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Connectivity and Population Structure in a Marginal Sea—A Review

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ABSTRACT

Aim: The current biodiversity crisis calls for conservation measures that limit or reduce the negative human impact on key habitats and vulnerable wild populations. To effectively protect biodiversity at all levels, including intra-specific diversity, conservation measures should, ideally, be aligned with the connectivity and genetic structure of wild populations. In this review, we synthesise the scientific literature on connectivity and population structure of marine species in a marginal sea.

Location: The study focuses on the Skagerrak—a marginal sea in the northeast Atlantic Ocean.

Methods: We reviewed a total of 172 scientific publications assessing connectivity or population structure in 48 species. From this material, we summarised the main patterns of connectivity and population structure across species, as well as the taxonomic and geographic representation of the scientific literature within this field.

Results: Our review shows that contemporary connectivity with adjacent seas is high, but asymmetric, for most species. Simultaneously, most species have multiple distinct populations in the Skagerrak, separate from those in adjacent seas. Within the Skagerrak, population structure is common both among coastal populations and between coastal and offshore populations, but less frequent among offshore populations. In many mobile species, multiple populations temporarily overlap in certain areas, but retain their genetic divergence through homing or other barriers to gene flow.

Main Conclusions: Even in one of the most intensively studied marine regions within the field of connectivity and population structure, there are still large knowledge gaps limiting both our understanding of connectivity and its application in management decisions. Nevertheless, it is evident that the presence of population structure despite high connectivity, and temporal variability in population assemblages, poses a challenge for area-based protection measures. This underscores the need for adaptive management that monitors and manages intra-specific diversity on multiple temporal and spatial scales.

1 | Introduction

Biodiversity loss is an ongoing crisis that negatively impacts both global and local ecosystems (Cardinale et al. 2012). A "sixth mass extinction" is underway (Cowie et al. 2022), caused by anthropogenic pressures such as climate change, habitat fragmentation, invasive alien species and overexploitation of wild populations (Pievani 2014; Ceballos et al. 2015). The loss of species is often preceded by loss of intra-specific diversity (Ceballos et al. 2017), and it has consequently been argued that the population, rather than the species, is the relevant unit for conservation (Reydon 2019; Allendorf et al. 2022; Norderhaug et al. 2024). Large populations with high genetic diversity are more resilient to environmental changes and are more likely to harbour alleles that may prove beneficial in future environments—referred to as evolutionary potential (Bürger and Lynch 1995; Frankham et al. 1999; Allendorf et al. 2022). For these reasons, the importance of conserving genetic diversity within species is increasingly recognised in international conventions and legislation, including Goal A and Target 4 in the recent Kunming-Montreal Global Biodiversity Framework (Convention on Biological Diversity 2022). Area-based protection is highlighted as one of the main tools to prevent biodiversity loss, especially in Target 3, stating that 30% of land and water areas should be protected by 2030 (Convention on Biological Diversity 2022). To be effective, however, area-based protection should build on a sound understanding of the spatial requirements of the target populations and the connectivity among different populations (Goetze et al. 2021; Beger et al. 2022).

Connectivity refers to the exchange of energy, biomass, or genetic material between populations or geographic locations (Beger et al. 2022). There are several types of connectivity, which can be conceptualised in different ways. In this review, which focuses on connectivity in the marine environment, we use a conceptual connectivity framework consistent with, e.g., Lowe and Allendorf (2010), Gagnaire et al. (2015), Selkoe et al. (2016) and SEA-UNICORN (Darnaude et al. 2022), depicted in Figure 1 and detailed in Box 1. In marine environments, connectivity is generally high and maintained by both passive dispersal of propagules with ocean currents and active dispersal (migration) of organisms through a continuous environment (Carr et al. 2003). As connectivity patterns are shaped by the specific dispersal traits of multiple life stages, they have the potential to be highly variable across different species and populations (e.g., Corell et al. 2012; Moksnes et al. 2014). Connectivity can promote the persistence of species and intra-specific genetic diversity through gene flow, but can also assist in restoring biodiversity at all levels after depletion, through the dispersal and movement of organisms and genetic material across populations, communities and ecosystems (Balbar and Metaxas 2019).

A related concept is population structure—the subdivision of species into multiple populations (Waples and Gaggiotti 2006; see also Box 1), which can only arise and persist when genetic connectivity between populations is low (Slatkin 1987). Differentiated populations within a species may harbour different genetic adaptations, enabling them to occupy different habitats or ecological niches (Stronen et al. 2022). Importantly,
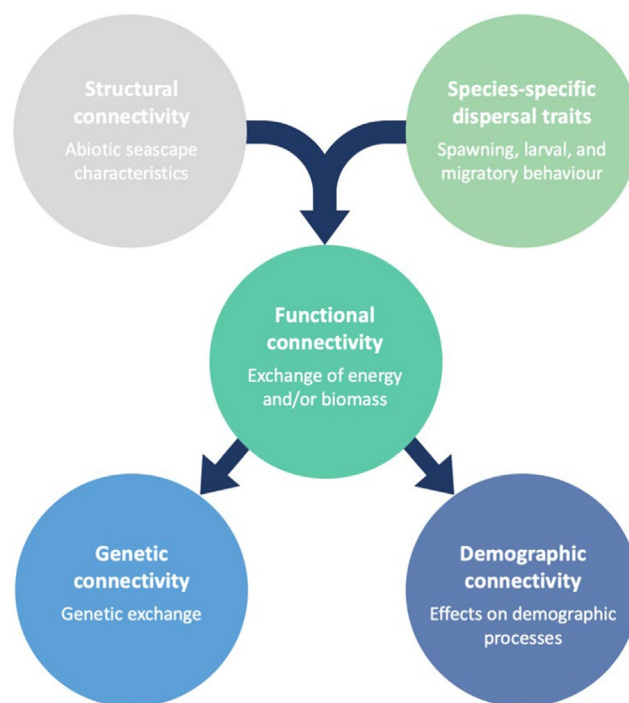
FIGURE 1 | Concept map visualising the relationships between different types of connectivity. The structural connectivity of the landscape/seascape interacts with species-specific dispersal traits to shape functional connectivity patterns – actualised exchange of biomass or energy between populations or locations. Functional connectivity does not necessarily lead to genetic connectivity (gene flow) or demographic connectivity (effects on population-level processes) between populations, but is a prerequisite for both.

however, functional and/or demographic connectivity can still be high among differentiated populations (Selkoe et al. 2016).

In addition to their evolutionary significance, connectivity and population structure have direct applications in conservation and stock management (Riginos and Beger 2022; Jahnke and Jonsson 2022). Knowledge on both the connectivity and population structure of managed species is essential for accurately delineating management units (e.g., fish stocks; see Reiss et al. 2009), as the distribution ranges of marine populations can vary widely, from trans-oceanic to highly local (Kerr et al. 2017), as well as overlap (e.g., Aarestrup et al. 2022). Still to this day, management units are often based on legislative borders between nations or regions, when they should ideally be based on species biology and delineate demographically and/or genetically independent populations (Palsbøll et al. 2007). Similarly, area-based protection measures such as marine protected areas (MPAs) should, ideally, cover a sufficient number of important and well-connected habitat patches to ensure the persistence of populations (Goetze et al. 2021; Beger et al. 2022). For instance, prioritising the protection of areas with high total larval contribution to adjacent sites, as well as high self-recruitment, has been shown to be effective in fisheries management (Krueck et al. 2022). Prioritising, however, requires sufficient knowledge on the connectivity of populations in an area to elucidate possible meta-population structures and source-sink dynamics (Beger et al. 2022). Synthesising information on both population structure and

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BOX 1 | Connectivity and Population Structure.

Connectivity

Fundamentally, there is **structural connectivity** – the connectivity of the landscape or seascape itself. In marine environments, this is dictated by various seascape features such as bathymetry, the shape of the coastline, and ocean currents at different depths. How this structural connectivity affects the connectivity of species depends on the **biological dispersal traits**, specific to the species or populations studied. The interactions of structural connectivity and biological dispersal traits creates **functional connectivity**, i.e., the realised exchange of biomass between populations or geographic locations, most commonly referring to the dispersal of individuals. However, dispersed individuals may not be considered as "recruited" to the new populations if they do not remain in the new population until reaching a certain age or size, or contribute with genetic material. Thus, functional connectivity is distinct from both **demographic connectivity** and **genetic connectivity**. **Demographic connectivity** describes the extent to which immigration and emigration affect demographic processes, such as population growth, and **genetic connectivity** refers to gene flow between populations, affecting evolution and adaptation (Selkoe et al. 2016). Importantly, connectivity may be asymmetric, meaning the flow of energy, biomass, and/or genetic material can be higher in one spatial direction than the other (Beger et al. 2010). This is particularly true in marine environments, where ocean currents often have one prevailing direction.

Connectivity Barriers

Areas where connectivity is distinctly lower than in surrounding regions are commonly referred to as connectivity breaks or **connectivity barriers**. Depending on the type of connectivity assessed, such barriers may be caused by either land- or seascape features (structural connectivity; Selkoe et al. 2016), strong environmental gradients (Johannesson and André 2006), or prezygotic isolation due to behavioural differences – e.g., assortative mating (Schumer et al. 2017) and/or natal homing (André et al. 2016) – or postzygotic incompatibilities (Orr and Turelli 2001).

