Patterns of Invasive Species in Tropical Marine Environments:

Biogeography, Taxonomy, and Life-History Characteristics

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Abstract

Marine invasive species present several ecological, economic, and social problems in practically every region of the world. Tropical systems retain some of the highest marine biodiversity in the world, and provide many ecosystem services such as coastal protection, nutrient cycling, and a great abundance of edible fish. Study of tropical marine invasive species is remarkably limited, but essential to informing management decisions to maintain biodiversity and ecosystem functioning of these tropical systems. The advent of frequent, global transportation contributes most to the spread and establishment of exotic marine species. This study compiles information on 133 tropical marine invaders and includes trends seen in biogeography, invasion pathways, taxonomy, and life history traits such as reproduction and trophic functions. Understanding commonalities among marine invasives highlights which species characteristics contribute most to invasion success and potential mitigation strategies. The information presented here is most useful at the regional level, where comparisons with native species and communities are possible and meaningful. Hawaii and Florida, the two most-invaded tropical marine regions in the world, are presented as case studies of how marine invasive species can affect management.

Keywords

Marine invasive species, invasion susceptibility, Hawaii, Florida, life-history traits

Introduction

Historically, species invasions have displaced competitors and other interacting species, disrupted ecosystems, and adversely affected commercial economies and cultures (Pimentel et al. 2005, Kennedy et al 2002). A non-native species may affect native community structure and ecosystem functioning in a variety of ways, depending on environmental characteristics, interactions with other species, and particular life history traits (Stachowicz and Tilman 2005). This warrants an understanding of the factors that contribute to invasion success, in order to prevent the unwanted negative consequences seen in some species invasions.

Marine invasions in particular, have been understudied, comprising only 13% of invasive species studies (Bruno et al. 2005). Furthermore, studies of species invasion in tropical marine environments are a small fraction of the total marine studies of species invasions (Coles and Eldredge 2002, Grosholz 2002). Yet, tropical systems harbor some of the world's most diverse environments, and provide several important ecosystem functions and services, including nutrient cycling, coastal protection, and an abundance of organisms for fisheries.

Our current understanding of tropical marine invasions largely derives from anecdotal observations, rather than comprehensive analysis of empirical data. Analyzing patterns of life history traits and environmental characteristics in invaded tropical marine communities will inform effective management practices to cope with the species invasion. Here I ask which reproductive, trophic, and taxonomic characteristics promote invasion success of nonindigenous species. This, when combined with biogeographic information and invasion pathways can inform management on a regional scale.

Environmental Characteristics That Foster Invasion

Even the most well-adapted and competent exotic species may not become established due to environmental factors (Gaines, pers. comm.). There are several vectors that make an environment more susceptible to invasion. The Diversity-Resistance Hypothesis suggests that regions with high biodiversity are resistant to species invasion, due to decreased availability of open niches (Kennedy et al. 2002). Native species in a more diverse system would better utilize the space and resources present, preventing the establishment of a nonindigenous species (Stachowicz and Tilman 2005). However, a less diverse community may have several open niches that a nonindigenous species could potentially occupy. Stachowicz et al. (1999) demonstrated support for this hypothesis in an experiment in a New England coastal ecosystem, in which species richness of sessile invertebrates in experimental communities decreased invasion success of a nonindigenous snail. Byers and Noonburg (2003) used theoretical models to show that invasion resistance increases with native species diversity, providing further support for the Diversity-Resistance Hypothesis.

In conjunction with biodiversity, anthropogenic disturbance is another prominent determinant of invasion success across ecosystem types. Anthropogenic disturbance may consist of conversion or destruction of habitat, the introduction of parasites and disease, or overexploitation of resources, among other impacts. Disturbance creates open niches that exotic species can occupy (Byers 2002). Moreover, in the face of disturbance, local adaptations of native species may become less viable, potentially making them inferior competitors to nonindigenous species (Byers 2002). Ports and harbors, for instance, are disproportionately susceptible to invasion, due to constant anthropogenic disturbance. Not only do pollution, dredging, artificial structures, and other anthropogenic stressors open niches for nonindigenous establishment, but there is a constant flux of ships, many of which harbor foreign species (Byers 2002).

In an analogous fashion, parasites and disease are often introduced with species that are either carriers or have resistance to infection (Grosholz 2002). The introduced parasites and disease can have a devastating effect on native species that lack resistance, giving a competitive advantage to the exotic species.

Geographically isolated regions are particularly susceptible to invasion, due in part to high rates of endemism (Reaser et al. 2007, Sax et al. 2005). These regions with high rates of endemism may support specialist communities, which are also particularly susceptible to species invasion (Byers and Noonburg 2003). Organisms that require specific resources for survival may be out-competed by an exotic species that utilizes the same resource. A generalist exotic species may use that resource that the specialist requires, decreasing resource availability for the native specialist. This leads to decreased fitness of the native species and possible extirpation. The Hawaiian Islands, for example, are geographically isolated in the Central Pacific and are particularly susceptible to invasion, where 7% of all marine species present are invasive (Allison et al. 1995).

In some invasions, the nonindigenous species lack predators which allow them to expand their population rapidly (Bruno et al. 2005, Ricklefs et al. 2005). In some instances, potential native predators are naïve to the nonindigenous species, preventing biological control and effective predation of the exotics. This issue is compounded if the nonindigenous species has allelopathic (chemical) defenses that a predator in its former environment had evolved resistance to. For example, the Red Lionfish (*Pterois volitans*) lacks predators in its invaded environment, the Caribbean, whereas in its native range—the Indo-Pacific—its population is controlled by a single predator, the Blue Cornetfish (*Fistularia commersonii*), that co-evolved resistance to the lionfish's venomous spines (Meister et al. 2005).

Invasion Pathways

Marine systems are particularly susceptible to invasion, particularly since the advent of global travel and shipping (Bax et al. 2003). Shipping is the most common invasion pathway, carrying invasive species in ballast or as fouling organisms and has contributed to 69% of all marine introductions (Molnar et al. 2008). Ports and harbors tend to be hotspots for invasive species due to heavy ship traffic and these locations are often preferentially studied when compared with other marine environments (Hewitt et al. 2002).

Aquaculture is the second largest contributor to marine species invasions. 41% of marine invasive species were introduced from aquaculture practices when individuals escape or are released (Molnar et al. 2008). Exotic marine fishes or invertebrates will often be introduced to a region via aquaculture practices as an economical investment. Hawaii was subject to this in the 1950s, when several fishes were introduced to the islands for food and sport fishing (Randall 1987). Though many were unsuccessful, 13 species established breeding populations, four of which had substantial negative economic and ecological effects (Randall 1987).

Molnar et al. (2008) report that 17% of marine invasive species occur via the construction of canals. Canals typically connect two biogeographically distinct bodies of water, creating the high potential for species interchanges. The Mediterranean Sea maintains many international trade routes and is also connected to the biologically diverse Red Sea via the Suez Canal (Galil 2000). Since the construction of the Suez Canal, there have been many introductions of species from the Red Sea into the Mediterranean, though the opposite is rarely the case due to the substantial differences in regional biodiversity (Galil 2000; Galil 2008). Exchange of species also occurred with the establishment of the Panama Canal, which enabled passage between the Atlantic and Pacific Oceans (Galil et al. 2007).

Other means of species introduction include aquarium trade, intentional and unintentional releases, live-fish trade, and natural range expansion. On a global scale, these means of introduction are not as common, but may be prevalent at the local or regional scale. For example, the aquarium trade contributes to only 6% of global marine invasions, but is particularly common in Florida, where aquarium fishes are kept and traded frequently (Molnar et al. 2008, USGS-NAS 2009). Given all the pathways of invasion, management should focus on areas that are most affected by shipping, aquaculture practices, or canal construction, but also take regional variation in ecology and economic activity into account.

Common Characteristics of Invasive Species

Hutchings et al. (2002) describe an invasive species as widespread, tolerant, generalist, competitive, and pioneering. These characteristics allow an invasive species to become biologically dominant in a region, often, but not always, with adverse effects (Sax et al. 2005). Species that can tolerate environmental extremes maintain a certain versatility and can occupy a broad range of environments. The red algae, *Gracilaria salicornia,* for example can tolerate a wide range of temperatures and salinities, contributing to its invasion success in Hawaii (GISD 2007).

Invasive species often originate from biologically diverse environments, which can render them with highly evolved, superior adaptations (Stachowicz and Tilman 2005). Such adaptations may include allelopathic or physical defenses, such as the venomous spines of two widely-established marine invasives: the Red Lionfish (*Pterois volitans*) and the Crown-of-Thorns Sea Star (*Acanthaster planci*) (Stachowicz and Tilman 2005; GISD 2006; GISD 2007).

