PHYLOGEOGRAPHY AND EVOLUTION OF MESOPHOTIC CORAL ECOSYSTEMS

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By

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OBITUARY

Joshua “Josh” Michael Copus, scientific explorer, died unexpectedly on November 13, 2019 while exploring deep reefs off of Mborokua Island in the Solomon Sea. Josh was born on March 5, 1980 in Phoenix, Arizona to Carol (McRann) and Michael Copus. He was 39.

Raised for most of his younger years in Hulett, Wyoming, Josh later returned to Arizona and graduated from Moon Valley High School.

Having no prior experience with the ocean, Josh had a life-changing experience while taking a scientific diving class in Tahiti during his undergraduate degree. Here he developed a fascination with both scuba diving and coral reef fishes. The first in his family to attend college, Josh earned a Bachelor’s degree (2008) and Master’s degree (2011) in Biology from Northern Arizona University. Both his undergraduate and master’s projects focused on butterflyfishes with a growing interest in population genetics. In 2011, Josh started working on his doctorate degree in the Zoology department at the University of Hawai’i at Manoa with a focus on deep-reef fishes. He was 3 months away from defending his dissertation: Phylogeography and Mesophotic Coral Ecosystems. Based on his prolific record of scientific publications, Josh will posthumously receive his Ph.D. in Zoology from the University of Hawai’i at Manoa.

Josh’s scientific legacy lives on in many ways. He authored 21 (and counting) scientific publications. He described three new fish species and made many additional discoveries which will continue to be published posthumously. Josh dove to places that no person had ever seen, and discovered species no one knew existed. Over 100 scientists, to date, have used his publications. His valuable insights and contributions to marine biology will continue to influence scientific research and exploration for decades to come. In that light, he has taken his rightful place alongside the giants of science whom he admired.

Josh married his wife, Cassie Ka‘apu-Lyons, on March 19, 2011. In their time together, Cassie knew him not only as an amazing scientist, but first and foremost he was her best friend, her soul mate, her avid supporter, and her biggest fan. Josh was also a dedicated, loving father. He was the perfect punching bag, favorite chair, and epic superhero to his son Isaac, and he was proudly awaiting the arrival of their unborn child.

Josh is survived by his spouse and soul mate, Cassie, his children, Isaac and unborn child, his mother Carol (Dan McRann), his sisters Ambershea (Sean Sears), Kaylon (Zach Pike), father-in-law Dan Lyons, mother-in-law Cynthia, sister-in-laws Sydney Lyons, Kanoe Grioni, Ryenn Lyons, grandparents Chuck and Mary Copus, aunt's, uncles and numerous nieces, nephews and cousins. He is preceded in death by his infant brother Cory Copus, father Michael Copus, and grandparents Lillian and W.B. (Tom) Thomas.

Josh touched many lives in his 39 years, leaving those lives and this world in a better place. Through these impacts his presence will continue to live on.

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Without my family and friends, there is no way that I would complete the journey to a Ph.D. I especially want to thank my parents Carol and Michael Copus, my stepfather Dan McRann, and my sisters Ambershea and Kaylon. You have been there for me every step of the way. I love you guys. To my Hawaiʻi ʻohana - I could not have done this without you. Your friendship and love helped ground me.

Finally, I extend my deepest love and appreciation to my soulmate Cassie Kaʻapu-Lyons, my son Isaac, and the one not yet born. You made my life happy, fulfilling, and whole.
Mahalo nui loa

ABSTRACT

In this dissertation, I begin to address the phylogeography and evolution of the unique reef fish fauna of the mesophotic zone, generally regarded as beginning at 30 - 150 m depth. Chapter 1 is an introduction to the topic and background for subsequent chapters. As the field of mesophotic research matures, we can move beyond descriptive studies and begin to construct hypotheses for the origins and evolution of mesophotic reef fishes. Accordingly, Chapter 2 describes the habitat persistence hypothesis (HPH), which postulates that mesophotic reef fish communities are older and more stable than their shallow water counterparts. This hypothesis is based on two fundamental observations; 1) Mesophotic communities are extend below the surface waters that are subject to glacial sea level changes on a scale of 10^6 years, and 2) The shallow water biodiversity gradient, extending from the Coral Triangle (between Philippines, Indonesia, and New Guinea) to Rapa Nui in the eastern Pacific, may not apply to mesophotic communities. This chapter is a formal description of the HPH, and outlines a set of testable hypotheses to evaluate the validity of the HPH. Chapter 3 is a description of the mesophotic fish species *Neoniphon pencei.* Chapter 4 is a description of the mesophotic fish species *Luzonichthys seaver*, and Chapter 5 is a description of the mesophotic fish species *Prognathodes geminus*. These data will provide some of the first descriptions of MCE fishes, and provide a beginning point for testing phylogenetic hypotheses about the origins of mesophotic fishes. Chaper 6 provides a brief conclusion.

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CHAPTER 1

Introduction

Coral reefs are home to greater fish diversity (~6,000 species; almost one-fifth of all fishes) than any other single habitat (Pyle 1996*,* Myers 1999) and coral reef associated fishes exhibit vast diversity in color, behavior, ecology, phylogenetic relationships, and biogeographic patterns. However, diversity of coral reef fishes is not evenly distributed across space (Briggs 1999), and the causes of these diversity imbalances remain hotly debated. In tropical marine waters exist biodiversity hotspots, areas with very high numbers of species. These hotspots include the Indo-Australian Archipelago (IAA) between the Philippines, Indonesia, and New Guinea, the Caribbean Sea in the western Atlantic, and the Western Indian Ocean and biodiversity declines with distance from these hotspots (Bowen et al. 2013). For example, the IAA hosts ~3000 fish species, Hawaiʻi in the Central Pacific has ~630, while Rapa Nui (Easter Island), and has ~ 130. This pattern applies to vertebrate, invertebrate and plant phyla which indicates a universal evolutionary process effecting these biodiversity patterns (Bellwood & Wainwright 2002). In addition to this diversity gradient, another key feature is areas of high endemism. These endemism hotspots are not measured in absolute numbers of species but rather the relative number of endemic species at a given location. Some of these hotspots include Hawaiʻi (25% endemic fish species), Rapa Nui (22%), Red Sea (13%) and Marquesas (10%) (Randall 1998, Randall 2007, DiBattista et al. 2016). Biodiversity and endemism hotspots are the focus debate in the biogeography of tropical marine fauna, but the processes underpinning these patterns are not yet understood (Rocha & Bowen 2008, Cowman & Bellwood 2013, Hodge et al. 2014, Bowen et al. 2016).

The vast majority of scientific research on coral reefs has been confined to the shallowest 40m, leaving two thirds of the total depth ranges of coral-reef environments largely unexplored and drastically understudied. Consequently our foundational knowledge of coral reefs is biased to a fraction of the depth range of this ecosystem. The reason for this gap is due to physiological and technological limits imposed by breathing gases composed of a constant fraction of oxygen (F_{O2}) at elevated pressures on an open-circuit SCUBA system. Photosynthetic hermatypic corals have been found as deep as 98m in the Bahamas (Hartman 1973), 112m at Enewetak (Colin et al*.* 1986), 145m in the Red Sea (Fricke & Schuhmacher 1983) and 165m in Hawaiʻi (Kahng & Maragos 2006). Furthermore, photosynthetic algae have been observed to depths of 120m in the Bahamas (Porter 1973) and 140m at Enewetak (Colin et al*.* 1986, Hills-Colinvaux 1986). The historical shallow depth bias may obscure key evidence of the processes that affect biodiversity in tropical marine systems and comprehensive analysis of the communities at deeper depths may resolve the ongoing debate regarding biodiversity and endemism hotspots.

Recent advances in diving technologies have invigorated the scientific community and increased access to deeper reefs, called Mesophotic Coral Ecosystems (MCEs; light dependent ecosystems between 30-150m; Pyle & Copus 2019). However, the vast majority of recent publications (Kahng et al. 2014) are almost exclusively based on upper MCEs (~30-60m). These depths have been shown to be an extension of shallow coral-reef habitat where (depending on the location) a transition to what becomes a unique deep reef community begins (Hinderstein et al. 2010). The available evidence reveals the presence of unique communities of organisms at the lower MCEs (Copus et al. 2015a, Copus et al. 2015b, Pyle et al. 2016). However, little more is known about the ecology, distribution, or physiology of these unique fish communities. Additionally, exploration and research of MCEs has been geographically constrained to few areas in the Caribbean, Pacific and Red Sea due to the logistical challenges of conducting extended range decompression diving in remote locations, leaving most MCEs undiscovered and unexplored (Pyle & Copus 2019). Exploration of MCEs across the Pacific are ongoing and discoveries of new taxa abound (e.g. Copus 2015a, b, 2019; Pyle et al. 2018, Pyle et al. 2019), confirming that associated fish communities at these depths belong to taxonomic families typical of shallow-water coral reef habitat. Further, these discoveries are increasing known endemism rates on MCEs (Kosaki et al. 2017). At the same time, thousands of reef-associated fish species have yet to be discovered and described.

Biogeographic Hypothesis Testing

Two primary explanations for biodiversity gradient away from the IAA are the "center of speciation" hypothesis (Briggs 2003; Mora et al. 2003), and the "center of accumulation" hypothesis (Ladd 1960; Jokiel & Martinelli 1992). The former states that species are formed through intense competition in the high-diversity IAA and subsequently radiate outward, whereas the latter asserts that speciation occurs external to this center of diversity, with species accumulation towards the IAA (Bellwood & Hughes 2001). Similar to the "center of accumulation" hypothesis is the "overlap" hypothesis, which proposes that the high diversity of the IAA results from overlap of biogeographic provinces (Bellwood & Wainwright 2002; Gaither & Rocha 2013). It is important to note that these hypotheses invoke processes operating on time-scales involving speciation (10^7–10^8 yr) and rely on diversity patterns observed on the shallowest (<30m), least-stable fraction of reef habitat.

Much of the work addressing the evolutionary history of coral reef organisms, other than the few groups that leave a relatively strong fossil record, has been conducted on extant species and current distributions, and how current geology, and biodiversity interact to produce contemporary patterns of biogeography (Bellwood & Wainwright 2002; Bowen et al. 2013). Additional studies have focused on ancient vicariance such as the rise of the Isthmus of Panama ~3 million years ago (MYA) to explain the biodiversity patterns we see today (Bellwood & Wainwright 2002; Barber & Bellwood 2005). However, more recent historical processes and the importance of these processes in driving biodiversity patterns are often underappreciated.

Sea-level fluctuations associated with glacial cycles have also been invoked to explain patterns of marine biodiversity (Barber & Bellwood 2005; DiBattista et al. 2012). Throughout the Pleistocene (~2.5 Million years ago to 11.7 thousand years ago), the Earth has experienced cyclic fluctuations in temperature. These fluctuations, caused by long-term Milankovitch Cycles in the Earth's rotation and orbit, are made up of long periods of extreme cold called glacials and shorter periods of warming called interglacials. In the early half of the Pleistocene, these cycles were on the order of about 41 thousand years. After the Mid-Pleistocene Transition, however, the frequency of these cycles increased to a period of about 100 thousand years. During the glacials, much of earth's water is trapped in ice sheets (mostly in the higher latitudes) resulting in a drop in sea level much lower than present day levels (-120m). As the shorter warming periods cycle through, much of this water is released causing a rise in sea level to present day levels and higher. Although there is little debate about the existence of the Milankovich Cycles or their timing, duration, or amplitude, it is unclear how these events affect the biogeography of marine organisms, with many researchers still subscribing to a modern-centric paradigm of biogeography.

Remarkably, the sea level has been 30m or lower than current conditions for as much as 84.5% of the last glacial cycle (104 thousand years). Only about 11 thousand years ago did MSL rise above the -30m (below current MSL) depth. Consequently, the majority of present day coral-reef habitat was dry land for most of the glacial cycle and most shallow coral reefs are less than ten thousand years old. Due to the bathymetry of the world's oceans; a drastic drop in available habitat (~90%; Copus unpublished) for many marine organisms accompanies the drastically lower sea-levels that is the true norm for marine environments. This pattern has huge implications for marine biodiversity such as: 1) Glacioeustatic sea-level fluctuations may be a mechanism for causing population expansion and contraction in tropical-marine species as a result of fluctuating habitat availability and habitat fragmentation through time. This is not to say that all tropical marine species experience bottlenecks and expansions simultaneously. Instead these expansions coincide with availability of habitat, which is species specific. For instance, species that live in bays, estuaries, or lagoons may undergo bottlenecks during glacial cycles while species that are surge specialists may actually see population expansions due to the increase in the circumference of the surge zone in many locations. 2) Glaceoeustatic sea-level fluctuations could be a mechanism for speciation whereby intense competition resulting from reduced habitat availability or adaptive radiations into new unoccupied habitats with increases in sea level. Due to the capacity of most marine species for long distance dispersal, these geographic range of these radiations is not on the same scale as terrestrial organisms but likely on much broader scales (Bowen et al. 2020). These rapid radiations could explain patterns of recent divergences observed in some reef fishes such as the pygmy angelfishes (genus *Centropyge*; Gaither et al. 2014). 3) Species will experience range changes throughout the glacial cycle as organisms track suitable habitat. As sea-level rises and drops, the shifting bathymetric profile and changes in local environment will determine what habitat types (i.e. lagoons, bays, walls, etc.) are accessible at any given time. A species' range could be drastically affected by this fluctuation in available habitat. For example, during glacials, most of the Pacific Islands become steep wall habitat and lose much of the complex shallow habitat that currently exists. Species that rely on habitats such as bays, estuaries, and mangrove will likely not persist at many Pacific Islands through the glacial cycle. 4) In marine biogeography it is widely believed that 120m drops in sea level may limit gene flow between regions, causing temporary isolation or extirpations. However, because low sea levels predominate for most of the glacial cycle (~80%) it would be more accurate to say that the interglacial period represents a temporary population expansion prior to subsequent return to a more typical fragmented state. Therefore, many species will not experience temporary bottlenecks at the LGM but instead will experience temporary yet rapid population expansions during the interglacials due to huge increases in available habitat. Similarly, sea-level drop does not cause temporary barriers to dispersal (such as the Red Sea), but rather sea level rise may cause temporary connectivity where normally none exists. 5) It is postulated that during glacials many species will "hold out" in refugia (McCoy & Heck 1976) and subsequently expand outward when sea levels rise and habitat returns. However, it is misleading to assume refugia are required for tropical marine species that evolve in conjunction with these cyclic environmental pressures, wherein the glacials are the primary condition and the warmer interglacials are the exception.

It is necessary to escape the dogma that current sea level and current habitat availability are the baseline in which to compare the historical biogeography and evolution of populations and species, where changes in sea level may leave a temporary mark on an organism, before returning to the "normal" state of the present day. An example of this can be found in the Hawaiian Islands which contains over 600 near-shore fish species, of which approximately 25% are endemic (Randall 2007), the highest level of endemism of near-shore fishes anywhere in the world. This high rate of endemism is attributed to isolation, with hydrology often considered the main isolating factor because Hawaiʻi is not directly connected to the major Pacific currents. Recent research has revealed a gradient of endemics from the northern end of the archipelago (where nearly 100% of the fishes found on the deep reefs are endemic) (Kane et al. 2014; Kosaki et al. 20167) to the south (where many of the endemics are absent or are very deep). This gradation in abundance and depth distribution correlates to a cline in temperature across the archipelago. In Hawaiʻi a reduction of 3^{o}C (Lee et al. 2001) during the last glacial maxima (LGM) forced tropical marine fauna out of the higher latitudes. During glacials, tropical marine fauna may shift down the chain from the northwest to the southeast which have higher temperatures and more complex bathymetry. The fauna that persist in the higher latitudes are sub-tropical species with broad thermal tolerances, or deep reef species that can move shallower with reduced surface temperature. Species that persist in the lower Main Hawaiian Islands will be those that can use the limited habitat that persists during glacials. As temperatures slowly warm, tropical species are able to disperse away from their temperature refuges and recolonize the rest of the chain, extirpated species recolonize Hawaiʻi from other locations across the Pacific, and species with lower temperature tolerances are forced to the cooler waters of the northwestern end of the archipelago or into the deeper waters of the mesophotic coral ecosystems. It is not difficult to imagine that over the Pleistocene, glacial cycles act like a species pump, giving the Hawaiian fauna opportunities for diversification.

Endemic fish abundances increase latitudinally in the Northwest Hawaiian Islands both at shallow and MCE depths and MCEs have higher rates of endemism than their shallow counterparts at a particular location (Kane et al 2014). This increase in endemism coincides with the temperature decline with latitude. The Hawaiian archipelago, that spans over 10 degrees of latitude, also spans a surface thermal gradient of approximately 9^{o}C. Kane et al. (2014) report temperatures at mesophotic depths to be consistently cooler than surface waters suggesting thermal tolerances drive adaptive radiations in Hawaiʻi. Presence and absence reports (Mundy 2005) of fish species across the archipelago reveal 28 species of fish at Johnston Atoll (1390 km southwest of Hawaiʻi Island) that do not make it to the cooler waters of Hawaiʻi. Similarly, 30 species of fish are found at Hawaiʻi Island (in the far southeast) that have not been reported further north while another 30 species are found on the northern atolls of the archipelago but not in the warmer waters of the southern islands. Comparisons of occurrences of population expansions and bottlenecks among fishes from both shallow and deep waters (Copus unpublished) suggest that communities at different depths respond differently to glaciation. Further, consistent genetic breaks among taxa across the archipelago indicate that connectivity within the Hawaiian Archipelago is limited (Toonen et al. 2011). This pattern may be explained by differing thermal tolerances between organisms as SST warm resulting in variability in timing of recolonization from refuges or, the structure across the archipelago may be due to some lineages being more temperature tolerant than others.

The Habitat Persistence Hypothesis

Exploration of MCEs have revealed two qualitative patterns among fishes inhabiting deep-reef habitats that are inconsistent with patterns observed among shallow-reef habitats (i.e., the patterns upon which virtually all biogeographical hypotheses of coral-reef organisms are based). First, species restricted to deep reefs tend to have smaller geographical ranges than species restricted to shallow reefs, indicating that a greater proportion of fishes on deep reefs are endemic to specific geographical regions (Pyle 1999, Pyle 2000, Kane et al. 2014, Pyle et al. 2016, Pyle & Copus 2019). Second, the general pattern of high diversity in the Indo-Australian Archipelago (IAA), with attenuating diversity eastward across the tropical Pacific – well documented for many groups of organisms inhabiting shallow coral reefs – does not appear to exist among organisms inhabiting deep coral reef environments (Pyle 2000, Pyle & Copus 2019). These two fundamental differences between shallow and MCEs resulted in a new hypothesis for explaining the biogeographic patterns for tropical coral reef organisms called the Habitat Persistence Hypothesis (HPH; Chapter 2). The primary premise of the HPH is that the persistence of habitat over ecological and evolutionary timescales is correlated with the persistence of populations (or lack thereof) over those timescales, and broadly influences both the biogeographic distribution of organisms and their associated patterns of evolution. Six additional premises of the HPH are as follows:

1) *Relative sea level has changed throughout oceanic regions on a global scale* – During the last glacial maximum (LGM), a period that lasted from approximately 26.5 to 19 – 20 thousand years ago (ka), global sea level was approximately 120 m lower than it is today (Fairbanks 1989, Pillans et al. 1998, Peltier & Fairbanks 2006, Clark et al. 2009, Rohling et al. 2014, Lambeck et al. 2014). Fluctuations in relative sea-level (RSL) of approximately the same magnitude (depending on specific local factors that affect RSL compared to eustatic sea level; ESL) have occurred throughout tropical regions in association with glacial cycles at approximately 100-ka intervals during the mid-to-late Pleistocene (Hanebuth et al. 2000, Voris 2000, Bintanja et al. 2005, Bintanja & van de Wal 2008, Rohling et al. 2009, Elderfield et al. 2012).

2) *Falling RSL results in more substantive loss of shallow-reef habitats where existing bathymetry is steep or vertical, relative to gently sloping bathymetry that allows lateral habitat shifts as RSL falls* – Many oceanic atolls and islands are characterized by steep or vertical bathymetry extending downward hundreds of meters. By contrast, many continental islands (e.g., the IAA) and large volcanic archipelagos within Oceania (e.g., Hawaiian Archipelago, Fiji Islands and Marquesas Islands; see Pyle 2019b, Cabioch et al., 2008, respectively) have more gradually sloping bathymetry and/or shelves spanning the upper 150 – 200 m (hereinafter referred to as "sloped bathymetry"). As RSL falls, shallow-reef habitats such as mangroves, lagoons, patch reefs, barrier reefs, spur and groove habitats, and shallow fore-reefs (among others), disappear from oceanic atolls and islands with steep bathymetry (Kosaki et al. 1991, Fletcher & Sherman 1995, Nunn 1998, Dickinson 2004, Camoin & Webster 2015, Ludt & Rocha 2015, Coleman et al. 2018). Conversely, shallow-reef habitats are more likely to shift along bathymetric contours (and thereby persist across glacial cycles) in regions with more gradually sloped bathymetry.

3) *Loss of shallow-reef habitats leads to extirpation of populations of reef-associated species that require such habitats for part of their life cycles* – Classic island biogeography maintains that increased rates of local extinction will result from a decrease in habitat area (MacArthur & Wilson 1967). Many reef-associated species require shallow ecosystems for some or all of their life cycles, depend on shallow ecosystems for food or habitat, and/or rely on cues associated with

shallow-reef habitats for larval settlement (among other possible dependencies). During low RSL, shallow-reef habitat in the Pacific was reduced by approximately 90%, and in the Gulf of Mexico and Caribbean Sea by as much as 92% (Bellwood et al. 2015, Ludt & Rocha 2015). Complete or near-complete loss of these shallow-reef habitats in regions with steep bathymetry would likely lead to the demise of local populations of many reef-associated species (Kosaki et al. 1991, Nunn 1998, Ludt & Rocha 2015). By contrast, populations of reef-associated species are more likely to persevere across glacial cycles at regions with sloped bathymetry, where shallow-reef habitats are more likely to persist (Myers 1999, Tager et al. 2010).

4) *Restoration of high RSL generally leads to restoration of shallow-reef habitats in regions with steep bathymetry* – As RSL rises during inter-glacial periods, the various shallow-reef habitats are enhanced or restored at locations with steep bathymetry. The current shallow-reef habitats at oceanic atolls and islands have existed for only about ~8–9 ka, as the sea surface approached modern levels (Dickinson 2004). In regions with sloped bathymetry (including the IAA hotspot), shallow-reef habitats generally continue to persist as they shift along bathymetric contours upward with the rising RSL.

5) *Natural restoration of shallow-reef habitats in regions with steep bathymetry allows recolonization of previously extirpated species from regions where shallow-reef habitats persist* – As the geomorphological structure of shallow-reef habitats are restored with rising ESL, the potential to support previously extirpated species is likewise restored. Over time, these restored habitats are recolonized via dispersal from populations inhabiting regions with sloped bathymetry, where the shallow habitats (and the associated species) persist. Patterns of recolonization vary among species, depending on many factors (e.g., larval duration and other factors affecting dispersal potential, habitat specificity, restoration of ecological networks, oceanographic patterns, stochastic factors, distance from source, etc.), with some species able to recolonize relatively quickly across broad geographical ranges, and others less so.

6) *Deep-reef habitats and associated organisms are likely to persist, regardless of bathymetric profile* – Deep-reef habitats should persist during all RSL states regardless of whether the bathymetry is steep or sloped, because in most cases these habitats are already situated along mostly vertical bathymetry. Exceptions include regions where deep-reef habitat is dramatically reduced or eliminated during low RSL, such as certain regions around the Arabian Peninsula (DiBattista et al. 2018) and IAA (Myres 1999). In the majority of locations, however, a lowering of RSL by 120 m or more would not fundamentally change the geologic structure or other environmental parameters of these habitats. As RSL falls and rises, these deep-reef habitats should simply move up and down the steep slopes or vertical drop-offs, maintaining the same depth, habitat, and geophysical characteristics. However, deep-reef species may be subject to extirpation similar to shallow-reef species if they require shallow ecosystems for a part of their life cycles, depend on shallow ecosystems for food, and/or rely on cues associated with shallow-reef habitats for larval settlement (among other possible habitat dependencies).

