

Improbable Colonists: Helminth Parasites of Freshwater Fishes on an Oceanic Island¹

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Abstract—Eleven species of helminth parasites were found in 5 species of native gobioid and 4 species of introduced poeciliid stream fishes from 29 aquatic habitats on the islands of Hawai‘i, O‘ahu, and Kaua‘i in the Hawaiian archipelago. Mechanisms by which these parasites originally colonized Hawai‘i, either naturally or by means of human activities, were investigated. Two sources of native, or naturally occurring parasites, were identified: marine fishes and migratory piscivorous birds. Four native species, of which the roundworm *Spirocamallanus istiblenni* was the most numerous, originated in marine fishes. An additional 3 parasites used migratory piscivorous birds as final hosts and fishes as intermediate hosts. The remaining 4 species of parasites were introduced into Hawai‘i by man. Three of these species of helminths, a roundworm *Camallanus cotti*, a tapeworm *Bothriocephalus acheilognathi*, and a leech *Myzobdella lugubris*, introduced when exotic poeciliid fishes were brought to the archipelago, were the most widespread and abundant helminths parasitizing stream fishes. Biological characteristics that enhance the probability of colonization of oceanic islands by parasites include: broad host specificity, the utilization of vagile final hosts, and the use of common and ubiquitous intermediate hosts. The colonization potential of both allogenic and autogenic parasites of freshwater fishes on oceanic islands is compared with results of previous studies of allogenic and autogenic colonists of continental islands.

Introduction

When scientists examine the flora and fauna that populate oceanic islands, it is important to distinguish between those species that colonize the islands by natural means and the species that are introduced to the islands by human activities. Among the most improbable colonists of oceanic islands are species of freshwater fishes, for it is difficult to imagine a mechanism by which a freshwater fish could

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reach an oceanic island without human assistance. In the Hawaiian archipelago, the native stream fish fauna is depauperate and consists of only 5 species (Fitzsimons & Nishimoto 1995). The taxonomic relationships and life histories of these 5 species, however, immediately suggests the manner by which colonization was accomplished. All 5 species of native Hawaiian stream fishes are gobioids, 4 gobies (Gobiidae) and 1 sleeper (Eleotridae). Each of these stream fishes is amphidromous, meaning that although the adult fishes are restricted to fresh water, the larvae of these species are required to spend the early portion of their life history in the ocean (Mc Dowall 1988). Following a planktonic marine larval phase, the post-larval fishes return to stream mouths, and move upstream to occupy the habitats in which they are found as adults (Kinzie 1991). Recently, Radtke & Kinzie (1996) have shown that even the most isolated of these stream fishes, i.e. adult *Lentipes concolor* living above waterfalls of both permanent and intermittent streams have patterns of strontium deposition in their otoliths that indicate that they began life as marine larvae. Kinzie (1990) hypothesized that initial colonization of Hawaiian streams by the ancestral amphidromous gobioids occurred as planktonic marine larvae. Indeed, although many marine gobies occur in Hawai'i, they are not the closest relatives of stream gobioids. Rather, the sister taxa of the amphidromous stream gobioids in Hawai'i are amphidromous gobioids found in streams elsewhere in Micronesia (Watson 1991, 1992).

This paper presents data on the colonization of these native Hawaiian stream fishes by helminth parasites. Their colonization of oceanic islands is perhaps even more improbable than that of freshwater fishes. Font & Tate (1994) offered data

