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Synthesising Support for the Entrainment Hypothesis Through Spatially Explicit Life Cycles, Vagrancy and Collapse of Atlantic Tarpon (*Megalops atlanticus*)

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ABSTRACT

Understanding spatial dynamics and migratory behaviours of fish populations is essential for effective fisheries management. We focus on the migratory Atlantic tarpon (*Megalops atlanticus*) to explore how movement strategies and spatial life cycle patterns shape stock dynamics, contingent structure and mechanisms for collapse and recovery. The entrainment hypothesis posits that migratory routes are socially transmitted from experienced repeat spawners to younger conspecifics, resulting in distinct contingents within a population. Using a combination of literature review, life history data, mark-and-recapture records and electronic tagging, we evaluated five biological hypotheses related to entrainment mechanisms, habitat conservatism and phenotypic plasticity within Atlantic tarpon populations. Our findings provide evidence for migratory connectivity and the role of entrainment in shaping Atlantic tarpon contingent structure across the Western Atlantic. Movement and mark-and-recapture data revealed spatially discrete contingents with some intermixing, highlighting behavioural conservatism and phenotypic plasticity. Examples of vagrancy showed Atlantic tarpon caught far from their capture contingent, suggesting vagrant movements may contribute to colonising new habitats under suitable conditions. Straying by a subset of individuals may also increase the recovery and resilience of Atlantic tarpon stocks following collective memory loss in migratory routes. Research on contingent structure, larval recruitment patterns and abundance trends is needed to inform management measures to ensure the maintenance of migratory knowledge. This approach provides a framework for understanding Atlantic tarpon and other migratory marine fish stock dynamics, while underscoring the importance of coordinated management and conservation efforts across contingent boundaries.

1 | Introduction

Understanding the spatial distribution and migratory patterns of fish is essential for fisheries science and population management (Sinclair 1988). Migratory patterns influence fish stock structure, population fluctuations and resilience to collapse caused by overfishing or habitat loss (Cadrin and Secor 2009; Lowerre-Barbieri et al. 2019). Within large marine fish stocks, subgroups often form that reflect distinct ecological and behavioural strategies. One such subgroup is the spawning unit, which can consist of multiple units, that is, local populations, that separate during spawning but may share feeding and nursery grounds at other stages of their life cycle (Petitgas et al. 2006). Beyond reproduction, fish stocks also exhibit broader groupings known as life history types (Hjort 1914) or contingents (Clark 1968). Contingents are defined as a 'discrete segment of a population that diverges spatially along an alternative migratory pathway during the course of life history' (Kraus and Secor 2004). The formation and persistence of contingents are not solely driven by genetic structure but are shaped by environmental forcing, phenotypic plasticity and behavioural conservatism, where learned behaviours become habitual (Secor 1999; Corten 2002; Petitgas et al. 2010). Oceanographic processes, such as larval retention and adult migratory pathways, further play an important role in structuring and maintaining the spatial distributions and life cycle patterns of contingents (Harden-Jones 1968; Sinclair 1988). By partitioning risk and diversifying habitat use, contingents help to increase population resilience and buffer against localised disturbances (McQuinn 1997a; Kerr et al. 2010).

The entrainment hypothesis posits that migratory routes develop in fish populations through the interactions between experienced, repeat spawners and their inexperienced conspecifics (Petitgas et al. 2006). These social interactions facilitate the transmission of migratory knowledge and collective memory, providing a mechanism for the persistence of life cycle spatial patterns that give rise to separate contingents within populations despite having a potentially near-homogenous genetic structure (Chambers 2021). Thus, if collective memory is lost, it may be the precursor to the loss of spawning units or entire population collapse (De Luca et al. 2014; Macdonald et al. 2018; MacCall et al. 2019). Ultimately, phenotypic diversity and proportion of successful re-establishment arising from vagrancy (i.e., non-entrained individuals that disperse and reconnect regions) can allow for recolonisation and potential for recovery from either depletion or complete collapse (Petitgas et al. 2010; Chambers 2021).

Synchronised biological processes (e.g., spawning migrations), which suggest entrainment, have been identified as key factors in maintaining contingent structure of fish populations (ICES 2007). These mechanisms are particularly relevant in explaining the migratory behaviours, depletion, collapse and subsequent recovery of multiple species, ranging from Atlantic herring (*Clupea harengus*) (McQuinn 1997a, 1997b; Corten 2002), to striped bass (*Morone saxatilis*) (Secor and Piccoli 2007) and Atlantic bluefin tuna (*Thunnus thynnus*) (Fromentin and Powers 2005; Fromentin et al. 2014). For example, the distribution expansion of Atlantic bluefin tuna in the 1960s from the western stock in temperate North Atlantic to equatorial waters off Brazil highlights the potential role of these mechanisms (ICES 2007). Informed by seasonal catch trends, the established contingent in the Caribbean and Gulf of Mexico (GOM) was believed to be connected to the new migratory contingent separate from the previously understood distribution of Atlantic bluefin tuna (Fromentin et al. 2014). Then, following extensive fishing efforts in the Caribbean and GOM and due to the potential loss of migratory behaviours (Secor 2015), the new equatorial Brazilian contingent rapidly disappeared (Fromentin and Powers 2005). More recent reports of occasional Atlantic bluefin tuna catches in the South Atlantic suggest the presence of potential vagrants from the western stock. If suitable habitats are available, these potentially non-entrained 'would-be contingent leaders' or 'exploratory platoons' could pioneer novel life cycle patterns and facilitate the establishment of new migratory pathways or the re-establishment of lost contingents (Secor 1999, 2015; ICES 2007). Ultimately, establishing migratory pathways through entrainment and subsequent disruption can alter the dynamics and recovery of different stocks.

