

Sex- and age-biased mortality of three shearwater species in longline fisheries of the Mediterranean

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ABSTRACT: Hundreds of thousands of seabirds die annually as a result of being bycaught in longline fisheries, and these rates are unsustainable for many seabird populations worldwide. To understand effects at the population level, it is essential to assess sex- and age-biased mortalities, since uneven mortalities may exacerbate bycatch impacts. In the Mediterranean, bycatch is the main cause of population declines for the 3 endemic shearwater species (Scopoli's *Calonectris diomedea*, Balearic *Puffinus mauretanicus* and Mediterranean shearwater *P. yelkouan*), but little is known about population biases of the birds caught in longliners. From 2003 to 2015, we collected 639 shearwater carcasses from Spanish longliners operating in the north-western Mediterranean, determined their age and sex and examined their spatial and temporal patterns and the origin of ringed birds. Most shearwaters caught in longliners were adults, but the proportion of immatures and subadults increased in the late breeding period. Adult Scopoli's shearwaters were mostly caught around the breeding colonies. In contrast, all *Puffinus* birds were caught on the Iberian shelf. Catches of Scopoli's shearwaters were male-biased, particularly during the pre-laying period and close to the breeding colonies. Catches of *Puffinus* shearwaters were also male-biased during the pre-laying period, but adult catches were female-biased during chick-rearing. Ring recoveries revealed that most birds were ringed in the nearby Balearic Islands, but some Scopoli's shearwaters ringed in France and Italy were also caught during their migration, indicating that the impacts of the Spanish longliners extend well beyond the Spanish colonies. The adult-biased and sex-biased mortality found in this study may aggravate bycatch impacts on populations and highlights the urgent need for conservation action.

KEY WORDS: Seabirds · Sex ratio · Bycatch · North-western Mediterranean · Colonies of origin · Differential susceptibility

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INTRODUCTION

Seabirds are amongst the most threatened group of birds in the world, especially due to the pressures induced by human activities (Croxall et al. 2012). In particular, bycatch in commercial longline fisheries represents one of the major threats to many seabird species, since it causes the annual death of several hundred thousand birds worldwide (Anderson et al. 2011). The incidental mortality on longlines occurs

when seabirds attempt to steal bait from the hooks during line setting, become hooked or entangled in the fishing gear and drown. The seabirds most frequently caught in longline fisheries are procellariiform species (albatrosses, petrels and shearwaters) (Anderson et al. 2011). These seabirds show slow life-history strategies, which make them particularly sensitive to additive mortality and therefore unable to cope with the mortality caused by fisheries (Arnold et al. 2006, Croxall et al. 2012, Genovart et

al. 2017b). As a result, many seabird populations exhibit negative population trends linked to these incidental catches (Weimerskirch et al. 1997, Lewison & Crowder 2003, Poncet et al. 2017). Consequently, determining bycatch rates has been a prime issue in seabird conservation worldwide over the last 2 decades (e.g. Anderson et al. 2011, Cortés et al. 2017). However, not only numbers are important; a greater effect on adult birds and uneven mortality among sexes can also exacerbate demographic impacts of bycatch (Lewison et al. 2012, Komoroske & Lewison 2015). Despite their potential importance, these biases have scarcely been recorded.

Incidences of bycatch on different age classes can vary widely among species, regions and seasons (Phillips et al. 2010, Gianuca et al. 2017). The most common pattern found in longline fisheries is adult-biased bycatch (Nel et al. 2002, Phillips et al. 2010, Gianuca et al. 2017). However, in some species, regions and fishery types, catches of immature birds may also predominate (Murray et al. 1993, Gales et al. 1998), suggesting that the susceptibility to bycatch among age classes is determined by differences in their spatial and seasonal distribution and overlap with fisheries, rather than by a differential ability in gaining access to bait and discards (Riotte-Lambert & Weimerskirch 2013, Gianuca et al. 2017). In long-lived species, such as seabirds, adult survival is the most important demographic parameter for the population growth rate (Lebreton & Clobert 1991). Therefore, additional mortality in this age class in particular can have immediate and large effects on seabird population trends (Arnold et al. 2006, Barbraud et al. 2012, Genovart et al. 2016). Moreover, procellariiforms are monogamous birds with strong intra-pair cooperation (Bried & Jouventin 2002); thus, the most immediate effect of bycatch mortality of adults is the pair-bond disruption due to the loss of a partner. This can lead to breeding failure when the partner dies during the breeding season (Belda & Sánchez 2001), and may delay the next breeding cycle until the remaining bird finds a new mate; this may also reduce reproductive success due to a mate familiarity effect (Bradley et al. 1995, Ismar et al. 2010, Sánchez-Macouzet et al. 2014). On the other hand, a high mortality rate of immature birds may also substantially influence population viability by reducing the recruitment level necessary to maintain population stability over the medium to long term (Arnold et al. 2006, Votier et al. 2008, Finkelstein et al. 2010, Penteriani et al. 2011).

The incidence of the sex-biased incidental mortality is also important, since the sex ratio imbalance reduces the effective population size, which has a significant impact on fecundity and population viability (Jouventin et al. 1999, Mills & Ryan 2005). In some species, bycatch mortality is most frequently skewed towards males (Phillips et al. 2010, Gianuca et al. 2017), although this bias may vary both seasonally and regionally (Gales et al. 1998, Nel et al. 2002, Gianuca et al. 2017). Many albatross and petrel species show sexual segregation in foraging areas and diet, in particular during the pre-laying period (Phillips et al. 2017). Thus, the uneven mortality between males and females is usually driven by sex differences in their spatio-temporal distribution and the resultant variation in the relative spatial overlap with high-risk fisheries (Bugoni et al. 2011, Jiménez et al. 2016, Gianuca et al. 2017).