Adaptations such as resistance to parasites and disease or better utilization of a given resources may contribute to competitive dominance. This is exemplified in the exotic snail, *Batillaria attramentaria*, in San Francisco Bay, which out-competes the native snail, *Cerithidea californica*, by using resources more efficiently than the native species and developing resistance to parasitic infection (Byers, 2000; Byers and Goldwasser 2001). Generalist species, such as filter-feeders and plants, also have a high potential to become invasive, due to their lack of specific resource needs (Byers and Noonburg 2003).

The most successful invaders tend to have rapid growth rates, mature quickly, and produce many viable offspring (Ricklefs 2005). These characteristics contribute to rapid colonization and establishment of an invasive species, particularly in disturbed environments. Despite these common themes, it is important to note that not every nonindigenous species becomes widely established and invasive. For example, the Allee Effect may prevent the production of viable offspring, or water currents may carry offspring into inhospitable environments (Stephens and Sutherland 1999).

Tropical Marine Environments: A Lack of Information

When compared to terrestrial species invasions, relatively little is known about marine invasions, particularly in tropical environments (Grosholz, 2002; Coles and Eldredge 2002). Without an understanding of native biodiversity in a particular region, it is inherently difficult to make inferences as to which species are exotic. This can largely be attributed to the information gaps in tropical marine biodiversity. For example, the Ocean Biogeographic Information System (OBIS) provides regional marine biodiversity data across the globe, but lacks distribution data for 80% of the 230,000 positively identified marine species (Grassle et al. 2005). Temperate ocean systems in the northern hemisphere are preferentially included in OBIS, which contributes to inconsistency of biodiversity and invasive species estimates (Grassle et al. 2005). For example, the Mediterranean Sea and the San Francisco Bay tend to be heavily studied for marine invasive species, as they are environments that are particularly susceptible to species invasion (Galil 2000; Cohen and Carlton 1998). A more comprehensive understanding of tropical marine biodiversity across the globe would provide more accurate information with regard to species invasions.

In environments where native diversity is not well known, species which cannot be identified as native or exotic are deemed cryptogenic (after Carlton 1996). In such situations, life histories, written historical records, coevolution, and interactions with other species are used to infer whether a species is indigenous or not (Carlton 1996).

Until the study by Molnar et al. (2008), no comprehensive analysis of marine invasions on a global scale was available. The researchers compiled biogeographic information on 329 invasive species, reporting the ecological impact, invasion pathway, and taxonomic information for each species. In their study, Molnar and colleagues assessed invasion pathway, taxonomic distribution, ecological impact, and biogeographic extent of marine invasive species. Their research is paramount to a global and regional understanding of marine invasions, and provides a baseline that further studies may build upon.

Many studies of life history traits of invasive species are largely observational, meagerly supported by empirical evidence. For my thesis research, I addressed this issue and examined the life-history traits of tropical marine invasive species reported in the database by Molnar et al. (2008) more thoroughly. Reproduction, trophic level, habitat, diet, and size, among other life history traits were analyzed for 133 tropical marine invasive species. I also investigated which biogeographic regions have the highest invasion rates, and the environmental characteristics that contribute to these regions' invasibility. Geographic origins of tropical marine invasive species are also examined, in conjunction with invasion pathways.

Methods

Molnar et al (2008) provide the first comprehensive list of marine invasive species and their reported ecological effects. A database of these species is publicly available at http://conserveonline.org/workspaces/global.invasive.assessment. Species are organized biogeographically into ecoregions, provinces, and realms. The database provided information regarding taxonomy, origin of species, invasion pathway, geographic distribution, and brief descriptions of ecological impacts. I expanded upon this dataset by collecting information on the life history traits of tropical marine invasive species specifically. Life history data includes diet, trophic level, size, sexual characteristics, population growth potential, frequency of reproduction, and the primary reproductive strategy which contributed most to the invasive species' success. I then focus in on two of the world's most highly invaded tropical marine ecoregions: Hawaii and Florida.

Biogeographic Data

Origins of the marine invasive species are listed, but not confined to ecoregions and may cover geographic expanses as large as the Indo-Pacific. Invasion pathways are described as the means by which the invasive species were introduced to exotic environments. These pathways are as follows: hull-fouling, ballast, aquaculture, natural spread, animal trade, canals, biocontrol, the bait industry, and climate change.

The total number of invasive species was listed for each tropical ecoregion. This particular aspect provides insight as to which ecoregions are most affected by invasive species. To account for bias, these most-affected ecoregions were compared to the number of studies for each ecoregion.

From the data, I compiled a list of ecoregions with the highest number of invasive species recorded. I then compare the invisibility of these regions to the number of studies done on marine invasive species in these regions. Some of the regions (e.g. Greater Antilles, Southern Caribbean, and Southwestern Caribbean) have distinct names and were simplified (e.g. "Caribbean") for the regional search. Only the number of invasive species from the most invaded of these combined regions was included. This serves as a conservative estimate of the invasibility of these regions. Each region was searched in the Web of Science from the years 1973 to 2010. Within these results, topics were refined to ecology, marine and freshwater biology, environmental sciences, environmental studies, zoology, evolutionary biology, fisheries, water resources, biodiversity conservation, biology, and plant sciences. The results were further refined by the keyword "marine" and again by the words "invasive", "alien", "exotic", "nonnative", or "introduced". A Spearman Rank Correlation was used, based on the number of invasive species and the number of articles found on each region.

Life History Data

The taxonomic distribution of tropical marine invasives was determined by designating each species as one of the following taxa: algae, annelid, arthropod, ascidian, bryozoan, cnidarian, echinoderm, fish, mollusk, porifera (sponges), reptile, or tunicate.

Diet was categorized by major prey items of each species (e.g. generalist carnivore or omnivore) or by means of feeding (e.g. filter feeder or photosynthetic autotroph). Trophic levels for each species are closely related to their diets. For example, an herbivore only consumes plants and would always have a trophic level of 2. For species with a wider range of prey items, trophic levels vary. FishBase and SeaLifeBase provided trophic level estimates. For many species, and for the remainders, I estimated trophic level based on published diet information. For example, filter feeders were assigned an estimated trophic level of 2.5, based on the assumption that they consume similar amounts of phytoplankton and zooplankton.

Sexual characteristics describe a species as dioecious (has two separate sexes), monoecious (has only one sex) or hermaphroditic. Protandrous and protygynous hermaphrodites were limited to fish species and included in the broader category of "hermaphroditic".

Frequency of reproduction was determined by whether a species could reproduce continuously throughout the year or with seasonal peaks. In some occurrences, the invasive species could reproduce asexually and sexually, where sexual reproduction would exhibit a seasonal peak and asexual reproduction could occur continuously. In such cases, both "seasonal" and "continuous" are listed.

Population growth potential reflects characteristics of r-selected and K-selected individuals. Thus, "rapid" growth potential would be typical of r-selected species where K-selected individuals exhibit “slow” growth. “Moderate” species cannot be clearly classified as either r-selected or K-selected. Population growth potential was influenced by fecundity, age of reproduction, and individual growth rates.

Primary reproductive strategies are listed as the invasive species’ predominant reproductive mode. These modes include external fertilization, internal fertilization, fragmentation, regeneration, binary fission, heterogamy, and asexual reproduction. If the organism was capable of both asexual and sexual reproduction with neither appearing dominant, “A/S” is listed.

Results

Biogeography and Invasive Pathways

To better understand environmental characteristics that contribute to marine invasions, a closer look is necessary at which regions are most invaded and regions where the invasive species originate. This gives insight into drivers of invasion as well as characteristics that make an environment susceptible. Invasion pathways also provide information regarding the transport of species and potential areas where management can be effectively employed.

The Hawaiian Islands is the world’s most invaded region for marine species, serving as a host to 74 (56%) of the 133 marine invasive species in this study (Fig. 1). The second-most invaded region is Florida, with 44 (33%) marine invasive species. All other ecoregions had 14 marine invasives or less. The Caribbean is also particularly susceptible to invasion. Of the Caribbean’s several ecoregions, the Greater Antilles, Southern Caribbean, and Southwest Caribbean are among the top five most highly invaded environments, with 14, 14, and 12 marine invasives respectively. Other notable invaded ecoregions include the Southern Gulf of Mexico, South-Central Great Barrier Reef, Northern Great Barrier Reef, Southern China, and the South Kuroshio Current.

A Spearman Rank Correlation revealed that there was no significant correlation ($p = 0.344$) between the number of invasive species in each region and number of related studies for that same region. This result suggests that the ranking of most invaded regions is not due to differential sampling effort.

The Indo-Pacific was the origin for the distinctive majority (19%) of the marine invasive species studied (Fig. 2). The Western Pacific and the Eastern Pacific were the origin for 7% and 8%, respectively. The Northwest Atlantic, Northeast Atlantic, Caribbean, and Western Atlantic contributed to 7%, 10%, 11%, and 12% respectively. The Mediterranean was also a notable area of origin, representing 12% of the marine invasive species studied.

