

ICES WKVHES REPORT 2012

SCICOM STEERING GROUP ON SUSTAINABLE USE OF ECOSYSTEMS

ICES CM 2012/SSGSUE:05

REF. SCICOM, ACOM

Report of the Workshop on the Value of Coastal Habitats for Exploited Species (WKVHES)

25–29 June 2012

Copenhagen, Denmark



ICES

International Council for
the Exploration of the Sea

CIEM

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Recommended format for purposes of citation:

ICES. 2012. Report of the Workshop on the Value of Coastal Habitats for Exploited Species (WKVHES), 25-29 June 2012, Copenhagen, Denmark. ICES CM 2012/SSGSUE:05. 66 pp. <https://doi.org/10.17895/ices.pub.9033>

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Participants at the ICES Workshop on the Value of Coastal Habitats for Exploited Species.

From left: Ulf Bergstrom, Dave Eggleston, Håkan Wennhage, Joel Fodrie, Rochelle Seitz, Rom Lipcius, Rita Vasconcelos, Jaap van der Meer, Ingrid Tulp, Olivier Le Pape, Karen van de Wolfshaar (not pictured: Tom Ysebaert).

Executive Summary

This report summarizes the work of the 2012 ICES Workshop on the Value of Coastal Habitats for Exploited Species (WKVHES) held 25–29 June 2012 at ICES headquarters in Copenhagen, Denmark. There were 12 participants (one additional individual, absent but contributing via email) from six countries; participants included scientific and technical experts with extensive experience dealing with fishery management and conservation issues.

The primary goal of this workshop was to provide the foundation for integrating habitat value quantitatively in models of the population dynamics of exploited species, for which ICES gives management advice, as well as those species that are important in the food web of ICES species.

The workshop sought to lay the foundation for determining the relative value of coastal nursery habitats (e.g. seagrass beds, salt marshes, kelp beds, rocky bottom), feeding grounds, and spawning areas for the suite of species of interest to ICES by (i) documenting and evaluating case studies where the quantity and quality of coastal habitats can be linked directly to the population dynamics of exploited species; (ii) producing reviews that synthesize and critically evaluate the evidence for the importance of coastal habitats to exploited species; and (iii) establishing quantitative methods for determining how coastal habitats influence population abundance and fishery yield. We expect the workshop findings to aid in improving predictions of fishery yield, age-class strength and long-term population status for species of commercial and recreational value, and to define key habitats for restoration efforts.

The workshop goals are important because many exploited marine and estuarine populations have experienced significant reductions in spawning stock biomass and recruitment. Concurrently, fishery production of these species is lower than historical levels, such that their commercial value has similarly declined. Moreover, essential habitats such as nursery and foraging grounds have been degraded in many areas such that these critical habitats are no longer adequate to fulfill nursery, feeding or reproductive functions.

The workshop meeting consisted of a series of introductory talks by various participants, followed by working sessions by three subgroups (Annex 1). At the end of the workshop, a draft report was generated and subsequently revised and submitted after the end of the workshop.

The key findings of the workshop were that: (i) there is limited information on how fish utilize some coastal habitats, particularly hard-bottom habitats such as kelp forests, rocky shores and macroalgae, but the available information suggests that these habitats are essential for many species; (ii) the majority (71%) of commercial species in the ICES area utilize coastal habitats, but for most species, there is inadequate information to judge the degree to which these coastal habitats limit population growth and fishery production; (iii) to attain quantitative estimates of the importance of habitats for fish and invertebrates, information is needed both on population fitness in different habitats (habitat quality), and on the availability of different habitat types (habitat quantity), specifically comprehensive habitat maps; and (iv) there are various diverse mathematical modeling approaches that can provide answers to the preceding questions.

The WKVHES therefore recommends that: (i) studies be undertaken on the suite of habitat types to attain quantitative data on habitat use by fish and invertebrates of

importance to ICES; (ii) mathematical models be employed along with quantitative habitat data to estimate the value of coastal habitats to population abundance and fishery production of representative species with diverse life histories and habitat use; (iii) WKVHES be formed into a working group, which in collaboration with WGMHM (marine habitat mapping working group) work on compiling information on habitat distributions and modeling their importance for exploited species of relevance to ICES to establish the foundation for ecosystem-based fishery management.

1 Introduction

Many exploited marine and estuarine populations have experienced significant reductions in spawning stock biomass and recruitment. Concurrently, fishery production of these species is lower than historical levels, such that their commercial value has similarly declined. Moreover, essential habitats such as nursery and foraging grounds (e.g. seagrass beds) have been degraded in many areas such that these critical habitats are no longer adequate to fulfill nursery, feeding or reproductive functions.

Although the influence of coastal habitats on survival, growth, and reproduction of exploited marine species has been demonstrated widely, the absolute value of these habitats to their population dynamics has rarely been quantified. Consequently, it has been difficult to estimate the optimal extent of habitat required for the persistence and sustainable use of exploited species, and therefore, to effectively manage habitat with respect to abundance of exploited species. In addition, recent research indicates that many species inhabit linked sets of primary (e.g. seagrass beds) and secondary (e.g. salt marsh fringed coves and shorelines) nurseries. Yet there is little to no information on the relative value of these critical nurseries to the population dynamics of exploited species. Thus, there is a critical need to define the value of coastal habitats to population abundance (and ultimately, fishery yield) of exploited species.

This workshop seeks to lay the foundation for determining the relative value of coastal nursery habitats (e.g. eelgrass beds, salt marsh fringed coves and coastal beaches), feeding grounds, and habitats necessary for reproduction. In addition, the workshop will aim to establish linkages between the diverse suite of coastal habitats, and how these habitat linkages influence population abundance and fishery yield. Subsequently, we expect the workshop findings to aid in improving predictions of fishery yield, age-class strength and long-term population status for species of commercial and recreational value, and to define key habitats for restoration efforts.

ICES is well positioned to support the integration of habitat features into quantitative models of population dynamics. With a network of more than 1600 scientists from 200 institutes linked by an intergovernmental agreement and meeting in over 100 expert groups, it can add significant value to national and international research efforts, co-ordinate data collection and analysis, provide a forum for sharing expertise and offer impartial and consensual scientific advice. ICES also acts as a major custodian and provider of population dynamics data.

The goal of this workshop was to provide the foundation for integrating habitat value quantitatively in models of the population dynamics of exploited species, for which ICES gives management advice, by achieving the following objectives:

- Document and evaluate case studies where the quantity and quality of coastal habitats can be linked directly to the population dynamics of exploited species;
- Produce a review paper(s) that synthesizes and critically reviews the evidence for the importance of coastal habitats to exploited species and general patterns that may be applicable over a broad range of situations
- Develop guidelines for further work in ICES to aid in the quantitative links between coastal habitat and population dynamics of exploited species, particularly with reference to ecosystem-based management.

2 Coastal habitats

2.1 Classification of coastal habitats

In the following The ICES Science Plan states that coastal zone habitats include near-shore areas and productive estuaries and bays, which are essential nursery grounds for many commercial and recreational fish and shellfish species. These areas are also critical to successful mariculture operations. We have consulted several sources of information regarding coastal habitats of importance to European countries, including 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). In addition, we added habitats based on our literature review of habitat utilization by exploited species. Our classification is detailed in Table 2.1.

Table 2.1. 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 salt marshes
	Salt marshes	Low coastal grassland frequently flooded by tidal flow
Shallow vegetated	Seagrass beds	Beds of rooted, flowering plants (4 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	Intertidal 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

Although there are various definitions of “coastal habitat” in use by EU countries (Box 1), we classified coastal habitats based on their ecological characteristics so that there would be a standard description that could be adapted for fisheries management by individual countries or management authorities.

Box 1. Definitions of coastal habitats adopted by various countries (ICES 2010)

- CANADA – 2010, Between low water mark and 12 nm line
- DENMARK – 2009, Between 3 km inland and either 6 m depth or 1 nm seaward
- IRELAND – 2008, No, coastal boundaries defined by WFD, EEZ, ICES areas
- NORWAY – 2010, No, EU WFD definition of ‘coastal water’: 1 nm off the baseline*
- GERMANY – 2010, In the national ICZM strategy the EEZ; coastal waters and transitional waters in the sense of the WFD, and in estuaries those waters that are influenced by the tide are included
- SPAIN – 2009, EU WFD definition of ‘coastal water’: 1 nm off the baseline of interior waters
- UK – 2010, Guidance Note 20 on coastal planning offers guidance on defining coastal zone

* Coastal water means surface water on the landward side of a line, every point of which is at a distance of 1 nm on the seaward side from the nearest point of the baseline from which the breadth of territorial waters is measured, extending where appropriate up to the outer limit of transitional waters.

2.2 Description of coastal habitats

In the following sections, we provide a brief description of the coastal habitat types (Table 2.1) and their ecological importance. For further details, and for additional information regarding threats to the various habitats, consult Airoldi & Beck (2007) whose habitat descriptions we have adapted below.

2.2.1 Coastal wetlands and salt marshes

As Airoldi & Beck (2007) note, the coastline of Europe is characterized by estuaries, lagoons and intertidal bays intertwined with salt marshes and irregularly flooded wetlands. Coastal wetlands are highly productive, and provide nursery, feeding and spawning grounds for commercially and ecologically important fishes, shellfish, and birds. Coastal wetlands are patchworks of sand, mud flats and salt marshes. Salt marshes are low coastal grasslands with structurally complex vegetation and distinctive patches that are regularly flooded by tidal flow, and which are distributed throughout Europe (Figure 2.1).



Figure 2.1. Distribution of salt marshes in Western Europe (adapted from Boorman, 2003).

2.2.2 Shallow vegetated habitats

The key vegetated habitats in shallow water include seagrass meadows (Figure 2.2), macroalgal beds, and patches of benthic algae. Seagrasses are rhizomatous, clonal, marine plants forming beds that provide food and refuge for many commercial species, and which aid in nutrient cycling, enhance water quality, and sediment dynamics (Duarte 2002; Airoidi and Beck, 2007). Seagrasses can colonise a variety of coastal habitats from estuarine to marine, subtidal to intertidal, sedimentary to rocky. Several seagrass species occur along the European coastline, including the natives *Zostera marina*, *Z. noltii*, *Ruppia maritima*, *R. cirrhosa*, *Cymodocea nodosa* and *Posidonia oceanica* (endemic to the Mediterranean Sea) plus *Halophila stipulacea*, which was recently introduced in the Mediterranean Sea.

Macroalgal beds are comprised of erect brown and red macroalgae, such as kelps and furoids, 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, cobbles and artificial structures from intertidal to subtidal habitats as deep as 30 m from the intertidal down to more than 30 m in depth (Airoidi and Beck, 2007). The most common species in the Mediterranean Sea are in the genera *Cystoseira* and *Sargassum*, whereas *Laminaria* and *Fucus* dominate the northwestern European coastline.

2.2.3 Biogenic reefs and beds

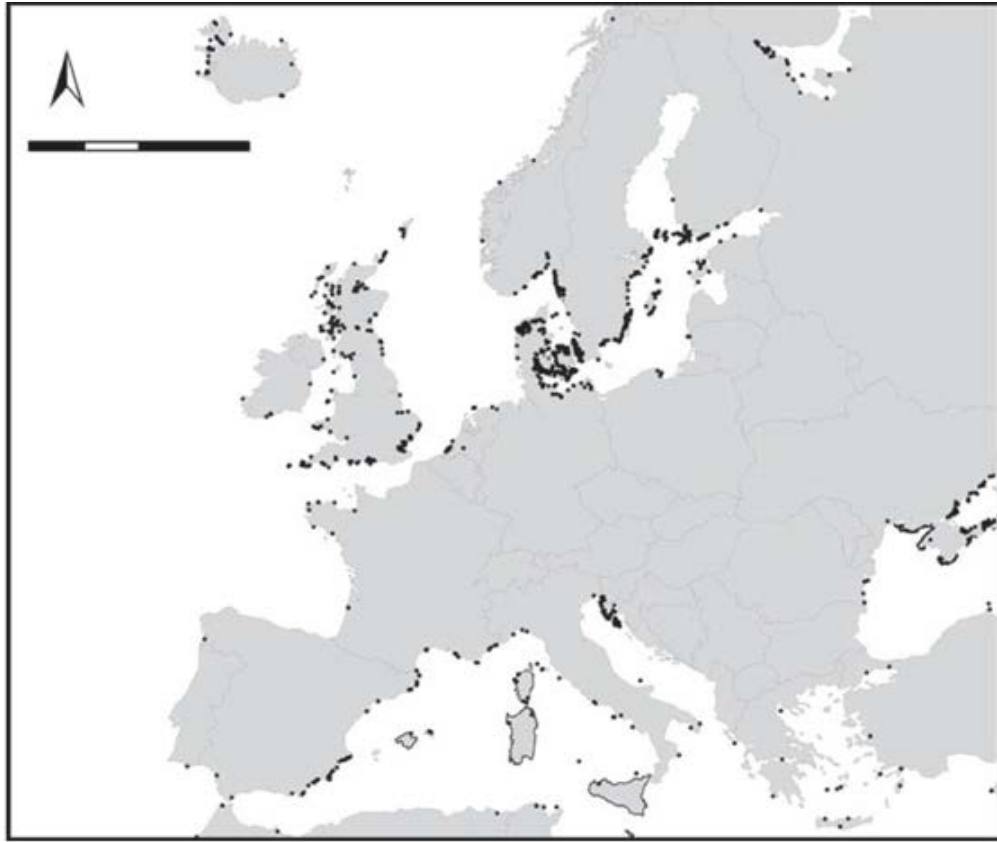


Figure 2.2. Distribution of seagrass beds in Western Europe (adapted from Airolidi and Beck 2007).

The biogenic reefs and beds are three-dimensional structures created by oysters or mussels growing on a firm substrate, and with subsequent generations attached to older individuals, often forming clusters. Oyster species include the native European flat oyster (*Ostrea edulis*) and the introduced Pacific oyster (*Crassostrea gigas*), which is easier to cultivate than the native oyster. Three-dimensional structures are also constructed by marine polychaete worms in the family Sabellariidae, and 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 cm 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 individuals per square meter.

Maerl (rhodolith beds) encompasses various species of unattached, crust-forming, calcareous red algae that can form substantial beds of live and dead material (Figure 2.3), not unlike coral reefs and oyster reefs. The main maerl-forming European species are *Phymatolithon calcareum*, *Lithothamnion corallioides* and *L. glaciale*. Maerl beds occur from the surface down 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.



Figure 2.3. Distribution of maerl beds in Western Europe (from Airoidi and Beck, 2007).

2.2.4 Mariculture beds and aggregations

Aquaculture represents a growing contributor to the production of aquatic food worldwide. 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.

Shellfish farming is primarily based on bivalves that are born in the wild (i.e. natural spatfall) and rely on food (i.e. mainly 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. 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 has 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 macro-tidal 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. Two species are being cultured, the blue mussel (*Mytilus edulis*) and the Mediterranean mussel (*Mytilus galloprovincialis*). European aquaculture of mussels relies almost entirely on natural spatfall. Besides mussels, two species of oysters are cultured, the Pacific oyster (*Crassostrea gigas*) and the native European flat oyster (*Ostrea edulis*). Of the two oys-

ter species, the Pacific oyster dominates in mariculture operations. Other shellfish species cultured in Europe include clams, scallops and abalones.

2.2.5 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, 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 are defined as those shallower than 30 m depth.

3 Quantitative habitat assessment

3.1 Introduction

Population dynamics are driven by both density-dependent (regulation) and – independent (limitation) processes, which, in turn, can be mediated by the structural complexity of a species' habitat. Density dependence can either be (1) direct, whereby input rates (birth and immigration) vary inversely with population size and/or loss rates (mortality and emigration) vary directly with population size, or (2) inverse, whereby input rates vary directly with population size and/or loss rates vary inversely with population size (i.e. the opposite of direct density dependence) (Hixon *et al.*, 2002). In contrast, density independence is the absence of (substantial) change in these demographic rates in response to changes in population size (Hixon *et al.*, 2002). Mechanisms most often proposed for how structural complexity of marine habitats influences demographic rates of a given species are that food supplies and survival increase with habitat structural complexity (Heck *et al.*, 2003, Minello *et al.*, 2003). There is equivocal evidence, however, for the role of habitat type and complexity in driving patterns of population dynamics and overall abundance due, in part, to limited data on the components of demographic rates and assessing the role of those rates at the population level. Herein we review the literature on habitat effects on population demographic rates such as Birth, Death, Immigration and Emigration, as well as local density. Because most marine populations are demographically open, we combine Births and Immigration as "Recruitment."

