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Abstract:

Speciation in tropical reef fish occurs through a variety of methods. It occurs allopatrically when larvae are isolated and populations are geographically distinct from one another. Allopatric speciation also occurs in the marine environment due to physical changes in the environment over large time scales. Sympatric speciation also occurs in the marine environment and is divided into several unique methods that include the following models: stepping stones, adaptive radiations, color morphologies, and the presence of cryptic species. In the following sections explore the causes of speciation in tropical reef fish and addresses the following questions: What are the driving forces behind reef fish speciation and how did genetic divergence occur initially? And, how is it possible that the diversity of reef fish is so high when the competitive exclusion principle states that only one specie may exist in a given ecological niche?

Introduction:

Allopatric speciation occurs when a single large population is divided into smaller subpopulations by physical barriers. If genetic exchange between these populations ceases then genetic divergence may occur leading to reproductive isolation and eventually speciation. If these barriers are crossed or broken down the now distinct species will not be able to interbreed and selection may actually occur to increase reproductive isolation even more (Palumbi, 1994).

Founder events are another manner in which reproductive isolation leading to speciation may occur by allopatry. Founder events occur when a few individuals are moved to a new habitat, become isolated from the source population and speciate due to the lack of gene flow between populations. Because there are so few individuals first arriving, the gene pool

becomes dominated by their genes only. If a small subpopulation of a given species breaks off from the main population, the small population may be subject to founder events, in which case genetic differences from the main population may accumulate quickly causing the smaller population to diverge from the main population (Palumbi, 1994).

According to Paulay and Meyer (2002), in a marine system, founder events are most likely to cause speciation when just a few pelagic larvae enter in the water column and survive while at the same time traveling a large distance. The species that are most likely to undergo founder speciation are those that have just a few larvae in the water column, but that have a high survivorship over the distances they are dispersed. Many first generation larvae may never become successfully established in a founder event because the larvae may have become too spread out to meet potential mates in the future.

Tropical reef species present a challenge to the idea of allopatric speciation; they often have high fecundity and larvae that are highly dispersive. Gene flow across large areas is common and there are few impassable barriers in the open ocean, therefore widely separated areas may be genetically connected. Additionally, marine populations, especially amongst reef fish tend to be large which may slow genetic divergence between populations (Palumbi, 1994).

In addition to allopatric speciation events, sympatic speciation may also occur. Under this method populations do not become isolated by physical barriers as is the case with allopatric speciation. Instead populations evolve and eventually speciate while living in the same geographic area. In this case speciation may occur due to changes in niche specialization, external morphologies, or mate selection (Freeman and Herron 2004). This method of speciation is common in tropical reef fish and there are several species that have been studied in the past fifteen years that have shown evidence of sympatric speciation.

It is difficult to differentiate between speciation events that have occurred allopatrically as opposed to sympatrically and research is currently being conducted to determine how and when similar species have diverged from ancestral populations. In addition, one of the most prevalent issues related to speciation research is to distinguish between changes that have occurred during speciation and those that have occurred afterward due to the effects of reproductive isolation. Reproductive isolation may occur due to barriers in pre-zygotic or post-zygotic life cycle phases. For example in pre-zygotic isolation, if two individuals cannot produce a viable offspring reproductive isolation is present. In post-zygotic isolation for example, if an individual is unable to locate a mate of the same species, reproductive isolation is present. In addition to reproductive isolation, mate preference is common in tropical reef fish. In some species spawning is almost exclusively between individuals of the same color pattern. Habitat specialization limits reproductive possibilities as well, for example depth and temperature limit the possible ranges of reef fish species (Palumbi, 1994).

Even with the high possibility of reproductive isolation in the marine environment tropical reef fish have evolved to be both diverse and numerous. Tropical reef fish have evolved to share many of the same ecological niches, but the competitive exclusion principle, as explained by Karleskint at. al. (2006), states that no two species should be able to occupy the same niche. In coral reef environments 60-70% of reef fish are general carnivores and the rest graze on algae or coral. There are four hypotheses that attempt to explain how this phenomenon is possible—the competition model, the predation disturbance model, the lottery model, and the resource limitation model. Under the competition model each species has a unique, highly specialized niche based on factors such as the time of day they feed, the size of the prey they catch, their position in the water column, etc. The predation disturbance model

implies that there is competition between species but that competition is limited because mortality rates due to predation and other factors maintain populations at low enough levels that competitive exclusion is prevented. The lottery model assumes that chance alone regulates which larvae will settle on a reef and which species will occupy any given niche. Finally, the resource limitation model assumes that the larvae available to colonize any given area are limited and this limitation on available larvae prevents any species from ever reaching its carrying capacity. It is not yet fully understood which of these possible models is most important in explaining how the diversity of reef fish could be so high.

