Demographics and exploitation of two 'Near Threatened' freshwater-eels, Anguilla bengalensis and A. bicolor in small-scale subsistence fisheries and implications for conservation

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1

Demographics and exploitation of two Near Threatened freshwater eels, *Anguilla bengalensis* and *Anguilla bicolor* in small-scale subsistence fisheries and implications for conservation

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Abstract

1. Tropical freshwater eels (*Anguilla bengalensis* and *Anguilla bicolor*) contribute a major share of the world's wild-caught eel production, having become the next major target owing to the declines in availability of both *A. japonica* and *A. anguilla*, species that have traditionally contributed to eel aquaculture and trade.

2. Although both *A. bengalensis* and *A. bicolor* are assessed as Near Threatened on the IUCN Red List, these assessments are primarily based on anecdotal information and local knowledge on population declines.

3. Demographics and exploitation levels of *A. bengalensis* and *A. bicolor* were determined from small coastal river systems, and their adjoining aquascapes in the Western Ghats hotspot of southern peninsular India, and the value of these data for future conservation planning discussed.

4. The computed estimates of annual catch data for freshwater eels from the study region are between 0.17 (*A. bicolor*) to 0.30 t (*A. bengalensis*). Virtual population analysis of exploitation, showed a drastic decline (in number) in the length groups > 45 cm for both species, suggesting that they were less likely to attain their asymptotic length in the region.

5. Current exploitation rates of *A. bengalensis* are unsustainable, while those for *A. bicolor* are almost close to reaching this level. Exploitation of all life stages from yellow eels to adults (29–171 cm) are likely to cause recruitment failure, and significant mortality of spawning individuals of both species.

6. An integrative conservation approach including raising awareness (leading to voluntary restrictions), fishing closures in reservoirs, village-level quotas, and regular monitoring of populations will ensure a sustainable future for the freshwater eel species in the Western Ghats hotspot, and elsewhere in the tropics where these species are exploited.

Keywords: anguillid eels, catadromy, freshwater eel, overfishing, small-scale fisheries

1 | INTRODUCTION

Anguillid eels comprise a group of facultatively catadromous fishes distributed throughout tropical and temperate waters, known for their role in diets, folklore, literature and culture, and having been studied, fished, traded and consumed for centuries (Kuroki, Righton & Walker, 2014). At present, the genus comprises 16 valid species (and an additional three sub-species) (Tsukamoto, Kuroki & Watanabe, 2020) inhabiting the fresh, estuarine and coastal waters of more than 150 different countries (International Union for Conservation of Nature (IUCN), 2014), where they are a valuable aquatic resource, with various life stages from juveniles to adults harvested, farmed and traded on local and international markets (Shiraishi & Crook, 2015; Gollock et al., 2018). This increasing demand has led to indiscriminate exploitation both of adults and young eels, and together with a range of human stressors (pollution, hydropower development), has resulted in the population decline of many species (Righton et al., 2021).

The artificial spawning of anguillids has evaded success, and remains in the research and development stage (Okamura et al., 2014; Righton et al., 2021), and as a result the rapidly growing global aquaculture industry continues to be supplied exclusively with wild-caught glass eels (juveniles). This exploitation is considered to be one of the major causes for the catastrophic declines (going back as far as the 1970s) of several eel populations (Arai, 2014, 2016; Stone, 2003). Populations of the European (*Anguilla anguilla*), American (*Anguilla rostrata*) and Japanese (*Anguilla japonica*) eels are considered to be overfished, and current fisheries unsustainable (Arai, 2016; Dekker, 2003; Busch & Braun, 2014). Synergistic impact of a range of human stressors including pollution, fragmentation and loss of habitats, alien parasites, climate change, and the impact of commercial and recreational fisheries (Drouineau et al., 2018), have resulted in all three species listed as threatened on the IUCN Red List (*A. anguilla* – Critically Endangered, *A. japonica* and *A. rostrata* – Endangered).

The three popular and iconic species, *A. anguilla*, *A. rostrata* and *A. japonica*, together contributed to an average of about 56% of the world's wild-caught anguillid fishery between 2008 and 2017 (Food and Agriculture Organization (FAO), 2019), the rest (minus *A. australis* contributing <1%) is contributed by a group of species that the FAO puts together as 'freshwater eels' (*Anguilla* spp.). In 2017, these 'freshwater eels', accounted for more than 60% of the world's wild-caught eel production (FAO, 2019), largely comprising two tropical species, *Anguilla bengalensis* and *Anguilla bicolor*. These two species have a natural distribution range spanning the inland and marine waters of the Indian (*A. bengalensis, A. bicolor*) and the Western-Pacific Ocean (*A. bicolor*) rim countries, where they are the target of subsistence and commercial fisheries, and international trade (live and frozen products), including on Business to Business (B2B) marketplaces/trade platforms (Pike et al., 2020a, Pike et al., 2020b).

As a result of declines in the availability of both *A. japonica* and *A. anguilla*, species that have traditionally contributed to eel aquaculture and trade, *A. bicolor* has become the next preferred target (Pike et al., 2020b; Arai, 2014). Although there is little quantitative information available to infer the population status of *A. bicolor*, the growing interest in, and demand for, the species in East Asian markets is likely to lead to a considerably greater threat from increased exploitation (Pike et al., 2020b; Arai, 2014). The same trend may also be more or less applicable to *A. bengalensis*, which has shown local population declines of 30% over the last 10 years (Islam, 2015), and is now known to be absent from many parts of its global range (Pike et al., 2020a).

5

Both *A. bengalensis* and *A. bicolor* have been assessed as Near Threatened on the IUCN Red List of Threatened Species (Pike et al., 2020a, Pike et al., 2020b). For *A. bengalensis*, it has been suspected that a reduction of close to 30% has probably occurred across its distribution range over the last 36 years (three generations), based on reports of local declines (Pike et al., 2020a), whereas for *A. bicolor* it is suspected that a reduction in population size of close to 30% will occur over the next 21 years (three generations) given its current and future demand in the global eel markets (Pike et al., 2020b). If these levels of exploitation continue to increase, this may pose a significant threat to the populations of both species at a global scale (Pike et al., 2020a, Pike et al., 2020b), necessitating the need to upgrade the conservation status of the two species, and initiate effective species conservation planning and management.

