Fish in sand and gravel habitats in the North Sea and adjacent shelf seas: A systematic literature review

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Short Running Title: Fish use of sand & gravel habitats

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ABSTRACT

Sedimentary habitats such as sand and gravel are among the most widespread seafloor environments in shelf ecosystems, yet fish–habitat relationships in these substrates remain poorly understood. Although these habitats support diverse and productive benthic communities, ecological information on how fish use them is fragmented, limiting the effectiveness of conservation frameworks such as EUNIS, the EU Habitats Directive, and ecosystem-based fisheries management. To address this gap, we conducted a systematic review of peer-reviewed studies reporting associations between fish species and sandy and gravelly substrate types across the Northeast Atlantic shelf. The review identified 104 studies covering 77 species associated with these substrate types, divided into littoral ecozones down to 200 m depth. Study frequency strongly influenced the number of habitat types in which species were recorded, complicating assessments of habitat specialisation based on available data. Across ecozones, sand consistently supported the highest species richness, and most nursery areas were linked to sand in the littoral and infralittoral zone. Species of conservation concern (IUCN) occurred across all substrate types; however, we highlight particular concern for gravel habitats as spawning grounds and as habitat for several red-listed species, given their more limited distribution compared to sand. Commercially important species dominated reports of spawning and nursery functions. This synthesis provides a comprehensive overview to date of fish–habitat associations in sedimentary environments of the Northeast Atlantic shelf. The resulting literature list, database and habitat-specific species lists offer a valuable foundation for marine spatial planning and area-based conservation, including the identification of Essential Fish Habitat.

Keywords: Marine sedimentary habitats; sand habitat; gravel habitat; fish–habitat associations; Northeast Atlantic; marine conservation; Essential Fish Habitat; EUNIS

I. INTRODUCTION

Habitat loss and other spatially explicit threats are driving declines in marine species abundance, richness, and diversity, highlighting the need for management measures that account for the specific habitat needs and locations these species rely on (Turner et al., 2024). Sedimentary habitats, those composed of sand, gravel, and mixed seabed sediments, are among the most widespread environments in the world's oceans (Holland and Elmore, 2008; Heap and Harris, 2011). Although they may appear barren at first glance, they are anything but. These habitats are dynamic, productive, and essential to marine life. Decades of research have demonstrated that they support rich communities of microbes, worms, crustaceans, and other invertebrates that form the foundation of seafloor ecosystems (Snelgrove, 1999; Lenihan and Micheli, 2001; Gray, 2002). Despite this, surprisingly little is known about how fish species associate with and depend on these habitats (Pittman et al., 2004; Knudby et al., 2010; Brown et al., 2019).

Across the North Sea, the English Channel, and the Skagerrak, the continental shelf is dominated by sandbanks, gravel plains, and mixed sandy sediments shaped by strong tides and waves. While the invertebrate communities living in these sediments are relatively well studied, the role of these habitats as Essential Fish Habitats (EFH), including nurseries, spawning grounds, and foraging areas, remains far less understood (Seitz et al., 2014; Kritzer et al., 2016). This includes how fish distributions respond to subtle differences in sediment grain size, depth, and wave exposure across littoral ecozones, from shallow coastal sands to the darker, deeper parts of the shelf.

Yet it is clear that many fish rely heavily on sand and gravel habitats. Inner-shelf sand ridges, for example, provide key habitat for several commercially and ecologically important species (Vasslides & Able, 2008). Sandeels (*Ammodytidae*), comprises several species that are trophic keystone species in sandy habitats, where they live, feed, spawn, and overwinter on and in sand

and gravel banks (Holland et al., 2005; Tien et al., 2017). Herring (*Clupea* sp.) often deposit their eggs on coarse sand, and several skate species (*Rajidae*) use sand and gravel seabeds as nursery grounds (Serra-Pereira et al., 2014; Campanella and van der Kooij, 2021; Heessen et al., 2023). Despite these examples, we lack a comprehensive overview across the coherent shelf system spanning the North Sea, UK waters, Bay of Biscay, and Western Baltic Sea.

Along with being a needed or preferred habitat for spawning or refuge, several species also forage on the rich invertebrate fauna living within and on the sediment. This infauna forms the prey base and habitat structure that many fish depend on, meaning that pressures on these seabeds can cascade through the ecosystem. Demand for sand and gravel is rising due to coastal erosion, beach nourishment, and large infrastructure projects, leading to intensified seabed extraction (Groot, 1986; De Jong et al., 2016; Torres et al., 2017). Although currently in decline in the North Sea and adjacent waters, bottom trawling remains another major disturbance, with impacts that vary depending on sediment type, hydrodynamic conditions, and the life histories of the organisms present (Hiddink et al., 2019; Nielsen et al., 2023; Sethi et al., in review).

To support conservation planning and management, Europe relies on habitat classification systems such as the EUNIS framework and the habitat types of the EU's Habitat Directive (e.g. Galparsoro et al., 2012; Ware and Downie, 2020). These systems provide standardised approaches for describing and assessing marine habitats across regions. However, their effectiveness is limited because large areas of the seafloor remain unmapped, and ecological information, particularly for mobile fauna, remains incomplete. Filling these knowledge gaps is therefore essential for achieving broader conservation goals, including the 30×30 target under the Kunming–Montreal Global Biodiversity Framework, the Nature Restoration Law, and Ecosystem-Based Fisheries Management (EBFM) as outlined in the Marine Strategy Framework

Directive (MSFD) and the Common Fisheries Policy (CFP), the implementation of which are progressing rapidly (e.g. Hering et al., 2023; Rodriguez-Perez et al., 2023).

Another key challenge is that we still lack clear expectations for which species and communities should occur in different sediment habitats under favourable ecological conditions. Without this baseline, it becomes difficult to assess habitat status or determine whether these environments continue to provide essential ecological functions, as required under the framework of Favorable Conservation Status (FCS) (Mehtälä and Vuorisalo, 2007). This need is especially challenging for sandy and gravelly habitats, which are often not defined by physical structures, but by the fauna that inhabit them (Dernie et al., 2003; Buhl-Mortensen et al., 2010).

The aim of this study is to systematically compile and assess peer-reviewed literature on fish–habitat associations, with a particular focus on sedimentary habitats ranging from muddy sands to gravel and pebbles across different littoral ecozones. The geographical focus is the Northeast Atlantic shelf, spanning the northern North Sea around the UK to the Bay of Biscay, a region characterised by shared ecological features, overlapping fish communities, and substantial trawling and sediment extraction, and where implementation of the 30×30 conservation targets is advancing rapidly. Furthermore, by synthesising this information within standardised habitat and conservation frameworks, we aim to strengthen the scientific basis for habitat assessment, conservation planning, and ecosystem-based management.