Global shipping appears to be the largest culprit for the transport and spread of invasive species (Fig. 3). Hull-fouling and ballast contribute to over 50% of all the invasions observed of the 133 tropical marine invasives in this study. Intentional and unintentional releases though aquaculture are the cause of 17% of all tropical marine invasions. Natural spread of existing population contributes to a further 15% of marine invasions. The remaining 18% invasion pathways can be attributed to (in descending order) the aquarium and animal trade, canals, biocontrols, the bait industry, and climate change.

Patterns in Invasive Species Characteristics

Among the 133 tropical marine invasive species studied, arthropods, mollusks, and algae are most common (Fig. 4). Of these marine invasive species, there are twelve trophic guilds: filter feeder, photosynthetic autotroph, generalist carnivore, deposit feeder, planktivore, herbivore, scavenger, omnivore, piscivore, and specialist diets that consist of only bryozoans, arthropods, or wood (Fig. 5). The most common trophic guild was filter feeders (43%), followed by photosynthetic autotrophs (16%), generalist carnivores (11%), and deposit feeders (8%). All other trophic guilds comprised 5% of less of the invasive species studied.

Mean trophic level often is closely related to the trophic guilds. For example, the invasive ascidians, bryozoans, annelids, mollusks, tunicates, and sponges all had an approximated mean trophic level of 2.5. This is largely because their diets consist of relatively similar amounts of zooplankton and phytoplankton. The photosynthetic autotrophs (plants and algae) had a mean trophic level of 1. Arthropods, cnidarians, fishes, and reptiles are more variable, having mean trophic levels of 2.8, 2.9, 3.3, and 4.5 respectively.

Forty percent of the invasive species studied used external fertilization as their primary reproductive strategy, followed by 23% with internal fertilization (Fig. 6). Nineteen percent of the species studied used a combination of asexual and sexual reproduction. Fragmentation was the primary reproductive mode for 10.5% of all species, though this was most common in algae and sponges. Heterogamy, regeneration, binary fission, and other forms of asexual reproduction contributed to less than 10% of all primary reproductive strategies.

The majority (50%) of the organisms were dioecious or species that had two separate sexes throughout their life history (Fig. 7). Monoecious species comprised 10.5% of all invasive species studied, though these were all algae. Thirty-six percent displayed some form (protandrous, protogynous) of hermaphroditism. The sexual characteristics of the remaining 3% were either unstudied or unknown.

Time of reproduction was also researched and categorized as continuous or with seasonal peaks (Fig. 8). Species that reproduced seasonally represented 44% of the studied species, whereas species that were capable of reproducing throughout the year represented 39%. There were five species (4%) with multiple reproductive strategies: they reproduce year-round asexually but show seasonal peaks in sexual reproduction. It is important to note that the timing of reproduction was unstudied or unknown for 19% of the invasive species listed.

Individual growth rates, fecundity, reproductive strategies, and time of reproduction were all taken into consideration when analyzing potential for population growth (Fig. 9). Because population growth is highly variable between taxa, population growth rate is relative to taxonomically similar, native species. Over 57% of all the invasive species showed a high potential for rapid population growth, where moderate and slow population growth consisted of 10% and 3% respectively. About 5% displayed variable population growth, often dependent on environmental factors. There was not enough data to discern the potential for population growth for 25% of the invasive species studied.

Discussion

Biogeography and Invasive Pathways

Global trends of tropical marine invasions can give insight into the underlying causes for invasion success. The Spearman Rank Correlation revealed that no significant correlation existed between the number of studies of each ecoregion and the number of invasive species listed there, eliminating sampling bias. Thus, differences between ecoregions can be attributed to environmental and/or anthropogenic factors. The situations in Hawaii, Florida, and the Caribbean highlight several environmental factors that contribute to a regions susceptibility to invasion.

I hypothesize that the extensive tourism development and the construction of ports and harbors Hawaii, Florida, and the Caribbean may create open niches, which nonindigenous species can then occupy. Although natural disturbance may also open new niches and weaken community structure, such natural events (e.g. hurricanes) are common across all tropical sites studied. However, experimental evidence is necessary to verify differences of natural and anthropogenic disturbance on invasion success in these regions.

Differences in biodiversity may also contribute to the variability of invasion success across ecoregions. As the Diversity-Resistance Hypothesis attests, regions with greater biodiversity are more resistant to invasion due to the fewer vacant niches that nonindigenous species may occupy (Kennedy et al. 2002). Hawaii, the most-invaded tropical ecoregion, has relatively fewer marine species than other tropical ecoregions due in part to geographic isolation (Reaser et al. 2007, Sax et al. 2005). Florida and the Caribbean, although not geographically isolated, maintain lower species diversity than ecoregions in the Indo-Pacific (Gray 1997). There are several ecoregions in the Indo-Pacific that have far fewer invasive species, due perhaps in part, to higher species richness and thus are of lesser concern for invasive species prevention.

A closer look of the 133 marine invasive species studied shows that over 25% originated in the Western Pacific or Indo-Pacific, the world's most species rich marine areas. Although not conclusive, this provides support that a higher percentage of species originate from species-rich environments and become established in less diverse regions. Species from diverse regions of the world are likely to have more highly evolved methods of utilizing resources and defense mechanisms, often giving exotic species a competitive edge (Stachowicz and Tilman 2005).

The species studied are introduced to new environments most commonly by hull-fouling and ballast (Molnar et al. 2008). Global shipping is the primary culprit and can be difficult to regulate and enforce (Molnar et al. 2008, O'Shea and Cangelosi 1996). Although regulations and enforcement occur at the local and regional level (discussed later), international mandates may help ameliorate the issue. Often, trans-oceanic ship load and unload ballast at ports during its voyage (O'Shea and Cangelosi 1996). This causes a direct exchange of seawater and associated coastal and intertidal species in comparable environments. If these ships were required to load and unload ballast while in open-water areas away from coastlines, it could reduce the number of introduced nonindigenous species that could survive successfully in ports. Alternatively, the ballast water could be filtered or treated prior to unloading. The use of excessive ultraviolet light may prove useful to sterilize ballast water prior to unloading. Chemical treatment of ballast water is not advisable, unless there are absolutely no negative effects on the ambient environment.

Hull-fouling regulations may be more difficult to employ and enforce. Currently, anti-fouling paints are commonly used on ship hulls to reduce drag and transportation of invasive species (Drake and Lodge 2007). While technological advances with these paints could further reduce the number of introduced species, hulls can be manually or mechanically cleaned while outside coastal waters, prior to entering a port. This would limit the number of introduced species to ports, but may not be realistic or feasible. Regions such as Hawaii, with particularly high rates of introduction from ballast and hull-fouling, should be especially strict with regulation and enforcement. Biogeographic information regarding invasive species is important to understanding how humans facilitate the transport of species and where regulations may need to be improved.

Patterns in Invasive Species Characteristics

Organisms that are typically found in ballast or on ship hulls are generally benthic colonial invertebrate or algal species. Many benthic colonial invertebrates rely on filter feeding as their primary feeding mode. The diet requirements for these organisms are exceptionally general, requiring only plankton in the ambient water. Algae require only sunlight for photosynthesis, an arguably common resource in the tropics. Generalist carnivores and deposit feeders also lack specific diet requirements and are two of the most common trophic guilds among invasive species. Invasive species with specialist diets do exist, though species with generalist diets are far more common.

As the most common functional group, filter feeders are a primary concern for management. If they become too numerous they alter community structure and decrease the abundance of commercially valuable crustaceans and fish with bipartite life cycles (GISD 2006). A management focus on ballast and hull-fouling may reduce further introductions of these organisms.

The mean trophic level of marine invasive species for each ecoregion can give insight as to whether the invasive species present have top-down or bottom-up effects. If the mean trophic level of invasive species in a region is 2.5 or less, herbivores and filter feeders may have more visible bottom-up effects. For example, the dominating presence of algal species could mean that invaded areas are affected by eutrophication. Alternatively, a low mean trophic level occurs when filter feeders out-compete other species in an ecosystem and can cause depletion of commercially and ecologically important plankton. On the other hand a region that has a mean trophic level of 3.0 may imply that predators and generalist carnivores are contributing more top-down effects on the ecosystem.

The most common reproductive strategy for the marine invasive species studied was external fertilization, a reproductive method utilized by several taxa: ascidians, annelids, arthropods, echinoderms, mollusks, tunicates, and fishes. External fertilization, or broadcast spawning, is common among sea life due to the ease of disseminating gametes through the water column. However, this reproductive strategy is only efficient if there are enough individuals in the proximity to limit the Allee Effect (Stephens and Sutherland 1999). Therefore, there must be an ample number of introduced species in a low-flow area with few currents (for gamete retention) in order for the species to become established in a new environment (Gaines, pers. comm.).

