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RD Seitz
Virginia Institute of Marine Science

H Wennhage

U Bergstrom

RN Lipcius

T Ysebaert

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Contribution to the Themed Section: 'The Value of Coastal Habitats for Exploited Species'

Review

Ecological value of coastal habitats for commercially and ecologically important species

Rochelle D. Seitz[1]*, Håkan Wennhage[2], Ulf Bergström[3], Romuald N. Lipcius[1], and Tom Ysebaert[4,5]

[1]*Virginia Institute of Marine Science, College of William & Mary, PO Box 1346, Gloucester Point, VA 23062, USA*
[2]*Department of Aquatic Resources, Institute of Marine Research, Swedish University of Agricultural Sciences, Turistgatan 5, 453 30 Lysekil, Sweden*
[3]*Department of Aquatic Resources, Institute of Coastal Research, Swedish University of Agricultural Sciences, Skolgatan 6, 742 42 Öregrund, Sweden*
[4]*IMARES - Institute for Marine Resources and Ecosystem Studies, PO Box 77, 4400 AB Yerseke, The Netherlands*
[5]*Netherlands Institute for Sea Research (NIOZ), PO Box 140, 4400 AC Yerseke, The Netherlands*

**Corresponding author: tel: +1 804 684 7698; fax: +1 804 684 7399; e-mail: seitz@vims.edu*

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Many exploited fish and macroinvertebrates that utilize the coastal zone have declined, and the causes of these declines, apart from overfishing, remain largely unresolved. Degradation of essential habitats has resulted in habitats that are no longer adequate to fulfil nursery, feeding, or reproductive functions, yet the degree to which coastal habitats are important for exploited species has not been quantified. Thus, we reviewed and synthesized literature on the ecological value of coastal habitats (i.e. seagrass beds, shallow subtidal and intertidal habitats, kelp beds, shallow open water habitats, saltmarshes, mussel beds, macroalgal beds, rocky bottom, and mariculture beds) as feeding grounds, nursery areas, spawning areas, and migration routes of 59 taxa, for which the International Council for the Exploration of the Sea (ICES) gives management advice, and another 12 commercially or ecologically important species. In addition, we provide detailed information on coastal habitat use for plaice (*Pleuronectes platessa*), cod (*Gadus morhua*), brown shrimp (*Crangon crangon*), and European lobster (*Homarus gammarus*). Collectively, 44% of all ICES species utilized coastal habitats, and these stocks contributed 77% of the commercial landings of ICES-advice species, indicating that coastal habitats are critical to population persistence and fishery yield of ICES species. These findings will aid in defining key habitats for protection and restoration and provide baseline information needed to define knowledge gaps for quantifying the habitat value for exploited fish and invertebrates.

Keywords: feeding, fisheries, migration, nursery, reproduction, spawning.

Introduction

Habitat and exploited species

Many exploited species are experiencing population declines. In addition to overfishing, habitat changes may potentially be involved to a large extent in these declines (Worm *et al.*, 2006). Consequently, a major effort is underway globally to adopt an ecosystem-based approach to fishery management, which includes the effects of fishing on habitat quality (e.g. Hollowed *et al.*, 2011), the use of marine protected areas (MPAs) based on habitat characteristics (e.g. Link *et al.*, 2011) and the effects of habitat availability on fishery yield (McClanahan *et al.*, 2011).

Coastal habitats are threatened by anthropogenic stressors, including coastal development and habitat degradation (Kennesh, 2002; Kemp *et al.*, 2005; Lotze *et al.*, 2006; Airoldi and Beck, 2007), such that 86% of the European coast is at high or moderate risk for unsustainable coastal construction and development (Bryant *et al.*, 1995; EEA, 1999). An established EU Natura2000 network of protected areas is aimed at conservation of the most threatened species and habitats, yet many of these species and habitats are still in jeopardy (Sundblad *et al.*, 2011). Often, degradation has modified coastal habitats to the degree that they no longer fulfil nursery, feeding, or reproductive functions (Beck *et al.*, 2001; Worm *et al.*, 2006). This has consequences for several ecosystem services provided by these coastal habitats. It has even been estimated that the ecosystem goods and services provided by coastal habitats, such as seagrass beds, intertidal habitats, and saltmarshes, are appreciably higher per unit area than those provided by terrestrial habitats (Costanza *et al.*, 1997).

Although the influence of coastal habitats on particular demographic rates such as survival, growth, and reproduction has been demonstrated (Chícharo *et al.*, 1998; Allain *et al.*, 2003; Kostecki *et al.*, 2011; Martin *et al.*, 2011; Vasconcelos *et al.*, 2013), the degree to which coastal habitats are important for exploited species at the population level has not been quantified. Many species rely on different coastal habitats to fulfil their life cycle; therefore, habitat quality and connectivity are considered essential characteristics of coastal ecosystems (Lipcius *et al.*, 2008). Thus, there is a critical need to define the integrated value of coastal habitats to population abundance, and ultimately fishery yield of exploited species (ICES, 2008). We reviewed the literature, examining links between coastal habitats and exploited species or species important in the foodweb of exploited species, to provide the foundation and justification for quantifying the production value of coastal habitats for exploited species and subsequently to integrate habitat quality in stock assessment and ecosystem-based fishery management.

Coastal habitats

Coastal habitats are defined in various ways by EU countries; we used several sources of information regarding coastal habitats to guide our definition. A general definition outlined in the ICES Science Plan states: "Coastal-zone habitat includes highly productive estuaries and bays, which are essential nursery grounds for a number of commercial and recreational fish species and home to a number of invertebrates (e.g. clams, crabs). As well, this habitat is critical to successful mariculture operations" (ICES, 2008). This definition was amended using the following sources to derive classifications of various habitats included in our review: the Habitats Directive (92/43/EEC), Marine Strategy Framework Directive (2008/56/EC) (MSFD), Water Framework Directive (2000/60/EC), a report of the ICES Working Group on Marine Habitat Mapping (ICES, 2010), and a recent scientific review (Airoldi and Beck, 2007; Table 1). For further details and for additional information regarding threats to the various habitats, consult Airoldi and Beck (2007), whose habitat descriptions we have adapted below.

Coastal tidal wetlands and saltmarshes

The coastline of Europe is characterized by estuaries, lagoons, and intertidal bays intertwined with saltmarshes and irregularly flooded wetlands (Airoldi and Beck, 2007). Coastal wetlands are highly productive and provide nursery, feeding, and spawning grounds for commercially and ecologically important fish, shellfish, and birds. Coastal wetlands are patchworks of sand flats, mud flats, tidal creeks, and saltmarshes. Saltmarshes are low coastal grasslands with structurally complex vegetation and distinctive patches that are regularly flooded by tidal flow and which replace mangroves in temperate and Arctic regions.

Shallow vegetated habitats

The key vegetated habitats in shallow water include seagrass meadows and macroalgal beds. Seagrasses are rhizomatous, clonal, marine plants forming beds that provide food and refuge for many commercial species and which enhance nutrient cycling, water quality, and sediment dynamics (Duarte, 2002; Airoldi and Beck, 2007). Seagrasses can colonize a variety of coastal habitats from estuarine to marine, subtidal to intertidal, and sedimentary to rocky. Several seagrass species occur along the European coastline, including the natives *Zostera marina*, *Z. noltii*, *Ruppia maritima*, *R. cirrhosa*, and *Cymodocea nodosa*.

