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REVIEW, CONCEPT, AND SYNTHESIS

Factors affecting the importance of myctophids in the diet of the world's seabirds

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Abstract

Mesopelagic myctophid fish are a key component of the world's ocean food webs, linking primary consumers and predators. Among marine predators, seabirds are globally significant consumers, but the extent to which they feed on myctophids has been investigated only at the regional scale. This global-scale review of analyses of the stomach contents of 228 seabird species reveals that the occurrence of myctophids in seabird diets is extremely variable. However, myctophids do constitute a considerable amount of the food of penguins, the Procellariidae (shearwaters/petrels, etc.), and storm-petrels; in locations where birds are foraging in oceanic basin/shelf slope habitat; and among birds that feed at night. Recent analyses of the fatty acid signature of stomach oil emphasize that myctophids can be important prey also for seabirds exploiting oceanic habitats. Current efforts to survey seabirds' distribution outside the breeding period, when they often become more oceanic, and their circadian activity may further support the global importance of myctophids as a pathway for carbon advection between marine compartments.

Introduction

The total biomass of mesopelagic fish at the global scale had previously been estimated to reach 10^9 t (Gjøsaeter and Kawaguchi 1980), but more recent estimates are even greater by at least an order of magnitude (Irigoien et al. 2014). Among mesopelagic fish, myctophids (family Myctophidae, also known as lanternfishes) are dominant (Collins et al. 2008), accounting for 75% of this biomass (reviewed in Catul et al. 2011). Myctophids are important predators of copepods and krill, which are themselves key primary consumers in pelagic ecosystems (Moku et al. 2000; Sassa and Kawaguchi 2004; Hopkins et al. 1996; Hill et al. 2006; Murphy et al. 2007). As such, myctophid fish are considered to be an essential component of the tertiary level of pelagic ecosystems (Pakhomov et al. 1996; Pusch et al. 2004; Cherel et al. 2010), transferring the energy from zooplankton to upper trophic levels (Saunders et al. 2015). Indeed myctophids are profitable prey in terms of energy content (Clarke and Prince 1980; Anthony and Roby 1996; Davis et al. 1998) and are consumed by a variety of underwater predators, including tuna (Battaglia et al. 2013; Young et al. 2010), sharks (Pethybridge et al. 2011; Kubodera et al. 2007; Markaida and Sosa-Nishizaki 2010), squid (Pethybridge et al. 2012; Lorrain et al. 2011), dolphins (Ohizumi et al. 1998, 2000) and other marine mammals (Rodhouse and Nigmatullin 1996).

Among this wide array of marine predators, seabirds are notable as significant consumers of marine resources across the world's oceans (Brooke 2004a). They are highly mobile, and they exploit a range of marine habitats through extremely diverse foraging adaptations, from the surface-feeding specialists such as albatrosses (Diomedeidae) and gulls/terns (Laridae) to the deep-diving penguins (Spheniscidae) and alcids (Alcidae) (Schealer 2002). As colonial and land-breeding species, seabirds are relatively convenient to study among marine predators, and their food has been well documented during the breeding season at many sites around

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the world. Diet studies have revealed that several seabird species forage on myctophids, but this has been documented only at the regional scale (e.g., Connan et al. 2007a). It has thus been difficult so far to apprehend the overall significance of myctophids as food for seabirds. In this paper, we review the food of all seabird species that we could find in the literature, with the aim of providing a global assessment of how much myctophid fish and seabirds are interconnected at the scale of the world's oceans.

We also explore site-specific and species-specific factors which may explain variations in the consumption of myctophids by seabirds. Myctophid–seabird interactions may well be enhanced or prevented because seabirds would exploit, respectively, identical or different habitats to those of myctophids. First, myctophids are distributed mainly in the oceanic domain and over the shelf slope, rather than over the shelf itself and in coastal waters (Beamish et al. 1999; Donnelly et al. 2004; Moteki et al. 2011; Pepin 2013; but see Vipin et al. 2012). In contrast, seabirds forage in a variety of marine habitats, including oceanic basin, shelf slope, shelf, coast, and inland brackish and freshwater biotopes (see SI Table 1). Thus, the marine habitat exploited could predict the extent to which seabirds feed on myctophids. Specifically, we expected that seabirds exploiting the oceanic domain or areas over the shelf slope would feed on myctophids more than those foraging over the shelf or in coastal areas. Second, many species of myctophids have broadly tropical or subtropical distribution patterns (Hulley 1995), but the largest biomass of myctophids is found in the Southern Ocean (Lubimova et al. 1987; reviewed in Catul et al. 2011). Indeed, the density of mesopelagic fish in the Pacific Ocean seems to be greater in subarctic and subantarctic areas (4.5–6.5 g/m^3) than in equatorial (2.6–3.0 g/m^3) and central areas (1.0–2.0 g/m^3) (Gjøsaeter and Kawaguchi 1980). Thus, we expected that latitude would affect the importance of myctophids in seabirds' diet. Third, an oceanic survey between 40° north and south showed that myctophids are more abundant in more productive waters (Irigoien et al. 2014). Therefore, we expected also that marine primary production within the range of each seabird population would affect the consumption of myctophids.

