Salacia-Marine
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Ecosystem niche review for species caught by commercial potting

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Ecosystem niche review: commercial potting species

Contents

Glossary

Ecological Niche: The role, and position, a species has in its environment - how it meets its needs for food and shelter, how it survives, and how it reproduces. A species' niche includes all of its interactions with the biotic and abiotic factors of its environment.

Fundamental niche: The ecospace an organism would occupy if free of interference and competition from other species.

Realised niche: The ecospace a species actually occupies at a particular moment in time. It is usually restricted in comparison to the fundamental niche, due to competition and interaction with other species. It is the ecospace a species is most adapted to.

Trophic level: The position of a species in a food chain (or web). It is determined by a species' predators (the trophic level above) and prey (the trophic level below).

Apex predator: Species at of the top of the food chain (or web).

Top-down regulator: A species which significantly influences species at lower trophic levels, via direct predation.

Bottom-up regulator: A species which significantly influences higher trophic levels due to its role as a prey species.

Trophic cascade: Top-down control of species assemblages via predator-prey interactions. Changes in predator abundance will affect species at lower trophic levels; leading to disruption of food chains (or webs) and, potentially, ecosystem function and stability.

Ecosystem function: The collective processes (or mechanisms) required to maintain ecosystem structure. It is how the ecosystem operates as a whole. The required processes can be biological, geochemical or physical.

Functional diversity: A measure of the number, type and distribution of functions performed by species within an ecosystem. The higher the functional diversity, the more stable and resilient an ecosystem is.

Functional trait: Morphological, biochemical, physiological, structural, phenological, or behavioural traits which are expressed by a species; and are of relevance to the response of the species to its environment, and/or its effects on ecosystem function. Variation in traits across species within an ecosystem is used to quantify 'functional diversity'.

Functional group: A group of species with similar functional traits. Note - species within functional groups may not all be of the same taxonomic faction.

Keystone species: A species which has a disproportionately large effect on an ecosystem, relative to its abundance. It is pivotal in maintaining ecosystem function.

Phase shift: Transition of an ecosystem from one stable state to another as a result of disturbance. The previous state ceases to exist.

Bioturbator: A species which reworks sediments, and therefore affects sediment texture, structure, bioirrigation and composition of species assemblages.

Biogenic engineer: A species which creates biological structures within its ecosystem.

Introduction

Static gear fisheries, specifically potting and trapping, take place around the British coast both within and without MPAs. There are eight key species targeted by these fisheries and are the focus of this review;

- the crustacean Brown crab *Cancer pagurus*, European lobster *Homarus gammarus*, European spiny lobster (also called crayfish or crawfish) *Palinurus elephas*, Velvet swimming crab *Necora puber*, Spider crab *Maja squinado*, and Langoustine *Nephrops norvegicus*, and;
- the molluscan Cuttlefish *Sepia officinalis*, Whelk *Buccinum undatum*.
- Other species such as the Palaemon spp. Prawns and green crabs are targeted on a smaller regional scale.

The fisheries take place across a wide range of habitats determined by the ecological requirements of each species; *H. gammarus* and *N. puber* fisheries are predominantly rocky ground fisheries whereas fisheries for *B. undatum* and *N. norvegicus* take place over soft sediment environments, the latter in muddy grounds.

All species inhabit a particular ecological niche, the relative position of each species in their ecosystem. A species niche determines how a population responds to resource abundance and number and severity of threats by increasing when resources are plentiful and effects of predators, parasites and pathogens are low. The species niche affects these same factors by consuming resources and supporting, through predation, population growth of predators. Beyond predator-prey relationships and food-web interactions the species niche determines how some species contribute to the function of their community through their interaction with the physical environment and such actions as biochemical cycling.

The understanding of ecological niche and related interactions is particular interest to marine fishery and conservation managers because it may be informative in the effective management of exploited ecosystems. Over exploitation or local extinction of some commercial species has been implicated in ecological perturbations such as phase shifts and trophic cascades.

Understanding the respective ecosystem niche that commercial potting species occupy will help understand what, if any, effect that removing them would have on the ecosystem functioning of the designated features or habitats.

The aim of this report is to undertake a literature review to enable an initial understanding of the ecological role these eight species occupy within a framework that considers their interaction with predators, prey and physical environment.

Beyond the review of the ecological role of these eight species we have attempted to assess the evidence and determine the possible ecosystem effects of commercial species removal.

We identify the information gaps and shortfalls in understanding associated with both ecological niche and effect of removal.

Finally, this study offers possible directions of study to address these shortfalls in understanding and signposts possible approaches and practical ways forward.

Methods and Approach

Literature review

The species review was undertaken drawing upon primary research literature and academic publications enabled by our research partnerships with UK Universities. Initial searches utilized academic search tools Web of Knowledge and Google Scholar.

In addition to the electronic sources Salacia-Marine drew upon our own library of grey literature. Further reports and publications were obtained through our network of colleagues in Government research bodies.

We endeavoured to identify and source details on current relevant research this underway and that may help to address shortfalls in understanding.

The results of individual species ecological niche reviews are presented in this report and in individual species datasheets formatted to help Natural England staff rapidly understand their ecology, trophic relationships and ecosystem role as well as key gaps in understanding.

All citations in the literature review have been stored in both Endnote and Mendeley citation databases for ease of access.

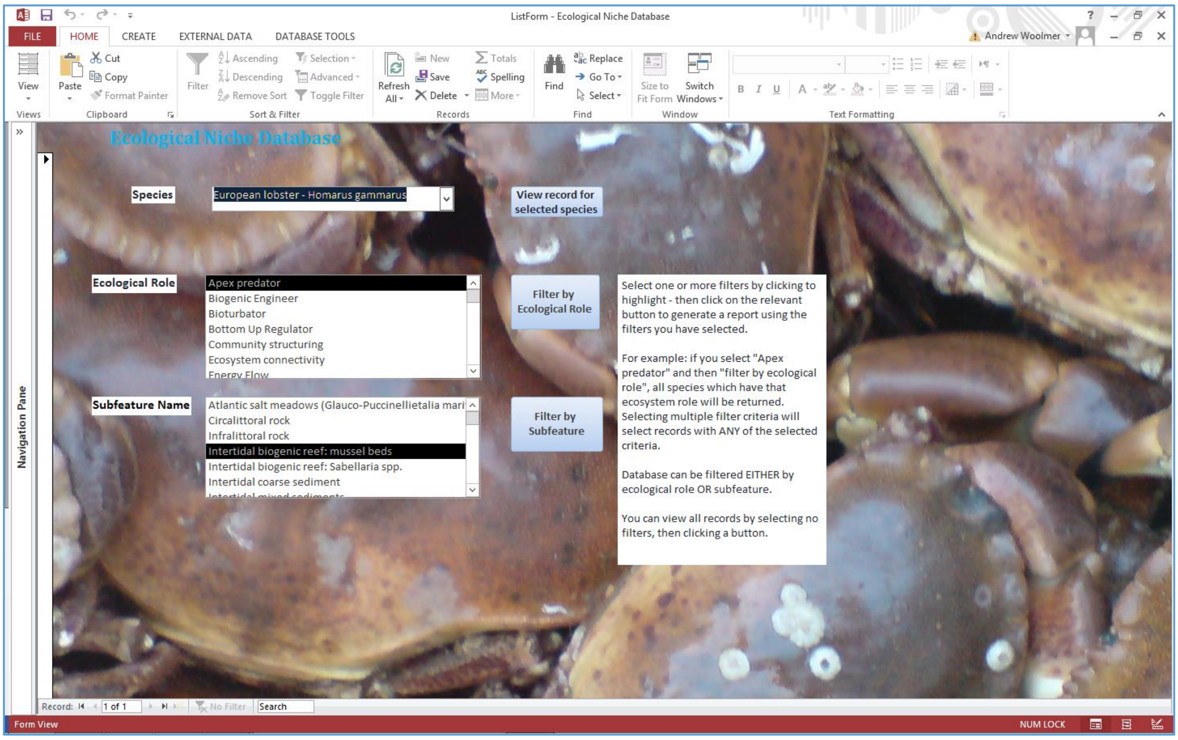
Species niche tool

Discussions with Natural England highlighted the requirement for an information discovery tool that will enable marine advisers and regulators to readily access species niche information in order that they are able to provide consistent and well evidenced conservation advice.

Initial attempts to tabularise outputs were even with only 8 species considered by the authors to be insufficiently intuitive enough for wider use. This resulted in the development of a MS Access database which enables the user to search on a suite of criteria based upon species ecology and on ecological roles. The end result enables the user to readily search for and be presented with species datasheets for each of the commercial species reviewed in this study.

Should future development and expansion be required, it is possible for the Access database to be exported to an SQL database in the future. The benefit of an SQL database for this purpose is that it can be located on a central server and new species added to it, and current species datasheets updated and appended as new information becomes available. A web interface would enable a wide group of users to utilise the tool without the need for the distribution of multiple individual copies.

See over for screenshot of search Tool



Ecological Niche Database

Species European lobster - Homarus gammarus

View record for selected species

Ecological Role

- Apex predator
- Biogenic Engineer
- Bioturbator
- Bottom Up Regulator
- Community structuring
- Ecosystem connectivity
- Energy Flow

Filter by Ecological Role

Subfeature Name

- Atlantic salt meadows (Glauco-Puccinellietalia mari
- Circalittoral rock
- Infralittoral rock
- Intertidal biogenic reef: mussel beds
- Intertidal biogenic reef: Sabellaria spp.
- Intertidal coarse sediment

Filter by Subfeature

Select one or more filters by clicking to highlight - then click on the relevant button to generate a report using the filters you have selected.

For example: if you select "Apex predator" and then "filter by ecological role", all species which have that ecosystem role will be returned. Selecting multiple filter criteria will select records with ANY of the selected criteria.

Database can be filtered EITHER by ecological role OR subfeature.

You can view all records by selecting no filters, then clicking a button.

Figure 1. A screenshot of the species niche search tool produced as part of this study.

The Ecological Niche

The term, '*ecological niche*' has a range of definitions and associated theories, and as such, has its own dedicated field of research under the general theme of 'Evolutionary biology'. The science of 'ecological niches' encompasses both empirical and theoretical aspects, using the natural environment, as well as mathematical modelling, to enhance our understanding of species' '*ecological niches*' and their subsequent survival in the natural world.

However, the description of an '*ecological niche*' can easily be simplified using this commonly employed definition in order to portray the concept to a general audience.

"An ecological niche is the role, and position, a species has in its environment - how it meets its needs for food and shelter, how it survives, and how it reproduces. A species' niche includes all of its interactions with the biotic and abiotic factors of its environment" (Anon)

On the presumption that no two species are identical, an ecological niche is considered to be unique to a particular species. However, in nature, it will be noted that species do share habitats and 'modes of life', and live cheek-by-jowl. This is a result of species' adapting to successfully survive under local competition for resources. As a consequence there are two categories of ecological niche – the '*fundamental*' and '*realised*' niche (Fig.2).

The '*fundamental niche*' of a species is the ecospace an organism would occupy if free of interference and competition from other species. It would exploit the full range of habitats and resources in which it could survive and reproduce. In reality, however, species are competing and interacting with each other, and as such, this pressure forces each species to occupy a more restricted niche; the one to which they are most adapted to. This is known as the '*realised niche*' and is the one a species actually occupies at a particular moment in time. There is, however, potential for the 'realised niche' to shift within the 'fundamental niche', if the constraints change. Once a niche becomes vacant, a different species will quickly fill the void.

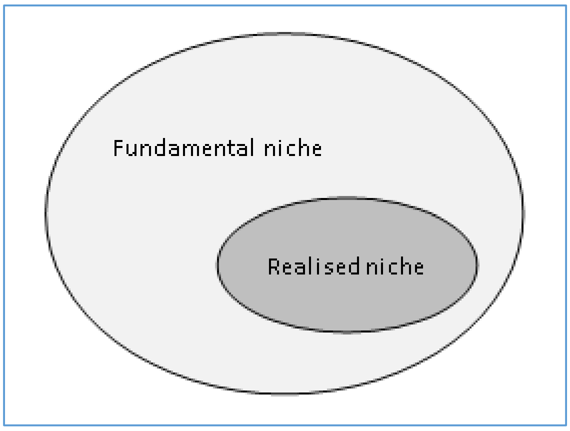


Figure 2. The Ecological Niche

The 'realised niche' is reiterated by the '*competitive exclusion principle*', which states that two species competing for the same resource cannot coexist at constant population values.

There are a variety of factors which define a species' ecological niche. They are both abiotic and biotic. Abiotic factors are those associated with the physical environment. In marine ecosystems, they can be, for example, substratum type; water depth, temperature and salinity, and tidal/current regimes. In contrast, biotic factors are those associated with the living organism itself, and include behaviour, diet, reproductive strategies, predation and disease. Competition for resources, resulting from coexisting species, is also considered a biotic factor.

Food chains (and food webs) within ecosystems provide valuable insight into a species' ecological niche. They provide detail on an organism's position within a community, and also on its predators and prey. It also offers information on the associated adaptations of a species to occupy a particular ecological niche. '*Trophic levels*' are used to describe the position of an organism in a food chain, and are determined by an organism's predators (trophic level above) and prey (trophic level below).

Ecologists have created the concept of '*trophic level pyramids*' (Fig. 2) to convey the fundamental principle of food chains and energy transfer within ecosystems. A food chain (or pyramid) can have up to 5 levels, depending on the complexity of the ecosystem. Level 1, is at the bottom of the pyramid, and as you progress up through the levels, the organisms on each level tend to become larger and more complex. However, in contrast to increased size and complexity of the organism as you move upwards; there is a loss of energy between each level, and this results in an overall decrease in biomass and numbers at higher trophic levels. Hence, the pyramidal shape. A generalised 'trophic level pyramid' of a marine ecosystem is presented in Figure 2. In summary, level 1 constitutes the photosynthetic organisms, such as phytoplankton and seaweed, which is then followed by herbivores (level 2), and then carnivores (levels 3, 4 and 5). Apex consumers/predators are those at of the top of the pyramid; and in marine ecosystems, are typically large carnivores such large fish, mammals and birds.

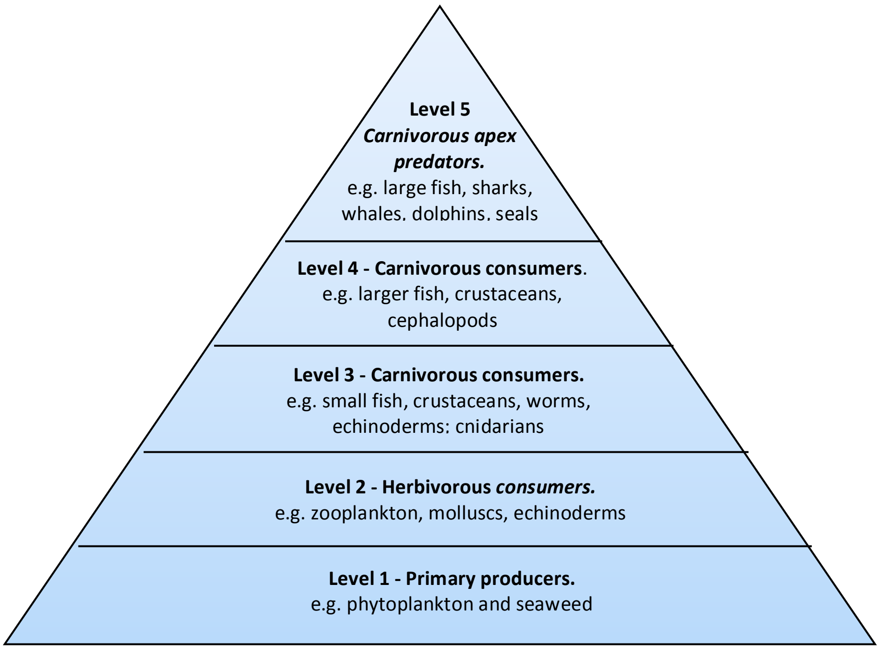


Figure 3. Trophic pyramid of a marine ecosystem

A specialised and powerful approach for determining the specific trophic level of an organism is the quantification of naturally-occurring stable isotopes within the organism's tissues (Jennings *et al*., 2008). Commonly, it is carbon and nitrogen stable isotopes which are measured. Nitrogen stable isotope data, for example, can provide information on intra- and inter-specific variation in trophic level, predator-prey size ratios, food chain length, relationships between predator and prey species diversity, and the dynamics of energy use (Chikaraishi *et al*., 2014). All of these parameters are extremely important in determining a species/organisms ecological niche.

Relationship between Ecological Niche and Ecosystem Function

What is ecosystem function?

There is no single definition of 'Ecosystem function'. In simple terms, it is the collective processes (or mechanisms) which are required to maintain ecosystem structure. It addresses how the ecosystem operates as a whole. The required processes can be biological, geochemical or physical. The major functional aspects are the abiotic and biotic processes involved in energy and mass transfer; particularly those related to biomass production, nutrient recycling and trophic interactions. Functioning within ecosystems is predominantly concerned with linking together different structural elements to create a stable system, and thus maintaining the ability to supply ecosystem goods and services. Understanding and interpreting ecosystem function greatly improves our ability to sustainably harvest and manage particular habitats and environments.

"Concepts of ecosystem structure and function may be useful in designing an overall framework for UK marine monitoring, as they are concepts that are inherent within the ecosystem approach and may help us to consider underlying processes, rather than monitoring at small spatial scales or of small ecological scope. There are significant challenges in understanding the ecosystem across different sectors and scales, and consideration of processes that link these elements may encourage integration". JNCC (2008).

Biodiversity and ecosystem function

Biodiversity and ecosystem function (commonly termed the 'BEF agenda or paradigm' Loreau *et al*., 2001), is a field of research which has emerged over the past 20 years. It emerged from the consensus that the increasing impact of human activities on natural and managed ecosystems is decreasing biodiversity in such systems. Hence, the question was raised of whether these impacted systems function less effectively than species-rich ecosystems; ultimately diminishing the ecosystems ability to deliver goods and services (Loreau, 2010; Cardinale *et al*., 2012).

Consequently, it was debated on whether it was the number of species *per se* (i.e. species richness) or the composition of species which drives and maintains ecosystem function. Classical biodiversity measurements are based on species richness, which assumes that all species, and individuals, are equal and distinct. However, in reality, the situation is far more complex, and as such, studies have shown that ‘richness’ effects are commonly less influential than ‘compositional’ effects in determining the BEF relationship (Hooper *et al.*, 2005; Arenas *et al*, 2006; Cadotte *et al.*, 2011) .

Furthermore, studies on species compositions have established that it is the functional roles of species within ecosystems which are pivotal in linking biodiversity and ecosystem function. Species richness and abundance, alone, are unable to fulfil the criteria of a stable functioning ecosystem. Ecosystem function revolves around the ‘*ecological niches*’ and ‘*functional traits*’ of encompassed species.

How is ecosystem function measured?

Describing or measuring ecosystem function can be difficult, as it encompasses a number of phenomena relating to the chemical, physical and biological components of the system (Hooper *et al.*, 2005). However, scientists are now generally in agreement that the concept of ‘*Functional diversity*’ is a measurable index which can provide much insight into ecosystem structure and function (Hooper *et al.*, 2002; 2005; Heemsbergen *et al.*, 2004). It overcomes the difficult, and often impossible, task of cataloguing all species present within an ecosystem. By focussing on processes and functions, it may be easier to establish how an ecosystem can be managed or protected. In addition, by protecting ecosystem function, the individual species performing these functions will be protected by default.

‘*Functional diversity*’ is a measure of the number, type and distribution of functions performed by organisms within an ecosystem (Diaz and Cabido, 2001). It is considered that the higher the functional diversity, the more stable and resilient is an ecosystem is. Functional diversity is not necessarily positively correlated with species diversity, and this highlights the potential for species redundancy (Naeem, 2002). For example, you can have an ecosystem with low species richness and diversity, but with high functional diversity (Tornroos *et al.*, 2014), thus highlighting that every species within that ecosystem has a unique functional role. Alternatively, there may be an ecosystem which is highly species-rich, but several of those species have the same functional role, hence low functional diversity. As a result, it is possible that the relative abundance of species in such an ecosystem can vary; or even become scarce or extinct, without compromising ecosystem functionality. However, in an ecosystem which has fewer species, all of which have a unique functional role, species cannot be lost without a detrimental effect to the ecosystem’s structure and function. An extreme example of a species exhibiting a unique functional role; is the ‘*keystone*’ species. Keystone species are those which have a disproportionately large effect on an ecosystem, relative to their abundance. They are critical to maintaining ecosystem function; hence, loss of a keystone species results in an ecosystem ‘*phase shift*’, with the previous ecosystem ceasing to exist.

Functional traits

How is an organism’s ecological function and role classified? The most widely applied approach is to use ‘*functional traits*’. Functional traits encompass a broad range of characteristics, and can be morphological, biochemical, physiological, structural, phenological, or behavioural traits which are expressed by individual organisms, and are relevant to the response of such organisms to their environment, and/or their effects on ecosystem function (Violle *et al., et al.,* 2007). The variation in traits across species within an assemblage (or ecosystem) can therefore be used to quantify 'functional diversity'. Such quantification generally involves grouping together species of similar functional traits, hence creating '*Functional groups*' of species. It must be noted that species within such '*functional groups*' may not all be of the same taxonomic faction. Functional groups can be created via subjective decision-making, or more objectively through mathematical or statistical methods (e.g. Bremner *et al*., 2003; McGill *et al*., 2006; Paganelli *et al*., 2012; Byrnes *et al* 2014).