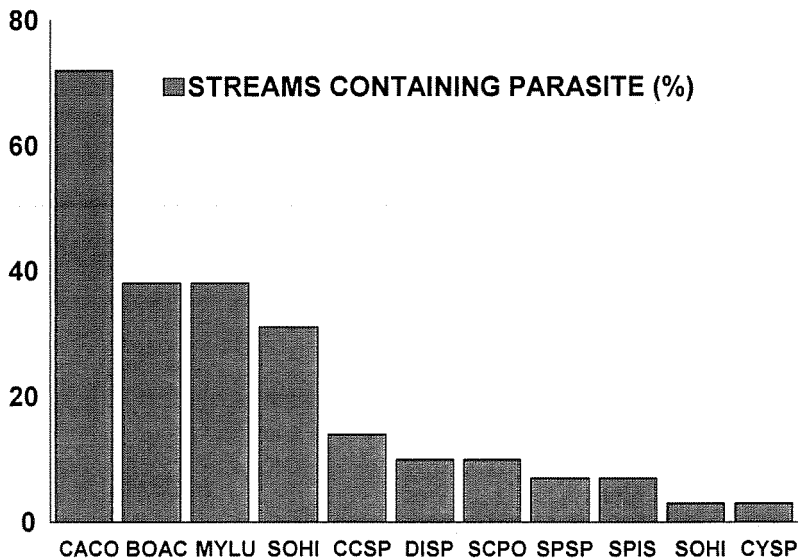


Figure 1. Frequency of occurrence, expressed as a percentage, of helminth parasites in 29 aquatic habitats in the Hawaiian archipelago. Abbreviations of scientific names of parasites are given in Table 2.

that indicated that the original larval amphidromous gobioids that first colonized Hawaiian streams brought no helminth parasites with them to Hawai‘i. Yet, in that same paper, they presented a list of 9 species of helminths that parasitized native Hawaiian stream fishes. It is important, then, to understand how these stream fishes were initially colonized by helminths, and to determine what life history characteristics of helminths increase the likelihood of colonization of oceanic islands. Much useful information on the ecology of helminth colonists of freshwater fishes on islands has been provided by the elegant studies of Kennedy et al. (1986), Esch et al. (1988) and Marcogliese (1992). However, the islands that they studied were continental islands where the constraints imposed by the extreme ecological isolation of oceanic islands do not apply. Esch et al. (1988) proposed the application of the felicitous terms “allogenic” and “autogenic” to parasites. These terms provide a conceptual framework for our understanding of the ecology of parasite colonization. Briefly, Esch et al. stated that autogenic parasites are species that could complete their entire life cycles within the confines of a single freshwater habitat. An example of an autogenic helminth parasite with a direct life cycle would be a fish leech which is transmitted directly from one fish host to another fish host. An autogenic helminth with an indirect life cycle would be a fish tapeworm in which the adult parasite occurs in a fish and the larval tapeworm occurs in an aquatic copepod. Conversely, allogenic parasites have life cycle stages that require non-aquatic hosts that transport them from a freshwater habitat where only a portion of the life cycle occurs. Some part of the life cycle occurs in a non-aquatic environment. An example of an allogenic parasite would be a trematode that uses a freshwater snail as a first intermediate host, a fish as a second intermediate host for larval development, and a fish-eating bird as the final host for the adult worm. The bird could transmit the parasite from one stream to another when parasite eggs are released in the bird’s feces to infect aquatic snails. Esch et al. (1988) applied their allogenic/autogenic concept to potential parasite colonists and presented both empirical data and theoretical reasons that indicated that allogenic parasites that could be carried from one aquatic habitat to another by vagile terrestrial hosts offered a greater probability of colonizing new habitats. Herein, I present data on the distribution of helminths in Hawaiian streams and provide information on the biological characteristics of helminths that allows predictions to be made regarding their ability to colonize oceanic islands and their subsequent spread among streams of an archipelago subsequent to the initial colonization event. The relationship of colonization of parasites by natural and by anthropogenic mechanisms is also examined.

Materials and Methods

Five species of native gobioid stream fishes, *Eleotris sandwicensis* (‘o‘opu ‘akupa) (Eleotridae), *Lentipes concolor* (‘o‘opu alamo‘o) *Sicyopterus stimpsoni* (‘o‘opu nōpili) *Awaous guamensis* (‘o‘opu nākea) and *Stenogobius hawaiiensis* (‘o‘opu naniha) (Gobiidae) and 4 species of introduced live bearers *Poecilia reticulata* (guppy) *P. mexicana* (shortfin molly), *Xiphophorus helleri* (green swordtail)

and *Gambusia affinis* (mosquitofish) (Poeciliidae) were examined for helminth parasites. They were collected from 29 aquatic habitats on the islands of Hawai'i, O'ahu, and Kaua'i, including permanent and intermittent streams, rivers, agricultural ditches, and a spring fed pond. All stream reaches were examined from the mouth to headwaters above waterfalls. A variety of collecting techniques were employed, including seining, spearing, hook and line fishing, dipnetting, and trapping. Most fishes were transported alive to the laboratory and held in aerated containers until necropsied within 72 hr of capture. Speared fishes were held on ice and examined within 3 hr. Some fishes were preserved in the field in 10% formalin for later examination.