Population Structure

Population structure refers to the subdivision of species into more-or-less distinct groups of individuals, or "populations" (Waples and Gaggiotti 2006). This subdivision can vary in strength, depending on environmental factors, the species' biology, and the geographical area. Population structure tends to be less pronounced in marine organisms, as they often have both large population sizes and high dispersal potential (e.g., Ward et al. 1994). While population structure is commonly referred to in population genetic terms, it can be assessed in a multitude of ways – including chemical isotope analysis, and morphometry – in addition to genetic methods.

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connectivity is, thus, crucial in establishing a biological baseline that informs adaptive and evidence-based management strategies.

This review summarises knowledge on connectivity and population structure in marine species in the Skagerrak—a marginal sea in the northeast Atlantic. The Skagerrak is one of

the world's most productive oceans (Olsson 1993), but both offshore and coastal Skagerrak ecosystems have been strongly impacted by anthropogenic pressures such as bottom trawling, depletion of fish stocks, pollution and trophic imbalances (e.g., Rosenberg et al. 1996; Svedäng and Bardon 2003; Baden et al. 2012; Eigaard et al. 2017). The region has received substantial attention from both fundamental and applied scientific disciplines, including research on connectivity and population structure, most likely due to the historically large fisheries (Eigaard et al. 2017) as well as the presence of multiple environmental (Gustafsson and Stigebrandt 1996) and genetic gradients (Johannesson et al. 2020). Despite this, both implementation and holistic assessment of connectivity and meta-population structure in this region are considerably lacking compared to similar marine regions (Roessger et al. 2022). Although several MPAs are established in the Skagerrak, including national parks and the MPA networks designated under OSPAR (the Convention for the Protection of the Marine Environment of the North-East Atlantic) and Natura 2000 (European Union (EU) Birds- and Habitats Directives), preliminary assessments show that the majority confer ineffective protection (Moland et al. 2025). Fisheries quotas in the Skagerrak are negotiated annually by the EU and Norway, based on recommendations from ICES (the International Council for the Exploration of the Sea). Management units within fished species are generally delineated geographically using ICES subdivisions, but do not explicitly account for population structure within these areas. Synthesising the current scientific knowledge on connectivity and population structure is an essential step toward establishing effective regional management practices, conserving genetic diversity and rebuilding depleted stocks.

More specifically, this review aims to interrogate whether there are general trends and common connectivity patterns across multiple taxa and if there are knowledge gaps that need to be addressed. Although population structure has been described in several species in the area, we here aim to assess whether population structure is the rule or the exception across all species that have been studied. In addition, we want to know if the patterns of population structure reflect patterns of connectivity in the area. The results are of fundamental relevance, especially in assigning management units and designing MPA networks. As the Skagerrak is among the most well-studied systems in the world within this research field, contains a wide range of habitats and is under strong anthropogenic impact, we also discuss how conclusions from the Skagerrak may be transferable to other systems. This enables more general conclusions about the relationship between connectivity, population structure and adaptive management of marine ecosystems under global change.

2 | Methods

2.1 | Study Area

The Skagerrak is a small sea sharing its borders with Norway, Denmark and Sweden (Figure 2). The area is characterised by the Norwegian Trench, following the Norwegian coast, with depths down to 700 m in the eastern Skagerrak and a deep sill in the west at approximately 270 m depth (Rodhe 1996). The

FIGURE 2 | The study area and some of its prominent seascape features. Depth is displayed as different shades of blue (darker = deeper) and idealised surface ocean currents are indicated with arrows (larger = stronger). Bathymetric data were sourced from EMODnet Digital Bathymetry (2022), coastlines from the European Environmental Agency (https://www.eea.europa.eu/en/datahub/datahubitem-view/af40333f-9e94-4926-a4f0-0a787 f1d2b8f), and ocean currents redrawn from Jonsson, Corell, et al. (2016) and Huserbråten et al. (2018). Note that the strength and direction of ocean currents may differ at different depths.

Norwegian and Swedish coastlines are convoluted and topographically complex, characterised by many small inlets and fjords, as well as the long Oslofjord, which extends approximately 90 km northwards. The Danish Skagerrak coast, on the other hand, mostly consists of a shallow sandy bottom with sporadic rocky reefs. Together with the Kattegat and Danish Straits, the Skagerrak is often referred to as a "transition zone" between the near-oceanic North Sea and the brackish Baltic Sea (Gustafsson and Stigebrandt 1996). The southern Skagerrak receives an inflow of water from the North Sea, turning in a counterclockwise direction along the Swedish and Norwegian Skagerrak coasts (Danielssen et al. 1997). Brackish water from the Baltic Sea flowing northward along the Swedish west coast also enters the Skagerrak and mixes with the North Sea water to form the Norwegian Coastal Current (Gustafsson and Stigebrandt 1996).

2.2 | Literature Search

We performed a systematic literature search for studies on connectivity and population structure in the Skagerrak on the Web of Science database on the 3rd of May 2023. Our search string was structured in three main sections, defining (a) the area of study, (b) the context and (c) the methodological approach. The search string in full was:

Skagerrak

AND

(marine OR sea* OR coast* OR offshore* OR estuar* OR fjord* OR inshore*)

AND

(egg* OR larv* OR propagul* OR ontogenetic* OR recruit* or dispers* OR connectivity OR migrat* OR "gene flow" OR "gene-flow" OR hydrodynamic* OR biophysical OR Lagrangian OR genetic* OR genomic* OR "population structure" OR "otolith chemistry" OR "otolith microchemistry" OR tag* OR telemetry)

The length of the third section reflects the highly variable methodological approaches available to assess connectivity and population structure. The Web of Science database only searches through the title, keywords and abstract of the original publications. Hence, we supplemented the list of publications from the systematic literature

search by manually adding scientific publications of relevance to this review. As the search string was highly inclusive regarding methodological approaches, the most likely reason that these publications were not found in the systematic literature search was that their title, keywords and abstract did not specifically mention either the Skagerrak, the marine context, or both.

2.3 | Screening

The full list of publications (Table S1) was screened according to a set of five exclusion criteria (A–E; see Table 1). Publications were excluded if they (A) had a non-marine context; (B) were not in the Skagerrak; (C) did not investigate connectivity of any marine species; (D) were a review, meta-analysis, short-format, or non-peer-reviewed article; or (E) were inaccessible.

The systematic literature search yielded a list of 413 unique scientific publications. Out of these, 113 (27%) were eligible for review. Most excluded publications were so based on thematic irrelevance, i.e., not explicitly assessing connectivity in marine species (exclusion criterion C; 58%). We supplemented the list of 113 publications by manually adding 59 relevant publications that the authors were aware of, or that were cited in reviewed publications. Thus, after screening, a total of 172 scientific publications were assessed as eligible for review (Figure 3A). A complete reference list for the reviewed publications is provided in Appendix 1.

2.4 | Data Extraction

Eligible publications were divided among the authors, who extracted information on study design and methodology and

TABLE 1 | Exclusion criteria used for the screening of publications.

Symbol	Exclusion criterion	Explanation
A	Context	The study does not focus on marine, coastal, estuarine, offshore, or inshore environments
B	Geographic area	The study area is outside the geographic area of interest (Skagerrak)
C	Theme	The study does not explicitly investigate connectivity of marine species
D	Study type	The study is a review, meta-analysis, response, comment, brief note, or is not peer-reviewed
E	Inaccessible	The study cannot be accessed
	Retain	No reason for excluding the study based on exclusion criteria A–E

summarised the relevant results. For a complete overview of the extracted information, see the extraction matrix (Table S2).

As connectivity operates on multiple time scales, we separated studies assessing contemporary connectivity (within one generation) from those assessing population structure (an outcome of low genetic connectivity both historically and currently). We sorted publications into three categories, based on both their methodology and the types of results presented: publications assessing (a) contemporary connectivity, (b) geographically defined barriers to connectivity and (c) population structure. Note that these categories are not mutually exclusive—a single publication may assess all three, in concert.

In the *contemporary connectivity* category, we included publications assessing either active (migration) or passive dispersal (e.g., egg and larval drift) within a single generation. We included publications assessing connectivity both to, from and within the Skagerrak. The main methodological approaches to assess contemporary connectivity were tagging studies (mark-recapture and acoustic telemetry) and biophysical modelling studies. We only included publications that provided explicit information on dispersal direction, dispersal distance, or home range in this category. As connectivity estimates differ substantially between studies, our classification of high and low connectivity was based on the relevant levels for the specific connectivity estimate used and the conclusions of the authors of the original publications (see Tables S3 and S4).

Publications were categorised into the *geographic connectivity barrier* category if they inferred or directly assessed geographically defined barriers to connectivity. Inference methods varied across publications but included both genetic methods to detect geographically distinct genetic barriers and biophysical modelling approaches to detect biophysical barriers. From these publications, we extracted information on the nature (genetic or biophysical) and geographic location of the inferred barriers.

Publications were included in the *population structure* category if they assessed the presence of distinct groups of individuals, or variation in specific traits, within species. The methodological approaches included population genetics, morphometry, or chemical isotope analyses. Studies were classified as describing population divergence when the specific divergence estimate used was statistically significant among populations, or when distinct population clusters were inferred *de novo* in the original study (see Table S5).

When synthesising results from multiple studies on the same species, we accounted for the reliability of the results from each original publication, based on a qualitative assessment of their respective methodology and conclusions. This was done for all three categories of publications (see Tables S2–S5).

