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A predatory use of counterillumination by the squaloid shark, *Isistius brasiliensis*

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Synopsis

A number of very unusual morphological and behavioral characteristics attributed to the cookie-cutter shark, *Isistius brasiliensis*, may be explained by a novel use of counterillumination. Specifically, it is proposed that a band of pigment, located beneath the jaw and bounded by ventrally directed bioluminescence, acts as a lure which mimics the search image of many upward-looking pelagic predators.

Introduction

The bioluminescent pelagic squaloid shark, *Isistius brasiliensis* (Figure 1), has acquired the common name of 'cookie-cutter shark' because of its very unusual feeding style, that apparently involves extracting cookie-shaped plugs of flesh from fast swimming, larger predators such as tunas, swordfish and porpoises. Evidence for this theory comes from the crater-shaped wounds found on fishes and cetaceans which match the plugs of flesh found in the stomachs of *Isistius brasiliensis*, as well as the unusual shape of this shark's dentition (Jones 1971) (Figure 2). Large whole squid (15-30 cm) are also commonly found in the stomachs of these small (29-46 cm) slow-swimming sharks (Strasburg 1963) which raises the obvious question: How does such a predator manage to attack larger and swifter prey? A unique and heretofore unsuggested application of bioluminescence is proposed as an answer to this riddle.

Distribution patterns

Isistius brasiliensis is a schooling dwarf shark found in tropical waters (Parin 1966). Specimens have been collected, both near shore and in the open ocean, using nets at trawling speeds as slow as 2.5 kts (Strasburg 1963). Although collections have been made as deep as 3500 m (Parin 1966), most specimens have been taken in surface waters at night and evidence seems to suggest that these sharks are vertical migrators (Strasburg 1963).

Specialized morphology

Isistius brasiliensis exhibits unique morphological adaptations related to a specialized feeding behavior. The upper and lower teeth are profoundly different, with the upper teeth being small, slender and thorn-like while the lower, mandibular teeth are much larger, flattened and triangular (Bigelow & Schroeder 1948) (Fig. 2). Although most sharks replace their teeth one at a time, in *I. brasiliensis* the mandibular teeth are interconnected in such a way

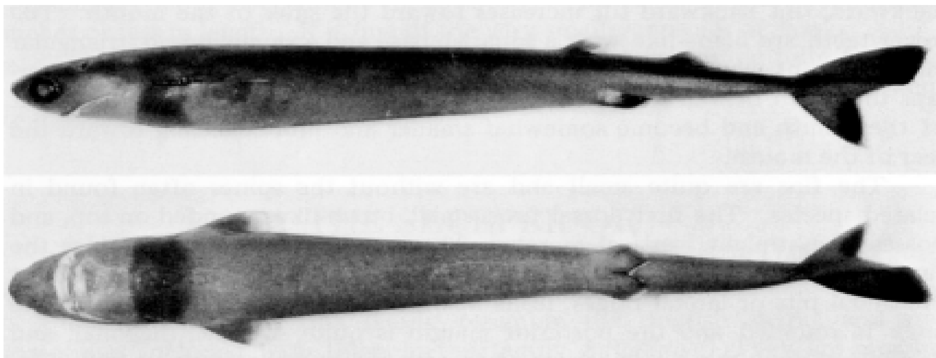

Figure 1. The bioluminescent shark, *Isistius brasiliensis*, showing the darkly pigmented 'dog collar' under the jaw. Approximate length, 50 cm (reproduced with permission from Tinker 1978).

that all the teeth must be shed at once and are replaced as a fully functional unit. To replace all the teeth when only one is damaged requires a considerable energy investment and points to strong selective pressures for maintaining a fully functional jaw. Additionally, this shark has a large gape and protruding lateral lips which enable it to pull an oral vacuum against a smooth surface by closing off the spiracles located on the top of the head and then retracting the tongue. On one occasion, when a living specimen of *I. brasiliensis* was presented with a fish in air, it produced an oral vacuum sufficient to lift the fish from a table (Jones 1971).

