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Abstract

Tropical cyclone activity is predicted to intensify with anthropogenic climate change. Therefore, there has been a call to action in the scientific community to increase knowledge of the impacts of tropical cyclones on ecosystems. In particular, there is a wide knowledge gap in the understanding of how tropical cyclones influence coastal marine ecosystems. Using a standardized Web of Science database search, I identified 101 peer-reviewed articles documenting the impacts of tropical cyclones on coastal marine ecosystems in the North Atlantic Ocean, including coral reefs, mangrove forests, salt marshes, and seagrass meadows. Here, I summarize the results of these articles with the aim of improving general understanding of how past tropical cyclones have affected coastal marine ecosystems. Specifically, I summarize the types of tropical cyclones that have most often been documented to impact ecosystems (tropical storms or Category 1 to 5 hurricanes), how often the impacts have been documented in each of the past 5 decades (1970s, 1980s, 1990s, 2000s, and 2010s), and at what level of biological organization most of the impacts have been recorded (organismal, population, community, or ecosystem). Category 3 or greater intensity hurricanes have been responsible for most of the impacts to marine ecosystems recorded in the literature. However, there is no clear increase or decrease in the number of impacts recorded in each decade. This result may be due to a time lag in the publication of research results that has reduced the number of reports in the most recent decade. Most of the impacts of tropical cyclones have been recorded at the population level, with a decrease in population abundance following a storm. The findings of this literature review can help create a larger view of how scientists should prepare for the consequences of these natural disasters.

MONTCLAIR STATE UNIVERSITY

Effects of Tropical Cyclones on Coastal Marine Ecosystems

by

Xenia Neal

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Thesis Committee

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EFFECT OF TROPICAL CYCLONES ON COASTAL MARINE ECOSYSTEMS

A THESIS

Submitted in partial fulfillment of the
requirements for the degree of Master of Science

By

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INTRODUCTION

Since the start of the second industrial revolution, CO₂ levels in the atmosphere have exponentially risen (Manoli et al. 2016). This rapid rise of CO₂ has resulted in warming of the earth's atmosphere and oceans (IPCC 2018). In response to climate change, there have been changes to precipitation patterns, accelerated sea-level rise, and changes to the intensity of tropical cyclones (IPCC 2019). The increase of destructive tropical cyclones occurs because warm waters have more energy to fuel these storms (Walsh 2015). Intense precipitation events can cause serious flooding as a result of tropical cyclones (Trenbeth 2011). Furthermore, sea level rise can contribute to storm surge during a tropical cyclone, which can cause immense damage to densely populated cities (Walsh 2015). In addition to the risks to human populations, tropical cyclones have the potential to impact coastal marine ecosystems (Mumby et al. 2011, Pruitt et al. 2019).

There is growing concern about the impacts of anthropogenic activity, and how this activity will influence coastal marine ecosystems. Understanding of tropical cyclone impacts in coastal marine ecosystems is incomplete (Pruitt et al. 2019). The preservation of coastal marine ecosystems is important, as they provide many economic and ecological services (Barbier et al. 2011). Ecosystems like coral reefs, mangrove forests, salt marshes, and seagrass meadows provide important resources to humans and marine organisms (Barbier 2017). Coasts are known to host roughly one-third of the world's population, and contain 90% of the catch from marine fisheries (Barbier 2017). These ecosystems are a large economical contributor for many countries, providing resources for hunting, and fuelwood extraction (Barbier 2012). Mangrove forests are documented to help prevent against coastal erosion, and salt marshes have properties that allow filtering of pollutants from surrounding waters. The cultural significance of these ecosystems is also a reason for preservation and protection; local human populations put non-monetized value on having access to coastal resources (Barbier 2012). Furthermore, coastal ecosystems protect inland residential homes and commercial establishments from the damages of ocean waves during strong storms.

The purpose of this study is to examine the influence that tropical cyclones have on dominant coastal marine ecosystems in the North Atlantic Ocean. The amount of peer-reviewed literature regarding the impact of strong storms on coastal marine ecosystems is

staggering. By collating this information, there can be a stronger understanding of the future of coastal environments, making it easier to develop plans for conservation and guide future research.