Macroalgal beds are made up of erect brown and red macroalgae, such as kelps and fucoids, which are ecosystem engineers by forming complex, productive habitats utilized by various commercially and recreationally exploited species. Macroalgae colonize shallow hard substrates such as rock, boulders, cobble, and artificial structures from intertidal to subtidal habitats as deep as 30 m (Airoldi and Beck, 2007). The dominant macroalgae of the northwestern European coastline include *Laminaria hyperborea*, *L. digitata*, *Saccharina latissima*, *Fucus serratus*, and *Alaria esculenta*.

Biogenic reefs and beds

Biogenic reefs and beds are three-dimensional structures created by oysters, mussels, or polychaete worms. Subsequent generations often attach to older individuals, forming distinct clusters. Oyster species include the native European flat oyster (*Ostrea edulis*) and

Table 1. Classification of coastal habitats of importance to exploited species in the eastern North Atlantic Ocean and Mediterranean Sea.

Class	Habitat	Description
Coastal wetlands/marshes	Coastal wetlands	Patchwork of sand flats, mud flats, and saltmarshes
	Saltmarshes	Low coastal grassland frequently flooded by tidal flow
Shallow vegetated	Seagrass beds	Beds of rooted, flowering plants (four species)
	Kelp beds	Kelps, fucoids, and other complex, erect macroalgae
	Benthic algae	Bushy, flat, or crustose algae
Biogenic reefs and beds	Oyster reefs	Three-dimensional structures created by oysters, mussels, or marine polychaete worms spanning intertidal to subtidal areas
	Mussel beds	
	Worm reefs	
	Cockle beds	Aggregations of buried cockles in shallow sand/mud flats
	Maerl	Coralline algae growing in beds in the sublittoral habitats
Mariculture beds	Oyster beds	As above, three-dimensional structures of oysters and mussels formed by aquaculture operations in intertidal and subtidal areas near the coast
	Mussel beds	
Soft bottom	Intertidal flats	Intertidal mud and sand flats
	Subtidal soft bottom	Subtidal mud, sand, and mixed sediments
Hard structure	Rocky shore	Intertidal and subtidal rock, boulders, and cobble
	Artificial substrates	Manmade structures constructed of hard substrates
Open water	Shallow open water	Water depths shallower than 30 m but not directly next to the coast

the introduced Pacific oyster (*Crassostrea gigas*), which is easier to cultivate than the native oyster. Blue mussel (*Mytilus edulis*) beds are also common along the Northeast Atlantic coast. Generally, the mussel bed community is more species rich and contains different species than the surrounding soft sediment habitat (Commito *et al.*, 2008; Buschbaum *et al.*, 2009; Ysebaert *et al.*, 2009). Three-dimensional structures are also constructed by marine polychaete worms in the family Sabellariidae, primarily *Sabellaria alveolata* and *Lanice conchilega* in European waters. These structures consist of sediments consolidated by a mucoprotein cement produced by the worms. Biogenic reefs occur in the intertidal to subtidal zones.

Cockle beds are composed of aggregations of cockles buried a few centimetres below the surface in shallow sand, mud, and gravelly flats from the intertidal to subtidal zones. The most widespread is the edible, common cockle (*Cerastoderma edule*), though another cockle (*C. glaucum*) can also be locally abundant. Cockles can occur in extremely dense aggregations reaching more than 1000 ind. m^{-2}.

Maerl (a rhodolith bed) encompasses various species of unattached, crust-forming, calcareous red algae that can form substantial beds of live and dead material, not unlike coral reefs and oyster reefs, and which can serve as nursery habitat (Steller and Cáceres-Martínez, 2009). The main maerl-forming European species are *Phymatolithon calcareum*, *Lithothamnion corallioides*, and *L. glaciale.* Maerl beds occur from the surface to 100 m in depth, though most are at 20–30-m depths. *Phymatolithon calcareum* forms brittle, purple-pink, branched structures that look more like small corals than algae, and which grow as spherical nodules at sheltered sites or as twigs or flattened medallions at more exposed sites. Maerl is an important habitat for many species and is vulnerable to damage from trawling and dredging.

Mariculture beds and aggregations

Aquaculture represents a growing contributor to the production of aquatic food worldwide (www.fao.org). In the EU, aquaculture production is an important economic activity in many coastal and estuarine areas. In terms of production, shellfish farming represents the most important sector (Bostock *et al.*, 2010). Shellfish farming is primarily based on bivalves that are born in the wild (i.e. natural spatfall) and rely on food (e.g. phytoplankton) provided by the natural environment in which they are cultured. Two main categories of farming are practiced in the EU: suspended or off-bottom culture and bottom culture (McKindsey *et al.*, 2011). Suspended culture is used in deeper, subtidal waters and includes suspended ropes and longlines from floating rafts for mussel and other shellfish species. This technique was developed to take advantage of spatfall locations as well as areas of good water quality and food availability. Off-bottom culture is mainly carried out in intertidal areas with macrotidal regimes, with off-bottom trays for oysters and poles or stakes (bouchots) for mussels. Bottom shellfish culture is a type of culture where juvenile or adult animals are placed or relayed on the bottom for on-growing. This type of culture is mainly conducted in shallow coastal and estuarine areas, both intertidal and shallow subtidal.

Mussels are the main shellfish species produced in Europe (Smaal, 2002). Two species are being cultured: the blue mussel (*M. edulis*) and the Mediterranean mussel (*M. galloprovincialis*). European aquaculture of mussels relies almost entirely on natural spatfall. Besides mussels, two species of oysters are cultured: the Pacific oyster (*C. gigas*) and the native European flat oyster (*O. edulis*). Of the two oyster species, the Pacific oyster dominates in mariculture operations. Other shellfish cultured in Europe include a number of species of clams, scallops, and abalones.

Unvegetated soft bottom, hard structure, and open water

These habitats are widespread in western European waters and include intertidal and shallow subtidal mud flats, sand flats (exclusive of coastal tidal wetlands), bottoms of mixed sediments, and hard-bottom habitats such as rock, boulders, and cobble. Manmade hard structures include those used as artificial reefs and erosion-control structures that can also provide valuable habitat. Open waters in the coastal zone are defined as those shallower than 30-m depth, but are not directly next to the coast.

Exploited species

Commercial species from the Northeast Atlantic are poorly represented in the literature covering quantitative habitat assessments or habitat-specific demographic rates in coastal areas (Vasconcelos *et al.*, 2013). It was, therefore, of interest to establish to what degree commercial species use coastal habitats. The present review was focused on the species for which ICES gives advice (hereafter "ICES-advice species"), directing this summary compilation to important stocks for ICES Member Countries (i.e. Belgium, Denmark, Estonia, Finland, France, Germany, Iceland, Ireland, Latvia, Lithuania, the Netherlands, Norway, Poland, Portugal, Russia, Spain, Sweden, and the UK; US and Canadian fish stocks are not included in the advice, though these are ICES Member Countries) and to taxa for which information on the influence of coastal habitats could be incorporated in future ecosystem-based advice.

ICES gave advice for 59 taxa in 2012 (ICES, 2012; Table 2). Stocks with full analytical assessment were included together with data-poor stocks or species for which only precautionary advice is given. To increase the cover of invertebrate species, we investigated a number of molluscs and crustaceans that are important economically or ecologically, specifically for ICES Member Countries.

