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ARTICLE

Multiscale Investigation of Water Chemistry Effects on Fish Guild Species Richness in Regulated and Nonregulated Rivers of India's Western Ghats: Implications for Restoration

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Abstract

Tropical rivers across the world are experiencing rapid degradation and loss of fish species due to flow regulation, pollution, and other anthropogenic pressures. Knowledge of how flow alterations at different scales affect tropical fish diversity remains limited, especially in terms of how resulting changes in water chemistry affect fish communities. We investigated fish guild composition and responses of guild richness to water chemistry in 120 river segments with and without local-scale water removals and pollution. This included two regulated subbasins (with flow regulation by barrages and large-scale water diversions) and two nonregulated subbasins (flows not regulated by these barriers) in India's Western Ghats. Using multivariate ordination and regression models, we identified covariates related to water chemistry and environmental characteristics that explained differences in fish species composition and species richness of three water column position-based fish guilds in the study area. At the subbasin scale, effects of water chemistry were stronger for individual river segments. At the segment scale, no differences in water chemistry were found between segments with and without water removals or pollution in both regulated and nonregulated subbasins. Guild-

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wise species richness, especially of surface-dwelling fishes, was positively correlated with water temperature and total dissolved solids across regulated and nonregulated subbasins. In regulated subbasins, total alkalinity was positively correlated with species richness of bottom-dwelling and mid-column-dwelling fishes. Landscape-scale flow alterations and degree of flow regulation by river barriers significantly influenced fish composition and species richness over and above local water withdrawal or pollution. River restoration at both the local (segment) and landscape (basin) scales is crucial for fish conservation. To sustain fish guild diversity, maintenance of ecological flow regimes downstream of barriers needs to receive priority over mitigating local disturbances in regulated river catchments of the Western Ghats.

Freshwater is vital to sustaining biodiversity as well as human wellbeing (Baron et al. 2003; Dudgeon et al. 2006; Vorosmarty et al. 2010), but freshwater ecosystems are among the most affected by anthropogenic impacts across the globe (Dudgeon 2010; Strayer and Dudgeon 2010; Vorosmarty et al. 2010). As a result, a high proportion of riverine biodiversity is highly threatened, especially freshwater fishes (more than 5,000 species worldwide), according to the International Union for Conservation of Nature (IUCN; Dudgeon 2000; Nel et al. 2007; Darwall et al. 2008; Moreno and Rodriguez 2010; Reid et al. 2013). Tropical river fishes are affected by hydrological barriers, such as dams, barrages, and other forms of flow regulation. Reduction in flows or other aberrations can lead to minor to major changes in water chemistry, to which river fishes might be sensitive. River fishes are also threatened by local water withdrawals for irrigation and by water pollution from domestic waste, sewage, and agrochemical runoff (Tejerina-Garro et al. 2005; Kanno and Vokoun 2010; Winemiller et al. 2016). Such local disturbances are often strongly related to the degree of catchment regulation, with highly regulated basins also being more polluted and disturbed, thereby impacting biodiversity (Jackson et al. 2001; Kanno and Vokoun 2010; Mims and Olden 2013; Shen et al. 2017). This makes it important to assess the independent and combined impacts of flow regulation (at the landscape level) and water removal (at the local level) on water chemistry and, in turn, freshwater fish diversity and ecosystem services (fisheries), which are not well understood in many tropical freshwater ecoregions (Bunn and Arthington 2002; Moreno and Rodriguez 2010; Poff and Zimmerman 2010).

Stream fish communities are influenced by both biotic factors (competition and predation) and abiotic factors (catchment characteristics, channel morphology, discharge, habitat heterogeneity, water chemistry, changes in land use patterns, and human activities) at local, regional, and basin scales (Schlosser 1991; Chapman 1996; Matthews 1998; Gido and Jackson 2010; Sannadurgappa 2010; Pease et al. 2011; Atkore 2017), but the relative importance of these factors for influencing fish assemblages is still uncertain (Pease et al. 2011). Hydrological barriers disrupt the longitudinal and lateral connectivity of river systems (Vannote et al. 1980; Pringle 2001), often with highly negative impacts on fish communities (Poff and Allan 1995; Malmqvist and Rundle 2002; Konar et al. 2013). These barriers have both immediate as well as long-term effects on the life histories of fishes (Vasconcelos et al. 2014). Hydrological barriers and impoundments due to dams, barrages, and reservoirs may benefit some generalist (and particularly invasive) fish species (Chu et al. 2015); however, they negatively affect the overall diversity and abundance of native and endemic fish species as well as their life history traits, survival, and breeding success (Dudgeon 2000; Pringle 2001; Mims and Olden 2012, 2013; Reid et al. 2013).

Apart from hydrological, environmental, and biological factors, anthropogenic disturbances, such as land use changes or water removals, can also influence fish communities (Gilliam et al. 1993; Jackson et al. 2001; Kanno and Vokoun 2010). Local water withdrawals, pollution, excessive fishing, and substrate mining pose additional threats to fish breeding habitats in regulated hill streams and rivers of the Western Ghats (WG) region, a global biodiversity "hot spot" in Peninsular India that harbors significant endemic fish species richness and diversity (Daniels 2002). Local disturbances can directly affect fish communities or the impacts of local disturbances can be aggravated by flow regulation at the catchment scale. Thus, it becomes difficult to separate local anthropogenic effects from correlated larger basin-scale effects—especially in terms of influences on water quality—to prioritize conservation efforts. Hence, there is a need to generate knowledge on how changes in water chemistry affect freshwater fish diversity across multiple scales in tropical river systems in India (Bhat 2002; Rao 2016; Atkore 2017).

Earlier studies on fish diversity have described functional responses of fish guilds to riverine habitat gradients or stream characteristics (De Silva et al. 1979; Bhat 2004; Weliange and Amarsinghe 2007; Johnson and Arunachalam 2012; Oliveira et al. 2012; Chakrabarty and Homechaudhuri 2013). In India, despite a highly diverse freshwater fish fauna and numerous taxonomic studies, factors driving persistence of various fish guilds in hydrologically altered and human-modified river systems remain less studied (Jayaram 2010; Kundu et al. 2014; Atkore et al. 2017; Grubh and Winemiller 2018; Jumani et al. 2018). Guild-based approaches can provide an intuitive understanding of the functional responses of fish communities to alterations (Villéger 2008) and can help to develop a broad understanding of the impacts of river modification on fishes (Mouillot et al. 2013). Previous studies have shown that fish communities partition habitat space based on their ecomorphology, stream substrate use (Bhat 2005; Johnson and Arunachalam 2010), rainfall events (Grubh and Winemiller 2004, 2018), and elevational gradients (Raghavan et al. 2008). Flow-regulated rivers (with dams/barrages) in the WG differed substantially from nonregulated rivers (without dams/barrages) in fish assemblage structure (Bhat and Magurran 2007). Recently, a study on small hydropower projects in the WG showed that dewatering and changes in daily natural flow regimes negatively affected the abundance, size structure, and diversity of many fish species (Jumani et al. 2018). Atkore et al. (2017) showed that river fish species recovered as a function of distance from upstream hydrological barriers. These studies did not quantify the effects of water chemistry and environmental covariates in relation to flow regulation and local effects, which was the focus of the present study.

For this study, we defined regulated river subbasins (RSBs) as catchments with flow regulation by barrages and large-scale water diversions, and we defined nonregulated river subbasins (NRSBs) as those not regulated by these barriers and maintaining near-natural flows. Both RSBs and NRSBs can be subject to local effects of disturbance by human activities unrelated to flow regulation (e.g., fishing, pollution, local water withdrawals, etc.). Based on comparisons of RSBs and NRSBs, our current study addressed three questions: (1) “How do fish guild richness and composition vary across RSBs and NRSBs?”; (2) “How do water chemistry and other environmental variables differ between (a) RSBs and NRSBs and (b) across sites with and without local water removal/human disturbance in RSBs and NRSBs?”; and (3) “How does fish guild richness respond to water chemistry and other environmental variables across segments in the different basins?”

Based on predictions from previous studies (Brasher 2003; Merz 2013; Macnaughton et al. 2016), we hypothesized that river segments in RSBs would have higher temperatures and poorer water quality indices than river segments in NRSBs, which in turn would have variable effects on the fish species richness of different guilds. We predicted that surface-dwelling (SD) fishes would be more sensitive to changes in water chemistry and temperature than mid-column-dwelling (MCD) and bottom-dwelling (BD) fish species. To test this, we quantified the species richness of fish guilds (based on position in the water column) in response to differences in water chemistry within and between RSBs and NRSBs and across sites with local impacts of pollution and water withdrawals. We discuss the implications of our findings for mitigating the effects of flow regulation, prioritizing fish conservation in river habitats, and developing guidelines to maintain ecological flow regimes for fish conservation in India's WG and similar tropical river basins elsewhere.