In this article, the demographics and exploitation levels of *A. bengalensis* and *A. bicolor* (Figure 1) are determined from small coastal river systems, and their adjoining aquascapes in the Western Ghats biodiversity hotspot of southern peninsular India, and the value of these data for future conservation planning are discussed. The Western Ghats as a discrete biogeographical region is known not only for its exceptionally rich freshwater biodiversity, but also as a region that continues to face extensive human impacts on its freshwater ecosystems through habitat fragmentation, hydropower dams, pollution and overfishing (Dahanukar et al., 2011). The Western Ghats has also been particularly flagged as an area from where *A. bengalensis* has reportedly become absent in recent times (Pike et al., 2020a). There is also a general lack of knowledge on basic life history and population parameters such as age, growth and maturation of tropical freshwater eels compared with temperate freshwater eels (Arai, 2016; Gollock et al., 2018), and assessing health and dynamics of stocks and generating management advice continues to remain a basic topic of anguillid eel research (Castonguay &

Durif, 2016; Righton et al., 2021). In this context, the present article will not only provide primary information on two poorly known freshwater eel species, but also serve as a baseline to inform future research needs, to determine robust conservation assessments, and to develop sustainable levels of exploitation and management strategies.

2 | MATERIALS AND METHODS

2.1 | Species and sub-species

Allocation of common names to anguillid eels is known to be a challenge especially for those that have sub-species (Tsukamoto, Kuroki & Watanabe, 2020). Two sub-species are currently recognized for *A. bengalensis*: the Indian Bengal eel (formerly, Indian mottled eel), *Anguilla bengalensis bengalensis* Gray, 1831 distributed in the marine and inland waters of the Indian subcontinent, extending into the Andaman Sea and peninsular Malaysia; and the African Bengal eel (formerly, African mottled eel), *Anguilla bengalensis labiata* Peters, 1852 restricted to Western Africa (Tsukamoto, Kuroki & Watanabe, 2020). Similarly, *A. bicolor* has two recognized sub-species, the Indian bicolor eel, *Anguilla bicolor bicolor* McClelland, 1844 (formerly, the Indian shortfin-eel) distributed in the Indian Ocean, peninsular Malaysia and Indonesia; and the Pacific bicolor eel, *Anguilla bicolor pacifica* Schimdt, 1928 (formerly, the Pacific shortfin-eel) found in Australia and the Pacific (Tsukamoto, Kuroki & Watanabe, 2020). Throughout this article, the species names *Anguilla bengalensis* (referring to *A. bengalensis bengalensis*) and *A. bicolor* (referring to *A. bicolor bicolor*) are used, as they are the oldest available names, and would be retained if the sub-species status is elevated.

7

2.2 | Study sites and data collection methodology

Data were collected by visiting local fish markets and landing sites along three small rivers: the Chalakudy, Periyar and Muvattupuzha draining the southern part of the Western Ghats hotspot, and their associated backwater and estuarine systems (Figure 2; Table 1). *Anguilla bengalensis* and *A. bicolor* are caught by local small-scale fishers primarily using hook and line, and rarely in gill nets (Figure 1), and sold either in local markets or consumed directly in the fisher households. Local fishers are able to distinguish both species effectively, which are known under different vernacular names.

Regular visits were undertaken to markets and landing centres along these river systems to understand the nature of the anguillid eel fishery, finalize sampling sites (based on information on anguillid catches), and interact with local fishers targeting the two species. From February 2019 until June 2020, weekly surveys were carried out at 30 sites (10 in the River Chalakudy, 14 in the River Periyar, three in the River Muvattupuzha, and three in the Vembanad backwaters), comprising stream, floodplain wetlands, reservoirs as well as adjoining backwaters, and estuaries (Table 1). As the aim of the study was to understand the fishing pressure on the two eel species, only length measures of fish caught by local fishers were taken, and no experimental fishing was undertaken specifically for the purpose of the study. Entire catch irrespective of the life stage and size (juveniles, sub-adults and adults) are brought to the market, and no eels are released back into the wild.

On each sampling day, measurements were made of the length (to the nearest cm) and weight (to the nearest g) of all *A. bengalensis* and *A. bicolor* caught by local fishers at the specific sampling site visited, or kept for sale at the adjoining market. A total of 712 length

8

measurements, comprising 387 individuals of *A. bengalensis* and 325 individuals of *A. bicolor*, were used for the length–frequency analysis. Weight measurements were available for 375 individuals of *A. bengalensis* and 282 individuals of *A. bicolor*.

2.3 | Data analyses

Analysis of the data is based on cumulative catches of all fishers in a given month. Length–weight relationships were determined using the allometric equation $W = aL^b$ (Pauly, 1984) and logarithmically transformed into log (W) = log (a) + b log (L). The values of a and b were estimated by least square regression (Zar, 1984). Goodness of fit was determined using the coefficient of determination (R^2). The null hypothesis that the species grows isometrically, i.e. $b = 3$, was tested using a two-tailed t test (Zar, 1984).

Length–frequency distributions were used to study growth patterns, mortality and exploitation. Data were arranged in a length–frequency table with 5 cm as the mid-length of the group and with a 10-cm class interval. Parameters related to growth, mortality and exploitation were estimated from the length–frequency data using FAO-ICLARM Stock Assessment Tools II (FiSAT II) software (Gayanilo, Sparre & Pauly, 2005), which has been previously used for understanding the stock assessment and population dynamics of anguillid eels (Simon, 2007; Leander et al., 2012; Robinet et al., 2013). The von Bertalanffy growth formula (VBGF) was fitted using the equation, $L(t) = L_\infty\ [1\text{-exp}(-K(t-t_0))]$, where L_∞ is the asymptotic length, K is the growth constant, $L(t)$ is growth at time t; and t_0 is hypothetical age at which the organism will have zero size. Parameters of VBGF were estimated employing ELEFAN 1 routine (Pauly, 1984). The parameter t_0 was estimated using the equation, log ($-t_0$) = -0.3922 - 0.2752 log L_∞ - 1.038 log K (Pauly, 1979). Potential longevity (t_{max}) was estimated using the formula t_{max} =

$(3/K) + t_0$ (Pauly, Moreau & Gayanilo, 1998). Based on the values of L_∞ and K, the growth performance index ($\phi' = 2*\log L_\infty + \log K$) was estimated (Pauly & Munro, 1984). Growth parameters were used to determine the freshwater recruitment pattern of the young (Moreau & Cuende, 1991) by reconstructing the recruitment peaks from a time series of length–frequency data to estimate the number of pulses per year and the relative strength of each peak (Gayanilo, Sparre & Pauly, 2005).

