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Using multivariate autoregressive state-space models to examine stock structure of Greenland halibut in the North Atlantic

J. Úbeda[1,2] | A. Nogueira[2] | N. Tolimieri[3] | M. Vihtakari[4] | B. Elvarsson[5] | M. Treble[6] | J. Boje[2,7]

[1]University of Alicante, Alicante, Spain

[2]Greenland Institute of Natural Resources, Nuuk, Greenland

[3]Conservation Biology Division, Northwest Fisheries Science Center, NOAA Fisheries, Seattle, Washington, USA

[4]Institute of Marine Research, Tromsø, Norway

[5]Marine and Freshwater Institute, Reykjavik, Iceland

[6]Fisheries and Oceans Canada, Winnipeg, Manitoba, Canada

[7]DTU Aqua, Lyngby, Denmark

Correspondence
J. Úbeda, University of Alicante, Alicante, Spain.
Email: julioubedaquesada@gmail.com

Abstract

Accurate information on population structure is essential for effective fisheries management. Greenland halibut (*Reinhardtius hippoglossoides*) in the North Atlantic is managed as four separate offshore stocks. We use Multivariate Autoregressive State-Space (MARSS) models to assess population structure by means of abundance and biomass trends in four regions (Norwegian Sea, Iceland, Southeast Greenland, and Northwest Atlantic) where three offshore stocks are recognized: (1) Baffin Bay–Davis Strait (Northwest Atlantic stock), (2) Southeast Greenland and Iceland (West Nordic stock (WNS)), and (3) the Barents and Norwegian Seas (Northeast Arctic stock). We formulated model alternatives, using bottom trawl survey data from each region for 1996–2019, to evaluate support for different population structures. Abundance and biomass observations from each region were linked to growth rate parameters in MARSS models and the impact of climate (North Atlantic Oscillation Index) and fishing (commercial catches) on stock dynamics was investigated. Top models identified the Northwest Atlantic as an independent population. Best-fit models treated Greenland halibut in the WNS as two independent populations (east and west), with potential connections between eastern Iceland and the western Barents Sea. These results suggest a mismatch between current stock perception and management boundaries in the Northeast Atlantic.

KEYWORDS
multivariate autoregressive state-space models, NAO index, North Atlantic Ocean, population structure, *Reinhardtius hippoglossoides*, sustainable fisheries management

1 | INTRODUCTION

Correctly identifying species' geographic population structures (Holmes et al., 2012), distributions, and dynamics are needed for most management and conservation strategies (Pauly et al., 2002).

Populations are often managed based on political boundaries that may not reflect biology (Hutchinson, 2008) or incomplete information, because demography and mixing of subpopulations are difficult to quantify, which generates ambiguity in advice on utilization (Begg et al., 1999; Schindler et al., 2010). Consequently, resources

may be over- or under-exploited (Benestan, 2019; Reiss et al., 2009), thereby causing economic losses, and wider ecosystem effects, such as reductions in biodiversity and cascading impacts on the food web (Hilborn et al., 2003; Mölman & Diekman, 2012). Thus, proper identification of the structure and distribution of an exploited population is crucial to establish effective sustainable harvest strategies (Moritz, 2002).

Greenland halibut (*Reinhardtius hippoglossoides*, Walhaum, 1792; also known as Greenland turbot or black halibut) is a large flatfish distributed primarily in arcto-boreal cold and deep waters, with continuous populations along continental slopes of the North Pacific, Atlantic, and Arctic Oceans (Hedges et al., 2017; Vihtakari et al., 2021). The species exhibits strong sexual dimorphism with females growing larger (~120 cm vs. 70 cm), older (>30 years vs. >20 years; Treble et al., 2008), and maturing later (L/A50 61 cm/15 years vs. 44 cm/8 years; Morgan et al., 2003; Yan et al., 2022) than males (estimates from the Institute of Marine Research (IMR) database). Mark–recapture studies have shown that Greenland halibut can be a highly migratory species (Albert & Vollen, 2015; Boje, 2002; Vihtakari et al., 2022). The species inhabit depths of 50–2000 m and temperatures between −2 and 8°C (Bowering & Nedreaas, 2000; Vihtakari et al., 2021).

Currently, the Greenland halibut fishery in the North Atlantic is managed as four discrete offshore stocks (Figure 1): (1) Northeast Arctic Stock (NEAS) around the Barents Sea; (2) West Nordic Stock (WNS) in Southeast Greenland, Iceland, and the Faroe Islands waters; (3) Northwest Atlantic Stock (NWAS) in Baffin Bay and Davis Strait; and (4) eastern Canadian Stock along the Newfoundland and Labrador coast, as well as Grand Banks and Flemish Cap. Tagging studies suggest a connection between the NEAS and WNS and a possible connection between the NWAS and Southeast Greenland (Albert & Vollen, 2015; Vihtakari et al., 2021; see further discussion below). Our research team had easy access to survey data from the NEAS, WNS, and NWAS; therefore, we have chosen to focus our analysis on these three stocks.

The Northeast Atlantic Stock has been fished over the advice since the 1990s and is declining at the time of writing (ICES, 2021), while WNS has had a relatively stable catch and population biomass since 2005 (ICES, 2022). In the NWAS, catch has been within the total allowable catch (TAC) in most years. The TAC has increased during 2000–2019, due to an expansion of the fishery northward into Baffin Bay, as well as in response to a stable or slightly positive trend in population biomass during this period (Treble & Nogueira, 2020).

Three spawning areas for Greenland halibut are assumed for North Atlantic stocks (Figure 1). The spawning area for NEAS is along the Norwegian continental slope, west of the Barents Sea (Albert & Vollen, 2015), and nursery grounds are found in the northern Barents Sea waters around Svalbard and Franz Josef Land. Based on egg and larvae observations and gonad development, the spawning area for NWAS is located between eastern Canada and West Greenland, at the southern slope of the Davis Strait. Egg and larval drift from this spawning area is assumed to supply the nursery grounds on the West Greenland banks and in Disko Bay (Jørgensen, 1997; Riget et al., 1992) and on the eastern Canadian shelf from Baffin Island to Labrador (Vihtakari et al., 2022). As a result, the NWAS and the eastern Canadian Stock are considered to comprise a single large population (Morgan & Bowering, 1997; Roy et al., 2014). The third spawning ground in the WNS is the least documented, but based on observations of females in running condition and observations of larvae, the location is Southwest of Iceland (Magnússon, 1977). No main nursery grounds have been observed for this stock area, but recruitment could be from the surrounding NEAS and NWAS (Vihtakari et al., 2022). However, nursery grounds may be situated along the southeast coast of Greenland, in fjords or on eastern Iceland shelves (Gundersen et al., 2013).

A lack of reliable spawning information (Albert et al., 2002), and mixing of Greenland halibut stocks in the North Atlantic (Ådlandsvik et al., 2004; Albert & Vollen, 2015; Vihtakari et al., 2022), raises a question whether current management units match the spatial population delineation (Benestan, 2019). A strong connectivity between Northeast Atlantic Stock and the Iceland portion of the WNS has been demonstrated by a number of studies. Some studies also include the Southeast Greenland portion as well. Therefore, the North Atlantic may consist of two major offshore populations, with a boundary somewhere between Iceland and Southeast of Greenland (Vihtakari et al., 2022). The recovery of a substantial proportion of juveniles tagged in Svalbard nursery area and recovered in the West Nordic area suggested that NEAS and WNS should be treated as one population (Albert & Vollen, 2015). Genetic studies also suggested that Greenland halibut in the Northeast Atlantic should be treated as panmictic population, instead of two separated populations (Gislason et al., 2023; Knutsen et al., 2007; Westgaard et al., 2017). Based on a particle-tracking model, eggs and larvae of Greenland halibut may be distributed from the NEAS spawning ground toward Southeast Greenland and Iceland waters following ocean currents (Ådlandsvik et al., 2004). Despite these reports, two offshore stocks in the Northeast Atlantic are currently considered separated populations for management purposes.

