ECOSYSTEM PROFILE OF AMERICAN PLAICE

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Background

The distribution of American plaice extends along the Atlantic coast of North America, primarily in the Gulf of Maine and Georges Bank. Ocean properties in the Gulf of Maine are highly influenced by the Labrador current, which flows in a general northeast to southwest direction into the Gulf of Maine region (Nye et al. 2010; Brickman et al. 2021). More specifically, sources of water in the Gulf of Maine include the relatively cooler, fresher, surface Scotian Shelf Water which enters via the Nova Scotian Shelf, and warmer, saltier Slope Water that enters the Gulf of Maine at intermediate and greater depths through the Northeast Channel (Townsend et al. 2015; Pettigrew et al. 2005). The flow of water through the Gulf of Maine is cyclonic, or counter-clockwise (Townsend et al. 2015; Chang et al. 2016), where the flow is driven in part by density differences between the Scotian Shelf water and the Slope Water (Brooks 1985). When the Labrador current is strong, water temperatures in the Gulf of Maine decrease and when the strength of Labrador current is weak, a higher proportion of warm water coming from the Gulf Stream enters the Gulf of Maine, increasing Gulf of Maine water temperatures (Nye et al. 2010). The position of the Gulf Stream has shifted northward (Nye et al. 2010; Pershing et al. 2015; Brickman et al. 2021) and the Gulf of Maine has seen temperature warming rates much higher than that of the global average in recent decades (Pershing et al. 2015). While some attribute the warmed temperatures to this northward shift in the Gulf Stream (Nye et al. 2010; Saba et al. 2016), others attribute this to the strength of the Gulf Stream (Alexander et al. 2020). Temperature is considered to be one of the most influential environmental factors for many species across the Northwest Atlantic and has been associated with effects of growth, maturity, survival, metabolism, recruitment, and other aspects of life history (Nye et al. 2010; Runge et al. 2010; Lesser 2016). Many species along the Northwest Atlantic coast have thermal preferences between 5 and 15°C and thermal habitat within this range has decreased, while habitat outside of this range (both colder and warmer) has increased (Nye et al. 2010).

Nutrient profiles in the Gulf of Maine have also changed in the past few decades. Deep (>100m) waters in the Gulf of Maine have become both fresher and colder with increasing silicate and lowering nitrate levels (Townsend et al. 2010). Although changes in the predominating form of slope water that enters the Gulf of Maine (Labrador Slope Water or Warm Slope Water) are correlated with the North Atlantic Oscillation (NAO, Smith et al. 2001; Greene and Pershing 2003; Thomas et al. 2003; Townsend et al. 2006), Townsend et al. (2010) found that the increasing silicate levels of the Gulf of Maine were not correlated with the current NAO cycle, but rather better coincided with the melting of the Arctic ice sheet.

Changes in nutrient concentrations are important driving forces in determining the species composition of phytoplankton in an ecosystem (Townsend et al. 2010). The Gulf of Maine's food web complexity has increased from the mid-2000s, indicating a more stable ecosystem than prior decades (Han et al. 2021). Changes in the composition of species that serve as the foundation of this food web may however, result in significant impacts on higher trophic levels or changes in primary productivity (Nye et al. 2010).

Other observed and expected changes in the Gulf of Maine region include increases in precipitation (Wake et al. 2006), acidification (Nye et al. 2010), sea level rise (Rhamstorf 2007), species invasions, and/or dominance by more "warm water" species (Harris and Tyrrell 2000; Nye et al. 2010; Kleisner et al. 2017). With the expected increase of warm water species in the Gulf of Maine also comes the likelihood of projected loss of suitable habitat (Kleisner et al. 2017), and increases in natural mortality (Jorgensen and Holt 2012) of species that currently or have historically resided in the Gulf of Maine.

Although ecosystem profiles are transforming along the Northeast U.S Shelf, the temperatures at which many species are observed has not significantly changed over time (Nye et al. 2010). This suggests that species are shifting their distributions to seek out their ideal habitat conditions. Shifts in spatial distributions are hypothesized to be one of the first responses to unfavorable changes in species' environments (Walther et al. 2002; Parmesan and Yohe 2003). Thus, it is important to identify how various ecosystem and climate influences are affecting distributions, stock dynamics, and other life history characteristics of species in the Gulf of Maine, so that informed conservation or management decisions can be implemented.