In the Mediterranean Sea, high seabird mortality in longline fisheries has been documented, particularly of the 3 endemic and threatened shearwaters of the Mediterranean: Scopoli's *Calonectris diomedea*, Balearic *Puffinus mauretanicus* and Mediterranean shearwaters *P. yelkouan* (Belda & Sánchez 2001, García-Barcelona et al. 2010a, Báez et al. 2014, Cortés et al. 2017). However, little is known about the population biases of this mortality and their spatial and temporal patterns, or about the origin of the affected birds. Only 1 study has provided data about bycatch age composition from 38 ringing recoveries collected in the longline fleet operating near the Columbretes Islands (western Mediterranean) (Belda & Sánchez 2001). Those authors found that most birds were adults (60%) that had been ringed in the Columbretes archipelago and other neighbouring Spanish colonies (Balearic Islands). However, that study was restricted to a specific area and season, limiting the generalizability of the results. To date, no information on age- and sex-biased mortality is available for any of the 3 species of shearwaters. Nevertheless, some studies have pointed out that during the pre-laying period, females usually perform longer foraging trips whereas males visit the colony more often than females do (Bourgeois et al. 2008, Guilford et al. 2012, J. González-Solís unpubl. data). These sexual differences in foraging behaviour could lead to a differential interaction with longline fisheries and result in sex-biased mortality. Population effects of this unnatural mortality have recently been illustrated in the 3 shearwaters of the Mediterranean (Oppedal et al. 2011, Genovart et al. 2016, 2017b). Considering equal survival between sexes and parity in population sex ratios, demographic models showed

that the population viability of these species is compromised by adult mortality caused by fisheries. Moreover, in the case of Scopoli's shearwaters, Sanz-Aguilar et al. (2016) found that this loss of breeders is buffered by immigration, since local recruitment is not enough to compensate this loss. Furthermore, the Spanish breeding colonies of Scopoli's shearwater show variation in adult survival among colonies, which is related to the degree of spatial overlap between the foraging areas and longline fisheries (Genovart et al. 2017a).

To understand the potential consequences of uneven mortality between sex and age classes and the geographical extent of the impacts, we investigated the ages and sexes of shearwater carcasses and the provenance of the rings recovered by the Spanish demersal and pelagic longline fleet operating in the north-western Mediterranean.

MATERIALS AND METHODS

Study area

The study was conducted in the north-western Mediterranean, which includes the regions of Catalonia (Iberian Peninsula) and the Balearic Islands. This area contains important breeding colonies of endemic and sensitive seabirds (Zotier et al. 1999, Arcos et al. 2009). Most shearwater colonies are distributed along the Balearic archipelago, but birds primarily forage over the Iberian continental shelf in addition to the waters around the colony (Arcos et al. 2012b, Meier et al. 2015). The Iberian shelf also attracts Scopoli's and Mediterranean shearwaters from colonies beyond the study area, including French and Italian colonies (Péron et al. 2012, Péron & Grémillet 2013). Concurrently, an important longline fleet operates in this region (FAO 2016), mainly composed of artisanal demersal (medium and small scale) and semi-industrial pelagic vessels (Féral 2004).

The demersal longline fleet in the region consists of artisanal boats ranging from 7 to 15 m in length and 1 to 4 crew members that usually make 1 d fishing trips. Main fishing grounds are located over the continental shelf or in shelf-break areas close to the fishing ports of origin (Cortés et al. 2017). Generally, the medium-scale vessels employ demersal longlines year round, but the small-scale vessels are polyvalent, so several boats use demersal longlines seasonally. The fishing effort of the demersal medium-scale vessels in the north-western Mediterranean is mainly concentrated on the

continental shelf of Catalonia (Cortés et al. 2017). In contrast, the effort of the small-scale vessels is widely distributed along the continental shelf of the study area.

In the case of pelagic longline fisheries, the fleet is composed of vessels ranging from 9.5 to 25 m in length and 3 to 10 crew members, and the time spent at sea per fishing trip ranges from 1 to 9 d (normally 3 or 4 d). The fleet operating in the study area shows a highly variable spatial and temporal distribution, but the main fishing grounds are located around the Balearic Islands and in Levantine region waters, including both neritic and oceanic waters. For detailed information about the gear characteristics of both longline fleets, see Cortés et al. (2017), García-Barcelona et al. (2010a) and Macías et al. (2012).

Seabird dissections

We collected 639 shearwaters accidentally caught between 2003 and 2015 by different longline fleets operating in the north-western Mediterranean: (1) demersal (medium-scale longliners; $n = 314$ birds; small-scale vessels; $n = 103$) and (2) semi-industrial pelagic fleet ($n = 222$). The specimens were either collected during on-board observations or were voluntarily offered by longline fishermen when there was no observer onboard.

All collected birds were labelled indicating date, fishing harbour, name of the vessel, species and position. After being landed, seabird carcasses were immediately frozen at -20°C until dissection. All specimens were dissected to determine the age and sex by inspecting and measuring the sexual organs, following Van Franeker (2004). We also examined the moulting stage as an additional criterion for ageing birds. We classified birds into 4 age classes: juveniles (hatch-year), immatures, subadults and adults mainly based on gonadal development (see Figs. S1–S8 in the Supplement at www.int-res.com/articles/suppl/m588p229_supp.pdf). To distinguish the juvenile and immature birds from adults, we also used the presence and size of the bursa of Fabricius (Broughton 1994). The subadult category included both immature birds close to adult age and non-breeding adults, since gonadal development of these 2 stages is difficult to differentiate (Hector et al. 1986). Therefore, we were only able to confirm the adult stage when birds were in breeding state (Van Franeker 2004). In males, testes gradually become larger and turn from blackish to greyish, reddish or pinkish with age, but only the

testicles of breeding males acquire a creamy colour and reach sizes $>30 \text{ mm}^2$ (Phillips et al. 2010). In females, the development of the ovarian follicles and the oviduct increase with age, from an ovarium without developed follicles ($<0.1 \text{ mm}$) and very thin and straight oviduct to larger follicles and an enlarged oviduct, but only breeding females develop prominent follicles ($>2 \text{ mm}$) and a wider, curved oviduct.

