ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

DOCTORAL THESIS NO. 2025:32
FACULTY OF NATURAL RESOURCES AND AGRICULTURAL SCIENCES

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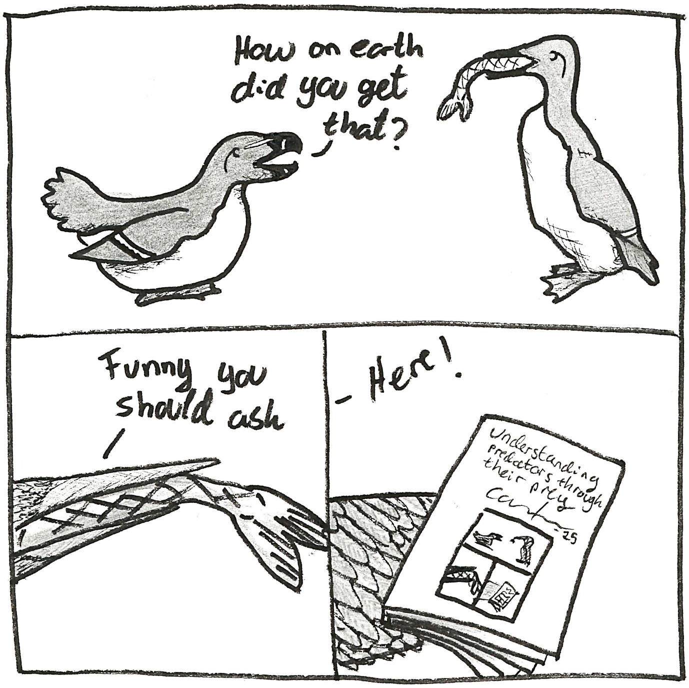

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OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS
Uppsala 2025

Acta Universitatis Agriculturae Sueciae
2025:32

Cover: “Long story long” by Astrid A. Carlsen, 2025.

ISSN 1652-6880
ISBN (print version) 978-91-8046-467-3
ISBN (electronic version) 978-91-8046-517-5
https://doi.org/10.54612/a.2dpu51qvq6

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Print: SLU Grafisk service, Uppsala 2025

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Abstract

Seabirds are the most threatened of all birds, with half of all populations being on decline due to anthropogenically driven changes to their environment. Many of the issues affecting seabirds are directly or indirectly tied to their foraging, but tracking seabirds' food resources has been challenging due to their extensive ranges. With novel technologies, fine-scale information on prey distributions is increasingly accessible, enabling new insights into predator-prey interactions. In this thesis, I contribute with knowledge on how diving seabirds utilize and respond to dynamic prey landscapes, with a particular focus on niche divergence among closely related predators. I explored the ecological consequences of predator adaptations in relation to foraging behaviour, environmental variability, and the consequences of adaptations to seabirds' conservation on a global scale. I first investigated the utility of hydroacoustic prey data monitored using an unmanned surface vehicle from April-July in 2019-2023 and predicted the spatiotemporal distribution of the small pelagic fish community. Then, I used biologging (GPS and dive loggers) of two diving seabirds, common guillemot (*Uria aalge*) and razorbills (*Alca torda*), to investigate their responses to diel distribution patterns of prey and found that their niche partitioning could be traced to divergent responses to prey distribution patterns and sensitivity to light levels. I further showed how common guillemots were dependent on predictable and stable foraging sites, but with clear responses in distance moved based on prey abundance and depth of site indicating active search. I finally zoomed out to the world's seabirds and demonstrated how species-specific potential foraging range could be predicted by morphometrics and flying mode. This relationship was used to conclude that only 1% of the global seabirds' foraging habitats during their breeding season are fully protected. By developing new methods and linking fine-scale behavioural responses to prey with broad-scale, trait-based conservation frameworks, this thesis provides a multiscale perspective on how foraging ecology in predators relates to marine ecosystems and prey fields. Such insights can inform biologically grounded conservation strategies for wide-ranging marine predators in a rapidly changing ocean.

Keywords: Predator-prey, spatiotemporal distribution, hydroacoustics, biologging, niche, diel behaviour, foraging behaviour, conservation

Förstå rovdjur genom deras byte

Abstract

Många av de problem som påverkar sjöfåglar är direkt eller indirekt kopplade till deras födosöksbeteende, men att spåra sjöfåglarnas födoresurser har varit utmanande på grund av eras omfattande utbredningsområde. Med ny teknik kan mer information om finskaliga variationer i bytesfördelningar erhållas. I denna avhandling utökar jag kunskapsluckan i hur dykande sjöfåglar reagerar på dynamiska bytesdjurslandskap genom förutsägbarhet och tillgänglighet, med särskilt fokus på nischdivergens bland närbesläktade rovdjur. Jag utforskar de ekologiska konsekvenserna av rovdjursanpassningar i relation till födosöksbeteende, miljövariationer, och konsekvenserna för bevarande på global skala. Jag undersökte först funktionaliteten i ekolod data som samlades med en autonom seglande drönare under perioden april-juli i 2019–2023 och gjorde en rumslig-tidsmässig bytesfördelningsmodell. Sedan använde jag spårningsdata (GPS och djupmätare) från två dykande havsfåglar, sillgrissla (*Uria aalge*) och tordmule (*Alca torda*) för att undersöka mönster i predatorers tidsmässig bytesfördelning, och fann att nischdivergens härrör till olika distributionsmönster och ljuskänslighet. Jag visar vidare hur sillgrisslor är beroende av förutsägbara och stabila födosöksplatser och tydligt svarar på variation i bytesförekomst och havsbottnens djup, vilket indikerar aktivt sökbeteende, antingen för en specifik bytestyp eller livsmiljö. Jag tog sedan mig an världens sjöfåglar och visade hur deras födosöksområden kunde förutsägas med enkla analyser av morfometri, vilka användes för att dra slutsatsen att endast 1% av sjöfåglarnas potentiella livsmiljöer skyddas under deras häckningsperiod. Genom att koppla finskaliga beteendemässiga reaktioner på bytesdjur till bredskaliga, egenskapsbaserade bevaranderamverk, ger denna avhandling ett flerskaligt perspektiv på hur födosöksekologi hos rovdjur relaterar till marina ekosystem och bytesdjursfält. Sådana insikter kan ligga till grund för biologiskt grundade bevarandestrategier för ett brett spektrum av marina rovdjur i ett snabbt föränderligt hav.

Keywords: Predator-bytesdjur, spatiotemporal distribution, hydroakustik, biologgning, nisch, dielt beteende, födosöksbeteende, bevarande

Preface

Don’t take it too seriously, it will all be old news soon.

Dedication

Til Sørfolda.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Astrid A. Carlsen, Michele Casini, Francesco Masnadi, Olof Olsson, Aron Hejdström, Jonas Hentati-Sundberg (2024). Autonomous data sampling for high-resolution spatiotemporal fish biomass estimates. Ecological Informatics 84, 102852. https://doi.org/10.1016/j.ecoinf.2024.102852.

II. Astrid A. Carlsen, Claire Saraux, Elin Andersson Sjöholm, Camilla Menestrina, Mica Bohacek, Natalie Isaksson, Michele Casini, Samantha Patrick, Jonas Hentati-Sundberg. Diel prey distribution patterns shape predators shared strategies and niche divergence (manuscript).

III. Astrid A. Carlsen, Quentin Queiros, Michele Casini, Samantha Patrick, Jonas Hentati-Sundberg. Relying on Predictable Prey: A Deep Diving Forager in a Spatially Variable System (manuscript).

IV. Quentin Queiros, Astrid A. Carlsen, Bethany Clark, David Grémillet, Kyle Elliott, Jacob Gonzáles-Solís, Stephen Votier, Jonathan A. Green, Samantha Patrick, Steffen Oppel, Thomas A. Clay, John Arnould, Jonas Hentati-Sundberg. Alarmingly poor global protection of seabird foraging areas (manuscript).

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The contribution of Astrid A. Carlsen to the papers included in this thesis was as follows:

I. Conceptualization, fieldwork and data collection, public data sourcing, data preparation, investigation and statistical work incl. modelling, wrote original draft, main and corresponding author in publishing process.

II. Conceptualization, fieldwork and data collection, data preparation, investigation and statistical work incl. modelling, wrote original draft, main author and corresponding author in submission process.

III. Conceptualization, fieldwork and data collection, public data sourcing, data preparation, investigation and statistical work incl. modelling, wrote original draft, main author.

IV. Fieldwork and data collection, conceptualization and methodological advisor, discussion framing, initial rounds of manuscript editing, second author.

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Abbreviations

USV	Unmanned Surface Vehicle
BDCr	Bottom-to-Dive Cycle ratio
Ch.	Chapter
Guillemot	Common guillemot (*Uria aalge*)
Stickleback	Three-spined Stickleback (*Gasterosteus aculeatus*)
CPF	Central Place Foraging

1. Background

Foraging behaviour reflects adaptations to environmental conditions and selective pressures over time. Understanding predator foraging requires examining prey ecology, as this provides context for predator adaptations, allows investigation into predator responses, and helps identify which prey traits influence the predators under natural conditions, and how. This framework reveals how extensive anthropogenic impacts on animals' energy allocation are, thus the future prospective for biodiversity (Marske *et al.*, 2023). Marine ecosystems are undergoing rapid transformations due to interacting effects of climate change and commercial fishery which enhance pressures on predators through bottom-up effects (Cury *et al.*, 2011; Grémillet *et al.*, 2018; Keogan *et al.*, 2018; Dias *et al.*, 2019; Hammerschlag *et al.*, 2019; Montevecchi, 2022; Layton-Matthews *et al.*, 2024). Seabirds have since long been identified as 'sentinels of the sea', due to how their behaviour, survival and reproduction reflect the stability of marine ecosystems (Brisson-Curadeau *et al.*, 2017; Grémillet *et al.*, 2020; W. J. Sydeman *et al.*, 2021; Hentati-Sundberg *et al.*, 2023). While it is critical to investigate how climate change and fisheries contribute to the extensive decline in seabird populations, it is not yet clear exactly how many seabirds respond to natural variation in prey availability in the first place (Grémillet and Boulinier, 2009; Barbraud *et al.*, 2012; Montevecchi, 2022; Renner *et al.*, 2024). Without this baseline, predicting future anthropogenic impacts is like solving a function without knowing the intercept. A clearer understanding is especially needed of how seabirds partition resources and their behavioural flexibility to changes in prey availability. Linking fine-scale predator-prey dynamics to broader patterns in seabirds' potential foraging range reveal how resource partitioning relates to ecosystem resilience, and help guide more effective, targeted conservation efforts. This thesis builds on the idea that understanding predator foraging requires simultaneous insight into prey behaviour (Gilg *et al.*, 2012; Chave, 2013). By developing methods and integrating high-resolution data on both predators and prey, I investigate the foraging niches of two highly specialized sympatric diving seabirds, and what these reveals about ecological flexibility, species coexistence, and conservation needs.

1.1 The art of foraging

1.1.1 Optimal Foraging and Energetic Trade-offs

Sustaining energetic balance is the most important aspect of living, as without energy there is no life. However, paradoxically, it takes energy to gain energy: energy is costly to locate, harvest, transfer and store. This implies that animals must achieve a favourable cost-gain ratio, where the energy gained sufficiently exceeds the energy spent (Carbone and Houston, 1996; Walton, Ruxton and Monaghan, 1998; Langton, Davies and Scott, 2014). Foraging profitability typically follows a diminishing returns curve, due to decreasing prey availability (e.g. by exploitation or escape), individual state/storage limits (e.g. stomach, mouth, beak), cost of transportation, fatigue, amongst other physiological (e.g. thermoregulation) and ecological (e.g. light, parental care) constraints (Charnov, 1976; Wetterer, 1989; Langton, Davies and Scott, 2014; Alerstam, Bäckman and Evans, 2019; Menezes, 2022). Thus, prey energetic value becomes important, as dietary shifts toward low-energy food, even when abundant, can negatively impact an animals' survival and fecundity due to the skew in cost-gain relations (Wanless *et al.*, 2005; Österblom *et al.*, 2008; Montevecchi, 2022). Such energetic constraints shape how animals search for, exploit and adapt to resources with patchy distributions.

To optimize energy gain, animals often rely on cost-effective search strategies, such as Area-Restricted Search, Lévy Flight and random search (Fauchald, 1999; Dorfman, Hills and Scharf, 2022). Further, many food resources are quite predictable since they are distributed according to environmental drivers which are related to recognizable traits, such as in topography, elevation or specific vegetation (Giske, Huse and Fiksen, 1998). Animals that can identify, learn or track these traits over time gain an advantage of predicting where food is likely available (Guisan and Zimmermann, 2000). For animals specializing on predictable resources, memory and temporal cues can decrease the cost of search, thus improving the foraging cost-gain ratio and reduce energetic risk (Benhamou, 1994; Kamil and Roitblat, 1985). When prey is widely distributed or less predictable in space and/or time (e.g. wind dispersed resources), specialized senses and cost-efficient movement allow predators to search for and find foraging locations (MacArthur and Pianka, 1966; Abrams, 2000; Williams and Safi, 2021). To reduce costs and unprofitable investments, animals have evolved ways to evaluate patch quality (Bedoya-Perez *et al.*, 2013; Bonte *et al.*, 2012; Mella *et al.*, 2018). They choose between foraging patches and the time spent in each, weighing prey availability with travel costs (Charnov, 1976). According to the Marginal Value Theorem, an animal should leave a patch if the rate of energy gain, thus foraging efficiency, becomes equal to or lower than the mean of the environment (Charnov, 1976). However, as travel costs increase, more energy must be gained. The cumulative gains and losses in previous patches during a multi-patch foraging event, along with expectations of further investments (e.g. distance to new patch), may affect the decisions made in the focal patch (Menezes, 2022).

1.1.2 Competing for energy: niche divergence

In environments with shared resources, competition further shape foraging strategies (Holt and Bonsall, 2017). Competition for resources, such as energy, has been a key driver of species evolution often leading to interspecific niche divergence, the process by which species differentiate in traits such as morphology, physiology, or behaviour to reduce competition. The ecological outcome of this process is niche partitioning, where species coexist by using different resources, or using the same resource in different ways or at different times (Pearman *et al.*, 2008). Intraspecific niche divergence is also common, such as through sexual dimorphism, age, life stage and size classes (Selander, 1966; Nakazawa, 2015; Carlsen, Lorentsen and Wright, 2021). Niche partitioning provides individuals potential advantages in resource competition (Pearman *et al.*, 2008). It also facilitates a wider distribution of resources across taxa, promoting biodiversity and thus ecosystem stability and resilience (Chapin *et al.*, 1997). Niche partitioning can range from coarse-scale patterns, such as broad habitat separation, to fine-scale behavioural differences. More broadly, partitioning reflects the spectrum from generalists adapted to a wide range or variable conditions, to specialists adapted to excel in a narrow range or predictable conditions (Sexton *et al.*, 2017). While generalists can switch between its range of potential resources when needed, the flexibility comes at a cost, with competitive disadvantage to specialists on overlapping resources (Julliard *et al.*, 2006). Specialists, however, excel when resources are stable, but with higher risk if the predictability of resources change (Sexton *et al.*, 2017).

1.1.3 Central place foraging and range

Many animals have evolved central place foraging (CPF) strategies, returning to a specific site between foraging events, for example to provision offspring, avoid predation, or shelter from environmental extremes (Orians & Pearson 1979). In species with CPF, selection has shaped morphological traits, such as wing size to body mass ratio, to align with the opportunities of their foraging environment (Norberg, 1995; Orians & Pearson 1979). Across taxa, a larger ratio correlates with a larger foraging range from the central place (Norberg, 1995). Indeed, animals with the ability to fly excel in CPF, due to their ability to move large distances quickly and cost efficiently (Williams and Safi, 2021). Since the area accessible to an animal increase with the square of the radius ($A=\pi r2$), each additional kilometre adds disproportionately more area. This creates a steep gradient in the marginal value of distance, where the outermost distance allows access to vast new habitat and foraging opportunities. However, beyond a certain threshold, increasing foraging area may exceed the animals' capacity to efficiently search prey, particularly if prey is unpredictable (Langton, Davies and Scott, 2014). Since an animal is expected to maximize food return per unit of time, distant patches must return proportionally greater rewards (Orians & Pearson 1979). This cost-gain trade-off can manifest as an upper extent in foraging range, due to diminishing returns (Langton, Davies and Scott, 2014). An alternative strategy is therefore to specialize in exploiting nearby resources. As morphological adaptations for long-range travel often are incompatible with traits that enhance manoeuvrability, both abilities are rarely adapted together (Norberg, 1995; Thaxter *et al.*, 2010). Understanding how morphology and foraging strategies shape species' ecological roles is key to predicting how animals will respond to environmental shifts and changes in food resources in the near future (Sexton *et al.*, 2017).

1.2 Marine predator-prey interactions

1.2.1 On forage fish ecology

Forage fish are the key prey species in aquatic systems, acting as a crucial link in food chains by supporting higher predators, and are thus fundamental to the apparent competition (Engelhard *et al.*, 2014; Holt and Bonsall, 2017). Forage fish are small-medium sized pelagic fish whose abundance, distribution, and accessibility are fundamental to their predators' survival and reproductive success (Wanless *et al.*, 2005; Engelhard *et al.*, 2014; Searle *et al.*, 2023). However, forage fish are also living organisms with life histories and ecological driving forces independent of predation (Chellappa *et al.*, 1989; Cardinale *et al.*, 2003; Casini, Cardinale and Arrhenius, 2004; Solberg, Klevjer and Kaartvedt, 2012; Bergström *et al.*, 2015; Frisk *et al.*, 2015; Solberg, Røstad and Kaartvedt, 2015; Palermino *et al.*, 2024). They are primarily predators themselves, with habitat restrictions and ecological niches relating to foraging strategies, metabolic regulation and reproduction (Frisk *et al.*, 2015). As the habitats suitable to forage fish's niche is limited, they have adapted to reduce predation risk without compromising frequent opportunity to meet all other needs (Jensen *et al.*, 2011; Ahrens, Walters and Christensen, 2012). Indeed, the strong seasonal patterns associated with forage fish circular spawning-to-feeding ground migrations play a key role in shaping their predictability to predators across space and time (Cushing, 1969; Holst *et al.*, 2002; Nøttestad *et al.*, 2007).

1.2.2 Predator avoidance and seabird strategies

The range of predators hunting strategies specialized for forage fish is staggering, with attacks from any angle and in any size, from whales gulping entire schools to small fish predating fish eggs and larvae (Cury *et al.*, 2000; Fauchald *et al.*, 2011; Griffiths, Olson and Watters, 2013; Olin *et al.*, 2022). This width suggests that anti-predator adaptations in forage fish are shaped not necessarily to single threats, but rather by the cumulative pressure of a wide and persistent predator field (Holt and Bonsall, 2017). In forage fish, two main responses have been identified as most effective in reducing predation risk across predator strategies: changing the spatial density of individuals by aggregating in different forms (Magurran, 1990; McNamara and Houston, 1992), and changing visibility and availability in response to light, such as depth migrations (Hays, 2003; Häfker *et al.*, 2022). Notably, aggregation and reduced exposure serve many purposes to aquatic organisms, including feeding, cost efficient swimming, thermal metabolic regulation, digestion, reduction of UV-exposure, social behaviour and reproduction (Cardinale *et al.*, 2003; Sims *et al.*, 2005; Jensen *et al.*, 2006, 2011). This underlines that there is spatiotemporal predictability in these behavioural responses, based on environmental factors beyond predation alone. Overall, prey's spatial distribution, abundance, and body condition are primarily determined by bottom-up processes (e.g., food availability) and environmental constraints (e.g. oceanography), rather than through top-down effects (Casini *et al.*, 2014; Montevecchi, 2022; Novotny *et al.*, 2022).

Predators have in turn adapted to overcome such prey behaviours by collaborating with conspecifics and other species, adapting their senses and/or to exploit windows of vulnerability when disadvantageous prey behaviours are less expressed (Axelsen *et al.*, 2001; Regular, Hedd and Montevecchi, 2011; Lett *et al.*, 2014; Sutton, Hoskins and Arnould, 2015; Thiebault *et al.*, 2016). Such predator adaptations are often niche dependent, where different species have specialized on one or few specific prey vulnerabilities (Pulliam, 2000; Pearman *et al.*, 2008; Sexton *et al.*, 2017). Seabirds are excellent study species for niche specific predator-prey interactions with forage fish, due to their wide range of foraging strategies and mobility adaptations (Schreiber & Burger, 2001). The strategies include surface feeding (e.g. Frigatidae), plunge diving (e.g. Sulidae), highly adapted under-water swimming (e.g. Phalacrocoracidae) and deep diving (e.g. Spheniscidae and Alcidae).

1.2.3 Predictability of forage fish

Specializations to foraging strategies make many seabird species dependent on predictability of foraging conditions (Weimerskirch, 2007). Predictability of prey abundance distributions is even more important during CPF, due to the commitment to a specific area/range, where the food resource must be left between every foraging event (Burke and Montevecchi, 2009). Importantly, the scale at which predictability matters differ across foraging strategies and relates to the foraging range of the animal (Fauchald, Erikstad and Skarsfjord, 2000; Jenouvrier, Barbraud and Weimerskirch, 2003; Weimerskirch, 2007). Specialist divers, such as alcids and penguins, with strong morphological constraints and relatively narrow foraging ranges, rely on fine-scale, local, and temporally stable prey availability. In contrast, wide-ranging flyers like albatrosses may tolerate greater local-scale unpredictability but are still dependent on larger-scale spatial predictability.

By returning to the same patch every time (i.e. site fidelity), a seabird relying on predictable food resources can know the location of a sufficient food source and how it changes over time, while trading away the possibility to know of other, potentially better, sites (Weimerskirch, 2007; Regan *et al.*, 2024). If there is abruption and/or unpredicted change in the chosen foraging area, a predator adapted to highly predictable resources may have few options (Bradshaw *et al.*, 2004; Renner *et al.*, 2024). While few environments remain completely unchanged over evolutionary timescales, stability in key ecological characteristics such as resource availability, habitat structure, or climate patterns can drive adaptations of specialized species (Poisot *et al.*, 2011). Specialization to predictability can still occur in dynamic environments if changes are gradual. For example, seasonal prey availability (e.g., seasonally driven migration routes of fish) can stabilize predator demographics by influencing timing of breeding, colony size, or foraging behaviour (Cushing, 1969). Similarly, slow shifts in prey distribution can drive behavioural plasticity in foraging strategies, such as travel distances or shifts in diet composition (Burke and Montevecchi, 2009) but they can also be problematic if they accumulate over time or exceed the species' adaptive capacity (Bustnes *et al.*, 2013; Grémillet *et al.*, 2018; Amélineau *et al.*, 2019). The ongoing climate change is concerningly rapid, and it remains unclear how flexibly animals can respond to shifts in environmental predictability (Elith and Leathwick, 2009; Summers *et al.*, 2012; Bates *et al.*, 2014; Meier *et al.*, 2021; Renner *et al.*, 2024; Wernberg *et al.*, 2024). Understanding the global status of key prey populations is essential to assessing the full impact of environmental change on biodiversity (Wernberg *et al.*, 2024).

1.3 Global status for foraging predators

Higher predators are particularly vulnerable to changes in prey resources due to their high metabolic demands, extensive habitat requirements, and often specialized reliance on specific prey species or prey behaviours (Ripple *et al.*, 2014). Over the past two centuries, higher predator populations have significantly declined worldwide because of human activities, due to habitat degradation and fragmentation, affecting predators foraging opportunities (Heithaus *et al.*, 2008; Ripple *et al.*, 2014; Dias *et al.*, 2019). However, higher predators play essential roles within ecosystems by regulating food webs, influencing nutrient cycling, shaping habitat structures, and limiting ecological invasions (Sergio *et al.*, 2008; Hammerschlag *et al.*, 2019). Consequently, higher predators’ rapid disappearance has triggered unexpected shifts in food webs and ecosystem services, with cascading effects on numerous species (Hammerschlag *et al.*, 2019). Seabirds are incredibly diverse higher predator group, with some of the most extreme adaptations and behaviours of the animal kingdom (Schreiber & Burger, 2001). The ~360 species include some of the most cost-efficient flyers (e.g. Albatrosses), longest distance migrators (e.g. *Sterna paradisaea*), to flightless species (e.g. penguins). Of the few things the myriads of seabirds have in common, they are all long-lived with relatively slow life histories as compared to many other bird groups (e.g. Passerines). Further, they are all impacted by anthropogenic activities (Dias *et al.*, 2019).

1.3.1 Seabird foraging in a changing ocean

Currently, 38% of the world's seabird species are classified as globally threatened or near threatened by the International Union for Conservation of Nature (IUCN), while half of all seabird populations are on decline (Grémillet *et al.*, 2018). This has resulted in an estimated 19% decrease in seabirds' prey consumption between the 1970s and 2000s. Meanwhile, commercial fisheries targeting the same prey species have increased their catch by approximately 10% over the same period, leaving little room for seabird populations to regrow (Grémillet *et al.*, 2018). However, the effects of climate change and fisheries on prey abundance and distribution in marine ecosystems overlap and interact, and cannot easily be teased apart (Barbraud *et al.*, 2012). Morphologically, both fisheries and warming waters can be 'size selective' of prey, such as forage fish, in that they tend to decrease the average body size in remaining populations (Shackell *et al.*, 2010; Baudron *et al.*, 2014; Kraak *et al.*, 2019). Physiologically, moderate fisheries can improve body conditions of forage fish through decreased food competition (Casini *et al.*, 2011), but climate change is likely to counter such effects as warmer water reduces primary production and thus forage-fish food availability (Gregg *et al.*, 2003; Kulk *et al.*, 2020). Further, climate models predict increasing water stratification (e.g. in thermal, salinity, oxygen and nutrients distribution) caused by warming (Meier *et al.*, 2021). Stratification affects the behaviour of zoo plankton and forage fish depth distribution, in addition to limiting nutrient input into the epipelagic zone, with further cascading effects to abundance and distribution of such key populations (Liblik and Lips, 2019; Weidner *et al.*, 2020; Meier *et al.*, 2021). Fisheries make local abundances in historically predictable foraging sites less reliable for predators and can also alter depth distribution of forage fish directly (Frederiksen *et al.*, 2008), and indirectly when larger predator fish are harvested (Montevecchi, 2022). In addition, both warming waters and fishery may lead to changes in aggregation patterns of fish, such as schooling density or size, through a range of effects such as reduced water oxygen, water stratification, reduced visual distance, reduced food availability and altered predation pressures (Pavlov and Kasumyan, 2000; Domenici, Steffensen and Marras, 2017; Holubová *et al.*, 2019; Kasumyan and Pavlov, 2023; Kuruvilla *et al.*, 2023). Thus, climate change and fisheries jointly make prey abundance and distribution patterns less predictable, while altering prey availability through their behaviour (Frederiksen *et al.*, 2008; Barbraud *et al.*, 2012; Hammerschlag *et al.*, 2019).

Seabirds may buffer against decreased prey availability through behavioural plasticity, such as increasing foraging effort or switching prey type, but these strategies have energetic and spatiotemporal limits, and are largely niche dependent (Jenouvrier, Barbraud and Weimerskirch, 2003; Regular, Hedd and Montevecchi, 2011). Decreased prey abundance and/or prey quality led seabirds to experience elevated foraging costs, with accelerating consequences for reproductive success and demography (Durant *et al.*, 2005; Österblom *et al.*, 2008; Sabarros *et al.*, 2012; Searle *et al.*, 2023; Layton-Matthews *et al.*, 2024). Moreover, shifting prey distribution, both fine-scale (e.g., aggregation density, depth) and broad-scale (e.g., seasonal migration, latitudinal shifts), can severely affect predator foraging success (Frederiksen *et al.*, 2008; Boyd *et al.*, 2015; Montevecchi, 2022). Thus, sustaining marine resources for higher predators requires understanding of both prey ecology and broader ecosystem processes (Ahrens, Walters and Christensen, 2012; Sydeman *et al.*, 2017; Montevecchi, 2022).

1.4 Protecting seabirds foraging grounds

While conservation efforts for seabirds have been made, globally and for decades, seabird populations across taxa keep decreasing, highlighting the need to examine the underlying drivers (Barbraud *et al.*, 2012; Grémillet *et al.*, 2018; Dias *et al.*, 2019; Pike *et al.*, 2024). Primarily, we should expand on our understanding of how species-specific adaptations and niches reflect seabirds needs, considering spatiotemporal habitat use under natural variation (Grémillet and Boulinier, 2009). Several studies have shown direct links between changes in prey dynamics and seabird population dynamics

(Frederiksen *et al.*, 2008; Dias *et al.*, 2012; Bustnes *et al.*, 2013; Montevecchi, 2022), yet IUCN classify food shortages as a lower ranking threat to most seabirds (Dias *et al.*, 2019). A recent assessment of threats to seabirds identified the major issues as invasive species (affecting 46% of species), bycatch (28%), hunting/trapping (27%), climate change (27%), disturbance (20%), pollution (29%), with overharvest of marine resources only estimated to affect 15% of species (Dias *et al.*, 2019). Meanwhile, fisheries effort is at an all-time high and fish stocks around the world are on decline (Worm and Branch, 2012; Grémillet *et al.*, 2018). However, the measurability of prey resource effects may be a limiting factor in the investigations of threats to seabird populations, due to seabirds' formidable capacity in short-term buffering under poor foraging conditions (Burger and Piatt, 1990; Quillfeldt *et al.*, 2011; Regular *et al.*, 2014; Kadin *et al.*, 2016; Burke and Montevecchi, 2018). Effects of food shortages are likely to be slow, cumulative and, crucially, likely to interact with or accelerate these top threats, and to become a major issue in the future (Dias *et al.*, 2019; Grémillet *et al.*, 2018). Further, changes in food availability can have long lasting effects across individuals in a breeding population, directly or indirectly (Jenouvrier, Barbraud and Weimerskirch, 2003; Barbraud *et al.*, 2012; Montevecchi, 2022). Food shortages reduce the body condition of individuals by increasing energetic cost to gain, increasing mortality in particular for young or small (e.g. age or sex specific) individuals, reducing the number of individuals attempting to breed and ultimately lifetime fecundity (Grémillet *et al.*, 2018; Montevecchi, 2022). Low body condition due to starvation also makes animals more susceptible to disease and parasites, and to take more risks leading to elevated predation (Barbraud *et al.*, 2012). Indeed, the reduction in prey availability or quality may be a driving reason why seabirds end up foraging close to fishing vessels, which leads to an important point: bycatch primarily happen due to fisheries in seabirds foraging areas and during foraging times (Montevecchi, 2022). Additionally, climate change primarily affects seabirds through bottom-up effects, in addition to drive movement of species that can become problematic in new habitats (Barbraud *et al.*, 2012; Bustnes *et al.*, 2013; Bates *et al.*, 2014; Chaalali *et al.*, 2016; Grémillet *et al.*, 2018).