Methods

Literature review

We compiled relevant scientific literature on habitat use of the ICES-relevant species and of a number of additional invertebrates with high landings in the ICES Area or that are of ecological importance. The searches were made using Google Scholar, primarily by combining species name + habitat function (spawning, nursery, feeding, migration). In cases where no matches were found, we made searches by species name + habitat name and finally by habitat name + "fish" or "invertebrates" for habitats poorly represented in the original search. Depth ranges for various species were obtained from FishBase (Froese and Pauly, 2013). We also recognize that shellfish aquaculture is gaining importance and has the potential to greatly influence coastal benthic habitats; thus, we examined the influence of shellfish aquaculture on these habitats.

Habitats and habitat function

Coastal habitats were as defined above, but modifications had to be made to this classification to accommodate the lack of detailed habitat descriptions in the literature and the poor representation of some habitats in fish studies. We evaluated habitat use of commercially important fish species and invertebrates by examining four different ecological habitat functions: spawning, nursery, feeding, and migration. The categorization was mainly based on papers referring to these functions, but also, in some instances, on our conclusions referring to the definitions of functions in Table 1.

Table 2. Coastal habitat use of commercially important fish species for which ICES gave advice in 2012.

Species	Common name	Coastal habitat type: Seagrass	Intertidal soft bottom	Subtidal soft bottom	Kelp	Shallow open water	Saltmarsh	Mussel beds	Macroalgae	Rocky shore	Coastal	Depth range (m)	References
Ammodytes marinus	Sandeel			S, N, F		F					Yes	10–150	Holland *et al.* (2005)
Anguilla anguilla	Eel	N, F		N	N, F	M	N, F		N, F	N, F	Yes	0–700	Moriarty and Dekker (1997); Pihl and Wennhage (2002); Cattrijsse and Hampel (2006); Pihl *et al.* (2006); Bergström *et al.* (2011)
Aphanopus carbo	Black scabbard fish											200–1 700	Swan *et al.* (2003)
Argentina silus	Greater silver smelt											140–1 440	Magnússon (1996)
Beryx spp.	Alfonsinos/ Golden eye perch											100–1 000	Anibal *et al.* (1998)
Brosme brosme	Tusk											18–1 000	FAO (1990)
Capros aper	Boarfish											40–700	Blanchard and Vandermeirsch (2005)
Centrophorus squamosus	Leafscale gulper shark											145–2 400	Veríssimo *et al.* (2012)
Centroscymnus coelolepis	Portuguese dogfish											150–3 700	Veríssimo *et al.* (2011)
Cetorhinus maximus	Basking shark					F					Yes	0–2 000	Sims (2008)
Chelidonichthys cuculus	Red gurnard											15–400	Lopez-Lopez *et al.* (2011)
Chelidonichthys spinosus	Spiny red gurnard											25–615	
Clupea harengus	Herring	S				N, F		S	S	S	Yes	0–364	Rajasilta *et al.* (1989); Nøttestad *et al.* (1996); Pihl and Wennhage (2002); Polte and Asmus (2006); Jensen *et al.* (2011)
Coryphaenoides rupestris	Roundnose grenadier											180–2 600	
Dalatias licha	Kitefin shark											37–1 800	
Dicentrarchus labrax	European sea bass	N					N				Yes	10–100	Jennings and Pawson (1992); Laffaille *et al.* (2001)
Engraulis encrasicolus	Anchovy					N					Yes	0–400	Motos *et al.* (1996); Drake *et al.* (2007)
Eutrigla gurnardus	Grey gurnard											10–340	

Continued

Table 2. *Continued*

Species	Common name	Coastal habitat type: Seagrass	Intertidal soft bottom	Subtidal soft bottom	Kelp	Shallow open water	Saltmarsh	Mussel beds	Macroalgae	Rocky shore	Coastal	Depth range (m)	References
Gadus morhua	Cod	N		N	N, F				N	N	Yes	0–600	Uzars and Plikshs (2000); Pihl and Wennhage (2002); Norderhaug *et al.* (2005)
Glyptocephalus cynoglossus	Witch											18–1 570	
Hoplostethus atlanticus	Orange roughy											180–1 809	
Lamna nasus	Porbeagle											0–715	
Lepidorhombus boscii	Fourspot megrim											7–800	
Lepidorhombus whiffiagonis	Megrim											100–700	
Limanda limanda	Dab		N	N							Yes	0–100	Bolle *et al.* (1994); Gibson *et al.* (2002)
Lophius budegassa	Black-bellied anglerfish											20–1 000	
Lophius piscatorus	Anglerfish											20–1 000	
Mallotus villosus	Capelin		S	S							Yes	0–700	Penton *et al.* (2012)
Melanogrammus aeglefinus	Haddock											10–200	
Merlangius merlangus	Whiting	N		N					N		Yes	0–100	Pihl and Wennhage (2002)
Merluccius merluccius	Hake											30–1 000	Santos and Monteiro (1997)
Micromesistius poutassou	Blue whiting											150–1 000	
Microstomus kitt	Lemon sole											10–200	
Molva dypterygia	Blue ling											150–1 000	
Molva molva	Ling											100–1 000	
Mullus surmuletus	Striped red mullet			N			N				Yes	5–100	Santos and Monteiro (1997); Rogers *et al.* (1998); Mathieson *et al.* (2000)
Nephrops norvegicus	Norway lobster											20–800	
Pagellus bogaraveo	Red sea bream											<700	
Pandalus borealis	Northern prawn											20–1 000	
Phycis blennoides	Greater forkbeard											10–800	
Platichthys flesus	Flounder		N	N, F			N				Yes	0–100	Cattrijsse and Hampel (2006); Florin *et al.* (2009)
Pleuronectes platessa	Plaice		N	N, F			N				Yes	0–100	Gibson (1999); Cattrijsse and Hampel (2006)

Pollachius pollachius	Pollack			N	N				N	N	Yes	0–200	Pihl *et al.* (1994); Norderhaug *et al.* (2005)
Pollachius virens	Saithe			N	N				N	N	Yes	0–300	Pihl and Wennhage (2002); Norderhaug *et al.* (2005)
Reinhardtius hippoglossoides	Greenland halibut											1–2 000	Godø and Haug (1989)
Salmo salar	Salmon	M	M	M	M	M			M	M	Yes	0–30	McCormick *et al.* (1998)
Salmo trutta	Sea trout	F	F	F	F	F, M			F	F	Yes	0–10	Pihl and Wennhage (2002)
Sardina pilchardus	Sardine					F					Yes	10–100	Elliott and DeWailly (1995)
Scomber scombrus	Mackerel					N, M					Yes	0–100	Eltink (1987); Jamieson and Smith (1987)
Scophthalmus maximus	Turbot		N	S, N							Yes	<70	Gibson (1973); Øie *et al.* (1997); Iglesias *et al.* (2003)
Scophthalmus rhombus	Brill		N	S, N							Yes	5–50	Gibson (1973, 1994); Chanet (2003)
Sebastes marinus	Golden redfish											50–300	Pikanwski *et al.* (1999)
Sebastes mentella	Beaked redfish											300–1 400	Pikanwski *et al.* (1999); Roques *et al.* (2002)
Solea solea	Sole		N, F			S, M					Yes	<60	Dorel *et al.* (1991); Koutsikopoulos *et al.* (1991); Cabral (2000); Grioche *et al.* (2000); Laffaille *et al.* (2000)
Sprattus sprattus	Sprat		N,			N, F	N				Yes	<150	Elliott *et al.* (1990); Laffaille *et al.* (2000); Voss *et al.* (2003); Gorokhova et al. (2004); Baumann *et al.* (2006)
Squalus acanthias	Spurdog											<200	
Trachurus picturatus	Blue jack mackerel											<300	
Trachurus trachurus	Horse mackerel											100–1 000	
Trisopterus esmarkii	Norway pout			F							Yes	50–300	Pihl *et al.* (2006)

The function of coastal habitats for species was divided into (S) spawning area, (N) nursery ground, (F) feeding area, and (M) migration route. Coastal habitat types constitute a subset of the habitats in Vasconcelos *et al.* (2013) for which there was information on species habitat use. Depth ranges were collated from FishBase.

