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INSHORE FISHES OF HOWLAND ISLAND, BAKER ISLAND, JARVIS ISLAND, PALMYRA ATOLL, AND KINGMAN REEF

BY

BRUCE C. MUNDY, RICHARD WASS, EDWARD DEMARTINI,
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AND CRAIG MUSBERGER

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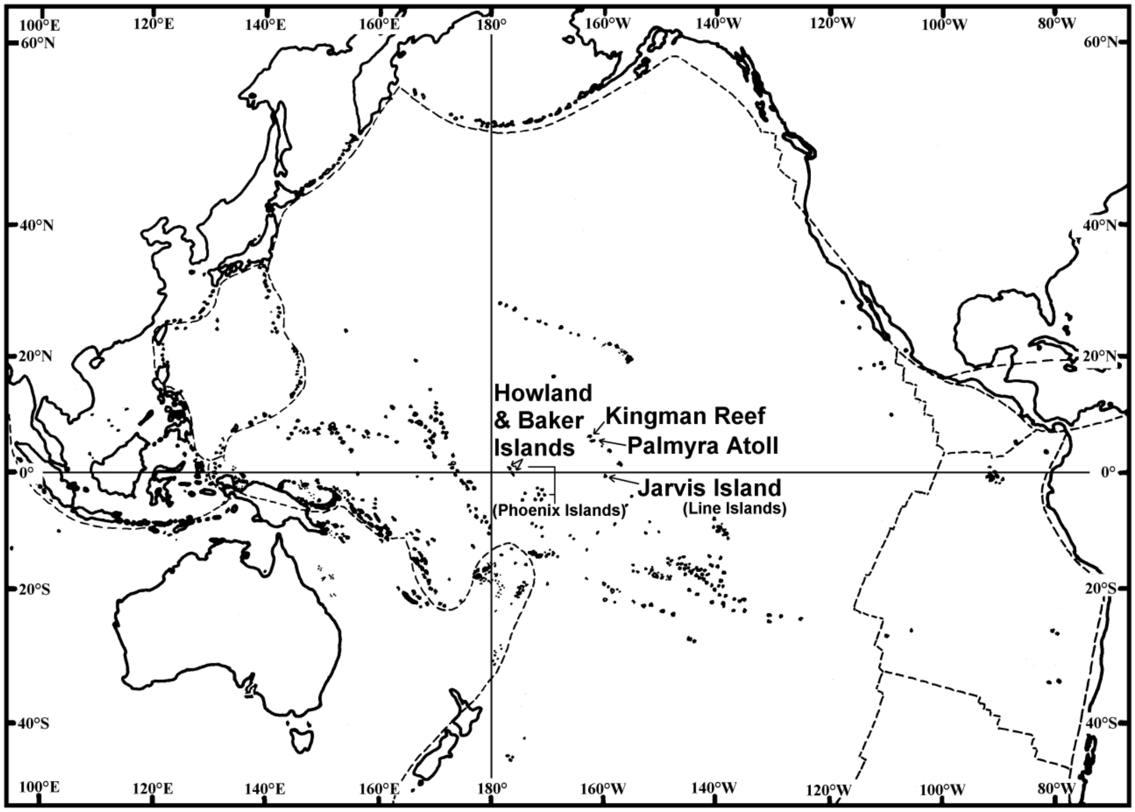

Figure 1. Locations of Kingman Reef, Palmyra Atoll, Jarvis Island, Howland Island, and Baker Island in relation to the major central Pacific island groups. Dashed lines represent the tectonic plate boundaries in the Pacific Ocean.

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ABSTRACT

A list is given of shore fishes known from Howland and Baker Islands, outliers of the Phoenix Islands group, and Jarvis Island, Palmyra Atoll, and Kingman Reef in the Line Islands group. The list was compiled from literature sources, museum collection databases, and surveys conducted in 2000–2008 by the NOAA Pacific Islands Fisheries Science Center's Coral Reef Ecosystem Division (CRED). A total of 506 shore-fish species and 27 epipelagic species were recorded from the five islands. Of the shore-fish species, 41 (8.1%) were first noted in our CRED surveys. Numbers for the individual islands are: Howland Island—328 species of which 166 (50.8%) are first records from CRED sampling; Baker Island—268 species with 188 (70.1%) as new CRED records; Jarvis Island—274 species with 176 (64.2%) as new CRED records; Palmyra Atoll—395 species with 113 (28.6%) as new CRED records; and Kingman Reef—270 species with 212 (78.5%) as new CRED records. Fifteen additional species whose identifications are in need of verification were reported in our surveys or previous efforts. An additional 16 are considered suspect identifications of species that probably do not occur at the Line or Phoenix Islands. Differences in the species composition of the five islands are discussed in the context of habitat diversity, historic sampling effort, and regional oceanography. The evolution of shore-fish species found at these central Pacific islands is reviewed in the context of phylogeographic information, geology of Pacific islands, and regional oceanography. It is argued that oceanography and dispersal have played a larger role than geologic adjacencies in the evolution of central Pacific oceanic island fishes. Knowledge of the fish fauna of the central equatorial Pacific remains incomplete, in part, because of limited sampling of small, nocturnal, or otherwise cryptic species. These five islands are

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unique among United States possessions in having a few reef fish species found nowhere else in the country. The isolated islands of the central Pacific remain one of the most poorly understood regions on earth for knowledge of biodiversity.

INTRODUCTION

Howland Island, Baker Island, Jarvis Island, Palmyra Atoll, and Kingman Reef are United States possessions in the central Pacific Ocean (Fig. 1, Table 1). Howland and Baker Islands are outliers of the Phoenix Islands, while Jarvis Island, Palmyra Atoll, and Kingman Reef are part of the Line Islands group. They were designated as part of the Pacific Remote Islands Marine National Monument on January 6, 2009, under the authority of the Antiquities Act of 1906. The five islands are managed by the U.S. Fish and Wildlife Service (USFWS), with Palmyra Atoll managed in partnership with the Nature Conservancy. These islands are tiny relative to the Hawaiian Islands, American Samoa, Guam, or the Commonwealth of the Northern Marianas that, together with Wake Island and Johnston Atoll, comprise the other U.S. Pacific islands. Maragos et al. (2008) and Miller, Maragos et al., (2008) summarized their geography, history, geology, climate, oceanography, and biology.

Little information exists on the marine biota of the U.S. equatorial Pacific islands compared to more populated Pacific locations. Until recently, this region of the Pacific (10°N–10°S by 145°W–180°) was one of the most poorly investigated portions of the world's oceans outside of the polar regions. Beginning in 2000, ecological surveys of the shallow coral reef habitats of the U.S. equatorial Pacific islands were conducted by the Coral Reef Ecosystem Division (CRED) of the National Oceanographic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NMFS or NOAA Fisheries), Pacific Islands Fisheries Science Center (PIFSC). In this paper, we report the species composition of the fishes observed with visual inventories during the first six CRED survey cruises to the five islands on the NOAA Ship *Townsend Cromwell* (TC) in 2000, 2001, and 2002, on the NOAA Ship *Oscar Elton Sette* in 2004, and the NOAA Ship *Hi`ialakai* in 2006 and 2008. We also review previous surveys of the fishes of these islands (excluding deep-sea species) from published sources, unpublished reports of the U.S. Fish and Wildlife Service, larval fish surveys conducted from the *Townsend Cromwell* during 1990 and 1992, and online databases of specimens from these islands in several U.S. museum ichthyology collections.

PREVIOUS ICHTHYOLOGICAL SURVEYS

The earliest fish collection at these islands of which we are aware was at Baker Island in 1864 by Captain Joseph Hammond, represented by two specimens of *Istiblennius* in the collection of the Academy of Natural Sciences (ANSP) of Philadelphia, ten in the collection of the Museum of Comparative Zoology (MCZ) at Harvard University, and two at the Bernice P. Bishop Museum (BPBM) at Honolulu. The

Table 1. Characteristics of Howland Island, Baker Island, Jarvis Island, Palmyra Atoll, and Kingman Reef (from Grigg et al., 1988; Defense Mapping Agency, 1988; Maragos, 1997; Central Intelligence Agency, 2001; Spalding et al., 2001; Maragos et al., 2008).

	Howland Island	Baker Island	Jarvis Island	Palmyra Atoll	Kingman Reef
Position	0°48'04''N, 176°38'4''W	0°11'40'N, 176°28'43'' W	0°23'25'S, 160°0'50''W	5°52'34"N, 162°4'32"W	40 mi. north of Palmyra, ca. 6°24′N, 162°22′W
Emergent island area (hectares)	184.1	163.9	439.5	275.2	1.2
Year of refuge status	1974	1974	1974	2001	2001
Island type	Island	Island	Island	Atoll, highly modified	Tilted Atoll, mostly submerged
Marine refuge area (km^2)	131.73	128.43	151.83	2086.69	1958.99
Maximum height above sea level (m)	3–6	5–8	6–7	2–3	1–2, varying among years
Mean rainfall (mm/yr)	< 500	< 500	< 500	> 5080	> 5080
Coastline (km)	6.4	4.8	8.0	14.5	< 0.1 (3.0 for reef shoals)

first fish species described from these islands was *Serranus howlandi* by Günther in 1873 [now *Epinephelus howlandi* (Günther, 1873)], based on a specimen collected by Andrew Garrett and held in the collection of the Natural History Museum (earlier known as the British Museum, Natural History).

Streets (1877) reported on a small collection of fishes from the 1873-1874 expedition of the U.S. Ship *Portsmouth* to "the Fanning Islands" [= Line Islands], including Palmyra Atoll. The collection localities for most species in Streets (1877) were reported only as "Fanning Islands" or "Fanning Group," making it impossible for us to determine which were collected at Palmyra vs. other islands of the archipelago. Some of Streets' specimens were deposited at the National Museum of Natural History, Smithsonian Institution (USNM).

Small expeditions from Honolulu visited Palmyra in July 1913 and the summer of 1922 (Edmondson, 1923). The 1913 expedition included H. E. Cooper, then the island's owner, J. F. Rock, a botanist from the College of Hawai`i (now the University of Hawai`i), and C. M. Cooke, Jr., a malacologist from the BPBM. The 1922 expedition included L. A. Thurston and D. Thaanum of Honolulu. Fishes collected by Cooke, Thurston, and Thaanum were deposited in the BPBM collection, where they were initially analyzed by the visiting ichthyologist H. W. Fowler in the 1920s. Fowler was the ichthyology curator at ANSP and he transferred many duplicate fish specimens from BPBM collections to ANSP. He reported many of the fishes from the Bishop Museum in his reviews of the fishes of Oceania (Fowler, 1928, 1931, 1934, 1949).

In 1924, scientists from the *Whippoorwill* Expedition, part of the larger *Tanager* Expedition to several Pacific islands, collected fishes at Jarvis, Howland, and Baker Island, and at Palmyra Atoll (as well as other Line Islands). These are also now divided between the BPBM and ANSP collections. Fowler (1927) described the *Whippoorwill* Expedition fishes and later included information on the fishes from the equatorial Pacific islands in his 1928-1949 reviews.

The 1933 Templeton Crocker Expedition to Polynesia and Melanesia collected a few fishes at Palmyra Atoll. These are archived at the California Academy of Sciences (CAS) ichthyology collection.

Specimens collected at some of these islands by smaller expeditions in the early 20th Century are held at the BPBM. These were incorporated in Fowler's 1928-1949 reviews. The smaller expeditions include those designated in BPBM collection records as the 1935 "Dr. Dana Coman Expedition" and collections from the U.S. Coast Guard vessel *Itasca* beginning in 1936. Dr. E. H. Bryan of BPBM may have participated in the Coman Expedition, as indicated by the collection data for BPBM 10133 (a *Myrichthys colubrinus*). The *Itasca* specimens were products of an astonishing, but until recently little known, effort by the United States to claim Howland, Baker, and Jarvis Islands by "colonizing" them with Hawaiian high-school students (Burlingame, 2002). The tasks given to these students included the collection of natural history specimens. The students were not told what their destinations were and lived on these bleak islands for 6 months or more at a time. Of ca. 135 students participating in this effort, 3 died; 1 from appendicitis-induced peritonitis and 2 during a shelling of Howland Island by the Japanese Navy on December, 1941 (Burlingame, 2002; Tengan, 2008). The fish specimens that they collected for BPBM are part of their legacy.

In 1937, the George Vanderbilt South Pacific Expedition, on the auxiliary schooner *Cressida*, collected 56 fish specimens of 5 species at Jarvis Island and 33 specimens of 21 species at Palmyra Atoll. These were also reported by Fowler (1938) and the specimens were placed in the ANSP collection.

There are several specimens in the BPBM collection that were collected during February 1948 and June 1949, but no collectors or vessels are named in the collection data for these.

In August 1951, Earl S. Herald, Robert R Rofen (Harry), and others collected fishes at Palmyra Atoll during a second George Vanderbilt Foundation (GVF) effort, its Equatorial Expedition, from the vessel *Pioneer*. Specimens from that expedition were originally placed in the Stanford University (SU) ichthyology collection and are now archived at CAS, as are other fish specimens from Stanford (Brittan, 1997).

Suspected ciguatoxic and other poisonous fishes were surveyed at Kingman Reef, Palmyra Atoll, and Jarvis Island during cruises from the USFWS Pacific Oceanic Fishery Investigations Laboratory (POFI, now the PIFSC) in 1950-1953. Large species taken in these surveys were recorded by Halstead and Schall (1958). Some of these remain in the ANSP and USNM collections. An unpublished report by Halstead (1951) from the preliminary sampling for that study contains one record of a species from Kingman Reef (*Lutjanus fulvus*) omitted from Halstead and Schall's (1958) published paper.

The University of Hawai`i (UH) sent expeditions to Palmyra Atoll on several occasions in the 1950s and early 1960s. Specimens from 1953, collected by J. E. King and others, are listed in the BPBM collection as having been transferred from the UH fish collection. In late 1959 and early 1960, fishes were collected by W. Gosline, then the UH professor of ichthyology, and his students, D. Strasburg, A. H. Banner, and P. Helfrich. The BPBM also has collections, transferred from the UH fish collection, from Palmyra in1962 by Helfrich, P. S. Miles, L. G. Eldredge, and others.

POFI vessels made collections at and near these islands on several occasions during 1950–1966, including cruises by the R/V *J. M. Manning* in 1954, the R/V *H. M. Smith* in 1956, and the R/V *C. H. Gilbert* in 1960 and 1966. These fishes are in the BPBM collection, but most are oceanic species and are not included in this report. A few of the fishes captured by trolling and longlining by POFI, but not retained, were reported by Murphy and Shomura (1953, 1955) and Iversen and Yoshida (1956, 1957).

In 1963 and 1964, the Smithsonian Institution collected fishes at the islands, including samples of small, cryptic species that have otherwise not been surveyed at these locations. Most of these are now in the USNM. The Smithsonian's Pacific island surveys, primarily terrestrial in emphasis, were known by several names. Initially, the surveys were called only the Southern Island Cruises but were soon formally named the Pacific Ocean Ornithological Project to better reflect their primary emphasis (Clapp, 2002). Shortly thereafter, however, the program was renamed the Pacific Ocean Biological Survey Project (POBSP) by someone who was acronym attentive and perhaps who had less humor. The origin and history of this program are controversial (MacLeod, 2001), but those controversies do not affect the value of the resultant ichthyological surveys. Fish specimens from this effort are listed in the Smithsonian's database under the more recent and euphonious acronym for the Smithsonian Institution Pacific Ocean Biological Survey program (SIPOBS). No summary report was published describing the SIPOBS fishes.

In 1968 and1977, J. E. Randall, H. A. Randall, J. McVey, W. Hashimoto, R. McNair, G. S. Haywood, and G. Friedholm, scientists from the UH and BPBM aboard the research vessel *Westward*, collected fishes at Palmyra Atoll. These were deposited at BPBM.

In 1986, D. K. McDermond and R. C. Wass (USFWS) compiled a list of reef fishes from visual observations during seven snorkeling surveys at Howland Island and two at Baker Island (McDermond and Wass, 1986).

In 1990 and 1992, the NOAA Fisheries scientists aboard the *Townsend Cromwell* surveyed larval fish distributions in the vicinity of Palmyra Atoll, collected samples of shallow-dwelling midwater fishes with plankton nets and midwater trawls, and made a few *in-situ* observations of adult inshore fishes by snorkeling surveys. Specimens from those cruises, TC9007 and TC9201, remain among the uncataloged larval fish collection at the PIFSC. A few of these records were reported by Boehlert and Mundy (1993; their table 2).

A few other small collections from the five islands are not reviewed here, although several specimens from them were included in our inventory.

METHODS

The surveys at the five islands that initiated our study were at visual rapid ecological assessment stations in March–April 2000, January-February 2001, and January-February 2002. Two or three scuba divers would descend at a location and survey diurnally active, non-cryptic, reef-associated, shallow-dwelling fishes between 3 and 20 m for ca. 50–60 minutes. Much of the time was occupied with counting the fishes seen along measured transects. Two observers conducted the fish survey stations in 2000 and 2002. A third observer participated in 2001, with the primary task of roving the area around transects and identifying all fish species seen. Additional records were obtained from towed-diver transects, rapid ecological assessment surveys, and stationary point count stations. The survey methods are described in more detail by Brainard et al. (2005).

Most of our stations at Howland, Baker, and Jarvis Islands were at the leeward slopes of their western sides (Figs. 2–4). Easterly winds dominate weather at Howland, Baker, and Jarvis Islands. The swells are likewise usually from the east or northeast, making the western reef slopes the most protected areas. The abrupt shoaling of the bottom at these islands causes large surf to result at the shelf breaks, making small boat operations hazardous. Stations at Palmyra Atoll were more uniformly distributed around that atoll (Fig. 5), although surveys at the eastern end were limited by the stronger winds and swells there. Our stations at Kingman were concentrated in the eastern half of the reef, primarily in the lagoon and along the protected inner edges of the reef (Fig. 6). Currents at Kingman Reef are often very strong along the outer north and south edges of the atoll, and they intensify from the east to the west in the lagoon.

Station locations were obtained with Global Positioning System (GPS) units on the dive skiffs. The fish team did not record GPS locations for their stations during the first cruise, but instead relied on positions recorded by the coral survey biologist (J. Maragos, USFWS). This provided location data for most stations, but in a few instances the fish team surveyed stations not surveyed by the coral biologist, leaving some stations without position data. In addition, the quality of the GPS units and satellite position data was less during 2000 than in 2001, and most accurate in 2002. In most instances, text descriptions of the station locations written during our sampling enabled us to resolve these problems.

Effort varied at the different islands in different years (Table 2a, b). Howland and Baker Islands had about the same level of effort, while Jarvis Island had slightly more. Kingman Reef and Palmyra Atoll had more effort expended because of their sizes and, for Palmyra, diversity of habitats.

Our identifications are based almost entirely on visual criteria. Almost no specimens were collected, and few photographs were taken to confirm identifications. Our identifications cannot be definitive without voucher specimens or photographs.

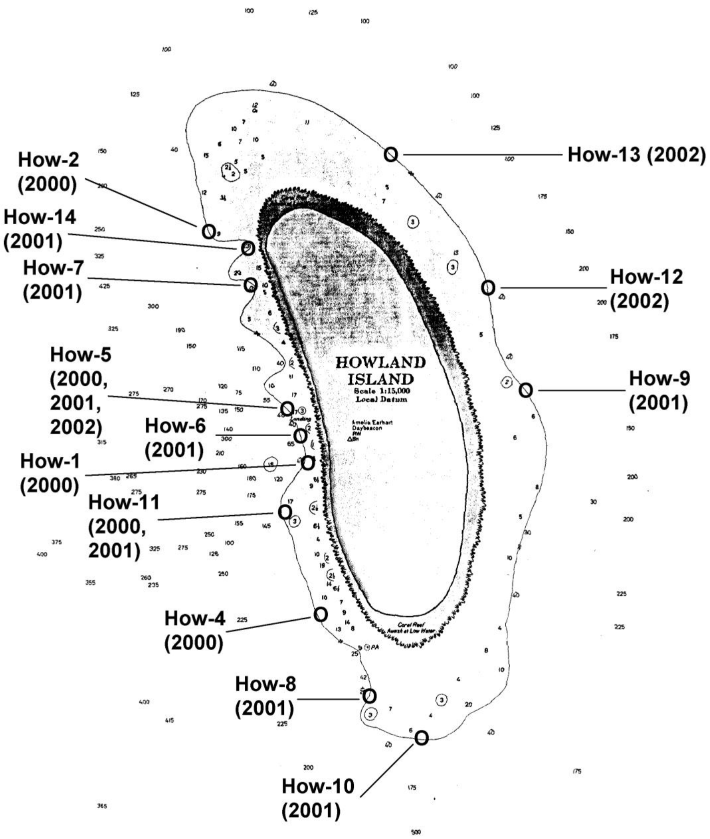

Figure 2. Howland Island as shown on NOAA navigational charts prior to 2003, with the locations of the NOAA Fisheries fish observation stations in 2000–2002.

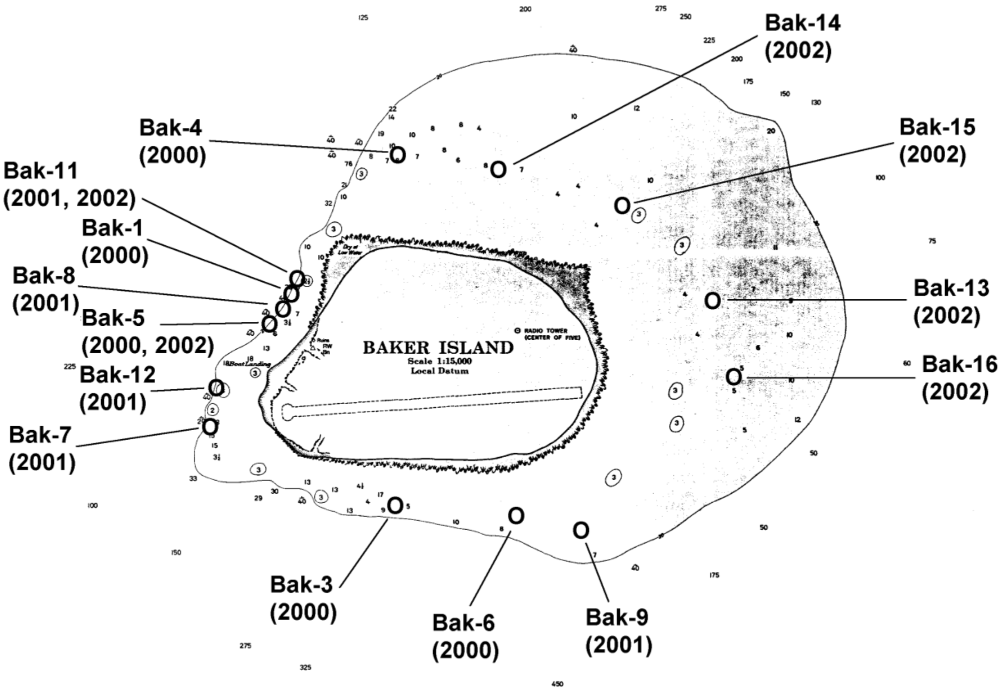

Figure 3. Outline of Baker Island as shown on NOAA navigational charts prior to 2003, with positions of NOAA fish transect stations.

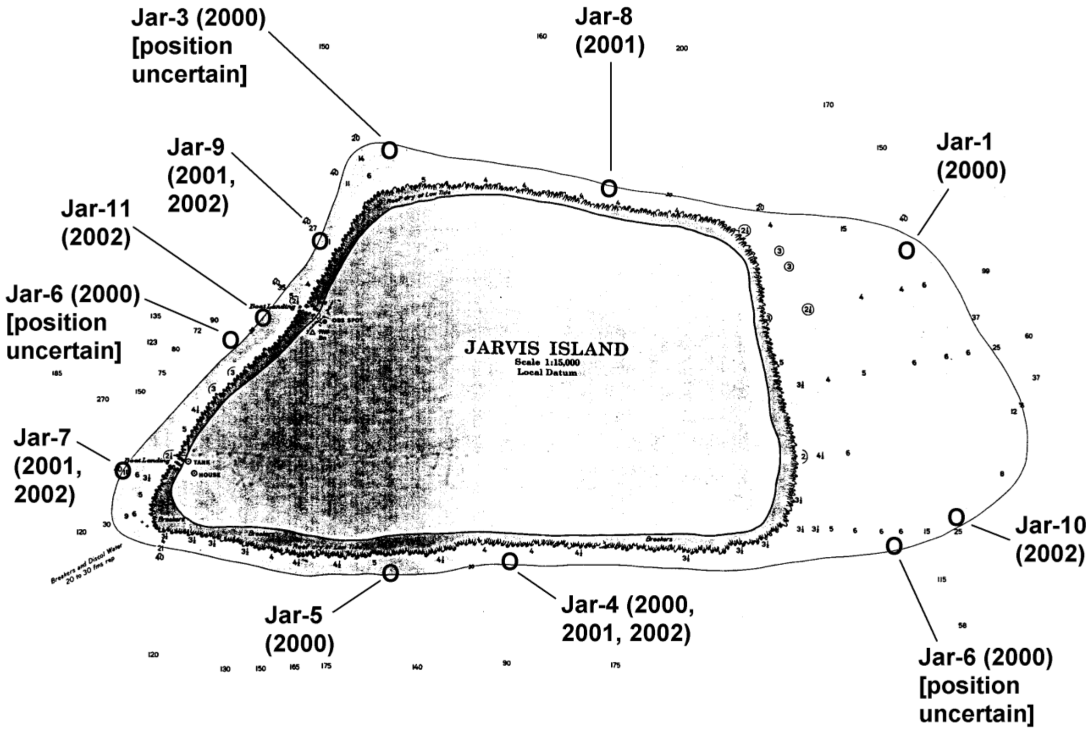

Figure 4. Outline of Jarvis Island as shown on NOAA navigational charts prior to 2003 with station locations for NOAA fish surveys.

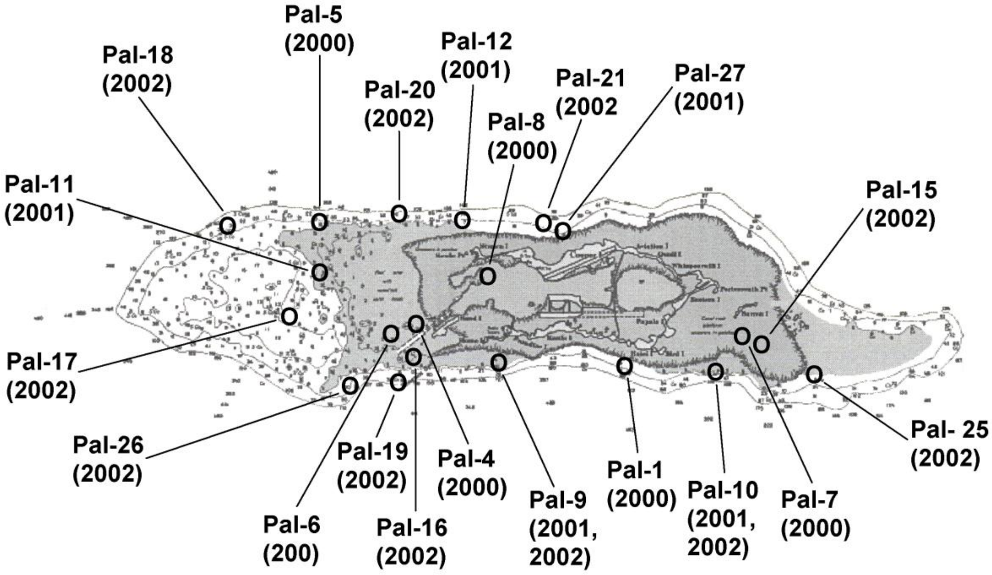

Figure 5. Outline, position, and bathymetry of Palmyra Atoll as shown in NOAA navigational charts prior to 2003.

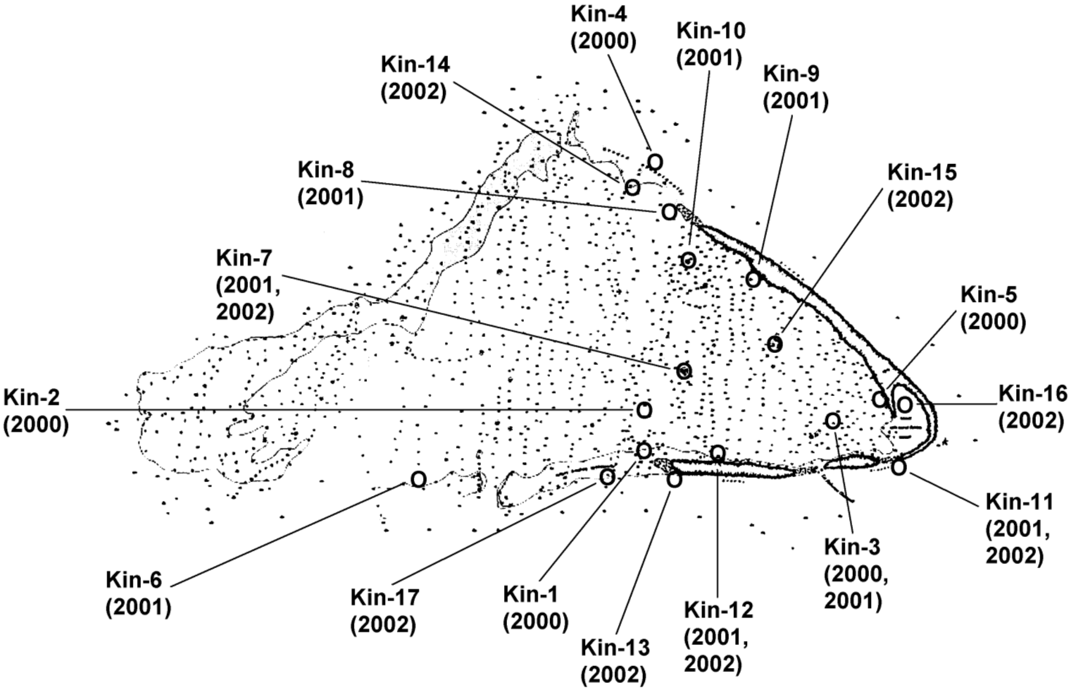

Figure 6. Outline and position of Kingman Reef as shown on NOAA navigational charts prior to 2003, with locations of NOAA Fisheries fish transect stations.

Nevertheless, we are confident that most of the identifications of the larger, distinctively colored species are correct as based on information in the taxonomic works in our literature cited. Our identifications of the smaller, visually less distinctive species need verification. For this reason we made the effort to incorporate into this report records from taxonomic publications and from collections of the four major museums (CAS, ANSP, BPBM, and USNM) that archive specimens from the equatorial Pacific islands. No effort was made to verify the identifications of those specimens by examination, but by listing them we hope to give interested researchers information that will prompt future efforts to verify the identifications of fishes from these islands. Museum collection numbers for the museum records listed below are available upon request from the first author. The information from the USNM database was provided with the permission of the National Museum of Natural History, Smithsonian Institution, 10th and Constitution Ave. N.W., Washington, DC 20560-0193. (http://www.nmnh.si.edu/); access to the USNM data is available at http://vertebrates.si.edu/fishes/fishes_collections.html. The information from the Academy of Natural Sciences of Philadelphia Information was provided with the permission of The Academy of Natural Sciences, Philadelphia, PA.

The order in which families are listed is that of J. Nelson (2006), except that we follow Smith and Craig (2007) in recognizing the Epinephelidae as a family distinct from the Serranidae. A few changes to the taxonomy of shore-fish species in the region are worth noting, to explain why some names used herein differ from those in common usage prior to 2010. Craig and Hastings (2007) placed *Aethaloperca* and *Gracila* as junior synonyms of *Cephalopholis*, and we follow their conclusion. Marshall et al. (2009) demonstrated that there are two species of *Manta* in the region. We identified the mantas in our surveys as *M. birostris* (Walbaum), following the practice prior to Marshall et al. (2009) of considering the genus to contain only that species. Marshall et al. (2009)

Table 2a. CRED sampling effort at each island in 2000-2008.

Island	2000 # Stations (2 observers)	2001 # Stations (3 observers)	2002 # Stations (2 observers)	2004 # Stations (3 observers)	2006 # Stations (3 observers)	2008 # Stations (4 observers)	Total number of stations	Total number of observers X stations
Howland Island	4	6	6	6	6	12	40	122
Baker Island	5	6	5	6	8	7	37	108
Jarvis Island	5	4	5	6	9	20	49	157
Palmyra Atoll	6	5	11	10	13	28	73	230
Kingman Reef	6	9	9	9	16	23	72	215
Total	26	30	36	37	52	90	271	832

Table 2b. Expeditions to each island

Howland: 12 expeditions, 11 reef sampling
- Günther (1873-1875) – Andrew Garrett specimen
- *Whippoorwill* expedition – 1924
- Dr. Dana Coman Expedition – 1935
- *Itasca* – 1936
- POFI *H. M. Smith* cruise - 1950
- SIPOBS – 1963
- SIPOBS - 1964
- SIPOBS - 1966
- McDermond and Wass (1986)
- TC0001
- TC0101
- TC0201
- OES0401
- HI0601
- HI0801

Baker: 11 expeditions, 11 reef sampling
- Capt. Joseph Hammond—1864
- *Whippoorwill* expedition—1924
- Dr. Dana Coman Expedition—1935
- *Itasca*—1936
- SIPOBS—963
- SIPOBS—1964
- SIPOBS—1966
- McDermond and Wass (1986)
- TC0001
- TC0101
- TC0201
- OES0401
- HI0601
- HI0801

Jarvis: 16 expeditions, 12 reef sampling
- *Whippoorwill* expedition—1924
- Dr. Dana Coman Expedition—1935
- *Itasca*—1936
- POFI—1951
- Unidentified expedition—1952
- POFI—1953
- Halstead and Bunker (1954)
- Iversen and Yoshida (1957)
- Halstead and Schall (1958)
- SIPOBS—1963

SIPOBS—1964
SIPOBS—1966
Unidentified Expedition (SIPOBS?) —1969
TC0001
TC0101
TC0201
OES0404
HI0604
HI08-03

Palmyra: 36 expeditions, 30 reef sampling
Streets (1877)
Cooper, Rock, and Cooke—1913 (Edmondson, 1923)
Cooke—1916
Thurston and Thaanum—1922
Whippoorwill Expedition—1924
Templeton-Crocker Expedition—1933
Dr. Dana Coman Expedition—1935 (same as 1935 Bryan expedition?)
George Vanderbildt Expedtion, *Cressida*—1937
Vasconcellos—1940
W. Chapman—1944
Unidentified expedition (M. Schaefer) —1948
Peterson/*Calistar*—1949
“Unidentified expedition” = POFI, *H. M. Smith* cruise—1950
George Vanderbilt Foundation, Herald and Rofen *et al.* —1951
POFI—1951
J. King (POFI), *H. M. Smith* Cruise—1953 (Murphy and Shomura, 1953?)
Unidentified—1955 (Shomura and Murphy, 1955)
Iversen and Yoshida (1956?)
Iversen and Yoshida (1957)
Halstead and Schall (1958)
Gosline, Strasburg, Banner, Helfrich, Strasburg—1959–1960
Helfrich, Miles, Eldredge et al. —1962
SIPOBS—1963
SIPOBS—1964
SIPOBS—1966
BCF Vessel *Gilbert*—1966
Westward (Randall, Randall, McVey, Hashimoto, McNair, Haywood, and Friedholm) — 1968
Westward (Randall, Randall, McVey, Hashimoto, McNair, Haywood, and Friedholm) —1977
McDermond and Wass (1986)
TC9007
TC9201

Nelson and Seibel—2001
TC0001
TC0101
TC0201
Handler and James—2006
OES0404
HI0604
HI0803

Kingman: 15 expeditions, 8 reef sampling
Commonwealth cruise—1950
POFI—1951
POFI—1953
Halstead (1951)
Murphy and Shomura (1953)
Unidentified expedition—1955 (same as below?)
BCF vessel *J. R. Manning*—1956
Iversen and Yoshida (1957)
Halstead and Schall (1958)
Gilbert cruise (POFI)—1960
Westward—1968 or 1977
McDermond and Wass (1986)
TC0001
TC0101
TC0201
OES0404
HI0604
HI0803

demonstrated that the smaller species occurring more frequently close to shore in the Indo-Pacific is *M. alfredi* (Krefft), but we now identify the mantas recorded herein only as *Manta* species in the absence of data to confirm the species to which they belonged. White et al. (2010) demonstrated that the Indo-Pacific spotted eagle ray previously identified as *Aetobatus narinari* (Euphrasen) is a distinct species taking the name *A. ocellatus* (Kuhl), and we follow their conclusion herein. We also use the name *Acanthurus nigros* Günther for the Indo-Pacific population of the surgeonfish usually called *A. nigroris* Valenciennes, following advice that *A. nigroris* should be recognized as an endemic Hawaiian Islands species (Randall et al*.,* in press).

A number of oceanic, epipelagic species that have been recorded from the vicinity of the islands are listed separately. These include literature records and species, seen by us, swimming just offshore of our survey stations. Some of the latter moved toward us briefly, enabling us to obtain good identifications. Others were seen only at a distance, making their identifications tentative. The division between the inshore fishes and the oceanic epipelagic species is arbitrary, but generally follows conventions in commonly used guides to tropical Pacific fishes (e. g., Myers, 1999; Randall, 2005). A good example showing how difficult it is to establish a precise distinction between inshore and oceanic species may be found in our record of *Ablennes hians*, a clearly oceanic species usually not found over reefs; however, these fishes were found swimming over the shallow top of a patch reef inside of the Kingman Reef lagoon. We, therefore, classify some otherwise oceanic species as inshore if they were found swimming directly above reefs, as opposed to swimming or having been captured in waters offshore of reefs within our survey depths. Thus, we list *Manta* species and *Ablennes hians* among the inshore fishes, although they are certainly as pelagic in habitat as are species such as *Euthynnus affinis* and *Psenes cyanophrys* that we list as oceanic epipelagics.

In our results, new records from our surveys at the five individual islands are those for which only "CRED", reference 1 (Brainard et al., 2005), or reference 2 (Miller et al., 2008) are given. References 1 and 2 summarize results of CRED surveys. Species that are newly recorded in our surveys from all of the Line or Phoenix Islands are listed in Table 3. The tabulations of numbers and percentages of inshore species at each island and island group used taxa identified to species, or to genera when no species within a genus was identified from an island at which the genus was recorded.

