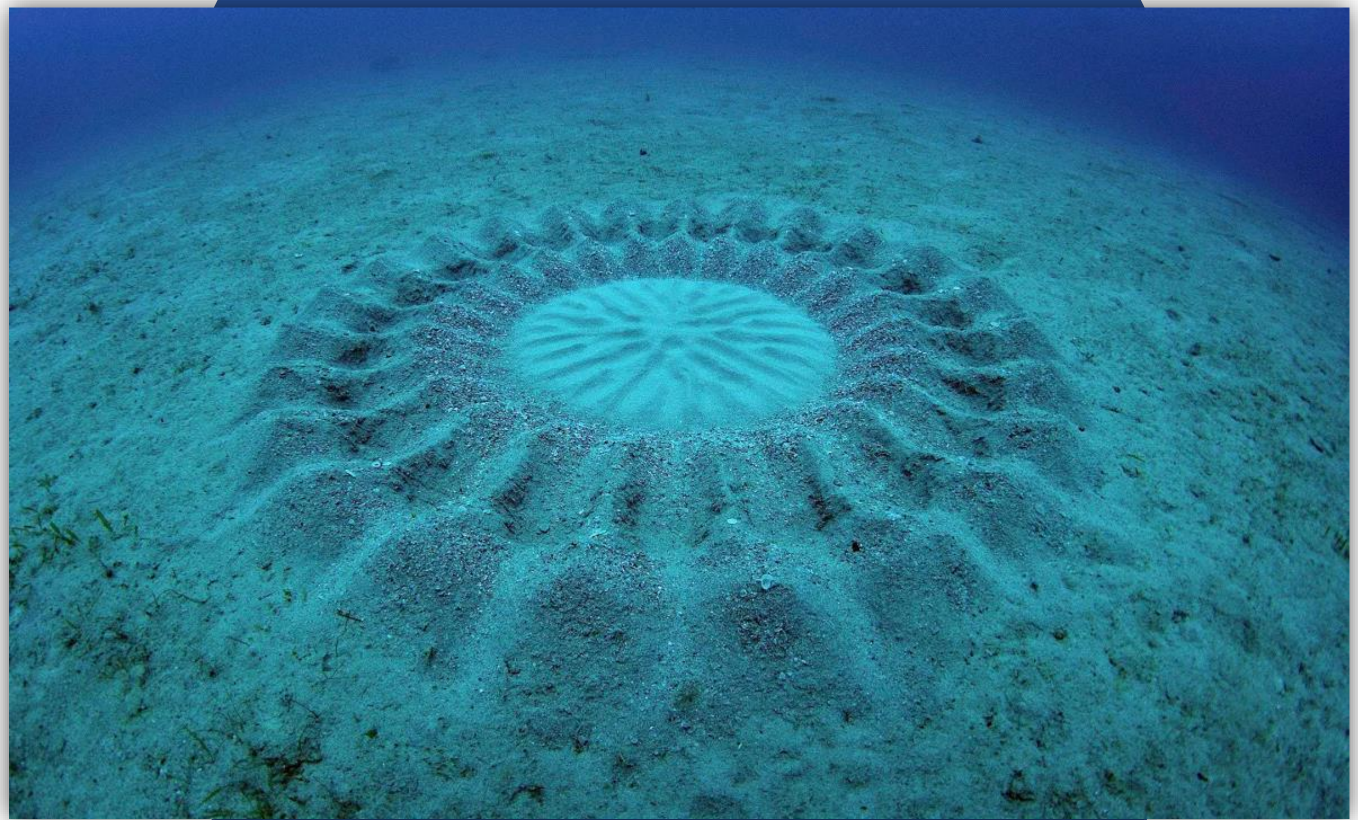
Sand Architects: The Nesting Advantages of Sand Circle Construction by the White-Spotted Pufferfish *(Torquigener albomaculosus)*



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Introduction

In 1995 a geometric circular sand structure was discovered of the coast of southern Amami-Oshima Island in subtropical Japan (Kawase et al., 2013). The origin of these circles remained unknown until 2011, when Japanese scientist discovered a small male pufferfish to be the architect of these circular structures (Kawase et al., 2013). These circles had a diameter of approximately 2 meters wide and were observed between depths of 10 and 30 meters (Kawase et al., 2013, 2014). This species named *Torquigener albomaculosus* or white spotted pufferfish (not be confused by the white spotted puffer) was officially recorded in 2014 by Keiichi Matsuura. It has been hypothesized to be distributed along sandy bottoms at depths around 15 and 18 meters in the tropic region of the West Pacific. (Matsuura, 2014). This small fish of around 120 mm in length (Kawase et al., 2013) has garnered some attention with its unique construction of these marvelous circles. It is known that the white-spotted pufferfish uses the sand circle as a nest to incubate its eggs, but it differs greatly in the complexity of nest construction from other fish (Kawase et al., 2013, 2014, 2017). On the contrary, certain species of filefish (Kawase & Nakazono, 1996; Nakazono & Kawase, 1993) and triggerfish species (Kawase, 2002, 2003) release their eggs on the sandy sea floor without even making a nest. Evenly interesting, some fish make nests from coral rubble like the Yellow-margin triggerfish (Gladstone, 1994). But no other recorded fish has come close to creating sand nests showing the same peaks, valleys, and complexity as the nest of the white-spotted pufferfish (Kawase et al., 2013). This begs the question, why a small pufferfish of only 12 centimeters would construct a nest which is 16 times its size. Thus this report will try to answer the question: *What benefits does the white spotted pufferfish (Torquigener albomaculosus) gain from constructing a sand circle nest?*

Since its discovery in 2011 (Kawase et al., 2013) and its documentation in 2014 (Matsuura, 2014) much of the pufferfish still remains a mystery. Almost nothing is known about the ecology and biology of this tiny pufferfish and the research that has been performed mainly focusses on the complex sand nests they build (Kawase et al., 2013, 2017; Matsuura, 2014; Mizuuchi et al., 2018; Shameem et al., 2021). In this report, we shall go over the existing knowledge related to the nest of the white-spotted pufferfish. Furthermore, we will explore potential benefits observed in other animal species that might hold relevance and applicability for the pufferfish.

