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BIORESUSPENSION BEHAVIORS OF THE GOBIID, *VALENCIENNEA PUELLARIS,* AND THE BIOGENIC SEDIMENTARY STRUCTURES IT PRODUCES

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ABSTRACT: **Biologically mediated fabrics are disturbed sediment by organisms that resemble primary physical structures. In this aquaria-based study, the sand-sifting goby, *Valenciennea puellaris*, produced biogenic sedimentary structures resembling planar lamina and ripple cross lamina with grain sizes ranging from fine sand to gravel. *Valenciennea puellaris* moved and re-deposited fine- and coarse sand and gravel used in this study, but dug only in fine- to coarse sand. Gravel-sized particles were too large to pass through its gills and therefore the goby moved them individually. Through the bioresuspension behaviors of feeding, digging, and resting, the *V. puellaris* produces *Piscichnus*-like craters and moves about nine mouthfuls of sediment a minute, i.e., 0.18 cm^3. The biogenic fabrics produced by *V. puellaris* in this study are similar to primary sedimentary fabrics produced by hydrologic flow. Similar behaviors and feeding styles are widespread and found in larger fish and marine mammals. While *V. puellaris* has only been around since the Eocene, burrowing Actinopterygians date back to 400 Ma, suggesting that similar biogenic sedimentary structures may have a long history in the geological record.**

INTRODUCTION

Actinopterygians (ray-finned) fish burrowing is well documented (Parker 1892; Kerr 1898; Rao 1939; Dôtu and Mito 1955; Colin 1973; Rice and Johnstone 1972; Clayton and Vaughan 1986; Pelster et al. 1988; Atkinson and Froglia 2000; Itani and Uchino 2003; De Schepper et al. 2007; Nico et al. 2009; Dinh et al. 2014). In addition to excavating burrows, fish disturb sediment by feeding and digging (Atkinson and Taylor 1991). The resulting reworked sediment commonly resembles primary physical sedimentary structures rather than burrows or bioturbation (Schäfer 1962; Aller and Yingst 1978; Graf and Rosenburg 1997; McIlroy 2010). These biodepositional sedimentary fabrics (Larson and Rhoads 1983) may be subtle and difficult to recognize.

Biodepositional sedimentary fabrics include cryptobioturbation, burrow mottling, biostratification, biowinnowing, biodeformation and bioresuspension (e.g., Schäfer 1962; Rhoads 1963, 1974; Howard and Frey 1975; Wetzel 1983; Bromley 1990; Graf and Rosenberg 1997; Meysman et al. 2005; Pemberton et al. 2008; Table 1). Most of these fabrics are emplaced by the activities of infaunal invertebrates (Table 1). Biologically mediated resuspension (bioresuspension), the process by which organisms (bivalves, decapod crustaceans, fish) resuspend sediment in the water column above the sediment-water interface (Rhoads 1963, 1974; Graf and Rosenberg 1997) is the focus of this study. Although it is an important aspect of sedimentation and sediment reworking, few investigations have quantitatively determined bioresuspension-induced sediment fluxes across the sediment-water interface. Bender and Davis (1984) investigated the surface and subsurface deposit-feeding bivalve *Yoldia limatula* (Say 1831) and observed that deposit-feeding *Y. limatulu* expelled 10 to 200 times its body weight in sediment /solid waste daily. McIlroy (2010) examined the shrimp, *Alpheus bellulus* (Miya and Miyake 1969), in poorly sorted, coarse-grain sand, and observed that this shrimp was able to produce structures closely resembling ripple cross-lamination.

Biologically mediated deposition studies on fish are limited to remotely operated vehicles or mounted camera-based studies that help understand fish bioturbation behaviors and rates of bioturbation but lack understanding on the resulting sedimentary fabrics (Sasko et al. 2006; Yahel et al. 2002, 2008; Katz et al. 2009, 2012, 2016). Fish-induced sediment resuspension is regarded as an important regulator of phytoplankton dynamics in shallow, hypereutrophic lakes; fish introduce nutrients from the sediments to the water column, and that influx results in increased algal biomass and dominance by small, r-selected taxa (Havens 1991). It is uncertain how the fish-associated biogenic sedimentary structures affect the texture of the deposited sediments.

Gobiids are well-known sediment reworkers (Bromley 1990; Atkinson and Taylor 1991). The genera *Amblygobius*, *Coryphopterus*, *Pholidichthys*, *Rhinogobiops*, and *Valenciennea* are commonly known as substrate-sifting gobies in the hobby aquarium (Michael 1999). These fish have two distinct behaviors that result in sediment bioresuspension: feeding and ecosystem engineering.

Previous studies (Atkinson and Taylor 1991; Takegaki and Nakazono 1999; Clark et al. 2000) on gobiid biologically mediated deposition focused on bioturbation behaviors rather than the resulting sedimentary fabrics and did not quantify bioturbation rates. Data on sediment bioturbation rates are sparse, although limited observations have been provided for fish that deposit-feed within their burrows and behavioral observations on feeding rates (Atkinson and Taylor 1991; Takegaki and Nakazono 1999; Clark et al. 2000).

This study examines the sedimentary fabrics produced by bioresuspension behaviors of the gobiid *Valenciennea puellaris* (Tomiyama and Ab-E 1956) on substrate of various grain sizes in the absence of hydraulic flow. We examine and describe biodepostional fabrics produced by gobiid bioresuspension and quantify the amount of sediment reworked by individual *V. puellaris*.

MATERIAL AND METHODS

Subject Taxon.—The orange-spotted sleeper-goby *Valenciennea puellaris* (Tomiyama 1956) is a tropical goby that resides within lagoon

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TABLE 1.—*Biogenic sedimentary fabrics and processes.*

Fabric	Process	Taxa
Cryptobioturbation	the disruption of physical sedimentary textures by the action of interstitial meiofauna	Blood worms, Amphipods
Burrow mottling	complete destruction of physical sedimentary fabric by the mixing effects of burrowing	Bivalves, decapod crustaceans
Biostratification	biological formation of horizontal sedimentary laminae	Bivalves, worms
Biowinnowing	selective deposit-feeding on specific grain constituents at depth in the sediment	Blood worms
Biodeformation	liquefaction caused by biological pumping of water into the near-burrow environment	Bivalves, decapod crustaceans
Bioresuspension	resuspend sediment in the water column above the sediment-water interface allowing redeposition	Bivalves, decapod crustaceans, fish, whales

and outer reef habitats with sandy substrates (Hoese and Larson 1994). *Valenciennea puellaris* occupies water depths ranging from 2 to 84 m and has an Indo-Pacific (Red Sea to Samoa, north to southern Japan, south to the Great Barrier Reef and New Caledonia) geographic distribution of (Fricke et al. 2011). *Valenciennea puellaris* feeds on infauna by processing the sediment in which the invertebrates dwell. Copepods form the main part of their diet (~ 60%), with amphipods, ostracods, nematodes, and shelled protozoa (foraminifera) also being common prey (Michael 1999).