Ehrlich has theorized that the level of diversity found among tropical fish residing on coral reefs today is due largely to the fact that reefs have remained constant over a very long time period which has likely allowed the allopatric evolution of many fish species to fill broad and diverse niches (Ehrlich 1975). Species have been able to successfully remain on these reefs due to the patchy nature of the habitat and the randomized recruitment and loss processes common among reef fish. Ehrlich believed that the extremely high levels of fish diversity on a coral reef are ultimately made possible by the extremely narrow niche each species occupies (1975).

More recently, in the past 30 years, in order to fully understand the cause of high diversity levels in tropical reef fish, studies have focused on speciation events and sources of genetic divergences. Since this research began around 30 years ago, there have been enormous advances in the understanding of how genetic evidence can be used to help classify distinct fish species. Today genetic sequencing and gel electrophoresis of proteins and DNA provide extensive information often within a couple hours of completing said procedures. In the 1970's, Hinegardener and Rosen reviewed genetic studies that were often done by simply

counting chromosomes or measuring the amount of DNA in an organism. During the time of their research, it was believed that more advanced organisms would have a larger amount of DNA per cell (1972). Current research demonstrates that this is not the case and that organisms are distinct from one another not by the number of chromosomes in their genome but by the information encoded by the chromosomes they poses. In the 1970's it was assumed that fish evolved and eventually speciated due to an increase in DNA content caused by a polyploidy event that is followed by a gradual decrease in DNA content (1972).

This paper will not focus on genetic tests and DNA sequencing but rather on how and when speciation events have occurred in tropical reef fish and what has caused these speciation events. The causes of speciation that will be analyzed include the scale of larval dispersal in association with the role of niche specialization followed by reproductive isolation, and temporal changes in the entire ocean habitat.

I. Larval dispersal as a source of speciation:

Tropical reef fish have pelagic larvae meaning that they are planktivorous and are moved by ocean currents (Shulman 1998). The pelagic larval stage may last from just a few days to a few months. Damselfish species, for example have pelagic larvae that remain in the water column for 15-35 days (Bernardi et. al., 2001) whereas bonefish have pelagic larval stages lasting from 2-24 months (Colborn et. al., 2001). Theoretically larvae should be dispersed as far as they can be carried by ocean currents before settling out of the water column and developing into juveniles and eventually adult forms that spend the remainder of their lives within the vicinity of a single coral reef. Additionally, the longer the individual is in the pelagic stage, the further it may be able to disperse from its home range and thus the greater the gene

flow from location to location. A species with pelagic larvae may not necessarily have enormous, wide ranging populations (Ehrlich, 1975). Many long lived planktonic larvae may actually stay within the vicinity of the area where they originate due to the varied behavioral factors of both larvae and adult forms (Paulay and Meyer, 2002). There are several barriers to the dispersal of larvae including life history traits such as high mortality rates (Paulay and Meyer, 2002), low probabilities of larvae settling in locations favorable to growth and development, or becoming reproductively isolated upon maturation (Palumbi, 1994). In addition to life history barriers, there are also physical boundaries that may inhibit the movement of pelagic larvae that include steep temperature gradients (Ehrlich, 1975), the circulation patterns of ocean currents (Paulay and Meyer, 2002), extreme depths that may be impassable (Lessios et. al., 1998), and spatial segregations that cannot be overcome by certain larval species.

Small planktonic larvae often have high mortality rates while large larvae have much lower mortality rates; the longer the plankontic stage of an organism lasts, the greater geographic range that species may be able to cover (Paulay and Meyer, 2002). Larvae may live for many days and they may drift across an entire ocean, however successful transport and establishment may actually be rare. Larvae that travel long distances have a higher chance of settling in unfavorable environments than larvae that stay within the vicinity of their parents. Also the density of larvae decreases with increased distance from the source and they are therefore unlikely to settle in an area where they will ultimately find a breeding partner (Palumbi, 1994).