To distinguish between the 2 *Puffinus* species, we considered plumage colouration and biometrics and conducted genetic analyses in 66% and isotopic analyses in 20% of the specimens ($N = 88$) to confirm the species (Militão et al. 2014, García-Barcelona et al. 2016). However, some specimens (5%) could not be identified due to the overlap of both species in some traits, so we refer to them as *Puffinus* spp.

Data analysis

We analysed the seasonal and spatial demographics of the seabirds caught by the longline fleet operating in the study area. To evaluate seasonal variability, we defined different time periods for each shearwater species in accordance with their phenology (see Fig. 1) (Ruiz & Marti 2004, Bourgeois & Vidal 2008, Reyes-González & González-Solís 2011, Raine et al. 2013). We examined the annual and seasonal deviation from the 1:1 expected sex ratio for each shearwater species. To calculate the sex ratio, we considered 2 data groups: (1) all individuals, where all age classes were included in the analysis, and (2) adult individuals. In addition, we compared the annual and seasonal age-related proportion (adults, subadults and immatures plus juveniles) for each shearwater species. Furthermore, in the case of Scopoli's shearwater, we compared the proportion of adults, males and sex ratio between areas, i.e. Catalonia and the Balearic archipelago. These differences were tested using a chi-squared test with Yates's correction for continuity.

To determine the origin of the individuals caught by the longline fleet in the region, we used the recovered rings that came either from the collected carcasses or from ring data reported by fishermen. We recorded the place and time of the first capture to determine the breeding colony of origin and the accurate (if it was ringed as a chick) or approximate age of the banded birds when they died.

Table 1. Number of dead shearwaters collected in the longline fisheries operating in the north-western Mediterranean. Data are grouped into 2 main areas: Catalonia and the Balearic Islands. Also shown is the overall proportion for the different age classes considered in this study: adults (AD), subadults (SA) and immatures plus juveniles (IM). N_1 refers to the total number of birds collected (N_1) or to the number of birds for which we were able to identify the age (N_2)

	Catalonia	Balearic Is.	N_1	AD (%)	SA (%)	IM (%)	N_2
Scopoli's shearwater	162	89	251	72	12	16	215
Balearic shearwater	188	0	188	40	31	29	182
Mediterranean shearwater	182	0	182	45	29	26	170
<i>Puffinus</i> spp.	18	0	18	31	25	44	16
Total	550	89	639	–	–	–	583

RESULTS

Seabird dissections

Most birds were recovered from the Catalonia area (86%, 550 birds of 639 caught in total during the study, Table 1) and all *Puffinus* shearwaters were collected from the shelf of this region. Almost all Balearic shearwaters (93%) and a large proportion of the Mediterranean shearwaters (75%) were caught by vessels operating in the central-southern area. However, we also registered catches in areas further north, especially of the Mediterranean shearwater (25%). In the case of Scopoli's shearwaters (Table 1), the majority of the carcasses were collected in Catalonia (65%), but they were equally distributed over the shelf off northern and central-southern Catalonia and the Balearic Islands (32, 33 and 36%, respectively).

Carcasses were mainly collected during the pre-laying and incubation periods (for Scopoli's shearwater) and the chick-rearing period (*Puffinus* shearwaters; Fig. 1). However, we also recovered a high number of *Puffinus* carcasses during the pre-laying period and of Scopoli's shearwaters during the late chick-rearing period.

Adults were the age class caught most often in the 3 species of shearwaters (Table 1), followed by subadults and immatures (juvenile and immature birds). Adults of Scopoli's (SS) and Mediterranean shearwaters (MS) were more abundant than subadults (SS: $\chi^2_1 = 150.11$, $p < 0.001$, MS: $\chi^2_1 = 9.07$, $p < 0.01$) and immatures (SS: $\chi^2_1 = 127.14$, $p < 0.001$, MS: $\chi^2_1 = 13.83$, $p < 0.001$), while in the case of Balearic shearwaters (BS), the proportion of adults was only significantly higher than that of immatures (BS: $\chi^2_1 = 4.38$, $p < 0.05$). Moreover,