Marine species that rely on internal fertilization, on the other hand, does not require low-flow areas in order to propagate. This reproductive strategy is used almost exclusively by arthropods and mollusks among the marine invasive species in this study. Similarly, other reproductive strategies of invasive species tended to be limited to certain taxa. For example, fragmentation allows for comparatively easy establishment for introduced species and was limited to algae and sponges. Fragmentation is a type of asexual reproduction which does not require other individuals of the same species for propagation. Because of this, a population of invasive species can originate from a single introduced individual. Moreover, physical disturbance, such as wave action, can contribute to the spread of fragments and population growth of species using fragmentation. Species utilizing this strategy must be monitored and contained carefully for effective management.

Some taxa are capable of both asexual and sexual reproduction, such as bryozoans, cnidarians, and some algae seen in this study. Often with these species, sexual reproduction occurs on a seasonal basis while asexual reproduction can occur continuously throughout the year. The reproductive capacity of these species contributes to competitive success and rapid population growth.

Species capable of regeneration, although not common, must be monitored and managed with caution. Although only one of the 133 species could regenerate, it had exceptional population growth. This species is an annelid (*Chaetopterus sp.*) capable of regenerating from any intact segment, forming dense aggregations that dominate the benthic substrate (Hawaii Biological Survey 2002). Similar to other asexually-reproducing species, these dense aggregations are likely genetically homogenous and may be particularly susceptible to disease or chemical stress. Any management strategy involving these species must be carefully determined, being wary of secondary environmental damages.

Frequency of reproduction did not appear to have a large effect on the ecological impact rating, established by Molnar et al. (2008). While this life history trait is especially useful in the management of a single species, it is not inherently helpful for management at a regional or global scale. Similarly, the sexual characteristics of the invasive species (dioecious, monoecious, hermaphroditic) were not significant and would not be particularly helpful for management.

The majority of the invasive species in this study displayed characteristics of rapid population growth. This highlights the observation that many invasive species retain the ability to grow and establish populations quickly. However, even slowly maturing species can have extensive ecological impacts, such as the Mangrove Monitor (*Varanus indicus*) in the Pacific (GISD 2007). While the rapidity of population growth is difficult to manage, it is necessary to understand how quickly introduced species can become established.

With all of these reproductive traits, it is necessary to have a native species assemblage for comparison. In addition, the most applicable reproductive trait to inform regional management is the primary reproductive strategy. A comparison of the native distribution of reproductive strategies with those of invasive species will highlight which strategies may influence invasion success most. Furthermore, reproductive strategies contributing to invasion success are also likely connected with particular aspects of environmental susceptibility to invasion, such as notable anthropogenic or natural disturbance. These observations, however, are necessary to apply in a regional context for management efforts to be truly effective.

Regional Patterns of Marine Invasion Success

Global patterns of life histories and biogeography of tropical marine invasive species is of little use to management unless applied in a regional context. Life history patterns of invasive species also require the context of trends among naturally-occurring species in order to make more accurate conclusions. The Hawaiian Islands and Florida are two of the world's most invaded tropical marine environments, necessitating a better understanding of invasive species in each region. Each region is analyzed more closely to determine possible reasons as to why invasive species have become so prevalent in those areas and possible management strategies to cope with such issues.

The Hawaiian Islands

Hawaii is the world's most invaded tropical marine environment (Fig. 1). The region's susceptibility to invasion is due largely in part to the region's biogeography. The Hawaiian Islands are geographically isolated from any mainland and have been for millions of years. Despite the tropical environment, Hawaii supports fewer species when compared to other tropical areas (Gray 1997). Moreover, the species have a high rate of endemism with many specialist communities, contributing further to a distinct susceptibility to introduced, generalist species from other more diverse regions (Byers and Noonburg 2003).

The Hawaiian Islands have 74 marine invasive species with a reported ecological impact (Molnar et al. 2008). Among these, 42 have characteristics typical of rapid population growth, allowing them to grow and spread quickly. Of the 74 marine invasive species in Hawaii, 17% (12) had ecosystem-wide effects while 42% (30) had repercussions at the community level. Less than 6% (4) of the invasives had species-level effects and 4% (3) had negligible effects on the marine environment. However, the ecosystem impact of 32% of these invasive species were unstudied, a short-coming which certainly warrants further research. The underlying issue with the presence of invasive species is that they compete with native organisms and can hinder ecosystem functioning of an environment. With over 58% of the invasive species having effects at the ecosystem or community level, native biodiversity and ecosystem functioning of Hawaii's coral reef systems is at risk.

Understanding those species that have more widespread effects is necessary. For species with an ecosystem-wide impact, 50% are photosynthesizing algae. These algae often form thick mats during blooms, which can smother other species and create hypoxic conditions (Norkko and Bonsdorff 2007). Although they can improve water clarity and quality, 33% of species with an ecosystem-wide impact rely on plankton as primary food source, severely interrupting the life cycle of native species with early planktonic stages of development (GISD 2006). The remaining 17% of species with ecosystem-wide effects are deposit feeders that interfere with soil chemistry and dynamics, negatively affecting benthic ecology.

Thirty of the 74 invasive species in Hawaii affected the environment at the community-level, primarily by competition within similar functional groups. Seventy-seven percent of these species were filter feeders, photosynthetic autotrophs, and deposit feeders, the most common trophic groups with an ecosystem-level impact as well. Current reactive management should focus on species within these trophic groups, as they appear to have the largest effects on the community and ecosystem. These species are well-established and would be difficult to remove with manpower alone. Monitoring and prevention of further spread may prove to be the best management strategy for these species. Total removal could prove to be extremely difficult and if attempted, must be focused on single species.

The taxonomic distribution of marine invasives in Hawaii is displayed in Figure 11. Resembling the global patterns, the most invasive taxa are arthropods, followed by mollusks and algae. Other taxa present include cnidarians, annelids, bryozoans, sponges, fishes, ascidians, echinoderms, and tunicates.

Bishop Museum, Hawaii's State Museum of Cultural and Natural History, provided biodiversity data for natural assemblages of marine species, provided in Figure 12. Fishes are the most diverse taxa, followed by arthropods, mollusks, and algae. Within each taxon, the percentage of invasive species to naturally-occurring species was calculated (Fig. 10). The taxa with the highest potential for invasibility were ascidians, sponges, bryozoans, and tunicates.

The invasive ascidians, sponges, bryozoans, and tunicates are all filter feeders and colonial organisms. Their diet on plankton is generalized and do not require a specific food source. Like several other marine invertebrates, they are also all hermaphroditic. The sponges rely on fragmentation for reproduction, allowing for continuous reproduction year-round (Hawaii Biological Survey 2002). However, potential population growth for sponges is variable and is dependent on environmental conditions (Hawaii Biological Survey 2002). Ascidians and bryozoans on the other hand, have potential for rapid population growth. Moreover, all of the invasive ascidians, bryozoans, sponges, and tunicates are benthic colonial organisms that can easily spread laterally across the seafloor. The threat exists that they may out-compete native benthic organisms, such as corals and sponges. Despite this, the extent of ecological is unstudied in 47% of these species. Given the presence of these organisms, their population growth potential, and threat to native communities they should be carefully monitored, studied, and attempted to be removed from the environment.

Two of the largest contributors to Hawaii's problem of marine invasive species are introductions via ballast and hull-fouling. Eighty-three percent of Hawaii's marine invasive species were introduced by one of these pathways. Furthermore, all of the aforementioned ascidians, bryozoans, sponges, and tunicates were introduced to Hawaii by ballast or hull-fouling. As the taxa with the highest invasion potential, this is particularly concerning. Moreover, 92% of the species with ecosystem-level impact were introduced by ballast and/or hull-fouling. Several of the species that are introduced with these pathways have an apparently large impact on Hawaii's marine environment, warranting more effective management. As an island nation in the Pacific, Hawaii relies on many imports brought in by ships. Ballast and hull-fouling can be attributed almost wholly to commercial global shipping practices.

Stricter regulations and enforcement are necessary for incoming ships to Hawaiian waters to reduce introductions from ballast and hull-fouling. Suggestions of added regulations are previously mentioned and include unloading of ballast in open water, treatment or filtering of ballast water prior to unloading, and the manual or mechanical cleaning of ship hulls prior to entering a port. Technological advances in anti-hull-fouling paints may help as well. These reformations in regulation are particularly necessary for Hawaii, given the particularly high numbers of species introduced by hull-fouling and ballast.