METHODS

Literature Review

For this study, I conducted a systematic literature review of scholarly articles from 1970–2019 documenting the impacts of North Atlantic tropical cyclones on dominant coastal marine ecosystems: coral reefs, mangrove forests, salt marshes, and seagrass meadows. To find the relevant articles, I searched the database “Web of science” for article titles with the following search string: TI=(hurricane* OR cyclone* OR "tropical storm*") AND TI=(coral* OR alga* OR macroalga* OR macrophyt* OR seagrass* OR eelgrass* OR "submerged aquatic vegetation" OR seaweed* OR mangrove* OR marsh*). I searched titles of scholarly articles, not abstracts for the search string. Abstracts are unavailable for many articles before the year 1990, therefore the search with that inclusion would create bias in the literature towards later publication years (Ward and Lafferty 2004).

To further narrow the search and use of articles for the review, a criterion was developed. Articles were excluded if they were not located in the North Atlantic region, if they were based off a purely modeling experiment (for these papers do not have empirical data), if the articles were not ecologically-based research (e.g., geological studies), and if there was not a biological impact observed (i.e., a negative result). Only three of the original group of articles contained no impact.

For each scholarly article that fit the criterion (n = 101 articles), I datamined information on the type of ecosystem impacted (coral reef, mangrove forest, salt marsh, or seagrass meadow), the type of biological response observed (see details below), the year of the storm impact, the name of the storm, and the location (latitude and longitude) where the storm made landfall. The name of the storm was cross-referenced against the National Hurricane Center database (<https://www.nhc.noaa.gov/>) to determine the storm’s maximum intensity on the Saffir Simpson scale: ranked from tropical storms to Category 1 to 5 hurricanes (weakest to strongest). To determine the exact location of landfall,

coordinates were calculated from 'Google Earth' based on the field site information provided in the scholarly article.

Biological Responses

Biological responses to tropical cyclones documented in the articles were divided into four different levels of biological organization, defined by a hierarchy of complexity and scale: organismal, population, community, and ecosystem (Table 1, Table A1). I recorded the biological response at the highest level of biological organization impacted for each article. An organismal response is further broken down into five categories of growth, behavior, condition, phenology, and physiology. The growth response occurs when a storm increases or decreases organismal growth rate. The condition response occurs when a storm causes superficial, non-lethal damage to the organism. A phenology response results in a change in reproductive timing. Lastly, the physiology response occurs when there is a change in normal physiological functions as a result of a storm (Table 1).

At the population level, responses were divided into three categories of abundance, demography, and genetics (Table 1). The abundance response occurs when there is a change in the number of individuals in a population. The demography response occurs when there is a change in the age or size structure of a population. Lastly the genetic response occurs when there is a change in the genetic diversity of a population (Table 1).

At the community level, responses were defined as changes to species richness/composition and species interactions (Table 1). Species richness/composition is defined as a change in the number of total species or the relative abundances of species. Species interactions are defined as a change in competition, consumption, symbiosis, or commensalism (Table 1).

Lastly, at the ecosystem level, responses were divided into three categories including localized ecosystem regime shifts, changes to energy cycling, and changes to nutrient cycling (Table 1). A localized regime shift is described as the dominant habitat-forming (foundational) species changing in the location of storm impact. The change is abrupt and persistent, with recovery not expected within one generation of foundational species. Energy cycling is defined as a change in how energy moves through the ecosystem.

Nutrient cycling is defined as a change in how nutrients move throughout the ecosystem (Table 1).

Data Analysis

To analyze the data, I examined the percentage of scholarly articles that recorded storm impacts in each of the four ecosystem types (coral reef, mangrove forest, salt marsh, or seagrass meadow), at each of six levels of storm intensity (tropical storm, Category 1, Category 2, Category 3, Category 4, or Category 5 hurricane), in each of five decadal periods (the 1970s, 1980s, 1990s, 2000s, or 2010s), and at each of the levels of biological organization (organismal, population, community, or ecosystem). I then determined whether the percentage of the four levels of biological responses differed among ecosystem types, storm intensities, or decades using contingency table analyses ($\alpha = 0.05$). In the analysis, Category 3 and weaker storms were pooled due to few observations at these intensity levels. Observations from the 1980s and 1970s were also pooled due to limited number of observations.

Three hypotheses were tested. The first hypothesis (H1) was that all four ecosystems would produce similar percentages of reports at each level of biological organization, as I had no specific reason to expect ecosystems would respond to storms differently. The second hypothesis (H2) was that greater intensity storms would have a reported impact at a higher level of biological organization (i.e., community and ecosystem levels vs. organismal and population levels) given that stronger storms are more disruptive events. My third hypothesis (H3) was that more recent decades would have impacts reported at a higher level of biological organization given that storm strengths have been increasing through time. Contingency table analyses were conducted in an Excel spreadsheet.

