Spawning phenology of Yellowtail Flounder: analysis of reproductive condition determined on NEFSC bottom trawl surveys

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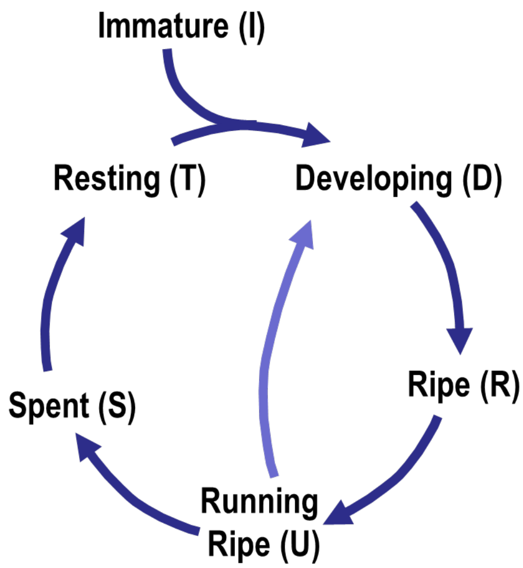
Background/rationale

Spawning phenology, the annual timing of reproduction, determines when spawning occurs and is therefore important to understanding individual fish energetics and condition, as well as the timing and location of release of eggs. Fish undergo seasonal (annual) patterns of weight gain and loss related to spawning. In some extreme cases, gonad weight can be > 30% body weight, therefore estimates of fish condition based on fish weight can be influenced by reproductive state. Thus, shifts in survey timing and/or spawning seasonality over time could produce changes in calculated weight based condition indices. Oocyte development in Yellowtail Flounder has been reported in detail (Howell 1983; Howell and Kesler 1977); they are batch spawners with group synchronous oocyte development and determinate fecundity (McElroy et al. 2015), similar to other flatfish in the region (e.g. American Plaice, Witch Flounder; Murua and Saborido-Rey 2003). Based on estimates of total and batch fecundity of Yellowtail Flounder on the Grand Bank, Zamarro (1991) estimated that an individual 42 cm female would spawn about 7 times during the spawning season. In a more detailed laboratory study that followed individual females across multiple spawning seasons, Manning and Crim (1998) report 14-22 batches per year with near daily spawning over a period of a month. Maturity data collected on NEFSC bottom trawl surveys were evaluated to determine spawning seasonality, and to investigate if this may have changed over the available time series of data. The spring bottom trawl survey (SBTS) coincides with the spring/summer spawning period (March-August, Burnett et al. 1989). O'Brien et al. (1993), further describe the spawning season as April-August with peak May-June for all three stocks. The autumn bottom trawl survey (ABTS) occurs during the non-spawning period. Although some early developing fish are sampled in the fall, these individuals have low gonadal-somatic index (GSI; Wuenschel et al. 2019), and the early stage of development is not expected to have significant impact on the overall weight.

Methods

Spawning phenology of Yellowtail Flounder was evaluated using macroscopic maturity data collected during routine NEFSC spring and fall bottom trawl surveys. The macroscopic scheme includes six stages – immature, developing, ripe, running ripe, spent, and resting- and criteria are described in Burnett et al. (1989). Beginning in the fall of 2006, the classification of ripe changed, from >50% of eggs hydrated (clear) to the presence of any hydrated eggs. In this scheme, fish mature once in their life, and then cycle through developing to resting stages annually.



As batch spawners, Yellowtail Flounder would be developing leading up to spawning, then undergo cycles of ripe and running ripe as individual batches mature, hydrate and are released. After each batch is released, they would return to a developing stage and repeat until the last batch is released, after which they would proceed to the spent and resting stages. Therefore individuals in the developing stage could either be prespawning, or in between batches, which cannot be distinguished macroscopically (ovarian histology can differentiate these two based on the presence of postovulatory follicles). At the population level, the occurrence of developing fish with some ripe is indicative of active spawning. The present analysis is restricted to mature females, since males are generally prepared to spawn over a broader time period than females. Histological verification of the macroscopic staging, and formal quantification of error rates have not been evaluated for Yellowtail Flounder. However, for species that have been evaluated, the error rates have been relatively low (McBride et al. 2013, Wuenschel and Deroba 2019). The rates of misclassifications are assumed to be minor compared to the volume of correct classifications. The survey data was not edited in any way, and it is likely there are some erroneous classifications included, therefore caution should be exercised when interpreting subsets of the data where sample sizes become limited. Data was analyzed for each of the three stock regions (Cape Cod- Gulf of Maine, Georges Bank, and Southern New England) using the survey strata sets (Table 1) identified for each stock. Specifically, the proportions developing, ripe, spent, and resting were calculated for each stock region and survey. For simplicity, both ripe and running ripe stages, which both represent spawning active fish (Brown-Peterson et al. 2010), were combined into a single ripe stage. The period from 1971 to 2023 was analyzed for the spring survey and the period 1981-2022 was analyzed for the fall survey. The mean size of mature females that were sampled was also calculated for the following reasons; 1) for many species larger and older females are ready to spawn earlier in the year and spawn for a longer period (Trippel 1995), and 2) size based sampling protocols have changed over the years, especially with the development of FSCS 2.0 (in fall of 2011) that enabled greater flexibility to sample more of the larger fish captured. The bottom temperature at collection and day of year associated with mature females sampled were also plotted to evaluate trends. For the spring surveys, the proportions in each maturity stage were also summarized by temperature bin (1 °C) and week of year to evaluate influence of each. These relations (binned bottom temperature and week of year) were also summarized by decade to explore temporal changes over the past few decades (1970s to 2020s). The same series of summary/diagnostic plots are presented for each stock area. The data summaries allow visual interpretation of patterns and trends.

Multinomial logistic regression was used to summarize and evaluate the relative significance of sampling week, bottom temperature, and time block on the spawning condition of fish sampled during spring surveys. For this analysis, developing fish were considered 'prespawning', both ripe and ripe and running classes were considered 'spawning', and the spent and resting classes were combined into 'postspawning'. Although there is some order to these three classifications, they represent more of a cycle, and given Yellowtail Flounder are batch spawners and go from developing to ripe and back to developing multiple times before becoming spent. Therefore, multinomial regression was chosen over ordinal regression. The stock specific multinomial log-linear models took the form:

(Spawning condition) ~ (Week of year) + (Bottom Temperature) + (Time block)

Where spawning condition of individual fish is Prespawning, spawning, postspawning; as outlined above), Week of Year, Bottom Temperature (°C), and Time block (10year periods) are associated with each sample. Models were fit using *multinom* function in the *nnet* library (Venables and Ripley 2002) in R with Hess= True to calculate coefficient standard errors. The three probabilities (prespawning, spawning, postspawning) sum to one, only two need to be estimated. The resulting odds ratios were used to estimate probabilities using the R package ggeffects (Ludecke 2018) for visualizations of marginal effects. The significance of variables in the model was evaluated with likelihood ratio test using *Anova* in the R package (car) (Fox and Weisberg 2019).

The fall bottom trawl survey provides a shorter time series of Yellowtail flounder maturity, with data for 1971, then continuous from 1981. As mentioned above, the fall occurs during the non-spawning period, when overall fish weights should not be influenced by maturity stage. Nevertheless, the time series of spawning condition was plotted for each stock to confirm this, but further exploration of the data by week of year, bottom temperature, time block, and multinomial models were not performed for the fall time series.

Results and Discussion

CC GOM Yellowtail Flounder (Figures 1-6)

The spring survey (SBTS) generally occurs during the spawning season, capturing a mix of developing (spawning capable phase, sensu Brown-Peterson et al. 2010), ripe (spawning active phase), spent (regressing phase), and resting (regenerating phase) individuals (Figure 1). The mean size of mature females sampled slightly declined early the time series. The time series indicates a lower proportion of post spawning fish collected at higher temperatures more recently. Although the dates sampled were similar early and late in the time series, the temperatures occurring on these dates was higher late in the time series. Spawning condition was related to bottom temperature, with samples from higher temperatures having a lower proportion of prespawning fish (Figure 2). The proportion of spawning fish increased with week of year sampled (Figure 2). Together, these increases in prespawning and spawning fish as temperature and week of year sampled increases, indicate that the spring survey captures the peak to end of annual spawning depending on the year.

When summarized by decade, the most recent decades (2010s-2020s) sampled fish at slightly warmer temperatures and had a lower percentage of resting fish as compared to the 1970s to 2000s (Figure 3). Sampling has also occurred later into the spring in the recent decades (2010s-

2020s) but has collected slightly higher proportions of prespawning and spawning fish combined 1970s to 2000s that had few observations beyond week 18 (Figure 4).

The multinomial model indicated significant effects of bottom temperature, week of year, and decade on the probability of individual females being in a prespawning, spawning, or postspawning condition (Table 2). Pattern of increasing spawning and postspawning and decreasing prespawning with both week of year and temperate was evident (Figure 5). The pattern by decade indicated an increase in prespawning and decrease in postspawning groups after 2000; however, data is limited for the most recent decade. The increase in prespawning fish through time indicates sampling has shifted from the beginning or early portion of the spawning season up to the 1990s to occurring closer to the peak of the spawning season since 2000.

The autumn survey (ABTS) occurs in the non-spawning season and captures mostly resting individuals early in the time series before including many more developing fish since 2005 when sampling as occurred later in the year (Figure 6). The mean size of mature females sampled did not change over time. Although some developing fish are sampled in the fall, especially lately, these are most likely individuals early in development with low gonadosomatic index (GSI) that are still approximately 6 months away from spawning (see Wuenschel et al 2019, monthly GSI plot). There seem to be more developing fish present at later dates sampled in the fall. This indicates the fall survey generally occurs as fish are transitioning from resting into early developing as they prepare for the next spawning season. Given the overwhelming proportion of resting and early developing fish sampled during the fall survey, with little effect on overall weight, additional analyses (e.g. binning by temperature, week of year, decade) were not explored in more detail.

Georges Bank Yellowtail Flounder (Figures 7-12)

The spring survey (SBTS) generally occurs during the spawning season, capturing a mix of developing (spawning capable phase, sensu Brown-Peterson et al. 2010), ripe (spawning active phase), spent (regressing phase), and resting (regenerating phase) individuals (Figure 7). The mean size of mature females sampled varied over the time series. The time series indicates a similar proportion of post spawning fish collected at higher temperatures more recently. Although the dates sampled were similar, early and late in the time series, with a few exceptions, the temperatures occurring on these dates was higher late in the time series. Spawning condition was related to bottom temperature, with ripe fish declining at temperatures above 8 C, spent fish increasing with temperature, but little change in developing and resting fish over the range of temperatures (Figure 8). The proportion of developing fish decrease, while ripe, spent and resting fish increased with week of year sampled (Figure 8). Together, these increases in prespawning and spawning fish as temperature and week of year sampled increases, indicate that the spring survey captures the peak to end of annual spawning depending on the year.

When summarized by decade, for the most recent decades no clear patterns in the proportion of developing fish were evident, however more spent fish were encountered in the in the recent decades since 2000 (Figure 9). Sampling has also occurred later into the spring in the recent decades (2010s-2020s) and has collected slightly higher proportions of spent and resting fish sampled at later weeks compared to the period from the 1970s to 2000s that had few observations beyond week 17 (Figure 10).

The multinomial model indicated significant effects of bottom temperature, week of year, and decade on the probability of individual females being in a prespawning, spawning, or postspawning condition (Table 2). A pattern of increasing spawning and postspawning and decreasing prespawning with week of year was evident (Figure 11). Bottom temperature had the reverse effect, with increasing prespawing fish but decreasing spawning and spawning fish as temperature increased. The pattern by decade indicated relatively minor changes in the predicted probability of each spawning group over time, and sampling has consistently occurred close to the peak spawning period.

