Hard-bottom habitats support commercially important fish species: a systematic review for the North Atlantic Ocean and Baltic Sea

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Hard-bottom habitats span a range of natural substrates (e.g. boulders, cobble) and artificial habitats (e.g. the base of wind turbines, oil platforms). These hard-bottom habitats can provide a variety of ecosystem services, ranging from the enhancement of fish biomass and production to providing erosion control. Management decisions regarding the construction or fate of hard-bottom habitats require information on the ecological functions of these habitats, particularly for species targeted in ecosystem-based fisheries management. This study provides a systematic review of the relationships of various hard-bottom habitats to individual commercially harvested species that are managed jointly across the Atlantic by the International Council for the Exploration of the Sea (ICES). We systemically reviewed peer-reviewed publications on hard-bottom habitats including both some natural and artificial reefs, after applying various exclusion criteria. Most studies were conducted on near-shore hard-bottom habitats, and habitat importance varied according to fish species and region. We quantified the frequency with which studies demonstrate that natural and artificial hard-bottom habitats function as spawning grounds, settlement and nursery areas, and foraging grounds, as well as provide stepping-stones during migration, or new home ranges. Hard-bottom habitats generally support higher fish densities than surrounding habitat types, although not all fish species benefit from hard-bottom habitats. Of the commercially important species, cod (*Gadus morhua*) was the most frequently studied species, with enhanced biomass, density, feeding, and spawning on hard-bottom habitats compared to unstructured habitats. Moreover, hard-bottom habitats appear to be of particular importance for spawning of herring (*Clupea harengus*). Collectively, data indicate that loss of hard-bottom habitats may translate into less-favourable conditions for spawning and biomass of diverse commercial species, including

cod and herring.

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32 ## Abstract

33 Hard-bottom habitats span a range of natural substrates (e.g. boulders, cobble) and artificial habitats (e.g.

34 the base of wind turbines, oil platforms). These hard-bottom habitats can provide a variety of ecosystem

35 services, ranging from the enhancement of fish biomass and production to providing erosion control.

36 Management decisions regarding the construction or fate of hard-bottom habitats require information on

37 the ecological functions of these habitats, particularly for species targeted in ecosystem-based fisheries

38 management. This study provides a systematic review of the relationships of various hard-bottom habitats

39 to individual commercially harvested species that are managed jointly across the Atlantic by the

40   International Council for the Exploration of the Sea (ICES). We systemically reviewed peer-reviewed

41   publications on hard-bottom habitats including both some natural and artificial reefs, after applying

42   various exclusion criteria. Most studies were conducted on near-shore hard-bottom habitats, and habitat

43   importance varied according to fish species and region. We quantified the frequency with which studies

44   demonstrate that natural and artificial hard-bottom habitats function as spawning grounds, settlement and

45   nursery areas, and foraging grounds, as well as provide stepping-stones during migration, or new home

46   ranges. Hard-bottom habitats generally support higher fish densities than surrounding habitat types,

47   although not all fish species benefit from hard-bottom habitats. Of the commercially important species,

48   cod (*Gadus morhua*) was the most frequently studied species, with enhanced biomass, density, feeding,

49   and spawning on hard-bottom habitats compared to unstructured habitats. Moreover, hard-bottom

50   habitats appear to be of particular importance for spawning of herring (*Clupea harengus*). Collectively,

51   data indicate that loss of hard-bottom habitats may translate into less-favourable conditions for spawning

52   and biomass of diverse commercial species, including cod and herring.

53   **Keywords:** reefs; fish abundance; spawning grounds; essential fish habitat

Introduction

55   Natural hard-bottom habitats are vital to the health and function of coastal ecosystems (Stål et al., 2007;

56   Kovalenko et al., 2012; Simon et al., 2013; Lefcheck et al. 2019). These structures provide a range of

57   services, including structural refuge for juveniles and feeding grounds for commercially important fish

58   species. Hard-bottom habitats include a wide variety of topographic forms (e.g. high vertical profile, high

59   complexity), substratum types (e.g. boulders, rocks, cobble, artificial materials), and degree of rugosity

60   (e.g. smooth surfaces, perforated materials), with well-documented effects of increasing biodiversity with

61   habitat complexity (Wilhelmsson et al., 2006; Kovalenko et al., 2012; Wehkamp and Fischer, 2013). As

62   such, these hard substrates often comprise a three-dimensional structure, which means they can offer

63   increased complexity in an otherwise two-dimensional landscape. Hard-bottom habitats provide substrate

64   for the attachment of macrophytes, such as kelp and other macroalgae that further increase the

65   complexity of the benthos and associated biodiversity, compared to unstructured habitat (Norderhaug et

66   al., 2005; Christie et al., 2007, 2009). Reviews on the importance of coastal habitats for exploited species

67   identified a lack of information on how fish utilize some habitat types in the North Atlantic, particularly

68   complex natural and artificial hard-bottom habitats (e.g. rocky shores, foundations of wind farms, oil-rigs;

69   Seitz, 2014; Seitz et al., 2014, Fowler et al. 2018).

70   Artificial reefs have been used as a tool for restoration of marine habitats and as mitigation for damage to

71   other marine habitats. Artificial reefs may be constructed using natural stone (Støttrup et al., 2017) or,

72   more commonly, using a range of man-made materials including concrete units or scrap materials, such

73   as decommissioned ships and oilrigs (Jensen, 2002; Soldal et al., 2002). Artificial reefs have been widely

74   deployed to (1) enhance fisheries (Seaman and Sprague, 1991; Bombace et al., 1994; Brock, 1994), (2)

75   mitigate damage to specific bottom habitats such as seagrass beds (*Posidonia* sp.; González-Correa et

76   al., 2005), (3) increase the recreational value of an area (Wilhelmsson et al., 1998) or (4) as a tool for

77   rehabilitation of coastal ecosystems (Pickering et al., 1999). Artificial reefs can be intentional (i.e.

78   anthropogenic explicit creation of a reef) or unintentional (i.e. created as a by-product of other

79   anthropogenic activities, such as oil platforms and wind turbines, hereafter referred to "*de facto*" reefs).

80   Artificial reefs generally harbor higher fish densities and biomass than surrounding natural reefs (e.g.

81   Wilhelmsson et al., 1998), which is attributed to their form and complexity (Hunter and Sayer, 2009;

82   Degraer et al., 2020) and/or food abundance (Rilov and Benayahu, 2000; Fabi et al., 2006; Glarou et al.

83   2020), but artificial reefs may also increase abundance and richness of the fish community (Rilov and

84   Benayahu, 2000). Moreover, effects of artificial reefs may vary by individual fish species (Leitão et al.,

85   2008; Krone et al., 2013). Findings on the importance of artificial habitats for species managed by the

86   International Council for the Exploration of the Sea (ICES) could be important for management decisions

87   regarding habitat restoration and protection of fisheries species.

88   In Europe, hard-bottom habitats are one of the few marine habitat types included in the European Union's

89   Habitat Directive (1170 Reef Habitat; EEC, 1992). For this reason, reef areas are included in several

90   Natura 2000 networks such as the Danish Natura 2000 network. Surprisingly, the importance of

91   temperate reefs is rarely considered in fisheries management and in fish population assessments (Lipcius

92   et al., 2019, and references therein), and the importance of hard-bottom reefs may differ for different

93   fishery species. Management decisions require the best available information on specific ecosystem

94   services that, in some cases, can be monetized (Costanza et al., 1997; Cavanagh et al., 2016). As such,

95   the goal of this study was to summarize the existing information on ICES-managed fish species and their

96   use of temperate hard-bottom habitats in an effort to (1) inform scientists interested in the ecological

97   function of these habitats for some key fish species, and (2) inform managers (especially ICES managers)

98   and conservation groups focused on coastal habitats of the potential importance of hard-bottom habitats

99   to certain fish species. ICES is an inter-governmental marine science organization whose advisory

100   committee translates science to management on "the sustainable use and protection of marine species,"

101   and their work is relevant to extensive coastal areas, for example throughout Europe and the United

102   States. Focusing our review on ICES-managed species is important because ICES-managed species are

103   common throughout coastal areas of North America and Europe, and many commercial and recreational

104   fisheries for these species are in poor condition, which causes concerns among conservationists as well

105   as those dependent on fisheries as an economic activity or food source (ICES Science Plan 2013).

Materials & Methods

107   The overarching objective was to review the literature to quantify the ways in which hard-bottom habitats

108   support commercially important fish species in temperate regions, particularly the North Atlantic, and

109   Baltic and North Seas. We targeted the value of natural hard-bottom habitats and artificial reefs on

110   exploited fish species by (1) summarizing increases or decreases in demographic variables (e.g. growth,

111   survival, biomass, spawning rates) for individual commercial fishery species associated with hard-bottom

112   habitats, and (2) highlighting the importance of these habitats for certain fish species so that managers

113   and conservation groups can act on this knowledge. The spatial focus was on temperate, hard-bottom

114   habitats (excluding subtropical and tropical areas, and the Mediterranean Sea), and we excluded some

115   natural hard-bottom habitats such as coral reefs and biogenic habitats (see negative keywords in the

116   search string below). We also focused on species important for management by ICES (see species-

117   related keywords below), therefore, we did not include all commercially important species. In addition, we

118   excluded rockfish in the Pacific Ocean, which have a separate body of literature targeted towards them,

119   and which are not managed by ICES. Thus, our conclusions cannot be applied to all species in every

120   area, and our focus was on non-biogenic or anthropogenically created reefs. We were most interested in

121   habitat enhancement from the physical structure provided by hard-bottom habitats, and thus excluded

122   biogenic reefs, which provide additional ecological benefits such as increased nutrients (e.g. from faeces

123   and pseudofaeces on mussel beds; Thiel and Ullrich, 2002).

