How do cephalopods become available to seabirds: can fish gut contents from tuna fishing vessels be a major food source of deep-dwelling cephalopods?

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Received 3 July 2012; accepted 28 September 2012; advance access publication 24 October 2012.

Cephalopods are important prey for numerous seabird species. However, the physical mechanisms by which cephalopods (particularly species considered as deep-dwelling) become available to seabirds are poorly understood, and it has recently been suggested that the discarded stomachs of gutted fish captured by tuna longliners can be a major source of deep-dwelling species. Here, we identify some deep-dwelling cephalopods that appear in the diet of seabirds, review what is known of their vertical distribution and movements. We then compare the stomach contents of commercially captured tuna with those of seabirds foraging in the same area. The limited available information leads us to conclude that tuna longliners are unlikely to be a major source of deep-dwelling cephalopods for seabirds. However, much more information is required on the ecology of seabird prey, particularly commercially unexploited cephalopod species, which may be obtained from scientific cruises devoted to cephalopod biological research. In addition multispecies/foodweb modelling studies may be required to explore potential interactions between seabirds, their predators and prey, and commercial fishing operations.
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seabirds that forage in the same areas. As a case study example, we compared the diet of wandering albatrosses breeding at South Georgia with the stomach contents of tuna caught by the longline fishery off the coast of Brazil.

Deep-dwelling cephalopods found in the diet of seabirds include species of the following families: Architeuthidae, Backeteuthidae, Bolitenidae, Brechoteuthidae, Chiroteuthidae, Grimalditeuthidae, Mastigoteuthidae, Nectoteuthidae, Promachoteuthidae, Vampyroteuthidae (Vaske, 2011), and Bathyteuthidae (Rooper, 1969). However, some species are probably not exclusively deep-diving, performing vertical migrations into the upper water column (Rooper and Young, 1975). For example, the brachiotethid Slosarczykivia circumantarctica migrates towards the surface at night where it is commonly caught in open-close nets typically deployed at depths <400 m (Piatakowsky et al., 1994; Rodhouse and Piatakowsky, 1995); the neoteuthid Alluroteuthis antarcticus has been observed at depths <100 m in the water column (Filippova and Pakhomov, 1994); and the vamprotyeuthid Vampyroteuthis infernalis occasionally migrates to the lower limits of the epipelagic zone at night (Rooper and Young, 1975). In addition, juvenile specimens of Architeuthis dux (considered a deep-diving species) have been found in stomach contents of Alepisaurus ferox, which mainly forage the upper 300 m of the water column (Rooper and Young, 1972; Varghes et al., 2010). However, for numerous species, the data are too sparse to describe distributions with depth (Collins and Rodhouse, 2006). The postulated vertical distributions of numerous cephalopod species are primarily based on captures of juveniles in small scientific nets (Piatakowsky et al., 1994; Rodhouse and Piatakowsky, 1995; Xavier et al., 1999; Collins and Rodhouse, 2006) or in deep-water trawlnets which remain open between the fishing depth and the surface, and consequently we do not know the precise depth at which individuals were captured (Rooper and Young, 1975; Clarke, 2006).

Cephalopods may also become available to seabirds after they die. These cephalopods may be classified as ‘muscular’—and consequently they sink after they die—or ‘ammoniacal’ with a gas-filled endoskeleton or high concentrations of ammonium chloride—and consequently they float up towards the surface, where they become available to predators (Lipinski and Jackson, 1989). For some cephalopod species, it is not clear if they are muscular or ammoniacal, e.g. Kondakivia longimana is muscular, though it will float up to the surface after death as the muscles decompose. Furthermore, adults of some species migrate towards the surface to mate and/or to spawn, and those that are semelparous die after spawning where they become available to surface predators (Rodhouse et al., 1987). This information complicates our understanding of vertical distributions and migrations of cephalopods and the extent to which deep-diving species might be available to seabirds (Cherel and Weimerskirch, 1999).