As the world's most invaded tropical marine environment, Hawaii requires a change in current management. Geographically isolation has made the islands prone to invasion, particularly with the onset of global transportation (Allison et al. 1995). Proactive and preventative management measures include more restrictions and enforcement of the dumping of ballast in ports and cleaning of ship hulls prior to entry in Hawaiian ports. Many marine invasive species are already established in Hawaiian waters that require reactive management approaches. While removal of these species may be too difficult to be realistic, monitoring and further study of the organisms with the greatest impact is necessary.

Florida

Florida is the second-most-invaded tropical marine ecoregion in the world. Unlike Hawaii, Florida is not geographically isolated and its invasion susceptibility is driven by other mechanisms (Allison et al. 1995, Byers 2002, Reaser et al. 2007, Sax et al. 2005, Semmens et al. 2004). Coastal south Florida is densely populated with people, many of which partake in coastal activities that contribute to continued anthropogenic disturbance. The region also is impacted extensively by hurricanes and storms, contributing to natural disturbance of coastal communities. The disturbance creates vacancies in niches that can be occupied by species that are introduced to the area (Byers 2002).

According to this study, hull-fouling and ballast contributed to 49% of the marine species invasions in Florida, which is comparable to the global trend of 50%, but still accounted for the most common invasion pathways. Aquaculture poses the second-largest source of invasive species, accounting for 19% of the species introduction, also comparable to the global trend. Animal and aquarium trade however, contribute to 16% of Florida introductions, 4% higher than the global pattern. Florida is especially known for the imports and exports of tropical fishes and its aquarium culture, so this observation is somewhat unsurprising.

The Florida ecoregion has 44 marine invasive species with a reported ecosystem impact (Molnar et al. 2008). Arthropods, fish, and mollusks represent the majority of these species with 11, 9, and 9 species respectively. Other invasive taxa in Florida include cnidarians, bryozoans, annelids, tunicates, and plants. Invasive algal species, however, are far less common in Florida than seen in global trends or Hawaii, comprising only 2 of the 44 marine invasives. Florida's invasive species taxonomic distribution needs to be compared to that of its native species to determine which taxa have the highest potential for invasion in Florida, exemplified in the analysis of Hawaii. Unfortunately, a taxonomic distribution for Florida's native biodiversity was unavailable during the time frame of this study.

Of Florida's invasive species, 57% were dioecious, higher than the global average for invasive species. This is likely attributed to the greater percentages of invasive fishes and arthropods in Florida, many of which are dioecious. Thirty-four percent were hermaphroditic and included at least one species from each non-photosynthesizing taxon, though represented most by bryozoans, cnidarians, and tunicates. Despite the distribution, the sex characteristics of the invasive species appeared to have little consequence on invasive species effectiveness

Although filter feeders still remain the most common (34%) trophic guild among the Florida invasives, generalist carnivores are far more common than global trends suggests and account for 18% of the invasive species. Additionally, herbivores appear more common in Florida than in other ecoregions, accounting for over 11% of the invasives present. Three of the generalist carnivores and all of the herbivores are fish species. Of the invasive fishes found in Florida, 89% have ecosystem- or community-level effects that range from top-down controls like excessive predation to bottom-up controls such as depletion of aquatic vegetation. Upon closer inspection, every single invasive fish species was introduced to Florida by the aquarium trade. As a taxa that has broad-ranging effects on the coastal ecosystem, exotic fishes involved in the aquarium trade need to be monitored and handled more carefully. Many aquarium enthusiasts may release unwanted aquarium fish into coastal waters, introducing exotic fish to Florida waters (Semmens et al. 2004). While many of these people may view releasing unwanted fish as humane, they must be educated as to the ramifications of invasive species. Improving awareness of invasive fish impacts on Floridian coastal environments may prove helpful.

Over 20% of the invasive species in Florida have an impact that alters the ecosystem, while just over 43% of the species have community-level impacts. Eight of these species are fishes, whose environmental consequences and suggestions for management were mentioned previously. Three cnidarians have ecosystem-level impacts involving over-consumption of plankton, which can altar species composition and community structure. Excessive consumption of plankton can also decrease the number of commercially important fishes and crustaceans that Florida's fisheries depend upon (GISD 2006). The ecological impact of several (25%) of Florida's marine invasives remains unstudied, warranting further research and monitoring.

Similar to Hawaii, Florida needs to focus on stricter regulations and enforcement with regard to shipping, as hull-fouling and ballast introductions remain the most common invasive pathway. Proactively, Florida should also inform the public and particularly aquarium enthusiasts about the consequences of releasing exotic aquarium fish into coastal waters, due to the noticeable presence of invasive fishes in Florida when compared to other tropical ecoregions. These strategies are primarily to prevent further species introductions into Florida's coastal waters. However, there are many invasive species that are already well-established in Florida's ecoregion. These species must be closely monitored and studied for ecological impacts and range expansion. Removal of established invasive species can be extremely difficult, if not impossible. Ecosystem managers must try to limit the negative, wide-ranging effects of the species with ecosystem-level and community-level impacts. These species should receive particularly close observation and the brunt of management efforts.

Future Research

Molnar et al. (2008) provided the first and only comprehensive study of marine invasive species throughout the world. Their research served as a basis for this study and was extremely helpful in discerning global trends in biogeography, invasion pathways, and taxonomy. However, research by Molnar et al. (2008) presented 329 marine invasive species where there was a documented ecological impact, 133 of which occupied tropical ecoregions and were discussed in this study. There are likely far more than 329 marine invasive species found globally. Cranfield et al. (1998) listed 159 marine species that had invaded New Zealand alone. Another study by Allison et al. (1995) showed that over 343 marine invasive species exist in Hawaii. Although not tropical, the Mediterranean has over 550 invasive species, shown in research by Galil (2008). The point is that although numbers of invasive species have been observed and recorded for several regions of the world, associated ecological impacts often go unstudied or unreported. There is a distinct need to monitor and research the ecological effects of these species so that we may understand how they alter marine ecosystems and to further develop global databases that incorporate this information.

Marine biodiversity research would further knowledge of invasive species as well. Marine species did not receive ample study until recently, primarily because of their inaccessibility. Native, marine biodiversity is a particularly important area of study and informs the environmental history and current contributors to ecosystem functioning of a region. Life history traits of hundreds of marine species are unstudied. For 25% of the marine species in this study, there was not enough fecundity, growth to sexual maturity, or individual growth data to provide an accurate estimate of potential population growth. Moreover, some trophic levels, trophic guilds, and reproductive traits of species in this study had not been explicitly researched and thus, my estimates were based on characteristics of taxonomically similar species. Furthermore, explicit life history research of marine species is necessary to further knowledge of marine biodiversity, species linkages within communities, and functioning of the marine ecosystem.

Finally, an understanding of what species are native to ecosystems provides insight to which species are nonindigenous to the area. Many species observed in marine systems are given the title “cryptogenic” because their nativity to the area is not truly known (Carlton 1996). A study by Coles and Eldredge (2002) displayed that 26 species in Pearl Harbor alone were cryptogenic. Genetic analysis, interspecific connections, and written histories can aid future research in understanding the marine biodiversity and discerning between native and nonindigenous species.

In summary, tropical marine systems and the exotic species that invade them have been understudied. As some of the world’s most biodiverse systems with several economically and ecologically important ecosystem functions, their integrity is of utmost concern. A better understanding of individual species’ life history traits can aide in the effective management of established species and mitigation of their negative impacts. Discerning patterns of taxonomy, biogeographic information, pathways, reproduction, and trophic groups can inform how regional systems are collectively affected by marine invasive species and will contribute to proactive management of marine systems. Managing for marine invasive species is ecologically, economically, and socially important given the extent of regional and even global impacts of these species.