RESULTS

Overall Patterns in Reporting

In Figure 1a, coral reefs had 34% of overall storm impact reports, mangrove forests had 32%, salt marshes had 24%, and seagrass meadows had 11%. In Figure 1b, Category

5 hurricanes caused 59% of ecosystem impact reports, Category 4 hurricanes caused 23%, Category 3 hurricanes caused 9%, Category 2 hurricanes caused 0%, Category 1 hurricanes caused 2%, and tropical storms caused 1%. Out of all the recorded storm impacts in this study, 90% were from Category 3–5 hurricanes, which are considered Atlantic major hurricanes (Yan et al. 2017). In Figure 1c, 25% of the recorded hurricane impact reports took place in the decade 2010, 41% in the 2000s, 21% in the 1990s, 25% in the 1980s, and 2% in the 1970s.

In Figure 2a, at the organismal level of biological organization, 50% of reports were the condition response, 20% were the physiological response, 20% were the phenology response, and 10% were the growth response. In Figure 2b, at the population level, 89% of reports were the abundance response, 9% were the demography response, and 2% were the genetic response. In Figure 2c, at the community level, 95% of reports were the species richness/composition response and 5% were the species interaction response. In Figure 2d, 77% of the articles reported an ecosystem regime shift response, 15% were nutrient cycling responses, and 8% were energy cycling responses.

Regarding reported responses to a hurricane impact, results show that with all four ecosystem types, the population response is the largest category (Figure 3a). The next most common biological response reported is a community response (Figure 3a). The contingency table analysis indicated no difference among ecosystem types in the percentage of the four biological responses, thus supporting H1 ($\chi^2 = 10.4$, $p = 0.31$). However, it is interesting to point out that ecosystem regime shifts were recorded only since the 1990s (Figure 3a).

Amongst the storm intensities, population level responses were again the most common biological response reported at all storm intensities (Figure 3b). The community response is seen as the second most observed, except under the Category 3 storm (Figure 3b). With the Category 3 storm, it is shown that the organismal level was the second most common response (Figure 3b). However, contingency table analysis indicated no differences among storms in the percentage of the four biological responses ($\chi^2 = 9.38$, $p = 0.153$). Based on the data I can reject H2; there is no evidence that greater storm intensities have effects reported at a greater biological level.

In each decadal period, the most common biological response reported was again at the population level (Figure 3c). The second most common response was at the community level. The contingency table analysis indicated no difference among storms in the percentage of the four biological responses ($\chi^2 = 5.91$, $p = 0.749$). This data leads me to reject H3; decade had no influence on reported impact levels of biological organization.

Ecosystem-Specific Findings

Coral Reefs. After reviewing the articles of tropical cyclone impacts on coral reefs, all levels of biological organization were represented. For the organismal level, individuals were affected by sediment deposition which aided or inhibited individual growth (Hillis and Bythell 1998, Reardon 2018). Coral colonies were also reported to experience damage and fragmentation after a tropical cyclone (Highsmith et al. 1980). Tropical cyclones were also recorded to bring in cool influxes of water which allowed individuals to recover from coral bleaching (Manzello et al. 2007), but it was also noted that there was reduced calcification from lowered levels of pH (Manzello et al. 2013). Additionally, population abundance changed due to death of coral colonies following a storm (Knowlton et al. 1981, Woodley et al. 1981, Fenner 1991, Fong and Lirman 1994, Wulff 1995, Fong and Lirman 1997, Nowlis et al. 1997, Rogers and Miller 2001, Adams and Ebersole 2004, Alvarez and Gil 2006, Gleason et al. 2007, Alvarez et al. 2009, Edmunds 2019, Wright et al. 2019). Tropical cyclone impacts have also caused changes in demography with a reduction in coral recruitment in some areas (Mumby 1999, Malella and Crabbe 2009, Lugo and Gravois 2010), while in other areas the strong waves increased larval dispersal (Lugo and Gravois 2010). There was one report of tropical cyclones aiding in the eradication of an invasive marine species (Lapointe et al. 2006). Coral reef communities were also influenced by storms. Some articles mentioned that the surrounding fish and benthic invertebrate species richness were lost (Moran and Reaka-Kudla 1991, Adams 2001), while in other articles there was a change in fish species composition (Anonymous 1998, Rousseau et al. 2010). There were also reports of a loss of both corals and sponges (Bythell et al. 1993, Bythell et al. 2000). There was only one report of an ecosystem level response (regime shift). After the storm passed through a coral reef ecosystem, it disturbed the reef yielding a takeover by a macroalgae bed ecosystem (Steneck et al. 2019).