In this review, we differentiate between component and demographic effects (Stephens *et al.* 1999, Kramer *et al.* 2009). A component effect changes a component of fitness while a demographic effect changes the overall fitness at the population level (Stephens *et al.*, 1999). A component effect can suggest there is potential for a demographic effect, which is much harder to demonstrate than a component effect (Stephens *et al.*, 1999). In some of the examples cited in our report, a positive relationship between habitat complexity and juvenile density is a component effect, which can translate (but not always) into a positive relationship between habitat complexity and population fitness. To disentangle the role of habitat versus other factors in driving population dynamics and overall abundance, we need information on habitat-specific demographic rates that can be used to parameterize population dynamics models. We thus review the literature for habitat-specific demographic rates of exploited fish and invertebrates.

3.2 Methods

Our intent was to select and review publications on immigration, emigration, growth, mortality and density of fish and macroinvertebrates in coastal habitats. We limited our search to commercially exploited species in view of the scope of the workshop. Search and selection of publications was conducted haphazardly, based on our individual publication databases and a search of the ISI Web of Knowledge literature data-base search engine--priority was given to studies that compared and contrasted a demographic rate(s) across multiple habitats, as well as to studies focusing on several demographic rates simultaneously and that presented empirical data. For each study, information was gathered on the geographical area and precise location, type of approach of the study (correlative, experimental or meta-analysis), habitat types, species (scientific name), species group (fish, crustacean or mollusc), life stage (larvae, juvenile or adult) and demographic rates considered in the study (immigration, emi-

gration, mortality, growth, density), as well as availability of empirical data on the study and its conclusions (Table 3.1). We then selected a few representative examples of species-specific studies in which demographic rates have been quantified in different habitats and provided those in Table 3.2.

3.3 Results

We selected 124 papers for this study (Table 3.1). Six of these studies were meta-analyses, and 117 were original research papers. Of the latter, 84 were descriptive studies identifying correlations between habitats and demographic rates, 36 were experimental studies, of which the majority were field experiments, and several were experimental habitat choice studies in the laboratory or in mesocosms. Seven of the original research papers had both a descriptive and an experimental component.

The number of demographic rates studied in the different papers differed. Most studies (85) measured densities in one or more habitats and related these to habitat characteristics. Growth and mortality were measured in 52 studies. In only 18 papers were growth, mortality and density compared simultaneously. Post-settlement processes such as growth and survival were studied in 70 papers, and pre-settlement processes such as substrate selection by larvae in 9.

The spatial scale of studies varied from 1 m² to > 1000 km². Most of the studies (35) were performed on a scale of only several square meters. Thirty studies took place on a scale of 1 km². The intermediate scale (10 km²) was least represented (2), while research effort increased again at the larger scales (13 at 100 km², and 17 at scales over 1000 km²).

With regards to habitats involved, the majority of studies took place on soft bottom (64) or sea grass (42). Salt marshes, unvegetated bottom adjoining salt marshes, mangroves, coral reefs and shallow open waters were each represented in approximately 15 studies. Less than 10 studies were performed on kelp, macroalgae, oyster beds, mussel beds, other biogenic structures, rocky shores or artificial habitats. Many studies investigated one or more demographic rates in a single habitat. Two habitats were compared in 33 studies, and three or more habitats in 25 studies.

Most studies were carried out in North America (53) and Europe (36), with fewer studies in Asia (6), Africa (2), the Caribbean (14) and Oceania (9). Fish were over-represented in the selection (106), with fewer (14) invertebrate examples. Two studies included fish and invertebrates.

Although the literature search was not carried out in an objective manner and was highly influenced by the background of the participants, there are some general patterns that can be derived from the literature on habitat-specific demographic rates. Below, we summarize the main findings organised by the four distinguished demographic rates: immigration and emigration, growth and survival, and density as an integrative indicator of demographic rates.

3.3.1 Immigration (larval/postlarval settlement)

Replenishment of marine benthic populations typically involves “settlement” from pelagic larval to benthic juvenile habitats (e.g. Gleason *et al.*, 2009, Eggleston *et al.*, 2010). Within the context of overall larval dispersal and settlement (Figure 3.1), at relatively small scales in time and space, habitat features, such as structural complexity, chemical and sound cues, and location within the seascape can influence settlement success (Armsworth *et al.*, 2004).

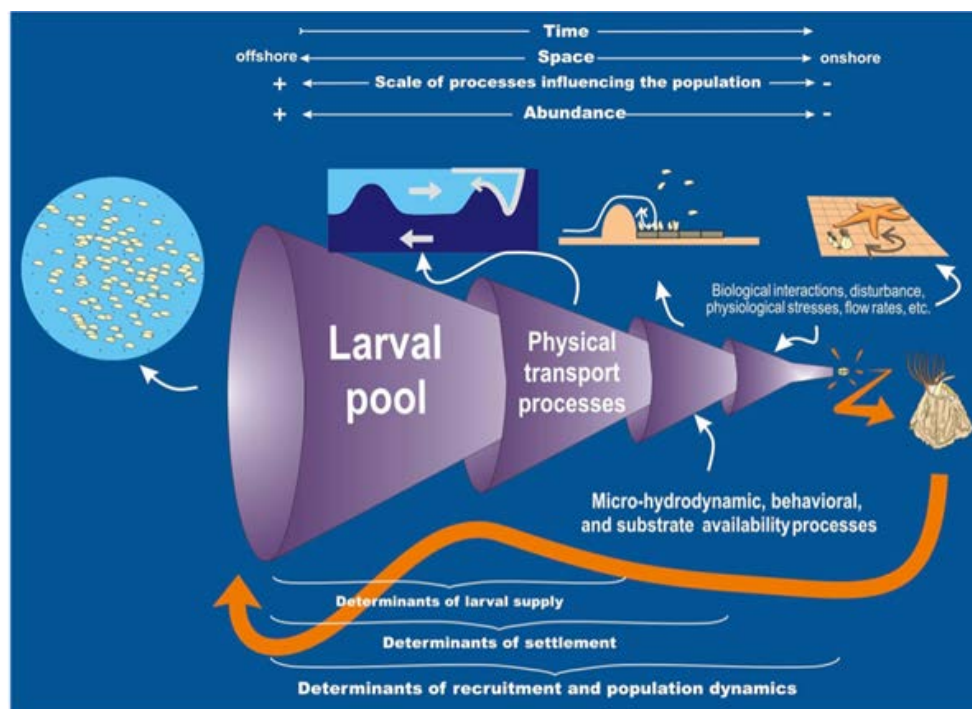


Figure 3.1. Schematic of hierarchical processes influencing larval settlement and subsequent population dynamics of marine benthic populations. Processes are both serial, and ordered in space, starting with processes in the larval pool, far from the settlement site, and ending in processes occurring around the settlement site. There is also a scale correspondence, with larger spatial scale processes occurring in the larval pool, followed by physical transport processes, and smaller scale processes occurring at the settlement site. The present review focused primarily on substrate availability processes. Schematic adapted from Pineda, 2000.

Despite considerable research efforts during the past 30 years on quantifying substrate selection behavior by competent larvae under laboratory and field condition (e.g. Birrell *et al.*, 2008), our review of the literature found relatively few quantitative estimates of habitat-specific settlement compared to information on habitat-specific demographic rates such as growth and survival (5 of 123 examples in Table 3.1). Experimental approaches usually involve exposing naturally settling larvae in the field to different settlement substrates (e.g. Eggleston and Armstrong, 1995), to synoptic surveys of different habitat types during intense recruitment periods (Nash *et al.*, 2007), to laboratory habitat choice experiments that expose competent larvae to a range of habitat types or varying substrate complexity (Ray and Stoner 1995; VanMontfrans *et al.*, 2003). In our examples, differences in settlement sometimes spanned 1-2 orders of magnitude between habitat types (Ray and Stoner, 1995; Eggleston and Armstrong, 1995; VanMontfrans *et al.*, 2003). In one case, high settlement patterns by settling-stage Dungeness crabs (*Cancer magister*) in oyster shells versus soft-bottom habitats were de-coupled within 48 hours due to post-settlement mortality, resulting in no differences in crab density between shell and mud after 48 hours (Eggleston and Armstrong 1995). In other cases, relatively high settlement in one habitat versus another was preserved in the juvenile population for several weeks post-settlement (e.g. blue crabs in seagrass: Heck *et al.*, 2003). There is a strong need for more experimental studies that quantify the effects of different substrates in larval settlement and post-settlement processes such as emigration, growth and survival.

3.3.2 Emigration (secondary dispersal)

The degree to which populations are considered demographically open is often defined by an organism's dispersal capability, and is generally life-stage dependent. For example, many marine organisms undergo long-distance dispersal during a pelagic larval phase, before settling to benthic habitats where they remain as juveniles and adults (Scheltema, 1986), often with ontogenetic changes from juveniles in restricted nursery grounds to subadults and adults more widespread. While larval dispersal can have significant population-level consequences (e.g. maintain spatially-separated sub-populations, enhance gene flow, alter distribution and abundance patterns), the same may be true of pelagic, post-settlement emigration (secondary dispersal) by juveniles or adults following initial settlement to the benthos (Caley *et al.*, 1996; Reyns and Eggleston, 2004). Similar to larval transport, secondary dispersal can occur over relatively large distances (Beukema and de Vlas, 1989; Etherington and Eggleston, 2003), and thus has the capacity to enlarge a species' distributional range (Armonies, 1992), as well as restructure populations and communities (Caley *et al.*, 1996, Palmer *et al.*, 1996, Etherington and Eggleston, 2003; Reyns and Eggleston, 2004). Moreover, a rapidly growing body of literature suggests that secondary dispersal is more prevalent than previously believed in aquatic systems, with examples from diverse taxa including marine meiofauna (Palmer, 1988), marine and stream benthos (Günther, 1992), and reef fishes (Hindell *et al.*, 2003).

Despite this rapidly growing area of research, our review of the literature found very few quantitative estimates of habitat-specific emigration from initial settlement habitats for commercially exploited species (2 of 124 examples in Table 3.1). Watson *et al.* (2002) disentangled post-settlement movement and mortality to explain loss of recently settled snapper (*Ocyurus chrysurus*) in tropical seagrass beds in the British Virgin Islands. They found that fish < 8 cm total length were consistently observed in seagrass, but were never recorded in censuses of adjacent rocky habitat, where older juveniles occurred. Thus, settlement-stage fish were assumed to reside in seagrass for several weeks (Watson *et al.*, 2002). Second, average home ranges for fish of 2 – 2.5 cm and 3 – 3.5 cm total length were estimated to be 2.3 m² and 6.3 m², respectively, indicating that movement of newly settled *O. chrysurus* was negligible compared to the size of the census area (1250 m²). Third, late pelagic-stage *O. chrysurus* caught with light traps in adjacent waters were tagged sub-cutaneously with fluorescent elastomer tags, and released at the center of the seagrass grid the evening after their capture. Ninety-six individuals were released over three evenings in September 1999. Concurrent aquarium studies showed tagging mortality was 13%. Over the following eight days, 32 re-sightings were made. Only one fish was seen more than 2 – 3 m distant from where it was sighted on the first census after releases were completed, providing convincing evidence of site fidelity after settlement (Watson *et al.*, 2002).

In another example, Reyns and Eggleston (2004) examined environmental (wind, diel cycle, tidal phase) and biological (ontogenetic, density-dependent) factors that contribute to the secondary dispersal of a benthic marine invertebrate, the blue crab (*Callinectes sapidus*) in Pamlico Sound, North Carolina, USA (Figure 3.2). Field studies conducted in relatively large (0.05 km²) seagrass beds determined that secondary dispersal is primarily undertaken by the earliest juvenile blue crab instar stages (J1 crabs). These crabs emigrated pelagically from seagrass settlement habitats using nighttime flood tides during average wind conditions (speed ~ 5 m s⁻¹), and during all diel and tidal cycles when winds exceeded 15 m s⁻¹. Moreover, the secondary dispersal of J1 crabs was density-dependent and regulated by intra-cohort (J1) crab density in seagrass. Their results suggest that dispersal occurs rapidly following settlement,

and promotes blue crab metapopulation persistence by redistributing juveniles from high-density settlement habitats to areas characterized by low postlarval supply. Collectively, these two contrasting examples illustrate that seagrass can serve as an initial settlement habitat where settlers display high site fidelity on the scales of weeks to months before exhibiting an ontogenetic shift to coral reefs (e.g. Watson *et al.*, 2002), or that seagrass can serve as an initial “landing strip” in which increasing intra-cohort densities can drive secondary dispersal to alternative nursery habitats and thereby alter initial settlement patterns (Reyns and Eggleston, 2004). Future studies should emphasize the spatiotemporal scales at which secondary dispersal occurs in exploited species to better define settlement habitats, and the degree of connectivity between primary and secondary settlement areas.

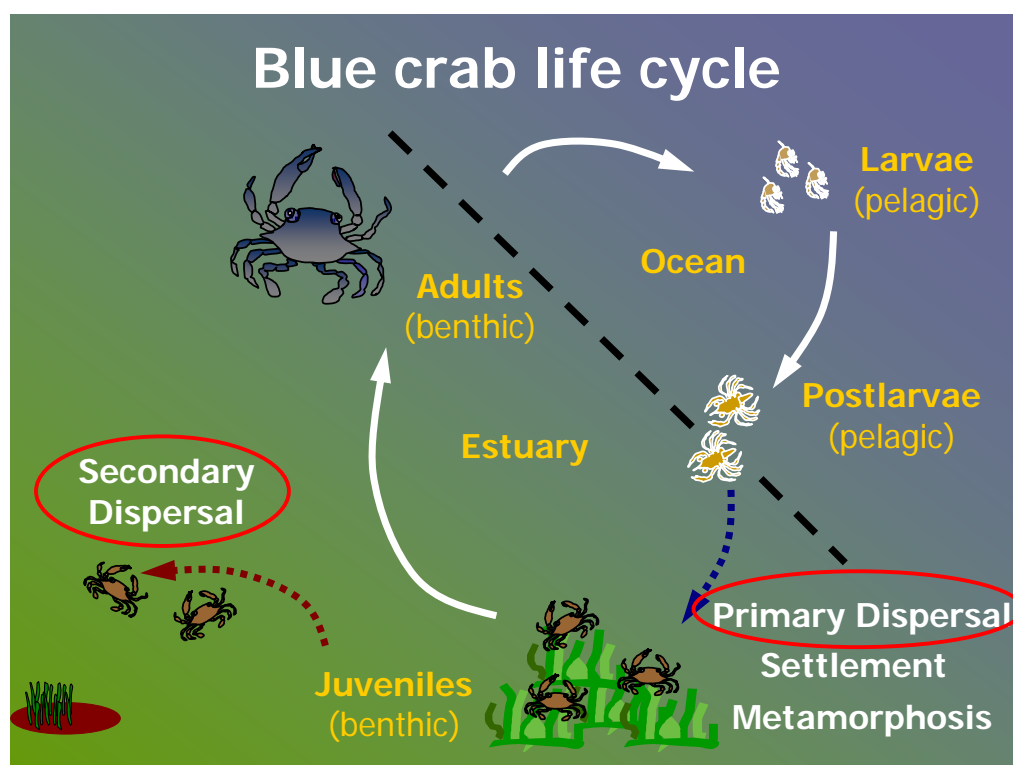


Figure 3.2. Schematic of secondary dispersal of recently settled blue crabs (*Callinectes sapidus*) from seagrass to alternative nursery habitats, such as shallow marsh detritus, after initial settlement of postlarvae from the plankton to seagrass. Adapted from Reyns and Eggleston (2004).

3.3.3 Growth rate

Food availability and predation on nursery grounds are the main drivers of habitat choice and individual fitness during the juvenile stages of many species. Size-selective mortality appears especially important during the first benthic life stage following larval settlement, and can reflect structural refuge provided by a given habitat, as well as abiotic factors of a given habitat, or simply reflect relatively high survival during the larval stage that is maintained post-settlement (“larval inertia”) (Searcy *et al.*, 2007 a,b). Below, we summarize the effects of habitat type on growth rate and survival.

