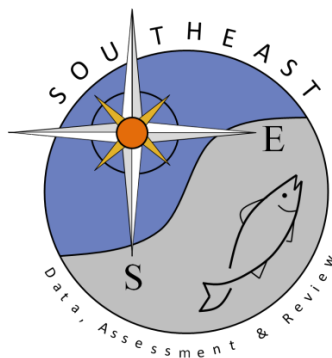


King mackerel (*Scomberomorus cavalla*) egg indices of relative
abundance and their spatial distribution from SEAMAP Fall Plankton Surveys,
2013 to 2025

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King mackerel (*Scomberomorus cavalla*) egg indices of relative abundance and their spatial distribution from SEAMAP Fall Plankton Surveys, 2013 to 2025

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Abstract: *Information on spawning activity can complement traditional data sources used to assess king mackerel (*Scomberomorus cavalla*) in the Gulf of America. We used DNA-barcoded eggs collected with a Continuous Underway Fish Egg Sampler during surveys from 2013 through 2025 to explore the development of fishery-independent indices of relative abundance and evaluate changes in spawning distribution in the eastern Gulf. We estimated annual indices using delta-lognormal and negative binomial models and assessed spatial patterns using egg-weighted centroids and measures of spatial dispersion. King mackerel eggs occurred at 35 of 231 stations (15.2%). All index formulations indicated generally higher spawning activity during the early survey years and lower activity during recent years, including no egg detections in 2022 and 2024. In 2025, egg detections were concentrated within a smaller area and farther northwest than during 2013-2019. The spread of egg locations around their centroid contracted from 237 km during 2013-2019 to 92 km in 2025, whereas the spatial extent of sampling effort remained similar between periods. The egg-weighted centroid also shifted approximately 274 km to the northwest. These results indicate that DNA-barcoded eggs provide useful fishery-independent information on king mackerel reproductive activity and suggest that spawning in the eastern Gulf was reduced and more spatially concentrated in recent survey years. Continued sampling and Gulf-wide barcoding will be necessary to determine whether these patterns persist and to develop an egg-based index suitable for use in stock assessment.*

Introduction

King mackerel (*Scomberomorus cavalla*) support valuable recreational and commercial fisheries throughout the Gulf of America (hereafter *Gulf*). Information on spawning activity can inform stock assessment because reproductive output is reflected in the abundance, occurrence, and distribution of early life stages. Fishery-independent surveys of fish eggs and larvae are important tools for monitoring spawning populations, particularly when conducted consistently over broad spatial and temporal scales (McClatchie et al. 2014). Long-term ichthyoplankton datasets can be used to develop indices of relative abundance

and to characterize spatial patterns in spawning activity, providing complementary information on population dynamics through time.

The Southeast Area Monitoring and Assessment Program (SEAMAP) has conducted ichthyoplankton surveys throughout the Gulf since 1982 and has generated one of the longest continuous records of larval fish abundance in the region (McClatchie et al. 2014). Larval collections from these surveys have been used to describe spawning activity of marine fishes, including king mackerel, and larval indices of relative abundance have been incorporated into multiple stock assessments (e.g., Hanisko et al. 2022, Hanisko et al. 2026). Fish eggs have also been collected via standard SEAMAP bongo-net samples since the inception of the surveys. SEAMAP later added a Continuous Underway Fish Egg Sampler (CUFES; Checkley et al. 1997) to obtain targeted samples of near-surface fish eggs. Whereas larvae can often be identified visually by trained taxonomists, species-level identification of most marine fish eggs is generally not possible using morphological characteristics alone. As a result, egg samples collected during SEAMAP surveys were archived for future study. In 2020, the Spawning Habitat & Early-life Linkages to Fisheries (SHELF) program initiated a collaboration with SEAMAP to apply DNA barcoding techniques to archived and newly collected egg samples (e.g., Stallings et al. 2024; Keel et al. 2025), allowing us to create a species-specific dataset of king mackerel egg occurrence and abundance in the eastern Gulf.

Egg-based observations complement traditional larval indices by providing information closer in space and time to spawning events. Because eggs remain in this developmental stage for a relatively short period (e.g., 36-48 hours) and lack the capacity for directed swimming, they generally experience less transport from their spawning location than larvae. Their occurrence and abundance may therefore provide a more direct indicator of reproductive activity and spawning location than later developmental stages. As a result, DNA-barcoded egg collections offer a unique opportunity to evaluate both temporal variation in spawning output and changes in the spatial distribution of spawning activity within the sampled region.

King mackerel spawning occurs from May through early October in the Gulf, with a peak in September (McEachran et al. 1980; Finucane et al. 1986; Grimes et al. 1990). The SEAMAP Fall Plankton Survey occurs annually from late August through September over the Gulf continental shelf and therefore coincides with peak king mackerel spawning. The objectives of this working paper were to (1) explore the development of fishery-independent indices of relative abundance for king mackerel based on DNA-barcoded eggs collected during selected SEAMAP Fall Plankton Surveys from 2013 through 2025 and (2) evaluate temporal patterns in the spatial distribution of king mackerel eggs within the

survey domain. Together, these analyses evaluate the potential for DNA-barcoded eggs to provide complementary information on king mackerel spawning activity and identify the sampling and analytical needs for developing a more complete egg-based index.

Methodology

Egg Collections

Fish eggs were collected using a CUFES during SEAMAP Fall Plankton Surveys in 2013, 2014, 2019, 2022, and 2024, and during a complementary September survey conducted by SHELF in 2025. The CUFES continuously pumps seawater from approximately 3 m depth while the survey vessel is underway (Checkley et al. 1997). During transits between SEAMAP sampling stations, CUFES samples were collected at 30-minute intervals. Water was passed through a concentrator fitted with a 500- μ m mesh net, and retained material was preserved in 95% ethanol for subsequent laboratory processing and species identification.

Collections were conducted aboard the NOAA ships *Pisces* in 2013 and 2019 and *Gordon Gunter* in 2014, 2022, and 2024. The 2025 collections were conducted aboard the FIO ship *Weatherbird II* (Table 1). Because SHELF is supported through the Florida RESTORE Act Centers of Excellence Program (FLRACEP), which emphasizes waters east of 87.5°W longitude, we restricted all analyses to the eastern Gulf / West Florida Shelf to maintain a common spatial domain among years (Figures 1-6).

CUFES samples were also collected during SEAMAP Fall Plankton Surveys in 2015, 2017, 2018, and 2023, but these surveys had limited coverage within the study domain. We have therefore not yet barcoded samples from those years. No CUFES samples were collected during 2020 or 2021 because of disruptions associated with the COVID-19 pandemic. The 2024 survey was shortened by the approach of Hurricane Helene and covered only the northern portion of the study domain. We retained 2024 as a reference year, evaluated its influence through sensitivity analyses, and excluded it from comparisons requiring consistent spatial coverage.

DNA Barcoding and Species Identification

We processed archived and newly collected fish egg samples through a collaboration between SHELF and SEAMAP. First, we manually isolated individual eggs under a dissecting microscope, extracted DNA from each egg using the HotSHOT protocol, and amplified a fragment of the mitochondrial cytochrome oxidase I (COI) gene using universal fish barcoding primers. We Sanger sequenced successful amplicons and compared the resulting sequences to reference databases including the Barcode of Life Data System

(BOLD) and the GenBank nucleotide (nt) database to assign taxonomic identities. Detailed laboratory and bioinformatic procedures followed those described by Keel et al. (2025).

Frequency of Occurrence and Indices of Relative Abundance

To define a biologically relevant sampling universe, we identified the minimum and maximum water depths and latitudes associated with stations containing king mackerel eggs. We used these values to define the portion of the survey domain over which king mackerel eggs were observed and excluded stations outside this range from subsequent analyses. This procedure retained 231 of 326 candidate stations. The resulting sampling universe encompassed water depths from 13.9 to 88.6 m and latitudes from 25.0004°N to 30.2884°N.

We calculated frequency of occurrence (FOC) as the proportion of stations within the trimmed sampling universe that contained one or more king mackerel eggs. We estimated annual indices of relative abundance using two complementary approaches. First, we implemented a delta-lognormal framework with a binomial submodel for occurrence and a lognormal submodel for positive egg counts. We calculated annual index estimates as the product of the probability of occurrence and expected abundance conditional on occurrence. Second, we fit negative binomial (NB) models to egg-count data from all stations within the trimmed dataset. We evaluated separate formulations that treated year either as a categorical factor or as a continuous variable describing temporal trends. Because the dataset contained many more zero than positive stations, we also fit a zero-inflated negative binomial (ZINB) extension of each NB formulation. We compared AIC values between paired NB and ZINB models to determine whether the additional zero-inflation component improved model fit, and used likelihood-ratio tests as supporting evidence. Because neither model type was clearly favored across the two model formulations for the year term (see Results), we report standardized indices from both NB and ZINB models. We standardized each index series to a mean of one across the years represented within that series.

We quantified the precision of annual indices using coefficients of variation (CV) and an approximate 95% confidence interval, calculated as the standardized index multiplied by $\exp(\pm 1.96 \times CV)$, a log-scale approximation that keeps both bounds positive. For delta-lognormal indices, we combined CVs from the occurrence and positive-catch submodels following the approach of Lo et al. (1992). For NB and ZINB models, we calculated CVs directly from model predictions and their associated standard errors. We combined the nominal annual sample size, number of positive stations, proportion positive, total eggs, and mean count with each model's standardized index, standard error, CV, and confidence interval into a single summary table.

We assessed the delta-lognormal model using standard residual histograms and Q-Q plots. For the NB and ZINB models, we used DHARMA simulation-based scaled residuals (Hartig 2022) rather than raw Pearson residuals, since the latter are difficult to interpret for sparse count data because they tend to be dominated disproportionately by a small number of high-count stations. We generated DHARMA residuals by simulating 1,000 data sets from each fitted model and ranked each observation within its own simulated distribution, producing residuals that were approximately uniform (0,1) under a correctly specified model. We evaluated residual uniformity, dispersion, and outlier frequency using DHARMA's standard Kolmogorov-Smirnov, dispersion, and outlier tests, respectively.