Mangrove forests. At an organismal level, the mangrove ecosystem responded with a change in condition; the storm resulted in trees losing their foliage (Graneck et al 2007). At the population level, there were reports of tree mortality and canopy loss (McCoy et al. 1996, Sherman et al. 2001, Milbrandt et al. 2006, Piou et al. 2006, Ross et al. 2006, Greenwood et al. 2007, Han et al. 2008, Zhang et al. 2008, Doyle et al. 2009, Whelan et al. 2009, Sharpe 2010, Barr et al. 2012, Fickert 2018, Sharpe 2010, Imbert 2018, Proffit et al. 2019, Rivera et al. 2019, Walcker et al. 2019, Zhang et al. 2019), this was also paired with some areas that were impacted losing genetic diversity (Bologna et al. 2019). One article reported a mass mortality of mangrove trees that occurred some years after the storm originally passed (Feller et al. 2015). It was also noticed that tree mortality would change the structure and species composition in mangrove forests (Roth 1992, Vogt et al. 2012, Baldwin et al. 2001 ,and Rogers 2019). Additionally, with the passing of large storms it was recorded that there was a reduction of invasive species (Vogt et al. 2012). There were also articles involving ecosystem level responses. Cahoon et al. (2003) and Smith et al. (2009) mention that after the passage of Hurricane Mitch, the surveyed area turned into mudflats. There were articles discussing changes to nutrient cycling involving the increase of litterfall, and nutrient pool alterations (Smith et al. 1994, Adame et al. 2013). Lastly there was one ecosystem level article that mentioned the change in how energy is cycled after a storm passing (Castaneda et al. 2010).

Salt Marshes. At the organismal level, seed germination in salt marsh grasses was affected by saltwater intrusion (Middleton 2009). Additionally, local bird behavior shifted by migrating to a different area of the marsh (Benscoter et al. 2019). On a population level, salt marshes experienced loss in marsh grass abundance and coverage (Chabreck and Palmisano 1973, O'Connell and Nyman 2011, Williams and Flanagan 2009, Williams and Liu 2019), but this loss was recovered in some areas (McKee and Cherry 2009, Williams and Delinger 2009, Williams and Delinger 2013, Gittman et al. 2014, Baustian et al. 2015). There were also records of loss in abundances of organisms that inhabit the salt marsh area. Population abundances of voles and mosquitoes changed due to the influence of tropical cyclones (Longenecker et al. 2018, Lucas et al. 2019). Salt marsh community level was affected with changes in plant communities (Courtemache et al. 1999, Piazza et al. 2009,

Else-Quirk 2016). A similar response was noticed with freshwater salt marshes in Louisiana (Neyland 2007). Not only was there a change in plant communities, but alterations in the diatom community was noted as well (Parsons 1998). Due to the strength of large storms, some areas of marsh were converted into open water from erosion (Jackson et al. 1993, Kahanna et al. 2017), or they were replaced with mudflats (Williams 2012).

Seagrass Meadows. A few areas of seagrass meadows experienced unusual synchronous spawning in response to a tropical cyclone passing, indicating an organismal level effect on phenology (van Tussenbroek et al. 2006). Population level effects included loss of seagrass cover (van Tussenbroek 1994, Carlson et al. 2010). Steward et al. (2006) mentioned that the meadows were reduced due to sediment burial. Macrophyte community compositions were influenced by tropical cyclone activity (van Tussenbroek et al. 2008, Cole et al. 2018, Congdon et al. 2019). Two of the reports for this ecosystem recorded an ecological regime shift of seagrass meadows that were later dominated by calcareous green algae (Guimaraes et al. 2003, Fourquaran and Rutten 2004).

DISCUSSION

I studied broad patterns in hurricane impacts on marine ecosystems based on a literature review. The 101 articles that were used in this study were separated into different categories regarding ecosystem type, storm intensity, and decades. The highest percentages recorded for storm intensities were the Atlantic major hurricanes (Categories 3, 4, and 5). This information suggests that the strongest storms are influencing marine ecosystems. This influence may escalate under global climate change given a predicted increase in the frequency of these most intense storms (Knutson et al. 2020). I did not however see a clear increase in reports of storms from 1970s to 2010s. In fact, reports decreased from the 2000s to 2010s. This result could be due to a time lag with the data available, as it is likely that not all storm impacts from the 2010s have been reported (published) yet.