The autumn survey (ABTS) occurs in the non-spawning season and captures mostly a mix of resting and developing individuals early and late in the time series when sampling has occurred later in the year (Figure 12). The mean size of mature females sampled did not change over time. Although some developing fish are sampled in the fall, including lately, these are most likely individuals early in development with low gonadosomatic index (GSI) that are still approximately 6 months away from spawning (see Wuenschel et al. 2019, monthly GSI plot). There seem to be more developing fish present at later dates sampled in the fall. This indicates the fall survey generally occurs as fish are transitioning from resting into early developing as they prepare for the next spawning season. Given the overwhelming proportion of resting and early developing fish sampled during the fall survey, with little effect on overall weight, additional analyses (e.g. binning by temperature, week of year, decade) were not explored in more detail.

Southern New England Yellowtail Flounder (Figures 13-18)

The spring survey (SBTS) generally occurs during the spawning season, capturing a mix of developing (spawning capable phase, sensu Brown-Peterson et al. 2010), ripe (spawning active phase), spent (regressing phase), and resting (regenerating phase) individuals (Figure 13). The mean size of mature females sampled varied over the time series. The time series indicates a higher proportion of ripe fish collected early and late in the time series. The dates sampled have varied over time, with later sampling occurring 1977-1982, and more recently. The bottom temperatures showed a similar pattern for the recent period, however for the earlier period sampled late in the year, the water temperatures were much lower. Spawning condition was related to bottom temperature, with ripe fish increasing at temperatures above 5 °C, spent fish increasing with temperature, developing fish decreasing and resting fish increasing over this range. At lower temperatures, the patterns were reversed, but there were fewer observations (Figure 14). The proportion of developing fish decreased, while ripe, spent and resting fish increased with week of year sampled (Figure 14). Together, these increases in spawning and postspawning fish as temperature and week of year sampled increases, indicate that the spring survey captures the peak to end of annual spawning depending on the year.

When summarized by decade, the most recent decades indicate higher proportions of developing fish with subsequent declines in ripe fish compared to the earliest decade (Figure 15), however only a single mature female was sampled in the most recent decade. Sampling has also occurred during similar weeks (1970s-2010s) and has collected slightly higher proportions of spent and resting fish sampled in the 1990s at warmer temperatures (Figure 16).

The multinomial model indicated significant effects of bottom temperature, week of year, and decade on the probability of individual females being in a prespawning, spawning, or postspawning condition (Table 2). Pattern of increasing postspawning and decreasing spawning and prespawning with week of year was evident (Figure 17). The effect of bottom temperature differed, with increasing spawing and postspawning fish but decreasing prespawning fish as temperature increased. The pattern by decade indicated an increase in prespawning and decrease in spawning from the 1970s to 1990s, with little change since (ignoring the most recent decade, which is represented by a single fish). In the late 1970s and early 1980s SNE samples were collected later in the spring and contained large numbers of ripe fish, in the peak of spawning. From the mid-1980s to 2010 sampling occurred earlier and collected mostly prespawning fish.

The autumn survey (ABTS) occurs in the non-spawning season and captures mostly a mix of resting and developing individuals early and late in the time series when sampling has occurred slightly later in the year (Figure 18). The mean size of mature females sampled was variable, and few fish sampled recently were smaller. Although some developing fish are sampled in the fall, including lately, these are most likely individuals early in development with low gonadosomatic index (GSI) that are still approximately 6 months away from spawning (see Wuenschel et al. 2019, monthly GSI plot). There seem to be more developing fish present at later dates sampled in the fall. This indicates the fall survey generally occurs as fish are transitioning from resting into early developing as they prepare for the next spawning season. Given the overwhelming proportion of resting and early developing fish sampled during the fall survey, with little effect on overall weight, additional analyses (e.g. binning by temperature, week of year, decade) were not explored in more detail.

Conclusions

Yellowtail Flounder spawn during the spring months in the region, with the spring survey sampling fish during the spawning season. There is evidence that spawning condition is related to the bottom temperature, week of year, and decade sampled for each of the three stocks and survey timing and environmental conditions (bottom temperature) have been variable over time. The analysis of macroscopic data presented here provides some evidence for a change in the spawning season of CC GOM and SNE stocks. Early in the time series, sampling captured the beginning/early portion of spawning season, while later in the time series sampling has captured more of the peak in spawning. However, some caveats to this general conclusion are warranted. First, since Yellowtail Flounder are batch spawners, individuals cycle from developing, to ripe, to running ripe, and back to developing for each of many batches over a >1 month period. As such, the developing class includes a mix of individuals that have not released any batches yet (true prespawners) and others who are ‘in between batches (i.e. partially spent, but before a next batch). Gonadal histology and/or GSI data could help to refine categorization of these stages, but such data does not exist for the long time series presented. Second, the analysis by decadal timeblocks presented is a rather coarse approach to investigating long term trends in spawning condition. More appropriate methods should be explored and evaluated in future studies. Nevertheless, even with significant inter-annual variability, the approach presented should detect directional change in spawning seasonality over the time series. Subtle shifts to earlier spawning, accompanied by more individuals sampled later in their annual reproductive cycle (e.g. closer to spent), were evident in CC GOM and SNE stocks. Even small changes in spawning seasonality and/or sampling timing can affect the total weight of individuals sampled given the gonad of Yellowtail Flounder females can reach 35 % of their body weight (Wuenschel et al. 2019), with the ovary declining in weight over a period of months as batches of eggs are shed. Therefore, consideration of spawning condition when interpreting fish weight and relative condition during the spring season should be considered. Although sampling was not specifically designed to detect changes in spawning seasonality of Yellowtail Flounder, the present analysis provides a preliminary evaluation of spawning timing over a long time series (1971-2023).

The post spawning Yellowtail Flounder would be expected to have lower relative condition due to shedding of gametes, depletion of liver (used for oocyte development and maturation), and higher water content of muscle and liver tissue, as has been reported in cod (Lambert and Dutil 2000) and flatfishes (Wuenschel et al. 2019). Some fishes also reduce or cease feeding during spawning, for behavioral or physical (e.g. gonad occupying most of the body cavity) reasons. The annual cycle of energy acquisition, storage, and depletion is lowest immediately following spawning in capital breeders such as haddock (McBride et al. 2015). Manning and Crim (1998) estimated female weight loss associated with spawning to be 22-23% in a laboratory study of Yellowtail Flounder. Although the reduction in weight and condition due to spawning is temporary, comparisons of relative condition (weight at length) across years that sampled varying proportions of active and post spawning fish (whether due to spawning timing or survey timing) should be considered with caution. The results presented for mature females should be applicable to mature males as well, but immature fish of both sexes will not undergo weight loss due to spawning. Therefore, comparison of condition in proximity to spawning season across years that contain varying proportions of immature and mature fish will also be problematic. Given the temporal separation from spawning, relative condition estimates derived from autumn surveys will be less influenced by alterations in timing of surveys or spawning season.

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Table 1. NEFSC bottom trawl survey strata used for each Yellowtail Flounder stock unit.

Stock unit	Spring Strata	Fall Strata
GB	Offshore 13-21	Offshore 13-21
CC-GOM	Offshore 25,26,27,39,40, Inshore 56,57,59,60,61,62,64,65,66	Offshore 25,26, 39,40, Inshore 56,57,59,60,61,62,64,65,66
SNE	Offshore 1,2,5,6,9,10,69,73,74 Inshore	Offshore 1,2,5,6,9,10

Table 2. ANOVA summaries for stock specific multinomial regression models.

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

	N	Chi Sq.	Df	Pr(>Chisq)
CC GOM YT SPAWNCOND ~ WOY+TEMP+TIMEBLOCK	2,985			
WOY		20.067	2	4.391-05***
TEMP		25.334	2	3.154e-06***
TIMEBLOCK		144.059	10	<2.2e-16***
GB GOM YT SPAWNCOND ~ WOY+TEMP+TIMEBLOCK	3,929			
WOY		80.046	2	<2.2e-16***
TEMP		33.155	2	6.316e-16***
TIMEBLOCK		79.959	10	5.115e-13***
SNE GOM YT SPAWNCOND ~ WOY+TEMP+TIMEBLOCK	3,144			
WOY		48.325	2	3.209e-11 ***
TEMP		7.031	2	0.02973 *
TIMEBLOCK		242.634	10	< 2.2e-16 ***

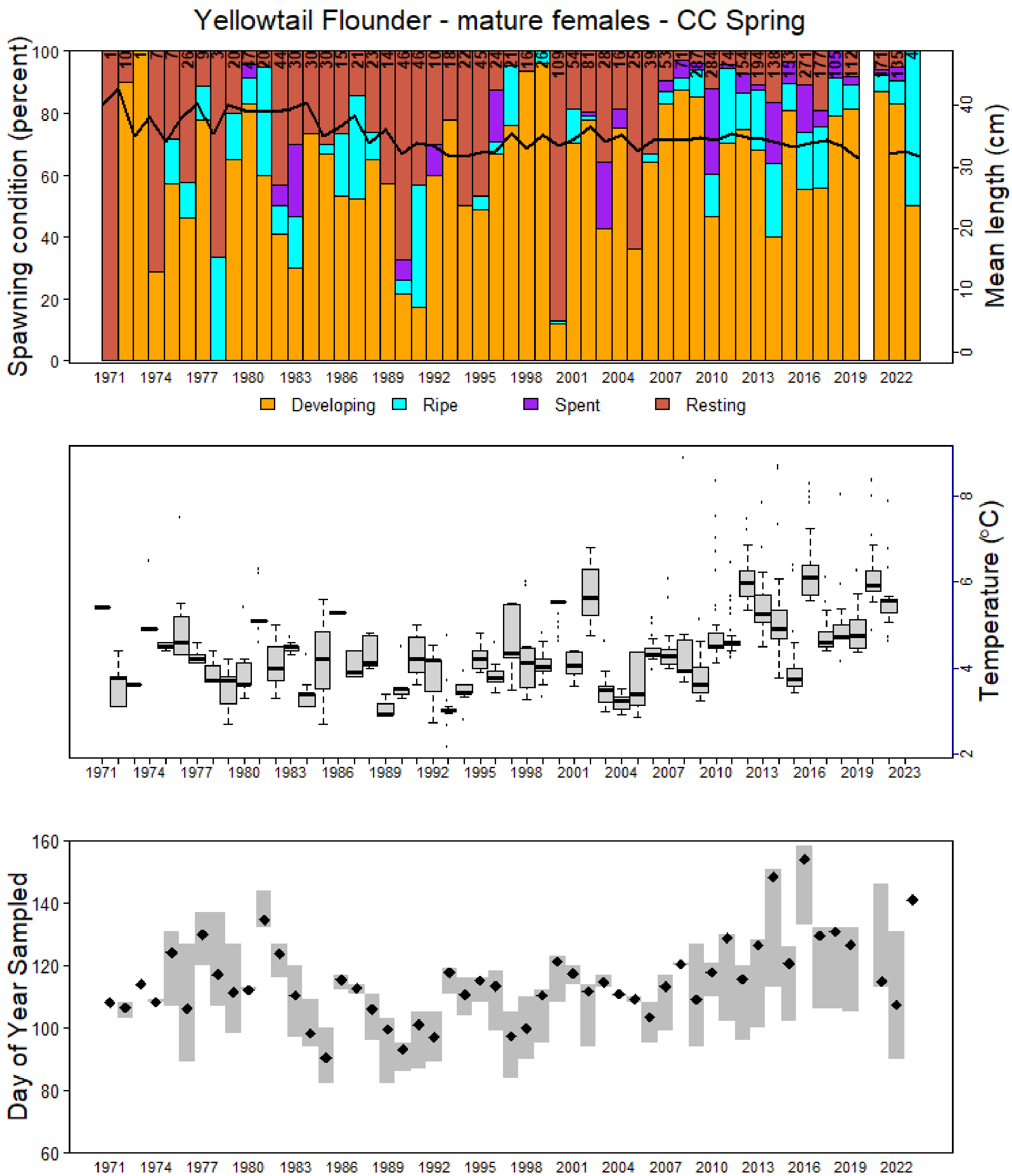

Figure 1. Spawning condition of mature female CC GOM Yellowtail Flounder sampled during the NEFSC SBTS (1971-2023). The mean size (black line in top panel), and bottom temperatures, and day of year sampled associated with those captures are shown.