Total mortality (Z) was estimated from the length-converted catch curve. The length at first capture (L_C) was determined using a logit function on the probability of capture. Natural mortality (M) was determined using Pauly's M equation, which is known to work well, particularly for tropical fishes, $\ln(M) = -0.0152 - 0.279\ln(L_\infty) + 0.6543\ln(K) + 0.463\ln(T)$, where T is the average annual temperature (26°C for the current study area). Fishing mortality (F) was calculated as $F = Z - M$, and the current exploitation level (E) was calculated as $E = F/Z$ (Pauly, 1984).

Growth and mortality related parameters were then used to model the Virtual Population Analysis or VPA (Hilborn & Walters, 1992), and for estimating the exploitation level of the species using relative yield-per-recruit (Y'/R) and relative biomass-per-recruit (B'/R) analysis with a knife edge selection procedure (Beverton & Holt, 1966). Plots of Y'/R vs. E and of B'/R vs. E were used to estimate E_{max} (exploitation ratio producing maximum yield) and E_{50} (exploitation ratio under which the stock has been reduced to 50% of its unexploited biomass).

3 | RESULTS

3.1 | Habitat use

Anguilla bengalensis was caught from locations spread across an altitudinal range of 0–415 m above sea level (m asl), and *A. bicolor* from a lower altitudinal range between 0 and 75 m asl (Table 1). The highest percentage of individuals of *A. bengalensis* were recorded between 30 and 40 m asl, and those of *A. bicolor* between 0 and 10 m asl (Figure 3b). Whereas 45% of the exploited *A. bengalensis* occurred in reservoirs, only 1% of *A. bicolor* were caught from the same locations (Table 1). Interestingly, only a single individual of *A. bengalensis* was caught from the habitats with tidal influence compared with 26 individuals of *A. bicolor*. The largest individuals of both species were caught from rivers, compared with medium-sized fish in reservoirs (Table 1). In the backwaters and estuary, only small-sized (50–56 cm) *A. bengalensis* were caught, while a larger size range (41–104 cm) was observed for *A. bicolor* (Table 1).

3.2 | Characterization of exploited populations

Both *A. bengalensis* (54%) and *A. bicolor* (46%) contributed to the local fisheries in three river systems and their adjoining backwaters in the southern Western Ghats in almost equal quantities. Exploited populations of *A. bengalensis* were contributed by individuals in the size ranges between 29 and 171 cm, and those of *A. bicolor* between 38 and 125 cm (Table 1). Fish in the length groups of 51–70 cm dominated the catches of *A. bengalensis*, and those in the length groups of 61–70 cm dominated the catches of *A. bicolor* (Figure 3a). Distinct seasonal trends were observed in the fishery of the two species with catches of *A. bicolor* peaking in the months of July and August, and *A. bengalensis* in November and December. For the 1-year period, from July 2019 to June 2020, 0.30 t of *A. bengalensis* and 0.17 t of *A. bicolor*, were caught and sold in the markets.

3.3 | Growth, longevity and mortality

Length–weight relationships of *A. bengalensis* and *A. bicolor* were represented by the equations $W = 0.0015L^{3.0775}$ ($R^2 = 0.9259$, $P < 0.001$) and $W = 0.0013L^{3.0805}$ ($R^2 = 0.9230$, $P < 0.001$), respectively. For both species, the exponent was not significantly different from the expected cubic value under isometric growth (*A. bengalensis*: $b = 3.0775 \pm 0.0451$, $t = 1.7189$, $P = 0.0865$; *A. bicolor*: $b = 3.0805 \pm 0.0532$ $t = 1.5135$, $P = 0.1313$).

VBGF fitted to both species (Figure 4) predicted a greater asymptotic length ($L_\infty = 183.75$ cm) for *A. bengalensis* (Table 2). Growth-related parameters varied between the two species, with a comparatively higher K value for *A. bicolor* suggesting that this species approaches its asymptotic length more quickly than *A. bengalensis* (Figures 4a, c). This was also reflected in the lower longevity (8.02/yr) for *A. bicolor* compared with *A. bengalensis* (13.17/yr). However, the growth performance index (ϕ) of both species was not considerably different, although *A. bengalensis* had slightly higher values (Table 2). Between the two species, *A. bicolor* had a greater natural mortality (M) (0.59/yr), compared with *A. bengalensis* (0.39/yr). Statistical analysis of recruitment revealed two peaks for *A. bengalensis* (Figure 4b) and one peak for *A. bicolor* (Figure 3d), indicating that there are variations in reproductive and spawning strategies of the two species.

3.4 | Exploitation

Computed estimates of annual catch data from the study region are between 0.17 (*A. bicolor*) to 0.30 t (*A. bengalensis*). Greater levels of fishing mortality (F) were observed in *A. bicolor* (1.13/yr), compared with its sympatric congener, *A. bengalensis* (0.70/yr). The estimated mean length at first capture (L_c) for *A. bicolor* was 59.58 cm and for *A. bengalensis* was 63.08 – around 45% and 34% of their asymptotic lengths.

VPA showed a steady decrease in the population resulting from natural losses until the mid-length of 45 cm for both species, after which there was a drastic reduction in the surviving population with increasing fishing mortality (Figures 5a, c). Fishing pressure was greater for *A. bicolor* (Figure 5c) than for *A. bengalensis* (Figure 5d), and individuals of both species were less likely to attain their asymptotic length in the region because of exploitation. Current exploitation rate (E) of *A. bengalensis* was greater than both its E_{max} (i.e. exploitation rate producing maximum yield) and E_{50} (i.e. exploitation rate under which the stock has been reduced to 50% of its unexploited biomass (Figure 5b, Table 2), suggesting severe fishing pressure and overfishing. A high exploitation pressure also exists for *A. bicolor* with its current exploitation rate (E) almost twice its E_{50}, and very close to reaching the predicted E_{max} (Figure 5d, Table 2).

4 | DISCUSSION

Complications and uncertainties regarding the spatial pattern of anguillid eel life histories, particularly the mysteries surrounding the marine phase of tropical species such as *A. bengalensis* and *A. bicolor*, continue to be a challenge for developing conservation and management plans. Some studies have revealed that the migration of 'freshwater eel' species such as *Anguilla bicolor bicolor* into fresh water is not an obligatory behaviour (Chino & Arai, 2010). Although recent research has started to address this knowledge gap and helped improve our understanding of their natural reproduction (Arai & Chino, 2019; Arai et al., 2020), there are regions where anguillid eels have been poorly studied (e.g. South Asia: Jacoby et al., 2015).

