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

Patterns and processes of habitat-specific demographic variability in exploited marine species

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Population dynamics are governed by four demographic rates: births, deaths, immigration, and emigration. Variation in these rates and processes underlying such variation can be used to prioritize habitat conservation and restoration as well as to parameterize models that predict habitat-specific effects on population dynamics. The current understanding of patterns of habitat-specific demographic variability in exploited marine species, as well as processes underlying these patterns, was reviewed. We describe patterns of (i) habitat-specific density, followed by ontogenetic changes in habitat use, such as (ii) immigration (i.e. use as a settlement habitat) and (iii) emigration (i.e. use as a habitat for secondary dispersal to and from), and demographic rates such as (iv) growth, and (v) mortality. Despite the importance of coastal habitats for fish and invertebrate species and the vulnerability of these habitats to human impacts, there was ambiguous evidence on their role in driving of population dynamics. Roughly 63% of the studies were descriptive, 21% experimental, and 11% used a combination of descriptive and experimental approaches, whereas 5% used meta-analyses. Habitat-specific density was the most common pattern quantified, followed by growth and mortality, with relatively few examples of studies of habitat-specific larval settlement. There were many examples of the influence of coastal habitats on survival, growth, and movement, especially at young stages, and there was an emerging focus on the effects of habitat degradation on demographic rates. There needs to be an increased effort on quantifying habitat-specific demographic rates and integrating these to better predict the effects of coastal habitats on the dynamics of exploited marine populations.

Keywords: coastal area, demographic rates, fish, habitat, invertebrates, population dynamics.

Introduction

Coastal areas and their habitats are widely acknowledged as valuable for fish and invertebrates. Their role as nurseries for early life stages of many species, as well as foraging and spawning grounds, has been the subject of several recent reviews (e.g. [Beck et al., 2001](#); [Elliott and Hemingway, 2002](#)). One of the major challenges that marine fisheries scientists are facing is predicting and then testing how population

dynamics are driven by habitat characteristics. There is ambiguous evidence regarding the importance of habitat characteristics in driving patterns of population dynamics. Knowledge of the role of habitat use is particularly valuable from a conservation and management perspective, since the vulnerability of coastal habitats to anthropogenic stressors is increasing ([Lotze et al., 2006](#); [Halpern et al., 2007](#); [França et al., 2012](#)). Marine ecosystems have been

degraded in many areas such that critical coastal habitats are no longer available or adequate to provide nursery, feeding, or reproductive functions, with negative consequences on production and renewal of populations (Worm *et al.*, 2006; Barbier *et al.*, 2011). Reductions in spawning-stock biomass and subsequent recruitment and fishery production in many exploited marine and estuarine populations have increased concerns over the multiple effects of fishing, as well as habitat loss and degradation on the resilience and persistence of exploited marine fisheries populations (Pauly *et al.*, 2002; Halpern *et al.*, 2008).

Despite the vast number of studies that have focused on coastal habitat use by fish and invertebrates, quantitative data on habitat-specific demographic rates appear relatively more scarce (e.g. Levin and Stunz, 2005; Maes *et al.*, 2005; Fodrie *et al.*, 2009) yet is critical to estimating the optimal extent of habitat required for the persistence and sustainable use of exploited species, and therefore, to effectively manage these habitats.

Although there is a critical need to define the value of coastal habitats to population abundance and growth of exploited species, quantifying the value of coastal habitats at the population level represents a complex task. For example, a common assumption is that relative high densities of a given species equate to high habitat value (Beck *et al.*, 2001). Although density may provide some insight on habitat value, it does not reflect the functional role of habitats, such as its role in population connectivity among habitats and life stages within a given seascape. Moreover, the use of a single demographic rate as a proxy for the habitat value can be misleading (Beck *et al.*, 2001; Wennhage and Pihl, 2001; Heck *et al.*, 2003; Le Pape *et al.*, 2003a; Dahlgren *et al.*, 2006; Fodrie and Levin, 2008; Vasconcelos *et al.*, 2011).

Population dynamics is primarily defined by four demographic (vital) rates: reproduction, mortality, immigration, and emigration (e.g. Hixon and Johnson, 2009). Moreover, population dynamics are driven by both density-dependent (regulation) and -independent (limitation) processes (Hixon and Johnson, 2009). Density-dependence occurs when a parameter varies as a causative function of density. It can either be: direct (compensation), in which input rates (growth, reproduction, or immigration) decrease with increase in population size or loss rates (mortality and emigration) increase with population size; or inverse (depensation), in which the opposite patterns occur. In contrast, density-independence is the absence of change in these demographic rates in response to changes in population density. Though standard population models assume that fitness increases as density declines (direct density-dependence), fitness can also be reduced at lower densities via reduced reproductive success (Gascoigne and Lipcius, 2004).

Thus, density-dependent and -independent processes include compensatory and compensatory reproduction, growth and survival, and environmental influences on demographic rates. These complex processes interact and are reflected in population and related fisheries dynamics of estuarine and coastal exploited species.

In this study, the current understanding of the pattern of habitat-specific demographic variability in exploited species, as well as processes underlying these patterns, was reviewed. There were many examples of the influence of coastal habitats on survival, growth, and movement, especially at young stages, and there was an emerging focus on the effects of habitat degradation on demographic rates. There needs to be an increased effort on quantifying habitat-specific demographic rates to better predict the effects of coastal habitats on the dynamics of exploited marine populations and sustainable exploitation rates.