Necropsy techniques used for parasitological examination employed the methodology described by Font & Tate (1994). Briefly, following anaesthization in TMS-222, all external surfaces, viscera, and musculature were examined under magnification. Parasites were enumerated and fixed according to methods appropriate for each taxonomic group. Subsequently, using standard parasitological techniques, whole mount specimens were made and examined microscopically so that specific identifications could be made. Voucher specimens have been deposited in the United States Parasitological Collection.

RESULTS AND DISCUSSION

A total of 11 species of helminth parasites were found in native gobioid stream fishes. For each of these species of parasites, the manner of original colonization of streams (i.e. natural or introduced by humans) was determined, as well as the probable source of the parasite from which colonists were recruited (Table 1). Table 1 also indicates whether the parasite occurs as a juvenile or larval stage, utilizing the fish as an intermediate host, or whether the parasite occurs as an adult, using the fish as a definitive (= final) host.

Table 1. Helminth parasites of native Hawaiian stream fishes, including method of colonization of the Hawaiian archipelago, whether naturally (i.e. native) or by human introduction, source of colonists, life cycle stage that occurs in fish, and type of life cycle host represented by the fish.

Scientific name	Colonization	Source	Stage	Type host
<i>Southwellina hispida</i>	native	birds	cystacanth larva	intermediate
Cyclophyllidea	native	birds	cysticercus larva	intermediate
Strigeoidea	native	birds	metacercaria larva	intermediate
<i>Spirocamallanus</i> <i>istiblenni</i>	native	marine fish	adult	definitive
<i>Scolex polymorphus</i>	native	marine fish	plerocercoid larva	intermediate
Didymozoidae	native	marine fish	larva	intermediate
<i>Cystobranchus</i> sp.	native (?)	marine fish (?)	adult	definitive
<i>Camallanus cotti</i>	introduced	exotic fish	adult	definitive
<i>Bothriocephalus</i> <i>acheilognathi</i>	introduced	exotic fish	adult	definitive
<i>Myzobdella lugubris</i>	introduced	exotic fish or crustacean	adult	definitive
<i>Ascocotyle tenuicollis</i>	introduced	exotic fish	metacercaria larva	intermediate

Two sources of native parasites were identified, piscivorous birds and marine fishes. Adult specimens of *Southwellina hispida*, a spiny-headed worm (Acanthocephala) have been reported previously from both Palearctic and Nearctic herons and the cystacanth larvae of this species are known from Old World and New World fishes and amphibians. Herons, e.g. the black crowned night heron, *Nycticorax nycticorax*, have colonized the Hawaiian archipelago naturally (Pratt et al. 1987), and likely introduced this spiny headed worm to native stream fishes. Interestingly, this parasite has been reported from herons on another isolated oceanic archipelago, the Galapagos Islands (Van Cleave 1940). Two species of flatworms were rare (prevalence <1%) parasites of stream fishes. Because of their immaturity, neither the larval cyclophyllideans (Cestoda) nor strigeoids (Trematoda) could be identified more specifically, but both groups are known to use migratory birds as definitive hosts and are assumed to have colonized Hawai'i in this manner. In addition, native lymnaeid snails which can host strigeoids were found in the streams where native fishes were infected with these metacercariae.

Marine fishes are the sources of all remaining native helminths parasitizing stream fishes. The most common hosts for the roundworm (Nematoda) *Spirocamallanus istiblenni* are tidepool and coral reef fishes (Noble 1966, Hasagawa et al. 1991, Rigby & Font, in press) and the proximity of these habitats to lower reaches of streams accounts for its occasional occurrence in sleepers, *Eleotris sandwicensis* that occupy stream mouths. Both *Scolex polymorphus* and didymozoids are flatworms and as larvae they parasitize marine fishes when these fishes ingest infected copepods. Amphidromous gobioids may feed on copepods during their marine larval stage and become infected, carrying these marine parasites into the streams. Because the normal definitive hosts of these helminths are marine teleosts and elasmobranchs that become infected by eating smaller fishes harboring the larval parasites, the rare occurrence of these parasites in streams represents a dead end for both parasites. The discovery of a single specimen of a leech (Hirudinea) in the genus *Cystobranchus* parasitizing a sleeper in the mouth of one stream provides an inadequate amount of information to account for its occurrence in Hawai'i.