Construction of the sand circle

A male, white-spotted pufferfish starts his construction of the circle by pressing his body against the sand thus creating some indents in the sand (Kawase et al., 2017). This way the pufferfish creates an area of approximately 85 by 75 centimeters of several depressions in the sand (figure 1A and 1B) (Kawase et al., 2017). This stage is, as called by Hiroshi Kawase, the early stage of the sand circle construction. It is not known why the pufferfish starts off his construction by making indents, but it is hypothesized by Mizuuchi and Kawase that the pufferfish uses these small depressions in the sand as an orientation marker to build its nest circle around (Kawase et al., 2017; Mizuuchi et al., 2018). After completing the early stage of the nest construction the pufferfish starts to dig channels. It will lay down on the sand and swim towards the center of the circle while using its pectoral fins, anal fins, and caudal fins to stir up sand (figure 1C-G) (Kawase et al., 2013). Mizuuchi (2018) found that by following simple rules which are always swimming in a straight line and starting excavations at lower positions it is able to create channels. This in combinations with a lot of repetition makes the pufferfish able to create the complex structure of peaks and valleys which is also referred to as the outer ring (Mizuuchi et al., 2018). The width of the channels that are dug by the pufferfish thus corresponds to the width of the pufferfish itself (Kawase et al., 2013). During the end of the middle stage the pufferfish will also start to move from the inward to the outside in the outer ring while starting excavation when halfway through the outer circle (Mizuuchi et al., 2018) this creates a second peak along the inner border of the outer ring. Finally the pufferfish makes inward and outward lines in the middle of the circle creating a maze-like pattern in the inner circle (Mizuuchi et al., 2018). With the construction of the circle finished the construction process enters the final stage (figure 1H). During this stage the male pufferfish decorates the peaks in the outer ring with shell and coral fragments (Kawase et al., 2017). After mating the male pufferfish stops maintaining the circle and the circle slowly erodes away (Kawase et al., 2013; Shameem et al., 2021). The time it takes for a male pufferfish to complete a nest circle from a flat seabed, ranges from 7 to 9 days, but it is not known what causes these differences in construction time (Kawase et al., 2013).

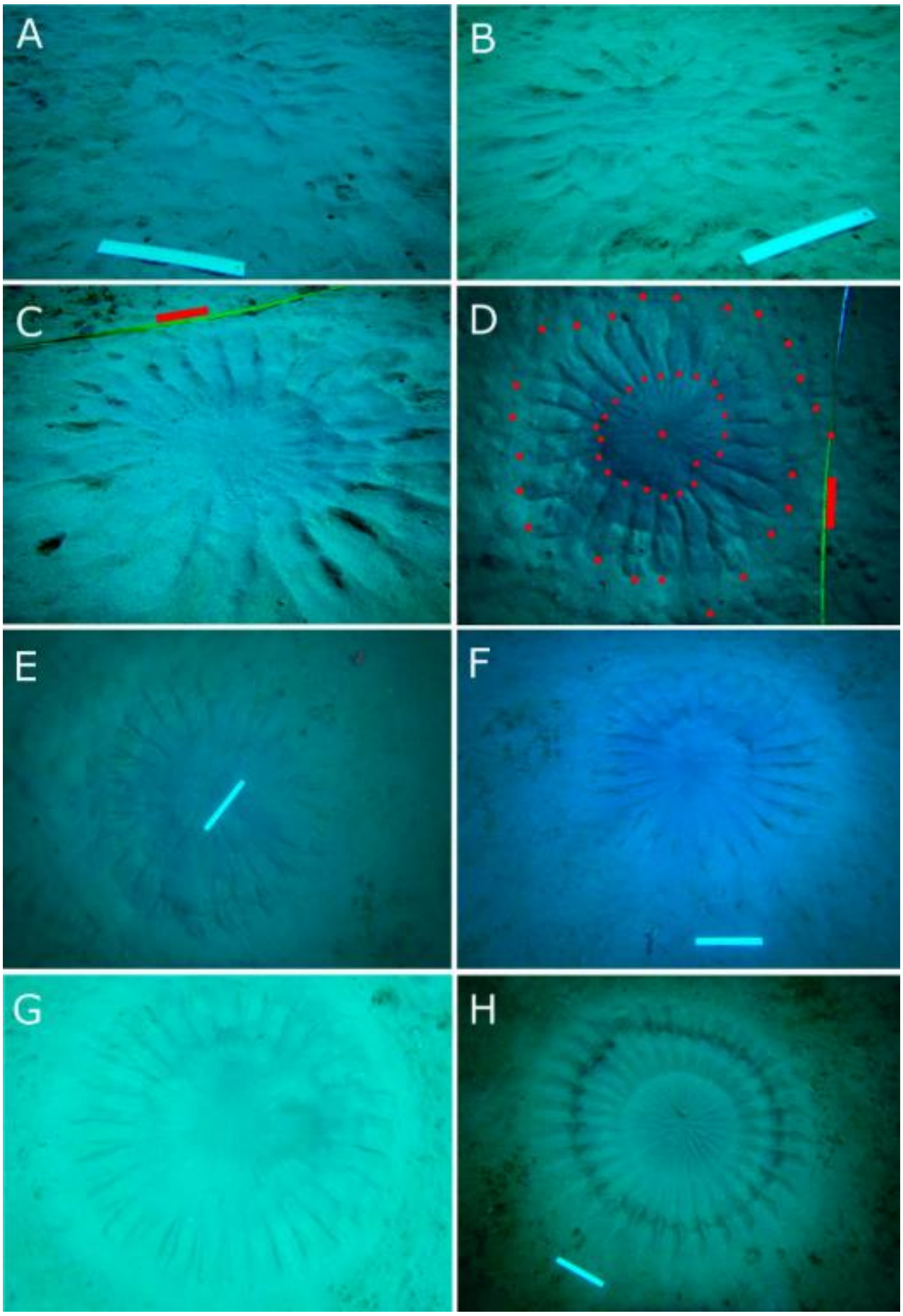

Figure 1. *Development of the mystery circle constructed by the pufferfish Torquigener albomaculosus. The earliest stage (**A,B**), early stage (**C-F**), middle stage (**G**) and the final stage (**H**) of construction are shown. Scale length in (**A,B,E,F,H**) is 30 cm. Red bar in (**C,D**) represents 20 cm. Source: Discovery of an Earliest-Stage "Mystery Circle" and Development of the Structure Constructed by Pufferfish, Torquigener albomaculosus, Kawase et al. 2017*

Hydrology

Due to its unique shape the sand circle also has been studied on its hydrology. One of the main characteristics of the sand circle is that no matter from which side the water flows, the water runs through the valleys, slows down in the middle, and exits through the valleys on the other side (Kawase et al., 2013, 2022; Shameem et al., 2021).

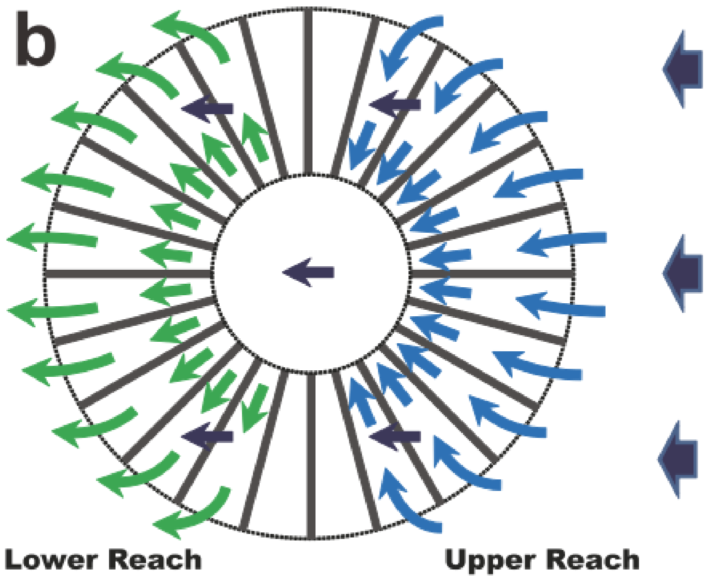

Figure 2. *Schematic diagram of the circular structure and direction of water flow. Source: Role of huge geometric circular structures in the reproduction of a Marine pufferfish, Kawase et al. 2013*