Many of the existing hypotheses that attempt to explain the distribution of shallow-reef organisms yield overlapping predictions, confounding attempts to interpret which hypothesis best explains any given set of evidence. In Chapter 2, I present seven specific predictions that result from the HPH, most of which do not overlap the predictions from other diversity-gradient hypotheses.

This dissertation is a starting point for testing the predictions of the HPH. Rigorous evaluation of the HPH will require relatively complete inventories of, and collected samples from, both shallow and deep species assemblages at multiple localities across large geographical regions to assess patterns of diversity attenuation, establish rates of endemism (i.e., endemics can only be asserted as such when their absence from adjacent localities can be confidently established), and assess population genetic features. Additionally, it will be helpful to distinguish classes of species with respect to the habitats they occupy. In particular, species that are restricted to shallow-reef habitats are most likely to demonstrate patterns of extirpation during low RSL and subsequent recolonization in regions with steep bathymetry during high RSL. Likewise, species restricted to deep-reef habitats are less likely to be impacted by changes in RSL, and should reflect fundamentally different distributional and genetic patterns across their geographical ranges, compared to species restricted to shallow reefs. Evidence supporting or refuting predictions of the HPH will be less apparent when considering species that occupy both shallow- and deep-reef habitats. For such species, the persistence of deep-reef habitats would reduce the probability of extirpation from regions with steep bathymetry during low RSL; but populations of these depth generalists in regions with steep bathymetry may nevertheless be more heavily impacted by changes in RSL than they would be in regions where both shallow and deep habitats persist. Therefore, we expect a mixture of evidence from species with broad depth ranges.

Another class of species to consider when evaluating the HPH is the set of species that inhabit rocky shoreline habitats. Although the bulk of habitat that is expected to persist across glacial cycles in regions with steep bathymetry involves habitat below a depth of about 30 m, the foundation of the HPH concerns habitat persistence. One such habitat that we would expect to persist in all tropical regions (including those with steep bathymetry) is rocky shoreline, including intertidal and shallow subtidal habitats. Species inhabiting rocky shoreline habitats would have patterns concordant with species inhabiting deep-reef habitats, including regions with steep bathymetry. Documenting rocky shoreline habitats and associated species at uplifted islands (see fifth case study above) would help reveal which specific species are most likely to be included within this class.

In this dissertation, I begin to amass quantitative evidence to test the validity of the HPH in Chapter 2. To do this, I have attempted to compile species-level inventories of coral-reef fishes. Coral-reef fishes are among the most compelling targets for completing species-level inventories in marine environments because they provide an optimal combination of high diversity, extensive existing data content and information infrastructure, and large potential for discovery. Existing platforms like the *Catalog of Fishes*, Zoobank, FishBase, GBif, and Explorer's Log have provided tremendous digital resources for nomenclature, distribution data, and integration of multiple data sources. These resources have provided the ability to compile the most comprehensive dataset to date of coral-reef fishes unmatched in both completeness and accuracy to test the HPH. Additionally, I have collected and completed broad sampling of all members of a mesophotic coral reef fish sub-genus to assess the phylogenetic relationships of fishes on MCEs as well as population level sampling of two MCE fishes. With these samples I will provide the first data to test the predictions of the HPH. Chapter 3 is a description of the mesophotic fish species *Neoniphon pencei.* Chapter 4 is a description of the mesophotic fish species *Luzonichthys seaver*, and Chapter 5 is a description of the mesophotic fish species *Prognathodes geminus*. These data will provide some of the first descriptions of MCE fishes, hopefully providing a foundation to test some fundamental and potentially paradigm shifting patterns of biodiversity in the tropical coral-reef ecosystems.

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CHAPTER 2

The Habitat Persistence Hypothesis: A New Perspective on the Distribution of Coral-Reef Organisms

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Abstract

We reviewed patterns of biogeographical distributions of organisms inhabiting tropical coral reefs from both published and unpublished sources, incorporating our documented observations accumulated over three decades of exploration on deep coral-reef habitat (30 – 150 m) throughout the Pacific, and formulated the HPH to account for biogeographical patterns observed on both shallow and deep coral reefs. Initial observations and data suggest that species occurring on deep coral reefs show higher rates of endemism and less eastward diversity attenuation than their counterparts inhabiting shallow coral reefs. The HPH accounts for these biogeographical differences by stipulating that shallow-reef habitats tend to persist across glacial cycles and associated relative sea-level changes in regions with sloped bathymetry (e.g., continental regions and large islands), but are largely extirpated during periods of low relative sea-level in regions with steep bathymetry (e.g., coral atolls); in contrast to deep-reef habitats, which tend to persist in most regions. The HPH suggests that regions with habitat persistence are characterized by higher rates of endemism, and that patterns of attenuating diversity with increasing distance from centres of species richness are shaped by relatively recent recolonization of less persistent habitats from regions with greater habitat persistence. following subsequent restoration of those habitats. Whereas most existing hypotheses that attempt to explain biogeographical patterns observed on coral reefs rely on observations limited to shallow (<30 m) coral-reef habitat and invoke processes operating on speciation time-scales (10^7 – 10^8 yr), the HPH additionally incorporates patterns observed within the remaining 80% of coral-reef habitat (30 – 150 m) and invokes processes operating on time scales associated with sea-level changes (10^5 – 10^6 yr). The HPH posits seven specific predictions that can be directly tested to distinguish its role in shaping coral-reef biogeography from existing hypotheses.

Introduction

Much has been written about the observed distribution patterns of organisms inhabiting tropical coral reefs. Coral-reef biodiversity peaks in the western equatorial regions of the three major tropical oceans, with attenuating diversity along eastward and latitudinal gradients (Stehli & Wells 1971; Briggs 1974; Rosen 1984; Veron 1995; Myers 1999; Bellwood & Wainright 2002; Mora et al. 2003; Bellwood & Meyer 2009; Carpenter & Springer 2005). This pattern is most evident in the Pacific Ocean (Fig. 1). There is far less agreement on hypothesized mechanisms to explain the origin and causes of this general pattern (Bowen et al. 2013; Gaither & Rocha 2013; Bellwood et al. 2015). A thorough review of the various hypotheses is beyond the scope of this work; however, the different perspectives can be broadly clustered into several categories, including *vicariance models* (Springer 1982; McCoy & Heck 1976; Rosen 1984; Paulay 1990; Pandolfi 1992; Santini & Winterbottom 2002), *centres of origin* (Ekman 1953; McCoy & Heck 1983; Briggs 2003; Mora et al. 2003; Timm et al. 2008; Carpenter et al. 2011; Barber et al. 2011; Cowman & Bellwood 2013; Tornabene et al. 2015), *centres of accumulation* (Ladd 1960; Jokiel & Martinelli 1992; Connolly et al. 2003; Budd & Pandolfi 2010), *regions of overlap* (Woodland 1983; Hobbs et al. 2008; Gaither & Rocha 2013), *centres of survival* (McCoy & Heck 1976;

Barber & Bellwood 2005; Cowman & Bellwood 2013), and *models based on environmental and ecological parameters* (Newell 1971; Stehli & Wells 1971; Vermeij 1978; Springer & Williams 1990; Fraser & Currie 1996; Bellwood & Hughes 2001; Renema et al. 2008; Keith et al. 2013; Brown 2014).

No clear consensus has emerged for any of these hypotheses, and most recent treatments acknowledge that elements of several hypotheses are likely at play (Randall 1998; Wilson & Rosen 1998; Bernardi et al. 2004; Allen & Erdmann 2012; Bowen et al. 2013; Hodge et al. 2014; Bellwood et al. 2015; Bowen et al. 2016). These different biogeographical hypotheses are supported by varying degrees of empirical evidence, but in some cases different hypotheses have similar or congruous predictions, so it is not always clear which alternative biogeographical mechanism best explains the available evidence. Moreover, available evidence is fragmentary, and in some cases woefully lacking. Even for the most studied coral-reef organisms (fishes, scleractinian corals), accurate distribution patterns are not uniformly available. Comprehensive regional inventories of species exist only for a few localities (particularly throughout the Pacific and Indian Oceans), and even the fishes and corals are plagued by incomplete or unstable taxonomy (Forsman et al. 2010; Gaither et al. 2015). Perhaps the most significant limitation of existing hypotheses for coral-reef biogeography is that essentially all of the documented patterns of species distributions, "hotspots", endemism, and general diversity have been limited to observations of species occurring on the shallowest 30 m of coral-reef habitat, primarily due to the depth limitations of conventional SCUBA technology (Pyle 1998; Parrish & Pyle 2002; Pyle 2019a). Despite the limited knowledge of deep-reef habitats, hermatypic corals have been found at 98 m in the tropical Atlantic (Hartman 1973; Fricke & Meischne 1985; Reed 1985; Appeldoorn et al. 2019; Dustan & Lang 2019; Frade et al. 2019; Francini-Filho et al. 2019; Goodbody-Gringley et al. 2019; Reed et al. 2019; Slattery & Lesser 2019; Smith et al. 2019), 112 m at Enewetak (Colin et al. 1986), 145 m in the Red Sea (Fricke & Schuhmacher 1983; Eyal et al. 2019), and 165 m in Hawaiʻi and Johnston Atoll (Strasburg et al. 1968; Maragos & Jokiel 1985; Kahng & Maragos 2006; Pyle et al. 2016; Spalding et al. 2019a). Nearly 100% coral cover has been reported at 70 m on the Great Barrier Reef (Hopley 1991; Hopley et al. 2007; Bridge et al. 2011a, 2011b, 2012; 2019) and in Hawaiʻi (Pyle et al. 2016; Spalding et al. 2019a), and up to 60% coral cover at 60 – 75 m at Pulley Ridge in the Gulf of Mexico (Jarrett et al. 2005; Reed et al. 2019). Photosynthetic algae have been observed at similar or deeper depths (Porter 1973; Littler et al. 1985; Colin et al. 1986; Hills-Colinvaux 1986; Wagner et al. 2011; Spalding et al. 2019b), and fish species on reef habitats down to about 150 m belong almost exclusively to families typical of shallower coral-reef environments (Pyle 1996; Pyle 1999; Pyle et al. 2019b). Thus, the evidence about distribution patterns of coral-reef organisms is based on incomplete species inventories with inadequate taxonomic resolution, and limited to approximately one-fifth of coral-reef habitat. It should, therefore, come as no surprise that mechanisms underlying coral-reef biogeographical patterns remain unresolved.

Over the past three decades, the authors and collaborators have conducted dozens of surveys of deep coral-reef habitat (mesophotic coral ecosystems [MCEs]; 30 – 150 m; see Hinderstein et al. 2010; Baker et al. 2016; Loya et al. 2019) at twenty localities throughout the tropical Pacific (Fig. 1) (e.g., Pyle 1996; Pyle 1999; Pyle 2000; Wagner et al. 2014; Kane et al. 2014; Coleman et al. 2018; Pyle et al. 2016). These surveys (which serve as the basis for a large-scale biogeographical analyses currently in development) have revealed two qualitative patterns among species inhabiting deep-reef habitats that were both unexpected, and inconsistent with patterns observed among shallow-reef habitats (i.e., the patterns upon which virtually all biogeographical hypotheses of coral-reef organisms are based). First, species restricted to deep reefs tend to have smaller geographical ranges (on average) than species restricted to shallow reefs, which also means that *a greater proportion of species on deep reefs are endemic to specific geographical regions* (Pyle 1999; Pyle 2000; Kane et al. 2014; Pyle et al. 2016; Pyle & Copus 2019). Second, the general pattern of high diversity in the Indo-Australian Archipelago (IAA), with attenuating diversity eastward across the tropical Pacific – well documented for many groups of organisms inhabiting shallow coral reefs – *does not appear to exist among organisms inhabiting deep coral reef environments* (Pyle 2000; Pyle & Copus 2019).

Herein we describe a generalized explanatory model for patterns of coral-reef biogeography that includes distribution patterns observed throughout the entire depth range of coral-reef habitats. We do not represent this model as "the" explanation for patterns of species richness and endemism on coral reefs; rather, we introduce it as another possible mechanism shaping biodiversity patterns as they currently exist on coral reefs worldwide. Moreover, the model is rudimentary. The dynamics that have led to modern-day distribution patterns of coral reef biodiversity are likely almost as diverse as the organisms themselves. In our ongoing efforts to evaluate this model, we expect to find exceptions and idiosyncratic distribution patterns (as is the case for all generalized models of biogeography). Although this perspective was largely inspired by observations of species distributions on deep coral reefs throughout the Pacific (to be published elsewhere), its greatest implications relate to mechanisms affecting the distribution patterns of shallow-reef species. The section that follows represents a formal description of a novel biogeographical hypothesis relating to distribution patterns of coral-reef organisms, based on the relative persistence of habitat over evolutionary time-scales. Although the hypothesis itself is very general and may apply to biogeographic patterns in any environment involving different degrees of habitat persistence over time, herein we focus particularly on what is likely to be among the most important factors influencing persistence of coral-reef habitat: changes in sea level in response to glacial cycles and the corresponding influence of bathymetric profile. The aim of this paper is not to "prove" the application of the hypothesis with respect to coral-reef ecosystems; rather our intention is to clearly define the hypothesis, including a clear articulation of both the premises that under-pin it, and the specific predictions that result from it. Data necessary to support or refute the hypothesis will only come from many decades of future research involving careful documentation of biogeographic patterns, depth distributions, and ecology of species throughout many locations, and across the entire depth range of coral-reef ecosystems.

The Habitat Persistence Hypothesis

The general concepts behind the Habitat Persistence Hypothesis (HPH) were first outlined in the context of explaining biological diversity, richness and endemism of coral-reef fishes at Johnston Atoll (Kosaki et al. 1991). It was later developed into a generalized model, initially proposed as the "Center of Refuge" hypothesis (Pyle 2005). However, that label was easily confused with the "area of refuge" hypothesis (McCoy & Heck 1976; Paulay 1990; Bellwood & Hughes 2001; Carpenter & Springer 2005), as well as hypotheses about deep coral reefs serving as ecological refugia for shallow reefs (Hughes & Tanner 2000; Riegl & Piller 2003; Hinderstein et al. 2010; Bongaerts et al. 2010; Kahng et al. 2014; Baker et al. 2016; Bongaerts & Smith 2019).

The underlying premise of the HPH is that the persistence of habitat over ecological and evolutionary timescales is correlated with the persistence of populations (or lack thereof) over those timescales, and broadly influences both the biogeographic distribution of organisms and their associated patterns of evolution. Herein we provide a comprehensive description of the HPH in the context of tropical coral-reef ecosystems, with particular emphasis on the effects of sea-level changes and their effects on habitat persistence in regions with different bathymetric profiles. We include a detailed description of six premises and seven predictions related to the HPH in this context, as well as a discussion of key areas for future testing and other implications.

Premises

The six basic premises of the HPH in the context of coral-reef ecosystems, as illustrated in part in Fig. 2, are as follows:

1) *Relative sea level has changed throughout oceanic regions on a global scale* – During the last glacial maximum (LGM), a period that lasted from approximately 26.5 until 19 – 20 thousand years ago (ka), global sea level was approximately 120 m lower than it is today (Fairbanks 1989; Pillans et al. 1998; Peltier & Fairbanks 2006; Clark et al. 2009; Rohling et al. 2014; Lambeck et al. 2014). Fluctuations in relative sea-level (RSL) of approximately the same magnitude (depending on specific local factors that affect RSL compared to eustatic sea level; ESL) have occurred throughout tropical regions in association with glacial cycles at approximately 100-ka intervals during the mid-to-late Pleistocene (Hanebuth et al. 2000; Voris 2000; Bintanja et al. 2005; Bintanja & van de Wal 2008; Rohling et al. 2009; Elderfield et al. 2012; Lambeck et al. 2014). Although frequency and magnitude of historical sea-level changes (as well as differences between eustatic and relative sea level) vary, the core principles of the HPH apply regardless and are particularly applicable to how biogeographic patterns have been shaped since the LGM.

2) *Falling RSL results in more substantive loss of shallow-reef habitats where existing bathymetry is steep or vertical, than in regions where existing bathymetry allows lateral habitat shifts as RSL falls* – As illustrated in Fig. 2, many oceanic atolls and islands are characterized by steep or vertical bathymetry extending downward hundreds of metres (hereinafter referred to as "steep bathymetry"). By contrast, many continental islands (e.g., the IAA) and large volcanic archipelagos within Oceania (e.g., Hawaiian Archipelago, Fiji Islands and Marquesas Islands; see SOEST 2014; Pyle 2019b; Cabioch et al., 2008, respectively) have more gradually sloping bathymetry and/or shelves spanning the upper 150 – 200 m (hereinafter referred to as "sloped bathymetry"). As RSL falls, shallow-reef habitats such as mangroves, lagoons, patch reefs, barrier reefs, spur and groove habitats, and shallow fore-reefs (among others), disappear from oceanic atolls and islands with steep bathymetry (Kosaki et al. 1991; Nunn 1998; Dickinson 2004; Camoin & Webster 2015; Ludt & Rocha 2015). Conversely, shallow-reef habitats are more likely to shift along bathymetric contours (and thereby persist across glacial cycles) in regions with sloped bathymetry (see Fig. 2a-c). Although examples of both sloped and steep bathymetry can be found within many particular archipelagos and other similarly-sized geographic regions (e.g., Toomey et al. 2013), the important factor for the purposes of the HPH is the presence of substantial sloped bathymetry within a relatively small (~10's – 100's of km) geographic scale; such that meaningful amounts of shallow-reef habitat persists within the geographic range of a particular population of reef-dwelling organisms. It should also be noted that a *rise* in RSL can lead to shallow-reef habitat loss at coral atolls, in cases where the rise exceeds the rate at which corals and other reef-building organisms can grow vertically – the "Darwin Point" (Grigg 1982). In such cases, the resulting submerged reef ("drowned atoll") will also lack the suite of shallow-reef habitats as described above. However, this is not as likely to

have as broad-scale impact on species distribution as RSL drops, which affect the availability of shallow-reef habitats throughout all regions with steep bathymetry.

3) *Loss of shallow-reef habitats leads to extirpation of populations of reef-associated species that require such habitats for part of their life cycles* – Classic island biogeography maintains that increased rates of local extinction will result from a decrease in habitat area (MacArthur & Wilson 1967). Many reef-associated species require shallow ecosystems for some or all of their life cycles, depend on shallow ecosystems for food or habitat, and/or rely on cues associated with shallow-reef habitats for larval settlement (among other possible dependencies). During low RSL, shallow-reef habitat in the Pacific was reduced by approximately 90%, and in the Gulf of Mexico and Caribbean Sea by as much as 92% (Bellwood et al. 2015; Ludt & Rocha 2015). Complete or near-complete loss of these shallow-reef habitats in regions with steep bathymetry would likely lead to the demise of local populations of many reef-associated species (Kosaki et al. 1991; Nunn 1998; Ludt & Rocha 2015). By contrast, populations of reef-associated species are more likely to persevere across glacial cycles at regions with sloped bathymetry, where shallow-reef habitats are more likely to persist (Myers 1999; Tager et al. 2010).

4) *Restoration of high RSL generally leads to restoration of shallow-reef habitats in regions with steep bathymetry* – As RSL rises during inter-glacial periods, the various shallow-reef habitats are restored at locations with steep bathymetry (Fig. 2d). The current shallow-reef habitats at oceanic atolls and islands have existed for only about ~8–9 ka, as the sea surface approached modern levels (Dickinson 2004). In regions with sloped bathymetry, shallow-reef habitats generally continue to persist as they shift along bathymetric contours upward with the rising RSL. Certain exceptions to this exist (e.g., Webster et al. 2010); but in general, most locations relevant to the HPH have remained geologically stable at least since the LGM (e.g., Teger et al. 2010).

5) *Natural restoration of shallow-reef habitats in regions with steep bathymetry allows recolonization of previously extirpated species from regions where shallow-reef habitats persist* – As the geomorphological structure of shallow-reef habitats are restored with rising ESL, the potential to support previously extirpated species is likewise restored. Over time, these restored habitats are recolonized via dispersal from populations inhabiting regions with sloped bathymetry, where the shallow habitats (and the associated species) persist (Fig. 2d). Patterns of recolonization vary among species, depending on many factors (e.g., larval duration and other factors affecting dispersal potential, habitat specificity, restoration of ecological networks, oceanographic patterns, stochastic factors, distance from source, etc.), with some species able to recolonize relatively quickly across broad geographical ranges, and others less so.

6) *Deep-reef habitats and associated organisms are likely to persist, regardless of bathymetric profile* – Deep-reef habitats should persist during all RSL states regardless of whether the bathymetry is steep or sloped, because in most cases these habitats are already situated along mostly vertical bathymetry (Fig. 2). Exceptions include regions where deep-reef habitat is dramatically reduced or eliminated during low RSL, such as certain regions around the Arabian Peninsula (DiBattista et al. 2018) and IAA (Myres 1999). In the majority of locations, however, a lowering of RSL by 120 m or more would not fundamentally change the geologic structure or other environmental parameters of these habitats. As RSL falls and rises, these deep-reef habitats should simply move up and down the steep slopes or vertical drop-offs, maintaining the same depth, habitat, and geophysical characteristics. It should be noted that species inhabiting deep reefs may be subject to local extirpation similar to shallow-reef species if they require shallow ecosystems for a part of their life cycles, depend on shallow ecosystems for food, and/or rely on

cues associated with shallow-reef habitats for larval settlement (among other possible habitat dependencies).

In the context of these six premises, we hypothesize that the biogeographical patterns of shallow coral-reef ecosystems (i.e., the basis for competing hypotheses about the biodiversity gradient) are strongly shaped by *relatively recent (~10^5 – 10^6 yr) recolonization from regions across glacial cycles and associated RSL changes*. Specifically, certain regions (e.g., continental margins, the IAA, and major archipelagos such as the Hawaiian Archipelago, Fiji Islands and Marquesas Islands) allow shallow-reef habitats and their associated species to persist across multiple glacial cycles. This pattern has been documented at Papua New Guinea (region of sloped bathymetry), where every one of 76 coral, calcareous red algae, and formanifera taxa persisted across both high and low sea-level stands during the the past ~416 kyr (Tager et al. 2010). Populations in these regions serve as source populations that recolonize similar shallow-reef habitats in regions with steep bathymetry. Deep-reef habitats, by contrast, would persist at most localities across glacial cycles, regardless of the bathymetric profile. Thus, many deep-reef species assemblages would not be shaped by the same cyclical extirpation/recolonization process that shapes shallow-reef assemblages, and, therefore, should reveal different biogeographical patterns. Fig. 2 illustrates the hypothesized process with respect to RSL across a single glacial cycle.

A fundamental difference between the HPH and most other diversity-gradient hypotheses is that the latter invoke processes that occur across "evolutionarily significant time" (i.e., 10^7 – 10^8 years), whereas the former invokes processes that occur across "ecologically significant time" (i.e., 10^5 – 10^6 years) (Veron 1995). Premise 5 of the HPH presumes that many (if not most) coral-reef organisms are capable of long-distance dispersal to varying degrees, and that the process of recolonization of shallow-reef habitats in regions with steep bathymetry is driven largely by dispersal from regions with sloped bathymetry.

Predictions

Many of the existing hypotheses that attempt to explain the distribution of shallow-reef organisms yield overlapping predictions, confounding attempts to interpret which hypothesis best explains any given set of evidence. Here we assert seven specific predictions that result from the HPH, most of which do not overlap the predictions from other diversity-gradient hypotheses.

1) *There should be proportionally higher endemism in regions where habitats persist across evolutionary time-scales, than in regions where habitats are eliminated during low RSL* – If species that require shallow-reef habitats are more likely extirpated from islands with steep bathymetry, then populations of these species resulting from rare (>100 ka) colonization events are less likely to persist across evolutionary time scales. Consequently, they have a much shorter timeframe to diverge into unique (endemic) species. Instead, the shallow-reef habitats of islands with steep bathymetry should harbor proportionally more species that have been recolonized since the current high sea-level stand was re-established from other regions with sloped bathymetry. By contrast, regions with sloped bathymetry that favour shallow-reef habitat persistence should have proportionally higher rates of endemism among species that require shallow-reef habitats (compared to regions with steep-slope bathymetry), because populations resulting from rare colonization events at localities with sloped bathymetry are more likely to persist across evolutionary time scales, and thus have a longer timeframe to evolve into distinct species. Similarly, if deep-reef habitats persist through changing RSL due to glacial cycles at most localities (regardless of bathymetric profile), then novel populations of deep-reef species

resulting from rare colonization events are more likely to persist across evolutionary time scales, and thus ultimately evolve into distinct species. Differences in rates of endemism between deep-reef species and shallow-reef species in regions with sloped or steep bathymetry would be most pronounced when comparing species that are exclusive to each respective habitat depth (i.e., species restricted to deep reefs vs. species restricted to shallow reefs).