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Figure 1. Top 10 Most Invaded Tropical Marine Ecoregions

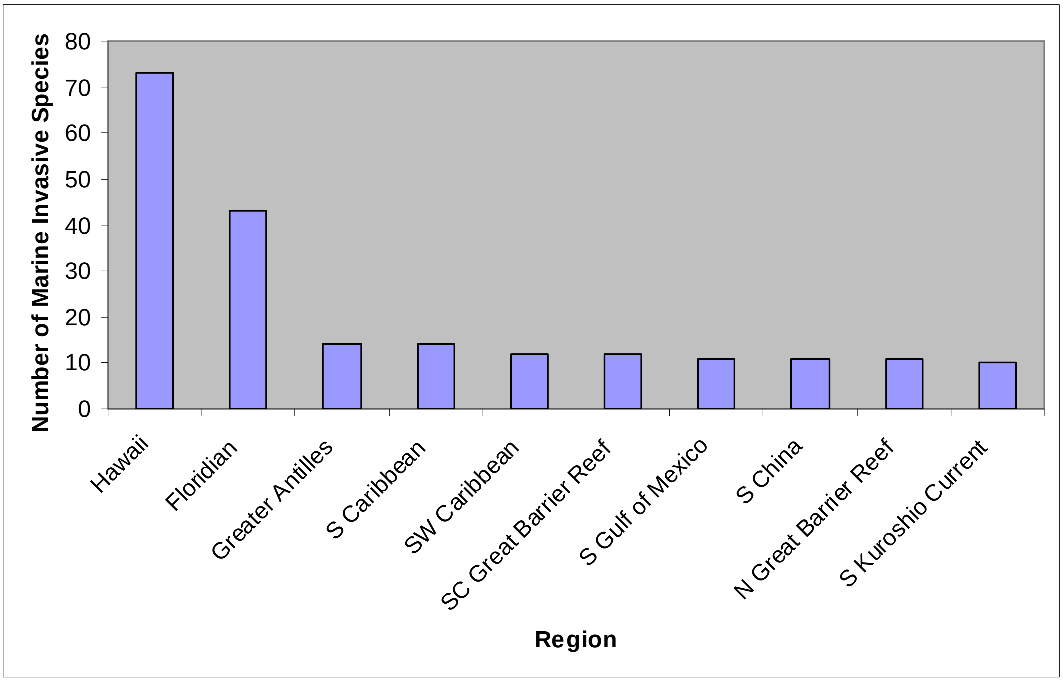

Fig 1. The top 10 tropical marine ecoregions with the most marine invasive species censused. Hawaii is the most invaded with 74 species, followed by Florida with 44 species.

Figure 2. Top 10 Most Common Places of Origin

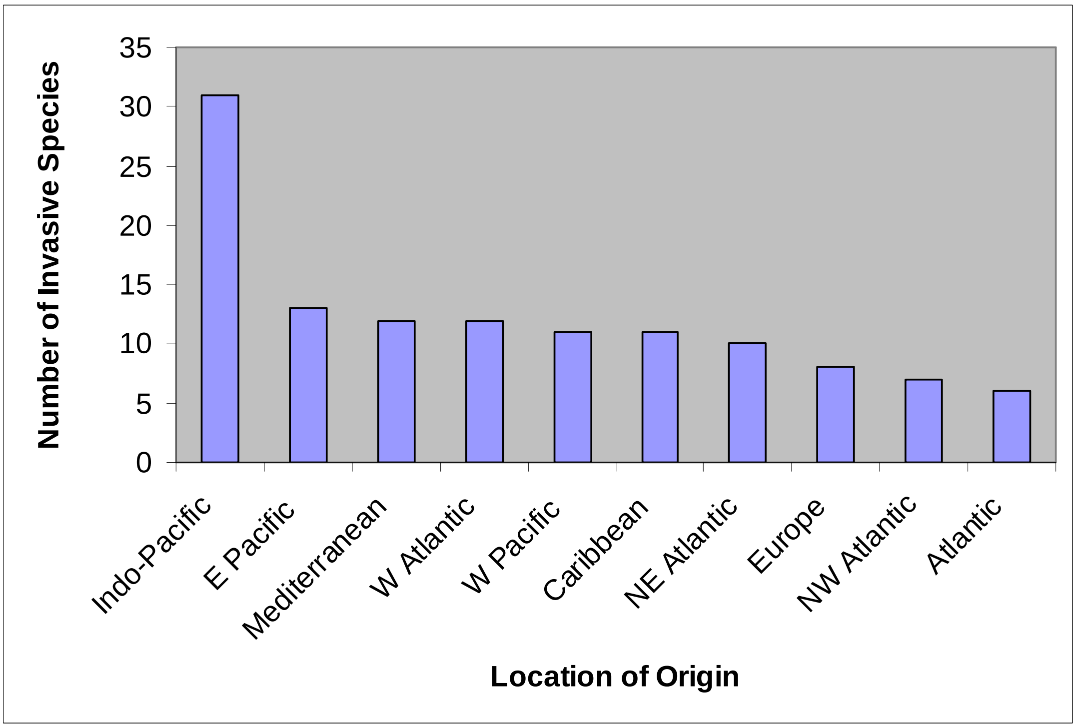

Fig 2. This chart displays the most common areas of origin for the marine invasive species in tropical marine ecoregions. The Indo-Pacific was the most common, with 31 species.

Figure 3. Invasion Pathways

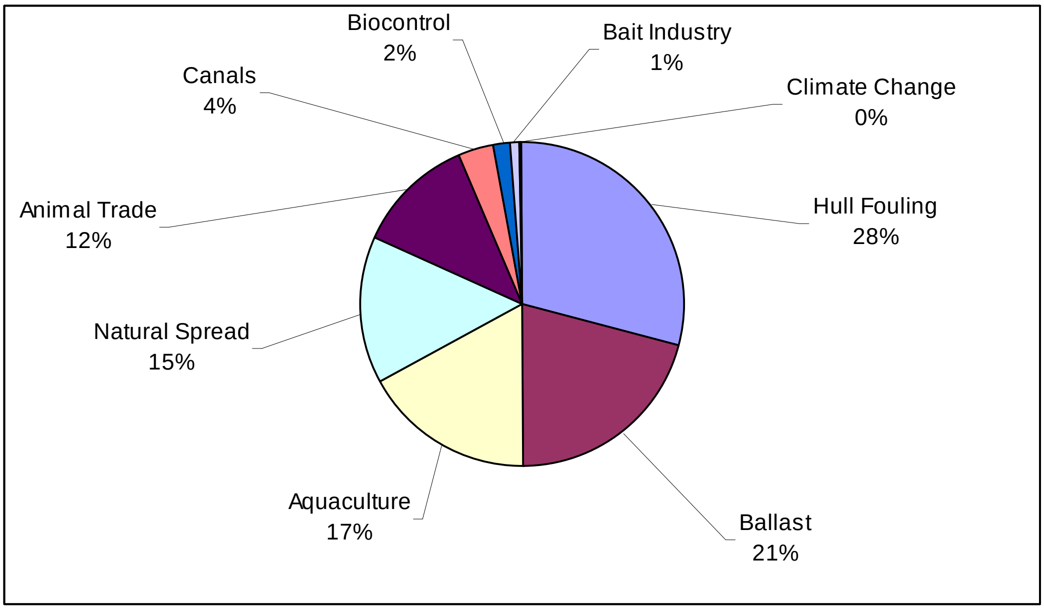

Fig 3. This chart displays the pathways by which invasive species are introduced to novel tropical marine environments across the globe. Hull-fouling and ballast are the most common and closely related to shipping.

Figure 4. Taxonomic Distribution

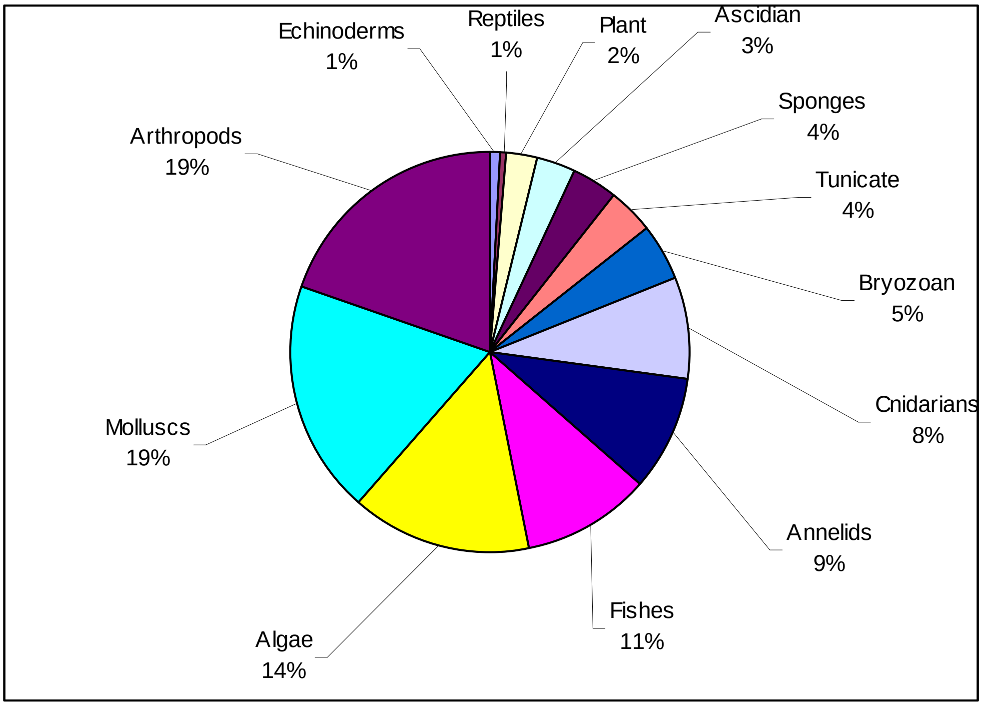

Fig 4. This graph shows the taxonomic distribution of invasive species found in tropical marine environments globally. The most common taxa are arthropods, mollusks, algae, and fishes.