The following questions guided the systematic literature review as well as the data extraction and processing:

I. What species have been studied in sandy and gravelly habitats? What species are reported to have been observed in or have a preference for these habitats, and how many IUCN Red Listed species are represented?
II. What geographic areas are represented in these studies?

III. What temporal trends are there in the types of studies and fish-habitat associations studied for sand/gravel habitats?

IV. What information is reported about the substrate classes in studies (e.g., is grain-size information provided, explicit substrate categories without grain-size data, or no explicit substrate details)?

V. Based on a broad classification of substrate types based on the information provided in studies (i.e., *muddy sand*, *sand*, *coarse sand*, *gravel*, *pebble*, and *mixed*), which and how many species have reported fish-habitat associations with each substrate class?

VI. Which species are found in the different substrate types across different littoral ecozones (e.g., 0–5 m (littoral), 5–20 m (infralittoral), and 20–200 m (circalittoral))?

VII. Are specific habitat functions for specific species provided for certain substrate types (e.g., spawning, nursery)?

II. METHODS

Search Strategy and Protocol

This study followed a standard systematic review protocol consistent with established guidelines for the field (i.e., PRISMA/PRISMA Eco-Evo; Moher et al., 2009; O'Dea et al., 2021). A review protocol was pre-registered prior to data extraction (19/01/2025; available via Open Science Framework, https://osf.io/7c9sb; DOI: 10.17605/OSF.IO/7C9SB).

Database searches were conducted in Web of Science ('WoS', 15/10/2024) and Scopus (16/10/2024) from the University of Melbourne. A standardised query was used, including terms relating to: (i) the study area of interest (i.e., '*"North Sea" OR "Dogger Bank" OR "Kattegat" OR "Skagerrak" OR "Baltic Sea" OR "English Channel" OR "Celtic Sea" OR "Irish Sea" OR*

*("Atlantic" W/5 "north*east*"))*'); (ii) the habitat of interest (e.g., "*("sandbank*" OR "sandbar*" OR "gravel*" OR "pebble*" OR "sediment type*" OR (("sediment*" OR "sand*" OR "seafloor*" OR "seabed*" OR "benthic*") AND ("habitat*" OR "ecosystem*" OR "biotope*")))*"), and (iii) studies on fish (i.e., including "**fish**" or any one of 201 fish species scientific names known to occur in the North Sea area; based on Carl and Møller (accessed on 16/09/2024). See full database-specific search queries in Supplementary Materials, Appendix S1. Duplicates were removed both in R via the package 'revtools' (v0.4.1; Westgate, 2019) and using the web screening tool Rayyan (https://rayyan.ai/; Ouzzani et al., 2016), giving 1,566 original records for screening.

Study Selection

Studies were included if they met the following three key criteria: (1) the study is within the following geographical regions: North Sea, Western Baltic, Kattegat, Skagerrak, Celtic Sea, Irish Sea, English Channel and Bay of Biscay, corresponding to biogeographic region 3 in Costello et al. (2017), down to a depth limit of 200 m; (2) the study includes sandy and gravelly sediment habitats, where sediment types may include anything from fine sand to pebbles, within the photic zone; and, (3) the study includes original data/quantitative analysis of fish interaction with (or occurrence on) sand or gravel bank habitats, including specific ecological interactions if mentioned (e.g., reproduction, foraging, refuge, etc.). Locations in non-marine areas, such as river outlets and lakes, were excluded. Studies were excluded where the full text record could not be accessed, where papers were in languages other than English or Nordic languages. Finally, only peer-reviewed records were included.

Title-abstract screening was conducted by 2 reviewers (MVD, OH) via Rayyan, and two 5% randomised samples were conducted to check the consistency of inclusion decisions. 20% of records were double-screened, and conflicting decisions were discussed and resolved collaboratively. From this, 424 records were included for full-text screening, which was conducted by 5 reviewers (MVD, PL, OH, MB, TB). To ensure that criteria were applied consistently, a practice set of 15 papers was randomly selected for full-text screening by all five reviewers, and any conflicting decisions were resolved collaboratively. No major issues were identified, so the remaining papers were assessed by a single reviewer. Additional secondary records (5) were also identified from the references of papers and were screened against the inclusion criteria. Screening records, extraction databases, and PRISMA records are available at Open Science Framework (https://osf.io/sa3ew, [DOI to be added, currently accessible via review link https://osf.io/sa3ew/overview?view_only=557aef6f212d42e7be07371657b4f37a]) and are archived at data.dtu.dk [doi to be added upon acceptance]. See also further screening details in Supplementary Materials, Appendix S1.

Data Extraction and Preparation

138 studies were initially identified as meeting our pre-registered inclusion criteria, with data extracted and analysed from 104 studies. A subset of initially included studies was excluded from data extraction and analysis due to limitations in data reporting or analysis that prevented us from extracting data on fish-habitat associations, as well as studies that showed negative or null results (23 studies). A further subset was subsequently excluded during data extraction to better focus the analysis on empirical studies that present data relating to fish-habitat associations within the most relevant habitats and locations (11 studies; e.g., excluding laboratory and modelling studies, studies from estuarine and eelgrass habitats, studies from northern Norway, Portugal). These studies are still considered included within the broader criteria used for the systematic review, but are not incorporated into summary data or qualitative data analysis describing fish-habitat associations.

Data from each included study were extracted by a single author (primarily MVD) at the study level. Data from a subset of papers (10%) were also reviewed by a second author (MB, JB) to confirm the accuracy of the information extracted. This included details about the focal species, life stage (e.g., juvenile, adult, etc.), types of fish-habitat association reported (e.g., habitat preference, or specific ecological interactions such as nursery, reproduction, feeding/foraging, refuge, or torpor/hibernation), location and habitat information, and any details about how the study reported substrate types and ecological zones (for further classification, as described below). See further details of data extraction methods in Supplementary Materials, Appendix S2.

