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Title: Environmental factors influencing local distributions of European green crab (*Carcinus maenas*) for modeling and management applications

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Abstract

Environmental factors determine the habitat selection, use and distribution of species at various spatial scales. Understanding the factors driving these distributions can help predict areas of higher species occurrence, and be used in species conservation, and management strategies. In this study we reviewed 71 publications to evaluate the most relevant factors shaping local, fine-scale distribution of a globally invasive species, the European green crab (*Carcinus maenas*). We compared these studies to determine how factors differ (i) between adult and juvenile life stages, (ii) with the influence of internal and temporal variables, and (iii) among clades. Factors of depth, biotic interactions, vegetation, presence of shelter and salinity were found to be important, although the supporting evidence varied between juvenile and adult stages. Internal variables of size, carapace color and sex, and temporal variables such as seasonal, tidal and diel cycles played a role in determining how crabs responded to environmental factors. The importance of environmental factors also varied by clade. All of these factors and variables may be expected to play a role in the local, fine-scale distribution of *C. maenas*.

These variations affect the efficacy of using a single model to anticipate local green crab distribution (e.g., spatial distribution model). Application of different models for adult and juvenile subsets of the population, clades, and accounting for temporally shifting distribution may help accommodate some of this variation. The relative presence of factors in a region and the availability of local, fine-scale environmental data may further influence the efficacy of modeling. The combined effects of such considerations will make predictive local modeling at fine scales challenging, if not impossible, with existing knowledge, data and technology. Nonetheless, our results provide insight into the environmental characteristics most relevant to shaping local distributions of *C. maenas,* which may inform management strategies such as efficient trap-setting within an ecosystem.

Keywords: habitat, species distributions, green crab, *Carcinus maenas,* environmental factors

Introduction: The need to identify environmental factors influencing local, fine-scale European green crab (*Carcinus maenas*) distributions

Habitat quality and availability are recognized determinants of population success (Hodgson et al. 2011). Habitat ties in closely with the niche concept, the sum of resources and environmental conditions that permit an individual's survival and reproduction (Whittaker et al. 1973, Krausman 1997). Habitat quality is often represented in terms of population density, and higher population densities can act as an indicator for habitat quality (Van Horne 1983). By extension, habitat quality may be considered a proxy for areas with high harvesting potential, and may be used in a number of management contexts, such as targeted removals of an invasive species or harvest of a commercial species (e.g., Chang et al. 2012).

As habitat selection is a hierarchical process that occurs at a variety of spatial scales, different factors are more or less important depending on the scale under consideration (Hutto 1985, Specziár et al. 2013, Svensson et al. 2013). At regional or global scales, important variables typically include climatic factors such as latitudinal temperature and precipitation that delineate the absolute limit of a species' range (Blach-Overgaard et al. 2010, Compton et al. 2010). At finer scales, resource availability and biotic interactions are thought to more often influence habitat selection, although there is some contention (Chuine 2010, Wisz et al. 2013). Furthermore, distribution may change with habitat use, the division of resources for different activities such as foraging, spawning, protection or other necessary life tasks (Litvatis et al., as cited in Krausman 1997). Collectively, these mechanisms drive the spatial and temporal distribution of species.

Within regions where invasion and establishment of a non-native species has occurred, understanding forces that drive habitat selection is beneficial to predicting areas of high population densities. However, this can be a complex process. Species responses to environmental factors vary in time and space, including seasonal, diel and tidal movements. This is further complicated by internal population structure if movements vary by sex and phenological condition (e.g., spawning or moulting). Furthermore, habitat requirements of individuals often shift as they mature (Snover 2008). These variables make species distributions challenging to predict (e.g., Silva et al. 2010, Dambach and Rödder 2011, Dalmau et al. 2013, Martin et al. 2013). Nonetheless, if management of a species is imperative, this information may prove valuable in developing effective management plans.

The European green crab, *Carcinus maenas,* represents a case where understanding these factors may be key to management. This invasive crustacean poses ecological and economic threats to many regions along Canada's Northwest Atlantic Coast. Eelgrass (*Zostera marina*), and commercial bivalves such as softshell clam (*Mya arenaria*) and blue mussel (*Mytilus edulis*) are among the native species predated by *C. maenas* (Davis et al. 1998, Miron et al.2002). As a consequence of such impacts, there is a push for monitoring and management of *C. maenas*. Models have been constructed to address habitat-related concerns around *C. maenas*. These aim to predict the likelihood of the species appearing within a given water body, or potential economic or ecological impacts (Colnar and Landis 2007, U.S. Environmental Protection Agency 2008, Grosholz et al. 2011). Models focus less on predicting distribution *within* an invaded area, as the factors driving local, fine-scale distributions are generally not known. Manual removal is the preferred means of control of *C. maenas*, and improved understanding of their fine-scale distributions within local areas (e.g., an inshore water body, such as a harbor, estuary or other region where trapping may be feasible) may help improve trapping efficiency for removals. Such understanding may also increase the effectiveness of other management activities such as identifying areas where crabs will next invade and lucrative sites for commercial fisheries. Accordingly, there is a need for increased understanding of environmental factors that reliably drive fine-scale distributions in local waterbodies, for modeling, monitoring and other management practices.