Striking differences between the internal anatomy of *Isistius brasiliensis* and that of another dwarf pelagic shark, *Euprotomicrus bispinatus*, further highlight the specialized morphology of the cookie - cutter shark. While the skeleton of *E. bispinatus* is soft and lacking in calcification, as is often the case in neutrally buoyant pelagic dwarf species, in *I. brasiliensis* the cranial and labial cartilages are hard and calcified. However, the additional weight resulting from this heavy jaw structure is apparently offset by the fact that, compared to *E. bispinatus, I. brasiliensis* has an exceptionally enlarged liver, that

Figure 2. The unusual jaw, dentition and suctional lips of *Isistius brasiliensis.* Approximate length of specimen, 38 cm (reproduced from California Polytechnic State University computer data base, photo by Don Nelson).

fills almost the entire body cavity (Hubbs et al. 1967)

Bioluminescence

Isistius brasiliensis is bioluminescent, possessing thousands of extremely tiny photophores (0.03-0.05 mm in diameter) that form a dense network around the edges of the scales and cover the entire ventral surface of the body, except for a darkly pigmented band just behind the mouth, in the pharyngeal area (Parin 1966) (Figure 1). Bioluminescence in *I. brasiliensis* was first described by Bennett (1840) who provides the most detailed description, yet reported, of luminescence in these sharks. The following observations were made on a specimen collected at night and taken into a dark room: 'The entire inferior surface of the body and head emitted a vivid and greenish phosphorescent gleam, imparting to the creature, by its own light, a truly ghastly and terrific appearance. The luminous effect was constant, and not perceptibly increased by agitation or friction. I thought, at one time, that it shone brighter when the fish struggled, but I was not satisfied that such was the fact. When the shark expired (which was not until it had been out of the water more than three hours) , the luminous appearance faded entirely from the abdomen, and more gradually from other parts; lingering the longest around the jaws and on the fins.

The only part of the under surface of the animal which was free from luminosity was the black collar around the throat; and while the inferior surface of the pectoral, anal[1], and caudal fins shone with splendor, their superior surface (including the upper lobe of the tail-fin) was in darkness, as also were the dorsal fins, back and summit of the head.

I am inclined to believe that the luminous power of this shark resides in a peculiar secretion from the skin. It was my first impression, that the fish had accidentally contracted some phosphorescent matter from the sea, or from the net in which it was captured; but the most rigid investigation did not confirm this suspicion; while the uniformity with which the luminous gleam occupied certain portions of the body and fins, its permanence during life, and decline and cessation upon the approach and occurrence of death, did not leave a doubt in my mind that it was a vital principle, essential to the economy of the animal.

The small size of the fins would appear to denote that this fish is not active in swimming; and since it is highly predaceous, and evidently of nocturnal habits, we may perhaps indulge in the hypothesis, that the phosphorescent power it possesses is of use to attract its prey, upon the same principle as the Polynesian Islanders, and others, employ torches in night fishing'. (Bennett 1840).

The ventrally directed bioluminescence, that Bennett describes in *Isistius brasiliensis*, is a common attribute among mesopelagic organisms, that use luminescence to camouflage their silhouettes. In the dim twilight depths of the ocean where many animals operate at the very limits of visual perception, the brightest light for seeing comes from above and the only objects that are visible are those that are silhouetted against that dim light. Many predators, therefore, hunt for prey by searching the waters above for a dark silhouette that may reveal the presence of a fish, squid or shrimp. To avoid detection by these predators, many prey have evolved a concealment mode, known as counter-illumination, which involves replacing the filtered sunlight that is absorbed or reflected by their body tissues with bioluminescence (Clark 1963) (Figure 3). The effectiveness of this camouflage strategy demands that the bioluminescence provide a close match to the color, intensity and angular distribution of the downwelling light field and it has been found that animals have met this evolutionary challenge with a remarkable variety of solutions (see Buck 1978, Young 1983 and Widder 1998, for reviews). The extent of convergent evolution associated with counterillumination is a testament to the extreme selective advantage afforded by this trait.

In most cases counterillumination is produced by discrete photophores, the effect of which is to produce a disruptive pattern, which breaks up the silhouette and, at a distance, blends with the background light, making it that much more difficult for

[1]Since squaloid sharks lack an anal fin, Bennett probably meant to indicate the pelvic fins.