Valenciennea puellaris was selected for this study due to its small size, availability through the aquarium industry, and its diverse behaviors. The ability to compare behavior observed in the lab with aquarium enthusiast's videos posted online also proved beneficial. Four *V. puellaris* were utilized in this study, with two gobiids participating in the grain-size experiments. To validate observations of gobiid sediment movement, 10 YouTube videos from home aquaria were used to help understand rates of sediment movement. These videos are recorded at a perspective that allows constant footage of a *V. puellaris* behavior.

Several experiments were conducted including observing the feeding behavior of the fish and recording the sedimentary fabrics produced by this activity. Sediment fabrics produced by the goby were observed along the margins of the aquarium. Observations of fish behavior and sedimentary fabrics were conducted in our display tank and experimental setups described below. Photographs and videos were taken of the gobies' behaviors. Agisoft PhotoScan® was used to process the images.

Grain Size Experiment.—An isolated tank was used in the experiments to produce a system with minimal currents. The tank was a $21 \times 26 \times 41$ cm, 22.3 l aquarium. For each experiment, an 8 cm-thick layer of sediment was placed in the aquarium. Experiments were run with fine sand (25–250 μm), coarse sand (0.5–1 mm), and very fine to medium gravel (2–16 mm). The sediment was collected from the intertidal zone of Craig Bay, British Columbia and sieved at the University of Alberta. To add contrast to the sediment the fine- and coarse sand were interlayered with fine black magnetite sand. Water in the experiment was kept to marine conditions using Red Sea Coral Pro Salt®. The seawater was kept at 20°C and oxygenated using a small air pump. Although the pump generated a weak rotational current, it had negligible effect on sediment movement.

Sediment Transport Experiment.—To observe and document sediment transport volumes a separate tank ($30.5 \times 15 \times 20.5$ cm) was used. Sediment in this tank consisted of #13 grade abrasive glass bead (88.9–43.18 μm): the beads were used to keep a constant density, which was desirable for our mass-to-volume assessments. A small mylar sheet was used to collect sediment. The sheet was placed outside the gobiid's burrow and removed after the gobiid deposited one mouthful of sediment on the sheet. Each sample was then flushed with deionized water to remove any salt from the sample. The samples where then dried and weighted. Volume for each mouthful of sediment was calculated using the equation volume = mass/density, with an internal sediment porosity of 40%. The porosity of 40% is used based on modern sandy offshore environments where the average porosity of sand was determined to be 37.7%, 42.3%, and 46.3% for packed, natural (*in situ*), and loose packing conditions, respectively (Curry et al. 2004). The density of the glass bead used for this part of the study is 2.65 g/cm^3.

RESULTS

Valenciennea puellaris used in these experiments were found to be prolific ecosystem engineers, constantly moving sediment. Three distinct bioresuspension behaviors were differentiated: feeding, digging, and resting. The first two behaviors (feeding and burrowing behaviors) involved grabbing mouthfuls of sand, where the resting behavior involved full body movement.

Feeding Behaviors.—*Valenciennea puellaris* feeds on infaunal invertebrates found in the sediment. To feed, the fish typically inserts its head up to 3 cm into the sediment and secures a mouthful of sand (Figs. 1, 2A–2D). As the fish withdraws from the substrate with the mouthful of sediment, it sifts the sediment with its mouth to isolate food from the sediment. Sediment is expulsed through the gills while food is retained within its mouth. While sifting, the fish rests on, or just above, the substrate, and the resuspended sediment settles to the substrate surface proximal to the feeding location. Once all of the sand has been expelled from its mouth, the fish repeats the process.

The gobiids used in this experiment processed several mouthfuls of sediment per minute, producing light currents in the process. Processed sediment settled back upon the substrate surface, draping feeding pits and undisturbed substrate. As the fish obtains a mouthful of sediment from below the substrate surface, it transfers significant amounts of sediment from several centimeters below the sediment-water interface to the surface. Sediment movement rates are presented below.

Burrowing Behavior.— *Valenciennea puellaris* digs burrows, excavating sediment from underneath rocks by grabbing mouthfuls of sediment, transferring it above the sediment-water interface and expulsing the sediment (Fig. 2A–2C, 2E). The entrance to the burrow is commonly lined with small pieces of rubble or shells, and sand is piled over the top of the rocks or shells that were used as the roof (Hoese and Larson 1994). In some instances a shell is used as a door to the burrow entrance. This 'door' is moved to the side of the burrow, and subsequently pulled back into place when they enter. *Valenciennea strigata* (Broussonet 1782) uses clumps of calcareous alga for this purpose (Hoese and Larson 1994).

Valenciennea puellaris digs in a method similar to its feeding behavior. The fish buries its head in the sand bed and retracts with a mouthful of sediment. During burrowing activity, the sediment is not passed through the gills but rather is expelled out of its mouth. The *V. puellaris* expels the sediment either at the place of digging or travels across its territory and dumps the sediment at an alternative location. The sediment is most often ejected from the gobiids mouth at a height of ~ 1–2 cm above the sediment water interface but occasionally the gobiid will swim well above the sediment-water interface (~ 20 cm) and drop the sediment. The sediment