Because the 2024 fall cruise was cut short by an approaching tropical cyclone and covered only the panhandle portion of the shelf, we conducted a sensitivity analysis that excluded 2024 from the abundance indices. We conducted this sensitivity analysis for the NB and ZINB year-as-trend indices (the only formulations in which 2024 contributes a fitted data point) and the raw coefficient of variation of abundance (the only other quantity 2024 affects) with and without that year, to evaluate whether its truncated spatial coverage affected the results.

Spatial Distribution Analysis

We evaluated temporal changes in spawning distribution using two complementary metrics that describe different aspects of spatial structure: centroid location and spatial extent. Centroid analyses quantified shifts in the geographic center of spawning activity, whereas dispersion analyses quantified changes in the spatial spread of egg occurrences around that center.

For each year containing positive detections, we calculated egg-weighted centroid latitude and longitude as abundance-weighted means of station coordinates. We evaluated differences among annual centroids using permutation tests in which we randomly reassigned year labels among positive stations while retaining observed egg counts. We used an omnibus test to evaluate differences among all years with positive detections. Preliminary examination of annual egg distributions suggested that spawning activity may have shifted during 2025 relative to earlier years. To further evaluate this pattern, we conducted a targeted comparison between the 2025 distribution and the pooled distributions observed during 2013, 2014, and 2019. We could not include comparisons with 2022 or 2024 because no king mackerel eggs were observed during those cruises.

We quantified spatial extent using inertia (Woiillez et al. 2007), calculated as the egg-weighted mean squared distance of observations from their annual centroid. Lower inertia values indicate a more spatially concentrated distribution, whereas higher values indicate

a broader distribution. We used permutation tests analogous to those applied to the centroid analyses to compare inertia between the pooled 2013-2019 period and 2025.

To determine whether variation in survey coverage could explain observed changes in egg distributions, we conducted parallel centroid and inertia analyses using all attempted CUFES transects regardless of king mackerel occurrence. We calculated annual sampling-effort centroids from unweighted station locations so that each transect contributed equally to the analysis and calculated sampling inertia using the same procedures applied to egg distributions. We then applied identical permutation tests to the sampling-effort data. Because the 2024 cruise was shortened and covered only the panhandle portion of the shelf, we treated its sampling-effort centroid as a reference point rather than pooling it with fully-sampled years. Note that it was already excluded from the egg distribution analysis since it automatically excludes years with no observed king mackerel eggs. We conducted a sensitivity analysis that compared effort between pooled years that included and excluded 2024 to evaluate whether its truncated coverage affected results. By comparing patterns in egg distributions with those observed for sampling effort, we evaluated whether apparent changes in spawning location or spatial extent reflected biological changes in spawning activity or variation in survey coverage. For visualization purposes, we converted inertia values to equivalent-radius circles centered on annual centroids. These circles represent dispersion around the centroid and should not be interpreted as estimates of occupied habitat area.

We conducted all analyses in the R statistical environment (version 4.6.1; R Core Team 2026). We used the libraries *MASS* for the delta-lognormal models (Venables and Ripley 2002), *glmmTMB* for negative binomial and zero-inflated negative binomial models (Brooks et al. 2017), and *DHARMa* (Hartig 2022) for model diagnostics.

Results and Discussion

We identified king mackerel eggs at 35 of 231 stations (15.2%) within the trimmed sampling universe, demonstrating that archived and newly collected SEAMAP samples provide a useful fishery-independent record of king mackerel spawning activity on the West Florida Shelf. Two primary patterns emerged from analyses of these samples. First, egg-based indices suggested reduced spawning activity in recent years compared to earlier ones, including complete absences of king mackerel eggs during the 2022 and 2024 surveys. Second, the spatial footprint of spawning activity changed substantially through time. Relative to 2013-2019, king mackerel eggs observed in 2025 were concentrated within a smaller geographic area and occupied a different portion of the West Florida Shelf. Together, these results suggest that king mackerel spawning activity in the eastern Gulf has become both less abundant and more spatially restricted in recent years.

Frequency of Occurrence and Indices of Relative Abundance

Frequency of occurrence and all index formulations showed broadly similar temporal patterns (Figure 7). Occurrence and abundance were generally higher during the early years of the survey compared to more recent years. The complete absence of king mackerel eggs during 2022 and 2024 was particularly noteworthy.

We evaluated whether the high frequency of zero observations warranted the use of zero-inflated models by comparing ZINB and standard NB formulations (Table 2). Model comparisons provided little evidence that the additional zero-inflation component improved model performance. The simpler NB model was favored for the year-as-factor formulation ($\Delta\text{AIC} = 2.0$), whereas the ZINB year-as-trend formulation was favored by only 1.3 AIC units. Consistent with these results, standardized indices derived from NB and ZINB models were nearly identical in both magnitude and temporal pattern (Table 3; Figure 7). Collectively, these findings suggest that the simpler NB models adequately described the data and that inferred abundance trends were robust to model structure.

Diagnostic plots indicated adequate model fit for all index formulations (Figures 8-12). DHARMA simulation-based residual analyses provided no evidence of lack of fit for either the NB or ZINB models, with tests of residual uniformity, dispersion, and outliers all yielding non-significant results. Although caution is warranted given the relatively short time series and modest sample sizes, the consistency among index formulations suggests that recent reductions in egg occurrence are unlikely to be artifacts of model structure or standardization approach. Sensitivity analyses further supported this conclusion. Excluding 2024 from the year-as-trend models altered individual annual index values but did not change the overall pattern of higher abundance during the early years of the survey and lower abundance in recent years (Table 4). Similarly, exclusion of 2024 had little effect on the coefficient of variation of raw egg abundance.

The absence of king mackerel eggs during 2022 and 2024 is consistent with broader evidence of reduced abundance and reproductive capacity in recent years. The SEAMAP larval index declined during the terminal years of its time series, although uncertainty prevented distinguishing that decline from the longer-term stable trend (Hanisko et al. 2026). Fishery-dependent indices showed similar patterns. Standardized commercial handline catch rates decreased slightly in recent years after a period of relative stability, and standardized headboat catch rates declined in both the eastern and western Gulf (Pawluk and Thompson 2026; Nuttall 2026). These trends coincided with substantial declines in commercial and recreational landings (Turley et al. 2026). Biological changes may also have reduced reproductive output. Mean length-at-age of older king mackerel, particularly females, declined by approximately 10%, corresponding to an estimated

reduction of more than 30% in total reproductive output (Turley et al. 2026). Increasing Gulf temperatures may have further affected larval survival, adult growth, migration, or spawning distribution, but the relative contributions of fishing, environmental conditions, and changes in stock distribution remain unresolved (Turley et al. 2026). The egg index therefore provides an additional fishery-independent signal consistent with several other data sources suggesting recent changes in the Gulf king mackerel population.

Spatial Distribution Analysis

In addition to changes in abundance, the spatial distribution of king mackerel eggs differed between the early and recent survey years. Egg occurrences during 2013, 2014, and 2019 were broadly distributed across the West Florida Shelf, whereas detections during 2025 were concentrated within a smaller region in the northwestern portion of the sampling domain (Figure 13). Centroid and dispersion analyses characterized differences in the location and spatial extent of these observations (Figure 14).

The egg-weighted centroid shifted 274 km between the pooled 2013–2019 period and 2025 ($p = 0.052$). Although the magnitude of this shift was substantially greater than the corresponding shift in the sampling-effort centroid over the same period (26 km; $p = 0.071$), neither difference was significant at $\alpha = 0.05$. Analyses of SEAMAP larval data show that annual centers of distribution on the West Florida Shelf can also vary considerably when larvae occur at few stations, indicating that centroid estimates based on sparse detections may be sensitive to individual observations.

Changes in spatial extent provided stronger evidence of redistribution. The root mean square distance of egg occurrences from their centroid declined from 237 km during 2013–2019 to 92 km during 2025 ($p = 0.049$). Expressed as an equivalent circular area, this represents an 85% reduction in spatial dispersion, from 176,690 km² to 26,489 km². These values describe the spread of observations around their centroid and do not represent the actual area occupied by eggs or the extent of suitable spawning habitat. In contrast, the dispersion of sampling effort did not differ between periods (234 km versus 244 km; $p = 0.936$), and its equivalent area increased by approximately 9%. Thus, the concentration of egg detections in 2025 cannot be attributed to a comparable contraction in survey coverage.

These findings indicate that the distribution of observed spawning activity was more spatially concentrated in 2025 than during 2013–2019. However, the short and discontinuous time series, the small number of positive transects in 2025, and documented interannual variability in the distribution of larvae on the West Florida Shelf limit broader inference. The observed pattern could represent a persistent contraction or

redistribution of spawning activity, but it could also reflect high interannual variability within a region outside the principal concentration of Gulf-wide spawning. Continued sampling will be necessary to distinguish these alternatives.

Changes in spawning distribution can affect the interpretation of fishery-independent indices by altering the proportion of reproductive activity captured within a fixed survey domain. If spawning becomes concentrated within a smaller portion of the eastern Gulf, reproductive output in this region may also become more sensitive to local environmental conditions and disturbances. Continued monitoring of both abundance and spatial distribution will therefore provide useful context for comparing trends among egg, larval, fishery-dependent, and assessment-derived indicators.

Conclusions

DNA-barcoded fish eggs provide a useful fishery-independent record of king mackerel spawning activity in the eastern Gulf. We detected king mackerel eggs at 15.2% of stations within the analysis domain, similar to the 16% occurrence of larvae reported for the eastern Gulf in the SEAMAP larval index (Hanisko et al. 2026). These detections supported exploratory indices of relative abundance and comparisons of spawning distribution among survey years.

The egg-based indices generally indicated higher spawning activity during the early survey years and lower activity during recent years, including no detections in 2022 or 2024. The spatial distribution of egg detections was also more concentrated in 2025 than during 2013–2019. The equivalent area associated with egg dispersion decreased by approximately 85%, whereas the dispersion of sampling effort remained similar between periods. However, the short and discontinuous time series, incomplete survey coverage in 2024, and small number of positive stations in 2025 limit inference about whether these patterns represent sustained changes in spawning activity or strong interannual variability in the eastern Gulf.