We also investigated other factors related to seabird species-specific foraging capacities. Most myctophids remain at 200–1500 m depth during the daytime, while at night some (but not all) of them migrate to the upper 200-m euphotic zone to feed (Watanabe et al. 1999). In contrast, seabirds exploit mostly the surface layer and feed during daylight hours (with a few exceptions: see SI Table 1), as they generally need to see their prey to capture it. These traits may limit the opportunities for seabirds to feed on myctophids. Exceptions are king penguins, red-legged kittiwakes (*Rissa brevirostris*) and Kerguelen petrels (*Pterodroma brevirostris*). King penguins are able to dive deeply (150–250 m) and reach myctophids that remain in deep waters during the daytime (Bost et al. 2002). In contrast, red-legged kittiwakes and Kerguelen petrels actively feed on myctophids at the surface during the night (Harper 1987; Ainley et al. 1991, Kokubun et al. 2016). The red-legged kittiwake has noticeably larger eyes than the closely-related black-legged kittiwake (*Rissa tridactyla*) (Storer 1987), and the Kerguelen petrel has a greater number of retinal ganglion cells than any other procellariiform species (Hayes and de Brooke 1990), and in both cases it is believed that these peculiarities enable nocturnal feeding. Thus, we expected that specialized feeding on myctophids may be limited to those seabird species that dive deep or feed nocturnally. Further, as body mass might limit dive depth (Kooyman 1989; Schreer and Kovacs 1997), we expected that larger seabird species would forage on myctophids more than smaller species.

In this paper, we review the proportion of myctophid fish found in the stomach, regurgitations or bill-loads of seabirds over the world's oceans. Using these data, we examine whether seabird foraging habitat or behaviour would affect the importance of myctophids in their diet. We then discuss the potential bias inherent in samples collected in colonies using other sources of information such as chemical markers, and debate the possibility of nocturnal foraging by surface feeders that consume myctophids. Finally, we discuss how recent studies of animal behaviour outside the breeding season may change our view of seabird species' trophic niche.

Materials and methods

Data sources

To evaluate the importance of myctophids in seabird diets, we first considered review papers (Croxall and Lishman 1987; Prince and Morgan 1987), books (Brooke 2004b; Gaston and Jones 1998; Williams 1995; Nelson 2005) and papers analysing multiple seabird species in colonies (Croxall et al. 1988, 1997; Schneider and Hunt 1984; Harrison et al. 1983; Ridoux 1994) or at sea (Ainley et al. 1991; Spear et al. 2007). We then considered studies describing the diet of single species, using the Web of Science search engine (with "diet", "seabird" and "myctophids" as key words) up to May 2016. Most diet studies of seabirds are based on examination of (1) the regurgitations (or pukes), (2) the contents of the oesophagus, proventriculus and gizzard, which we refer to collectively (though inaccurately) as stomach samples (Ratcliffe and Trathan 2011), or (3) the prey brought back to the chicks crosswise in the bills as bill-loads. From the diverse prey species identified in the stomach samples and bill-loads (see SI Table 1), we categorized the seabird diets as consisting mainly of copepods, krill, crustaceans, squid, other marine invertebrates (including shellfish, sea stars and sea urchins), myctophids, or non-myctophid fish, including epipelagic schooling fish (sardine/anchovy), bottom-living fish (flatfish, blennies, sculpin), and fish eggs. Some seabirds also fed on carrion, eggs or chicks of other seabirds, terrestrial animals (mammals or insects) or garbage. Hence, we assigned to each seabird population its main prey categories according to the literature (SI Table 1).

Analyses

To examine the importance of myctophids as prey among seabird families, we compared the number of confamilial species that fed on myctophids at at least one study site (based on all types of diet analyses from SI Table 1). For statistical analyses, we then used the percentage (by mass or volume) of myctophids given in the studies as a metric of their importance in the seabirds' diet, for each species at each study site. If the values varied between years, seasons or studies for the same species at the same location, we used the mid point of the range. When values were reported as "$< x\%$", we used half of this range in statistical analyses (e.g., "$< 11\%$" in SI Table 1 became 6%). The distribution of the response variable (percentage of myctophids in diets) was highly skewed to lower values (SI Fig. 1).

The marine habitat of the study site (colony or area at sea where seabirds were sampled) was categorized as oceanic basin and slope habitat (BE, encompassing both oceanic waters > 400 m deep and within 100 km of the shelf slope) or shelf and coastal habitat (SC, including ≤ 200 m shelf waters, mainland coastal areas, and freshwater-related habitats (see SI Table 1). For effects of latitude, we used absolute values; for study areas with wide latitudinal ranges, we used middle values. To examine the relationship between biological productivity and the consumption of myctophids, we extracted sea-surface chlorophyll-*a* concentrations at each study site, using the function "xtracto_3D" from the package "xtractomatic" in R v. 3.4.2 software (R Core Team 2015), from the average value of all SeaWiFS satellite data (1997–2010, monthly composite, 0.0417° resolution) in a 5° × 5° box centred on the site's coordinates. These long-term data are expected to limit the seasonal or annual effects in chlorophyll-*a* concentration patterns and facilitate comparisons among sites, although it is possible that the averages may be biased towards the summer values, given the potential reading limitations for the satellite during winter due to sea-ice and cloud coverage. The 5° × 5° spatial box was chosen as a compromise between measuring site-specific characteristics in productivity and accounting for the movements of foraging seabirds around each site. In the case of studies with several sites that spread beyond the 5° × 5° box, a box was drawn for each site; in the case of studies covering a regional marine sector, the boundaries of the studied region were directly used to draw a single box.

The body masses of the seabird species were drawn from Schreiber and Burger (2001), Brooke (2004b), and Nelson (2005) (SI Table 1). Species-specific feeding techniques were previously assigned to pursuit dive (pd), surface dive (sd), surface plunge (sp), pursuit plunge (pp), aerial plunge (ap), surface seizure (ss), surface filtering (sf), dipping (dp), aerial catch (ac), scavenging (sv), and kleptoparasitism (kp) (Ashmole 1971; Gaston and Jones 1998; Williams 1995; Brooke 2004b; Nelson 2005) (SI Table 1). To evaluate the effect of a species' diving capacity on its consumption of myctophids, we simplified these categories into two contrasting feeding techniques: diving (D; equivalent to pd) and surface feeding (S; comprising ss, sf, dp, ac, sv, kp, sd, sp, pp, and ap) (SI Table 1). Information about nocturnal feeding was drawn from Harper (1987), Phalan et al. (2007) and the above-cited reviews. In the eastern tropical Pacific, analysis of otoliths in relation to the time of day when birds were collected showed that some procellariiform species caught prey primarily between 20:00 and 24:00 (Spear et al. 2007), and thus we assumed that these species were nocturnal feeders. We categorized species as nocturnal (N) when significant nocturnal feeding was determined from these studies, or non-nocturnal/unknown (U) otherwise.