All remaining species of parasites listed in Table 1 have been introduced to Hawai'i by human activity, namely the release of exotic fishes into Hawaiian streams. Each of these four species has been found in introduced poeciliid fishes and has transferred to native gobioid stream fishes living syntopically in streams with exotic fish hosts. They were absent from streams in which exotic fishes did not occur. Both the roundworm *Camallanus cotti* and the tapeworm *Bothriocephalus acheilognathi* occur commonly in many species of freshwater fishes of the Orient, have been disseminated globally by man, and use ubiquitous copepods as intermediate hosts. The leech *Myzobdella lugubris* has been reported frequently from freshwater fishes in North America and Sawyer et al. (1975) has recorded the occurrence of cocoons of *M. lugubris* cemented to the carapace of blue crabs, *Callinectes sapidus*, from low salinity estuaries of the Gulf of Mexico. Thus, either blue crabs or a species of North American fish which have been introduced into Hawai'i (Eldredge 1995) could be the source of this leech which is now wide-

spread in Hawaiian streams. Metacercariae of the trematode *Ascocotyle tenuicollis* infect the hearts of mosquitofish, *Gambusia affinis* in North America and in Hawai'i, they also parasitize *E. sandwicensis* when these sleepers occur syntopically with infected introduced mosquitofish. Thiarid snails, native to the Far East, widely disseminated throughout Micronesia, and introduced by man into North and South America, also occur in Hawai'i, and serve as the first intermediate host for *A. tenuicollis* in the archipelago. Piscivorous birds harbor adults of this heterophyid trematode.

Table 2 records the Hawaiian streams and other freshwater habitats in which each of these 11 species of parasites were found and presents the ranked order of prevalence (percentage of fish infected with each parasite). By far, the most widespread and prevalent parasite was the introduced nematode, *Camallanus cotti*. Of the 29 aquatic habitats included in this study, *C. cotti* was found in 21 (72%) of these, and was the most prevalent parasite in 20 of the 21 streams in which it occurred. This parasite also displayed the broadest host specificity, infecting all species of exotic poeciliids and 4 of the 5 native gobioids. Only *Sicyopterus stimpsoni* was uninfected with this roundworm, a consequence of its diet which does not include copepod intermediate hosts (Font & Tate 1994). Two more introduced parasites, the tapeworm *Bothriocephalus acheilognathi* and the leech *Myzobdella lugubris* ranked next with regard to their distribution among streams and typically ranked second and third in prevalence. The final introduced species *Ascocotyle tenuicollis* was not widely distributed among streams, a consequence of its dependence on thiarid snail intermediate hosts which are uncommon in Hawaiian streams.

The most widely distributed native parasite was the spiny-headed worm *Southwellina hispida*, a parasite that is disseminated by its avian definitive hosts. The marine nematode *Spirocamallanus istiblenni* was locally common in sleepers at Lokoaka Pond and near the mouth of the Wailoa River because of their proximity to infected tidepool fishes, especially zebra blennies, *Istiblennius zebra*, but was uncommon elsewhere, indicating that its movement into freshwater habitats is dependent upon local ecological conditions. All other species of parasites were found at low prevalence (<10%) in fishes and were restricted to few (<15%) streams.

From these data we can detect patterns of parasite distribution and obtain insight regarding those biological characteristics of parasites that make colonization and dispersal more or less probable. Clearly, one important attribute of parasites that have high colonizing potential is broad host specificity, and the introduced parasites *C. cotti*, *B. acheilognathi*, and *M. lugubris* serve as excellent examples. Colonization of freshwater habitats on oceanic islands is definitely more probable for parasites of migratory birds, and this same dispersal mechanism also enhances the dissemination of parasites among streams within an archipelago, as is exemplified by *S. hispidus*. Conversely, data obtained from these stream fishes indicate that colonization of freshwater fishes by marine parasites is unimportant, at least in Hawai'i. Three marine helminths were found in freshwater fishes, but each of these were either rare (*Scolex polymorphus* and didymozoid larvae) or restricted to ecologically unusual habitats (*Spirocamallanus istiblenni*). The occurrence in fresh

Table 2. Ranked order of prevalence (percentage of fishes infected) of helminth parasites in native gobioid stream fishes and introduced fishes in Hawai'i. Number 1 indicates highest prevalence.