The most difficult decision to make is which functional traits to use for functional group creation and analysis. Choosing traits depends on the specific aims of the study, but in general, only traits which are important for the function of interest must be included; traits that are functionally uninformative must be omitted (Petchey and Gaston, 2006). If careful thought is put into the choice of functional traits, and they are used appropriately, there is potential to provide significant insight into community dynamics and ecosystem processes using this method.

Functional traits & ecological niche

When exploring the general functioning of an ecosystem, and the roles particular organisms play in determining ecosystem integrity and stability, the functional traits used for such an assessment are often based on the factors involved in determining a species' '*ecological niche'*. In particular, the factors of habitat, trophic level and feeding behaviour. Species are considered to have functional traits that are uniquely adapted to their '*ecological niche'*. Hence, in this respect, the factors (or 'functional traits') used in the present report to describe the ecological niche and functional role of the 8 targeted commercial shellfish species, will be used to assess whether each species' loss from an ecosystem will have detrimental effects on their ecosystem's function and stability and; hence provision, of ecosystem goods and services.

Major drivers of ecosystem function

The major drivers of ecosystem function are considered to be '*trophic dynamics*' and '*resource partitioning and competition*'. 'Trophic dynamics' refers to the ecosystem food web, and the 'Bottom-up' (prey) and 'top-down' (predator) control of species. It is, therefore, the principle process of energy and nutrient transfer between organisms; and as such, strongly influences ecosystem structure and function. Breakdown or disturbance of the ecosystem food web may have deleterious consequences. Thus, when assessing a species' role in ecosystem function, it is important to establish its trophic level, hence; providing insight into the species' predators and prey, as well as its potential to belong to a 'functional group'. Functional groups of species tend to be larger at lower trophic levels; hence, the trophic pyramidal shape, and therefore ecosystem function may be more resilient to any change in particular species within such a group.

'Resource partitioning and competition' describes how similar species within an ecosystem use limiting resources. As such, it helps to explain how species can coexist in the same ecosystem without species driving one another to extinction through competition. Understanding 'resource partitioning and competition' will, therefore, help determine how a species' decline or increase will impact ecosystem function and stability (Griffin and Silliman, 2011). Important resources to consider when evaluating the 'functional role' and 'ecological niche' of species are habitat, food and reproductive mates.

Ecosystem function and stability – what happens as a result of disturbance?

Disturbance within an ecosystem can be catastrophic and extremely obvious, as in the case of an environmental disaster such as an oil spill; or more subtle and gradual, as in changes in species abundance and richness, and thus community structure. In the present day, gradual changes are commonly associated with human fishing activity, climate change and disease. Disturbance, in the form of species removal (or significant decrease in abundance) from an ecosystem, can induce both direct and indirect effects on ecosystem function and stability. For example, with regard to human fishing activities, the target species often occupies a high trophic level, and therefore belongs to a small functional group of species. In some instances, it may be the apex predator. Thus, fishing (and reducing) the population of such a species will ultimately affect species at lower trophic levels; potentially altering ecosystem structure and function. Such changes will not automatically result in deleterious consequences, because the outcomes for each scenario are idiosyncratic. Deleterious consequences are more probable if the removed species is a '*keystone*' species or performs a unique ecological role, and thus doesn't belong to a functional group. Disturbance to one (or few) species will not only directly affect the species themselves, there may be indirect costs associated with the change. Indirect directs commonly manifest themselves as '*trophic cascades*'.

'Trophic cascades' are classified as the top-down control of species assemblages via predator-prey interactions. Changes in abundance of predatory species can have drastic and long-lasting effects on species at lower trophic levels, ultimately disrupting food web structure and, potentially, ecosystem function and stability. Density-mediated effects occur when changes in abundance of one species effects the abundance of others, through direct predation. Such changes can cascade through several trophic levels. Alternatively, there are behaviour (or trait)-mediated effects that are non-lethal, but result in prey species altering their behaviour (or morphology) in order to avoid predation. This may reduce species fitness via shifts to less favourable ecological niches and/or reductions in optimal foraging. A classic and well-studied example of a marine 'trophic cascade' is the sea urchin grazing scenario, whereby changes in sea urchin abundance, via predation, determine whether the benthos is dominated by macroalgae (forests; lack of grazing urchins) or crustose coralline algae (barrens; abundant grazing urchins) (e.g. Shears and Babcock, 2002; Behrens and Lafferty; 2004; Guidetti, 2006). Such trophic cascades can lead to a persistence of alternative community states (Shears and Babcock, 2003), which are also known as ecosystem '*phase shifts*'. The more stable an ecosystem is, the more resilient it is to 'phase shifts'.

Unfortunately, MPAs provide ideal ecosystems for 'trophic cascades', and potential 'phase shifts'. Human fishing activities commonly target the species within high trophic levels down, such as large predatory fish or crustaceans. Hence, in MPAs or marine reserves where human fishing activity is prohibited, such apex species are released from predation, thus allowing increases in their abundance and size. This direct species effect is the most commonly reported beneficial phenomena of marine reserve implementation. However, the majority of studies have not investigated what effect this drastic increase in predatory abundance is having on lower trophic levels and overall ecosystem function and stability. The few scientists who have investigated such potential indirect effects have frequently reported trophic cascades; and as such, have concluded that not all species, or ecosystems, will benefit from marine reserve or MPA protection (e.g. Pinnegar *et al* 2000; Shears and Babcock 2003; Guidetti, 2006; O'Sullivan and Emmerson, 2011; Noble *et al*., 2013).

The Lundy Island No-Take Zone (NTZ), UK, also exhibits signs of trophic cascades. Several studies have demonstrated a significant increase in the abundance of European lobster, *Homarus gammarus*, inside the NTZ, with a coinciding decrease in co-existing decapod crustaceans, such as the Brown crab, *Cancer pagurus,* and the Velvet swimming crab, *Necor puber* (Hoskin *et al*., 2011; Wootton *et al*., 2012; Davies *et al*., 2014; in prep). Lobsters appear to be the current apex consumer in the Lundy NTZ, and since they are free from predation due to fishing prohibition, their dominant, aggressive and highly territorial nature, may be allowing them to exert both density- and behaviour-mediated effects on other resident decapod species. Such species may have been preyed upon by resident lobsters and/or physically displaced from their ecological niche within the NTZ. Whatever the precise reason, there appears to be a dramatic decline in the abundance of some species within the NTZ, and thus the possibility of a trophic cascade. Further in-depth monitoring of the NTZ, to include more species at various trophic levels, would determine nature of this cascade and ascertain whether it is deleterious to species biodiversity and abundance, and ultimately, ecosystem function and stability.

However, the inconspicuous nature of trophic cascades; resulting from their cumulative impact on less apparent lower trophic levels and the temporal scales required for trophic cascades to become visible (e.g. Edgar *et al* 2009; Babcock *et al* 2010; Estes *et al* 2011), means that investigations into such phenomena are commonly overlooked and not incorporated into management strategies of natural resources.

Additional indirect costs of ecosystem disturbance include disease, parasitism and invasive non-native species, all of which may compromise overall ecosystem function and stability. For example, with regard to disease and parasitism, climate change and anthropogenic stimuli are both considered to be increasing disease and parasitic outbreaks within the marine environment, and potentially destabilising ecosystem function (e.g. Harvell *et al*., 1999, Ward and Lafferty, 2004; Altizer *et al*., 2013). Increases in disease and parasitism have also been reported within MPAs (e.g. Sasal *et al*., 2004; McCallum *et al*., 2005; Lebarbenchon *et al*., 2007; Page *et al*., 2009; Wootton *et al*., 2012, Davies *et al*., 2014) which is disconcerting when considering the objective of MPA implementation on ecosystem structure and function. In terms of non-native species, a meta-analysis by Byrnes *et al*., (2007) on coastal marine food webs showed that the majority of species loss is occurring at high trophic levels, whilst most species invasions are occurring at low trophic levels. Thus, these opposing changes are significantly altering trophic dynamics, and as a consequence impacting ecosystem structure and function.

The final implication of changes to ecosystem function and stability, and subsequent potential deleterious costs, is loss of ecosystem goods and services to human populations. These include the food, transport, energy and amenities provided by the marine environment. The importance of such good and services has led to the development of ecosystem-based management (EBM). EBM is a management strategy by which the marine ecosystem is addressed as a whole. It is an integrated and interdisciplinary approach which considers the full array of sectors and aspects of the ecosystem, including humans (McLeod *et al.*, 2005).

Species reviews

The intention of the species reviews is to review the ecological niche of commercial shellfish species occupying English waters. The principle influential factors in defining the ecological niche for each species will be discussed. They will include both biotic and abiotic factors, and are as follows:

- Habitat and physical environment.
- Behaviour.
- Trophic level, predators and prey.
- Niche competitors.

Shellfish species included in the review:

- **Brown crab** - Cancer pagurus
- **European lobster** - *Homarus gammarus*
- **European spiny lobster** - *Palinurus elephas*
- **Velvet swimming crab** - *Necora puber*
- **Spider crab** - *Maja squinado*
- **Cuttlefish** - *Sepia officinalis*
- **Whelk** - *Buccinum undatum*
- **Langoustine** - *Nephrops norvegicus*

For each species, a general overview of the '***General biology & ecology***' of the species will also be included to put the review of its ecological niche into context.

Further to the review on ecological niche, emphasis will then be placed on evaluating the role of each species in '***Ecosystem function and stability'*** and then subsequently the ***'Consequences of removal on ecosystem function and stability'.***

The majority of the target species in this review possess larval planktonic stages; however, due to the objectives of this review, the main focus will be on the benthic life stages of such species. It is these life stages which constitute the commercial fisheries, and are of principle importance during the MPA designation process.

Summary tables are presented at the end of this section outlining significant functional roles (Table 2) and potential risk of effect of species removal (Table 3).

Brown crab (Cancer pagurus)

General biology & ecology

Cancer pagurus is one of the largest native UK decapod crustaceans. It is an orange/brown coloured crab which can grow up to 27 cm in carapace width (CW). It is characterised by a 'pie crust' edge around the dorsal carapace, and large black tipped claws/pincers. The species is distributed throughout the Northeast Atlantic, North Sea and English Channel; and is ubiquitous around British and Irish coasts. Adult crabs live a solitary epibenthic existence on a variety of substratum, both inter- and sub-tidally (up to 100m in depth). They are generally considered a nocturnal species, which actively predates and scavenges on a wide range of invertebrate prey.

C. pagurus reaches sexual maturity at approximately 11-12 cm CW (circa. 10 years old; Tallack 2007, Ungfors 2007a), and copulation takes place during spring and summer, when females are undergoing ecdysis (moulting; Edwards 1966, Woll 2003). Females generally moult once a year, however, the inter-moult period may increase in very large females. After copulation, females store the sperm until winter (or until optimal environmental conditions occur) and internally fertilise the eggs (250,000 – 3,000,000 eggs) during the spawning process. She will then externally incubate the eggs (on the underside of her abdomen) for several months prior to releasing planktonic larvae. The larvae remain in the plankton for several weeks (Nichols *et al.,* 1982, Eaton *et al.,* 2003, Weiss *et al.,* 2009), before settling in the intertidal zone and metamorphosing into juvenile benthic crabs. The juvenile crabs generally inhabit the intertidal benthos until they become 60-70cm in CW. Subsequently, they migrate offshore into deeper waters, and at this point, are considered to have been recruited to the adult population. Such recruitment takes place at 4-6 years of age. Average life expectancy of an adult crab is 15 -25 years, although it is possible for them to reach 100 years old.

Adult *C. pagurus* have been shown to exhibit migratory behaviour, with individual crabs translocating several kilometres. Females tend to migrate larger distances than males, and this is thought to be related to reproductive success (Bennett and Brown 1983, Ungfors *et al.,* 2007, Hunter *et al.,* 2013).

Ecological Niche

Habitat & physical environment

Planktonic larval stages: These life stages are at the mercy of the physical environment. The larvae, therefore, will be influenced by numerous physical factors; including water temperature and salinity, and tidal/current regimes (Lindley 1987, Kirby *et al.,* 2008, Lindley *et al.,* 2010). Research has shown that such variables will impact on *C. pagurus* larval distribution, development, viability and settlement (e.g. Eaton *et al.,* 2003, Weiss *et al.,* 2009).

Epibenthic life stages: The ubiquitous nature of adult *C. pagurus* around UK coasts highlights its ability to tolerate and inhabit a range of physical environments. This species has been found residing in substratum ranging from fine clean sand through to muddy gravel, bedrock and boulders. They can inhabit the intertidal zone through to the subtidal zone (e.g. Silva *et al.,* 2014). Salinity is not a strong limiting factor in the biogeographic distribution of this species because individuals have been found to tolerate salinities in the range of 18 – 50 psu (i.e. brackish water to hypersaline water) (Neal and Wilson 2008, Smyth *et al.,* 2014). Benthic *C. pagurus* can also cope with moderately exposed locations (Silva *et al.,* 2010), including tidal flows of up to 3 knots (Neal and Wilson 2008).

The drivers behind the type of physical environment *C. pagurus* inhabits are primarily the age and sex of the crab. The species expresses an ontogenetic shift in habitat. For example, juvenile crabs inhabit rocky intertidal zones, where they bury themselves in the substrate, shelter under rocks/boulders or seaweed, or reside in cracks and crevices during tidal exposure to prevent desiccation. These rocky intertidal habitats are considered the nursery grounds of *C. pagurus*. Intertidal habitation results in the juveniles experiencing a wide range of environmental conditions; including fluctuations in temperature, salinity and wave action. Hence, it is not surprising that juvenile *C. pagurus* have been found in estuaries, as well as open coastal locations (e.g. Thrupp *et al.,* 2013); and can cope with lower salinity environments than adult crabs (Wanson *et al.,* 1983).

The ontogenetic shift in habitat results in crabs moving into deeper water as they increase in size and age (Brown and Bennett 1980). Although adults can be found co-habiting the intertidal zone with juveniles, the majority of large adult crabs are found offshore, in waters up to 100 m deep (Neal and Wilson 2008). Adult crabs tend to prefer rocky environments, where they can shelter in crevices or under boulders, either to avoid predation or ambush prey. Female adult crabs, however, will be found in soft sediments, where they create, and reside in, pits of sand or gravel; particularly when they are 'berried' (ovigerous; egg-bearing; Edwards, 1966). It is thought that ovigerous females inhabit a soft substratum during spawning in order to enhance the adherence of eggs to their abdomens (Ungfors 2008). Hence, there is a certain amount of sex segregation; with males, in comparison to females, being more commonly found on rocky substrates in comparison (Pawson 1995). Furthermore, the maternal migratory behaviour of ovigerous female crabs requires them to tolerate a wider range of physical environments.

Habitats:
- Juveniles – *intertidal zone*
- Adults – *intertidal & subtidal zone*
- All substratum – *particularly rocky*

Behaviour

Epibenthic life stages: Several behavioural traits are key to determining the ecological niche of *C. pagurus*. Firstly, both juvenile and adults crabs exhibit nocturnal activity (Karlsson and Christiansen 1996, Skajaa *et al.,* 1998) probably to reduce predator encounters. During the day, crabs will shelter in crevices, under boulders, or bury themselves in soft sediment. Secondly, they are solitary organisms which exhibit aggressive behaviour towards their prey, conspecifics and competing species. This allows the species to exert authority and thus enhance their chance of survival

Key behavioural traits:
- Nocturnal
- Aggressive
- Solitary
- Migratory
- Predatory
- Scavenger

and reproduction within a community. As a result, their ecological niche will be well-established, and as such, potentially occupy a higher trophic level in the ecosystem.

Finally, the species exhibits migratory behaviour; particularly female crabs. Females are thought to migrate in order to optimise mating, egg development and larval release. This equates to survival of the species. A well-documented *C. pagurus* migration in UK waters is the westward movement of adult (sexually mature) female crabs in the English Channel (e.g. Bennett and Brown, 1983, Pawson 1995, Hunter *et al.,* 2013). This westward movement is against the prevailing current; hence it is thought that the females take advantage of the current to transport their planktonic progeny to suitable nursery sites. Similar female migrations have been observed in the North Sea (Nichols *et al.,* 1982, Eaton *et al.,* 2003). Such migrations, often in excess of 50km, highlight ecological niche segregation between adult male and female crabs during certain stages of their life history.

Trophic level, predators & prey

Planktonic larval stages: The larval stages of *C. pagurus* constitute zooplankton, thereby generally considered to occupy the 2nd trophic level (i.e. primary consumers). There is, however, an ontogenetic shift in size and diet during each metamorphosis (Ingle 1981). Brachyuran crabs, such as *C. pagurus,* produce herbivorous, omnivorous and carnivorous larval stages, which feed on both phytoplankton and zooplankton (Le Vay *et al.,* 2001). Each larval stage will therefore occupy a different trophic level (and ecological niche) between trophic levels 2-3 of marine ecosystem. *C. pagurus* larvae are, in turn, predated upon by numerous organisms at higher trophic levels.

Epibenthic life stages: Juvenile and adult crabs are considered first-level carnivorous consumers, which constitutes the 3rd trophic level of a generalised marine ecosystem . They therefore act as both predators and prey within a community. Juvenile and adult crabs are active predators and foragers, feeding mainly at night (e.g. Karlsson and Christiansen 1996, Silva *et al.,* 2010). Their diet is very varied, but composes mainly of invertebrates, such molluscs and crustaceans (Lawton 1989, Lawton and Hughes 1985; Mascaro and Seed 2001, Grefsrud *et al.,* 2003). They also exhibit cannibalism (Lawton 1989); particularly during ecdysis, when their new shells are soft (Amaral *et al.,* 2009). Adult crabs have also been documented to excavate pits in soft sediments in order to reach bivalve prey (Hall *et al.,* 1991).

Size differences between juvenile and adult crabs will lead to an occupation of different trophic levels. Hence, there will be variations in levels of predation on *C. pagurus*. Predators of *C. pagurus* include crustaceans, fish, cephalopods and seals. Small juvenile crabs in the intertidal zone are likely to experience much higher levels of predation than the larger individuals offshore. In some ecosystems, it is feasible that large aggressive adult crabs may be apex predators.

Trophic levels:

- Planktonic larval stages – ***Level 2-3*** (primary & secondary consumers)
- Juvenile & adult crabs - ≥ ***Level 3*** (carnivorous consumers)

A study using ratios of naturally- occurring stable isotopes to determine a more precise trophic level for *C. pagurus*, found the species to occupy a trophic level of 2.9 within a kelp forest (Fredriksen 2003).

Niche competitors

Planktonic larval stages: As a consequence of the large number of UK decapod crustaceans, and the high fecundity of many of these species; decapod larvae are dominant in temperate water zooplankton assemblages (Lindley *et al.,* 2010). Hence, there are numerous competing species which could competently fulfil the ecosystem niche of *C. pagurus* larvae, if this species was to dramatically decline in abundance.

Epibenthic life stages: Juvenile and adult *C. pagurus* share their habitats with numerous other decapod species, particularly in rocky environments. For example, Robinson and Tully (2000a) found 29 different benthic decapod species inhabiting a subtidal cobble habitat in Ireland. *C. pagurus*, together with 8 other species, were present at the site all year round. In a second study by Robinson and Tully (2000b), a range of different benthic habitats were sampled, from mud to boulders. They encountered 17 different decapod species, including *C. pagurus*. Furthermore, on rocky shores in North Wales, UK; Lawton (1989) noted several decapod crustaceans to be sympatric with *C. pagurus*; including *Carcinus maenas*, *Galathea squamifera*, *Pilumnus hirtellus*, *Pisidia longicornis,* and *Porcellana platycheles*. Such observations strongly suggest that epibenthic *C. pagurus* encounters numerous niche competitors, with all competitors inhabiting restricted ‘realised ecological niches’. It is highly unlikely that a vacant niche would remain so for very long.

In UK benthic ecosystems:
- 50-60 known decapod crustacean species
- > 50% of species are Brachyuran crabs

It must be noted, however, that as *C. pagurus* increases in size, and subsequently moves up through trophic levels, the potential for niche competitors drastically decreases. *C. pagurus* is one of the largest UK decapod species, and once it has been recruited to the adult population, its main niche competitor is the European lobster, *Homarus gammarus*. Both species are highly aggressive, therefore, there is potential for agonistic interspecies behaviour (Addison 1995) and niche restriction.

Invasive non-native species possess high potential to outcompete native organisms. With regards to *C. pagurus*, there are several non-native competitors; including the Chinese mitten crab (*Eriocheir sinensis*), Asian shore crab (*Hemigrapsus sanguineus*), and Marbled Rock crab (*Pachygrapsus marmoratus*).

Non-native niche competitors:
- Chinese mitten crab (*Eriocheir sinensis*)
- Asian shore crab (*Hemigrapsus sanguineus*)
- Marbled Rock crab (*Pachygrapsus marmoratus*)

Role in ecosystem function & stability

As significant predators in both plankton and benthic communities, *C. pagurus* can manipulate productivity and structure communities in the majority of ecosystems they inhabit.