124   **Search protocol:**

125   We followed the protocol for a systematic literature review proposed by Pullin and Stewart (2006), which

126   set forth guidelines for planning the review to analysis of the data. We systematically reviewed the

127   literature and evaluated papers returned by three different databases (DTU-Findit, Web of Science, and

128   Scopus) for relevance based on our inclusion criteria (Table 1). Screening was conducted at the level of

129   title, abstract, and full text (Pullin and Stewart, 2006) to each of several ecological study variables (see

130   "search string" below), using the PRISMA protocol (Moher et al., 2009)(Fig. 1). The first author of this

131   publication screened each paper by title to eliminate non-relevant papers, and a subset of articles was

132   sent to all co-authors to compare the group's decisions and ensure we came to consensus on what

133   should be discarded. Then, the same procedure was followed for examining the abstracts of the

134   remaining papers. Finally, we divided the papers for full-text examination among all authors and each

135   person independently extracted data, with a group discussion of which papers were relevant and why,

136   and resolving any discrepancies on what should be included. The search was run on the three different

137   databases on April 7th, 2017. The papers returned by the three different databases were evaluated for

138   relevance based on the inclusion criteria (Table 1), applied at three successive levels: (1) title, (2) abstract

139   and (3) full-text. It is important to note that there are some limitations of our approach, and that we may

140   have missed some research that did not fall into our selected categories based on the search terms we

141   used, and results are only applicable to the species we incorporated into our search (namely ICES-

142   managed species). Our review focused on the species for which ICES gives advice, which resulted in

143   examining the species of importance for ICES Member Countries (i.e. Belgium, Canada, Denmark,

144   Estonia, Finland, France, Germany, Iceland, Ireland, Latvia, Lithuania, the Netherlands, Norway, Poland,

145   Portugal, Russia, Spain, Sweden, United Kingdom, and United States of America; US and Canadian fish

146   stocks are not included in the advice, though these are ICES Member Countries). Therefore,

147   interpretations of these data apply only to the species and habitats we incorporate. Additionally, we

148   examined the current literature (2017-2022) for more recent papers on the same ICES-managed species

149   using hard bottom habitats (database from B. Ciotti pers. comm.), which allowed us to identify a couple of

150   case studies to serve as a check on validity of conclusions from our systematic search.

151

152   **Search string**

153   The following search keywords were chosen for each of the ecological variables we wanted to examine:

154   Biomass, Density, Biodiversity, Condition, Mortality, Growth, Feeding, Spawning, Nursery, Settling, Diel

155   cycle, Site fidelity, Migration. Separate searches with all other keywords in combination with each of the

156   ecological search keywords were conduced (Table 2). Location-related keywords and exclusion keywords

157   were also included to narrow the search results.

158   **Importance-related keywords** (note: asterisks represent a search engine wild-card and were used to

159   broaden the search by finding multiple words that start with the same letters):

160   Fish attraction, fish production, fish biomass, fish diversity, fish growth, fish survival, fish density, fish

161   migration, demographic rate*, fish reproduction, fish mortality and fish juvenile*, feeding, nursery, spawn*.

162   **Ecosystem-related keywords:** Hard bottom, rocky reef*, stone reef*, riprap, seawall*, groin*, groyne*,

163   offshore wind energy structure*, wind farm*, wind turbine*, artificial reef*, fish attraction device*, FAD*,

164   shipwreck*, oil rig*, oil platform* oil pipe*, gas rig*, gas platform*, gas pipe*, offshore platform*, rig* to

165   reef*, decommission*.

166   **Species-related keywords:** *Alopias* spp., *Amblyraja radiata*, *Ammodytes* spp., *Anguilla anguilla*,

167   *Aphanopus carbo*, *Argentina silus*, *Beryx* spp., *Brosme brosme*, *Capros aper*, *Centrophorus squamosus*,

168   *Centroscymnus coelolepis*, *Cetorhinus maximus*, *Chelidonichthys cuculus*, *Clupea harengus*,

169   *Coryphaenoides rupestris*, *Dalatias licha*, *Dicentrarchus labrax*, *Dipturus batis-complex*, *Engraulis*

170   *encrasicolus*, *Gadus morhua*, *Galeorhinus galeus*, *Galeus melastomus*, *Hoplostethus atlanticus*, *Lamna*

171   *nasus*, *Lepidorhombus* spp., *Leucoraja circularis*, *Leucoraja fullonica*, *Leucoraja naevus*, *Limanda*

172   *limanda*, *Lophius budegassa*, *Lophius piscatorius*, *Macrourus berglax*, *Mallotus villosus*, *Melanogrammus*

173   *aeglefinus*, *Merlangius merlangus*, *Merluccius merluccius*, *Micromesistius poutassou*, *Molva dypterygia*,

174   *Molva molva*, *Mullus surmuletus*, *Mustelus* spp., *Pagellus bogaraveo*, *Phycis blennoides*, *Platichthys*

175   *flesus*, *Pleuronectes platessa*, *Pollachius pollachius*, *Pollachius virens*, *Raja brachyura*, *Raja clavata*,

176   *Raja microocellata*, *Raja montagui*, *Raja undulata*, *Reinhardtius hippoglossoides*, *Rostroraja alba*, *Salmo*

177   *salar*, *Salmo trutta*, *Sardina pilchardus*, *Scomber scombrus*, *Scophthalmus maximus*, *Scophthalmus*

178   *rhombus*, *Scyliorhinus canicula*, *Scyliorhinus stellaris*, *Sebastes* spp., *Solea solea*, *Sprattus sprattus*,

179   *Squalus acanthias*, *Squatina squatina*, *Trachurus picturatus*, *Trachurus trachurus*, *Trachyrincus scabrus*,

180   and *Trisopterus esmarkii*.

181   **Location-related keywords:** Belgium, Canada, Denmark, Estonia, Finland, France, Germany, Iceland,

182   Ireland, Latvia, Lithuania, Netherlands, Norway, Poland, Portugal, Russia, Spain, Sweden, United

183   Kingdom, United States of America, Northeast Atlantic, Atlantic Iberian, Biscay, English Channel, Bristol

184   Channel, North sea*, Irish sea*, Cantabrian sea*, Belt sea*, Bothnian sea*, Celtic sea*, Azores,

185   Skagerrak, Kattegat, Bornholm, Baltic, Gulf of Gdansk, Gulf of Riga, east Gotland, Faroe grounds,

186   Iceland grounds, Greenland, Rockall, Bothnian bay, Reykjanes Ridge, Dogger bank*, Viking bank*,

187   Bergen bank*.

188   **Negative (Excluded) keywords:** Biogenic reef*, eelgrass, mussel bed*, coral reef*, tropical, subtropical,

189   Australia, Mediterranean, Caribbean, Indian sea.

190   **Data extraction:**

191   Our primary question was: "What is the habitat importance of hard-bottom natural and artificial structures

192   for temperate fish species managed by ICES?" To answer this question, for each paper we determined

193   the studied habitat, the ecosystem type, and species targeted, as detailed below. We broke down habitat

194   importance into the following four main components: (1) distribution-related variables, (2) community-

195   related variables, (3) fitness-related variables, and (4) reproduction-related variables (see details below).

196   **Habitat importance:** Fish species receive numerous benefits from benthic habitats, such as food,

197   shelter, or spawning grounds. Such benefits may translate into measurable demographic variables (e.g.

198   growth, survival, biomass, spawning rates), which allow researchers to assess the importance of various

199   habitats. We initially grouped the data into the following four broad categories: (1) species distribution, (2)

200 community, (3) fitness, and (4) reproduction. Distribution-related variables included papers targeting diel

201 cycles, site fidelity, or migration patterns. Community-related variables included papers targeting fish

202 biomass, density, or biodiversity. Fitness-related variables included papers targeting condition, mortality

203 rates, growth, and feeding. Lastly, reproduction-related variables included papers targeting spawning

204 habitats, nursery potential, and settling (both of adults to newly formed habitats or of juveniles).

205 **Ecosystem type:** A species' ecological niche may encompass different ecosystems. Therefore, we

206 targeted coastal marine environments and transitional areas, such as fjords and estuaries. Though we

207 excluded biogenic reefs, we did include literature that dealt with macrophyte cover in temperate regions.

208 **Target species:** To improve future fisheries management, this review included fish species targeted for

209 advice by the International Council for the Exploration of the Sea (ICES). Targeted species are listed

210 above in "Species-related keywords."