We tested the statistical effect of these factors on the proportion by mass or volume of myctophids in each seabird species' diet using a Generalized Linear Mixed-effect Modelling (GLMM) approach, in which the proportion by mass or volume of myctophids in the seabirds' diet was the response variable (assuming a binominal distribution); marine habitat (BE vs SC), latitude (absolute value), sea-surface chlorophyll-*a* concentration of the sampling site, species body mass, feeding technique (D vs S) and daily timing of feeding (N vs U) were explanatory factors; and seabird species was a random factor. The model selection procedure followed Akaike's Information Criteria corrected for small samples ($\mathrm{AIC_c}$), using the packages lme4 and MuMIn in R v. 3.2.1 software. Models with $\Delta \mathrm{AIC_c} < 2.00$ were denoted as equally supported. When multiple models were selected, parameter estimates were calculated using the model averaging procedure for all equally supported models. All Variance Inflation Factor values were < 5, indicating no colinearity (Zuur et al. 2009).

Results

We reviewed 252 publications, encompassing 228 seabird species from 12 families studied at 174 sites or regions around the world (SI Table 1).

Taxonomic comparison

The importance of myctophids in the diet varied extensively among bird families. In six families, more than half of the reviewed species fed to some extent on myctophids, at at least one study site (SI Table 1): penguins (Spheniscidae, 9/14, 64%); albatrosses (Diomedeidae, 6/11, 55%); shearwaters/petrels/giant petrels/fulmars/prions (Procellariidae, 33/45, 73%); storm petrels (Hydrobatidae, 10/13, 77%); diving petrels (Pelecanoididae, 2/3, 67%); and skuas and jaegers (Stercorariidae, 3/4, 75%). By contrast, a minority of species fed on myctophids among alcids (Alcidae, 2/18, 11%), boobies (Sulidae, 1/9, 11%), and cormorants and shags (Phalacrocoracidae, 2/13, 15%). Intermediate values were found for gulls and terns (Laridae, 10/32, 31%) and for tropicbirds (Phaethontidae, 1/3, 33%). We found no evidence of any population of frigate birds (Fregatidae) for which myctophids would be significant prey. The percentage mass of myctophids in the diet (Fig. 1) also indicates that myctophids constitute a considerable amount of food for penguins, shearwaters/petrels/giant petrels/fulmars/prions and storm petrels, but with large variation within each family.

Effects of foraging habitat and technique

Because of the inherent correlation of seabird family with feeding technique, habitat and latitude, effects of family could not be examined along with other factors. When all seabird data were used, habitat and timing of feeding are selected in all four equally supported models (all-species models in Table 1). The seabirds tend to feed on myctophids more in oceanic basin and slope than in shelf and coastal habitat (Fig. 2a, SI Table 2) and seabirds that feed at night tend to feed more on myctophids than those that do not feed at night (Fig. 2b, SI Table 2). Latitude, feeding technique and body mass, however, were selected in only one of the four equally supported models, and primary production was not selected.

When the analysis was restricted to Procellariidae species only, which are all surface feeders and thus feeding technique was omitted as a potential factor, habitat and body

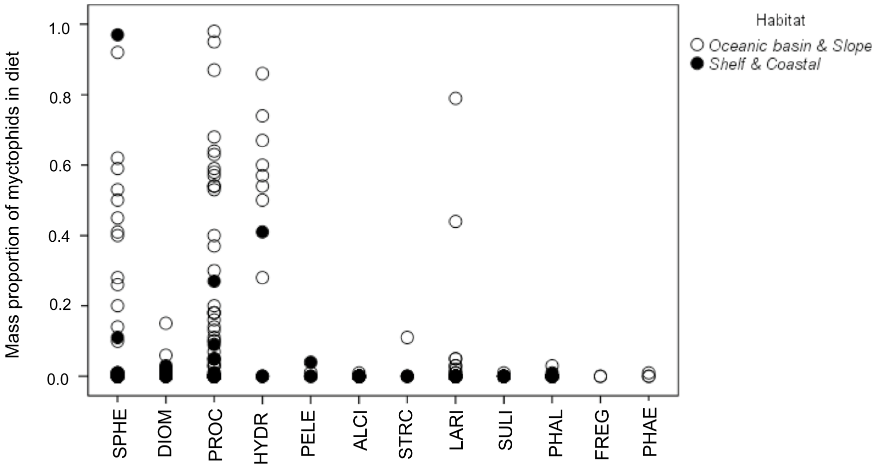

Fig. 1 Proportion of myctophids (by mass) in seabirds' diet across families (*SPHE* spheniscidae, *DIOM* diomedeidae, *PROC* procellariidae, *HYDR* hydrobatidae, *PELE* pelecanoididae, *ALCI* alcidae, *STRC* stercorariidae, *LARI* laridae, *SULI* sulidae, *PHAL* phalacrocoracidae, *FREG* fregatidae, *PHAE* phaethontidae). Values shown are for each site–species combination in open circle oceanic basin and slope habitat and filled circle shelf and coastal habitat