2) *There should be more examples of closely-related "species complexes" and "incipient species" in regions where habitats persist across evolutionary time-scales, than in regions where habitats are eliminated during low RSL* – In the same way that higher rates of endemism are predicted for persistent habitats, examples of species "complexes" (i.e., closely-related but taxonomically distinct sibling species) and "incipient species" (i.e., species with geographical variation and/or recognized as distinct at the subspecific level) are more likely to be present in regions with persistent habitat (deep-reef habitats and shallow-reef habitats in regions with sloped bathymetry). By contrast, if species restricted to shallow reefs in regions with steep bathymetry are primarily represented by recent recolonizations, then there should be fewer examples of young and incipient speciation.

3) *There should be greater average population genetic structure among species in persistent habitats, than in regions where habitats are eliminated during low RSL* – If shallow populations in regions with steep bathymetry are largely the product of recent recolonization, then such species should tend to have greater propensity for dispersal and, therefore, greater average gene flow. Consequently, there should be relatively low population genetic structure among species restricted to shallow-reef habitats in regions with steep bathymetry across geographical ranges (a possible signature of recent colonization). This pattern has been reported for shallow-reef species distributed across the Central-West Pacific (Craig et al. 2007; Reece et al. 2011; DiBattista et al. 2012; Gaither et al. 2015). By contrast, species capable of inhabiting deep-reef habitats, which are more likely to persist at most localities regardless of bathymetric profile, should include a mixture of species with high dispersal potential and gene flow, and species with lower dispersal potential and gene flow. Therefore, species inhabiting deep-reef habitats should tend to show greater average population structure across their geographical ranges, and genetic signatures consistent with older, more stable populations, compared with shallow-reef species in regions with steep bathymetry.

4) *There should be lower average genetic diversity among populations of shallow-reef species in regions with steep bathymetry, relative to conspecifics in regions with sloped bathymetry, or among populations of deep-reef species* – For genetic loci that are not under strong selection, genetic diversity is a function of effective population size (N_e), the mean number of successfully reproducing adults averaged across thousands of generations (Gillespie 2004). However, N_e is based on a harmonic mean, which is strongly influenced by population bottlenecks. If contemporary populations of species restricted to shallow-reef habitats in regions with steep bathymetry are the result of relatively recent recolonization (or persistence in small refugia), then the average genetic diversity should be lower, relative to populations of species that have persisted in sloped bathymetry or deep habitats. Indeed, some fish populations in shallow lagoon habitats around oceanic islands show genetic signatures of recent colonization (Fauvelot et al. 2003; Thacker 2004; Ludt et al. 2012).

5) *Genetic signals of recent population expansions should be less common in regions where habitats persist across evolutionary time-scales, than in regions where habitats are eliminated during low RSL* – Population expansion during the last 20 ka will leave distinctive genetic signatures which include an overabundance of rare closely-related haplotypes (Fu & Li 1993). If

species restricted to shallow reefs in regions with steep bathymetry are experiencing population expansions following RSL rise, we expect that these populations should have significant negative values of Fu's F_S statistic (Fu 1997). By contrast, populations on deep reefs and shallow reefs with sloped bathymetry should tend to have equilibrium N_e values.

6) *There should be less eastward attenuation of diversity among species in persistent habitats, compared with regions where habitats are eliminated during low RSL* – Regions with sloped bathymetry (e.g., east Africa and Madagascar, the IAA, Caribbean, eastern Brazil) tend to dominate in the western parts of the three major tropical oceans, whereas central and more eastern regions (particularly in the Pacific) tend to be dominated by oceanic islands and coral atolls with steep bathymetry. According to the HPH, the pattern of eastward diversity attenuation of shallow-reef species is largely the result of recolonization of oceanic atolls and islands with steep bathymetry following RSL drops and associated shallow-reef habitat loss. If deep-reef habitats are more persistent across longer time periods at oceanic atolls and islands, then there should be less-pronounced habitat loss and species extirpation from deep-reef habitats following RSL drops. Instead, the distribution pattern among deep-reef organisms should show a more homogeneous pattern of diversity across large geographical areas.

7) *There should be an attenuation of diversity among shallow-reef species in regions with steep bathymetry correlating with increasing distance from regions with sloped bathymetry* – Most biogeographical hypotheses concerning coral-reef organisms focus on patterns of diversity as they relate to regions with high diversity (e.g., the IAA, western Indian Ocean, Caribbean). By contrast, the HPH focuses on patterns of diversity as they relate to regions with habitat persistence. Although regions with high diversity are mostly congruous with regions of hypothesized habitat persistence, there are key exceptions. Specifically, within the Pacific Ocean, the HPH predicts that certain regions with sloped bathymetry (e.g., the Hawaiian Archipelago, Fiji Islands, Marquesas Islands, Easter Island) are also characterized by persistent shallow-reef habitat. Rather than patterns of distribution radiating only from "hotspots" of shallow-reef diversity, the HPH predicts patterns of distribution of shallow-reef organisms that radiate from regions with shallow-reef habitat persistence. As such, we predict that shallow-reef species assemblages on oceanic atolls and islands with steep bathymetry will be most similar to those at nearby localities with sloped bathymetry (including certain archipelagos without high diversity). Moreover, species with greater dispersal potential should, on average, recolonize further from regions with shallow-reef persistence than species with less dispersal potential.

DISCUSSION

Testing the predictions of the Habitat Persistence Hypothesis requires relatively complete inventories of, and collected samples from, both shallow and deep species assemblages at multiple localities across large geographical regions – to assess patterns of diversity attenuation, establish rates of endemism (i.e., endemics can only be asserted as such when their absence from adjacent localities can be confidently established), and assess population genetic features. It is difficult to amass this level of quantitative data among shallow-reef assemblages; to do so among deep-reef species requires many field expeditions using advanced diving technologies, submersibles, or remote survey technologies. Direct, quantitative evidence to test these predictions is ongoing.

Nevertheless, our extensive observations on deep coral reefs throughout the Pacific (Fig. 1) qualitatively support two key predictions of the HPH. The first (and least quantified) observation is that deep-reef fish communities appear no more diverse in terms of species richness within the IAA (e.g., Indonesia, Philippines, New Guinea) and other western-Pacific localities (e.g., Ryukyu Islands, Taiwan, Palau, Vanuatu, Fiji), than they do in Central Pacific regions (e.g., Kiritimati, Cook Islands, Society Islands) (Prediction 6).

The second pattern we have observed supports Prediction 1: proportionally higher rates of endemism among deep-reef species compared to endemism among shallow-reef species (Pyle 2000; Kane et al. 2014; Pyle et al. 2016). Fig. 3 shows a comparison of species overlap among both deep- and shallow-reef fish species between Palau, Papua New Guinea and Fiji. Species overlap is nearly ten times greater among shallow reef fishes than among deep-reef fishes. Less species overlap indicates more restricted distributions, and thus higher rates of endemism.

Although the concept behind the HPH was inspired by observations made throughout the tropical Pacific, the principles should also apply to the Indian Ocean and potentially the tropical Atlantic Ocean as well (albeit to a much lesser extent). This may be observed when comparing regions with complex bathymetry within the upper 200 m (e.g., eastern African continent, Madagascar in the Indian Ocean; eastern American continent, Caribbean, and eastern Brazil in the Atlantic Ocean) to regions with primarily vertical bathymetry across this depth range (e.g., Chagos Archipelago, Maldives in the Indian Ocean; Bermuda, Ascension, St. Helena, and St. Paul’s Rocks in the Atlantic Ocean). The application of the HPH within the tropical Atlantic is limited. The entire Caribbean is comparable in both scale and general bathymetric characteristics to the IAA, and as such, we would not expect the predictions of the HPH to be borne out within the Caribbean any more than we would expect them to be within the IAA. As noted above, only a few isolated oceanic islands exist within the tropical Atlantic, so while it is possible that the mechanisms of the HPH may have influenced the broader distribution of species in parts of the tropical Atlantic, the potential for testing the predictions is far lower than in the Pacific and Indian Oceans. Nevertheless, a comparison of the broader Caribbean with oceanic islands such as Bermuda, Ascension, St. Helena, and St. Paul’s Rocks could prove insightful, as shallow-reef habitat in the latter locality would be reduced to a narrow band along the sloping sides of the Bermuda Platform (Armstrong & Singh 2011; Locke et al. 2013). Indeed, both Ascension and St. Paul’s Rocks harbor a number of endemic species, most of which are known to inhabit deeper-reef environments. Below we provide some considerations when gathering and analyzing evidence in the context of the HPH.

Key Locations for Future Testing

We have identified several key locations where robust documentation from existing and future studies of both deep and shallow species assemblages would allow direct tests of patterns predicted by the HPH and other biogeographical hypotheses.

One example, for which extensive data has already been published, involves the Hawaiian Archipelago. The bathymetry of most of the Archipelago is very well established (Miller et al. 2006; Hawaiʻi Mapping Research Group 2014; PIBHMC 2015), and the distribution of many reef-associated organisms (particularly fishes) inhabiting both shallow and deep coral reefs are well documented (Randall 2007; Pyle et al. 2016; Spalding et al. 2016a). The bathymetry throughout most of this archipelago is dominated by gradual slopes and/or near-horizontal shelves, with evidence that shallow shoreline habitats (such as spur-and-grooves) existed at lower sea levels (Stearns 1978; Fletcher & Sherman 1995; Webster et al. 2009; Faichney et al. 2010, 2011) (Figs 4 & 5). High rates of shallow-reef endemism among Hawaiian species, as well as even higher rates of endemism among deep-reef species (Kane et al. 2014; Pyle et al. 2016; Spalding et al. 2019a) support Prediction 1. Comparisons have already been made to nearby Johnston Atoll, a coral atoll with near-vertical bathymetry, which initially inspired the HPH (Kosaki et al. 1991; Wagner et al. 2014). Johnston Atoll has fewer total species of reef and shore fishes (323 vs. 622 in Hawaiʻi) and only one endemic fish species (*Centropyge nahackyi* Kosaki 1989; occasionally reported from Hawaiʻi), in contrast to about 25% endemism among reef and shore fishes in the Hawaiian Archipelago (Kosaki et al. 1991; Randall 2007; Wagner et al. 2014; Pyle et al. 2016). However, this comparison is confounded by the much smaller size of Johnston Atoll. In terms of genetic diversity, Johnston Atoll and Hawaiʻi have similar levels of mtDNA variability in a number of reef fishes, including *Centropyge loriculus* (Günther, 1874) (Schultz et al. 2007), *Chaetodon multicinctus* Garrett, 1863 (Craig et al. 2010), *Zebrasoma flavescens* (Bennett, 1828) (Eble et al. 2011), *Halichoeres ornatissimus* (Garrett, 1863) (Ludt et al. 2012), and *Parupeneus multifasciatus* (Quoy & Gaimard, 1825) (Szabo et al. 2014). However, the surgeonfish *Acanthurus nigroris* Valenciennes, 1835 (DiBattista et al. 2011) has significantly lower mtDNA haplotype diversity at Johnston Atoll ($h = 0.22$) versus Hawaiʻi ($h= 0.52$), consistent with Prediction 4. Notably, this species may be the best test of HPH predictions, because it shows strong isolation between Johnston Atoll and Hawaiʻi (most of the others do not), indicating independent population trajectories. Similar comparisons between Hawaiian reef populations and those at Johnston Atoll could be made with populations occurring at Minami Tori-Shima (formerly Marcus Island).

Another example is the Marquesas Islands, which are similar to the Hawaiian Archipelago both in terms of bathymetric profile and shallow-reef endemism. Unlike the Hawaiian Archipelago, the deep-reef communities of the Marquesas have not yet been documented. Doing so would allow testing of HPH predictions. In particular, the proximity of the Marquesas to the Society Islands (dominated by atolls and islands with steep bathymetry) will allow robust testing of Prediction 7, especially given that the HPH predicts patterns that contrast with other coral-reef biogeographical hypotheses.

The third example involving the IAA, Palau, and Fiji is represented in Fig. 3 (see also Pyle & Copus 2019). Preliminary data reveal greater overlap among shallow-reef fish species between localities compared with deep-reef species (and, hence, higher endemism among deep reefs). Palau is a group of islands with mostly vertical bathymetry, and is less than 1,000 km north and east of the IAA. Fiji is a group of islands with sloped bathymetry, and is more than 3,000 km east of the IAA. Traditional hypotheses of coral-reef biogeography would predict much greater biological affinity between the IAA and Palau among both shallow- and deep-reef species relative to Fiji, based on geographical proximity. By contrast, the HPH would predict similar degrees of biological affinity among deep-reef species at all three locations, and much less difference in faunal affinity among the shallow-reef species; or perhaps even greater affinity between the IAA and Fiji than between the IAA and Palau. The HPH predicts that more shallow-reef species would persist in the IAA and Fiji across glacial cycles relative to Palau (which the HPH would predict is still being recolonized from the IAA after shallow-reef habitat loss during the LGM). More comprehensive surveys of both deep- and shallow-reef species of these regions would allow effective testing of such HPH predictions.

The fourth example would involve a comparison of both deep and shallow species at Rapa Nui (Easter Island), with nearby Pitcairn and Rapa islands, and the Tuamotu Archipelago. The bathymetry of Rapa Nui, Pitcairn and Rapa is sloped, so shallow-reef habitats are more likely to persist across glacial cycles than shallow-reef habitats within the Tuamotu Archipelago. As with the Marquesas, a comparison of both shallow and deep species at these localities would represent an effective test of all of the HPH predictions, especially Prediction 7.

The fifth example involves uplifted islands. One of the premises of the HPH is that at times of lower RSL there will be a loss of shallow-reef habitats in regions with steep bathymetry, which in turn results in the loss of species that require shallow-reef habitats for part of their life cycles. Several islands throughout the Pacific (e.g., Henderson, Makatea, Niue, Fais) are geologically anomalous in that they are uplifted relative to the current high sea-level stand, and thus represent what many islands and atolls throughout the Pacific would look like during periods of lower sea level (McNutt & Menard 1978). Comprehensive surveys of uplifted Pacific islands should result in reduced numbers of species compared to nearby islands that are not uplifted (and therefore maintain the full complement of shallow reef habitats).

The sixth example involves regions where shallow-reef habitat persists across glacial cycles, but deeper habitat does not. In particular, the region around the Arabian Peninsula (including the Red Sea) is such that deep habitats may be largely extirpated during low RSL (Ludt & Rocha 2015). In these cases, the HPH predicts that the deep-reef would be less persistent and therefore reflect patterns similar to those of shallow-reef habitat in areas of steep bathymetry. Conversely, the shallow-reef habitats in these areas would more likely persist, reflecting patterns consistent with other areas with sloped bathymetry. High rates of endemism and persistent populations across glacial cycles have been documented for butterflyfishes in this region (DiBattista et al. 2018).

Finally, seamounts may represent other useful examples in terms of their availability as coral-reef habitat and stepping-stones during periods of lower RSL. Among those listed in the Global Seamount Database (Kim & Wessel 2011), 645 seamounts within tropical latitudes reach depths shallower than 300 m of the current sea surface level (and thus the lower limits of coral-reef habitat, 150 m, during the lowest sea-level stands). It is possible that some of these seamounts may have played a role in facilitating dispersal of deep-reef species, and possibly to a lesser degree shallow-reef species during low sea-level stands. Seamounts may have allowed deep-reef habitat to persist in regions where shallow reef habitat did not exist during the Pleistocene, and as such may have played a role in impacting Predictions 1 and 2.

Species Classes

To test the predictions of the HPH, it is helpful to distinguish several classes of species with respect to the habitats they occupy. Evidence supporting or refuting predictions comparing shallow-reef species to deep-reef species should be most apparent in species restricted to each of these respective habitats. In particular, species that are restricted to shallow-reef habitats are most likely to demonstrate patterns of local extirpation during low RSL and subsequent recolonization in regions with steep bathymetry during high RSL. Likewise, species restricted to deep-reef habitats are less likely to be impacted by changes in RSL, and should reflect fundamentally different distributional and genetic patterns across their geographical ranges, compared to species restricted to shallow reefs.

Evidence supporting or refuting predictions of the HPH will be less apparent when considering species that occupy both shallow- and deep-reef habitats. For such species, the persistence of deep-reef habitats would reduce the probability of extirpation from regions with steep bathymetry during low RSL; but populations of these depth generalists in regions with steep bathymetry may nevertheless be more heavily impacted by changes in RSL than they would be in regions where both shallow and deep habitats persist. Therefore, we expect a mixture of evidence from species with broad depth ranges.

Another important class of species to consider when evaluating the HPH predictions is the set of species that inhabit rocky shoreline habitats. Although the bulk of habitat that is expected to persist across glacial cycles in regions with steep bathymetry involves habitat below a depth of about 30 m, the foundation of the HPH concerns habitat persistence. One such habitat that we would expect to persist in all tropical regions (including those with steep bathymetry) is rocky shoreline, including intertidal and shallow subtidal habitats. Species inhabiting rocky shoreline habitats would be expected to have patterns concordant with species inhabiting deep-reef habitats, including regions with steep bathymetry. Documenting rocky shoreline habitats and associated species at uplifted islands (see fifth case study above) would help reveal which specific species are most likely to be included within this class.

Alternate Hypotheses

Clearly, the HPH does not account for all biogeographical patterns in reef-associated species. Under a strict interpretation of the HPH, if shallow-reef habitat in the Hawaiian Archipelago has persisted for as long as shallow-reef habitats within the IAA, then we would expect the same level of diversity among shallow-reef species. Clearly this is not the case: the shallow coral-reef biodiversity within the IAA is five to six times greater than that of the Hawaiian Archipelago (Randall 2007; Allen & Erdmann 2012). The discrepancy in total diversity is no-doubt a result of multiple factors, such as much larger total habitat area (at all sea levels), greater overall diversity of habitat types within IAA (Woodland 1990; Randall 1998), overlapping of species from the Indian Ocean and Pacific Ocean (Gaither & Rocha 2013), historical factors (Cowman & Bellwood 2013; Hodge et al. 2014), and many other processes operating on both evolutionary and ecological time scales.

The HPH shares some characteristics with the ‘Centre of Survival’ hypothesis (McCoy & Heck 1976). However, this and similar discussions (Barber & Bellwood 2005; Cowman & Bellwood 2013) focused on the IAA, maintaining that lower extinction rates are (at least partially) responsible for high biodiversity. The HPH is a more generalized explanation that applies to the IAA as well as other regions in all tropical seas where differences in habitat persistence (both geographically and across depths) show different levels of endemism and genetic signatures of persistence.

It is not clear how extensively the principles of the HPH may be operating in continental margins in the eastern tropical oceans (in terms of serving as persistent source populations to recolonize nearby islands with steep bathymetry); other factors operating in eastern oceans, such as annual temperature cycles and oceanic current patterns, geological history, the distribution and paucity of oceanic islands and atolls with steep bathymetric profiles, and a multitude of other factors lead us to believe that the principles of the HPH may impact biogeographical patterns of marine organisms less extensively within the eastern oceans. Moreover, the HPH is primarily focused on coral-reef habitats and their associated organisms. While scleractinian corals flourish in eastern oceans, the nature and extent of coral-reef ecosystems are dramatically different from those of western and central tropical oceans.

As stated earlier, we do not represent the HPH as "the" explanation for patterns of biological diversity, richness and endemism on coral reefs. However, the HPH addresses patterns of endemism and the general pattern of eastward attenuation of shallow-reef species diversity across all three tropical oceans, which are the major patterns that have shaped biogeographical hypotheses of coral-reef organisms.

Alternate Environments

Although the HPH was conceived and formulated in response to observed biogeographic patterns of organisms within coral-reef ecosystems, its general principles apply to any environment. We would expect analogous biogeographic patterns to exist among organisms in other marine and terrestrial ecosystems that have experienced differences in degrees of broad-scale habitat persistence across ecological and evolutionary timescales. For example, Jacquet et al. (2015) found that climatic oscillations over the Pleistocene probably played a major role in shaping the genetic diversity within a species complex of African Shrews, which may be analogous to the effects of glacial cycles on tropical coral reefs. A detailed review of the potential relevance of the HPH to other environments is beyond the scope of this paper; however, it is likely that the general principles outlined in the premises and predictions described herein could be adjusted for any environments (terrestrial or marine) where heterogeneous habitat persistence may have played a role in shaping biogeographic patterns.

Summary

According to the HPH as applied to tropical coral-reef ecosystems, most coral-reef habitats (both shallow and deep) tend to persist across glacial cycles and associated changes in RSL in regions with sloped bathymetry within the upper 200 m, because these habitats are likely to shift along the bathymetric profile during periods when RSL changes. In regions characterized by steep or vertical bathymetry (e.g., oceanic islands and atolls), deep-reef habitats (which already exist on vertical or near-vertical bathymetry) persist by shifting up and down with changes in RSL; whereas many shallow-reef habitats (and the associated organisms that require them) disappear or are greatly reduced during low RSL. Speciation is more likely to occur in regions where habitat persists across evolutionary time scales – an expected feature of most deep coral reefs and those shallow reefs that exist in regions with sloped bathymetry. By contrast, populations of shallow-reef organisms are less likely to persist in regions characterized by steep bathymetry (such as many oceanic islands and atolls), and therefore biogeographical patterns are more likely to be shaped by relatively recent recolonizations from regions with persistent shallow-reef habitat during the past ~8 – 9 ka (i.e., ecological time scales). Thus, the HPH posits that much of the pattern of eastward attenuation in species diversity observed in tropical oceans is shaped by patterns of relatively recent recolonization, rather than patterns of speciation. Whereas most other hypotheses concerning coral-reef biogeography are based only on shallow-reef species, the HPH is more consistent with observed distribution patterns of species throughout the entire depth range of coral-reef habitat. A series of predictions resulting from the HPH can be tested through more complete documentation of distribution patterns of both shallow- and deep-reef species distributions, and associated patterns of genetic diversity and phylogeography.

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Figure Legends

Figure 1. Map of the tropical Pacific, showing pattern of eastward attenuation of shallow-reef species diversity, overlayed with locations of preliminary deep-reef exploration surveys conducted during the past two decades.