In southern peninsular India, which encompasses the drainages of Western Ghats and their extensive network of backwaters, anguillid eels have received little research attention. This is despite anecdotal observations, particularly from the northern part of Western Ghats suggesting that populations of anguillid eels are declining, and are probably extirpated from many localities (Kharat et al., 2003; Kumkar et al., 2017). However, quantitative estimates to support the decline in population of *Anguilla* species are relatively rare. Three previous studies have used similar methods to those in the present study (data collected by visiting markets and fish landing sites) to estimate catches of anguillid eels. Kurup et al. (1995) reported 0.63 t of *A. bicolor* during 1988–1989 from a relatively smaller study area in Kerala State, compared with only 0.17 t in the present study, suggesting that the population of this species may have been reduced by at least 70% in the last 30 years, but comparative data are not available for *A. bengalensis*. Fishery catch data (from 2009 to 2011) based on much smaller study areas – for example, the rivers Bharathapuzha and Muvattupuzha in Kerala – showed the range of annual exploitation of *A. bengalensis* to be between 0.12 and 2.40 t – constituted by fish in the length group of 26.8–71.2 cm (Renjithkumar, Roshni & Kurup, 2016; Renjithkumar, Roshni & Kurup, 2021). The catch estimates of *A. bengalensis* in the present study was 0.30 t, but for a much larger area, and included specimens of comparable size range (29.0 to 71.1 cm).

4.1 | Habitat use

Although not the direct focus of the current study, the results obtained suggest a differential habitat preference and use for the two sympatric species, *A. bengalensis* and *A. bicolor*, similar to previous observations. In many parts of its distribution range, *A. bicolor* inhabits the middle to downstream parts of the rivers including areas of tidal influence, in contrast to the middle reaches to cooler hill-streams preferred by *A. bengalensis* (Arai & Kadir, 2017b; Arai & Chino, 2019; Arai et al., 2020). The highest elevation at which *A. bengalensis* was caught was 415m. Although there is no information on the highest elevations inhabited by *A. bengalensis*, there are records of the species from reservoirs located >800m in the Western Ghats (Radhakrishnan & Kurup, 2010). There was also a significant difference in the use of lacustrine habitats between the two species, with most catches of *A. bengalensis* (45%) contributed by reservoirs in the study region (against only 1% of *A. bicolor*), suggesting that *A. bicolor* seldom makes long vertical migrations and prefers the lower reaches of rivers (also see Cumaranatunga et al., 1997). This is also confirmed by the occurrence of *A. bengalensis* (but not *A. bicolor*) in upland reservoirs (Odyuo & Nagesh, 2012), and in mountain aquascapes in the Bhutan Himalaya (Gurung & Thoni, 2015), both located >1000 km from the nearest tidal region. It is also interesting to note that no individuals below 29 cm in length in *A. bengalensis* and 38 cm in *A. bicolor* were caught in the fishery in the study region. Whether glass eels, elvers and early yellow eels use a different habitat is yet to be understood. Similar bias in the length groups were seen in studies carried out in Southeast Asia where the smallest individual of *A. bengalensis* measured 35 cm and in *A. bicolor* was 20 cm (Arai & Kadir, 2017b; Arai et al., 2020). Future research on these two species should focus on sampling entire estuarine habitats including areas in the tidal zones to improve our understanding of the ontogenetic ecology and population dynamics of glass eels.

4.2 | Demographics

Although *A. bicolor* and *A. bengalensis* occur sympatrically in most parts of the Indian Ocean including the Andaman Sea and Malacca strait, *A. bicolor* is known to be the dominant species contributing to local fisheries, and experimental fishing efforts (e.g. 76–88% in peninsular

Malaysia, Arai & Kadir, 2017a, Arai & Kadir, 2017b; Arai et al., 2020). This is in contrast to the present study, where *A. bengalensis* was the dominant species, although the percentage share of catches was not substantially different from *A. bicolor* (56 vs. 46%). This difference is most likely due to the fact that the habitats covered by this study were within a wider elevational range (0–415 m asl).

The maximum observed length (L_{max}) of the Indian Ocean sub-species of *A. bicolor* (*A. bicolor bicolor*) has been suggested to be 80 cm (Skelton, 2001 cited in Righton et al., 2021), with a recent study observing that most of the individuals in a population comprise the 21–75 cm length class (Arai et al., 2020). Individuals of *A. bicolor* measuring 125 cm (66 individuals between the size ranges of 80–125 cm) observed in the present study extends the maximum recorded length of the Indian Ocean sub-species by 45 cm. In comparison, the largest *A. bengalensis* caught in the fishery measured 171 cm, which is smaller than the maximum reported size of the species (i.e. 200 cm; Righton et al., 2021).

Despite their fisheries and the conservation significance of these species, no reliable length–weight or demographic estimates of *A. bengalensis* and *A. bicolor* are available (Froese & Pauly, 2021), making it impossible to compare data meaningfully. A study carried out in the early 1950s based on a sample size of 3500 *A. bengalensis* estimated the length–weight relationship *b* value at 3.202 (Pantulu, 1957). Based on the length–frequency data of glass eels (mean size of 5 cm) of an anguillid species (presumably *A. bicolor*) caught in the Cimandiri River, Java, Indonesia, the growth rate (*K*) was computed at 0.50 yr^{-1} (Triyanto et al., 2020), which is greater than the *K* value estimated in the present study (0.36 yr^{-1}). This is probably because the present study incorporated a larger size range of individuals (from juveniles to adults), compared with only glass eels in the study from Indonesia.

4.3 | Exploitation

Direct exploitation of different life stages including glass, yellow and silver eels is carried out throughout the countries in their range using a variety of gear and effort, but the impacts of such fisheries on population status and trends remain poorly quantified (Righton et al., 2021). High levels of fishing mortality (F=3.05 yr^{-1}) and exploitation rate (E=0.77 yr^{-1}) of glass eels of *A. bicolor* has been documented from Indonesia (Triyanto et al., 2020). Similar levels of fishing mortality and exploitation rates in both *A. bengalensis* and *A. bicolor* were observed in the present study, also indicating that individuals of both species were less likely to attain their asymptotic length in the region.

