

Abstract—Intensive sampling at a site over the Galapagos Rift hydrothermal vents in the tropical eastern Pacific Ocean yielded 1338 shorefish larvae. At least 77 species in 29 families of shorefishes were identified using mitochondrial DNA barcoding and morphology. The species were not characteristic of the Galapagos or Cocos Island faunas, but included continental marine, brackish, and freshwater species not recorded on the offshore islands. Larvae of 3 species of freshwater amphidromous *Sicydium* gobies were present, including an undescribed species from the Rio Pichende in Panama. Also captured were larvae of 5 continental brackish and estuarine gobioid species and about 20 other species from soft-bottom, continental shelf habitats not found on the islands, some ranging south only to Panama or Colombia. Among reef fishes, the barcodes of 3 species did not match the Galapagos Islands population: the scorpionfish *Scorpaenodes* matched the continental nominal species, while the razorfish *Xyrichtys* species and chameleon wrasse (*Halichoeres dispilus*) matched populations from Panama, about 1000 km to the northeast. The range of sizes and ages of some species were especially wide, indicating a continuing inflow of continental shorefish larvae. The youngest larvae were 23 d old, and the youngest Panama-sourced larvae were 6 weeks old, indicating straight-line offshore transport of at least 15–20 km/d.

Rapid long-distance multispecies transport of shorefish larvae to the oceanic tropical eastern Pacific, revealed by DNA barcodes and otolith aging of larvae captured over the Galapagos Rift

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Introduction

One of the more intractable questions in marine fish biology is identifying where pelagic larvae of shorefishes go during the weeks and months after spawning (Jones, 2015). The duration of the larval stage varies greatly among species, with pelagic larvae of most shorefishes spending 2 weeks to several months offshore at varying distances. Studying this question quantitatively involves two main challenges: 1) the densities of shore-sourced propagules are expected to decrease significantly with increasing distance from the shore, and 2) identifying source populations is necessary to evaluate basic aspects of dispersal. In general, identifying sources is difficult due to the complex geography of many coral reef regions, where many potential point sources exist within any particular range. Furthermore, large tropical regions with many stepping-stone islands, including the Caribbean Sea and Coral Triangle, share much of their fauna. Some recent genetic studies have shown that long-distance larval dispersal, spanning hundreds of kilometers, occurs within some reef-fish populations, such as clownfish (*Amphiprion*) (Simpson et al., 2014) and groupers (Epinephelidae) (Williamson et al., 2016).

Studies to date of pelagic larvae of shorefishes in the tropics have primarily focused on modeling the dispersal and return of successful recruits (e.g.,

Bode et al., 2019). While this is undeniably a key factor underlying shorefish population dynamics, it represents only a small proportion of the eggs and hatchlings released from reefs and other coastal habitats.

Other interesting questions arise regarding the pelagic life of advected shorefish larvae that do not return to a suitable shore or shelf habitat such as assessing dispersal abilities of species (which can determine biogeography over ecological time and divergence and speciation in evolutionary time), understanding larval behaviors and habits, and, as a potentially important component of the oceanic food web, resolving the population ecology of pelagic larval shorefishes in offshore waters.

The tropical eastern Pacific (TEP) region provides a more manageable geography, with a long, mostly linear, continental coastline and a few very isolated offshore islands. In addition, the fauna of the various islands and coastal segments can be very different, resulting from the diverse habitats and areas that are influenced in varying ways by cold upwelling and El Niño–Southern Oscillation-induced warming. The isolation of offshore islands and segments of the linear continental shelf results in genetic divergences among some populations and species complexes, which can help identify the origin of individual larvae. At present, after a number of comprehensive surveys, the fish fauna in the re-

gion is well documented by the Food and Agriculture Organization of the United Nations' guides (Fischer et al., 1995), Grove and Lavenberg (1997), and especially the online guide for the Shorefishes of the Tropical Eastern Pacific by Robertson and Allen (2024). The fish species list for the Galapagos Archipelago has been updated by Grove et al. (2022) and Victor et al. (2024).

Advances in technology have also provided insights into the offshore life of shorefish larvae. Daily otolith increments allow the age and growth of larvae to be determined, potentially to the precise day, depending on otolith quality and clarification of the core region. Otolith microchemistry can also preserve the record of the marine environment each larva has experienced. Most recently, the development of the DNA-barcoding database, the Barcode of Life Database (available from <https://www.boldsystems.org/>) has allowed identification of larvae by matching sequences to adults of known species. At present, the barcode coverage for the TEP and the tropical western Atlantic (TWA) has become sufficiently comprehensive to reliably identify most shorefishes of the region, with the TEP database now including systematic surveys from Mexico, Panama, Peru, and the Galapagos Archipelago.

Fortunately, larvae maintained in ethanol for preserving otoliths can be DNA-sequenced, permitting individuals to be aged and identified to species, revealing age-and-growth history and even potentially revealing the actual location of the source population. Victor (1987) reviewed the larvae of Labridae and Pomacentridae collected in the Galapagos Rift sample reported here, but without the benefit of DNA-barcode identification. Many genera were identified morphologically, but species could not be determined and source populations could not be identified. The age and growth of 6 identified genera were analyzed and the larvae ranged widely in age from about 3 weeks to 4 months, indicating a wide variety of cohorts were present with continuous inflow of reef-fish larvae to the study site.

A series of large-scale fish larval surveys were conducted in the region, beginning in the 1960s by Ahlstrom (1971, 1972). These surveys found almost no shorefish larvae beyond the shelf margin zone of about 200 km from shore, the "inshore pattern" of Ahlstrom (1971), with the exception of certain groups, such as eel leptocephali (mostly inshore and shelf species of snake eels of Ophichthidae and conger eels of Congridae) (Raju, 1985), and some species in the family Scorpaenidae (Moser et al., 1977). These findings reinforced the concept that most shorefish larvae, especially reef-fish larvae, tend to stay nearshore, or, at least, do not survive long when advected away from shelf waters. In the present study, a more intensive sampling with gear targeting larger larvae obtained a large and diverse collection of shore (including shelf) fish larvae far beyond nearshore waters. The purpose of this paper is to document the presence

and rate of transport of shorefish larvae in oceanic waters of the equatorial eastern Pacific Ocean, based on larvae identified using mitochondrial DNA (mtDNA) barcodes and aged using daily otolith increments.