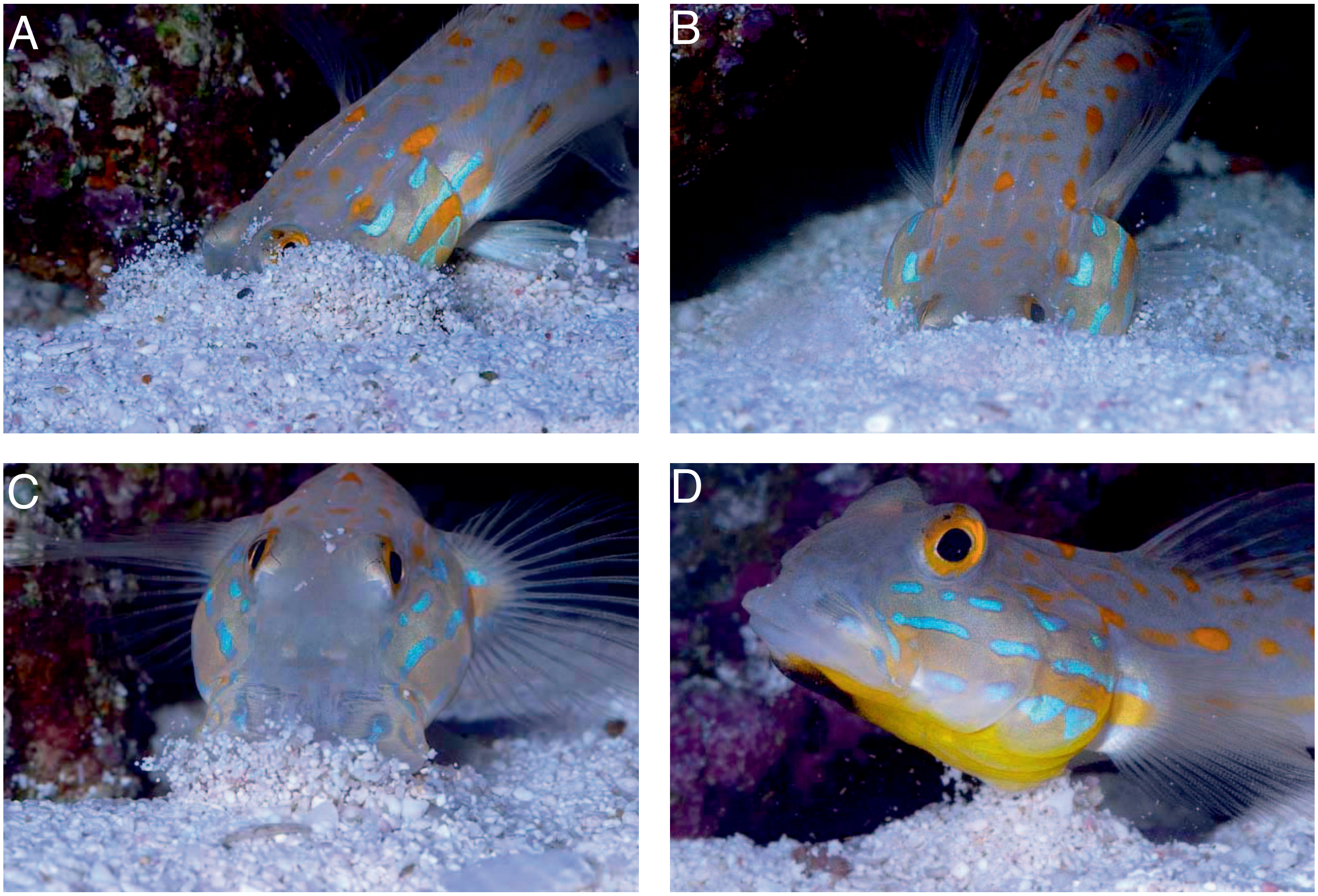

FIG. 1.—Gobiid feeding process. **A**, **B**) The gobiid *Valenciennea puellaris* buries its mouth up to 3 cm deep into the sand bed and engulfs a mouthful of sand. **C**) As the fish retracts from the sand bed with a mouthful of sand, it begins the process of sifting the sand in search of food. **D**) Hovering on or just above the substrate, the fish expels sand sifted and stripped of invertebrates. After the sand is passed through its gills, the sediment falls to the sediment-water interface under conditions set by the *V. puellaris*. Photos courtesy of Greg Rothschild of Mother Nature's Creations.

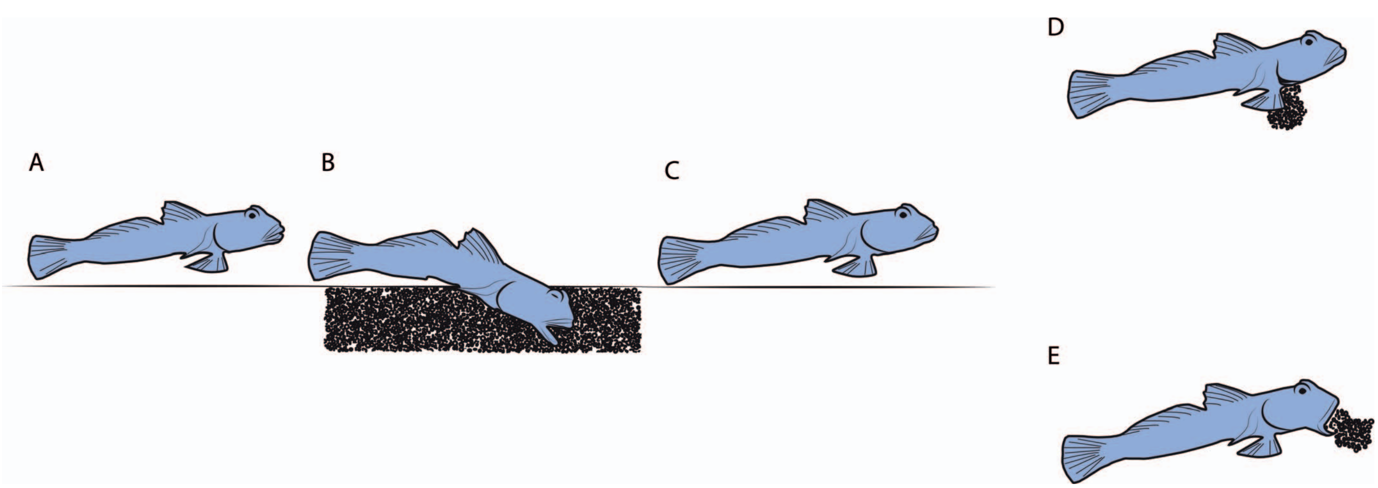

FIG. 2.—Schematic diagram of feeding and digging of the gobiid *Valenciennea puellaris*. **A**) The gobiid at rest. **B**) The gobiid burying its head and engulfs a mouthful of sand. **C**) The gobiid in motion to a new location. **D**) The gobiid collecting food and passing sediment through its gills. **F**) The gobiid ejecting sediment out its mouth

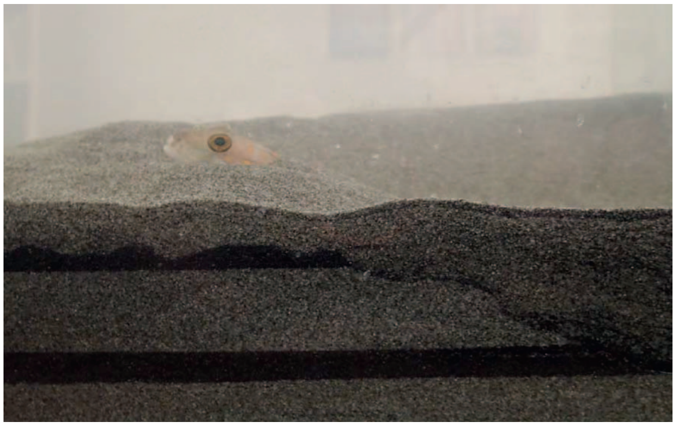

FIG. 3.—*Valenciennea puellaris* at rest. To bury itself in sediment, *V. puellaris* uses its caudal fin and posterior of its body to thrash side to side until it resuspends sediment that is then deposited around its body until only its eyes or head are above the sediment.