The effects of habitat type on growth rates was quantified in 45% of the selected studies (Table 3.1). The scales of studies ranged from large (1000 km², depth gradient, estuarine / non estuarine systems) to medium (km², intra-ecosystem gradients) to small (m², local habitats). In ~ 50% of these growth studies, there was no effect of

habitat type on growth rates. In many of these cases, however, growth rates were influenced by factors other than structural aspects of the habitat, such as salinity and temperature. Thus, considering only growth as an indicator of habitat suitability could lead to spurious conclusions (Searcy *et al.*, 2007 a,b). There was also evidence of density-dependent growth in certain cases, which when combined with density-dependent mortality, can regulate local populations. Another issue that arose in this study was related to variation in methods used to estimate growth (increase in size for different periods of life and with different time steps, increases in weight, body mass at weight and body condition such as mass at size, or biochemical condition such as ARN/AND or lipid content, otolith increment). Thus, it is important for future studies of habitat-specific growth rates to standardize response variables and methods whenever feasible, and integrate abiotic characteristics of a given habitat along with pre-settlement growth trajectories (e.g. Searcy *et al.*, 2007 a,b).

Despite these caveats, several patterns regarding habitat-specific growth emerged:

- i) Evidence of density-dependent mortality due to food deprivation and size-selective predation;
- ii) Preponderance of studies on habitat-specific rates of species in seagrass at medium to local spatial scales, and among shallow habitat types at the large scale in estuaries;
- iii) Recognition of the importance of watershed characteristics (freshwater influx, organic mater loading) and location within the seascape (immigration success), and adjacent habitats (food web) on the nursery role of a given focal habitat type; and
- iv) Recognition of the negative consequences to growth of degradation in habitat characteristics and water quality on growth and immigration.

3.3.4 Mortality

In the present review, approximately 35% of the selected references mention mortality as an important factor driving habitat suitability, but only a low proportion provided quantitative estimates of mortality or survival rates, especially for mobile species. Understandably, survival estimates are more easily quantified in sessile invertebrates such as oysters, or invertebrates with relatively low mobility such as certain crustaceans, compared to more mobile fish. Moreover, it was not possible to discriminate mortality from immigration-emigration processes in most of the studies reviewed.

The majority of studies quantified mortality as a function of habitat complexity, or as a function of habitat degradation. The effects of habitat type on mortality had the greatest impact on recently settled stages of organisms compared to later stages. Given that mortality is especially high during the first life stages, habitat-specific differences in mortality rates can lead to large differences in subsequent recruitment success of juveniles. The lack of approaches coupling estimates of growth and mortality, which would allow for integrated quantitative estimates of habitat suitability, is evident from Table 3.1. Although the selection of references focusing on habitat suitability was directed at multi-habitat comparisons, only 15% combined a focus on growth, mortality and density.

3.3.5 Density

Population density, a key response variable in assessing a species' abundance patterns and certain types of resource management strategies, can modify demographic

rates and regulate populations (Caley *et al.*, 1996). Density of individuals was the most commonly quantified variable in our review, probably due to the relative ease with which it can be quantified compared to other demographic rates. Many of these studies quantified density of a given species across multiple coastal habitats simultaneously.

Many of the examples from this study demonstrated an order of magnitude difference in animal density between habitats at different scales, especially for juvenile fish. For example, several reviews and meta-analyses (e.g. Minello *et al.*, 2003, Heck *et al.*, 2003) found that densities were highest in relatively shallow vegetated habitats compared to unstructured and relatively deep habitats. Many studies also demonstrated how habitat quality can vary according to both biotic and abiotic factors (e.g. salinity, temperature, prey-availability, refuge), which can vary in space for a given habitat type, and for a given species (Table 3.1). One emerging area of research is related to the ability of a habitat to serve as a barrier to successful establishment of an invasive species (Reusch and Williams 1999), or comparing the nursery role of an endemic versus invasive species of vegetated structure (Carroll *et al.*, 2010). Another active area of research concerns the effects of habitat degradation on a species' demographic rates.

3.4 Conclusions

We conclude that there is: (i) a strong need to standardize demographic rates across studies and habitats, (ii) relatively little information on emigration and immigration, both key ecological processes that connect spatially separate populations, and (iii) relatively little experimental quantification of demographic rates within and among habitat types. Quantitative data are key to disentangling the role of pre- versus post-settlement processes underlying habitat-specific differences in species densities. This review provides an important step towards integrating habitat-specific demographic data into population models that can, in turn, evaluate the role of habitat on population dynamics for species selected in this review (Table 3.1).

Table 3.1. Selected studies on quantitative relationships between demographic rates of exploited species in coastal habitats. Data shown are: type of study (C - correlative, E - experimental, M - meta-analysis), habitats included, group of species (F - fish, C - crustacean, M - mollusc), species, life stage (L - larvae, J - juvenile, A - adults), demographic rate, and reference.

Type	Habitats	Group	Species	Life stage	Demographic rate	Source
Asia						
C	Soft bottom	F	<i>Lateolabrax japonicus</i>	J	growth, emigration	Islam Tanaka et al. 2006
C	Soft bottom	F	<i>Platichthys bicoloratus</i>	J	mortality, density	Yamashita et al. 2000
C	Seagrass, Soft bottom	F	<i>Lateolabrax labrus</i>	L/J	growth rate, density	Yube et al. 2006
E	Seagrass, Coral reef, Soft bottom	F	<i>Lethrinus atkinsoni</i>	J	growth rate, mortality	Nakamura et al. 2012
E	Mangrove	F	<i>Apogon amboinensis</i> , <i>Gerres erythrouus</i>	J	survival	Nanjo et al. 2011
E	Seagrass	F	<i>Pagrus major</i>	J	mortality (predation)	Shoji et al. 2007
Oceania						
C	Coral reef, Soft bottom, Biogenic reefs and beds	F	Several	All	density	Fitzpatrick et al. 2012
C	Coral reef	F	<i>Dascyllus aruanus</i>	J	density	Holbrook et al. 2000
C	Kelp, Mangrove, Soft bottom	F	Several	J	density	Laegdsgaard et al. 2001
C	Soft bottom	F	<i>Sillaginodes punctatus</i> , <i>Arripis georgianus</i>	J/A	growth	Potter et al. 2011
C	Soft bottom	F	<i>Pristipomoides filamentosus</i>	J	density	Parrish et al. 1997
E	Soft bottom, Artificial	F	>20 species	J	density	Dempster Kingfors 2004
E	Mangrove	F	<i>Chromis viridis</i>		mortality	Lecchini et al. 2007
M	Mangrove	F	14 species	J/SubA	mortality, density	Hixon Jones, 2005
M	Macroalgae	F/C	8 species	J	mortality, density	Manson et al. 2005
Europe						
C	Shallow open water	F	<i>Engraulis encrasicolus</i>	L	growth	Allain et al. 2003
C	Shallow open water	F	<i>Engraulis encrasicolus</i>	L	density	Allain et al. 2004
C	Soft bottom	F	<i>Solea solea</i>	J	growth	Amara et al. 2007
C	Soft bottom	F	<i>Solea solea</i>	J	growth	Amara et al. 2008
C	Shallow open water	F	<i>Engraulis encrasicolus</i>	J	growth	Basilone et al. 2004
C	Soft bottom	F	<i>Dicentrarchus labrax</i>	J	growth, density	Cabral Costa 2001
C	Shallow open water	F	<i>Sardina pilchardus</i>	L	mortality	Chicharo et al. 1998

Type	Habitats	Group	Species	Life stage	Demographic rate	Source
C	Shallow open water	F	<i>Engraulis encrasicolus</i>	L	growth (condition), mortality	Cutitta et al. 2006
C	Soft bottom	F	<i>Solea solea</i>	J	growth, density	Darnaude et al. 2004
C	Soft bottom	F	<i>Solea solea</i>	J	growth	Dierking et al. 2012
C	Unvegetated marsh	F	<i>Pleuronectes platessa</i> , <i>Limanda limanda</i>	J	density	Gibson et al. 2002
C	Soft bottom	F	<i>Solea solea</i>	J	growth	Gilliers et al. 2006
C	Shallow open water	F	<i>Clupea harengus</i>	L	growth	Hook 2008
C	Soft bottom	F	<i>Dicentrarchus labrax</i>	J	growth, density	Kelley 2002
C	Soft bottom	F	<i>Solea solea</i>	J	growth, density	Kostecki et al. 2010
C	Saltmarsh, Unvegetated marsh	F	<i>Pleuronectes platessa</i> , <i>Solea solea</i> , <i>Limanda limanda</i>	J	growth	Kostecki et al. 2011
C	Saltmarsh	F	<i>Dicentrarchus labrax</i>	J	growth, density	Lafaille et al. 2000
C	Soft bottom	F	<i>Solea solea</i>	J	mortality, density	Le pape et al. 2003
C	Soft bottom	F	<i>Solea solea</i>	J	mortality, density	Le pape et al. 2003
C	Soft bottom	F	<i>Solea solea</i>	J	growth	Le pape et al. 2003
C	Soft bottom	F	<i>Solea solea</i>	J	density	Le pape et al. 2007
C	Saltmarsh, Unvegetated marsh, Soft bottom	F	<i>Solea solea</i>	J	growth	Le pape et al. 2012
C	Seagrass, Soft bottom	F	<i>Gadus morhua</i>	J	growth, mortality	Lekje et al. 2003
C	Soft bottom	F	<i>Solea solea</i>	J	density	Nicolas et al. 2008
C	Seagrass	F	Several	J	density	Parlier et al. 2006
C	Saltmarsh	F	Several	J	density	Parlier et al. 2006
C	Seagrass, Soft bottom	F	<i>Gadus morhua</i>	J	mortality, density	Pihl et al. 2006
C	Seagrass, Soft bottom	C	<i>Crangon crangon</i>	J	density	Polte et al. 2005
C	Soft bottom, biogenic reefs and beds	F	<i>Pleuronectes platessa</i>	J	density	Rabaut et al. 2010
C	Soft bottom	F	<i>Solea solea</i>	J	density	Rijnsdorp et al. 1992
C	Soft bottom	F	<i>Solea solea</i>	J	density	Rochette et al. 2010
C	Shallow open water	F	<i>Engraulis encrasicolus</i>	L	mortality, density	Ruiz et al. 2009
C	Shallow open water	F	<i>Sardina pilchardus</i>	J	density	Tsagarakis et al. 2008
C	Soft bottom	F	<i>Pleuronectes platessa</i>	J	density	van der Veer et al. 2001
C	Unvegetated marsh	F	<i>Pleuronectes platessa</i>	J	mortality, density	Wennhage Pihl 2001

Type	Habitats	Group	Species	Life stage	Demographic rate	Source
	Soft bottom	F	<i>Pleuronectes platessa</i>	J	growth, mortality, emigration, density	Nash et al. 2007
Africa						
C	Shallow open water	F	Several	L	density	Cury Roy 1989
C		F	Several	J	mortality, density	Lamberth et al. 2009
North-America						
C	Seagrass, Kelp,	F	<i>Lagodon rhomboides</i>	J	growth, mortality, density	Adams et al. 2004
C	Soft bottom	F	<i>Parophrys vetulus</i>	J	mortality, density	Chittaro et al. 2009
C	Soft bottom, biogenic reefs and beds	F	Several	J	density	Diaz et al. 2003
C	Shallow open water, Biogenic reefs and beds, Rocky shore	F	Several	J	density	Diaz et al. 2003
C	Seagrass, Mangrove, Coral reef, Biogenic reefs and beds	C	<i>Panulirus argus</i>	J	density	Eggleston Dahlgren 2001
C	Seagrass, Coral reef, Biogenic reefs and beds	F	Several		density	Eggleston et al. in review
C	Mangrove	F	<i>Cyprinodon variegatus</i>	J	density	Ellis Bell 2004
C	Unvegetated marsh, Soft bottom	F	<i>Paralichthys lethostigma</i>	J	growth, density	Glass et al. 2008
C	Seagrass, Saltmarsh, Macroalgae, Unvegetated marsh, Soft bottom	F	<i>Pseudopleuronectes americanus</i>	J	density	Goldberg et al. 2002
C	Saltmarsh	F	<i>Fundulus heteroclitus</i>	J	growth	Goto Wallace 2010
C	Rocky shore	F	<i>Sebastes mystinus</i>	J	mortality, density	Johnson 2007
C	Kelp, Soft bottom	F	<i>Paralichthys dentatus</i> , <i>Pseudopleuronectes americanus</i>	J	mortality, density	Manderson et al. 2000
C	Kelp, Soft bottom	F	<i>Pseudopleuronectes americanus</i>	J	density	Meng et al. 2005
C	Soft bottom	F	<i>Lutjanus synagris</i>	J	growth, mortality, density	Mikulas Rooker 2008
C	Soft bottom	F	<i>Lutjanus campechanus</i>	J	growth, mortality, density	Rooker et al. 2004
C	Seagrass	F	<i>Sciaenops ocellatus</i>	L / J	growth, density	Rooker et al. 1997a
C	Seagrass	F	<i>Sciaenops ocellatus</i>	L / J	growth, density	Rooker et al. 1997b
C	Soft bottom	F	<i>Pleuronectes vetulus</i>	J	mortality, density	Rooper et al. 2004

Type	Habitats	Group	Species	Life stage	Demographic rate	Source
C	Soft bottom	F	<i>Leiosoutheastern xanthurus</i> and <i>Micropogonias undulatus</i>	J	growth, mortality, density	Ross 2003
C	Unvegetated marsh	F	<i>Sciaenops ocellatus</i>	L/J	growth, mortality, density	Sharf 2000
C	Macroalgae, Coral reef	F	<i>Epinephelus morio</i> and <i>Mycteroperca bonaci</i>	J	density	Sluka et al. 2001
C	Shallow open water	F	<i>Clupea harengus</i>	J/A	growth	Stokesbury et al. 1999
C	Soft bottom	F	<i>Lepidopsetta polyxystra</i>	J	density	Stoner et al. 2007
C	Saltmarsh, Soft bottom, oyster reef	F/C	59 species	J	density	Stunz et al. 2010
C	Seagrass	F	<i>Seriola dumerili</i>	J	growth, mortality, density	Wells Rooker 2004
C	Kelp	F	<i>Paralabrax clathratus</i>	J	density	White Caselle 2008
C	Soft bottom	F	5 species	J	growth, mortality, density	Woodland et al. 2012
C	Seagrass	C	<i>Callinectes sapidus</i>	J	emigration	Reyns Eggleston 2004
C / E	Kelp	F	<i>Tautoglabrus adspersus</i>	L	mortality, emigration	Levin 1993
E	Seagrass	M	<i>Argopectin irradians</i>	J/A	growth	Carroll et al. 2010
E		F	<i>Leiostomus xanthurus</i>	J	growth, mortality, density	Craig et al. 2007
E	Shallow open water	F	<i>Cynoscion regalis</i>	L	growth	Duffy et al. 1996
E	Soft bottom, Artificial	F	<i>Pseudopleuronectes americanus</i> , <i>Tautoga onitis</i>	J	growth	Duffy-Anderson Able 1999
E	Kelp, Soft bottom, Rocky shore	M	<i>Mytilus edulis</i>	J/A	growth, mortality, density	Eckman Duggins 1991
E	Soft bottom, oyster reef	C	<i>Cancer magister</i>	L/J	mortality, density	Eggleston Armstrong 1995
E	Seagrass, Soft bottom, Oyster reef	C	<i>Cancer magister</i>	J	mortality, density	Fernandez et al. 1999
E	Seagrass, Artificial	F	<i>Fundulus heteroclitus</i>	J	growth	Halpin 2000
E	Seagrass, Soft bottom	M	<i>Argopectin irradians</i>	J/A	growth, mortality, density	Irlandi et al. 1995; Irlandi 1999; Bologna Heck 1999
E	Saltmarsh, unvegetated marsh	C	<i>Callinectes sapidus</i>	J	mortality, density	Johnson Eggleston 2010
E	Saltmarsh, Macroalgae, Unvegetated marsh	F	<i>Pseudopleuronectes americanus</i> , <i>Tautoga onitis</i>	J	growth	Kuorpat et al. 2002
E	Saltmarsh, Unvegetated marsh	C	<i>Callinectes sapidus</i>	J	mortality	Lipcius et al. 2005

Table 3.2. Examples of habitat-specific demographic rates. Life stage (J - juvenile, A - adult).

