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DIETARY ECOLOGY OF SEABIRDS: A CRITICAL REVIEW OF PATTERNS OF PREY USE, METHODOLOGICAL ADVANCES, AND RESPONSES TO ENVIRONMENTAL CHANGE

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ABSTRACT

Seabirds occupy diverse trophic positions in marine food webs and consume prey ranging from zooplankton and euphausiid krill to forage fish, mesopelagic fishes, cephalopods, crustaceans, carrion and, in some generalist species, terrestrial or anthropogenic food. Their diets are shaped by prey availability, body size, feeding morphology, diving capacity, habitat, season, breeding constraints and interactions with fisheries. This review synthesizes literature on seabird diet, emphasizing prey composition, dietary specialization and flexibility, spatial and temporal variation, methods of diet determination, and implications of dietary change for conservation. A systematic thematic approach was adapted from the methodology used in the accompanying methodological review, with recent literature emphasized for 2020-2025 and older studies retained when they established foundational methods, global patterns or long-term ecological context. The evidence indicates that no single seabird diet is representative of the group: penguins and several Procellariiformes may rely strongly on krill, myctophids, fish or squid; auks often target energy-rich forage fish and zooplankton; gannets, cormorants and many terns are predominantly piscivorous; whereas gulls and skuas display greater trophic plasticity and frequently incorporate carrion, discards and terrestrial resources. Conventional stomach, pellet and regurgitate analyses provide direct taxonomic information but are affected by digestion and sampling biases. Stable isotopes and fatty acids extend inference to assimilated diet and trophic niche, while DNA metabarcoding can substantially improve prey identification, although quantitative interpretation remains constrained by DNA degradation, primer bias and reference-database limitations. Collectively, the literature supports a complementary, multi-method approach to seabird diet research and demonstrates that diet is both an ecological trait and a sensitive indicator of marine ecosystem change.

Keywords: Seabirds; Diet Composition; Trophic Ecology; Prey Selection; Stable Isotopes; DNA Metabarcoding

1 INTRODUCTION

Seabirds are among the most conspicuous predators of the marine environment and occupy an exceptional range of ecological niches. Their feeding ecology links planktonic and nektonic production to higher trophic levels and, through the transport of marine-derived nutrients to breeding colonies, can also connect oceanic and terrestrial nutrient cycles. Global estimates have placed seabird food consumption at approximately 96 million tonnes annually [2, 16], although such estimates remain uncertain because diet information is incomplete for many species and is often derived from breeding-season observations [2, 16].

Despite this importance, the phrase "seabird diet" conceals marked taxonomic, spatial and temporal heterogeneity. Procellariiformes such as albatrosses, shearwaters and petrels consume fish, cephalopods and crustaceans, with some species relying strongly on squid or mesopelagic fishes. Penguins may consume krill, fish and cephalopods depending on region and species. Auks commonly exploit zooplankton and small schooling fish, whereas gannets, cormorants and many terns are primarily piscivorous. Gulls and skuas are comparatively opportunistic and may combine marine prey with carrion, fishery discards, terrestrial foods and other birds [2, 7, 23].

Diet is a functional expression of how seabirds interact with the physical and biological environment. Prey distributions are sometime spatially patchy and temporally dynamic, and therefore seabirds must locate profitable prey while meeting energy requirements associated with flight, diving, thermoregulation, reproduction and moult [10, 12]. In the Gulf of Cádiz, seabird distributions were more strongly related to prey abundance than to broad oceanographic predictors alone, illustrating that the biological prey field can be a proximate driver of predator distribution [12]. At South Georgia, dietary segregation among seabirds sharing krill resources was associated with differences in foraging range and feeding mode, demonstrating that species can partition a common prey field through spatial and behavioral mechanisms [10].

Understanding seabird diet is important because diet reveals trophic position and food-web connectivity, indicates the availability of prey that can be difficult to survey directly, influences breeding and survival, and exposes interactions with fisheries, climate-driven changes in prey distribution and quality, and pollution. Seabird diet studies are therefore relevant to ecosystem-based fisheries management and marine conservation [2, 18].

However, seabird diet research is also methodologically challenging. Birds are highly mobile, many forage far offshore, and diet samples obtained at colonies often represent a short period or a particular life-history stage [5]. Conventional techniques may over represent prey with durable hard parts, whereas molecular techniques can reveal prey that are difficult to identify morphologically but may not provide unbiased quantitative estimates. Modern trophic tools have therefore shifted the field from a simple "what was eaten?" question toward integrated inference concerning prey identity, trophic position, habitat use and dietary niche [5].

The present review critically synthesizes the literature on seabird diet, emphasizing: (1) the principal prey categories consumed by major seabird groups; (2) mechanisms driving dietary variation; (3) conventional and modern approaches used to determine diet; (4) the influence of fisheries, climate change and pollution on dietary pathways; and (5) methodological and research gaps that should guide future seabird trophic studies.

2 CONCEPTUAL FRAMEWORK

Seabird diet may be understood as the outcome of interacting environmental, biological and methodological processes. Prey abundance and energy density constrain the available food field; seabird morphology and behavior determine which components of that field can be accessed; life-history demands alter energetic requirements and prey selection; and the method used to observe diet determines which components are detectable. Figure 1 emphasizes that observed diet is not identical to the total diet consumed: it is the intersection of actual prey consumption, assimilation and detectability.

