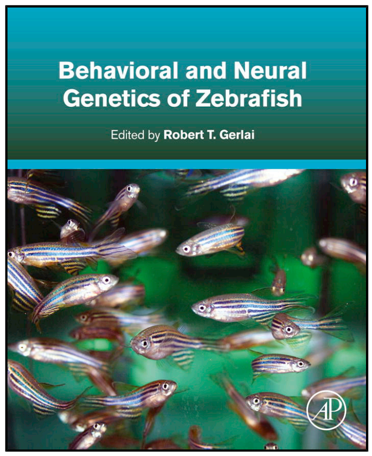

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CHAPTER

1

The biotic and abiotic environment of zebrafish

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Introduction

The zebrafish, *Danio rerio*, was recognized for its potential utility in developmental genetics (Chakrabarti et al., 1983; Kimmel, 1989; Grunwald and Eisen, 2002; Varga, 2018), but the species has become increasingly valuable for understanding behavior and the neurobiology underlying behavior (Kalueff et al., 2013; Gerlai, 2014; Orger and de Polavieja, 2017; Zabegalov et al., 2019). Viewed simply as a model system, the zebrafish can provide insights that may be generalizable to other vertebrates. Viewed as a species—with its own evolutionary history and selection regimes past and present—the zebrafish can inform our understanding of how behaviors, life history characteristics, morphology, developmental genetics, and physiology have been shaped in the wild. Whereas the former perspective requires only zebrafish and facilities to study them, the latter perspective requires the integration of such tools and resources with an intimate knowledge of the species' natural history.

To this end, we briefly review what is known of the zebrafish range, its evolutionary origins, and the abiotic and biotic environments in which it occurs. Given the fragmentary nature of this information and the limited scope of field studies thus far, our goal is not to paint a detailed portrait of how zebrafish behave in the natural world, but rather to collect some of the salient observations and to suggest avenues for future efforts.

Geographic distribution and phylogeny

The genus *Danio* presently comprises 26 valid species distributed across South Central and Southeast Asia (Tang et al., 2010; McCluskey and Postlethwait, 2015; Froese and Pauly, 2019). Encompassing a large geographical region, and studied in the wild by relatively few

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Behavioral and Neural Genetics of Zebrafish, First Edition, 2020, 3–16

researchers, it seems likely that additional danios await discovery. Indeed, the number of recognized species has increased markedly in recent years (Fig. 1.1A).

The zebrafish itself is also distributed widely, with historical or more recent records from India, Nepal, Bangladesh, and Myanmar (Spence et al., 2006, 2007b, 2008; Engeszer et al., 2007; Whiteley et al., 2011; Arunachalam et al., 2013; Suriyampola et al., 2015; and references therein) (Fig. 1.1B). The fish may also occur in Pakistan (Daniels, 2002). The limits of the range are somewhat unclear given the paucity of sampling. Adding to this uncertainty, morphologically similar, striped danios also having ill-defined ranges, including *Danio quagga* and *D.* aff. *kyathit* (which may itself be *D. quagga*), could be mistaken for zebrafish in the eastern states of India, or vice versa in Myanmar (Fang, 1998; Quigley et al., 2005; Kullander et al., 2009; McCluskey and Postlethwait, 2015).

The phylogeny of zebrafish relative to other *Danio* species has been examined in several contexts, using different approaches and coming to different conclusions (Meyer et al., 1993, 1995; McClure, 1999; Parichy and Johnson, 2001; Sanger and McCune, 2002; Fang,

