Ecology of the Caribbean Reef Squid Sepiotheuthis sepioidea (Phylum Mollusca, Class Cephalopoda)

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Cephalopods are fascinating and intelligent creatures with a long history. Ancestors of modern cephalopod molluscs which include octopus, squid, cuttlefish, and the nautilus have existed since the Cambrian (550 mya) (Hanlon and Messenger 1996). The earliest cephalopods had straight external shells referred to as orthocones that eventually developed into a spiral (Vandetti, 2006). Many cephalopods eventually lost their external shells, for example Coleoids (includes all living squid, octopus and cuttlefish) (Monks 2015). Changes in the skin also occurred and became important for communication and camouflage (Hanlon and Messenger 1996; Young et al. 2012). In the late Triassic to Jurassic (about 200 mya) cephalopods developed an internal shell (Vandetti 2006). The loss of the external shell has allowed for changes in habitat because intense pressure can implode the shell in water deeper than 500m (Monks 2015). Modern coleoids (squid) are thought to have appeared in the Jurassic, but may have been around as early as the Devonian (Hanlon and Messenger 1996). Fossil cephalopods are much more diverse than living ones today (Vandetti 2006). The Caribbean reef squid (Sepiotheuthis sepioidea) evolved from the Neocoleoidea which is a monophyletic group evidenced by the presence of suckers, and is a part of the Coleoidea (Young et al. 2012).

Today, Caribbean reef squids are found throughout the tropical waters of the western Atlantic Ocean (Moynihan and Rodaniche 1982). They belong to the genus Sepiotheuthis, which consists of three species of reef squids (S. sepioidea, S. lessoniana and S. australis) that live in tropical to temperate waters across the globe (Vecchione and Young 2010). Reef squid can grow to 30cm in length and are often light brown in colour with a white stripe along their dorsal surface, but this can vary (Moynihan and Rodaniche 1982). Reef squids are typically found in and around shallow coral reefs at depths of 1.5-8m below the surface and have been seen as far down as 100m (Marine Bio Conservation Society 2013). They do not often feed on the bottom or at the surface, possibly due to the risk of predation (Moynihan and Rodaniche 1982).

Throughout their lives they tend to be found in different locations in the water column. They can be found closer to the surface, in deeper water, or in open water depending on their level of growth and the time of day (McKay and Anderson 2015). The newly hatched young are often found near the surface in places with sandy bottoms (Moynihan and Rodaniche 1982). Juveniles are found closer to shore and in turtle grass (Thalassia testudnum), but tend to avoid being too close to the surface (Moynihan and Rodaniche 1982). Reef squid that are older, but not yet fully mature, tend to prefer turtle grass and shallower water (McKay and Anderson 2015). They are found near the surface during the day and

closer to the bottom at night (McKay and Anderson 2015). Medium sized and adult squids stay away from the grass and have been found to travel between reefs (McKay and Anderson 2015). They are found near the shore during the day and offshore at night (McKay and Anderson 2015). Once larger, the reef squid will find refuge in places other than turtle grass (Moynihan and Rodaniche 1982).

Breeding age adults (around 6 months old) are usually found on the reef during the day and in deeper water at night (McKay and Anderson 2015). Breeding itself occurs on the reef where the water is shallower (Moynihan and Rodaniche 1982). Overall they are found closer to the substrate than most other squid (McKay and Anderson 2015). This may be because they can change colour in order to be camouflaged with their surroundings (Wood et al. 2010).

Caribbean reef squid have a relatively short life cycle: they reach maturity in six months and are semelparous (that is they die after reproducing) (Moynihan and Rodaniche 1982; Marine Bio Conservation Society 2013). Females only lay one clutch of eggs before dying but males are able to fertilize multiple females (MarineBio 2013). Courtship can occur at any time of the year and is mostly seen occurring in the morning and early afternoon (Moynihan and Rodaniche 1982). Fertilization is internal, but there is little physical contact between males and females (McKay and Anderson 2015).

Males must compete with other males in order to gain access to breed with a female (Marine Bio Conservation Society 2013). Once a male has outcompeted other males, by flashing zebra patterns or light colours, he will approach the female and gently stroke her with his tentacles (Marine Bio Conservation Society 2013). When initially approached, females may react with alarm by flashing a distinct, usually zebra pattern, but are calmed by the male when he blows water at her and gently jets away (Moynihan and Rodaniche 1982; MarineBio Conservation Society 2013; McKay and Anderson 2015). The male will re-approach repeatedly until a female accepts him (MarineBio 2013). This can continue for up to an hour (MarineBio 2013). Once he is accepted, a male will reach out and present the female with a sticky sperm packet (spermatophore) while at the same time displaying a pulsating pattern (MarineBio Conservation Society 2013). He then attaches the spermatophore inside the mantle chamber of her body (MarineBio 2013). The female will then place the packet into her seminal receptacle (MarineBio 2013). The female may toss away a sperm packet if she chooses (McKay and Anderson 2015). Once fertilized, the female will find an appropriate location to place her egg clusters, usually hidden somewhere in a protected area then she will die (MarineBio 2013). The eggs are laid 7 to 8 in a row within a capsule (McKay and Anderson 2015). These capsules are common among squid, but the number laid varies with species (McKay and Anderson 2015). Once hatched, the young will start feeding within 10-15 hours (McKay and Anderson 2015).