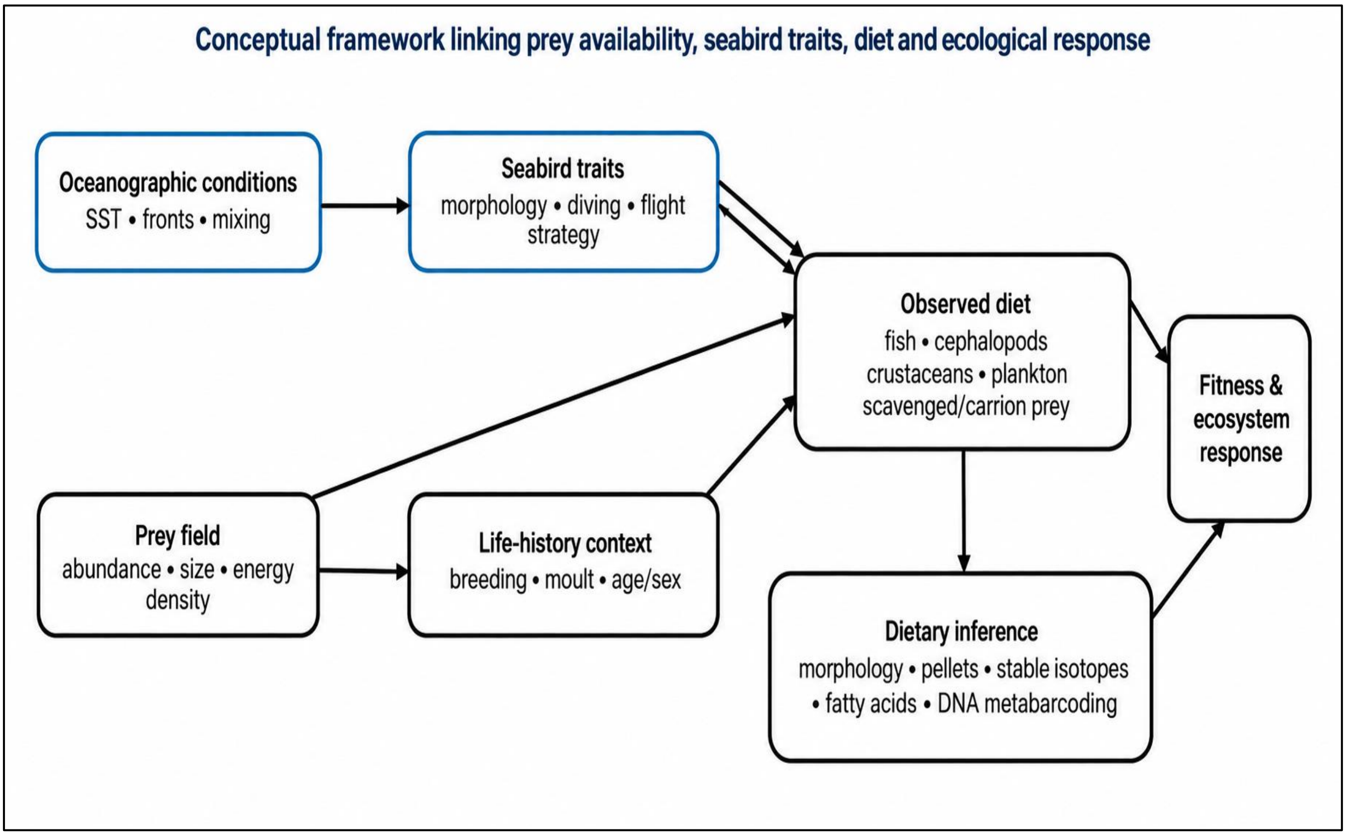

Figure 1: Seabird Diet Conceptual Framework

3 MATERIALS AND METHODS

3.1 Search Strategy

A systematic thematic literature review was conducted using academic search engines, bibliographic databases, publisher platforms, and open-access repositories to identify globally relevant literature on the diet, feeding ecology, prey composition, and trophic ecology of seabirds. The search strategy prioritised recent peer-reviewed studies published between 2020 and 2025 to provide current information on advances in seabird dietary research, including the application of molecular and biochemical techniques such as DNA metabarcoding and stable-isotope analysis. Older publications were also used where relevant, particularly when they provided foundational information on seabird feeding ecology, dietary composition, trophic relationships, and conventional methods used to study seabird diets.

The search refinement was guided by thematic keywords, including “diet of seabirds,” “seabird diet,” “seabird feeding ecology,” “seabird prey,” “seabird prey composition,” “seabird trophic ecology,” “seabird foraging ecology,” “seasonal variation in seabird diet,” “spatial variation in seabird diet,” “methods to study seabird diet,” “DNA metabarcoding of seabird diet,” “stable isotopes and seabird diet,” “climate change and seabird diet,” and “fisheries and seabird diet.”

Additional searches were conducted using terms related to major seabird groups, including albatrosses, petrels, shearwaters, storm petrels, penguins, auks, gulls, terns, gannets, boobies, and cormorants, together with terms relating to their principal dietary resources, including fish, cephalopods, crustaceans, krill, zooplankton, and mesopelagic prey.

The review was designed to capture literature examining seabird diets from several ecological perspectives. These included direct studies of prey composition, investigations of temporal and spatial variation in diet, dietary specialisation and flexibility, prey switching, trophic segregation, foraging ecology, marine food-web relationships, climate-related changes in prey availability, and interactions between seabirds and fisheries. Literature on conventional and modern methods used to investigate seabird diets was also included. The present review further aligns its reporting logic with Figure 2 for transparent identification, screening and synthesis of literature.

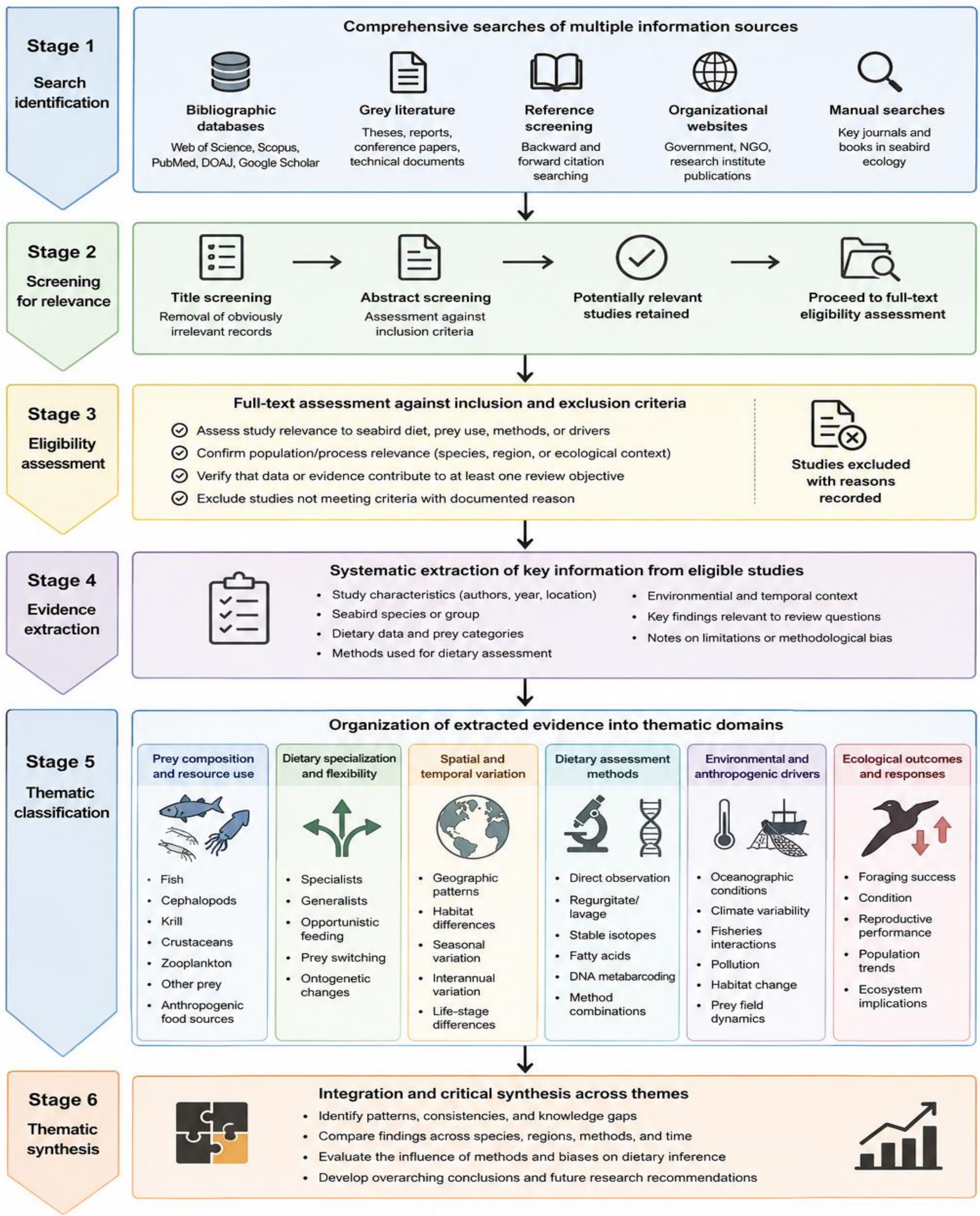

Figure 2. Literature search, screening and thematic synthesis framework.
This framework outlines the six conceptual stages used to identify, screen, assess, extract, classify, and synthesize literature relevant to seabird diet, prey use and associated drivers.