While morphological traits have evolved to optimize energy use and reduce interspecific competition for seabirds, they may function as ecological traps under the current environmental change, locking species into maladaptive foraging strategies while prey availability or predictability declines (Schlaepfer, Runge and Sherman, 2002; Grémillet *et al.*, 2018). However, one of the major reasons effects of foraging conditions are so hard to pinpoint to seabird population dynamics is due to the sheer scale and complexity of the study systems.

1.5 Novel technologies for studying far-ranging seabirds

Understanding predator-prey interactions in marine systems remains a significant challenge, particularly when dealing with far-ranging predators and highly mobile prey (Weimerskirch, 2007). While the complexity and dynamic nature of these interactions are well recognized, prey is often, by necessity, treated as a relatively static resource in studies of predator functional responses (Hunsicker *et al.*, 2011). This is largely due to the logistical difficulties of concurrently capturing fine-scale predator behaviours and prey dynamics at a matching temporal and spatial scale (Brisson-Curadeau *et al.*, 2017). With the development of small trackers that can be carried by animals with body masses well below 1kg (Brisson-Curadeau *et al.*, 2017), remote sensing (Wilson *et al.*, 2002; Schaeffer *et al.*, 2008; Kulk *et al.*, 2020; Hentati-Sundberg *et al.*, 2023), and recently, autonomous vehicles for monitoring prey, the collection of extensive fine-scale data across large geographical areas and over extended time periods can now be feasible (Ghani *et al.*, 2014; Liu *et al.*, 2016). These advances include autonomous underwater vehicles (AUVs), gliders, drones, and bio-logging devices equipped with GPS, accelerometers, and cameras, as well as satellite and acoustic remote sensing tools for mapping prey fields and oceanographic conditions (Ponganis, 2007; Liu *et al.*, 2016; McKinnon and Love, 2018; Le Traon *et al.*, 2019; Chung, Lee and Lee, 2021; De Robertis *et al.*, 2021; Wullenweber *et al.*, 2022; Hentati-Sundberg *et al.*, 2025). Studying seabirds during breeding is, admittedly, much more feasible than during non-breeding, due to their commitment to the breeding site constraining their available foraging habitat. Although adult survival is typically the key demographic driver in long-lived species with slow life histories, such as seabirds, sustained reproductive failure across multiple taxa has shifted attention to the breeding period as a critical window for population recovery and growth (Layton-Matthews *et al.*, 2024). Unmanned surface vehicles (USVs) with environmental sensors can allow for long-term spatiotemporal prey surveys and thus become key in approaching the knowledge-gaps in seabirds behavioural responses to fine-scale variation in foraging conditions (De Robertis *et al.*, 2019, 2021). However, significant uncertainties are associated with technologies under development, such as the practicality of data sampling and the resulting quality of data (Ghani *et al.*, 2014; Liu *et al.*, 2016). Once the reliability and applicability of these tools are better assessed, we may be one step closer to understanding predator responses to varying prey fields, with resolutions traditional approaches have not been able to provide (Hunsicker *et al.*, 2011; De Robertis *et al.*, 2019, 2021).

2. Knowledge gaps

Diving seabirds rely on prey that is highly variable in space and time, yet our understanding of how they respond to natural variation in prey availability, distribution, and behaviour remains limited (Benoit-bird and Au, 2003; Strod *et al.*, 2008; Regular *et al.*, 2010; Regular, Hedd and Montevecchi, 2011). This is particularly true for fine-scale prey traits such as aggregation and depth, which can strongly affect underwater predators but are difficult to observe (Masello *et al.*, 2010; Regular, Hedd and Montevecchi, 2011; Shoji, Aris-Brosou and Elliott, 2016; Thiebault *et al.*, 2016; Chimienti *et al.*, 2017; Montevecchi, 2022). The inherent problem of collecting sufficient data on prey or on predators under enough varying foraging conditions makes it hard to disentangle predator species-specific constraints from broader patterns of behavioural flexibility (Sabarros *et al.*, 2012; Linnebjerg *et al.*, 2015; Gulka, Ronconi and Davoren, 2019; Petalas *et al.*, 2021). Additionally, while predictable food resources are considered essential for breeding seabirds, prey data are often based on short-term snapshots, limiting our ability to evaluate what constitutes "good" foraging conditions (Weimerskirch, 2007). Improving this understanding is especially urgent given the accelerating pressures from fisheries and climate change, and the many seabird species with unknown or poorly assessed conservation status (Worm *et al.*, 2006).

3. Aim of thesis

This thesis aims to improve the understanding of what characterizes favourable foraging conditions for two sympatric diving seabird species during the breeding season, and how this knowledge can support seabird conservation. I examine how seabirds respond to variation in prey abundance, predictability, and behaviour using novel tools that provide fine-scale, long-term concurrent predator-prey data.

To address this, I focus on four aspects of prey availability: Prey abundance and spatiotemporal distribution **(Ch. I, II and III)**, prey aggregation numbers **(Ch. II)** and prey diel vertical migration **(Ch. II)**, all studied in relation to environmental variation across months. Finally, the morphologically determined foraging range of the world's seabirds were estimated to investigate their conservation status during central place foraging **(Ch. IV,** Fig. 1**)**. I approached this using three methods of data collection: (i) Autonomous unmanned surface vehicles to collect hydroacoustic and environmental data for high-resolution estimates of prey abundance and prediction of distribution; (ii) Animal tracking to reveal seabird movement and foraging behaviour; (iii) Global data repositories to assess seabird distributions, environmental conditions, and conservation coverage.

Research questions by chapter:

I. What are the advantages and limitations of implementing autonomous data collection in ecological monitoring for high resolution long-term data and species distribution models?

II. Can niche partitioning between two closely related sympatric species be explained by diel light cycles and prey distribution patterns?

III. How dependent is a dive-specialized predator on stability and predictability of prey abundance during breeding?

IV. How protected are the worlds seabirds potential foraging range during central place foraging and how can non-studied species and colonies be better protected?

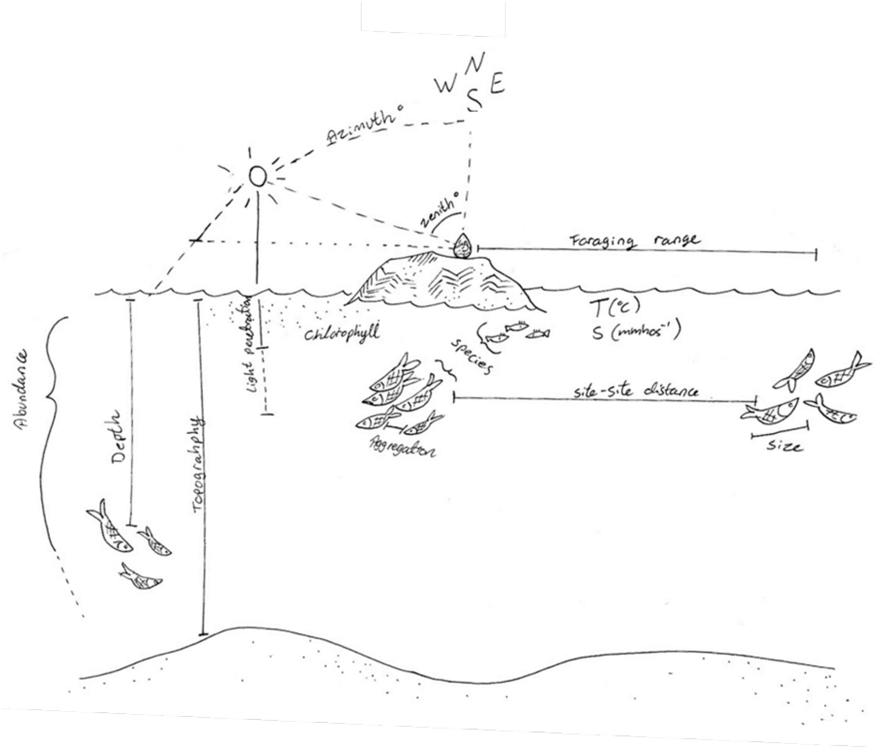

Figure 1. Aspects of prey distribution for central place foraging seabirds (illustrated by position of the egg) touched upon in this thesis. Inspired by Montevecchi (2022), Fig. 3.1. By A.A. Carlsen, 2025.

4. Methods

4.1 Study system

Studies in **chapter I-III** were performed in the Baltic Sea, Sweden, off the island of Stora Karlsö (Fig. 2), that hosts the largest seabird colony in the region. The Baltic Sea is a relatively simple ecosystem, where few species contribute significantly to food web interactions. Further, it is one of the areas in the world most rapidly impacted by climate change with considerable fisheries occurring (Meier *et al.*, 2021). Uniquely, the seabird populations at Stora Karlsö have increased near exponentially over the past 30 years and are still growing (BSP unpublished data). The development is attributed to changes in foraging conditions, where the collapse of the local cod stock led to large increases in small pelagic fish abundances (Österblom *et al.*, 2006). I here studied two forage fish dependent, diving seabirds, the common guillemot (*Uria aalge*) and the razorbill (*Alca torda*). Previous studies have shown variation in behavioural responses in these predator species to prey quality and quantity, primarily based on observations in the colony and tracking of the seabirds foraging trips (Österblom *et al.*, 2006, 2008; Kadin *et al.*, 2012, 2016; Isaksson *et al.*, 2019). Based on the environmental shifts, the current prey status and previous studies on predator responses to prey quality, this is an interesting system to investigate predator responses to spatiotemporal fluctuations in prey distribution (**Ch. II-III**). While there are morphological trade-offs that discriminate the foraging behaviour of the two seabird species, their responses in these studies are likely to reflect behavioural decisions within relatively comfortable foraging conditions compared to declining populations. Here, a seabird quitting foraging under certain conditions is more likely to reflect the reaching of a goal or avoidance of unnecessary costs rather than limitations due to lack of abilities/unsuitable environment. The qualities of this Baltic Sea study system thus allow my results to serve valuable baseline knowledge of how seabirds behave while their populations grow.

For **Chapter IV**, I changed the scope to the world's seabird populations, including data from 79 species from 217 breeding colonies, representing ten seabird families across both the northern and southern hemisphere, while extrapolating for three lesser studied families.

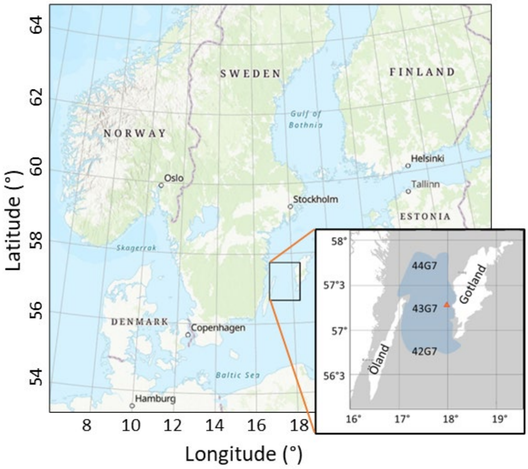

Figure 2. Study system for chapters I-III in the Baltic Sea, Sweden. Diving seabirds breeding at Stora Karlsö (orange triangle in zoom in), with foraging area between Öland and Gotland, in International Council for the Exploration of the Sea's (ICES) subdivision 27, statistical squares 42G7-44G7. Drone survey area marked in blue in zoom-in window.

4.1.1 About the Baltic Sea predators

To study predator behaviour in **chapters I-III**, I used two diving seabirds of the Alcid family, the common guillemot and the razorbill. These species breed alongside each other, utilizing the same food resources with spatiotemporal overlap, and are both single prey loaders in this system (Kadin *et al.*, 2016; Olsson and Hentati-Sundberg, 2017). Both species have a modest horizontal foraging range compared to e.g. surface feeders, but with differences between the two species in wing-to-body size ratio (Fig. 3), suggesting they respond differently to fine-scale distribution patterns in prey abundance and behaviour (Thaxter *et al.*, 2010). While guillemots (Fig. 3A) are one of the deepest diving seabirds (<250m), and by far the deepest diving of birds that can fly (Chimienti *et al.*, 2017), the razorbills, which have large overlaps in foraging niche, are slightly more adapted to flight but can only dive a fraction of the guillemots depth (<60m; Fig. 3B) (Thaxter *et al.*, 2010). The largest seabird populations at Stora Karlsö are ~26,000 pairs of guillemots, ~12,000 pairs of razorbills, and ~2,000 pairs of great cormorants (*Phalacrocorax carbo sinensis*). These top predator species forage on small pelagic fish (Lundström *et al.*, 2010; Kadin *et al.*, 2012; Hentati-Sundberg *et al.*, 2018; Engwall, Waldenström and Hentati-Sundberg, 2022).

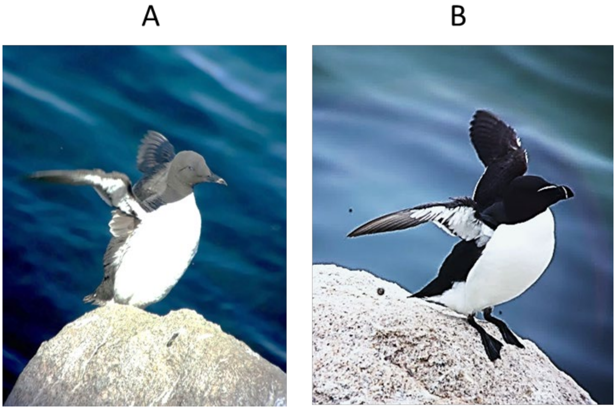

Figure 3. The marginal wing-to-body size ratio difference between two closely related species, represents niche differences. The smaller ratio in (A) Common guillemot (*Uria aalge*) makes them more efficient divers, while the slightly larger ratio in (B) razorbill (*Alca torda*) give them a larger potential foraging range (Thaxter et. al., 2010). By A.A. Carlsen.

4.1.2 About the Baltic Sea prey

Of the small pelagic fish in the area studied in **chapters I-III**, the three most abundant species (Fig. 4) are the two commercially sought clupeid species sprat (*Sprattus sprattus)*, and herring (*Clupea harengus)*, and the three-spined stickleback (*Gasterosteus aculeatus) (*Olsson *et al.*, 2019; ICES, 2021, 2023). The three species have some overlap in utilized food resources, primarily dependent on individual size, season and life stage (e.g. feeding versus spawning focused period) (Novotny *et al.*, 2022). All three forage fish species exhibit distinct fine-scale spatial distribution patterns (**Ch. II**). Clupeids undergo large-scale diel vertical migrations, with portions of the population ascending towards the surface at dusk and descending back to the seabed or depths of 70–80 m at dawn, depending on their size, maturation and physiological state (Cardinale *et al.*, 2003; Nilsson *et al.*, 2003). All three fish species exhibit facultative aggregation behaviour, adjusting their group density in response to various biotic and abiotic factors (Jurvelius *et al.*, 1996; Nilsson *et al.*, 2003). Clupeids tend to form aggregations during vertical migration and, to some extent, throughout the day (Zwolinski *et al.*, 2007; Solberg and Kaartvedt, 2017). Sticklebacks, in contrast, have a less pronounced vertical migration, typically increasing their depth by 10-20 m from their nocturnal distribution, while forming dense aggregations under peak daylight conditions (Jurvelius *et al.*, 1996). Although sticklebacks may be a lower-quality prey option for alcids due to their smaller size and potentially higher handling costs (Wasserman *et al.*, 2021), their high daytime availability at shallower depths makes them accessible to diving predators. Spawning migrations and sites of spawning in forage fish is important to their spatiotemporal predictability to predators (**Ch. III**) (e.g. Regular *et al.*, 2014). When fish species specific abundance is unavailable, information on their periodical behaviour can aid in inferring their distribution, and thus their availability to the seabirds. The study period of this project partially overlaps with the spawning season of all three forage fish species (Jørgensen, Hansen and Loeschcke, 2005; Candolin, Engström-Öst and Salesto, 2008; Ojaveer and Kalejs, 2010). Herring spawn in batches by age/size (March-May) in shallow seabed habitats along the coast (Aro, 1989; Jørgensen *et al.*, 2005; ICES, 2021). Sprat spawn up to several times per individual during the summer (April-August) in deep water basins with >0.6% salinity (Aro, 1989), overlapping in time with the spawning of sticklebacks (May-July). However, the sticklebacks utilise shallow spawning depths similar to herring habitats (Olin *et al.*, 2022).

Figure 4. Examples of relative sizes of mature small pelagic fish from the Baltic Sea included in abundance data, from the top: three-spined stickleback (*Gasterosteus aculeatus*); Sprat (*Sprattus sprattus*), Herring (*Clupea harengus*). By A.A. Carlsen.

4.2 Prey monitoring and variables

Prey data (for **Ch. I-III**) was collected using the remotely operated Unmanned Surface Vehicle (USV) Sailbuoy (Offshore Sensing AS, Bergen, Norway), equipped with an echosounder, a conductivity-temperature (CT) sensor and a fluorometer (Fig. 5). Sampling followed transects designed to cover the foraging area of breeding seabirds from Stora Karlsö (Evans *et al.*, 2013; Isaksson *et al.*, 2019), spanning approximately 60-80 km from the island and returning to 2-5 km offshore (Fig. 2). Surveys were conducted from late April to late July between 2019 and 2023. The USV, was powered by sail and steered via an electronic rudder, while all electronic systems on-board were solar powered, making the operation fully reliant on renewable energy. Prey abundance and distribution was assessed from hydroacoustic data collected with a Simrad Wide Band Transceiver WBT-mini echosounder with an ES-200CDK transducer from Kongsberg Maritime (frequency sweep 185-255 kHz). Prey information was extracted with Echoview Software Pty. Ltd. (v.13) after calibration, filtering and cleaning of data. Prey abundance is given in Nautical Area Scattering Coefficients (NASC; m^2 nmi^{-2}) (Simmonds and MacLennan, 2005). See **chapter I** for more information on the USV and prey data collection.

A range of spatiotemporal prey abundance models were tested (**Ch. I**) to conclude which method to go forward with for studies overlapping with seabird tracking data (**Ch. II** and **III**). All models tested had ln-transformed NASC-value as response variable. Predictors were based on literature for fish distribution (Aro, 1989; Giske, Huse and Fiksen, 1998; Cardinale *et al.*, 2003; Sabatini, Reta and Matano, 2004; Schaeffer *et al.*, 2008; Watson, Stock and Sarmiento, 2015; Pennino *et al.*, 2020), and by data availability for the area and time of the study. See chapter I for more information on prey distribution estimates. Prey depth (**Ch. II**) was extracted as the mean depth of the median layer, at which the cumulative backscatter accounted for 50% of the water column sum, to inform on prey vertical migration and abundance per depth. Depths were based on 36,292 water columns summaries. Prey aggregations (i.e. schools/shoals) were detected through image processing of the raw echograms in Python 3.11 using Echoedge, which relies on Echopype 0.8.1 for reading and pre-processing of raw data (Lee *et al.*, 2024). Aggregations (**Ch. II**) were extracted through thresholding methods with a minimum size fixed to 2x2m and excluding aggregations within 1m from the seabed. The final dataset had 40,570 observations of single aggregations, that when summarized into bins of 10° solar azimuth (40min time-periods /1.3km with average USV speed) per date, concluded 7,089 bins. See chapter II for more information on extraction of aggregations. Prey stability and predictability was investigated through the rate of change in prey abundance, calculated as first derivative of the estimated abundance in a site (i) from one week to the next (i.e. Week-to-week stability) and (ii) for a specific week from one year to the next (i.e. week-across-year predictability). See chapter III for more information.

Figure 5. Unmanned Surface Vehicle Sailbuoy (Offshore Sensing AS, Norway). By A.A. Carlsen, 2025.

4.3 Predator tracking and variables

From 2019 to 2023, 17 common guillemots were equipped with Global Positioning System devices (GPS) (**Ch. III**), while from 2010 to 2023, 54 guillemots and 16 razorbills were fitted with time/temperature depth recorders (TDRs) (**Ch. II & III**). GPSs were attached to lower-back feathers using TESA© tape, while TDRs were attached to plastic leg rings with cable ties. The alcids were captured on nest, both on natural cliffs and on an artificial breeding ledge (Hentati-Sundberg *et al.*, 2025) using noose-pole and trapdoors. Deployment periods varied, spanning from 24h to year-round data sampling, but only data from May-July was selected for this project. Breeding stages included were 'incubation', 'chick-rearing', 'post-fledge' or 'non-breeding' (i.e. lost their egg/chick during the study or never had one). See **chapter II** for more information.

Variables for predators' behaviour were selected based on their likelihood of representing different aspects of foraging behaviour and efficiency (**Ch. II & III**), while being generalizable across species to simplify comparison. These were: surface and dive durations, dive efficiency, depth- and number of dives, bout length (n dives), distance moved between bouts and distance from colony (**Ch. II-IV**). Number of dives were summed per 10° azimuth per day/individual (**Ch. II**). Bottom-dive-cycle ratio (BDCr) was used to estimate the predators dive efficiency, giving an idea of time cost-gain ratio (Carbone and Houston, 1996) (**Ch. II**). In addition, time/energy budget were calculated for the guillemots foraging trips (**Ch. III**).

Figure 6. Seabird capturing and tracking work. (A) Razorbill nestbox entrance with slits for trapdoor. (B) Test of modified GPS with 3D printed charger cask. (C) Tagging of guillemot with TDR for over-winter tracking. (D) Floor hatch and noose-pole for catching guillemots. By Baltic Seabird Project.

4.4 Externally acquired and publicly available data

For prey distribution models and depth at predators foraging sites, data on environmental variables and topography (**Ch. I & III**) was downloaded from the European Union Copernicus Marine Service Information. The area was limited to a rectangle slightly exceeding the size of the area sampled with USV in latitude (56.50824°-57.80822°) and longitude (16.93013°-18.23579°), while the temporal selection was limited to the earliest and latest USV sampling Julian day. See chapter I for more information on variables. All light variables were calculated using the R package suncalc (**Ch. II**). The variation in zenith sun elevation ranged from 33 to 103° for the period of predator dives and from 33 to 111° for prey observations, with a cyclic relation to hour of the day. The Azimuth solar position provided unique values throughout the day, with its range of 0-360°. See **chapter II** for more information on light variables.

For global seabird analyses, all available GPS-data from breeding seabirds were downloaded from the global seabird databases MoveBank and BirdLife International Seabird Tracking Database (**Ch. IV**) (Kays *et al.*, 2022; Carneiro *et al.*, 2024). Global seabird colony data were compiled from many sources, including: the Global Seabird Data Portal, World Seabird Union; Joint Nature Conservation Committee and Digital and Data Solutions; CSIRO National Collections and Marine Infrastructure; OBIS Canada Digital Collections; OBIS Australia; BirdLife International; and Norwegian Institute for Nature Research. When colony location from the seabird tracking data was unavailable in these sources, colony position was determined using literature or based on first GPS trip locations. See **chapter IV** for more information. Important Bird and Biodiversity Areas (IBAs) and Marine Protected Areas (MPAs) data were downloaded from the World Database of Protected Areas.

For each species and colony, the foraging range within which 90% of trips occurred (FR90) was estimated and aggregated by seabird family (**Ch. IV**). Exclusive Economic Zones (EEZs) and High Sea were sourced from Flanders Marine Institute. See **chapter IV** for more information.

4.5 Statistical analyses

The analyses in this project have largely been based on models of different complexities, including Linear Mixed effect Models (**Ch. IV**), Generalised Linear (Mixed effect) Models (GLM(M); **Ch. I-IV**), and Generalised Additive (Mixed effect) Models (GAM(M); **Ch. I-III**) (Wood, 2017; Anderson *et al.*, 2022). Models were attempted to keep as simple as was meaningful, but model type where chosen based on its flexibility and ability to represent the complexity of the responses modelled (**Ch. I-VI**). When reliable, simpler statistical analyses such as ANCOVA (**Ch. I-III**) and permutation tests (**Ch. III**) were used, or simple base statistics were examined (**Ch. I-III**).

4.6 Ethical statement

The permit for handling birds was granted by Linköpings Djurförsöksetiska Nämnd (dnr 2477-2021). The handling of birds was kept to a minimum by reducing the measurements made during capture, and the number of captures per individual. The environment around the catching were purposefully kept calm and respectful, yet I acknowledge the impact I have caused on the seabirds and the disturbance on their environment.

5. Results and discussion

In this thesis, I use novel technologies to link fine- and broad-scale patterns in prey abundance and distribution to the foraging responses of two morphologically distinct diving seabird species, identifying key features of favourable prey conditions. I further demonstrate that global seabird foraging ranges can be predicted from wing morphology and flight mode, revealing alarmingly low conservation coverage of foraging ranges. The thesis explores chapter-specific findings in relation to broader ecological insights and across-chapter implications. In the following sections, I first discuss the key results from **chapters I–III**, then place them within the wider context of breeding-stage dependent foraging strategies and natural prey field variation, before connecting them to **chapter IV**'s trait-based conservation framework.

5.1 Autonomous monitoring and multi-source data

The first aim of the thesis was to establish the advantages and limitations of autonomous data sampling for large-scale high-resolution ecological monitoring and for species distribution models, here performed with data sampled using an unmanned surface vehicle (USV; **Ch. I-III)**. Considering USV operation, there were some technical challenges, ranging from steering in difficult weather, crossing ships wayfaring line, repairing of damages, retrieving terabytes of data in the docks and in calibrating equipment. However, the overall handling and manoeuvring of the USV was highly feasible and quick, both the USV and equipment were rather robust, and thus the data successfully collected at most times. The main challenges to overcome were maintenance of environmental sensors and modification of data storage unit due to unforeseen wave impact on the USB contact. The hydroacoustic data **(Ch. I)** had little disturbance (e.g. no engine turbulence) (DuFour *et al.*, 2021), high resolution and were near continuously sampled (7/10 minutes), from ~1.5m depth from the surface and down to the seabed/beyond the anoxic zone. The shallow depth of the USV meant it was excellent for sampling data near-surface and in vulnerable habitats. Cleaning and analysing the hydroacoustic data were a challenge **(Ch. I)** due to the large amount of data (~1TB/season), which made manual data cleaning unfeasible. Thus, much of the data cleaning was performed using a relatively conservative automatic bottom detection and broad-scale cleaning thresholds, which may have its drawbacks in excluding abundances of species with diel vertical migration particularly during daytime (Mello and Rose, 2009). The time between each visit to a general area was large due to the speed of the wind-driven USV **(Ch. I)**, which varied constantly. The varying speed and exclusion of fish near the seabed made the raw observations unreliable without a spatiotemporal context. For example, with the common speed of ~1m/s **(Ch. I)** the USV could cover 2 km in a straight line in ~30 minutes and so the distance would be highly represented by the time of day it was sampled. With no wind at times, the USV would lay still, resampling the same approximate site continuously for hours and even days. When cross-sailing up-winds, the USV could track back and forth over a large prey aggregation several times. Thus, the only way to properly analyse abundance and distributions of forage fish was by modelling, which can have its pitfalls in accuracy (Elith and Leathwick, 2009).

I ended up with a rather philosophical problem: Large data demands large data. In example, when predicting high resolution distribution of forage fish, environmental data for the entire area predicted upon was crucial. However, the resolution of the environmental data was coarser than the observations and perhaps so, the predictors struggled to describe the variance observed. Further, while one could fit a range of environmental sensors as on the USV, this data would be of no transferable value to spatiotemporal predictions or to matching with seabird tracking. The surface bound USV collected environmental variables could be used to explore habitat traits in the aquatic species studied, but for predictions or daisy-chaining data and models **(Ch. II-III)**, one would again either need perfect spatiotemporal overlap of observations or already accessible data of the entire area. In addition, few fisheries surveys in the area were available to compare catch with observations, making species specific prey models unfeasible.

The fine resolution of the data allowed correcting for the acoustic dead zone near the seabed (Mello and Rose, 2009) as a function of time of day in abundance distribution predictions **(Ch. I & III)**, likewise estimating the dynamics of diel vertical migration **(Ch. II)**. To establish how the diving predators responded to site specific dynamics in depth and aggregations **(Ch. II)**, a complete overlap between the diving predator and the prey, or a spatiotemporal distribution model of aggregations and prey depths, would have been necessary. As shown by Elin Andersson-Sjöholm, this is still difficult, with rare instances of reasonable spatiotemporal overlap between

USV and seabirds foraging sites recorded (Sjöholm, 2024). Hence, for diel prey distribution patterns, I needed to assume that dynamics across the foraging area was similar dependent on temporal variables such as time of day and week of the year. The long periods of observation became key when addressing variability in prey abundance and distribution, to fully capture the dynamics in predator-prey interactions. In the end, I found significant and meaningful relationships between the diel prey behaviour **(Ch. II)**, distribution and abundance **(Ch. I-III)** estimated from the USV-data, and the predators' responses in behaviour **(Ch. II & III)**, suggesting that successful prey, environment and predator data chaining was achieved.

This study demonstrates that autonomous data collection can provide large-scale yet cost-effective and low-impact ecological monitoring, particularly useful for highly mobile prey and long-range predators in dynamic systems. The findings show that while autonomous methods like the USV can provide ecologically meaningful results, they demand careful planning, understanding of data limitations and a recognition of scale when integrating multiple data sources. The details from the spatial distribution model in **chapter I**, and every connection between predators and prey confirmed in **chapter II & III** showcase only a small part of the benefits from the autonomous data sampling of prey.