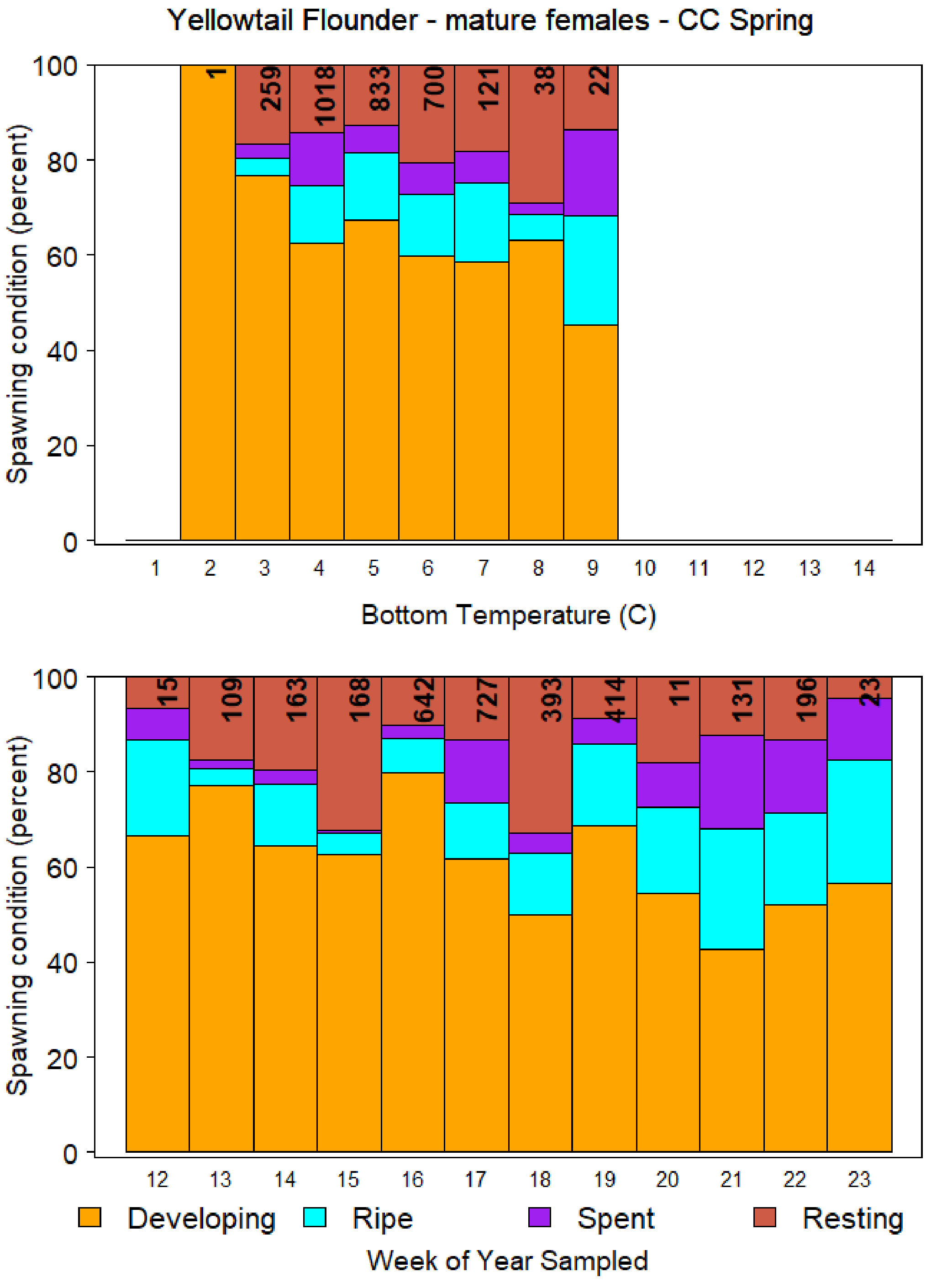

Figure 2. Spawning condition of mature female CC GOM Yellowtail Flounder sampled during the NEFSC SBTS (1971-2023), binned by bottom temperature and week of year sampled.

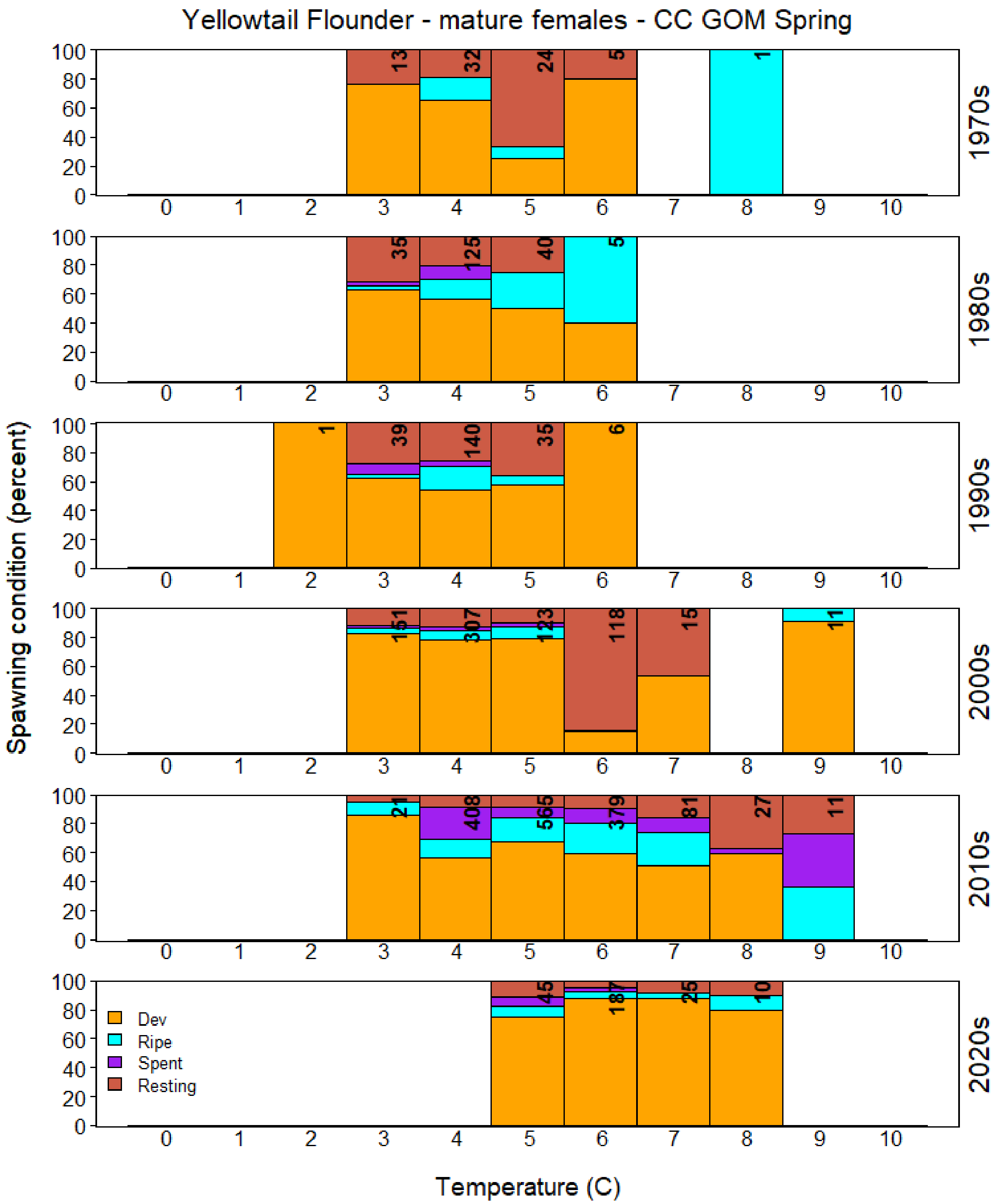

Figure 3. Spawning condition of mature female CC GOM Yellowtail Flounder sampled during the NEFSC SBTS (1971-2023), binned by bottom temperature and decade.

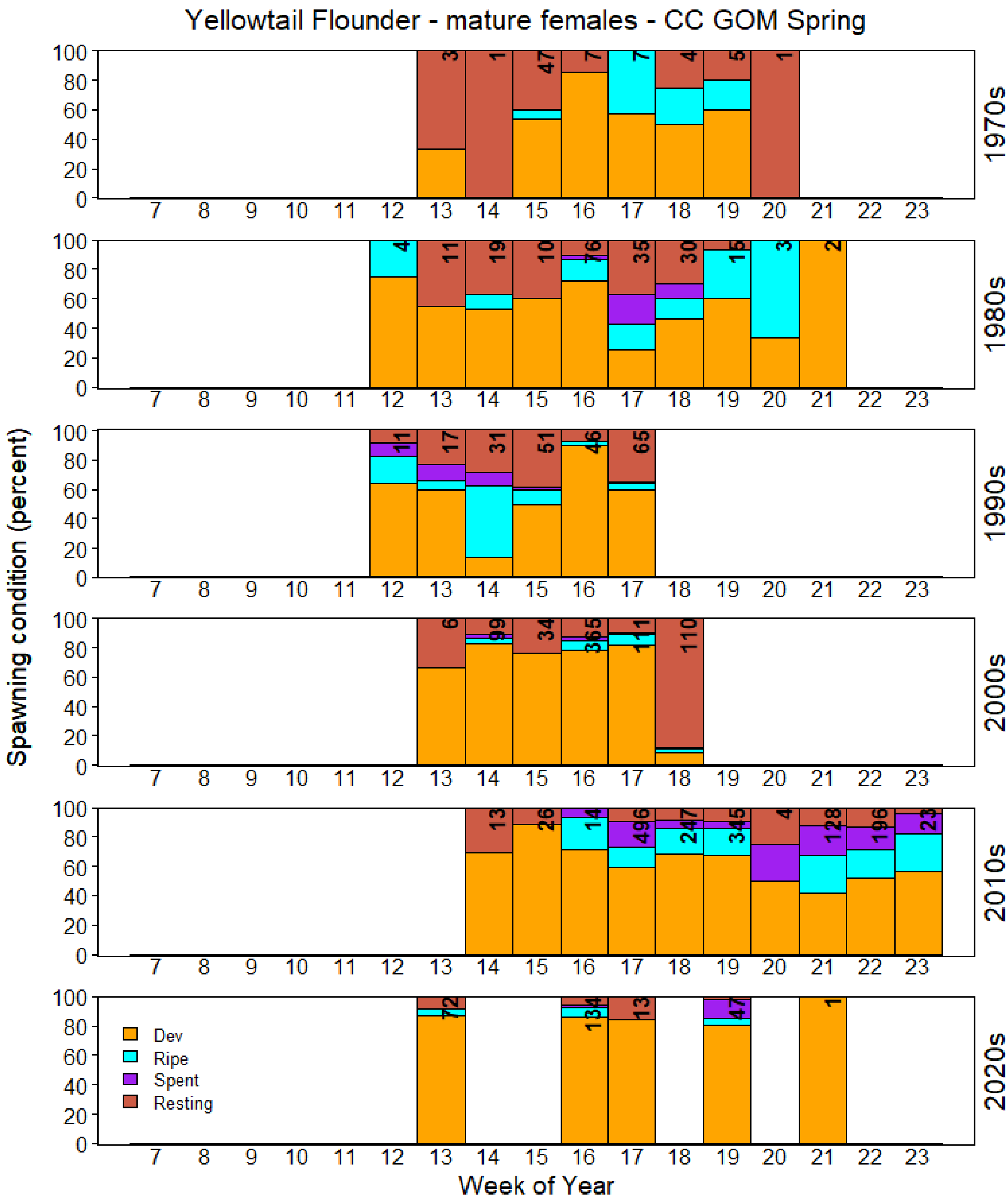

Figure 4. Spawning condition of mature female CC GOM Yellowtail Flounder sampled during the NEFSC SBTS (1971-2023), binned by week of year sampled and decade.