These limitations are particularly important because the eastern Gulf encompasses only part of the Gulf-wide spawning distribution. SEAMAP larval data indicate that king mackerel larvae occur more frequently and at higher abundance in the western Gulf than in the eastern Gulf, suggesting that the principal concentration of spawning activity lies outside the domain analyzed here (Hanisko et al. 2026). Although the spatial limitation of our data may prevent the indices from being suitable for tuning a Gulf-wide assessment model, they provide an independent source of information against which assessment outputs, larval indices, and fishery-dependent indicators can be compared. Agreement among these data

sources would increase confidence in inferred stock trends, whereas discrepancies could identify spatial variation or processes not fully represented by existing assessment inputs.

Future work should extend DNA barcoding to archived and newly collected SEAMAP egg samples throughout U.S. Gulf waters. Gulf-wide coverage, together with more consistent annual sampling and increased processing of available samples, would provide a stronger basis for evaluating whether egg data can support assessment tuning. Expanded barcoding would also provide species-specific fishery-independent information for other federally managed species whose eggs have already been collected through SEAMAP but remain unidentified.

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Table 1. Summary of CUFES sampling effort east of -87.5W in the Gulf of America. The 2024 cruise was cut short due to an approaching tropical cyclone (Hurricane Helene).

Year	Vessel	Number of CUFES samples
2013	NOAA Ship <i>Pisces</i>	316
2014	NOAA Ship <i>Gordon Gunter</i>	269
2019	NOAA Ship <i>Pisces</i>	200
2022	NOAA Ship <i>Gordon Gunter</i>	225
2024	NOAA Ship <i>Gordon Gunter</i>	90
2025	FIO Vessel <i>Weatherbird II</i>	352

Table 2. Comparison of negative binomial (NB) and zero-inflated negative binomial (ZINB) models. ΔAIC was calculated as $\text{AIC}(\text{NB}) - \text{AIC}(\text{ZINB})$, such that positive values favor ZINB and negative values favor NB. Likelihood-ratio test (LRT) p -values are provided as supporting evidence only because the zero-inflation parameter lies on the boundary of the parameter space under the null hypothesis, violating the assumptions of the standard chi-square test.

Comparison	AIC (NB)	AIC (ZINB)	ΔAIC (NB–ZINB)	LRT p -value
Year as factor	325.3	327.2	–2.0	0.846
Year as trend	345.2	344.0	+1.3	0.072

Table 3. Standardized indices of relative abundance for king mackerel based on the trimmed station set. *N* is the annual sample size; *NPos* is the number of positive stations; *PPOS* is the proportion of positive stations; *TotalEggs* is the total number of king mackerel eggs; and *MeanCount* is the mean number of eggs per station. *StdIndex* is the annual index standardized to a mean of one across the years included in each model. *SE* and *CV* are the standard error and coefficient of variation of the standardized index, respectively. *CI low* and *CI high* are the lower and upper bounds of an approximate 95% confidence interval calculated on the log scale as $StdIndex \times \exp(\pm 1.96 \times CV)$. Delta-lognormal, NB year-as-factor, and ZINB year-as-factor models exclude 2022 and 2024 because no eggs were detected in those years; NB and ZINB year-as-trend models include all years.

(Table 3 is on the next page)

Table 3.

Model	Year	N	NPos	PPOS	TotalEggs	MeanCount	StdIndex	SE	CV	CI low	CI high
Delta-lognormal	2013	54	17	0.315	66	1.222	2.065	0.606	0.294	1.162	3.671
Delta-lognormal	2014	41	5	0.122	9	0.220	0.434	0.250	0.576	0.140	1.342
Delta-lognormal	2019	44	8	0.182	42	0.955	1.021	0.456	0.447	0.425	2.451
Delta-lognormal	2025	35	5	0.143	13	0.371	0.480	0.275	0.572	0.156	1.473
NB, year as factor	2013	54	17	0.315	66	1.222	1.766	0.704	0.399	0.809	3.859
NB, year as factor	2014	41	5	0.122	9	0.220	0.317	0.174	0.548	0.108	0.929
NB, year as factor	2019	44	8	0.182	42	0.955	1.380	0.617	0.448	0.574	3.317
NB, year as factor	2025	35	5	0.143	13	0.371	0.537	0.293	0.547	0.184	1.567
ZINB, year as factor	2013	54	17	0.315	66	1.222	1.712	0.714	0.417	0.755	3.879
ZINB, year as factor	2014	41	5	0.122	9	0.220	0.317	0.171	0.540	0.110	0.914
ZINB, year as factor	2019	44	8	0.182	42	0.955	1.428	0.680	0.476	0.562	3.633
ZINB, year as factor	2025	35	5	0.143	13	0.371	0.543	0.294	0.541	0.188	1.568
NB, year as trend	2013	54	17	0.315	66	1.222	1.908	0.707	0.371	0.923	3.945
NB, year as trend	2014	41	5	0.122	9	0.220	1.682	0.558	0.332	0.878	3.224
NB, year as trend	2019	44	8	0.182	42	0.955	0.897	0.222	0.248	0.552	1.457
NB, year as trend	2022	29	0	0.000	0	0.000	0.615	0.196	0.320	0.329	1.150
NB, year as trend	2024	28	0	0.000	0	0.000	0.478	0.190	0.398	0.219	1.043
NB, year as trend	2025	35	5	0.143	13	0.371	0.421	0.186	0.442	0.177	1.002
ZINB, year as trend	2013	54	17	0.315	66	1.222	1.807	0.548	0.303	0.998	3.273
ZINB, year as trend	2014	41	5	0.122	9	0.220	1.665	0.452	0.272	0.978	2.835
ZINB, year as trend	2019	44	8	0.182	42	0.955	0.981	0.292	0.298	0.547	1.758
ZINB, year as trend	2022	29	0	0.000	0	0.000	0.653	0.272	0.417	0.289	1.477
ZINB, year as trend	2024	28	0	0.000	0	0.000	0.483	0.254	0.525	0.172	1.352
ZINB, year as trend	2025	35	5	0.143	13	0.371	0.412	0.242	0.588	0.130	1.304

Table 4. Standardized year-as-trend indices from negative binomial (NB) and zero-inflated negative binomial (ZINB) models fit with and without 2024. The models excluding 2024 provide no estimate for that year; estimates for the remaining years differ because removing 2024 alters the fitted temporal trend.

Model	Year	StdIndex (with 2024)	CV (with 2024)	StdIndex (no 2024)	CV (no 2024)
NB, year as trend	2013	1.908	0.371	1.526	0.353
NB, year as trend	2014	1.682	0.332	1.394	0.315
NB, year as trend	2019	0.897	0.248	0.887	0.257
NB, year as trend	2022	0.615	0.320	0.677	0.346
NB, year as trend	2024	0.478	0.398	—	—
NB, year as trend	2025	0.421	0.442	0.516	0.478
ZINB, year as trend	2013	1.807	0.303	1.488	0.304
ZINB, year as trend	2014	1.665	0.272	1.392	0.273
ZINB, year as trend	2019	0.981	0.298	0.931	0.290
ZINB, year as trend	2022	0.653	0.417	0.692	0.413
ZINB, year as trend	2024	0.483	0.525	—	—
ZINB, year as trend	2025	0.412	0.588	0.497	0.581

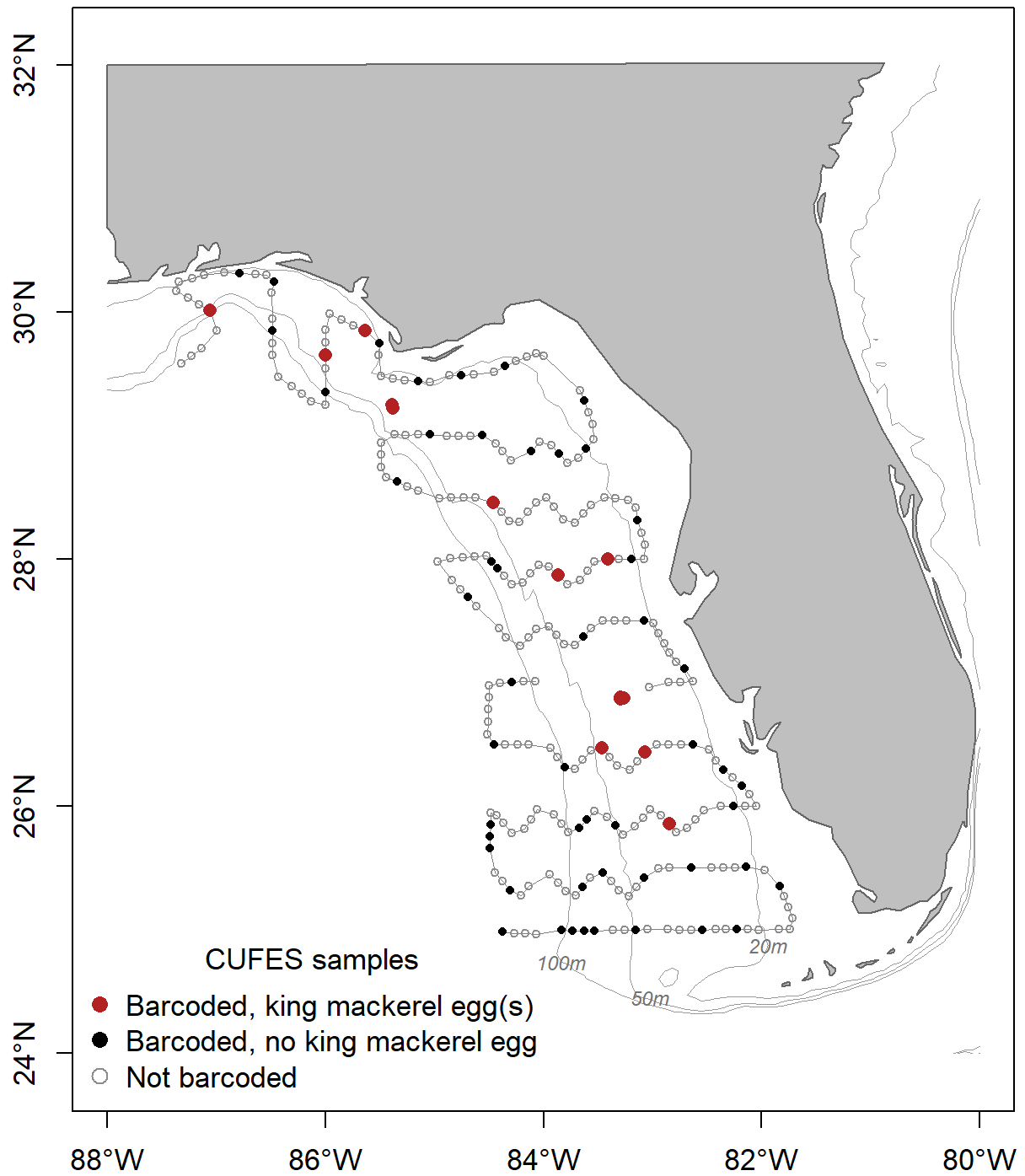


Figure 1. Cruise track displaying CUFES collections made in 2013 and samples that were DNA barcoded.