Figure 2: Literature Search, Screening and Thematic Synthesis Framework

3.2 Inclusion Criteria

This review aimed to evaluate existing literature on the diet and feeding ecology of seabirds. The selection of articles was based on the following inclusion criteria:

Relevant and recent peer-reviewed journal articles published between 2020 and 2025 were prioritised to demonstrate the current state of research on seabird diets, trophic ecology, and modern dietary assessment techniques.

Publications published before the 2020-2025 period were also reviewed when they contained relevant and foundational information. Older studies were included to establish a baseline for understanding seabird prey composition, feeding ecology, trophic relationships, dietary variation, and traditional methods used to study seabird diets.

Articles that examined the diet, prey composition, feeding behaviour, foraging ecology, or trophic ecology of seabirds.

Studies that identified or discussed major seabird prey categories, including fish, cephalopods, crustaceans, krill, zooplankton, mesopelagic organisms, and other marine prey.

Research focusing on dietary variation among different seabird species, families, orders, geographical regions, marine habitats, seasons, breeding stages, and life-history stages.

Papers examining dietary specialisation, dietary flexibility, prey switching, trophic segregation, and resource partitioning among seabirds.

Studies that investigated the effects of environmental conditions, oceanographic variability, climate change, prey distribution, marine productivity, and other ecological factors on seabird diets.

Articles examining the relationship between fisheries and seabird feeding ecology, including resource overlap, competition for prey, fishery discards, and anthropogenic influences on prey availability.

Studies describing conventional and advanced methods used to investigate seabird diets, including stomach-content analysis, regurgitate analysis, pellet analysis, prey remains, stable-isotope analysis, fatty-acid analysis, DNA metabarcoding, compound-specific isotope analysis, and multi-method approaches.

Papers that provided taxonomic information on seabird species, families, and orders, where available, and/or identified prey to the lowest practical taxonomic level.

Papers written and available in English.

4 RESULTS

Literature for this review was sourced from various academic search engines, bibliographic databases, publisher platforms, and open-access repositories, including Google Scholar, ResearchGate, Academia, Semantic Scholar, R Discovery, OiPub, ScienceDirect, PubMed/MEDLINE, SpringerLink, Web of Science, Scopus, Wiley Online Library, SciSpace, and institutional repositories. Reference lists of relevant review articles and primary research papers were also examined to identify additional literature relating to seabird diet and feeding ecology. The majority of journal articles were accessible through open-access platforms, publisher websites, institutional access, or other academic repositories. Where articles were identified through their Digital Object Identifiers (DOIs), the DOI was used to locate the original publication or an accessible version of the article.

An extensive collection of published literary works was accumulated when the selected search terms were utilised. The searches focused on literature relating to the diet, prey composition, trophic ecology, feeding behaviour, environmental influences, and methods used to investigate seabird diets. The principal search categories were as follows:

Diet of seabirds: Literature examining the general composition of seabird diets and the major prey groups consumed.

Seabird feeding and foraging ecology: Studies investigating how seabirds locate, capture, and utilise prey in coastal, pelagic, offshore, and marine environments.

Seabird prey composition: Research identifying fish, cephalopods, crustaceans, krill, zooplankton, mesopelagic organisms, and other prey consumed by seabirds.

Seabird trophic ecology: Studies examining trophic position, dietary niche, resource partitioning, and food-web relationships.

Seasonal variation in seabird diets: Research investigating changes in prey use among breeding and non-breeding periods and across different seasons.

Spatial variation in seabird diets: Studies comparing dietary composition among geographical regions, habitats, colonies, and foraging areas.

Methods to study seabird diets: Literature examining conventional dietary methods, stable-isotope analysis, fatty-acid analysis, DNA metabarcoding, and other approaches.

DNA metabarcoding of seabird diets: Studies using molecular methods to identify prey from faecal samples, regurgitates, stomach contents, or other biological materials.

Stable isotopes and seabird diets: Research using isotopic techniques to investigate trophic position, long-term dietary patterns, and marine food-web relationships.

Climate change and seabird diets: Studies examining how changes in temperature, oceanographic conditions, marine productivity, and prey distribution influence seabird feeding ecology.

Fisheries and seabird diets: Research examining fisheries interactions, competition for prey, resource overlap, and the use of fishery discards by seabirds.

The literature included recent publications from 2020-2025 and earlier foundational studies. The search results were subsequently refined by publication relevance, subject area, year of publication, taxonomic focus, and the extent to which individual papers contributed to the objectives of the review.

The literature eventually selected for the review included publications addressing several major dimensions of seabird dietary ecology. These consisted of studies directly identifying prey consumed by seabirds, investigations of differences in diet among species and families, and research examining changes in dietary composition across seasons, habitats, geographical regions, and life-history stages. Some studies were selected because they provided information on the ecological mechanisms underlying seabird dietary variation, including prey availability, oceanographic conditions, climate variability, marine productivity, competition, and fisheries activities.

However, not all papers retrieved for this review focused directly on identifying the prey consumed by seabirds. Some papers focused primarily on seabird foraging behaviour and movement patterns, while others examined trophic relationships and resource partitioning among sympatric seabird species. Several studies investigated the effects of climate change and environmental variability on marine prey, thereby providing indirect but relevant information for understanding changes in seabird diets. Still, other papers examined fisheries interactions, including competition between seabirds and fisheries for shared resources and the consumption of fishery discards.

Some publications focused specifically on methods used to investigate seabird diets. These included conventional techniques such as stomach-content analysis, regurgitate analysis, pellet analysis, prey-remains analysis, and observation of prey delivered to chicks. Other studies examined more recent methods, including stable-isotope analysis, fatty-acid analysis, DNA metabarcoding, and compound-specific isotope analysis. These studies were relevant because they demonstrated that different methods may provide different perspectives on seabird diets. Conventional methods may provide direct evidence of prey consumed but may underestimate prey that are soft-bodied or highly digested, whereas molecular approaches can improve prey identification but may be influenced by methodological and amplification biases. Stable-isotope techniques can provide information on longer-term trophic relationships but generally do not provide the same level of direct prey identification as morphological or molecular dietary analyses.

The results further demonstrated that seabird diets are highly variable among taxa and are primarily composed of fish, cephalopods, crustaceans, krill, zooplankton, and mesopelagic organisms [2, 7, 23]. However, the contribution of these prey groups differed among seabird species, families, and ecological guilds. Some seabirds demonstrated relatively specialised diets, whereas others were more generalist and capable of changing prey use in response to environmental conditions and resource availability term [17]. This information was considered important in evaluating the relationship between dietary flexibility, prey availability, environmental change, and seabird ecological resilience.

A major finding was that studies of seabird diet are not evenly distributed across all geographical regions or seabird groups. Substantial information is available for some temperate, polar, subpolar, and well-studied marine ecosystems, while comparatively less information is available for several tropical and developing coastal regions. Furthermore, important gaps remain concerning the diets of juvenile and immature seabirds, non-breeding populations, long-term dietary changes, quantitative prey consumption, prey energy content, and the consequences of dietary changes for reproduction and survival.

Therefore, although a substantial body of literature was identified, the final studies used in this review were selected based on their relevance to the central objective of understanding what seabirds eat, how seabird diets vary, which environmental and ecological factors influence prey selection, and which conventional and modern methods are available for studying seabird dietary ecology. Information considered relevant from these papers was grouped thematically and synthesized in the subsequent sections of this review.