A preliminary search revealed no studies focused on prioritizing key factors to consider in predicting fine-scale distribution of *C. maenas*. Previous reports (e.g., Klassen and Locke 2007, Leignel et al. 2014) have described green crab habitat preferences, noted their biotic interactions and/or described their physiological tolerances to environmental factors; however, they did not provide quantifiable evidence for factors warranting priority consideration. Furthermore, most existing models are constructed with the intent of inferring invasion risk of *C. maenas* along shorelines, or consider suitability of estuaries and inshore spaces as a whole (Colnar and Landis 2007, U.S. Environmental Protection Agency 2008, Grosholz et al. 2011). Our review is primarily directed at understanding fine-scale population distributions *within* local areas where *C. maenas* has already invaded; many of the factors considered in other studies and models (i.e., distance to adjacent invaded regions) are therefore irrelevant, and even those that are relevant may vary in influence. Consequently, we provide a synthesis and evaluation of existing literature on biotic and abiotic drivers of fine-scale distributions of *C. maenas* in localized areas. We compile a representative listing of key environmental factors that have been identified as determinants of *C. maenas* distribution in other studies. We evaluate the factors according to the established support for their significance on green crab distributions, and their practical use in local distribution modeling. We compare these studies to determine how environmental factors differ (1) between adult and juvenile life stages, (2) with the influence of internal and temporal variables, (3) in native and non-native regions, and (4) across clades. We highlight key considerations for understanding fine-scale distributions important to modeling and other management applications. These results can help inform strategies for monitoring and control, such as determining effective locations for traps, as well as highlighting areas warranting further research.

Delimiting the literature, the scale and the factors

Following a similar methodology to Snickars et al. (2014), we searched for key documents on the subject; these included peer-reviewed journal publications, scholarly theses and government research reports. These were (1) revealed in searches of online databases (Google Scholar, Worldcat, and Web of Science) using key terms[1], (2) recommended by databases upon accessing a searched item, (3) provided by key informants, and (4) noted in the works cited sections of these sources. Articles were scanned for relevant titles; abstracts were reviewed to filter ineligible papers; and, if relevance was not immediately evident, the full article was read. Further papers were revealed using a pearl-growing method from the works cited in the selected articles.

Articles were considered that involved: (1) one or more experiments containing results explicit to green crab; (2) field or lab-based studies of relationships between environmental factors and green crab distribution, including considerations for internal, temporal or clade-based influences at fine scales; or, (3) testing of relationships to environmental factors with a high potential for influencing distribution in the field. No restrictions were placed on the geographic location and date of studies, however these were noted to clarify the clade most likely addressed. In total, 71 studies (63 published research articles, six government reports, one book chapter and

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[1] See Table S1a (supplementary material) for a list of search keywords.

one graduate thesis) were selected for full review, the majority of which contributed multiple records (i.e., unique observations of factors).

The review focused on environmental factors and related internal and temporal variables associated with local fine-scale spatial distribution. Environmental factors refer to salinity gradients, water depth, temperature and bottom type. Internal variables refer to demographic and density-based features of *C. maenas* populations, including individual carapace color (closely tied to moult stage, usually changing from green to red as it ages (Styrishave and Rewitz 2004)), carapace size, and sex. Temporal variables refer to changes that occur with daily, tidal or seasonal cycles.

The studies considered addressed local sites (extents of 1-10 km) in terms of fine-scale differences in green crab distribution, such as along sheltered or limited coastal waters (e.g., bays, estuaries, mudflats, straits, or even limited stretches of shoreline). *C. maenas* often inhabit such areas, and thus they are target sites for removals and other management projects (e.g., Rivera et al. 2007, MTRI and Parks Canada 2013). Studies were not considered that conducted research at coarser scales (i.e., comparing distribution of crab between sheltered water bodies, at the regional or global scale). Furthermore, since a key purpose of this research is to inform trapping strategies, studies of green crab larvae were not considered.

Biotic interactions underpin species distributions, however they are rarely explicitly studied in green crab (Wisz et al. 2013, Snickars et al. 2014). Adequate food resources are integral to survival, reproduction and persistence; and, competition for resources or predation may detract from individual fitness and make habitat uninhabitable (e.g., McLoughlin et al. 2010). For such reasons we explored studies of food source preferences of *C. maenas*. These studies concerned: (1) predation on prey species in open water versus exclusions; (2) predation intensity in cages with prey and green crab; (3) predation on prey species of varying sizes; and, (4) direct predation and competition among individuals, where avoidance, displacement or mortality were considered to be significant interactions, and co-inhabitancy of species without significant displacement or mortality were considered non-significant interactions.

In our review, we also noted: (1) spatial scale (only results comparing variation at the fine scale were considered); (2) age classes (whether adult and/or juveniles were sampled; sometimes inferred from carapace size, with juveniles at or under 35 mm carapace width) or differing distribution according to internal variables of crab populations studied; (3) temporal variables (fluctuations on a tidal, daily or seasonal scale); and, (4) geographic origin, as behavioural differences have been noted between allopatric populations (Rossong et al. 2011, Haarr and Rochette 2012). Geographic origin was categorized according to boundaries illustrated in Roman and Palumbi (2004) and Brian et al. (2006), who identified four distinct native populations in Europe (Fig. 1).