Methods

The definition of coastal habitat used in this study integrated various definitions of coastal areas in use by countries worldwide (e.g. coastal waters are defined in the European Union Water Framework Directive as extending 1 nautical mile from the coastline). Within these coastal areas, we classified habitats based on their ecological characteristics so that there would be a standard description applicable in a management and conservation perspective. Fifteen coastal habitat types were considered: seagrass, kelp, salt-marsh, macroalgae, mangrove, coral reef, unvegetated marsh, soft bottom, shallow open water, oyster reefs, mussel reefs, other biogenic reefs and beds, mariculture beds, rocky shore, and artificial.

Due to the paucity of available information on habitat-specific demographic effects, we mainly focus on component effects (Stephens *et al.*, 1999), namely: reproduction, mortality, immigration, and emigration (the four primary demographic rates which define population dynamics) and also individual growth, as well as density.

We searched various academic search services (Thomson Reuters Web of Knowledge and Web of Science) for publications in the period between 1980 and 2012 using combinations of the following topics: habitat, fish, invertebrate, reproduction, mortality, immigration, emigration, growth, and density. Based on the results of these literature searches and our collective personal libraries, we selected a set of 120 studies to review (Supplementary material).

Results and discussion

General characterization of literature

We selected 120 articles for this study (Supplementary material). Only 5% of the reviewed articles were meta-analyses or reviews, and 95% were original research articles (Figure 1a). Among the latter, 63% of the total were descriptive studies identifying correlations between habitat characteristics and demographic rates, whereas 21% were experimental studies, of which most were conducted in the field, and several in the laboratory or mesocosm. In all, 11% of the studies reviewed had both a descriptive and an experimental component.

Most studies were carried out in North America (45%) and Europe (27%), with fewer studies in Central and South America (11%), and in Oceania, Asia, and Africa (under 10% each). The spatial scale of studies varied from 1 m to over 1000 km. A similar percentage of studies reviewed were conducted at small (1 – 2 m², 30% of studies), medium (1 km, 25% of studies), and large (100 – 1000 km, 25% of studies). About habitats involved, the majority of studies took place on soft bottom (56%) or seagrass (37%; Figure 1b). Saltmarsh, macroalgae, mangrove, coral reef, and shallow open water were each represented in 10 – 20% of studies. Less than 10% of studies were performed on kelp, unvegetated marsh, oyster reef, other biogenic reefs and beds, rocky shores, or artificial habitats. Most studies investigated demographic rates in a single habitat (55%), whereas two habitats were compared in 20% of studies and three or more habitats in 25% of studies.

Fish were the most abundant group studied (86% of the studies), with only 17% of studies focusing on invertebrates and even fewer (4%) on both fish and invertebrates within the same study. The number of demographic rates studied simultaneously in each study differed, with half the studies quantifying one rate (50%) and about one quarter quantifying two rates (28%). Most studies (73%) measured densities in one or more habitats and related these to habitat characteristics (Figure 1c). Growth and mortality