Materials and methods

Fourteen midwater-trawl tows were performed between 2 and 19 March 1985 at a single site on the equator (Rose Garden, 00°48.247'N, 86°13.478'W, depth about 2470 m), off the R/V *Atlantis* during a follow-up *Alvin* expedition after the initial discovery of the hydrothermal vents on the Galapagos Rift (Hessler et al., 1988). The site is about midway between the continent and the Galapagos Archipelago, about 350 km from Galapagos, 460 km from Cocos Island, 575 km west of Ecuador, and 1000 km southwest of the Panama Bight (Fig. 1).

Oblique tows were conducted for 30–90 min at variable speeds (typically about 3 km/h) from varying depths up to 200 m back to the surface with a 1-m by 3-m Tucker trawl with 2-mm mesh, mainly targeting cnidarians. The cod-end was refrigerated and a subsample of the fish larvae was then sorted and some selected for preservation. The volume of fish larvae was not documented, and varying portions of the catch were examined. A subsample of larvae that appeared to be from non-midwater species was then selected by eye and fixed in 95% ethanol. Subsequently, larvae were identified morphologically using a variety of sources, some primary literature (there is no comprehensive guide to TEP ichthyoplankton), but also larval guidebooks for adjacent areas, such as inshore Colombia (Beltran-Leon and Herrera, 2000) and the California Current and TWA, e.g., Moser et al. (1984), Moser (1996), Richards (2006), and, for the eels, Smith in Böhlke et al. (1989). The collection will be accessioned at the Marine Vertebrate Collection of Scripps Institution of Oceanography.

Recently, with mtDNA barcoding feasible, some larvae were tissue-sampled for sequencing the cytochrome *c* oxidase subunit I marker at the Barcode of Life program for fishes at the Centre for Biodiversity Genomics at the University of Guelph, Canada. In general, success of DNA amplification on the 30-year-old tissues was about 30%. Sequences were compiled in the Barcode of Life Database, where it is possible to compare a query sequence to a large number of barcode sequences, including a significant portion from private projects. The Barcode of Life Database assigns sequences to a lineage, a barcode index number (BIN), which clusters barcode sequences algorithmically (Ratnasingham and Hebert, 2013). These lineages can be identified as species or as genovariant populations within a species with cryptic lineages. The BIN permits a thorough evaluation of what species it represents; it includes photographs of vouchers, locations of collections, names

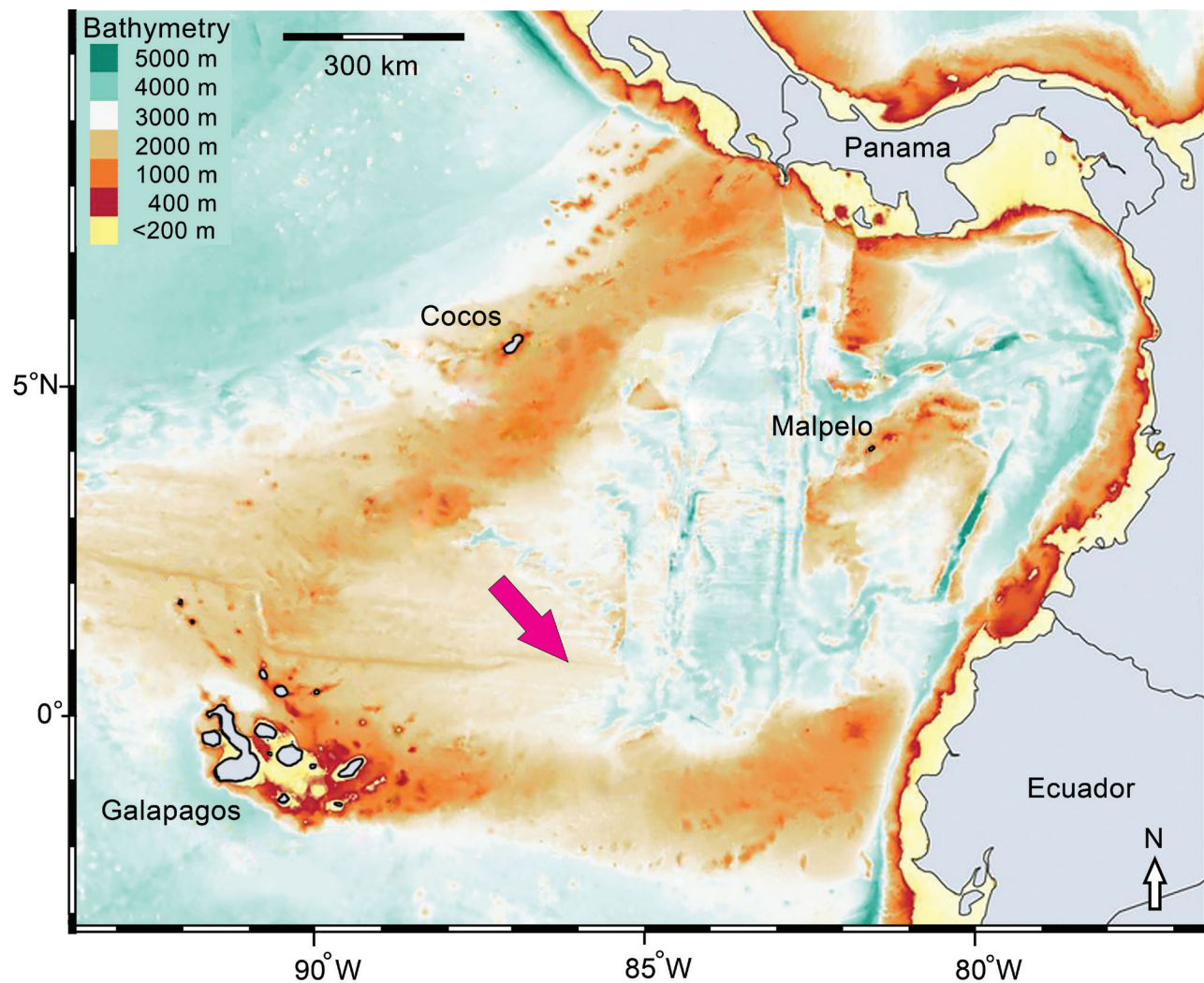


Figure 1

Bathymetric map of the central tropical eastern Pacific Ocean region. The arrow indicates the location of the Rose Garden Galapagos Rift site where larvae were collected between 2 and 19 March 1985. Adapted from Fig. 1 in Cambra et al. (2021) from PLOS ONE under a CC-BY 4.0 license; based on bathymetry data obtained from ETOPO1 1 Arc-Minute Global Relief Model under a CC BY license, with permission from NOAA National Centers for Environmental Information, original copyright 2009 (courtesy Marta Cambra).

assigned by various contributors, comments by reviewers, and the nearest-neighbor BIN, which adds additional information for identification, often a sister species in the TWA. Importantly, it assigns an identifier code (often also a digital object identifier) to a lineage for future assessment and communication. In general, tropical marine fish species do conform to a one-species one-BIN model, but there are many exceptions where species break up into 2 or more lineages and relatively fewer where more than one species share a single lineage (for the Greater Caribbean, see Victor et al. [2015]). Reported sizes of specimens are in standard length.