Additionally, planktonic larvae may not be widely dispersed because there are density and temperature factors that may interact to create circulation patterns that prevent planktonic

larvae from being carried out to sea (Ehrlich, 1975). Boundaries created by steep temperature gradients and near-shore currents may hinder gene flow and species may also be limited to a certain tectonic plate despite their potential for crossing plate boundaries (Palumbi, 1994). In the Indo-Pacific Ocean basin for example, the extreme longitudinal separation of coral reefs has long been considered one of the major barriers to dispersal of pelagic larvae due to the immense distance a larvae would have to travel to ensure continued gene flow between populations for genetic divergence to not occur (Klanten et al., 2006). As mentioned previously, the scale of pelagic larval dispersal is also partially responsible for limiting the dispersal capabilities of a larva. Pelagic larval dispersal may occur on large, medium, or small scales. Large scale dispersal refers to the dispersal of larvae across distances greater than 1000 km, medium scale dispersal refers to the dispersal of larvae across distances of 200-1000 km, and small scale larval dispersal refers to the dispersal of larvae across distances of less than 200 km (Shulman 1998).

Large scale dispersal:

Of the species of tropical reef fish that have been studied thus far across distances of over 1,000 km, most species have not show significant genetic differentiation; 36% of these species showed some significant level of differentiation while 64% did not (Shulman, 1998). Lessios, Kessing, and Robertson (1998) provide an example of gene flow across a large distance known as the Eastern Pacific Barrier. The EPB is 5,400 km of uninterrupted open ocean between the central and eastern Pacific. The Eastern Pacific Barrier is an area of extremely deep water and is known as the greatest barrier to the dispersal of shallow water marine organisms. Some species, such as the *Echinothrix diadema* actually occur on both sides of the barrier. This species, which was the focus of their research, is actually a species of

urchin. Although their study did not deal with tropical reef fish, their findings still provide a relevant example as urchins have pelagic larvae that are capable of dispersal across large distances.

Lessios et. al. claim that dispersal biogeographers believe that larvae are dispersed across the barrier easily due to the movement of the Line Islands into the North Equatorial Counter-Current since the Plesistocene era. Vicariant biogeographers on the other hand believe that the similar species on both sides of the barrier are relict populations that were previously contiguous; they believe larvae are unlikely to survive the long journey across the barrier. It has been proposed by Lessios et. al. (1998) that the most probable solution to this controversy is that some species are able to cross the barrier, especially during El Niño events which increase current velocity. In this case the barrier would act more like a filter than an impermeable wall. They predicted that in order for larvae to be transported across the EPB, they must be picked up by the Northern Equatorial Countercurrent which takes water particles 100-155 days to cross the boundary, however during El Niño events the time is shortened to 50-81 days. Paulay and Meyer have also suggested that storms are especially important for transporting larvae to new and distant locations; a storm may cause a specimen to be moved hundreds of kilometers in a relatively short time frame (2002).

For clarification, vicariant speciation comes from the fact that the isolation of some populations is the result of some genetic or climatic break or a physical barrier. Some scientists have rejected the idea of speciation by vicariance in marine systems due to the fact that there are an insufficient number of taxa supporting this theory. But, research has shown that both genetic and biogeographic patterns favor the theory of vicariant processes to explain diverging genetic structures in many species (Planes and Fauvelot, 2002). Speciation occurs if the

frequency of dispersal is very low, i.e. founder effects, or when dispersal probability decreases over time so that gene flow approaches zero, i.e. vicariant speciation. Paulay and Meyer (2002) provide three scales that are used to determine if founder or vicariant speciation is more likely to occur in any probable speciation event. The first deals with the location and size of the speciation zone, the second scale looks at the spatial scale of temporal fluctuations within the speciation zone, the third scale deals with genetic fluctuations due to temporal dynamics.

Medium and small scale dispersal:

According to a review by Shulman, most of the previously studied tropical reef fish show no significant genetic differentiation at the medium scale. At the small scale however there are several species that show statistically significant levels of genetic differentiation. Several different studies have proposed various explanations as to how this sympatric speciation may have occurred. A few of the best documented examples of sympatric speciation deal with the following models: stepping stones, adaptive radiations, color morphologies, and the presence of cryptic species.

