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Retention and export of planktonic fish eggs in the northeastern Gulf of Mexico

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Abstract

To help determine whether planktonic eggs of fishes on the West Florida Shelf (WFS) are retained locally or exported elsewhere, we collected fish eggs by plankton net from 17 locations (stations) and identified them using DNA barcoding. We then entered the station coordinates into the West Florida Coastal Ocean Model (WFCOM) and simulated the trajectories of the passively drifting eggs over 2 weeks at three depths (surface, midwater, and near bottom). The results indicated there were two groups of trajectories: a nearshore group that tended to be retained and an offshore group that tended toward export and potential long-distance dispersal. We also found evidence of a relationship between retention and higher fish-egg abundance; nearshore stations were associated with higher fish-egg abundances and higher retention. We suggest this is the result of (1) increased spawning in high-retention areas, (2) increased drift convergence in high-retention areas, or both processes acting together. Community analysis using SIMPROF indicated the presence of a depth-related (retention-related) difference in species assemblages. Fish-egg species were also categorized as pelagics or non-pelagics; there was no evidence of pelagic species being more likely to be exported.

KEYWORDS
aberrant drift, community structure, habitat connectivity, hydrodynamic model, Loop Current, metapopulation, self-recruitment

1 | INTRODUCTION

Ecosystem connectivity and modularity influence the community structure and perturbation resilience of connected ecosystems, and these features are, in turn, influenced by the transport of the planktonic early stages of marine organisms among connected ecosystems (Paris et al., 2020). In fishes, the passive, planktonic eggs and early (preflexion-stage) larvae are most likely to be dispersed by ocean currents as they drift during their pelagic phases. Larval dispersal can result in two main outcomes: export or retention. Export is the movement of eggs and larvae away from a region of interest (Jones et al., 2009), which can result in either aberrant drift or habitat connectivity (Jones et al., 2009). Aberrant drift involves the dispersal of eggs and larvae away from essential larval and juvenile habitat in a manner that likely results in mortality (Faillettaz et al., 2018; Hjort, 1926). Habitat connectivity is the movement of a reproductive cohort (i.e., progeny) to viable habitats used by successive life stages; it is part of the broader concept of ontogenetic habitat shift (Cowen &

Sponaugle, 2009). In contrast, when fish eggs and larvae are found to both originate and remain within a region of interest, the process is referred to as retention or self-recruitment (Cowen & Sponaugle, 2009; Jones et al., 2009). Dynamic coastal processes such as frontal convergences or sub-mesoscale eddies (Bassin et al., 2005; Sponaugle et al., 2005) can have direct and indirect influences on fish egg and larval retention and connectivity. These dynamic coastal processes are thus responsible for influencing egg transport, larval growth, and survival.

Aside from being buoyant, planktonic fish eggs are considered to be passive particles (Paris & Cowen, 2004). The buoyancy of pelagic fish eggs and early larvae depends on several internal characteristics such as lipid content in oil globules or the large quantities of aqueous fluid in the egg (Craik & Harvey, 1987). In addition to buoyancy and passive drift, active swimming by larvae, either individually or in schools, can modulate larval trajectories (Ben-Tzvi et al., 2012; Berenshtein et al., 2018; Irisson et al., 2015; Nelson & Grubesic, 2018); the entire time period during which eggs and larvae exist in the water column is known as the pelagic larval duration, or PLD (Kendall et al., 2013). The PLD differs among species, ranging from days to months, typically ending when the larvae transition to structural habitats (non-pelagic species) or metamorphose into schooling juveniles (pelagic species) (Shanks, 2009). Most reef-associated fishes in the Gulf of Mexico (GoM) have a relatively short PLD. For example, the Red Snapper (*Lutjanus campechanus*) egg incubation period is 20 to 27 h before hatching into larvae. The total PLD for this species is approximately 26 days (Hernandez et al., 2016). More generally, the average PLD for marine fishes is 36 days (Fuiman & Werner, 2009).

Flexion is a development stage or process during which fish larvae go through morphological transformations that involve the flexion of the notochord and the development of the caudal fin, which is coincident with behavioral changes that involve swimming and increased schooling. In the postflexion larval stage, fish change morphologically and become yet better able to swim. Multiple studies have published evidence of rapid developmental changes that occur in association with reaching the postflexion larval stage. To name a few, these changes include allometric growth (i.e., changes in morphometry), changes in swimming mode, inflation of the swim bladder, the onset of schooling behavior, increased vertical migration, advances in internal organ growth, or changes in feeding behavior (Somarakis & Nikolioudakis, 2010).

To investigate the movements of eggs and larvae, a variety of techniques are now being employed such as larval tagging (i.e., incorporation of isotopes or chemicals by the embryo from the mothers or via incubation), DNA sequencing (i.e., genetic analysis leading to identification of species), or biophysical circulation models (i.e., numerical simulation of behavior-influenced trajectories) (Jones et al., 2009; Karnauskas et al., 2022; Thorrold et al., 2002). Weisberg et al. (2014) used a numerical circulation model, the West Florida Coastal Ocean Model (WFCOM), which is similar to the one employed for the Deepwater Horizon (DWH) oil spill (e.g., Weisberg et al., 2017), to explain the movement of Gag (*Mycteroperca microlepis*) larvae on the West Florida Shelf (WFS). The authors compared surface and near-bottom trajectories to determine which pathway led to known locations of pre-settlement fish and how the larvae were transported to settlement sites. This study found that Gag most likely use bottom currents to move from spawning locations to juvenile habitats. This approach has also been used in other regions of the world. George et al. (2011) investigated the larval dispersal of fish in the Gulf of Kachchh (west coast of India) using a two-dimensional numerical model and confirmed the retention of fish larvae in that region. Integrating biological features into ocean models is becoming more common and can be expanded and used for predicting fish-egg and early-larval trajectories. The overall goal of this work was to investigate the movement of fish eggs and larvae on the WFS using high-resolution hydrodynamic models (Aiken et al., 2007; Cowen et al., 2006; James et al., 2002). Advances in DNA barcoding have allowed monitoring of planktonic fish eggs that previously could not be reliably identified (e.g., Burghart et al., 2014; Burrows et al., 2018). As part of the Florida Restore Act Centers of Excellence Program (FLRACEP), planktonic fish-egg distributions on the entire WFS are being monitored annually for a period of up to 15 years or longer.

Egg distributions observed by the FLRACEP egg monitoring program can potentially be modified by subsequent, variable egg export or retention on the WFS after spawning (Karnauskas et al., 2022), which could interfere with the use of data from the egg survey as a local fisheries management index. If egg production is a rough proxy for spawning stock biomass, variable loss of eggs through export would interfere with interpretation of the egg abundance time series, especially because loss of eggs (via export) is likely to be highly variable from year to year (Walsh et al., 2009). Thus, the purpose of the present effort was to develop preliminary methods for investigating egg retention on the WFS. More specifically, the primary objective was to determine whether planktonic eggs are being retained on the WFS or exported away from it by local flow patterns.

We used numerical models to simulate the drift of planktonic fish eggs and early larvae from 17 locations (stations) on the WFS. DNA barcoding of fish eggs from these locations was used to assign taxonomic identities to the simulated trajectories. Although detection of the drifting eggs of a given species provided definitive evidence that spawning had occurred, advection caused an unknown spatial offset between spawning and our subsequent collection of the drifting eggs. The reason for estimating the trajectories of different taxa was to determine whether certain types of fish were more likely to have their eggs retained on the WFS than others. For example, it might be expected that pelagic species such as tunas would be less adapted to retention than reef-associated fishes such as snappers.

The null hypotheses for this study were:

1. Fish eggs and larvae on the WFS are not likely to be exported. This is relevant to population connectivity between the WFS and other areas.
2. Sites with higher fish-egg abundance are not more likely to result in retention than sites with lower egg abundance. This relates to the idea that fish may spawn more heavily in areas where their

eggs are more likely to be retained or (conversely) in areas where eggs are likely to be exported.

3. Eggs and larvae of pelagic fish species are not more likely to be exported away from the WFS than eggs and larvae of non-pelagic species. The idea here is that non-pelagic fishes may have undergone more selection for retention of eggs near structural habitats used by post-settlement stages.
4. There is no depth-related community structure in fish eggs on the WFS. This hypothesis is related to the idea that deep-ocean epipelagic species (e.g., tunas) may only spawn near the deep-ocean epipelagic zone.

2 | MATERIALS AND METHODS

2.1 | Study domain: the WFS

The WFS is a large continental shelf in the eastern GoM with a width from 25 to 250 km and a length of about 900 km. It contains a variety of bottom features, including open sand, hard bottoms, and low-relief, exposed rock ledges, and paleoshorelines (Hine & Locker, 2011).

