



Review Article

A toolkit to study seabird–fishery interactions

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Seabirds and fisheries have been interacting from ancient times, sometimes with mutual benefits: Seabirds provided fishermen with visual cues of fish aggregations, and also fed upon food subsidies generated by fishing activities. Yet fisheries and seabirds may also compete for the same resources, and their interactions can lead to additional seabird mortality through accidental bycatch and diminishing fishing efficiency, threatening vulnerable seabird populations. Understanding these complex relationships is essential for conservation strategies, also because it could enhance and ease discussion between stakeholders, towards a common vision for marine ecosystem management. As an aid in this process, we reviewed 510 scientific publications dedicated to seabirds–fisheries interactions, and compiled a methodological toolkit. Methods employed therein serve four main purposes: (i) Implementing distribution overlap analyses, to highlight areas of encounter between seabirds and fisheries (ii) Analysing movement and behavioural patterns using finer-scale information, to characterize interaction types (iii) Investigating individual-scale feeding ecology, to assess fisheries impacts at the scale of bird populations, and (iv) Quantifying the impacts of seabird–fishery interactions on seabird demography and population trends. This latter step allows determining thresholds and tipping points with respect to ecological sustainability. Overall, we stress that forthcoming studies should integrate those multiple approaches, in order to identify and promote best practices towards ecosystem-based fisheries management and ecologically sound marine spatial planning.

Keywords: at-sea surveys, biologging, bycatch, demography, discards, ecosystem-based fisheries management, marine spatial planning, movement ecology, spatial analyses, stable isotopic analyses.

Introduction

Seabird and fisheries occur in all areas of the world ocean. In aquatic environments exposed to global changes, they share common challenges linked to e.g. vanishing fish resources. Their relationships are ancestral but the development of fishing and research technologies has transformed their many interactions, and our capacity to study these processes and rate their ecological consequences.

Notably, seabirds are conspicuous scavengers (Figure 1a; Hudson and Furness, 1988; Catchpole *et al.*, 2006; Depestele *et al.*, 2016) and have been feeding on fishery waste around the world ever since humans started harvesting marine organisms. For instance, the albatross sung by Charles Baudelaire (Baudelaire, 1857) probably followed ships in search of food.

Depending on the species involved, seabirds feed on fishery discards or on offal, whereby birds tend to target energy-rich organs (Hudson and Furness, 1988). In addition to discards and offal, Procellariiforms have been shown to target baits used in longline fisheries (e.g. Brothers, 1991; Kumar *et al.*, 2016). Furthermore, even if a limited number of cases have been reported in the literature, some diving species (e.g. cormorants and gannets) are strongly suspected to depredate fishing devices underwater (Ferrari *et al.*, 2015), as already well-described in marine mammals (Guinet and Bouvier, 1995). Finally, slippage and escapees from purse seine and trawl fisheries represent another potential food source for seabirds. Exploiting such easily accessible food may be advantageous for some species (Tasker *et al.*, 2000; Furness, 2003), at least when natural prey is scarce (Tew-Kai

et al., 2013). These supplementary prey items represent an important part of the diet in some species, and have been shown to potentially promote seabird population growth (Bicknell *et al.*, 2013). However, when it is of lower nutritional value, fishery waste may set ecological traps for seabirds (Grémillet *et al.*, 2008). Overall, these predictable anthropogenic food subsidies (Oro *et al.*, 2013) have shaped seabird communities, to the advantage of generalist predators (Votier *et al.*, 2004).

To benefit from fishery wastes seabirds need to approach fishing vessels, exposing themselves to bycatch on fishing gear (Figure 1b). The proximity between seabirds and fishing vessels also arises from the use of seabirds as indicators of profitable harvesting grounds (Figure 1c). This ancestral fishing strategy (Crawford and Shelton, 1978) uses the fact that seabirds aggregate when foraging on pelagic fish shoals, and can then be easily spotted from a distance. This technique is still commonly used today, especially by the tuna fishing fleet, which uses radars to spot seabird aggregations at sea. This specific fishing strategy enhances spatial overlaps between seabirds and fishing vessels, increasing the probability of interaction.

Three major types of casualties (bycatch on longlines, entanglement in gill nets and collision with trawling cables) and several other risks to seabirds are reported in the literature (Figure 1b). Notorious are bycatches of procellariiforms on the hooks of longline fishing fleets. Such bycatch has been described in numerous areas, e.g. albatrosses in Patagonian toothfish fisheries (Wienecke and Robertson, 2002; Delord *et al.*, 2005), albatrosses in Japanese tuna longline fisheries (Brothers, 1991), shearwaters in Mediterranean longline fisheries (Garcia-Barcelona *et al.*, 2010), albatrosses and petrels in Brazilian longline fisheries (Bugoni *et al.*, 2008). Worldwide, bycatches in longline fisheries have been estimated to at least 160 000 seabirds annually (Anderson *et al.*, 2011), with albatrosses making up to 80% of the bycaught individuals in some areas (Jiménez *et al.*, 2009). Entangling of diving seabirds in gill-nets, especially alcid (Darby and Dawson, 2000; Osterblom *et al.*, 2002; Cardoso *et al.*, 2011), is another common case of incidental catch. Żydelis *et al.* (2013) estimated that >400 000 seabirds are accidentally caught by worldwide gillnet fisheries each year. Trawl fisheries also represent a major threat to