METHODS

Our sampling unit was the river segment, defined as a stream reach of approximately 150 m in length with one or more instream riverine habitats (run, riffles, or pools). We adopted a guild-based approach to assess the ecological responses of fish species richness in three guilds (based on position in the water column) to differences in water chemistry across regulated river segments (by hydrological barriers) and nonregulated river segments (without hydrological barriers) as well as from local water withdrawal and pollution effects (Chapman 1996; Wei et al. 2009; Mantel et al. 2010; Muller et al. 2011). Our exploratory investigation was conducted in hill streams of two RSBs and two NRSBs within the central WG of India. For the study, we used the definition of a “guild” as “a group of fish with significant overlap in multidimensional resource niche space” (Simberloff and Tamar 1991; Wilson 1999). River barriers were defined as “anthropogenic modifications of river flow regimes by dams or barrages” (Bunn and Arthington 2002).

Study Area Description

The study was conducted in the states of Karnataka and Goa in the central WG of India from 2011 to 2014 (Figure 1; Tables S.1.1 and S.1.2 available in the Supplement in the online version of this article). The WG mountain range along the western coast of India is a distinct zoogeographical subdivision of Peninsular India (Bhimachar 1945) and is a part of the WG–Sri Lanka global biodiversity hot spot and world heritage site (Cincotta et al. 2000; Das et al. 2006). It is also a highly populous biodiversity hot spot, witnessing intense anthropogenic pressure on freshwater ecosystems from irrigation dams, hydropower projects, mining, agricultural intensification, and destructive fishing activities (Collins et al. 2012; Atkore 2017). We conducted fish sampling across two RSBs (Malaprabha River and Mhadei [also known as Mahadayi or Mandovi] River) and two NRSBs (Tunga and Bhadra rivers). The Malaprabha and Mhadei rivers originate from the same hill range at an elevation of 760 m above mean sea level (AMSL) bordering the states of Karnataka and Goa. The headwater catchments of the Malaprabha and Mhadei rivers are dominated by tropical moist evergreen forests, and the downstream plains are mostly covered by open scrub forests and agricultural land. These subbasins receive most of their annual precipitation during the southwest monsoon between June and September. In upper catchments of the Malaprabha River, the annual rainfall varies between 2,000 and 3,500 mm and the average annual

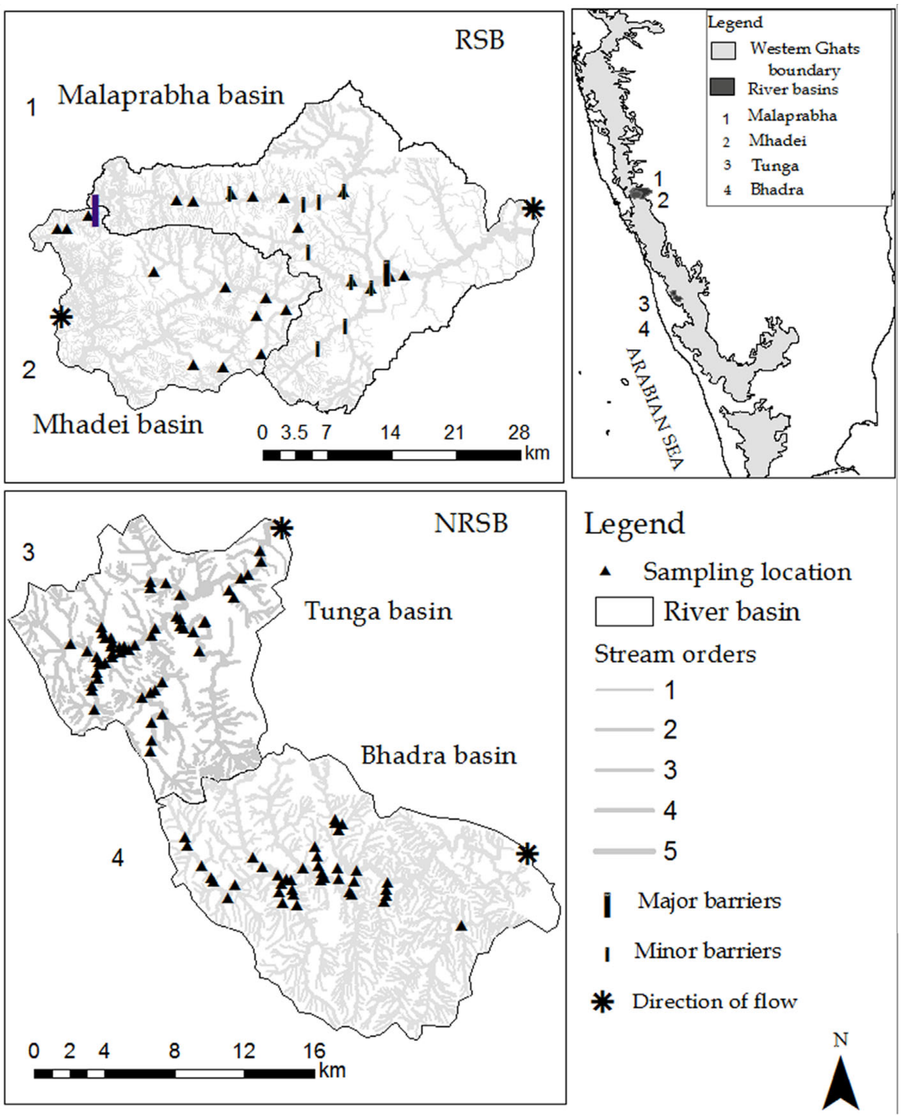

FIGURE 1. Sampling locations in the four subbasins of India's central Western Ghats (RSB = regulated river subbasins; NRSB = nonregulated river subbasins).

stream discharge recorded at the Khanapur gauging station for the year 2007 was approximately 450 m^3/s. Annual rainfall in the upper catchments of the Mhadei River varies from 1,800 to 3,500 mm, and average annual river discharge measured at Ganjem for the year 2007 was about 55 m^3/s (Ibrahampurkar 2012; Water Resource Development Organization, Karnataka and Goa, unpublished data).

River Flow Data

Data on river discharge were obtained for the Malaprabha River subbasin (1976–2007) and the Mhadei River subbasin (1979–2013; Table S.2). We also extracted daily rainfall (mm) time series data from the APHRODITE (Asian Precipitation–Highly Resolved Observational Data Integration towards Evaluation) data set and estimated basin average annual rainfall from 1979 to 2007 for the Malaprabha River subbasin and from 1979 to 2013 for the Mhadei River subbasin (Table S.2; Figure S.1 available in the Supplement in the online version of this article; and see associated references).

There are numerous check dams and barrages built on both rivers to store flows from the headwater catchments for irrigation (Ibrahampurkar 2012). A massive interbasin water transfer project has been constructed on headwater tributaries of the Mhadei River subbasin to divert 1,038.09 million cubic meters of water annually into the Malaprabha River subbasin for domestic water supply to towns and villages in northern Karnataka (Water Dispute Tribunal 2018). This diversion is likely to threaten fish species in both subbasins. In the last two decades, the cropping pattern in the Malaprabha River catchment has also drastically shifted from rain-fed crops, such as millets and pulses, to water-intensive crops, such as sugarcane, vegetables, and oilseeds. As a result, water extraction from the river and aquifer has intensified (Heller et al. 2012), affecting streamflows during both the monsoon and the dry season. Pollution in the river due to municipal wastewater and agrochemical residues from agricultural fields have lowered river fish productivity according to local communities in the area. Other local disturbances to stream biota are from intensive instream fishing and sand-boulder mining (Atkore et al. 2017).

The nonregulated Tunga and Bhadra River subbasins flow through the Chikkamagaluru, Dakshina Kannada, and Udupi districts of Karnataka. The headwater streams originate at an elevation of 1,160 m AMSL in Kudremukh National Park. The region receives more than 6,000 mm of rainfall annually (Krishnaswamy et al. 2006). These subbasins have evergreen forests in the headwaters, whereas downstream reaches have mixed land uses comprising paddy fields and coffee plantations.

Ethics Statement

We obtained legal research permissions from the Karnataka Forest Department and the Goa Forest Division to conduct this study, and we adhered to their ethical guidelines and standardized methods for fish and water sample collections. We followed standard guidelines as prescribed by the Committee for the Purpose of Control and Supervision of Experiments on Animals, India (http://cpcsea.nic.in/Auth/index.aspx). In addition, we followed guidelines for wild fishes as prescribed by the American Fisheries Society and American Society of Ichthyologists and Herpetologists (2003). Fewer than five individuals were collected for identification of unknown fish species. They were fixed in 4% formaldehyde and later transferred to 70% ethyl alcohol for confirmatory taxonomic identification. For rare species, we collected no more than two individuals as a precaution based on IUCN guidelines for the collection of threatened species (IUCN 2011). Other fishing gears, such as gill nets and electrofishing, were not employed for sampling in this study due to their negative impacts on fish reproduction (Snyder 2003) and mortality of small fish and macroinvertebrates. Electrofishing is also prohibited in protected areas under India's Wildlife Protection Act of 1972; a Karnataka Forest Department order (Annexure Government Order FEE-404-FWL-2014; January 20, 2015); the Karnataka Inland Fisheries (Conservation, Development, and Regulation) Act of 1996; and the Goa, Daman, and Diu Fisheries Rules of 1981.

