Evaluating the impact of invasive seagrass *Halophila stipulacea* on settlement, survival, and condition factor of juvenile yellowtail snapper, *Ocyurus chrysurus*, in St. Thomas, USVI

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By
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Abstract:

Yellowtail snapper, *Ocyurus chrysurus,* are one of the most commercially important fish species within the United States Virgin Islands (USVI). Like many reef fish, juvenile yellowtail snapper rely on seagrass habitats as critical nursery areas prior to an ontogenetic transition to coral reef ecosystems. Native seagrasses *Syringodium filiforme* and *Thalassia testudinum* provide juvenile fish with foraging habitat and protection during this vulnerable stage of life. However, these essential habitats are threatened by numerous anthropogenic stressors, including increased sediment runoff, pollution, and invasive species. In 2002 an invasive seagrass *Halophila stipulacea* was discovered off the coast of Grenada and has since spread rapidly throughout the Caribbean, arriving in St. Thomas, USVI in 2013. This invasive seagrass poses additional threats to native seagrasses as it displaces native species. A shift in community composition could have damaging effects on juvenile reef fish populations that depend on these habitats as nurseries. The purpose of this study was to determine the effects of *H. stipulacea* on juvenile yellowtail snapper settlement, mortality, and condition in St. Thomas, USVI. Settlement and mortality of juvenile yellowtail snapper was compared among *H. stipulacea, S. filiforme,* and *T. testudinum* seagrass habitats around southern St. Thomas, USVI. Juvenile yellowtail snapper (n=260) were trapped and measured for length and weight to derive the condition factor as a measurement of health. Significantly higher settlement and similar trends in mortality were seen in invasive seagrass habitats when compared to native seagrasses. There was no significant difference in condition factor of juvenile yellowtail snapper among seagrass species, although trends demonstrated a higher condition in native than invasive seagrass habitats. These results could suggest that *H. stipulacea* does not have as negative an impact on newly settled and juvenile yellowtail snapper populations and condition as previously hypothesized. This study is the first of its kind to try to understand the direct effects of *H. stipulacea* during the early life history stages of commercially important fish species in St. Thomas, USVI.

Keywords: *Halophila stipulacea*; *Ocyurus chrysurus;* Settlement; Mortality; Condition Factor; Invasive Species

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I understand that my thesis will become part of the permanent collection of the University of the Virgin Islands Library. My signature below authorizes the release of my thesis to any reader upon request.

Sophia Victoria Costa

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CONTRIBUTION OF AUTHORS

Sophia Costa contributed to the experimental design, completion of data collection and field and lab work, data analysis and writing of this thesis. Major advisor, Dr. Richard Nemeth, contributed to the project development, data collection and field work, and data analysis. Dr. Sennai Habtes provided guidance with the lab work and statistical analysis. Dr. Demian Willette assisted in the experimental design. All authors contributed to the editing of this document.

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DEDICATION

My thesis is dedicated to my dear grandmother, Sue Gilbreath, and dear friend Stephanie Hibberts. Without the support they gave me I would not have been able to get to where I am today. I miss you both every day.

CHAPTER 1
General Introduction

Fishing Industry in the United States Virgin Islands (USVI)

The United States Virgin Islands (USVI) is comprised of three islands (St. Thomas, St. John, and St. Croix) located in the northern sector of the Lesser Antilles, just southeast of Puerto Rico (Figure 2.01). St. Thomas and St. John are on the large, shallow-water shelf that includes Puerto Rico and the British Virgin Islands (Rogers et al. 2008, Kadison et al. 2017). St. Croix is 65 kilometers south of the northern U.S. Virgin Islands, which is separated by the Virgin Islands Basin (Fratantoni et al. 1997, Rogers et al. 2008, Fischel et al. 2017, Kadison et al. 2017). Due to the depth of the basin, there is limited migration of many commercially important reef fish species between the northern islands (St. Thomas, St. John) and St. Croix (Kadison et al. 2017). Nonetheless, the tropical waters of the USVI yield a diverse and vibrant marine ecosystem (Rogers et al. 2008).

Currently and historically within the USVI, the fishing industry is consistently one of the most important economic industries (NOAA Economic Report 2016, Yandle et al. 2020). Between the years 2005 to 2015, the USVI commercial fishing industry produced on average $7.4 million per year (Kojis et al. 2017). Due to St. Thomas and St. Croix’s economic reliance on marine resources, these islands are considered fishing-dependent communities (Stoffle et al. 2020). According to a 2016 economic census of ocean dependencies for the USVI, an estimated seven percent of the island population relied solely on ocean industries for their livelihood, which is more than three times higher than the United States average (NOAA Report Summary 2016). However, that estimate is believed to be under-representative of the true number of individuals within the USVI that depend on the ocean industries for their livelihood (NOAA Report Summary 2016). For example, in 2017 two category 5 hurricanes, Irma and Maria, devastated the USVI and inhibited numerous vital supplies. This resulted in the local community relying predominantly on the sea for many valuable resources (Stoffle et al. 2020, Yandle et al. 2020). The dependency on the local fishery creates a dire need for protection as pressures on marine ecosystems continue to increase throughout the world (Caddy 2008). As anthropogenic effects and climate change become more pressing issues, the local fishing industry in the USVI is more vulnerable than ever. One study found that due to the extended Puerto Rican shelf, the majority of the fishing around St. Thomas was in shallower waters (Brandt et al. 2011), which could make the fishing industry more vulnerable to nearshore impacts.

Global climate change has placed immense stress on the local, fishing industry in the Virgin Islands (Kojis et al. 2017). As global temperatures continuously rise, increased water temperatures around the world are believed to affect the abundance, growth, and mortality of many commercially important fish species (Mills et al. 2013). Fish are most vulnerable to these environmental changes during their larval phase and immediately after post-settlement recruitment. Lett et al. (2010) stated that increased effects of global climate change, like increased water temperatures and possible changes in oceanic circulation, could have a major effect on larval fish survival and dispersal. It has been suggested that with increased seawater temperature, major shifts in spawning season, increased larval mortality, and possible shorter larval duration could be seen (Lett et al. 2010). Additionally, as oceanic circulation changes, the distribution patterns and connectivity could leave larval fish more vulnerable than ever (Lett et al. 2010). Understanding these processes and how they are projected to changes is critical for manager to make informed decision on fish regulations. However, it is also important for managers to understand the vulnerability fish populations face during their juvenile stages. There are numerous factors that contribute to the success of newly settled juvenile fish, including food availability, competition, predator presence, and habitat structure (Grenouillet et al. 2002). Food resources are often considered one of the most important factors in overall success of a fish (Grenouillet et al. 2002, Nunn et al. 2012, Cushing 1990, Mayer and Whal 1997). The lack of prey availability could not only reduce the growth of an individual, but also result in the starvation and eventual death (Nunn et al. 2012, Cushing 1990, Mayer and Whal 1997). Grenouillet et al. (2002) found that with increased food availability, higher abundance and species richness of fish was seen. However, if a habitat becomes too saturated with individuals, the competition for resources could also leave the juvenile fish vulnerable to mortality (Wilson and Osenberg 2002). Not only does the competition in resources affect fish recruitment and success, but also the presence of predators has been seen to be an important post-recruitment factor (Beets 1997). Increased habitat complexity allows newly settled juvenile fish more area to hide from predators, therefore providing essential nursery habitat (Grenouillet et al. 2002). One such nursery habitat are seagrass ecosystems that provide food and structural support to many commercially important fish species (Parrish 1989, Laegdsgaard and Johnson 2001, Heck et al. 2003, Nagelkerken 2009, Grol et al. 2014).

Native Seagrasses

Seagrasses are a vital marine ecosystem globally because they supply numerous ecosystem services including carbon sequestration (Vaughn 2021, Rodemann et al. 2021), water filtration (Zimmerman et al. 1991, Short et al. 1996, Platenberg and Valiulis 2018), and structure in otherwise barren, sandy seafloors (Duffy 2006, Worm et al. 2006). This structure offers protection to many species of fish and invertebrates from large predators and is a major food source for megafauna species including turtles and stingrays (Zimmerman et al. 1991, Duffy 2006, Platenberg and Valiulis 2018). Not only do seagrasses provide shelter for many marine fauna, but they also dissipate wave energy which decreases sediment resuspension and the uprooting of benthic flora (Zimmerman et al. 1991, Platenberg and Valiulis 2018, Rodemann et al. 2021). Due to the available shelter and food abundance within these habitats, seagrasses act as a critical nursery area for many reef fish (Parrish 1989, Laegdsgaard and Johnson 2001, Heck et al. 2003, Nagelkerken 2009, Grol et al. 2014). Studies have shown that numerous commercially important species use seagrass habitats during the juvenile phase prior to transitioning to reef environments (Turano et al. 2000, Mateo et al. 2011, Grol et al. 2014).

There are four native seagrasses found within the USVI: *Syringodium filiforme*, *Thalassia testudinum*, *Halodule wrightii,* and *Halophila decipiens* (Delgado and Stedman 2004, Platenberg and Valiulis 2018, Jerris 2019). The three most common seagrass species *S. filiforme, H. wrightii*, and *T. testudinum*, have a similar elongated blade structures that offer ample coverage for juvenile fish (Platenberg and Valiulis 2018). *S. filiforme*, otherwise known as manatee grass, has a long, thin blade that is round and hollow in cross-section (Platenberg and Valiulis 2018). *Halodule wrightii*, otherwise known as shoal grass, is often found in shallower and more disturbed waters (Platenberg and Valiulis 2018). *H. wrightii* has a thin, circular blade that resembles *S. filiforme*, however, it is not hollow throughout the blade like *S. filiforme* (personal observation). Both *H. wrightii* and *S. filiforme* are important pioneer species in disturbed areas (Gallegos et al. 1994, Jerris 2019). The third common seagrass species is *T. testudinum*, otherwise known as turtle grass. *T. testudinum* has a long, ribbon-like blade with a deeper root system compared to the other two native seagrasses and is a climax species that is slow to arrive but quickly becomes dominant (Platenberg and Valiulis 2018, Jerris 2019). *T. testudinum* provides critical habitat and a food source for numerous fish, turtle, and invertebrate species found in the Virgin Islands (Platenberg and Valiulis 2018).

However, seagrass ecosystems are threatened by many anthropogenic impacts. Some scientists suggest that with increased impacts of global climate change, invasive species are expected to have a dramatic negative effect on already fragile native ecosystems (Canning-Clode et al. 2011, Hobbs 2000). An invasive species is defined as a non-native species that alters an ecosystem or reduces biodiversity within its invaded area (Gurevitch and Padilla 2004). One such invasive seagrass species is *Halophila stipulacea*, that has become an increasing threat as it has rapidly spread throughout the Caribbean Sea (Willette and Ambrose 2009, Willette et al. 2014). This species could not only threaten native seagrasses but also juvenile fish that depend on this habitat as nursery areas.

The Invasion

Native to the Red Sea and Western Indian Ocean, *H. stipulacea* is a Lessepsian species that was first observed in the Mediterranean Sea in the late 19th century (Willette and Ambrose 2009, Winters et al. 2020). Researchers and historians believe this species first invaded the region after the opening of the Suez Canal in 1869

(Willette et al. 2014, Winters et al. 2020). For several decades, *H. stipulacea* remained in the eastern Mediterranean Sea along the Albanian coast (Procaccini et al. 1999, Gambi et al. 2018). Throughout the next century, *H. stipulacea* spread into the Tyrrhenian Sea and western Mediterranean Sea (Gambi et al. 2009). Due to habitat preference, the impacts of *H. stipulacea* on native seagrasses within the Mediterranean seemed to be minimal (Rogers et al. 2014). However, because the invasion occurred within the Mediterranean Sea over a century prior to the subsequent invasion of the Caribbean Sea, it is difficult to know exactly how the species affected native Mediterranean environments.

In 2002, *H. stipulacea* was first reported in the Caribbean Sea off the coast of Grenada (Ruiz and Ballantine 2004). The rate of expansion has been well documented as *H. stipulacea* has spread rapidly throughout the Caribbean Sea (Willette and Ambrose 2009, Winters et al. 2020). Within five years, *H. stipulacea* spread north to Dominica, and then spread over 700 miles north to Puerto Rico and south to Venezuela (Willette and Ambrose 2009, Vera et al. 2014, Chiquillo et al. 2018). By 2013, the species had reached St. Thomas, USVI and by 2016 had spread to St. Croix (Olinger et al. 2017). Scientists predict that in due time the invasive species will be found throughout the entire Caribbean Sea (Olinger et al. 2017).

There are many characteristics that make *H. stipulacea* successful at invading new territories. In the Caribbean, *H. stipulacea* is seen in monospecific or polyspecific seagrass beds possibly demonstrating impacts of the invasion through competition with native seagrasses (Chiquillo et al. 2018). Evidence suggests this seagrass has the ability to rapidly colonize previously disturbed areas and has a high fragment settlement rate (Gambi et al. 2009, Willette et al. 2014, Jerris 2019, Willette et al. 2020). After small- and large-scale disturbances, *H. stipulacea* demonstrated a high resilience growing at an exponential rate and outcompeting native Caribbean seagrasses while capitalizing on any available space (Jerris 2019, Willette et al. 2020). Willette and Ambrose (2012) observed *H. stipulacea* overtaking native *S. filiforme* seagrasses, which suggests a devastating effect of the invasive species on this important pioneer species throughout the Caribbean Sea. Viana et al. (2019) suggested that *H. stipulacea* acts as a pioneer species after a disturbance providing suitable habitat for species that rely on seagrasses quicker than native seagrasses. Therefore, higher frequency and severity of disturbances could allow *H. stipulacea* to further outcompete native seagrasses throughout the greater Caribbean region.

Additionally, *H. stipulacea*'s biological characteristics have allowed the seagrass to quickly assimilate to conditions in the Caribbean Sea. The invasive seagrass can tolerate a wide range of depth from 2 to 50 meters and rapidly expands through fragmentation and lateral expansion (Willette and Ambrose 2009, Willette and Ambrose 2012, Olinger et al. 2017). It primarily reproduces sexually in its home range but reproduces primarily by asexual reproduction in the invaded Caribbean region (Chiquillo et al. 2018). *H. stipulacea* has also been seen to tolerate high variability of salinity (Oscar et al. 2018). When exposed to hyper- and hypo-saline conditions, the seagrass was seen to reduce density and blade size during these extreme situations to survive (Oscar et al. 2018). Upon returning to normal condition, *H. stipulacea* recovered density and biomass, demonstrating signs of high resilience (Oscar et al. 2018).

Unlike the most common native seagrasses in the Caribbean, *H. stipulacea* has short, serrated blades found in dense quantities (Willette and Ambrose 2009). Some researchers have suggested that the increased density of *H. stipulacea* seagrass beds may be more beneficial than previously presumed because it provides a refugia in otherwise barren seafloors (Rogers et al. 2014, Van Tussenbroek et al. 2016, Viana et al. 2019). Van Tussenbroek et al. (2016) compared nutrient content of densely formed areas of *H. stipulacea* versus areas with sparsely grown *H. stipulacea* and discovered higher nutrient concentrations in areas with the invasive seagrass. These potential benefits of the invasive species could have a positive impact on fish populations that depend on seagrass habitats by providing more food and habitat.

This Study

This study aims to understand the effects of the invasion of *H. stipulacea* on juvenile yellowtail snapper, *Ocyurus chrysurus*, in St. Thomas, USVI. We examined settlement and initial mortality of juvenile yellowtail snapper in native and invasive seagrass habitats in five bays off the southern coast of St. Thomas from May 2020 to June 2021. Additionally, juvenile yellowtail snapper were trapped in native and invasive seagrasses to analyze the health of individuals among seagrass species. The goal of this study was to (1) demonstrate the impact of invasive seagrass *H. stipulacea* on juvenile yellowtail snapper settlement selectivity, (2) demonstrate the impact of invasive seagrass *H. stipulacea* on juvenile yellowtail snapper post-settlement mortality rate, and (3) demonstrate the impact of invasive seagrass *H. stipulacea* on juvenile yellowtail snapper condition.

CHAPTER 2

Evaluating the effects of invasive seagrass *Halophila stipulacea* on settlement and survival of juvenile yellowtail snapper, *Ocyurus chrysurus*, in St. Thomas, USVI

Abstract:

As anthropogenic impacts increase in coastal areas, it is critical to understand how their consequences will affect commercially important fish species. Many of these species, like yellowtail snapper (*Ocyurus chrysurus)*, depend on seagrass beds as critical nursery habitat. Since 2002, an invasive seagrass, *Halophila stipulacea,* has become widespread throughout the Caribbean Sea, arriving in St. Thomas in 2013. The impacts of *H. stipulacea* on juvenile yellowtail snapper habitat are not well understood, yet, have the potential to disrupt essential fish habitats and reduce important fishery resources. Previous studies have demonstrated that *H. stipulacea* can reduce juvenile fish health and diversity, suggesting that *H. stipulacea* may have a strong negative effect on juvenile reef fishes (Olinger et al. 2017). In this study, we analyzed the impacts of *H. stipulacea* on the settlement and survival of juvenile yellowtail snapper. Results from this study demonstrate a higher settlement of yellowtail snapper in *H. stipulacea* seagrass habitats than in native *S. filiforme* and *T. testudinum* seagrass habitats. Juvenile yellowtail snapper survival was lowest in *S. filiforme* seagrass habitats, followed by *H. stipulacea*, then *T. testudinum.* Therefore, the effects of *H. stipulacea* might not be as harmful to juvenile yellowtail snapper populations as previously hypothesized.

Keywords: Settlement; Mortality; Yellowtail Snapper; *Halophila stipulacea*; St. Thomas, USVI; Invasive Species

Introduction:

Many coral reef fish have complex life histories that are typically comprised of a pelagic larval phase, benthic settlement phase, then an ontogenetic shift to coral reef ecosystems (Victor 1991, Öhman et al. 1998) To maintain fish populations it is critical to understand how individuals are affected throughout their life cycle, particularly in early life stages when individuals are most vulnerable (Richmond et al. 2018, Lecchini and Galzin 2005). Studies have demonstrated that many larval fish use olfactory, visual, and auditory cues to actively select suitable habitat for settlement (Lecchini et al. 2005, Lecchini and Galzin 2005, Pollux et al. 2007). Environmental variables such as lunar cycle (Robertson 1992), solar radiation and temperature (McCormick and Molony 1995, Bergenius et al. 2005), oceanographic processes (Sponaugle et al. 2005), as well as habitat suitability (Öhman et al. 1998) influence recruitment and settlement selectivity of many reef fish (Rankin and Sponaugle 2014).

Habitat selection is a critical variable in settlement selectivity as individuals depend on these areas for food and protection (Öhman et al. 1998, Nagelkerken et al. 2000). Seagrasses provide newly settled individuals with necessary resources and are often considered an essential nursery habitat to many species of reef-associated fishes before an ontogenetic shift to coral reef ecosystems (Parrish 1989, Muehlstein and Beets 1992, Verweij et al. 2008, Dahlgren and Eggleston 2000, Nagelkerken et al. 2000, Nagelkerken et al. 2002, Pollux et al. 2007, Turano et al. 2000, Watson et al. 2002). *Thalassia testudinum* and *Syringodium filiforme* are native seagrass species in the greater Caribbean region that fill this roll for many economically important fish species (Nagelkerken et al. 2000, Watson et al. 2002, Renán et al. 2006, Willette and Ambrose 2012, Olinger et al. 2017). The structural complexity of these habitats may provide many reef fishes with the necessary protection to reduce vulnerability from predators (Shulman 1985, Nagelkerken et al. 2000). To ensure the long-term survivability and fitness of many commercially important fish species, the maintenance of these essential seagrass nursery habitats is critical.

In 2002, *H. stipulacea* was reported in the Caribbean Sea off the coast of Grenada (Ruiz and Ballantine 2004). This invasive seagrass then spread north to Dominica, and continued to Puerto Rico, south to Venezuela, and west to Curaçao (Willette and Ambrose 2009, Willette et al. 2014, Chiquillo et al. 2018). By 2013 it reached St. Thomas, USVI and spread to bays around the island (Olinger et al. 2017). *H. stipulacea* has been found in large quantities in highly disturbed areas within the Caribbean (Willette et al. 2014). The invasive species is highly adaptable to a wide range of depths (2-50 m) and is documented to expand laterally at a rapid rate, allowing it to outcompete native seagrasses for space (Willette and Ambrose 2009, Olinger et al. 2017, Jerris 2019). A potential community shift to a dominant invasive seagrass habitat could disrupt critical ecological functions resulting in negative effects on fish populations that are dependent on these areas.

The direct effects of *H. stipulacea*, which is structurally dissimilar from native Caribbean seagrasses, on juvenile reef fish is not well understood. Native seagrasses *T. testudinum* and *S. filiforme* have elongated blades reaching on average 18 cm in length (Bradley and Houser 2009, Steiner and Willette 2013, Olinger et al. 2017, Platenberg and Valiulis 2018). In comparison, *H. stipulacea* has short, serrated blades reaching on average 5 cm in height (Willette and Ambrose 2009, Olinger et al. 2017). Due to its height difference, *H. stipulacea* could have disadvantageous impacts on species that rely on seagrass beds for food and development. Willette and Ambrose (2012) found significantly larger fish, and greater species abundance in *H. stipulacea* seagrass habitats than in *S. filiforme.* However, two times more juvenile fish were present in native than invasive seagrass habitats (Willette and Ambrose 2012). It is not known if juvenile reef fish are selecting *H. stipulacea* habitats during settlement, migrating to the invasive seagrass habitats after settlement, or if they have higher post-settlement survivorship in *H. stipulacea* habitats than in native seagrass habitats. Therefore, it is necessary to better understand how recruitment and post-settlement processes are affecting the abundance of juvenile reef fish in native and invasive seagrass habitats.