In order to understand the importance of cephalopods (including those that are classified as deep-diving above) in the diets of birds obtained from gut contents of fish caught by longliners, we must compare the diet of seabirds with those of fish targeted by longliners (with the foraging areas of the seabirds overlapping with the location of the longlining fisheries). If seabirds do feed significantly on gut contents, we would expect a degree of dietary overlap. However, it is noticeable that the diet of tropical seabirds is quite different from that of tunas from the same tropical area (Cherel et al., 2008), suggesting that fish gut contents are not an important component of seabird diet. Similarly, there is minimal taxonomic overlap in the cephalopod component of the diet of wandering albatrosses breeding at South Georgia (for which foraging ranges extend to Brazilian subtropical waters; Xavier et al., 2004) with that of tunas caught by longliners off southern Brazil (Santos and Haimovic, 2002), despite wandering albatrosses (and other seabirds) following fishing vessels and potentially feeding from their offal and discards (Xavier et al., 2004). Wandering albatrosses mainly feed on non deep-diving Histiotethus, Onychoteuthis, and Cranchiidae, which together represented >70% by number of individuals of cephalopods in one diet study, compared with <6% for all deep-diving cephalopods (Xavier et al., 2003b), whereas tunas mostly feed on Omastrephes, Sepiolid, Lycoteuthis, and Chiroteuthis (Santos and Haimovic, 2002).

Another potential route by which deep-dwelling cephalopods (from fish gut contents) become available to Southern Ocean seabirds (both Atlantic and Indian) is via the Patagonian toothfish longline fisheries that operate in these waters. However, from our albatross diet data (Cherel and Weimerskirch, 1999; Cherel et al., 2000, 2002; Xavier et al., 2003a, b), the diets of wandering, grey-headed, and black-browed albatrosses breeding at South Georgia and Kerguelen clearly do not overlap—the most important cephalopods (numerically) in the diet of Patagonian toothfish being octopods (South Georgia; Xavier et al., 2002) and Chiroteuthis and Mastigoteuthis (Kerguelen; Cherel et al., 2004), which are rarely observed in the stomachs of albatross species. Therefore, these albatrosses potentially do not ingest (or ingest very few) cephalopods obtained from toothfish fishing vessels. Furthermore, when comparing the beak sizes of cephalopod species found in Patagonian toothfish and albatrosses (Roberts et al., 2011), the size distributions of the main prey (e.g. Kondakivia longimana) present in both predators are quite different (K. longimana beaks in toothfish stomachs were considerably bigger than those found in the diet of all albatross species), supporting the view that albatrosses do not solely depend on offal and discards from Patagonian toothfish fishing vessels in order to access deep-diving cephalopods.

Deep-dwelling cephalopods might also become available to seabirds through marine mammal–seabird interactions. For example, sperm whales Physeter macrocephalus, that feed on deep-dwelling cephalopods, vomit periodically to empty their stomachs of indigestible items, including cephalopod beaks (Clarke, 1980; Clarke et al., 1981, 1993; Clarke, 1996). Deep-diving cephalopods recently vomited from whale stomachs have been observed on the sea surface, and seabirds have been observed feeding on these (Clarke et al., 1981). However, given the energy requirements of seabird metabolism, it is unlikely that sufficient cephalopods would be made available by this route to form an important contribution to seabird diet.

In conclusion, the information currently available leads us to conclude that longline fishing operations are unlikely to be a major source of deep-diving cephalopods for seabirds, even though seabirds are known to follow, and obtain food from, fishing vessels. This may in part be due to longline fisheries targeting species that do not feed extensively on deep-diving cephalopods, rather than a lack of interaction between fishing vessels and seabirds. It is clear that much more information on the ecology of cephalopods is required. This would be facilitated by increased numbers of scientific cruises devoted to biological research on cephalopods and the development of improved methods for capturing deep-water cephalopods (Xavier et al., 2007) in order to
better understand their vertical distribution (e.g. through the development of nets to catch bigger squid, using bigger open–close nets) and their biology (e.g. through the characterization of adult cephalopods found at the sea surface, following post-spawning mortality). Similarly, there is a need to focus on the dynamics of seabird–marine mammal–cephalopod interactions, as much of the relevant information on cephalopods also comes from the diet of natural predators (Xavier et al., 2004, 2011), to allow a critical evaluation of the relative ‘scavengability’ of different cephalopod species.

Acknowledgements
This work would not have been possible without the valuable input and numerous discussions with Richard Phillips on predator–prey interactions and the role of cephalopods in the feeding and foraging behaviour of top predators in the Southern Ocean.

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Handling editor: Jason Link