(i) Spawning: records of ripe adults, observation of spawning, or the presence of newly spawned eggs;

(ii) Nursery: reference to the concentration of juvenile stages or at least the presence of juveniles;

(iii) Feeding: the use of habitats by adults as feeding grounds or at least the presence of adults not related to spawning; and

(iv) Migration: mainly refers to the directional movement of diadromous species.

Catches of species using coastal habitats and ICES-advice species were then related to the total catch in the Northeast Atlantic using data from ICES catch statistics for 2010 (http://www.ices.dk/fish/CATCHSTATISTICS.asp).

Results

Coastal habitat use by ICES-advice species

Out of the 59 ICES species investigated, 26 species (44%) were considered to use coastal habitats. None of these 59 species seemed to be resident in a single coastal habitat, and for the large majority of species, the life cycle also had a non-coastal component (Table 2). In addition, a number of species used more than one type of coastal habitat. Overall, the nursery function was the most prevalent function, occurring in 30% of the ICES species, followed by feeding grounds for 20%, spawning areas for 10%, and migration routes for 8% (Figure 1).

In our review, representatives of ICES-advice species utilized most habitats that we investigated, and all habitats except kelp, saltmarshes, and mussel beds supported all the four functions for at least one species (Figure 2). Subtidal soft bottom was the habitat used as spawning and nursery areas by the largest proportion of species, and intertidal soft bottom was also used heavily as nursery grounds. The most prevalent habitat for feeding and migration among the ICES species was shallow open water, though subtidal soft bottom was also used by many species for feeding (Figure 2). In addition, our literature review showed that there is a specific lack of information on fish from complex hard bottom habitat types, including kelps and macroalgae, particularly in Europe.

Coastal habitat use by invertebrates

A considerable number of commercial invertebrates use coastal habitats. ICES gives advice for only two invertebrate species—Norway lobster (*Nephrops norvegicus*) and northern shrimp (*Pandalus borealis*). One reason for this may be that many commercially important invertebrates are less mobile than fish, such that the local populations are, therefore, managed nationally. We chose to do a close examination of coastal habitat use for commercially important invertebrates that had a substantial percentage of fishery landings in the ICES Area, as well as for a number of species of particular interest due to their major contribution to other fishery landings in the Atlantic (e.g. *Callinectes sapidus*) or as important prey species (e.g. *Macoma balthica*) for other commercially important species (Table 3).

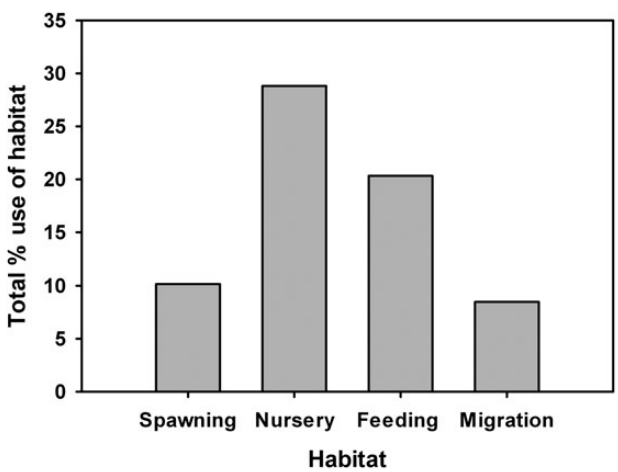

Figure 1. Percentage (%) of ICES-advice fish species using coastal habitats for spawning, as nursery grounds, for feeding, and for migration.

Of the 12 invertebrate species examined, all used coastal habitat during some phase of their life history (Table 3). All habitats except kelp and saltmarsh were used by several of the invertebrate species we examined. Shallow open water was the habitat most commonly used by invertebrates for spawning, whereas intertidal and subtidal soft-bottom habitats were used by the largest proportion of invertebrates as nurseries. Subtidal soft-bottom habitats were used most commonly for feeding. Most of the coastal habitats investigated, except kelp, were used by invertebrates for the nursery function (Figure 3).

Of the coastal habitats investigated, shallow subtidal and intertidal habitats were the most commonly used by invertebrates, with 16–25% of the invertebrate species we investigated using these two habitats for spawning, 50% of species using these habitats for nursery grounds, and 25–58% of species using these habitats for feeding (Figure 3). Shallow open water habitats were used not only for invertebrate spawning, but also for nursery grounds and feeding. Rocky shores were also commonly used for feeding (16% of species) or as nursery grounds.

Catches of ICES-advice species using coastal habitats

Total landings of fish and invertebrates reported within the ICES Area were estimated to be 8 514 820 t for 2010. Herring (*Clupea harengus*) comprised the highest tonnage of catch and the largest percentage of total catch in the Northeast Atlantic (~23%); this species utilized coastal habitats for nursery grounds, spawning, and feeding (Tables 2 and 4). Cod (*Gadus morhua*) and mackerel (*Scomber scombrus*) represented the next highest tonnages and percentages, together accounting for over 20% of total catch (Table 4). They utilized coastal habitats for nursery, feeding, and migration areas (Table 2). Blue whiting (*Micromesistius poutassou*), sprat (*Sprattus sprattus*), capelin (*Mallotus villosus*), sandeel (*Ammodytes marinus*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), and blue jack/horse mackerel (*Trachurus* spp.) rounded out the top ten species in terms of tonnage, with seven of these ten species utilizing coastal habitats (Table 4).

The species associated with coastal habitats made up 71% of the total landings and 77% of the cumulative landings of ICES-advice species in the Northeast Atlantic (Table 4). Although the Norway lobster is a commercially important invertebrate species in Europe and represented the largest percentage of total ICES catch of any invertebrate, it accounted for less than 1% of the total fishery catch in the Northeast Atlantic (Table 4).