Multivariate autoregressive (MAR) time-series models provide a way to model multiple population processes with structure or interactions. A Multivariate Autoregressive State-Space (MARSS) model is a state-space version of an MAR model, which runs in parallel separate multivariate state and observation components (Holmes et al., 2012). What we aim to estimate is the state (e.g., abundance estimate); the data are the observations of this state (Tolimieri et al., 2017). These models have been used in a variety of ecological and fisheries applications, including analysis of spatial structure of populations (Tolimieri et al., 2017; Ward et al., 2010), dynamics factor analysis for large fishery datasets (Zuur et al., 2003), and species interactions and community stability (Hampton et al., 2013; Ward et al., 2010). For example, survey indices from two different vessels and time periods were combined to estimate the spatial structure of three redfish stocks on the Flemish Cap and examine the influence of environmental covariates and commercial catches on their abundance trends (Nogueira et al., 2019).

Our objective was to determine if data support the current stock delineation or whether alternate population structures should be considered for three offshore stocks of Greenland halibut in the North Atlantic: NWAS, WNS, and NEAS. Biomass and abundance indices were examined, using data from Norway, Iceland, Canada, and Greenland research bottom trawl surveys carried out between 1996 and 2019. A second objective was to investigate the impact of climate (the North Atlantic Oscillation index, NAO) and fishing (commercial catches) on population dynamics of Greenland halibut.

2 | METHODS

2.1 | Study area

The study area encompassed regions of eastern Arctic Canada and western Greenland, waters around Iceland and Southeast Greenland, and western Barents Sea (Figure 1). These areas

play a significant role in the North Atlantic Ocean where climate changes have had a profound impact on the oceanic circulation system (Stolz & Baumann, 2010), and consequently its productivity (Martinez-Sanchez et al., 2019). The North Atlantic Ocean serves as a transitional zone between the cold and productive regime of the Subpolar gyre at higher latitudes and the warm and oligotrophic waters of the Subtropical gyre (Holliday et al., 2008; Sarafanov, 2009).

Fisheries in the northwestern Atlantic are managed by the Northwest Atlantic Fisheries Organization (NAFO), while those in the northeastern Atlantic are overseen by the International Council for the Exploration of the Sea (ICES), with the boundary located in South Greenland. Key commercially harvested species representative of both eastern and western North Atlantic habitats include round grenadier (*Coryphaenoides rupestris*), Atlantic cod (*Gadus morhua*), blackbelly rosefish (*Helicolenus dactylopterus*), American plaice (*Hippoglossoides platessoides*), Greenland halibut (*Reinhardtius hippoglossoides*), and beaked redfish (*Sebastes mentella*), including in areas beyond national jurisdictions (Morato et al., 2020).
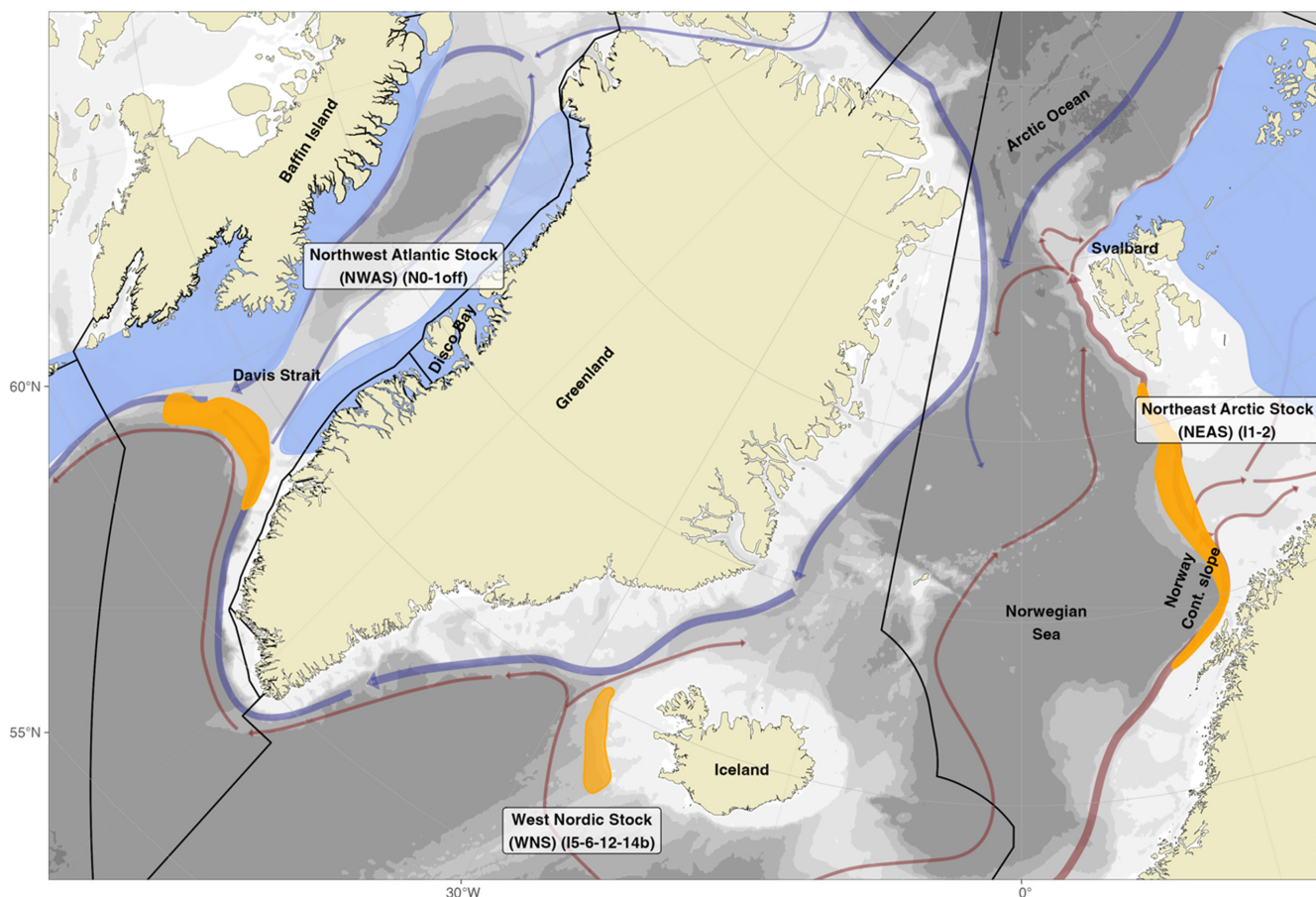

FIGURE 1 Map of the study area showing the three stocks of Greenland halibut examined in the North Atlantic: (1) The Northeast Arctic Stock (NEAS) of ICES in Subareas 1 and 2; (2) the WNS of ICES in Subareas 5, 6, 12, and 14b; and (3) the NWAS of NAFO in Subareas 0 and 1 (offshore). Two nursery regions are represented in light blue: shelf in eastern Canada from Baffin Bay to Labrador, banks of West Greenland and in Disco Bay, North, and East of Svalbard. Three spawning regions are represented in orange: Davis Strait, waters between East Greenland and Iceland, and Norwegian Continental slope. The direction of prevailing oceanic currents is indicated in blue for Arctic currents and red for Atlantic currents. Depth is indicated using shades of white (shallow shelf areas) to grey (deep offshore waters). This map is modified from Vihtakari et al. (2022).

2.2 | Data sources

Biomass and abundance indices were available from four different surveys conducted in four regions: West Greenlandic and Canadian eastern Arctic (in the NWAS), Southeast Greenland (in the WNS), Iceland (in the WNS), and Norwegian slope (in the NEAS) for the period 1996–2019 (Table 1). Southeast Greenland and Iceland are two regions in the WNS. Although the NWAS survey indices did not cover the whole stock area, these surveys were considered representative of stock distribution. The biomass index better represented the fishable part of populations while the abundance index better captures recruitment events resulting from many small individuals (Kimura & Somerton, 2006). In separate analyses for biomass and abundance indices, MARSS was used to combine time series from four different surveys.