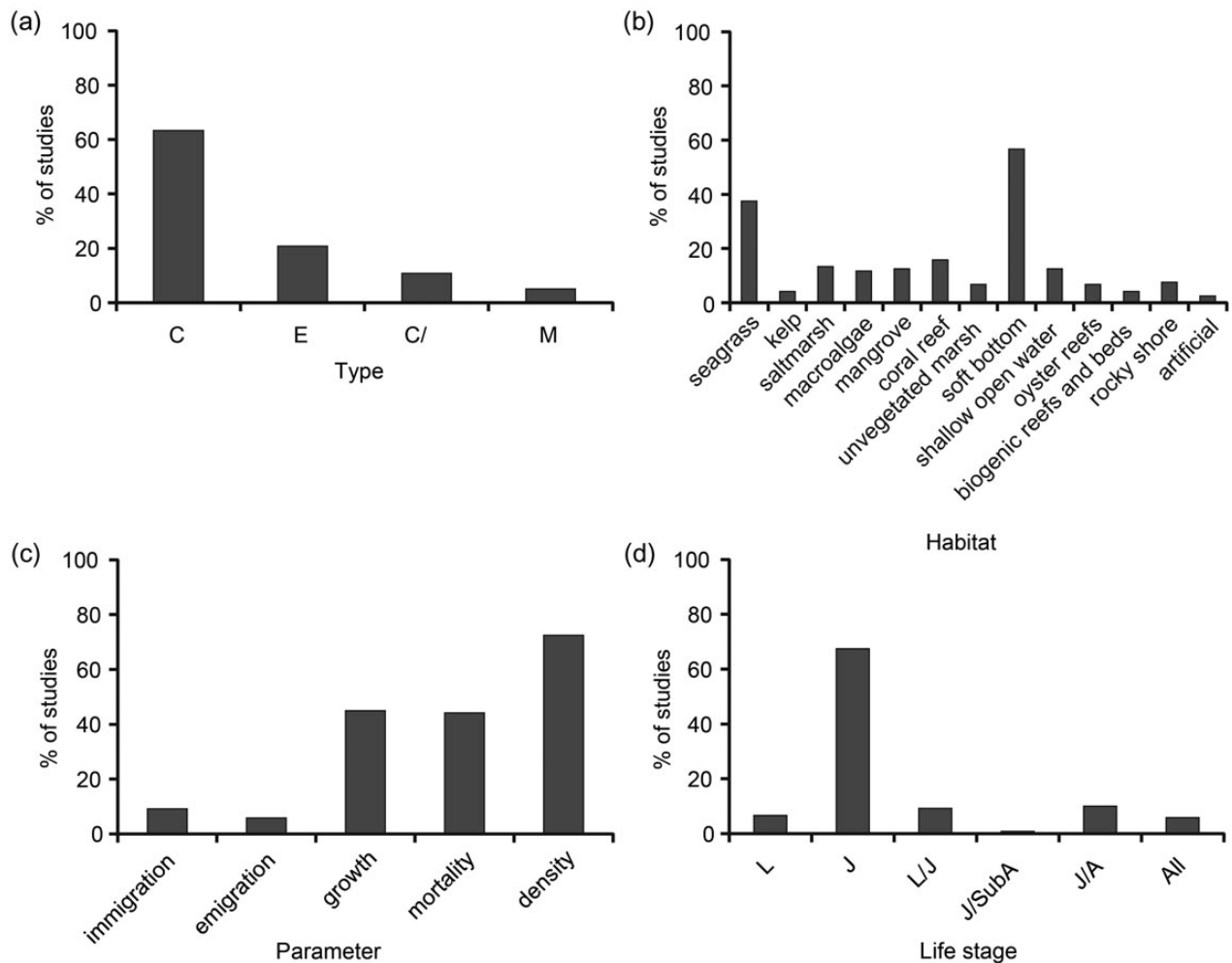


Figure 1. Proportion of selected publications (%) quantitatively estimating of the value of coastal habitats for fish and invertebrate species according to: (a) the type of approach (C, correlative; E, experimental; C/E, correlative and experimental; and M, meta-analysis or reviews), (b) the habitats (seagrass, kelp, saltmarsh, macroalgae, mangrove, coral reef, unvegetated marsh, soft bottom, shallow open water, oyster reef, other biogenic reefs and beds, rocky shore, and artificial), (c) the parameters (immigration, emigration, growth, mortality, and density), and (d) the life stages studied (L, larvae; J, juvenile; L/J, larvae and juvenile; J/SubA, juvenile and subadult; and A, adult; $n = 120$).

were each measured in ~45% of studies, while emigration and immigration were each determined in less than 10% of studies. Only in 15% of the studies were growth, mortality, and density compared simultaneously. Most studies focused only on post-settlement processes involving juveniles (68%), whereas pre- and post-settlement processes involving larvae and juveniles were studied simultaneously in 9% of the studies and pre-settlement processes alone in only 7% of the studies (Figure 1d).

The findings below are organized according to (i) habitat-specific patterns of density, followed by ontogenetic changes in habitat use, such as (ii) immigration (i.e. settlement habitat) and (iii) emigration (i.e. habitat for secondary dispersal to and from), and demographic rates, such as (iv) growth and (v) mortality. Within a given topic, the order of results are generally given as (i) the number of studies on the subject and the range in habitats studied, (ii) different methods used, (iii) conclusions regarding patterns and processes (when available), and (iv) remaining gaps of knowledge. We then conclude with a discussion of the effects of habitat degradation on demographic rates and integration of habitat-specific demographic rates and population dynamics.

Density

Population density is important in assessing a species' distribution and abundance patterns, as well as for certain resource management strategies. Habitat-specific density was the most common response variable in the studies we examined [73% of studies (87 of 120); Figure 1c], probably due to its relative ease of quantification compared with other demographic rates. Typical methods used were throw traps and trawls. Many studies quantified density of a given species across multiple coastal habitats simultaneously, such as among seagrass, soft-bottom, and macroalgae. Habitat suitability models have been used to link the distribution and abundance of a given species to habitat features at different scales such as geographic location, abiotic features, associated fauna, and food availability (Le Pape *et al.*, 2003b, 2007; Nicolas *et al.*, 2007). There are still limited data on quantitative comparisons of a given species among different habitats, especially in instances where habitat gear efficiency is known and densities can be adjusted for such differences in gear efficiency in a way that densities among habitats can be compared statistically. Many of the reviewed

examples demonstrated an order of magnitude difference in density of invertebrates or fish between habitats at different scales, especially for juveniles (Le Pape *et al.*, 2007). Previous reviews and meta-analyses found that densities were highest in relatively shallow vegetated habitats compared with unstructured deeper habitats (Heck *et al.*, 2003; Minello *et al.*, 2003). Habitat-specific animal densities can reflect structural refuge provided by a given habitat, as well as abiotic and biotic factors (e.g. salinity, temperature, prey availability, refuge from predators), which can also vary in space and time for a given habitat type. In particular, the link between food availability and juvenile fish density in shallow soft bottom systems has been widely demonstrated for flatfish (Manderson *et al.*, 2000; Le Pape *et al.*, 2007; Stoner *et al.*, 2007; Vasconcelos *et al.*, 2010), as well as its influence on interannual variability in juvenile density and distribution (Nicolas *et al.*, 2007).

Ontogenetic habitat changes along the life cycle

The degree to which populations are considered demographically open is often defined by an organism’s dispersal capability, which is generally life stage dependent. For example, many marine species undergo long-distance dispersal during a pelagic larval phase before settling to benthic habitats where they remain (Scheltema, 1986; Figure 2), and many species also undergo further ontogenetic changes in habitat use from juvenile stages (in restricted nursery grounds) to subadult and adult stages (more widespread; Figure 3). While larval dispersal can have significant population-level consequences [e.g. maintain spatially-separated subpopulations, enhance gene flow, and alter distribution and abundance patterns (Rochette *et al.*, 2012)], this may also be

true for post-settlement emigration (secondary dispersal) by juveniles or adults following initial settlement to the benthos (Dorel *et al.*, 1991; Caley *et al.*, 1996; Reyns and Eggleston, 2004; Figure 3).