211

212 **Results & Discussion**

213 Our study indicates that hard-bottom substrates may benefit multiple fish groups, such as elasmobranchs

214 (e.g. Martin et al., 2012; Rodríguez-Cabello et al.,2008), gadoids (e.g. Reubens et al., 2014 b; Ross,

215 Rhode, and Quattrini, 2015; van Hal et al., 2017), and other teleosts such as seabass (Dicentrarchus

216 labrax; Leitão et al., 2008). Furthermore, hard substrates serve as: (1) stepping stones, where species

217 may find shelter during migration events (Gascon and Miller, 1982), (2) spawning grounds for demersal

218 eggs (Johannessen, 1986), (3) settlement grounds for young fish migrating out of nurseries (Santos et al.,

219 2005), (4) foraging areas with increased prey densities (Leitão et al., 2008b) or (5) new home ranges,

220 with newcomers developing high site fidelity rates, as observed for novel constructions such as marine

221 wind farms (Reubens et al., 2013).

222 **Review selection process**

223 The search process returned an initial 2,651 papers, paring down to 2,333 papers after exclusion of

224 duplicate references. Of those, 45 papers were returned after the subsequent screening criteria and were

225 examined for full-text data extraction (as detailed below and in Fig. 1).

226 **Title analysis:** The title reviewing process led to the exclusion of 2036 papers (87% of the initial 2333),

227 leaving 297 papers for abstract analysis. Most of the exclusions (54%) represented off-topic papers

228 dealing with, for example, energy production, aquaculture, human health, oil spills, or physiology.

229 Additionally, 35% of the excluded papers were explicitly related to non-target organisms (e.g. zebrafish,

230 rainbow trout, invertebrates). A total of 9.5% excluded papers either studied non-target locations or other

231 ecosystems (e.g. Hawaii or soft-bottom ecosystems, respectively). Lastly, 1.4% of the excluded titles

232 either did not correspond to peer-reviewed papers or were not written in English.

233 **Abstract analysis:** From the 297 analysed abstracts, a total of 136 failed to comply with the inclusion

234 criteria (46%), leaving 161 papers for full text analysis. Most of the exclusions represented papers related

235 to non-target species (32%), followed by papers that did not relate to the target topics (25%). A total of

236 30% excluded papers either studied non-target locations or other ecosystems. Additionally, 13% of the

237 analysed search results were not peer-reviewed literature.

238 **Full text analysis:** From the 161 full texts analysed, 116 (72%) did not comply with the exclusion criteria.

239 Most of the papers were excluded based on location (49%), corresponding mostly to studies targeting

240 rockfish in the Pacific Ocean. A total of 21% exclusions represented papers related to non-target species,

241 while 13% studied non-target ecosystems and 7% did not relate to the target topics. A total of 11 papers

242 were excluded for "other" reasons: four were not peer-reviewed, four were reviews, and for three it was

243 not possible to obtain a full text version of the document. Therefore, the review focused on 45 studies

244 distributed along the Baltic and North Seas and northern Atlantic Ocean (Fig. 2). We quantified the

245 numbers of papers or percentage of papers reviewed as a function of the various response variables

246 emphasized.

247 **Papers reviewed as a function of response variables emphasized**

248 Distribution-related variables (i.e., diel cycle, site fidelity, migration) were studied in six papers (13.4%).

249 These targeted primarily site fidelity and migration patterns of Atlantic cod (*Gadus morhua*; e.g. Reubens

250 et al., 2014 a, b).

251 Community-related variables (i.e. density, biodiversity, biomass) were the most frequently studied

252 amongst the papers reviewed, being analysed in two thirds of the studies (Fig. 3). Most research targeted

253   a few species (i.e. Atlantic cod, herring [*Clupea harengus*], and saithe [*Pollachius virens*]) and a limited

254   set of variables (i.e. biomass, density, biodiversity, and feeding). Cod was the species most commonly

255   studied in community-related (i.e., density, biodiversity, biomass) studies (Table 2).

256   Fitness-related variables (i.e. condition, mortality, growth, feeding) were studied in 17 papers (38% of the

257   total number of analysed papers). Feeding was studied primarily on cod and saithe, showing a tendency

258   for fish use of hard-bottom habitats for foraging (Fig. 4; e.g. Johannessen, 1986; Malek et al., 2016;

259   Wennhage and Pihl, 2002). Interestingly, with the exception of cod, little research has been carried out on

260   the remaining fitness-related variables (Table 2).

261   Reproduction-related variables (i.e. spawning, settling, nursery) were studied in six papers (13.4%).

262   Spawning was studied primarily on herring and cod, with papers on nursery and settling being almost

263   absent for other species in the reviewed literature (Table 2). From the species targeted in our review,

264   hard-bottom substrates appeared to be of particular importance for herring spawning (Aneer and

265   Nellbring, 1982; Johannessen, 1986; Kääriä et al., 1997; Šaškov et al., 2014).

266   There was a clear predominance in the study of community-related variables in the analysed research

267   (Fig. 3). Broadening the scope of studied variables and targeted species may prove essential to fully

268   understand the relationships of hard-bottom reefs with commercially important species. For example,

269   more quantitative research at the community level reveals the value of hard-bottom habitats for fish

270   populations (essential fish habitat, *sensu* Valavanis, 2008; or effective habitat, *sensu* Dahlgren et al.,

271   2006), and integrating this information into assessment and management may provide considerable

272   advances towards ecosystem-based fisheries management (e.g., fish production estimates that can be

273   monetized).

274   **Ecosystems explored**

275   Research was nearly equally distributed across natural and artificial reef structures, with 26 and 27

276   papers related to each, respectively, and eight targeting both natural and artificial structures

277   simultaneously (Fig. 4, Table 3). Furthermore, 21 papers (46.7%) that resulted from our search performed

278   comparisons of hard-bottom habitats with soft-bottom habitats. The review indicated that different regions

279   of the world have different research foci. All papers on the north-western shore of the Atlantic Ocean

280 focused on natural reefs, with one paper also targeting an intentional artificial reef (Fig. 5). Similarly, there

281 was a greater focus on natural reef research in the Baltic Sea, with nine out of eleven papers targeting

282 natural reefs, as well as three papers targeting artificial *de facto* reefs, and only one paper targeting

283 intentional artificial reefs. Conversely, in the North Sea, only 3 out of 15 papers targeted natural reefs,

284 while 14 targeted *de facto* artificial reefs (most of which explored the effects of wind farms). Finally, on the

285 north-eastern coast of the Atlantic Ocean, there were nearly equal numbers of papers on natural and

286 artificial reef research (six and five papers, respectively, plus two papers that targeted both reef types

287 simultaneously). However, of the papers targeting artificial reefs, only one studied *de facto* artificial reefs,

288 while the remaining explored artificial intentional artificial reefs. There was a noticeable paucity of studies

289 in the northern regions. Additionally, most of the analysed research has been conducted near-shore.

290 Broadening the scientific knowledge on the importance of different habitats, areas, and regions along a

291 depth gradient away from shore may provide crucial insights for future management.

292 **Frequently studied species**

293 There has been a consistent research effort towards multiple morphological and behavioural aspects of

294 cod, with this species being researched twice as frequently as herring, the second-most-researched

295 species (25 vs 12 papers, respectively; Table 2). Furthermore, while research on cod and herring is

296 spread across the four groups of ecological variables considered in our review (i.e. species distribution,

297 community, fitness, reproduction), research is lacking for most reviewed species on variables not related

298 with community (e.g. condition, settling, site fidelity; Table 2).

299 The presence of hard-bottom habitat was associated with enhanced biomass in cod and saithe and,

300 conversely, was negatively associated with biomass in herring and whiting (*Merlangius merlangus*; Fig.

301 6). Most papers compared fish densities in multiple habitats, and higher densities of cod on hard-bottom

302 habitats were demonstrated in several papers, with only one paper suggesting fewer cod on hard-bottom

303 compared to adjacent soft-bottom habitats. Both positive and negative relationships of hard-bottom

304 habitats with density were demonstrated for herring, saithe, striped red mullet (*Mullus surmuletus*),

305 whiting, pollock (*Pollachius pollachius*), plaice (*Pleuronectes platessa*), and sole (*Solea solea*). Cod,

306 herring, saithe, striped red mullet, whiting, and pollock appeared to benefit from foraging on hard-bottom

307   habitat (i.e. for plaice feeding, only negative relationships of hard-bottom habitats were reported, as plaice

308   feed less frequently over hard-bottom habitats). Few papers targeted spawning on hard-bottom habitats,

309   and those that did reported associated benefits for cod and herring.

310   **Changes in fish distribution**

311   Research has demonstrated positive effects of the presence of hard-bottom substrates on cod biomass

312   and density (e.g. Krone et al., 2013; Pihl and Wennhage, 2002). With a few exceptions, natural hard-

313   bottom habitats and artificial reefs harbor significantly higher abundances of fish than adjacent

314   unstructured habitats (Rodríguez-Cabello et al., 2008; Fujii, 2016). Fish movement patterns reflected

315   relatively high site fidelity to structures (e.g. Hartman, 1987; Reubens et al., 2014 a, b), and the stomach

316   contents of fish residing on reefs (excluding biogenic reefs) reflected the prey assemblages associated

317   with the reefs (e.g. Reubens et al., 2014a), suggesting extended residency and foraging in the reef areas.