seabirds, which are killed or injured through collision with wrap cables (Gonzalez-Zevallos *et al.*, 2007; Croxall, 2008; Watkins *et al.*, 2008). Further, seabird mortality through artisanal fisheries is hard to assess, but is also considered as non-negligible (Suazo *et al.*, 2013). Overall, even in omission of substantial mortalities caused by abandoned fishing gear (Rodriguez *et al.*, 2013), threats caused by fisheries activities to seabird populations have been confirmed as a major conservation issue (Lewison *et al.*, 2004; Croxall *et al.*, 2012).

As the capture of non-target organisms such as seabirds is also detrimental to fishing efficiency, there is a global concern and a common interest for fishery management and seabird conservation stakeholders to eradicate bycatch. This led to the publication of a special guideline by the Food and Agriculture Organization by the United Nations in 1999 (International plan Of Action—Seabirds), prescribing mitigation measures built upon technical solutions (Cooper *et al.*, 2001), and enhanced specific actions for dedicated organisms (e.g. BirdLife International and Agreement on the Conservation of Albatrosses and Petrels, 2009). Those efforts gathering non-governmental organizations, scientists, managers and fishermen led to substantially reduced impacts (Agnew *et al.*, 2000; Abraham *et al.*, 2009; Bull, 2009), even if bycatch could not be eradicated, and may still arise through uncontrolled and/or illegal fisheries (Grémillet *et al.*, 2015). Synoptically, research conducted across the last two decades triggered a paradigm shift in fisheries management. Evidence that humans affect fish populations and marine ecosystems around the world (Jackson *et al.*, 2001; Christensen *et al.*, 2003; Myers and Worm, 2003; Chavance *et al.*, 2004) led to a shift from single-species approaches to ecosystem-based fishery management (Pikitch *et al.*, 2004). In this context, several new legislations have been implemented to reduce the collateral damages of fishing activities. For example, in Europe, the new Common Fishery Policy enforces a reduction of discarding practices through a landing obligation of all organisms for species under quotas, which is predicted to modify seabirds–fisheries interactions (Bicknell *et al.*, 2013).

However, despite these new insights, marine conservation is now facing the same research-implementation gap as its

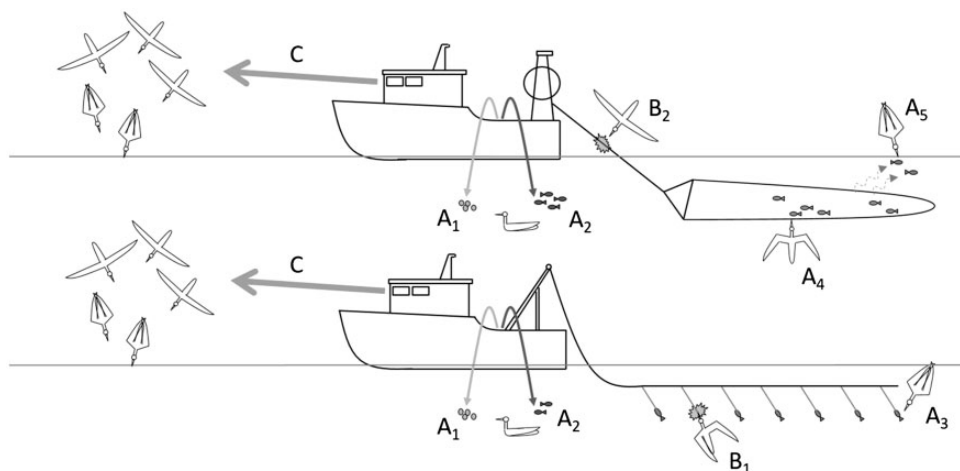


Figure 1. Schematic representation of direct interactions between seabirds and fisheries. (a) Seabirds forage on food subsidies from fishing activity. A1, Offal; A2, Discards; A3, Baits; A4, Depredation; A5, Escapes. (b) Foraging in the vicinity of fishing vessels causes accidental mortality for seabirds. B1, Bycatch; B2, Collision. (c) Fishermen cue on seabirds for profitable fishing grounds.

terrestrial counterpart (Knight *et al.*, 2006, 2008; Ban and Klein, 2009; Biggs *et al.*, 2011), partly stemming from the difficulty to develop true cooperation among typically diverse stakeholder groups, whose interests, norms, values, powers or communication skills may diverge. To overcome this hurdle, Lescroël *et al.* (2016) proposed to use charismatic marine predators, such as seabirds, as ambassadors of global ocean conservation to “see the oceans through the eyes of seabirds” and foster stakeholder cooperation. Part of this approach requires improved knowledge of seabird-fisheries interactions. Specifically, forthcoming research should enhance operational approaches, to better understand and forecast the impact of management policies on fishing practices and seabird populations. As an aid to these developments, we propose a methodological review and synthesis of the best methodologies currently available for the study of seabird–fishery direct interactions (see Sydeman *et al.*, 2017 for a review of competition interaction), with additional suggestions for future key developments.

