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Long-term changes in the maturation and growth of Cape Cod/Gulf of Maine yellowtail flounder *Limanda ferruginea*

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ABSTRACT: Yellowtail flounder *Limanda ferruginea* in the Gulf of Maine have been harvested by commercial fisheries since the 1930s, and the most recent stock assessment estimated that from 1985 to 2016 fishing mortality rates exceeded the fishing mortality reference point ($F_{40\%}$) in all but one year. The objective of this study was to understand changes in the maturation and growth of Cape Cod/Gulf of Maine yellowtail flounder by examining fisheries-independent data from cohorts produced over a 38 yr period (1976 to 2014). Maturity ogives demonstrated that the length and age at 50% maturity declined for cohorts throughout that time period. Probabilistic maturation reaction norms (PMRNs), which describe the probability that an immature individual will become mature at a certain age and size class, demonstrated a shift towards maturation at younger ages and smaller sizes. For age 3 female and male yellowtail flounder, the size at which the probability of becoming mature was 0.5 declined from 30.8 and 26.0 cm to 23.9 and 16.4 cm, respectively. Using von Bertalanffy growth curves, a decrease in asymptotic length (L_∞) and an increase in the growth rate (K) was estimated for both sexes. Taken together, these life history changes are suggestive of fisheries-induced evolution. However, although the PMRN approach is designed to account for phenotypic plasticity associated with growth and survival, further work is needed to determine whether other factors (e.g. temperature and body condition) could be responsible for the changes in maturation observed in this study.

KEY WORDS: PMRN · *Limanda ferruginea* · Fisheries-induced evolution · Maturation · Von Bertalanffy

1. INTRODUCTION

Maturation and growth are important components of productivity for fish populations. At an individual level, maturation and growth influence fitness, fecundity, and the potential number of lifetime reproductive opportunities. At the population level, these life history traits impact stock dynamics, recruitment, spawning stock biomass (SSB), and the yields that can be harvested by the fishery. Maturation schedules in flatfish are thought to be governed by tradeoffs involving mortality, reproduction, and growth (Roff 1983). Energy allocated to gonadal development detracts from somatic growth, and therefore the age at which an individual first reproduces influences their adult body size (Roff 1983, Lester et al. 2004). Because egg production increases proportionally with body size, individuals that mature at a smaller size exhibit reduced fecundity (Roff 1982, Grift et al. 2003). Further, females maturing at smaller sizes may have reduced reproductive success, as egg size and quality are positively correlated with body size (Trippel et al. 1997, Barneche et al. 2018).

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Natural variability in the length and age at maturation is generally small for stable populations (Trippel 1995, Walsh & Morgan 1999). However, many exploited fish stocks have demonstrated substantial changes in their maturation schedules, with these changes occurring across relatively short time periods (e.g. Jørgensen et al. 2007, Sharpe & Hendry 2009). Several hypotheses have been advanced to explain the observed variability in size and age at maturation. In some instances, trends in maturation and growth have been characterized as a phenotypic response to environmental variability. For instance, the temperature–size rule dictates that the temperatures experienced by ectotherms during their early development influence their adult size (Atkinson 1994, Kingsolver 2009). In teleosts, the temperature encountered during early stages is directly related to the probability of maturing at a given size (Grift et al. 2003), as warmer waters may be associated with faster reproductive development (Goldberg et al. 2019). Phenotypic plasticity in maturation and growth can also arise as a density-dependent response to population abundance. Intraspecific competition is reduced in depleted populations, enabling individuals to grow faster and become mature at younger ages (Morgan & Colbourne 1999, Wheeler et al. 2009). This plasticity may allow an individual to increase egg production, enabling depleted stocks to recover more quickly than stocks without this flexibility in their life history (Trippel 1995). Directional changes in the environment, such as increasing temperatures, changes in food availability, or the introduction of endocrine-disrupting chemicals, can also contribute to life-history evolution by altering maturation schedules (Kraak 2007, Law 2007). An alternative explanation is that size-selective fisheries alter the mortality schedule in a fish population by increasing mortality of older fish, leading to nonrandom selective pressures that change the genetic composition of the population to favor earlier maturation (e.g. Law 2000, Ernande et al. 2004, Jørgensen et al. 2007). When fisheries are size-selective or when fish stocks experience intense exploitation, individuals that are genetically predisposed to mature at younger ages and smaller sizes have a greater probability of passing on their genes than their slow-maturing counterparts (Law 2000, Barot et al. 2005). Over time, if the magnitude of fishing mortality is sufficiently high, the year classes of an exploited stock will become increasingly composed of the offspring from individuals that matured at a younger age or smaller size (Trippel 1995, Fenberg & Roy 2008). This phenomenon is known as fisheries-induced evolution. Trait heritability and strong artificial selective pressures upon those traits are considered the necessary prerequisites for fisheries-induced evolution to occur (Heino & Dieckmann 2008, Kuparinen & Festa-Bianchet 2017). Although there is uncertainty about the rate at which fisheries-induced evolution can operate in wild populations (Law 2000, Kuparinen & Festa-Bianchet 2017), there is increasing evidence that life history traits are heritable and can be modified by harvesting over relatively short time scales (Jørgensen et al. 2007, Sharpe & Hendry 2009, Kinnison et al. 2011, Therkildsen et al. 2019). Fisheries-induced evolution has been implicated as the causal factor for reductions in the size and age at maturation for several exploited fish stocks including North Sea plaice and sole (Grift et al. 2003, Mollet et al. 2007, van Walraven et al. 2010), Gulf of Maine cod (Barot et al. 2004a), and pikeperch in the Baltic Sea (Kokkonen et al. 2015).