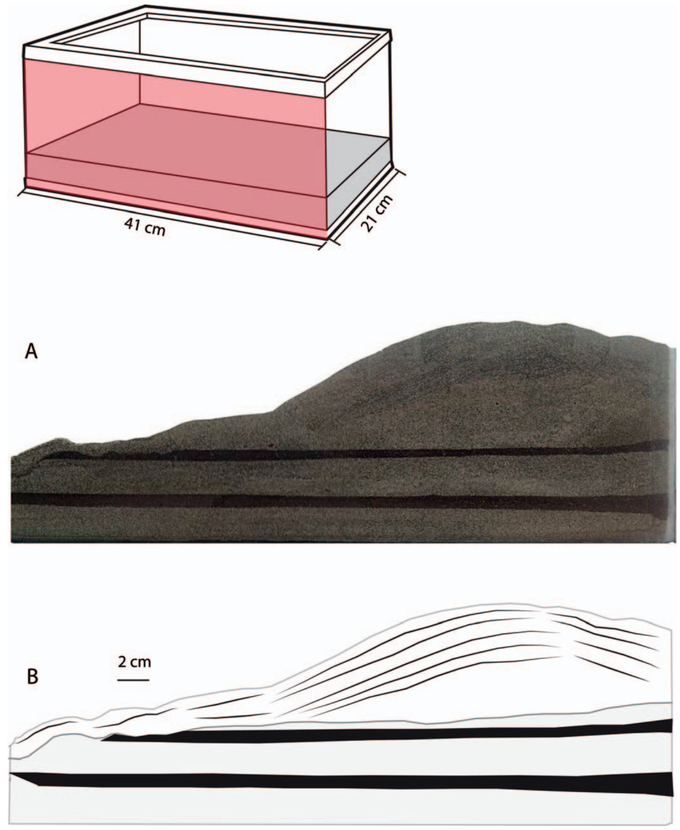

FIG. 4.—Long side of experimental tank. **A**) Orthophoto of a long side of the experimental fine sand aquarium sediment bed after 1 day of exposure to *Valenciennea puellaris*. The tan material is fine-grained quartz and black material fine-grained magnetite to help distinguish fabrics. **B**) Sketched representation of the orthophoto.

resuspended by the gobiid is then deposited under the conditions set by the gobiid.

Resting Behavior.— The resting behavior of *Valenciennea puellaris* is dramatically different from its other biodepostional behaviors. *Valenciennea puellaris* buries its body in the sand, leaving its eyes or head above the sediment (Fig. 3). To accomplish this, the fish swipes its tail and lower body back and forth, both resuspending the sediment and pushing it to the side with its body. These behaviors produce cross laminae that are similar to unidirectional ripple laminae in cross section and sinuous ripples in plan view. Review of laminae and ripples can be found in Campbell 1966 and Newton 1968.

Gobiid-Produced Sedimentary Fabrics.—*Valenciennea puellaris* were able to bioturbate all grain sizes used in the study (fine- and coarse sand and gravel). Through bioturbation activities the gobiid produced sedimentary fabrics that, depending on the cross-sectional view, bear similarities to primary physical sedimentary structures. Sediment structures produced by gobies were observed along the aquaria walls and include planar to parallel cross laminae, planar to discontinuous cross laminae and apparent ripple cross-laminae (Figs. 4, 5). Although *V. puellaris* biodepostional fabrics resemble hydrodynamically produced sedimentary structures, the goby is able to produce these features in the absence of external water flow.

The gobies resuspend sediment by intruding, biting, moving, and swimming with the sediment, and extruding it through its gills or mouth. Sediment is passively sorted when it passes through the gills and by the different settling velocities of the differently sized grains. The individual laminae are produced by a single gobiid expulsion of sediment or an amalgamation of expelling events. The laminae appear to be normally graded, likely due to the effects of gravity. Grain flows on the lee side of the asymmetric bedding structure (ripple) enhances the cross lamination. The ripples are 1–3 cm in height and include catenary, linguoid, to lunate features. In both the laminae and cross-laminae structures, grain sorting appears to be observed within the bed.

In all experiments the fish disturbed the sediment to a depth of approximately 2 cm although in places they excavated to a maximum depth of 6 cm. This large amount of bioturbation is likely magnified because of the confines of the aquarium. This magnification of results may also be present in the scale of the sedimentary fabrics found at walls of the aquarium.

In the experiments that used fine- and coarse sand substrates, the goby displayed feeding, digging, and resting behaviors. In gravel substrates, *V. puellaris* exhibited only digging behavior, which they did by picking up individual gravel clasts and moving them across the tank. Similar to the surface excavations of *Alpheus bellulus* conducted by McIlroy (2010), *V. puellaris* produces crater-like circular depressions in gravel with loosely consolidated cavities, rather than those maintained by a burrow wall. The resulting crater-like structure resembles a *Piscichnus*-like trace fossil. Foresets were produced as the gobiid dispels sediment from its mouth. The direction of the slope in the foresets is determined by the local topography. Commonly cross-lamina and foresets generated by gobies build up to the angle of repose.

The *Piscichnus*-like pit produced in these experiments has two distinct sizes. The smaller size is produced by a single burrowing/feeding event (Fig. 6) and range between 0.5 to 1 cm in diameter and are up to 0.3 cm deep. The second, larger size is more than an order of magnitude larger (up to 20 cm in diameter and up to 2 cm deep) and is produced by multiple feeding and digging events (Fig. 6). Both single and multiple event pits are circular to oval with gently tapering sides to a smooth base with slopes at angles of 10–25° relative to the substrate surface. The pits produced during one feeding session rarely overlap, with approximately 1 to 2 cm spacing between individual feeding pits. The smaller pits are highly distinctive features that together produce a horizon that separates the unbioturbated sediment below from settled, biogenically resuspended sediment above. In cross-section the pits produce a very irregular surface at the substrate-water interface.

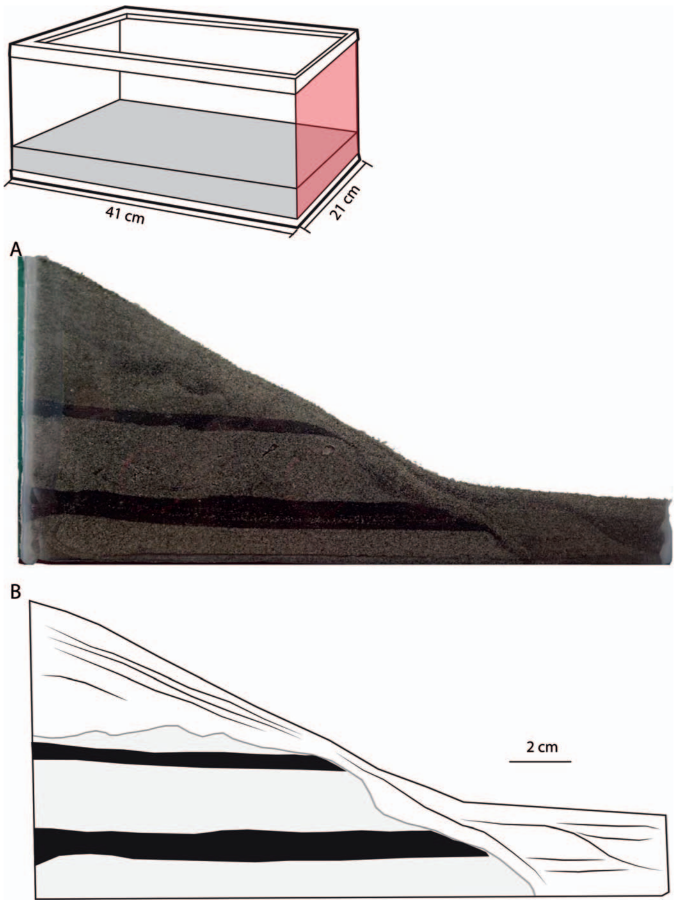

FIG. 5.—Short side of experimental tank. **A**) Experimental fine sand aquarium sediment bed after one day of exposure to *Valenciennea puellaris*. The tan material is fine-grained quartz and black material fine-grained magnetite to help distinguish fabrics. **B**) Sketched representation of the orthophoto.