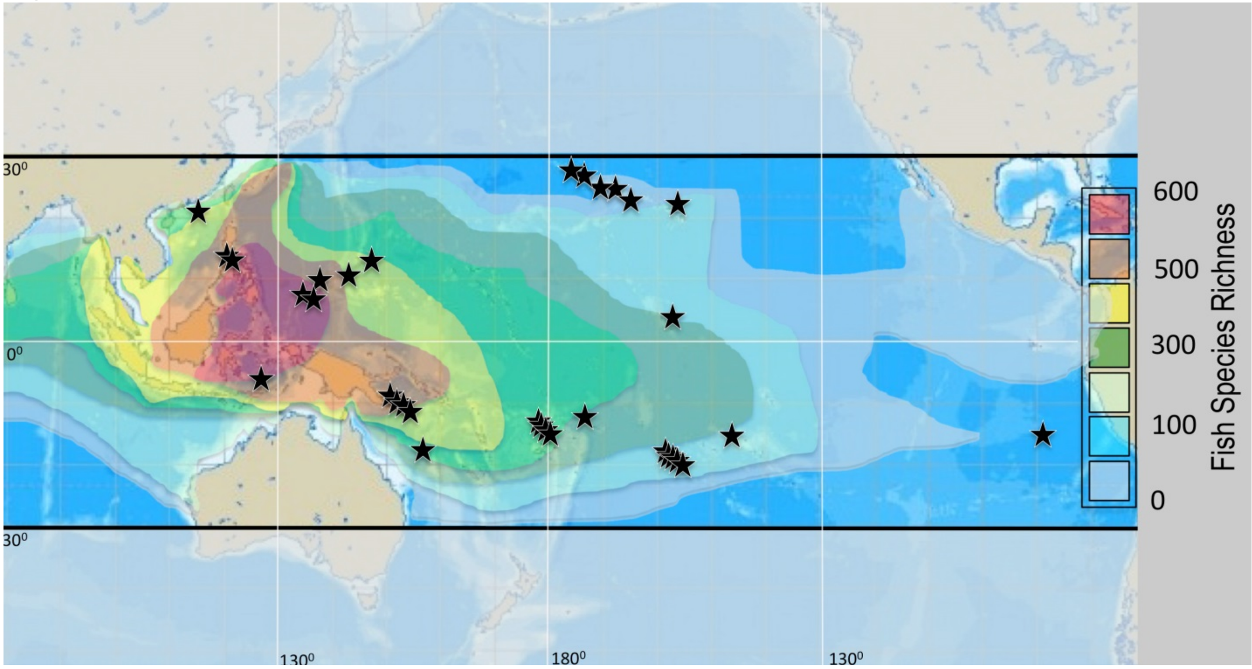
Figure 2. A diagramatic representation of the mechanism underlying the Habitat Persistence Hypothesis, showing the effects of different phases of a single glacial cycle and associated changes in relative sea level (RSL) on shallow and deep coral-reef habitats (and associated species assemblages) at locations with different bathymetric profiles. a) At the end of an interglacial high RSL, shallow- and deep-reef habitats exist at all localities. b) As RSL drops, shallow and deep habitats shift along the bathymetric contours of localities with sloped bathymetry, but disappear from localities with steep bathymetry. c) During periods of low RSL, most shallow and deep habitats persist at localities with sloped bathymetry, but only deep-reef habitats persist at localities with steep bathymetry. d) After high RSL is restored, shallow-reef habitats at localities with steep bathymetry are likewise restored, and these habitats are recolonized from source populations that persisted across all phases of the glacial cycle at localities with gradually sloping bathymetry. Thus, biogeographical patterns among shallow-reef organisms on many islands with steep bathymetry are more likely shaped by relatively recent dispersal from regions with persistent shallow habitat, whereas patterns of deep-reef organisms are shaped proportionally more by speciation processes operating on longer time scales. Diagrams modified from Pyle 2005.

Figure 3. Comparison of species overlap between Palau, Papua New Guinea and Fiji for shallow-reef fishes and deep-reef fishes. Less species overlap among deep-reef species implies higher rates of endemism. Modified from Pyle (2005).

Figure 4. Ancient shoreline 60 m deep in the Hawaiian Archipelago. Such features are common throughout the Archipelago at approximately 30 m, 60 m, 90 m, and 120 m depth, and closely resemble analogous habitats along modern shorelines. This, in part, supports Premise 2 of the Habitat Persistence Hypothesis in that shallow-reef habitats migrate along with changes in relative sea level at localities with gradually sloping bathymetry in the upper 0-100 m depth. Photo: R. L. Pyle.

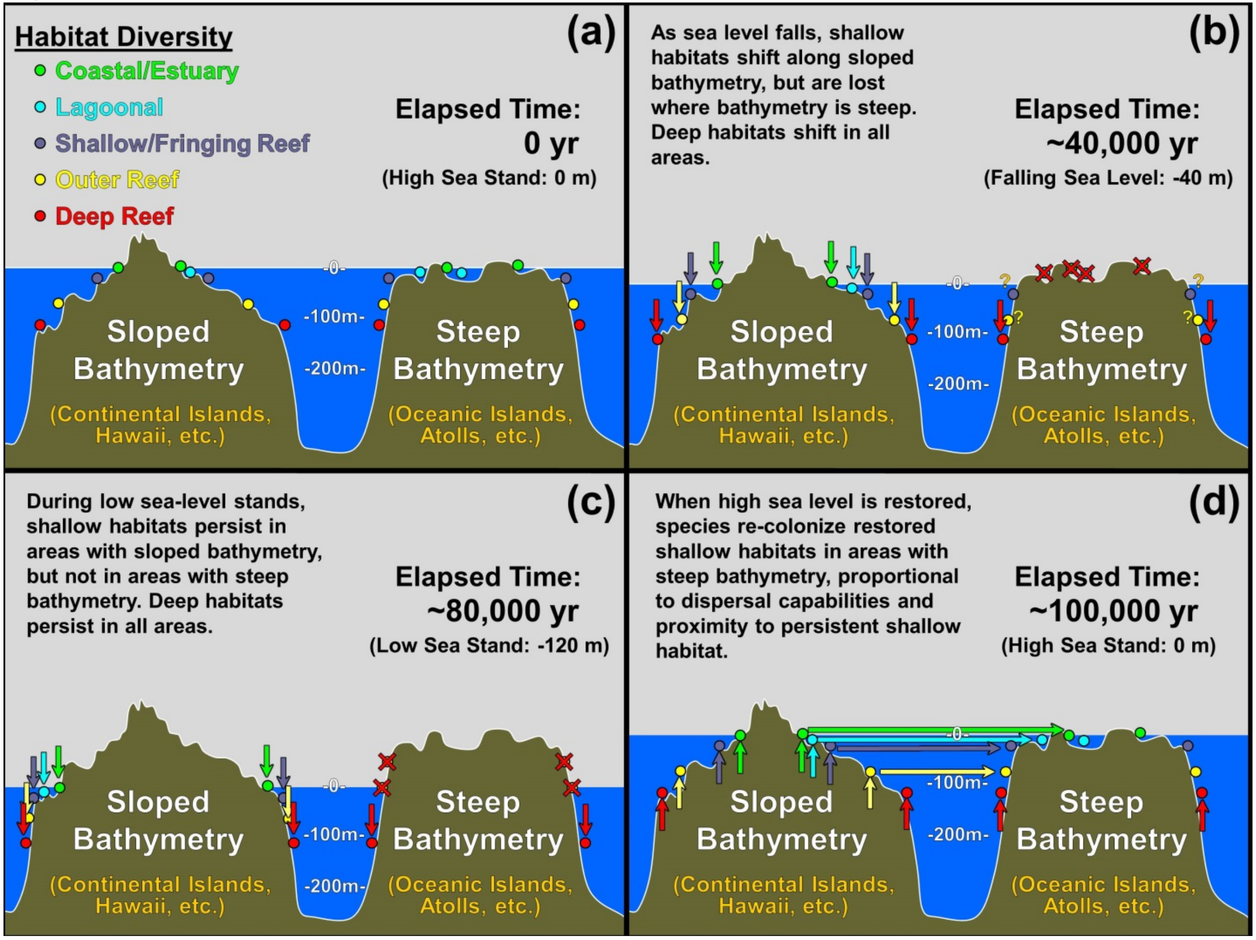
Figure 5. Spur-and-groove habitat along the northwestern coast of Pearl and Hermes Atoll in the Northwestern Hawaiian Islands with identical reef geomorphology at the surface and 30 m (a) and further offshore in the same general area at 60 and 90 m (b), demonstrating that shallow-reef habitats persisted at times of lower relative sea level. White areas represent missing bathymetric data. Data from the Pacific Islands Benthic Habitat Mapping Center (http://www.soest.hawaii.edu/pibhmc/pibhmc_nwhi.htm), and map image prepared by Daniel Wagner.

Figure 1.



30⁰
0⁰
30⁰
130⁰
180⁰
130⁰
600
500
300
100
0
Fish Species Richness

Figure 2.



As sea level falls, shallow habitats shift along sloped bathymetry, but are lost where bathymetry is steep. Deep habitats shift in all areas.

During low sea-level stands, shallow habitats persist in areas with sloped bathymetry, but not in areas with steep bathymetry. Deep habitats persist in all areas.

When high sea level is restored, species re-colonize restored shallow habitats in areas with steep bathymetry, proportional to dispersal capabilities and proximity to persistent shallow habitat.

Figure 3.

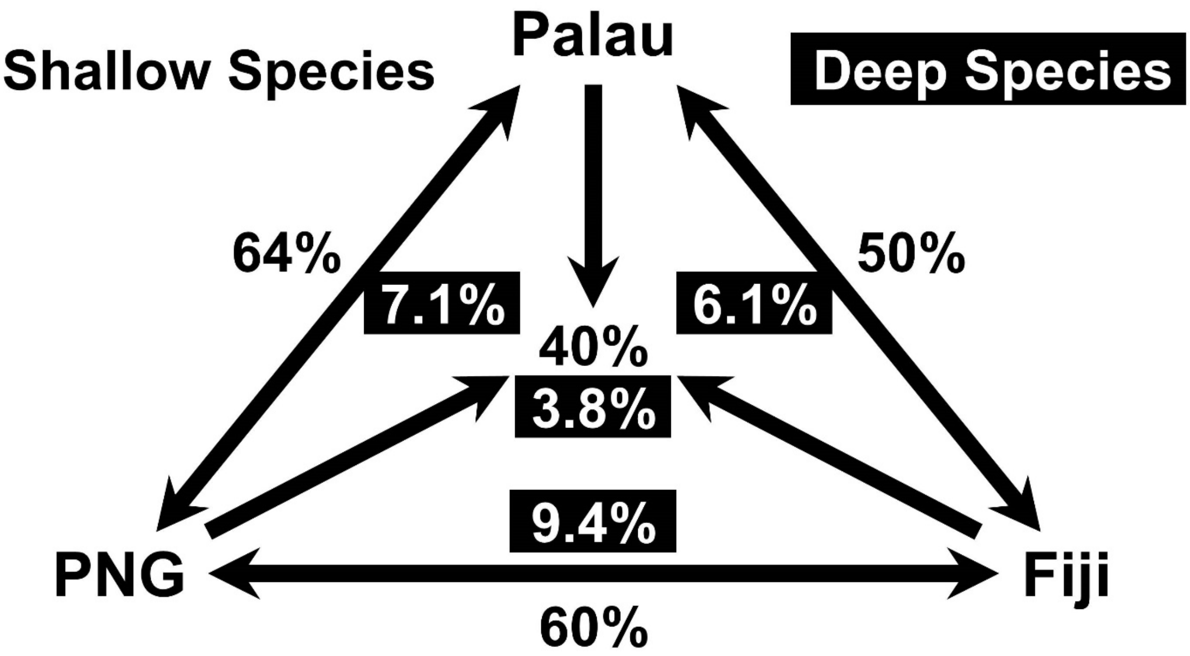

Shallow Species
Palau
Deep Species
64%
7.1%
6.1%
50%
40%
3.8%
9.4%
PNG
Fiji
60%

Figure 4.

Figure 5a.

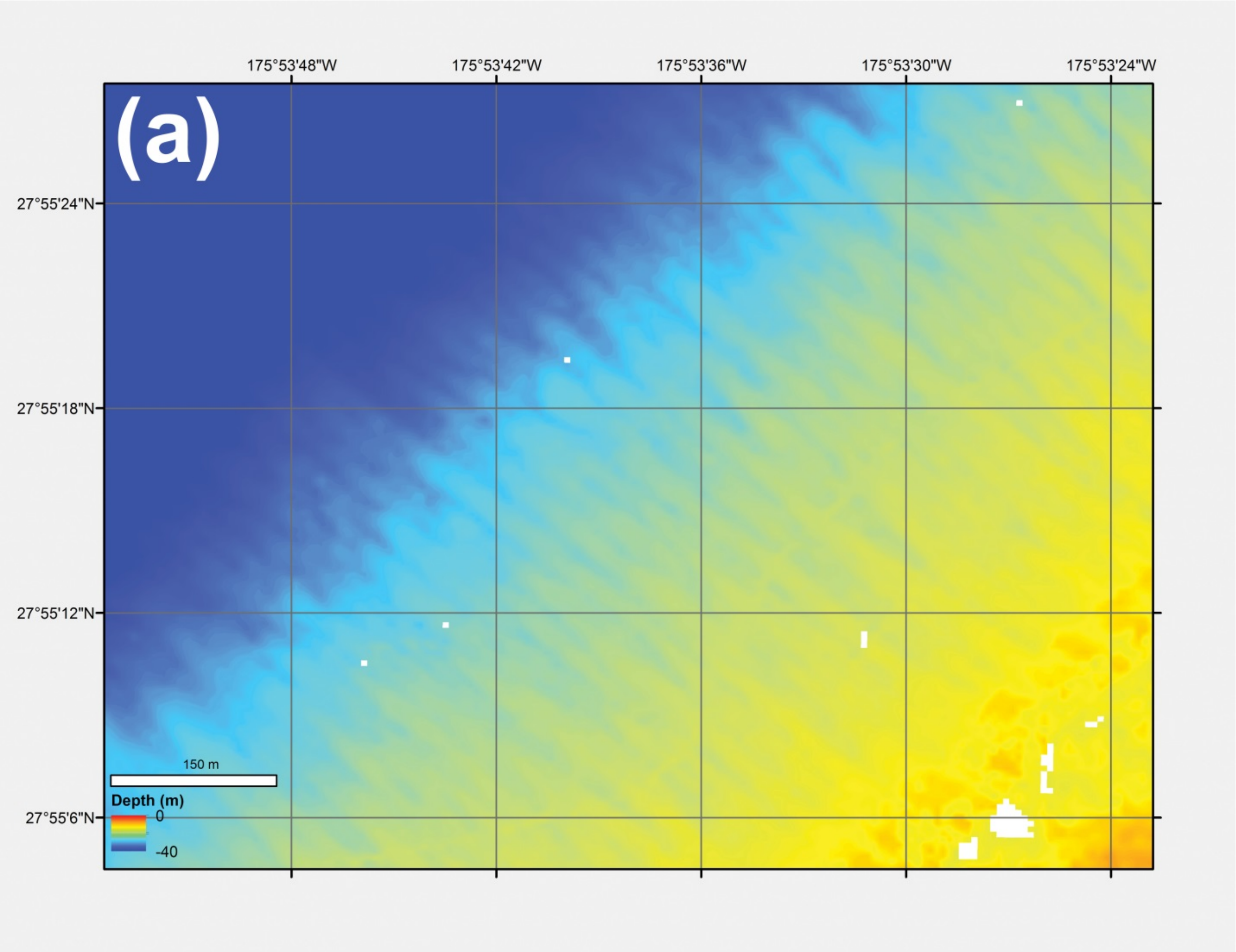
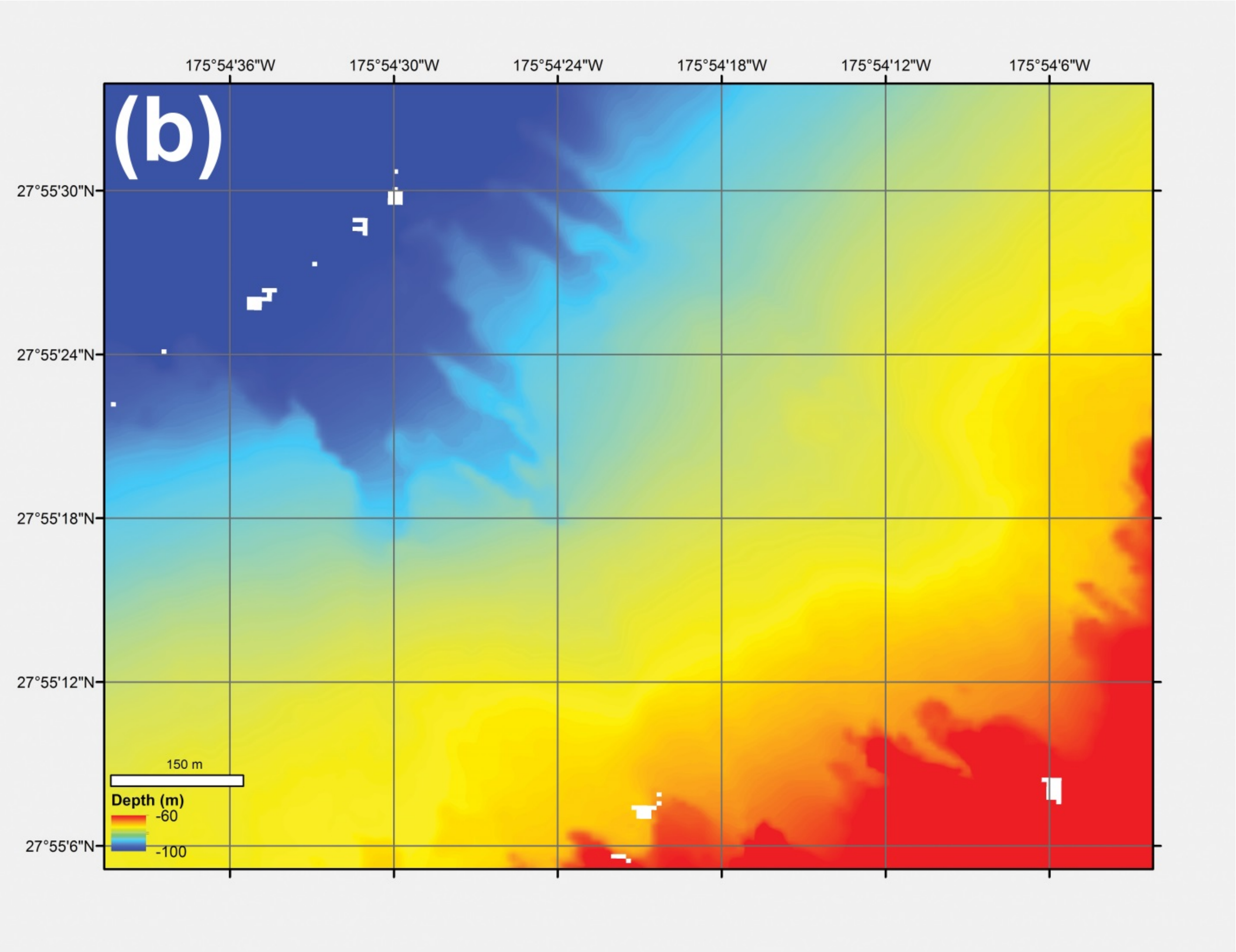

(a)
175°53'48"W
175°53'42"W
175°53'36"W
175°53'30"W
175°53'24"W
27°55'24"N
27°55'18"N
27°55'12"N
27°55'6"N
150 m
Depth (m)
0
-40

Figure 5b.


175°54'36"W
175°54'30"W
175°54'24"W
175°54'18"W
175°54'12"W
175°54'6"W
(b)
27°55'30"N
27°55'24"N
27°55'18"N
27°55'12"N
27°55'6"N
150 m
Depth (m)
-60
-100

CHAPTER 3

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Neoniphon pencei, a new species of holocentrid (Teleostei: Beryciformes) from Rarotonga, Cook Islands

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Abstract

Neoniphon pencei, n. sp., is described from thirteen specimens, 132-197 mm standard length (SL) collected from mesophotic coral ecosystems (MCEs) at Rarotonga, Cook Islands by divers using mixed-gas closed-circuit rebreathers. It differs from all other species of the genus in number of lateral line scales, scales above and below lateral line, elements of life color, and in COI and cytochrome b DNA sequences. Of the five other known species of *Neoniphon*, it is most similar to the Indo-Pacific *N. aurolineatus* and the western Atlantic *N. marianus* both morphologically and genetically.

Keywords

Holocentridae, *Neoniphon*, new species, Mesophotic Coral Ecosystems, MCE, Rarotonga, Cook Islands

Introduction

Collections of shore fishes at mesophotic depths (~30-200 m) across the Indo-Pacific are yielding a surprising number of undescribed species (Pyle 2000). Here, we describe a new species of the genus *Neoniphon* from depths of 90-115 m at Rarotonga, Cook Islands, raising to six the number of species within this genus.

The genus *Neoniphon* Castelnau 1875 includes five currently recognized species: *N. argenteus* (Valenciennes in Cuvier and Valenciennes 1831), *N. aurolineatus* (Liénard 1839), *N. opercularis* (Valenciennes in Cuvier and Valenciennes 1831) and *N. sammara* (Forsskål 1775) from the tropical Indo-Pacific, and *N. marianus* (Cuvier in Cuvier and Valenciennes 1829) from the tropical western Atlantic. Woods and Sonoda (1973) placed these five species (referring to *N. argenteus* by the junior synonym *laevis* [=*læve*] Günther 1859, and to *N. aurolineatus* by the junior synonym *scythrops* Jordan and Evermann 1903) within the genus *Flammeo* Jordan and Evermann 1898, on the grounds that the earlier name *Neoniphon* (type species: *N. armatus* Castelnau 1875) was "based on a species whose status is uncertain" (p. 345). Randall and Heemstra (1985) treated the four Indo- Pacific species of the genus, and confidently asserted that the original description of *N. armatus* Castelnau 1875 (the type species of*Neoniphon*) is conspecific with *N. sammara*, and therefore considered *Neoniphon* as a valid genus with higher nomenclatural priority, to apply to the the four Indo-Pacific species as well as *N. marianus* from the tropical Atlantic. The lead author is working on a larger phylogeographic study involving this genus, which will be published at a later time.

Materials and methods

Type specimens of the new species *Neoniphon pencei* from Rarotonga, Cook Islands have been deposited in the Bernice P. Bishop Museum, Honolulu (BPBM); the California Academy of Sciences, San Francisco (CAS); and the U.S. National Museum of Natural History, Washington, D.C. (USNM).

Measurements and counts given here follow the methods outlined in Randall (1998). Lengths of specimens are given as ratios of: standard length (SL) measured from the tip of the snout to the base of the caudal fin at the end of the hypural plate; body depth, taken at the point of maximum depth; or head length, measured from the median anterior point of the upper lip to the end of the longest opercular spine. Meristics and measurements were compared with data obtained from the literature for all five currently recognized species (Shimizu and Yamakawa 1979).

Tissue samples were obtained from each of the thirteen individuals of *N. pencei* collected at Rarotonga, Cook Islands by spear at 90-115 m. Tissue samples were also obtained from twenty-two specimens of the five other species of *Neoniphon*: *N. sammara* (n=6) collected from Diego Garcia, British Indian Ocean Territory; *N. opercularis* (n=2) collected from Moorea, French Polynesia; *N. aurolineatus* (n=7) collected from Oahu, Hawaii; *N. marianus* (n=1) collected from the Commonwealth of the Bahamas; and *N. argenteus* (n=6) collected from the Republic of Kiritimati. Total genomic DNA was extracted from each sample using the 'HotSHOT' protocol (Meeker et al. 2007). A 577-bp fragment of the mtDNA cytochrome *b* (*Cyt b*>) region was amplified using modified primers from Song et al. (1998) (5'- TGAAGTTGTCGGGATCTCCT-3') and Taberlet et al. (1992) (5'- TGCCGTGACGTAAACTATGG-3'). Polymerase chain reaction (PCR) was performed in a 15 µl reaction containing 7.5 µl BioMix Red (Biolone Inc., Springfield, NJ, USA), 0.2 µM of each primer, 5-50 ng template DNA, and nanopure water (Thermo Scientific* Barnstead, Dubuque, IA, USA) to volume. PCR cycling parameters were as follows: initial 95°C denaturation for 10 min. followed by 35 cycles of 94°C for 30 sec, 60°C for 30 sec, and 72° C for 30 sec, followed by a final extension of 72°C for 10 min. PCR products were visualized using a 1.5% agarose gel with GelStarTM (Cambrex Bio Science Rockland, Inc., Rockland MA, USA) and then cleaned by incubating with 0.75 units of Exonuclease and units of Shrimp Akaline Phosphate (ExoSAP; USB, Cleveland, OH, USA) per 7.5 µl of PCR product for 30 min. at 37°C followed by 85°C for 15 min. Sequencing was conducted in the forward direction and reverse direction when needed using a genetic analyzer (ABI 3130XL, Applied Biosystems, Foster City, California) at the Hawai'i Institute of Marine Biology EPSCoR Sequencing Facility. The sequences were aligned, edited and trimmed to a common length using Geneious Pro (v.5.6.6) DNA analysis software (Drummond et al. 2012). Twelve representative *Cyt b*> haplotypes were deposited in GenBank (accession numbers KJ188431-188436 and KJ201921-201926). jModelTest v.2.1.4 (Darriba et al. 2012, Guindon and Gascuel 2003) was used with an Akaike information criterion (AIC) test to determine the best nucleotide substitution model for the data. The GTR+G model with gamma parameter 0.1840 was identified to be the best suited model for phylogenetic inference. Maximum Likelihood, Neighbor-Joining, and Maximum Parsimony tree-building methods were implemented using Mega v.5.2.2 (Tamura et al. 2011). *Sargocentron rubrum* (Genbank accession number AP004432.1) was used to root a maximum likelihood phylogenetic reconstruction. Clade support was evaluated by bootstrapping 1,000 replicates in all cases (Felsenstein 1985).