Influence of shellfish aquaculture on benthic habitats

Although there are many anthropogenic influences on coastal habitats, shellfish aquaculture is a major one of increasing concern. Potential positive and negative environmental effects of different shellfish aquaculture practices are widely described in the scientific and technical literature (e.g. Kaiser *et al*., 1998; Newell, 2004; Borja

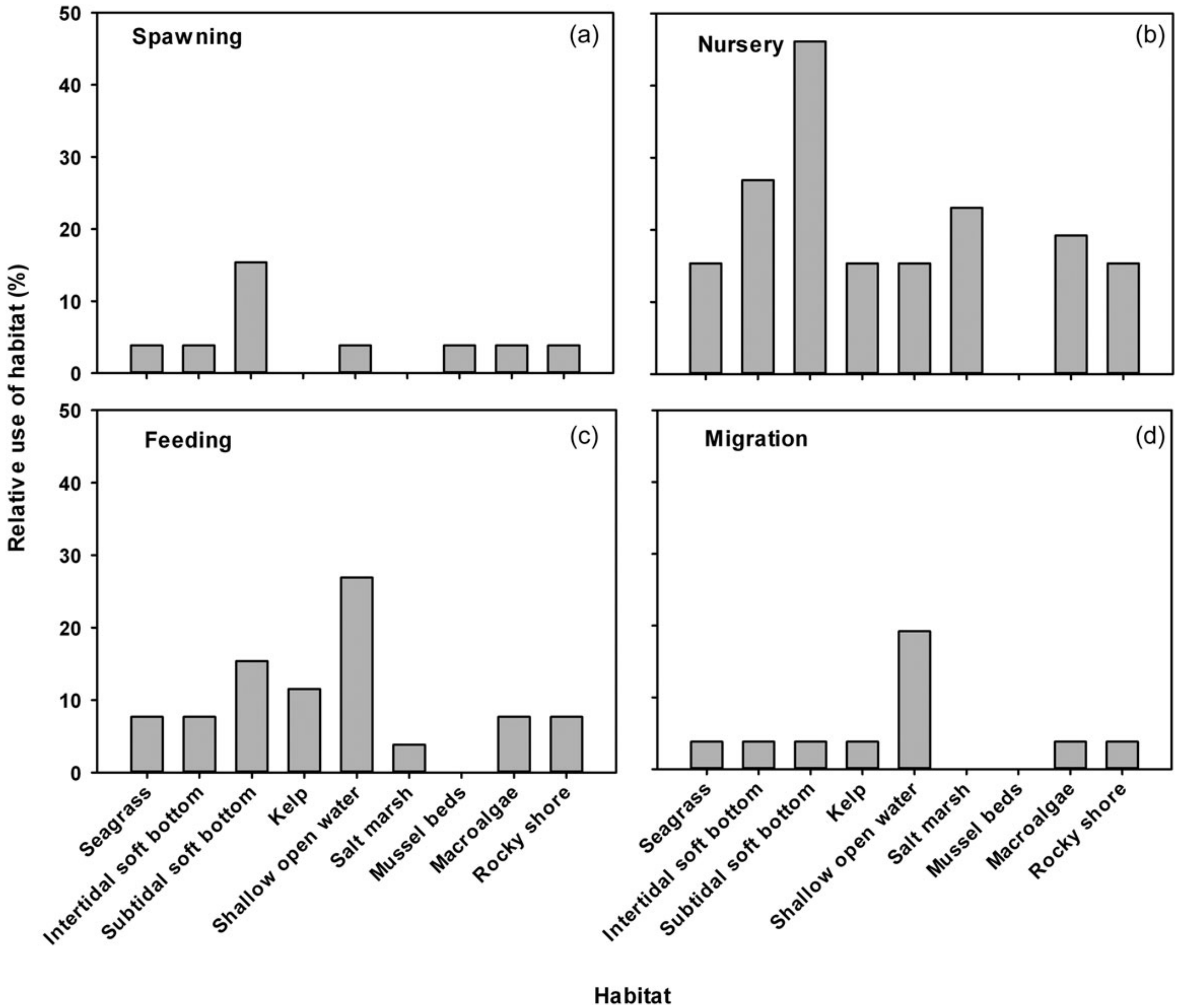

Figure 2. Relative contribution (%) of the different coastal habitats for the main functions (spawning, nursery, feeding, migration) identified among the ICES-advice fish species that use coastal habitats (26 species).

et al., 2009; Forrest *et al.*, 2009; Ysebaert *et al.*, 2009; McKindsey *et al.*, 2011; Shumway, 2011; Cranford *et al.*, 2012). Environmental concerns are related to how shellfish culture interacts with or controls basic ecosystem processes (Cranford *et al.*, 2012). The effects of different aquaculture systems depend on various factors, such as the local hydrographic conditions, the sedimentary habitat in which aquaculture occurs, the type of cultured organisms, the culture and production methods, and management practices (Henderson *et al.*, 2001). The effects are also site-specific and depend largely on the local environmental conditions (Read and Fernandes, 2003). The sensitivity of the ecosystem, the habitats in which culture practices occur, and the assimilative capacity of the surrounding environment are key to determining the magnitude and significance of the impact (Cranford *et al.*, 2012; Bunting, 2013).

Shellfish populations rely on the natural availability of nutrients and algae for their growth (Smaal and Van Stralen, 1990; Dame, 1996). Highly productive areas are preferred, such as shallow bays and estuaries (Nunes *et al.*, 2003). A healthy ecosystem is, therefore, of utmost importance for shellfish aquaculture. These areas are also often rich in biodiversity and act as important nursery grounds for fish and crustaceans and feeding areas for birds (Sequeira *et al.*, 2008). Because of this, many of these areas are internationally protected and are part of the European Natura2000 network. This can lead to conflicts with shellfish operations, as was the case in the Netherlands. Proper planning and location of activities should proceed in a sustainable manner and at sustainable levels, according to the carrying capacity of particular areas. Recently, focus is not solely on carrying capacity in terms of the maximum sustainable yield (MSY) of the bivalve culture, but also on potential changes in ecosystem structure and functioning and ecological variability over different spatial and temporal scales (Cranford *et al.*, 2012). An ecosystem-based management policy that balances the different needs is in the long-term interest of coastal communities and sustainable development of coastal resources.

Coastal habitat use by individual species

To provide concrete examples of the ecological value of coastal habitats for fish and invertebrates, we highlight a selection of commercially important species from the ICES Area and describe their

Table 3. Coastal habitat use by selected commercially or ecologically important invertebrates.

		Coastal habitat type											
Species	**Common name**	**Seagrass**	**Intertidal soft bottom**	**Subtidal soft bottom**	**Kelp**	**Shallow open water**	**Saltmarsh**	**Oyster Reef**	**Mussel beds**	**Macroalgae**	**Rocky shore**	**Coastal**	**References**
Crangon crangon	Common shrimp	N,F	N, F	F		S, M	N						Pandian (1970); Nichols and Lawton (1978); Howard and Bennett (1979); Tully and Céidigh (1987); Wahle and Steneck (1991); Jensen *et al.* (1994); Cattrijsse *et al.* (1997); Polte *et al.* (2005)
Ostrea edulis	Oyster							S, N, F					Launey *et al.* (2002)
Callinectes sapidus	Blue crab	N	N	N		S	N	N	N	N			Lipcius *et al.* (2008)
Homarus gammarus	European lobster			N, F		S					N, F		Pandian (1970); Nichols and Lawton (1978); Howard and Bennett (1979); Tully and Céidigh (1987); Jensen *et al.* (1994); Wahle and Steneck (1991)
Macoma balthica	Baltic clam		S, N, F	S, N, F		S							Bachelet (1980); Olafsson (1986); Beukema and de Vlas (1989); Armonies and Hellwig-Armonies (1992); Hiddink (2002)
Cancer pagurus	Edible crab		N	F		M					N	S	Brown and Bennett (1980); Bennett and Brown (1983); Hall *et al.* (1993); Sheehy and Prior (2008)
Palaemon serratus	Common prawn	N	N, F	N						N			Berglund (1982); Guerao and Ribera (1996, 2000)
Placopecten magellanicus	Atlantic sea scallop			F		S, N, F							MacDonald and Thompson (1985); Packer *et al.* (1999); Hart (2006)
Arctica islandica	Ocean quahog		F			S,N, F							Thompson *et al.* (1980)
Mytilus edulis	Blue mussel		S, N, F	S, N, F				S, N, F	S, N, F		S, N, F		Lintas and Seed (1994); Prins and Smaal (1994); Hilgerloh (1997); Walter and Liebezeit (2003)
Cerastoderma edule	Common cockle		S, N, F	S, N, F									Boyden and Russell (1972); Seed and Brown (1978)
Buccinum undatum	Whelk			S, N, F									Himmelman and Hamel (1993)

The function of coastal habitats for species was divided into (S) spawning area, (N) nursery ground, (F) feeding area, and (M) migration route. Coastal habitat types constitute a subset of the habitats in Vasconcelos *et al.* (2013) for which there was information on species habitat use.