SPECIES	LOCATION	HABITAT	LIFE STAGE	DEMOGRAPHIC		SOURCE
				RATE	VALUE	
Fish						
<i>Pseudopleuronectes americanus</i>	Navesing River, New Jersey	bare soft bottom	J	mortality	70 (%/day)	Manderson <i>et al.</i> 2000
		algae			38 (%/day)	
		eelgrass			15 (%/day)	
<i>Pseudopleuronectes americanus</i>	Nagarranset Bay, Rhode island)	upstream anthropogenic pressure	J	growth	0.33 (mm/day)	Meng <i>et al.</i> 2001
		upstream (low anthropogenic pressure)			0.53 (mm/day)	
		downstream (low anthropogenic pressure)			0.42 (mm/day)	
<i>Pseudopleuronectes americanus</i>	Nagarranset Bay, Rhode island)	beach cove	J	density	0.072	Meng <i>et al.</i> 2005
		beach no cove			0.041	
		deep zone cove			0.01	
		deep zone no cove			0.005	
<i>Pseudopleuronectes americanus</i>	Connecticut	mud shell litter	J	density	5.05	Howell <i>et al.</i> 1999
		mud wood litter			2.39	
		mud no litter			3.57	
		sand litter			1.2	
		sand no litter			0.8	
<i>Solea solea</i>	coasts of France	highly contaminated estuaries	J	growth	5	Gilliers <i>et al.</i> 2006
		"clean" estuaries			8.2	
<i>Solea solea</i>	Bay of Vilaine	high biomass of invertebrates	J	density	244	le Pape <i>et al.</i> 2007
		low biomass of invertebrates			2.72	

SPECIES	LOCATION	HABITAT	LIFE STAGE	DEMOGRAPHIC	VALUE	SOURCE
				RATE		
<i>Solea solea</i>	Eastern English Channel	mud	J	density	1.8	Rochette <i>et al.</i> 2010
		gravel			3.3	
		< 3m			6.04	
		>8m			1.2	
<i>Solea solea</i>	bay of Biscay	invasive mollusc covering soft bottom	J	density	15	Le Pape <i>et al.</i> 2004
		no invasive mollusc covering soft bottom		density	45	
<i>Solea solea</i>	bay of Biscay	estuaries	J	growth	19.7	le Pape <i>et al.</i> 2003
		coastal systems			17.5	
<i>Mullus surmuletus</i>	Venice Lagoon	seagrass bed	J	density	0.02/100m2	Franco <i>et al.</i> ECSS 2006
		sparsely vegetated habitat	J	density	0.37/100m2	
		bare sand habitat	J		1.35/100m2	
		mudflat	J		0.04/100m2	
		saltmarsh creek	J		0.03/100m2	
<i>Plathichtus flesus</i>	Venice Lagoon	seagrass bed	J		0.15/100m2	
		sparsely vegetated habitat	J		0.17/100m2	
		bare sand habitat	J		0.3/100m2	
		mudflat	J		2.17/100m2	
		saltmarsh creek	J		0.99/100m2	
<i>Solea vulgaris</i>	Venice Lagoon	seagrass bed	J		0.02/100m2	
		sparsely vegetated habitat	J		1.14/100m2	
		bare sand habitat	J		1.34/100m2	
		mudflat	J		1.35/100m2	
		saltmarsh creek	J		1.03/100m2	

SPECIES	LOCATION	HABITAT	LIFE STAGE	DEMOGRAPHIC		SOURCE
				RATE	VALUE	
<i>Dicentrarchus labrax</i>		salt marsh	J	density	5.31/min	Parlier <i>et al.</i> Cah. Biol. Mar. 2006
		salt marsh deteriorated (mowed+inv species)	J		2.07/min	
		salt marsh deteriorated (mowed+inv species)	J		0.17/min	
<i>Pleuronectes platessa</i>	Belgium coast	beach without lanice	J	density	4.7/sample	Rabaut <i>et al.</i> 2010
		beach with lanice	J		15.5/sample	
<i>Apogon aboinensis</i>	Japan, Urauchi River estuary	mangrove, mangrove-root	J	mortality	50%/30 min	Nanjo <i>et al.</i> 2011
		mangrove, unvegetated central area			85%/30 min	
<i>Gerres erythrouros</i>	Japan, Urauchi River estuary	mangrove, mangrove-root	J	mortality	70%/30 min	
		mangrove, unvegetated central area			85%/30 min	
<i>Engraulis encrasicolus</i>	Venice Lagoon	seagrass bed	J	density	0/360m2	Franco <i>et al.</i> 2006
		sparsely vegetated habitat			0.28/360m2	
		bare sand habitat			8.91/360m2	
		mudflat			4.28/360m2	Franco <i>et al.</i> 2006
		saltmarsh creek			1.57/360m2	
<i>Clupea harengus</i>	Aiguillon Bay/Mont Saint Michel Bay	salt marsh	J	density	1.61/min	Parlier <i>et al.</i> 2006
<i>Lethrinus atkinsoni</i>	Japan, Ishigaki Island	seagrass	J (small)	mortality	55%/hr	Nakamura <i>et al.</i> 2012
		coral reef			28%/hr	
		seagrass	J (medium)		66%/hr	
		coral reef			70%/hr	

SPECIES	LOCATION	HABITAT	DEMOGRAPHIC		VALUE	SOURCE
			LIFE STAGE	RATE		
		seagrass	J (large)		100%/hr	
		coral reef			100%/hr	
		seagrass	J (small)	growth	0.3 mm/day	
		coral reef			0.11 mm/day	
		seagrass	J (medium)		0.18 mm/day	
		coral reef			0.6 mm/day	
Argopectin irradians	Gulf of Mexico	seagrass edge	J + A	growth	0.031 mg dry wt./day	Bologna and Heck 1999
		seagrass interior			0.019 mg dry wt./day	
		unstructured soft-bottom			0.012 mg dry wt./day	
		seagrass edge		mortality	20% loss/day	
		seagrass interior			5% loss/day	
		unstructured soft-bottom	J + A	mortality	5% loss/day	
		seagrass edge		density	0.75 indvs/m2	
		seagrass interior			0.36 indvs/m2	
		unstructured soft-bottom			0.00 indvs/m2	
Mollusc						
Strombus gigas	Bahamas	seagrass (high density)	J (small)	growth	0.272 mm/day	Ray and Stoner 1995
		seagrass (low density)			0.306 mm/day	
		sand			0.285 mm/day	
		seagrass (high density)	J (medium)	growth	0.51 mm/day	
		seagrass (low density)			0.49 mm/day	
		sand			0.395 mm/day	
		seagrass (high density)	J (large)	growth	0.37 mm/day	
		seagrass (low density)			0.39 mm/day	
		sand			0.27 mm/day	
		seagrass (high density)	J (small)	mortality	High	
		seagrass (low density)			Lowest	
		sand			Highest	
		seagrass (high density)	J (medium)	mortality	High	

SPECIES	LOCATION	HABITAT	LIFE STAGE	DEMOGRAPHIC		SOURCE
				RATE	VALUE	
		seagrass (low density)			Lowest	Ray and Stoner 1995
		sand			Highest	
		seagrass (high density)	J (large)	mortality	High	
		seagrass (low density)			Lowest	
Crustacean		sand			Highest	
<i>Callinectes sapidus</i>	Chesapeake Bay	seagrass -low density crabs	J	growth	14 mm ³ /day	Perkins-Visser <i>et al.</i> 1996
		seagrass -high density crabs			18 mm ³ /day	
		soft-bottom (low density crabs)			7 mm ³ /day	
		soft-bottom-high density crabs			10 mm ³ /day	
		seagrass -low density crabs		mortality	0.71%/day	
		seagrass -high density crabs			1.57%/day	
		soft-bottom (low density crabs)			1.08%/day	
		soft-bottom-high density crabs			2.5%/day	

4 Coastal habitat use of commercial species relevant to ICES

4.1 Introduction

Commercial species from the Northeast Atlantic were poorly represented in the literature covering quantitative habitat assessments in coastal areas (see Section 3). It was therefore of interest to establish to what degree commercial species use coastal habitats. The present review was limited to the species for which ICES gives advice, focusing this initial compilation to important stocks within the ICES area and to taxa for which information on the influence of coastal habitats could potentially be incorporated in future advice.

ICES gave advice for 59 taxa in 2012 (ICES in prep). 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 occur in the coastal zone and that are important economically or ecologically. Catches of species using coastal habitats and for which ICES provides advice 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>).

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 reporting area. 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" for habitats poorly represented in the original search. Depth ranges were obtained from FishBase.

4.2 Habitats and habitat function

Coastal habitats are defined in Section 2 of this report, 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 commercial fish species and invertebrates by listing four different ecological functions. The categorisation was mainly based on papers referring to these functions, but in some instances also on our conclusions referring to the definitions below.

- 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.

4.3 Coastal habitat use by ICES species

Out of the 59 ICES species investigated, 25 species corresponding to 42%, were considered to use coastal habitats to some extent. None of these 59 species seemed to be

resident in a single coastal habitat, and for the large majority of species the life cycle had a non-coastal component (Table 4.1). Overall, the nursery function was the most prevalent function found for 29% of the ICES species, followed by feeding grounds for 20%, spawning areas for 10%, and migration route for 8% (Figure 4.1).

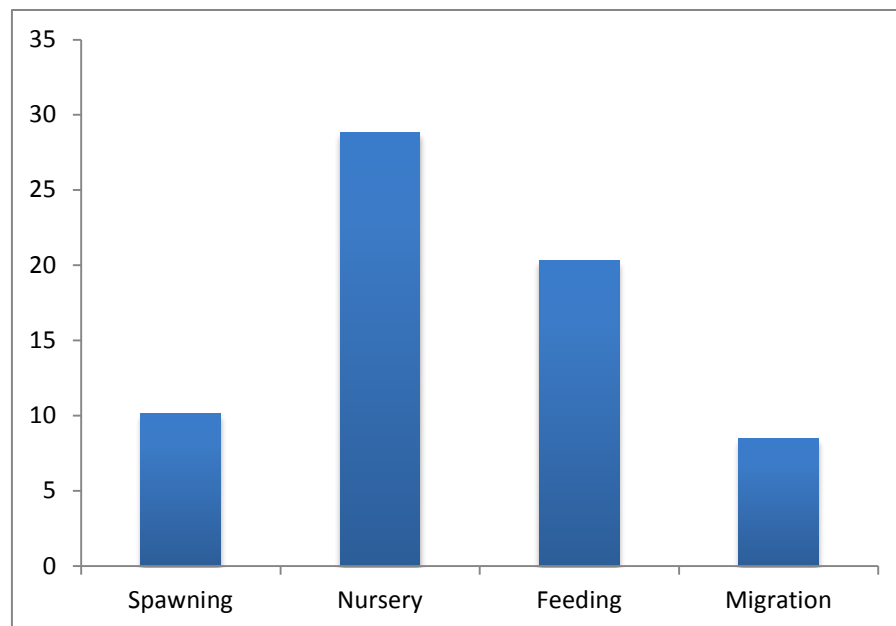


Figure 4.1. Proportion (%) of ICES species using coastal habitats for spawning, feeding, migration, and as nursery grounds.

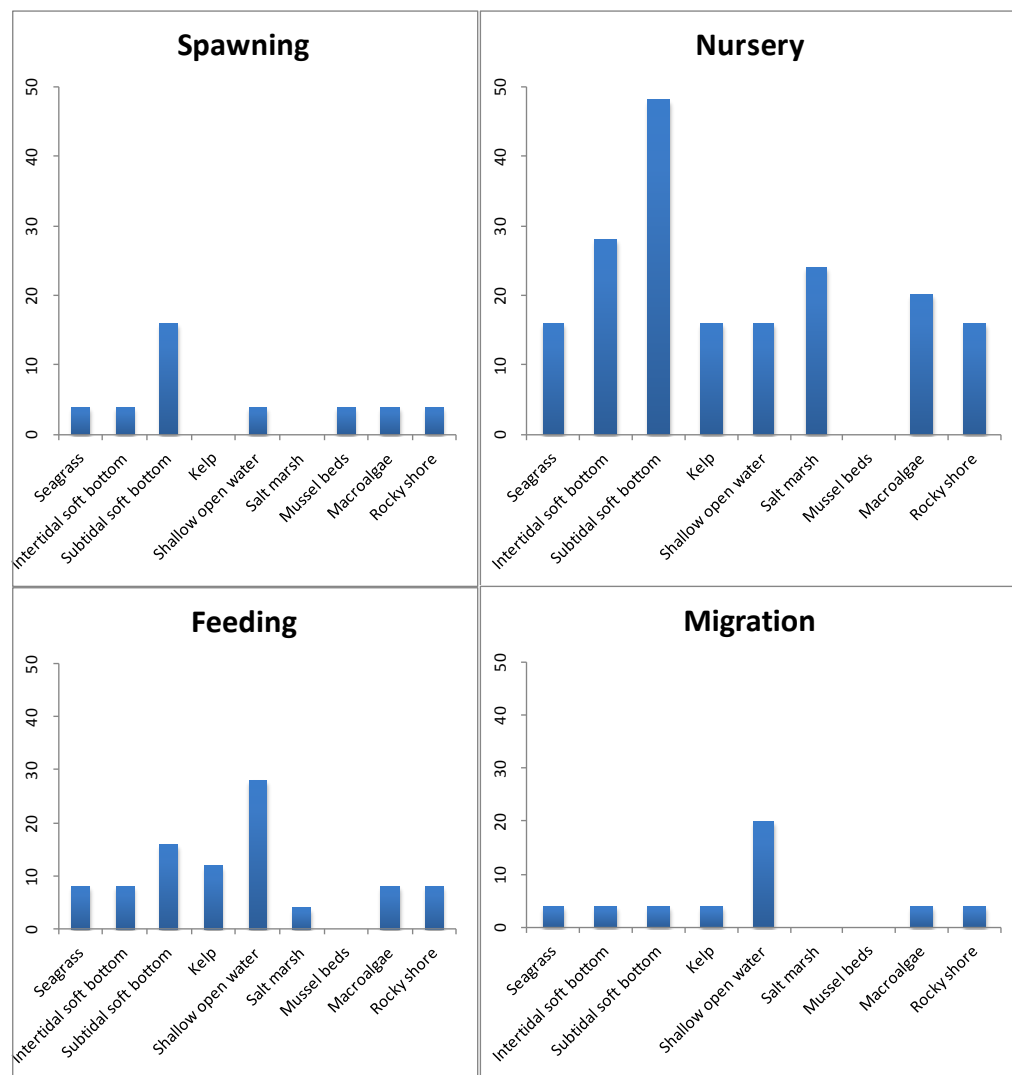


Figure 4.2. Relative contribution (%) of the different coastal habitats for the main functions (Spawning, Nursery, Feeding, Migration) identified among the ICES advice species that use coastal habitats.

Table 4.1 (Continued). Coastal habitat use of commercial species for which ICES gives advice in 2012. 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 section 3 for which there was information on species habitat use. Depth ranges were collated from FishBase.