The Loop Current (Figure 1) is a large-scale circulation feature that dominates the eastern GoM beyond the continental shelf (Hurlburt & Thompson, 1980; Liu, Weisberg,, Vignudelli, et al., 2016; Ohlmann & Niiler, 2005; Romanou et al., 2004). It is a deep ocean current that enters the GoM through the Yucatan Channel, flows northward to various extents at various times, and exits through the Florida Straits between Cuba and the Florida Keys (Nickerson et al., 2022; Vukovich et al., 1979; Weisberg, & Liu, 2017). The Loop Current does not pass directly over the WFS, yet it influences the circulation on the WFS (Hine & Locker, 2011; Liu, Weisberg, Lenes, et al., 2016; Weisberg et al., 2005; Weisberg & He, 2003).

The circulation on the WFS itself is driven by multiple physical features. It is mainly influenced by local winds and also by offshore forcing through the interaction between the Loop Current and the shelf slope (Weisberg et al., 2005; Weisberg & Liu, 2022). The long-term mean circulation pattern is upwelling with seasonal and interannual variability (Liu & Weisberg, 2012; Weisberg et al., 2009). Additionally, in shallow waters, the circulation in the inner shelf is mainly driven by wind forcing and is more subject to seasonal variations. More specifically, in the summer, the southerly winds drive the currents in shallow water and create a downwelling-favorable system. From fall to spring, the northerly winds generate an upwelling system (Liu & Weisberg, 2005, 2012). The outer-shelf circulation is mainly influenced by the loop current, its eddies, and their interaction with the shelf slope; it is less likely to vary seasonally and more likely to vary with the flow variations of the Loop Current (Liu et al., 2016; Weisberg & He, 2003).

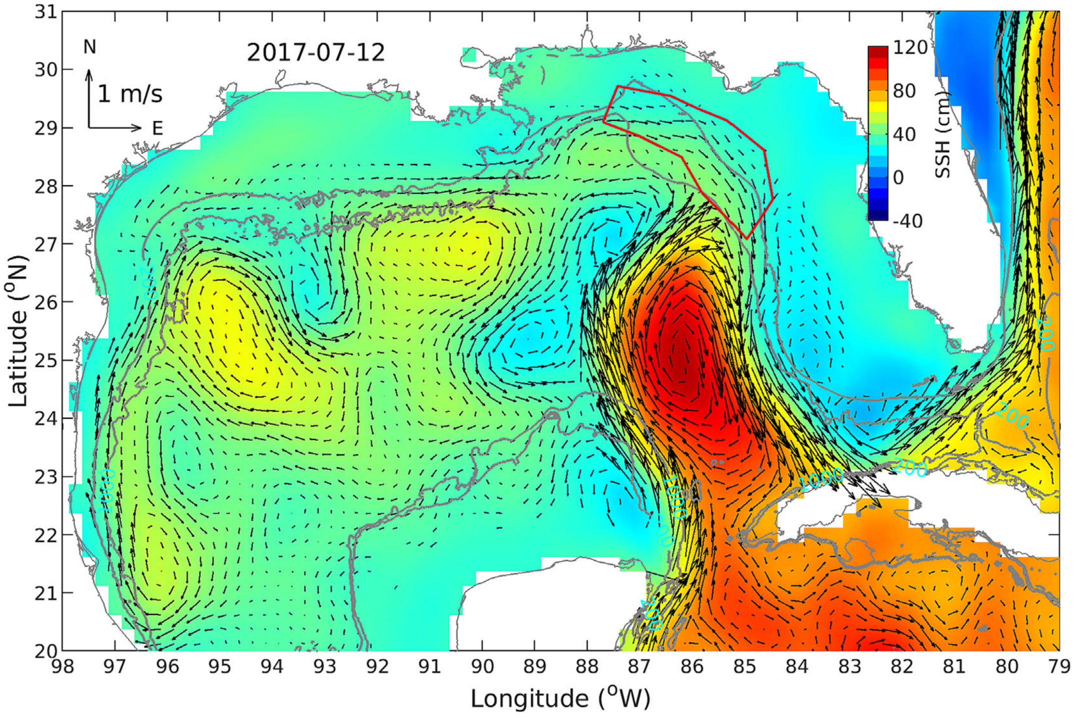

FIGURE 1 Altimetry-derived surface geostrophic currents showing the Loop Current intrusion (large arrows) into the GoM during July 2017. Isobaths of 100 and 200 m are shown as gray contours. The red polygon identifies an area where fish eggs could be transported into the Loop Current system. This altimetry product was generated following the procedure described by Liu, Weisberg, Lenes, et al. (2016), Liu, Weisberg, Vignudelli, et al. (2016), and Weisberg and Liu (2017). GoM, Gulf of Mexico.

2.2 | Fish-egg collection

On July 12, 2017, eight vessels sampled drifting eggs via plankton-net tows across 17 stations (Figure 2). Four commercial fishing vessels operated out of Panama City, Florida, USA (stations 1–2, 3–4, 5–6, and 7–8) and two operated out of the St. Petersburg area, Florida, USA (stations 9–10 and 11–12). Two larger research vessels operated out of St. Petersburg by the Florida Institute of Oceanography were used at stations 13–14 and 15–17. With one exception, each vessel sampled two stations, with the first station sampled at 0600 h EDT and the second station sampled at 1200 h. The exception was one of the research vessels, which sampled a third station, station 17, at 1800 h.

At each station, two types of plankton net tows were conducted: (1) a single, horizontal tow and (2) three replicate vertical tows. The purpose of the horizontal tow was to collect eggs for DNA barcoding and to estimate proportional compositions of the encountered taxa, and the purpose of the vertical tows was to estimate the number of eggs under one square meter of sea surface. For the horizontal tow, a 335-μm mesh, conical plankton net (3:1 aspect ratio) was towed for 15 min at idle speed (4–6 knots), using a three-point bridle to connect the net to the tow line. The conical net had a 0.73-m mouth and was equipped with a flowmeter. The net was attached to the aft gunwale of the vessel, with the net ring maintained at the surface by an attached float. The net was towed close to the vessel and ahead of the propeller wash. Vertical tows used identical gear without the float and with a 0.9 kg weight suspended from the cod end. The vertical net was lowered by hand, cod-end-first, to 30-m depth or the bottom, whichever was shallower. Once retrieved, time of day and latitude/longitude were recorded for each deployment. Flowmeter

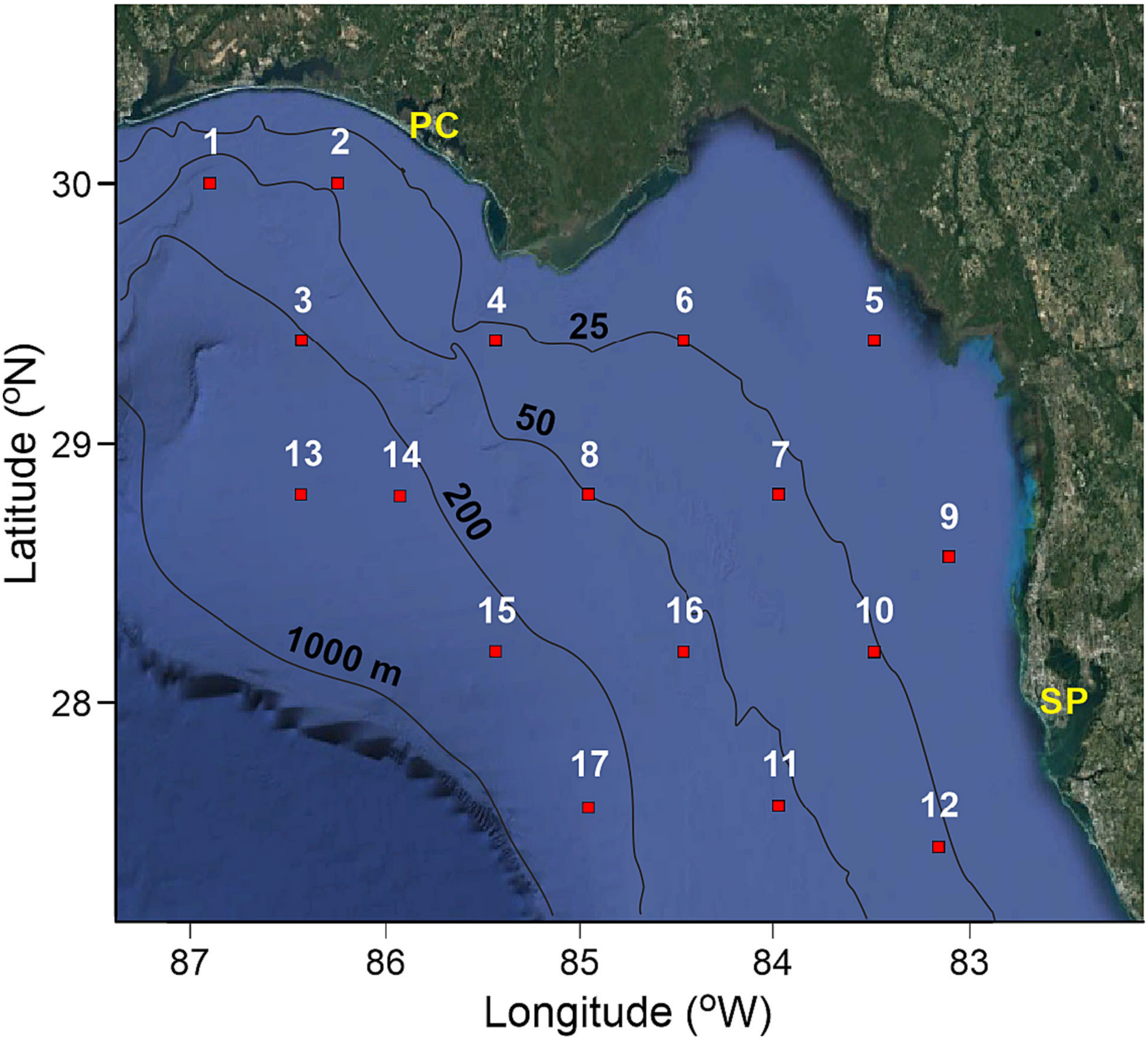

FIGURE 2 Locations of fish-egg collection stations sampled on July 12, 2017. PC is Panama City, Florida and SP is St. Petersburg, Florida. Background is a Landsat/Copernicus image (Data SIO, NOAA, U.S. Navy, NGA, GEBCO).