Fish Sampling Protocol

Fish communities were sampled, and data on corresponding environmental variables were collected from 150-m-long river segments across the four subbasins. Habitats within river segments chosen for sampling included pool, run, and riffle habitats that fish utilize at different stages of their life cycle (Schlosser 1991; Haur and Lamberti 2007). The chosen river segments located in both RSBs and NRSBs had similar elevation ranges (600–930 m AMSL), land uses, stream orders (2–6), and habitat characteristics (pools, runs, and riffles) to control for the effects of these variables on species turnover. At each of these river segments, fish sampling was conducted by using cast nets (0.5- × 0.5-cm mesh, 1.7 m deep; and 1.1- × 1.1-cm mesh, 2.8 m deep). Cast nets were preferred over other fishing methods because they are known to provide better coverage and capture of different fish guilds (irrespective of position in the water column) in WG rivers (Abraham and Kelkar 2012; Han et al. 2016). Furthermore, cast nets constitute a nondestructive fishing technique with the lowest fish mortality among competing intensive methods (Johnson and Arunachalam 2010; Abraham and Kelkar 2012; Ahmad et al. 2013). However, cast nets do have some limitations; for instance, they may be inefficient for sampling bottom dwelling fish at depths greater than 2.5–3.0 m.

We acknowledge that there are tradeoffs in choice of nets and gears for fish sampling based on efficiency and coverage and that the literature on stream fish sampling recommends electrofishing techniques to achieve catch efficiency and stream coverage. However, we chose to use cast nets for sampling due to adverse impacts of electrofishing on stream invertebrates and endemic fishes, the issue of high costs, and legal and ethical considerations (Snyder 2003). Ease of operation, relatively high sampling efficiency, and portability also enable cast nets to provide better access to sampling locations and habitats in relatively remote river reaches (Han et al. 2016).

In each segment, cast-net sampling was carried out strategically based on initial checks for the feasibility of sampling different run, riffle, and pool habitats. Each replicate included the total occurrence data from all casts (10–26) conducted over approximately 120 min at each river segment (Figure S.2.1). Our overall cast-net effort captured 79 fish species, which represented nearly 75% of the total pool (i.e., 105 known species) from the study area (Rema Devi et al. 2013), suggesting that the overall sampling effort was sufficient. However, the number of casts or throws varied among subbasins: Bhadra ($n = 40$), Tunga ($n = 53$), Malaprabha ($n = 15$), and Mhadei ($n = 11$) rivers. Sampling was continued until saturation was achieved with respect to species accumulation with increasing cast-net effort (based on Abraham and Kelkar 2012). During the dry season our sampling effort was the most concentrated. Species richness was similar across seasons, so we pooled our seasonal species richness data. Data on fish species richness varied over the 3 years of field data collection (Figure S.2.2). Across sampling periods, 40 species were sampled in 2011, 44 species were sampled in 2012, and 48 species were sampled in 2013–2014 (Figure S.2.3).

At each river segment, fish were caught, identified, measured (TL, cm), and released alive back into the river. Standard field guides (Daniels 2002; Jayaram 2010) were used for species-level identification, which was confirmed with the latest taxonomic updates (Fricke et al. 2020). Any evidence of disease or deformity in the sampled fish species was recorded. Environmental variables, such as river depth, width, substrate type, and canopy cover, as well as water chemistry variables, such as temperature, dissolved oxygen concentration (DO), calcium hardness, total dissolved solids (TDS), alkalinity, inorganic nitrates, and inorganic phosphates, were measured at all segments (Table S.1.2). For all segments, we recorded the presence or absence of water abstraction activity (e.g., pumping), pollution point sources, and other human activities causing disturbance to fish habitats (e.g., substrate mining). The richness of each water column position-based guild (SD, MCD, and BD) was defined as the response variable for further analyses.

Guild-Based Classification of Fish Species

We grouped all sampled fish species according to six classification schemes (see analysis methods and Table 1) based on field surveys and an intensive review of published (journal articles and field guides) and unpublished (reports and monographs) literature. Fish species were classified based on depth or water column use as follows: surface dwellers, mid-column dwellers, or bottom dwellers (Lowe-McConnell 1975, 1987; Arunachalam 2000; Bhat 2002). Fishes' feeding preferences were categorized as phytophagous (algivore, herbivore, and detritivore), heterotrophic (insectivore and carnivore), or omnivorous (Arunachalam 2000; Bhat 2002; Weliange and Amarsinghe 2007; Johnson and Arunachalam 2012; Froese and Pauly 2016). The flow responses of fish species were classified as eurytopic, limnophilic, or rheophilic (Aarts and Nienhuis 2003; Chakrabarty and Homechaudhuri 2013). Reproductive strategies were lithopelagophilic, lithophilic, pelagophilic, phytolithophilic, phytophilic, or psammophilic. Life history strategies were assigned as equilibrium, opportunistic, periodic/seasonal, or intermediate (Table S.3; Welcomme 1985; Bhat 2002; Welcomme et al. 2006; Winemiller et al. 2008; Das et al. 2013; Froese and Pauly 2016). Fish species were also classified based on endemicity to the WG (Daniels 2002; Dahanukar and Raghavan 2013). While compiling these data, we realized that there was a lack of species-specific information from the WG region. Due to the lack of information, we therefore assumed that in some cases, certain congeneric species shared similarities in habitat preferences and feeding traits, but not with respect to reproductive guild (Bhat 2002; Johnson and Arunachalam 2012). Therefore, we used a combination of available literature and reports on life history traits of some fish species and our own observations to assign guild classification to congeneric species for which information was not available (Welcomme 1985; Bhat 2002; Winemiller et al. 2008; Das et al. 2013; Atkore 2017). This led to redundancy in our classification, as one type of guild classification would be correlated strongly with other types. To address this problem, we conducted multivariate analyses to select which guild classification scheme was the most representative and optimal for broadly describing fish life history trait variation (see below).

Data Analysis

Selection of representative fish guilds.— To choose a representative guild classification for further analyses, we used ordination analyses to identify how species with similar guild classifications clustered together. We used nonmetric multidimensional scaling (NMDS), an ordination method that calculates dissimilarities from fish species occurrence data collected across sites or other categories in which species may or may not occur. Based on calculated dissimilarity values, groups (typically sites) with similar assemblages cluster closer to each other than those with relatively dissimilar assemblages (Borcard et al. 2011). Here, we used a trait-by-species (or guild) analogy of conventional "site-by-species" ordination methods. A presence–absence matrix was prepared for all species (in columns) and all guild classifications or traits (in rows) to run the NMDS analysis until it attained a stable configuration (Borcard et al. 2011). The guild-based analysis also helped to overcome biases resulting from unknown heterogeneity in taxonomic resolution or systematic biogeographic variations in fish species richness across RSBs and NRSBs. The most stable NMDS configuration was identified to select the best representative guild classification (see Results).

Variation in fish species composition across regulated and nonregulated subbasins.— Nonmetric multidimensional scaling was used to check whether species composition differed across river segments (sites) in the four subbasins. The NMDS ordination was unconstrained by environmental variables and driven only by species composition (Rowe 2007). All of the scaled water chemistry variables, such as total alkalinity (TA), electrical conductivity (EC), calcium hardness, free CO_2, and inorganic nitrates, were subsequently fitted on the NMDS ordination axes to examine which variables were correlated with dissimilarities in fish community composition using the Bray–Curtis measure of dissimilarity (Borcard et al. 2011). Analysis of similarity (ANOSIM; Clarke 1993) was performed to check whether the species composition differed between RSBs and NRSBs. These analyses were conducted using

TABLE 1. Systematic list of fish (revised as per Fricke et al. 2020), with multiple guild definitions of fish species sampled across regulated subbasins (ML = Malaprabha River; MH = Mhadei River) and nonregulated subbasins (TN = Tunga River; BH = Bhadra River) in the Western Ghats study area. Asterisks indicate species that are endemic to the Western Ghats region. Water column position was the selected representative guild classification (SD = surface dwelling; MCD = mid-column dwelling; BD = bottom dwelling).

		Basis of guild definition				
Order, family, and species	Subbasin(s)	Water column position	Feeding preferences	Flow response	Life history cues	Reproductive strategy
Cyprinodontiformes						
Aplocheilidae						
Striped Panchax *Aplocheilus lineatus*	TN, ML	SD	Heterotrophic	Rheophilic	Opportunistic	Lithophilic
Beloniformes						
Belonidae						
Freshwater Garfish *Xenentodon cancila*	BH, TN	SD	Heterotrophic	Rheophilic	Intermediate	Phytophilic
Cypriniformes						
Balitoridae						
Slender Stone Loach *Balitora mysorensis**	BH, TN	BD	Phytophagous	Rheophilic	Periodic	Lithophilic
Western Ghat Loach *Bhavania australis**	BH, TN	BD	Omnivorous	Rheophilic	Periodic	Psammophilic
Nemacheilidae						
Mesonoemacheilus sp. 1	TN	BD	Phytophagous	Rheophilic	Periodic	Lithophilic
Zodiac Loach *Mesonoemacheilus triangularis**	BH, TN	BD	Phytophagous	Rheophilic	Periodic	Phytophilic
Mongoose Loach *Nemachilichthys rueppelli**	ML	BD	Omnivorous	Rheophilic	Periodic	Lithophilic
Common Spiny Loach *Lepidocephalichthys thermalis*	ML, MH	BD	Phytophagous	Rheophilic	Periodic	Lithophilic
Maharashtra Zipper Loach *Paracanthocobitis mooreh**	TN, ML	BD	Heterotrophic	Rheophilic	Periodic	Lithophilic
Schistura denisoni	TN, ML, MH	BD	Omnivorous	Rheophilic	Periodic	Lithophilic
*Schistura semiarmata**	TN	BD	Phytophagous	Rheophilic	Periodic	Lithophilic
Botiidae						
Zebra Loach *Botia striata*	BH, TN	BD	Omnivorous	Rheophilic	Periodic	Psammophilic
Cyprinidae						
Malabar Baril *Barilius bakeri**	BH, TN	SD	Omnivorous	Rheophilic	Periodic	Lithopelagophilic

TABLE 1. Continued.