Methods

We used the Web Of Science database with the following combination of search terms for the 1990–2017 time period: [seabird* OR gull* OR gannet* OR albatross* OR petrel* OR shearwater* OR fulmar* OR penguin* OR skua* OR kittiwake* OR tern* OR guillemot* OR shag* OR cormorant*] AND (fisher* OR bycatch* OR discard* OR offal* OR longline* OR gillnet* OR trawl* OR seine*]. After eliminating studies focussed on food competition between seabirds and fisheries (methods reviewed in Sydeman *et al.*, 2017), and incorporating some missing studies rated as important by our group of authors, we obtained 510 papers of interest for our synthesis. To quantify the diversity of approaches reported in the literature, we specifically focussed on 249 original studies, putting aside reviews and technical studies relative to mitigation measures and their implementation. We classified these studies according to four broad categories, which may nonetheless partially overlap: (i) Analyses of large-scale distributional overlaps between seabirds and fisheries, (ii) Analyses of their movement and behaviour, (iii) Analyses of seabird feeding ecology and dependence from fishery subsidies, and (iv) Quantification of the impacts of these interactions on seabird demography and population trends. For each of these four categories, we critically evaluated methodological processes, from data acquisition to statistical analyses, and provided a synthetic summary table to guide choices and rank methodologies.

Distribution overlap analyses

The main objective of distribution overlap analyses is to identify areas of potential interactions between seabirds and fisheries, based on separately acquired data sets on seabird and fishery distributions (Table 1[A]).

The major difficulty has always been to acquire information about seabird distributions, as some of their ranges may stretch over several ocean basins (Egevang *et al.*, 2010). Therefore, except for some species for which presence can be studied from land (such as gulls, e.g. Castilla and Perez, 1995; Arcos and Oro, 1996), knowing where seabirds go requires advanced logistics and methodologies. At-sea surveys from either scientific cruises (Jespersen, 1924; Garthe, 1997; Camphuysen and van der Meer, 2005; Guy *et al.*, 2013) or fishing vessels (Cabezas *et al.*, 2012) are the primary source of knowledge about large-scale seabird at-sea distributions. From these ships, observers will report the presence and

number of the different species, associated with the position of the boat (Tasker *et al.*, 1984). Aerial survey transects can also be used to estimate seabird at-sea distribution at large spatial scales (Certain and Bretagnolle, 2008). Benefiting from developments in telemetry technologies, animal-borne devices have also been developed to monitor the movements of wild animals. Three main electronic devices are used for the study of seabird at-sea distributions. Platform terminal transmitters (PTTs) linked to the Argos system are the most commonly used (43% of distribution overlap studies). These platforms emit a signal which is received by a satellite and transferred to a ground receiving station. They can provide ~10–12 locations per day with a relative accuracy of up to a few kilometres (e.g. Nel *et al.*, 2002; Cuthbert *et al.*, 2005; Hatch *et al.*, 2016). Global positioning system (GPS) loggers are used in 25% of all distribution overlap studies. Contrary to PTTs, GPSs do not emit, but receive signals from a satellite network. Locations are accurate to 3–5 m and can be sampled at any frequency, starting from 1 s. They can be either stored onboard and retrieved after recovery of the device, or downloaded remotely via Argos, ultra high frequency, or the cellphone network. In the latter cases, tracking can therefore be performed in near-real time (Navarro *et al.*, 2016), i.e. as with PTTs, but with greater positioning accuracy. For both PTTs and GPSs, the recording duration is limited by power supply and attachment to the tracked birds (devices attached to the feathers will be shed during molt). Recent advent of solar-powered devices has drastically expanded deployment durations in some species, to several months, or even years (Bouten *et al.*, 2013). GPS device mass has also been reduced to a few grams (Amélineau *et al.*, 2016). Global location sensors (GLS) is the third main type of loggers used in distribution overlap analyses. Those devices record light level and time, which after processing can provide one to two daily positions (outside of the equinox periods) with an accuracy of ± 190 km (Wilson, 1992; Phillips *et al.*, 2004). GLSs are small and light enough (<1 g) to be affixed to a bird ring, and deployed for one to several years (Weimerskirch *et al.*, 2014). very high frequency tags have been used occasionally to study distribution overlap between seabirds and fisheries (Manosa *et al.*, 2004; Hamel *et al.*, 2008), but the logistical costs of mapping large-scale bird presence (aerial detection) make its implementation too difficult for a more common use.