To align the extracted data with relevant policy frameworks, we assigned each species record to a substrate type based on the EUNIS habitat classification approach and the sediment classification systems in Folk (1954) and Wentworth (1922). The main categories were: *sand* (63 µm - 2.0 mm), *coarse sand* (0.5 mm - 1.0 mm), and *gravel* (2.0 mm - 4.0 mm), adopted from the original Wentworth scale (Wentworth, 1922). These grain size range definitions for *sand* and *gravel* are also directly comparable to the EUNIS system (Long, 2006; modified from Folk, 1954). *Coarse sand* was included to allow a division between finer and coarser *sand* in the analysis, although subclasses of sand are not considered in the EUNIS system. Instead, EUNIS deals with "coarse sediments" defined as the range from gravelly sand to gravel. Other Wentworth *sand* subclasses (i.e. *medium* and *fine sand*) were rarely specified in the studies from which data were extracted and, to reduce complexity, not included as a separate category in the analysis. Habitat descriptions using terms such as "sandy substrate", "beach," or "sandbank" were also classified as *sand* during the analysis unless the text indicated dominance of coarser material, in which case the record was assigned to *coarse sand* or *gravel*, depending on the information provided.

Within the scope of this study we included *muddy sand* and *pebble*. *Muddy sand* and *sandy mud* are EUNIS substrate categories and not defined by grain sizes, but refer to sand with a large proportion of mud or vice versa (Long, 2006). Studies mentioning “muddy sand” explicitly or in any way report the presence of mud in relation to sandy substrate were placed in this category. Studies describing mud without reference to sand were considered outside the scope of this analysis. Pebble is a Wentworth category and covers the size range from 4 mm to 64 mm. In the EUNIS system, pebble is part of the category of coarser sediment. Lastly, we found the need to also include a *mixed* category in the analysis. The category *mixed* was used when the authors themselves refer to the substrate type as *mixed* and when species are associated with a sandbank containing various sandy and gravel substrate types, but without specific information on the exact substrate in which the fish were observed. Hence, the use of “mixed” in this study is not directly comparable to how “mixed” is used in the EUNIS system (Long, 2006).

To further align the data with relevant policy frameworks, we also adopted the ecozone definitions of the EUNIS habitat classification system (https://era.org.mt/topic/marine-habitats/). In this scheme, the *littoral zone* comprises tidally influenced habitats associated with coastlines; the *infralittoral zone* extends from the subtidal fringe and is characterised by algal‑dominated communities, typically including kelp and other macroalgae; and the *circalittoral zone* marks the transition to depths where algal growth is no longer sustained. At the upper boundary of the circalittoral, a limited number of low‑light‑tolerant algae (e.g., some red algae) may still occur. We use the term *substrate type* when referring to sediment characteristics, such as *sand* or *gravel*, and *habitat type* to refer to a combination of substrate type and littoral zone (e.g., “infralittoral sand”).

Depth boundaries between littoral zones vary with environmental conditions such as turbidity, light penetration, and tidal range. Based on literature from geographically relevant regions, we defined the zones as follows: 0–5 m (*littoral*), 5–20 m (*infralittoral*), and 20–200 m (*circalittoral*) (as per Marine Habitat Classification; JNCC, 2022). Depths beyond 200 m were considered bathyal and were excluded from the study. When a study spanned multiple depth zones, we assigned it to the zone representing its primary focus. For example, studies conducted between 10 and 30 m were classified as infralittoral. In rare cases where studies covered very broad depth ranges (e.g., 10–100 m), we assigned them to a more general category (e.g., *sublittoral*). If depth was not explicitly reported, we approximated it using the study location and the EMODnet Map Viewer (https://emodnet.ec.europa.eu/geoviewer/).

The data reported from each study were categorised based on whether they provided evidence of substrate preference for the fish species investigated, as opposed to merely reporting species presence on a given substrate. Studies in the first category often surveyed multiple habitat types and reported relative species abundances across them, allowing inference of habitat preference (e.g., species A occurring more frequently in one habitat type than another). Statistical testing was not required for a study to be considered as "evidence of substrate preference". Studies in the second category included, for example, surveys conducted exclusively on a sandbank, where species occurrences were reported without comparison to alternative habitat types.

To characterize the type of substrate information provided, we categorized studies as follows: (1) studies reporting explicit grain-size information; (2) studies using a terminology matching the substrate categorization defined above for the present study, but without grain-size data to confirm the categorization; (3) studies using vague substrate descriptions (e.g., "sandy substrate"); and (4) studies providing only indirect or non-differentiated descriptions, such as those referring broadly to beaches or sandbanks without specifying substrate type. For the latter category, substrate type was always classified as sand during data extraction.

Habitat function was recorded as either *spawning* or *nursery*. If a study explicitly stated that specimens were juveniles or provided length measurements indicating juvenile status, habitat function was registered as *nursery*. Only if explicit reports of spawning activity were noted in the study was it registered as *spawning*.

Many studies included multiple species and often reported species-specific habitat preferences. Consequently, the final database therefore often contained multiple entries per study, with each entry representing a species and the substrate type and littoral zone with which it was associated. In some cases, fish were identified only to family (e.g., *Clupeidae* sp.) or genus (e.g., *Pomatoschistus* sp.). IUCN Red List categories for all species were obtained via the European Red Lists of species, 2009-2022 (European Environment Agency, 2025). The final database is available at Open Science Framework (https://osf.io/sa3ew, [DOI to be added, currently accessible via review link https://osf.io/sa3ew/overview?view_only=557aef6f212d42e7be07371657b4f37a]) and is archived at data.dtu.dk [doi to be added upon acceptance]. Variations from pre-registered analysis methods are described in Supplementary Materials, Appendix S3.

III. RESULTS

A total of 104 unique studies were retained for further analysis, yielding a total of 453 data entries. Where multiple species are assessed within one study, or if a study species is assessed across multiple habitat types within the same study, each species- and habitat-specific record is treated as a separate data entry. Likewise, if a study distinguishes between juveniles and adults of the same species, each life-stage observation is recorded as an individual data entry.

The data contains 77 unique species and an additional 8 species groups (fish identified only to the nearest genus or family). The species groups do not necessarily represent additional species.

The subset of these species that show some evidence of a habitat preference for sandy and gravelly habitats is 59. Although notably, habitat preference may include species that show a preference for *gravel* compared with finer sediments, or it may favour *sand* relative to other habitat types that were not covered in this review.

Most studies originated from the North Sea, followed by the English Channel, although all regions within the broader Northeast Atlantic shelf study area were represented (Fig. 1). The number of studies reporting fish associations with sandy and gravelly habitats has increased over time, with a marked rise after the year 2000. This increase was particularly driven by studies that provided inference about substrate preference (Fig. 2).