<i>Mullus surmuletus</i>	Striped red mullet			N			N			Yes	5-100	Rogers et al 1998, Mathieson et al 2001, Santos and Monteiro 1997
<i>Nephrops norvegicus</i>	Norway lobster										20-800	
<i>Pagellus bogaraveo</i>	Red seabream										<700	
<i>Pandalus borealis</i>	Northern prawn										20-1000	
<i>Phycis blennoides</i>	Greater forkbeard										10-800	
<i>Platichthys flesus</i>	Flounder		N	N, F			N			Yes	0-100	Florin et al. 2009, Cattrijsse and Ampel 2006
<i>Pleuronectes platessa</i>	Plaice		N	N, F			N			Yes	0-100	Gibson et al 1999, Cattrijsse and Ampel 2006
<i>Pollachius pollachius</i>	Pollack			N	N				N	Yes	0-200	Pihl et al 1994, Nordehaug et al 2005
<i>Pollachius virens</i>	Saithe			N	N				N	Yes	0-300	Pihl & Wennhage 2002, Nordehaug et al 2005
<i>Reinhardtius hippoglossus</i>	Greenland halibut										1-2000	Godo & Haug 1989
<i>Salmo salar</i>	Salmon	M	M	M	M	M			M	Yes	0-30	McCormick et al 1998
<i>Salmo trutta</i>	Sea trout	F	F	F	F	F, M			F	Yes	0-10	Pihl & Wennhage 2002
<i>Sardina pilchardus</i>	Sardine					F				Yes	10-100	Elliott & DeWailly 1995
<i>Scomber scombrus</i>	Mackerel					N, M				Yes	0-100	N, S, F = Jamieson & Smith 1987; M = Eltink 1987
<i>Scophthalmus maximus</i>	Turbot		N	S, N						Yes	<70	N, M, S = Iglesias et al. 2001; F = Gunvor et al. 1997; N = Gibson 1973
<i>Scophthalmus rhombus</i>	Brill		N	S, N						Yes	5-50	N = Gibson 1994, 1973; Denial 2006
<i>Sebastes marinus</i>	Golden redfish										50-300	N = R. K. Pikanowski 1999
<i>Sebastes mentella</i>	Beaked redfish										300-1400	N = R. K. Pikanowski 1999, Roquez et al. 2002
<i>Solea solea</i>	Sole		N, F			S, M				Yes	<60	N, = Lafaille et al. 2000; S = Koutsikopoulos et al. 1991 and Grioche et al. 2000; M = Derel et al. 1991; F = Cabral 2000
<i>Sprattus sprattus</i>	Sprat		N,			N, F	N			Yes	<150	N, = Lafaille et al. 2000 and Elliott et al 1990 and Voss et al. 2003; F = Voss et al. 2003 and Gorkhova et al. 2004; S, M = Baumann et al. 2006
<i>Squalus acanthias</i>	Spurdog										<200	F = Koen Alanso 2002
<i>Trachurus picturatus</i>	Blue jack mackerel										<300	
<i>Trachurus trachurus</i>	Horse mackerel										100-1000	
<i>Trisopterus esmarkii</i>	Norway pout			F						Yes	50-300	Pihl et al. 1992

The review also showed that representatives of ICES species using coastal habitats were found in the great majority of habitats and that all habitats except kelp, salt marshes, and mussel beds supported all of the four functions for at least one species (Figure 4.2). Subtidal soft bottom was the habitat used as spawning and nursery areas by the largest proportion of species. The most prevalent habitat for feeding and migration among the ICES advice species was shallow open water (Figure 4.2).

4.4 Coastal habitat use by exploited invertebrates

ICES gives advice for only two invertebrate species--Norwegian lobster (*Nephrops norvegicus*) and northern shrimp (*Pandalus borealis*). One reason for this may be that many commercial invertebrates are less mobile than fish and that the local populations are therefore managed nationally. A considerable number of commercial invertebrates are, however, coastal.

We chose to do a close examination of coastal habitat use for commercially important invertebrates that had a substantial percentage of fisheries landings in ICES areas, as well as for a number of species of particular interest due to their major contribution to other fisheries landings (e.g. *Callinectes sapidus*) or as important prey species (e.g. *Macoma balthica*) for other commercial species (Table 4.2). Of the 12 invertebrate species examined, all used the coastal habitat during some phase of their life history. All

habitats except kelp and salt marsh were used by several species. Shallow open water was the habitat most commonly used by invertebrates for spawning. Most habitats were used for Nursery function except kelp (Figure 4.3). Shallow subtidal and intertidal habitats were the most commonly used of the coastal habitats, with 16-25% of invertebrate species 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 4.3). Rocky shores were also commonly used for feeding (16% of species) or as nursery grounds.

Table 4.2. Coastal habitat use of selected commercially or ecologically important invertebrates of interest. 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 section 3 for which there was information on species habitat use.

Species	Common name	Coastal habitat types										References
		Seagrass	Intertidal soft bottom	Subtidal soft bottom	Kelp	Shallow open water	Salt marsh	Oyster Reef	Mussel beds	Macroalgae	Rocky shore	
<i>Crangon crangon</i>	Common shrimp	N, F	F			S, M						Howard & Bennett 1979; Jensen et al 1994; Tully and Ceidigh 1987; Nichols & Lawton 1978; Pandian 1970; Whale & Steneck 1991
<i>Ostrea edulis</i>	Oyster							S, N, F				Launey et al. 2001
<i>Callinectes sapidus</i>	Blue crab	N	N	N		S	N	N	N	N		Lipcius et al. 2007
<i>Homarus gammarus</i>	European Lobster			N, F		S					N, F	Pandian 1970; Nichols & Lawton 1978; Howard & Bennett 1979; Tully and Ceidigh 1987; Jensen et al 1994; Whale & Steneck 1991
<i>Macoma balthica</i>	Baltic clam		S, N, F	S, N, F		S						Bachelet 1980; Olafsson 1986; Beukema & De Vlas 1989; Armonies & Armonies 1992; Hiddink 2002
<i>Cancer pagurus</i>	Edible crab		N	F		M					N	S Brown & Bennett 1980; Bennett & Brown 1983; Hall et al. 1993; Sheehy & Prior 2008
<i>Palaemon serratus</i>	Common prawn	N	N, F	N						N		Anders 1982; Guerao & Ribera 1996; Guerao & Ribera 2000
<i>Placopecten magellanicus</i>	Atlantic sea scallops			F		N, F, S						MacDonald & Thompson 1985; Packer et al. 1999; Hunter and Sayer 2009
<i>Arctica islandica</i>	Ocean quahog		F			S, N, F						Thompson et al. 1980
<i>Mytilus edulis</i>	Blue mussel								S, N, F		S, N, F	Lintus & Seed 1994
<i>Cerastoderma edule</i>	Common cockle		N, F, S	N, F, S								Boyden & Russell 1972; Seed and Brown 1978
<i>Buccinum undatum</i>	Whelk			N, F, S								Himmelman and Hammel 1993

4.5 Catches of ICES species using coastal habitats

Total landings of fish and invertebrates reported within the ICES area was estimated to be 8,514,820 tons for 2010. The ICES species found to be associated with coastal habitats made up 71% of the total landings, and 77% of the landings of ICES species in the Northeast Atlantic (Table 4.3).

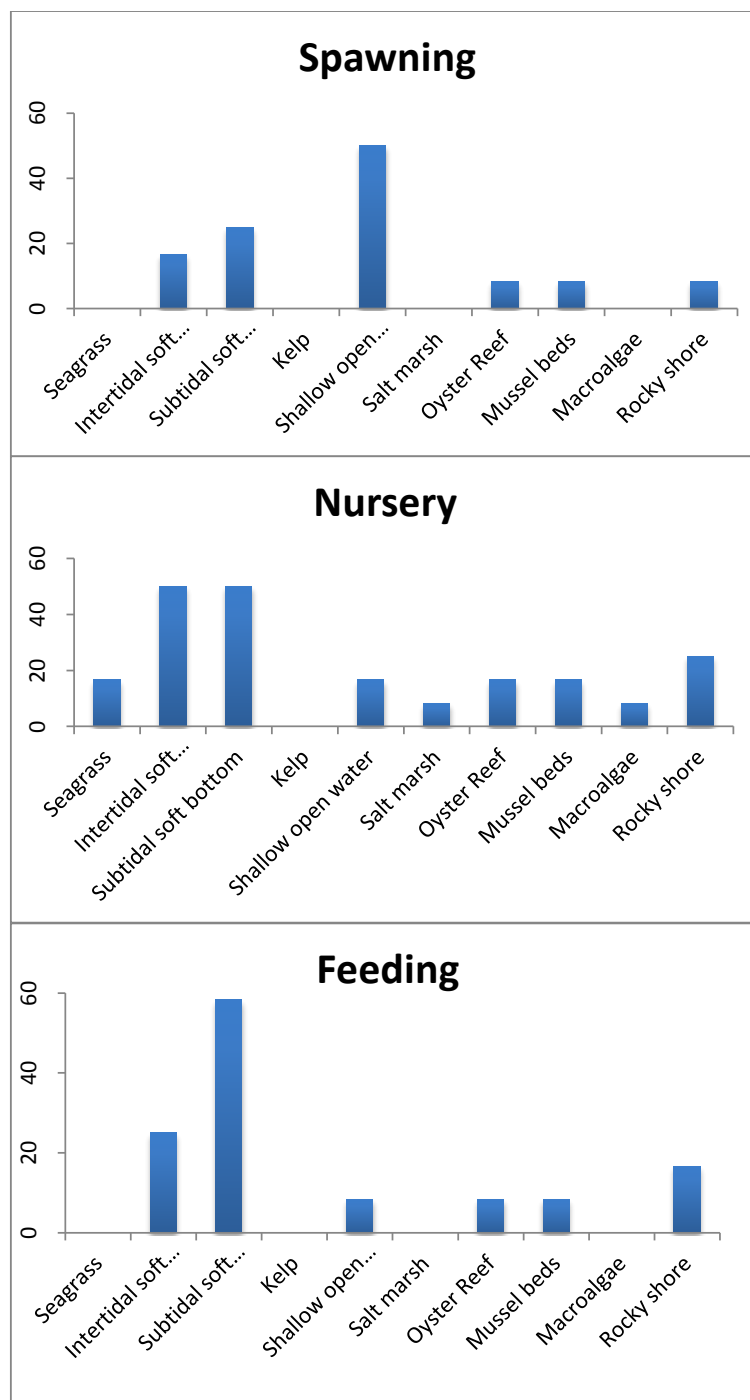


Figure 4.3. Relative contribution (%) of the different coastal habitats for the main functions (Spawning, Nursery, Feeding) identified among the invertebrate species investigated.

Table 4.3. Catches of ICES species with coastal habitat use (Yes/No) according to Table 4.1, and related to the total catch in the Northeast Atlantic (% of catch). Catches from ICES catch statistics for 2010.

Species	Catch (tons)	% of catch	Coastal habitat use
Herring	1986630	23.33	Yes
Cod	909008	10.68	Yes
Mackerel	831878	9.77	Yes
Blue whiting	546026	6.41	
Sprat	538105	6.32	Yes
Capelin	477679	5.61	Yes
Sandeel	422422	4.96	Yes
Haddock	364082	4.28	
Saithe	336504	3.95	Yes
Blue jack mackerel + horse mackerel	236745	2.78	
Golden redfish + beaked redfish	138300	1.62	
Boarfish	137678	1.62	
Norway pout	137079	1.61	Yes
Sardine	125997	1.48	Yes
Plaice	83967	0.99	Yes
Pollack	63743	0.75	Yes
Norway lobster	59010	0.69	
Hake	58957	0.69	
Anglerfish + black-bellied anglerfish	55141	0.65	
Northern prawn	43537	0.51	
Greenland halibut	41171	0.48	
Ling	33858	0.40	
Whiting	31430	0.37	Yes
Tusk	30372	0.36	
Flounder	26438	0.31	Yes
Sole	25020	0.29	Yes
Megrim + fourspot megrim	17201	0.20	
Anchovy	15365	0.18	Yes
Blue ling	12639	0.15	
Dab	11165	0.13	Yes
Lemon sole	11066	0.13	
Witch	10206	0.12	
European seabass	8263	0.10	Yes
Greater forkbeard	7191	0.08	
Roundnose grenadier	7094	0.08	
Black scabbard fish	6892	0.08	
Striped red mullet	5396	0.06	Yes
Turbot	4731	0.06	Yes
Greater silver smelt	4593	0.05	
Red gurnard + spiny red gurnard	4405	0.05	
Brill	2958	0.03	Yes
Red seabream	1172	0.01	
Eel	1152	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	0.00	
Portuguese dogfish	118	0.00	
Porbeagle	97	0.00	
Orange roughy	88	0.00	
Kitefin shark	6	0.00	
Basking shark	0	0.00	Yes
Spurdog	0	0.00	

4.6 Mariculture species in coastal habitats

4.6.1 Influence of shellfish aquaculture on benthic habitats

Potential effects of different shellfish aquaculture practises are widely described in the scientific and technical literature. The effects of different aquaculture systems depend on a number of factors, among which the local hydrographic conditions, the natural sedimentary habitat in which the culturing is taking place, the type of cultured organisms and the culture and production method, management practices, etc.

The effects are highly site specific and depend largely on the local environmental conditions. The sensitivity and resilience of the ecosystem and the assimilative capacity of the environment are key to determine the magnitude and significance of the impact.

Shellfish operations rely largely on the natural availability of nutrients and algae for their growth. High-productive areas are therefore preferred. Often these areas are also rich in biodiversity, and act as important nursery grounds for fish and crustaceans and feeding areas for birds. Because of this, many of these areas are internationally protected and are part of the European Natura 2000 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. Balancing these needs is in the long-term interest of coastal communities and sustainable development of coastal resources.

4.6.2 Importance of coastal habitats for shellfish aquaculture

Shallow coastal and estuarine habitats are the environment where most of the shellfish aquaculture is being practised. These environments are highly productive environments, providing the necessary food for filter feeding bivalves. But also these environments must provide the necessary larvae and juveniles, as shellfish aquaculture almost entirely relies on natural spatfall of larvae. These can be collected from natural substrates, or through specially designed collectors. A healthy ecosystem is therefore of utmost importance for the shellfish aquaculture,

4.6.3 Threats to coastal habitats that can impact shellfish aquaculture

The threats to nearshore coastal and estuarine ecosystems today arise from a vast range of human activities, from coastal development and industrial fishing to 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 impact on shellfish aquaculture to some extent.

4.7 Coastal habitat use of individual species

To illustrate the potential threats and value of coastal habitats for fish and invertebrates a selection of commercially important species from the ICES area are presented below.

4.7.1 Plaice (*Pleuronectes platessa*)

Plaice is found on sandy and muddy substratum of the European shelf from the Barents Sea to the Mediterranean including most of the Northeast Atlantic (Figure 4.3). The species normally occurs down to a depth of 100 m and gradually moves towards deeper habitats with increasing body size. Plaice is an example of flatfish species using shallow coastal habitats as nursery grounds. Other examples among the ICES species include turbot (*Scophthalmus maximus*), brill (*Scophthalmus rhombus*) and sole (*Solea solea*).

There is a targeted fishery for plaice, especially in the North Sea and in the Irish Sea. The species is mainly caught with beam trawls, Danish seines and gill nets. Plaice is also caught in mixed fisheries and as bycatch, for example in sole and *Nephrops* fisheries.

The North Sea stock has increased recently and is presently fished at MSY. In the Western Channel SSB is above B_{MSY} , but F is above target. For the other stocks there is insufficient information and precautionary advice is given (ICES, 2012). The stock structure in the Skagerrak, Kattegat and Western Baltic has been revised in 2012 because the analytical stock assessment has failed and needs to be improved.

Plaice are dependent on shallow (0–5 m) sediment substratum as nursery grounds during their early juvenile stage, and this habitat is only a small fraction of the species distribution range (Gibson, 1999). For plaice, 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 to settlement density, indicating that density-dependent processes are acting on the nursery grounds (Pihl *et al.*, 2000). These nurseries are important for the stock dynamic since a relationship between the nursery size and the population abundance exists, a relationship that has been conveyed as the “nursery size hypothesis” (Rijnsdorp *et al.*, 1992; van der Veer, 2000). The Wadden Sea is considered the largest and most important nursery ground in the North Sea. Spawning grounds are located so that eggs and larvae will be transported with prevailing currents towards the nursery grounds. Plaice larvae may then use selective tidal stream transport to reach the shallow most productive areas (Rijnsdorp *et al.* 1985). In the microtidal areas of Skagerrak, Kattegat and Western Baltic, wind-driven transport of larvae from offshore sources onto the nursery grounds means that the importance of different parts of the coast as nursery grounds may differ among years. Newly settled plaice are vulnerable to predation by *Crangon crangon* (van der Veer & Bergman, 1987) and *Carcinus maenas* (Ansell *et al.*, 1999). Plaice leave their nursery grounds at the end of their first summer and then gradually move towards deeper waters with increasing size.

Since plaice use shallow soft-bottom areas as nursery grounds, the early juvenile stage is vulnerable to new construction, such as harbours and road banks, and to land reclamation (Ronnback *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.