Table 1 Factors affecting the proportion of myctophids (by mass or volume) in the diet of all seabird species ($n=268$ species–sites) and Procellariidae (petrels/shearwaters, $n=73$ species–sites)

All species model						Procellariidae model					
Model	*df*	logLik	AIC$_c$	ΔAIC$_c$	wt	Model	*df*	logLik	AIC$_c$	ΔAIC$_c$	wt
HAB + night	**4**	**−68.1**	**144.4**	**0.00**	**0.25**	HAB + mass	**4**	**−27.3**	**63.1**	**0.00**	**0.23**
HAB + mass + night	**5**	**−67.9**	**146.0**	**1.60**	**0.11**	HAB + mass + night	**5**	**−26.4**	**63.7**	**0.58**	**0.17**
HAB + lat + night	**5**	**−68.0**	**146.1**	**1.77**	**0.10**	HAB + PP + mass	**5**	**−27.0**	**64.8**	**1.68**	**0.10**
HAB + ftech + night	**5**	**−68.1**	**146.4**	**1.99**	**0.09**	HAB + PP + mass + night	6	−26.0	65.3	2.21	0.08
HAB + PP + night	5	−68.1	146.4	2.07	0.09	HAB + lat + mass	5	−27.3	65.4	2.31	0.07

Generalized linear mixed-effect models used the following explanatory variables: marine habitat (HAB: oceanic basin and shelf slope versus shelf and coastal), latitude (Lat, absolute value), sea surface primary production (PP), body mass (Mass), feeding surface technique (Ftec: diving versus surface feeding), and timing of feeding (night: documented nocturnal feeding versus undocumented). Species was treated as a random factor. Model selection was based on ΔAIC$_c$. The five best models are shown, and equally supported models are in bold. Akaike weight (wt) is shown

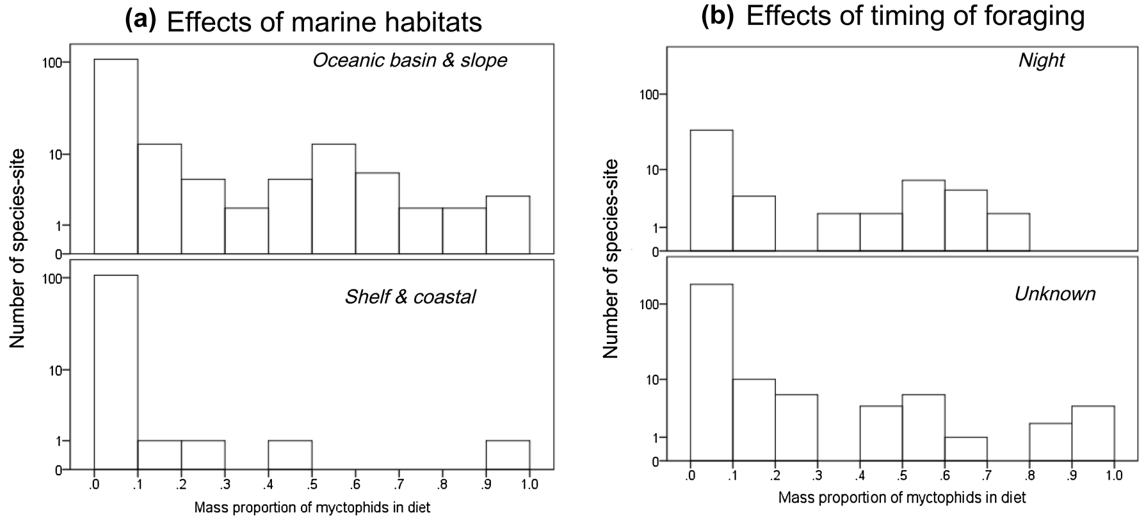

Fig. 2 Frequency distributions of the proportion (by mass) of myctophids in the diet of **a** all sampled seabirds ($n=268$ species–site combinations) in oceanic and basin versus shelf and coastal habitats and **b** species reported to feed nocturnally versus species not reported to feed nocturnally. Note that vertical axis uses log scale

mass were selected in all three equally supported models (Procellariidae models in Table 1). Although parameter estimates for all factors were not significant (SI Table 2), Procellariidae species tend to feed on a higher proportion of myctophids in oceanic basin and slope than in shelf and coastal habitat (Fig. 3a). Smaller species seem to feed on myctophids more (Fig. 3b), but when the two largest species (northern giant petrel, *Macronectes halli*, and southern giant petrel, *M. giganteus*) were excluded, body mass was not selected in the five equally supported models (SI Table 3). Primary production and timing of feeding were selected in only one of the three models, and latitude was not selected in any.

Discussion

Although we could not separate taxonomic effects from those of latitude, habitat and feeding techniques, our analysis, accounting for species as a random factor, suggests that