Current exploitation rates of *A. bengalensis* and *A. bicolor* are greater than their E_{50} values, and the exploitation rate of *A. bengalensis* is greater than its $E_{\max}$, suggesting an uncertain future for the local populations if management attention is not directed towards these species. No studies have investigated the exploitation rates of freshwater eels using length–frequency, or catch data, and this is also the case for most anguillid species around the world (Pike et al., 2020a, Pike et al., 2020b). The estimated mean length at first capture (L_c) ranged between 59.58 cm and 63.08 cm, suggesting that a large share of the catches is contributed by immature juveniles.

Anguilla bicolor is known to mature between 45–72 cm and *A. bengalensis* between 89–120 cm (Arai & Kadir, 2017a; Chai & Arai, 2018). In addition, most eels caught in local fisheries in the southern Western Ghats measured between 51–70 cm (a range of 29–171 cm in *A. bengalensis*, and 38–125 cm in *A. bicolor*) suggesting that mature adults and spawning individuals are being exploited. However, in the absence of information on the reproductive stages of the fish caught this cannot be verified, but is flagged as a cause for concern and an area for future research.

4.4 | Challenges for the conservation and management of anguillid eels in the Western Ghats

Existing conservation assessments for tropical freshwater eels are primarily based on anecdotal information and local knowledge on population declines (Pike et al., 2020a; Pike et al., 2020b). The present study is probably the first to demonstrate that freshwater eels are subjected to heavy exploitation pressure even in small-scale subsistence fisheries, and that local populations are vulnerable to collapse in the absence of future management interventions.

The migratory behaviour of the glass eel life stage of other temperate and tropical anguillid species is known to make them highly vulnerable to exploitation in estuarine environments (Harrison et al., 2014) and in doing so presents a major conservation challenge (Stone, 2003). The high economic value of glass eels and the absence of any organized fishery/collection of this life-stage of freshwater eels in India suggests that very young juveniles of *A. bengalensis* and *A. bicolor* either enter estuaries at a more advanced stage of their development or exhibit a novel, and more cryptic, mechanism of ascending estuaries. Despite being of less economic importance and viability (Knights, 2001), exploitation of yellow and silver eels is the major fishing activity for anguillid eels in India, catering to the food security and livelihoods of mostly rural and forest-dwelling communities. In some regions of the Western Ghats they are also consumed for their perceived medicinal properties (R. Raghavan, pers. observ.).

The fact that all life stages of anguillids, from yellow eels to adults (29–171 cm), are exploited indicates that the fishery is not size-selective, and is likely to cause recruitment failure, and significant mortality of spawning individuals. In addition to subsistence fisheries such as the one that is described in this article, anguillid eels are also caught in the region through unsustainable fishing practices including the 'monsoonal floodplain fishery' which specifically targets mature individuals during their spawning migration (Shaji & Laladhas, 2013).

Restrictions on the gear (e.g. mesh/net size) or limits on the size of the fish caught (minimum legal size) are a challenge to enforce because most eels are captured using hook and line. Also, unlike temperate species of anguillid eels, *A. bengalensis* and *A. bicolor* are thought to spawn year-round (Setiawan et al., 2001; Arai & Kadir, 2017a), and therefore mature eels are likely to move towards the sea or tidal reaches during several months of the year. Imposing a closed season in tandem with the spawning seasons, when fishing is either voluntarily or persuasively stopped is therefore not totally feasible for the two species of eels. The dispersed nature of fisheries and direct consumption in fisher households is a challenge for developing management plans for small-scale subsistence harvest of freshwater eels in the Western Ghats. Involving fishers and ensuring their participation is therefore crucial for the success of any management plans. Raising awareness of local fishers as well as entire riverine households on the perilous state of riverine eels and the need for immediate conservation and management interventions may help evoke changes in their behaviour, leading to voluntary reductions of harvests (including possibilities of developing village-level catch quotas) and consumption. Such voluntary restrictions and strategies have been considered for effective management of recreational fisheries (Cooke et al., 2013). Compared with streams and rivers, management of fisheries in reservoirs is comparatively easier given the existence of fisher-cooperatives and self-help groups, where interventions can be successfully implemented and enforced. Temporal or permanent closure of a fishery, a ban on harvests of juveniles, and allocation of catch quotas for adult eels can be initiated at all reservoirs in the region, which can then be monitored by the Department of Fisheries. Catch quotas can also be developed for each fishing village in consultation with local fishers. Indiscriminate harvests of eels (and other freshwater fish species) during their spawning migration (monsoon floodplain fishery) although banned by the Kerala Inland Fisheries and Aquaculture Act, 2013 and 2015 (Amendments), continue unabated, despite attracting a fine up to 10,000 Indian rupees (~US$ 130) and imprisonment up to 3 months. Strict field monitoring and enforcement of this legislation can help reduce harvests of mature, ready-to-spawn adults. In many countries of South and Southeast Asia, there are small-scale fisheries for freshwater eels that are vulnerable to similar sustainability issues as demonstrated in the present article. The aquascapes, human-dimensions of fisheries and fisheries legislation and governance are similar throughout much of South Asia, and therefore the management strategies that have been suggested in the present study can be adopted with local modifications to ensure a sustainable future for freshwater eel fisheries in these regions.

Freshwater eels are also exposed to multiple threats in their habitats, with these stressors acting either individually or synergistically (Jacoby et al., 2015). In the study region (Chalakudy, Periyar and Muvattupuzha Rivers), there are several continuing, as well as predicted future threats to freshwater biodiversity including flow alterations as a result of the cascade of hydropower dams, high levels of pollution, and extreme climatic events (Dahanukar et al., 2011; Raj et al., 2021). Combined effects of these threats will certainly result in changes to the habitat use, growth and reproduction of the two species of freshwater eels, making them more vulnerable to drastic declines and local extinctions, as has already been witnessed in the northern part of the Western Ghats (Kharat et al., 2003; Kumkar et al., 2017). Future hydropower development in the region should invariably consider fish-friendly infrastructure facilities such as ladders and fish passes, which are now absent from the dams in the region.

The present study, from one of the critical freshwater ecoregions of the Western Ghats hotspot, shows that small-scale subsistence fisheries pose a significant risk to anguillid eels, and in the absence of strict management are likely to lead to the collapse of local populations. Despite being a country with excellent data collection and research on aquatic environments, research on anguillid eels in India has been very scanty. There is an urgent need to understand the status and threats to freshwater eels across the river systems draining the eastern and western coasts of the country, and in their adjoining aquascapes such as reservoirs, estuaries and backwaters. Such studies also need to be complemented by those on ecology, habitat use and reproductive biology. For example, otolith microchemistry can be a potential tool to help contextualise exploitation rates such as those generated by this study, and facilitate the conservation management of anguillid eels in the region.