5 DISCUSSION

5.1 General trends and emerging patterns in the literature

The literature demonstrates that seabird diets are wide-ranging at the level of the entire clade but often strongly structured within species and populations. Foundational reviews emphasize fish, cephalopods and crustaceans as recurrent prey categories, while global analyses show substantial differences among taxa and oceanographic regions [2, 7. 23]. Recent studies increasingly reveal previously under-detected prey diversity through molecular methods. DNA metabarcoding of Arctic seabird faeces detected a wide range of fish and macrofaunal prey in little auks, black-legged kittiwakes and Brünnich's guillemots, including prey diversity that equaled or exceeded that obtained through conventional approaches in some comparisons [13].

The evidence also shows a methodological transition. Earlier work was dominated by morphological identification of stomach contents, regurgitates and pellets, whereas stable isotopes, fatty acids and molecular tools have expanded the temporal and taxonomic dimensions of diet inference [1, 4, 14]. McInnes *et al.* (2016) [18], in a systematic review of 109 albatross diet papers representing 296 study combinations, found that while morphological analyses remained important, stable-isotope approaches had become increasingly prominent. More recent studies demonstrate rapid adoption of DNA metabarcoding and multi-method designs [1, 4, 14]. Table 2 presents the principal dietary categories of seabirds.

Table 2: Principal dietary categories of seabirdsFish as a dominant dietary resource among seabirds

Seabird group	Representative species	Family	Dominant / Recurring prey	Representative ecological pattern	Major drivers of dietary variation	Key literature (Author & Year)
Albatrosses	Wandering albatross (*Diomedea exulans*); Black-browed albatross (*Thalassarche melanophris*)	Diomedeidae	Fish, squid, crustaceans, carrion and fishery discards	Large, highly mobile Procellariiformes that commonly exploit energy-rich fish and cephalopods and may scavenge at the ocean surface.	Oceanographic fronts, prey availability, fisheries, foraging range and breeding stage	Cherel & Klages (1998) [7]; McInnes *et al.* (2016) [18]; Kuepfer *et al.* (2023) [17]
Petrels and shearwaters	Manx shearwater (*Ardenna puffinus*); Sooty shearwater (*Ardenna grisea*); Northern fulmar (*Fulmarus glacialis*)	Procellariidae	Fish, squid, krill, crustaceans and mesopelagic fishes	Highly mobile oceanic foragers with substantial variation in feeding strategy, including surface feeding and pursuit of vertically migrating prey.	Foraging habitat, prey migration, season, diel cycle and oceanographic conditions	Cherel & Klages (1998) [7]; Watanuki & Thiebot (2018) [23]; Carreiro *et al.* (2020) [4]; Austad *et al.* (2025) [1]
Storm-petrels	European storm-petrel (*Hydrobates pelagicus*); Wilson's storm-petrel (*Oceanites oceanicus*)	Hydrobatidae / Oceanitidae*	Small fish, crustaceans, zooplankton, krill and myctophids	Small-bodied surface feeders that exploit patchy, near-surface prey and may use olfactory and oceanographic cues to locate food.	Surface productivity, prey size, season, wind conditions and colony location	Ceia *et al.* (2022) [5]; Carreiro *et al.* (2020) [4]; Watanuki & Thiebot (2018) [23]
Penguins	Emperor penguin (*Aptenodytes forsteri*); King penguin (*Aptenodytes patagonicus*); African penguin (*Spheniscus demersus*)	Spheniscidae	Krill, fish and cephalopods	Wing-propelled pursuit divers that obtain prey throughout the water column; dietary composition varies strongly among species and regions.	Sea-ice conditions, prey depth, prey size, breeding / moult demands and oceanographic conditions	Croxall *et al.* (1997) [10]; Cherel & Kooyman (1998) [8]
Auks and puffins	Common guillemot (*Uria aalge*); Brünnich's guillemot (*Uria lomvia*); Atlantic puffin (*Fratercula arctica*)	Alcidae	Forage fish, zooplankton and crustaceans	Diving seabirds frequently targeting energy-rich schooling fish, particularly during chick provisioning.	Prey size, abundance, colony distance, season and water temperature	Barrett *et al.* (2007) [2]; de Leeuw *et al.* (2024) [13]
Gannets and boobies	Northern gannet (*Morus bassanus*); Blue-footed booby (*Sula nebouxii*)	Sulidae	Mainly pelagic fish, with squid and other marine prey	Visual plunge-divers that exploit surface-associated or schooling prey, often through spectacular high-speed dives.	Fish-school abundance, prey depth, frontal systems, surface conditions and fisheries	Barrett *et al.* (2007) [2]; de la Cruz *et al.* (2022) [12]

Cormorants and shags	Great cormorant (*Phalacrocorax carbo*); European shag (*Gulosus aristotelis*)	Phalacrocoracidae	Fish, crustaceans and other aquatic organisms	Nearshore and continental-shelf diving predators that commonly exploit benthic and demersal as well as pelagic fish.	Local fish assemblage, depth, habitat structure, season and prey accessibility	Barrett *et al.* (2007) [2]
Terns	Common tern (*Sterna hirundo*); Arctic tern (*Sterna paradisaea*); Roseate tern (*Sterna dougallii*)	Laridae	Small pelagic fish, crustaceans and other small marine prey	Often capture individual prey items and transport them to chicks, making prey-delivery observations particularly useful.	Prey size, schooling behavior, colony distance, season and availability of small pelagic fish	Barrett *et al.* (2007) [2]
Gulls	Herring gull (*Larus argentatus*); Great black-backed gull (*Larus marinus*)	Laridae	Fish, molluscs, crustaceans, carrion, fishery discards, birds and terrestrial food	Highly opportunistic generalists capable of exploiting marine, intertidal, terrestrial and anthropogenic food resources.	Prey scarcity, fisheries, urbanization, waste availability, season and habitat	Barrett *et al.* (2007) [2]; Kuepfer *et al.* (2023) [17]
Skuas	Great skua (*Stercorarius skua*); Brown skua (*Stercorarius antarcticus*)	Stercorariidae	Fish, seabirds, carrion, eggs, krill and fishery discards	Predatory and kleptoparasitic seabirds with broad diets; may obtain food directly or by forcing other seabirds to surrender prey.	Availability of seabirds, fisheries, carrion, marine prey and breeding-colony activity	Barrett *et al.* (2007) [2]; Croxall *et al.* (1997) [10]

Fish are the most recurrent major prey category across many seabird lineages, but "fish-eating" does not imply dietary uniformity. Seabirds exploit prey that differ in size, depth, schooling behavior, lipid content and accessibility. Forage fish such as anchovies, sardines, herring, sprat, sand eels and capelin can be particularly important because they aggregate into dense schools and can provide high energetic returns [9]. In south-western African waters, anchovy represented about 31% of seabird food consumption in the regional model, followed by pelagic goby and hake, illustrating how a few abundant prey groups can dominate regional seabird energy intake [9].

Recent DNA metabarcoding of Manx shearwater faeces identified European sprat, blue whiting, Atlantic herring, northern rockling, sandeel and a cottoid fish, demonstrating that molecular methods can resolve prey that may be difficult to identify from degraded remains [21]. A complementary buccal-swab study of Manx shearwaters and northern fulmars detected 14 fish taxa, with amplification success differing strongly between species and sampling stages, illustrating both the power and sampling sensitivity of molecular diet inference [14].