Stepping stone model:

In 2001 Bernardi et. al. conducted a study on three species of damselfish which differed morphologically on the basis of coloration. In their study they investigated the genetic differences between the three fish species of damselfish from an initial island's reef to a neighboring island's reef and so forth at various distances across the Indo-Pacific. They found that at greater distances from the initial island's reef, that the genetic divergence was increased both between separate species as well as between the same species. Although genetic divergence was increased as the study moved further from the source, they determined that the island reefs act as stepping stones for pelagic larvae. It is most likely that high mortality rates

during pre-settlement of the pelagic larvae may limit dispersal to nearby islands. Due to the size and age of the samples from neighboring islands that were collected by Benardi and his colleagues, they were able to determine that when settlement does occur, it occurs in waves which are probably associated with altered current flows like those associated with El Niño events. These events may increase the velocity of ocean currents thus allowing for increased distances of larval dispersal, this is similar to the changes in the dispersal of larvae across the EPB during El Niño events. Finally, gene flow across the Pacific was very low for all three species; estimated gene flow between the most distant localities was estimated at less than one individual per generation. Thus, in the marine environment speciation may occur even when populations are connected by stepping stone habitats.

Adaptive radiation model:

Before an example of speciation due to adaptive radiation is discussed it is first necessary to define adaptive radiation. Taylor and Hellberg (2004) provide the following background on adaptive radiation: Genetic differentiation may not only occur due to the isolation of sub-populations as is the case with allopatric speciation; it may also occur sympatrically on a small scale due to ecological specialization or specialized mate recognition morphologies or actions. In the case of ecological specialization resource competition may be the primary factor contributing to speciation. Speciation at the small scale occurs as adaptive radiation in stages for many species. Adaptive radiation refers to the occurrence of an initial major break in habitat utilization followed by the divergence of habitat use into more and more specialized niche occupation. After the initial break in niche usage, speciation occurs rapidly in order to exploit all of the new possible niche availabilities as efficiently as possible. Finally a division occurs in sensory communication and thus new species are created sympatrically with

very similar sister taxa. Larval retention would then be responsible for maintaining localized populations that ultimately evolve into distinct species.

The first example of adaptive radiation that will be reviewed comes from a study conducted by Ruber et. al. in 2003 on American seven spined gobies. They found that habitat shifts are responsible for the early splitting of goby lineages and later divergences were caused by niche specialization. They determined several lines of evidence that support the theory that gobies have diverged due to adaptive radiation. First of all, the genetic tests they conducted provided evidence that within the goby species', there was an early burst of speciation followed by a slowdown in speciation which is typical of adaptive radiations. They believe that the decrease in speciation rate may be due to a decrease in the number of opportunities for speciation to occur as ecological and geographical spaces are filled. Furthermore molecular analysis has shown that ecology has played a more important role than biogeography in evolution of these Gobies. They observed shifts in ecology that are associated with specific cladogenetic events and that as ecological shifts are associated with recent speciation events that closely related taxa show pronounced ecological differences. In other words branching is shown in closely related lineages and if this were not the case most shifts in niche specialization would be seen close to the root of the tree.

In 2002, Streelman and colleagues studied parrotfish speciation. Parrotfish, like the gobies also likely experienced adaptive radiations throughout their evolutionary history. Approximately 42 million years ago, two major clades of parrotfish diverged, those that are associated with coral reefs and those that are associated with seagrass beds. This was concluded because a phylogenetic analysis of DNA indicated a clear break in parrotfishes. After this major branching event, specialists for each habitat began to evolve and ultimately

parrotfish diverged on the basis of breeding behaviors due to sexual dimorphic coloration. Most importantly, adaptive radiation among parrotfish began with an initial radiation was due to ecological segregation; additional radiations resulted from organismal variation between different places and times. Figure 1. from Streelman et. al. provides a clear diagram showing divergences due to ecological specializations and distinctive color morphologies.