To examine the applicability of the entrainment hypothesis within a given population, Petitgas et al. (2006) outlined the need for agreement across multiple biological hypotheses supported by three distinct but interconnected types of evidence. First, the evidence must be consistent, meaning it does not contradict with other observations; supportive, meaning it is not readily explained by alternative hypotheses or theories, and demonstrative, meaning it clearly shows the mechanisms by which entrainment occurs and is maintained. There needs to be consistent evidence that juvenile and adult distributions temporarily overlap, providing the potential for cross-generational learning. Additional consistent lines of evidence can be assessed following a fishery collapse, with different spawning units exhibiting variable recovery patterns. Consistent evidence may also support that colonisation could occur through either juvenile vagrancy or adult migratory changes driven by external and environmental forcing. Indicative of entrainment, supportive evidence includes identifying behavioural changes in juveniles when in proximity to adults or observational differences in geographical distributions for individuals that never overlapped with migrant adults (non-entrainment). Finally, using techniques such as DNA, electronic tagging and mark-recapture tagging programs to track the movement and distribution of different contingents can provide demonstrative evidence of entrainment mechanisms. Demonstrative evidence approaches can also uncover the presence and role of phenotypic plasticity in migratory behaviour, which is an important component for entrainment.

Atlantic tarpon (*Megalops atlanticus*) provides an excellent case study to evaluate the entrainment hypothesis. Atlantic tarpon is a migratory mesopredator fish that occurs across the Eastern and Western Atlantic Ocean (McMillen-Jackson et al. 2005) and supports a multimillion-dollar recreational fishing industry in the southeastern region of the United States of America (US) (Smith et al. 2022). Seasonally migrating hundreds to thousands of kilometres, Atlantic tarpon in the northern hemisphere move northward in the summer months from likely spawning areas towards foraging grounds and then southwards as temperatures decrease in the fall (Griffin et al. 2018; Luo et al. 2020; Drymon et al. 2021; Friess et al. 2021; Lowerre-Barbieri et al. 2021; Griffin, et al. 2022, 2023; Stephens et al. 2024). Adults have high levels of conservatism with repeatable migrations between pre-spawning and foraging grounds (Griffin, et al. 2022, 2023). Although gene flow between the Eastern and Western Atlantic populations is believed to be limited, genetic relatedness varies across the Western Atlantic, with some regions, such as Costa Rica, showing higher levels of isolation (McMillen-Jackson et al. 2005). Moreover, within the Western Atlantic populations, multiple contingents are thought to exist, with the three most well understood contingents being the Western GOM, Eastern GOM and Eastern US Seaboard contingents (Griffin, et al. 2023; Stephens et al. 2024). The Western and Eastern GOM contingents are believed to overlap but divide near the Mississippi Delta in Louisiana (Stephens et al. 2024), while the Eastern GOM and Eastern US Seaboard contingents overlap in South Florida during spawning and overwintering months (Griffin, et al. 2023). Despite some plasticity, within the Eastern GOM and Eastern US Seaboard contingents, Atlantic tarpon generally migrate northward following spawning in separate directions, one along the west coast of Florida and the other along Florida's east coast. Thus, while contingent structures exist, there appears to be some level of overlap in 'mixing areas'.

Despite their ecological, economic and cultural importance, little is known about the stock dynamics and which mechanisms drive the development and maintenance of Atlantic tarpon contingents. Local ecological knowledge from an angler perception survey suggests that the Atlantic tarpon fishery has declined in recent decades in the southeastern US (Griffin, et al. 2023). This highlights the need for a better understanding of stock structure and connectivity to inform effective management strategies, especially since they are listed as 'vulnerable' by the IUCN (Adams et al. 2019). Using the Petitgas et al. (2006) outline to assess the entrainment hypothesis with Atlantic tarpon in the Western Atlantic can thus provide important insights that can guide their conservation and management.

In the following sections, we assess five biological hypotheses as questions underlying the three evidence types (i.e., consistent, supportive and demonstrative; Petitgas et al. 2006) needed to support the entrainment hypothesis for Atlantic tarpon. First, we assess evidence of spatial or temporal overlap between juvenile and adult Atlantic tarpon that would enable entrainment (consistent evidence). Second, we assess evidence on whether all spawning units recover uniformly following a collapse (consistent evidence). Third, we assess evidence on whether juvenile vagrancy and environmental forces can drive the colonisation of new habitats (consistent evidence). Fourth, we assess evidence on whether juveniles show behavioural differences in the presence of adults compared to when isolated (supportive evidence). Finally, we assess evidence and provide an analysis of mark-and-recapture to assess if adult Atlantic tarpon overlap or cross between contingents (demonstrative evidence). Collectively, we aim to provide a tool for understanding stock dynamics, contingent structure and resilience in Atlantic tarpon. We expect that this is an approach applicable to other marine species facing similar stock management challenges and anthropogenic pressures.

2 | Biological Hypotheses

2.1 | Biological Hypothesis 1: Is There Spatial and Temporal Overlap Between Juveniles and Adults?

