

# Individual specialization in the foraging and feeding strategies of seabirds: a review

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**Abstract** Trophic relationships are a central theme in ecology and play a crucial role in the survival of organisms, because the availability of food resources varies over time and space. Until recently, most ecological studies treated conspecific individuals as ecologically equivalent, but intra-specific variation in individual foraging and feeding strategies can be large. Studies documenting the occurrence of individual specialization in seabirds ( $n = 94$ ) increased substantially since the year 2000, and rapid and significant advances are being made since then. This review summarizes existing knowledge within this subject, examines the relative incidence of individual specialization and investigates the possible ecological implications of individual specialization in seabirds. Our results show that, to date, the incidence of individual specialization is documented in around 12 % of the total extant seabird species although some studies ( $n = 12$ ) did not find evidences of individual specialization in the foraging and feeding strategies of some seabird populations. Most studies were conducted at higher latitudes, leading to a lack of knowledge on the incidence of this trait in tropical seabird populations. Results suggest that the incidence of individual specialization may be potentially widespread within seabirds, but may fluctuate spatio-temporally among/within species and populations due to the frequency of specialists, predictability of

resources or environmental conditions. This study supports the hypothesis that individual specialization may have important ecological consequences at both individual and population levels, such as implications in breeding performance or in intra-specific competition and, consequently, a high impact on ecological processes and foraging dynamics. Further investigation is required to identify the mechanisms that generate individual specialization and its ecological implications at both population and individual levels.

## Introduction

Ecologists have long used niche theory to define the ecological niche of a species or population as a whole, assuming that all individuals are similarly affected and ecologically equivalent. However, many apparently generalized and specialized species and natural populations are in fact composed of ecologically heterogeneous individuals that repeatedly differ in foraging behaviour and use different subsets of the available resources (Bolnick et al. 2002; Bearhop et al. 2004; Bell et al. 2009). Such intra-specific variation in individual foraging strategies can be large and vary according to factors such as sex, age, morphology and individual specialization (Bolnick et al. 2003). Individual specialization refers to the use of a relatively limited fraction of the possible range of available resources, resulting in inter-individual niche variation, which could be consistent over short- and/or long-term periods, and is known to be widespread across a diverse set of taxa (Bolnick et al. 2003; Bell et al. 2009), including several seabird species (e.g. Woo et al. 2008; Votier et al. 2010a; Ceia et al. 2012). The inter-individual variation in resource use may have a strong impact on ecological processes and population dynamics, and there is evidence that such traits may reduce

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intra-specific competition among individuals promoting their ecological segregation (Bolnick et al. 2003; Patrick and Weimerskirch 2014a). However, its ecological implications at the individual and population level are still poorly known (Araújo et al. 2011), particularly for pelagic seabird species, as most of them spend the majority of their annual cycle at sea, often changing habitats and foraging strategies throughout their annual cycle (Mackley et al. 2010; Weimerskirch et al. 2014).

As marine top predators, seabirds are closely dependent on highly patchy distributed food resources they can find at sea, which are predictable at large spatial scales (100 s–1000 s of kilometres) (Weimerskirch 2007). To cope with these conditions, seabirds developed specific morphological characteristics and foraging strategies that enable them to conserve the maximum energy possible while foraging at sea (Nelson 1980). Therefore, individuals may retain different strategies in order to get food, leading to variability not only among species, but also within species and populations, and promoting disruptive selection and ultimately speciation (Bolnick 2004). Moreover, all seabirds are central-place foragers for at least part of the breeding season, which could potentially lead to partition in the use of available resources within and between species, according to the principle of competitive exclusion (Pianka 2011, e.g. Wakefield et al. 2013). Notwithstanding, it is not sufficient to document the foraging ecology of a species or a population as a whole, but it is crucial to study inter-individual variation in resource use within populations and to investigate its wider implications. This is important to understand trophic relationships between seabirds and the marine environment, in order to support theoretical ecological hypotheses and develop conservation strategies (Wakefield et al. 2011). Individual specialization does not refer only to behaviour associated with the foraging and feeding strategies of seabirds, but is also associated with the mate choice and territories at the colony sites, among other traits (Jouventin and Bried 2001). Nonetheless, this review is focusing on the foraging (i.e. searching for food) and feeding (i.e. diet and prey choice) strategies of seabirds, which are among the main traits directly related to the survival of the organism.

Typically, a given population or species could be considered as “specialist” or “generalist” according to the feeding habits of its conspecific individuals. A specialist population assumes that all its individuals are preying on the same food resources and have similar ecological niches, resulting in an overall small dietary niche width. On the other hand, generalist populations that show a large dietary niche width might be composed by generalist individuals all taking a wide range of food types (Type A generalization) or individuals each specializing on a different but narrow range of food types (Type B generalization) (Bearhop et al. 2004;

Jaeger et al. 2009; Vander Zanden et al. 2010). However, the potential types of individual specialization in the foraging and feeding strategies of seabirds are not restricted to the diet consumed and may also include specialization in the foraging, searching and diving behaviour, site fidelity, consistency in the migratory and foraging routes and consistency in the non-breeding areas.

The fact that individuals of the same species or population may use different resources across time is crucial for constructing models of intra-specific competition, predator–prey interactions and food-web structure. However, understanding this issue using conventional approaches (e.g. pellets, regurgitates or stomach contents) requires laborious sampling of individuals over extended time periods, which is often logistically constrained, especially when working with pelagic seabirds as they spend most of their lifetime at sea. Determining at-sea distribution and habitat use using census at sea is also very challenging because seabirds are often patchily distributed over vast ocean areas. The use of stable isotope analyses (SIA) to infer diet and habitat selection is a powerful approach, as stable isotope ratios can integrate dietary information over different temporal scales depending on the tissue analysed (Inger and Bearhop 2008). For instance, blood retains information on diet up to the previous 3–4 weeks of sample collection (Hobson and Clark 1993) and feathers represent diet during the moult, unrelated to the sampling period since feather keratin is metabolically inert after synthesis (Quillfeldt et al. 2010; Ramos et al. 2011). Hence, the isotopic signature of different tissues provides information on the short- and long-term consistency in the isotopic niche of an individual (Ceia et al. 2014a). Logger devices (e.g. GPS, activity recorders, stomach temperature probes, geolocators, time-depth recorders, accelerometers) can be used simultaneously to obtain information on successive foraging trips, behaviour, foraging and feeding locations, and long-range movements of individual birds in the wild (Hunt and Wilson 2012). These techniques are particularly useful in the study of ecological niche mutually in space, time and trophic dimensions, especially when their use is combined (Navarro et al. 2013). These characteristics of SIA and tracking devices make them appealing to examine isotopic variance and differences in feeding behaviour within and among individuals and thus can be an effective way to investigate individual specialization (Newsome et al. 2007).