readings for the horizontal tows and depth of deployment for the vertical tows (usually 30 m) were also recorded. The net was rinsed on board with seawater and samples were preserved in 7:3 isopropanol:seawater.

Egg abundances from the three vertical tows were averaged. DNA barcoding followed the genetic identification and data analysis methods of Kerr et al. (2020). DNA was extracted from individual eggs (e.g., Breitbart et al., 2023) and amplified using a COI primer cocktail from Ivanova et al. (2007). Sequences are available in GenBank under accession numbers MK976037-MK976646. When barcoding of eggs from horizontal tows was not successful, eggs from vertical tows were used. Three stations (14, 15, and 17) did not provide successful egg identifications due to very low egg catches or poor preservation of genetic material, which was caused by large amounts of bycatch (non-egg) biomass in the samples.

2.3 | The West Florida coastal ocean circulation model (WFCOM)

In 2012, Zheng and Weisberg (2012) developed an application of the Finite Volume Community Ocean Model (FVCOM) that they called the WFCOM (Figure 3). WFCOM is a numerical model that combines local forcing with remote forcing acting upon coastal ocean circulation and it is a nesting of the FVCOM (Chen et al., 2003; Weisberg & Zheng, 2006) into the Global Hybrid Coordinate Model (HYCOM) (Chassignet et al., 2009). The WFCOM has a higher-resolution domain within the FVCOM. It is a fully three-dimensional model with 30 sigma layers in the vertical direction. The vertical velocity component was included in the Lagrangian trajectory simulations. The vertical diffusion coefficient is calculated using the modified Mellor and Yamada (MY) level 2.5 turbulence scheme (Mellor & Yamada, 1982), and the horizontal diffusivity is calculated using the Smagorinsky eddy parameterization method (Smagorinsky, 1963). More detailed information about the WFCOM settings can be seen from early publications (Weisberg et al., 2014; Zheng & Weisberg, 2012).

2.4 | Fish-egg trajectories

As in Weisberg et al. (2014), trajectories of fish eggs and larvae were simulated at surface (the depth of capture for the eggs), midwater, and near bottom. Drifts at these depths were modeled because the trajectories extended well beyond the egg stage, and the depths at which swimming-capable larvae traveled were unknown. The fish eggs were seeded as passive particles into the model for July 11, 2017; we assumed that the eggs were <24 h old when collected. We simulated egg drift over a 15-day period, which is a little less than half of the average PLD of marine species (36 days) and represents a generalized time between the spawning of eggs and the larval flexion stage. We consider this period to be a largely passive stage for larvae during which they live in the plankton, before the development of stronger swimming abilities; this time period avoids much of the behavior-related modulation of transport such as ontogenetic vertical migration and settlement (Paris et al., 2020). The movement of fish eggs and larvae was, therefore, forecasted from July 11, 2017 to July 25, 2017. While no identifiable eggs were found at station 17, trajectories were created to provide a general trend for this location.

Only the horizontal direction of planktonic fish eggs and larvae was considered in the trajectory simulations. We did not integrate vertical migrations or other biological responses to environmental factors (e.g., salinity, temperature, light, food availability, and currents) because of the limited information available regarding behavior during these life stages; this lack of information largely exists due to the lack of in-situ observation and experimental constraints on observing wild larvae after capture (Paris & Cowen, 2004; Somarakis & Nikolioudakis, 2010).

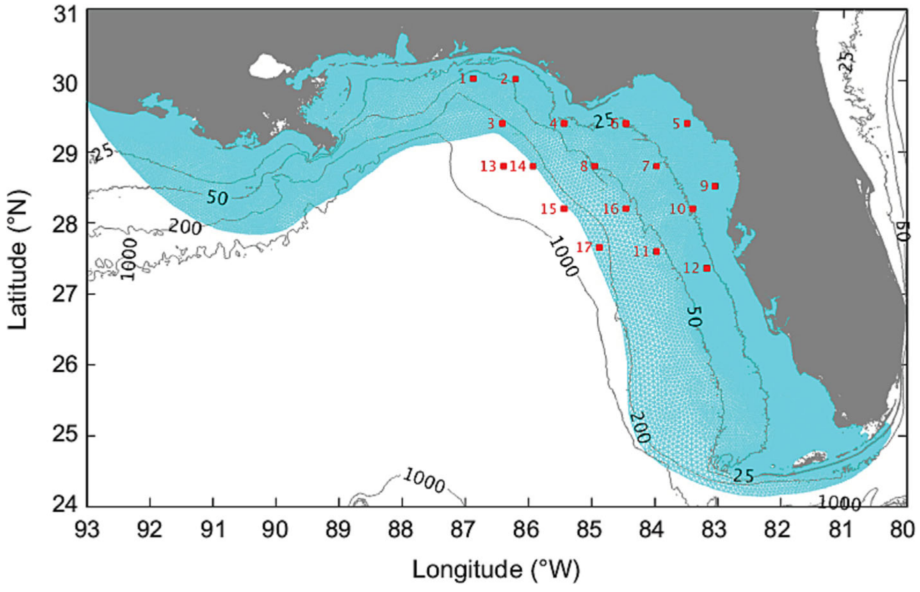

FIGURE 3 WFCOM domain and grid system (blue) with fish-egg collection stations (modified from Figure 1 of Liu et al., 2020). WFCOM, West Florida Coastal Ocean Circulation Model.

TABLE 1 Categorization of pelagic and non-pelagic species.

Family	Species	Common name	Pelagic versus non-pelagic
Achiridae	*Achirus lineatus*	Lined sole	Non-pelagic
Carangidae	*Selene setapinnis*	Atlantic moonfish	Non-pelagic
Carangidae	*Selene vomer*	Lookdown	Non-pelagic
Cyclopsettidae	*Syacium papillosum*	Dusky flounder	Non-pelagic
Chaetodontidae	*Chaetodon ocellatus*	Spotfin butterflyfish	Non-pelagic
Ephippidae	*Chaetodipterus faber*	Atlantic spadefish	Non-pelagic
Gerreidae	*Eucinostomus argenteus/Eucinostomus gula*	Spotfin mojarra/silver jenny	Non-pelagic
Gerreidae	*Eucinostomus* spp.	Mojarra	Non-pelagic
Haemulidae	*Haemulon aurolineatum*	Tomtate	Non-pelagic
Lutjanidae	*Lutjanus apodus*	Schoolmaster	Non-pelagic
Lutjanidae	*Lutjanus griseus*	Mangrove snapper	Non-pelagic
Lutjanidae	*Pristipomoides aquilonaris*	Wenchman	Non-pelagic
Lutjanidae	*Rhomboplites aurorubens*	Vermillion snapper	Non-pelagic
Ophidiidae	*Ophidion selenops*	Mooneye cusk-eel	Non-pelagic
Paralichthyidae	*Cyclopsetta fimbriata*	Spotfin flounder	Non-pelagic
Rachycentridae	*Rachycentron canadum*	Cobia	Non-pelagic
Sciaenidae	*Equetus lanceolatus*	Jackknife fish	Non-pelagic
Serranidae	*Rypticus bistrispinus*	Freckled soapfish	Non-pelagic
Serranidae	*Rypticus maculatus/saponaceus*	Whitespotted soapfish/greater Soapfish	Non-pelagic
Serranidae	*Rypticus* sp.	Soapfish	Non-pelagic
Serranidae	*Serraniculus pumilio*	Pygmy Sea bass	Non-pelagic
Synodontidae	*Saurida normani*	Shortjaw lizardfish	Non-pelagic
Synodontidae	*Synodus foetens/macrostigmus*	Inshore lizardfish/largespot lizardfish	Non-pelagic
Synodontidae	*Synodus intermedius*	Sand diver	Non-pelagic
Synodontidae	*Trachinocephalus myops*	Bluntnose lizardfish	Non-pelagic
Triglidae	*Prionotus martis*	Gulf of Mexico barred Searobin	Non-pelagic
Triglidae	*Prionotus ophryas*	Bandtail searobin	Non-pelagic
Triglidae	*Prionotus punctatus/Prionotus rubio*	Bluewing searobin/blackwing searobin	Non-pelagic
Triglidae	*Prionotus rubio*	Blackwing searobin	Non-pelagic
Carangidae	*Chloroscombrus chrysurus*	Atlantic bumper	Pelagic
Carangidae	*Decapterus punctatus/Decapterus tabl*	Round scad/roughear scad	Pelagic
Carangiformes	*Caranx crysos*	Blue runner	Pelagic
Scombridae	*Euthynnus alletteratus*	Little tunny	Pelagic
Scombridae	*Scomberomorus cavalla*	King mackerel	Pelagic
Scombridae	*Scomberomorus maculatus*	Atlantic Spanish mackerel	Pelagic
Scombridae	*Thunnus atlanticus*	Blackfin tuna	Pelagic