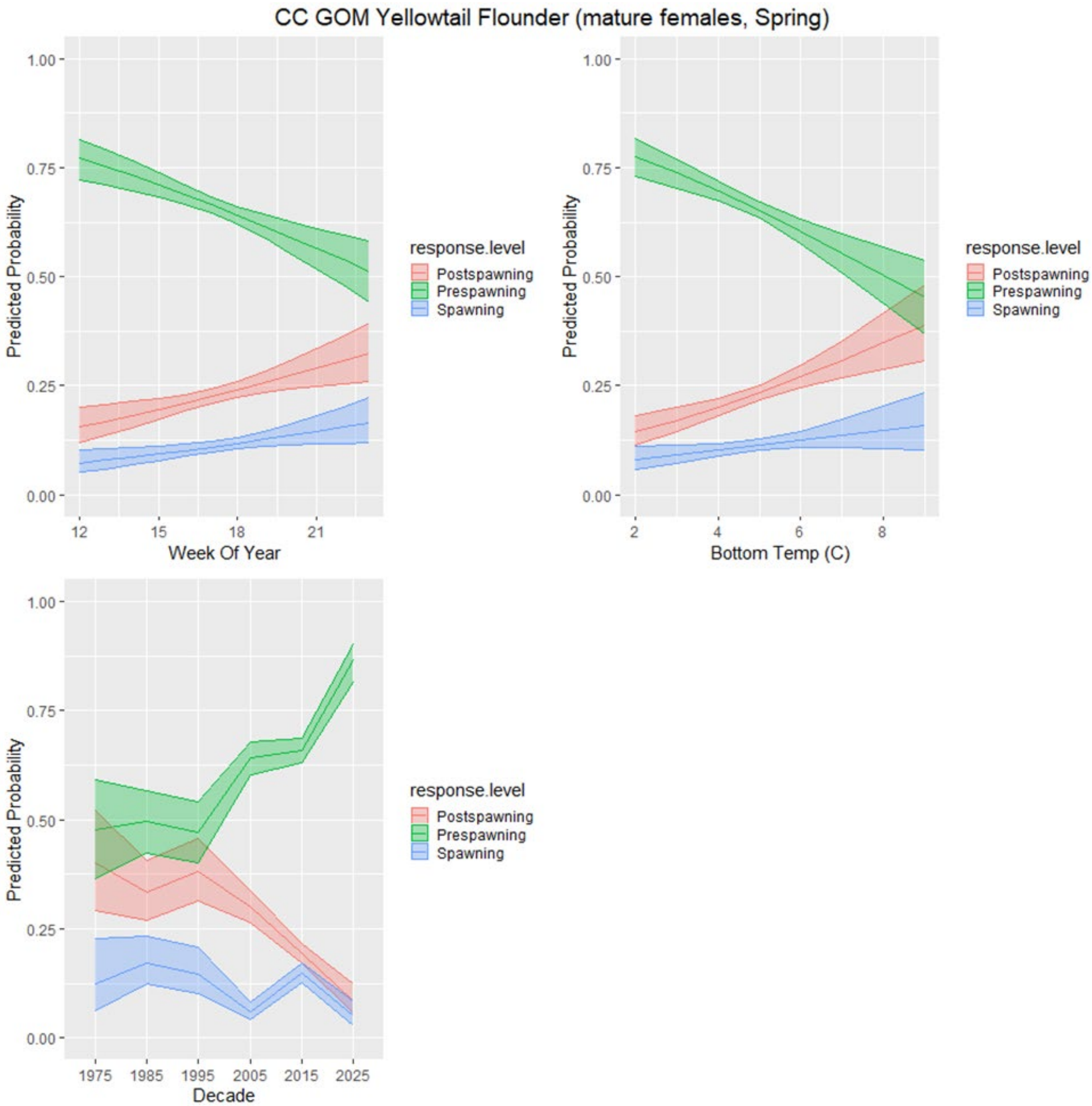

Figure 5. Predicted probabilities of spawning condition for female CC GOM Yellowtail Flounder from multinomial regression model as a function of week of year, bottom temperature, and decade. Note: 10 year time blocks are plotted by midpoint of each decade.

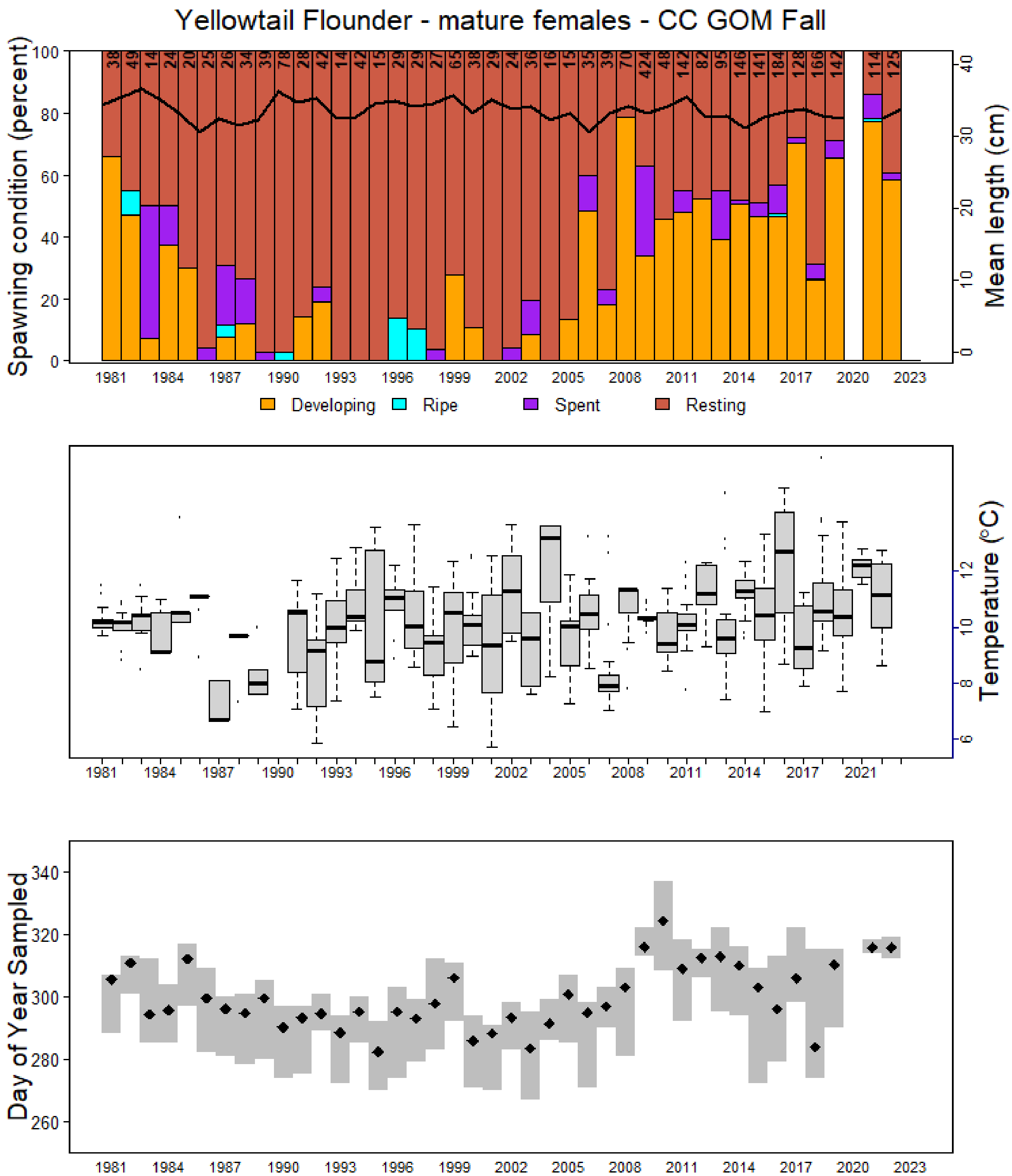

Figure 6. Spawning condition of mature female CC GOM Yellowtail Flounder sampled during the NEFSC ABTS (1981-2023). The mean size (black line in top panel), and bottom temperatures, and day of year sampled associated with those captures are shown.