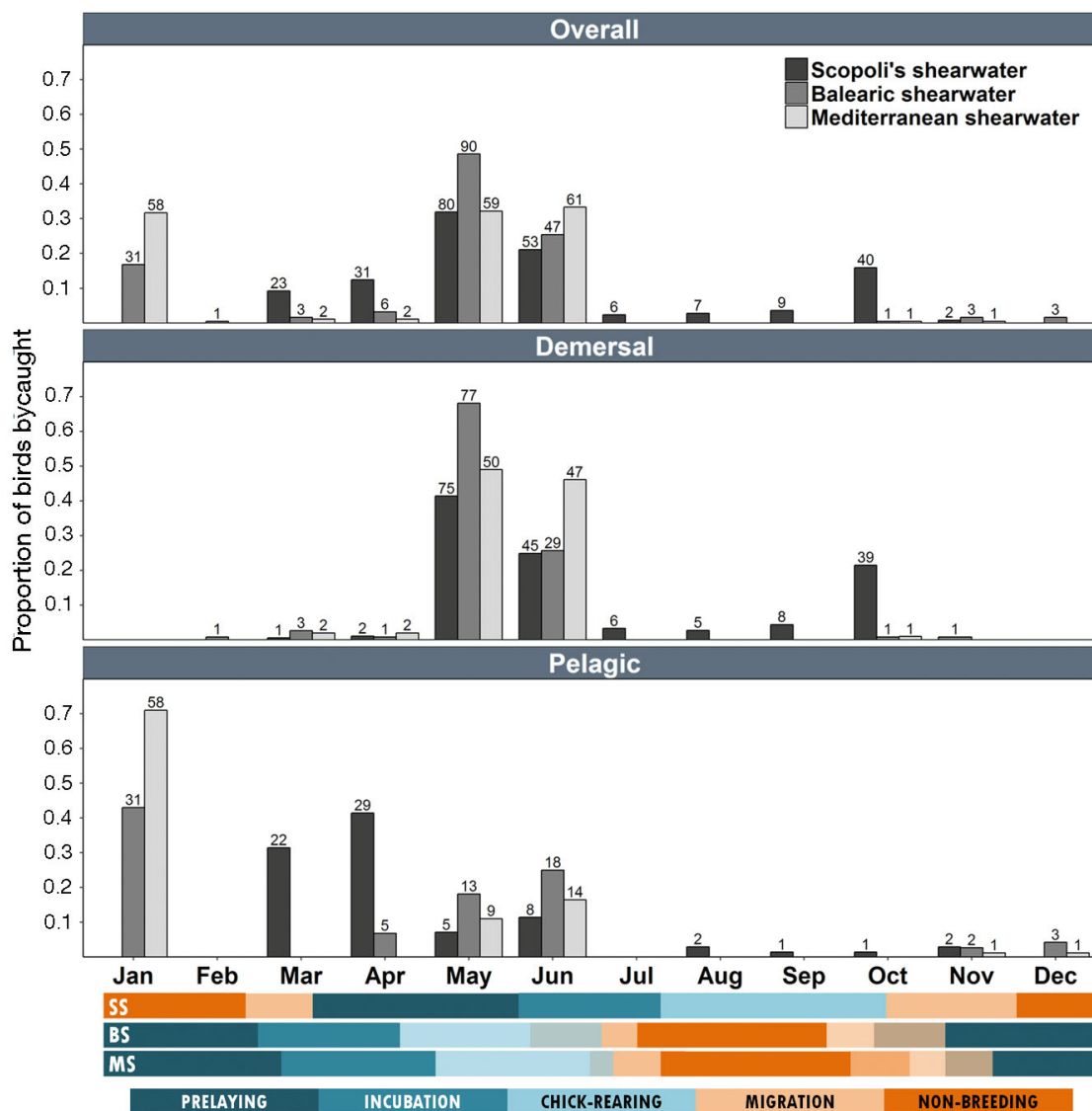


Fig. 1. Proportion of Scopoli's shearwaters (SS: dark, $N = 251$), Balearic shearwaters (BS: grey, $N = 185$) and Mediterranean shearwaters (MS: light grey, $N = 184$) accidentally caught by month in longliners, considering the overall fleet ($N = 620$ birds) and the demersal ($N = 396$) and pelagic longliners ($n = 224$) separately. Numbers above bars indicate the number of birds caught; colour bars indicate the breeding cycle for each species

adults of Scopoli's shearwaters were more abundant around the Balearic Islands (Fig. 2a; SS: $\chi^2_1 = 29.42$, $p < 0.001$), while immatures were almost exclusively caught over the Iberian shelf (Fig. 2b; SS: $\chi^2_1 = 23.19$, $p < 0.001$). Adult shearwaters were predominantly caught during the pre-laying period, but also during incubation for Scopoli's shearwater (Fig. 3). However, in this latter species, the proportion of subadults and immatures increased as the breeding season progressed, reaching their maximum in the chick-rearing period (Fig. 3a, SS: $\chi^2_2 = 64.93$, $p < 0.001$). Instead, in *Puffinus* shearwaters, immatures were caught in equal proportions

throughout the breeding period, while the proportion of subadults increased during chick-rearing (Fig. 3b, BS: $\chi^2_1 = 11.24$, $p < 0.01$; Fig. 3c, MS: $\chi^2_1 = 6.62$, $p < 0.01$).

Overall mortality showed a significant sex ratio bias only in Scopoli's shearwaters towards males (Table 2). In this species, the proportion of males was higher in the Balearic archipelago (70%) than in the Iberian area (56%; Fig. 2c and Table 3; SS: $\chi^2_2 = 4.12$, $p < 0.05$). Male-biased mortality was also found when only adults were considered (Table 2). However, when we considered breeding periods separately, male-bias was only significant in the pre-laying