This creates a constant supply of slowed fresh salt water to the center of the circle (Kawase et al., 2013; Shameem et al., 2021). Not only does the constant flow of water provide the eggs with fresh oxygen rich water, but the reduced flow also reduces the stress on the eggs (Kawase et al., 2013, 2022; Shameem et al., 2021). Further analysis by Shameem et al. (2021) shows that more is happening to the water flowing through the circle. When water passes over the ridge a recirculation zone is created, this causes water to flow in a circular motion in this zone (Shameem et al., 2021). This is visually shown in figure 3 which is taken from a 2D simulation of a cross view of the pufferfish nest. This increases the aeration of the inner circle on top of the steady flow which enters and exits the circle (Shameem et al., 2021). Another important function of the peaks in the outer ring to is absorb the wall shear stress which is created by the ocean floor's current (figure 4a,b) (Shameem et al., 2021). Furthermore, because of the absorption of the shear stress by the peaks the mean shear stress on the inner circle is less than the mean shear stress on the seabed outside the circle (figure 4b) (Shameem et al., 2021). Which means that the eggs laid inside the inner circle undergo less shear stress in comparison to if they would have been deposited on the seabed. Lastly, Shameem's model has shown that the behavior of decorating the peaks with seashells and coral fragments actually increased the shear strength in regions which undergo high shear stress, which made the peak more resilient against shear stress.

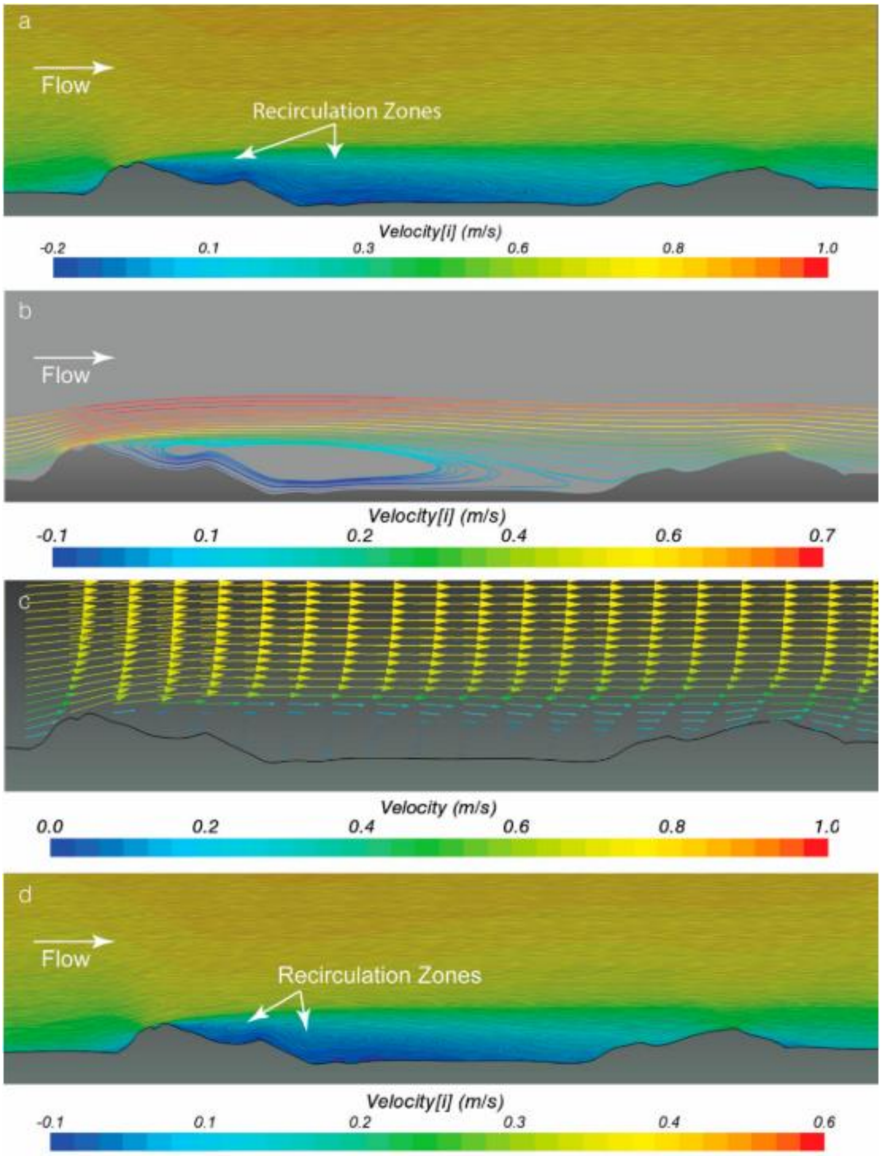

Figure 3. ***(a)*** *Mean streamwise velocity distribution of ridge section;* ***(b)*** *Streamline visualization of the ridge section;* ***(c)*** *Velocity vectors of ridge section;* ***(d)*** *Mean streamwise velocity distribution of ridge section one with 50% reduction in inlet velocity. Source: A Fluid Dynamics Approach for Assessing the Intelligent Geomorphic Design of the Japanese Pufferfish Nest, Shameem et al. 2021*

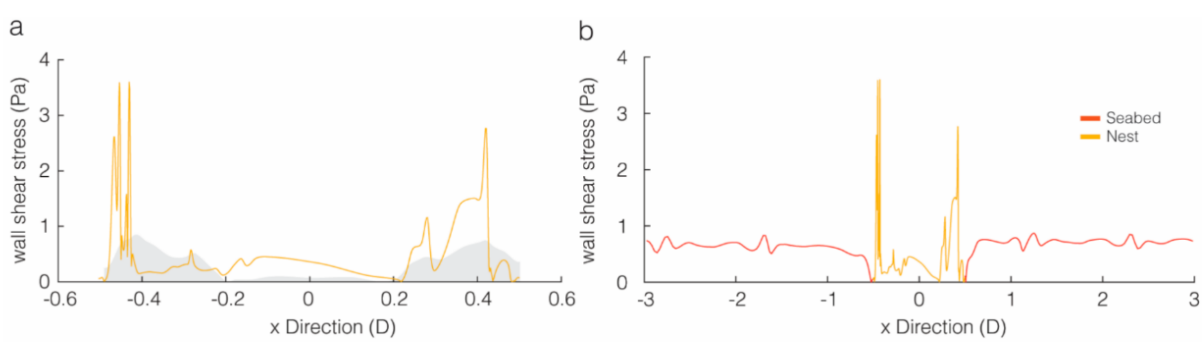

Figure 4. *Wall shear stress distribution along the nest and surrounding seabed in terms of nest diameter D. (a) Wall shear stress distribution within the nest; (b) Comparison of the surrounding seabed wall shear stress distribution against the wall shear stress within the nest. Source: A Fluid Dynamics Approach for Assessing the Intelligent Geomorphic Design of the Japanese Pufferfish Nest, Shameem et al. 2021*

Spawning substrate

The sand in the middle of the circle consists of finer grain size (0.5mm) (Shameem et al., 2021) than the sand in the outer ring (figure 5) (Kawase et al., 2022; Shameem et al., 2021). The male pufferfish separates the fine and coarse and during the excavation of the channels in the outer ring (Kawase et al., 2013, 2022; Shameem et al., 2021). When the sand is stirred up, finer sand particles need a lower flow velocity to settle than larger sand particles (Hjulström, 1935) and thus finer sand particles are deposited in the inner circle while the larger particles settle in the outer ring (Kawase et al., 2013, 2022; Shameem et al., 2021). The sand particles are mainly propelled by the fin movement of the fish (Kawase et al., 2013, 2022; Shameem et al., 2021) and there is no literature available if the pufferfish is influenced by the direction in which the water enters the circle while he is suspending the fine sand particles.