Although it is proven that individual specialization exists in many populations of seabirds (see Table 1), to our knowledge no studies summarized its incidence and investigated its wider implications. Therefore, the objectives of this review are to: (1) identify seabird populations with the incidence of individual specialization and (2) summarize all data gathered on this issue. For a better perception of the

**Table 1** Literature review (up to April 2015) of type of individual specialization in the foraging and feeding strategies of seabirds

Species (common, scientific)	Order	Family	Marine zone	FAO fishing area (ocean region)	Study site	Type of individual specialization	References
<i>(a) Studies documenting any evidence of individual specialization (positive results)</i>							
Wandering albatross <i>Diomedea exulans</i>	Pro	Dio	O	Southern Atlantic Ocean	Bird Island, South Georgia	Short- and long-term consistency in the foraging niche (S, A)	(Ceia et al. 2012)
Wandering albatross <i>Diomedea exulans</i>	Pro	Dio	O	Southern Indian Ocean	Possession Island, Crozet Archipelago	Short-term consistency in foraging behaviour; Short-term consistency in the foraging area (S)	(Jaeger et al. 2010) (Weimerskirch et al. 1993)
Sooty albatross <i>Phoebastria fusca</i>	Pro	Dio	O	Southern Indian Ocean	Possession Island, Crozet Archipelago	Short-term consistency in foraging behaviour	(Jaeger et al. 2010)
Light-mantled albatross <i>Phoebastria palpebrata</i>	Pro	Dio	O	Southern Indian Ocean	Possession Island, Crozet Archipelago	Short-term consistency in foraging behaviour	(Jaeger et al. 2010)
Indian yellow-nosed albatross <i>Thalassarche carteri</i>	Pro	Dio	O	Western Indian	Amsterdam Island	Searching behaviour (ARS) (S)	(Pinaud and Weimerskirch 2005)
Black-browed albatross <i>Thalassarche melanophrys</i>	Pro	Dio	O	Southern Atlantic Ocean	Bird Island, South Georgia	Site fidelity during the non-breeding season (S)	(Phillips et al. 2005)
Black-browed albatross <i>Thalassarche melanophrys</i>	Pro	Dio	O	Southern Indian Ocean	Canon de Sourcils Noirs, Kerguelen Archipelago	Foraging consistency during chick-rearing (related to personality traits and fitness) (S)	(Patrick and Weimerskirch 2014a, b)
Grey-headed albatross <i>Thalassarche chrysostoma</i>	Pro	Dio	O	Southern Atlantic Ocean	Bird Island, South Georgia	Foraging consistency during non-breeding season (S)	(Croxall et al. 2005)
Shy albatross <i>Thalassarche cauta</i>	Pro	Dio	O	Eastern Indian	Albatross Island, Tasmania	Site fidelity to foraging habitat (S)	(Hedd et al. 2001)
Cory's shearwater <i>Calonectris borealis</i>	Pro	Proc	O	Northeast Atlantic	Berlenga Island, Portugal	Short-term consistency in the isotopic niche	(Ceia et al. 2014b)
Cory's shearwater <i>Calonectris borealis</i>	Pro	Proc	O	Eastern Central Atlantic	Selvagem Grande Island, Madeira Archipelago	Site fidelity during the non-breeding season (wintering areas) (S, A); Consistency in migratory routes	(Dias et al. 2011, 2013)
Cory's shearwater <i>Calonectris borealis</i>	Pro	Proc	O	Eastern Central Atlantic	Gran Canaria Island, Canary Islands	Foraging site fidelity (related to spatial and temporal predictability of the resources)	(Navarro and González-Solís 2009)
Scopoli's shearwaters <i>Calonectris diomedea</i>	Pro	Proc	O	Mediterranean Sea	Linosa, Sicily, Italy	Consistency in migration strategies (S)	(Muller et al. 2014)