The purpose of this study was to analyze the effects of *H. stipulacea* on the settlement and survival of juvenile yellowtail snapper around St. Thomas, US Virgin

Islands. Juvenile fish habitat preference and suitability was compared among invasive *H. stipulacea* and native *T. testudinum* and *S. filiforme* seagrass habitats. These data will provide important insight on how the invasion of this species may impact commercially important fish populations in the US Virgin Islands.

Methods:

Site Selection

Four bays in St. Thomas, USVI (18.3381°N, 64.8941°W) were selected for this study. Each bay contains monotypic stands (>75%) of native seagrass species (*S. filiforme* and *T. testudinum*) and invasive seagrass (*H. stipulacea*): Saba Island, Lindbergh Bay, Frenchmans Bay, and Sprat Bay (Figure 2.01). The three target species of seagrasses in each of these sites ranged in depth from 3.7 m to 10.3 m (Table 2.01). Brewers Bay was also selected as an alternative site, even though there are no longer native seagrasses in this bay, to compare settlement patterns among shallow (2.4 m) and deep (16.4 m) *H. stipulacea* beds (Table 2.01, Figure 2.01).

Study Species

The yellowtail snapper (*Ocyurus chrysurus*) is a commercially important reef fish species found from the northeastern United States through the Caribbean to southern Brazil, including parts of the Gulf of Mexico (Riley et al. 1995, Turano et al. 2000, Gutiérrez-Sigeros et al. 2018, Lindholm et al. 2005, Manooch and Drennon 1987, Zajovits 2021, Garcia et al. 2003). With relatively slow growth rates as juveniles, yellowtail snapper can reach about 160 mm in total length after one year (Turano et al. 2000, Garcia et al. 2003). They are a gonochoristic species that reaches sexual maturity around 250 to 310 mm in length (McClellan and Cummings 1998, Gutiérrez-Sigeros et al. 2018). Spawning occurs year-round with large pulses in spring and summer (Turano et al. 2000, Farmer and Ault 2011, Zajovits 2021, Figuerola et al. 1998, Munro et al. 1973, Trejo-Martinez et al. 2011). After about 30 days in larval form, settlement of yellowtail snapper has been documented to occur a few days prior to the new moon (da Silva et al. 2015, Watson et al. 2002). After settlement juvenile yellowtail snapper are most often found in seagrass habitats, and occasionally in mangrove habitats for several weeks at a time, prior to an ontogenetic shift when adults migrate to coral reefs, rocky ledges, and hard bottom habitats (Turano et al. 2000, Nagelkerken et al. 2000, Watson et al. 2002). Verweij et al. (2008) found that roughly 98% of yellowtail snapper spend some time in seagrass habitats during the first two years of their lives. Previous studies have demonstrated that native seagrass found throughout the Caribbean region, like *Thalassia testudinum* and *Syringodium filiforme,* provide the necessary protection for juvenile yellowtail snapper less than 7.5 cm in total length (Turano et al. 2000, Watson et al. 2002). Watson et al. (2002) considered fish ≤3 cm to be a newly settled individuals and found that these fish showed strong site fidelity to their settlement location with a home range of 6.3 m^2 in seagrass habitats around Tortola, British Virgin Islands (BVI).

Settlement Plot Establishment

Settlement patterns and survival rates of juvenile yellowtail snapper among seagrass species (*H. stipulacea*, *S. filiforme*, and *T. testudinum*) were measured by establishing one 8 m x 8 m plot in each seagrass type in each bay with an effort to keep plots within ±5 m depth of one another (Table 2.01). Brewers Bay had two plots established in *H. stipulacea* at 16 m and 3m in depth to examine settlement variability between depth (Table 2.01). Settlement plots were established in the five bays between February 2020 and June 2020. Two additional plots were established in June 2020 in each seagrass species at Saba Island to examine within site variability among seagrass types. Each of the four corners of the plot were marked with steel rebar stakes pounded into soft sediment and outlined with a neon nylon line. Plot dimensions were determined based on Watson et al. (2002) who found newly settled yellowtail snapper (20 - 30 mm TL) have a home range less than 7.5 m^2.

Settlement and Survival Surveys

To better understand settlement patterns and survival of juvenile yellowtail snapper, visual surveys were conducted 3 to 7 days prior to the new moon in each plot.

Within each plot, two divers swam parallel to one another and recorded the size category of each juvenile yellowtail snapper observed (0 - 20 mm, 21 - 30 mm, 31- 40 mm, 41- 50 mm, 51- 100 mm, 101- 150 mm, 151- 200 mm, 201 - 300 mm, and 301 mm). Each diver used a two-meter PVC T-bar with 1 cm and 5 cm black and white markings to help estimate the size class. T-bars were pushed along just above or in the seagrass which improved sighting and counting of newly settled yellowtail snapper, especially in seagrass beds with longer blades. Surveys prior to the new moon provided a baseline population estimate before settlement pulses. Once a settlement pulse was detected (>10 individuals), surveys were repeated daily for seven days, then every other day for the following 8 days, and then weekly until the following settlement month (n=16 surveys) in the bays where a settlement pulse was detected. If the number of fish counted in a plot reached zero individuals for two consecutive surveys, the plot was no longer surveyed during that pulse.

Environmental Variables

A HOBO Pendant temperature 64k data logger (Onset, Massachusetts) was attached to a steel rebar stake in the center of one plot in each bay, and data was recorded every 15 minutes from May 2020 to September 2021. All bays had one HOBO logger, except Brewers Bay where one logger was placed in both shallow and deep-water plots. Upon retrieval of HOBO Pendant loggers, one MiniDOT oxygen/temperature logger (Precision Measurement Engineering, Inc., California) was attached to the same steel rebar stake and recorded data every 10 minutes. In Brewers Bay, only one MiniDOT logger was deployed in deep water. MiniDOT loggers were installed in September 2021 and retrieved for data offload in January 2022.

Seagrass Characteristics

Seagrass characteristics were recorded as blade height, blade density, and percent cover (from this point the three will be called seagrass characteristics) in each survey plot. Two divers would divide the plot in half and collect density information from 5 randomly placed 10 cm^2 quadrats in each half of the 8 m^2 plot. Divers would begin with their quadrats at 90^o and 1 m from the edge of the plot and would then follow random placement for a distance pattern of 1 m, 2 m, 1 m, and 2 m. Random placement was designed using a random angle generator and setting the parameters from 45^{o} to 120^{o} to ensure quadrats stayed within the plot. For each quadrat divers collected the total blade density (total blade count), percent coverage of the target seagrass of the plot, and five measurements of maximum blade height. These values were averaged for each plot to get the total density of each plot. Seagrass characteristics were collected twice throughout the study to see if there was a shift in benthic composition. The first collections were from July to December 2020 in all plots except SI-HS1, SI-TT1, SI-TT2, SI-SF2, SI-HS3, and SI-TT3 (Table 2.02). Seagrass characteristics were collected from all plots again from October 2021 to January 2022. Seagrass lateral growth or expansion rate was also collected for *H. stipulacea (H.s.)*, *S. filiforme (S.f.)*, and *T. testudinum (T.t.)* in Frenchmans Bay (*H.s, S.f, T.t*), Sprat Bay (*H.s, S.f, T.t*), Saba Island (*S.f, T.t*), and Brewers Bay (*H.s*) from December 2019 to January 2022. Lateral expansion was recorded by placing six steel rebars at the edge of a seagrass bed, then measured by tying a transect tape to the steel bar and measuring perpendicularly to the new growth edge of the seagrass. If a seagrass plot had merged with a bordering seagrass bed, measurements were halted (FB-HS, FB-SF, and BB-HS Shallow).

Data Analysis

Overall peak settlement of yellowtail snapper was determined by summing the number of newly settled yellowtail snapper (≤30 mm) observed across all surveys by days from the new moon. Comparisons of the number of settled yellowtail snapper were made using survey data of individuals ≤30 millimeters (mm) for months which had greater than 10 settlers (May, June, August, October 2020, and May 2021). When comparing settlement values among bays or seagrass types only bays including one plot of each seagrass type were used including, Saba Island plot set 1, Lindbergh Bay, Sprat Bay, and Frenchmans Bay. Settlement data from Brewers Bay deep and shallow plots and all replicate plots from Saba Island were used to determine within bay settlement trends. Settlement data did not meet parametric assumptions of Analysis of Variance (ANOVA), therefore, non-parametric Kruskal-Wallis and Dunn’s tests were used to test effects of seagrass species, bay, and month on settlement, as well as the effect of seagrass species on size class observed. Friedman Rank tests were used to test the effect of the interactions of bay and seagrass species as well as month and seagrass species on settlement.

To determine persistence and mortality rate of yellowtail snapper, only settlement months with ≥ 20 newly settled yellowtail snapper at peak settlement were used. For the purpose of this study, peak settlement was defined as the single day with maximum number of newly settled yellowtail snapper (≤30 mm), persistence is defined as the number of survived newly settled yellowtail snapper in a given day following the day of peak settlement, and mortality is defined as the difference between the two. Percent persistence and daily mortality rate were determined using the equations:

$$P: \frac{P_d}{P_p} \text{ x } 100$$

P: Percent Persistence; P_d: Daily Population; P_p: Population at Peak Settlement

$$M_r = \frac{(P_d - P_d^{+1})}{(TP_d)} \text{ x } 100$$

M_r: Daily Mortality Rate, P_d: Daily Population, $\underline{P_d}^{+1}$: Population Size from subsequent survey, T: Time Between P_d & $\underline{P_d}^{+1}$

Daily population was defined as the population size on any given day. Population at peak settlement was defined as the maximum number of individuals observed in a settlement month. Population size from the subsequent survey is the size of the population observed in the consecutive survey. Time is defined as the number of days between surveys. Percent persistence was used to approximate the survivability of newly settled yellowtail snapper. Daily mortality rate represented the rate of loss of newly settled yellowtail snapper within each seagrass species between each survey (i.e. 24 hr mortality rate). Overall persistence was calculated by averaging daily mortality rates per seagrass type relative to peak settlement.

Upon collection of the Hobo temperature loggers, data was offloaded using Onset HOBOware software version 3.7.23. Data from the placement of each logger on May 27, 2020 to August 22, 2021 when the loggers stopped recording were used to determine variability of seawater temperature among bays. From September 2, 2021 to January 7, 2022 MiniDOT O2 loggers recorded data within each bay, then offloaded using the MiniDOT software version 4.05. Outliers above 14 mg/l were removed from these data because they were outside of previous reported dissolved oxygen concentrations found in St. Thomas (Duffing Romero et al. 2021). Only data of dissolved oxygen concentrations in Frenchmans Bay from September 2021 to December 2021were used because of logger malfunction. The first data point from each bay at a randomly selected hour, using a random number generator, on the day of the new moon each month was used to compare variability of temperature and dissolved oxygen concentrations among bays. Seagrass characteristics were averaged for each plot for the beginning and end of the study respectively. Mean percent cover, blade density, and blade height from the end of the study were used for data analysis because metrics were recorded in each plot (n=20) unlike the beginning of the study (n=14).

Environmental variables, seagrass blade density and seagrass blade height did not meet parametric assumptions of Analysis of Variance (ANOVA) tests, therefore, non-parametric Kruskal-Wallis and Dunns tests were used to test the effect of bay on dissolved oxygen concentrations (mg/l), temperature (^{o}C), and seagrass characteristics, as well as to analyze the effect of seagrass species on blade density and blade height. A one-way ANOVA and Tukey’s Honest Significance Difference tests were used to test the effect of seagrass species on percent cover. To compare the change of seagrass characteristics from the beginning to the end of this study, a T-test was run. A Generalized Linear Model (GLM) using Gaussian distribution was run to understand which environmental variables and seagrass characteristics influenced settlement. Mean temperature and mean dissolved oxygen concentrations for each bay, as well as seagrass characteristics from the end of this study were used in this model. All statistical tests were run in R-Studio version 3.6.2 (R Core Team, 2019).

Results:

From May 2020 to June 2021, a total of 68 survey days were completed around St. Thomas, USVI (Table 2.03). In May, June, and August 2020, settlement pulses of yellowtail snapper were detected at Saba Island and Frenchmans Bay (Table 2.03). Additionally, in May 2020 there was a settlement pulse in Brewers Bay (Table 2.03). There were two settlement pulses in October 2020 (Frenchmans Bay, Sprat Bay, and Brewers Bay) and May 2021 (Frenchmans Bay, Sprat Bay, and Lindbergh Bay; Table 2.03). In total, two settlement pulses of greater than 100 individuals were detected in *H. stipulacea* (May 2020 n= 242; June 2020 n=194) seagrass habitats and two in *T. testudinum* (May 2020 n=110; June 2020 n=103) seagrass habitats. Eight settlement pulses of less than 100 individuals were observed in *H. stipulacea*, three times in *S. filiforme*, and three times in *T. testudinum* seagrass habitats. Within bay comparison of seagrass species at Brewers Bay and Saba Island demonstrated no significant difference in settlement rates.

Peak settlement of yellowtail snapper occurred between 4 and 0 days before the new moon (Figure 2.02). In Frenchmans Bay, peak total settlement occurred four days prior to the new moon in May, August, October 2020, and May 2021. Peak settlement was three days before new moon at Saba Island in May, June, and August 2020 and Sprat Bay in October 2020 and May 2021. In Lindbergh Bay, peak settlement occurred two days prior to the new moon in May 2021, however no settlement surveys were conducted three days prior to the new moon in this bay. Peak settlement occurred on the new moon in Brewers Bay during May and October 2020.

Seagrass species had a significant effect (p=1.15e-5) on yellowtail snapper settlement (Table 2.04; Figure 2.03). There were significantly more newly settled yellowtail snapper (≤30 mm) in *H. stipulacea* (n=1,367) seagrass habitats than in native *S. filiforme* (n=384) and *T. testudinum* (n=1,008) seagrasses (Figure 2.03). There was also a significant effect (p=2.39e-7) of month on settlement (Table 2.04; Figure 2.04). In May and June 2020 there was a significantly greater number of newly settled yellowtail snapper (≤30 mm) than in August 2020, October 2020, or May 2021 (Table 2.04; Figure 2.04). There was no significant difference in the number of yellowtail snapper that settled between May and June 2020, and no significant difference of settled individuals among August 2020, October 2020, and May 2021. The greatest number of individuals settled in June 2020 (n=1,118; Figure 2.04). There was no significant interaction ($p>0.05$) between settlement month and seagrass species.

There was a significant effect (p=9.44e-9) of bay on settlement (Table 2.04; Figure 2.05), with more settlement at Saba Island (n=1,584) than at Lindbergh Bay (n=231), Sprat Bay (n=334), or Frenchmans Bay (n=607), which were not significantly different from on another (Figure 2.05). There was a significant effect of the interaction of bay and seagrass (p=0.0138; Table 2.04; Figure 2.06). During all settlement months at Frenchmans Bay and Lindbergh Bay, a higher number of individuals settled in *H. stipulacea* seagrass habitats than in native seagrasses (Figure 2.06). However, at Saba Island more individuals settled in *T. testudinum* seagrass habitats than *H. stipulacea* or *S. filiforme* in May 2020 (Figure 2.06). Similarly, at Sprat Bay more newly settled yellowtail snapper were seen in *T. testudinum* seagrass plots than the other two seagrass species for all months but May 2020 (Figure 2.06). There was no significant difference of settlement in the same seagrass species within a site, however, at Saba Island there was a significant difference of settlement among seagrass species (p=0.019; Table 2.03). Significantly greater settlement of yellowtail snapper occurred in *H. stipulacea* and *T. testudinum* seagrass habitats than in *S. filiforme* seagrass habitats (Figure 2.06). There was no significant difference of settlement between *H. stipulacea* and *T. testudinum* at Saba Island.

Throughout the entire study, the number of individuals surveyed between 21-30 mm was significantly higher than any other size class ($p=<0.001$; Table 2.04). A higher number of yellowtail snapper ≤40 mm and from 110 mm to 300 mm in total length were observed in *H. stipulacea* seagrass habitats (Figure 2.07). Individuals from 41 mm to 100 mm were more commonly seen in *T. testudinum* seagrass habitats (Figure 2.07).

The GLM demonstrated that month (p=7.4e-8) and temperature (p=0.005) were significant predictor values of yellowtail snapper settlement (Figure 2.08; Table 2.05). The strength of the model fit improved with a reduction of deviance of about 25% with the addition of these variables when compared to the null model (Table 2.06). Although the fit of the model was not greatly reduced, this does indicate some influence of month and temperature on settlement. Dissolved oxygen levels and seagrass characteristics were not significant predictors for settlement of juvenile yellowtail snapper.

Average daily mortality rate of yellowtail snapper was highest in *S. filiforme* seagrass habitats with an average rate of 4.65% day^{-1} of the total new settlers (≤30 mm) followed by *H. stipulacea* (2.73% day^{-1}) and *T. testudinum* (2.35% day^{-1}). All seagrass species demonstrated similar trends of a rapid decrease of percent persistence (Figure 2.09). Analysis of monthly differences in yellowtail snapper (Figure 2.10) survival found the two highest mortality rates of any settlement month or seagrass type at Frenchmans Bay *H. stipulacea* in August 2020 (16.67 % day^{-1}) and Brewers Bay deep *H. stipulacea* in May 2020 (17.86% day^{-1}). The lowest mortality rate of yellowtail snapper among all bays, seagrasses, and months was observed in *H. stipulacea* at Saba Island in June 2020 with a rate of 0.81% day^{-1}. Mortality rate for *S. filiforme* was only recorded in June 2020 at Saba Island as 9.84% day^{-1}. *T. testudinum* mortality rates were recorded at Saba Island in May 2020 (6.28 % day^{-1}) and June 2020 (7.45 % day^{-1}), and Sprat Bay in May 2021 (4.91% day^{-1}).

There was no significant effect of bay on temperature (^{o}C; p>0.05) or dissolved oxygen concentrations (mg/l; p>0.05; Table 2.04). Water temperature varied among all bays with the lowest temperature recorded as 22.5 ^{o}C in May 2020 in Brewers Bay Deep, and the highest temperature recorded as 31.1 ^{o}C in September 2021 at Sprat Bay (Figure 2.11). Dissolved oxygen concentrations also varied among all bays; Lindbergh Bay had the lowest recorded dissolved oxygen at 0.04 mg/l in

December 2021, and Sprat Bay had the highest recorded dissolved oxygen at 13.99 mg/l in December 2021.

Seagrass characteristics (percent cover, blade density, and blade height) for each seagrass species were similar among bays (Table 2.02). There was no significant change ($p>0.05$) in percent cover, blade density, and blade height from the beginning to end of this study. However, differences of seagrass characteristics were seen among seagrass species (Table 2.04; Figure 2.12). *H. stipulacea* had significantly greater percent cover ($p=0.0034$), higher blade density ($p=<0.001$), and shorter blades ($p=0.0021$), than *S. filiforme* and *T. testudinum*, which were not significantly different from one another in each seagrass characteristics (Table 2.04; Figure 2.12). Brewers Bay shallow *H. stipulacea* expansion had the highest mean growth of 2.1 cm day^{-1} and Frenchmans Bay *T. testudinum* had the lowest mean growth of -0.2 cm day^{-1} throughout this study (Table 2.07).

Discussion:

This is the first study to look at the effects of *H. stipulacea* on the settlement and mortality of a commercially important fish species that depend on seagrass nursery habitats. Results of this study demonstrate that yellowtail snapper actively settle into *H. stipulacea* seagrass habitats at greater rates than native seagrasses. This is similar to Willette and Ambrose (2012) that found a greater abundance of adult yellowtail snapper in *H. stipulacea* seagrass habitats than in *S. filiforme* seagrass habitats using fish traps. Olinger et al. (2017) also saw similar results of a greater abundance of juvenile snapper in *H. stipulacea* seagrass habitats than in native *S. filiforme, T. testudinum,* or bare sand. These findings suggests that snapper species do not avoid the invasive seagrass habitat, instead juvenile yellowtail snapper could be actively settling in *H. stipulacea* seagrass habitats.

Not only was settlement frequency higher, but also yellowtail snapper in *H. stipulacea* and *T. testudinum* habitats had similar trends of mortality that were at a lower rate than *S. filiforme*, suggesting that the invasive seagrass could be a more suitable nursery habitat for yellowtail snapper. However, the low persistence rate in *S. filiforme* could be due to the lower number of individuals settled in this seagrass habitats when compared to the other two seagrass types. As suggested by Caley (1998), the smaller the sample size the more likely mortality rates could be flawed. In this study we compensated for those flaws by only analyzing settlement of greater than 20 individuals. Nonetheless, the smaller sample size in *S. filiforme* should be considered when trying to understand the mortality rate of this seagrass species. These results suggest that *S. filiforme* not only is utilized by fewer individuals for settlement but additionally a higher mortality rate occurs in this native seagrass. This could suggest that either the habitat is less suitable for foraging or camouflaging juvenile yellowtail snapper, or due to the lower blade densities of this seagrass higher mortality is expected.

Similar trends of rapid mortality were seen among all seagrass types as previously described in many tropical reef fish, with a sharp decline in population size following settlement (Roberts 1996, Watson et al. 2002). Watson et al. (2002) reported an estimated 79% mortality of newly settled yellowtail snapper in *T. testudinum* seagrass habitats over the course of 30 days. However, similar to results of this study, they suggest a low sample size could be causing an inaccurate estimation of mortality. Previous studies have suggested that mortality could be density independent, meaning greater settlement may bring greater survival rates (Sissenwine 1984, Watson et al. 2002, Sponaugle et al. 2006). Interestingly, individuals in *H. stipulacea* seagrass habitats displayed similar trends in mortality rates to those in *T. testudinum*. These data suggest no distinctive difference in survival among *H. stipulacea* and *T. testudinum* seagrass habitats.