A DNA barcode (cytochrome c oxidase I; COI) was completed for the holotype and one paratype (BPBM **41196**) using the primers from Baldwin et al. (2009), Fish-BCH (5'- ACTTCYGGGTGRCCRAARAATCA-3') and Fish-BCL (5'-TCAACYAATCAYAAAGATATYGGCAC-3') using the following PCR protocol: initial 95°C denaturation for 10 min. followed by 35 cycles of 94°C for 30 sec, 55°C for 30 sec, and 72° C for 30 sec, followed by a final extension of 72°C for 10 min. All other procedures were as described above. Both individuals possessed the same COI haplotype, so only one record was deposited in GenBank (http://www.ncbi.nlm.nih.gov/; accession number KJ188437) and BOLD (www.boldsystems.org; dx.doi.org/10.5883/DS-NPE511).

Taxon treatment

Neoniphon pencei Copus, Pyle, and Earle, sp. n.

i. ZooBank urn:lsid:zoobank.org:act:43F5CABA-6E4B-42BB-8569-8F93D3502DE9

ii. Barcode of Life NPE001-14

iii. GenBank KJ201926

iv. GenBank KJ188437

Materials

Holotype:

a. scientificName: *Neoniphon pencei*; originalNameUsage: *Neoniphon pencei* Copus, Pyle and Earle, 2014; originalNameUsageID: 43f5caba-6e4b-42bb-8569-8f93d3502de9; namePublishedIn: Copus, Joshua M., Richard L. Pyle & John L. Earle. 2014. *Neoniphon pencei*, a new species of holocentrid from Rarotonga, Cook Islands. Biodiversity Data Journal.; namePublishedInID: bbdce765-389b-4338-9c36-68def122f4fc; nameAccordingTo: Copus, Joshua M., Richard L. Pyle & John L. Earle. 2014. *Neoniphon pencei*, a new species of holocentrid from Rarotonga, Cook Islands. Biodiversity Data Journal.; nameAccordingToID: bbdce765-389b-4338-9c36-68def122f4fc; acceptedNameUsage: *Neoniphon pencei* Copus, Pyle and Earle, 2014; acceptedNameUsageID: 43f5caba-6e4b-42bb-8569-8f93d3502de9; taxonID: 43f5caba-6 e4b-42bb-8569-8f93d3502de9; scientificNameID: 43f5caba-6e4b-42bb-8569-8f93d3502d e9; parentNameUsageID: b047f156-f8da-4ec6-9f64-87345b68a759; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Pence's Squirrelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; specificEpithet: pencei; scientificNameAuthorship: Copus, Pyle & Earle; waterBody: Pacific Ocean; islandGroup: Cook Islands; island:

Rarotonga; country: Cook Islands; countryCode: CK; locality: E side; Matavera; off Charles J. Boyle's house; verbatimLocality: Cook Islands; Rarotonga; E side; Matavera; off Charles J. Boyle's house; verbatimDepth: 115 m; minimumDepthInMeters: 115; maximumDepthInMeters: 115; decimalLatitude: -21.223798; decimalLongitude: -159.728123; geodeticDatum: WGS 84; coordinateUncertaintyInMeters: 300; georeferenceSources: Google Earth; samplingProtocol: Spear; eventDate: 2012-07-02; year: 2012; month: 7; day: 2; habitat: small cave near base of vertical drop-off; individualCount: 1; lifeStage: adult; preparations: 55% Isopropyl; catalogNumber: 41197; recordedBy: David F. Pence; disposition: in collection; associatedSequences: GenBank KJ201926 (*cyt b*); KJ188437 (COI); identifiedBy: Richard L. Pyle; dateIdentified: 2012-08-07; modified: 2014-10-09T23:30:00Z; language: en; collectionID: urn:lsid:biocol.org:col:1001; institutionCode: BPBM; collectionCode: Fish; basisOfRecord: PreservedSpecimen

Paratypes:

- scientificName: *Neoniphon pencei*; originalNameUsage: *Neoniphon pencei* Copus, Pyle and Earle, 2014; originalNameUsageID: 43f5caba-6e4b-42bb-8569-8f93d3502de9; namePublishedIn: Copus, Joshua M., Richard L. Pyle & John L. Earle. 2014. *Neoniphon pencei*, a new species of holocentrid from Rarotonga, Cook Islands. Biodiversity Data Journal.; namePublishedInID: bbdce765-389b-4338-9c36-68def122f4fc;

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samplingProtocol: Spear; eventDate: 2012-07-03; year: 2012; month: 7; day: 3; habitat: small cave near base of vertical drop-off; individualCount: 1; lifeStage: adult; preparations: 55% Isopropyl; catalogNumber: 41196; recordedBy: David F. Pence; disposition: in collection; associatedSequences: GenBank KJ201926; identifiedBy: Richard L. Pyle; dateIdentified: 2012-08-07; modified: 2014-10-09T23:30:00Z; language: en; collectionID: urn:lsid:biocol.org:col:1001; institutionCode: BPBM; collectionCode: Fish; basisOfRecord: PreservedSpecimen

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Journal.; nameAccordingToID: bbdce765-389b-4338-9c36-68def122f4fc; acceptedNameUsage: *Neoniphon pencei* Copus, Pyle and Earle, 2014; acceptedNameUsageID: 43f5caba-6e4b-42bb-8569-8f93d3502de9; taxonID: 43f5caba-6 e4b-42bb-8569-8f93d3502de9; scientificNameID: 43f5caba-6e4b-42bb-8569-8f93d3502d e9; parentNameUsageID: b047f156-f8da-4ec6-9f64-87345b68a759; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Pence's Squirrelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; specificEpithet: pencei; scientificNameAuthorship: Copus, Pyle & Earle; waterBody: Pacific Ocean; islandGroup: Cook Islands; island: Rarotonga; country: Cook Islands; countryCode: CK; locality: E side; Matavera; off Charles J. Boyle's house; verbatimLocality: Cook Islands; Rarotonga; E side; Matavera; off Charles J. Boyle's house; verbatimDepth: 115 m; minimumDepthInMeters: 115; maximumDepthInMeters: 115; decimalLatitude: -21.223798; decimalLongitude: -159.728123; geodeticDatum: WGS 84; coordinateUncertaintyInMeters: 300; georeferenceSources: Google Earth; samplingProtocol: Spear; eventDate: 2012-07-03; year: 2012; month: 7; day: 3; habitat: small cave near base of vertical drop-off; individualCount: 1; lifeStage: adult; preparations: 55% Isopropyl; catalogNumber: 41196; recordedBy: David F. Pence; disposition: in collection; associatedSequences: GenBank KJ201926; identifiedBy: Richard L. Pyle; dateIdentified: 2012-08-07; modified: 2014-10-09T23:30:00Z; language: en; collectionID: urn:lsid:biocol.org:col:1001; institutionCode: BPBM; collectionCode: Fish; basisOfRecord:

PreservedSpecimen

- scientificName: *Neoniphon pencei*; originalNameUsage: *Neoniphon pencei* Copus, Pyle and Earle, 2014; originalNameUsageID: 43f5caba-6e4b-42bb-8569-8f93d3502de9; namePublishedIn: Copus, Joshua M., Richard L. Pyle & John L. Earle. 2014. *Neoniphon pencei*, a new species of holocentrid from Rarotonga, Cook Islands. Biodiversity Data Journal.; namePublishedInID: bbdce765-389b-4338-9c36-68def122f4fc; nameAccordingTo: Copus, Joshua M., Richard L. Pyle & John L. Earle. 2014. *Neoniphon pencei*, a new species of holocentrid from Rarotonga, Cook Islands. Biodiversity Data Journal.; nameAccordingToID: bbdce765-389b-4338-9c36-68def122f4fc; acceptedNameUsage: *Neoniphon pencei* Copus, Pyle and Earle, 2014; acceptedNameUsageID: 43f5caba-6e4b-42bb-8569-8f93d3502de9; taxonID: 43f5caba-6 e4b-42bb-8569-8f93d3502de9; scientificNameID: 43f5caba-6e4b-42bb-8569-8f93d3502d e9; parentNameUsageID: b047f156-f8da-4ec6-9f64-87345b68a759; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Pence's Squirrelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; specificEpithet: pencei; scientificNameAuthorship: Copus, Pyle & Earle; waterBody: Pacific Ocean; islandGroup: Cook Islands; island: Rarotonga; country: Cook Islands; countryCode: CK; locality: E side; Matavera; off Charles J. Boyle's house; verbatimLocality: Cook Islands; Rarotonga; E side; Matavera; off Charles J. Boyle's house; verbatimDepth: 115 m; minimumDepthInMeters: 115; maximumDepthInMeters: 115; decimalLatitude:

  -21.223798; decimalLongitude: -159.728123; geodeticDatum: WGS 84; coordinateUncertaintyInMeters: 300; georeferenceSources: Google Earth; samplingProtocol: Spear; eventDate: 2012-07-03; year: 2012; month: 7; day: 3; habitat: small cave near base of vertical drop-off; individualCount: 1; lifeStage: adult; preparations:

55% Isopropyl; catalogNumber: 41196; recordedBy: David F. Pence; disposition: in collection; associatedSequences: GenBank KJ201926; identifiedBy: Richard L. Pyle; dateIdentified: 2012-08-07; modified: 2014-10-09T23:30:00Z; language: en; collectionID: urn:lsid:biocol.org:col:1001; institutionCode: BPBM; collectionCode: Fish; basisOfRecord: PreservedSpecimen

- scientificName: *Neoniphon pencei*; originalNameUsage: *Neoniphon pencei* Copus, Pyle and Earle, 2014; originalNameUsageID: 43f5caba-6e4b-42bb-8569-8f93d3502de9; namePublishedIn: Copus, Joshua M., Richard L. Pyle & John L. Earle. 2014. *Neoniphon pencei*, a new species of holocentrid from Rarotonga, Cook Islands. Biodiversity Data Journal.; namePublishedInID: bbdce765-389b-4338-9c36-68def122f4fc; nameAccordingTo: Copus, Joshua M., Richard L. Pyle & John L. Earle. 2014. *Neoniphon pencei*, a new species of holocentrid from Rarotonga, Cook Islands. Biodiversity Data Journal.; nameAccordingToID: bbdce765-389b-4338-9c36-68def122f4fc; acceptedNameUsage: *Neoniphon pencei* Copus, Pyle and Earle, 2014; acceptedNameUsageID: 43f5caba-6e4b-42bb-8569-8f93d3502de9; taxonID: 43f5caba-6 e4b-42bb-8569-8f93d3502de9; scientificNameID: 43f5caba-6e4b-42bb-8569-8f93d3502d e9; parentNameUsageID: b047f156-f8da-4ec6-9f64-87345b68a759; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Pence's Squirrelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; specificEpithet: pencei; scientificNameAuthorship: Copus, Pyle & Earle; waterBody: Pacific Ocean; islandGroup: Cook Islands; island: Rarotonga; country: Cook Islands; countryCode: CK; locality: E side; Matavera; off Charles J. Boyle's house; verbatimLocality: Cook Islands; Rarotonga; E side; Matavera; off Charles J. Boyle's house; verbatimDepth: 115 m; minimumDepthInMeters: 115; maximumDepthInMeters: 115; decimalLatitude:

  -21.223798; decimalLongitude: -159.728123; geodeticDatum: WGS 84; coordinateUncertaintyInMeters: 300; georeferenceSources: Google Earth; samplingProtocol: Spear; eventDate: 2012-07-02; year: 2012;

month: 7; day: 2; habitat: small cave near base of vertical drop-off; individualCount: 1; lifeStage: adult; preparations: 55% Isopropyl; catalogNumber: 237596; recordedBy: David F. Pence; disposition: in collection; associatedSequences: GenBank KJ201926 (*Cyt b*); KJ188437 (COI); identifiedBy: Richard L. Pyle; dateIdentified: 2012-08-07; modified:
2014-10-09T23:30:00Z; language: en; collectionID: urn:lsid:biocol.org:col:1003; institutionCode: CAS; collectionCode: Fish; basisOfRecord: PreservedSpecimen

- scientificName: *Neoniphon pencei*; originalNameUsage: *Neoniphon pencei* Copus, Pyle and Earle, 2014; originalNameUsageID: 43f5caba-6e4b-42bb-8569-8f93d3502de9; namePublishedIn: Copus, Joshua M., Richard L. Pyle & John L. Earle. 2014. *Neoniphon pencei*, a new species of holocentrid from Rarotonga, Cook Islands. Biodiversity Data Journal.; namePublishedInID: bbdce765-389b-4338-9c36-68def122f4fc; nameAccordingTo: Copus, Joshua M., Richard L. Pyle & John L. Earle. 2014. *Neoniphon pencei*, a new species of holocentrid from Rarotonga, Cook Islands. Biodiversity Data Journal.; nameAccordingToID: bbdce765-389b-4338-9c36-68def122f4fc; acceptedNameUsage: *Neoniphon pencei* Copus, Pyle and Earle, 2014; acceptedNameUsageID: 43f5caba-6e4b-42bb-8569-8f93d3502de9; taxonID: 43f5caba-6 e4b-42bb-8569-8f93d3502de9; scientificNameID: 43f5caba-6e4b-42bb-8569-8f93d3502de9; parentNameUsageID: b047f156-f8da-4ec6-9f64-87345b68a759; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae;

Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Pence's Squirrelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; specificEpithet: pencei; scientificNameAuthorship: Copus, Pyle & Earle; waterBody: Pacific Ocean; islandGroup: Cook Islands; island: Rarotonga; country: Cook Islands; countryCode: CK; locality: N side; off Avarua Harbor; verbatimLocality: Cook Islands; Rarotonga; N side; off Avarua Harbor; verbatimDepth: 90 m; minimumDepthInMeters: 90; maximumDepthInMeters: 90; decimalLatitude: -21.198947; decimalLongitude: -159.781353; geodeticDatum: WGS 84; coordinateUncertaintyInMeters: 300; georeferenceSources: Google Earth; samplingProtocol: Quinaldine; eventDate: 2012-06-22; year: 2012; month: 6; day: 22; individualCount: 1; lifeStage: adult; preparations: 55% Isopropyl; catalogNumber: 431482; recordedBy: John L. Earle; disposition: in collection; otherCatalogNumbers: Formerly BPBM 41195; associatedSequences: GenBank KJ201926; identifiedBy: Richard L. Pyle; dateIdentified: 2012-08-07; modified: 2014-10-09T23:30:00Z; language: en; collectionID: urn:lsid:biocol.org:col:1002; institutionCode: USNM; collectionCode: Fish; basisOfRecord: PreservedSpecimen

Other materials:

- scientificName: *Neoniphon sammara*; acceptedNameUsage: *N. sammara* (Forsskål 1775); parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Sammara squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Indian Ocean; islandGroup: Diego Garcia; country: British Indian Ocean Territory; countryCode: IOT; verbatimLocality: Diego Garcia; samplingProtocol: Spear; year: 2002-2011; individualID: NSA128; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences:

Genbank-KJ188433; identifiedBy: Matt Craig; language: en

- scientificName: *Neoniphon sammara*; acceptedNameUsage: *N. sammara* (Forsskål 1775); parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Sammara squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Indian Ocean; islandGroup: Diego Garcia; country: British Indian Ocean Territory; countryCode: IOT; verbatimLocality: Diego Garcia; samplingProtocol: Spear; year: 2002-2011; individualID: NSA129; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences:
  Genbank-KJ188434; identifiedBy: Matt Craig; language: en
- scientificName: *Neoniphon sammara*; acceptedNameUsage: *N. sammara* (Forsskål 1775); parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Sammara squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Indian Ocean; islandGroup: Diego Garcia; country: British Indian Ocean Territory; countryCode: IOT; verbatimLocality: Diego Garcia; samplingProtocol: Spear; year: 2002-2011; individualID: NSA130; individualCount: 1; lifeStage: adult; preparations:

DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences:

Genbank-KJ188435; identifiedBy: Matt Craig; language: en

- scientificName: *Neoniphon sammara*; acceptedNameUsage: *N. sammara* (Forsskål 1775); parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Sammara squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Indian Ocean; islandGroup: Diego Garcia; country: British Indian Ocean Territory; countryCode: IOT; verbatimLocality: Diego Garcia; samplingProtocol: Spear; year: 2002-2011; individualID: NSA131; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences:

  Genbank-KJ188436; identifiedBy: Matt Craig; language: en
- scientificName: *Neoniphon sammara*; acceptedNameUsage: *N. sammara* (Forsskål 1775); parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Sammara squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Indian Ocean; islandGroup: Diego Garcia; country: British Indian Ocean Territory; countryCode: IOT; verbatimLocality: Diego Garcia; samplingProtocol: Spear; year: 2002-2011; individualID: NSA132; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences:

  Genbank-KJ188434; identifiedBy: Matt Craig; language: en
- scientificName: *Neoniphon sammara*; acceptedNameUsage: *N. sammara* (Forsskål 1775); parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank:

species; vernacularName: Sammara squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Indian Ocean; islandGroup: Diego Garcia; country: British Indian Ocean Territory; countryCode: IOT; verbatimLocality: Diego Garcia; samplingProtocol: Spear; year: 2002-2011; individualID: NSA133; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences:

Genbank-KJ188433; identifiedBy: Matt Craig; language: en

- scientificName: *Neoniphon aurolineatus*; acceptedNameUsage: *N. aurolineatus* Liénard 1839; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Yellowstriped squirelfish; nomenclaturalCode: ICZN; genus:*Neoniphon*; waterBody: Pacific Ocean; islandGroup: Hawaii; island: Oahu; country: United States; countryCode: USA; verbatimLocality: Hawaii; samplingProtocol: Spear; year: 2012; individualID: NAU1; individualCount: 1; lifeStage: adult; preparations: DMSO;recordedBy: Andrew Gray; disposition: in collection; associatedSequences: Genbank-KJ201925; identifiedBy: Andrew Gray; language: en
- scientificName: *Neoniphon aurolineatus*; acceptedNameUsage: *N. aurolineatus* Liénard 1839; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class

Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Yellowstriped squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Hawaii; island: Oahu; country: United States; countryCode: USA; verbatimLocality: Hawaii; samplingProtocol: Spear; year: 2012; individualID: NAU2; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Andrew Gray; disposition: in collection; associatedSequences: Genbank-KJ201923; identifiedBy: Andrew Gray; language: en

- scientificName: *Neoniphon aurolineatus*; acceptedNameUsage: *N. aurolineatus* Liénard 1839; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Yellowstriped squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Hawaii; island: Oahu; country: United States; countryCode: USA; verbatimLocality: Hawaii; samplingProtocol: Spear; year: 2012; individualID: NAU3; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Andrew Gray; disposition: in collection; associatedSequences: Genbank-KJ201924; identifiedBy: Andrew Gray; language: en
- scientificName: *Neoniphon aurolineatus*; acceptedNameUsage: *N. aurolineatus* Liénard 1839; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Yellowstriped squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Hawaii; island: Oahu; country: United States; countryCode: USA; verbatimLocality: Hawaii; samplingProtocol: Spear; year: 2012; individualID: NAU4; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Andrew Gray; disposition: in collection; associatedSequences: Genbank-KJ201923; identifiedBy: Andrew Gray; language: en
- scientificName: *Neoniphon aurolineatus*; acceptedNameUsage: *N. aurolineatus* Liénard 1839; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class:

Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Yellowstriped squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Hawaii; island: Oahu; country: United States; countryCode: USA; verbatimLocality: Hawaii; samplingProtocol: Spear; year: 2012; individualID: NAU5; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Andrew Gray; disposition: in collection; associatedSequences: Genbank-KJ201922; identifiedBy: Andrew Gray; language: en

- scientificName: *Neoniphon aurolineatus*; acceptedNameUsage: *N. aurolineatus* Liénard 1839; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Yellowstriped squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Hawaii; island: Oahu; country: United States; countryCode: USA; verbatimLocality: Hawaii; samplingProtocol: Spear; year: 2012; individualID: NAU6; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy:

Andrew Gray; disposition: in collection; associatedSequences: Genbank-KJ201925; identifiedBy: Andrew Gray; language: en

- scientificName: *Neoniphon aurolineatus*; acceptedNameUsage: ***N. aurolineatus*** Liénard 1839; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Yellowstriped squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Hawaii; island: Oahu; country: United States; countryCode: USA; verbatimLocality: Hawaii; samplingProtocol: Spear; year: 2012; individualID: NAU7; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Andrew Gray; disposition: in collection; associatedSequences: Genbank-KJ201925; identifiedBy: Andrew Gray; language: en
- scientificName: *Neoniphon opercularis*; acceptedNameUsage: *Neoniphon opercularis* Valenciennes 1831; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Blackfin squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Society; island: Moorea; country: French Polynesia; countryCode: PYF; verbatimLocality: Society; samplingProtocol: Spear; year: 2002-2011; individualID: NOP1; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences: Genbank-KJ188432; identifiedBy: Matt Craig; language: en
- scientificName: *Neoniphon opercularis*; acceptedNameUsage: *Neoniphon opercularis* Valenciennes 1831; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Blackfin squirelfish; nomenclaturalCode: ICZN;

genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Society; island: Moorea; country: French Polynesia; countryCode: PYF; verbatimLocality: Society; samplingProtocol: Spear; year: 2002-2011; individualID: NOP2; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences: Genbank-KJ188432; identifiedBy: Matt Craig; language: en

- scientificName: *Neoniphon argenteus*; acceptedNameUsage: *Neoniphon argenteus* Valenciennes 1831; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Clearfin squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Line; island: Kiritimati; country: Republic of Kiritimati; countryCode: KIR; verbatimLocality: Line; samplingProtocol: Spear; year: 2002-2011; individualID: NAR1; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences: Genbank-KJ188431; identifiedBy: Matt Craig; language: en
- scientificName: *Neoniphon argenteus*; acceptedNameUsage: *Neoniphon argenteus* Valenciennes 1831; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom:

Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Clearfin squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Line; island: Kiritimati; country: Republic of Kiritimati; countryCode: KIR; verbatimLocality: Line; samplingProtocol: Spear; year: 2002-2011; individualID: NAR2; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences: Genbank-KJ188431; identifiedBy: Matt Craig; language: en

- scientificName: *Neoniphon argenteus*; acceptedNameUsage: *Neoniphon argenteus* Valenciennes 1831; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Clearfin squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Line; island: Kiritimati; country: Republic of Kiritimati; countryCode: KIR; verbatimLocality: Line; samplingProtocol: Spear; year: 2002-2011; individualID: NAR3; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences: Genbank-KJ188431; identifiedBy: Matt Craig; language: en
- scientificName: *Neoniphon argenteus*; acceptedNameUsage: *Neoniphon argenteus* Valenciennes 1831; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Clearfin squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Line; island: Kiritimati; country: Republic of Kiritimati; countryCode: KIR; verbatimLocality: Line; samplingProtocol: Spear; year: 2002-2011; individualID: NAR4; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection;

associatedSequences: Genbank-KJ188431; identifiedBy: Matt Craig; language: en

- scientificName: *Neoniphon argenteus*; acceptedNameUsage: *Neoniphon argenteus* Valenciennes 1831; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Clearfin squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Line; island: Kiritimati; country: Republic of Kiritimati; countryCode: KIR; verbatimLocality: Line; samplingProtocol: Spear; year: 2002-2011; individualID: NAR5; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences: Genbank-KJ188431; identifiedBy: Matt Craig; language: en
- scientificName: *Neoniphon argenteus*; acceptedNameUsage: *Neoniphon argenteus* Valenciennes 1831; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Clearfin squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Pacific Ocean; islandGroup: Line; island: Kiritimati; country: Republic of Kiritimati; countryCode: KIR; verbatimLocality: Line; samplingProtocol: Spear; year: 2002-2011; individualID: NAR6; individualCount: 1;

lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences: Genbank-KJ188431; identifiedBy: Matt Craig; language: en

- scientificName: *Neoniphon marianus*; acceptedNameUsage: *Neoniphon marianus* Cuvier 1829; parentNameUsage: Neoniphon Castelnau, 1875; higherClassification: Animalia; Deuterostomia; Chordata; Craniata; Gnathostomata; Actinopterygii; Beryciformes; Holocentroidei; Holocentridae; Neoniphon; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Beryciformes; family: Holocentridae; taxonRank: species; vernacularName: Longjaw squirelfish; nomenclaturalCode: ICZN; genus: *Neoniphon*; waterBody: Atlantic Ocean; islandGroup: Bahamas; island: Bahamas; country: Commonwelth of the Bahamas; countryCode: BHS; verbatimLocality: Bahamas; samplingProtocol: Spear; year: 2013; individualID: NMA1; individualCount: 1; lifeStage: adult; preparations: DMSO; recordedBy: Matt Craig; disposition: in collection; associatedSequences: Genbank-KJ201921; identifiedBy: Casey Benkwitt; language: en

Description

Dorsal rays XI, 13, the last ray branched to base; anal rays IV,9, the last ray branched to base; principal caudal rays 17, the upper and lower unbranched; upper procurrent caudal rays 7, the first spinous, the last slender and segmented; lower procurrent caudal rays 6, the first 5 spinous, the last slender and segmented; pectoral rays 14, the uppermost rudimentary, the second and lowermost unbranched; pelvic rays I,7; lateral line scales 49 (48-52); scales above lateral line to base of dorsal spines 5; scales below lateral line to origin of anal fin 6 (6-7); oblique rows of scales on cheek 5; vertical row of 9 (8-10) scales on opercle; gill rakers 6+13 (6-7+13); vertebrae 25; body depth 3.2 (2.9-3.3) in SL; head length 2.8 (2.6-2.9) in SL; snout length 3.5 (3.4-3.8) in head length; orbit diameter 3.0 (2.6-3.0) in head length; interorbital width 4.8 (4.1-4.8) in body depth; upper-jaw length 2.3 (2.3-2.6) in head length; preopercular spine 2.2 (2.0-2.9) in orbit diameter; caudal peduncle depth 3.9 (3.7-4.3) in body depth; caudal peduncle length 7.3 (6.5-7.7) in SL, predorsal length 2.7 (2.4-2.7) in SL; preanal length

1.3 (1.2-1.3) in SL; prepelvic length 2.4 (2.4-2.6) in SL; first dorsal spine 3.5 (3.3-4.1) in head length; third dorsal spine longest, 2.3 (2.0-2.8) in head length; first anal spine 29.5 (19.0-29.5) in head length; second anal spine 9.0 (7.2-9.0) in head length; third anal spine 1.3 (1.1-1.3) in head length; fourth anal spine 2.0 (1.7-2.0) in head length; longest anal ray 2.0 (1.9-2.2) in head length; caudal-fin length 5.0 (3.3-5.2) in SL; caudal concavity 2.9 (2.0-2.9) in head length; pectoral-fin length 4.1 (3.6-4.2) in SL; pelvic-spine length 2.3 (2.2-2.5) in head length; pelvic-fin length 4.9 (4.3-4.9) in SL.