Planktonic larval stages: The planktonic larval stages represent the lowest trophic level of *C. pagurus*, and are generally found in high abundance in zooplankton assemblages. For example, In the North Sea, where *C. pagurus* is a dominant planktonic taxa (Lindley *et al.,* 1993), the decapod larval community is thought to be responsible for propagating climate-driven signals through the food web (Lindley and Kirby 2010, Lindley *et al.,* 2010). Furthermore, a study by Kirby and Beaugrand (2009) demonstrated that the North Sea larval decapod community enforces bottom-up control (either directly or indirectly) on commercial fish stocks of such cod, plaice and sole. Hence, Lindley and Kirby (2010) imply that understanding such interactions is important in establishing a successful ecosystem-based approach to future management of North Sea fisheries.

Significant functional roles of *C. pagurus* larvae:

- Propagation of climate-driven signals
- Bottom-up control of commercial fish stocks

Epibenthic life stages: The epibenthic life stages of *C. pagurus* assume different ecological roles to that of the planktonic life stages. As occupants of the 3rd trophic level and above, juvenile and adult crabs can exert both top-down and bottom-up control on food webs and community structure. A recent review by Boudreau and Worm (2012) provides a comprehensive overview of the ecological roles of epibenthic crabs; therefore, only the roles with relevance to the current report will be discussed here.

As voracious predators and scavengers of molluscs, crustaceans and some juvenile fish; the top-down control by epibenthic crabs includes significantly influencing commercial fish and shellfish stocks (e.g. Sant 1978, van der Veer and Bergman 1987, Philippart *et al.,* 2003, Grefsrud *et al.,* 2003, Beukema and Dekker 2005, Cardoso *et al.,* 2007). A well-documented example is the predator-prey interaction between *C. pagurus* and the scallop, *Pecten maximus*. *C. pagurus* is thought to deleteriously impact scallop populations through direct predation; and studies have suggested a scallop minimum release size of cultured animals in order to reduce predation, and hence mortality, of commercially farmed scallops stocks (Grefsrud *et al.,* 2003).

Top –down control by *C. pagurus*, via predatory behaviour, is also considered to play a key role in structuring intertidal communities (Lawton 1989, Silva *et al.,* 2008a, b). Such predation is particularly pertinent if the prey is a '*keystone*' species. For example, there is the predation of the herbivorous limpet, *Patella vulgata* by crabs on intertidal rocky shores. *P. vulgata* is considered a '*keystone*' species, because it regulates community structure through grazing micro and macroalgae (Hawkins and Hartnoll 1983, Power *et al.,* 1996). *Cancer pagurus* is a known predator of the limpet, *P. vulgata* (Silva *et al.,* 2008a; b), and therefore *C. pagurus* presence may significantly impact the structure of intertidal communities, and thus overall ecosystem function and stability.

C. pagurus is also thought to be important in the connectivity between the intertidal and subtidal environments, via small scale migrations of individuals in search of food. A recent study by Silva *et al.,* (2014) observed several crab species, including *C. pagurus*, moving between the two environments. The theory is that individual crabs migrate up into the intertidal zone during high tide to forage on the wealth of intertidal prey items. Individuals then move back into the subtidal zone as the tide ebbs. Hence, similar to other crab species, the intertidal zone is used as a feeding ground for both intertidal and subtidal *C. pagurus* populations (Hunter and Naylor 1993,Burrows *et al.,* 1999, Silva *et al.,* 2014), thus exerting significant pressure on intertidal ecosystems, and potentially influencing ecosystem function and stability.

Finally, there is the pit-digging phenomenon of *C. pagurus* in soft substrates, which is used to access burrowing bivalve prey. This behaviour is thought to disturb benthic communities on a local scale, possibly creating biogenic ecosystems and enhancing spatial heterogeneity (Thrush 1986; Hall *et al.,* 1991, Zajac 2004). However, the significance of such disturbance at the ecosystem level is currently unproven (Hall *et al.,* 1993).

The bottom-up control (i.e. predation) of epibenthic *C. pagurus* in ecosystems is less pronounced than their top-down control, and hence is far less influential. There are numerous explanations. First, is their nocturnal activity in order to minimise their exposure to predators. Second, *C. pagurus* possess robust carapaces, particularly in individuals >10 cm CW. This means that predators require strong physical mechanisms to overcome such a carapace. Hence, their main predators are restricted to large fish (e.g. cod and hake), seals, and cephalopods. Currently, the populations of large predatory fish are not considered high enough to strongly impact populations of large decapods (Frank *et al.,* 2005,Baum and Worm 2009, Boudreau and Worm 2012). In addition, crabs only constitute a small proportion of the diet of seals and cephalopods. Therefore, in some ecosystems, large *C. pagurus* may be released from predation and thus become the apex predator. This allows substantial populations of large *C. pagurus* to become established, subsequently producing commercially-viable fisheries.

Significant functional roles of epibenthic *Cancer pagurus*:

- ***Top-down regulator****: Of molluscs, crustaceans & fish, including commercial species*
- ***Community structuring****: Intertidal communities*
- ***Ecosystem connectivity****: Intertidal & subtidal ecosystems*
- ***Apex predator****: Large subtidal individuals & commercially-viable fisheries*

Potential consequences of removal on ecosystem function & stability

C. pagurus is a voracious predator and scavenger of wide range of molluscan and crustacean species. It is also known to prey on small fish. Hence, this crab species exerts general top-down control in all the ecosystems it inhabits.

With regard to the top-down control by epibenthic *C. pagurus*, numerous studies have revealed similarities between the prey species of *C. pagurus* and that of coexisting, hence niche-competing, crab species (e.g. Mascaro and Seed 2001, Griffin *et al.,* 2008, Silva *et al.,* 2008). One study, in fact, compared a range of crab species feeding on the commercial scallop*, P. maximus* (Lake *et al.,* 1987). All crabs, including *C. pagurus*, were found to prey on the scallops; however, *C. pagurus* was able to consume a larger scallop size range. Therefore, due to the large number of brachyuran crabs species in the UK (50-60 species), and the general consensus and evidence that such species possess very similar diets and behaviour; it is likely that the majority belong to a large 'functional group' of species. As a consequence, it is unlikely that removal (or drastic reduction in abundance) of *C. pagurus* would significantly modify the existing top-down control of commercial fish and shellfish stocks, and thus negatively impact ecosystem function and stability .

Similarly, structuring of intertidal communities via predation (top-down control) of '*keystone*' species may also be under the influence of a large 'functional group' of species. Numerous other crab species inhabit the intertidal zone along with juvenile *C. pagurus*, and Silva *et al* (2008a; b) examined the predator-prey relationship between crabs and the keystone limpet, *P. vulgata*, and found that several co-existing crab species, one of which being *C. pagurus,* were feeding on the limpets and, hence, influencing the abundance of this keystone species; consequently affecting intertidal community structure. Therefore, it is unlikely that removal of *C. pagurus* from rocky shores would significantly impact ecosystem structure, function and stability, because another species of the 'functional group' would expand its ecological niche to fill the void created by the loss of *C. pagurus*.

Another recent study by Silva *et al.,* (2014) has highlighted the connectivity between intertidal and subtidal environments via small scale migrations of individual epibenthic crabs in search of food. Several crab species, including *C. pagurus*, were found to move between the two environments. Due to the fact that several different crab species have been shown to undertake these tidal migrations (Silva *et al.,* 2014); once again, it is unlikely that removal of specific *C. pagurus* migrations would substantially change the existing intertidal ecosystem structure and function.

Examination of the functional role of large adult *C. pagurus* within ecosystems, suggests that there may be potential for adverse effects of *C. pagurus* removal in some instances. For example, large individuals may constitute the apex predator in some ecosystems, particularly in the subtidal zone; and as such, belong to a smaller 'functional group' of species. A co-existing species in such environments is the European lobster, *Homarus gammarus;* and it is possible that this species, together with *C. pagurus*, form a very small 'functional group'. Hence, if *C. pagurus* was lost as an apex predator, it is feasible that *H.*

gammarus would be able to fill the vacant ecological niche and ecosystem function of *C. pagurus*. Studies and observations have revealed agonistic and competitive behaviour between the two species (e.g. Addison 1995,Skerritt 2014), thus highlighting their similar ecological niches and functional roles. Furthermore, within the Lundy Island No-Take Zone (NTZ) there is a negative correlation between the abundance of the two species. There are significantly fewer *C. pagurus* in the NTZ (where *H. gammarus* is extremely abundant), compared with the control zone (where *H. gammarus* is of very limited abundance) (pers. obs, Hoskin *et al.,* 2011, Wootton *et al.,* 2012, Davies *et al., in prep*). These findings suggest that they are niche competitors; and in the case of the Lundy Island NTZ, it implies that *H. gammarus* is the more dominant species.

However, there is potential for ecological perturbation such as detrimental trophic cascades and associated ecological change in a situation where *H. gammarus* is unable fill the vacant apex predator ecological niche and functional role of *C. pagurus*. As such, the ecosystem goods provided by *C. pagurus*, as a commercial Brown crab fishery would be diminished, and this may result in significant economic loss to fisheries stakeholders and communities.

Overview of *C. pagurus* in ecosystem structure & function

Decapod crustaceans are one of the most abundant groups of marine benthic organisms around UK coasts, with between 50-60 known species. Epibenthic crabs constitute >50% of such species; the majority of which, exhibiting very similar functional traits and ecological niches. For that reason, it allows for a confident assumption of multiple niche competitors of *C. pagurus* (both native and non-native), and consequently, a large ‘functional group’ of epibenthic crabs with comparable roles in ecosystem function. Hence, in terms of top-down control by *C. pagurus*, it is unlikely that the removal of *C. pagurus* from an ecosystem would drastically compromise ecological processes; and, in turn, be detrimental to overall ecosystem function, stability and resilience. Since, if *C. pagurus* abundance was diminished, a coexisting species within the ‘functional group’ would likely expand its own ‘realised’ ecological niche to fill the void, and thus absorb the ecological function of *C. pagurus*. Furthermore, *C. pagurus* is not considered a ‘keystone’ species; hence, the probability of deleterious trophic cascades and phase shifts due to species loss is considered to be low. The only possible concern of *C. pagurus* removal is to the ecosystem goods provided by the species, in the form of the Brown crab fishery. If the crab was to be lost as apex predator, then the commercial viability of the fishery may be compromised.

To the best of our knowledge there are no documented studies on assessing the consequences of removal of *C. pagurus* from ecosystems. However, the contrasting hypothesis was tested in the Lundy Island No-Take Zone (NTZ), where cessation of fishing was enforced, and as such, previously fished species freed from significant top-down control . Under this scenario, however, *C. pagurus* was not found to increase in abundance within the NTZ after the fishing ban was implemented (per obs; Hoskin *et al.,* 2011, Davies *et al., in prep*). This highlights the complexity of ecosystem functioning and subsequent management strategies; and thus the need for robust scientific research.

The majority of the implications of *C. pagurus* removal from ecosystems discussed in the present report are based on conjecture and inference from numerous independent studies on *C. pagurus*. Therefore, in order fully elucidate the functional role of this decapod crustacean within an ecosystem, it is highly recommended that Before-After Control-Impact (BACI) studies are undertaken to test specific hypotheses. These are essential in an environment which encompasses ‘sliding/shifting baselines’ due to human exploitation of marine species over the past millennium. Present day data must therefore be used as the ‘Before impact’ baseline.

European lobster (*Homarus gammarus*)

General biology & ecology

The European lobster (*Homarus gammarus*) is a large decapod crustacean, native to UK waters. It commonly reaches 50 cm in total length (Wilson 2008), with a lifespan of several decades. The species is ubiquitous around UK coasts, inhabiting waters down to approximately 100 m in depth. The species prefers rocky habitats, where it shelters in crevices in daylight (Bannister *et al.,* 1994, van der Meeren 1997), emerging at dusk to actively hunt or scavenge on a range of prey species. Adults have well developed chelipeds (i.e. claws) which are used in both intraspecific agonistic behaviour and predator deterrence (Barshaw *et al.,* 2003). Both juveniles and adults retain favourable crevices in suitable habitat and can remain upon a section of reef for over two years (Jensen *et al.,* 1994); however, individuals searching for improved habitats can travel up to 20 km (Bannister *et al.,* 1994).Therefore, migratory patterns are most likely coincidental from larger adults moving offshore in search of new habitat (Pawson 1995, Smith *et al.,* 2001).

Little is known about the juvenile biology and ecology of *H. gammarus* (Skog 2008). Whilst laboratory experiments have identified preferred habitats (e.g. Howard and Nunny 1983, Linnane *et al.,* 2000), and suggested potential feeding behaviours (Skog 2008), a lack of field observations means validating lab experiments is difficult.

Juveniles reach sexual maturity after 5 to 8 years (Prodöhl *et al.,* 2006), with a carapace length (CL) of between 79 - 110 mm, depending on location. The reproductive cycle begins with mating in spring-summer, becoming ‘berried’ (i.e. egg-bearing) in early autumn and brooding the eggs for approximately 9 months, before hatching and release of planktonic larvae in late spring - summer the following year (Pawson 1995, Agnalt *et al.,* 2007). Immediately after hatching, the females moult and copulation takes place whilst the female’s new carapace is still soft. Females reproduce annually, or biannually, depending on size and location (Agnalt *et al.,* 2007, Laurans *et al.,* 2009). Fecundity is a size-dependent, with larger females (>130 mm CL) producing up to 40,000 eggs (Lizárraga-Cubedo *et al.,* 2003, Agnalt 2008).

Ecological niche

Habitat & physical environment

*Planktonic larval stages**:*** Although the hatching of eggs has an endogenous element (Ennis 1973), there are also various exogenous factors which influence hatching. Seasonal variations in day length and photoperiod play an important role, as does temperature (Branford 1978, Jackson *et al.,* 2014). Temperature and salinity also affect the survival of larvae in the water column; with above 30 °C and below 15 – 17 ‰ salinity, instantaneous mass mortality has been observed (Gruffydd *et al.,* 1975, Charmantier *et al.,* 2001).

There is very limited information on the ecology of *H. gammarus* larval stages; particularly in the wild, where sampling has recovered very few larvae. However, growth and development are thought to be temperature and light-dependent, with the complete planktonic larval phase lasting several weeks (Harding *et al*., 1987, Pawson 1995, Prodöhl *et al.,* 2006). Results from *in situ* water column sampling have been variable, however it appears that *H.*

gammarus larvae are not commonly found in surface waters, instead highest concentrations are located at depths of 15 – 16 m, incidentally below a halocline (Øresland and Ulmestrand 2013).

Epibenthic life stages: In comparison to the American lobster, *Homarus americanus*, very little is known about early benthic phase (EBP) and juvenile European lobsters, *H. gammarus*. Despite numerous attempts, EBP nursery grounds and habitats remain elusive (e.g. Linnane *et al.,* 2001, Mercer *et al.,* 2001). A mesocosm study, however, by Linnane *et al.,* (2000) found that juveniles preferred substratum with larger interstitial spaces (i.e. cobble and bivalve shells), over sand and coralline algae environments. However, EBP juveniles will burrow in softer sediments and create extensive burrows, if necessary (Howard and Bennett 1979, Howard and Nunny 1983, Linnane *et al.,* 2000). Using *H. americanus* as an analogy, it is likely that juvenile *H. gammarus* settle in shallow waters with a rocky substratum, thus providing food and shelter (Howard and Nunny 1983, Pawson 1995)

Habitats:

- EBP & juveniles – ***unknown***
- Adults –***subtidal zone***
- Substratum –***rocky***

More knowledge exists on the ecology of adult *H. gammarus*, because of ease of sampling. There is an ontogenetic shift in habitat preference for *H. gammarus*, with the species extending its habitat range further offshore with size (Tully 2004). Therefore, adults can be found in sublittoral zones to depths of 200 m, although they are rarely found below 100 m (Pawson 1995, Galparsoro *et al.,* 2009, Moland *et al.,* 2011). *Homarus gammarus* still retains a preference for rocky substrates in the adult stage, but loses the ability to make burrows in softer sediments, most likely due to its large size (Howard and Nunny 1983). The majority of populations are found along the boundary between rock and sediment habitats (Galparsoro *et al.,* 2009, Skerritt *et al.,* 2013). Further habitat modelling identified that the distance to a rocky substrate is best environmental predictor for *H. gammarus* habitat (Galparsoro *et al.,* 2009). This is because *H. gammarus* spends the majority of its time sheltering in crevices or burrows, only emerging at night to feed (Bannister *et al.,* 1994, van der Meeren 1997).

Furthermore, as *H. gammarus* is commonly found in high wave energy environments, individuals seek out troughs in the topography to reduce exposure (Galparsoro *et al.,* 2009), because normal behaviour is impaired in currents exceeding 27 cm s^{-1} (Howard and Nunny 1983). *Homarus gammarus* is tolerant of a range of physical conditions, with a lower temperature limit for functioning of 5 °C (Smith *et al.,* 1999) and mortality in salinities below 10 ‰ (Charmantier *et al.,* 2001).

Behaviour

Key behavioural traits:
- Nocturnal
- Aggressive
- Solitary
- Territorial
- Predatory
- Scavenger

Epibenthic life stages: Homarus gammarus is a solitary and nocturnal species. It shelters in rocky cracks and crevices ('dens') during daylight hours, and only emerging and becoming active at night (Smith *et al.,* 1999, Moland *et al.,* 2011). Similar to other decapod crustaceans, they are active predators and scavengers of a variety of invertebrates and fish. *H. gammarus* is also an aggressive and territorial species, and in nocturnal hours when individuals are active, both sexes assert dominance towards conspecifics (Skog 2008). Agonistic encounters are common and not dependent on habitat availability (Linnane *et al.,* 2000). Extensive research on *H. americanus* has revealed that such aggressive behaviour results in a dominance hierarchy, with large males exerting dominance over resources such as food, mates and shelter. Using cheliped losses as an indication of fighting, a study by Linnane *et al* (2000) on *H. gammarus* recorded 11.3 – 27 % of lobsters having one or both chelipeds missing over a nine month period, leading to the conclusion of a clear hierarchical dominance in *H. gammarus* populations, with strong dominant-subordinate relationships (Linnane *et al.,* 2000). Both male and female subordinates will avoid recognisable dominant conspecifics, although males will exhibit agonistic behaviour towards unknown individuals; whilst females will avoid them if they assert dominance (Skog 2008). By blocking chemoreceptors, Skog (2008) identified that urine release was a key factor in dominance, with increased quantities being excreted by winners.

Homarus gammarus movement is influenced by temperature (Smith *et al.,* 1999, Moland *et al.,* 2011) and light (Schmalenbach and Buchholz 2013). As such, juveniles show extensive nocturnal activity in laboratory experiments (Mehrtens *et al.,* 2005, Schmalenbach and Buchholz 2013), and this has been identified as a predatory avoidance mechanism (Schmalenbach and Buchholz 2013). Larger adults exhibit reductions in both shelter reliance and nocturnal activity (Mehrtens *et al.,* 2005), but the behavioural influences are retained to some degree on a seasonal scale. Activity and body movements are greater in late summer, when water temperatures are higher (Smith *et al.,* 1999, Moland *et al.,* 2011).

Homarus gammarus exhibits no regular migratory behaviour; any movements remain small and random and are most likely prompted by competition and ontogenetic habitat shifts as adults outgrow crevices (Pawson 1995, Smith *et al.,* 2001). Furthermore, adult males and females (berried or unberried) do not then differ in their movements; however, a recent study by Skerritt (2014) revealed that males had a larger home range than females. For their size and mobility, *H. gammarus* has a relatively small home range (Smith *et al.,* 1999), with 90 % of excursions remaining within 8 m of the home 'den' (Mehrtens *et al.,* 2005). However, tag-recapture studies have found juveniles up to 45 km from the release site (Smith *et al.,* 2001), but 95 % of individuals did remain within 1 - 4 km (Smith *et al.,* 2001, Agnalt *et al.,* 2007). Similar studies with adult *H. gammarus* recorded individuals 15 – 20 km from the release site, but average distances were between 5 – 7 km (Bannister *et al.,* 1994, Jensen *et al.,* 1994). Observing home ranges using acoustic telemetry has revealed large differences between populations, ranging from (mean ± SD) 19,879 ± 2,152 m^2 (Moland, Olsen, Andvord, *et al.,* 2011) to 170,660 ± 125, 519 m^2 (Wiig *et al.,* 2013). Such differences have been linked to water temperature (Smith *et al.,* 1999), but also to reduced competition in sparse populations, thus allowing individuals to expand their home range (Wiig 2012).

Local knowledge of the environment has also been shown to influence behaviour. Lobsters transplanted into a new environment exhibited a lack of nocturnal activity and increased roaming behaviour for several days before normal behaviour returned (van der Meeren 1997). This knowledge also applies to resident individuals, with movement patterns varying between individuals, depending on the environment (Wiig 2012). Where patterns are patchy, individuals are moving between known feeding areas, whilst slender patterns are a result of individuals using known routes to access different areas (e.g. rocky ridges or troughs) (Wiig 2012)

Trophic level, predators & prey

Planktonic larval stages: In conjunction with other decapod crustaceans, the larval life stages of *H. gammarus* constitute zooplankton in marine ecosystems. They are obligate planktotrophs, thus consuming both phytoplankton and zooplankton. As zooplankton, they are generally considered to occupy the 2nd trophic level, however their diet of both phyto- and zooplankton, places them in trophic levels 2-3. Information on their natural diet does not exist; however, laboratory investigations and aquaculture programmes have reared larvae on a range of live prey and commercial feeds (Jackson *et al*., 2014, Daniels *et al.,* 2013; Schoo *et al.,* 2014). A recent study determined that this is an ontogenetic shift, with older larvae exhibiting less dependence on nutrient quality of prey (Schoo *et al.,* 2014). Numerous planktotrophic species at higher trophic levels will feed on the larvae of *H. gammarus*.