Results

At least 77 species of shore and shelf fishes in 29 families (total of 1338 larvae) were identified and 62 of those species were DNA-sequenced from the Galapagos Rift larval sample (Table 1; larval photographs archived at <https://doi.org/10.5281/zenodo.7779563>). Most are shallow-water reef, sediment, or estuarine species, a few others are found on the shelf (up to 200 m deep) or on the adjacent slope (200–500 m deep), before depths abruptly plunge beyond 1000 m to the Panama Basin where depths range between 2000 m and 4000 m (Fig.

Table 1

The geographic distribution, maximum depth, number of larvae captured, and minimum and maximum standard lengths (SL) for species of shorefish larvae identified in ichthyoplankton samples collected over the Galapagos Rift between 2 and 19 March 1985. The barcode index number (BIN) code, an algorithmically derived mitochondrial DNA lineage from the Barcode of Life Database (BOLD), provides a record for the identification of the species. A blank cell in the BIN column indicates a sequence was not obtained. The geographic distribution of the larvae included the following locations within the tropical eastern Pacific (TEP): Galapagos (gal), Cocos (coc), Malpelo (mal), Ecuador continental (ecu), Colombia continental (col), Panama (pan), Costa Rica continental (cr), Nicaragua (nic), and Mexico (mex). Shaded cells highlight pertinent absences from sites of interest. The maximum depth recorded for each species is based mostly on Fischer et al. (1995), Grove and Lavenberg (1997), and Robertson and Allen (2024).

Family	Genus	Species	BOLD BIN	gal	coc	mal	ecu	col	pan	cr	nic	mex	max depth (m)	# larvae	min SL (mm)	max SL (mm)
Blenniidae	<i>Ophioblennius</i>	<i>steindachneri</i>		1	1	1	1	1	1	1	1	1	20	3	9.0	15.8
Bothidae	<i>Bothus</i>	<i>leopardinus</i>	AAN0843	1	1	1	1	1	1	1	1	1	120	33	8.9	24.0
	<i>Engyophrys</i>	<i>sanctilaurentii</i>	AAF6514				1	1	1	1	1	1	235	32	8.0	27.1
	<i>Monolene</i>	<i>dubiosa</i>							1	1	1	1	209	1	8.3	
	<i>Perissias</i>	<i>taeniopterus</i>	ABA4569				1	1	1	1	1	1	160	26	7.5	17.0
Callionymidae	<i>Synchiropus</i>	<i>atriliabatus</i>	AAI0127	1	1	1	1	1	1	1	1	1	235	69	5.0	23.1
Carangidae	<i>Decapterus</i>	<i>macarellus</i>	AAC4792	1	1	1	1	1	1	1	1	1	200	4	28.0	55.0
	<i>Selene</i>			1	1	1	1	1	1	1	1	1	50	1	16.3	
Carapidae	<i>Echiodon</i>	<i>exsilium</i>	AEY1488	1	1		1	1	1	1	1	1	90	12	36.0	115.0
Chaetodontidae	<i>Chaetodon</i>	<i>humeralis</i>	AAD9262	1	1	1	1	1	1	1	1	1	55	1	8.9	8.9
Chlopsidae	<i>Chlopsis</i>	<i>bicollaris</i>	ABV5198	1	1								585	323	65.0	100.5
Congridae	<i>Ariosoma</i>	<i>gilberti</i>	ABW4528	1	1	1	1	1	1	1			100	15	78.0	223.0
	<i>Bathycongrus</i>	<i>macrurus</i>	ABW4413		1	1	1	1	1	1	1	1	590	36	109.0	169.0
	<i>Bathycongrus</i>	<i>varidens</i>	ABU7082	1	1	1	1	1	1	1	1	1	935	1	235.0	
	<i>Chilconger</i>	<i>dentatus</i>	ABU7221	1	1	1	1	1	1	1	1	1	55	20	43.0	153.0
	<i>Heteroconger</i>	<i>klausewitzii</i>	ABU6366	1	1	1	1	1	1	1			20	1	66.8	
	<i>Paraconger</i>	<i>californiensis</i>	ABU6929	1	1	1	1	1	1	1	1	1	50	24	78.5	165.0
	<i>Paraconger</i>	<i>similis</i>	ABU6931	1					1	1	1	1	150	5	47.0	261.0
	<i>Rhynchoconger</i>	<i>nitens</i>	ADM4964				1	1	1	1	1	1	90	5	83.0	115.0
Cyclopoetidae	<i>Citharichthys</i>	<i>platophrys</i>	ABU6511				1	1	1	1	1	1	145	61	6.5	15.1
	<i>Cyclopoetta</i>	<i>panamensis</i>	AAH9976				1	1	1	1	1	1	114	2	7.4	16.0
	<i>Syacium</i>	<i>latifrons</i>	ABU6133	1	1		1	1	1	1	1	1	95	8	5.6	8.0
	<i>Syacium</i>	<i>ovale</i>	AAH9977				1	1	1	1	1	1	90	24	5.4	7.5
Eleotridae	<i>Erotelis</i>	<i>armiger</i>	AAX7828					1	1	1	1	1	5	10	8.9	14.0
	<i>Gobiomorus</i>	<i>maculatus</i>	AAC5593	1	1		1	1	1	1	1	1	5	14	7.0	11.9

Table continued

Table 1 (continued)