Results from this study suggest that for juvenile yellowtail snapper, *H. stipulacea* may be acting more as a non-native species than an invasive because it possibly is benefiting populations overall. With higher settlement, increased population sizes could be seen over time adding more individuals to the fishery. Due to yellowtail snapper being the most landed fish species in St. Thomas (Olsen et al. 2007), it is important for management to understand that *H. stipulacea* may have a positive impact on this commercially important fish species based on the evidence of this present study. Viana et al. (2019) also suggested that *H. stipulacea* could be adding beneficial ecosystem services to its invaded range, such as nursery habitat. The implications of these findings could demonstrate that *H. stipulacea* could be benefiting other important fish species as well by adding suitable settlement habitat in otherwise baren sea floor as seen in deep Brewers Bay.

No significant difference of settlement was observed between deep and shallow water habitats in Brewers Bay, although trends demonstrated roughly two times more yellowtail snapper settled in shallow waters compared to deeper habitats. These data could demonstrate that water depth does not have a significant effect on yellowtail snapper settlement. Booth and Beretta (1994) also found no effect of depth on settlement of tropical reef fishes in the USVI. Although fewer individuals overall settled in deep Brewers Bay than in shallow Brewers Bay, settlement was not significantly less and was actually higher in August and October, indicating that this additional seagrass area could be beneficial as it provides additional settlement habitat. The deep Brewer Bay plot is located at 16.5 m deep next to a small patch reef, which is much deeper than the depth range of native *S. filiforme* or *T. testudinum* seagrasses in St. Thomas (Willette et al. 2014, Platenberg and Valiulis 2018, Jerris 2019, Winters et al. 2020). This promising result could be beneficial for commercially important species as it may provide expanded habitat for settlement, as well as a deep water refugia in times of intense weather activity or increased anthropogenic effects. Due to settlement patterns of yellowtail snapper being quite variable, it is important for future studies to better understand how these deep habitats could be impacting the fishery long term.

Variability of settlement patters was observed across five bays and three seagrass types. For instance, in Frenchmans Bay new recruits were more likely to settle in *H. stipulacea* seagrass habitats, but in Sprat Bay more individuals settled in *T.*

testudinum seagrass habitats. At Saba Island, there was no difference of settlement between each of these seagrass types, but there was higher settlement in *H. stipulacea* and *T. testudinum* than in *S. filiforme*. Due to the relative proximity of each plot within these bays, settlement patterns were expected to be uniform if individuals were not actively selecting for habitat types (Pollux et al. 2007). While oceanographic variables are known to influence larval dispersal and settlement patterns (Kingsford 1988, Sponaugle et al. 2005, Booth and Beretta 1994), results from this study suggest that newly settled yellowtail snapper are actively selecting suitable habitat for settlement because uniform settlement did not occur throughout each bay. Due to no difference of settlement detected within bay and seagrass species at Brewers Bay and Saba Island, results suggest that yellowtail snapper may be selecting settlement habitat by seagrass species. Findings from this study suggest that *T. testudinum* and *H. stipulacea* offer the most suitable habitat for new recruits.

Overall peak settlement was observed for yellowtail snapper in May and June. After spending 30 days in larval form, juvenile yellowtail snapper settle into seagrass habitats (da Silva et al. 2015). Therefore, following settlement trends seen in this study, maximum spawning would have occurred in April and May, similar to a previous study that found peak spawning in yellowtail snapper in Puerto Rico and the USVI in March and April (Zajovits 2021). However, maximum spawning and settlement could vary from year to year, as seen in this study with maximum settlement occurring in June 2020 and no settlement detected across all five bays in June 2021. Watson et al. (2002) found settlement of juvenile yellowtail snapper in September 1999 to be larger than either April-May or June-July 2000 in Tortola, BVI. This further confirms that peak spawning and settlement varies by year. Studies suggest that many environmental variables influence spawning rates and success of larvae prior to settlement, including solar ultraviolet radiation, temperature, shore winds, and oceanic currents (McCormick and Molony 1995, Bergenius et al. 2005, Sponaugle et al. 2006). As these variables fluctuate, so could peak spawning and settlement.

This study is similar to Watson et al.'s (2002) findings that monthly peak settlement occurred on or a few days prior to the new moon. In this study, peak settlement was found between 0 and 4 days prior to the new moon during settlement pulse months. Although each bay displayed a peak settlement that differed slightly among months (Figure 2.02), the maximum settlement was seen within this period around St. Thomas, USVI. Each month's peak settlement followed an east to west pattern, with individuals first settling at Frenchmans Bay (4 days before new moon (nm)), then Sprat Bay and Saba Island (3 days before nm), followed by Lindbergh Bay (2 days before nm) and Brewers Bay (0 day of nm). No surveys were conducted during a settlement month at Lindbergh Bay 3 days prior to the new moon, therefore we cannot say if settlement at Lindbergh Bay follows the same trends as Sprat Bay and Saba Island. Robertson et al. (1999) suggests that oceanographic factors, such as tide, have the largest influence on larval dispersion. Oceanographic variables such as tides and currents were not analyzed in this study.

Of the environmental variables analyzed, results from the GLM suggest that temperature and month were significant predictor values for settlement of juvenile yellowtail snapper. Previous studies have documented that water temperature can have a significant influence on all life history stages of tropical reef fish (Sissenwine 1984, McCormick and Molony 1995, Robertson et al. 1999, Sponaugle et al. 2006). Temperature has demonstrated a strong correlation to settlement frequencies of tropical reef fish, where higher seawater temperature yields earlier settlement (McCormick and Molony 1995). Cure et al. (2015) found similar trends in recruitment, that with higher temperature higher settlement occurred. Findings from this study demonstrate that each month a settlement pulse was observed there was an increase in water temperature from the month prior within the settlement bay. Studies have demonstrated that as water temperature increases overall fitness of juvenile fishes improves (Peres and Oliva-Teres 1999, Sponaugle et al. 2006). Therefore, as suggested in the results of this study as well as previous studies temperature could be a key variable in yellowtail snapper selection of suitable settlement habitat. However, this study was limited by a lack of observations on additional factors that are known to impact settlement and mortality rates. As previously mentioned, oceanographic patterns were not analyzed in this study, but could explain some of the variability of settlement among bays (Robertson et al. 1999). Additionally, a better understanding of inter- and intra- species competition could also help explain the settlement patterns and mortality rates of juvenile yellowtail snapper (Grenouillet et al. 2002). Predator-prey interactions were also not recorded in this study but have been known to have a strong influence on post-recruitment behavior and mortality (Beets 1997).

Challenges faced by Watson et al. (2002) in estimating rapid mortality rate in juvenile yellowtail snapper after a settlement pulse were also experienced in this study, including low sample size in most settlement months. For this reason, rapid mortality rate is often an estimate of what might be occurring in the environment (Connell 1997, Watson et al. 2002). The growth-mortality hypothesis suggests that individuals are most vulnerable to increased predation at smaller size classes throughout all ontogenetic shifts (Anderson 1988). Although no predation was observed during this study, increased numbers of predatory fish (i.e., jack spp., adult snapper spp.) were observed in seagrass beds closer to the new moon throughout this study. This increased presence could likely result in higher mortality following peak settlement. Additionally, in this study delayed settlement or migration into the plot was observed. For example, in June at Saba Island, a secondary settlement was believed to have occurred in *H. stipulacea* and *T. testudinum* four days following the peak settlement causing the mortality rate to drop to 49% day^{-1} and -17% day^{-1} respectively between days 3 and 4. Due to the size increase of individuals, it is believed another small settlement occurred, however, there is a chance this resulted from migration into the plot.

Behavioral changes in yellowtail snapper were observed if settlement occurred simultaneously with other species. Although not common, if population sizes were large enough or a concurring settlement of grunts occurred, schooling behavior was observed in some surveys. This behavior could allow individuals to reduce mortality rates due to heterospecific schooling behavior and expand their home range further than what was previously expected since schools of grunts were more mobile than yellowtail snappers (personal observation). However, this is a behavior that should be further studied. To compensate for potential variation introduced by these factors, percentage of the population was calculated, and analyses were limited to settlements of 20 or more individuals was used to compensate for the variation in the data. Nonetheless, these data demonstrate varying trends among all three seagrass types.

The results of this study demonstrate that juvenile yellowtail snapper may prefer *H. stipulacea* seagrass habitats for settlement, and mortality rates of newly settled individuals was lower in invasive seagrass habitats than in native *S. filiforme*. These results coupled with the addition of suitable settlement areas in deep water habitats suggests that the establishment of *H. stipulacea* seagrass habitats may positively impact commercially important yellowtail snapper populations. However, further research is necessary to understand the longer-term impacts of *H. stipulacea* on large juvenile and adult yellowtail snapper populations to properly assess how the seagrass is affecting the fishery overall.

Tables:

Table 2.01: Summary of plot characteristics from five bays surveyed around St. Thomas, USVI. The total number of surveys completed from all settlement months are summarized in the final column of this table.

Bay	**Seagrass**	**Plot ID**	**Depth (ft)**	**Depth (m)**	**Surveys Completed**
Brewers Bay	*Halophila stipulacea*	BB-HS1 (Shallow)	8	2.4	23
Brewers Bay	*Halophila stipulacea*	BB-HS2 (Deep)	54	16.5	19
Lindbergh Bay	*Halophila stipulacea*	LB-HS	18	5.5	22
Lindbergh Bay	*Syringodium filiforme*	LB-SF	19	5.8	16
Lindbergh Bay	*Thalassia testudinum*	LB-TT	12	3.7	16
Saba Island	*Halophila stipulacea*	SI-HS-SET1	27	8.2	20
Saba Island	*Syringodium filiforme*	SI-SF-SET1	31	9.4	20
Saba Island	*Thalassia testudinum*	SI-TT-SET1	34	10.4	20
Saba Island	*Thalassia testudinum*	SI-TT-SET2	30	9.1	7
Saba Island	*Halophila stipulacea*	SI-HS-SET2	30	9.1	7
Saba Island	*Syringodium filiforme*	SI-SF-SET2	34	10.4	7
Saba Island	*Halophila stipulacea*	SI-HS-SET3	28	8.5	5
Saba Island	*Syringodium filiforme*	SI-SF-SET3	31	9.4	7
Saba Island	*Thalassia testudinum*	SI-TT-SET3	30	9.1	8
Frenchmans Bay	*Halophila stipulacea*	FB-HS	16	4.9	36
Frenchmans Bay	*Syringodium filiforme*	FB-SF	16	4.9	30
Frenchmans Bay	*Thalassia testudinum*	FB-TT	16	4.9	30
Sprat Bay	*Halophila stipulacea*	SB-HS	15	4.6	14
Sprat Bay	*Syringodium filiforme*	SB-SF	26	7.9	12
Sprat Bay	*Thalassia testudinum*	SB-TT	12	3.7	23

Table 2.02: Seagrass characteristic metrics, including percent cover, blade density (#/ 10 cm^2) and blade height (mm) for each plot from the beginning of this study (July - December 2020) and the end of this study (October 2021 - January 2022).

Plot ID	**First Sample Date**	**Second Sample Date**	**Number of Days Between Samples**	**Percent Cover Start (±std. dev)**	**Percent Cover End (±std. dev)**	**Blade Density Start (±std. dev)**	**Blade Density End (±std. dev)**	**Blade Height Start (mm; ±std. dev)**	**Blade Height End (mm ; ±std. dev)**
BB-HS-SET1	Oct. 25, 2020	Oct. 8, 2021	348	62% (±20)	74% (±19)	166 (±109)	139 (±33)	47 (±4)	60 (±21)
BB-HS-SET2	Oct. 25, 2020	Oct. 8, 2021	348	45% (±23)	85% (±16)	92 (±34)	110 (±20)	54 (±5)	68 (±19)
FB-HS-SET1	July 23, 2020	Oct. 10, 2021	444	90% (±16)	83% (±20)	143 (±51)	82 (±38)	84 (±36)	65 (±18)
FB-SF	July 23, 2020	Oct. 10, 2021	444	51% (±41)	34% (±23)	28 (±12)	26 (±13)	173 (±30)	181 (±46)
FB-TT	July 23, 2020	Oct. 10, 2021	444	85% (±17)	12% (±12)	23 (±7)	8 (±5)	252 (±39)	54 (±35)
LB-HS	July 28, 2020	Oct. 8, 2021	437	54% (±25)	26% (±19)	70 (±35)	47 (±27)	51 (±7)	58 (±13)
LB-SF	July 28, 2020	Oct. 8, 2021	437	20% (±17)	5% (±3)	26 (±15)	12 (±7)	219 (±30)	136 (±36)
LB-TT	July 27, 2020	Oct. 8, 2021	437	53% (±11)	13% (±14)	21 (±4)	17 (±5)	166 (±24)	127 (±36)
SB-HS	Aug. 2, 2020	Oct. 14, 2021	438	44% (±21)	51% (±23)	66 (±19)	31 (±15)	45 (±3)	44 (±6)
SB-SF	Aug. 2, 2020	Jan. 7, 2022	523	19% (±17)	15% (±8)	44 (±12)	25 (±7)	139 (±16)	144 (±49)
SB-TT	Aug. 2, 2020	Oct. 14, 2021	438	26% (±11)	64% (±36)	17 (±5)	11 (±5)	199 (±42)	151 (±33)
SI-HS-SET 1	NA	Nov. 11, 2021	NA	NA	50% (±19)	NA	59 (±26)	NA	48 (±5)
SI-SF-SET 1	Dec. 7, 2020	Nov. 11, 2021	339	20% (±11)	19% (±15)	38 (±21)	23 (±15)	168 (±28)	137 (±20)
SI-TT-SET 1	NA	Nov. 16, 2021	NA	NA	22% (±17)	NA	13 (±6)	NA	150 (±24
SI-HS-SET 2	Dec. 7, 2020	Nov. 16, 2021	344	40% (±13)	47% (±23)	86 (±31)	58 (±16)	47 (±2)	49 (±5)
SI-SF-SET 2	NA	Nov. 16, 2021	NA	NA	14% (±12)	NA	21 (±9)	NA	167 (±38)
SI-TT-SET 2	NA	Nov. 16, 2021	NA	NA	21% (±11)	NA	14 (±5)	NA	144 (±37)
SI-HS-SET 3	NA	Jan. 7, 2022	NA	NA	29% (±16)	NA	60 (±31)	NA	41 (±4)
SI-SF-SET 3	Dec. 7, 2020	Nov. 11, 2021	339	24% (±12)	19% (±11)	40 (±11)	23 (±9)	176 (±15)	161 (±30)
SI-TT-SET3	NA	Nov. 11, 2021	NA	NA	28% (±16)	NA	13 (±5)	NA	140 (±24)

Table 2.03: Dates for settlement and survival surveys for yellowtail snapper from April 2020 to May 2021.

Month	**Year**	**Date of New Moon**	**Settlement Survey Dates**	**Survival Survey Dates**	**Settlement (number of fish)**
April	2020	22	Apr 17, 22	n/a	Preliminary, no settlement
May	2020	22	May 19-28	June 2, 6	Settlement at Saba (n=129), Brewers (n=186, Frenchmans (n=38)
June	2020	21	Jun 16-22	June 24, 29	Settlement at Saba (n=334)
July	2020	20	Jul 13-19,24	n/a	No settlement
August	2020	18	Aug 11-16	Aug 18, 20, 22	Settlement at Saba (n=117), Frenchmans (n=68)
September	2020	17	Sep 10-12,16	n/a	No settlement
October	2020	16	Oct 9-15, 18,20	n/a	Settlement Frenchmans (n=21), Sprat (n=19), Brewers (n=11)
November	2020	15	Nov 13	n/a	No settlement
December	2020	14	Dec 11	n/a	No settlement
January	2021	13	Jan 15	n/a	No settlement
February	2021	11	Feb 16	n/a	No settlement
March	2021	13	Mar 12	n/a	No settlement
April	2021	12	Apr 9	n/a	No settlement
May	2021	11	May 5-11	May 13,17,19,25	Settlement at Frenchmans (n=18), Sprat (n=40), Lindbergh (n=13)

Table 2.04: Statistical summary table of all statistical tests from settlement data, environmental variables, and seagrass characteristics in this study.

Dependent	**Independent**	**n**	**Test stat**	**d.f.**	**p-value**	**Post-hoc**
Settlement	Seagrass Species	259	$X^2 = 22.74$	2	1.15e-5	*Hs>Tt,Sf*
Settlement	Month	259	$X^2 = 36.40$	4	2.39e-7	M2020,J>A,O, M2021
Settlement	Seagrass Species X Month	259			>0.05	
Settlement	Bay	259	$X^2 = 40.25$	3	9.44e-9	SI>LB,SB,FB
Settlement	Bay x Seagrass Species	259	F = 2.73	6	0.0138	
Abundance	Size Class	2,736	$X^2 = 1{,}083.4$	7	<0.001	21-30>“≤20”>31-40>41-50>60-100,101-150,151-200,201-300
Dissolved Oxygen (mg/l)	Bay	24			>0.05	
Temperature (ºC)	Bay	90			>0.05	
Percent Cover	Seagrass Species	20	F = 8.08	2	0.0034	*Hs>Sf, Tt*
Blade Density	Seagrass Species	20	$X^2 = 15.59$	2	<0.001	*Hs>Sf, Tt*
Blade Height	Seagrass Species	20	$X^2 = 12.29$	2	0.0021	*Hs<Sf, Tt*
Change in Percent Cover from Beginning and End of Study	Seagrass Percent Cover	14			>0.05	
Change in Seagrass Blade Density from Beginning and End of Study	Seagrass Blade Density	14			>0.05	
Change in Blade Height from Beginning and End of Study	Seagrass Blade Height	14			>0.05	
Settlement (within bay)	Brewers Bay *H.s.* Plots	25			>0.05	
Settlement (within bay)	Saba Island *H.s.* Plots	18			>0.05	
Settlement (within bay)	Saba Island *S.f.* Plots	23			>0.05	
Settlement (within bay)	Saba Island *T.t.*. Plots	23			>0.05	
Settlement (within Saba Island)	Seagrass Species	101	$X^2 = 7.95$	2	0.019	*Hs>Tt>Sf*

Table 2.05: Statistical summary table of predictor variables from the Generalized Linear Model. * indicates a significant predictor variable.

Predictor Variable	Standard Error	t-value	p-value
Month*	0.50	-5.50	7.4e-8
Dissolved Oxygen (O2)			>0.05
Seawater Temperature*	24.00	-2.81	0.005
Blade Height			>0.05
Blade Density			>0.05
Percent Cover			>0.05

Table 2.06: Model summary table from the Generalized Linear Model

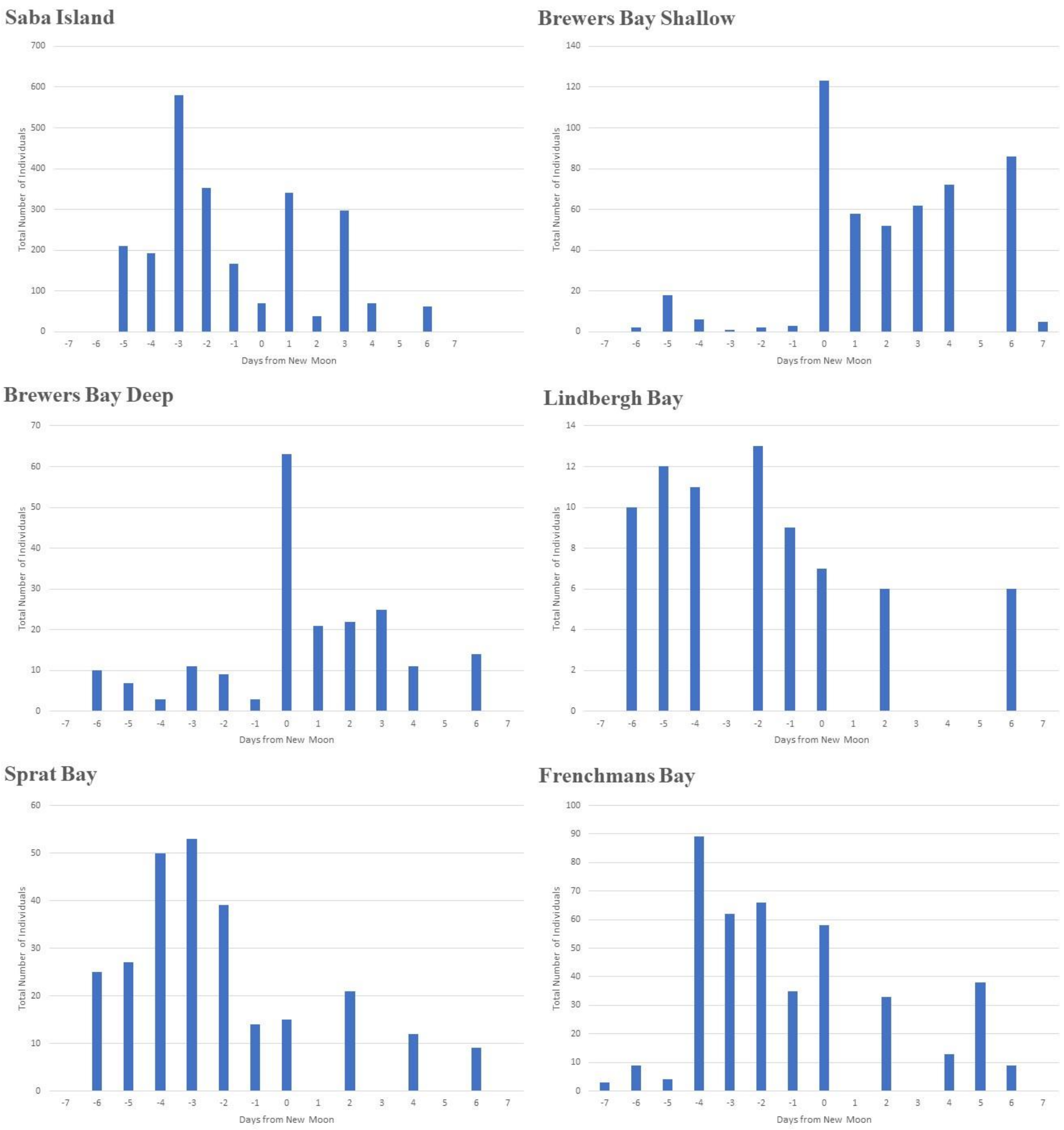
Model	Deviance	d.f.
Null	138,025	341
Residual	103,284	335
AIC: 2,939.5		

Table 2.07: Expansion measurements from December 2019 to January 2022 in bay and seagrass type with range of growth and standard deviation of all expansion measurements.