Publications were further sorted into subcategories based on the number of sampled sites in the Skagerrak, and whether they assessed connectivity or population divergence between the Skagerrak and adjacent seas (the North Sea, Kattegat, or Baltic Sea), or within the Skagerrak. Here, we define the North Sea as ICES Subarea 4, the Skagerrak and Kattegat as ICES subdivisions 20 and 21, respectively, and, following the outer boundary of the OSPAR area, we define the Baltic Sea as ICES subdivisions
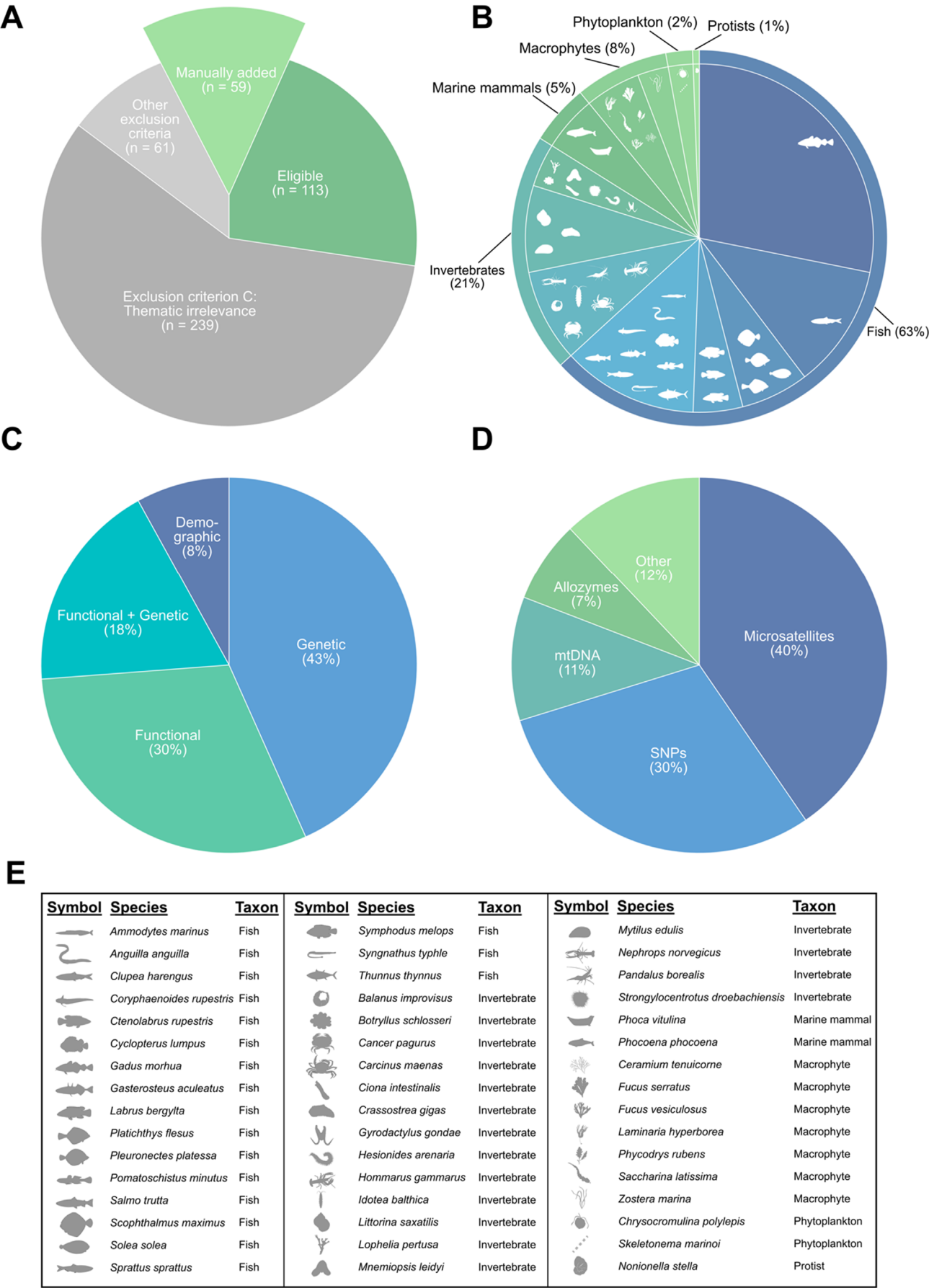
FIGURE 3 | Legend on next page.

FIGURE 3 | Summary of the scientific publications assessed in this review. (A) Overview of the 413 publications from the systematic literature search on Web of Science, with pie slices representing the proportion deemed eligible (green) or ineligible (grey) for this review. The 59 manually added publications are represented as the proportion in relation to the 413 publications in the systematic literature search. Subplots (B–D) summarise the studies included in this review: (B) the relative numbers of studies per taxon (outer pie chart) and species or species group (inner pie chart); (C) the types of connectivity assessed; and (D) which genetic marker types have been used in the genetic studies. In cases where a single publication fits multiple categories (e.g., a publication studied two different species), the publication has been represented as multiple studies in subplots (B–D) (e.g., one study on species I and one study on species II). Subplot (E) lists all 48 species included in this review.

22–32 (Figure 2). To account for the differences in geographic scope among publications, our synthesis below presents results from studies assessing connectivity between the Skagerrak and adjacent seas separately from those that assess connectivity within the Skagerrak.

2.5 | Barrier Analysis

To explore the location of genetic barriers further, we used the program BARRIER 2.2 (Manni et al. 2004) to re-analyse pairwise genetic distance estimates from 24 studies on 17 species, to infer barriers between the sample pairs with the most abrupt genetic dissimilarities (Manni et al. 2004). Specifically, we only included studies on native species with at least three sampling sites in the Skagerrak, which provided both pairwise F_{ST} or G_{ST} estimates and geographic coordinates for the sampling sites. The study area, as defined in BARRIER, was between latitudes 55.6° and 60.0° N, and longitudes 4.0° and 13.2° E. As different studies used different genetic markers, genetic distance estimates from different studies on the same species could not reliably be combined. Therefore, analyses were run separately for each study. Similarly, the statistical significance of inferred barriers could not be assessed since this information requires replicate divergence matrices (Manni et al. 2004). The number of barriers ranged from one to six, based on the number of study sites in the Skagerrak (see Tables S6 and S7).

3 | Results

3.1 | Literature Summary

Connectivity and population structure is a research field that has been gaining interest in recent years in Skagerrak species (Figure 4). The first included study was published in 1990, and the number of studies per year has increased gradually since, especially during the 2000s and 2010s. At present, around 10 studies on connectivity and population structure in the Skagerrak are published every year.

Connectivity and/or population structure has been assessed in 48 unique species in the Skagerrak (Figure 3E). The scientific literature on population structure and connectivity is strongly dominated by fish species (63% of studies; Figure 3B) and has been so since the 1990s (Figures S1 and S2). Atlantic cod (*Gadus morhua*; 28%) and Atlantic herring (*Clupea harengus*; 11%) alone account for 39% of the studies. Invertebrates are the second most represented taxonomic group (21%), with mainly crustacean (9%) and mollusc species (8%) studied. The marine mammals,

harbour porpoise (*Phocoena phocoena*; 4%) and harbour seal (*Phoca vitulina*; 1%), make up 5% of studies. Macrophytes are the subject of 8% of studies, with 5% on macroalgae and 3% on eelgrass (*Zostera marina*). Phytoplankton and protists are the least studied taxa in the Skagerrak, covered by 2% and 1% of studies, respectively, and represented by three species in total (*Chrysochromulina polylepis*, *Skeletonema marinoi* and *Nonionella stella*).

Most studies have assessed either genetic connectivity (43%, including papers assessing genetic population structure) or functional connectivity (30%), while 18% of the studies studied both in concert—an approach that appears to be slowly gaining popularity in recent years (Figure S3). Fewer studies (8%) assessed demographic connectivity (Figure 3C). Studies using genetic tools differ in the types of genetic markers used (Figure 3D). Microsatellite (40%) and single-nucleotide polymorphism (SNP) loci (30%) are the most common overall. The use of SNPs has increased since the mid-2010s and has almost completely replaced other markers in recent years (Figure S4).