Table 1 continued

Species (common, scientific)	Order	Family	Marine zone	FAO fishing area (ocean region)	Study site	Type of individual specialization	References
Streaked shearwater <i>Calonectris leucomelas</i>	Pro	Proc	O	Northwest Pacific	Sangan, Mikura and Awa Islands, Japan	Site fidelity and consistency in behaviour during the non-breeding season (wintering areas) (S)	(Yamamoto et al. 2014)
White-chinned petrel <i>Procellaria aequinoctialis</i>	Pro	Proc	O	Southern Indian Ocean	Possession Island, Crozet Archipelago	Short-term consistency in foraging behaviour	(Jaeger et al. 2010)
White-chinned petrel <i>Procellaria aequinoctialis</i>	Pro	Proc	O	Southern Atlantic Ocean	Bird Island, South Georgia	Site fidelity during the non-breeding season (wintering areas)	(Phillips et al. 2006)
Common diving petrel <i>Pelecanoides urinatrix</i>	Pro	Proc	O	Southern Indian Ocean	Mayes Island, Kerguelen Archipelago	Consistency in wintering areas	(Cherel et al. 2006)
Slender-billed prion <i>Pachyptila belcheri</i>	Pro	Proc	O	Southwest Atlantic	New Island, Falkland Islands	Short-term consistency in the feeding ecology (in chicks); Moulting areas (migratory specialization) (S)	(Quillfeldt et al. 2008, 2010)
Yellow-legged gull <i>Larus michahellis</i>	Cha	Lar	C	Northeast Atlantic	Berlenga Island, Portugal	Short- and long-term consistency in the feeding ecology	(Ceia et al. 2014a)
Yellow-legged gull <i>Larus michahellis</i>	Cha	Lar	C	Mediterranean Sea	Benidorm Island, Spain	Diet (some individual special-ists in storm petrels <i>Hydrobates pelagicus</i> ) (A)	(Oro et al. 2005; Sanz-Agui-lar et al. 2009)
Lesser black-backed gull <i>Larus fuscus</i>	Cha	Lar	C	Northeast Atlantic (Bay of Biscay)	Gipuzkoa, Spain	Consistency in the feeding ecology between breeding and winter periods (A)	(Arizaga et al. 2013)
Arctic herring gull <i>Larus smithsonianus</i>	Cha	Lar	C	Northeast Atlantic (Norwegian Sea)	Northern Norway	Site fidelity to wintering areas	(Helberg et al. 2009)
Arctic herring gull <i>Larus smithsonianus</i>	Cha	Lar	C	Northwest Atlantic	Great Island, Newfoundland, Canada	Diet (related to reproductive performance)	(Pierotti and Annett 1991)
Arctic herring gull <i>Larus smithsonianus</i>	Cha	Lar	C	Northwest Atlantic	Sable Island, Nova Scotia, Canada	Short-term consistency in trophic level (related to body condition) (A)	(Ronconi et al. 2014)
Western gull <i>Larus occidentalis</i>	Cha	Lar	C	Eastern Central Pacific	Alcatraz Island, California, USA	Diet (related to reproductive performance) (S, A)	(Annett and Pierotti 1999)
Mediterranean gull <i>Larus melanocephalus</i>	Cha	Lar	C	Mediterranean Sea	NE Spain (Wintering areas)	Site and route fidelity to wintering areas (A)	(Carboneras et al. 2013)
Dolphin gull <i>Larus scoresbii</i>	Cha	Lar	C	Southwest Atlantic	New Island, Falkland Islands	Foraging behaviour and diet (S)	(Masello et al. 2013)
Slaty-backed gull <i>Larus schistisagus</i>	Cha	Lar	C	Northwest Pacific	Teuri Island, Japan	Diet (seabird prey, related to reproductive success) (S)	(Watanuki 1992)
Laughing gull <i>Larus atricilla</i>	Cha	Lar	C	Northwest Atlantic	Northampton County, Virginia, USA	Diet (estuarine vs. marine prey)	(Knoff et al. 2001)

Table 1 continued

Species (common, scientific)	Order	Family	Marine zone	FAO fishing area (ocean region)	Study site	Type of individual specialization	References
Black-legged kittiwake <i>Rissa tridactyla</i>	Cha	Lar	C (breed.) O (n.b.)	Northeast Pacific (Gulf of Alaska)	Shoup Bay, Prince William Sound, Alaska	Foraging area fidelity (S); Fidelity to wintering habitat (S)	(Irons 1998) (McKnight et al. 2011)
Brown skua <i>Catharacta antarctica</i>	Cha	Ste	C (breed.) O (n.b.)	Southern Atlantic Ocean	Bird Island, South Georgia	Inter-annual consistency in the isotopic niche during non-breeding season (S); Diet (related to chick hatch date) (S)	(Phillips et al. 2007) (Anderson et al. 2009)
Great skua <i>Catharacta skua</i>	Cha	Ste	C (breed.) O (n.b.)	Northeast Atlantic	Hermaness, Shetland, UK	Diet (seabird prey and fishery discards); Diet (seabird prey, related to hatch date)	(Votier et al. 2004a, b)
Great skua <i>Catharacta skua</i>	Cha	Ste	C (breed.) O (n.b.)	Northeast Atlantic St	Foula, Shetland; St Kilda Archipelago; UK	Long-term consistency in trophic level and diet (related to mercury levels) (S, A); Diet (S)	(Thompson et al. 1991; Bearhop et al. 2000); (Furness et al. 2006; Käckelä et al. 2006, 2007)
Great skua <i>Catharacta skua</i>	Cha	Ste	C (breed.) O (n.b.)	Northeast Atlantic	Bjørnøya, Svalbard, Norway	Consistent use of winter areas (S)	(Magnusdottir et al. 2012)
Thick-billed murre <i>Uria lomvia</i>	Cha	Alc	N (breed.) O (n.b.)	Arctic Sea (Hudson Bay)	Coats Island, Nunavut, Canada	Diving behaviour and site fidelity; Diet and diving behaviour (S, A)	(Elliott et al. 2008) (Woo et al. 2008; Elliott et al. 2009a, b)
Thick-billed murre <i>Uria lomvia</i>	Cha	Alc	N (breed.) O (n.b.)	Arctic Sea	Akpatok Island, Eastern Canadian Arctic	Diet (S)	(Provencher et al. 2013)
Thick-billed murre <i>Uria lomvia</i>	Cha	Alc	N (breed.) O (n.b.)	Arctic Sea	Prince Leopold, Coats and Digges islands Eastern Canadian Arctic	Site fidelity during the non-breeding season (wintering areas) (S)	(Tranquilla et al. 2014)
Thick-billed murre <i>Uria lomvia</i>	Cha	Alc	N (breed.) O (n.b.)	Northwest Atlantic	Minarets, Eastern Canada	Diet (S)	(Provencher et al. 2013)
Thick-billed murre <i>Uria lomvia</i>	Cha	Alc	N (breed.) O (n.b.)	Northwest Atlantic	Gannet Island, Eastern Canada	Site fidelity during the non-breeding season (wintering areas) (S)	(Tranquilla et al. 2014)
Thick-billed murre <i>Uria lomvia</i>	Cha	Alc	N (breed.) O (n.b.)	Northeast Atlantic (Greenland Sea)	Spitsbergen Island, Svalbard Archipelago	Site fidelity to foraging areas	(Mehlum et al. 2001)
Common murre <i>Uria aalge</i>	Cha	Alc	N (breed.) O (n.b.)	Northwest Atlantic	Gannet, Funk and Gull islands, Eastern Canada	Site fidelity during the non-breeding season (wintering areas) (S)	(Tranquilla et al. 2014)
Pigeon guillemot <i>Cephus columba</i>	Cha	Alc	N	Northeast Pacific (Gulf of Alaska)	Naked Island, Prince William Sound, Alaska	Diet	(Golet et al. 2000)
Pigeon guillemot <i>Cephus columba</i>	Cha	Alc	N	Northeast Pacific (Gulf of Alaska)	Kachemak Bay, Alaska	Diet	(Litzow et al. 2000)
Atlantic puffin <i>Fratercula arctica</i>	Cha	Alc	N (breed.) O (n.b.)	Northeast Atlantic	Skomer Island, Wales, UK	Consistency in migratory routes	(Guilford et al. 2011)