5.2 Cephalopods and the importance of squid in seabird diet

Cephalopods, especially squid, are a major component of the diet of many Procellariiformes. Their importance is partly explained by the ability of some seabirds to forage over deep or oceanic habitats and exploit prey that become accessible near the surface during diel vertical migration. Albatrosses in particular are recognized as consumers of fish, cephalopods and, in some species, crustaceans [7, 18].

Squid beaks are durable and can remain in the digestive tract for long periods, so repeated recovery of beaks may overestimate the contribution of cephalopods if retention is not considered [2]. Barrett *et al.* (2007) [2] emphasized that differential digestion and retention of hard parts are major sources of bias in morphological diet studies. This demonstrates why prey occurrence should not automatically be interpreted as proportional dietary biomass.

5.3 Krill, zooplankton and mesopelagic prey

Krill and other zooplankton are particularly important in polar and subpolar food webs. At South Georgia, five of six simultaneously studied seabird species relied on Antarctic krill as their principal food during chick rearing, with krill accounting for 39-98% of diet mass in those species; the grey-headed albatross instead relied predominantly on the squid *Martialia hyadesi* [10]. Thus, even within the same ecosystem, dietary segregation can emerge from differences in foraging range, feeding method and prey selection.

Mesopelagic myctophid fishes constitute another important but historically under-recognized prey pathway. A global review covering stomach-content analyses from 228 seabird species found that myctophids were particularly important for penguins, Procellariidae and storm-petrels, especially in oceanic or shelf-slope habitats and among nocturnal foragers [23]. This has major implications because myctophids link surface productivity with deeper ocean food webs and may become increasingly relevant as seabirds alter foraging strategies in response to changing surface prey distributions [23].

5.4 Crustaceans and benthic invertebrates

Crustaceans occupy an intermediate position between specialist and opportunistic prey categories. Krill are central to several Antarctic seabirds, while amphipods and other crustaceans can supplement diets of prions, penguins and other planktivorous species [13]. Coastal seabirds, gulls and some diving birds may also consume benthic crustaceans and molluscs. Their contribution is often underestimated when studies focus on fish remains because soft-bodied or small invertebrates may be rapidly digested or poorly represented in pellets [13]. DNA metabarcoding can partly address this blind spot by detecting taxonomic signatures that are difficult to recover morphologically [13].

5.5 Dietary specialization versus flexibility

The literature supports a continuum from relative specialization to marked generalism. Specialization may confer efficiency when a high-quality prey resource is predictably available, but it can create vulnerability when prey abundance, distribution or phenology changes. Generalists can buffer environmental variability by switching among prey, but dietary flexibility does not necessarily guarantee demographic resilience. In the Falkland Islands black-browed albatrosses, fishery discards increased when natural foraging conditions were poor, yet switching to discards did not compensate for poor natural foraging conditions over the longer term [17].

Diet composition should therefore be evaluated together with prey size, energetic density, lipid content and the proportion of prey delivered to chicks. A prey item can be numerically dominant but energetically less important than a less abundant, lipid-rich alternative. Consequently, occurrence, biomass and energetic contribution should be reported as separate dietary metrics.

5.6 Spatial and temporal variation of seabird diet

Seabird diets vary across geographic scales because prey communities and oceanographic regimes differ among shelves, fronts, upwelling systems, polar waters and oligotrophic gyres. Within regions, diet can vary among colonies separated by relatively short distances. At South Georgia, differences among seabird species consuming the same broad krill resource were associated with spatial and behavioral segregation [10]. In the Gulf of Cádiz, seabird distributions tracked prey abundance, indicating that fine-scale prey fields may explain predator aggregation better than generalized environmental descriptors [12].

Diel changes are especially important for myctophid-feeding seabirds because many mesopelagic fishes migrate toward the surface at night. Seasonal variation also arises from breeding, chick provisioning, moult and migration. Adults may choose prey differently from adults provisioning chicks, and non-breeding birds may exploit oceanic prey fields that are inaccessible to colony-based sampling.

Methods used to determine seabird diet

Methodologies for investigating the diet of seabirds has evolved from direct inspection of digestive contents and prey delivery toward an integrated toolbox. Figure 3 and Table 3 illustrate the trade-off between taxonomic resolution, ecological context, temporal integration and invasiveness.

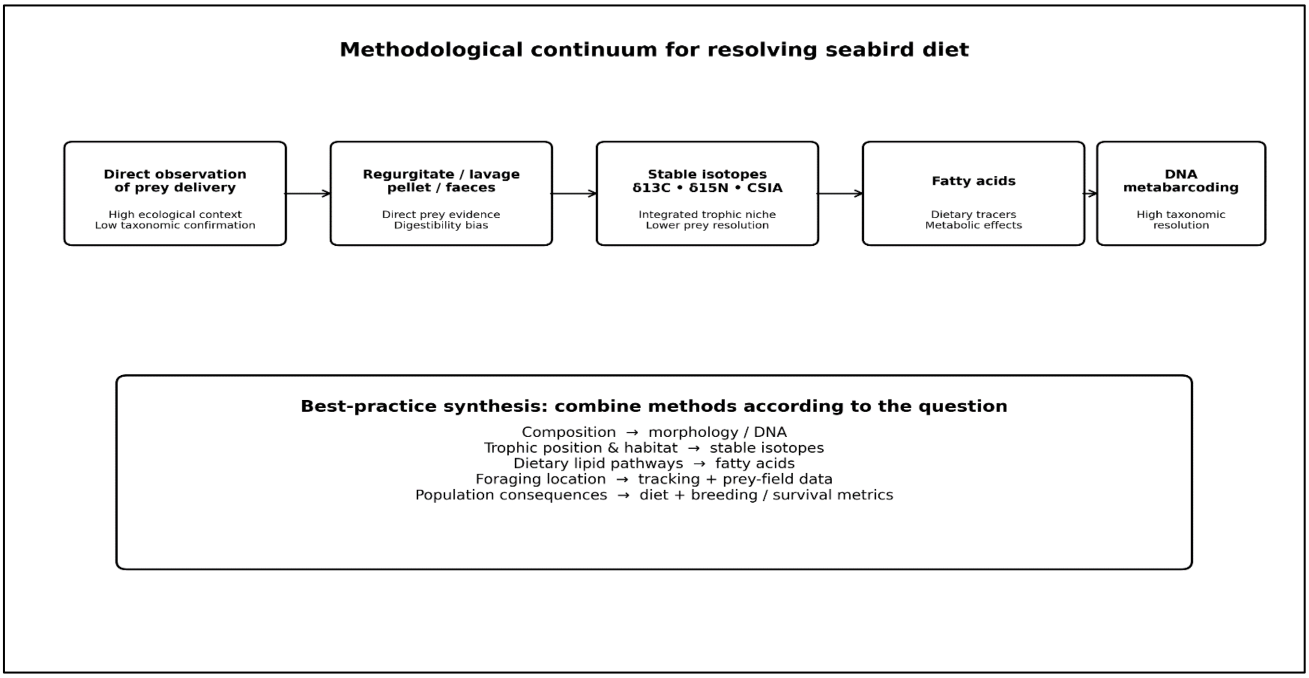

Figure 3: Methodological continuum for assessing seabird diet

Table 3: Methods used to investigate the diet of seabirds based on literature

Method	Strengths	Principal biases/limitations	Best use	Representative literature (Author & Year)
Stomach contents / necropsy	Direct prey evidence; prey size and mass can be estimated.	Invasive/lethal; digestion and retention biases; carcasses may be non-representative.	Detailed diet composition when ethical and permitted.	Barrett *et al.* (2007) [2]; McInnes *et al.* (2016) [18]
Regurgitate / lavage	Often provides identifiable prey with limited invasion; repeatable at colonies.	Disturbance; incomplete emptying; differential regurgitation; short time window.	Breeding-season prey composition and chick provisioning.	Barrett *et al.* (2007) [2]