We used the DNA barcoding identification to categorize species as being either pelagic or non-pelagic (Table 1) and visually compared their trajectories. While all of the eggs we collected were pelagic, we classified pelagic species as those that do not have any connection with a substrate throughout life and non-pelagic species as all others that use or relate to substrate at one or more times during their lifetime. This gave insight into whether certain types of fish are more or less likely to have their eggs retained on the WFS.

2.5 | Interpretation of trajectories

The model outputs are shown in the form of maps with trajectories. Categorizing the trajectories as resulting in retention or export can be complex because the spatial scale over which they are interpreted should be considered. Here, we consider retention on and export from the WFS. Trajectories can indicate short- or long-distance movement and can have different directions (e.g., toward the coast, along the coast, and toward the open ocean). Additionally, the trajectories

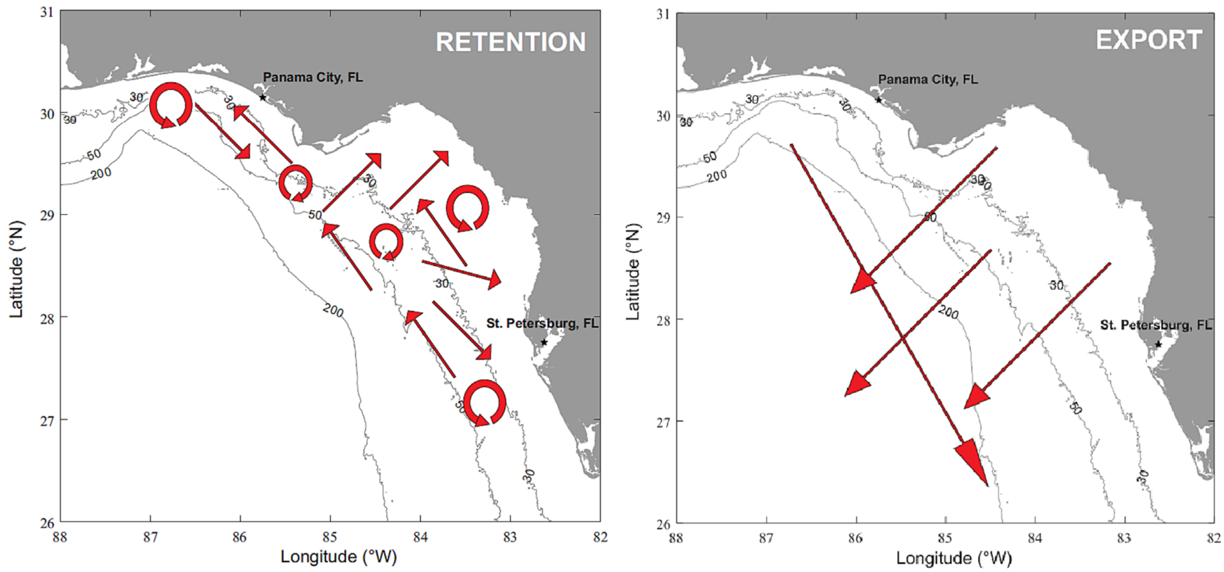

FIGURE 4 Schematic for interpretation of drifting fish-egg trajectories on the northern West Florida shelf. On the left, movement toward the coast or along the coast on the WFS is considered retention. On the right, movement toward the open ocean and away from the coast is considered export. WFS, West Florida Shelf.

cannot be precisely qualified as resulting in aberrant drift or connectivity because we do not have information regarding the outcome of the drift (e.g., mortality rate, proportion of settlers, and exact settlement site). On the WFS, trajectories that brought the eggs and larvae toward the coast or along the coast while remaining on the shelf were considered retained. Eggs that left the WFCOM model domain and moved toward the open ocean and away from the coast, or moved rapidly along its outer periphery (i.e., due to entrainment in the loop current) were considered exported (Figure 4).

The distance of dispersal was calculated as the distance from the initial station coordinates (day 1, first day of tracking) to the final coordinates (day 15, final tracking day). The haversine formula was used to calculate the great-circle distance between two points using coordinate inputs. The distances were generated through an online calculator using that formula.

Three stations (13, 14, and 15) were outside the WFCOM geographic domain, and thus no trajectories were generated. This lack of trajectory does not indicate a lack of movement, and these stations were identified with a distinct symbol from the other stations on the trajectory maps (Figure 3).

2.6 | Community analysis

Multivariate community analyses were conducted (1) to determine the distribution of eggs and larvae of pelagic species among stations and their likelihood of being exported, and (2) to determine whether species assemblages grouped by location on the WFS. For each station, the density of fish eggs was calculated from the vertical tows as the number of eggs under one square meter of water surface (number of eggs m^{-2}). This approach avoids the problem of egg abundance varying with depth (i.e., due to differences in buoyancy or variation in vertical mixing of eggs from station to station). The horizontal tows filtered more water and collected far more eggs than the vertical tows and were used to identify the proportion of each fish taxon at each station. The abundance of eggs for each fish taxon was then calculated as the proportion of the average total egg abundance ($n = 3$ vertical tows) at each station according to the formula

$$\text{Species A abundance} = \text{Proportion of species A}_{\text{horizontal}} \times \text{Mean total egg abundance}_{\text{vertical}}$$

PRIMER 7 software (v. 7.0.13, PRIMER-E, Auckland, New Zealand) was used to analyze fish-egg community structure. Egg abundance was square root transformed, and Bray–Curtis similarity was calculated for all possible station pairs. Cluster analysis was performed using these Bray–Curtis similarities, and a similarity profile analysis (SIMPROF) was used to identify statistically significant groupings of stations within the results of the cluster analysis (Kilborn et al., 2017). A seriated heatmap was generated to allow simultaneous visual comparisons of (1) station compositional similarity and (2) species associations. The PRIMER 7 heatmap algorithm re-arranges both axes (station similarities and species associations) to maximize diagonal trends in the heatmap without changing quantitative relationships within the cluster-analysis results (i.e., by re-arranging the horizontal connectors in the cluster-analysis dendrograms). SIMPROF groups were geographically mapped and non-metric multidimensional scaling (nMDS) was performed.

TABLE 2 Distance of dispersal from the initial coordinates of sites to the last coordinates of trajectory after 2 weeks of tracking from the fish-egg collection sites.

Dispersal distance (km)				
Station	**Bottom depth (m)**	**Surface**	**Midwater**	**Near bottom**
5	10	31.1	5.6	6.3
9	16	67.8	11.3	10.6
10	19	76.9	11.1	13.0
7	21	71.6	15.0	13.5
6	22	24.4	57.8	16.1
12	29	107.6	20.5	28.5
4	30	86.0	38.4	56.9
2	34	57.6	24.6	84.0
11	39	128.5	5.7	50.1
8	43	292.4	144.5	67.8
16	59	46.6	38.2	90.4
1	120	38.1	385.3	109.4
3	298	438.2	458.6	191.1
17	412	60.2	66.5	28.2
Average dispersal distance (km)		109.1	91.6	54.7
Range of dispersal distance (km)		24.4–438.2	5.6–458.6	6.3–191.1

Note: Stations are ordered by bottom depth.

3 | RESULTS

For the following description and observations, the trajectories are named after the station number. Dispersal distances are summarized in Table 2.

3.1 | Trajectories

Trajectories from sites that were closer to the coast on the inner shelf (on the shallower side of the 50-m isobath) tended to result in retention near the originating stations and on the WFS, compared to trajectories from sites that were farther out on the WFS (where the ocean floor was deeper than the 50-m isobath) that appeared to result in export from the WFS.