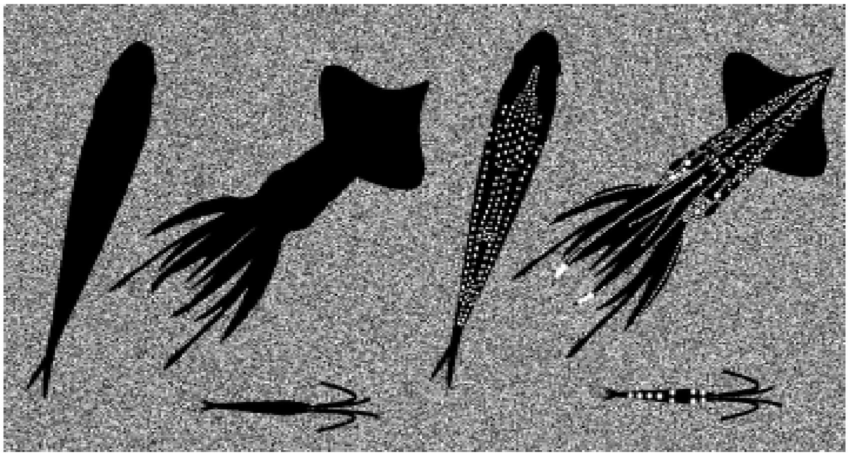

Figure 3. Illustration of how ventral photophores camouflage the silhouettes of midwater organisms, as seen from below, against a background of dim downwelling solar irradiance (based on a diagram from Edmunds 1974). The fish *Neoscopelus*, the squid *Abraliopsis* and a euphausiid, are shown against the background light field as seen without bioluminescent photophores, on the left, and with bioluminescent photophores, on the right. Scattering of light in the ocean reduces contrast causing the photophore patterns to blur and blend in with the background at a distance. Additionally, animals may assume postures which enhance the effect, such as rolling the fins over the back, in the case of the squid (*Neoscopelus*: after Herring 1978, p. 316; *Abraliopsis*; after Herring 1978, p. 209; euphausiid after Herring 1978, p. 224).

predators to recognize the silhouettes of their prey. Presumably the grain of the photophore pattern may be taken as a measure of the perceptive powers of the eyes that it must deceive. In this respect, the exceptionally high density of extremely small photophores found in *Isistius brasiliensis* is remarkable, in that the pattern is so fine-grained that the luminescence appears as a diffuse glow to the human eye, even under close inspection (Bennett 1840). This suggests that this luminescence pattern is directed toward visual predators with unusually high acuity or that it must function at unusually close range.

A predatory use of counterillumination

Since any mismatch between ventrally directed bioluminescence and the background light field would be visible to predators and therefore selected against, such an obvious aberration as the non-luminescent band found on the ventral surface of *Isistius brasiliensis* requires explanation. Sometimes referred to as the ‘dog collar’, this region is not only wholly lacking in photophores but is also darkly pigmented and tapered at the ends and would therefore produce the effect of a dark, fusiform silhouette against the downwelling lightfield (Figure 4). This apparent mimicry of the search image employed by many upward looking predators, and the location of the collar right behind the mouth, suggest that this unusual counterillumination pattern might function as a lure. Although the use of bioluminescence as a lure is well known, in angler fish, viper fish and flashlight fish, to name just a few of the better known examples, in this case, it appears that the actual lure is non luminescent. However, the form of the lure is defined by the bioluminescence that surrounds the area and serves to conceal the true outline of the shark.

Therefore, the answer suggested here, to the riddle of how these sharks manage to attack larger and swifter prey, is that the prey are lured into striking distance by what appears to be the silhouette of a small fish. The extremely fine grain of the ventral bioluminescence on *Isistius brasiliensis* is therefore accounted for as a means of ensuring that the prey will not recognize its mistake and abort the attack too soon. On the other hand, the large, oval eyes of the shark may permit it to see the prey in time to execute an evasive maneuver. The upward attack of the larger and swifter prey could then be used to the shark’s advantage, allowing *I. brasiliensis* to latch on to the side of its victim, as the prey’s upward

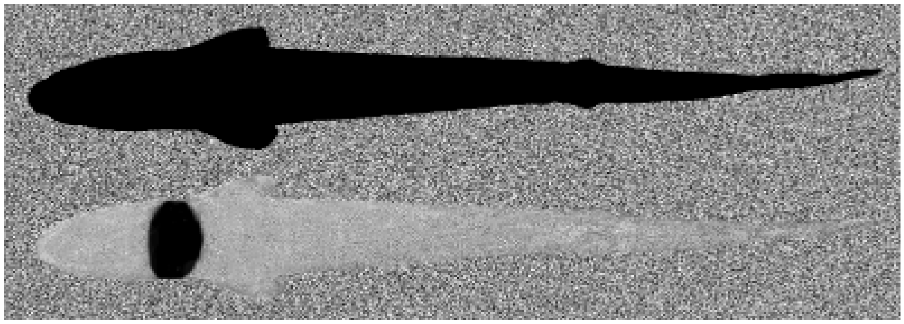

Figure 4. Illustration of how the counterillumination pattern of *Isistius brasiliensis,* shown below, masks the true outline of the shark, shown above. The high density of very small photophores which cover the entire ventral surface, except for the 'dog collar', produce a near perfect match with the background light field, leaving only the fish-shaped lure visible. The illustration was generated using outlines copied from the photograph in Figure 1.

momentum carries it past the shark. Once the shark has locked onto its victim, the mismatch between upper and lower teeth requires that the body of the shark rotate around the point of attachment, in order to allow the mandibular teeth to carve out a plug of flesh. The prey's propulsion may provide most of the rotational energy required for this maneuver, as the drag of the water on the shark's torpedo shape and the dorsal fins positioned on the posterior half of the trunk will cause it to rotate into the direction of flow produced by its victim and as Jones (1971) so aptly describes it, the teeth will 'act in the manner of a melon-ball cutter' leaving a crater-shaped wound on the victim. If the victim thrashes about in an attempt to shake off the shark, then so much the better, as *I. brasiliensis* can use its ability to pull an oral vacuum in order to remain attached until the gyrations of the victim provide sufficient rotational energy to pull the plug free.