Regarding the spatial and temporal distribution of fisheries, researchers benefit from diverse sources of data produced by a wide range of fishery stakeholders, although not all are easily available. Historically, these consist in logbooks from individual boats recording fishing zones and the number of sets, hauls, as well as gear type, together with indices of fishing effort such as numbers of hooks set per unit area (e.g. Cuthbert *et al.*, 2005; Bugoni *et al.*, 2009; Reid *et al.*, 2013). This information is collated and archived by international governance instances such as the International Commission for the Conservation of Atlantic Tunas (ICCAT) or the Indian Ocean Tuna Commission (IOTC) for tuna longline fisheries, or by national instances as the National Oceanic and Atmospheric Administration (NOAA) in the United States or the Marine Fisheries Agency in the United Kingdom. Such official statistics have nonetheless been demonstrated to be underestimates, both in terms of catch volumes and exploited areas (Pauly and Zeller, 2016). More recently, a specific application of monitoring commercial fishing boats, the vessel monitoring system (VMS), has been implemented worldwide. VMS is particularly useful as a database of fishing vessels positions, which allows

Table 1. Methods used in 206 original publications dedicated to the description, characterization, and quantification of seabird-fisheries interactions.

General purpose	Specific objective	Method examples	Identify seabirds	Identify fisheries	Localize interaction	Sample size	Logistics required	Invasiveness	Data accessibility	Identify interaction	Quantify interaction	Analysis complexity	Utilization frequency % (Σ)	
A. Where do seabirds and fishing vessels meet?	Detect at-sea presence of both seabirds and fisheries	At-sea and aerial survey	+	++	++	+++	+++	-	++	+			8, 3 (17)	
		PTTs GPS GLS	+++	-	+++	+	+	+++					25, 2 (52)	
	Learn where fishing takes place	VMS	-	+++	+++	+++	-	-						16, 5 (34)
		Logbook-Fishing effort Kernel analyses										+	+	13, 6 (28)
	Estimate spatial utilization	Map overlap												
		UDOI												
	Estimate spatial overlap	Cuthberg method												
		Spearman correlation												
	Assess the influence of overlap on space use	Generalized models												
		Multivariate analyses												
B. How do seabirds behave in the vicinity of fishing vessels?	Assess interactions visually from fishing vessels	Fisheries Observers	+++	+++	+++	+	+++	-	++	+++			49, 5 (102)	
		Seabird observers												
	From the birds' point of view	Video Cameras	+++	++	+++	+	++	++	+++					7, 3 (15)
		Bird-born cameras												
	Estimate bycatches	Electronic devices												
		Scale up observation										+++	++	18, 9 (39)
	Evaluate food subsid consumption	Generalized models												
		Bayesian models												
	Analyze common movements of seabirds and fishing vessels to detect interactions	Foraging Success Index												
		Bioenergetics												
Detect seabird prey in seabird food bowls	Tracks overlap													
	Activity overlap													
Do seabirds feed on food subsids from fisheries?	Behavioural switch													
	Regurgitations		+++	-	-	++	++	++	+++	++			21, 8 (45)	
Trace chemical signatures of seabird prey	Pellets													
	Stomach contents													
Evaluate food subsid consumption	Stomach extractions													
	Isotopic analyses		+++	-	-	+	+	+	+++				11, 7 (24)	
SIAR	Fatty acid analyses													
	Quantitative													
Qualitative	SIAR													
	Quantitative										++	++	21, 8 (45)	

Methods for data acquisition are given in *italics* in position to methods for data analysis. The utilization frequency index (% of occurrence and number of studies) gives the frequency of use in the literature for different group of methods pursuing a common objective. The corresponding references are given in aendix (Supplementary Table S1).

accurate tracking of their movements at 30 min to 3 h intervals (Granadeiro *et al.*, 2011; Copello *et al.*, 2014; Patrick *et al.*, 2015). The automatic identification system (AIS) developed to prevent ship collisions has also proved extremely useful (Robards *et al.*, 2016), notably to map fishing activities (Mazzarella *et al.*, 2014; Natale *et al.*, 2015) and will soon be used extensively to study seabirds–fisheries interactions. Further, bird-borne devices coupling a GPS and a ship radar/AIS detector (Weimerskirch *et al.*, 2017) enable recording seabird–ship encounters, as well as the AIS registration number of the vessels. This enables using seabirds as sentinels of fishing activities, being legal or illegal; especially in areas where surveillance is logistically challenging (e.g. West Africa, the Southern Ocean). Finally, fishing vessels distribution can be estimated from reported presence during scientific at-sea surveys, producing data equivalent to those from seabird direct observations.

