Splatoon was recently released (second quarter of 2015) for the Wii U, receiving a warm welcome by Nintendo fans (it’s nigh unthinkable for the company to launch a new IP like this) and generating a flood of fan art on the Internet. The game is a third-person shooter with ink instead of bullets. It features two races, inklings (the playable one) and octarians (the enemies), and revolves around the fierce dispute against each other. (In multiplayer though, its inkling against inkling.) Inklings and octarians (especially the elite soldiers called “octolings”) are based, respectively, on squids and octopuses (Fig. 1), two of the most awesome kinds of animals out there.

These animals are mollusks, and, more specifically, cephalopods. The mollusks are the second largest animal group on Earth (after the arthropods, of course) and includes gastropods (snails and slugs), bivalves (clams, mussels and oysters), cephalopods (we’ll come back to them soon) and the little known scaphopods (tusk shells), monoplacophorans, aplacophorans, polyplacophorans (chitons) and some fossil oddities. For those who remember their biological classification, we can put it like this: the class Cephalopoda belongs to the phylum Mollusca.

Cephalopoda is a group that contains a vast array of marine animals. Besides squids and octopuses, it counts with cuttlefish, nautiloids and the fossil belemnites and ammonoids. Today, cephalopods are found everywhere in the sea, from the polar regions to the tropics and from the surface to depths over 5,000 m. There are over 800 known living species of cephalopods, but the fossil record counts with more than 17,000 species (Boyle & Rodhouse, 2005; Rosenberg, 2014).

The class appeared over 450 million years ago during the late Cambrian, the first period of the Paleozoic era (Boyle & Rodhouse, 2005; Nishiguchi & Mapes, 2008). Cephalopods enjoyed a high amount of diversity during the Paleozoic and Mesozoic eras, with hundreds of species of nautiloids and ammonoids (Monks & Palmer, 2002). Most of these forms, however, did not survive to this day. Ammonoids and belemnites were completely extinguished and today we have just a handful of Nautilus species and the group consisting of cuttlefish, squids and octopuses. This group is a latecomer in cephalopod history: it appeared only during the
Mesozoic, although some late Paleozoic fossils have tentatively been classified as squids (Boyle & Rodhouse, 2005; Nishiguchi & Mapes, 2008). OK, so we can all see that Splatoon is a cephalopod-themed game. But before we can say something about the critters starring in Splatoon, we must first clear some Biology stuff. The foremost of these issues is: there is a long-lived and persistent confusion in popular knowledge, art and fiction, regarding squids and octopuses. People just do not seem to know which is which. Many biologists have bemoaned this and tried to set things right in popular works for quite a while (e.g., Lee, 1883; Salvador & Tomotani, 2014). Since these animals are our main theme here, we feel obliged to explain what, after all, are the differences between a squid and an octopus.

Figure 1. Top left: an inkling girl in human form (original model from the game). Top right: *Loligo vulgaris*, an example of a squid species (photo by Hans Hillewaert, 2005; image modified from Wikimedia Commons). Bottom left: an elite octarian soldier, a.k.a. octoling (original artwork from the game). Bottom right: *Octopus rubescens*, an example of an octopus species (photo by Taolland82, 2007; image modified from Wikimedia Commons).
SQUID OR OCTOPUS?

For the uninitiated (i.e., those whose sad childhoods did not include wildlife documentaries and visits to zoos and/or aquariums), squids and octopuses look the same. However, if one pays attention and carefully compare one to the other, many differences start to pop up. The first one is the overall shape of their bodies (Fig. 2): squids usually have a bullet-like shape and a more hydrodynamic body, with a pair of fins on their extremity; octopuses have a globose body, which is capable of some serious shape-changing. These animals’ shapes are linked to their way of life: squids are active swimmers, while octopuses live on the sea floor, hiding under rocks or inside burrows.

![Figure 2](image.png)

Figure 2. Diagrams of a squid (above) and an octopus (below), accompanied by the proper scientific terminology of their body parts. Image reproduced from Salvador & Tomotani (2014).