2.2.1 | Norwegian slope survey 1996–2019: NEAS

The Norwegian IMR conducted an autumn survey since 1996 along the continental slope between mainland Norway and Svalbard from 68°N to 80°N (Figure 2), using the Alfredo 3 or 5 bottom trawls. Greenland halibut in their spawning and main-fishing grounds is the target species for this survey. It samples both small maturing (>30 cm) and large mature fish having a mode at 45–50 cm. The survey was conducted annually until 2009 and biannually thereafter (Harbitz et al., 2010; ICES, 2020a). The survey indices were calculated using a stratified random design with depth strata of 400–500, 500–700, 700–1000, and 1000–1500 m. The survey index was an estimate of total all fish in the area using swept area indices over all strata (Høines & Gundersen, 2008).

2.2.2 | Icelandic survey (ICE) 1996–2019: WNS

The Icelandic Marine and Freshwater Research Institute (MFRI) completed a groundfish survey during autumn on the continental shelf and slope, using a Granton-type bottom trawl every October since 1996 (Figure 2), except 2011. The survey consisted of a stratified fixed survey design, where station placements were randomly located on important Greenland halibut fishing grounds of west, north, and east Iceland (Sólmundsson et al., 2010). Total abundance and biomass were estimated using swept area indices summed across all strata (Cochran, 1977), with registered sizes between 7 and 108 cm. The distribution of sizes is observed to be unimodal, with modes ranging between 50 and 60 cm (MFRI Assessment Reports, 2020).

2.2.3 | Southeast Greenlandic survey (EG) 1998–2016: WNS

The Greenland Institute of Natural Resources (GINR) conducted an annually buffered random stratified (Kingsley et al., 2004) survey using the Alfredo 3 bottom trawl from 1998 to 2016 (except 2001, when the vessel was not available). The survey covered 60°N to 67°N, although areas below 61.45°N were barely surveyed between the 3.0 nm and the 200 nm or middle line to Iceland (Figure 2). The survey index was calculated as the total estimate from 400 to 600, 600–800, 800–1200, 1200–1400, and 1400–1500 m depth strata, using the swept area method. The target species was Greenland halibut. Registered lengths ranged from 18 to 96 cm. Generally, the length distributions in the different depth strata were dominated by one mode between 50 and 55 cm (Nogueira et al., 2023).

2.2.4 | West Greenlandic and Canadian eastern Arctic surveys 1997–2019: NWAS

The GINR and Department Fisheries and Oceans Canada (DFO) conducted buffered random depth stratified bottom trawl surveys using an Alfredo 3 trawl (Figure 2). One survey was in NAFO Divisions 1CD (Greenland) from 1997 to 2019, except 2018, and a second survey was in NAFO Division 0A (Canada) from 1999, 2001, 2004, 2006, 2008, 2010, 2012, 2014, 2017, and 2019. Both surveys were stratified in six depth strata ranging from 400 to 1500 m. Greenland halibut was the main species caught and modal size has varied between 40 and 55 cm. Total biomass and abundance were not available due to gear selectivity (largest fish are able to avoid the trawl) and ages were not available. Biomass and abundance indices were estimated using the swept area method

TABLE 1 General information of four survey indices of Greenland halibut conducted in four regions in the North Atlantic Ocean, and their associated stocks for the period 1996–2019 (Table 1).

Stock	Survey	Regions	Time-series	References
Northeast Arctic Stock (NEAS)	Norwegian slope (NEAS)	South-West Svalbard (Slope)	1996–2019	Harbitz et al. (2010), ICES (2020a)
West Nordic Stock (WNS)	Iceland (ICE)	ICES Subareas 5, 6, and 12	1996–2019	Sólmundsson et al. (2010)
	Southeast Greenland (EG)	ICES Subdivision 14b	1998–2016	Kingsley et al. (2004)
Northwest Atlantic Stock (NWAS)	West Greenland and Canadian eastern Arctic (NWAS)	NAFO Divs. 1CD + Div. 0A-South (to approximately 72°N)	1997–2017 and 2019	Treble (2020), Nogueira and Estévez-Barcia (2020)

Note: Southeast Greenland and Iceland are two regions in the WNS. References are related to the survey information.
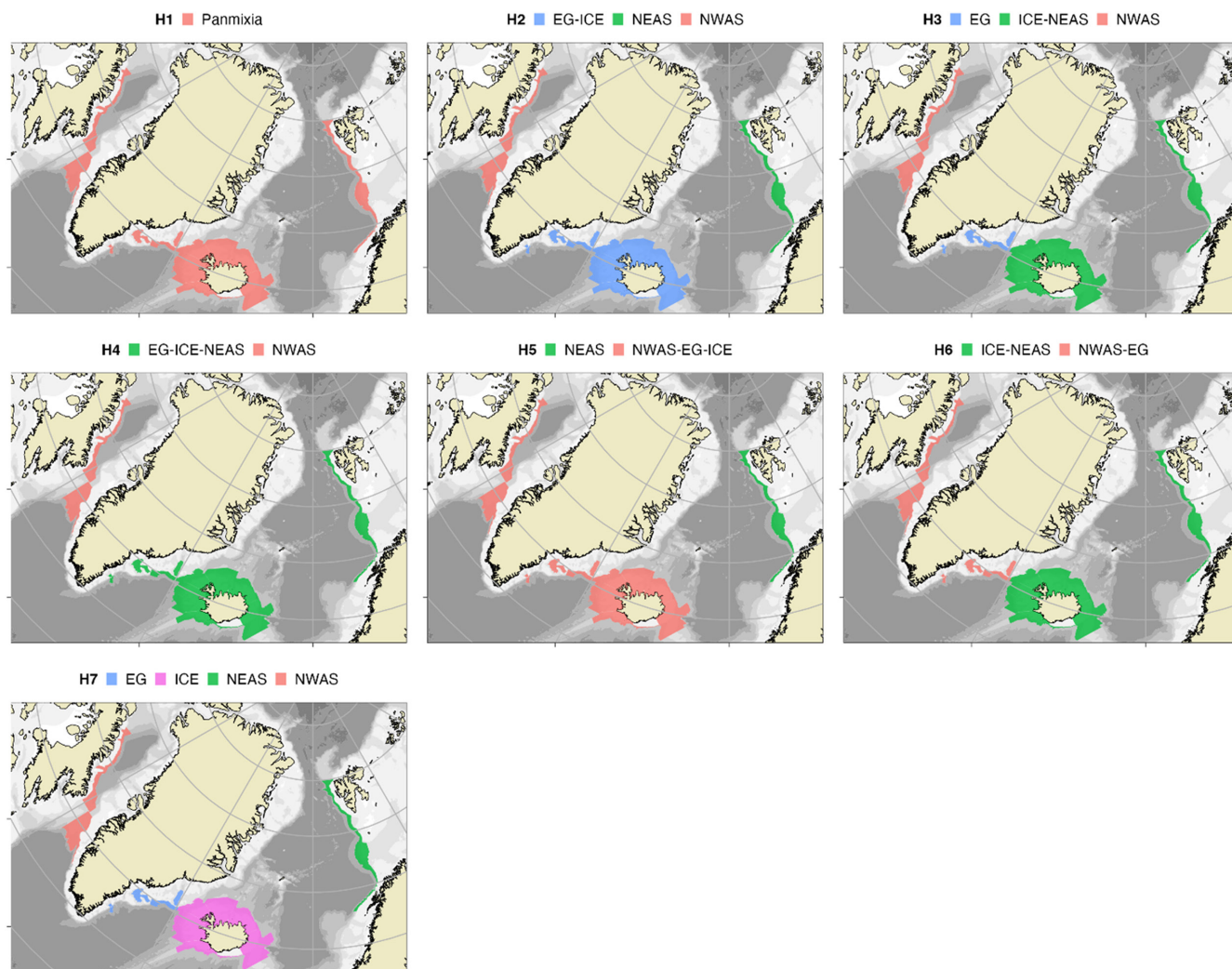
FIGURE 2 Seven hypotheses of Greenland halibut population structures using survey index values in four regions in the North Atlantic Ocean, by manipulating the **Z** matrix in Equation 1b. Survey regions: Canada and West Greenland and Canadian eastern Arctic (NWAS), Southeast Greenland (EG), Iceland (ICE), and the Norwegian slope (NEAS). Depth is indicated using shades of white (shallow shelf areas) to grey (deep offshore waters). Same colors encompassed same estimated populations.