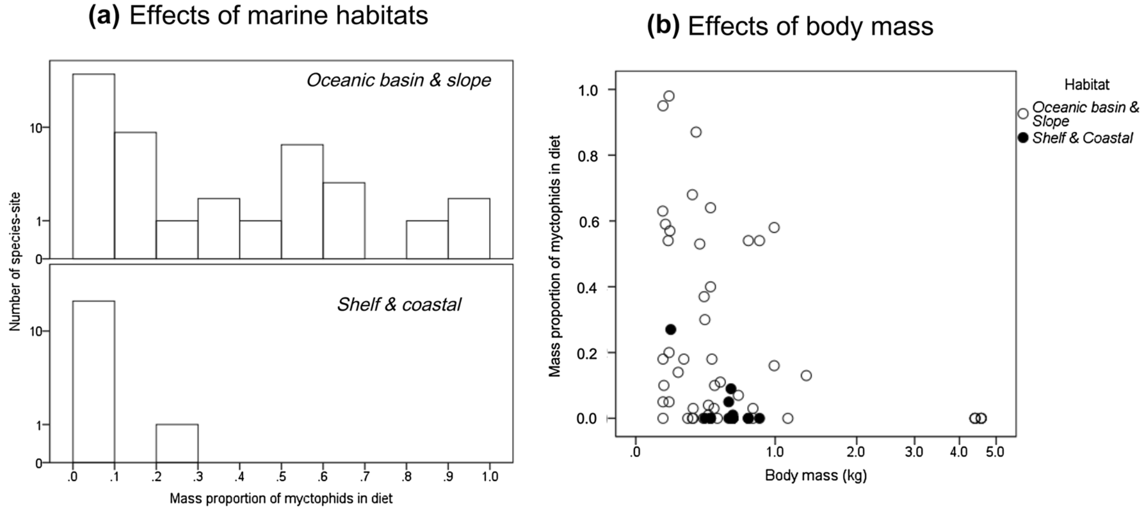

Fig. 3 **a** Frequency distributions of the proportion (by mass) of myctophids in the diet of Procellariidae seabirds ($n=73$ species–site combinations) in oceanic and basin versus shelf and coastal habitats. Note that vertical axis uses log scale. **b** Effect of body mass on the proportion (by mass) of myctophids in the diet. Values shown are for each site–species combination in open circle oceanic basin and slope habitat and filled circle shelf and coastal habitat

myctophids are important for some seabird species which exploit oceanic habitats with appropriate foraging behaviour. Latitude and primary production were not selected as important factors in any models. Sampling sites were biased in relation to both, which might partly explain why these environmental factors were not significant. Body mass and feeding technique (surface feeding vs diving) were not selected either. Surface feeders might feed on mesopelagic myctophids when the latter come close to the surface.

Foraging habitat

The all-seabirds models and the Procellariidae models indicate that marine habitat explain the importance of myctophids in the diet. Birds tend to feed more on myctophids in oceanic basin and slope than in shelf and coastal habitat. A comparison between the congeneric king (*Aptenodytes patagonicus*) and emperor penguins (*A. forsteri*) in the Southern Ocean illustrates this point. Both penguin species perform deep dives. During the breeding season, king penguins, which typically forage in open oceanic waters (e.g., Bost et al. 1997), feed mainly on myctophids (Croxall and Lishman 1987; Ratcliffe and Trathan 2011), while emperor penguins, which forage mainly over the shelf or the shelf break areas around Antarctica (Kirkwood and Robertson 1997; Raymond et al. 2016), do not. The latter, however, feed on some myctophids when they forage in oceanic waters (Ainley et al. 1991, 1992), which supports this inference.

Within-species variation in myctophid consumption also supports the effect of marine habitat. For example, chinstrap penguins (*Pygoscelis antarctica*) rearing chicks on Elephant Island feed mainly on krill over the shelf area, but they also bring back myctophids after long overnight foraging trips to offshore waters (Ichii et al. 2007). Similarly, short-tailed shearwaters (*Puffinus tenuirostris*) breeding in Tasmania forage both in neritic waters near their colonies (Tasman Sea, Bass Strait) and in remote oceanic waters (sub-Antarctic and Antarctic waters) (Klomp and Schultz 2000; Einoder et al. 2010; Cleeland et al. 2014). Stomach contents of this species sampled in the colonies commonly show krill, fish larvae, squid and copepods, but after long foraging trips (ca. a week), presumably to the Southern Ocean, myctophids may constitute ca. 10% by mass of the stomach contents (SI Table 1). In the Bering Sea, black-legged kittiwakes (*Rissa tridactyla*) have been consuming more myctophids and less walleye pollock (*Theragra chalcogramma*) since 1970 (Renner et al. 2012). In response to decreasing pollock stocks, black-legged kittiwakes have increased their foraging activity in the oceanic area and at night, targeting myctophids (Paredes et al. 2014). Red-legged kittiwakes also consume myctophids when they forage in the oceanic domain at night during the breeding season (Kokubun et al. 2016), but when they remain over the shelf areas during the non-breeding period, they typically show diurnal feeding patterns, with hence little opportunity to capture myctophids (Orben et al. 2015). Finally, among breeding Cory's shearwaters (*Calonectris diomedea*), foraging activity becomes predominantly nocturnal when the birds are specifically exploiting the cold and deep oceanic waters, presumably because vertically migrating mesopelagic prey species are locally abundant during the night (Dias et al. 2012). These study cases all support the general conclusion that seabirds foraging in the oceanic domain feed more on myctophids, especially if they are able to forage at night, when these mesopelagic fish move closer to the surface.

Nocturnal foraging

Results from our all-seabirds models imply that the known nocturnal foragers tend to feed more on myctophids than species not known to forage nocturnally. Irrespective of their feeding technique, seabirds would feed on myctophids that come closer to the surface during the night. Yet recent studies using animal-borne data loggers revealed that at least some surface-feeding albatrosses, shearwaters/petrels/giant petrels/fulmars/prions and gulls show more flexible circadian foraging patterns than previously known through direct observation (Table 2). The daily activity patterns of these birds are, therefore, difficult to categorize strictly. This may limit the ability of our review, based on conservative categorizations, to detect any linkage between nocturnal feeding and the importance of myctophids in the diet of the Procellariidae.