There is also no research available on why the pufferfish fills its inner circle with fine sand but a comparison with other fish species might give more insight into why the pufferfish might prioritize fine sand over rough sand. The Atlantic salmon (Sear et al., 2014) and the European river Lamprey (Silva et al., 2015) lay their eggs in gravel. By laying their eggs in coarse gravel they ensure that the eggs receive enough oxygen from the water by making the substrate just coarse enough so that fresh water can reach the eggs (Sear et al., 2014; Silva et al., 2015). This is essential to these species since the salmon and lamprey leave their eggs after spawning and thus do not fan or steer fresh water over their eggs (Sear et al., 2014; Silva et al., 2015). Furthermore, research performed by Palm et al. 2009 has shown that salmon thread a fine balance when picking the right size of spawning substrate. As explained before salmon choose a big grain size so that the eggs receive enough oxygen, but if they pick a grain size which is too big it will increase the odds of egg predation (Palm et al., 2009). Palm et al. found that predation by European sculpin increases with the increase of substrate particle size, thus salmon needs to balance aeration of the eggs with egg predation when picking the right size of substrate. Even though there are big differences between salmon spawning in a river and pufferfish spawning on the seabed, it is an indication of the importance of balancing substrate size. Since the pufferfish gathers fine sand, it might indicate that the nest circle combined with the male's parental care provides enough aeration for the eggs, while the fine sand offers protection against predation.

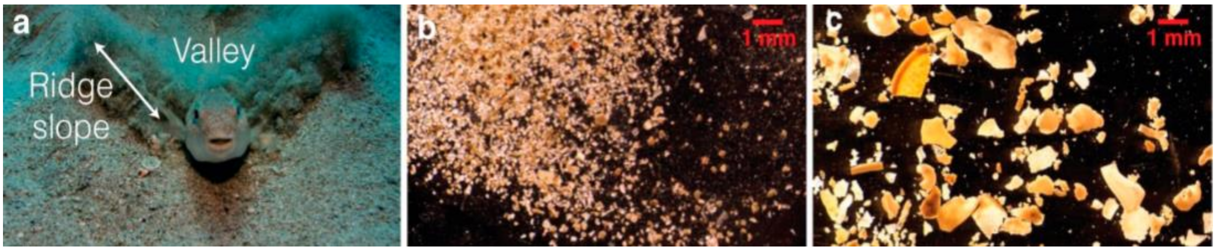

Figure 5. *Sand particle deposition during excavation of the nest.* ***(a)*** *Male pufferfish is moving through a valley while digging the sand using its pectoral, anal and caudal fins. This results in the stirred-up sand particles depositing on either side of the valley surface;* ***(b)*** *Photomicrograph of sand particles collected from a nest site the day before spawning;* ***(c)*** *Photomicrograph of sand particles collected from a nest site the day before hatching. Source: A Fluid Dynamics Approach for Assessing the Intelligent Geomorphic Design of the Japanese Pufferfish Nest, Shameem et al. 2021*

Spawning behavior

The spawning period for the white-spotted pufferfish is from spring until summer (April – September) during which water temperatures ranged between 20-29 °C (Kawase et al., 2014). Mating starts with a female pufferfish approaching the nest circle (Kawase et al., 2014). When the female pufferfish is noticed by the male, the male will start steering up the fine sand in the inner circle (figure 6A) (Kawase et al., 2014). If the female then decides to enter the nest, the male will repeat a rush and retreat behavior which is directed to the female (figure 6B) (Kawase et al., 2014). If the female then decides to mate with the male pufferfish, she will slowly descend to the seafloor in the inner circle, with the male approaching the female (figure 6C) (Kawase et al., 2014). Usually when a female turns down a male, she will leave the nest when the male is steering up sand or is performing the rush retreat behavior (Kawase et al., 2014). This is an indication that the behavior of steering up sand and rush and retreat shown by the male is to entice the female to lay her eggs in the nest. Slightly buried in the sand, both pufferfish start to vibrate during which the female releases her gametes and the male releases his sperm, this takes approximately 1 second (Kawase et al., 2014). During this time the male also lightly bites the rearmost outer part of the female's mouth (figure 6D) (Kawase et al., 2014). After the female has released her eggs she leaves the nest, but she may decide to return to perform another mating ritual. At that time the male does not steer up the sand anymore but only performs the rush retreat behavior (Kawase et al., 2014). Kawase et al. observed females partaking in the mating ritual from 4 times up to females partaking 43 times in 38 minutes. The scientists also observed a female chasing away another female (Kawase et al., 2014). In this instance the female pufferfish mated 3 times with a male pufferfish, until she got chased away by another female who proceeded to mate with the male pufferfish once. Furthermore, multiple female pufferfish may visit one male's sand circle nest (Kawase et al., 2014). This polygamy combined with multiple mating with different females is unique to the white spotted pufferfish (*Torquigener albomaculosus*) and no related fish species show this kind of mating behavior (Gladstone, 1987; Kawase, 2003; Kawase' & Nakazono, 1995; Kawase & Nakazono, 1996).

The importance of nests has been studied in a wide range of animals which has led to the discovery of multiple functions which a nest might serve. In species such as stickle bass (Barber et al., 2001) and Satin Bowerbirds (Borgia & Collis, 1989, 1990) nests serve as an indication of fitness. These indications help the female to make an educated choice if she should mate with a certain male (Barber et al., 2001; Borgia & Collis, 1989, 1990). Male fiddler crabs build sand hoods at the entrance of their burrows which are shown to be more attractive to female crabs than a male without a sand hood (Christy et al., 2002). Not only do these hoods attract females, but they also guide the female crab to the entrance of the male's burrow and thus act as a way for female crabs to orient themselves (Christy et al., 2002). In Barn swallows, nests are used by female swallow to assess the parental investment of the male swallow (Soler et al., 1998). All these functions can be applicable to the white-spotted pufferfish. The nest might serve as an indication for the male puffer's fitness, it may be an indicator of male parental investment and the nest might serve as a way for the females to find the males on a baren sandy sea bottom. Especially when considering the 12 cm size of the pufferfish and human scientists having trouble finding the fish themselves when they are not present in the nests (Kawase et al., 2014). But there yet has to be research conducted into these nest functions for the white-spotted pufferfish. On top of this, the fitness of building a nest would be hard to determine as long as there are no observations of male pufferfish not building a nest, let alone the question if male pufferfish that not build a nest even exist in the first place. Alternatively you could measure the fitness of a pufferfish nest by the number of offspring relative to the number of eggs. By then comparing different nests on survival rate and features like number, width, and depth of valleys and also sand grain size of the inner circle, you would be able to conclude which features indicate a better fitness. However, with this data you would not be able to compare non-nest building pufferfish with nest building pufferfish, thus you will not be able to conclude anything about the fitness of building a nest compared to not building one.