Bay	**Seagrass**	**Depth**	**Date of Establishment**	**Date of Final Measurement**	**Days from first and last measurement**	**Mean Growth (+/- Std. Dev.)**	**Range of Total Expansion**
Frenchmans Bay	*H. stipulacea*	4.88 m	Dec. 9, 2019	Sept. 2, 2021	632	1.5 cm day^{-1} (+/- 1.4)	45 - 810 cm
Frenchmans Bay	*S. filiforme*	4.88 m	Oct. 22, 2020	May 13, 2021	203	1 cm day^{-1} (+/- 0.9)	-12 -240 cm
Frenchmans Bay	*T. testudinum*	4.88 m	Oct. 22, 2020	Sept. 2, 2021	315	-0.2 cm day^{-1} (+/- 1.4)	-308 - 303 cm
Sprat Bay	*H. stipulacea*	6.00 m	Dec. 9, 2019	Sept. 22, 2021	632	0.4 cm day^{-1} (+/- 0.4)	-43 - 235 cm
Sprat Bay	*S. filiforme*	7.92 m	Nov. 5, 2020	Jan. 7, 2022	428	0.9 cm day^{-1} (+/- 0.9)	-147 - 76 cm
Sprat Bay	*T. testudinum* 1	3.66 m	Oct. 5, 2020	Sept. 22, 2021	315	0.8 cm day^{-1} (+/- 0.7)	7 - 149 cm
Sprat Bay	*T. testudinum* 2	1.52 m	Nov. 5, 2020	Sept. 22, 2021	301	0.1 cm day^{-1} (+/- 0.2)	-10 - 79 cm
Saba Island	*S. filiforme*	9.45 m	Sept. 16, 2020	Nov. 11, 2021	421	0.9 cm day^{-1} (+/- 0.6)	42 - 590 cm
Saba Island	*T. testudinum*	9.14 m	Sept. 16, 2020	Nov. 11, 2021	421	0.6 cm day^{-1} (+/- 0.4)	5 - 370 cm
Brewers Bay Deep	*H. stipulacea*	18.00 m	Feb. 4, 2020	Oct. 8, 2021	668	0.1 cm day^{-1} (+/- 0.4)	-70 - 178 cm
Brewers Bay Shallow	*H. stipulacea*	1.22 m	Dec. 10, 2019	Oct. 8, 2021	668	2.1 cm day^{-1} (+/- 1.8)	43 - 2100 cm

Figures:

Figure 2.01: Site map showing the location of five bays around St. Thomas, USVI. Map insert shows the location of St. Thomas outlined in a black box within the greater Caribbean region. Yellow dots show the location of each bay in southern St. Thomas; letters within each circle correlate to bay name as seen in figure legend: A). Saba Island, B. Brewers Bay, C. Lindbergh Bay, D. Sprat Bay, and E. Frenchmans Bay. Map insert letters correlate to the bay letter and demonstrate magnified focus of each bay with plots outlined in colored boxes.


Saba Island

Brewers Bay Shallow

Brewers Bay Deep

Lindbergh Bay

Sprat Bay

Frenchmans Bay

Figure 2.02: Total number of individuals observed in settlement surveys from May 2020 to May 2021 by bay relative to the new moon. Y-axes are scaled independently depending on settlement within each bay.

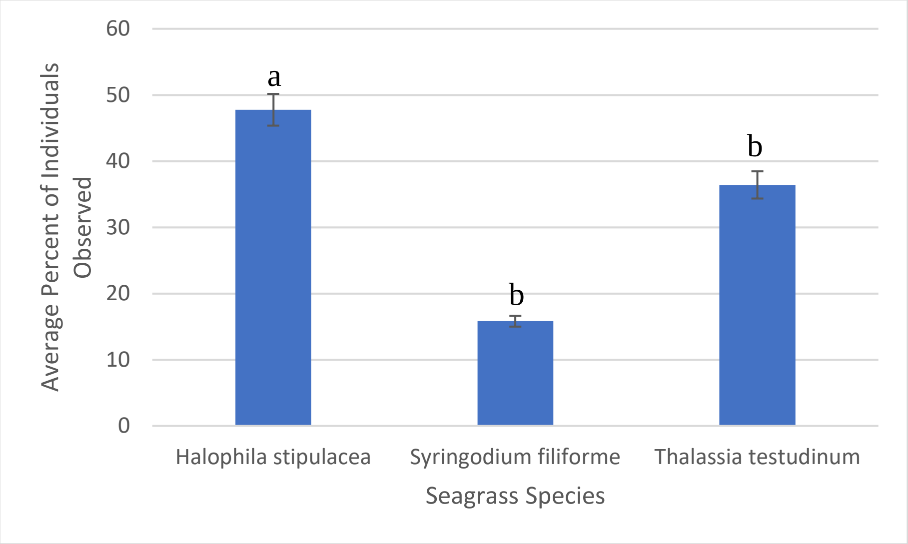


Figure 2.03: Average percent of newly settled juvenile yellowtail snapper (≤30 mm) observed in *H. stipulacea*, *S. filiforme*, and *T. testudinum* seagrass plots with ±SE bars. Percent observed was determined by averaging the total number of individuals by total number of surveys conducted per seagrass type. Seagrass species had a significant effect on settlement (p=1.15e-5). Only data from Saba Island (Set 1), Lindbergh Bay, Sprat Bay, and Frenchmans Bay included in this figure.

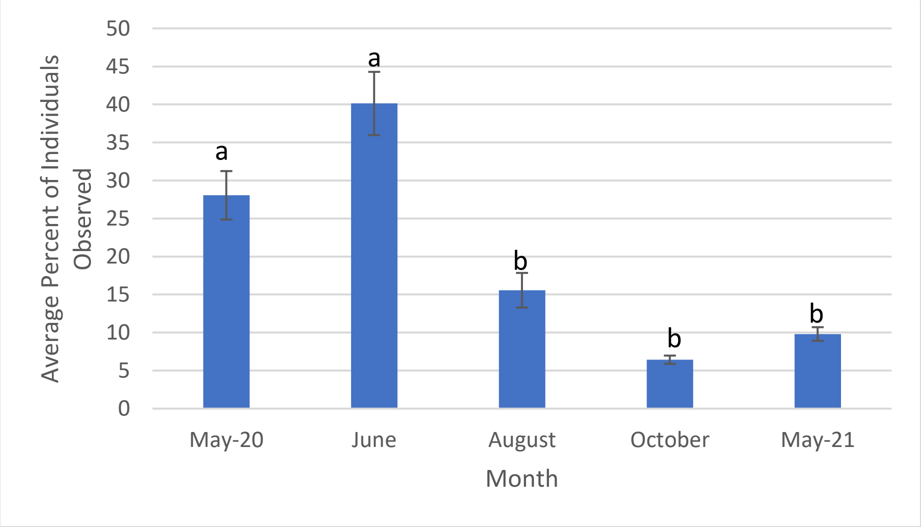


Figure 2.04: Average percent of newly settled juvenile yellowtail snapper (≤30 mm) observed in May, June and August, October 2020 and May 2021 with ±SE bars. Percent observed was determined by averaging the total number of individuals by total number of surveys conducted each month. Month had a significant effect on settlement (p=2.39e-7). Only data from Saba Island (Set 1), Lindbergh Bay, Sprat Bay, and Frenchmans Bay included in this figure.

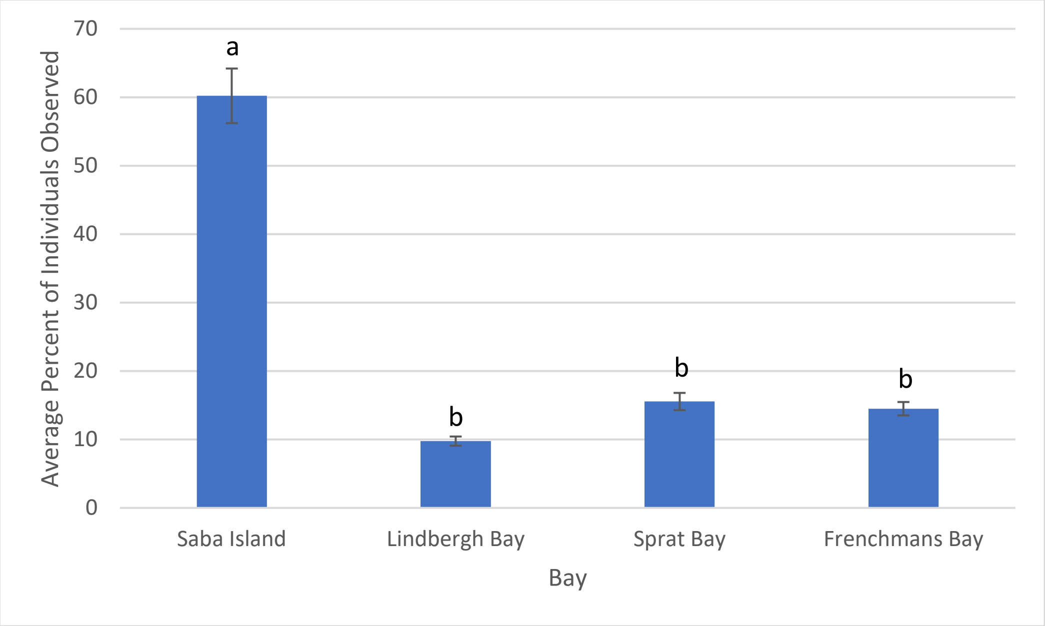


Figure 2.05: Average percent of newly settled juvenile yellowtail snapper (≤30 mm) observed in each bay with ±SE bars. Percent observed was determined by averaging the total number of individuals by total number of surveys conducted in each bay. Bay had a significant effect on settlement (p=9.44e-9). Only data from Saba Island (Set 1), Lindbergh Bay, Sprat Bay, and Frenchmans Bay included in this figure.

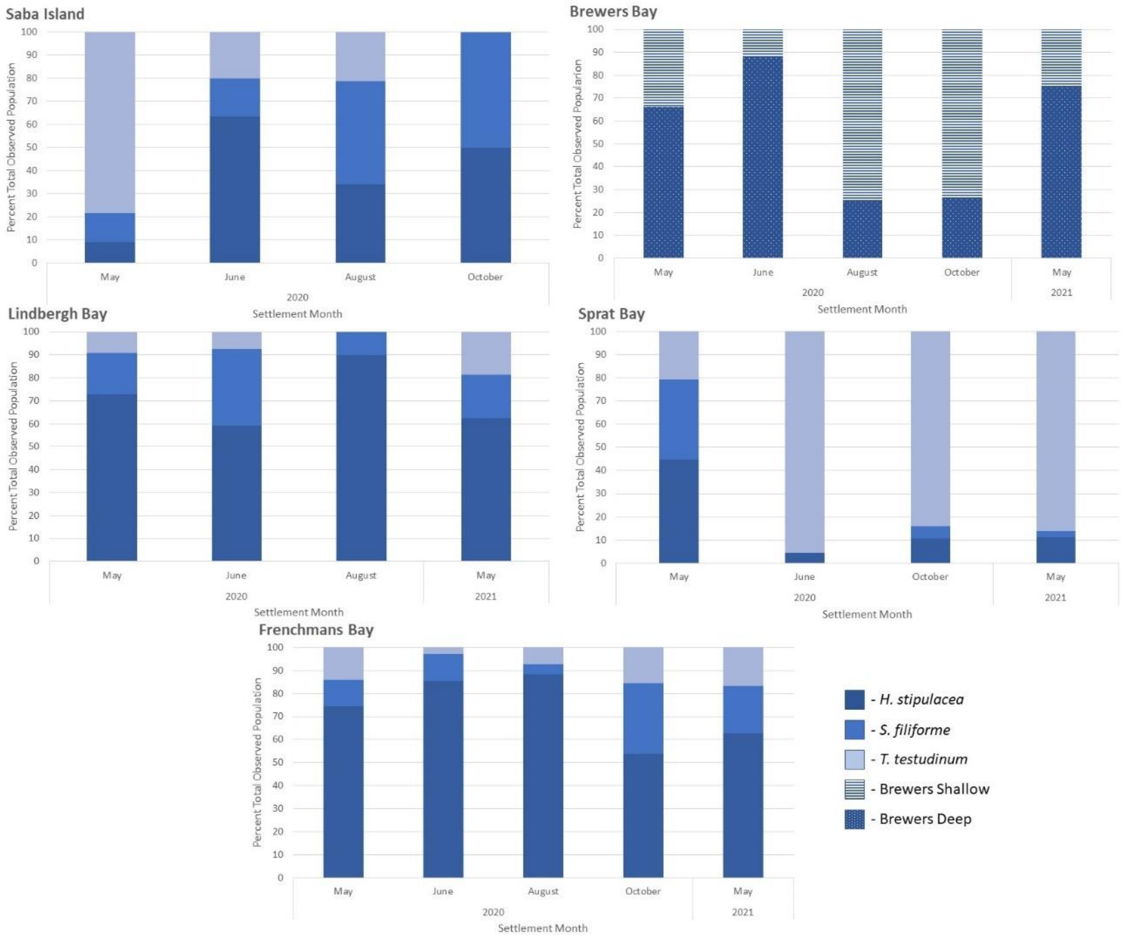


Figure 2.06: Percent of newly settled juvenile yellowtail snapper (≤30 mm) observed by seagrass and month, for May, June and August, October 2020 and May 2021 at Saba Island, Brewers Bay, Lindbergh Bay, Sprat Bay, and Frenchmans Bay.

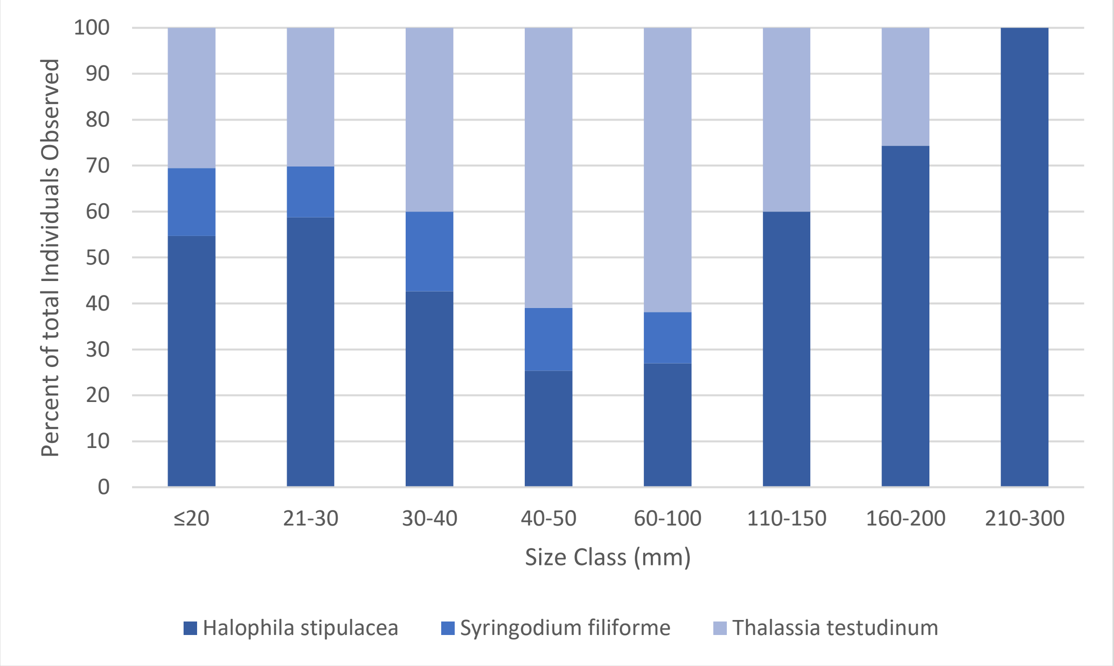


Figure 2.07: Percent of total number of individuals surveyed by seagrass and size class during settlement months in St. Thomas, USVI.

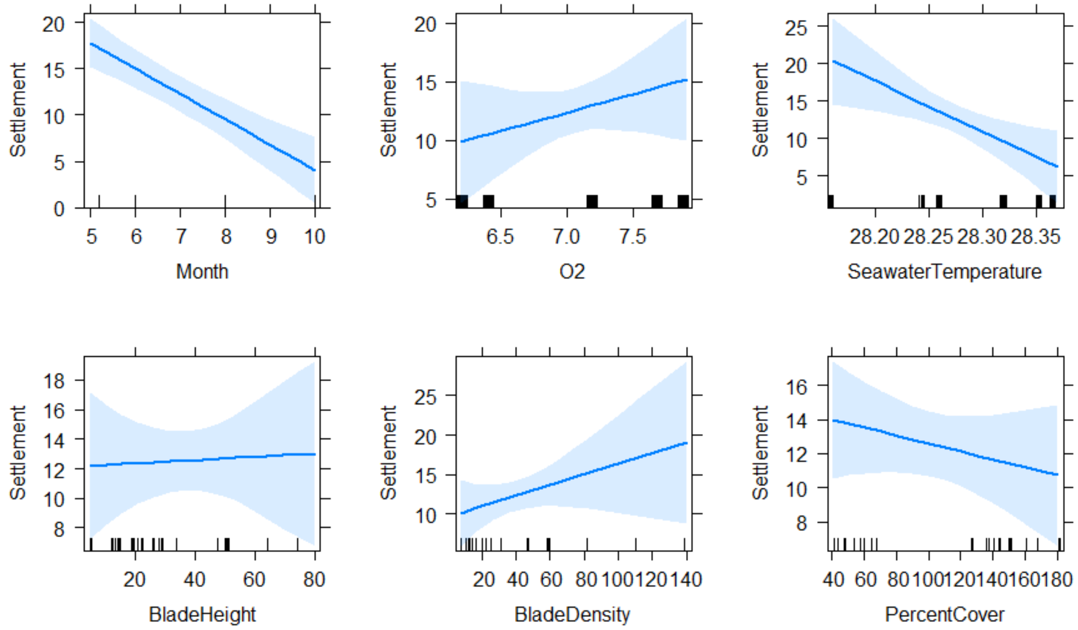


Figure 2.08: Response variable curves based on generalized linear model of possible predictor effects of settlement of juvenile yellowtail snapper. Month (p = 7.4e-8) and seawater temperature (°C; p = 0.005) are significant predictors for settlement.