Nevertheless, there is an even more striking difference (Fig. 2): an octopus has only eight arms, while a squid has eight arms and two tentacles (readily identifiable: they are more slender and usually longer than the arms).
The difference in meaning between “arm” and “tentacle” is crucial, but these words unfortunately are used interchangeably in popular writing. The arms of both squids and octopuses are covered with suction cups (or suckers) on their inner surface. (These suckers are sessile in octopuses, but squids have stalked mobile ones.) The tentacles, present only in squids, are smooth (i.e., without suckers) along almost their entire length; only the tentacle’s tip (called “club”) has suckers (Fig. 2).

Despite the popular confusion of squid/octopus and arm/tentacle, it seems Splatoon’s developers took care to be as accurate as they could with their cartoonish squids. The inklings, when in squid form, have the correct number of arms, with the two tentacles clearly differentiated (Figs. 4, 9). Incredibly, this is also true for an inkling in human form and the game’s official Japanese Twitter took some pains to show it is so (Fig. 3).

Finally, the last main difference lies inside their bodies. As anyone can tell, the most obvious feature of mollusks is their shells; just think of a snail or a clam and you immediately picture their shells. However, most living cephalopods do not have shells (nautiluses and the tiny Spirula spirula are the exception).

Squids have only a remnant of a shell called a “pen” (or gladius) that serves as a skeletal support for their bodies. Octopuses, however, have absolutely no shell whatsoever. In all other respects, squids and octopuses are very similar, since they are both cephalopods. So now we will dabble a little in cephalopod anatomy, because we will need some concepts to discuss other features from Splatoon.

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**Figure 3.** Diagram showing the correspondence of arms between an inkling (in human form) and a real squid. The tentacles are numbered as 1 and 2, while the remaining arms are numbered 3 to 10. Image taken from Splatoon’s official Japanese Twitter (https://twitter.com/SplatoonJP).

**CEPHALOPOD ANATOMY**

Before moving on to other topics, we have one final note on tentacles. The inkling boy’s tentacles, more specifically the club on the tip of each tentacle, are smaller than the inkling girl’s is. The official artwork seems to suggest that this is the case (Fig. 4) and this was confirmed in-game at least for the inklings in human form (it was difficult to compare squid forms due to all the shooting). Moreover, this is clearly seen on the Amiibo figures, where the boy’s tentacle clubs are about half the size of the girl’s (Fig. 5).

Sexual dimorphism (i.e., male and female of the same species looking different) is rather common in cephalopods and the difference usually lies on overall body size: in some species the males are larger while in others the females are the larger ones (Boyle & Rodhouse, 2005). However, differences in the size of tentacles and clubs seem to be rare, known only from cuttlefish (Bello & Piscitelli, 2000). Perhaps this matter was not investigated enough in other species, meaning that differences in tentacle or
club size could be more widespread in cephalopods. In any case, Bello & Piscitelli (2000) studied the species *Sepia orbignyana*, in which the females are larger than the males. They discovered that the female’s tentacle clubs were also proportionately larger (in relation to the body) than the male’s. They discuss that this feature is linked to feeding: cuttlefish use their tentacles to capture prey and, since females are larger and need more food, individuals with larger clubs have an advantage (they are able to capture larger prey) and were thus selected through the species’ evolutionary history.

**Figure 4.** Inking girl (top) and boy (bottom) in both human and squid forms. (Original artwork from the game.)

**Figure 5.** Photos of the Amiibo figures of the inkling girl (left) and boy (right) in human form. Note how the girl’s tentacles are much larger than the boy’s.

Now, moving on with the anatomy. The mouth of a cephalopod is located in the middle of the circle formed by the arms. It contains a pair of powerful chitinous mandibles, which together are called a “beak” due to their resemblance to a parrot’s beak (Fig. 6).

Inside the mouth lies the radula, a rasping tongue-shaped structure equipped with many rows of small chitinous teeth (Fig. 7). The animals use the radula to “scratch” their food and pluck small portions of it. (Note that the radula is a feature common to all mollusks, with the notable exception of the bivalves, which are filter feeders and have lost the radula in the course of evolution.) In Splatoon, the designers’ care is shown here once more: inklings in human form have pointed teeth to emulate the sharp beaks of squids.

Cephalopods breathe through gills located inside the mantle cavity (Fig. 8). The water enters this cavity through apertures on the mantle edge close to the head and brings dissolved oxygen to the gills. The water is then expelled from the cavity by a structure called
“funnel”. The funnel is also capable of expelling a powerful gush of water, which is responsible for the fast jet propulsion movement of cephalopods.