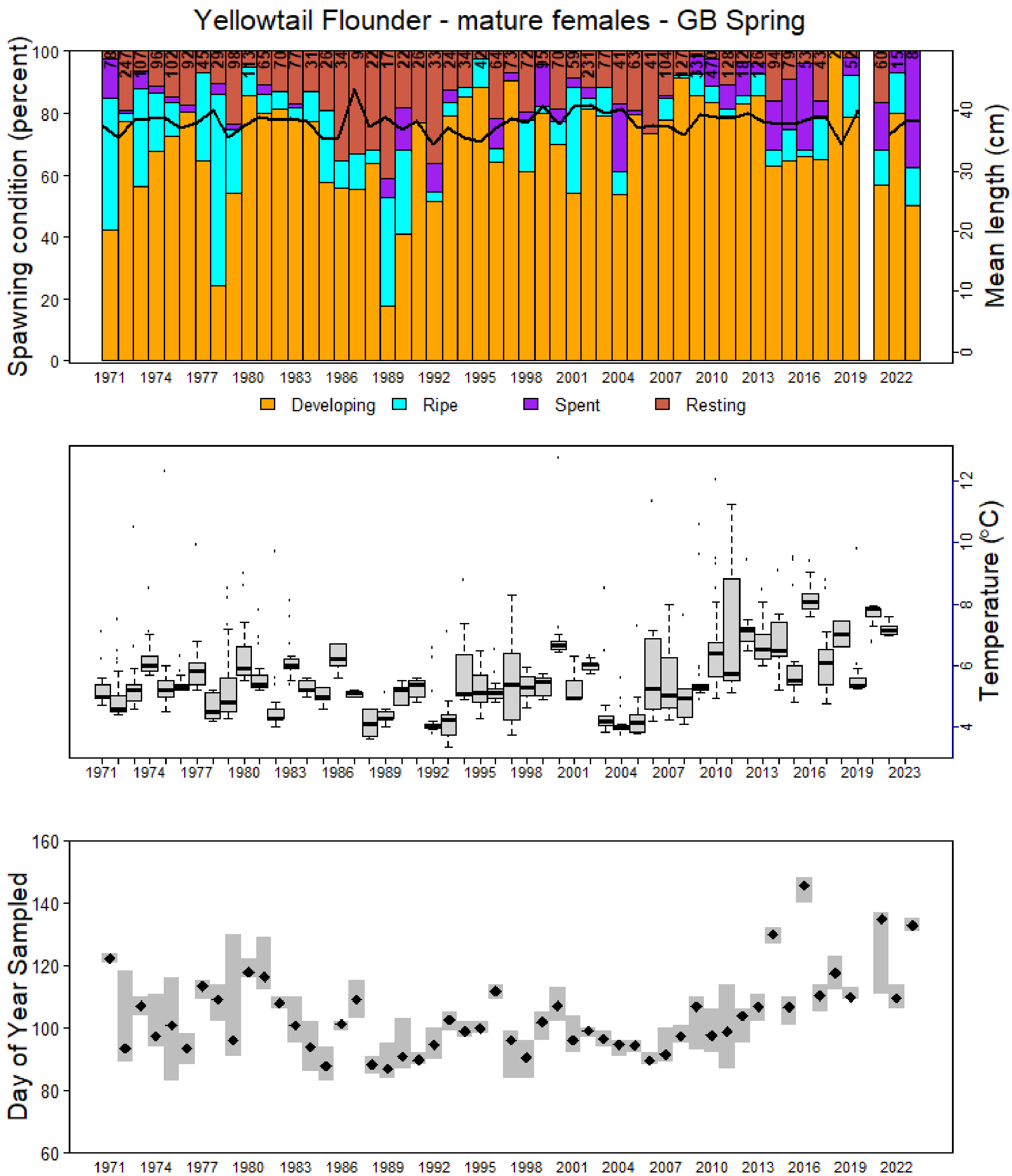

Figure 7. Spawning condition of mature female GB Yellowtail Flounder sampled during the NEFSC SBTS (1971-2023). The mean size (black line in top panel), and bottom temperatures, and day of year sampled associated with those captures are shown.

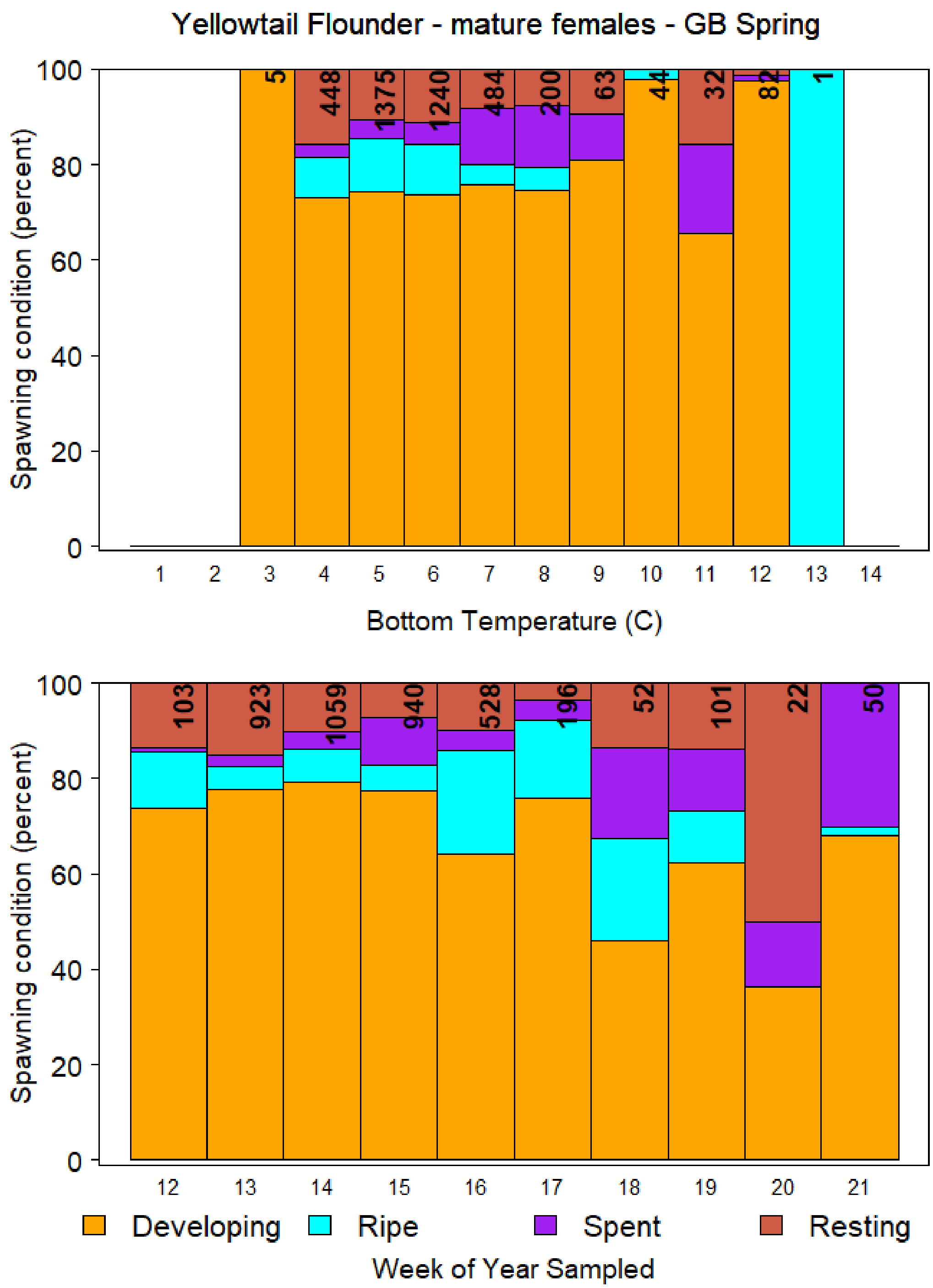

Figure 8. Spawning condition of mature female GB Yellowtail Flounder sampled during the NEFSC SBTS (1971-2023), binned by bottom temperature and week of year sampled.

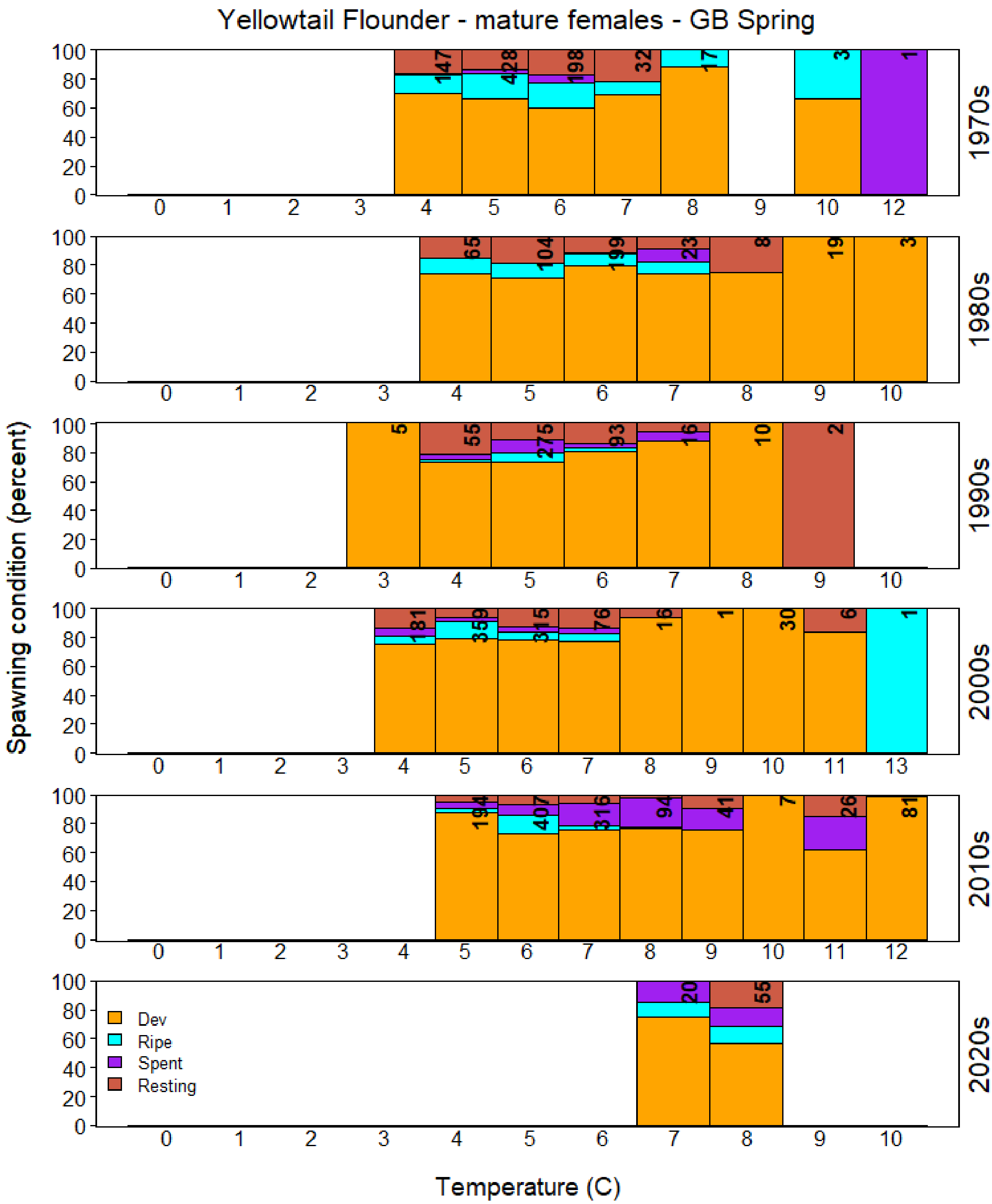

Figure 9. Spawning condition of mature female GB GOM Yellowtail Flounder sampled during the NEFSC SBTS (1971-2023), binned by bottom temperature and decade.