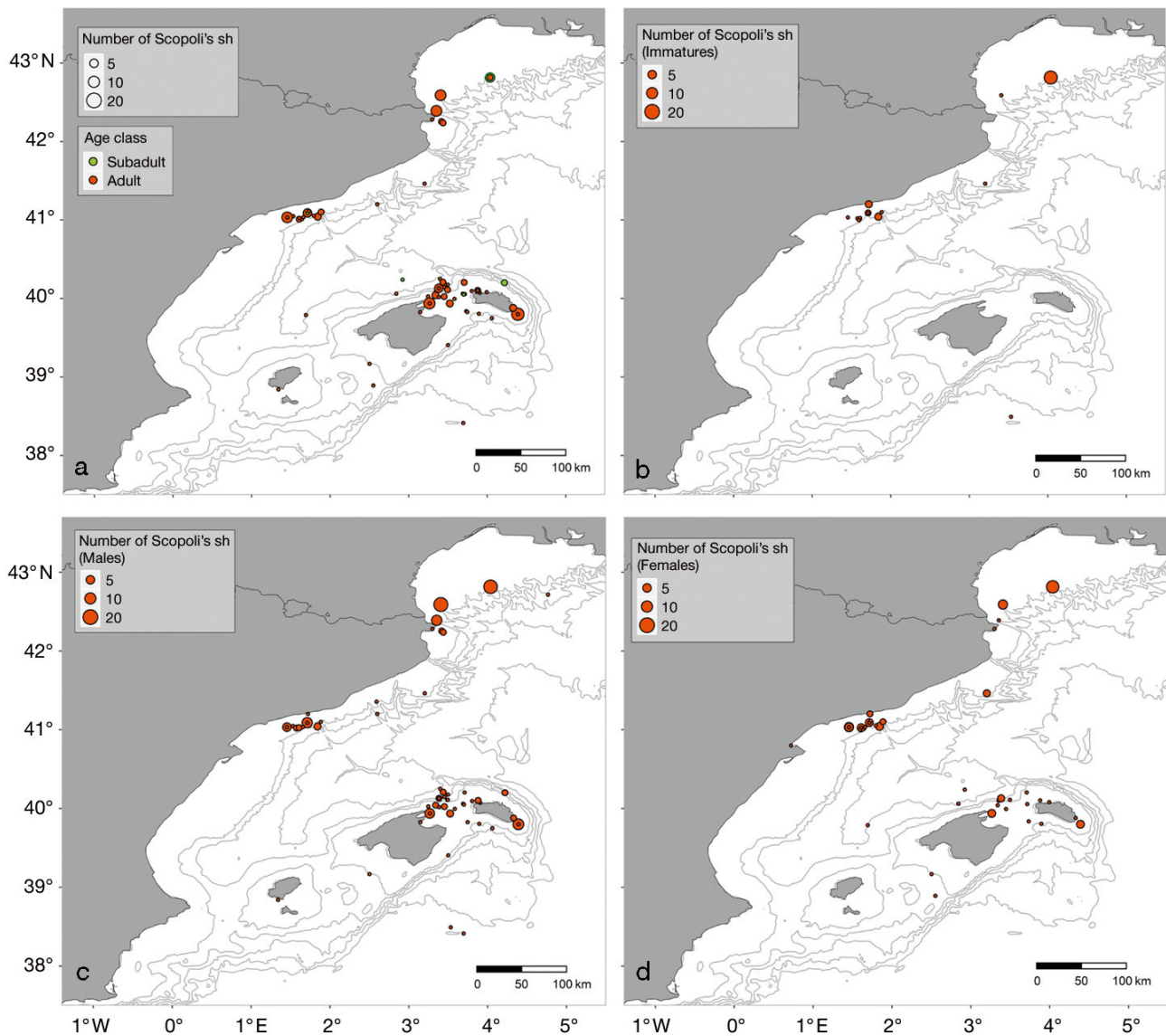


Fig. 2. Spatial distribution of the different Scopoli's shearwater age and sex classes killed by longlines: (a) adults + subadults (N = 200 birds), (b) immature + juveniles (N = 35), (c) males (N = 146) and (d) females (N = 95). Lines indicate the 200, 1000, 2000 and 3000 m isobaths

period. When we examined sex ratio occurring off Catalonia and the Balearic Islands independently (Table 3), we only found significant male-biased mortality in the Balearic Islands both year round and in the pre-laying period.

In the case of *Puffinus* shearwaters (Table 2), we also found male-biased mortality during the pre-laying period when all individuals and only adults were considered. In contrast, female-biased mortality was evident during the chick-rearing period. However, for Balearic shearwaters, this bias was only significant in adult birds caught during both the chick-rearing period and year round.

Ring recoveries

Ring recovery data obtained from birds caught in longliners operating in the study area over the same study period (N = 34 recoveries) showed that most ringed individuals were Scopoli's shearwaters (88%) caught throughout the breeding period and during migration (Table S1 in the Supplement). Birds were ringed in different breeding colonies of the western Mediterranean located in the Balearic (63%), French (27%) and Italian (10%) islands, but their origins differed across the Catalan coast; most Scopoli's shearwaters caught in northern Catalonia were ringed in