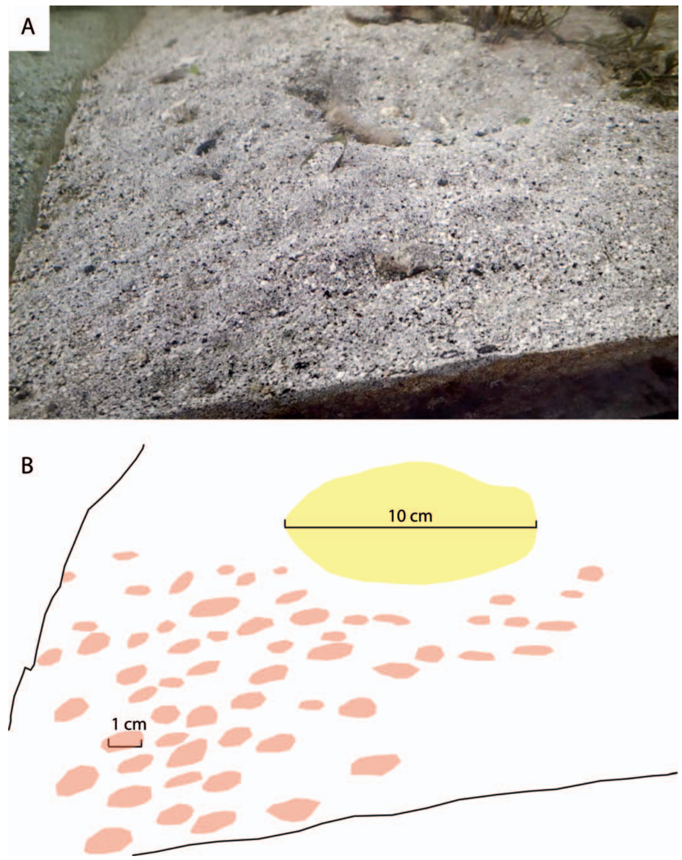

FIG. 6.—Feeding grounds of a *Valenciennea puellaris*. **A**) Photograph showing both large and small *Pisichnus*-like pits. **B**) Annotated sketch of the photograph showing small cm scale *Pisichnus*-like pits in red and large 10 cm *Pisichnus*-like digging pit.

Gobiid Sediment Transport.—As discussed above, *V. puellaris* are proficient sediment processors and can easily rework all of the sediment in the aquarium (~ 7,500 cm^3) given sufficient time. Typically within 24 hours a *V. puellaris* will rework sediment to a depth of 2–3 cm. Observations of *V. puellaris* feeding consist of 190.5 min and 1838 acts of feeding (mouthfuls of sediment) from University aquaria and 795 sec and 134 acts of feeding from YouTube® videos (Table 1). Observations of the gobiid burrowing consist of 253 minutes and 2642 acts of digging (mouthfuls of sediment) recorded in our own work and 619 sec and 104 acts of digging from YouTube® videos (Table 2). This averages 9.65 $\pm$ 2.9 feedings and 10.43 $\pm$ 0 3.6 acts of digging per minute. These rates are determined during active time for the fish and does not account for prolonged periods of rest.

Measurements (Table 3) of the amount of sediment in one gobiid mouthful were collected from a 10 cm long *V. puellaris*, by placing a mylar sheet outside the gobiid burrow and removing it after the gobiid expelled one mouthful of sediment onto the sheet. A total of 23 gobiid mouthfuls were collected, measured, and volumes calculated (Table 3). The average mass of a *V. puellaris* mouthful is 0.478 $\pm$ 0.17 g with an approximate volume of 0.18 cm^3.

DISCUSSION

Biogenic structures that resemble physical sedimentary structures illustrate the potential difficulties of misinterpreting biological processes within the sedimentological record. The parallel, discontinuous, and apparent ripple cross-laminae produced in this study show that biogenically mediated sedimentary structures are very similar to those produced by currents. Biogenically mediated sedimentary structures correspond to the movement of the responsible organisms. In this study the gobiid expelled sediment at rest or with little movement and produced structures that are cross laminated and resembled ripple cross-laminae. The gobiid expelling sediment while moving produced planar laminae.

The biogenic structures produced by *V. puellaris* in these experiments are similar to those produced by the shrimp *Alpheus bellulus* (McIlroy 2010). Contrasting with those produced by *A. bellulus*, the sediment fabrics produced by *V. puellaris* record sorting due to differential settling after the sediment grains were resuspended by the fish. However, similar to those produced by *A. bellulus,* the ripple cross-lamina and foresets generated by gobies are commonly at or close to the angle of repose (McIlroy 2010). Cross-laminae are produced as the gobiid feeds in one place or expels sediment in one place forming a mound with apparent foresets. The biogenic cross-laminae highlighted in Figure 5 are similar to those from hydraulically produced cross-laminae. The implications being that the variables that produce hydraulically produced and biogenically mediated structures are independent of each other.

The contact between the biogenic meditated sediment above and the underlying sediment is identifiable as an undulatory contact. The undulatory nature of the contact is produced by the gobiids feeding behavior, which is preserved as centimeter-scale *Piscichnus*-like traces. The contact expressed as a plane should have the same morphology as the

TABLE 2.—*Observed number of feeding acts, elapsed time and rate of feedings per minute for the fish in this study (IRG Fish) and from YouTube movies. Totals consist of 1972 acts of feeding over 210.83 minutes with an average rate of 9.35 feedings per minute with a standard deviation of 2.9.*

Video	No. of feeding acts	Elapsed time (min)	Rate of feeding	Link
IRG Fish	1838	190.58	9.64	
Youtube 2	36	9.57	3.76	https://www.youtube.com/watch?v=9PQeOTJGEXA
Youtube 3	9	0.77	11.74	https://www.youtube.com/watch?v=6nY2cQK5-kc
Youtube 4	14	1.32	10.63	https://www.youtube.com/watch?v=IEXGDkNakho
Youtube 6	29	3.98	7.28	https://www.youtube.com/watch?v=2c-6SDg_g6U
Youtube 7	15	1.47	10.23	https://www.youtube.com/watch?v=rM9UbNYpCIQ
Youtube 10	31	3.15	9.84	https://www.youtube.com/watch?v=xG8zPPAQWvY
Total	1972	210.83	9.35 ± 2.9	

small, connected feedings pits (Fig. 5). In cross-section the contact is composed of small 1-cm scale pits with columns of sediment left between them. The physical scour pits are a distinct and contain feature consistent with other scour pits such as a small-scale asymmetric combined-flow ripples as 3D planform, round crest, and convex-up sigmoidal profile with local pronounced scour at the toe of the stoss side (Dumas et al. 2005). Pits formed by gobiid feeding appear similar to scour pits caused by flow.