Our analysis quantified the percentage of studies and number of records concerning a given environmental factor. Documents often compared multiple experiments, geographic populations, environmental factors and other variables, and lab and field tests, producing unique results for each; these were catalogued as individual ‘records’. Special considerations were made for studies conducted with more than one *C. maenas* clade, multiple experiments and multiple statistical outputs[2]. Environmental factors were analyzed for (1) adults, (2) juveniles and (3) all records of *C. maenas*, regardless of age. Studies excluding information on age or carapace size were only included in the pooled analysis. The separate evaluation of adult and juvenile studies

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[2] The decision-making framework for managing these studies is outlined in Table S1b of supplementary material.

were to determine whether different factors govern different life stages, as other crustacean species demonstrate shifts to different habitats through their life cycle (Pallas et al. 2006, Andrade et al. 2014). General qualities of each factor (e.g., the 'type' of bottom most often emphasized) were noted[3]. To evaluate whether the importance of environmental factors differed by region, consistency of the records across geographic populations was assessed.

Environmental factors revealed

From the 71 studies, eleven environmental factors were identified and organized into five categories (adapted from Snickars et al 2014): 1) bottom topography; 2) biotic features; 3) hydrography; 4) exposure; and, 5) substrate (Table 1). Of these studies, 26 involved *C. maenas* of mixed native origins, 20 involved northern European populations, and 25 involved southern European populations. Thirty-four of the studies were conducted in Europe, three in Australia and 34 in North America. Studies entailed field and lab work from 1958 to 2012, more than 70% of which were conducted within the last 20 years. Our review revealed the most prevalent environmental factors associated with fine-scale spatial distribution of *C. maenas*. These are presented by age class, internal and temporal variables, geographic origin and clade.

Environmental factors for adult C. maenas

Agonistic interactions, food source and water depth, including location in the tidal column, were frequently acknowledged factors for adults (acknowledged in 23%, 22% and 22% of reviewed studies, respectively). These results had the highest number of records with statistically significant support (Table 2a). Agonistic interactions occurred with a number of species and ranged from displacement to predation and mortality; the outcome was dependant on

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[3] See Table S5 (supplementary material) for further details.

the species as well as size disparities between *C. maenas* and the individual with which it was interacting[4]. *C. maenas* were found to use a wide range of food sources; again these were dependant on the species and prey size. Adult *C. maenas* were most commonly found from six meters of depth to the shoreline, with larger adults in deeper water.

Environmental factors for juvenile C. maenas

Environmental factors indicated for juvenile *C. maenas* varied from those for adults. While agonistic interactions ranked highly in both demographic groups, vegetation and shelter were important for juveniles (in 21%, 29% and 21% of studies, respectively) (Table 2b). Vegetation and shelter for juveniles included discarded shells, live mussel beds, rocks, *Zostera*, kelp, algae and rockweed. Depth and food source were less frequently acknowledged (14% and 11% of studies, respectively), and bore fewer statistically significant results. As found with adults, juvenile agonistic interactions occurred with a number of species and the outcome depended largely on the species and size.

Environmental factors for combined C. maenas *studies*

When studies were combined ignoring age class, agonistic interactions, depth, food source and vegetation were most frequently acknowledged (23%, 19%, 19% and 14% respectively). Agonistic interactions had a high number of statistically significant records as well as the highest number of non-significant records (either where *C. maenas* was shown to not compete with or to avoid agonistics, or was shown to produce significant mortality rates to an agonistic). Agonistic interaction studies were most often conducted in a laboratory. Depth bore

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[4] See Table S5 (supplementary material) for further details.

more statistically significant records than did vegetation; no studies found a non-significant effect of depth on *C. maenas* distributions.

Salinity, temperature, bottom type, dissolved oxygen, flow and pH were less frequently identified as factors. Preferred salinity ranged from 22-35‰, with ‘red’ crabs (in reference to carapace color or moult stage) preferring more saline conditions. Temperature was found to primarily act with seasonal changes, affecting the depth at which *C. maenas* was found, as opposed to directly affecting distribution through fine-scale temperature differences. Bottom type was variable, noting mud, silt, sand and cobble. Dissolved oxygen appeared to affect crabs with a specific carapace color or moult stage (‘red’ crabs). Influence of flow was inconsistent: while in some cases *C. maenas* was found at higher densities in areas with a current, they were aversive to direct wave exposure and common in low-flow sites when foraging. pH was the least frequently addressed, and never found to exert a significant effect on *C. maenas* distributions.

Interactions between environmental factors and internal and temporal variables

Internal variables (i.e., size, carapace color, and sex) and temporal variables (i.e., seasonal, tidal or diel cycle) played a role in crab responses to environmental factors. Interactions with these variables were noted in 54% of records, and affected all environmental factors. For adult *C. maenas*, water depth demonstrated the broadest range of interactions with both internal and temporal variables (Table 3). The outcomes of biotic interactions (food sources as well as agonistic interactions) depended upon size disparities between predator and prey. Salinity preferences were affected by sex or carapace color (moult stage) in adult specimens. Dissolved oxygen was only found to substantially affect *C. maenas* distributions when carapace color was taken into account. Size (or size disparities between *C. maenas* and interacting species) and carapace color were found to interact with the most environmental factors in adults, and depth was the factor most often affected by internal and temporal variables. Interactions were less commonly recorded in juvenile studies. Size was the only significant variable, interacting with a number of environmental factors, including depth, vegetation, shelter, and temperature. The outcomes of biotic interactions (namely food sources and agonistic interactions), as with adults, were affected by size or size differences between interacting individuals. When findings from all studies (juvenile, adult, and non-specified) were combined, size influenced the most environmental factors. Depth was again the factor with the broadest range of interactions. Temperature changes affecting distribution were frequently (≥ 63% of supporting records) associated with temporal shifts in season.