318   Interestingly, catch per unit effort (CPUE) of cod was greater adjacent to wind farms than in shipwrecks in

319   the Belgian part of the North Sea (Reubens et al., 2014b), suggesting attraction towards wind farms. It is

320   important to note that the studied wind farms were closed to fisheries, while the shipwreck sites had no

321   fisheries restrictions, possibly biasing the comparison.

322   Gadoids such as saithe, haddock (*Melanogrammus aeglefinus*) and cod were the most common species

323   at the "Miller" oil and gas platform, in the North Sea (Fujii, 2016). Cod abundance was approximately four

324   times higher at the platform than in nearby shipwrecks or sandy bottom. Using trawl data, Martin et al.

325   (2012) modeled distributions of ten demersal elasmobranchs of the eastern English Channel in relation to

326   the environment, with female small-spotted catshark (*Scyliorhinus canicula*) occurring at higher densities

327   on hard substrate.

328   Within four years after the deployment of artificial reefs in an area previously closed to trawl fisheries in

329   the Bay of Biscay, there was a rapid increase in the biomass of small-spotted catshark (Rodríguez-

330   Cabello et al., 2008). Importantly, four to eight years after deployment, axillary sea-bream (*Pagellus*

331   *acarne*), horse mackerel (*Trachurus trachurus*), and striped red mullet demonstrated the most significant

332   increases in biomass. The observation that horse mackerel responded positively to the addition of

333   artificial reefs demonstrates that schooling pelagic species may also benefit from these hard-bottom

334   habitats.

335   Reefs (excluding biogenic reefs) may also enhance economic returns. For example, in one location,

336   reefs near Algarve and Faro, Portugal, raised catch rates and economic returns (Neves Santos and Costa

337   Monteiro 1998). Specifically, CPUE at the reefs exceeded CPUE at the control sites by a factor of 2.03 –

338   2.28 for the protected reef and by a factor of 1.11 – 1.86 for the exploited reef. In some artificial reef

339   systems, the economic return per unit of effort was higher at the reefs than at the control sites. Fishing on

340   artificial reefs would be expected to yield 2.2 times the economic return compared to the control sites

341   (Neves Santos and Costa Monteiro 1998). The productivity of reefs increased throughout the 15-year

342   period, implying that the interaction between the hard substrate and the marine environment may take

343   many years to produce the full effects on the carrying capacity (Whitmarsh et al., 2008). A distinct spatial

344   pattern of fishing activity around the reefs was detected, with a concentration of fishing gear on the

345   periphery of the reef area and a lower gear density at farther distances. A concentration of fishing gear

346   nearby the reef would suggest that the improved fishing opportunities offered by the reefs have been

347   recognized by fishermen. Fishermen likely take advantage of the spill-over of fish from the reefs,

348   consistent with recent studies (Rosemond et al., 2018).

349   The inclusion of quantitative data on hard-bottom habitats in the monitoring of fish populations may

350   further resolve a mismatch between fish population assessments and catches in fisheries of several fish

351   species with a patchy distribution due to their high affinity for hard-bottom habitats (e.g. cod; Wieland et

352   al., 2009). The mismatch between fish population assessments and catches of fish species with a patchy

353   distribution may be further exacerbated during stock recovery, where the most suitable habitats (i.e. hard

354   bottoms) will be populated first according to the ideal free distribution theory of MacCall (1990).

355   Not all fish species benefit from hard-bottom or marine constructed structures. Neutral or negative

356   relationships with biomass and density were recorded for flatfish such as plaice (*Pleuronectes platessa*)

357   and sole (*Solea solea*), as well as for whiting (*Merlangius merlangus*). For example, Støttrup et al. (2014)

358   found decreasing densities of sole post restoration of a natural reef, and Bergström et al. (2013) only

359   found whiting before the implementation of a wind farm. Neutral or negative relationships with hard-

360   bottom habitat for some species reflects the preferred habitat of the different species, with both flatfish

361   and whiting occurring primarily on soft-bottom habitats (Stål et al., 2007).

362   The rapid growth of offshore wind farms, coupled with the high abundance and biomass of fish associated

363   with wind farms, suggest that these *de facto* marine protected areas (MPAs) could be relatively easy to

364   enforce, serve as broodstock sanctuaries that benefit fished populations, and optimize use of the seafloor

365   (Fowler et al., 2018). Moreover, the economic impact of artificial reefs also appears high relative to

366   unstructured control sites. Although the potential positive relationships of artificial reefs with fish

367   populations are encouraging, it is important to recognize the attraction effect of artificial reefs and how

368   such a process can facilitate overfishing (Bohnsack, 1989; Smith et al., 2015, and references therein).

369   Artificial reefs, however, can also enhance growth and survival, for example by providing hard substrate

370   for sessile fouling communities that provide food to fish (Todd et al., 2018). Quantitative evidence may

371   also guide modeling efforts to assess the role of artificial reefs on population dynamics of exploited

372   species. Lastly, given that unstructured seafloor (i.e. flat, soft-bottom habitat) can be many orders of

373   magnitude greater in areal footprint than artificial reefs, it is important to recognize that unstructured

374   habitats can serve as effective juvenile habitat (*sensu* Dahlgren et al., 2006) for exploited fishery species.

375   Unstructured habitat is especially important for species for which ICES gives advice. For example, in

376   comparing coastal habitat use among various structured (e.g. seagrass, kelp, marsh) and unstructured

377   habitats, subtidal soft-bottom was the habitat used as a spawning or nursery area by the largest

378   proportion of ICES species examined, with intertidal soft-bottom habitat as the next most important

379   habitat (Seitz et al., 2014).

380   **Habitat heterogeneity enhances biodiversity**

381   Overall, both natural and artificial hard-bottom or reef structures tend to have a high attraction potential

382   and house densities of fish superior to surrounding habitats (e.g. Bergström et al., 2013; Støttrup et al.,

383   2014; Whitmarsh et al., 2008). In one study, natural structured habitats (rock, shell, rubble) compared to

384   bare sand had positive effects on density, growth, and survival of juvenile fishes and invertebrates, with a

385   greater positive effect for arthropod invertebrates than vertebrates (Lefcheck et al., 2019). When man-

386   made structures are placed on surrounding soft-bottom areas (e.g. wind turbine foundations, oil

387 platforms), they represent beacons of habitat heterogeneity that are capable of attracting new residents

388 (Gascon and Miller, 1982; Stenberg et al., 2015; Castège et al., 2016; Fujii, 2016). For example, cod

389 appears to have a clear affinity for hard-bottom substrates, with increased fish densities and/or biomass

390 near natural hard-bottom reefs (Stål et al. 2007; Støttrup et al. 2017; Kristensen et al. 2017), offshore

391 wind farms (Bergström et al., 2013; Reubens et al., 2013; van Hal et al., 2017), oil-platforms (Fujii, 2015),

392 shipwrecks (Wieland et al., 2009; Krone et al., 2013) and other man-made structures (Langhamer and

393 Wilhelmsson, 2009; Wehkamp and Fischer, 2013). Similarly, pollock generally restricted its movement to

394 a submerged reef area in Loch Ewe, Scotland, while saithe ranged more widely during daytime and

395 returned to the reef during night-time (Sarno et al., 1994). Specific age groups of cod and pouting

396 (*Trisopterus luscus*) can have high residency and site fidelity to the bases of marine wind turbines,

397 feeding on the dominant epifaunal prey growing on these introduced habitats (Reubens et al., 2014a, b).

398 Different species react differently to the addition of hard-bottom substrates, and recent literature reports

399 on various outcomes even within a species. For example, whiting can occur in relatively high abundance

400 on hard substrates (e.g. shipwrecks and offshore wind farms; Krone et al., 2013; Lindeboom et al., 2011;

401 Pihl and Wennhage, 2002), as well as on soft substrates (Stål et al. 2007; van Hal et al. 2017).

402 Additionally, in some cases, the attraction of reef-associated demersal fish species such as bogue (*Boops*

403 *boops*), horse mackerel, and axillary sea-bream may make them more vulnerable to predation, as the

404 probability of prey–predator encounters increases compared to unstructured habitats (Leitão et al. 2008).

405 Lastly, some commercially important species, such as dab (*Limanda limanda*) and sole, may avoid rocky

406 substrates, with decreasing abundances whenever there is a shift from soft to hard bottom (van Hal et al.

407 2017). Thus, the relationship of hard-bottom structures with fish distribution and abundance patterns in

408 the North Sea and Baltic Sea are species-dependent, a factor that must be considered during

409 management and restoration actions.

410 **Improved fitness and reproduction capacity**

411 Selection by fish for complex, hard-bottom habitats generally improved fitness in those species occupying

412 these habitats. Enhanced foraging opportunities improved condition in cod and pouting when occupying

413 wind farm areas (De Troch et al., 2013). However, this is not always the case. For example, Mathers et al.

