Life history spatial constraints of sub-arctic marine fish species

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Abstract

Climate change influences ecological processes and biogeochemical cycles of marine environments. Species may respond and adapt to these changes through shifting spatial distributions, but options may be limited by the required occupancy of essential habitats which are anchored in space. Marine fish species typically have complex life cycles composed of multiple life stages with different degrees of habitat preferences. Limited knowledge of when spatial constraints are most likely to occur in marine fish life cycles has impeded the development of realistic distribution forecasts. In this study, we develop and implement analytical techniques to identify spatial constraints, defined by both the *consistency* through which a particular geographic area is used year after year, and by the *extent* of such area with respect to the entire population range. This approach is applied to ten case studies including six groundfish species from the Eastern Bering Sea, three from the Scotian Shelf, and one from the Barents Sea. Our analyses illustrate that the early phase of the species' life cycle is more spatially constrained than older life stages, and that adult stages are more closely associated with particular temperatures or climate velocities. We detected significant species-specific variability in both the degree to which species are anchored in space throughout their life cycle, and the ontogenetic changes of the geographic association. Some of this variability can be explained by the species life history strategy and this provides promising avenues to extend similar analyses to data poor species. The presence of life history spatial constraints, particularly during early life stages, indicates restrictions exist to changes of spatial distribution and thus questions the assertion that global warming will uniformly result in an increase of harvest at higher latitudes and decreases at lower latitudes. Species distribution models are often parameterized from data based on life stages that are highly variable in space, such as the adult stages during summer months which may result in unrealistic forecasts of distribution. Our study develops ecological and analytical insights that are critical for developing accurate projections of species distributions under different climate change scenarios.

Key words: Life history, marine subarctic, spatial distribution, ontogeny, constraint

Introduction

A focal point in the study of fisheries oceanography is to understand and predict how fish populations respond to climate change, and to regional and local scale oceanographic variability (Kendall and Duker, 1998; Cury et al., 2008; NOAA et al., 2014a). Within this framework, a great challenge exists which is to quantitatively characterize the adaptive potential of marine organisms (Merilä and Hendry, 2014). Climate change is affecting ecological processes and biogeochemical cycles of many marine environments. Species may respond and adapt to these changes through both phenotypic plasticity and microevolutionary adaptations (Crozier and Hutchings, 2014). For example, one way in which adult marine fish quickly adapt to climate change is by shifting their spatial distribution (Poloczanska et al., 2013). Commercial exploitation has also shown to result in spatial shifts, in particular a deepening among older age groups (Frank et al., 2018). Retrospective analyses of long-term monitoring or survey programs have documented several shifts of marine fish spatial distribution across both latitudinal and bathymetric gradients (Perry, 2005; Nye et al., 2009; Pinsky et al., 2013; Pinsky et al., 2020). These trends are particularly evident in sub-arctic and temperate environments (Kleisner et al., 2017), where the effects of global warming appear to be the primary driver (Saba et al., 2016). Range shifts of marine fish are now impacting coastal communities that are dependent on commercial fisheries (Selden et al., 2020; Rogers et al., 2019).

There are limits to how far individuals in a population can adapt to a changing climate. Marine fish species have complex life cycles composed of multiple life history stages that undergo ontogenetic changes of spatial distribution and habitat requirements. As a consequence they exhibit different degrees of habitat preferences during their life cycle (Barbeaux and Hollowed, 2018; Bartolino et al., 2011). During some life stages individuals are constrained in space due to the presence of critical habitats and oceanographic conditions, such as bathymetry, sediment characteristics, or topographically induced currents and tides, which are also fixed in space and time. (Lough et al., 2006; Ciannelli et al., 2010; Stuart-Smith et al., 2021). Imprinted behavior (Cury, 2019) and social facilitations (Corten, 2002) also contribute to the presence of persistent spatial aggregations of individuals in geographically fixed habitats. Examples of spatially constrained habitats include spawning sites (Ciannelli et al., 2014), nursery areas (Beck et al., 2001), and dispersal pathways between them (Petitgas et al., 2013). During other life stages the same individuals are able to change their distribution and track climate velocities (e.g., Alvarez-Berastegui et al., 2014).

The effects of climate variability on species distributions are often assessed by examining a single or few life history stages based on readily available data (e.g., Wisz et al., 2015; Thorson et al., 2016; Kleisner et al., 2017). However, parameterizing species distribution models based on one or a few life stages may produce results that over-estimate the degree of spatial re-distribution in response to climate change, and misinterpret the processes involved in driving such spatial responses (Asch and Erisman, 2018). Recognizing where and when in the species' life cycle these spatial constraints occur is important to produce more realistic distributional forecasts. To date, there is no systematic knowledge of when in marine fish life cycles such spatial constraints are most likely to occur. Spatially constrained stages may act as a bottleneck to adaptation, and can have fitness repercussions (Caddy, 2014). Therefore, identifying these constraints has important implications for monitoring and managing marine fish species in a changing climate.