Variations in environmental factors by clade and native/non-native region

The relative distribution of records for environmental factors differed between geographically separated regions (Fig. 2 A, C). This may partly be due to the imbalance in total studies collected between these locations. In general, studies in areas with mixed clades of crabs (UK, Australia, parts of North America) emphasized depth, and those with populations of southern (mainly native regions) and mixed clades emphasized agonistic interactions. The majority of studies concerning food sources originated from invaded regions, whereas vegetation studies were emphasized in native regions.

Modeling and management implications of complexity in *C. maenas* distributions

Water depth and biotic interactions were revealed as the primary environmental factors affecting *C. maenas* distributions. Depth preference of *C. maenas* was frequently influenced by internal and temporal variables such as seasonal changes in water temperature. Several studies suggested that *C. maenas* migrates inshore with warmer seasons and to deeper areas with colder temperatures (e.g., Atkinson and Parsons 1973, Sharp et al. 2003). These movements are intermingled with tidal migration, as well as circadian rhythm of crab activities, with different depth preferences and greater activity at night (see for example Aagaard et al. 1995, Ansell et al. 1999). How strongly these movements are exhibited is further influenced by the age, sex, or carapace color of the individual, as each demographic has different habitat requirements and sensitivities. While depth may exert strong influences on *C. maenas* distribution (and perhaps be more feasibly monitored), the influence of depth on distribution is highly contextual. Exactly how these interactions will impact the distribution of *C. maenas* warrants consideration when conducting removals (i.e., when setting traps). Tidal fluctuations in *C. maenas* distributions are unlikely to be the primary consideration because most trap soak periods exceed the span of a single tidal cycle, however they may play a role in optimal setting sites in areas with large tides. Seasonal fluctuations may also be important in tracking *C. maenas* movements to greater depths.

The outcomes of biotic interactions (i.e., competition, predation and food sources) were found to depend on size differences of interacting pairs (e.g., predator and prey or competing individuals). This study did not break down biotic interactions to prey and predator species-specific outcomes when paired with *C. maenas*, which will inevitably play a role in fine-scale *C. maenas* distribution within a region. While *C. maenas* was frequently the victor in agonistic interactions, it was also found to be outcompeted or to not interact agonistically at all in other studies, likely due to the species with which it was paired and other demographic (i.e., size, carapace color or sex) variables. Agonistic interactions are more likely when microhabitat and resources are shared (Schoener 1983); understanding the factors characterizing species' respective niches and the amount of overlap between these is important. However, a large portion of the studies we collected for biotic interactions were lab-derived; these may mask the occurrence of niche overlap between interacting species and the effects of other environmental gradients in the field. This may make prediction of biotic interactions in the field difficult. Similarly, many studies of food sources were conducted in invaded regions, as opposed to regions where it is native. Concerns about *C. maenas'* impact as an invader on local fisheries and ecosystems have generated studies to understand its interaction with vulnerable (i.e., prey) species. This may explain the emphasis on food sources compared to other environmental factors, especially in regions where *C. maenas* is not native. Accordingly, these factors should only be considered with caveats and a strong understanding of the local environmental context. Despite recognition of these challenges to our understanding, the importance of incorporating biotic interactions to improve model performance has been noted (Mitchell 2005, de Araújo et al.2014, Snickars et al. 2014). Biotic interactions and other factors may be accounted for using certain models, although there are a number of acknowledged challenges. These include accounting for the effects of simultaneous interactions among multiple species, and variability in the nature of biotic interactions in space and time (Wisz et al. 2013; Loots et al. 2011, Brummer et al. 2013).

Many studies noted effects of interactions with internal and temporal variables, as well as interactions between environmental factors. Demographic habitat segregation is common among crustaceans; Andrade et al. (2014) noted age-related habitat differences in the redfinger rubble crab (*Eriphia gongaria*), and demographic differences in blue crab (*Callinectes sapidus*) and other Brachyurans (Pardieck et al. 1999, Pallas et al. 2006). In many species it is common for juveniles to segregate into regions with more available shelter or different substrate types or vegetation; this was observed in our comparisons between adult and juvenile *C. maenas*. There is evidence of sex-mediated distribution of American lobsters (*Homarus americanus*) at the local scale according to temperature differences (Jury and Watson 2013). Such differences are associated with life-stage or sex-related requirements, as different environmental risks and benefits are experienced. The majority of species distribution models, however, aim to explain species distribution through environmental factors without accounting for internal variables (Planque et al. 2011). While models that can account for multiple demographic or phenological situations simultaneously are rare, it is possible to address demographic subsets using separate models. Planque et al. (2011) suggest a multi-model approach to better understand which factors and variables exert the greatest effects. While our study noted the presence of many internal variables, only a few (sex, size, carapace color) were consistently acknowledged among environmental factors. These internal variables can exert a strong influence on fine-scale abundance levels (Loots et al. 2011), and their omission may have consequences for model performance at finer scales.