To assess support for *Biological Hypothesis 1*, we conducted a literature review primarily focused on peer-reviewed studies of nursery habitat use and ontogenetic habitat shifts in Atlantic tarpon. Relevant studies were identified using combinations of keywords such as 'Atlantic tarpon', 'juvenile recruitment', 'nursery habitat' and 'ontogenetic shift' via the search engine, Google Scholar. Our aim was to synthesise literature that provided insight into spatial and temporal overlap between life stages, a key mechanism that underpins potential entrainment.

Following the planktonic leptocephalus stage lasting 20–40 days (Shenker et al. 2002), post-metamorphic juveniles recruit to nearshore areas that can vary from freshwater to marine environments (Brown and Severin 2008; Rohtla and Vetemaa 2016). These diverse juvenile habitats can range from upper estuarine zones, mangrove swamps, marshes and ephemeral coastal ponds (Wade 1962; Adams et al. 2014; Kurth et al. 2019; Wilson et al. 2019; Navarro-Martínez et al. 2020; Bunting et al. 2024; Stevens et al. 2024). The highly vascularised swim bladders of Atlantic tarpon allow for their survival in anoxic and hypoxic conditions by air-gulping, allowing them to exploit habitats that are inaccessible to most predators and competitors (Seymour et al. 2008). Juveniles remain in these low-oxygen back-water areas typically until they reach ~30 cm fork length (~1 year old) or sometimes until ~60 cm fork length (~2 years old) if recruited to ephemerally connected sites (Adams, A. J., unpublished data; Bunting et al. 2024; Stevens et al. 2024). As larger juveniles approach maturity, they will typically shift towards estuarine habitats and begin to shift to exposed coastal regions at around 10.5 years and a size of 125 cm fork length (Crabtree et al. 1997; Kurth et al. 2019). This progression towards coastal zones at the end of the juvenile and sub-adult life history phases has been consistently observed (Wade 1962; Rickards 1968; Cyr 1991; Crabtree et al. 1992; Crabtree 1995; Zerbi et al. 2001; Stein III et al. 2012; Adams and Cooke 2015; Seeley et al. 2017; Seeley and Walther 2018; Navarro-Martínez et al. 2020). This ontogenetic shift towards coastal areas allows sub-adults or pre-spawn adults to intersect with repeat spawners during spawning or foraging migrations (Griffin, et al. 2023; Stephens et al. 2024). First-time migrants may then follow older conspecifics during their seasonal migrations, facilitating entrainment through the social transmission of migratory knowledge. Following this, adults move offshore to spawn (Luo and Ault 2012; Luo et al. 2020), initiating widespread dispersal mechanisms. The prolonged larval stage results in broad spatial distribution of recruits (Elmo et al. 2021; Graham et al. 2021), increasing the likelihood that juveniles settle in regions occupied by specific adult contingents with distinct migratory behaviours. This spatial overlap may expose juveniles to local environmental cues and, eventually, the movement patterns of older conspecifics, reinforcing contingent-specific migratory behaviours as they mature. Collectively, these patterns suggest a plausible mechanism for entrainment, supported by consistent observations and evidence of habitat overlap between juveniles and adults.

2.2 | Biological Hypothesis 2: Do all Spawning Units Recover?

To assess support for *Biological Hypothesis 2*, we conducted a literature review on long-term trends in Atlantic tarpon population dynamics, with a primary focus on historical fishery collapses and evidence for variable recovery across regions. Relevant literature was identified using combinations of keywords such as 'Atlantic tarpon', 'spawning unit', 'stock collapse', 'recovery', 'vulnerable', 'exploitation', 'harvest' and 'regional abundance' via Google Scholar. Our aim was to synthesise available evidence for spatial heterogeneity in collapse and recovery among spawning units to evaluate whether entrainment may influence the likelihood of recovery.

Despite recent angler and fishing guide perceptions of decline in the Atlantic tarpon abundance impacting the recreational fishery (Griffin, et al. 2023), the reduction in abundance has been most isolated to the Western GOM and the South American coast (Adams et al. 2019), with the most notable occurring in Texas (Holt et al. 2005). Historically, Port Aransas, Texas, was labelled as the 'Tarpon Capital of the World' in the 1920s and peaked in the 1930s. By the 1960s, the fishery had collapsed, a decline often linked to recruitment failure caused by degraded nursery habitats due to freshwater diversions, prey base depletion and water quality issues (Holt et al. 2005; Stilwell 2011). Though, considering Atlantic tarpon are long-lived and have late maturity (Crabtree et al. 1997; Puga et al. 2018), they are at an increased risk of collapsing if substantial losses occur (Navarro-Martínez et al. 2024). While this collapse is specific to the Texas region, it serves as a proxy for the broader Western GOM contingent, given the lack of available data elsewhere in the region. Contributing factors likely included recreational overfishing in Texas and subsistence fishing across the greater region (Adams et al. 2019). Moreover, the collapse and prevention of recovery may also have been compounded by lack of suitable habitat for adults or other environmental catastrophes that disrupted larval recruitment in the area, like the 1979 Ixtoc-I oil spill in the southwestern GOM (Soto et al. 2014), or even more recently, the persistent effects of the 2010 Deepwater Horizon oil spill (Pasparakis et al. 2019). In contrast, during the same period (1957–2003) and adjacent to the northwestern GOM collapse, sightings and mean weights of Atlantic tarpon at the International Grand Isle Tarpon Rodeo in Louisiana remained relatively stable, suggesting the recreational fishery was resilient to the nearby collapse (Dailey et al. 2004). More recently, the adult Atlantic tarpon fishery in Texas has begun to recover, with increasing juvenile abundances since the 1990s, possibly related to resurgence of sexually mature adults in the area (Stephens et al. 2024). Despite the putative mixing area between the Western and Eastern GOM contingents at the Mississippi Delta (Dance, M. A., unpublished data), the recovery process in the Western GOM contingent took multiple decades.