Order, family, and species	Subbasin(s)	Basis of guild definition				
		Water column position	Feeding preferences	Flow response	Life history cues	Reproductive strategy
Barna Baril *Barilius barna*	TN	SD	Omnivorous	Rheophilic	Periodic	Lithopelagophilic
Jerdon's Baril *Barilius canarensis**	BH, TN	SD	Omnivorous	Rheophilic	Periodic	Lithopelagophilic
Indian Hill Trout *Barilius bendelisis*	BH, TN	SD	Omnivorous	Rheophilic	Periodic	Lithopelagophilic
Barilius sp. 1	TN	SD	Omnivorous	Rheophilic	Periodic	Lithopelagophilic
Wayanad Mahseer *Neolissochilus wynaadensis**	BH, TN	MCD	Omnivorous	Rheophilic	Periodic	Psammophilic
Deccan White Carp *Cirrhinus fulungee*	ML	MCD	Omnivorous	Rheophilic	Periodic	Lithophilic
Cirrhinus sp. 1	TN	MCD	Omnivorous	Rheophilic	Periodic	Lithophilic
Silver Hatchet Chela *Chela cachius*	ML	MCD	Omnivorous	Rheophilic	Periodic	Phytolithophilic
Malabar Danio *Devario malabaricus*	BH, TN, ML, MH	MCD	Heterotrophic	Rheophilic	Opportunistic	Phytolithophilic
Arulius Barb *Dawkinsia arulius**	BH, TN	MCD	Omnivorous	Rheophilic	Intermediate	Phytophilic
Blackspot Barb *Dawkinsia filamentosa**	MH	MCD	Omnivorous	Rheophilic	Intermediate	Phytophilic
Tunga Garra *Garra bicornuta**	BH, TN, ML, MH	BD	Phytophagous	Rheophilic	Opportunistic	Lithopelagophilic
Mullya Garra *Garra mullya*	BH, TN, ML, MH	BD	Phytophagous	Rheophilic	Opportunistic	Lithopelagophilic
Niligiri Garra *Garra stenorhynchus*	BH, ML, MH	BD	Phytophagous	Rheophilic	Opportunistic	Lithopelagophilic
Curmuca Barb *Hypselobarbus curmuca**	BH, TN, ML	BD	Omnivorous	Rheophilic	Periodic	Phytophilic
Krishna Carp *H. dobsoni**	TN, ML	BD	Phytophagous	Rheophilic	Periodic	Lithophilic
Nilgiri Barb *H. dubius**	ML	BD	Omnivorous	Rheophilic	Periodic	Lithophilic
Jerdon's Carp *H. jerdoni**	BH, TN	MCD	Phytophagous	Rheophilic	Periodic	Lithophilic

TABLE 1. Continued.

		Basis of guild definition				
Order, family, and species	Subbasin(s)	Water column position	Feeding preferences	Flow response	Life history cues	Reproductive strategy
Red Canarese Barb *H. thomassi**	BH, TN	MCD	Phytophagous	Rheophilic	Periodic	Lithophilic
Fringed-lipped Peninsula Carp *Labeo fimbriatus*	ML	BD	Phytophagous	Limnophilic	Periodic	Lithophilic
Bombay Labeo *Labeo porcellus**	ML	BD	Phytophagous	Limnophilic	Periodic	Lithophilic
Labeo sp. 1	TN	BD	Phytophagous	Limnophilic	Periodic	Lithophilic
Cosuatis Barb *Oreichthys cosuatis*	ML	MCD	Heterotrophic	Rheophilic	Periodic	Phytophilic
Nash's Barb *Osteochilichthys nashii**	BH, TN, ML	MCD	Omnivorous	Rheophilic	Periodic	Lithophilic
Pethia sp. nov.*	ML	MCD	Heterotrophic	Rheophilic	Intermediate	Phytophilic
Narayan Barb *Pethia setnai**	TN, ML, MH	MCD	Heterotrophic	Rheophilic	Intermediate	Phytophilic
*Pethia striata**	TN	BD	Phytophagous	Rheophilic	Periodic	Phytophilic
Ticto Barb *Pethia ticto*	TN, ML	MCD	Omnivorous	Eurytopic	Periodic	Phytophilic
Scarlet-banded Barb *Puntius amphibius*	ML, MH	MCD	Heterotrophic	Rheophilic	Intermediate	Phytophilic
Chola Barb *Puntius chola*	ML	MCD	Omnivorous	Rheophilic	Intermediate	Phytophilic
Long-snouted Barb *Puntius dorsalis*	ML	MCD	Phytophagous	Rheophilic	Intermediate	Phytophilic
Indian Maharaja Barb *Puntius sahyadriensis**	BH, TN, ML	MCD	Omnivorous	Rheophilic	Intermediate	Phytophilic
Pool Barb *Puntius sophore*	ML	MCD	Heterotrophic	Eurytopic	Periodic	Phytophilic
Slender Rasbora *Rasbora daniconius*	BH, TN, ML, MH	MCD	Heterotrophic	Eurytopic	Opportunistic	Phytophilic
*Rasbora labiosa**	ML, MH	MCD	Omnivorous	Eurytopic	Opportunistic	Phytophilic
Vatani Rohtee *Rohtee ogilbii**	TN	MCD	Phytophagous	Rheophilic	Periodic	Phytophilic
Large Razorbelly Minnow *Salmostoma bacaila*	ML, MH	SD	Omnivorous	Limnophilic	Periodic	Phytophilic

TABLE 1. Continued.

Order, family, and species	Subbasin(s)	Basis of guild definition				
		Water column position	Feeding preferences	Flow response	Life history cues	Reproductive strategy
Boopis Razorbelly Minnow *Salmostoma boopis*	BH, TN, ML, MH	SD	Heterotrophic	Limnophilic	Periodic	Phytophilic
Novacula Razorbelly Minnow *Salmostoma novacula**	ML	SD	Heterotrophic	Limnophilic	Periodic	Phytophilic
Nukta *Schismatorhynchus nukta*	ML	BD	Phytophagous	Rheophilic	Periodic	Lithophilic
Olive Barb *Systomus sarana*	ML	MCD	Phytophagous	Limnophilic	Intermediate	Phytophilic
Systomus subnasutus	ML	MCD	Phytophagous	Limnophilic	Intermediate	Phytophilic
Deccan Mahseer *Tor khudree**	BH, TN, ML, MH	MCD	Omnivorous	Rheophilic	Periodic	Lithophilic
Mastacembeliformes						
Mastacembelidae						
Zig-zag Eel *Mastacembelus armatus*	BH, TN	BD	Heterotrophic	Rheophilic	Equilibrium	Phytophilic
Osteoglossiformes						
Notopteridae						
Bronze Featherback *Notopterus notopterus*	TN	BD	Omnivorous	Rheophilic	Intermediate	Lithophilic
Perciformes						
Ambassidae						
Indian Glassy Fish *Parambassis ranga*	TN, ML	MCD	Heterotrophic	Eurytopic	Intermediate	Phytophilic
Western Ghat Glassy Perchlet *Parambassis thomassi**	TN	MCD	Heterotrophic	Eurytopic	Intermediate	Phytophilic
Elongate Glass-perchlet *Chanda nama*	TN	MCD	Heterotrophic	Eurytopic	Intermediate	Pelagophilic
Channidae						
Dwarf Snakehead *Channa gachua*	ML	BD	Heterotrophic	Eurytopic	Equilibrium	Pelagophilic
Malabar Snakehead *Channa diplogramma**	ML	BD	Heterotrophic	Eurytopic	Equilibrium	Pelagophilic
Spotted Snakehead *Channa punctata*	ML	BD	Heterotrophic	Eurytopic	Equilibrium	Pelagophilic
Striped Snakehead *Channa striata*	BH, TN, ML, MH	BD	Heterotrophic	Eurytopic	Equilibrium	Pelagophilic

TABLE 1. Continued.