Temporal fluctuations in species distributions and abundance are well recognized in the literature, including for crustaceans (e.g., Jesse and Stotz 2002, Rewitz et al. 2004, Robinson et al. 2004, Andersen 2006, Silva et al. 2014). Consequently, the need to account for spatio-temporal shifts of species in models has been noted (D’Heygere et al. 2003, Caixia et al. 2014). D’Heygere et al. (2003) demonstrated the utility of modeling spatio-temporal relations to understand migratory dynamics. Caixia et al. (2014) illustrated not only the utility of temporal considerations, but how considering the proper temporal scale in modeling (week, fortnight, month) may affect model performance. These are often necessary to account for changes in distribution related to temporal movements, such as seasonal migration. In general, model predictions of where higher densities of *C. maenas* may be found are likely to be compromised if temporal and internal variables (such as depth preference during summer versus winter) are not taken into account.

There are some other general considerations for all of the environmental factors and variables highlighted. Certain environmental factors may be contingent on others, or combined may have different effects on *C. maenas* distribution. For example, predation by other agonistics on juvenile *C. maenas* may have a greater effect on distribution in areas where these small crabs have less access to shelter. Many studies did not account for interaction effects between environmental factors, and these were not recorded in our literature review when they did appear. However, such interactions are important to understanding local environments and predicting local distributions. From a modeling point of view, such variations in local contexts may affect the generalizability of any model and the reliability of its output. Furthermore, coarse-scale environmental variations (i.e., latitudinal temperature changes) may also interact to affect distribution at finer scales, as highlighted in other studies attempting to generalize models (McAlpine et al. 2008). Future works may wish to account for site-specific variations as well as different scales of influence.

At the fine scale, the environmental conditions of the site need to be taken into context. Different inshore regions vary in their topography, hydrodynamics, flora and fauna. While factors are likely to lie within some bounds in order to permit initial establishment, the full amplitude of an environmental gradient warrants consideration, as this may vary between water body types. The sample size in this study did not allow for direct comparison of factors by water body type. Regardless, site characteristics may have implications for the main factors shaping local *C. maenas* distribution, particularly if environmental gradients are enhanced, reduced or absent altogether.

A further consideration for integrating these findings into management is availability of data. Some inshore regions, which are more intensively studied (for instance, protected park areas), may already yield environmental data at an acceptable resolution, derived from previous studies. For example, Little Port Joli estuary, in Kejimkujik National Park & National Historic Site, Nova Scotia, Canada, already yields a wealth of information on bathymetry, sediment distribution, and vegetation monitoring among other factors (e.g., Brylinsky et al. 1987, Pelletier 2009). In most other locations, it is less likely that environmental information will have been collected for factors important to *C. maenas* distribution. In areas that are heavily invaded, initial removal efforts may benefit from monitoring relevant environmental factors alongside removals in order to provide additional information for modeling and for trapping efforts. In areas of inshore fisheries, local harvesters may already be familiar with important environmental factors and use them as an intuitive guide to setting traps.

Limitations

The results of this review are based on existing literature on fine-scale distributions of *C. maenas*; however, it is rarely feasible to source all relevant documents. *C. maenas* has been extensively studied and papers are frequently published. Furthermore, while steps were taken to ensure a relatively objective collection of data, there is potential for subjectivity in interpreting the results. This is especially applicable to descriptive studies that may not provide explicit supporting data. Consistency in analytical methods was prescribed to reduce this. It is reassuring that separate analyses of descriptive studies and statistically significant records supported similar factors. We have also assumed that the approaches used in the various studies to support results around biotic interactions were sound; however, these studies were largely focused on the ability of green crab to predate or be displaced by species, and may not accurately reflect other factors and interactions in the field. Direct competitive interactions were largely considered in lab studies, which also represent simplifications of field conditions and may not highlight effects of indirect competition.

Our research assumes that the numbers of records yielding supporting evidence for a factor provides an indication of its importance in shaping fine-scale distributions of *C. maenas*. This method is vulnerable to unequal emphasis on different environmental factors in the literature. Imbalances in research priorities may exist due to biased interests (Nasser and Welch 2013), and regional variations in interest may simply indicate that different research questions are emphasized. Consequently, other quantitative indicators, such as a ratio of studies supporting versus refuting each factor, may provide a different picture of importance. However, our method highlights key factors, the number and age of studies related to and supporting each factor, and potential areas warranting further research.

Conclusions

This study highlights the key factors established in the scientific literature affecting fine-scale habitat distribution of *C. maenas*. While green crabs generally showed potential for distribution according to depth and presence of biotic interactions, the driving factors for different life stages differ somewhat, with juveniles and adults being variously influenced by vegetation characteristics, shelter, salinity and presence of food sources. Other internal and temporal variables were found to interact with distributions along different environmental gradients, such as age, sex, carapace color, and seasonal, diel and tidal effects. These interactions affected the specific environmental conditions preferred, and how they changed at day or night, or over an annual cycle. There is also potential for factors to vary between clades. Such results illustrate the complexity of factors influencing fine-scale distributions of this species.