To identify areas used by seabirds and fisheries from these data, the most common method is kernel analysis. This algorithm calculates a density distribution of the locations and a probability distribution in space use, termed utilization distribution (UD). Thereby, the density matrix is estimated via fixed kernel home-range analyses following Worton (1989; see also Brothers *et al.*, 1998; Nel *et al.*, 2000, 2002; Copello *et al.*, 2014), with potential modifications following (Wood *et al.* 2000; Xavier *et al.*, 2004; Bugoni *et al.*, 2009). Contour plots can be generated, over which areas of overlap between seabirds and fisheries are visually identifiable. The degree of overlap can also be quantified using a UD overlap index (UDOI, Fieberg and Kochanny, 2005) derived from the estimated UDs. It has been used extensively to quantify large-scale overlaps between seabirds and fisheries (e.g. Granadeiro *et al.*, 2011, 2014; Copello *et al.*, 2014). Two other important overlap indices can be computed without relying on probability distribution in space: (i) A Spearman correlation coefficient (r_s), calculated between geographical grid cells for the density of presence of both seabirds and fisheries (Camphuysen and Garthe, 1997; Hyrenbach and Dotson, 2003); (ii) A measure of the overlap between individual seabird geographical density and fishing effort (Cuthbert *et al.*, 2005). This latter index is the simple multiplication of the density of birds by the fishing effort (number of hooks, hours of trawling) reported to unit area. It is commonly used to study overlaps with longline fisheries (Hamel *et al.*, 2008; Thiers *et al.*, 2014; Jiménez *et al.*, 2016), and with trawling fisheries (Guy *et al.*, 2013). In the literature, such overlap indices are not always calculated, and fishing effort or distribution are handled as environmental variables susceptible to impact modelled seabird space utilization. The corresponding statistical methods are principal component analyses (Garthe, 1997; Weichler *et al.*, 2004) or generalized models (e.g. generalized linear model (GLM), Cama *et al.*, 2012; Catry *et al.*, 2013 or generalized additive model (GAM), Weimerskirch *et al.*, 2010; Renner *et al.*, 2013) with seabird presence or density as the response variable and fishing effort or distribution and other environmental variables as explanatory variables.

Whatever the method used, distribution overlap approaches have the huge advantage of identifying areas with strong probability of encounter between seabirds and fisheries. It allows defining high-risk areas deserving specific conservation efforts (e.g. Tancell *et al.*, 2016) and their projection following global change scenarios (e.g. Krüger *et al.*, 2018). Yet, overlap does not always mean direct interaction. Sharing the same resources, seabirds and fishing vessels are targeting the same areas (e.g. Pichegru *et al.*,

2009), but conservation and management measures will largely depend upon interaction types. This calls for the downscaling of impact studies, to include information on the actual behavioural patterns of seabirds and fishing units (Table 1[B], Torres *et al.*, 2013).

Analysis of movement and behaviour

Using direct observations and tracking data, it is possible not only to define space use in seabirds and fisheries, but also to associate at-sea positions with specific behaviours. For instance, dedicated observers onboard fishing boats (hereafter seabird observers) can record the characteristics of seabird feeding aggregations (mainly species and broad age composition), as well as the different behaviours displayed by seabirds, with respect to prey choice, intra- and interspecific competition and rank-order (Hudson and Furness, 1988; Garthe and Huppopp, 1994; Otley *et al.*, 2007; Carniel and Krul, 2011; Depestele *et al.*, 2016), and also interaction types, food choices and any potential accidental mortality (Bugoni *et al.*, 2008). Specifically, efforts have been made by concerned nations to deploy fisheries observers on at-risk fisheries (such as longline and gillnet fisheries), so as to record accidental seabird bycatch (Reviewed in Anderson *et al.*, 2011; Żydelski *et al.*, 2013). Yet observers focus on caught seabirds and hardly take in account individuals injured or killed that are not hauled on board. Furthermore, costs incurred limit the number of deployed observers and the rate of monitored fisheries is still low, some remaining unmonitored (Pauly *et al.*, 2014). At-sea observations using video-based monitoring (McElderry, 2008) could be a solution in the future. This approach still requires research and development (e.g. observation event detection algorithms for automatic analysis of video sequences) and enhanced co-construction of video monitoring programmes with fishery stakeholders (Lescroë *et al.*, 2016).