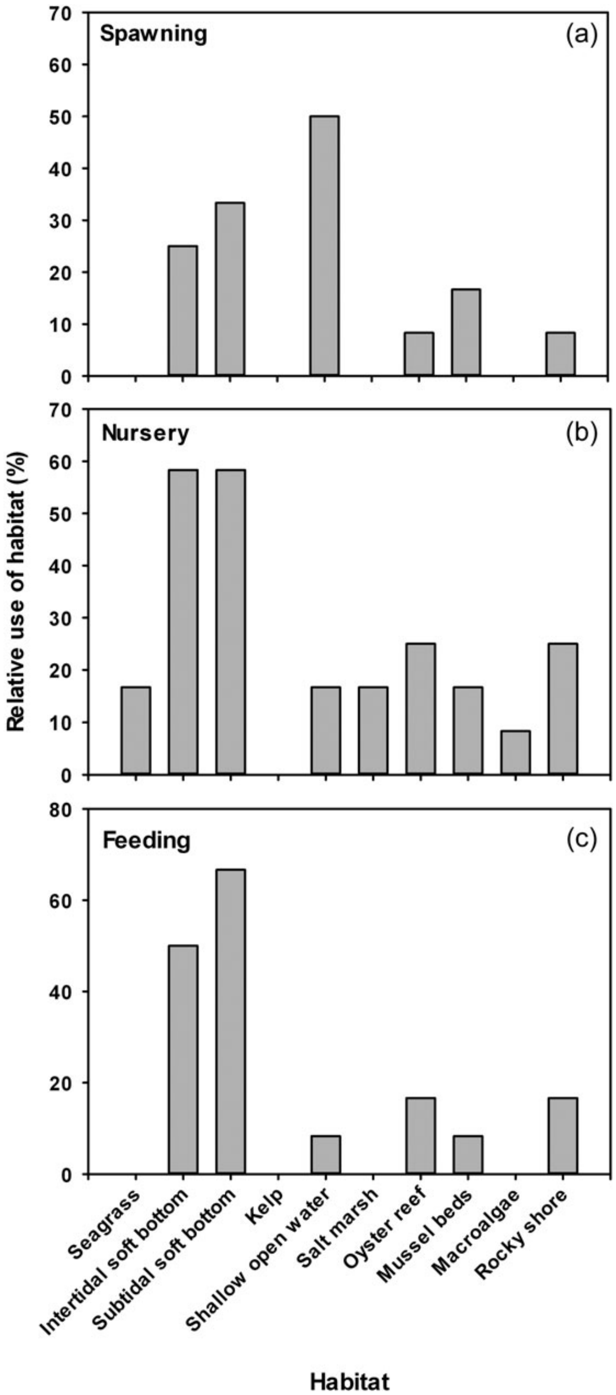

Figure 3. Relative contribution (%) of the different coastal habitats for the main functions (spawning, nursery, feeding) identified among the invertebrate species investigated. Few invertebrate species used coastal habitats for migration, so these are not depicted.

specific use of coastal habitats. Other coastal species may also use coastal habitats similarly.

Plaice (*Pleuronectes platessa*)

Plaice occur on sandy and muddy substrata of the European shelf from the Barents Sea to the Mediterranean including most of the

Table 4. Catches of ICES species with coastal habitat use (Yes, or No = left blank) according to Table 2 and related to the total catch in the Northeast Atlantic (0% catch means < 0.01%).

Species	Catch (t)	% of catch	Coastal habitat use
Herring	1 986 630	23.33	Yes
Cod	909 008	10.68	Yes
Mackerel	831 878	9.77	Yes
Blue whiting	546 026	6.41	
Sprat	538 105	6.32	Yes
Capelin	477 679	5.61	Yes
Sandeel	422 422	4.96	Yes
Haddock	364 082	4.28	
Saithe	336 504	3.95	Yes
Blue jack mackerel + horse mackerel	236 745	2.78	
Golden redfish + beaked redfish	138 300	1.62	
Boarfish	137 678	1.62	
Norway pout	137 079	1.61	Yes
Sardine	125 997	1.48	Yes
Plaice	83 967	0.99	Yes
Pollack	63 743	0.75	Yes
Norway lobster	59 010	0.69	
Hake	58 957	0.69	
Anglerfish + black-bellied anglerfish	55 141	0.65	
Northern prawn	43 537	0.51	
Greenland halibut	41 171	0.48	
Ling	33 858	0.4	
Whiting	31 430	0.37	Yes
Tusk	30 372	0.36	
Flounder	26 438	0.31	Yes
Sole	25 020	0.29	Yes
Megrim + fourspot megrim	17 201	0.2	
Anchovy	15 365	0.18	Yes
Blue ling	12 639	0.15	
Dab	11 165	0.13	
Lemon sole	11 066	0.13	
Witch	10 206	0.12	
European sea bass	8 263	0.1	Yes
Greater forkbeard	7 191	0.08	
Roundnose grenadier	7 094	0.08	
Black scabbard fish	6 892	0.08	
Striped red mullet	5 396	0.06	Yes
Turbot	4 731	0.06	Yes
Great silver smelt	4 593	0.05	
Red gurnard + spiny red gurnard	4 405	0.05	
Brill	2 958	0.03	Yes
Red sea bream	1 172	0.01	
Eel	1 152	0.01	Yes
Salmon	784	0.01	Yes
Grey gurnard	634	0.01	
Alfonsinos	575	0.01	
Sea trout	490	0.01	Yes
Leafscale gulper shark	149	0	
Portuguese dogfish	118	0	
Porbeagle	97	0	
Orange roughy	88	0	
Kitefin shark	6	0	
Basking shark	0	0	Yes
Spurdog	0	0	

Catches from ICES catch statistics for 2010.

Northeast Atlantic to a depth of 100 m (Kottelat and Freyhof, 2007; Froese and Pauly, 2013). Plaice are dependent on shallow (0–5 m) sediment substratum as nursery grounds during their early juvenile stage, which is only a small fraction of the species' distribution range (Gibson, 1994). Variation in year-class strength is generated during the pelagic stages and subsequently dampened during the early juvenile stage (van der Veer, 1986; Beverton, 1995). Growth rate is negatively correlated and mortality positively correlated with settlement density, indicating that density-dependent processes are acting in the nursery grounds (Pihl *et al*., 2000). These nurseries are important for stock dynamics, since a relationship between nursery size and population abundance exists, a relationship that has been conveyed as the "nursery size hypothesis" (Rijnsdorp *et al*., 1992; van der Veer *et al*., 2000).