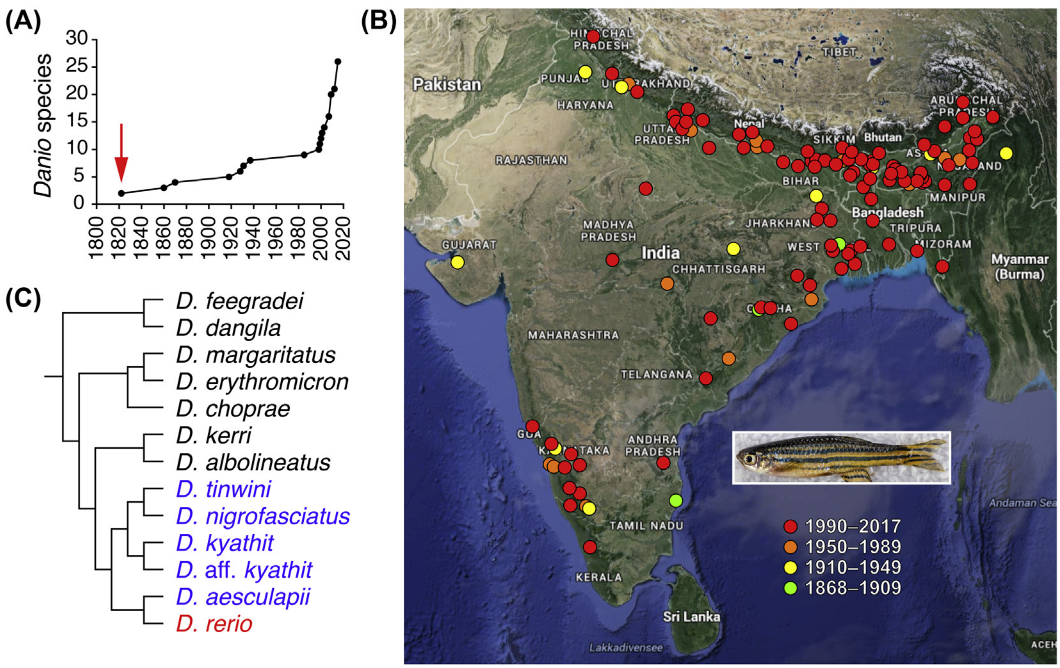

FIGURE 1.1 **Zebrafish evolution and range.** (A) Cumulative numbers of *Danio* species, beginning with *Danio rerio* (arrow) (Hamilton, 1822). (B) Historical and recent sites at which *D. rerio* has been reported. Inset, Example adult *D. rerio* caught at a site in northeastern India (Engeszer et al., 2007). (C) Phylogenetic relationships of several *Danio* species, with the *D. rerio* species group shown in blue and red. Tree shown is only one of several recovered topologies. Images of *Danio* species with an emphasis on pigmentation and its evolution have been published (Quigley et al., 2004, 2005; Mills et al., 2007; Patterson et al., 2014; Spiewak et al., 2018; Lewis et al., 2019; Patterson and Parichy, 2019) in addition to species descriptions (Fang, 1997b, 2000; 1997a; 1998; Fang and Kottelat, 1999, 2000; Roberts, 2007; Sen, 2007; Kullander and Fang, 2009b, 2009a; Kullander et al., 2009, 2015; Kullander, 2012, 2015; Kullander and Britz, 2015; Kullander and Noren, 2016). *(C) After (McCluskey and Postlethwait, 2015).*

Behavioral and Neural Genetics of Zebrafish, First Edition, 2020, 3–16

2003; Mayden et al., 2007; Fang et al., 2009; Tang et al., 2010). The most recent analyses using genome-wide data point to a *D. rerio* species group within which relationships are difficult to discern, owing at least in part to extensive introgression of chromosomal segments across phylogenetic lineages (McCluskey and Postlethwait, 2015). New opportunities for understanding the evolution of behavior and other traits may become apparent as genomes of new *Danio* species are placed within this developing framework.

Features of the abiotic and biotic environment

Table 1.1 summarizes observations of five studies plus unpublished field observations that documented zebrafish habitats in India and Bangladesh (McClure et al., 2006; Spence et al., 2006; Engeszer et al., 2007; Arunachalam et al., 2013; Suriyampola et al., 2015). Although the different studies emphasized different features of the environment, some generalities emerge. Some examples of sites at which zebrafish have been found are shown in Fig. 1.2.

Zebrafish have been found at elevations from just above sea level to over 1500 m. At these locations, zebrafish are most often found in shallow streams, backwaters, blind channels connected stably or intermittently to streams, or pools at stream edges. Substrates are commonly fine—mud, silt, or sand—but also can be pebbles, larger rock, or of mixed types. Not limited to natural bodies of water, zebrafish are found in rice paddies, irrigation ditches, and artificial ponds as well. Whether natural or artificial sites, zebrafish most often occupy still or slow moving water, sometimes adjacent to main channels having considerably faster flow. Banks are often well-vegetated, and waters frequently have overhanging and surface vegetation. Aquatic or submerged plants are often abundant. Vegetation presumably confers shade and considerable microenvironmental complexity, likely exploited for spawning, growth of larvae, and avoidance of predators. Indeed, still or nearly still waters with abundant plant material have been found to harbor apparently spawning zebrafish, and also juvenile zebrafish. Nevertheless, the life cycle of zebrafish in the wild and the relevance of laboratory observations to specific environments and behaviors in the field remain poorly understood (Spence et al., 2007a, 2007b; Engeszer et al., 2008; Suriyampola et al., 2015).