It was most common for studies to have either "clear substrate description" or "unclear substrate description" (see specific definitions above), each occurring in 37.1% of the studies, while only 8.6% of studies reported explicit grain-size information. A similar proportion lacked any substrate description beyond broad terms such as "beach" or "sandbank" (Fig. 3A). *Sand* was the most frequently reported substrate type (reported in 69.5% of all studies), followed by *gravel* (21.0%) and *coarse sand* (16.2%) (Fig. 3B). This dominance of *sand* is not unexpected, as the category also encompassed several less well-defined substrate descriptions (e.g. "sandy sediment").

Within the littoral zone, nearly all fish-substrate associations occurred on sand (Fig. 4A), with 23 species reported in this combination. In the infralittoral zone, the highest species richness was also associated with *sand* (50 species), followed by *coarse sand* (9 species) and *muddy sand* (8 species). In the circalittoral zone, the highest richness was found on *mixed* substrates (27 species). *Muddy sand*, *sand*, *coarse sand*, and *gravel* all supported roughly similar numbers of species in the circalittoral zone (ranging from 8 on *coarse sand* to 14 on *muddy sand*), while only three species were reported on substrate type *pebble*.

For species with information on habitat function (nursery or spawning), nursery areas were most frequently associated with *sand* (25 species) and *muddy sand* (10 species) (Fig. 4B). In total, nursery function was indicated for 38 species. Spawning function was reported for only 11 species, distributed across *muddy sand* (1), *sand* (5), *coarse sand* (2), and *gravel* (3).

Species of conservation concern according to the European IUCN Red List (VU, NT, EN) were found across all substrate types. The only endangered species (EN), *Squalus acanthias*, was recorded on *mixed* substrate. Near-threatened species (NT), including *Raja clavata*, *R. microocellata*, *R. brachyura*, *R. undulata*, *Scyliorhinus stellaris*, and *Cyclopterus lumpus*, were found across all other substrate types (Fig. 5).

There was a clear positive relationship between how frequently a species has been studied and the number of habitat types in which it has been recorded. This relationship was best described by a Michaelis-Menten asymptotic curve (AIC = 297), rather than a linear model (AIC = 332) (Fig. 6A). However, the fitted curve suggests that most species, possibly with *Pleuronectes platessa* as an exception, have not been studied sufficiently to infer their full habitat range. Consequently, the data cannot be used to distinguish habitat specialists from generalists, as the number of habitat types associated with a species largely reflects study effort. Rare or non-commercial species are studied far less frequently than commercially important species such as *P. platessa* and various gadoids.

A similar positive relationship was found between study effort within a habitat type and the number of unique species recorded in that habitat. Linear and Michaelis-Menten models produced comparable AIC values (Fig. 6B), indicating that a substantial number of studies are required to approach the true species richness of a habitat type. The number of studies needed will also depend on the geographical scope of the question.

Only 10 species had more than 10 entries (Fig. 7). These were primarily common commercial flatfish (e.g., *P. platessa*, *Limanda limanda*, *Solea solea*) and gadoids (e.g., *Gadus morhua*, *Merlangius merlangus*, *Melanogrammus aeglefinus*). These same species were also among the few for which spawning habitat function was reported (Table 1), mostly within the sublittoral (infralittoral + circalittoral) zone and predominantly on *sand* and *coarse sand*. *M. merlangus* was the only species recorded spawning exclusively on *gravel*, while flatfish generally spawned on *sand* (with the exception of *P. flesus*). *Clupea harengus* and *Clupeidae* sp. were also well represented among studies reporting habitat function, with a clear preference for coarser substrates (i.e. c*oarse sand*, *gravel*, *pebble*).

Supplementary figures S2 and S3 provide an overview of species occurrences across habitat types (see Supplementary Materials, Appendix S4). These figures allow users to identify species of interest and consult the corresponding studies in the supplementary database (see Supplementary Materials, Appendix S5). Occurrence frequencies were weighted by whether the study reported simple observations or evidence of a substrate-specific preference, which were given twice the weight of studies reporting only presence. The overview is split into juveniles (nursery function; see Fig. S2) and all other records (Fig. S3). IUCN Red List categories are shown for each species.

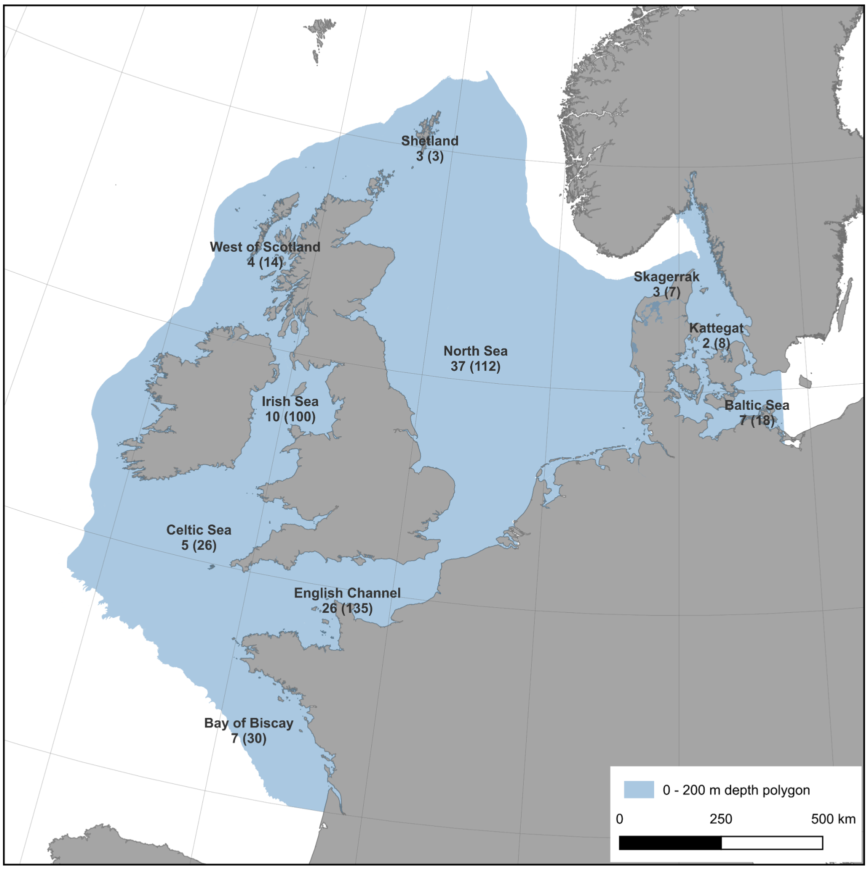

Figure 1. Number of studies and total number of data entries (value in parentheses) by geographical area. One data entry represents unique information about a species found in association with a given substrate type, and a given study can address multiple species-substrate combinations. The geographical areas are the Bay of Biscay, English Channel, Celtic Sea, Irish Sea, Shetland Islands, West of Scotland, North Sea, Skagerrak, Kattegat, and Western Baltic Sea. Besides the geographical areas, the scope of the study goes from 0 to 200 m depth (illustrated by the light blue shading on the map).