414   (1992) examined growth rates in saithe using biochemical indicators and found no differences in growth

415   rates on an oil platform as compared to the open sea. Further, while pouting condition was enhanced in a

416   wind farm area relative to sandy areas, condition of cod was similar in both habitat types (Reubens et al.,

417   2014b). The similar growth rates or condition of fish on oil platforms or wind farms compared to

418   unstructured areas suggests that although production was evident on a local scale (i.e. wind farm

419   foundations), this may have had little effect on the larger spatial scale (i.e. the Belgian part of the North

420   Sea). In a related example, oil and gas platforms in the North Sea provided unique feeding grounds for

421   commercially important gadoids such as cod, saithe, and haddock (Fujii, 2016). For example, haddock

422   predominantly consumed ophiuroids that occurred in high abundances on platforms at all depths,

423   whereas temporal changes in the presence and abundance of saithe reflected the occurrence and

424   availability of euphausiids (Fujii, 2016). These findings indicate that gadoids utilized the platform for

425   foraging.

426   A tagging study revealed that spawning activities of cod in the Gulf of Maine occurred around specific

427   bottom features, such as humps and ridges (Siceloff and Howell, 2013). Cod tended to move in groups

428   after spawning, as 14 of 26 tagged and recaptured cod shifted to deep water (>100 m) within 23 to 50

429   days after tagging, with females tending to leave before males. While these findings indicate that the

430   pelagic spawning of cod may be associated with large offshore hard-bottom structures, relatively shallow,

431   complex habitats with rocks and cobble may enhance survival among the juveniles after benthic settling

432   (Tupper and Boutilier, 1995).

433   A recent study highlighted the potential role of offshore oil and gas platforms as spawning sites for

434   lumpsucker (*Cyclopterus lumpus*; Todd et al., 2018). *C. lumpus* was observed during different stages of

435   reproduction on an offshore oil and gas structure in the North Sea, providing novel evidence of spawning

436   offshore at depths of around 40-45 m. Examples from the literature also show positive relationships of

437   hard-bottom habitats with spawning and recruitment for several fish species, with much of the relevant

438   literature coming from natural hard-bottom habitats. In a survey of natural hard bottoms in western

439   Norway, spawning of herring generally occurred on hard-bottom substrates down to a depth of 10 m, with

440   little evidence of spawning on soft-bottom habitats (Johannessen, 1986).

441   In the Baltic Sea, the vegetation usually attached to hard substrates seems to play an important role for

442   successful spawning of Baltic herring (*C. harengus membras*). In a survey of natural hard bottoms in the

443   northern Baltic Sea (Sweden), herring eggs were only found on filamentous algae (*Pilayella littoralis*)

444   attached to hard substrates (Aneer and Nellbring 1982) and not on the surrounding hard or soft bottoms.

445   Likewise, in the southwestern archipelago of Finland, Baltic herring spawning beds occurred in areas with

446   vegetation growing on hard bottoms (down to a depth of 4 m); usually close to the regions' deepest zones

447   (down to 60 m depth; Kääriä et al., 1997). The complex habitat established by the algae may provide

448   refuge from predators, as birds and other fish are responsible for a majority of the predation of herring

449   eggs (Aneer and Nellbring 1982). Areas without spawning beds generally had soft sediments with narrow

450   bands of vegetation. Filamentous green algae (*Cladophora* sp.), brown algae (*Ectocarpus* sp., *Pilayella*

451   sp.) and *Potamogeton pectinatus* made up the most common vegetation where divers observed eggs

452   (Kääriä et al. 1997). For Baltic herring spawning on the Lithuanian coast (eastern coast of the Baltic),

453   eggs were found on red algae *Furcellaria lumbricalis* and *Polysiphonia fucoides*, as well as hard habitat

454   covered with mussels at 4-8 m depth (Šaškov et al. 2014). The dependence of Baltic herring on

455   vegetation as substrate for the eggs may render this species vulnerable to pressures such as

456   eutrophication that negatively affect macroalgal growth.

457   Modeling studies can be informative in assessing the effects of habitat on recruitment success. One

458   model was used to assess the effects of MPAs on juvenile cod recruitment success (Lindholm et al.,

459   2001). MPAs can maintain habitat complexity (i.e. more pebble-cobble substratum) compared to areas

460   that are fished with dredges or trawls that damage the seafloor and reduce complexity (Ocean Studies

461   Board & National Research Council 2002). Modeled survival of juvenile cod on natural reefs showed that

462   survival was density-dependent (i.e. affected by predation or cannibalism; Wikan and Eide, 2004) and

463   increased with seafloor habitat quality (modeled as increased size of an MPA). Juvenile cod had higher

464   survival rates at low densities and in large MPAs, thus linking juvenile cod survival to seafloor habitat

465   complexity (Lindholm et al. 2001). Modeled improved survival associated with complex sea-floor habitats

466   is consistent with previous laboratory studies and may explain why various fish species prefer habitats

467   with gravel and cobble where they can find shelter in the crevices (Gotceitas and Brown 1993;

468   Christoffersen et al. 2018).

469   The review process that we used did not include all commercially important species, but rather was

470   targeted towards species important for management by ICES, and we only examine temperate, non-

471   biogenic reefs. The results from our study are limited to those specific species and the physical structure

472   provided by hard-bottom, non-biogenic habitats. Our search terms were very specific and we

473   acknowledge that this approach may have missed relevant research from habitats that we excluded.

474   Therefore, interpretations of these data apply only to the species and habitats we incorporate.

475   **Recent Case Studies**

476   Although the literature for this study was not reviewed beyond those papers published in early April 2017,

477   a related study reviewing methods that have examined the nursery role of different habitats included

478   search terms relevant to hard-bottom habitats and fishery species of interest to ICES (Ciotti et al., in

479   prep.). We highlight several recent case studies below that reflect this updated literature review. In the

480   first example (Elliott et al. 2017), stereo baited remote underwater video (SBRUV) surveys were

481   conducted in the nearshore, Scottish waters of the Firth of Clyde during summer 2013 and 2014 to

482   determine the habitat of juvenile Atlantic cod, haddock and whiting. The fishery stocks of all three species

483   declined in the late 20th century, and recruitment and spawning stock biomass remains relatively low in

484   the Firth of Clyde despite efforts to re-build the stocks (Fernandes and Cook 2013, Holmes et al. 2014,

485   ICES 2016a,b,c). Understanding juvenile gadoid habitat is particularly important given that settlement and

486   post-settlement survival is thought to be the best means to understanding gadoid population regulation

487   (Olsen and Moland 2011, Laurel et al. 2016). Atlantic cod were most abundant in shallow, sheltered areas

488   composed of gravel−pebble containing maerl. Haddock and whiting predominated over deeper sand and

489   mud. Relative abundances of Atlantic cod and whiting were positively related to the diversity of epibenthic

490   and demersal fauna. Thus, spatial conservation measures to benefit demersal fish should consider

491   habitat type and diversity (Elliot et al. 2017).

492   Another case study examined the environmental benefits of leaving de-commissioned

493   offshore infrastructure, such as oil and gas platforms and wind turbines, in the ocean due to benefits such

494   as biodiversity enhancement, provision of reef habitat, and protection from bottom trawling (Fowler et al.

495   2018). The rationale for this study was that the *in situ* ecosystem value of platforms and the negative

496   impacts of removal are not factored into decommissioning decisions in regions such as the North Sea,

497   where over 80% of oil structures are more than a decade old (OSPAR Commission 2017a) and are likely

498   integrated to at least some extent into existing ecosystems (Fowler et al. 2018). The removal policy is

499   based on the assumption that "leaving the seabed as you found it" will minimize negative impacts on the

500   marine environment. A total of 200 experts spanning academia, government, and private organizations

501   were sent surveys seeking their opinions on the following: (1) appropriateness of the current removal

502   policy, (2) identification of viable alternatives to complete removal of offshore infrastructure, (3) key

503   environmental considerations and trade-offs for decommissioning decisions, and (4) advice on

504   decommissioning considerations between platforms and wind turbines. Of most relevance to this review

505   of hard-bottom habitats, 78% of the 40 respondents thought that artificial habitats with environmental

506   value should be maintained and protected due to enhanced ecosystem services (Fowler et al. 2018).

507   Evidence includes harboring threatened species (Bell and Smith 1999), providing reef habitat (Coolen

508   2020), boosting recruitment of overfished species (Love et al. 2006), producing fish biomass at a greater

509   rate than any other marine ecosystem (by as much as a factor of ten; Claisse et al. 2014), and acting as

510   foraging sites for top-order predators (Todd et al. 2009). Fowler et al. (2018) concluded that the

511   traditional view that artificial structures must be removed from marine ecosystems simply because they do

512   not "belong" there has shifted to one of environmental optimization based on comparative assessment

513   (Fowler et al. 2015). Each decommissioning option will have positive and negative impacts that must be

514   carefully weighed, while also accounting for site-specific characteristics and the broader environmental

515   context of the disturbance.