These competing explanations (phenotypic plasticity and fishery-induced evolution) are not mutually exclusive and can operate in a confounding manner, making it difficult to determine the relative importance of each driver, especially in the absence of experimental controls (Barot et al. 2005, Sharpe & Hendry 2009, Kuparinen & Festa-Bianchet 2017). Fortunately, phenotypic plasticity can be characterized using reaction norms, which are estimated at the population level and describe how a single genotype (or group of genotypes) will give rise to different phenotypes across a range of environmental conditions (Ernande et al. 2004, Heino & Dieckmann 2008). Probabilistic maturation reaction norms (PMRNs) were developed to assess changes in the maturation process independently of changes in growth and survival, allowing evolutionary changes in maturation to be disentangled from some sources of phenotypic plasticity (Heino et al. 2002, Barot et al. 2004b). PMRNs describe the probability that an immature individual will become mature at a certain age and size class during a given time interval (Heino et al. 2002). PMRNs are commonly depicted using their contour lines, and the midpoint (L_{p50}) describes the size at which the probability of maturation is 0.5 at a certain age (Barot et al. 2004b). A downward shift in the contour lines of the reaction norm is typically interpreted as supportive evidence for fisheries-induced evolution (Ernande et al. 2004, van Walraven et al. 2010), although directional changes in the environment can also contribute to shifts in the maturation reaction norm (Law 2007).

The objective of this study was to use data collected during the Massachusetts Division of Marine

Fisheries (MADMF) and the Northeast Fisheries Science Center (NEFSC) spring bottom trawl surveys (1978 to 2018) to investigate trends in the maturation and growth of yellowtail flounder *Limanda ferruginea* off the coast of Massachusetts, USA. Yellowtail flounder in US waters are managed as 3 unit stocks: Cape Cod/Gulf of Maine, southern New England, and Georges Bank (Cadrin 2010); the Cape Cod/Gulf of Maine stock was the focus of this investigation.

Yellowtail flounder are a commercially important flatfish that have been harvested in New England for over a century, although the fishery did not typically target yellowtail flounder until the early 1930s (Royce et al. 1959). In the Gulf of Maine and east of Cape Cod, yellowtail flounder are captured along with several species including Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, and winter flounder *Pseudopleuronectes americanus* in a mixed-species fishery that primarily uses otter trawls and gillnets. A minimum landing size of 28 cm was established in 1982; it was subsequently increased to 30 cm in 1986 and 33 cm in 1989 (NEFSC 2003). A minimum mesh size of 13 cm was established for the otter trawl fishery in 1982, and minimum mesh size requirements were later increased to 14 cm in 1983, 15.3 cm in 1994, and finally 16.5 cm in 1999 (NEFSC 2003). According to the most recent stock assessment (NEFSC 2017), the Cape Cod/Gulf of Maine yellowtail flounder stock is classified as overfished, because current estimates of SSB are below the maximum sustainable yield management target (SSB_{MSY}). During the time period estimated by the most recent assessment (1985 to 2016), SSB has fluctuated between 600 and 2500 mt (NEFSC 2017), which is considerably less than the SSB_{MSY} target of 4640 mt (Fig. 1). Further, with the exception of one year (2015) the stock has experienced overfishing throughout the time series of the stock assessment, as the estimated fishing mortality (F) has exceeded the $F_{40\%}$ reference point (NEFSC 2017; Fig. 1). Fishery removals were relatively low in the 1930s, and increased to moderate levels from the 1940s to the early 1970s (Fig. 1). The highest removals were observed between 1976 and 1983, when annual catches routinely exceeded 2000 mt. Catches fluctuated at intermediate levels from the late 1980s until 2004, at which point catches decreased to relatively low levels. Total catches did not exceed 500 mt from 2014 to 2016, which are the lowest catch levels observed in the time series (NEFSC 2017). From 1996 to 2003, a period of intermediate landings, Cape Cod/Gulf of Maine yellowtail flounder were worth roughly \$3 000 000–7 000 000 USD annually (NEFMC 2003). However, the value of the fishery is currently diminished, as landings in 2017 were worth less than \$1 000 000 USD (NEFMC 2019).