In keeping with structural and biological richness of their habitat, zebrafish in the wild have been found to eat animal material, especially insects of both terrestrial and aquatic origin, but also detritus, algae, and higher plant matter (McClure et al., 2006; Spence et al., 2007b; Arunachalam et al., 2013).

Waters containing zebrafish tend to be clear, although zebrafish can also be found occasionally in more turbid conditions, sometimes associated with rainfall or other disturbances. Details of light spectra and intensities in the aquatic environment—as experienced by zebrafish themselves—have yet to be documented unfortunately. Nevertheless, these data will be critical to interpreting behaviors and potential signals that are employed in agonistic interactions, courtship, shoaling, and predation avoidance (Rosenthal and Ryan, 2005; Rosenthal, 2007; Engeszer et al., 2008; Kalueff et al., 2013; Lewis et al., 2019; Zabegalov et al., 2019).

Although zebrafish in the laboratory are typically maintained at ~28°C, they experience a considerable thermal range in nature, having been documented in waters from 12 to 39°C. It seems certain that some populations of fish experience colder conditions as well because

TABLE 1.1 Abiotic conditions for zebrafish in the field.

				Substrate[d]				Conditions				Study		
Location	Elevation (m)[a]	Parent water body[b]	Depth (cm)[c]	A	B	C	D	Flow[e]	Temp	pH	Transparency[f]	Source[g]	Source site	Month
Bangladesh	~2	Ditch	80	X				Still	20	8	Clear	A	1	January
Bangladesh	~5	Isolated channel small river	50	X				Still	22	8	Intermediate	A	9	January
Bangladesh	~16	Cultivated pond	15	X				Still	21	8	Clear	A	15	January
Bangladesh	~16	Pond	40	X				Still	20	8	Intermediate	A	16	January
Bangladesh	~16	Pond	103	X				Still	17	8	Intermediate	A	17	January
Bangladesh	~18	Pond	96	X				Still	21	8	Intermediate	A	22	January
Bangladesh	~18	Ditch of paddy fields	50	X				Still	23	8	Clear	A	23	January
Bangladesh	~18	Pond	65	X				Still	33	8	Intermediate	A	23	January
Bangladesh	~18	Irrigation channel	75	X				Still	33	8	Intermediate	A	25	January
Bangladesh	~18	Creek adjacent to river	120	X				Flowing	30	8	Intermediate	A	26	January
India NW, N, NE	~6, ~129, ~520	Rice paddy, slow streams	16−57					Slow	27−34	7.9−9.2	Clear	B	2,4,5	September, October
India NE	51	Swamp by second-order stream	nd[c]	X				Slow	25	6.8	Clear	C	1	July
India NE	63	Second-order stream	nd	X				Medium	34	6.5	Clear	C	3	July
India NE	63	Second-order stream	nd	X				Medium	33	6.4	Intermediate	C	4	July
India NE	63	Second-order stream	nd	X				Medium	32	6.3	Clear	C	5	July
India NE	63	Rice paddy	nd	X				Very slow	39	7.3	Clear	C	6	July
India NE	54	Second-order stream	nd	X				Slow−medium	27	7.1	Clear	C	9	July