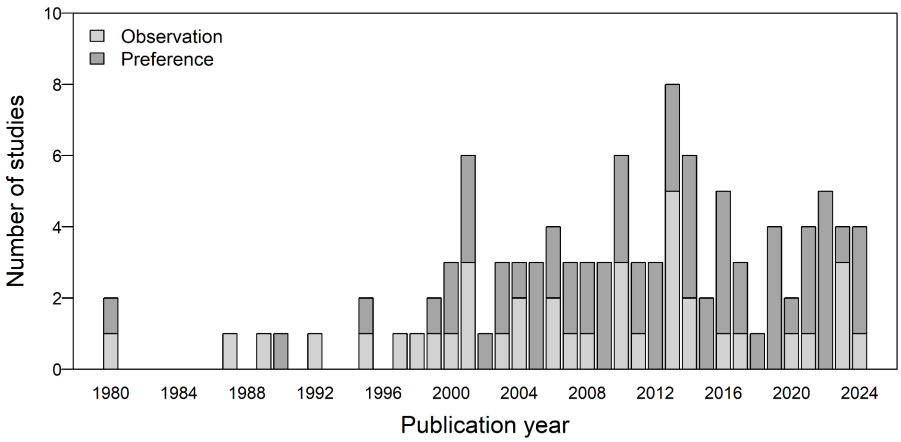

Figure 2. Number of studies by publication year. Studies are further divided by the type of association reported between fish and habitats: Light grey indicates studies that report observations/simple presence, whereas dark grey represents studies that indicate a specific preference for that habitat.

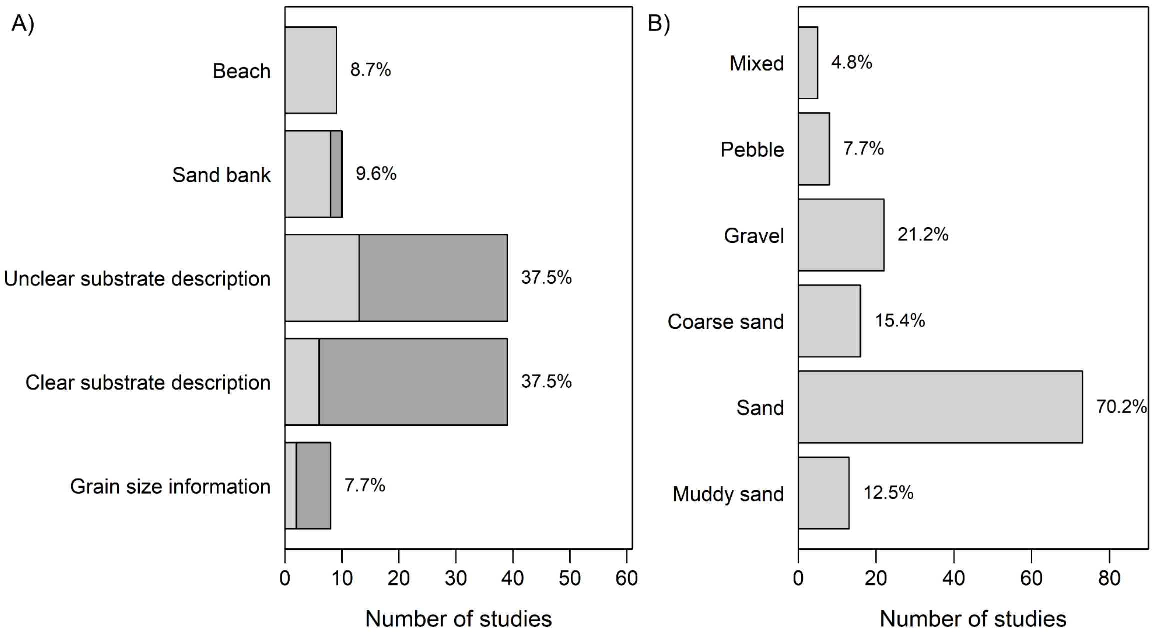

Figure 3. (A) Substrate description and the type of association reported between fish and sand/gravel habitats (i.e., observations v preference). Substrate descriptions were grouped into five categories. These included cases where grain-size information was available; cases with clear descriptive distinctions between substrate categories but lacking quantitative measures such as grain size; cases where unclear substrate descriptions were used, such as "sandy substrate"; cases where "sandbank" or "beach" was used as the habitat descriptor without further additional specification. Light grey indicates studies reporting simple presence, and dark grey indicates studies that include some inference of preference. The percentages represent the relative proportion of studies in which each type of substrate description was applied. (B) Number of studies by substrate type. A single study may be represented under multiple substrate types if it examines more than one substrate type. Hence, the number of studies by substrate type sums to more than the 104 studies from which data were extracted. The percentages provide the relative proportions of the studies in which a given substrate type was included. Note, as a study may contribute multiple data entries across classifications, percentages do not sum to 100.