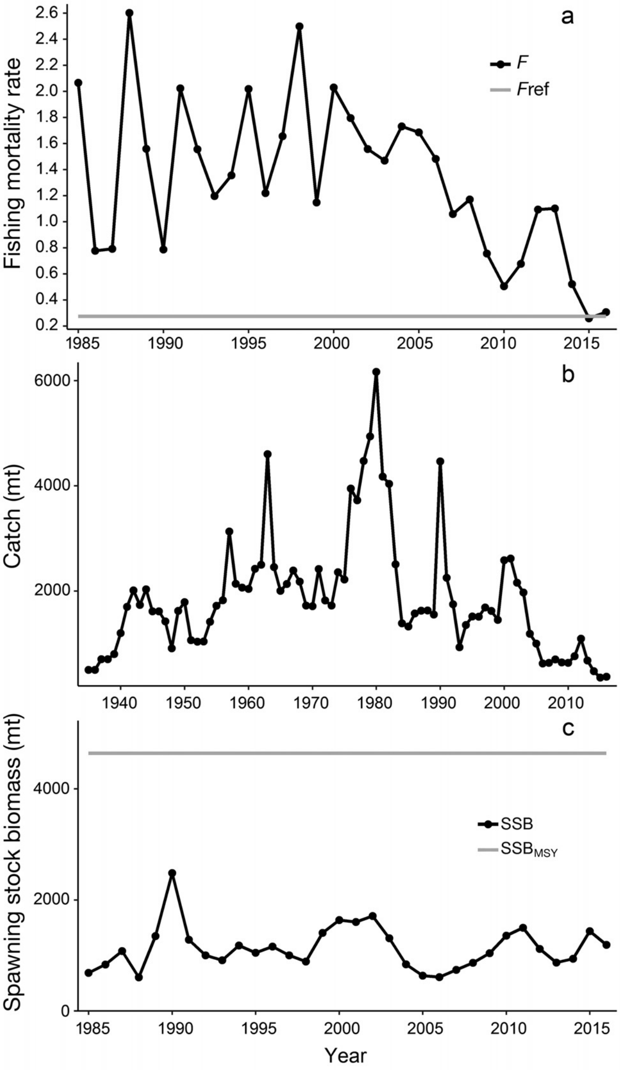

Fig. 1. Estimates of (a) fishing mortality (F), (b) fishery catch, and (c) spawning stock biomass (SSB) for Cape Cod/Gulf of Maine yellowtail flounder. Fref: fishing mortality target reference point; SSB_{MSY}: spawning stock biomass maximum sustainable yield reference point. All values were reported in the 2017 stock assessment (NEFSC 2017)

2. MATERIALS AND METHODS

2.1. Data collection

The MADMF has conducted a biannual bottom trawl survey in Massachusetts coastal waters since 1978, with the spring and fall surveys occurring in May and September, respectively. The NEFSC has completed a spring (March–May) bottom trawl survey on the northeast US shelf since 1968 and a fall (September–November) bottom trawl survey since 1963. Both surveys were executed on research vessels using a stratified random design, with stratification based on depth and geographic region (Grosslein 1969, King et al. 2010). On the MADMF trawl survey, all tows were completed during daylight hours, and the target tow duration was 20 min. The MADMF survey vessel was changed from the FV 'Frances Elizabeth' to the RV 'Gloria Michelle' in 1982, but no other changes were made to the survey gear or methodology. The NEFSC trawl survey samples 24 h d^{-1}. Several changes were made to the NEFSC survey in 2009 when the RV 'Albatross IV' was replaced by the RV 'Henry B. Bigelow'; the survey net was changed, and the target tow duration was reduced from 30 to 20 min (Politis et al. 2014).

Both trawl surveys collect detailed biological data for fish and invertebrate species, and age structures and maturity observations were collected from yellowtail flounder with a length-stratified design to ensure that comparable numbers of fish were sampled within each 1 cm length bin. Scales were obtained from the caudal peduncle for age determination, and sex and maturity stage were determined macroscopically. Since 1989, 6 stages of maturity have been assigned to the sampled fish: immature (*I*), developing (*D*), ripe (*R*), ripe and running (*U*), spent (*S*), and resting (*T*) based on criteria developed by Burnett et al. (1989). Prior to 1989, yellowtail flounder maturity was classified macroscopically according to either 5 or 8 maturity stages, and Burnett et al. (1989) described the evolution of the maturity staging criteria employed on the bottom trawl survey. Importantly, the changes in maturity classification would not be expected to affect the discrimination of mature and immature individuals. Analysis of maturation was restricted to observations collected during the spring trawl survey, which coincides with the spawning season for Cape Cod/Gulf of Maine yellowtail flounder (Cadrin 2010). Using maturity data from the period closest to the spawning season is expected to lead to more reliable classifications of sex and maturity stage (Witherell & Burnett 1993). A wide range of size and age classes are represented in the survey data, and both surveys use a trawl net with a small mesh codend liner (<3 cm), thus avoiding issues with size-selectivity that can confound growth and maturation estimates derived from fisheries-dependent sampling (Lester et al. 2004).

From 1988 to 2016, bottom water temperature was recorded using temperature loggers (Onset) every 2 h at 2 locations in Cape Cod Bay off the coast of Massachusetts (Fig. 2). The 'Manomet Boulders' monitoring site (41° 54′ 9″ N, 70° 30′ 49″ W) is located at 55 m depth, while the 'Mars Wreck' monitoring site (41° 58′ 0″ N, 70° 26′ 22″ W) has a depth of 110 m. The mean annual bottom temperature was calculated for each site, and a linear regression was used to examine trends in mean annual temperatures at each location from 1988 to 2016.

