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CHARACTERIZING THE RELATIONSHIP BETWEEN SPECIES RICHNESS AND THE SEASONAL PHENOMENON OF TROPICAL FISH DISPERSAL IN NEW ENGLAND WATERS

A Thesis Presented

by

MICHAEL E. O'NEILL

Submitted to the Office of Graduate Studies,
University of Massachusetts Boston,
In partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2021

Marine Science and Technology Program

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ABSTRACT

CHARACTERIZING THE RELATIONSHIP BETWEEN SPECIES RICHNESS AND THE SEASONAL PHENOMENON OF TROPICAL FISH DISPERSAL IN NEW ENGLAND WATERS

May 2021

Michael E. O’Neill, B.A. & B.S., Boston College
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The Gulf Stream exerts tremendous influence over oceanographic conditions in the Northwest Atlantic as it transports tropical water to higher latitudes. As the Gulf Stream’s path traverses the east coast of North America, there are implications for the biogeography of marine ecosystems within this range and beyond. While the meandering eddies and warm core rings generated by the Gulf Stream persist year-round, the seasonal warming of New England’s coastal waters afford many tropical species transported by the current temporary residence through the summer and fall. Many aspects that shape this phenomenon and its impact on coastal ecosystems remain a mystery. There is evidence that habitat choice by larval fish affects their distribution within tropical waters. Based on this evidence, tropical species incidence may serve as an indicator of critical nursery habitat and biodiversity hotspots for targeted conservation efforts. From 2015 to 2017, a biodiversity survey of Pleasant Bay, Massachusetts gathered incidence data to estimate species richness at unique sites within the estuary. This survey asserts that sampling species incidence may be a viable and efficient small-scale method to extrapolate native species richness and indicate desirable habitat for non-native tropical species. The distribution of teleost species is the result of many factors. To begin to address the conditions that shape observed richness, characteristics including sediment type and dominant benthic communities were applied as criteria to cluster survey sites for species richness analysis through sample-based rarefaction. The results of this study indicate that small-scale species incidence sampling can be used to highlight critical habitat for conservation protections. The evidence for habitat choice by juvenile fishes highlights the importance of evaluating biodiversity as an indicator for ecosystem health and resiliency. Paired with a broader citizen science network, characteristics including reported species frequency and a review of species life history, are beginning to reveal potential ecosystem impacts that result from the dispersal of expatriated species by the Gulf Stream. As climate change continues to alter marine coastal environments, furthering our understanding of the role expatriated species play in New England waters may improve the allocation of conservation effort and help anticipate future ecosystem changes.

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And to my parents, Jim and Carol, and my wife, Alison, whose love and support helped push me across the finish line.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

FACTORS SHAPING THE GULF STREAM ORPHAN PHENOMENON

Introduction

The Gulf Stream has been the fascination of scientists and sailors for centuries. Numerous indices have been developed to quantify its activity and there are many global processes that influence its productivity. Regardless of underlying variations in its path, the Gulf Stream is responsible for an enormous amount of warm water being carried through the Florida Straits and the South Atlantic Bight, northeast beyond Cape Hatteras (Zeng and He, 2016). As the Gulf Stream meanders, swirling eddies of warm water and large meanders that break off as Warm Core Rings (WCRs) proceed northward to the coast of North America. These vectors of warm water can be of considerable depth and more than a hundred kilometers across (Olson and Backus, 1985). Contained within these rings and eddies of warm water are the flora and fauna of its tropical origins. Through this mechanism, a wide variety of species in their planktonic stages including eggs, larvae, and juvenile fishes are transported beyond their native geographic range throughout the temperate coastal range of North America (Gawarkiewicz et al. 2018). Influencing the Gulf Stream's activity are large-scale fluctuations in both seasonal and inter-annual conditions making the relationships between Gulf Stream activity and other climate processes complex. The peak in WCR formation is May, June, and July providing a method for large volumes of tropical water to be transported northward at the time of year that many tropical and subtropical finfish species are spawning. Gangopadhyay et al. (2019) found that a substantial inter-annual variation in WCR formation has led to increasing WCR numbers in recent years (2000-2017). Regardless of the variation in WCR production, it remains unclear as to the correlation between WCR activity and abundance of tropical fish in northern latitudes.

Between 25°N and 45°N latitude the North American coastline spans transitioning environmental characteristics. A variety of life history strategies across different families of fish combines with these transitioning environments to create a complex biogeographic distribution of species assemblages. A comprehensive review of all factors involved with this topic are too broad for the scope of this paper. A few aspects of fish biology, considered most critical by the author and discussed here, will assist in the focus on tropical species distribution due to Gulf Stream transport. Several historical reports and anecdotal evidence via personal communication indicate that occurrence of these "Gulf Stream Orphans" (GSOs) and the species represented has been variable and decreasing in recent years compared to previous decades. Due to the geographic range throughout which the phenomenon occurs, it is likely that fluctuations in WCR formation and Gulf Stream transport may lead to both increases and decreases in abundance along different portions of the North American coastline.

In an effort to confront the "needle in a haystack" characteristic of the phenomenon, a citizen science network entitled "The Gulf Stream Orphan Project" was launched in 2016 to assemble sightings of unusual tropical species (termed "Gulf Stream Orphans" or GSOs) in the Northwest Atlantic. Paired with the launch of this broader data-gathering effort, a survey of 24 different seine and trawl locations within Pleasant Bay in Orleans, Massachusetts was conducted over three years. Species incidence data were gathered at each site in order to compute rarefaction curves to estimate species richness at each sampling site.

In addition to the physical processes that bring tropical species northward in the Atlantic Ocean, there is significant evidence for habitat choice by reef species having an impact on distribution of species in their native range. Based on this evidence, it is hypothesized that these wayward tropical fish may also exercise habitat choice in the selection of micro-habitat that parallels characteristics of their native reefs. The Pleasant Bay survey indicates that sampling species incidence may be a viable small-scale method to extrapolate species richness and indicate desirable nursery habitat for non-native tropical species and critically biodiverse areas for native species. Assessment of biodiversity often requires large, well-resourced sampling efforts of both incidence and abundance data to establish estimates of species richness and evenness. The initial findings of these survey efforts will help guide further areas of exploration to more accurately describe the biological and physical factors that shape the observed incidence of expatriated tropical fish species in New England waters.

Seasonal Temperature

While the Gulf Stream and its associated variation is responsible for the transport of tropical species into the Northwest Atlantic, there are several environmental parameters that are required for the development and sustained residence of these species at northern latitudes. Chief among these is ambient water temperature and the associated thermal tolerance of tropical and subtropical species. Sea surface temperature data collected for over a century in Woods Hole, Massachusetts indicate that mean winter water temperature ranged from 1.2-3.6° C and mean summer water temperature ranged from 19.3-20.4° C over the course of the 20th century (Nixon et al. 2004). The average summer temperature is well within the range tolerated by subtropical and tropical fish species and the seasonality provides several months of favorable conditions for these expatriated species to survive beyond their native range. The preferred temperature range of several subtropical species detected in Gulf Stream Orphan surveys generally possess a lower limit of 14° C (Kaschner et al. 2019). Evidence gathered in Woods Hole, MA from the longest coherent coastal sea surface temperature record in North America reveals that this lower limit temperature is present along the Massachusetts coastline from May to October on average and the warming effects of anthropogenically induced climate change has only expanded that seasonal window (Nixon et al. 2004). The seasonal warming of New England waters in summertime allows for tropical species transported by the Gulf Stream to not only survive, but to complete their larval development through flexion, settlement, and into their juvenile life stages over several months. The observed temperature conditions along New England's coastal waters during this time indicate a relatively broad window of opportunity for these tropical and subtropical species to inhabit an ecological niche once transported northward. Water temperature is the foundational condition that opens the door for the occurrence of this phenomenon.

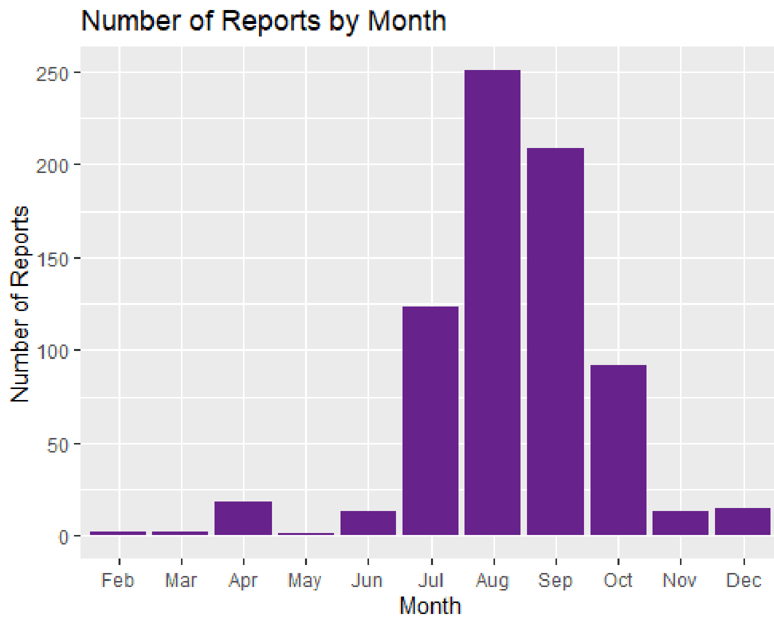


Figure 1. Number of Reports by Month. *Reports of potential "Gulf Stream Orphans" collected by the Gulf Stream Orphan Project from citizen scientists, public aquaria, and other marine research institutions.*

A comparison of reporting frequency by month (Figure 1) illustrates the influence of seasonal temperature on species occurrence in northern latitudes. As previously stated, water temperature along the New England coastline generally exceeds the thermal minimum for many subtropical and tropical species from May to October when the highest frequency of reports is also observed. This distribution is also compounded by the correlation with highest rates of observer effort and participation by citizen scientists. Reports to the Gulf Stream Orphan Project outside of the July-September range are generally received from fishermen at sea where sampling methods vary and from citizen scientists throughout the mid-Atlantic region where water temperatures may reach tolerable ranges earlier in the year.

Beyond water temperature, consideration must then be given to numerous biological factors that further shape the observed phenomenon. The duration and successful residence by many species indicates that the microhabitats within Pleasant Bay and other coastal areas in New England can sustain the ecological resources and functions needed by these fishes over several months.

Spawning of Reproductive Populations

The sighting prevalence of different species in northern waters varies widely and gives rise to several questions as to the factors causing such drastic differences in distribution and abundance. It is likely that variation in life history traits among species plays a role in increased or decreased dispersal by the Gulf Stream. Many fishes, particularly those residing in lower latitudes, produce large numbers of eggs over a protracted spawning season in order to address the challenges of a diffuse and patchy open ocean environment (Houde, 1989; Roberston, 1991; D'Alessandro et al. 2011). Several biological factors at the genesis of the Gulf Stream Orphan phenomenon include the timing and reproductive methods of spawning populations as well as the progression of larval development through settlement to subsequent young-of-the-year populations.

Different tropical species seen along the coast of New England may be transported as egg, larvae, or juveniles depending on life history strategies and development. A principal difference impacting dispersal is spawning strategy amongst reef fish species. Many of the most frequently reported Gulf Stream Orphan species disperse off-spring via buoyant pelagic eggs and/or pelagic juvenile life stages including *Fistularidae, Priacanthidae, Balistidae,* and *Chaetodontidae* (Hardy, 1978; Curran, 1989). Broadcast spawning and pelagic dispersal is likely the most prevalent strategy to result in transport by the Gulf Stream. Many of the ichthyoplankton present in the Northwest Atlantic possess these pelagic characteristics that would enhance dispersal by the Gulf Stream and several species reported in northern latitudes come from spawning populations that participate in prolonged spawning seasons that peak in spring and summer (Fahay, 1983). Many broadcast-spawning species also participate in spawning aggregations that could play a role in their prevalence in Gulf Stream transport. Spawning aggregations are generally divided into two forms, transient fish spawning aggregations (tFSAs) and resident aggregations. Dozens of species across 10 different families of fish in the Caribbean region are known to use tFSAs including notable groups like snapper (*Lutjanidae*) and grouper (*Serranidae*) that have also been reported as Gulf Stream Orphans. Other known GSO's that participate in resident aggregations include surgeonfish (*Acanthuridae*), and goatfish (*Mullidae*), (Kobara et al. 2013). Spawning aggregations, and particularly tFSAs rely on a suite of environmental and ecological cues that are also not fully understood or explored. It is likely that natural phenomena like spawning aggregations could play a role in the distribution of tropical species by the Gulf Stream as well as observed inter-annual variation in reported species and abundance. It would seem less likely that alternative reproductive strategies including nesting with demersal eggs and mouth brooding would yield the same opportunity for transport via major ocean currents.

Geographic Distribution of Spawning Populations

Combined with spawning strategy is the geographic location of spawning aggregations as well as the population ranges that would increase the likelihood of Gulf Stream transport. Along with species that participate in transient fish spawning aggregations that may be located near the Gulf Stream, many reef species inhabit live-bottom habitat in the

South Atlantic Bight (SAB). A review of bottom trawl survey data in the SAB found numerous reef fish species determined to be warm-temperate or subtropical-tolerant species can reside year-round in the intermediate open-shelf zone (Miller and Richards, 1980). Fifty species discovered on live-bottom sites in the SAB have been reported as Gulf Stream Orphans through the GSO Project. Farmer et al. (2017) found in an analysis of spawning reef fish populations off the southeastern coast of the United States that spawning females of reported GSO species, including several grouper (*Serranidae*) species have been sampled off the coast of South Carolina and their peak spawning occurred in the spring and summer from February to August depending on the species. Lunar phase also influences the timing of these reproductive populations with several grouper species reported in northern latitudes being most commonly observed spawning from May to August during particular phases of the lunar cycle (Farmer et al. 2017). Evidence of stable reef fish populations and spawning activity in the SAB present a likely origin point for the Gulf Stream Orphan phenomenon. Based on the path of the Gulf Stream and its proximity to these live-bottom habitats, it is likely that broadcast spawning species native to this region provide the eggs and larvae picked up by the Gulf Stream as opposed to reproductive populations further south into the Caribbean.

