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Diurnal feeding behavior of the American Eel *Anguilla rostrata*

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ABSTRACT

Despite potential to structure ecosystem food webs through top-down effects, the trophic interactions of the American Eel *Anguilla rostrata* remain largely understudied. All previous research on the trophic ecology of American Eel in inland aquatic ecosystems has been conducted in temperate continental regions of the species' range. These studies have led to a paradigm that American Eel is a nocturnally active benthic predator, which most commonly consumes benthic invertebrates. Tropical island streams and rivers have habitats and communities that are distinct from temperate counterparts, but comprise a large portion of the adult habitat in the American Eel's range. We documented a previously undescribed diurnal feeding behavior by American Eel in a Caribbean river and demonstrate that this behavior, and a shift toward more frequent daytime feeding, is linked to periodic mass migrations of postlarvae of amphidromous fish taxa, including the Sicydiine goby *Sicydium* spp. Our findings indicate that periodic mass migrations of amphidromous postlarvae could function as a potentially important food source for American Eel in tropical regions of its distribution, despite the intermittence of availability. Furthermore, this suggests that the American Eel plays an important role in the structure of tropical lotic food webs through top-down effects that are potentially augmented by instream barriers.

The American Eel *Anguilla rostrata* has the potential to broadly and profoundly affect both marine and freshwater aquatic food webs through its role as a predator. American Eel are native to the Western North Atlantic basin from Greenland to Venezuela, including the Caribbean and Gulf of Mexico drainages (Benchetrit and McCleave, 2016). In lotic and lentic freshwaters, estuaries, and marine coastal environments, American Eel can become a large-bodied predator and can attain high population biomasses, which indicates strong potential to influence community structure through top-down trophic interactions (Ogden, 1970; Facey and Van Den Avyle, 1987; Lookabaugh and Angermeier, 1992). Despite this potential to disproportionately influence food webs, the current understanding of American Eel trophic ecology is limited in both number of observations and spatial extent, particularly in freshwater riverine habitats. Therefore, new information that describes the feeding behavior and diet of American Eel is crucial to understanding its functional role in diverse and complex food webs.

Studies that have quantified the American Eel diet in streams and rivers have indicated that benthic macroinvertebrates are a primary food source for small- and medium-sized individuals, with ontogenetic shifts toward piscivory and larger macroinvertebrates (e.g., crayfishes) in larger individuals (Ogden, 1970; Lookabaugh and Angermeier, 1992). Nocturnal foraging behavior and general activity (e.g., movement; Helfman et al., 1983) have been observed (Helfman, 1986; Sorensen et al., 1986) and applied to develop a widely accepted, generalized description of American Eel as a nocturnally active, generalist benthic predator, that most frequently consumes macroinvertebrates (Shepard, 2015). However, the aforementioned studies of behavior and diet encompass a relatively small spatial extent (i.e., United States, Canada) of the American Eel distribution and habitats.

No studies have been previously published on American Eel feeding behavior and trophic ecology in the southern portion of its range, which includes the entire Caribbean basin. Important habitat and community composition differences in tropical portions of the American Eel range could influence feeding behavior and subsequent trophic interactions. One profound difference between temperate continental and tropical island lotic ecosystems is the prevalence of amphidromous taxa including fishes, shrimps (Caridea), and snails (Gastropoda), which are dominant components of Caribbean stream ecosystems (Smith et al., 2003). For instance, the catadromous American Eel is the only non-amphidromous, native stream fish in Puerto Rico (Kwak et al., 2016). Moreover, amphidromous gobioids, undergo synchronous, pulsed, migrations from the ocean into rivers as postlarvae, which are frequently

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accompanied by migrations of postlarval shrimps (Winemiller and Ponwith, 1998; Keith and Lord, 2011; Engman, 2017; Engman et al., 2017). These mass migrations of diverse groups of larval and juvenile organisms may represent a valuable food source for American Eel in tropical portions of its distribution. Therefore, observations of American Eel feeding behavior and quantification of its diet during pulsed migrations of amphidromous fishes and other aquatic taxa are crucial to understanding American Eel trophic ecology.