At the surface (Figure 5b and Table 3), we observed that the trajectories from stations 2, 4, 5, 6, 7, 9, 10,11, 12, and 16 had a northwest direction for the first 7 to 10 days. The trajectories then turned toward the coast whether it was northward, northeastward, or eastward. Trajectories from those stations indicated that fish eggs and larvae collected from those stations would have most likely been retained close to the areas where they were spawned. For station 1, the direction of the trajectories were southwest for 3 days and then northeast toward the coast. Those trajectories are considered retained near station 1 and on the WFS. Trajectories from stations 3 and 8 were southeastward and could result in export from the WFS because of the long-distance transport of 292 to 438 km. The trajectory from station 17 was tracked over 6 days before leaving the WFCOM domain. This trajectory most likely resulted in export.

At midwater (Figure 5c and Table 3), we observed that the trajectories from stations 1, 3, and 8 had a southeast direction along the WFS, parallel to the coast. Those trajectories indicated passive particles could have traveled long distances (as long as 458 km) over a 2-week period. Fish eggs and larvae that followed those trajectories would be considered exported from the WFS because of the long distance they traveled in a short time. Trajectories from stations 2, 4, 5, 6, 7, 9, 10, 11, 12, and 16 had nominal movement. The observed trajectory from station 4 had a northwest then southeast and west direction. At station 8, the trajectory had a southwest direction and followed the shape of 30-m isobath. The trajectory from station 16 had a northward direction. Fish eggs and larvae from those stations were more likely to have been spawned and have remained in the same areas. They can be considered to have been retained on the WFS. The trajectory from station 17 was tracked over 4 days before leaving the WFCOM domain, and most likely resulted in export.

Near the bottom (Figure 5d and Table 3), the observed trajectories from stations 2, 4, 8, and 11 had a southeast direction where the fish eggs and larvae seemed to be transported over short distances. The movement appeared to result in retention on the WFS. Trajectories initialized from stations 5, 6, 7, 9, 10, and 12 had very nominal movement, and eggs and larvae collected from those stations were considered to have been likely retained on the WFS; the simulated larvae traveled only short distances of 15 km on average. At stations 1 and 3, the trajectories could potentially indicate export from the WFS, with the trajectory from station 1 having a direction toward the open GoM over 109 km and trajectory from station 3 having a length of 191 km. At station 16, the trajectory appears to indicate export. The trajectory from station 17 was tracked over 6 days before

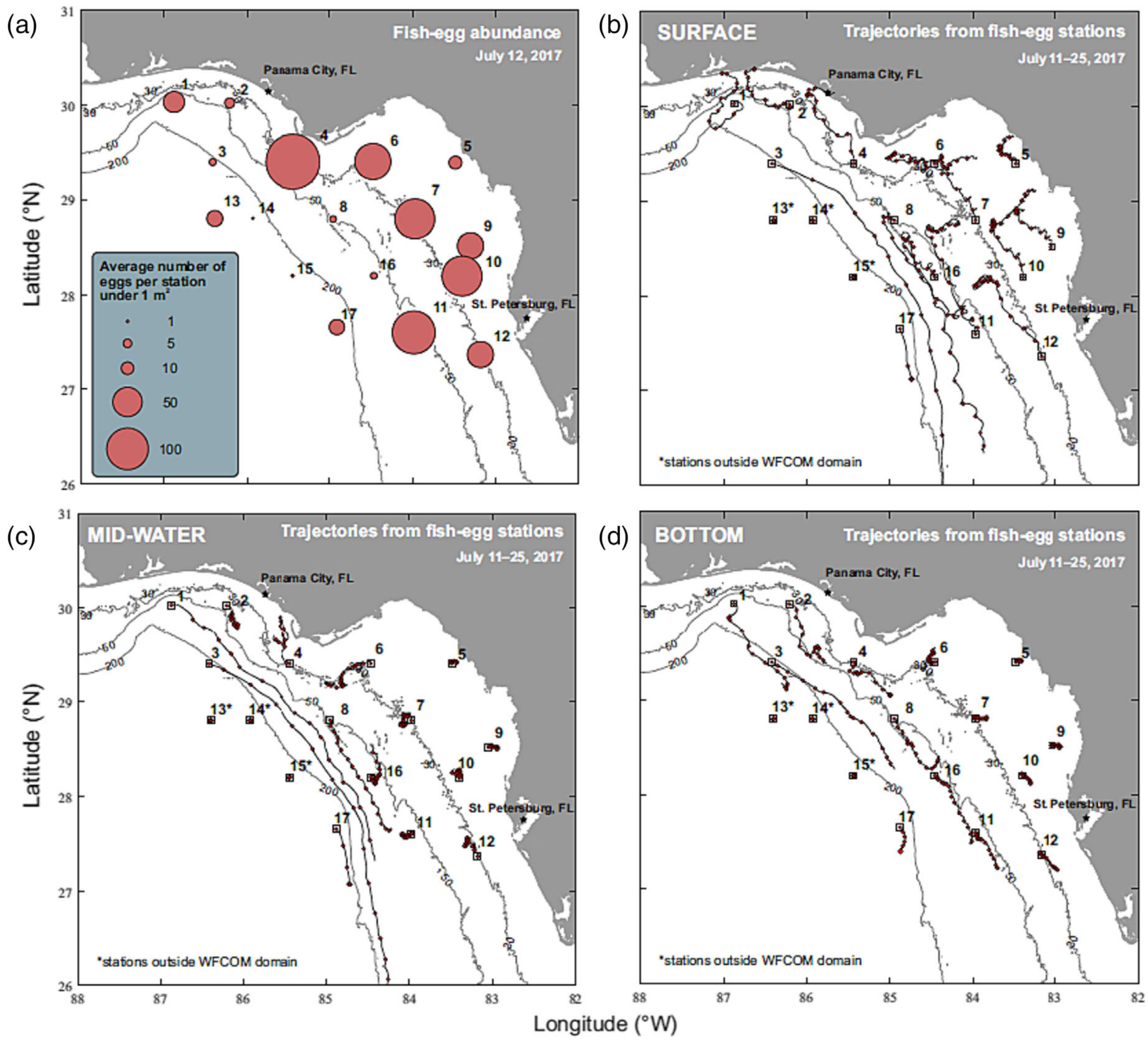

FIGURE 5 Fish-egg trajectories generated by the West Florida Coastal Ocean Model (WFCOM). The trajectories were initialized from the fish-egg collection sites. The trajectories suggest a retention pattern toward and along the coast. (a) Fish-egg abundance per site on the northern WFS. (b) Surface trajectories. (c) Midwater trajectories. (d) Near-bottom trajectories. WFS, West Florida Shelf.

leaving the WFCOM domain. That trajectory most likely resulted in export.

Overall, at all depths, the trajectories simulated from inshore, shallow-water stations appeared to result in retention on the WFS. In contrast, trajectories that were generated from offshore, deep-water stations appeared to result in potential export from the WFS. The strongest potential export of fish eggs and larvae away from the WFS resulted from trajectories that originated at the most offshore stations at the surface and at midwater.

3.2 | Fish-egg abundance and retention

Fish-egg abundance was generally higher closer to shore on the inner shelf (Figure 5a and Table 4). Nguyen (2020) projected egg trajectories from sites where spawning adult fishes were collected (i.e., known spawning locations), and these results suggested the area near station 4 experienced a convergence of egg trajectories. Generally, however, stations with higher fish-egg abundance (6, 7, 9, 10, 11, and 12) had trajectories with nominal movement at midwater and near the bottom and were considered to result in retention. Also, the surface trajectories from those stations, for the majority, had a northwest and then toward-the-coast direction, where fish eggs and larvae would also be considered to be retained. Stations with lower fish-egg abundance (1, 2, 3, 8, 16, and 17) were farther out on the WFS and corresponded with trajectories that resulted in apparent export. This suggests a relationship may exist between retention and locations with higher fish-egg abundance.

3.3 | Species assemblages and pelagic versus non-pelagic difference in retention

The results for the SIMPROF analysis are summarized in Figures 6 and 7. Figure 6 is a heatmap of the fish-egg taxa, with a dendrogram indicating species associations and vertical lines identifying

TABLE 3 Trajectory characteristics by station and position in the water column.