Spawning Season and Larval Transport via the Gulf Stream

There are several temporal factors to consider in the occurrence of the Gulf Stream Orphan phenomenon. The confluence of spawning season along with larval development and the timing of transport of the Gulf Stream all play a role in the arrival and success of expatriated species in the Northwest Atlantic. Perhaps another factor in the disparity between different species arriving and surviving beyond their native range is due to differences in the duration of larval development and how it relates to the arrival of warm water in northern latitudes. In the case of the butterflyfishes (*Chaetodontidae*), settlement of larval fish occurs at approximately 40 days-post-hatch (Leis, 1989). This coincides with the transport time of warm water by the Gulf Stream so that these larvae are settling as they reach the coast of New England. Analysis of 87 Warm Core Rings formed over 10 years of Gulf Stream activity found that WCR lifespan had a bimodal distribution divided at 140 days, with short-lived rings (<140 days) having a mean lifespan of 54 days, and long-lived rings (>140 days) having a mean lifespan of 229 days (Brown et al. 1986). These durations indicate that the occurrence of GSO's in New England waters may be shaped by the selective pressures created within WCR environments and the larval ecology of potential GSO species during the first few weeks to months of development. Contained within a dispersed larval population can be numerous variations in traits that can result in selective loss due to food availability, temperature, and other environmental factors (Sponaugle and Grorund-Colvert, 2006; Sponaugle et al. 2006). WCR environments likely shape these conditions, influencing the survivorship of different tropical and subtropical species based on food sources during larval and juvenile stages of development and water temperature and chemistry as the rings migrate through the Northwest Atlantic and eventually disperse along the continental shelf. The timing of peak WCR formation from May to July and the transport time to the coast of New England are both characteristics of the physical oceanography of the Gulf Stream that may play a critical role in the occurrence of this phenomenon. As these rings form along the

Gulf Stream, entraining tropical fish eggs and larvae, the transport time and seasonality of their formation align with the dispersal and development of reef fish species to result in the residence of these wayward tropical species temporarily in the Northwest Atlantic. Variation in WCR formation and the frequency of tropical species sighted along the coast of the United States may be attributed to the region in which rings form. While total numbers of WCRs have increased from 2000-2017 in comparison to the 20 years prior, the total number generated in the western-most region between 75° W and 70° W longitude has seen the fewest births (Gangopadhyay et al. 2019). Anecdotal reports indicate that the prevalence of Gulf Stream Orphans has been lower in the last decade indicating that correlation with WCR formation may not be directly related. WCRs may provide a mechanism for punctuated arrival of tropical water containing planktonic flora and fauna but perhaps the smaller eddies that are shed off of the Gulf Stream closest to the coast are responsible for a more continuous dispersal of tropical fish from year to year. Regardless, the physical transport of warm tropical water is only one of a multitude of factors worthy of examination in understanding this phenomenon.

Developmental Biology of Larval Reef Fish

Habitat Partitioning

Fish distribution in varying habitats within their native range is extensively documented for tropical species (Berumen et al. 2005). Differing habitat types including rocky bottom, sandy bottom, algae-dominant, and coral-dominant settings provide a diverse array of habitat-choice for reef species. On top of this, life-history strategies vary by reef species as to what habitats are used as nurseries for juveniles versus residences for adults. In some species, rigid life stage-habitat partitioning may exist while other species may be ubiquitously distributed across habitat types and life history stages. Gratwicke et al. (2006) found that bays and lagoons are important nursery habitat for reef-dwelling fishes in that all species that demonstrated partitioning between bays and reefs used bay habitat as juveniles before moving to reefs in adulthood. Outside of their native range, it is likely that the juveniles of these reef-dwelling species would seek out the same habitat characteristics in the bays and sheltered estuaries of temperate regions.

Habitat Selection

Larval reef fish are capable of selecting desirable habitat through several factors that may apply to the habitats in New England waters. While the broad dispersal of larval and juvenile reef fishes is largely dependent on ocean currents and tidal activity, post-settlement marine fishes do have opportunity to select for habitat on small spatial scales (<1km) (Jones, 1991). Upon arrival in New England waters, it is safe to assume that similar environmental conditions and habitat characteristics of their native ranges play a role in shaping the selection and distribution of these fishes. Specialization in habitat exploitation and fluctuations in environmental conditions likely combine to shape variation in fish assemblages (Igulu et al. 2014; Ebner et al. 2016; Da Silva et al. 2018). Behavioral characteristics seen in their native ranges such as site fidelity are also exhibited by these tropical fish in temperate environments and indicate viable survivability once settled in New England waters while environmental conditions are tolerable. In a study published in 1998, McBride and Able found 35% of marked *C. ocellatus* were recaptured between September 1 and October 20, 1991 during a study along the coast of New Jersey. In conjunction with described behavior and residence time while in New England waters, there continues to be a growing body of evidence indicating that passive dispersal cannot be the sole factor in the distribution of larval reef fish (Sale et al. 1984; Montgomery et al. 2001). Many reef fish species also exercise habitat partitioning across life stages indicating that many species that are reef-associated as adults may depend on estuaries and lagoons in early stages (Gratwicke et al. 2006). Several potential cues and behaviors are now thought to influence habitat choice. It is worth considering these factors in assessing how expatriated reef fish select habitat along the New England coastline. While it appears larval reef fish are capable swimmers and possess several sensory perceptions to enhance navigation to suitable habitat (described below), little is known about how those qualities may affect habitat selection in non-native ranges.

Swimming Ability

Research on the swimming ability of larval fishes indicates that reef fish species have a distinctly higher capacity for locomotion than non-reef species. While non-reef species are capable of traveling at speeds from 0.5-5 cm/sec (Blaxter, 1986; Montgomery et al. 2001), late-stage reef fish larvae can swim at speeds of 13.5cm/sec for several days (Stobutzki and Bellwood 1994, 1997; Stobutzki, 1998; Dudley et al. 2000; Montgomery et al. 2001). Larval swimming ability also varies amongst different reef fish families and several groups that are sighted as Gulf Stream Orphans demonstrate extensive capacity for sustained swimming including *Acanthuridae, Chaetodontidae, Monacanthidae, Pomacentridae* and *Pomacanthidae* which are all able to exceed 50 hours or approximately 25 kilometers and at a swimming speed of 13.5cm/sec (Stobutzki and Bellwood, 1997). There can also be variation within families and swimming ability generally increases with size and age of larval fishes (Fisher et al. 2000). Physiological differences amongst species during larval development and how the developmental stage aligns with Gulf Stream transport may offer another avenue for variability for these expatriated tropical species.

Larval Orientation

There is a growing body of evidence to suggest that larval reef fish may rely on a variety of sensory and environmental cues during the settlement process in order to select for viable habitat. This is another aspect of the Gulf Stream Orphan phenomenon that relates to the underlying ecology of northern coastlines that may influence the recruitment of expatriated tropical fish. In native reef habitat, many of these cues are dependent on larval sensory perception through auditory, chemical, oceanographic, and visual cues. It is likely that these retain some degree of relevance to habitat orientation in non-native environments. Larval reef fish at settlement stage orient towards high frequency noise produced by marine invertebrates on reefs (Simpson et al. 2008). While invertebrate cohorts vary greatly between reefs and temperate coasts, perhaps concentration of invertebrate noise remains a relevant indicator for viable nursery habitat for larval fishes. In tropical environments sound peaks at night over summer new moon periods when settlement often occurs on reefs and can be elevated beyond ambient noise tens of kilometers away (Milichich et al. 1992). There is also evidence to support that reef fish can detect conspecifics through chemical signals and orient towards those habitats though this information has generally thus far been proven only on small spatial scales (Lecchini et al. 2005). With respect to Gulf Stream Orphans, detection of conspecifics may not correlate with the recruitment of larval fish to established populations as the seasonality of the occurrence results in annual novel settlement but could be responsible for a concentration of conspecifics on small spatial scales within specific nursery sites of a larger ecosystem. Physical oceanographic cues are also thought to influence larval fish navigation and dispersal. It is possible for larval fish to use swell, wave-action, and currents to orient towards reefs and settlement sites (Montgomery et al. 2001). Lastly, though generally thought to be used by larval fish and juveniles for small-scale habitat selection, visual cues also provide signals for larval fish settlement (Montgomery et al. 2001). These may be relevant cues to tropical species beyond their native range though potentially on even smaller spatial scales as turbidity in northern latitudes during summer is generally far higher than tropical waters. Visual cues therefore likely only guide settlement cues on the smallest-scale distribution and may impact territory selection following settlement in species with high site fidelity.

Diet Specialization

Another piece to the puzzle for consideration is the trophic guild and foraging behavior of expatriated tropical species. Within native geographic ranges, variation in resource availability and quality has significant effects on physiological condition, fitness and abundance of coral reef fishes (Shulman, 1985; Munday et al. 1997; Holbrook et al.

2000; Berumen et al. 2005). Following dispersal of larvae and settlement, there is evidence to suggest that prey availability in different habitats can impact physiological condition of fishes which then shape growth and survivorship (Jones and McCormick, 2002; Berumen et al. 2005). It is plausible that reef fish species with a highly specialized diet are least likely to sustain themselves beyond their native range. Successful Gulf Stream Orphan species must have viable foraging ability and prey abundance considering the duration of residence by some species through the summer and fall in New England waters. Expatriated species may also benefit from inherent diet plasticity and tolerance to varying conditions that is known to benefit their distribution across habitat types in their native ranges (DaSilva et al. 2018). There are several complexities to consider in regard to target prey and foraging, as the diet of reef fishes from larval stages to adulthood can vary tremendously (D'Alessandro et al. 2011). It is also worth considering that some of the larval fish that reach northern latitudes may develop into juveniles successfully without ever transitioning to the diet specialization that would have occurred in its native tropical range.

Historical Reports

Concern continues to grow for the implications of climate change on the biogeography of marine species. Marine environments are experiencing some of the greatest observed impacts due to climate change and are commonly causing shifts to the distribution of species (Burrows et al. 2011; Poloczanska et al. 2013). On-going environmental sampling and documentation of organism dispersal by the Gulf Stream is critical to understanding the alteration of biogeography in the Northwest Atlantic as climate change progresses. While it is easy to jump to the conclusion that the occurrence of tropical species beyond their native range is a sign of climate alterations, it is important to consider the historical context of this phenomenon. Documented dispersal of many of the same tropical species seen today along the east coast of the United States dates back more than 150 years. Some of the earliest reported specimens date back to the mid-19th century including a Short Bigeye, *P. alta*, sighted in Marblehead, MA in 1859 and a Bluespotted Cornetfish, *F. tabacaria*, reported in Rockport, MA in September of 1865 (Bigelow and Schroeder, 1953). Reports from the United States Fish Commission Bulletin published in 1898 reported Northern Sennet, *S. borealis*, occurring along the southern coast of Massachusetts in 1882 and refer to the occurrence of a few individual Spotfin Butterflyfish, *C. ocellatus,* "nearly every year," via seining in the vicinity of Woods Hole, MA (Smith, 1898). The Gulf Stream has been shaping biological activity in the Northwest Atlantic since its inception and monitoring its functionality and role in shaping ecosystems is vital to understanding the future of species dispersal and fish assemblage composition of the east coast of North America.

Citizen Science Participation

In order to expand the viable dataset for further study of this phenomenon, a citizen science network (www.GSOproject.org) was launched in 2015 to assemble reports from recreational divers and other engaged community members of coastal New England. Citizen science reports, institutional collection data from public aquaria, and historical accounts from the literature have provided a dataset of thousands of records to be analyzed in future efforts. The sightings indicate that the phenomenon spans a range of North American coastline from

Virginia to Nova Scotia. In 2016, this citizen science effort was expanded to include the iNaturalist.org platform which allowed for the inclusion of previously reported species on the platform to be absorbed into the Gulf Stream Orphan Project. The geo-referencing of photographs through iNaturalist also provides an added level of data quality verification and the mobile-friendly app makes user experience and reporting more convenient while in the field. Since 2015, citizen scientists have submitted over 200 reports to the GSO Project.

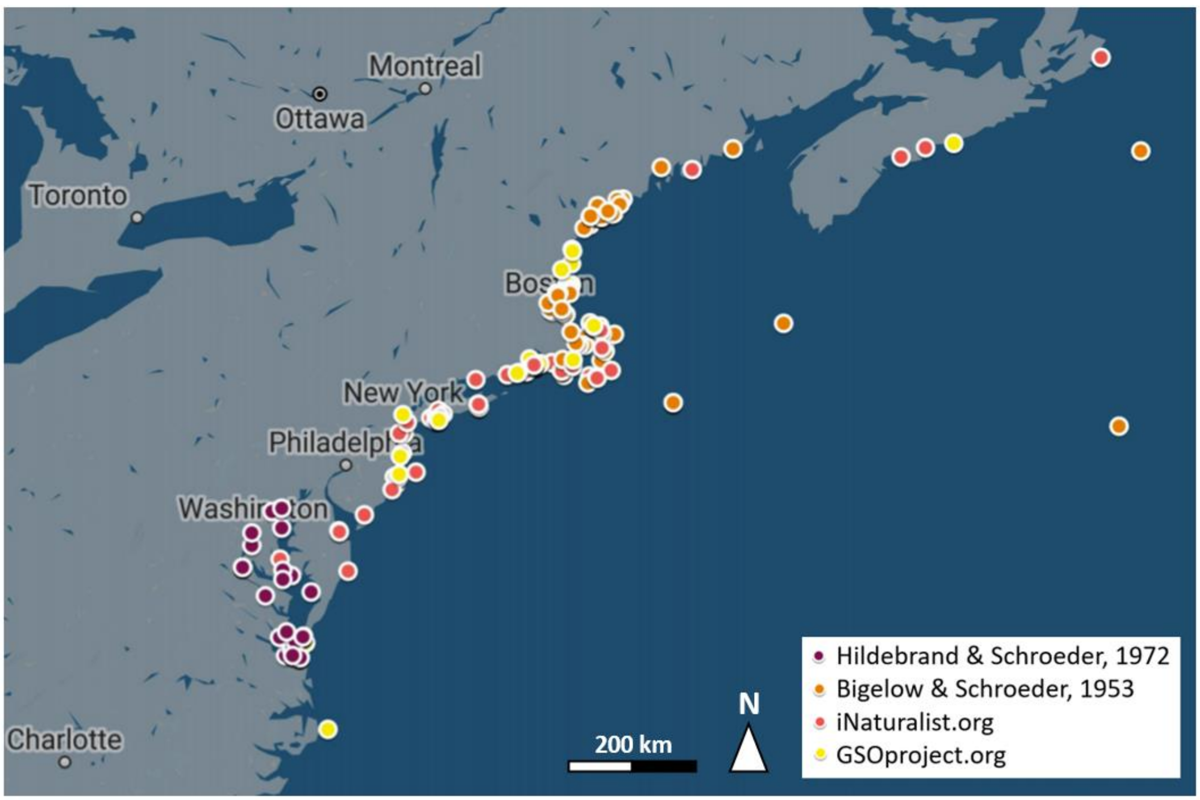


Figure 2. Gulf Stream Orphan Sightings. *The distribution of Gulf Stream Orphan sightings including citizen scientist submissions to GSOproject.org and iNaturalist.org as well as non-native teleost species recorded in Fishes of the Chesapeake Bay (Hildebrand & Schroeder 1972) and Fishes of the Gulf of Maine (Bigelow & Schroeder, 1953).*

CHAPTER 2

BIODIVERSITY SURVEY OF PLEASANT BAY, MA

Introduction

Sightings of juvenile tropical reef fish along the New England coastline are often considered rare. Due to environmental characteristics and mechanisms used by larval reef fish to select beneficial habitat in their native range, it is predicted that wayward tropical fish, referred to as Gulf Stream Orphans (GSOs) within the citizen science network, can select for and reside in critical nursery habitat beyond their native range. The seasonal influx of tropical and subtropical reef fish to New England waters through dispersal by the Gulf Stream results in the short-term residence of these fishes in areas that provide vital habitat characteristics and adequate prey abundance. Assessment of species richness is one of several biodiversity metrics that can be employed to compare fish assemblages at unique survey sites. Comparing richness at sites with varying habitat characteristics may provide insight into the environmental factors that shape observed species distributions. Biodiversity surveys often require extensive resources and large sample sizes to accurately quantify various diversity metrics (Chao et al. 2009). Sampling species incidence rather than abundance affords survey effort to be maximized by decreasing processing time per sample so that more sites can be surveyed, and more total samples gathered. The use of sample-based rarefaction can control for under sampling bias in survey data and differences in the number of samples collected (Gotelli and Colwell, 2001). Using these methods, small-scale surveys of relatively broad and complex ecosystems can be accomplished to highlight unique habitat areas that support critical ecosystem functions. This technique was used in Pleasant Bay, MA from 2015-2017 to assess species richness for the fish assemblage at unique sites within the estuary. Unusual species detected during the survey include members of several different taxonomic families. Aspects of their ecology and development are discussed here to better understand their status as GSOs and their role as indicators of critical habitat within the broader survey environment. Pleasant Bay is a hydrologically complex system and provides environmental services to a broad group of community stakeholders with varying degrees of ecosystem impacts. The bay is well documented for providing habitat to a wide range of marine animals including those of significance to both commercial and recreational fisheries (Fiske et al. 1967; Nichols et al. 2020). By sampling the species incidence of fishes present at different sites within an estuary, estimated species richness at each site may serve as an indicator for the areas likely to harbor non-native tropical species. Understanding of species richness within an ecosystem is often used to guide conservation effort and its maximization is generally emphasized as a goal of these efforts (May, 1988). Sites within the estuary with elevated species richness may compare favorably to the ecosystems within tropical species' native range, maximizing their success and residence time while underlying environmental conditions are within their tolerances. Due to the growing evidence in support of active habitat selection by larval fish and reef-associated species in particular, the assessment of smaller patches of habitat within a study area may be critical to accurately interpreting species distributions. The presence of these non-native species at individual sites may highlight valuable nursery micro-habitat and local biodiversity hotspots crucial for habitat restoration and preservation. As ecosystem dynamics in the Northwest Atlantic are altered by broader climate phenomena, a comprehensive understanding of species assemblages is critical to effective conservation and stewardship. The use of this small-scale survey technique and statistical estimation affords coastal communities a viable and cost-effective method for assessing and prioritizing local habitat conservation areas that in turn promote the environmental function, use, and stewardship of larger estuarine systems.