The relationship of shore-fish numbers at the five islands to those at other Pacific islands and archipelagos was analyzed with principals of island biogeography theory. The four parameters investigated were the distance along the Indo-Pacific diversity gradient from the Indo-Australian Archipelago center of diversity (IAA), isolation from other islands, island area, and island age (e. g., MacArthur and Wilson, 1963; Connolly et al., 2003; Bellwood et al., 2005; Whittaker et al., 2008). Fish habitat area is a more meaningful measure of effective biogeographic area than simple island size (R. Brainard, PIFSC, pers. comm.), but we could not use data on fish habitat area in our analysis because those data were not available for many of the Pacific islands or island groups at which shore-fish species have been inventoried. Regression analyses were done with Sigmaplot©. Linear or exponential functions were fitted to the data depending upon the theoretical functions proposed for the relationships (MacArthur and Wilson, 1963; Connolly et al., 2003; Whittaker et al., 2008) and the visually apparent relationships of species numbers vs. the four parameters. For analysis of distance from the IAA, the center of Sulawesi was arbitrarily chosen as the location of the IAA center, as Sulawesi is approximately in the middle of the triangle defined by Indonesia, the Philippines, and New Guinea. The relationship between species number and distance from the center of the IAA was an exponential decay function. Our first exploration of the best fit to the data produced a curve with several inflection points and an unrealistic negative species number for the farthest distance from the IAA. We, therefore, rejected this and constrained the regression to one with a single inflection point, for parsimony, and with its origin at the observed values for Easter Island, the island with the smallest species number and greatest distance from the IAA. Unconstrained linear functions gave the best fit to the three other relationships. The relationship of species number to island age was analyzed with the ATT^2 model of Whittaker et al. (2008) with the function: log, (island area) + island age + (island age)^2. Indonesia, the Philippines, New Guinea, and New Caledonia were included in the analyses of distance, isolation, and area to provide data on species numbers in the center of biodiversity, but were excluded from the analysis of island age because they are groups of continental islands of composite ages, with

Table 3. New records from our surveys of fish species from the U.S. Line and Phoenix Islands. (Note that the new records for the Phoenix Islands below are based on occurrences at Howland and Baker Islands. Those islands are most similar to the Line Islands in species composition, not the main Phoenix Islands. Therefore, records of fish species from Howland and Baker may not indicate that those species can be expected in the main Phoenix Islands.)

Nebrius ferrugineus—new record for the Line Islands.
Carcharhinus albimarginatus—new record for the Line Islands.
Sphyrna lewini—new record for the Phoenix Islands.
Sphyrna mokarran—new records for the Line and Phoenix Islands.
Taeniura meyeni—new record for the Phoenix Islands.
Aetobatus ocellatus—new record for the Phoenix Islands.
Gymnomuraena zebra—new record for the Phoenix Islands.
Gymnothorax breedeni—new record for the Phoenix Islands.
Unidentified deepwater *Conger* species—new record for the Phoenix Islands.
Neoniphon opercularis—new record for the Phoenix Islands.
Sargocentron diadema—new record for the Phoenix Islands.
Cephalopholis rogaa—new records for the Line and Phoenix Islands.
Cephalopholis aurantia—new record for the Phoenix Islands.
Epinephelus howlandi—new record for the Line Islands, but identification needs to be confirmed.
Epinephelus lanceolatus—new record for the Line Islands.
Epinephelus retouti—new record for the Phoenix Islands.
Epinephelus spilotoceps—new record for the Phoenix Islands.
Pseudanthias bicolor—new record for the Phoenix Islands.
Pseudanthias cooperi—new record for the Phoenix Islands.
Pseudochromidae species—new family record from the Line Islands based on collection of larvae, genus and species undetermined.
Heteropriacanthus cruentatus—new record for the Phoenix Islands.
Ostorhinchus apogonides—new records for the Line and Phoenix Islands.
Atule mate—new record for the Line Islands.
Caranx ignobilis—new record for the Phoenix Islands.
Mulloidichthys mimicus—new record for the Phoenix Islands.
Parupeneus cyclostomus—new record for the Phoenix Islands.
Sectator ocyurus—new record for the Phoenix Islands.
Paracirrhites arcatus—new record for the Phoenix Islands.
Paracirrhites xanthus—new record for the Line Islands.
Abudefduf vaigiensis—new record for the Phoenix Islands.
Chromis agilis—new records for the Line and Phoenix Islands.
Chromis caudalis—new record for the Phoenix Islands
Chromis xanthura—new record for the Phoenix Islands.
Plectroglypidodon phoenixensis—new record for the Line Islands.
Stegastes fasciolatus—new records for the Line and Phoenix Islands.
Anampses melanurus—new record for the Line Islands.
Anampses meleagrides—new record for the Phoenix Islands.
Bodianus axillaris—new record for the Phoenix Islands.

Cheilinus oxycephalus—new records for the Line and Phoenix Islands.
Cheilinus trilobatus—new record for the Line Islands.
Halichoeres melasmopomus—new record for the Phoenix Islands.
Halichoeres claudia—new record for the Phoenix Islands.
Hemigymnus fasciatus—new record for the Phoenix Islands.
Labrichthys unilineatus—new records for the Line and Phoenix Islands, but identifications need verification.
Labroides bicolor—new record from the Phoenix Islands.
Labroides rubrolabiatus—new record from the Phoenix Islands.
Labropsis xanthonota—new record from the Line and Phoenix Islands.
Pseudocheilinus evanidus—new records from the Line and Phoenix Islands.
Pseudocheilinus octotaenia—new record for the Phoenix Islands.
Pseudocoris heteroptera—new records for the Phoenix Islands.
Thalassoma lutescens—new record for the Phoenix Islands.
Thalassoma trilobatum—new record for the Line Islands.
Scarus trilobatus—new record for the Phoenix Islands.
Exallias brevis—new record for the Line Islands.
Amblyeleotis fasciata—new record for the Line Islands.
Valenciennea strigata—new record for the Phoenix Islands.
Ptereleotris evides—new record for the Phoenix Islands.
Ptereleotris zebra—new record for the Phoenix Islands.
Zanclus cornuta—new record for the Phoenix Islands.
Acanthurus maculiceps—new record for the Phoenix Islands.
Acanthurus mata—new records for the Line and Phoenix Islands.
Acanthurus pyroferus—new record for the Phoenix Islands.
Acanthurus thompsoni—new records for the Line and Phoenix Islands.
Ctenochaetus hawaiiensis—new record for the Phoenix Islands.
Naso brevirostris—new record from the Phoenix Islands.
Naso caesius—new record from the Phoenix Islands.
Naso hexacanthus—new record from the Phoenix Islands.
Naso unicornis—new records for the Line and Phoenix Islands.
Naso vlamingii—new record for the Phoenix Islands.
Paracanthurus hepatus—new record for the Phoenix Islands.
Zebrasoma rostratum—new record for the Phoenix Islands.
Gymnosarda unicolor—new record for the Line Islands.
Ostracion meleagris—new record for the Phoenix Islands.
Canthigaster amboinensis—new record for the Phoenix Islands.
Canthigaster janthinoptera—new record for the Phoenix Islands.

accreted terrains, to which Whittaker et al.'s (2008) model was not intended to apply. Although the four regressions were not intended to be a rigorous statistical analysis in a model of island species richness, r^2 values were calculated as an indication of the relative strengths of the relationships of the relative contributions of distance from the IAA, island isolation, island area, and island age to the variability of species numbers at Pacific islands and archipelagos.

As a heuristic tool for investigating the biogeographic relationships of reef fishes at the U.S. equatorial Pacific islands, a similarity analysis of species presence/

absence relationships was done to compare the islands with other Pacific Plate islands or archipelagos at which reasonably complete species inventories exist. Only taxa identified to species, or to genus if no species within the genus were specifically identified from a locale, were included in the species lists for each island or archipelago. Locales included in this analysis and the sources of species lists for them were: this study for the U.S. equatorial Pacific islands; Chave and Eckert (1974) and an unpublished species list by R. Pyle (BPBM, pers. comm.) for the central Line Islands of Fanning and Christmas; Myers (1999) for the Marshall Islands; Randall (1955a) for the Gilbert Islands (Kiribati); Schultz (1943), Stone et al. (2001), and Obura and Stone (2003) for the Phoenix Islands; Mundy (2005) and Randall (2007) for the Hawaiian Islands; Randall et al. (1985) and Kosaki et al. (1991) for Johnston Atoll; Wass (1984) for American Samoa; Williams et al. (2006) for Wallis Island; Zug et al. (1988) for Rotuma; Randall (1985) and an unpublished list by J. Leis (Aust. Mus., pers. comm.) for the Society Islands and Tuamotu Archipelago; Randall and Earle (2000) for the Marquesas; and Randall (2005) for all of those locales when they were specifically mentioned as within the ranges of individual species. The Dice coefficient (Equation 1) was chosen as the dissimilarity index, in part, because it approximates a binary analog of the Bray-Curtis coefficient based on relative abundance that is frequently used in ecological and biogeographic analysis (Boesch, 1977).

Equation 1: $D_{sm} = [2(N_{AB})]/[2(N_{AB}) + N_A + N_B]$
Where: D_{sm} = Dice similarity coefficient with values of 0-1 where 0 = complete dissimilarity and 1 = complete similarity;
N_{AB} = the number of species in common between island groups A and B;
N_A = the number of species found only at island group A; and
N_B = the number of species found only at island group B.

The Dice coefficient was also selected because it gives greater weight to species that are present at both entities (locations in this case) of the pair that are compared, relative to species that are absent at one or the other locations. This was preferred because sampling problems created uncertainty about the completeness of discovery of many species at many of the locations, because of differences in sampling techniques in the various historical surveys, temporal changes in sampling intensity, and differences in the probability of finding naturally rare species at multiple locations.

Relationships of similar pairs of localities identified by the Dice coefficients were then determined for all localities using the unweighted pair-group mean average clustering strategy (UPGMA; Equation 2) to construct a similarity dendrogram that included all of the localities. The UPGMA is a hierarchical, agglomerative, space-conserving strategy. It is a frequently used clustering technique in ecology (Boesch, 1977).

Equation 2: $D_{hk} = (N_i/N_k)D_{hi} + (N_j/N_k)D_{hj}$
Where: D_{hk} = the similarity distance between groups h and k;
N_i = the number of entities in group i;
N_k = the number of entities in group k;

D_{hi} = the similarity distance between groups h and i;
N_j = the number of entities in group j; and
D_{hj} = the similarity distance between groups h and j.

For our exploration of vicariance biogeography and geologic processes that might have affected biogeography at central Pacific islands, paleolocations of the U.S. Line and Phoenix Islands were estimated with the flow line technique of Wessel and Kroenke (1997). Island paleotrajectories were estimated on tracks parallel to the flow line of the Emperor Seamount— Hawaiian Ridge, with extensions for ages earlier than 81 million years ago (ma) estimated from the hypothesized location of ancient Emperor Seamount edifices in the Bering Sea (Steinberger and Gaina, 2007), after accounting for tectonic displacement as the hypothesized edifices transferred from the Pacific Plate to the Kula and North American Plates. Ages used for the Line Islands were those of 86–81 ma and 73–68 ma from Davis et al. (2002). Ages for the Phoenix Islands are unknown. Miller, Lundblad et al. (2008) argued that the best evidence suggests that the five U.S. Line and Phoenix Islands formed in the second, primarily Paleocene, period of 73–68 ma. This projection relies on plate tectonic theory of Pacific Ocean development, rejecting the expanding earth hypothesis advocated by some biogeographers (e. g., McCarthy, 2005), and also relies on the hot-spot hypothesis of Hawaiian Island and Emperor Seamount origins (e. g., Wessel and Kroenke, 1997: Pilger, 2007) rather than the alternate hypothesis of shallow-source volcanism from latitudinally progressive fracturing during lithospheric extension (e. g., Smith, 2007).

For our purposes, great precision in paleotrajectory estimation was not required. We, therefore, did not include hypothesized finer details of plate motion, such as the putative change in plate movement in the past 5 ma (Wessel and Kroenke, 1997). Given numerous uncertainties about island ages, and the trajectory, expansion, and possible rotation of the Pacific Plate, we consider it appropriate to use a highly generalized, first order hypothesis of paleotrajectories for our discussion.

RESULTS

Inshore Fishes

Shore-fish species recorded at the five islands are listed in the following tables. In the tables, abbreviations for sources of the records are: A = ANSP, B = BPBM, C = CAS, CRED = original data from our observations and others in the NOAA PIFSC Coral Reef Ecosystem Division, L = Natural History Museum of Los Angeles County, M = MCZ of Harvard University, N = The Natural History Museum (London), U = USNM, 1 = Brainard et al. (2005), 2 = Miller et al. (2008), 3 = Fowler (1927), 4 = Fowler (1938), 5 = Halstead and Schall (1958), 6 = McDermond and Wass (1986), 7 = Friedlander et al. (2008), 8 = Handler and James (2006), 9 = Böhlke and Randall (2000), 10 = Böhlke et al. (1989), 11 = McCosker and Randall (1982), 12 = Streets (1877), 13 = McCosker (1998), 14 = McCosker and Rosenblatt (1993), 15 = Kanazawa (1958), 16 = Boehlert and Mundy (1993), 17 = Pietsch and Grobecker (1987), 18 = Parin et al. (1980), 19 = Collette (1974), 20 = Fowler (1949), 21 = Randall and Greenfield (1996), 22 = Randall (1998a), 23 = Dawson (1985), 24 = Dawson (1981), 25 = Poss in Carpenter and Niem (1999), 26 = Randall and Eschmeyer (2001), 27 = Randall and Heemstra (1991), 28 = Günther (1873–1875), 29 = Randall (2005), 30 = Fowler (1928), 31 = Randall and Taylor (1988), 32 = Randall and Baldwin (1997), 33 = Mooi (1995), 34 = Starnes (1988), 35 = Greenfield (2001), 36 = Gon (1993), 37 = Fraser (2008), 38 = Fraser and Randall (2003), 39 = Fraser and Lachner (1985), 40 = Goe and Halstead (1955), 41 = Smith-Vaniz and Randall (1994), 42 = Iversen and Yoshida (1957), 43 = Smith-Vaniz and Staiger (1973), 44 = Allen and Talbot (1985), 45 = Halstead (1951), 46 = Carpenter (1987), 47 = Randall and Guézé (1980), 48 = Randall (2004c), 49 = Randall and Myers (2002), 50 = Allen et al. (1998), 51 = Randall and Randall (2001b), 52 = Allen and Emery (1985), 53 = Randall (1972a), 54 = Randall (1999a), 55 = Randall (1999b), 56 = Randall (2000), 57 = Randall and Edwards (1984), 58 = Bruce and Randall (1985), 59 = Schultz (1958), 60 = Fricke (1997), 61 = Springer and Williams (1994), 62 = Williams (1988), 63 = Springer (1967), 64 = Strasburg (1956), 65 = Springer and Gomon (1975), 66 = Bath (2004), 67 = Jewett and Lachner (1983), 68 = Lachner and Karnella (1980), 69 = Randall and Greenfield (2001), 70 = Thacker (2004b), 71 = Winterbottom and Burridge (1989), 72 = Hoese and Larson (1994), 73 = Randall and Hoese (1985), 74 = Randall (1956), 75 = Randall and Earle (1999), 76 = Randall and Clements (2001), 77 = Randall (1955b), 78 = Randall (1960), 79 = Murphy and Shomura (1953), 80 = Iversen and Yoshida (1956), 81 = Randall and Klausewitz (1973), 82 = Randall et al. (1978), 83 = Hutchins (1986), 84 = Su and Tyler (1986), 85 = Shomura and Murphy (1955), 86 = Howell and Kobayashi (2006), 87 = Butler (1979), 88 = Møller and Schwarzhans (2008), ? = tentative identification, in need of verification, "or" = Palmyra, Kingman Reef, or both, without specification to individual island in McDermond and Wass (1986).

	Howland	**Baker**	**Jarvis**	**Palmyra**	**Kingman**
Ginglymostomatidae					
Nebrius ferrugineus (Lesson, 1831)	-	-	-	-	CRED
Carcharhinidae					
Carcharhinus albimarginatus (Rüppell, 1837)	-	-	CRED	-	CRED
Carcharhinus amblyrhynchos (Bleeker, 1856)	1, 2, CRED	1, 2, CRED	1, 2, 3, 4, CRED	1, 2, 5, CRED	1, 2, CRED
Carcharhinus galapagensis (Snodgrass and Heller, 1905)	1?, CRED?	1?, CRED?	-	-	-
Carcharhinus melanopterus (Quoy and Gaimard, 1824)	U, 1, 6, CRED	1, CRED	1, 2, CRED	B, 4, 1, CRED	1, CRED
Galeocerdo cuvier (Péron and LeSueur in LeSueur, 1822)	-	-	-	CRED	CRED
Triaenodon obesus (Rüppell, 1837)	1, 2, 6, CRED	1, 2, CRED	1, 2, CRED	1, CRED	1, 2, CRED

	Howland	Baker	Jarvis	Palmyra	Kingman
Sphyrnidae					
Unidentified *Sphyrna* species	1, CRED	1, CRED	CRED	CRED	CRED
Sphyrna lewini (Griffith and Smith, 1834)	2, CRED	2, CRED	2, CRED	CRED	CRED
Sphyrna mokarran (Rüppell, 1837)	-	CRED	1, 2, CRED	-	CRED
Dasyatidae					
Taeniura meyeni Müller and Henle, 1841	CRED	CRED	CRED	-	-
Myliobatidae					
Aetobatus ocellatus (Kuhl, 1823)	CRED	CRED	-	CRED	CRED
Manta species	6, CRED	CRED	1, 2, CRED	2, CRED	CRED
Albulidae					
Unidentified *Albula* species	-	-	-	C, 5, CRED	-
Albula glossodonta (Forsskål, 1775)	-	-	-	C, 7	-
Anguillidae					
Anguilla marmorata Quoy and Gaimard, 1824	-	-	-	8 (waifs?)	-
Moringuidae					
Unidentified *Moringua* species	-	-	-	B	-
Moringua macrochir Bleeker, 1855	-	-	-	B	-
Chlopsidae					
Unidentified *Kaupichthys* species	-	-	-	C	-
Kaupichthys hyoproroides (Strömman, 1896)	-	-	-	-	B
Muraenidae					
Unidentified *Anarchias* species	-	-	-	B	-
Anarchias allardicei Jordan and Starcks in Jordan and Seale, 1906	B	-	-	A	-
Anarchias cantonensis (Schultz, 1943)	B	-	-	-	-
Anarchias seychellensis Smith, 1962	-	-	-	A, B, C, 9	-
Channomuraena vittata (Richardson, 1845)	-	-	-	A, 10	-
Unidentified *Echidna* species	-	-	A	C	-

	Howland	**Baker**	**Jarvis**	**Palmyra**	**Kingman**
Echidna nebulosa (Ahl, 1789)	A, B, 3, 4, 9	B, 3, 4	A, 9	B, C, 9	-
Echidna polyzona (Richardson, 1845)	A	-	-	-	-
Echidna unicolor Schultz in Schultz *et al*., 1953	-	-	-	C	-
Enchelycore pardalis (Temminck and Schlegel, 1846)	A, 9	-	CRED	-	-
Enchelynassa canina (Quoy and Gaimard, 1824)	-	-	A, 9, CRED	-	-
Gymnomuraena zebra (Shaw in Shaw and Nodder, 1797)	CRED	-	CRED	-	-
Unidentified *Gymnothorax* species	A, B	CRED	A	B	-
Gymnothorax breedeni McCosker and Randall, 1977	CRED	CRED	CRED	-	-
Gymnothorax buroensis (Bleeker, 1857)	-	-	-	B, C, 9	-
Gymnothorax chilospilus Bleeker, 1864	A	-	-	C	-
Gymnothorax enigmaticus McCosker and Randall, 1982	-	-	-	B, C, 11	-
Gymnothorax fimbriatus (Bennett, 1832)	-	-	-	B, C	-
Gymnothorax flavimarginatus (Rüppell, 1830)	A, B, 6, 9, CRED	A, 9, CRED	CRED	B, C, 9, CRED	-
Gymnothorax javanicus (Bleeker, 1859)	CRED	-	CRED	A, B, C, 5, 9, CRED	CRED
Gymnothorax margaritophorus Bleeker, 1864	-	-	-	B, C	-
Gymnothorax marshallensis (Schultz in Schultz *et al*., 1953)	A	-	-	-	-
Gymnothorax meleagris (Shaw in Shaw and Nodder, 1795)	3, 4, CRED	-	CRED	B, C, 3, 4, CRED	CRED
Gymnothorax monostigma (Regan, 1909)	-	-	A	-	-
Gymnothorax pictus (Ahl, 1789)	A, B, 3, 4, 9	A, B, 3, 4, 9	A, B, 3, 4, 9	A, B, C, U, 4, 5, 9, 12, CRED	-
Gymnothorax rueppellii (McClelland, 1844)	A, 9	B, 3, 4, 9	A, 9	B	-
Gymnothorax thyrsoideus (Richardson, 1845)	A	-	-	-	-
Gymnothorax undulatus (Lacepède, 1803)	A, 3, 4, 9, CRED	-	-	B, 9	-
Unidentified *Uropterygius* species	B, A	A	A	C	-
Uropterygius concolor Rüppell, 1838	-	-	-	3, 4	-
Uropterygius macrocephalus (Bleeker, 1864)	-	-	-	4	-
Uropterygius marmoratus (Lacepède, 1803)	B	A, B, U, 3, 4, 9	B	-	-
Uropterygius micropterus (Bleeker, 1852)	-	A	-	-	-

	Howland	**Baker**	**Jarvis**	**Palmyra**	**Kingman**
Uropterygius polyspilus (Regan, 1909)	-	-	-	C	-
Uropterygius superforatus (Regan, 1909)	-	-	-	B, 9	-
Uropterygius xanthopterus Bleeker, 1859	-	-	A	-	-
Ophichthidae					
Callechelys catostoma (Schneider and Forster in Bloch and Schneider, 1801)	-	-	-	B, 4, 13	-
Leiuranus semicinctus (Lay and Bennett, 1839)	-	-	-	B, C	-
Muraenichthys schultzei Bleeker, 1857	-	-	-	C	-
Myrichthys colubrinus (Boddaert, 1781)	-	-	-	A, B, C, U, 4, 14	-
Myrichthys maculosus (Cuvier, 1816)	A, B, 3, 4, 14	-	-	B, C, 14	-
Scolecenchelys gymnotus (Bleeker, 1857)	-	-	-	C	-
Scolecenchelys macroptera (Bleeker, 1857)	-	-	-	B	-
Congridae					
Unidentified deepwater *Conger* species	CRED	-	-	-	-
Conger cinereus Rüppell, 1830	-	-	-	C, 15	-
Clupeidae					
Unidentified *Dussumieria* species	-	-	-	CRED	-
Chanidae					
Chanos chanos (Forsskål, 1775)	6, CRED	-	-	A, 4, CRED	1, CRED
Synodontidae					
Saurida gracilis (Quoy and Gaimard, 1824)	-	-	-	C	-
Unidentified *Synodus* species	CRED	-	CRED	CRED	CRED
Synodus variegatus (Lacepède, 1803)	-	-	-	CRED?	CRED?
Ophidiiformes					
Unidentified “Brotulidae”	-	-	-	C	-
Ophidiidae					
Unidentified *Brotula* species	-	-	-	CRED	-
Brotula multibarbata Temminck and Schlegel, 1846	-	-	-	C	-

	Howland	Baker	Jarvis	Palmyra	Kingman
Bythitidae					
Unidentified Dinematichthyini	-	-	-	C, 16	-
Alionematichthys piger (Alcock, 1890)	-	-	U, 88	B, 88	-
Antennariidae					
Antennarius coccineus (Cuvier in Lesson, 1831)	-	-	-	A, B, 4, 17	-
Antennatus tuberosus (Cuvier, 1817)	U, 17	-	-	U, 17	-
Mugilidae					
Unidentified Mugilidae species	-	-	-	CRED	-
Crenimugil crenilabrus (Forsskål, 1775)	-	B, 3, 4	-	B, 3, 4	-
Liza macrolepis (Smith, 1846)	-	-	-	5?	-
Liza vaigiensis (Quoy and Gaimard, 1825)	-	-	-	B, 3, 4, 5, CRED	-
Neomyxus leuciscus (Günther, 1872)	-	A, B, 3, 4	-	B, C, 3, 4, CRED	-
Unidentified *Valamugil* species	-	-	-	B	-
Valamugil engeli (Bleeker, 1859)	-	-	-	A, B, 3, 4, 5	-
Hemiramphidae					
Unidentified Hemiramphidae species	-	CRED	-	CRED	CRED
Hemiramphus depauperatus Lay and Bennett, 1839	-	-	-	B, 18	CRED?
Unidentified *Hyporhamphus* species	-	-	-	-	B
Hyporhamphus acutus acutus (Günther, 1871)	-	-	B, 18, 19	B, C, U, 18, 19	18
Hyporhamphus affinis (Günther, 1866)	-	-	-	-	U, 18
Hyporhamphus dussumieri (Valenciennes in Cuvier and Valenciennes, 1847)	-	-	-	5	B
Belonidae					
Unidentified Belonidae species	-	-	-	CRED	CRED
Ablennes hians (Valenciennes in Cuvier and Valenciennes, 1946)	-	-	-	CRED	B, CRED
Platybelone argulus platyura (Bennett, 1832)	U	A, B, 3, 4	20	A, B, 4, 5	-
Holocentridae					
Unidentified *Myripristis* species	-	-	CRED	CRED	CRED

	Howland	Baker	Jarvis	Palmyra	Kingman
Myripristis adusta Bleeker, 1853	-	-	-	CRED	CRED
Myripristis amaena (Castelnau, 1873)	CRED	CRED	CRED	B, C, 5, 21, CRED	CRED
Myripristis berndti Jordan and Evermann, 1903	2, CRED	2, CRED	CRED	5, CRED	CRED
Myripristis kuntee Valenciennes in Cuvier and Valenciennes, 1831	-	-	-	CRED	CRED
Myripristis murdjan (Forsskål, 1775)	-	-	CRED?	C, 5	CRED?
Myripritis pralinia Cuvier in Cuvier and Valenciennes, 1829	-	-	-	B, 5, 21	-
Myripristis vittata Valenciennes in Cuvier and Valenciennes, 1831	CRED?	-	-	-	-
Myripristis woodsi Greenfield, 1974	CRED or	or CRED	-	CRED	-
Neoniphon opercularis (Valenciennes in Cuvier and Valenciennes, 1831)	-	CRED	-	5, CRED	CRED
Neoniphon sammara (Forsskål, 1775)	CRED	CRED	-	C, CRED	CRED
Sargocentron caudimaculatum (Rüppell, 1838)	CRED	CRED	CRED	B, 22, CRED	CRED
Sargocentron diadema (Lacepède, 1802)	CRED	-	-	C, CRED	CRED
Sargocentron microstoma (Günther, 1859)	CRED	-	-	B, C, 5, 22	CRED
Sargocentron punctatissimum (Cuvier in Cuvier and Valenciennes, 1829)	U, 22	A, B, 3, 4, 22	-	C	-
Sargocentron spiniferum (Forsskål, 1775)	6, CRED	-	CRED	B, C, L, 5, 22, CRED	CRED
Sargocentron tiere (Cuvier in Cuvier and Valenciennes, 1829)	CRED	CRED	CRED	B, 22, CRED	CRED
Syngnathidae					
Choeroichthys sculptus (Günther, 1870)	U, 23	-	-	-	-
Doryrhamphus excisus excisus Kaup, 1856	-	-	-	C, 24	-
Aulostomidae					
Aulostomus chinensis (Linnaeus, 1766)	CRED	CRED	CRED	B, CRED	CRED
Fistulariidae					
Unidentified *Fistularia* species	-	-	-	B	-
Fistularia commersonii Rüppell, 1838	CRED	-	-	4, CRED	CRED
Scorpaenidae					
Unidentified Scorpaenidae species	U	-	CRED	-	-
Dendrochirus biocellatus (Fowler, 1938)	-	-	CRED	C	-

	Howland	Baker	Jarvis	Palmyra	Kingman
Pterois antennata (Bloch, 1787)	CRED	-	-	B, C, 25?	CRED
Pterois radiata Cuvier in Cuvier and Valenciennes,1829	B, U, 3, 4	-	-	CRED	CRED
Pterois volitans (Linnaeus, 1758)	CRED	-	CRED	-	-
Unidentified *Scorpaenodes* species	-	-	-	C	-
Scorpaenodes guamensis Quoy and Gaimard, 1824	-	-	-	B, C	-
Scorpaenodes hirsutus (Smith, 1957)	-	-	-	B	-
Scorpaenodes kelloggi (Jenkins, 1903)	-	-	-	C	-
Scorpaenodes parvipinnis (Garrett, 1864)	-	-	-	B, C	-
Unidentified *Scorpaenopsis* species	-	-	CRED	-	-
Scorpaenopsis diabolis (Cuvier, 1829)	-	-	CRED	C, 26	-
Sebastapistes cyanostigma (Bleeker, 1856)	A, 3, 4, CRED	CRED	CRED	A, B, 4	CRED
Sebastapistes mauritiana (Cuvier in Cuvier and Valenciennes, 1829)	B, U, 3	-	U	B, C	-
Sebastapistes tinkhami (Fowler, 1946)	-	-	-	B	-
Taenionotus triacanthus Lacepède, 1802	CRED	CRED	-	-	-
Caracanthidae					
Caracanthus maculatus (Gray, 1831)	A, B, 3, 4, 6, CRED	CRED	CRED	A, B, 3, 4, CRED	CRED
Caracanthus unipinnis (Gray, 1831)	U	-	-	A, B, 3, 4	-
Perciformes (Percoidei)					
Unidentified percoid species	-	CRED	-	-	-
Epinephelidae					
Unidentified *Cephalopholis* species	-	-	-	B	-
Cephalopholis [Gracila] albomarginatus Fowler and Bean, 1930	1, 2, CRED	1, 2, CRED	CRED	CRED	CRED
Cephalopholis argus Bloch and Schneider, 1801	1, 2, CRED	A, 1, 2, CRED	A, B, 1, 3, 4, 27, CRED	A, B, L, 1, 3, 4, 5, 27, CRED	1, CRED
Cephalopholis aurantia (Valenciennes in Cuvier and Valenciennes, 1828)	B, CRED	-	-	-	-
Cephalopholis leopardus (Lacepède, 1801)	CRED	CRED	CRED	B, 27, CRED	-
Cephalopholis miniata (Forsskål, 1775)	1, 2, CRED	1, 2, CRED	1, 2, CRED	C, CRED	-
Cephalopholis [Aethaloperca] rogaa (Forsskål, 1775)	CRED	CRED	-	-	-

	Howland	**Baker**	**Jarvis**	**Palmyra**	**Kingman**
Cephalopholis sexmaculata (Rüppell, 1830)	CRED?	CRED?	CRED?	-	-
Cephalopholis spiloparaea (Valenciennes in Cuvier and Valenciennes, 1828)	CRED	CRED	-	-	-
Cephalopholis urodeta (Forster in Bloch and Schneider,1801)	1, 2, CRED	1, 2, CRED	1, CRED	A, 1, 4, 5, 27, CRED	1, CRED
Unidentified *Epinephelus* species	CRED	-	-	-	-
Epinephelus fasciatus (Forsskål, 1775)	1, CRED	1, CRED	B, 3, 4, CRED	A, 4, 27, CRED	CRED
Epinephelus hexagonatus (Forster in Bloch and Schneider, 1801)	CRED	6, CRED	B, 27, CRED	B, 5, 27, CRED	CRED
Epinephelus howlandi (Günther, 1873)	N, 27, 28, CRED	CRED	CRED	CRED	CRED
Epinephelus lanceolatus (Bloch, 1790)	-	CRED?	-	-	2, CRED
Epinephelus macrospilos (Bleeker, 1855)	U, 4, 27, CRED	U, 27, CRED	CRED	A, B, C, 4, 5, 27, CRED	-
Epinephelus melanostigma Schultz in Schultz *et al*., 1953	A, U, 27, CRED	A, U, 27, CRED	CRED	B, 27, 29, CRED	CRED
Epinephelus merra Bloch, 1793	A, B, 3, 4, 27, CRED	3, 4, CRED	3?, 4?, CRED	B, C, 4, 5, 27, CRED	CRED
Epinephelus polyphekadion (Bleeker, 1849)	-	-	-	L, 1, 4, 5, 6, 27, CRED	1, 5, CRED
Epinephelus retouti Bleeker, 1868	CRED	B, CRED	A, B, 3, 4, 27, CRED	CRED?	-
Epinephelus socialis (Günther, 1873)	-	-	5, 27	5, 27	-
Epinephelus spilotoceps Schultz in Schultz *et al*. 1953	CRED	CRED	A, 27, CRED	B, 3, 30, CRED	CRED
Epinephelus tauvina (Forsskål, 1775)	A, U, 27	CRED	B, 3, 27, CRED	A, B, C, 4, 5, 27, CRED	CRED
Grammistes sexlineatus (Thunberg, 1792)	-	-	-	B	-
Liopropoma susumi (Jordan and Seale, 1906)	-	-	-	B, C, 31	-
Plectropomus laevis (Lacepède, 1801)	6	-	-	5	-
Pogonoperca punctata (Valenciennes in Cuvier and Valenciennes, 1830)	-	-	U, CRED	-	-
Pseudogramma polyacanthum polyacanthum (Bleeker, 1856)	-	-	-	B, C, 32	-
Suttonia lineata Gosline, 1960	-	-	-	29	-
Variola albimarginata Baissac 1953	-	-	-	CRED?	CRED?
Variola louti (Forsskål, 1775)	CRED	CRED	1, CRED	B, 1, 4, 5, 27, CRED	CRED

	Howland	Baker	Jarvis	Palmyra	Kingman
Serranidae					
Luzonichthys whitleyi (Smith, 1955)	1, 2, CRED	1, 2, CRED	2, CRED	-	-
Pseudanthias bartlettorum (Randall and Lubbock, 1981)	1, 2, CRED	1, 2, CRED	2, CRED	CRED	-
Pseudanthias bartlettorum (Randall and Lubbock, 1981) var. "red-spot" [Blue head and yellow dorsal fin with red underneath extending onto caudal fin.]	CRED	CRED	CRED	-	-
Pseudanthias bicolor (Randall, 1979)	-	CRED	-	-	-
Pseudanthias cooperi (Regan, 1902)	CRED	CRED	-	-	-
Pseudanthias dispar (Herre, 1955)	CRED	CRED	CRED	CRED	-
Pseudanthias olivaceus (Randall and McCosker, 1982)	CRED	CRED	CRED	CRED	CRED
Pseudanthias pascalus (Jordan and Tanaka, 1927)	-	CRED?	-	-	-
Pseudochromidae					
Unidentified Pseudochromidae species	-	-	CRED	CRED	-
Plesiopidae					
Plesiops corallicola Bleeker, 1853	A, B, 3, 4, 33	A, B, 3, 4, 33	-	-	-
Priacanthidae					
Unidentified Priacanthidae	-	-	-	-	CRED
Heteropriacanthus cruentatus (Lacepède, 1801)	CRED	-	-	B, 34	B, CRED
Priacanthus hamrur (Forsskål, 1775)	-	-	-	5	-
Apogonidae					
Unidentified Apogonidae	-	-	-	U	-
Apogon crassiceps Garman, 1903	U	-	-	U	-
Apogon susanae Greenfield, 2001	-	-	U, 35	C?	-
Cheilodipterus quinquelineatus Cuvier in Cuvier and Valenciennes, 1828	CRED	-	CRED	B, C, 36, CRED	CRED
Unidentified *Fowleria* species	-	-	-	B	-
Fowleria isostigma (Jordan and Seale, 1906)	-	-	-	B, C	-

	Howland	**Baker**	**Jarvis**	**Palmyra**	**Kingman**
Fowleria vaiulae (Jordan and Seale, 1906)	-	-	-	C	-
Fowleria variegata (Valenciennes, 1932)	-	-	-	B, C	-
Unidentified *Gymnapogon* species	-	-	-	CRED	-
Nectamia savayensis (Günther, 1872)	-	-	-	C, 37	-
Ostorhinchus angustatus (Smith and Radcliffe in Radcliffe, 1911)	CRED	CRED	CRED	CRED	-
Ostorhinchus apogonides (Bleeker, 1856)	CRED	CRED	CRED	-	-
Ostorhinchus taeniophorus (Regan, 1908)	U, 38	U	U	-	-
Pristiapogon exostigma (Jordan and Starcks, 1906)	-	-	-	B, C, 39	-
Pristiapogon fraenatus (Valenciennes, 1832)	CRED	-	-	6 or	or 6
Pristiapogon kallopterus (Bleeker, 1856)	-	-	-	B, C, 39	-
Pristiapogon taeniopterus (Bennett, 1835)	-	-	-	C, 39	-
Unidentified *Siphamia* species	-	-	-	-	CRED
Malacanthidae					
Malacanthus brevirostris Guichenot, 1848	CRED	-	CRED	-	-
Malacanthus latovittatus (Lacepède, 1801)	CRED?	-	-	-	CRED
Carangidae					
Alectis ciliaris (Bloch, 1787)	-	-	B	-	-
Atule mate (Cuvier in Cuvier and Valenciennes, 1833)	-	-	-	CRED?	-
Carangoides ferdau (Forsskål, 1775)	CRED	CRED	CRED	B, CRED	-
Carangoides orthogrammus (Jordan and Gilbert, 1882)	CRED	CRED	CRED	A, C, 5, CRED	CRED
Unidentified *Caranx* species	-	-	-	C	-
Caranx ignobilis (Forsskål, 1775)	2, CRED	2, CRED	CRED	1, 2, 5, 40, CRED	CRED
Caranx lugubris Poey, 1860	1, 2, CRED	1, 2, CRED	A, 1, 2, 3, 41, CRED	C, 1, CRED	1, CRED
Caranx melampygus Cuvier in Cuvier and Valenciennes, 1833	1, 2, CRED	A, 1, 2, CRED	1, CRED	B, C, 1, 5, CRED	1, CRED
Caranx sexfasciatus Quoy and Gaimard, 1825	1, 6, CRED	B, 3, 4	2, CRED	C, 5, CRED	1, CRED
Unidentified *Decapterus* species	-	-	-	B, CRED	-