India NE	74	Swamp	nd	X				Still	27	6.3	Clear	C	11	July
India NE	50	Second-order stream and pools	nd	X				Slow–medium	28	6.1	Clear	C	12	July
India NE	1323	Second-order stream	nd	X				Medium	27	6.5	Clear	C	14	July
India NE	1323	Second-order stream	nd	X				Slow	26	6.2	Clear	C	15	July
India NE	1323	Second-order stream, adjacent pools	nd	X				Still–very slow	28	5.9	Clear	C	16	July
India NE	1234	Second-order stream	nd	X				Fast	25	nd	Clear	C	18	July
India NE	14	Fish pond	nd	X				Still	32	8.1	Turbid	C	24	July
India NE	14	Fish pond	nd	X				Still	31	7.8	Turbid	C	26	July
India NE	647	First-order stream	nd	X	X			Slow	20	6.3	Clear	D	11	December
India NE	675	Stream	nd	X	X			Slow	19	6.9	Clear	D	12	December
India NE	710	Stream	10–15	X	X			Slow	20	7.3	Clear	D	13	December
India NE	236	Pond off large river	nd	X	X			Slow	22	7	Clear	D	14	November
India NE	214	Fish pond	70		X	X		Medium–fast	21	7.2	Clear	D	15	November
India NE	274	Beel	nd	X					22	7.3	Turbid	D	16	November
India NE	342	Stream	10–60	X	X			Medium	20	7.1	Clear	D	17	November
India NE	218	Small river	20–60		X	X	X	Medium–fast	19	6.3	Clear	D	18	November
India NE	396	Third-order stream	nd		X			Fast	21	7.3	Clear	D	19	November
India NE	341	Third-order stream	1–15	X	X	X		Slow	20	6.5	Clear	D	20	November
India NE	1576	Pool near stream	nd						12	6.2	Clear	D	21	June
India N	268	Third-order stream	30	X				Medium	28	6.4	Clear	D	9	May
India N	656	Fish farm	nd	X				Medium	24	7.5	Clear	D	10	May
India E	418	Fourth-order stream	15–35		X	X		Medium	27	6.6	Clear	D	5	May

(*Continued*)

TABLE 1.1 Abiotic conditions for zebrafish in the field.—cont'd

				Substrate[d]				Conditions				Study		
Location	Elevation (m)[a]	Parent water body[b]	Depth (cm)[c]	A	B	C	D	Flow[e]	Temp	pH	Transparency[f]	Source[g]	Source site	Month
India E	432	Third-order stream	10–80		X	X		Medium	27	6.4	Clear	D	6	May
India E	245	Second-order stream	10–50	X				Medium	27	7.2	Turbid	D	7	August
India E	238	Second-order stream	nd		X			Medium	25	9.8	Turbid	D	8	August
India SW	328	Second-order stream	10–35		X	X		Medium	26	6.7	Clear	D	1	June
India SW	680	River	10–32		X	X		Medium	26	7.1	Clear	D	2	March
India SW	615	Stream	10–110		X	X	X	Slow	17	7.9	Clear	D	3	May
India SW	599	Third-order stream	30–45		X	X	X	Slow–medium	17	7.1	Intermediate	D	4	May
India NE	12	Rice paddy	15	X				Still	27	7.7	nd	E	SV	October, November
India NE	12	Irrigation channel	13	X				Still	27	7.4	nd	E	SN	October, November
India NE	41	Stream	10	X				Fast	27	7.5	nd	E	FM	October, November
India N Central	324	Stream	15	X				Slow	27	7.5	nd	E	FV	October, November
India NE	690	Puddle in road	5		X			Medium	37	nd	Clear	F		August
India NE	1410	Rice paddy	10–20	X				Slow	23	6.22	Clear	F		August

[a] ~, *Inferred from locality data through Google Earth.*
[b] *In some instances fish may have been collected in pockets at stream edges.*
[c] *nd, not determined.*
[d] *A, mud or silt; B, sand; C, pebble, gravel or cobble; D, boulder or bedrock.*
[e] *Still, no detectable flow; slow, <6 cm/s; medium, 6–12 cm/s; fast, >12 cm/s.*
[f] *Clear, to bottom or ≥30 cm deep; intermediate, <30 cm deep; turbid, dirty, muddy or <5 cm deep.*
[g] *A, Spence et al. (2006); B, McClure et al. (2006); C, Engeszer et al. (2007b); D, Arunachalam et al. (2013); E, Suriyampola et al. (2015); Postlethwait et al. field observations.*

FIGURE 1.2 **Examples of zebrafish habitat.** (A–D) Stream with still pools and rice paddies in the Indian state of Meghalaya (sites 14–16 of Engezer et al., 2007). (A) Aerial view, recorded on November 2009 (Google Earth) showing locations and directions from which images in B, C, and D were taken during July 2006. N, North. (B) Small stream with well-vegetated banks. (C) Paddy fields above stream. (D) Still water with submerged vegetation adjacent to stream, flooded during the monsoon season, but dry in aerial view. Inset shows two zebrafish of a small shoal, adjacent to surface detritus (arrow, in main panel). (E) Small stream in West Bengal, India (site 3 of Engeszer et al., 2007). (F) Turbid pond with zebrafish and farmed fish in state of Orissa, India (site 24 of Engeszer et al., 2007). (G, H) Sites in Meghalaya, including a flooded road surface waters at 37°C (25.740610, 91.806707) and a small stream adjacent to a town (25.604767, 91.896118). Insets in G show a small shoal of zebrafish in shallow water as well as a single fish, with characteristic—and oddly conspicuous—spot of reflective iridophores that decorate the heads of zebrafish (arrow) (field observations, Postlethwait, Raman, Chatterjee, Dey, and Mylliemngap, unpublished).