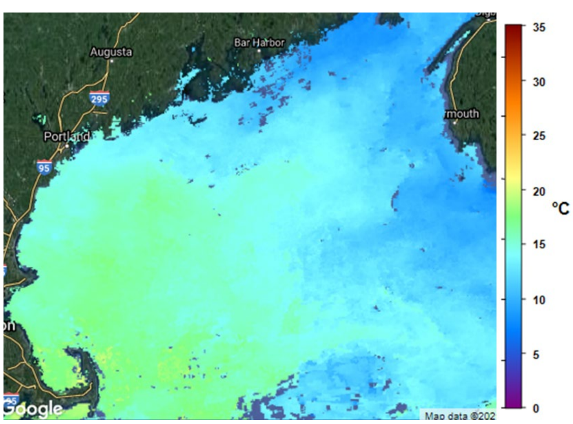

Figure 5. Surface temperature in the Gulf of Maine (June 15 2016, https://eastcoast.coastwatch.noaa.gov/region_gm.php).

Ecosystem Influences on Distribution and Habitat Use

Temperature is an important driver of American plaice distribution. Hare et al. (2016) categorized American plaice as having 'high' sensitivity to climate change, and high associated potential for climate-related distribution change. Fredston-Hermann et al. (2020) found significant positive association between range edge position and surface isotherms (northward shift), and significant negative association between range edge position and bottom temperatures (southward shift). Areas of high plaice densities have been correlated with depths between 60-90 m and mean temperatures <2 °C on the Magdalen Shallows (Swain et al. 1998). Correspondingly, in the Gulf of St. Lawrence, a spatial analysis of plaice catch from 2002-2010 revealed high densities of plaice were associated with areas of mid-depth (66.1 m), salinities <32, max monthly temps between 1-3 °C at mean depth, and annual temperatures 0.5-1.5 °C at mean depth, whereas low densities were associated with highly saline and warm, deep channel locations (Chouinard et al. 2014). However, upon analysis of plaice catch from a longer time series (1971-2010), warm, deep channel locations were not associated with low densities (Chouinard et al. 2014). Through the use of a high-resolution global climate model, Kleisner et al. (2017) estimated the surface and bottom temperatures over an 80-year future time period to increase by approximately 3.7 °C and 3.9 °C, respectively in the Gulf of Maine. Due to these forecasted warming conditions, Kleisner et al. (2017) projected a loss in suitable thermal habitat for American plaice in the U.S. Northeast Continental Shelf marine ecosystem.

Anomalous temperatures can drive shifts in a species' productivity, which may be difficult to reverse (Robertson et al. 2021). From 1985-2018 an influx of cold water into the Grand Bank resulted in a 200km southward shift in the distribution of American plaice, resulting in a contraction, and declines in biomass (Robertson et al. 2021). Fish stocks limited to the Gulf of Maine appear to respond to warming by moving into deeper waters. Nye et al. (2009) found that American plaice in the Northeast U.S. waters shifted to deeper water at a rate of 0.53 m/year from 1968 to 2007, based on changing ocean conditions (e.g., the North Atlantic Oscillation and Atlantic Multidecadal Oscillation). In other studies, depth played a role (12% R^2) in determining spatial patterns and abundance of juvenile plaice in the Grand Bank (Walsh et al. 2004). In relation to seasonality, American plaice in the Gulf of St. Lawrence occupied deeper and warmer water in the winter (374-426 m and 5.2-5.4 °C) compared to summer (58-67 m and -0.1 to 0.3 °C; Swain et al. 1998). This seasonal migration pattern has also been observed in other coastal Canadian waters (Powles 1965).

One study found that habitat associations in the Gulf of St. Lawrence were not consistently stronger when comparing depth and temperature variables, but did note that using both depth and temperature in models improved plaice density prediction capabilities (Swain et al. 1998). Additionally, Nye et al. (2009) found the relationship between area occupied and abundance was not strong. In generalized additive models (GAMs), adding spatial location improved model fit and better described influences of environmental variables on distribution (Figure 6; Walsh et al. 2004). In that study, temperature, depth, and sediment were the top predictor variables for American plaice and yellowtail flounder distribution (Walsh et al. 2004).