Owing to their presence in a wide range of aquatic habitats from estuaries, backwaters, tidal reaches of rivers, large reservoirs and upper reaches of rivers, anguillid eels are ideal surrogate species for conservation (Itakura et al., 2020). No other species in the Western Ghats and southern peninsular India occupy such a wide range of aquatic habitats, help maintain connectivity between mountain streams and estuaries, and at the same time demonstrate panmixia, and face multiple threats including from exploitation. Implementing the management strategies that have been suggested here can help promote sustainable populations of *A. bengalensis* and *A. bicolor* and their fisheries not only in the aquascapes of southern peninsular India, but elsewhere in South and Southeast Asia where riverine eel species are indiscriminately harvested.

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Table 1. Details of local markets and landing centres along three river systems, and associated aquascapes in the southern Western Ghats, India, and length data of *Anguilla bengalensis* and *A. bicolor* collected in the study.

Location	River System	Habitat	Latitude (°N)	Longitude (°E)	Altitude (m asl)	*Anguilla bengalensis*		*Anguilla bicolor*	
						N	Length (cm)	N	Length (cm)
Pariyaram	Chalakudy	River	10.317	76.376	5	39	42-94	-	-
Poringalkuthu	Chalakudy	Reservoir	10.314	76.635	415	2	104-117	-	-
Konnapilly	Chalakudy	River	10.296	76.407	21	3	43-103	-	-
Chalakudy	Chalakudy	River	10.294	76.346	10	5	53-70	19	49-80
Ezhattumugham	Chalakudy	River	10.293	76.468	40	4	63-79	-	-
Konnakuzhi	Chalakudy	River	10.290	76.423	26	16	48-64	2	78-84
Vettilapara	Chalakudy	River	10.289	76.509	64	8	45-110	3	51-125
Athirapilly	Chalakudy	River	10.285	76.559	75	27	45-120	6	48-81
Edamalayar	Periyar	Reservoir	10.241	76.698	153	2	100-135	-	-
Annamanada	Chalakudy	River	10.237	76.331	6	7	44-100	12	46-100
Mookannur	Periyar	River	10.218	76.395	6	1	87	1	40
Krishnankotta	Periyar	River	10.208	76.224	1	-	-	5	59-70
Thiruthipuram	Periyar	River	10.202	76.220	1	-	-	1	87
Aanapuzha	Periyar	Estuary	10.197	76.213	2	1	50	18	41-82
Illithod	Periyar	River	10.196	76.559	4	2	95-109	-	-
Angamaly	Periyar	River	10.191	76.363	5	2	76-81	6	51-76
Gothuruth	Periyar	River	10.191	76.218	1	-	-	1	83
Kottuvallikadu	Periyar	River	10.186	76.189	3	2	51-54	63	38-97
Kodanad	Periyar	River	10.182	76.507	5	6	46-95	4	40-100
Vadattupara	Periyar	River	10.181	76.727	55	6	29-135	3	41-111
Vadakkumpuram	Periyar	River	10.180	76.225	4	1	89	-	-
Munambam	Periyar	Estuary	10.179	76.164	0	-	-	2	69-71
Kanakkankadavu	Chalakudy	River	10.173	76.273	1	13	50-96	33	54-90
Kalady	Periyar	River	10.167	76.451	2	11	44-100	1	67
Paravur	Periyar	River	10.154	76.232	3	-	-	3	64-84
Manjaly	Periyar	River	10.150	76.273	1	1	110	7	43-80
Bhoothathankettu	Periyar	Reservoir	10.137	76.662	24	23	45-96	2	61-100
Perumbavoor	Periyar	River	10.123	76.453	2	22	30-99	14	38-86
Thattekad	Periyar	River	10.112	76.704	29	2	87-91	-	-
Cheriyapilly	Periyar	River	10.124	76.249	3	-	-	2	67-79
Varapuzha	Periyar	River	10.072	76.280	3	10	51-99	100	42-100
Neriyamangalam	Periyar	River	10.056	76.784	36	1	91	-	-
Kothamangalam	Periyar	River	10.054	76.631	19	13	47-123	4	48-100
Chambakkara	Vembanad Lake	Backwaters	9.954	76.329	4	-	-	3	86-87
Thodupuzha	Muvattupuzha	River	9.894	76.716	26	8	34-171	2	54-69
Aroor	Vembanad Lake	Backwaters	9.883	76.292	0	-	-	1	122
Panangad	Vembanad Lake	Backwater	9.882	76.335	0	1	56	2	82-104
Muvattupuzha	Muvattupuzha	River	9.881	76.585	83	1	64	-	-
Malankara dam	Muvattupuzha	Reservoir	9.852	76.745	39	147	33-127	2	70-86
Vaikom	Muvattupuzha	River	9.725	76.387	0	-	-	3	59-64

734 **Table 2.** Growth, mortality and exploitation parameters of *Anguilla bengalensis* and *A. bicolor*
735 in three small river systems and associated aquascapes of Western Ghats, India

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Parameter	*A. bengalensis*	*A. bicolor*
Asymptotic length (L_∞, cm)	183.75	131.25
Growth constant (K, yr^{-1})	0.22	0.36
Potential longevity (t_{max}, yr)	13.17	8.03
Growth performance index (ϕ')	3.87	3.79
Length at first capture (L_c, cm)	63.08	59.58
Total mortality (Z, yr^{-1})	1.09	1.72
Natural mortality at 26°C (M, yr^{-1})	0.39	0.59
Fishing mortality (F, yr^{-1})	0.70	1.13
Exploitation rate (E, yr^{-1})	0.65	0.66
Exploitation rate reducing stock to 50% (E_{50})	0.32	0.35
Exploitation rate producing maximum yield (E_{max})	0.56	0.68

737

738

LIST OF FIGURES

FIGURE 1 Freshwater eels in the catches of local fishers in River Chalakudy, Southern part of Western Ghats, India. (a) *Anguilla bengalensis* adult caught in a hook and line, (b) local fisher with a catch of *A. bengalensis*, (c) small-scale subsistence fisher and (d) local fisher exhibiting his daily catch of *A. bengalensis*.

