Alien vs. Predator: interactions between the colossal squid (*Mesonychoteuthis hamiltoni*) and the Antarctic toothfish (*Dissostichus mawsoni*)

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Data collected onboard two South Korean longliners in 2011–2014 targeting Antarctic toothfish provided insights into trophic interactions between two Antarctic top predators: the colossal squid *Mesonychoteuthis hamiltoni* and the Antarctic toothfish *Dissostichus mawsoni*. Adults of each species opportunistically prey upon weakened representatives of the other species: squid will feed on longline-caught toothfish, and toothfish on dying and dead squid. The highest occurrence of squid attacks was recorded in the Davis Sea and Commonwealth Sea, and the lowest in the Ross Sea. Squid depredation rates were around 1% on average, though regionally they might rise to 2–3%, which is of a similar magnitude to rates caused by sperm whales and killer whales in some areas.

**Keywords:** longline; depredation; colossal squid; Antarctic toothfish; *Mesonychoteuthis hamiltoni*

**Introduction**

The colossal squid (*Mesonychoteuthis hamiltoni* Robson, 1925) is one of the largest known cephalopods that has ever existed, attaining a maximum mantle length (ML) of about 250 cm, and maximum recorded weight of 495 kg (Roper and Jereb 2010). The species was originally described from the remains found in a sperm whale (*Physeter macrocephalus*) stomach (Robson 1925) and until recently was recorded mostly from stomachs of these whales (Korabelnikov 1959; Klumov and Yukhov 1975; Clarke 1980; Filippova 2002). The large specimens are captured occasionally by trawls (Figure 1) or on longlines while preying on hooked toothfish (Petrov 2008).

Colossal squid occurs across the Southern Ocean in waters from the Antarctic Convergence to 70°S (Figure 2), although it occasionally might penetrate as far north as 40°S, particularly off South Africa. It is a mesopelagic to bathypelagic species from late juvenile stages onwards, inhabiting depths of 500–2000 m. It is believed to feed on mesopelagic fishes (mainly myctophids), Patagonian toothfish, sleeper shark and other squids, and in turn is preyed upon by sperm whale and Antarctic toothfish (Roberts et al. 2011). Early juvenile squids also are preyed upon by albatrosses and Antarctic fulmars (Roper and Jereb 2010).

The flesh is rumoured to be of ‘excellent quality and very flavourful’, but this needs to be reconfirmed (Roper and Jereb 2010). One of authors (VL) tried a boiled

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piece of a tentacular stalk of a large animal and found it delicious, the taste being similar to that of *Illex* and *Todarodes*, different from *Loligo* and *Thysanoteuthis*, and incomparably better than flesh of *Dosidicus* and *Sthenoteuthis*.

This paper investigates the impact of colossal squid depredation on the Antarctic toothfish fisheries in the Southern Ocean. The term ‘depredation’ defines fish removed from the gear by predators during hauling (Söffker et al. 2015).

**Materials and methods**

Data on colossal squid depredation on captured toothfish were collected between December 2011 and March 2012 (FV 701 *Hong Jin*) and December 2012 to January 2014 (FV *Sunstar*) in the Indo-Pacific sector of the Southern Ocean including the Ross Sea, D’Urville Sea, Davis Sea, Mawson Sea, Commonwealth Sea and Amundsen Sea (Figure 2). Vessels were fishing in the CCAMLR area using a trotline system. Lines of 13.7 km middle length were set between 600 and 2600 m depth.

A total of 8031 toothfish was sampled during the study. The total length was measured within 1 cm, body weight taken within 1 kg, and stomach contents examined. Colossal squid predation events, which were identified by the presence of scratches from the suckers and hooks and deep wounds caused by squid beak, were recorded in 71 toothfish (Figure 3). Remains of colossal squid (beaks, arms, tentacles and large pieces of mantle) were found in the stomachs of 57 toothfish
The percentage of toothfish damaged on the line due to colossal squid attacks was considered to be the depredation rate.

Mantle length of the squid prey was recalculated from 13 tentacular club lengths (which is mean 14% ML – K. Bolstad, pers. comm.) and from lower rostral length of five beaks (Xavier and Cherel 2009).