Adult and juvenile American plaice showed distribution overlap which can lead to possible spatial competition between these two age groups (Walsh et al. 2004). Juvenile plaice were found to be abundant on sand/shell hash sediments, less abundant on muddy sand & rock/sand sediments, and almost absent from mud sediments (Walsh et al. 2004).

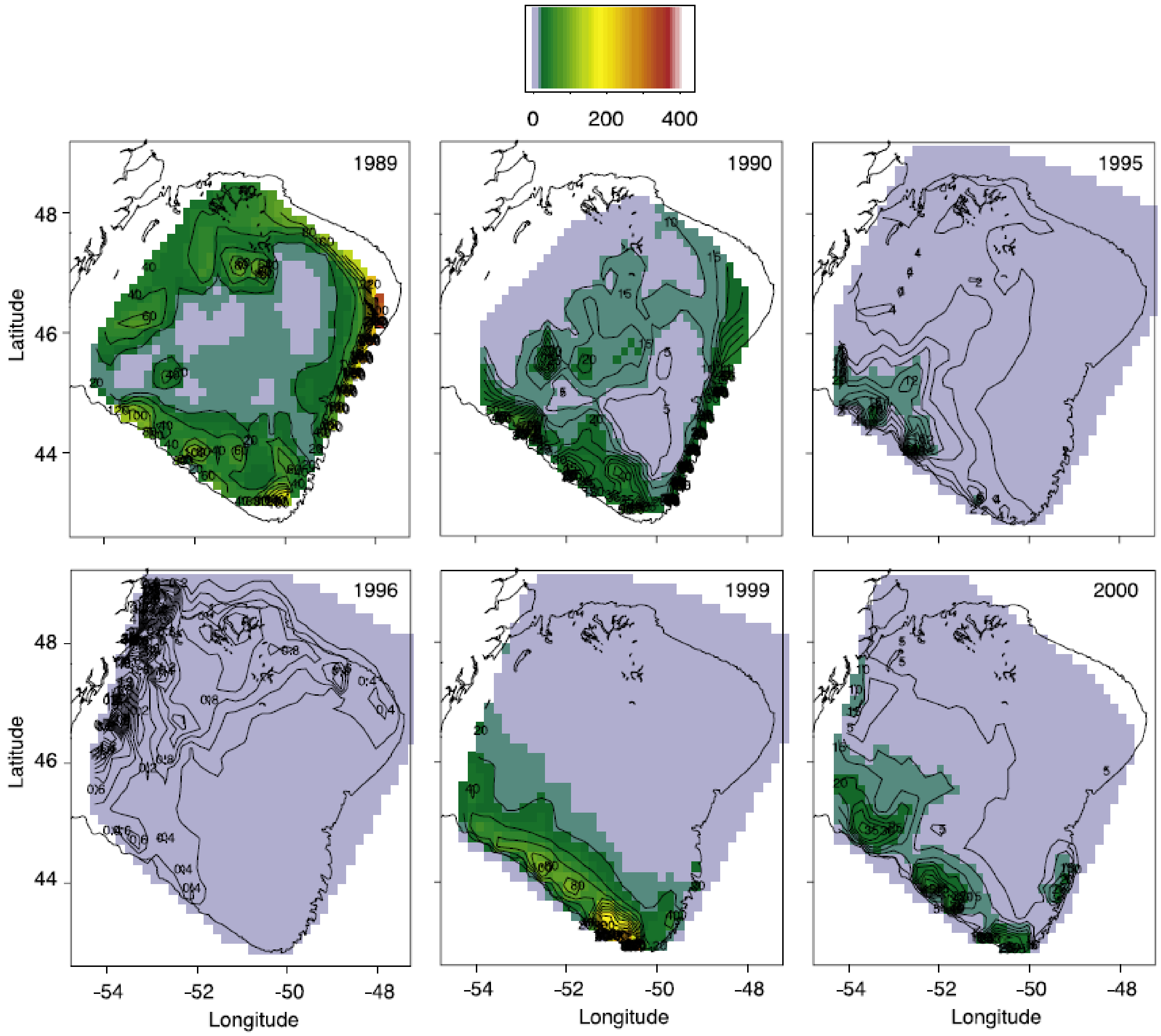

Figure 6. Contour plots (catch in numbers) showing the spatial distribution of age 1 American plaice in annual surveys of the Grand Bank from 1989–2000 based on the generalized additive model. The blue represents the area covered in the survey. Sourced from Walsh et al. 2004.