A mobile species such as *C. maenas* may be a challenge to model at a fine scale. Given regional and temporal fluctuations, recommendations for any "best" factors for modelling distributions may be difficult to prescribe. Considering the inherent complexity of environmental interactions and the significance of local context, existing modeling technologies may be challenged in creating a practical model for *C. maenas*. Nonetheless, this review provides key delimitations concerning some of the most scientifically supported environmental factors and influencing variables. These may inform practical considerations for management recommendations, such as when first prioritizing local research or locations for trap placement within an invaded water body. Inclusion of internal and temporal variables may help to better predict the fine-scale distribution and movements of *C. maenas*. This may guide management direction for future parks-based, community or government-led removal, exploratory fishery or other initiatives by understanding factors driving distribution.

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Category	Factor	Explanation
Bottom topography	Depth	Considering movements within the tidal column, onshore exposure and sub tidal preferences
	Shelter	Focusing on use of stones and discarded shells or mussel beds in lab or field settings
Biotic Features	Vegetation	Algae and macroalgal growth
	Food source	Fauna actively predated on in lab or field observations
	Agonistics	Including competition with, avoidance of, displacement or predation by other species
Hydrography	Salinity	Either preferences for a set salinity or tolerance to salinity changes
	Temperature	Aversion to or preference for given temperature ranges
	Dissolved Oxygen	Avoidance of particularly low or high amounts of dissolved oxygen
	Water pH	Preference for a specific pH/range
Exposure	Flow	Current and wave exposure
Substrate	Bottom type	Primary sediment type, i.e. mud or sand

Table 1

A) Adult Studies	**Depth**	**Shelter**	**Vegetation**	**Food Source**	**Agonistics**	**Salinity**	**pH**	**DO**	**Temperature**	**Flow**	**Bottom Type**
% Studies with Factor	**22**	**2**	**2**	**22**	**23**	**17**	**0**	**3**	**5**	**2**	**3**
P < 0.005	3	1	0	9	8	1	0	1	1	1	0
0.005 < p < 0.05	3	1	0	8	5	2	0	0	0	2	0
Descriptive Support	14	0	1	3	3	3	0	0	1	0	2
Discussed Support	0	0	0	0	2	3	0	0	0	0	0
ns; P > 0.05 or refuted	**0**	**0**	**0**	**3**	**9**	**1**	**0**	**1**	**1**	**1**	**0**
Total Records (interactions)	**7 (13)**	**0 (2)**	**1 (0)**	**5 (18)**	**25 (2)**	**5 (5)**	**0**	**1 (1)**	**1 (2)**	**1 (3)**	**1 (1)**
Total Statistically Significant Records (interactions)	**2 (4)**	**0 (2)**	**0**	**4 (13)**	**11 (2)**	**1 (2)**	**0**	**0 (1)**	**0 (1)**	**1 (2)**	**0**

Table 2

B) Juvenile Studies	**Depth**	**Shelter**	**Vegetation**	**Food Source**	**Agonistics**	**Salinity**	**pH**	**DO**	**Temperature**	**Flow**	**Bottom Type**
% Studies with Factor	**14**	**21**	**29**	**11**	**21**	**0**	**0**	**0**	**4**	**0**	**0**
P < 0.005	1	1	1	1	0	0	0	0	0	0	0
0.005 < p < 0.05	1	3	3	2	5	0	0	0	0	0	0
Descriptive Support	2	3	3	0	0	0	0	0	1	0	0
Discussed Support	0	0	1	0	0	0	0	0	0	0	0
ns; P > 0.05 or refuted	**0**	**0**	**0**	**0**	**2**	**0**	**0**	**0**	**0**	**0**	**0**
Total Records (interactions)	**0 (4)**	**3 (10)**	**4 (4)**	**1 (2)**	**4 (3)**	**0**	**0**	**0**	**0 (1)**	**0**	**0**
Total Statistically Significant Records (interactions)	**0 (1)**	**2 (5)**	**3 (1)**	**1 (0)**	**2(3)**	**0**	**0**	**0**	**0**	**0**	**0**

Table 2 (continued)

C) All Studies	**Depth**	**Shelter**	**Vegetation**	**Food Source**	**Agonistics**	**Salinity**	**pH**	**DO**	**Temperature**	**Flow**	**Bottom Type**
% Studies with Factor	**18**	**14**	**20**	**27**	**32**	**17**	**1**	**7**	**14**	**4**	**8**
P < 0.005	6	5	3	11	11	1	0	1	1	1	1
0.005 < p < 0.05	8	5	4	10	10	2	0	0	2	2	0
Descriptive Support	36	5	7	6	8	5	0	2	6	1	5
Discussed Support	0	0	2	0	2	3	0	0	0	0	0
ns; P > 0.05 or refuted	**0**	**0**	**0**	**3**	**15**	**1**	**1**	**2**	**5**	**1**	**6**
Total Records (interactions)	**13 (37)**	**3 (12)**	**10 (6)**	**7 (23)**	**39 (7)**	**7 (5)**	**1 (0)**	**2 (3)**	**4 (8)**	**2 (3)**	**2 (4)**
Total Statistically Significant Records (interactions)	**6 (8)**	**2 (8)**	**5 (2)**	**5 (16)**	**13 (10)**	**1 (2)**	**0**	**0 (1)**	**1 (2)**	**1 (2)**	**1 (0)**

Table 2 (continued)