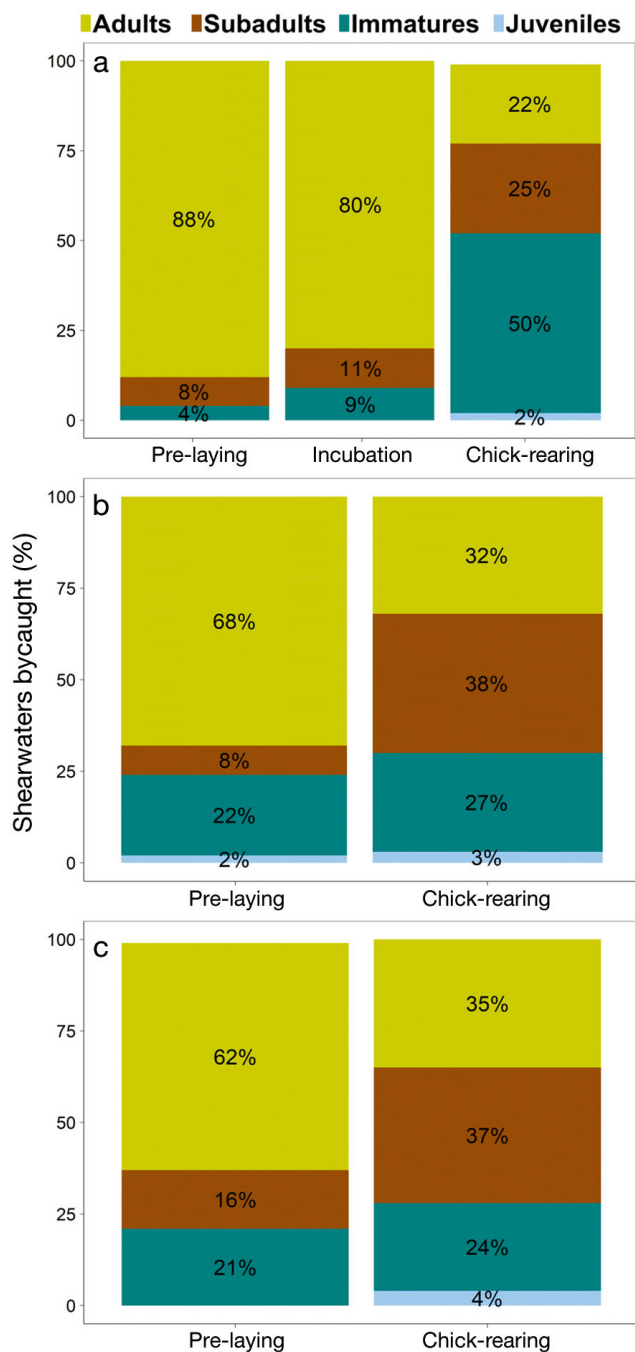


Fig. 3. Percentage of each age class (adults, subadults, immatures and juveniles) accidentally caught in different time periods for each shearwater species: (a) Scopoli's (pre-laying, $N = 102$ birds; incubation, $N = 64$; chick-rearing, $N = 40$), (b) Balearic (pre-laying, $N = 41$; chick-rearing, $N = 132$) and (c) Mediterranean shearwaters (pre-laying, $N = 62$; chick-rearing, $N = 111$)

France or Italy, while birds caught in the central-southern area and in waters around the Balearic archipelago were mostly ringed in the Balearic Islands (Fig. 4a). For those ringed birds for which we

Table 2. Proportion (%) of males and sex ratio (SR), considering all age classes or only adults (adult sex ratio, ASR), of the shearwater species killed in the north-western Mediterranean by longline fisheries annually and in each breeding period. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Species/ period	% Male	N	SR (M:F)	% Adult males	N	ASR (M:F)
Scopoli's shearwater						
Annual	61	242	1.6:1***	66	151	1.9:1***
Pre-laying	64	105	1.8:1**	69	91	2.2:1***
Incubation	62	80	1.6:1	59	51	1.4:1
Chick-rearing	52	52	1.1:1	67	9	2.0:1
Balearic shearwater						
Annual	51	182	1.1:1	34	73	0.5:1*
Pre-laying	73	41	2.7:1**	74	27	2.8:1*
Incubation	33	6	–	0	3	–
Chick-rearing	45	132	0.8:1	12	43	0.1:1***
Mediterranean shearwater						
Annual	48	174	0.9:1	43	77	0.8:1
Pre-laying	71	62	2.4:1**	82	38	4.6:1**
Chick-rearing	35	111	0.5:1**	0.1	39	0.1:1***

could determine age (67 %, $N = 30$ Scopoli's shearwaters), adults were the age class most often recovered (86 %, $N = 20$ birds of known age), ranging from 6 to a maximum of 17 yr. In the case of ring recoveries from Balearic (6 %, $N = 34$) and Mediterranean (6 %) shearwaters, all ringed specimens were adults caught during the chick-rearing period. Balearic shearwaters were ringed on Majorca Island (Balearic archipelago), while 1 individual classified as a Mediterranean shearwater was ringed on Minorca Island (Balearic archipelago) and another in a French colony (Fig. 4b). Catches of *Puffinus* shearwaters occurred in central-southern Catalonia, although the Mediterranean shearwater from the French colonies was caught in the northern part of the study area.

DISCUSSION

This is the first comprehensive study on age- and sex-related variation in seabirds caught by longline fisheries in the Mediterranean. The examination of the catches from demersal and pelagic longline vessels revealed clear differences in mortality among age classes and sex, which varied across areas and seasons and among the 3 endemic shearwater species of the Mediterranean: Scopoli's, Balearic and Mediterranean. In addition, ring recoveries showed that bycatch mortality is affecting breeding populations from the western Mediterranean, both in and outside of the study area.

Table 3. Proportion (%) of adults, males and adult males of Scopoli's shearwaters caught annually and in each breeding period, considering catches that occurred off Catalonia and the Balearic Islands separately. The sex ratio (SR) was obtained considering all age classes or only adult birds (adult sex ratio, ASR). Total number of birds is indicated in brackets. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Period	Catalonia					Balearic Islands				
	% Adults	% Males	SR	% Adult males	ASR	% Adults	% Males	SR	% Adult males	ASR
Annual	62 (123)	56 (153)	1.3:1	60 (70)	1.5:1	92 (87)	70 (89)	2.3:1***	70 (81)	2.2:1***
Pre-laying	64 (28)	52 (29)	1.1:1	56 (18)	1.3:1	97 (74)	70 (76)	2.3:1**	73 (73)	2.7:1***
Incubation	83 (54)	61 (70)	1.6:1	62 (45)	1.6:1	60 (10)	60 (10)	1.5:1	33 (6)	–
Chick-rearing	19 (37)	49 (49)	1:1	57 (7)	–	67 (3)	100 (3)	–	100 (2)	–

The incidental mortality of Scopoli's shearwater was registered in the shelf off the Iberian coast but also close to the Balearic Islands, an important foraging ground for shearwaters breeding in western Mediterranean colonies (Louzao et al. 2009, Péron & Grémillet 2013). Conversely, all *Puffinus* shearwaters were caught on the Iberian shelf during the pre-laying and chick-rearing periods. The Balearic shearwater was more frequently caught in central-northern (93% of the catches) than in northern Catalonia, an area well known as a major foraging hotspot for the species year round (Louzao et al. 2009, Arcos et al. 2012b). In the case of the Mediterranean shearwater, the incidental catches were important in central-northern (75%), but also in northern Catalonia (25%), which is considered one of the most important foraging area of the species in the western Mediterranean (Arcos et al. 2012b, Péron et al. 2013).