Ecosystem Influences on Recruitment

American plaice eggs are buoyant and incubate for 11-14 days in the upper water column, hatching as pelagic larvae (Bigelow and Schroeder 1953, Colton and Temple 1961, Johnson et al. 1999). Thus, sea surface temperature is an important consideration for plaice recruitment. The thermal limit for survival and incubation of American plaice eggs is 14ºC (Howell and Caldwell 1984), and recent sea surface temperatures in late spring-early summer (the end of the spawning season) have exceeded that threshold (e.g., Figure 5). Reproductive rate (recruits per spawner) of American plaice is significantly related to temperature and the North

Atlantic Oscillation, where greatest recruitment rates occur at extreme cold temperatures (Brodziak and O'Brien 2005). Sea surface temperature emerged as a better predictor for range edge positions than bottom temperature for many demersal fish species, including American plaice (Fredston-Hermann et al. 2020). Some species' distributions are driven by larval distributions, where sea surface temperature and juvenile survival may impact future population distributions (Fredston-Hermann et al. 2020). For juvenile plaice, depth was also found to be a significant driver for determining abundance and spatial locations in the Grand Bank (Walsh et al. 2004).

Adult plaice spatial structure influences the proportion of nursery area utilized by juvenile plaice. Walsh et al. (2014) noted that an increase in adult American plaice stock size typically correlated with a wider distribution of juveniles. Noting increases in juvenile populations are important as wider distributions signify juveniles are likely exposed to a broader range of environmental conditions, which may decrease model performance if not accounting for spatial heterogeneity (Walsh et al. 2004). Other variables such as salinity were not found to be a significant driver of plaice recruitment (Walsh et al. 2004), but potential changes in currents may lead to transportation of larvae to suboptimal nursery habitats (Nye et al. 2009).

One study found constant recruitment was more appropriate than assuming recruitment was proportional to stock size in describing the stock-recruitment data for 8 different flatfish stocks, including American plaice (Iles 1994). A major caveat of a model utilizing constant recruitment however, is that it assumes positive recruitment at a stock size of zero, which is biologically implausible (Iles 1994). Another study found models that utilized autocorrelated stock recruitment relationships (SRRs) were more similar to observed patterns, however stock assessment models using autocorrelated SRRs also tended to demonstrate increased risk of overfishing in simulation, by overestimating recruitment in forecasts and thus fishing beyond F_{msy} (Zhang et al. 2020). In addition, the SRRs in Zhang et al.'s (2014) study also demonstrated strong variation, which suggests presence of temporal nonstationarity.

Ecosystem Influences on Growth and Maturity

Between 1978-2005, size at maturity was larger in the southern part of the Grand Bank American plaice population than the northern part (Zheng et al. 2020). Warmer temperatures have been associated with accelerated growth rates, reductions in body size, and earlier ages at maturity (Levangie et al. 2021). Female plaice have been found in warmer waters than male plaice during September in the Gulf of St. Lawrence, and have also been determined to have a higher growth rate than males (Nye et al. 2009). This could be a trade-off between foraging rate and predation risk. Females may accept a higher predation risk than males to obtain more food, and would thus be expected to prefer warmer temperatures (Nye et al. 2009). From 1960-1970, age at 50% (A_{50}) maturity for female American plaice in the Grand Bank was typically >9, but from 1970-1990, estimates demonstrated declines in A_{50} throughout the area (Zheng et al. 2020, Figure 7). These declines in A_{50} were most pronounced on the northwestern bank and less pronounced on the southwestern bank (Zheng et al. 2020). After 1990, model estimates from Zheng et al. (2020) show an increasing trend in female age at 50% maturity again (Figure 7).