Table 1 continued

Species (common, scientific)	Order	Family	Marine zone	FAO fishing area (ocean region)	Study site	Type of individual specialization	References
Little penguin <i>Eudyptula minor</i>	Sph	Sphe	N	Eastern Indian	Penguin Island, Australia	Diving behaviour (S)	(Ropert-Coudert et al. 2003)
Adelie penguin <i>Pygoscelis adeliae</i>	Sph	Sphe	N (breed.) O (n.b.)	Southern Indian Ocean	Hukuro Cove, Syowa Station, Antarctica	Site fidelity (feeding area specialization – 63 % of birds) (S)	(Watanuki et al. 2003)
Gentoo penguin <i>Pygoscelis papua</i>	Sph	Sphe	N (breed.) O (n.b.)	Southern Indian Ocean	Penn Island and Estacade, Kerguelen Archipelago	Diet (related to mercury levels)	(Carravieri et al. 2013)
Macaroni penguin <i>Eudyptes chrysolophus</i>	Sph	Sphe	N (breed.) O (n.b.)	Southern Indian Ocean	Possession Island, Crozet Archipelago	Short-term specialization in the foraging niche during winter	(Cherel et al. 2007)
King penguin <i>(Aptenodytes patagonicus)</i>	Sph	Sphe	N (breed.) O (n.b.)	Southwest Atlantic	Volunteer Point, Falkland Islands	Short-term consistency in the foraging routes	(Baylis et al. 2015)
Northern gannet <i>Morus bassanus</i>	Sul	Suli	N	Northeast Atlantic	Grassholm Island, Wales, UK	Short-term consistency in the foraging niche; Searching behaviour (in immatures); Foraging site, foraging consistency, searching behaviour (S)	(Votier et al. 2010a, b) (Patrick et al. 2014)
Northern gannet <i>Morus bassanus</i>	Sul	Suli	N	Northeast Atlantic (North Sea)	Bass Rock Island, Scotland, UK	Foraging site fidelity	(Hamer et al. 2001; 2007)
Northern gannet <i>Morus bassanus</i>	Sul	Suli	N	Northwest Atlantic	Funk Island, Canada	Site fidelity to foraging areas; Winter-site fidelity (S)	(Montevecchi et al. 2009) (Fifield et al. 2014)
Northern gannet <i>Morus bassanus</i>	Sul	Suli	N	Northeast Atlantic	Vesterålen and Storstappen, Norway	Short-term consistency in the foraging routes	(Pettex et al. 2012)
Masked booby <i>Sula dactylatra</i>	Sul	Suli	N	Southeast Atlantic	Ascension Island	Short-term consistency in the foraging trip characteristics (presumably related to high intra-specific competition) (S)	(Oppel et al. 2015)
Great cormorant <i>Phalacrocorax carbo</i>	Sul	Pha	C	Northeast Atlantic	Chausey Islands, France	Foraging site fidelity (S)	(Grémillet et al. 1999)
Pelagic cormorant <i>Phalacrocorax pelagicus</i>	Sul	Pha	C	Northeast Pacific (Gulf of Alaska)	Middleton Island, Alaska	Diving behaviour (in males) (S)	(Kotzerka et al. 2011)
European shag <i>Phalacrocorax aristotelis</i>	Sul	Pha	C	Northeast Atlantic (North Sea)	Isle of May, Scotland, UK	Winter-site fidelity (S, A)	(Grist et al. 2014)
Kerguelen shag <i>Phalacrocorax verrucosus</i>	Sul	Pha	C	Southern Indian Ocean	Mayer Island, Kerguelen Archipelago	Long-term consistency in the foraging niche (both prey type and foraging area) (S)	(Bearhop et al. 2006)
Imperial shag <i>Phalacrocorax atriceps</i>	Sul	Pha	C	Southwest Atlantic	Punta Leon, Argentina	Short- and long-term consistency in foraging behaviour (S)	(Harris et al. 2014)