This study has the dual goals of first *developing* analytical techniques to identify spatial constraints on a species' life cycle, and then *implementing* these new analytical techniques to compare patterns of life history spatial constraints across species with contrasting life history strategies. Data rich species/populations from sub-arctic systems in both the North Atlantic

(Scotian shelf and Barents Sea) and the North Pacific (Bering Sea) (Fig. 1) are evaluated, although we envision future application of these techniques to species from temperate and subtropical systems. The selection of species in this study balances the need to include contrasting life history strategies and highly resolved life cycle data . Here we define the degree of spatial constraint by both the *consistency* at which a particular geographic area is used year after year, and by the *extent* of such area with respect to the entire population range. Consequently, life history stages that occupy the same areas over time, and are concentrated in a relatively small area compared to the population range, are deemed highly constrained. In discussing our results, relevance is given to global climate change and the ways in which species can adapt even in the presence of strong spatial constraints. With these study goals and methodologies, we anticipated the existence of bottlenecks to species adaptability through changes of spatial distribution, to generate hypotheses to link a species' life history and the processes affecting the selection of habitat through the life cycle, and to develop spatial distribution models that consider multiple life history stages and that can be used to project species distributions in relation to future climate change scenarios.

Methods

The methodology is organized in two sections. First, we describe the quantitative metrics for assessing habitat constraints, and in the second, we describe the application of these metrics to a selection of ten sub-arctic fish populations that are representative of contrasting life history strategies and habitat requirements.

Metrics for assessing habitat constraint

We defined the habitat constraint (*HC*) for a species (*s*) at a target age or size (*a*), as the product of the *consistency C*, dimensionless, ranging from 0 (not consistently occupied) to 1 (consistently occupied) at which a specific habitat is occupied, and the geographic *extent E,* dimensionless, ranging from 0 (small extent) to 1 (large extent) of that habitat:

$$HC_a = C_a(1 - E_a) \qquad (1)$$

As such, the habitat constraint metric can only range from 0 to 1. It approaches 1 when, over the studied period, fish at a target age or size are consistently using a very small fraction of the area where the population is known to occur. Conversely, the constraint metric will be close to zero when target age or size distribution is highly variable from year to year and widely spread over the population range. Note that the habitat constraint changes for each species, however in equation (1) the sub index for species has been omitted.

We used Generalized Additive Models (GAM) to determine C_a. GAMs allow for nonlinearities between covariates and response, and therefore are well suited to capture unique patterns of spatial dependency over space (Wood, 2017). Let $X_{a,lat,lon,y}$ be the natural log of the local abundance of the studied species at the target age or size *a*, collected over multiple years *y*, at locations defined by geographic coordinates (*lat*, *lon*). We quantify the consistency of habitat use (C_a) as the difference of the residual error between the *base* model (2), which only includes yearly variable intercepts ($\beta_{a,y}$) and the day of the year effect (i.e., phenology *d*),

$$X_{a,lat,lon,y} = \beta_{a,y} + s_a(d) + \varepsilon\_b_{a,lat,lon,y} \qquad (2)$$

and the *habitat* model (3), which includes also the effect of geographic coordinates (*lat, lon*)

$$X_{a,lat,lon,y} = \beta_{a,y} + s_a(d) + g_a(lat, lon) + \varepsilon\_h_{a,lat,lon,y} \tag{3}$$

The parameter $\beta_{a,y}$ is a stage and year specific intercept that accounts for interannual changes in abundance, g is a two-dimensional smooth function that varies by stage, s is a one-dimensional smooth function that also vary by stage, and ε is a random error assumed to be normally distributed (on the log scale) with mean equal to zero and variance equal to the residual variance of the model. Models 2 and 3 are fitted separately for each age or size-group of a population.

Given the base and habitat models in 2 and 3, the consistency metric is derived as follows:

$$C_a = \frac{\sum(e\_b_{a,lat,lon,y})^2 - \sum(e\_h_{a,lat,lon,y})^2}{\sum(e\_b_{a,lat,lon,y})^2} \tag{4}$$

If a target age or size group consistently uses the same habitat year after year, then the error of the habitat model ($\varepsilon\_h_{a,lat,lon}$) will be small, the ensuing C_a metric will be high, and approaching 1. Vice-versa, for a habitat used very inconsistently from one year to the next, C_a will approach 0. The determination of C_a from models (2) and (3) is executed on presence only data (i.e., positive, non-zero catches). However, corresponding logistic regression models are also implemented to the presence-absence data to estimate the probability of occurrence of the target stage, and the presence-absence and the presence only models are used together to predict density over a regularly spaced array of stations for the calculation of habitat extent, as discussed in the next paragraph.