Trophic levels:
- Planktonic larval stages – ***Level 2-3*** (primary & secondary consumers)
- Juvenile & adult crabs - ≥ ***Level 3*** (carnivorous consumers)

Epibenthic life stages: Feeding strategies and prey species of wild EBP juvenile *H. gammarus* are not documented due to their elusive nature, thus preventing sampling and research. However, it has been suggested that they rely on suspension feeding (Loo *et al.,* 1993), or use the same predatory and scavenging methods as adults, but on smaller prey items (Mehrtens *et al.,* 2005). More information is available on the diet of adults, with *H. gammarus* known to be an opportunistic scavenger (Bremner *et al.,* 2003) and predator; consuming a wide variety of prey, including bivalves (Côté and Jelnikar 1999, Prodöhl *et al.,* 2006), echinoderms (Jones *et al.,* 2000), small or juvenile crustaceans (Števčić 1971, Prodöhl *et al.,* 2006) and polychaete worms (Prodöhl *et al.,* 2006). *Homarus gammarus* has also exhibited suspension feeding (Loo *et al.,* 1993), with analyses revealing that suspension feeding offers a nutritional reward (Loo *et al.,* 1993). The well-studied American lobster, *H. americanus* is considered a generalist feeder with adaptability; it will feed on slow moving prey in its local environment. Hence, prey items will vary according to location and environmental temperature, prey availability, lobster size and moult cycle (Cobb and Castro 2006). It is very likely that *H. gammarus* exhibits very similar diet strategies and behaviour to that of *H. americanus*.

With regard to predation of *H. gammarus,* there is a clear ontogenetic shift; which is not only evident through observations, but also through morphology. EBP and juvenile lobsters are at a much higher risk of predation than adult lobsters. Adults possess large chelipeds (i.e. claws) which act as deterrents to potential predators (Barshaw *et al.,* 2003). Therefore, as the lobster grows larger, predation will be reduced as capture success for the predator may be compromised by injury. Juvenile *H. gammarus* are thought to be predominantly predated upon by visually oriented fish found commonly on rocky reefs (Ball *et al.,* 2001, Mercer *et al.,* 2001; Schmalenbach and Buchholz 2013), including bull rout (*Myoxocephalus scorpius*), long-spined bullhead (*Taurulus bubalis*), rock cook wrasse (*Centrolabrus exoletus*), gobies (*Pomatoschistus minumus*) and rockling (*Ciliata mustela*). The shore crab (*Carcinus maenas*)*,* and cuttlefish (*Sepia officinalis*), have also been observed preying on EPB lobsters (Mercer *et al.,* 2001)

In contrast to juveniles, adult *H. gammarus* have very few predators. Large groundfish, such as cod, are thought to be the principle predators, and in the case of the American lobster, *H americanus,* it is thought that the demise of cod populations created the present day thriving (and sustainable) lobster fishery. Large groundfish are not abundant around UK coasts, hence it is likely that *H. gammarus* is also exempt from natural top-down predation. There are anecdotal reports of groundfish predating upon adult *H. gammarus* (Tully, 2004), but direct evidence is absent. Therefore, the only current top-down control of large adult *H. gammarus* is human fishing activity, and this has been demonstrated in the Lundy Island No-Take Zone, where there has been a boom in lobster abundance since the No-Take Zone was enforced (Hoskin *et al.,* 2011, Wootton *et al.,* 2012, Davies *et al.,* 2014)

A field experiment on adult *H. gammarus* in Israel, identified triggerfish (*Balistes carolinensis*) as a predator, attacking in groups and exhibiting unique behaviour to capture lobsters (Barshaw *et al.,* 2003). In the same experiment, octopuses were also observed to feed upon lobsters, but were never observed subduing one (Barshaw *et al.,* 2003).

A large ecosystem study placed *H. gammarus* at a trophic level of 3.26 (Pranovi *et al.,* 2014). However, because *H. gammarus* consumes a very wide range of prey species, and possesses the ability to suspension feed, it can occupy trophic level 2 and above. Large adult lobsters, free from natural predation, are therefore, apex predators.

Niche competitors

Planktonic larval stages: Our very limited knowledge of *H. gammarus* larvae, and their potential scarcity in the marine environment, means that determining their precise niche competitors is currently impossible. However, it is likely that they belong to the general decapod larval community which is dominant in temperate water zooplankton assemblages (Lindley *et al.,* 2010). Hence, there are numerous competing species which could competently fulfil the ecosystem niche of *H. gammarus* larvae, if this species was to dramatically decline in abundance.

Epibenthic life stages: Niche competition is highly dependent on the size of *H. gammarus*. EBP and juvenile lobsters, presumably living in cracks and crevices of hard substratum for protection, will encounter numerous niche competitors, particularly other decapod crustacean species. The lack of EBP and juvenile observations, and hence nursery grounds, during an EU-funded research project dedicated to gathering field and experimental data on EBP lobsters (LEAR - Lobster Ecology And Recruitment project: 1998-1999, Mercer *et al.,* 2001), revealed high numbers of potentially co-existing species in benthic habitats. Unsurprisingly, decapod crustaceans predominated. Therefore, one suggestion for the absence of EBP lobsters during the project was very high levels of niche competition, and thus exclusion of EBP lobsters from such environments (Linnane *et al.,* 2001, Mercer *et al.,* 2001). A comparison table provided by Butler *et al.,* (2006), revealed that EBP *H. americanus* encounters far less niche competition than EBP *H. gammarus* and may, therefore, be a significant factor in establishing thriving adult *H. americanus* populations in the Gulf of Maine, USA (Table 1).

	UK	**Ireland**	**Gulf of Maine**
EBP lobsters (no./m^2)	0	0	1.5
Decapod density (no. / m^2)	85.5	86.5	8.6
No. Decapod families	13	14	4
No. of Decapod species	15	32	5
Dominant genus/family	Porcellinidae	Porcellinidae	Homarus

Table 1. Niche competitors Homarus sp. (Adapted from Butler et al., (2006))

In comparison to EBP and juvenile *H. gammarus*, adults experience far less niche competition. They are large and aggressive individuals, and thus commonly occupy high trophic levels within marine ecosystems (Addison and Bannister 1998). Their most likely native competitor is the Brown crab, *Cancer pagurus*, who will compete for both food and shelter resources. Inter-specific behaviour has been observed between the two species, particularly around baited creels/pots (Addison 1995, Skerritt 2014). However, studies in the Lundy Island No-Take Zone (NTZ) reveal that *H. gammarus* prevails as the dominant species. There is a negative relationship between *H. gammarus* and *C. pagurus* abundance within the NTZ (Hoskin *et al.,* 2011, Wootton *et al.,* 2012, Davies *et al., in prep*). The high density of lobsters within the NTZ appears to have outcompeted *C. pagurus,* with only large *C. pagurus* being able to withstand competition from *H. gammarus* and therefore remain within the NTZ (Hoskin *et al.,* 2011). In addition, a recent study on interspecies competition around baited pots, demonstrated that the presence of *H. gammarus* within a pot, significantly decreased the catchability of *C. pagurus* and velvet swimming crabs, *N. puber*; thus reinforcing the hypothesis of *H. gammarus* being the dominant species amongst decapod crustaceans (Skerritt 2014).

A further potential niche competitor is the non-native American lobster*, H. americanus*. There are numerous records of the American lobster (*Homarus americanus*) inhabiting UK waters, most commonly on the south coast of England (Stebbing *et al.,* 2012). *H. americanus* has very similar niche requirements to that of *H. gammarus*, but is considered the more aggressive species (Skog 2008). Therefore, there is a risk of competition between the two Homarus *spp*., with possible disruption of dominance hierarchies and hybridisation (Skog 2008, Stebbing *et al.,* 2012). Whilst there are thought to be no established populations in the UK, in Norwegian waters where invading *H. americanus* are more commonly sighted, mating has occurred between the two species, resulting in viable hybrid offspring (Agnalt, *pers. comm.*)

Role in ecosystem function & stability

Due to our very limited knowledge of larval, EBP and juvenile *H. gammarus*, it is not possible to determine their specific roles in ecosystem function and stability. However, due to the large number of niche competitors at these *H. gammarus* life stages, particularly other decapod crustacean species, it is likely that *H. gammarus* belongs to a large 'functional group' of organisms, and as such, the ecological roles of larval, EBP and juvenile *H. gammarus* are probably not unique. It is adult *H. gammarus* which are likely to significantly influence ecosystem function and stability.

Epibenthic life stages: The role of adult *H. gammarus* in ecosystem function and stability is centred around their large size, and dominant and aggressive nature; with the ability to occupy the niche of apex predator in many ecosystems. They are both predators and scavengers, consuming a wide variety of prey species; and due to their highly territorial (and non-migratory) behaviour are thought to adapt their diet to the availability of prey species in their local environment. Therefore, on a local scale and/or in high densities, their top-down control may significant impact community structure and function. Furthermore, the dominant and aggressive nature of *H. gammarus* may indirectly affect communities via behaviour-mediated responses. For example, *H. gammarus* may outcompete other decapod crustaceans for food and shelter, hence causing such species to move/migrate into areas containing less *H. gammarus*, and hence, less competition. The high trophic level of adult *H. gammarus* (levels 4-5) suggests that numerous lower trophic levels may be affected by their presence and behaviour; with the possibility of inducing a trophic cascade and fundamentally changing ecosystem structure, function and stability.

The risks of significantly affecting ecosystem function and stability will probably only occur in areas of high *H. gammarus* density. For example, in the Lundy Island NTZ where several studies have shown significant reductions in the abundance of decapods species (including the commercial species of velvet swimming crab, *N. puber* and brown crab, *C. pagurus*), coinciding with significant increases in *H. gammarus* abundance (Hoskin *et al.,* 2011, Davies *et al., in prep*, *pers. obs*). The overall impact of these changes on ecosystem function and stability is unknown, because other species at lower trophic levels were not investigated. However, to date, *H. gammarus* has not been classified as a keystone species in European habitats (Smith *et al*., 2014). Studies on the Leigh marine reserve (NTZ) in New Zealand have conclusively revealed deleterious trophic cascades within the reserve, which have been attributed to increased top-down control from thriving spiny lobster (*Jasus edwardsii*) and snapper (*Pagrus auratus*) populations (Shears and Babcock 2002, 2003).

The final functional role of *H. gammarus* is provision of ecosystems goods via a commercially viable fishery. However, the fishery and landings are not expanding at the same rate as the thriving (and sustainable) American lobster, *H. americanus,* fisheries in the Gulf of Maine and Canada.

Significant functional roles of adult *Homarus gammarus*:

- ***Top-down regulator****: Of molluscs, crustaceans & other invertebrates, including commercial species*

Potential consequences of removal on ecosystem function & stability

According to the CEFAS stock status of *H. gammarus* around English coasts, the species is generally is considered to be moderately-heavily exploited (http://www.cefas.defra.gov.uk/our-science/fisheries-information/commercial-species/shellfish.aspx), suggesting that current ecosystems are functioning under low levels of *H. gammarus* of habitation. Unfortunately, due to the 'sliding baseline' phenomenon it is unfeasible to determine the impact of *H. gammarus* removal on ecosystem structure, function and stability. However, using the converse scenario where *H. gammarus* is freed from top-down control via prohibition of human fishing activities, as in the Lundy NTZ; and as such, the population allowed to boom, some insight made be gained into the role this species plays in ecosystem function. As discussed previously, the current circumstance in the Lundy NTZ is the rapidly expanding *H. gammarus* population (as the apex predator) at the expense of contracting other species' populations. Therefore, contrary to belief, lower *H. gammarus* populations may be beneficial in increasing community biodiversity and maintaining ecosystem function and stability. The risk of deleterious trophic cascades may also be minimised.

In terms of the ecosystem goods provided by the *H. gammarus* fishery, continued removal of the species may allow its niche competitor, the Brown crab, *C. pagurus,* to extend its ecological niche and occupy habitats vacated by *H. gammarus*. Unfortunately, the commercial value of *H. gammarus* is significantly less than that of *C. pagurus*; therefore, there may be an overall economic loss to fisheries stakeholders.

Overview of *H. gammarus* in ecosystem structure & function

The principle outcome of this review on the ecological niche and functional role of *H. gammarus* is that the species appears to be the dominant decapod crustacean of UK waters. Adult H. gammarus will outcompete potentially co-existing species, such the Brown crab, *C. pagurus* and the Velvet swimming crab, *N. puber,* and as a result, *H. gammarus* is commonly the apex predator in UK benthic marine ecosystems.

However, our in-depth understanding of such functional roles of this species is very limited, and the majority of information is inferred from the well-studied (but closely-related)

American lobster, *H. americanus*. There are currently significant gaps in our general ecological knowledge of *H. gammarus* which are hindering interpretation of present day observations and findings. The key knowledge deficits are larval dispersal and settlement processes, ecology of EBP and juvenile lobsters, and status of adult populations. Understanding larval dispersal and settlement is an important factor in deciphering meta-population connectivity and location of nursery grounds; whilst improving our knowledge on the ecology of EBP and juveniles is imperative because successful settlement and recruitment of EBP lobsters is thought to drive the demography of adult lobster populations. We currently have no documented evidence on sightings of EBP and juvenile lobsters, and as such, nursery habitats remain elusive. Whether it is because EBP and juvenile lobsters are so scarce or, in fact, studies have been looking in the wrong place, is unknown. Finally, data on the status of adult populations should be treated with caution, because as both scientists and fisheries stakeholders are aware, passive sampling via pots is very discriminate, with *H. gammarus* catchability being influenced by numerous internal and external stimuli; and hence, not truly reflecting the population status.

Recent in-depth research into the abundance, interaction and movement of a *H. gammarus* population has been carried out by Skerritt (2014), in conjunction with Newcastle University, Northumberland IFCA, Natural England and the MMO. Key findings included observations of high site fidelity; catchability differences between sexes (leading to female-skewed density estimates); the presence of *H. gammarus* significantly lowering the catchability of crab species; and male *H. gammarus* exhibiting significantly larger home-ranges than female *H. gammarus*, potentially leading to increased catchability of males in baited pots. The fundamental ecological research carried out as part of this study has furthered our understanding of *H. gammarus* population dynamics and of the species' behaviour. Both aspects are important in implementing successful management strategies and MPA designations.

An ongoing project in Lyme Bay Marine Protected Area (MPA), Dorset, is assessing the impact of potting density on seabed biodiversity and target species within the Lyme Bay MPA. This study is being carried out by the Marine Institute Plymouth University in partnership with the Blue Marine Foundation and members of the local fishing industry. The study is gathering a wide range of data, including video images of seabed habitats and species; quantitative data on mobile species utilizing the MPA; data on target species under standardised fishing conditions; and finally an assessment of potential spill-over from control areas. *H. gammarus* is one of the project's target species. Ultimately, the study will provide valuable insight into the ecological functioning of the Lyme Bay MPA, with emphasis on shellfish potting activity and biodiversity.

Finally, the Lundy Island NTZ has illustrated the repercussions of prohibiting *H. gammarus* fishing activities. The subsequent boom in *H. gammarus* abundance within the NTZ may have significant implications for ecosystem structure, function and stability, due to the overriding presence of *H. gammarus* as apex predator. Initial studies suggest that there may be detrimental consequences to the co-existing species in the NTZ. However, further studies investigating multiple species, at different trophic levels, are required to determine the presence of trophic cascades due to ecosystem dominance by *H. gammarus*. However, the limiting factor of all studies carried out within the Lundy NTZ, to date, is that relevant baseline data was not collected prior to NTZ designation. Thus, before-after comparisons cannot be made. Fortunately, due to the ‘sliding baselines’ phenomenon and use of various control sites, Lundy Island NTZ still remains a valuable research site for studying ecosystem structure, function and stability.

European spiny lobster (*Palinurus elephas*)

General biology & ecology

The European spiny lobster (*Palinurus elephas*), also known as the Crawfish or Crayfish, is a large decapod crustacean whose UK populations represent the northerly limit of the species distribution (Jackson *et al.,* 2009). Growing as large as 600 mm in length, but more commonly 400 – 500 mm, *P. elephas* is an epibenthic species that relies on shelter from crevices and caves during daylight hours, emerging to feed at night (Díaz *et al.,* 2001, Buscaino *et al.,* 2011, Gristina *et al.,* 2011). It inhabits rocky environments in the subtidal zone, in waters up to 200m deep (Groeneveld *et al.,* 2013). As the common name of 'spiny lobster' suggests its carapace is heavily armoured with spines; which may compensate for the absence of large cheliped claws, which are present on the native European lobster, *Homarus gammarus*. The UK population of *P. elephas* is extremely small, as a result of overfishing and/or environmental change. Within England, populations are restricted to the south west coast. As a consequence, it is considered a UK priority Biodiversity Action Plan species (JNCC 2010).

Size of sexual maturity (SOM) is at approximately 70-80 mm carapace length, and takes place between two hard-shelled individuals during June-October. In comparison to other spiny lobster species, *P. elephas* has a low fecundity (Jackson *et al.,* 2009). Eggs are externally fertilised, and then brooded, on the underside of the female for between 4 – 10 months, depending on temperature (Goñi and Latrouite 2005). Commonly between March-June, 23,000 - 202,000 eggs are released into the water column (Goñi *et al.,* 2003); where they may disperse > 1 km (Jackson *et al.,* 2009). The larval stages of *P. elephas* exist for between 65 – 149 days (Kittaka *et al.,* 2001); and consist of 10 phyllosoma stages, followed by a puerulus stage. Metamorphosis into the post-pueruli stage marks the beginning of epibenthic life for the species, where it will reside in crevices and sustain an omnivorous diet (Goñi *et al.,* 2001). Upon maturation, *P. elephas* undergoes an ontogenetic migration offshore in winter, with a return migration inshore during the following spring for mating purposes (Ansell and Robb 1977, Hunter 1999). The species exhibits annual moulting, peaking in September for both males and females (Hunter *et al.,* 1996) and lasting 2 – 5 weeks (Hepper 1977). The lifespan of *P. elephas* is considered to be > 25 years.

Ecological Niche

Habitat & physical environment

Planktonic larval stages: There are ten phyllosoma larval stages of *P. elephas*, all of which are pelagic (Hunter 1999, Kittaka *et al.,* 2001). They rely on offshore drifting for directional movement, as the larvae are poor horizontal swimmers and can only control vertical movement (Goñi and Latrouite 2005).

Early-stage phyllosomas are positively phototrophic (Hunter 1999, Goñi and Latrouite 2005). However, a series of samples from the English Channel found an absence of phyllosomas in the top 10 m of water (Russell 1927 in Goñi and Latrouite 2005), suggesting that later stages may become negatively phototrophic. Temperature influences growth and moult cycles of all crustacean species (Chittleborough 1976), which causes geographical variations in larval periods for *P. elephas* (Hunter 1999). This has been directly observed in *P. elephas*, as larval period is negatively related to temperature. Phyllosomas are rarely caught in the wild, so dispersal patterns are largely inferred from puerlus settlement and population genetics (Groeneveld *et al.,* 2013).

After metamorphosis to the pueruli stage, larval *P. elephas* are no longer phototrophic and remain in the mid to lower water column; most likely due to their increased weight (Goñi and Latrouite 2005). Very little is known about this stage (Hunter 1999), except that it is more common in inshore waters (Goñi and Latrouite 2005 and refs within). This is possibly because although the pueruli stage is technically planktonic, it has been suggested that they utilise small crevices and seaweed as shelter (Bouvier 1914, Fage 1927 in Goñi and Latrouite 2005), thus making them difficult to sample.

Epibenthic life stages: Recent observations suggest that pueruli settlement occurs over a wider bathymetric and substratum range than previously thought (Abelló *et al.,* 2008). Previously, it was considered that settlement was defined by a very narrow temperature range and water depth; in waters 10 – 15 m deep, when sea surface temperatures start to increase in May (Díaz *et al.,* 2001). However, post-pueruli (8.5 -16 mm CL) have been observed at 73 m depth, and also on artificial collectors on sandy substratum (Díaz *et al.,* 2004). Furthermore, the limited observations of post-pueruli by Díaz (2010), led to uncertainty over earlier theories of ontogenetic movements from shallow (settlement habitat) to deep waters (adult habitat)

However, post-pueruli are thought to rely crevices in rocks for suitable habitat, exhibiting complete fidelity (Díaz *et al.,* 2001). They have a strong preference towards limestone rock due to the presence of holes left by the rock-boring bivalve *Lithophaga lithophaga*, of which post-pueruli exclusively use (Díaz *et al.,* 2001). For this reason, abundances are lower on calcareous metamorphic rock and completely absent on siliceous metamorphic rock due to lack of such holes (Díaz *et al.,* 2001). Hole size is closely related to body size in the absence of predators, although in their presence, individuals show no selection (Gristina *et al.,* 2009). Post-pueruli prefer sub-vertical surfaces for avoidance of light and siltation (Díaz *et al.,* 2001), but also as avoidance from predators (Gristina *et al.,* 2009).

Adult *P. elephas* reside in coastal areas down to depths of 200 m (Barshaw *et al.,* 2003, Goñi and Latrouite 2005). However, overfishing in shallower waters has resulted in an almost complete absence of adult *P. elephas* in depths of less than 40 m across its entire distribution (Goñi and Latrouite 2005). Adults prefer shallow inshore rocky reefs and coralligenous substrates due to the higher presence of vertical surfaces (Ansell and Robb 1977). Such environments offer small caves and crevices as temporary protection for *P. elephas* (Ansell and Robb 1977, Goñi and Latrouite 2005), as it mainly resides in open ground or among weeds on rocky surfaces (Ansell and Robb 1977). Currents are higher in rocky habitats, and *P. elephas* is tolerant of such exposure as a result (Ansell and Robb 1977).