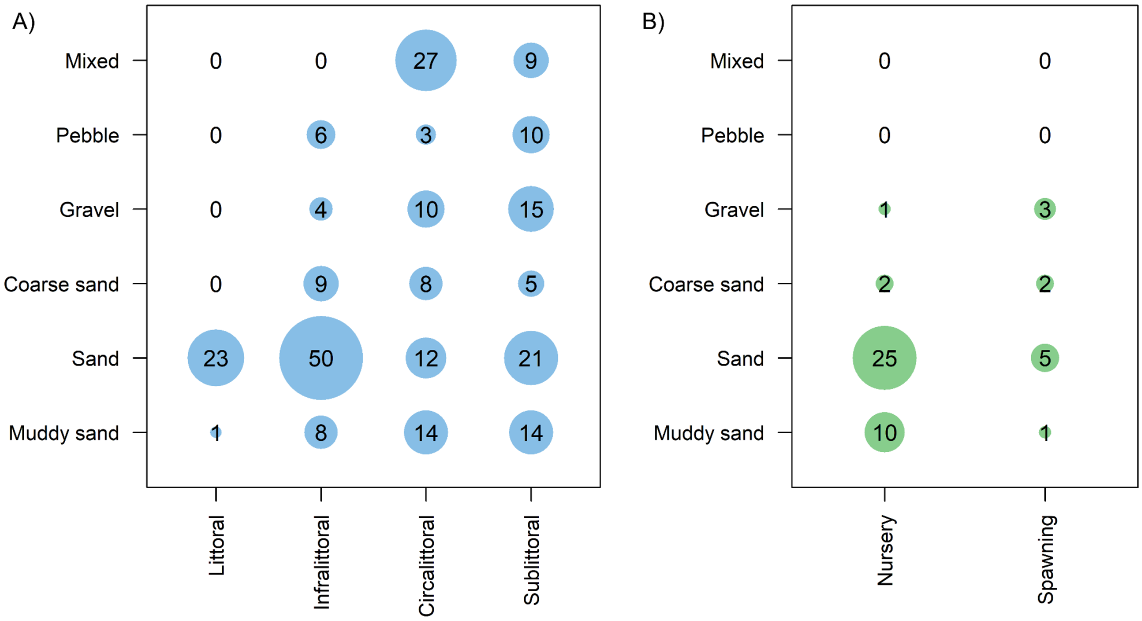

Figure 4. (A) Number of unique combinations of species, littoral zone, and substrate type. Numbers inside the bubbles indicate the number of species associated with each substrate–zone combination. The category *sublittoral* includes cases where study areas spanned both the infralittoral and circalittoral zones to an extent that prevented assigning records to one zone exclusively. (B) Number of unique combinations of species, habitat function, and substrate type. Numbers inside the bubbles indicate the number of species associated with each substrate type for which a habitat function was identified. Records were assigned to *Nursery* when studies explicitly stated that individuals were juveniles or provided length measurements confirming juvenile status. Records were assigned to *Spawning* only when spawning activity by the species was explicitly reported in the study.

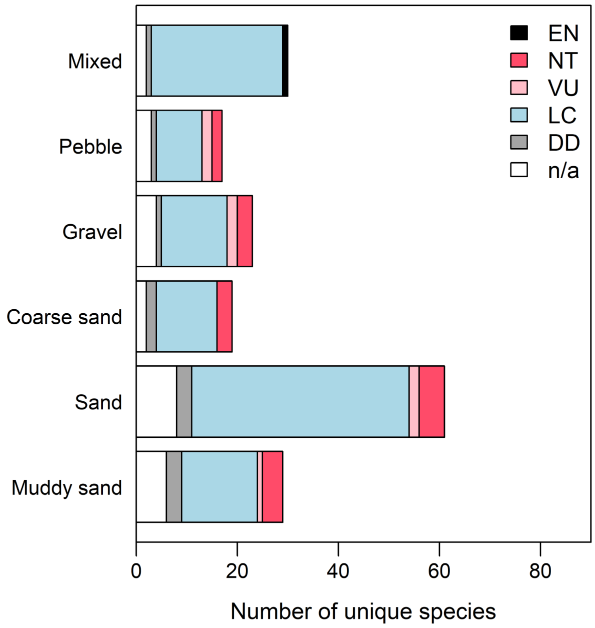

Figure 5. Number of unique species reported by substrate type and IUCN Red List category: not available (white), data deficient DD (dark grey), least Concern LC (Light blue), vulnerable VU (pink), near threatened NT (red), endangered EN (black).

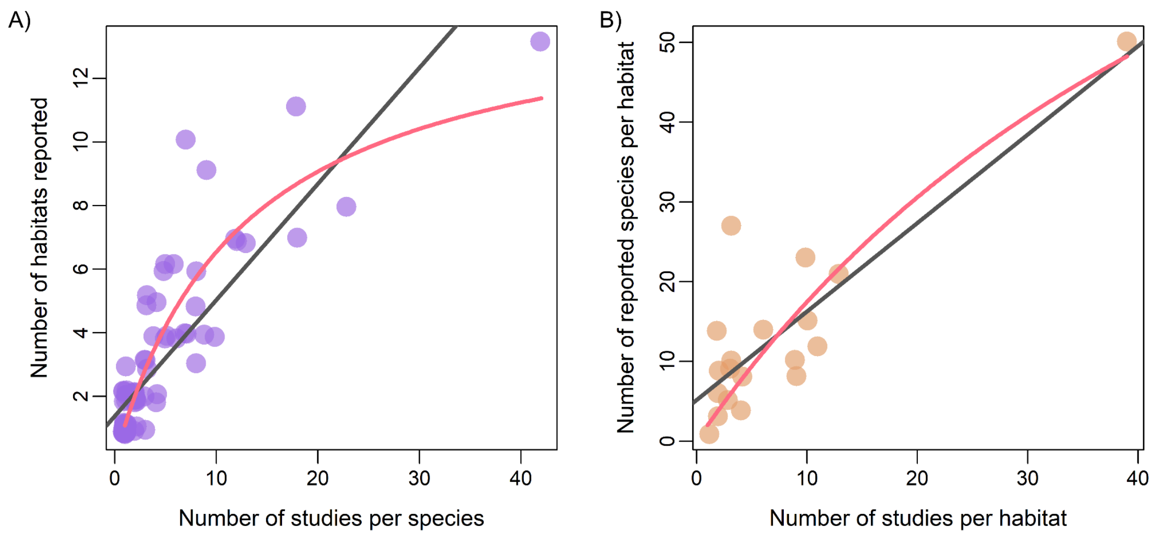

Figure 6. (A) Relationship between the number of studies in which a given species is reported and the number of habitat types in which the same species is found. Each point in the plot represents a single species. A linear model (AIC: 332) and a Michaelis-Menten asymptotic curve (AIC: 297) were fitted to the data points, respectively. (B) Relationship between the number of studies per habitat type and the number of species per habitat type. Each point in the plot represents a single habitat type. A linear model (AIC: 130) and a Michaelis-Menten asymptotic curve (AIC: 133) were fitted to the data points, respectively.