Figure 6. A (dead) specimen of the squid species *Loligo sanpaulensis*. The top image show the whole body of the animal. The bottom left image shows the mouth region on the center of the ring of arms and tentacles. The bottom right inset shows a close-up of the mouth, with the beak barely visible on its center. The last two insets on the very bottom right show the beak (removed from the specimen) in frontal and lateral views.
Figure 7. The radula (removed from the specimen of Fig. 6), shown straightened out. Notice the neat rows of pointy little “teeth”.

Figure 8. The arrows indicate the way in which water passes through the squid’s body, entering the mantle cavity (shown in transparency), passing by the gills and exiting via funnel (shown in two positions, for forward and backwards movement). Image reproduced from Richard E. Young, 2000, The Tree of Life Web Project (Creative Commons Attribution Non Commercial License 3.0).

If inklings can leap very high from a pond of ink when in squid form, jet propulsion is the reason why. This might better be called “ink-jet-propulsion”, though (Fig. 9).

As a matter of fact, the funnel has an important role in the most characteristic aspect of cephalopod biology: inking. And this is what we will turn to now.

INK

Inside the mantle cavity there is an organ known as “ink sac”, which, as the name implies, is a reservoir of ink. The animals can expel this ink through the funnel and they do this in two very ninja-like manners: as clouds or as pseudomorphs (Derby, 2007). Ink clouds are pretty straightforward, functioning as a smoke screen to allow the cephalopod to escape (Fig. 10); although some recent observations show that they can also be used to confuse and sneak attack prey (Sato et al., 2016). Pseudomorphs (meaning “false-shapes”) are more curious things. They are made of ink and mucus and appear as a well-defined and stable form (maintaining its physical integrity for a while after it is released). These pseudomorphs can be almost as large as the animal releasing them. It is thought they serve as a decoy, a fake double of the cephalopod which will distract the predator and allow it to escape unharmed. Finally, cephalopods’ ink might also contain organic compounds that act either as toxins to deter or damage enemies or as signals to warn...
Inconspecifics (members of the same species) of any danger (Derby, 2007).

**Figure 10.** Ink cloud created by a Humboldt squid, *Dosidicus gigas*. Image reproduced from Bush & Robinson (2007).

In Splatoon, the main purpose of the ink is, well, to ink stuff. Inklings shoot ink through guns (not funnels), hoping to beat their opponents senseless (“splat” them, as the game puts it) and to ink the largest portion of the battlefield to achieve victory (Fig. 11).

**Figure 11.** A chaotically inked Splatoon battlefield. (Screenshot from the game.)

Inklings’ ink is the same color as their body (Fig. 12). True cephalopods’ ink is always dark (due to its main constituent, melanin), of course, but we can all agree that different colors of ink was a fair gameplay necessity. And, speaking of body color, cephalopods are the most colorful animals out there (sorry, birds).

**Figure 12.** An inkling’s ink is always the same color as its body. (Original models from the game.)

**COLORFUL AND SMART CREATURES**

Cephalopods are so colorful because they can actually change their body color and also their color patterns. They have specialized cells in their skin called cromatophores, which enable them to instantly change color to camouflage themselves (either to evade predators or to ambush prey; Fig. 13), to communicate with conspecifics, or to ward off predators (Hanlon & Messenger, 1996; Hanlon, 2007; Mäthger et al., 2012). Some scientists even argue that cephalopods can produce waves of changing color patterns to mesmerize prey and make them easier to catch (e.g., Mauris, 1989; Mather...
& Mather, 2006), but this remains scarcely proved.

Doing justice to cephalopod coloration, inklings come in many colors: turquoise, lime green, purple, pink, orange and blue. And they change colors basically for each battle.

Figure 13. Photo sequence showing an octopus decamouflaging itself. Image reproduced from Hanlon (2007).

Box 1. Ink and slime
Inklings can only move freely on ink of the same color as theirs; they get stuck in other colors of ink (i.e., those produced by their opponents). Cephalopods, of course, have no such restriction of movement, but another kind of mollusk does. Land snails and slugs produce a mucous slime in order to move; they actually “glide” on top of it. Was this an intentional decision by the game developers, based on actual knowledge of mollusks? Or was this merely a gameplay choice that resulted in a nice molluscan coincidence?

A land snail leaving a silvery slime trail on its wake. Photo by “snail ho”, 2007; image modified from Wikimedia Commons.