(Nogueira & Estévez-Barcia, 2020; Treble, 2020). In 2018, the GINR research vessel was retired, and in 2019, a charter vessel of similar length and tonnage to the previous vessel was used to conduct both surveys, using the same Alfredo 3 trawl and rigging. While vessel changes can affect catchability and introduce variability to time-series models (Thorsen & Ward, 2014), in this case, the vessel change was for the final year only, and when we tested the model with and without the 2019 data, the results did not change. We concluded that selectivity was similar and chose to retain the 2019 data as part of the NWAS survey series.

2.3 | Covariates

To investigate potential impacts of environmental and anthropogenic drivers on survey indices for Greenland halibut, eight covariates were included in modeling:

North Atlantic Oscillation (NAO) index: The NAO is a cyclical climate oscillation, measured as the difference in atmospheric pressure between the Icelandic low and Azores high (Figure 3). This index has been used by Albert and Høines (2003) to assess Greenland halibut distribution, as well as by Roberts et al. (2019) to evaluate climate effects on population distribution of seven commercial fish species in the southern Atlantic, off the coast of the United States.

North Atlantic Oscillation (NAO) index "lagged": The effect of NAO on recruitment was examined using the approach of Pérez-Rodríguez et al. (2012), by using a 5-year moving average of NAO values (i.e., $\text{NAOlagged}\_1996 = \sum_{y=1992}^{1996} \text{NAO}y / 5$).

(3-4-5) Commercial catches: Greenland halibut catches (kilotons) in NAFO Subareas 0 and 1 (NWAS offshore, Treble & Nogueira, 2020); ICES Subareas 5, 6, 12, and 14b (WNS, ICES, 2020b); ICES Subareas 1 and 2 (NEAS, ICES, 2020a) were included to evaluate the impact of fishing (Figure 4). Impact on population indices would be reflected in the same year.
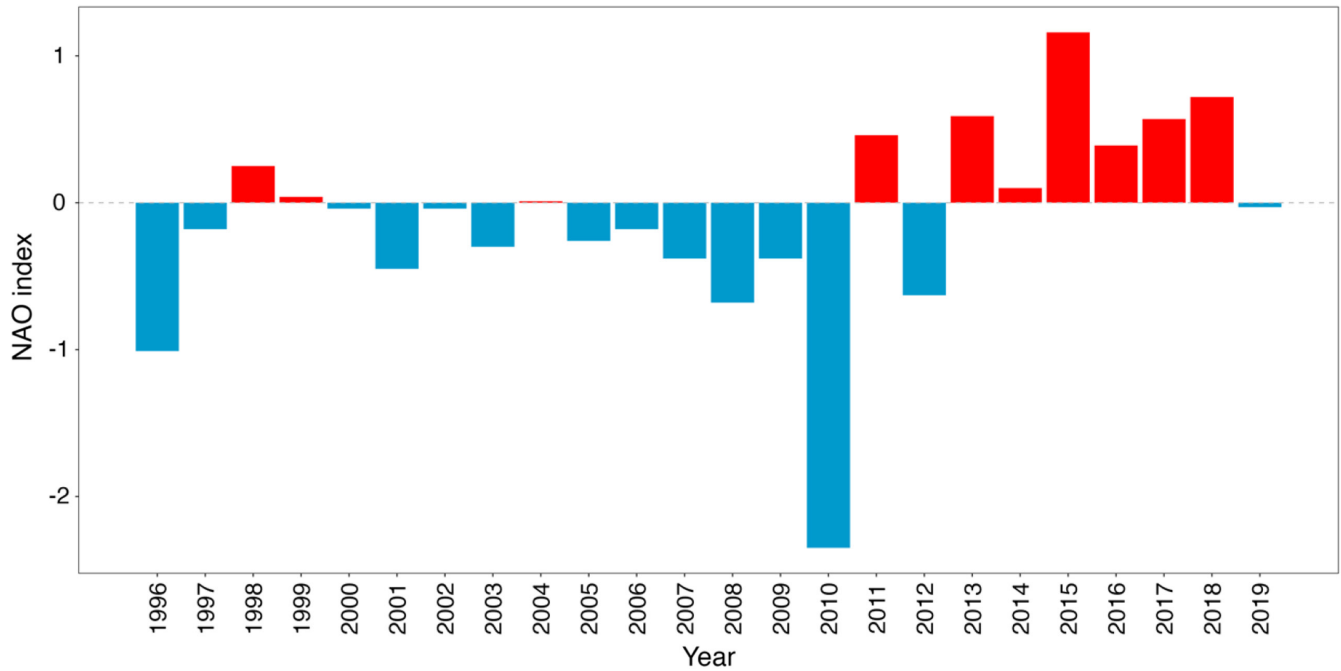
FIGURE 3 North Atlantic Oscillation (NAO) index, measured as the difference in atmospheric pressure between the Icelandic low and Azores high, from 1996 to 2019. Red columns represent positive values. Blue columns represent negative values. Data source: Jones et al. (1997).

(6-7-8) Commercial catches "lagged": Fishing impact on the Greenland halibut indices of respective stocks would be reflected 1 year later.

Survey index maps were created using the ggOceanMaps package (Vihtakari, 2022), with land polygons from Natural Earth Data (https://www.naturalearthdata.com/) and depth polygons from the ETOPO 1 arc-minute bathymetry grid (Amante & Eakins, 2009). During model investigation covariates were examined in various combinations; however, these models were poorly supported and we chose to focus on models that examined covariates one at a time.

2.4 | Statistical methodology: MARSS

Survey data were analyzed by fitting linear MARSS models with Gaussian errors using the "MARSS" package (Holmes et al., 2021) in R 4.1.2 (R Core Team, 2022). Survey data and catch covariates were log-transformed prior to analysis.

The MARSS model was described by the following equations:

$$x_t = x_{t-1} + u + C_t c_t + w_t, \quad \text{where } w_t \sim \text{MVN}(0, Q) \quad (1a)$$

$$y_t = Z x_t + a + v_t, \quad \text{where } v_t \sim \text{MVN}(0, R) \quad (1b)$$

Equation 1a was the process equation, to model the set of true but estimated population trajectories (state processes were on a log scale because data were transformed). We defined population as x_t, an $n \times 1$ vector of state values (index values) at time t and at region n. The u parameter was a column vector of long-term population

growth rate (e.g., for each x_t in x_{t-1}). The C_t was a matrix of parameters that allowed the covariates, c_t, to affect population growth rate. The w_t parameter was process error, which is unexplained deviations from the mean growth rate (real variation in population size due to unobserved processes like recruitment, rather than observation error). Process error was modeled as a multivariate normal distribution (MVN) with variance–covariance matrix Q (random effects).

Equation 1b was the observation equation, to relate the observed survey time series (y_t) which is an $n \times 1$ vector, at time t and at region n, to the estimated population (the x_t in Equation 1a). The Z parameter was a matrix that defined how observations related to underlying hypothetical estimated populations. For example, if all regions would merge into one population (x_t), Z would define only one population. The a parameter was a scaling term for each observational time series, to allow time-series estimates across different scales to be combined, such as differences among vessels or fishing gears (Nogueira et al., 2019; Tolimieri et al., 2017). The observation error v_t also followed an MVN with variance–covariance matrix R.