Our goal was to describe the feeding behavior and quantify the diet of American Eel in the lower reaches of the Río Grande de Arecibo, Puerto Rico. The Río Grande de Arecibo headwaters rise in the Cordillera Central Mountain Range, the river flows north through the Karst geologic region, and meets the Atlantic Ocean at 18.473^0 N, 66.711^0 W. The mouth of the Río Grande de Arecibo is notable as a site of monthly mass-recruitment episodes (i.e., migrations from marine to freshwater lotic habitat) of amphidromous fish postlarvae that occur over several days of the last quarter moon phase during the wet season (i.e., June–January; Engman et al., 2017). Sirajo Goby (*Sicydium* spp.) and River Goby (*Awaous banana*) postlarvae are commonly abundant during mass-recruitment episodes but other gobioids and amphidromous shrimps also migrate into the river during these times (Engman, 2017). Moreover, gobioid postlarvae—colloquially referred to as cetí—are harvested in an artisanal fishery in Puerto Rico, and the Río Grande de Arecibo is considered one of the most culturally and economically significant rivers on the island for the postlarvae fishery (Erdman, 1961; Engman, 2017). Postlarvae that escape the fishery at the river mouth encounter the first impediment to their upstream migration toward adult habitats at the Cambalache Dam (18.456^0 N, 66.704^0 W; Cooney and Kwak, 2013). The Cambalache Dam is a low-head dam, built of local Karst limestone, and is located 2.6 km upstream of the Río Grande de Arecibo mouth. The dam is approximately 4.0 m high, 43.9 m wide, and 11.4 m long. The dam allows flow through and over natural boulders, however, construction has created a small cascade with a deep pool below the dam (Fig. 1). Adult and post-larval Sirajo Goby, like many other Sicydiine gobies, can ascend waterfalls using suction-cup-like, fused, pelvic fins (Maie et al., 2012). In the Río Grande de Arecibo, postlarval Sirajo Goby have been repeatedly observed climbing the face of the Cambalache Dam 24 to 48 h after the detection of the initiation of a mass-recruitment episode (hereafter referred to as a postlarvae run) at the river mouth (Engman, 2017).

American Eel diets were monitored over a nine-day period in July 2015 to quantify the contribution of pulsed, amphidromous postlarvae migrations to diurnal feeding. The sampling period included six days before a postlarvae migration event (July 3–8) and during a postlarvae migration event (July 9–12; hereafter referred to as before the run and during the run periods). We captured American Eel by daytime (between 0720 and 1400) pulsed-DC boat electrofishing at locations from 1.6 km upstream of the river mouth to the large pool below the Cambalache Dam located 2.6 km upstream of the mouth. We immediately euthanized captured individuals with an overdose of buffered MS-222 and extracted their stomach contents by foregut excision (Garvey and Chipps, 2012). After extraction, all diet items were immediately preserved in a 10% buffered formalin solution. Preserved diet samples were examined for the presence of any prey items, and the occurrence of gobioid (i.e., all gobies and eleotrids) and Sirajo Goby postlarvae was noted for all stomachs containing prey.

We estimated the percentage of stomachs that contained any prey items (number of eels with prey in stomach/total number eels examined × 100) as an indicator of feeding frequency (Arrington et al., 2002). We also calculated the percent frequency of occurrence (%*F*) of Sirajo Goby and all gobioid postlarvae as:

$$\%F = \frac{J_i}{P} \times 100$$

where J_i is the number of eels containing prey item i, and P is the number of eels with prey in their stomach. We tested the hypothesis that the relative proportions of American Eel with prey, and with empty stomachs was independent of the run status (before run versus during run) with a two-tailed Fisher's exact test on a 2 × 2 contingency table with the statistical package R 3.3.1 (R Development Core Team, 2016).