Table 1 continued

Species (common, scientific)	Order	Family	Marine zone	FAO fishing area (ocean region)	Study site	Type of individual specialization	References
Macquarie shag <i>Phalacrocorax (atriceps) purpurascens</i>	Sul	Pha	C	Southwest Pacific	Macquarie Island, Australia	Diving behaviour (in females) (S)	(Kato et al. 2000)
South Georgia shag <i>Phalacrocorax (atriceps) georgianus</i>	Sul	Pha	C	Southern Atlantic Ocean	Bird Island, South Georgia	Long-term consistency in the foraging niche (both prey type and foraging area) (S) Diving behaviour (in females) (S)	(Bearhop et al. 2006) (Ratcliffe et al. 2013)
Crozet shag <i>Phalacrocorax (atriceps) melanogenis</i>	Sul	Pha	C	Southern Indian Ocean	Possession Island, Crozet Archipelago	Foraging area fidelity; Consistency in daily activity patterns and diving profile (S)	(Cook et al. 2006)
(b) Studies documenting lack of evidence of individual specialization (negative results)							
Black-browed albatross <i>Thalassarche melanophrys</i>	Pro	Dio	O	Southern Atlantic Ocean	New Island and Steeple Jason, Falkland Islands	Short-term consistency in the foraging behaviour (associated with fisheries – 5 % of birds)	(Granadeiro et al. 2011)
Black-browed albatross <i>Thalassarche melanophrys</i>	Pro	Dio	O	Southern Atlantic Ocean	Steeple Jason, Falkland Island	Long-term trophic consistency (associated with fisheries)	(Granadeiro et al. 2014)
Cory's shearwater <i>Calonectris borealis</i>	Pro	Proc	O	Northeast Atlantic	Berlenga Island, Portugal	Short-term consistency in the isotopic niche	(Ceia et al. 2014b)
Common diving petrel <i>Pelecanoides urinator</i>	Pro	Proc	O	Southern Atlantic Ocean	Bird Island, South Georgia	Consistency in wintering areas	(Cherel et al. 2006)
Brown skua <i>Catharacta antarctica</i>	Cha	Ste	C (breed.) O (n.b.)	Southern Atlantic Ocean	Bird Island, South Georgia	Diet (seabird prey) (S)	(Carneiro et al. 2014)
Great skua <i>Catharacta skua</i>	Cha	Ste	C (breed.) O (n.b.)	Northeast Atlantic	Foula and Hermaness, Shetland, UK	Diet (seabird prey) (S)	(Votier et al. 2007)
Common murre <i>Uria aadge</i>	Cha	Alc	N (breed.) O (n.b.)	Northeast Atlantic (North Sea)	Isle of May, Scotland, UK	Foraging area fidelity	(Wanless et al. 1990)
Razorbill <i>Alca torda</i>	Cha	Alc	N (breed.) O (n.b.)	Northeast Atlantic (North Sea)	Isle of May, Scotland, UK	Foraging area fidelity	(Wanless et al. 1990)
Atlantic puffin <i>Fratricula arctica</i>	Cha	Alc	N (breed.) O (n.b.)	Northeast Atlantic (North Sea)	Isle of May, Scotland, UK	Foraging area fidelity	(Wanless et al. 1990)
Northern gannet <i>Morus bassanus</i>	Sul	Suli	N	Northeast Atlantic	Les Etacs, Alderney, Channel Islands	Short-term consistency to specific foraging areas	(Soanes et al. 2013)
Northern gannet <i>Morus bassanus</i>	Sul	Suli	N	Northeast Atlantic	Great Saltee, Ireland	Foraging site fidelity	(Hamer et al. 2001)

Table 1 continued

Species (common, scientific)	Order	Family	Marine zone	FAO fishing area (ocean region)	Study site	Type of individual specialization	References
Masked booby <i>Sula dactylatra</i>	Sul	Suli	N	South Atlantic	St. Helena Island	Short-term consistency in the foraging trip characteristics (presumably related to low intra-specific competition) (S)	(Oppel et al. 2015)

*Short term* within season, *long term* across seasons and/or years. Order: *Cha* Charadriiformes, *Pro* Procellariiformes, *Sph* Sphenisciformes, *Sul* Suliformes. Family: *Alc* Alcidae, *Dio* Diomedidae, *Lar* Laridae, *Pha* Phalacrocoracidae, *Proc* Procellariidae, *Sph*e Spheniscidae, *Ste* Stercorariidae, *Suli* Sulidae. Marine zone: *O* oceanic, *N* neritic, *C* coastal (breed. breeding period, *n.b.* non-breeding period, *S* controlled for sex, *A* controlled for age)

current knowledge worldwide, we summarized the documented incidence of individual specialization systematically by species, families and orders of seabirds, and ocean regions. Possible aspects on the ecological implications of individual specialization in seabirds based on what has been referenced are also discussed.

## Methods

We reviewed a broad array of scientific publications, published in international scientific journals, to collate available data on individual specialization in the foraging and feeding strategies of seabirds. The literature sources were identified from a systematic search on the Internet and academic databases (e.g. ISI Web of Science and Scopus and ScienceDirect) up to April 2015, including a combination of the search term “seabird” or additional terms reflecting the main types of seabird “albatross”, “shearwater”, “petrel”, “prion”, “gull”, “kittiwake”, “tern”, “skua”, “jaeger”, “auk”, “murre”, “guillemot”, “puffin”, “penguin”, “gannet”, “booby”, “cormorant” or “shag”, and any of the terms “individual specializ(s)ation”, “foraging specializ(s)ation”, “consistency”, “route fidelity”, “foraging fidelity” or “site fidelity”. We also examined other studies otherwise known to authors of this review. Despite our extensive literature review, we acknowledge that there is a publication bias because researchers that did not find significant specialization within individuals (negative result) may not have reported their results. We focused this review on individual specialization in foraging and/or feeding strategies within seabird populations relying on the marine environment for at least part of the year, both in the short term (within season) and in the long term (across seasons and/or years). We excluded studies focusing on differences in foraging and feeding strategies between sexes (e.g. Phillips et al. 2011), colonies (e.g. Catry et al. 2011) or subcolonies (e.g. Ceia et al. 2015), and age classes (e.g. Lecomte et al. 2010), unrelated to the individual level and that could confound “true individual specialization”. Many seabird species are sexually dimorphic leading to different morphological characteristics that potentially promote sex-specific foraging and/or feeding specialization, and ideally, this should be controlled for before assessing the repeatability in foraging behaviour and diet (Ratcliffe et al. 2013). Likewise, we did not review studies focusing on the variability in the foraging and feeding strategies of seabirds from different colonies or subcolonies. For the most literature sources, we were unable to distinguish data in relation to age because many seabirds sampled in those studies were of undefined age class. However, it should be noted that comparing foraging and feeding strategies between sexes, colonies and



age classes should provide insights into the degree of specialization in different groups.