Given an age or size group *a*, its geographical *extent* (E_a), is determined by the smallest fractions of the total occupied habitat that contains a pre-specified fraction (e.g., $f=0.75$) of the predicted total abundance of the species at the targeted age or size. Namely,

$$E_a = \frac{A_{f,a}}{A_t} \Big/ f \qquad (5)$$

where $A_{f,a}$ is the smallest area containing a fraction *f* of the species total abundance at the targeted age/size, and A_t is the total area occupied by the population. Because available surveys are likely to cover areas where the targeted species has never occurred, A_t is here defined by a regular array of equally spaced grid points that are less than 30 km away from a location with positive occurrence of the targeted species. $A_{f,a}$ is equal to the aerial sum of all the grid cells (H), each with area (*h*), and whose cumulative fraction of predicted abundance is less than or equal to *f*:

$$A_{f,a} = \sum_{i=1}^{H} h_i$$

We choose the fraction *f* equal to 75% of the predicted biomass within the area A_t, and for three of the ten case studies examined, we assessed the sensitivity of *f* to the habitat extent and habitat constraint metrics (Appendix S1). To predict the density of the targeted species and stage at each location in the array ($\hat{d}_{h_i,a}$), we use the delta method (Porter and Ciannelli, 2018), by taking the product between the probability of occurrence (*u)* and the abundance (*x)* of the target stage and species predicted from a presence-absence and presence only habitat model (3), respectively:

$$\hat{d}_{h_i,a} = \hat{u}_{hi,a}\hat{x}_{hi,a}.$$

To predict $A_{f,a}$, the array units (h) are first sorted in decreasing order of the respective predicted density, such that $\hat{d}_{h\_i} \geq \hat{d}_{h_1+1}$, and their respective areas are summed until the fractional biomass threshold f is reached. When so derived, the extent metrics (E_a) can only range from 0 to 1. It approaches 0 when the target stage is spatially clustered within the species distribution range, and 1, when the target stage is uniformly distributed across the species distribution range.

Applying constraint metrics to species with contrasting life histories

We implemented the habitat constraint models to ten case studies, including six groundfish species from the Eastern Bering Sea, three from the Scotian Shelf, and one from the Barents Sea (Table 1). For each studied system, fish distribution data are collected as part of long-term survey programs conducted by the agencies that oversee fisheries management and assessment in the region, including the National Oceanic and Atmospheric Administration (NOAA) for USA (Lauth et al., 2019), the Canadian Department of Fisheries and Oceans (DFO; Frank et al., 2018), and the Institute of Marine Research (IMR), Norway (Fall et al., 2018) and the Polar Branch of Russian Federal Research Institute of Fisheries and Oceanography (VNIRO) for Russia (Stige et al., 2019) in cooperation for the Barents Sea. We only included stages of species for which the available survey coverage clearly captured the distribution core of the targeted age or size, and we only included years in which there were more than 40 stations sampled. In general, the timing of the juvenile and adult survey is summer, while that of eggs and larval stages changes depending on the spawning phenology of the species. Additional information about each survey, including years and months covered, is provided in the Appendix S2.

To compare patterns of habitat constraint across the ten case studies we first derived an index of ontogenetic development ($O_{s,a}$) as the ratio between the size or age of the examined life history stage and the maximum size or age of the species. We are aware that ontogeny does not linearly scale with either age or size. Therefore, we also tried alternative ways of calculating the ontogenetic index, e.g., as the log of the age or size over the log of maximum age or size. Results were not sensitive to the way in which the ontogenetic index was calculated, and we opted for the simpler linear formulation. We then fit a GAM to the habitat constraint versus ontogenetic index metrics. In these analyses, the inter-species variability was first included as a random term, which allowed us to estimate an average relationship across the ten combinations of species and populations, and the variance components associated with the fixed and random terms:

$$HC_{s,a} = \beta + g(O_a) + \delta_s + \varepsilon_a \qquad (6)$$

where β is a model intercept, g is a smooth non-parametric function, δ_s is a random effect varying by combinations of species and population (10 estimates) assumed to be normally distributed, and $\varepsilon_a$is the residual variation, also normally distributed.

In a second GAM formulation, the inter-population variability was modeled as a fixed effect, which allowed us to estimate a single smooth term and elevation for each examined population:

$$HC_{s,a} = \beta_s + g_s(O_{s,a}) + \varepsilon_a \qquad (7)$$

In GAM formulations (6) and (7), the maximum degrees of freedom for the one-dimensional smooth terms was limited to three, to avoid overfitting.

We applied the above analyses to multiple life history stages, including eggs, larvae, and eight or nine progressively larger or older juvenile and adult stages. Not all stages were available for all populations. Some case studies missed the egg and larval stages due to lack of taxonomic resolution (arrowtooth flounder, *Atheresthes stomias*) or life history characteristics (Pacific cod, *Gadus macrocephalus,* have demersal eggs), and all of the Scotian Shelf case studies did not include the egg stage. For the Bering Sea case studies, juvenile and adult stages were partitioned into eight size groups, with size thresholds chosen to even out sample size. For the Scotian Shelf and Barents Sea case studies, juvenile and adult stages were partitioned into nine age groups, (age-0 to age-8 and older). For each species, we only included data from sampled stations that are less than 30 km away from a sampled location that had at least one positive occurrence of the targeted species at any age or size. Thus, we eliminated surveyed stations where the targeted species had never occurred.