Environmental Conditions Shaping the Gulf Stream Orphan Phenomenon

Gulf Stream Activity

The Gulf Stream is the major driver of water transport and influence on climate in the North Atlantic (Frankignoul et al. 2001). The path of the Gulf Stream hugs the eastern coast of Florida and the southeastern United States before traveling northeast across the Atlantic. Its activity is dictated by fluctuations in meandering instability of the stream and large-scale shifts in lateral positioning due to seasonal and interannual variation (Frankignoul et al. 2001). One of the significant activities associated with Gulf Stream transport is the formation of Warm Core Rings (WCRs), pinched off from large meanders in the current, entraining a core of warm southerly water and traveling into the Northwest Atlantic before dispersing into the slope sea and continental shelf water of North America (Gangopadhyay et al. 2019). These WCRs have a range of lifespans from 11-300 days, and a bimodal distribution of longevities with short-lived rings (<140 days) having a mean lifespan of 54 days, while long-lived rings (>140 days) possess a mean lifespan of 229 days (Brown et al. 1986). During the time of a WCR's existence, the biological contents within the core, marine phytoplankton and zooplankton, continue to develop as they are transported beyond the lower latitudes of the Gulf Stream's origin. It is through this mechanism, and the associated streamers and eddies of the Gulf Stream, that tropical and sub-tropical species of marine fish are thought to reach the temperate water of the Northwest Atlantic.

Pleasant Bay Sea Surface Temperature

Assisting in the successful residence of non-native tropical and subtropical marine fishes in New England waters is the seasonal fluctuation in water temperature. Many species distinguished by native ranges in the tropics prefer temperatures only present in the Northwest Atlantic during the warmest times of the year. Mean summer temperatures collected in Woods Hole, MA since the 1890's indicates a range from 19.3-20.4 °C (Nixon et al. 2004). This is well above the lower limit of the preferred temperature window for subtropical species around 14°C (Kaschner et al. 2019). The seasonality of temperature variation in New England also shapes the duration of tolerable temperature ranges for expatriated marine species. The surface temperature data collected during the Pleasant Bay, MA survey indicates that the survey sites maintain a thermal range tolerable to tropical and subtropical marine species from May to November (Figure 2.2.1) and the longest coherent temperature record in North America sampled at Woods Hole, MA indicate that this has been the case for more than a century and that the duration has expanded during the most recent few decades (Nixon et al. 2004). McBride and Able (1998) found the hypothermal mortality in Spotfin Butterflyfish, C. *ocellatus,* to be within a range of 10-12° C.   They further observed that *C. ocellatus* displayed additional negative, though non-lethal behaviors including a lack of appetite at temperatures below 15° C. These observations indicate that sustained temperatures above 15° C are a critical environmental condition supporting the phenomenon of tropical species in the Northwest Atlantic.

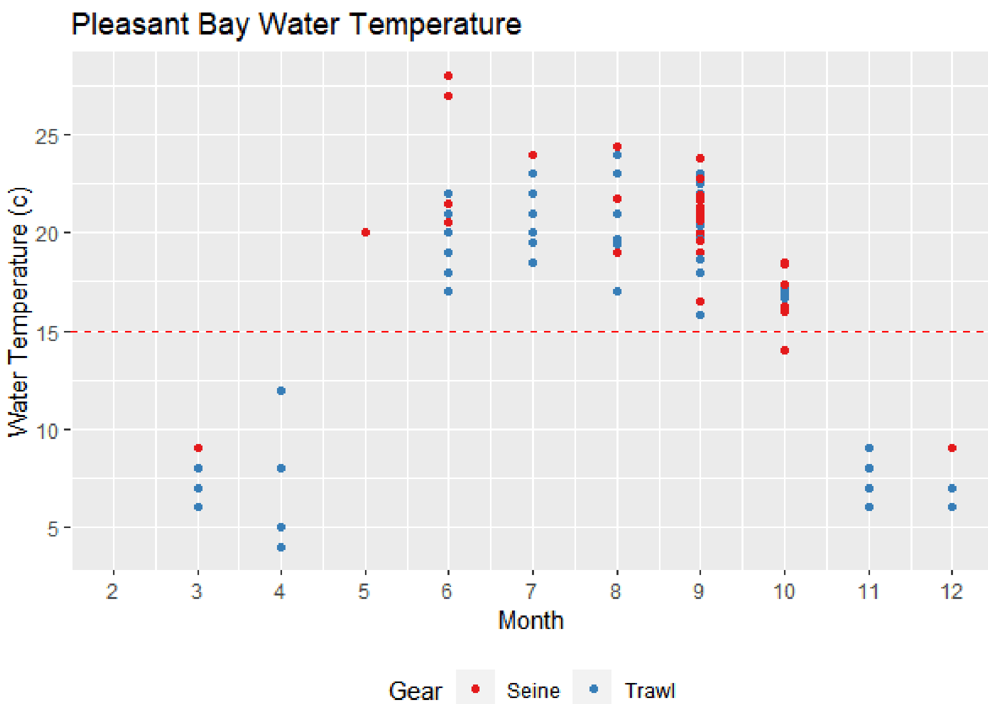


Figure 3. Pleasant Bay Water Temperature. *Water temperatures by month from trawl and seine sites in Pleasant Bay, Orleans, MA. Temperatures from May to October exceed the thermal threshold for C. ocellatus according to McBride & Able 1998 while temperatures leading to hypothermal mortality were measured in April and November. The horizontal line at 15°C indicates the temperature at which C. ocellatus exhibits loss of appetite.*

Developmental Biology and Ecology of Gulf Stream Orphans

Aside from the seasonal variation in environmental characteristics that allow for the survivorship of subtropical and tropical species in New England waters, there are several components of the developmental biology and ecology of fishes that likely shape the observed GSO phenomenon. Aspects of reproduction, larval ecology, diet, and habitat selection all play a role in the process. Members of the *Belonidae, Carangidae, Chaetodontidae*, and *Sphyraenidae* families were detected during the Pleasant Bay survey, and while some aspects of their biology remain unclear, there are components that may be pieced together to improve our understanding of GSO abundance in the Northwest Atlantic. Due to the diffuse and patchy nature of the ocean environment, a common reproductive strategy used by many tropical fish species is to produce vast quantities of eggs over an extended spawning season (Houde, 1989; Robertson, 1991; D'Alessandro et al. 2011). Variation of traits within the larval population combine with diverse environmental conditions to produce selective pressures that shape the abundance and success of dispersed fishes through settlement and early development (Sponaugle and Grorud-Colvert, 2006; Sponaugle et al. 2006). It is likely that broadcast spawning by species along the southeastern coast of the United States in springtime provides the initial source of subtropical and tropical fish larvae which ultimately reach the Northwest Atlantic. In the case of sphyraenids, D'Alessandro et al. (2011) found larval sennets in the Straits of Florida (SOF) were located predominantly in the upper 25m of the water column and were most abundant from November to June for sennet species. This seasonality, location, and early larval distribution all appear to coincide with potential transport via the Gulf Stream as spawning by western Atlantic sphyraenids appears to occur at the juncture of coastal and oceanic circulation (de Sylva, 1963). This transport then results in the observed residence of young-of-year sennets detected in this survey of Pleasant Bay, MA as well as coastal New Jersey during the summer and fall (Able and Fahay, 1998). The gut contents of sphyraenids sampled in the SOF also indicate that beyond 8mm in length, a size achieved within days of hatching, larval and juvenile sennets transition from a diet of calanoid copepods to one of piscivory (D'Alessandro et al. 2011). This diet must then be maintained throughout larval dispersal within Gulf Stream waters, and into the juvenile stage while residing along the New England coastline.

The occurrence and distribution of fish in the family *Chaetodontidae* (butterflyfishes) due to Gulf Stream transport appears to support the role that diet specialization and other life history components may play in shaping the Gulf Stream Orphan phenomenon. Of the 2,765 sightings collected and reviewed by the Gulf Stream Orphan Project, 22.7% are of the butterflyfishes. Within that group 91.4% of the reported butterflyfishes are of the Spotfin Butterflyfish (*C. ocellatus*) while all other species reported in the family comprise 8.6% (aggregate of C. *capistratus, C. striatus, C. sedentarius*). As described, a confluence of biological factors likely influences the distribution of *Chaetodontidae* northward and trophic guild or diet may be a principle selective pressure. *C. ocellatus* is a documented omnivore and generalist (Randall, 1967; Aiken, 1975; Motta, 1989) with a diet spanning algae, polychaetes, amphipods, crustaceans and more. *C. striatus* and *C. capistratus* are more specialized, feeding primarily on polychaetes and coral polyps including anthozoa and gorgonians (Randall, 1967; Aiken, 1975; Motta, 1989). This diet specialization may contribute to a lower success rate of sustained residence by larval and juvenile individuals of these species during summer and fall in northern latitudes. *C. sedentarius* shares some diet commonality with *C. striatus* and *C. capistratus*, though it is considered a more generalist feeder (Motta, 1989), likely indicating that additional factors beyond diet specialization shape reported occurrence along the coast of the United States. Though a generalist feeder, the scarcity of reports of *C. sedentarius* in the Northwest Atlantic more closely mirrors the incidence of *C. striatus*.

Beyond diet and its associated specialization by species, there is a broad spectrum of behavioral and habitat characteristics that shape survivorship of juvenile fishes. It is likely that variation in swimming ability by different families of fish and mechanisms of habitat selection all play a role in the resulting abundance of non-native fish species within particular ecosystems. Many of the fishes reported frequently as GSO's are members of the *Acanthuridae, Chaetodontidae*, *Monacanthidae*, *Pomacentridae* and *Pomacanthidae* families which possess some of the highest capacity for larval swimming ability (Stobutzki and Bellwood, 1997). While much of the broad distribution of fishes is due to transport and dispersal by the Gulf Stream, post-settlement reef fishes are capable of habitat selection on small spatial scales (Jones, 1991; Berumen et al. 2005). Beyond habitat choice, sustained behavioral characteristics exhibited by reef fishes have also been demonstrated to influence fish distribution and abundance. The most reported GSO, *C. ocellatus,* was found to exhibit strong site fidelity during a mark and recapture study from September 1 and October 20, 1991 along the coast of New Jersey (McBride and Able, 1998). It is well established that specialization in habitat exploitation combines with dynamic environmental conditions to shape observed fish assemblages (Igulu et al. 2014; Ebner et al. 2016; Da Silva et al. 2018). The influx of non-native species to the New England coastline introduces additional levels of complexity to fish assemblages and ecosystem dynamics and is worthy of further exploration.

Methods

Gulf Stream Orphan Evaluation Rubric

A wide range of species are reported by citizen scientists, fishermen, and avid scuba divers to the Gulf Stream Orphan Project; not all of which are considered tropical reef fish though their presence in the Northwest Atlantic may still be a result of Gulf Stream activity. Numerous temperate and sub-tropical species participate in pelagic life stages or have transient seasonal populations (McBride and McKown, 2000). Aspects of species life history including stage of development, geographic distribution of the native range, temperature tolerance, and habitat association must be evaluated to filter reports and consolidate analysis. Several species that are seasonally abundant in the Mid-Atlantic and New England coastal waters employ overwintering strategies and migratory routes that are independent of the Gulf Stream transport discussed here. For the purposes of this study, species categorized with tropical distribution or subtropical distribution that extends to 26°N latitude and juvenile (<6 months) life stages, will be considered as likely evidence of expatriated fish due to Gulf Stream transport. The "Preferred Temperature" parameter described in Figure 2.4.1 is derived from the environmental envelopes modeled by AquaMaps.org (Kaschner et al. 2019) based on large occurrence data sets from the Global Biodiversity Information Facility (GBIF.org) and the Ocean Biodiversity Information System (OBIS.org), as well as the literature cited within FishBase.org. Habitat association with reefs further strengthens the status of several species, though it is appropriate to consider that a broader group of habitat associations for species that exhibit other supportive characteristics are still subject to larval dispersal by the Gulf Stream.

	Spotfin Butterflyfish *Chaetodon ocellatus*	Snowy Grouper *Hyporthodus niveatus*	**Northern Sennet** *Sphyraena borealis*	**Atlantic Needlefish** *Strongylura marina*	**Atlantic Moonfish** *Selene setapinnis*	Grey Triggerfish *Balistes capriscus*	**Tautog** *Tautoga onitis*	**Cunner** *Tautogo-labrus adspersus*
Preferred Temp (° C)	23.89-28.18	23.04-28.19	13.44-26.9	14.84-28.19	14.44-28.07	12.76-27.94	8.65-22.41	6.74-13.59
Tropical	✔							
Reef- Associ.	✔		✔	✔		✔	✔	✔
Juvenile	✔	✔	✔		✔		✔	✔
Subtropical		✔	✔	✔	✔	✔	✔	
Demersal		✔						
Bentho-pelagic					✔			
Temperate								✔
Adult				✔		✔		

Figure 4. Gulf Stream Orphan Evaluation Rubric. *Sample Gulf Stream Orphan evaluation rubric for commonly reported species. Comparisons based on categorizations from species habitat-associations, geographic distributions, and preferred temperature range courtesy of Aqua Maps (www.Aquamaps.org). Supporting evidence of characteristics associated with the Gulf Stream Orphan phenomenon are color coded (Green=Likely, Yellow= Neutral, Red = Unlikely). Species in bold were sampled during the survey of Pleasant Bay.*

As displayed in Figure 4, there are several factors that can be evaluated to assess species reported as Gulf Stream Orphans. Fundamental characteristics including thermal tolerance, broad habitat associations, and life stage are relatively straight-forward for incorporation into a rubric, while other aspects of life history are more complex. A comparison of species that display neutral temperature preferences illustrates the difficulty in confirming their status as Gulf Stream Orphans. While *S. borealis, S. marina, S. setapinnis*, and *B. capriscus* possess subtropical distributions and some may be reef-associated, reports of adult *S. marina* and *B. capriscus* indicate they are unlikely to be dispersed by Gulf Stream activity alone and are rather opportunistic migrants in the northernmost outskirts of their habitable range. Furthermore, in the case of *S. marina*, reports of this species participating in anadromous reproductive migration in mid-Atlantic states (Massman, 1954) would indicate that the occurrence of adult *S. marina* in estuarine environments of New England is a result of seasonal range expansion during summer months. Conversely, reports of *S. setapinnis* and *S. borealis* are consistently of specimens displaying young-of-year morphology indicating their transport beyond their native range was more likely due passive dispersal by the Gulf Stream and subsequent habitat selection.