Studies of the amount of time spent on the water, the numbers of take-off/landing on the water, or the sinuosity of tracks have suggested nocturnal feeding in six species of albatrosses, four species of shearwaters/petrels, and two species of kittiwakes/gulls (Table 2). Nocturnal prey ingestions were confirmed by measuring stomach temperature or body acceleration in two species of albatrosses and one species of kittiwake. Thus, nocturnal feeding may be more widespread among seabirds than previously thought, and may allow surface feeders to further exploit mesopelagic myctophid fish, although direct evidence is still limited. Thus, at present, this review indicates that flexibility of seabirds' foraging behaviour, especially in time, in surface-feeding species may promote myctophid consumption. Direct exploration of nocturnal feeding in surface feeders using animal-borne data loggers would be important for further understanding of the global trophic interactions between seabirds and myctophids.

Chemical markers

To look at the importance of myctophids in seabirds' diets, we consider stomach contents, regurgitations and bill-loads that reflect food that is consumed a few hours before

Table 2 Nocturnal feeding of seabird species, as suggested or confirmed through the use of animal-borne data recorders on surface-feeding seabird species

Species	Method	Device	Nocturnal feeding	Main foraging	References
Wandering albatross	Tracking, on water	GPS, wet–dry	Suggested	Day	Phalan et al. (2007)
Wandering albatross	Tracking, prey ingestion	PTT, ST	Confirmed	Day	Weimerskirch et al. (2005)
Gray-headed albatross	Tracking, on water	GPS, wet–dry	Suggested	Day	Phalan et al. (2007)
Gray-headed albatross	Tracking, on water, prey ingestion	GPS, wet–dry, ST	Confirmed	Day	Catry et al. (2004)
Gray-headed albatross	Activity	Temp	Suggested	Day and night	Weimerskirch and Guionnet (2002)
Black-browed albatross	Tracking, on water	GPS, wet–dry	Suggested	Day	Phalan et al. (2007)
Black-browed albatross	Activity	Temp	Suggested	Day and night	Weimerskirch and Guionnet (2002)
Yellow-nosed albatross	Activity	Temp	Suggested	Day	Weimerskirch and Guionnet (2002)
Shy albatross	Tracking	PTT	?	Day	Hedd et al. (2001)
Sooty albatross	Activity	Temp	Suggested	Day	Weimerskirch and Guionnet (2002)
Light-mantled sooty albatross	Tracking, on water	GPS, wet–dry	Suggested	Day	Phalan et al. (2007)
Cory's shearwater	Tracking, on water	wet–dry	Suggested	Day	Dias et al. (2012)
Scopoli's (Cory's) shearwater	Activity	Compass	Suggested	Day	Rubolini et al. (2015)
Streaked sheawater	Activity, depth	DT, AC	?	Day	Matsumoto et al. (2012)
Streaked sheawater	Activity	wet–dry		Day	Yamamoto et al. (2008)
White-chinned petrel	Tracking, on water	wet–dry	Suggested	Night?	Mackley et al. (2011)
Barolo shearwater	Tracking, on water, dive	wet–dry, MDS	Suggested	Day and night	Neves et al. (2012)
Red-legged kittiwake	Tracking, activity	GPS, AC	Confirmed	Night	Kokubun et al. (2016)
Audouin's gull	Tracking	GPS	Suggested	Day	Bécares et al. (2015)

Feeding was suggested from the time spent on water, successive take off/landing on water behaviour (using wet–dry sensors, temperature recorders or compass sensor), or the sinuosity of bird movement [tracked using GPS loggers or satellite transmitters (PTT)]. Food ingestion was confirmed using stomach temperature recorder (ST) or by the detailed recording of activity using acceleration data loggers (AC). Some on water activities were observed during the nights but were not determined as foraging (?). See SI Table 1 for scientific names of species

sampling (Wilson et al. 1985; Jackson and Ryan 1986; Hilton et al. 2000), so the importance of prey items which are consumed well before the return to the colony tends to be underestimated (Barrett et al. 2007; Connan et al. 2007b). A comparison of the diet of Procellariiformes between the Scotia–Weddell Sea offshore area (57–62°S; Ainley et al. 1986, 1991, 1992) and the Crozet Islands (46°S; Ridoux 1994), both in the oceanic basin, illustrates how this digestion bias masks the importance of myctophids in seabirds' diets (SI Table 1). The stomach contents of breeding seabirds returning to the colony to feed chicks at Crozet, which reflect prey taken around the colony, contained few myctophids (0–5%, 8 species; SI Table 1). However, myctophids were important prey items in the stomachs of birds (40–95% by mass, median value for each of seven species) that were collected in the Scotia–Weddell Sea, possibly reflecting prey taken in the oceanic basin. Elevated nitrogen-stable isotope values of the muscle tissues of seabirds collected in the Scotia–Weddell Sea (Rau et al. 1992) confirmed that these birds fed on high-trophic-level prey.

Determining the profile of fatty acids (FA) and fatty alcohols (FAlc) of seabirds' stomach oil and body tissue may complement the information obtained by inspecting their stomach contents (Karnovsky et al. 2012). Comparison of the compositions of FA and FAlc in lipids with those of potential prey species using multi-variable statistical techniques can estimate the most probable prey species in samples of predator tissue (Iverson et al. 2005, 2007), with some limitations (Wang et al. 2010; Williams and Buck 2010). Stomach oil, which consists of undigested lipids of prey species [triacylglycerols (TAGs) and wax esters (WEs); Imber 1976; Clarke and Prince 1976; Jacob 1982], is often found in adult Procellariiformes returning from long (ca. a week) foraging trips (Weimerskirch and Cherel 1998; Chaurand and Weimerskirch 1994; Matsumoto et al. 2012; Einoder et al. 2013). Therefore, the FA profile of WEs and TAGs in stomach oil may reflect the prey which were consumed about a week earlier. Studies of FA profiles of stomach oil, thus clearly highlight digestion bias, and reveal that adult birds feed on myctophids in the oceanic basin (Table 3). For example, stomach contents of breeding short-tailed shearwaters coming back from foraging trips consist mainly of krill, fish larvae, squid and copepods (Weimerskirch and Cherel 1998; Einoder et al. 2013), whereas the lipids of their stomach oil originated mainly from myctophids (Table 3; Connan et al. 2005, 2007a). Similarly, stomach content analyses showed that adult blue petrels (*Halobaena caerulea*) at Kerguelen Island brought back mainly crustaceans (> 70% by mass)