While increased fishing pressure has been thought to promote growth and earlier maturation due to reduction in resource competition, decreases in age and length at maturity coincided with timing of prolonged intensive fishing from 1970s to early 1990s in the Grand Bank (Zheng et al. 2020). Similarly, growth rates may also be affected by population abundance, as Rijnsdorp and Van Leeuwen (1992, 1996) found decreased growth rates in plaice when abundance was high. However, another study found that fishing pressure did not affect the rate of growth in plaice from 1957-1961 (Powles 1965).

Spatial location affects growth rates. Powles (1965) found that slower growth rates in plaice typically occur in deeper waters in the Gulf of St. Lawrence, compared to other areas. This effect on growth rate may also be due to differences in temperature. Increased growth rates have been correlated with areas of higher temperatures (Salter et al. 2018). In the northwest Atlantic, Johnson et al. (1999) reported that the fastest growth rates occur in the Gulf of Maine, which correlates well with the high warming rate of the Gulf of Maine (Pershing et al. 2015). However, another study found plaice on Georges Bank have faster growth rates than Gulf of Maine plaice (Salter et al. 2018).

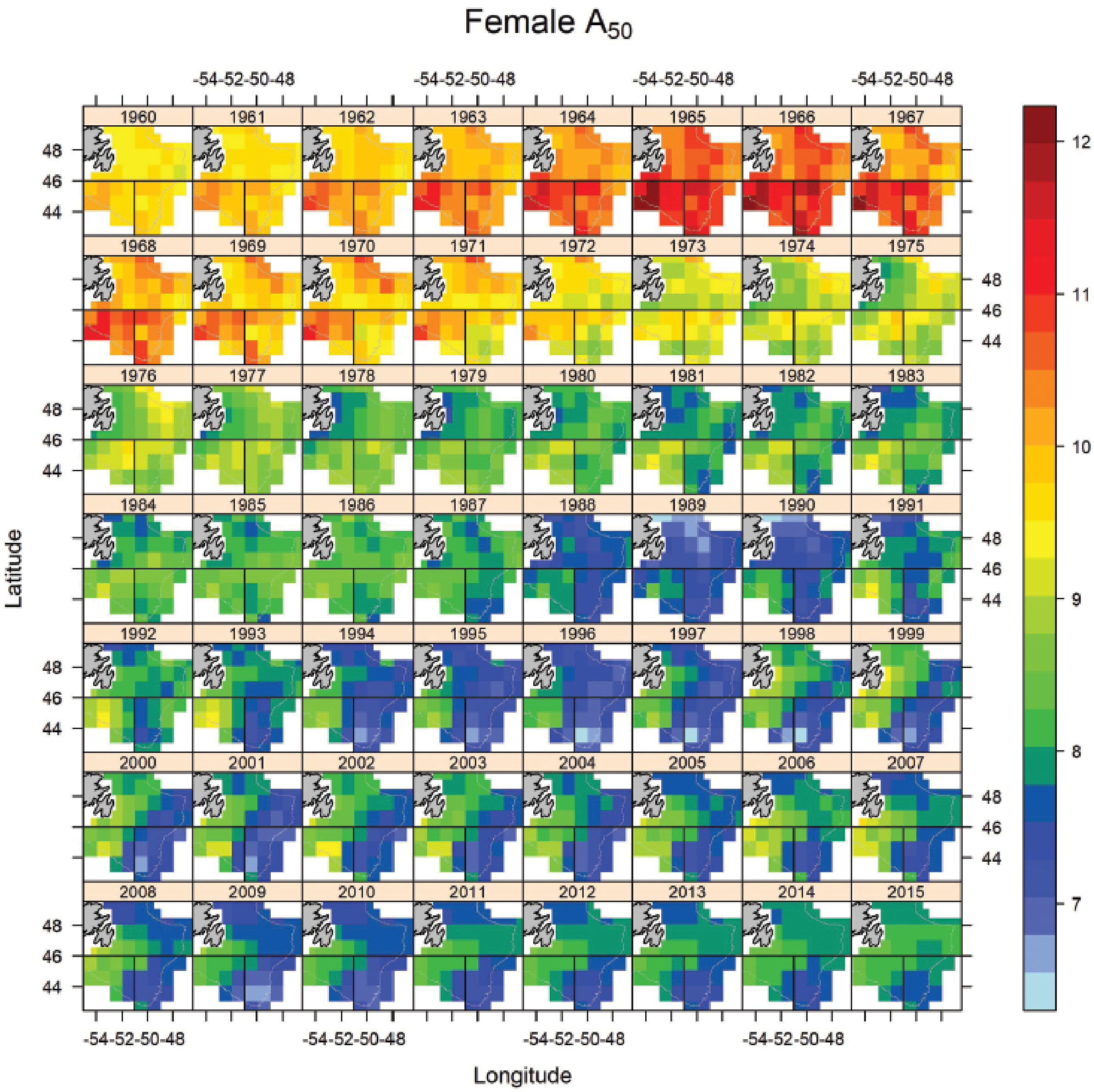

Figure 7. Spatial distribution of female American plaice age at 50% maturity. The number above each panel gives the cohort year. These distributions were generated from the grid models used in Zheng et al. (2020). This figure was sourced from Zheng et al. 2020.

Ecosystem Influences on Natural mortality

Warmer conditions may increase mortality at the southern extent of a species' range, particularly in early life stages, by means of eggs hatching at lethal temperatures and by reduced growth rates which may increase predation and starvation (Nye et al. 2009; Levangie et al. 2021). In addition, unusually cold temperatures have also been associated with increases in natural mortality levels in Canadian waters (Committee on the Status of Endangered Wildlife in Canada 2009). In a multispecies analysis of the Scotian Shelf system, Levangie et al. (2021) estimated an increase in natural mortality rate of American plaice associated with warming and a decrease in maximum size.