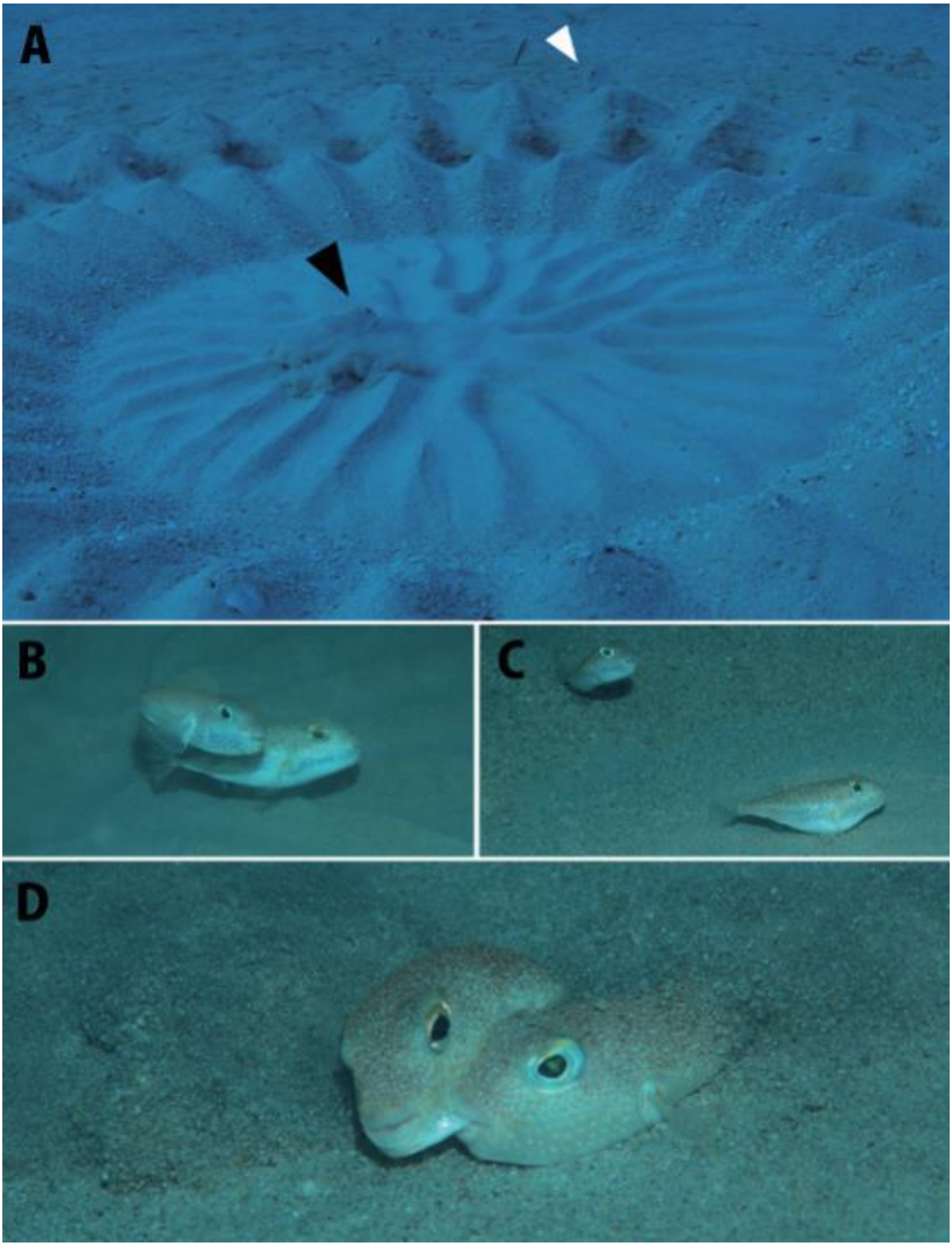

Figure 6. *Mating behavior of Torquigener albomaculosus.* ***(A)*** *Male (black arrow) stirring up of fine sand particles, creating irregular pattern on the nest, after detecting a female (white arrow);* ***(B)*** *male (left) rush and retreat directed at the female (right) that enters the nest;* ***(C)*** *female (right) descending to the bottom of the nest just before spawning;* ***(D)*** *releasing of gametes by a pair at the bottom (female = left). Source: Spawning behavior and paternal egg care in a circular structure constructed by pufferfish, Torquigener albomaculosus (Pisces: Tetraodontidae), Kawase et al. 2014*

After mating the female pufferfish leaves the nest and the male pufferfish will remain to care for the eggs (Kawase et al., 2013, 2014). Male pufferfish will perform several behaviors to take care of the eggs. Male pufferfish will flap their fins on the nest site (figure 7A), remove debris which has floated into the nest (figure 7B) and chasing away fish that passed too close to the nest (Kawase et al., 2014). Hatching of the eggs occurred in the evening around sunset with nests made in July taking 5 days to hatch (Kawase et al., 2014). On the evening when the eggs are hatching the male pufferfish will significantly stay longer on the nest and perform parental care behavior more frequently than on days without hatching eggs (Kawase et al., 2014). Larvae will hatch synchronously with the male pufferfish fanning his fins on the nest (figure 7C). After hatching the male will leave the nest circle to start construction on a new circle elsewhere (Kawase et al., 2014).