2.4.1 | Tested models

Seven hypotheses of Greenland halibut population structures were evaluated using survey index values in four regions in the North Atlantic Ocean, by manipulating the Z matrix in Equation 1b. Hypotheses were based on previous work on the distribution of Greenland halibut in the North Atlantic, complemented by our own hypotheses considering other possible geographic population structures (Table 2; Figure 2). The seven population structure hypotheses tested are:
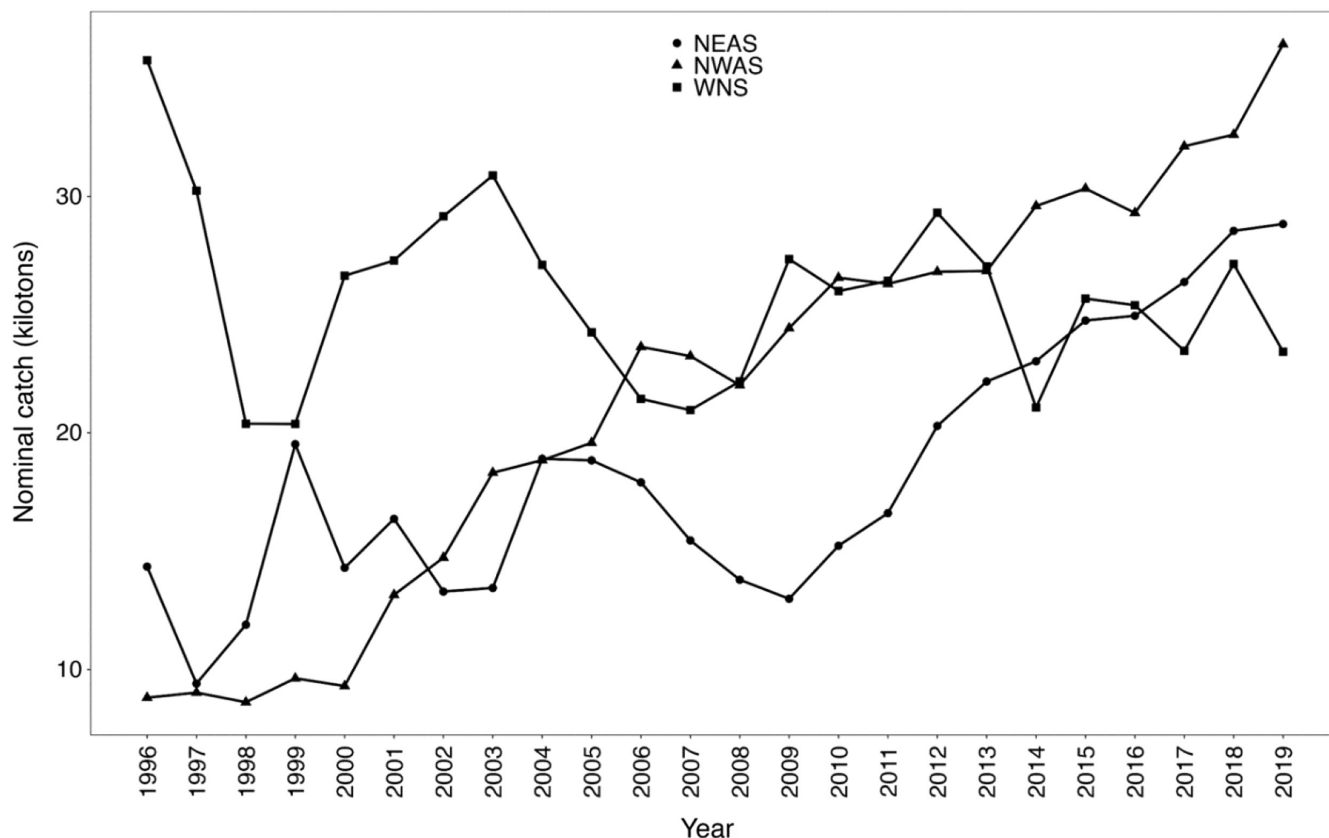
FIGURE 4 Commercial catches of three stocks of Greenland halibut in the North Atlantic Ocean from 1996 to 2019: (1) Northeast Arctic Stock (NEAS, dots) in the ICES Subareas 1 and 2, (2) NWAS (triangles) in NAFO Subarea 0 + 1(offshore), and (3) WNS (squares) in ICES Subareas 5, 6, 12, and 14b.
Data source: NWAS (Treble & Nogueira, 2020); NEAS (ICES, 2020a); WNS (ICES, 2020b).

1. Describes one trajectory for all regions, based on genetic research suggesting a single, panmictic population throughout the North Atlantic (Vis et al., 1997).
2. Describes the current situation with three populations. Possibly related to geographic adjacency, to test whether Southeast Greenland and Iceland regions might enclose a single population, separate from the other two (Albert et al., 2002).
3. Describes three different populations, based on tagging and egg and larval drift studies suggesting a connection between Norwegian slope and Iceland (Ådlandsvik et al., 2004; Albert & Vollen, 2015).
4. Describes two major populations in the North Atlantic, merging the Norwegian slope, Iceland, and South Greenland regions in a unique population separated from West Greenlandic and Canadian eastern Arctic region, which is suggested by genetic studies (Gislason et al., 2023; Knutsen et al., 2007; Westgaard et al., 2017).
5. Describes two major populations in the North Atlantic, merging the West Greenlandic and Canadian eastern Arctic, Iceland, and Southeast Greenland regions in a unique population separated from the Norwegian slope. Although this hypothesis is less supported than the previous one, tagging studies also found migrations between NWAS and WNS (Boje, 2002; Vihtakari et al., 2022).
6. Describes two major populations with boundaries somewhere between Iceland and Southeast Greenland, based on migrations noted by Boje (2002) and Vihtakari et al. (2022) from NWAS toward Southeast Greenland.
7. It was set to check if all four regions might support unique populations.

For each hypothesized population, equal (all populations follow the same growth rate) and unique (separated growth rate across populations) population growth rates (u) were tested. The variance–covariance matrix structure (Q) was tested as: (1) "diagonal and equal" which means populations share a variance term (off-diagonal values were 0 and diagonal values were equal), (2) "diagonal and unequal" which means populations each have their own estimated variance (off-diagonal values were 0 and diagonal values were different), and (3) "unconstrained" (off-diagonal and diagonal values differed by allowing for covariance among populations; Holmes et al., 2012). The dataset included different surveys, methodologies, and vessels, so we assumed an independent observation variance–covariance matrix (R) and did not explore other structures. However, Southeast Greenland and West Greenlandic and Canadian eastern Arctic data were assigned the same observational variance because the same ship surveyed both areas.

TABLE 2 Seven hypotheses of Greenland halibut population structures with four regions in the North Atlantic Ocean: West Greenlandic and Canadian eastern Arctic (NWAS); Southeast Greenland (EG); Iceland (ICE); and Norwegian slope (NEAS); by manipulating the number of hypothetical estimated population (Z matrix) in Equation 1b.

Hypothesis	Number of hypothetical estimated populations (Z)	Method of delineation	References
1	(1) NWAS–EG–ICE–NEAS	Genetics	Vis et al. (1997)
2	(1) NWAS (2) EG–ICE (3) NEAS	Tagging	Albert et al. (2002)
3	(1) NWAS (2) EG (3) NEAS–ICE	Egg/larval drift modeling; Tagging	Ådlandsvik et al. (2004), Albert and Vollen (2015)
4	(1) NWAS (2) EG–ICE–NEAS	Genetics; Tagging	Knutsen et al. (2007), Westgaard et al. (2017), and Vihtakari et al. (2022)
5	(1) NWAS–EG–ICE (2) NEAS	Tagging	Boje (2002), Vihtakari et al. (2022)
6	(1) NWAS–EG (2) ICE–NEAS	Tagging; Genetics	Boje (2002), Westgaard et al. (2017), Vihtakari et al. (2022)
7	(1) NWAS (2) ICE (3) EG (4) NEAS	–	*Own assumptions*

Note: References relate to previous work on the distribution of Greenland halibut in the North Atlantic, complemented by our own assumptions considering other possible geographic population structures. The method of delineation corresponding to each reference is also indicated.

2.4.2 | Model selection

A specifically designed bootstrap version for state-space models of Akaike's information criterion (AICb, estimated within the "MARSS" package; Holmes et al., 2021) was used to select the most parsimonious model (Cavanaugh & Shumway, 1997). This version of AIC was used to deal with the small-sample problem and avoid underestimating complexity of models (Cavanaugh & Shumway, 1997; Holmes et al., 2012). The model with the lowest AICb value was selected as the most parsimonious, and models with ΔAICb <2 were similarly supported (Burnham & Anderson, 1998). For similarly supported models, the model with the fewest parameters was chosen as the most parsimonious. Approximated 95% confidence intervals (CI) for MARSS parameters were computed using numerical estimation of the Hessian matrix for the best-fit model or models.