Habitats:

- Juveniles & adults – **subtidal zone**
- Up to **200 m** water depth
- **Rocky** substratum

An offshore migration is present in adult *P. elephas* and has been suggested as the definitive characteristic of the adult stage (Díaz *et al.,* 2001). Linked with the reproductive cycle, it occurs after egg laying (September onwards), with a return to shallower waters in the spring for mating (Ansell and Robb 1977, Hunter 1999, Goñi and Latrouite 2005). The migration is highly temperature dependent (Hunter 1999), coinciding with the passing of the annual peak water temperature in September (Ansell and Robb 1977).

Behaviour

Epibenthic life stages: Adult *P. elephas* can be solitary, or occur in pairs or small groups (Goñi and Latrouite 2005), and is therefore considered a gregarious species (Hunter 1999, Jackson *et al.,* 2009). However at high densities, aggression will increase, regardless of food availability (Follesa *et al.,* 2007a). Cooperative defence strategies can occur where groups share dens or crevices, but are not fundamental mechanisms for defence against predators (Buscaino *et al.,* 2011 and refs within), as they often abandon their tight formations when directly threatened. Audial behaviour has been observed in *P. elephas* as an alert mechanism against predators (Buscaino *et al.,* 2011). The sound is produced from a specialised organ on its head, and is increased when single lobsters are threatened in comparison to grouped lobsters (Buscaino *et al.,* 2011), suggesting it is an intimidation tactic rather than group behaviour.

Key behavioural traits:
- Predatory
- Nocturnal
- Gregarious
- Migratory

Increased nocturnal activity is present in both juvenile and adult *P. elephas* as predatory avoidance mechanism (Díaz *et al.,* 2001, Gristina *et al.,* 2009, Buscaino *et al.,* 2011). This avoidance behaviour dictates their diurnal cycles, as *P. elephas* will remain sedentary in daylight hours, emerging to feed only at night (Hunter 1999).

Reproduction takes place between June and October, depending on the region (Hunter 1999, Goñi and Latrouite 2005). Copulation involves the male depositing spermatophores on the female's sternum (Goñi and Latrouite 2005), which the female uses to fertilise the eggs by shedding the eggs over them. Incubation varies geographically, with shorter periods in Mediterranean waters (4 – 5 months) compared to Atlantic populations (6 – 10 months) (Goñi and Latrouite 2005 and refs within). The reproductive behaviour of *P. elephas* has a strong, annual migratory element (Díaz *et al.,* 2001). After mating and egg laying throughout October to November in shallow waters, individuals migrate offshore to deeper waters (Ansell and Robb 1977, Lenihan 1999). Remaining offshore throughout the winter, the subsequent inshore migration occurs in spring and summer months (Ansell and Robb 1977, Hunter 1999), with males migrating earlier than females (Ansell and Robb 1977). Tag-recapture studies have revealed adult migrations of between 2-20 km (Hepper 1967, Goni *et al.,* 2000, Giacalone *et al.,* 2006, Follesa *et al.,* 2007b). However, recent study by Follesa *et al.,* (2015) has revealed that the homing abilities of *P. elephas* are impeded when displaced >0.5 km.

Trophic level, predators & prey

Planktonic larval stages: Being planktonic in their larval stage, *P. elephas* are susceptible to non-selective predation from planktivorous consumers. In their phyllosoma stages, *P. elephas* are rapacious predators (Kittaka and Ikegami 1988). Their low survival in diatom rich water and morphological adaptations of the mouthparts provide evidence for a carnivorous diet (Goñi and Latrouite 2005). Lab cultures of *P. elephas* phyllosoma have identified fish larvae to be an important dietary component, with higher survival rates if they are consumed (Kittaka *et al.,* 2001). The diet of the pueruli stage is unknown, but lab experiments have achieved survival on a diet of *Mytilus edulis* flesh (Kittaka *et al.,* 2001). Although larval *P. elephas* are planktonic and therefore a within the zooplankton community, the presence of fish larvae and survival on bivalve flesh in their diet places them in the 2nd - 3rd trophic level of a marine ecosystem.

Trophic levels:
- Planktonic larval stages – ***Level 2-3*** (primary & secondary consumers)
- Juvenile & adult crabs - ≥ ***Level 3*** (carnivorous consumers)

Epibenthic life stages: Newly settled post-puerulus are the most vulnerable benthic life stage of *P. elephas* (Butler *et al.,* 2007). Small juveniles have weak defences and rely entirely on avoidance of predators (Díaz *et al.,* 2001). Predators include octopus (Quetglas *et al.,* 2001, Butler *et al.,* 2007, Gristina *et al.,* 2009), crab (Butler *et al.,* 2007) and numerous pelagic and demersal fish (Goñi and Latrouite 2005 and refs within, Butler *et al.,* 2007). As *P. elephas* increases in size, individuals have an increasing chance of defending themselves against predators, even attacking their predators when threatened (Barshaw *et al.,* 2003). Adults reach large sizes at maturity (400 – 500 mm total length; Jackson *et al.,* 2009), so only large predators can successfully predate them. Fish and elasmobranchs are common predators of adult *P. elephas* due to their agility, and thus avoidance defensive strategies (Buscaino *et al.,* 2011 and refs within). Specific to the UK, the European conger eel (*Conger conger*) and common octopus (*Octopus vulgaris*) are known predators of *P. elephas* (Buscaino *et al.,* 2011), with the latter eliciting dramatic defensive responses from *P. elephas* (Gristina *et al.,* 2011).

Palinurus elephas often jettison their stomach upon capture (Campillo and Amadei 1978 in Hunter 1999) and exhibits poor and erratic feeding behaviour in captivity (Hunter *et al.,* 1996), so understanding their diet has been difficult. However, it is considered a generalist, opportunistic feeder, with a diet adapted to the local abundances of prey sources (Goñi *et al.,* 2001, Goñi and Latrouite 2005). The diet of *P. elephas* is very extensive and includes crustaceans (Hunter 1999, Goñi, Quetglas, *et al.,* 2001), echinoderms (Ansell and Robb 1977, Hunter 1999, Goñi *et al.,* 2001, Guidetti 2004), fish (Hunter *et al.,* 1996, Goñi *et al.,* 2001), polychaetes (Goñi *et al.,* 2001) and molluscs (Ansell and Robb 1977, Hunter *et al.,* 1996, Hunter 1999, Goñi *et al.,* 2001), as well as algae (Ansell and Robb 1977, Goñi *et al.,* 2001).

Diets do not vary between sexes, but the species exhibits a progressive ontogenetic change in diet from gastropods and crustaceans to other prey sources such as fish (Goñi *et al.,* 2001). Furthermore, feeding rate increases at maturity due to the higher energy demands of gonadal and egg development (Goñi *et al.,* 2001). There are no documented cases of cannibalism in *P. elephas*, probably due to the gregarious nature of the species. Any calcium deficiencies in the diet that would encourage cannibalism are met from other sources such as mollusc shells and other crustacean species (Goñi *et al.,* 2001).

Palinurus elephas is an omnivorous species (Hunter 1999) and therefore spans multiple trophic levels. As a juvenile, the preference towards molluscs and small crustaceans leads to *P. elephas* occupying the 3rd trophic level. The gradual ontogenetic shift towards increased fish prey and larger crustaceans in their diet (Goñi *et al.,* 2001) will allow larger individuals to occupy the 4th trophic level as secondary carnivorous consumers. As this change in diet is dictated by growth (Goñi *et al.,* 2001), there is no discrete point in its life history where the trophic shift can be identified. However, the presence of algae in the diet of P. elephas of all sizes (Ansell and Robb 1977, Goñi *et al.,* 2001) clearly demonstrates that it simultaneously occupies the level of herbivorous consumer (2nd trophic level).

There are no documented studies of *P. elephas* assuming the role of apex predator within an ecosystem. This may be related to lack of research and their low abundance levels. However, the fact that the species the species can occupy the 4th trophic level, and potentially produce a commercially-viable fishery, suggests that *P. elephas* may be able to assume apex predator in some ecosystems.

Niche competitors

Planktonic larval stages: There is no documented information on the niche competitors of *P. elephas* larvae; and due to their scarcity in the marine environment, determining their precise niche competitors is currently impossible. However, it is possible that they belong to the general decapod larval community which is dominant in temperate water zooplankton assemblages (Lindley *et al.,* 2010). Hence, there are numerous competing species which could competently fulfil the ecosystem niche of *P. elephas* larvae.

Epibenthic life stages: Palinurus elephas is an omnivorous consumer that simultaneously occupies three trophic levels (levels 2-4). It adapts its prey selection to local variations in prey abundance (Goñi *et al.,* 2001, Goñi and Latrouite 2005), producing highly niche-specific diets (Hunter *et al.,* 1996, Boudreau and Worm 2012). Therefore, it has been acknowledged that *P. elephas* does not experience any trophic competition as it can simply alter prey sources if competition arises (Hunter *et al.,* 1996).

In contrast, habitat is a source of competition for *P. elephas*. Understandably, there will be multiple species that require the shelter of small caves and crevices in rocky subtidal environment. At smaller life stages (post-pueruli), *P. elephas* will be out-competed by the majority of competitors, as it is generally a prey source for such species. With adult *P. elephas*, niche competitors include the Conger eel (*C. conger*) and the Common octopus (*O. vulgaris*). They require the same physical habitat for shelter (i.e. crevices and holes) and are known predators of *P. elephas*. Hence, it is considered that they will always out-compete *P. elephas* for such ecological niches (Quetglas *et al.,* 2001, Buscaino *et al.,* 2011, Gristina *et al.,* 2011). Other potential niche competitors of adult *P. elephas* include the Brown crab, *Cancer pagurus*, and the European lobster, *Homarus gammarus*. Both these large decapod competitors possess a more aggressive nature than *P.elephas,* and have the added advantage of large cheliped claws for attack and defence. Hence, it is likely that the clawless *P. elephas* will be the subordinate species during confrontation, and thus be out-competed. Although there is no direct evidence of such competition, comparison of species' distribution, show that while *C. pagurus* and *H. gammarus* are ubiquitous in all coastal waters of the UK, *P. elephas* has very patchy distributions, isolated to discrete sites in the south and west of England Wales, and confined to the west coast in Scotland (Jackson *et al.,* 2009).

Lacking enlarged cheliped claws, *P. elephas* relies on a thicker carapace and escape tactics to avoid predation (Barshaw *et al.,* 2003). As clawless lobsters are more common in lower latitudes, it is hypothesised that clawed lobsters were excluded from lower latitudes due to "some intrinsic factor such as the maintenance cost of large claws that precluded an evolutionary increase in shell thickness" (Barshaw *et al.,* 2003). Therefore, it could be deduced that *P. elephas* will exhibit increased predation pressure at its northerly distribution limit in UK waters, unlike *C. pagurus* and *H. gammarus* which have evolved appropriate defence mechanisms.

Role in ecosystem function & stability

Epibenthic life stages: Palinurid decapods, in general, are recognised for their influence on the structuring of benthic habitats. For example, exclusion of the spiny lobster, *Panulirus interruptus* from exposed intertidal rocky shores in Santa Catalina Island, California resulted in the rapid expansion of *Mytilus* spp. beds, replacing pre-existing algal turfs (Robles and Robb 1993). Another study, by Lafferty (2004), revealed that the predation of *P. interruptus* on sea urchins in a Californian National Park, was maintaining a kelp forest ecosystem, which would not be the case under high densities of grazing sea urchins. This has led to *P. interruptus* to be classified as a 'keystone' species, and thus capable of inducing trophic cascade. However, whilst *P. elephas* consumes both of these prey types, there is no recognised top-down control, or keystone status, of this species. Reasons for this may include, very low population densities of *P. elephas* and also the fact that they consume such prey species as part of a much broader diet (Goñi *et al.,* 2001, Guidetti 2004). Lack of research is also a limiting factor.

It may be concluded that ascertaining the roles of *P. elephas* in ecosystem function and stability is currently an impossible task. Present UK populations of *P. elephas* are very small and patchy; hence measuring the impact such the species has on an ecosystem is unfeasible. Additionally, there is little, if no, early documented evidence on the ecological roles of *P. elephas* prior to the population crash in the 1970's. Furthermore, few of the MPAs which have been established in the Mediterranean Sea to protect and enhance current *P. elephas* populations, have monitoring programmes; and of those that do, the programmes commonly only investigate the target species of *P. elephas* (Goni *et al.,* 2003, Follesa *et al.,* 2008, 2009, Bevacqua *et al.,* 2010, Diaz *et al.,* 2011). Therefore, the impact of increased *P. elephas* abundance on community assemblages, and hence ecosystem function and stability, cannot be determined. Monitoring of solely one target species within an MPA is a common oversight, and unfortunately will not provide any insight into trophic cascades, and overall ecosystem health and resilience.

Based on conjecture and research on other palinurid species; if UK population levels were that of pre-1970, it is possible that *P. elephas* could exert significant top-down control within ecosystems. Similar to other large decapod crustaceans, it may be possible that *P. elephas* is able to assume the apex predator role in some environments. Furthermore, the migratory behaviour of *P. elephas*, resulting in it annually alternating between coastal and offshore habitats may enhance ecosystem connectivity. The migrations are thought to be timed in response to changing water temperature, which may result in large transfers of biomass from shallow to deep water environments on a very short timescale.

Potential functional roles of epibenthic *Palinurus elephas*:

- ***Top-down regulator**: Of molluscs, echinoderms, polychaetes, crustaceans & fish*
- ***Community structuring:** If occupying 4th trophic level*
- ***Ecosystem connectivity**: Coastal & offshore ecosystems*

It must be reminded that the ‘potential’ functional roles discussed above are tentative; due to current low levels of *P. elephas* abundance and lack of specific research.

Potential consequences of removal on ecosystem function & stability

Due to very limited *P. elephas* populations, as a result of overexploitation and/or environmental change, it may be assumed that UK ecosystems have been functioning without such a species for almost 50 years. Hence, current ecosystem scenarios reflect *P. elephas* removal. However, over the past 50 years the marine environment has under gone significant change, with a multitude of influential factors (anthropogenic and non-anthropogenic); hence, in combination with the lack of scientific research on *P. elephas,* it is impossible to determine the impact of *P.elephas* removal on ecosystem function and stability.

However, other large decapod crustaceans native to the UK (e.g. *Cancer pagurus* and *Homarus gammarus*) probably belong to the same functional group as *P. elephas*; hence, fulfilling the vacant ecological niche of *P. elephas*; including the provision of ecosystem goods via commercially-viable fisheries. It is, therefore, unlikely that the diminished populations of *P.elephas* in UK waters induced deleterious effects on overall ecosystem function and stability.

Overview of *P. elephas* in ecosystem structure & function

In summary, there is a significant knowledge gap in the role of *P. elephas* in ecosystem structure and function; mainly as a result of overexploitation, environmental change, and the lack of research into the biology and ecology of the species. This is particularly pertinent with regard to wild populations (especially in the UK), and early benthic phase and juvenile ecology. In order to facilitate population recovery, knowledge of suitable nursery grounds is vital. Current research is primarily focused on Mediterranean, not UK, populations. The only current UK research project appears to be the tagging of *P. elephas* within the Isles of Scilly

MCZ, in order to monitor populations. The project is being managed by the Isles of Scilly IFCA, and is currently in its 3rd year (2015).

Despite the now limited *P. elephas* fishery in UK waters, the population, however, does not appear to be recovering. This may be due to lack of data, or possibly the population size being below the effective threshold required for net growth. In addition, it is possible that *P. elephas* is currently subordinate to co-existing clawed decapods crustaceans (e.g. *C. pagurus* and *H. gammarus*), and unable to enhance its own ecological niche. Current marine climates may also be hindering its revival.

MPA designation within the Mediterranean Sea has reported increases in abundance, biomass and size of *P. elephas* within protected areas (e.g. Goni *et al.,* 2010, Follesa *et al.,* 2008, 2009), together with 'spillover' in adjacent fisheries. However, the effects on the long-term recovery of *P. elephas* populations is currently unknown, and is hindered by our lack of knowledge on larval dispersal, subsequent nursery grounds and, hence, population connectivity. Furthermore, we do not have insight into the indirect effects of increased *P. elephas* abundance within MPAs, such trophic cascades and changes in functional (and bio) diversity, which ultimately effect ecosystem structure, function and resilience. One study by Diaz *et al* (2005), however, did record increased levels of juvenile *P. elephas* predation within the reserve, probably as a result of the simultaneous protection afforded to the predatory fish within the MPA.

Norway lobster (Nephrops norvegicus)

General biology and ecology

The Norway lobster (*Nephrops norvegicus*) is a small lobster (< 25 cm) found throughout the UK, although populations are more common in Scottish waters (Sabatini and Hill, 2008). It is an infaunal/benthic species found in waters between 20-800 m in depth. *N. norvegicus* is a solitary animal; however, its strong substrate preference for muddy sediments results in dense localised populations, leading to frequent intraspecific interactions, often over burrow possession (Sabatini and Hill, 2008). This has also led to evidence of density-dependent growth due to food resource limitations (Johnson *et al.*, 2013; Tuck *et al.*, 1997). *N. norvegicus* exhibits burrowing behaviour (Farmer, 1974a; Rice and Chapman, 1971) as a means of protection against predators. Such burrowing activity dramatically influences the surrounding environment in areas where burrow density is high (Johnson *et al.*, 2013). Regularly emerging from the burrow only feed, *N. norvegicus* is an opportunistic predator that feeds on a wide range of prey species, in particular, crustaceans (Cristo and Cartes, 1998).

The typical life span of *N. norvegicus* is 5-10 years, with size at sexual maturity varying greatly, even on small spatial scales (tens of km). In the Firth of Clyde, Scotland, for example, size at sexual maturity ranges from 21 – 34 mm carapace length (CL) in females and 29 – 46 mm CL in males (Tuck *et al.*, 2000), and is known to be similar in Irish Sea populations (Sabatini and Hill, 2008). Such high variations in size are due to differential growth rates between populations (Tuck *et al.*, 2000). *N. norvegicus* is a post-moult mater (Farmer, 1974b), with egg laying generally occurring between August – September and hatching in April – June (Farmer, 1974b). Following a 50 day larval period (Johnson *et al.*, 2013), the larvae metamorphose and settle on the seabed, where they find shelter in the form of burrows (Chapman, 1980).

N. norvegicus is considered a non-migratory species, with adults rarely moving more than a few hundred metres. This may be related to unsuitable sediments and their heavy reliance on the protection afforded to them by their burrows (Bell *et al.*, 2013).

Ecological niche

Habitat and physical environment

Planktonic larval stages: Although the biology and morphology of larval *N. norvegicus* is well documented (Farmer, 1974b), the ecology is less well known. Like all crustacean planktonic life stages, *N. norvegicus* larvae remain suspended in the water column, relying entirely on advection for transport (Johnson *et al.*, 2013). Although it is suggested that external recruitment is possible, self-recruitment is more common (Johnson *et al.*, 2013). For example, mud substratum in the Irish Sea is geographically isolated and therefore confines *N. norvegicus* populations to two distinct areas (White *et al.*, 1988). A seasonally forming gyre over one of the areas has been suggested to act as a self-recruitment mechanism for the resident population (Hill *et al.*, 1996), allowing larvae to remain within the water column above the muddy sediment until settlement.

Epibenthic life stages: Once settled, *N. norvegicus* require muddy habitats where burrowing is most effective (Johnson *et al.*, 2013); typically in substratum containing > 40% silt and clay (Bell *et al*., 2006). However, in the Irish Sea, *N. norvegicus*, has been found inhabiting substratum of between 4 – 90 % silt and clay content (Tully and Hillis, 1995). Although *N. norvegicus* can inhabit sandy substrates, densities are dramatically lower due to the increased fluidity of the sediment (Johnson *et al.*, 2013). As a result, *N. norvegicus* is commonly found offshore where wave exposure is negligible and tidal strengths are below 1 knot (Sabatini and Hill, 2008). *N. norvegicus* has been recorded at between water depths of 20 – 800 m (Katoh *et al.*, 2013; Maynou and Sardà, 1997; Sabatini and Hill, 2008), inhabiting the infra- and circalittoral zones (Sabatini and Hill, 2008).

It is especially important for juveniles to find shelter as soon as they metamorphose into the epibenthic life stage, as they are highly vulnerable to predation by fish feeding on the sediment surface. They therefore prefer to occupy empty adult burrows , as these can provide more substantial protection (Chapman, 1980; Tuck *et al.*, 1994). However, juveniles will build their own burrows in areas where burrow densities are low (Chapman, 1980). Burrows of adult *N. norvegicus* are considered semi-permanent structures, and can reach up to 33 cm below the surface (commonly 2 – 3 times the length of the animal).They are very simple U-shaped structures, consisting of a wide-mouthed tunnel for entry and a smaller ventilation shaft at the rear (Rice and Chapman, 1971).

Habitats:
- Larvae – *plankton*
- Juveniles & adults – *subtidal benthos*
- Substratum – *muddy soft sediment*

The creation of their own burrows highlights their very specific substrate requirements and this specificity is also shown in their salinity tolerance (31.8 – 38.8 PSU) (Johnson *et al.*, 2013; Sabatini and Hill, 2008). In contrast, however, *N. norvegicus* can tolerate a wider temperature range, from 6.4 – 17.3 °C (Johnson *et al.*, 2013).