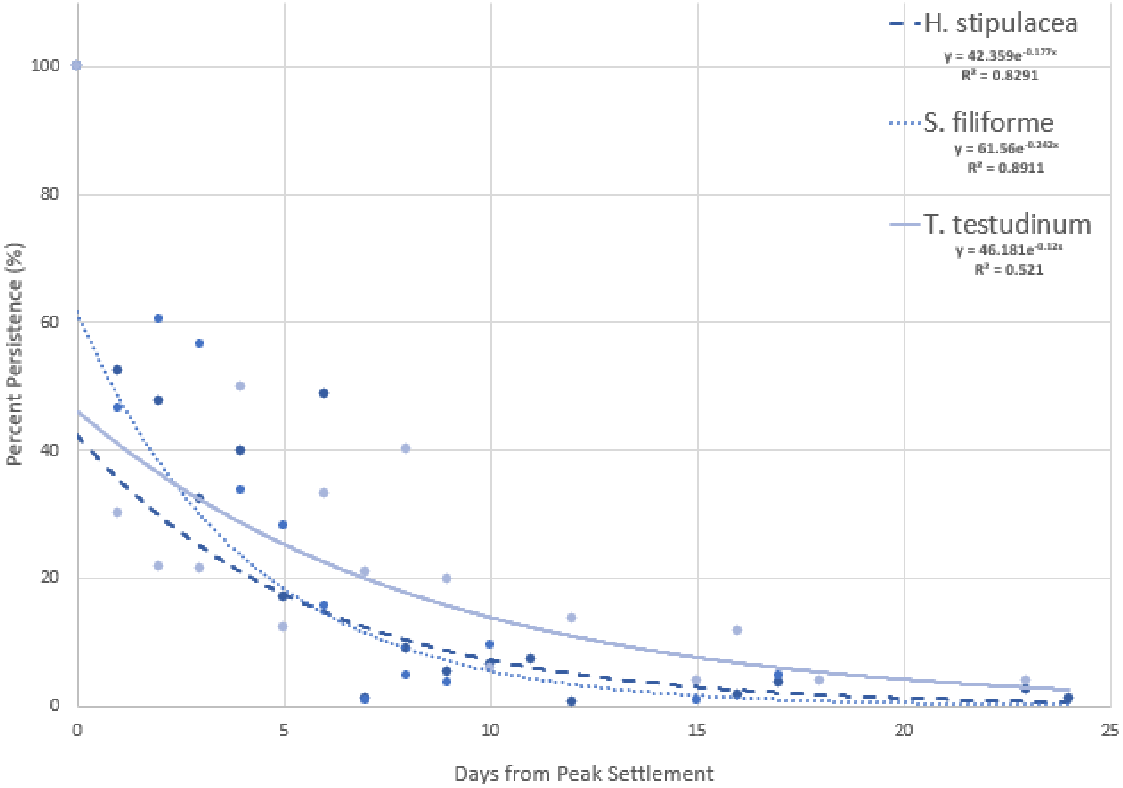
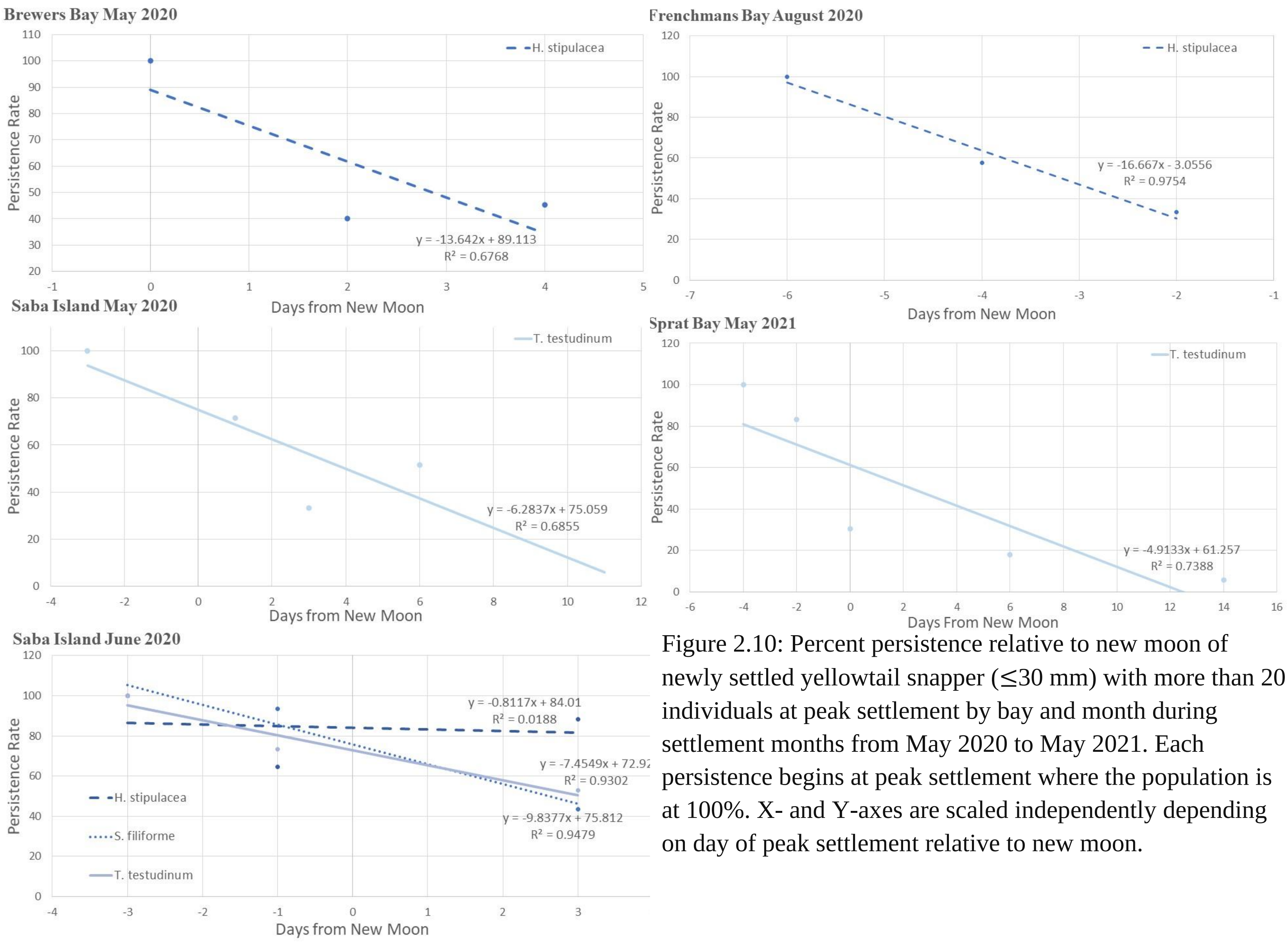


Figure 2.09: Percent persistence of newly settled juvenile yellowtail snapper (≤30 mm) per seagrass type on subsequent days from new moon during settlement months from May 2020 to May 2021. Each data set begins at peak settlement where the population is at 100% persistence but some points are covered and not shown.



Brewers Bay May 2020

Frenchmans Bay August 2020

Saba Island May 2020

Sprat Bay May 2021

Saba Island June 2020

Figure 2.10: Percent persistence relative to new moon of newly settled yellowtail snapper (≤30 mm) with more than 20 individuals at peak settlement by bay and month during settlement months from May 2020 to May 2021. Each persistence begins at peak settlement where the population is at 100%. X- and Y-axes are scaled independently depending on day of peak settlement relative to new moon.

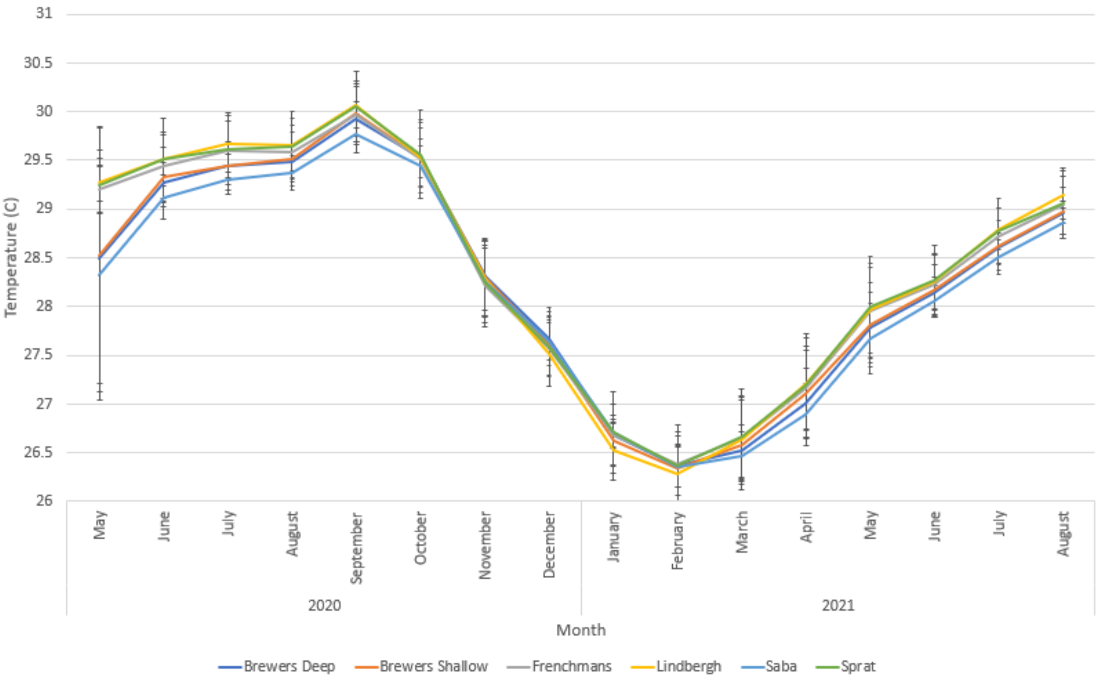


Figure 2.11: Average monthly seawater temperature per bay from May 2020 to August 2021 in St. Thomas, USVI. There was no significant difference of temperature among bays.

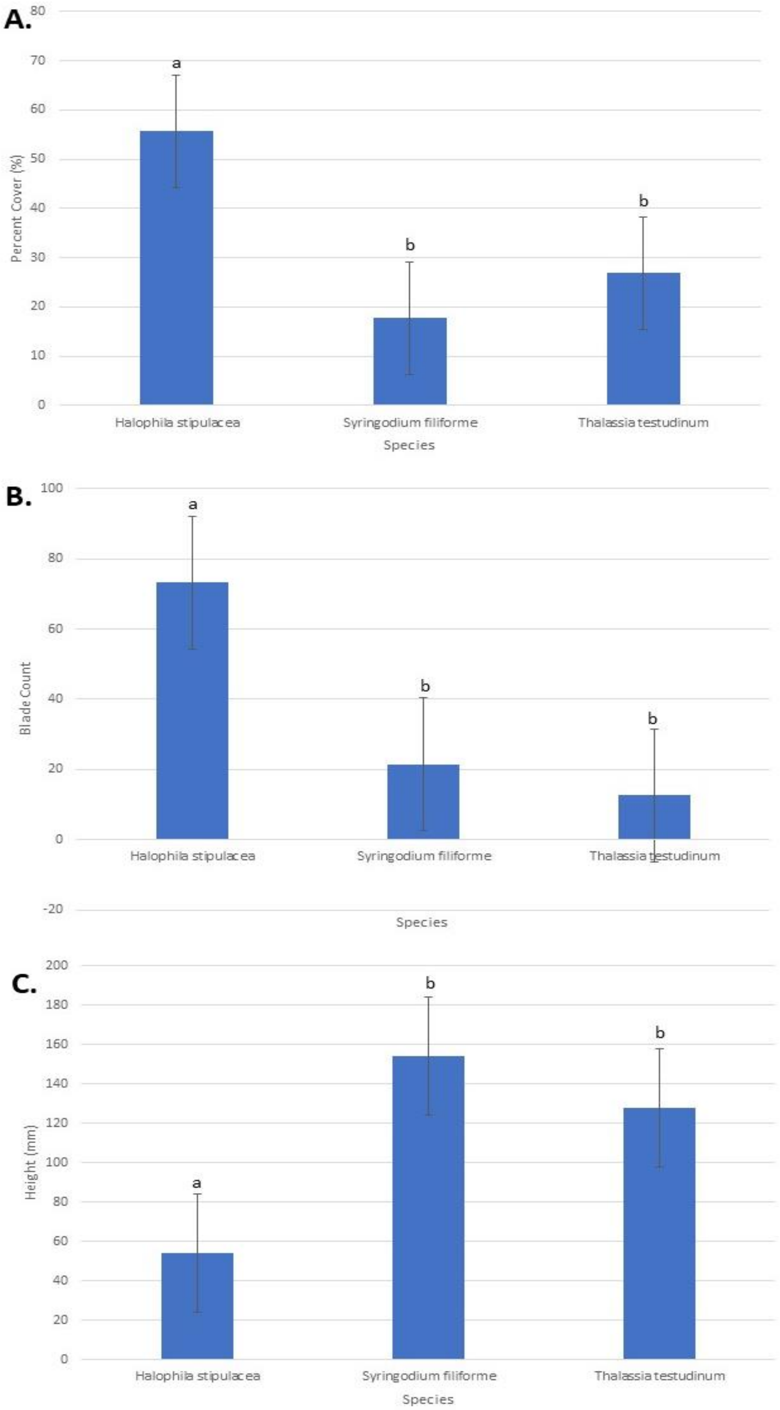


Figure 2.12: Seagrass characteristics among seagrass species with ±SE bars. A. Average percent cover (%), B. Average blade density, C. Average maximum blade height (mm).

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CHAPTER 3

Evaluating the effects of invasive seagrass *Halophila stipulacea* on condition (K) of juvenile yellowtail snapper, *Ocyurus chrysurus*, in St. Thomas, USVI

Abstract:

Since its invasion in 2002, *H. stipulacea* has become widespread throughout the Caribbean, arriving in St. Thomas in 2013. The impacts of *H. stipulacea* on juvenile yellowtail snapper habitat is not well understood, yet, have the potential to disrupt essential fish habitats and reduce important fishery resources. Previous studies have demonstrated that *H. stipulacea* can reduce fish health (Green 2017), suggesting that *H. stipulacea* may have a strong negative effect on economically important reef fishes. This study aims to examine the effects of the invasive seagrass *H. stipulacea* on the condition factor (K) of juvenile yellowtail snapper (*Ocyurus chrysurus*) in St. Thomas, US Virgin Islands. A total of 260 juvenile fish (19 - 72.5 mm) were caught to analyze for condition factor of individuals among invasive (*H. stipulacea*, n=116) and native (*S. filiforme*, n=66; *T. testudinum*, n=78) seagrasses. Condition factor is a measurement derived from the length and weight of an individual. Results of this study show no significant effect of seagrass species on juvenile yellowtail snapper condition, however, trends demonstrate a higher condition of individuals caught in native seagrasses than invasive. These data will provide resource managers with a better understanding of how *H. stipulacea* may be impacting important fishery species.

Keywords: *Halophila stipulacea*; Yellowtail Snapper; St. Thomas; Condition Factor; Invasive species; Seagrass

Introduction:

Yellowtail snapper (*Ocyurus chrysurus*) are an economically important lutjanid species found throughout the tropical and subtropical waters of the western Atlantic shelf (Clarke et al. 1997, Turano et al. 2000, Vasconcellos et al. 2008, Saillant et al. 2012). In St. Thomas, US Virgin Islands (USVI) the economy is dependent on the fishing sector both for tourism and commercial fishing (NOAA Economic Report 2016). Tourists are attracted to the Caribbean for the excellent sport fishing, and yellowtail snapper are a highly desirable species due to their high-quality meat, making it one of the top three commercially landed species within the U.S. Caribbean (Clarke et al. 1997, Turano et al. 2000, Gutiérrez-Sigeros et al. 2018, Collins 1984, Manooch and Drennon 1987, Watson et al. 2002, Zajovits 2021). Olsen et al. (2007) determined that 22% of the fishing landings in St. Thomas consisted of yellowtail snapper, making it the most prevalent and important finfish on the island. However, there is still insufficient data on yellowtail snapper populations to properly evaluate the species conservation ranking (IUCN Red List 2019, Zajovits 2021).

As opportunistic feeders, yellowtail snapper eat consistently throughout the day to optimize their foraging ability (Zajovits 2021). Optimal foraging theory suggests that predators select prey based on availability that allows them to maximize their energy gains versus the cost of energy needed to catch, ingest, and digest its prey (Pyke 1984). Therefore, to maximize energy yellowtail snapper are generalist carnivores that feed above the substrate, primarily in the water column, and have diverse food preferences consuming crabs, small fish, and shrimps as adults (Bortone and Williams 1986, Zajovits 2021). As juveniles and larvae, yellowtail snapper primarily feed on zooplankton and small invertebrates found in seagrass habitats (Boehlert 1996, McClellan and Cummings 1998, Nunn et al. 2012). Feeding habits of fish is often a good indication of the overall health of an ecosystem as it provides an insight into the amount of food available in a habitat (Kara et al. 2017, Latuconsina et al. 2022, Green 2017, Zhou et al. 2007, Brosset et al. 2016), which can be measured using condition factor. Condition (K) is a measurement derived from the weight and length of a fish and can be a non-lethal index to estimate health of an individual, where heavier fish of a length are considered to have better condition and therefore health (Sutton et al. 2000, Robinson 2010, Mazumder et al. 2016). These measurements are often used in fisheries management to help determine the overall success of a population in regard to growth, reproduction, and survival (Mazumder et al. 2016, le Cren 1951). Due to the yellowtail snapper's generalized diet, the condition factor of these individuals not only demonstrates the populations overall health but can also be a good indicator for overall health of an ecosystem.

Yellowtail snapper are most commonly seen in seagrass habitats as juveniles prior to an ontogenetic transition to reef habitat where they spend their adult life (Turano et al. 2000, Nagelkerken et al. 2000, Watson et al. 2002). Seagrasses provide essential habitat for newly settled individuals not only due to prey availability, but also seagrass blades provide necessary protection for individuals during this vulnerable phase (Dahlgren and Eggleston 2000, Nagelkerken et al. 2000, Nagelkerken et al. 2002, Pollux et al. 2007). Shifts in structural complexity of seagrass, which consists of blade height, density, and percent cover, have been seen to alter fish species abundance and diversity (Hori et al. 2009, Willette and Ambrose 2012, Gatwicke and Speight 2005, Green 2017). These shifts within seagrass communities can ultimately negatively affect the overall health of a fish (Green 2017).

In 2002, an invasive seagrass species, *Halophila stipulacea,* was first reported off the coast of Grenada (Ruiz and Ballantine 2004). Originally from the Red Sea, *H. stipulacea* first invaded the Mediterranean Sea after the opening of the Suez Canal in 1869 (Por 1971). This Lessepsian species is believed to have been transferred to the Caribbean unintentionally, but has since spread rapidly arriving in St. Thomas, U.S. Virgin Islands in 2013 (Willette et al. 2014, Olinger et al. 2017, Winters et al. 2020, Vaughn 2021). *H. stipulacea* is a highly successful invasive species due to its ability to adapt to variable salinity, light, depth, and sediment quality (Willette and Ambrose 2012, Winters et al. 2020). This species has been seen to displace native seagrasses throughout its invaded region possibly resulting in major shifts of seagrass composition throughout the Caribbean region (Jerris 2019, Winters et al. 2020).

Little is known about the effects of the invasion of *H. stipulacea* on fish communities and their health. Studies have shown varied abundance of fish assemblages and diversity between native and invasive seagrass habitats (Willette and Ambrose 2012, Olinger et al. 2017, Winters et al. 2020), however, little is known about the direct effects of seagrass community composition shifts on fish health. Green (2017) reported trends of higher condition in juvenile Nassau grouper in mixed seagrass habitats than in monotypic *H. stipulacea* seagrass habitats. Green (2017) suggested these results are due to a lower canopy height, which does not allow as much protection for individuals while foraging as native seagrasses. Although trends demonstrated higher condition in monotypic native than monotypic invasive seagrasses, the results were not significant for juvenile Nassau grouper (Green 2017). Therefore, it is still unclear what the direct impacts of *H. stipulacea* are on juvenile Nassau grouper or other economically important fish species, like yellowtail snapper.

The purpose of this study was to better understand the effects of the invasion of *H. stipulacea* on the condition of juvenile yellowtail snapper. It was hypothesized that individuals caught in *H. stipulacea* seagrass habitats will have a significantly lower condition than individuals in either native *Syringodium filiforme* or *Thalassia testudinum* seagrass habitats.

Methods:

Study Site

St. Thomas, USVI is located in the northern Lesser Antilles of the Caribbean Sea (18.3381^{O}N, 64.8941^{O}W). Five bays (Brewers Bay, Lindbergh Bay, Frenchmans Bay, Sprat Bay, and Saba Island) were selected in southern St. Thomas for their monotypic seagrass habitats and relative proximity to one another (Figure 2.01). Lindbergh Bay, Frenchmans Bay, Sprat Bay, and Saba Island consist of expansive seagrass habitats of the native *T. testudinum* and *S. filiforme* as well as invasive *H. stipulacea* seagrass meadows. Brewers Bay was selected due to the presence of expansive *H. stipulacea* seagrass habitat across a broad depth range (2-18 meters).

Fish Collection and Condition Factor

Juvenile yellowtail snapper were primarily collected in June 2020. Sample sizes were below our target minimum of 50 individuals per seagrass, therefore we continued fish collections opportunistically until May 2021 (Table 3.01). Divers used two clear vinyl-sided nets (29 cm x 29 cm x 48 cm deep) with fine mesh (1.5 mm) bottom to catch juvenile yellowtail snapper (19 – 73 mm) in each seagrass habitat. Individuals were then transferred to a designated Ziploc bag underwater. Once back on the boat, the fish were humanely euthanized by placing them on ice. Each fish was then measured for weight (± 0.01 g), total length (± 0.5 mm), and fork length (± 0.5 mm), then transferred to a preservative consisting of 95% ethanol.

A correlation analysis was run between total length and fork length to determine if there was a relationship between each metric. Condition factor (K) was then determined using total length and weight of each individual using the equation:

$$K = \frac{W}{L^3} \times 100$$

W: Weight(g); L^3: Total length cubed (mm)

Plankton Traps

Within each bay, one passive plankton trap was attached to a steel rebar stake in the center of a bed of each seagrass species (n=17; Table 3.02). Within Brewers Bay, one plankton trap was placed in deep (16 m) habitat and one in shallow (3 m) habitat. A second set of traps were also placed in each seagrass species at Saba Island. Passive plankton traps were clear acrylic tubes (60 cm long, 5 cm diameter) that were filled with 10% buffered formaldehyde, seawater, and a few drops of green food coloring to help see the level of formaldehyde solution remaining in the trap (Yund et al. 1991, Nemeth 1997). As plankton, invertebrates, and vertebrates drifted into the trap, the buffered formaldehyde euthanized and fixed each organism. The tube traps were used to estimate potential food resources available in each seagrass type and location. About every two months from May 2020 to September 2021, the tube traps were collected and filtered through 0.075 mm sieve, then immediately replaced. The samples were then split into macro-species samples, course samples, and fine samples by filtering each sample through 2 mm, 0.5 mm, and 0.075 mm sieves, respectively. Individuals were classified to at least ordinal level in each sample. At the macro-species and course sample levels, individuals were identified and counted using a dissecting microscope. A plankton splitter was used to make volumetric splits of fine samples, with each sample split four times. After the fourth split, the quarter sample was then analyzed under a Leica M205C microscope, where individuals were identified to at least ordinal level and counted. The number of individuals of each taxonomic group were then multiplied by four to quantify the total number of individuals in the sample.