I classified each biological organization level into more defined tropical cyclone responses. The largest category reported within the organismal level was changes in condition. With organisms being damaged from passing tropical cyclones, this would result

in energy going into healing instead of other functions, like reproduction (Lindsay 2010). Within the population level, abundance was the most common biological response reported. Often tropical cyclones affected abundances of foundational species (Knowlton et al. 1981, McCoy et al. 1996 ,Alvarez et al. 2009, Walcker et al. 2019). The destruction of foundational species could ultimately result in the reduction of ecosystem functionality (Ellison 2019). At the community level, changes to species richness/composition were reported the most in response to tropical cyclones. This could indicate that ecosystems lose diversity in response to tropical cyclones. This is unfortunate, as diversity keeps ecosystems healthy by boosting productivity. A loss in species can weaken the ecosystem's resilience (Mori et al. 2012). Regime shifts were revealed to be the most reported response for the ecosystem level. This observation indicates changes in broad dynamics in an ecosystem, creating internal feedbacks which can result in unknown impacts on ecosystem services to societies (Mollmann et al. 2015).

The contingency table analysis compared the distribution of biological responses across ecosystems, storm intensities, and decadal periods. From the data, population levels were the most common response reported, indicating that marine populations are at risk from tropical cyclone influence. Results reveal that all levels of biological organization can be influenced by storms. This is significant because it contributes to the understanding of ecosystem fragility, and conservation importance. Additionally, ecological regime shifts were not documented until after the 1990s, strengthening the argument that anthropogenic effects change the structure of ecosystems.

Referring to H1, the results indicate that all ecosystems can produce similar reported responses to tropical cyclone activity. Population level is the most prominent level of response throughout coral reefs, mangroves forests, salt marshes, and seagrass meadows. This prominence could act as an aid in conservation. When researching a resolution for one ecosystem it may also assist in the progression of another, giving scientific studies increased guidance. The rejection of H2 indicates that greater intensity storms (Categories 3, 4, and 5) have reported impacts on all levels of biological organization. This enforces the importance of studying interactions and relationships of coastal marine ecosystems since there is not a quantitative amount of knowledge of the various interconnections within those ecosystems. H3 indicates later decades do not have a reported influence at higher

biological levels of organization. This can be due to decadal shifts in climatic oscillations that complicate climate patterns. Climate oscillations like El Nino and La Nina, are seen to coincide with warm and cool weather events. These events may also help alternate the energy given to Atlantic tropical cyclones (Patricola et al. 2014). This finding reminds researchers that there are many aspects influencing tropical cyclones. Carefully reviewing information on these influences can help attain a greater understanding of this subject.

Due to the nature of this research, there are various aspects that could have contributed to bias in the data. One factor possibly contributing to bias is researching efforts changing. There is more literature concerning tropical cyclones influences on coastal marine ecosystems in recent decades. Scientists also surveyed damaged areas opportunistically, resulting in sites not being selected randomly (Highsmith et al. 1980, Bythell et al. 1993, van Tussenbroek et al. 2006, Walcker et al. 2019). Reporting bias may also be a contributing factor. Ecologists may be most interested to study population-level effects. Another factor is scientists may gravitate towards studying areas with higher population density. Research opportunities are limited, so damaged areas with a low population density might be overlooked. Additionally, Atlantic major hurricanes could be more documented because they produce the strongest wind and waves, attracting the attention of researchers. This may cause lower intensity storm categories (Tropical storms, Categories 1 and 2) to be understudied because they are less obvious events. A small number of articles mentioned islands or natural structures protecting coastal marine ecosystems from storms. They create a barrier minimizing damage brought on from tropical cyclone-generated waves (Piou et al. 2006, Elsey-Quirk 2016) and may alter the relative impact of storms of various intensities. Finally, as mentioned above, research conducted in the 2010s may not yet be published, creating bias towards earlier studies. Overall the research in this study could be improved with a meta-analysis that looks at standardized effect sizes in biological responses across ecosystems.

Climate change will contribute to the severity of tropical cyclones. Increased carbon emissions due to anthropogenic activity will result in increased strong storm activity (Knutson et al. 2020). Public education of tropical cyclone damaging effects is a way to prevent the destruction of coastal marine ecosystems. Americans believe that global warming is a serious issue, but many participate in a “wait and see” tactic where there is

little involvement until serious damage by anthropogenic activities has been done (Sterman and Sweeney 2002). Providing accurate and cohesive information to the public is the best way to organize public thinking in the direction of preservation. It is also critical that the public applies pressure on policy makers to create and follow regulations helping with increased greenhouse gas emissions (Huisinigh et al. 2012). Huisinigh et al. (2012) states that many developed countries have the largest contributions to carbon emissions and are the ones that need to commit to cutting down the carbon output. A new source of primary energy is needed. Currently fossil fuels are the most used, but the excessive use is causing changes to tropical cyclones.