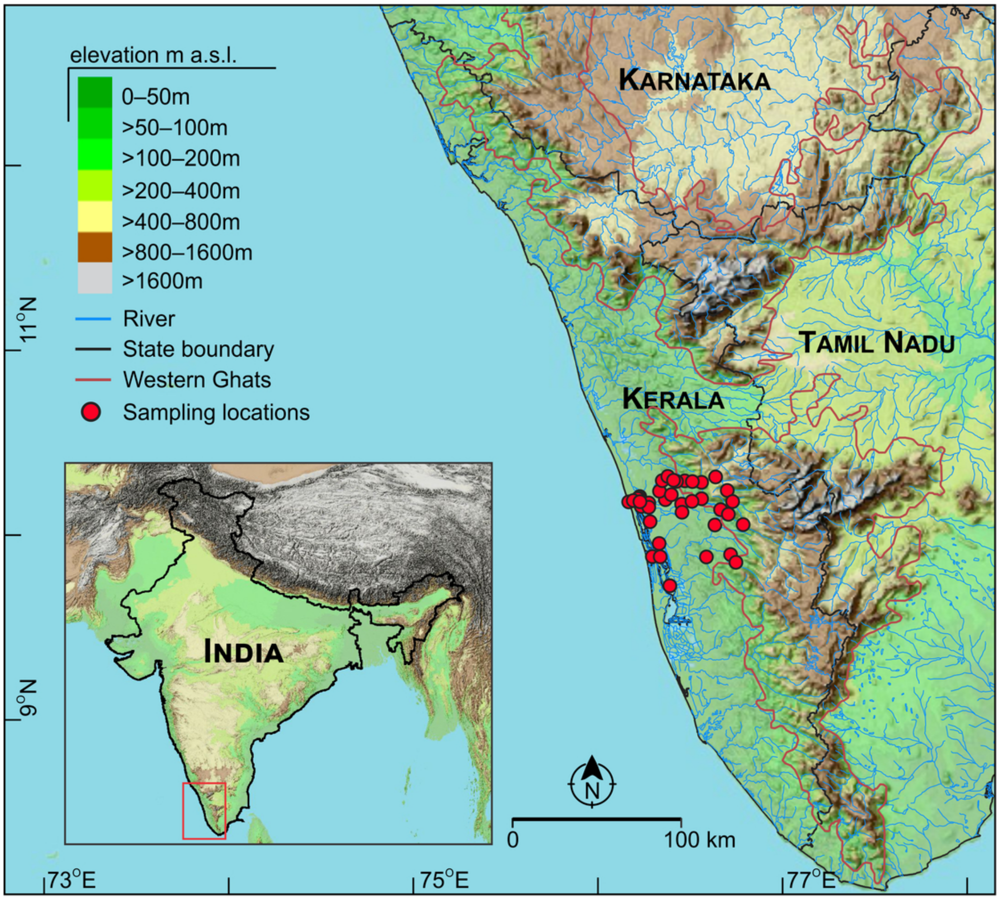
FIGURE 2 Map showing the location of markets and landing centres along Periyar, Chalakudy and Muvattupuzha river systems and associated backwater and estuarine aquascapes in the Western Ghats biodiversity hotspot, India which formed the source of data on catches of *Anguilla bengalensis* and *A. bicolor*

FIGURE 3 Length group and altitudinal distribution frequency distribution of *Anguilla bengalensis* and *A. bicolor* populations in three river systems and associated aquascapes in the southern Western Ghats, India. (a) Histogram of length frequency distribution, and (b) histogram of altitudinal distribution.

FIGURE 4 The von Bertalanffy growth function (VBGF) and recruitment of young in *Anguilla bengalensis* and *A. bicolor* in three river systems and associated aquascapes in the southern Western Ghats, India. VBGF for (a) *Anguilla bengalensis* and (c) *A. bicolor*. Dashed line indicates asymptotic length. Recruitment of young in (b) *A. bengalensis* and (d) *A. bicolor* fitted with normal distributions.

FIGURE 5. Virtual population dynamics (VPA) and relative yield-per-recruit (Y′/R) and relative biomass-per-recruit (B′/R) analysis of exploited *Anguilla bengalensis* and *A. bicolor* populations in three river systems and associated aquascapes in the southern Western Ghats, India. (a) VPA and (b) Y′/R and B′/R analysis of *A. bengalensis*. (c) VPA and (d) Y′/R and B′/R analysis of *A. bicolor*. In (b) and (d), current exploitation ratio E is marked on x-axis by an asterisk.

Freshwater eels in the catches of local fishers in River Chalakudy, Southern part of Western Ghats, India (a) Anguilla bengalensis adult caught in a hook and line, (b) local fisher with a catch of A. bengalensis, (c) small-scale subsistence fisher and (d) local fisher exhibiting his daily catch of A. bengalensis.