4.7.2 Cod (*Gadus morhua*)

Cod is widely distributed in the north Atlantic and Arctic (Figure 4.4), and is found in a variety of habitats, from the shoreline down to the continental shelf. Juveniles prefer shallow waters with complex habitats, which provide shelter from predators (Juanes, 2007). When maturing, the optimum temperature of cod decreases and the larger fish are mainly found in deeper and colder waters.

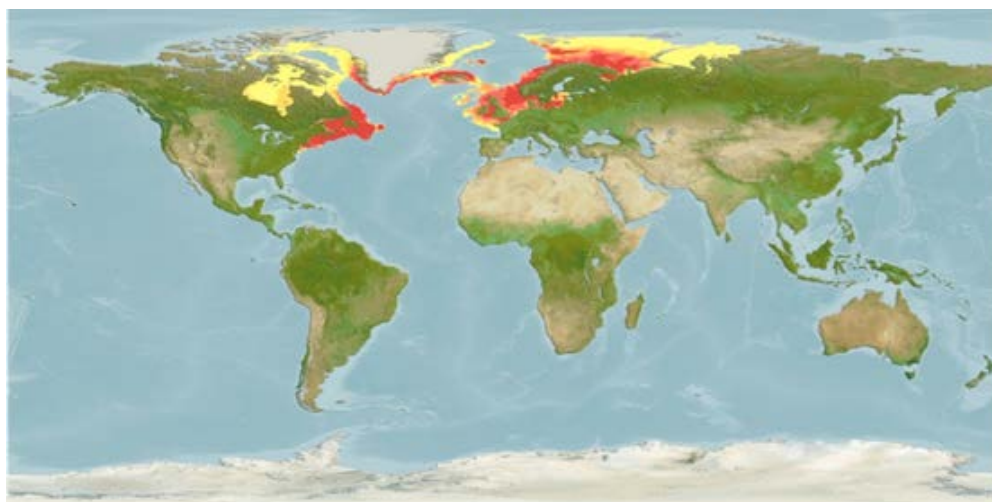


Figure 4.4. Cod (*Gadus morhua*) distribution map (FishBase 2012).

Cod has historically been by far the most important demersal species of North Atlantic fisheries, and continues to be so even though many cod stocks have been severely depleted. Most catches are taken in trawls, but also seines, gillnets and hook and line are important gear types. The landings of cod within the ICES area peaked in 1956, and in 2010 they were down to 40% of maximum with 909,000 tons. After a few years of lowered TAC (Total Allowable catch) in combination with other management measures, several stocks have now started to increase.

Cod spawn in the pelagic zone, usually in offshore areas. Eggs and larvae drift with currents, and after some months as pelagic larvae, at a size of 25–80 mm, cod settle to the seafloor (Juanes, 2007). As juveniles they are mainly found in complex habitats, such as seagrass beds, kelps, rocky shores and gravel bottoms with cobbles and attached fauna (Pihl and Wennhage, 2002, Norderhaug *et al.*, 2005, Lindholm *et al.*, 2004). Mortality risk of 0-group cod is lower in complex habitat types than in simple habitats, indicating that cod recruitment may be a function of habitat availability (Juanes *et al.*, 2007). Older life stages of cod are less dependent on specific habitat types, probably as a consequence of a lower vulnerability to predation.

Since cod is dependent on complex coastal habitats during early demersal life stages, loss of these habitat types may be detrimental to the populations. 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, Airoidi 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 loss due to harvesting of algae (Tegner and Dayton, 2000; 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).

4.7.3 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 fisheries species, especially in the North Sea. This species is tolerant of a multitude of environmental conditions and its distribution ranges along the European coast from the White Sea to Morocco, and includes the Mediterranean and Black Seas. The northern distribution is thought to be

regulated by egg and larval development needs, whereas the southern distribution is limited by maintenance costs (Campos, 2009).

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 tonnes landed; this was dominated by Germany and the Netherlands, with total catches of 12,000 to 16,500 tonnes, while Denmark, France, and the UK landed another 5,000 tonnes (Tulp *et al.*, 2011). There is a lack of management in the fishery, but the ICES *Crangon* working group has suggested that management should be implemented.

Though the status of the *C. crangon* stock is stable and EU landings have been steadily climbing since the 1970s, the fishery could be made more efficient. The fishery currently uses unselective gear in shallow coastal nursery areas, which results in excessive discards and damage to the environment (Tulp *et al.*, 2011).

Aside from the pelagic larval stage, this species is resident in shallow coastal areas of 1–20 m in sand or muddy sand habitats, though there have been records of this species obtaining 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. *Crangon crangon* can be found in high densities in tidal pools at low tide and regularly use tide pools and creeks (Cattijss and Hampel, 2006). They leave the tidal zone at about 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 tidal communities in Sweden, as they feed in tidal areas. They bury in the sediment during the day and are nocturnal (Pihl and Rosenberg, 1984). In the coastal zone of Holland, calanoid copepod blooms are linked with the settlement of *C. crangon*, suggesting the importance of resources for recruitment (Boddeke *et al.*, 1986). The major ecological threats to the species involve habitat degradation. Non-selective gear use in shallow habitats can destroy these fragile areas.

4.7.4 European lobster (*Homarus gammarus*)

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 in the Baltic Sea (Holthius 1991). Its distribution southward extends along the mainland European coast around Britain and Ireland, to a southern limit of about 30°N latitude on the Atlantic coast of Morocco (Figure 4.5). The species also extends throughout the coastal and island areas of the Mediterranean Sea, though less abundantly, and has been reported from the westernmost end of the Black Sea in the Straits of Bosphorus (Phillips *et al.*, 1980).

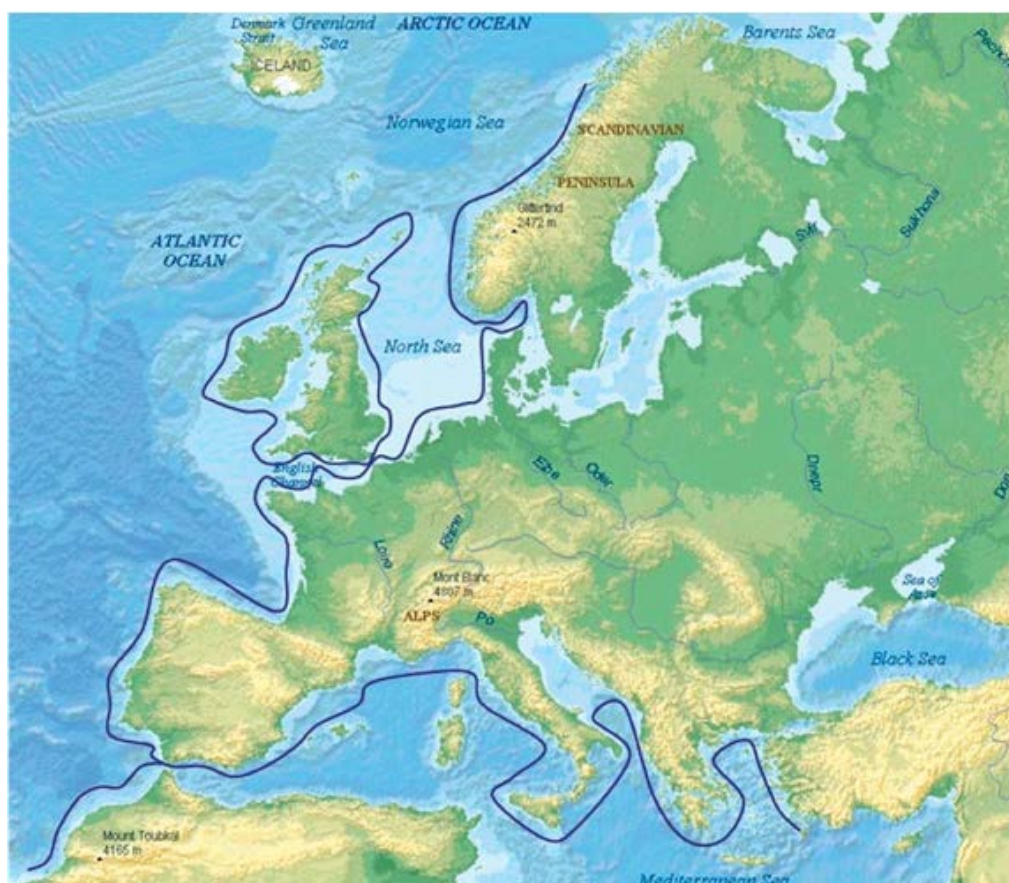


Figure 4.5. Distribution of *Homarus gammarus* (from Prodohl *et al.*, 1991).

Total annual European landings have varied between 1,600 and 5,000 tonnes in the recent past (Holthius, 1991; Prodohl, 2006), with a slow increase since the 1970s, and lobster catches vary considerably between countries (Prodohl 2006; FAO, 2006). Lobster aquaculture is also developing, based on some local declines and increases in demand, but production rates are still 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).

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. Adult *H. gammarus* live on the continental shelf and use a rock crevice habitat (Howard and Bennett, 1987). Early-benthic-phase juveniles of the closely related *H. americanus* in the Northeastern US are restricted to shelter-providing shallow cobble habitats, whereas adults are found in ledge and sedimentary substrata. Gravel and cobble are thought of as 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 spawned in shallow bays in Ireland and displayed diel vertical migration with high densities in the neuston (i.e. surface waters) at dawn and dusk (Tully and Ceidigh, 1987). Spawning begins in July and a spawning peak occurs in August (Panidian, 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).

5 Modelling habitat value for exploited populations

5.1 Continuous-time models

The continuous time models, or differential equation models, that could be used for studying species are suited for time and equilibrium analysis of the system. In general this type of model describes a population with one equation or consists of multiple equations representing stages. They may or may not incorporate a spatial component, whereby habitat is not, or implicitly or explicitly taken into account. When habitat is explicitly taken into account this type of model could be used to aid management directly, whereas when habitat is only implicitly or not accounted for, these models allow for a more general approach. The outcome of this type of model is population dynamics, mostly presented as equilibria or as numerical solutions. This approach also allows discovery of conditions for which alternative stable states exist.

St. Mary *et al.* (2000) used two life stages, juveniles and adults that occupy different habitats (Figure 5.1). In addition, for each stage two habitats were used, a marine reserve and an area outside the reserve. Migration to and from the reserve was allowed to examine source/sink function of the reserve. Density dependence in either stage or both was incorporated. They concluded that based on the socio-economic values, protecting only juveniles or both stages could be considered as suitable option for preserving the population.

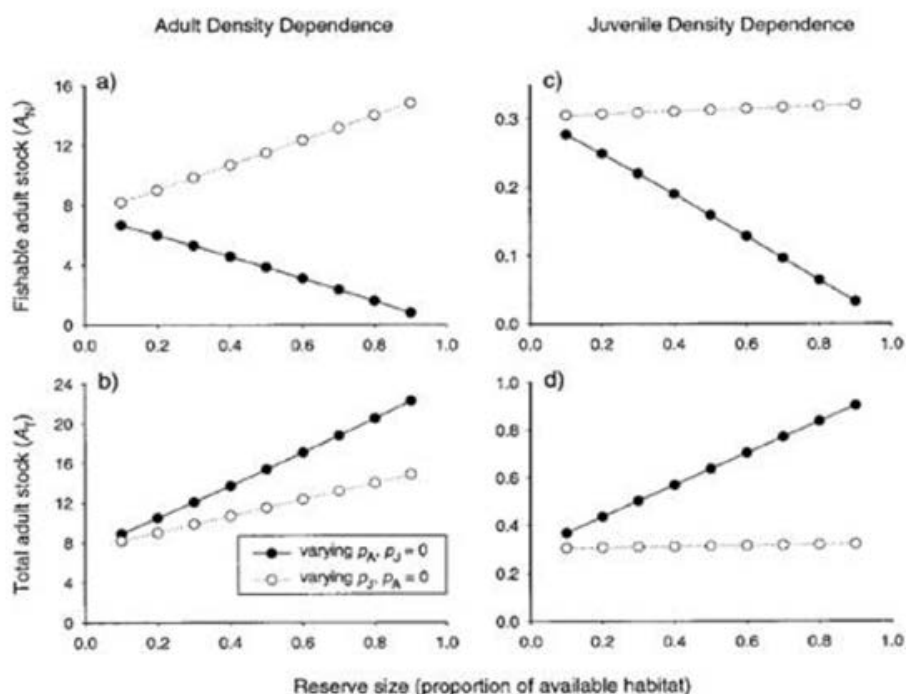


Figure 5.1. The effect of reserve size as studied by St. Mary *et al.* (2000). The effects of varying the size of adult or juvenile reserves on the fishable adult stock (panels A, C) and the total adult stock (C, D). In each panel the effect of adult reserves is presented in filled circles and the effect of juvenile reserves in open circles (D.B. Eggleston, unpublished manuscript).

Van de Wolfshaar *et al.* (2011) used a model with juveniles and adults, and included resources for these stages separately (Figure 5.2). In this manner spatial segregation of juveniles and adults was incorporated, resulting in resource competition within stages and not between stages. The relative difference between adult and juvenile habitat productivity was used to study effects on population dynamics. This difference between relative productivity resulted in alternative stable states with most biomass in either the juvenile or the adult stage. Fishing mortality on adults was added to the model. One of the main results of the study was that improving juvenile habitat could be more effective in increasing adult biomass than a reduction in fishing mortality.

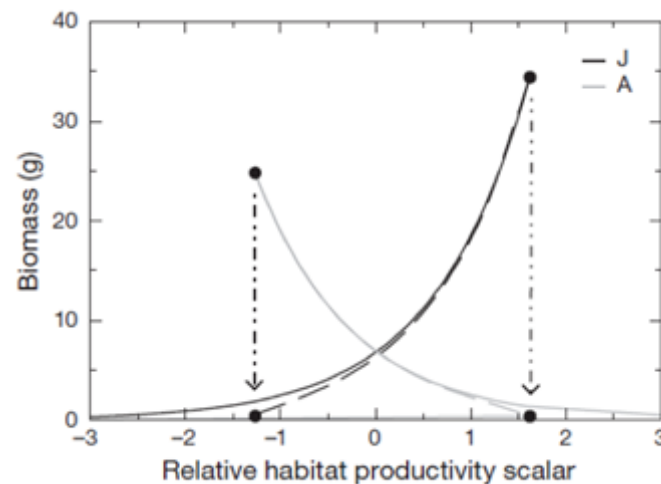


Figure 5.2. Example of the results of a differential equation model from Van de Wolfshaar *et al.*, (2011). Adult and juvenile equilibrium biomass as function of the relative habitat productivity scalar. Negative values of the scalar indicate that the adult habitat is more productive than the juvenile habitat, and positive values that the juvenile habitat is more productive than the adult habitat. Stable equilibria are solid and unstable equilibria are dashed. Alternative stable states occur between the hatched arrows, at which one of the alternative equilibria collapses and beyond which only one stable equilibrium occurs.

Jordan-Cooley *et al.*, (2011) used a set of differential equations to study the effect of live and dead oysters and sedimentation rates on the viability of oyster reefs (Figure 5.3). The model was developed to study the possibility and conditions of alternative stable states in oyster reefs. Three equations were used, live and dead oysters and the sediment layer. They found that the initial height of the oyster reef determined the equilibrium state. Only when the reef was high enough was the non-trivial equilibrium reached. This study therefore may aid restoration projects in creating viable artificial reefs.

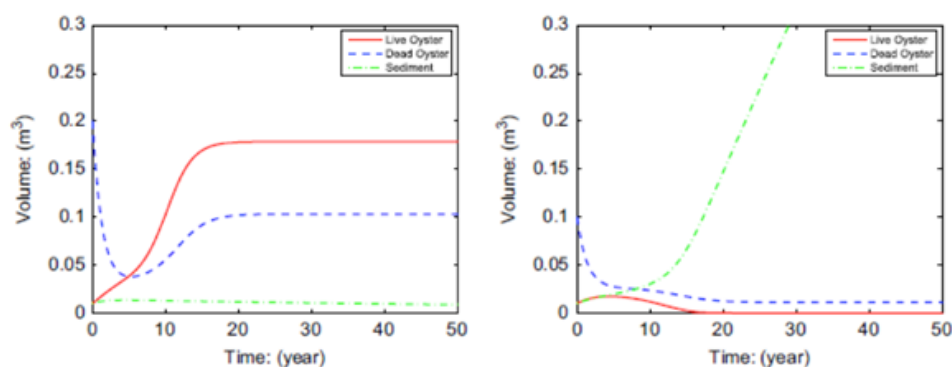


Figure 5.3. Numerical result from the model presented by Jordan-Cooley *et al.* (2011). Displayed is the change in live oysters, dead oysters and the sediment layer in time for different initial reef heights. The panel on the left shows an increase in live oysters reaching a non-trivial equilibrium in time when starting at a sufficiently high reef height. The panel on the right shows an increase in sediment and decrease in live oyster biomass and accreting reef when initial reef height is too low.