Order, family, and species	Subbasin(s)	Basis of guild definition				
		Water column position	Feeding preferences	Flow response	Life history cues	Reproductive strategy
Cichlidae						
Green Chromide *Etroplus suratensis*	ML	BD	Omnivorous	Eurytopic	Equilibrium	Lithophilic
Gobiidae						
Tank Goby *Glossogobius giuris giuris*	ML	BD	Heterotrophic	Eurytopic	Opportunistic	Lithophilic
Sisoridae						
Lonah Catfish *Glyptothorax lonah*	TN	BD	Heterotrophic	Rheophilic	Periodic	Lithophilic
Glyptothorax sp. 1	BH	BD	Heterotrophic	Rheophilic	Periodic	Lithophilic
Glyptothorax sp. 2	ML	BD	Heterotrophic	Rheophilic	Periodic	Lithophilic
Siluriformes						
Bagridae						
Sharavati Batasio *Batasio sharavatiensis**	BH, TN	BD	Heterotrophic	Eurytopic	Periodic	Phytophilic
Day's Mystus *Mystus bleekeri*	ML	BD	Heterotrophic	Eurytopic	Equilibrium	Phytophilic
Gnagetic Mystus *Mystus cavasius*	ML	BD	Heterotrophic	Rheophilic	Periodic	Phytophilic
Long Whiskers Catfish *Mystus gulio*	TN, ML	BD	Heterotrophic	Rheophilic	Periodic	Phytophilic
Keletius Mystus *Mystus keletius*	ML	BD	Heterotrophic	Rheophilic	Periodic	Phytophilic
Clariidae						
Valenciennes Clariid *Clarias dussumieri*	ML	BD	Omnivorous	Eurytopic	Opportunistic	Phytophilic
Siluridae						
Butter Catfish *Ompok bimaculatus*	ML	BD	Heterotrophic	Eurytopic	Periodic	Polyphilic
Goan Catfish *Ompok malabaricus**	TN	BD	Heterotrophic	Eurytopic	Periodic	Polyphilic
Ailiidae						
Goongwaree Vacha *Eutropiichthys goongwaree*	ML	BD	Heterotrophic	Rheophilic	Periodic	Phytophilic

the metaMDS and envfit routines of the "vegan" package in R version 3.2.1 (R Development Core Team 2015).

Effects of environmental variables on guild-wise fish species richness.— To test our hypothesis on the effects of flow regulation and anthropogenic disturbance (including water extraction) on environmental variables, we checked for statistically significant differences between values of environmental and water chemistry variables across (1) RSBs and NRSBs and (2) across river segments with and without local water withdrawals and pollution (presence of vehicle oil, agricultural runoff sources, and town sewage outlets) in each of the subbasins. In terms of basin-level hydrological regulation due to barriers, the Malaprabha River subbasin (744 km^2) had 10 barriers and the Mhadei River subbasin (426 km^2) had 1 barrier (the inter-basin link described earlier). Local water withdrawals and pollution were also higher in RSBs but were not absent from the NRSBs. Local threats mainly included dewatering for agricultural purposes to meet the domestic water demands of townships. In some places, fish harvesting by destructive fishing methods was observed.

Principal components analysis (PCA) was used to decompose multiple correlated environmental variables measured in the study to a set of orthogonal and uncorrelated axes referred to as principal components (PCs). The PCA helped in identifying correlated variables and in selecting variables for further regression analyses. Log-linear regression models were used to explore the influences of normalized environmental and water chemistry variables on the log-transformed values of guild-wise fish species richness separately for each subbasin. Data were analyzed independently for each subbasin to account for potential variation in fish species detectability (which could not be estimated in this study) and any other sampling effects. We tested the effects of local water removals and the presence of local pollution sources on segment-wise fish guild richness in each subbasin. We also used mixed-effects regression models with "subbasins" as random effect variables; however, we found that those models provided estimates with inconsequential random effects and hence they were not used. Variables with similar positive or negative effects on fish guild richness across subbasins were later identified from model summaries. The model equation used was

$$Y = AX + C + \varepsilon,$$

where Y is guild type; A is the slope for covariates X, which are environmental or water chemistry variables; C is the model intercept; and ε is the normal error term.

Measures of model fit (multiple R^2 and adjusted R^2) and Akaike's information criterion (AIC) were used to evaluate and compare between log-linear models. This was done for two reasons. First, the actual fit of the model was important for understanding the model's ability to explain the variation in the response (guild richness). Second, AIC uses the model likelihood for calculating fit but provides only a relative measure of fit—that is, with respect to the other models' fit and complexity. Thus, AIC could risk selection of a "best model" with respect to other poorly fitting or limited candidate models for a particular data set. Models with the highest fit and lowest AIC scores were chosen as the best models. All analyses were performed in R (R Development Core Team 2015).

RESULTS

Fish Species Richness in Different Guilds

In total, 12,840 individuals comprising 79 fish species belonging to 7 orders and 17 families were sampled in the four subbasins across the wet season (June 2011; June 2012; June, November, and December 2013; and January 2014) and dry season (April 2011, March 2012, May 2013, and May 2014). Cypriniformes was the most dominant order, with 54 species (28 species of these were endemic to the WG region) and 94.3% of the collected individuals. The most consistent and representative guild classification among the different classifications was the one based on fish position in the water column (Figure 2). Bottom-dwelling fishes consisted of 5 orders, 14 families, and 42 species; MCD fishes belonged to 2 orders, 2 families, and 26 species; and SD fishes comprised 3 orders, 3 families, and 11 species (Table 1 contains details of traits associated with BD, MCD, and SD fishes).

Fish Species Composition across Regulated and Nonregulated Subbasins

Fish species composition clearly differed across RSBs and NRSBs (Figure 3). The RSBs (Malaprabha and Mhadei rivers) also differed from each other in species composition. Exploratory analyses indicated that 39.2% (31 of 79 species) were WG endemic species. About 48.4% (15 of 31) of the WG endemic species were restricted to the NRSBs (Tunga and Bhadra rivers), while 25.8% (8 of 31) were found only in the RSBs, and 22.6% (7 of 31) were common to both RSBs and NRSBs. Nonregulated basins (Tunga and Bhadra rivers) and regulated basins (Malaprabha and Mhadei rivers) differed in species composition (ANOSIM: $R = 39.83$, $P = 0.001$). The two RSBs also clearly differed from each other. We observed that TA, calcium hardness, EC, free CO_2, and inorganic nitrates were correlated with dissimilarities in fish species composition, whereas water temperature (WT) and pH were not significantly correlated with dissimilarities in community composition. This indicated that differences in water chemistry would best explain differences in fish species composition between RSBs and NRSBs. The SD guild species richness was found to be higher in NRSBs than in RSBs, whereas MCD species richness and BD species richness were higher in RSBs than in NRSBs (Table 2).

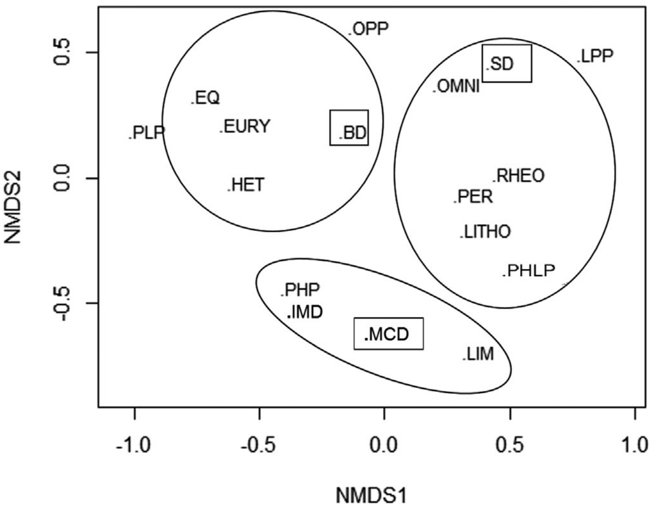

FIGURE 2. Trait-by-species nonmetric multidimensional scaling (NMDS) ordination axes and plot, with three clusters showing correlated guild classifications for fish species across the four subbasins. We chose three guilds based on the position of fishes in water column as the most stable and representative classification (water column position: SD = surface dwelling, MCD = mid-column dwelling, BD = bottom dwelling; life history: EQ = equilibrium, OPP = opportunistic, PER = periodic, IMD = intermediate; flow response: EURY = eurytopic, LIM = limnophilic, RHEO = rheophilic; reproductive strategy: PLP = polyphilic, LITHO = lithophilic, PHP = phytophilic, PHLP = phytolithophils, LPP = lithopelagophilic).

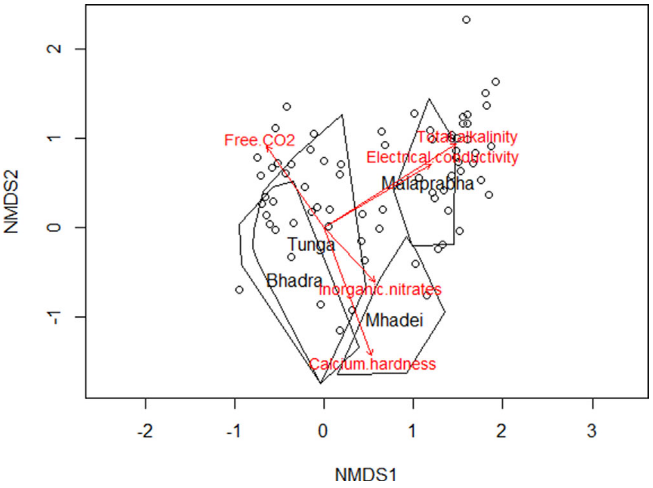

FIGURE 3. Nonmetric multidimensional scaling (NMDS) ordination plot, showing dissimilarity in fish species composition across the four subbasins (open circles indicate species). Nonregulated subbasins (Bhadra and Tunga rivers) and regulated subbasins (Malaprabha and Mhadei rivers) differed distinctly in species composition. The two regulated subbasins also clearly differed from each other. Water chemistry variables fitted to the NMDS axes are also shown in the ordination space.