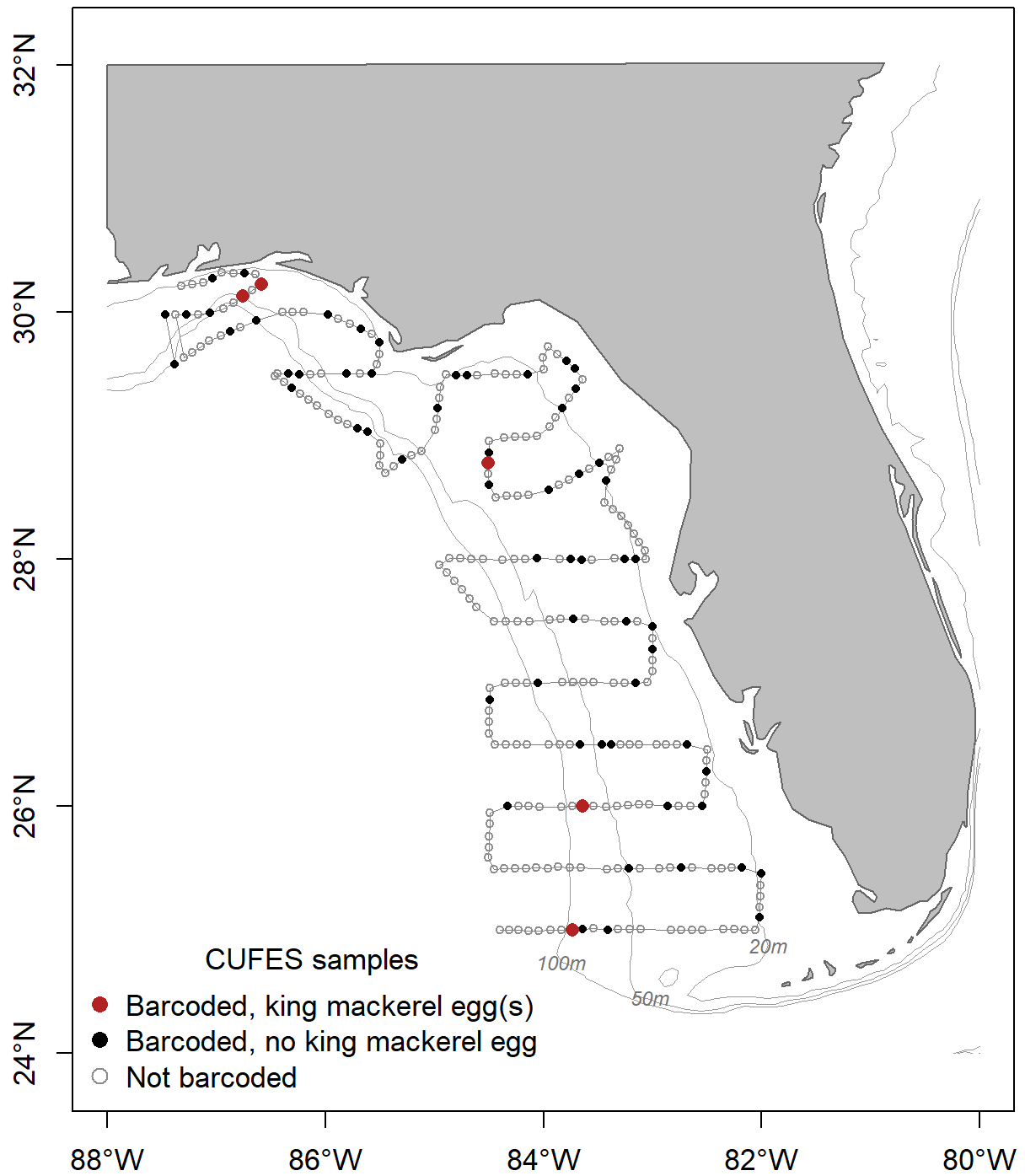


Figure 2. Cruise track displaying CUFES collections made in 2014 and samples that were DNA barcoded.

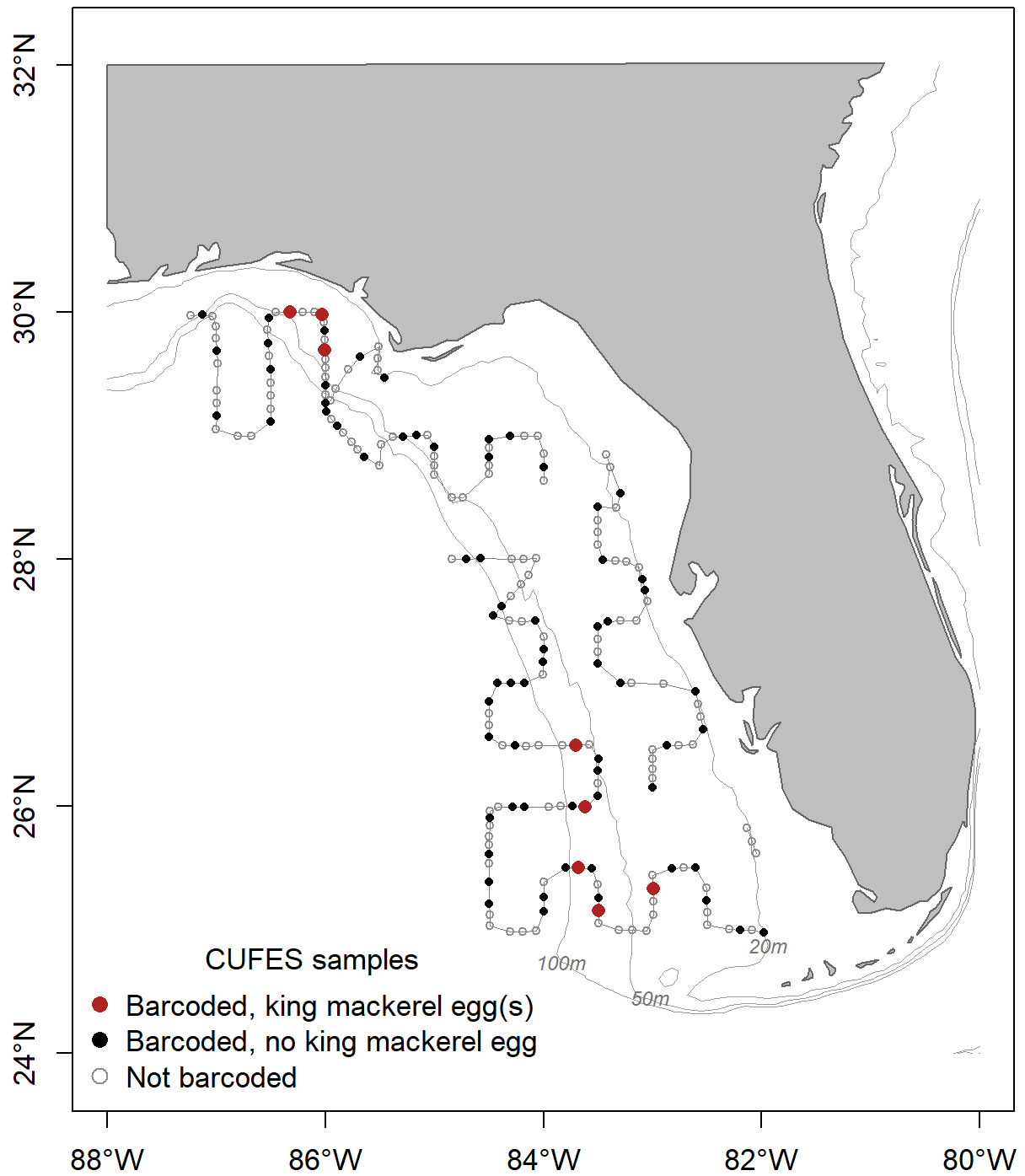


Figure 3. Cruise track displaying CUFES collections made in 2019 and samples that were DNA barcoded.