These types of models (i.e. differential equations) have not been used very often in this context, most likely due to the spatially explicit research questions concerning habitat use by species and habitat selection for conservation purposes, as well as the generic nature of these models. They do however provide insight into population behaviour in the context of spatial- and habitat-specific questions with relatively little parameterization effort. The simplicity of differential equation models is both a strong point and a weakness.

5.2 Discrete-time models

Many fish and invertebrate species are able to select among a diverse portfolio of habitat alternatives for reproduction, foraging or evading predators. Variability in habitat choice among individuals within a species, as well as ontogenetic migrations among habitats as fishery species age, add significant complexity for quantifying the functional value of purported essential fish habitats. Despite a general appreciation for the importance of high-quality habitat in promoting healthy fisheries (Figure 5.4), as well as a vast literature on habitat-specific growth and mortality rates (See Section 3), there is no synthetic approach that scales up from specific habitat use and vital-rate components to population dynamics, which has limited the formal and meaningful inclusion of habitat into fishery management plans and stock assessments (NMFS 2010).

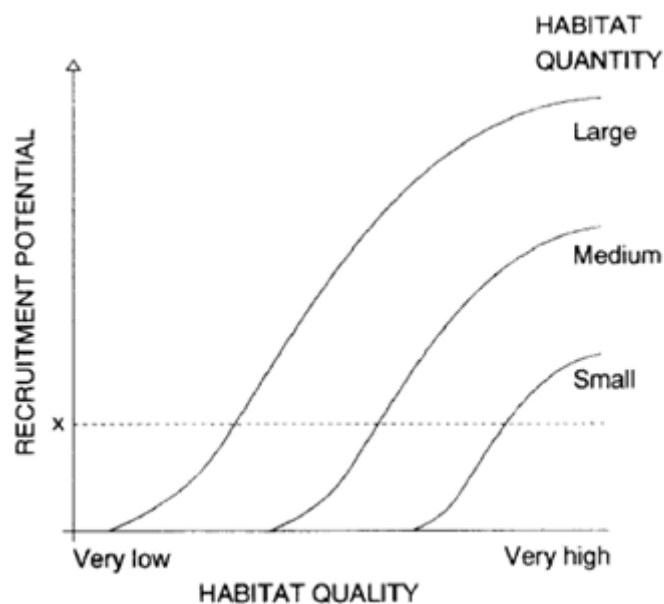


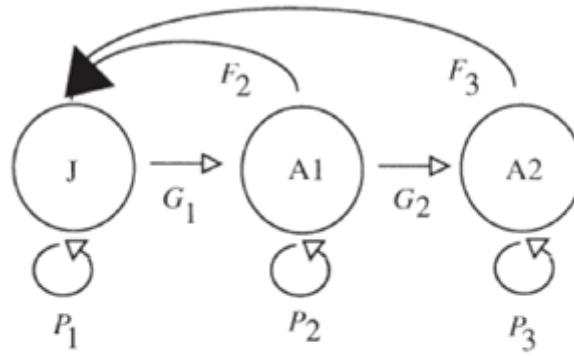
Figure 5.4. Hypothetical relationship between habitat quality and habitat availability in supporting healthy fisheries stocks (e.g., recruitment potential here). Beyond general models such as this one, quantitative relationships between habitat and population dynamics of exploited species remain elusive, and require improved modelling approaches. Figure taken from Gibson (1994).

In this section, we review two forms of discrete models that have the potential to (i) integrate habitat-related vital rates (growth, survivorship, fecundity) across life histories of fishes or invertebrates, and (ii) demonstrate the quantitative relationships between habitat use and population dynamics: population projection matrix models and finite time-step population models.

5.2.1 Population projection matrix models

The fitness of any population can be defined by its population growth rate λ (Leslie 1945). Lambda is a function of growth, survivorship and fecundity schedules, all of which may vary across space or through time. A population (or biomass) increases in circumstances where $\lambda > 1$, decreases in situations where $\lambda < 1$, and is stable in cases where $\lambda = 1$.

Given the complex life histories of most exploited species that include larval, juvenile and adult phases, populations can be best expressed as groups of connected age (Leslie, 1945), size or stage (Lefkovitch, 1965) classes. The basic form of these life histories and corresponding demographic vital rate matrices are shown in Figure 5.5. Subsequently, projecting changes in population size (and age/stage structure) can be accomplished by simple matrix algebra, and over the long-term by determination of the dominant eigenvalue (λ) of the vital rate matrix (Caswell, 2001). Because λ integrates vital rate information from all life-history stages into a single measure of overall population fitness, it can provide a clear and easily understandable metric of habitat value.



$$n_{t+1} = An_t$$

$$\begin{pmatrix} J_{t+1} \\ A1_{t+1} \\ A2_{t+1} \end{pmatrix} = \begin{pmatrix} P_1 & F_2 & F_3 \\ G_1 & P_2 & 0_3 \\ 0 & G_2 & P_3 \end{pmatrix} \times \begin{pmatrix} J_t \\ A1_t \\ A2_t \end{pmatrix}$$

Figure 5.5. Representative life-cycle diagram and associated vital rate projection matrix of marine species with complex life histories. Figure redrawn from Davis and Levin (2002).

We conducted a literature search for applications of age- or stage-based matrix models used to link habitat use with population dynamics (λ). Using the Web of Science platform, we examined all records identified using one of the following search combinations: “demography” or “demographic matrix” or “matrix model” or “leslie” or “population fitness” or “lefkovitch” paired with “fish” and “habitat.”

Marine (including those studies related to salmon) records pertaining to environmental gradients in habitat types, habitat quality, fishing pressure or spatio-temporal gradients in individual vital rates, as well as records that considered metapopulation dynamics were extracted for further analyses ($N = 24$). Only references dealing with single species were included, unless full model explanations were included for each species in the published article. These records highlight the broad applicability of projection matrix models. For instance, records covering bony fishes, elasmobranchs, invertebrates, mammals and reptiles are included in this list. Research themes were concentrated around detecting the consequences of pollution ($N = 5$), harvest ($N = 3$), environmental variability ($N = 4$), reserve establishment ($N = 2$), nursery habitat use ($N = 2$), metapopulation connectivity ($N = 2$), other environmental threats ($N = 5$), and restoration activities ($N = 2$). Among publications, demographic matrices were populated from a mix of study-related sampling, literature reviews or both. While most projection models were density independent, three of the studies did incorporate density dependence to estimate λ . Notably, we detected a strong bias (22 out of 24 records) towards published records arising from North American coastal waters (western Atlantic and eastern Pacific). Nine studies explicitly considered the fitness consequences of alternative habitats used by fishes or invertebrates.

Nearly all studies incorporated some form of sensitivity analysis (20 out of 24), consisting of both prospective (e.g. elasticities that reveal how sensitive λ is to proportional changes in matrix entries) and retrospective (e.g. decomposition analyses that calculate the actual contribution of age- or stage-specific growth, survival and fecundity rates to changes in λ across some degree of environmental variability).

To further demonstrate the value of this modeling approach in linking habitat use to population dynamics, we specifically consider the two studies noted above that investigated the population-level effects of nursery habitat utilization/selection in greater detail. Including population fitness as a metric of nursery value, a technique that considers the influence of each life-history stage, seems particularly advantageous for species in which the relative impacts of perturbations to both early (e.g. habitat degradation, bycatch) and late (e.g. harvest) life-history stages of a fluctuating population confound one another (Crouse *et al.*, 1987). Therefore, it is surprising that the quantitative effects of juvenile habitat utilization on fish or invertebrate demography have been largely neglected as a management tool.

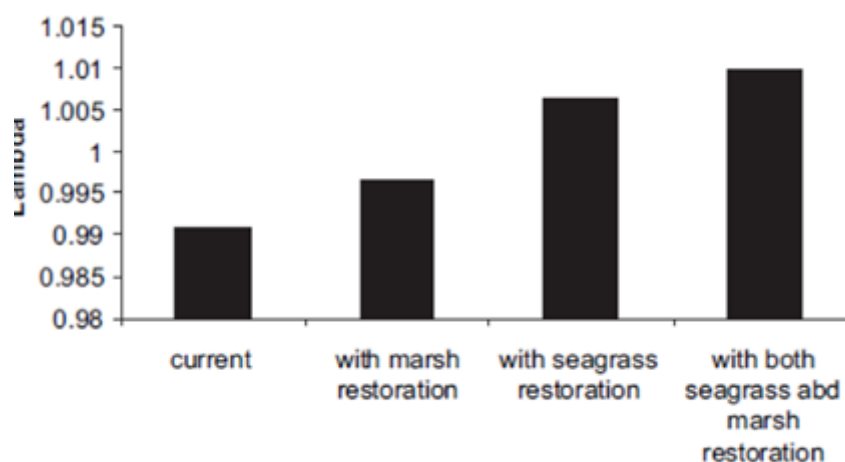


Figure 5.6. The projected population fitness (λ) of red drum following a series of hypothetical restoration activities. Figure taken from Levin and Stunz (2005).

Levin and Stunz (2005) utilized stage-structured models of red drum, *Sciaenops ocellatus*, to demonstrate that comprehensive wetlands restoration could lead to a 2% increase in population growth without any changes in fishing practices (Figure 5.6). This change resulted in a shift from negative to positive population growth for this species.

Fodrie *et al.* (2009) also considered the demographic consequences related to utilization of alternative nursery habitats by juvenile California halibut, *Paralichthys californicus* (Figure 5.7). Recently, the most widely-used metrics of nursery value have been (i) total production of individuals to an adult stock, and (ii) unit-area production to an adult stock. These authors, however, demonstrated that these metrics of nursery value could be decoupled from the impacts nursery use has on population growth rate (λ). Although alternative juvenile habitats (exposed coast and coastal embayments) could contribute an approximately equal number of recruits to the adult stock, positive overall population growth ($\lambda > 1$) depended critically on the subpopulations of juveniles that utilized coastal embayments (bays, lagoons, and estuaries). Conversely, the juvenile subpopulation along the exposed coast contributed negatively to overall population growth ($\lambda < 1$) in three of the four years of the study due to elevated local mortality in that habitat (Figure 5.7).

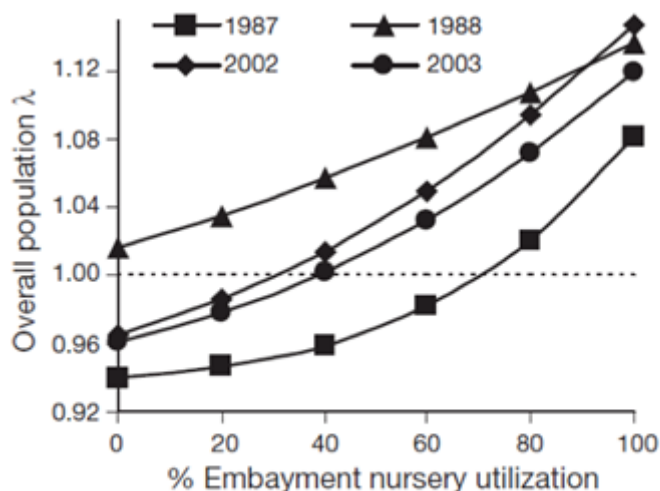


Figure 5.7. Fitness of California halibut populations resulting from the percentage of juvenile fish that utilized exposed coast versus embayment habitat as nurseries during 1987, 1988, 2002, and 2003. Dashed line represents a stable population ($\lambda = 1$). Figure taken from Fodrie *et al.* (2009).

Effective ecosystem-based management also increasingly recognizes the need to incorporate spatial ecology into management plans, and projection matrix models are amenable to metapopulation modelling approaches in which multiple demes are connected via dispersal (emigration) and connectivity (immigration) of larvae. Both Carson *et al.* (2010) and Eggleston *et al.* (unpublished data) combined local demographic matrices with larval connectivity matrices to explore the local and regional population dynamics of exploited bivalves. For instance, Eggleston and colleagues conducted mark-recapture studies and fecundity analyses to measure local demographics at 10 eastern oyster, *Crassostrea virginica*, spawning sanctuaries, and also used a 3-dimensional hydrodynamic model to estimate larval connectivity among this network of no-take oyster reserves (Figure 5.8). Their measurements indicated that oyster growth, survival, and reproduction varied greatly among reserves, such that certain reserves could be classified as the “growers” (i.e. reserves with fastest growth), others the “survivors,” and yet others the “spawners” (Figure 5.8). Inter-reserve connections were rare and relatively low in magnitude ($< 5\%$), while self-recruitment was relatively high in magnitude (20-50%) when present (3 of 10 sites). Limited connectivity and reserve-specific demographics resulted in an exponential decline in metapopulation size over time (overall $\lambda < 1$). Thus, these researchers concluded that the network of oyster reserves, as currently configured, was not capable of persisting through time.

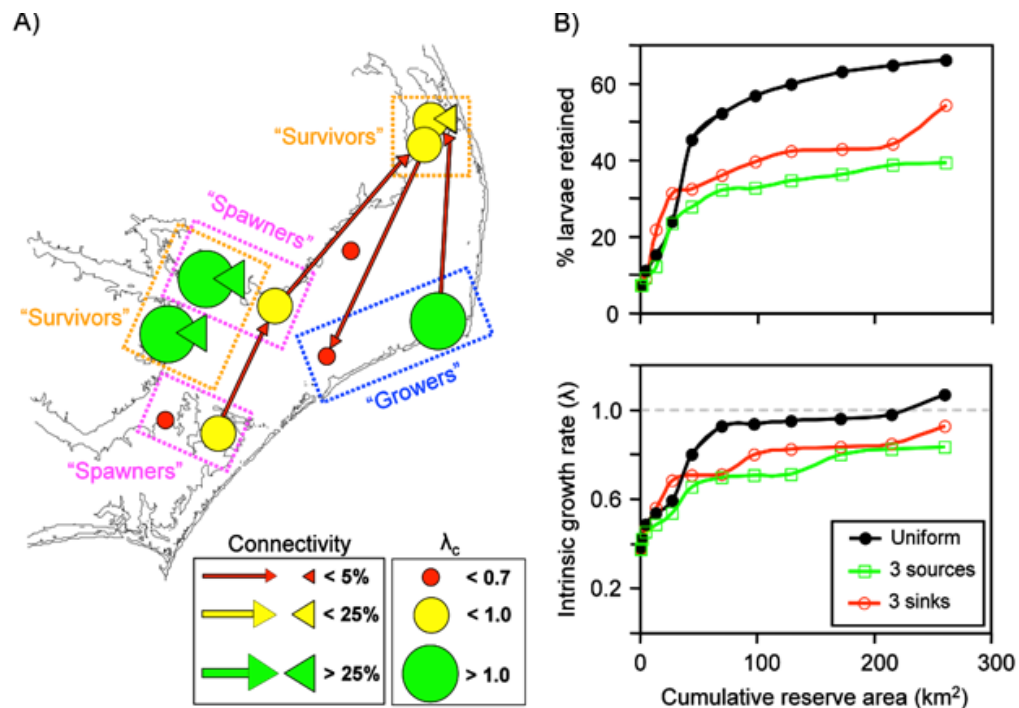


Figure 5.8. A) Map of no-take oyster reserves (circles) in Pamlico Sound, North Carolina, USA. Oyster demographic superlatives (e.g., fastest growing oysters) are indicated by the dashed boxes. Larval connectivity is proportional to the thickness of the arrows and triangles, which depict inter-reserve dispersal and self-recruitment, respectively. Metapopulation source (largest circle, $\lambda_c > 1$) and sink reserves ($\lambda_c < 1$) are denoted by the circle size at each reserve. B) Results of model simulations to determine the impact of increasing reserve size (measured as cumulative reserve area) on the percentage of larvae retained within the metapopulation (top panel) and growth rate of the metapopulation (bottom panel) for three scenarios whereby size increases were allocated (1) uniformly among all reserves (closed circles), (2) among the 3 source reserves (open squares), and (3) among the 3 worst sinks (open circles). The initial points on each panel represent the current state of the reserve network.