Atlantic tarpon overexploitation, declines in abundance and delayed recovery have been observed elsewhere, notably in Brazil (Menezes 1967; Fernandes et al. 2022) and Colombia (Garcia and Solano 1995). Indeed, global historical landings declined by > 80% between 1965 and 2007 (Adams et al. 2014). Despite these declines, detailed information on their current status and recovery processes are limited (Spotte 2016). In Colombia, Garcia and Solano (1995) reported that at a single port alone, the Atlantic tarpon commercial fishery approached nearly 600 t annually in the 1960s before collapsing completely. Interestingly, while no recovery has been observed along the northwest coast of Colombia (i.e., the Caribbean side), an increase in Atlantic tarpon abundance was observed in the Tropical Eastern Pacific following the opening of the Panama Canal (Castellanos-Galindo et al. 2019). Atlantic tarpon are now found as far as 700 km from the canal ranging from Guatemala to Peru (Neira and Acero 2016; Barraza 2018; Castellanos-Galindo et al. 2019; Hooker 2025). While this expansion is beginning to support a growing sport fishing industry in the Pacific region of Colombia, Panama and Costa Rica (Castellanos-Galindo et al. 2019), the Caribbean fishery in this region struggles to recover. Taken together, these examples suggest consistent spatial variability in recovery and that spawning unit recovery potential may be shaped by entrainment.

2.3 | Biological Hypothesis 3: Which Fish Are the Colonisers?

To assess support for *Biological Hypothesis 3*, we reviewed available literature on occurrences of Atlantic tarpon outside their established range, with a focus on identifying which life stages, juveniles or adults, may act as potential colonisers. We searched for instances of vagrancy, atypical movement and habitat shifts using combinations of keywords such as 'Atlantic tarpon', 'vagrancy', 'new record', 'migration', 'survival', 'temperature range', 'colonisation' and 'climate change' via Google Scholar. Our aim was to assess consistent evidence on whether movements beyond typical geographical boundaries are associated with juvenile vagrancy or external environmental forcing that could disrupt entrainment and support the colonisation of new habitats.

Anecdotal reports from anglers suggest juvenile Atlantic tarpon (≥ 1 year in age) inhabit areas outside their typical range, such as South Carolina, North Carolina and Mississippi, raising questions about juvenile vagrancy. Although smaller juveniles (typically < 30 cm and < 1 year in age) recruit via larval transport to these areas (Elmo et al. 2021; Graham et al. 2021), it is unlikely these metamorphosed juveniles survive beyond winter months since juvenile Atlantic tarpon have a mean minimum lethal temperature of 13.7°C (Mace et al. 2017). Multi-year survival is possible if thermal refuges like deepwater access or warm water discharges from power plants are present (Mace et al. 2020). Still, even if these refuges occur, the potential for these juveniles to reach coastal areas remains uncertain. Tracking data indicate that large juveniles (> 30 cm fork length) can be either resident or nomadic (Griffin, et al. 2023), suggesting that the observed juveniles in these unexpected areas have either become entrained earlier than the age/size at maturity or are vagrants. Although further empirical data is needed to confirm these patterns, guides and anglers have reported juveniles associating with schools of adult tarpon in these regions.

For adult Atlantic tarpon, reports and tracking data have substantiated that adults are capable of vagrancy, with individuals documented in unexpected areas beyond their typical range. Such areas include the cooler, temperate waters off Nova Scotia, the Azores and across northwest Europe, such as Ireland, France, Spain and Portugal (Twomey and Byrne 1985; Bañón et al. 2019; Luo et al. 2020). Whether the vagrants reported in Europe came from the Western Atlantic or Eastern Atlantic waters is debated (Bañón et al. 2019), and these unusual occurrences are believed to be influenced by external environmental forces. Since adult Atlantic tarpon are believed to use 26°C isotherms as migratory cues (Luo et al. 2020), oceanic features associated with the Gulf Stream (e.g., eddies, altered currents) may occasionally interrupt entrained movements and lead to vagrancy. This mechanism might allow adult Atlantic tarpon to reach and colonise new habitats, provided the environmental conditions are conducive to their biology and ecology.

Vagrancy involves exploratory or atypical movements driven by immediate environmental forcing or man-made structures (i.e., the Panama Canal), whereas climate-driven shifts represent broader population responses to long-term habitat changes. However, climate change may open previously unsuitable habitats by shifting thermal regimes, improving prey availability or reducing historical cold-water barriers. In such cases, vagrants reaching these areas may find them increasingly suitable, facilitating their persistence and even supporting range expansions over time. Indeed, acoustically tagged Atlantic tarpon have exhibited potential vagrant movements, being detected as far as coastal waters in Virginia, Maryland and Delaware (Griffin, et al. 2023) and anglers have reported an apparent increase in Atlantic tarpon in more northern areas, including the Chesapeake Bay, Virginia, Long Island, New York and Cape Cod, Massachusetts (e.g., Clarke 2024).