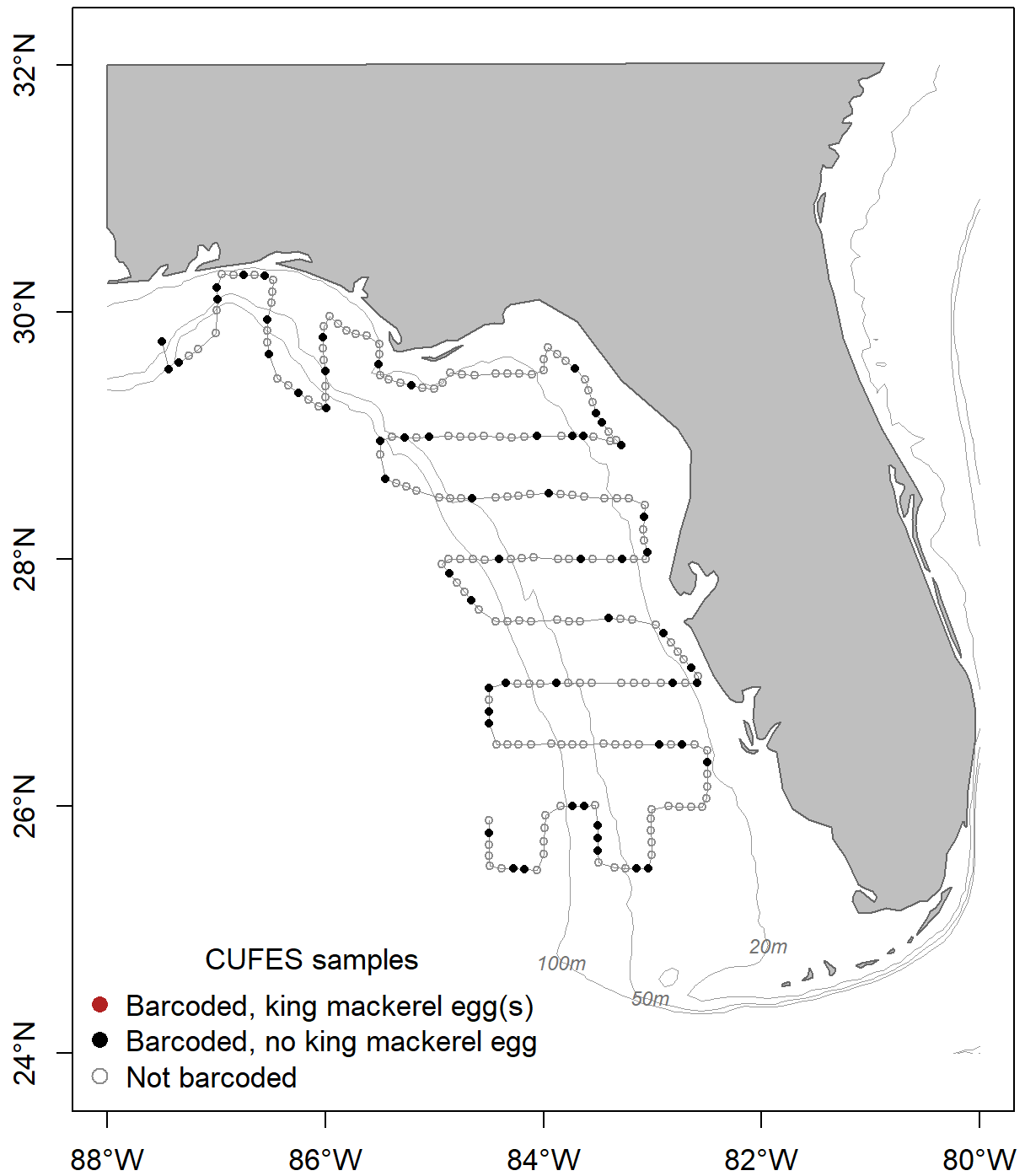


Figure 4. Cruise track displaying CUFES collections made in 2022 and samples that were DNA barcoded.

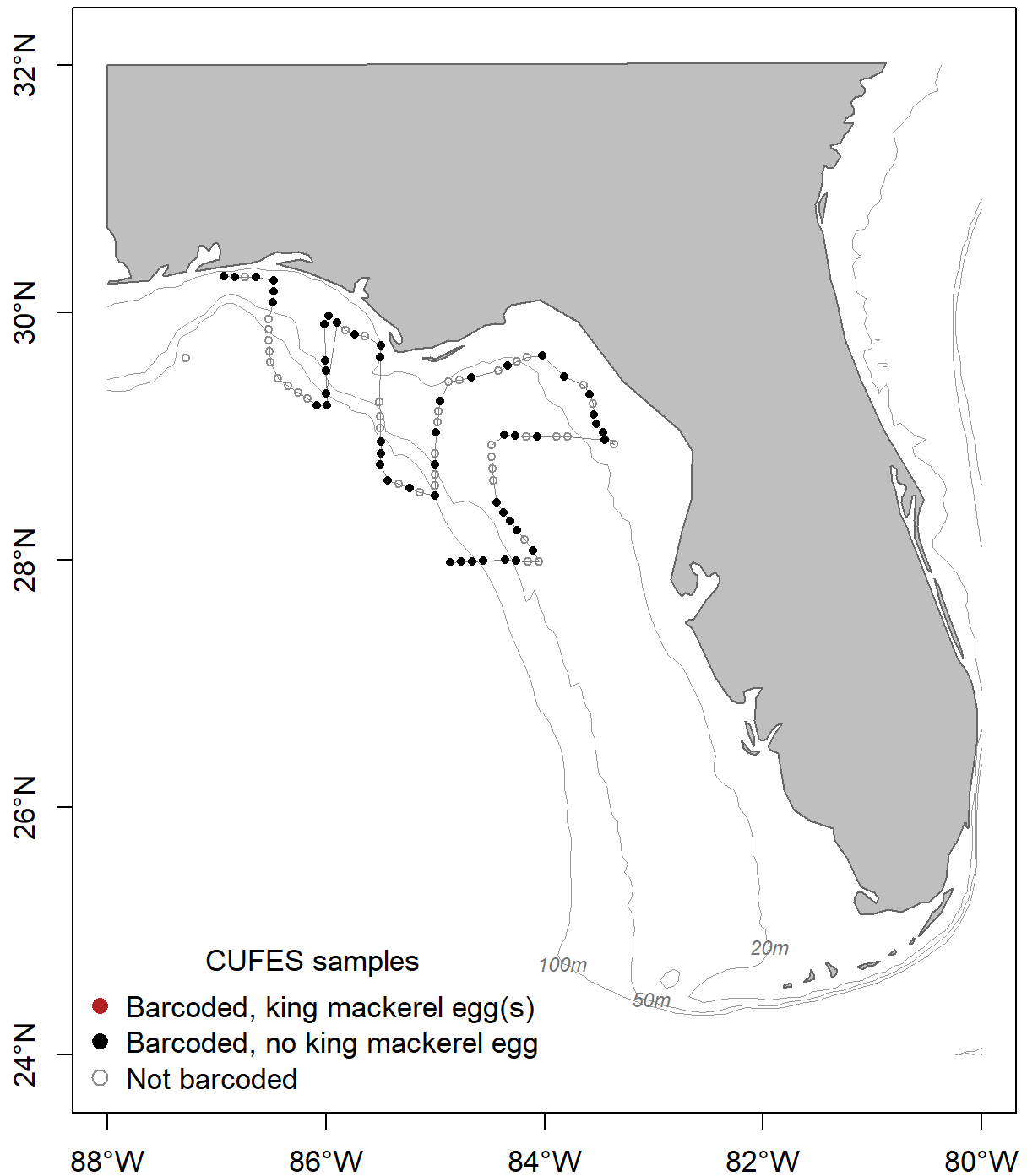


Figure 5. Cruise track displaying CUFES collections made in 2024 and samples that were DNA barcoded. Th 2024 cruise was shortened due to the approach of a tropical cyclone (Helene).

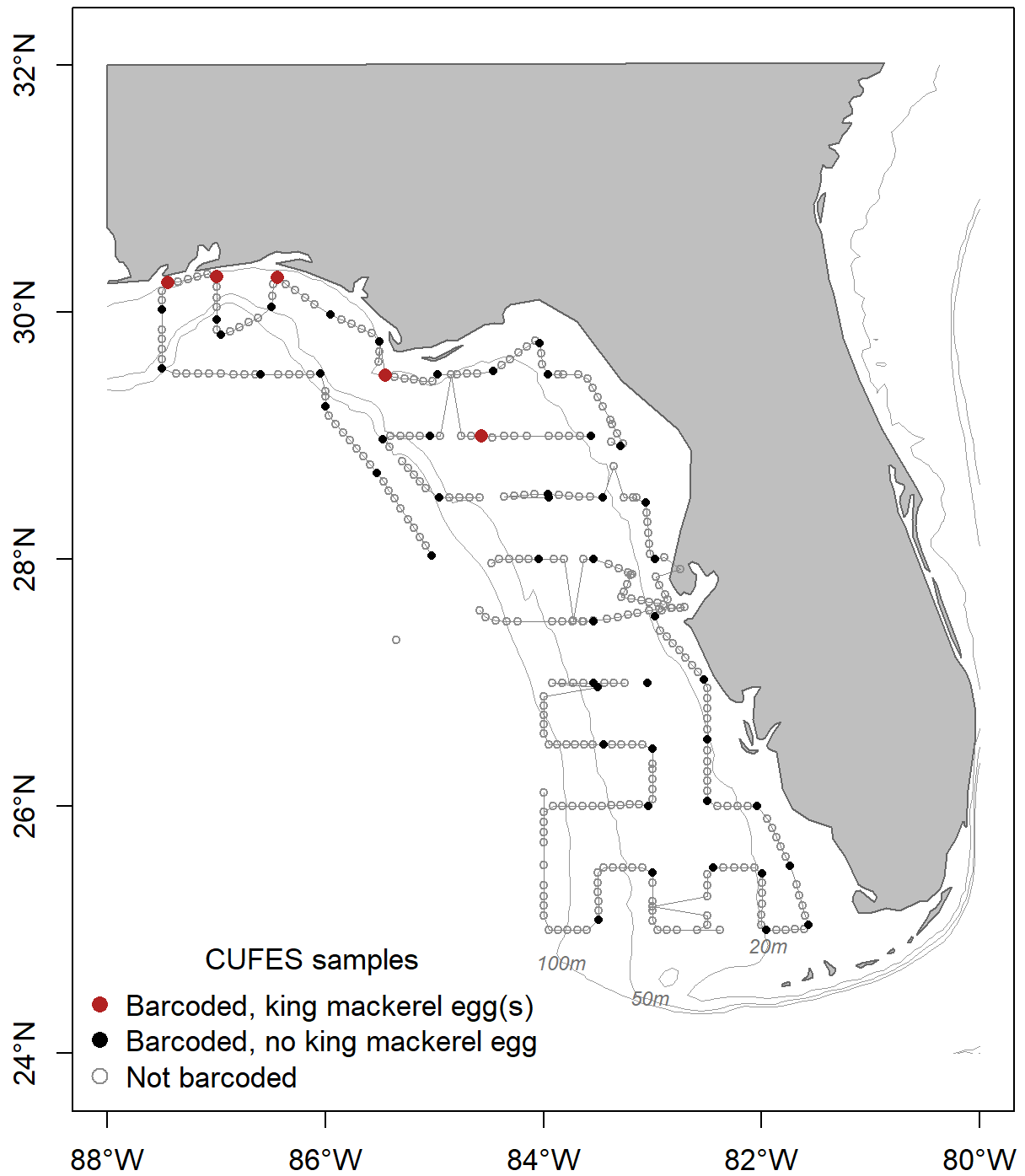


Figure 6. Cruise track displaying CUFES collections made in 2025 and samples that were DNA barcoded.