5.2.2 Statistical and individual-based models

Next to matrix projection models, which build on the classical work of Leslie (1945) and Lefkovich (1965) and that were popularized by Caswell, (2001), and the so-called physiologically structured population models (PSPMs) introduced by Metz *et al.* (1986) and further developed by De Roos and co-workers (e.g. De Roos *et al.*, 1992), a third type of model is the individual-based model (IBM) advocated by DeAngelis and Mooij (2005) and Grimm and Railsback (2005).

These models have the advantage that model individuals are unique entities that can be characterized by a range of state variables. The exact choice of the variables depends upon the questions the model has to answer. The changes in the state variables over time occur according to specified rules and may depend upon the number and characteristics of all other individuals in the model, and on characteristics of the modeled abiotic environment. The fate (do they survive or die), growth and reproduction of the individuals depend upon their state and possibly the environment. The dynamics of population characteristics then simply follow from summing over all individuals.

This strength of the IBM approach is at the same time also its weakness. Choices of state variables and of rules how the variables change are easily made on an ad-hoc

basis, which makes it difficult to appreciate the results of IBM model analyses and compare them with other studies (Grimm, 1999). One goal of science is to describe phenomena within a unified framework and IBMs published so far cannot be considered a coherent set of models.

Recently, Martin *et al.* (2012) made a plea for using Dynamic Energy Budget (DEB) theory (Kooijman, 2010) as a unifying framework to describe the role of individual organisms in terms of the acquisition of resources, the allocation to maintenance, growth and reproduction, and the consequences for survival. DEB theory also highlights the central role of the individual in studies of mass and energy balances, and as such is an ideal basis for IBMs. An overview of DEB theory and its applications can be found in Kooijman (2010). Van der Meer (2006) and Nisbet *et al.* (2008) provide accessible introductions. The standard DEB model can in principle be used for all species, with only the parameters differing among species. An overview of species for which DEB models have been parameterized is given on the DEB website (<http://www.bio.vu.nl/thb/deb/index.html>).

As Martin *et al.* (2012) write “DEB is appropriate as a building block for IBMs because it is a relatively simple model that translates environmental conditions to individual performance (growth, survival and reproduction) and is consistent with first principles such as conservation of energy. This is important because the tradeoffs in life-history traits that DEB specifies (growth vs. reproduction, time and size to maturation) turn out to strongly influence population dynamics ... Moreover, because DEB is a generic theory, it can be applied to virtually all species, which would facilitate broader insight from specific studies and comparisons between species.”

So far DEB models have been used to model the population dynamics of a few marine species (e.g. Kooi and Van der Meer, 2010; Van der Meer *et al.*, 2011), but not within a spatial context as discussed in the present paper.

We examined three papers that use IBMs to evaluate the importance of specific habitats for the population dynamics of commercially valuable marine species (Rose 2000, Butler *et al.*, 2005, Maes *et al.*, 2005). Rose (2000) describes a simulation model of spiny lobster survival in Florida Bay from the time of settlement to emigration about 18 months later. Growth, survival, and movement of individuals were simulated in a 7 x 35 grid of cells. Habitat, among other things characterized by the abundance of sponges and algae, differed among cells. Each incoming post-larval lobster was assigned an initial cell. A suite of rules was used to simulate the complex behaviors of developing lobsters. Empirical estimates of immigration of post-larvae were used to drive the model. Predicted population abundances showed surprisingly remarkable resilience in response to drastic variability in the abundance of sponges and algae (Figure 5.9).

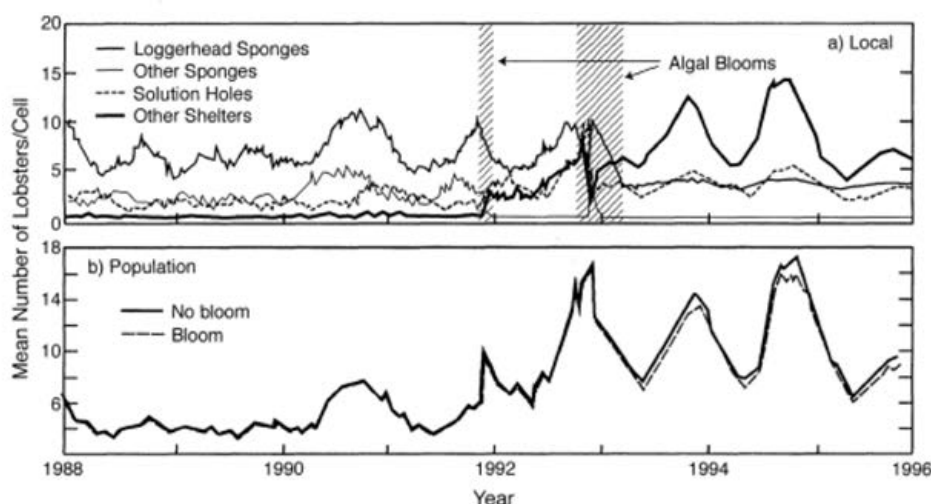


Figure 5.9. Predicted spiny lobster densities from post-larval settlement to emigration in Florida Bay, USA. Shaded periods show when algal blooms that eliminated sponges in selected cells of the model grid were simulated. (a) Lobster densities in each of the habitat types. (b) Population densities summed over all habitats and cells for simulations with and without algal blooms. Adapted from Rose (2000).

Rose also describes a fresh water example on how two trout species in Appalachian streams respond to climate-related local environmental changes. Butler *et al.* (2005) basically describe the same spiny lobster model as Rose (2000), but in more detail. Maes *et al.* (2005) model the habitat use of young herring *Clupea harengus* in an estuary. The area is divided in five zones ranging from the upper estuary to the open sea. Spatio-temporal gradients occur in the environmental variables temperature, turbidity, food availability and predation risk. Growth and survival depend upon the environment. The method of dynamic programming (Mangel and Clark, 1988) was used to assess the optimal habitat choice strategy, where optimal means having the highest chance to survive the period at a certain minimum mass. It appeared that particularly in the initial phase the herring should choose the upper estuary as it is safer than the coastal zone and the open sea. This choice comes though at the price of reduced growth (Figures 5.10 and 5.11).

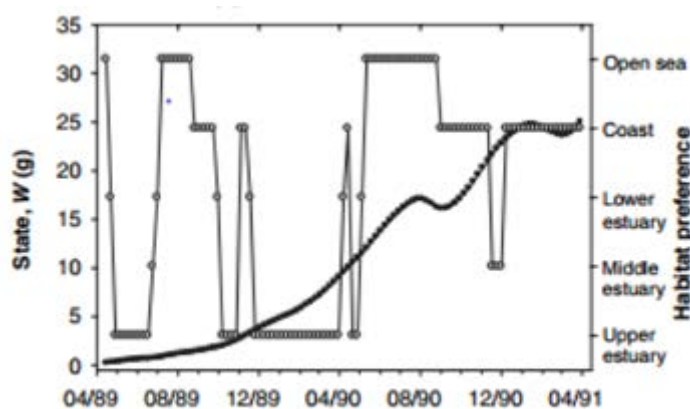


Figure 5.10. Optimal habitat (open circles) and growth (filled circles) as herring grow and mature. From Maes *et al.* (2005).

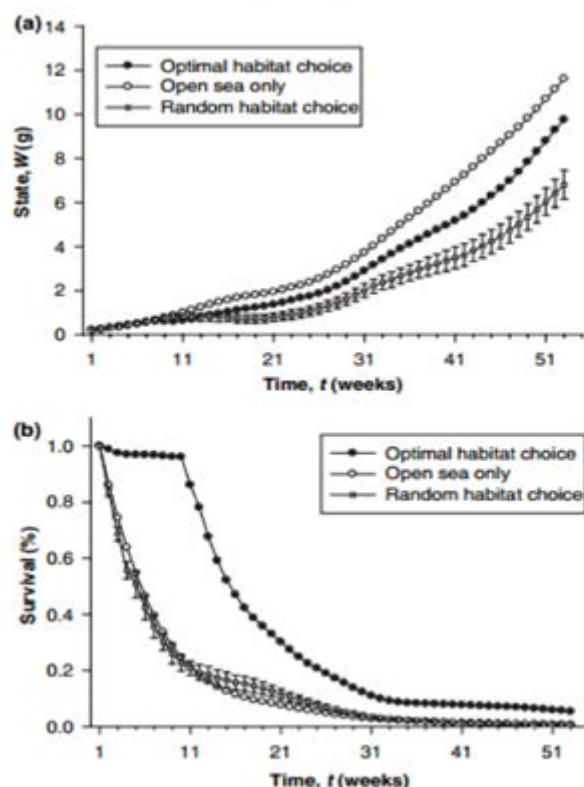


Figure 5.11. Growth and cumulative survival of three different migration strategies: optimal habitat choice, a forced stay at open sea, and random habitat choice. Error bars for the random migration represent standard errors of the means of 10 randomized trajectories drawn from a uniform distribution. From Maes *et al.* (2005).

Finally, more statistically oriented model approaches have been used to quantify the relative role of habitat types in population dynamics. One example is provided by Van der Meer *et al.* (2003) who used 30 years of age-structured data of the bivalve *Macoma balthica*, sampled at more than 10 different locations, to estimate spatial differences in life-time egg production rates. Assuming that growth is of the von Bertalanffy type, mortality rate is constant, egg production is related to condition and length according to an empirically derived function, they observed (on the basis of estimates of growth, survival and condition) that life-time egg production was lowest in the upper shore (Figure 5.12).

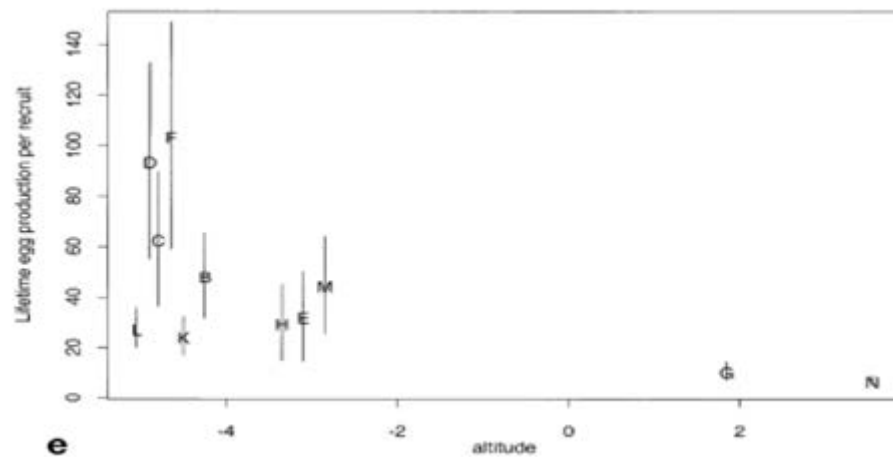


Figure 5.12. For each site, estimated means for lifetime egg production include 95% confidence intervals. From Van der Meer *et al.* (2003).

Recruit densities were nevertheless highest at these sites. They explain this apparent discrepancy by pointing to the fact that all larvae initially settle in the upper shore zone, and the animals thus have to balance a risky journey to better sites lower down with a safer staying in the poor habitat upshore. The approach resembles the matrix modeling discussed earlier, although it only considers the recruit to egg phase and does not deal with the egg to recruit phase.

5.3 Perspective

Different questions often ask for different approaches, yet often several approaches are possible to tackle a question. The table below provides an outline of the types of models that would be suitable given a set of characteristics that define an ecological or management problem. Multiple-species questions limit the model options. The number of suitable models increases with increasing coarseness of the spatial extent. All model types presented here can deal with full life cycles, however, only IBM and statistical models are useful when considering only part of a life cycle (e.g. recruitment to age 1).

		MATRIX MODEL	DIFFERENTIAL EQUATIONS	IBM	STATISTICAL MODEL	FOOD WEB MODEL
Number of species	single spe- cies	y	y	y	y	n
	predator- prey	n	y	y	n	y
	multiple species	n	n	y	n	y
Spatial component	grid	n	n	y	n	y
	meta- population	y	y	y	n	n
	habitat	y	y	y	y	n
Life cycle	full	y	y	y	y	y
	partial	n	n	y	y	n

In the table below, we provide details of the various examples cited previously and their characteristics.

Reference:	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Time (discrete/continuous)	d	c	c	c	d	d	d	d	d	d	d	d	d	c
Structured	y	n	y	y	y	y	y	y	y	y	y	y	y	
Density	y	y	y	y	n	n	n	n	n	y	y	y	y	
Spatial	y	n	y	y	y	y	y	n	n	y	y	y	y	
Resource	n	n	y	y	n	y	n	n	n	n	n	n	n	
Habitat (implicit/explicit)	n	yi	yi	n	ye	ye	yi	ye	yi	n	n	ye	n	
IBM						y	y	y						
Statistical														y

1: Gardmark; 2: Jordan-Cooley; 3: Van de Wolfshaar; 4: St. Mary's; 5: Fodrie; 6: Maes; 7: Rose; 8: Butler; 9: Levin; 10: Kerr; 11: Yakubu; 12: Whitlatch; 13: Hare; 14: Van der Meer.

6 Summary and recommendations

- 1) There is an obvious lack of information on how fish utilize some habitat types in the ICES area. This is particularly true for complex hard-bottom habitats such as kelp forests, rocky shores and macroalgae, where many census techniques are inadequate. The little information available suggests that these habitats may be essential for many species. A recommendation from WKVHES would be to focus studies on these habitat types to attain quantitative data on fish and invertebrates (both population and individual level data) from these habitats.
- 2) It is clear from our analysis that many commercial species in the ICES area utilize coastal habitats. For most species, however, there is not enough 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. Since many species use coastal habitats as spawning, feeding and nursery areas, and these life stages usually have very specific habitat demands, it may be anticipated that habitat availability may actually be a bottleneck for many populations. A recommendation from WKVHES would be to focus future studies on attaining quantitative estimates of the importance of habitats for species that are important for the ICES community.
- 3) To attain quantitative estimates of the importance of habitats for fish and invertebrates, we need information not only on population fitness in different habitats (habitat quality), but we also need quantitative estimates of the availability of different habitat types (habitat quantity), specifically comprehensive habitat maps. Comprehensive maps of coastal habitats are so far available only for small and scattered portions of the ICES area. However, the EU Marine Strategy Framework Directive puts demands on member states to map these habitats to make sure that they have a Good Environmental Status, so there are new and planned initiatives. A recommendation would be that WKVHES is formed into a working group, which in collaboration with WGMHM (working group on marine habitat mapping) could work on compiling information on habitat distributions, their importance for commercial and threatened species (i.e. the species that EU cares about), and threats to these habitats.

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Annex 1: Agenda

25 – 29 June 2012 (ICES, Copenhagen, Denmark)

Monday	25 June	1300 – 1700
Tuesday	26 June	0900 – 1700
Wednesday	27 June	0900 – 1700
Thursday	28 June	0900 – 1700
Friday	29 June	0900 – 1200
<i>Lunch daily:</i>		<i>1200 – 1300</i>

Monday, 25 June 2012

Time	Agenda
1300	Welcome
1330	Discussion of workshop goals and products
1400	Group activities
1515	Coffee Break
1530	Group activities
1630	Summary of progress and planning for next day's activities
1700	Adjourn

Tuesday – Thursday, 26–28 June 2012

Time	Agenda
0900	Plan of day's activities
0930	Group activities
1030	Coffee Break
1045	Group activities
1200	Lunch
1300	Group activities
1430	Coffee Break
1445	Group activities
1630	Summary of progress and planning for next day's activities
1700	Adjourn

Friday, 29 June 2012

Time	Agenda
8:00 AM	Plan of day's activities
8:30-10:00	Summary of workshop
10:00-10:15	Coffee Break
10:15 AM -12:00 PM	Summary of workshop
12:00-1:00	Lunch
1:00 PM	Adjourn

Annex 2: List of Workshop participants

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