	Caco	Boac	Mylu	Disp	Scpo	Sohi	Aste	Srsp	Cysp	Ccsp	Spis
Hawai'i											
H-HAKA	1	3	2	4					6	5	
H-HAMA	1										
H-HONO	1		2								
H-KEAN	1										
H-KOHA	1										
H-KOHK	1		2								
H-KOLE	1	2									
H-LOKO		3	5			2	4				1
H-MANO	1										
H-NANU	1			2							
H-WAIK	1										
H-WAIL	1	3	2			5					4
H-WAIM	1										
H-WAIU	1										
O'ahu											
O-HAKI	1	3				2					4
O-KAHA	1					2					3
O-KAHU		1						2			
O-KAIP											
O-KAIW											
O-KALU	3		1			2					4
O-KAMO	1										
O-WAIA	1	2	4			3					
O-WAIN	1	2	4			3					
O-WAIH	1	2	4			3					
O-WAIK	1	2	3			4					
O-WAIM			1								
Kaua'i											
K-HANA					2	1					
K-NUAL					2	1					
K-WAIN		1		2	3			4			

Abbreviations of scientific names. Caco *Camallanus cotti*, Boac *Bothriocephalus acheilognathi*, Mylu *Myzobdella lugubris*, Disp Didymozoidae, Scpo *Scolex polymorphus*, Sohi *Southwellina hispida*, Aste *Ascocotyle tenuicollis*, Srsp Strigeoidea, Cysp *Cystobranchus* sp., Ccsp Cyclophylloidea, Spis *Spirocamallanus istiblenni*.

Abbreviation of names of streams and other aquatic habitats. Hawai'i (H) — HAKA Hakalau Stream, HAMA Hamakua Ditch, HONO Honoli'i Stream, KEAN Keanuimano Stream, KOHA Kohala Ditch, KOHK Kohakohau, KOLE Kolekole Stream, LOKO Lokoaka Pond, MANO Manoloa Stream, NANU Nanue Stream, WAIK Wailuku River, WAIL Wailoa River, WAIM Waiku'amalo Stream, WAIU Wai'ula'ula Gulch. O'ahu (O) — HAKI Hakipu'u Stream, KAHAKAHA Kahana Stream, KAHU Kahuku Stream, KAIP Kaipapau Stream, KAIW Kaiwainui Marsh, KALU Kaluanui Stream, KAMO Kamo'oali'i Stream, WAIA Waiahole Stream, WAIN Wai'anu Stream, WAIH Waihe'e Stream, WAIK Waikane Stream, WAIM Waimea River. Kaua'i (K) — HANA Hanakapi'ai Stream, NUAL Nu'alolo Stream, WAIN Wainiha River.

water of the first 2 of these 3 species represents dead ends for the parasites where completion of the life cycles in streams is highly unlikely. Thus, their presence in freshwater is without ecological or evolutionary significance.

It is important to consider also attributes of parasites with limited colonizing ability to appreciate how their biological characteristics affect, in a negative manner, the probability of colonization. Although the habitats of marine fishes, many of which harbor monogene parasites (Yamaguti 1968), are traversed by larval amphidromous gobioids, these gobioids do not become parasitized. Lack of transfer of parasites from marine to freshwater fishes is most likely due to the extremely narrow host specificity of most monogenes, but may also be due to the intolerance of freshwater by these marine ectoparasites, or even to their inability to attach to the minute gills of larval fishes. Yamaguti (1970) also recorded hundreds of species of trematodes parasitizing marine fishes in Hawai'i, yet none of these infect native gobioid stream fishes. Apparently the inability of these parasites or their intermediate hosts to tolerate the salinity extremes of both of these aquatic environments represents a barrier to their colonization of fresh water. Narrow host specificity also decreases the probability of spread of parasites. We found several species of freshwater monogenes in the genus *Salsuginus* on introduced stream poeciliids, but none of these infected syntopic native gobioids. Similarly, the narrow host specificity of two species of introduced heterophyid trematodes *Centrocestus formosanus* and *Haplorchis taichui* prevented their transfer from syntopic poeciliids to gobioids.