Immigration (larval/post-larval settlement): primary dispersal

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 larval dispersal and settlement (Figure 2) at relatively small temporal and spatial scales, habitat features such as structural complexity, chemical and sound cues, and location within the seascape can influence settlement success (Armstrong, 2000).

Despite considerable research efforts during the past 30 years on quantifying substrate selection behaviour by competent larvae under laboratory and field conditions, relatively few examples (only 9%; 11 of 120 studies) of habitat-specific immigration and settlement rates were found in our review. The approaches included experimental laboratory and mesocosm habitat choice experiments that exposed larvae or post-larvae that were competent to settle to a range of habitats or to varying substrate complexity (van Montfrans *et al.*, 2003), field experiments with post-larvae settling on different substrates (e.g. Eggleston and Armstrong, 1995), and also synoptic surveys of habitats during intense recruitment periods (Nash *et al.*, 2007). In our examples, settlement differed up to 2 orders of magnitude between habitats (Eggleston and Armstrong, 1995; van Montfrans *et al.*, 2003). In one case, high settlement in oyster shells vs. mud by settling-stage Dungeness crabs *Metacarcinus magister* was decoupled from high density within 48 h due to post-

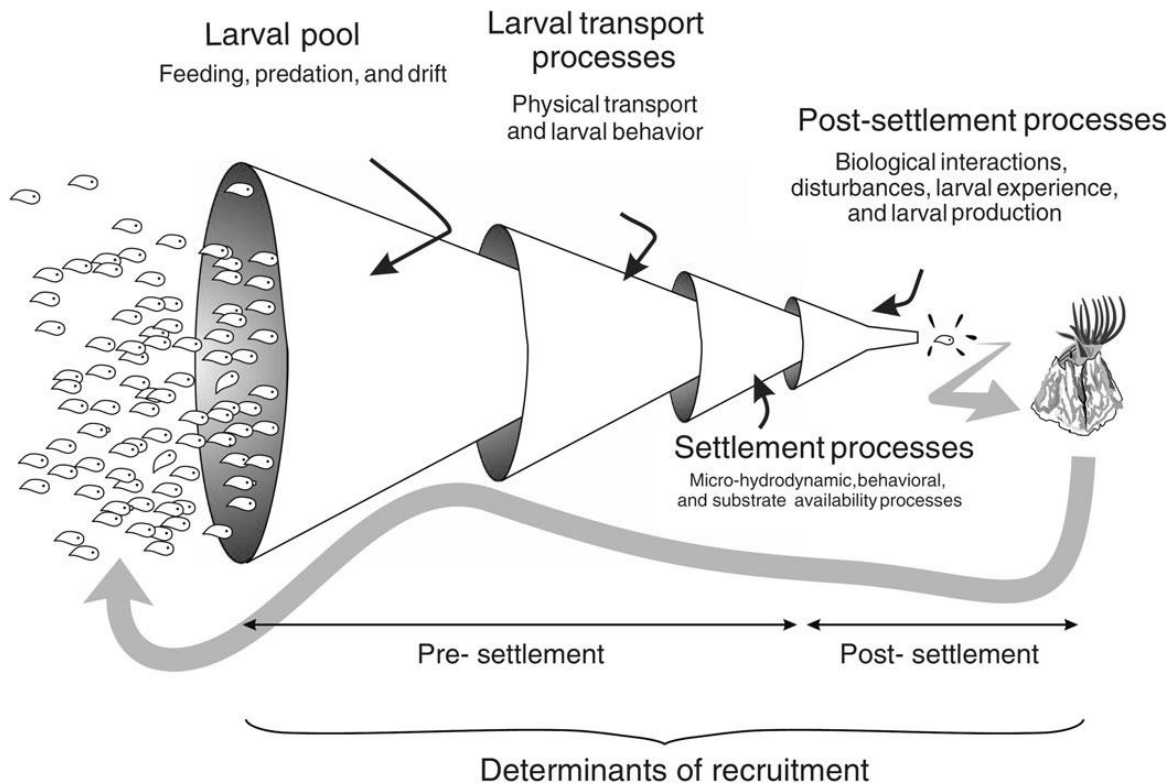


Figure 2. Schematic diagram of hierarchical processes influencing larval settlement and subsequent population dynamics of marine benthic populations, from Pineda *et al.* (2009). Processes are both serial, and ordered in space, starting with processes in the larval pool, far from the settlement site, 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.