Although Petitgas et al. (2006) identify both juvenile vagrancy and environmentally forced adult colonisation as plausible mechanisms for the formation of new contingents, our review found more consistent evidence for adult vagrancy. However, supportive observations of juveniles in atypical habitats, particularly those older than 1 year, suggest that juvenile vagrancy is possible and could play a role under certain conditions. Together, these findings support the idea that both life stages may initiate colonisation and, if new entrainment is established, facilitate the persistence of novel migratory patterns.

2.4 | Biological Hypothesis 4: Do Juveniles Change Their Behaviour in the Presence of Adults?

To assess support for *Biological Hypothesis 4*, we reviewed literature on juvenile behaviour and ontogenetic shifts in different regions with different types of migratory propensities. We used search terms such as 'Atlantic tarpon', 'ontogenetic shift', 'migration', 'repeatability' and 'elements and isotopes' via Goole Scholar. Our aim was to assess supportive evidence focused on identifying behavioural changes in juveniles potentially influenced by the presence or absence of adults, indicating the possible for social learning transmission.

Inferred from a multi-year acoustic telemetry dataset, large juvenile Atlantic tarpon were generally resident or nomadic until nearing maturity, at which point they began to adopt adult-like migratory behaviours with high levels of repeatability, that is, conservatism (Griffin, et al. 2023). These individuals exhibit seasonal migratory behaviours that align spatially and temporally with adult Atlantic tarpon, appearing to migrate with repeat spawners to and from pre-spawning aggregation sites or to putative foraging areas. Among migrants, there was no relationship between size and migratory behaviour. Individuals displayed high-intra-individual variability and high inter-individual repeatability in migratory strategies (Griffin, et al. 2023). This pattern suggests that movement strategies may not be solely driven or shaped by environmental cues or swimming capacity, but by social facilitation or learning.

Examining changes in stable isotope (e.g., $\delta^{15}N$, $\delta^{13}C$) and element (e.g., Sr.:Ca, Ba:CA) values across calcified structures such as scales and otoliths in Atlantic tarpon has proven valuable for identifying ontogenetic shifts and detecting movement across salinity gradients or into new systems, as inferred from baseline tracer values (Brown and Severin 2008; Woodcock and Walther 2014; Rohtla and Vetemaa 2016; Seeley and Walther 2018; Kurth et al. 2019). Comparing $\delta^{15}N$ values between Atlantic tarpon from Puerto Rico, where distinct migratory contingents are not observed, and those from Texas (Western GOM contingent), Woodcock and Walther (2014) found contrasting patterns in ontogenetic isotopic shifts. In Texas, $\delta^{15}N$ values increased from the core (younger age) to the edge of their scales (older age), reflecting an ontogenetic shift in trophic level consistent of moving into new food web systems. In contrast, scales from Puerto Rico displayed more variable patterns, with some individuals showing little increase in $\delta^{15}N$ from the core to the edge. This lack of change suggests that some individuals remained resident throughout ontogeny (Woodcock and Walther 2014). With no overlap with migrant repeat spawners, like that in the GOM, these fish may not have been entrained into a migratory contingent but formed a resident contingent, also highlighting how selection pressures to migrate or not vary regionally. Although direct evidence of juvenile behaviour in the absence of adults is limited, the available data support that adult presence may influence post-maturity behaviour in Atlantic tarpon through entrainment.

2.5 | Biological Hypothesis 5: Do Individuals Migrate Between Contingents?

To assess support for *Biological Hypothesis 5*, we examined evidence from genetic and electronic tagging studies, as well as from a mark-and-recapture program, to determine whether individuals form distinct contingents, exhibit phenotypic plasticity in their migratory behaviours and regularly move between contingents. The literature review was completed using combinations of keywords such as 'Atlantic tarpon', 'genetics', 'population dynamics', 'tracking', 'migration', 'spawning', 'conservatism' and 'phenotypic plasticity' via Google Scholar. We analysed data from the National Marine Fisheries Service (NMFS)

Cooperative Tagging Center Mark-and-Recapture Program. This dataset spans from 1961 to 2015 and includes fish tagged with intramuscular dart/anchor tags [multiple series (R, T, HM), Floy Tag Mfg, ~120 mm plastic streamer, Southeast Fisheries Science Center's Cooperative Tagging Center (https://contingent.fisheries.noaa.gov/southeast/atlantic-highly-migratory-species/cooperative-tagging-program)]. Associated angler-reported data provided capture and recapture dates, locations and estimated fish size. The majority of this effort was based on the tags distributed to cooperative fishers all over the Atlantic and its associated water bodies. Direct interpretation of recapture rates from angler-reported data assumes that angler-fishing effort is equal across the entirety of the stock and that any recaptures are equally likely to be reported. However, this is almost certainly not the case. As such, we report and interpret recapture rates within and across contingents and putative pre-spawning/mixing areas (e.g., Mississippi Delta, South Florida) as an indication of the scale of movements that are possible, rather than as an indicator of how frequently they occur within the broader population. By combining insights from the literature review and analysis of long-term mark-and-recapture data, our aim was to assess demonstrative evidence for the role of phenotypic plasticity in Atlantic tarpon population dynamics, particularly as it relates to cross-contingent movement.