Color in life (Figs 1, 2, 3): Body silvery white with an orange-red tint above lateral line. Scales above lateral line with orange-red borders. Approximately eleven red to orange- red stripes following and sometimes bisecting scales of each horizontal scale row, width of stripes on body alternating between very narrow stripes and stripes over three times wider, except for two consecutive wide stripes, numbers six and seven counted ventrally from the thin dorsal-most stripe, the eleventh ventral-most stripe thin and barely visible on some specimens. Preopercle silvery white with a narrow orange-red posterior border, faint on some specimens. Opercle, nape and interorbital space orange-red. Prominent red bar of less than pupil width extending across nape to level of pectoral axil when viewed underwater. Pectoral axil orange-red. Dorsal fin spines and rays light orange red. Membranes of spinous portion of dorsal fin red with white tips and a white semicircular spot encompassing the middle vertical third of each membrane, its greatest length along the preceding anterior spine and not extending to the posterior spine. Some specimens without a white spot on the first membrane. Soft dorsal fin, pectoral fin, anal fin and pelvic fins with transparent membranes, except anal fin with translucent white membrane between longest spines. Pectoral fin and pelvic fin rays with faint pinkish tint. Anal fin spines white with a faint orange tint on some specimens. Anal fin rays orange-red. Caudal fin rays orange-red, faint on inner rays, membranes translucent white.

Figure 1.

Holotype of *Neoniphon pencei*, BPBM 41197, Rarotonga, Cook Islands. Photo: Richard Pyle and Brian Greene.

Color in alcohol: Body pale yellowish-white. Narrow orange-tan stripes bisecting scales of horizontal scale rows, except for lateral line scale row, the stripes above lateral line faint, barely visible on some specimens. Preopercle white with narrow yellow-tan border. Opercle, nape and interorbital space yellow-tan. Spinous dorsal fin membranes translucent with a white tint. Soft dorsal fin, anal fin pectoral fin and pelvic fin membranes transparent. Caudal fin with orange-tan blotch on upper and lower base, extending faintly on to upper and lower rays. Middle third of caudal fin rays and membranes transparent.

Figure 2.
Neoniphon pencei at approximately 70 m in Rarotonga, Cook Islands. Cropped from a video frame taken by J.L. Earle.

Figure 3.
An apparent *Neoniphon pencei* at approximately 90 m in Moorea. Cropped from a video frame taken by R.K. Whitton.

Diagnosis

Dorsal rays XI,13; anal rays IV,9; pectoral rays 14; lateral-line scales 48-52 (usually 49); scales above lateral line to base of dorsal spines 5; scales below lateral line to base of anal fin 6-7; oblique rows of scales on cheek 5; gill rakers 6-7+13 (usually 6+13); body slender, the depth 2.9-3.3 in SL; head length 2.6-2.9 in SL; orbit diameter 2.7-3.0 in head length; interorbital width 4.1-4.8 in body depth; upper jaw length 2.3-2.6 in head; lower jaw strongly protruding; preopercular spine 2.0-2.9 of orbit diameter; first dorsal spine 3.3-4.1 in head length; last dorsal spine shortest; third anal spine the longest, its length 1.1-1.3 in head length; body red with white stripes dorsally, front edge of pelvic and anal fins white, white on base of dorsal fin; reaches 24cm.

Etymology

Named for David F. Pence, Diving Safety Officer for the University of Hawai'i, a member of the deep diving team that discovered this species, in recognition of his efforts to collect the type specimens.

Distribution

All type specimens of *N. pencei* were collected at Rarotonga, Cook Islands. An individual *Neoniphon* closely matching the life colors of *N. pencei* (and different from all other known species) was captured on video by Robert K. Whitton at a depth of 90 m at Moorea, in February 2012 (Fig. 3). It is likely that the species is more broadly distributed throughout the southeastern tropical Pacific, but has escaped noticed due to insufficient collecting activities at mesophotic depths in this region.

Analysis

Genetic results

After alignment and editing, a 377-bp partial sequence of *Cyt b* was obtained for all thirty- five *Neoniphon* samples, resulting in twelve unique haplotypes. All three phylogenetic methods used resulted in congruent tree topologies and are presented as a Maximum Likelihood reconstruction (Fig. 4). Phylogenetic reconstruction recovered strong support for clades corresponding to known *Neoniphon* species. The species *N. pencei* showed strong clade support (100% bootstrap support for all three methods) for belonging to a single clade distinct from currently described *Neoniphon* species. There was not enough signal to resolve the sister relationship between some members within the genus *Neoniphon*; however, this description is not necessary for the goals of this study. *Neoniphon pencei* shows 9-12.5% uncorrected sequence divergence and 34-47 mutations between all other known *Neoniphon* species and posesses 8 diagnostic sites unique from all other species of *Neoniphon* within this this region of *Cyt b*. This is consistent with species level sequence divergence found in other fish taxa (Bellwood et al. 2004, Fessler and Westneat 2007, Randall and Rocha 2009, Rocha 2004, Rocha et al. 2008).

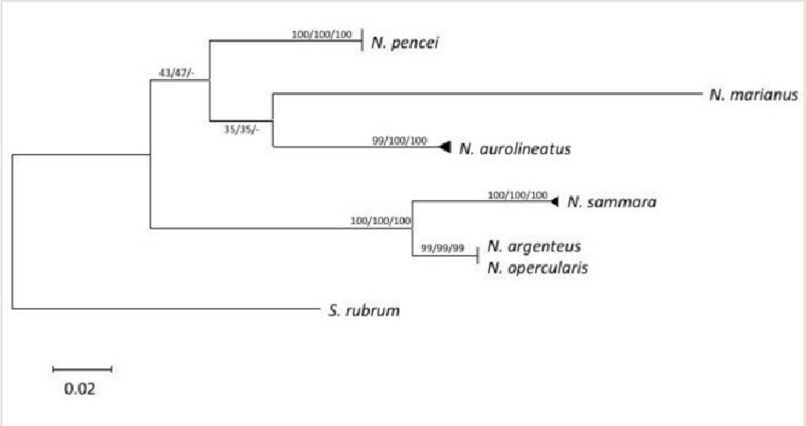

Figure 4.

Maximum likelihood phylogenetic reconstruction for the genus *Neoniphon* based on *Cyt b* sequences from 35 individuals, yielding 12 unique haplotypes, rooted with *Sargocentron rubrum*. Branch support values are Maximum Likelihood, Neighbor-Joining, and Maximum Parsimony bootstrap percent values respectively. Triangles at branch termini represent multiple haplotypes; vertical bars at branch termini represent multiple individuals with identical haplotypes.

Discussion

Most recent authors who have reported on *Neoniphon* (e.g., Randall and Heemstra 1985, Randall and Heemstra 1986, Kotlyar 1996, Kotlyar 1998, Randall and Greenfield 1999, Greenfield 2003, Satapoomin 2009) consider it to be a valid genus (a senior synonym of *Flammeo*), distinct from other genera in the subfamily Holocentrinae (particularly *Sargocentron*; Fowler 1904), primarily on the basis of the position of the last dorsal-fin spine (relative to the penultimate dorsal-fin spine and first dorsal-fin ray), and the protruding lower jaw in species of *Neoniphon* (Randall and Heemstra 1985). A more recent phylogenetic analysis of holocentrids by Dornburg et al. (2012), however, reported evidence that *Sargocentron* and *Neoniphon* are paraphyletic. Specifically, they found that four of the five species of *Neoniphon* (they did not include *N. aurolineatus* in their analyses) cluster among several subclades that include nine of the seventeen species of *Sargocentron* they analyzed (*S. coruscum*, *S. diadema*, *S. inaequalis*, *S. ittodai*, *S. microstoma*, *S. punctatissimum*, *S. suborbitalis* [=suborbitale], *S. vexillarium* and *S. xantherythrum*). The other eight species of *Sargocentron* they analyzed (*S. caudimaculatum*, *S. cornutum*, *S. melanospilos*, *S. praslin*, *S. rubrum*, *S. seychellense*, *S. spiniferum* and *S. tiere*) form a separate clade (their "*Sargocentron* group 1"). They argue that the characters used to differentiate these species are ecologically plastic and therefore current relationships represent ecotypes rather than their evolutionary relationships. We acknowledge the results of this study and welcome a new comprehensive analysis of the entire Holocentrinae in light of new genetic evidence. However, in the absence of observed morphological characters that are consistent with the genetic results, we choose to retain these six species within the genus *Neoniphon*, to the exclusion of *Sargocentron*, thereby maintaining nomenclatural stability. *Neoniphon pencei* clearly differs from all species placed in the genus *Sargocentron* on the basis of a closer association of the last dorsal-fin spine with the first soft-ray rather than the penultimate spine and the strongly protruding lower jaw (Randall and Heemstra 1985) as well as life color.

Meristic data of the type specimens of *Neoniphon pencei* are included in Table 1, and proportional measurements are included in Table 2. *Neoniphon pencei* is distinctive from all other species of holocentrids, both morphologically and genetically. Table 3 summarizes morphological differences between *N. pencei* and other species in the genus. It differs most substantially from all other *Neoniphon* in number of lateral line scales (48-52, compared with 38-47 among all other species), number of scales above the lateral line to the origin of the dorsal fin (5, compared with 2.5-3.5) and number of scales below the lateral line to the origin of the anal fin (6-7, compared with 7-9). It also differs from *N. aurolineatus*, *N. opercularis*, and *N. argenteus* in proportional length of the upper-jaw (2.3-2.6 in head length, compared with 2.0-2.3), and proportional length of of the third and fourth anal spines (1.1-1.3 and 1.7-2.0, compared with 1.4-1.9 and 1.9-2.7, respectively). It is further distinguished from *N. aurolineatus* in total number of gill rakers (19-20, compared with 15-17); from *N. opercularis* in head length (2.6-2.9 in SL, compared with 2.9-3.1), orbit diameter (1.2-1.4 in head length, compared with 3.0-3.5), snout length (1.2-1.4 in orbit diameter, compared with 1.2-1.5), and interorbital width (1.7-1.9 in orbit diameter, compared with 1.2-1.5); from *N. argenteus* in number of pectoral rays (14, compared with 12-13), interorbital width (1.7-1.9 in orbit diameter, compared with 1.2-1.7), and first dorsal-spine length (3.3-4.1 in head length, compared with 2.4-3.1); and from *N. sammara* in number of soft dorsal-fin rays (13, compared with 11-12), interorbital width (1.7-1.9 in orbit diameter, compared with 1.3-1.6), and first dorsal-spine length (3.3-4.1 in head length, compared with 2.2-3.0). In addition to these morphometric characters, *N. pencei* differs from all other species of *Neoniphon* in life color, particularly in the pattern of white spots on the dorsal fin and overall body color, and the lack of yellow coloration on the body (as in *N. aurolineatus* and *N. marianus*). Genetically, it differs in its *Cyt b* sequence from *N. argenteus* by 9.8%, *N. aurolineatus* by 9-9.6%, *N. marianus* by 11.7%, *N. opercularis* by 9.8%, and *N. sammara* by 12-12.5%.

Table 1.

Meristic data of the type specimens of *Neoniphon pencei*.

Holo-type	**Paratypes**											
BPBM	BPBM	BPBM	BPBM	BPBM	BPBM	BPBM	BPBM	BPBM	BPBM	BPBM	USNM	CAS
41197	41196	41196	41196	41196	41196	41196	41196	41196	41196	41196	431482	237596

	175	197	172	170	159	157	162	150	160	160	135	165	132
Dorsal Fin Rays	XI,13	XI,13	XI,13	XI,13	XI,13	XI,13	XI,13	XI,13	XI,13	XI,13	XI,13	XI,13	XI,13
Anal Fin Rays	IV,9	IV,9	IV,9	IV,9	IV,9	IV,9	IV,9	IV,9	IV,9	IV,9	IV,9	IV,9	IV,9
Pectoral Fin Rays	14	14	14	14	14	14	14	14	14	14	14	14	14
Pelvic Fin Rays	I,7	I,7	I,7	I,7	I,7	I,7	I,7	I,7	I,7	I,7	I,7	I,7	I,7
Principal Caudal Rays	9+8	9+8	9+8	9+8	9+8	9+8	9+8	9+8	9+8	damaged	9+8	9+8	9+8
Upper Pro-current Caudal Rays	7	7	7	7	7	7	7	7	7	damaged	7	7	7
Lower Pro-current Caudal Rays	6	6	6	6	6	6	6	6	6	damaged	6	6	6
Lateral Line Scales	49	49	49	49	49	49	49	48	49	damaged	49	52	49
Scales Above Lateral Line	5	5	5	5	5	5	5	5	5	5	5	5	5
Scales Below Lateral Line	7	7	6	7	6	6	6	6	6	6	6	6	7

Cheek Scales	5	5	5	5	5	5	5	5	5	5	5	5	5
Opercle Scales	9	9	10	10	9	10	8	9	10	10	9	9	9
Gill Rakers	6+13	7+13	6+13	6+13	6+13	6+13	6+13	6+13	7+13	6+13	7+13	6+13	6+13
Verte-brate	25	25	25	25	25	25	25	25	25	25	25	25	25

Table 2.

Proportional measurements of type specimens of *Neoniphon pencei* as percentages of standard length[1], head length[2], orbit diameter[3], or body depth[4].

	Holo-type	**Paratypes**											
	BPBM 41197	BPBM 41196	BPBM 41196	BPBM 41196	BPBM 41196	BPBM 41196	BPBM 41196	BPBM 41196	BPBM 41196	BPBM 41196	BPBM 41196	USNM 431482	CAS 237596
Standard length (mm)	175	197	172	170	170	157	162	150	160	160	135	165	132
Body depth[1]	3.15	3.30	3.04	3.06	3.09	2.90	3.16	3.06	3.02	3.06	3.16	3.08	3.03
Head length[1]	2.82	2.93	2.77	2.79	2.83	2.60	2.72	2.69	2.74	2.70	2.81	2.84	2.73
Snout length[2]	3.54	3.60	3.70	3.49	3.69	3.54	3.72	3.78	3.66	3.43	3.76	3.63	3.66
Orbit diameter[2]	3.02	2.80	2.73	2.94	2.82	3.01	2.90	2.75	2.72	2.96	2.63	2.76	2.73
Inter-orbital width[4]	4.83	4.69	4.11	4.72	4.78	4.70	4.18	4.45	4.51	4.35	4.38	4.46	4.61
Upper-jaw length[2]	2.30	2.32	2.38	2.35	2.35	2.41	2.45	2.59	2.29	2.42	2.34	2.27	2.31
Preoper-cular spine[3]	2.16	2.00	2.39	2.44	2.66	2.86	2.34	2.53	1.95	broken	2.61	2.00	2.54
Caudal-peduncle depth[4]	3.90	3.92	4.04	3.83	3.79	4.00	3.73	3.77	3.93	dama-ged	4.28	4.12	4.17

Caudal peduncle length[1]	7.30	6.74	7.24	7.23	7.16	6.82	6.48	6.45	6.81	dama-ged	7.01	6.88	7.68
Predorsal length[1]	2.66	2.72	2.52	2.64	2.54	2.43	2.58	2.53	2.43	2.46	2.53	2.61	2.52
Preanal length[1]	1.32	1.34	1.26	1.34	1.29	1.27	1.31	1.21	1.30	1.25	1.23	1.40	1.31
Prepelvic length[1]	2.44	2.48	2.51	2.48	2.64	2.43	2.57	2.49	2.60	2.46	2.52	2.62	2.48
First dorsal spine[2]	3.50	4.14	3.99	broken	3.66	4.09	3.65	3.54	3.86	3.65	3.45	3.84	3.33
Longest dorsal spine[2] **First**	3.34	2.44	2.30	2.37	2.31	2.37	2.25	2.03	2.40	2.68	2.24	2.85	2.21
anal spine[2] **Second anal**	29.5	25.0	25.2	23.2	27.4	23.6	23.2	25.2	26.0	22.3	24.9	25.7	19.1
spine[2] **Third anal**	9.00	8.17	8.09	7.24	8.52	8.25	8.26	7.84	8.29	7.66	7.88	7.95	7.34
spine[2] **Fourth anal spine[2]**	1.34	1.24	1.21	1.20	1.25	1.22	1.26	1.16	1.13	1.17	1.13	1.18	1.16
Longest anal ray[2]	1.98	1.97	1.80	1.89	1.89	1.93	2.03	2.00	1.74	1.99	1.71	1.89	1.88
Caudal-fin length[1] **Caudal**	2.05	2.05	1.92	1.96	2.0	2.09	2.13	2.12	1.94	2.21	1.89	2.12	1.97
concavity[2] **Pectoral-fin length[1]**	5.00	5.18	4.30	4.25	4.25	3.65	3.77	3.33	3.76	4.00	4.50	4.71	3.53
Pelvic-spine	2.88	2.54	2.23	2.30	2.47	1.98	2.20	2.45	2.21	dama-ged	2.78	2.90	2.16
length[2]	4.12	4.08	4.14	4.20	4.0	3.63	3.90	3.92	4.05	3.79	3.88	4.29	4.11

	2.32	2.26	2.21	2.26	2.31	2.51	2.33	2.23	2.29	2.37	2.29	2.47	2.43
Pelvic-fin length^{1}	4.93	4.83	4.74	4.42	4.59	4.30	4.63	4.41	4.44	4.54	4.58	4.93	4.57

Table 3.

Comparison of selected morphological characters for species of *Neoniphon*. Data for *N. argenteus*, *N. aurolineatus* (as *Flammeo scythrops*), *N. sammara*, and *N. opercularis* are from Shimizu and Yamakawa (1979); data for *N. marianus* are from Woods (1955).

Characters that differ from *N. pencei* are shown in bold. 1 as a proportion of Standard Length; 2 as a a proportion of orbit diameter; 3 as a proportion of head length.

Character	***N. pencei***	***N. argenteus***	***N. aurolineatus***	***N. marianus***	***N. opercularis***	***N. sammara***
Head Length^{1}	2.6-2.9	2.7-3.4	2.8-3.1	2.6-2.9	**2.9-3.1**	2.9-3.2
Snout Length^{2}^{2}	1.2-1.4 | 9.2-10.6^{1}	1.2-1.6	1.2-1.5	9.5-10.6^{1}	**0.8-1.0**	1.1-1.3
Orbit Diameter^{3}	2.6-3.0^{3} | 7.4-8.5^{1}	2.4-3.0	2.5-2.9	6.5-8.2^{1}	**3.0-3.5**	2.5-3.0
Interorbital Width^{2}	1.7-1.9^{2} | 12.5-15.4^{1}	**1.2-1.7**	1.6-2.1	11.5-14.8^{1}	**1.2-1.5**	**1.3-1.6**
Upper-jaw Length^{3}	2.3-2.6^{3} | 6.3-7.0^{1}	**2.2-2.3**	**2.0-2.3**	5.9-6.7	**2.1-2.2**	^{1} 2.2-2.4
First Dorsal-spine Length^{3}	3.3-4.1^{3} | 9.1-12.1^{1}	**2.4-3.1**	3.2-4.5	14^{1}	3.1.-3.6	**2.2-3.0**
Third Anal-spine Length^{3}	1.1-1.3^{3} | 3.1-3.8^{1}	**1.4-1.6**	**1.4-1.6**	3.4-4.4	**1.5-1.9**	^{1} 1.1-1.5
Fourth Anal-spine Length^{3}	1.7-2.0	**1.9-2.4**	**2.1-2.7**	-	**2.0-2.7**	1.8-2.2
Dorsal-fin soft rays	13	11-13	12-13	12-13	13	**11-12**
Pectoral-fin Rays	14	**12-13**	14	14	13-14	13-14
Lateral-line Scales						
Scales Below Lateral Line						
Scales Above Lateral Line						

48-52**38-43 44-46** 5**2.5 3.5 3.5 2.5 2.5**
46-47 38-40 39-43

6-7**7-8 8-9 8 8 8**

Gill Rakers	19-20	12-19**15-17**	18-19	17-19	13-20

Neoniphon pencei appears most similar to *N. aurolineatus* and *N. marianus*, based on having the the fewest number of differences in morphometrics, greatest genetic similarity, and most similar aspects of life coloration with these two species. It is also similar to *N. aurolineatus* in the depth and habitat it occupies. However, the differences between *N. pencei* and these two species as noted above clearly warrant recognition of *N. pencei* as a distinct species. A more comprehensive phylogenetic analysis of the species of *Neoniphon* and related genera based on both morphology and genetics (with verified voucher specimens) is beyond the scope of this work.

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We are especially grateful to Charles "Chip" Boyle for logistical support in the field, and to David F. Pence for collecting most of the type specimens of the new species. Radiographs were produced by Loreen R. O'Hara, and curatorial support was provided by Arnold Y. Suzumoto. We would also like to thank Casey Benkwitt, Tye Kindinger, Alix Davis, Lillina Tuttle, Mark Hixon, Matthew Craig, Athline Clarke, Richard Coleman, Brian Bowen, John Randall, Brian D. Greene and Robert K. Whitton for their help on various aspects of this work. We would also like to thank the reviewers for their invaluable comments.