The proportion test (R Core Team 2013) was used to test the null hypothesis that the occurrence of colossal squid attacks on Antarctic toothfish are different between study areas.

(Figures 4 and 5). The percentage of toothfish damaged on the line due to colossal squid attacks was considered to be the depredation rate.

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Results

Identification of colossal squid attacks on Antarctic toothfish

Imprints of squid suckers on toothfish bodies (Figure 3) have the appearance of rings of 1–2 cm in diameter, sometimes up to 2.5–3 cm. The distinctive dots of puncture wounds left by the teeth of suckers (Figure 3) prove that they do belong to the colossal squid. Another large Antarctic squid, Kondakovia longimana (Onychoteuthidae) has smooth sucker rings. Among the scars of arm suckers, occasional scars of 5–10 cm long were observed, presumably left by tentacular hooks. Deep wounds on the body caused by bites of the enormous beak of M. hamiltoni reflect squid predation. There might be several of such wounds simultaneously on the different parts of the body, but more often on the soft belly.

Attacks by colossal squid on Antarctic toothfish were recorded throughout the study area, although with different intensities that varied from 0.15% to 2.27% between different seas (Table 1). In the Ross, Mawson and Commonwealth Seas, the frequency of occurrence was statistically different from the average of the entire area sampled. The highest occurrence of squid attacks was recorded in the Davis Sea and the Commonwealth Sea, and possibly in the D’Urville and Amundsen Seas, where differences with total sample were not statistically significant. Attacks of captured toothfish occurred rarely throughout the Ross Sea.
Identification of colossal squid body pieces in stomachs of Antarctic toothfish

The most common remains of the colossal squid in toothfish stomachs were beaks, arms and tentacles of large specimens (Figure 4), although pieces of mantle and fins were observed occasionally. Estimated mantle lengths of squids, based on the measurements of beaks \( n = 5 \) varied from 120 to 220 cm, and those estimated from tentacle clubs \( n = 13 \) ranged from 178 to 239 cm.

One of the most impressive findings in the stomach of a toothfish (185 cm L\(_T\); 70 kg total weight) was a tentacle with two attached arms. The length of the tentacle was 242 cm, with a tentacular club 29 cm (estimated ML 207 cm), and the lengths of the arms were 127 and 114 cm, respectively. The total weight of flesh in that stomach was 7.0 kg (Figure 5).

Total lengths of fish in which stomach squid remains were found varied from 125 to 195 cm (mean 153 cm). The lengths of fish attacked by squid ranged between 95 and 170 cm (mean 142 cm). Comparison of length frequencies of the toothfish subjected to attack on the colossal squid and preying on this species demonstrated the similarity of fish size between the two samples. However, Antarctic toothfish as a predator turned out to be slightly larger (152.7 cm versus 142.8 cm of L\(_T\) ) than when prey \( t = 94.2, p < 0.0001 \).

Discussion

There is no information about the natural diet of large, adult colossal squid. Adult \( M. hamiltoni \) (120–240 cm ML; 100–400 kg in weight) are much larger than Antarctic

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**Figure 4.** Remains of large colossal squids in Antarctic toothfish stomachs. (A) Arms; (B) a tentacle; (C) beak; (D) a piece of mantle with cartilage. Photos by A. Remeslo.
toothfish (usually about 50–80 kg). In consequence, it is likely that toothfish is a usual part of their diet. Moreover, it is supposed that colossal squid are not voracious predators capable of high-speed predator–prey interactions, but rather ambush or sit-and-float predator that use the hooks on its arms and tentacles to ensnare prey that unwittingly approach (Rosa and Seibel 2010). Therefore, immobilized, weakened

Figure 5. Large tentacle and two arms recovered from a toothfish stomach. Photo by A. Remeslo.
toothfish captured by longline are easy prey for this predator (Yukhov 2012). The depredation rates do not seem to be very high: c.1% on average, though they might rise to 2–3% regionally, becoming similar to those caused by sperm and killer whales in some Australian areas (Arangio 2012).

Determining the depths at which tooth fish were attacked by colossal squid was not possible. However, it is probable that it occurs in the water column when the lines are being lifted, and not in the bottom layers, as the fish were never eaten to an extensive degree. Usually, the weight of the flesh eaten away did not exceed usually more than 1–2 kg, so the squid had eaten a few mouthfuls.