	Howland	**Baker**	**Jarvis**	**Palmyra**	**Kingman**
Decapterus macarellus (Cuvier in Cuvier and Valenciennes, 1833)	-	-	-	CRED	CRED
Elagatis bipinnulata (Quoy and Gaimard, 1825)	1, CRED	1, CRED	42, CRED	42, CRED	2, 42, CRED
Gnathanodon speciosus (Forsskål, 1775)	-	-	-	16	-
Scomberoides lysan (Forsskål, 1775)	CRED	-	CRED	B, C, 5, 43, CRED	-
Selar crumenophthalmus (Bloch, 1793)	-	-	-	CRED	-
Seriola dumerili (Risso, 1810)	6	-	-	-	-
Trachinotus baillonii (Lacepède, 1801)	A, 6	A	-	-	-
Lutjanidae					
Aphareus furca (Lacepède, 1801)	2, CRED	2, CRED	CRED	A,1, 4, CRED	1, CRED
Aphareus rutilans Cuvier in Cuvier and Valenciennes, 1830	-	CRED	-	-	-
Aprion virescens Valenciennes in Cuvier and Valenciennes, 1830	CRED	CRED	-	CRED	CRED
Lutjanus bohar (Forsskål, 1775)	1, 2, CRED	1, 2, CRED	1, 42, CRED	B,1, 2, 4, 5, 42, 44, CRED	1, 2, 42, CRED
Lutjanus fulvus (Forster in Bloch and Schneider, 1801)	CRED	CRED	A, B, 3, 4, CRED	A, B, C, U, 3, 4, 5, 44, CRED	45, CRED
Lutjanus gibbus (Forsskål, 1775)	U, 6, CRED	CRED	CRED	A, B, 1, 3, 4, 5, 44, CRED	1, CRED
Lutjanus kasmira (Forsskål, 1775)	CRED	CRED	CRED	44	-
Lutjanus monostigma (Cuvier in Cuvier and Valenciennes, 1828)	2, CRED	A, B, 2, 3, 4, CRED	A, B, 3, 4, CRED	A, B, 1, 3, 4, 5, 44, CRED	-
Lutjanus semicinctus Quoy and Gaimard, 1824	CRED	-	-	-	-
Macolor niger (Forsskål, 1775)	CRED	CRED	-	-	-
Pristipomoides filamentosus (Valenciennes in Cuvier and Valenciennes, 1830)	-	CRED	-	-	-
Caesionidae					
Caesio teres Seale, 1906	CRED	CRED	CRED	CRED	2, CRED
Pterocaesio cf. *lativittata* Carpenter, 1987 [Probably an undescribed species, J. Earle, BPBM, pers. comm., May 2009]	CRED or	or CRED	-	CRED	CRED

	Howland	**Baker**	**Jarvis**	**Palmyra**	**Kingman**
Pterocaesio marri Schultz in Schultz et al., 1953	CRED	-	-	CRED	CRED
Pterocaesio tile (Cuvier in Cuvier and Valenciennes, 1830)	CRED	CRED	-	B, 46, CRED	CRED
Lethrinidae					
Gnathodentex aureolineatus (Lacepède (ex Commerson), 1802)	CRED	CRED	CRED	CRED	CRED
Unidentified *Lethrinus* species	-	CRED	-	5?	-
Lethrinus olivaceus Valenciennes in Cuvier and Valenciennes, 1830	CRED	-	CRED	4?, CRED	CRED
Lethrinus xanthochilus Klunzinger, 1870	-	CRED	-	B, CRED	CRED
Monotaxis grandoculis (Forsskål, 1775)	CRED	CRED	CRED	B, CRED	CRED
Mullidae					
Mulloidichthys flavolineatus (Lacepède (ex Commerson), 1801)	6, CRED	CRED	-	A, B, 4, 5, CRED	CRED
Mulloidichthys mimicus Randall and Guézé, 1980	CRED	CRED	CRED	B, 3, 4, 47 CRED	CRED
Mulloidichthys vanicolensis (Valenciennes in Cuvier and Valenciennes, 1831)	CRED	CRED	CRED	C?, 5, CRED	CRED
Unidentified *Parupeneus* species	-	-	-	B	B
Parupeneus barberinus (Lacepède (*ex* Commerson), 1801)	-	-	CRED	C, 48, CRED	CRED
Parupeneus cyclostomus (Lacepède, 1801)	CRED	-	CRED	CRED	CRED
Parupeneus insularis Randall and Myers, 2002	CRED	CRED	B, 2, 3, 4, 49 CRED	C, 5, 49, CRED	CRED
Parupeneus multifasciatus (Quoy and Gaimard, 1825)	CRED	CRED	CRED	B, C, 48, CRED	CRED
Parupeneus pleurostigma (Bennett, 1831)	CRED?	-	-	-	-
Upeneus arge Jordan and Evermann, 1903	-	-	-	A, B, 4, 5	-
Pempheridae					
Pempheris oualensis Cuvier in Cuvier and Valenciennes, 1831	CRED	U, CRED	CRED	5, CRED	CRED

	Howland	**Baker**	**Jarvis**	**Palmyra**	**Kingman**
Kyphosidae					
Unidentified *Kyphosus* species	CRED	-	CRED	CRED	CRED
Kyphosus cinerascens (Forsskål, 1775)	B, 3, 4, 6, CRED	B, U, 3, 4, CRED	CRED	CRED	CRED
Kyphosus vaigiensis (Quoy and Gaimard, 1825)	6?	CRED?	CRED?	C, CRED?	-
Sectator ocyurus (Jordan and Gilbert, 1882)	CRED	CRED	-	-	-
Chaetodontidae					
Unidentified *Chaetodon* species	-	-	-	-	B
Chaetodon auriga Forsskål, 1775	6, CRED	CRED	CRED	A, B, C, 3, 4, 5, CRED	CRED
Chaetodon bennetti Cuvier in Cuvier and Valenciennes, 1831	CRED	-	-	CRED	CRED
Chaetodon citrinellus Cuvier (ex Broussonet) in Cuvier and Valenciennes, 1831	6, CRED	CRED	-	CRED	CRED
Chaetodon declivis Randall, 1975	CRED	CRED	-	-	-
Chaetodon ephippium Cuvier in Cuvier and Valenciennes, 1831	-	-	CRED	C, 5, CRED	CRED
Chaetodon kleinii Bloch, 1790	6, CRED	-	-	B, 3, 4, CRED	CRED
Chaetodon lineolatus Cuvier (ex Quoy and Gaimard) in Cuvier and Valenciennes, 1831	-	CRED	-	CRED	CRED
Chaetodon lunula (Lacépède, 1802)	B, CRED	CRED	CRED	B, C, 5, CRED	CRED
Chaetodon lunulatus Quoy and Gaimard, 1824	-	-	-	5, M, L, CRED	CRED
Chaetodon meyeri Bloch and Schneider, 1801	CRED	CRED	CRED	CRED	CRED
Chaetodon meyeri x *reticulatus* hybrid	-	-	-	-	CRED
Chaetodon ornatissimus Cuvier (ex Solander) in Cuvier and Valenciennes, 1831	CRED	CRED	CRED	CRED	CRED
Chaetodon pelewensis Kner, 1868	-	-	-	CRED?	CRED?
Chaetodon punctatofasciatus Cuvier in Cuvier and Valenciennes, 1831	-	-	-	CRED	CRED
Chaetodon quadrimaculatus Gray, 1831	CRED	CRED	CRED	CRED	CRED

	Howland	Baker	Jarvis	Palmyra	Kingman
Chaetodon reticulatus Cuvier in Cuvier and Valenciennes, 1831	CRED	CRED	-	CRED	CRED
Chaetodon semeion Bleeker, 1855	-	-	-	CRED	CRED
Chaetodon trifascialis Quoy and Gaimard, 1825	CRED	CRED	CRED	B, C, CRED	CRED
Chaetodon ulietensis Cuvier in Cuvier and Valenciennes, 1831	CRED	CRED	-	B, C, CRED	CRED
Chaetodon unimaculatus Bloch, 1787	6	CRED	CRED	CRED	CRED
Chaetodon vagabundus Linnaeus, 1758	CRED	CRED	-	CRED	CRED
Forcipiger flavissimus Jordan and McGregor in Jordan and Evermann, 1898	CRED	CRED	CRED	CRED	CRED
Forcipiger longirostris (Broussonet, 1782)	6, CRED	-	-	-	CRED
Hemitaurichthys thompsoni Fowler, 1923	-	-	CRED	-	CRED
Heniochus acuminatus (Linnaeus, 1758)	CRED	CRED	-	-	-
Heniochus monoceros Cuvier in Cuvier and Valenciennes, 1831	CRED	CRED	-	-	-
Heniochus varius (Cuvier, 1829)	CRED	-	-	-	-
Pomacanthidae					
Apolemichthys griffisi (Carlson and Taylor, 1981)	CRED	CRED	CRED	-	CRED
Apolemichthys xanthopunctatus Burgess, 1973	50, CRED	50, CRED	CRED	CRED	CRED
Centropyge bicolor (Bloch, 1787)	CRED	CRED	-	-	-
Centropyge bispinosus (Günther, 1860)	-	CRED	-	-	-
Centropyge fisheri (Snyder, 1904)	-	-	-	CRED	CRED
Centropyge flavissima (Cuvier in Cuvier and Valenciennes, 1831)	2, CRED	2, CRED	CRED	B, C, CRED	CRED
Centropyge loricula (Günther, 1874)	2, CRED	2, CRED	CRED	CRED	CRED
Centropyge flavissima x *Centropyge vrolikii* hybrid	CRED?	-	-	-	-
Centropyge multifasciata (Smith and Radcliffe, 1911)	CRED	CRED	-	-	-
Centropyge vrolikii (Bleeker, 1853)	CRED?	-	-	-	-
Pomacanthus imperator (Bloch, 1787)	CRED	CRED	CRED	CRED	CRED
Pygoplites diacanthus (Boddaert, 1772)	CRED	CRED	-	-	CRED

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Kuhliidae					
Unidentified *Kuhlia* species	-	-	B	-	-
Kuhlia petiti Schultz, 1943	U	-	5	-	-
Kuhlia sandvicensis (Steindachner, 1876)	-	A, B, 3	B, 3	A, 4, CRED	-
Cirrhitidae					
Cirrhitichthys oxycephalus (Bleeker, 1855)	U, CRED	CRED	CRED	A, B, CRED	CRED
Cirrhitops hubbardi (Schultz, 1943)	CRED	CRED	CRED	-	-
Cirrhitus pinnulatus (Forster in Bloch and Schneider, 1801)	U, CRED	B, 3, 4, CRED	CRED	CRED	CRED
Neocirrhites armatus Castelnau, 1873	CRED	CRED	CRED	-	-
Paracirrhites arcatus (Cuvier in Cuvier and Valenciennes, 1829)	2, CRED	2, CRED	CRED	A, B, C, 3, 4, CRED	CRED
Paracirrhites forsteri (Schneider in Bloch and Schneider, 1801)	CRED	CRED	CRED	CRED	CRED
Paracirrhites hemistictus (Günther, 1874)	CRED	CRED	CRED	B, CRED	CRED
Paracirrhites nisus Randall, 1963	-	-	CRED	-	-
Paracirrhites xanthus Randall, 1963	-	CRED	CRED	-	-
Pomacentridae					
Unidentified *Abudefduf* species	-	B	-	-	-
Abudefduf cf. *notatus* (Day, 1869)	A?, B?, 3?	-	CRED	-	-
Abudefduf septemfasciatus (Cuvier in Cuvier and Valenciennes, 1830)	B, U, 6	U	CRED	A, 4, 5,12	-
Abudefduf sordidus (Forsskål, 1775)	A, B, U, 3, 4, 6	A, B, U, 3, 4	A, B, U, 3, 4, 5, CRED	A, B, 3, 4, 5, 12, CRED	-
Abudefduf vaigiensis (Quoy and Gaimard, 1825)	-	CRED?	-	-	CRED?
Amphiprion chrysopterus Cuvier in Cuvier and Valenciennes, 1930	6, CRED	CRED	-	-	-
Amphiprion perideraion Bleeker, 1855	CRED	-	-	-	-
Chromis acares Randall and Swerdloff, 1973	CRED	CRED	CRED	2, CRED	CRED
Chromis agilis Smith, 1960	CRED	-	CRED	CRED	CRED
Chromis atripes Fowler and Bean, 1928	-	-	CRED?	-	-
Chromis caudalis Randall, 1988	B, CRED	CRED?	-	-	-
Chromis lepidolepis Bleeker, 1877	-	-	-	CRED	CRED

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Chromis margaritifer Fowler, 1946	U, CRED	CRED	CRED	B, 2, 4, CRED	CRED
Chromis vanderbilti (Fowler, 1941)	U, CRED	CRED	CRED	B, 2, CRED	CRED
Chromis viridis (Cuvier (ex Ehrenberg) in Cuvier and Valenciennes, 1930)	-	-	-	C, CRED	CRED
Chromis weberi Fowler and Bean, 1928	6?	-	-	-	-
Chromis xanthura (Bleeker, 1854)	CRED	CRED	CRED	CRED	CRED
Chrysiptera biocellata (Quoy and Gaimard, 1824)	-	-	-	B, 4	-
Chrysiptera brownriggi (Bennett, 1828)	U, 6	U	-	-	-
Chrysiptera glauca (Cuvier in Cuvier and Valenciennes, 1830)	A, B, U, 3, 4	A, B, U, 3, 4	B	A, B, C, 5, CRED	-
Dascyllus aruanus (Linnaeus, 1758)	-	-	-	A, B, C, 4, CRED	CRED
Dascyllus auripinnis Randall and Randall, 2001	CRED	CRED	-	B, C, 51, CRED	CRED
Lepidozygus tapeinosoma (Bleeker, 1856)	1, 2, CRED	1, 2, CRED	2, CRED	CRED	CRED
Unidentified *Plectroglyphidodon* species	-	-	-	B	-
Plectroglyphidodon dickii (Liénard, 1839)	CRED	CRED	B, CRED	A, B, C, 4, CRED	CRED
Plectroglyphidodon imparipennis (Vaillant and Sauvage, 1875)	U, 6	U, CRED	U, CRED	CRED	CRED
Plectroglyphidodon johnstonianus Fowler and Ball, 1924	CRED	CRED	CRED	CRED	CRED
Plectroglyphidodon lacrymatus (Quoy and Gaimard, 1825)	4, CRED	CRED	-	-	-
Plectroglyphidodon leucozonus (Bleeker, 1859)	A, U, 6	U	-	-	-
Plectroglyphidodon phoenixensis (Schultz, 1943)	U, 6	U, CRED	U, CRED	CRED	CRED
Unidentifed *Pomacentrus* species	-	-	-	C	-
Pomacentrus coelestis Jordan and Starks, 1901	CRED	-	CRED	B, CRED	CRED
Unidentified *Stegastes* or *Pomacentrus* species (Brown head and anterior body, pale caudal area)	-	CRED	CRED	-	-
Unidentified *Stegastes* species	-	-	-	CRED	-
Stegastes albifasciatus (Schlegel and Muller, 1839)	B, U, 6, CRED	B, U	CRED	B, C, 52, CRED	-

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Stegastes aureus (Fowler, 1927)	A, B, U, 3, 4, 52, CRED	U, CRED	B, U, CRED	B, C, 52, CRED	CRED
Stegastes fasciolatus (Ogilby, 1889)	U, CRED	CRED	CRED	CRED	CRED
Stegastes nigricans (Lacepède, 1802)	A, B, U, 3, 4	B, 3, 4, 6, CRED	B	B, C, 5, CRED	-
Stegastes punctatus (Quoy and Gaimard, 1825)	-	-	-	6 or	or 6
Labridae					
Unidentified labrid species (juvenile *Halichoeres melanurus* (Bleeker, 1851)?)	-	-	-	CRED	CRED
Anampses caeruleopunctatus Rüppell, 1829	53, CRED	B, 53, CRED	CRED	B, CRED	CRED
Anampses melanurus Bleeker, 1857	-	-	CRED	CRED	CRED
Anampses meleagrides Valenciennes in Cuvier and Valenciennes, 1840	CRED	CRED	CRED	CRED	CRED
Anampses twistii Bleeker, 1856	CRED	-	-	B, CRED	CRED
Bodianus axillaris (Bennett, 1832)	CRED	CRED	CRED	CRED	CRED
Bodianus loxozonus (Snyder, 1908)	-	-	CRED	CRED	CRED
Bodianus prognathus Lobel, 1981	CRED	CRED	CRED	CRED	CRED
Cheilinus oxycephalus Bleeker, 1853	CRED	CRED	-	CRED	CRED
Cheilinus trilobatus Lacepède, 1801	4, 6, CRED	CRED	CRED	B, CRED	CRED
Cheilinus undulatus Rüppell, 1835	1, 2, CRED	1, 2, CRED	2, CRED	2, CRED	-
Cirrhilabrus exquisitus Smith, 1957	CRED	CRED	CRED	CRED	CRED
Coris aygula Lacepède, 1801	6, CRED	CRED	B, 3, 54, CRED	CRED	CRED
Coris centralis Randall, 1999	CRED	CRED	CRED	CRED	CRED
Coris gaimard (Quoy and Gaimard, 1824)	6, CRED	CRED	CRED	CRED	CRED
Epibulus insidiator (Pallas, 1770)	-	-	CRED	B, C, 5, CRED	CRED
Gomphosus varius Lacepède, 1801	CRED	CRED	CRED	B, C, CRED	CRED
Unidentifid *Halichoeres* species	-	-	-	C	-
Halichoeres biocellatus Schultz in Schultz *et al*. (1960)	CRED?	-	-	-	-
Halichoeres claudia Randall and Rocha, 2009	CRED	CRED	CRED	CRED	CRED
Halichoeres hortulanus (Lacepède, 1801)	CRED	CRED	CRED	CRED	CRED

	Howland	Baker	Jarvis	Palmyra	Kingman
Halichoeres margaritaceus (Valenciennes in Cuvier and Valenciennes, 1839)	A, B, 3, 4	-	CRED	CRED	-
Halichoeres marginatus Rüppell, 1835	-	-	-	CRED	-
Halichoeres melasmapomus Randall, 1981	CRED	-	CRED	-	CRED
Halichoeres pallidus Kuiter and Randall, 1995	-	-	CRED	-	CRED
Halichoeres trimaculatus (Quoy and Gaimard, 1834)	6, CRED	-	CRED	B, C, CRED	CRED
Hemigymnus fasciatus (Bloch, 1792)	CRED	CRED	CRED	CRED	CRED
Unidentified *Hologymnosus* species	-	-	-	CRED	-
Hologymnosus annulatus (Lacepède, 1801)	-	-	CRED	-	CRED
Hologymnosus doliatus (Lacepède, 1801)	-	-	-	6	CRED
Labrichthys unilineatus (Guichenot, 1847)	-	CRED?	-	CRED?	CRED?
Labroides bicolor Fowler and Bean, 1928	CRED	CRED	CRED	B, CRED	CRED
Labroides dimidiatus (Valenciennes in Cuvier and Valenciennes, 1839)	CRED	CRED	CRED	B, C, CRED	CRED
Labroides rubrolabiatus Randall, 1958	CRED	CRED	CRED	B, CRED	CRED
Labropsis xanthonota Randall, 1981	CRED?	CRED?	CRED?	CRED?	CRED?
Macropharyngodon meleagris (Valenciennes in Cuvier and Valenciennes, 1839)	CRED	CRED	CRED	CRED	CRED
Novaculichthys taeniourus (Lacepède, 1801)	6, CRED	CRED	CRED	CRED	CRED
Oxycheilinus bimaculatus (Valenciennes in Cuvier and Valenciennes, 1840)	-	CRED	-	-	-
Oxycheilinus digrammus (Lacepède, 1801)	-	-	-	CRED?	CRED?
Oxycheilinus unifasciatus (Streets, 1877)	CRED	CRED	CRED	B, C, CRED	CRED
Pseudocheilinus evanidus Jordan and Evermann, 1903	CRED	-	-	CRED	CRED
Pseudocheilinus hexataenia (Bleeker, 1857)	CRED	CRED	CRED	A, B, C, 4, 55, CRED	CRED
Pseudocheilinus octotaenia Jenkins, 1901	CRED	CRED	CRED	B, C, 55	CRED
Unidentified *Pseudocoris* species	CRED	CRED	-	-	-
Pseudocoris heteroptera (Bleeker, 1857)	CRED	CRED	CRED	CRED	CRED
Pseudodax moluccanus (Valenciennes in Cuvier and Valenciennes, 1840)	CRED	CRED	CRED	CRED	CRED
Unidentified *Pseudojuloides* species	-	-	-	CRED	CRED
Pseudojuloides cerasinus (Snyder, 1904)	-	-	CRED	CRED	-

	Howland	Baker	Jarvis	Palmyra	Kingman
Stethojulis bandanensis (Bleeker, 1851)	U, 56, CRED	U, 56, CRED	U, CRED	B, C, 56, CRED	CRED
Unidentified *Thalassoma* species	-	-	-	B, C	-
Thalassoma amblycephalum (Bleeker, 1856)	B, 2, 3, 4, CRED	2, CRED	CRED	B, C, CRED	CRED
Thalassoma hardwicke (Bennett, 1830)	-	CRED	-	B, C, CRED	CRED
Thalassoma lunare (Linnaeus, 1758)	-	-	-	B, C, 3, 4, CRED	CRED
Thalassoma lutescens (Lay and Bennett (ex Solander), 1839)	CRED	6, CRED	CRED	B, C, CRED	CRED
Thalassoma purpureum (Forsskål, 1775)	U, CRED	A, B, U, 3, 4, CRED	B, 3, 4, CRED	B, CRED	CRED
Thalassoma quinquevittatum (Lay and Bennett, 1839)	U, CRED	CRED	CRED	B, C, 57, CRED	CRED
Thalassoma trilobatum (Lacepède, 1801)	U, 57, CRED	U, CRED	U, CRED	CRED	CRED
Scaridae					
Unidentified Scaridae	-	-	-	C	-
Bolbometopon muricatum (Valenciennes in Cuvier and Valenciennes, 1840)	-	-	2, CRED	2, CRED	-
Calotomus carolinus (Valenciennes in Cuvier and Valenciennes, 1840)	6, CRED	CRED	CRED	B, 58, CRED	CRED
Cetoscarus ocellatus (Valenciennes in Cuvier and Valenciennes, 1840)	-	-	CRED?	-	-
Chlorurus frontalis (Valenciennes in Cuvier and Valenciennes, 1840)	CRED	-	CRED	B, U, 3, 4, 5, 12, L, CRED	CRED
Chlorurus microrhinus (Bleeker, 1854)	6, CRED	CRED	1, CRED	B, 2, 5, CRED	1, 2, CRED
Chlorurus sordidus (Forsskål, 1775)	6, CRED	-	CRED	5, 59, CRED	CRED
Hipposcarus longiceps (Valenciennes in Cuvier and Valenciennes, 1840)	-	-	CRED	CRED	-
Unidentified *Scarus* species	CRED	CRED	5, CRED	B, C, CRED	CRED
Scarus altipinnis (Steindachner, 1879)	6	-	CRED	B, 5, CRED	-
Scarus festivus Valenciennes in Cuvier and Valenciennes 1840	-	-	-	-	CRED?
Scarus forsteni (Bleeker, 1861)	-	-	CRED?	B?, CRED?	CRED?
Scarus frenatus Lacepède, 1802	2, CRED	2, CRED	B, C, U, 1, 5, 59, CRED	U, 5, 59, CRED	CRED
Scarus ghobban Forsskål, 1775	-	-	CRED	CRED	CRED

	Howland	Baker	Jarvis	Palmyra	Kingman
Scarus globiceps Valenciennes in Cuvier and Valenciennes, 1840	-	-	-	B, 59, CRED	CRED
Scarus niger Forsskål, 1775	6	CRED	CRED	CRED	CRED
Scarus oviceps Valenciennes in Cuvier and Valenciennes, 1840	6, CRED	CRED	3, 4, CRED	B, CRED	CRED
Scarus psitticus Forsskål, 1775	-	CRED	CRED	4, CRED	CRED
Scarus rubroviolaceus Bleeker, 1847	2, CRED	2, CRED	A, 1, 3, 4, CRED	U, 5, 59, CRED	CRED
Scarus spinus (Kner, 1868)	-	-	-	CRED	CRED
Scarus tricolor (Bleeker, 1847)	CRED	CRED	CRED	CRED	CRED
Creediidae					
Crystallodytes cookei enderburyensis Schultz, 1943	-	-	U	-	-
Tripterygiidae					
Unidentified Tripterygiidae	-	-	-	C	B
Unidentified *Enneapterygius* species	U	-	-	-	-
Enneapterygius nigricauda Fricke, 1997	B, 3, 4, 60	-	U, 60	-	-
Enneapterygius tutuilae Jordan and Seale, 1906	-	-	-	B, 60	-
Helcogramma chica Rosenblatt in Schultz *et al*., 1960	A, B, 3, 4, 60	-	-	-	-
Helcogramma striatum Hansen, 1986	CRED	-	-	CRED	CRED
Blenniidae					
Unidentified Blenniidae	CRED	CRED	B, CRED	-	-
Aspidontus taeniatus Quoy and Gaimard, 1834	-	-	B, CRED	B	-
Blenniella caudolineata (Günther, 1877)	U, 29, 61	-	-	-	-
Blenniella gibbifrons (Quoy and Gaimard, 1824)	U, 61	U, 61	U, 61	C, 61	-
Blenniella paula (Bryan and Herre, 1903)	A, B, U, 3, 4, 61	4	U, 61	A, B, C, 4, 61	-
Unidentified *Cirripectes* species	CRED	CRED	CRED	CRED	CRED
Cirripectes polyzona (Bleeker, 1868)	U, 62, CRED	U, 62	CRED	B, C, CRED	B, CRED
Cirripectes quagga (Fowler and Ball, 1924)	U, 62	U, 62	U, 62	-	-

	Howland	Baker	Jarvis	Palmyra	Kingman
Cirripectes variolosus (Valenciennes in Cuvier and Valenciennes, 1836)	CRED	CRED	U, 62, CRED	A, B, C, U, 4, 62, CRED	CRED
Ecsenius midas Starck, 1969	B, CRED	CRED	CRED	-	-
Unidentified *Entomacrodus* species	B	-	-	-	-
Entomacrodus cymatobius Schultz and Chapman, 1960	-	-	U, 63	-	-
Entomacrodus sealei Bryan and Herre, 1903	-	-	U, 63	-	-
Entomacrodus striatus (Quoy and Gaimard, 1836)	U, 63	-	U, 63	-	-
Entomacrodus thalassinus thalassinus (Jordan and Seale, 1906)	U, 63	-	U, 63	C?	-
Exallias brevis (Kner, 1868)	CRED	-	-	-	CRED
Unidentified *Istiblennius* species	U	-	-	A, B, 3, 61	-
Istiblennius edentulus (Schneider in Bloch and Schneider, 1801)	A, B, U, 3, 4, 61	A, B, M, 3, 4, 61	U, 61	A, B, 61	-
Istiblennius lineatus (Valenciennes in Cuvier and Valenciennes, 1836)	U, 61	-	-	-	-
Meiacanthus atrodorsalis (Günther, 1877)	-	CRED?	-	-	-
Omobranchus rotundiceps obliquus (Garman, 1903)	-	-	-	B, C, 64, 65	-
Plagiotremus laudandus (Whitley, 1961)	-	CRED?	-	-	-
Plagiotremus rhinorhynchos (Bleeker, 1852)	CRED	CRED	CRED	CRED	-
Plagiotremus tapeinosoma (Bleeker, 1857)	CRED	CRED	CRED	CRED	CRED
Rhabdoblennius rhabdotrachelus (Fowler and Ball, 1924)	U	-	U, 66	-	-
Rhabdoblennius snowi (Fowler, 1928)	U	U, 66	-	-	-
Gobiesocidae					
Lepidichthys minor Briggs, 1955	B, 29	-	-	16?	-
Callionymidae					
Unidentified Callionymidae	CRED	-	CRED	-	-
Eleotridae					
Unidentified Eleotridae	-	-	-	C	-
Eleotris fusca (Schneider and Forster in Bloch and Schneider, 1801)	-	-	-	B?, 4?	-

	Howland	Baker	Jarvis	Palmyra	Kingman
Gobiidae					
Unidentified Gobiidae	B	-	CRED	C	CRED
Amblyeleotris fasciata (Herre, 1953)	-	-	-	-	CRED
Unidentified *Amblygobius* species	-	-	-	C, 16	-
Amblygobius decussatus Bleeker, 1855	-	-	-	C?	-
Amblygobius nocturnus (Herre, 1945)	-	-	-	C	-
Amblygobius phalaena (Valenciennes in Cuvier and Valenciennes, 1837)	-	-	-	C, U, CRED	-
Unidentified *Asterropteryx* species	-	-	-	C	-
Asterropteryx ensiferus (Bleeker, 1874)	-	-	-	B	-
Asterropteryx semipunctata Rüppell, 1830	-	-	-	A, C, 4	-
Unidentified *Bathygobius* species	-	-	-	U	-
Bathygobius cocosensis (Bleeker, 1854)	U	-	-	-	-
Bathygobius fuscus (Rüppell, 1830)	A?, B?, 3?, 4?	-	-	A?, B?, 4?	-
Unidentified *Cabillus* species	-	-	-	C	-
Unidentified *Eviota* species	A, 3, 30	-	-	B, U, 30	CRED
Eviota cometa Jewett and Lachner, 1983	-	-	-	C, 67	-
Eviota distigma Jordan and Seale, 1906	-	-	-	B, C, U, 68	-
Eviota epiphanes Jenkins, 1903	B?	-	-	-	-
Eviota infulata (Smith, 1956)	-	-	-	C, 68	-
Eviota nebulosa Smith 1958	-	-	-	C, 68	-
Eviota prasites Jordan and Seale, 1906	-	-	-	B?	-
Eviota saipanensis Fowler, 1945	A, B, 3	-	-	C	-
Eviota zonura Jordan and Seale, 1906	-	-	A?	A?	-
Unidentified *Fusigobius* species	-	-	-	C	-
Fusigobius neophytus (Günther, 1877)	-	-	-	C	-
Unidentified *Gnatholepis* species	CRED	-	-	C	-
Gnatholepis anjerensis (Bleeker, 1851) [including specimens *G. scapulostigma* of Thacker (2004b), in part]	-	-	-	B, C, 69, 70	-
Gnatholepis cauerensis Bleeker, 1853 [including specimens *G. scapulostigma* of Thacker (2004b), in part]	-	-	-	C, 70	CRED
Unidentified *Gobiodon* species	-	-	-	B	-
Gobiodon citrinus (Rüppell, 1838)	-	-	-	A, B, 3	-

	Howland	Baker	Jarvis	Palmyra	Kingman
Gobiodon rivulatus (Rüppell, 1830)	-	-	-	A, 4	-
Macrodontogobius wilburi Herre, 1936	-	-	-	C	-
Unidentified *Oplopomus* species	-	-	-	C	-
Oplopomus oplopomus (Valenciennes in Cuvier and Valenciennes, 1837)	-	-	-	B, C	-
Unidentified *Paragobiodon* species	-	-	-	C	-
Paragobiodon echinocephalus (Rüppell, 1830)	-	-	-	B, C, 3, 4	-
Priolepis semidoliatus (Valenciennes, 1837)	B, 3, 4	-	-	C	-
Priolepis squamogena Winterbottom and Burridge, 1989	U, 71	-	U, 71	C	-
Unidentified *Silhouettea* species	-	-	-	C	-
Unidentified *Trimma* species	-	-	-	B, C	-
Trimmatom nanus Winterbottom and Emery, 1981	-	-	-	C	-
Valenciennea sexguttata (Valenciennes in Cuvier and Valenciennes, 1837)	-	-	-	U, 72	-
Valenciennea strigata (Broussonet, 1782)	CRED	-	CRED	C	CRED
Microdesmidae					
Unidentified *Gunnellichthys* species	-	-	-	CRED	-
Gunnellichthys curiosus Dawson, 1968	CRED	CRED	-	-	-
Ptereleotridae					
Nemateleotris magnifica Fowler, 1938	CRED	-	-	CRED	CRED
Ptereleotris evides (Jordan and Hubbs, 1925)	6, CRED	-	-	B, C, 73, CRED	CRED
Ptereleotris heteroptera (Bleeker, 1855)	CRED	-	-	-	CRED
Ptereleotris microlepis (Bleeker, 1856)	-	-	-	C, CRED	-
Ptereleotris zebra (Fowler, 1938)	-	CRED	-	CRED	CRED
Schindleriidae					
Schindleria praematura (Schindler, 1930)	-	-	-	16	-
Ephippidae					
Unidentified *Platax* species	-	-	-	CRED	CRED
Platax boersii Bleeker, 1852	CRED	-	-	-	-

	Howland	Baker	Jarvis	Palmyra	Kingman
Platax orbicularis (Forsskål, 1775)	CRED	CRED	-	-	-
Platax teira (Forsskål, 1775)	CRED	-	CRED	CRED	CRED
Zanclidae					
Zanclus cornutus (Linnaeus, 1758)	CRED	CRED	CRED	CRED	CRED
Acanthuridae					
Unidentified Acanthuridae	CRED	CRED	CRED	C, U, CRED	U, CRED
Acanthurus achilles Shaw, 1803	CRED	CRED	A, B, 3, 4, CRED	C, CRED	CRED
Acanthurus blochii Valenciennes in Cuvier and Valenciennes, 1835	6, CRED	CRED	CRED	CRED	CRED
Acanthurus dussumieri Valenciennes in Cuvier and Valenciennes, 1835	-	-	CRED	CRED	-
Acanthurus guttatus Forster in Bloch and Schneider, 1801	6	CRED	A, B, 3, 4, CRED	A, 4, CRED	CRED
Acanthurus leucochilus Herre, 1927	CRED	CRED	CRED	CRED	CRED
Acanthurus lineatus (Linnaeus, 1758)	20, CRED	CRED	20, CRED	B, C, 4, 74, CRED	CRED
Acanthurus maculiceps (Ahl, 1923)	6	CRED	CRED	CRED	CRED
Acanthurus mata Cuvier, 1829	6, CRED	CRED	CRED	-	CRED
Acanthurus nigricans (Linnaeus, 1758)	2, CRED	2, CRED	B, 1, 2, 3, 4, 20, CRED	B, C, 5, CRED	CRED
Acanthurus nigricauda Duncker and Mohr, 1929	CRED	B, CRED	CRED	5, CRED	CRED
Acanthurus nigrofuscus (Forsskål, 1775)	CRED	CRED	CRED	CRED	CRED
Acanthurus nigros Günther, 1861	20, CRED	CRED	B, 3, 4, CRED	5, CRED	CRED
Acanthurus olivaceus Bloch and Schneider (ex Forster), 1801	CRED	B, 75, CRED	CRED	CRED	CRED
Acanthurus pyroferus Kittlitz, 1834	CRED	CRED	-	-	CRED
"*Acanthurus rackliffei*" Schultz, 1943 (= *A. achilles* x *A. nigricans* hybrid)	CRED	-	CRED	CRED	CRED
Acanthurus thompsoni (Fowler, 1923)	CRED	CRED	CRED	CRED	CRED
Acanthurus triostegus triostegus (Linnaeus, 1758)	A, B, 2, 3, 4, CRED	A, B, U, 2, 3, 4, 74, CRED	A, B, 3, 4, CRED	A, B, C, 3, 4, 5, 74, CRED	CRED
Acanthurus xanthopterus Valenciennes in Cuvier and Valenciennes, 1835	6, CRED	CRED	B, 3, 74, CRED	A, B, C, 3, 4, 5, CRED	CRED

	Howland	**Baker**	**Jarvis**	**Palmyra**	**Kingman**
Unidentified *Ctenochaetus* species	CRED	CRED	CRED	B, CRED	CRED
Ctenochaetus binotatus Randall, 1955	-	-	-	-	CRED
Ctenochaetus cyanocheilus Randall and Clements, 2001	6, 2, CRED	2, CRED	2, CRED	A, 4, CRED	CRED
Ctenochaetus flavicauda Fowler, 1938	76, CRED	76, CRED	76, CRED	CRED	CRED
Ctenochaetus hawaiiensis Randall, 1955	CRED	CRED	1, CRED	CRED	CRED
Ctenochaetus marginatus (Valenciennes in Cuvier and Valenciennes, 1835)	2, CRED	2, CRED	B, C, 2, 3, 4, 77, CRED	CRED	CRED
Ctenochaetus striatus (Quoy and Gaimard, 1825)	CRED	CRED	CRED	B, C, 5, 76, CRED	CRED
Unidentified *Naso* species	CRED	-	-	B	-
Naso annulatus (Quoy and Gaimard, 1825)	-	CRED	-	CRED	-
Naso brevirostris (Valenciennes in Cuvier and Valenciennes, 1835)	CRED	-	CRED	CRED	CRED
Naso caesius Randall and Bell, 1992	CRED	CRED	CRED	CRED	-
Naso hexacanthus (Bleeker, 1855)	CRED	CRED	CRED	CRED	CRED
Naso lituratus (Forster in Bloch and Schneider, 1801)	2, CRED	2, CRED	CRED	CRED	CRED
Naso unicornis (Forsskål, 1775)	CRED	CRED	-	CRED	CRED
Naso vlamingii (Valenciennes in Cuvier and Valenciennes, 1835)	CRED	CRED	CRED	CRED	CRED
Paracanthurus hepatus (Linnaeus, 1766)	CRED	CRED	-	-	-
Zebrasoma rostratum (Günther, 1873)	CRED	CRED	CRED	5, 78, CRED	CRED
Zebrasoma scopas (Cuvier, 1829)	CRED	CRED	CRED	CRED	CRED
Zebrasoma veliferum (Bloch, 1795)	CRED	CRED	-	CRED	CRED
Sphyraenidae					
Unidentified *Sphyraena* species	2	CRED	B	-	CRED
Sphyraena barracuda (Walbaum, 1792)	CRED	CRED	CRED	B, 4, 5, 42, 79, 80, CRED	42, 79, CRED
Sphyraena helleri Jenkins, 1901	-	-	CRED	CRED	-
Sphyraena qenie Klunziger, 1870	-	CRED	2, CRED	CRED	2, CRED
Scombridae					
Gymnosarda unicolor (Rüppell, 1836)	CRED	CRED	CRED	-	-

	Howland	**Baker**	**Jarvis**	**Palmyra**	**Kingman**
Bothidae					
Unidentified Bothidae	-	-	-	B	CRED
Unidentified *Bothus* species	-	-	-	CRED	-
Bothus mancus (Broussonet, 1782)	U, 20	20	U	B, U, 4, 30	-
Balistidae					
Unidentified Balistidae species	-	-	-	B	-
Balistapus undulatus (Park, 1797)	2, CRED	2, CRED	CRED	C, 5, CRED	CRED
Balistoides conspicillum (Bloch and Schneider, 1801)	CRED	-	-	-	-
Balistoides viridescens (Bloch and Schneider, 1801)	CRED	CRED	CRED	CRED	CRED
Melichthys niger (Bloch, 1786)	CRED	CRED	CRED	C, CRED	CRED
Melichthys vidua (Richardson (ex Solander), 1845)	CRED	CRED	U, 81, CRED	CRED	CRED
Odonus niger (Rüppell, 1836)	6, CRED	CRED	CRED	CRED	-
Pseudobalistes flavimarginatus (Rüppell, 1829)	CRED	CRED	CRED	4, 30, CRED	CRED
Rhinecanthus aculeatus (Linnaeus, 1758)	-	-	-	A, B, C, 3, 4, 5, 30, CRED	-
Rhinecanthus rectangulus (Bloch and Schneider, 1801)	A, CRED	B, 20, CRED	5, CRED	CRED	CRED
Sufflamen bursa (Bloch and Schneider, 1801)	CRED	CRED	CRED	CRED	CRED
Sufflamen chrysopterum (Bloch and Schneider, 1801)	A, CRED	CRED	CRED	5	CRED
Sufflamen fraenatum (Latrielle, 1804)	CRED	CRED	CRED	-	-
Xanthichthys auromarginatus (Bennett, 1832)	6	-	CRED	CRED	-
Xanthichthys caeruleolineatus Randall, Matsuura, and Zama, 1978	CRED	U, 82, CRED	CRED	CRED	CRED
Monacanthidae					
Aluterus scriptus (Osbeck, 1765)	CRED	CRED	CRED	CRED	CRED
Amanses scopas (Cuvier, 1829)	CRED	CRED	CRED	CRED	CRED
Cantherhines dumerilii (Hollard, 1854)	CRED	CRED	CRED	CRED	CRED
Cantherhines pardalis (Rüppell, 1837)	6, CRED	CRED	CRED	-	CRED
Pervagor marginalis Hutchins, 1986	-	-	CRED?	B, 83, CRED?	CRED?