Survey Methods

From 2015 to 2017, a survey was conducted across 23 different sites within Pleasant Bay in Orleans Massachusetts. Sampling was conducted 11 out of 12 months of the year, with peak sampling efforts from June to November. Sampling was contingent upon weather and sea conditions. Seine and trawl sampling sites were selected based on accessibility, diversity of habitat type, and included a subset of sites previously surveyed within the bay where Gulf Stream Orphans have been reported (Nichols et al. 2020). In total the survey conducted 54 seines across 7 different sites, and 117 trawls from 16 different sites (Figure 5).

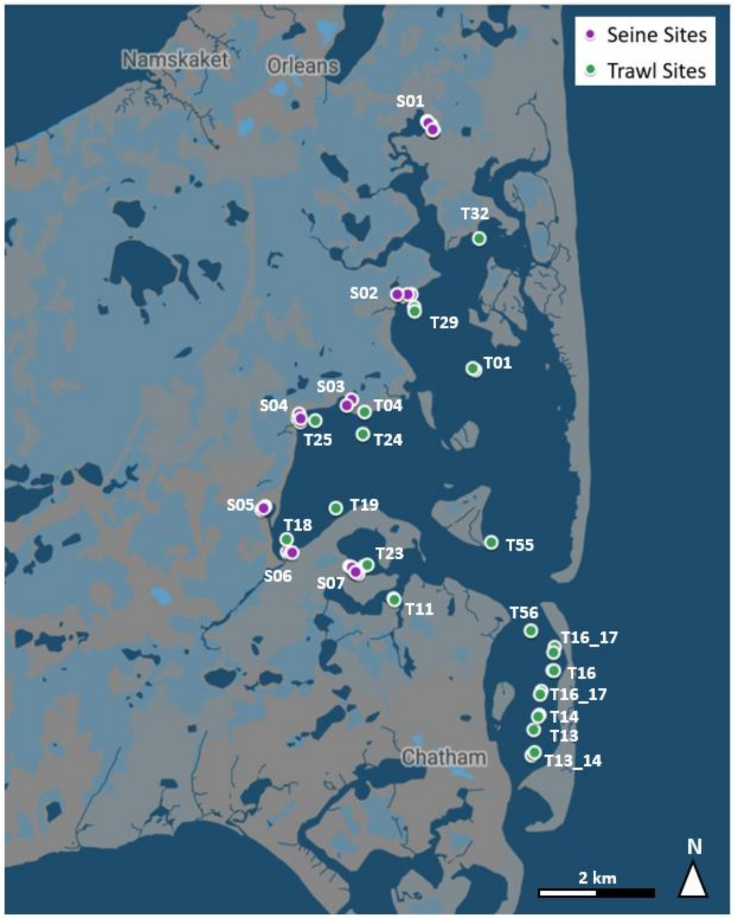


Figure 5. Pleasant Bay Survey Sites. *Survey site map of Pleasant Bay, Orleans Massachusetts.*

Seine sampling of the intertidal zone was performed using a 50' (15.2 m) long by 4' (1.2 m) deep, black, knotless seine with 3/16" (4.8mm) mesh and 4' by 4' (1.2m x 1.2m) square bag fabricated by Memphis Net & Twine Co., Inc. Seine sampling was conducted following the standardized methods described in Nichols et al. 2020. Following successful operation of the seine, sampled species were sorted into 5-gallon buckets for species identification and photo documentation until the entire sample had been processed and returned to the site. Supplemental information recorded included environmental conditions as well as invertebrate species identification. A duplicate haul was then made adjacent to the initial sample without overlap.

Subtidal surveys were conducted on board the R/V Shackleton, a 20' (~7 m) center-console v-hull vessel with a 110hp outboard engine. The trawl net used was a 30' (9.1 m) sweep Wilcox shrimp trawl with 3.8cm stretched mesh and 8.2 m head rope. The comprehensive trawl configuration used is described in Nichols et al. (2020) and was replicated for the sampling in this survey. Trawl sampling was conducted with a duration of 5 minutes at a speed of 2 knots and GPS data was collected at the start and end of each trawl via a Garmin 76 GPS and temperature and depth information was collected using the R/V Shackleton's Faria Instruments DS1002 echosounder. Immediately following each trawl, a duplicate was conducted adjacent to the initial tow. The fish and invertebrate species contained in each trawl were sorted onboard the R/V Shackleton for immediate recording and photo documentation. Environmental conditions including weather, tides, air, and water temperatures were recorded at the start of each tow along with any additional notes following sample processing.

Analysis

Environmental conditions and species detected within each sample and survey site was compiled into a master data frame and analyzed using the open-source software "R Studio" and the package "ggplot2" to establish an overview of the teleost assemblage in Pleasant Bay, Orleans (R version 3.6.1, R Core Team, 2019). To begin to address the question of whether there was a significant difference in fish assemblages and species richness at sites where Gulf Stream Orphans were detected, a comparison of total teleost species detected per seine or trawl sample was made to understand variation in sampling method prior to individual site analysis. Following that initial exploratory analysis, seine and trawl survey results were divided into separate groups for further analysis. Comparisons of sampling technique and species detected further illustrate differences in sampling method and likely differences in habitat at each sampling site resulting in the presence of different fish assemblages. Exploratory analysis of the frequency distribution of total teleost species detected per seine and trawl with regards to GSO presence or absence was then conducted. Due to the small sample size of the survey, Fisher's exact test with simulated p-values was used to determine the independence of the teleost species detected per sample at GSO-detected sites with GSO-undetected sites for each survey methods. In order to determine the underlying variations in native species detected, the incidences of GSO species themselves were removed from the analysis.

In order to estimate species richness differences across the survey sites within Pleasant Bay, species incidence data was analyzed using the ChaoSpecies function for Hill Numbers ($q = 0$) within the R package "SpadeR: Species Richness and Diversity Estimation in R" (Chao et al. 2016). To perform this assessment, incidence data is based on sampling units, therefore seine and trawl sample datasets were analyzed separately. Data frames for seine and trawl sites were organized by site with the presence/absence data of each species per sample for all samples at each location. Sample-based rarefaction to compare species richness requires several assumptions including sufficient sampling. Due to the small scale of the Pleasant Bay survey, there are several sites that do not meet a suitable sample size, leading to estimated confidence intervals that were quite broad in some cases. The additional assumptions to complete the rarefaction analysis regarding comparable sampling method, taxonomic similarity, and independent and random sampling were met.

To address limited sample sizes and examine possible correlation of GSO occurrence with various environmental characteristics, the sample sites within each survey method were clustered using three different parameters: geographic proximity, biotope, and biotic group. The biotope and biotic group distinctions of Pleasant Bay as described in the US Coastal and Marine Ecological Classification Standard (CMECS) and determined through acoustic surveys and benthic samples by Mittermayr et al. 2020 were applied to both the seine and trawl sites of this survey to dictate the clusters. Each biotope is comprised of both physical habitat characteristics and associated species (FGDC 2012). Mittermayr et al. 2020 described and mapped five unique biotopes within Pleasant Bay distinguished by dominant indicator species and sediment grain size characteristics summarized in Table 1. As nearly all trawl sites share the same biotope, the clustering of trawl sites by biotope was then further divided by geographic proximity.

BIOTOPE	DESCRIPTION
BIOTOPE 1	Haustoriidae on positively skewed sediment
BIOTOPE 2	*Streblospio benedicti* on symmetrically skewed silt
BIOTOPE 3	*Ameritella agilis* on symmetrically skewed coarse sediment
BIOTOPE 4	*Ampelisca sp.* On symmetrically skewed, heterogeneous sediment
BIOTOPE 5	*Gemma gemma* on symmetrically skewed, homogeneous sediment

Table 1 Biotopes of Pleasant Bay. *Biotopes contained within Pleasant Bay, MA as determined by Mittermayr et al. 2020.*

Sample-based rarefaction curves using species incidence data for Hill number (q = 0) were constructed to graphically represent the asymptotic estimator for species richness at each sample site using the "iNEXT - iNterpolation and EXTrapolation" and "ggplot2" packages in "R" (Hsieh and Chao, 2014). iNEXT was also used to compute bootstrap confidence intervals for each rarefaction curve at 95%. Sample-based rarefaction preserves the species aggregation or segregation present in the dataset between sampling sites and is therefore a preferred analysis over individual-based rarefaction as it maintains independence of sampling units (Gotelli and Colwell, 2011). Rarefaction and extrapolation can be used to assess the magnitude of difference between communities (Chao and Jost, 2012). Each rarefaction curve can then be analyzed to better understand the richness of the fish assemblage at each site. In order to compare native species richness as the underlying condition that may be correlated with GSO incidence, the presence or absence of the detected GSOs themselves were removed from each survey site incidence matrix.

Results

Gulf Stream Orphan Evaluation Results

The broader GSO Project sighting data reveals approximately 80 different teleost species and several invertebrates have been reported as non-native species along the coast of North America. From this larger group, four species were detected during the Pleasant Bay survey that warranted close examination of their potential incidence being attributable to Gulf Stream transport. Those species are listed among other reference species in Figure 4. (*C. ocellatus, S. vomer, S. marina. S. setapinnis*). Three of the four possess likely and/or neutral characteristics indicative of Gulf Stream transport with *C. ocellatus* being the most prototypical example. *S. marina* was removed from the "Gulf Stream Orphan" cohort based on the reported occurrence of adults within the GSO Project database and documented anadromy in the literature (Massman, 1954). Following the evaluation of these four species, the analysis of their incidence at sites within Pleasant Bay could be undertaken to provide insight into the correlation of their occurrence and the estimated species richness at each survey site.

Comparing all reports collected by the GSO Project reveals a total of 738 reports and 2,741 individual fish for consideration as Gulf Stream Orphans. Figures 6 and 7 display the distribution of reports and individual fish by taxonomic family. The species sampled during the survey of Pleasant Bay echo those most commonly reported families in the broader data collection effort. Atlantic Moonfish (*S. setapinnis*) and Spotfin Butterflyfish (*C. ocellatus*), members of the *Carangidae* and *Chaetodontidae* families respectively, are both the most reported species (117 reports each), and most numerous fish sighted (*Carangidae*, n=802; *Chaetodontidae*, n=639). Northern Sennet (*S. borealis*) of the *Sphyraenidae* family is the 6th most reported family (38 reports), and 5th most reported number of individuals (n=109).

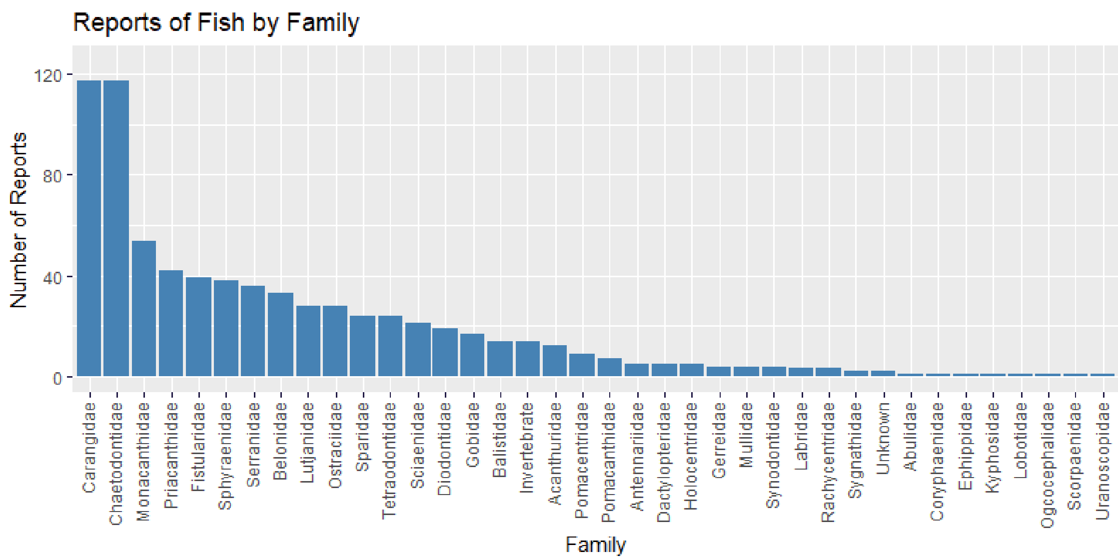


Figure 6. Reports of Fish by Family. *Number of reports assembled by the GSO project grouped by taxonomic family of fish.*

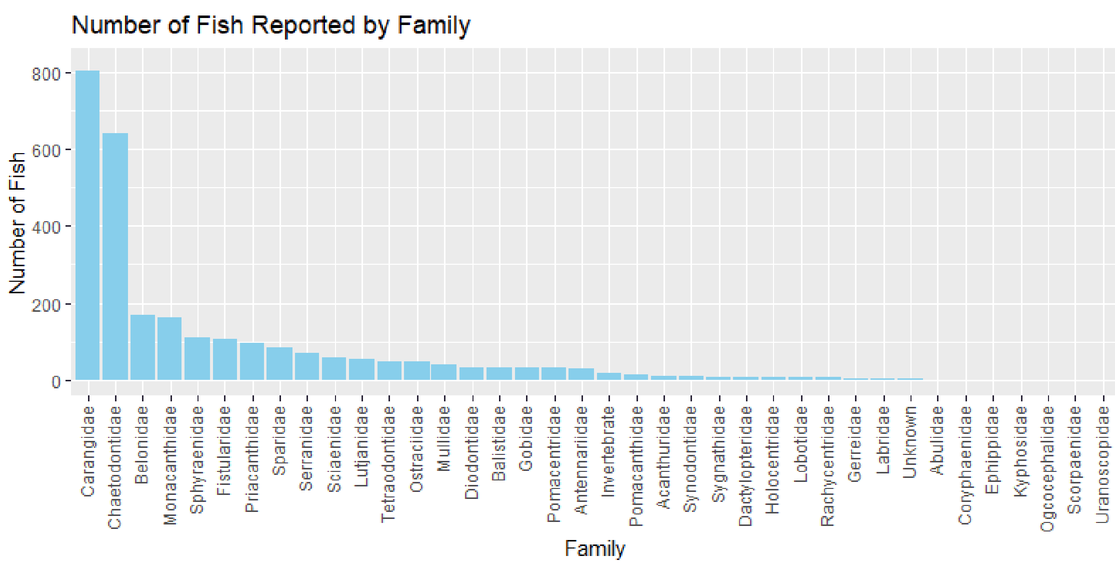


Figure 7. Number of Fish Reported by Family. *Total number of individual fish assembled by the GSO Project grouped by taxonomic family.*

Pleasant Bay Survey Results

The presence/absence data for all detected species in the survey were tabulated for each trawl and seine sample to determine the species incidence across the entire survey. Atlantic Silversides (*M. menidia*), Fourspine Sticklebacks (*A. quadracus*), and Winter Flounder (*P. americanus*), were the three most frequently sampled species out of 35 different teleost species (and 2 unidentifiable species) detected across trawl and seine sampling methods combined for the entirety of Pleasant Bay (Figure 8).