Color morphology model:

In the past patterns of color differences have been used to analyze marine fish speciation; however, new evidence suggests that coloration may not have much to do with tropical fish speciation (Bernardi et al., 2002). As Bernardi et. al. has noted in 2002, color variation leading to speciation has not been entirely ruled out by many present day scientists and therefore it will be used here to investigate the possible relationship between morphological differences such as color, and speciation. Many different geographically localized color morphologies exist between quite a few closely related coral reef species such as damselfish. This is notable as tropical reef fish tend to have long pelagic larval stages and a therefore large dispersal capability which implies that genetic divergence should be limited between a single species found at more than one location. Historically populations have been classified as unique species if color morphology is distinctive between locations. Different color morphs have often been shown to develop allopatrically due to depth segregation in species such as the gopher and black and yellow rockfish, the cabrilla seabass, and the arc-eye hawkfish. These examples of divergent species due to color morphologies have not actually diverged significantly at the genetic level from closely related species. If different color morphs correlate with speciation events then each color variation should represent closely

related monophyletic lineages that were previously described as a single species. Bernardi et. al. have demonstrated that this is not the case among damselfish.

Bernardi and colleagues (2002) conducted a genetic comparison between four species of closely related damselfish which differed in color morphology as well as in geographic range. The four species were grouped together in the paraphyletic clades, meaning that they are assumed to be closely, but distinct enough to be considered individual species based on morphological appearances. Research proved that some species were more closely retated than previously believed and that some were in fact genetically distinct but did not show morphological divergences. For example, the three species encompassed in the clade, *Dascyllus trimaculatus,* which was previously divided into three paraphyletic clades, actually show high levels of genetic divergence and in reality may be three cryptic species.

Similarly, Bernardi et. al. (2002) found that two species, *Dascyllus albisella* and *Dascyllus strasburgi*, from the Hawaiian and Marquesas islands showed significant genetic divergence and were placed into two monophyletic groups. In the fourth species of damselfish, *Dascyllus auripinnis*, monophyletic status was also rejected due to genetic similarities. The genetic divergence between members of this species may be due to recent speciation events or this particular color pattern may have developed in the same species at different locations in parallel. Ultimately the four different color morphs of damselfish that this study was based on divide individuals into five different clades and indicate that the different color morphs do not correspond to strict partitions among natural groups. The pattern may be explained by the presence of cryptic species that were previously undetected (Bernardi et al., 2002).

McMillan et. al. (1999) presented speciation in butterflyfishes due to color morphologies and their work will be presented here. In some species, such as the

butterflyfishes, differing color patterns evolve very rapidly and color morphology is often the only trait separating closely related species. In this group, color patterns are considered extremely important in mate recognition and choice. There are more than 125 different species of butterflyfish and both males and females are brightly colored, theoretically to assist in mate recognition. In a study on three species of butterflyfish collected from across the Pacific Ocean genetic comparisons were done to determine the significance of color variation in speciation and mate recognition. Molecular data indicates that these three species diverged from their Indian Ocean sister species between one and two million years ago and those have diverged from each other from 260,000 to 870,000 years ago. The three species used in this study were, *Chaetodon multicincts, C. punctatofasciatus,* and *C. pelewensis*. Of these three morphologically distinct species, only *C. multicinctis* exhibits selective pairing and distinct genetic traits; the other two species, one isolated in the Phillippines, the other endemic to Fiji, show little genetic difference and will mate readily with one another when placed in the same location such as a lab setting. The selective pairing of *C. multicinctus* is probably due to a divergence of color pattern which eventually led to reproductive isolation. The color variations among the other two species are most likely explained due to either differences in fixation regarding coloration because of different selection pressures or because the two distinct patterns evolved in the past and the two species are now hybridizing, which would explain the genetic similarities. All three of the groups have shown that the evolution of color morphology can occur prior to the evolution of reproductive isolation and assortive mating.

Cryptic species model:

Marine speciation is complicated by the presence of often undetected cryptic species which show genetic differences but are identical in regards to morphology and in coloration

(Bernardi et al., 2002). One example of this phenomenon is in the bonefish, which unlike most tropical marine fish species shows very little morphological or ecological variation in different locations (Colborn et. al. 2001). According to Colborn et. al. (2001), speciation in bonefish, *Albula* species, has been allopatric as inferred from mtDNA, however the divergent groups occupy similar habitat niches in different locations. Some of these locations include Hawaii, the Caribbean, the Gulf of California, off the coast of South Africa, and the Philippines. The maintenance of consistent desired habitat characteristics may be responsible for the minimal morphological and ecological divergences among species of *Albula*. As it is very difficult to distinguish different species of *Albula* without a genetic analysis, their different species may be cryptic.