5.2 Niche partitioning and foraging conditions

5.2.1 Good conditions are niche dependent

The second aim was to determine if the niche partitioning between two closely related sympatric species could be explained by diel light cycles and prey distribution patterns. I here found that diel variation in prey behaviour significantly shaped the foraging patterns of guillemots and razorbills, with between-species similarities and species-specific capacities **(Ch. II)**. Both seabird species showed heightened foraging effort and dive efficiency during twilight, particularly at dusk, compared to the high-light period. These peaks aligned with changes in prey availability: while prey abundance near the surface increased by night due to vertical migration, the number of prey aggregations showed a distinct diel asymmetry, peaking in the late morning before declining rapidly around noon and early afternoon. These prey dynamics created a temporal 'foraging window' of elevated opportunity in the late day, during which 56% of all guillemot dives and a staggering 70% of all razorbill dives were concentrated. Guillemots indeed foraged with symmetry around noon, timely matching with preys' vertical migrations in both directions. Razorbills on the other hand, timed their foraging to periods where the number of aggregations were lower, while light levels were higher than what was used by guillemots. Notably, the timing of foraging in razorbills implied a trade-off between foraging under acceptable light conditions, while avoiding large numbers of aggregations. Razorbills are not adapted to such diving depths as guillemots (Thaxter *et al.*, 2010) and thus their vision and other sensory systems are likely to be less adapted to 'fishing in the dark' (Regular, Hedd and Montevecchi, 2011). However, this does not necessarily imply that razorbills are struggling under the focal conditions (Engwall, Waldenström and Hentati-Sundberg, 2022). Rather, I am comparing the two species at the guillemots' turf **(Ch. II)**, where high specialization to under-water mobility, light and pressure is key for species with horizontally short foraging range (Thaxter *et al.*, 2010). Razorbills strength is more likely to lay in their small but significant increase in foraging range **(Ch. IV)** that makes it less costly to go further or sample multiple sites in a trip (Thaxter *et al.*, 2010). However, previous studies have shown that the razorbills in this colony do not necessarily realize this potential. Indeed, Isaksson *et al.*, (2019) showed that half of the razorbills' trips went to a deep basin where most guillemots foraging trips went **(Ch. III)**, while the other half of razorbills' trips traced the closer edge of the continental shelf off the west coast of Gotland (Isaksson *et al.*, 2019). An intriguing explanation could be that the difference in responses of the two seabird species was driven by difference in foraging habitat selection based on target prey. Razorbills provide their chicks with overall slightly smaller clupeids than the guillemots (Thaxter *et al.*, 2013; Engwall, Waldenström and Hentati-Sundberg, 2022). These clupeids may have a different spatial distribution than the large sprat (Cardinale *et al.*, 2003) primarily provisioned by guillemots (Kadin *et al.*, 2016). Thus, despite all similarities, the sympatric seabirds had different fine-scale responses to changes in prey distribution patterns, that likely affects their selected foraging habitats **(Ch. II-III)**. The difference in responses suggests guillemots might adapt more readily to fluctuations in small scale behavioural changes in prey (i.e. within a foraging site) due to their excellent dive abilities (Layton-Matthews *et al.*, 2024; Chimienti *et al.*, 2017). However, the similarities in response curves to prey aggregations and depths revealed that the guillemots may only be one step ahead of razorbills **(Ch. II)**. If there are large prey distribution changes, particularly in timing and depth of prey, guillemots will have elevated foraging costs which may propagate into long-term demographic effects (Jenouvrier, Barbraud and Weimerskirch, 2005; Eilertsen, Barrett and Pedersen, 2008; Reed, Harris and Wanless, 2015; Amélineau *et al.*, 2019; Dunn *et al.*, 2019; Whelan *et al.*, 2021). Under behavioural changes in prey, razorbills could do worse due to their primary dependence on condition available once-per-day, particularly during chick-rearing as offspring are fed several times per day (Harris and Wanless, 1986). Razorbills could instead be more resilient to changes in larger scale distributions or predictability of prey distributions as their cost of visiting several sites are likely to be lower due to larger wing-to-body mass ratio (Thaxter *et al.*, 2010), and in this system clearly utilize a wider range of foraging habitats **(Ch. III;** Isaksson *et al.*, 2019) suggesting more active search behaviour and thus potentially wider knowledge of available foraging sites. This nuanced difference not only improves the two species individual survival chances but also ensures stability in the broader ecosystem, potentially allowing one species to succeed when the other struggles (Mooney *et al.*, 2009). These findings highlight how morphological adaptation, and energetic trade-offs drive niche separation, reducing interspecific competition and shaping predator responses to prey behaviour. Further, I here reveal both species-specific strategies and shared constraints in how seabirds cope with a patchy and shifting marine environment, that could be used as baseline for comparative studies.

While it is tempting to conclude that aggregations are the ultimate problem to these diving seabirds, and that aggregations must be omitted through depth and/or time selectivity to enhance foraging efficiency, I must confess that this is not completely clear. A study on a closely related diver, the Atlantic puffins (*Fratercula arctica)*, showed that they were highly successful in hunting herring schools (Axelsen *et al.*, 2001), while studies on the dives of Cape gannets *Morus capensis* showed that they were most successful when schools were actively broken up by group-foraging seabirds (Thiebault *et al.*, 2016). Another study on little penguins (*Eudyptula minor*) showed that such collaborative approaches to aggregations were driven by ability to detect prey rather than to increase capture rate (Sutton, Hoskins and Arnould, 2015). In this study, I could not tell if the prey aggregations changed sizes or density over the season, nor fish species or size group. Thus, I advise some caution in concluding on the specific future perspectives of diving seabirds' response to aggregations, beyond that if aggregation behaviour in prey is reduced it may not be of an issue to these diving seabirds which mainly foraged at the time of day when aggregation numbers were minimal **(Ch. II)**. To clarify these results, future studies should focus on explaining changes in aggregation behaviour by species and size groups in long-term monitoring with large variations in environmental factors (Whitton *et al.*, 2020).

5.2.2 Predictability of prey

The third aim was to determine how dependent diving predators were on stability and predictability of prey abundance. Diving guillemots utilised sites with short-term stable and long-term predictable fish abundances, more than what could be expected at random **(Ch. III)**. Despite this, they showed responses in distance moved to in-site prey abundances and habitat aspects (i.e. depth of seabed) that could best be described as 'giving-up' on a foraging site, with transition to searching behaviour and/or visitation of new sites. I did not deeply investigate the search behaviour, as others have before (Fauchald *et al.*, 2000; Davoren, Montevecchi and Anderson, 2003). The major goal of including search was to establish if deterministic responses to the focal environment were detectable, as opposed to under strict site fidelity. More importantly I seek to determine if predictability of prey abundance were relevant and recognizable to the guillemots' foraging behaviour. The areas chosen by guillemots for foraging typically had a depth of seabed deeper than 70 meters, but a rather low abundance of prey compared to the available environment. Further, it was intriguing to see how guillemots abandoned high abundance areas (of potential prey) with large spatial steps, for sites with low, stable and predictable abundances **(Ch. III)**. This implied that the guillemots may have searched for a habitat associated with a specific prey type, rather than the highest abundance of any potential prey species (Waggitt *et al.*, 2018). The sought area indeed overlapped with the estimated high-probability-of-spawning area of sprat (Parmanne, Rechlin and Sjöstrand, 1994). Unfortunately, I could not distinguish if the short-term stability were due to the low abundance of fish or due to a continued flux of fish, though the width of spawning season and the traits of habitats selected for spawning by sprat is likely to explain such long-term predictability (Aro, 1989; Parmanne, Rechlin and Sjöstrand, 1994).

When modelling the prey abundance, I tested for different scales of prediction and found an aggregated data-based model to perform somewhat better than the full resolution data model (R^2: 0.30 versus 0.38 respectively). However, this came with a trade-off between number of observations used as foundation for the model (42,000 versus 1,800) and the degree of significant temporal autocorrelation (<0.2 across >50 observations versus 0) **(Ch. I)**. The overall model performances here were equal to, or somewhat lower than, many species distribution models for similar species based on much shorter-term traditional vessel data (Pennino *et al.*, 2020; Schickele *et al.*, 2020; Palermino *et al.*, 2024). Whether this is due to the accumulation of at least three species of fish in a time with very different species-specific habitat requirements (Aro, 1989; Olsson *et al.*, 2019), or small-pelagic fish not being very predictable on this spatiotemporal scale could not easily be disentangled.

The temporal patterns in depth and number of aggregations by time of day and season add another dimension to prey predictability for seabirds **(Ch. II)**. As clupeids exhibit a stronger diel vertical migration than sticklebacks, it is fair to assume that the foraging close to dusk and dawn is related to the predictability of clupeid biomass near the surface (Jurvelius *et al.*, 1996; Cardinale *et al.*, 2003; Regular *et al.*, 2010; Regular, Hedd and Montevecchi, 2011; Elliott and Gaston, 2015). Interestingly, the time-related number of aggregations **(Ch. II)** shows that aggregations in this system may not be predictable on a 12-24h scale (e.g. Weimerskirch, 2007), but here rather only for a few hours. However, aggregation behaviour is typically dependent on conspecific abundance, season and the environment (Pavlov and Kasumyan, 2000). In the core foraging areas of guillemots, the abundance was stable or changed slowly **(Ch. III)**. Thus, such stable sites (i.e. scale dependent) are likely to have similar amounts of schools/aggregations at the same time of day **(Ch. II)** over significant time periods (e.g. weeks, Fauchald, 1999), till there are sufficient changes in conspecific abundance, or other environmental aspects affecting aggregation behaviour have happened **(Ch. III)** (Pavlov and Kasumyan, 2000). Though the alcids in this study system seemed rather uninterested in fish aggregations, many of the worlds' seabirds **(Ch. IV)** are highly dependent on schools to detect and hunt prey (Axelsen *et al.*, 2001; Litzow *et al.*, 2004; Sutton, Hoskins and Arnould, 2015; Thiebault *et al.*, 2016).

The findings in **chapter III** suggest that for highly specialized diving predators like guillemots, long-term predictability and short-term stability in prey availability are crucial, supporting the idea that niche divergence can evolve in response to reliable access to specific prey types rather than opportunistic foraging.

5.2.3 Natural variation in foraging conditions

I wish to shortly put focus on the natural variations in prey field throughout this study. Early studies on marine systems have emphasized the high degree of stochasticity in spatiotemporal biomass distributions (Weimerskirch, 2007), before tools to successfully predict species distributions in respect to their niches were developed (e.g. Giske, Huse and Fiksen, 1998). With this thesis, I here point back towards complexity, not in the form of randomness, but rather in the presence of large, seasonal and annual variations and fluctuations that predators must have adapted to tackle in their natural environment **(Ch. I-III)**. In this study, prey availability within the seabirds' foraging range varied substantially by time of day and season **(Ch. I-III)**. This included variation in, and rate of changes in, prey abundance (Fig 7A; **Ch. I & II**), prey depth (Fig. 7B), abundance in shallow water **(Ch. II)**, and number of aggregations (Fig. 7C). In addition, there was significant variation in spatiotemporal prey distribution **(Ch. I)** and rate of change **(Ch. III)** on both a fine and coarse spatiotemporal scale. Diving seabirds were tracked from May 16th (week 20) at the earliest to August 05. (week 31) at the latest (Table 1), while there were dramatic decreases in both the number of aggregations and depth of prey per time of day. While prey distribution patterns may follow predictable diel and seasonal patterns, the width of conditions a predator must respond to over a season (Fig. 7) requires a behavioural and sensory flexibility that allow them to cope with these environmental fluctuations, razorbills and guillemots alike. Indeed, the large variation in foraging distances used both by closely related seabird species and across families (**Ch. IV**) reflect such large variations in conditions during breeding (Fig 8A). Thus, the key challenge for foragers may not lie in handling a wide range of prey distributions patterns or abundances per se. Rather, the challenge likely lies in the cumulative costs of long lasting sub-optimal conditions, and the need to remain flexible across a wide range of dynamic conditions (Keogan *et al.*, 2018; Dunn *et al.*, 2019, 2020). Changes in prey distribution patterns over extended time periods have consequences for cost of foraging (**Ch. II**), which are highly likely to manifest as slow and cumulative consequences over time rather than immediate and easily recorded effects. These findings also point to the importance of timing of high-cost life-stages to favourable prey distribution patterns beyond sheer abundance for successful reproduction and long-term survival (Durant *et al.*, 2005; Regular *et al.*, 2014).

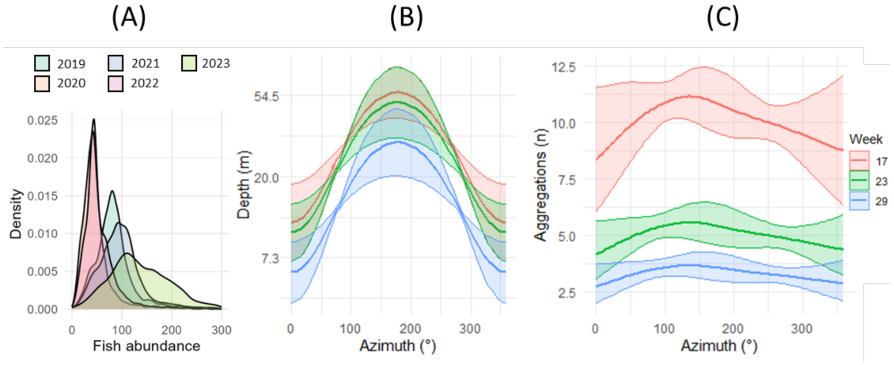

Figure 7. Seasonal variation in estimated (A) abundance (m^2 nmi^{-2}) by year, and (B) depth & (C) number of aggregations, per degree Azimuth estimated across 12 weeks, presented for 3 weeks of the year. Abundances in A were derived from Ch. I & III, and models of prey distribution patterns in B and C were derived from Ch. II.

Table 1. Number of dives observed per Julian week of the year by species.

Week	Guillemot	Razorbill
20	141	0
21	310	0
22	1042	0
23	2486	28
24	4099	1108
25	6057	1101
26	7363	1958
27	3833	1183
28	3207	941
29	2987	696
30	2603	788
31	699	202

5.2.4 Stage dependent and non-dependent foraging

When investigating the responses of seabirds to variations in prey availability across the breeding season, one cannot omit the dimension of stage and thus state-dependence of foraging behaviour (Shepard *et al.*, 2009; Regular *et al.*, 2014; Amélineau *et al.*, 2021; Cleasby *et al.*, 2023). For most years of GPS tracking, the guillemots returned to the same general area during chick rearing (Fig. 8B), despite areas with much larger concentrated abundances, being available closer to the colony **(Ch. III)**. Under the high energetic demands of chick rearing, predictability in prey availability may be more important than sheer abundance (Regular *et al.*, 2014). The preference for specific, low-abundance sites suggests that reliable access to suitable prey (i.e. species, size) was prioritized during this critical breeding stage (Golet *et al.*, 2000; Kadin *et al.*, 2012; Regular *et al.*, 2014).

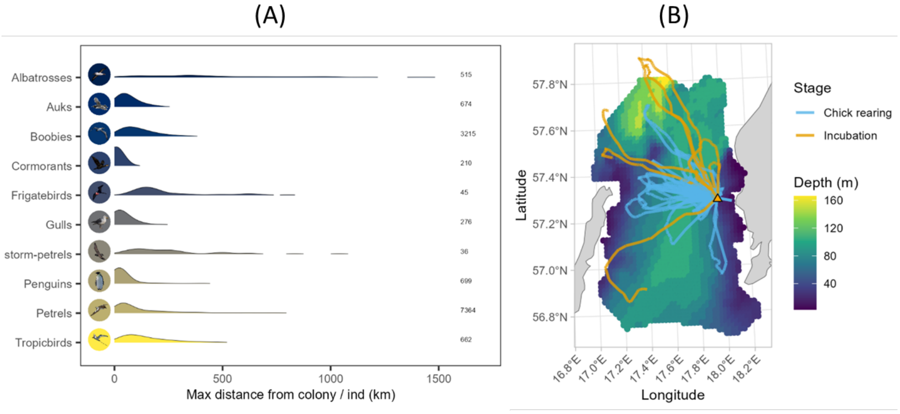

Figure 8. Variation in foraging ranges (A) across seabird families, with number of individuals on the right, and (B) of the Stora Karlsö guillemots by breeding stage. A as derived from Ch. IV and B from Ch. I & III.

Interestingly, diel foraging patterns of guillemots remained consistent throughout the breeding season, with little variation across stages or over time despite large changes in trip frequency and dive numbers associated with the shift from incubation to chick rearing (Bohacek, 2022). Although the Scandinavian summer nights are never completely dark **(Ch. II)**, there are significant changes in light conditions from May to July. During incubation in May, midnight light levels were lower than in late June-early July, while during daylight, prey were deeper and aggregation numbers higher (**Ch. II** and Fig. 7). Yet, the guillemots showed no clear shift in the timing of dives. Given all that is known about guillemots ability to forage in the dark, low light levels were unlikely a limiting factor for diving at midnight in this period (Regular, Hedd and Montevecchi, 2011; Chimienti *et al.*, 2017) Instead, foraging less during peak conditions at midnight (Fig. 9) is more likely a strategic choice tied to maximizing the opportunity to forage on clupeids under relatively favourable conditions. By feeding in early morning and late evening, guillemots could use the elevated foraging conditions made available by shallow prey twice per day instead of once at midnight **(Ch. II)**. Guillemots' tendency to feed the chick in the evening and then again early in the morning too fits this time budget (Bohacek, 2022). Yet, from incubation and non-breeding data it became clear that timing for chick-feeding was unlikely to be the driving force to timing of dives in guillemots **(Ch. II)**. This is particularly interesting from a life-history perspective of long lived species that may skip entire breeding seasons (Reed, Harris and Wanless, 2015), as it reflects that while the parent guillemot has to return with prey to the chick and switch on watching the nest, they do not seem to change *when* they feed to fit the chicks needs. The feeding is still primarily driven by prey-patterns and efficiency of foraging, thus good foraging conditions **(Ch. II)**. To the razorbills, chick rearing along with changing light levels and aggregation patterns, are more likely to be driving factors of timing of dives. This is particularly likely when it comes to foraging during the middle of the day and around noon, primarily done during chick rearing (Fig. 9). The underlying reason could be the higher sensitivity to low-light conditions and the need to provide chicks multiple times during the day, that persuade razorbills to utilize poorer conditions around noon during chick-rearing **(Ch. II)**. The shift to foraging at midday during chick rearing could come with high costs for razorbills, suggesting that they are more limited in timing of efficient foraging (Shoji *et al.*, 2016). Compared to guillemots, this may indicate a steeper trade-off between parental care and foraging efficiency (O'Rourke and Renn, 2015). It highlights how species-specific adaptations to foraging windows for foraging can shape the actual cost of reproduction under variable prey and light conditions. Notably, chick rearing in razorbills happens in the beginning of July, around 2 weeks later than guillemots (Engwall, Waldenström and Hentati-Sundberg, 2022), while the numbers of aggregations were at the lowest recorded.

(A) (B)

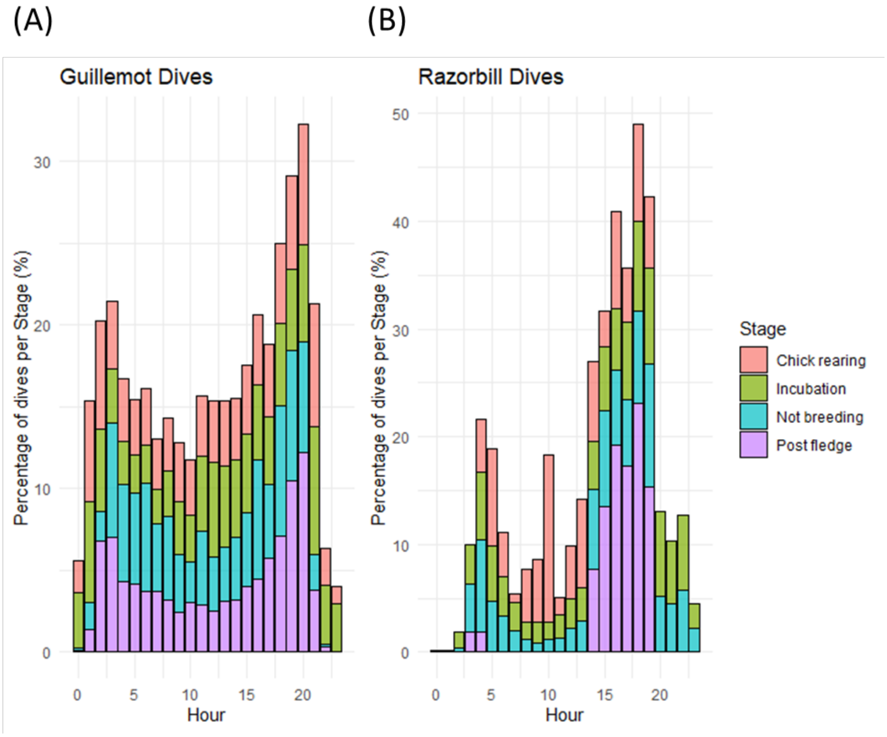

Figure 9. Hour of dives in the Stora Karlsö colony by Stage for (A) guillemots and (B) Razorbills. A as derived from Ch. II.

5.3 Conservation actions for foraging seabirds

For the fourth aim, I determined that the worlds' seabirds are not well protected with respect to their potential foraging range **(Ch. IV)**. This was established from confirming that seabirds potential foraging ranges could be well predicted using primarily simple flight-related traits including wing aspect ratio (i.e. width-length ratio) and flying style, subsequently matching the foraging range with current MPAs. The connection between birds potential foraging range, wing morphology and flight mode is not a novel idea (e.g. Thaxter *et al.*, 2012), but thanks to global and open databases, such large-scale analyses can be performed and used to create new baselines tools for conservation. Importantly, the modelled foraging ranges allowed the inference of potential foraging ranges of less studied species such as those breeding in remote colonies, using morphology as a proxy.

Notably, when the modelled foraging range of a species deviated from the estimates, the most likely reason was tied to the species foraging niche (Schreiber and Burger, 2001). For example, skuas (*Stercorariidae*) were overestimated, probably because they partially are kleptoparasites, stealing food from other species or scavenging. The common tern (*Sterna paradisea*) too was highly overestimated, where their strategy of hunting in short distance from exposed nests was obscured by wing morphology adapted for long-distance migration. Meanwhile, shearwater and petrel (*Procellariidae*) foraging ranges were typically underestimated, likely due to their provisioning strategy reliant on crop milk. This highly energetic residual of feed allows them to stay away from chicks for extended time periods (Kooijman, 2020). Thus, knowledge on areal usage by foraging habitat and mode, both specific to species and across species with similar niches, can aid in better estimating potential foraging range **(Ch. II-III;** Boyd *et al.*, 2015; Hickcox *et al.*, 2022; Regan *et al.*, 2024). Large scale prey distribution and/or habitat models based on autonomously sampled data can add further information on key areas to protect, when tagging of predators or large-scale vessel surveys are less feasible **(Ch. I)**. Further, knowledge about the behavioural responses in seabirds to prey distribution patterns **(Ch. II-III)** can be highly valuable to understand which aspects of prey to consider for protection, particularly when food availability is the core issue (Buchholz, 2007). Indeed, for seabird species that forage at specific times of day **(Ch. II)**, reducing temporal overlap of fishing effort with foraging times can potentially reduce bycatch (Gilman *et al.*, 2023). By combining predicted foraging ranges with prey information **(Ch. I),** predators habitat selection and behavioural insights **(Ch. II-III)**, we can better identify core aspects for effective protection during breeding, aligned with both species-specific needs and broader ecosystem functioning (Thaxter *et al.*, 2012).

We found that the foraging areas of breeding seabirds only covered ~10% of the global ocean, but almost all of them (95%) were in exclusive economic zones (EEZ; **Ch. IV**). This is likely the major reason for the currently poor conservation status of foraging ranges around breeding colonies (Grémillet *et al.*, 2018; Cury *et al.*, 2011). However, conserving seabirds foraging ground have positive effects on entire ecosystems (Sabarros *et al.*, 2012; Young *et al.*, 2015; Erisman *et al.*, 2017), where rapid positive effects on local prey populations may lead to a gradual reduction in the area necessary to protect (Sydeman *et al.*, 2021). In systems where foraging sites of seabirds are predictable due to spawning habitats of their prey, protecting these areas can create positive feedback loops enhancing prey availability, thus supporting seabird reproduction also in the coming years (Sabarros *et al.*, 2012). Indeed, seabirds are brilliant umbrella species when conserved, due to their flexibility in space and variety in habitats and prey species sought, in addition to their tendency to breed in mixed colonies with other seabird species of differing niche (Young *et al.*, 2015; Veit and Harrison, 2017). Further, many seabirds hunt in coalition with subsurface predators, such as *Gadidae* and *Scombridae* species (Sabarros *et al.*, 2012). The effects subsurface predators have on depth distribution and detectability of prey to seabirds may have been a significant driver of many seabirds' adaptations to marine resource dependence and are key to efficient foraging for many seabirds (Ceia and Ramos, 2015). Industrial fisheries targeting large predator fish as well as forage fish exacerbate shifts in such fine-scale forage fish distribution patterns (Frederiksen *et al.*, 2008; Sabarros *et al.*, 2012; Montevecchi, 2022). For less depth-adapted divers, plungers and surface feeders, there may be detrimental impacts, but also for deep divers' additional energetic costs through decreased foraging efficiency may have long lasting effects (Montevecchi, 2022). The conservation principle "one third for the birds" (Cury *et al.*, 2011) suggests setting aside a portion of forage fish stocks to support seabird reproduction, but this may only hold if a sufficient proportion of that prey remains physically and behaviourally available to the birds (Waggitt *et al.*, 2018). By protecting more of the core foraging areas for diving seabirds, safe havens can be generated also to larger sub-surface predators that assure prey availability, balancing a healthy ecosystem fundamental for mitigating further biodiversity loss.

For well-studied seabird species, core foraging area and site fidelity could be determined through tracking as well as knowledge about prey species distributions, abundances and habitat **(Ch. III)**. However, for less studied species, combining the knowledge of their potential foraging range **(Ch. IV)** with knowledge from behaviour of closely related species or species with likely similar foraging niche **(Ch. II)** can be enough to retain successful protection.

5.4 Limitations and future studies

Firstly, I'd like to discuss the missing dimension of prey niche. Ironically, while spending great effort in understanding and describing the range of niches from the extremely fine-scale differences between two sympatric seabirds **(Ch. II)** to the spatial use of the global diversity in seabirds **(Ch. IV)**, I here could only estimate the spatial distribution on community level for small pelagic fish, without taking into consideration their species and size/maturation specific niches (Aro, 1989; Bergström *et al.*, 2015). While the areas most used by guillemots showed an overall increase in prey abundance from year to year **(Ch. III)**, it is not possible at the time to attribute the positive development to a species level. Similarly, there were large abundances of potential prey close to the breeding colony **(Ch. I)**, but with no species information inferences on birds' prey selection versus habitat knowledge cannot be made. There are methods for inferring species and size classes based on hydroacoustic data (Dragonette, 1999; Pedersen and Korneliussen, 2009; Palermino *et al.*, 2021), and I, with my research team, made an effort to improve the accuracy of identifying local small pelagic fish species to this project (Hentati-Sundberg *In. Prep*). However, it is still a long way from being implementable to the multiple terabytes of data collected in this study. For species inferences, more automated approaches such as supervised learning could be a future alternative. Before that, site specific case studies, such as comparing stable versus variable sites across the season, combined with trawling may aid in understanding prey distribution on species and size-class level. Detailed studies of spatial patterns in small pelagic fish, especially contrasting spawning migrations with non-spawning distributions, could clarify seabird site selection and prey predictability. In addition, more understanding of fine-scale prey behaviour under varying environmental conditions and future climate change predictions would be valuable in predicting the future of seabirds.

Secondly, I wish to discuss the predator effects on prey distribution. From this study it was apparent that while predation from above was most intensive during late summer (i.e. seabird chick rearing), the forage fish was found in shallower depths and with fewer aggregations **(Ch. II)**. At the same time, prey abundance was increasing from June to July **(Ch. I and III)** close to the colony of the ~100,000 fish-eating seabirds (including non-breeders). Though the Baltic Sea may be a particular system, the seabird populations are growing while the sites used the most has no traceable negative change neither on a short nor long term scale **(Ch. III)**. Indeed, the changes in prey patterns are completely opposite to what would be expected of predator avoidance behaviour in prey **(Ch. II & III)**, raising questions about the preys' perceptions of predation risk (Gaynor *et al.*, 2019; Magurran, 1990; Elliott *et al.*, 2009; Mehner, 2012; Benoit-Bird, Moline and Southall, 2017; Kasumyan and Pavlov, 2023). I thus suggest long-term studies of diel distribution patterns (e.g. across seasons) in relation to environmental variables beyond light, with more information on the fish species, to understand the underlying forces. Further, more information on prey species distribution and local changes in fish species and size class specific abundance can inform if there are notable effects of the seabirds foraging in the prey composition.

Thirdly, the predator-GPS tracking should be evaluated. In total, I had 6 weeks of overlapping predator-prey data with GPS **(Ch. III)** and 12 weeks of overlap with TDR data **(Ch. II)**, but there was a lack of across-year repetition in seabird GPS-tracking data for each sampled week **(Ch. II-III)**. While much time and effort were spent planning the data sampling with the USV, more effort invested in planning the concurring data sampling from predators would have been valuable. Only after 3 years of USV survey were seabirds tracked during incubation (2022), revealing that their foraging range in this period largely outmatched the survey area of the USV. 5 out of 10 foraging trips recorded ended outside of the survey area during incubation **(Ch. III)**, and one trip had to be completely excluded as there were only a few kilometres overlap before the bird travelled a baffling rout to the north of Gotland (Fig. 2). Thus, prey variables for the further most dives in **Chapter III** were estimated solely based on environmental variables, week of the year, and in correspondence to the mean of the area.

Lastly, I wish to elaborate on the investigations of scales. While the scale of observation is a central consideration in ecological analyses of responses between predators and prey (Fauchald, 1999; Fauchald, Erikstad and Skarsfjord, 2000; Weimerskirch, 2007), this thesis has largely maintained a consistent focus on the finest meaningful resolution available. This decision was motivated by the exceptional detail of the dataset; it seemed important to first explore the system at its finest level before considering broader data grouping, while different scales were investigated before numerous decisions. For example, in **Ch. I**, I compared two spatial and temporal resolutions in the small pelagic fish distribution model. In **Ch. II**, I summarized prey aggregations within 10-degree azimuth intervals (approximately 40 minutes), although both finer and coarser resolutions were explored. I also grouped dives into bouts based on surface durations from literature, as in my data a natural segregation point was unclear. Although scale was not in focus across chapters, it is an important underlying dimension. A thesis worth of studies could probably have focused on understanding how the observed predator-prey interactions shift with scale alone. Such investigations could help explain some of the uncertainties in model fit and bird response patterns observed in this thesis.

6. Conclusions

In this thesis, I addressed a central knowledge gap in seabird ecology: how diving predators respond to natural variation in prey landscapes, and how such responses shape niche divergence, foraging flexibility, and conservation vulnerability. By integrating fine-scale predator behaviour with prey distribution data and trait-based conservation frameworks, I explored how foraging dynamics scale up to influence ecosystem use and biodiversity resilience. In **chapter I**, I demonstrated the utility of autonomous sampling with an unmanned surface vehicle (USV) in marine ecological research. This method offered high-resolution, near-continuous data over extended timescales, but with limitations related to speed variability and lack of sensor maintenance. Using USV-data, I estimated forage-fish distribution, comparing model performance on data with fine and coarse spatiotemporal scales. In **chapter II**, I revealed how prey depth and aggregation patterns followed diel dynamics, and diverging predator responses to these patterns. Guillemot foraging was linked to prey depth, while razorbills responded to light levels and prey aggregation, demonstrating a strong example of niche partitioning under shared environmental conditions. In **chapter III**, I showed that guillemots consistently and actively selected deep-water foraging sites characterized by stable prey availability across the breeding season and increasing abundance across years. In **chapter IV,** I confirmed that simple morphological traits and flight mode can predict seabird potential foraging range. Applying these traits to global species distributions revealed that existing marine protected areas cover only 1% of seabird foraging habitats.