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CHAPTER 4

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Luzonichthys seaver, a new species of Anthiinae (Perciformes, Serranidae) from Pohnpei, Micronesia

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ZooBank: urn:lsid:zoobank.org:pub:EDB2B394-7D15-42A5-AC89-D979AF29AAA7

Abstract

Luzonichthys seaver, n. sp., is described from two specimens, 42-46 mm standard length (SL) collected from Pohnpei, Micronesia. Collections were made by divers on mixed-gas closed-circuit rebreathers using hand nets at depths of 90-100 m. *Luzonichthys seaver* is distinct from all other species of the genus in the characters of lateral line scales, gill rakers, pelvic fin length, caudal concavity and coloration. Of the six species of *Luzonichthys*, it appears to be morphologically most similar to *L. earlei* and *L. whitleyi*.

Keywords

Serranidae, Luzonichthys, new species, Mesophotic Coral Ecosystems, MCE, Pohnpei, Micronesia

Introduction

The genus *Luzonichthys* Herre 1936 consists of six species of small, slender serranids within the subfamily Anthiinae, distributed throughout the tropical Indo-Pacific. The genus is distinguished from other anthiine genera in general body size and shape, and in possessing two fully separated dorsal fins, two opercular spines, and 11+15 vertebrae (Randall 1981, Randall and McCosker 1992). The currently recognized species include *L. earlei* Randall 1981, *L. microlepis*(Smith 1955),*L. taeniatus* Randall and McCosker 1992, *L. waitei* (Fowler 1931), *L. whitleyi* (Smith 1955), and *L. williamsi* Randall and McCosker 1992. Fowler (1931) originally established *L. waitei* within the genus *Mirolabrichthys* Herre 1927. Herre (1936) established the genus *Luzonichthys* with *waitei* as the type species, but classified it (as did Fowler 1931) within the family Pomadasyidae. Whitley and Colefax 1938 described the new genus and species *Naurua waitei*, and Smith 1955, unaware of Herre's genus *Luzonichthys*, described two additional species (*microlepis* and *addisi*) within*Naurua*, also placing *M. waitei* Fowler 1931 in this genus, thereby establishing *N. waitei* Whitley and Colefax 1938 as a secondary homonym of *M. waitei* Fowler 1931. Smith (1955) proposed the new name *N. whitleyi* as a replacement for Whitley and Colefax's species. Smith (1956) later reassigned the two species he described to *Luzonichthys* and suggested the two other species of *Naurua* may also belong to that genus. Fourmanoir (1977) proposed the species *L. robustus* from seven specimens taken from Mare, Loyalty Islands and one specimen from Kwajalein, Marshall Islands. Randall (1981) described the species *L. earlei* from specimens taken off Oahu, Hawaii and suggested that *L. addisi* and *L robustus* were junior synonyms of *L. waitei*, noting the type series of*robustus* included 4 different species of *Luzonichthys*, the holotype being *L. waitei*. Finally, in a revision of the genus *Luzonichthys*, Randall and McCosker (1992) described two additional new species of the genus, *L. taeniatus* and *L. williamsi*. With the description of the new species, *L.*

seaver herein, the number of recognized species within *Luzonichthys* is raised to seven.

Materials and methods

Type specimens of the new species, *Luzonichthys seaver*, were collected at Pohnpei, Micronesia by hand net from depths of 90-100 m and deposited in the Bernice P. Bishop Museum, Honolulu (BPBM). Measurements and counts given here follow the methods outlined in (Randall and McCosker 1992). Proportional measurements are given as ratios of: standard length (SL; measured from the tip of the snout to the base of the caudal fin at the posterior edge of the hypural plate); head length (HL, measured from the median anterior point of the upper lip to the end of the longest opercular spine), or body depth (BD, measured as the maximum depth from the base of the spinous portion of the dorsal fin). Character values for the paratype are presented in parentheses, if different from those of the holotype. Meristics and measurements were compared with data obtained from the literature (Randall and McCosker 1992) for the six currently recognized species of *Luzonichthys*: *L. earlei (n= 26)*, *L. microlepis (n= 13)*, *L. taeniatus (n= 8)*, *L. waitei (n= 57)*, *L. whitleyi (n=33)*, and *L. williamsi (n= 8)*.

Tissue samples were obtained from the two individuals of *L. seaver*. Total genomic DNA was extracted from both samples using the 'HotSHOT' protocol (Meeker et al. 2007). A 690-bp fragment of the mtDNA cytochrome c oxidase 1 (CO1) region was amplified using modified primers from (Baldwin et al. 2009): Fish-BCH(5' ACTTCYGGGTGRCCRAARAATCA-3') and Fish-BCL (5'-TCAACYAATCAYAAAGATATYGGCAC-3'). Polymerase chain reaction (PCR) was performed in a 15 µl reaction containing 7.5 µl BioMix Red (Biolone Inc., Springfield, NJ, USA), 0.2 µM of each primer, 5-50 ng template DNA, and nanopure water (Thermo Scientific* Barnstead, Dubuque, IA, USA) to volume. PCR cycling parameters were as follows: initial 95°C denaturation for 10 min. followed by 35 cycles of 94°C for 30 sec, 55°C for 30 sec, and 72°C for 30 sec, followed by a final extension of 72°C for 10 min. PCR products were visualized using a 1.5% agarose gel with GelStarTM (Cambrex Bio Science Rockland, Inc., Rockland MA, USA) and then cleaned by incubating with 0.75 units of Exonuclease and 0.5 units of Shrimp Akaline Phosphate (ExoSAP; USB, Cleveland, OH, USA) per 7.5 µl of PCR product for 30 min. at 37°C followed by 85°C for 15 min. Sequencing was conducted in the forward and reverse direction using a genetic analyzer (ABI 3730XL, Applied Biosystems, Foster City, California) at the ASGPB Genomics Sequencing Facility at the University of Hawaii at Manoa. The sequences were aligned edited and trimmed to a common length using Geneious Pro v.6.1.6 DNA analysis software (Biomatters. http://www.geneious.com/). CO1 haplotypes were deposited in GenBank (accession numbers KP110513 and KP110514) and BOLD (dx.doi.org/10.5883/DS- LSE001).

Taxon treatment

Luzonichthys seaver Copus, Ka'apu-Lyons, and Pyle 2015, sp. n.

- ZooBank urn:lsid:zoobank.org:act:68D04709-50C1-48D5-820C-FA4EC1BEF301

Materials

Holotype:

a. scientificName: *Luzonichthys seaver* Copus, Ka'apu-Lyons and Pyle; originalNameUsage: *Luzonichthys seaver* Copus, Ka'apu-Lyons and Pyle; originalNameUsageID: 68d04709-50c1-48d5-820c-fa4ec1bef301; namePublishedIn: Copus J, Ka'apu-Lyons C, Pyle R (2015) *Luzonichthys seaver*, a new species of Anthiinae (Perciformes, Serranidae) from Pohnpei, Micronesia. Biodiversity Data Journal 3: e4902.; namePublishedInID: edb2b394-7d15-42a5-ac89-d979af29aaa7; nameAccordingTo: Copus J, Ka'apu-Lyons C, Pyle R (2015) *Luzonichthys seaver*, a new species of Anthiinae (Perciformes, Serranidae) from Pohnpei, Micronesia. Biodiversity Data Journal 3: e4902.; nameAccordingToID: edb2b394-7d15-42a5-ac89-d979af29aaa7; acceptedNameUsage: *Luzonichthys seaver* Copus, Ka'apu-Lyons and Pyle sec Copus, Ka'apu-Lyons and Pyle; acceptedNameUsageID: 68d04709-50c1-48d5-820c- fa4ec1bef301; taxonID: 68d04709-50c1-48d5-820c-fa4ec1bef301; scientificNameID: 68d04709-50c1-48d5-820c-fa4ec1bef301; parentNameUsageID: 5b101671-671b-4200-8b57-17c8548a7180; parentNameUsage: *Luzonichthys* Herre 1936; higherClassification: Animalia, Deuterostomia, Chordata, Craniata, Gnathostomata, Actinopterygii, Perciformes, Percoidei, Serranidae, Anthiinae, *Luzonichthys*; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Perciformes; family: Serranidae; taxonRank: species; verbatimTaxonRank: Species; vernacularName: Seaver Splitfin; nomenclaturalCode: ICZN; genus: ***Luzonichthys***; specificEpithet: ***seaver***; scientificNameAuthorship: Copus, Ka'apu-Lyons and Pyle; higherGeography: Pacific Ocean, Western Pacific Ocean, Micronesia, Caroline Islands, Senyavin (Pohnpei) Islands; waterBody: Pacific Ocean; islandGroup: Caroline Islands; island: Ahnd (Ant) Atoll; country: Federated States of Micronesia; countryCode: FM; stateProvince: Pohnpei; locality: southwest end; verbatimLocality: Pacific Ocean, Western Pacific Ocean, Micronesia, Caroline Islands, Senyavin (Pohnpei) Islands, southwest end of Ahnd (Ant) Atoll; verbatimDepth: 90-100m; minimumDepthInMeters: 90; maximumDepthInMeters: 100; decimalLatitude: 6.79018; decimalLongitude: 158.034245; geodeticDatum: WGS84; coordinateUncertaintyInMeters: 30; georeferenceProtocol: GPS; samplingProtocol: Hand net; eventDate: 07/10/2014; year: 2014; month: 7; day: 10; habitat: rock outcrop along steep slope at top of drop-off; individualID: afba0d7b-3eba-43a3-98a5-8edf341836d2; individualCount: 1; lifeStage: adult; preparations: 55% Isopropyl; catalogNumber: 41205; recordedBy: Richard L. Pyle; disposition: in collection; identifiedBy: Richard L. Pyle; dateIdentified: 08/01/2014; modified: 2014-10-29T23:30:00Z; language: en; collectionID: http://biocol.org/urn:lsid:biocol.org:col:1001; institutionCode: BPBM; collectionCode: I; ownerInstitutionCode: BPBM; basisOfRecord: PreservedSpecimen

Paratype:

a. scientificName: *Luzonichthys seaver* Copus, Ka'apu-Lyons and Pyle; originalNameUsage: *Luzonichthys seaver* Copus, Ka'apu-Lyons and Pyle; originalNameUsageID: 68d04709-50c1-48d5-820c-fa4ec1bef301; namePublishedIn: Copus J, Ka'apu-Lyons C, Pyle R (2015) *Luzonichthys seaver*, a new species of Anthiinae (Perciformes, Serranidae) from Pohnpei, Micronesia. Biodiversity Data Journal 3: e4902.; namePublishedInID: edb2b394-7d15-42a5-ac89-d979af29aaa7; nameAccordingTo: Copus J, Ka'apu-Lyons C, Pyle R (2015) *Luzonichthys seaver*, a new species of Anthiinae (Perciformes, Serranidae) from Pohnpei, Micronesia. Biodiversity Data Journal 3: e4902.; nameAccordingToID: edb2b394-7d15-42a5-ac89-d979af29aaa7; acceptedNameUsage: *Luzonichthys seaver* Copus, Ka'apu-Lyons and Pyle sec Copus, Ka'apu-Lyons and Pyle; acceptedNameUsageID: 68d04709-50c1-48d5-820c- fa4ec1bef301; taxonID: 68d04709-50c1-48d5-820c-fa4ec1bef301; scientificNameID: 68d04709-50c1-48d5-820c-fa4ec1bef301; parentNameUsageID: 5b101671-671b-4200-8b57-17c8548a7180; parentNameUsage: *Luzonichthys* Herre 1936; higherClassification: Animalia, Deuterostomia, Chordata, Craniata, Gnathostomata, Actinopterygii, Perciformes, Percoidei, Serranidae, Anthiinae, *Luzonichthys*; kingdom: Animalia; phylum: Chordata; class: Actinopterygii; order: Perciformes; family: Serranidae; taxonRank: species; verbatimTaxonRank: Species; vernacularName: Seaver Splitfin; nomenclaturalCode: ICZN; genus: ***Luzonichthys***; specificEpithet: ***seaver***; scientificNameAuthorship: Copus, Ka'apu-Lyons and Pyle; higherGeography: Pacific Ocean, Western Pacific Ocean, Micronesia, Caroline Islands, Senyavin (Pohnpei) Islands; waterBody: Pacific Ocean; islandGroup: Caroline Islands; island: Ahnd (Ant) Atoll; country: Federated States of Micronesia; countryCode: FM; stateProvince: Pohnpei; locality: southwest end; verbatimLocality: Pacific Ocean, Western Pacific Ocean, Micronesia, Caroline Islands, Senyavin (Pohnpei) Islands, southwest end of Ahnd (Ant) Atoll; verbatimDepth: 90-100m; minimumDepthInMeters: 90; maximumDepthInMeters: 100; decimalLatitude: 6.79018; decimalLongitude: 158.034245; geodeticDatum: WGS84; coordinateUncertaintyInMeters: 30; georeferenceProtocol: GPS; samplingProtocol: Hand net; eventDate: 07/10/2014; year: 2014; month: 7; day: 10; habitat: rock outcropalong steep slope at top of drop-off; individualID: ff70b774-16f8-4469-8229-b2e0a9b655fa; individualCount: 1; lifeStage: adult; preparations: 55% Isopropyl; catalogNumber: 41206; recordedBy: Richard L. Pyle; disposition: in collection; identifiedBy: Richard L. Pyle; dateIdentified: 08/01/2014; modified: 2014-10-29T23:30:00Z; language: en; collectionID: http://biocol.org/urn:lsid:biocol.org:col:1001; institutionCode: BPBM; collectionCode: I; ownerInstitutionCode: BPBM; basisOfRecord: PreservedSpecimen

Description

Dorsal rays X,16, the first two soft rays simple; anal rays III,7, the first spine very small and difficult to detect; first ray simple; pectoral rays 21 (19), the upper most and lower most rays simple; branched pelvic rays I,5; branched caudal rays 13; simple upper and lower segmented caudal rays 4; upper and lower procurrent caudal rays 13; lateral line scales 63 (64); scales above lateral line to origin of dorsal fin 5; scales below lateral line to origin of anal fin 12; gill rakers 8+19 (8 +18) (Table 1).

Table 1.

Counts of dorsal rays, anal rays, pectoral rays, lateral line scales, and gill rakers of the species of *Luzonichthys*.

	Dorsal rays	Anal rays	Pectoral rays	Lateral line scales	Gill rakers
*L. seaver*X,16	III,7		19-21	63-64	8+18-19
*L. earlei*X,16-17	III,7		19-21	59-68	6-9+19-22
*L. microlepis*X,16	II,9		21-22	70-76	7-8+21-23
*L. taeniatus*X,16	III,7		19	56-60	7+19
*L. waitei*X,15-17	III,7		17-21	51-59	7-10+19-22
*L. whitleyi*X,16	III,7		19-22	65-74	7-9+20-23
*L. williamsi*X,16	II,9		21-23	70-78	7-8+21-22

Body moderately elongate, the depth 3.86 (4.6) in SL, and compressed, the width 1.83 (1.25) in BD; head length 3.54 (3.41) in SL; snout short and bluntly rounded, 4.0 (3.86) in HL. Orbit diameter 3.43 (3.8) in HL; the least width of interorbital space 3.0 (3.38) in HL; caudal peduncle depth 2.4 (2.45) in HL; caudal peduncle length about twice its depth, 1.09 (1.23) in HL. Mouth terminal and oblique, the maxilla reaching posterior to rear edge of pupil but not posterior to rear edge of orbit; the upper jaw length 1.6 (1.93) in HL; corners of maxilla rounded, its greatest depth about equal to pupil diameter. Opercle with 2 flat spines, the lower acute, in line with center of eye and opercular flap, the upper spine at dorsal end of gill opening poorly developed. Lateral line only slightly arched above pectoral fin, gradually descending below soft portion of dorsal fin, straightening toward the peduncular region; scales on body ctenoid; head scaled except snout; dorsal, anal, and pelvic fins naked; caudal fin with small scales extending about three-fourths distance to posterior margin; basal fifth of pectorals with small scales. Origin of dorsal fin above eighth lateral-line scale; first dorsal spine short, 8.0 (9.0) in head; fourth dorsal spine longest, 2.4 (2.45) in HL; longest dorsal soft ray 2.4 (2.45) in HL; origin of anal fin below base of sixth dorsal soft ray; first anal spine very short, about 12(13.5) in HL; second anal spine 6.0 (6.75) in HL; first anal soft ray very slender and only partly segmented, 2.4 (2.7) in HL; longest anal soft ray 2.0 (2.45) in HL; caudal fin forked, with filamentous rays, the fin length 4.05 (3.83) in SL, the caudal concavity 8.5 (8.36) in SL; middle pectoral rays longest, 3.86 (4.38) in SL; origin of pelvic fins below lower base of pectorals; second pelvic soft ray longest, 5.67 (6.57) in SL (Table 2).

Table 2.

Proportional measurements of type specimens of*Luzonichthys seaver*expressed as percentages of standard length

	Holotype BPBM 41205	**Paratype BPBM 41206**
Standard length (mm)	42.5	46
Body depth	25.9	21.7
Body width	14.1	17.4
Head length	28.2	29.3
Snout length	7.1	7.6
Orbit diameter	8.2	8.7
Interorbital width	9.4	8.7
Upper jaw length	17.6	15.2
Caudal peduncle depth	11.8	12.0
Caudal peduncle length	25.9	23.9
Predorsal length	35.3	34.8
Preanal length	62.4	70.0
Prepelvic length	33.0	32.6
First dorsal spine	3.5	3.3
Second dorsal spine	9.4	8.7
Third dorsal spine	10.6	8.7
Forth dorsal spine	11.8	12.0
Longest dorsal spine	11.8	12.0

First anal spine	2.4	2.2
Second anal spine	4.7	4.3
First anal ray	11.8	10.9

Longest anal ray	14.1	12.0
Caudal fin length	24.7	26.1
Caudal concavity	11.8	12.0
Pectoral fin length	25.9	22.8
Pelvic spine length	9.4	7.6
Pelvic fin length	17.6	15.2

Color of holotype in life: head excluding operculum predominately yellow (many scales with yellow margins and pink centers), yellow extending posteriorly on upper half of body from a line starting at approximately the tip of the opercular flap and top of pectoral fins to the eighth dorsal ray, fading to bright pink posteriorly. Operculum to lower half of body salmon pink. Pectoral and pelvic fins pale. Dorsal fins yellow with bases of rear dorsal rays pink. Anal fin rays yellow with pale membranes. Upper and lower base of caudal fin pink, extending posteriorly to approximately halfway to the tips; center of base of caudal fin white, fading to pale; posterior half of caudal fin yellow. Lower base of caudal peduncle with yellow band (Fig. 1).

Figure 1.

Holotype of*Luzonichthys seaver*,**BPBM 41205**, Pohnpei, Micronesia. Photo: Brian D. Greene.

Color of holotype in alcohol: Pale, all fins colorless except the caudal which has purple spots on the base of each of the upper and lower segments, the upper extending anteriorly, dorsally on the caudal peduncle.

Diagnosis

Dorsal rays X,16; anal rays III,7; pectoral rays 19-21; lateral line scales 63-54; gill rakers 8+18-19; Body moderately elongate, the depth 3.86-4.6 in SL; head length 3.41-3.54 in SL; snout 3.86-4.0 in HL; caudal fin forked, with filamentous rays, caudal concavity 8.36-8.5 in SL; pectoral fins 3.86-4.38 in SL; pelvic fins 5.67-6.54 in SL.

Etymology

Named *seaver*, as a noun in apposition, for the Seaver family in recognition of support from the Seaver Institute for marine research.

Distribution

Type specimens of*L. seaver*were collected from Pohnpei, Micronesia. A single larva of what may be this species (98.2-99.5% similarity at CO1) was collected in Moorea, French Polynesia (BOLD: FPFLB281-12; GenBank: KJ967845.1; Hubert et al. 2014), but the taxonomic identity of the Moorea specimen could not be confirmed by the authors. Therefore, it is possible that adults of this species will be discovered in Moorea and other locations across the Pacific.

Taxon discussion

Luzonichthys seaver is distinct from all other species within the genus in life coloration. It is most similar in color to *L. earlei* (Fig. 2); however, it differs from that species in coloration of head, upper half of body, and dorsal and anal fins (yellow in *L. seaver*, compared with orange in *L. earlei*), and in the distinctive color pattern on the caudal fin (bright pink blotches on the base of both caudal lobes with bright yellow distally in *L. seaver*, compared with drab, diffuse orange blotches and pale yellow distal caudal lobes in *L. earlei*). We have examined enough individuals of *L. earlei* from many localities to confirm that these color characteristics do not vary signigicantly within that species. Morphologically, it differs from all other species except *L. earlei* in number of lateral line scales (63-64, compared with 51-60 or 65-78 for other species), and from all other species except *L. whitleyi* in caudal concavity (8.4-8.5 in HL, compared with 4.0-8.3 for other species). It further differs from all other species except *L. earlei*, *L. waitei* and *L.*

taeniatus in number of gill rakers (8+18-19, compared with 7-10+20-23 for other species), and from *L. williamsi* and *L. microlepis*in number of anal-fin spines and rays (III, 7 compared with II, 9), as well as snout length, orbit diameter, and caudal peduncle depth (Table 3). *Luzonichthys seaver* is further distinct from *L. williamsi* in its body depth and pectoral fin length, and from *L. taeniatus* in snout length, caudal peduncle depth, and longest dorsal spine (Table 3). Overall, *L. seaver* is most similar morphologically to *L. earlei* and *L. whitleyi*; however, in addition to character differences outlined above, it can be further distinguished from these two species by caudal peduncle depth (both species) snout length (*L. whitleyi*), and head length (*L. earlei*) (Table 3). Molecular data are not used for comparative purposes in this description because these data do not exist for any of the other species of *Luzonichthys*. The CO1 barcodes produced in this study represent the first sequences publicly available for this genus, aside from the afore mentioned and previously unclassified larval specimen from Moorea.

Table 3.

Comparison of selected morphological characters for species of *Luzonichthys*.

Character		***L. seaver***	***L. earlei***	***L. microlepis***	***L. taeniatus***	***L. waitei***	***L. whitleyi***	***L. williamsi***
Body depth	in SL	3.9-4.6	3.6-4.1	4.1-4.4	3.7-4.0	3.3-3.8	4.15-5.0	5.2-5.4
Head length	in SL	3.4-3.5	3.15-3.4	3.5-3.7	3.3-3.5	3.0-3.6	3.4-3.8	3.4-3.5
Snout length	in HL	3.9-4.0	3.9-4.3	4.0-4.3	4.2-4.4	3.7-4.7	4.2-4.8	4.3-4.6
Orbit diameter	in HL	3.4	3.1-3.9	4.1-4.4	3.0-3.5	3.5-3.9	3.2-3.6	2.7-3.3
Caudal peduncle depth	in HL	2.4-2.5	2.6-2.9	2.5-2.7	1.5	2.3-2.6	2.5-2.9	2.8-2.9
Caudal concavity	in SL	8.4-8.5	6.1-7.3	6.0-6.8	5.1-5.5	4.0-5.6	5.2-9.0	6.7-8.3
Longest dorsal spine	in HL	2.4-2.5	2.1-2.6	2.4-2.8	2.2-2.4	2.2-2.6	2.0-2.6	2.2-2.5
Pectoral fin length	in SL	3.9-4.4	3.7-4.0	4.1-4.7	3.6-3.7	3.2-3.5	3.7-4.4	4.4-4.7
Pelvic fin length	in SL	5.7-6.6	4.4-5.2	5.0-5.8	4.6-4.9	3.9-4.7	4.6-6.0	4.8-5.8

Figure 2.

Luzonichthys earlei, from the Hawaiian Islands. Photo: John E. Randall.