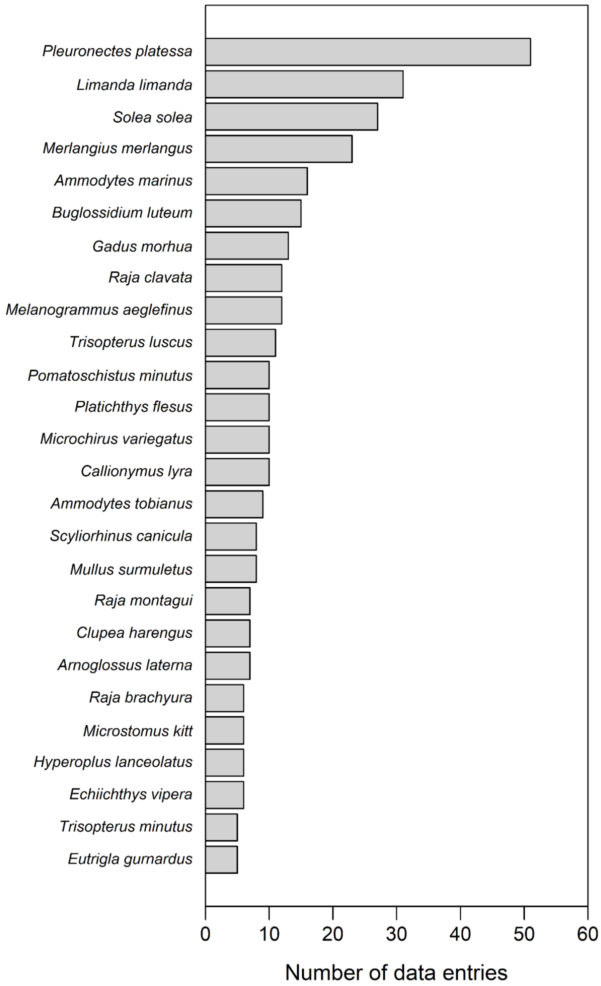

Figure 7. Species with the highest data availability in the literature review. Only species with five or more data entries are shown.

Habitat	Species	References
Muddy sand littoral	*Entelurus aequoreus*	Polte & Buschbaum, (2008)
Sand Sublittoral	*Gadus morhua, Limanda limanda, Pleuronectes platessa*	Lelievra et al., (2014); Gonzales et al. (2016)
Sand Circalittoral	*Melanogrammus aeglefinus, Solea solea*	Eastwood et al., (2001); Gonzales et al. (2016)
Coarse sand Sublittoral	*Gadus morhua*	Gonzales et al. (2016)
Coarse sand Circalittoral	*Clupeidae sp., Melanogrammus aeglefinus*	Vallet & Dauvin, (1998); Gonzales et al. (2016)
Gravel Sublittoral	*Clupea harengus, Merlangius merlangus*	Maravelias, (2001); Lelievra et al., (2014)
Gravel Infralittoral	*Platichthys flesus*	Grioche et al., (1997)
Gravel Circalittoral	*Clupea harengus*	Maravelias et al., (2000)
Pebble Circalittoral	*Clupeidae sp.*	Vallet & Dauvin, (1998)

Table 1. Species by habitat type for which it was explicitly indicated that the habitat was used for spawning.

IV. DISCUSSION

Sedimentary habitats such as sand and gravel are widespread and ecologically important, yet fish-habitat relationships in these environments remain poorly understood. These substrates support key ecological functions across the North Sea region, as feeding grounds and spawning and nursery areas (e.g. Amara et al., 2001; Maravelias, 2001; Amezcua et al., 2003; Amara et al., 2004; Lelievre et al., 2014; González-Irusta et al., 2016). Achieving conservation targets, such as 30×30 and ecosystem-based fisheries management, requires robust ecological data on how fish use these habitats. Our synthesis contributes to this need by consolidating current knowledge across the Northeast Atlantic shelf.

This review identified 104 studies covering 77 fish species reported in associations with sandy and gravelly habitats, and for 59 species, some degree of substrate comparison or preference was made (as opposed to merely reporting the observation of a species on sandy substrate). Substrate descriptions were sometimes vague, lacking grain-size measurements or quantitative definitions of substrate types. *Sand* was the most commonly reported substrate, followed by *gravel* and *coarse sand*.

Study frequency influenced the number of habitats a species appeared in, making habitat specialisation difficult to determine. Across ecozones, sand consistently supported the highest species richness, and most nursery areas were associated with *sand* or *muddy sand*. Species of conservation concern occurred across all substrate types, though commercially important species dominated the records. Relatively few studies explicitly identified habitats or substrates as spawning grounds, but among those that did, commercially important species were again the most frequently reported.

Although the North Sea is the largest region and the source of most studies, the English Channel produced the highest number of data entries (unique species–habitat records). This reflects the fact that several English Channel studies were multispecies surveys, whereas many North Sea studies focused on only one or a few species (e.g., Amara and Paul, 2003; Creutzberg and Witte, 1989). The pattern is even more pronounced in the Irish Sea: although only ten studies were identified, they generated 100 data entries, likely reflecting the long history and strong traditions of trawl surveys in the UK (Hunt et al., 2024). A clear temporal trend was also evident, with a marked increase in studies providing quantitative inference on habitat preference rather than simple presence records.

Surprisingly many studies did not provide explicit grain-size information with the substrate types (e.g., Amezcua and Nash, 2000). Most did, however, use a terminology consistent with either Wentworth (1922) or Folk (1954), but without reporting the underlying grain-size ranges in the article itself. In some cases, it was possible to trace these definitions through cited sources (e.g., Martin et al., 2012). When grain-size information was provided, it was generally consistent with Wentworth (1922) and therefore also with the substrate type definitions used for this study (e.g. Amezcua et al., 2001; Prista et al., 2003; Holland et al., 2005; Carl et al., 2008; De Jong et al., 2014; Langon et al., 2021). Nearly 20% of the studies did not describe substrate characteristics at all, referring instead to locations such as “sand bank” or “beach”. Although less precise in terms of substrate detail, this approach can still convey ecologically relevant information: sand banks imply shallow topography that may generate upwelling (e.g., Martinez et al., 2013), while beaches indicate environments strongly shaped by wave action (e.g., Jones et al., 2020).

Sand was the most frequently reported substrate type. For two gadoid species and three flatfish species (Pleuronectiformes), spawning activity on sublittoral sand was documented (Eastwood et al., 2001; Lelievre et al., 2014; Gonzalez-Irusta and Wright, 2016). Among the flatfishes, only *P. flesus* was reported to spawn on infralittoral *gravel* (Grioche et al., 1997). Although *sand* dominated the records, 16.2% and 21% of studies referred to *coarse sand* and *gravel*, respectively, and 7.6% mentioned *pebble*. Coarser sediments, including *gravel* and *pebble*, are more spatially restricted than *sand* or *muddy sand*. According to the EMODnet Seabed Habitats (Broad-scale seabed habitat map for Europe), sand alone covers a surface area twice as large as coarse sediments (when calculated for the study area shown in Fig. 1).