We mentioned above that cephalopods can communicate with each other by changing their color pattern (Shashar et al., 1996; Mäthger et al., 2009). This kind of communication can only work if the animals using them possess a high degree of intelligence. And indeed they do. Cephalopods can solve puzzles, cause all sort of embarrassments for caretakers in aquariums
and zoos, and even use tools (Mather, 2008; Finn et al., 2009). Their nervous system is the most complex among invertebrates and, actually, their brain-to-body mass ratio falls between those of endothermic (birds and mammals) and ectothermic (all the others) vertebrates (Nixon & Young, 2003).

In Splatoon, the inklings and octarians are clearly intelligent enough to build cities and weapons. One of the Sunken Scrolls (a kind of game collectible that tells more about the backstory) reveals that the two races evolved when rising sea levels (yes, that’s Global Warming) wiped out humans and allowed sea creatures to take over (Splatoon Wiki, 2016).

**SPECIES IDENTIFICATION**

Now, after such a long immersion in cephalopod biology, it’s past time we try to identify which species exactly (if any) served as the basis for Splatoon’s inklings. (Unfortunately, octarians have a way too generic octopus design to allow some proper identification.)

The game’s developers have not stated which squid species (or number of species) they used as basis for the inklings. However, gamers on the Internet have referred to the Humboldt squid (Splatoon Wiki, 2016) or to the Japanese flying squid (on some forums). The Humboldt squid (Fig. 14), *Dosidicus gigas*, in the first place, is not a Japanese species (we assume Japanese game developers basically only use Japanese stuff for their games; see the majority of critters in Pokémon, for instance). The Humboldt squid is found on the Pacific coast of the Americas (Zeidberg & Robinson, 2007). As such, the Japanese flying squid (Fig. 14), *Todarodes pacificus*, would seem a good choice.

The Japanese flying squid belongs to the same family (Ommastrephidae) as the Humboldt squid. The squids in this family, as their common names imply, use jet propulsion to “fly” above the sea surface, covering a few tens of meters in each jump. This behavior is thought to be related to predator avoidance or to save energy as the squids migrate across vast ranges. It could be safely assumed that the jet-propelled jumps of the inklings in Splatoon (Fig. 9) were based on squids from this family. As a matter of fact, other flying squids of the family Ommastrephidae can be found in Japanese waters, such as the “neon flying squid”, *Ommastrephes bartramii*.

Ommastrephidae species also have a shape similar to the inkling’s squid form (Fig. 14), with large fins forming a triangle on the tip of the body, a tubular section of the mantle leading from it to the head and small arms. As such, it is safe to assume that this family of squids served as inspiration for both behavior and design of the inklings. However, the tubular section in the inkling is where the eyes are located and could thus be interpreted as the whole head. As such, there is another possible species that might have influenced the inkling’s design: the diamond squid (Fig. 14), *Thysanoteuthis rhombus* (family Thysanoteuthidae). As its name implies, the fins give the animal a diamond shape and extend all the way to its head (as the inkling’s head seem to be immediately below the fins). Moreover, it has short and strong arms and tentacles, like the inklings. This species can be found worldwide, but is an important catch for the Japanese fishing industry (Bower & Miyahara, 2005) and it is to this topic that we will turn next.
THE FISHING INDUSTRY

It is very common for gaming developers to come up with jokes for April Fools’ and last year even Nintendo joined in. A post on Splatoon’s official Tumblr page read: “So... this whole time I thought ‘Splatoon’ was going to be the name of the game, but it’s not. Splatoon is actually a hot new snack that’s coming out in May! You gotta be squiddin’ me! Now you can have your squid and eat it too! Unless you’re a squid, then... maybe don’t because that’s weird and kinda creepy. Maybe just eat a quesadilla.” A photo of the supposed snack’s package (Fig. 15) accompanied the post.

While it may be a cute April Fools’ joke (the Japanese seem to love these strange snacks), it brings up a very serious question: Japan’s destructive fishing practices. As remarked above, the diamond squid is a very important species for the Japanese fishing industries, but the Ommastrephidae flying squids also consist in large portions of their catch (FAO, 2015a). As a matter of fact, all of these species are heavily exploited and the species are in steady decline.
Squids, octopuses and lots of ink

(Bower & Ichii, 2005; Bower & Miyahara, 2005; FAO, 2015a).