3 | RESULTS

Biomass and abundance indices were correlated for surveys in West Greenland and Canadian eastern Arctic (Pearson's correlations = 0.64), Southeast Greenland (0.93), Iceland (0.91), and the Norwegian slope (0.73; Figure 5). In West Greenland and Canadian eastern Arctic, biomass and abundance were both highest, with a peak in 2016, followed by a sharp decline in 2017. In Southeast Greenland, biomass and abundance were lowest, and decreased after 2006. In Iceland, biomass and abundance contrasted, with peaks in

2003 and 2013. In the Norwegian slope, biomass was variable, abundance increased before 2009, and both declined thereafter.

3.1 | Abundance

For abundance, one candidate model (Model 1) supported Hypothesis 3 that combined Iceland and Norwegian slope regions into a single population, while leaving West Greenland and Canadian eastern Arctic and Southeast Greenland regions as separate populations (Table 3). The model included catch as a covariate and estimated a single population growth rate of $u = -0.007$; 0.7% decrease in abundance per year, but the 95% confidence interval included zero (Table 4; Figure 6). None of the top 10 models could estimate process variance (Q), likely because of the large number of missing survey years for Norwegian slope and West Greenlandic and Canadian eastern Arctic surveys (Figure 5) that resulted in a diagonal and equal structure in all cases. Models 1–7 all supported Hypothesis 3, while Models 8–10 supported Hypothesis 7, which included four populations, but were less supported.

Model 4 was the best model with no covariates to evaluate actual rates of population change when not accounting for catch. Model 4 also supported Hypothesis 3, but included different population growth rates among the three regions. The population in West Greenland and Canadian eastern Arctic region declined at a much higher rate ($u = -0.097$, or 9.7% per year) than in Southeast Greenland ($u = -0.006$ or 0.6% decrease per year) or Iceland and the Norwegian slope ($u = -0.007$ or 0.7% decrease per year; Table 4).
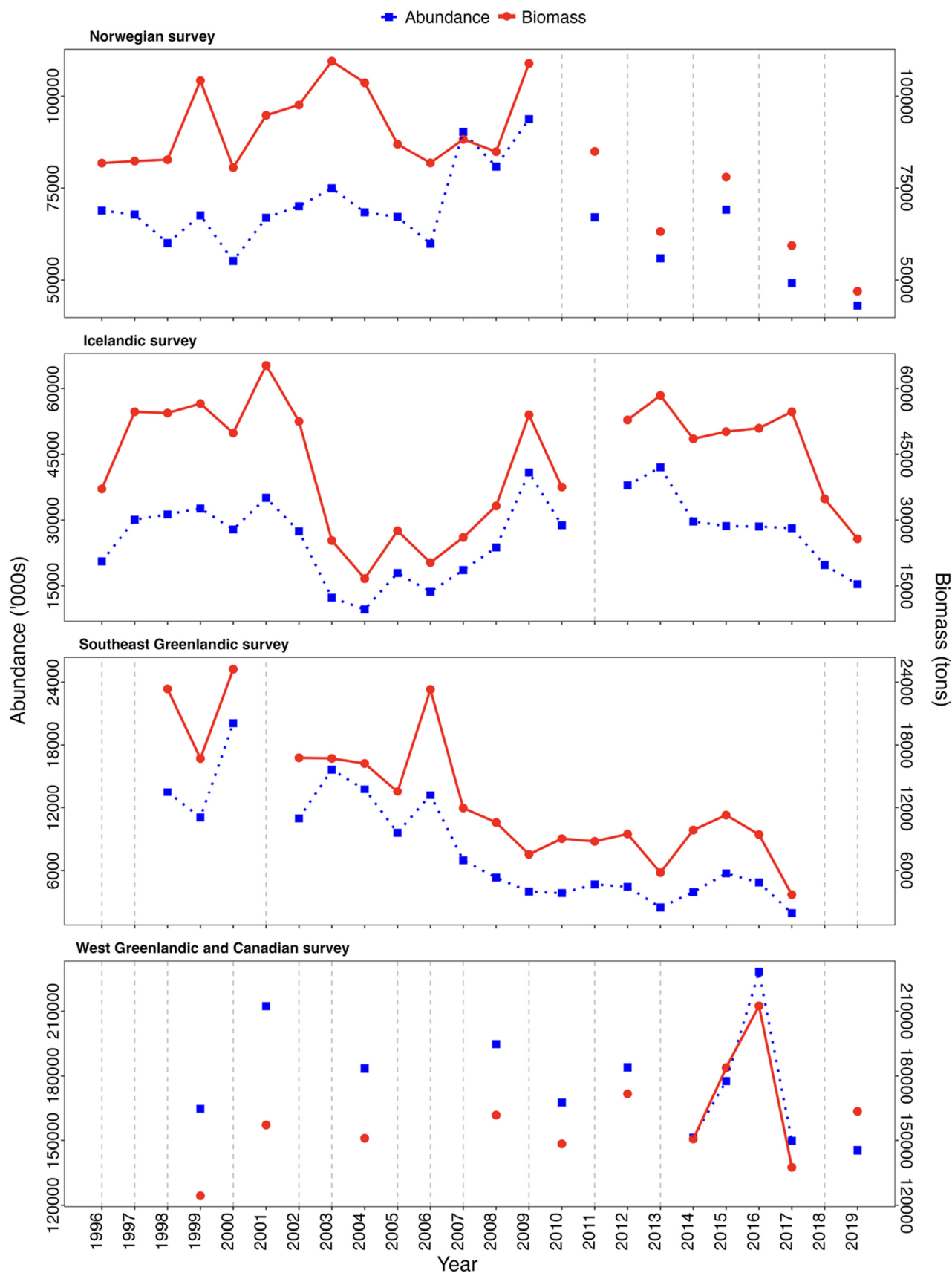
FIGURE 5 Greenland halibut abundance (blue squares) and biomass (red dots) indices for the Norwegian slope survey (NEAS), Icelandic survey (WNS), Southeast Greenland survey (WNS), and West Greenland and Canadian eastern Arctic survey (NWAS) from 1996 to 2019. The vertical dashed lines represent years without data.

TABLE 3 Top 10 MARSS models using abundance indices.

Model	Hypothesis	Covariates	*u*	*Q*	*Z*	*K*	AICb	ΔAICb
1	**3**	**Catch**	**Equal**	**Diagonal & equal**	**3**	**12**	**42.34**	**0.00**
2	3	Catch-L	Equal	Diagonal & equal	3	12	44.60	2.26
3	3	Catch	Unequal	Diagonal & equal	3	14	44.92	2.58
4	3	–	Unequal	Diagonal & equal	3	11	45.32	2.97
5	3	NAO	Unequal	Diagonal & equal	3	12	45.78	3.44
6	3	NAO-L	Unequal	Diagonal & equal	3	12	46.10	3.76
7	3	Catch-L	Unequal	Diagonal & equal	3	14	47.53	5.19
8	7	Catch	Unequal	Diagonal & equal	4	15	47.99	5.64
9	7	Catch-L	Unequal	Diagonal & equal	4	15	52.13	9.79
10	7	NAO	Unequal	Diagonal & equal	4	13	52.78	10.44

Note: Hypothesis: see Table 2; Covariates: Catch=commercial catches (L=lagged) and NAO=North Atlantic Oscillation index (L=lagged); *u* is the population growth rate (Unequal=independent *u*; Equal=same *u*); *Q* is the process variance (Diagonal and equal=same value on the diagonal and 0 in the off diagonal); *Z* is the number of hypothetical estimated populations; *K* is the number of estimated parameters; AICb: bootstrap version of the Akaike's information criterion; and ΔAICb the AICb difference to the best-fitting model. Bold indicates the best-fit model based on the lowest ΔAICb and the fewest parameters.