	Howland	**Baker**	Jarvis	Palmyra	Kingman
Ostraciidae					
Lactoria diaphana (Bloch and Schneider, 1801)	-	-	-	B	-
Ostracion meleagris Shaw in Shaw and Nodder, 1796	6, CRED	CRED	4, CRED	CRED	CRED
Tetraodontidae					
Arothron hispidus (Linnaeus, 1758)	B, 3, 4	-	-	A, B, U, 4, 5, 12	-
Arothron meleagris (Lacepède (ex Commerson), 1798)	U, 84, CRED	CRED	CRED	5, CRED	CRED
Arothron nigropunctatus (Bloch and Schneider, 1801)	-	CRED	-	C	CRED
Canthigaster amboinensis (Bleeker, 1865)	A, 6, CRED	CRED	CRED	CRED?	CRED
Canthigaster janthinoptera (Bleeker, 1855)	CRED	-	CRED	B, CRED	CRED
Canthigaster solandri (Richardson (ex Solander), 1845)	CRED	CRED	-	A, B, C, CRED	CRED
Diodontidae					
Diodon hystrix Linnaeus, 1758	CRED	CRED	CRED	CRED	CRED
Unidentified					
Unidentified fish	-	-	-	B	-

Epipelagic oceanic species recorded near inshore areas

	Howland	**Baker**	**Jarvis**	**Palmyra**	**Kingman**
Rhincodontidae					
Rhincodon typus Smith, 1828	-	-	1, CRED	-	-
Carcharhinidae					
Carcharhinus altimus (Springer, 1950)	-	-	42, 85	42, 85	42
Carcharhinus longimanus (Poey, 1861)	-	-	85	85	-
Engraulidae					
Encrasicholina punctifer Fowler, 1938	-	-	-	16	-

	Howland	Baker	Jarvis	Palmyra	Kingman
Exocoetidae					
Unidentified Exocoetidae	-	B	-	-	-
Cheilopogon atrisignis (Jenkins, 1904)	-	-	-	A, 4	-
Cheilopogon furcatus (Mitchill, 1815)	-	-	A, 4	-	-
Cheilopogon suttoni Whitley and Colefax, 1938	-	-	-	C	-
Unidentified *Hirundichthys* species	-	-	A, 4	-	-
Oxyporhamphus micropterus micropterus (Valenciennes in Cuvier and Valenciennes, 1847)	-	-	-	A	-
Hemiramphidae					
Euleptoramphus viridis (van Hasselt, 1823)	-	-	-	A, 4, 18	-
Coryphaenidae					
Unidentified *Coryphaena* species	-	-	-	C	-
Coryphaena equiselis Linnaeus, 1758	-	-	-	A, B, C, 4	-
Coryphaena hippurus Linnaeus, 1758	B	-	-	42	-
Echeneidae					
Unidentified Echeneidae species (gray body)	CRED	-	-	-	CRED
Echeneis naucrates Linnaeus, 1758	CRED	-	-	-	-
Remora remora (Linnaeus, 1758)	-	B, 3, 4	B	-	-
Carangidae					
Naucrates ductor (Linnaeus, 1758)	-	-	B	-	-
Scombridae					
Unidentified Scombridae	CRED	-	-	C	-
Acanthocybium solandri (Cuvier in Cuvier and Valenciennes, 1832)	-	-	42	B, 2, 42, 80	42, 79, CRED
Euthynnus affinis (Cantor, 1849)	CRED	CRED	CRED	42	-
Katsuwonus pelamis (Linnaeus, 1758)	-	CRED	85	42, 85	42
Thunnus alalunga (Bonnaterre, 1788)	-	-	85	-	-
Thunnus albacares (Bonnaterre, 1788)	U	-	42, 85	2, 42, 79, 80, 85, CRED	
Thunnus obesus (Lowe, 1839)	-	-	-	80, 86	-

	Howland	Baker	Jarvis	Palmyra	Kingman
Istiophoridae					
Istiophorus platypterus (Shaw in Shaw and Nodder, 1792)	-	-	-	-	CRED
Kajikia audax (Philippi, 1887)	-	-	-	-	CRED
Nomeidae					
Unidentified Nomeidae	-	-	B	-	-
Cubiceps pauciradiatus Günther, 1872	-	-	87	-	-
Nomeus gronovii (Gmelin,1789)	-	-	-	30	-
Psenes cyanophrys Valenciennes in Cuvier and Valenciennes, 1833	-	-	B	-	-
Balistidae					
Canthidermis maculatus (Bloch, 1786)	-	CRED	CRED	-	-

Records from our surveys of species that might occur in the region, but for which we have great uncertainty about identifications

	Howland	Baker	Jarvis	Palmyra	Kingman
Belonidae					
Tylosurus crocodilus crocodilus (Peron and Lesueur in Lesueur, 1821)	CRED?	CRED?	CRED?	-	CRED?
Holocentridae					
Myripristis chryseres Jordan and Evermann, 1903	CRED?	-	-	-	-
Caesionidae					
Caesio caerulaurea Lacepède (ex Commerson), 1801	-	-	-	-	CRED?
Kyphosidae					
Kyphosus hawaiiensis Sakai and Nakabo, 2003	6?, CRED?	CRED?	-	5?, CRED?	CRED?
Chaetodontidae					
Chaetodon melannotus Bloch and Schneider, 1801	CRED?	-	-	-	-
Pomacentridae					
Chromis amboinensis (Bleeker, 1857)	-	-	CRED?	-	-
Chromis ternatensis (Bleeker, 1856)	-	-	-	-	CRED?

	Howland	Baker	Jarvis	Palmyra	Kingman
Labridae					
Labroides pectoralis Randall and Springer, 1975	CRED?	-	-	CRED?	-
Labropsis australis Randall, 1981	-	-	-	-	CRED?
Pseudocheilinus tetrataenia Schultz in Schultz *et al*., 1960	CRED?	CRED?	CRED?	CRED?	-
Blenniidae					
Ecsenius bicolor (Day (ex Tickell), 1888)	CRED?	-	-	-	-
Scombridae					
Scomber japonicus Houttuyn, 1782	-	-	-	A?, 5?	-
Diodontidae					
Diodon liturosus Shaw, 1804	6?	-	-	-	-

Questionable records of species that seem unlikely to occur in the region based on their known distributions

	Howland	Baker	Jarvis	Palmyra	Kingman
Muraenidae					
Gymnothorax albimarginatus non (Temminck and Schlegel, 1846)	-	-	-	C?	-
Bythitidae					
Dinematichthys iluocoetoeides non Bleeker, 1855	-	-	-	C?	-
Mugilidae					
Mugil species	-	-	-	C?	-
Epinephelidae					
Epinephelus maculatus non (Bloch, 1790)	6?	-	-	-	-
Epinephelus malabaricus non (Bloch and Schneider, 1801)	-	-	-	A?, 4?	-
Serranidae					
Pseudanthias pleurotaenia non (Bleeker, 1857)	-	6?	-	-	-

	Howland	Baker	Jarvis	Palmyra	Kingman
Pomacanthidae					
Apolemichthys trimaculatus non (Cuvier (ex Lacepède) in Cuvier and Valenciennes, 1831)	6?	-	-	-	-
Pomacentridae					
Amblyglyphidodon aureus non (Cuvier (ex Kuhl and van Hasselt) in Cuvier and Valenciennes, 1830)	-	6?	-	-	-
Pomacentrus bankanensis non Bleeker, 1853	U?	-	-	-	-
Labridae					
Diproctacanthus xanthurus non (Bleeker, 1856)	-	6?	-	-	-
Thalassoma ballieui non (Vaillant and Sauvage, 1875)	-	-	-	C?	-
Thalassoma duperrey non (Quoy and Gaimard, 1824)	-	-	-	C?	-
Scaridae					
Chlorurus perspicillatus non (Steindachner, 1879)	-	-	-	A?, C?, 4?, 30?	-
Blenniidae					
Salarias species	-	-	-	C?	-
Gobiidae					
Valenciennea muralis non (Valenciennes (ex Guoy and Gaimard) in Cuvier and Valenciennes, 1837)	-	-	-	C?	-
Acanthuridae					
Acanthurus leucopareius non (Jenkins, 1903) [as *Acanthurus umbra* non (Jenkins, 1903)]	-	-	-	C?, CRED?	-

DISCUSSION

Numbers of Species

A total of 506 shore-fish species and 27 epipelagic species are recorded from the U.S. equatorial Pacific islands in this survey. Of the shore-fish species, 41 (8.1%) were first noted in our CRED surveys, including some species that are new records as seen in their entirety (Table 3) for the Line or Phoenix Islands. We also report an additional 26 (5.1%) species that were found by earlier surveys but were not recorded in previously published literature. Together, these 67 species comprise 13.3% of the fish species known to date from the U.S. Line and Phoenix Islands. Totals of 354 species were recorded from Howland and Baker, and 450 species from the three U.S. Line Islands. Numbers for the individual islands are: Howland Island— 328 species of which 166 (50.8%) are first records from CRED sampling; Baker Island—268 species with 188 (70.1%) as new CRED records; Jarvis Island—274 species with 176 (64.2%) as new CRED records; Palmyra Atoll—395 species with 113 (28.6%) as new CRED records; and Kingman Reef—270 species with 212 (78.5%) as new CRED records. Fifteen additional species whose identifications are in need of verification were reported in our surveys or previous studies. An additional 16 are considered suspect identifications of species that probably do not occur at the Line or Phoenix Islands. Neither of the latter two groups is included in the numbers of species reported above.

There were some noteworthy findings from our CRED surveys compared to previous surveys of the Line Islands (e.g ., Chave and Eckert, 1974; Randall, 2005) and Phoenix Islands (e. g., Schultz, 1943; Stone et al., 2001; Obura and Stone, 2003). We found 27 new records for the Line Islands and 62 for the Phoenix Islands, with 13 of those originating from both archipelagos. Our new records for the Phoenix Islands were based on occurrences at Howland and Baker Islands. As discussed later, Howland and Baker are more similar to the Line Islands in species composition than to the main Phoenix Islands. Therefore, records of fish species from Howland and Baker may not indicate that they occur in the main Phoenix Islands. The high number of new records from Howland and Baker in our surveys, in part, reflects the lesser historical sampling effort there than in the Line Islands. For noteworthy taxa, we recorded hammerhead sharks (*Sphyrna* species) at both the U.S. Line and Phoenix Islands, whereas they had previously only been recorded from the Line Islands. Surprisingly, *Taeniura meyeni*, *Chromis agilis*, *Platax* species, and *Naso vlamingii* do not appear to have been recorded from the main Phoenix Islands or the central Line Islands prior to our surveys. *Abudefduf vaigiensis* is another widespread Indo-Pacific species that was not recorded from those archipelagos prior to our surveys, but our identifications need verification because of uncertainties about the ranges of that species and the similar *A. conformis* Randall and Earle, 1999, a species thought to be a Marquesan endemic (Randall, 2005) that may occur in the central Line Islands (J. Earle, BPBM, pers. comm., May 2009). Records of Gobiesocidae, Shindleriidae, and Microdesmidae from Palmyra (Boehlert and Mundy, 1993) are the first of those families for both archipelagos, as are our records of Callionymidae. In contrast, there were numerous smaller species, and several larger ones, recorded previously from the Line or Phoenix Islands that we did not observe in our surveys. For example, we did not record moringuids and atherinids from Howland and Baker, nor carapids from the Line Islands. We did not record *Centropyge nigriocellus*, *Cymolutes* species, *Parapercis* species, and several gobiid species from either archipelago. These are species that occur in habitats or that have habits that make them unavailable to census by our visual scuba surveys.

Estimates of species richness at the individual islands need to be standardized by sampling effort. In the CRED surveys the number of observers times the numbers of stations in 2000-2002, the years in which focused efforts were made to accumulate lists of all fish species present, and the years for which data are readily available in the form needed for this analysis, can serve as a crude measure of effort (Table 2). The total numbers of species observed at each island in those surveys divided by the number of observer-stations are: Howland Island = 166/38 = 4.37 sp./sta., Baker Island = 188/38 = 4.95 sp./sta., Jarvis Island = 212/32 = 6.63 sp./sta., Palmyra = 113/49 = 2.31 sp./sta., and Kingman = 212/57 = 3.72 sp./sta. For the total numbers of species recorded at each island, it is difficult to quantify the effort expended in an absolute manner because information is incomplete on the number of individual samples taken in historical collections. A crude metric of effort can be obtained from the number of expeditions to each island in which specimens were recorded. Excluding those expeditions in which only pelagic species were recorded, the numbers of species/expedition are: Howland Island = 327/14 = 23.4, Baker Island = 267/14 = 19.1, Jarvis Island = 273/14 = 19.5, Palmyra Atoll = 393/32 = 12.3, and Kingman Reef = 257/10 = 25.7. We suggest that these numbers reflect the species accumulation curves from sampling intensity, following the well-known phenomenon of declining numbers of species added to totals as sampling effort increases.

Palmyra Atoll has been the most intensively surveyed of the five islands, with the greatest number of species recorded. The number of expeditions to Palmyra was about three times the number to each of the other islands. This greater effort at Palmyra will continue now that it has a research station. Kingman Reef was the least often sampled of the five islands prior to our surveys. Although 17 expeditions recorded fishes from Kingman, only 10 reported reef or shore fishes, and of those only 8, including our surveys, listed many species. Kingman Reef is the only one of the five islands at which small or otherwise cryptic species have not been sampled.

Published records of shore fishes from the entire Line and Phoenix Island archipelagos yielded records of 647 shore-fish species from the Phoenix Islands, 587 from the Line Islands, and 647 species from both archipelagos combined. Thus, at the U.S. islands we recorded about 78% of the known shore-fish fauna of these island groups. The remaining 22% of the region's species may be found at the U.S. islands with either better sampling of a greater variety of habitats or with the passage of time during which species from nearby islands may recruit there. The U.S. Line and Phoenix Islands are small with limited habitat area. This, according to island biogeography theory (MacArthur and Wilson, 1963), prompts the prediction that populations of some fish species there are transitory, appearing and disappearing in part due to chance events of colonization and local extinction. Such changes may become more frequent as strengthening signals of global climate change are increasingly overlain on environmental changes from El Niño and La Niña events, and decadal regime shifts (Munday et al., 2008). We, therefore, hypothesize that the populations of the least abundant inshore-fish species at these small central Pacific islands will be unstable in the coming decades.

It was surprising that we could not find previously published records at the Line and Phoenix Islands for certain conspicuous species for which we had anticipated reports. These included a number of the best known, distinctive, and widespread fish species for which recent taxonomic revisions have not been needed: *Galeocerdo cuvier*, *Taeniura meyeni*, *Aulostomus chinensis*, *Fistularia commersonii*, the echeneidid species, many Carangidae, *Aphareus furca*, *Aphareus rutilans*, *Aprion virescens*, *Pristipomoides filamentosus*, *Monotaxis grandoculis*, *Gomphosus varius*, *Hemigymnus fasciatus*, *Novaculichthys taeniourus*, *Oxycheilinus unifasciatus*, *Pseudodax moluccanus*, many scarid species, *Exallias brevis*, *Zanclus cornutus*, *Sphyraena qenie*, *Bothus mancus*, most of the balistids, *Aluterus scriptus*, *Amanses scopas*, *Cantherhines dumerilii*, *Arothron hispidus*, and *A. meleagris*. Distribution maps and range descriptions for these species usually only give ranges as a general area, without specific records from individual islands or archipelagos except at the species' distributional limits.

Family Composition

There are 75 fish families recorded from the U.S. Line and Phoenix Islands, including 7 with only epipelagic species. At the familial level, the fauna is typical for the Indo-Pacific. The most species-rich families were the Labridae (51 species), the Pomacentridae and Acanthuridae (each with 34 species), and the Muraenidae and Gobiidae (each with 32 species). Other families represented by more than 10 species were the Epinephelidae (29 species), Chaetodontidae (26 species), Blenniidae (22 species), Scaridae (18 species), Apogonidae (16 species), Holocentridae and Carangidae (15 species each), Balistidae and Scorpaenidae (14 species each), and Lutjanidae and Pomacanthidae (11 species each).

Williams et al. (2006) found that the Gobiidae, Labridae, Pomacentridae, and Apogonidae were the most species-rich families at Wallis Island. Our results for the Line and Phoenix Islands differ most noticeably by the lower number of gobiids and apogonids, and the higher numbers of epinephelids, muraenids, and acanthurids. The gobiids and apogonids are mostly small, cryptic species which were likely undersampled by our survey techniques. In contrast, most of the epinephelid and acanthurid species at the U.S. islands were likely recorded in our surveys because those fishes are large and diurnally active. Even so, some aspects of the rankings may reflect real biogeographic patterns. The Muraenidae ranks higher in relative species richness in the Hawaiian Islands than elsewhere (Randall, 2007), and its high ranking at the U.S. Line and Phoenix Islands may reflect a gradient in familial species richness northeastward in the central Pacific. The Gobiidae and Apogonidae have demersal eggs and, in the case of the former family, species with larvae often found primarily close to shore (Leis, 1991; Kobayashi, 1989; Boehlert and Mundy, 1993). Their lower relative rank in species richness at isolated archipelagos in the central Pacific, compared to less isolated archipelagos of the western Pacific, may be real, reflecting reduced dispersal ability (J. Williams, NMNH, pers. comm., 19 April 2007).

Sampling Biases in Our Surveys

The absence in our surveys of some species, from the Line and Phoenix Islands, recorded by others may be due in part to the focus of our efforts on moderately shallow reef habitats. We likely missed almost all sand-dwelling species such as *Cymolutes praetextatus*, *Iniistius* species, *Parapercis* species, many microdesmids, most burrowing gobiids, callionymids, bothids, and samarids. We also did not record deeper-dwelling reef species such as *Pseudanthias aurulentus*, *Bodianus sepiacaudus*, or *Pseudocheilinus ocellatus*.

Many of the littoral species collected in numbers by early expeditions to these islands were absent or rare in our observations because we did not survey shallow shoreline habitats well. Examples of such littoral species include *Gymnothorax pictus*, *Epinephelus socialis*, *Chrysiptera glauca*, *Abudefduf septemfasciatus*, and *Abudefduf sordidus*. The numerous specimens of *Gymnothorax pictus* in older collections may be due to its shallow, often intertidal, habitat. Intertidal observations were not made in our surveys.

Williams et al. (2006) found at Wallis Island that the Carangidae, Caesionidae, Lethrinidae, Chaetodontidae, Scaridae, Scombridae, and Tetraodontidae were recorded only in visual scuba surveys and not with rotenone or spear sampling. These families were among those that we found to be well sampled by our visual surveys.

Most of the species known from the Line and Phoenix Islands that we did not record at the five U.S. islands were small, nocturnal, or otherwise cryptic species. A few cryptic species recorded in our surveys were only represented by larvae collected in plankton tows around Palmyra Atoll in 1990 and 1992. These included species in the Bythitidae, Gobiesocidae, Gobiidae, Microdesmidae, and Schindleriidae. Williams et al. (2006) found that about 43% of the fish species that they recorded from Wallis Island were only sampled by rotenone collections. Those species were primarily in the Muraenidae, Ophichthidae, Bythitidae, Antennariidae, Holocentridae, Scorpaenidae, Apogonidae, Creediidae, Blenniidae, Gobiesocidae, and Gobiidae. In the western North Atlantic, where the fish fauna is less similar to the Line and Phoenix Islands than that of Wallis Island, rotenone collections revealed that otherwise unsampled cryptic species comprised 45.5% of the fish fauna of Navassa Island (Collette et al. (2003) and about 56% at Buck Island National Monument, St. Croix, U.S. Virgin Islands (Smith-Vaniz et al., 2006). The results of Collette et al. (2003), Williams et al. (2006), and Smith-Vaniz (2006) suggest that the 22% of the Line and Phoenix Islands fauna not sampled by our visual surveys may greatly underestimate the number of cryptic species still to be discovered at these islands.

Samples of small, nocturnal, or otherwise cryptic fish species from the Line and Phoenix Islands would increase our understanding of the fish assemblages there and the biogeography of the region's ichthyofauna. Rotenone sampling has been advocated as the most suitable method of collecting these species (Collette et al., 2003; Smith-Vaniz, 2006; Williams et al., 2006; Robertson and Smith-Vaniz, 2008) despite popular antipathy to its use from misconceptions about its effects and the persistence of its impacts (Robertson and Smith-Vaniz, 2008). Conservation management of the five U.S. islands as U.S. Fish and Wildlife Service wildlife refuges prohibits the use of rotenone or other ichthyocides for sampling there, based on the strong effort to minimize anthropogenic damage to coral reef habitats in the refuges. Knowledge of the diversity of the entire fish fauna of the Line and Phoenix Islands will, therefore, necessarily come from islands that are not U.S. wildlife refuges. As a result, the extent of fish diversity at the U.S. Line and Phoenix Islands can only be inferred, not known.

Identification Problems

There are a number of taxa recorded in our surveys and in published papers that have problematic identifications, described in more detail in supporting materials for this paper available from the first author. They include the following.

We have doubts about the validity of our early records of *Tylosurus crocodilus*. Misidentified *Myripristis earlei* are probably conflated in our records of *M. berndti* (*fide* J. Earle, BPBM, pers. comm., May 2009). We are not confident in many cases of our visual identifications of spotted *Epinephelus*, including *E. hexagonatus*, *E. howlandi*, *E. macrospilus*, *E. melanostigma*, *E. merra*, *E. polyphekadion, E. spilotoceps*, and *E. tauvina*. We are also uncertain about our identifications of black-striped *Ostorhinchus* species seen in our surveys, with potential for confusion of *O. angustatus, O. novemfasciatus*, *O. nigrofasciatus*, and *O. taeniophorus*. Verification is needed of our records of *Pterocaesio marri*. We followed Randall (2005) in considering *Pempheris otaitensis* Cuvier to be a synonym of *P. oualensis* Cuvier, although we are now aware that Mooi (2001) considered the two species to be distinct. We, therefore, may have misidentified the *Pempheris* in our surveys. We may have misidentified *Paracirrhites nisus* among the *P. arcatus* in our surveys, although all of our voucher photographs of *Paracirrhites* that might have been either species are clearly identifiable as *P. arcatus*, and the two are visibly distinct when seen underwater (J. Earle, BPBM, pers. comm., May 2009). Brown or gray damselfish in our surveys were difficult or impossible to identify. We are, therefore, not confident of our records listed as unidentified *Stegastes* or *Pomacentrus* species, unidentified *Stegastes* species, *S. fasciolatus*, *S. nigricans*, and *S. punctatus*. These may have been any of those species or even indistinctly marked *Chrysiptera*. Likewise, there is potential for misidentification in our records of small brownish damselfish with white bars or blotches on the body and tail, including *Chrysiptera biocellatus*, *Chrysiptera brownriggi*, *Plectroglyphidodon leucozonus*, and perhaps *Stegastes albifasciatus*. The predominance of records of *Oxycheilinus digrammus* and *O. unifasciatus* during different years in our visual records indicates potential misidentifications of these similar species. Our records of *O. digrammus* might have been of young *O. unifasciatus* (J. Earle, BPBM, pers. comm., May 2009). Moderately large, round-headed *Acanthurus* seen on many occasions in the water column offshore of our sampling transects were usually identified *A. mata* but were also recorded as *A. nubilus* (Fowler and Bean, 1929); we now assume that these were all *A. mata* but this needs further investigation. *Acanthurus nubilus* has otherwise not been reported from east of the Marianas in the Northern Hemisphere (Randall, 2001b). We are also uncertain about the identifications of large, dark, demersal *Acanthurus* that were seen from distances that likely obscured diagnostic color patterns. The identification of small *Pervagor* species that were seen briefly as they swam into cover is problematic; we recorded both *P. marginalis* and *P. janthinosoma* on our data sheets but list only *P. marginalis* here based on the ranges reported by Hutchins (1986) and Randall (2005). The white-spotted, blackish *Canthigaster* species seen in our surveys were assumed to have been *C. janthinoptera* instead of *C. jactator* or *C. punctatissimus*, but voucher specimens or photographs were not obtained to verify these identifications.

There was one fish that we could not identify at all, even though a reasonably good voucher photograph was obtained. This was a small blue and gold percoid that was actively darting in the water column. This fish was most similar to, and may have been a juvenile of, *Caesio teres*, but its behavior, including flitting in the water, was more similar to an anthiin serranid. It was also solitary, not in a school as expected of *C. teres.* The possible identity of this fish could not be determined despite inquiries with several ichthyologists familiar with the fauna of the region (e. g., J. Randall, BPBM; R. Pyle, BPBM; K. Carpenter, Old Dominion Univ., pers. comm., 2006 and 2007).

Genera needing revision before the identities of specimens from the U.S. Line and Phoenix Islands can be determined include *Moringua*, *Kaupichthys*, *Anarchias*, *Fowleria* and *Trimma*. Although central Pacific species in the the goby genus *Eviota* were revised by Lachner and Karnella (1980) and Jewett and Lachner (1983), additional review is needed because of the continued discovery of new species and questions about the identities of museum specimens from the U.S. Line and Phoenix Islands.

Questions about historical records include the following. What species was recorded by Greenfield (1974) from the Line Islands as *M. parvidens*? What was the species reported by McDermond and Wass (1986) from Howland Islands as *Epinephelus maculatus*, and does *E. maculatus* occur at the Line or Phoenix Islands, where it has not previously been recorded? What was the species reported from Palmyra Atoll by Fowler (1938) as *E. malabaricus* non (Bloch and Schneider, 1801), a species otherwise not known from east of the Solomon Islands along the equator, nor north of Fiji and Tonga in the central Pacific Ocean (Randall and Heemstra, 1991)? Were Fowler's (1927, 1938) reports of *Chaetodon trichrous* from the Line Islands valid or misidentifications of the similar *C. kleini*? Was his (1938) report of *Scomber japonicus* valid? Finally, in conjunction with Fowler's publications (Fowler and Ball, 1925; Fowler, 1927), the identities of Line and Phoenix Island chubs in the *Kyphosus bigibbus* group (sensu Sakai and Nakabo, 2004) remain puzzling (Randall, 2004a). Records of *K. bigibbus* and *K. fuscus* from the U.S. Line and Phoenix Islands are herein provisionally listed as *K. hawaiiensis*, but more work needs to be done on the identification of *Kyphosus* species from the central Pacific islands.

BIOGEOGRAPHIC RELATIONSHIPS

The Species Definition Problem

Our analysis of central Pacific shore-fish biogeographic patterns, reliant on the tabulation of species, is subject to uncertainties arising from changes in how species are defined. A recent trend by ichthyologists increasingly identifies numerous species with restricted distributions from geographic populations within what had previously been recognized as widespread species (e. g., Gill and Kemp, 2002). This is partly due to the availability of more specimens from more areas, which allows improved empirical understanding of morphological differences among populations, but it is also partly due to changes in the definition of "species" (Isaac et al., 2004). The literature on species concepts is too voluminous and contentious to be reviewed here, but it has resulted in several competing theories about what the systematic level "species" is and how it should be defined (e. g., Wheeler and Meier, 2000; K. de Quiroz, 2005). Nevertheless, the practices of most recent ichthyologists working on Indo-Pacific shore fishes appear to conform with Cracraft's (2002) suggestion that, regardless of which species definition they favor, taxonomists are converging on the practical solution of recognizing species as the smallest clusters of populations in which individual specimens can be reliably diagnosed as distinct from individuals from other clusters. Emphasis on the smallest clusters leads to a recognition of greater numbers of species, often with limited geographic ranges (Isaac et al., 2004). This concept corresponds approximately with the secondary level of diagnosable species in K. de Queiroz's (2005) unified lineage species concept. This is the level at which nonexclusive species diagnoses are avoided (McCabe, 2008), a condition regarded by us as useful even though it was explicitly rejected as a consequence of K. de Queiroz's (2005) unified species concept. For Indo-Pacific shore fishes the trend toward recognizing species as the smallest clusters of populations that can be exclusively diagnosed as distinct has perhaps been given its most extreme advocacy by Gill (1999) and Gill and Kemp (2002). They argued that all subspecies or other diagnosable geographic variants of shore-fish taxa should be recognized and named as full species. But, as has long been recognized, the variability in relative character-state frequencies in populations of Indo-Pacific species, as a likely consequence of the different temporal positions of populations in their evolutionary trajectories, makes this extreme position operationally less useful than Gill (1999) and Gill and Kemp (2002) advocate.

The present state of Pacific shore-fish taxonomy includes recognition of a gradient of diversification among populations, subspecies, and species that reflects an acceptance of evolution as a continuing process at varying stages of differentiation within clades. Populations that have diverged in character states to the point at which they can be consistently and unequivocally diagnosed are recognized as distinct species. Populations that have diverged to points at which only the majority of individuals can be diagnosed, or populations that are diagnosed by statistical analyses such as by mean or modal values of counts, are usually recognized as subspecies, varieties, or unnamed morphs. Some are simply described as having geographic differences that may be clinal or that have phenotypic differences maintained by selection pressures despite gene flow among the populations. We argue that the resolution of all taxa to absolutely distinct species or even completely diagnosable subspecies is incongruent with an acceptance of evolution as an active and ongoing process, regardless of which species concepts are used. Although most Indo-Pacific shore-fish taxa may be at periods of stasis in cladogenesis (Gould, 2002), there is good evidence that some taxa are at various stages in cladal differentiation that may, or may not, result in their speciation. The range of differentiation in species integrity from incipient to complete is predicted if, as Rocha and Bowen (2008) have argued, parapatry is the prevalent mode of speciation for reef fishes.

The full range of operational and theoretical interpretations of species definitions can be found in fishes from the U.S. Line and Phoenix Islands. These include several examples of how the increased availability of larger sample sizes from various archipelagos have allowed what were previously considered individual variants of a single, widespread species to be identified as diagnosable species with more restricted ranges. Sometimes the subtle differences between specimens described as species from different archipelagos are at levels of distinctiveness that would have been considered geographic variants of single species in earlier times. For instance, Greenfield (2001) was able to disentangle the identification of an "*Apogon erythrinus*" species group from other species of cardinal fish with which the clade had been confused, and describe three new species in the clade. He restricted *A. erythrinus* to the Hawaiian population as an endemic species, described a Marquesan endemic *A. marquesensis*, and described two species found at the Line and Phoenix Islands, a Pacific Plate endemic *A. susanae*, and an Indo-west/central Pacific species, *A. indicus*. But the last species had a mosaic of geographic character variability that Greenfield (2001) could not use for further taxonomic division.

In an analysis that found somewhat less subtle diagnostic characters, Hutchins (1986) distinguished six similar species of *Pervagor*, two of which he described as new, that had usually been identified as wide-ranging *P. melanocephalus*. Of these, *P. marginalis* is a Line Island and Marquesan endemic. Hutchins (1986) mentioned that "Due to the presumed close relationship between *Pervagor marginalis* and the allopatric *P. aspricaudus*, some researchers might prefer to recognize these taxa at the subspecific level only. However, specimens of *P. aspricaudus* examined during this study from widely separated insular localities … show no significant variation. It is the opinion of the author that the differences between *aspricaudus* and *marginalis* presented above are specific in magnitude."

For the hogfish genus *Bodianus*, Gomon (2006) recognized three closely related species in the subgenus *Paralepidaplois*, including the Line and Phoenix Islands endemic, *B. prognathus*. He commented "*Bodianus prognathus* may represent a relatively recent divergence resulting from the isolation of a small population of the ancestral form common to *B. dictynna* and it, or … all three of the species in the subgenus. If so, it demonstrates the rapidity with which morphological variation can occur." Note, however, that Gomon (2006) only had data on the morphological degree of divergence among these species, and not on its rate, to support a conclusion about timing.

Winterbottom and Burridge (1989) studied populations of what had previously been recognized as a widespread Indo-Pacific goby species, *Priolepis cincta*, and described specimens from the Line and Phoenix Islands to French Polynesia as *P. squamogena*. In that description, they noted that "Of the nontype material, the Howland Island specimen and the two specimens from Kiritimati, Line Islands, may represent different species." Randall (2005) also recognized *P. squamogena* as distinct from *P. cincta*, but commented "Some might prefer to regard *P. squamogena* as a subspecies of *P. cincta*, differing chiefly in having scales on the cheek."

Randall and Clements (2001) provided one of the clearest examples of more restricted biogeographic distributions resulting from a splitting of species within a previously recognized single, widespread species. They recognized four almost allopatric species among populations of what had previously been regarded as *Ctenochaetus strigosus*. They restricted *C. strigosus* to the Hawaiian Islands population as an endemic species, resurrected *C. flavicauda* as a central-south Pacific endemic known from the Phoenix Islands southeast into the Pitcairn group, described *C. cyanocheilus* as a new species with a range from the eastern Indian Ocean to the Phoenix Islands and Samoa, and described *C. truncatus* as a new Indian Ocean species.

One of the earliest and most enduring recognitions of subspecies in Pacific shore fishes, for *Acanthurus triostegus*, used Line and Phoenix Islands specimens to support its argument. Based on differences in the color pattern below the pectoral-fin base, Schultz and Woods (1948; as discussed in Schultz and Woods in Schultz et al., 1953) recognized the subspecies *A. t. sandvicensis* from the Hawaiian Islands, *A. t. marquesensis* from the Marquesas, and *A. t. triostegus* from elsewhere in the Indo-Pacific. Specimens from the Phoenix Islands had pectoral-fin base markings that included variations seen in all three subspecies, as well as intermediate states. The Phoenix Islands specimens were used to argue that incomplete but clearly evident morphological differentiation indicated evolution to a point at which subspecies, but not distinct species, could be recognized. Although *A. sandvicensis* has sometimes been recognized as a full species, the conclusion of Schultz and Woods (1948) was accepted by the subsequent, more detailed research of Randall (1956, 2001b). However, Lessios and Robertson (2006) presented evidence that the genetic divergence of *A. t. sandvicensis* from eastern Pacific and Line Islands *A. t. triostegus* populations is at a level found between species in other genera.

At a different point along the species-definition spectrum, Gill and Kemp (2002) gave *Epinephelus fasciatus* as an example of a taxon currently considered to be a single species that might be split into several species. They noted that in the last review of the genus, Randall and Heemstra (1991) recognized six diagnosable geographic forms. The latter authors stated that “It is clear that the population of *E. fasciatus* on the Pacific Plate has diverged from elsewhere, but in our opinion not at the species level” and they also considered the Marquesan population similarly differentiated. Randall and Heemstra (1991) concluded that “In our opinion more material and more exhaustive study are needed before attempting to recognize any of these populations nomenclaturially [sic].”

In an example that resulted in a conclusion counter to the prevailing trend to recognize geographically restricted species among populations of a formerly recognized widespread species, McMillan et al. (1999) argued that the butterflyfish species pair *Chaetodon punctatofasciatus* and *C. pelewensis* are populations divergent in phenotype in which color differences are maintained by selection pressures despite a lack of genetic isolation. They concluded that continued recognition of the color variants as distinct species was impossible “under most current species definitions”, a recommendation accepted by Smith et al. (2003), who synonymized the species. This example demonstrates how the “recognition concept” for species definition discussed by Cracraft (2002) has failed to resolve the old problem of creating a definition for the concept “species”. In the example of *C. punctatofasciatus/pelewensis*, opposing conclusions about the status of the two species are largely due to the criteria, genetic vs. phenotypic, used to identify the smallest clusters of populations in which individual specimens can be reliably diagnosed as distinct from individuals from other clusters. This problem, therefore, continues to affect biogeographic analysis by use of techniques of species inventories and analyses of the ranges of endemic species.

A last example also illustrates the occasional discrepancy between changing morphological species concepts and the results of genetic analysis of population relationships. *Dascyllus auripinnis* was described by Randall and Randall (2001b) for

Line, Phoenix, and northern Cook Islands populations that had been regarded as a color variant of the widespread Indo-Pacific *D. trimaculatus*. Bernardi et al. (2002, 2003) examined genetic relationships of four species in the *Dascyllus trimaculatus* clade, including *D. auripinnis*, and found that *D. auripinnis* specimens were nested within one of three clades of *D. trimaculatus* that might be interpreted as a cryptic species of the latter. This indicates that *D. auripinnis* and *D. trimaculatus* are not monophyletic species. Bernardi et al. (2002) suggested three hypotheses that might explain this result: that *D. auripinnis* is not a valid species, but is only a phenotypic variant of *D. trimaculatus*; that the two species are valid but have hybridized with consequent genetic introgression, or; that *D. auripinnis* is the result of a recent speciation event with incomplete lineage sorting with respect to *D. trimaculatus*. They mentioned that the sympatry of nominal *D. auripinnis* with *D. trimaculatus* at Penrhyn and Suwarrow, northern Cook Islands, might be taken as evidence for their status as distinct species, presumably based on the biological species concept, with the implication that their second or third hypotheses would be favored. Bernardi et al. (2003) commented that if hybridization of the two morphospecies is occurring at Penrhyn and Suwarrow Islands, their relative abundance suggests that the *D. auripinnis* haplotypes would likely introgress those of *D. trimaculatus*.

In the *Dascyllus trimaculatus* clade, the lack of concordance between color phenotypes diagnostic for nominal species and genetic population structure is very similar to the lack of concordance found by McMillan et al. (1999) for the nominal *Chaetodon pelewensis* and *C. punctatofasciatus*. The confusing results of these genetic analyses are an indication of the variety of stages in evolutionary histories in which lineages of Indo-Pacific shore fishes exist. Rocha et al. (2007) suggested that in such cases, color and morphological differences diagnostic for morphospecies can evolve without congruent changes to the portion of the genetic sequences used in phylogeographic studies to identify genetic species. They suggested that divergence due to adaptation to local conditions and disruptive natural selection in combination with assortative mating might be two possible explanations for this discrepancy. In particular, they suggested that analysis of gene sequences related to color might be necessary to investigate the relation of morphospecies to genetic species in coral reef fishes.