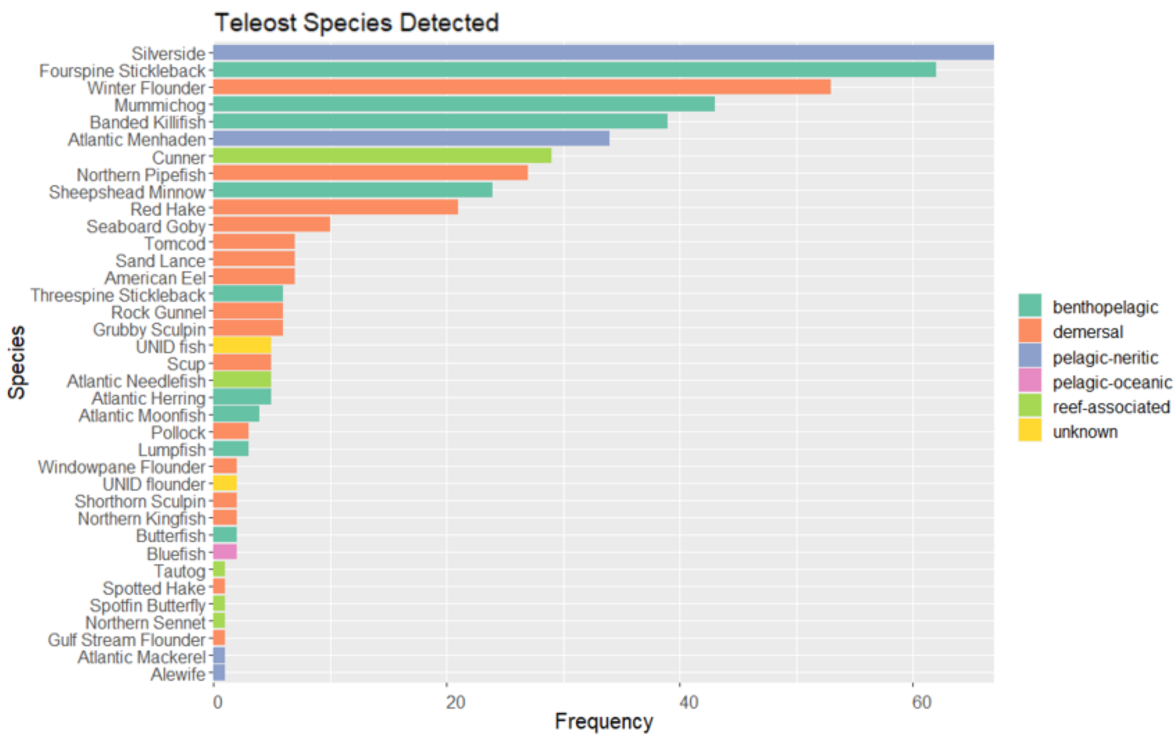


Figure 8. Teleost Species Detected. *Frequency of species sampled in Pleasant Bay, Orleans, across all sites and sampling methods and their habitat association (as described via www.FishBase.org, Froese and Pauly 2000)*

Visual representation capturing the frequency of species detection as well as the geographic distribution and habitat association of each can be reviewed in Figures 8 and 9. Species with temperate distribution and bentho-pelagic, demersal, or pelagic-neritic association were sampled with the greatest frequency overall. The second most frequently sampled group has a sub-tropical distribution and two species (*T.onitis* and *T. adspersus*) within this group are also reef-associated. As illustrated in Figure 4 the preferred thermal range and geographic distribution indicate that Pleasant Bay is within their native range as opposed to being the result of Gulf Stream transport (Kaschner et al. 2019). Figure 2.5.5 displays the frequency of species detected by each sampling method, with the demersal Winter Flounder (*P. americanus*) being the most frequently sampled via trawl method, while the Fourspine Stickleback (*A. quadracus*) and Atlantic Silverside (*M. menidia*) were most frequently sampled via seine net.

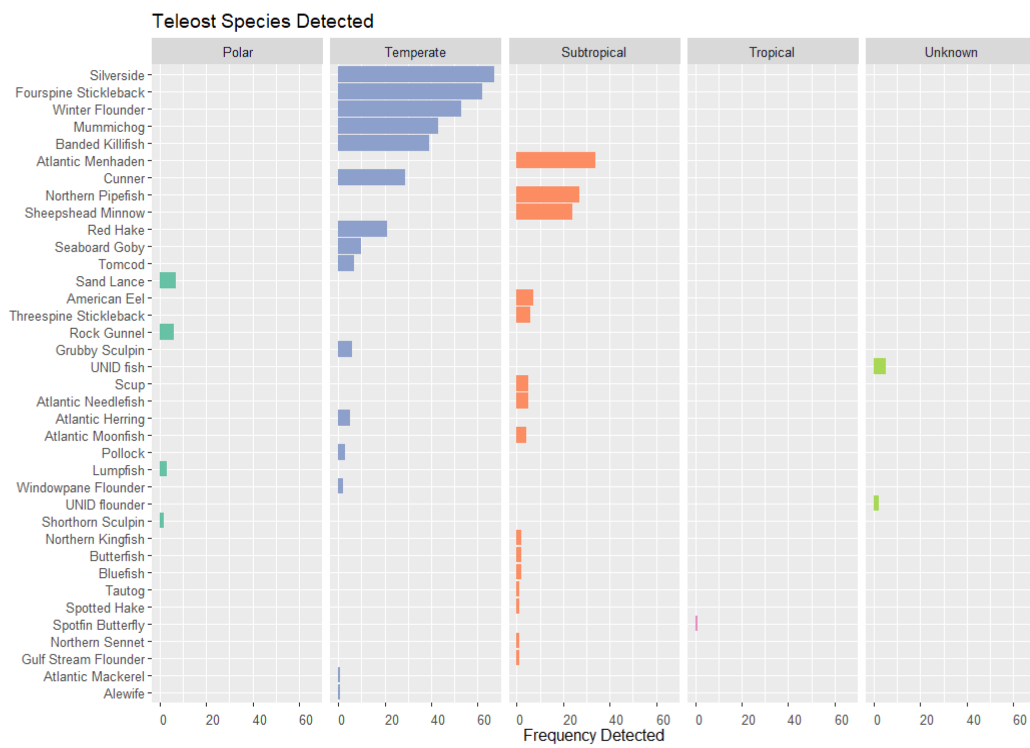


Figure 9. Teleost Species Detected by Distribution. *The frequency of species detected across all sampling techniques and sights displayed according to geographic distribution. Most of the teleost sampling in Pleasant Bay was composed of species distributed across temperate and subtropical ranges.*

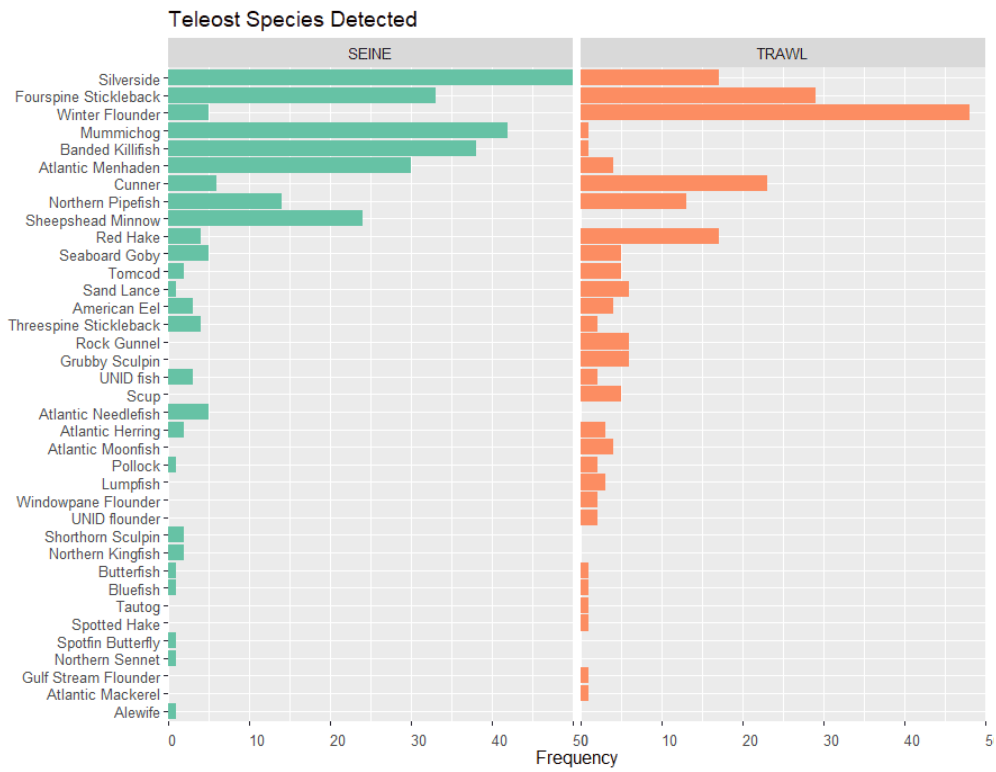


Figure 10. Teleost Species Detected by Seine and Trawl. *Comparison of species detected and frequency differences by sampling technique. Demersal species such as Winter Flounder (P. americanus) being the most frequently sampled species via trawl method, while seine sampling detected Fourspine Stickleback (A. quadracus) and Atlantic Silverside (M. menidia) with the highest frequency.*

A comparison of sampling technique found the mean teleost species per seine to be 5.19 species per sample while mean teleost species sampled per trawl was 1.92 species per sample. This difference in teleost species per sample site is visually distinct for each method in Figure 11 which displays a boxplot of teleost species per sample at each site. This difference between sampling methods is attributable to several factors including net mesh size, sampling method, area coverage, sampling effort, fish assemblage and environmental differences.

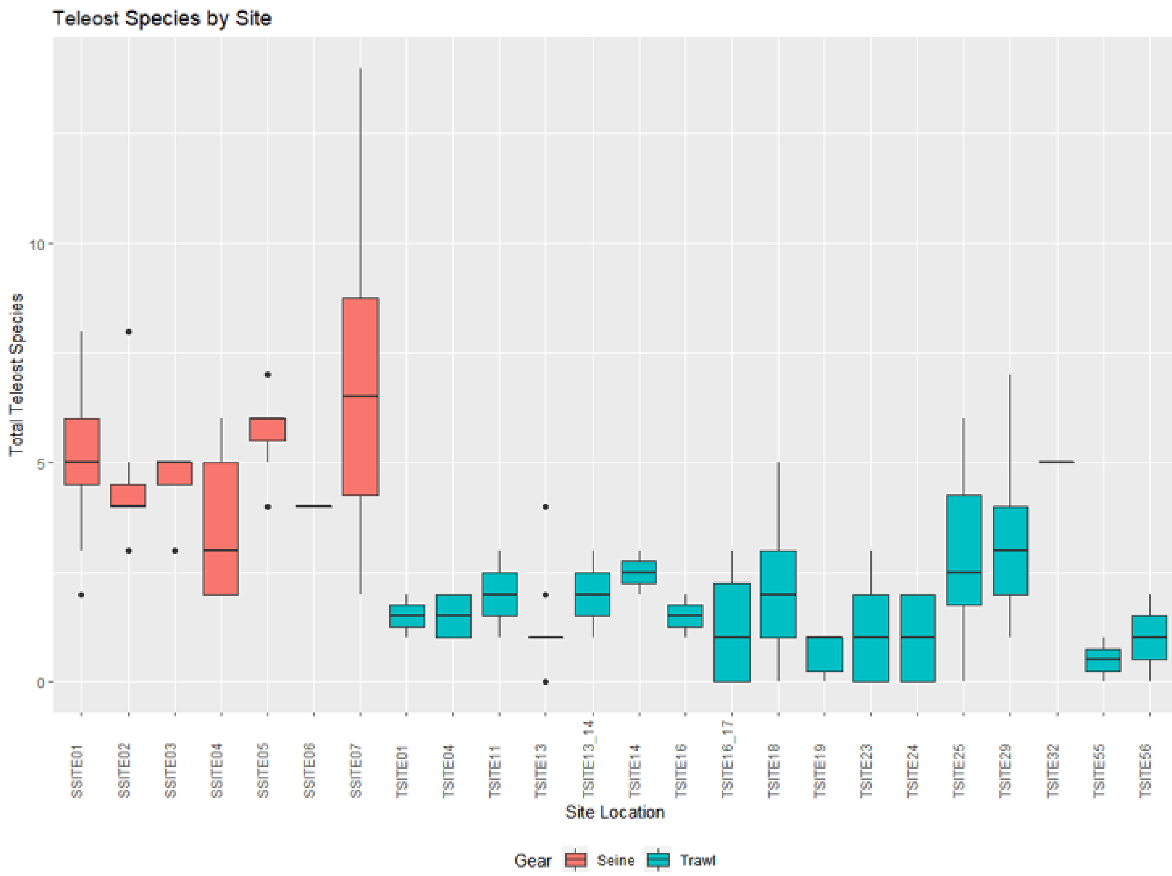


Figure 11. Teleost Species by Site. *Total teleost species detected per sample at each survey site. Teleost species sampled at seine sites was higher (mean = 5.19) compared to those sampled via trawl (mean=1.19).*

At three of the survey sites (one seine site and two trawl sites), an unusual tropical or subtropical species worth investigation was sampled. These sites are identified as Seine Site 07, Trawl Site 18 and Trawl Site 25. Determination of the incidence of each species to be the result of transport northward beyond their native range by Gulf Stream was done using the evaluation rubric in Figure 4. Of the 35 different teleost species surveyed in Pleasant Bay, three were uncommon species, worthy of further investigation: Atlantic Moonfish, Northern Sennet, and Spotfin Butterflyfish.

Because of the differences in sampling techniques and small sample size, a Fisher's exact test was used to examine the relationship between the frequencies of total teleost species per sample at GSO-detected and GSO-undetected sites for each sampling technique. Figure 12 shows the frequency distribution of total teleost species detected per seine and trawl survey sample, subdivided by samples from sites where GSOs were detected and undetected (enumerated in Table 2). Incidence of GSO species were removed from each sample total in order to compare native teleost species per sample. The Fisher's Exact Test with simulated p=values based on 2000 replicates for seine samples yielded a p-value = 0.09845. The same testing method for trawl samples resulted in a p-value = 0.03048. These p-values indicate that the null hypothesis cannot be rejected for seine samples (p-value > 0.05), while a p-value < 0.05 for trawl samples does indicate a rejection of the null hypothesis and supports the alternative hypothesis that the number of native teleost species detected per sample is different at sites where GSOs were detected when compared with sites where no GSOs were found.