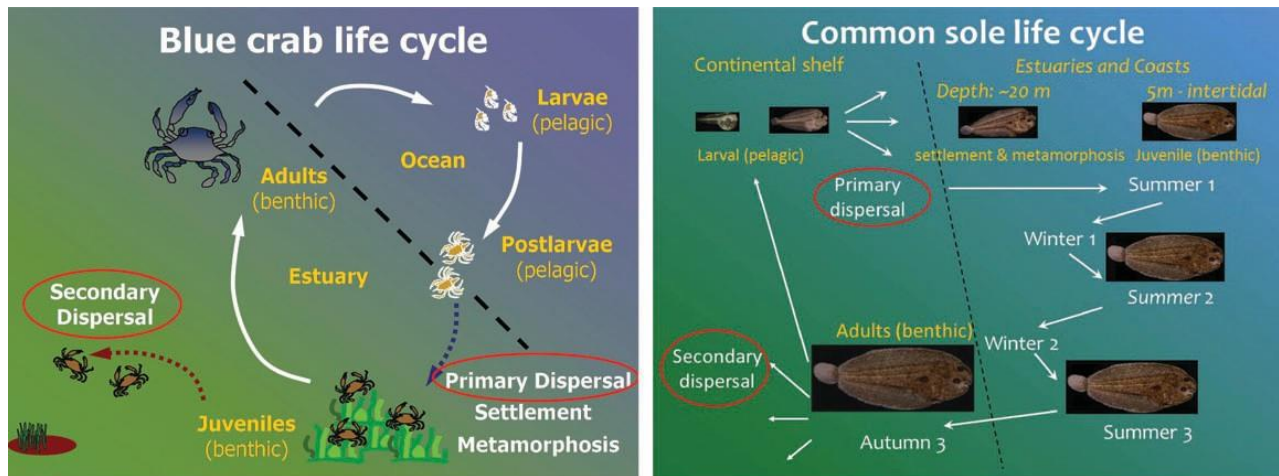


Figure 3. Examples of coastal and estuarine dependent life cycle of fish and macro-invertebrates, including habitat-related stages and dispersal phases: (a) blue crab *C. sapidus* (Reyns and Eggleston, 2004); (b) common sole *S. solea* (Dorel et al., 1991).

settlement mortality, resulting in no differences in density between habitats after 48 h (Eggleston and Armstrong, 1995).

Moreover, in especially favourable coastal habitats, differences in immigration and settlement time among species can limit niche overlap between juveniles (Fonseca et al., 2006). With the increasing emphasis on population connectivity in marine ecology and spatial fisheries management such as networks of Marine Protected Areas connected by larval dispersal, it is important to generate more information on the role of specific benthic habitats as settlement sites for larvae (Botsford et al., 2003; Cowan et al., 2007).

Emigration (migration from initial settlement habitats): secondary dispersal

Similar to larval transport and habitat-specific larval settlement, secondary dispersal of post-larvae can occur over relatively large distances (Beukema and de Vlas, 1989; Armonies, 1992; Etherington and Eggleston, 2003; Reyns and Eggleston, 2004) and thus has the capacity to enlarge a species distributional range, as well as restructure populations and communities (Caley et al., 1996; Palmer et al., 1996). A growing body of literature suggests that secondary dispersal is more prevalent than previously believed in aquatic systems, with examples from diverse taxa including marine benthic invertebrates (Günther, 1992) and fish (Hindell et al., 2003).

Despite this rapidly growing area of research, our review of the literature found few quantitative estimates of habitat-specific emigration from initial settlement habitats for commercially exploited species [6% (7 of 120 examples)]. For example, Watson et al. (2002) disentangled the effects of post-settlement movement (negligible) and early mortality (high) to explain loss of recently settled yellowtail snapper *Ocyurus chrysurus* in tropical seagrass beds, and high density of younger juveniles in seagrass and older juveniles in adjacent rocky habitat. In another example, Reyns and Eggleston (2004) examined factors that contributed to the secondary dispersal of a benthic marine invertebrate, blue crab *Callinectes sapidus* (Figure 3a). Field studies in large seagrass beds (0.05 km²) determined that secondary dispersal is primarily undertaken by the earliest juvenile instar stage which emigrated pelagically from seagrass settlement habitats. Moreover, secondary dispersal was density-dependent and regulated by intra-cohort density. Their results suggested that dispersal occurs rapidly following settlement and promotes blue crab

meta-population persistence by redistributing juveniles from high-density settlement habitats to areas characterized by low post-larval supply. These two contrasting examples illustrate how a habitat (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 another habitat (coral reefs; Watson et al., 2002) and how a habitat (seagrass) can serve as an initial settlement habitat in which increasing intra-cohort densities can drive secondary dispersal to alternative nursery habitats thereby altering initial settlement patterns (Reyns and Eggleston, 2004).

Moreover, when habitat use and secondary dispersal are examined on larger temporal and spatial scales, ontogenetic habitat shifts can reach large distances. Juvenile common sole *Solea solea* progressively migrate tens of kilometres from shallow estuarine waters to deeper coastal waters throughout successive juvenile stages during the first years of life, before performing a larger migration (hundreds of kilometres) at sexual maturity (Dorel et al., 1991; Figure 3b). Future studies should emphasize the spatio-temporal scales at which successive secondary dispersal occurs in exploited species to better define settlement habitats, the degree of connectivity between primary and secondary settlement habitats, and the level of dependence of subadult and adult populations on these essential coastal habitats.

Demographic rates

Food availability and predation on nursery grounds are the main drivers of habitat suitability and individual condition during the juvenile stages of many species in coastal areas (Gibson, 1994; Van der Veer et al., 2000). Size-selective mortality (resulting from the combined effects of growth and mortality) appears especially important during the first benthic life stage following larval settlement and can modify demographic rates and regulate populations (Ellis and Gibson, 1995; Gibson et al., 1995; Caley et al., 1996; Nash and Geffen, 2012).