Figure 5. Functional Groups

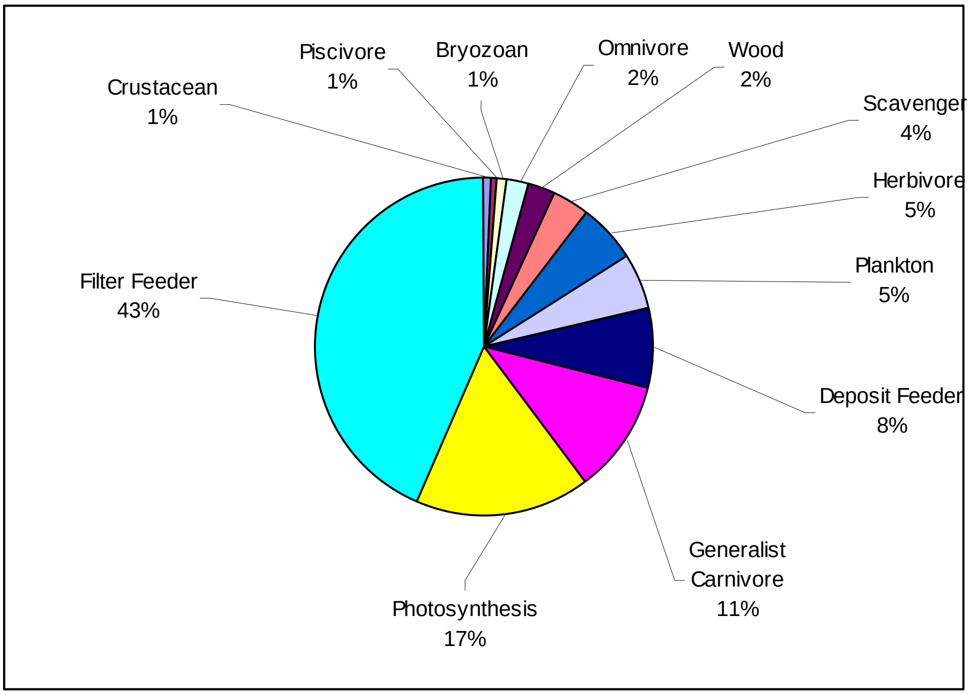

Fig 5. Functional groups are closely related to diet. The above classifications describe the means or the resources that marine invasive species use to acquire the majority of their energy.

Figure 6. Primary Reproductive Strategy

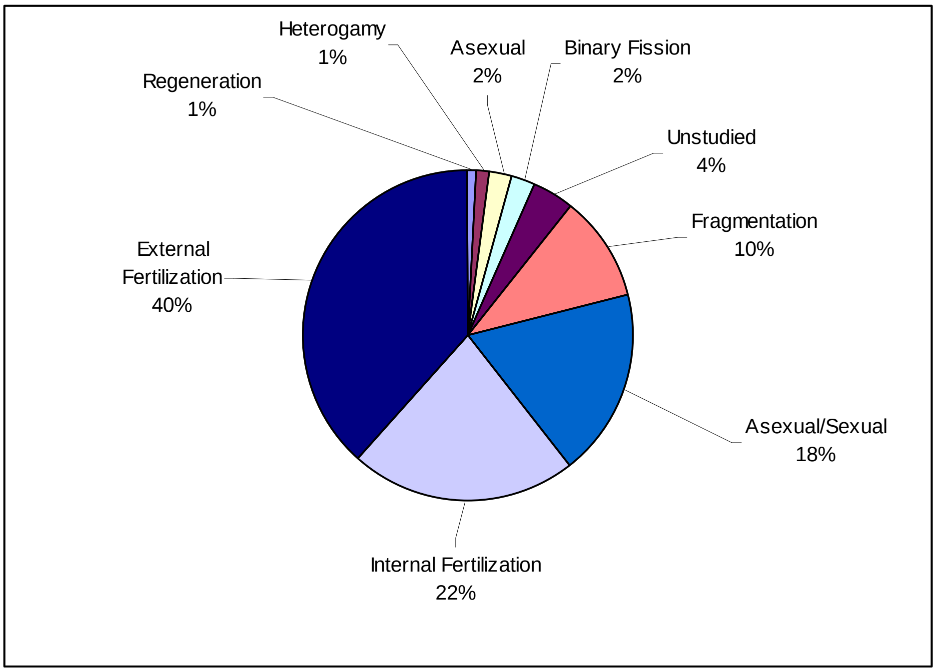

Fig 6. This graph displays the reproductive strategy that the marine invasive species rely on most. The asexual/sexual classification shows that the species reproduces in both ways in similar extent.

Figure 7. Sexual Characteristics

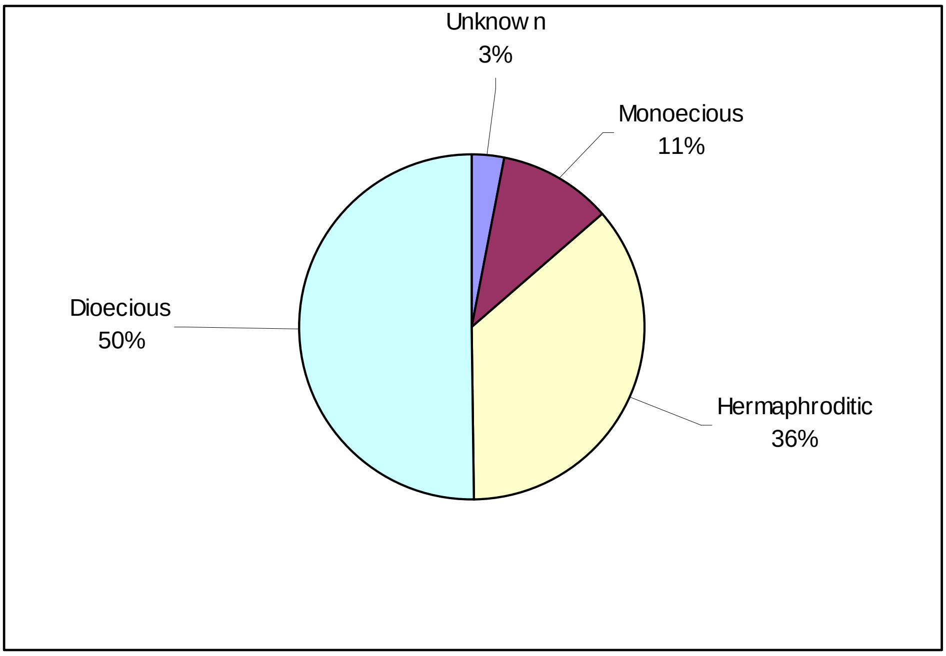

Fig 7. This graph displays the reproduction characteristics of the marine invasive species. Dioecious species have two separate sexes that remain so throughout their lifetime. Monoecious organisms have only one sex and hermaphroditic organisms may display characteristics of either sex at various times throughout their lives.

Figure 8. Time of Reproduction

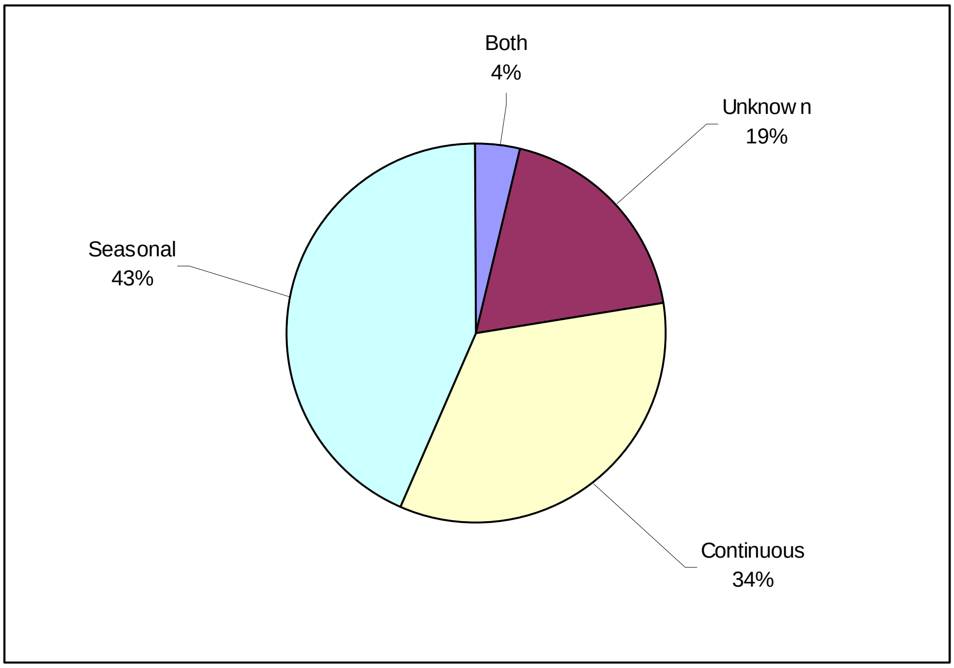

Fig 8.   This chart shows whether the marine invasive species reproduce with seasonal peaks or are capable of reproducing throughout the year. A species that reproduces in one manner (e.g. sexually) with seasonal peaks and continuously with another (e.g. asexually) is given the title of “both.”