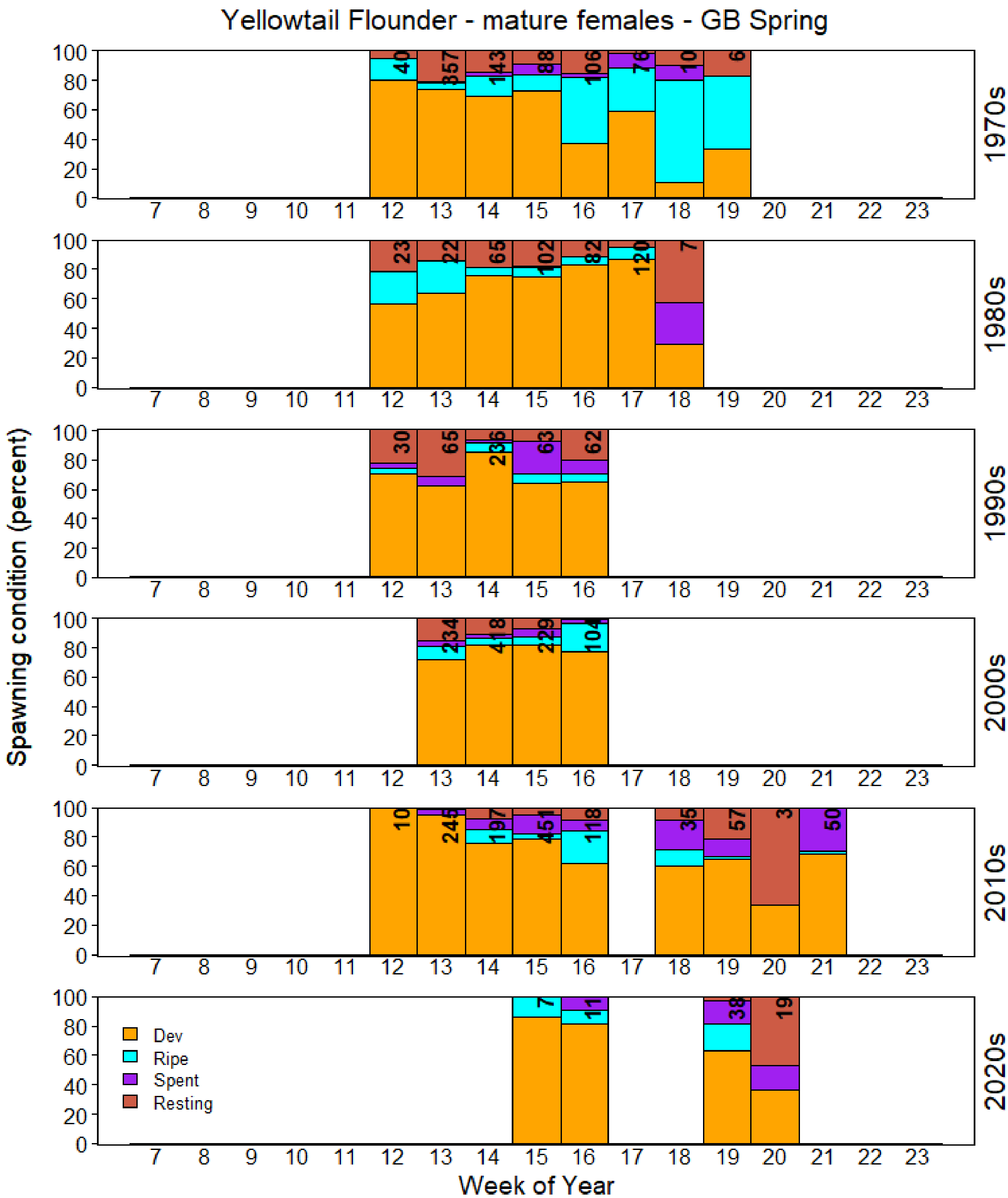

Figure 10. Spawning condition of mature female GB Yellowtail Flounder sampled during the NEFSC SBTS (1971-2023), binned by week of year sampled and decade.

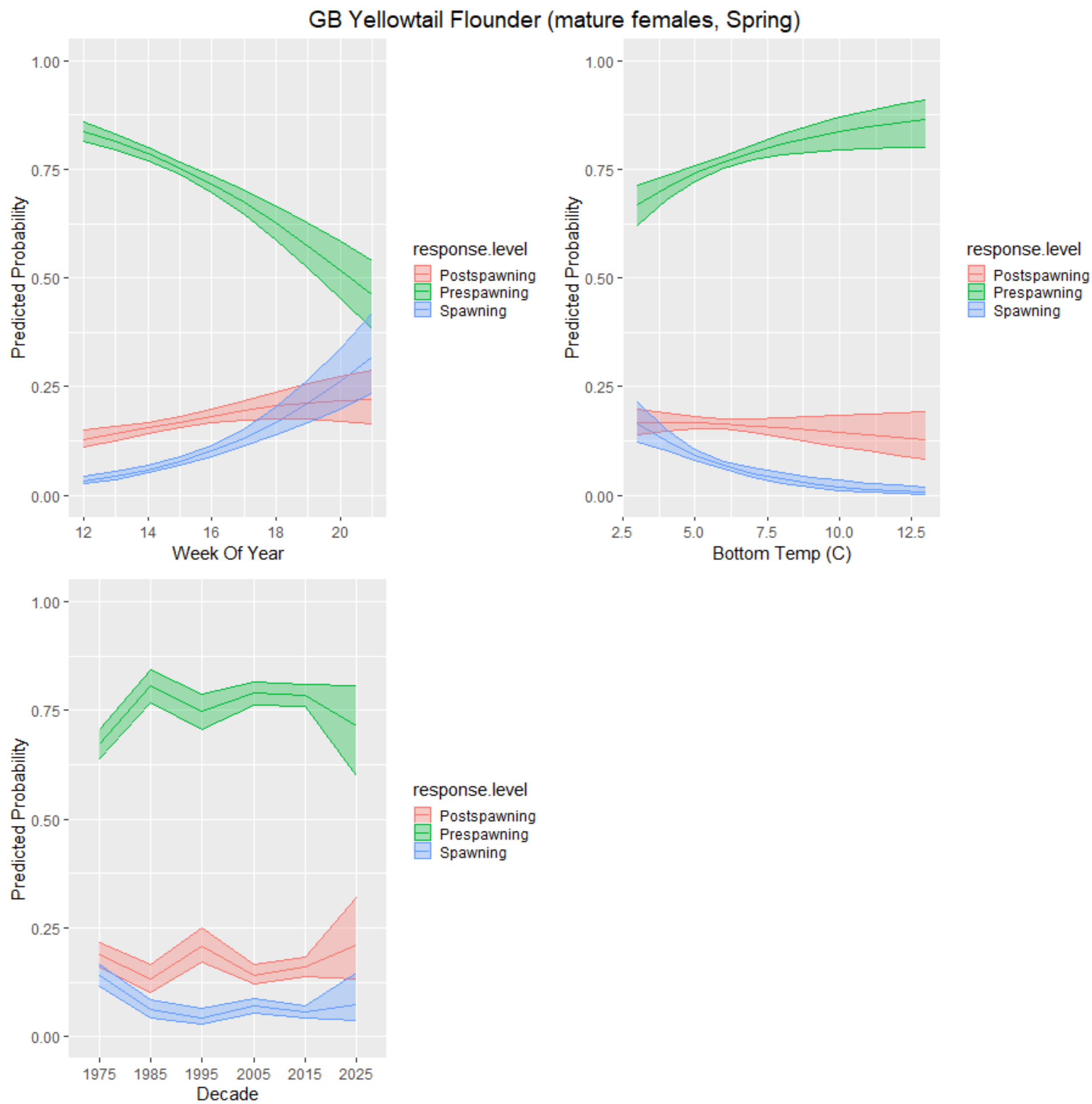

Figure 11. Predicted probabilities of spawning condition for female GB Yellowtail Flounder from multinomial regression model as a function of week of year, bottom temperature, and decade. Note: 10 year time blocks are plotted by midpoint of each decade.

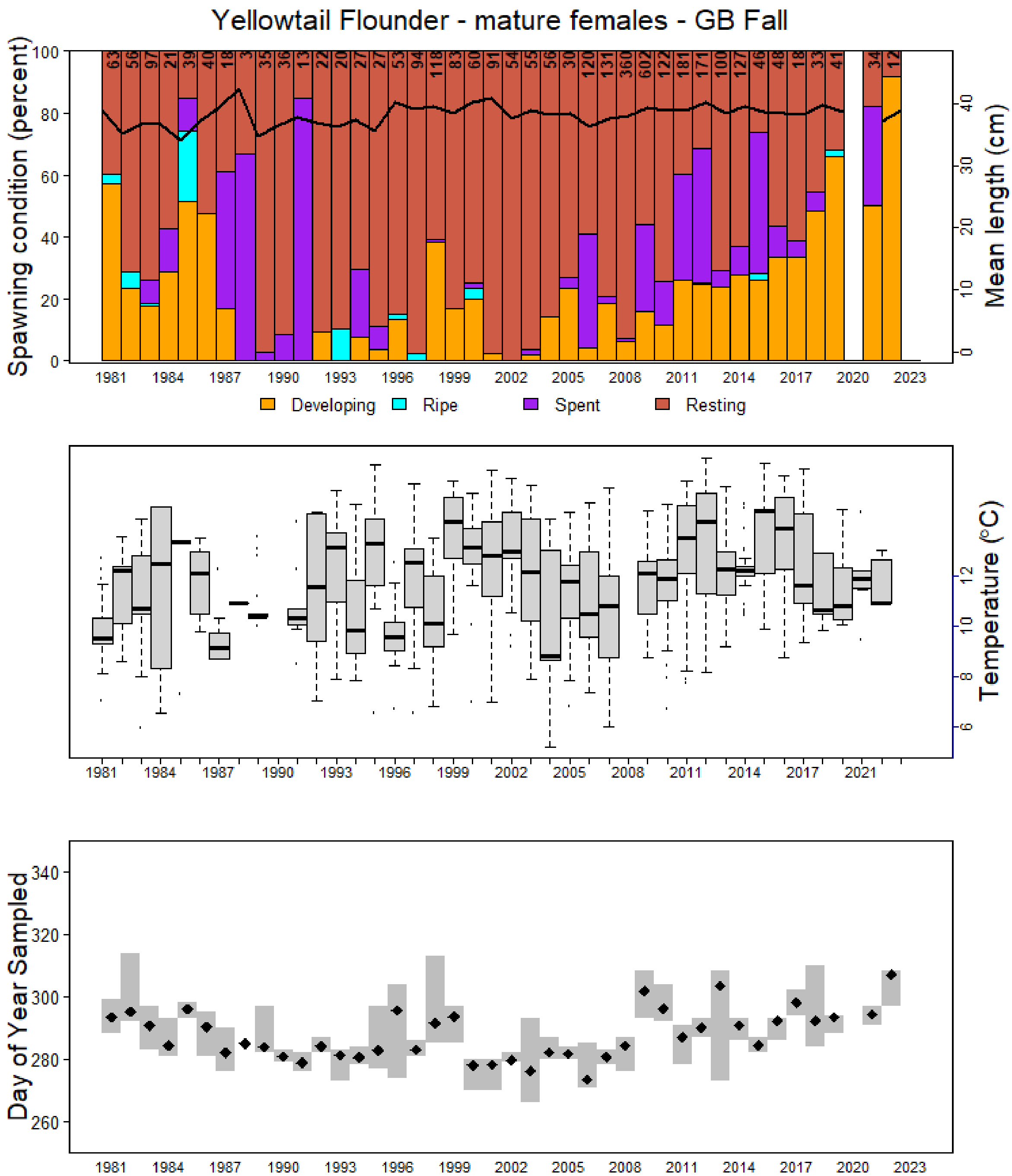

Figure 12. Spawning condition of mature female GB Yellowtail Flounder sampled during the NEFSC ABTS (1981-2022). The mean size (black line in top panel), and bottom temperatures, and day of year sampled associated with those captures are shown.

