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Habitat loss due to dam development may affect the distribution of marine-associated fishes in Gabon, Africa

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Abstract. The planned construction of 38 hydropower dams will impact the fish species inhabiting freshwater ecosystems in the megadiverse African country of Gabon. Many of Gabon's most culturally and economically important fish species are marine-associated, moving between fresh and salt or brackish waters. However, we know little about their life histories or movement patterns, which makes it difficult to predict the impacts of dam development on biodiversity and fisheries in Gabon. Here, we apply MaxEnt distribution modeling to predict the distribution of marine-associated fishes in Gabon's freshwaters. The model predicts a high likelihood of these fishes occurring in every coastal watershed, throughout the undammed Nyanga drainage, and extending ~400 km into the Ogooué River and its tributaries Ngounie and Abanga. If all 38 dams are constructed, marine-associated fishes will lose approximately 17% of riverine habitats (7400 km) including 7% of the best quality habitat (460 km). Proposed dams pose a substantial threat to Gabon's most culturally and economically important fishes.

Key words: Afrotropics; connectivity; conservation planning; distribution modeling; endangered; freshwater; habitat fragmentation; ichthyology; MaxEnt; migration; Nyanga; Ogooué.

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INTRODUCTION

Freshwater ecosystems cover 0.8% of Earth's surface but are home to ~40% of the world's fish biodiversity (Dudgeon et al. 2006). This diversity is concentrated in large tropical rivers, including the Amazon (2320 freshwater fish species), Mekong (599 species), Congo (1296 species), and the Ogooué River (308 species; Winemiller et al. 2016, Mbega 2004). Yet, freshwater ecosystems are among the most imperiled in the world and approximately 20% of the assessed freshwater fishes are threatened with extinction (Strayer and Dudgeon 2010, IUCN 2019). Dams have changed the morphology, hydrology, and function of many freshwater ecosystems, thereby causing major shifts in species distribution and abundance, including extinctions (Bunn and Arthington 2002, Poff and Schmidt 2016).

At present, large free-flowing rivers persist in only a few regions including remote parts of the Arctic, Amazon, and central Africa (Grill et al. 2019). There are three large (>500 km) free-flowing rivers in the central African nation of Gabon (Fig. 1): the Ivindo, flowing uninterrupted for 1063 km; the Nyanga, undammed along its 559 km length; and the Ogooué, flowing uninterrupted for 557 km of its 1200 km total length (Grill and Lehner 2019). Large dams and their reservoirs impede movement of freshwater fauna, fragmenting these systems worldwide (Adams and Hughes 1986, Holmquist et al. 1998,