Table 2. Frequency of Teleost Species Detected per Sample

Teleost Species Totals	Seine			Trawl	
	GSO-detected	GSO-undetected		GSO-detected	GSO-undetected
0	0	0		5	16
1	0	0		8	26
2	1	4		11	20
3	1	4		6	7
4	2	11		4	3
5	1	9		7	2
6	3	9		1	0
7	1	1		0	1
8	1	2		0	0
9	2	0		0	0
10	1	0		0	0
11	0	0		0	0
12	0	0		0	0
13	1	0		0	0

Table 2. Frequency of Teleost Species Detected per Sample. *The frequency of total teleost species detected per survey sample. Sample totals were grouped by survey method and then divided by those samples from sites where GSOs were detected and those where GSOs were undetected. Species totals for survey samples containing GSOs have ben adjusted to compare only native species totals.*

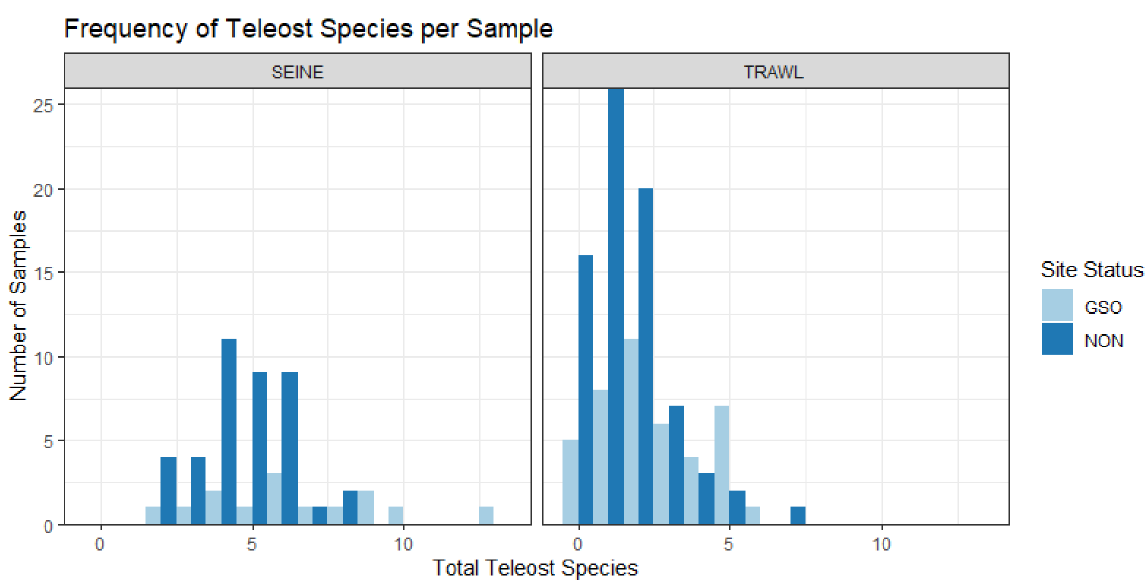


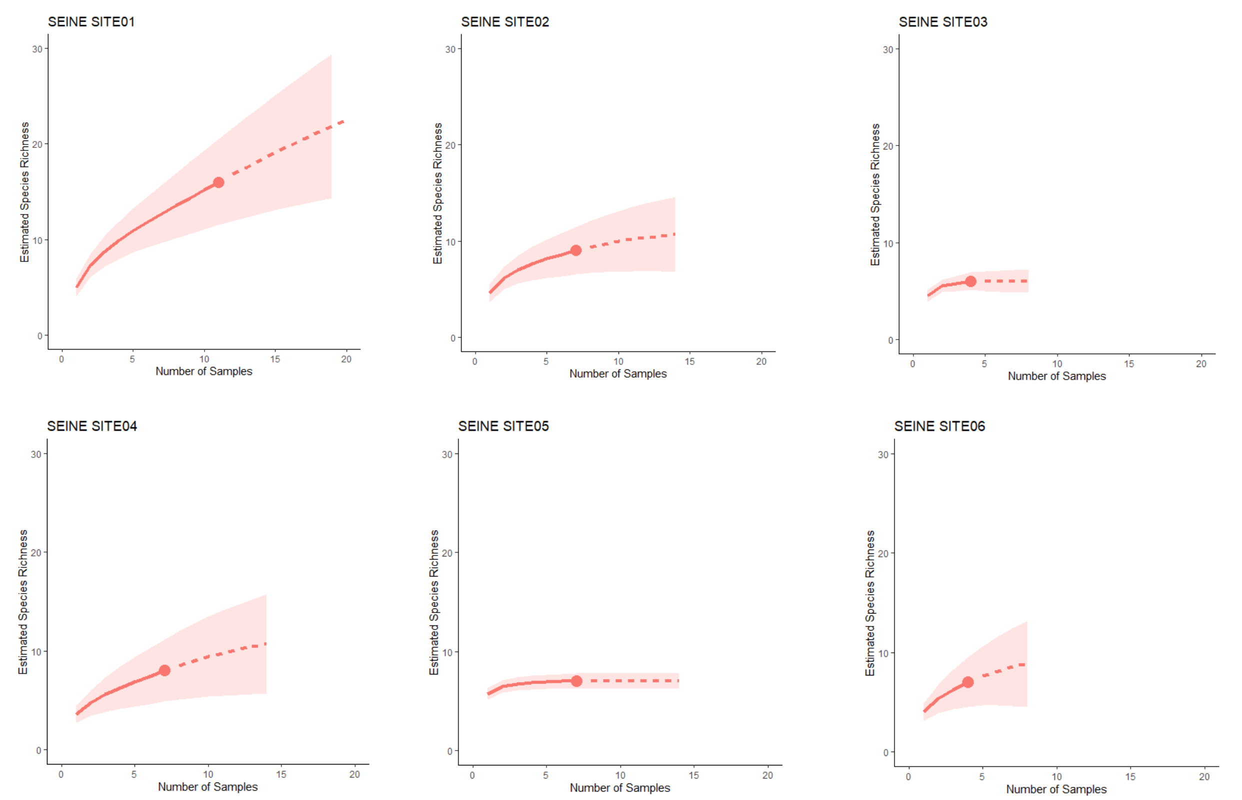
Figure 12. Frequency of Teleost Species per Sample. *The frequency of total teleost species detected per survey sample. Sample totals were grouped by survey method and then divided by those samples from sites where GSOs were detected and those where GSOs were undetected. Species totals for survey samples containing GSOs have been adjusted to compare the native teleost species detected.*

Comparing native teleost species totals and sampling frequencies by method does not accurately assess biodiversity at each sampling site but rather indicates that more detailed analysis is needed. Metrics to evaluate biodiversity generally include both incidence and abundance data among others to calculate species richness and evenness for various assemblages. From these sampled values, several biodiversity indicators may be calculated. It is often problematic to infer conclusions based on differences in raw taxon counts alone as characteristics including sampling effort, observation and collection will influence these counts and present misleading results (Gotelli and Colwell, 2001).

Species richness estimates for each seine site, the standard error, and 95% confidence interval are summarized in Table 3. Seine Site 07, shaded in gray, was the only seine site location to detect Gulf Stream Orphans with both *C. ocellatus* and *S. borealis* sampled at that location. Within the 95% confidence interval, there is overlap in the estimated value of species richness amongst several sites. Richness estimates for Seine Site 01 and Seine Site 07 do appear distinctly elevated from sites 02-06, though only sites 03 and 05 appear to approach an asymptote with an upper bound that does not overlap with the other sites. While Seine Site 07 was the only GSO-positive site in the survey, Atlantic Needlefish, (*S. marina*) which, though a sub-tropical and reef-associated species, was determined to be inconclusive as a Gulf Stream Orphan, was found at Seine Site 01 which appears to have elevated richness, like that of Seine Site 07.

Table 3. Seine Survey Species Richness Estimation						
	Number of Samples	**Observed Species**	**Estimated Species Richness**	**Est. s.e.**	**95% Lower**	**95% Upper**
Seine Site 01	11	16	48.727	23.287	25.335	130.742
Seine Site 02	7	9	11.571	3.881	9.304	30.758
Seine Site 03	4	6	6.000	0.423	6.000	7.523
Seine Site 04	7	8	13.143	6.129	8.815	40.469
Seine Site 05	7	7	7.000	0.337	7.000	7.828
Seine Site 06	4	7	10.375	5.473	7.365	38.241
Seine Site 07	14	16	16.619	1.23	16.052	23.381

Visual comparison of the rarefaction curve generated for each seine site can be inspected in Figure 13. As was alluded to in the comparison of seine sites via Table 3, sites 03 and 05, clearly indicate the species richness approaching an asymptotic value of 6 and 7 teleost species, respectively. Though these two sites had fewer samples collected (n=4 and n=7 respectively), these sample sizes were comparable to sites 02, 04, and 06 which did not approach an asymptote as definitively. The rarefaction curves for sites 01, 02, 04, and 06 demonstrate a consistent positive slope, leading to a larger upper limit of species richness that additional sampling effort would likely shape towards a more precise asymptote. Though the estimated values for species richness and associated confidence intervals may have been honed by increased sample size, sample-based rarefaction of incidence data in this survey of Pleasant Bay has provided valuable insight into the local species richness at each sample site.



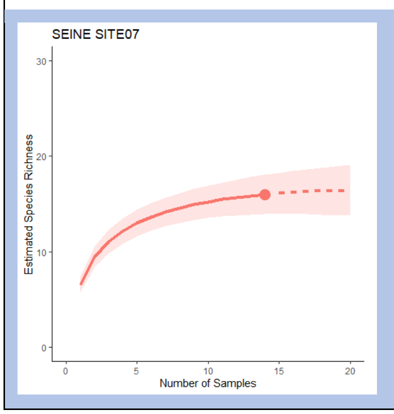


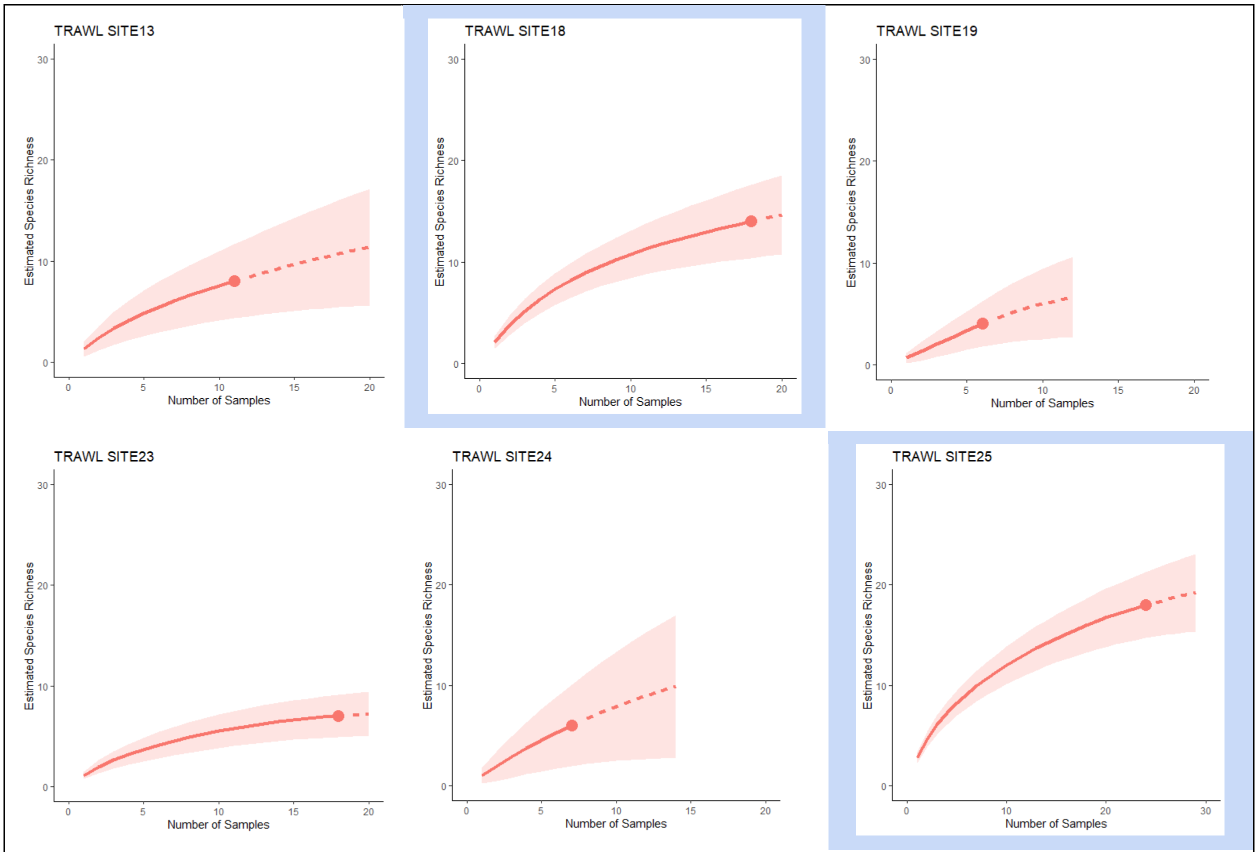
Figure 13. Seine Site Rarefaction Curves. *Species Rarefaction Curves for each of the 7 seine survey sites in Pleasant Bay. Estimated species richness is calculated only for native species detected and does not include incidence of Gulf Stream Orphans. Interpolated richness based on samples is indicated by the solid line while extrapolated species richness beyond sampled values is indicated by the dashed line. The pink shaded area indicates the 95% confidence interval. Seine Site 07 is highlighted in blue to indicate its status as a site where Gulf Stream Orphans were found. The remaining sites did not harbor any GSOs though Site 01 did harbor Atlantic Needlefish, S. marina, which has been discussed here as a potential GSO.*

Species richness estimates and sample-based rarefaction curves were also created for the trawl sites of the Pleasant Bay survey. A summary of the trawl survey samples and estimated species richness values as well as 95% confidence intervals are provided in Table 4. Sites 18 and 25 are highlighted in blue as they were GSO-positive sites where Atlantic Moonfish, *S. setapinnis* were sampled.

Table 4. Trawl Survey Species Richness Estimation

	Number of Samples	Observed Species	Estimated Species Richness	Est. s.e.	95% Lower	95% Upper
Trawl Site 13	11	8	19.364	15.614	9.51	93.53
TSITE 18 w/o GSOs	18	14	22.5	9.633	15.431	64.473
Trawl Site 19	6	4	9	5.839	4.812	34.79
Trawl Site 23	18	7	7.63	1.247	7.053	14.475
Trawl Site 24	7	6	16.714	14.743	7.421	86.784
TSITE 25 w/o GSOs	24	18	22.696	4.659	18.927	41.788
Trawl Site 29	10	14	16.25	2.706	14.353	28.352

The initial trawl survey of Pleasant Bay consisted of 16 different sampling locations. In order to estimate species richness, locations that were sampled $n \geq 6$ times were included in this analysis. Trawl sites 18 and 25, both positive for GSO species incidence were the two sites with highest estimated species richness though their 95% confidence interval overlapped with all but one other trawl site. Trawl sites 13, 18, and 24 all possess elevated upper-bound estimates, which are illustrated in the positive slope of their rarefaction curves in Figure 14.