Conclusions and implications for management

517   Our systematic review has elucidated that Atlantic cod, the most frequently studied species of the group

518   of species managed by ICES, had increased biomass, density, feeding, and spawning associated with

519   hard-bottom habitats compared to unstructured habitats. Spawning of herring, was increased in hard-

520   bottom habitats, which appear to be of importance for this species. We detected that most research was

521   conducted on Atlantic cod, herring, and saithe, and the most commonly studied variables included

522   biomass, density, biodiversity, and feeding. Cod was the species most commonly studied, and studies

523   were mostly on community-related variables (i.e., density, biodiversity, biomass). However, not all

524   responses to the presence of hard-bottom habitat were positive. For herring, saithe, striped red mullet,

525   whiting, pollock, plaice, and sole, we quantified positive and negative relationships between fish density

526   and hard-bottom habitats. Thus, we achieved our goal of summarizing the existing information on ICES-

527   managed fish species and their use of temperate hard-bottom habitats. This information should help

528   inform scientists interested in the ecological function of hard-bottom habitats for some key fish species,

529   and inform managers and conservation groups focused on coastal habitats of the potential importance of

530   hard-bottom habitats to certain fish species.

531   Natural hard-bottom reefs, if removed or destroyed, can only be restored by human intervention. Thus, it

532   would be wise if management focuses on protecting natural reefs and finding the most cost-effective

533   solutions for restoring reefs. In support of ecosystem-based fisheries management, research should

534   provide additional scientific information on the value of hard-bottom habitats for biodiversity or for

535   individual species on a local, national and regional scale. While this information is slowly being produced

536   (e.g. Christoffersen et al., 2018; Liversage and Benkendorff, 2013; Liversage et al., 2017), the economic

537   value of hard-bottom habitats remains largely unknown. This is in contrast to other complex marine

538   habitats (e.g. eelgrass) where several recent studies have estimated the annual economic values per

539   area (McArthur and Boland, 2006; Tuya et al., 2014; Cole and Moksnes, 2016). Similar economic

540   valuation studies are needed for hard-bottom habitats, so that policy makers may assess the economic

541   importance of protective measures related to these habitats. In areas where hard-bottom habitat has

542   been removed or destroyed, consideration should be given to the economic and ecological benefits or

543   disadvantages of removing decommissioned marine structures (e.g. Fowler et al., 2018). These

544   structures could be equated to shipwrecks that become *de facto* reefs and are generally not removed.

545   The value of reef habitats and the need for their protection ultimately depends on the occurrence of that

546   habitat type in the area/region and the potential for hard-bottom habitats to represent value as a resource.

547   For example, in Denmark, although the extraction of boulders and larger stones from reef areas has

548   ceased, extraction of smaller stones or gravel continues to take place, even though these hard bottom

549   types are important habitats for juvenile eel and cod (Gotceitas et al., 1995; Christoffersen et al., 2018).

550 Research should provide the necessary information to allow for an effective restoration of the functions of

551 destroyed reefs. Studies are increasingly investigating restoration methodologies for hard-bottom reefs

552 (Støttrup et al., 2017; Liversage and Chapman, 2018). However, the currently available information is

553 insufficient to conduct a restoration program that is not, in itself, explorative. From a cautionary

554 standpoint, we recommend that anthropogenic activities degrading hard-bottom habitats should be

555 carefully considered, and weighed against the accumulating evidence that highlights the importance of

556 various hard-bottom habitats for several commercially important species.

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Admission/exclusion criteria

Admission/exclusion criteria for hard-bottom review

1   Table 1: Admission/exclusion criteria

Criteria	Include	Exclude
Peer-reviewing	Peer-reviewed	Everything else
Text Language	English	Everything else
Ecosystem	Natural and artificial hard-bottom reefs in marine or contiguous salt water environments (i.e. fjords and estuaries)	Biogenic reefs or other structures placed at non-marine environments
Target species	Fish species managed by ICES	No fish species managed by ICES present
Location	North hemisphere, temperate zone (not including Mediterranean Sea)	Mediterranean Sea, everything else
Type of study	Field studies	Everything else

Total number of papers (no parentheses) and percentage of papers in relation to the total of papers (in parentheses) for each of the top eight fish species that were most commonly selected in our review, in relation to the different ecological variables o

The groups of variables are delineated by the grey horizontal lines: community-, fitness-, reproduction- and distribution-related (from top to bottom; terms defined in the Materials & Methods section). In the "Total" column, the percentage of papers is shown in relation to the total number of papers reviewed (i.e. 45). Note that any given paper may simultaneously target more than one species and/or variable. Most research has targeted few species (i.e. cod, herring, and saithe) and a limited set of variables (i.e. biomass, density, biodiversity, and feeding). Full genus names given in "Species-related keywords" section.

1   Table 1: Total number of papers (no parentheses) and percentage of papers in relation to the total of papers (in parentheses) for each of the top
2   eight fish species that were most commonly selected in our review, in relation to the different ecological variables of interest in the review. The
3   groups of variables are delineated by the grey horizontal lines: community-, fitness-, reproduction- and distribution-related (from top to bottom;
4   terms defined in the Materials & Methods section). In the "Total" column, the percentage of papers is shown in relation to the total number of
5   papers reviewed (i.e. 45). Note that any given paper may simultaneously target more than one species and/or variable. Most research has
6   targeted few species (i.e. cod, herring, and saithe) and a limited set of variables (i.e. biomass, density, biodiversity, and feeding). Full genus
7   names given in "Species-related keywords" section.

	G. morhua	*C. harengus*	*P. virens*	*M. surmu.*[a]	*M. merlangus*	*P. pollachius*	*P. platessa*	*S. solea*	Total
Biomass	3(12)	1(8.3)	1(9.1)	3(30)	3(30)	2(22.2)	1(11.1)	0(0)	6(13.3)
Density	15(60)	6(50)	5(45.5)	7(70)	7(70)	6(66.7)	7(77.8)	5(62.5)	24(53.3)
Biodiversity	6(24)	4(33.3)	5(45.5)	7(70)	6(60)	5(55.6)	5(55.6	7(87.5)	15(33.3)
Condition	3(12)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	3(6.7)
Mortality	2(8)	2(16.7)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	3(6.7)
Growth	1(4)	0(0)	1(9.1)	0(0)	0(0)	0(0)	0(0)	0(0)	2(4.4)
Feeding	8(32)	2(16.7)	4(36.4)	1(10)	1(10)	2(22.2)	2(22.2)	0(0)	12(26.7)
Spawning	1(4)	4(33.3)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	5(11.1)
Nursery	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Settling	1(4)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	1(2.2)
Diel cycle	4(16)	1(8.3)	2(18.2)	1(10)	1(10)	2(22.2)	1(11.1)	1(12.5)	4(8.9)
Site fidelity	3(12)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	3(6.7)
Migration	1(4)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	1(2.2)
Total	25(55.6)	12(26.7)	11(24.4)	10(22.2)	10(22.2)	9(20)	9(20)	8(17.8)	45

8   [a] *Mullus surmuletus*

Distribution of papers per fish species and different hard-bottom structures.

Artificial reefs are further split into intentional and de facto reefs, with de facto reefs further subdivided into the various structures that form de facto reefs. "Other" includes wave-energy foundations and coastal-protection structures (i.e. riprap and breakwater tetrapods). The percentage of papers in relation to the total of papers for each species is shown in the brackets. In the "Total" column and row, the proportion of papers is shown in relation to the total number of papers reviewed (i.e. 45). Note that any given paper may simultaneously target more than one species and/or more than one hard-bottom structure. Overall, data shows an even distribution of research between natural and artificial reefs, despite the spatial patterns noted in Figure 4. Full genus names given in "Species-related keywords" section.

1   Table 1: Distribution of papers per fish species and different hard-bottom structures. Artificial reefs are further split into intentional and *de facto*

2   reefs, with *de facto* reefs further subdivided into the various structures that form *de facto* reefs. "Other" includes wave-energy foundations and

3   coastal-protection structures (i.e. riprap and breakwater tetrapods). The percentage of papers in relation to the total of papers for each species is

4   shown in the brackets. In the "Total" column and row, the proportion of papers is shown in relation to the total number of papers reviewed (i.e. 45).

5   Note that any given paper may simultaneously target more than one species and/or more than one hard-bottom structure. Overall, data shows an

6   even distribution of research between natural and artificial reefs, despite the spatial patterns noted in Figure 4. Full genus names given in

7   "Species-related keywords" section.

	G. morhua	C. harengus	P. virens	M. surmu.[a]	M. merlangus	P. pollachius	P. platessa	S. solea	Total
Natural Reefs	12(48)	9(75)	9(81.8)	5(50)	5(50)	7(77.8)	5(55.6)	3(37.5)	26(57.8)
Artificial Reefs	18(72)	4(33.3)	7(63.6)	6(60)	7(70)	4(44.4)	6(66.7)	7(87.5)	27(60)
Intentional	3(12)	1(8.3)	3(27.3)	2(20)	1(10)	3(33.3)	1(11.1)	2(25)	8(17.8)
De facto	15(60)	3(25)	4(36.4)	4(40)	6(60)	1(11.1)	5(55.6)	5(62.5)	19(42.2)
Wind Farms	10(40)	3(25)	1(9.1)	3(30)	6(60)	0(0)	5(55.6)	5(62.5)	12(26.7)
Shipwrecks	3(12)	0(0)	1(9.1)	1(10)	1(10)	0(0)	1(11.1)	0(0)	4(8.9)
Platforms	2(8)	0(0)	3(27.3)	0(0)	0(0)	0(0)	0(0)	0(0)	3(6.7)
Other	3(12)	0(0)	0(0)	1(10)	0(0)	1(11.1)	0(0)	0(0)	4(8.9)
Total	25(55.6)	12(26.7)	11(24.4)	10(22.2)	10(22.2)	9(20)	9(20)	8(17.8)	45

8   [a] *Mullus surmuletus*

Figure 1

PRISMA flow diagram for our hard-bottom systematic review showing numbers of papers at different stages in the review.