The larger *Piscichnus*-like crater produced by the gobiid digging behavior could easily be misidentified as a feeding trace of a much larger organism. This is due to *V. puellaris* compulsive nature to move sediment. These biogenic structures are a form of cryptic organism-sediment interaction that could easily be misidentified unless studied in great detail. The presence of climbing ripples and planar lamina is commonly taken to indicate strong current energy and abundant sediment load; failure to recognize biogenic cross-laminae and planar laminae could lead to incorrect paleoenvironmental interpretation (McIlroy 2010). Despite the fact that biologically induced sedimentary fabrics are numerous, their origins are ambiguous or difficult to explain. The preservation potential of the biogenically produced sedimentary fabrics probably differs from that of primary sedimentary fabrics. Biogenically produced sedimentary fabrics will be found in association with and oxygenated water column and sediment because both the organisms producing the fabric and their prey need oxygen to survive. This leads to a reduced rate of preservation compared to primary sedimentary fabrics that don't rely on chemical properties of the surrounding water and sediment. Biogenically produced sedimentary fabrics are more likely preserved in near-shore environments.

Many organisms are capable of producing biogenically mediated structures, but few do it as well as fish. Fish date back to the early Paleozoic (Atkinson and Taylor 1991; Near et al. 2012) and are likely responsible for substantial sediment resuspension and bio-mediated deposition over their history. Gobiid actinopterygians, the focus of this study, have a global distribution and date back until at least the Eocene (Bajpai and Kapur 2004; Thacker 2015). Thus their role in biogenic sediment reworking probably dates back well into the Cenozoic.

Gobiids inhabit modern sandy and muddy substrates to a depth of 100 m (Michael 1999) which are conditions ideal for producing biogenic sedimentary structures. Other fish display behaviors similar to the gobiid behaviors identified in this study. The Sand Drum, *Umbrina coroides* (Cuvier 1830) feeds by foraging along the sea floor, burying its mouth in the sand and ejecting sediment through its mouth and gill openings, producing a dense sandy cloud (Zahorcsak et al. 2000). Similarly, the common Mojarra, *Eucinostomus gula* (Quoy and Gaimard 1824) protrudes its mouth and sinks it into the sand, after which it ejects sediment through its mouth and gill openings, producing a scattered sandy cloud of thin sediment (Zahorcsak et al. 2000).

Studies of *Valenciennea* gobbids show high amount of sediment movement and feeding rates. In the wild, paired male and female sleeper striped gobies, *Valenciennea longipinnis* (Lay and Bennet 1839) share the division of labor of burrowing with both sexes taking approximately the same frequency of feeding bites (Takegaki and Nakazono 1999).

Through SCUBA recordings Clark et al. (2000) recorded a pair of two-stripe gobies, *Valenciennea helsdingenii* (Bleeker 1858) as they moved up to 90 pieces of rubble in 10 min. The pair fed up to 259 times in one 10-minute observation period, with an average rate of 3.7 times per fish per minute (Clark et al. 2000). In the wild *Valenciennea muralis* (Valenciennes 1837) have been observed continuous foraging and feeding with a mean feeding rate of 153.9 bites per 10-minute period, and feeding observed in 82% of the observation period (Herler et al. 2011). Herler et al. (2011) also found a considerable amount of sedimentary material was ingested during the feeding process (e.g., 24 to 27 % by weight and volume in the gut of *V. muralis*), and suggest high feeding rates may be required to overcome the ingestion of such large amounts of indigestible material.

The speed and volume of sediment that a single gobiid is capable of reworking has not previously been established, however the rapid and complete sediment reworking observed in our aquaria experiments suggests that it is significant. Based on digging rates and volumes calculated from aquaria observations, it is estimated that it would take a single gobiid 5.4 days to completely rework a square meter of sediment (with an internal sediment porosity of 40%) to a depth of 2 cm. This time

TABLE 3.—*Observed number of digging, elapsed time and rate of feedings for the fish in this study (IRG Fish) and from YouTube movies Totals consist of 2746 acts of digging over 263.32 minutes with an average rate of 10.43 digging per minute with a standard deviation of 3.7.*

Video	Observed digging	Elapsed time (min)	Rate of digging	
IRG FISH	2642	253	10.4	
Youtube 1	27	2.32	11.7	https://www.youtube.com/watch?v=XWRc0FaRxgI
Youtube 2	15	0.90	16.7	https://www.youtube.com/watch?v=2ijSepBFw0E
Youtube 5	44	5.00	8.8	https://www.youtube.com/watch?v=PKnqaxTsH9Y
Youtube 8	6	1.07	5.6	https://www.youtube.com/watch?v=yQ2NIrC9Rko
Youtube 9	12	1.03	11.6	https://www.youtube.com/watch?v=7P35LpkWzxw
Total	2746	263.32	10.43 ± 3.7	

would significantly decrease with the addition of more gobiids. In addition, this time length may be greatly affected by the size of the gobiids, a parameter not assessed in our experiments.

Foraging within sediment substrates for prey, similar to *Valenciennea puellaris*, has been documented for many taxa including chondrichthyans (e.g., Gregory et al. 1979; Kotake and Nara, 2002; Sasko et al. 2006), a variety of osteichthyans (e.g., Cook 1971; Yahel et al. 2002; Pearson et al. 2007; Yahel et al. 2008; Katz et al. 2009), sea otters (e.g., Shimek 1977; Calkins 1978), whales (e.g., Nerini 1984; Oliver and Slattery 1985; Nelson and Johnson 1987; Klaus et al. 1990; Dunham and Duffus 2001), walruses (e.g., Oliver et al. 1983; Fukuyama and Oliver 1985; Gingras et al. 2007), crabs (Zaklan and Ydenberg 1997), ophiuroids (Mángano et al. 1999), and sea stars (Fukuyama and Oliver 1985). *Valenciennea puellaris* is dwarfed in comparison to most of these organisms but the effects of biogenic reworking on sediment inside a small aquarium is profound, with complete reworking in hours by a relatively small fish. The range of burrowing and feeding behavior of a variety of fishes are summarized in Schäfer (1962).