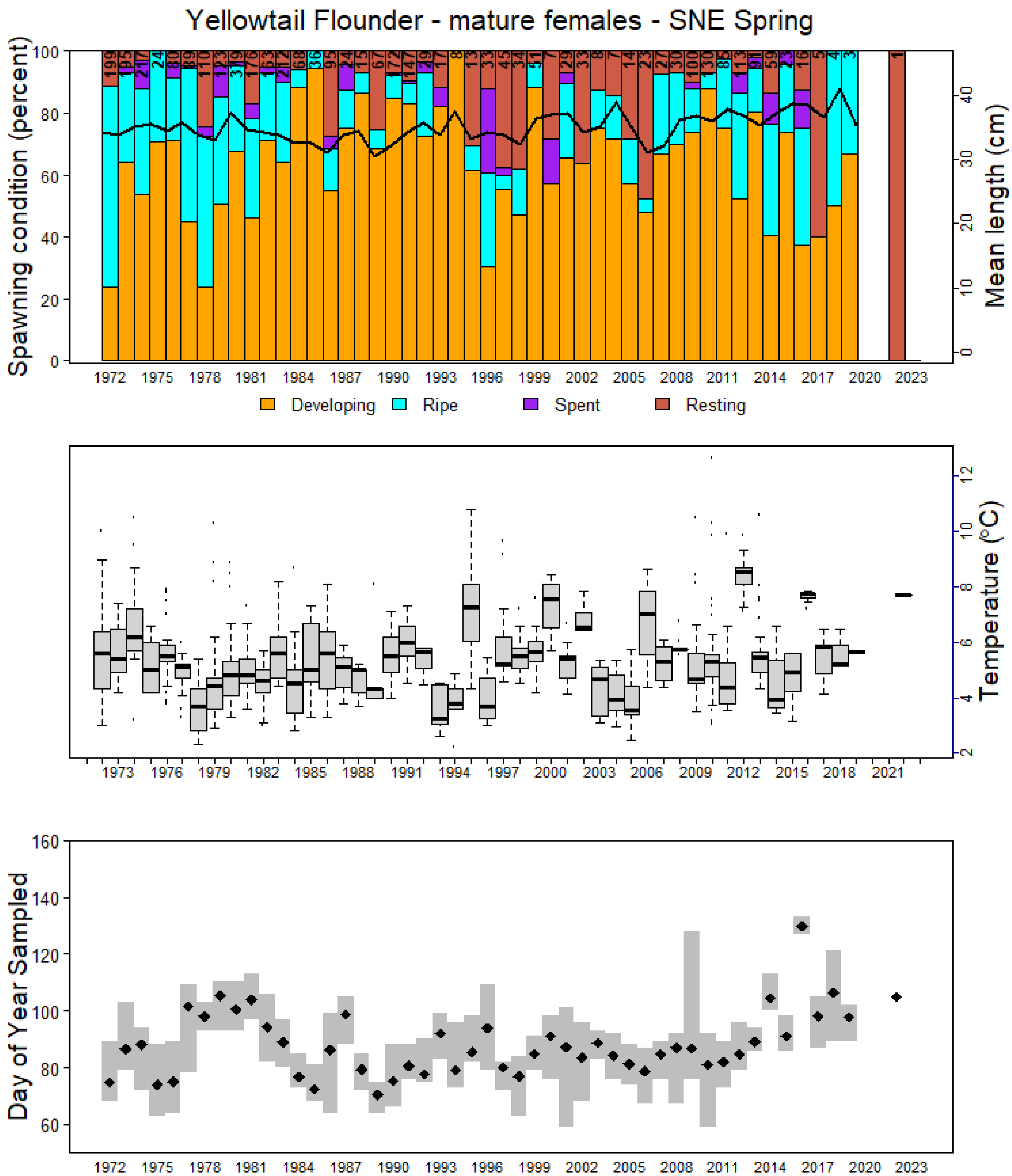

Figure 13. Spawning condition of mature female SNE Yellowtail Flounder sampled during the NEFSC SBTS (1971-2023). The mean size (black line in top panel), and bottom temperatures, and day of year sampled associated with those captures are shown.

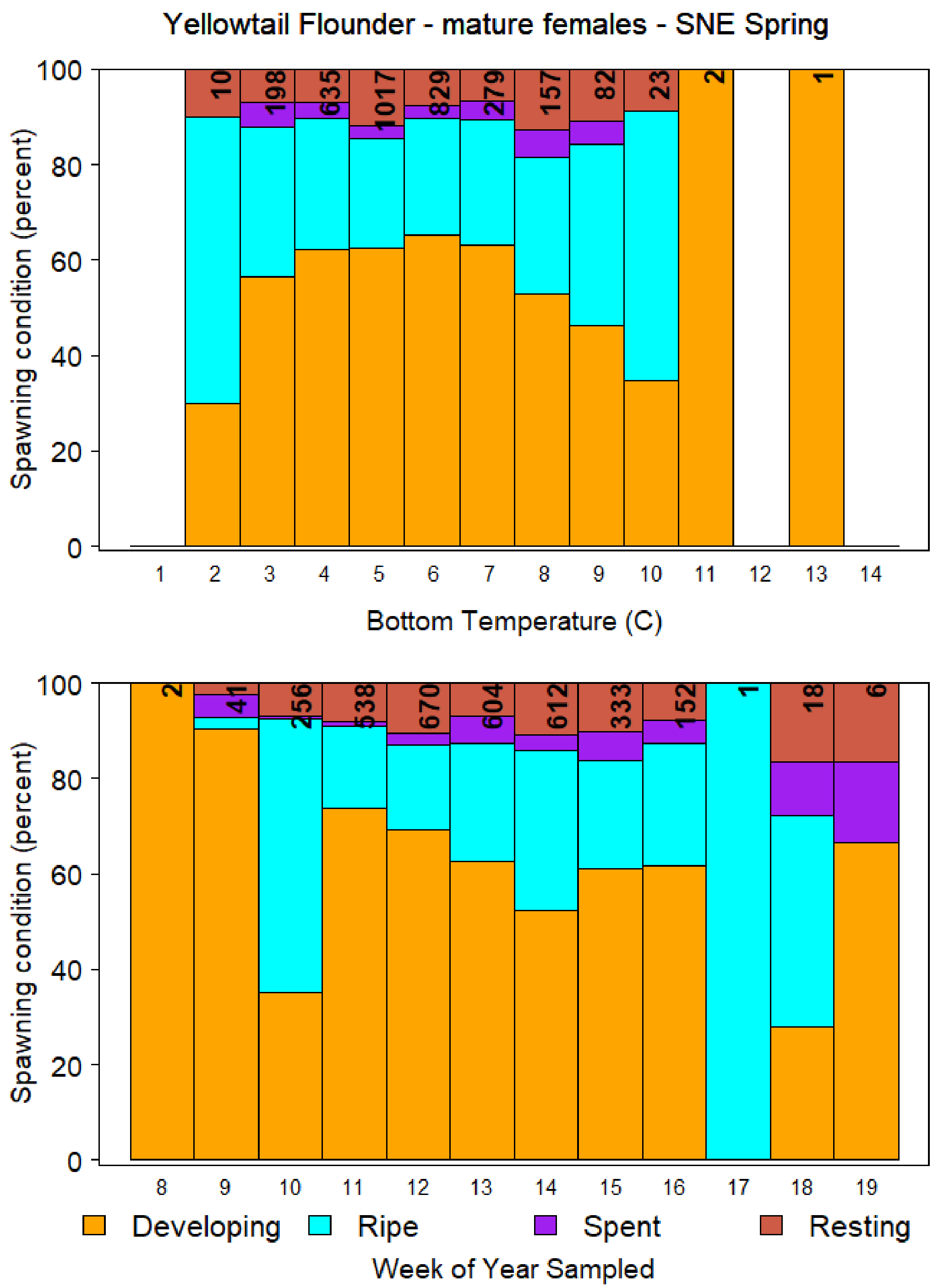

Figure 14. Spawning condition of mature female SNE Yellowtail Flounder sampled during the NEFSC SBTS (1971-2023), binned by bottom temperature and week of year sampled.

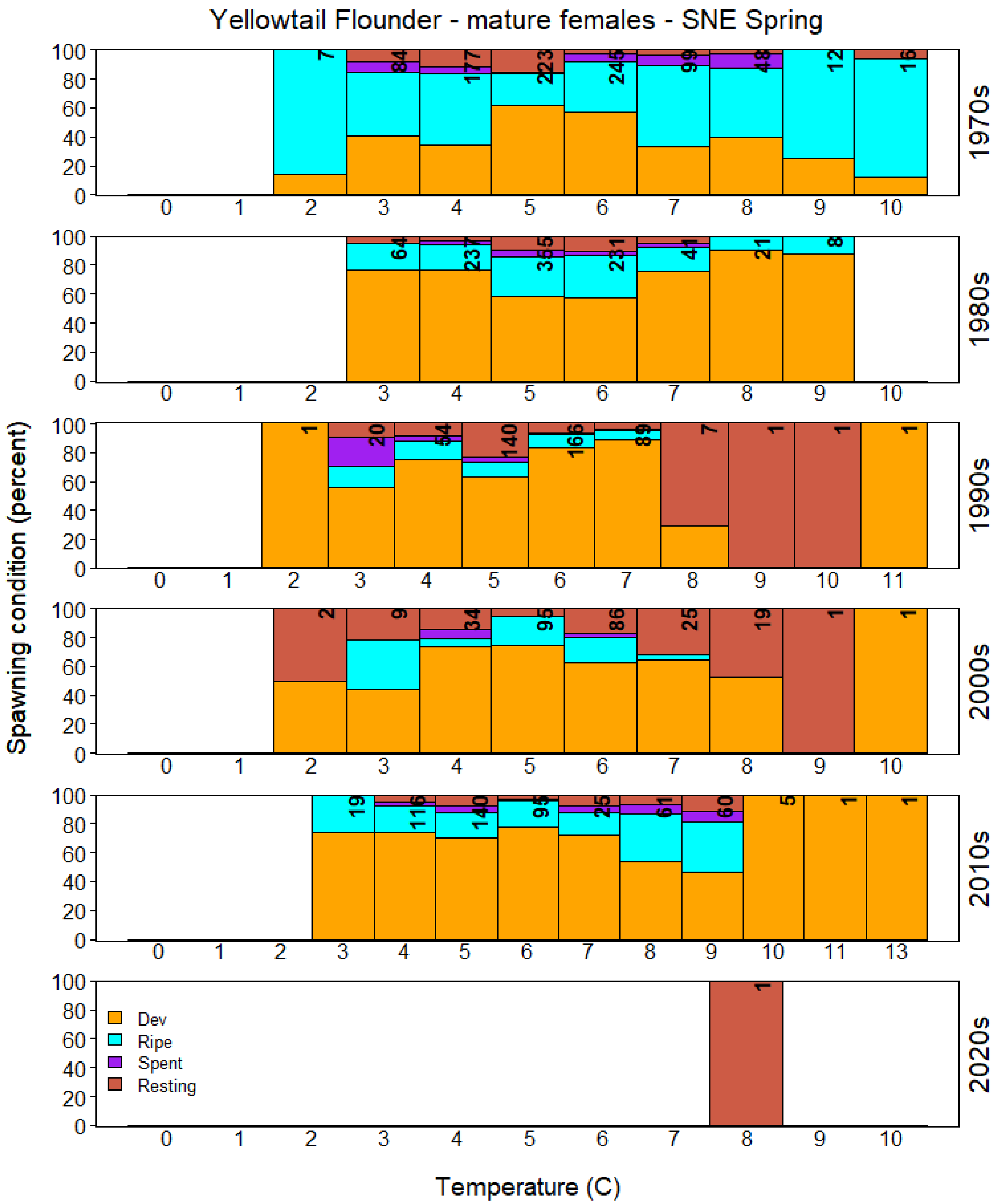

Figure 15. Spawning condition of mature female SNE Yellowtail Flounder sampled during the NEFSC SBTS (1971-2023), binned by bottom temperature and decade.