Categorising studies assessing contemporary connectivity and population structure separately showed that 93 studies assessed contemporary connectivity (55%), 12 explicitly assessed geographic barriers to connectivity (7%) and 131 assessed population structure (78%). Note, again, that these categories are not mutually exclusive. A detailed overview of the reviewed studies, as well as their respective methodologies and results is given in Table S2.
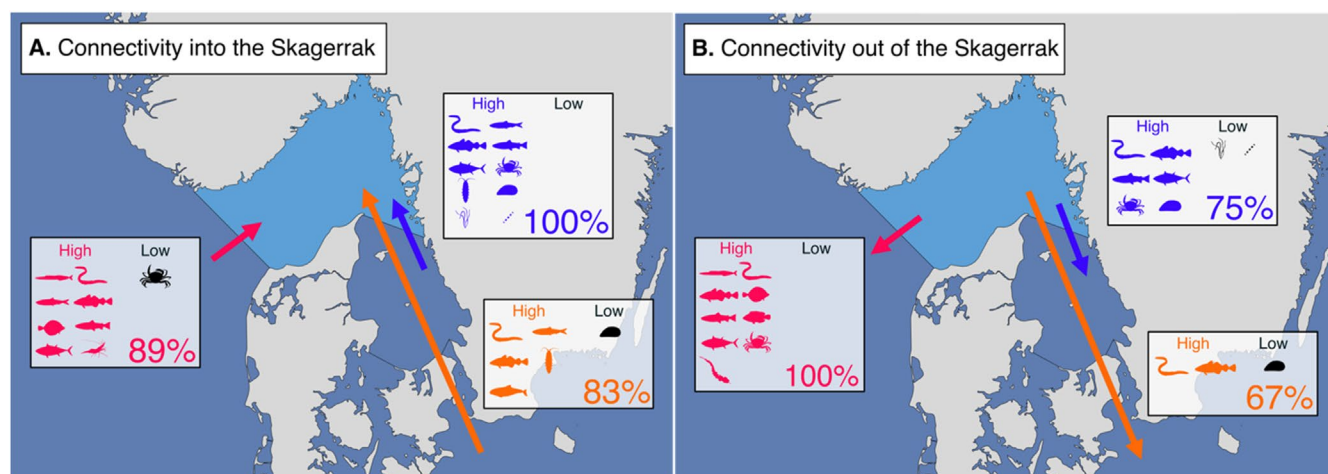
3.2 | Contemporary Connectivity

3.2.1 | Connectivity With Adjacent Seas

Connectivity is generally high between Skagerrak populations and populations in the North Sea, Kattegat and Baltic Sea (Figure 5; Table S3), both from the west (North Sea: 89% of species) and the south (Kattegat: 100%; and Baltic Sea: 83% of species; Figure 5A). Connectivity out of the Skagerrak is, similarly, high into the North Sea (100% of species), but slightly fewer species show connectivity in the southward direction (Kattegat: 75%; and Baltic Sea: 67% of species; Figure 5B). There are, however, fewer studies explicitly assessing southward connectivity rather than northward connectivity in the Skagerrak–Baltic Sea region, likely due to the prevailing ocean current patterns. The main direction of passive dispersal is in the northward direction for organisms with shallow-drifting propagules and southward for those with deeper drift depths (Pacariz, Björk, Jonsson, et al. 2014; Pacariz, Björk, and Svedäng 2014; Jonsson, Nilsson Jacobi, and Moksnes 2016).
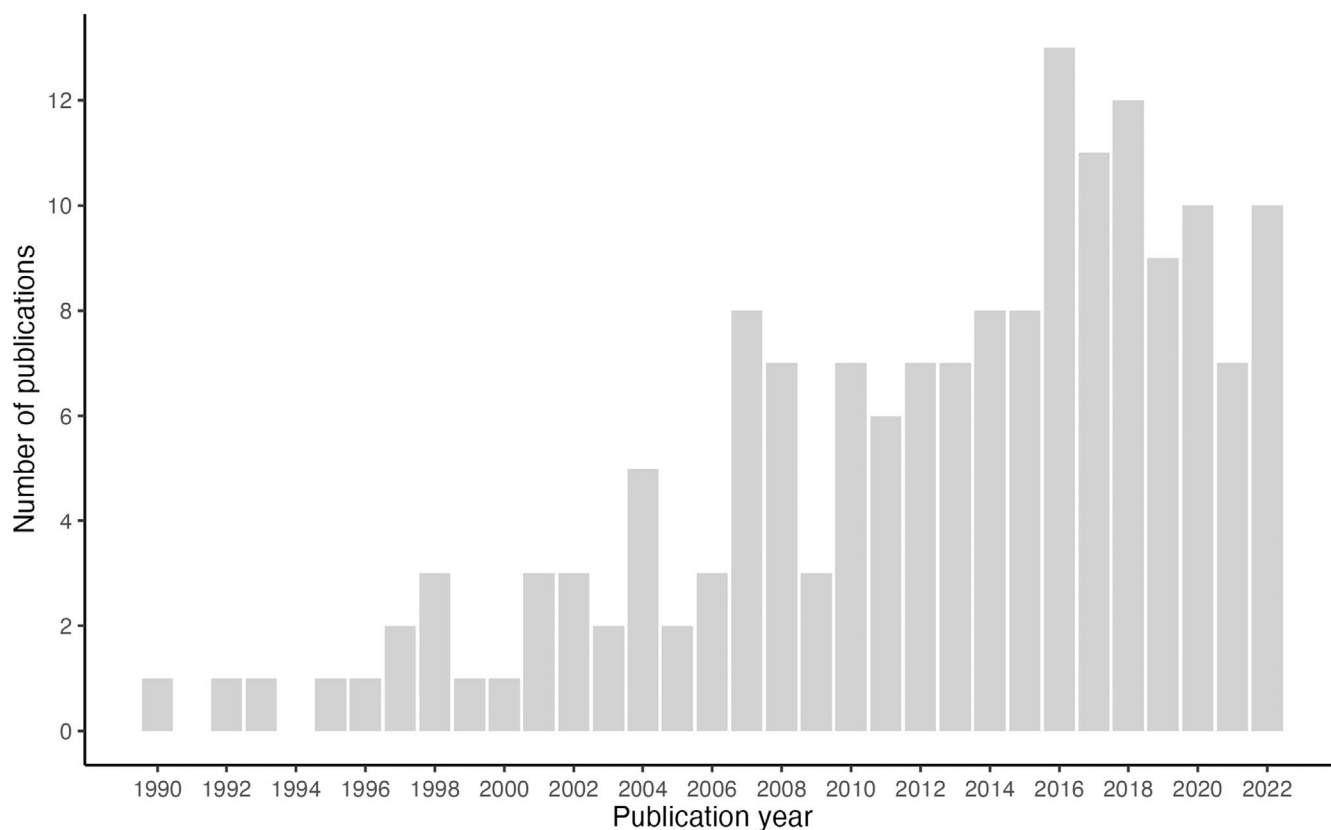
FIGURE 4 | Publication years of the studies included in this review. The bar heights represent the numbers of studies eligible for this review, published each year. As the literature search was performed in March 2023, studies published in 2023 are excluded from this figure. Hence, only results from whole years are displayed.

FIGURE 5 | Contemporary connectivity of Skagerrak species with the adjacent North Sea (pink), Kattegat (blue), and Baltic Sea (orange). The figure summarises functional and demographic connectivity within one generation (A) into, and (B) out of the Skagerrak. The boxes show which species have been assessed, and the proportion of these species for which connectivity has been found (in colour). The data underlying this figure can be found in Table S3, and a key for the species symbols is found in Figure 3E.

3.2.1.1 | Passive Dispersal. For species with little to no active migration at any life stage, dispersal tends to be highly asymmetric in this region. Most passive dispersal occurs in the northwesterly direction, from the Baltic or Kattegat, into the Skagerrak and out into the North Sea, as seen for e.g., blue mussels (*Mytilus* spp), the isopod *Idotea balthica*, tangle (*Laminaria hyperborea*), eelgrass and the phytoplankton *S. marinoi* (Table S3). Larval dispersal traits also affect the direction

of dispersal, as illustrated by European shore crab (*Carcinus maenas*). Shore crab larvae in the Skagerrak and Kattegat have a circadian vertical migration behaviour, meaning they can disperse between the Skagerrak and Kattegat in both directions, and from both seas out into the North Sea, while the tidal migration behaviour of North Sea larvae seems to create a dispersal barrier from the North Sea into the Skagerrak (Jahnke et al. 2022).

Even in larger, mobile species, connectivity with adjacent seas can, in part, be shaped by passively dispersing life stages. For example, in lesser sandeel (*Ammodytes marinus*), eel (*Anguilla anguilla*), herring and cod, large amounts of eggs and larvae are passively brought into the Skagerrak from populations spawning in the North Sea or further out in the Atlantic Ocean (Table S3). In cod, a large proportion of eggs and larvae also passively drift into the Skagerrak from the Kattegat and western Baltic Sea (Jonsson, Corell, et al. 2016; Barth et al. 2017).

3.2.1.2 | Active Dispersal. All of the more mobile species that have been studied display high connectivity between seas. In eel, herring and cod, some individuals originating from offshore spawning populations migrate westwards out of the Skagerrak after reaching sexual maturity (Table S3). Active dispersal between seas also appears to be high in European plaice (*Pleuronectes platessa*), as 15%–20% of spawning fish tagged in the North Sea migrate into the Skagerrak, and *vice versa* (Ulrich et al. 2017). Similarly, sea trout (*Salmo trutta*) kelts tagged in the North Sea, Skagerrak and Kattegat appear to migrate long distances between all three areas during their time at sea, regardless of natal origin (Kristensen et al. 2019). Tagging and otolith chemistry show that adult cod also readily migrate between the Skagerrak, Kattegat and the Western Baltic Sea (André et al. 2016; Hüssy et al. 2022).

In certain species, migration between areas only occurs at specific times of the year, causing the population assemblages in the Skagerrak to be temporally variable. For example, the feeding migration of adult herring from the Western Baltic means that at least three herring populations mechanically mix (i.e., coexist, but do not interbreed) in the Skagerrak in the summer (Ruzzante et al. 2006; Berg et al. 2017). Similarly, harbour porpoises from the Western Baltic population migrate into the Kattegat and Skagerrak in the winter to feed (Börjesson and Berggren 1997). Another example, on a much larger geographic scale, is the feeding migration of Atlantic bluefin tuna (*Thunnus thynnus*), where individuals from both the western and eastern Atlantic populations migrate into the Skagerrak in late summer–autumn (Aarestrup et al. 2022).