Given a species, with the exception of the Barents Sea case study, we limited the analyses to overlapping years of data availability across the stages examined. So, for the Scotian shelf case studies, we restricted the analyses from 1979 to 1982, which are the years in which ichthyoplankton collections are available. For the Bering Sea, data were available from 1982 to 2018 for adults and juveniles, and from 1988 to 2018 for eggs and larvae, however, the exact years changed among the species examined due to the necessity of including no less than 40 sampled stations within each year. For the Barents Sea, temporal coverage differed between stages. Eggs and larvae were only available from 1981 to 1993, while the autumn juvenile and adult surveys are only available from 2003. More information about the years and months included in the analyses is provided in the Appendix S2.

To estimate the relationship between habitat constraint and the ontogenetic index (Eqs. 6 and 7), we only included species and stages that had more than 400 stations with positive catches through all years, which correspond to less than the 10% quantile of available sample sizes across all examined species and stages. A minimum of 400 stations was deemed necessary to simultaneously fit one- and two-dimensional smooth functions of phenology and distribution in model (3). This caused the removal of yellowfin sole eggs (n = 33), Alaska plaice larvae (n = 253), Scotian shelf haddock (n = 160) and cod (n = 262) larvae, Scotian shelf cod age-0 (n = 262) and age-1 (n = 333), Scotian shelf hake age-0 (n = 372), and Scotian shelf haddock age-0 (n = 283) and age-1 (n = 342). To reduce model uncertainties, the size or age specific data should ideally capture the distribution range and have similar sample size across size or age groups. In our applications, we removed yellowfin sole larvae because their distribution was clearly truncated at the northern end of the sampled area, in spite of this stage including 603 stations. For the remaining cases, the area monitored include clusters of high numerical density, and covers bathymetric and oceanographic values that are representative of the habitat variability experienced throughout the population range. Thus, we are confident that the data analyzed capture well the degree to which different size or age groups distribute over space. All analyses were conducted in R (version 3.6.2) and GAM models were fitted with the mgcv library (1.8-33). With the exception of data from the Barents Sea case study, all other R codes and data are deposited in: https://github.com/lciannel/lifehistoryconstraint.

Results

Implementing habitat constraints analyses

The distribution of walleye pollock in the Eastern Bering Sea changes for different ontogenetic stages and size groups (Fig. 2). At the egg and larval stages, the majority of the estimated biomass is confined to the Alaska Peninsula and to the Pribilof Islands regions, which are known spawning locations. The slight difference in distribution between egg and larval stages is attributable to passive transport by currents from spawning to juvenile habitats. As individuals grow in size they occupy larger areas of the outer (depth 100-200 m) and middle (depth 50-100 m) shelf regions, illustrated by a progressive increase of the habitat extent for these stages (Fig. 2).

Unlike the pollock case study, in which distribution changes across life stages, the spatial distribution of haddock in the Scotian shelf does not change through different life stages. Despite this, there are differences in the consistency and extent of habitat use across life history. High concentrations of haddock larvae are located at the southern and western portion of the Scotian shelf, corresponding to Browns and Emerald Banks, which are known spawning grounds. Consequently, the majority of the estimated larval biomass is confined to these two locations (Fig. 3). Habitat expansion and increased dispersion is observed during the age-0 stage, (probably due to greater mobility of these juveniles), while distribution becomes concentrated and patchier again at older and reproductively mature life stages (age-1+) (Fig. 3). Note that we provide similar sets of figures to those for walleye pollock and haddock shown here for the other eight case studies in the Appendix S3.

For walleye pollock in the Bering Sea, estimates of habitat constraint decline with ontogeny, ranging from 0.22 at the egg stage to 0.06 at an intermediate adult stage. This is due to both a higher interannual spatio-temporal variance associated with larger sized individuals, and a progressive increase of habitat extent (Fig. 4). The consistency at which a stage occupies a specific geographic area decreases notably for individuals in the middle of size ranges, between 383 mm and 444 mm in length, denoting large interannual variability of spatial distribution at corresponding size ranges (Fig. 4).

Haddock's metrics of habitat constraints are higher than those of pollock, and are highest between age-2 (0.26) and age-4 (0.27) to then decline for older life stages, at age-8 (0.17) and age-9+ (0.18). During the larval and age-0 stages, haddock metrics of constraint are also low, but the sample size for these stages is small compared to that of other stages, and may have contributed to the high interannual variability and low consistency of spatial distribution (Fig. 5).

By including population as a random term (Eq. 6), we found a significant and linear effect of the ontogenetic index on habitat constraint across all species (Fig. 6). This outcome implies that younger stages and size groups, on average, tend to be more highly constrained in space than older stages and larger size groups. However, the variance component of the random term (population) is three orders of magnitude greater than the variance explained by the ontogeny effect, underscoring high inter-population (or species) variability in this relationship (Table 2).