For juvenile and small plaice, cod are main predators, but mortality from cod predation has decreased due to declines in large cod abundance (Powles 1965). A predation study was conducted between juvenile Atlantic cod *Gadus morhua*, Atlantic herring *Clupea harengus* (predators) and American plaice larvae (prey) at natural temperature extremes (8 and 13 ºC), to assess the effects of water temperature on predator-prey interactions (Fuiman and Batty 1994). They found cod and herring to have a 96% and 83% predation success rate on plaice larvae, respectively, and that predator capture and prey evasion rates were not affected by water temperature (Fuiman and Batty 1994).

Fishermen's Perspectives on Ecosystem Impacts

Pavlowich et al. (2021?) elicited information from fishermen to address the assessment of American plaice in the rapidly changing Gulf of Maine ecosystem. They selected initial research questions regarding changes in stock distribution and habitat use and discussed any changes they had observed over their fishing careers and received information about a variety of topics related to ecology, management, decision making, and stock assessments. They also examined the state of the science and management of American plaice to identify the topics about which least is known and the factors that have the biggest impact on management decisions. The insights and ideas gathered from fishermen were applied to analyses of data from fisheries-independent and dependent sources. [summarize results]

Table 1

Environmental Impacts on	Gulf of Maine/ Georges Bank Notes	References
Recruitment	1. American plaice recruits per spawner was significantly related to temperature and the NAO, with greatest recruitment rates at extreme cold temperatures. 2. The thermal limit for survival and incubation of American plaice eggs is 14ºC. SSTs at end of spawning season have exceeded this threshold. 3. Depth played a major role in determining spatial patterns and abundance of juvenile plaice (in Grand Bank). a. Spatial structure of adult plaice population also influences the amount of nursery area utilized by juvenile plaice. Increase in adult stock size = juveniles more widely distributed (and subsequently exposed to a wider range of environmental influences, decreasing model performance). b. Strong year classes in North Sea plaice are often associated with cold sea temperatures.	1. Brodziak and O'Brien 2005 2. Howell and Caldwell 1984 3. Walsh et al. 2004 4. Nye et al. 2009 5. Zhang et al. 2020 6. Parretti and Thorson 2019.