A wide range of fish produce feeding pits, including flatfish. Feeding pits produced by the smooth flounder *Liopsetta pinnifasciata* (Kner 1870) and winter flounder *Pseudopleuronectes americanus* (Walbaum 1792) produced 2–3 cm diameter pits, 3–5 cm deep at a density as high as 20 per m^2 at the Bay of Fundy (Risk and Craig 1976). Flatfish will also use their bodies to rework sediment, the slender sole, *Lyopsetta exilis* (Jordan and Gilbert 1880) will completely rework surface sediment every 2.5 days with a daily resuspension rate of 1.3 ± 0.7 l bulk sediment m^{-2} d^{-1} in the Saanich Inlet, British Columbia, Canada (Yahel et al. 2008). Large fish, such as Atlantic sturgeon, will produce and displace more sediment. *Acipenser oxyrinchus* (Mitchill 1815) can resuspend 3.9 to 105.9 cm^3 of sediment with each feeding excavation and are responsible for resuspension and redeposition of 44.9–1,220.9 m^3 of sediment across the entire intertidal mud flat at Mary's Point, New Brunswick, Canada over a time span of approximately 6–8 weeks (Pearson et al. 2007). Another large fish, the tilefish, *Lopholatilus chamaeleonticeps* (Goode and Bean 1879) can excavate pits 5 m in diameter and 1 m deep and can reach a density 2,500 burrows per km^2 near the Hudson Canyon, Gulf of Mexico (Coleman and Williams 2002).

Marine mammals also account for vast amounts of sediment reworking. The Pacific walruses, *Odobenus rosmarus divergens* (Illiger 1815), physically and hydraulically root in the sediment, creating $47 \times 0.4 \times 0.1$ m linear furrows (Nelson and Johnson 1987; Nelson et al. 1987). The largest known sediment redepositing organism is the gray whale, *Eschrichtius robustus* (Lilljeborg 1861), that creates $1.5 \times 2.5 \times 0.1$ m pits by ingesting both sediment and prey (Oliver and Slattery 1985; Nelson and Johnson 1987; Nelson et al. 1987). The ingested sediment is either expelled on the sea floor or, more often, near the water's surface. Gray whale and walrus are responsible for the erosion and redistribution of approximately 106–195 m^3 of sediment in one feeding season (Nelson and Johnson 1987; Nelson et al. 1987). All of the animals highlighted may produce structurally similar, biogenic sedimentary fabrics to *V. puellaris*.

The recent development of large-scale modern fishing and whaling by humans has likely diminished the effect of biologic influence on sedimentary deposition in modern oceans compared to the past. Implications based on observations of current population densities likely underestimate the effect of ancient populations. For example, the gray whales are estimated to have had a global population of 76,000–118,000 individuals prior to the whaling era whereas they currently have a population of $\sim$ 19,000 (Alter et al. 2012) and are now completely absent in the North Atlantic (Rice 1998).

Biogenic Structures in the Rock Record.—The pits found in this study are similar to the trace fossil *Piscichnus*. The *piscichnus* trace fossil was originally considered a sedimentary structure such as a load marks and potholes (Howard et al. 1977). Now it is reconciled as feeding traces formed when organisms such as fish, rays, and walrus eat benthic animals living in the sediments (Howard et al. 1977; Gregory 1991; Pearson et al. 2007). In the case of the ichnofossil *Piscichnus waitemata* (Gregory 1991) the pit is filled in with grading structures formed when particles of the host sediment were redeposited (Gregory 1991). *Piscichnus waitemata* can be found at modern sites such as the Azores, Baja Calaifornia Sur (Mexico), and New Zealand as well as in the Pliocene of Santa Maria Island (Uchman et al. 2018).

Biogenic structures produced by gobiid-style feeding, burrowing and resting behaviors are not limited to Cenozoic macro fauna (Fig. 7). Mesozoic macro fauna such as the long-necked plesiosaurs have been interpreted as benthic rather than planktonic predators. This is supported by evidence from stomach contents containing a significant amount of sand (McHenry et al. 2005). Ichthyosaurs, plesiosaurs, and crocodilians stomach contents have also been found to contain large amounts of sand, suggesting that these animals ingested a significant amount of sediment whilst feeding (Zhuravlev 1943; Martill 1992; Geister 1998). Large, gutter-like traces, discovered in the Middle Jurassic Callovian Marl of Liesberg in Switzerland have been interpreted to represent the feeding traces of plesiosaurs (Geister 1998). Similar traces are also known from the Upper Jurassic of Spain and have been given the ichnotaxonomic name *Megaplanolites ibericus* (Calvo et al. 1987). As with the *Piscichnus-like* craters produced by the gobiid from this paper, the *Megaplanolites ibericus* tracemaker excavated the grooves and deposited the sediment some distance away. Similar to the activity of gobiids, sediment deposited by the *Megaplanolites ibericus* tracemaker look similar to physical sedimentary structures. Large scale *Piscihnus* have been found in La Posa, Isona, Spain and were originally interpreted as dinosaur Tracks (Martinell et al. 2001). These behaviors of feeding are all different and can range from actions as sieving, harrowing, rubbing, flattering, puffing water jets, digging, shoveling, but they all create conditions of bioresuspension and biogenetically induced sedimentary fabrics.

Paleozoic large fish, such as armored heterostracans, are believed to have shared similar behaviors to the gobiids in this study (e.g., predators that selectively scooped and ingested inactive prey; Northcutt and Gans 1983; Gans 1989). These fish date back to the Wenlockian (Silurian), 430 Ma (Soehn and Wilson 1990). As mentioned above, gobiids date back to at least the Eocene (Bajpai and Kapur 2004; Thacker 2015) and burrowing actinopterygians date back to the Devonian (400 Ma) (Near et al. 2012). This strongly suggests that sedimentary fabrics within post-Silurian strata may record biologically mediated redeposition.

Temporally, these behaviors could date back to near, or shortly after, the origin of mobile predators, as early life was concentrated at the sediment-water interface. The earliest known organisms with possible similar behaviors to the gobiid in this study are the Cambrian *Pikaia*, *Haikouichthys*, and *Myllokunmingia*. These three genera all appeared around 530 Ma. All of these early vertebrates lacked jaws and likely relied on filter feeding close to the seabed as they likely ejected water and excess inorganics entering the mouth and pharynx through pharyngeal pores or slits sifting food particles (Lacalli 2012). If early chordates such as *Pikaia* and Heterostracans used this behavior to feed, then they likely would have redeposited sediment in a similar manner to the gobiids studied in this paper. The advent of mobile, process-feeding predators likely heralded a profound change in the nature of seafloor sediments. Since the Cambrian, large aquatic organisms capable of widespread sediment reworking have been prevalent including Paleozoic fish, Mesozoic marine reptiles and actinopterygians, and Cenozoic marine mammals and actinopterygians (Fig. 7). Arguably, vertebrate-produced sedimentary fabrics may have appeared in the mid-Cambrian, become common by the mid-Paleozoic and become dominant in some depositional settings during the Cenozoic.