In all 3 shearwater species, most catches were adult birds, particularly during the pre-laying period. This high prevalence of adults was also found in the ringing and recovery data collected in this study. However, the proportion of adults decreased with the progression of the season. In Scopoli's shearwater, incidental mortality of adults peaked during the incubation period, and thereafter we found an increase in catches of immatures and subadults, which possibly resulted from the increase in numbers of these age classes in the area. During

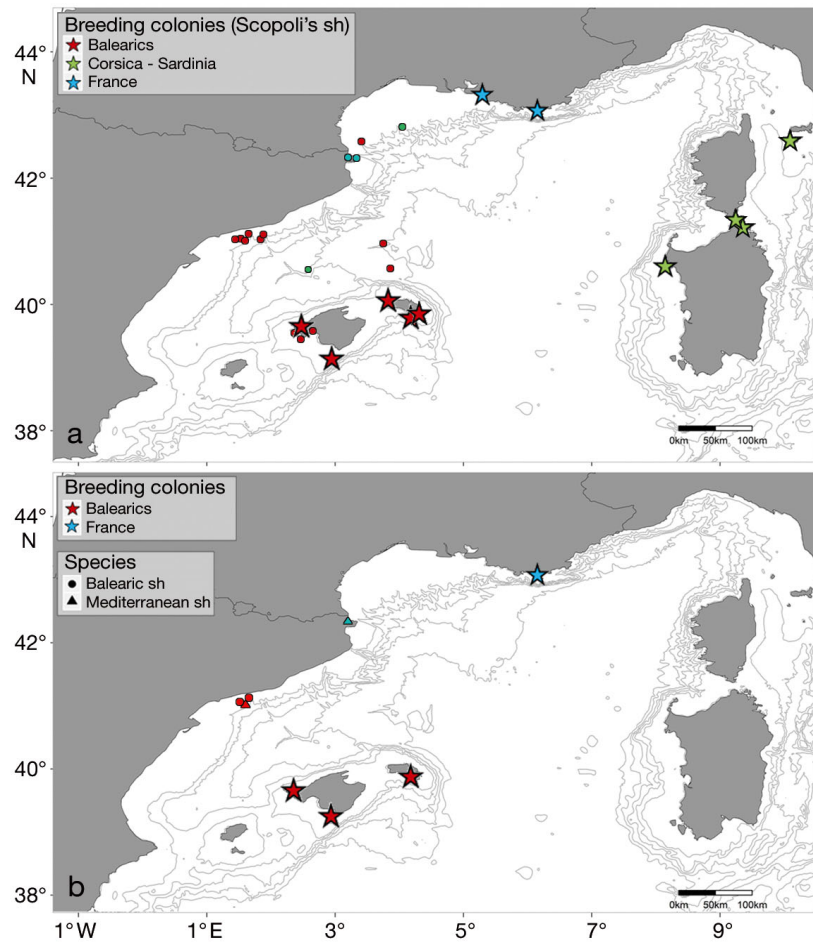


Fig. 4. Spatial locations of ringed birds caught by longline fisheries operating in the north-western Mediterranean and their breeding colonies of origin for (a) Scopoli's shearwater ($N = 30$ banded birds) and (b) the *Puffinus* shearwaters (Balearic and Mediterranean shearwater, $N = 4$). The breeding colonies shown in the map correspond to the banding locations of the ringed birds collected in longline vessels. These colonies are grouped in 3 different regions: Balearic Islands (red), France (green) and Corsica-Sardinia (blue). Lines indicate the 200, 1000, 2000 and 3000 m isobaths

the pre-migration period, immature and subadult Scopoli's shearwaters come into the area from more eastern breeding colonies (Péron & Grémillet 2013),

with a consequent increase in by-catch risk. In the case of the *Puffinus* shearwaters, we only found an increase in the proportion of subadults from the pre-laying to the chick-rearing period, while immatures were evenly caught throughout the breeding season. However, the number of adults in the late breeding period may have also been underestimated due to gonadal regression (Hector et al. 1986), which makes it difficult to differentiate adult breeders from subadults late in the season. This bias may be particularly important in *Puffinus* shearwaters, since most birds were collected during the chick-rearing period.

Interestingly, the spatial distribution of the age classes was not uniform. Adult Scopoli's shearwaters were caught in higher proportions in waters close to their major breeding site in the area (Balearic Islands, 92% of total individuals caught) than along the Iberian coast (62%), whereas the reverse was true for other age classes. Indeed, juvenile and immature birds were nearly exclusively caught along the Iberian coast, and the proportion of subadults was also larger in this area. Our findings agree with a previous study that also found a high proportion of adults caught in the longline fleet operating nearby Columbretes Island (Iberian Peninsula), where a small breeding colony of the species occurs (Belda & Sánchez 2001). A higher proportion of adults caught near the breeding colonies may be related to differences in distribution among age-classes derived from the constraints of central place foraging in breeding birds (Phillips et al. 2017b) and the avoidance of intraspecific competition in the vicinity of the colonies by non-breeders (Weimerskirch et al. 2006, Votier et al. 2011).