Figure 7. Standardized indices of relative abundance for king mackerel eggs collected during surveys from 2013 through 2025. Panels show (a) nominal mean egg count, (b) delta-lognormal index, (c) negative binomial (NB) index with year as a categorical factor, (d) zero-inflated negative binomial (ZINB) index with year as a categorical factor, (e) NB index with year as a continuous trend, and (f) ZINB index with year as a continuous trend. Each series was standardized to a mean of one across the years included in the corresponding model. Points show annual estimates, and gray ribbons and vertical bars show approximate 95% confidence intervals. The delta-lognormal and year-as-factor models exclude 2022 and 2024 because no king mackerel eggs were detected in those years; the year-as-trend models include all survey years. Lines connect successive estimates to illustrate temporal patterns and do not imply observations during unsampled years.

(Figure 7 is on the next page)

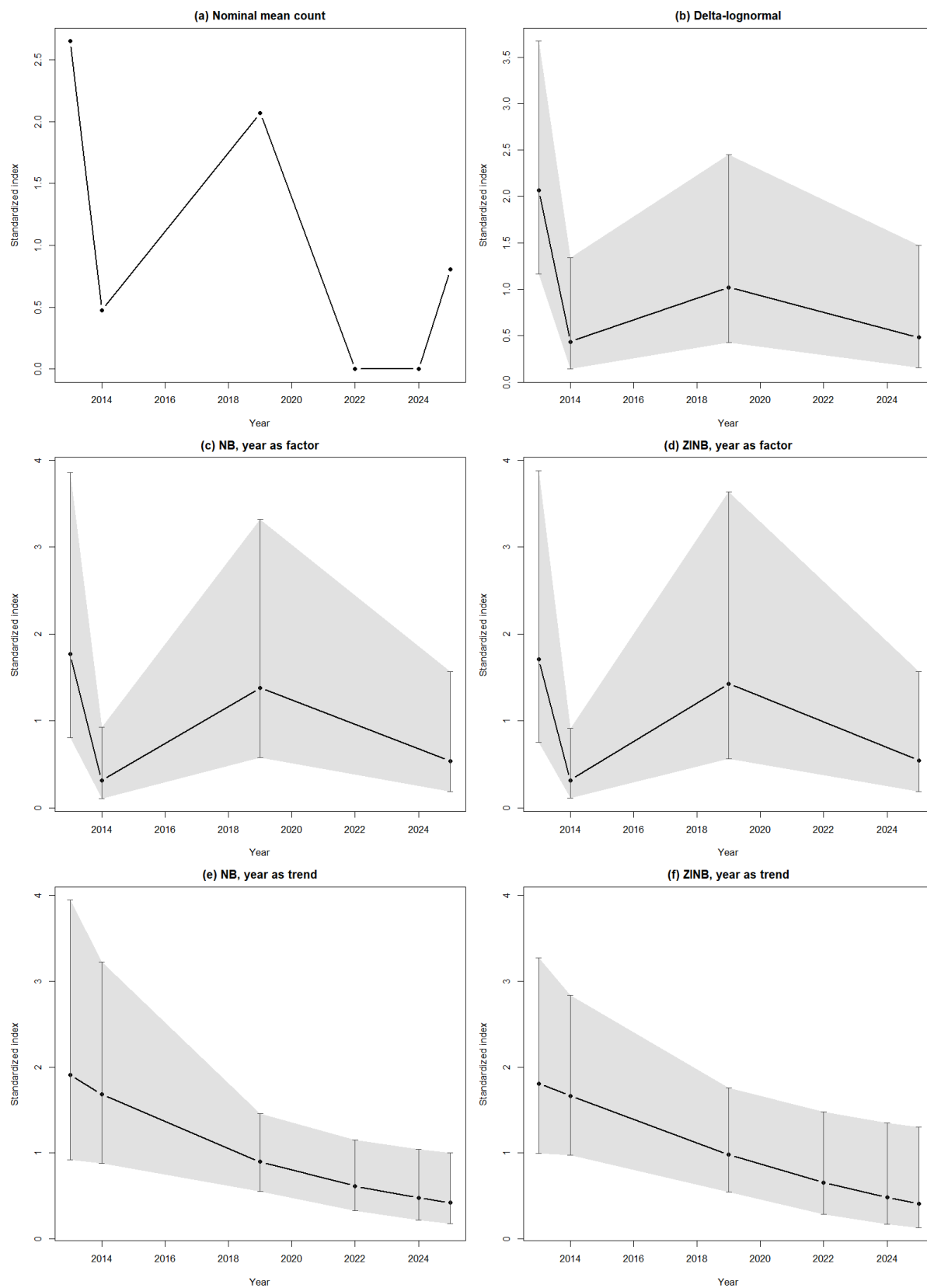


Figure 7.

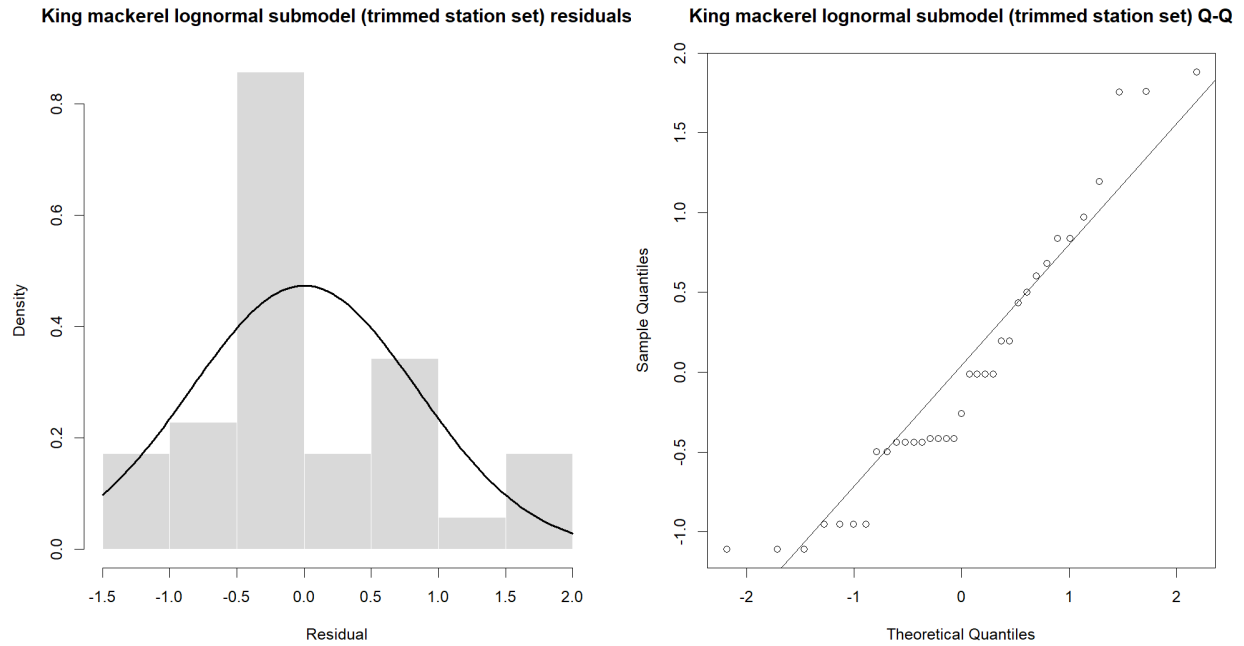


Figure 8. Diagnostic plots for the lognormal positive-catch submodel based on the trimmed station set. The residual histogram with overlaid normal density curve (left) and normal Q-Q plot (right) were used to evaluate the distribution of model residuals.

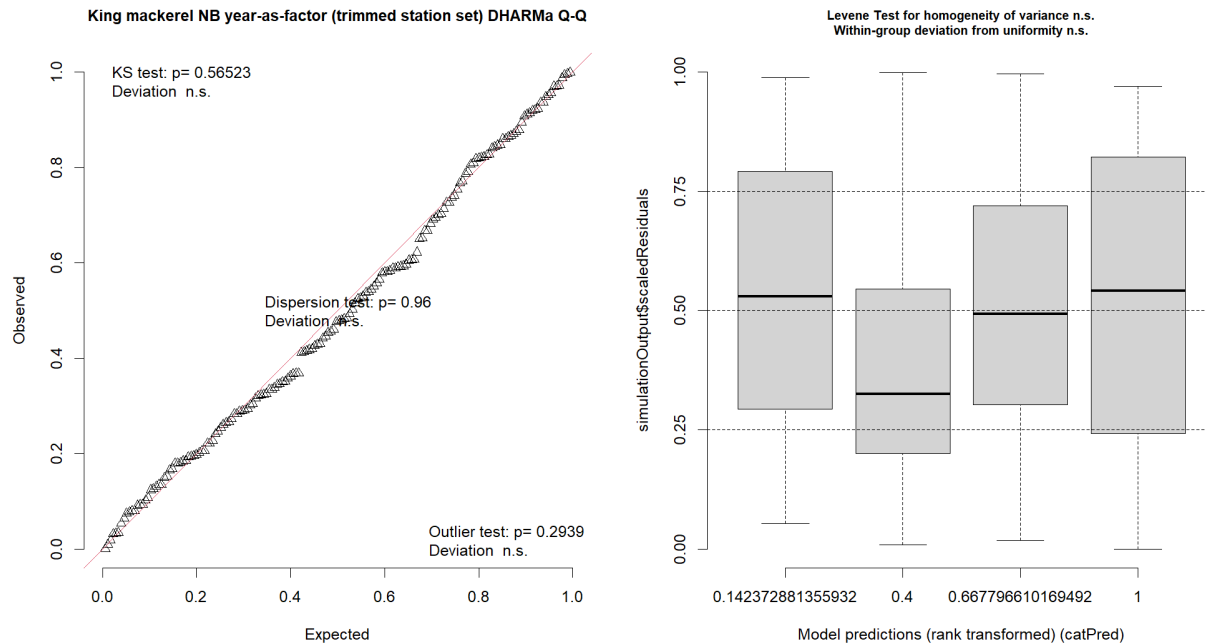


Figure 9. DHARMA simulation-based residual diagnostics for the negative binomial model with year treated as a categorical factor. The quantile-quantile plot (left) evaluates residual uniformity, dispersion, and outliers. Boxplots of scaled residuals across ranked model predictions (right) evaluate variation in the residual distribution across fitted values. None of the diagnostic tests indicated significant lack of fit.