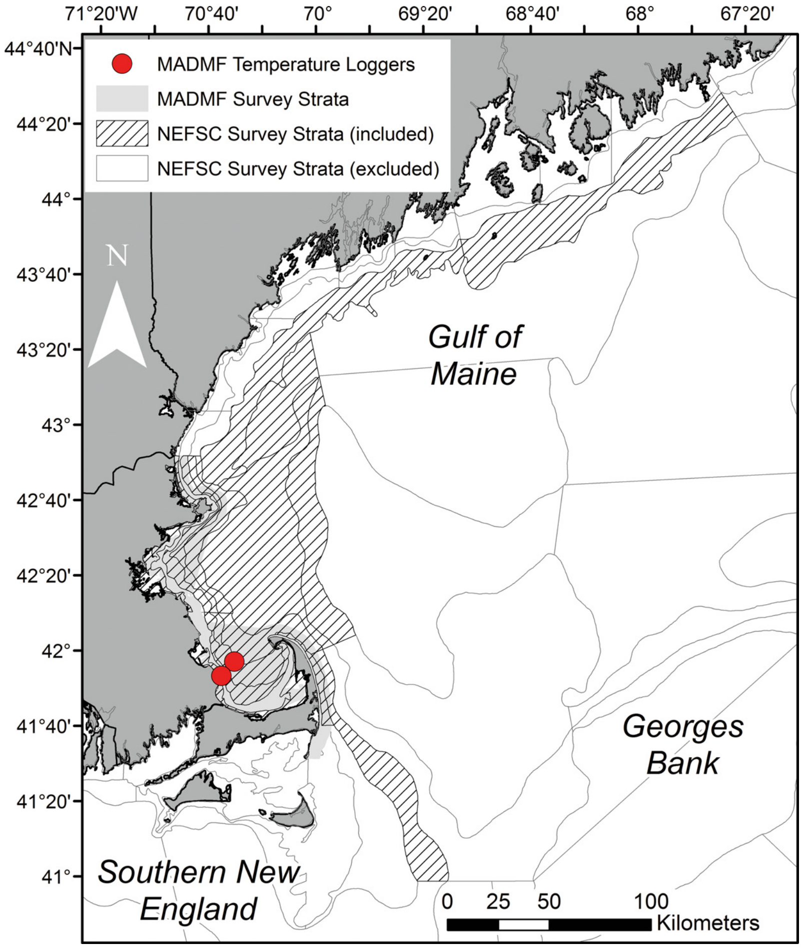

Fig. 2. Survey regions from the Massachusetts Division of Marine Fisheries (MADMF) and the Northeast Fisheries Science Center (NEFSC) bottom trawl surveys that were included in the analysis for Cape Cod/Gulf of Maine yellowtail flounder

2.2. Maturation analysis

Analysis of maturation and growth was limited to yellowtail flounder that were captured in the survey strata that are included the Cape Cod/Gulf of Maine stock assessment (Fig. 2). For the MADMF trawl survey, this included yellowtail flounder captured in survey strata 18–36. NEFSC survey observations were limited to individuals captured in survey strata 25–27, 39, 40, 56, 57, and 59–66. Biological data were pooled from both surveys and included cohorts produced from 1976 to 2014 (i.e. the cohorts for which representative samples were available to estimate size and age at maturity). The MADMF spring survey did not collect biological data for yellowtail flounder in 1982, 1983, or 1996. Maturation and growth were analyzed independently for males and females.

Maturity ogives were estimated as a first step towards investigating temporal changes in the size and age at maturation. For each cohort produced from 1976 through 2014, a generalized linear model with a logit link function was fit to the observed proportions of fish mature at each length and age. Maturity was treated as a binomial response variable; fish that were observed to be state *I* were assigned a maturity value of 0, while the other developmental stages (*D*, *R*, *U*, *S*, *T*) were considered to be mature and assigned a maturity value of 1. The median age (A_{50}) and length (L_{50}) at maturity were calculated for each cohort and sex. For each regression, non-parametric bootstrap methods (200 iterations) were used to derive the median values and confidence intervals of the A_{50} and L_{50} estimates using the R package 'sizeMat' (Torrejon-Magallanes 2018).

Changes in the size and age at maturation were also investigated using PMRNs, following the demographic estimation method described by Barot et al. (2004b). For nearly all cohorts, the sample size requirements of the PMRN method recommended by Barot et al. (2004b) were not achieved. Therefore, following the approach employed by Pérez-Rodríguez et al. (2009) and van Walraven et al. (2010), cohort groupings were used to investigate growth and maturation for each sex (Table 1). A total of 4 cohort groupings were created to ensure that the sample sizes were representative and adequate within each grouping. The objective of this analysis was to investigate temporal trends in the PMRNs; therefore, fish in each of the 4 cohort groupings were treated as discrete populations in the analyses. For each sex and cohort grouping, the probability of an individual being mature $m(a,l)$ was estimated using logistic regression by:

$$\text{logit}(m) = \beta_0 + \beta_1 l + \beta_2 a + \varepsilon \tag{1}$$

where m is the proportion of mature fish in each age and length class, a is the age of the individual, l is total length (cm), βs are regression parameters, and ε is a binomial error term. A full model including an interaction term between length and age was also tested, but a comparison of Akaike's information criterion (AIC) values demonstrated that the interaction term did not improve the model fit. The maturity data were not corrected to account for the length-stratified sampling scheme used on the trawl surveys, which may introduce a source of bias into the estimated proportions of maturity-at-age (Morgan & Hoenig 1997). For yellowtail flounder, first-time spawners could not be differentiated from repeat spawners using the macroscopic classification methods employed on the trawl surveys. Therefore, the demographic estimation method of the PMRN was applied, which makes the assumptions that mature and immature individuals exhibit the same growth rates and survival probabilities, and that growth is independent of size within an age class (Barot et al. 2004b). Barot et al. (2004a) showed that the demographic estimation method is robust to these assumptions, while Pérez-Rodríguez et al. (2009) demonstrated high agreement between PMRNs estimated using the direct and demographic methods for Flemish Cap cod. The probability of becoming mature at a given age and size, $p(a,l)$, was estimated for each sex and cohort grouping by:

$$p(a,l) = \frac{m(a,l) - m(a-1,l-\Delta l)}{1 - m(a-1,l-\Delta l)} \tag{2}$$

where Δl is the length increment grown in the course of a year by individuals in age group a. Linear interpolation was used to calculate the reaction norm midpoint (L_{p50}) for each cohort group and age.