Imbalance in the sex ratio of the catches was noticeable in some periods and areas. In particular, in the 3 shearwater species most catches of pre-laying adults were males. This may result from sex-related differences in the at-sea distribution during this period. Indeed, pre-laying males forage closer to the breeding colonies than females in many procellariiform species (Phillips et al. 2017), including Balearic, Mediterranean and Scopoli's shearwaters (Bourgeois et al. 2008, Guilford et al. 2012, J. González-Solís unpubl. data). This is typically related to the different role of males and females in this period, since females have to form the egg and engage in long pre-laying exodus often far from the breeding colonies, whereas males are more involved in nest defence and remain in areas closer to the breeding colony than females (Hedd et al. 2014, Phillips et al. 2017b). Similarly, the skewed mortality towards females in adult Balearic and Mediterranean shearwaters dur-

ing the chick-rearing period is possibly related to sex-specific differences in food-provisioning behaviour influencing the likelihood of interaction with longlines. Indeed, in the sibling species, the Manx shearwater *P. puffinus*, females make longer trips and have lower feeding rates than males during chick-rearing (Gray & Hamer 2001). Alternatively, the sex-biased mortality observed in this study may actually reflect an imbalance in adult sex ratios (ASRs) at the population level. In fact, skewed ASRs, in particular towards males, have been observed in many bird species (Bessa-Gomes et al. 2004, Donald 2007), with this tendency being more pronounced in species with a poor conservation status (Donald 2007). Previous studies carried out in 2 different populations of Scopoli's shearwater (Spain and Greece) did not find significant deviation of parity in sex ratios at hatching and fledging (Genovart et al. 2005, Karris et al. 2013), although a slight male bias was reported in the population of Greece. Nevertheless, in monogamous birds, a skew in the ASR primarily results from differential mortality between sexes rather than differences in the offspring sex ratio (Awkerman et al. 2007, Donald 2007, Székely et al. 2014). Sex-specific survival rates may occur because males and females have different behaviour, ecology and life histories (Kokko & Jennions 2008, Székely et al. 2014), which lead to unequal exposure to potential sources of mortality. The lack of information about population structure does not allow us to rule out the possibility of a pre-existing sex bias in the shearwater populations; however, because bycatch in longline fisheries is the main source of mortality for these species, it is to be expected that the sex-biased mortality found in this study could be having a large influence on population sex ratios (Awkerman et al. 2007).

We also examined the origin of birds caught in longliners based on 34 ring recoveries. Most recoveries of Scopoli's shearwaters corresponded to birds ringed at the closest breeding site (63%, $N = 30$ Scopoli's shearwaters), the Balearic islands (53% from Majorca and 10% from Minorca), similar to previous studies (Belda & Sánchez 2001). Genovart et al. (2017a) built a longline bycatch risk map for Scopoli's shearwater from 3 distant Spanish breeding colonies, and linked this with their adult survival. The authors found colony-specific sensitivity to bycatch, with Pantaleu (Majorca) and Columbretes Island being the colonies most affected. Our study corroborates this high incidence on colonies of Majorca, particularly in the Cabrera archipelago (37% of the total rings from Spanish breeding colonies) and Pantaleu

(32%). Nevertheless, we also found a significant proportion of birds ringed in French and Italian colonies (37%) which were mainly caught in the north of Catalonia (82%, $N = 11$), particularly during the migration period. This is because the Spanish western Mediterranean is an important stopover site during the post-breeding migration for Scopoli's shearwaters from more eastern breeding colonies (Péron & Grémillet 2013). On the other hand, the 4 rings from *Puffinus* shearwaters were recovered on the Catalan coast, basically corresponding to breeding colonies within or near the Spanish western Mediterranean. Two Balearic shearwaters were ringed as chicks in Majorca, the closest breeding site for the species. Two Mediterranean shearwaters were ringed at Porquerols (southern France) and the Balearic/Mediterranean shearwater hybrid population of Minorca.

CONCLUSIONS

Although we would expect immature birds to be more numerous in the population (Arcos et al. 2012a, Garcia et al. 2016, Sanz-Aguilar et al. 2016), we found adult birds to be by far the most common age class among birds caught by the longliners in the 3 shearwater species. In the case of Scopoli's shearwaters, the proportion of adults was particularly high in the vicinity of their breeding colonies. These results show that the longline fleet operating in the north-western Mediterranean is mainly affecting the survival of breeding birds, the most sensitive and critical demographic parameter in long-lived seabirds (e.g. Genovart et al. 2017b). We also found a number of imbalances in the sex ratio of the 3 shearwater species across areas and seasons due to sex-specific differential mortality in longline fisheries, which may exacerbate bycatch impacts on population dynamics (Mills & Ryan 2005, Awkerman et al. 2006), in particular on species with small populations (Bessa-Gomes et al. 2004), such as the Critically Endangered Balearic shearwater (BirdLife International 2017). Overall, our study shows population biases in bycatch, which may aggravate demographic implications for populations of the 3 endemic shearwater species. Moreover, impacts are more pronounced, but not limited, to the Spanish breeding colonies, affecting birds from other western Mediterranean colonies while using the area as a stopover site during the migration period.

The strong temporal pattern of the shearwater bycatch found in this study supports the recommendation of implementing a temporal closure of the

longline fleet, both demersal and pelagic, to minimize the bycatch rate in the study area (García-Barcelona 2010b, Báez et al. 2014, Cortés et al. 2017). Indeed, in the pelagic longline fleet, this type of temporary closure has already been implemented in the past, such as in October and November 2009 (ICCAT Recommendation 08-03), and from January to March 2017 (ICCAT Rec. 16-05). Although these closures were primarily oriented to recover fish stocks, they could also be very beneficial for shearwaters if implemented in the more critical periods of bycatch, such as April to June and October. Furthermore, our findings show the importance of achieving a comprehensive spatial and temporal coverage of the fleet to properly assess the bycatch impact on seabird populations. Further detailed studies are needed on the foraging distributions of shearwaters and their overlap with fisheries to better interpret the causes of the age- and sex-related variations in the bycatch mortality by longline fisheries. Moreover, demographic models on the population viability of the 3 endemic shearwaters of the Mediterranean should be improved by incorporating the population biases found in the present study.

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