Figure 9. Population Growth Potential

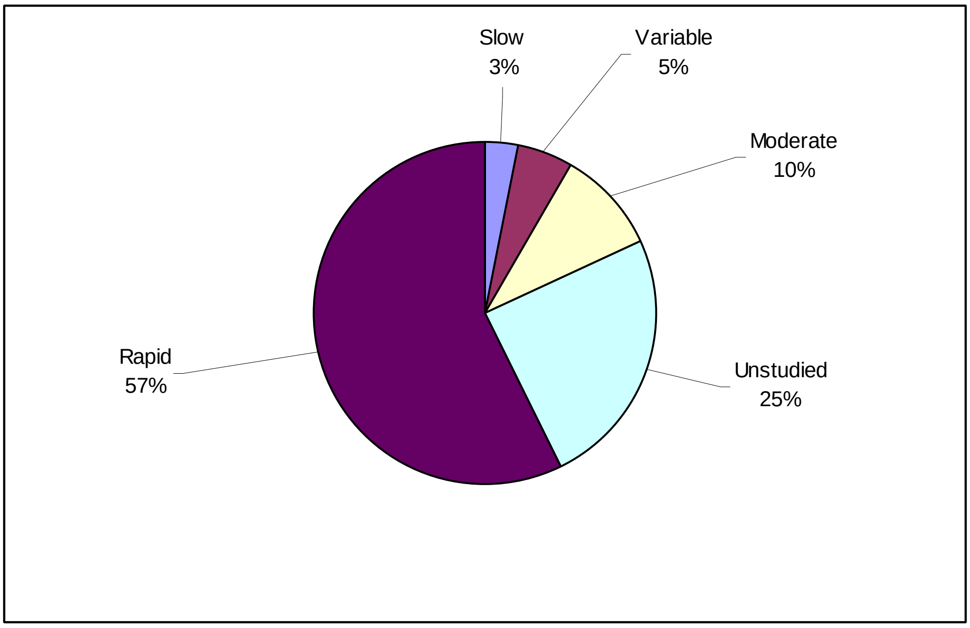

Fig 9. This chart displays the population growth potential of the marine invasive species. The designation of slow, moderate, and rapid population growth potential constitutes fecundity, growth to maturity, and individual growth. "Variable" species are highly dependent on environmental conditions.

Figure 10. Taxonomic Invasive Percentage

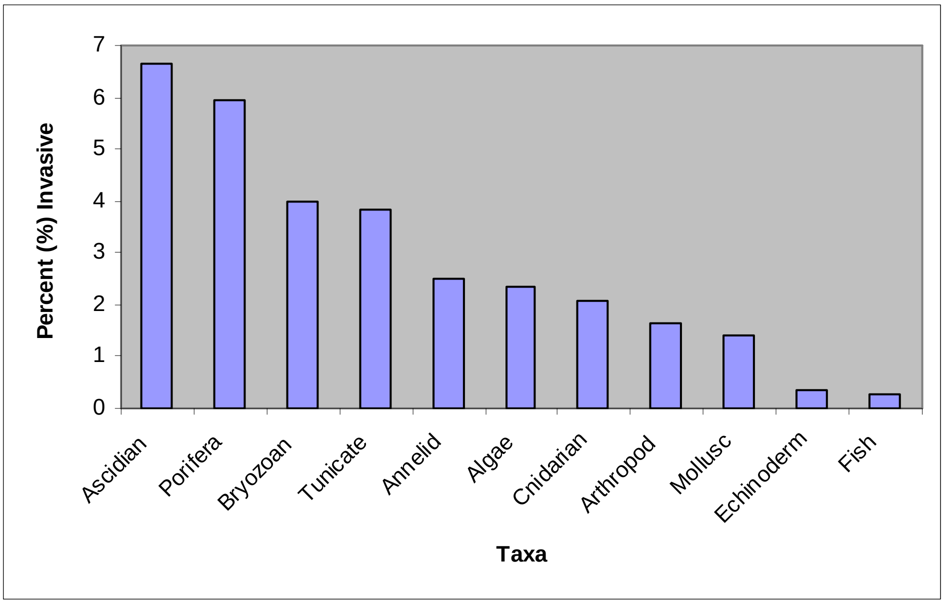

Fig 10. This chart displays a comparison of invasive species to native species within each taxa in the Hawaii ecoregion. This was determined by dividing the number of invasive species by the number of native species of that same taxa in Hawaii. This graph shows which taxa may have the greatest potential to become invasive.

Figure 11. Invasive Taxa of Hawaii

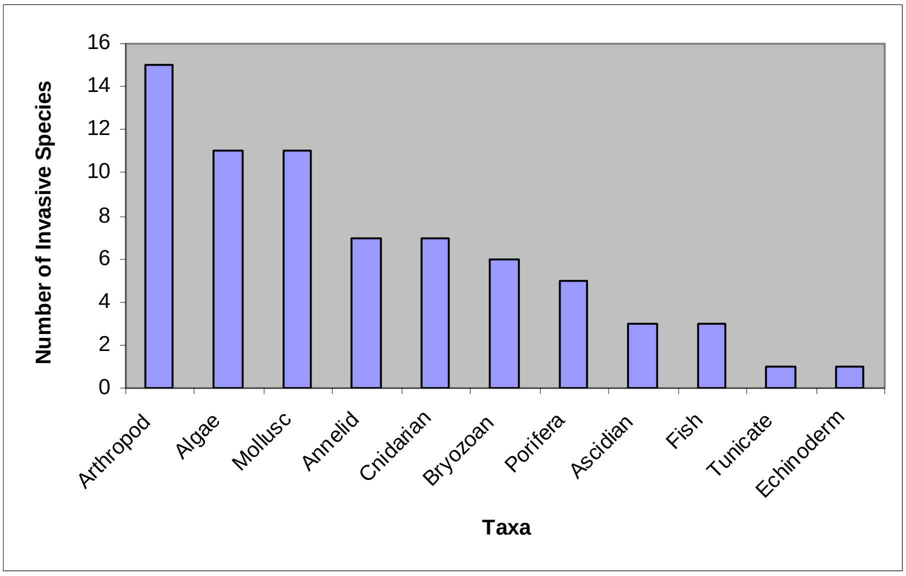

Fig. 11. This graph shows the taxonomic distribution of Hawaii's invasive marine species.

Figure 12. Native Taxa of Hawaii

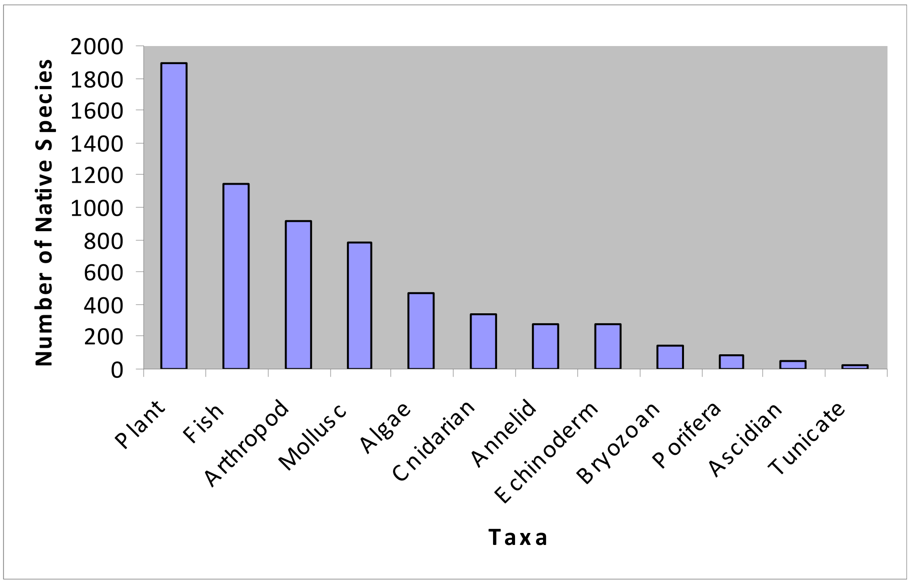

Fig. 12. This graph shows the taxonomic distribution of Hawaii's native marine species. No invasive or cryptogenic species are included in these biodiversity estimates of Hawaii's marine species.