At the global scale, McMillen-Jackson et al. (2005) reported high genetic differentiation and low gene flow between Atlantic tarpon populations in the Western Atlantic and Africa. However, within the Western Atlantic, genetic analyses have produced mixed results. Using nuclear DNA markers, Ward et al. (2004) identified distinct population structure and genetic differentiation between the Western and Eastern GOM contingents. In contrast, a subsequent study by Ward et al. (2008), which used microsatellite DNA markers, found no substantial genetic distinction between these contingents. This discrepancy in genetic differentiation within the GOM may, in part, be explained by the potential spawning behaviours of the Atlantic tarpon off Louisiana (Stein III et al. 2012, 2016; Graham et al. 2017; Luo et al. 2020). Considering that the Western and Eastern GOM contingents overlap here (Stephens et al. 2024), low genetic differentiation may occur because of spawning overlap and larval dispersal mechanisms (Gehringer 1959; Eldred 1967). Indeed, 1-day-old Atlantic tarpon leptocephalus larvae have been captured in this region (Shenker, J. M., unpublished data). While overlap occurs at the Mississippi Delta (Dance, M. A., unpublished data), no data from acoustic telemetry (Griffin, et al. 2023; Stephens et al. 2024) or satellite telemetry (Luo et al. 2020; Drymon et al. 2021) have documented instances of Atlantic tarpon fully crossing from the Western and Eastern GOM contingents, for example, from Texas to Florida or vice versa. In contrast, within the Eastern GOM contingent, multi-year acoustic telemetry data has demonstrated around 20% of tagged individuals were detected moving across both the Eastern GOM and Eastern US Seaboard contingents at least once (Griffin, et al. 2023).

From 1961 to 2015, the NMFS Cooperative Tagging Center Mark-and-Recapture Program recorded 195 recaptures from 10,384 tagged and captured Atlantic tarpon, providing insights into inter- and intra-contingent movement patterns. Among these recaptures, 28% ($n=55$) involved movements across regions, including crossings between contingents or mixing areas such as the Mississippi Delta and South Florida (Figure 1, Table 1). For fish tagged in the Eastern US Seaboard contingent, 38% ($n=6$) were recaptured within the same contingent, while another 38% ($n=6$) were recaptured in the mixing area of South Florida. Four individuals (24%) were recaptured outside this contingent, with two (12%) in the Eastern GOM and two (12%) in Cuba. Similarly, for fish tagged in the Eastern GOM, 75% ($n=69$) were recaptured within the same contingent. The remaining recaptures included 18% ($n=17$) in South Florida, 5% ($n=5$) in the Eastern US Seaboard contingent and 1% ($n=1$) in Cuba. For fish tagged in South Florida, 80% ($n=55$) were recaptured within the same region, while others were recaptured in the Eastern GOM (10%, $n=7$), the Eastern US Seaboard (7%, $n=5$), the Mississippi Delta (1%, $n=1$) and the Western GOM (1%, $n=1$). Fish tagged in the Mississippi Delta were recaptured in the Eastern GOM (60%, $n=6$), within the Mississippi Delta (20%, $n=2$) and the Western GOM (20%, $n=2$). In contrast, Atlantic tarpon tagged in the Western GOM ($n=2$) and Puerto Rico ($n=1$) were exclusively recaptured within their respective tagging regions. Overall, most recaptures occurred within the same region or adjacent mixing areas. However, movements across multiple contingent groups and from the US to Cuba (i.e., vagrancy), provide evidence of phenotypic plasticity in migratory behaviour within the Atlantic tarpon population.

3 | Discussion

Examining the life history, migratory patterns and recovery processes of fish species with complex life cycles can lead to support for the entrainment hypothesis, which suggests that juveniles and first-time spawners learn migratory behaviours from repeat spawners (Petitgas et al. 2006). Here, by integrating life history knowledge for Atlantic tarpon, prior research findings and mark-and-recapture data, we demonstrate the likelihood of entrainment through consistent, supportive and demonstrative lines of evidence framed by five underpinning biological hypotheses. These findings highlight how entrainment and phenotypic plasticity in migration may increase the resilience of Atlantic tarpon stocks to collapse.

Entrainment mechanisms can shape behavioural consistency within populations and under certain conditions, may reinforce ecological separation across populations. For example, unlike the contingents within the GOM that migrate along the coast, in Costa Rica, Atlantic tarpon extensively migrate inland into freshwater systems. Using otolith microchemistry, Brown and Severin (2008) found that many Atlantic tarpon in Costa Rica, including those caught in Lake Nicaragua (190 km inland via the San Juan River), spend their entire adult phase, if not their lives, in freshwater environments. Unique to Costa Rica, an entire Atlantic tarpon recreational fishery has emerged in freshwater rivers, some located many kilometres from the Caribbean coast (Enderlin, T., pers. comm.). Genetic analyses have identified Atlantic tarpon in Costa Rica as distinct from other Western Atlantic populations (McMillen-Jackson et al. 2005; Ward et al. 2008), indicating a higher likelihood of local recruitment and reproductive isolation. Notable differences in life history traits further support this isolation, including differences in size at sexual maturity between Atlantic tarpon in Costa Rica and