Data Analysis

Condition factor data did not meet parametric assumptions of Analysis of Variance (ANOVA) tests, therefore non-parametric analyses were used instead. Kruskal-Wallis and Dunn tests were used to test the effect of seagrass species, bay, and size class on condition factor of juvenile yellowtail snapper. Species richness of plankton found within each plankton trap was used as a measurement of diversity and compared by bay and seagrass type using a Kruskal-Wallis and Dunn tests. A Friedman Rank test was used to test the effect of the interaction of seagrass species and bay, as well as seagrass species and size class on the condition factor of juvenile yellowtail snapper. A Generalized Linear Model (GLM) using Gaussian distribution was run to test the effect of environmental variables and seagrass metrics (see Chapter 2) as predictor values for condition. Mean temperature and mean O2 for each bay, as well as seagrass characteristics from the end of this study, and overall species richness from each plankton trap were used in this model. All statistical tests were run in R-Studio version 3.6.2 (R Core Team, 2019).

Results:

Between June 2020 and May 2021, a total of 260 fish between the sizes of 19 mm TL and 72.5 mm TL were collected across all five bays (Table 3.01; Table 3.03). A strong correlation was found between total length and fork length (y = 1.0862x - 0.4177; R^2= 0.99). Of all the fish caught, 116 were trapped in monotypic *H. stipulacea* seagrass, 66 in *S. filiforme* seagrass, and 78 in *T. testudinum* (Figure 3.01) Of all the individuals caught, 51% were collected in the 21-30 mm size class (n=134; Figure 3.02; Table 3.03). Of the 134 individuals in the 21-30 mm size class, 81 fish were caught in *H. stipulacea* seagrass (Figure 3.03). The highest number of individuals were caught at Saba Island (n=67), followed by Sprat Bay (n=59), Frenchmans Bay (n=50), Lindbergh Bay (n=45), Brewers Bay (total n=39, shallow n=24, deep n=15; Figure 3.04). Of the 67 fish caught at Saba Island, most individuals (TL n=32) were in the 21-30 mm size class range (Figure 3.05).

Condition values ranged from 0.000756 K to 0.00225 K. There was no significant effect ($p>0.05$) of seagrass species on condition, however trends demonstrate higher condition in individuals caught in *S. filiforme* (0.001206), followed by *T. testudinum* (0.001194), then *H. stipulacea* (0.001160; Figure 3.06). There was a significant effect of bay on the condition of juvenile yellowtail snapper (p = 7.106e-5; Figure 3.07). Individuals from Brewers Bay Deep (0.001067) had a significantly lower condition than individuals caught in Brewers Bay Shallow (0.001206), Frenchmans Bay (0.001231), and Sprat Bay (0.001239). Additionally, individuals from Saba Island (0.001138) had a significantly lower condition than individuals from Sprat Bay (Figure 3.07). The results from the Friedman Rank test also showed a significant effect of the interaction between bay and seagrass (p=2.67e-7; Figure 3.08). Condition factor varied among bay and seagrass species. Condition factor was highest in *S. filiforme* at Saba Island and Lindbergh Bay, highest in *T. testudinum* at Sprat Bay, and highest in *H. stipulacea* in Frenchmans Bay (Figure 3.08). Within Brewers Bay, individuals from shallow seagrass habitats had a higher condition than individuals in deep-water habitats.

Size class (p=0.005) as well as the interaction of size class and seagrass (4.72e-6) had a significant effect on the condition factor of individuals caught. Juvenile yellowtail snapper ≤20 mm had a significantly higher condition (0.001586) than individuals caught in any other size class (Figure 3.09). Similar trends as seen in cumulative condition factor (Figure 3.06) were seen in the smaller size classes (≤20, 21-30, 31-40 mm) of individuals where a higher condition was seen in individuals in *S. filiforme* than in *H. stipulacea* (Figure 3.10). However, individuals from size classes 41-50 mm and 51-60 mm had a trend of higher condition in *H. stipulacea* than in either native *S. filiforme* or *T. testudinum* (Figure 3.10). No individuals were caught in *H. stipulacea* between 61 mm to 75 mm (Figure 3.10).

The Generalize Linear Model indicated that seawater temperature (p=0.04) and seagrass percent cover (p=0.01) were the strongest predictors for the condition of juvenile yellowtail snapper (Table 3.04; Figure 3.11). The strength of the model fit improved with a reduction of deviance of about 6% with the addition of these variables when compared to the null model (Table 3.05). Although the fit of the model was not greatly reduced, this does indicate some influence of seawater temperature and seagrass percent cover on condition of juvenile yellowtail snapper. Dissolved oxygen, plankton trap species richness, average blade height, and blade count were not strong predictors of condition factor of juvenile yellowtail snapper caught in this study.

There was no significant effect of bay or seagrass on plankton species richness of the plankton traps (Figure 3.12). Overall, ten taxonomic phyla were identified in plankton traps among all bays and seagrass species (Table 3.02). *S. filiforme* had the highest abundance at 37% of individuals, followed by *H. stipulacea* that consisted of 33%, and *T. testudinum* at 30%. Lindbergh and Frenchmans Bays had the highest reported abundances at 28% each, followed by Saba Island (24%) and Sprat Bay (19%).

Discussion:

There was no significant effect of seagrass species on the condition factor of juvenile yellowtail snapper caught in this study. However, trends within the data demonstrated a higher condition in individuals in native *S. filiforme* and *T. testudinum* than in invasive *H. stipulacea*. These findings are similar to trends seen in Green (2017) that used seagrass height as a proxy for species and found higher canopy height yielded a higher condition for juvenile Nassau grouper, suggesting individuals caught in native seagrass had a higher condition than those caught in *H. stipulacea*. The results from this study and Green (2017) suggest that although fish living in *H. stipulacea* did not have as high of a condition as those from native seagrasses, they are not significantly lower. Trends demonstrate there were no significant differences in yellowtail snapper condition factor and plankton diversity among seagrass types, but each factor was higher in *S. filiforme* habitats. Grorud-Colvert and Sponaugle (2006) found that when *Thalassoma bifasciatum* were fed at higher rates they not only had higher condition, but also greater overall fitness. Due to yellowtail snapper being generalist carnivores (Bortone and Williams 1986), the higher diversity of plankton available within the *S. filiforme* could be positively affecting their condition factor. Further research should be conducted on gut content of juvenile yellowtail snapper to better understand how plankton availability and diversity influence condition factor of juvenile yellowtail snapper.

Although *H. stipulacea* is providing habitat that otherwise would not be there in Brewers Bay deep (see Chapter 2), the individuals from that area had a lower condition than all other bays. Hoey et al. (2007) found that depth has a significant effect on growth rates of individuals, where individuals had higher initial growth rates but lower average asymptotic lengths in deeper habitats. This suggests deep habitats created by *H. stipulacea* could be beneficial for newly settled yellowtail snapper initially allowing individuals to grow quickly. Studies have suggested that rapid initial growth of individuals could positively affect survival rates of individuals as it allows juveniles to rapidly grow out of vulnerable life stages and reduces predator pressure according to the growth-mortality hypothesis (Johnson 2008, Hoey and McCormick 2004, Grorud-Colvert and Sponaugle 2006). However, if deep habitats negatively affect fish growth over time (Hoey et al. 2007), depth could ultimately negatively affect fish populations, as seen in this study. Johnson (2008) suggests that early life history condition measurements could better represent overall fitness of fish populations and individuals over time. Therefore, if deep-water habitat, like Brewers Bay, are producing less healthy individuals it is critical to understand how that could affect the fishery long-term in the USVI and invaded Caribbean region.

An additional next step could be to look at the condition factor of adults foraging over habitats of native and invasive habitats to determine if the effects of seagrass community composition change is accumulating and resulting in adults with significantly lower condition factor and health. It was seen in this study that newly settled individuals (≤20 mm) had a significantly higher condition than individuals in any other size class. This finding is consistent with previous studies that have found higher condition (K) in smaller size classes of individuals (Lizama et al. 2002). Seagrass, bay, and the interaction of each factor had a significant effect on the condition factor of individuals in this study. Newly settled individuals (≤20 mm) from native seagrass habitats had a higher condition factor than those in invasive seagrass habitats. Interestingly this trend continues until reaching 40 mm at which point the condition factor of individuals in *H. stipulacea* is slightly higher. This could be a result of a change in diet or ability to forage for food. Although in this study, no significant difference of prey diversity was seen, previous studies have demonstrated higher diversity of invertebrates in invasive seagrass habitats in the Caribbean (Willette and Ambrose 2012). Therefore, as yellowtail snapper grow, increased diversity in prey availability could explain why condition factor increases in *H. stipulacea* seagrass habitats in higher size classes. No individuals were caught in the highest juvenile size class (61-75 mm) in *H. stipulacea* seagrass habitats; therefore, we cannot say if the trend continues. Although a potential shift in condition factor is seen in the larger size classes collected, it is difficult to be certain as the sample size was small. Further examination of individuals in larger class sizes is necessary to understand how condition could shift with size class.

Temperature (^{o}C) and seagrass percent cover (%) were strong predictors for condition of juvenile yellowtail snapper. Percent cover of seagrass was the strongest predictor of condition factor. Yeager et al. (2012) found a higher abundance of fish in areas with increased seagrass coverage. Previous research suggests higher percent cover and biomass of seagrass yields more diverse and greater species abundance (Hooks et al. 1976, Heck and Orth 1980, Horinouchi 2007). Due to *H. stipulacea* having a significantly higher percent cover than native seagrasses, it would have been expected that a higher abundance and diversity would have been seen in invasive habitats. However, no significant difference of species richness from the plankton traps was seen among seagrass types. Further research is necessary to better understand how density affects condition of individuals.

Temperature was also a significant predictor of condition of juvenile yellowtail snapper. When comparing temperature by bay (Figure 2.12) to condition factor by bay (Figure 3.07) similar trends are demonstrated with Sprat Bay having higher temperature and condition than deep Brewers Bay. It would have been expected that temperatures were higher in Sprat Bay because it is shallower than deep Brewers Bay. The findings of this study are similar to numerous studies that have found higher water temperatures yield higher condition factor in fish (Kodama et al. 2002, Peres and Oliva-Teres 1999, Grorud-Colvert and Sponaugle 2006, Mazumder et al. 2016). Peres and Oliva-Teres (1999) found that with increased water temperatures growth rate and feeding efficiency improved in juvenile fish, while other studies have suggested that growth rates in fish slow as water temperatures decrease because metabolic rate slows in cooler temperatures resulting in lower condition of fish (Kodama et al. 2012).

If temperature and percent seagrass cover are strong predictor variables, it would have been expected that individuals caught in seagrass habitats with the highest percent cover in the bays with the highest temperature would have had the greatest condition. Due to these variables having an effect on the prediction of condition factor, individuals caught in *H. stipulacea* seagrass habitats in Lindbergh Bay or Sprat Bay would be expected to have the highest condition. While individuals caught in Sprat Bay had high condition that correlated with these predictions, individuals from Lindbergh Bay did not. In both Sprat Bay and Lindbergh Bay, individuals caught in *S. filiforme* seagrass habitats had the higher condition than individuals collected in *H. stipulacea* or *T. testudinum* seagrass habitats. These findings suggest there is greater complexity to condition factor among seagrass habitats than analyzed in this study, like sex, age, gut content, or parasitism (Ndiaye et al. 2015). However, due to the limitation of this study none of these variables were recorded that could be having a great influence on the condition of juvenile yellowtail snapper. Additional limitations of this study were caused by the opportunistic sampling that occurred when divers were available. Because resources were limited, sampling occurred simultaneously with settlement surveys (Chapter 2). Therefore, sampling within the bays was not done randomly or consistently throughout the bays, but instead a bay would be revisited repeatedly when a settlement pulse occurred (see Chapter 2). This limitation implies a lack of randomization in the sampling technique, which should be considered when understanding the difference of condition of fish among bays. However, the target question of this study was to understand the difference of condition among seagrass species not necessarily bays. Therefore, further data on commercially important fish among these habitats and bays is necessary to better understand condition of fish among invasive and native seagrass habitats.

No significant difference of condition factor was seen among seagrass species in this study. Although, more research is necessary as seagrass community composition shifts to better understand how condition factor could change among individuals of varied size classes. *H. stipulacea* is providing habitat in deeper waters that otherwise might lack seagrasses completely. This added benefit of more area for juvenile fish could have a stronger positive outcome than the negative of a lower condition than individuals seen in shallower native habitats. Future studies should focus on collecting a greater number of samples from deeper habitats in multiple bays to understand the realized effects of these deep habitats.

Tables

Table 3.01: Summary of average fish characteristics with standard deviation by day, bay, and seagrass species of individuals caught from June 2020 to May 2021 in bays around St. Thomas, USVI.

Date	Bay	Seagrass	Number Caught	Average Length	Average Weight
6/2/2020	Brewers Deep	*H. stipulacea*	5	25(±2.3)	0.16(±0.04)
6/2/2020	Brewers Shallow	*H. stipulacea*	5	29.2(±4.7)	0.31(±0.20)
6/2/2020	Frenchmans	*H. stipulacea*	5	29.4(±6.0)	0.31(±0.19)
6/2/2020	Frenchmans	*S. filiforme*	1	38	0.67
6/2/2020	Lindbergh	*H. stipulacea*	5	26.8(±3.1)	0.22(±0.08)
6/2/2020	Saba Island	*H. stipulacea*	5	27.4(±2.3)	0.23(±0.06)
6/2/2020	Saba Island	*S. filiforme*	5	37.6(±14.1)	0.83(±1.06)
6/2/2020	Saba Island	*T. testudinum*	4	37.5(±5.9)	0.62(±0.34)
6/5/2020	Frenchmans	*S. filiforme*	5	27(±3.8)	0.24(±0.11)
6/5/2020	Lindbergh	*S. filiforme*	6	38.7(±9.2)	0.80(±0.60)
6/5/2020	Lindbergh	*T. testudinum*	5	29.6(±7.3)	0.34(±0.24)
6/5/2020	Sprat	*H. stipulacea*	11	31.8(±5.6)	0.42(±0.22)
6/5/2020	Sprat	*S. filiforme*	5	42.2(±7.2)	0.95(±0.36)
6/5/2020	Sprat	*T. testudinum*	5	31.2(±5.2)	0.38(±0.20)
6/6/2020	Frenchmans	*T. testudinum*	2	38(±9.9)	0.59(±0.43)
6/16/2020	Frenchmans	*T. testudinum*	3	24.7(±1.9)	0.16(±0.03)
6/17/2020	Frenchmans	*H. stipulacea*	2	31.7(±13.8)	0.48(±0.52)
6/17/2020	Lindbergh	*H. stipulacea*	1	35	0.53
6/17/2020	Saba Island	*H. stipulacea*	2	23.2(±0.4)	0.12
6/19/2020	Saba Island	*H. stipulacea*	4	26(±6.0)	0.22(±0.15)
6/19/2020	Saba Island	*S. filiforme*	4	23.9(±2.5)	0.18(±0.07)
6/19/2020	Saba Island	*T. testudinum*	9	27.7(±7.3)	0.30(±0.27)
6/20/2020	Frenchmans	*H. stipulacea*	4	31.5(±17.0)	0.72(±1.06)
6/20/2020	Frenchmans	*T. testudinum*	3	24.3(±0.6)	0.19(±0.02)
6/20/2020	Lindbergh	*H. stipulacea*	1	21	0.15
6/20/2020	Saba Island	*H. stipulacea*	6	23.9(±3.4)	0.16(±0.04)
6/20/2020	Saba Island	*S. filiforme*	1	25	0.16
6/22/2020	Lindbergh	*H. stipulacea*	12	27.4(±7.9)	0.27(±0.27)
6/22/2020	Lindbergh	*S. filiforme*	2	46.7(±16.6)	1.36(±1.25)
6/22/2020	Lindbergh	*T. testudinum*	2	57.2(±8.1)	2.22(±0.91)
6/29/2020	Brewers Shallow	*H. stipulacea*	12	27.8(±3.1)	0.27(±0.09)
7/8/2020	Brewers Deep	*H. stipulacea*	6	31(±3.5)	0.30(±0.09)
7/13/2020	Saba Island	*H. stipulacea*	1	46	1.12
7/13/2020	Saba Island	*S. filiforme*	3	52.8(±4.5)	1.53(±0.38)
7/13/2020	Saba Island	*T. testudinum*	2	46.7(±4.6)	1.18(±0.27)
7/15/2020	Brewers Deep	*H. stipulacea*	3	23.7(±2.9)	0.18(±0.10)
7/15/2020	Brewers Shallow	*H. stipulacea*	3	27(±7.2)	0.27(±0.23)

7/15/2020	Saba Island	*H. stipulacea*	3	33.7(±8.5)	0.48(±0.29)
7/15/2020	Saba Island	*S. filiforme*	6	47.5(±5.2)	1.27(±0.39)
7/15/2020	Saba Island	*T. testudinum*	2	37.2(±4.6)	0.63(±0.20)
7/16/2020	Frenchmans	*H. stipulacea*	2	22.5(±0.7)	0.14(±0.01)
7/16/2020	Frenchmans	*T. testudinum*	1	72.5	4.27
9/10/2020	Frenchmans	*S. filiforme*	1	43	0.98
9/10/2020	Lindbergh	*H. stipulacea*	1	40	0.70
9/10/2020	Lindbergh	*T. testudinum*	1	44	1.13
9/10/2020	Saba Island	*H. stipulacea*	1	48	1.32
9/10/2020	Saba Island	*T. testudinum*	1	48	1.28
9/10/2020	Sprat	*S. filiforme*	1	36	0.52
9/10/2020	Sprat	*T. testudinum*	2	20	0.10(±0.01)
9/13/2020	Frenchmans	*H. stipulacea*	1	21	0.14
9/14/2020	Saba Island	*H. stipulacea*	1	39	0.65
9/14/2020	Saba Island	*S. filiforme*	2	51.5(±9.2)	1.65(±0.80)
9/14/2020	Saba Island	*T. testudinum*	3	52.3(±6.6)	1.46(±0.79)
9/15/2020	Lindbergh	*H. stipulacea*	1	45	1.27
9/16/2020	Saba Island	*S. filiforme*	1	60	2.68
10/29/2020	Frenchmans	*S. filiforme*	3	32(±2.6)	0.46(±0.12)
11/5/2020	Frenchmans	*S. filiforme*	5	45.8(±12.5)	1.26(±0.93)
11/5/2020	Frenchmans	*T. testudinum*	2	42.5(±10.6)	0.95(±0.68)
11/5/2020	Sprat	*S. filiforme*	4	42.6(±11.4)	1.06(±0.72)
11/5/2020	Sprat	*T. testudinum*	9	36.1(±6.8)	0.59(±0.42)
11/13/2020	Saba Island	*S. filiforme*	1	22	0.15
5/6/2021	Brewers Deep	*H. stipulacea*	1	23	0.13
5/6/2021	Frenchmans	*H. stipulacea*	2	24(±1.4)	0.14(±0.02)
5/6/2021	Frenchmans	*S. filiforme*	2	21.2(±0.3)	0.12(±0.01)
5/6/2021	Lindbergh	*H. stipulacea*	1	22	0.13
5/6/2021	Lindbergh	*S. filiforme*	1	40.5	0.78
5/6/2021	Lindbergh	*T. testudinum*	3	26.7(±7.2)	0.22(±0.15)
5/6/2021	Sprat	*S. filiforme*	1	21	0.08
5/6/2021	Sprat	*T. testudinum*	7	21.2(±1.4)	0.13(±0.03)
5/7/2021	Brewers Shallow	*H. stipulacea*	4	23(±1.4)	0.15(±0.03)
5/7/2021	Frenchmans	*H. stipulacea*	1	39.5	0.71
5/7/2021	Frenchmans	*S. filiforme*	1	31	0.32
5/7/2021	Lindbergh	*H. stipulacea*	2	27.5(±6.4)	0.26(±0.11)
5/10/2021	Frenchmans	*H. stipulacea*	2	20	0.12
5/10/2021	Frenchmans	*S. filiforme*	1	19	0.11
5/10/2021	Sprat	*T. testudinum*	7	25.1(±5.3)	0.24(±0.18)
5/11/2021	Frenchmans	*S. filiforme*	1	20	0.16
5/11/2021	Sprat	*S. filiforme*	2	52(±5.6)	1.82(±0.63)
5/11/2021	Sprat	*T. testudinum*	5	28(±8.5)	0.34(±0.29)
5/17/2021	Lindbergh	*S. filiforme*	1	48	1.12

Table 3.02: Plankton trap summary table of total abundance and the average plankton species richness (±standard deviation) per trap. Traps were placed in May 2020, and samples were taken July and October 2020, and February, April, and September 2021. Brewers Bay Deep had an extra sample in December 2020 due to low volume of formaldehyde. Plankton taxa identified: Anthropoda, Chordata, Annelida, Mollusca, Chaetognath, Nemertea, Cnidaria, Echinodermata, Platyhelminthes, and Forminifera.