Coarser sediments (e.g. *gravel* and *pebble*) are also recognised as ecologically important habitats (Evans et al., 2018). They are especially significant as spawning grounds for several species, with herring (*C. harengus*) being the most frequently studied in the region (Maravelias et al., 2000; Maravelias, 2001; Lelievre et al., 2014; Flavio et al., 2023). Burying species such as sandeels (e.g. *Ammodytes marinus*) also depend on coarse sediments with low silt content (Holland et al., 2005; Tien et al., 2017). In this review, the IUCN-listed species associated with *gravel* and *pebble* were *R. clavata*, *R. brachyura*, and *S. stellaris* (Martin et al., 2012; Dedman et al., 2015).

Consequently, when identifying EFH and considering red-listed species in marine spatial planning (MSP), *coarse sand*, *gravel*, and *pebble* substrates in the circalittoral and infralittoral zones warrant particular attention and may require explicit inclusion in MSP to ensure adequate protection of key spawning grounds and other limited habitat resources. Gravel, in particular, is also heavily targeted for material extraction (Groot, 1986; De Jong et al., 2016; Torres et al., 2017), and the impact of trawling on its associated benthic communities is relatively high (Nielsen et al., 2023).

Juvenile records were classified as nursery habitat whenever specimens were described as juveniles, and these records were more common than spawning observations. As in the broader dataset, *P. platessa* dominated juvenile records and was primarily associated with *sand* in the littoral and infralittoral ecozones, mainly coastal areas, which also hosted most juvenile occurrences across species. Other commercially important species, such as *Limanda limanda* and *S. solea*, were also frequently reported. Although these substrates may not be inherently limited, their proximity to coastal areas exposes them to substantial anthropogenic pressures (Feist and Levin, 2016).

Two juvenile elasmobranchs, *S. canicula* and the Near Threatened skate *R. clavata*, were reported from sublittoral *muddy sand* (Martin et al., 2012). At the opposite end of the sediment-coarseness spectrum, *gravel*, only two species were recorded as juveniles, *L. limanda* and *Microchirus variegatus*, both in the sublittoral zone (Amezcua et al., 2003). Species also differ in whether they use littoral or sublittoral areas as nursery habitat, indicating that no single habitat type can be universally defined as a nursery. However, infralittoral sand emerges as the most common nursery habitat and is, fortunately, both widespread and relatively less vulnerable to trawling, although trawling can still affect juveniles through bycatch (Stäbler et al., 2016).

Across littoral ecozones, sand supported the highest number of species. While this might suggest higher biodiversity, the strong relationship between species richness and study effort indicates that sampling bias is the dominant driver. With the exception of *P. platessa*, most species–habitat accumulation curves showed no sign of saturation, implying that at least ~20 studies per habitat type are needed to approach true species richness. Consequently, this review cannot reliably infer comparative biodiversity across substrate types.

There is also a clear tendency for scientific attention to be disproportionately directed toward commercially valuable or visually appealing species, while many threatened fishes receive little or no research focus, a well-known literature bias (Mouquet et al., 2024). Our dataset reflects this pattern. Frequently encountered commercial species such as *P. platessa*, *S. solea*, and *A. marinus* have the highest number of data entries. However, among studies with five or more entries, several skates in the Rajidae family, such as *R. clavata* and *R. brachyura*, both listed as

Near Threatened on the European IUCN Red List, are also well represented. Notably, some small, non‑commercial species, including *Buglossidium luteum* and *Pomatoschistus minutus*, have ten or more entries. This suggests that the dataset may offer valuable insights for conservation planning and marine spatial planning (MSP) beyond fisheries‑focused species. Still, as noted above, caution is needed when using these data for species‑richness or biodiversity meta‑analyses.

This review provides a comprehensive synthesis of fish-habitat associations, with particular emphasis on sandy and gravelly substrates. The resulting overview offers a useful foundation for MSP, including initiatives aimed at achieving area‑based conservation targets such as the 30×30 goal. In several cases, information relevant to EFH was also available, further increasing the potential applicability of this review in management and conservation contexts. It is important to note that the absence of a species in a given habitat type within the dataset does not imply that the species does not use that habitat.

Figures S2 and S3 (see Supplementary Materials, Appendix S4) allow users to identify species associated with specific habitat types aligned with EUNIS categories, while users interested in a particular species can consult the same figures to determine the range of habitat types in which that species has been observed. The full publicly available review database also enables more detailed queries across species-substrate combinations and provides direct access to the underlying literature. The dataset also includes essential information on the type of association reported between fish and sand/gravel habitats, including whether ecosystem functions were mentioned and whether the evidence reflects simple observations or quantitative inference about habitat preference.

Although the dataset may support optimisation of area‑based protection strategies, for example, to safeguard habitats used by many species, by commercially important species, or by

IUCN-listed species, it is essential to emphasise that habitat type alone should not determine conservation priorities. A wide range of biological, physical, and climatic factors influences species presence and the extent to which habitats function as EFH. These factors should be integrated into MSP and conservation planning to ensure robust and ecologically meaningful outcomes. Nevertheless, comparing the species observed in sedimentary habitats with the communities typically associated with these habitats could offer a valuable step toward assessing habitat status and even help to clarify whether signs of degradation arise from the condition of the habitat itself or from external pressures.

SUPPLEMENTARY MATERIALS

Appendix S1. Search Strategy and Study Selection

Appendix S2. Data Extraction Methods

Appendix S3. Pre-Registration Details, Departures, and Justifications

Appendix S4. Supplementary Results

Appendix S5. Included References

DECLARATIONS

Acknowledgements: TBC

Funding: This work was supported by the Horizon Europe project MARHAB (grant no. 101135307) (Improving marine habitat status by considering ecosystem dynamics)

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Data accessibility: Data and code used to process our systematic searches, screening records, and data extracted from studies to reproduce all results are all available through Open Science Framework (https://osf.io/sa3ew, [DOI to be added, currently accessible via review link https://osf.io/sa3ew/overview?view_only=557aef6f212d42e7be07371657b4f37a]) and are archived at data.dtu.dk [doi to be added upon acceptance]).

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