The Wadden Sea is considered the largest and most important nursery ground in the North Sea. Spawning grounds are located such that eggs and larvae are transported with prevailing currents towards the nursery grounds, then they use selective tidal-stream transport to reach the shallow productive areas (Rijnsdorp *et al*., 1985). Plaice leave their nursery grounds at the end of their first summer then gradually move towards deeper waters with increasing size.

There is a targeted fishery for plaice using beam trawls, Danish seines, and gillnets, especially in the North Sea and the Irish Sea. The North Sea stock has increased recently and is currently fished at MSY. In the Western Channel, spawning-stock biomass (SSB) is above B_{MSY}, but fishing pressure (F) is above target. For the other stocks, there is insufficient information, and precautionary advice is given (ICES, 2012).

Cod (*G. morhua*)

Cod is widely distributed in the North Atlantic and Arctic (Froese and Pauly, 2013) and is found in a variety of habitats, from the shoreline down to the continental shelf. When maturing, the optimum temperature for cod decreases, and the larger fish are mainly found in deeper, colder waters.

Cod spawn in pelagic habitats usually offshore, and eggs and larvae drift with currents for months before settling to the seabed (Juanes, 2007). As juveniles, they are mainly found in complex habitats, such as seagrass beds, kelps, rocky shores, and gravel bottoms with cobble and attached fauna, which provide shelter from predation (Pihl and Wennhage, 2002; Lindholm *et al*., 2004; Norderhaug *et al*., 2005; Juanes, 2007). Mortality risk of 0-group cod is lower in complex habitat types than in simple habitats, suggesting that cod recruitment may be a function of habitat availability (Juanes, 2007). Older life stages of cod are less dependent on specific habitat types, probably as a consequence of a lower vulnerability to predation.

Cod has historically been by far the most important demersal species of North Atlantic fisheries, and it continues to be so although many cod stocks have been severely depleted. Most catches are taken in trawls, but they are also taken in seines, gillnets, and hook and line gear. Landings of cod within the ICES Area peaked in 1956; in 2010, they were down to 909 000 t, which is 40% of the maximum historical catch (Table 4). After a few years of lowered total allowable catch in combination with other management measures, several stocks have now started to increase, whereas others remain at a low level (Cardinale *et al*., 2013).

Brown shrimp (*Crangon crangon*)

An abundant species in European waters, the brown shrimp, also known as the common shrimp, is important ecologically and as a fishery species, especially in the North Sea. This species tolerates diverse environmental conditions, and its distribution ranges along the European coast from the White Sea to Morocco, including the Mediterranean and Black Seas.

Aside from the pelagic larval stage, this species is resident in shallow coastal areas of 1–20 m in sand or muddy sand habitats, although there have been records of this species found in depths of 130 m (FAO, 1999). In the Wadden Sea, shallow intertidal habitats are nurseries for *C. crangon* from February through June, dependent on temperature. Brown shrimp can be found in high densities in tide pools at low tide (Cattrijsse and Hampel, 2006). They leave the tidal zone at ~30 mm in carapace length from July through September, when there is a large recruitment to the adult stock. In winter, adults spawn again, and in spring, larvae migrate inshore and settle in the intertidal zone (Kuipers and Dapper, 1984). In the UK, there are seasonal migrations between Severn Estuary and Bristol Channel (Henderson and Holmes, 1987). Ecologically, there is evidence that *C. crangon* is a major structuring force for shallow, soft-bottom communities, where they are a dominant predatory species.

Crangon crangon is fished in Germany, the Netherlands, Denmark, UK, Belgium, and France. For this species, there is no official ICES advice given, but it is of prime concern, and there has been an ICES Working Group for this species. In 2010, in the North Sea, there were 36 000 t landed, dominated by Germany and the Netherlands, and the stock is stable (ICES, 2011). There is no management plan for the fishery, although there are some mesh-size regulations (Innes and Pascoe, 2007), and the ICES Working Group on *Crangon* fisheries and life history has suggested that further management should be implemented. The fishery currently uses unselective gear in shallow coastal nursery areas, which results in excessive discards and damage to the environment (ICES, 2011); thus, the fishery could be made more efficient.

European lobster (*Homarus gammarus*)

The European lobster has a broad geographic distribution in the eastern Atlantic from northwestern Norway (Lofoten Islands) to southeastern Sweden and Denmark, but possibly because of low salinity and temperature extremes, it is absent from the Baltic Sea (Charmantier *et al*., 2001; FAO, 2012). Its distribution southward extends along the mainland European coast around Britain and Ireland, to a southern limit of ~30°N latitude on the Atlantic coast of Morocco (Prodöhl *et al*., 2006).

There is little information on the juvenile phases of *H. gammarus*. In England, habitats with suitable crevices are sought out, and in lab experiments, juveniles also can bury in fine, cohesive mud. Early juvenile stages of their close relative *H. americanus* use cobble as their main habitat, and this habitat is thought to be a demographic bottleneck to those populations (Wahle and Steneck, 1991). Given their similar life cycles, it is reasonable to believe that the same might be true for the European lobster. Adult *H. gammarus* live on the continental shelf and use a rock crevice habitat (Howard and Bennett, 1979). Gravel and cobble are thought to be the prime nursery habitats. Moreover, adults colonized artificial reefs in the UK. In England, areas with habitats that include less structure and fewer large-scale outcrops for adults produce lobsters of smaller size than other areas, indicating the importance of the habitat for growth (Howard, 1980). Larvae are spawned in shallow bays in Ireland and display diel vertical migration with high densities in the neuston (i.e. surface waters) at dawn and dusk (Tully and Céidigh, 1987). Spawning begins in July, and a spawning peak occurs in August (Pandian, 1970).

There is little information on the *H. gammarus* fishery, and a lack of official registration of catches, which may mean that population size is underestimated. Because of this, management is difficult, and stock status is not well known (Galparsoro *et al.*, 2009). Total annual European landings have varied between 1600 and 5000 t in the recent past (Holthuis, 1991; Prodöhl *et al.*, 2006), with a slow increase since the 1970s. Moreover, lobster catches vary considerably between countries (FAO, 2006; Prodöhl *et al.*, 2006). Lobster aquaculture is also developing, based on some local declines and increases in demand, but production rates are low. Local populations should be managed separately as self-recruiting stocks, as local stocks vary among countries. In some areas, stocks have locally collapsed. For example, the Norwegian stock collapsed between 1960 and 1980 (Agnalt *et al.*, 2007).

We have some detailed information on coastal habitat use for a few important species, as discussed above. However, in general, there is poor knowledge regarding habitat dependence even for many common species.

Discussion

The present assessment demonstrates clearly the use of coastal habitats by commercially and ecologically important species and thus suggests the importance of those habitats to population dynamics and fishery yield. Of all ICES-advice species, a large percentage (44%) utilizes coastal habitats during some portion of their life history, indicating the ecological value of coastal habitats. Moreover, those advice species using coastal habitats were responsible for a majority (71%) of the fishery landings in ICES Member Countries, demonstrating the economic value of coastal habitats. Unfortunately, for most species, there was inadequate information to judge the degree to which these coastal habitats limit population growth and fishery production. There is an obvious lack of information on how fish utilize some habitat types in the ICES Area, particularly complex hard-bottom habitats such as kelp forests, rocky shores, and macroalgae, where many census techniques are inadequate. The collective information suggests that these habitats may be essential for many species. One recommendation is to focus future studies on these habitat types to attain quantitative data on fish (both population- and individual-level data) and their dependence on these habitats.