Table 1. Cohort groupings and sample sizes that were used to estimate the maturity ogives and probabilistic maturation reaction norms for Cape Cod/Gulf of Maine yellowtail flounder

Cohort grouping	Females n	Females Immature	Females Mature	Males n	Males Immature	Males Mature
1976–1986	1088	583	505	1056	364	692
1987–1996	1619	830	789	1853	369	1484
1997–2005	2027	600	1427	2175	225	1950
2006–2014	2967	639	2328	2843	227	2616

The Δl increments were derived by fitting ordinary von Bertalanffy growth curves to length-at-age data for individuals, ages 1 through 6. To examine temporal variability, growth curves were fit separately for each sex, and cohort group:

$$l_t = L_\infty - (L_\infty - L_0)\mathrm{e}^{-Kt} \quad (3)$$

where l_t is the length at age t, L_∞ is the mean asymptotic length, K is the Brody growth coefficient, and L_0 is the length at which $t = 0$. Following the convention of van Walraven et al. (2010), the curve was forced to go through the origin ($L_0 = 0$) to help interpret changes in growth over time.

PRMNs are estimated by combining the results from non-linear growth and maturity ogive functions, and as a result, direct calculation of uncertainty measures is not possible. To derive 95% confidence intervals for the PRMNs, we used a bootstrap approach by resampling the raw observations, stratified by cohort grouping, age, and sex. Each bootstrapped sample, obtained by resampling individuals from the original sample (with replacement, to produce a new population of the same size), was then used to estimate growth curves and maturity ogives from which the new PRMNs were derived (Manly 1991). This process was repeated 200 times for each population (cohort grouping and sex), and the confidence limits of the L_{p50} were estimated as the 2.5th and 97.5th percentiles of the distribution of the 200 midpoints of each population.

3. RESULTS

The length (L_{50}) and age at 50% maturity (A_{50}) declined in cohorts of Cape Cod/Gulf of Maine yellowtail flounder over the time series (Fig. 3). Values of L_{50} and A_{50} were generally consistent for cohorts born in the late 1970s and 1980s, but declined throughout the latter part of the time series. Changes in maturity were greater for males than females. From 1978 to 2014, L_{50} values declined approximately 34.5% (9.9 cm) for males and approximately 17% (4.7 cm) for females. The A_{50} for male yellowtail flounder declined by 24%, from 2.6 yr in 1977 to 1.9 yr in 2014. For females, A_{50} declined nearly 15%, from 2.7 yr in 1976 to 2.3 yr in 2014.

Large changes were observed in the PMRNs across the 4 cohort groupings for both male and female yellowtail flounder in the Cape Cod/Gulf of

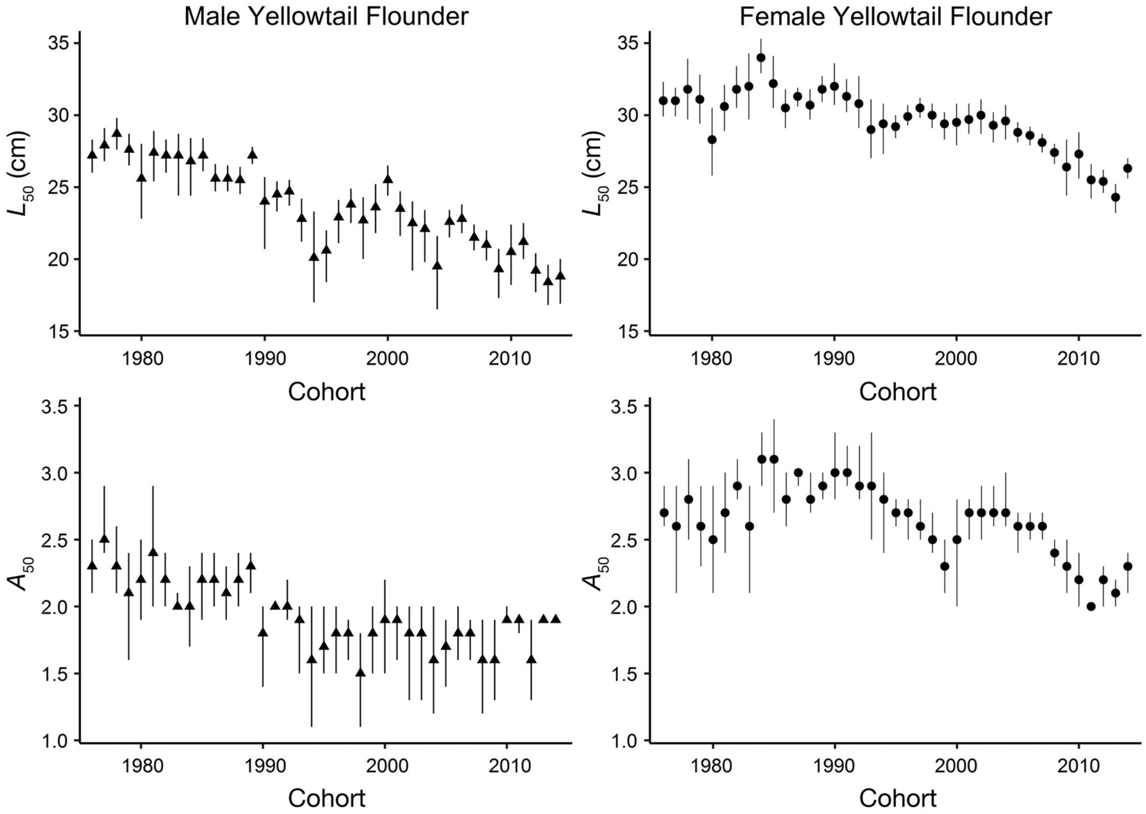

Fig. 3. Age (A_{50}) and length at 50% maturity (L_{50}) for male and female cohorts of yellowtail flounder in the Cape Cod/Gulf of Maine stock. Vertical lines: 95% CI