Station	Bottom depth (m)	Trajectory position	Trajectorydescription	Potential outcome
5	10	Surface	NW for 7 to 10 days then NE toward the coast	Retention
5	10	Midwater	Nominal movement	Retention
5	10	Near bottom	Nominal movement	Retention
9	16	Surface	NW for 7 to 10 days then NE toward the coast	Retention
9	16	Midwater	Nominal movement	Retention
9	16	Near bottom	Nominal movement	Retention
10	19	Surface	NW for 7 to 10 days then NE toward the coast	Retention
10	19	Midwater	Nominal movement	Retention
10	19	Near bottom	Nominal movement	Retention
7	21	Surface	NW for 7 to 10 days then NE toward the coast	Retention
7	21	Midwater	Nominal movement	Retention
7	21	Near bottom	Nominal movement	Retention
6	22	Surface	NW for 7 to 10 days then SE	Retention
6	22	Midwater	SW movement	Retention
6	22	Near bottom	Nominal movement	Retention
12	29	Surface	NW for 7 to 10 days then remains in same area going SW and NE	Retention
12	29	Midwater	Nominal movement	Retention
12	29	Near bottom	SE toward the coast	Retention
4	30	Surface	NW for 7 to 10 days then NE toward the coast	Retention
4	30	Midwater	NW for 7 days then SE	Retention
4	30	Near bottom	SE along the coast	Retention
2	34	Surface	NW for 7 to 10 days then NE toward the coast	Retention
2	34	Midwater	SE then NW	Retention
2	34	Near bottom	SE along the coast	Retention
11	39	Surface	NW for 7 to 10 days then NE toward the coast	Retention
11	39	Midwater	Nominal movement	Retention
11	39	Near bottom	SE along the coast	Retention
8	43	Surface	NW for 3 days then SE along the coast	Export
8	43	Midwater	SE along the WFS	Export
8	43	Near bottom	SE along the coast	Retention
16	59	Surface	NW for 7 to 10 days then SE along the coast	Retention
16	59	Midwater	NW movement	Retention
16	59	Near bottom	SE along the coast	Export
1	120	Surface	SW for 3 days then NE toward the coast	Retention
1	120	Midwater	SE along the WFS	Export
1	120	Near bottom	SE toward open ocean	Export
14	285	Surface	Outside domain of WFCOM	N/A
14	285	Midwater	Outside domain of WFCOM	N/A
14	285	Near bottom	Outside domain of WFCOM	N/A
3	298	Surface	SE along the WFS	Export
3	298	Midwater	SE along the WFS	Export
3	298	Near bottom	SE along the coast	Export
15	323	Surface	Outside domain of WFCOM	N/A
15	323	Midwater	Outside domain of WFCOM	N/A
15	323	Near bottom	Outside domain of WFCOM	N/A
13	397	Surface	Outside domain of WFCOM	N/A

TABLE 3 (Continued)

Station	Bottom depth (m)	Trajectory position	Trajectorydescription	Potential outcome
13	397	Midwater	Outside domain of WFCOM	N/A
13	397	Near bottom	Outside domain of WFCOM	N/A
17	412	Surface	SE along the WFS for 3 days before going off domain of WFCOM	Export
17	412	Midwater	SE along the WFS for 4 days before going off domain of WFCOM	Export
17	412	Near bottom	SW for 6 days before going off domain of WFCOM	Export

Note: Stations are ordered by bottom depth. NE = northeast, SE = southeast, SW = southwest, NW = northwest, WFCOM = West Florida Coastal Ocean Model, WFS, West Florida Shelf, and N/A = not applicable.

TABLE 4 Number of fish species identified per station and average number of eggs under 1 m^2 per station, with stations ordered by bottom depth.

Station	Bottom depth (m)	Number of species per station	Average number of eggs under 1 m^2
5	10	7	31.9
9	16	10	59.7
10	19	7	92.4
7	21	10	87.6
6	22	13	82.8
12	29	5	55.8
4	30	7	130.6
2	34	5	21.5
11	39	11	99.6
8	43	9	16.7
16	59	2	14.3
1	120	4	47.0
14	285	0	4.0
3	298	4	12.7
15	323	0	7.3
13	397	1	35.8
17	412	0	40.6

statistically significant station associations (SIMPROF groups). The SIMPROF analysis produced four groupings among 14 stations (stations 14, 15, and 17 did not have identifiable fish eggs and were excluded). For each of the four groups, the stations were mapped with a unique symbol in Figure 8. From this representation, a geographic grouping can be observed from west to east and from deep to shallow waters, with group *a* being the farthest west and in deeper water than groups *b*, *c*, and *d*, in that order.

In Figure 6, blue outlines indicate pelagic species. Pelagic species were found in all four groups of stations and were found at 12 stations out of 14. Figure 7 is an nMDS plot that shows the groupings of stations according to their Bray–Curtis similarity.

4 | DISCUSSION

The first hypothesis considered the potential retention and export of fish eggs. Evidence of export of fish eggs and larvae away from the WFS was found; trajectories initiated from stations on the outer shelf and in deeper waters (offshore of the 50-m isobath) more likely resulted in export away from the WFS. In contrast, trajectories initiated from stations on the inner shelf and in shallower waters (inshore of the 50-m isobath) more likely resulted in retention on the WFS. The first null hypothesis, which stated that fish eggs and larvae on the WFS are not likely to be exported, was thus rejected.

It is important to consider the general ocean circulation features of the WFS when interpreting these different trajectories. In general,

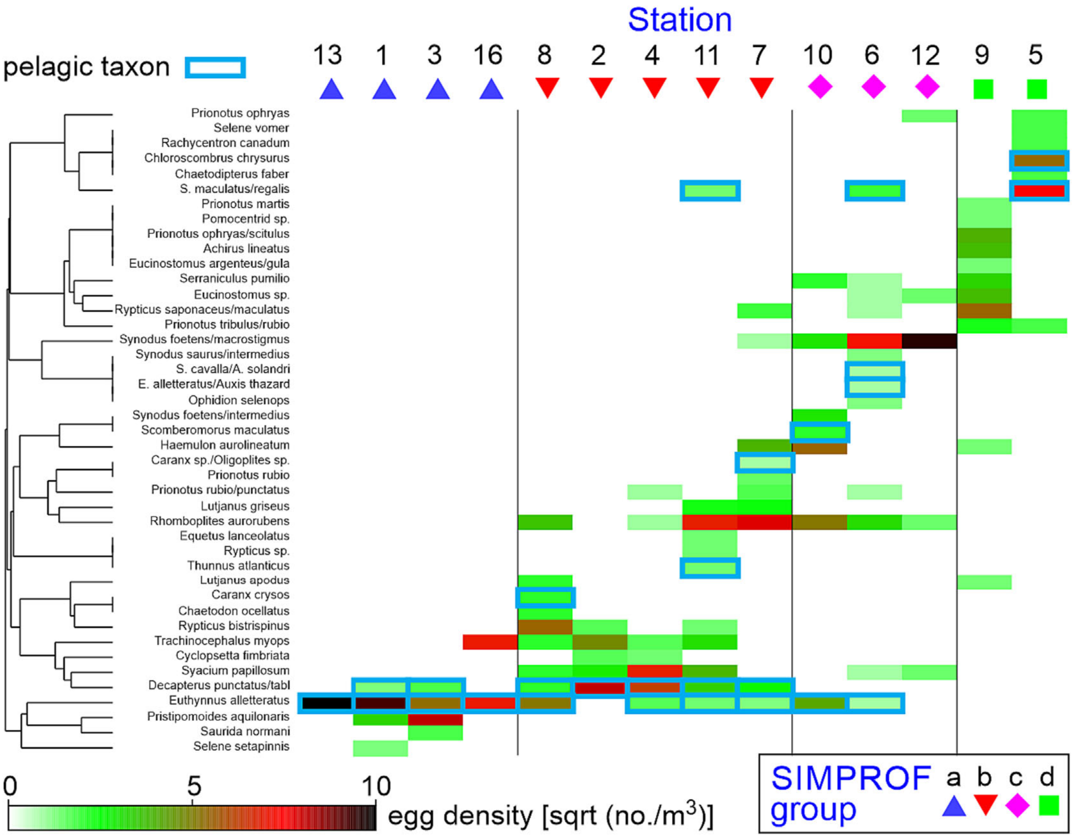

FIGURE 6 Seriated heatmap of the fish-egg taxa, with a dendrogram indicating species associations (index of association) and vertical lines delineating four statistically significant station groupings (SIMPROF groups). Blue outlines on rectangles indicate pelagic taxa.

the WFS is upwelling-favorable with seasonal variability. The circulation on the WFS is known to be influenced by multiple hydrodynamic features. In particular, the circulation in shallow water is influenced by wind forcing, whereas the circulation in deeper waters on the outer part of the WFS is influenced by the Loop Current and its eddies. More specifically, in the summer months, southerly winds tend to have a stronger influence on surface currents, especially in shallow water (Liu & Weisberg, 2012). With Ekman transport, the deflection of the surface current in shallow water should be 45–90° to the right (depending on depth). From this, water circulation would result in downwelling. However, from the trajectories near the surface, at midwater, and near the bottom, there was no strong evidence of downwelling or movement away from the coast and toward the open ocean (during the time period considered here). Two explanations are plausible in this case: the winds were not strong enough to create downwelling, or the influence of the Loop Current was stronger than the downwelling process and countered it, slowing the water flow at shallow depths. Daily-averaged winds for our period of observation had the same patterns as the surface trajectories in shallow water, confirming that surface water flow was influenced primarily by winds.