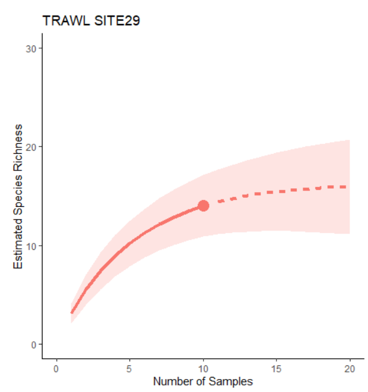


Figure 14. Trawl Site Rarefaction Curves. *Species Rarefaction Curves for the 7 trawl survey sites in Pleasant Bay with sample sizes n ≥ 6. Interpolated richness based on samples is indicated by the solid line while extrapolated species richness beyond sampled values is indicated by the dashed line. The pink shaded area indicates the 95% confidence interval. Trawl sites 18 and 25 are highlighted in blue to indicate GSO-positive sites. The remaining sites did not harbor any "Gulf Stream Orphans."*

To compare the relationships between different environmental characteristics and species richness, the seine and trawl survey samples were clustered according to three different categories: geographic proximity, biotope, and biotic group. Both the biotope and biotic group distinctions were mapped for Pleasant Bay by Mittermayr et al. 2020 and defined using CMECS (FGDC, 2012). The clustering of sites based on these characteristics also served to improve sample size within each group to improve the resulting rarefaction curves. Across all clustering parameters, there is substantial overlap at the 95% confidence interval between GSO-detected and undetected groups. Estimated richness in clusters that contain GSO-detected sites do show elevated richness across each scenario and rank at least one group as the highest or second highest estimated richness group in all three clustering scenarios. Clustering by biotic group in Figures 19 and 20 show the strongest evidence in support of the hypothesis with GSO-detected groups displaying the highest or second highest estimated richness across both sampling methods. The need for increased sampling persists regardless of clustering parameter. Group 01 in all three seine survey clustering methods presents a unique estimate for further study and expanded sampling as the estimated richness and 95% CI is consistently the most elevated.

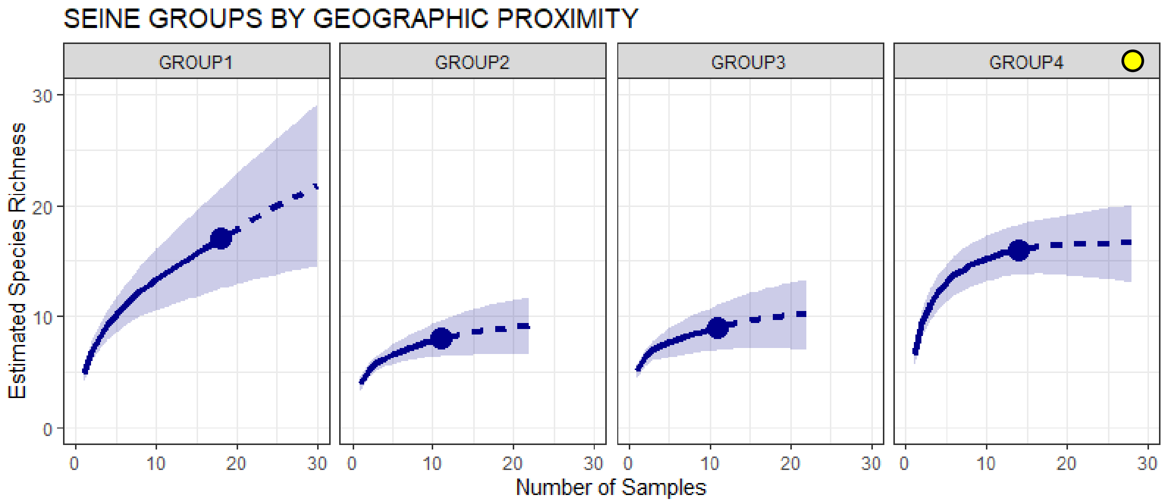


Figure 15. Seine Groups by Geographic Proximity. *Species Rarefaction Curves for the seine survey sites of Pleasant Bay grouped by geographic proximity. Estimated species richness is calculated for native species detected and does not include incidence of Gulf Stream Orphans. Interpolated richness based on samples is indicated by the solid line while extrapolated species richness beyond sampled values is indicated by the dashed line. The shaded area indicates the 95% confidence interval. Group 4 contains Seine Site 07 where Gulf Stream Orphans were found. The remaining grouped sites did not harbor any GSOs though Site 01 did harbor Atlantic Needlefish, S. marina, which has been discussed here as a potential GSO.*

Table 5. Species Richness Estimation for Seine Sites Grouped by Geographic Proximity

	Number of Samples	Observed Species	Estimated Species Richness	Est. s.e.	95% Lower	95% Upper
GROUP 01 (S01, S02)	18	17	43.444	20.17	24.014	116.705
GROUP 02 (S03, S04)	11	8	9.818	3.426	8.163	28.295
GROUP 03 (S05, 06)	11	9	10.818	3.426	9.163	29.295
GROUP 04 (S07)	14	16	16.619	1.23	16.052	23.381

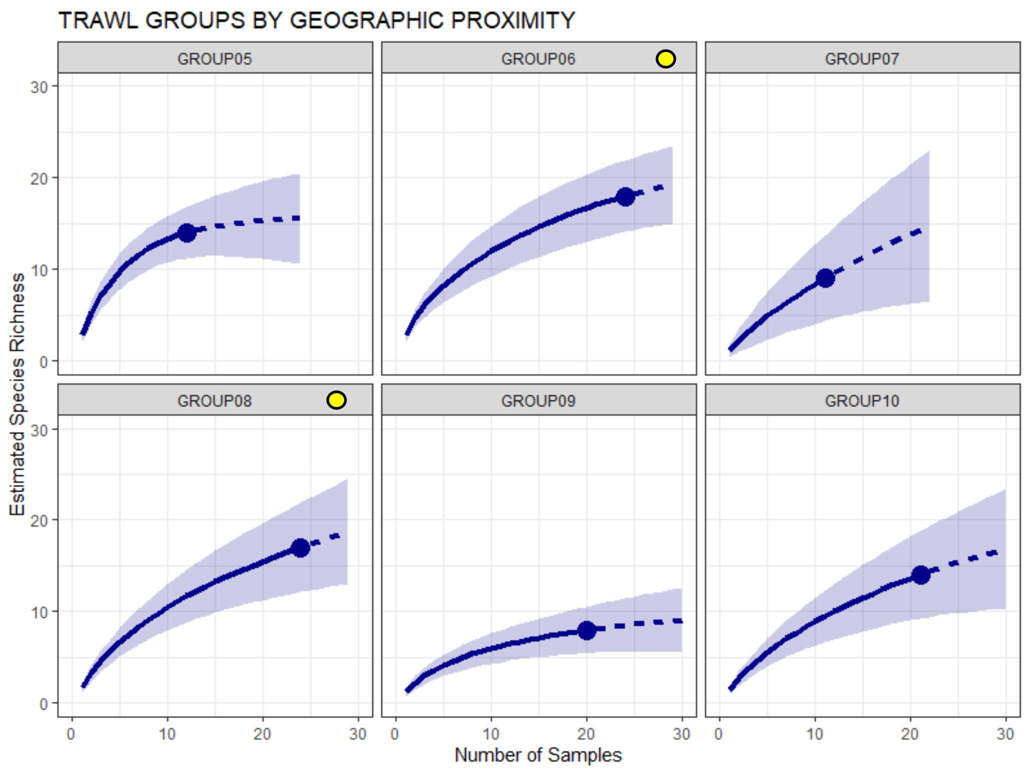


Figure 16. Trawl Groups by Geographic Proximity. *Species Rarefaction Curves for the trawl survey sites in Pleasant Bay grouped by geographic proximity. Interpolated richness based on samples is indicated by the solid line while extrapolated species richness beyond sampled values is indicated by the dashed line. The shaded area indicates the 95% confidence interval. Groups 06 and 08 represent sites 25 and 18 respectively and are marked with yellow dots to indicate GSO-positive sites. The remaining sites did not harbor any "Gulf Stream Orphans."*

Table 6. Species Richness Estimation for Trawl Sites Grouped by Geographic Proximity

	Number of Samples	Observed Species	Estimated Species Richness	Est. s.e.	95% Lower	95% Upper
GROUP 5 (T01, T29)	12	14	15.8333	2.457	14.251	27.374
GROUP 6 (T025)	24	18	22.696	4.659	18.927	41.788
GROUP 7 (T04, T24)	11	9	28.091	15.68	13.674	86.984
GROUP 8 (T18, T19)	24	17	36.406	19.367	20.805	115.988
GROUP 9 (T11, T23)	20	8	10.137	3.243	8.251	26.202
GROUP 10 (T13-T17)	21	14	24.159	9.806	16.071	63.836

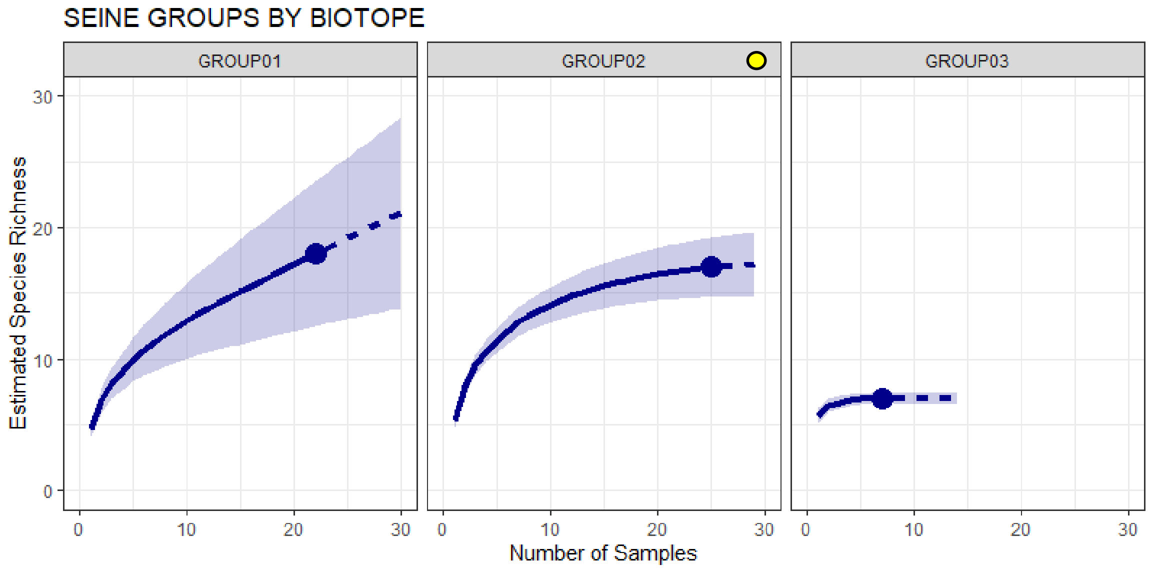


Figure 17. ***Species Groups by Biotope.*** *Species Rarefaction Curves for the seine survey sites of Pleasant Bay grouped by biotope. Estimated species richness is calculated for native species detected and does not include incidence of Gulf Stream Orphans. Interpolated richness based on samples is indicated by the solid line while extrapolated species richness beyond sampled values is indicated by the dashed line. The shaded area indicates the 95% confidence interval. Group 02 contains Seine Site 07 where Gulf Stream Orphans were found. The remaining grouped sites did not harbor any GSOs though Group 01 does contain Seine Site 01, which did harbor Atlantic Needlefish, S. marina, which has been discussed here as a potential GSO.*

Table 7. Species Richness Estimation for Seine Sites Grouped by Biotope

	Number of Samples	Observed Species	Estimated Species Richness	Est. s.e.	95% Lower	95% Upper
GROUP 1 (S01, S02, S03) – Biotope1	22	18	52.364	24.46	27.798	138.522
GROUP 2 (S04, S06, S07) – Biotope 4	25	17	17.48	0.999	17.038	23.061
GROUP 3 (S05) – Biotope 2	7	7	7	0.337	7	7.828

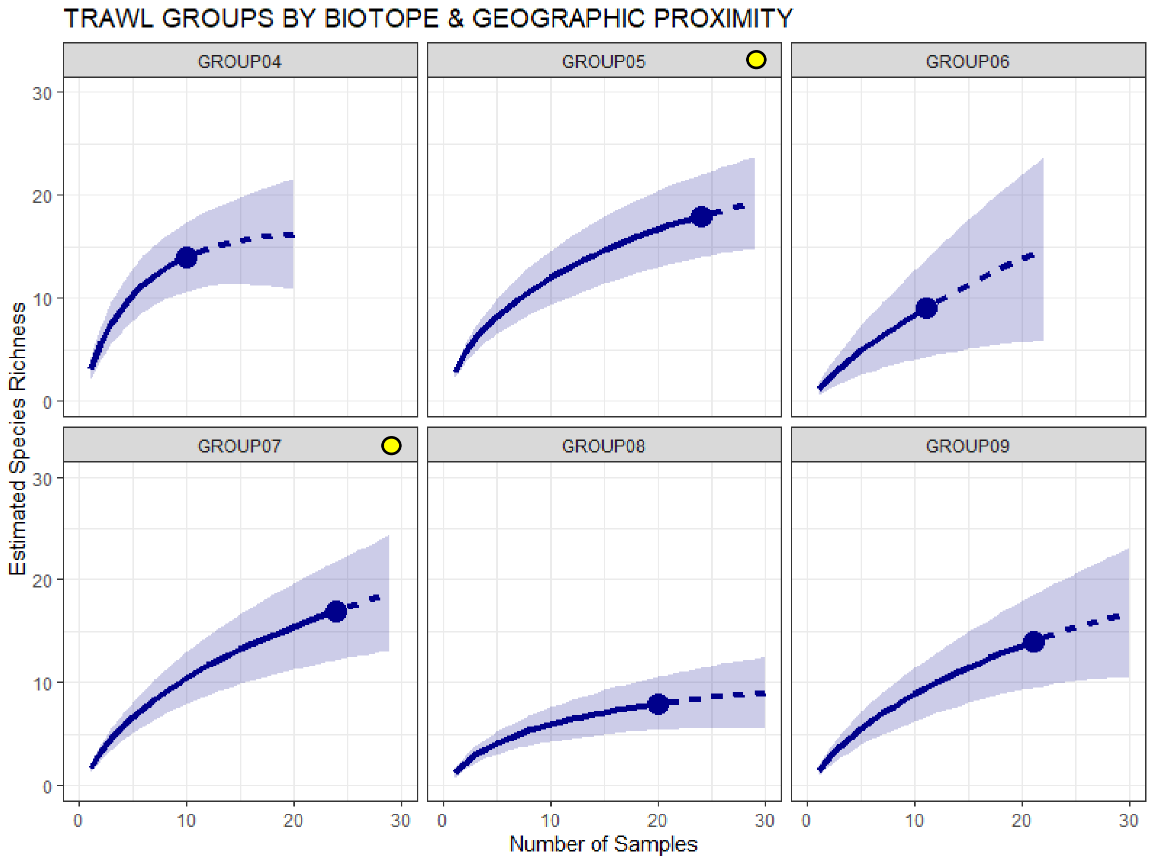


Figure 18. Trawl Groups by Biotope and Geographic Proximity. *Species Rarefaction Curves for the trawl survey sites in Pleasant Bay grouped by biotope and geographic proximity. Interpolated richness based on samples is indicated by the solid line while extrapolated species richness beyond sampled values is indicated by the dashed line. The shaded area indicates the 95% confidence interval. Groups 05 and 07 represent sites 25 and 18 respectively and are marked with yellow dots to indicate GSO-positive sites. The remaining sites did not harbor any "Gulf Stream Orphans."*