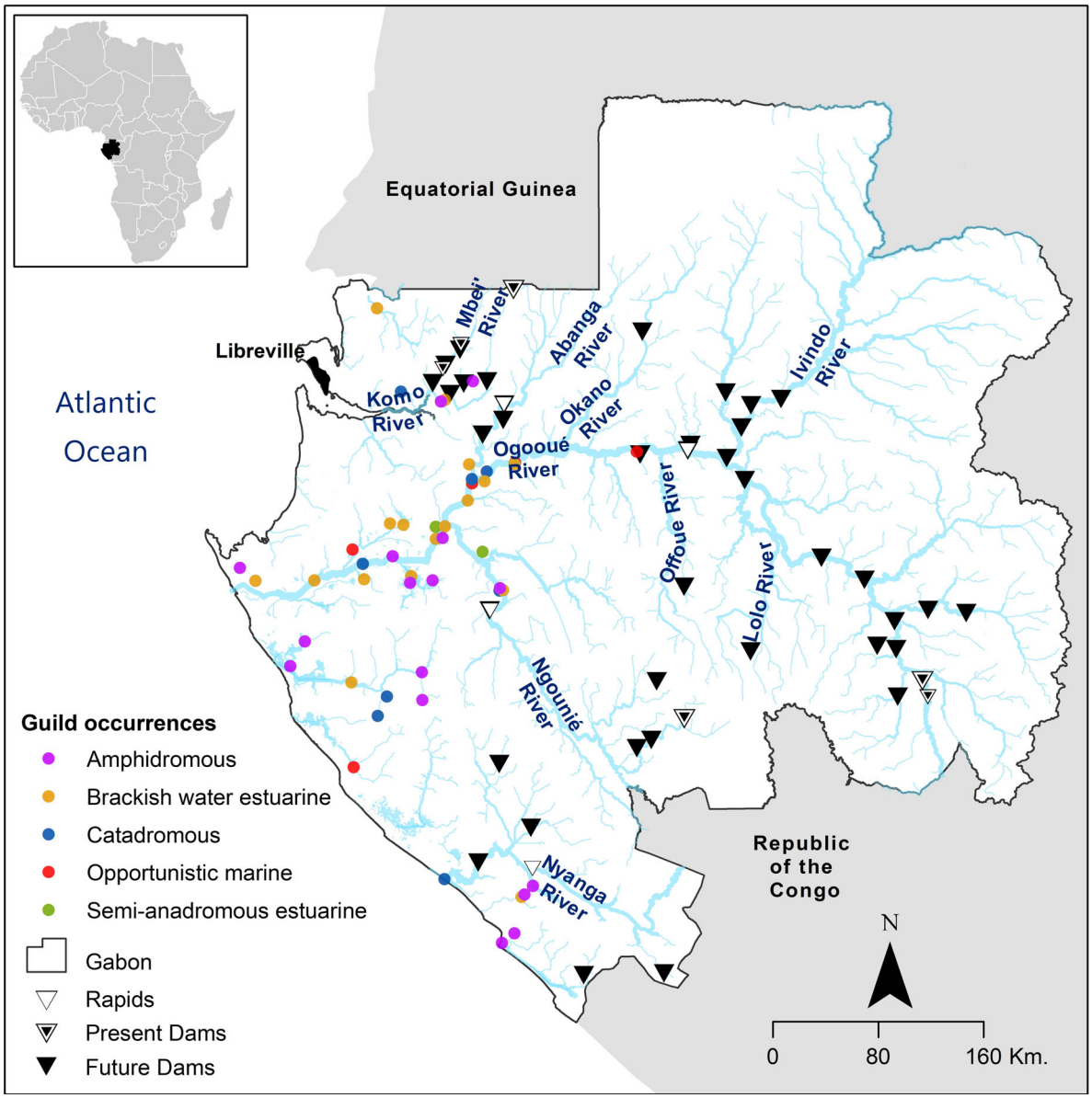

Fig. 1. Map of Gabon showing the river networks and all sites where marine-associated fishes have been documented in freshwaters (color points), rapids (white triangles), existing dams (filled triangles), and proposed dams (black triangles).

Pringle et al. 2000, Richter et al. 1997, Dudgeon et al. 2006, Anderson et al. 2018, Oliveira et al. 2018). Migratory fishes, including marine-associated fishes that rely on multiple distinct habitats, are particularly susceptible to dam construction (Aleem 1972, Drinkwater and Frank 1994, Stanford and Ward 2001, Rowell et al. 2008, Stone 2011). Developing large-scale freshwater conservation strategies requires understanding patterns of connectivity between marine, estuarine, and freshwater ecosystems (Flitcroft et al. 2019), but few studies have incorporated the entire range of habitats required by marine-associated fish species in tropical river systems.

Gabon has identified 38 potential dam sites, including 28 in the Ogooué watershed (Figs. 1

Table 1. List of proposed and existing dams in Gabon.

Name	Code	MW
Chutes Booue	CB	1000
Tsengue-Leledi	T-L	565
Derivation Ogooue-Lolo	O-L	550
Mingouli	Min	460
Kouata-Mango	K-M	445
Kongue	Ko	435
Grand Poubara†	GP	157
Lifoula	Lf	135
Liboka	Lb	121
Ngoulmendjim	Ng	100
Mafoula Matato	MM	88
Souka-Minimal	S-M	85
Angouma	An	85
Chutes de l'Imperatrice	CI	84
Akieni	Ak	76
Nemguembani	Ne	74
Tchimbele†	Tc	68.4
Ibola	Ib	61
Kinguele aval	KAv	60
Kinguele†	Ki	57.6
Tchimbele aval	TAv	55
Lebombi	Le	42
Kinguele amont	KAm	41
Poubara 1 & 2†	Pb	38
Faga	Fa	37
Omvan amont	OAm	35
Fe II	Fe	35
Omvan aval	OAv	25
Dibwangui	Di	10
Mounana	Mn	5
Makongonio	Ma	5
Igotchi	Ig	5
Ovan	Ov	3.5
Booue	Bo	2
Iroungou	Ir	2
Iboundji	Ib	0.4
Mbigou†	Mbi	0.3
Mboungou	Mb	0.3
Medouneu†	Med	0.2
Mouyanama	My	0.2
Guietsou	Gu	0.1
Ndindi	Nd	0.1
Moulengui-Bindza	M-B	0.1
Lope	Lo	0.05