TABLE 4 Parameter estimates for the best-fit model (Model 1, Hypothesis 3) and the best-fit model for with no covariates (Model 4, Hypothesis 3) using abundance data, including trajectories and estimated parameters: Number of hypothetical estimated populations (*Z*), process variance (*Q*); growth rate (*u*); observational variance (*R*).

Model 1 (*Z*=3)		Model 4 (*Z*=3)	
Trajectories	**Parameter estimates**	**Trajectories**	**Parameter estimates**
u-All	−0.007 (−0.033, 0.019)	*u*-NWAS	−0.097 (−0.118, −0.075)
–	–	*u*-EG	−0.006 (−0.021, 0.009)
–	–	*u*-ICE-NEAS	−0.007 (−0.032, 0.018)
Q	0.000 (−0.0004, 0.0004)	*Q*	0.000 (−0.0005, 0.0005)
R-Canada & Greenland	0.079 (0.038, 0.119)	*R*-Canada & Greenland	0.074 (0.036, 0.112)
R-Iceland	0.150 (0.064, 0.240)	*R*-Iceland	0.150 (0.063, 0.238)
R-Norway	0.030 (0.006, 0.033)	*R*-Norway	0.030 (0.010, 0.50)
Catch (*c*)—WNS	0.108 (0.032, 0.184)	–	–
Catch (*c*)—NWAS	−0.121 (−0.201, −0.042)	–	–
Catch (*c*)—NEAS	−0.112 (−0.191, −0.033)	–	–

Note: Survey time series: Canada and West Greenland and Canadian eastern Arctic (NWAS), Southeast Greenland (EG), Iceland (ICE), and the Norwegian slope (NEAS). Values in parentheses are upper and lower 95% CI (note that they include zero for *u*'s).

The 95% CI of *u* for Southeast Greenland and Iceland and the Norwegian slope included zero (Table 4), which suggested that populations were neither increasing nor decreasing in these regions.

3.2 | Biomass

For biomass, two models (Models 1 and 3) supported Hypothesis 3, which combined Iceland and Norwegian slope regions into one population, while a third model (Model 2) supported Hypothesis 7, with four populations (Table 5). All three models included catch or lagged catch as a covariate, but Model 2 included three more parameters, so Model 1 was selected as the preferred model (Table 6). As for the abundance model, the biomass, Model 1

included a single population growth of *u*=0.011 or 1.1% increase per year, but the 95% confidence interval included zero for all three populations (Figure 7).

As with abundance, most models failed to separate process and observation variance, and models either estimated a single zero process variance for all populations or separate but small process variances. While the preferred model supported Hypothesis 3 (three populations), Hypothesis 7 was also supported, with the second-best model and three of the top 10 models having four separate populations or stocks. Models with no covariates (Model 7 three populations; and Model 10 four populations) differed by 0.76 AICb points and one parameter.

Model 7 was the best model with no covariates (Table 6). As with abundance, excluding catch as a covariate resulted in unequal

population growth among populations. Greenland halibut biomass declined in West Greenlandic and Canadian eastern Arctic at 6.7% per year ($u=-0.067$). Biomass did not increase or decrease in Southeast Greenland, Iceland, and the Norwegian slope regions, because 95% confidence interval included zero.
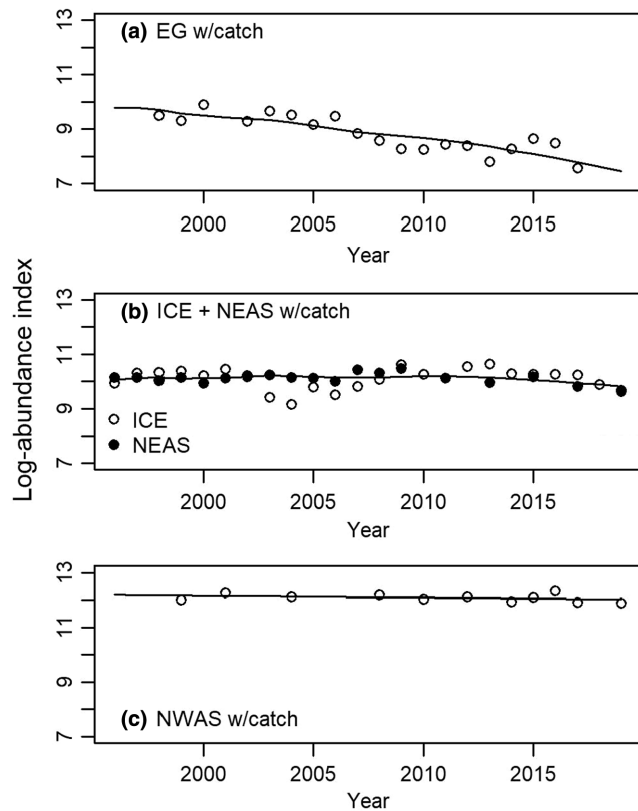

FIGURE 6 Estimated log-abundance trajectories from the best-fit model (Model 1, Hypothesis 3) for Greenland halibut in each estimated region from 1996 to 2019: Canada and West Greenland and Canadian eastern Arctic (NWAS), Southeast Greenland (EG), Iceland (ICE), and the Norwegian slope (NEAS). Lines indicate the estimated state, and points indicate observed data.

4 | DISCUSSION

Understanding how populations of Greenland halibut are interconnected is challenging, because the species can migrate long distances that cross international boundaries (Albert & Vollen, 2015; Boje, 2002; Vihtakari et al., 2022). Currently, four different offshore stocks of Greenland halibut are managed separately in the North Atlantic. We used MARSS models to test whether three of those stocks (Northwest Atlantic, West Nordic, and Northeast Arctic) could be treated as a single complex for management purposes or whether there was data support for separating them into as many as four separate stocks or populations (dividing the WNS into Southeast Greenland and Iceland regions). Abundance and biomass models supported combining Iceland and Norwegian slope regions (corresponding to the NEAS) into one population, while retaining West Greenlandic and Canadian eastern Arctic (corresponding to the NWAS) and Southeast Greenland regions as separate populations. However, biomass indices somewhat supported four separate populations (Hypothesis 7).

Abundance and biomass analyses identified the NWAS as an independent population, which implies that the population was not connected with adjacent populations, specifically those in Southeast Greenland. There have been observations in Icelandic ichthyoplankton surveys of eggs/larvae drifting from western Iceland and Southeast Greenland toward West Greenlandic and Canadian eastern Arctic and tagged fish moving from West Greenlandic and Canadian eastern Arctic to Southeast Greenland region (Vihtakari et al., 2022). However, some exchange (eggs/larvae, juveniles, or adults) between Northwest Atlantic and Southeast and Iceland

TABLE 5 Top 10 MARSS models using biomass indices.

Model	Hypothesis	Covariates	*u*	*Q*	*Z*	*K*	AICb	ΔAICb
1	**3**	**Catch**	**Equal**	**Diagonal & equal**	**3**	**12**	**26.35**	**0.00**
2	7	Catch	Unequal	Diagonal & equal	4	15	26.96	0.61
3	3	Catch-L	Equal	Diagonal & equal	3	12	27.45	1.10
4	3	Catch-L	Equal	Diagonal & unequal	3	14	28.42	2.07
5	7	Catch-L	Unequal	Diagonal & equal	4	15	28.92	2.58
6	3	Catch	Equal	Diagonal & unequal	3	14	29.20	2.85
7	3	–	Unequal	Diagonal & equal	3	11	30.49	4.14
8	3	Catch	Unequal	Diagonal & equal	3	14	30.79	4.44
9	3	Catch-L	Unequal	Diagonal & equal	3	14	30.94	4.59
10	7	–	Unequal	Diagonal & equal	4	12	31.25	4.90

Note: Hypothesis: see Table 2; Covariates: Catch=commercial catches (L=lagged) and NAO=North Atlantic Oscillation index (L=lagged); *u* is the population growth rate (Unequal=independent *u*; Equal=same *u*); *Q* is the process variance (Diagonal and equal=same value on the diagonal and 0 in the off diagonal); *Z* is the number of hypothetical estimated populations; *K* is the number of estimated parameters; AICb: bootstrap version of the Akaike's information criterion; and ΔAICb the AICb difference to the best-fitting model. Bold indicates the best-fit model based on the lowest ΔAICb and the fewest parameters.