Reef squid have an active lifestyle and so will feed more frequently than sessile organisms (O'Dor et al. 2002). They are generalist feeders and will prey

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on many species of fish including: the dusky anchovy (Anchola lyolepis), dwarf herring (Jenkinsia lamprotaenia), and hardhead silversides (Atherinomorus stipes) (Moynihan and Rodaniche 1982). They are also known to eat arthropods such as shrimp but do not appear to eat crabs (Moynihan and Rodaniche 1982). An adult squid will eat fish up to 12cm in length (Moynihan and Rodaniche 1982). Reef squid have also been seen to feed in open water on what researchers believe to be small arthropods such as copepods (Moynihan and Rodaniche 1982). Reef squid hunt most actively just after dark, but have been observed hunting throughout the day (Moynihan and Rodaniche 1982). Hunting squid will often change colour which can vary from yellow streaks to stripes and spots, but these patterns are not restricted to hunting behaviors (Moynihan and Rodaniche 1982). These colour changes are more commonly seen before attacking a fish, likely to confuse and distract the prey (Moynihan and Rodaniche 1982). This behavior implies there may be an element of fear for the squid because a larger fish can potentially damage the tentacles (Moynihan and Rodaniche 1982).

Once they have a fish in their tentacles, the squid will bite it behind the head in order to kill it (Moynihan and Rodaniche 1982). When feeding on a fish the squid do not eat the head, vertebrae, or tail, but will consume the fleshy parts of the fish (Moynihan and Rodaniche 1982). As squid mature they tend to prefer fish to other prey items (McKay and Anderson 2015). In order to catch shrimp, squid will disturb the substrate to flush out prey (McKay and Anderson 2015). Although squid feed on smaller fish, schools of juvenile reef fish have been seen in association with groups of squid without being attacked (Nunes et al. 2007). Reef squid have also been seen with other species of squid (Loligo plei) as well as with goatfish (Mullidae) which they associate with when the goatfish are feeding, but the associations to goatfish are unclear (McKay and Anderson 2015). Caribbean reef squid are not cooperative hunters but have been seen to alert one another to food if it is near (McKay and Anderson 2015).

Reef squid are not only predators, but are also prey to a variety of fish. Some predators include mutton snapper (Lutjanus analis), French grunts (Haemulon flavolineatum), barracudas (Sphyraena spp.), bar jack (Caranax ruber), purplemouth moray eels (Gymnothorax vicinus) and spotted snake eels (Ophichthidae) depending on their geographical location (McKay and Anderson 2015; Wood et al. 2010; Mather 2010). In addition, the surface of the water is avoided due to the presence of predators such as pelicans (Pelecanus spp.), herons (Ardeidae), kingfishers (Alcedines), terns (Sternidae) and egrets (Ardeidae) (Moynihan and Rodaniche 1982). Squid are known to have sentinels within a group in order to watch for potential predators and to alert the group when danger appears (McKay and Anderson 2015).

Squid have multiple defense strategies to avoid predation. Inking is a common response (Wood et al. 2010). This is where a squid will squirt ink from an ink sac, located internally just posterior to the head, in order to confuse a predator and to cover its escape (Wood et al., 2010). Also, jet assisted locomotion is efficient for short bursts, but not for long distances since it is

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energetically costly (Mather 2010). Since they live in groups (up to 150 individuals) the inking behavior of one squid can also trigger responses, such as jetting away, from other squid in the group (Moynihan and Rodaniche 1982; Wood et al. 2010). When inking, a squid will turn a dark colour eject its ink then turn a lighter colour as it jets away (Wood et al. 2008). The ink may have chemical properties that deter predators by being unpalatable (Wood et al. 2008). Another response to potential predation is changing colour (Wood et al. 2008). Changes such as "eye spotting," which is the colouring of large spots on the sides of the animal to make it appear larger than it is, are common and has been seen in response to other squid inking (Wood et al., 2008). Also, patterns, such as zebra displays, have been seen in response to predators (Mather 2010). Because the cephalopods have no protective shell (except the nautilus) they are particularly vulnerable to predators. These animals must balance predator avoidance with necessities such as feeding therefore they may elicit different responses to varying levels of threats (Mather 2010). Different fish species have been observed to approach to different distances from squid before triggering a response (Mather 2010). Once a predator has been spotted by a squid's exceptional vision, the group of squid will move closer to each other to form a school (Mather 2010).

Squid are a popular food for humans and they are commonly found in many restaurants. With increased fishing of these squid, along with the potential reduction of prey fish as a result of climate and ocean changes, we may see a decrease in the numbers of these animals in the future. Squid are often used as bait by fishermen (McKay and Anderson 2015) which can reduce their numbers as well as increase the squid's competition for prey. The Caribbean reef squid is has not yet been assessed by the IUCN (International Union for Conservation of Nature) so it is hard to determine how much of an impact humans and climate are having on overall populations.

Reef squid are important predators in their marine ecosystem and how they may respond to human caused changes such as warming and acidification is unpredictable. If their populations do become negatively affected, this may cause widespread changes on reefs including increased populations of fish and invertebrates that they prey upon, leading to disruption of the balance of the entire ecosystem.

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