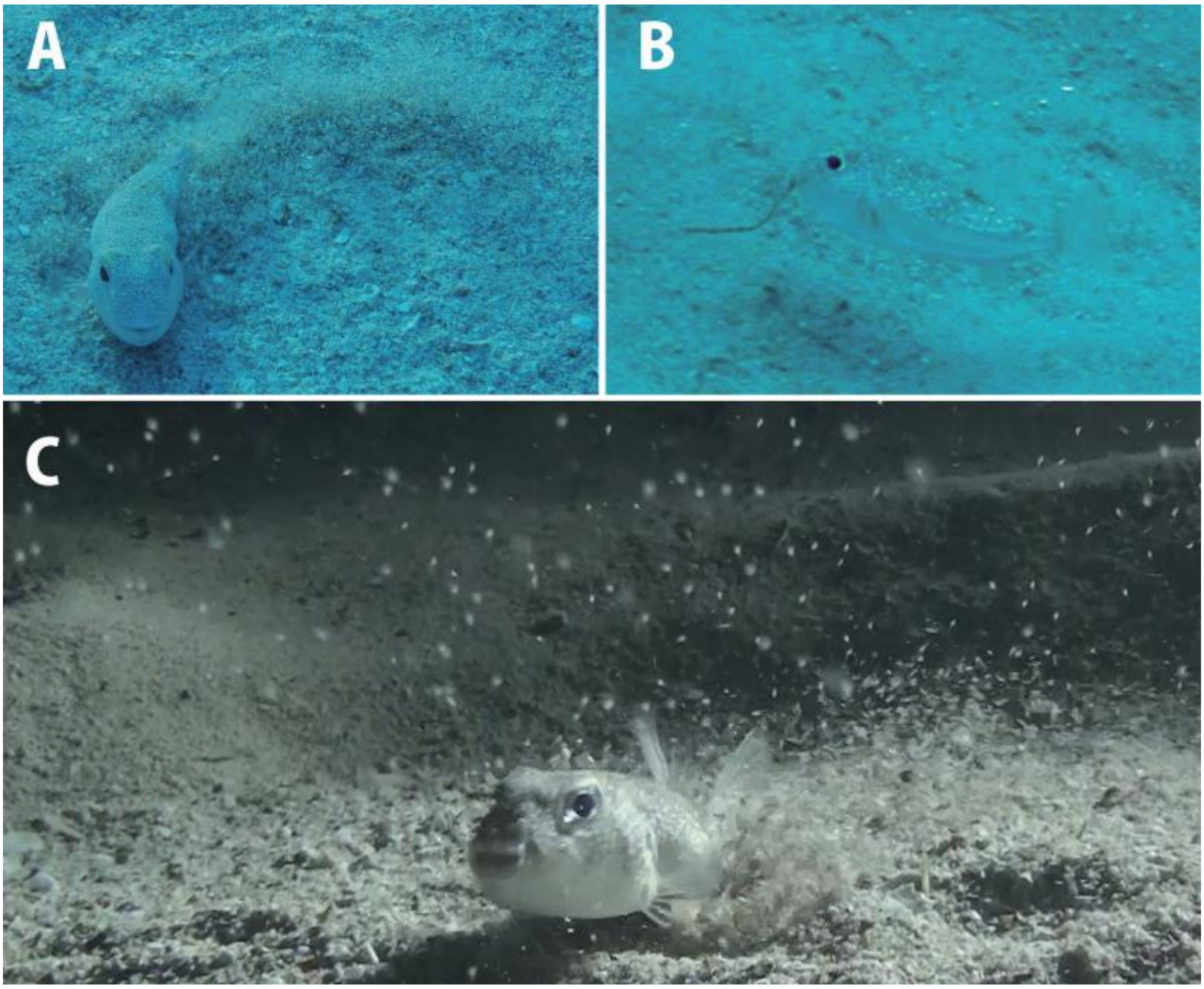

Figure 7. *Paternal egg care and hatching of Torquigener albomaculous. Parental male cares for the eggs deposited on the nest by flapping his fins* ***(A)*** *and by removing debris* ***(B)****. Parental males promote hatching around sunset; white dot-like figures are newly hatched larvae* ***(C)****. Source: Spawning behavior and paternal egg care in a circular structure constructed by pufferfish, Torquigener albomaculosus (Pisces: Tetraodontidae), Kawase et al. 2014*

Discussion

Due to the research being predominate focused on the male perspective it is hard to conclude on any advantages that the female gains from the nest. This has mostly likely to do with the fact that the circles build by male pufferfish are easier to find and thus male pufferfish that stay with their sand circle are easier to observe. As such, more research will be required to fully determine all advantages that the nest brings to the pufferfish. Further subjects that would need to be researched should in my opinion be focused around identifying more abiotic or biotic influences that have pushed the pufferfish to make these nests. I would suggest starting with finding these influences by testing the benefits gained from the nest. This approach will enable you to assess whether these benefits derived from the nests are essential for the eggs' survival and thus if they are key influences for building the nest. Some suggestions would be testing the effect of water flow over the eggs, the effect of shear stress and the effect of grain size on the eggs.

All known and researched benefits have to do with egg protection by sheltering it from things like seabed current, which begs the question why the pufferfish did not seek out preexisting shelters like other related species such as the grass puffer which lays its eggs on pebbles in intertidal zones (Honma et al., 1980; Yamahira, 1994). Potentially, this is caused by lack of shelters, the interspecies competition for shelters. Alternatively, the particular nest choice of the pufferfish could be part of its reproduction strategy to invest more energy into parental care than a fish like the filefish you lay their eggs on a bare sandy seabed (Kawase & Nakazono, 1996; Nakazono & Kawase, 1993). By building a sand circle nest they then would increase survivor rate of the pufferfish larvae. Furthermore, the whole life stadium between larvae and adult is also still unknown and would possibly hold further insight into the reason why these pufferfish construct such elaborated nests.

In 2020 during surveillance of deep-sea pipelines by a remote operated vehicle, similar sand circles were discovered as the ones observed in Japan (Bond et al., 2020). These circles were observed approximately 130 kilometers off the Australia's Northwest coast in the southern region of the North West Shelf at a depth around 130 meters. The pufferfish which was present close to the circles was only identified by a low-resolution camera (figure 8) and thus it is hard to definitively conclude that this species is indeed the white spotted pufferfish (*Torquigener albomaculosus*). This might be an indication that the white spotted pufferfish is actually living at greater depths than the depth which was observed in Japan. Furthermore, Bond et al. noticed that the pufferfish had only build nest along pipelines which were dug into the seabed, and that no nests were present at pipelines which laid on the seabed ((Bond et al., 2020). This might be an indication of how we as humans impact deep sea ecosystems with our pipe laying.

Figure 8. *Examples of pufferfish found in close proximity to Australian circles. Left and center (14/19): dorsal view of two individuals of Torquigener sp. recorded by the hybrid autonomous underwater vehicle downward-looking still camera along the Echo-Yodel umbilical close to pufferfish circles. Right (22): lateral view of an individual recorded by the baited remote underwater stereo-video system. Source: Mystery pufferfish create elaborate circular nests at mesophotic depths in Australia, Bond et al. 2020*

In April of 2023, Thomas et al. published a paper proposing bio-inspired wave breakers. One of these proposed designs was inspired by the nest of the white spotted pufferfish (*Torquigener albomaculosus*). Even though the wave breakers were designed as a form of coastal protection, I believe the application of the design of the white spotted pufferfish can also aid in the reintroduction of mangroves, seagrass, mussels and oysters. Mangrove populates (Asian Development Bank, 2018; Makowski & Finkl, 2018), seagrass (Gräfnings et al., 2022; van Katwijk et al., 2016), mussels (Alder et al., 2021), and oysters (Goelz et al., 2020) all cope with the fact that in the early stages of life as a larva or during germination they are at their most vulnerable and thus require shelter. It should be investigated whether small structures based on the design of the white spotted pufferfish (*Torquigener albomaculosus*) nest may aid in the survival rate during these early stages and thus benefit the reintroduction of these species. Furthermore, if made out of biodegradable material it could be placed without the need of retrieving it later. Further research into the application of these concepts would be needed to confirm the effectiveness of the proposed 'circle shelter'.