The variability in the shape and elevation of the smoothed ontogenetic index is evident from the results of the fixed effect model (Eq. 7). Three of the populations exhibit habitat constraints that persist to juvenile or even adult stages (Alaska plaice, yellowfin sole, flathead sole) and for two of these species the relationship between the ontogenetic index and habitat constraint is nonlinear (e.g., flathead sole and yellowfin sole) (Fig. 7). Five populations have a gradual linear decline of habitat constraint with ontogeny (Barents Sea cod, Bering Sea pollock and cod, and Scotian shelf haddock and cod), while the remaining two populations have no significant relationship between habitat constraint and ontogeny (arrowtooth flounder, silver hake). In addition to variability in the shape of the ontogenetic effect we also found significant variability in the elevation associated with each population (Table 2). Yellowfin sole, Alaska plaice and flathead sole have the highest intercept estimates, indicating a stronger overall affinity of these populations to location or substrate, compared to other examined cases. The relationships between the metrics of habitat constraint and extent with the ontogenetic index did not change with changes of the parameter *f* (fraction of biomass for the habitat extent metric) (Appendix S1).

Discussion

Drivers of life history spatial constraints

Our analyses illustrate that marine fishes, particularly during the early phase of their life cycle, are more constrained in space than other stages. The existence of life history spatial constraints is common and well documented in terrestrial vertebrates and invertebrate species, and have practical implications for conservation. For example, stopover sites of long-distance migratory birds, such as the bar-tailed godwits (*Limosa lapponica)* in the eastern Atlantic flyway (Scheiffarth et al., 2002), are critical to the completion of the species' annual migration. Likewise, migrating and overwintering generations of the eastern monarch butterflies *Danaus plexippus* are known to concentrate from a 4.5 million km^2 breeding ground during spring and summer, down to an approximately 1 km^2 area in winter (Reppert and de Roode, 2018). In contrast to these examples of strong spatial affinity and site fidelity for terrestrial species, the current paradigm for marine sub-arctic fish, (especially pelagic species; Cheung et al., 2015), is that of a loose association with geographic locations. This is in part because of their highly dispersing life history strategy, and in part because of the highly spatially dynamic nature of seascapes. This is the basic premise behind the postulate that fish species can adapt to global warming by shifting their spatial distribution, leading to a redistribution of global catches, with loss at the tropics and gains at higher latitudes (Cheung et al., 2010; Meredith et al., in press) . While there is ample evidence that many marine fish species are redistributing, here we show that some species from sub-arctic seas consistently occupy restricted geographic locations during early phases of their life cycle. The existence of these spatial constraints will limit the degree to which these species can adapt to climate change by re-distributing to higher latitudes.

We did not address the drivers of these spatial constraints, but it is reasonable to expect that natal homing (Cury, 2019) and a life history strategy tuned to the presence and persistence of topographic, sediment, and bathymetric characteristics are the primary reasons. In the Bering Sea for example, organic content and sediment characteristics are correlated with higher trophic level community composition and abundance in benthic habitats (Grebmeier et al., 1989). Flatfish abundance has strong associations with sediment characteristics, and it is hypothesized that these associations are the result of diet preferences and benthic prey availability (McConnaughey and Smith, 2000). Similarly, in the Scotian shelf there are strong habitat associations of the three gadids studied here (cod, silver hake and haddock) and sediment types (Scott, 1982a; Waiwood and Buzeta, 1989), and in the nearby Georges Bank newly settled juvenile cod and haddock are associated with pebble-gravel deposits in the northeast side of the bank (Lough et al., 1989). Bathymetric-driven circulation features, important for the dispersal of fish eggs and larvae, are also potential drivers of spatial constraint during early life stages. In the Bering Sea, canyons along the continental slope drive topographically steered circulation (Ladd, 2014) and affect the transport pathways of slope spawning flatfish eggs and larvae (Sohn et al., 2016). On the shelf, circulation features (e.g. gyres) can also aggregate and retain eggs and larvae in spatially restricted areas around banks (O'Boyle et al., 1984; Smith and Morse, 1985; Lough et al., 2006). In our analyses of the Scotian shelf, haddock and cod larvae generally occupied Browns and Emerald banks, and silver hake was found in the vicinity of Western Bank. These are known gadid spawning locations in the Scotian shelf region (Hurley and Campana, 1989; Brickman, 2003), and previous studies have underscored the importance of larval retention around these banks (O’Boyle et al., 1984). While in principle during spatially constrained phases of a fish life cycle, water temperature may not be an important driver of spatial distribution, temperature may still be an important covariate during other life history stages. For example, the spawning habitats of walleye pollock, in both the Eastern Bering Sea and western Gulf of Alaska, do not geographically change in relation to changes of water temperature (Bacheler et al., 2010, Bacheler et al., 2012), while adult stages of walleye pollock outside of the spawning season shift northward during warm years (Thorson et al., 2020).