TABLE 2. Differences in guild-wise fish species richness (mean, with range in parentheses) across two regulated river subbasins (RSBs) and two nonregulated river subbasins (NRSBs) in the Western Ghats region (SD = surface-dwelling; MCD = mid-column-dwelling; BD = bottom-dwelling). Statistical significance of differences was assessed with a Welch *t*-test (with unequal variance for groups; $\alpha = 0.05$; $^{***}P \leq 0.001$).

	Fish species richness			Welch *t*-test	
Guild	NRSBs	RSBs	df	*t*	*P*
SD fishes	3.00 (0–7)	2.19 (0–4)	52.41	3.43	0.001***
MCD fishes	2.79 (0–6)	5.38 (0–11)	27.38	−3.39	0.001***
BD fishes	2.42 (0–8)	6.00 (0–16)	27.00	−3.98	0.0004***

Ecological Variable Selection for Further Modeling

The PCA results showed that the first three PCs accounted for 83.0% of the total variation in environmental covariates. Canopy cover was correlated with PC1, and water chemistry variables were correlated with PC2. Canopy cover was correlated with WT, so we used WT for our regression analyses. We also specifically tested for the effects of TA, TDS, DO, EC, and pH on guild-wise fish species richness. Substrate characteristics and free CO_2 were correlated with PC3 based on the loadings on PC axes. We also analyzed the effects of substrate composition on fish species richness (Figure S.3).

Differences in Environmental Variables in Relation to River Regulation and Disturbance

Water temperature was significantly higher in the RSBs than in the NRSBs (Tables 3 and S.4; Figure 4). Calcium hardness and inorganic nitrates were higher in RSBs, indicating poorer water quality. Total dissolved solids also showed a similar pattern, but DO did not differ significantly between the RSBs and NRSBs (Table 3; Figure 4). However, we did not detect significant differences in water chemistry variables in river segments with and without local water withdrawals when compared within RSBs and within NRSBs (Table 4). Within NRSBs, DO was lower in segments with the presence of local pollution sources than in segments without (Table 5). Within RSBs, water chemistry did not differ between segments with and without local pollution sources (Table 5); the exception was the concentration of inorganic nitrates, which was higher in segments with local pollution than in those without (Tables 5 and 6).

Effects of Water Chemistry and Other Variables on Guild-wise Fish Species Richness

Overall, WT, TDS, and TA emerged as the most consistent predictors affecting fish species richness of all guilds. The effect of WT on species richness of the guilds in all basins was positive except in the west-flowing and regulated Mhadei River (where WT had a negative effect on SD fishes). The SD and MCD species richness in both

TABLE 3. Differences in water chemistry variables (mean, with range in parentheses) between regulated river subbasins (RSBs) and nonregulated river subbasins (NRSBs) in the Western Ghats region. Temperature was higher and water quality was generally poorer (as seen in higher levels of total dissolved solids [TDS], calcium hardness, inorganic nitrates, and total alkalinity) in RSBs as compared to NRSBs (DO = dissolved oxygen concentration). Statistical significance of differences was assessed with a Welch *t*-test (with unequal variance for groups; $\alpha = 0.05$; $^{**}P \leq 0.01$, $^{***}P \leq 0.001$).

			Welch *t*-test		
Variable	NRSBs	RSBs	df	*t*	*P*
Water temperature (°C)	20.86 (16–27)	24.76 (20.00–29.88)	45.2	−8.25	<0.001***
TDS (mg/L)	0.011 (0.00–0.035)	0.052 (0.01–0.12)	25.27	−6.15	<0.001***
Calcium hardness (mg/L)	7.93 (3.69–56.11)	110.69 (11.22–347.89)	21.16	−4.41	0.0002***
DO (mg/L)	7.80 (6.17–9.14)	8.35 (4.50–11.13)	27.77	−1.28	0.21
Inorganic nitrates (mg/L)	0.17 (0.01–0.43)	0.38 (0.075–1.450)	23.09	−3.13	0.0046**
Total alkalinity (mg/L)	24.42 (11–44)	58.45 (30.00–98.50)	23.43	−8.62	0.000***

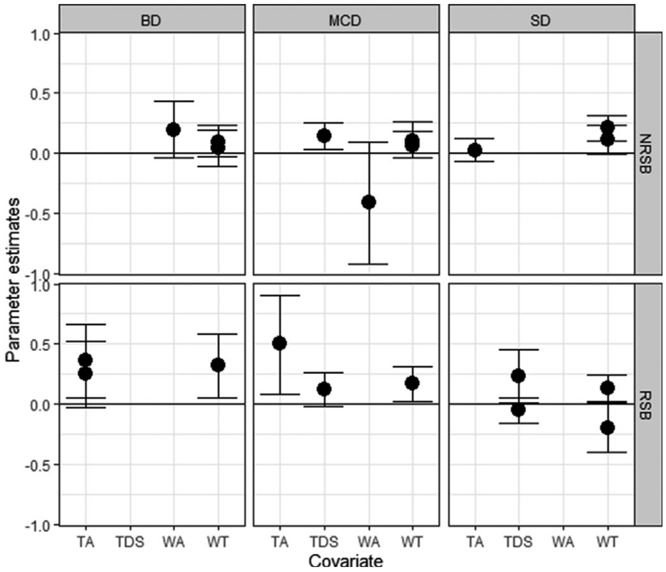

FIGURE 4. Parameter estimates for species richness of fish guilds (BD = bottom dwelling; MCD = mid-column dwelling; SD = surface dwelling) in regulated subbasins (RSB) and nonregulated subbasins (NRSB) in the central Western Ghats region. Effect sizes are shown for total alkalinity (TA), total dissolved solids (TDS), water abstraction/removal (WA), and water temperature (WT). Species richness of SD fish was negatively affected by WT only in the Mhadei River subbasin (RSB) and by TA in the Tunga River subbasin (NRSB). Mid-column-dwelling fishes were less diverse in segments with WA in the Tunga River subbasin. Effects of TDS and WT were otherwise generally positive for all guilds. In RSBs, MCD and BD fish species richness was higher when TA was higher.

RSBs and NRSBs was positively related to TDS (Tables 6 and S.4). Additionally, SD species richness was negatively correlated with TDS in the Malaprabha River subbasin and positively correlated with TA in the nonregulated Tunga River subbasin. The MCD and BD guild richness had a positive correlation with TA in the RSBs (Figure 4). The MCD species richness was negatively correlated with effects of local water withdrawals in the Bhadra River subbasin (Table 6). Among RSBs, the effects of TDS were stronger and positive for the SD guild in both subbasins, but negative in the Malaprabha River subbasin. Similarly, the effects of TA were stronger and positive for MCD and BD guilds in RSBs. The effects of WT on fish guild richness were strongest in the Malaprabha River basin (Tables 6 and S.4). This was perhaps attributable to the Malaprabha River having a greater density of impoundments and local disturbances than the Mhadei River.

DISCUSSION

Our major finding was that fish responses to river flow regulation were related to water temperature and altered water chemistry (especially TDS and alkalinity) between RSBs and NRSBs. Fish responses to water chemistry are complex and driven by multiscale processes, including direct local disturbances and the indirect effects of regulation. We discuss the relevance of our findings for river flow management and fish conservation in human-modified tropical catchments of the WG, which are undergoing rapid land cover changes, water infrastructure development, and further flow regulation.

Differences in Fish Community Composition across Subbasins

Despite interbasin differences in catchment characteristics (basin area, flow regime, and disturbances), we found distinct differences in fish guild richness, species composition, and endemic species richness across regulated and nonregulated subbasins in the WG of India. Water chemistry differences between RSBs and NRSBs were significantly greater than those within individual subbasins, which had river segments with and without local water removals and pollution. The RSBs had higher concentrations of inorganic nitrates and calcium hardness than the NRSBs. Fish community composition also differed between the two regulated subbasins, the Malaprabha and Mhadei rivers. The effects of WT, alkalinity, and TDS on

TABLE 4. Differences in water chemistry (mean, with range in parentheses) of river segments with (present) and without (absent) local water removal within regulated river subbasins (RSBs) and nonregulated river subbasins (NRSBs) in the Western Ghats region (TDS = total dissolved solids; DO = dissolved oxygen concentration). No significant differences were found within both RSBs and NRSBs. Statistical significance of differences was assessed with a Welch *t*-test (with unequal variance for groups; α = 0.05).