	c. Relationship between plaice recruitment and salinity was NOT found to be significant (in Grand Bank) d. Food availability, predation, and abiotic factors can impact recruitment variability. e. A model of constant recruitment was found to more appropriately describe the S/R data than one in which recruitment was proportional to stock size. 4. Potential changes in currents may lead to transportation of larvae to suboptimal nursery habitats 5. Models that utilized autocorrelated SRRs were more similar to observed patterns (Grand Bank). a. However, autocorrelated SRRs also tended to demonstrate increased risk of overfishing by going beyond Fmsy. b. SRRs showed strong temporal variations, suggesting nonstationarity in the SRRs. 6. Recruits demonstrated a faster northward shift in distribution compared to spawners, suggesting that increased spawner abundance may not be a driving factor for the shift in recruits observed.	
Natural Mortality	1. Warming may increase mortality at the southern extent of a species' range, particularly in early life stages. a. Reduced growth rates under warming temperatures may indirectly cause natural mortality though potential increases in physiological stress (Scotian Shelf), predation and starvation 2. Cod are main predators of small plaice but mortality from cod predation has decreased due to declines in large cod abundance (Gulf of St. Lawrence). 3. Unusual cold water conditions might have played a role in increases of natural mortality seen (Canada).	1. Nye et al. 2009; Levangie et al. 2021 2. Powles 1965 3. Committee on the Status of Endangered Wildlife in Canada 2009
Growth and Maturity	1. Female plaice have a higher growth rate than males. Female plaice were typically found in warmer waters than male plaice in September. This could be a trade-off between foraging rate and predation risk. Females may risk a higher foraging rate than males to obtain more food, and would thus be expected to prefer warmer temperatures (in Gulf of St. Lawrence). 2. Decreases in age and length at maturity coincided with timing of prolonged intensive fishing from 1970s - early 1990s (Grand Bank) a. Increased fishing pressure can promote growth and earlier maturation due to reduction in resource competition b. Larger sizes of plaice maturation occurred in the southern portion of the Grand Bank and smaller sizes at maturation occurred in the northern portion. c. Temperature may by a strong driver for maturity variability 3. Fastest growth rates occurred in the Gulf of Maine compared to other areas of northwest Atlantic 4. Slower growth rates observed in deeper waters (Gulf of St. Lawrence) a. Fishing did not affect rate of growth in plaice from 1957-1961 5. GBK palice have faster growth rates than Gulf of Maine plaice a. Increased growth rate at higher temperatures 6. Decreased growth rates in plaice when abundance was high 7. Changes in growth rate and smaller maximum size associated with warming (Scotian Shelf)	1. Swain et al. 1998 2. Zheng et al. 2020 3. Johnson et al. 1999 4. Powles 1965 5. Salter et al. 2018 6. Rijnsdorp and Van Leeuwen (1992, 1996) 7. Levangie et al. 2021

Distribution and Habitat Use	1. American plaice of the northeast U.S. shifted to deeper water at a rate of 0.53 m/year from 1968 to 2007 associated with climate changes (e.g., the NAO and AMO). a. The relationship between area occupied and abundance is not strong b. Stocks limited to the Gulf of Maine appear to respond to warming by increasing their depth preference. 2. Projected loss in suitable thermal habitat for American plaice in the U.S. Northeast Continental Shelf marine ecosystem. 3. Depth played a major role (12%) in determining spatial patterns and abundance of juvenile plaice (in Grand Bank) a. Adding spatial location to GAM improved model fit and better described influences of environmental variables on distribution. b. Adults and Juveniles showed distribution overlap -> possible spatial competition between juvenile and adult plaice. c. Juvenile plaice are abundant on sand/shell hash sediments, less abundant on muddy sand & rock/sand sediments, and almost absent from mud sediments. 4. Plaice distribution hot spots were associated with areas of mid-depth, salinities <32, max monthly temps between 1-3°C at mean depth, and annual temperatures 0.5-1.5°C at mean depth (Gulf of St. Lawrence). a. Cold distribution spots were associated with highly saline and warm, deep channel locations. 5. Significant positive association with SST isotherms, and significant negative association with sea bottom temperatures. 6. Influx of cold water from 1985-2018 in the Grand Bank resulted in a plaice shift of 200 km southwards, resulting in contraction of distribution, and declines in biomass without recovery. a. Anomalous temperatures can result in shifts in species stable-states, which may be difficult to reverse. 7. Habitat associations were not consistently stronger with one variable than the other, when comparing depth and temperature variables (in Gulf of St. Lawrence). a. Using both depth and temperature in the models improved plaice density prediction capabilities b. Occupied deeper and warmer water in the winter compared to summer.(58-67 m and -0.1to 0.3°C in September and 374-426 m and 5.2-5.4°C in January).	1. Nye et al. 2009 2. Kleisner et al. 2017 3. Walsh et al. 2004 4. Chouinard et al. 2014 5. Fredston-Hermann et al. 2020 6. Robertson et al. 2021 7. Swain et al. 1998

Table 2. Candidate drivers of American plaice dynamics, hypothetical impact and potential time series (and data source) that may index this impact.