Family	Genus	Species	BOLD BIN	gal	coc	mal	ecu	col	pan	cr	nic	mex	max depth (m)	# larvae	min SL (mm)	max SL (mm)
Fistulariidae	<i>Fistularia</i>	<i>commersonii</i>		1	1	1	1	1	1	1	1	1	130	4	26.0	59.0
Gerreidae	<i>Eucinostomus</i>			1	1	1	1	1	1	1	1	1	100	1	10.6	10.6
Gobiidae	<i>Ctenogobius</i>	<i>manglicola</i>	AAF8708				1	1	1	1	1	1	5	12	6.5	9.0
	<i>Evorthodus</i>	<i>minutus</i>	AAJ0337				1	1	1	1	1	1	5	5	7.6	8.3
	<i>Gobioides</i>	<i>peruanus</i>	AAF8263				1	1	1	1	1	1	15	2	10.4	12.1
	<i>Lythrypnus</i>			1	1	1	1	1	1	1	1	1	150	1	5.4	
	<i>Sicydium</i>	<i>salvini</i>	AAF4136						1	1	1		0	12	10.5	19.0
	<i>Sicydium</i>	sp. Darien	AAH6892						1				0	4	11.7	14.0
	<i>Sicydium</i>	sp. 2	AEX8908										0	2	14.5	15.5
Haemulidae	<i>Haemulon</i>			1	1	1	1	1	1	1	1	1	100	1	9.7	
Holocentridae	<i>Neomiphon</i>	<i>suborbitalis</i>		1	1	1	1	1	1	1	1	1	25	1	6.8	
Labridae	<i>Bodianus</i>			1	1	1	1	1	1	1	1	1	75	1	9.9	
	<i>Decodon</i>	<i>melasma</i>	AAI9623	1	1		1	1	1	1	1	1	220	5	13.4	20.0
	<i>Halichoeres</i>	<i>dispilus</i> (Panama)	ABZ0764						1	1	1	1	75	4	9.4	13.5
	<i>Sagittularia</i>	<i>inornata</i>	AAI1946	1	1	1							150	31	7.7	14.1
	<i>Thalassoma</i>	spp.		1	1	1	1	1	1	1	1	1	65	9	7.7	11.7
	<i>Xyrichtys</i>	<i>mundiceps/perlas</i>	AAD4975						1				30	36	9.9	16.7
Lophiidae	<i>Lophiodes</i>	<i>caulinaris</i>	AAF0897		1	1	1	1	1	1	1	1	380	3	4.6	4.9
Microdesmidae	<i>Cerdale</i>	<i>ionthas</i>	AAZ6311				1	1	1	1			2	1	10.7	
	<i>Microdesmus</i>	<i>affinis</i>	AAZ5433						1	1	1	1	10	1	15.4	
Mugilidae	<i>Mugil</i>			1	1	1	1	1	1	1	1	1	25	1	27.0	
Muraenidae	<i>Muraeninae</i>	spp.		1	1	1	1	1	1	1	1	1	125	11	48.0	66.0
Nettastomatidae	<i>Hoplunnis</i>	<i>pacifica</i>	ABU6420				1	1	1	1	1	1	275	21	80.0	146.0
	<i>Saurencbelys</i>	sp.	ABW4200	1	1	1	1	1	1	1	1	1	200	7	80.0	104.0
Ophichthidae	<i>Myrichthys</i>	<i>aspetocheiros</i>	ABV9127		1				1	1	1	1	64	1	64.0	
	<i>Myrichthys</i>	<i>xysturus</i>	AAG2542	1	1		1	1	1	1	1	1	25	1	64.5	
	<i>Myrophis</i>	<i>vafer</i>					1	1	1	1	1	1	12	3	73.0	83.0
	<i>Ophichthus</i>	<i>apachus</i>	AAx0445 ¹					1	1	1	1	1	8	1	81.0	
	<i>Ophichthus</i>	<i>mecopterus</i>	ABV9668						1	1	1	1	80	2	60.5	64.0
	<i>Ophichthus</i>	<i>triserialis</i>	ABW6641				1	1	1	1	1	1	20	50	38.0	85.0

Table continued

Table 1 (continued)

Family	Genus	Species	BOLD BIN	gal	coc	mal	ecu	col	pan	cr	nic	mex	max depth (m)	# larvae	min SL (mm)	max SL (mm)
	<i>Ophichthus</i>	<i>zophochir</i>	AAI1203				1	1	1	1	1	1	100	8	93.5	161.0
	<i>Pseudomyrophis</i>	<i>micropima</i>	ABV9785					1	1	1		1	200	4	85.0	101.0
Ophidiidae	<i>Brotula</i>	<i>clarkae</i>	ABA7631	1	1		1	1	1	1	1	1	650	3	40.5	55.0
Polynemidae	<i>Polydactylus</i>	<i>approximans</i>	AAF1341		1	1	1	1	1	1	1	1	30	1	15.0	
Pomacentridae	<i>Abudefduf</i>	<i>troschelii</i>	AAC8011	1	1	1	1	1	1	1	1	1	15	1	7.3	
	<i>Azurina</i>	<i>atrilobata</i>	AAC8581	1	1	1	1	1	1	1	1	1	80	1	11.7	
	<i>Stegastes</i>			1	1	1	1	1	1	1	1	1	38	8	4.8	7.6
Scorpaenidae	<i>Pontinus</i>	<i>furcibinus</i>	ACE3449	1	1	1	1	1	1	1	1	1	300	3	7.2	12.7
	<i>Pontinus</i>	<i>sierra</i>	ABA3845	1			1	1	1	1	1	1	247	4	5.8	14.0
	<i>Pontinus</i>	sp. A "rosy"	ABA3844	1			1	1	1	1	1	1	399	166	5.4	13.0
	<i>Scorpaena</i>	<i>histrion</i>	ABA2570	1	1	1	1	1	1	1	1	1	157	37	4.6	8.6
	<i>Scorpaenodes</i>	<i>chincha</i>	ABA7033				1	1	1	1	1	1	50	48	5.4	9.6
Serranidae	<i>Pronotogrammus</i>	<i>multifasciatus</i>	ABU7042	1	1	1	1	1	1	1	1	1	300	7	4.6	5.9
	<i>Serranus</i>	<i>aequidens</i>	AAZ5418	1	1		1	1	1	1	1	1	265	8	7.4	24.3
Cynoglossidae	<i>Symphurus</i>	<i>callopterus</i>	ABU6159				1	1	1	1	1	1	317	5	15.0	38.0
	<i>Symphurus</i>	<i>chabanaudi</i>	ABA7064				1	1	1	1	1	1	60	34	13.8	18.0
	<i>Symphurus</i>	<i>elongatus</i>	ABA8355				1	1	1	1	1	1	100	13	11.0	15.5
	<i>Symphurus</i>	<i>melanurus</i>	ABA8354				1	1	1	1	1	1	35	9	21.7	24.0
	<i>Symphurus</i>	<i>prolatinaris</i>					1	1	1	1	1	1	162	8	23.3	26.0
	<i>Symphurus</i>	sp. 2	AEY8993											1	14.0	
	<i>Symphurus</i>	<i>undecimfasciatus</i>	ABU6158				1	1	1	1	1	1	56	2	34.0	43.0
Tetraodontidae	<i>Sphoeroides</i>	<i>lobatus</i>	AAJ3304	1	1	1	1	1	1	1	1	1	107	2	11.1	12.0

¹Transisthmic sister lineage of *O. apachus* which does not yet have a BIN assignment.