TABLE 6 Parameter estimates for the best-fit model (Model 1, Hypothesis 3) and the best-fit model with no covariates (Model 7, Hypothesis 3) for biomass data, including trajectories, and estimated parameters: Number of hypothetical estimated populations (Z); process variance (Q); growth rate (u); observational variance (R).

Model 1 ($Z = 3$)		Model 7 ($Z = 3$)	
Trajectories	**Parameter estimates**	**Trajectories**	**Parameter estimates**
u-All	0.011 (−0.011 to 0.033)	u-NWAS	−0.069 (−0.867, −0.051)
–	–	u-EG	−0.016 (−0.032, 0.001)
–	–	u-ICE-NEAS	0.011 (−0.010, 0.032)
Q	0.000 (−0.0004, 0.0004)	Q	0.000 (−0.001, 0.001)
R-Canada & Greenland	0.055 (0.026, 0.083)	R-Canada & Greenland	0.051 (0.023, 0.079)
R-Iceland	0.169 (0.071, 0.267)	R-Iceland	0.151 (0.063, 0.238)
R-Norway	0.013 (0.003, 0.023)	R-Norway	0.027 (0.008, 0.046)
Catch (c)—WNS	0.121 (0.059, 0.183)	–	–
Catch (c)—NWAS	−0.134 (−0.198, −0.069)	–	–
Catch (c)—NEAS	−0.129 (−0.193, −0.064)	–	–

Note: Survey time series: Canada and West Greenland and Canadian eastern Arctic (NWAS), Southeast Greenland (EG), Iceland (ICE), and the Norwegian slope (NEAS). Values in parentheses are upper and lower 95% CI (note that they include zero for u's).
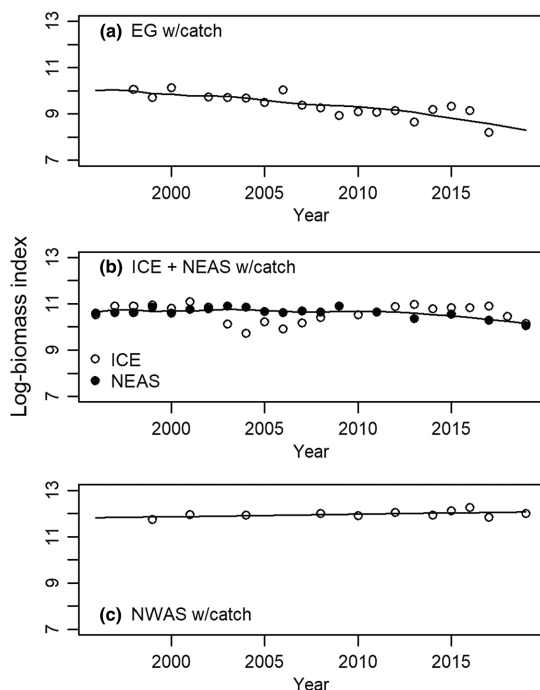

FIGURE 7 Estimated log-biomass trajectories from the best-fit model (Model 1, Hypotheses 3) for Greenland halibut in each estimated region from 1996 to 2019: Canada and West Greenland and Canadian eastern Arctic (NWAS), Southeast Greenland (EG), Iceland (ICE), and the Norwegian slope (NEAS). Lines indicate the estimated state, and points indicate observed.

is primarily supported by spawning in the Davis Strait (Gislason et al., 2023; Gundersen et al., 2010).

Our findings supported combining Iceland and Northeast Atlantic stocks into a single population, which means that abundance trends (e.g., population growth rate and interannual variation) were similar enough to not distinguish two separate populations (Tolimieri et al., 2017). Combining Iceland and Northeast Arctic into one population agrees with previous genetic and tagging studies that found high connectivity of Iceland waters and Northeast Arctic regions (Ådlandsvik et al., 2004; Albert & Vollen, 2015; Vihtakari et al., 2022; Westgaard et al., 2017). Such intermingling of populations would likely be caused by feeding and reproductive movements or dependency on prevailing oceanic currents carrying eggs and larvae (Ådlandsvik et al., 2004). Our most parsimonious biomass model also combined Iceland and Northeast Arctic into one population, along with seven of the top 10 biomass models. Although the second-best biomass model supported separate Iceland and Northeast Arctic. This situation could be because the model fails to reflect the migration rate of juveniles (9–29 cm) among these two regions, found in tagging studies (Albert & Vollen, 2015; Vihtakari et al., 2022), since the surveys reflect the dynamics of the species at depths >400 m, where juveniles are rarely found (Bowering & Nedreaas, 2000). Probably the biomass index was more influenced by this fact than the abundance index, as it was measured by weight, and this tends to vary to a lesser extent compared to recruitment peaks (Kimura & Somerton, 2006).***

None of our best-fit models or similarly supported models combined Southeast Greenland and Iceland regions into a single population or supported the current management structure (Hypothesis 2). One possible cause could be related to a dependence on recruitment from neighboring populations (Northwest Atlantic and Northeast Atlantic stocks), which would differently impact population dynamics

populations does not seem inconsistent with our results based on abundance/biomass trends. Also, our finding is consistent with previous genetic studies (Knutsen et al., 2007; Westgaard et al., 2017) and the current understanding, which assumes that the NWAS

in Southeast Greenland and Iceland, and suggest a mixing zone for two or more populations in the WNS (Vihtakari et al., 2022). Another explanation could be that spawning in Southeast Greenland fjords leads to differences between Southeast Greenland and Iceland populations (Gundersen et al., 2013).

4.1 | Our findings supported the importance of fishery harvest, but not NAO, as descriptors of Greenland halibut abundance and biomass

Best-fit models of abundance and biomass supported including catch as a covariate, with many of the top 10 models including catch or lagged catch, likely because quotas are set based on these survey indices. However, the correlation was often negative and population growth rates were the same among populations when harvest was considered. Abundance models that included the NAO were among the top 10, while none of the top 10 biomass models included the NAO. Inclusion of the NAO in abundance models may represent the impact of climatic variation on recruitment, which would make abundance estimates more sensitive to the NAO than biomass. Greenland halibut recruitment is correlated to the NAO (e.g., distribution of juveniles, Albert & Høines, 2003; northward displacement of juvenile Greenland halibut when temperature in the Barents Sea increased and a more southern distribution when temperature decrease, Albert et al., 1997). Despite these findings, the effect of climate variation on the species' distribution is poorly understood and should be studied further.

5 | CONCLUSION

Different combinations of MARSS models we examined indicate that the NWAS is likely independent of other stocks, but questions are raised about current management in the Northeast Atlantic. Our findings support combining Iceland and Norway slope populations into one stock, although the full range of biological information available for this species should inform any such decision. Top 10 abundance and biomass models separated Southeast Greenland and Iceland into two populations, which suggested that the WNS comprised at least two populations one in Southeast Greenland and the other in Iceland waters, as a potential mixing zone between western and eastern North Atlantic (Vihtakari et al., 2022). While this delineation still needs to be confirmed, fisheries managers could begin to identify implications, in terms of fishery productivity (Benestan, 2019), for what could be a mixed stock fishery in the West Nordic area. Thus, our findings warn that the current political boundaries of the stocks of Greenland halibut in the Northeast Atlantic do not reflect the biology of species. Managers should take a precautionary approach when establishing harvest strategies over the stocks in the North Atlantic due to the ambiguity in advice on utilization (Schindler et al., 2010), in order to avoid economic losses of the fishery industry and reductions on biodiversity (Mölman &

Diekman, 2012). We encourage future studies to increase understanding of the synchronicity between populations of Greenland halibut in Southeast Greenland and Icelandic waters to shed light on what appears to be a mixing zone between two large populations in the North Atlantic.

CONFLICT OF INTEREST STATEMENT

The authors and their afiliation whose names are listed here certify that they have no involvement in any organization with finantial interest in the subject matter or materials discussed in this manuscript.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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