Rocha et al. (2007) also mentioned that some of the incongruent matches of genetic lineages with morphological differentiation may be due to hybridization. This is pertinent to hybridization processes in reticulate patterns of evolution like those proposed for reef-building corals (Veron, 1995), in which lineages diverge and then rejoin. Reticulate evolution has received less attention for fish species than for corals, but it is consistent with the parapatric mode of speciation suggested as the dominant mode for reef fishes by Rocha and Bowen (2008). Rocha et al. (2007) commented that mtDNA may flow easily between species in hybrid contact zones, and that phylogeographic patterns found in mtDNA analyses may not correspond to the evolutionary history of populations that hybridize, but merely to the history of the mitochondria. Their conclusion was that mtDNA should not be solely relied upon when hybridization is suspected, and that nuclear DNA should also be analyzed. By inference, this would be particularly important for species in which reticulate evolution is a possibility. Reliance on mtDNA alone would only track maternal contributions to lineage histories, while a combination of mtDNA and nuclear DNA might allow for identification and understanding of genetic mosaics among populations that could indicate potential lineage divergence and merging.

General Distribution Patterns

Widespread Indo-Pacific taxa dominate the fish fauna of the U.S. Line and Phoenix Islands, comprising 69.1% of the species. These species' ranges extend from the Indian Ocean (usually from east Africa) to the central South Pacific (usually to French Polynesia). The dominance of Indo-Pacific species has been found in surveys of shore fishes throughout the Pacific (Randall, 1998b). A smaller component of the fauna, with 9.9% of the species, is comprised of taxa found from the eastern Indian Ocean through the central Pacific. These may be Pacific species that have dispersed into the fringes of the eastern Indian Ocean (Read et al., 2006). Only 3.8% of the species are circumtropical found in the Atlantic, Indian, and Pacific Oceans. Most of these are semi-pelagic species such as *Aluterus scriptus*, *Elagatis bipinnulata*, and *Melichthys niger*. A small portion (1.8%) is too poorly known to state species' general distributions with confidence. Most of these are cryptic species that are not well sampled anywhere. *Gunnellichthys* species are an example, for which the alpha taxonomy is reasonably well known but which have been recorded from Palmyra Atoll only as larvae unidentified to species.

The remaining 15.4% of the species are Pacific endemics. One species, *Sectator ocyurus*, is an eastern Pacific endemic that disperses to the central Pacific. Wide-ranging Pacific Ocean species, with distributions from Asia to the central South Pacific that cross boundaries of tectonic plates and ocean-current gyres, comprise 53.8% of the Pacific endemic component (8.3% of all species present). Examples are *Myripristis amaena* and *Chaetodon reticulatus*. Most of the Pacific endemics, 41.0% (6.3% of all species), are restricted to the Pacific tectonic plate (see Springer, 1982). Examples are *Pseudanthias bartlettorum* and *Apolemichthys xanthopunctatus*. Of the Pacific Plate endemics, 25% are restricted to the central and central-south Pacific including the Line or Phoenix Islands, some or all of French Polynesia, and sometimes the Cook Islands or the Marquesas (e.g., 10.3% of the Pacific-wide endemics; 15.8% of all species). An additional two are otherwise known as Hawaiian Island and Johnston Atoll endemic species (6.0% of the plate endemics; 2.6% of the Pacific-wide endemics; 0.4% of all species). Only two of the shore-fish species recorded in our inventory are Line or Phoenix Island endemics (6.0% of the plate endemics; 2.6% of the Pacific-wide species; 0.4% of all species).

Endemism

Six species are known from the Line and Phoenix Islands and nowhere else - a small percentage of endemic species compared to the Marquesas or the Hawaiian Islands. *Dascyllus auripinnis* would be considered a Line and Phoenix Island endemic species were it not for its occurrence in the northern Cook Islands. Of these local endemics, we recorded only *D. auripinnis*, *Bodianus prognathus* and *Coris centralis* in our inventory, although the likely undescribed species of *Pterocaesio* similar to *P. lativittata* might be another of these (J. Earle, BPBM, pers. comm., May 2009). All occur in both the Line and Phoenix Islands. We did not observe the other Line or Phoenix Island endemics: *Pseudanthias aurulentus* Randall and McCosker, 1982, *Chrysiptera albata* Allen and Bailey, 2002, *Parapercis latus* Randall and McCosker, 2002, or *Amblyeleotris harrisorum* Mohlmann and Randall, 2002.

Parapercis latus is known from both the Line and Phoenix Islands. It rests on rubble or sand at 5-55 m (Randall, 2005) and was likely not seen in our surveys because we concentrated our efforts on coral habitats. *Chrysiptera albata* is the one species known only from the Phoenix Islands. It is a small, shy species (Randall, 2005) that could have been easily overlooked in our surveys. Two of the endemic species not seen by us are only recorded from the Line Islands. *Pseudanthias aurulentus* Randall and McCosker, 1982, apparently only known from Fanning and Christmas Islands, occurs deeper than our surveys, at > 30 m (Randall and McCosker, 1982; Randall and Pyle, 2001; J. Earle, BPBM, pers. comm., May 2009). *Amblyeleotris harrisorum* lives in alpheid shrimp burrows in sandy rubble and is known only from a single collection from a steep outer reef habitat at 32 m (Mohlmann and Randall, 2002). We did not survey habitats as deep as those inhabited by *A. harrisorum*, although we do have a new record from the Line islands of its shallow-dwelling congener *A. fasciata*. All of the species now recorded as Line and Phoenix Island endemics might be found to have wider distributions once appropriate sampling is done at nearby islands and archipelagos. The two Line Island endemic species, as well as *Cirripectes auritus* and *Acanthurus leucochilus*, were not included in Randall's (2005) review of central and South Pacific fishes primarily because the northern Line Islands and Jarvis Island were excluded from the region of coverage in that volume, with only the southern outliers of the archipelago included. This leaves the northern and central Line Islands as the only central Pacific island group not included in recent reviews of central Pacific fishes (e. g., Myers, 1999; Randall, 2005; Randall, 2007).

Waifs

Individual fishes found at localities where reproducing populations of their species do not exist are variously called waifs, vagrants, or expatriates. At the U.S. Line and Phoenix Islands, examples might be *Anguilla marmorata*, *Sectator ocyurus*, and the *Platax* species. Handler and James (2006) discussed the possibility that *Anguilla marmorata* found at Palmyra Atoll may have been from a recent colonization of that island by waifs. They did not discuss whether *A. marmorata* at Palmyra has a reproducing and self-recruiting population that will persist. *Sectator* and *Platax* are moderately large, distinctive, diurnally active fishes that swim in the open and school in their native ranges. We suggest that more individuals of *Sectator* and *Platax* would have been seen in our surveys if reproductive populations existed at the U.S. equatorial Pacific islands. *Sectator ocyurus* is indigenous to the eastern Pacific, but has been recorded as waifs from localities across the Pacific Ocean, including the Hawaiian Islands, the Society Islands, Guam, and Japan (Randall and Earle, 2000; Mundy, 2005; Randall, 2007). Observations of large numbers of individuals at the Marquesas Islands prompted Randall and Earle (2000) to suggest that *Sectator* has a reproducing population there. The species is semi-pelagic, associating with floating objects as well as topography, which may explain its sporadic appearance at distant localities (Randall, 2007). *Platax* species are less well known as waifs, but individuals of questionable origin have been recorded in the main Hawaiian Islands and at Midway Atoll in the Northwestern Hawaiian Islands (Mundy, 2005; Randall, 2007). The *P. boersii* recorded from Midway Atoll during 1980 (Randall, 2007) were likely waifs. The *Platax* species reported from the main Hawaiian Islands were most likely introduced from the ornamental aquarium-fish hobby and trade, a source improbable for the uninhabited or sparsely populated U.S. equatorial Pacific islands.

The presence of waifs at Pacific islands such as the Hawaiian Archipelago and perhaps the U.S. Line and Phoenix Islands is consistent with the much-debated theory of island biogeography (MacArthur and Wilson, 1963: e. g., Brown and Lomolino, 2000; Kadmon and Allouche, 2007; Heaney, 2007). A core prediction from that theory is that the species composition at islands will vary somewhat over ecological time scales. Populations of some species will disappear and new colonizers will arrive, although populations of many species will persist through great periods of time (Heaney, 2007). Thus, the shore-fish species inventory at the U.S. Line and Phoenix Islands can be expected to change naturally, at least for rare species more at risk for local extinction and for species with good colonization abilities that can sporadically disperse to these islands.

There is evidence that the dispersal of waifs is influenced by climatological changes including El Niño and La Niña events (Robertson et al., 2004). For the years of our surveys, neither 2000 nor 2001 were El Niño years (Howell and Kobayashi, 2006), but an El Niño event began in May-July 2002 and reached its peak in October 2002 through January 2003 (McPhaden, 2004). Our surveys were done in January-February of that year, prior to the development of the El Niño conditions. Oceanographic changes in the region during El Niño, La Niña, and intermediate years were discussed by Johnson et al. (2002). These might have affected species composition for interannual comparisons, particularly recruitment of waifs, at the five equatorial Pacific islands. Concerns about this for our inventory are diminished by the probable time lags between these physical changes and their biotic effects, within the few years of our surveys. Continued monitoring of these islands may detect changes in species composition and community structure due to interannual climate and oceanographic effects.

Introduced Species

In biogeographic studies, the possibility must now be considered that not all of the species found are native. The increasing introductions of nonindigenous species by human activity in the past century makes it likely that some of the ranges found for organisms result from human transportation, rather than natural dispersal and colonization (e. g., Coles and Eldredge, 2002; Hutchings et al., 2002; Paulay et al., 2002). Introductions may accelerate the dynamic processes of colonization and extinction in some island environments. Chapman and Carlton (1991) suggested criteria for corroboration of the identification of species as introduced: 1) whether the species is previously unknown in the region, 2) if the species has a post-introduction range expansion, 3) if there is a probable method of human introduction, 4) if the species is associated with other known introductions, 5) if the species is associated with new or artificial environments, 6) if the species has a discontinuous regional distribution, 7) if the species has a disjunct global distribution, 8) if the species has insufficient life history adaptations for global dispersal, 9) if there are insufficient passive global dispersal mechanisms to explain the distribution, and 10) if the species has an "exotic evolutionary origin." These are alternative criteria and not all are necessary to corroborate an introduction.

Omobranchus rotundiceps obliquus is widely distributed in a variety of nearshore habitats of the western Pacific from the Mariana Islands south through the Philippines and eastern Indonesia, and eastward to Fiji and Samoa. This species is known on the Pacific tectonic plate only from harbors of O`ahu and Palmyra Atoll (Springer and Gomon, 1975). It meets at least half of the ten criteria that identify nonindigenous species. Blennies such as *O. r. obliquus* are associated with fouling communities and can be transported to boat harbors such as those of Oahu and Palmyra by ship traffic (Mundy, 2005; Randall, 2007; criterion 3). The western lagoon at Palmyra Atoll, the only location in the Line or Phoenix Islands where *O. r. obliquus* has been found, was dredged into a military harbor in World War II, and was a favorite stopping point for yachts sailing across the Pacific (Grigg et al., 1988; Keating, 1992; Maragos, 1997; Maragos et al., 2008; criterion 5). The species has a disjunct distribution, with no collections eastward of the Marianas, Yap, Palau, Vanuatu, Fiji, or Samoa except those from harbors of Palmyra and O`ahu (criteria 6 and 7). The species has demersal eggs, and in the Hawaiian Islands, has apparently been unable to disperse from the island of its introduction (Randall, 2007; criteria 8). Strasburg (1956) and Englund and Baumgartner (2000) suggested that *O. r. obliquus* is an introduced species at O`ahu. Based on the isolation of the *O. r. obliquus* populations at O`ahu and Palmyra from the next nearest populations, and on the limitation of those populations to boat harbors, we suggest that this species is also introduced at Palmyra Atoll, perhaps even from the population at O`ahu. This raises the possibility that other small, cryptic fishes at the five equatorial Pacific islands could also have been introduced by transportation on ship or boat hulls, given the military activity there during World War Two and yacht or fishing vessel traffic thereafter. Transport of organisms in hull-fouling communities and in ballast water is well-documented vectors for the introduction of organisms. Blennioids, gobioids, and pomacentrids are the groups that have the best-documented history of such introductions at other Pacific islands (Myers, 1999; Mundy, 2005; Randall, 2007). In contrast, and unlike at the Hawaiian Islands, there is no evidence of introductions for larger, non-benthic fishes at these islands.

Comparison of Shore-fish Species Numbers to Those of Other Pacific Islands

The numbers of shore-fish species that we record from the U.S. equatorial Pacific islands are similar to those at other islands of their size and location in the Pacific (e.g., Fig. 2 of Randall, 1998b; Fig. 7 of Myers, 1999). The U.S. equatorial Pacific island numbers are at the low end of the range for localities investigated to date with the notable exception of Easter Island, the most distant Indo-Pacific location for which numbers were available (129: Randall et al., 2005). Other islands with similarly low numbers of shore-fish species include, by increasing numbers of species, Midway Atoll (266: Randall et al., 1993; Myers, 1999), Rapa (268: Randall et al., 1990), Johnston Atoll

(285: Kosaki et al., 1991; Myers, 1999), Wake Atoll (321: Lobel and Lobel, 2004), and the Pitcairn Islands (335; Randall, 1999c). The Gilbert Islands (Kiribati) have only 396 shore-fish species recorded, but that archipelago has not been resurveyed since Randall (1955a) and more species will undoubtedly be found there with more intensive sampling. For comparison, recent estimates of the numbers of shore-fish species at other Pacific islands are: 415 at the Marquesas (Randall and Earle, 2000); 425 at Rotuma (Zug et al., 1988); 622 at the Hawaiian Archipelago (Randall, 2007); 633 at the Society Islands and Tuamotu Archipelago (Myers, 1999); 647 at the Phoenix Islands (Schultz, 1943; Stone et al., 2001; Obura and Stone, 2003); 648 at Wallis Island (Williams et al., 2006); 653 at Ouvéa Atoll near New Caledonia (Kulbicki and Williams, 1997); 801 at the Ogasawara Islands (Randall et al., 1997); 915 at the Samoa Islands (Randall, 1998b); 919 at Fiji (Myers, 1999; but this number will increase greatly as the results of recent surveys by D. Greenfield, J. Randall, and others are published); 936 at the Marshall Islands (Myers, 1999; Randall et al., 2005); 1118 in the Caroline Islands (Randall, 1998b); 1162 at Tonga (Randall et al., 2003); 1106 at the Mariana Islands (Myers and Donaldson, 2003); 1387 at Palau (Myers, 1999); and 1610 at New Caledonia (Myers, 1999). The low number of shore-fish species at the U.S. equatorial Pacific islands is consistent with Connolly et al.'s (2003) finding that shore-fish species richness in the mid-Pacific is lower than that predicted by the null hypothesis mid-domain model for species-richness gradients in the Indo-Pacific. This finding is also congruent with Springer's (1982) identification of distinct Indo-West Pacific and Pacific Plate components to the Indo-Pacific shore-fish fauna, in which many species have ranges that do not extend to oceanic islands of the plate.

Distance along the Indo-Pacific diversity gradient, isolation from other islands, small area, restricted habitat diversity, island age, and the evolutionary histories of the clades represented are factors often identified in island biogeography as primary influences on species richness (e. g., Connolly et al., 2003; Bellwood et al., 2005; Kadmon and Allouche, 2007; Ricklefs, 2007; Whittaker et al., 2008).

Indo-Pacific shore-fish species numbers decline with increasing latitudinal and longitudinal distance from a region of greatest species diversity that includes Indonesia, the Philippines, New Guinea, and the Solomon Islands (Randall, 1998b). That region is variously called the East Indies triangle (Briggs, 2000), the Indonesian and Philippine region (IPR; Mora et al., 2003), Indo-Malay-Philippines Archipelago (IMPA; Carpenter and Springer, 2005), or Indo-Australian Archipelago (IAA, used hereafter; Connolly et al., 2003; Bellwood et al., 2005). The numbers of shore-fish species recorded at each of the U.S. Line and Phoenix Islands are at the low end of the range for all Pacific islands or archipelagos for which species inventories exist. Even so, the numbers recorded at the U.S. equatorial Pacific islands (257–393) are nested among those of the less diverse islands at the distance at which they reside from the IAA (Fig. 7). The r^2 for the relationship of distance from the IAA to species numbers was 0.68, indicating a strong effect of distance relative to isolation and island age discussed below.

Isolation of islands from continents and other islands limits colonization rates, according to the island biogeography theory of MacArthur and Wilson (1963). To examine the relationship of isolation and species richness at the U.S. equatorial Pacific islands compared to other Pacific islands and archipelagos, species numbers were plotted against the island isolation indices of Dahl (1991). As with distance from the IAA, species numbers for the U.S. equatorial Pacific islands fell within the ranges expected for their isolated locations, although Palmyra Atoll had slightly more species than might have been expected (Fig. 8). An r^2 of 0.56 was found as a general indication of the importance of island isolation on shore-fish species numbers at Pacific islands and archipelagos, suggesting a less strong relationship than with distance from the IAA. In the central Pacific, though, distance from the IAA is related to isolation because islands become more widely separated proceeding eastward from the western Pacific.

A direct relationship between island area and species richness has long been proposed; indeed, that relationship was the starting point from which MacArthur and Wilson (1963) began their development of the classic dynamic theory of island biogeography. The U.S. equatorial Pacific islands have very small areas compared to most localites for which shore-fish species inventories have been generated. The low numbers of shore-fish species at these islands fall within the range expected for Pacific islands of such small size, although Palmyra Atoll again had slightly more species than might have been expected (Fig. 9). A linear function fit to species number versus log(area) gave an r^2 of 0.70, indicating a relationship between those parameters roughly as strong as that between species number and distance from the IAA. Island areas in the central equatorial Pacific are generally smaller with increasing distance from the IAA, though. Thus, those two parameters are not independent in the region of the U.S. Line and Phoenix Islands.

It has been suggested that area is often directly proportional to habitat heterogeneity, and that habitat heterogeneity is the true explanation for the greater species numbers at islands of larger sizes. Connolly et al. (2003) and Bellwood et al. (2005) concluded that habitat-area effects were at least partially consistent with the deviations that they found between observed latitudinal shore-fish species richness gradients, including low observed species numbers in the mid-Pacific, and the predictions of their mid-domain model's null hypothesis. The relationship between total area, habitat area, habitat heterogeneity, and species richness is not straightforward, though. In theory, increased habitat heterogeneity sometimes exists at the expense of area for each habitat within the total island area, which in turn increases risk of stochastic extinction of species within those small habitats (Kadmon and Allouche, 2007). This effect would be most pronounced at small islands. Aspects of habitat diversity at the U.S. equatorial Pacific islands that might affect species richness are discussed later, but we note here that Palmyra has greater habitat diversity than the other four islands. That may explain why Palmyra has more species than would be expected relative to numbers at other Pacific islands of comparable size and isolation.

The use of shore-fish habitat area instead of simple island area might give a more robust relationship to species number than simple island area, once those data become available. For example, Kingman Reef has a very small emergent land area, but has a shore-fish habitat area that is relatively large compared to the other four islands in our study (R. Brainard, PIFSC CRED, pers. comm.).

Whittaker et al. (2008) suggested a general model of island biogeography in which they found variation of terrestrial species richness among individual oceanic islands to be well explained by the function: log (island area) + island age + $(\text{island age})^2$

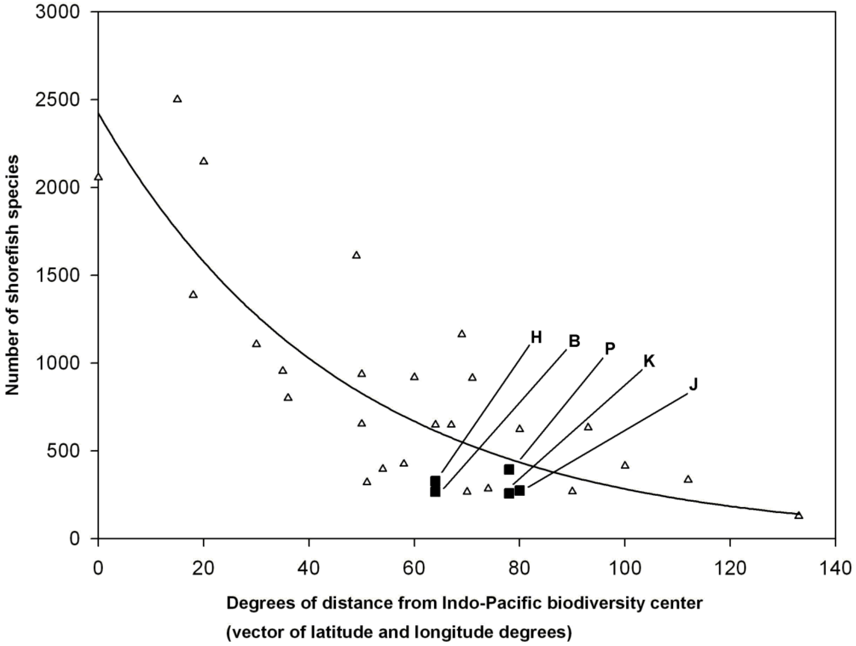

Figure 7. The relationship between the number of shorefish species recorded at Pacific islands and archipelagos, and the distance of those locations from the center of Indo-Pacific biodiversity: Indonesia, the Philippines, and New Guinea (see text for the method of distance estimation). Black squares = the U.S. Line and Phoenix Islands; white triangles = other islands and archipelagos; B = Baker Island; H = Howland Island; J = Jarvis Island; K = Kingman Reef; P = Palmyra Atoll.

(abbreviated as the ATT^2 model in their paper). We found little relationship when we plotted shore-fish species numbers against the ATT^2 model (Fig. 10), in contrast to simply plotting species numbers vs. the log (area), isolation index, or distance from the IAA. In the absence of a clearly different form to the data, a simple linear relationship was selected between the ATT^2 model and species richness. An r^2 of 0.07 resulted, which was a much weaker relationship than those found for distance from the IAA, island isolation, or island area. The lack of fit of central Pacific shore-fish species richness to Whittaker et al.'s (2008) ATT^2 model may largely be caused by our lack of data on species numbers, island ages, and shore-fish habitat areas for most individual central Pacific islands. This forced us to rely on data for entire archipelagos, likely obliterating any relationship that may exist between species numbers and the ATT^2 model at individual central Pacific oceanic islands. Complications from using conglomerate data from island groups with multiple ages of origin were discussed by Whittaker et al. (2008). Another explanation might be that Whittaker et al.'s (2008) ATT^2 model fits less well for marine organisms, with good dispersal capabilities between island groups, than it does for the terrestrial organisms for which the ATT^2 model was developed.

Similarity of the Shore-fish Fauna to That At Other Pacific Island Groups

The similarity analysis of shore-fish species composition at the U.S. equatorial Pacific islands and other central Pacific islands showed both expected and unexpected patterns (Figs. 11 and 12). The five U.S. equatorial Pacific islands were generally similar to each other in species composition (Fig. 11) as expected from their locations (Fig. 12). Howland and Baker Islands were most similar to Jarvis Island, a result

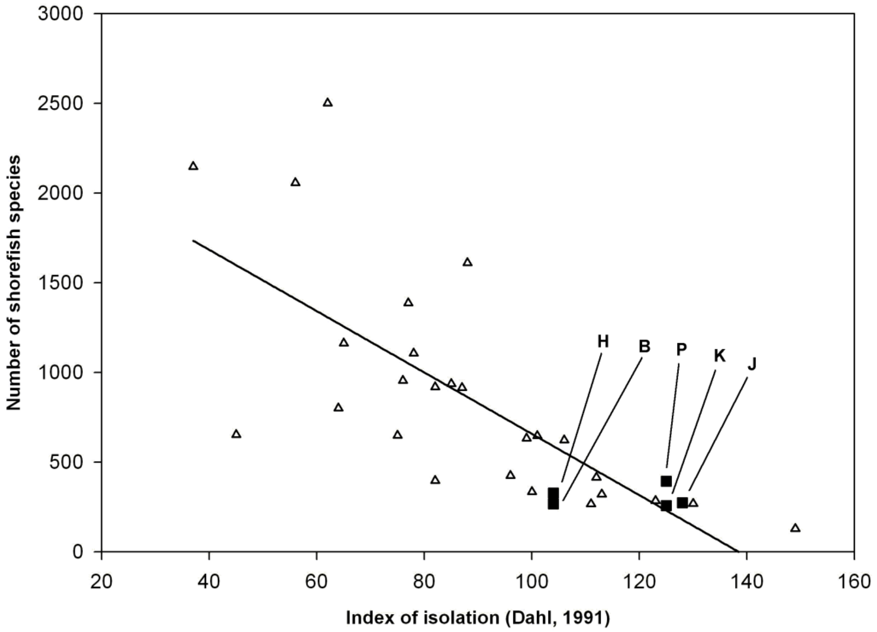

Figure 8. The relationship between the number of shorefish species recorded at Pacific islands and archipelagos, and the isolation of those locations from the other islands and continents. The measure of isolation is the value of the isolation index from Dahl (1991) for a single island or the lowest value for any island in a group. Black squares = the U.S. Line and Phoenix Islands; white triangles = other islands and archipelagos; B = Baker Island; H = Howland Island; J = Jarvis Island; K = Kingman Reef; P = Palmyra Atoll.

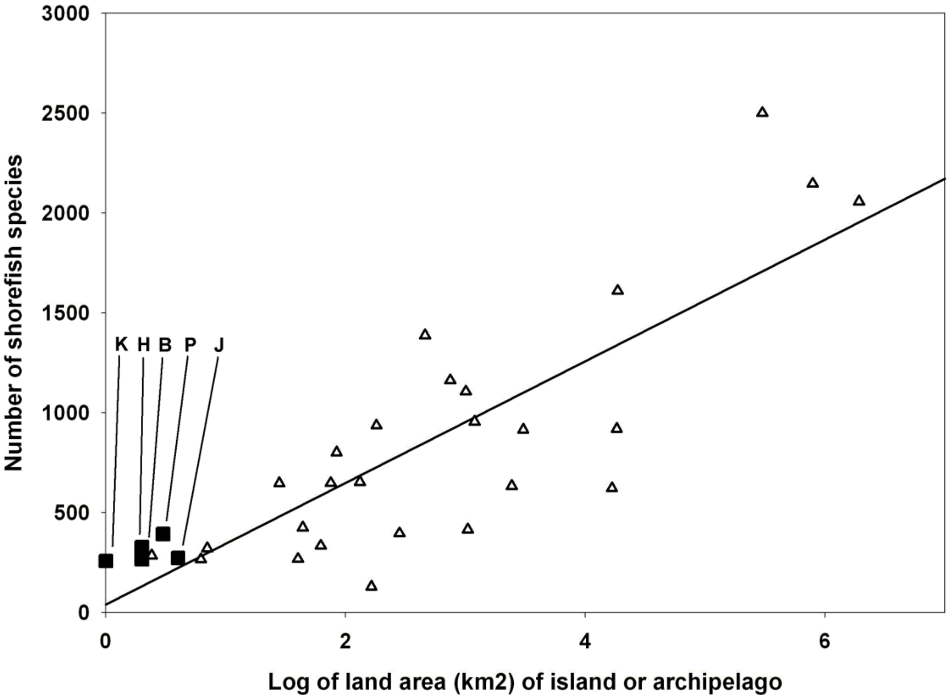

Figure 9. The relationship between the number of shorefish species recorded at Pacific islands and archipelagos, and the log10 of the land areas (km2) of those locations. Black squares = the U.S. Line and Phoenix Islands; white triangles = other islands and archipelagos; B = Baker Island; H = Howland Island; J = Jarvis Island; K = Kingman Reef; P = Palmyra Atoll.

unexpected given the proximity of Howland and Baker to the main Phoenix Islands and the geological location of Jarvis Island on the Line Islands ridge together with Palmyra and Kingman Reef. That result is consistent with the location of the three islands in the prevailing geostrophic flow of the South Equatorial Current, though. This suggests that oceanographic currents have a larger effect on fish species composition in this region than does geologic history.

Kingman Reef was most similar to the island group of Howland, Baker, and Jarvis, but not to nearby Palmyra Atoll. This was an unexpected result, given that Kingman Reef and Palmyra Atoll are only about 60 km apart. Palmyra was most similar to the central Line Islands, which may be a result of greater habitat diversity at these larger islands, as well as to the greater sampling effort at these locations compared to the smaller, less hospitable islands.

The next node in our similarity analysis links the five U.S. equatorial Pacific islands plus the central Line Islands (Kiribati; Figs. 11 and 12) to Wake Island far to the northwest. This defines a faunal region of small, very isolated low oceanic islands in the central Pacific (Fig. 12). The faunal similarity of the islands that comprise this central Pacific low oceanic island region is not congruent with either the simple oceanographic or geologic contexts in which those islands are located. The islands of this region are in different large-scale ocean currents. Wake is in the east-to-west flowing North Equatorial Current. Palmyra Atoll and Kingman Reef are also in east to west flowing currents for at least half of the year, but differ because they are in the path of the Equatorial Countercurrent that flows in the opposite direction for a portion of the time. Howland, Baker, and Jarvis are in the east-to-west flowing South Equatorial Current. Geologically, Wake is the northernmost emergent feature of the Marshall Island Ridge; Howland and Baker are on the Tokelau Ridge; and Jarvis, Palmyra, and Kingman are on the Line Islands Ridge. We, therefore, suggest that habitat diversity, or lack thereof, as well as geographic isolation from other island groups, are primary factors influencing the fish fauna of this biogeographic region.

The isolated low islands of the central Pacific region are next most similar to the archipelagos of French Polynesia to the southeast: the Marquesas, Society Islands, and the Tuamotu Archipelago. The most unexpected result of the analysis was that the main Phoenix Islands were not most similar in shore-fish species composition to nearby Howland and Baker Islands (Fig. 11). Instead, the Phoenix Islands had greater similarity to French Polynesia. The dissimilarity of the fish fauna of Howland and Baker with that of the main Phoenix Islands is consistent with the composition of marine benthic algae, in which only 38% of the species recorded from Howland and Baker are known from the other Phoenix Islands (Tsuda et al., 2008). The biogeographic relationships of the Phoenix Islands and French Polynesia are not consistent with either the geology of those groups or with the oceanography of the central Pacific, but may be more understandable in an oceanographic than geologic context. The Phoenix and Marquesas Islands are in the same general regime of the South Equatorial Current, but are as distant from each other, as Palmyra and Kingman are from the dissimilar Marshall Islands (Fig. 12). In aggregate, the low isolated central Pacific islands, the islands of French Polynesia, and the Phoenix Islands are a well-defined ichthyofaunal region distinct in species composition from islands to the west and south, and the Hawaiian faunal region.

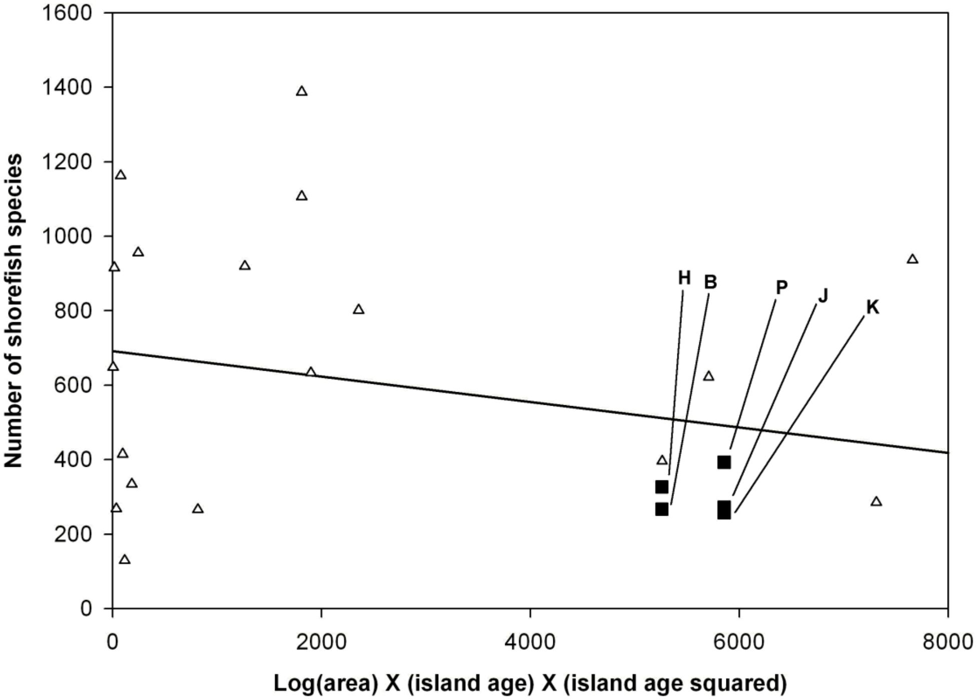

Figure 10. The relationship between the number of shorefish species recorded at oceanic Pacific islands and archipelagos, and the the island-age model [log(island area) + island age + (island age)2] of Whittaker et al. (2008). Black squares = the U.S. Line and Phoenix Islands; white triangles = other islands and archipelagos; B = Baker Island; H = Howland Island; J = Jarvis Island; K = Kingman Reef; P = Palmyra Atoll. Indonesia, the Philippines, New Guinea, and New Caledonia, included in the previous three figures, were excluded from this analysis because Whittaker et al.'s (2008) model does not apply to continental islands and accreted terrains.

The central Pacific cluster of islands was next most similar to a large and diverse group of islands to the west and southwest. This large cluster represents the species-rich and highly connected western/central Pacific fish fauna. The species-similarity relationships of island groups within that western/southwestern cluster of our analysis are complicated. They were likely not well resolved because our analysis was confined to oceanic islands, excluding continental areas like the Philippines, New Guinea, Indonesia, and the Great Barrier Reef with which the westernmost islands in our analysis, such as Palau and Ouvea, may have greater similarity. For the large cluster of islands to the west and southwest of the central Pacific region, an unexpected result was that American Samoa and Tonga of the Southern Hemisphere were most similar in shore-fish composition to the Mariana and Marshall Islands of the Northern Hemisphere. These were most similar in turn to Palau, and that larger group was in turn most similar to Wallis Island and Ouvea near New Caledonia. Another unexpected result was that the small Gilbert Islands (Kiribati) were more similar to Ifaluk in the Caroline Islands than to the closer Marshall Islands, Howland and Baker, or the Phoenix Islands. We have no explanation for this result. The basal islands in the large cluster of western and southwestern islands were Pohnpei in the Caroline Islands and Rotuma. Rotuma is near Fiji, a species-rich archipelago closer to the IAA and less isolated from other westward island groups than are the islands of the central equatorial Pacific.

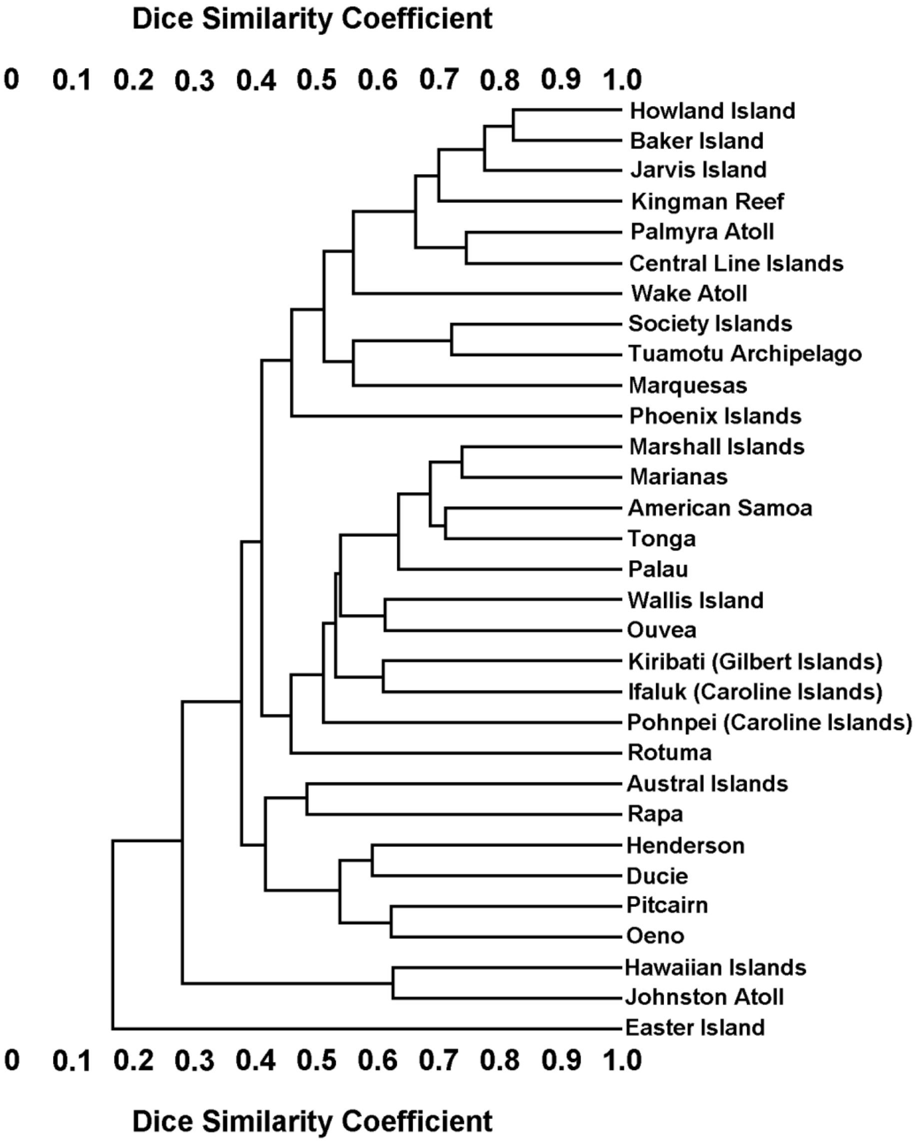

Figure 11. Similarity dendrogram for reef-fish species composition at selected central Pacific islands and island groups, calculated with the Dice similarity coefficient using presence/absence data for those species.

A distinct faunal region was found in our analysis comprised of isolated islands of the southernmost central Pacific, south of French Polynesia but excluding Easter Island. This region was comprised of the Austral Islands, Rapa, and the Pitcairn Group, islands dissimilar in species composition from French Polynesia, the group of central Pacific islands that includes the five U.S. equatorial Pacific islands, and the diverse group of species-rich islands of the western-central Pacific.

Finally, the Hawaiian Islands (faunally including Johnston Atoll) and Easter Island were the least similar to other islands in this analysis because of their high percentage of endemic species and the absence of many widespread Indo-Pacific species (Randall et al., 2005; Mundy, 2005; Randall, 2007). Only two shore-fish species, *Kyphosus hawaiiensis* and *Eviota epiphanes*, are known only from the Line or Phoenix Islands and the Hawaiian Islands or Johnston Atoll. The fish fauna of the U.S. Line and Phoenix Islands has little similarity to that of the Hawaiian Islands.