We examined the excised stomach contents of 32 American Eel (16 before run, 16 during run). Of these, one (6.3%) contained prey before the run and seven (43.8%) contained prey during the run. A Fisher's exact test indicated that the observed proportion of American Eel with prey was not independent of the run status ($P = 0.02$), revealing that diurnal feeding frequency in American Eel increased significantly during the postlarvae run. The observed increase in feeding frequency was confirmed to be related to consumption of postlarval gobioids (71.4% frequency of occurrence in diets), which were predominately Sirajo Goby (57.1%).

In addition to diet quantification in 2015, we directly observed American Eel feeding on Sirajo Goby postlarvae during synchronous ascent over the Cambalache Dam throughout postlarvae runs over three consecutive years in July. Specifically, observations were made on 3

Fig. 1. Cambalache Dam, Río Grande de Arecibo, Puerto Rico (18.456^0 N, 66.704^0 W). Sirajo Goby postlarvae are often observed ascending this impediment to upstream migration 24–48 h after ingress to the river mouth from the Atlantic Ocean. In inset: American Eel *Anguilla rostrata* feeding on Sirajo Goby postlarvae during dam ascent.

July 2013; 20 July 2014; and 11 July 2015; all observations were between 1000 and 1630 h, AST. On 20 July 2014 and 11 July 2015, the feeding behavior was documented with video (S1). American Eel were observed in small pools within the dam and made repeated feeding strikes at Sirajo Goby postlarvae that were ascending wetted rocks above the surface of the water. During feeding strikes, the American Eel's head and often large portions of their bodies were raised out of the water. We documented two distinct feeding strikes by one individual on 11 July 2015 and multiple feeding strikes by a separate individual on 20 July 2014 (S1).

Our results demonstrate that the presence of a periodically abundant food resource (i.e., amphidromous fish postlarvae) is associated with shifts in the diel feeding schedule and behavior of American Eel, an important riverine predator. Prior to the postlarval fish run, nearly all the diurnal samples of American Eel diet were empty, which aligns with the prevailing paradigm of American Eel as a nocturnally active predator. However, during the postlarval run, American Eel was observed using a previously undescribed behavior to consume migrating postlarvae of Sirajo Goby during the daytime. Daytime feeding rates increased during the run, as nearly half of the American Eel diets that were sampled contained prey in this time period and almost all had empty stomachs before the run. The pulsed migration of postlarval gobies appears to have increased daytime feeding in American Eel and was confirmed by high frequencies of occurrence of postlarval Sirajo Goby and other gobioid postlarvae. Thus, migrating amphidromous postlarval fishes appear to be an important, periodically available food resource for American Eel. American Eel likely consume amphidromous postlarvae in lotic and estuarine ecosystems throughout large portions of its native range, because mass migrations of postlarval gobioids are known to occur throughout the Caribbean region including islands and continental drainages (Kwak et al., 2016). Furthermore, anguillid eels co-occur with amphidromous species in insular streams throughout the tropics and subtropics (Smith et al., 2003), which suggests similar trophic interactions could occur on a global scale.

Predation by American Eel may interact with the effects of dams and other instream barriers to influence the abundance, distribution, and composition of amphidromous goby species. Prior research has highlighted the role that dams, other anthropogenic instream barriers, and natural waterfalls can have in structuring stream fish assemblages by selectively limiting and extirpating native migratory species from upstream reaches (March et al., 2003; Cooney and Kwak, 2013). American Eel is often found at its highest density directly below barriers (Machut et al., 2007), and dam tailraces have been identified as areas of concentrated predation on the young stages of other migratory fish species (e.g., salmonids; Ward et al., 1995). Sirajo Goby are able to surpass barriers tall enough to exclude all other native fish species in Puerto Rico, and their superior climbing ability provides them access to predator-free habitats above waterfalls. We observed postlarvae migrating the Cambalache Dam in large numbers, so this small dam is not a direct impediment to Sirajo Goby migrations. However, this and other low-head dams may slow migration progress and concentrate predation on migrating postlarvae, thus increasing the effects of American Eel predation on amphidromous populations.

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