Together, these findings illustrate how closely related species can diverge in their foraging strategies through different responses to environmental variability and prey field, and how such divergence supports niche partitioning and coexistence. Trait-based predictors, in turn provide a valuable approach for assessing conservation risks, especially for species and regions less studied. By linking fine-scale predator-prey interactions with global-scale conservation frameworks, this thesis provides a multiscale perspective on foraging ecology and its role in shaping biodiversity outcomes under anthropogenic impacts. As prey landscapes continue to shift with climate and fisheries pressure, the behavioural flexibility and constraints in predator foraging strategies will play a crucial role in determining both species persistence and ecosystem resilience.

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Popular science summary

Food is crucial to survival, due to its energy that allows for life to take its course. Paradoxically, it takes energy to gain energy: without enough food it becomes impossible to gain more food in the long run. Due to this, many of the unique traits you see in organisms are specifically adapted to finding and eating as efficiently as possible. In example, having good eyesight, a strong nose can be great assets to locating food quickly. However, one must also be able to move, often fast and far. If the food is distributed in patches rather than evenly in the environment, then it can take a lot of time and thus wasted energy searching 'in the blind'. Indeed, if it is far between good feeding spots, then having a good search strategy may be crucial for success. In example, learning what to look for, such as landscapes, vegetation or light conditions that may indicate the preferred foods likelihood of presence, or remembering where one found food at the same time last year may be simple ways to increase the success rate. However, this means the food is somewhat predictable, based on the hints of the environment, but this is not always the case. For animals looking for food that floats freely on the surface of the sea, the time food may be found can be somewhat predictable, based on how high the temperature is or how late in the season it is, but the position can be next to impossible to know without checking every now and then, or even looking anew every time one needs food.

As with anything highly sought, food sources can be very popular, with many different animals wanting to share it. Thus, animals have developed unique features and a wide range of strategies to do better in the competition. Seabirds is an incredibly diverse group of animals, due to their large range in specialisations and behaviours. They all find their food in relation to the sea, at least parts of the year, and are experts in finding and chasing food in this difficult and abrupt environment. However, the oceans are changing because of large human activity. As the sea becomes warmer, many of its feature's change, which affects how available and predictable food is. The same is true with fisheries, pollution and destruction of under-water habitats, and these effects become even stronger when the climate change. This change in predictability of food resources is becoming problematic for animals, such as many seabirds, that have spent millions of years specializing to rely on that predictability. Suddenly, food is not found in a specific site used for generations, or there is so little food that the competition is too high.

Or there is enough food, but it is impossible to catch because it is too deep in the water or to spread out to catch efficiently. Even the quality of the food can change, so if it is as hard to catch as before then less energy is gained for each mouthful. During most part of the year seabirds may be free to follow moving prey around, but this is more difficult when they lay eggs and raise their chicks. In this time, the birds need to return to the nest in between feeding, to warm and protect the eggs or to bring food to the chick(s). In this period, the availability of food is restricted to how far the bird can fly, how deep it can dive or how easily it can catch the prey. The thing is, while we know that fisheries and climate change affect both the prey abundance and all sorts of prey behaviours essential to many seabirds, we don't actually know very well how birds use these food sources in the first place. This is due to the simple problem of being in the right place and the right time. Seabirds can go really far to find food, while the food is under the surface of the water, so it is very hard for us to know where the birds will go and be there to monitor the activity at the same time. However, with new technologies such as drones, we are now able to move scientific equipment far and for long with very low costs. In addition, the birds can share their movements with us, with little GPS's telling us when and where they go, and pressure sensors that reveal when and how they dive.

For my thesis, I used five summers of data from a small sailboat-like drone with an echosounder, a salt- and temperature measurer and sensor for measuring algal activity, all giving me information necessary to find out where the seabirds preferred little fish spends their time. In addition, a gang of deep-diving seabirds, common guillemots and razorbills, shared information on their foraging behaviour. I matched all this together to see how the two species behaved under different fish-prey conditions, to get a better understanding of when the birds thrived and not. As the two species are slightly different, they were expected to also respond differently to prey distributions. In addition, I looked at how far all the worlds' ~360 species of seabirds, with all their different adaptations, moved when looking for food. As seabirds are highly threatened by human activities, and particularly when they are out looking for food, I used the information on how far they go to assess how well they currently are protected by legislations.

Using statistical analyses, I firstly found that using the sail drone to determine where fish was present worked well. There were a lot of challenges on the way, which affects how we can and cannot use the information from the drone, but in all I found that a lot of useful and new information could be retrieved, which has been very hard to get with large boats, such as surveying shallow depth areas, or large areas for a long period of time continuously. I used this information, along with the diving behaviour of guillemots and razorbills to look at how the depth distribution and schooling patterns of fish under different light conditions affected the two seabirds dive behaviour and found that razorbills were quite sensitive to aggregations and preferred to forage when there were less of them, while the light conditions were good. The guillemots, however, dove deeper and in lower light conditions, and didn't seem to mind the aggregations that much. Interestingly, the guillemots diving reflected the depth of fish, where they dove more when fish was closer to the surface during the night and less when the fish was in deeper depths during the day. Meanwhile, the razorbills would dive most in the afternoon and evening, which turned out to fit well with the time of day when the numbers of fish schools were low while light conditions were good. This means that if there are changes in these fish behaviours, the two seabirds that have their nests on the same island at the same time of the year could do very differently as a result. I then focused only on the guillemots, investigating what places they went to when looking for food, and if they seemed to search actively or just go straight to predictable places, they knew to be good. I found that, contrary to my expectations, the birds did not go to the places with the most food. Instead, they went to deep areas where there was relatively little food abundance, yet where the food was predictable across years and stable over the season. This is probably because they are looking for a specific type of food and/or habitat, likely the spawning sprat in the mid basin, which is the food they bring most to their chicks. However, this clarified one of the main limitations of the drone collected data, it could not tell the species nor size of the fish, just how much fish there were, within the size range the birds hunted. Finally, I could conclude that the distance flown to find food by all the worlds' seabirds, guillemots and razorbills included, were related to the size of their wings and the way they fly. With this information, I could determine that they were very poorly protected when foraging. Penguins were one of the groups that were better protected, likely because they are cute and far away from cultural fishery. However, additional information on foraging behaviour and site selection in seabirds could aid these models greatly in determining how to protect seabirds foraging grounds in the future.

In conclusion, drones can be used for large scale marine ecosystem studies. Deep-diving seabirds have very different approaches to how they forage, which makes each species unique but also vulnerable in its own way. The deep-diving and short ranging guillemot depend on predictable and stable food sources but have some active search behaviour as well- they do not only depend on their memory. And the worlds' seabirds need better protection that is based on where they forage, and how available the food is to them so they can forage efficiently, not just that food is abundant enough.

Populärvetenskaplig sammanfattning

Mat är avgörande för överlevnad, eftersom den ger den energi som krävs för att livet ska kunna fortsätta. Paradoxalt nog krävs det energi för att få energi: utan tillräckligt med mat blir det omöjligt att få i sig mer mat i längden. På grund av detta är många av de unika egenskaperna du ser hos organismer specifikt anpassade för att hitta och äta så effektivt som möjligt. Att till exempel ha bra syn och lukt kan göra det lättare att hitta mat. Du behöver också kunna röra dig, gärna snabbt och långt. Om maten fördelas fläckvis snarare än jämnt i miljön kan det ta mycket tid att söka "i blindo" och därmed slösa energi. Om det är långt mellan områden med god tillgång till mat kan en bra sökstrategi vara avgörande för att nå framgång. Att till exempel lära sig vad man ska leta efter, som hur typ av landskap, växtlighet eller ljusförhållanden kan indikera hur sannolikt det är att den mat man föredrar finns på platsen, eller komma ihåg var man hittade maten vid samma tidpunkt förra året, kan vara enkla sätt att öka hur frekvent man är framgångsrik. Det betyder att förekomst av mat kan vara förutsägbar baserat på signaler från omgivningen, men så är det inte alltid. För djur som söker efter föda som till exempel flyter fritt på havsytan kan tidpunkten för när födan finns tillgänglig till viss del vara förutsägbar baserat på temperatur är eller tid på säsongen, men exakt var födan finns kan vara nästan omöjligt att veta utan att då och då explicit undersöka omgivningarna, eller till och med varje gång det är dags att äta.

Som med allt som är eftertraktat kan områden med god tillgång till matvara mycket populära, med många olika djur som vill få del av maten. Djur har därför utvecklat unika egenskaper och ett brett register av strategier och knep för att överträffa varandra. Sjöfåglar är en grupp med stor mångfald, med stor variation i olika specialiseringar och beteenden. De får alla sin föda från havet, åtminstone under delar av året och är därför experter på att hitta mat i denna utmanande miljö. Men miljön håller på att förändras, på grund av alla de storskaliga mänskliga aktiviteterna. När havet värms upp förändras många av dess egenskaper, vilket påverkar hur förutsägbar tillgång har utvecklat sin förmåga att hitta mat genom att förlita sig på havets förutsägbarhet. Plötsligt finns det ingen mat på den specifika plats som använts i generationer, eller så finns det så lite mat att konkurrensen om den blir väldigt hög. Även om det finns lämplig föda, kan den vara omöjlig att få tag på det eftersom den finns för djupt i vattnet, eller är för utspridd för att fångas tillräckligt effektivt. Dessutom kan kvaliteten på maten vara lägre än tidigare, vilket innebär att det blir mindre energi kvar vid varje fångst. Under större delen av året kan fåglarna fritt att följa sina födoresurser, men det är svårare under den tid på året när de lägger ägg och föder upp ungar. Under denna tid måste fåglarna återvända till boet mellan sina jaktturer, för att värma och skydda äggen och get mat till ungarna. Under denna period begränsas därför tillgången på mat av hur långt fåglarna kan flyga, hur djupt de kan dyka eller hur effektivt de kan fånga sina byten. Saken är den att även om vi vet att både fiske och klimatförändringar påverkar såväl mängden föda som alla typer av beteenden hos de små fiskar som är väsentliga för många sjöfåglar, så vet vi faktiskt inte särskilt mycket om hur fåglarna använder dessa födokällor. Detta beror på att det är svårt att vara på rätt plats vid rätt tidpunkt. Sjöfåglar kan flyga väldigt långt för att hitta fisk, vilken dessutom kan befinna sig långt under vattenytan, vilket innebär att det är väldigt svårt för oss att vara där på plats och observera när fågeln söker föda. Men med ny teknik, som drönare, kan vi nu flytta och använda vetenskaplig utrustning långt bort och med brett sökfält till mycket låg kostnad. Dessutom kan fåglar dela sina rörelser med oss, med hjälp av små GPS:er som talar om för oss när och var de flyger, och med trycksensorer som avslöjar när och hur de dyker.

Under mitt avhandlingsarbete tillbringade jag fem somrar med att samla in data från en liten segelbåtsliknande drönare med ekolod, salt- och temperaturmätare och sensor för mätning av algaktivitet. Detta gav mig all den information jag behövde för att ta reda på var deras små bytesfiskar tillbringar sin tid. Dessutom delade en flock djupdykande sjöfåglar med GPS:er och djupmätare, inklusive sillgrisslor och tordmular, information om sitt födosöksbeteende. Jag kombinerade alla dessa data för att se hur de två arterna betedde sig beroende på utbredingen av deras bytesfisk, för att få en bättre förståelse för när fåglarna har mer eller mindre gynnsamma förhållanden. Eftersom de två arterna är något olika, förväntades även skillnader i deras beteenden. Dessutom tittade jag på hur långt alla världens ~360 arter av sjöfåglar, med alla sina olika anpassningar, rörde sig när de letade efter föda. Eftersom sjöfåglar är starkt hotade av mänskliga aktiviteter, och särskilt när de är ute och letar efter föda, använde jag informationen om hur långt de färdas för att bedöma hur väl de är skyddade av den lagstiftning som finns för att skydda dem under häckningssäsongen.

Vid at använda statistiska analyser upptäckte jag först och främst att det fungerade ganska bra att använda segeldrönaren för att ta reda på var fisken fanns. Även om det var många utmaningar på vägen som påverkar hur vi kan och inte kan använda informationen från den, fann jag över lag att den gav mycket användbar och ny information som tidigare varit väldigt svårt att få tag på med stora båtar. Det handlar till exempel om att kartlägga ytor på grunda djup, eller stora områden över en lång tidsperiod kontinuerligt. Jag använde denna information, tillsammans med sillgrisslans och tordmularnas dykbeteende, för att titta på hur djupfördelningen och fiskstimmens under olika ljusförhållanden påverkade de två sjöfåglarnas dykbeteende. Jag fann att tordmularna var ganska känsliga för förekomst av fiskstim och att de helst jagade efter föda när stimmen var färre och ljusförhållandena var goda. Sillgrisslorna dök djupare och under sämre ljusförhållanden än tordmularna och verkade inte bry sig så mycket om förekomst av fiskstim. Faktum är att sillgrisslornas dykbeteende reflekterade de djup som fisken befann sig på. De gjorde fler dyk när fisken var närmare ytan vid soloppgång och solnergång, och färre när fisken uppehöll sig på större djup under dagen. Tordmularna dök mest på eftermiddagen och kvällen, vilket sammanföll med den tid på dygnet då antalet fiskstim var mycket lägre. Det betyder att om det sker förändringar i fiskarnas beteende kan de två sjöfåglarna komma att svara på dessa på olika sätt, trots att de har sina bon på samma ö vid samma tid på året. Sedan fokuserade jag på sillgrisslorna, och undersökte vilka områden de använda när de letade efter mat, och om de sökte mat aktivt eller bara flög till förutsägbara eller välbekanta platser varje gång. Jag upptäckte att fåglarna, tvärtemot mina förväntningar, inte nyttjade till de platser som hade mest mat. I stället sökte de sig till djupa områden där det fanns relativt lite mat, men där födotillgången var förutsägbar under flera år och stabil över säsongen. Detta beror troligen på att de letar efter en specifik typ av föda, mest trolig skarpsill som leker i djupet vid den här tiden på året. Skarpsill är också den föda de oftast ger sina ungar Detta visade dock på en av drönarens huvudsakliga begränsningar: den kan för närvarande inte säga vilken art fisken är eller vilken storlek den har, bara att det är fisk av den storlek som fåglarna jagade. Slutligen kunde jag dra slutsatsen att den distans alla världens sjöfåglar, inklusive sillgrisslor och tordmular, flyger för att hitta föda är relaterad till storleken på deras vingar. Med denna information kunde jag sedan konstatera att de är mycket dåligt skyddade vid födosök, då bara runt 1% av dom tillgängliga jaktområdena omfattas avskydd, och dessutom bara för få arter. Pingviner var en av de grupper som skyddades bäst, förmodligen för att de är söta och lever långt ifrån där vi människor bor. Ytterligare information om sjöfåglarnas födosöksbeteende och platsval skulle dock kunna hjälpa dessa modeller i hög grad för att avgöra hur sjöfåglar ska skyddas i framtiden.

Sammanfattningsvis visar min avhandling hur drönare användas för att studera sjöfåglars födosöksbeteende. Mina studier visar hur sjöfåglar som dyker djupt kan skilja sig åt väldigt mycket i hur de söker föda, vilket gör varje art unik men också sårbar på sitt sätt. Sillgrisslor är beroende av förutsägbara och stabila födokällor, men har också ett visst aktivt sökbeteende - de är därför inte bara beroende av sitt minne vid födosök, utan har specifika krav på bytestillgänglighet och de habitat de söker upp. Slutligen behöver världens sjöfåglar ett bättre skydd som utgår från var de faktiskt söker föda och hur tillgänglig födan är för dem - inte bara från hur mycket föda som finns.

Acknowledgements

Thank you to main supervisor **Jonas** for giving me the opportunity to join the Baltic Seabird Project, for supervision and room to expand as a researcher. You have opened my eyes to the opportunities that come with new (and well-installed old) technologies and given me a different view on the future of research. Thank you for all those good times at Stora Karlsö and Gotland, practical field challenges, and opportunity to realise my dream of becoming a researcher. Thank you to my co-supervisor **Michele**, for the meetings, supervision and feedback provided during the course of this work, it's always a pleasure to see you! Thank you to my co-supervisor **Sam**, for the guidance and support, for including me in your research group and receiving me in Liverpool. Thank you to **Henrik Österblom** for leading the overarching project 'Sustainability science, dialogues and novel technologies for understanding and managing ocean ecosystem tradeoffs', and for all interest, support and feedback on my work. Thank you to **Olof Olsson** and all the participants in the **Baltic Seabird Project** for the many wonderful experiences and interesting challenges we've faced together, I think of the time at Stora Karlsö with great joy and cherish the field seasons, both the first feast-week of the year, and into the late days of pasta with lentils. I will miss the island, the community and all of you greatly! See you up the road (…up fyrtrappan)! A special thank you to the **Sailbuoy Team** (98% being **Aron**) and the **AI-team** (**Sofia** and **Joakim**) for all aid, collaboration and support throughout the years.

Thank you to all my coauthors for your efforts and support! A special thank you to **Quentin** for your team spirit, for all the great research discussions and for your purest generosity, for the amazing trip to Coimbra and the fieldwork at Stora Karlsö. Thank you for all your support on writing the third paper and for considering all my suggestions regarding the 4th chapter. You have been essential to my work spirit the last two years, and I truly aspire to establish The Great Seabird Triangle with you and **Marianna** in the future! A great thank you to **Claire Saraux** that received me in Strasbourg, and for all the support and guidance in writing the 2nd chapter! The greatest thank you goes to my dear **Francesco** for every single little thing over the last four years. You believed in me when my despair was the greatest, you helped me take my ideas and bring them to life and gave me the tools I needed to write the 1st chapter. The extent of your care and support

is unmatched and I could not have written this thesis without you helping me and pushing me forward.

Thank you to my students, **Camilla**, **Mica** and **Elin**, what superstars you are in mind and spirit!! You all kept on doing excellent work after we parted ways. Take care, and I look forward to seeing you again up ahead.

Thank you to **André Chiaradia** for the great learning opportunities and for taking care of me on Phillips Island, during my research exchange. Thank you to **Marianna Chimienti** for inviting me to visit and hold a seminar at the University of Bangor, in Menai Bridge. I greatly appreciate all the encouragement, advice and all the good times we've shared there, in Australia and in Sweden. Also, thank you to **Prof. Nonnis-Marzano** at the University of Parma, for trusting me to open the 19th Italian Ichthyological Associationas (AIIAD, 2024) as key-note speaker. Thank you to the **ICES WGFAST** for great scientific meetings, discussions, and for the brilliant time in Brest, France (2024).

A huge thank you (and many hugs) to my fellow **PhD-students** and post-docs, at SLU, in Liverpool (the brilliant **SEAGUL/AEGUL** people), in Strasbourg, in Norway, in Denmark, in Canada, in the Netherlands, and elsewhere. Particularly thank you to the **Aqua PhD-students**, and those at Ultuna which has become like a family the last years, I will miss our camaraderie greatly. Know that you are all obliged to let us know if you are heading for the North so we can take you in!! And thank you to **Lilia**, my sister-in-arms working with the drone and diving birds in Strasbourg and on Philip Island simultaneously with me! Your brilliance is inspiring, your kindness is endless, and I look so much forward to see what more you will get out of your work!

Thank you to all my **colleagues in Lysekil** and **SPRAS-team** on **RV Svea**, and to the people that made me feel alive there when covid was all-joy-supressing! To you that helped me when I didn't know where to turn (**Jessica**), that showed me where they first heard Frank Zappa (**Perry**), that took me on mushroom expeditions (**Massimiliano**) and that sang Hunger Strike with me over wine in the late evenings (**Eros & Fra**). Thank you to the **Department of Aquatic Resources**, my colleagues and many now friends, for discussions, laughs and cake. So much cake.

I need to express a special thank you to all the people that took care of me when I didn't know where to turn, that eased my confusion, made me feel seen and understood, and helped me foster my ideas into publishable stories.

Particularly thank you to **Magnus Huss** for being a diplomatic rock when diplomatic rock was needed. Also thank you for your brilliant humour; very, very important.

Thank you to **my family**, for supporting my journey and being so present in developing our plans ahead. Thank you to my closest friends in Sweden, at home and in Spain. Especially to **Yao** for being the best at base, **Sarah** for being the best in the sun, and **Krispo** for being the best at home! So much bestness, ladies! No you-no mental health, that's for sure!! Particularly thank you to **Niu Jingyao**, primarily for your existence which has been such an important asset to life in Uppsala. Life at the office would have been bleaker without you, but our best moments are still all the escape from the work scape, on travels, at home with food and in the many forests and lakes. Thank you for being there and for being savage when I needed it the most! Well, you already got a speech, you can just paste it here haha

There are so many who deserve thanks for standing by me and supporting me throughout this climb, -as you know from all the times you've been there for me. Many of you were not expected to take on this role, which only makes you more remarkable and valuable. Thank you to all that read and commented on my work. Thank you to those that created scenes for scientific exchange and safe discussions (**Anna Gårdmark, Örjan Östman** and **Josefin Sundin**), and to those that held the fort in protecting PhD-students rights through demands, salary and legislations (**Magnus Huss, Jessica Petersson** and **Noel Holmgren**). Thank you to those that took on responsibilities for us when we felt lost and confused.

A great thank you to **my funders**, this work could not have been done without your resources and trust -in a time where research is being deprived of it. Field work was supported by WWF Sweden, Milkywire and field travels by Karlsö Klubben. My thesis work was supported by Marcus and Marianne Wallenbergs stiftelse. I would also like to thank SLU for the PhD-travel grants I received twice, that made the trip to Australia and Liverpool possible. My attendance to The XVI International Seabird Group Conference in Coimbra, Portugal, was supported by Stiftelsen Edvard Nonnens stipendiefond, Stiftelsen J.M. Svenssons donationsfond and Stiftelsen Nilsson-Aschans stipendiefond, through Kungliga Skogs- och Lantbruksakademien. Keep funding, you are essential for development!!

Finally, thank you to **whoever read this thesis** and thus showed interest in my work.

Appendix

Ecological Informatics 84 (2024) 102852

Contents lists available at ScienceDirect

Ecological Informatics

journal homepage: www.elsevier.com/locate/ecolinf

Autonomous data sampling for high-resolution spatiotemporal fish biomass estimates

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ARTICLE INFO

Keywords:
Species distribution modelling
Remote sensing
USV
Hydro-acoustic
Spatiotemporal modelling
Small pelagic community

ABSTRACT

Many key ecological dynamics such as biomass distributions are only detectable on a fine spatiotemporal scale. Autonomous data collection with Unmanned Surface Vehicles (USV) creates new possibilities for cost efficient and high-resolution aquatic data sampling. However, the spatial coverage and sampling resolution remain uncertain due to the novelty of the technology. Further, there is no established method for analysing such fine-scale autocorrelated data without aggregation, potentially compromising data resolution. We here used a USV with an echosounder, a conductivity-temperature sensor and a flourometer to collect data from April–July 2019–2023 in a 60x80km area in the central Baltic Sea. The USV covered a total distance of 8000 nmi, over 42–81 days per year, with an average speed of 0.5 m/s. We combined the hydroacoustic data with publicly available oceanographic data from Copernicus Marine Service Information (CMSI) to describe seasonal distribution dynamics of a small pelagic fish community. Key oceanographic variables collected by the USV were correlated with CMSI estimates at daily/monthly resolution, respectively, to test for suitability to scale (Temperature 0.99/0.97; Salinity −0.77/−0.26; Chlorophyll-a 0.12/0.28). We investigated two approaches of Species Distribution Models (SDMs): generalized additive models (GAM) versus spatiotemporal generalized linear mixed effect models (GLMM). The GLMMs explained the observed data better than the GAMs (R^2 0.31 and 0.20, respectively). The addition of environmental variables increased the explanatory capability of GAM and GLMM by 25 % and ~ 3 %, respectively. Due to the high data resolution, we found significant amounts of positive autocorrelation (R: 0.05–0.30) across more than 50 sequential observations (>6 hours). However, we found that diel patterns in fish detection strongly affected the abundance estimates due to vertically migrating species hiding in the ‘acoustic dead zone’ near the seabed. Such dynamics could only be estimated and corrected for in predictions on the high-resolution data, complicating the trade-off between autocorrelation and high-resolution for SDMs. We compared estimates and effect sizes/directions in identical SDMs on 2x2km/month aggregated (i.e non-autocorrelated) observations and non-aggregated (i.e. autocorrelated) observations, and found relatively little difference in spatiotemporal estimates ($r = 0.80$). For the first time, we predicted the distribution of a small pelagic fish community at a high spatial resolution, in an area essential to breeding top predators, opening up for new applications in ecological studies locally and globally.

1. Introduction

The spatiotemporal distribution of organisms is key in understanding population dynamics. Such distributions are influenced by the organisms’ dispersal capabilities (Chaalali et al., 2016; Pulliam, 2000), the presence of interacting species (Wisz et al., 2013) and specific habitat requirements (Guisan and Zimmermann, 2000). As such, organisms distribute in an environment based on factors such as resource

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https://doi.org/10.1016/j.ecoinf.2024.102852
Received 19 April 2024; Received in revised form 7 October 2024; Accepted 7 October 2024

availability (Charnov, 1976), competition (Fretwell and Calver, 1969; Křivan et al., 2008), predation (Benoit-Bird et al., 2017; Fauchald, 2009; Moody et al., 1996), life stage (La Mesa et al., 2010; Maathuis et al., 2023) and environmental conditions (Elith and Leathwick, 2009). Because animals interact with each other, disperse and migrate, reproduce and die, population numbers and spatial distributions vary through time. This variation leads to the persisting challenge of mapping species at a high temporal resolution accurately and efficiently (Giske et al., 1998; Hughes et al., 2021; J. Miller, 2010; Patterson et al., 2008; Waldock et al., 2022). However, small-scale and short-term spatiotemporal dynamics in abundance of species can be crucial for ecosystem functions (Elith and Leathwick, 2009), e.g. during reproduction for predators (Durant et al., 2005; Hilborn et al., 2017; Keogan et al., 2018).

In surveys of aquatic environments, pelagic species demography is assessed by combining measurements of hydro-acoustic backscatter with biological sampling, e.g. by pelagic trawling (Giske et al., 1998; Pennino et al., 2020; Simmonds and MacLennan, 2005). However, the main aim of these surveys is to provide estimates of the fish population indices (usually abundance or biomass) to be used in stock assessment for fisheries management (WGFAST, ICES, 2023.2). The surveys are typically short, covering extensive areas with a low spatial and temporal resolution, often without resampling within the same year due to the high running costs (e.g. vessel time, crew, instrumentation). This results in loss of details in the inherent dynamics of the population changes that may be of high ecological significance (Durant et al., 2005; Elith and Leathwick, 2009; Hilborn et al., 2017; Phillips et al., 2022; Robinson et al., 2011). In contrast, long-term continuous hydro-acoustic data is frequently sampled by moored equipment at a fixed position, providing important insights in fish ecology (e.g. Egerton et al., 2018; Kaartvedt et al., 2023; Maathuis et al., 2023), but the area covered is inherently restricted. Therefore, both large scale, short-term vessel surveys and long-term studies at fixed positions present limitations for studies where high spatiotemporal resolution is needed.

In the recent decade, various types of unmanned surface vehicle (USV) have become available for scientific data collection (Ghani et al., 2014; Swart et al., 2016), providing an alternative way to monitor large areas with high resolution over long time periods (De Robertis et al., 2021). USVs can collect a range of data types continuously, without demanding on-site crew besides during deployment and retrieval, dramatically decreasing the costs of operation (Liu et al., 2016). Further, they can often operate in areas that larger vessels cannot access, such as shallow water and fragile ecosystems (Liu et al., 2016), decreasing spatial sampling bias (Hughes et al., 2021). Equipped with several different sensors, USVs can simultaneously sample a range of environmental variables such as salinity, temperature, phytoplankton and depth of water column (Swart et al., 2016), important for generating informative spatial predictions of fish over time (Panzeri et al., 2023; Pennino et al., 2020; Rooper and Zimmermann, 2007). While large public databases (e.g. from E.U. Copernicus Marine Service Information; hereafter CMSI) aid with important information on physical and biogeochemical oceanographic variables, they mainly constitute of model estimates with coarse spatiotemporal resolution (Ghani et al., 2014; Michener, 2015). This creates an uncertainty tied to the compatibility to own resolution, and so in-situ sampled data can provide a valuable opportunity to compare.

Species distribution models (hereafter SDMs) comes in a wide range of approaches that integrate abundance and oceanographic data (Robinson et al., 2011), with the ability to predict if species are likely to occur in non-sampled locations or time periods (Panzeri et al., 2023; Pennino et al., 2020). SDMs are routinely used in Ecosystem-Based Fisheries Management, to provide valuable information on Essential Fish Habitats and Vulnerable Marine Ecosystems, as well as to inform protection and restoration strategies (Lauria et al., 2017; Panzeri et al., 2023). They also help defining stock changes (Orio et al., 2019) and habitat suitability under projected climate change scenarios (Palermino et al., 2024; Panzeri et al., 2024).

When implemented in SDMs, high-resolution data comes with a significant challenge of spatiotemporally autocorrelation (Robinson et al., 2011). For weaker correlations, adding correlation structures (i.e. for temporal and/or spatial autocorrelation) to complex SDM model frameworks (Robinson et al., 2011), or including relevant predictive variables (i.e. finer time or space variables) or order/group the correlated data in a meaningful way (Carlsen et al., 2023) can be sufficient. For stronger or longer lasting correlations, the most common approach is to simply aggregate the data (ICES, 2021c) consequentially compromising the high resolution and important ecological dynamics in it. Thus, defining meaningful ways to conserve high data resolution while producing trustworthy predictions is essential.

We here investigate the utility of USV-based collection of spatiotemporally high-resolution hydroacoustic and environmental data as a new tool for studies of ecological dynamics. For the first time, we investigate high-resolution SDMs for a community of small pelagic fish over an extended period of time and in a ~ 480 km^2 area essential for vulnerable seabird species. We perform a stepwise procedure of fish distribution analyses in an attempt to conserve the high resolution of the data, and investigate the effects of autocorrelation on a spatial prediction. This paper specifically:

1) Report the coverage and utility of a USV for scientific monitoring.
2) Correlate environmental data sampled by USV with environmental variable estimates from CMSIs database.
3) Produce and compare SDMs of different complexities (i.e. model type, explanatory variables, error structures, data sources and data resolution) for a community of small pelagic fish, to investigate the gains and limitations of the information retrieved.
4) Estimate the spatiotemporal distribution and variations in biomass, detailing out the effects of each variable, and contrast two different data aggregations (i.e. the full-resolution versus 2x2km spatial aggregations within the month of the year), to evaluate the autocorrelated high-resolution model estimates.
5) Present spatiotemporal fish distribution predictions for future ecological studies.