The large whole squid, that have also been found in the stomachs of these sharks (Strasburg 1963), may be accounted for by a very similar technique. Assuming the shark can identify its prey, then with squid, no evasive maneuver is necessary. In the moment before the squid strikes, the shark need only open its jaws, close the spiracles and raise the tongue, to apply suction, and predator becomes prey as the attacking squid is consumed whole.

Since the illusion of the fish silhouette will only work at depths where the intensity of the shark's ventrally directed bioluminescence can match the downwelling light, the fact that *Isistius brasiliensis* vertically migrates is of critical importance to maintaining the illusion. Small rapid changes in downwelling irradiance, due to passing clouds, may be adjusted for through a variety of physiological feedback control mechanisms, that allow counter-illuminators to alter their bioluminescence to match the downwelling light. However, changes in cloud cover generally encompass a range of less than an order of magnitude. Over the course of a 24 hour cycle, light changes some six orders of magnitude, between full sunlight and full moonlight and nine orders of magnitude between sunlight and starlight (Lythgoe 1979). Therefore, counterilluminators must adjust their depth in order to remain within the relatively narrow light range that their bioluminescence can match (see Young 1983 and Widder 1998, for reviews). Vertical migration by *I. brasiliensis* is thus a behavioral adaptation that serves to attract visual predators, rather than to hide from them, which is the function most often attributed to this behavior.

Another behavior that may serve to enhance the effect of the lure is the schooling of *Isistius brasiliensis*. In a group, these counterilluminating sharks would appear like a school of small fish, which should make the lure both more conspicuous and more tempting. Schooling may also explain how these very small sharks avoid a counterattack from the very large predators such as swordfish and porpoises on which their crater wounds are commonly found. The damage these sharks inflict would make their company as appealing as a swarm of wasps.

Discussion

In the evolutionary arms race between predators and prey, predators that can not outrun their prey often resort to deception and ambush. This is a feeding style that appears to explain several highly unusual attributes connected with the morphology and natural history of *Isistius brasiliensis*. Primary among these is the dark pigment band that appears to mar what is an otherwise near-perfect counter-illumination pattern. That this band seems to mimic the silhouette, which is the search image of most mesopelagic predators and that it is located in such close proximity to the unique and relatively massive jaw structure of these very small sharks, suggests that it may function as a lure. Although the idea that *I. brasiliensis* might be using its bioluminescence to attract prey was first suggested by Bennett (1840) more than 150 years ago and was restated by Jones (1971), neither of these authors mentioned the 'dog collar' in this regard.

In his comprehensive description of adaptive coloration in animals, Cott (1957) describes one form of disruptive pattern, known as differential blending, where some areas blend in with the background while other, highly contrasted, areas stand out starkly against the same background. The illusion of the lure in *I. brasiliensis* is a consequence of differential blending, where bioluminescence masks the true outline of the shark while defining the outline of the darkly pigmented 'dog collar'. Since this illusion will only work against a background radiance comparable to that which the shark can match with its bioluminescence, the illusion is dependent on the vertical migration behavior of these sharks.

Both bioluminescence and vertical migration require energy. However, so does searching for prey, especially in the open ocean. The use of a lure is an energy conserving tactic that allows a predator to take advantage of the muscle power of prey. Some evolutionary consequences of this strategy are the small fins, flabby musculature and neutral buoyancy commonly associated with such sit-and-weight pelagic predators as angler fish. *I. brasiliensis* apparently exhibits these same traits, except for the relatively massive and calcified jaw structure needed to attach and hold onto large and fast moving prey. However, the weight of the jaw is counterbalanced by an exceptionally enlarged liver, thus providing the neutral buoyancy expected of a sit-and-wait predator.

Bioluminescence is believed to serve a multitude of different functions in different animals (see Buck 1978, Morin 1983; Young 1983, Herring 1990, and Widder 1998). These functions fall into the three broad categories of finding food, finding mates and defending against predators. Counterillumination is generally assigned to the last category since it is thought to be an adaptation of prey to avoid detection by visual predators. However, *Isistius brasiliensis* appears to represent a case where counterillumination serves the first category, finding food and therefore, the use of bioluminescence in these very unusual sharks, should be assigned a predatory function.

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