Potential Driver	Hypothetical Impact	Time series	Data Source

Decadal-scale climate variability	Time-varying growth or natural mortality, recruitment	Climate indices such as North Atlantic Oscillation, Atlantic Multidecadal Oscillation, and Gulf Stream Index	NOAA National Centers for Environmental Information https://www.ncei.noaa.gov/
Climate warming trend	Time-varying growth or natural mortality, recruitment, ssb, center of biomass location, maturity	Sea surface or bottom temperature anomaly for region	NASA Optimum Interpolation Sea Surface temp. (OISST) https://www.ncei.noaa.gov/products/optimum-interpolation-sst or modeled bottom temp. (FVCOM) http://www.smast.umassd.edu:8080/thredds/catalog/models/fvcom/NECOFS/Archive/Seaplan_33_Hindcast_v1/catalog.html
Unaccounted for predation	Time-varying natural mortality	Predator abundance time series (e.g., spiny dogfish) or diet information	NOAA stock assessment output, NOAA food habits database https://www.fisheries.noaa.gov/inport/item/8083
Fish distribution shift	Time-varying catchability in survey or fishery	Sea surface or bottom temperature anomaly for region	NASA Optimum Interpolation Sea Surface Temp. (OISST) or FVCOM (bottom temperature)
Changes in currents	Larval transport (recruitment),	Current direction, speed, or anomalies?	Northeastern Regional Association of Coastal Ocean Observing Systems (NERACOOS)? http://www.neracoos.org/
Fishing pressure	Growth, maturity, abundance (which also affects growth)	Fishing effort time series	Stock SMART https://www.st.nmfs.noaa.gov/stocksmart?app=chart-time-series

Table 3: American Place life history conceptual model

Developed from the NOAA Essential Fish Habitat Source Document (Johnson 2004) and COSEWIC Assessment and Status Report (COSEWIC 2009).

Stage	Habitat & Distribution	Phenology	Age, Length, growth	Energetics	Diet	Predators/ Competitors
Adult	For western North Atlantic: Labrador – New York. Clear preference for fine sand over coarse gravel substrate.	Migrate to deeper offshores in winter and shallower waters in spring.	Average length 27-66 cm TL.	Found 1-12℃ in spring, and 3-15℃ in fall. Physiological stress and natural mortality associated with warming, low O2, and size	Opportunistic (small benthic crustaceans, echinoderms, cnidarians, and polychaetes).	Redfish, cod, Greenland sharks, halibut, goosefish, spiny dogfish, grey seals, harbour seals, seabirds.
Spawning	Batch spawners – eggs released every few days during spawning period. Occurs depths <90 m, near shelf edges. No significant spawning migration.	Gulf of Maine spawning season: March- mid June. Begins north of Cape Cod in March.	Spawning begins earlier in larger fish and fish in deeper waters	Cold water cues around 4.4℃ in Gulf of Maine.		
Juvenile	Descent towards bottom beings as eye migration completes.		Higher first-year growth rates in warmer waters.	Found between 2-10℃ (spring), 4-16℃ (Fall), Physiological stress and natural mortality associated with warming, low O2, and size	Small crustaceans, polychaetes, cumaceans.	Feeding competition between young plaice and cod.
Larvae	Susceptible to drift transport, found in shallow waters	Pigmentation begins ≈4-6 mm.	Hatch at 2.4 mm. Migration of left eye begins ≈20 mm and completes by 30-40 mm.	Typically caught between 4-14℃. Most abundant 5-8℃ (March/Jun) and 10-12℃ (July/Aug)	Plankton, diatoms, copepods.	Commonly consumed by redfish.
Egg	Depth zones > 56 m. Tend to be retained near spawning areas.	Buoyant, float near surface for ≈2 weeks.	Growth rate at 10 ℃ was fastest. Average diameter of egg is 2.5 mm.	Incubate for 11-14 days at 3.9℃. Mortality at temps >14 ℃.		

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