Fisheries observer's data may nonetheless be an important input, allowing an evaluation of interaction levels at a broader scale (Gilman *et al.*, 2017). A simple method consists in up-scaling observed bycatch rates, taking into account overall fishing effort (Francis and Sagar, 2012). But as incidental catches are rare events, even recorded at large regional scales, error margins are substantial (Lewison *et al.*, 2004). Methods to model rare events have been recently improved, and their application to bycatch estimates offers fruitful perspectives. Notably, generalized models have been used in this field (e.g. Winter *et al.*, 2011; Yeh *et al.*, 2013), but Bayesian frameworks providing robustness for uncertainty accounting may soon become the norm (e.g. Martin *et al.*, 2015). Another problem to address when estimating mortality from bycatch observer data is to identify the origin of individuals incidentally caught. However solutions based on the application of biochemical and molecular markers have been implemented (Burg, 2007; Lavers *et al.*, 2013; Jiménez *et al.*, 2015; Techow *et al.*, 2016). Relevantly, Burg *et al.* (2017) have been able to differentiate origins of intraspecific groups of albatrosses using mitochondrial DNA extracted from blood or feathers of bycaught individuals. Furthermore, seabird observer data are essential to quantify the amount of subsid prey fed to seabirds. Foraging success indices can be calculated by species (Garthe and Huppopp, 1998; Jodice *et al.*, 2011), providing feeding rates upon which total consumed amounts can be estimated. Some studies go further, by using bioenergetics modelling so as to estimate the implications of discard consumption for seabird energy balances (Lilliendahl and Solmundsson, 1997; Walter and Becker, 1997;

Arcos and Oro, 2002). Even though ecophysiological modelling tools (Votier *et al.*, 2004; Fort *et al.*, 2009) offer great perspectives, estimating the amount of consumed subsid prey is still complex. Notably, direct seabird observations do not provide any information on the number of other fishing vessels visited by seabirds during their foraging trips.

A solution is to reverse the viewpoint, from the birds towards fishing vessels, which is difficult to obtain, but can be achieved with novel electronic tools. The most obvious ones are bird-borne cameras, which can directly record the visual landscape of the bird. It is then possible to detect when fishing vessels are present in the vicinity of the birds and whether there are direct interactions with them (Grémillet *et al.*, 2010; Votier *et al.*, 2013; Lescroël *et al.*, 2016). However, in the case of video recordings, the battery size of such portable devices is still limiting the duration of image acquisition to a few hours. Progress in automatic image processing is also required to detect and characterize interactions more efficiently (e.g. Spampinato *et al.*, 2010). For these reasons, the most commonly used devices to study behavioural interactions between seabirds and fisheries remain GPS recorders, but the use of radar detector loggers (see previous section, Weimerskirch *et al.*, 2017) could soon become important to. Two types of analyses are performed using GPS tracks; the first is in the continuity of distribution overlap studies, and aims at detecting overlaps between individual birds and fishing vessel trajectories. The second aims at identifying specific seabird behavioural patterns as they approach fishing vessels. The two approaches are dependent upon fine-scale localization of fishing vessels, mostly via VMS. When individual tracks from both seabirds and fishing vessels are available, interactions can simply be assumed when tracks overlap spatially and temporally (Granadeiro *et al.*, 2011; Torres *et al.*, 2011; Tew-Kai *et al.*, 2013). To go further, and contrary to overlap analyses, seabird foraging tracks can be analysed individually to extract characteristics such as foraging trip duration, path length and maximum distance reached (e.g. Mattern *et al.*, 2013; Garcia-Tarrason *et al.*, 2015). The influence of fisheries on seabird foraging behaviour can then be assessed by modelling the effect of fishery activity patterns (e.g. weekdays vs. weekends, Garcia-Tarrason *et al.*, 2015; Tyson *et al.*, 2015) on these characteristics using GAMs or generalized linear mixed models. Some studies go further and identify the strict periods of active foraging within seabird tracks (i.e. excluding resting and travelling periods, see Barraquand and Benhamou, 2008; Torres *et al.*, 2017 for a specific discussion), usually using residence time methods. Seabird specific overlap with active vessels is then identified and differentiated from “natural” foraging, i.e. in the absence of fishing vessels (Votier *et al.*, 2010; Patrick *et al.*, 2015). The second approach focuses on identifying seabird behavioural changes when in the vicinity of a fishing boat. There again, movement analysis methods are used to track specific behavioural signatures or responses in bird tracks interacting with fishing vessels. For example, birds may redirect flight trajectories towards boats (Collet *et al.*, 2015) or adopt vessel cruising pattern (Torres *et al.*, 2011). In this way, Bodey *et al.* (2014) showed that seabirds switched between foraging and commuting behaviour according to the fishing activity of the followed vessel. As this method is based on the preliminary identification and isolation of behavioural sequences that are specific to interactions with fishing vessels, it avoids confounding direct interactions and mere spatial overlap of two entities co-existing in the same area, because targeting the same resources. However, automatic detection of such behaviour

can be difficult, and is strongly dependent upon individualities in behavioural patterns.

Feeding ecology and dependence on fishery subsidies

Another powerful way to quantify the dependence of a given seabird species or population on food sources originating from fisheries is to search for traces of these food sources (Table 1[C]) in bird stomach contents (diet sampling) or tissues (usually blood or feathers, using biochemical methods). This relies on the assumption that prey items provided by fisheries are different from natural prey targeted by the studied species. The most obvious example is the case of seabirds naturally targeting pelagic prey and eating discards from demersal fishing activities (Kakela *et al.*, 2010).