Behaviour

Epibenthic life stages: The behavioural ecology of *N. norvegicus* is almost entirely defined by its burrowing behaviour (Chapman, 1980; Johnson *et al.*, 2013). *Nephrops norvegicus* is a highly territorial species (Farmer, 1974a), with individuals attempting to retain burrows in areas of high resources. There is no strict burrow fidelity in populations (Johnson *et al.*, 2013), as dominant individuals, such as large males, will regularly attempt to evict conspecifics in preferred burrows (Chapman and Rice, 1971). Therefore, larger males tend to retain burrows for longer periods, although eviction can still occur (Chapman and Rice, 1971). Using burrows for predatory avoidance (Johnson *et al.*, 2013), individuals will leave the burrow only to feed (Chapman and Rice, 1971) and reproduce (Powell and Eriksson, 2013).

Key behavioural traits:
- Burrower
- Engineer
- Territorial
- Solitary
- Diurnal

Laboratory observations of burrowing mostly resemble behaviour in the field (Farmer, 1974a). However, whilst females and small males create normal burrows, larger lab-reared males have been observed to create shallower depressions rather than burrows (Farmer, 1974a). Larger males (> 4 cm carapace length) exhibit higher aggression due mainly to resource and mating competition (Chapman and Rice, 1971). As individuals frequently change burrows and attempt to evict smaller conspecifics (Chapman and Rice, 1971), it was suggested that males do not expend energy creating large burrows in order to devote more time and energy into defending territory (Farmer, 1974a). Maintained at high densities, laboratory animals created a large system of interconnected burrows with up to thirteen entrances (Farmer, 1974a). In wild populations, such discrete tunnel groups have not been observed, with wild burrows only possessing a maximum of two entrances (Rice and Chapman, 1971).

Behaviour has been shown to be strongly diurnal in *N. norvegicus* (Atkinson and Naylor, 1976; Chapman and Rice, 1971; Farmer, 1974c; Hammond and Naylor, 1977). Emergence from burrows is influenced by exogenous factors and is highly depth-dependent (Hammond and Naylor, 1977). In shallow waters (10-50 m), *N. norvegicus* only emerges at night to feed, and returns by dawn (Chapman and Rice, 1971; Katoh *et al.*, 2013). With increasing depth, emergence becomes more common in daylight hours (Katoh *et al.*, 2013). Light intensity, a common cause of depth-dependent behaviour, has only an indirect control on emergence (Atkinson and Naylor, 1976). Rather, it is suggested that *N. norvegicus* responds to diurnal patterns in predator and prey activity (Katoh *et al.*, 2013). Increased activity within the burrow at night is an endogenous rhythm (Atkinson and Naylor, 1976; Hammond and Naylor, 1977) and therefore does not vary spatially.

Fished individuals caught in pots and creels have commonly exhibited small circular punctures in the carapace and claws, indicating aggression and fighting behaviour between individuals (Chapman and Rice, 1971). *In situ*, it has been observed that fighting commonly occurs when an individual approaches a conspecific's burrow. Such aggressive behaviour lasts between 10 – 20 minutes and commonly occurs between large males (Chapman and Rice, 1971).

Trophic level, predators & prey

Planktonic larval stages: Decapod larvae are predated upon by ctenophores, meduase and pelagic fish species (such as herring, *Clupea harengus* in UK waters; Farmer 1975). In the latter, feeding rates are proportional to their availability in the water column, suggesting no evidence of targeted predation (Boudreau and Worm, 2012). Larval *N. norvegicus* are themselves opportunistic carnivores, actively predating upon copepods, mysids, other decapod larvae, as well as small Sagitta spp. (Farmer, 1975). At abnormally high densities (observed in laboratory conditions), cannibalistic behaviour has been recorded (Farmer, 1975). The grazing on zooplankton places larval *N. norvegicus* in the 2nd -3rd trophic levels (i.e. primary and secondary consumers).

Epibenthic life stages: Juvenile and adult *N. norvegicus* are generally considered first-level carnivorous consumers, which constitutes the 3rd trophic level of a generalised marine ecosystem. They therefore act as both predators and prey within a community. In terms, of predators of *N. norvegicus*, predation is highest in the early stages of benthic life. With a strong substrate preference, individuals will be vulnerable if they have settled in an area with a low density of burrows (Boudreau and Worm, 2012). Analysis of nearly 100,000 North Sea cod (*Gadus morhua*) stomachs found *N. norvegicus* to occur in 93 % of stomachs (ICES, 1997). A study in the Irish Sea found similar results, concluding that cod is the most significant predator of *N. norvegicus* (Pinnegar and Platt 2011). The North Sea study (ICES, 1997) also found *N. norvegicus* in other predatory fish including haddock (*Melanogrammus aeglefinus*), Atlantic wolfish (*Anarhichas lupus*), grey gurnard (*Eutrigla gurnardus*), megrim (*Lepidorhombus whiffiagonis*), herring (*Merlangius merlangus*) and turbot (*Psetta maxima*), as well as various elasmobranch species including skate and lesser-spotted dogfish (*Scyliorhinus canicula*) (Howard, 1989).

Trophic levels:

- Larval stages – ***Level 2-3*** (primary & secondary consumers)
- Juvenile & adult crabs - ***Level 3*** (carnivorous consumers)

N. norvegicus, itself, is a generalist predator and scavenger (Johnson *et al.*, 2013), with variations reflecting local availability (Parslow-Williams *et al.*, 2002). A study comparing *N. norvegicus* populations in the Mediterranean Sea and the adjacent Atlantic Ocean identified 119 different prey species in *N. norvegicus* stomach contents (Cristo and Cartes, 1998). The most common prey groups targeted by *N. norvegicus* were polychaetes (Baden *et al.*, 1990; Parslow-Williams *et al.*, 2002), molluscs (Baden *et al.*, 1990; Parslow-Williams *et al.*, 2002), crustaceans (Cristo and Cartes, 1998; Farmer, 1974c; Parslow-Williams *et al.*, 2002), echinoderms (Cristo and Cartes, 1998; Parslow-Williams *et al.*, 2002) and fish (Cristo and Cartes, 1998; Farmer, 1974c). *N. norvegicus* has also been observed to consume plankton through suspension feeding (Loo *et al.*, 1993), as well as exhibit cannibalism at high densities in the wild (Baden *et al.*, 1990; Cristo and Cartes, 1998). Such a varied diet of *N. norvegicus* means that it inhabits a broad range of trophic levels within the ecosystem food web.

Stable isotope studies confirm that *N. norvegicus* is a consumer of suspension and deposit-feeding invertebrates, and both epibenthic and burrowing crustaceans; and thus occupies the 3rd trophic level (i.e. first level carnivorous consumers; Loc'h & Hily 2005, Hill 2007).

Niche competitors

Planktonic larval stages: As a consequence of the large number of UK decapod crustaceans, and the high fecundity of many of these species; decapod larvae are dominant in temperate water zooplankton assemblages (Lindley *et al.*, 2010). Hence, there are numerous competing species which could competently fulfil the ecosystem niche of *N. norvegicus* larvae, if this species was to dramatically decline in abundance.

Epibenthic life stages: In the juvenile stage, the only potential niche competitor is the gobiid fish *Lesueurigobius friesii* (Chapman and Rice, 1971; Farmer, 1975). The fish occupies *N. norvegicus* burrows, but there is no evidence of direct competition, as *L. friesii* only inhabits empty burrows. Interspecific burrow competition is not deemed an important factor for *N. norvegicus*, with incidences occurring only in specific populations or at specific times when competitor abundances are abnormally high (Farmer, 1975).

Occupying a broad range of trophic levels, adult *N. norvegicus* can compete with many species for resources; such as fish (Farmer, 1975) and other mud-dwelling crustaceans, including the squat lobster, *Munida rugosa* (Farmer, 1975; Trenkel *et al.*, 2007), angular crab, *Gonneplax rhomboides* (Trenkel *et al.*, 2007), portunid crabs, *Macropipus* spp. (Farmer, 1975), the deepwater crustacean, *Polycheles typhlops* (Farmer, 1975) and thalassinidean crustaceans (Hughes and Atkinson, 1997). Interactions may involve competition for burrow space, food or direct predation (Cristo and Cartes, 1998).There are also competing cephalopod species (Farmer, 1975). However, most of these competitors are in low enough numbers to not pose a direct threat the ecological niche and function roles of *N. norvegicus* (Farmer, 1975). In the case of *G. rhomboides*, competition is mitigated by foraging at different times of the day, or by spatial segregation into interspecies clumps (Trenkel *et al.*, 2007). This may allow for coexistence between *N. norvegicus* and other crustacean species (Hartley and Shorrocks, 2002). A study by Maynou *et al.,* (1997) actually found positive correlations between the density of *N. norvegicus* and other crustacean species.

Role in ecosystem function & stability

As significant predators in plankton and benthic communities, *N. norvegicus* can manipulate productivity and structure communities in the majority of ecosystems they inhabit.

Planktonic larval stages: The large number of UK decapod crustacean species, and the high fecundity of many of these species; leads to decapod larvae, including that of *N. norvegicus*, being dominant in temperate water zooplankton assemblages (Lindley *et al.*, 2010). This zooplankton assemblage, as a large 'functional group' of species is thought to be responsible for propagating climate-driven signals through the food web (Lindley and Kirby, 2010; Lindley *et al.*, 2010) and enforce bottom-up control (either directly or indirectly) on commercial fish stocks (Kirby and Beaugrand, 2009).

Epibenthic life stages: N. norvegicus has a very well described and prominent ecological role due to its burrowing behaviour. However, research has predominantly been fisheries related, and therefore focussed upon the biology and population dynamics of the species, rather than the ecosystem role (Johnson *et al.*, 2013). Nevertheless, some studies have been undertaken on the topic.

The network of semi-permanent burrows created by the species, due to dense localised populations, lends itself to *N. norvegicus* being classified as a biogenic engineer. By burrowing in mud, which is highly susceptible to oxygen depletion, *N. norvegicus* acts as a bioturbator, supplying oxygen to the subsurface, as well as circulating nutrients that would otherwise be sequestered (Johnson *et al.*, 2013). This action notwithstanding, *N. norvegicus* still demands a certain level of oxygen and cannot survive in oxygen-deficient sediments (Gray and Elliott, 2009). Burrowing, irrigation and the associated sediment-water flux are considered influential functional roles of *N. norvegicus.*

Aside from bioturbation, the burrows also increase the habitat heterogeneity in an otherwise low energy homogeneous muddy seabed habitat (Tuck *et al.*, 1994), and this is associated with increased biodiversity (Thrush *et al.*, 2001). The burrowing behaviour creates habitats for fish, such as the red band fish (*Cepola rubescens*) (Gray and Elliott, 2009) and goby (*Lesueurigobius friesii*) (Tuck *et al.*, 1994); as well as for the echiuran worm, *Maxmuelleria lankesteri,* and the thalassinidean crustacean, *Jaxea nocturna* (Tuck *et al.*, 1994). There is evidence of interspecies burrow use, as well as physical burrow interconnection between different species (Chapman and Rice, 1971; (Tuck *et al.*, 1994). Furthermore, in high density areas of *N. norvegicus,* and in the absence of fish predators due to overfishing, *N. norvegicus* will be an important influence of benthic community structure (Baden *et al.*, 1990). Hence it is not surprising that *N. norvegicus* has been classified as a '*keystone*' species, due to its promotional roles in engineering, habitat and biodiversity (Smith *et al.*, 2014)

On a trophic level basis, *N. norvegicus* plays a larger role as a prey source than a predator, hence acting as a bottom-up regulator (rather than a top-down regulator). Although a wide range of fish feed on *N. norvegicus*, only in cod does *N. norvegicus* have high occurrence in stomach contents - 93% of cod investigated (ICES, 1997; Pinnegar and Platt, 2011). Therefore, it could be suggested that *N. norvegicus* only shows bottom-up control over cod, and not any other predators. The role of *N. norvegicus* as a bottom-up regulator of fish and cephalopod populations is a highly complex scenario, and very difficult to interpret with present day insight and data. For example, with cod being considered the main predator of *N. norvegicus*, there is controversy over whether *N. norvegicus* consumption is due to availability or preference (Bjornsson and Dombaxe, 2004; Pinnegar and Platt, 2011; Serrano *et al.*, 2003). Secondly, due to the significant reduction in cod and (and other ground fish) stocks over the past century, *N. norvegicus* will have been released from significant 'natural' top-down control, potentially allowing *N. norvegicus* populations to thrive. As a consequence, this may have created the viable commercial fishery, and thus permit the species to cope with the significant fishing pressure of human activities. Recent estimates are that cod eat 0.61 thousand tonnes of *N. norvegicus* annually in the Irish Sea, whilst 8.4 thousand tonnes are harvested annually by fishers (Pinnegar and Platt 2011). However, in contrast, a modelling study by Coll *et al.,* (2006) considered benthic cephalopods to be the most important consumer of *N. norvegicus*.

A further functional role of *N. norvegicus* is the flow of carbon through benthic ecosystems. In muddy habitats, where the species is highly abundant, the population may represent a large proportion of the benthic biomass and production (Johnson *et al.*, 2013). A study in the Irish Sea, which used stable isotopes to investigate the flow of carbon and nitrogen within the ecosystem, revealed that *N. norvegicus* accounted for 96% of the total biomass at trophic level 3 (Hill, 2007). In addition, the input of carbon to the benthos (via primary production) was equal to the removal of carbon from the benthos via the *N. norvegicus* fishery.

N. norvegicus may also exert indirect functional roles within the ecosystem as a consequence of the *N. norvegicus* commercial fishery. For example, the trawling gear used in some fisheries may significantly impact the benthos, subsequently changing the species assemblages. It is suggested that burrowing crustaceans will dominate benthic communities; as such species can evade the trawling gear. Furthermore, the sediment mobilised by the trawling process may smother filter-feeding species, thus excluding them from the habitat (Queirós *et al.*, 2006). The high by catch rates of the *N. norvegicus* fishery may also have significant impacts on ecosystem function and stability. Firstly, the bycatch may contain numerous fish species (e.g. plaice, sole, cod and whiting), some which are commercially sensitive species. Secondly, the bycatch, and subsequent discards, are thought to account for up to 37% of the food resource for certain marine scavengers, such as the hag fish (Catchpole *et al.*, 2006). Hence, the consequences of the *N. norvegicus* fishery on ecosystem function and stability may be important.

Significant functional roles of epibenthic *Nephrops norvegicus*:

- ***Biogenic engineer & keystone species****: Burrow construction*
- ***Bioturbator****: Burrow irrigation & sediment-water flux*
- ***Community structuring****: Increased habitat heterogeneity & biodiversity via bioturbation*
- ***Bottom-up regulator****: Of fish and cephalopods*
- ***Energy flow****: Carbon & biomass transfer in benthic food webs*
- ***Indirect fishery consequences:*** *Community and habitat structuring*

Potential consequences of removal on ecosystem function & stability

Due to the heavy exploitation of *N. norvegicus* populations, many of the significant functional roles of this species in ecosystem structure and stability are, in fact, a consequence of constant removal of individuals through the process of commercial fishing. However, *N. norvegicus* appears to be relatively resilient to fishing and thrive in disturbed environments. This is illustrated by some areas being fished more than 7 times a year, but with landings being maintained at approximately Maximum Sustainable Yield (MSY) (Seafish, 2013). Nonetheless, there are limits to the level of fishing pressure that *N. norvegicus* can withstand, as some populations have shown a decline (Fariña and González Herraiz, 2003). The stable commercial fishery of *N. norvegicus* within repeatedly-fished discrete fishing grounds, suggests that *N. norvegicus* is the dominant species in such ecosystems, with few significant niche competitors. It also implies that *N. norvegicus* belongs to a small ‘functional group’ of species, with very few other species capable of fulfilling the same functional role as *N. norvegicus* in overall ecosystem structure, function and stability. This substantiates its classification as a ‘keystone’ species (Smith *et al.*, 2014). Keystone species are those which exert significant pressure on community structure and overall ecosystem function and stability; therefore loss of *N. norvegicus* from an ecosystem may result in large scale consequences.

For example, constant removal of *N. norvegicus* via fishing, not only regularly restructures benthic communities via physical disturbance; it also promotes the burrowing activities of *N. norvegicus*. This is because burrows may be damaged during the fishing process, thus requiring reconstruction (Johnson *et al.*, 2013). Harvesting (i.e. removal) also induces the influx of new *N. norvegicus* recruits into the newly created ecological niche void. Such increased burrowing behaviour will therefore enhance burrow irrigation, sediment-water fluxes and habitat heterogeneity. The reworking of the sediment is thought to favour other burrowing species; and have a negative impact on filter feeders (due to smothering or burial), and other species that stabilise the sediment (Pillay and Branch, 2011). Therefore, if the *N. norvegicus* fishery ceased, it is possible that an ecosystem 'phase shift' may occur, with the creation of a less dynamic, but more stable, benthic community; which may not include dense aggregations of the keystone species, *N. norvegicus*. The newly created ecosystem, may be structurally and functionally-different to its predecessor.

The role of *N. norvegicus* as a bottom-up regulator of fish and cephalopod populations is a highly complex scenario, and very difficult to interpret with present day insight and data. However, stocks of cod and other ground fish are currently rebuilding in response to improved management across Europe, in particular, in response to Maximum Sustainable Yield (MSY) targets. Hence, there may be repercussions on *N. norvegicus* populations due to resurgence of their 'natural' predators; and removal by both human fishing activities and natural predators may exert significant pressure on *N. norvegicus* populations, and as a consequence there may be a similar ecological 'phase shift' to more stable benthic environment, as discussed above.

Finally, as highlighted by Hill (2007), *N. norvegicus* can constitute the majority of the carbon and biomass (96%) in the 3rd trophic level of benthic ecosystems. The removal of such, via fishing activities, equated to the same carbon loss as that that was transferred to the benthos via primary production. This large carbon, and hence energy, loss from the marine food web and ecosystem, is likely to be influential to overall ecosystem function and stability. If fishing, and *N. norvegicus* removal, was halted, and the energy retained within marine ecosystem, there may be significant alterations to community assemblages and functional diversity of the present day ecosystem.

Overview of Nephrops norvegicus in ecosystem structure & function

Currently, there are extensive knowledge gaps in our understanding of the role of *Nephrops norvegicus* in ecosystem structure and function. The predominant limiting factor is the lack of unexploited *N. norvegicus* populations for study. Without robust comparisons between control (i.e. unfished) and experimental (i.e. fished) populations, hypotheses cannot be rigorously tested. Some studies have attempted such comparisons by using unfished wrecks as control sites (Ball *et al.*, 2000; Hall *et al.*, 1993), but doubt has been cast over the validity of such research. Research is further hampered by the fact that behaviour of *N. norvegicus* under laboratory conditions is not always comparable to that of it in its natural environment; particularly with regard to burrow construction (Farmer, 1974a). Furthermore, attempts to understand the role of *N. norvegicus* burrows in sediment-water fluxes have concluded that it is a highly complex and variable process to measure and quantify (Aller, 1980; Gilbert *et al.*, 2003; Hughes and Atkinson, 1997); and as such, extensive replication in space and time is required to fully understand the ecological implications (Hughes *et al.*, 2000).

MPA reference areas are a potential solution for legitimately investigating the functional role of *N. norvegicus* in ecosystem function and stability. The closest example of a reference area is the annual spatio-temporal closure (3 months per year) of a section of the Porcupine Bank *N. norvegicus* fishery ground in the Irish Sea (Stokes and Lordan, 2011). The area is primarily closed and surveyed each year to gain data on the residing *N. norvegicus* stock. The closure is not implemented to investigate the effects of fishing cessation on *N. norvegicus* population structure and ecosystem function. Hence, the annual surveys do not encompass comparisons between the fished and unfished areas. Nonetheless, the 2012 survey did include underwater video surveys to gather ecological data on *N. norvegicus* burrow density, and coexisting macro-benthic species (Lordan *et al.*, 2012). This limited spatio-temporal closure and survey of *N. norvegicus* fishery stocks highlights the potential of No-take references areas in gaining valuable information on the ecology of *N. norvegicus*.

Velvet swimming crab (*Necora puber*)

General biology & ecology

The velvet swimming crab, *Necora puber* (synonyms: *Portunus, Macropipus* or *Liocarcinus puber*) is a ubiquitous brachyuran crab of UK coasts. It is easily identifiable by prominent red eyes and velvety texture of the carapace, from which it gets its name. It is the largest species of UK swimming crab. With a life span of approximately five years (Bakir and Healy 1995), males reach a larger size of 98 – 109 mm carapace length (CL) compared to females (83 – 98 mm CL) (Hearn 2002 and refs within). Size at sexual maturity (SOM) is not as sexually dimorphic as maximum size, with males maturing at 37.5 – 52.3 mm CL compared to females that mature at 42 – 54.7 (Hearn 2002 and refs within). SOM occurs when the crabs are approximately one year old.

Necora puber is known for its aggression, as it is a highly solitary species that often initiates and wins fights against much larger conspecifics (Smith *et al.,* 1994, Thorpe *et al.,* 1994, Huntingford *et al.,* 1995), as well as against potential predators (Grisley *et al.,* 1996). It predominantly inhabits the infra- and circalittoral zone (Choy 1988, Norman and Jones 1992), but is known to migrate into the intertidal zone on high tides to feed (Silva *et al.,* 2008, 2010, 2014). It has a very broad diet with ontogenetic, spatial and seasonal variations, generally in response to food availability (Norman and Jones 1992). Its high levels adaptability result in a very successful species of UK ecosystems.