1). Epipelagic, mesopelagic, bathypelagic, bathyal, and abyssal species were not included. The mtDNA barcodes obtained either matched to known species lineages or a sister species match in the Caribbean fauna identified the sequence; a few required morphological identification to confirm the species identity. DNA-barcode coverage in the TEP is moderate, with a very rough estimate of half of the shorefish species barcoded, and many of those in private projects only.

Size of larvae

The shorefish larvae collected covered a wide range of sizes, from 4.6 mm in spottedtail goosefish (*Lophiodes caularis*) (Lophiidae) to 235 mm in the leptocephalus of the largehead conger (*Bathycongrus varidens*) (Congridae). For reef fishes, the range was 4.8 mm in *Stegastes* (Pomacentridae) and *Scorpaena*, to 24.3 mm in deepwater serrano (*Serranus aequidens*) (Serranidae), to 55 mm in Pacific bearded brotula (*Brotula clarkae*) (Brotulidae), to 58 mm in *Fistularia* (Fistulariidae), and to 135 mm in leptocephali of yellow snake eel (*Ophichthus zophochir*) (Ophichthidae). For non-reef species, notably large larvae included amphidromous gobies (*Sicydium* spp.) (Gobiidae) larvae at 19 mm, Pacific leopard flounder (*Bothus leopardinus*) (Bothidae) at 23 mm, and speckledtail flounder (*Engyophrys sanctilaurentii*) (Bothidae) at 29 mm. For inshore pelagic species, *Decapterus* (Carangidae) juveniles ranged up to 55 mm and *Mugil* (Mugilidae) juveniles to 27 mm. Several taxa were far larger than the maximum sizes reported in the literature for their species or genus, either in the TEP (Moser, 1996; Beltran-Leon and Herrera, 2000) or TWA (Richards, 2006): blackspot wrasse (*Decodon melasma*) (Labridae) at 20.0 mm versus 8.0 mm (TWA); deepwater serrano at 24.3 mm versus 10.8 mm (TEP) and 14.0 mm (TWA); and blacklip dragonet (*Synchiropus atrilabiatus*) (Callionymidae) at 23.1 mm versus 12.5 mm (TEP), 4.3 mm (TWA), and 5.1 mm maximum pelagic size for any Indo-Pacific callionymid (Leis and Carson-Ewart, 2000).

The tonguefishes (Cynoglossidae) were exceptional, with some occurring as fully transformed juveniles, eyes completely migrated, and bodies scaled and pigmented—these were also often particularly large, with transformed juveniles of imitator tonguefish (*Symphurus undecimpterus*) at 43.0 mm, chocolate tonguefish (*Symphurus callopterus*) at 38.0 mm, halfstriped tonguefish (*Symphurus prolatinarius*) at 26.0 mm, and drab tonguefish (*Symphurus melanurus*) at 24.0 mm.

Source populations

Galapagos Archipelago and Cocos Island

Despite the proximity to the offshore islands, only about half of the species detected occurred in Galapagos Ar-

chipelago or Cocos Island, and those were virtually all pan-TEP species. No species endemic to the offshore islands, Galapagos, Cocos, or Malpelo, were detected, with the exception of the deepwater collared false-moray eel (*Chlopsis bicollaris*). Originally described as an endemic species in Galapagos, it more recently has been photographed from a submersible at Cocos Island (Starr et al., 2012) and may be present undetected on the continental slope.

The series of larvae of the cape wrasse (*Sagittalarva inornata*) (Labridae) was instrumental in establishing that the century-old, unique, juvenile holotype of *Pseudojulis inornatus* (Gilbert, 1890), from the tip of Baja California, was a synonym of the deep-water labrid described as *Halichoeres raisneri* by Baldwin and McCosker (2001) from Galapagos. The mtDNA sequences from the larvae matched an adult collected at the type location of *Pseudojulis inornatus*, and the description of *Halichoeres raisneri* fits that of Gilbert's *Pseudojulis inornatus* (Victor et al., 2013). Beltran-Leon and Herrera (2000) have now documented the species from Colombia (as larvae); it is also known from Galapagos, Cocos, and Malpelo, as well as Baja California.

Continental shelf

Larvae of 7 species of *Symphurus* were identified, but notably, the 6 that could be assigned to species are not found on the offshore islands. Four cynoglossid species occur on the offshore islands (Munroe and McCosker, 2001; Cortés, 2012): halfspotted tonguefish (*Symphurus atramentatus*) (widespread in the TEP), devil's tonguefish (*Symphurus diabolicus*) (Galapagos, Cocos, and Panama), whitetail tonguefish (*Symphurus oligomerus*) (continent and Cocos), and mottled tonguefish (*Symphurus varius*) (Galapagos, Cocos, Malpelo, and Panama). Among the larvae identified was the chocolate tonguefish, with a large and very characteristic exterilium larva (Evseenko, 1990). The additional identified species comprised darkcheek tonguefish (*Symphurus chabanaudi*), elongate tonguefish (*Symphurus elongatus*), drab tonguefish, halfstriped tonguefish, and imitator tonguefish. These are all soft-bottom species limited to the continental shore and shelf, from Mexico to Peru.

A number of leptocephalus larvae of a variety of eels, particularly snake eels and conger eels, were identified. Four of the 7 ophichthid species identified do not occur on any offshore islands, and notably 3 extend only as far south as the Panama Bight: thin snake eel (*Ophichthus apachus*), longarmed snake eel (*O. mecopterus*), and plain worm eel (*Pseudomyrophis micropinna*). In addition, yellow snake eel (*O. zophochir*) is found along the continental margin from California to Peru. Two conger and pike-conger eels limited to the continental shelf from Baja to Peru were identified: needletail conger

(*Rhynchoconger nitens*) and silver pikeconger (*Hoplunnis pacifica*).

Larvae of 7 species of flounder were identified, and 5 of them do not occur on the offshore islands, but are limited to the continental shelf from Baja California to Peru: *Engyophrys* and *Perissias* in Bothidae and small sanddab (*Citharichthys platophrys*), panamic flounder (*Cyclopsetta panamensis*), and oval flounder (*Syacium ovale*) in Cyclopsettidae.