3.2.2 | Connectivity Within the Skagerrak

Studies focusing on contemporary connectivity on smaller scales, within the Skagerrak, are limited to 28 studies on 10 species—Atlantic cod, Atlantic herring, sea trout, turbot (*Scophthalmus maximus*), broadnosed pipefish (*Syngnathus typhle*), brown crab (*Cancer pagurus*), European lobster (*Homarus gammarus*), blue mussel, harbour seal and eelgrass (Table S4). Atlantic cod was the subject of 12 of these studies, with the remaining 16 studies distributed across the other nine species.

3.2.2.1 | Passive Dispersal. For passively dispersing species or life stages, local retention of propagules spawned inside Skagerrak fjords is common. This is the case for Atlantic cod eggs, blue mussels, and, to some extent, eelgrass (Table S4). For the two assessed species with sessile adult life stages, blue mussel and eelgrass, passive dispersal of propagules along the coast appears to be within 10–45 km (Stuckas et al. 2017; Jahnke et al. 2020). Interestingly, blue mussel larvae do not seem

to disperse between the western and eastern Skagerrak or Kattegat (Stuckas et al. 2017).

3.2.2.2 | Active Dispersal. For the two most-studied species, cod and herring, mechanical mixing of genetically differentiated populations is well documented (Tables S3–S5). Applying this knowledge in studies on active dispersal has unravelled complex spatiotemporal dynamics and population-specific dispersal behaviours. For instance, dispersal distances of cod in the Skagerrak range from a few to hundreds of kilometres, depending on their genetic origin (Table S4). Cod of the "coastal"/"fjord" ecotype tend to be resident in Skagerrak fjords (on the timescales studied), while "offshore ecotype" cod show more migratory behaviour out of the fjords (Table S4). Similar to cod, sea trout in a Norwegian fjord appear to consist of two behavioural phenotypes coexisting in the same habitat—resident "stayers" and "dispersers" migrating out of the fjord (Thorbjørnsen et al. 2019). Two migratory phenotypes are also present in brown crab, but here it is the sexes that differ. Males are more or less stationary, while females tend to migrate longer distances, sometimes even offshore (Karlsson and Christiansen 1996; Ungfors et al. 2007).

Studies on herring in the artificial estuary Landvikvannet in southern Norway further exemplify how complex the spatiotemporal dynamics of coastal populations can be. During the spawning season in spring, three distinct populations coexist in the area: a "local" population and small proportions of oceanic Norwegian spring spawners and coastal Skagerrak spring spawners (Eggers et al. 2014, 2015). Interestingly, even the "local" herring do not appear to be resident in this estuary, but instead migrate to other coastal areas after the spawning season (Eggers et al. 2015).

There are also several species with very limited active dispersal in the Skagerrak. For example, tagging studies suggest dispersal distances below 1 km for adult European lobster (Table S3) and less than 50 km for both juvenile turbot (Bergstad and Folkvord 1997) and harbour seals (Härkönen and Hårding 2001). Broadnosed pipefish is one of the mobile species with the lowest dispersal potential, with a spatial decorrelation scale of 2.4 km, indicating that functional and demographic connectivity along the coast is very low (Knutsen et al. 2022).

3.3 | Geographic Connectivity Barriers

Out of the 12 publications assessing connectivity barriers, two publications on goldsinny wrasse (*Ctenolabrus rupestris*) and Pacific oyster (*Crassostrea/Magallana gigas*) found no barrier in the Skagerrak or to the adjacent North Sea and Kattegat (Faust et al. 2017; Jansson et al. 2017). Seven publications describe a barrier located between the North Sea and the Skagerrak shared among several coastal fish species (e.g., Mattingsdal et al. 2020; Seljestad et al. 2020; Knutsen et al. 2022) and shore crab (Moksnes et al. 2014). One study has also described a barrier for eelgrass between the Kattegat and the Skagerrak (Jahnke et al. 2018). The only geographic barriers identified within the Skagerrak were within fjord systems, for the passively dispersing blue mussel (Pastor et al. 2021) and eelgrass (Jahnke et al. 2020).

The exploratory re-analysis of genetic distance estimates with BARRIER suggests three main categories of genetic connectivity barriers within the study area, based on data from 24 studies (Table S7). In line with previous studies, we inferred a genetic barrier on the southwestern tip of Norway, between the Skagerrak and the North Sea (Figure 6A). The barrier is shared among ballan wrasse (*Labrus bergylta*), corkwing wrasse (*Symphodus melops*), pipefish and tangle. Barriers in this area were also indicated in several other fish and crustacean species, but with lower support (Figure 6B,C; thin lines).

We also inferred various forms of barriers between fjords or coastal locations, for eight species, including fishes, crustaceans and eelgrass (Figure 6B). Lastly, seven fish species also have genetic barriers inferred in the southern parts of the area, both between the Skagerrak and Kattegat and within the Kattegat (Figure 6C). For Atlantic cod and sea trout, different studies have inferred barriers in different regions, likely reflecting differences in geographic scope in the original studies. In contrast, all four studies on corkwing wrasse infer similar barriers, in the western part of the study area. Most
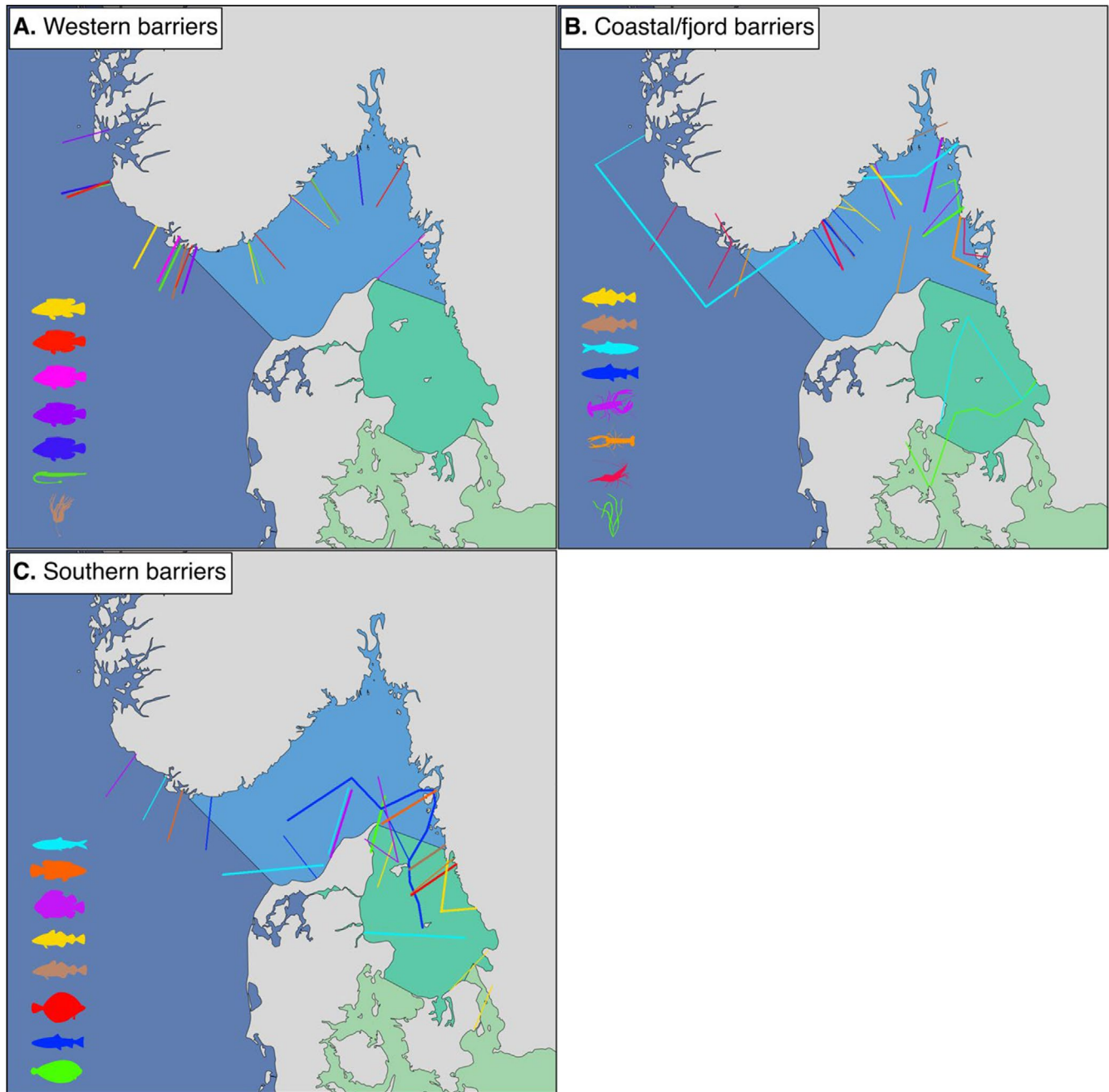
FIGURE 6 | Inferred genetic barriers from the re-analysis of genetic divergence estimates in BARRIER, displayed as lines on maps. Line colours represent different species and studies while line thicknesses indicate the relative level of support within each study. The subplots group studies based on the location of the main inferred genetic barrier: (A) off southwest Norway, (B) between coastal locations or fjords, and (C) in the southern Skagerrak/Kattegat. Note that results from different studies on the same species are presented separately. The studies underlying this figure are listed in Table S7, and a key for the species symbols is found in Figure 3E. Note that the divergence data from the original studies did not enable accounting for potential mechanical mixing of different populations, or assessing the statistical significance of barriers.