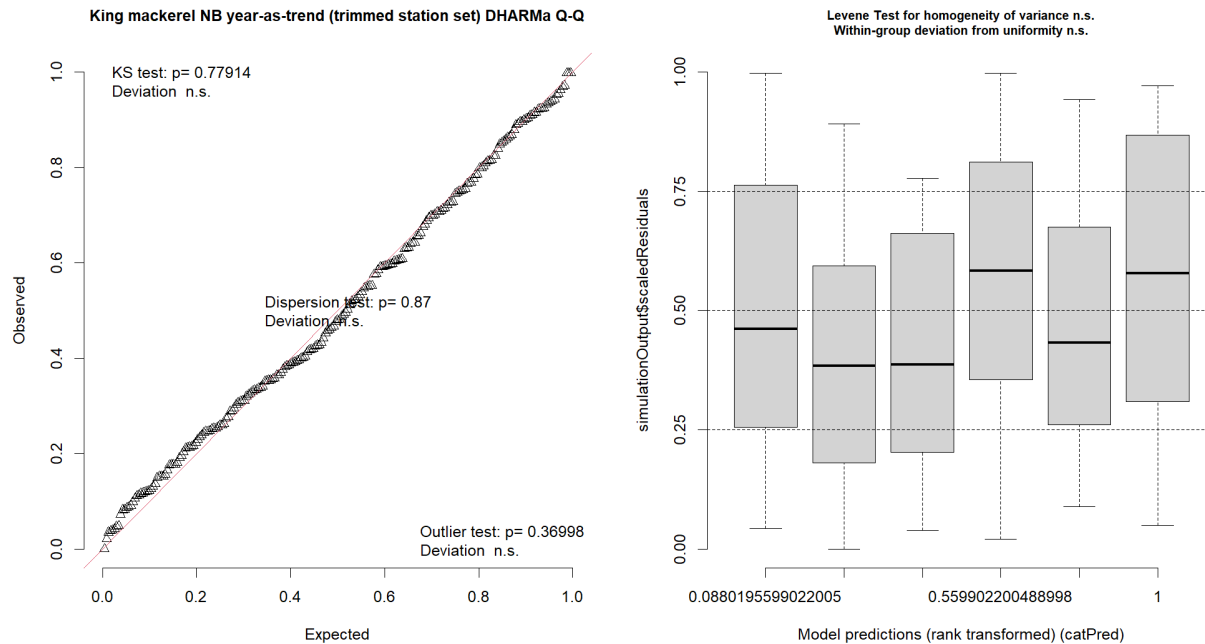


Figure 10. DHARMA simulation-based residual diagnostics for the negative binomial model with year treated as a continuous trend. The quantile-quantile plot (left) evaluates residual uniformity, dispersion, and outliers. Boxplots of scaled residuals across ranked model predictions (right) evaluate variation in the residual distribution across fitted values. None of the diagnostic tests indicated significant lack of fit.

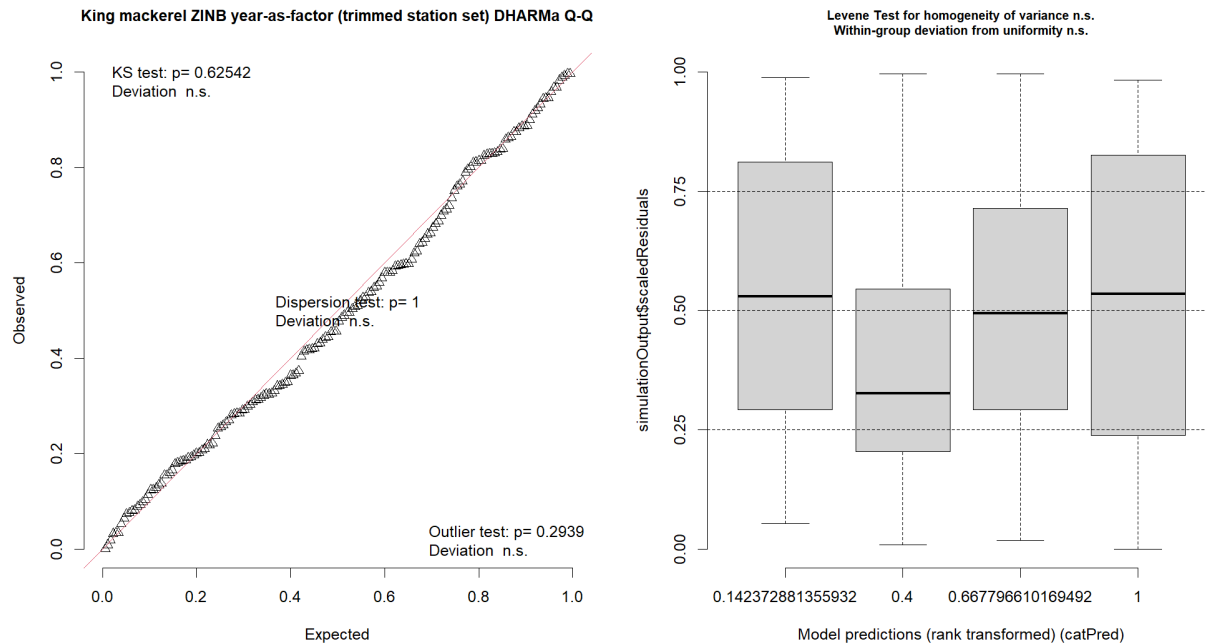


Figure 11. DHARMA simulation-based residual diagnostics for the zero-inflated negative binomial (ZINB) model with year treated as a categorical factor. The quantile-quantile plot (left) evaluates residual uniformity, dispersion, and outliers. Boxplots of scaled residuals across ranked model predictions (right) evaluate variation in the residual distribution across fitted values. None of the diagnostic tests indicated significant lack of fit.

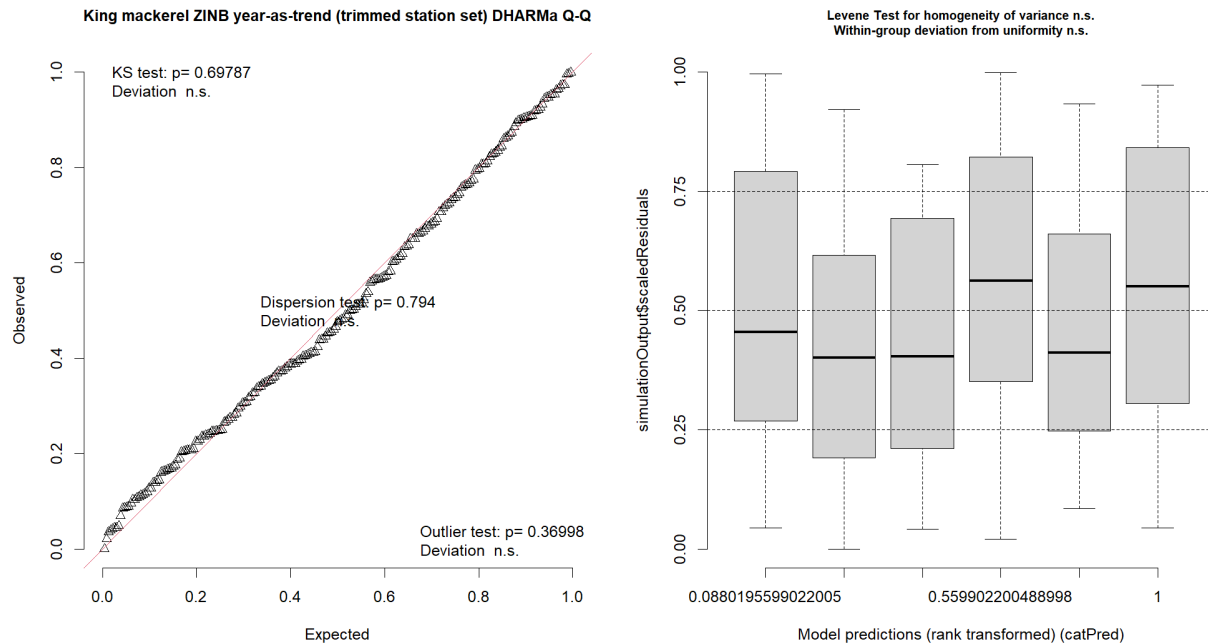


Figure 12. DHARMA simulation-based residual diagnostics for the zero-inflated negative binomial (ZINB) model with year treated as a continuous trend. The quantile-quantile plot (left) evaluates residual uniformity, dispersion, and outliers. Boxplots of scaled residuals across ranked model predictions (right) evaluate variation in the residual distribution across fitted values. None of the diagnostic tests indicated significant lack of fit.