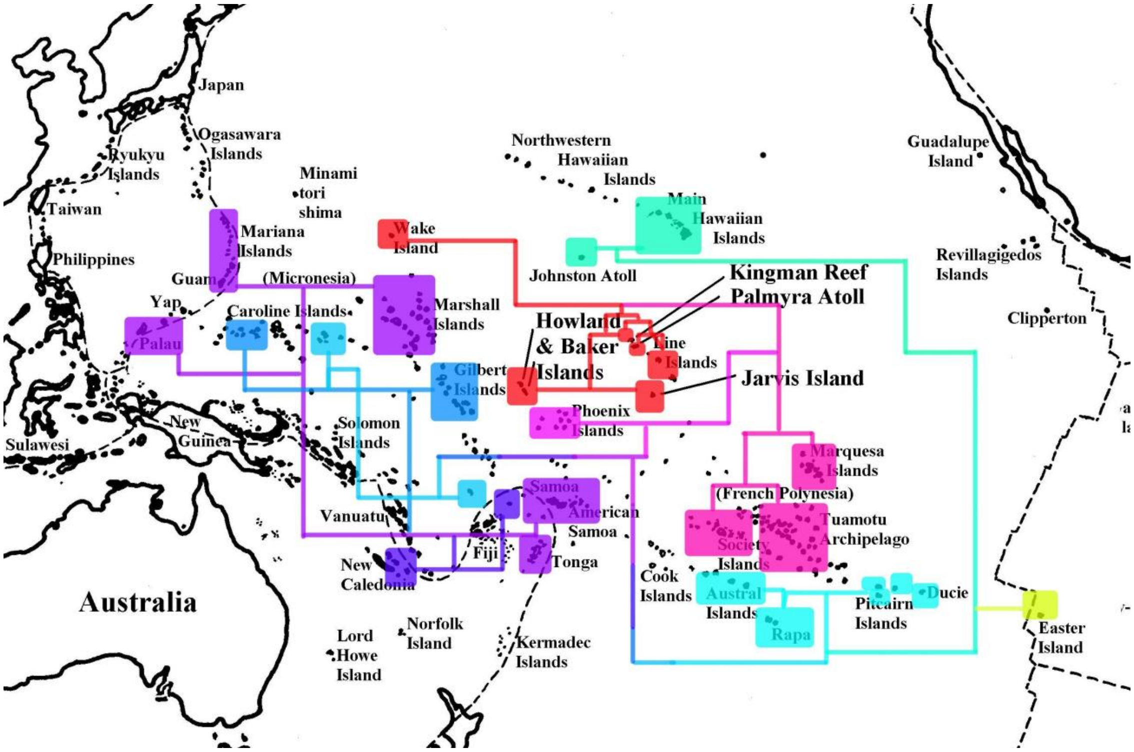

Figure 12. Schematic diagram of island and island-group similarity relationships based on reef- and shore-fish composition. Distances of the dendrogram branches in this diagram are not to scale for the similarity distances, but are distorted to better illustrate the geographic relationships of the groups shown in Figure 9. Color groupings were selected to show major clusters of similar islands and island groups identified as distinct between 40 and 60% similarity levels.

East-West and North-South Differences in Fish Distributions at the U.S. Line and Phoenix Islands

About half the species recorded in our inventory of the five U.S. equatorial Pacific islands were found to range broadly throughout the region, across Howland and Baker to the eastern Line Islands as well as south to north from the three equatorial islands to Palmyra or Kingman Reef. But 13% were restricted to Howland and Baker and 31% to the eastern Line Islands. In addition, 23% were recorded only at the three islands proximate to the equator, while an equal percentage was recorded only from Palmyra and Kingman Reef to the north. About 56.6% of the species that were recorded in our inventory were reported from only one or two collections or sightings, making conclusions about their ranges suspect. More confidence can be given to hypotheses about limited ranges for species that were recorded several times at several stations. With this limitation, we can confidently say that 32.0% of the species were recorded as ranging throughout all or most of the five islands; 2.7% of the species were recorded only from Howland and Baker; 6.0% were recorded only from the Line Islands; 5.4% from the three southern islands of Howland, Baker, and Jarvis; and 4.8% from the two northern atolls of Palmyra and Kingman Reef.

East-west differences (U.S. Phoenix vs. Line Islands). Differences in the species compositions at Howland and Baker vs. the Line Islands are representative of regional east-west differences in the distributions of fish species. In our inventory, 55 shore-fish species are recorded from Howland and Baker Islands but not the U.S. Line Islands, disregarding taxa for which species indentifications were problematic. Likewise, there were records of 131 species from the U.S. Line Islands but not Howland and Baker. Almost all of these species are more wide-ranging than these limits indicate, though, with most of those not recorded from the U.S. Line Islands ranging to French Polynesia, and most of those not recorded from Howland and Baker ranging westward from the region. Nevertheless, some species have their eastern range limits at the Phoenix Islands, and some their western range limits at the Line Islands.

The easternmost distribution of shore fishes in the Pacific is primarily limited by the distribution of islands, banks, and seamounts (Briggs, 1961; Leis, 1984; Robertson et al., 2004). The Line Islands are the easternmost emergent land in the region of the equator, but to the south the Marquesas, Tuamotus, Pitcairn Islands, Easter Island, and Sala-y-Gomez extend the Indo-Pacific biogeographic region eastward (Parin, 1991). It is, therefore, noteworthy that a number of species are recorded eastward to the Phoenix or Line Islands, but not into French Polynesia and farther to the southeast (Randall, 2005).

Species that have been recorded eastward only to the Samoa and Phoenix Islands include, with various qualifications: *Gymnothorax marshallensis, Uropterygius micropterus*, *Epinephelus fuscoguttatus*, *Epinephelus* [*Anypernodon*] *leucogrammus*, *Epinephelus howlandi, Epinephelus timorensis*, *Plectropomus areolatus*, *Nectamia fusca, Macolor niger*, *Amphiprion perideraion*, *Parapercis clathrata*, *Helcogramma capidatum*, *Helcogramma hudsoni*, *Rhabdoblennius snowi*, and *Macrodontogobius wilburi*. To these can be added *Oplopomus atherinoides*, reported east to Wallis Island and the Phoenix Islands, and two species that have been recorded eastward only to the Phoenix and Cook Islands, *Plesiops corallicola* and *Cabillus tongarevae*.

Species that have been recorded eastward only to the Samoa and Line Islands (including Johnston Atoll) are, with various qualifications: *Moringua macrochir*, *Kaupichthys hyoproroides*, *Anarchias cantonensis*, *Channomuraena vittata*, *Muraenichthys schultzei*, *Sargocentron inequalis*, *Sargocentron violaceum*, *Penetopteryx taeniocephalus*, *Sebastapistes cyanostigma*, *Pseudanthias cooperi*, *Pseudanthias dispar*, *Cephalopholis miniata*, *Cephalopholis* [*Aethaloperca*] *rogaa, Cephalopholis sonnerati*, *Liopropoma susumi*, *Malacanthus latovittatus*, *Lutjanus argentimaculatus*, *Caesio teres*, *Chrysiptera biocellata*, *Hologymnosus doliatus*, *Labrichthys unilineatus*, *Scarus tricolor*, *Cirripectes polyzona*, *Lepidichthys minor, Eviota prasites*, *Valenciennea sexguttata*, *Ptereleotris hanae*, *Acanthurus maculiceps*, *Ctenochaetus cyanocheilus*, *Paracanthurus hepatus*, *Balistoides conspicillum*, *Sufflamen chrysopterum*, and *Arothron nigropunctatus*. To these can be added species that occur eastward only to the Line Islands and the Philippines (*Cirripectes auritus*), Palau and the Phoenix Islands (*Halichoeres pallidus*; our records of a second species having this distribution, *Pterocaesio lativittata*, are probably based on a similar undescribed species [J. Earle, BPBM, pers. comm., May 2009]), Guam (*Iniistius pentadactylus*), New Caledonia (*Amblyeleotris ogasawarensis*), the Loyalty Islands (*Luzonichthys whitleyi*), the Solomon and Marshall Islands (*Pseudanthias bartlettorum*, *Chromis caudalis*), Fiji (*Bodianus sepiacaudus*, *Helcogramma striatum*, *Eviota nebulosa*, *Platax teira*), the Marshalls (*Chaetodon punctatofasciatus*, *Apolemichthys griffisi*), Tuvalu (*Acanthurus leucochilus*), Tonga (*Chaetodon meyeri*, *Chromis lepidolepis*, *Thalassoma lunare*), the Cook Islands (*Epinephelus melanostigma*, *E. spilotoceps*), and the Hawaiian Islands (*Onuxodon parvibrachium*, *Pseudanthias bicolor*, *Chaetodon kleini* [with a waif in the Galapagos]). *Apolemichthys xanthopunctatus* is a central Pacific endemic known from Kapingamarangi and the Gilbert Islands to the Line Islands.

A small number of shore-fish species in the region are south-central Pacific endemics, with ranges that extend from French Polynesia to the Line or Phoenix Islands but not to the west (Randall, 2005). *Pseudanthias olivaceus* is a central-south Pacific endemic recorded from the Society Islands, Tuamotus, and Cook Islands eastward to Niue, the Line Islands (where the species is most common), and the Phoenix Islands. *Kuhlia petiti* is recorded only from the Marquesas, the Line Islands, and the Phoenix Islands including Howland and Baker. *Paracirrhites nisus* is known only from Oeno Atoll in the Pitcairn Islands, the Tuamotus, the northern Cook Islands, and southern Line Islands including Jarvis Island west to the main Phoenix Islands. *Paracirrhites xanthus* is known from the Marquesas, the Tuamotus, the Society Islands, the southern Line Islands including Jarvis Island, and the main Phoenix Islands west to Howland and Baker. *Crystallodytes enderburyensis*, elevated to species status from a subspecies of *C. cookei* by Randall (2005), is known from Ducie and Pitcairn Islands westward to the Phoenix and Samoa Islands. *Priolepis squamogena* was described as the central-south Pacific sister species to the Indo-Pacific *P. cincta* from material collected in the Marquesas, the Tuamotu Archipelago, the Society Islands, and Malden and Jarvis in the Line Islands, with specimens from Howland and Kiritimati Islands as nontype material. *Ctenochaetus flavicauda* is recorded from the Pitcairn, Austral, Marquesas, Tuamotu, Society, Cook, Line, and Phoenix Islands.

The east-west differences in the fish fauna of the region reflect both regional endemism at central Pacific islands (Randall, 1998b) and the gradient of declining species numbers with distance from the IAA (Mora et al., 2003; Connolly et al., 2003).

North-south differences (Howland, Baker, and Jarvis vs. Palmyra and Kingman). The similarity of the shore-fish faunas of Howland and Baker Islands with Jarvis Island, vs. the similarity of Palmyra and Kingman with the central Line Islands (Figs. 11 and 12), is indicative of north/south differences in the fish fauna of the region. A number of species were recorded only at Howland and Baker, or only at Jarvis and one or both of the U.S. Phoenix Islands, but not at the two northern Line Islands. Likewise, many species were recorded only from the northern Line Islands of Palmyra and Kingman, but not the three equatorial islands.

Some of these differences are undoubtedly sampling artifacts from different survey efforts throughout the years and from the different techniques used at the different islands. Palmyra Atoll, in particular, had more intensive sampling with a greater variety of techniques than the other islands. A large number of small or otherwise cryptic species are known at the five islands only from Palmyra, but might be expected at least at Kingman Reef and perhaps the other islands if techniques that sample cryptic fishes could be used there. Examples of cryptic species known only from Palmyra are *Moringua macrochir*, *Uropterygius concolor*, *Scolecenchelys macropterus*, *Scorpaenodes hirsutus*, *Fowleria isostigma*, *Eviota distigma*, and *Schindleria praematura*.

The positions of Howland, Baker, and Jarvis in the westward-flowing South Equatorial Current, vs. the positions of Palmyra and Kingman Reef at various times in the eastward-flowing North Equatorial Countercurrent or westward-flowing North Equatorial Current, place the two sets of islands in different and often opposing regimes of presumed larval transport (Maragos et al., 2008). This may partially explain why some shore-fish species are found only in the northern or southern sets of islands. Shears, fronts and other discontinuities of temperature, water density, turbidity, plankton composition, or other attributes of the opposing currents might act as barriers to the dispersal of larvae across the currents, but this is speculation because little is known about the factors that limit dispersal of larvae across fronts or other transitions between currents and water masses. In contrast, eddies and other mesoscale features, perhaps including tropical instability and inertial waves, could act to transport larvae and other particles across zonal current shears, as discussed later. Nevertheless, conventional thought in marine biogeography is that zonal geostrophic currents exert a strong influence on the distributions of marine organisms (e. g., Randall, 1998b; many other papers). We have no explanation other than the effects of currents to explain the absence at the two northern islands of such species as *Taeniura meyeni*, *Enchelycore pardalis*, *Gymnothorax breedeni*, *Ostorhinchus apogonoides*, *Kuhlia petiti*, *Cirrhitops hubbardi*, *Neocirrhites armatus*, and *Paracirrhites xanthus*. The low number of all large pomacanthids at Palmyra and Kingman Reef was one of the more noticeable results of our surveys for which we cannot offer a corroborated explanation.

Habitat differences. Differences in habitat diversity may explain some of the differences in the shore-fish faunas of the southern vs. northern U.S. equatorial Pacific islands (Maragos et al., 2008). Howland (Fig. 2), Baker (Fig. 3), and Jarvis (Fig. 4) are low islands without lagoons, and these islands are in a region of very low rainfall. Palmyra (Fig. 5) is an atoll with moderately extensive emergent land enclosing central lagoons. Kingman Reef (Fig. 6) is a tilted atoll with small slips of emergent reefs or sandbars on its eastern half and submerged atoll reefs on the western half, which combine to encircle the large, open lagoon that comprises most of Kingman. Palmyra and Kingman are in a narrow region of very high rainfall (Miller, Lundblad et al. 2008).

The elongate shape of Howland Island makes it the only one of the equatorial Pacific islands that lacks a lee to protect reef habitats when the winds and swells come from the prevailing north or south directions. It has the narrowest reef flat of the five islands. Nevertheless, branching *Acropora* stands have been found on the small southeastern terrace of Howland Island. Baker Island has a much wider shallow reef shelf than Howland Island. The narrow western and southern shelves are steep and terraced, but the wide eastern and northern shelves deepen gradually. The wider shelf area on the east side of Baker Island is dominated by branching *Acropora* corals that form extensive fields interrupted only occasionally by pockets of rubble and coralline algal reef. The north side of Baker Island also has branching corals, but areas of coral rubble habitat are more extensive. The shallow, subtidal reef shelf at Jarvis is intermediate in morphology between that of Howland and Baker, with branching *Acropora* stands also on its eastern side. The western and other narrow, terraced shelves of Howland, Baker, and Jarvis Islands provide habitat for a diverse assemblage of reef fishes, including swarms of small anthiines and many roving large predators. Semi-pelagic predators and planktivores are abundant in open water just off the steep slopes. The western reef slopes also have numerous undercut ledges that provide habitat for nocturnal and other cryptic reef species. Coral diversity is low at Jarvis Island compared to the other equatorial Pacific islands, perhaps as a result of the great distance between it and the nearest islands upstream in the surface currents that might transport coral larvae (Maragos et al., 2008). The lower coral diversity at Jarvis Island may also be due to upwelling at its southwestern side producing a shallow thermocline below 14 m. The thermocline at Jarvis is marked by an abrupt transition from hermatypic corals in the warmer surface layer to soft corals (predominantly *Sinularia* species) that formed a noticeable band at 14-20 m in cooler water (Maragos et al., 2008).

Palmyra Atoll is very different from the three southern islands. The reef shelves along the northern and southern sides of Palmyra are narrow, but wide shallow reef shelves extend off the western and eastern ends. The shelves of both the eastern and western ends of Palmyra at all depths are scattered with patch reefs extending upward into shallower water. Northeasterly trade winds predominate at Palmrya, with swells on the northern and eastern sides of the island. The western and southern reefs are usually in the lee of the island, and most of our stations were along those sides. Four lagoons and two pools are present at Palmyra in part due to alteration of the atoll by human activity. The largest, western lagoon is connected to the ocean by a channel and is ca. 40 m deep. The three eastern lagoons are shallow reef flats. Reefs in the lagoons were destroyed directly by human modification of the atoll (Keating, 1992; Brainard et al. (a) in Maragos et al., 2008.). With the exceptions of the biologically rich eastern two pools, corals, crustose coralline algae, and other lagoonal species are rare or absent from the highly altered lagoons of Palmyra Atoll (Maragos et al., 2008). The eastern and western reef shelves at Palmyra have much patchier habitats than the reefs at Howland, Baker, and Jarvis, with extensive areas of dead coral covered with coralline algae and interspersed with rubble and sand habitat. The western terrace has an extensive central depression rimmed by shallower reef except where the pass was cut. The outer reef slopes of Palmyra Atoll are less steep than the western reef slopes of Howland, Baker, and Jarvis Islands. Undercut crevices of reef edges adjacent to sand patches provide cover for cryptic reef species at Palmyra (CRED surveys, unpublished data, 2000-2002).

Kingman Reef is very different from the four other islands. It is a tilted atoll reef roughly triangular in shape with apices at the north, east, and west, but the tilting has resulted in land emerging only as a crescent extending westward and northwestward from the eastern apex. Otherwise, Kingman Reef is a drowned atoll reef, ca. 16.6 km long east/west by ca. 9.3 km wide north/south, with a perimeter of shallow reef surrounding a sunken lagoon of ca. 18->100 m. The south side of the reef perimeter is cut by several passes. The lagoon has many patch reefs, some large, arising as shallow as ca. 9 m. Kingman Reef is only ca. 62 km north of Palmyra Atoll and is in the same weather regime. Winds, swells, and the absence of a lee at most of Kingman Reef restricted our sampling to the eastern part of the lagoon or to the sheltered south-southeastern edge of the fore reef. The outer reef crests and slopes, exposed to swells, are highly variable in habitat composition. Strong wave energy may contribute to this patchiness and the presence of dead coral on the outer reefs of Kingman at < 5–8 m. The reefs at Kingman Reef differ qualitatively from those at the other islands. Coral diversity is greatest at Kingman Reef of all the five islands (J. Maragos, USFWS, pers. comm., Feb. 2001). Branching *Acropora* corals are not abundant at Kingman Reef (also true of Palmyra), but table *Acropora* are common in the lagoon. *Acropora*, *Pocillopora*, and *Montipora* diminish in abundance moving westward in the atoll, with *Porites* remaining as the only consistently common coral genus in the shallow reefs in the western part of the atoll. An unusual assemblage of soft corals, including *Pachyseris* and *Subergorgia* sea fans, is found at 35 m in a pass off the western rim of the atoll (Maragos et al., 2008). Weakly branched pocilloporids and acroporids dominate the more shallow outer reef faces, western fore-reef terraces, and northeasterly facing fore reefs (E. DeMartini, PIFSC, pers. obs.).

The exposure of the five islands to energetic swells limits the amount of sediment substrate that accumulates in unprotected areas and forms habitat for fish species that utilize soft sediments. Exposure to energetic swells also creates high energy habitat for some species that occur almost exclusively in surge areas. Wave energy is a well-recognized controlling factor for coral-reef community structure in highly energetic regions (Grigg, 1983; Dollar and Tribble, 1993; Jokiel, 2008; Rooney et al., 2008; Grigg et al. 2008). Wave energy likely also has a strong influence on the biotic composition of reef habitats at the U.S. central Pacific islands as well (Maragos et al., 2008). Long-term mean measures (for example Cornett, 2008) give a basin-wide overview of differences in wave energy in the regions of the various central Pacific island groups, useful as measures of persistent although often seasonal long-period swell conditions that are important as a habitat component most of the time (Grigg, 1983). A more powerful control on coral-reef community structure, although perhaps more temporary in evolutionary time, is likely exerted by occasional brief episodes of intense wave energy from proximate or distant storms (Dollar and Tribble, 1993). Thus, both long-term and event-based measures of wave energy are important for evaluating the effects of wave energy on community structure in coral reef habitats. At the scale of individual small islands or atolls, wave energy is now thought to be one of the primary determinants in structuring both the habitat and species assemblages. On larger, climatological scales, wave energy and storm tracks need to be considered as structuring mechanisms (R. Brainard, PIFSC, pers. comm.).

Both long-term wave energy and the frequency and intensity of epidsodic storms generally decrease in the central Pacific moving from north to south (R. Hoeke, PIFSC CRED, pers. comm.; see also figures 4 and 10 in Cornett, 2008). Thus, Howland, Baker, Jarvis, Palmyra, and Kingman experience lower levels of wave energy than the Hawaiian Islands or Johnston Atoll. Most of the wave energy at the five islands comes from winter storms to the northwest. Lower-energy but persistent trade-wind swells from the northeast dominate at other times. Swells from storms to the northwest are less frequent and generally smaller at Howland and Baker than at the three Line Islands. At the three most equatorial islands, trade-wind swells dominant all year long with northeast trades in boreal winter and southeast trades in the boreal summer. The influence of trade winds is less dominant at Jarvis Island than at Howland and Baker, although the northwest swell and episodic waves from the northwest and southeast are more frequent at Jarvis. Trade-wind swells are much more dominant at Palmyra and Kingman, which are more firmly within the northeast trade-wind zone than the three southern Islands. But with their more northern locations, they receive more frequent and more energetic long-period distant-source episodic swells (R. Hoeke, PIFSC CRED, pers. comm.).

Palmyra and Kingman Reef have more protected area than the three equatorial Pacific islands. Species recorded only at Palmyra and Kingman that are associated with soft sediments include *Abula glossodonta*, ophichthid eels, *Upeneus arge*, *Amblyeleotris fasciata*, *Amblygobius phalaena*, *Valenciennea sexguttata, Ptereleotris heteroptera*, and *Gunnellichthys* species. While these species may prove to be present at the three southern islands, the limited amount of their habitat at those islands makes observation of those species less likely than at the two northern islands. The paucity of areas with extensive sediments at all five islands, compared to high islands or Kiritimati Island with four *Iniistius* species (J. Earle, BPBM, pers. comm., May, 2009), may explain why razor wrasses in the genera *Cymolutes*, *Iniistius*, and *Xyrichtys*, a conspicuous component of the fish fauna at places like the main Hawaiian Islands, were absent in our inventory.

An opposite influence of wave energy on species composition may be in creating persistent habitat for fish species that are most abundant and occur most frequently in high energy surge areas. Examples of such species are *Kuhlia petiti*, *Plectroglyphidodon phoenixensis*, *Thalassoma purpureum*, *T. trilobatum*, *Entomacrodus cymatobiotus*, *Acanthurus achilles*, and *A. guttatus*. The comparative biogeography of surge-associated versus non-surge species is poorly investigated, and would be an interesting topic for further research.

Although wave energy is becoming a topic of greater interest in studies of coral reef community structure (R. Brainard, PIFSC CRED, pers. comm.), its influence on the biogeographic distributions of reef fishes on an evolutionary time-scale is almost totally unknown. The role of wave energy in determining coral reef community structure on ecological time scales is now the subject of very active research. The variability of basin or archipelago scale wave-energy patterns on interannual time scales (e.g., ENSO or Pacific Decadal Oscillation scales) is a topic within some of that research. The variability of wave energy on geologic or evolutionary time scales (e.g., glacial and interglacial periods, or longer) is almost totally unknown at present. The importance of wave energy to the formation biogeographic patterns, relative to temperature, productivity, and ocean circulation variability, would be an interesting topic for future investigation (R. Hoeke, PIFSC, CRED).

The steep drop-offs at each island provide habitat favorable to the occurrence of certain species. Differences in the relative area of drop-off habitat may explain some of the differences in fish species found between the northern and southern islands. The sampling bias in our surveys at Palmyra and Kingman toward more protected, less steep habitats may have also contributed to differences in fish assemblages that we recorded. These topographic factors are difficult to separate from the influence of others, including finger coral habitat, algal growth, and plankton availability due to upwelling or intensified currents at points and drop-offs. Plankton abundance is likely enhanced by local, topographically induced upwelling caused by the impingement of the Equatorial Undercurrent on the steep flanks of Howland, Baker, and particularly Jarvis Island (Brainard et al., 2008b; Gove et al., 2006). These three islands are also located solidly within the regional equatorial upwelling zone (Fig. 13; Sette, 1955; Barber and Chavez, 1991; Chavez et al., 1996). Palmyra Atoll and Kingman Reef are on the fringes of this upwelling zone and likely influenced by it more sporadically, as discussed in the subsequent section of this paper on oceanography. The combined influences of regional equatorial upwelling (Fig. 13) and topographically induced local upwelling from the Equatorial Undercurrent place Howland Island, Baker Island, and Jarvis Island in more productive waters than Palmyra Atoll or Kingman Reef (Brainard et al., 2008b; Gove et al., 2006).

Points or drop-offs with locally enhanced plankton availability are habitats where large numbers of benthopelagic planktivorous shore fish are seen. The combination of regional Equatorial upwelling, local topographically induced upwelling, and our sampling bias at Howland, Baker, and Jarvis for drop-off habitats not far from points may explain the high numbers of benthopelagic planktivores seen at those islands in contrast to Palmyra and Kingman. *Pseudanthias bartlettorum* and *Lepidozygus tapeinosoma* were very abundant at the three southern islands but not the two northern ones. *Luzonichthys whitleyi* was the most abundant fish at the southern islands, seen in swarms of thousands, but was not recorded at all at Palmyra and Kingman. Those three species, together with the much less abundant blenny *Ecsenius midas,* form a well known suite of planktivorous shore fishes that have social mimicry in color and behavior in the Line and Phoenix Islands (Randall and McCosker, 1993). Island differences in upwelling and drop-off habitats do not explain the apparent replacement of *Pseudanthias bartlettorum* by the much less abundant *P. dispar* at Palmyra and Kingman.

Upwelling has another possible effect on shore-fish occurrences. This is the intrusion of cooler water from deeper sources into shallow depths that may facilitate the shallow occurrences of otherwise deeper living species. The triggerfish *Xanthichthys caeruleolineatus* seen at Howland, Baker, and Jarvis may be an example because this species is generally found below 80 m throughout its Indo-Pacific range (Randall, 2005). However, it was recorded in our surveys from depths less than 80 m at Palmyra and Kingman, where topographically induced upwelling is less pronounced than at Howland, Baker, and Jarvis.

The northern and eastern shelves of Baker and Jarvis, the western and eastern shelves of Palmyra, and the lagoonal habitats of both Palmyra and Kingman Reef differ substantially in other ways that may provide habitat most suitable for different species. The eastern terraces of Baker and Jarvis Islands have extensive staghorn *Acropora* cover, although Plate *Montipora* is abundant on the shelf of Jarvis (Maragos et al., 2008). *Pseudanthias olivaceus* is an example of a shore-fish species that was abundant in the staghorn *Acropora* habitat. The dense fields of staghorn *Acropora* coral created a labyrinthine, lattice framework with numerous, deep interstices in which fishes could easily hide. It is likely that we were unable to see many fish species in that habitat, and it is equally likely that the *Acropora* habitat was poorly sampled, if at all, by earlier surveys.

Among the five islands, lagoonal habitats are found only at Palmyra Atoll and Kingman Reef, but there are trenchant differences between the lagoons of those two atolls (Maragos et al., 2008). Maragos et al. (2008) observed that typical lagoon species of invertebrates and algae were almost entirely absent in the altered, "dead" lagoons of Palmyra Atoll. In our surveys, lagoon fishes were recorded mostly from the large western lagoon that has a channel open to the sea. Many of the fishes found there were large, mobile species, such as *Manta* sp. and *Carcharhinus melanopterus*, or species that are found in lagoonal habitats elsewhere, such as *Lutjanus fulvus*, *Parupeneus barberinus*, *Chrysiptera glauca*, and *Amblygobius phalaena*. Ichthyoplankton sampling inside the lagoon found a diverse assemblage of larval gobiids which could not be identified to species, as well as the unusual progenetic gobioid *Schindleria praematura* (Boehlert and Mundy, 1993). In contrast to the damaged lagoons of Palmyra, the lagoon at Kingman Reef has very healthy reef habitats (Maragos et al., 2008). Fish species observed in sand habitats of Kingman but not the southern Islands included *Amblyeleotris fasciata* and *Ptereleotris heteroptera*. Fish species observed on the lagoon floor and pinnacles included *Chromis viridis*, *Dascyllus aruanus*, and *Pomacentrus coelestis*, but none of the fishes recorded in these habitats at Kingman were unique to Kingman's lagoon among the five islands.

Differences in freshwater input at the five islands may also influence the species composition of their fishes. Dramatic differences in rainfall characterize the climate of these five islands (Barkley, 1962; Keating, 1992; Mueller-Dombois and Fosberg, 1998). Jarvis Island is within the driest part of the equatorial Pacific that extends from the eastern Pacific along the equator, receiving on average of < 500 mm/yr of rain. Christophersen (1927) said that "... Jarvis Island has a desert climate." Howland and Baker, on the edge of the driest part of this zone, receive slightly more rainfall averaging 750 mm/yr. Hague (cited in Christophersen, 1927) noted that warming of the coral rock of Howland and Baker Islands creates thermal convection that often causes rain squalls approaching these islands to separate and bypass them, giving the islands even less rainfall than the surrounding ocean. In contrast, Palmyra Atoll is in the Intertropical Convergence Zone, the climatic equator with the heaviest rainfall in the central Pacific. Palmyra has an average rainfall of ca. 5000 mm/yr, evidenced by its lush forest. Kingman Reef is even closer to the wettest portion of the Intertropical Convergence Zone, but the lack of permanent emergent land with soil to support vegetation gives little evidence of this (Mueller-Dombois and Fosberg, 1998). Heavy rainfall at Palmyra and Kingman sporadically reduces salinity at the sea surface, creating pseudo-estuarine conditions at those islands. Freshwater runoff and other effects of heavy rainfall at Palmyra have been observed to be strong enough to temporarily modify lagoonal and nearshore circulation (Brainard et al. (b) in Maragos et al., 2008.). Marine habitats at Palmyra may receive greater terrigenous inputs of nutrients than those at the other islands because of Palmyra's rainfall and vegetated terrestrial habitats, although nutrient inputs from the bird populations at Howland, Baker, and Jarvis are likely also important in the nearshore productivity systems of those islands in addition to equatorial and topographically induced upwelling.

The pseudo-estuarine conditions at Palmyra and Kingman may be favorable for the persistence there of fish families, such as the Albulidae, Engraulidae, and Chanidae, which are primarily associated with continental areas or high islands with freshwater

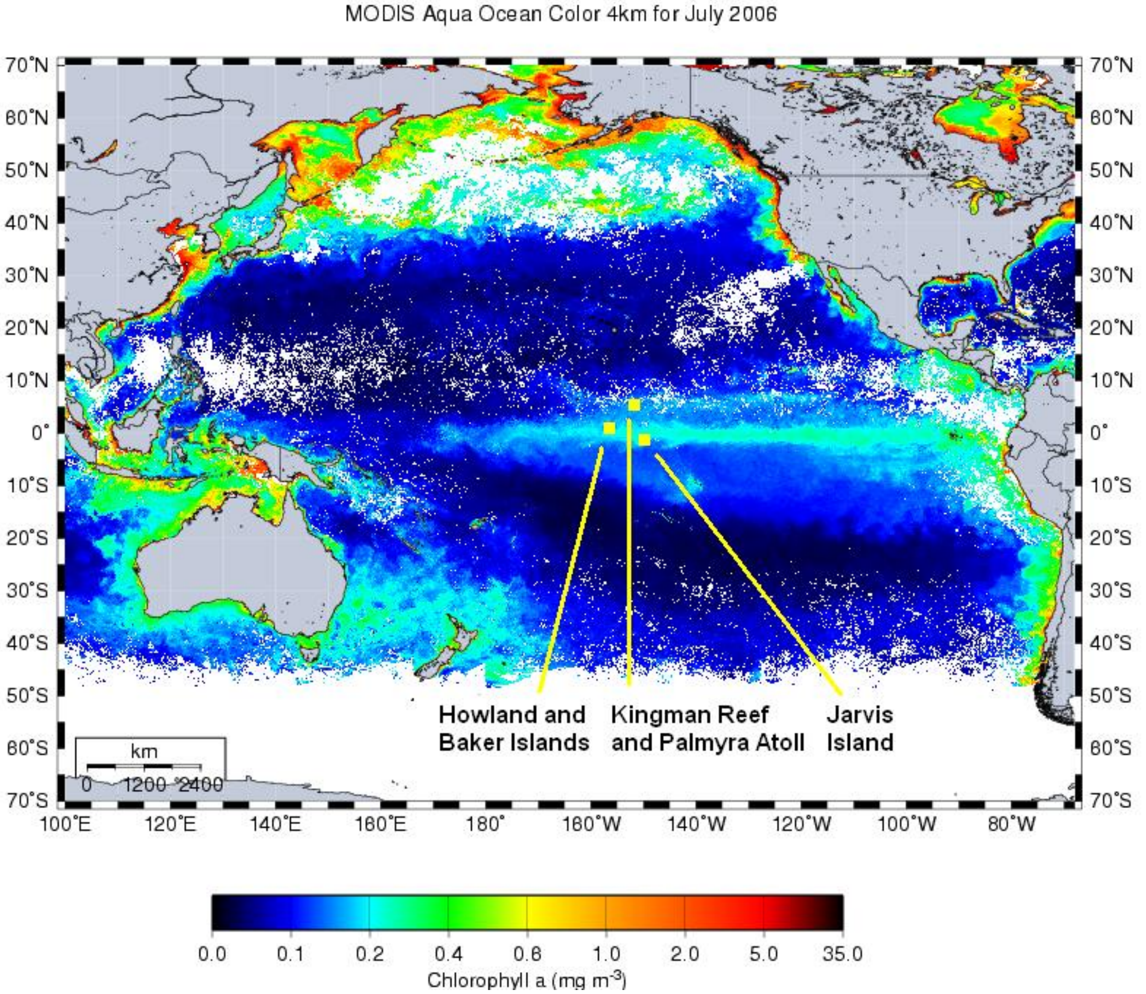

Figure 13. Sea surface chlorophyll a concentrations in the Pacific Ocean basin during July 2006, from MODIS Aqua Ocean Color satellite imagery, exemplifying regional patterns in primary productivity. Note the band of moderately high productivity, compared to the regions of the central Pacific gyres, extending westward along and just to the north of the equator between the coast of South America and ca. 170°W. This is the region of Equatorial upwelling that influences biological productivity at the U.S. central Pacific equatorial islands, particularly Howland Island, Baker Island, and Jarvis Island. July, 2006 was a transitional time moving into a moderately strong El Niño, when equatorial upwelling and resultant primary productivity were diminished, after weak La Niña conditions, when the equatorial chlorophyll band was well developed. The white areas are places where cloud cover or other water vapor prevented the satellite from obtaining good data on ocean color. Image courtesy of Lucas Moxey, NOAA OceanWatch - Central Pacific program (http://coastwatch.nmfs.hawaii.edu/oceans.html).

streams and estuaries. The anchovy *Encrasicholina punctifer* was the most abundant fish in surface trawl samples taken around Palmyra Atoll in 1990 and 1992. That species is considered to be the most oceanic of a family otherwise associated with freshwater effluent in continental areas. On a transect that followed the 155°W meridian, Ozawa and Tsukahara (1973) found larvae of *E. punctifer* to be much more abundant at ca. 10°N that to the north or south. That location is roughly within the band of high rainfall within which Palmyra and Kingman Reef are located. The high abundance of *E. punctifer* in this region may be related to the freshwater input, as has been suggested for other engraulid species elsewhere (Whitehead et al., 1988).

EVOLUTION OF THE FISH FAUNA AT THE U.S. LINE AND PHOENIX ISLANDS

Phylogenetic Biogeography of Fishes at the U.S. Line and Phoenix Islands

Too little is known of the phylogenies of shore-fish species found at the U.S. Line and Phoenix Islands to speculate about the evolutionary processes that formed this fauna. The combined data of restricted areas of endemism and robust phylogenies necessary for strong biogeographic analyses (Mooi and Gill, 2002) are almost nonexistent for fishes in the central Pacific. Regional endemics, excluding Hawaiian Island species, are not included in phylogenies available to date with the exception of species in the *Dascyllus trimaculatus* species complex including *D. auripinnis* (i.e., McCafferty et al., 2002; Bernardi et al., 2002, 2003), and the French Polynesian endemic butterflyfish *Chaetodon trichrous* (i.e., Hsu et al., 2007). There are few well-supported morphology-based phylogenetic analyses that include even the more broadly distributed Pacific plate endemic species. The species with the most restricted ranges included in available phylogenetic analyses have distributions that range across the Pacific Basin from Indonesia or the Philippines to the Phoenix Islands or French Polynesia, and many of these are placed only in unresolved polychotomies in those studies.

The wide geographic ranges of the species included in resolved phylogenies, together with the multiplicity of phylogeographic histories indicated, result in a daunting problem of disparate temporal origins for different species with similar ranges, in addition to a bewildering variety of times and ranges for their sister taxa. We do not have the computing power or skills to analyze these patterns for confounding factors such as paralogy (Nelson and Ladiges, 1996) or concordant dispersal events that might be aliased as vicariant phenomena (Zink et al., 2000; A. de Queiroz, 2005), nor are there enough studies that include estimates for the timing of cladal divergences to distinguish between congruent, pseudo-congruent, incongruent, and pseudo-incongruent patterns (Donoghue and Moore, 2003).

We, therefore, leave the task of cladistic biogeographic analysis of central Pacific fishes to others, but we mention here, for the benefit of those interested in this topic, that studies giving promising beginnings for this task include: Colborn et al. (2001), *Albula*; Markle and Olney (1990), Carapidae; Bowen et al. (2001), *Aulostomus*; Craig and Hastings (2007), Epinephelini; Mooi (1995), *Plesiops*; Mabuchi et al. (2006), Apogonidae; Miller and Cribb (2007), Lutjaninae; Carpenter (1990), Caesionidae; Littlewood et al. (2004), Hsu et al. (2007), and Fessler and Westneat (2007), Chaetodontidae [with somewhat different phylogenies likely resulting from different taxon sampling]; Bellwood et al. (2004), Pomacanthidae; Quenouille et al. (2004), Pomacentridae, particularly *Amphiprion* and *Abudefduf*; Westneat and Alfaro (2005), Labridae; Gomon (2006), *Bodianus*; Barber and Bellwood (2005), *Halichoeres*; Read et al. (2006), *Macropharyngodon*; Bernardi et al. (2004), *Gomphosus* and *Thalassoma*; Williams (1988), *Cirripectes*; Springer and Williams (1994), *Istiblennius*, *Blenniella*, and *Paralticus*; Harold et al. (2008), Nemophini, Smith-Vaniz (1976); *Gobiodon*; Winterbottom and Burridge (1989), *Priolepis*; Winterbottom (1990), *Trimmatom*; Thacker (2000), Microdesmidae; and Borden (1998), Dayton (2001), and Klanten et al. (2004), *Naso*.