Despite the benefit of quantifying habitat-specific growth and mortality simultaneously, which would allow for combined estimates of habitat suitability, there were relatively few studies (22%) that did so, and many did not present quantitative estimates. Integrated approaches whereby growth and mortality are quantified simultaneously will facilitate understanding the role of habitat

characteristics (e.g. complexity and connectivity) in optimizing growth and survival (e.g. trade-off between protection and foraging) and enhancing juvenile fitness. In the studies reviewed here, the basic question “how do animals optimize habitat-specific growth and survival to enhance fitness?” is often mentioned without quantitatively testing it. Below, we summarize the effects of habitat on growth rate and survival.

Growth

The effects of habitat type on growth rates or proxies were quantified in 45% (54 of 120 studies) of the selected studies (Figure 1c). The spatial scales ranged from large (1000 km, depth gradient, estuarine vs. non-estuarine systems) and medium (km, intra-ecosystem gradients) systems to small (m, local habitats). Many experimental approaches quantified habitat-specific growth in seagrass and other biotic structures at medium to local spatial scales using enclosures and mark-recapture techniques (Perkins-Visser *et al.*, 1996; Bologna and Heck, 1999), whereas correlative field studies examined the effects of estuarine gradients at large scales (Vasconcelos *et al.*, 2009). The studies reviewed revealed a notable variety of response variables used to estimate growth, ranging from increase in length for different life periods or time intervals, or increase in weight, to increase in the size increment of fish otoliths, as well as proxies for growth such as body condition (mass at size) or biochemical condition (RNA:DNA or lipid content). In about half these studies, there was no significant effect of habitat type on growth rates. Often, however, growth rates were influenced by factors other than structural aspects of the habitat, such as salinity and temperature, or biotic factors such as density of conspecifics or larval inertia *sensu* Searcy *et al.* (2007).

Despite these caveats, several patterns regarding habitat-specific growth emerged in the studies reviewed. For example, there was evidence of density-dependent growth under conditions of low food availability (Gilliers *et al.*, 2006; Amara *et al.*, 2007). Habitat suitability, which is linked to food quality and availability, is highly influential on growth of juveniles, and density-dependent effects related to food limitation can influence recruitment variability and population dynamics (Cowan *et al.*, 2000; Nash *et al.*, 2007). Similarly, local primary production and organic matter input (e.g. freshwater flow) are important for coastal foodwebs and for the influence of coastal habitats as nursery grounds for exploited marine species (Le Pape *et al.*, 2003a, c).

Considering growth alone as an indicator of habitat suitability can lead to spurious conclusions (Searcy *et al.*, 2007; Vasconcelos *et al.*, 2011). 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 growth trajectories.

Mortality

The effect of habitat type on mortality rates was quantified in 44% (53 of 120 studies) of the selected studies (Figure 1c); however, not all provided quantitative estimates of mortality or survival rates, especially for mobile species. Survival estimates are more easily quantified in invertebrates which are sessile such as oysters, or have low mobility such as certain crustaceans, than in more mobile fish. Moreover, in many of the reviewed studies, it was not possible to discriminate losses due to mortality vs. those from emigration (e.g. Nash *et al.*, 2007; Johnson and Eggleston, 2010). The majority of studies quantified mortality as a function of habitat complexity or degradation. For example, experimental tethering

techniques determined that predation-induced mortality of bay scallops (*Argopecten irradians*) decreased from the edge to interior of seagrass patches and was ~60% lower in seagrass compared with macroalgae (Bologna and Heck, 1999; Carroll *et al.*, 2010). For mobile fish, a combination of tethering and field cage enclosure experiments demonstrated that survival of juvenile (5 cm TL) Pacific yellowtail snapper (*Lethrinus atkinsoni*) was higher in seagrass than adjacent coral reefs (Nakamura *et al.*, 2012). Repeated trawl surveys found that the combined effect of density-dependent mortality and predator density on larval supply were shown to define variation in post-settlement densities of a flatfish across coastal soft bottom habitat (Wennhage and Pihl, 2001), and a combination of trammel net surveys, stomach content analyses, and laboratory predator-prey experiments determined that seagrass enhanced survival of two species of flounder by providing shelter and refuge compared with macroalgae or bare sand (Manderson *et al.*, 2000).

Given that mortality is especially high during the early juvenile stages, habitat-specific differences in mortality rates can lead to large differences in subsequent recruitment success of juveniles. Mortality in nursery habitats influences recruitment and contributes to regulate variability in year-class strength (Scharf, 2000; Van der Veer *et al.*, 2000; Levin and Stunz, 2005; Fodrie *et al.*, 2009), and there needs to be more research effort on quantifying habitat-specific and life-history stage mortality rates to properly estimate the function and the value of coastal habitats.

Negative consequences of anthropogenic pressure

The reviewed literature showed growing interest on anthropogenic impacts on the functions and services of habitats and ecosystems. Reduced densities of juvenile fish were shown to be significantly lower in estuarine and coastal habitats affected by increases in human disturbances (concentration of xenobiotics; Gilliers *et al.*, 2006; Rochette *et al.*, 2010) or density of invasive molluscs (Kostecki *et al.*, 2011). Variations in growth rates in relation to the level of human development have also been investigated (Meng *et al.*, 2001). Moreover, Rochette *et al.* (2010) used historical maps of the highly degraded Seine estuary back to 1850 to retrospectively build quantitative maps based on habitat suitability models for the common sole *Solea solea* and showed that habitat loss led to more than 40% decrease in nursery capacity.