TABLE 1.2 Teleost species co-occurring with zebrafish.

Family	Genera and species
Adrianichthyidae	*Oryzias carnaticus*, *O.* sp.
Ambassidae	*Chanda nama*
Anabantidae	*Anabas testudineus*, *Badis badis*, *Colisa chun*, *C. fasciatus*, *C. lalia*, *Parambassis lala*, *P. ranga*
Anguillidae	*Anguilla bengalensis*
Aplocheilidae	*Aplocheilus lineatus*, *A. panchax*
Badidae	*Badis blosyrus*, *Dario dario*, *Da.* sp.
Bagridae	*Mystus bleekeri*, *M. cavasius*, *M. tengara*, *M. vittatus*
Belonidae	*Xenedonton cancila*
Channidae	*Channa gachua*, *Ch. orientalis*, *Ch. punctatus*, *Ch. stewartii*, *Ch.* sp. 1, *Ch.* sp. 2
Cichlidae	*Oreochromis niloticus*
Clupeidae	*Corica soborna*, *Gudusia chapra*
Cobitidae	*Botia almorae*, *B. dario*, *B. rostrata*, *Lepidocephalichthys annandalei*, *L. guntea*, *L. irrorata*, *L.* sp. 1, *L.* sp. 2,
Cyprinidae	*Amblypharyngodon mola*, *Aristichthys nobilis*, *Aspidoparia jaya*, *Barilius barna*, *Ba. bendelisis*, *Ba. gatensis*, *Ba. vagra*, *Chagunius chagunio*, *Chela fasciatus*, *Chela khujairokensis*, *Chela laubuca*, *Cirrhinus cirrhosus*, *Ci. mrigala*, *Ci. reba*, *Crossocheilus latius*, *Cyprinus carpio*, *Danio aequipinnatus*, *Danio dangila*, *Danio meghalayensis*, *Devario aequipinnatus*, *De. assamensis*, *De. devario*, *Esomus danricus*, *Garra annandelei*, *G. lissorhynchus*, *G. mullya*, *G. nasuta*, *Hypophthalmichthys molitrix*, *Hypselobarbus jerdoni*, *Hypselobarbus kolus*, *Labeo bata*, *La. boga*, *La. boggut*, *La. calbasu*, *La. gonius*, *La. pangusia*, *La. rohita*, *Neolissochilus hexastichus*, *Osteobrama cotio peninsularis*, *Osteochilichthys nashi*, *Puntius bimaculatus*, *Pu. carnaticus*, *Pu. chola*, *Pu. conchonius*, *Pu. fasciatus*, *Pu. gelius*, *Pu. phutunio*, *Pu. sarana*, *Pu. shalynius*, *Pu. sophore*, *Pu. stoliczkanus*, *Pu. terio*, *Pu. ticto*, *Pu.* sp., *Raiamas bola*, *Rasbora daniconius*, *R. rasbora*, *Salmophasia bacaila*, *S. boopis*, *S. horai*, *S. phulo*, *Tor khudree*, *Tor mosal mahanadicus*, *T. tor*
Erethistidae	*Pseudolaguvia ribeiroi*
Gobiidae	*Brachygobius nunus*, *Glossogobius giuris*, *Gobiopterus chuno*
Mastacembalidae	*Macrognathus aculeatus*, *Ma. aral*, *Ma. pancalus*, *Ma.* sp., *Mastacembelus alboguttatus*, *Mas. armatus*
Nandidae	*Nandus nandus*
Nemacheilidae	*Acanthocobitis botia*, *Nemacheilus* sp., *Schistura arunachalensis*, *Sc.* sp.
Notopteridae	*Notopterus notopterus*
Olyridae	*Olyra longicaudata*
Osphronemidae	*Colisa sota*, *Ctenops nobilis*
Psilorhynchidae	*Psilorhynchus balitora*, *Ps. sucatio*, *Ps. tenura*, *Ps.* sp.