Maine stock (Table 2, Fig. 4). The negative slope of the reaction norms for males and females indicates that the probability of becoming mature at a given size increases as the fish gets older. The intersection of the reaction norm and the average growth curve depicts L_{50} and A_{50}. For females, this intersection shifted from about 31.5 cm and 2.8 yr for cohorts of females produced from 1976 to 1986 to approximately 26.8 cm and 2.3 yr for cohorts born between 2006 and 2014. For males, the intersection was reduced from approximately 27.8 cm and 2.3 yr for the earliest cohorts to 20.9 cm and 1.5 yr for the most recent cohort grouping.

For both sexes, the L_{p50} values declined at all ages across the 4 cohort groupings. For example, the L_{p50} of age 3 females decreased from 30.8 cm for cohorts born from 1976 to 1986 to 23.9 cm for cohorts born from 2006 to 2014 (Fig. 4). Similarly, the L_{p50} of age 3 male yellowtail flounder decreased from 26.0 to 16.4 cm over the time period (Fig. 4). For female and male yellowtail flounder, the L_{p50} estimates were most precise at ages 3 and 2, respectively, which is when most of the individuals become mature (Table 2).

Marked changes in growth were estimated for cohort groupings of male and female yellowtail flounder. For females, the estimated L_∞ decreased from 52.22 cm for cohorts produced between 1976 and 1986 to 40.93 cm for cohorts born from 2006 to 2014, while estimates of K increased from 0.32 to 0.49. For males, estimates of K increased from 0.32 for cohorts born from 1976 to 1986 to 0.49 for cohorts produced from 2006 to 2014, while the estimated L_∞ decreased from 44.21 to 35.98 cm.

The mean annual bottom water temperature increased at both locations in Cape Cod Bay from 1988 to 2016 (Fig. 5). For both locations, the increase in annual mean temperatures was significant ($p < 10^{-5}$) and the slope of the regression was 0.059 °C yr^{-1}.

Table 2. Probabilistic maturation reaction norm midpoints for each cohort grouping of female and male Cape Cod/Gulf of Maine yellowtail flounder. 95% confidence limits for each midpoint estimate are shown in parentheses

Age	1976–1986	1987–1996	1997–2005	2006–2014
Female cohort groupings				
2	34.41 (31.99–34.51)	36.39 (35.02–38.60)	32.28 (31.06–33.43)	28.56 (28.40–29.78)
3	30.76 (29.69–30.80)	29.75 (29.73–30.89)	28.87 (28.03–29.21)	23.93 (23.11–25.12)
4	28.15 (25.55–29.19)	22.98 (20.93–26.23)	24.47 (22.35–26.64)	20.62 (18.83–21.77)
Male cohort groupings				
1	29.98 (28.90–31.67)	27.67 (27.10–31.09)	27.03 (24.08–29.08)	22.47 (21.35–27.17)
2	28.34 (27.97–28.74)	24.32 (24.10–25.93)	22.47 (21.27–22.53)	20.1 (19.40–20.66)
3	26 (24.27–27.24)	21.48 (20.52–22.76)	19.37 (16.21–20.23)	16.43 (15.81–19.39)

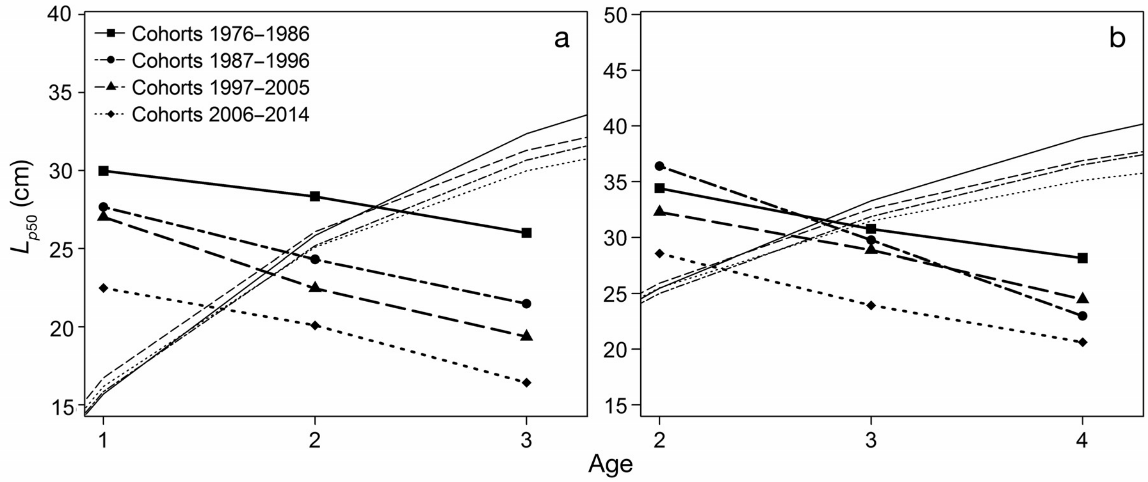

Fig. 4. Probabilistic maturation reaction norms for (a) male and (b) female yellowtail flounder in the Cape Cod/Gulf of Maine stock unit depicting the length at which the probability of becoming mature is 0.5 (L_{p50}) for the 4 cohort groupings. Thin lines: von Bertalanffy growth curves for each cohort grouping