2. Methods

2.1. Study design and general description of study site

2.1.1. Study design

We collected data using a remotely operated USV, Sailbuoy, (Offshore Sensing AS, Bergen, Norway) equipped with an echosounder, a conductivity- and temperature sensor (CT), and from 2021 on, a fluorometer (see *2.2 Scientific sensors* below). The study was performed in the Central Baltic Sea (International Council for the Exploration of the Sea, ICES, subdivision 27; statistical squares 42G7-44G7), off the island of Stora Karlsö, Sweden (Fig. 1), that hosts the largest seabird colonies in the Baltic Sea. Sampling was performed in transects that were typically sailed in bows between four virtual geolocation cursors, with a range of ~60–80 km from, and back to ≥2 km from Stora Karlsö (Fig. 2). The sampling transects were designed to cover the area in which the breeding seabirds at Stora Karlsö perform their foraging trips (Evans et al., 2013; Isaksson et al., 2019) from late April to late July, years 2019–2023.

2.1.2. Upper trophic levels of the study system

Island of Stora Karlsö hosts 26,000 pairs of common guillemot (*Uria aalge*), 12,000 pairs of razorbill (*Alca torda*), and 2000 pairs of great cormorant (*Phalacrocorax carbo sinensis*), amongst other species. In addition a significant population of grey seals (*Halichoerus grypus*) is present in the area (Ahlgren et al., 2022), with daily observations at Stora Karlsö in the summer months. These top predator species forage on small pelagic fish (Hentati-Sundberg et al., 2018; Kadin et al., 2012; Lundström et al., 2010) of which the three most abundant species in the

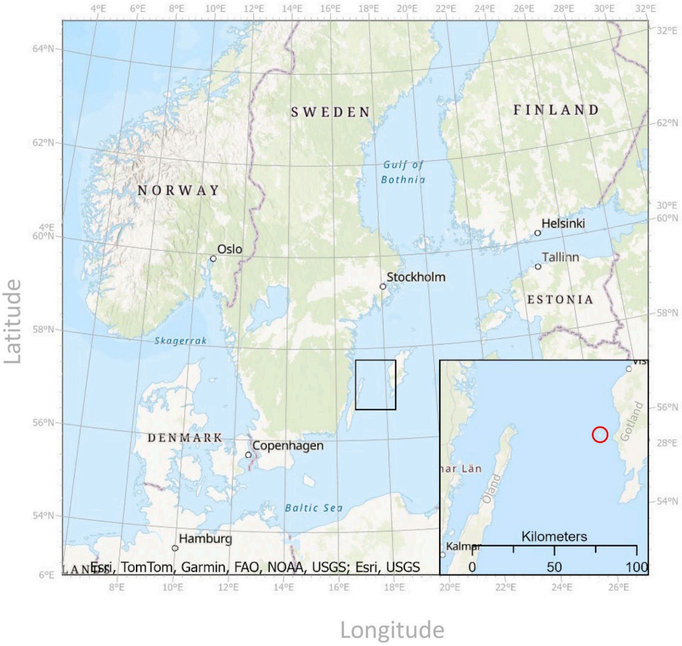


Fig. 1. Map of area and zoom in on survey area and with Stora Karlsö, 57°17′1″N 17°58′19″E (red circle). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

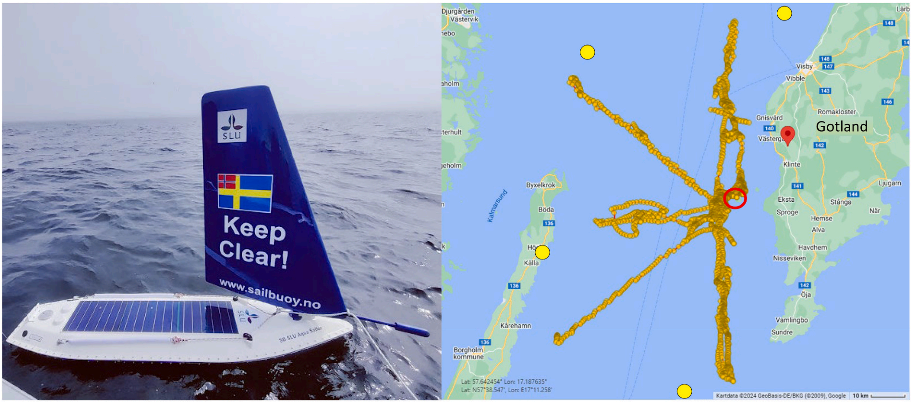


Fig. 2. The USV Sailbuoy (Offshore Sensing AS) (left) and five example sampling transects performed by the USV in May 2021 (right) from and back to Stora Karlsö (red circle). Yellow circles indicate the four virtual geolocation cursors used to define sampling transects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

study area are the two commercially sought clupeid species sprat *Sprattus sprattus* and herring *Clupea harengus,* and three-spined stickleback *Gasterosteus aculeatus*. No other fish species are nearly as numerous in the study region (ICES, 2021b). The entire Baltic Sea spawning stock biomass (SSB) was estimated to be 1,380,565 t for sprat in 2022 (ICES, 2023), and 364,981 t for herring in 2020 (ICES, 2021a). Although there is no stock assessment for sticklebacks, the relative abundance has increased drastically in recent years (Bergström et al., 2015; Olin et al., 2022; Olsson et al., 2019). All three species interchangeably utilize the area for spawning and feeding during the period of this study (Candolin et al., 2008; Jørgensen et al., 2005b; Ojaveer and Kalejs, 2010). Spring spawning herring utilize the shallow seabed areas from March to May

(Jørgensen et al., 2005a, 2005b) partially alongside sticklebacks which spawn continuously from May to July (i.e. coast-wards migration starts in April). Sprat on the other hand perform spawning migrations to and from deeper basin areas from March to July where one individual can spawn several times over the season (Aro, 1989). While the Baltic Sea also host autumn (from July) spawning herring, their population size is low and their use of this area is unknown (ICES, 2013).

2.2. Data collection

2.2.1. USV operation

The USV was 2 m long and weighed ~60 kg. It moved by sail, with an electronic rudder. Every twenty minute, the position of the sail and rudder was reassessed, sailing in one of four possible directions (i.e. 'tacks') in relation to the wind (two headwind and two downwind). The USV was primarily operated in autopilot mode, where a waypoint was given, and an algorithm based on wind direction and sailing speed automatically chose the best tack. The route was limited to a given radius from the transect as to decrease chances of sailing onto land. All remote communication with the USV was accomplished through Iridium Communication Incorporation's global satellite interface, where both steering, vessel and sensor settings could be adjusted, and data from both the vessel log and scientific sensors (see 2.2. *Scientific sensors* below) could be inspected in near real time (ten minutes delay). For more information about the USV structure, mechanical and electronic features see Wullenweber et al. (2022).

Using wind for propulsion, the USV would usually not move with wind strengths <2 m/s, leading to the decision of integrating data by time instead of distance (Ghani et al., 2014). All electronic parts of the USV were solar powered, and therefore the entire USV operation was solely driven on renewable energy.

2.2.2. Scientific sensors

Hydro-acoustic data for fish distribution estimates were collected using a Simrad Wide Band Transceiver (WBT)-mini scientific echosounder with an ES-200CDK transducer, produced by Kongsberg Maritime. The echosounder was mounted on a gimbal in the hull at 0.6 m depth. All hydroacoustic data acquisitions was planned in Simrad EK Mission Planner 3.3.x. The echosounder was run in wideband mode (frequency sweep 185–255 kHz) with a ping rate of 1/1.4 s to suit the low speed of the USV. Data was recorded to 100 m depth, as a permanent stratification (halocline) and anoxia in the study area prevents fish from distributing below 70-80 m (Weidner et al., 2020). The echosounder was calibrated using a 38.1 mm tungsten sphere, with the same settings as used in the data collection, one-two times per year in the study area following internationally standard methodology (ICES, 2021c).

Salinity and water temperature were collected with a Cabled CT Sensor produced by NBOSI, at 0.3 m depth. Fluorescence and turbidity were collected with an ECO-triplet-w fluorometer with a self-cleaning system, produced by Sea-Bird Scientific, at ~20 cm depth facing downwards. The frequencies collected were Chlorophyll-a (Chl) (470/695 nm, excitation/emission), Phycocyanin (Pc) (630/680 nm, excitation/emission), and turbidity/backscatter (700 nm). The data was collected in ten minutes acquisition loops, with one sensor at the time (order: (1) CT-sensor; (2) fluorometer, (3) echosounder continuously for 7 min, (4) full shut-off of all sensors).

2.3. Data treatment and dataset information

All raw echosounder data treatment, including calculation of calibration values, were performed in Echoview Software Pty Ltd. v. 13. Our hydroacoustic data cleaning followed a 3-step approach. In Step 1, we visually inspected echograms to familiarize ourselves with the possible NASC range of fish data. Step 2 involved generating surface (Fraser et al., 2017) and bottom exclusion lines using statistical methods, which we tested across various depths and habitats. In Step 3, we reviewed all exclusion lines visually on exported echograms and adjusted them as necessary, iterating back to Step 2 when needed. Echo integration (Simmonds and MacLennan, 2005) was performed for depth layers of 4 m over 7 min intervals, each constituting of 300 pings. The integrals were summarized as Nautical Area Scattering Coefficient (hereafter NASC), with unit m^2 nmi^{-2}, which is used as a proxy for biomass in this study (see Table 1). We examined a range of the highest values in the dataset, returning to Step 1 to identify likely extreme integration cells for direct inspection, removing any cells or intervals where values were unlikely to represent fish. We set the upper NASC limit at 10,000 $m^2 nmi^{-2}$ per integrated cell (4 m depth * 10 min time range) for two reasons: (1) visual inspection of raw data often showed cells reaching 6000–8000 $m^2 nmi^{-2}$, suggesting higher values were possible, and (2) it represented a natural cut-off in the data distribution, as detailed in Appendix A1. All further statistical analyses were performed using R versions 3.6.3 and 4.2.2 (R Core Team). The GPS-position for each data point gives the mean position of all pings within the seven minutes of sampling. All depth layers of the water column within the same time interval were cumulated, giving a dataset of NASC per mean time and position for each interval, in total 41,292 observations. For analyses on aggregated data, the mean of all observations within 2 × 2 km squares per month of the year was extracted, resulting in a dataset of 1899 observations. All dates and times were set to local time (CEST).

Data gathered from the European Union Copernicus Marine Service Information (hereby CMSI; last download 09.10.2023) was limited to a rectangle slightly exceeding size of the area sampled with USV in latitude (56.50824°-57.80822°) and longitude (16.93013°-18.23579°), while the temporal selection was limited to the earliest and latest date sampled with the USV. The datasets were downloaded in two resolutions, monthly average- and daily average estimates (Table 1), and the bathymetry was also retrieved from CMSI. CMSI model estimates for years 2022 and 2023 had not been corrected by the same standard as models from previous years at the time of this study (i.e. due to a 2 year lag in verification, see Le Traon et al., 2019), and may thus still contain occasional errors. However, the data was visually inspected for outliers, and none were identified.

2.4. Statistical analyses

Correlation tests were performed using Pearson correlation analyses (i.e. through the 'R base' function cor()) for observations and model estimates, Variance Inflation Factor ('car' function vif()) for model predictors and temporal autocorrelations assessments ('R base' function acf()), along with visual inspections (e.g. Appendix A7 and A8.3).

2.4.1. Models setup and relevant variables

Generalized additive model (GAMs; mgcv), and spatiotemporal generalized mixed effect model (GLMM; sdmTMB, see Anderson et al., 2022) with spatiotemporal fields and smooths/priors (i.e. mimicking GAMMs), were used as SDMs to model the distribution of the small pelagic fish community in the sampled area. While GAMs could be constructed with spatiotemporal random fields (i.e. through Stochastic Partial Differential Equations, or SPDE, see D. L. Miller et al., 2020), GLMM models within the framework of sdmTMB hold great advantages in explaining data with complex structures. This is especially due to the variety of options for spatiotemporal field realizations such as the possibility to define suitable spatial meshes to the specific data, and the use of separable versus non-separable time-space effects (Anderson et al., 2022). However, GAMs have advantages in being highly flexible in defining non-linear relationships without assumptions, and in explaining complex data with less information (e.g. non-parametric). Thus, the simplest models (i.e. without spatiotemporal structure) here were performed as GAMs, while more complex spatiotemporal models were fundamentally GLMMs. All models used in this study are presented in Table 2.

All models tested used 'NASC' as response variable, which was log-

Table 1
Data variable information. See *Literature* for dataset sources Anonymous a–d.

Variable	Unit	Sensitivity	Resolution	Total sensor range	Variable range	Source	Collection method	Variable status
Nautical Area Scattering Coefficient (NASC)	m^2 nmi^{-2}		Hourly mean		0.0001–8000	USV	Simrad WBT mini, 70 cm depth	Observation
Salinity	Mmhos /cm	+/− 0.005	Hourly mean	0–60	0–11.9	USV	NBOSI CT 40 cm depth	Observation, Sea surface
Temperature (Temp)	°C	+/− 0.002	Hourly mean	0–30	3.1–25.9	USV	NBOSI CT 40 cm depth	Observation, Sea surface
Chlorophyll (Chl)	µg/l	+ − 0.025	Hourly mean	0–50	0–7.3	USV	Sea Bird ECO triplet 20 cm depth	Observation, Sea surface
Salinity	PSU (~Mmhos/ cm)	−0.01	Monthly and daily on 2x2km grid		6.3–7.4	CMSI (Anonymous c, Anonymous d)	Moored monitoring stations, CTD and ferry boxes	Estimate, Sea surface
Temperature (Temp)	°C	0-5 m: −0.4 5-30 m: 0.1 30–80:m 0.3 80–200: 0.3	Monthly and daily on 2x2km grid		3.3–20.6	CMSI (Anonymous c, Anonymous d)	Moored monitoring stations, CTD, L3 satellite imagery and ferry boxes	Estimate, Sea surface
Chlorophyll (Chl)		−0.72	Monthly and daily on 2x2km grid		0.5–4.1	CMSI (Anonymous a, Anonymous b)	Moored monitoring stations, CTD, L3 satellite imagery and ferry boxes	Estimate, Sea surface
North-South currents (NS_current)	m/s	−0.08 - 0.23 m/s −17° - 38°	Monthly on 2x2km grid		−0.1-0.1	CMSI (Anonymous c, Anonymous d)	Moored monitoring stations	Estimate, weighted average of water column
East-West currents (EW_current)	m/s	−0.08 - 0.23 m/s −17° - 38°	Monthly on 2x2km grid		−0.1-0.1	CMSI (Anonymous c, Anonymous d)	Moored monitoring stations	Estimate, weighted average of water column
Current speed	m/s	−0.08 - 0.23 m/s	Monthly on 2x2km grid		0.003–0.128	CMSI (Anonymous c, Anonymous d)	Moored monitoring stations	Estimate
Depth of seabed (Depth)	meter	−749 - 0	2x2km grid		−166.4 - 0	CMSI (Anonymous a)		Observation
Week	Julian week				16–31	USV		Observation
Hour	Cyclic 24 h				00–23	USV		Observation
Year	Julian year				2019–2023	USV		Observation
Month	Julian month				4–7	USV		Observation
X,Y	UTM coordinates, CRS 33 N				X: 619.4–697.1 Y: 6290–6311	Calculated from USV latitude, longitude		Observation

transformed due to its wide range in values and their near Poisson distribution (see fig in Appendix A1). Explanatory variables were chosen based on literature for fish distribution (e.g. Aro, 1989; Cardinale et al., 2003; Giske et al., 1998; Maravelias & Reid, 1995; Pennino et al., 2020; Sabatini et al., 2004; Schaeffer et al., 2008; Watson et al., 2015) and availability of environmental variables from the area and time of the study (Table 1). While temperature (Nøttestad et al., 2007), salinity and chlorophyll are established variables for determining abundance in SDMs of many aquatic species, hour of the day was expected to affect the detection rather than the true abundance (Cardinale et al., 2003; Mello and Rose, 2009). Both 'Week' and 'Month' was included for different scales of seasonal dynamics, as they were not correlated (i.e. as tested by Variance Inflation Factor, VIF = 0.03) while improved the models. Water currents were included as they can affect availability of food for planktivores (Sabatini et al., 2004; Schaeffer et al., 2008; Watson et al., 2015), organisms metabolic cost and movement (Maathuis et al., 2023; Simmonds and MacLennan, 2005). Currents can also affect organisms distance to the seabed /topographic structures (Maravelias, 1999), along with the stratification of the water- and thus the detectability by echosonar (Mello and Rose, 2009). The effect of, 'depth' (i.e. of the seabed) is likely to interact with the time of day, as benthic hiding/acoustic dead-zone is primarily a problem when depth of the seabed is shallower than the anoxic zone. However, to reduce model complexity and avoid over-parametrization we chose 'hour' to detail out the cyclic pattern in fish detection.

The GLMMs were fitted on a spatial mesh based on the coordinates of observations across all years. The temporal field of the model was by months as the entire survey area was aimed to be resampled once per month. In addition, all environmental variables from CMSI were monthly averages in fish biomass models. The variable Julian 'week' was added to capture finer scale changes in fish biomass due for example to short-term weather patterns and behaviour in general. Models were initially tested against simplified models in terms of fixed and random effects included, and smooth structures, where the models with best log likelihood (LL) were selected for further analyses. The final model evaluation was based on the statistical estimates of log likelihood, maximum absolute error (MAE), root mean square error (RMSE) and coefficient of determination (R^2) of the highest ranked models. Best models were selected based on explanatory ability through cross validations of 70/30 % training/test data (see *Results*). Autocorrelation structures of models were checked with the function *acf()* (Appendix A7). Explanatory variables were checked for correlation using R base function *cor()* (see Appendix A3) and variables representing the same environmental variable (e.g. 'Temperature' from the USV versus CMSI) were never present in the same model. While water column averages of CMSI estimates for temperature and chlorophyll explained the fish distribution better than surface estimates (Appendix A3), we proceeded with the surface estimates due to the wish to correlate the variables against the observations made by the USV (i.e. which was only able to collect data at the surface). Residuals and goodness of fit were visually inspected, and several distribution families for log NASC were tested before student distribution with 4 degrees of freedom was selected as the

Table 2
Numbered overview of all the models. The smoothers were b-spline 's(...)', cyclic s(...,bs='cc'), random intercept (1|...). For spatiotemporal and spatial models, the random fields are given in [brackets], and the correlation structure (i.e. Autoregression = AR1; Identical and independent = IID) is indicated.

Model name	Model formula/structure	Rationale	Model type
Model 1	*log_NASC ∼ s(Week) + s(Hour, bs = 'cc') + s(Depth) + Year*	Baseline GAM model	GAM
Model 2	*log_NASC ∼ s(Week) + s(Hour, bs = 'cc') + s(Depth) + s(NS_current) + EW_current + Current_speed + s(Temp) + s(Chl) + s(Salinity) + Year*	Model 1 with CMSI environmental variables	GAM
Model 3	*log_NASC ∼ s(Week) + s(Hour, bs = 'cc') + s(Depth) + (1|Year); [Month, X/Y]; Correlation structure AR1;*	Baseline GLMM model	GLMM
Model 4	*log_NASC ∼ s(Week) + s(Hour, bs = 'cc') + s(Depth) + s(NS_current) + EW_current + Current_speed + s(Temp) + s(Chl) + s(Salinity) + (1|Year); [Month, X/Y]; Correlation structure AR1;*	Model 3 with CMSI environmental variables	GLMM
Model 5	*log_NASC ∼ s(Week) + s(Hour, bs = 'cc') + s(Depth) + s(NS_current) + EW_current + Current_speed + s(Temp) + s(Chl) + s(Salinity) + (1|Year); [Month, X/Y]; Correlation structure AR1;*	*Model 4 with 'Temperature' and 'chlorophyll' from USV, years 2021–2023*	GLMM
Model 6	*log_NASC ∼ s(Week) + s(Hour, bs = 'cc') + s(Depth) + s(NS_current) + EW_current + Current_speed + s(Temp) + s(Chl) + s(Salinity) + (1|Year); [Month, X/Y]; Correlation structure AR1;*	*Model 4 on years 2021–2023*	GLMM
Model 7	*log_NASC ∼ s(Depth) + NS_current + EW_current + Current_speed + s(Temp) + s(Chl) + s(Salinity) + (1|Year) + (1|Month); [X/Y]; Correlation structure IID;*	*Spatial Model 4 without 'Week' and 'Hour' for 2X2km data aggregation*	GLMM
Model 8	*log_NASC ∼ s(Depth) + s(NS_current) + EW_current + Current_speed + s(Temp) + s(Chl) + s(Salinity) + (1|Year); [Month, X/Y]; Correlation structure AR1;*	*Model 4 without 'Hour' and 'Week', for comparison with Model 7*	GLMM
Model 9	*log_NASC ∼ s(Hour, bs = 'cc') + s(Depth) + s(NS_current) + EW_current + Current_speed + s(Temp) + s(Chl) + s(Salinity) + (1|Year); [Month, X/Y]; Correlation structure AR1;*	Model 4 without 'Week' for simplified time structure in prediction	GLMM

best available option (see Appendix A1). Space-time was separable for all full-data GLMMs through 'autoregressive' correlation structure (AR1), but inseparable for the aggregated data GLMM through 'identical and individual distributed' autocorrelation (IID) (Lindgren et al., 2023). The decisions were based on residual fit and the time and space span between observations (i.e. $\geq$ 10 min in full-data and 1 month in the aggregated data).

2.4.2. *Analyses workflow*

First, we tested how well the fish distribution in 2019–2023 could be estimated by two different model types: a GAM and a spatiotemporal GLMM (Table 2). Two different complexities were investigated, with and without additional environmental variables (GAM Models 1 and 3 and GLMM Models 2 & 4 respectively), to see if information on monthly average of a set of environmental parameters (i.e. CMSI provided salinity, temperature, chlorophyll-a and current direction/speed) could improve the two different model types.

The discrepancy between USV observations and CMSI model estimates of temperature, salinity and chlorophyll-a was evaluated in two ways. First, a correlation test, with CMSI estimates versus USV observations were performed between the high-resolution daily averages of CMSI estimates to the USV observations, contrasted with low-resolution monthly averages of CMSI estimates. As the year 2021 was the only year with both Chlorophyll data from the USV and verified CMSI daily estimates (Le Traon et al., 2019), the fine resolution correlation was based solely on this year, but with cross references to the correlations of monthly estimates to all available years (2019–2023). Second, the significance of the discrepancy was tested through model performances in two contrasting GLMMs using USV (Model 5) and CMSI (Model 6) sea-surface variables respectively (monthly CMSI estimates), with the baseline structure as provided below. The variables compared in the GLMMs were temperature and chlorophyll-a values from the years 2021 to 2023. As the local salinity measures from the USV deviated significantly from the CMSI estimates (and also from the Swedish Metrological and Hydrological Institute data, see Results), we chose to proceed with CMSI values for salinity also in Model 5.

To address the potential effects of autocorrelation, we compared the model estimates from a simplified spatiotemporal GLMM (Model 8) with a model on spatiotemporally aggregated data, using mean values for 2x2km by month/year (Model 7), to verify direction and sizes of variable effects on a non-correlated dataset. The only difference between the models were the correlation structure (see Table 2).

The final prediction of biomass distribution was produced using Model 9, where 'week' was selected out for a simplified time structure in the prediction. The predictive grid was constituted of CMSI values for a slightly increased area (as compared to observations). The chosen grid value for 'hour' was 01 (CEST) to utilize the maximum biomass estimates during diel vertical migrations (Mello and Rose, 2009).

3. Results

3.1. *Data collections*

The number of operating days per year for the USV were 42 days in 2019; 81 days in 2020; 67 days in 2021; 81 days in 2022; 52 days in 2023 (Fig. 3a). The average sailing speed of the USV in the Baltic Sea was 0.55 ms^{-1}; 1.1 knots (Range: 0-3 ms^{-1}, see Appendix A4) and the total distance sailed was ~8000 nmi (14,752 km) across all five years. The shallowest areas the USV was operated in was <2 m deep and the deepest were > 150 m. Each round-trip, from Stora Karlsö to the outer edge of the study area and back, typically took 2–10 days, and thus, approximately five such trips were sampled each month. The USV had a running cost of 100 SEK per day, and a purchase cost of 1,750,000 SEK (in 2019), leading to an overall operation cost of ~5500 SEK per day. The calculation does not include piloting, which typically took 5–15 min per day, and 4 h per deployment/retrieval for one person (on average 6 per season), including calibrations.

The log NASC values observed ranged from: lower extreme −2.32, 1st quartile 3.49, median 4.26, mean 4.31, 3rd quartile 5.04 and upper extreme 9.63 (Fig. 4). These observations include all pelagic species, and are exemplified as echograms in Fig. 4. The lower extreme essentially represent no fish detected, and 1st quartile and mean shows small and medium dense fish aggregations <50 m depth. The 3rd quartile shows two layers of fish aggregations around 10-20 m and 60 m depth respectively, and the upper extreme shows one extremely dense layer of fish around 50-60 m depth.

3.2. *Surface environment variables in pelagic fish biomass/distribution*

The correlation tests between USV observations and CMSI estimates

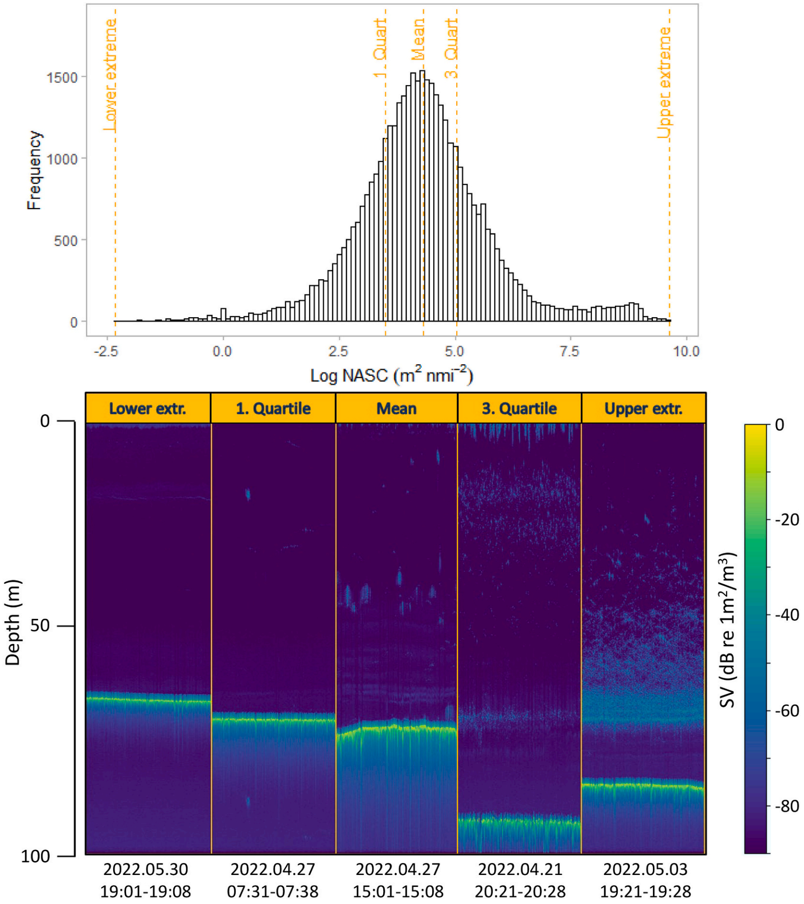


Fig. 3. Number of acoustic observations by the USV per Julian day in each year of operation.

shows that daily averages of temperature (Table 3 and Fig. 5a) were highly correlated between the USV and CMSI ($R = 0.99$), while the monthly averages still represent the observations well ($R = 0.92$) (Table 3 and Fig. 5d). There was a rather low correlation in chlorophyll-a values, due to a mismatch in the estimated versus observed peak bloom timing and level in June/July (Fig. 5c). The monthly average estimates from CMSI (Fig. 5f), which included two more years (2021–2023 versus 2021), was more correlated to the USV observations than the daily averages ($R = 0.28$ versus 0.12). Especially the correlation in salinity data stood out (Table 4 and Fig. 5b and e), with a strongly negative correlation both in the monthly average and especially in the daily average of CMSI data against USV observations ($R = -0.26$ and $-$ 0.77 respectively). The difference increased over the season. With reference to observations from an SMHI-station outside of Stora Karlsö (BY38) we found that the error was tied to the USVs measurements rather than the CMSI estimate (see Appendix A5), where the USVs CT-sensor had a consistent time drift over season, reoccurring in all years (see Appendix A5.2). The discrepancy between the two high-resolution data sources (daily average of CMSI estimates versus USV observations, 2021) is shown in Fig. 5.

When testing for the effects of monthly CMSI estimates in SDMs, we found that the GAM was improved by about 25 % (R^2: 0.16 for Model 1 versus 0.20 for Model 2), while the corresponding spatiotemporal GLMM was improved only by <3 % (R^2: 0.305 for Model 3 versus 0.313 for Model 4) upon inclusion of these three variables (see Table 4). However, the GLMM (Model 4) gave an overall better fit, as determined through LL, MAE and RMSE (Table 4), and were deemed important also in GLMM (Model 4) regardless of the variable effect sizes and significance. When contrasting the model effects of CMSI monthly averages (Model 5) with identical models based on USV collected versions of the environmental surface variables we found that the models' abilities to estimate the observations differed very little (R^2: 0.380 for CMSI, Model 5, versus 0.383 for USV, Model 6; <1 % difference). While R^2 was higher for the model with USV observations, all other metrics were slightly better for the CMSI based model.

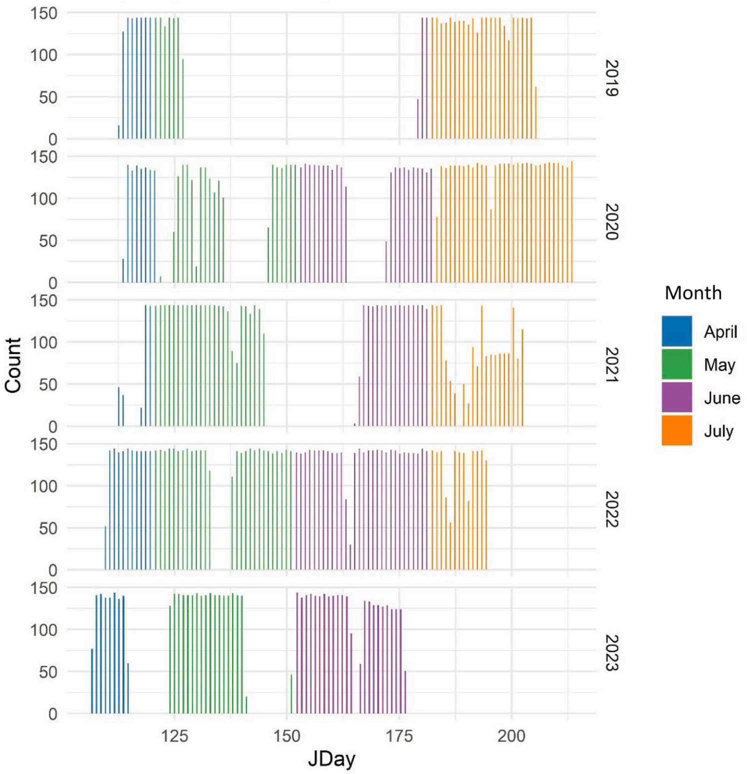


Fig. 4. Absolute distribution of Log NASC (m^2 nmi^{-2}) values (above) and example echograms of fish aggregations (below) at lower extreme (−2.32), 1st quartile (3.49), mean (4.31), 3rd quartile (5.04) and upper extreme (9.63). Strong lower echo line reflects the bottom topography, and in 3rd quartile there was surface turbulence; these echo's are not included in the calculations.