Exploitation and predator-prey interactions may also contribute to changes of habitat constraints through ontogeny. Sub-arctic systems are characterized by relatively few species, some of which are commercially harvested, with strong trophic interactions (Livingston, 2000; Frank et al., 2006). Strong exploitation erodes spatial structure and exploitation status is another important driver of spatial constraint (Ciannelli et al., 2013). In the Scotian shelf, Frank et al., (2018) found that exploitation drives ontogenetic-like deepening of Atlantic cod. Thus, one recommendation for future analyses would be compare patterns of range shifts in relation to exploitation status of the stock. Trophic interactions may shape the degree of patchiness, especially in pelagic fish species. For example, (Frank et al., 1993) found that capelin larvae on the Southeast Shoal of the Grand Banks were patchy during early stages, followed by increased dispersion, and then, with the onset of schooling behavior, distributions became patchier and were closely associated with their primary food sources. Some species, such as adult Atlantic cod and walleye pollock, are prone to eating smaller and younger conspecific individuals. So, their movement and distribution is linked to that of their prey (Ciannelli et al., 2007; Fall et al., 2018).

Expanding these analyses to other case studies

The assessment of life history spatial constraints requires spatial data collected over multiple age or size groups of a species' life cycle, ideally during oceanographically contrasting years, and for most of the population distribution range. Not surprisingly, such data are limited, but notable exceptions exist, and they have been included in our study. If data are available over different seasons, it is best to separate the analyses accordingly, as species can undergo seasonal contraction and expansions in their distribution. This is evident in the Barents Sea cod, with winter distribution range limited by low temperature under sea ice, and therefore more constrained compared to summer (Appendix S3, Figs. S14 and S16).

Life history spatial constraints inferred from data rich cases, may provide insight for data poor species. In cases we examined, three patterns of spatial constraint across life histories were evident (Fig. 7). The first pattern is characterized by a gradual and monotonic decline of spatial constraint, resulting in the adult spawning individuals and eggs being most spatially constrained, and the non-spawning adult individuals instead being more spatially dispersed. Gadids, including walleye pollock, Scotian shelf cod and haddock, Pacific cod and Barents Sea cod follow this pattern in so far as their populations have the simultaneous presence of spatially constrained and highly mobile individuals. These species have strong site fidelity at spawning (e.g., Hurley and Campana, 1989; Rose, 1993; Neidetcher et al., 2014) and highly mobile adults during the nonbreeding seasons. Tagging studies of adult stages of Pacific cod (> 50 cm length) indicate widespread movement and occupancy during summer, and directional movement to slope spawning areas during winter (Shimada and Kimura, 1984). Similarly, mature Barents Sea cod undertake extensive southwards countercurrent migrations during winter toward spawning grounds along the Norwegian coast and migrate northwards to vast feeding grounds in the summer (Ottersen et al., 2014).

The second pattern is characterized by a delayed (flathead sole) or protracted (Alaska plaice, yellowfin sole) period of high spatial constraint, persisting into juvenile and sub-adult stages, before declining at later stages. Previous work has pointed to strong associations of yellowfin sole abundance in sandy substrate, flathead sole in mixed sand and mud, and Alaska plaice in mixed gravel and sand (McConnaughey and Smith, 2000). In the Bering Sea shelf, bathymetry is negatively correlated with sediment size and, not surprisingly, all three species have a strong affinity with specific depth ranges (Swartzman et al., 1992). Adult yellowfin sole perform annual spring and fall migrations to and from spawning areas (Wilderbuer et al., 1992). The timing of these migrations is influenced by water temperature and sea ice extent on the Bering Sea shelf, and in turn influences availability to the survey (Nichol et al., 2019). So, it is possible that the rapid decline of habitat constraint of adult yellowfin sole may be driven by the changes in timing of their migration and availability to the summer survey, rather than interannual distribution changes.

The third pattern includes cases with a relatively constant level of spatial constraint through the species life cycle, indicating either a loose (e.g., arrowtooth flounder) or high (e.g., silver hake) lifetime spatial associations. Species that conform to this pattern are at the northernmost extreme of their range, and their spatial distribution and annual abundance may be particularly sensitive to changes of water temperature. For example, arrowtooth flounder in the Bering Sea avoids water below 2^{o}C, which is typically observed in the middle shelf during summer on the Bering Sea (Ciannelli et al., 2012). Similarly, silver hake in the Scotian shelf tends to occupy warmer water of the central and southwest portion of the shelf while avoiding the colder northeast shelf (Scott, 1982b), and bottom water temperature on the shelf is an important driver of their abundance (Reed et al., 2018). We note that our cross-section of species only includes those residing in sub-arctic systems, and with either benthic or demersal strategies during the adult phase. Thus, augmenting these analyses with more species, including those from temperate and tropical reef species, as well as species with pelagic life history strategies during the adult phase (e.g., Muhling et al., 2013), would be instrumental to validate the trends of habitat constraint across the life cycle, and to establish the link with life history strategies. Ultimately, this broader level of investigation would further enable inference about habitat use and adaptability to climate change for data poor species, for which life history trait information is known but spatial data for multiple life stages is not available.