Plot	**Bay**	**Seagrass**	**N**	**Total Abundance**	**Average Plankton Spp. Richness (±Std. Dev)**	**Months Not Sampled**
BB-HS-Shallow	Brewers	*H. stipulacea*	5	375	7 (±5.4)	
BB-HS-Deep	Brewers	*H. stipulacea*	6	484	10 (±4.2)	
FB-HS	Frenchmans	*H. stipulacea*	5	597	10 (±4.4)	
FB-SF	Frenchmans	*S. filiforme*	5	569	11 (±2.9)	
FB-TT	Frenchmans	*T. testudinum*	4	557	10 (±7.2)	September 2021
LB-HS	Lindbergh	*H. stipulacea*	4	321	9 (±7.0)	July 2020
LB-SF	Lindbergh	*S. filiforme*	5	601	11 (±6.6)	
LB-TT	Lindbergh	*T. testudinum*	5	544	12 (±5.9)	
SB-HS	Sprat	*H. stipulacea*	5	282	7 (±4.0)	
SB-SF	Sprat	*S. filiforme*	5	719	11 (±2.2)	
SB-TT	Sprat	*T. testudinum*	4	212	4 (±6.5)	April 2021
SI-HS-SET1	Saba	*H. stipulacea*	4	497	12 (±1.2)	October 2020
SI-HS-SET2	Saba	*H. stipulacea*	3	245	6 (±5.7)	February and April 2021
SI-SF-SET1	Saba	*S. filiforme*	5	553	9 (±5.3)	
SI-SF-SET2	Saba	*S. filiforme*	4	445	8 (±4.6)	February 2021
SI-TT-SET1	Saba	*T. testudinum*	4	220	6 (±5.6)	October 2020
SI-TT-SET2	Saba	*T. testudinum*	4	654	9 (±6.4)	February 2021

Table 3.03: Summary of average fish characteristics with standard deviation by size class of juvenile yellowtail snapper trapped in bays around St. Thomas, USVI from June 2020 to May 2021.

Size Class	N	Average Fork Length	Average Total Length	Average Weight
≤20	9	18.8 (±0.44)	19.8(±0.5)	0.12(±0.03)
21-30	133	23.1(±2.57)	24.6(±2.78)	0.18(±0.07)
31-40	68	32.8(±2.82)	35.1(±2.94)	0.52(±0.14)
41-50	31	42.5(±3.01)	45.8(±3.26)	1.09(±0.23)
51-60	15	51.5(±2.51)	55.5(±3.01)	1.98(±0.36)
61-75	4	59.8(±3.59)	65.0(±5.02)	3.13(±0.76)

Table 3.04: Statistical summary table of predictor variables from the Generalized Linear Model. * indicates a significant predictor variable.

Predictor Variable	Standard Error	t-value	p-value
Dissolved Oxygen (O2)			>0.05
Seawater Temperature *	2.35	2.07	0.04
Plankton Species Richness			>0.05
Blade Height			>0.05
Blade Density			>0.05
Percent Cover *	7.90	2.53	0.01

Table 3.05: Model summary table from the Generalized Linear Model

Model	Deviance	d.f.
Null	85,471	259
Residual	80,252	253
AIC: 2,244.2		

Figures

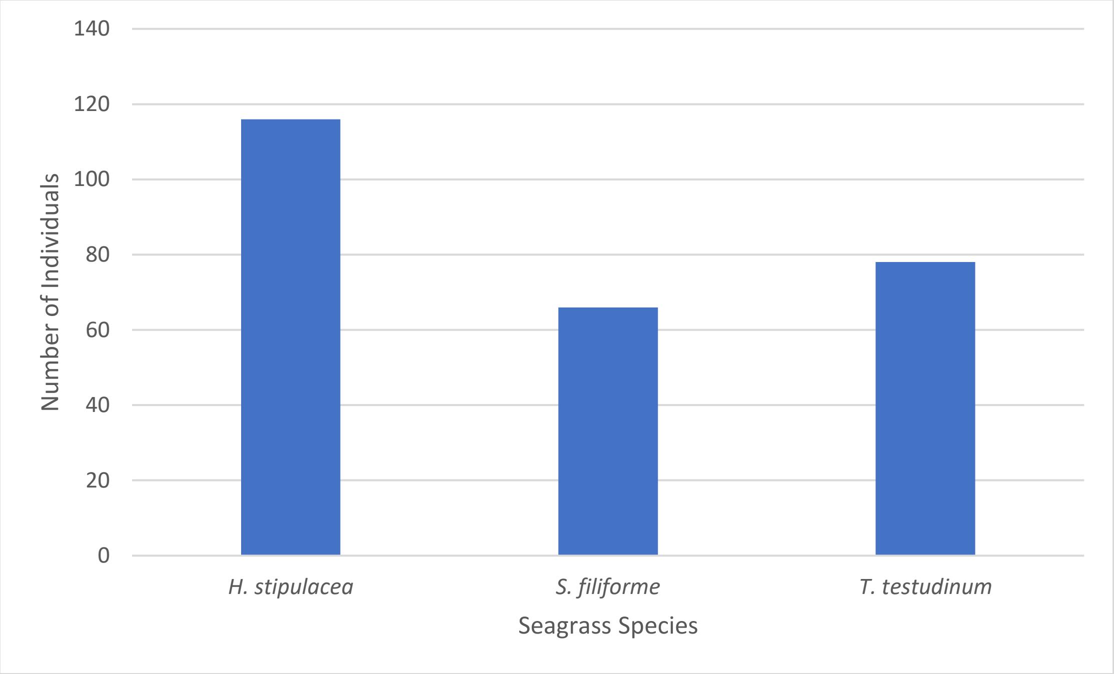

Figure 3.01: Number of yellowtail snapper collected in each seagrass species from June 2020 to May 2021 in St. Thomas, USVI.

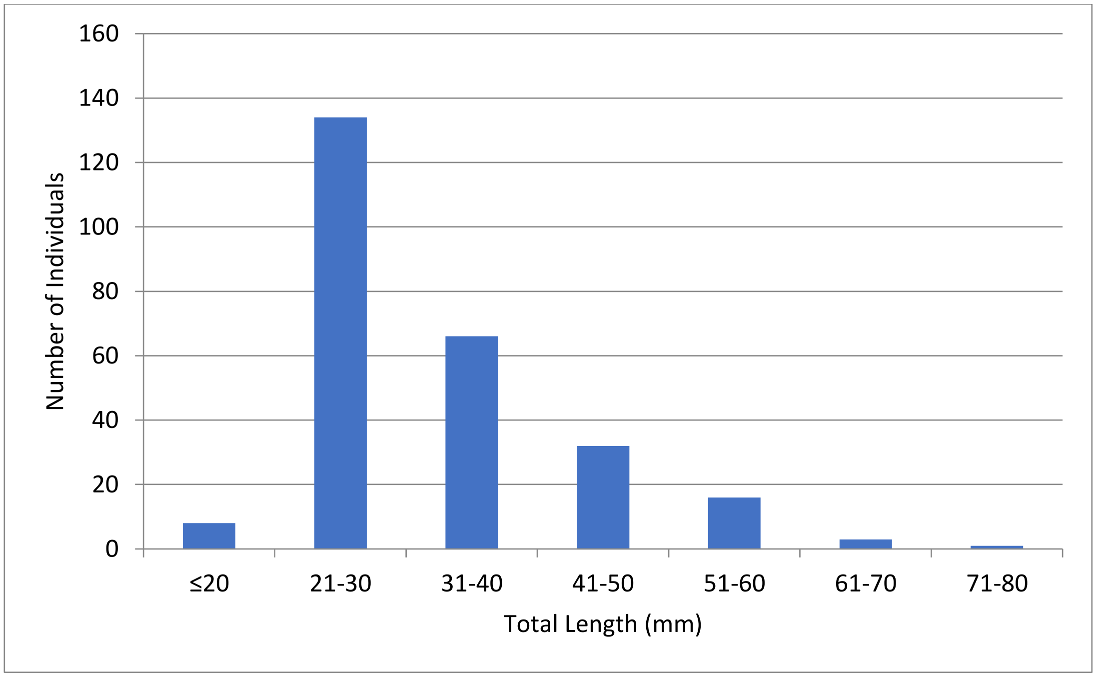

Figure 3.02: Number of yellowtail snapper collected by size class of total length from June 2020 to May 2021 in St. Thomas, USVI.

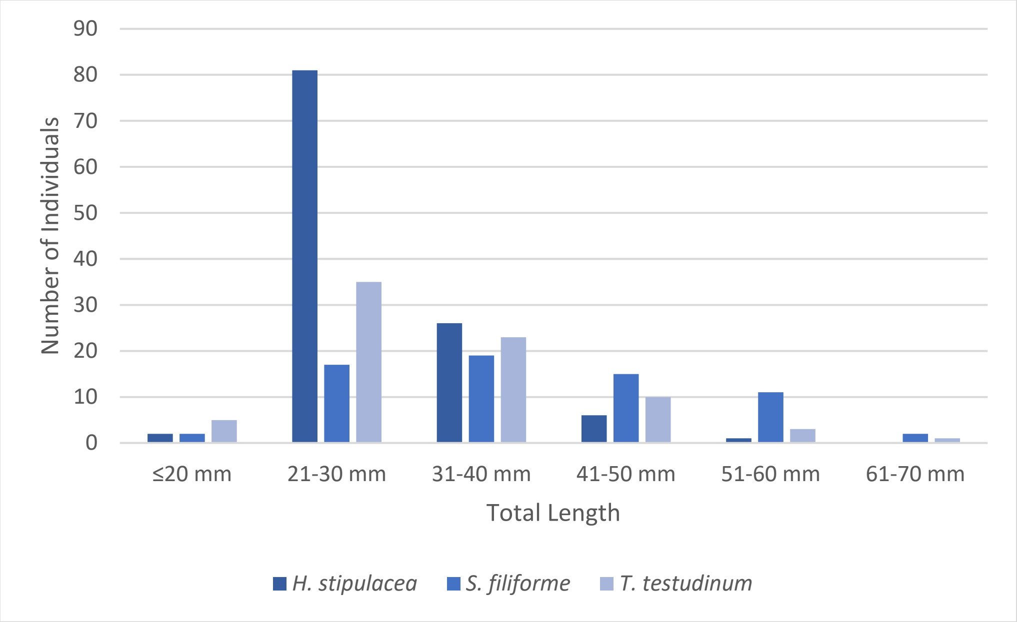

Figure 3.03: Number of yellowtail snapper collected by size class of total length by seagrass from June 2020 to May 2021 in St. Thomas, USVI.

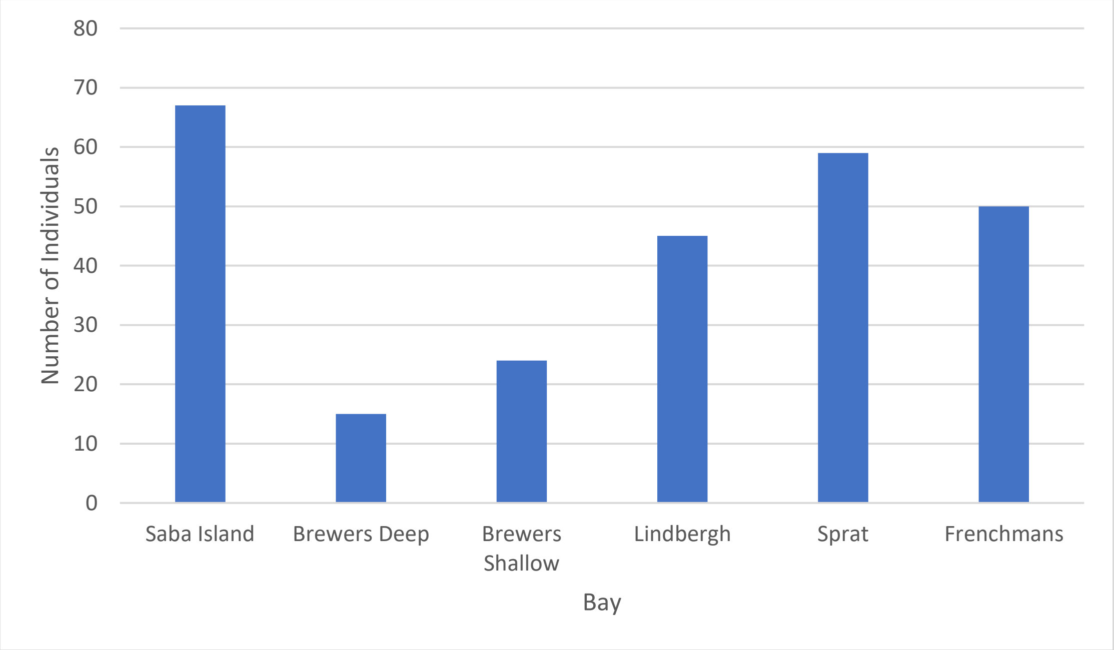

Figure 3.04: Number of yellowtail snapper collected in bays around St. Thomas, USVI from June 2020 to May 2021.

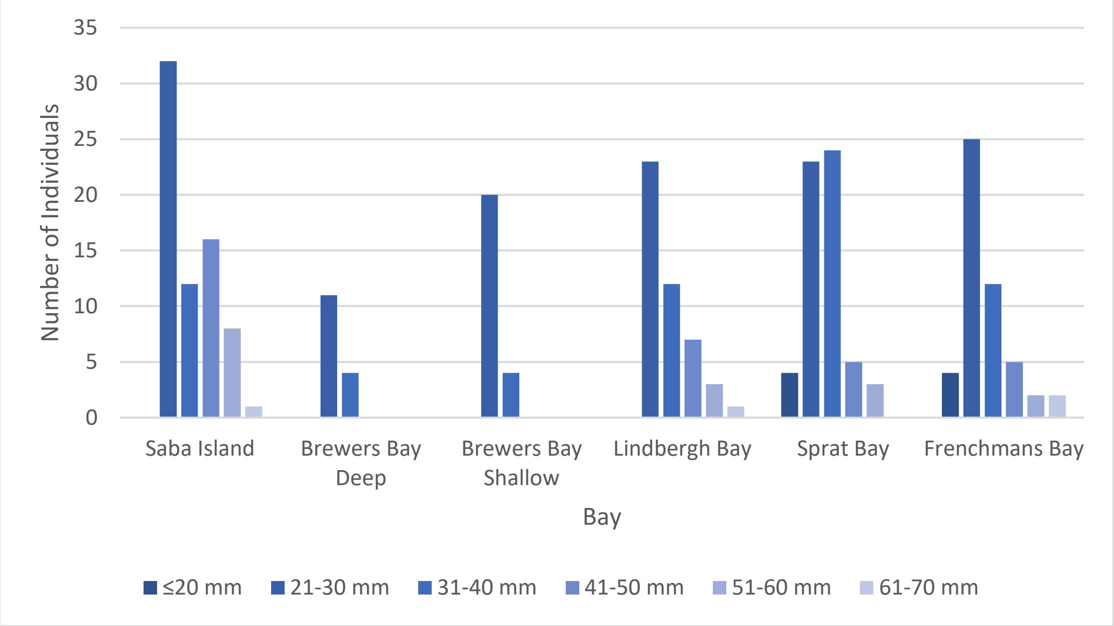

Figure 3.05: Number of yellowtail snapper collected by size class of total length by bay from June 2020 to May 2021 in St. Thomas, USVI.

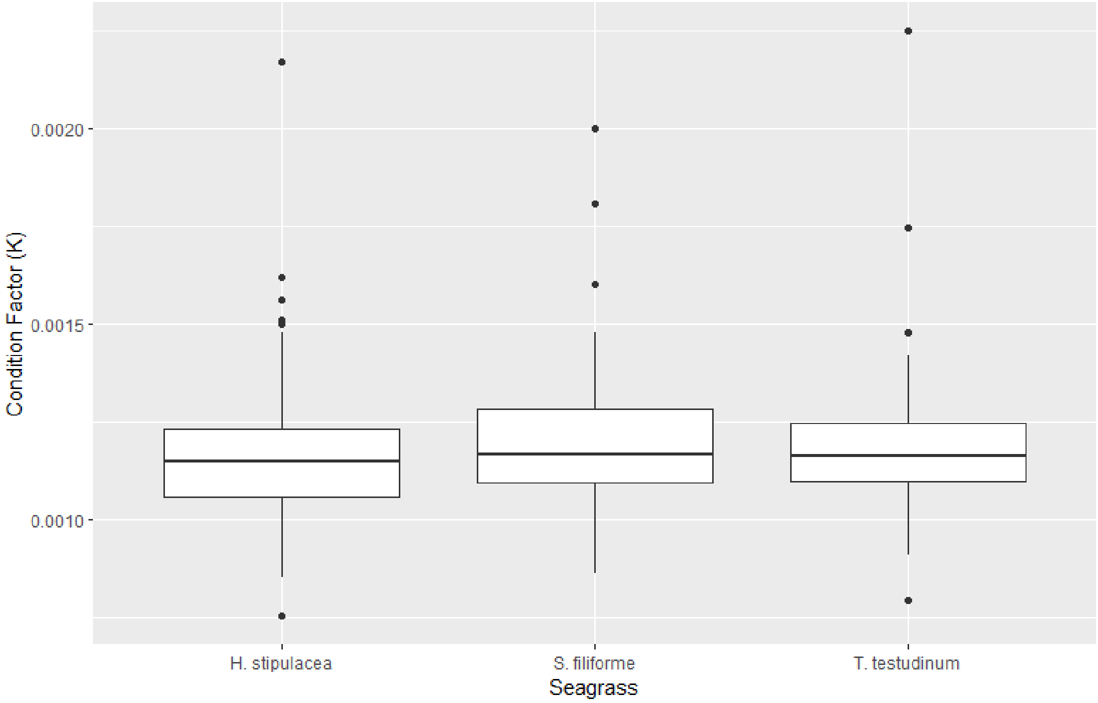

Figure 3.06: Box and whisker of average condition factor of all fish collected by seagrass species from June 2020 to May 2021. Black lines represent the mean temperature for each bay, whiskers represent the range of temperatures for each bay, and black dots represent individuals outside of this range. No significance was seen among seagrass species.

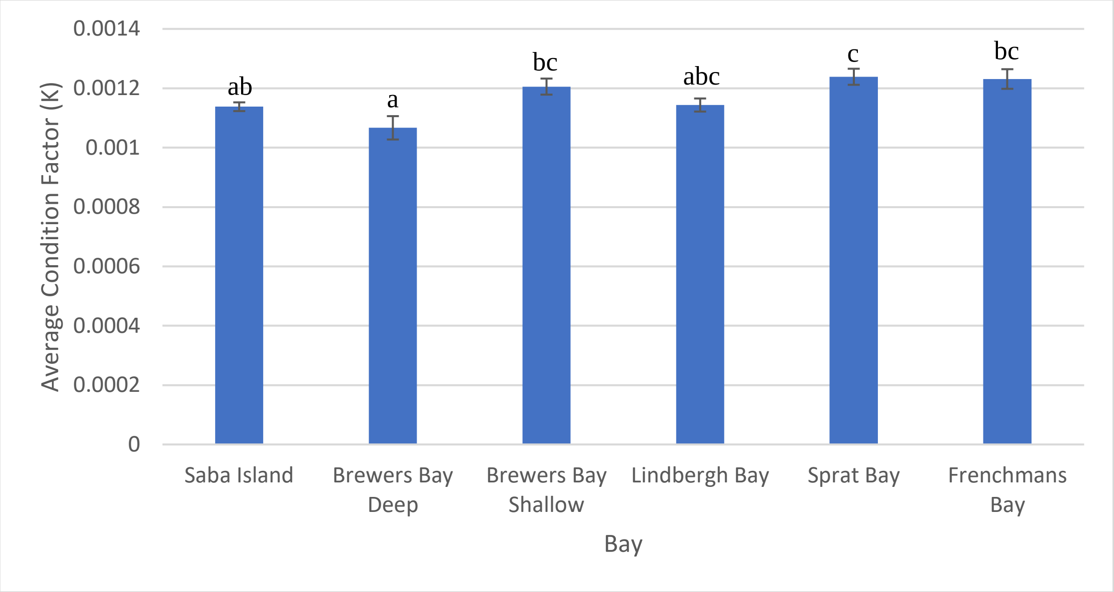

Figure 3.07: Average condition factor (K) of all fish collected by bay from June 2020 to May 2021 with ±SE bars. A significant effect of bay on condition factor (K) was seen (p = 7.106e-5).

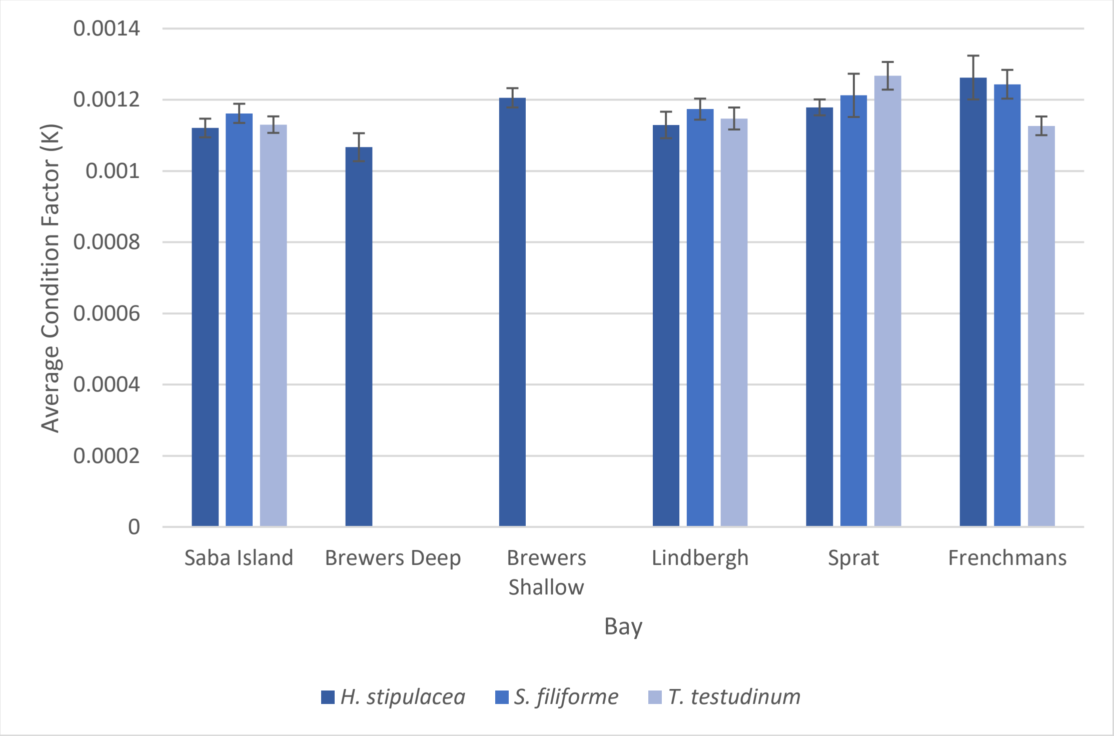

Figure 3.08: Average condition factor (K) by seagrass and bay of all juvenile yellowtail snapper collected between May 2020 and June 2021 with ±SE bars. A significant interaction of bay and seagrass was seen (p = 2.76e-7).