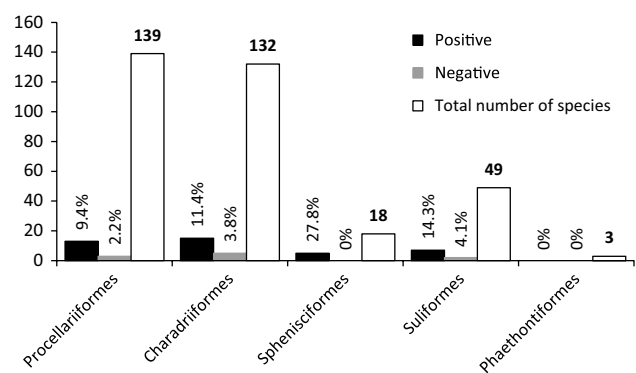
During the search, we considered extant seabird species belonging to the orders, and respective families, of Procellariiformes (families: Diomedidae, Procellariidae, Hydrobatidae and Oceanitidae), Charadriiformes (families: Laridae, Stercorariidae and Alcidae), Sphenisciformes (family: Spheniscidae), Suliformes (families: Sulidae, Phalacrocoracidae and Fregatidae) and Phaethontiformes (family: Phaethontidae). We excluded wader bird families belonging to the order of Charadriiformes from our search. Additionally, members of the family Anhingidae (Suliformes) were not considered because they are mainly found in freshwater lakes and streams. Thus, seabird populations considered in the present study belong to three groups according to the typical (i.e. year-round) marine zone exploited: “oceanic” (marine waters above open ocean, typically >200 m in depth), “neritic” (marine waters above continental shelf or around near-shore oceanic islands, typically <200 m in depth) and “coastal” (marine waters along coasts including estuaries, typically <8 km from the shoreline) (Croxall et al. 2012). The results were then summarized by orders, families and species or subspecies. We documented the type of individual specialization in the foraging and feeding strategies of seabirds identified in each study analysed, and we used FAO fishing area boundaries (<http://www.fao.org/fishery/area/search/en>) to classify the 19 core ocean regions corresponding to the study sites, which were then combined into ten main geographic areas to reduce some of the smaller-scale sampling biases. We followed the taxonomy of BirdLife International (2014).

### The documented incidence of individual specialization

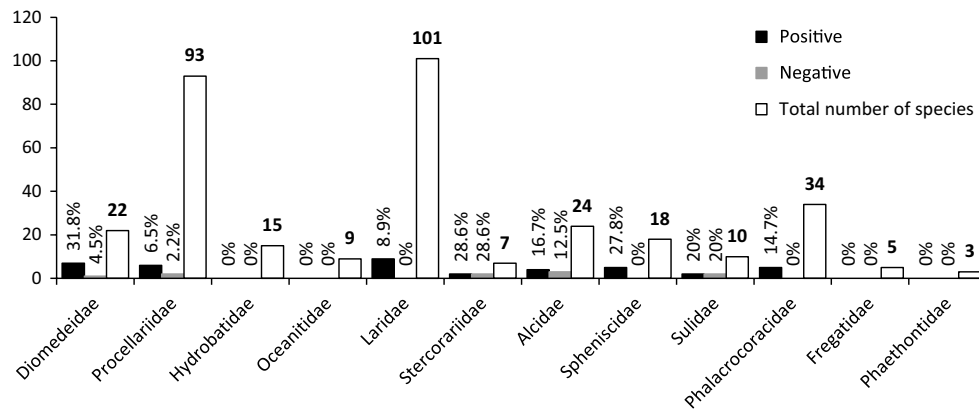
In total, we identified 81 scientific publications searching for any type of individual specialization in the foraging and feeding strategies of 42 seabird species (Table 1). Some publications examined individual specialization in different seabird species, years and/or study sites, resulting in a total of 94 records (hereafter studies), of which 82 identified any type of individual specialization (positive result) and only 12 documented little or no individual specialization (negative result). Although the database of published studies used in this review goes back to 1980, the great majority of the studies were published after the year 2000 (i.e. 89.4 %), highlighting the increasing focus on individual specialization in the foraging and feeding strategies of seabirds during the past 15 years. Overall, we found that most studies focused on the order Charadriiformes ( $n = 42$ ) and that an intermediate number focused on Procellariiformes ( $n = 26$ ) and Suliformes ( $n = 21$ ). Five studies focused on Sphenisciformes and none in the order Phaethontiformes.

### Evidences of individual specialization

It is clear that with the development of new technology, such as tracking devices and stable isotope analyses, it became possible to increase our knowledge on individual specialization of seabirds by investigating accurately and repeatedly their feeding ecology. To date, 40 species representing 11.7 % of the total extant seabird species (i.e. 341 seabird species, BirdLife International (2014)) exhibited some type of individual specialization in foraging and/or feeding strategies, but this proportion is certainly limited by existing studies. Our review shows that individual specialization is documented in all seabird orders (Fig. 1), with the exception of Phaethontiformes (possibly because no studies are available yet), which comprises only one family and three species, and hence potentially widespread among seabirds. No studies documented the incidence of individual specialization in the families Hydrobatidae and Oceanitidae (Procellariiformes), but this is not surprising as these Procellariiform families include species that are too small to study with currently available data-loggers. Additionally, we found no studies documenting individual specialization in the families Fregatidae (Suliformes) and Phaethontidae (Phaethontiformes; Fig. 2). The eight members of these two families (i.e. five frigatebird and three tropicbird species) are predominantly from tropical ocean regions, and there are no studies available in these species concerning individual specialization. In fact, our results showed that a greater number of studies were conducted in ocean regions at higher latitudes (i.e. in temperate and polar regions) than at lower latitudes (i.e. tropical regions; Fig. 3). This