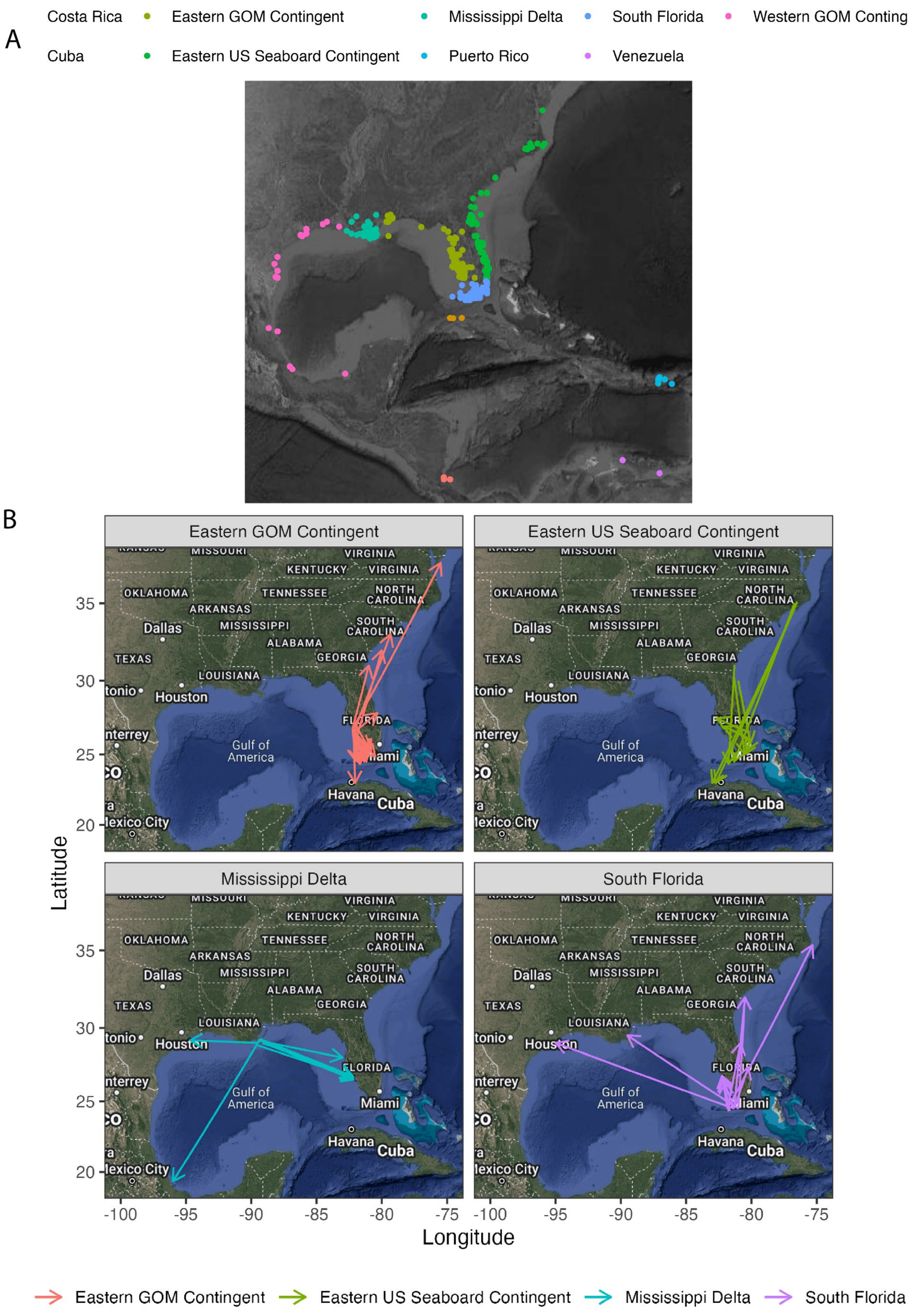

FIGURE 1 | Legend on next page.

FIGURE 1 | Tagging and recapture information from the National Marine Fisheries Service Cooperative Tagging Center Mark-and-Recapture Program with Atlantic tarpon (*Megalops atlanticus*) from 1961 to 2015, with (A) all tagging and recapture locations within the Western Atlantic and (B) to-from recaptures across contingents and putative spawning/mixing areas, such as Mississippi Delta and South Florida.

TABLE 1 | Tagging and recapture information from the National Marine Fisheries Service Cooperative Tagging Center Mark-and-Recapture Program with Atlantic tarpon (*Megalops atlanticus*) from 1961 to 2015.

Tagging location	Recapture location	Recapture number	Proportion
Western GOM contingent	Western GOM contingent	2	1
Mississippi Delta	Eastern GOM contingent	6	0.6
	Mississippi Delta	2	0.2
	Western GOM contingent	2	0.2
Eastern GOM contingent	Eastern GOM contingent	69	0.75
	South Florida	17	0.18
	Eastern US Seaboard contingent	5	0.05
	Cuba	1	0.01
South Florida	South Florida	55	0.8
	Eastern GOM contingent	7	0.1
	Eastern US Seaboard contingent	5	0.07
	Mississippi Delta	1	0.01
	Western GOM contingent	1	0.01
Eastern US Seaboard contingent	Eastern US Seaboard contingent	6	0.38
	South Florida	6	0.38
	Cuba	2	0.12
	Eastern GOM contingent	2	0.12
Puerto Rico	Puerto Rico	1	1

Note: Only data from recaptured are shown, and proportion is the number of recaptures in a given location relative to their shared tagging locations.

their Florida counterparts (Crabtree et al. 1997). These observations imply the potential for isolation and entrainment mechanisms have allowed Atlantic tarpon to develop conservatism in unique habitats in Costa Rica, such as inland freshwater habitats.