Implications for species distribution models

Assessment of habitat constraints through the species life cycle have important implications for accurate predictions of species distribution in relation to climate change. The presence of strong spatial dependency for some stages indicates that within the range of examined values, water temperature may not be a primary driver of spatial distribution (Stuart-Smith et al., 2021), and calls into question projections of species or catch distributions based solely on water temperature. Additionally, species distribution models are often parameterized using data from stages that are highly variable, such as the adult stages during summer months, which is when most groundfish surveys occur in sub-arctic areas. Our analyses indicate that adult stages are more likely to follow temperature or climate velocities because they are less constrained in space. Consistently, stage-specific models have different prediction outcomes compared to those parameterized on only one life stage (Asch and Erisman, 2018). Life history stages with high habitat constraint will limit future distribution shifts and can be used as a “mask” increasing accuracy of current species distribution model predictions.

To what degree can range shift offset climate change?

Populations that have the simultaneous occurrence of spatially constrained and spatially unconstrained life stages (e.g., walleye pollock and Pacific cod) can experience a further separation among their stage-specific habitats and therefore be challenged to close their life cycle. This appears to be the case for both Pacific cod and walleye pollock in the Bering Sea, where in recent years the juvenile and adult summer distribution has been shifting progressively northward (Stevenson and Lauth, 2019), while spawning habitats are fixed in space at the southern edge of their distribution range (Neidetcher et al., 2014; Bacheler et al., 2012).

When species are constrained in space during certain stages they will need to adapt to new habitat conditions in order to change their distribution. Adaptive changes are needed when the distribution of the most limiting stage is 1) geographically controlled, and/or 2) the physiological tolerance limits (e.g. temperature-dependent development) of the most limiting stage have been reached. In 1), for species to shift distribution, adaptation must occur by linking the new geographic cues (e.g. deeper waters) to the environmental conditions associated with suitable habitat. In 2), if physiological tolerance limits have been reached, adaptation in the physiological response to the environment would be needed before further shifts could occur. In the Gulf of Alaska for example, water temperature is significantly warmer than the Bering Sea, and laboratory and modeling analyses indicate that Pacific cod eggs may be experiencing thermal stress at their traditional spawning sites, which may further limit recruitment (Laurel and Rogers, 2020). To adapt to these changes Pacific cod will need adaptation to 1) develop new cues and spawn in cooler habitats within the Gulf of Alaska, and/or 2) shift the thermal tolerance of embryos. Models that account for life history constraints as outlined here, that are extended to also include physiologically based relationships (e.g., Kearney and Porter, 2009) of environmental covariates in addition to a fixed spatial term, can be used to simulate plastic and adaptive responses of fish to climate. Furthermore, modelling of free-drifting life stages and energy budget modelling of migratory adults might be needed to assess whether different spatial constraints across life stages will necessitate evolutionary adaptations in order for the species to close its life cycle in a future climate.

There is unfortunately a chasm in the marine sciences literature with fisheries oceanographers being more keenly aware of plastic responses of fish to climate change and life-history biologists being more keenly aware of evolutionary adaptations (e.g.,. Hutchings, 2011). Bridging this gap between plasticity and adaptations (Schoener, 2011; Anderson et al., 2012) to understand and model how marine species respond to climate change and variability, as well as other anthropogenic stressors, will be an important advancement in marine ecology.

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Table 1. List of case studies examined. NOAA: National Oceanic and Atmospheric Administration; DFO: Department of Fisheries and Ocean; IMR: Institute of Marine Research, VNIRO: Russian Federal Institute of Fisheries and Oceanography. Stages with an asterisk (*) were not included in the analyses of habitat constraints vs ontogenetic index (Equations 6 and 7) due to a small sample size. For additional information about sample sizes, years, and months included in each case study, see Appendix S2 (Table S1).

Common and scientific names	**Area**	**Max size or age**	**Survey type**	**Stages available**	**Source**
Walleye pollock (*Gadus chalcogrammus*)	Eastern Bering Sea	910 mm	Ich, BT	Eggs, larvae, juveniles, adults	NOAA
Flathead sole (FH, *Hippoglossoides elassodon*)	Eastern Bering Sea	650 mm	Ich, BT	Eggs, larvae, juveniles, adults	NOAA
Arrowtooth flounder (ATF, *Atheresthes stomias*)	Eastern Bering Sea	980 mm	BT	Juveniles, adults	NOAA
Pacific cod (*Gadus macrocephalus*)	Eastern Bering Sea	1170 mm	BT	Juveniles, adults	NOAA
Alaska plaice (AP,	Eastern	720 mm	BT	Eggs,	NOAA

Pleuronectes quadrituberculatus)	Bering Sea			larvae*, juveniles, adults	
Yellowfin sole (YFS, *Limanda aspera*)	Eastern Bering Sea	700 mm	BT	Eggs*, larvae, juveniles, adults	NOAA
Atlantic cod (*Gadus morhua*)	Barents Sea	15 years	Ich, MT, BT	Eggs, larvae, juveniles, adults	IMR, VNIRO
Atlantic cod (*Gadus morhua*)	Scotian shelf	15 years	Ich, BT	Larvae*, juveniles*, adults	DFO
Silver hake (*Merluccius bilinearis*)	Scotian shelf	15 years	Ich, BT	Larvae, juveniles*, adults	DFO
Haddock (*Melanogrammus aeglefinus*)	Scotian shelf	15 years	Ich, BT	Larvae*, juveniles*, adults	DFO

Ich= Ichthyoplankton survey, BT = bottom trawl survey, MT = midwater trawl.