of the inferred genetic barriers in the south are more-or-less latitudinal, separating northern and southern populations. Sea trout is an interesting exception to this, as the strongest barrier is between western and eastern populations in the Skagerrak–Kattegat. Note, however, that this analysis does not explicitly account for mechanical mixing of multiple populations at a single sampling location.
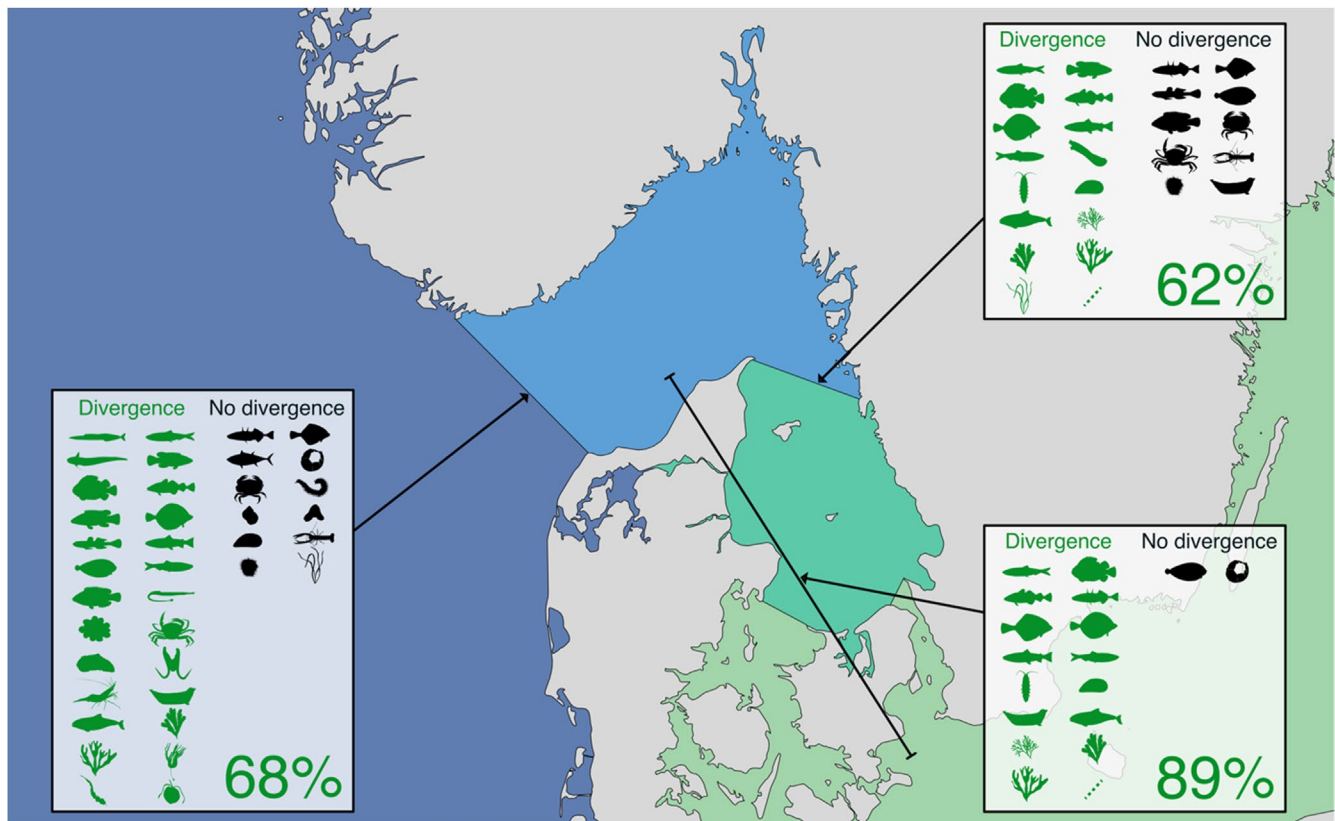
3.4 | Population Structure

3.4.1 | Population Divergence Between the Skagerrak and Adjacent Seas

Based on the reviewed scientific literature, divergence between Skagerrak populations and adjacent populations in the North Sea, Kattegat and Baltic Sea seems to be the rule rather than the exception (Figure 7). Divergence between the North Sea and Skagerrak has been assessed in the largest number of species ($n = 38$), and the divergent populations are documented in 68% of these species. The corresponding numbers for the Kattegat ($n = 26$) and Baltic ($n = 18$) are 62% and 89%, respectively (Table S5). Note that divergence has not been assessed between all areas in all species.

In some species, the Skagerrak populations diverge from populations in all three adjacent seas—Atlantic herring, lumpfish (*Cyclopterus lumpus*), Atlantic cod, European plaice, sea trout, harbour porpoise, toothed wrack (*Fucus serratus*) and bladderwrack (*F. vesiculosus*) (Figure 7; Table S5). In several other species, one or more areas have not been compared to the Skagerrak; however, differences have been found between all the areas that have been compared (Figure 7; Table S5) – lesser sandeel, roundnose grenadier (*Coryphaenoides rupestris*), Pacific oyster, northern shrimp (*Pandalus borealis*) and sugar kelp (*Saccharina latissima*). Yet, for other species, there is no known population divergence between any of the areas (Figure 7; Table S5), e.g., bay barnacle (*Balanus improvisus*), Norway lobster (*Nephrops norvegicus*) and green sea urchin (*Strongylocentrotus droebachiensis*).

For corkwing wrasse, star tunicate (*Bothryllus schlosseri*), Pacific oyster and harbour seal, genetic connectivity between the Skagerrak and adjacent seas has been inferred indirectly, by using population genetic distance estimates to estimate rates of gene flow. In all four species, there appear to be some levels of gene flow between the North Sea and the Skagerrak (Table S3). In harbour seals, some levels of gene flow have been inferred between all areas, though roughly three times higher between the Skagerrak and Kattegat compared to between the Skagerrak and North Sea or Baltic Sea (Goodman 1998). Note, however, that such analyses of genetic connectivity cannot distinguish between contemporary and historic gene flow.

FIGURE 7 | Population structure between the Skagerrak and the adjacent North Sea, Kattegat, and Baltic Sea. The boxes show the species for which population structure between two areas has been assessed, and the proportion of species for which population structure has been found (in green). The data underlying this figure can be found in Table S5, and a key for the species symbols is found in Figure 3E.
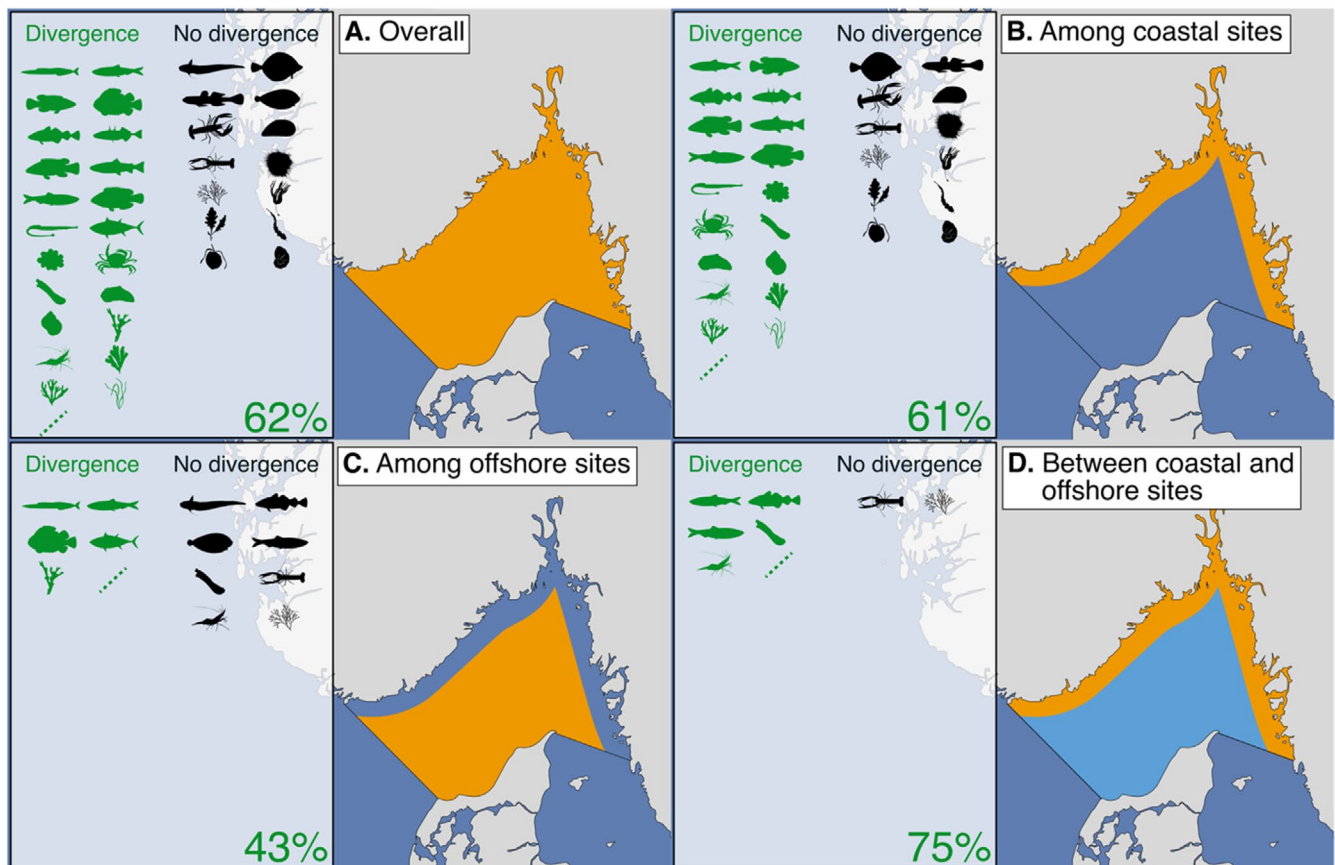
3.4.2 | Population Structure Within the Skagerrak