Table 3
Correlation between sea surface values from CMSI versus USV, with two CMSI data resolutions: daily averages from 2021 and monthly averages from all years of available USV data. See Fig. 5a-c of daily estimates versus observations, and Fig. 5d-f of the discrepancy between USV and CMSI on a monthly resolution.

CMSI resolution	Sea surface variables	Correlation (R)	Years
Daily	Temperature	0.99	2021
Monthly	Temperature	0.92	2019–2023
Daily	Salinity	−0.77	2021
Monthly	Salinity	−0.26	2019–2023
Daily	Chlorophyll-a	0.12	2021
Monthly	Chlorophyll-a	0.28	2021–2023

3.3. *Spatiotemporal biomass estimates and prediction*

3.3.1. *Final model estimates*

The final spatiotemporal fish distribution estimate was based on Model 4 (Fig. 6). The predictor 'week' (Fig. 6a) detailed out the general pattern observed over the season where fish biomasses were highest at the beginning and end of the season, but with significantly lower levels in weeks 20–25, from mid-May to mid-June. The effects of 'hour' (Fig. 6b) and 'depth of seabed' (Fig. 6c) on fish biomass was the most stable across models in terms of effect sizes and regression (Appendix A8). 'Hour' showed a distinct cyclic pattern of higher levels detected during dusk/dawn/night hours (19–05 CEST) than during the day (05–19 CEST). Both temperature (Fig. 6d) and salinity (Fig. 6e) had overall positive effects on fish biomass, but note that temperature in particular was very even across the area (Appendix A13). Chlorophyll (Fig. 6f) did not have a clear effect on biomass, returning an undulating regression. We estimated more fish during stronger currents from the north (Fig. 6g), south and west (Fig. 6h), but lower total current speed (Fig. 6i) seemed to overall increase fish detections. Note that lower current speeds were the dominant type in this area with mean; 0.04 m/s; range: 0.003–0.13 m/s (See Appendix A14). The models log NASC estimates (mean: 4.23, range: −0.69–7.12) fitted well with the observations (mean: 4.31, range: −2.32 - 9.63), though with a slight underestimation and a narrower distribution (Fig. 6j).

3.3.2. *Autocorrelation and data aggregation*

As expected, model 4 returned a consistent autocorrelation across >50 lags (Appendix A7), starting at $R = 0.30$, reduced to <0.20 after 4 lags (i.e. 4 × 10 minutes). To test the robustness of the variable effect directions and sizes, a spatial model on aggregated data (Model 7; identical to model 4 without the fine-scale time variables 'Week' and 'Hour') was compared to a full data version (Model 8), which returned R^2's of 0.310 and 0.364, respectively. The aggregated data resulted in much improved residual fit (Appendix A1), no autocorrelation across

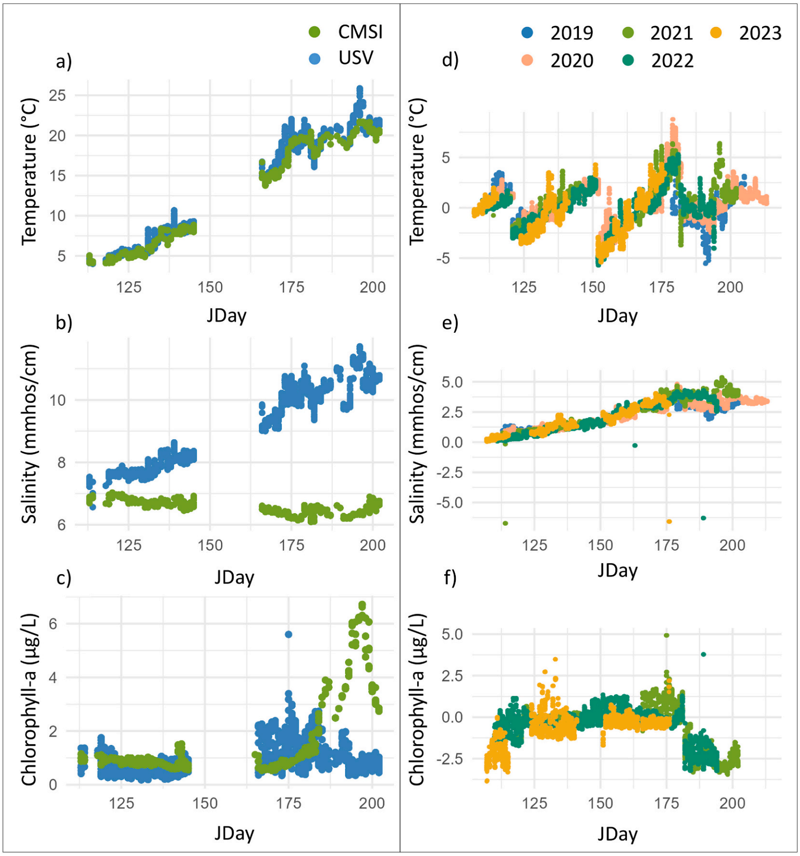


Fig. 5. Seasonal trends in daily surface environmental estimates from CMSI (green) versus in situ observations by the USV (blue) in 2021, for a) Temperature, b) salinity and c) chlorophyll-a. Further, the discrepancy between CMSI monthly surface environmental estimates subtracted from in-situ observations by the USV for all years (2019–2023), for d) Temperature, e) salinity and f) chlorophyll-a. See Appendix A5 for more information. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Model statistics for goodness of fit by Log Likelihood, coefficient of correlation (R^2), maximum absolute error (MAE) and root mean square error (RMSE). Cross validation of 70/30 % training/test data, values mean of 5 reiterations. See all model structures in Table 2. Datasets refer to foundational data for comparability of log likelihood: A = full data; B = subset of 2021–2023; C = 2x2km aggregated NASC values.

Model name	Log Likelihood	R^2	MAE	RMSE	Datasets	SDM type
Model 1	−52,625.3	0.164	0.928	1.325	A	GAM
Model 2	−51,802.9	0.204	0.897	1.292	A	GAM
Model 3	−45,988	0.305	0.783	1.210	A	GLMM
Model 4	−45,673.6	0.313	0.775	1.204	A	GLMM
Model 5	−28,260.5	0.380	0.784	1.204	B	GLMM
Model 6	−28,269.3	0.383	0.783	1.201	B	GLMM
Model 7	−2015.2	0.364	0.466	0.645	C	GLMM
Model 8	−45,845.6	0.310	0.780	1.208	A	GLMM
Model 9	−46,587.0	0.292	0.798	1.222	A	GLMM

observations (Appendix A7), and yet it showed similar variable interpretations as the non-aggregated data model in terms of direction and range of effects (Appendix A7). All effects sizes were higher in the aggregated data model (Model 8). The predicted biomass estimates had a mean of 4.38 log NASC, and the range 2.76 to 6.05 log NASC, which matched the observations (mean: 4.38, range: 1.51 to 7.27) well, though the estimated range was much narrower than observed (Appendix A8). In comparison, the corresponding values from the non-aggregated data model (Model 8) were: mean 4.22 log NASC, range − 0.60 to 7.61 log NASC, when the non-aggregated dataset had a mean of 5.04 log NASC, and a range of −1.32 to 9.63 log NASC.

When predicted on a spatiotemporal grid, the mean estimate of Model 7 was 4.46, ranging from 2.43 to 6.88 (Appendix A8). Model 8 had a mean of 4.81 log NASC, and range of −0.54 to 8.77, returning a much wider range corresponding better to the fine scale observations (Appendix A8). The two predictions from Model 7 and 8 had a correlation of $r = 0.80$. When inspecting the direction and sizes of effects, Model 7 came out with slightly stronger effects and larger ranges than Model 8, but overall with very similar directions of effects for all

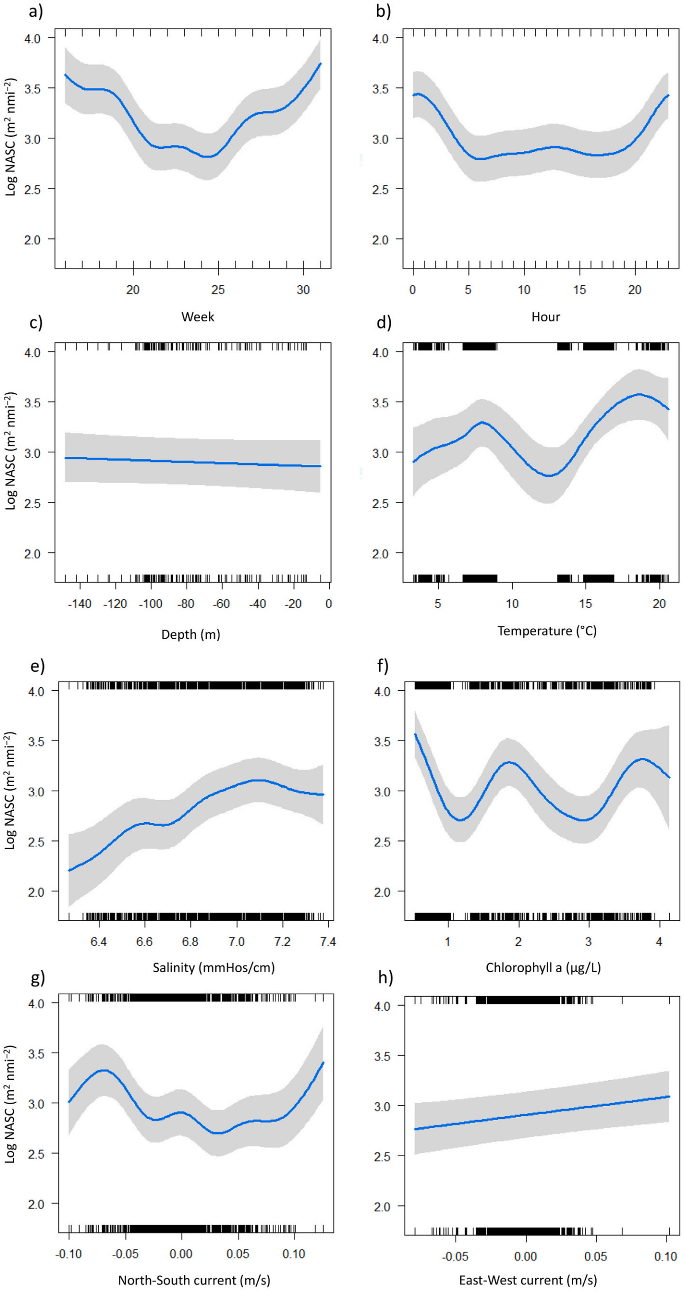


Fig. 6. Effect sizes of each explanatory variable on log NASC, from spatiotemporal GLMM with environmental variables from CMSI monthly averages (Model 4). $R^2 = 0.313$. See Appendix A6 for model summary.

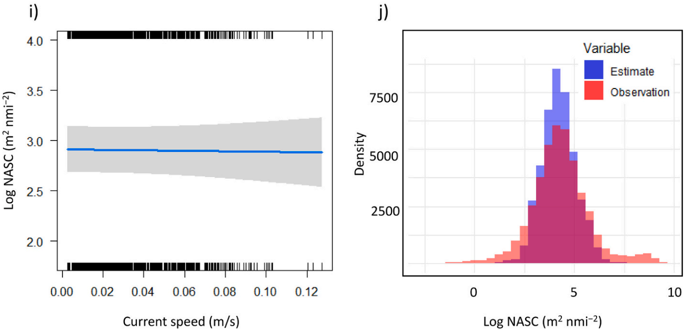


Fig. 6. (*continued*).

explanatory variables (Appendix A8). However, as shown in Fig. 6, the hour of the day strongly affects the detection of pelagic fish, and > 30 % of the observations were made during daytime (between hour 04–21) and at depths shallow enough (<80 m) to expect acoustic dead zones (50 % of the data was sampled in areas shallower than 100 m during daytime). This means high risk of under-estimation of true biomass values that cannot be corrected for under a grid prediction. Thus, we here continue with the non-aggregated data for a spatiotemporal grid prediction (see Appendix A9 for aggregated data grid prediction and estimate discrepancies between Model 7 and Model 8).

3.3.3. *Spatial prediction*

When the final fish distributions were predicted on a grid (Fig. 7), 'Week' was excluded to simplify the time structure (Model 9). The highest biomasses were detected in shallow areas (e.g. close to Gotland and Öland, ref. Fig. 1), but not strictly. Some areas, like north-east of Öland consistently had higher levels of fish than others. There were significant seasonal patterns of change across months, as reflected on a finer scale in the predictor 'week' from Model 4, where overall higher levels of fish were found in the beginning and end of the season, with an estimated dip in June. The model predicts very similar trends in months across years (see Appendix 13 for environmental variable trends), where the same general areas were predicted to produce upper quantile levels of fish (see Appendix A14 for distribution of observed upper quantiles). Strongest of all, however, were the 'year' effects, where years with high biomass such as 2023 contrasts with poorer years, like 2022 (See Appendix A1 for year values). As no data was gathered in or after July 2023 we have chosen not to include this month in the prediction (see Appendix A14).

4. Discussion

We here show how we collected and analysed high-resolution spatiotemporal hydroacoustic data for estimating fish biomass distributions at a community level over time. The area selected and the speed of the USV facilitated the possibility to cover a large and diverse area with high revisiting rate across the season each year, which gave a solid foundation for describing trends in pelagic fish distribution and amounts. Further, it enhanced the possibilities to predict also in non-sampled areas and times, and even to estimate changes in detected fish abundance on a scale as fine as by hours. The details picked up in the hydroacoustic data were on a remarkably fine scale (as shown in Fig. 3), from 1 to 100 m depths, with next to no noise due to the low speed and lack of propulsion from the USV (DuFour et al., 2021). In all, the cost effectiveness of the observations, and the extension in space and shallow water depths possible to monitor provide great opportunities for ecological studies on yet under-sampled habitat types (e.g. upper water column, shallow-water areas and fragile ecosystems). Further, the sampling design of always starting and returning to the same area (i.e. close to Stora Karlsö, see Fig. 1) provided an important advantage: high but discrete re-visitation rate to a concentrated area, providing a stronger foundation for estimating fish biomass in similar areas that were less frequently observed. In addition, the travel from east to west sampled the range of water depths several times weekly (See Appendix A12), under different environmental conditions such as currents and hour of the day. In 2019 there was a break in data collection of ∼1.5 months (May–June), which impacted the ability to explain the distribution trends (i.e. R^2 Model 4: 0.31; Model 5: 0.38), underlining the value of high resolution and frequent resampling to inform spatiotemporal models.

We found high consistency between the CMSI estimates of surface temperature and our in-situ observations. However, the CMSI estimates for chlorophyll-a was less consistent with our observations. The low correlation was likely due to the annual late summer chlorophyll-a bloom which did not match the observations well, neither in timing nor level (see Fig. 5 and Appendix A5). The match in the initial season may explain why the models containing chlorophyll-a as a variable still did better in cross validations than the ones without (the salinity observations are dealt with below). Notably, the variation in USV-observations of temperature and chlorophyll-a was partly due to the fine resolution of hour and level of solar irradiance. High temperature/irradiance leads to sensors exaggerating chlorophyll measurements (Rousso et al., 2021), but on a USV there is no possibility for in-situ sensor corrections nor determination of calibration values. While the environmental variables, the semi-random movement pattern and speed of the USV, and the time of day decreased problematic autocorrelation (Appendix A7), it was not completely removed. For that, we needed to aggregate the data before modelling (Model 7), a procedure resulting in more accurate estimates but on fewer and more conservative observations (i.e. smaller CIs). Nevertheless, when comparing the aggregated model prediction (from Model 7) with the non-aggregated one (Model 8), the general trends were similarly described. The aggregated data variant gave stronger effect sizes and better residual fits, along with non-significant autocorrelation. However, the aggregated models also returned larger variations in effect sizes though a smaller overall range in estimates, diffusing the significance of variables which made it

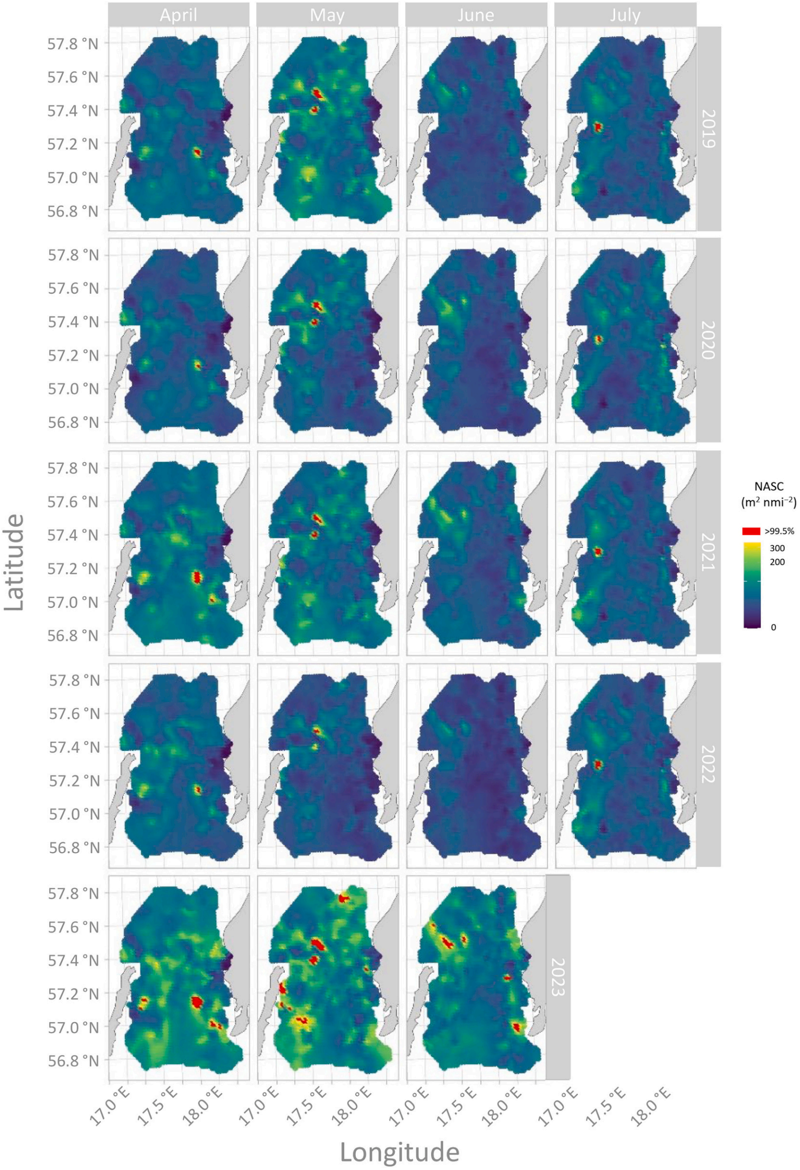


Fig. 7. Predicted fish biomass distribution in NASC (m^2nmi^{-2}) with upper 0.005 quantile marked in red, by months (April–July) per year (2019–2023). Prediction was based on 'hour' 01, using Model 9 (See Table 2) with full-data and autoregressive correlation structure. See Appendix A6 for model summary. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

unclear how successful this aggregation was in terms of unit size (i.e. 2x2km). Without a reference system for biologically significant entities (Schneider and Piatt, 1986; Weimerskirch, 2007), we aggregated to the same resolution as the by-month CMSI data. Preliminary tests found that other time aggregations (e.g. week or even day of the year) resulted in similar number of observations as by month (by JDay: $n = 3220$; Week: $n = 2458$; Month: $n = 1920$; no aggregation: 41292), while any finer scale (e.g. 1, 3 and 6 h intervals, respectively) still had significant autocorrelation.

4.1. Environmental variables and SDMs on community level

Any prediction extending in space and/or time from observations depend on models containing explanatory variable values comparable to what is available on the predictive grid. The correlation procedures were intended to verify the suitability of scale (i.e. monthly resolution and 2x2km means in CMSI variables versus the hourly means of USV variables), in case the effects deviated from the expectations (Andersson et al., 2023; Candolin et al., 2008; Fey, 2001; Jørgensen et al., 2005a, 2005b; Lefébure et al., 2011, 2014; Novotny et al., 2022). We spotted a critical time drift in our own salinity measurements. The USVs CT sensor, without filters or flushing system, was likely cumulating a biological film (i.e. bacterial/algae) over time (Ando et al., 2005). This is a direct consequence of miniature equipment along with the lack of maintenance by an on-site crew. In contrast, the fluorometer had a mechanical cleaning wiper to prevent growth, but still returned a large difference in chlorophyll-a measurement as compared to CMSI estimates. As the USV moved over large areas the problem is unlikely to be due to a spatial mismatch or short-term local levels (see Appendix A12). Notably, the model containing USV-collected temperature and chlorophyll-a variables (Model 6) performed slightly better than its CMSI counterpart (Model 5) in the evaluation process. In models, the environmental variables in general correlated positively (i.e. depth inverted) with NASC levels, except the non-significant chlorophyll-a and current speed. Whilst the general direction of the environmental effects remained similar across models and data aggregation, the effect sizes and thus their significance needs to be evaluated with caution due to the uncertainty of the underlying data (i.e. autocorrelation in fish observations, and mismatch between CMSI estimates and USV observations). Though the models presented here explained the distribution of the pelagic fish community reasonably well ($R^2 > 0.30$), the environmental effects could not be viewed as essential. However, there may be alternative reasons to why the variable effects were less clear than expected. Firstly, surface variable estimates for chlorophyll-a, salinity and temperature are unlikely to be the best predictors for pelagic fish distributions (see Appendix A3), especially in highly stratified waters like the Baltic Sea (Liblik and Lips, 2019; Muchowski et al., 2023). Secondly, the models were based on aggregated NASC values from a community of at least three fish species, when even different species of cohabitant clupeids can respond to hydro-climatic forces in significantly different ways (Pennino et al., 2020). In addition, the species in this community have different spawning times and conditional demands during the studied time-period and, even within species, the dynamics depended on size and reproductive state (Andersson et al., 2023; Cardinale et al., 2003). In order to disentangle data by species, size compositions and proportions for realistic biomass estimates (i.e. kg/km^2), biological samples such as trawling are still essential and cannot be performed by the USV. Alternatively, species and size composition can be inferred by Target Strength (TS) equations to the raw acoustic data (Didrikas and Hansson, 2004). For now, methods are primarily under development for species of commercial importance (Fässler et al., 2008; Ona, 2003). Further development on this topic would be desirable to improve the results of trawling-independent acoustic monitoring such as USV surveys.

4.2. Autocorrelation and data aggregation

Spatiotemporal autocorrelation was unavoidable in the USV observations, with no standardized method for handling such data without heavily aggregating it. However, beyond compromising the resolution, aggregating the data is problematic for several reasons. Firstly, the speed of the USV varied, and the areas sampled were opportunistic based on wind directions, meaning that the number of observations within each spatial and temporal aggregation would vary drastically amongst areas. While weighting estimates for the number of observations could aid, we would still face the problem of detected fish biomass varying drastically with hour of the day (Fig. 6). This variation reflects one of the main challenges in hydroacoustic data treatment: distinguishing fish close to the seabed (Mello and Rose, 2009). Two of the species highest represented in the area, herring and sprat, perform diel vertical migrations (Cardinale et al., 2003). During daylight hours they can be inseparable from the seabed, even by visual inspection. Due to the anoxic zone, fish were rarely detected in deeper depths, and so whenever the seabed was deeper, a loss of fish detection was unlikely. However, more than 1/3 of our observations were made during low-detection hours (see Fig. 6) and at depths shallower than the typical depths of the anoxic zone. While the models were trained on all hours of the day, we decided to predict on the estimated night distribution (01 am CEST), to compensate for the change in detection rate by time of day. For future studies, the key areas for change in biomass by time of day could be estimated prior to spatiotemporal modelling, to correct for observations in areas and times where an acoustic 'dead zone' (Mello and Rose, 2009) is likely to exclude fish. Though a large proportion of the clupeids often remains close to the seabed also during the night (Cardinale et al., 2003), finding a way to, at least partially, compensate for non-detected fish before aggregating data would be ideal.

4.3. Final remarks and potential contributions to future research

Despite the complexity of environmental effects, fish behaviour and autocorrelation, the final distribution of small pelagic community predicted in this study is in line with what is expected for the Baltic during late spring-summer (Candolin et al., 2008; Jørgensen et al., 2005; Ojaveer and Kalejs, 2010), as for similar species around the globe (e.g. sardines and anchovy in Mediterranean Sea: Pennino et al., 2020; sprat in the Adriatic Sea: Palermino et al., 2024). The varying spawning times and bathymetric requirements, means that movement between suitable spawning sites is expected with strong month specific patterns and similarities across years.

There are possibilities for technical development in smaller USVs and miniature sensors, especially with focus on autonomous calibrations and maintenance for longer lasting surveys. The continuity of the data makes it potentially highly correlated, whilst robust tools for handling such data is still under development. In the meantime, stepwise analysis can clarify the strengths and weaknesses in the data, and can reveal meaningful dynamics and insights on the way. While data aggregation still proved the best way to reduce problematic data structures like autocorrelation, crucial details were lost in the process. However, both with aggregated and non-aggregated data, we estimated similar effects and distributions, which revealed important ecological dynamics and highlighted that some areas consistently offered favourable habitats for small pelagic species. Overall, hydroacoustic surveys can become much more cost effective with the inclusion of USVs for pre-surveys, simultaneous co-operative surveys (e.g. pre-sailing transects) though with limitations in comparability between obtained values between larger vessels and USVs. The majority of biomass in our study was observed in water too shallow (<15 m) for larger ships to monitor effectively, and significant abundances were found in shallow-seabed areas (<20 m) that are often inaccessible to larger vessels. Even in comparable depths, aligning the ping rate to survey speed between vessels would be difficult. Finally, the USVs variance in speed with fixed ping rate results in greater data variability as compared to large vessel surveys. In any case, the USV would be highly useful for extending surveyed areas and habitat types, and for coping with issues of larger vessels, such as disturbance to the observed environment. The possibility to model fish distribution on a fine scale could be a valuable tool for ecosystem-based management of small pelagic fish, and for detailed ecological studies of their role in marine ecosystems (Cury et al., 2011; Hilborn et al., 2017; Pikitch et al., 2014). Here, we estimated the detailed spatial distribution of the small pelagic fish community in high resolution, in an area important to avian predators throughout their reproductive period (Galatius et al., 2020; Österblom et al., 2006). The next steps should be to find a solution to the effects of time of day, and match the spatiotemporal distribution of prey to the foraging sites of the local top predators dependent on them.

CRediT authorship contribution statement

Astrid A. Carlsen: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Michele Casini:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Investigation, Funding acquisition. **Francesco Masnadi:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Olof Olsson:** Project administration, Methodology, Funding acquisition. **Aron Hejdström:** Data curation. **Jonas Hentati-Sundberg:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation.

Declaration of competing interest

None.

Data availability

All data are publically available through the Swedish National Data Service (SND) https://doi.org/10.5878/9m27-vg06. R-codes are published at Github Inc., https://github.com/Astidac/Autonomous-data-sampling-for-high-resolution-spatiotemporal-fish-biomass-estimates.

Acknowledgements

We owe many thanks to everyone involved in the Baltic Seabird Project, especially those tied to the USV work. We'd also like to thank the crew at RV Svea for aid and assistance during the voyages of the Sailbuoy. Thank you to Max Lindmark for feedback in the modelling procedure, and Agnes Olin for feedback on the manuscript and on the modelling procedure. AAC was supported by Marcus and Marianne Wallenbergs stiftelse, JHS was supported by Vetenskapsrådet and Formas. Field work was supported by WWF Sweden and Milkywire. We also wish to thank three anonymous reviewers for valuable revision of the manuscript.

Jonas Hentati-Sundberg, Olof Olsson and Astrid Carlsen were supported by Marcus and Marianne Wallenbergs stiftelse (grant number 2018-0093). Jonas Hentati-Sundberg was also supported by Vetenskapsrådet (grant number 2021- 03892) and Formas (grant number 2021-02639).

Appendix A. Appendix

A.1. Distribution of response variable, NASC

The biomasses observed ranged from 0.1 to 15,174.9 m2 nmi − 2, with 1st quartile of 32.9 m2 nmi − 2, median of 70.74 m2 nmi − 2, mean of 293.8 m2 nmi − 2 and 3rd quartile of 154.6 m2 nmi − 2, meaning strongly Poisson distributed. For all analysis, NASC values were log transformed to approach the assumption of normal distribution (Fig. A1.1). There was still a slight upper skew likely reflects larger aggregations of fish.

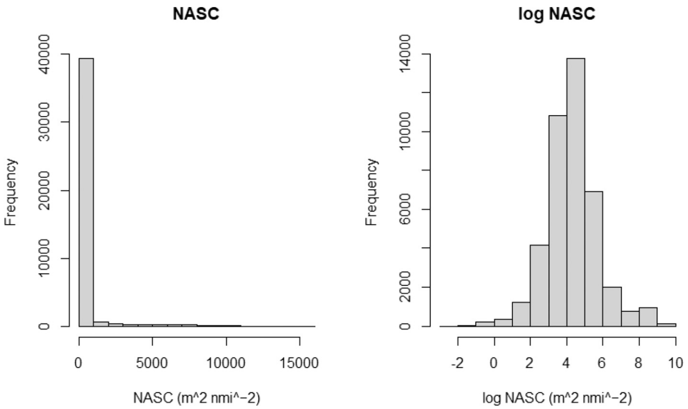


Fig. A1.1. Distribution of response variable NASC before and after log transforming.

Distribution family for the models were chosen after stepwise tests and inspecting residual distributions. The final best distribution for the response variable log-NASC was student distribution, with df = 4 (fig. A1.2).