Discriminating anthropogenic disturbances from natural patterns is a complex endeavour, as the more disturbed systems are often the more suitable, especially in estuarine systems, as presented in the Estuarine Quality Paradox (Elliott and Quintino, 2007). Anthropogenic disturbances can influence the capacity of coastal and estuarine nurseries and, thus, potentially the recruitment and the renewal of populations (Johnson *et al.*, 1998; Cowan *et al.*, 2007; Peterson *et al.*, 2000; Scharf, 2000; Peterson, 2003). Habitat loss and degradation are currently considered one of the most serious threats to the recovery of fish stocks, with ~70% of nursery habitats worldwide impaired (Worm *et al.*, 2006; Barbier *et al.*, 2011). Thus, there is a need to maintain and restore the ecological function of coastal nursery grounds to sustain marine fish populations and related fisheries (Elliott *et al.*, 2007); however, direct estimates of the consequences of habitat loss or degradation to populations have been seldom attained as well as estimates of population effects of restoration (Cordier *et al.*, 2011). There is an urgent need for more quantitative data on the effects of degraded habitats on demographic rates and the mechanisms underlying such changes compared with non-impacted controls.

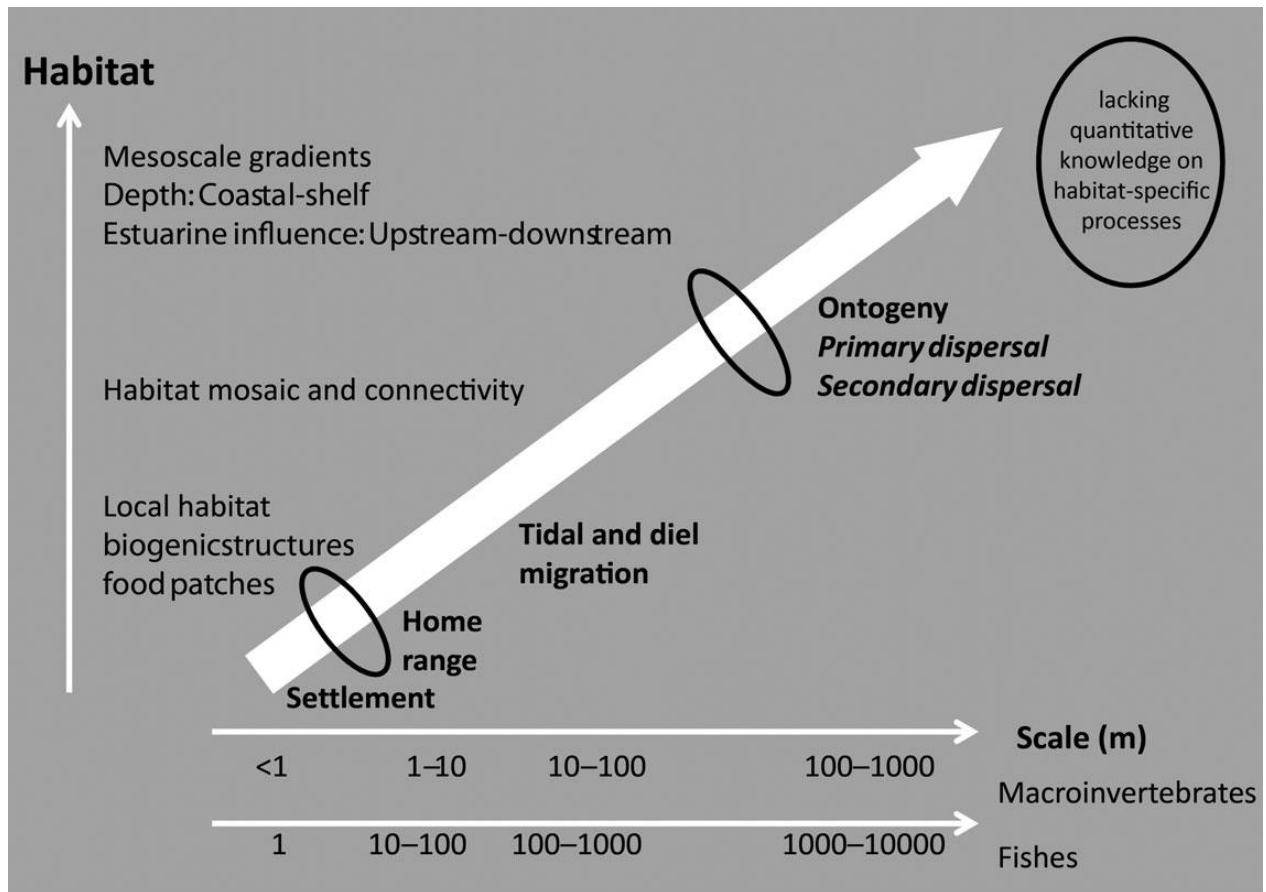


Figure 4. Habitat-specific demographic process for coastal fish and invertebrate species.