Among the scorpaenids, 3 deep-water *Pontinus* species were identified, and 2 of them are not documented on offshore islands: speckled scorpionfish (*Pontinus sierra*) and *Pontinus* sp. A “rosy” scorpionfish (a recognized species awaiting description for some decades due to unresolved species character boundaries) (Robertson et al., 2017). However, the distribution of *Pontinus* species is poorly documented and there may be additional undescribed species.

Brackish and tidepool

Five gobioids (suborder Gobioidi) that are found in fresh and brackish waters and only along the continental shores were identified: mangrove goby (*Ctenogobius manglicola*), small goby (*Evorthodus minutus*), Peruvian eel-goby (*Gobioides peruanus*), and Pacific sleeper (*Gobiomorus maculatus*), found from Baja California to Peru, but notably also flathead sleeper (*Erotelis armiger*), which ranges south only to Colombia in the Panama Bight.

Two larvae of wormfishes (Microdesmidae) were sequenced, but did not have close barcode matches because the family is poorly represented in the TEP barcode database. Both were identified by a diagnostic fin-ray count. Spotted worm-goby (*Cerdale ionthas*) is documented only south to Colombia in the Panama Bight and does not occur on any of the offshore islands. The second species, olivaceous wormfish (*Microdesmus affinis*), has been collected south only to Panama; its fin-ray count excludes banded wormfish (*Microdesmus dipus*), the only microdesmid collected on any of the offshore islands, which has many fewer dorsal-fin elements. In any case, the sole island record is a single translucent fish from a Galapagos tidepool collected in 1938, presumably a vagrant, originally described as the new species *Microdesmus reidi*.

Freshwater

The presence of *Sicydium* larvae in the sample was particularly interesting. Adults of these amphidromous gobies live in rivers and streams along the TEP continental coastline (and one Cocos Island endemic species), including several widespread species and some localized species; their larvae are widely dispersed in oceanic waters (Lord et al., 2015; Moody et al., 2015). Three species of *Sicydium* were successfully sequenced, and one matched

to a wide-ranging continental species, multispotted goby (*Sicydium salvini*), which has DNA-barcode records obtained from Mexico, Costa Rica, and Panama. The second DNA lineage, however, matched to a sequence obtained only from an undescribed species collected above the mouth of the Rio Pichende in the Darién Province of Panama, at 7 m altitude (BSFFA804-07, from the Smithsonian Tropical Research Institute; GenBank MG937265). The third species does not match any lineage in the databases, so the Cocos Island endemic species cannot be excluded.

Coral reef fishes

Three intriguing cases of reef-fish larvae are notable, showing the power of DNA barcoding for revealing unexpected results. In general, the suite of common reef-fish families, such as Pomacentridae and Labridae, mostly comprise widespread TEP species and thus some of their larvae from the Galapagos Rift collection were not sequenced. However, the larval sequence obtained from the chameleon wrasse, a widespread species that would otherwise be of little use in tracking source populations, turned out to be a special case. This species has subpopulations with different mtDNA lineages within the TEP, and the barcode sequence of the larva collected over the hydrothermal vents matches to the Panama population and not the Galapagos population (which diverges by 3.3%).

The second example comprises the larvae of *Xyrichtys* razorfish (Labridae), which are not identifiable to species morphologically. Five species occur in the TEP, but only one species occurs in each region (Victor et al., 2001). The mtDNA sequences of the larvae collected match the species from Baja California, cape razorfish (*Xyrichtys mundiceps*), but that species is found only in Mexico. However, the population from the Bay of Panama, described as the Panamanian razorfish *Xyrichtys perlas*, is a close sister species (or the same) as *X. mundiceps*, and these larvae are therefore most likely *X. perlas*. The Panamanian razorfish has only been found in Panama, extending westward a short way from its type location in the Perlas Islands. Notably, the congener found in the Galapagos and Cocos Islands, the Galapagos razorfish, *Xyrichtys victori*, comprises a distant unrelated mtDNA lineage (12.0% divergent).

The third example is the reef-based scorpionfish *Scorpaenodes* (Scorpaenidae), which is present in 2 distinct DNA lineages in the TEP (7.5% divergent). The Galapagos (and Clipperton and Baja California) populations of rainbow scorpionfish (*Scorpaenodes xyris*) are very close to the Indo-Pacific populations of cheekspot scorpionfish (*Scorpaenodes evides*), whereas the continental mainland population from Central America to Peru, nominally *Scorpaenodes chincha*, is a sister species to the deepreef scorpionfish (*Scorpaenodes tredecimspinosus*)

found in the Caribbean. The *Scorpaenodes* larvae in the sample (12 sequenced from 48 larvae) all matched to the continental mainland species.

Discussion

The application of DNA barcoding to larval dispersal studies can not only identify larvae to species, often not possible with morphology alone, but also potentially identify source populations when species have restricted ranges or when species have regional genetic lineages. In this study, barcoding proved useful to identify species that have adults only on the continent or endemic to islands, and even to link larvae to specific locations where adults are known to occur. In the past, it was difficult to identify most larvae to species and, without comprehensive guides to larvae in the TEP, many were often misidentified. For example, Evseenko and Shtaut (2005) used the guide to larvae for the California Current (Moser, 1996) to identify larvae from Costa Rica, and so listed Baja Californian species that occur nowhere near Costa Rica (e.g., rock wrasse [*Halichoeres semicinctus*], sargo [*Anisotremus davidsoni*], plain cardinalfish [*Apogon atricaudus*], and California lizardfish [*Synodus lucioceps*]). Another example was Beltran-Leon and Herrera's (2000) identification of unusual labrid larvae off Colombia as *Halichoeres* cf. *malpelo* (*Halichoeres malpelo* is the endemic member of the golden wrasse [*Halichoeres melanotis*] complex on Malpelo Island offshore of Colombia), however the same distinctive larval type at the Galapagos Rift was DNA-matched to *Sagittalarva inornata*, known until then only from Baja California, Cocos, and Galapagos Islands.

Shorefish larvae in far offshore waters

The prevailing view of the distribution of shorefish larvae in the TEP is that they are limited to inshore waters <200 km from shore, with a few exceptions in some groups with long-lived larvae, such as eel leptocephali (Raju, 1985), a subset of flatfishes, and some scorpaenids (Moser et al., 1977). Other than those, the occurrence of shorefish larvae far from shore is usually interpreted as rare long-distance transport of vagrant individuals, such as those Indo-Pacific species that cross the East Pacific Barrier and show up as occasional individuals in the Galapagos Islands (Grove and Lavenberg, 1997; Robertson et al., 2004; Victor et al., 2024). Indeed, Leis (1983) captured 4 labrid larvae 600 to 1200 km into the East Pacific Barrier, apparently from the Line Islands, showing that very long-distance transport does occur, but is only rarely detected. A few other anecdotal reports of shorefish larvae far from native shores in the TEP are documented, such as a single giant larva of a continental

tonguefish captured near the Galapagos Islands (Munroe and Krabbenhoft, 2010), and those captures were interpreted as a rare "expatriation" of a long-lived larva with delayed metamorphosis.