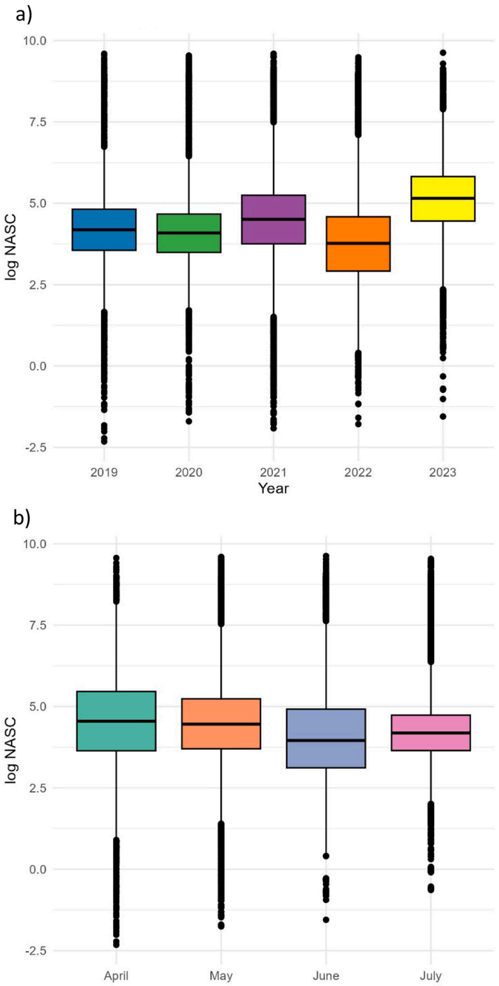


Fig. A1.2. Distribution of log-transformed NASC values across (a) years and (b) months.

A.2. Model residuals

Model residuals were inspected visually to select the best distribution family for each model.

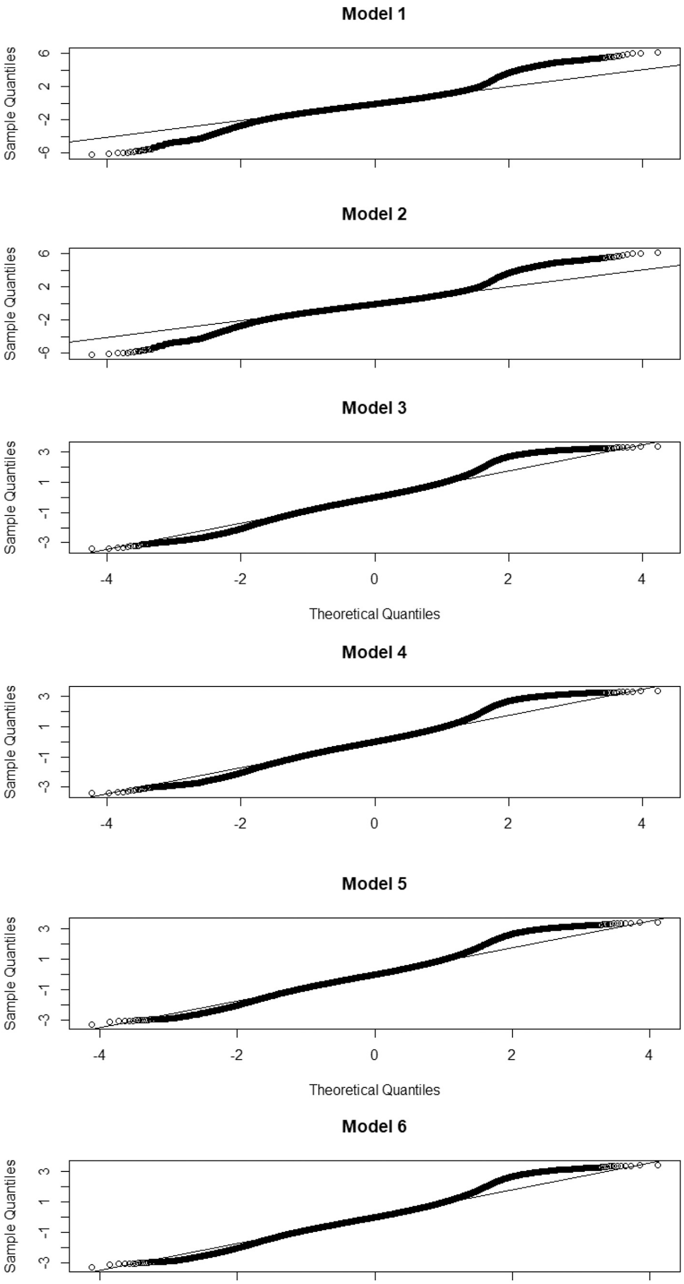


Fig. A2. Residual distributions for Model 1–9, all fitted with student distribution (link ‘identity’, df = 4), models 1–6 and 8–9 had correlation structure ‘AR1’, Model 7 had correlation structure ‘iid’.

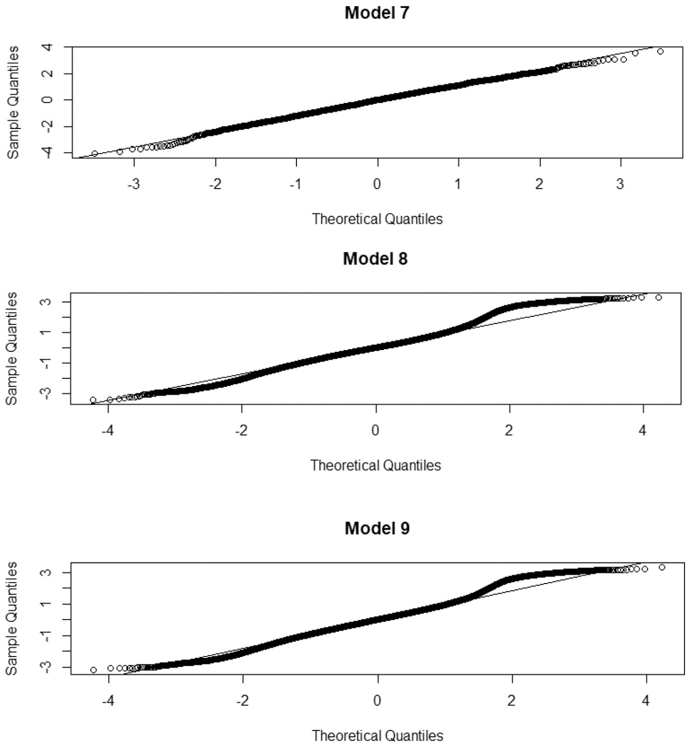


Fig. A2. (*continued*).

A.3. Correlation tests predictive variables

General correlation between mean water column estimates and sea –surface estimates of chlorophyll-a, salinity and temperature were produced, to test how similar they were (Table A3.1). While water column estimates for temperature and chlorophyll explained the fish distribution better than surface estimates (Table A3.2), water column estimates should be used with cation due to their high level of uncertainty as e.g. remote sensing is less accurate. Further, the USV can per now only perform surface observations, and so for any discrepancy test on values for salinity, temperature and chlorophyll-a we'd have to rely on surface values from CMSI anyways. The correlation between water column means (weighted for depth, where surface values are weighted heavier) shows that there is a rather large discrepancy between them, inferring the strong stratification of the water column in the Baltic sea. This reflects why it may be problematic to base models for fish distribution of pelagic species on surface variables, and why the models didn't improve more when these core variables are included.

Table A3.1
Correlations between surface and water column averages by CMSI.

Variables	Correlation
Chlorophyll: water column vs surface, CMSI	0.52
Salinity: water column vs surface, CMSI	−0.05
Temperature: water column vs surface, CMSI	0.72

Table A3.2
Estimated effects and prediction power of distribution model when using mean of the water column versus sea-surface versions of the variables chlorophyll-a, salinity and temperature from CMSI.

Variable	Effect (SE)	Pr(>|t|)	R2-Adj.
Mean water column Chlorophyll	0.14 (0.013)	<2e-16	0.003
Sea surface Chlorophyll	0.06 (0.007)	8.59e-15	0.001

(*continued on next page*)

Table A3.2 (*continued*)

Variable	Effect (SE)	Pr(>|t|)	R2-Adj.
Mean water column salinity	−0.11 (0.013)	<2e-16	0.002
Sea surface salinity	−0.63 (0.029)	<2e-16	0.011
Mean water column temperature	−0.07 (0.003)	<2e-16	0.011
Sea surface temperature	−0.03 (0.002)	<2e-16	0.007

A.4. Sailing velocity of USV

While the drone were in movement for most of the time, more than 700 observations were made laying completely still, and more than 2500 were made with a speed of more than 1 m per second. With a speed of 0.5 m per second, 7 min of sampling aggregated contains fish detections over 210 m, while a speed of 1 m/s an observation would cover a distance of 420 m. Distance covered must be seen as a conservative measurement as the drone sometimes would sail in a straight line, and sometimes in zig-zag to maintain the direction set by waypoint, meaning that including distance and/or speed directly in any model is far from straight forward.

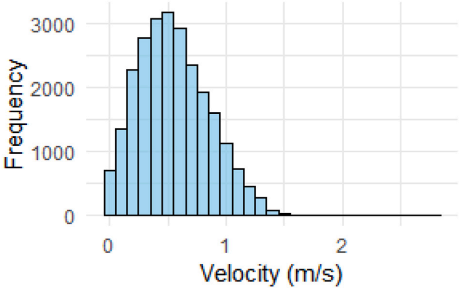


Fig. A4. Velocity of USV per NASC observation across all years.

A.5. Salinity by month of year at Karlsö by SMHI 2021–2023

To verify the deviating salinity levels observed by the USV versus CMSI estimates, we obtained observations from the local hydrology station of Swedens Metrological and Hydrological Institute (SMHI). The hydrological measuring station is situated just outide of Stora Karlsö, within the study area. The observations by SMHI, which is also included in the data for estimates of surface temperature by CMSI, closely resembles the CMSI estimates, with the same clear deviation from the USV observations, supporting the impression that we had technical issues with our equipment.

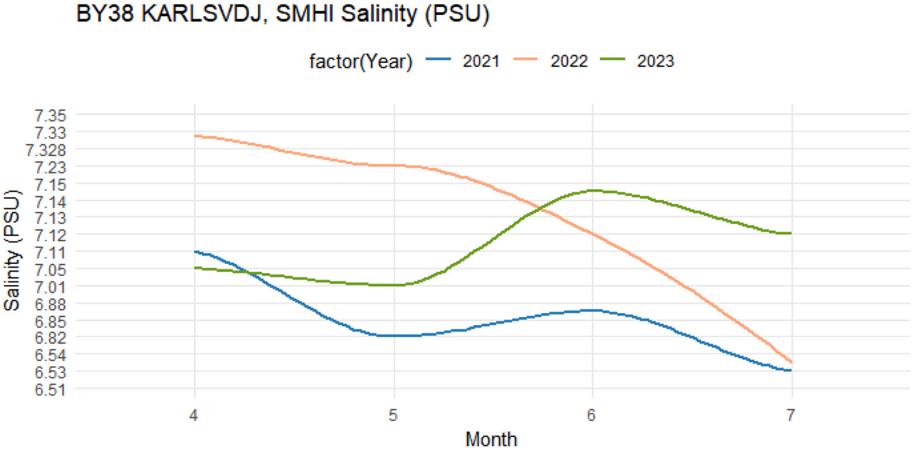


Fig. A5.1. Local sea-surface salinity measurements by SMHI across three years for reference in range and direction of effects as compared to the daily resolution 2021 estimates by CMSI and the USV.

A.6. Model output /results

Model output for the models described in more detail in the result section: Model 4, Model 7, Model 8 and Model 9. Model outputs include information about the general structure of the model, effect sizes and information on model validation summarized. Visualisations of variable effects for model 4 is given in *Results* Fig. 6, and for Model 7 and 8 Appendix A8 Fig. A8.1 and A8.2, respectively.

Table A6
Model output for Key SDMs: Model 4, Model 7, Model 8 and model 9.

Model 4:			**Model 7:**		
Spatiotemporal model fit by ML ['sdmTMB']			Spatiotemporal model fit by ML ['sdmTMB']		
Time column: Month			Time column: Month		
Family: student(link = 'identity')			Family: student(link = 'identity')		
	coef.est.	coef.se		coef.est.	coef.se
(Intercept)	4.35	0.24	(Intercept)	4.57	0.26
Mean_EW_uo_Wclm	1.79	0.63	Mean_EW_uo_Wclm	4.28	1.45
Mean_current_speed	−0.24	1.22	Mean_current_speed	−1.09	2.66
sWeek	0.18	0.16	sDepth	−0.27	0.23
sDepth	−0.02	0.02	sMean_thetao_SST	0.13	0.43
sMean_thetao_SST	0.02	0.31	sSO_surf	0.19	0.06
sSO_surf	0.12	0.16	sChl_surf	−0.52	0.53
sChl_surf	−1.14	0.37	sMean_NS_vo_Wclm	0.49	0.27
sMean_NS_vo_Wclm	0.7	0.11			
Smooth terms:			Smooth terms:		
	Std. Dev.			Std. Dev.	
sds(Week)	2.23		sds(Depth)	0.75	
sds(Hour)	0.08		sds(Mean_thetao_SST)	0.97	
sds(Depth)	0		sds(SO_surf)	0	
sds(Mean_thetao_SST)	1.12		sds(Chl_surf)	5.14	
sds(SO_surf)	1.4		sds(Mean_NS_vo_Wclm)	1.53	
sds(Chl_surf)	5.32				
sds(Mean_NS_vo_Wclm)	2.53				
Random intercepts:			Random intercepts:		
	Std. Dev.			Std. Dev.	
Year	0.5		Year	0.5	
			Month	0.08	
Dispersion parameter:	0.72		Dispersion parameter:	0.49	
Spatiotemporal AR1 correlation (rho):	0.12		Matérn range:	20.96	
Matérn range:	7.3		Spatial SD:	0.2	
Spatial SD:	0.31		Spatiotemporal IID SD:	0.45	
Spatiotemporal marginal AR1 SD:	0.77		ML criterion at convergence:	2012.305	
ML criterion at convergence:	60,590.05				
Model 8:			**Model 9:**		

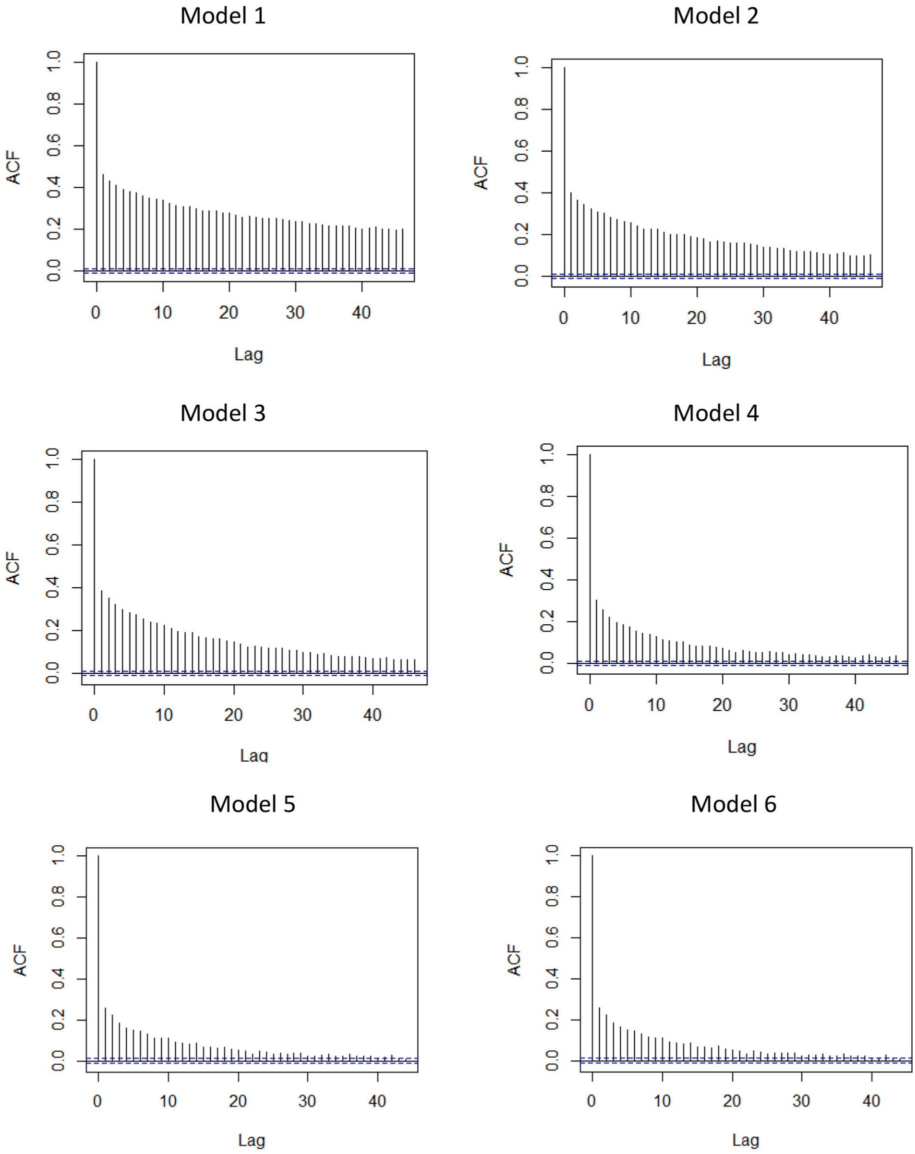
(*continued on next page*)

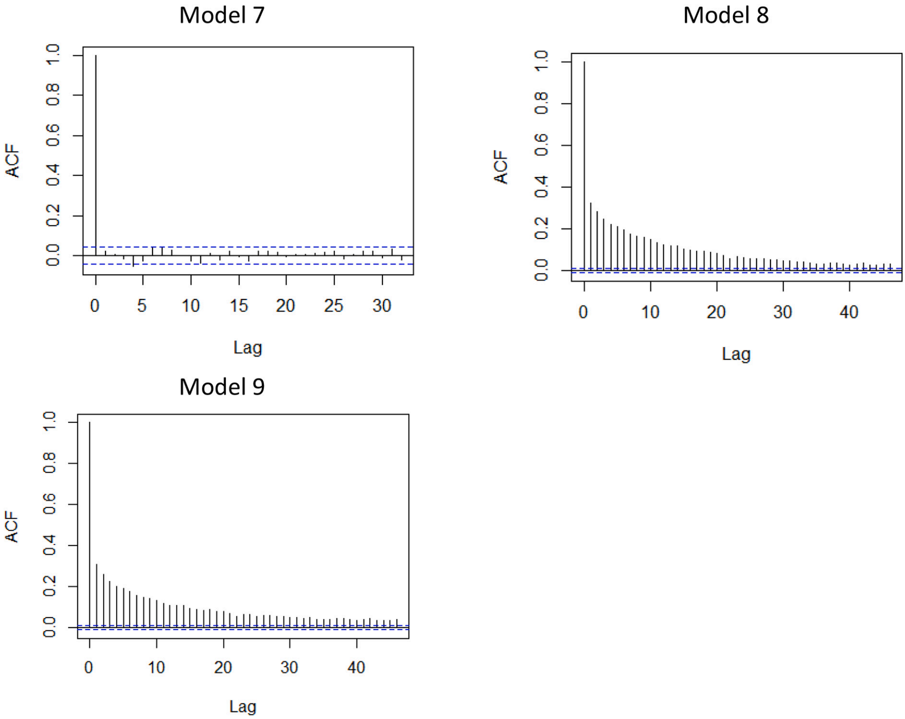
Table A6 (*continued*)

Model 8:			**Model 9:**		
Spatiotemporal model fit by ML ['sdmTMB'] Time column: Month			Spatiotemporal model fit by ML ['sdmTMB'] Time column: Month		
Family: student(link = 'identity')			Family: student(link = 'identity')		
	coef.est.	coef.se		coef.est.	coef.se
(Intercept)	2.46	0.69	(Intercept)	4.37	0.24
Mean_thetao_SST	−0.01	0.01	Mean_EW_uo_Wclm	1.83	0.63
SO_surf	0.29	0.09	Mean_current_speed	0.1	1.25
Chl_surf	−0.04	0.02	sDepth	0	0.02
Mean_EW_uo_Wclm	0.41	0.62	sMean_thetao_SST	−0.16	0.37
Mean_current_speed	0.65	1.28	sSO_surf	0.03	0.18
sDepth	−0.09	0.18	sChl_surf	−1.79	0.38
sMean_NS_vo_Wclm	0.75	0.11	sMean_NS_vo_Wclm	0.74	0.11
Smooth terms:			Smooth terms:		
	Std. Dev.			Std. Dev.	
sds(Depth)	1.02		sds(Hour)	0.08	
sds(Mean_NS_vo_Wclm)			sds(Depth)	0	
			sds(Mean_thetao_SST)	1.87	
Random intercepts:			sds(SO_surf)	1.61	
	Std. Dev.		sds(Chl_surf)	6.25	
Year	0.45		sds(Mean_NS_vo_Wclm)	2.72	
Dispersion parameter:	0.75		Random intercepts:		
Spatiotemporal AR1 correlation (rho):	0.05			Std. Dev.	
Matérn range:	7.17		Year	0.51	
Spatial SD:	0.37				
Spatiotemporal marginal AR1 SD:	0.83		Dispersion parameter:	0.72	
ML criterion at convergence:	62,028.04		Spatiotemporal AR1 correlation (rho):	0.12	
			Matérn range:	7.21	
			Spatial SD:	0.3	
			Spatiotemporal marginal AR1 SD:	0.77	
			ML criterion at convergence:	60,867.51	

A.7. Autocorrelation structures in models

The autocorrelation across 50 observations of NASC values for models 1–9. The autocorrelation is highest in models without environmental variables (Model 1 and 3), and further decreased for models including variables for high resolution time structures, i.e. 'hour' and 'week' (Model 4–6 and 9). All models had highly significant autocorrelation structures except the aggregated data model (Model 7).


Model 1
Model 2
Model 3
Model 4
Model 5
Model 6
ACF
0.0
0.2
0.4
0.6
0.8
1.0
Lag
0
10
20
30
40



. (*continued*).

A.8. *Variable regressions from comparative models with different data aggregation levels*

To validate the results from a spatial prediction model based on autocorrelated data, we compared the effect sizes and directions in two models with the same model structure, based on non-autocorrelated aggregated data (Model 7) versus non-aggregated autocorrelated data (Model 8). See *Results* for more details. The model output for Models 7 and 8 is given in Table A6.

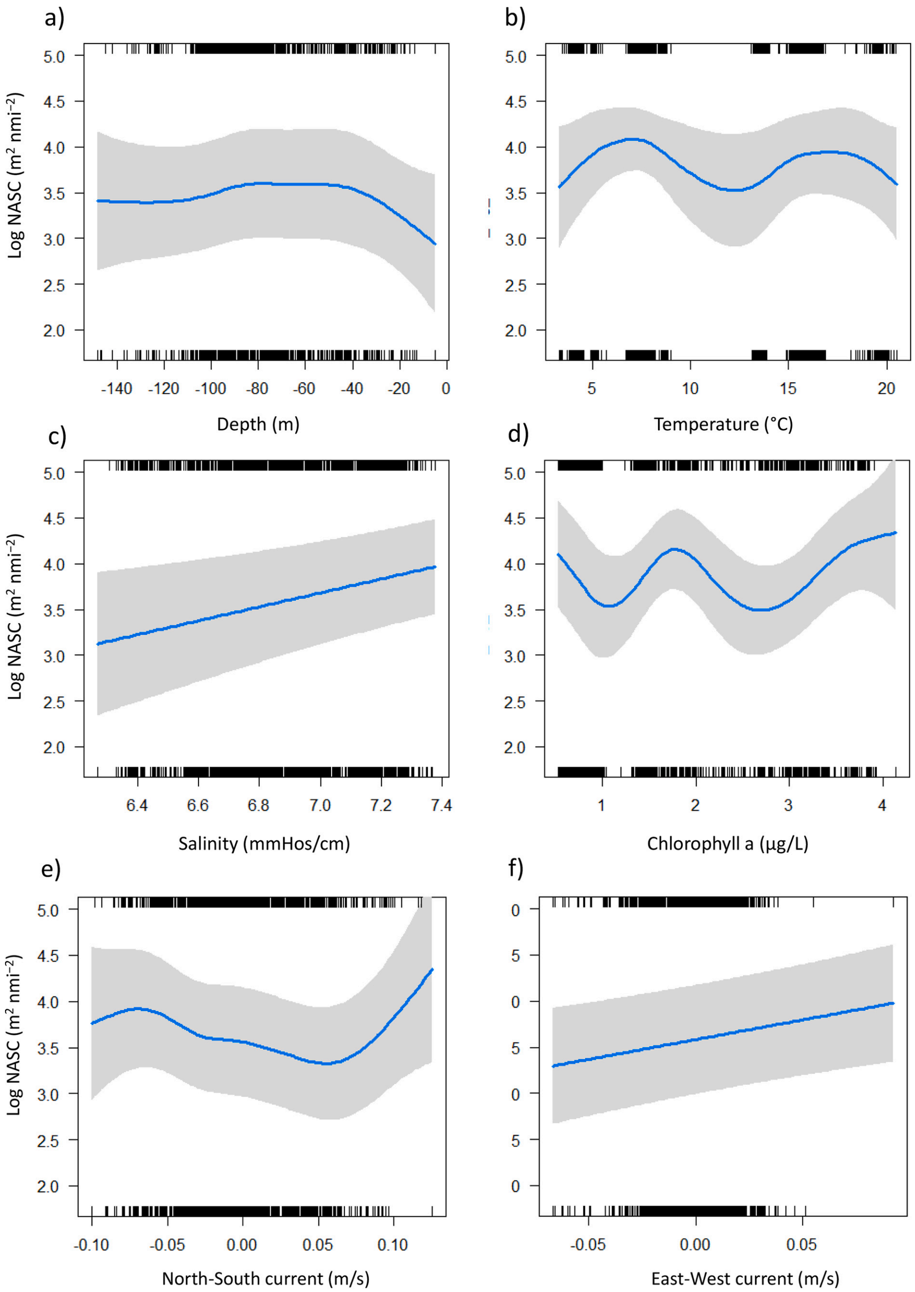


Fig. A8.1. Model 7 (2×2 km spatially aggregated data) effect sizes of each explanatory variable on log NASC, from the GLMM with environmental estimates from CMSI. See Appendix A6 for model summary and Table 4 for model validation and performance.

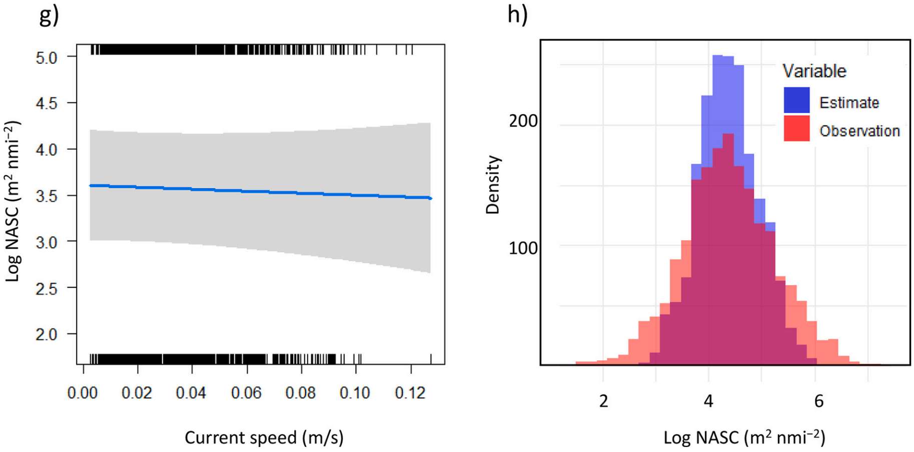


Fig. A8.1. (*continued*).

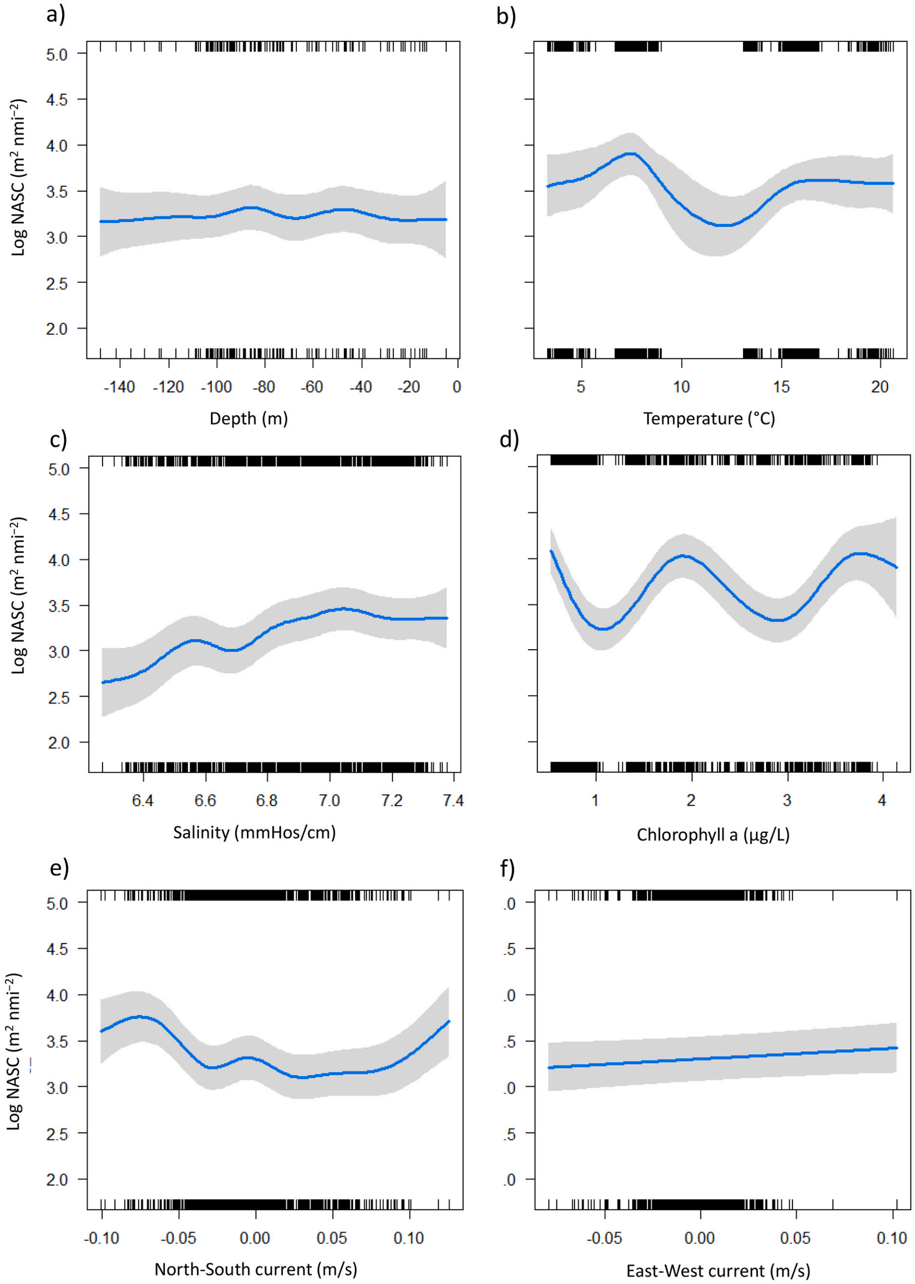


Fig. A8.2. Non-aggregated data model (Model 8) effect sizes of each explanatory variable on log NASC, from the GLMM with environmental estimates from CMSI. See Appendix A6 for model summary and Table 4 for model validation and performance.