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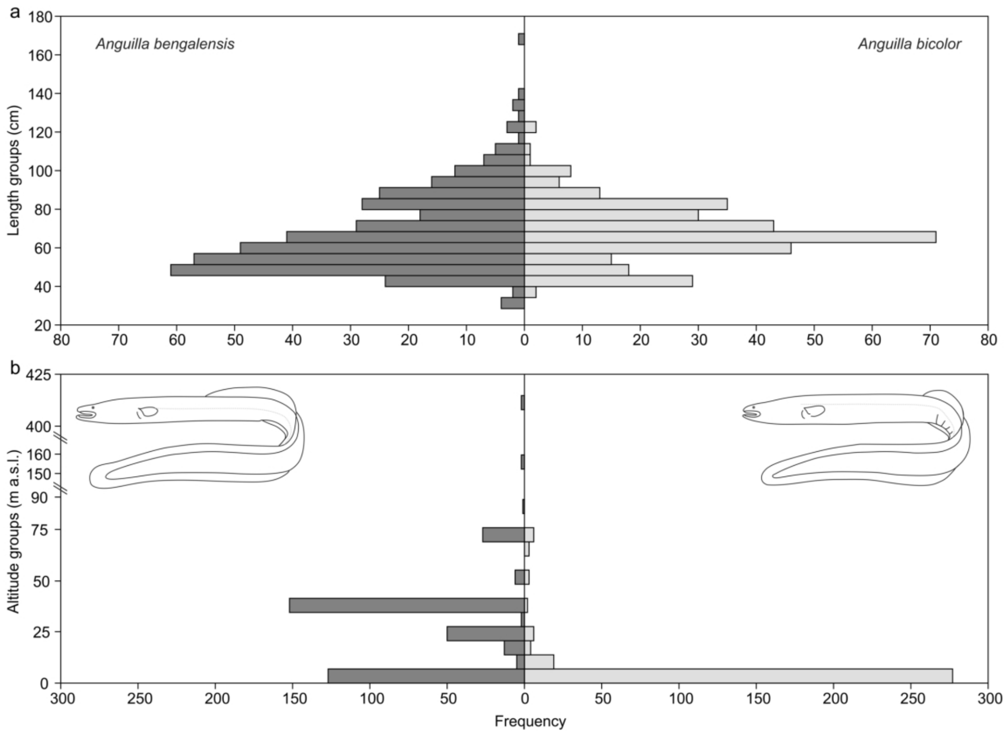
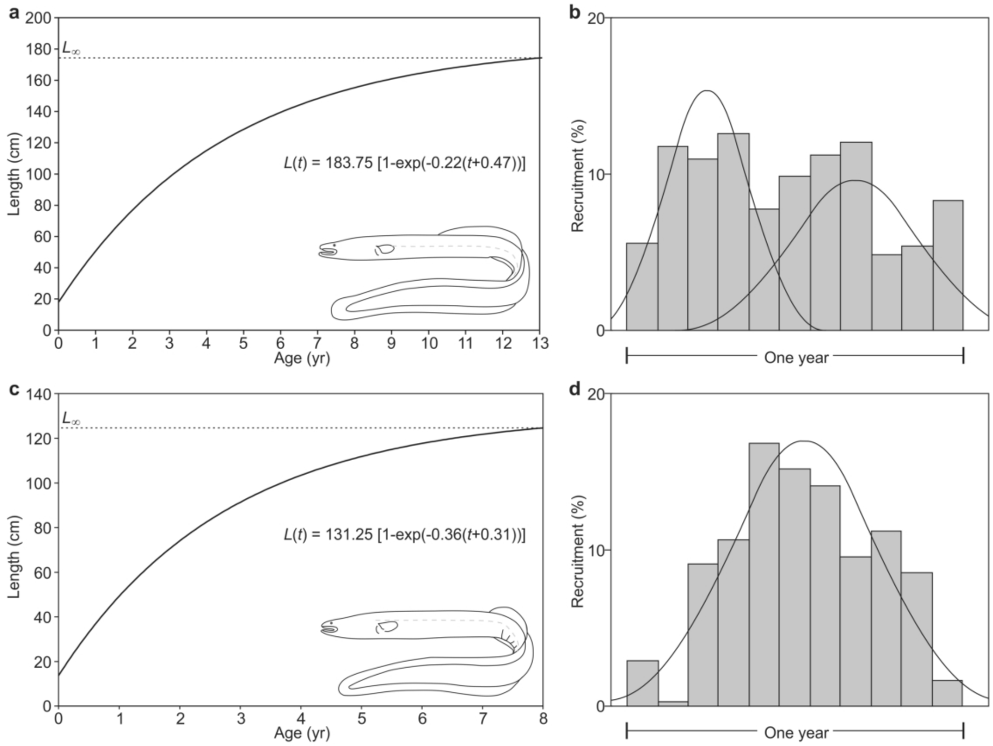


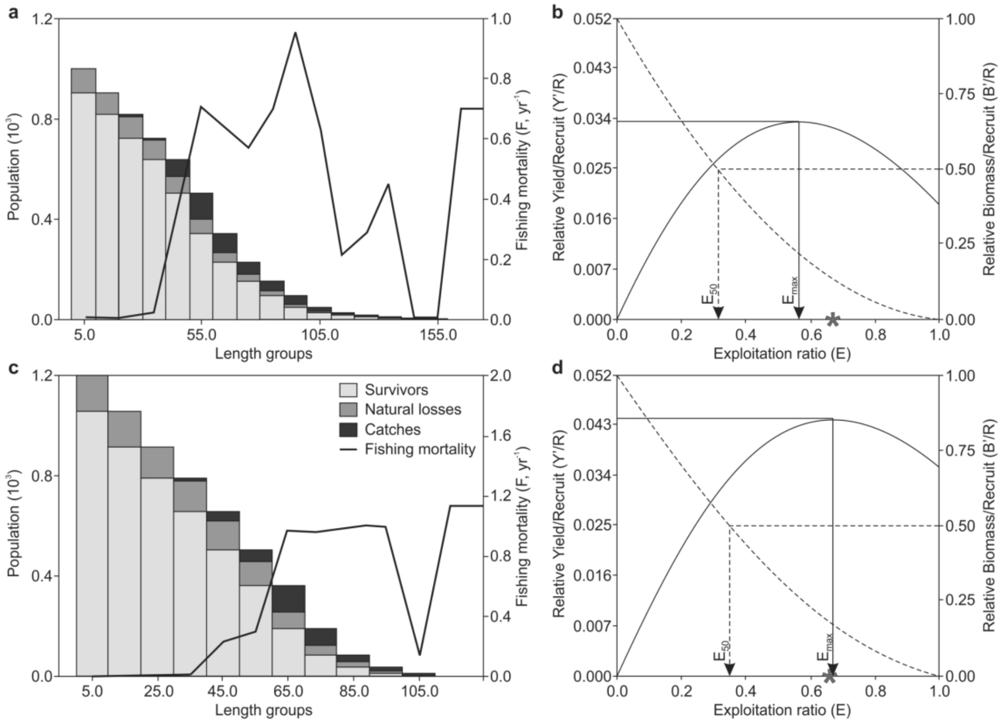
Length group and altitudinal distribution frequency distribution of Anguilla bengalensis and A. bicolor populations in the river systems and associated aquascapes of Western Ghats, India. (a) Histogram of length frequency distribution, and (b) histogram of altitudinal distribution.

186x135mm (300 x 300 DPI)



The von Bertalanffy growth function (VBGF) and recruitment of young in Anguilla bengalensis and A. bicolor in the river systems and associated aquascapes of Western Ghats, India. VBGF for (a) Anguilla bengalensis and (c) A. bicolor. Dashed line indicates asymptotic length. Recruitment of young in (b) A. bengalensis and (d) A. bicolor fitted with normal distributions.

180x135mm (300 x 300 DPI)



Virtual population dynamics (VPA) and relative yield-per-recruit (Y′/R) and relative biomass-per-recruit (B′/R) analysis of exploited Anguilla bengalensis and A. bicolor populations in the river systems and associated aquascapes of Western Ghats, India. (a) VPA and (b) Y′/R and B′/R analysis of A. bengalensis. (c) VPA and (d) Y′/R and B′/R analysis of A. bicolor. In (b) and (d), current exploitation ratio E is marked on x-axis by an asterisk.

185x133mm (300 x 300 DPI)