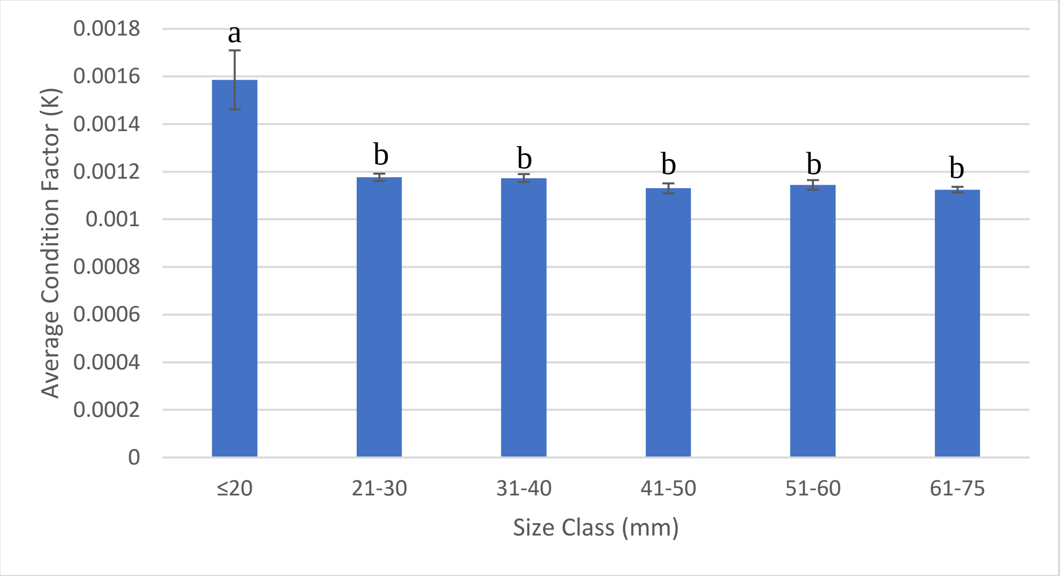

Figure 3.09: Average condition factor (K) by size class of all juvenile yellowtail snapper collected between May 2020 and June 2021 with ±SE bars. A significant difference was seen among size classes (p = 0.005) and significantly higher condition factor (K) was seen in individuals from ≤20 mm than any other size class.

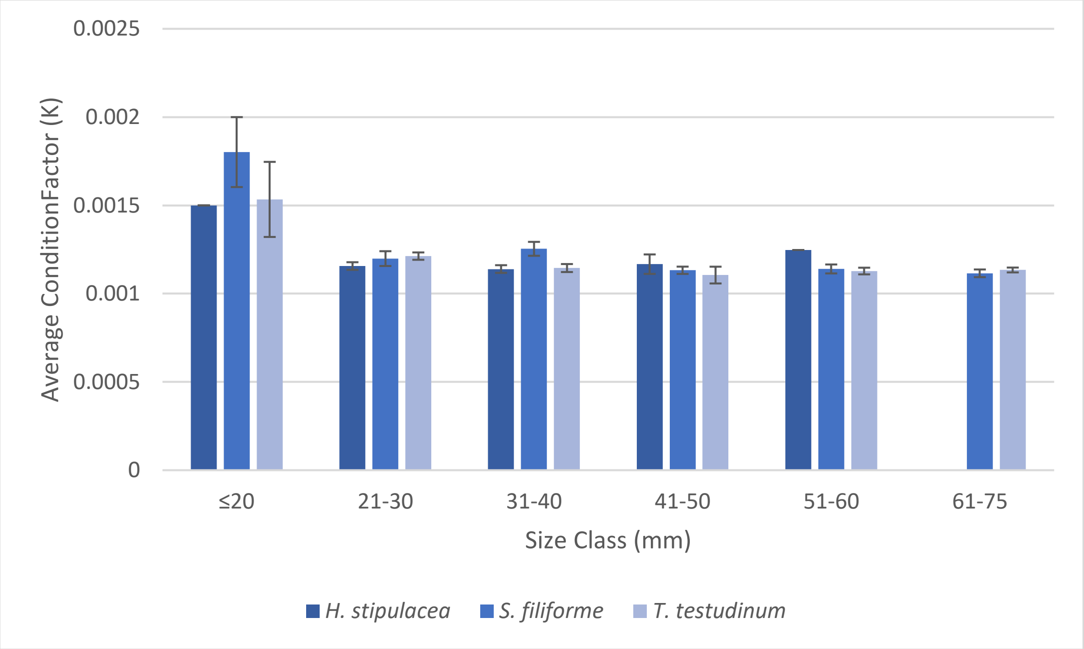

Figure 3.10: Average condition factor (K) by size class and seagrass of all juvenile yellowtail snapper collected between May 2020 and June 2021 ±SE bars. A significant effect of the interaction of size class and seagrass species was seen (p = 4.72e-6).

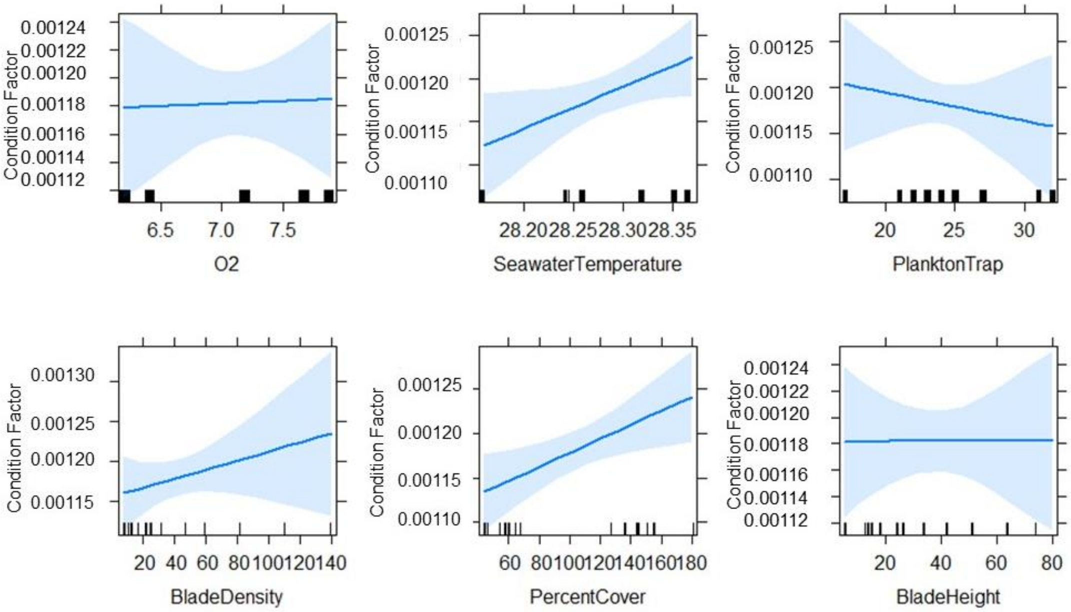

Figure 3.11: Response variable curves based on the generalized linear model of possible predictor effects on condition factor (K) of juvenile yellowtail snapper. Seawater temperature (^oC; p = 0.04), and percent cover (p = 0.01) are significant predictors of condition factor.

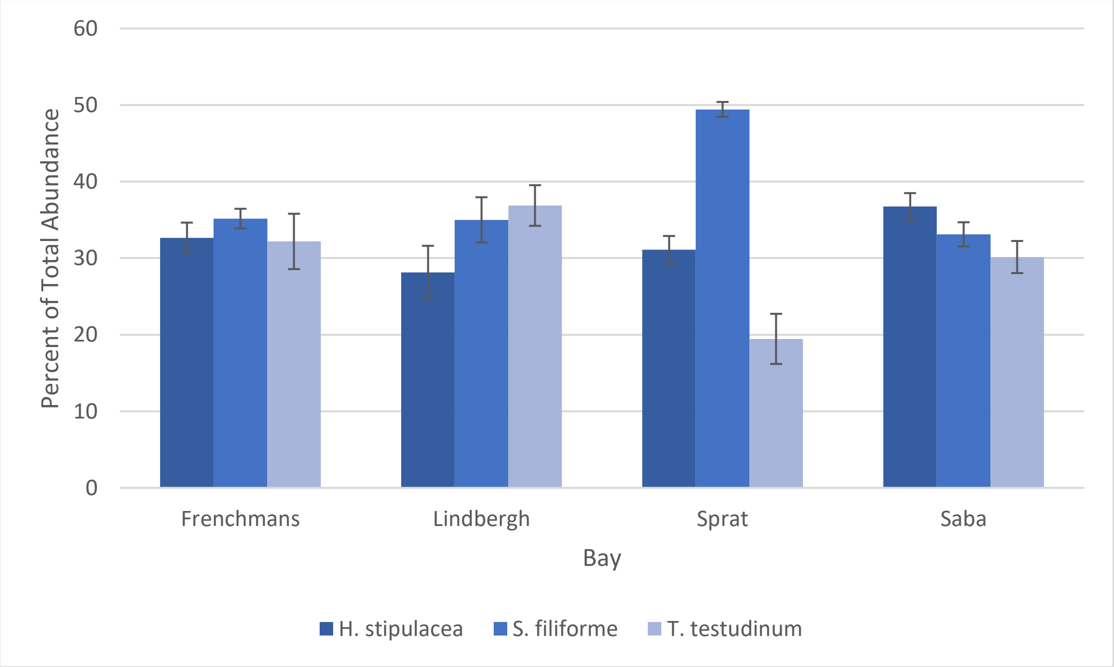

Figure 3.12: Percent of total abundance of different planktonic organisms collected in plankton traps in each seagrass species from May 2020 to September 2021. The abundance of individuals from Brewers Bay are not reflected in this figure.

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CHAPTER 4
General Discussion

This study was the first of its kind to look at the effects of *H. stipulacea* on juvenile yellowtail snapper settlement, mortality, and condition in St. Thomas, USVI. When analyzing these three measurements in juvenile yellowtail snapper among *H. stipulacea*, *S. filiforme,* and *T. testudinum* seagrass habitats overall results suggest that *H. stipulacea* might not be as detrimental to yellowtail snapper fish populations as previously hypothesized. Settlement of yellowtail snapper increased, mortality was lower, and condition factor did not significantly differ in invasive seagrass habitats than in native seagrass habitats. Therefore, if *H. stipulacea* does outcompete *S. filiforme* after a disturbance as suggested by Jerris (2019), it could have a positive effect on yellowtail snapper populations. Not only does more settlement occur, but also lower mortality is seen while condition remains statistically similar in juvenile yellowtail snapper in *H. stipulacea* seagrass habitats.

Positive impacts on yellowtail snapper populations could be seen in particular within deeper habitats. While only one plot was established in deeper habitats in this study, promising results in recruitment and settlement demonstrate potential positive effects of the invasion of *H. stipulacea* on commercially important fish species. Although settlement and condition were not as high in deep Brewers Bay than in shallow Brewers Bay, results show that roughly 30% of all fish observed in Brewers Bay were seen in the deep plot. These data suggest that yellowtail snapper are not only utilizing deep habitats for settlement, but additionally their condition was statistically similar. These findings suggest an overall possible benefit of *H. stipulacea* seagrass habitats. Prior to the establishment of *H. stipulacea* many of these deeper habitats were most likely barren seafloor, because these depths are beyond all native seagrass ranges except for *Halophila decipiens* (Jerris 2019). Therefore, the additional suitable nursery habitat could be more beneficial to yellowtail snapper populations than the possibility of lower condition in those individuals. In this study, only one deep plot was analyzed and no native *H. decipiens* habitats were observed. Therefore, future studies should compare potential settlement and condition between each of these seagrass types.

Although these promising results could be beneficial for yellowtail snapper populations, the loss of sandy areas could be detrimental to ground fish species that depend on this habitat throughout their life. Guidetti (2000) found distinct groupings of species associated with sand habitats than seagrass or rocky-algal habitats. These findings could demonstrate an association of species to the sandy ecosystems. Therefore, if *H. stipulacea* capitalizes on patches of barren sandy areas, it could have a harmful effect on demersal fish populations that have a specialized niche in sandy habitats. Further understand of the effects of the loss of sand habitats on demersal fish would help management make a more informative decision on *H. stipulacea.*

Another potential benefit of *H. stipulacea* could be quick establishment following disturbances. With reports of major seagrass die off throughout the Caribbean (Muehlstein and Beets 1992, Rodemann et al. 2021) and increased impacts from storms (Jerris 2019) causing major loss in seagrass area, *H. stipulacea*'s rapid growth rate and ability to adapt to a range of conditions could be beneficial to fish populations. Jerris (2019) found *H. stipulacea* outcompeted native *S. filiforme* after hurricanes Irma and Maria in St. Thomas, USVI. With higher settlement rate, lower mortality, and no distinct difference of condition factor in yellowtail snapper, this shift in community structure could be beneficial for snapper population sizes around St. Thomas. However, *H. stipulacea* could also be threatened by seagrass die off like native seagrasses in the area. In August 2020, a large settlement of *Lobophora variegata* was observed in Sprat Bay. A sharp decline of *H. stipulacea* was observed after the settlement of the algae occurred. While initial density measurements were taken after *L. variegata* arrival, density of the plot did not recover to what was observed in the beginning months of this study (Table 2.03; personal observations). Although *H. stipulacea* is highly adaptable, possibly with time, population sizes will be regulated naturally through competition with native species. Occurrences like the one observed in this study should be closely monitored, because the total loss of native and invasive seagrass could be devastating to yellowtail snapper populations.

Although not strongly represented in results from this study, data suggest possible negative effects of *H. stipulacea* on yellowtail snapper in larger juvenile size classes. The absence of individuals in *H. stipulacea* seagrass habitats in the larger juvenile size class (40-75 mm) was evident in this study (Figure 2.06). During settlement surveys reported in Chapter 2, more individuals in larger juvenile size classes (41-75 mm) were seen in native seagrass habitats than in invasive seagrass habitats, which might suggest a threshold size of individuals in invasive seagrass habitats. The average size blade of *H. stipulacea* is significantly shorter than native seagrasses (Figure 2.09), which could prevent juvenile yellowtail in the larger size classes from camouflaging or hiding from predators resulting in higher mortality of larger juveniles. While it is possible juvenile yellowtail snapper in these larger size classes are migrating to nearby native seagrass habitats that provide higher blades for increased shelter, it is unlikely because high numbers of individuals would have been reported in these size classes in native seagrass species during surveys reported in Chapter 2. This could imply that there is a higher mortality rate of individuals in invasive seagrass habitats in the higher size classes, however, further research is necessary to test this theory. This study focused primarily on individuals less than 30 mm in total length. Therefore, future studies should look at the behavior, mortality, and condition of larger juveniles to better understand what could be occurring.

In addition to seagrass species, the environmental variables that strongly affected juvenile yellowtail snapper were bay and temperature. Temperature trends follow similar patterns in each bay, with no significant difference observed among bays. This study found that increased temperatures in bays not only resulted in higher settlement, but also higher condition of juvenile yellowtail. Numerous studies explain that temperature has a strong effect on the overall fitness of fish (Kodama et al. 2002, Peres and Oliva-Teres 1999, Grorud-Colvert and Sponaugle 2006, Mazumder et al. 2016), similar to the findings of this study. Cure et al. (2015) suggests that as seawater temperatures increase globally there could be initial positive effects on fish populations. However, other studies have demonstrated that fish may reach a maximum threshold in water temperature that would then decrease the overall fitness of the fish when stressed (Johansen et al. 2014). Although this was not specifically tested in this study, results from Brewers Bay demonstrate that during months of increased water temperature, like August and October, that there was higher settlement in deep habitats than shallow. This could show that these deep habitats are offering possible refugia for juvenile yellowtail snapper with increased water temperatures. With further research, this potential trend might suggest that deep *H. stipulacea* seagrass habitats could become necessary nursery areas for juvenile fish as sea water temperatures increase.

Settlement, mortality, and condition are known to be variable in juvenile reef fish (Victor 1991, Öhman et al. 1998, Beets 1997, Nunn et al. 2012, Wilson and Osenberg 2002, Sutton et al. 2000, Robinson 2010, Mazumder et al. 2016). Therefore, additional environmental variables could have contributed to these results, but due to the limitations of this study were not recorded. These variables include but are not limited to predator presence (Beets 1997), competition among juvenile yellowtail snapper for space and resources (Nunn et al. 2012, Wilson and Osenberg 2002), oceanographic patterns (Sponaugle et al. 2005), or water quality (Thorensen et al. 2010). Each of these variables could impact the settlement, survival, and condition factor of juvenile yellowtail snapper. This study was also limited spatially and temporally to the divers available and the bays in southern St. Thomas. This study was conducted during Covid-19, which limited the diver availability greatly. Therefore, the original experimental design could not be fulfilled each month with continued mortality surveys throughout each month or random collection of juvenile yellowtail snapper consistently throughout each bay. These spatial and temporal limitations should be considered when analyzing the findings of this study. Due to the complexity of yellowtail snapper life history, management should look further into how *H. stipulacea* may be impacting environmental variables as well as settlement, survival, and condition factor on a broader scale to properly evaluate the overall impact of this invasive species on yellowtail snapper populations.

Food-Energy-Water Nexus

This study was the first to look at how the shift in seagrass community structure could be impacting food-energy-water systems (FEWS) in the USVI. FEWS thinking is an interdisciplinary approach to understanding the complexity of food, energy, and water interdependence to provide managers with a better understand of a system as a whole (Scanlon et al. 2017). For instance, the conclusions from this study in addition to previous studies demonstrate the complexity of the invasive seagrass *H. stipulacea* by providing some positive (i.e. more settlement habitat) and negative (i.e. reduces diversity [Olinger et al. 2017]) effects on fish populations. This study focused on the food and energy cycling within the invasive and native seagrass habitats.

Food systems were the primary focus of this study; not only did this study aim to answer how could the community composition shift affect the yellowtail snapper fishery overall, but additionally tried to understand what food was available in each seagrass type for newly settled individuals. As previously mentioned, yellowtail snapper is one of the most landed fish species within the Virgin Islands (Olsen et al. 2007). Therefore, any impact to this species would have an effect on the food systems within the territory. The dependence on the fishery made it critical to understand how a shift in the ecosystem would affect the early life history stages of this commercially important species. It was found there was a potential positive impact on the yellowtail snapper populations with more suitable settlement habitats, which could increase population sizes of yellowtail snapper. Additionally, similar prey diversity and abundance among each seagrass type was found, which demonstrates no significant difference of food availability within each seagrass habitat. These findings suggests positive impacts on yellowtail snapper populations, and answer some questions of the impacts of *H. stipulacea* on the food systems within St. Thomas, USVI.

This study also sought to answer how could this community composition change be affecting the energy system within the ecosystem. Condition factor has often been used as a measurement to understand the fatty reserves of a fish, which can be used as energy reserves during times of stress (Robinson 2010; Ndiaye et al. 2015). Using condition as a proxy for energy within the system, it was found that although not significant *H. stipulacea* might have a detrimental effect on fish’s energy reserves. These findings demonstrate that *H. stipulacea* could have a long-term impact on fish populations energy cycling. If the condition factor of fish found in *H. stipulacea* seagrass habitats is lower than those found in native seagrasses, then the individuals feeding over invasive seagrasses might also have lower condition. This effect could be impacting the food chain as predators feed on prey with lower condition. While this impact on the energy cycle was not looked at in this study, the effects of *H. stipulacea* on early life history stages of yellowtail snapper were identified. However, there are many gaps to still be filled for management to conclude on the overall impacts of *H. stipulacea* on marine ecosystems.

A broader ecosystem-based approach is necessary to truly answer the question on how environmental variables and prey availability might differ among seagrass types. Due to *H. stipulacea*'s rapid expansion rate (Table 2.04) and ability to outcompete native seagrasses (Jerris 2019, Winters et al. 2020), the shift in community composition could have long term impacts that were not represented in this study. By better understanding how the shift in community composition could change for the entire ecosystem, it would be easier to predict how *H. stipulacea* could impact commercially important fish species long-term. For instance, Stuij (2018) found a more diverse and specialized microbial community in *H. stipulacea* than in native seagrasses, but less differentiation between above and below substrate diversity. This could result in a decreased diversity in microbiome communities resulting in less or different prey availability over time. For fish species that have a more specified diet than yellowtail snapper, this shift in prey availability could have a damaging effect on their populations, which could greatly impact the fishing industry within the USVI.

Additionally, this study did not answer any questions on the impacts of *H. stipulacea* on the water systems. One area of study that should be further explored is the possible differentiation of water quality among seagrass types. If there is a change in water quality among native and invasive seagrass habitats, it would be a critical step for management to better understand in order to make informed management decisions on *H. stipulacea*. As the seagrass continues to spread throughout the Caribbean, it is important for more information to be gathered on how *H. stipulacea* is impacting the FEWS in the USVI to better understand the overall impacts of its invasion. The findings of this study will be shared with local management to help them make an informed decision locally on the effects of *Halophila stipulacea* on commercially important yellowtail snapper populations.

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