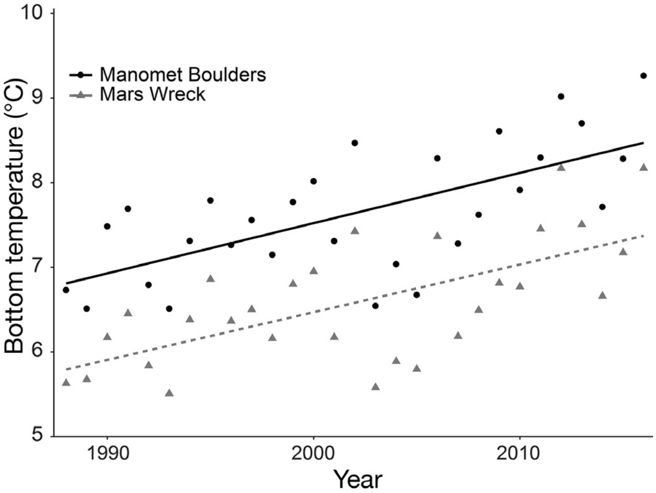

Fig. 5. Annual mean bottom water temperature observed at 2 locations off the coast of Massachusetts in Cape Cod Bay from 1988 to 2016. The trend line is a linear regression fitted to the observed mean annual temperatures at each location

4. DISCUSSION

This study documented substantial changes in the maturation schedules and growth of Cape Cod/Gulf of Maine yellowtail flounder over a period of nearly 40 yr. Using observations from the NEFSC trawl survey collected between 1970 and 1997, Begg et al. (1999) also reported decreases in the length (L_{50}) and age at maturation (A_{50}) for yellowtail flounder in the Gulf of Maine. Similarly, reductions in L_{50} and A_{50} were observed for yellowtail flounder stocks on the Grand Banks (Walsh & Morgan 1999) and in the Gulf of St. Lawrence (Beacham 1983). Trends towards maturation at younger ages and smaller sizes have been noted for other exploited flatfish stocks, including American plaice off Newfoundland (Morgan & Colbourne 1999, Barot et al. 2005) and in the Gulf of Saint Lawrence (Beacham 1983), female sole in the North Sea (Mollet et al. 2007), and plaice in the North Sea (Grift et al. 2003, van Walraven et al. 2010).

Estimates of A_{50} and L_{50} were relatively stable for cohorts of both sexes produced from 1978 until approximately 1990, after which maturation schedules changed markedly (Fig. 3). The cause of these changes in maturation is not readily apparent. It is unlikely that the sudden shifts in maturation were caused by density-dependent effects, as SSB was relatively consistent throughout the time series (Fig. 1). Further, although catches were relatively high in 1990, estimates of F were of similar magnitude to prior years (Fig. 1). One possible explanation is that the regulations on codend mesh size requirements and minimum landing sizes that were established in the 1980s may have shifted the selectivity of the fishery to preferentially harvest older and larger individuals.

PMRNs are designed to exclude the effects of phenotypic plasticity associated with variability in survival and growth, so changes in PMRNs provide much stronger evidence for genetic changes than trends in maturity ogives (Olsen et al. 2004, Swain 2011). However, the PMRN method employed in this study cannot be taken as definitive evidence of fishery-induced evolution, because environmental factors not included in the analysis could have also contributed to the shift in the reaction norm (Heino & Dieckmann 2008). The Gulf of Maine is one of the fastest warming ecosystems on Earth (Mills et al. 2013), and the observed increases in bottom water temperature in the nearshore Gulf of Maine (Fig. 5) may be at least partly responsible for the observed trends in maturation. Growth rates in the year prior to maturation can be a key determinant of whether or not a juvenile fish will mature (Kinnison et al. 2011), and cohorts of flatfish experiencing warmer temperatures during their juvenile stage have been shown to mature at younger ages and smaller sizes (Morgan & Colbourne 1999, Walsh & Morgan 1999). Temperature may also affect maturation schedules independently of growth (Dhillon & Fox 2004).

PMRNs can be extended to include explanatory variables other than age or size (Heino et al. 2002), such as temperature, body condition, and individual growth histories (Grift et al. 2003, Kraak 2007, Mollet et al. 2007, Siegel et al. 2018), and future analyses could consider multidimensional PMRNs to better understand the extent to which environmental and genetic sources of change are responsible for the observed trends in maturation for yellowtail flounder. The evaluation of multidimensional PMRNs was not possible for this analysis, given the cohort samples and concern about the validity of assessing the influence of environmental variation at the aggregated cohort level presented. Growth during critical life history periods can also be an important determinant of maturation (Kuparinen et al. 2008), and PMRNs that accounted for individual growth histories outperformed size-at-age PRMN models for Chinook salmon in Alaska (Siegel et al. 2018). Using multidimensional PMRNs, Kraak (2007) noted that temperature increases of 1°C corresponded to a decrease of 1.4 cm in the L_{p50} of age 3 female plaice in the North Sea, and thus while temperature partially explained long-term trends in L_{p50}, the residual trend in L_{p50} suggested that fishery-induced genetic change had occurred. In this study, the L_{p50} of yellowtail flounder declined by 6.8 and 8.2 cm for females at age 3 and males at age 2, respectively. Bottom temperature in Cape Cod Bay increased by approximately 2.5°C from 1988 to 2016 (Fig. 5), and this rapid warming likely contributed in part to the shifts in the reaction norms. However, the large magnitude of change in the L_{p50} values suggests that fishery-induced evolution has also occurred, and it is likely that genetic and phenotypic forces acted synergistically to drive the observed trends in maturation.