Pellets	Non-invasive; inexpensive; large sample sizes; useful for long-term monitoring.	Hard-part preservation bias; species attribution problems; prey-size uncertainty.	Cormorants, gulls, skuas and pellet-producing taxa.	Barrett *et al.* (2007) [2]
Faecal remains	Non-invasive and repeatable.	Rapid digestion can erase soft prey; usually poor prey-size information.	Long-term monitoring and molecular sampling.	Barrett *et al.* (2007) [2]; de Leeuw *et al.* (2024) [13]
Direct observation / prey delivery	Minimal disturbance; high behavioral context.	Taxonomic misidentification; observer error; limited to visible prey.	Auks, terns and species carrying discrete prey.	Barrett *et al.* (2007) [2]
Stable isotopes	Integrates assimilated diet; estimates trophic position and habitat.	Requires baseline knowledge; low prey taxonomic resolution; tissue turnover varies.	Trophic position, niche breadth and seasonal shifts.	Hobson *et al.* (1994) [15]; McInnes *et al.* (2016) [18]
Compound-specific isotopes	Improves trophic-position inference and reduces some baseline problems.	Costly; specialized laboratory methods; calibration needed.	Fine-scale trophic position and seasonal comparisons.	Wu *et al.* (2018) [25]; Quillfeldt & Masello (2020) [20]
Fatty acids	Useful trophic tracers; can indicate spatial/temporal diet patterns.	Metabolic modification; prey lipid variability; mixing assumptions.	Dietary pathways and prey-source discrimination.	Williams & Buck (2010) [24]
DNA metabarcoding	High taxonomic resolution; detects degraded/soft prey; minimally invasive sampling possible.	PCR/primer bias; reference-library gaps; read abundance is not automatically biomass.	Prey inventories and difficult-to-identify prey.	de Leeuw *et al.* (2024) [13]; Evans *et al.* (2025) [14]
Multi-method integration	Combines temporal, taxonomic and trophic information.	Higher cost and analytical complexity.	Robust ecological inference and monitoring.	Ceia *et al.* (2022) [5]; Austad *et al.* (2025) [1]

5.7 Conventional methods

Conventional approaches remain indispensable because they provide direct evidence of prey identity, size and, in favorable circumstances, biomass. Regurgitated samples from gannets, cormorants, gulls and terns can contain relatively intact prey and may be sampled repeatedly through the breeding season [2]. However, the amount regurgitated is not equivalent to meal size, and prey that differ in digestibility or retention can be systematically over- or underrepresented. Pellets are similarly more reliable for identifying diet than for estimating absolute consumption [2].

These biases can change ecological conclusions. If a hard-bodied prey item persists longer in the digestive tract than a soft-bodied prey, frequency-of-occurrence analysis may suggest that it is more important than it actually is. Conversely, highly digestible prey may disappear from morphological samples and appear unimportant. Thus, prey frequency, biomass, occurrence and energetic contribution are distinct response variables and should not be treated as interchangeable.

5.8 Stable isotopes and trophic position

Stable isotope analysis provides a different perspective because it reflects assimilated resources rather than only recently ingested material. Nitrogen isotope ratios ($\delta 15N$) can indicate relative trophic position, while carbon isotopes ($\delta 13C$) can help distinguish broad inshore/offshore or habitat-associated feeding. Hobson *et al.* (1994) [15] showed that stable nitrogen patterns across 22 marine bird species broadly agreed with conventional trophic interpretations while also suggesting greater importance of lower-trophic prey for some species.

Stable isotope analysis is valuable for birds that forage far from colonies, but interpretation requires knowledge of baselines, discrimination factors and tissue turnover. Compound-specific isotope analysis can improve trophic-position estimates and reduce some ambiguity [20, 25].

5.9 Fatty-acid analysis

Fatty-acid signatures provide another biochemical window into diet because dietary lipids can be incorporated into consumer tissues. Williams & Buck (2010) [24] emphasized their potential to identify key prey and resolve spatial and temporal variation. However, consumer lipid profiles are also influenced by life-history stage, diet quality and physiological condition. Quantitative interpretation therefore requires prey-specific calibration and explicit treatment of metabolic modification.

5.10 DNA Metabarcoding: a major methodological transition

DNA metabarcoding has become one of the most important recent developments in seabird diet research. It can identify multiple prey taxa from faeces, regurgitates or other biological material even when prey is too degraded for reliable morphological identification. Recent molecular studies of seabird regurgitate and faeces have demonstrated that DNA metabarcoding can recover broad fish, squid and macrofaunal diversity that is difficult to resolve morphologically; Arctic applications using COI and 18S markers provide a clear example [13].

Recent applications also show that molecular success depends on sample timing and sample type. Siddiqi-Davies *et al.* (2025) [21] identified six fish species from Manx shearwater faecal samples, but only 19 of 153 samples yielded sufficient DNA for prey identification. Evans *et al.* (2025) [14] found prey DNA in 68% of Manx shearwater samples but only 28% of northern fulmar samples. These results demonstrate that metabarcoding is powerful but not bias-free.

The principal quantitative limitation is that sequence-read abundance cannot automatically be converted into prey biomass because primer mismatch, PCR effects, prey DNA copy number, digestion and other biological and technical processes can alter sequence representation [22]. The most defensible current use of metabarcoding is therefore to improve prey detection and taxonomic resolution, while quantitative interpretation should be strengthened by calibration experiments, mock communities, standardized sampling and independent methods.

5.11 Integrated approaches

The strongest evidence increasingly comes from combining methods. DNA metabarcoding can identify prey taxa; stable isotopes can estimate trophic position and habitat; fatty acids can provide biochemical source information; tracking can establish where feeding occurs; and conventional observations can provide prey size and behavioral context. Carreiro *et al.* (2020) [4] demonstrated the value of combining metabarcoding, stable isotopes and tracking in storm-petrels, while Austad *et al.* (2025) [1] combined metabarcoding and stable isotopes to compare Mediterranean shearwaters. The emerging consensus is therefore methodological complementarity rather than methodological replacement.

5.12 Fisheries and fishery discards

Fisheries can influence seabird diet through two opposing pathways: depletion or competition for natural prey, and supplementation through discards or offal. Scavenging seabirds may benefit from fishery waste, but dependence on vessels can increase bycatch risk, alter foraging behavior and expose birds to nutritionally suboptimal prey. Kuepfer *et al.* (2023) [17] found that black-browed albatrosses increased discard use when natural foraging conditions were poor, yet switching to discards did not compensate for poor natural foraging conditions over the longer term.

Competition should therefore be evaluated using spatial and temporal overlap in prey use rather than assuming that similar diets automatically indicate direct competition [16]. Diet studies become substantially more informative when linked with fishery catch/discard data, prey surveys and seabird movement data.

5.13 Climate change and dietary change

Climate change can alter seabird diet through changes in prey abundance, phenology, distribution, size structure and energetic quality [3]. Warming can shift cold-water forage fish, alter stratification and modify the timing of plankton blooms. Marine heatwaves can produce abrupt food-web changes. Recent modelling in Britain and Ireland projects declines in seabird abundance under climate change, reinforcing the need to understand dietary mechanisms rather than treating population responses as purely demographic [11].