Table 2. Results of the GAM models for the analyses of habitat constraints versus ontogenetic index. Model results are shown for two different formulations, including the first in which population is a random term (Eq. 6), and the second with population as a fixed effect (Eq. 7). The values reported for the intercept terms (β) indicate their estimated mean, and the values reported for the smooth terms ($g(O)$) indicate the estimated degrees of freedom. For the fixed effect model, species are sorted in decreasing order of their p-value for the smooth term. Signif. codes: '***' <0.001, '**' < 0.01, '*' < 0.05, '.' < 0.1. YFS: Yellowfin sole. ATF: Arrowtooth flounder

Mixed effect model	$HC_a = \beta + g(O_a) + \delta_s + \varepsilon_a$ Adjusted R^2 = 0.673, Dev = 71.0%, n = 86		
	β	$g(O_a)$	δ_s
Estimate	0.201 ***	1.000 ***	
Var comp		4.05×10^{-5}	8.12×10^{-2}

Fixed effect model	$HC_{s,a} = \beta * I_s + g\left(O_{s,a}\right) * I_s + \varepsilon_a$ R^2 = 0.831, Dev = 97.7%, n = 86	
	$\beta * I_s$	$g\left(O_{s,a}\right) * I_s$
ATF	0.217 ***	1.691
Silver hake	0.249 ***	1.289
Pacific cod	0.065 ***	1.299
Scotian cod	0.153 ***	1.831 .
Barents cod	0.129 ***	1.000 *
Haddock	0.244 ***	1.000 *
Pollock	0.111 ***	1.710 *

Alaska plaice	0.279 ***	1.591 ***
Flathead sole	0.281 ***	1.970 ***
YFS	0.370 ***	1.983 ***

FIGURE LEGENDS

Figure 1. Study areas, including the Eastern Bering Sea (left panel), the Scotian Shelf (center panel), and the Barents Sea (right panel).

Figure 2. Spatial distribution of walleye pollock in the Bering Sea over different ontogenetic stages and size groups. Predictions are shown as color image in the units of number of individuals $10m^{-2}$ (eggs and larvae), or numbers of individuals per hectare (ha^{-1}) for all other size groups. Predictions were obtained from presence/absence and presence only GAM models (delta method, equation 3). Semitransparent grey bubbles are observed densities and the region delineated by a white cross ('+') represents the estimated habitat extent, or the portion of the surveyed area that contains 75% of the estimated total abundance. The stage or size range (in mm) examined is indicated in the lower left corner of each plot. The 200m depth isobath is shown.

Figure 3. Spatial distribution of haddock in the Scotian Shelf over different ontogenetic stages and age groups. Predictions are shown as color image in the units of number of individuals m^{-3} (larvae), or numbers of individuals per hectare (ha^{-1}) for all other age groups. Predictions were obtained from presence/absence and presence only GAM models (delta method, equation 3). Grey bubbles are observed densities and the region delineated by a white cross ('+') represents the estimated habitat extent, or the portion of the surveyed area that contains 75% of the estimated total abundance. The stage or age (in years) examined is indicated in the lower left corner of each plot. The 200m depth isobaths is shown.

Figure 4. Habitat constraint metrics applied to walleye pollock in the Bering Sea. These include the percentage of explained variance of the habitat model (top left, equation 3), mean square error

ratio (MSE ratio, bottom left) between the base (2) and habitat (3) models, the Habitat Extent (top right), representing the occupied and surveyed areas that contains *f=75%* of the total estimated biomass, and the Habitat Constraint (bottom right), calculated as the product of the previously two described metrics. The number of stations with positive catches included in the spatio-temporal models at each stage or size is indicated in the upper left plot.

Figure 5. Habitat constraint metrics applied to haddock in the Scotian shelf. These include the percentage of explained variance of the habitat model (top left, equation 3), mean square error ratio (MSE ratio, bottom left) between the base (2) and habitat (3) models, the Habitat Extent (top right), representing the occupied and surveyed areas that contains *f=75%* of the total estimated biomass, and the Habitat Constraint (bottom right), calculated as the product of the previously two described metrics. The number of stations with positive catches included in the spatio-temporal models at each stage or age is indicated in the upper left plot.

Figure 6. Average habitat constraint across ontogeny for all species, as estimated by the mixed effect GAM model where population is included as random effect (Equation 6). The shaded region represents the 95% confidence interval on the average relationship. The scatterplots are partial residuals and the rug represents data incidence. The scale of the y-axis is in estimated anomalies (i.e., deviations from 0).

Figure 7. Relationship between the habitat constraint metrics and the ontogenetic index for the ten populations examined in this study (Equation 7). The smooth solid lines are average

relationships determined by a fixed effect GAM between constraint and the linear ontogeny index. Dashed lines are 95% confidence intervals. The scale of the y-axis represents the response variable. Species are sorted in decreasing order of their p-value for the ontogenetic index (upper right corner on each plot). For species abbreviations see Table 1.