Diet sampling analysis can be performed on dead or live birds. On dead birds (e.g. from bycatch, Gould *et al.*, 1997) the stomach or the entire digestive track is removed and stored for latter identification of the content. These samples may be biased in populations containing diet-specialist, as all sampled birds are caught in the vicinity of fishing vessels, and naturally foraging individuals may be missed. To sample the diet of live birds, it is possible to retrieve stomach contents by stomach flushing (Wilson, 1984), but for those seabird species which vomit when captured, acquiring samples from regurgitation may be easier. Fresh food bowls can then be sorted and prey items can be directly identified when digestion is not too advanced (Blaber *et al.*, 1995; James and Stahl, 2000). When it is the case, rigid parts such as otoliths and cephalopods beaks are still identifiable (James and Stahl, 2000). Those non-digestive parts are evacuated by some species by the production of pellets, which can be collected and studied afterwards (Votier *et al.*, 2008). This method has limitations, as the otoliths of some species (e.g. clupeids) are very small and might be fully digested or simply not retrieved, with an overall bias towards larger prey (Alonso *et al.*, 2013).

Two different biochemical methods are used in the studies of interactions between seabirds and fisheries. Most prominent are stable isotopic analyses (SIA; Jaeger *et al.*, 2013; Mariano-Jelicich *et al.*, 2014; Edwards *et al.*, 2015). Those techniques rest on the measurement of the differential between stable isotopes for carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and further elements. Nitrogen ratios mainly reflect trophic level, and carbon ratios are linked to at-sea habitats (Bearhop *et al.*, 2001). SIA can be performed on different tissues which will have different properties for signalling diet specification. Inert tissues as feathers provide signals upon the diet during feather synthesis, which can be different from the isotopic signature of food items ingested later on (Jaeger *et al.*, 2009). Complementary information about the current diet of the studied animals can then be found in plasma or red blood cells (Mariano-Jelicich *et al.*, 2014). Isotopic signature is indicative of diet over at least a few days (plasma) and presents the big advantage of not being dependent upon a single meal. It avoids therefore the risk of sampling food caught by an adult bird, not for its own use, but for its chick (Grémillet *et al.*, 2008). Yet, specific items constituting the diet are not directly identifiable through SIA, although mixture models allow reconstruction of overall diet composition, provided SIA signatures are known for potential prey. Such stable isotope analysis in R (SIAR) models (Jackson *et al.*, 2009) which follow a Bayesian structure are being widely used (e.g. Meier *et al.*, 2015; Osterback *et al.*, 2015).

Second, fatty acid signatures measured in bird plasma may also help distinguishing natural from discarded prey (Kakela *et al.*, 2009, 2010). This method requires larger blood samples and has been used less extensively in the literature, because of its lower accuracy with respect to differentiating natural from subsid prey (but see Moseley *et al.*, 2012). Combining classical dietary analyses based upon e.g. stomach contents, with aforementioned biochemical methods reduces overall biases in estimating seabird diet composition (Karnovsky *et al.*, 2012). It is therefore recommended to cross those different approaches to detect and quantify the presence of fisheries subsidies in seabird diet (e.g. Jiménez *et al.*, 2017).

Dietary studies allow extensive sampling which can be performed within very limited time periods at seabird colonies, with modest associated field costs and, in most cases, without the need for at-sea campaigns. They are therefore a very powerful tool for the study of seabird-fishery resource overlap, even if necessary sample sizes have to be carefully determined with respect to the potential impact of sampling (e.g. stomach flushing, blood sampling) on animal well-being. Method standardization nonetheless strongly promotes the expansion of dietary studies from the individual, to the populational, meta-populational, and inter-specific levels, to yield better understanding of fisheries impacts on the diet of the entire seabird community (e.g. Phillips *et al.*, 1997; Votier *et al.*, 2008).

Impacts of fishery interactions upon seabird populations

Beyond characterizing and quantifying seabird-fishery at-sea interactions, evaluating the ultimate impact of these processes on seabird population dynamics is the most important step towards sound marine management and conservation (Table 2). At the populational level, one approach consists in confronting long-term seabird population trends with indicators of seabird-fishery interactions. Along these lines, population size can be observed in parallel to fishing effort, within shared areas, using discarded prey volumes as a covariate (Chapdelaine and Rail, 1997; Bunce *et al.*, 2002). This correlative approach may provide a qualitative view upon the level of interaction, but cannot rate impacts; neither provides metrics of sustainability thresholds. Specifically in the case of seabird bycatch, reference points are required to assess the sustainability of the bycatch level relative to a conservation objective. Those conservation reference points (reviewed and discussed in Moore *et al.*, 2013) can be used as a main indicator in the context of seabird mortality (e.g. Jiménez *et al.*, 2012; Genovart *et al.*, 2016). Primarily developed to estimate marine mammals allowable bycatch (Wade, 1998), the potential biological removal (PBR) is also an estimation of the additional mortality that can be sustained by a population each year. Calculation of the PBR rests on estimates of population size and its maximum annual recruitment rate (R_{\max} , sensu Dillingham and Fletcher, 2008). R_{\max} can be estimated from matrix population models when appropriate demographic information is available. However, it is seldom the case in seabird studies, even though Niel and Lebreton (2005) proposed a method allowing R_{\max} estimation in a data-poor context, while only relying on age at first reproduction and adult survival (See Dillingham and Fletcher, 2011 for details). By including those reference points (e.g. Tuck *et al.* 2011), ecological risk assessment (reviewed in Small *et al.*, 2013) offers a framework particularly relevant for the study of incidental seabird