A series of comprehensive larval fish surveys have been made in the TEP, most prominently by the large-scale EASTROPAC I and II surveys in the 1960s by Elbert Ahlstrom, who pioneered the study of fish larvae in the Pacific Ocean for the National Marine Fisheries Service. In those surveys, multiple ships sampled along 3000-km transects crossing the region. Ahlstrom (1972) noted that "shorefishes, however, were not an important element" of the ichthyoplankton, not surprising given the vast populations of midwater fishes in the region. In addition, although sampling was planned to be comprehensive over geographic scales, it was not intensive at any location, and shorefish larvae were not collected in large numbers offshore of the continental shelf. Those EASTROPAC surveys were followed by a series of additional surveys, including the Southwest Fisheries Science Center eastern tropical Pacific Ocean (ETP) dolphin surveys between 1987 and 1992 (Charter et al., 1998; Ambrose et al., 2000; Moser et al., 2000; Sandknop et al., 2000; Watson et al., 2000) and the Stenella Abundance Research Project in 1999 and 2000 (STAR99 and STAR00, respectively) (Ambrose et al., 2002; Watson et al., 2002).

These surveys yielded mostly midwater fish families, while shore or shelf fish families were collected in small numbers or were absent. Those captures were almost always within the inshore band but, even then, the catch was particularly low, with many prominent shorefish families with fewer than 10 individuals or absent from the collections, raising issues of gear selectivity and/or seasonality. For example, the EASTROPAC I surveys summarized in Ahlstrom (1971) were the most extensive, with 4 vessels conducting 482 hauls and collecting 95,109 fish larvae. Despite the transects starting at the shore with a large portion of trawls within the shelf, many prominent shorefish families were not represented at all, such as Blenniidae, Chaenopsidae, Tripterygiidae, Pomacentridae, Microdesmidae, Lutjanidae, Gerreidae, Scarinae, Haemulidae, Acanthuridae, Chaetodontidae, Diodontidae, and Tetraodontidae (and many other less prominent shorefish families). The shorefish families that were collected were almost all taken in the inshore band, with a few exceptions.

Two shorefish taxa were presented in Ahlstrom's (1971) maps: *Synodus* (lizardfishes), with 41 larvae, and the Pacific leopard flounder, with 50 larvae. The 2 groups showed different distribution patterns, with all but 3 *Synodus* larvae collected within a 200-km coastal band, Ahlstrom's "inner pattern." In contrast, the bothid larvae were distributed from inshore to far offshore and out to the Galapagos Archipelago. Moser et al. (1977) documented the distribution of the scorpaenid larvae from the

survey and most were collected within a coastal band of about 300 km, but some were up to half way from the continent to Galapagos, and *Pontinus* sp. A “rosy” larvae extended offshore broadly in the area between Galapagos, Cocos Island, and the continent.

Another group of shorefish larvae, eel leptocephali, included taxa that were not limited to the inshore larval distribution pattern. This is not unexpected, since the leptocephalus larval form is adapted to a large size and a long larval life (Miller and Tsukamoto, 2020). Ahlstrom (1971) noted that several groups of eels had larvae throughout the region between the continent and the Galapagos Islands. Raju (1985) reviewed the distribution of congrid larvae in the region, from 20 years of survey material, including EASTROPAC. He reported that larvae of these shelf congrids were found in a wide coastal band, but with occasional larvae very far out in the open ocean, for example a largehead conger leptocephalus was picked up at 5°N, 118°W, about 2000 km from the nearest shelf and 1000 km from remote Clipperton Atoll (about 10°N, 110°W). However, the largehead conger has a giant leptocephalus larva, up to 25 cm, presumably with a very long larval life. Similarly, an *Ariosoma* leptocephalus was collected at 12°N, 121°W, about equally isolated, and they also have very large larvae (up to 21 cm); the finding is more significant since *Ariosoma* is a relatively shallow-living eel (up to 100 m) and larvae would originate near the shoreline.

Subsequent surveys after EASTROPAC I were conducted between July and December and were less productive but repeated the pattern of few shorefish families, and those that were captured were almost all within the inshore band. As an example, the EASTROPAC II surveys, despite starting nearshore, captured only 11 pomacentrid and 6 blenniiform (Order Blenniiformes) larvae in total, with all other shorefish families as one or 2 individuals or absent. In the 1987 ETP dolphin surveys reported by Moser et al. (2000), other than some gerreid and haemulid larvae, all other non-pelagic shorefish families were represented by 5 or fewer larvae; this includes 3 synodontids (Synodontidae), 3 gobioids, 2 microdesmids, 2 pomacentrids, and a single leptocephalus (with no larval blennioids, labrids, scarines, serranids [Serranidae], or lutjanids). Charter et al. (1998) reviewed continued ichthyoplankton sampling in subsequent ETP dolphin surveys in 1989, and larvae of non-pelagic shorefishes were very rare, with 6 or fewer larvae of pomacentrids (*Chromis*, all from a tow off Guadalupe Island, Baja California) and holocentrids (*Sargocentron*), 3 larvae each of *Synodus*, *Bothus*, and haemulids, and one or 2 individuals of gobioids, labrids, scorpaenids, and all eels (with zero for all the remaining large shorefish families). Watson et al. (2002) reported that in the STAR99 surveys, larvae of

non-pelagic shorefishes were rarely captured, with fewer than 10 larvae captured for many large shorefish families (Congridae, Muraenidae, Serranidae, Sciaenidae, Kyphosidae, Pomacentridae, all blenniiform families), a single *Synchiropus* larva, and no larvae from the families Ophichthidae, Apogonidae, Holocentridae, Acanthuridae, Chaetodontidae, Labridae, Scarinae, or Microdesmidae. Evseenko and Shtaut (2005) reported on catches in the Costa Rican Dome area, up to 400 km off Central America, and showed a similar pattern of scarce shorefish larvae, with only eel leptocephali, scorpaenids, and some flatfishes with more than 10 larvae captured in the 200–400 km offshore zone, as well as about 50 unidentified gobioid larvae extending out to 300–400 km.