Note: Codes are used in Fig. 2.
† Denotes existing dam.

and 2, Table 1). These dams and their reservoirs can increase energy production, but they would fragment and alter relatively pristine river systems, and potentially threaten the fisheries that those intact rivers support. Many of the most culturally and economically important fish species in Gabon's rivers are marine-associated, meaning that they belong to one of several guilds of fishes that move between freshwater and marine or brackish ecosystems (Welcomme et al. 2006). These species include the Giant African threadfin (*Polydactylus quadrifilis*), snappers (*Lutjanus* spp.), croakers (*Pseudotolithus* spp.), Bonga Shad (*Ethmalosa fimbriata*), mullets (*Parachelon grandisquamis*, *Neochelon falcipinnis*), Atlantic Tarpon (*Megalops atlanticus*), and tongue soles (*Cynoglossus* spp.). Though these fishes are known to enter rivers regularly, most of the 38 potential dam sites have never been scientifically surveyed for presence of marine-associated fishes, and no formal studies of fish movement within Gabon's freshwater ecosystems have been conducted. Because of those data gaps, it is difficult to predict how the proposed dams may affect riverine biodiversity or alter habitats critical to Gabon's economically important fish species.

Here, we present a rapid appraisal of dam impacts on Gabon's marine-associated fish fauna using MaxEnt modeling. This technique facilitates assessment of potential impacts on critical fish guilds where data are limited and helps identify dams that will impact biodiversity, fisheries, and local economies.

Methods

Distributional data

We compiled presence records for fresh- and brackish-water fishes of Gabon and Equatorial Guinea from three databases that provide data on expertly identified museum specimens (Global Biodiversity Information Facility (GBIF), FAUNAFRI, and Oregon State University's Specify database). We applied filters to exclude records with low geographic precision (less than two decimal points) and points outlying the hydrography dataset (>300 m). In total, we included 314 species and 6060 point occurrences.

We assigned each fish species inhabiting Gabon's freshwater to one of the seventeen habitat-use guilds from Welcomme et al. (2006). Each such guild included fish species that shared similar ecological niches, inhabited waters with similar physiochemical and hydrological properties, and were predicted to respond similarly to changes in river hydrographs and to modifications of riverine geomorphology, habitat structure, and ecological

function (Vadas and Orth 2001). Members of fifteen guilds were present in Gabon: amphidromous, brackish-water estuarine, catadromous, eupotamonic benthic, eupotamonic lithophilic, eupotamonic pelagophilic, eupotamonic phytophilic, eupotamonic riparian, freshwater estuarine, opportunistic marine, paleopotamonic, parapotamonic, plesiopotamonic, rhithronic-riffle, and semi-anadromous estuarine. Of these fifteen guilds present in Gabon's freshwaters, five included species with some reliance on marine or brackish ecosystems; these guilds were considered marine-associated and formed the focus of this study. Members of the opportunistic marine guild are primarily marine species that breed in the ocean and occasionally enter freshwater. The catadromous guild includes migratory species with freshwater growth and oceanic reproductive phases, while the semi-amphidromous estuarine guild includes species that enter fresh or brackish water to breed or to use the lower reaches of the river as a nursery. Species in the amphidromous guild enter freshwaters to feed, often opportunistically, and brackish-water estuarine guild members are euryhaline species that tolerate fresh- and saltwater and move freely between those habitats near river mouths. All told, thirty marine-associated species from these five guilds (Table 2) were included in the final model, with 135 unique occurrences at 47 surveying localities (Fig. 1).

Table 2. Ecological guilds and species included in the final model.

Guild	Species	Unique occurrences
Opportunistic marine	*Caranx hippos*	1
	Citharichthys stampflii	1
	Eucinostomus melanopterus	1
	Lutjanus goreensis	3
	Monodactylus sebae	5
	Polydactylus quadrifilis	13
	Pomadasys jubelini	7
	Pristis pristis	3
	Pseudotolithus elongatus	12
	Trachinotus teraia	2
Amphidromous	*Aplocheilichthys spilauchen*	16
	Awaous lateristriga	6
	Bostrychus africanus	1
	Carcharhinus leucas	2
	Ethmalosa fimbriata	1
Semi-anadromous estuarine	*Dormitator lebretonis*	1
	Eleotris daganensis	4
	Eleotris senegalensis	3
	Eleotris vittata	2
	Kribia kribensis	2
Brackish-water estuarine	*Laeviscutella dekimpei*	3
	Microphis aculeatus	1
	Microphis brachyurus	2
	Neochelon falcipinnis	19
	Parachelon grandisquamis	2
	Parasicydium bandama	1
	Periophthalmus barbarus	3
	Porogobius schlegelii	1
Catadromous	*Elops lacerta*	12
	Enneacampus ansorgii	5
Total		135