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CHAPTER 5

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Prognathodes geminus, a new species of butterflyfish (Perciformes, Chaetodontidae) from Palau

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http://zoobank.org/d71a7fba-8539-47e2-9df1-e0d8bfda5005

Abstract

A new species of the butterflyfish genus *Prognathodes* (Chaetodontidae) is described from two specimens collected at a depth of 116 m off Ngemelis Island, Palau. *Prognathodes geminus* sp. n. is similar to *P. basabei* Pyle and Kosaki, 2016 from the Hawaiian Archipelago, and *P. guezei* (Maugé and Bauchot, 1976) from the western Indian Ocean, but differs from these species in the number of soft dorsal-fin rays, size of head, body width and body depth. There are also differences in the life color from both species, and a substantial genetic difference from the Hawaiian species ($d \approx 0.08$ in mtDNA cytochrome oxidase I). Although genetic comparisons with *P. guezei* are unavailable, we expect the genetic divergence between *P. guezei* and *P. geminus* to be even greater than that between *P. geminus* and *P. basabei*. It is named for the strikingly similar color pattern it shares with *P. basabei*.

Keywords

Mesophotic Coral Ecosystem, Closed-Circuit Rebreather, Butterflyfish, Micronesia, Systematic Ichthyology

Introduction

The butterflyfish genus *Prognathodes* Gill 1862 (type species *Chelmo pelta* Günther 1860 = *Chaetodon aculeatus* Poey 1860) currently includes twelve valid species: seven from the Atlantic [*P. aculeatus* (Poey, 1860), *P. aya* (Jordan, 1886), *P. brasiliensis* Burgess, 2001, *P. dichrous* (Günther, 1869), *P. guyanensis* (Durand, 1960), *P. marcellae* (Poll, 1950), and *P. obliquus* (Lubbock and Edwards, 1980)], two from the tropical eastern Pacific [*P. falcifer* (Hubbs and Rechnitzer, 1958), *P. carlhubbsi* Nalbant, 1995], one from the Hawaiian Islands [*P. basabei* Pyle and Kosaki, 2016], one from the central Indian Ocean and western Pacific [*P. guyotensis* (Yamamoto and Tameka, 1982)], and one from the western Indian Ocean [*P. guezei* (Maugé and Bauchot, 1976)], most of which are associated with deep coral-reef environments known as Mesophotic Coral Reef ecosystems (MCEs; 30-150 m; Hinderstein et al. 2010).

Several individuals of a butterflyfish with dark bars resembling both *P. guezei* from the Western Indian Ocean and a species from the Hawaiian Islands that was later described as *P. basabei* were recorded on video at depths in excess of 110 m during a series of submersible dives in Palau conducted by Patrick L. Colin and Lori Bell Colin in 2001. In April 2007, while conducting a series of deep exploratory dives off Ngemelis Island, Palau (Republic of Belau) in the Caroline Islands, authors Pyle and Greene collected two specimens of this unidentified *Prognathodes* at a depth of 116 m. The specimens were encountered among a patch of limestone rubble at the base of a prominent limestone outcropping.

Based on an examination of a combination of morphological and genetic characters of the Palauan specimens, in comparison to six specimens of *P. basabei* and two specimens of *P. guezei* (the two species that most closely resemble the Palauan specimens), we herein describe the new species, *Prognathodes geminus*.

Methods

Two specimens of *Prognathodes* were collected with hand nets during deep dives using mixed-gas, closed-circuit rebreathers off of Ngemelis Island (7.13791°W, 134.22181°N), at a depth of 116 m. Specimens were brought to the surface alive, and immediately following euthanization were photographed for retention of color. A tissue sample was taken from each specimen prior to being placed in formalin. Methods of counts and measurements follow Pyle and Kosaki (2016).

Head length, depth of body, width of body, snout length, predorsal length, preanal length, length of dorsal-fin and anal-fin bases, orbit diameter, interorbital width, caudal peduncle depth, and lengths of fin spines and rays are expressed as percent of SL. Counts and measurements for the paratype, if different from the holotype, are presented in parentheses after the value for the holotype.

The holotype has been deposited in the fish collection at the Bernice Pauahi Bishop Museum, Honolulu (BPBM), and the paratype has been deposited at the U.S. National Museum of Natural History, Washington, D.C. (USNM).

Total genomic DNA was extracted using the 'HotSHOT' protocol (Meeker et al. 2007). A 533-base pair fragment of the mtDNA cytochrome c oxidase 1 (CO1) region was amplified using primers from Baldwin et al. (2009). Polymerase chain reaction (PCR) was performed in a 15 µl reaction containing 7.5 µl BioMix Red (Biolone Inc., Springfield, NJ,USA), 0.2 µM of each primer, 5-50 ng template DNA, and nanopure water (Thermo Scientific Barnstead, Dubuque, IA, USA) to volume. PCR cycling parameters were as follows: initial 95°C denaturation for 10 min followed by 35 cycles of 94°C for 30 sec, 55°C for 30 sec, and 72°C for 30 sec, followed by a final extension of 72°C for 10 min. PCR products were visualized using a 1.5% agarose gel with GelStar^{TM} (Cambrex Bio Science Rockland, Inc., Rockland MA, USA) and then cleaned by incubating with 0.75 units of Exonuclease and 0.5 units of Shrimp Akaline Phosphate (ExoSAP; USB, Cleveland, OH, USA) per 7.5 µl of PCR product for 30 min. at 37°C followed by 85°C for 15 min. Sequencing was conducted in the forward and reverse direction using a genetic analyzer (ABI 3730XL, Applied Biosystems, Foster City, California) at the ASGPB Genomics Sequencing Facility at the University of Hawai‘i at Mānoa. The sequences were aligned, edited and trimmed to a common length using Geneious Pro v.6.1.6 DNA analysis software (Biomatters. http://www.geneious.com/). CO1 haplotypes were deposited in GenBank and the Barcode of Life Database (BOLD).

Description

Prognathodes geminus Copus, Pyle, Greene and Randall, sp. n.
http://zoobank.org/beab3b7f-b4b1-44f7-8181-2ff950ca466a

Figs. 1–3.

Type Locality

Caroline Islands; Palau; Ngemelis Island, northwest side, “Blue Holes” (7.13791°N, 134.22181°W), 116 m.

Holotype

BPBM 40857, GenBank MG895424, Barcode of Life PROGE001-17, 73.1 mm SL, Caroline Islands; Palau; Ngemelis Island, northwest side, “Blue Holes”, 7.13791°N, 134.22181°W: around limestone rock outcrop with limestone rubble, 116 m. Hand nets. R.L. Pyle. 27 April 2007.

Paratype

USNM 440390, GenBank MG895423, Barcode of Life PROGE002-17, 1:70.0 mm SL, same location, habitat, collecting method, and date as holotype, B.D. Greene collector.

Diagnosis

A species of *Prognathodes* (*sensu* Smith et al. 2003) distinguished by the following combination of characters: dorsal-fin soft rays 17–19; anal-fin soft rays 15; head 2.48–2.49 in SL; body depth 1.71–1.76 in SL; pelvic-fin spine length 4.18–4.46 in SL; color in life white with three black bands on each side of the body, the first band originating at origin of first dorsal-fin spine, extending diagonally to eye and continuing horizontally as a yellowish brown stripe from eye to tip of snout, the second band originating at and including third to seventh dorsal-fin spines, extending vertically at a slightly posterior angle to ventral surface of abdomen just anterior to anus, tapering slightly and curving slightly posteriorly below pectoral fin, the third band originating at and including last six dorsal-fin spines and covering entire first two to three dorsal-fin soft rays tapering down to base of last dorsal-fin soft rays, extending vertically at a slightly posterior angle to include base of anal-fin soft rays, a broad black margin on posterior edges of dorsal and anal fins extending as a narrow black band across base of the caudal fin, a narrow yellow band on dorso-posterior margin of operculum, extending ventrally to posterior angle of operculum, a yellow spot on upper one-third of pectoral-fin axis extending towards yellow band on operculum, pelvic fins white on spine and anterior one-third of fin, and yellowish brown on posterior two-thirds of fin.

Description

Dorsal fin XIII,17 (19), last soft ray branched to base; anal fin III,15, last soft ray branched to base; pectoral-fin rays 15; pelvic-fin rays I,5; principal branched caudal rays 15; pored lateral-line scales 26 (27); scale rows above lateral line to origin of dorsal fin 11 (10 in paratype); scale rows below lateral line to origin of anal fin 21 (20); gill rakers on upper limb 5 (6), on lower limb 10; vertebrae 24.

Body deep, depth 1.71 (1.76) in SL, and compressed, width 4.36 (3.2) in depth; head length 2.49 (2.48) in SL; snout produced, its length 2.37 (2.52) in head; orbit diameter 3.30 (3.53) in head; interorbital slightly convex, least bony width 4.59 (4.78) in head; least depth of caudal peduncle 4.59 (4.78) in head.

Mouth small, upper jaw 2.37 (2.52) in head, slightly diagonal, the gape forming an angle of about 20° to the horizontal, upper jaw slightly protruding; teeth in jaws densely setiform, longest 7.8 in orbit diameter; nostrils anterior to eye horizontally in line with center of iris, the anterior in a short membranous tube with a well-developed posterior flap, the posterior slightly larger, ovate, with a low fleshy rim. Lower edge of lacrimal smooth; margin of preopercle finely serrate; margins of other opercular bones smooth.

Lateral line forming a broad arc, ending below the base of third to fifth soft dorsal rays and within the second black band of the body. Scales ctenoid, moderately large on body except for chest and near origins of dorsal and anal fins, where small; head fully scaled except anterior portions of both jaws and around nostrils, scales on the head small; scales on fleshy sheath surrounding base of dorsal and anal fins moderately large anteriorly and proximally, reducing in size posteriorly and distally; scales on caudal peduncle and covering base of caudal fin small.

Origin of dorsal fin slightly anterior to upper end of gill opening, its base 1.5 (1.51) in SL; first dorsal-fin spine shortest, its length 4.03 in head; second dorsal-fin spine 1.85 (1.88),in head; fourth dorsal-fin spine longest, its length 1.18 (1.26) in head; third dorsal-fin spine nearly as long as fourth, its length 1.23(1.28) in head; fifth dorsal-fin spine shorter, its length 1.28 (1.29) in head; dorsal-fin spines progressively shorter posteriorly, the last 1.96 (1.89) in head; membranes between anterior dorsal-fin spines deeply incised, progressively less so posteriorly; first dorsal-fin soft ray the longest, approximately same length as last dorsal-fin spine, 1.87 (broken in paratype) in head, dorsal-fin soft rays progressively shorter posteriorly; first anal-fin spine shortest, its length 2.67 (2.56) in head; second anal-fin spine longest, its length 1.33 (1.38) in head; third anal-fin spine 1.44 (1.53) in head; first anal-fin soft ray longest, its length 1.40 (damaged in paratype) in head, anal-fin soft rays progressively shorter posteriorly; caudal fin damaged; pectoral fins damaged; pelvic spine 1.1.68 (1.8) in head; first soft ray of pelvic fin broken in both specimens.

Color in life as in Figures 1–2.
Body white with three dark brown bands, the first beginning narrowly at origin of dorsal fin, curving slightly as it passes, mostly one-half eye diameter in width, to eye; second band originating at tips of third to fifth dorsal spines and basal half of fifth spine, crossing body ventrally, progressively narrower below lateral line to end on mid-abdomen one-half eye diameter in width; second dark brown band originating from outer third of eighth dorsal spine and tip of first two soft rays of fin, passing obliquely, equal in width, to lateral line, then narrowing to half that width at mid-base of soft portion of anal fin, and crossing fin to end on outer half of third anal spine; a yellowish brown bar, one-half eye diameter in average width (narrowing gradually to mid-peduncle depth), across caudal peduncle and base of caudal fin; remainder of caudal fin whitish; a yellowish brown band of pupil width passing obliquely from eye, narrowing on its anterior half, to end at tip of snout; eye silvery white with an oblique dark brown band in alignment with nape band across eye, the dorsal part half-pupil width, and the ventral part one-half that; opercular membrane bright yellow; margin of soft portion of anal fin dark yellowish brown, about pupil width on last rays and membranes, progressively narrower to first rays; a similar terminal margin on dorsal fin; pectoral fins translucent with a semicircular light gray bar at base, preceded on upper half by a bright yellow bar. about half-pupil diameter in width, in alignment with yellow margin of operculum; spine and first ray of pelvic fins white, the white continuing progressively shorter on remaining rays that are dark orange-yellow, the membranes translucent dark yellowish.

Color in alcohol similar to life color, except body a uniform dull yellow, bands dark brown, and orange areas pale brown.

Morphometric data for selected characters of type specimens are provided in Table 1.

Distribution

Prognathodes geminus is positively known only from the island of Ngemelis in Palau. Individuals of what appear to be this species were collected by aquarium-fish collector Tim Bennett in the Coral Sea at a depth of 140 m (Fenton Walsh, personal communication), and video taken from a depth of about 120 m in New Caledonia (and reviewed by co-author Pyle) show what appears to be a similar fish. A similar species was recently described from the Hawaiian Islands (*P. basabei*), but numerous deep dives by the authors and others in regions between Palau and the Hawaiian Islands have not yielded any observations of this species, or any other members of the genus *Prognathodes*.

Habitat

Type specimens and other individuals observed from submersible by Patrick L. Colin (personal communication) in Palau were observed in association with limestone outcroppings on steep slopes at depths of 110–150 m. The type specimens were collected in an area with broken limestone rubble (Figure 3).

Etymology

We name this species *geminus*, meaning "one who is a twin", in reference to its similarity in color to *P. basabei* from the Hawaiian Islands.

Morphological Comparisons

Prognathodes geminus appears to be most similar in color and morphology to *P. basabei* collected at similar depths in the Hawaiian Archipelago. These two species differ from each other in number of dorsal-fin soft rays (17–19 for *geminus*, compared to 21–22 for *basabei*) and anal-fin soft rays (15 compared to 16–17). *P. geminus* has a larger head (2.48–2.49 in SL, compared to 2.63–2.80 in SL), its body more elongate, the depth 1.71-1.76 in SL, compared to 1.58–1.69 for *P. basabei*, more slender, the width 7.46–7.95 in SL compared to 6.40–7.04, and a shorter pelvic-fin spine (4.18–4.46 in SL, compared to 3.63–4.07 in SL)[1] than the Palau species. The two species also differ in certain aspects of life color. The posterior edge of the first black band of *P. geminus* (Figures 1–3) ends at the origin of the first dorsal spine while it includes the first dorsal spine in *P. basabei* (Figure 4). The anterior edge of the second black band of *P. geminus* originates at the third dorsal-fin spine, whereas this band originates on the fourth dorsal-fin spine in *P. basabei*. Moreover, both of the dark bands on *P. geminus* are proportionally broader dorsally, tapering more substantially ventrally than in *P. basabei*. Also, the pale areas between dark bands are white in *P. geminus*, but pale yellow in *P. basabei*, and the orangish coloration on the pelvic fins and posterior margin of the soft dorsal and anal fins of *P. geminus* are much darker (brownish) than in *P. basabei*.

P. geminus is also similar in color and morphology to *P. guezei* from the western Indian Ocean. It differs from that species morphologically in number of dorsal-fin soft rays (17–19 for *geminus*, compared to 20 for *guezei*), body depth (1.71–1.76 in SL, compared to 1.87–1.95 in SL), and body width (7.46–7.95 in SL, compated to 7.16–7.27). There are also several differences in life color between the two species. In particular, *P. guezei* (Figure 5) has more pronounced and discrete yellow bars on the body between the black bands, compared with more white in *P. geminus*. The two black bands on the body of *P. guezei* taper even more substantially than they do in the *P. geminus*. Also, the orangish coloration on the pelvic fins and posterior margin of the soft dorsal and anal fins of *P. guezei* are much paler and yellowish than in *P. geminus*.

Genetic comparisons

A comparison of mtDNA COI sequences obtained from the holotype and paratype of *P. geminus* and from the holotype and two paratypes of *P. basabei* reveal 8% uncorrected sequence

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[1] Pyle and Kosaki (2016) incorrectly stated that the pelvic-fin spine of *P. basabei* was "shorter" than that of this species, though they correctly presented the corresponding proportional measurements.

divergence, consistent with species-level divergences in other fish taxa (Johns and Avise 1998, Bowen et al. 2001, Bellwood et al. 2004, Fessler and Westneat 2007, Randall and Rocha 2009, Reese et al. 2010, Rocha 2004, Rocha et al. 2008). While no tissue samples or DNA sequences have been reported for *P. guezei*, we anticipate that given the geographic distributions of *P. guezei* in the western Indian Ocean, and *P. geminus* and *P. basabei* in the Pacific Ocean, a much greater genetic divergence between *P. guezei* and the other two species likely exists.

Discussion

Mixed-gas closed-circuit rebreather diving technology has revolutionized the exploration of the deeper depths of coral reef environments across the globe (Pyle 1996, 2000). *Prognathodes geminus* is just one of many new fish species being discovered on MCEs and many more species are yet to be discovered and described. One of the more interesting aspects of this new species is the contrast between the strikingly similar color pattern it shares with *P. basabei*, against the substantial genetic differences. While genetic comparisons with *P. guezei* are not possible without appropriate tissue samples from that species, we expect that the genetic divergence between that species and *P. geminus* to be even greater than that between *P. geminus* and *P. basabei*. The disparity between the degree of difference in color relative to the genetic difference is striking in comparison to many species of butterflyfishes, which tend to have more substantial color differences relative to genetic differences (Hemingson et al. 2018).

Prognathodes geminus is the thirteenth member of the genus. Given the proclivity for species of this genus to inhabit relatively poorly-explored MCEs, as well as the stark genetic differences between *P. basabei* and its closest known relative, it would not be unusual for other species of this genus to be discovered elsewhere throughout the tropical Indo-Pacific region. Indeed, video captured using a remotely operated vehicle at Rapa Nui (Easter Islands) reveals what appears to be another as-yet un-named species of banded *Prognathodes* inhabiting MCEs (Easton et al. 2017).

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Table 1. Morphometric and meristic data for selected characters of type specimens of *Prognathodes geminus*. Values of morphometric data (other than TL and SL) are represented as % of SL.

	Holotype	Paratype
Morphometrics	BPBM 40857	USNM 440390
Standard length (SL) in mm	73.1	70.1
Body depth	58	57
Body width	13	13
Head length	40	40
Snout length	16	17
Orbit diameter	12.2	11.4
Interorbital Width	9.0	8.0
Predorsal length	46	42
Preanal length	72	71
Base of dorsal fin	67	66
Base of anal fin	30	30
Caudal Peduncle Depth	8.8	8.4
Pelvic Spine	23.9	22.4
Pelvic Fin	-	-
First Dorsal Spine length	10	10
Second Dorsal Spine length	22	21
Third Dorsal Spine length	33	31
Fourth Dorsal Spine length	34	32
Fifth Dorsal Spine length	31	31
Last Dorsal Spine length	21	21
Longest Dorsal Ray length	21	
First Anal Spine length	15	16
Second Anal Spine length	30	29
Third Anal Spine length	28	26
Longest anal ray length	29	
Caudal fin length	-	-
Pectoral fin length	-	-
Meristics		
Dorsal Spines	XIII	XIII
Dorsal rays	17	19
Anal Spines	3	3
Anal Rays	15	15
Pectoral Rays	15	15
Caudal Rays	22	22
Pored lateral line scales	26	27
Dorsal scale rows	11	10
Ventral scale rows	21	20
Gill rakers	5+10	6+10

Figure 1. Holotype of *Prognathodes geminus* (BPBM 40857-1), collected at a depth of 116 at Palau off of xyz. Photo by R.L. Pyle

Figure 2. Paratype of *Prognathodes geminus* (BPBM 40857-2), collected at a depth of 116 m at Palau. Photo by R. L. Pyle.

Figure 3. Holotype of *Prognathodes geminus* in its natural habitat at a depth of 116 m off Ngemelis, Palau. Photo by J. L. Earle.

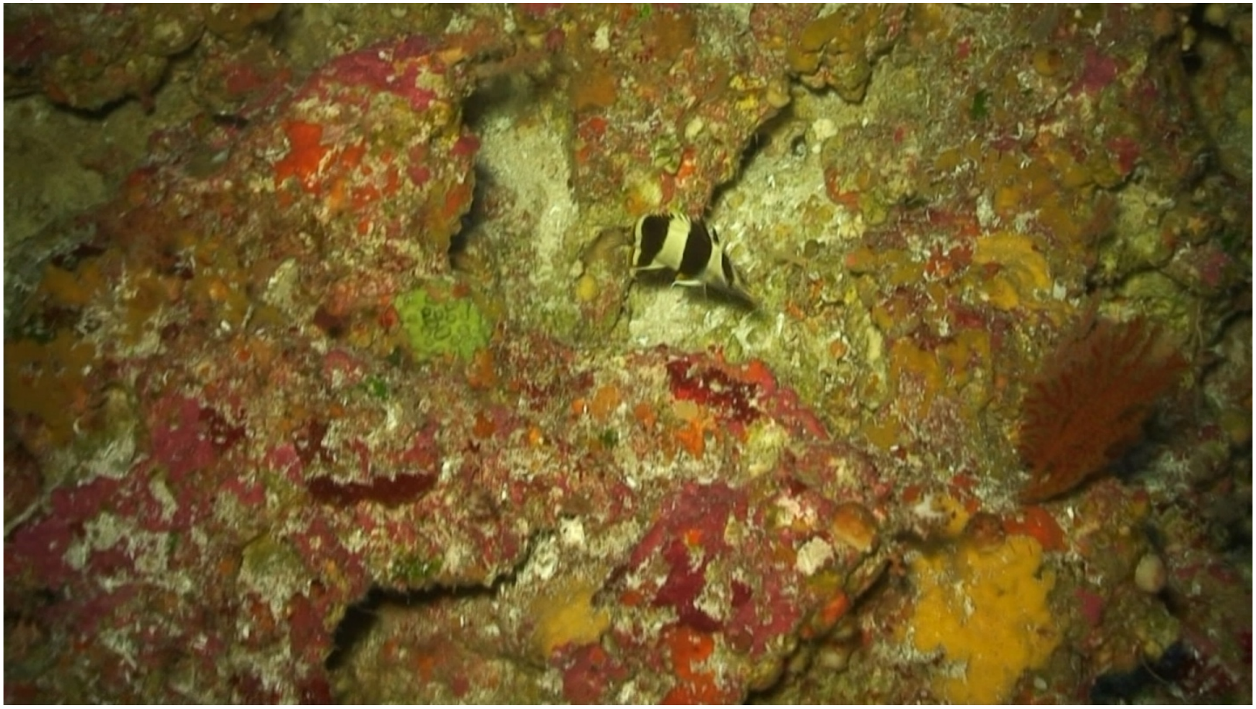

Figure 4. Holotype of *Prognathodes basabei* (BPBM 41290), collected at a depth of 61 m off Pearl and Hermes Atoll, Northwestern Hawaiian Islands. Photo by R. L. Pyle.

Figure 5. *Prognathodes guezei* at a depth of 117 m off Sodwana Bay, South Africa. Photo by R. L. Pyle.

CHAPTER 6

CONCLUSION

The existence mesophotic coral ecosystems (MCEs; light-dependent coral ecosystems from 30 to 150 m in depth) has been known since the nineteenth century, and focused scientific exploration of these zooxanthellate corals began over 50 years ago. However, more than 70% of all research on MCEs has been published only within the past seven years. MCEs represent approximately 80% of potential coral reef habitat worldwide, yet very little is known about them in comparison to shallow reefs. Many MCE species new to science have been discovered in the past decade, and many more await discovery. The term MCEs has been widely adopted by the scientific community since its 2008 inception; however, there is considerable inconsistency in how it is subdivided into "upper" and "lower" (and sometimes "middle") zones. Moreover, doing so may lead to artificial boundaries when habitats and ecological communities at different depth zones may blend together. Growing evidence suggests that MCEs harbor proportionally more geographically endemic species than their shallow-water counterparts, and initial indications are that major biogeographic patterns described for shallow reef organisms may not apply to MCEs. Although MCEs may serve as refugia for some shallow species, they are increasingly recognized as unique ecosystems, important in their own right. Future research on MCEs should aim to address gaps in our understanding of the basic physical and biological characteristics of MCEs including geography, taxonomic composition, depth distribution, ecology, physiology, and connectivity.

This dissertation is a starting point for research into the origins and evolution of reef fishes that inhabit the MCE. In particular the three species descriptions may provide some insight into the taxonomic affiliations of deep reef fishes. The evaluation of the habitat persistence hypothesis in Chapter 2 may provide some compass points for further exploration of these vastly understudied ecosystems.

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