Table 3 Estimation of seabirds' prey items based on the profile of fatty acids (FA) and fatty alcohol (FAlc) in triacylglycerols (TAGs) and wax esters (WEs) in the stomach oil of adult seabirds or chicks sampled at the colony after long at-sea trips, versus those in the lipids from the adipose, muscle or blood tissues

Species	Location	Material	Lipids	Fraction	Method	Prey (primary/secondary)	References
Adélie penguin	Mawson Station (S)	Adult blood	NI	FA	DF	Krill/fish	Tierney et al. (2008)
King penguin	Crozet Is (S)	Chick adipose	TAGs	FA	Similarity	Myctophids	Raclot et al. (1998)
King penguin	Crozet Is (S)	Stomach contents	TAGs	FA	Similarity	Myctophids	Raclot et al. (1998)
King penguin	Crozet Is (S)	Adult adipose	TAGs	FA	Similarity	Myctophids	Raclot et al. (1998)
White-chinned petrel	Crozet Is (S)	Stomach oil	WEs, TAGs	FA, FAlc	DF	Myctophids/squids	Connan et al. (2007a, b)
Blue petrel	Kerguelen Is (S)	Stomach oil	WEs, TAGs	FA, FAlc	DF	Myctophids/copepods or notothenids	Connan et al. (2007b, 2008)
Thin-billed prion	Kerguelen Is (S)	Stomach oil	WEs, TAGs	FA, FAlc	DF	Myctophids/copepods or notothenids	Connan et al. (2007b)
Thin-billed prion	Falkland Is (S)	Stomach contents	NI	FA	DF	Squids or crustaceans	Quillfeldt et al. (2011)
Antarctic prion	Kerguelen Is (S)	Stomach oil	WEs, TAGs	FA, FAlc	DF	Myctophids/copepods or notothenids	Connan et al. (2007b)
Short-tailed sheawater	Bruny Is (S)	Stomach oil	WEs, TAGs	FA, FAlc	DF	Myctophids/notothenids	Connan et al. (2005, 2007b)
Cape gannet	South Africa (S)	Adult blood	NI	FA	CA	Epipelagic schooling fish	Moseley et al. (2012)
Streaked shearwater	Awashima Is (N)	Stomach oil	TAGs	FA, FAlc	PC	Anchovy/pacific saury	Kurasawa et al. (2012)
Greater shearwater	NW Atlantic (non-breeding) (N)	Blood	NI	FA	DF	Krill/herring	Ranconi et al. (2010)
Sooty shearwater	NW Atlantic (non-breeding) (N)	Blood	NI	FA	DF	Krill or herring	Ranconi et al. (2010)
Balarctic sheawater	Mediterranean (N)	Adult blood	NI	FA	PC	Pelagic feeding	Käkelä et al. (2010)
Red-legged kittiwake	Pribilof Is (N)	Adult adipose	NI	FA	QFASA	Myctophids (c 90% lipid mass)	Iverson et al. (2007)
Black-legged kittiwake	Pribilof Is (N)	Adult adipose	NI	FA	QFASA	Myctophids (c 60% lipid mass)	Iverson et al. (2007)
Common murre	Pribilof Is (N)	Adult adipose	NI	FA	QFASA	Non-myctophid fish	Iverson et al. (2007)
Thick-billed murre	Pribilof Is (N)	Adult adipose	NI	FA	QFASA	Non-myctophid fish	Iverson et al. (2007)
Little auk	Svalbard Is (N)	Adult muscle	NI	FA	CA	High level of Calanus marker	Wold et al. (2011)
Thick-billed murre	Svalbard Is (N)	Adult muscle	NI	FA	CA	Low level of Calanus marker	Wold et al. (2011)
Black-legged kittiwake	Svalbard Is (N)	Adult muscle	NI	FA	CA	High level of Calanus marker	Wold et al. (2011)
Northern fulmar	Svalbard Is (N)	Adult muscle	NI	FA	CA	High level of Calanus marker	Wold et al. (2011)
Glaucous gull	Svalbard Is (N)	Adult muscle	NI	FA	CA	Diverse diet	Wold et al. (2011)

"NI" indicates that lipid type was not identified. Analytical methods used were discriminant function analysis (DF), principal component analysis (PC), quantitative fatty acid signature analysis (QFASA), correspondence analysis (CA), or Similarity. See SI Table 1 for scientific name of species. For location, N and S indicates Northern Southern hemispher, respecyively and some fish, mostly myctophids, to feed their chicks, whereas the FA profile of their stomach oil indicated that myctophids were the major diet component (Connan et al. 2008). These lines of information derived from the analysis of chemical markers also support the inference that pelagic seabirds feed on myctophids more often when foraging in the oceanic basin.