Environmental data

For a biologically meaningful characterization of the riverscape, we ran geoprocessing algorithms in ArcGIS Pro 2.6 to get local channel gradient, maximum gradient downstream, mean annual discharge, valley confinement, and distance to the ocean, based on a 12.5-m-resolution digital elevation model generated from an L-Band Synthetic Aperture Radar (ALOS PALSAR, Japan Aerospace Exploration Agency), and was radiometrically terrain-corrected (RTC, University of Alaska, Fairbanks, Alaska, USA). We computed zonal statistics of other potentially useful environmental predictors: land cover (CCI, ESA), tree canopy percent (USGS, University of Maryland, USA), erodibility, atmospheric temperature, and precipitation (WorldClim 2). We modeled two connectivity scenarios for Gabon's hydrological network: one based on barriers detected in the topographic relief data and existing dams (present connectivity), and a second scenario with proposed dams.

MaxEnt model

We used a MaxEnt approach for guild-level distribution modeling (Elith et al. 2011, Phillips et al. 2017). Guilds were initially grouped into lotic, lentic, eurytopic, marine-associated habitat types according to Welcomme et al. (2006). Parameters were set separately according to guild-specific traits and prevalence. Poorly performing guilds were set aside and parameters individually tuned. Using a Jenks natural breaks classification that detects natural classes in the distribution of the data, we ranked every reach in one of five categories of guild habitat

suitability including (1) zero, (2) low, (3) mid-low, (4) mid-high, and (5) high suitability (Fig. 2).

To assess habitat complementation between Gabon's marine and freshwater environments for species dependent on both, we trained our model to detect threshold relationships between the presence of marine-associated guilds and downstream gradients. The threshold-based model showed a very low likelihood of marine-associated guilds occurring upstream of reaches with more than 40% gradient which are likely to have waterfalls or steep changes in elevation that act as natural barriers for fish dispersal. Thus, we classified stream sections exceeding that threshold as disconnected from upstream movement. As none of the existing dams in Gabon are equipped with fish passages, we classified the