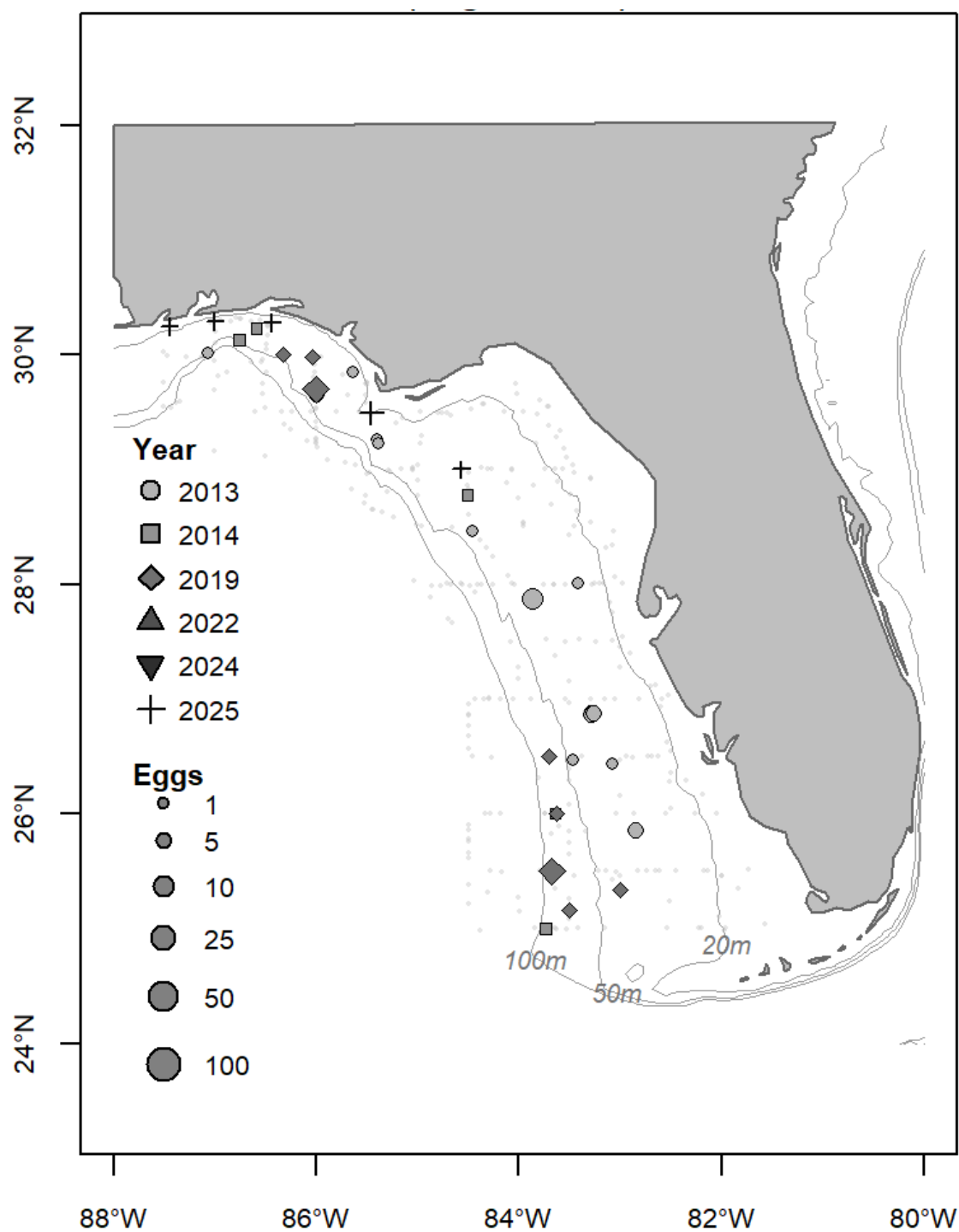


Figure 13. Distributions of king mackerel (*Scomberomorus cavalla*) eggs by year, 2013–2025. Small pale points mark every fall shelf transect with any sequenced taxon that year, for reference against overall station coverage. No king mackerel eggs were detected in 2022 or 2024.

Figure 14. Spatial distribution of king mackerel egg detections and CUFES sampling effort. (a) Annual egg-weighted centroids of stations where king mackerel eggs were detected. (b) Annual unweighted centroids of all CUFES transects, representing the spatial distribution of sampling effort. Crosses denote centroids for the pooled 2013, 2014, and 2019 observations. Solid and dotted circles show spatial dispersion around the pooled and 2025 centroids, respectively, with radii equal to the root mean square distance of positive stations, weighted by egg abundance, in panel (a) and of unweighted CUFES transects in panel (b). Dashed lines connect the pooled and 2025 centroids; labels indicate the distance between them. The 2024 effort centroid is shown for reference but was excluded from comparisons because the survey was shortened by the approach of Hurricane Helene and covered only the northern portion of the study domain. Dispersion circles are statistical summaries and do not represent the area occupied by eggs or the boundaries of suitable spawning habitat.

(Figure 14 is on the next page)

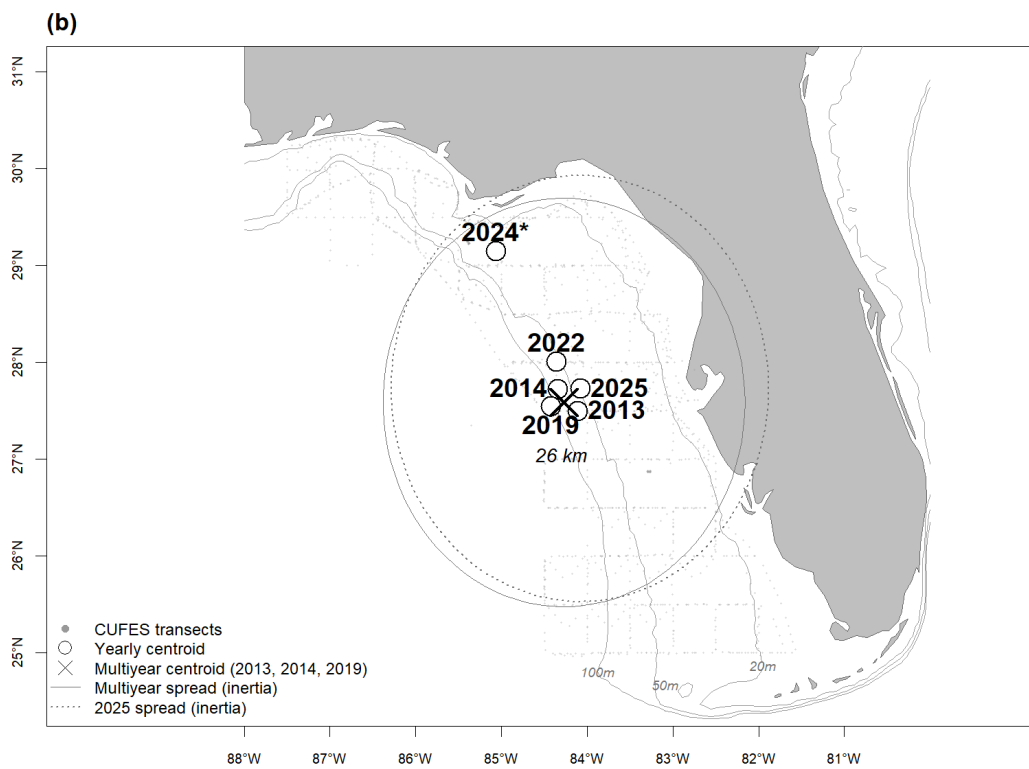
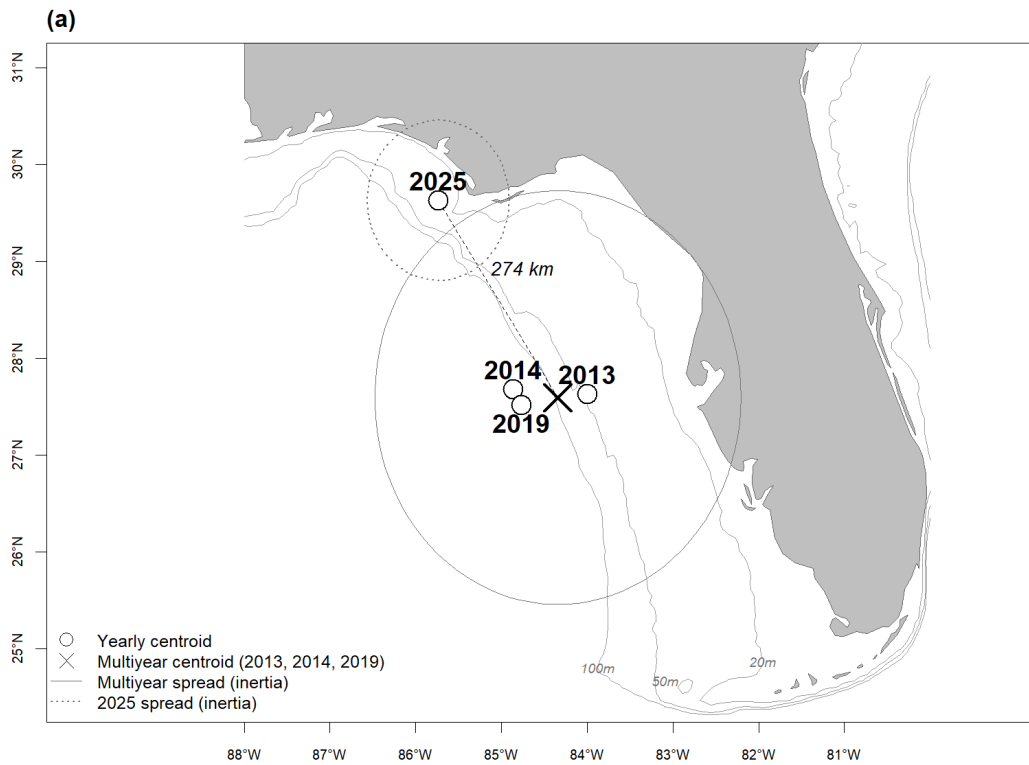


Figure 14.