Behavioral and Neural Genetics of Zebrafish, First Edition, 2020, 3−16

TABLE 1.2 Teleost species co-occurring with zebrafish.—cont'd

Family	Genera and species
Schilbeidae	*Eutropichthys vacha*
Siluridae	*Ompok bimaculatus*, *Wallago attu*
Sisoridae	*Bagarius bagarius*, *Gagata cenia*, *Glyptothorax* sp.
Synbranchidae	*Monopterus cuchia*
Syngnathidae	*Microphis deocata*
Tetraodontidae	*Tetraodon cutcutia*

Aggregated from: *Spence et al. (2006)*; *Engeszer et al. (2007b)*; *Arunachalam et al. (2013)*; *Suriyampola et al. (2015)*

high-altitude sites with the lowest recorded temperatures were surveyed during the summer months of June and July. Zebrafish have been found in waters with a pH from 5.9 to 9.2. These conditions suggest potentially interesting thermal and other physiological adaptations across populations. Understanding means and variances in these parameters across seasons, both within and among populations, will provide essential information for such efforts.

Of particular interest for understanding the origins of zebrafish morphology and behavior are the other fishes with which it shares a habitat. A large number of species have now been documented to occur in the same bodies of water with zebrafish (Table 1.2; Fig. 1.3). These include potential competitors, like killifish (*Aplocheilus*), minnows (*Esomus*), barbs (*Puntius*), and others. Also present are potential predators of egg and larvae, including catfish (*Mystus*), loaches (*Lepidocephalus*), spiny eels (*Mastacembelus*), and torrent minnows (*Psilorhynchus*). Potential predators of adults include snakeheads (*Channa*), leaffish (*Nandus*), needlefish (*Xenentodon*), large catfish, and others. Beyond teleosts, it is likely that odonate larvae and other aquatic invertebrates prey upon zebrafish. Whether terrestrial animals, including wading or diving birds, take zebrafish remains unclear. Formal documentation of predatory and competitive interactions would provide valuable insights into the selection regime experienced by zebrafish, and the ecological consequences of behavioral variation across life cycle stages (Engeszer et al., 2007a; Buske and Gerlai, 2011).

Environmental changes to zebrafish habitat

As for all species, human impacts on zebrafish in the wild are likely substantial. Specific types of habitat degradation have been noted (Engeszer et al., 2007b; Arunachalam et al., 2013) and anecdotal observations from the field suggest that many sites formerly populated by zebrafish no longer support them. Given the wide geographic distribution of these fish, and the enormous wealth of knowledge provided by genomic, developmental, and other analyses, zebrafish would seem to be a valuable model for assessing the impacts of human activities on natural habitats and ecological and evolutionary responses to them. A sentinel role for zebrafish could provide insights into population and genetic consequences of direct human population encroachment; exposure to household, agricultural, or industrial products; and overall impacts of changing global and regional climates. Opportunities for such insights

FIGURE 1.3 **Species that co-occur with zebrafish.** Only selected examples are presented. Color images of additional taxa can be found in Engeszer et al. (2007). *Esomus*, *Oryzias*, and other species might compete with zebrafish, whereas *Lepidocephalus*, *Channa*, *Mystus*, *Barilius*, and other species seem likely to be predators of zebrafish eggs, larvae, or adults. Large-bodied species of *Danio* and *Devario* often co-occur with smaller zebrafish; other small-bodied danio species occur typically further east than the known range of zebrafish (McCluskey and Postlethwait, 2015).

will require those who study zebrafish in the wild to consistently publish high-resolution GPS data to allow field sites to be visited and revisited for years to come.

Conclusions

The zebrafish already offers an outstanding system for developmental biology and developmental neurobiology, evolution, genomics, and toxicology. As the species is increasingly adopted for behavioral neuroscience or ethological investigations, a deeper understanding of its natural world will surely provide valuable context and may lead to insights that would not otherwise be apparent. Despite the geographical distance of wild zebrafish from the majority of labs that use the species, the studies reviewed here, and the authors' own experiences, indicate that field work is both tractable and illuminating. When done collaboratively, such efforts also can lead to valuable scientific and cultural bridges for investigators and trainees across the globe.

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Behavioral and Neural Genetics of Zebrafish, First Edition, 2020, 3−16