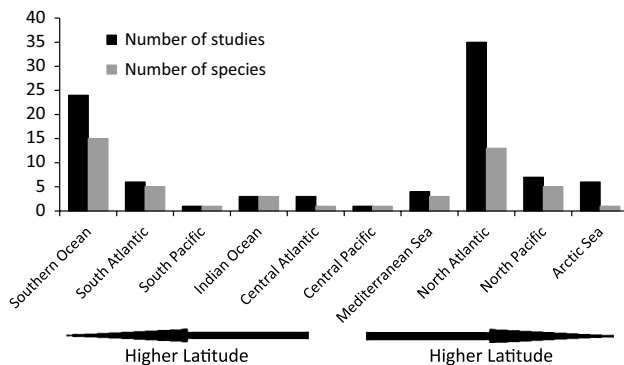


**Fig. 1** Number of seabird species in which any type of individual specialization in foraging and/or feeding strategies was positive and negatively documented, and total number of species for the five seabird orders, according to BirdLife International (2014). The fraction (%) between the number of studied species and the total number of species for each order is shown in the bars. The order of Charadriiformes does not comprise wading birds, and the order Suliformes does not comprise the family Anhingidae



**Fig. 2** Number of seabird species in which any type of individual specialization in foraging and/or feeding strategies was positive and negatively documented, and total number of species for the 12 extant seabird families in accordance with BirdLife International (2014)

(wading bird families and the family Anhingidae were not considered). The fraction (%) between the number of studied species and the total number of species for each family is shown in the bars



**Fig. 3** Ocean regions showing the number of studies (black bars) and seabird species (grey bars) in which any type of individual specialization in the foraging and/or feeding strategies of seabirds was documented (both positive and negative results). The ten ocean regions were combined based on FAO fishing area boundaries

fact leads to ambiguity when drawing conclusions. If, on the one hand, there is a general gap in the study of individual specialization of seabirds at lower latitudes, on the other hand this trait could be more conspicuous and common at higher latitudes. Overall, our results reinforced the need for documenting either the presence or the absence of individual specialization in the studied seabird populations, particularly for tropical regions, because both positive and negative results are crucial to better understand this issue.

We found few studies that documented little or no individual specialization in the foraging and feeding strategies of some seabird populations (Table 1b). Soanes et al. (2013) examined repeatability between the first and second foraging trips made by northern gannets *Morus bassanus* in the Northeast Atlantic and found no apparent short-term consistency to specific foraging areas (but see Wakefield et al.). Hamer et al.

(2001) described contrasting foraging strategies of individual northern gannets at two Northeast Atlantic colonies; their results indicate a much lower degree of foraging area fidelity at one of the studied colonies. Ceia et al. (2014b) showed fluctuations on short-term consistency in the isotopic niche along a three-year study in a Procellariiform species, the Cory's shearwater *Calonectris borealis*, at a Northeast Atlantic colony. Granadeiro et al. (2011) tracked 67 individual black-browed albatrosses *Thalassarche melanophrys* in order to study the interactions between individual birds and vessels in the Southwest Atlantic, and found that less than 5 % of the total birds returned to vessels with which they had interacted in a previous trip. Moreover, Granadeiro et al. (2014) found no long-term trophic consistency of individual black-browed albatrosses with regard to fisheries in the same region, suggesting that this species does not specialize in discards. Wanless et al. (1990) documented little foraging area fidelity in common murre *Uria aalge*, razorbills *Alca torda* and Atlantic puffins *Fratercula arctica* in the Northeast Atlantic. Votier et al. (2007) found high levels of annual variation in seabird consumption for great skuas *Catharacta skua* in two Northeast Atlantic colonies (Foula and Hermaness, UK) and Carneiro et al. (2014) found no clear evidence for specialist brown skuas *Catharacta antarctica* at South Georgia.

### Fluctuating selection of individual specialization

Individual specialization in foraging strategies, diets, locations or niches of seabirds has been described in several seabird populations (Table 1a), but not in others (Table 1b). The studies reviewed in this work show variability in individual specialization within species and populations. Nonetheless, it remains unclear why there

are such a high number of specialized and consistent individuals within some populations and not in others. Woo et al. (2008) suggest that the answer may be related to temporal changes in the predictability of resources, and Svanbäck and Persson (2004) showed that individual specialization in the perch *Perca fluviatilis* may fluctuate with population density through feedback mechanisms via resource levels. In fact, Ceia et al. (2014b) showed that individual variation in resources use during the short term may fluctuate over time (i.e. among years and periods) in a population of Cory's shearwaters depending on resource availability (i.e. individual short-term consistency was higher during periods with a regular availability of food resources and lower when food availability was either abundant or scarce). This agrees with the theory that dietary specializations at the individual level can disappear under influence of prey availability, and hence competition, and a generalist strategy be pursued by most individuals (Svanbäck and Bolnick 2005). Therefore, fluctuations on individual specialization in seabirds may be related to temporal changes in the availability and predictability of resources and, thus, vulnerable to extrinsic factors, as suggested by Hamer et al. (2001), Woo et al. (2008) and Ceia et al. (2014b). Similarly, studies in wading birds such as oystercatchers *Haematopus ostralegus* (van de Pol et al. 2010) show that individuals with different strategies present differences in fitness between years, and therefore, a specific individual specialization may fluctuate depending on biotic and abiotic conditions; Catry et al. (2014) show that individual specialization in black-tailed godwits *Limosa limosa islandica* may fluctuate between years due to the frequency of specialists, competitor density, prey abundance and environmental conditions. As a consequence, birds display distinct degrees of individual specialization in diet and habitat use, indicating the presence of both generalists and specialists within a population (Catry et al. 2014). This allows individual feeding preferences and adjustments to spatial, seasonal and inter-annual variations in resources by exploiting different foraging niches (Moreno et al. 2009; Ramos et al. 2011; Ceia et al. 2014a). That is really the only way that a diversity of specialization can be maintained indefinitely within the population. Overall, these studies showed intra-individual variability in the foraging and feeding strategies of some seabird populations, at least during specific periods, suggesting that this trait could differ between species and/or populations or even oscillate in the same population over time (i.e. it may vary spatio-temporally among/within species and populations).