On the deeper, outer part of the WFS, the circulation is influenced by several factors such as winds, eddies, and the Loop Current (Weisberg et al., 2005). The latter has the strongest influence on the outer shelf, even though its influence varies annually depending on how northward the Loop Current penetrates into the GoM (Figure 1). The trajectories that were initiated from stations at deep water were highly influenced by the Loop Current. In these cases, deepwater trajectories at all depths connected the northern WFS with the southern WFS (Figure 5), which are two retention provinces that otherwise tend to be isolated from each other at particle drift times of weeks to months (Miron et al., 2017). These long, southeastern trajectories tended to originate offshore, yet they occurred over bottom depths that were within the distributional range of adult reef fishes such as snappers.

Overall, fish eggs and larvae are more likely to be dispersed and transported over long distances by large-scale circulation features, and they are more likely to be retained locally by small-scale processes and the interaction of those processes and currents with bathymetry (Paris & Cowen, 2004). In general, the observed trajectories in shallow and deep water are consistent with the physical attributes of the WFS circulation.

Moreover, it is important to note that categorizing the trajectories cannot be solely based on hydrodynamic models. In this study, the trajectories were categorized according to relative retention versus export, and not to the further level of aberrant drift and habitat connectivity that are subcategories of export. More specifically, to make inferences on habitat connectivity, biophysical models are often used because of the incorporation of hydrodynamic data from ocean

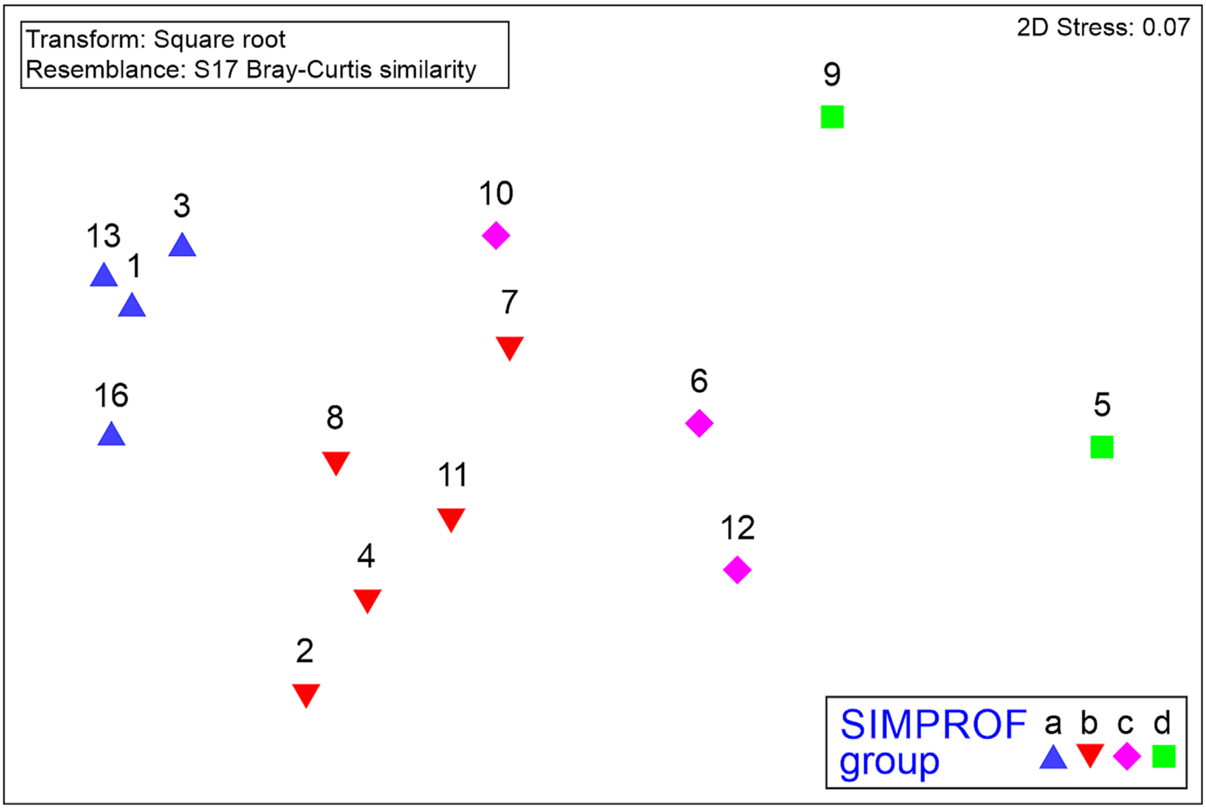

FIGURE 7 Non-metric multidimensional scaling (nMDS) plot indicating the compositional similarity of fish-egg samples (station numbers are above symbols), as indicated by Bray–Curtis similarity and SIMPROF analysis, with both based on square root-transformed densities (as in Figure 6).

circulation (e.g., current and other environmental parameters) and biological data (e.g., pelagic larval duration and larval behavior; Abesamis et al., 2016, Paris et al., 2020). Within the GoM, Paris et al. (2020) used a biophysical model to describe relatively good connectivity clockwise from Yucatan through the northern GoM and into the eastern GoM but identified relatively poor connectivity between the eastern GoM and Cuba. Establishing connectivity between the eastern GoM and the Carolinas, for example, would require larger-scale modeling. Existing genetic evidence is consistent with gene flow occurring between fishes in the GoM and the southeastern US coast (Zatcoff et al., 2004).

The offshore trajectories indicated strong advections of fish eggs and larvae. Indeed, the distance of dispersal was up to 458 km, reaching the southern half of the WFS in a period of 2 weeks. In the study of Gag larval transport by Weisberg et al. (2014), trajectories were simulated over 45 days, accounting for the approximate age of individuals approaching coastal nursery habitats. This suggests that the long-distance offshore movement of fish eggs potentially resulting in export could possibly reach the Florida Keys and be entrained in the Florida Current and continue its course in the Gulf Stream up to the southeastern United States, where similar fish assemblages occur. Indeed, recreational and commercial harvest occurs off North and South Carolina for some of the same species (e.g., snapper-grouper complex) that are captured on the WFS (Karnauskas et al., 2022; Overton et al., 2008). Connectivity between the WFS snapper-grouper complex and the one from the Carolinas could exist because of the possible export of the fish eggs and larvae away from the WFS (Denit & Sponaugle, 2004; Hare & Walsh, 2007; Karnauskas et al., 2022).

Specifically, for July of 2017, the penetration of the Loop Current into the GoM was far northward, and the northern part of the loop was in close contact with the shelf break (Figure 1); the shallowest isobath in Figure 1 is the 200-m isobath. Based on the trajectories originating from station 17, we observed that only 3 days at the surface and midwater and 6 days at the near bottom were represented before the trajectory went outside of the WFCOM domain and was not trackable anymore. Observation of the shape and movement of the Loop Current during that summer indicated advection of water from the WFS into the Loop Current and potential export of fish eggs and larvae that were spawned close to the shelf break (see surface trajectories in Figure 1). Those eggs and larvae could then be entrained in the strong currents described above (i.e., Florida Current, Gulf Stream) and brought to the Carolinas in a few weeks, where they could settle (Walsh et al., 2009). This time period can be estimated by considering the average velocity of 0.8 m s^{-1} for the Loop Current, 1.9 m s^{-1} for the Florida Current, and 2.5 m s^{-1} for the Gulf Stream (Milliman & Imamura, 1992; Niiler & Richardson, 1973). The distance between the point of contact between the Loop Current and the shelf