Albula are members of the Eloppmorpha group which have extremely long pelagic larval stages (2-24 months), so it would seem that the opportunity for wide-ranging dispersal would limit allopatric speciation events which could otherwise be caused by isolation due to barriers such as water temperature, ocean currents, and the ability of larvae to cross areas of deep water. Although it appears that allopatric speciation should not occur among the *Albula* species, their populations in the central and eastern Pacific show no evidence of contact since the Pliocene era thus indicating speciation by allopatry. Colborn et. al. hypothesized that speciation in bonefish occurs slowly and that genetic divergences has been shown to take 4-20 million years and most divisions are likely attributed to changes in geological boundaries that have appeared and disappeared over millions of years. Ultimately speciation in bonefish may be due to vicariant separations and the conservatism in niche use may represent stabilizing selection at a global scale in the tropics (2001).

II. Temporal changes as a source of speciation:

The diversity found in tropical marine fish may be due speciation over long time periods of sharing the same niche and not due to spatial segregation (Klanten et al., 2007). Genetic evidence in species such as *Naso valamingii* indicates that genetic differentiation has occurred temporally at a geological time scale for some species rather than spatially (Klanten et. al. 2007). Planes and Fauvelot (2002) have described how speciation may occur as species may have expanded and decreased their ranges during periods of climatic changes or geological changes. For example as the sea level has risen and fallen some reefs have been created and others have been lost. They present that distinct episodes of expansion and reconnection of populations over time from changes of physical barriers, such as changes in the depth of the ocean (revealing and covering landmasses) is responsible for speciation. Also some areas have been re-colonized or abandoned, thus leading to genetic divergence of some populations. Cycles of isolation, genetic divergence, and dispersal may have occurred multiple times in the history of a species, depending on its age, as the sea levels fluctuated. Throughout history there were probably four periods of isolation between locations since the Miocene period when sea levels were reduced and then increased. Then from the Miocene to Plestocene, sea levels dropped below their present day levels. It is quite possible that many populations have experienced both an expansion in their range due to a climatic change and a change in local demographics due to an increased area of available habitat. Range contractions on the other hand would reduce the number of populations and may bring together populations that were previously separated; these populations may or may not be able to interbreed.

Temporal fluctuations in gene flow may be caused by variations in inter-population distances, in the velocity of the transport medium, i.e. the water currents, or from variation in

the number of larvae entering into the water column (Paulay and Meyer, 2002). Klanten et. al.(2006) studied temporal partitioning in the reef fish, *Naso valamingii*. Despite a geographically comprehensive sampling array, they found evidence of temporal partitioning, not spatial as they predicted. They conducted genetic tests on their samples and concluded that the life history traits of this coral reef fish allow for substantial distribution geographically. The important life history traits of this fish include, long, overlapping generation times, long pelagic larval durations, larvae that have strong swimming abilities and adults that are semi-pelagic with an omnivorous diet. These life history traits combined with genetic analyses led Klanten et. al. to conclude that an extended, temporally distributed history along with the resilient life history of the species has produced temporal rather than spatial structuring of the populations of *Naso valamingii.*

Conclusions:

What are the driving forces behind reef fish speciation and how did genetic divergence occur initially? And, how is it possible that the diversity of reef fish is so high when the competitive exclusion principle states that only one specie may exist in a given ecological niche?