The socioeconomic aspect of increased hurricane activity is important to consider, as these storms influence people living in the path of natural disasters. An individual's racial group and socioeconomic status gives insight into who will suffer most as a result of natural disasters (Groen and Polvika 2010). Groen and Polvika (2010) state that one's social standing can additionally determine how easily that individual can recover from natural disasters. When Hurricane Katrina hit in 2005 extreme-poverty residential homes took the brunt of the storm, and many residents were black homeowners (Fussell et al. 2010). Human equality and ecosystem integrity are intimately linked, as socioeconomically vulnerable communities also often rely on marine resources for food and materials; and these resources are threatened by hurricane activity (Thomas et al. 2019, Medina et al. 2020).

The purpose of this study was to create a bridge of knowledge between tropical cyclones and coastal marine ecosystems. Due to the increase of carbon emissions from anthropogenic activities, there is growing concern on how this will influence the intensity of storms, which will impact local ecosystems. I found that all four ecosystems (mangroves, coral reefs, salt marshes, and seagrass meadows) all produce similar reported responses in biological organization (organismal, population, community, and ecosystem). I also found that greater intensity storms would have profound impacts at all levels of biological organization. Lastly, it is concluded that more recent decades do not appear to have had effects at a higher biological level of organization. This research brings more attention to the fact that there needs to be a deeper understanding of the consequences that can result from tropical cyclone damage. Not only would these consequences negatively

affect the marine individuals of these ecosystems, but also humans whose livelihood depends on them.

Table 1. Levels of biological organization affected by tropical cyclones.

Level of Organization	Response	Definition	Example
Organism	Growth	Increase or decrease in growth rate	Plate corals increased growth rate when a storm removed sediment from a reef (Hillis and Bythell 1998)
	Condition	Superficial (non-lethal) damage to body	A coral colony was abraded by storm waves (Highsmith et al 1980)
	Behavior	Change in activity level or type of activity	None found
	Phenology	Change in reproductive timing	Synchrony in macroalgal spawning occurred following a hurricane (van Tussenbroek et al 2006)
	Physiology	Change in the normal functions	Lower PH from storms reduces calcification potential and advances acidification stress (Manzello et al 2013)
Population	Abundance	Change in the quantity of individuals of a single species in a single location	The number of <i>Acropora</i> sp. colonies decreased due to hurricane mortality (Fong and Lirman 1994)
	Demography	Change in the age or size structure of a single species in a single location	Coral recruits (juveniles) were rarer following a hurricane (Mumby 1999)
	Genetics	Change in genetic diversity of a population	Lowered genetic diversity in impacted areas (Bologna et al. 2019)
Community	Species richness or composition	The number of total species or the relative abundances of species changed following a storm	Hurricanes affected macrophyte community structure (Cole et al. 2018)
	Species Interactions	Change in competition, consumption, symbiosis, or commensalism	Even with the death of herbivore <i>Diadema antillarum</i> macroalgae was kept in check due to grazing fish populations (Bythell et al. 2000)
Ecosystem	Localized ecosystem regime shift	The dominant habitat-forming (foundational) species changes in the location of storm impact. The change is abrupt and persistent (recovery not expected within one generation of foundational species) and the function of the ecosystem changes	Regime shift from mangrove forest to mudflat (Cahoon et al. 2003) or regime shift from coral dominated reef to macroalgal dominated reef (Steneck et al. 2019)
	Energy Cycling	Change in how energy is placed throughout a system	Change in habitat function due to raised soil elevation, sediment deposition, and higher nutrient pools (Castaneda et al. 2010)
	Nutrient Cycling	Change in how nutrients is placed throughout a system	Nutrient pools changed encouraging the development of an algal mat and phytoplankton bloom (Smith et al. 1994)

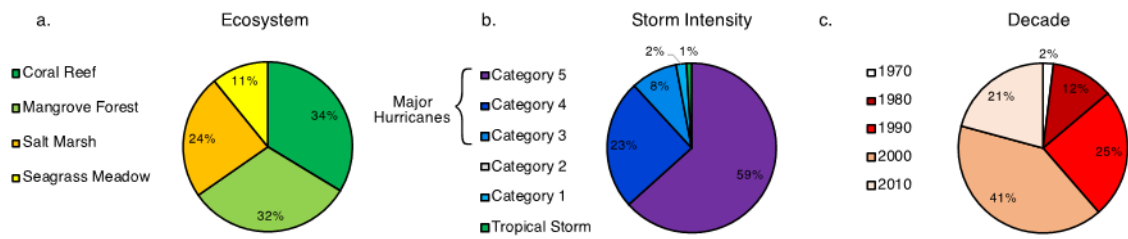


Figure 1. Here three pie charts show out of the total number of articles used in this study, the percentage that documented storm impacts among four different types of ecosystems (a) six different storm categories (b) and five decades (c).