Some insight may be gained by examining a list of parasites infecting poeciliid fishes in their native ranges to determine the probability of colonization. For instance, Hoffman (1967) records 19 species of helminths from North American mosquitofish, *Gambusia affinis*, but 18 of these were *not* introduced into Hawai'i with the introduction of this fish. It is more difficult to explain negative data, i.e. why a parasite has been unsuccessful as a colonist, and in some cases, the reason may be due to chance. But perusal of Hoffman's list shows that many of these non-colonists have very specific dependence upon intermediate hosts which are not found in Hawai'i. Clearly, parasites that do not depend upon intermediate hosts have greater colonizing potential than those parasites that do have intermediate hosts. And with regard to the latter category of parasites, those that have intermediate hosts with small geographic ranges or restrictive ecological requirements are less likely to colonize than parasites that have common, ubiquitous, or cosmopolitan intermediate hosts. For example, it is apparent that the use of copepod intermediate hosts by both *C. cotti* and *B. acheilognathi* has not limited their global dispersal because freshwater copepods have been transported globally and are common components of the fauna of oceanic islands.

Colonization of the Hawaiian archipelago by freshwater fish parasites is definitely limited; the native stream fish fauna harbors an assemblage comprised of only 7 native helminth parasites which is supplemented by 4 additional species that have been introduced by man. Among the factors responsible for this depauperate parasite community, the two most significant are the extreme isolation of the Hawaiian archipelago, situated 4000 km from the nearest mainland, and the de-

pauperate nature of the freshwater fish community itself. A reasonable hypothesis with regard to the parasite community of native stream fishes on certain other oceanic islands of Micronesia is that they are likely to be more species rich than that of Hawai'i. For example, it is predicted that the freshwater parasite community of Guam may be more diverse, based upon the fact that this oceanic island lies nearer to a continental landmass from which numerous freshwater fish parasites have been recorded, and because the native stream fish fauna of Guam is much more species rich than that of Hawai'i, containing not only more species of amphidromous gobioids, but also other non-gobioid species such as eels (J. Parham and S. Nelson, personal communication).

There exists much empirical data to support the hypothesis of Esch et al. (1988) that allogenic species which use vagile hosts have higher dispersal ability and should be more widespread geographically. Yet, the data gathered from the study of geographic distribution of Hawaiian stream fishes indicate that precisely the opposite pattern exists in this archipelago. The most widespread parasites are the roundworm *C. cotti*, the tapeworm *B. acheilognathi*, and the leech *M. lugubris*, each of which is autogenic, completing the entire life cycle in exclusively aquatic hosts. Furthermore, stream to stream dispersal of these 3 parasites in Hawai'i is prevented by geographical, physiological, and ecological barriers. Most Hawaiian streams lie within deep valleys and flooding events do not disperse fish among streams. The ocean also serves as a barrier to between stream dispersal of these freshwater parasites whose intermediate and final hosts are unable to withstand high salinities and cannot disperse from stream to stream via the marine environment. The answer to the seeming paradox of wider distribution of autogenic species in Hawai'i, however, is quite simple. These autogenic parasites with limited powers of dispersal are the most widespread species in Hawaiian streams because humans have introduced infected poeciliids into each and every stream where these parasites now occur in native fishes. Therefore, despite these data from Hawai'i, Esch's hypothesis is not invalidated. However, these results clearly demonstrate that studies of parasite colonization and dispersal must clearly distinguish between natural colonists and those parasites that have been introduced by man. Researchers must also realize the magnitude of the impact of anthropogenic introductions and the potential that these human effects have for confounding natural patterns of dispersal.

To illustrate this lesson with an anecdote, for the past 5 years, I have monitored, coincidentally, the population dynamics of *B. acheilognathi* infected mosquitofish in two artificial ponds on the campus of Southeastern Louisiana University. These ponds are separated by an earthen space that is <5m in width. In the south pond, 95% of the mosquitofish harbor these tapeworms at all times of the year. Yet, in the north pond, none of several thousand mosquitofish that have been examined has ever been found to be infected. It is a testament to the power of human intervention that a species of tapeworm that cannot traverse a 5m barrier on its own is now one of the most abundant parasites of freshwater fishes on the most isolated oceanic islands on our planet.

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