This paper offers no single answer to these questions, all methods are probably correct to some degree, it is probably different for different groups and length of larval period is also probably an important factor affecting large scale dispersal while niche specialization may be the driving force behind small scale speciations. Tropical reef fish speciation is driven mainly by spatial isolation, periods of temporal isolation, adaptive radiations, and reproductive isolation due to color morphologies and mate preference. The methods of speciation are nearly

as diverse as the number of different tropical reef fish species. In response to the second question, there is likely a very high level of diversity among reef fish due to their highly specialized niche occupations and many have the ability to speciate at very small scales thus further increasing the level of their niche specializations. Additionally it is interesting to note that species within the same taxonomic group seem to show similar methods of speciation. This could be a point of additional research. It may also be interesting in the future to address it was beneficial for so many color variations to evolve and why it is that many juveniles in closely related groups look almost identical in terms of color morphology.
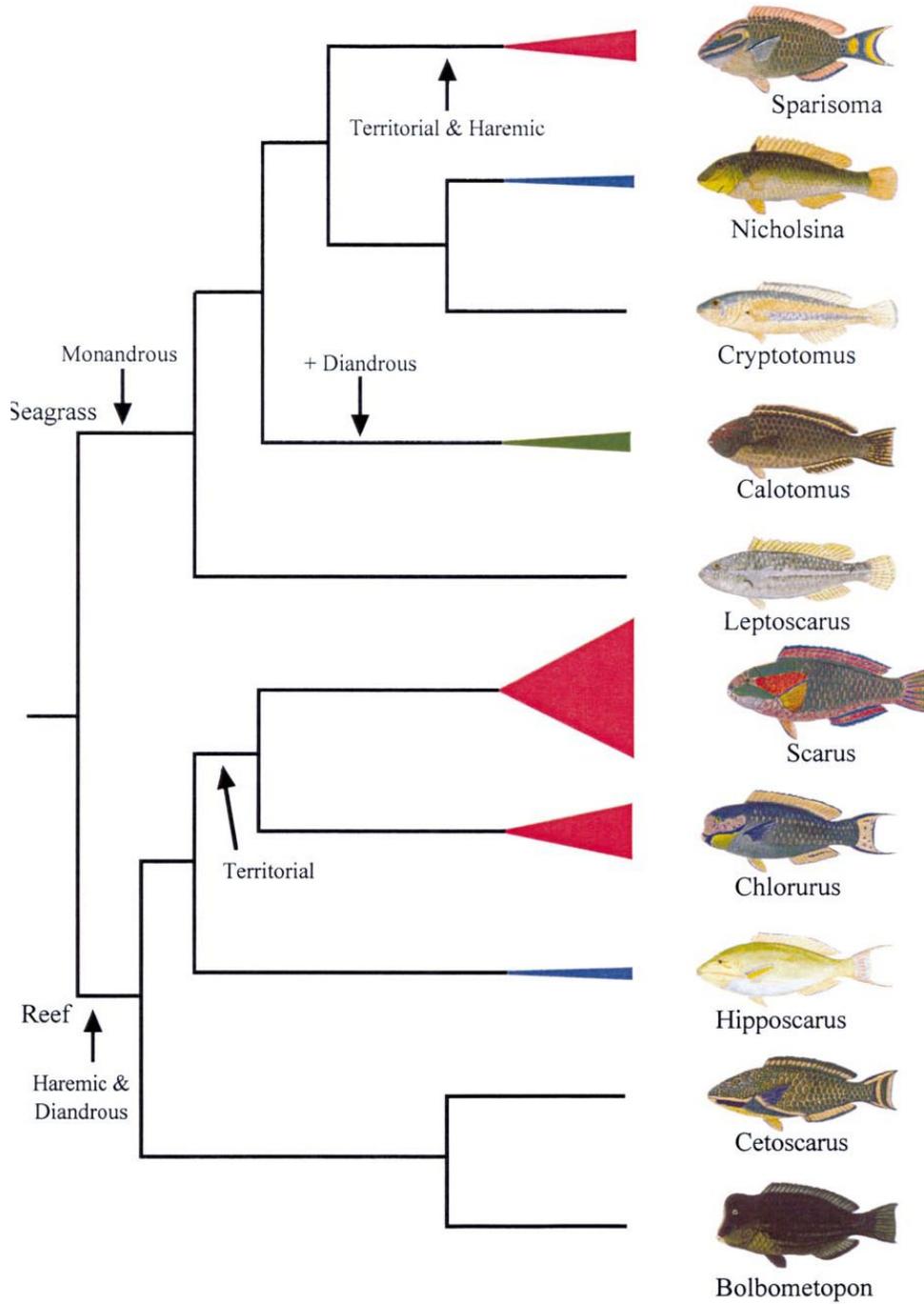
Figure 1. Evolution of male coloration and social breeding behavior (Streelman et. al., 2002).

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