Conclusion

Male white spotted pufferfish (*Torquigener albomaculosus*) make incredible nests to attract mates and to hatch their eggs. The circle is built in a way that provides reduced water flow over the inner circle of the nest and provides extra circulation of fresh salt water. This increases the aeration of the eggs while also protecting them by reducing the shear stress on the inner circle. Furthermore, the pufferfish is able to separate fine and rough sand for its inner circle during the construction leading to an accumulation of fine sand in the center of the circle. Comparisons with other fish species show the importance of the right size spawning substrate to balance aeration of the eggs and protection against predation, but if this is applicable to the pufferfish remains unknown and thus requires further research. Since the discovery of the fish in 2011 a lot has been uncovered about its nests, but there still remains much to discover. Due to a male nest-building dominated perspective in the literature not much is known about the benefits for the female pufferfish or the fitness of building a nest. Future studies are required to uncover the sex-specific benefits of the sand circle. By making some comparisons with other bird and marine species, we are able to investigate such benefits like the nest being an indication of fitness, presence of a male or parental investment. Since the pufferfish has a unique way of reproduction (polygamy and mating multiple times with different females) it can also be suggested that the circle serves a crucial role in the selection of a mate. So in the end the male pufferfish might use these circles to 'puff' its chest out in the name of love, but the circles do deserve a 'round' of applause for its near 'puff-fection'.

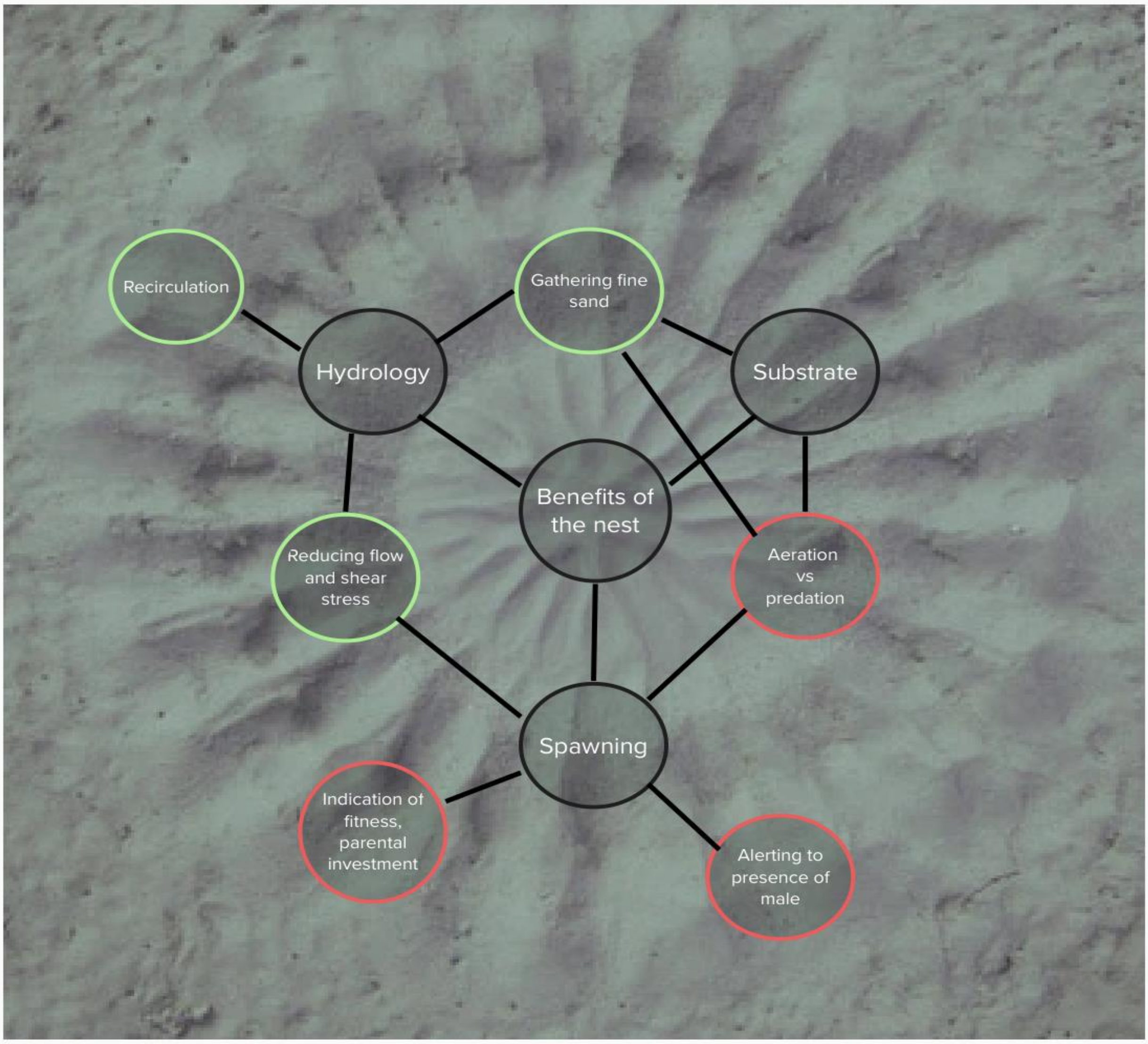

Figure 9. *Visualization of the benefits gained by the white spotted pufferfish nest building. All topics circled by green are proven by literature and all topics circled by red are parallels with other animals but yet to be confirmed by research into the pufferfish.*

References

Alder, A., Jeffs, A., & Hillman, J. R. (2021). Considering the use of subadult and juvenile mussels for mussel reef restoration. Restoration Ecology, 29(3). https://doi.org/10.1111/rec.13322

Asian Development Bank. (2018). A Community-Based Mangrove Planting Handbook for Papua New Guinea. https://doi.org/10.22617/TIM189796-2

Barber, I., Nairn, D., & Huntingford, F. A. (2001). Nests as ornaments: revealing construction by male sticklebacks. In Behavioral Ecology (Vol. 12).

Bond, T., Mueller, R. J., Birt, M. J., Prince, J., Miller, K., Partridge, J. C., & McLean, D. L. (2020). Mystery pufferfish create elaborate circular nests at mesophotic depths in Australia. Journal of Fish Biology, 97(5), 1401–1407. https://doi.org/10.1111/jfb.14506

Borgia, G., & Collis, K. (1989). Behavioral Ecology and Sociobiology Female choice for parasite-free male satin bowerbirds and the evolution of bright male plumage. Behav Ecol Sociobiol, 25, 445–454.

Borgia, G., & Collis, K. (1990). Parasites and Bright Male Plumage in the Satin Bowerbird (Ptilonorhynchus violaceus). Integrative and Comparative Biology, 30(2), 279–286. https://doi.org/10.1093/ICB/30.2.279

Christy, J. H., Backwell, P. R. Y., Goshimab, S., & Kreutera, T. (2002). Sexual selection for structure building by courting male fiddler crabs: an experimental study of behavioral mechanisms. Behavioral Ecology, 13(3), 366–374. https://doi.org/10.1093/BEHECO/13.3.366

Gladstone, W. (1987). The courtship and spawning behaviors of Cunthigaster valentini (Tetraodontidae). Environmental Biology of Fishes, 20(4), 2–261.