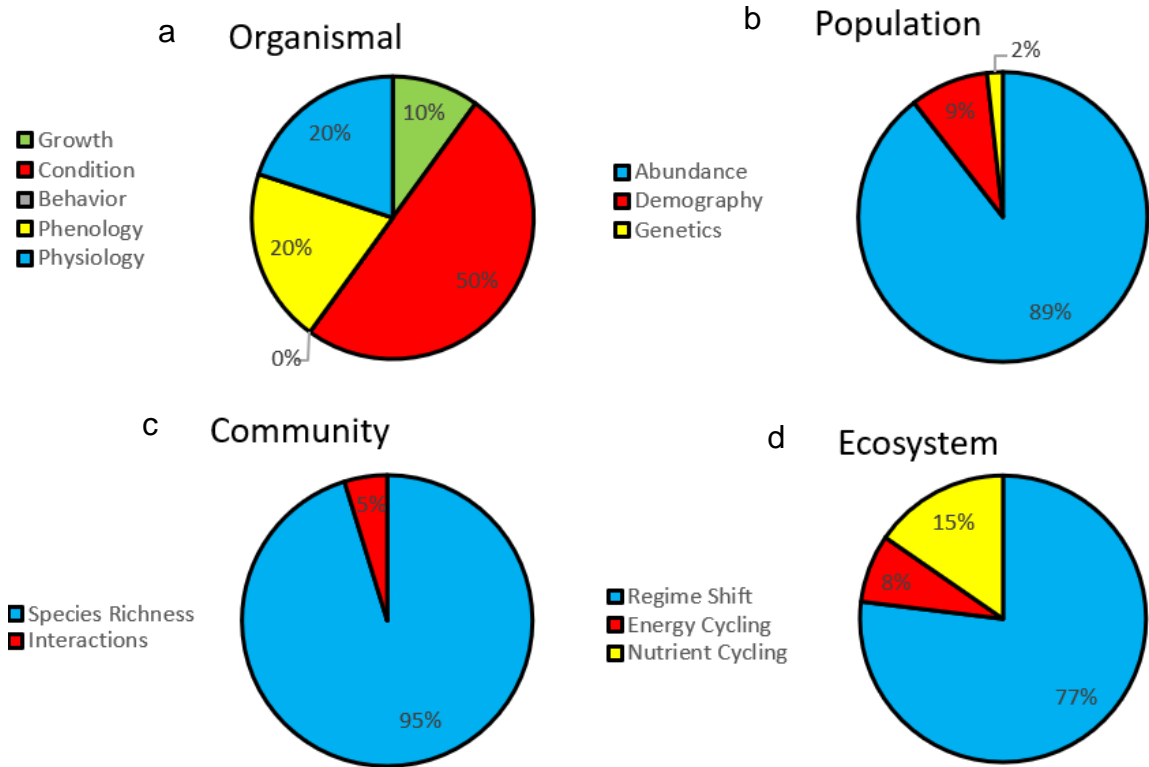


Figure 2. Here four pie charts show out of the total number of articles used in this study, the percentage that documented biological responses at each level of biological organization including (a) organismal, (b) population, (c) community, and (d) ecosystem.