	NRSBs					RSBs				
			Welch *t*-test					Welch *t*-test		
Variable	Removal absent	Removal present	df	*t*	*P*	Removal absent	Removal present	df	*t*	*P*
Water temperature (°C)	21.04 (16–27)	20.55 (17.0–23.5)	84.60	1.08	0.28	25.00 (21.5–26.7)	24.48 (20.00–29.88)	18.13	0.63	0.53
TDS (mg/L)	0.01 (0.00–0.03)	0.01 (0.01–0.02)	79.50	1.67	0.09	0.05 (0.01–0.12)	0.05 (0.01–0.12)	23.97	0.06	0.94
Calcium hardness (mg/L)	8.90 (3.69–56.11)	6.28 (5.29–8.66)	21.58	1.11	0.27	137.73 (11.22–347.89)	78.23 (11.7–291.78)	19.34	1.34	0.19
DO (mg/L)	7.86 (6.17–9.14)	7.60 (6.90–8.94)	7.95	0.61	0.55	8.29 (4.55–11.13)	8.42 (6.01–10.16)	16.60	−1.75	0.86
Inorganic nitrates (mg/L)	0.15 (0.01–0.26)	0.21 (0.12–0.43)	12.13	−1.61	0.13	0.36 (0.07–0.74)	0.40 (0.07–1.45)	13.07	−0.23	0.81
Total alkalinity (mg/L)	23.59 (11–44)	25.84 (18–32)	33	−1.36	0.18	58.87 (30.00–98.50)	57.95 (40–90)	19.80	0.12	0.90

TABLE 5. Differences in water chemistry (mean, with range in parentheses) of river segments with (present) and without (absent) local pollution within regulated river subbasins (RSBs) and nonregulated river subbasins (NRSBs) in the Western Ghats region (TDS = total dissolved solids; DO = dissolved oxygen concentration). Apart from differences in DO (mg/L) in NRSBs, no significant differences were found between the regulated and nonregulated basins. Statistical significance of differences was assessed with a Welch *t*-test (with unequal variance for groups; α = 0.05; $^{**}P \leq 0.01$).

	NRSBs					RSBs				
			Welch *t*-test					Welch *t*-test		
Variable	Pollution absent	Pollution present	df	*t*	*P*	Pollution absent	Pollution present	df	*t*	*P*
Water temperature (°C)	20.83 (16–27)	21.12 (16.0–23.5)	9.82	−0.35	0.72	24.51 (20.00–26.70)	25.10 (22.00–29.88)	20.86	−0.72	0.47
TDS (mg/L)	0.01 (0.00–0.03)	0.01 (0.01–0.02)	12.03	0.33	0.74	0.05 (0.02–0.12)	0.04 (0.01–0.10)	21.40	0.52	0.60
Calcium hardness (mg/L)	6.51 (3.69–17.50)	14.80 (4.81–56.11)	5.03	−1.00	0.36	109.60 (11.22–347.89)	112.26 (13.47–338.28)	16.91	−0.05	0.95
DO (mg/L)	8.03 (6.26–9.14)	6.77 (6.17–7.31)	8.33	4.02	0.003**	8.34 (4.55–11.13)	8.38 (6.21–9.18)	16.84	−0.06	0.95
Inorganic nitrates (mg/L)	0.18 (0.01–0.43)	0.15 (0.14–0.18)	23.70	1.37	0.18	0.27 (0.07–0.68)	0.53 (0.24–1.45)	10.62	−1.90	0.08
Total alkalinity (mg/L)	24.20 (11–32)	25.50 (19–44)	5.46	−0.32	0.75	59.30 (30.00–98.50)	57.22 (40–87)	19.94	0.27	0.78

TABLE 6. Selected best linear regression models, showing effect sizes of environmental variables on guild-wise (SD = surface dwelling; MCD = mid-column dwelling; BD = bottom dwelling) fish species richness for regulated river subbasins (RSBs) and nonregulated river subbasins (NRSBs) in the Western Ghats region (LCL = lower 95% confidence limit; UCL = upper 95% confidence limit; AIC = Akaike's information criterion; TDS = total dissolved solids; CH = calcium hardness; WT = water temperature; WA = water abstraction/removal; TA = total alkalinity). In the case of MCD species richness in NRSBs, no model was found to improve the fit over that of the null model. Statistical significance for parameter estimates is indicated ($\alpha = 0.10$ [90% CI]; *$P \le 0.10$, **$P \le 0.05$, ***$P \le 0.01$, ****$P \le 0.001$).

Subbasin	Guild	Parameter estimate	Slope (SE)	LCL	UCL	P	Multiple R^2	Adjusted R^2	Residual SE	AIC
Mhadei River (RSB)	SD	Intercept	1.06 (0.09)	0.85	1.28	<0.001****	0.79	0.71	0.24	5.12
		TDS	0.23 (0.09)	0.01	0.45	0.04**				
		WT	−0.20 (0.09)	−0.40	0.01	0.066*				
		TDS × WT	0.34 (0.16)	−0.04	0.72	0.076*				
	MCD	Intercept	0.84 (0.18)	0.40	1.26	<0.001****	0.38	0.22	0.62	25.24
		TDS	0.22 (0.21)	−0.26	0.71	0.31				
		WT	−0.30 (0.21)	−0.78	0.18	0.19				
	BD	Intercept	1.18 (0.12)	0.89	1.46	<0.001****	0.52	0.45	0.36	11.07
		TA	0.36 (0.13)	0.05	0.66	0.03**				
Malaprabha River (RSB)	SD	Intercept	1.22 (0.04)	1.11	1.32	<0.001****	0.40	0.30	0.18	−3.21
		WT	0.13 (0.05)	0.02	0.24	0.01***				
		TDS	−0.05 (0.05)	−0.16	0.05	0.27				
	MCD	Intercept	2.15 (0.06)	2.01	2.28	<0.001****	0.50	0.42	0.23	4.31
		WT	0.17 (0.07)	0.02	0.31	0.02**				
		TDS	0.12 (0.06)	−0.02	0.26	0.08*				
	BD	Intercept	2.14 (0.12)	1.88	2.41	<0.001****	0.51	0.41	0.43	19.93
		WT	0.32 (0.12)	0.05	0.58	0.02**				
		TA	0.25 (0.13)	−0.03	0.52	0.08*				
Bhadra River (NRSB)	SD	Intercept	1.26 (0.05)	1.14	1.38	<0.001****	0.08	0.06	0.37	38.11
		WT	0.11 (0.06)	−0.007	0.23	0.07*				
	MCD	Intercept	1.05 (0.07)	0.87	1.17	<0.001****	0.11	0.07	0.48	59.22
		WT	0.10 (0.07)	−0.04	0.26	0.16				
		WA	−0.41 (0.25)	−0.92	0.09	0.10*				
	BD	Intercept	1.04 (0.07)	0.91	1.18	<0.001****	0.05	0.02	0.41	47.98
		WT	0.09 (0.06)	−0.03	0.23	0.15				
Tunga River (NRSB)	SD	Intercept	1.37 (0.04)	1.28	1.47	<0.001****	0.28	0.25	0.34	40.31
		WT	0.21 (0.06)	0.10	0.31	0.001****				
		TA	0.02 (0.04)	−0.07	0.12	0.65				
	MCD	Intercept	1.44 (0.05)	1.33	1.56	0.01***	0.22	0.17	0.38	53.07
		WT	0.06 (0.05)	−0.04	0.18	0.24				
		TDS	0.14 (0.05)	0.03	0.25	0.01***				
		WT × TDS	−0.16 (0.08)	−0.32	−0.004	0.04**				
	BD	Intercept	1.04 (0.08)	0.86	1.22	<0.001****	0.23	0.18	0.42	65.35
		WT	0.04 (0.06)	−0.11	0.19	0.59				
		WA	0.19 (0.11)	−0.04	0.43	0.10*				
		WT × WA	0.27 (0.12)	0.02	0.52	0.03**				

fish guild richness differed between the two regulated rivers, potentially in relation to their different levels of regulation. Streambank erosion, agricultural runoff, sewage, and town pollution were higher in the Malaprabha River subbasin than in the Mhadei River subbasin. Differences in topography, rainfall–runoff relationships, and flow direction (e.g., westward flowing versus eastward flowing) could also explain some effects of environmental variables. Water temperature emerged as the most consistent predictor of species richness across SD, MCD, and BD fish guilds. In the regulated Mhadei River (the only westward-flowing river in our study), WTs were the highest and had a negative effect on the species richness of the SD guild. This was probably due to limited riparian cover (attributable to deforestation) and the shallower nature of streams in the Mhadei River basin headwaters.

Potential Drivers of Differential Responses of Fish Guilds

Surface-dwelling fishes are known to be sensitive to river regulation, as they depend on run–riffle habitats with high DO, a common feature of nonregulated, high-gradient streams (Johnson and Arunachalam 2010; Costa et al. 2013; Lujan and Conway 2015), such as the ones we sampled. Responses of SD fishes were different from those of MCD and BD fishes, which appeared more tolerant to the WT perturbations in RSBs. In fact, higher WTs in regulated rivers were perhaps more suitable for the BD and MCD guilds due to these fishes' preference for deep pools, which were abundant in regulated rivers. Subbasin-level differences in community composition can be explained mainly by the loss or replacement of SD species in regulated rivers relative to nonregulated rivers and the corresponding higher richness of MCD or BD species in regulated rivers.

Impacts of Altered Water Chemistry on Fish Guild Richness

Species richness of all fish guilds showed a positive correlation with the concentration of TDS in all subbasins. Mineral springs, wet and dry deposition of mineral salts (e.g., calcium, sodium, and sulfates), agricultural runoff, and point source/non-point-source wastewater discharges could be the potential sources of dissolved solids (Chapman 1996). This could be linked to higher inorganic productivity (for which TDS is considered a proxy) that might have supported a greater diversity of species. Other than WT and TDS, TA also had differing effects on the three fish guilds. Surface-dwelling fishes were negatively affected by TA, but the other two guilds seemed to tolerate higher levels of TA. Differences in alkalinity (or calcium hardness, as observed) were not only due to flow reduction after regulation. Local human disturbances, land use changes, and intensification of cropping, among other factors, also contributed, but their effects were weaker (Heller et al. 2012). Downstream of barriers, greater base flow contribution from groundwater sources to total streamflow could increase calcium hardness and lower the WT (Wurts and Robert 1992; Malkhede 2003; Central Ground Water Board 2007). Differences in water chemistry in segments with and without local withdrawals for irrigation were not significant within RSBs or within NRSBs. A limitation of our study was that we could not directly quantify the volume of local water removals, as these occur during the availability of power supply. In future studies, local water withdrawal rates should be estimated to assess their impacts on fish assemblages (Kanno and Vokoun 2010).