	------------Internal Variables-----------									------------Temporal Variables------------								
	Carapace width			Sex			Color			Time (season)			Time (tide)			Time (circadian)		
Factor	B	A	J	B	A	J	B	A	J	B	A	J	B	A	J	B	A	J
Depth	x	x	x	x	x		x	x		x			x	x			x	
Shelter	x		x															
Vegetation	x		x															
Food	x	x	x															
Agonistics	x	x	x															
Salinity				x	x		x	x										
Temperature			x	x						x								
pH																		
Dissolved Oxygen							x	x										
Flow																		
Bottom Type	x			x														

Table 3

Table 1. Primary environmental factors affecting local-scale distribution of *C. maenas* in the reviewed literature. These are grouped into five overlying environmental categories, adapted from work by Snickars et al. (2014). Each factor is accompanied by a brief description of the studies which were considered supportive of this factor.

Table 1. Comparisons of studies and records reporting descriptive or statistically significant (either $0.005 < p < 0.05$ or $p < 0.005$) evidence of factors posing an effect on *C. maenas* distribution in local-scale studies. Numbers are shown for A) all age classes, and solely B) juvenile or C) adult records. Records with interactions with temporal, phenological, ontogenetic or biotic factors are noted in brackets. DO = Dissolved Oxygen. Dotted lines group factors into five broad categories, respectively: bottom topography, biotic features, hydrography, exposure, and substrate.

Table 3. Prevalence of interactions between (internal and temporal) variables and environmental factors observed in this study. An 'x' indicates where an internal or temporal factor was found to interact with an environmental factor in more than two records. These were broken down according to: (B) all studies, regardless of age class; records of adult (A) crabs; or records of juvenile (J) crabs. Dotted lines group factors into five broad categories, respectively: bottom topography, biotic features, hydrography, exposure, and substrate.