Human population numbers have been increasing substantially in coastal habitats (Airoldi and Beck, 2007). Factors associated with natural and anthropogenic global change, including rising temperature and sea levels, changes in the magnitude of nutrient and sediment run-off, overfishing, dredging, and sand mining, and habitat loss, present increased threats to coastal habitats worldwide (Kennesh, 2002; Kemp *et al.*, 2005; Lotze *et al.*, 2006). Although management has attempted to ameliorate adverse effects of habitat degradation, to some extent, many management efforts do not go far enough in protecting these delicate habitats and the species that rely on them. It is estimated that 85% of European coastlines are degraded (EEA, 1999), and public awareness of prolonged habitat losses is limited (Lotze, 2004).

In our assessment, seagrass, shallow intertidal and subtidal soft bottoms, shallow open water, macroalgae, and rocky-shore habitats supported all four major ecological functions—nursery provision, spawning area, migration, and reproductive areas—among the species investigated. These habitats are threatened by anthropogenic disturbance and stress due to pollution, eutrophication, and increased turbidity leading to reduced water clarity, important for seagrass and macroalgae (Orth *et al.*, 2006), as well as direct habitat destruction from dredging, sand mining, and destructive fishing practices, such as trawling and dredging (Turner *et al.*, 1999; Jackson *et al.*, 2001). A synthesis of the interaction of human activities with marine ecosystems indicated that "no area is unaffected by human impact" (Halpern *et al.*, 2008), and other studies show coastal habitats are threatened by multiple anthropogenic impacts (Lotze *et al.*, 2006; Halpern *et al.*, 2007). Various threats may affect different coastal habitats differentially, as pollution and turbidity are important for vegetated habitats (Duarte, 2002), while destructive fishing practices are most damaging to biogenic habitats, such as oyster reefs and maerl beds (Barbera *et al.*, 2003). Gear effects from fishery activities have detrimental effects on coastal habitats in many areas (Thrush and Dayton, 2002; Chuenpagdee *et al.*, 2003; Hixon and Tissot, 2007; Hobday *et al.*, 2011). Moreover, the current distribution of key habitats still needs to be quantified, and recent efforts to do so are making progress in the right direction (Agardy and Alder, 2005), such as habitat classifications through the European Union Nature Information System (EUNIS) programme (Davies *et al.*, 2004), and through modelling techniques (Bekkby *et al.*, 2008; Sundblad *et al.*, 2011; Gorman *et al.*, 2013). Only when we have quantitative knowledge on both the spatial distribution of habitats (e.g. total area through mapping and remote sensing; quality through production per unit area) and on population fitness in different habitat types (i.e. secondary production per unit area in each habitat type) can we estimate the contribution of different habitat types to fish or invertebrate production and fisheries.

Many of the threats to coastal habitats can adversely affect specific important fish and invertebrate species. As one example, since plaice use shallow soft-bottom areas as nursery grounds, the early juvenile stage is vulnerable to new construction and infrastructural works, such as harbours and road banks, and to land reclamation (Rönnbäck *et al.*, 2007). Another threat to plaice nursery grounds is the reduction in habitat quality and quantity caused by the proliferation of macroalgae (Pihl *et al.*, 2005), which may be a sign of both eutrophication and a trophic cascade releasing predation pressure on grazers (Svensson *et al.*, 2012).

In another species-specific example, since cod depend on complex coastal habitats during early demersal life stages, loss of these habitat types may be detrimental to cod population recovery. A continuous loss of large, complex vegetation due to overgrowth by filamentous algae caused by eutrophication and excess sedimentation, augmented by coastal construction, is a serious threat to cod nursery grounds (Pihl *et al.*, 2006; Airoldi and Beck, 2007). Degradation of these habitats may also be triggered by a weakened trophic control, stemming from decreases in large predatory fish, as well as direct losses due to harvesting of algae (Tegner and Dayton, 2000). Thus, overfishing may indirectly cause degradation of coastal habitats, which may give rise to a feedback mechanism as recruitment of large predatory fish is impaired (Eriksson *et al.*, 2011). Further, loss of biogenic structures in gravel habitats due to bottom trawling may pose a threat to cod nursery habitats in areas with an intense demersal fishery (Lindholm *et al.*, 2004). In addition to these, other anthropogenic effects such as ocean acidification and climate warming also likely have negative effects on fish species, although the magnitude and direction of such effects depend on location and are difficult to predict (Jones, 2014).

Exemplifying the case of invertebrates, coastal habitats are very important for brown shrimp, and non-selective gear used in shallow habitats can destroy these fragile areas. Therefore, the major ecological threats to *C. crangon* are thought to involve habitat degradation (Broadhurst *et al*., 2006; ICES, 2011). Towed or dragged commercial fishing gear (benthic trawls or dredges) are responsible for over 50% of total fishery landings (Kelleher, 2005), and the habitat destruction and bycatch loss by such gear is substantial and alarming (Broadhurst *et al*., 2006).

The threats to nearshore coastal and estuarine ecosystems today arise from a vast range of human activities, including coastal development, industrial fishing, aquaculture, upstream dams, and water diversions. The impacts are manifold, including habitat loss and degradation, pollution, eutrophication, harmful algal blooms, changes in freshwater inflows or tidal patterns, loss of fish and shellfish populations, diseases, and invasive species. All these can have impacts on natural populations and also upon coastal shellfish aquaculture operations.

It is clear from our analysis that many commercially important species in the ICES Area utilize coastal habitats. For most species, however, there is insufficient information to judge whether these coastal habitats (or non-coastal habitats used during other parts of the life cycle) are actually essential and limiting to population growth and fishery production.

Since many species use coastal habitats as spawning, feeding, and nursery areas, and these life stages usually have very specific habitat demands, habitat availability may be a bottleneck for many populations (Fodrie and Levin, 2008; Sundblad *et al*., 2014). Further studies are needed to attain quantitative data on coastal habitat use by fish and invertebrates to aid the definition of key habitats for protection and restoration efforts and to integrate habitat quality in stock assessment and ecosystem-based fishery management.

Potential consequences of further degradation of coastal habitats could include decreased fishery landings, since such a large percentage of important fishery species depends on those habitats. Given the likelihood for strong dependence upon specific coastal habitats during juvenile stages in marine fish (Juanes, 2007), further reviews quantifying detailed use of habitats by exploited species are anticipated to give additional weight to arguments for habitat preservation through MPAs and other means (Agardy, 2000). There have been efforts and policies directed towards coastal and marine habitats of Europe that are threatened (Airoldi and Beck, 2007) and efforts to develop efficient networks of MPAs to protect such ecosystems (Sala *et al*., 2002; Fenberg *et al*., 2012). However, MPAs alone cannot protect habitats from all anthropogenic threats, such as pollution (Airoldi and Beck, 2007), aquaculture, and cross-ecosystem effects of fishing (Eriksson *et al*., 2011). Future fishery management efforts need to be directed not only at maintaining fish stocks, but also at preserving and restoring the habitats that are essential for fish and invertebrate populations, which is a major thrust of ecosystem-based management.

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