The FA profile of TAGs in subcutaneous fat reflects prey consumed over about a month (Iverson et al. 2004; Wang et al. 2010). FA signature analyses of the lipids in adipose tissue confirmed that king penguins and red-legged kittiwakes fed mainly on myctophids (Table 3), as determined by stomach content analyses (Cherel and Ridoux 1992; Ridoux 1994; Schneider and Hunt 1984; Sinclair et al. 2008; Kokubun et al. 2016), and revealed also that black-legged kittiwakes fed on myctophids to a larger extent than revealed by stomach content analyses (Iverson et al. 2007). However, excepting these two kittiwake species, the FA profile of lipids in the tissues does not indicate that myctophids are an important food resource for seabirds breeding or wintering in the Northern Hemisphere (Table 3). Qualitative FA signature analysis of lipids from muscle tissues suggests that the little auk (*Alle alle*), black-legged kittiwake, thick-billed murre (*Uria lomvia*), northern fulmar (*Fulmarus glacialis*) and glaucous gull (*Larus hyperboreus*) in Svalbard do not feed on myctophids (Table 3) as much as inferred from stomach content analyses (SI Table 1). Similarly, blood FA components, which allow the metabolic processes of prey consumption to be taken into account, also indicate that the Cape gannet (*Morus capensis*), balearic shearwater (*Puffinus mauretanicus*), greater shearwater (*P. gravis*) and sooty shearwater (*P. griseus*) feed on krill and non-myctophid fish (Table 3).

Non-breeding period

Our review indicates that seabirds exploiting oceanic basin and shelf slope habitats generally consume more myctophids than birds in other habitats. However, we based our analysis on diet relevant mainly to the breeding period. According to recent research (Marra et al. 2015), our understanding of the fundamental ecology of vertebrates, including seabirds, has been limited by a severe breeding-season research bias. In this regard, seabird ecologists are now trying to study individuals outside their breeding period, notably following the development of small, inexpensive light-based geolocation loggers, which can remain for over a year on birds with minimal disturbance (Bridge et al. 2011). One of the main outcomes of this research is the unexpected demonstration that seabirds are generally much more oceanic when they are not breeding, as they are freed from the typical nest-centred constraints that limit their foraging range during the breeding period (Hamer et al. 2002). Indeed, examples of such a habitat shift have been observed in nearly all seabird families: the Spheniscidae (Raya Rey et al. 2007; Thiebot et al. 2011), Diomedeidae (Weimerskirch and Wilson 2000; Thiebot et al. 2014), Procellariidae (Thiers et al. 2014), Hydrobatidae (Pollet et al. 2014), Pelecanoididae (Navarro et al. 2015), Alcidae (Jessopp et al. 2013), Laridae (Frederiksen et al. 2012; Egevang et al. 2010), Stercorariidae (Phillips et al. 2007), Phaethontidae (Le Corre et al. 2012) and Fregatidae (Weimerskirch et al. 2017). Although there are exceptions to this pattern, we suggest that throughout their life-cycle, most seabirds can hunt myctophids more often than indicated from the stomach contents of breeding birds. This is partly verified for the macaroni penguin, the single largest avian consumer of marine resources worldwide (Brooke 2004a): during the Austral winter, non-breeding adults from Crozet Island have the option of heading south, where they feed more on fish (Cherel et al. 2007; Bost et al. 2009).

Widened foraging range and foraging habitats may not be the only reasons why non-breeding birds would feed on myctophids more than during their breeding season. Indeed, profound ecological changes in the marine ecosystems across seasons may also support such prey switch. During the Austral winter, Antarctic seabirds feed on more energetically valuable prey, such as myctophids or squid, than in summer (Ainley et al. 1991). In this situation, krill, one of the main components of the summer diet, must feed close to the ice undersides in winter (Daly 1990). Hence, myctophids might provide an important alternative for normally krill-dependent avian predators, as illustrated when comparing either inter-seasonal diets or within-summer diet during years of lower krill availability (Murphy et al. 2007; Collins et al. 2008; Waluda et al. 2012).

However, this prey switch may not be universal, because myctophids may live more deeply in winter (Sabourenkov 1991; Cherel et al. 1993), restricting their availability to many of their predators, including seabirds. Feeding on myctophids to a greater extent during the non-breeding period would nevertheless still be achievable for those seabird species which may be free of summer breeding constraints, namely winter breeders and biennial breeders. As the biomass-dominant myctophids can live year-round in ecosystems supporting a rich and abundant community of seabirds (e.g., Saunders et al. 2017), we thus support the call for a year-round approach to animal ecology, and more specifically in this case, to seabirds' diet.

Conclusions and perspectives

Our review of the stomach contents in the global seabird community demonstrates global-scale contrasts in the importance of myctophids as food for seabirds. These mesopelagic fish seem to be especially consumed by seabirds that exploit oceanic or shelf slope habitats or that feed at night, at least to some extent. The recent studies of FA in stomach oil in several species of Procellariiformes give additional support to this result. The general biomass of predators and prey, the relative availability of shelf versus oceanic domains to seabirds, and the proportion of nocturnally surfacing mesopelagic fish all vary between marine regions (Klevjer et al. 2016). Hence, it is understandable that our review highlights contrasts in seabirds' consumption of myctophids between marine regions. In addition, interannual variations in the availability of these fish may also be detected in the seabirds' diet, with direct influence on the birds' reproductive success, in relation to the high energy contents of myctophids (Connan et al. 2008; Paredes et al. 2014).

Finally, considering their extremely large biomass in marine ecosystems (Catul et al. 2011; Irigoien et al. 2014), myctophids have the potential to serve as a gigantic pathway of carbon advection between the sea surface and the deeper layers in the world's oceans through their diel vertical migrations (Pakhomov et al. 1996, but see Hudson et al. 2014). Hence, it seems crucial to collect additional information on (1) the distribution and behaviour of both myctophids and seabirds on a circadian and circannual basis, and (2) on seabirds' diet through the use of a range of approaches, including chemical diet markers, to refine our estimates of the trophic relationships between these two groups at the global scale. Such estimates may bring a new perspective to clarify the role of myctophids in the active transport of carbon between marine compartments at the global scale.

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Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest.

Ethical approval This article does not contain any studies with human participants performed by any of the authors. This article is a review paper and does not contain any studies with animals performed by any of the authors.

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