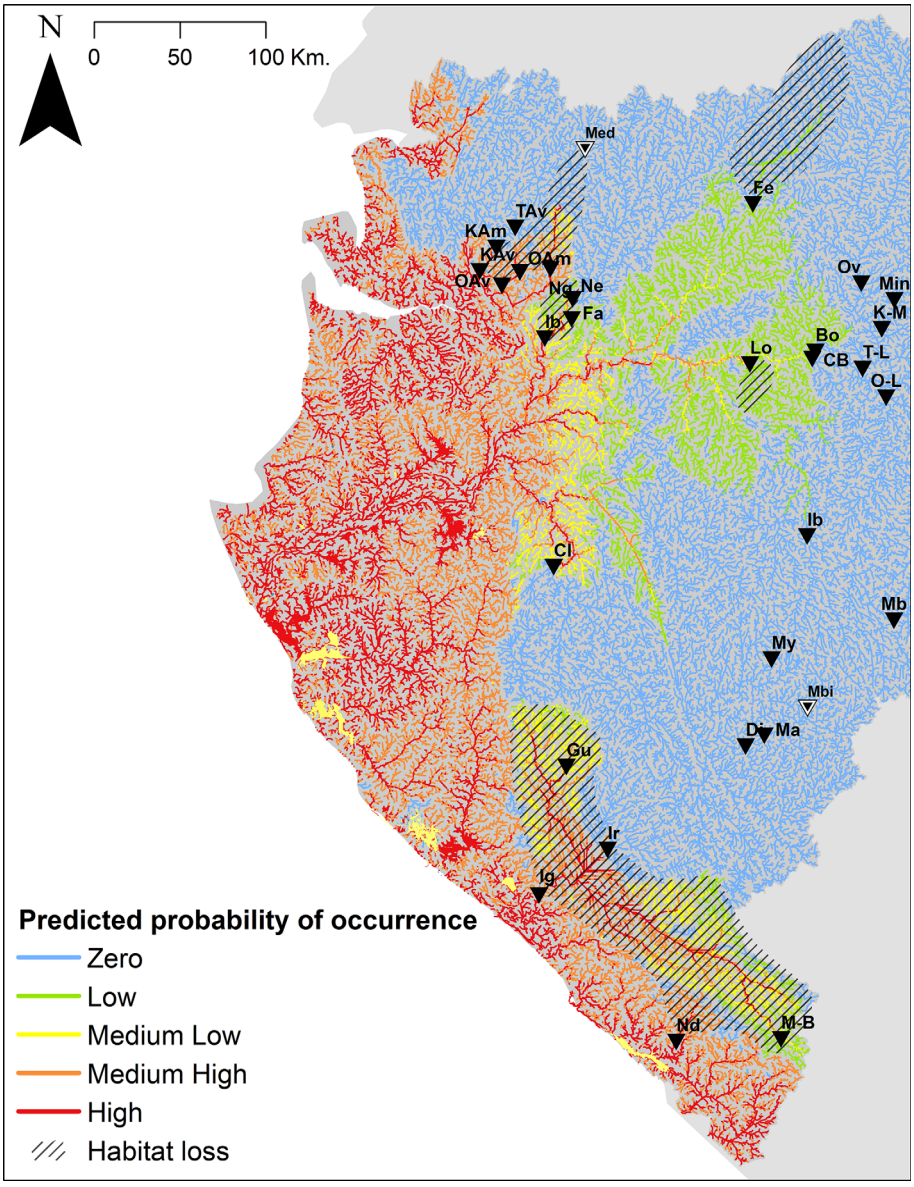

Fig. 2. Map of Gabon showing the predicted distribution of marine-associated fish guilds, and the potential habitat loss due to proposed hydropower development in Gabon. Dams coded as in Table 1.

few systems currently blocked by flow control structures as disconnected (e.g., on the Mbei and the Upper Ogooué).

For model optimization, we used R package MaxentVariableSelection. This package helps identify the most influential and uncorrelated environmental variables and uses an optimal regularization multiplier to avoid building overcomplex or overfitted models. This script varies parameters among stepwise MaxEnt runs and assesses performance with the area under the receiver operating characteristic (AUC) and the Akaike information criterion (AIC; Jueterbock et al. 2016). Final parameters were set by harmonizing models with highest AUC and lowest AIC values. During model optimization, mean annual atmospheric temperature was dropped from analysis due to collinearity with elevation ($r^2 = 0.95$), and land cover and tree cover percent were dropped due to their small contribution to predictions (<5%). Because fish surveys were biased toward Gabon's road system, we randomly selected 10,000 background samples (pseudoabsences) restricted to accessible reaches through main roads, existing sampling locations, and adjacent reaches.

Results

Our MaxEnt model performed very well (AUC = 0.93), and the most influential environmental variables for marine-associated fishes were distance to the ocean, mean annual discharge, and valley confinement. Marine-associated fish species had a high likelihood of traveling 400 km upstream into freshwaters and proposed dam development could result in loss of nearly 500 km of highly suitable marine-associated fish habitat (Fig. 2).

Our model predicted marine-associated fishes had a high likelihood of occurrence throughout coastal watersheds, including the Noya, Komo, Remboué, Nkomi, Rembo Ngové, Rembo Ndogo, and Louzibi, and had a high likelihood of occupying the mainstem Nyanga and its major tributaries (Fig. 2). We also predicted a high likelihood of marine-associated fishes occupying the entire lower Ogooué and mainstem Ogooué from its mouth to around Lopé, approximately 400 km upstream. In addition, we found high likelihood of occurrence in most Ogooué major tributaries including the Ngounie River to the Chutes de l'Imperatrice and the Abanga River to Nemguembani. Our model predicted that marine-associated fishes had low likelihood of occurring throughout the upper Ogooué River, upper Lolo River, and most of the Mvoung River drainage of the Ivindo River watershed. Large waterfalls (the Chutes de Booué, the Chutes de l'Imperatrice, and Nemguembani) might form natural biogeographical barriers on the Ogooué, Ngounie, and Abanga rivers, respectively, blocking upstream movement of marine-associated fishes. Most existing dams in Gabon were sited high in watersheds and thus are not expected to directly affect marine-associated fishes. The dam at Kinguele on the Mbei River is a notable exception as this dam blocked potential upstream movement of marine-associated fishes.

Marine-associated species had potential access (predicted probability of occurrence > 0.1) to 44,336 km of river, but if the 38 proposed hydropower dams were constructed, 17% or 7391 stream kilometers of previously accessible habitat would be lost (Table 3). Of those accessible

Table 3. Habitat suitability for marine-associated fishes in Gabon's freshwater ecosystems.