PRISMA flow diagram for our hard-bottom systematic review showing numbers of papers at different stages in the review.
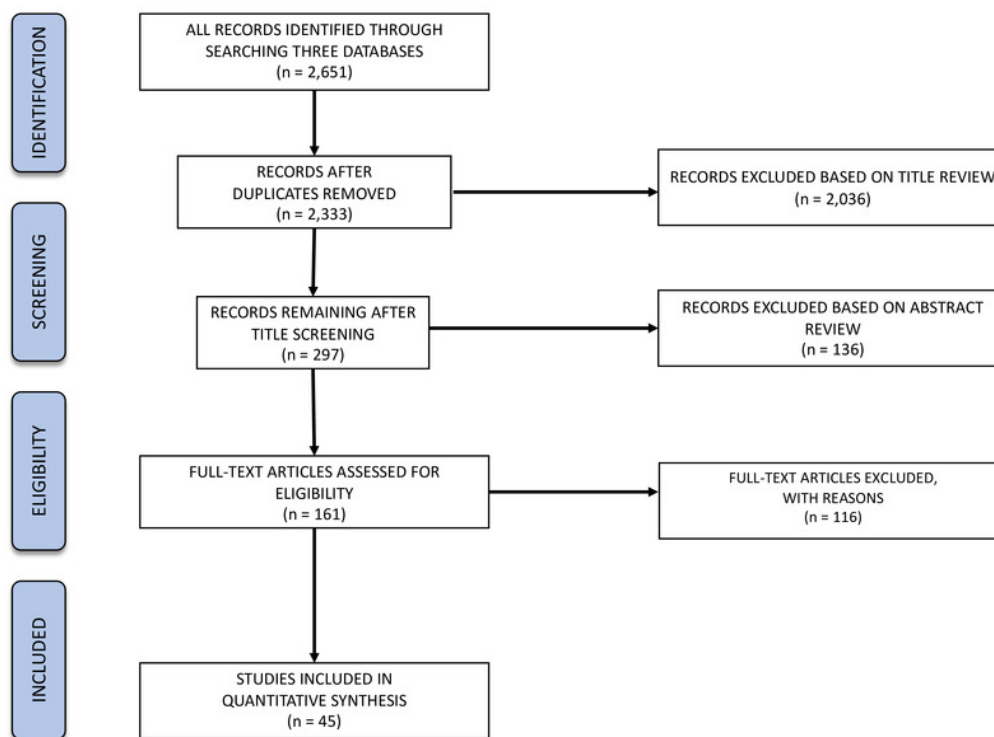
Figure 2

Geographical distribution of the papers that were included in the review.

Geographical distribution of the papers that were included in the review.
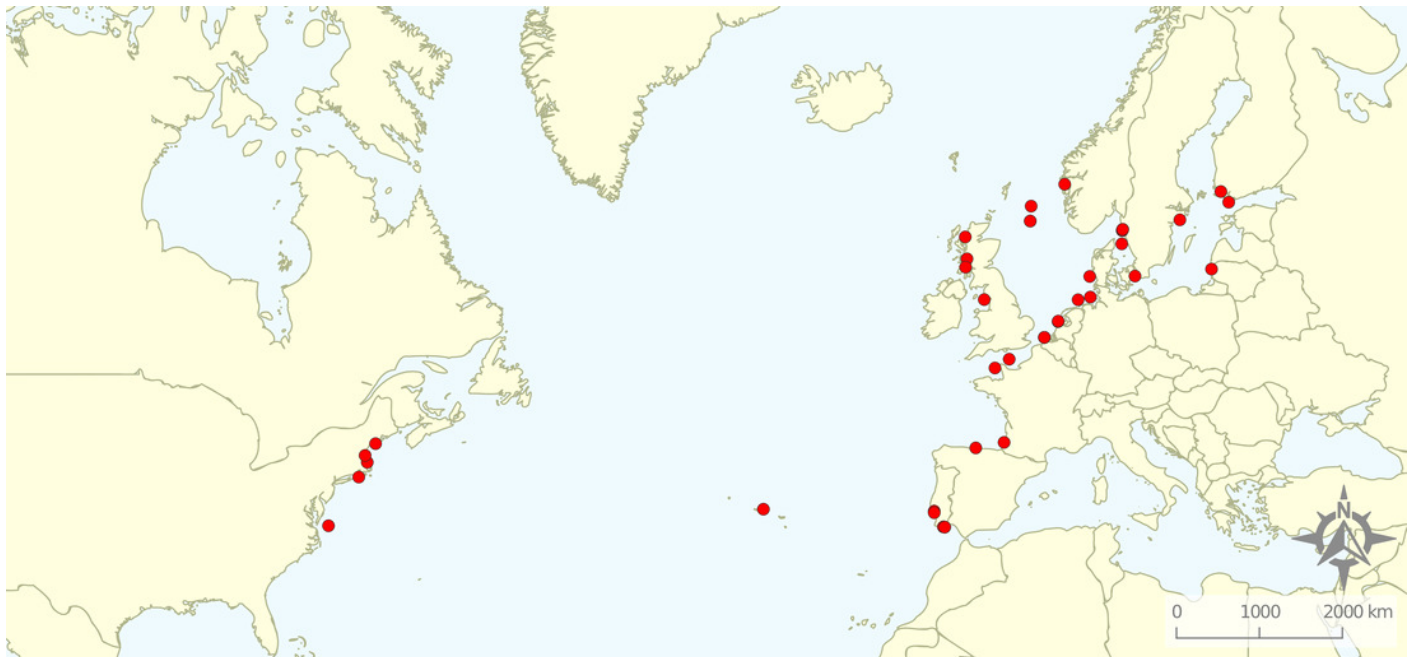
Figure 3

Number of papers targeting each of the ecological response variables recorded. Note that each paper may target more than one variable. Variables were grouped by colors, showing a clear dominance of community-related studies.

Number of papers targeting each of the ecological response variables recorded. Note that each paper may target more than one variable. Variables were grouped by colors, showing a clear dominance of community-related studies.
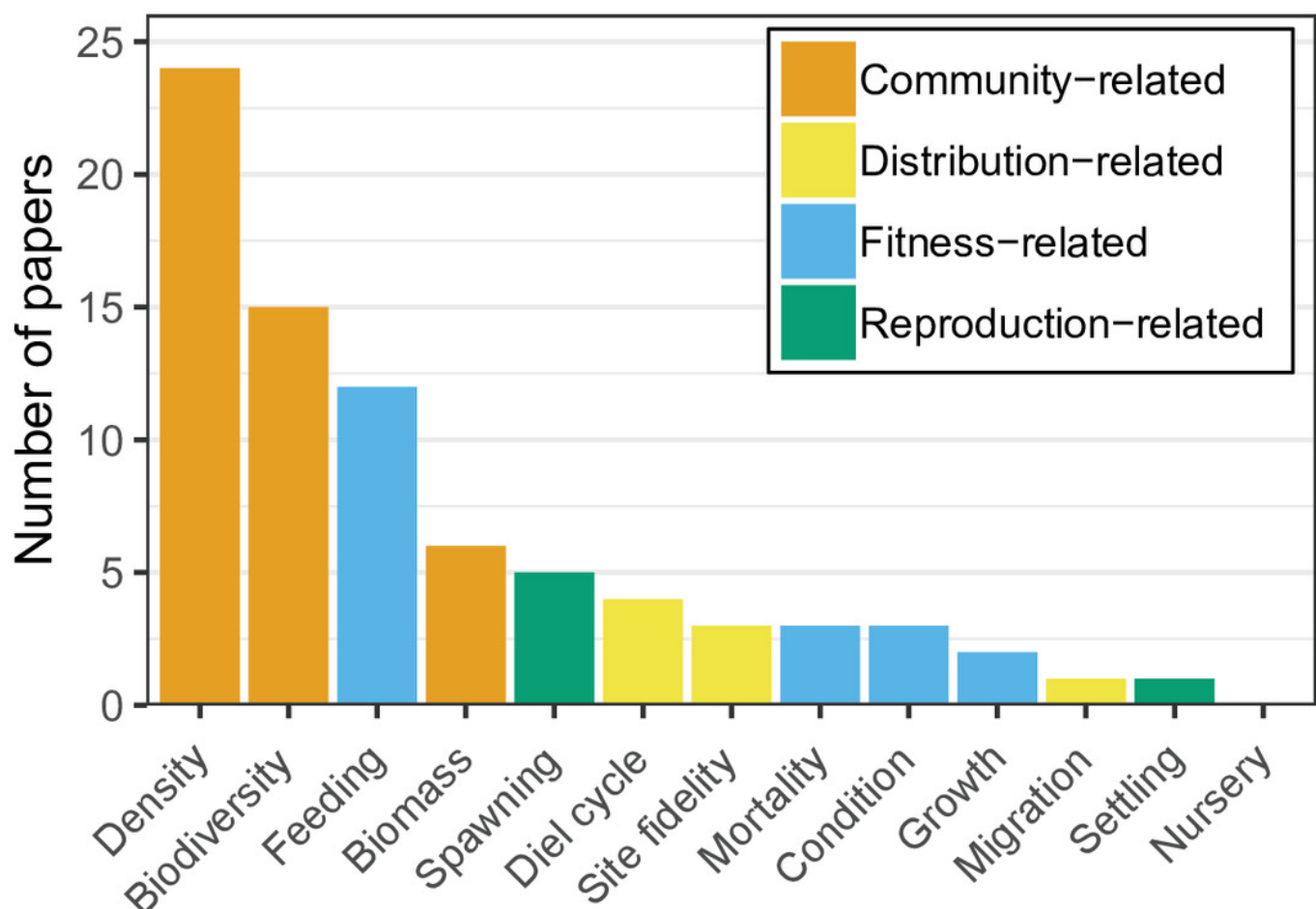
Figure 4