## Ecological implications of individual specialization

Many seabird populations may present a high number of specialized individuals in the foraging and feeding strategies, but it remains unclear what are the ecological implications of individual specialization at the individual and population levels. Few studies addressed this question, and information on the implications of specialization is scarce (Araújo et al. 2011). During our literature review, some studies (e.g. Woo et al. 2008; Ceia et al. 2012) did not find any apparent differences in the fitness of specialists and generalists. However, some evidences show that individual specialization over short-time periods may confer an advantage in terms of birds' condition status and breeding performance or foraging effort. For instance, Patrick and Weimerskirch (2014b) demonstrated that successful breeders of black-browed albatrosses had a considerably narrower niche width than unsuccessful breeders. Nevertheless, most studies showing some benefit in individual specialization were in seabird species with apparently broader niches such as skuas and gulls. Furness et al. (2006) demonstrated that the body condition, survival and breeding performance of individual great skuas may be improved by choosing to winter in areas where there are large fisheries providing discards. Anderson et al. (2009) found that individual specialization in the diet of brown skuas influenced timing of breeding and potentially the reproductive output of breeding pairs. Ceia et al. (2014a) showed that individual consistency was high and stable across two years of contrasting food availability in yellow-legged gulls, although birds differed in foraging behaviour and effort. Pierotti and Annett (1991) and Annett and Pierotti (1999) found that variation in diet choice was related to individual breeding performance in Arctic herring gulls *Larus smithsonianus* and western gulls *Larus occidentalis*, respectively. Similarly, Ronconi et al. (2014) showed that higher trophic level foraging in Arctic herring gulls was associated with better body condition. Watanuki (1992) showed that individuals of slaty-backed gulls *Larus schistisagus* specializing on seabird chick prey raised more fledglings than those delivering mostly fish. Overall, these studies suggest that the ecological implications of individual specialization at individual level, apparently more conspicuous in seabirds with broader species level niches, may lead to improvements in several ecological traits (especially in breeding performance) possibly due to substantial advantages in specialization on certain resources (e.g. higher energetic content, lower foraging effort). However, it should be noticed that these associations between individual specialization and fitness were found over short-time periods, and one breeding season (or part of it in many studies) is not enough to

draw any conclusions about the evolutionary importance of individual specialization. As previously reported, such selection for specialization often fluctuates; thus, we should be critical when considering that specialists tend to have higher breeding performance than generalists over long-time periods. If there was really directional selection for specialization, then all individuals would quickly become specialists, promoting speciation.

The repeatability of behaviour is a widespread phenomenon in animals, but the proximate reasons for it are unresolved. Therefore, at this point, we place the question “why do individuals specialize?” Possibly there are many and different reasons, and the answer could be related to the underlying causes of specialization such as variation in morphology, physiology, personality or cognitive abilities. Many animals, including seabirds, are highly variable among individuals but highly repeatable within individuals for hormone levels (e.g. Seltmann et al. 2012; Elliott et al. 2014b), basal metabolism (e.g. Bech et al. 1999) and metabolic rate (e.g. Careau et al. 2008; Biro and Stamps 2010; Elliott et al. 2014a), personality (e.g. van Oers et al. 2004) or cognitive abilities (e.g. Kitaysky et al. 2006). Moreover, recent research suggests that colonies may be important as sources of social information allowing animals to make decisions based on information sharing from conspecifics (Wakefield et al. 2013; Evans et al. 2015). Nevertheless, whatever the ecological implications and the underlying causes of specialization, individual specialization within a seabird’s population has an important role on its ecology, foraging behaviour and dynamics, and may contribute to reduce intra-specific competition among individuals (Ceia et al. 2012; Patrick and Weimerskirch 2014a; Opper et al. 2015), as suggested in other taxonomical animal groups (e.g. Svanbäck and Bolnick 2007, Vander Zanden et al. 2010, Matich et al. 2011).

## Final remarks

Our review documented, for the first time, a full list of studies identifying individual specialization in the foraging and feeding strategies of seabirds, an area in which the knowledge is scarce for the general diversity of taxa and particularly for seabirds. Some degree of individual foraging specialization was previously documented in a large range of marine taxa, such as invertebrates (e.g. Burrows and Hughes 1991), fishes (e.g. Matich et al. 2011), sea turtles (e.g. Thomson et al. 2012), marine mammals (e.g. Tinker et al. 2008) and seabirds (this review), suggesting that this could be a widespread phenomenon.

Overall, this review demonstrates that inter-individual variation in resource use occurs within several populations and species of seabirds, which is necessary for natural selection, and hence adaptation. By extension,

individual specialization may play an important role in the foraging dynamics of the populations by reducing, for instance, intra-specific competition, but further investigation is required in order to understand how ecological implications at individual level may be related to several traits such as reproductive success, body condition or foraging effort. Such implications though could vary according to species and spatio-temporal variation of the populations, and respective incidence of individual specialization.

## Future research

In general, a small number of reviews on individual specialization have been published, and this is the first one specifically on seabirds. Our review documented its occurrence at around 12 % of the extant seabird species. However, this proportion is most likely limited by existing studies (especially in small or tropical seabird species), and many unanswered ecological questions require future research as trophic interactions among individual conspecifics and their relationships with the marine environment are particularly complex. Apart from documenting the existence of individual specialization, further studies should explore the timescale at which an individual’s specialization is consistent (i.e. during the short and long term), investigate the relative incidence in different populations, species and communities, determine the fitness implications of different strategies, and, finally, identify the mechanisms that generate inter-individual variation. Given the long history of diet analyses in seabird ecology, there are a substantial number of appropriate data sets that in conjunction with recent powerful techniques such as stable isotope analyses, logger devices and software would permit a wide range of theoretical hypotheses of niche variation to be tested and validated. However, for that, it is essential to document the negative results (i.e. studies in which individual specialization was tested in a given population but not validated). Then, it would be possible to explore in a robust meta-analysis the general veracity of this hypothesis, its spatio-temporal fluctuations (among/within species and populations) and the implications for fitness, fecundity and survival.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Human rights and animal standards** This article does not contain any studies with human participants or animals performed by any of the authors.

**Informed consent** Informed consent was obtained from all individual participants included in the study.

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