mortalities through fisheries. Within vulnerable species or populations, it allows a focus on high-risk seasons and/or areas, facilitating specific bycatch mitigation measures.

When a seabird population is monitored in the longer term, the influence of interacting with fisheries can be evaluated through regression analyses. Typically, reproductive success and population size is then modelled as a function of discard availability (Oro *et al.*, 1995; Louzao *et al.*, 2006; Mullers *et al.*, 2009). Thereby, potential confounding effects can be tested, but forward projections are difficult using these methods. When capture-mark-recapture (CMR) data are available, classical CMR analyses can also be used to estimate different demographic parameters and confront them to interaction influence. Most of the studies implemented Cormack-Jolly-Seber like models to estimate adult survival in the population (e.g. Delamare and Kerry, 1994; Arnold *et al.*, 2006; Francis and Sagar, 2012), adding age-structured matrix models (Caswell, 2001) in most cases (Lewison and Crowder, 2003; Awkerman *et al.*, 2006; Barbraud *et al.*, 2008; Genovart *et al.*, 2016). This second step offers the possibility to estimate probabilities of transition from one age class to another. It is particularly relevant for the study of seabird-fishery interactions, as individual vulnerability may diverge according to age (e.g. Baker *et al.*, 2007). Those demographic models provide parameters that can be linked to environmental covariates, as incidental mortality from fisheries. Yet, they may also be calculation-intensive, in addition to the commitments and costs of long-term seabird CMR monitoring studies. However, they allow testing scenarios with different levels of interaction (e.g. mortality from fisheries; Lewison and Crowder, 2003; Baker and Wise, 2005), and exploring the populational impacts of positive or negative interaction with fisheries, as well as integrating, and so comparing, other effects, as climate change (Barbraud *et al.*, 2012; Pardo *et al.*, 2017). Therefore, they offer the possibility to detect non-viable levels of incidental seabird exploitation, to monitor population status in the case of positive fishery impacts on seabirds, and to assess the risk of generating ecological traps.

Conclusions

This synthesis allowed us to review the vast diversity of methods currently available to study direct interactions between seabirds and fisheries (Tables 1 and 2). Those interactions feature a complex system. Such complexity stems from the multiplicity of protagonists, amplified by their respective behavioural plasticity. Further, interactions are largely scale-dependent, both in time and space. Static representations are necessary at large scales, to evaluate areas of overlap, but they can be misleading if protagonists share ranges at different times. Finally, the nature of seabird-fishery interactions and their functioning is strongly influenced by environment constraints such as resource availability and abiotic factors (e.g. wind fields acting upon seabird travelling costs, Amélineau *et al.*, 2014). Overall, understanding this very particular case of association between wildlife and anthropogenic activities, and designing appropriate conservation strategies, requires the use of multiple approaches and methods in parallel. We hope that the panel of tools presented here will assist researchers and managers in understanding the ancestral association between fishermen and seabirds, in a globally modified ocean.

Table 2. Methods used in 43 original publications dedicated to evaluate the impact of interactions with fisheries, for seabird populations.

General purpose	Specific objective	Methods	Sample size	Logistics required	Invasiveness	Data accessibility	Quantify impact	Project scenarios	Help for decision making	Analysis complexity	Utilization Frequency % (Σ)	
What is the repercussion of interacting with fisheries for seabird populations?	Population monitoring	<i>Demography</i>	+++	++	+	+++					44, 2 (19)	
		<i>CMR data</i>	++	+++	++	+++					55, 8 (24)	
	Evaluate the sensibility of the population	Correlative approach						+	-	+	+	7 (3)
		Regression approach						++	++	+	++	32, 6 (14)
		PBR, reference point						++	+	+++	+++	11, 6 (5)
	CMR						+++	+++	++	+++	55, 8 (24)	

Methods for data acquisition are given in *italics* in opposition to methods for data analysis. The utilization frequency index (% of occurrence and number of studies) gives the frequency of use of each method in the literature. The corresponding references are given in [Supplementary appendix Table S1](#).

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Supplementary data

[Supplementary material](#) is available at the *ICESJMS* online version of the manuscript.

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