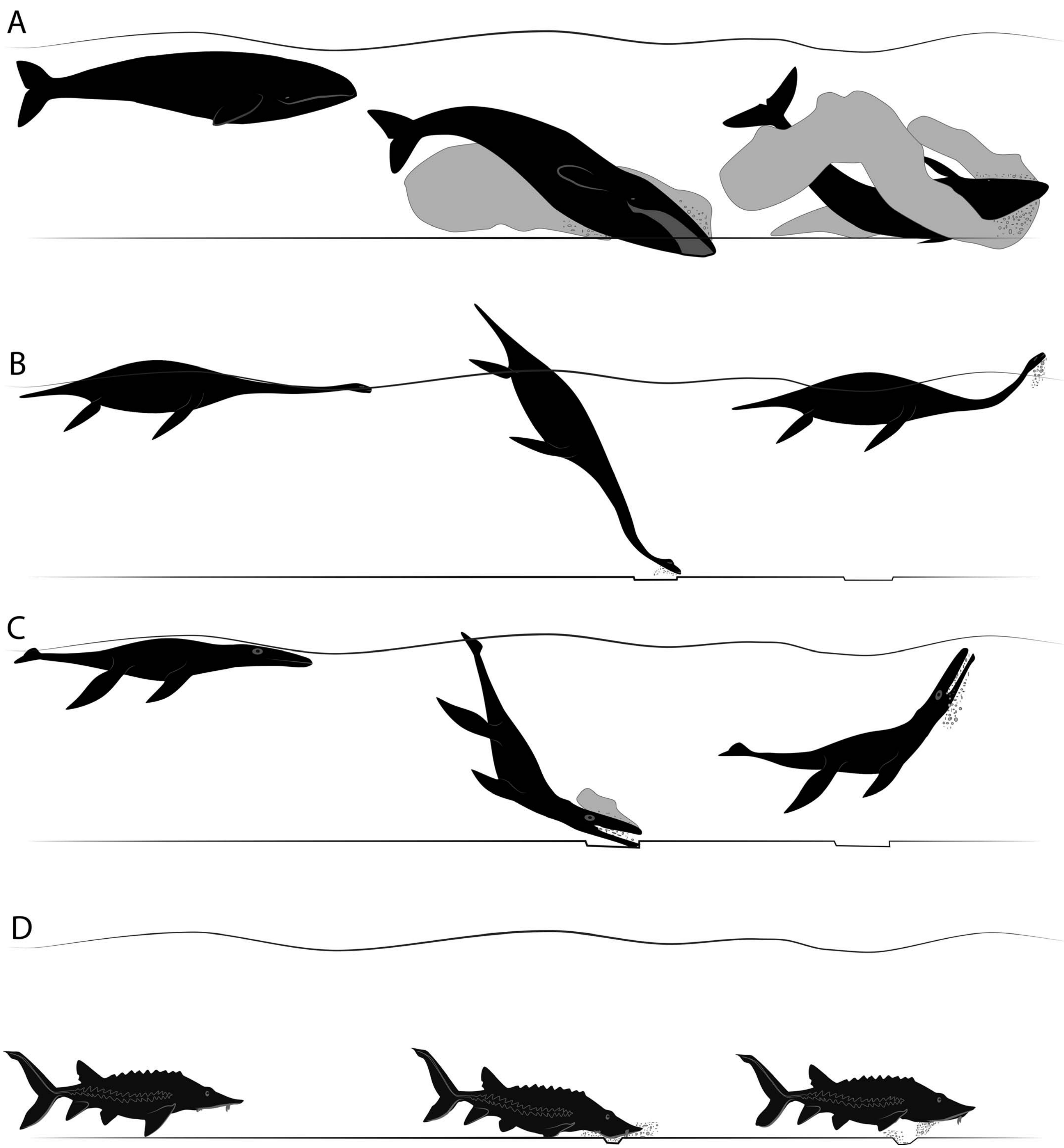

FIG. 7.—Schematic diagram showing feeding styles and bioresuspension behaviors of macrofauna from different time periods. **A**) Cenozoic Gray Whale (*Eschrichtius robustus*). **B**) Mesozoic plesiosaur. **C**) Mesozoic ichthyosa. **D**) Paleozoic sturgeon (*Acipenseridae*).

CONCLUSION

Aquaria-based experimental studies using the gobiid actinopterygian fish *Valenciennea puellaris* indicate that biological processes redeposit a substantial amount of sediment and that hydraulic flow may not be the dominant process responsible for some 'primary' sedimentary fabrics observed in shallow marine environments. The sets of experiments conducted herein show that the resuspension behaviors of *V. puellaris*, produce planar and lamination similar to cross-ripple laminae. The gobiids also produce surficial pits, some of which are similar to the trace fossil *Piscichnus*. These structures are a form of bioturbation that may be difficult or impossible to distinguish from primary physical sedimentary

TABLE 4.—*Mass and volume of sediment collected for individual measurements of gobiid mouthful. An average gobiid mouthful is 0.478 g with a standard deviation of 1.7 in mass and 0.18 cm^3 with a standard deviation of 0.07 in volume.*

Gobiid mouthful	Mass (g)	Volume (cm3)
Attempt 1	0.294	0.11
Attempt 2	0.342	0.13
Attempt 3	0.550	0.21
Attempt 4	0.360	0.14
Attempt 5	0.510	0.19
Attempt 6	0.720	0.27
Attempt 7	0.346	0.13
Attempt 8	0.656	0.25
Attempt 9	0.363	0.14
Attempt 10	0.250	0.09
Attempt 11	0.518	0.20
Attempt 12	0.770	0.29
Attempt 13	0.312	0.12
Attempt 14	0.581	0.22
Attempt 15	0.792	0.30
Attempt 16	0.324	0.12
Attempt 17	0.423	0.16
Attempt 18	0.362	0.14
Attempt 19	0.600	0.23
Attempt 20	0.780	0.29
Attempt 21	0.504	0.19
Attempt 22	0.360	0.14
Attempt 23	0.274	0.10
Average	0.478 ± 1.7	0.18 ± .07

fabrics. Sediment-reworking behaviors exemplified by *V. puellaris* activities occur in other extant organisms such as larger fish and marine mammals, highlighting the importance of these cryptic forms of organism-sediment interaction.

Through their bioresuspension behaviors, which include feeding, digging, and resting, *V. puellaris* excavates *Piscichnus*-like craters and transports approximately nine mouthfuls of sediment per minute or 1.62 cm^3/min (0.18 cm^3/mouthful) of sediment.

Valenciennea puellaris-style behavior and feeding is widespread and observed in association with larger fish and marine mammals. These depositional behaviors likely account for a significant amount of sediment fabrics in both modern and ancient sediments. While gobiids have only been around since the Eocene, burrowing Actinopterygians date back to 400 Ma. It is thus both possible and likely that a significant proportion of aquatic Phanerozoic sedimentary fabrics could consist of vertebrate-produced biologically mediated structures. This study emphasizes the importance of cryptic forms of organism-sediment interaction and is the first to examine the resulting sedimentary fabric of fish bioresuspension and suggests that a significant portion of sedimentary fabrics might be biologically mediated.

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