Dietary flexibility has limits because a replacement prey may differ in energy density or nutritional value. Consequently, future monitoring should record prey quality in addition to prey identity.

5.14 Plastic and non-food ingestion as a dietary contaminant pathway

Plastic is not a conventional component of diet, but it is increasingly inseparable from feeding ecology because plastics can enter the digestive tract alongside natural prey. Procellariiformes are particularly exposed because many forage at the ocean surface. Charlton-Howard *et al.* (2023) [6] documented extensive fibrosis associated with plastic exposure in the proventriculus of flesh-footed shearwater fledglings and described the condition as plasticosis. Such evidence indicates that dietary contamination can produce physiological consequences distinct from simple reductions in prey availability. Table 4 presents key studies, the method employed to assess bird diet, the principal finding of each study and interpretive significance.

Table 4: Synthesis of key studies

Author(s), year	Taxon / Context	Region	Method	Principal finding	Interpretive significance
Croxall *et al.* (1997) [10]	Penguins, petrels, albatrosses	South Georgia	Morphological diet analysis	Krill dominated five of six species; grey-headed albatrosses emphasized squid.	Dietary segregation can arise despite shared prey fields.
Hobson *et al.* (1994) [15]	22 marine bird species	NE Pacific	δ13C and δ15N	Stable N tracked trophic position; C differentiated broad habitat use.	Biochemistry can complement conventional diet studies.
Barrett *et al.* (2007) [2]	Multiple seabird taxa	Global	Methodological review	All methods contain biases; breeding-season bias is pervasive.	Standardization and complementary sampling are essential.
McInnes *et al.* (2016) [18]	Albatrosses	Global	Systematic review	109 papers representing 296 study combinations; major spatial/temporal gaps persisted.	Long-term standardized monitoring is needed.
Watanuki & Thiebot, (2018) [23]	228 seabird species	Global	Review of stomach contents	Myctophids important especially in penguins, Procellariidae and storm-petrels.	Mesopelagic prey are under-recognized.
Carreiro *et al.* (2020) [4]	Storm-petrel	Atlantic	Metabarcoding + isotopes + tracking	Integrated methods resolved trophic ecology across space and time.	Method integration improves ecological inference.
de la Cruz *et al.* (2022) [12]	Three seabird species	Gulf of Cádiz	At-sea distribution + prey surveys	Distribution related strongly to prey abundance.	Prey fields are proximate drivers of predator distribution.
Kuepfer *et al.* (2023) [17]	Black-browed albatross	Falkland Islands	Stomach contents + breeding data	Discard use increased under poor natural foraging but did not compensate long term.	Dietary flexibility has demographic limits.
de Leeuw *et al.* (2024) [13]	Kittiwake, guillemot, little auk	Svalbard	Faecal DNA metabarcoding	High diversity of fish and macrofaunal prey detected.	Non-invasive molecular monitoring is promising.
Austad *et al.* (2025) [1]	Scopoli's and Yelkouan shearwaters	Mediterranean	DNA metabarcoding + stable isotopes	38 prey families detected; strong dietary overlap.	Integrated methods reveal niche overlap.

Evans *et al.* (2025) [14]	Manx shearwater, northern fulmar	Western Europe	Buccal swab + DNA metabarcoding	Prey DNA success differed between species.	Sampling stage and species biology affect detectability.
Siddiqi-Davies *et al.* (2025) [21]	Manx shearwater	UK	Faecal DNA metabarcoding	Six fish species identified; low sample-level success.	Molecular studies require careful timing and sampling design.

The central findings indicate that seabird diet is best characterized as a dynamic trophic strategy rather than a fixed species trait. Fish, squid, krill, mesopelagic fishes and crustaceans form the core of marine prey use, but the relative importance of each category changes with morphology, foraging depth, habitat, season and prey availability. The most important distinction is between broad dietary capacity and realized diet: a seabird may be capable of consuming many prey types but exploit only a subset under particular environmental conditions.

The literature also demonstrates that dietary composition is strongly linked to spatial scale. Regional prey communities create the opportunity set, but fine-scale prey aggregation determines where birds forage. The finding that seabird distributions can track prey abundance more closely than broad oceanographic predictors supports a mechanistic view in which oceanography matters largely through its effects on prey fields [12]. Predictive models should therefore incorporate prey biomass, size structure and energetic quality wherever possible.

Another major finding concerns dietary specialization. Specialization can be advantageous when prey is abundant and predictable, but it creates exposure to mismatch when environmental conditions change. Generalists may respond to prey scarcity by switching resources, but such switching can have hidden costs. The Falkland Islands albatross evidence shows that access to fishery discards did not fully compensate for poor natural foraging conditions [17]. Dietary flexibility should therefore be interpreted as a potential buffering mechanism, not as proof of resilience.

5.15 Methodological implications

The review reveals a persistent mismatch between the question researchers want to answer and the methods they use to get these answers. Morphological methods are strongest for direct prey identification and size estimation but weak for rapidly digested prey and long-term diet. Stable isotopes integrate diet over longer periods but usually cannot identify individual prey taxa. Fatty acids provide source information but are affected by metabolism. DNA metabarcoding offers exceptional taxonomic sensitivity but currently has weaker quantitative calibration. Tracking reveals where a bird searches for food but does not, by itself, identify what it consumes [5].

The most scientifically defensible design is question-driven integration and if the objective is prey identity, metabarcoding plus conventional morphology is appropriate. When the objective is trophic position, stable isotopes or compound-specific isotopes should be emphasized. However, if the objective is dietary lipid pathways, fatty acids are useful. If the objective is linking prey use to habitat, diet analysis should be coupled with tracking and prey-field surveys. This approach follows the complementary-method principle emphasized in modern seabird trophic reviews [5].

Implications of seabird diet for seabird conservation

Dietary information has direct conservation value because it identifies the resources upon which populations depend. Conservation planning that protects nesting colonies without protecting critical feeding areas may therefore be incomplete. Marine Protected Areas, fisheries regulations and spatial planning should consider prey distributions and seabird foraging ranges.

For threatened albatrosses and petrels, diet is especially important because fishery interactions can simultaneously change prey availability, provide artificial food subsidies and increase mortality risk. Climate adaptation likewise requires diet monitoring because dietary shifts may provide earlier evidence of altered prey fields than demographic indicators.

5.16 Research gaps

In systematic reviews it is important to identify research gaps because it presents scope and opportunities to identify new areas of study and add new information to existing knowledge, and reduces the likelihood of repeating work that has already been done. In the context of seabirds and their diets, identifying research gaps maybe helpful in identifying inadequately studied seabird species, prey groups, ecological processes and geographic regions. Understanding these research areas could be useful for developing targeted investigations to better understand seabird feeding habits and dynamics of marine food webs.

Based on the findings of this review, the following research gaps were identified:

- Non-breeding-season diet remains poorly documented because many seabirds disperse over large oceanic areas, making direct sampling difficult [2].
- Geographic coverage is uneven. The North Atlantic, Antarctic and selected temperate systems are relatively well represented compared with many tropical and subtropical regions.
- Prey quality is underreported since many studies identify prey occurrence without quantifying energetic density, prey size or nutritional value.
- Molecular methods require calibration. Standardized sampling windows, validated primers, mock communities and improved regional reference libraries are needed.
- Long-term methodological continuity is essential. Changes in analytical method can create apparent dietary trends that actually reflect changes in detectability [18].
- Integrated datasets remain uncommon. Linking diet with prey abundance, fisheries, tracking, oceanography and demographic outcomes is necessary to distinguish dietary response from dietary cause.