Population structure within the Skagerrak appears to be the rule rather than the exception, with 62% of the assessed species exhibiting population structure in this region (Figure 8A; Table S5). Worth noting is that population structure within the Skagerrak is present in 64% of the species that simultaneously have high connectivity with adjacent seas (nine out of 14 species)—sandeel, herring, cod, sea trout, bluefin tuna, shore crab, northern shrimp, eelgrass and *S. marinoi*. The most studied form of divergence is among coastal populations and is found in 61% of the assessed species (Figure 8B). These include species from most of the major taxonomic groups represented in the literature: fishes, molluscs, crustaceans, macroalgae, seagrasses and phytoplankton (Table S5). Divergence among offshore populations is rarer and only described in six of the 14 assessed species (43%): lesser sandeel, herring, lumpfish, Atlantic bluefin tuna, the cold-water coral *Lophelia pertusa* and the phytoplankton *S. marinoi* (Figure 8C; Table S5). Divergence between coastal and offshore populations is found in six out of eight assessed species (75%): Atlantic cod, herring, sprat (*Sprattus sprattus*), vase tunicate (*Ciona intestinalis*), northern shrimp and *S. marinoi* (Figure 8D; Table S5). Despite being commonly found, the latter form of divergence has been studied in the fewest species. Lastly, there are 14 assessed species (38%) with no clear evidence for population structure within the Skagerrak, including representatives

from most of the major taxonomic groups: fish, crustaceans, molluscs, echinoderms, macrophytes, phytoplankton and protists (Figure 8A; Table S5).

4 | Discussion

The need to incorporate connectivity in marine resource management and conservation has been acknowledged over the last decade in a number of international agreements and policies. Nevertheless, recent studies show that the European network of MPAs suffers from low connectivity (Assis et al. 2021); hence, there is a clear need to increasingly incorporate connectivity estimates in spatial protection (Jonsson et al. 2020; Riginos and Beger 2022; Berkström et al. 2022) and fisheries management (Ramos Martins et al. 2021). In general, conservation management efforts have the highest probability of success when they are supported by scientific data that provides information on e.g., vulnerability, diversity, location and connectivity of ecotypes, populations and species (van Oppen and Coleman 2022). The level of detail required is therefore often at the intra-specific level, and generalisations across taxa and geographic regions are consequently associated with big caveats. In our review, we have explored patterns of connectivity and population structure specific to the marginal sea Skagerrak, but we deem some of the overarching patterns inferred here, as well as our recommendations for management,

FIGURE 8 | Consensus population structure within the Skagerrak for the species assessed in the scientific literature. Subplots show whether any population structure has been found (A) broadly within the Skagerrak, (B) among coastal sites, (C) among offshore sites, or (D) between coastal and offshore sites. The boxes show which species have been assessed, and the proportion of these species for which population structure has been found (in green). The data underlying this figure can be found in Table S5, and a key for the species symbols is found in Figure 3E.

to be more broadly applicable also to other geographic areas. Two of the most notable findings from this review are (a) that even species with wide distributions and high functional connectivity can be genetically distinct on small spatial scales and (b) that generalisations across species or taxonomic groups are challenging at the current state of knowledge, even in one of the most well-studied marine regions in the world. Our most important overarching management recommendation is to be aware of, and plan for, temporally and spatially variable connectivity patterns for many taxa, including—but not limited to—commercially and ecologically important species. The presence of multiple populations, potentially with local genetic adaptations and different functional roles in the ecosystem, has important consequences for both the current functioning and future resilience of marine ecosystems.

4.1 | Current State of Knowledge

A specific conclusion from our review is that functional connectivity of marine populations in the Skagerrak is generally high across most species, both within the Skagerrak and with adjacent seas. This is shaped by both the prevailing ocean currents in the region and, for some species, population-specific active dispersal behaviours. Despite the high functional connectivity, population structure is evident in the majority of Skagerrak species, which have populations in the Skagerrak that are genetically and/or morphologically distinct from those in adjacent seas. Several species also display finer-scale structure with multiple distinct populations within the Skagerrak, predominantly (but not exclusively) associated with the coastal habitat and fjords in particular. There are several potential explanations for this. In general, coastal habitats along convoluted coastlines are shaped by complex fine-scale circulation patterns, sharp environmental clines and other fine-scale environmental characteristics. Habitat discontinuity has been identified as the main driver of population differentiation in several species (e.g., Binks et al. 2019; Knutsen et al. 2022). Local retention of propagules in several fjords (e.g., Ciannelli et al. 2010; Virtanen et al. 2020), high prevalence of resident behaviour in multiple mobile species (e.g., Knutsen et al. 2011; Kristensen et al. 2019), and local genetic adaptations (e.g., Jorde et al. 2015) are also likely to contribute to the divergence of coastal populations. Population differentiation may also be explained by other behaviours, such as assortative mating (Schumer et al. 2017) and natal philopatry (André et al. 2016). Active dispersers may share feeding grounds or nursery areas during parts of the year or across certain life stages, while behavioural differences may ensure that spawning occurs in allopatry or at different times (e.g., Ruzzante et al. 2006; André et al. 2016; Aarestrup et al. 2022). Genetic differences themselves may also put limitations on the extent of gene flow across populations, for instance, if hybrid offspring are nonviable (Irwin 2020). Differences in the genetic architecture of populations may lead to heterogeneity in the levels of gene flow in different parts of the genome (Harrison and Larson 2016). For instance, chromosomal inversions, which have been described for herring and cod in the Skagerrak, may enable sympatric genetic divergence despite ongoing gene flow (Han et al. 2020; Sodeland et al. 2022).

The finding of differentiated populations despite high contemporary connectivity, although counterintuitive, is not specific to the Skagerrak. Sympatric yet differentiated populations are found in marine species in many other regions around the world, running the same risks of mismanagement unless accounted for (e.g., Le Moan et al. 2016; Moore et al. 2021; Díaz-Arce et al. 2024; Norderhaug et al. 2024). Indeed, the combination of both high connectivity and evident population structure illustrates the importance of appreciating that there are different types of connectivity of relevance in shaping population structure in marine species. A promising way forward, increasingly applied in the Skagerrak (Figure S3), is to jointly assess both genetic and functional connectivity, for instance by combining population genetics with biophysical modelling, tagging or otolith chemistry (Jahnke and Jonsson 2022; Legrand et al. 2024). Studying both population structure and functional connectivity in concert enables connecting genetic origins to phenotypes, hence moving past merely identifying populations and toward understanding the ecological relevance of population structure. Importantly, however, the high functional connectivity between populations, itself, has relevance for conservation management. The partial sympatry of genetically differentiated populations means a mechanical mix of individuals from different populations of the same species can coexist in the same place during different parts of the year. Population mixing is a considerable challenge when using purely geographic borders to delineate populations or define MPAs (Dahle et al. 2018; Bekkevold et al. 2023; Hüssy et al. 2024).

4.2 | Knowledge Gaps and Biases

Despite covering one of the world's most well-studied marine regions in terms of research on connectivity and population structure, this review points toward clear knowledge gaps and biases. Both scientists and managers should aim to fill these gaps to improve knowledge and enable science-based management.

One clear knowledge gap is the scarcity of studies on demographic connectivity. This is a notable finding, since knowledge on the demography and source-sink dynamics of populations may be the most important form of connectivity to consider for spatial management aiming to monitor and maintain population sizes. A key challenge is to accurately and consistently define when an individual has fully recruited into a new population, in demographic terms. Furthermore, estimation of demographic connectivity requires knowledge on both migration rates and intrinsic demographic rates of the populations (Lowe and Allendorf 2010). Such estimations require accurate identification and definition of populations A and B, which can be challenging if knowledge on the underlying population structure is lacking. Even in species with well-described population structure, estimates of population sizes may be unavailable.