Scenario	Occurrence index	Kilometers	Percentage lost
Accessible habitat			
Present	0.00–0.1	78433.494	50.6764342
Future	0.00–0.1	38686.196	
Habitat loss		39747.298	
Usable habitat			
Present	0.1–0.43	44336.10	16.67
Future	0.1–0.43	36944.30	
Habitat loss		7391.80	
Moderately to highly suitable habitat			
Present	0.44–0.59	22450.92	5.13
Future	0.44–0.59	21298.27	
Habitat loss		1152.66	
Highly suitable habitat			
Present	>0.6	6522.02	7.15
Future	>0.6	6055.73	
Habitat loss		466.29	

Notes: Scenario refers to level of dam construction with existing and 39 proposed dams. Occurrence index derived from MaxEnt model. Accessible habitats have an occurrence index of 0.00–0.10, usable habitats 0.11–0.43, moderately to highly suitable habitats 0.44–0.60, and highly suitable habitats have an occurrence index > 0.61.

areas, 6522 stream kilometers are considered highly suitable (predicted probability of occurrence > 0.6), and proposed dam development may result in a loss of 7% of highly suitable habitats or 466 stream kilometers. These losses were largest on the Nyanga, Ogooué, Mvoung, Lolo, Komo, and Okano rivers (Fig. 2). The losses are most visible in the Nyanga drainage, which is currently undammed in Gabon and has 679 km of highly suitable habitats. If the proposed dam at Igotchi were constructed, 392 km (or 57.7%) of highly suitable habitats would be lost.

Discussion

Gabon has some of the world's most pristine unimpeded river systems and high freshwater biodiversity. Many of Gabon's most culturally and economically important fish species move between marine or brackish ecosystems and freshwaters and rely on free-flowing rivers. Inaccessibility and lack of scientific effort have limited the understanding of the distribution patterns of freshwater fishes in Gabon's freshwater ecosystems. We demonstrate an original application of MaxEnt to predict the distribution of marine-associated fishes in Gabon's freshwaters.

With this model, we are able to examine whether and where proposed dams can block marine-associated fish passage. The MaxEnt model suggests strongly that proposed dam construction in Gabon will block access to freshwater habitat used by those species. Members of the five marine-associated fish guilds in Gabon have a high likelihood of occupying every coastal watershed, and thus, proposed dams close to the coast will likely have the most deleterious effects on those 30 species of marine-associated fishes. Proposed dams on the Nyanga, the Komo, the Ogooué downstream of the Chutes de Booué, and on the Ngounie downstream of the Chutes de l'Imperatrice would result directly in habitat loss for marine-associated fishes by blocking access to highly suitable habitat. Dam construction upstream of these sites may also threaten marine fish populations indirectly through changes in flow, sedimentation, and fragmentation (Agostinho et al. 2004, Caudill et al. 2007, Anderson et al. 2018) and similarly threaten purely freshwater fish species and fisheries (Cutler et al., *unpublished manuscript*).

Habitat suitable for marine-associated guilds also included the lower portion of Gabon's largest river (the Ogooué) as far inland as approximately 400 km from the coast. This finding corroborates reports from local fishers around Lopé who report capturing snappers and other marine-associated species and confirms that marine fishes can access freshwater habitat quite distant from the coastline. Even dams located within the interior apparently have the potential to restrict the movement and habitat available to the species upon which fisheries depend.

In summary, marine-associated fishes are culturally and economically important in Gabon and may see their available habitat reduced by planned dam construction. Our model predicts marine-associated fishes to occupy all coastal river systems in Gabon and suggests their ability to travel long distances (>400 km) upstream to breed, feed, or rear young. Proposed dams within regions of high suitability will block the movement of marine-associated fishes and threaten these species with habitat loss and fragmentation. In time, such habitat alterations could reduce fish populations, impact local fisheries, and cause local extinctions.

Before any of the proposed dams are constructed, we recommend conducting baseline surveys of the fishes present at the dam site and urge that dams not be constructed in areas that may affect dispersion of marine-associated fishes. We also recommend that existing dams within regions of high suitability for marine-associated species, particularly the dam at Kinguele on the Mbei, be outfitted with fish passages appropriate to migratory species in the area (Silva et al. 2018) or water management strategies to ensure minimum environmental flows that mimic natural conditions (Murphy et al. 2019). These actions should help to minimize negative impacts of dam development on fish biodiversity and fisheries production (Ferguson et al. 2011).

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