Integration of demographic rates with population dynamics and current gaps in knowledge

Only a few studies have reviewed and conducted meta-analyses of the literature for how habitat characteristics affect population demographic rates and habitat functions for populations [e.g. saltmarsh (Minello *et al.*, 2003) and seagrass (Heck *et al.*, 2003)]. In addition, the importance of some particular coastal habitat types for fauna has also been reviewed (e.g. Manson *et al.*, 2005; Adams *et al.*, 2006; Cattrijsse and Hampel, 2006; Nagelkerken *et al.*, 2008). The present paper identifies the main current findings on habitat-specific demographic rates and evidences of their influence on population dynamics, as well as the main gaps in knowledge. The availability of quantitative data is the key to disentangling the role of pre- vs. post-settlement processes underlying habitat-specific differences in species densities. From the 120 studies reviewed herein, some general patterns can be drawn regarding the lack of data: (i) relatively little experimental quantifications of demographic rates within and among habitat types are available; (ii) standardized methods to estimate demographic rates across studies and habitats are strongly needed; (iii) information on emigration and immigration, which are key ecological processes connecting spatially separated populations, is scant; and (iv) there is a need for integrated approaches, especially combining demographic components and densities to account for density-dependent processes in component estimates. Notably, two main gaps in knowledge are evident (Figure 4) and hinder quantitative integrations of coastal habitat function in population dynamics of marine species, as follows.

Influence of post-settlement habitat use at early stages

Contribution of individuals from nursery areas to adult population is not necessarily related to the density of recently settled post-larvae on available nursery habitats (Rooper *et al.*, 2004; Chittaro *et al.*, 2009). This indicates the importance of post-settlement regulation linked to habitat quality for juveniles. Density-dependent regulation of a cohort is hypothesized to occur at a critical size following larval settlement (Cowan *et al.*, 2000; Nash and Geffen, 2012), when fish are especially vulnerable. At this life stage, habitat-related density-dependent processes strongly modulate growth and mortality with relation to larval immigration (primary dispersal) and juvenile emigration (secondary dispersal; Nash *et al.*, 2007). For coastal marine species, nursery carrying capacity limits juvenile production and reduces variability in mean stock size related to larval supply (i.e. concentration hypothesis; Iles and Beverton, 2000). Thus, post-settlement mortality related to coastal nursery habitat capacity can affect future recruitment strength and population size (Rooper *et al.*, 2004; Nash and Geffen, 2012). Knowledge is lacking on ecological processes and habitat use during this critical post-settlement stage. The study of these very young fish and macro-invertebrates remains a challenge. The high spatio-temporal variability in larval supply, mortality, and emigration (and, thus, density) leads to high turnover rates and requires fine temporal (Fonseca *et al.*, 2006) and spatial strategies (De Raedemaeker *et al.*, 2012). Such studies are required to understand and quantify habitat-specific demographic processes at this critical post-settlement stage.

Connectivity, emigration, and recruitment to adult population

The dependence of marine species on coastal habitats has been studied at population scale with various approaches. For example, [Rijnsdorp et al. \(1992\)](#) demonstrated that the larger the nursery ground the higher the level of recruitment to the adult population of common sole *Solea solea*. From quantitative mapping of habitat use by juvenile common sole, [Le Pape et al. \(2003b\)](#) showed that shallow muddy habitat represented only 10% of coastal areas in the Bay of Biscay and hosted 80% of young of the year. In the Eastern Channel, a single coastal sector hosted about half the juvenile common sole and one-third the juvenile plaice *Pleuronectes platessa* ([Riou et al., 2001](#)). Similarly, estuarine contributions have been estimated for other species and populations using various approaches including the aforementioned quantitative habitat suitability modelling and mapping ([Fodrie and Mendoza, 2006](#); [Vasconcelos et al., 2010](#)) and also the effective contribution of juvenile to adult populations using tags such as otolith microchemistry ([Yamashita et al., 2000](#); [Fodrie and Levin, 2008](#); [Vasconcelos et al., 2011](#); [Tanner et al., 2013](#)).

[Fodrie et al. \(2009\)](#) explored the population-level consequences of habitat selection by juvenile California halibut *Paralichthys californicus* in southern California, focusing on population growth rate (L) as a measure of fitness. Nevertheless, similar approaches are scarce. Moreover, carrying capacity does not fully represent the population level changes following a habitat alteration ([Hayes et al., 1996](#)). The paucity of quantitative estimates of the dependence of marine species on essential coastal habitat use at juvenile stage, and the difficulty to link recruited subadults and adults to their nursery habitats were especially evidenced.

Conclusions

The present paper explores the current state of knowledge on the relative value of coastal habitats for population dynamics of exploited species. The major strengths and weaknesses in available knowledge were identified. The large influence of coastal habitats on component demographic rates (migrations, growth and mortality, and the resulting density) of coastal marine exploited species was evident from the selected studies. This influence can be observed at different spatial scales, from local habitat to mesoscale. The negative influence of anthropogenic pressures on the demographic component was also evidenced.

There is, however, a paucity of data relating demographic component effects to habitat condition experienced by fish especially during the first post-settlement life stage in coastal areas for marine species. Moreover, although studies determining habitat-specific vital rates were abundant for some species, they preferentially target some habitats (e.g. soft bottom, seagrass) and some vital parameters (e.g. density, growth) over others. As a result, only for some species do several vital rates seem to be available across several habitats, which greatly restricts our ability to predict the effects of varying habitat characteristics on population dynamics. Thus, obtaining data on habitat-specific demographic rates for various life-history stages should be priority for fisheries ecologists, so that such data can be integrated in population dynamics models which, in turn, should facilitate disentangling the role of habitat use vs. other factors in driving population dynamics as well as predicting sustainable harvest rates.

Supplementary data

Supplementary material is available at the *ICES/JMS* online version of the manuscript.

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