Table 8. Species Richness Estimation for Trawl Sites Grouped by Biotope and Geographic Proximity

	Number of Samples	Observed Species	Estimated Species Richness	Est. s.e.	95% Lower	95% Upper
GROUP 04 (T29)	10	14	16.812	3.334	14.448	31.643
GROUP 05 (TSITE 25)	24	18	22.696	4.659	18.927	41.788
GROUP 06 (T04, T24)	11	9	28.091	15.68	13.674	86.984
GROUP 07 (T18, T19)	24	17	36.406	19.367	20.805	115.988
GROUP 08 (T11, T23)	20	8	10.137	3.243	8.251	26.202
GROUP 09 (T13-T17)	21	14	24.159	9.806	16.071	63.836

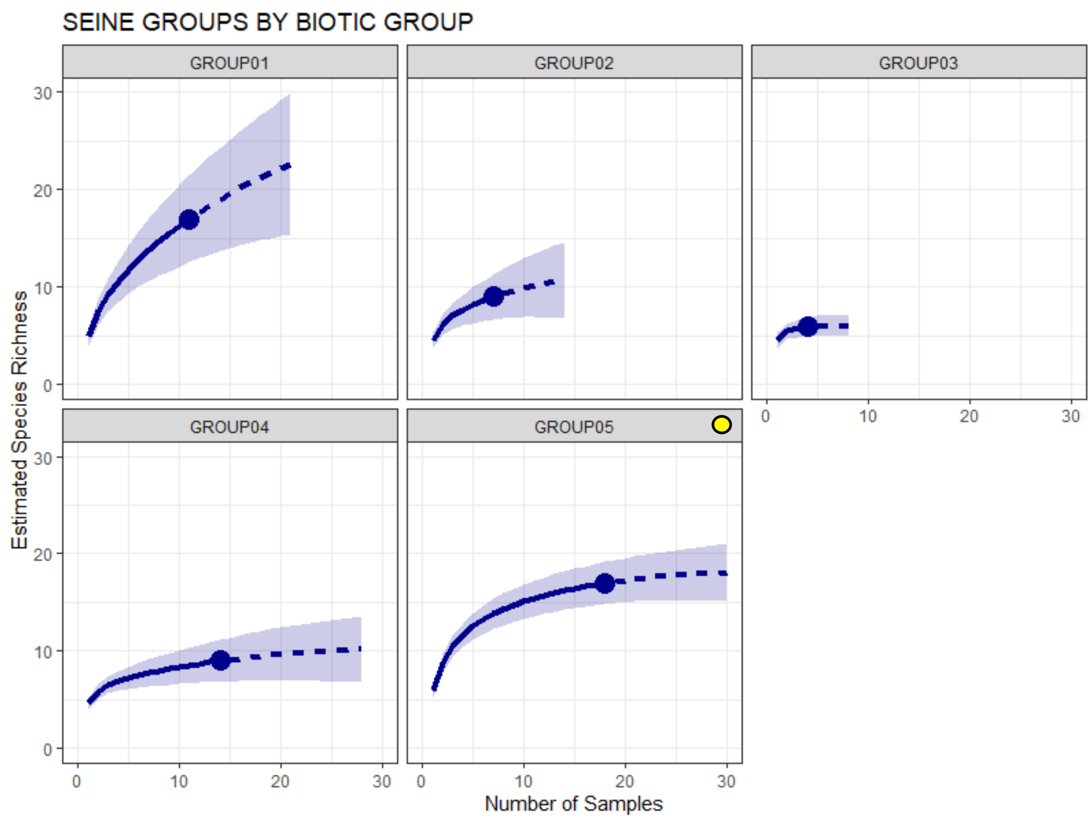


Figure 19. Seine Groups by Biotic Group. *Species Rarefaction Curves for the seine survey sites of Pleasant Bay grouped by biotic group. Estimated species richness is calculated for native species detected and does not include incidence of Gulf Stream Orphans. Interpolated richness based on samples is indicated by the solid line while extrapolated species richness beyond sampled values is indicated by the dashed line. The shaded area indicates the 95% confidence interval. Group 5 contains Seine Site 07 where Gulf Stream Orphans were found. The remaining grouped sites did not harbor any GSOs though Group 01 does contain Seine Site 01, which did harbor Atlantic Needlefish, S. marina, which has been discussed here as a potential GSO.*

Table 9. Species Richness Estimation for Seine Sites Grouped by Biotic Group

	Number of Samples	Observed Species	Estimated Species Richness	Est. s.e.	95% Lower	95% Upper
GROUP 01 (S01) *Mobil mollusk on soft sediment*	11	17	31.545	15.037	19.735	94.352
GROUP 02 (S02) *Seagrass bed*	7	9	11.571	3.881	9.304	30.758
GROUP 03 (S03) *Small surface burrowing fauna*	4	6	6	0.423	6	7.523
GROUP 04 (S04, S05) *Small tube-building fauna*	14	9	10.857	3.493	9.167	29.688
GROUP 05 (S06, S07) *Large tube-building fauna*	18	17	18.417	2.182	17.163	29.296

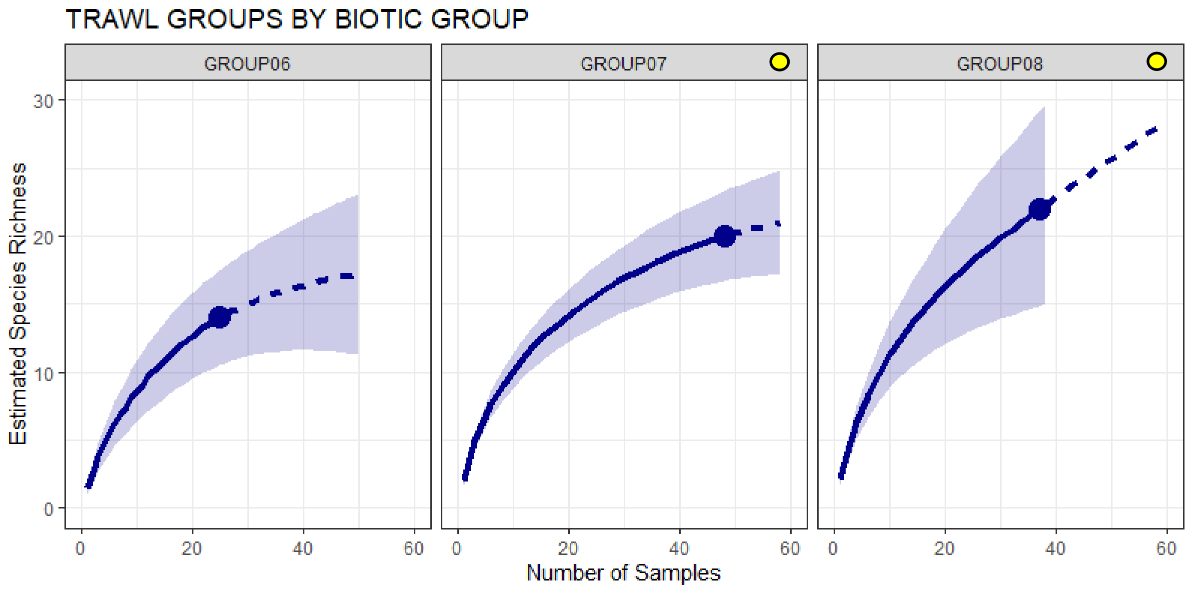


Figure 20. Trawl Groups by Biotic Group. *Rarefaction curves for the trawl survey sites of Pleasant Bay clustered by biotic group. Estimated species richness is calculated for native species detected and does not include incidence of Gulf Stream Orphans. Interpolated richness based on samples is indicated by the solid line while extrapolated species richness beyond sampled values is indicated by the dashed line. The shaded area indicates the 95% confidence interval. Group 07 contains Trawl Site 18, and Group 08 contains Trawl Site 25 where Gulf Stream Orphans were found.*

Table 10. Species Richness Estimation for Trawl Sites Grouped by Biotic Group

	Number of Samples	Observed Species	Estimated Species Richness	Est. s.e.	95% Lower	95% Upper
GROUP 06 (T04, T13-17) *Small surface burrowing fauna*	25	14	18.32	4.629	14.778	37.977
GROUP 07 (T11, T18, T23, T29) *Large tube-building fauna*	48	20	22.938	3.182	20.522	36.521
GROUP 08 (T19, T24, T25) *Small tube-building fauna*	35	22	80.865	69.166	31.487	387.258

Discussion

The occurrence of tropical reef fish in the Northwest Atlantic is due to a confluence of natural phenomena that shape the physical, biological, and ecological characteristics of the coastline of North America. From the physical transport of tropical water to the factors that influence and contribute to habitat choice by fish, the temporary residence of reef fishes in New England still has many unanswered questions.

Species richness, though difficult to measure in its totality, is viewed as one of the most straightforward descriptors of community diversity and is often referenced as an explicit objective for conservation efforts (May, 1988). Methods of standardization in ecosystem survey design, data collection and analysis such as sample-based rarefaction can help to eliminate sources of error that would influence richness values. Sample-based rarefaction can also help standardize against the fundamental trend in richness evaluation methods that increasing sampling effort leads to increasing species recorded for diverse taxa (Bunge and Fitzpatrick, 1993). Ultimately, with sufficient sampling, the value of a species accumulation curve would reach an asymptote as sampled species approached 100% of those in a particular environment, but often this degree of effort is beyond the scope of realistic survey design due to costs, sampling effort, and methods. Constraints on the realities of field work and survey effort are important to consider in the design of species richness estimation. As in the case of this Pleasant Bay survey, sampling species incidence rather than abundance data allowed for increased sampling effort by decreasing sample processing time. Likewise, standardizing the assessment through a sample-based approach and analyzing rarefaction curves can generate comparable results between survey sites, even in small-scale surveys where constraints in the field may impact survey effort allocation. While analysis and results of survey data can be improved with increasing sample sizes, species richness estimation of incidence data and sample-based rarefaction can determine significance in species richness across relatively small survey designs.

The clustering of survey sites by proximity, biotope, and biotic group incorporated additional environmental characteristics into the analysis and improved sample sizes for each rarefaction curve generated, though there were limitations. Mittermayr et al. (2020) found only 24.09% of benthic infauna species distribution was attributable to prevailing sediment types within Pleasant Bay, indicating many more factors likely play a role in the community structure. Further incorporation of both physical and biological factors including water chemistry, water movement, vegetation, and trophic interactions are necessary to achieve a more comprehensive understanding of fish assemblages within Pleasant Bay and the distribution of GSOs within the estuary.

Species richness estimates revealed seine site 01 as an intriguing location for further study as increased sampling effort may indicate it as a biodiversity hotspot. The estimated richness was substantially elevated and had broad range within the 95% CI when compared with other seine sites. No confirmed GSOs were sampled at this site, though incidence of Atlantic Needlefish (*S. marina),* a subtropical and reef-associated species, did occur. Perhaps the incidence of *S. marina* as a reef-associated species highlights that the site harbors certain environmental characteristics beyond those considered in this survey that increase its likelihood to harbor GSOs.

The survey methods and analysis presented here provide an effective evaluation method for small-scale survey initiatives. Increasing the reach and accessibility of environmental assessments through scientific surveys is critical to improving environmental conservation and stewardship efforts. Promoting viable methods for small-scale, cost-effective survey design and analysis may prove invaluable to coastal communities looking to accurately assess and prioritize their resources and conservation efforts. The methods described in this paper provide one example of a small-scale survey initiative to advance our understanding of a local estuary. The incorporation of citizen science reporting is another effective tool in developing our understanding of the breadth and context of natural phenomena for more detailed scientific analysis.

The Pleasant Bay survey resulted in the detection of three different tropical or sub-tropical species (*C. ocellatus*, *S. borealis*, and *S. setapinnis*) distinguished as "Gulf Stream Orphans." The presence of these species in Pleasant Bay is likely the result of transport and dispersal by the Gulf Stream to geographic areas beyond their native ranges. Following that dispersal, it is likely that the residence of these species at their detected sample locations is the result of both environmental characteristics and active habitat selection by these species for favorable conditions that parallel those within their native range. The three Gulf Stream Orphan species detected in Pleasant Bay were found at sample locations with three of the four highest estimated species richness across all individual seine and trawl sites, though substantial overlap was documented at the 95% confidence interval. This evidence would indicate that there may be a relationship between the incidence of tropical and subtropical species at sites of elevated species richness. An additional aspect of this relationship to explore is the variation and distribution of habitat type within Pleasant Bay and how habitat characteristics connect to selection by these expatriated species. Clustering of seine and trawl samples based on proximity as well as CMECS biotope and biotic groups was a viable technique to increase sample size for rarefaction and revealed promising trends to consider in future efforts. While these clustering techniques incorporated sediment characteristics and dominant benthic fauna into the analysis, there are many more habitat characteristics worthy of examination to understand the influences on fish assemblages and distributions within Pleasant Bay. Legare et al. (2020) explored the integration of environmental conditions and habitat characteristics with the distribution of microinvertebrate communities of Pleasant Bay to better assess the links between these factors within the broader ecosystem. The incorporation of habitat type, vegetation, community structure, and GSO incidence in survey and modeling efforts will also lead to a comprehensive understanding of the physical and biological phenomena shaping the estuary and improve conservation measures. The dozens of documented marine fish species reported as GSO's span 36 different taxonomic families, indicating that a variety of life histories exist amongst fish dispersed in the Northwest Atlantic. Nichols et al. (2020) demonstrated that additional GSO species are present within the Pleasant Bay system (Snowy Grouper, *H. niveatus*), and a diversified survey design with additional sampling and observation techniques is necessary to capture a more complete picture of the phenomenon.

The Northwest Atlantic and Gulf of Maine in particular has been subject to several distinct community changes in recent decades, influenced by four phenomena: harvesting of ground fish stocks, invertebrate population dynamics, sea surface temperature increase, and changes in dominance by introduced and opportunistic benthic community species (Harris and Tyrrell, 2001). The role that Gulf Stream transport plays in the dispersal and potential introduction of opportunistic species that may be capable of capitalizing on changing environmental conditions is worthy of further exploration. The influences on coastal ecosystem dynamics due to stakeholder use, compiled with amplified climate variations may result in novel opportunities for expatriated marine species to play a more significant role within coastal ecosystems of the Northwest Atlantic. Pleasant Bay presents as a fascinating microcosm of many of the interlocking processes that shape our coastal environments on a grand scale. Reviewing historical records, continued monitoring and expansion of data collection efforts will prove invaluable in shaping our understanding of potential changes to marine environments applicable on local and regional scales.

The presence of expatriated tropical and subtropical fish species in New England waters may serve as a valuable indicator of critical habitat and biodiversity hot spots. Survey efforts that expand our understanding of the phenomenon including citizen science reporting to more comprehensively describe their occurrence may yield valuable insight into high priority habitat that provides ecosystem services such as nursery habitat and preserves biodiversity. Creating a more robust understanding of the incidence of GSOs with underlying ecosystem conditions may help coastal stakeholders glean insight into target areas for conservation initiatives. The potential for citizen science reporting to amplify conservation targets beyond those studied through traditional survey methods deserves exploration. As reporting and associated research achieves a broader scale, biogeographic changes in species distribution along the east coast of North America may be revealed. A comprehensive understanding of the changes in fish assemblages of the Northwest Atlantic could be applied to shape ecosystem management and policy efforts moving forward.

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