Number of papers targeting each of the studied hard-bottom substrates. Note that papers may target more than one topic simultaneously.
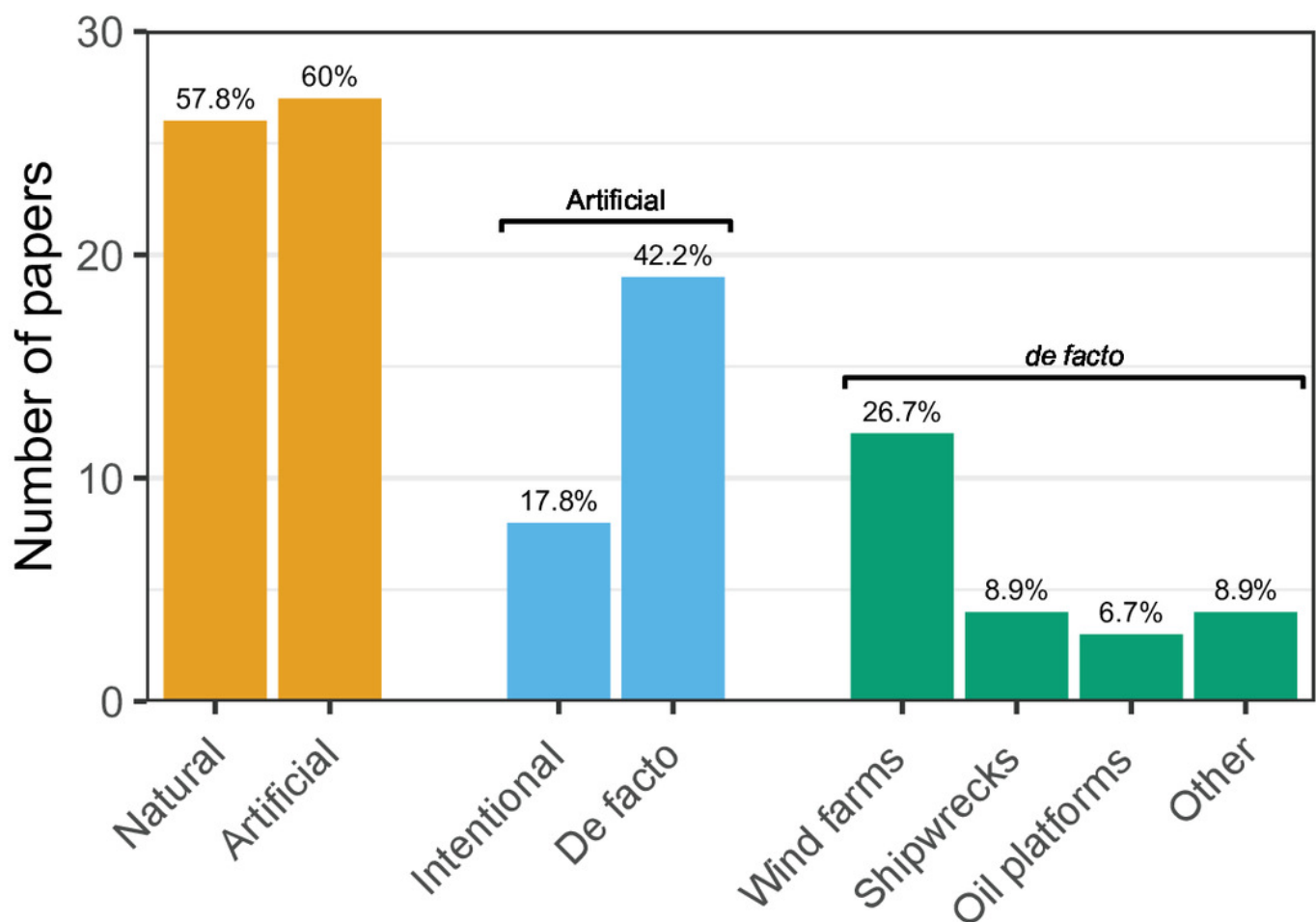
Figure 5

Distribution of papers with grouping of studied reef structures.

Distribution of papers with grouping of studied reef structures: natural reefs only (downward pointing green triangles); artificial reefs only (upward pointing blue triangles); both natural and artificial reefs (orange diamonds).
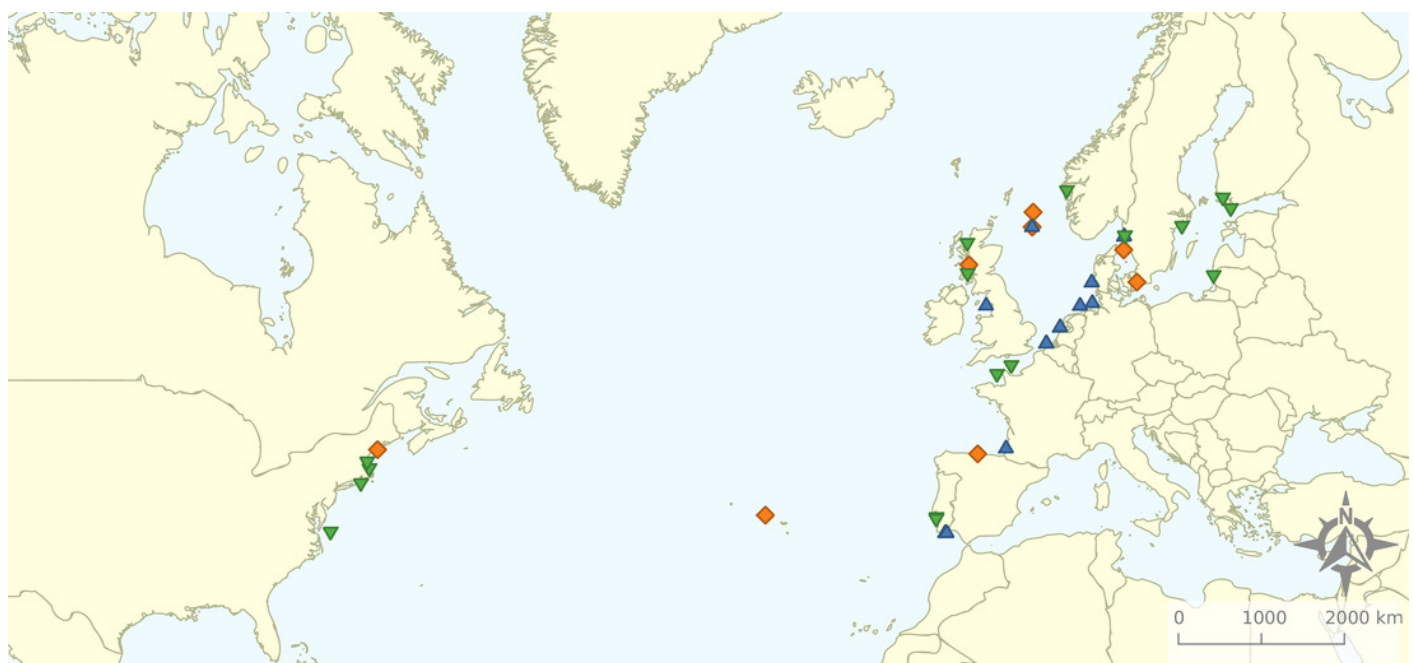
Figure 6

Effects of the presence of hard-bottom habitats on the most commonly studied variables.

Effects of the presence of hard-bottom habitats on the most commonly studied variables: biomass (B), density (D), feeding (F) and spawning (S), for the species most commonly targeted in recent research. Given the variety of methods used in literature the effects are listed as positive, neutral or negative. When no comparison was performed with a different substrate, the effect was considered unknown.