Gladstone, W. (1994). Lek-like spawning, parental care and mating periodicity of the triggerfish Pseudobalistes flavimarginatus (Balistidae). Environmental Biology of Fishes , 39, 249–257.

Goelz, T., Vogt, B., & Hartley, T. (2020). Alternative Substrates Used for Oyster Reef Restoration: A Review. Journal of Shellfish Research, 39(1), 1–12. https://doi.org/10.2983/035.039.0101

Gräfnings, M. L. E., Heusinkveld, J. H. T., Hoeijmakers, D. J. J., Smeele, Q., Wiersema, H., Zwarts, M., van der Heide, T., & Govers, L. L. (2022). Optimizing seed injection as a seagrass restoration method. Restoration Ecology, 31(3). https://doi.org/10.1111/rec.13851

Hjulström, F. (1935). Studies of Morphological Activity of Rivers as Illustrated by the River Fyris. Bulletin of the Geological Institute University of Uppsala, 25, 221–527.

Honma, Y., Ozawa, T., & Chiba, A. (1980). Maturation and Spawning Behavior of the Puffer,Fugu niphobles, Occurring on the Coast of Sado Island in the Sea of Japan (A Preliminary Report). In Japanese Journal of Ichthyology (Vol. 27, Issue 2).

Kawase, H. (2002). Simplicity and diversity in the reproductive ecology of triggerfish.

Kawase, H. (2003). Spawning behavior and biparental egg care of the crosshatch triggerfish, Xanthichthys mento (Balistidae). Environmental Biology of Fishes, 66, 211–219.

Kawase, H., Kitajima, Y., & Iwai, D. (2022). 3D model of the geometric nest structure, the "mystery circle," constructed by pufferfish. Scientific Data 2022 9:1, 9(1), 1–4. https://doi.org/10.1038/s41597-022-01466-4

Kawase, H., Mizuuchi, R., Shin, H., Kitajima, Y., Hosoda, K., Shimizu, M., Iwai, D., & Kondo, S. (2017). Discovery of an Earliest-Stage "Mystery Circle" and Development of the Structure Constructed by Pufferfish, Torquigener albomaculosus (Pisces: Tetraodontidae). Fishes 2017, Vol. 2, Page 14, 2(3), 14. https://doi.org/10.3390/FISHES2030014

Kawase', H., & Nakazono, A. (1995). Predominant maternal egg care and promiscuous mating system in the Japanese filefish, Rudarius encodes (Monacanthidae). Environmental Biology of Fishes, 43, 241–254.

Kawase, H., & Nakazono, A. (1996). Two alternative female tactics in the polygynous mating system of the threadsail filefish, Stephanolepis cirrhifer (Monacanthidae). Ichtyological Research, 43(3), 315–323.

Kawase, H., Okata, Y., & Ito, K. (2013). Role of huge geometric circular structures in the reproduction of a Marine pufferfish. Scientific Reports, 3. https://doi.org/10.1038/srep02106

Kawase, H., Okata, Y., Ito, K., & Ida, A. (2014). Spawning behavior and paternal egg care in a circular structure constructed by pufferfish, Torquigener albomaculosus (Pisces: Tetraodontidae). Bulletin of Marine Science, 91(1), 33–43. https://doi.org/10.5343/bms.2014.1055

Makowski, C., & Finkl, C. (2018). Threats to Mangrove Forests. http://www.springer.com/series/8795

Matsuura, K. (2014). A new pufferfish of the genus Torquigener that builds "mystery circles" on sandy bottoms in the Ryukyu Islands, Japan (Actinopterygii: Tetraodontiformes: Tetraodontidae). Ichthyological Research, 62(2), 207–212. https://doi.org/10.1007/s10228-014-0428-5

Mizuuchi, R., Kawase, H., Shin, H., Iwai, D., & Kondo, S. (2018). Simple rules for construction of a geometric nest structure by pufferfish. Scientific Reports, 8(1), 12366–12366. https://doi.org/10.1038/S41598-018-30857-0

Nakazono, A., & Kawase, H. (1993). Spawning and biparental egg-care in a temperate filef'ish, Paramonacanthus japonicus (Monacanthidae). Environmental Biology of Fishes, 37, 245–256.

Palm, D., Lindberg, M., BrännäS, E., Lundqvist, H., Östergren, J., & Carlsson, U. (2009). Influence of European sculpin, Cottus gobio, on Atlantic salmon Salmo salar, recruitment and the effect of gravel size on egg predation - implications for spawning habitat restoration. Fisheries Management and Ecology, 16(6), 501–507. https://doi.org/10.1111/j.1365-2400.2009.00705.x

Sear, D. A., Pattison, I., Collins, A. L., Newson, M. D., Jones, J. I., Naden, P. S., & Carling, P. A. (2014). Factors controlling the temporal variability in dissolved oxygen regime of salmon spawning gravels. Hydrological Processes, 28(1), 86–103. https://doi.org/10.1002/hyp.9565

Shameem, A. J., Valyrakis, M., & Zare-Behtash, H. (2021). A Fluid Dynamics Approach for Assessing the Intelligent Geomorphic Design of the Japanese Pufferfish Nest. V11 N22 (20210101): 22, 11(22), 22. https://doi.org/10.3390/geosciences11010022

Silva, S., Gooderham, A., Forty, M., Morland, B., & Lucas, M. C. (2015). Egg drift and hatching success in European river lamprey Lampetra fluviatilis: Is egg deposition in gravel vital to spawning success? Aquatic Conservation: Marine and Freshwater Ecosystems, 25(4), 534–543. https://doi.org/10.1002/aqc.2486

Soler, J. J., Cuervo, J. J., Pape Møller, A., & Lope, F. DE. (1998). Nest building is a sexually selected behaviour in the barn swallow. ANIMAL BEHAVIOUR, 56, 1435–1442.

Thomas, C., Lieunard, V., Oudon, B., Bain, O., Le Bivic, R., & Coutu, A. (2023). Bio-inspired wave breakers to reduce swell erosion in the Bay of Biscay using Computational Fluid Dynamics. Regional Studies in Marine Science, 62. https://doi.org/10.1016/j.rsma.2023.102965

van Katwijk, M. M., Thorhaug, A., Marbà, N., Orth, R. J., Duarte, C. M., Kendrick, G. A., Althuizen, I. H. J., Balestri, E., Bernard, G., Cambridge, M. L., Cunha, A., Durance, C., Giesen, W., Han, Q., Hosokawa, S., Kiswara, W., Komatsu, T., Lardicci, C., Lee, K. S., … Verduin, J. J. (2016). Global analysis of seagrass restoration: The importance of large-scale planting. Journal of Applied Ecology, 53(2), 567–578. https://doi.org/10.1111/1365-2664.12562

Yamahira, K. (1994). Combined effects of tidal and diurnal cycles on spawning of the puffer, Takifugu niphobles (Tetraodontidae). Environmental Biology of Fishes, 40, 255–261.