Using Position-Based Guilds to Represent Fish Tolerance of River Regulation

A small but significant methodological contribution of our study was in our choice of position-based fish guilds for analyses. This choice helped us to overcome redundancies across multiple guild classifications but also retained correlations of position in the water column with other life history strategies (e.g., reproductive guilds). This classification could be used for qualitative assessments in future studies on river fishes. The use of discrete fish guilds did not allow us to interpret clear continua in life history strategies of fishes as have been shown in American rivers (Winemiller 1989; Winemiller and Rose 1992), yet our approach helped to detect broad differences. In RSBs, fishes with a periodic life history strategy (e.g., *Barilius*, *Cirrhinus*, *Hypselobarbus*, and *Mystus* spp.) were more common than species with an opportunistic strategy (e.g., *Aplocheilus*, *Garra*, and *Rasbora* spp.) or an equilibrium strategy (e.g., *Channa* and *Etroplus* spp.). Insectivorous fish species (*Aplocheilus* and *Devario* spp.) were more abundant in NRSBs, but omnivorous (*Barilius* spp.) and phytophagous (*Hypselobarbus* and *Cirrhinus* spp.) species dominated the community composition in RSBs. This might be due to reduced flow causing greater submerged macrophyte biomass. Future studies could explore whether this might lead to greater bottom-up controls and trophic simplification of regulated rivers.

Species richness of WG endemic fishes was higher in nonregulated rivers than in regulated rivers. Consistently poorer water quality in regulated rivers could explain why many sensitive endemic species (e.g., *Neolissochilus*, *Rohtee*, *Barilius*, and *Tor* spp.; cascade specialists: e.g., *Balitora* and *Bhavania* spp.; and some rare substrate-dwelling fishes: e.g., *Batasio* spp.) were not detected in RSBs. Other disturbances and increases in turbidity/siltation (e.g., road networks and canal construction) within RSB headwaters might have also negatively affected torrent fishes, such as *Bhavania* (Ganasan and Hughes 1998; Das and Samanta 2006), which were likely absent in the upper reaches of the Malaprabha River basin. Generalist MCD species, such as Slender Rasbora *Rasbora daniconius*, Deccan White Carp *Cirrhinus fulungee*, and Scarlet-banded Barb *Puntius amphibius*, were dominant in regulated rivers, and these taxa could also be considered as indicators of poor water quality. Additionally, fish with physical deformities (~50 individuals of *Systomus*, *Puntius*, and *Cirrhinus* spp.) were recorded only from RSBs (our field observations). Deformities in fish can occur from exposure to chemical pollutants or direct physical damage (e.g., due to entrainment in and injury during dam water releases; Chapman 1996; Daniels 2002; Cunningham et al. 2005; Sun et al. 2009), so this observation is of great significance.

Overall, our results followed previously reported impacts of flow regulation on fish species. From a conservation standpoint, our results suggest that maintenance of ecological flow regimes suited for endemic fish species and their habitats should be a higher priority for fish conservation in the WG than managing local disturbances. Recently, Grubh and Winemiller (2018) reasoned that the spatial variation in local fish assemblages within few wetlands in the southern WG was due to species-specific habitat selection; however, they found that hydrologic regulation greatly reduced the seasonal fish assemblages in the wetland complex of the southern WG. Abraham and Kelkar (2012) showed that endemic species received coverage within the protected area network in Kerala's WG as an indirect outcome of mid-elevation siting of protected areas upstream of dam–reservoir catchments. In comparison with their study, our study area had a greater coverage of protected areas (elevation > 500 m ASL). Nevertheless, the impacts of flow regulation and local disturbance could have strongly affected endemic fish species despite existing protection in RSBs.

In the WG, differences in fish community composition between nonregulated and regulated rivers have been documented earlier (Bhat 2002). Studies from different parts of the world have generally found that SD rheophilic fishes are less abundant in regulated rivers, whereas eurytopic fishes belonging to MCD and BD guilds might benefit from flow regulation (David 1956; Aarts and Nienhuis 2003; Das and Samanta 2006; De Leeuw et al. 2007; Chakrabarty and Homechaudhuri 2013; Macnaughton et al. 2016). Worldwide, multiple studies assessing the impacts of dams on riverine fish communities have shown that dams strongly affect native species by physically obstructing their seasonal spawning migrations (Jackson and Marmulla 2001; Larinier 2001; Hoeinghaus et al. 2009; Gopal 2013). Dewatering downstream of a small dam in Costa Rica affected the life history strategies of fishes, such as cichlids, with similarly complex reproductive requirements (Anderson et al. 2006). A study of the Colorado River found that regions with high densities of dams benefited invasive and exotic species with equilibrium life history strategies over native fish species with opportunistic/periodic breeding and growth patterns (Pool et al. 2010). Similarly, hydropeaking operations downstream of the Itutinga Dam led to the disappearance of insectivorous fish communities in the Grande River basin, Brazil (Gandini et al. 2014). In our study area, upstream migration of SD and MCD fishes, such as Deccan Mahseer *Tor khudree*, Jerdon's Carp *Hypselobarbus jerdoni*, and Deccan White Carp, and MCD to BD fishes, such as *Pethia striata*, Tunga Garra *Garra bicornuta*, and Slender Stone Loach *Balitora mysorensis*, is affected by existing river barriers, thereby hindering the completion of their reproductive cycle, and such effects need to be studied in detail.

Implications for River Restoration and Conservation

Our results emphasize that the monitoring of water chemistry in RSBs is an integral part of ecological flow regime management. Specifically, we show that river flow regulation might strongly affect water quality at the landscape scale (basin scale). In such cases, local impacts of degraded water quality or water withdrawals appear to be less significant than the effects of barrages, but this needs extended investigation from multiple subbasins. Our main finding has significant implications for the recovery of fish assemblages downstream of river barriers. Our earlier study in the Malaprabha River basin (Atkore et al. 2017) showed that fish species recovered as a function of distance from upstream hydrological barriers largely due to the contribution of undammed tributaries below the dam. Recovery should be monitored specifically for endemic fishes and sensitive SD fish species. Importantly, the study identified that RSBs exhibited altered thermal regimes and degraded water quality (e.g., higher calcium hardness, inorganic nitrates, etc.), which influenced fish composition. Therefore, if basin-scale flow management is planned, tracking the exact mechanisms by which flow reduction could influence water chemistry must be accomplished with hydrological and laboratory instrumentation. Our exploratory study might be useful to policymakers and conservationists who are interested in prioritizing the scale of interventions for river restoration and fish conservation efforts. Water chemistry criteria could also be linked to estimation of flow release thresholds from barrages (Macnaughton et al. 2016). Such criteria could be prioritized in decision-making processes to mitigate the impacts of dams on sensitive species. Prescribing near-natural hydrological regimes through controlled impoundment releases might also benefit from the simultaneous tracking of improvements in water chemistry along river reaches downstream.

Prioritizing basin-scale restoration over addressing local river segment-scale impacts (e.g., habitat fragmentation due to deforestation) in RSBs will also be vital for addressing the ecological outcomes of future threats, such as interbasin water transfers. A headwater link between the Malaprabha and Mhadei rivers has already destroyed important headwater habitats for fish. Our field observations suggest that canal constructions can cause a further reduction in water quality and can seriously affect freshwater fish and endemic species diversity. The WG region is showing a trend of rapid urbanization and human population pressures, which are likely to cause further river regulation in the near future (McDonald et al. 2011; Konar et al. 2013). The region is the second highest in dam densities in India, and more than 352 small to medium hydropower projects (<25 MW) are under consideration in the state of Karnataka alone (Dandekar 2012). According to recent policy studies, dams could further threaten river biodiversity in this area (Dandekar 2012; Jumani et al. 2018). Maintenance of ecological flow regimes in RSBs can improve water quality not only for fish fauna but also for local human users of water (Macnaughton et al. 2016).

In NRSBs, the priority will obviously need to be reducing local-scale impacts of degraded water quality (especially related to nitrates). In the Tunga River in particular, local human disturbances and polluting activities are of concern for fish conservation. Thus, across the study area, the priorities of intervention will require a shift from managing water removals in the Tunga River to the maintenance of ecological flows for improving water quality in the Mhadei River or to controlling local pollution and water removal while optimizing ecological flow needs downstream of river barriers in the Malaprabha River. In light of these recommendations, fish conservation efforts by governmental or nongovernmental institutions can be scaled according to the basin and relative impacts of flow regulation and local disturbances. Scale-dependent prioritization of interventions can guide adaptive conservation planning and policy in current and future scenarios of river water use conflicts in the WG region.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.