6 CONCLUSIONS

The evidence garnered from this review demonstrates that seabird diets are highly diverse and dynamic, reflecting complex interactions among species-specific foraging adaptations, prey availability, environmental conditions, and anthropogenic pressures. Fish, cephalopods, crustaceans, krill, zooplankton, and mesopelagic organisms constitute the principal dietary resources, but their relative importance varies considerably among families, species, geographical regions, seasons, and life-history stages. This variation is further evidence that seabirds should not be treated as a single trophic group; rather, differences in morphology, body size, diving capacity, foraging range, prey-capture behaviour, and habitat use determine access to particular prey resources. Further, it should be noted that dietary flexibility may allow some species to respond to changing prey conditions, although a shift in diet does not necessarily indicate successful adaptation. In some cases, dietary changes may instead reflect reduced availability of preferred or nutritionally superior prey, with potential consequences for body condition, reproduction, survival, and population persistence.

Critically, this review establishes seabird diet as an important ecological link between changes in marine environments and responses at higher trophic levels. Oceanographic conditions, including temperature, productivity, currents, and other environmental processes, influence prey abundance and distribution, which subsequently affect prey accessibility, seabird foraging behaviour, and dietary composition. Seabird diet can therefore provide valuable insight into broader changes within marine food webs. However, the relationship is not always straightforward, since changes in diet may result from multiple interacting processes, including prey switching, competition, fisheries activities, climate variability, and differences in individual foraging strategies. The most informative interpretation of dietary change must therefore extend beyond identifying prey taxa and incorporate information on prey availability, prey quality, environmental conditions, foraging movements, reproductive performance, and population trends. This strengthens the value of seabird diet research as a tool for ecosystem monitoring while also demonstrating the limitations of interpreting dietary data in isolation.

Despite considerable advances in seabird trophic ecology, the available literature remains geographically and methodologically uneven. Important gaps persist regarding diets outside the breeding period, the trophic ecology of juvenile and immature birds, quantitative estimates of prey consumption, the energetic value of prey, and long-term responses to environmental change. Much of the evidence has originated from temperate, polar, subpolar, and relatively well-studied marine systems, creating uncertainty about the extent to which these findings can be generalised to tropical ecosystems. This represents a significant limitation because tropical and Neotropical marine environments differ substantially in oceanography, seasonality, prey communities, coastal processes, and human pressures. There is consequently a need for greater research throughout the Neotropics to determine whether the ecological relationships identified in well-studied regions operate similarly in tropical systems or whether region-specific trophic patterns exist.

This geographical gap is particularly relevant to Guyana, where there is a clear need for baseline research linking coastal and marine birds to the prey resources and food webs upon which they depend. While Guyana's coastal environment supports diverse resident and migratory bird communities, comparatively limited published information is available on the detailed diets, trophic positions, seasonal prey use, and foraging ecology of marine-associated birds. This absence of dietary data represents an important scientific research gap because Guyana's coastal ecosystems are influenced by distinctive interactions among riverine inputs, estuarine and coastal processes, mangrove-associated habitats, muddy intertidal systems, and the tropical Atlantic. Without systematic dietary information, it remains difficult to determine how changes in fisheries, coastal development, pollution, climate variability, habitat modification, and other emerging pressures may influence prey availability and subsequently affect bird populations. Guyana therefore represents an important opportunity for future research to establish the ecological links between environmental conditions, prey assemblages, avian diet, foraging behaviour, and population responses, thereby contributing evidence currently underrepresented in the global seabird literature.

Overall, the review highlights the need for future and continued seabird research, particularly in Guyana and the wider Neotropics, to adopt integrated and long-term approaches rather than relying solely on descriptive accounts of prey occurrence. Combining conventional dietary analysis with DNA metabarcoding, stable-isotope techniques, biologging, seasonal monitoring, and concurrent assessments of prey and environmental conditions would provide a more complete understanding of seabird trophic ecology.

Such research should prioritise comparisons among species, habitats, seasons, and life-history stages and should investigate how dietary patterns respond to climate variability, fisheries, pollution, and changing marine productivity. Addressing these gaps would not only improve knowledge of what seabirds consume but, more importantly, clarify how changes at lower trophic levels are transmitted through marine food webs to top predators. Consequently, expanded research in Guyana and the Neotropics is essential both to correct the present geographical imbalance in seabird dietary research and to establish the baseline ecological knowledge required for effective monitoring, conservation, and management of tropical marine ecosystems.

Recommendations

Based on the findings of this review, the following recommendations are made:

- Adopt standardized reporting of prey taxonomic resolution, prey size, mass, frequency of occurrence, biomass contribution and sampling effort.
- Prioritize non-invasive or minimally invasive sampling for threatened seabirds and use dead birds opportunistically rather than designing studies around lethal sampling.
- Expand sampling beyond breeding colonies and breeding seasons using tracking, autonomous sampling, remote observation and molecular approaches.
- Develop regional DNA reference libraries and validated metabarcoding protocols for marine prey taxa, especially in tropical and poorly sampled oceans.
- Couple seabird diet data with prey abundance, prey energy density, fisheries catch/discard data and oceanographic observations.
- Treat non-food ingestion, including plastics, as a parallel dietary-health variable rather than an incidental observation.
- Use at least two complementary diet research methods whenever feasible, particularly pairing conventional prey identification with stable isotopes or DNA metabarcoding.
- Establish long-term monitoring sites using consistent methods so genuine ecological change can be separated from changes in analytical methodology.

Limitations of the Review

This review is a systematic thematic synthesis rather than a quantitative meta-analysis. The heterogeneity of seabird taxa, sampling methods, response metrics and geographic coverage prevented formal pooling of dietary effect sizes. The search was designed around peer-reviewed English-language literature and may underrepresent relevant non-English studies. Database interfaces are dynamic and the present synthesis does not claim that its thematic search recovered every published seabird diet study. These limitations should be considered when interpreting apparent differences in the volume of evidence among taxa or regions.

STATEMENTS ON COMPLIANCE WITH ETHICAL STANDARDS

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors certify that this submission is original work and is not under review at any other publication. The authors hereby declare that this manuscript does not have any conflict of interest.

Statement of informed consent

The authors declare that informed consent was obtained from all individual participants included in the study. All work utilized in this study was fully cited and referenced so authors of prior researches are given their due credentials for their work.

Data Availability

Data will be made available on request.

Credit Authorship Contribution Statement

Lakhnarayan Kumar Bhagarathi- Conceptualization, methodology, literature search and screening, data curation, formal analysis, writing - original draft, writing - review and editing; Aarif Baksh- Conceptualization, methodology, literature search and screening, data curation, formal analysis, writing - original draft, writing - review and editing; Phillip N. B. Da Silva - Conceptualization, methodology, literature search and screening, data curation, formal analysis, writing - original draft, writing - review and editing; Vandevi Bhikam - Conceptualization, methodology, literature search and screening, data curation, formal analysis, writing - original draft, writing - review and editing; Ferial Pestano - Conceptualization, methodology, literature search and screening, data curation, formal analysis, writing - original draft, writing - review and editing; Sushmita Kalika-Singh - Conceptualization, methodology, literature search and screening, data curation, formal analysis, writing - original draft, writing - review and editing; Yunita Arjune - Conceptualization, methodology, literature search and screening, data curation, formal analysis, writing - original draft, writing - review and editing

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