Vicariance and Dispersal

The effects of topographic adjacencies and the influence of ocean current patterns are the main geophysical factors invoked in discussions of the origins and maintenance of biogeographic patterns for marine organisms (e. g., Springer, 1982; Veron, 1995). These factors are usually discussed from two aspects that reflect major and sometimes opposing paradigms in biogeographic theory. One paradigm emphasizes dispersal as the most important factor in determining distributions (e. g., Briggs, 2000; Mora et al., 2003). In this paradigm, the proximity and separations of islands, banks, seamounts, and continents within prevailing current flows are thought to exert a strong influence on connecting or isolating populations during the creation of distributional patterns by dispersal. This paradigm tends to be the one assumed in ecological studies (e. g., MacArthur and Wilson, 1963; Heaney, 2007), but is also the one most frequently found in discussions of Pacific shore-fish biogeography (e. g., Randall, 1998b) and genetic phylogeography (e. g., Lessios and Robertson, 2006). The other paradigm emphasizes the strong affinity of species for habitat topography and considers distributions to be records of the temporal changes in topographic adjacencies and divisions of the geologic features in which those habitats are found. Branches of this paradigm that are distinct in important respects, but which have some overlap in their assumptions (Humphries, 2000), include panbiogeography (Heads, 2005) and vicariance biogeography, which gave rise to and is sometimes considered identical with cladistic biogeography (Humphries, 2000; Donoghue and Moore, 2003). Some proponents of these theories dismiss dispersal as an important factor in determining biogeographic distributions (e. g., Heads, 2005; G. Nelson, 2006). The paradigm of a close linkage of geologic history with biogeography, albeit usually integrated with dispersal as an important concomitant process, is most frequently found in studies of taxonomy and morphology-based phylogenetic analyses that provide cladistic hypotheses (e. g., Springer and Williams, 1994; Springer, 1988; Mooi, 1995) although the paradigm also appears in discussions of general biogeographic theory of the Indo-Pacific Ocean biota (e. g., Springer, 1982; Santini and Winterbottom, 2002).

A few authors have attempted to interpret dispersal in a framework that considers changes in ocean currents as vicariance mechanisms directly equivalent to changes in topographic configurations through geologic history: hydrotectonics (White, 1994) or sea-surface vicariance (Veron, 1995). It is reasonable to consider dispersal, topographic vicariance, and sea-surface vicariance all as mechanisms for the formation of biogeographic distributions at central Pacific islands (Veron, 1995; A. de Queiroz, 2005; Cowie and Holland, 2006; Holland and Cowie, 2006).

GEOLOGIC HISTORY AND SPECIATION OF FISHES FOUND AT THE U.S. LINE AND PHOENIX ISLANDS

A Note About Alternative Geologic Theories in Biogeography

A scenario is given here of the evolution of the central Pacific shore-fish fauna in the context of geologic history. Before doing so, however, we acknowledge that alternative overarching geologic theories are sometimes discussed in the biogeographic literature (e. g., Cox, 1990). Our scenario is presented in the theory, prevailing among our geologist colleagues, of plate tectonics, mantle plume hot spots, expansion of the Pacific Plate, and contraction of the Pacific Basin, which seem to us to be the best supported among the alternatives in biogeographic discussions.

The major theory presented in opposition to plate tectonics is of an expanding earth (e. g., McCarthy, 2003, 2005), which itself has alternate formulations (e. g., Shields, 1991, 1996, 1997; Owen, 1990; Patterson and Owen, 1991). There are also alternate theories than mantle plume hot spots for oceanic island formation, even for the archetypal Hawaiian Islands; for example, Smith (2007) argued that progressive lithospheric extension and fracturing better explains the formation of the Hawaiian Islands than a mantle-plume hot-spot hypothesis (see also Koppers and Staudigel, 2005). Plate tectonic theory indicates that, since the Jurassic Age, the Pacific Basin has contracted as the Atlantic Ocean opened, and that the Pacific Plate has been expanding (e. g., Springer, 1982; Pilger, 2007; Smith, 2007). Expanding earth theory suggests that both the basin and plate have been expanding, but that plate expansion is of a different nature than in plate tectonic theory (e. g., McCarthy, 2003, 2005).

We are not geologists and cannot objectively evaluate the specific evidence for or against plate tectonic vs. expanding earth theories. Our geologist colleagues accept plate tectonics as the unifying theory of their field, with its ancillary theories of mantle plume hot spots, a contracting Pacific Basin, and an expanding Pacific Plate (e. g., Clague and Dalrymple 1989; Carson and Clague, 1995; Wessel and Kroenke, 1997; Tarduno et al., 2003; Sharp and Clague, 2006; Watts et al., 2006; Steinberger and Gaina, 2007; Pilger, 2007; Rooney et al., 2008). We therefore present our discussion in that paradigm.

The Geologic History of the Pacific Islands, Pacific Reef-fish Evolution, and the Formation of the Extant Shore Fish Fauna of the U.S. Line and Phoenix Islands

The seafloor upon which Howland and Baker reside formed between 130 and 123.8 ma, with 125.2-123.8 ma as the best estimate. The seafloor upon which Jarvis, Palmyra, and Kingman reside formed between 113-111.6 ma (Miller et al. in Maragos et al., 2008). The seafloor in this region, therefore, formed during the early to mid-Cretaceous period. In plate tectonic theory, the new seafloor would have been on an expanding Pacific Plate, at its junction with the Farallon Plate (Springer, 1982), in the midst of a much larger proto-Pacific Ocean (Panthalassia), and far from continental margins (Veron, 1995). Extant orders of fishes may have been diverging from their common ancestors during this time, but extant families, genera, or species had not yet evolved (Bellwood and Wainwright, 2002).

Howland and Baker are thought to have formed between 72 and 70 ma. Kingman Reef, Palmyra Atoll, and Jarvis Island are thought to have formed between 76 and 68 ma, with a more precise estimate of the age of Kingman at 69.76 ma (Miller et al. in Maragos et al., 2008; Miller, Maragos et al., 2008). These islands are, therefore, among the oldest in the Pacific and were present when there were few other oceanic islands in the Pacific Basin (Clouard and Bonneville, 2004). Deep seamounts and guyots of the Magellan, Mid-Pacific, Marcus-Wake, and Marshall seamount groups had formed prior to this time, beginning at ca. 140 ma for Look Seamount in the present-day Marshalls. Most of these seamounts now have summits below 1000 m. The shallower Cross Seamount and others of the Geologist Seamounts, now near the Hawaiian Islands, had also formed. Volcanic activity at the Hawaiian hot spot began at ca. 80–70 ma and Meiji Seamount, the oldest seamount in the Hawaiian/Emperor Seamount chain, formed at ca. 70–68 ma. This initiated formation of the Hawaiian Islands that persists to the present (Clague and Dalrymple, 1989), creating a continued presence of the central Pacific islands to the north of the Line Islands. Evidence from the age of nearby seamounts also suggests an age of formation for Caroline (Millenium) Island, one of the isolated Line Islands south of Jarvis, at 75–70 ma, although with a later, mid-Eocene period of secondary volcanism (Haggerty et al., 1982). Other islands formed by this time and remaining emergent today included: Johnston Atoll; Anewetak (Eniwetak), Erikub (Lokkworkwor), and probably other Marshall Islands (Clouard and Bonneville, 2004). The Gilbert Islands (Kiribati) likely formed at ca. 72.1–63.2 ma and the Tokelaus, or at least seamounts of the Tokelau Ridge, at 70.5–58.1 ma (Koppers and Staudigel, 2005). Few other Pacific islands existed. Thus, there were fewer "stepping stones" for colonization of organisms in the Pacific Basin at the time of formation of the U.S. Line and Phoenix Islands than at present.

Howland and Baker are part of the Tokelau submarine ridge that extends from Swains Island and the Tokelaus northward, but west of the main Phoenix Islands (Miller in Maragos et al., 2008). Howland and Baker may, therefore, have a different origin than the main Phoenix Islands, which are not on the Tokelau Ridge.

Davis et al. (2002) placed the area of origin of the Line Islands ridge in a region of great volcanic activity and shallow bathymetry - the South Pacific Superswell - approximately in the present-day area extending from Pitcairn Island to the Marquesas. Watts et al. (2006) suggested that the mismatch of ages for rock samples from the Line Islands, the age of the seafloor upon which the islands sit, and their predicted age from the elastic thickness of that seafloor all indicate that the islands were likely not formed on the spreading ridge of the Pacific Plate. They suggested that the ages of the Line Islands indicate their formation on a flank ridge or entirely off ridges. The projected placement of the Line Islands to the west of the spreading ridge at ca. 81 ma (Fig. 14) is consistent with the hypothesis that the islands were formed by off-ridge or flank-ridge events.

Formation of the Line Islands at the South Pacific Superswell has an interesting biogeographic implication for reef formation at the islands. At the time of their formation on the Superswell, these edifices would have been on an elevated seafloor relative to their present basal elevation, with consequent subsidence as they were moved northwestward off the Superswell by the motion of the Pacific Plate. Koppers et al. (2003) cited Winterer et al. (1993; not seen) in saying that the uplift was 200-700 m, and Adam and Bonneville (2005) gave a maximum amplitude for the uplift of 680 m, a large change in depth for the shores and upper slopes of the Line Islands. The subsidence of the islands from that maximum uplift, together with eustatic sea level changes over time, give a mechanism to explain the deep extent (> 800–1000 m) of ancient carbonate reef seen at the three U.S. Line Islands (B. Mundy and F. Parrish, PIFSC, unpubl. data, July 2005).

Global climate and oceanographic conditions were very different at the time of formation of the five U.S. equatorial Pacific islands than now, as was the biota of both the land and oceans. Scleractinian corals first begin to dominate tropical reefs at about 80 ma (Veron, 1995). The estimate of age for the oldest coral reef formation at the Line

Islands is in the late Cretaceous period, ca. 75–70 ma (Schlanger et al., 1984), close to the estimated ages of formation for Baker Island at ca. 70.1 ma (Miller, Maragos et al., 2008) and Kingman Reef at 69.76 (76–68) ma (Davis et al., 2002; Miller et al. in Maragos et al., 2008). Southern Italian fossil reef deposits with beryciform and perciform fishes, including the first appearance of precursors of modern reef fishes, date to this period (ca. 75 ma), although no extant reef taxa below the ordinal level were present (Bellwood and Wainwright, 2002). There is genetic evidence that the Labridae (*sensu lato*) may have diverged from its sister taxon at about 78–66 ma, but it seems more likely that the divergence was not trenchant until after the mass extinction event at the end of the Cretaceous period [the "K/T boundary" at 67 ma] (Westneat and Alfaro, 2005). The fish fauna of the U.S. Line and Phoenix Islands at their origin was very different from the fauna of today.

Massive extinctions at the K/T boundary set the stage for the origins of the modern shore-fish fauna of the U.S. Line and Phoenix Islands. Ocean primary productivity was reduced to an extreme low, and coral reefs likely became almost extinct, remaining negligible for more than a million years. Primary productivity and reef growth began to recover in the Paleocene period at ca. 66.5-64.5 ma (Veron, 1995). The basal evolutionary radiation of perciform fishes, the dominant order of reef-associated shore fishes, was underway at ca. 60-30 ma, when extant suborders and at least 11 extant genera were recognizable in the fossil record (Bellwood and Wainwright, 2002).

The first fossils of extant reef-fish families are known from the Eocene Monte Bolca fossil beds of Italy from ca. 50 ma. Those beds contain many extant reef fish families, including the Pomacentridae, Labridae, Acanthuridae, Ephippidae, Siganidae, and Zanclidae, but few extant genera (Bellwood, 1996). The divergence of the Pomacanthidae plus the Chaetodontidae from other percoid taxa is inferred from genetic evidence to have occurred at ca. 65-50 ma, around the Paleocene/Eocene boundary (Bellwood et al., 2004). By 50 ma, Howland and Baker would have been carried by the motion of the Pacific Plate from their southeastern area of origin to the present-day position of the northern Tuamotu Archipelago. Jarvis, Palmyra and Kingman would have been carried to an area east of the Marquesas' present-day location. At that time, the Austral Islands and Tuamotus had begun to form far southeast of their present positions, and the formation of the Hawaiian Chain continued with what are now Emperor Seamounts (Clouard and Bonneville, 2004). These increased the potential pathways for dispersal and colonization of Pacific insular organisms. The direction of movement of the Pacific Plate changed from northward to northwestward between ca. 67-50 ma (Koppers and Staudigel, 2005; Sharp and Clague, 2006). It has often been assumed that the trajectory of all Pacific islands changed from northward to northwestward at ca. 50 ma, the age of the bend in the Hawaiian Ridge/Emperor Seamount Chain that indicates the change in direction of that archetypical hot spot seamount and island trail (e. g., Wessel and Kroenke, 1997; Sharp and Clague, 2006; Pilger, 2007). However, age estimates for bends in the Gilbert and Tokelau Ridges indicate respective trajectory changes at ca. 67 ma and 57 ma. These asynchronous bends in seamount trails indicate that hypotheses of plate-motion constraint, fixed-plate movement vs. lithospheric extension, stationary hot spots, and mantle plumes need further testing (Koppers and Staudigel, 2005).

Genetic evidence suggests that the oldest identified divergence of an extant Pacific shore-fish species, *Naso minor* (not found in the central Pacific), from its sister clade occurred as early as 46.1-38.39 ma. Klanten et al. (2004) noted that the diversification of species in *Naso* contrasts noticeably with diversification in other reef-fish genera by having occurred from a slow accumulation of lineages over a great period of time, mostly since the Miocene period, but even from the Eocene period for early cladogenesis, instead of by more recent and rapid speciation.

Genetic evidence also suggests that the ancestor of the Scaridae existed at ca. 42 ma and that the Sparisomatinae and the Scarinae diverged at about that time (Streelman et al., 2002). The oldest of the Mariana Islands, Guam and Saipan, began to form at ca. 43 and 41 ma, respectively (Riegl et al., 2008). The Austral Islands and Hawaiian Chain

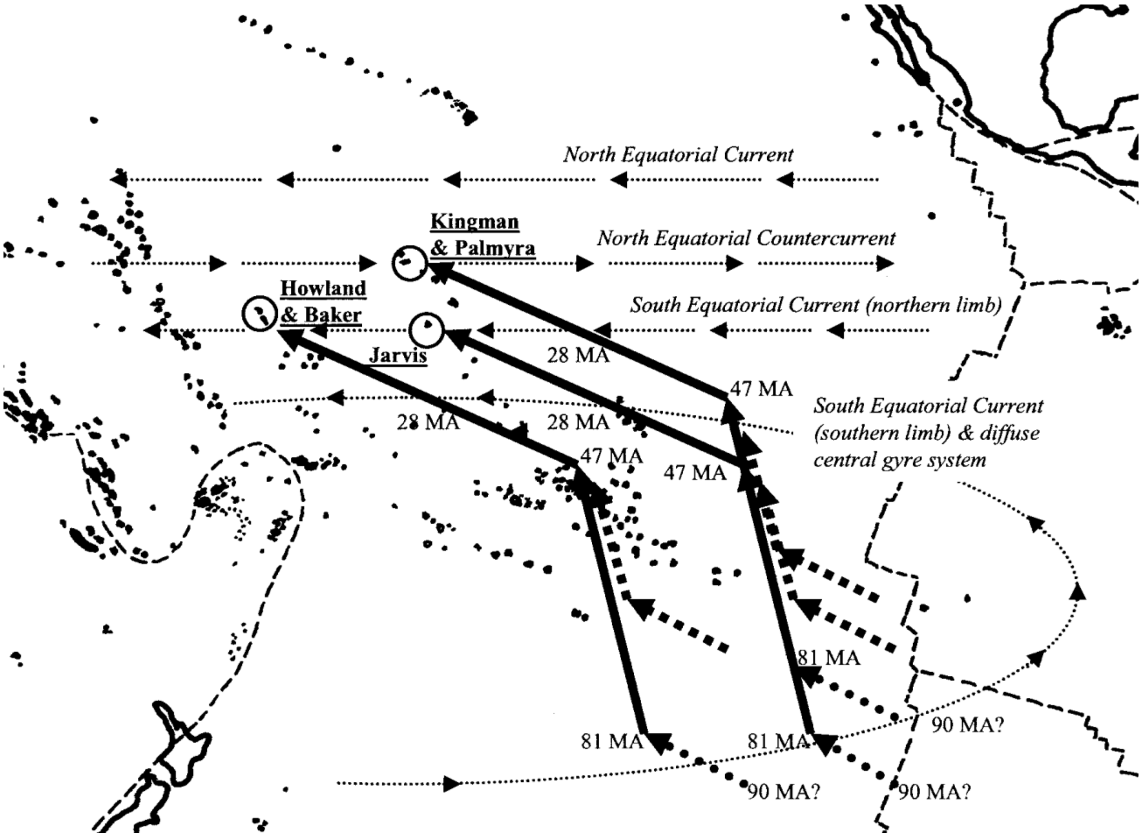

Figure 14. Schematic diagram of estimated trajectories (heavy arrows) for paleolocations of the U.S. Line and Phoenix Islands. The trajectories were plotted on tracks parallel to those of Meiji and Detroit Seamounts (ca. 71-81 ma; Duncan and Keller, 2004) described by the Hawaiian hot spot hypothesis (as for Suiko Seamount by Wessel and Kroenke, 1997), with additional projections for more ancient trajectories from ca. 90 ma (heavy dotted arrows) based on hypothesized positions of Hawaiian hot spot seamounts in the Bering Sea (Steinberger and Gaina, 2007). The heavy dashed arrows indicate shorter trajectories between 90 and 47 ma that would result from correction to account for a shift in the Hawaiian hot spot location of ca. 13° latitude to the south and ca. 3° longitude to the east between 81 and 49 ma (Duncan and Keller, 2004; Steinberger and Gaina, 2007). Projected trajectories do not account for plate rotation or shifted positions through time of the margins of the expanding Pacific Plate itself. The light dotted arrows indicate the general trends in major, contemporary geostrophic currents of the region (Tomczak and Godfrey, 2005).

continued to form (Clouard and Bonneville, 2004). Carson and Clague (1995) suggested that only low islands or atolls existed in the Hawaiian Chain during this period.

By 38 ma, approaching the Eocene/Oligocene boundary, the Tethys Sea closure and isolation of Antarctica led to global cooling, increased latitudinal temperature gradients, strengthened gyral circulation, and strengthened western boundary currents in the North Pacific. Global ocean circulation changed from primarily shallow and latitudinal to predominantly meridional. The modern thermohaline hydrographic regime was initiated as a consequence of deep, cold-water Arctic and Antarctic bottom-water formation near the poles. Glacial events began as a consequence (Veron, 1995). These changes in ocean circulation likely had profound effects on the biogeography of marine organisms with processes affecting both dispersal and vicariance. Between 38 and 26 ma, moving into the Oligocene period, many extant genera of fishes become recognizable in the fossil record (Bellwood and Wainwright, 2002). Volcanism at the Mariana Arc continued the formation of Guam and Saipan, as well as Rota, Aguijan, Tinian, and Farallon de Medinilla from ca. 32-20 ma continuing to 9-5 ma (Riegl et al., 2008).

In the late Oligocene to early Miocene periods, at ca. 28 ma, the circumantarctic current developed, enhancing global ocean cooling and climate change. Distinct seasonality and latitudinal temperature gradients developed as a result. The contemporary water masses of the world ocean began to form. For Pacific island diversity, the formation of the Hawaiian Islands continued with Kure and Midway Atolls, the oldest extant emergent islands of the chain (Clague and Dalrymple 1989; Carson and Clague, 1995; Clouard and Bonneville, 2004). Genetic evidence suggests that monacanthid clades began divergence as early as 38 ma when *Aluterus* split from its sister clade (Alfaro et al., 2007). Evidence suggests that the morphologically static bonefish genus *Albula* existed as early as ca. 30 ma (Colborn et al., 2001), as did the morphologically labile family Apogonidae, with evidence that the genus *Apogon* (*sensu stricto*) diverged from other apogonid clades at about 27 ± 2.6 ma (Mabuchi et al., 2006).

The Miocene period, beginning at 24 ma, saw major diversification of Pacific shore fishes, including the first divergences of species found at the U.S. Pacific islands. The continents had approached their present-day positions, but the mid-latitudes likely had Tethys Sea circulations through relatively unobstructed Indonesian and Central American Seaways. Global climate was warmer than at present, although not as warm as in the Cretaceous period. The upthrust of the Himalayan Mountains and central Asian Plateau started the Southeast Asian monsoonal climate and modern western Pacific weather patterns. As a consequence, El Niño events may have started at this time. Provincialism in modern coral families arose in the early to mid-Miocene period (Veron, 1995). The diversity of the Pacific islands increased somewhat during this time with the formation of the first Cook Island, Mangaia, at ca. 21.9-18.4 ma (Clouard and Bonneville, 2004). *Naso brevirostris* is the most ancient extant central Pacific shore-fish species identified thus far, with a divergence time from its sister clade of 23.7–19.78 ma (Klanten et al., 2004). The estimated time-range for divergence of *Gnatholepis knighti* (sensu Thacker, 2004a,b) from the clade containing *G. anjerensis* is 23.5–16.7 ma (Thacker et al., 2008). The oldest estimated time of divergence of *Pygoplites diacanthus* (*s.l.)* from American *Holacanthus* species is 23 ma, although with a wide range of 23–12.9 ma

(Bellwood et al., 2004). *Macropharyngodon* is estimated to have diverged from its sister clade at ca. 22.4 ma (Read et al., 2006). *Pristiapogon exostigma* may have diverged from its sister species, *P. kallopterus*, at about 22 ma (Mabuchi et al., 2006). Divergence and initial diversification of *Dascyllus* began at ca. 21 ma, continuing to 11.7 ma (McCafferty et al., 2002). *Naso unicornis* diverged from its sister clade at 20.19–16.81 ma (Klanten et al., 2004).

The mid-Miocene period from 20 to 13 ma was warm, with extensive tropical zones, preceding the formation of the modern polar ice caps. Ocean circulation patterns began to approximate present-day conditions. The Tethys Sea was reduced to a narrow band connecting the Indian Ocean while the Mediterranean Sea and the Caribbean Sea had only a shallow connection to the east Pacific. After initiation of closure of the Indonesia Seaway at ca. 17 ma, midlateral westerlies intensified, strengthening the northern subtropical gyre. Reef development was similar to today in distribution but extended to higher latitudes (Veron, 1995). The first fossils of the family Scaridae date to this time, but genetic evidence suggests that divergence of the family occurred much earlier at ca. 42 ma (Streelman et al., 2002). *Naso vlamingii* diverged from its sister clade at 19.86–16.54 ma (Klanten et al., 2004), *Diodon holacanthus* from its sister clade at 18–6 ma (Alfaro et al., 2007), and *Balistoides viridescens* from its sister genus *Xanthichthys* at 17–10 ma (Alfaro et al., 2007). Diversification of *Halichoeres* began at ca. 16 ma (Barber and Bellwood, 2005), as did divergence of *Ostorhinchus taeniophorus* from its sister clade (Mabuchi et al., 2006).

During 15–12 ma, the poles cooled and the tropics warmed for the first time in the Cenozoic. The Tethys circulation was terminated by complete closure of the Indonesian Seaway (Veron, 1995). The oldest of the Caroline Islands, Chuuk (Truk) began to form, starting at 14.8 ma (Fefan at 14.8-11.7 ma; Dublon at 14.4-10.0 ma; Uman at 11.3-8.4 ma; Tol at 10.6-4.8 ma; Ulalu at 4.3-4.0 ma) (Clouard and Bonneville, 2004), providing an enhanced dispersal pathway for central Pacific shore fishes from the west (i.e., the Caroline conduit of Springer, 1982). Formation of the Austral Islands continued with Rurutu at 12.9–0.03 ma, of the Cook Islands with Mitiaro Atoll at 12.3 ma, and the first of the Pitcairn Islands, Fangataufu and Moruroa, were formed at 12.95–9.64 and 11.8–9.45 ma, respectively (Clouard and Bonneville, 2004).

Numerous reef-fish species are estimated to have diverged from their sister clades beginning in the mid-Miocene age and continuing through the Pliocene period. This may have been in part due to the closing of the Indonesian Seaway that led to increased isolation of populations, with resultant vicariant events, enhanced by sea-level changes during the glacial and interglacial phases that began at this time. For Pacific Ocean fish evolution, it is estimated that the divergence of four population clades within *Naso vlamingii* occurred at 14.9–8.8 ma (Klanten et al., 2007). In contrast, the first major cladogenesis event for the entire genus *Albula* is estimated to have occurred at about the same time, at 14.4–10.2 ma (Colborn et al., 2001). *Gnatholepis scapulostigma* (*sensu* Thacker, 2004a,b) diverged from its Atlantic congener *G. thompsoni* (Thacker et al., 2008) at 14.3–8.9 ma, although the genetic coalescence times of extant populations of these nominal species are estimated as much more recent, 0.15-0.13 ma (Rocha et al., 2005). The Hawaiian endemic *Centropyge potteri* diverged from the clade containing *C. loricula* and *C. aurantonotus* 13.9–6.8 ma (Bellwood et al., 2004). Divergence of *Chaetodon trifascialis* from the clade containing *C. rainfordi* and *C. octofasciatus* occurred at 13–12 ma (Fessler and Westneat, 2007). *Canthigaster amboinensis* diverged from its sister clade at 13–8 ma (Alfaro et al., 2007) and *Dascyllus aruanus* from its sister species at 12.3–6.8 ma (McCafferty et al., 2002). The *Chaetodon punctatofasciatus* and *C.* "*rhombochaetodon*" species groups diverged at 12-5 ma (McMillan and Palumbi, 1995; McMillan et al., 1999). *Anampses scopas*, nested phylogenetically within the paraphyletic genus *Cantherhines*, also diverged from its sampled sister species, *C. dumerilii*, at 12–5 ma (Alfaro et al., 2007).

In the late Miocene period, mid-latitude warming progressed, the global thermal gradient increased, and the northern and southern Pacific mid-ocean gyres intensified. The first antitropical vicariance events likely began as a consequence. One of the greatest sea-level regressions of the earth's entire history occurred at the end of the Miocene period, during 9–5 ma. This was catastrophic for coral reef development (Veron, 1995) and probably for reef fish habitat. The central North and South Pacific gyres became isolated from the eastern Pacific and equatorial water masses at 9-8 ma. This may have started trichotomous sea-surface vicariant conditions for pelagic organisms, including larval stages of shore fishes, which began the separation of the eastern Pacific biota from the rest of the Indo-Pacific (White, 1994). Numerous Pacific islands formed during this time: Tubuai, Austral Islands, at 10.6–7.23 ma; Atiu Atoll, Cook Islands, at 10.34–7.39 ma; Easter Island 10.0–0.13 ma; Ponape, Caroline Islands, from several components between 8.6–3.0 ma; Aitutuki Atoll, Cook Islands, at 8.43–0.74 ma; Raivavae (Raevavae) Island, Austral Islands, at 7.57–5.2 ma; Nihoa, Hawaiian Islands at 7.5–6.9 ma; Mauke Island, Cook Islands, at 6.3–4.64 ma; and Gambier Island, Pitcairn Group, at 6.2–5.68 ma. The Marquesas first appeared with the formation of Eiao Atoll at 8.72 ma and the Society Islands with the formation of Bora Bora at 6.08–3.12 ma. Raiatea, Society Islands, formed at 5.6–2.38 ma (Clouard and Bonneville, 2004). The distance of the emergent Marquesas and Society Islands from the U.S. Line and Phoenix Islands would have been the same as today. For Pacific reef-fish evolution, *Arothron hispidus* and *A. nigropunctatus* diverged at ca. 10–4 ma (Alfaro et al., 2007; but note that other species in the genus were not sampled). *Forcipiger flavissimus* and *F. longirostris* diverged from each other at about 10 ma, as did *Heniochus varius* from a clade of four other *Heniochus* species (Fessler and Westneat, 2007). Divergence of *Ostorhinchus apogonoides* from the common ancestor of the clade containing *O. aureus* and *O. semilineatus* occurred at ca. 9 ma, as did divergence of *Nectamia savayensis* and *N. fusca* (assumed here to be the *N. guamensis* of Mabuchi et al., 2006, per Fraser, 2008). *Chaetodon bennetti* diverged from a clade of three other species in the genus at about 8–7 ma (Fessler and Westneat, 2007). At about 7 ma, *Ostorhinchus novemfasciatus* diverged from the common ancestor of *O. angustatus* and *O. nigrofasciatus* (Mabuchi et al., 2006). *Chaetodon quadrimaculatus* diverged from *C. citrinellus* at 7–6 ma (Fessler and Westneat, 2007), *Sufflamen bursa* and *S. chrysopterus* at 7–5 ma (Alfaro et al., 2007), *Albula oligolepis* from the clade containing *A. argentea* and *A. virgata* at 7.1–4.2 ma (Colborn et al. 2001), *Diodon hystrix* from *D. liturosus* at 7–3 ma (Alfaro et al., 2007), *Ostorhinchus angustatus* from *O. nigrofasciatus* at ca. 6.0 ma (Mabuchi et al., 2006), and *Chaetodon semion* from *C. ephippium* at 6.0–5.0 (Fessler and Westneat, 2007), the same time period estimated for genetic coalescence of the Pacific endemic *Centropyge loricula* with its sister clade (Schultz et al., 2006).

Beginning near the Miocene/Pliocene boundary, from ca. 5.5–5 ma, sea levels were generally low, and continental shelves were reduced in size. The North and South Pacific gyres reunified and then split apart, creating antitropical vicariant events. Corals proliferated in the eastern Pacific perhaps as a consequence of the movement of the northern Line Islands into the Equatorial Countercurrent, which might have reduced the effective size of the eastern Pacific open-water biogeographic barrier (Veron, 1995). Between 5.5–4 ma, more central Pacific islands appeared: Rapa, Austral Islands, at 5.2-4.13 ma; Kauai, Hawaiian Islands, at 5.3–3.9 ma; Ni`ihau, Hawaiian Islands, at 5.0–4.78 ma; Hauhine, Society Islands at 4.99–2.01 ma; and Nuku Hiva, Marquesas, at 4.96–2.1 ma; (Clouard and Bonneville, 2004). For fish evolution, the Pacific endemic *Naso lituratus* diverged from its Indian Ocean geminate sister species *N. elegans* at 5.62–4.68 ma (Klanten et al., 2007); the Pacific *Albula glossodonta* from its Atlantic sister species *A. vulpes* [*sensu stricto*]; *A. argentea* from *A. oligolepis* at ca. 5.5 ma (Colborn et al., 2001); the *Dascyllus trimaculatus* species group from its sister clade at 5.4–2.6 ma (McCafferty et al., 2002); and *Chaetodon auriga* diverged from *C. vagabundus* and *C. unimaculatus* at ca. 5 ma (Fessler and Westneat, 2007). The genetic coalescence time for populations comprising cryptic species of *Doryramphus excisus* is estimated at ca. 5.3 ma (Lessios and Robertson, 2006). *Rhinecanthus aculeatus* diverged from *R. assasi* and *Canthigaster solandri* from its sister clade, the *C. janthinoptera* species complex, at 5–3 ma (Alfaro et al., 2007).

At about 4 ma, the last part of the Tethyan circulation began to be severed as the Central American seaway shoaled, initiating one of the final great hydrotectonic events for Indo-Pacific biogeography. The eastern Pacific and Central Equatorial water masses and biotas became isolated from each other (Veron, 1995). Closure of the seaway was likely complete at about 3.1 ma. Events in the emergence of Pacific islands included: the western half of O`ahu, Hawaiian Islands, formed at ca. 3.8–3.5 ma; Fatu Hiva, Marquesas, at 3.72–1.30 ma; and Rarotonga, Cook Islands, at 3.64–1.10 ma (Clouard and Bonneville, 2004). For fish evolution: there is genetic coalescence for the western Atlantic *Aulostomus maculatus* with the common ancestor of the Indo-Pacific *A. chinensis* and the eastern Atlantic *A. strigosus* at ca. 4–3 ma (Bowen et al., 2001), and for Hawaiian populations of *Gnatholepis knighti* (sensu Thacker, 2004a, b) from populations elsewhere in the Pacific at 3.9–1.2 ma (Thacker et al., 2008). *Macropharyngodon geoffroy*, a Hawaiian endemic, and *M. meleagris*, likely a Pacific endemic with dispersal into the eastern Indian Ocean, diverged at ca. 3.8 ma (Read et al., 2006).

At ca 3.5–3.1 ma, the Panamanian Isthmus closed, the Caribbean and eastern tropical Pacific biotas were isolated from each other, and the last remnant of Tethyan circulation was blocked. The oxygen minimum layer of the eastern tropical Pacific developed. Extinctions, displacements, and vicariance may have occurred as a result. Sporadic cooling of east Pacific surface waters intensified because of upwelling. Tethyan scleractinians in the east Pacific become isolated from those in the Caribbean, but these unique east Pacific corals become extinct in the Pleistocene period. Northern hemisphere glaciation increased, along with the formation of Arctic "bottom water" in the North Atlantic, initiating the modern ice age cycle, enhancing global thermal gradients, seasonality, and ocean circulation patterns. Sea levels dropped by ca. 100 m (Veron, 1995). These changes may have led to increased deepwater and interior basin vicariance but increased shoreline dispersal. Continental shelf widths and estuarine areas were likely reduced, but island connectivity may have been increased. New Pacific islands emerged; the eastern part of O`ahu, Hawaiian Islands at 2.7–2.5 ma; Kusaie (Kosrae), Caroline Islands, at 2.6–1.2 ma; Moorea, Society Islands, at 2.45–1.15 ma; and Tahiti-Nui, Society Islands, at 2.29–0.23 ma. The first of the Samoa Islands, Upolu, was formed at 2.8–1.0 ma (Clouard and Bonneville, 2004). Events in central Pacific reef-fish evolution from the closure of the Tethyan Seaway until the end of the Pliocene period at ca. 1.6 ma were: the Pacific *Chaetodon lunulatus* diverged from its Indian Ocean geminate sister species *C. trifasciatus* at ca. 3.5 ma (Hsu et al., 2007), the surgeonfish *Naso hexacanthus* from its sister clade at 3.24–2.70 ma (Klanten et al., 2004); the butterflyfish *C. ornatissimus* from the clade of *C. reticulatus* and *C. meyeri* at ca. 3.22 ma (Fessler and Westneat, 2007) or, alternatively, from *C. meyeri* at 2.5 ma (Hsu et al., 2007); the Hawaiian Islands endemic bonefish *Albula virgata* from the western Pacific *A. argentea* at 2.7–2.0 ma (Colborn et al. 2001); and *C. vagabundus* from *C. decussatus* at ca. 2.5 ma (Hsu et al., 2007). The endemic Hawaiian Islands surgeonfish subspecies *Acanthurus triostegus sandwicensis* coalesces genetically with its Indo-Pacific sister subspecies, *A. t. triostegus*, at ca. 2.1 ma (Lessios and Robertson, 2006). At ca. 2 ma, the butterflyfish *Chaetodon lineolatus* diverged from its sister clade (Fessler and Westneat, 2007).

Near the Pliocene/Pleistocene boundary, starting at ca. 2 ma, sea level regression created many islands and banks that could have served as stepping stones for dispersal of Pacific organisms. Indonesia and Sahul were continental, and intensified upwelling created cool surface temperatures in the gap between them, likely leading to vicariance of Indian Ocean and Pacific species (Fleminger, 1986). With the emergence of the Pacific islands, Molokai of the Hawaiian Islands formed at 2.5–1.69 ma. Sala-y-Gomez, the easternmost island of the Indo-Pacific biogeographic realm (Parin, 1991), formed at 1.7 ma (Clouard and Bonneville, 2004). In the evolution of Pacific reef-fishes, the period of 2.0 to ca. 0.8 ma saw the divergence of: *Chaetodon lunula* from *C. fasciatus* (Fessler and Westneat, 2007); *Canthigaster janthinoptera* from its endemic Hawaiian sister species *C. jactator* (the third species in the complex, the eastern Pacific endemic *C. punctatissima*, was not sampled) (Alfaro et al., 2007); and the Pacific *Chaetodon punctatofasciatus* species group from the Indian Ocean *C. "rhombochaetodon"* group (McMillan and Palumbi, 1995; McMillan et al., 1999). The divergence of Indian and Pacific Ocean populations within *Halichoeres marginatus* at 1.9–1.7 m (Barber and Bellwood, 2005) occurred. *Naso caesius* diverged from a potentially unnamed sister species at 1.71–1.42 ma (Klanten et al., 2004).

In the Pleistocene period, after ca. 1.6 ma, biogeographic patterns are thought to have been influenced by numerous sea level fluctuations. Glacial invigoration of gyral strength may have increased larval dispersal during times of ice cap expansion and lowered sea levels. The Tethyan-derived corals of the east Pacific became extinct and recolonization of the east Pacific by dispersal of corals and other organisms from the Indo-Pacific began (Veron, 1995). The emergence of the Pacific islands included: Tutuila, Samoa Islands, at 1.4–1.03 ma; Lanai and the west Maui Mountains, Hawaiian Islands, at 1.36–1.24 ma; the northern Mariana Islands from Anatahan to Uracas from 1.2 ma to the present; Pitcairn Island at 0.9–0.5 ma; and Wallis Island between Fiji and the Samoa Islands at 0.82 ma (Clouard and Bonneville, 2004; Riegl et al., 2008). In the evolution of Pacific reef-fishes, two clades of *Dascyllus trimaculatus* (western-central Pacific and French Polynesian) coalesce genetically at 1.5–0.6 ma (Bernardi et al., 2003). *Chaetodon lineolatus* diverged from *C. oxycephalus* at ca. 1.5 ma (Hsu et al., 2007, but see Fessler and Westneat, 2007 for a different phylogeny). The divergence of the western North Pacific butterflyfish *Chaetodon punctatofasciatus*, the South Pacific *C. pelewensis*, and Hawaiian endemic *C. multicinctus* is estimated at 0.87–0.26 ma (McMillan and Palumbi, 1995; McMillan et al. 1999; Hsu et al., 2007). Diversification of the species within the *D. trimaculatus* group, including *D. trimaculatus, D. albisella*, *D. strasburgi*, and *D. auripinnis*, began at 0.6–0.5 ma. The Marquesan endemic *D. strasburgi* diverged first in the phylogeny of the group. The Hawaiian endemic *D. albisella* diverged last, but it is paraphyletic with populations of *D. trimaculatus*. Unfortunately for the present discussion, no age estimate was given for the one equatorial Pacific Plate endemic in this clade, *D. auripinnis*. The Society Island and Tuamotu Archipelago endemic *D. flavicaudus*, paraphyletic with populations of the polyphyletic morphospecies *D. reticulatus*, also diverged from its sister taxon in the past 0.5 ma (McCafferty et al., 2002). The French Polynesian endemic *Chaetodon trichrous* also diverged from its Indo-Pacific sister species, *C. kleini*, at ca. 0.5 ma (Hsu et al., 2007). Genetic coalescence of the Atlantic *Gnatholepis thompsoni* with the Indo-Pacific *G. cauerensis* (or *scapulotigma sensu* Thacker, 2004b) is estimated as 0.269–0.13 ma (Rocha et al., 2005). The most recent estimate for divergence of a Pacific reef-fish species is that of 260,000 years before the present (ybp) for *Chaetodon ulietensis* from its Indian Ocean sister species, *C. falcula* (Fessler and Westneat, 2007).