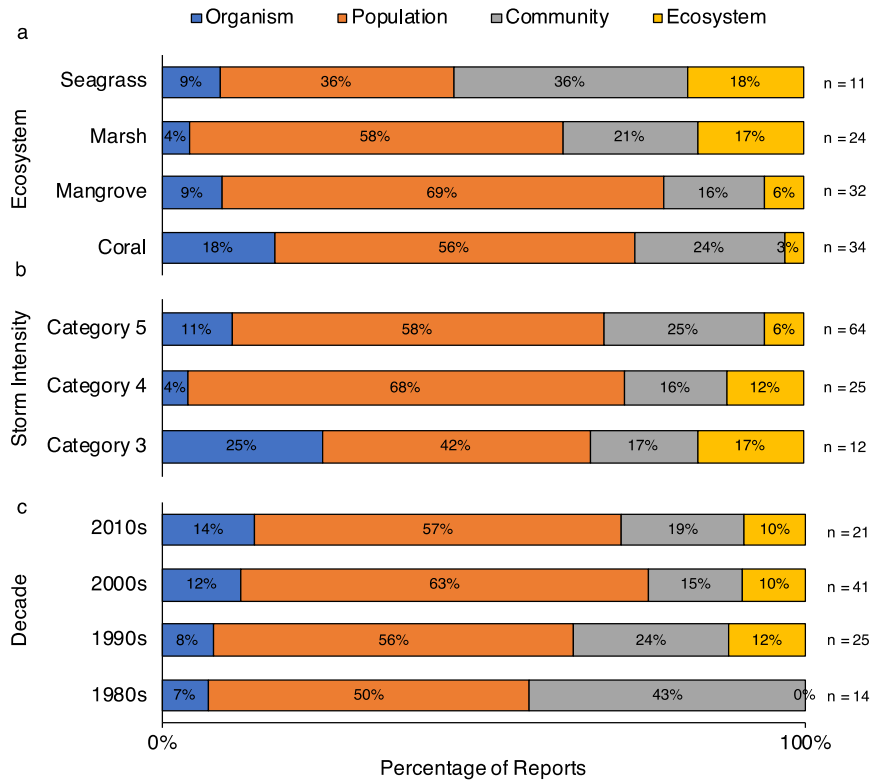


Figure 3. This figure shows how the different ecological responses present themselves in the total number of scholarly articles. It is broken down into the different types of ecosystems (a), different storm intensities (b), and different decades (c). n = the number of articles that apply to that specific grouping.

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Appendix A

Table A1. Levels of biological organization references

Level of Biological Organization	Response	References
Organism	Growth	Hillis and Bythell 1998
	Condition	Highsmith et al. 1980, Fong and Lirman 1995, Manzello et al 2007, Reardon 2018
	Behavior	None found
	Phenology	van Tussenbroek et al. 2006, Middleton 2009
	Physiology	Granek et al. 2007, Manzello et al. 2013
Population	Abundance	Chabreck and Palmisano 1973, Knowlton et al. 1981, Woodley et al. 1981, Fenner 1991, Fong and Lirman 1994, van Tussenbroek 1994, Wulff 1995, McCoy et al. 1996, Lirman and Fong 1997, Mumby 1999 Adams and Ebersole 2004, Alvarez and Gil 2006, Milbrandt et al. 2006, Piou et al. 2006, Proffit et al. 2006, Ross et al. 2006, Steward et al. 2006, Gleason et al 2007, Greenwood et al. 2007, Zhang et al. 2008, Williams and Flanagan 2009 Alvarez et al. 2009, Malella and Crabbe 2009, Doyle et al. 2009, Whelan et al. 2009, McKee and Cherry 2009, Lugo and Gravois 2010 Carlson et al. 2010, O'Connell and Nyman 2011, Schmidt et al. 2011, Barr et al. 2012, Williams and Denlinger 2013, Gittman et al. 2014, Feller et al. 2015, Baustian et al. 2015, Rangoonwala et al. 2015, Longenecker et al. 2018, Fickert 2018, Han et al. 2018, Imbert 2018, Benschoter et al. 2019, Edmunds 2019, Edmunds et al 2019, Rivera et al. 2019, Wright et al. 2019, Walcker et al. 2019, Zhang et al. 2019, Lucas et al. 2019, Williams and Liu 2019
	Demography	Sherman et al. 2001, Lapointe et al. 2006, Sharpe 2010
	Genetics	Bologna et al. 2019
Community	Species richness or composition	Wilkinson and Cheshire 1988, Moran and Reaka-Kudla 1991, Rogers et al. 1991, Roth 1992 Bythell et al. 1993, Anonymous 1998, Parsons 1998, Courtemanche et al. 1999, Baldwin et al. 2001, Adams 2001, Neyland 2007, van Tussenbroek et al. 2008, Piazza et al. 2009, Rousseau et al. 2010, Vogt et al. 2012, Elsey-Quirk 2016, Cole et al. 2018, Rogers 2019, Congdon et al. 2019, Cruz Perez 2019
	Interactions	Bythell et al. 2000
Ecosystem	Localized ecosystem regime shift	Jackson et al. 1993, Cahoon et al. 2003, Fourqurean and Rutten 2004, Smith et al. 2009, Williams 2012, Guimaraes et al. 2013, Kahanna et al. 2017, Campbell et al. 2017, Deis et al. 2019, Steneck et al. 2019
	Energy Cycling	Castaneda et al 2010
	Nutrient Cycling	Smith et al. 1994, Adame et al 2013

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