Similarly, other species have also developed distinct contingents and struggle to recover when collective memory of migratory knowledge is lost (Petitgas et al. 2010). For example, following the collapse of the Northern cod (Atlantic cod; *Gadus morhua*) population off Newfoundland and Labrador in the early 1990s, the offshore contingent, known for spawning at the shelf has not recovered while their abundance in coastal areas has (Rose et al. 2000; Smedbol et al. 2002; Hu and Wroblewski 2009). Considering migrating schools of Northern cod were size-structured aggregations with juveniles and adults and led by older 'scouts,' it has been hypothesised that the knowledge transfer of migration routes and offshore spawning habitats, intrinsic to the offshore contingent, has been lost (Rose 1993; Petitgas et al. 2010). For successful re-establishment, straying individuals from coastal and bay contingents may play a pivotal role (Hu and Wroblewski 2009). However, for successful recolonisation to occur, these individuals must overcome the Allee effect, a phenomenon wherein low adult abundance reduces reproductive success (Frank and Brickman 2000; Perälä et al. 2022). While low reproductive success exacerbates recovery challenges, vagrancy and dispersal behaviours across the population may offer a pathway to restore lost contingents. An analysis of nearly 100 years of Atlantic cod tagging data revealed that the population exhibits a wide range of migratory behaviours, with 41% remaining sedentary, 18% being accurate homers, 20% being inaccurate homers and another 20% acting as dispersers (Robichaud and Rose 2004). This highlights the importance of understanding and conserving the migratory behaviours within a population, as it may dictate their resilience and recovery strategies.

More recently, the re-emergence of Atlantic bluefin tuna in Nordic waters after nearly 50 years (MacKenzie and Myers 2007; Aarestrup et al. 2022) provides an example of how species form new contingents through the development of novel migratory pathways. The repeatable return of individual Atlantic bluefin tuna to the re-colonised foraging grounds in Nordic waters (Aarestrup et al. 2022) suggests that both vagrancy and entrainment have played roles in establishing this pattern of habitat conservatism (Petitgas et al. 2010). Drawing parallels to the Atlantic bluefin tuna fishery's emergence and subsequent collapse in Brazil during the 1960s (Secor 2015), it is critical to maintain unified management measures in Nordic waters and connected contingent units. Such measures aim to preserve collective migratory knowledge and prevent its loss (De Luca et al. 2014; Berdahl et al. 2018), ensuring the long-term sustainability and resilience of these migratory contingent units.

While Atlantic tarpon do not have the same level of management attention as Atlantic bluefin tuna or Atlantic cod, this species still holds considerable economic, ecological and cultural value (Kokomoor 2010; Mill et al. 2010; Davis 2017; Smith et al. 2022). Given the reported declines in Atlantic tarpon populations and fisheries (Griffin, et al. 2023) and a lack of formal stock assessments, addressing these challenges requires an integrated approach to management (Adams et al. 2023; Griffin et al. 2025). This approach should encompass and consider the various threats Atlantic tarpon encounter along their migratory pathways (Griffin, et al. 2023), from shark depredation and post-release mortality (Guindon 2011; Luo et al. 2020; Horowitz et al. 2023; Casselberry et al. 2024), harmful algal blooms (Griffin, et al. 2022), juvenile habitat degradation (Wilson et al. 2019; Bunting et al. 2024), to the effects of climate change (Carroll et al. 2023; Danylchuk et al. 2023). Ultimately, considering the likelihood of entrainment shaping Atlantic tarpon stock dynamics and contingent structure, management should be tailored to maintaining Atlantic tarpon migratory knowledge and its transfer to younger conspecifics. Prioritising research questions that explore the connections between contingents (e.g., population genetics, tagging at putative mixing areas), the mechanisms of colonisation and recruitment (e.g., additional tagging, larval transport models), the long-term trends in relative abundance (e.g., catch and mortality data, pre-spawning aggregation size estimates) and the impact of anthropogenic and environmental changes (e.g., stable isotope analysis, changes in space use, angler/boater avoidance) on different life stages of Atlantic tarpon will be key. Such research is fundamental for developing more complete management and conservation strategies that reflect the complex life cycles and migratory behaviours of Atlantic tarpon.

4 | Conclusion

These findings further our understanding of Atlantic tarpon stock dynamics and highlight the role of spatially explicit life cycles, vagrancy and entrainment mechanisms in management, resilience and recovery. The framework for evaluating the entrainment hypothesis (Petitgas et al. 2006) provides a structured approach to better understand migratory marine fish stocks, particularly those that have complex life cycles or are data deficient, like that of Atlantic tarpon. A strength is its clearly defined questions and emphasis on assessing the spatial and temporal connectivity across life stages, as well as how contingent structure emerges, persists and affects collapse and recovery dynamics. However, as demonstrated in our case study, generating clear lines of evidence for each biological hypothesis can be challenging due to species-specific nuances and data limitations. Nonetheless, applying this framework and examining each line of evidence revealed patterns consistent with entrainment and highlighted important knowledge gaps and research priorities. From a conservation standpoint, coordinated and targeted management strategies are key to maintaining connectivity across life stages and habitats and to preserve the transfer of migratory knowledge. As climate change, overharvest and habitat degradation increasingly threaten fisheries, this framework should help support biodiversity and healthy fisheries.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used in this manuscript are available upon request.

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