The late Pleistocene and Holocene periods were characterized primarily by sea level changes during glacial and interglacial periods (Veron, 1995). Continent, ocean basin, and ocean current configurations had achieved their present-day positions by this time. The present height of the Line and Phoenix Islands above sea level is thought to be due to relatively recent eustatic sea level change (Keating, 1992). It has been suggested that atoll formation by reef growth occurred during the rise in sea level following the Wisconsin glacial period, at ca. 10,000–12,000 ybp. Most of the islands would have been submerged at ca. 5000 ybp when sea levels were ca. 2 m above present. The tops of the islands may have been leveled by wave erosion then and as sea levels subsequently dropped. Lagoons at Howland, Baker, and Jarvis were filled as sea levels continued to drop. Keating (1992) hypothesized that rainfall and consequent karstic dissolution of emergent rock had a major influence on the physiographic development of these islands. Kingman Reef and Palmyra Atoll are nearly submerged and partially submerged atolls, respectively, in part as a result of high dissolution of emergent rock, while Howland, Baker, and Jarvis Islands are emergent with infilled lagoons, in part because of lesser dissolution from reduced rainfall, redistribution of sand and detritus to the interior of the atolls, and biogenic input from guano. Keating's (1992) hypothesis layers a more recent effect on island modification to the hypothesis of submergence and progressive erosion of younger to older islands usually invoked to explain the transition from high to low islands in chains created by volcanic hot spots (e. g., Walker, 1990 for the more recently formed Hawaiian Islands). Miller et al. in Maragos et al. (2008) noted that, according to contemporary hypotheses about Pacific Plate seafloor subsidence and atoll senescence, none of these islands should be above sea level. This remains a mystery to be solved by future research.

Phylogeography of Fish Populations at the U.S. Line and Phoenix Islands

The history of Pleistocene reef-fish evolution after ca. 0.75 ma is primarily of genetic divergence of populations within species, inferred mostly from back-calculated coalescence ages of genetic clades. Coalescence of cryptic species of the hawkfish *Cirrhitichthys oxycephalus* in the central and eastern Pacific is estimated at 0.75 ma and of eastern and central Pacific populations of the surgeonfish *Acanthurus triostegus* at 0.59 ma (Lessios and Robertson, 2006). Although there has been discussion of the effect of Pleistocene sea-level on reef-fish biogeography (e. g., Springer and Williams, 1990; Myers, 1999; Springer and Williams, 1994), the time since ca. 0.25-0.10 ma has apparently been too short for the development of a strong genetic signal of species divergence.

There is support from a few studies of species that occur at the Line and Phoenix Islands for the general observation that population haplotype divergence in shore fishes is much more recent than speciation events, suggested by Grant and Bowen (1998) to be a prevalent phenomenon in fish evolution. As mechanisms that could create recent population divergence times, Grant and Bowen (1998) proposed founder effects, population bottlenecks, local population extirpations with recolonization, and a large variance in reproductive success by individuals within populations that cause periods of low effective population sizes (e. g., few individuals in a population contributing to successful recruitment even though population sizes may remain large). They noted that species most susceptible to such effects would be those with high dispersal potentials and ranges lacking strong physical barriers to dispersal, but which are divided into small, isolated populations. That description surely applies to most of the shore fishes found at the U.S. central Pacific islands.

Friedlander et al. (2008) found that the population of *Albula glossodonta* at Palmyra Atoll was not significantly different in haplotype diversity from the population at Kiritimati, but was divergent from Hawaiian and Seychelle Island samples. They suggested that the lineages of Line and Hawaiian Islands *A. glossodonta* coalesce genetically to a common ancestor at a back-calculated age in the late Pleistocene period, ca. 250,000–331,000 years ago. Connectivity of populations among archipelagos and a selective sweep of an mtDNA type superior in natural selection were given as hypotheses to explain the relatively recent divergence of genotype variability. The late Pleistocene period was a time of relatively rapid and strong fluctuations in eustatic sea level change between ca. 25 and 200 m below present-day sea level during at least two glacial and one to three interglacial periods. The recent divergence of Line and Hawaiian Island populations of *A. glossodonta* relative to the more ancient species divergence within the clade is consistent with the general phenomenon of shallow population structure relative to deeper speciation times in shore fishes.

The late Pleistocene period's coalescence of Line and Hawaiian Islands *A. glossodonta* lineages is consistent with the results of Bernardi et al. (2002) and McCafferty et al. (2002) for the divergence time of *Dascyllus auripinnis* populations from populations of other nominal species in the *D. trimaculatus* clade. The studies differ, though, in that genetic structure was found by Bernardi et al. (2002) between *D. auripinnis* specimens from Kingman Reef and Kiritimati, but not by Friedlander et al. (2008) for *A. glossodonta* specimens from Palmyra and Kiritimati.

Craig et al. (2007) did not find evidence for strong genetic structure in central-western Pacific populations of *Myripristis berndti*, in a study that included samples from the main Phoenix and central Line Islands. Little evidence for isolation by distance in Pacific samples of *M. berndti* was found. The species shows evidence of recent dispersal on the ocean-basin scale of several thousands of kilometers. Craig et al. (2007) concluded that the weak genetic structuring of *M. berndti* populations is more similar to that of pelagic species than of most reef species studied to date. They found evidence for recent population expansions in *M. berndti* with coalescence times of ca. 300,000-1,000,000 years ago, which they also associated with habitat restrictions from rapid sea level changes during glacial changes. This time frame is consistent with those proposed for genetic changes that include Line Island populations of *Albula* and *Dascyllus*, although the effects of those changes are manifested at different systematic levels for the three genera.

Schultz et al. (2006) found no significant genetic differences among specimens of *Centropyge loricula* from several Pacific island groups, despite variation in color patterns that distinguish fish from the Hawaiian and Marquesas Islands from those elsewhere in the region. The lack of genetic differentiation between specimens from Howland, Baker, Palmyra, Kiritimati, Johnston Atoll, the Hawaiian Islands, the Marquesas, Moorea, the Marshall Islands, or Vanuatu therefore did not allow for an estimate of divergence of Line or Phoenix Island populations. Schultz et al. (2006) noted that the species shows evidence of having a population expansion from a population crash or founder event ca. 160,000 years ago. They estimated that *C. loricula* diverged as a species from its nearest extant related species in the "*C. bispinosus* complex" (*C. potteri*, *C. bispinosus*, *C. shepardi*, and *C. ferrugata*) at about 5-6 ma. Bellwood et al. (2004) estimated that *C. potteri* diverged from the clade containing *C. loricula* and the Atlantic species *C. aurantonota* at about 13.9 ma, with an alternate estimate of 10.1-6.8 ma. Recent population coalescence relative to ancient speciation is again supported.

Although the study did not include specimens from the Phoenix or Line Islands, Thacker (2004a) found evidence for population expansion into the central Pacific Cook Islands, Society Islands, and the Tuamotu Archipelago at ca. 88,000 years ago for *Gnatholepis anjerensis* [*G. anjerensis* or *G. cauerensis* in part of Randall and Greenfield, 2001, 2007] and ca. 237,000 years ago for *G. scapulostigma* [*G. cauerensis* in part of Randall and Greenfield, 2001, 2007]. Thacker (2004a) suggested (p. 362) that population expansion led to the relatively recent colonization of those islands "from continental-shelf refugia, such as Fiji, following glacially induced sea level drops." The time frame for this population expansion, with resultant shallow genetic structure relative to the age of the species, is consistent with that found for most other shallow-dwelling species at central Pacific islands.

In contrast to the other studies, one found older phylogeographic structure developed by repeated events since the divergence of the species from its sister taxon. Klanten et al. (2007) investigated the fine-scale phylogeography of *N. vlamingii* populations and found evidence for ancient diversification of four clades, in the mid- to late Miocene period between ca. 8.8 and 14.9 ma. The Line and Phoenix Islands were not among the locations from which samples were obtained; French Polynesia was the only central Pacific locale included in the study. Klanten et al. (2007) suggested that the phylogeographic structure of *N. vlamingii* indicates ancient but repeated range contractions into refugia during glacial periods, followed by massive, repeated dispersals throughout the Indo-Pacific, creating intermittent mixing of partitioned stocks that led to the present-day pattern of genetic diversity without strong spatial structuring across the two ocean basins. The relatively great ages of divergence and coalescence for clades within *N. vlamingii*, along with the absence of spatial structure to the species' genetic diversity, contrast strongly with the recent ages of diversification and spatial structure found within *Albula*, *Myripristis*, *Centropyge*, *Dascyllus*, and *Gnatholepis*.

Conclusions from Phylogenetic, Phylogeographic, and Geologic Information

The phylogenetic and phylogeographic information for species in the U.S. Line and Phoenix Islands is consistent with the general observations that extant reef-fish species diverged from their common ancestors beginning at the Oligocene/ Miocene boundary (ca. 28 ma), but mostly from the mid-Miocene (ca. 15 ma) into the Pleistocene period (0.5 ma) (Rocha and Bowen, 2008; preceeding sections). By the end of the Oligocene period, the U.S. Line and Phoenix Islands were certainly distant from continents and other island groups under the assumptions of both plate tectonic and expanding earth theory. According to plate tectonic theory, by 28 ma Howland and Baker would have moved to the present-day region of Starbuck Island, and Jarvis Island would have moved into the present day location of the Marquesas (which had not yet formed). That would have placed Howland, Baker, and Jarvis into the present-day oceanographic regime of the southern limb of the South Equatorial Current, assuming that geostrophic ocean-current positions then were the same as now. By 28 ma, Palmyra and Kingman had moved into a region north of the present-day location of the Marquesas and far to the east of the present-day location of Jarvis. That would have placed Palmyra and Kingman in the present region of the South Equatorial Current's northern limb. Factors that influenced the present-day biogeographic patterns of extant shore-fish species at the U.S. Line and Phoenix Islands operated from no earlier than the early Miocene period (28 ma). Many of the Pacific island and seamount groups for which age estimates have been obtained did not exist prior to the Miocene period, the exceptions being the Line Islands, Johnston Atoll, Marshall Islands, Austral Islands, Hawaiian/Emperor Seamount Chain, Necker Island, the Tuamotus, the Mid-Pacific Mountains, the Magellan Seamounts, and the Marcus-Necker Seamounts.

The origin of the Line and Phoenix Islands on the central Pacific Plate soon after the plate's appearance, the expansion of the plate since then, the distance of the early plate from continents, the larger size of the Pacific Basin in the past, and the absence of evidence or a mechanism of island integration for the Line and Phoenix Archipelagos all imply that simple topographic adjacencies unrelated to ocean current patterns were not the primary factors that shaped biogeographic patterns at these central Pacific islands. Evidence supports the hypothesis that both dispersal and sea-surface vicariance (hydrotectonics) in part formed the biogeographic patterns of shore fishes at the U.S. Line and Phoenix Islands.

Oceanography and Larval Transport in Relation to Line and Phoenix Island Biogeographic Patterns

Present-day oceanographic currents impinging on the equatorial Pacific islands are relatively strong because the islands are within the cores of equatorial segments of the north and south gyral currents and the opposing Equatorial Countercurrent between them (Tomczak and Godfrey, 2005). This would presumably enhance larval transport to and from the islands, even with the caveats by Leis (2006b) about flaws in the assumption that tropical reef-fish larvae cannot exert control on their movement in currents. Direct measurements of currents have only been published from Jarvis Island and Palmyra Atoll (Wyrtki, 1967; Roemmich, 1984; Hamann et al., 2004, Gove et al., 2006; Gove in Maragos et al., 2008). Inferences about currents at the other islands and in the region are otherwise drawn from transects at nearby latitudes in the central Pacific (e. g., Barkley, 1962).

The islands fall within two groups in different general surface current regimes flowing in opposite directions (Tomczak and Godfrey, 2005). Palmyra Atoll and Kingman Reef are often in the Equatorial Countercurrent (ECC) that flows from west to east, although this can vary with changes in current positions that are related to El Niño or La Niña conditions. Kingman Reef, in particular, is in an area that can be within the North Equatorial Current (NEC), ECC, or even the northern limb of the South Equatorial Current [SEC(N)], depending upon climatic conditions (Brainard et al. (b) in Maragos et al., 2008). The islands that are nearest upstream to Palmyra and Kingman are the Marshalls, although they are 1440 nmi away. Howland, Baker, and Jarvis Islands are solidly within the SEC(N) that flows from east to west, in the opposite direction of the surface current usually flowing past Palmyra and Kingman Reef. Howland and Baker Islands are downstream of the Line Islands by 1140 nmi in this current. In contrast, Jarvis Island is directly downstream only from the Galapagos Islands and Ecuador 3900 nmi to the east. All of these currents have great seasonal and interannual variability, particularly in velocity. Poorly understood meanders and eddies, particularly near the islands and reefs, add complexity to the oceanography of the region that is greatly in need of study. The Equatorial Undercurrent (EUC, or Cromwell Current), flows from west to east below the ocean thermocline (> ca. 100 m) at the latitudes of Howland, Baker, and Jarvis Islands. At the latitudes of Palmyra Atoll and Kingman Reef, the current flow remains generally from west to east in the upper 300 m but gradually diminishes in strength with depth.

There are significant differences in the oceanography between the eastern and western groupings of the U.S. equatorial Pacific islands that might influence the formation of biogeographic patterns, in addition to the north-south differences (Gove in Maragos et al., 2008). Howland and Baker are often more within the eastern edge of the western Pacific "warm pool" with sea surface temperatures of > 27°C, little seasonal variability in thermocline depth and current velocities, and often west of the influence of tropical instability waves discussed later in this section. In contrast, Jarvis, Palmyra, and Kingman are in the boundary region between the warm pool and the westward extension of cooler, more productive water, the equatorial cold tongue, which extends westward from the eastern Pacific. Jarvis, in particular, is within the cold tongue. Palmyra and Kingman are often just to the north of its boundaries, but seasonal and interannual variability in the positions and intensities of oceanographic features associated with the cold tongue and warm pool have a marked effect on the oceanography of the two northern islands. The influence of east-west differences of the islands in relation to oceanography means that Jarvis, Palmyra, and Kingman experience stronger effects than Howland and Baker from equatorial upwelling, the passage of fronts and eddies from tropical instability waves and other meridional transport mechanisms, and enhanced primary productivity from those mechanisms (Gove in Maragos et al., 2008).

The positions of islands with respect to the surface geostrophic currents, zonal in the equatorial region, are usually suggested as the major influence on the biogeography of the islands via the transport of larvae and pelagic juveniles from islands upstream (e.g., Randall et al., 2003; Maragos et al., 2008). For example, Clark (1995) concluded that larvae of shore fishes captured at stations between 5-8°N and 150-158°W°, far to the east of Palmyra and Kingman, likely came from those islands because of the prevailing eastward flow of the ECC, even though most of those stations were closest to Christmas Island in Euclidean distance. Clark (1995) also suggested Jarvis Island was the probable source for shore-fish larvae captured between 2°S and 2°N at the same latitudes. He concluded that the EUC was the means for transport, instead of the surface flow. However, eddies spinning off these currents, Ekman transport from upwelling, or meanders with significant meridional vectors could also transport larvae across the prevailing zonal current patterns. The distribution patterns of individual shore-fish species found at the equatorial Pacific islands clearly indicate that mechanisms of meridional dispersal are required, in addition to transport in the opposing, narrow, zonal geostrophic currents of the region (e. g., Bernardi et al., 2003).

There is diverse evidence for the geographic distribution, strength, and even direction of meridional transport in the central North Pacific. Wyrtki (1967) observed short-term changes in current directions with current-meter observations taken from a ship anchored during 14–25 March 1967, in a moderately strong La Niña year, at 6°25.8–24.0’N,157°46.5–53.2’W (variations in the location were caused by the necessity to re-anchor the ship when it broke free on two occasions). Currents at 20 and 100 m had a strong northwestern component during 14–16 and 18–19 March, a strong northern or slightly northeastern component during 23 March, were westerly during 20–23 March, and were variable with a frequent easterly set during 24–25 March.

Calculations from direct measurements of current velocities by acoustic Doppler current profiler surveys in this region estimated mean meridional sea-surface current velocities of 0–13 cm s^{-1}, with strong divergence at the equator and convergence from 5°N to 9°N (Johnson et al., 2001; averaged to the mean longitude in their study—135°W). These velocities are considerably less than the average zonal sea-surface velocities of 0–50 cm s^{-1} and almost an order of magnitude less than the EUC zonal velocities of 1–90 cm s^{-1} at 50–200 m. Nevertheless, meridional transport mechanisms may be influential for biogeography because of the shorter latitudinal distances between islands in this region compared to their longitudinal distances.

Evidence also exists for meridional transfer of productivity through trophic levels in the region (Fig. 13). The U.S. Line and Phoenix Islands are within or on the edge of a region between 5°N and 5°S of enhanced primary productivity relative to the central Pacific Ocean gyres to north and south of the equator (Sette, 1955; Barber and Chavez, 1991; Barber et al., 1996; Chavez et al., 1996). There is evidence that enhancement and concentration of phytoplankton from equatorial upwelling occur in fronts at the leading and trailing edges of tropical instability waves, discussed later, which have a meridional component (Barber et al., 1996; Strutton et al., 2001). Chlorophyll levels at these frontal areas of concentration can be twice to an order of magnitude greater than background levels. Strutton et al. (2001) concluded that enhanced productivity in the equatorial central-eastern Pacific is caused by complex interaction of enhanced upwelling, concentration of plankton at subductive fronts, horizontal mixing and shear, and poleward meridional advection. Zooplankton mean biomass is greater in the vicinity of the Line Islands from the Equator to Palmyra, relative to the mean biomass to the north and south (Sette, 1955).

Gaudy et al. (2004) found enhanced mesozooplankton biomass (e. g., copepods, chaetognaths) between 6°S and 5°N in their study at 8°S–8°N, 180° during La Niña conditions in which equatorial upwelling extended westward through that region. North of 6°N mesozooplankton biomass was relatively low. They attributed a meridional increase in heterotrophic zooplankton biomass moving away from the equator to the maturing of the ecosystem, with growing consumer populations as water was advected away from upwelling areas where new primary productivity was initially high. A meridional pattern of enhanced biomass for higher trophic-level organisms also exists in the region, offset somewhat to the north of the upwelling as a result of advection and temporal lags in trophic transfers of productivity resulting from the time needed for feeding, assimilation, growth and reproduction of zooplanktivores and their predators, including tuna (Sette, 1955; King, 1958). King (1958) found micronekton abundance to be offset from zooplankton abundance in the region during 1955, although both trophic groups had their highest biomass near the region of divergence, convergence, and frontal systems in the area of the ECC.

The classic model for equatorial Pacific meridional transport is that of a poleward component to water movement in the upper mixed layer due to Ekman transport during equatorial upwelling, with linked equatorward transport at the bottom of the mixed layer and in the thermocline (e. g., Wyrtki and Kilonski, 1984; Brown et al., 2007). Wyrtki and Kilonski (1984) suggested that the northward surface water transport is minimal in the Intertropical Convergence Zone (ICZ) region of 4°N (the doldrums), but more pronounced to the south and north. Johnson et al. (2001) found empirical evidence that the northward water transport north of the equator was greater than was predicted by wind patterns. They explained this, in part, by suggesting that the strong shears between the zonal currents of the region reduce the effective Coriolis parameter below its calculated value, allowing enhanced Ekman transport. They also suggested that the opposition of the NECC to the prevailing winds creates a greater stress north of 5°N, which would also allow increased Ekman transport. In contrast, a model by Meinen (2005) found that the northward meridional exchange of warm water was usually blocked by a vorticity front under the ICZ (see Fig. 15). The model suggested that the northward meridional transport in this region becomes progressively reduced with greater distance away from the equator, becoming negligible by 15°N. There was strong variability in meridional transport in different years, with enhanced movement during El Niños and reduced transport in La Niñas. Even during years of strong transport, warm water discharged across 5° and 8°N could not be tracked as far as 10°N, and most of the meridional transport in the region was across the equator to the south (Meinen, 2005). Brown et al. (2007) suggested that the poleward flow south of 8°N should be less strongly developed than suggested by Wyrtki and Kilonski (1984) or Johnson et al. (2001), and that the meridional flow south of 2°N would be equatorward and downwelled. Seasonally, their model predicted southward flow across the equator west of 140°W in summer, with northward flow from November to April. They suggested that the greater amount of the northward transport found by Johnson et al. (2001), vs. that which was predicted by their model, was due to the noise and brevity of the time series in Johnson et al.'s (2001) data. Clearly, more research is needed to understand meridional transport in the equatorial central Pacific.

Meridional flow from tropical instability waves confounds empirical observations of upwelling-induced meridional flow (Johnson et al., 2001; Brown et al., 2007). Tropical instability waves are westward-moving cusp-like signals detected by satellites measuring sea surface height and temperatures, among other techniques (Tomczak and Godfrey, 2005). They are strongly developed features of the equatorial Pacific that influence meridional transport and biological activity (Johnson, 1996; Strutton *et al*., 2001). For example, Johnson et al. (2001) suggested that a peak of variability in meridional transport at ca. 4.5°N might be a result of tropical instability waves. Foley et al. (1997) and Strutton et al. (2001) found enhanced chlorophyll density, and by implication enhanced primary productivity, at tropical instability wave fronts. Tropical instability waves develop at least in part from the shear along the separation zone between the SEC and NECC during June–February, and are most pronounced between 110° and 140°W (east of the region of concern for this paper), have periods of 20–25 days, and wavelengths on the order of 1000 km (Tomczak and Godfrey, 2005). Lyman et al. (2007) argued that what appears to be a single broad band of tropical instability waves in oceanographic data is, in theory, the resonant signal from two wave-forms which are best expressed with mean periods of ca. 17 days at ca. 2°N and ca. 33 days at ca. 5°N. These different tropical instability wave functions at different latitudes are clearly relevant to transport at the northern and southern groups of the U.S. central Pacific islands. Most authors discuss them as wave-forms, but Flament et al. (1996) and Kennan and Flament (2000) have argued that, upon inspection at finer scales, they are actually westward propagating trains of anticyclonic eddies.

Regardless of their wave or vortex nature, potential meridional transport of larvae during displacement by tropical instability waves could be an interesting topic for future research in the region of the U.S. equatorial Pacific islands. As evidence for such potential transport by tropical instability waves, Chavez et al. (1999) observed eastward advection of a concentrated chlorophyll patch within the central region of a propagating tropical instability wave at 105 (±5) km day^{-1}, or 1.2 m s^{-1}. Although they did not discuss meridional transport, the meanders shown in their Figs. 2 and 5 indicate that there was likely a substantial meridional component to this transport. Fronts of tropical instability waves also have been found to have chlorophyll concentrations and herbivorous zooplankton biomass enhanced at their leading edges (Barber et al., 1996) or decreased at the trailing edges (Gaudy et al. 2004). Conditions of enhanced plankton biomass, together with concentration of plankton by convergence in the fronts, could be favorable for the survival of fish larvae if changes in plankton community structure allow, provided that ichthyoplankton predator populations are not also enhanced there (Bakun, 2006). Variations across the fronts and convergences of temperature, a major influence on larval growth and developmental rates, could also have great influence on the survival and transport of fish larvae in these features, in conjunction with food and predator concentrations.

Eddies are thought to generally have a significant effect on larval transport and recruitment in fishes (e. g., Boehlert and Mundy, 1993; Cowen, 2002; Sponaugle et al., 2005). Howland, Baker, and Jarvis are in an unusual position for the influence of eddies, however, because they are in a region in which the Coriolis force, a significant parameter in eddy dynamics, is minimal (5°S – 5°N; Meinen, 2005). Nevertheless, there is ample evidence that eddies form in the southern and particularly northern parts of this latitudinal band (Flament et al., 1996; Kennan and Flament, 2000). In addition, eddies can form at even short distances from the equator when topography alters the prevailing flow, as discussed for divergent anticyclonic forced eddies by Bakun (2006). Eddies in the region of the U.S. equatorial Pacific islands are shown in satellite sea surface altimetry images (e. g., Fig. 15) in which well developed cyclonic eddies are present just north of Kingman Reef and Palmyra Atoll, less developed anticyclonic eddies are present between that region and the region of Howland, Baker, and Jarvis, and weak meanders or cyclonic eddies are present in the vicinities of the latter three islands (see also the discussion and Fig. 5 in Howell and Kobayashi, 2006). Eddies can influence meridional water transport and, therefore, distributions of larvae, either by direct transport or, as suggested by Meinen (2005) by creating fronts that block transport. The biological effects of eddies in the equatorial central Pacific deserve more research.

The effects of divergent upwelling, Ekman transport, tropical instability waves, and eddies on meridional transport are not independent, with interference of those combined processes creating localized enhancement and diminution of transport. For example, Johnson et al. (2001) noted that an analysis of drifter trajectories suggested that equatorial upwelling was more localized than the mean results of studies such as theirs would indicate, with concomitant greater velocities within those areas of localized upwelling than found in their averaged results. The possibility that larval dispersal and colonization events at the equatorial Pacific islands may be dependent on mechanisms that are ephemeral and spatially localized therefore needs more investigation.

As a cautionary thought, there is increasing evidence that present-day biogeographic patterns in tropical Pacific marine organisms may have more to do with ancient oceanographic regimes than they have to do with contemporary latitudinal oceanographic currents. For example, there is evidence that populations of some reef organisms had ancient genetic connections along southeast/northwest directions, parallel to existing central Pacific island chains, instead of along east-west directions that would be indicated by present-day geostrophic currents in the central Pacific (Benzie, 1999). In addition, it is clear that oceanographic currents have changed in the period of shore-fish evolution due to variations in climate, including glacial and interglacial periods, as well as more ancient changes in the configurations of continents and ocean basins.

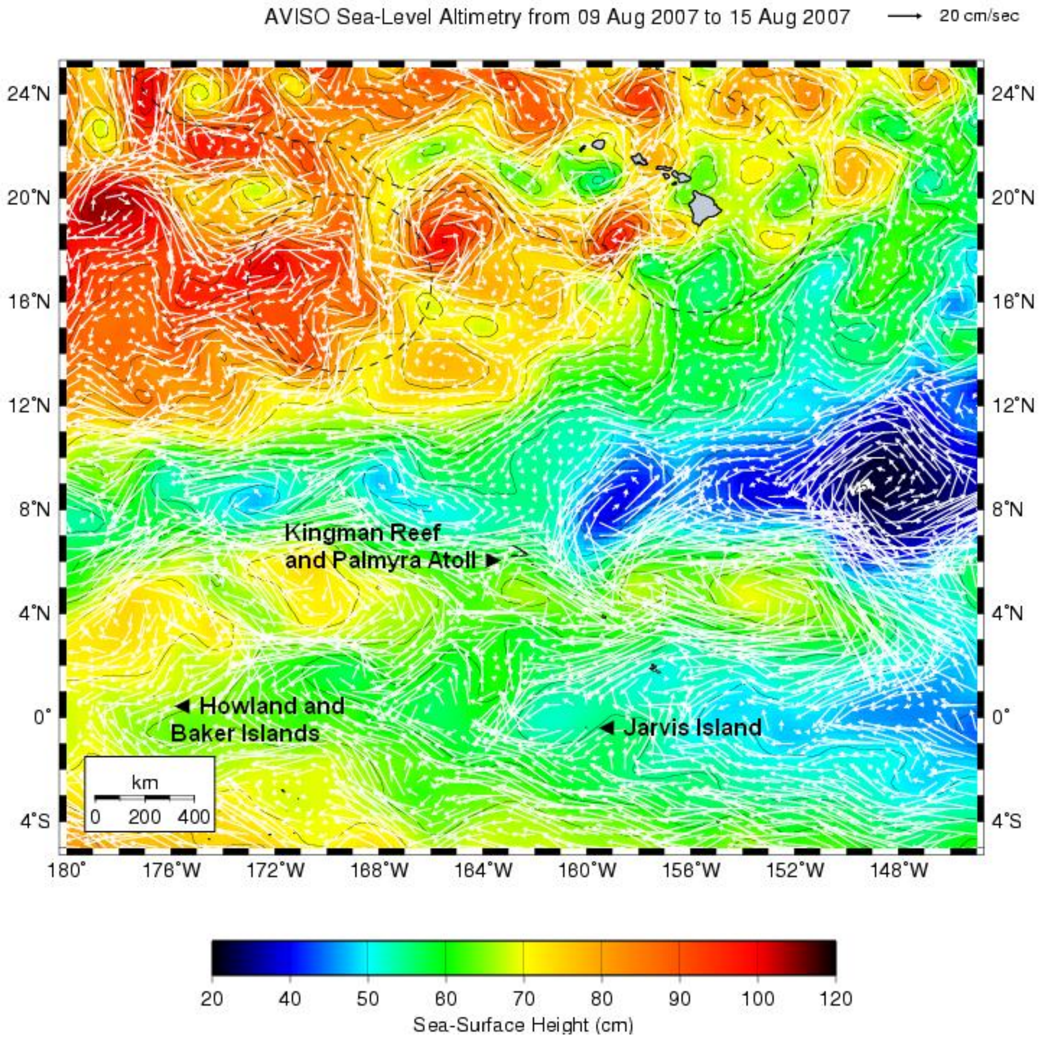

Figure 15. AVISO Sea-Surface Height map for the Line Islands region, 9–15 August 2007. Image courtesy of Lucas Moxey, NOAA OceanWatch - Central Pacific program (http://coastwatch.nmfs.hawaii.edu/oceans.html).

Regional Endemics, Peripheral Isolation, and Problems in Interpreting Their Distributions in Relation to Biogeographic Patterns of Central Pacific Shore Fishes

Speciation by peripheral isolation is a strong component in central Pacific shore-fish phylogenetic history. It clearly is an important part of the evolution of fishes in the Hawaiian Islands, Marquesas, and Easter Island, where a high percentage of species are found nowhere else in the world and presumably evolved *in situ* (Randall and Earle, 2000; Randall et al., 2005; Mundy, 2005; Randall, 2007). Peripheral isolation has been proposed, as the centripetal or vortex model of biogeography (Jokiel and Martinelli, 1992), as a general alternative to the center of origin or centrifugal model for Indo-Pacific biogeography (Briggs, 2000). Neither generalized model is supported by the diversity of origins in phylogenetic and phylogeographic analyses of shore fishes discussed in the previous sections on phylogeography, phylogenetic analysis, and geologic history, nor for other Indo-Pacific organisms (Reaka et al., 2008).

Although the vast majority of shore-fish species at the U.S. Line and Phoenix Islands have broad geographic ranges that give no indication of origins as central Pacific peripheral isolates, there are a small number of species that are central Pacific island endemics. Most of these are restricted to the Line Islands, Phoenix Islands, Cook Islands, or French Polynesia, including the Marquesas: *Pseudanthias olivaceus*, *Mulloidichthys mimicus* (also recorded as a waif from the Hawaiian Islands), *Kuhlia petiti, Cirrhitops hubbardi*, *Paracirrhites xanthus*, *Dascyllus auripinnis*, *Priolepis squamogena*, *Ctenochaetus flavicaudus*, and *Pervagor marginalis*. Other Marquesas, Line, and Phoenix Islands' endemics include *Myripristis earlei* (see Randall et al., 2003), *Apogon lativittatus*, and *Chaetodon declivis*, with subspecies recognized for the Marquesan (*C. declivis declivis*) and Line Islands populations (*C. declivis wilderi*) (see Randall, 2001a). Two species at the Line Islands are otherwise Hawaiian Island and Johnston Atoll endemics: *Kyphosus hawaiiensis* and *Eviota epiphanes*. The Line and Phoenix Island endemic shore-fish species are *Pseudanthias aurulentus*, *Chrysiptera albata*, *Bodianus prognathus*, *Coris centralis*, *Parapercis latus*, and *Amblyeleotris harrisorum*. Randall et al. (2003) suggested that *Myripristis earlei* became established in the Phoenix Islands from down-current dispersal of larvae from the Marquesas, although they did not know at that time that *M. earlei* is also abundant in the central Line Islands (J. Earle, BPBM, pers. comm., May 1999). They also suggested that *M. earlei* evolved as a peripheral isolate of *M. berndti* in the Marquesas after colonization during the past few thousand years, followed by a second colonization, without differentiation, of the Marquesas by *M. berndti* in more recent times. The Marquesas appear to be somewhat isolated from the Societies and Tuamotus by opposing gyral currents separated by shears and fronts. The hypothesized connection between the Marquesas and the main Phoenix Islands may partially explain why the shore-fish fauna of the main Phoenix Islands in our analysis was more similar to that of French Polynesia than to the fauna of the Line Islands, Howland, and Baker.

Connolly et al. (2003) found an excess of small-range shore-fish species in the South Pacific near 20°S relative to the prediction of their null-hypothesis mid-domain model. They suggested that the excess was due to a group of South Pacific endemic species found between the Great Barrier Reef and French Polynesia. *Stegastes aureus*, which ranges west to New Caledonia, and *Zebrasoma rostratum*, ranging west to American Samoa, are two such shore-fish species that range into the Line and Phoenix Islands. *Gymnapogon vanderbilti* may be another example (Gon, 2002). These species may have likely evolved as central-South Pacific peripheral isolates.

The Line and Phoenix Islands are in a region of overlap between several tropical Pacific faunal provinces - the northwestern, southeastern, central, Hawaiian, and possibly a south-central Pacific isolated island province (Maragos et al., 2008; this study). In addition, the fish fauna of the Line and Phoenix Islands are strongly influenced by the gradient of declining species numbers going eastward of the IAA. However, every island group in the central Pacific has some fish species that have their eastward or westward range limits there. In this regard, the faunal provinces of the central Pacific shore-fish biota might better be thought of as diffuse entities, i.e., as population centers with diminishing numbers of component species at increasing distances from the areas where the greatest numbers of those species are found (J. Earle, BPBM, pers. comm., 22 Sept.

2008). Those may also be areas where small-range endemic species have evolved by peripheral isolation. Candidate areas include the isolated southern Line Islands (J. Earle, BPBM, pers. comm., May 2009), the Marquesas, the Society and Tuamotu Archipelagos, the Marshalls, the Cook Islands, Fiji and Samoa, and, to a much lesser extent, the Phoenix Islands and main Line Islands. The Hawaiian Archipelago, including Johnston Island, might also be included, although very few species found elsewhere in the Pacific can unequivocally be interpreted as Hawaiian endemics that have dispersed outward.

There are conceptual difficulties in identifying species that originated as peripheral isolates at islands and have become more widespread by subsequent dispersal. Inferences can be drawn from species with very limited distributions, such as those few known only from the Hawaiian, Johnston, and the Line or Phoenix Islands. Inferences become difficult for those species which have wider central Pacific distributions (e. g., *Apolemichthys griffisi*, *Centropyge loricula*), even if they may have evolved as species in one of the archipelagos with a high percentage of endemics (e. g., the Hawaiian and Marquesas Islands).

These difficulties are particularly acute in the interpretation of potential occurrences of otherwise endemic Hawaiian and Johnston Atoll species at the Line Islands. The existence of a few Hawaiian-Line Island species makes it difficult to determine the validity of a few early records of otherwise endemic Hawaiian Island species in the Line Islands. These include *Thalassoma duperrey* and *Chlorurus perspicillatus*. Those records would be easily discounted as misidentifications or mislabelings of collection localities for museum specimens were it not for the verified records of two otherwise Hawaiian species in the Line Islands (*Kyphosus hawaiiensis* and *Eviota epiphanes*). (Some of the records of *C. perspicillatus* may be misidentifications of *Scarus festivus*, a species that is similar when seen in the field [J. Earle, BPBM, pers. comm., May 2009]). Evaluation of the validity of Line or Phoenix Island records of otherwise endemic Hawaiian and Johnston Island species therefore depends on the recency of the records and whether the identifications were done by taxonomists who were knowledgeable about the identifying characters of the species. The two presumed Hawaiian Island endemics reported in the late 20th Century from the Line Islands are assumed by us to be species that originated as Hawaiian Island endemics and dispersed southward. This hypothesis is based largely on the high percentage of endemic shore-fish species found in the Hawaiian Islands, indicating that it is a location of speciation through peripheral isolation. Alternative hypotheses are that these are species that originated as Line Island endemics and dispersed to Johnston Atoll and the Hawaiian Islands, or that they are species that were more widespread, but that have become extinct elsewhere in their original ranges.

The appearance of waifs in the Hawaiian Islands by likely dispersal from sources to the south (e. g., *Mulloidichthys mimicus*, *Halichoeres marginatus*, *Zebrasoma rostratum*), the opposite distributional phenonomenon, is well documented (Randall, 2007). These records were possible largely because there is a large, resident population of knowledgeable and watchful fish enthusiasts in Hawai`i. The near absence of such a resident population in the U.S. Line and Phoenix Islands, and perhaps lack of communication about unusual sightings in the Kiribati Line and Phoenix Islands, makes records of dispersal from Hawai`i to islands southward less likely than records of waifs in the Hawaiian Islands. This creates a sampling bias in our ability to record evanescent dispersal events in different directions to and from the Hawaiian Islands and other central Pacific areas of peripheral isolation. Identification of species that originated as peripheral isolates but later dispersed outward from their islands of origin is one of the major challenges to understanding the evolution of central Pacific shore fishes.

CONCLUSIONS

Howland, Baker, Jarvis, Palmyra, and Kingman Reef are unique among United States possessions in having reef fish species found nowhere else in the country. They include species that are part of a poorly understood endemic central Pacific fauna. The isolated islands of the central Pacific remain among the most poorly explored places on the Earth.

Our knowledge of the reef fish fauna is incomplete because of limited sampling of small, cryptic, nocturnal, and deepwater species. The wish to complete our knowledge of the reef fish species at these islands will have to be moderated by the requirements emplaced to give the islands their present protection as U.S. Fish and Wildlife Service wildlife refuges.

The oceanography of the region, as it influences biogeographic patterns of reef organisms, is understood at present only in its simplest, first-order form. The effects of mesoscale features such as tropical instability waves, fronts, and eddies deserve much more investigation in this region.

More investigation of the phylogeography of central Pacific reef fishes is needed to understand the evolution of this fauna. Both traditional morphology-based phylogenetic analyses and genetic phylogeographic studies need to be done that include endemic central Pacific species, to begin to understand their origins. That research will likely also increase understanding of basic concepts of what marine fish species are, in a general sense. The isolation and unique geologic histories of the central Pacific islands will provide insights into reef-fish evolution that can test the universality of hypotheses proposed from studies of continental species, and further our understanding of the unique evolutionary aspects of the biota of this fascinating region.

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Note added in proof

An additional paper on the fish fauna of Kingman Reef that appeared after this paper was written is:
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