The loss of a single squid species may not seem much to most people. But when a species go extinct, its absence may lead the whole ecosystem to a disastrous collapse. In the long run, the only thing we’ll be eating from a barren sea will be jellyfish burgers. Japan’s fishing industry is one of the most overexploiting in the world (Clover, 2004: Roberts, 2007; FAO, 2015b); besides, Japan is involved in a huge controversy regarding its whaling practice.

Moreover, seafood is a staple of Japanese cuisine. Even so, the fisheries could do better with some planning, to avoid species and ecosystems collapses. Some restrictions, accompanied by proper regulation, should be put in place. For us consumers, Clover (2004) offers advice on how to make a difference, buying only lawfully catch seafood (identified by seals of quality or similar markings) and always inquiring where said seafood comes from (to avoid buying something from threatened areas).

Box 2. Mario’s Famous Squid
The inklings’ squid form is also reminiscent of another famous Nintendo squid: Blooper. Everyone should be familiar with this recurrent antagonist from the Mario series, which is present in almost every underwater stage across several Mario titles (Cavallari, 2015). Despite Blooper’s simple design, it can be safely recognized as a squid (Cavallari, 2015) and it is curiously very similar to Splatoon’s inkling. However, according to the game’s developers, they did not use Blooper as a base for the inkling’s squid form design (Splatoon Wiki, 2016).

Figure 15. The April Fools’ Splatoon snack. Image taken from Splatoon’s official Tumblr (http://splatoonus.tumblr.com/).

Nobody is expecting people to just stop fishing; the sea is an amazing resource to feed the increasing number of humans on the planet.
CEPHALOPOD CONSERVATION

Typically, invertebrates are not a priority in conservation efforts, since they are usually faced with lots of antipathy. As such, the role of flagship species for raising people’s awareness about biodiversity loss and the dire need of conservation measures is often reserved for mammals and birds (and the eventual tiny cute frog). Cephalopods usually do not get much attention in conservation efforts, but they do have some charismatic species that can serve such purpose (and should definitely be used). Among the squids, the semi-mythic giant squid *Architeuthis* sp., the animal who originated the legend of the Kraken, is the most obvious choice (Guerra et al., 2011; Salvador & Tomotani, 2014). Among the octopuses, everyone should remember Paul, the “clairvoyant” cephalopod who predicted the results of the 2010 FIFA World Cup, and the little octopus *Opisthoteuthis* sp. that made the news everywhere this year just for being so damn adorable (Fig. 16).

There is no doubt that the media and works of fiction can help in environmental education and in raising ecological awareness. (It can work against it too, like when the movie *Jaws* started a shark-killing frenzy.) We believe that games can and should have a much more prominent role in these efforts. This is especially true for a game like Splatoon, which is more children-friendly. After all, we have to teach this ecological awareness to children (adults are already too narrow-minded to listen).

For instance, the game *Never Alone* (released November 2014) has its story and setting based on Inuit folklore and culture. As the player progresses in the game and encounters different things, he/she unlocks a series of short documentaries which explain facets of the Inuit culture, their arctic environment and arctic animals. This shows that games can both entertain and actually teach something of value.

A different (and more direct) kind of approach was taken by Rovio Entertainment Ltd., house of the famous *Angry Birds* franchise. The company joined forces with BirdLife International to fight against the extinction of the wondrous South Pacific birds. Unfortunately, their crowdfunding campaign reached only about half of its US$ 150,000 target in donations (Save the Birds of the Pacific, 2015). Just for comparison, games overhyped by the media (*e.g.*, Shenmue) were meanwhile gathering over 6 million dollars on Kickstarter; so gamers do have money to spend.

Could Splatoon be used for educating players and raising environmental awareness? Yes, it could. Could Nintendo do the same as Rovio did and join some cephalopod
conservation effort? Definitely. Will this ever happen? Likely not; as explained above, Japan is too busy eating all squids in the Pacific Ocean.

REFERENCES


**MATERIAL ANALYZED**

The material analyzed for this study (i.e., the inkling Amiibo figures) is deposited in the private collection of one of the authors (R.B.S.), next to a Kirby and an Elite Stealth Elf.

The squid specimen from Figs. 6 and 7 is deposited in the scientific collection of the Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil) under the record number MZSP 86430. No mollusks were harmed during this work.