The capture of so few and such a limited variety of shorefish larvae collected, even within the inshore band, suggests that the collection technique, size and mesh of the nets, and speed of towing explains the rarity of shorefish larvae in large-scale surveys, which typically use relatively small, fine-mesh plankton nets; indeed, when coarser mesh nets that filter more water at higher speeds are used, reef-fish larvae can be captured in large numbers more than 100 km offshore (Clarke [1995] with 6-mm mesh; Lo-Yat et al. [2006] with 5-mm mesh). In contrast to these broad surveys, the Galapagos Rift collection was intensive and used a larger Tucker trawl with coarser mesh. A single tow often yielded more shorefish larvae of many families than the entire EASTROPAC and Southwest Fisheries Science Center ETP and STAR99 surveys combined, including all inshore and offshore sampling. The Galapagos Rift collection yielded several hundred shore and shelf eel leptocephali, and, as one pertinent example, the sample of the blacklip dragonet included 69 larvae ranging from 5.0 to 23.1 mm versus 7 in all prior National Marine Fisheries Service sampling.

The large portion of the sampled larvae that originated on the continent and not the offshore islands suggests that shorefish larvae are transported in a wide variety and large numbers several hundreds of kilometers into the open ocean, at least within the central TEP Panama Basin region. Of particular interest, the subset of continental species whose larvae are present over the Galapagos Rift, but whose adult populations extend only as far south as Panama, implies that the distant Panama Bight, up to 1000 km in linear distance from the sampling site, is a source of some shorefish larvae in the sample. The Rio Pichende *Sicydium* goby is especially significant, since it appears to be an undescribed local species from the Darién region of southern Panama. Other widespread *Sicydium* species occupy large ranges in Central and South America, and larvae of one of those, multispotted goby, were also present in the Galapagos Rift sample. Furthermore, the barcode DNA match of the larval labrid chameleon wrasse to the Panama lineage,

and the presence of numerous larvae of a razorfish found only as far south as Panama, provide further evidence of a source location in Panama.

The current regime in this area is not well resolved. Kessler (2006) points out that the classic schema of circulation in the TEP (Wyrski, 1966) is less clear after more recent data are analyzed. In the classic description, the North Equatorial Countercurrent, flowing eastward toward the Panama Bight, is deflected southward to meet the westward-running South Equatorial Current, producing a flow out of the Panama Bight toward the Galapagos Islands along the equator. However, the modern schema (Kessler, 2006) shows greater uncertainty in that area, with a surface South Equatorial Current moving westward, a subsurface equatorial undercurrent moving eastward, and a circular flow within the Panama Bight. Willett et al. (2006) document prominent mesoscale eddies in the TEP, but those form well north of the study area. They do show, however, that tropical instability vortices are produced around the equatorial cold tongue and may occur in the study area where warm and cold currents meet. Notably, a diagram of current at depth at the area around the collection site (Kessler, 2006) reveals a westward surface current overlying a deeper eastward current running from 50–300 m depth, and, since many ichthyoplankton vertically migrate through these zones, a steady mixing of continental inflow and oceanic waters from the west and north could be expected.

In addition to evidence of mixing of larvae from a variety of sources, there is evidence of a continuous inflow of larvae. The size range of shorefish larvae was extreme, sometimes with unusually large pelagic juveniles present, and many taxa were collected in a broad size range (Table 1). The age and size distribution of labrid and pomacentrid larvae in the sample was very wide, 23–131 d and 4.8–16.7 mm (Victor, 1987), indicating multiple incoming cohorts of larvae. The youngest larva examined was a *Stegastes* damselfish (5.8 mm and 23 d since hatching; otolith photographs archived at <https://doi.org/10.5281/zenodo.7779587>), but *Stegastes* species are generally wide ranging in the TEP and cannot reveal their source population; if larvae 23 d old were from the nearest Galapagos Islands, the straight-line distance traveled was a minimum of 350 km, yielding a minimum transport rate of 15 km/d. Similarly, the youngest *Sagittalarva* larva was 27 d old, but that species is found on both the Galapagos Archipelago and Cocos Island and likely traveled a similar distance. The youngest *Xyrichtys* razorfish larva (with DNA matching to cape razorfish) was 46 d old (the oldest was 131 d old, and their size ranged from 10–17 mm) and it likely traveled from the Panama Bight in that period, yielding a minimum rate of transport of about 20 km/d.

These results raise the intriguing possibility that shorefish larvae may be present elsewhere in far-offshore waters, but have not yet been targeted with apparatus that can collect enough larvae to assemble a representative sample. Alternatively, this part of the Eastern Pacific Corridor may be oceanographically exceptional, with an unusual confluence of features promoting rapid offshore transport of continental water masses. It is notable that William Beebe (1926) devoted a chapter in his book on the 1925 Arcturus expedition to the Galapagos (via the Panama Canal) to a phenomenon that astonished him, a “gigantic current rip,” a wide area of strong currents in varying directions and speeds. He describes vast drifts of flotsam of continental origin, including entire trees, accompanied by a great number and variety of fishes, including hugely abundant fish larvae that immediately filled their nets. This was located about 200 km north of the vent site.

The application of DNA barcoding can reveal much more about shorefish larvae and has a remarkable potential for pinpointing source populations for pelagic larvae. This combination of approaches may well confirm that long-distance transport of shorefish larvae is a widespread phenomenon, at least in some tropical regions, and we may need to rethink the potential for dispersal of these fishes.

Conclusions

A site over the Galapagos Rift hydrothermal vents in the TEP Ocean yielded 1338 shorefish larvae. At least 77 species in 29 families of shorefishes were identified. They were not characteristic of the Galapagos or Cocos Island faunas, but included continental marine, brackish, and freshwater species not recorded on the offshore islands. Larvae of 3 freshwater amphidromous *Sicydium* goby species were present, including an undescribed species from a Panamanian river. Also collected were 5 continental brackish and estuarine gobioid species. About 20 species of other families were from soft-bottom, continental-shelf habitats not found on the islands, some species ranging south only to Panama or Colombia. Among reef fishes, the mtDNA sequences of 3 species did not match the Galapagos Islands population: *Scorpaenodes* matched the continental nominal species, *Scorpaenodes chinch*a, and the *Xyrichtys* razorfish and chameleon wrasse matched populations from Panama, about 1000 km to the northeast. The range of sizes and ages of some genera and species were especially wide and made up of multiple cohorts, indicating a continuing flow of continental shorefish larvae into the region. The youngest larvae were about 23 d old, and the youngest Panama-sourced larvae were 6 weeks old, indicating straight-line offshore transport of at least 15–20 km/d.

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