Ecological niche

Habitat & physical environment

*Egg stages**:*** Eggs are carried by females for the entirety of development, and so are influenced by the physical environment. Development is possible between 4 – 31 °C (Valdes *et al.,* 1991), but the incubation period is dependent on temperature, lasting 17.6 days at 25 °C and 76 days at 10 °C (Valdes *et al.,* 1991).

Planktonic larval stages: Larval hatching is successful between 8 – 20 °C and 20 – 40 PSU (Choy 1991). Development of the planktonic larvae is temperature dependent (Mene *et al.,* 1991, Valdes *et al.,* 1991, Nagaraj 1992), with high mortality observed at 10 °C (Nagaraj 1992), thus defining its lower survival limit, and also at 25 °C (Mene *et al.,* 1991), which indicates an upper limit. Whilst extreme temperatures halted larval development, low salinities only delay it, and are only influential in conjunction with temperature fluctuations (Mene *et al.,* 1991).

Larvae are released into the water column between April and August (Norman and Jones 1993, Bakir and Healy 1995), with megalopae (final larval stage) not exhibiting any large vertical migrations (Lee *et al.,* 2005). Megalopae have been found to be most abundant in surface waters, and more common on the flood tide; hence, causing a net transport shoreward (Lee *et al.,* 2005). The larval duration period can be up to several months. There is no information on specific larval dispersal and recruitment processes; however, it appears that larval development occurs offshore, in similar ways to other shallow-water portunid crabs (Lee *et al*., 2005).

Epibenthic life stages: Megalopae are thought to settle in structurally complex substratum of shallow rocky shores (Lee *et al.*, 2004); hence, juvenile *N. puber* are commonly found in the lower intertidal zone on rocky shores (Norman 1989). Having the ability to actively select substratum, juveniles will relocate to suitable substrata if necessary, but they do rely on hydrodynamic processes for initial settlement (Lee *et al.,* 2004). Maturity causes an ontogenetic shift in habitat, with migrations between inshore and offshore habitats (Silva *et al.,* 2014). Commonly inhabiting rocky or stony shores, adult *N. puber* is found in the infra-, circa- and sublittoral zones (Choy 1988, Norman and Jones 1992), probably due to its limited tolerance of aerial exposure (Johnson and Uglow 1985). *N. puber* is generally found in waters down to 80 m in depth. Gravid females exhibit stronger migratory behaviour, and, therefore, more commonly inhabit subtidal habitats (Norman and Jones 1992). The species will readily enter the intertidal zone on high tides to feed (Silva *et al.,* 2008, 2010, 2014).

Habitats:
- Juveniles – *intertidal & subtidal zone*
- Adults – *intertidal & subtidal zone*
- All substratum – *particularly rocky*

Behaviour

Epibenthic life stages: Necora puber is a highly solitary and aggressive species. Agonistic behaviour is present in both males and females (Smith *et al.,* 1994, Thorpe *et al.,* 1994) and occurs even in the absence of a direct resource (e.g. mate or prey item) (Thorpe *et al.,* 1994). Furthermore, individuals were equally as likely to initiate, and win, a second fight immediately after the first (Thorpe *et al.,* 1995). Fights follow general biological predictions, in that duration is inversely related to the size difference between the two crabs (Smith *et al.,* 1994). However, *N. puber* is different to other crab species in that smaller individuals will become offensive to larger opponents even after the initial displays (Smith *et al.,* 1994, Huntingford *et al.,* 1995). Smaller individuals persist longer in the presence of females, and an individual of any size is more likely to win a fight that they initiated (Huntingford *et al.,* 1995). This is evidence that motivation is the dominant resolving factor for fights, not size (Smith *et al.,* 1994, Huntingford *et al.,* 1995).

Key behavioural traits:
- Aggressive
- Solitary
- Predatory
- Scavenger
- Nocturnal
- Non-migratory

Moulting occurs between spring and autumn (Choy 1988, Bakir and Healy 1995) and is earlier in the season in males; because copulation occurs between hard-shelled males and soft-shelled females (Choy 1988). The reproductive period of *N. puber* is not as discrete, as for other crustaceans (Choy 1988), and varies spatially. Studies have reported breeding seasons beginning between February and May and peaking between May and August, respectively (Choy 1988, Bakir and Healy 1995). If males provide sufficient sperm, multiple spawning events are possible in one intermoult stage (Choy 1988). Females can store spermatophores for extended periods, thus allowing mating and gonadal development to be independent of each other (Bakir and Healy 1995).

It is generally thought that *N. puber* does not have any long-distance migrations (Kinnear and Mason 1987, Norman and Jones 1993), with movements being limited to approximately 100 m. However closer observations have identified an ontogenetic migration from infraand circa-littoral zones to deeper subtidal zones in winter (Choy 1988), which is pronounced in gravid (egg-bearing) females (Choy 1988, Norman and Jones 1993), but absent in juveniles (Norman 1989). However, little detailed information exists on seasonal migrations. In order to feed on prey high up in the intertidal zone (e.g. limpets and barnacles), *N. puber* is known to undertake small-scale diurnal migrations. Entering the littoral zone on nocturnal high tides (Silva *et al.,* 2008, 2010, 2014), this behaviour is a combination of semi-diurnal and diurnal influences.

Trophic level, predators & prey

Planktonic larval stages: Although there have been numerous studies on *N. puber* larval survival in different physical environments, there has been little focus on its feeding habits or trophic level. There is evidence, however, of dinoflagellates as selected prey items, with ingestion rates coinciding with dinoflagellate blooms in August (Fileman *et al.,* 2014). Fileman *et al.,* (2014) concluded that both pico- and nano-plankton are important components of larval *N. puber* diet. Laboratory rearing experiments on *N. puber* found that larvae did not reach the first juvenile stage when fed on a diet of *Artemia* or various diatom species (Harms and Seeger 1989). In concurrence with other decapod larvae, *N. puber* will occupy trophic levels 2-3 (primary and secondary consumers) of the marine food web, and thus act as a prey source, themselves, for numerous plankton-feeding species at higher trophic levels.

Epibenthic life stages: Juvenile *N. puber* experience extremely high levels of predation (58.5 – 99.4 % mortality year^{-1}), and as a result, can be the controlling factor of recruitment for annual cohorts (Lee *et al.,* 2006). With increasing size, *N. puber* is able to successfully fend of predators and, therefore, predation decreases. There is little information on specific predation of *N. puber*, but there is evidence of predation by the curled octopus, *Eledone cirrhosa* (Grisley *et al.,* 1996), common cuttlefish, *Sepia officinalis* (Pinczon du Sel and Daguzan 1997, Pinczon du Sel *et al.,* 2000), lobsters (Hoskin *et al.,* 2011) and the lesser black-backed gull, *Larus fuscus* (Luczak *et al.,* 2012).

Necora puber is an opportunistic, omnivorous predator (Norman and Jones 1992) and scavenger (Moore and Howarth 1996, Bremner *et al.,* 2003). This is a common feeding strategy of brachyuran crabs. It considered to be an adaptation to spatial and seasonal variability in food resources (Norman 1989, Norman and Jones 1992, Bakir and Healy 1995). For example, variations in diet have been observed between *N. puber* populations in the infralittoral, circalittoral and littoral zones (Norman and Jones 1992), as well as between soft sediment and rocky substrates (Freire and Gonzalez-Gurriaran 1995). Seasonal variations in primary food sources are not always observed (Freire and Gonzalez-Gurriaran 1995), and where present, have not yet been attributed to reproductive cycle (Bakir and Healy 1995).

Almost all intertidal taxa are predated upon by *N. puber*: including crustaceans (brachyuran crabs and barnacles) (Norman and Jones 1992), echinoderms (Freire and Gonzalez-Gurriaran 1995, Makra and Keegan 1999), bivalve, gastropod and cephalopod molluscs (Norman and Jones 1992, Freire and Gonzalez-Gurriaran 1995, Langridge *et al.,* 2007, Silva *et al.,* 2008, 2010, 2014, Langridge 2009), fish, polychaetes and sponges (Freire and Gonzalez-Gurriaran 1995), as well as algae (Norman and Jones 1992; Bakir and Healy 1995).

There are ontogenetic changes in diet with increasing size, relating to both variety and preference. An increase in fish, brachyuran, mussel, echinoid and sponge prey items was observed in one population, with decreases in foraging of gastropod egg cases and holothurians (Freire and Gonzalez-Gurriaran 1995). Although prey variety increases with size, the increase is marginal (0.26 species) and so does not show any distinct ecological effect.

The trophic level of *N. puber* has been calculated in numerous studies, and a comparison reveals a strong tidal zone gradient in trophic levels. Intertidal populations have been found to occupy a trophic level of 3.7 (Schaal *et al.,* 2008) whilst subtidal populations occupy a trophic level of 2.6 - 2.8 (Freire and Gonzalez-Gurriaran 1995, Schaal *et al.,* 2010, Vinagre and Costa 2014). Studies sampling *N. puber* from intertidal and subtidal zones found them to occupy the intermediate level of 3.2 (Choy 1986, Vinagre and Costa 2014). The presence of small fish, brittlestars and polychaetes in its di*et al*so places *N. puber* in the 4th trophic level. In addition, individuals have been found to simultaneously feed on algae, thus occupying the 2nd trophic level. The broad diet of *N. puber*, therefore, allows the species to occupy trophic levels 2-4. Evidence of *N. puber* acting as apex predator has not been documented; however, the ability of *N. puber* to occupy the 4th trophic level, combined with its abundance being high enough to warrant a commercial fishery, suggest that the species is dominant in some marine ecosystems. Refer to Loch Hyne marine reserve study under '*Role in ecosystem function and stability'* below.

Trophic levels:
- Planktonic larval stages – ***Level 2-3*** (primary & secondary consumers)
- Juvenile & adult crabs - ≥ ***Level 2*** (omnivorous consumers)

Niche competitors

Planktonic larval stages: Although there is no documented evidence on specific niche competitors of larval *N. puber*, similar to other decapod crustacean larvae it is likely that they belong to the large 'functional group' of zooplankton in temperate waters, and hence possess numerous co-existing and niche-competing species.

Epibenthic life stages: Necora puber inhabits the lower intertidal and subtidal zones where numerous other brachyuran crabs are present, such as the brown crab (*Cancer pagurus*), common shore crab (*Carcinus maenas*) and other swimming crabs (*Liocarcinus* spp.). However, the highly aggressive behaviour of *N. puber* is likely to be an advantage over other crab species. In addition, when *N. puber* enters the intertidal habitat (and fundamental ecological niche) of *C. maenas*, resource competition is avoided as *C. maenas* are better equipped to predate on softer prey items, such as crustaceans, whilst *N. puber* can handle the irregular, thicker shells of limpets (Rheinallt and Hughes 1985; Silva *et al.,* 2008). A study by Griffin *et al.,* (2008) revealed food resource partitioning between three co-existing crab species (*N. puber*, *C. pagurus* and *C. maenas*), with each species exhibiting a different prey preference. Hence, although their 'fundamental' ecological niches overlap, they have developed discrete 'realised' ecological niches, thus allowing them to co-exist. Similar resource partitioning has been observed with the swimming crab competitor, *Liocarcinus holsatus*; with *L. holsatus* feeding on fish and *N. puber* on brown algae (Choy 1986).

A study by Fahy *et al* (2008) on the *N. puber* pot fishery in Ireland, revealed that is terms of capture, the presence of *N. puber* in pots is negatively associated with the presence spider crab (*Maja brachydactyla*); probably as a result of *M. Brachydactyla* outcompeting *N. puber* in shallow water environments. In contrast, however, the presence of *N. puber* was positively associated with that of the Brown crab, *C. pagurus*; with the abundance of both species increasing with water depth. This positive relationship indicates that the two species have distinct 'realised' ecological niches, and thus are able to coexist in ecosystems.

Similar to the Brown crab, *C. pagurus*, there are invasive non-native crab species with the potential to outcompete native ones.
With regards to *N. puber* there are several non-native competitors; including the Chinese mitten crab (*Eriocheir sinensis*), Asian shore crab (*Hemigrapsus sanguineus*), and Marbled Rock crab (*Pachygrapsus marmoratus*).

Non-native niche competitors:

- Chinese mitten crab (*Eriocheir sinensis*)
- Asian shore crab (*Hemigrapsus sanguineus*)
- Marbled Rock crab (*Pachygrapsus marmoratus*)

Homarid lobsters may also compete with *N. puber* for resources, and the increased European lobster, *Homarus gammarus*, population in the No-Take Zone (NTZ) of the Lundy Island MCZ, is considered to be responsible for a decreased *N. puber* population within the NTZ (Hoskin *et al.,* 2011). Large *H. gammarus* will predate *N. puber,* and therefore out-compete, and remove, individual crabs, thus reducing the *N. puber* population. However, when the size of the two species are similar, is thought that competition will become more balanced (Hoskin *et al.,* 2011).

Role in ecosystem function & stability

As significant predators in both plankton and benthic communities, *N. puber* can manipulate productivity and structure communities in the majority of ecosystems it inhabits.

Planktonic larval stages: The planktonic larval stages represent the lowest trophic level of *N.puber*, and are commonly found in zooplankton samples. The decapod larvae planktonic community, as a whole, has been shown to be responsible for propagating climate-driven signals through the food web (Lindley and Kirby 2010, Lindley *et al.,* 2010). Furthermore, a study by Kirby and Beaugrand (2009) demonstrated that the North Sea larval decapod community enforces bottom-up control (either directly or indirectly) on commercial fish stocks of such cod, plaice and sole. Hence, Lindley and Kirby (2010) imply that understanding such interactions is important in establishing a successful ecosystem-based approach to future management of North Sea fisheries. No specific examples of *N. puber* larvae enforcing bottom-up control on commercial fish and shellfish stocks have been documented.

Potential functional roles of *N. puber* larvae:

- Propagation of climate-driven signals
- Bottom-up control of commercial fish stocks

Epibenthic life stages: By scavenging, *N. puber* can occupy the temporary niche produced by fishing disturbances (Moore and Howarth 1996; Strain *et al.,* 2012) and survive in areas of low abundances of live prey (Bremner *et al.,* 2003). Scavengers are important in marine food webs as they recycle energy back into the food web that would otherwise be sequestered in sediments.

A study focussing on *N. puber* populations surrounding mussel rafts in NW Spain found the species to be the second largest contributor to biomass in the area (González-Gurriarán 1981). *Necora puber* feeds on a very wide range of prey sources, but is more resistant to predation than other brachyurans, due to its higher aggression towards predators (Grisley *et al.,* 1996). Therefore, where *N. puber* has strong prey preference, it can exert top-down control on such a species. This may be the case in the mussel raft population where the anomuran crab, *Pisidia longicornis* constitutes 50 – 81 % of the *N. puber* diet (Freire and Gonzalez-Gurriaran 1995).

N. puber has also been documented as a significant predator of cultured scallop spat in Spain (Louro *et al.,* 2005); thus highlighting that *N. puber* can detrimentally impact commercial shellfish species and associated aquaculture growth and economy.

Smith *et al.,* (2014) who recently reviewed the keystone species of all European marine habitats did not classify *N. puber* as a keystone species. However, Silva *et al.,* (2008; 2010) revealed that *N. puber* is an effective predator of the limpet, *Patella vulgata* on rocky shores. *N. puber* was found to be able to predate a wide size spectrum of *P. vulgata*, and the study predicted that 94% of the *P. vulgata* population on rocky shores is vulnerable to *N. puber* attack. Hence, because *P. vulgata* is a keystone species, due to its algal grazing, *N. puber* can indirectly impose significant impact on rocky shore community assemblages, and subsequent ecosystem function and stability. This is an example of a deleterious trophic cascade.

A further example of a *N. puber*-related trophic cascade is in Loch Hyne, Northern Ireland. Loch Hyne was designated a marine reserve in 1981, and a study by O'Sullivan and Emmerson (2011) revealed a significant increase in *N. puber* abundance (occupying the 4th trophic level) and a simultaneous decrease in the abundance of the purple sea urchin, *Paracentrotus lividus* (occupying 2nd trophic level), since marine reserve designation, and simultaneous cessation of human exploitation. *P. lividus* is often considered a 'keystone' species on rocky shore dues to its herbivorous grazing activities. The decrease in *P. lividus* has led to a significant increase in macroalgal cover within the marine reserve (30% of shoreline was free of macroalgae in 1979, compared with only 0.91% in 2010). Direct predation on *P. lividus* by *N. puber* is considered an influential factor in the *P. lividus* population decline. There is also evidence of a trait-mediated indirect interaction between the two species, with *P. lividus* showing a habitat shift by living in boulder scree to avoid predation. Furthermore, increased macroalgal cover on the rocky shore has resulted in decreased habitat for the top shell, *Gibbula cineraria,* oyster, *Anomia ephippium* and scallop, *Chlamys varia* (all occupying 3rd trophic level), which concomitantly face increased predation from the spiny starfish, *M. glacialis.* In summary, this study of Loch Hyne marine reserve suggests a trophic cascade spanning 4 trophic levels, with significant changes to ecosystem structure and function. It also highlights that marine reserve protection is not beneficial to all species.

Finally, evidence has been provided for bottom-up control of the lesser black-backed gull colonies of the North Sea (*Larus fuscus*) by swimming crabs, including *N. puber* (Luczak *et al.,* 2012, 2013). Increase in abundance of the gull, *L. Fuscus*, coincided with that of swimming crabs. The study implicates that swimming crabs are an important food source for the gull, particularly for developing chicks; and as such the resultant nutrient flux from marine to terrestrial environments is heavily dependent on the availability of such prey (Luczak *et al.,* 2012). The authors concluded that the positive relationship between swimming crabs and the lesser black back gull provided ecosystem connectivity (marine – terrestrial) and as well influencing North Sea ecosystem structure and function. This relationship was later contested (Shamoun-Baranes and Camphuysen 2013), stating that fish contribute 80 – 90 % of *L. fuscus* diet by mass, negating the crustacean prey influence. However, this was discredited as it was shown that although consumed in smaller quantities, the crab carapace provides a valuable source of calcium for eggshells and bone development in chicks (Luczak *et al.,* 2013).

The lack of evidence for long-distance migratory behaviour in *N. puber* means that any resultant ecosystem connectivity will be weak (Norman and Jones 1993). However, stronger migrations in gravid females (Choy 1988) suggests some degree of connectivity is present.

Significant functional roles of epibenthic *Necora puber*:

- ***Top-down regulator****: Scavenges & predates wide range of prey species*
- ***Bottom-up regulator****: Of seagull populations*
- ***Community structuring****: When predating on 'keystone' species*
- ***Ecosystem connectivity****: Intertidal & subtidal; marine & terrestrial*
- ***Energy flow****: Scavenging behaviour resulting in high biomass & energy recycling*

Potential consequences of removal on ecosystem function & stability

Due to the objectives of this report, the potential ecological consequences of *N. puber* removal (or drastic change in abundance) from ecosystems will be focussed on the epibenthic life stages of this species. The prospective 'costs' to ecosystem function, stability and provision of ecological goods will be discussed in relation to the species' significant functional roles highlighted above.

N. puber belongs to a large 'functional' group of decapod crustaceans (50-60 UK species). There are, in fact, approximately 14 species of swimming crabs in the UK (family: Portunidae), of which *N. puber* is one of them. Hence, although *N. puber* is one of the more aggressive and abundant species, there is not any documented evidenced of *N. puber* fulfilling a unique role in ecosystem function and stability. Evidence is commonly related to either Brachyuran, or swimming, crabs acting as 'functional' group of species. Therefore, it is likely that another decapod crustacean could competently fill the ecological niche of *N. puber* if the species was to be removed, or drastically diminish in abundance. Such ecological niche expansion by other decapod crustaceans are likely to nullify the negative effects of *N. puber* loss on top-down and bottom-up regulation, community structuring, ecosystem connectivity and energy flow within ecosystems.

There is a commercial fishery for *N. puber* in the UK; however, they are generally caught as by-catch of other crustacean fisheries. There is evidence that *N. puber* landings are on the increase, particularly in Scotland; however, whether this related to increased fishing effort or increased *N. puber* abundance is unclear. There is suggestion that *N. puber*, which is thought to prefer warm water temperatures, is extending its biogeographical range as a result of climate change. In contrast, where local populations have been overfished, it has been noted that the shore crab, *Carcinus maenus*, is captured in pots instead *of N. puber* (Fahy *et al.,* 2008). This highlights the ability of other Brachyuran crab species to expand their ecological niche to fill the niche vacated by *N. puber*, and thus assume its functional role with ecosystems. A further example of *N. puber* removal from an ecosystem was the collapse of both the *N. puber* population and fishery in Brittany, France, during the 1980's. Catches were reduced by 94% (Wilheim and Miahle 1996). Mass mortalities of *N. puber* were reported, with research revealing that the dinoflagellate parasite, *Hematodinium* spp. was responsible (Wilheim and Miahle 1996). No knock-on effects of such a mass mortality on ecosystem function were documented; however, the *N. puber* fishery in Brittany does not appear to have recovered from the mass mortality. This highlights the potential detrimental impact of epizootic disease outbreaks within marine ecosystems.