Squid release prey before ascent to the surface of the sea, although there are known exceptions (Petrov 2008). Colossal squid were often reported from stomachs of Antarctic toothfish either as juvenile squid of 55–65 cm or as part of adult bodies, but generally the size of squid prey has not been reported in studies of the diet of toothfish (Yukhov 1982). Colossal squid are very important prey and represent c.20% of prey (by weight) in the Mawson Sea, 14% in the Davis Sea (Petrov and Istomin 2010), and 11–19% in the Lazarev Sea (Petrov and Tatarnikov 2011). In the Ross Sea unidentified squids occurred in 5–14% of stomachs (Fenaughty 2003); it is not clear what proportion were colossal squid, although obviously lower than in the Mawson, Davis and Lazarev Seas.

One of the possible explanations for toothfish foraging on squids larger than themselves is that *D. mawsoni* attacks dead and possibly dying *Mesonychoteuthis*. This supposition might be inferred also from the diet of a bottom scavenger and ambush predator – the Antarctic sleeper shark *Somniosus antarcticus* – in which colossal squid occurred in 66.1% of stomachs and represented 52% of cephalopod prey (by weight) around the Kerguelen Islands (Cherel and Duhamel 2004). However, because of their needle-like teeth, Antarctic toothfish are highly unlikely to tear apart the large pieces of mantle that were occasionally found in stomachs. Therefore the likely explanation for the remains of larger parts of colossal squid in Antarctic toothfish stomachs could be that toothfish scavenge the leftovers of other squid predators. Antarctic sleeper sharks

| Antarctic Sea and CCAMLR fishing area (SSRU) | n  | % D | % F | \( \chi^2 \) | p      |
|---------------------------------------------|----|-----|-----|-----------|--------|
| Ross Sea (northern part) – 88.1 B           | 688| 0.15| 0.73| 3.7605    | 0.050  |
| D’Urville Sea – 58.4.1 G                    | 349| 1.43| 6.30| N/A       | *      |
| Davis Sea – 58.4.1 E                        | 668| 0.95| 1.95| 7.8752    | 0.005  |
| Mawson Sea – 58.4.1 C                       | 2330| 0.39| 0.39| 1.1378    | 0.286  |
| Commonwealth Sea – 58.4.2 E                 | 2100| 1.33| 0.33| 5.7487    | 0.0165 |
| Ross Sea (south-eastern part, near shore) – 88.1 L, 88.1 H, 88.1 J | 1544| 0    | 0    | 15.6405   | <0.0001|
| Amundsen Sea – 88.2 H, 88.2 E               | 352| 2.27| 0.28| N/A       | *      |

Note: * Chi-squared approximation may be incorrect
Abbreviations: n – number of studied Antarctic toothfish; % D – depredation rate; % F – occurrence of toothfish with remains of colossal squid in stomachs.
occur generally in temperate and subantarctic waters north of 55°S (Díaz de Astarloa et al. 1999; Yano et al. 2007; Ebert 2013), i.e. outside of the Antarctic toothfish range but within the range of colossal squid. Sperm whales are rare in deep Antarctic waters and during the entire period of observation were noticed by two of the authors (A.R. and M.Y.) only twice. Another candidate for an enormous predator targeting colossal squid is the colossal squid itself. Intraspecific cannibalism, when squid attack smaller or just weakened animals, is very common among cephalopods including the giant squid Architeuthis (for a review see Ibáñez and Keyl 2010) and it is likely that the colossal squid would have similar behaviour. Also, while attacking conspecifics, squid target the body and not the arms (V.L. personal observations on Doryteuthis, Illex and Sthenoteuthis), thus avoiding the potentially dangerous beak of the prey, and so squid arms and tentacles are easily lost to the sea floor.

We can conclude that two top predators of Antarctic waters – the colossal squid and toothfish – forage on each other as adults but it is likely that predation does not often occur between healthy and free-swimming animals. Antarctic toothfish attack dead and dying squid (possibly together with other squids that simplifies taking large pieces) whereas colossal squid prey on captured (as well as possibly on weakened and dying) toothfish. This leads to horizontal transfer of nutrients within the upper level of the Antarctic food web.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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