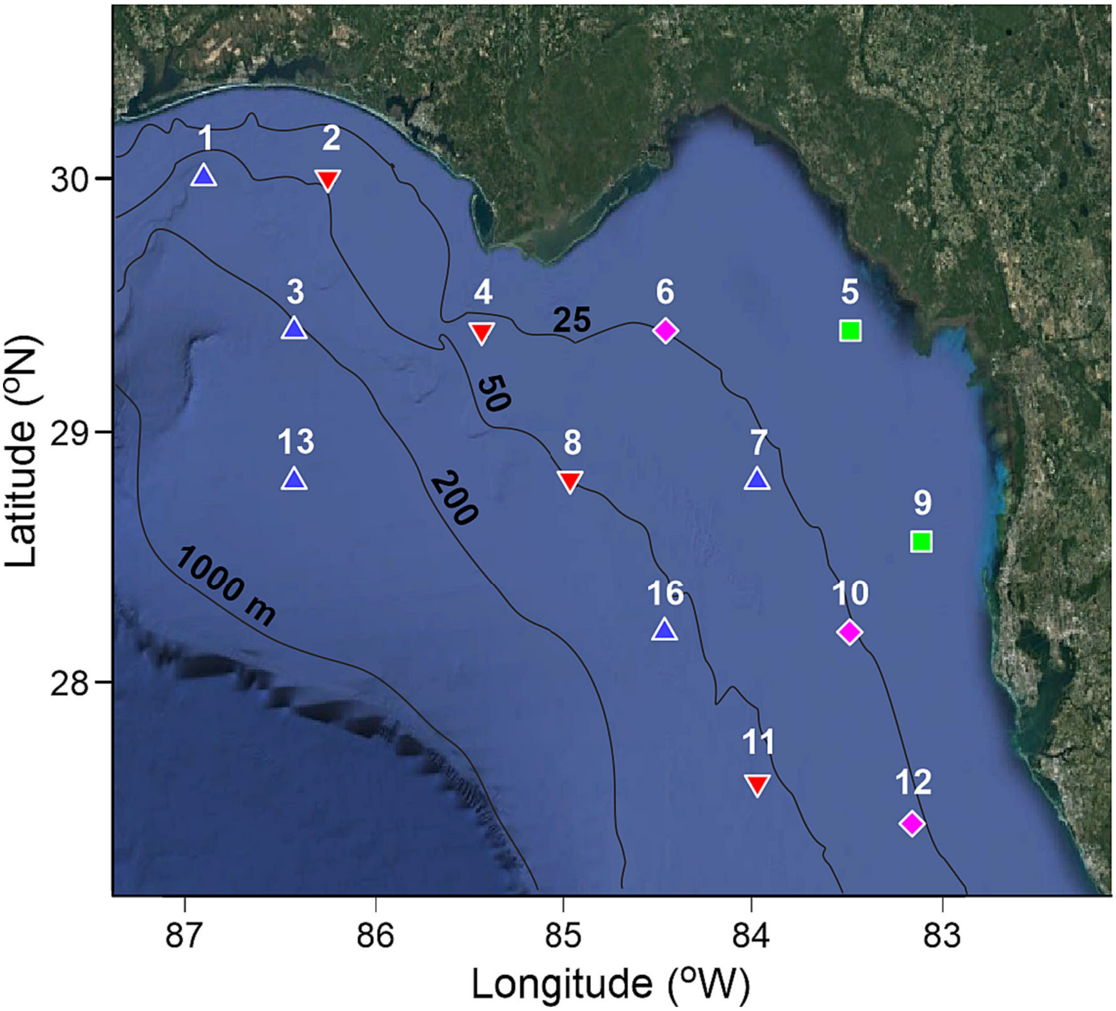

FIGURE 8 Geographic representation of the analysis results in Figures 6 and 7.

break and an area on the shelf off the coast of North Carolina can also be estimated. Such calculations result in an approximate period of transport of 2 weeks. This time period is reasonable for hypothesizing that, in the summer of 2017, when the Loop Current came into close contact with the WFS break, fish eggs and larvae that were spawned in that area could have been advected into strong currents and transported passively to the Carolinas where they could settle. This phenomenon of potential export and connectivity appears to be highly variable and dependent on years and seasons when the shape and degree of intrusion of the Loop Current into the GoM is conducive to this type of long-range connectivity.

Other evidence of this potential "shelf exit" in the Florida Keys was described by Kerr et al. (2020) and Karnauskas et al. (2022). DNA barcoding of fish eggs collected along a transect from the WFS to Cuba (i.e., across the Straits of Florida) distinguished reef-associated fish species from pelagic species. The results indicated the presence of (shallow water) reef-associated species in deeper water within the Straits of Florida. This was associated with the presence of a mesoscale cyclonic eddy that introduced water from the WFS into the Florida Current. That study is an additional demonstration of how considering ocean circulation in combination with biological data is fundamental to understanding how different processes work together, and would present another hypothesis regarding connectivity between the WFS and the Carolinas. Karnauskas et al. (2022) have previously supported this position by providing compelling evidence that Red Snapper on the southern WFS heavily subsidize their stocks in the southeastern US Atlantic Coast via export of larvae that are spawned south of Tampa Bay. Notably, Figures 1 and 5 suggest these subsidies may also originate from areas north of Tampa Bay, which would increase the size and potential importance of these progeny sources.

Our second hypothesis investigated fish-egg abundance in relation to retention. Fish-egg abundance appeared to be higher closer to shore, where the majority of fish-egg collection sites resulted in retention (Figure 5). Fish-egg abundance was nominally lower at sites in deeper water where trajectories were more likely to result in export. The apparent relationship between egg abundance and retention suggests we should reject the null hypothesis that sites with higher egg abundance were not more likely to result in retention. Note that this could represent increased spawning or higher fish biomass in these areas, increased drift convergence, reduced export, or all processes acting together. This finding is consistent with the concept of self-recruitment; an increase in self-recruitment is generally associated with retention zones that are found adjacent to the coast. It has been suggested that these coastal zones tend to retain eggs and larvae because of interactions between circulation and topography (e.g., bays, reefs, and other bottom features; Gawarkiewicz et al., 2007).

The third hypothesis was related to pelagic versus non-pelagic species. Pelagic species were thought more likely to be exported than non-pelagic fish species. No evidence of this was found during the present study. Pelagic species were found at most of the stations whether they were retained or exported, and the SIMPROF analysis found pelagics to be represented in all community groups. This is likely because some pelagic species, such as Spanish mackerel (*Scomberomorus maculatus*) and king mackerel (*Scomberomorus cavalla*), are not just pelagic, they are notably coastal and migratory within coastal waters, and are managed as "coastal migratory pelagics" by regional fishery management councils.

Lastly, the fourth hypothesis investigated whether there was spatial structure in the fish-egg species assemblages that occur within our study area. The SIMPROF analysis indicated the presence of geographic station groupings based on taxonomic composition. This analysis indicated a geographical grouping from west to east (from deep to shallow water). Even though physical and chemical properties were relatively constant, the topography or other currently unidentified factors seemed to influence the species composition at the different stations on the WFS. In most cases, species found in deeper water were not likely to be found in shallow water and vice versa. The sites that were geographically closer together yielded similar species. It is interesting that one relatively shallow station, station 7, was classified as being in SIMPROF group *a* (Figure 6), yet it plotted close to stations 6 and 10 in the shallow-water group *b* in the nMDS plot (Figure 7). Interestingly, stations 7 and 16 are located in the only area of the WFS where Yang et al. (1999) identified cross-shelf mixing of surface waters (their Figure 12). Because there was depth-related variation in the structure of these species assemblages, the fourth null hypothesis was rejected. This is consistent with findings by Huelster (2015) and Huelster and Peebles (2019). Based on stable-isotopic values from muscle tissue, these authors found isotopic separation between nearshore and offshore energy pathways that coincided with changes in fish assemblages. As in the present study, the Huelster (2015) SIMPROF analysis, which was based on trawl data, also separated fish communities into shallow and deep components. The reef-fish component (snappers, grunts, and porgies) favored the inner WFS. The analysis was repeated for 11 years from 2008 to 2018, and a similar shallow-deep division in community structure was found in 10 years out of 11 (Huelster & Peebles, 2019). In some years, shallow-water species extended their distributions toward deeper water, whereas in other years, they were more narrowly restricted to shallower waters, suggesting dynamic distribution behaviors in these fish assemblages.

In summary, our primary findings are as follows:

1. Shallow-water trajectories likely resulted in retention, and deep-water trajectories likely resulted in export.
2. There was higher egg abundance in shallow water that was also associated with a higher likelihood of retention, but this higher abundance also could have been caused by more spawning occurring in those areas.
3. Eggs from pelagic species were not more likely to be exported than eggs from non-pelagic species. That is because many pelagic species occur in inshore areas where retention is high.
4. The SIMPROF analysis indicated the presence of depth-related groupings of fish-egg assemblages.

Over the years, multiple studies have acknowledged that oceanographic processes and physical features can potentially influence the recruitment success of fish stocks (Hinrichsen et al., 1997). DNA barcoding is highly reliable in species identification of fish eggs (Burghart et al., 2014; Burrows et al., 2018; Ward et al., 2009), and tracking of movement via numerical models can be done efficiently in a timely manner once initial coordinates are identified and put into the model. The present study provides insight into the fate of planktonic fish eggs spawned at different locations on the continental shelf. However, our study was conducted using data collected during just 1 day. Repeated efforts at different times would be useful for evaluating any uncertainty in our results; this is most relevant to the third hypothesis (i.e., that the eggs of pelagic species are not more likely to be exported than those of non-pelagics), which was the only null hypothesis that was not rejected. If that hypothesis is given future consideration, it may be productive to consider coastal pelagics separately from pelagics that occur in the deep ocean.

AUTHOR CONTRIBUTIONS

Bich Vi Viviane Nguyen, Ernst B. Peebles, Robert H. Weisberg, and Steven A. Murawski designed the study. Makenzie Kerr and Eva-Maria S. Bønnelycke conducted the DNA barcoding of fish eggs under the guidance of Mya Breitbart. Bich Vi Viviane Nguyen conducted the numerical modeling of egg trajectories under the guidance of Yonggang Liu and Robert H. Weisberg. Bich Vi Viviane Nguyen interpreted the data and prepared the first draft of the manuscript as part of her Master's thesis; Ernst B. Peebles edited the first draft to prepare it for journal publication. All authors except Robert H. Weisberg, Steven A. Murawski, and Eva-Maria S. Bønnelycke edited intermediate drafts. All authors reviewed and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support our findings are available from the corresponding author upon request.

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