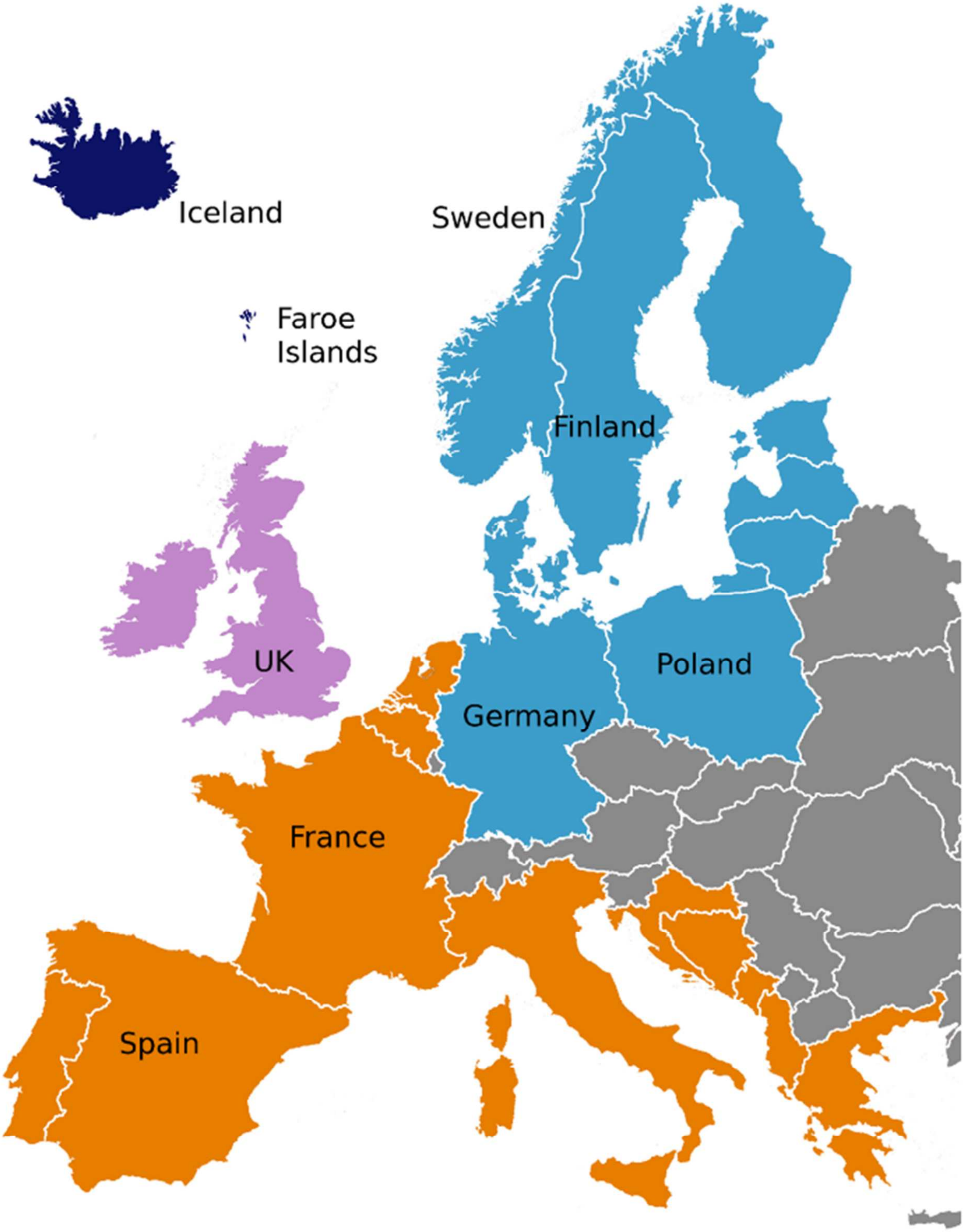
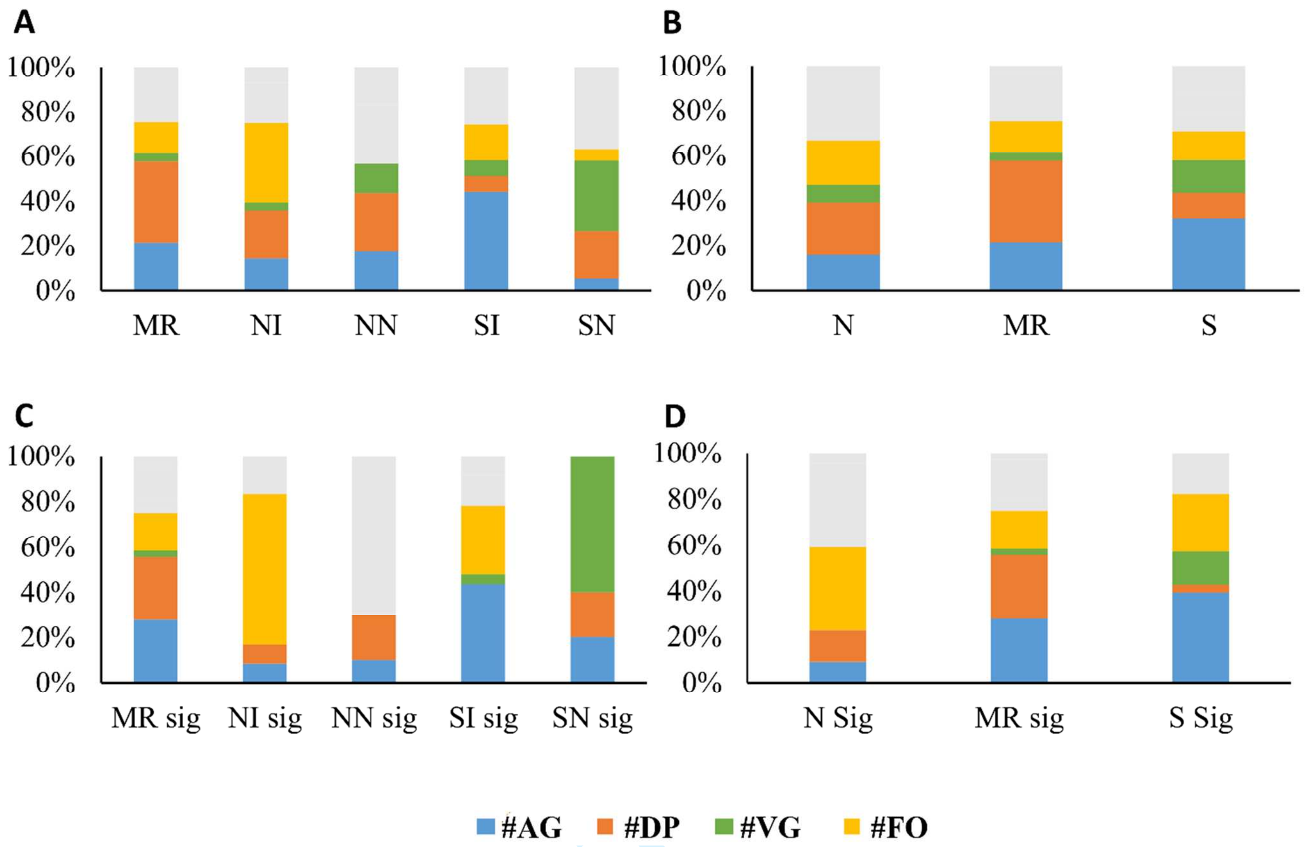

Iceland
Sweden
Faroe
Islands
Finland
UK
Poland
Germany
France
Spain

Figure 1


A
100%
80%
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NN sig
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D
100%
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MR sig
S Sig
#AG
#DP
#VG
#FO

Figure 2

Figure 1. Map of Western Europe. The greatest divisions of native *C. maenas* clades exist between Iceland/Faroe Islands (deep blue) and the rest of continental Europe; a smaller division exists at regions south of (orange) and north of (light blue) Germany. The UK (mauve) appears to contain individuals from both sides of the Germanic division, although primarily bears similarities to Western European (orange) populations and overall shows little genetic diversity across the island. *C. aestuarii* regions are also indicated (orange). (Clade divisions according to Roman & Palumbi (2004) and Brian, Fernandes, Ladle *et al.* (2006)). (Adapted from iStock.com/Rufus Young)

Figure 2. Percent (%) of records addressing the effects of environmental factors in Northern European (N), Southern European (S) and mixed origin (MR) *C. maenas* populations. Comparisons were made between A) invasive (I) and native (N) populations. Comparisons were also made B) looking solely at origin. Records only providing statistically significant support for factors (C and D) were also compared. Factors highlighted include agonistic interactions (AG), vegetation (VG), depth (DP) and food (FO). Other factors are grouped and not discussed (grey area).