Future work should also consider whether variation in length-based selectivity associated with the 2009 change in the NEFSC survey vessel and trawl net affects the estimation of maturity ogives. Length-based survey calibration coefficients have been estimated for yellowtail flounder (Miller et al. 2010) and Morgan (1999) demonstrated how estimates of maturity-at-age and weight-at-age can be adjusted to account for survey vessel changes.

In this study, males exhibited greater changes in length and age at maturity than females, which is congruent with sex-specific trends in maturation that were observed for yellowtail flounder on the Grand Bank (Walsh & Morgan 1999) and in the Gulf of Saint Lawrence (Beacham 1983), and for plaice stocks off Newfoundland (Morgan & Colbourne 1999, Barot et al. 2005). The energetic costs associated with reproduction are thought be greater in female flatfish than in males (Pandian 1970, Roff 1982), and Walsh & Morgan (1999) posited that females may be more constrained than males in terms of the minimum size or age required to reach maturity. Because male yellowtail flounder have lower energetic requirements for reproduction, they may respond more quickly to selection pressures imposed by harvesting or the environment. The reaction norm approach used here demonstrates that the greater reductions in L_{p50} values observed for males are due to the process of maturation itself, rather than sex-specific differences in survival or growth (Barot et al. 2005).

The results of this study have important implications for management and stock assessment. In New England, regulations including minimum landing sizes and mesh size requirements have been implemented to reduce mortality of juvenile fish and to optimize near-term yields. However, these well-intentioned management measures may contribute to fisheries-induced evolution by directing harvest pressure on the largest individuals in the population, ultimately favoring genotypes that exhibit smaller adult body sizes and earlier reproduction (Conover & Munch 2002, Kuparinen & Festa-Bianchet 2017). Populations that exhibit a genetic response to harvest may increase their resilience to fishing mortality, but will exhibit lower overall fitness than an unfished population (Dieckmann et al. 2009, Kuparinen et al. 2014). For example, reductions in size at maturity can lead to long-term declines in sustainable yield (Law 2000, Ernande et al. 2004, Jørgensen et al. 2007) as the energetic investment associated with earlier reproduction comes at the expense of somatic growth (Heino et al. 2002, Grift et al. 2003), and individuals that mature at smaller sizes may remain smaller for the rest of their lives (Baudron et al. 2014, Hunter et al. 2015). Because fecundity in flatfish increases with adult body size, there is also a tradeoff between early maturation and future egg production (Roff 1982). Reduced adult sizes may negatively impact recruitment because larger fish produce higher quality eggs with higher larval survival (Hsieh et al. 2010, Kinnison et al. 2011, Barneche et al. 2018), although the interaction between female size and egg quality in yellowtail flounder needs further research (McElroy et al. 2016).

There is recognition that failure to account for the consequences of fisheries-induced evolution can lead to overestimation of sustainable yields, and ultimately, overharvest (Kuparinen & Festa-Bianchet 2017). While the maturation trends observed in this study appear to have a genetic component, increasing temperatures in the Gulf of Maine may also be contributing to maturation at earlier ages and smaller sizes, and warming trends are projected to continue into the future (IPCC 2014). Therefore, these life history modifications will likely be difficult to reverse in the near term through fisheries management actions (Law 2000, Hunter et al. 2015). Some management strategies that have been suggested to counteract fisheries-induced evolution include the establishment of Marine Protected Areas, and maximum size limits to protect the largest individuals in the population (Conover & Munch 2002). In New England, fishery closed areas have been used for decades to reduce fishing mortality, protect sensitive habitat, and limit harvest on spawning aggregations (Department of Commerce 2018). Cape Cod/Gulf of Maine yellowtail flounder are primarily harvested using otter trawls (NEFSC 2017) and the intended conservation benefits of slot limits may not be recognized because the mortality of yellowtail flounder discarded in the trawl fishery is thought to be substantial (Barkley & Cadrin 2012). Law & Plank (2018) recently advocated that the directional selection pressures imposed by fishing can be reduced by employing a balanced harvesting strategy, where fishing mortality rates are set in proportion to the rate of somatic production. Implementing a balanced harvesting approach in New England would be challenging because yellowtail flounder are caught in a mixed-species groundfish complex that harvests multiple stocks simultaneously, but balanced harvesting strategies deserve further consideration in this region.

Taken together, the trends in life history traits observed in this study (increases in K; decreases in L_∞, L_{50}, and A_{50}) provide indirect evidence that natural mortality (M) may be increasing for Cape Cod/Gulf of Maine yellowtail flounder. Empirical relationships and size-spectrum theory demonstrate that K is directly proportional to the magnitude of M for a population (Pauly 1980, Andersen et al. 2009, Gislason et al. 2010, Then et al. 2015). Further, ecosystem models suggest that small decreases in body size can lead to increases in M because of increased predation (Audzijonyte et al. 2013). In addition, the mortality associated with reproduction is expected to increase as size and age at maturation decline (Swain 2011). For example, Beverton et al. (1994) observed that maturation cohorts of northeast Arctic cod that matured at younger ages exhibited decreased longevity and smaller asymptotic lengths compared to their later-maturing counterparts. The present study provides indirect evidence for nonstationarity in M for the Cape Cod/Gulf of Maine yellowtail flounder stock, but further research is needed to address this possibility more directly.

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