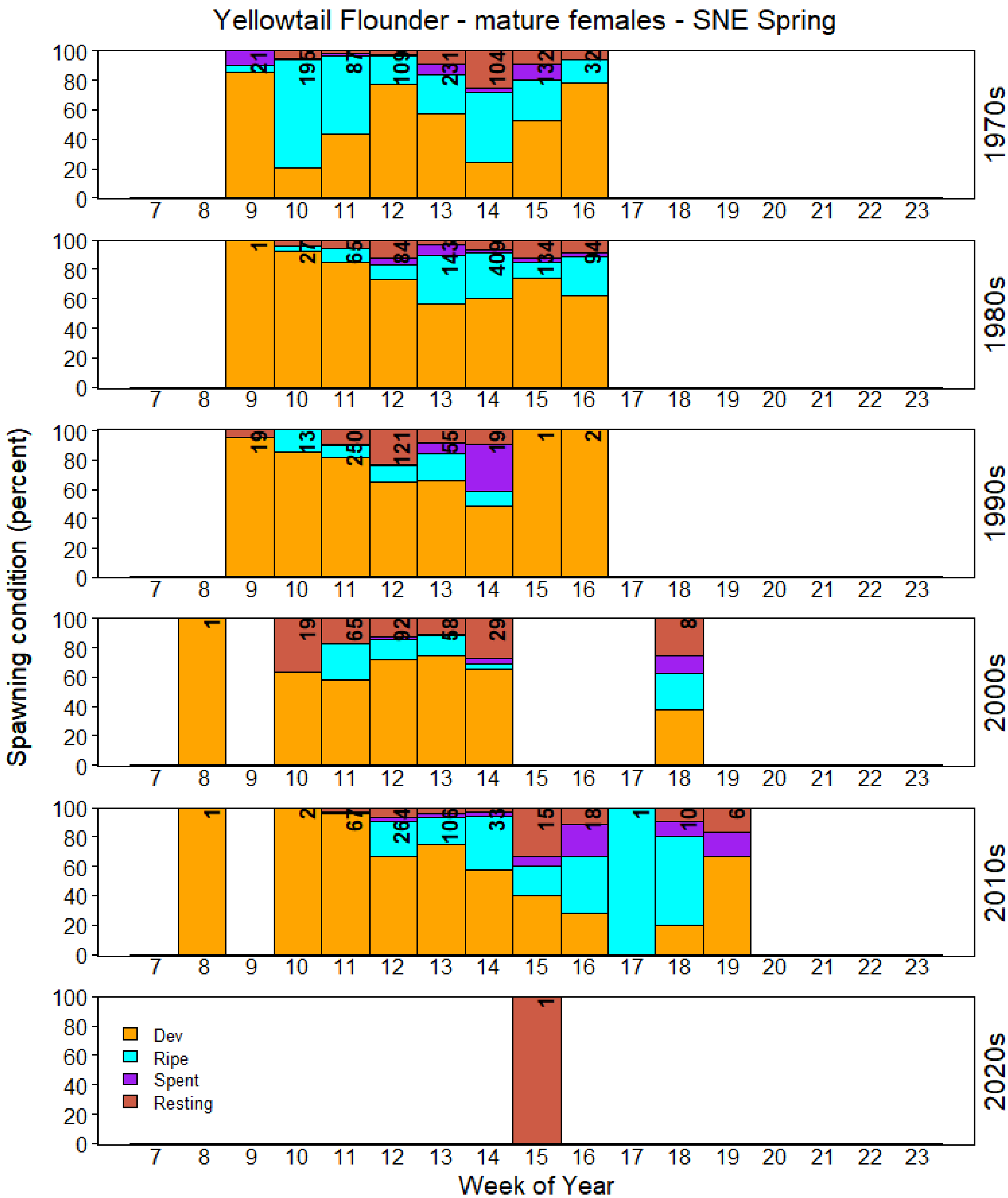

Figure 16. Spawning condition of mature female SNE Yellowtail Flounder sampled during the NEFSC SBTS (1971-2023), binned by week of year sampled and decade.

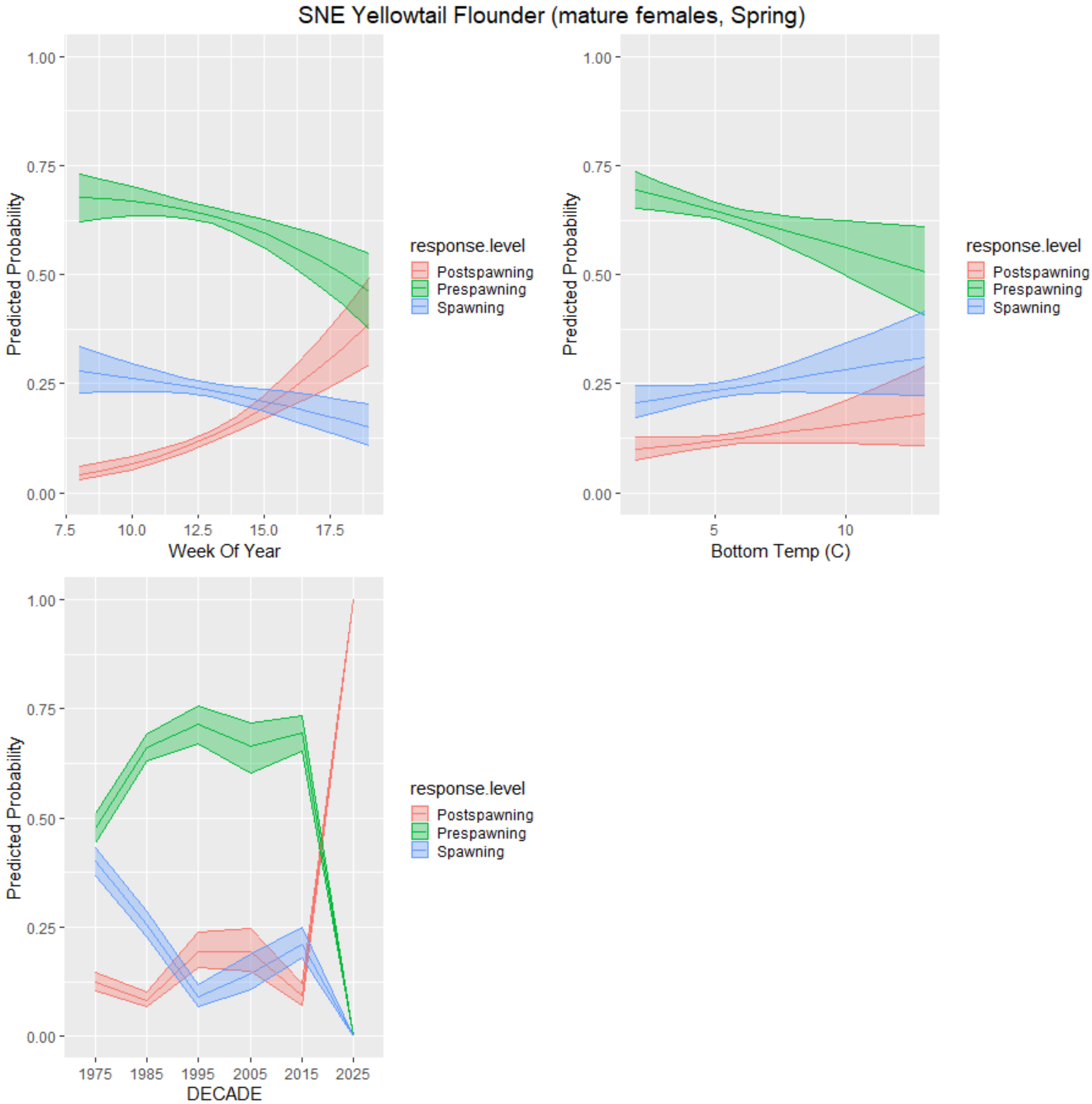

Figure 17. Predicted probabilities of spawning condition for female SNE Yellowtail Flounder from multinomial regression model as a function of week of year, bottom temperature, and decade. Note: 10 year time blocks are plotted by midpoint of each decade, and the last decade is represented by a single individual.

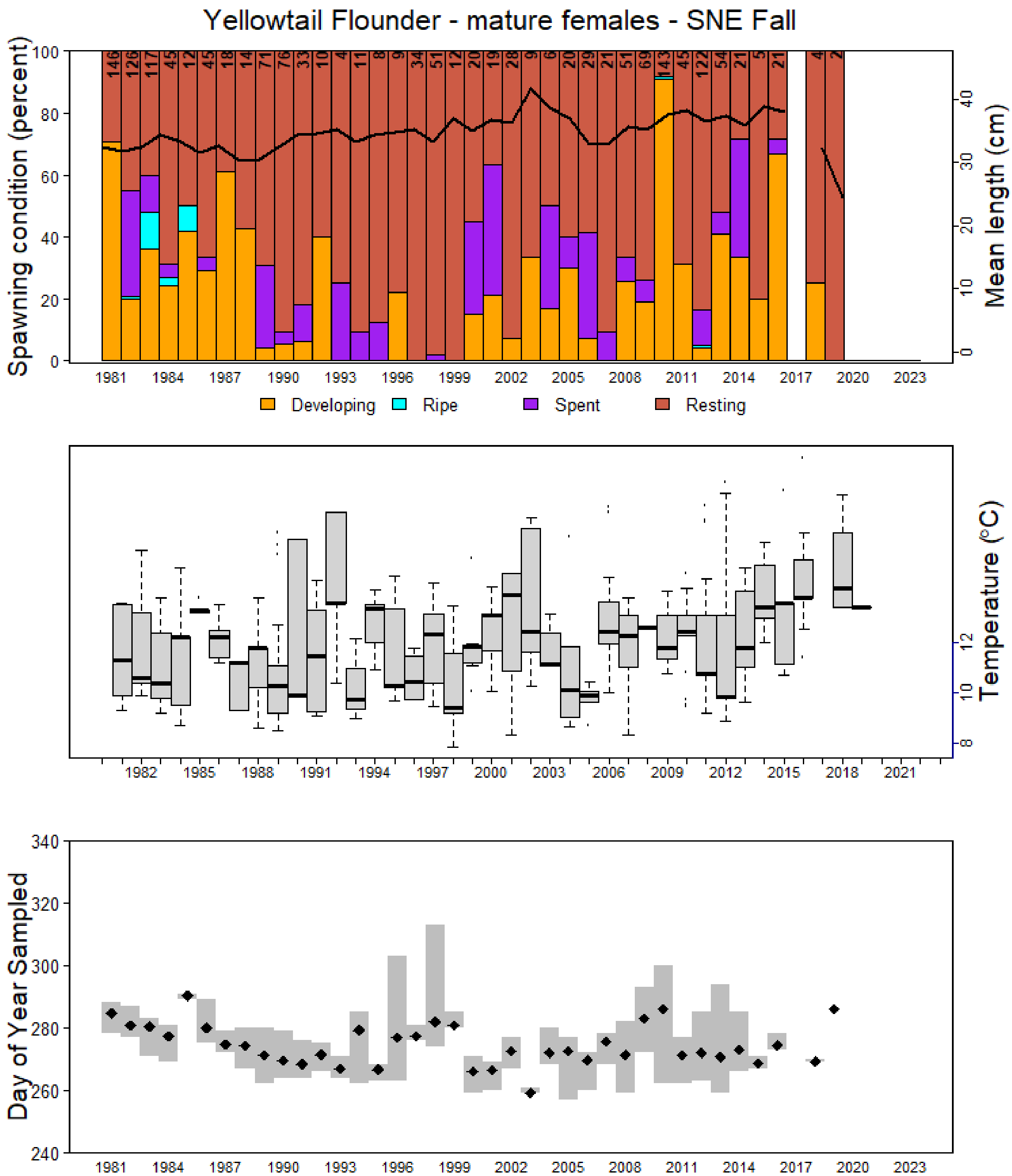

Figure 18. Spawning condition of mature female SNE Yellowtail Flounder sampled during the NEFSC ABTS (1981-2022). The mean size (black line in top panel), and bottom temperatures, and day of year sampled associated with those captures are shown.