Moreover, there is a tendency that population structure is more commonly described in species that have been extensively studied. There may be several underlying causes for this pattern. For instance, population structure is more likely to be discovered the more a species has been studied; conversely, species with known population structure may also be preferentially targeted for further research. This feedback loop can lead to knowledge being restricted to a few focal species, with limited possibilities for broader comparisons of patterns across taxa. Currently, connectivity research in the Skagerrak shows a clear taxonomic bias

toward fish species (Figure 3B). Extensive studies on focal species have, undoubtedly, provided key insights into marine evolutionary biology and connectivity research, helping move the entire research field forward. For instance, within Atlantic cod, there has been a gradual transition from previously estimating genetic divergence at the sample level to now using individual-based clustering methods to infer genetic origins. This has led to the discovery that individuals of multiple genetic origins may frequent the same geographic area (Barth et al. 2019) and can even spawn in the same fjord (Jorde et al. 2018; Svedäng et al. 2019). It is not unlikely that this is also the case in other species, but it has not yet been discovered due to the lack of studies. At present, knowledge on 46% of the species covered in this review is limited to single studies (22 out of 48 species). Non-fish taxa constitute 83% of these species (16 out of 22 species), which is 55% of all non-fish taxa represented in the literature (16 out of 29 species). The two only deep-sea species represented in the literature, roundnose grenadier and *L. pertusa*, were also only represented by single studies. This demonstrates that not only do we have very few studies on these taxa in general (Figure 3B), but knowledge is also highly restricted on the few species for which we have data. Moreover, information about connectivity and population structure is only available for a small fraction of the thousands of species documented in the Skagerrak. Large taxonomic differences in connectivity have been reported in other parts of the world (e.g., Virtanen et al. 2020; Assis et al. 2021). Thus, taxonomically broadening the knowledge on connectivity is important to enable generalising patterns of intra-specific diversity and connectivity across taxa and to avoid leaving the management of non-model species to guesswork. Furthermore, these understudied taxa may perform important ecosystem functions, such as being ecosystem engineers or forming the base of the food chain. Despite this, the relative dominance of fish taxa in the scientific literature has remained at the same level during the last 15-year period (Figures S1 and S2), providing no indication that the research field as a whole is currently working toward addressing the taxonomic biases and knowledge gaps in the Skagerrak.

A final major bias we identified is the geographic representation of studies in the Skagerrak. On the larger scale, the Danish Skagerrak is clearly underrepresented in the literature compared to the Swedish and Norwegian Skagerrak. Moreover, knowledge on population structure and connectivity is often restricted to small geographic areas, especially in species with low numbers of publications. The patterns that have been described for species with reduced geographic representation may not be the biologically most relevant, but rather artefacts from the geographic sampling design. For instance, in our BARRIER analysis, different studies on the same species inferred different genetic barriers, most likely due to differences in the geographic region sampled (see, e.g., sea trout and Atlantic cod in Figure 6B,C). Limited geographic extent may also bias analyses of connectivity. For example, the dispersal distances reported in small-scale tagging studies may depend on the extent of the telemetry arrays or the regions of recaptures. In some studies, individuals dispersing outside of the telemetry array are completely excluded from further analysis. This may be justifiable based on the scope of the original study, but likely underestimates dispersal distances. Herein, we have described the Skagerrak as a marginal sea. However, when considering the properties of the Norwegian trench—a submerged fjord—parts

of the Skagerrak could also be viewed as a miniature deep sea. Studies are scarce on the functional, demographic and genetic connectivity of deep-water benthos and infauna, and we underscore the urgency of advancing this knowledge, especially considering the chronic and ubiquitous impact of bottom trawling throughout Skagerrak and down to at least 500 m depth in the Norwegian trench (Eigaard et al. 2017).

Overall, the scarcity of demographic connectivity studies, as well as the biased taxonomic and geographic representation, limits our overall understanding of connectivity and population structure within the Skagerrak and with adjacent seas. Whether these knowledge gaps and biases lead to under- or overestimations of connectivity likely depends on the species as well as the geographic areas (not) considered.

4.3 | Implications for Management

Skagerrak populations in several species are genetically and/or morphologically distinct from surrounding populations in the North Sea, Kattegat and Baltic Sea. Despite this, functional connectivity on the large scale is high in most species, meaning individuals from several populations may coexist in certain areas during parts of the year, especially in highly mobile taxa. Accounting for this complex spatial and temporal connectivity is challenging but likely essential for achieving sustainable management of intra-specific biodiversity in the Skagerrak and elsewhere.

Functional connectivity is often the main limitation for species range shifts induced by climate change globally (Assis et al. 2024). For this reason, the high functional connectivity could be interpreted as positive for the future survival of Skagerrak species, as it may allow range shifts under global change. If intra-specific population sizes or genetic diversity are depleted locally, the connectivity with neighbouring populations may facilitate recolonisation and/or genetic rescue of local populations (Balbar and Metaxas 2019)—provided that dispersed individuals remain in the area and/or contribute to the local gene pool (i.e., if it leads to demographic and/or genetic connectivity; Selkoe et al. 2016). As our review clearly shows, however, the latter is not necessarily the case. Furthermore, if locally adapted populations are completely lost, the local recovery of the species may require genetic adaptations to arise anew and would, therefore, take a very long time (Allendorf et al. 2022). Thus, management strategies ensuring high connectivity are of little value if local populations are not simultaneously protected.

The high functional connectivity with adjacent seas, with populations dispersing in and out of the Skagerrak at different times, supports the notion of the Skagerrak as a transition zone between the North Sea and the Baltic Sea. Therefore, the management of marine populations in the area cannot treat the Skagerrak as an isolated system, but must account for large-scale connectivity within the Northeast Atlantic as well. As shown, however, the Skagerrak itself is not homogeneous. Most species have multiple differentiated populations, particularly along the coast, which are unique to the Skagerrak. Management of such species should be on a much finer geographic scale than the entire Skagerrak to preserve unique populations—often on the scale of 10s of kilometres, or of individual fjords. The Skagerrak is, thus, more than

just a transition zone—it is also a unique marginal sea requiring special attention in management strategies. This is essential to safeguard both coastal and offshore populations, as well as their up- or downstream demographic subsidiaries (Cardinale et al. 2023).

Perhaps the biggest challenge for management, again discussed here specifically for the Skagerrak, but likely widely applicable, is the temporal variability in population assemblages, particularly in mobile fish species. The temporal co-existence of multiple differentiated populations within a species in a given area demonstrates the shortcomings of using purely spatial methods to delineate management units. Management of these species should consider the temporal aspect of population mixing, and fisheries should implement mixed-stock management, where the relative proportions in catches over time are monitored, for instance using population genetic tools. One example of where such tools have been successfully implemented is the mixed-stock winter fisheries for Atlantic cod in northern Norway. By genetically determining the relative proportions of migratory Northeast Arctic cod (NEAC) and resident Norwegian coastal cod (NCC) in catches, management advice is updated weekly (Johansen et al. 2018; Dahle et al. 2018). If the proportional catch of the smaller NCC population is too high, fisheries are temporarily closed in this area (Dahle et al. 2018).

The scientific fields of connectivity and population structure are growing, gaining more research attention and more utility in legislation. Consequently, management strategies need to be not only spatiotemporally sensitive but also flexible enough to adapt to new scientific findings. For instance, management programmes for monitoring genetic diversity (e.g., Mastretta-Yanes et al. 2024) and real-time genetic monitoring of fisheries catches (e.g., Dahle et al. 2018) enable agile management in response to updated information on intra-specific diversity and connectivity (Norderhaug et al. 2024). Incorporating these monitoring tools in management would also aid in the estimation of population sizes, fundamental to analyses of demographic connectivity which are lacking in this region.

Considering connectivity and population structure has clear implications in conservation and fisheries management, but the taxonomic knowledge gaps are challenging, both in the Skagerrak and in other marine areas. If information is lacking for a species of interest, it is sometimes possible to use the knowledge on a species with similar life-history as a guide or proxy. However, we have found that different taxa are so unequally represented that more specific connectivity patterns cannot justifiably be generalised across species and/or life-history traits in more detail than has been done here (*cf.* Wennerström et al. 2013; Wray et al. 2024). While the knowledge on some species may suffice for informing the design of spatial management measures, improvement can only be gained from temporal and spatial connectivity assessments on a per species basis.

Synthesising knowledge on population structure and connectivity for multiple species, as we have done here, assists in providing the broader picture, but new and more detailed knowledge is generated for each species continuously. Hence, adaptive

management approaches combining spatial and temporal management are more likely to succeed in establishing a robust and future-proof management regime for biodiversity in the Skagerrak. To summarise, our main management recommendations synthesised from all available data on connectivity in the Skagerrak, but applicable to any marginal sea, are:

- Management of biodiversity in the target area needs to be based on up-to-date knowledge about species' population structure and connectivity.

- Management should be fine-scaled enough to capture population structure, often on the scale of 10s of km, especially along coasts and within fjords.

- Fisheries management, MPA design and marine spatial planning need to consider both coastal and offshore marine areas.

- Management needs to consider that different populations may coexist at certain times in a given area. This is especially relevant in fisheries management, when different stocks coexist, and where genetic mixed-stock analysis should be implemented to disentangle and estimate the proportions of the different stocks.

- More information on population structure and connectivity is needed for both sessile and mobile species. Non-fish taxa and deep-sea species are particularly underrepresented in the literature.

- Adaptive strategies incorporating both spatial and temporal management are more likely to succeed in creating a robust and future-proof biodiversity management.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data underlying this study is available as Supporting Information (Tables S1–S7). In all cases where data from another study has been re-analysed, we have listed where in the original study these specific data can be found.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Appendix 1

Reviewed Studies

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