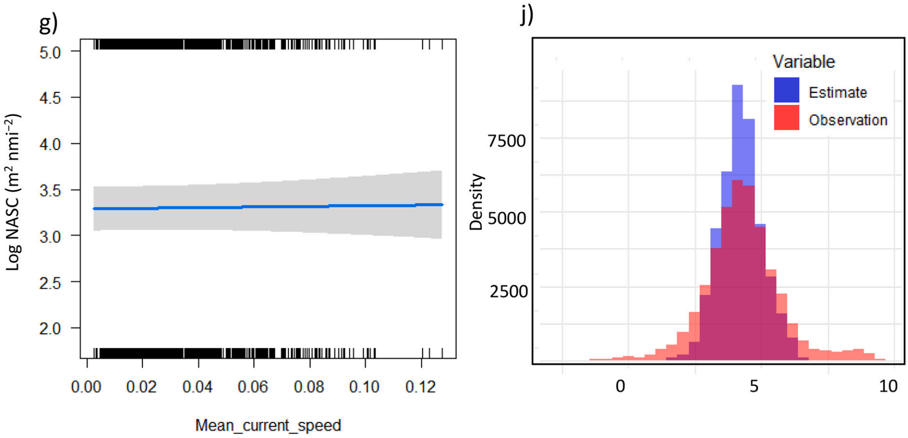


Fig. A8.2. (*continued*).

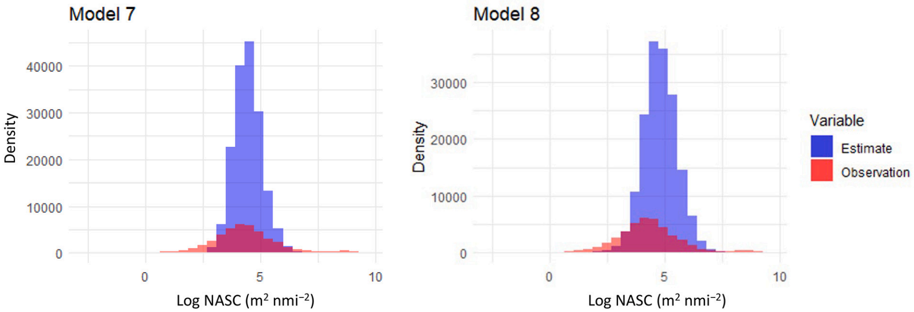


Fig. A8.3. Grid predicted values versus observations for Model 7: prediction on 2 × 2km aggregated data, versus Model 8: prediction on non-aggregated data. See Appendix A6 for model summary and Table 4 for model validation.

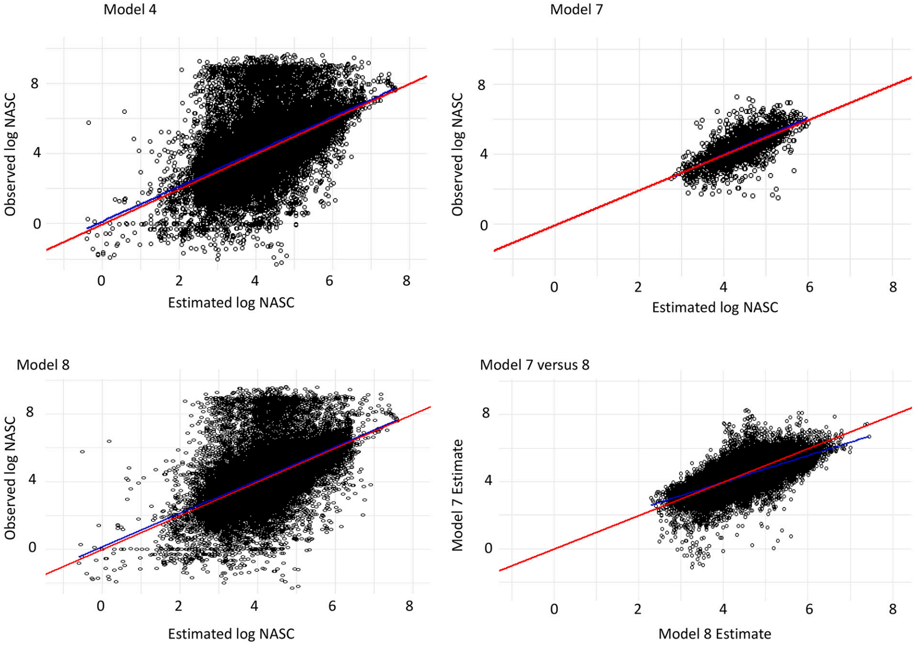


Fig. A8.4. Correlation of prediction versus observations for non-aggregated data model (Model 4), 2 × 2km aggregated data (Model 7), comparative non-aggregated model (Model 8) and Model 7 on Model 8 estimates. Red line indictes a 1-1 linear regression while blue line gives the observed regression.

A.9. Spatiotemporal prediction of Model 7

Spatial prediction based on aggregated data and Model 7. While much less upper quantile predictions are made, the general pattern of high abundance areas is similar to the patterns generated by the non-aggregated data Model 9.

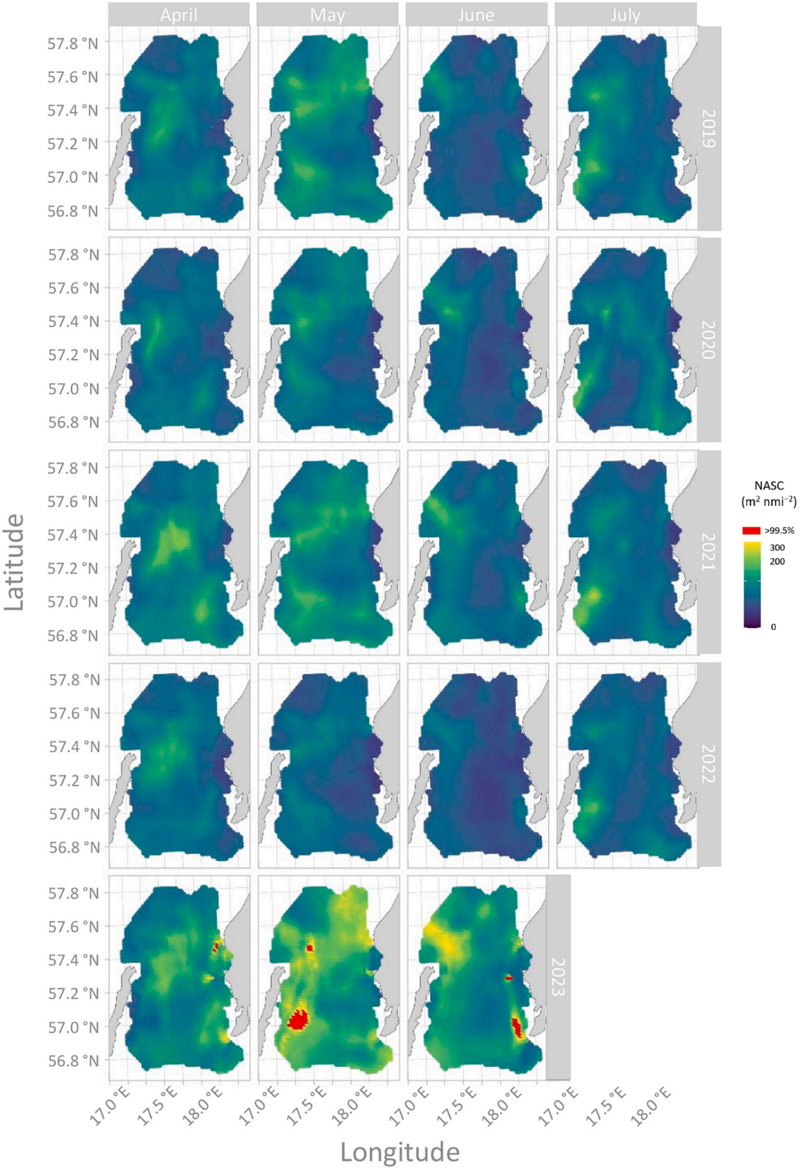


Fig. A9.1. Spatiotemporal prediction of aggregated data, Model 7.

A.10. Spatial distribution of model residuals

Residuals of model estimates

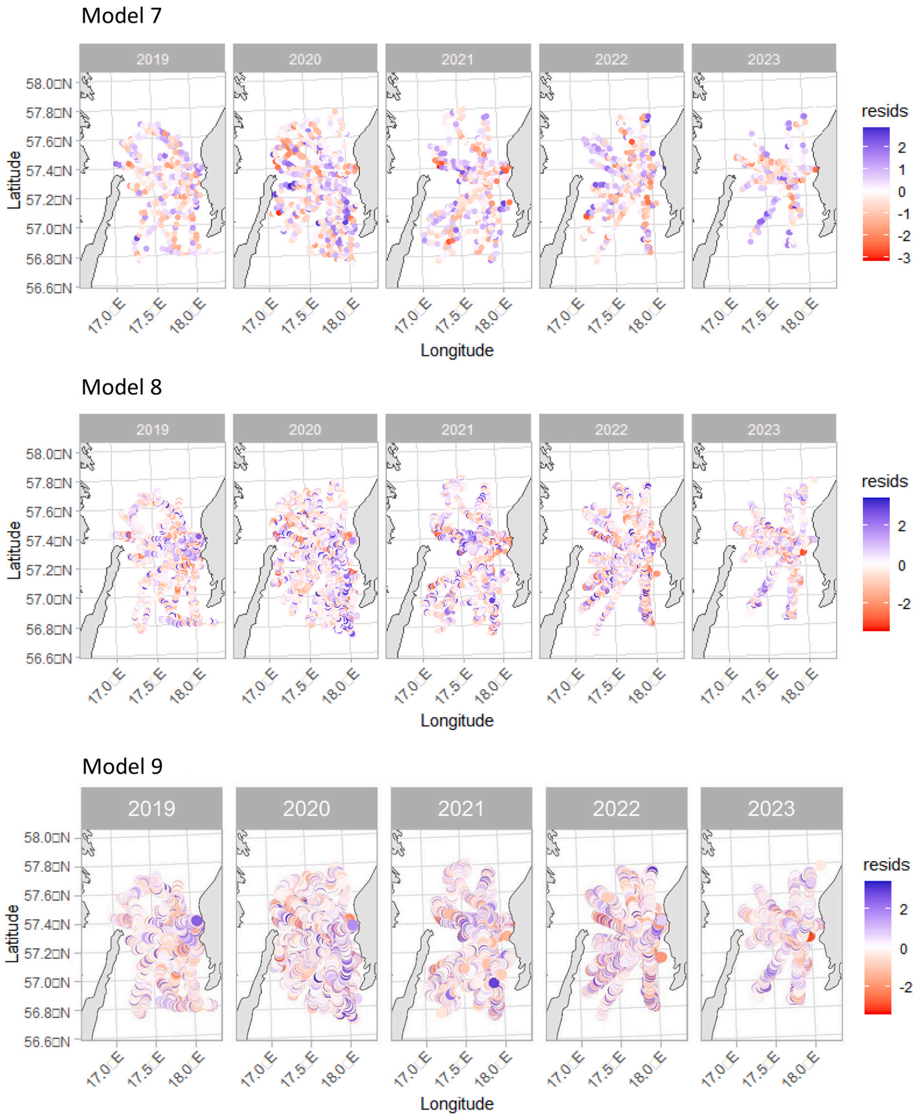


Fig. A10.1. Spatial distribution of residuals of Model 7, 8 and 9.

A.11. Model validations

The stepwise model selection and validation was based on the metrics R2, MAE, RMSE and LL, where we present the mean values in Table 3 (See *Results*). The mean value was based on 5 iterations of each model (Fig. A11.1), after performing 10 iterations and determining that the range of variation across 10 iterations was sufficiently small (Fig. A11.2).

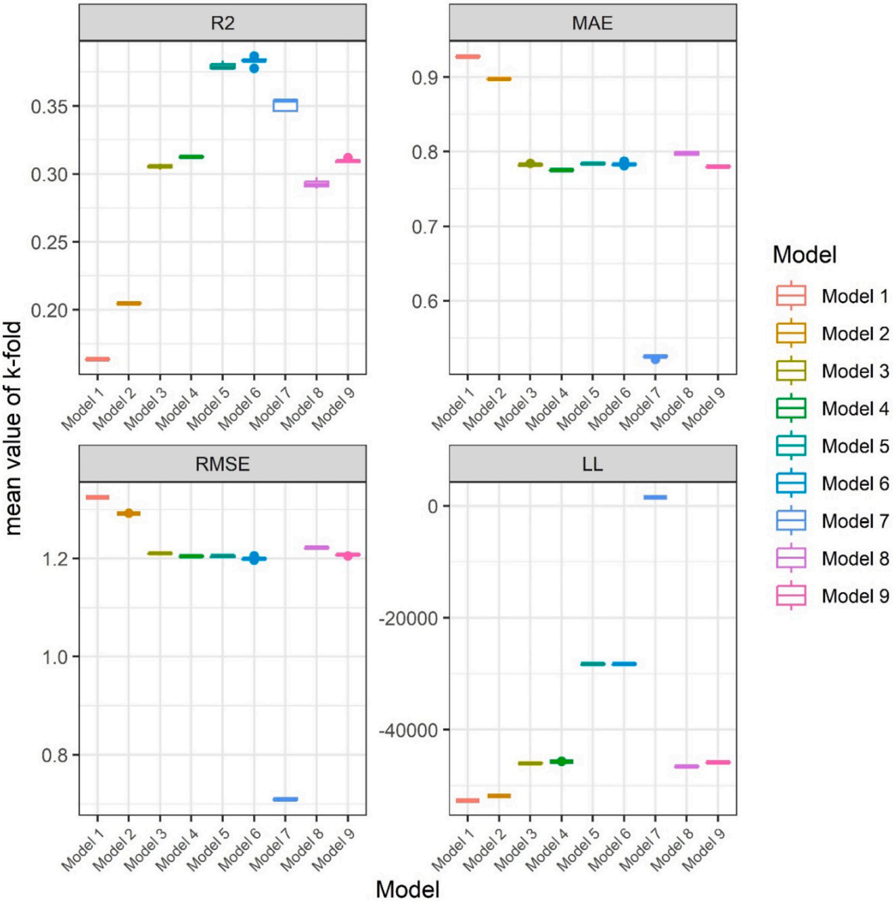


Fig. A11.1. Mean value of k-fold from 5 iterations of each model, with 70/30 % training/test data (See Fig. A11.2 for 10 iterations of first 4 models).

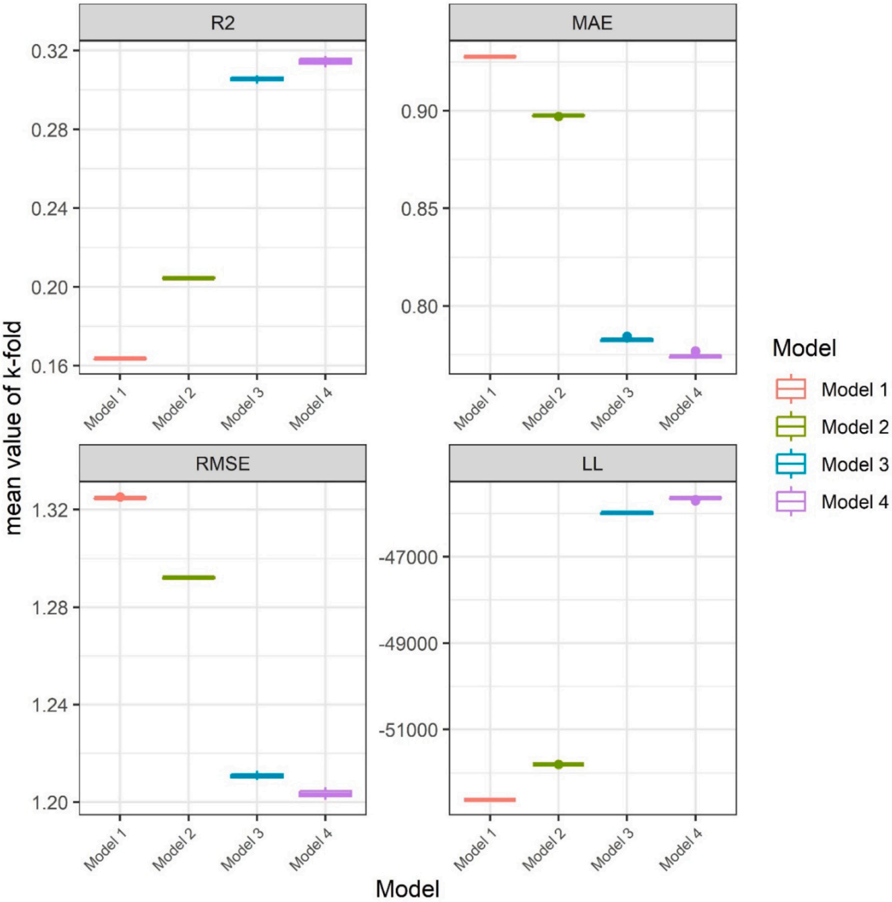


Fig. A11.2. 10 iterations, 70/30 % training/test data. The small variation amongst iterations were used to justify a smaller number of iterations for following models (Fig. A11.1) to save computation time.

A.12. Model validations

The study was performed within ICES statistical rectangles 42G7-44G7, in SD27 of the Central Baltic region.

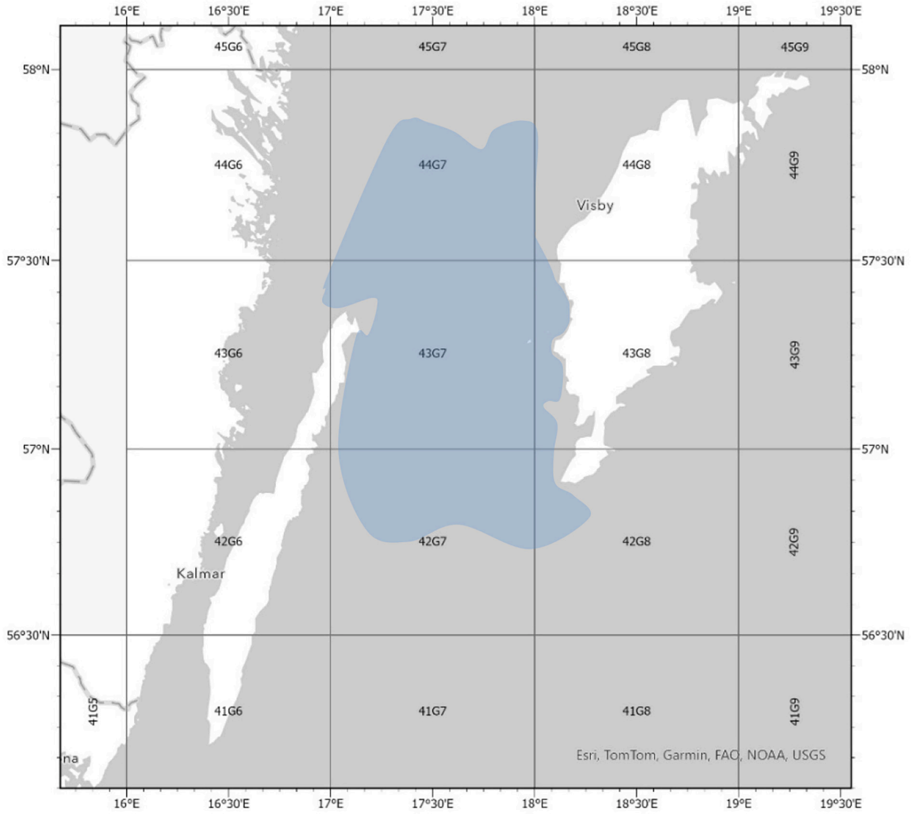


Fig. A12. ICES statistical units in the area surveyed with the USV (blue field) for reference. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

A.13. CMSI estimates of environmental variables

The CMSI environmental variables visualized on the area for reference.

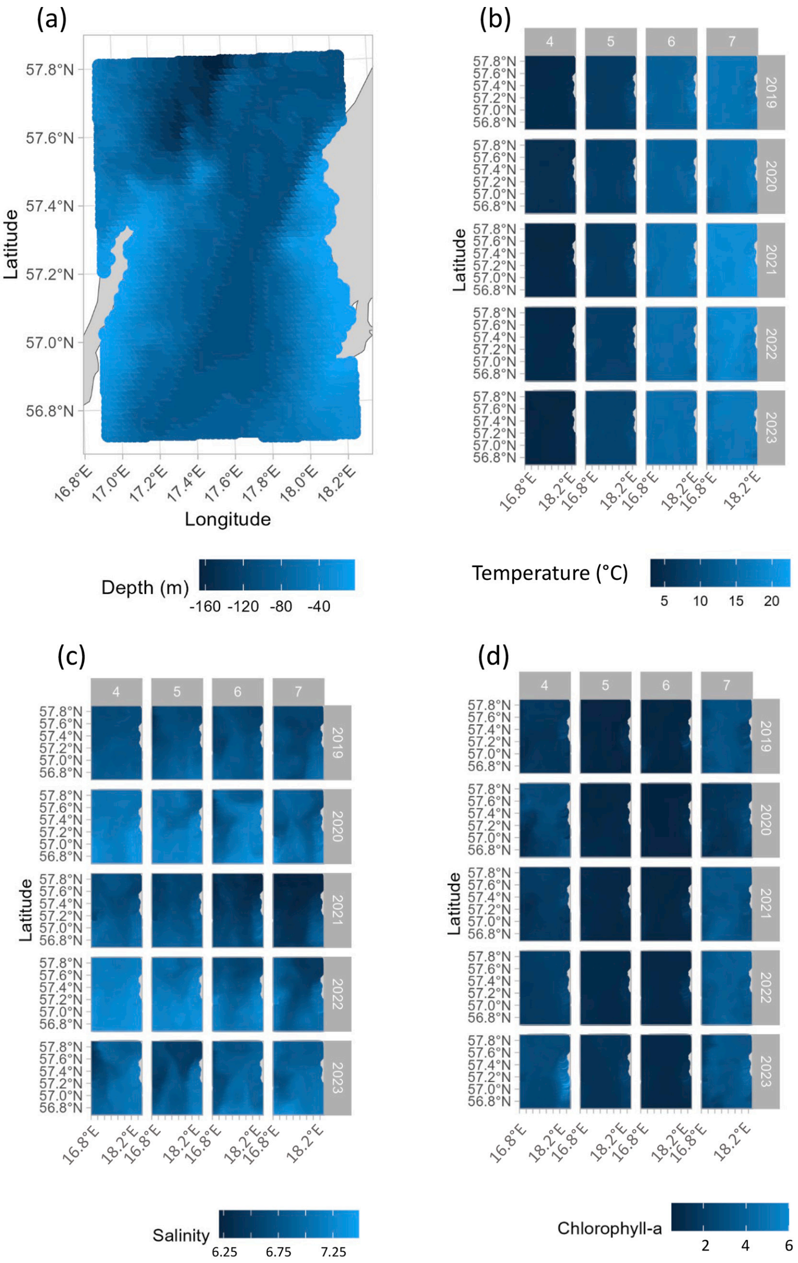


Fig. A13. Environmental variables from CMSI used for spatial prediction of fish distribution with monthly resolution: (a) depth, (b) temperature, (c) salinity, (d) chlorophyll, (e) north-south current, (f) east-west current and (g) current speed.

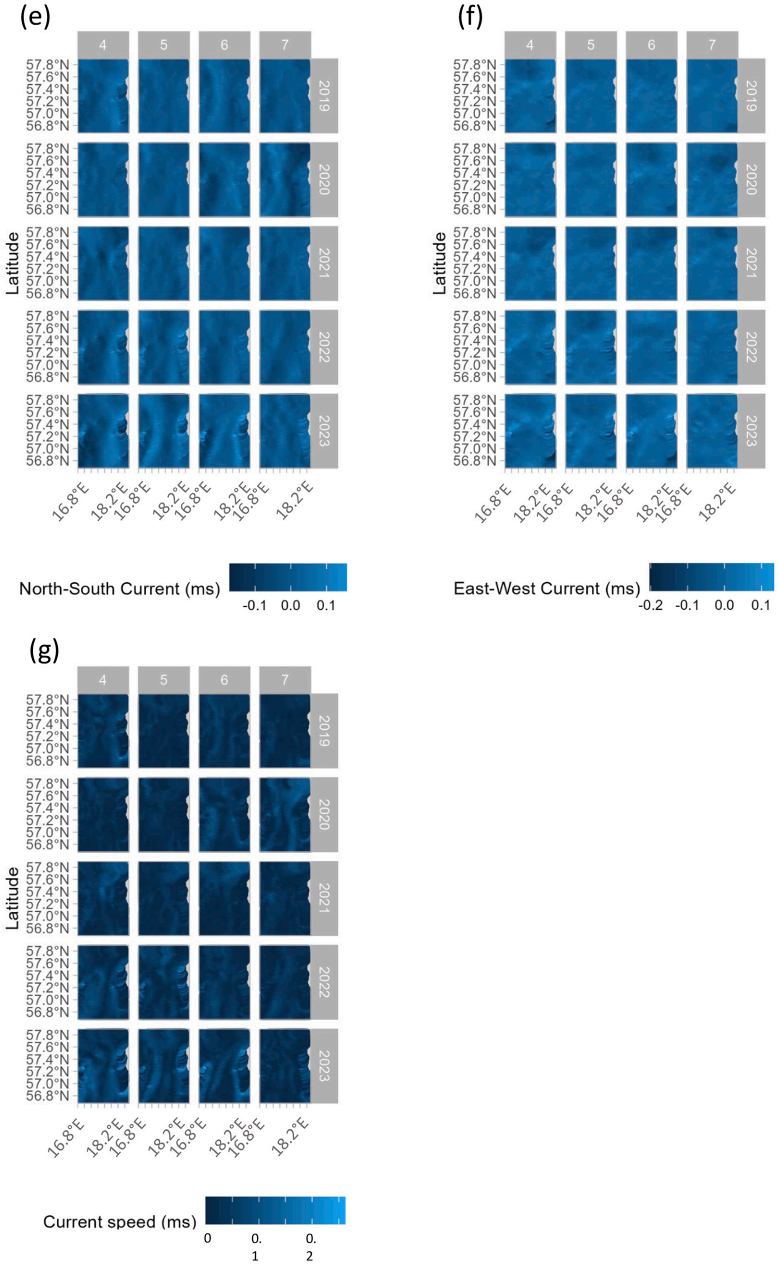


Fig. A13. (*continued*).

A.14. Data collection by month and upper quantiles (0.995) in raw data

The size of the areas sampled varied between months and years, where the wind direction and strength determined how large areas could be covered in the days of operation. Inspection of the distribution of upper quantiles in raw NASC values was needed when their spatial prediction was difficult to make (See Appendix A8 Fig. A8.3 and A8.4).

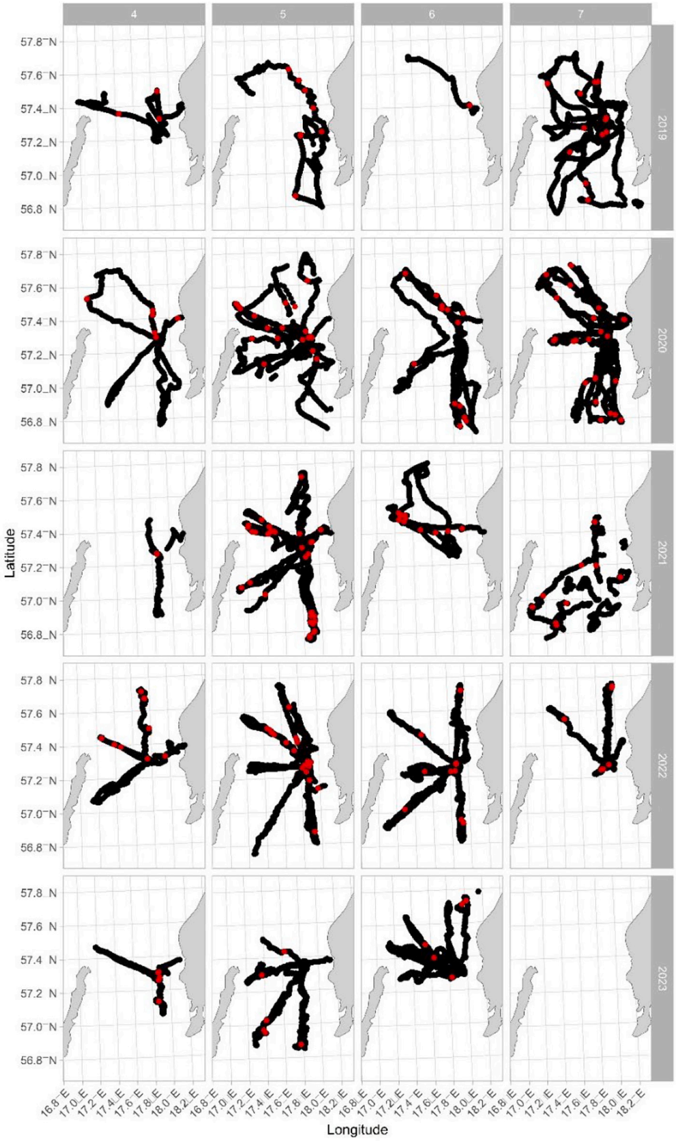


Fig. A14. All observations (black points) and upper 0.995 quantile observations (red points). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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Doctoral Thesis No. 2025:32

This thesis explores how seabird foraging behaviour responds to prey availability and environmental conditions across spatial and temporal scales. Using biologging, environmental data, and modelling, it examines diel patterns, behavioural plasticity, and morphological constraints in shaping foraging effort and preferences. A global analysis highlights gaps in marine protection during breeding. Together, the findings underscore the significance of seabirds as ecological indicators and the urgent need to incorporate behaviourally informed approaches into conservation strategies under the rapid environmental change.

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ISSN 1652-6880
ISBN (print version) 978-91-8046-467-3
ISBN (electronic version) 978-91-8046-517-5