The principle effect of *N. puber* removal from an ecosystem is the loss of ecosystem goods provided by the commercially viable fishery.

Overview of *N. puber* in ecosystem structure & function

In summary, *N. puber*, fulfils functional roles similar to that of other decapod crustaceans in ecosystem structure function and stability. However, it's highly aggressive nature may allow it to dominate over co-existing crab species, and thus occupy a slightly higher trophic level. This is evident in Loch Hyne marine reserve, Northern Ireland, where there has been a significant increase in the *N. puber* population, but not in the shore crab, *Carcinus maenus* population (O'Sullivan and Emmerson 2011). As a consequence, increased *N. puber* abundance appears to have induced a deleterious trophic cascade within the ecosystem.

Research on the ecology of *N. puber* is less than that on other decapod crustaceans, such as the Brown crab, *Cancer pagurus*, Norway lobster, *Nephrops* norvegicus and the European lobster, *Homarus gammarus*. Therefore, significant ecological roles of *N. puber* within ecosystem structure and function, and subsequent deleterious effects on removal of the species, may not yet have been discovered or documented.

Therefore, in order fully elucidate the functional role of this decapod crustacean within an ecosystem, it is highly recommended that Before-After Control-Impact (BACI) studies are undertaken to test specific hypotheses. These are essential in an environment which encompasses ‘sliding/shifting baselines’ due to human exploitation of marine species over the past millennium. Present day data must therefore be used as the ‘Before impact’ baseline.

Common spider crab (*Maja squinado*)

General biology and ecology

The common spider crab (*Maja squinado*) is the largest spider crab found in UK waters, growing up to approximately 208 mm carapace length (CL; Corgos and Freire 2006). Named in response to its long limbs, *Maja squinado* can each over 50 cm in total length. In inhabits rocky and sandy shores down to depths of approximately 100 m. It is considered a warmer water species, so is generally confined to the south-west coasts of England and Wales – the northerly limit of its biogeographic range. However, its range does appear to be extending, with populations now present on the west coast of Scotland (Hosie, 2009).

Until 2008, *M. squinado* was considered conspecific with *Maja brachydactyla*. However, morphological and genetic analyses identified them as two distinct species (Sotelo *et al.*, 2008), with *M. squinado* populations confined to the Mediterranean Sea and *M. brachydactyla* populations having an Eastern Atlantic distribution from Morocco to Scotland (Hosie, 2009). Although the distinction is important for conservation and research purposes (Sotelo *et al.*, 2008); from a functional perspective, the two species exhibit very similar ecology and biology, and therefore can be combined. Due to ambiguity between the two sibling species based on morphological features, it is common for both species to still be referred to as *M. squinado*; particularly in fisheries management (Sotelo *et al.*, 2008). Therefore, for the purpose of this report, information will be assimilated for both species and the species-complex will be referred to as *M. squinado* from here on in.

Juvenile *M. squinado* moult annually, increasing in size by a third every moult (Corgos *et al.*, 2007) up until the terminal moult, which occurs at a wide range of sizes depending on fitness (115 – 208 mm CL; Corgos and Freire 2006) where adults become sexually mature and begin annual migrations offshore to reproduce (González-Gurriarán and Freire 1994, Hines *et al.,* 1995, Carabel *et al.,* 2003, Corgos *et al.,* 2011). These migrations are not undertaken by juveniles, which instead rely upon the safety of inshore waters where they often aggregate into large 'mounds' to protect themselves from predation (Corgos *et al.*, 2010; Sampedro and González-Gurriarán, 2004; Števčić, 1971).

Maja squinado has a very broad diet of up to 100 components (Bernárdez *et al.*, 2000), but feeds commonly upon macroalgae and any surrounding animals that are sessile or of low mobility (Bernárdez *et al.*, 2000). Its predators are relatively unknown, although the reduction in predatory avoidance behaviour in post-terminal moult adults indicates there is a significant reduction in predation.

Ecological niche

Habitat & physical environment

Planktonic larval stages: Hatching of larvae in summer and autumn (Hines *et al.*, 1995) is closely linked to winter temperatures, with earlier hatching occurring when winter-spring temperature were higher (Martin and Planque, 2006). There is almost no directed research on the habitat or physical parameters of *M. squinado* larvae, with the majority of larval research focussing on growth, development, and to a lesser degree, feeding of larvae.

Hence, it is presumed that they fulfil a planktonic lifestyle similar to that of other decapod crustacean species.

Epibenthic life stages: Juvenile *M. squinado* settle in shallow (< 10 m) waters on rocky substratum throughout the summer and autumn (Freire *et al.*, 2009; Hines *et al.*, 1995). However, juveniles have been observed on sandy substratum, and telemetry studies have identified that juveniles utilise both habitats regularly, using sandy substratum for refuge and rocky substratum for feeding (Freire *et al.*, 2009).

After the terminal moult, when *M. squinado* becomes a sexually mature adult, there is a gradual ontogenetic shift in habitat use. Initially, individuals remain in rocky habitats due to its reliance for food (Bernárdez *et al.*, 2000), but exhibits a gradual movement to slightly deeper waters (10 – 15 m); however, the movement is not directionally orientated (Hines *et al.*, 1995). Subsequently, there is a defined highly directional migration, commonly during autumn, onto sandy substratum down to depths of 100 m (Carabel *et al.*, 2003; Corgos *et al.*, 2011; González-Gurriarán and Freire, 1994; Hines *et al.*, 1995). They remain in deeper waters for the duration of winter, but return to shallower waters the following spring (Hines *et al.*, 1995).

Habitats:
- Juveniles – *shallow (<10m) subtidal zone*
- Adults – *shallow & deep subtidal zone*
- Substratum – *rocky (juvenile) & sandy (adult)*

Behaviour

Planktonic larval stages: The morphology of the larval stages of *M. squinado* is similar to that of the other species studied from genus Maja (Guerao *et al.*, 2008; Paula, 1988; Rodriguez, 2002). Larval development of *M. squinado* consists of two zoeal stages and one megalopal stage and takes a total of 18 to 22 days at 18°C (Guerao and Rotllant, 2010). Details on the behaviour of the larvae are lacking, with studies concentrating on the growth and development of larvae under laboratory conditions. This is aimed at restocking the Mediterranean Sea via captive-bred individuals (Durán *et al.*, 2013). Knowledge of the general biology and ecology of wild larval populations is also non-existent.

Epibenthic life stages: Both juvenile and adult *M. squinado* are considered opportunistic predators and scavengers. They are omnivores with a very varied diet, and as such, will adapt to local food resources.

Juvenile *M. squinado* exhibit little movement during the daytime (Bernárdez *et al.*, 2005; González-Gurriarán and Freire, 1994; González-Gurriarán *et al.*, 2002). However, stable isotope analyses identified feeding in both rocky and sandy substrates, leading to the conclusion of nocturnal diurnal migrations into rocky substrates. *Maja squinado* exhibits no difference in oxygen consumption between day and night (Cerezo Valverde *et al.*, 2009), indicating the diurnal cycle is not physiological, but rather a behavioural mechanism to avoid predation (Freire *et al.*, 2009). Evidence also suggests that there is no migration between favourable

Key behavioural traits:
- Predatory
- Scavenger
- Migratory
- Aggregatory
- Gregarious
- Anti-predatory masking

habitats within juvenile populations, meaning adjacent populations remain separated (Corgos *et al.*, 2002, 2011; González-Gurriarán and Freire, 1994). The limited spatial movement of juvenile *M. squinado* lends them to being classified as sedentary.

In contrast to juveniles, adults are considered migratory. During autumn, 2-3 months after their terminal moult at 2-3 years of age, the now sexually mature crabs undergo a migration into deeper waters, up to 100 m in depth. The migrations are principally thought to be associated with reproduction. Taking anywhere between 1.3 to 13.6 days to complete (González-Gurriarán *et al.*, 2002), the timing of migration for individuals is determined not by physiological state, but by reproductive potential (Corgos *et al.*, 2006). Smaller males will migrate earlier to avoid competition by larger males for female mates (Corgos *et al.*, 2006). Due to the terminal moult in *M. squinado*, mating takes place between hard-shelled individuals. Mating is not confined to the offshore breeding grounds, as copulation has been observed in the migratory corridor (Corgos *et al.*, 2006). However the majority of the breeding season is known to occur offshore in overwintering grounds (González-Gurriarán *et al.*, 1995). The stable offshore environment increases reproductive success (González-Gurriarán and Freire, 1994) and reduces predation of larvae post-dispersal (Hines *et al.*, 1995). Main breeding season in south-west England is between July - September (Lebour, 1927); and in the UK and Ireland, only one brood is thought to be produced per year (Rodhouse, 1984). The migration is also thought to be related to adults to optimising energy resources in offshore environments, which is a too dangerous environment for juveniles due to increased predation risk (Hines *et al.*, 1995).

The following spring, adult *M. squinado* then migrate back into shallow waters (<10m); probably to take advantage of warmer water temperatures for physiological processes. Migration appears to be more common in female crabs, and this thought to be related to optimising spawning and egg/larval development and hatching (González-Gurriarán *et al.*, 1993, 2002). Hatching tends to occur in the shallow waters prior to the autumn migration back into deeper waters offshore. A study by Fahy and Carroll (2009) on Irish *M. squinado* populations revealed the migration of male *M. squinado* was less directional than that of females. All females moved predominately in the same south-eastward direction, suggesting that they were driven by external environmental stimuli.

Another key behavioural trait of *M. squinado* is strong aggregatory behaviour, classifying the species as gregarious (Sampedro and González-Gurriarán, 2004). The aggregations, commonly known as 'mounds', 'heaps' or 'pods' (Corgos *et al.*, 2010; Sampedro and González-Gurriarán, 2004; Števčić, 1971) can be very large, reaching widths of up to 300 m, and containing 1000's of individuals (Corgos *et al.*, 2010). Aggregations have only been documented at depths less than 10 m (Sampedro and González-Gurriarán, 2004). The behaviour was originally thought to only be exhibited by lower ranking individuals (juveniles and females), with males predominantly remaining solitary (Števčić, 1971). However, there are observations of single, and mixed, sex aggregations of both adults and juveniles. Although, there is little insight into the specific function of such aggregations, hypotheses include moulting, mating, breeding and spawning sites (Corgos *et al.*, 2010; González-Gurriarán *et al.*, 2002; Sampedro and González-Gurriarán, 2004). Aggregations have also been deemed a response to predation; with moulting and smaller individuals in the centre of aggregations (Sampedro and González-Gurriarán, 2004), leaving larger crabs to defend on the periphery (Števčić, 1971). Being a gregarious species, aggression is not a key behavioural trait of this species. However, some aggression has been documented between males during the mating season, probably over potential mates; and also within crab pots/creels, probably over bait (Fahy and Carroll, 2009; Rodhouse, 1984).

A final behavioural trait of all *Maja* spp., including *M. squinado*, is that of active masking (Fernández *et al.*, 1998; Parapar *et al.*, 1997). Individuals, particularly juveniles, decorate themselves with seaweed and hydroids to act as camouflage, and thus as an anti-predatory mechanism. In adults (i.e. after the terminal moult), the active masking is commonly replaced with passive colonisation of the carapace by sessile epibionts, which again acts as anti-predation via crypsis.

Trophic level, predators & prey

Planktonic larval stages: Little is known about the feeding behaviour of larval *M. squinado*, except for knowledge gained from aquaculture studies. However, in such studies, emphasis was placed on maximising growth and survival for subsequent stock enhancement, and did not reflect the natural diet of the species. Most experiments found a *Artemia* diet to be most successful (Andrés *et al.*, 2007, 2008, 2011), indicating that *M. squinado* larvae, like those of other crustaceans, are primary and secondary consumers and therefore are within trophic levels 2-3. Larvae are strongly reliant on food availability, with larval success falling rapidly after 2 – 3 days of starvation (Guerao *et al.*, 2012).

Trophic levels:
- Planktonic larval stages – ***Level 2-3*** (primary & secondary consumers)
- Juvenile & adult crabs - > ***Level 2*** (omnivorous consumers)

Epibenthic life stages: There has been no research attention on specific predator-prey relationships or rates of natural predation in *M. squinado*. However, considering the reduction in predatory avoidance behaviour in adults, it may be deduced that there is also a distinct reduction in predation threat at this life stage. In juveniles, the main predators are considered to be large epibenthic fish (Hines *et al.*, 1995), whilst the only documented predator of the adult life stage is the common octopus (*Octopus vulgaris*; Sampedro and González-Gurriarán 2004, Corgos *et al.,* 2010).

There have been few studies into the diet of *M. squinado.* The most extensive study determined that *M. squinado* (both juvenile and adult) has a highly diverse diet composed of up to different 100 components (Bernárdez *et al.*, 2000), therefore, confirming that *M. squinado* is a generalist, opportunistic feeder. Life history has very little influence over diet composition, with any changes in diet composition with size being due to habitat usage and not ontogenetic (Bernárdez *et al.*, 2000). Diet therefore largely reflects the abundance and availability of local resources and subsequently has a seasonal component due to life histories of their prey and migrations of mature individuals (Bernárdez *et al.*, 2000).

Macroalgae (*Laminaria* spp. and *Corrallina* spp.) have been noted as the dominant food source (Bernárdez *et al.*, 2000; Parapar *et al.*, 1997), both harvesting it from rocky habitats, but also from drift algae on sandy substrates (Freire *et al.*, 2009). Numerous molluscan, echinoderm, ascidian, brachyuran and crustacean species are also present in the diet, however, they are in lower quantities (Bernárdez *et al.*, 2000). It is evident that almost all prey species are either sessile or have little mobility (Bernárdez *et al.*, 2000). Thus, *M. squinado* is not an active predator and will most likely consume what is easily accessible in the immediate environment. Recent studies by Alaminos and Domingues (2008) and Domingues *et al.*, (2012) studied a range of diets on captive juvenile *M. brachydactyla*, and found that maximum growth and survival was obtained on a diet of fresh mussel, in comparison to frozen mussel, frozen shrimp, fish fillets and commercial fish pellets.

A study on a trophic food webs, placed *M. squinado* at a trophic level of 2.6 (Vinagre and Costa, 2014). Whilst this is definitive, it does not explain the variation in the diet, and therefore the broad trophic niche it occupies. Due to the high dependence on algae in studies (Bernárdez *et al.*, 2000), it occupies the 2nd trophic level of herbivorous consumer. But the consumption of various other species including polychaetes, echinoderms and molluscs means *M. squinado* can simultaneously occupy the 3rd and 4th trophic level. Considering this, the trophic level of 2.6 may indicate that although it occupies three levels (2 – 4), there is a bias towards lower trophic levels.

Niche competitors

Planktonic larval stages: Similar to other aspects of *M. squinado* ecology, there is documented information on the niche competitors of the planktonic larval life stages of this species. However, due to the planktonic life style, it is likely to a member of a large 'functional group' of decapod crustacean species within zooplankton assemblages. Hence, *M. squinado* larvae may experience numerous planktonic niche competitors.

Epibenthic life stages: Maja squinado is a generalist feeder whose diet consists of up to 100 components (Bernárdez *et al.*, 2000). It exhibits no specific food preference other than what is the most abundant source, which in most cases is algae (Bernárdez *et al.*, 2000; Freire *et al.*, 2009). Therefore it is likely, that there is very little scope for interspecific competition for food resources. Where any potential conflicts occur, *M. squinado* can either relocate or select another food source, thus partitioning the resources. In addition, *M. squinado* is the largest UK brachyuran crab, which in itself is anti-predatory feature. Furthermore, the species commonly forms large aggregations, which suggests that in such situations niche competition is non-existent. Whether there is niche competition between the two *M. squinado* sibling species has not been investigated. In addition, whether they have overlapping biogeographic ranges is unknown, probably resulting from the difficulties associated with morphologically separating the two species. There may be niche competition at biogeographic boundaries; however, it is unlikely to impact ecosystem function.

Role in ecosystem function & stability

Epibenthic life stages: Identifying the ecosystem functions of *M. squinado* is a difficult due to the weak evidence base and lack of research. The most obvious role in ecosystem function and stability is of ecosystem connectivity between shallow coastal waters and deeper subtidal environments, created by the migrations undertaken by the species each year (Carabel *et al.*, 2003; Corgos *et al.*, 2011; González-Gurriarán and Freire, 1994; Hines *et al.*, 1995).

The high percentage of macroalgae in the diet of *M. squinado* (Bernárdez *et al.*, 2000) could potentially indicate a degree of trophic pressure upon macroalgae beds; particularly during periods of aggregation. Aggregations can encompass 1000's of individuals, hence exerting an enormous amount of pressure on the local ecosystems. Due to their large size, *M. squinado*, will dominant the ecosystem during this time, potentially excluding other species; both directly and indirectly, as result of diminished resources and subsequent eviction. The aggregations commonly occur during the summer months and are temporary, only lasting a few weeks each year. It should be noted, however, that there is no empirical evidence of such top-down control to date, and Smith *et al.,* (2014) did not record *M. squinado* as a keystone species in European marine habitats.

The final functional role of *M. squinado* is the provision of ecosystems goods via a commercially-viable UK fishery. In such instances, the species may assume the role of apex predator.

The 'potential' roles of *M. squinado* in ecosystem structure and function listed below are only tentative. Such roles were gleaned from existing knowledge on the general biology and ecology of the species. As highlighted previously, research dedicated to the ecological role of the *M. squinado* species-complex is very limited.

Potential functional roles of epibenthic *Maja squinado*:

- ***Ecosystem connectivity***: *Migration between shallow & deep waters.*
- ***Top-down regulator:*** *Macroalgal diet & aggregatory behaviour*
- ***Apex predator:*** *Aggregations & provision of commercially-viable fishery*

Potential consequences of removal on ecosystem function & stability

Determining the potential consequences of *M. squinado* removal on ecosystem function and structure is difficult due to lack of evidence. Hence, the following insight is hypothetical.

M. squinado, once abundant in the Mediterranean Sea, is now rare (due to overfishing) and, as such, is currently a protected species under the UNEP Action Plan for the Mediterranean Sea. Hence, current research is dedicated to larval culture with the aim of carrying out re-stocking programmes (Rotllant *et al.*, 2014). This scenario in the Mediterranean Sea is an example of *M. squinado* species removal from an ecosystem. *M. squinado* populations diminished in the late 20th Century, however, there does not appear to be any documented evidence on the impacts of such a species loss to ecosystem function and stability. Whether this is due to lack of observed effect, or lack of research and data, is unknown. There is no routine stock assessment of *M. squinado* in the UK, hence accurate information on UK abundance and population structure does not exist. However, the UK *M. squinado* fishery appears to be increasing, possibly due to the increased insurgence of the species into inshore waters during spring and summer months. *M. squinado* is considered a pest species because in high densities they curtail other fisheries (e.g. demersal fish and lobsters; Pawson *et al.*, 2002).

Similar to other UK decapod crustaceans, it is likely that *M. squinado* belongs to a large 'functional' group of organisms, in terms of ecosystem function and stability. It is an omnivorous predator and scavenger of UK coastal waters. Its diet is very varied and will depend on local resources. It also appears to inhabit a range of physical environments. Thus, in summary, *M. squinado* does not appear to display any specialist functional traits which could not be fulfilled by another marine species. Therefore, it is expected that numerous other decapod crustaceans, and possibly fish, could competently fill the ecological niche and functional role of *M. squinado* if the species was to be removed from the ecosystem. It is unlikely that an ecosystem would suffer detrimental consequences to its function and resilience if this species was lost or significantly reduced in abundance.

With regard to the commercial fishery and loss of ecosystem goods; because *M. squinado* is generally considered a by-catch or pest species, it is likely that another large decapod crustacean species, such as the Brown crab, *Cancer pagurus*, or European lobster, *Homarus gammarus*, would fill the void with respect to a shellfish pot fishery. Particularly as *M. squinado* is thought to outcompete the commercially-valuable *H. gammarus* for bait in pots. Furthermore, the disruption caused to net fisheries by the high-density coastal insurgence of *M. squinado* may be reduced if the population was to diminish, thus allowing fishers to catch targeted fish species, rather than *M. squinado* as by-catch. Hence, loss of *M. squinado* may not be considered significantly detrimental to the provision of ecosystem goods.

Overview of Maja squinado in ecosystem structure & function

The limiting factor in determining the ecological roles of *Maja squinado* is lack of documented evidence and/or lack of research. There are also significant knowledge gaps in the species' general biology; ecology and abundance; particularly with regard to UK populations. There is insufficient knowledge on larval, juvenile and adult life stages. Current research is, in fact, is focussed on Mediterranean populations, due to the species' protected status in these waters and the incentive for re-stocking programmes. The principle areas to investigate, and thus understand, with regard to establishing the species' functional role in UK waters are the impacts of large aggregations of individuals (juveniles and adults) on the local ecosystem, and the implications of their macroalgal grazing. *M. squinado* is considered a warmer water species, with a similar biogeographic range to that of the velvet swimming crab, *Necora puber*; therefore, there are suggestions that rising sea temperatures are extending the range of both species northwards, further into UK waters. Hence, *M squinado* may become a more widespread and common species, and thus understanding its role in ecosystem function, structure and resilience is imperative.

Common whelk (*Buccinum undatum*)

General biology & ecology

The common whelk (*Buccinum undatum*) is a marine gastropod inhabiting predominantly subtidal environments (Ager 2008). Found on both hard and sediment substrates, it is common along almost all UK coastlines. It is a slow growing species, living up to 12 years and reaching maturity after 7 – 8 years (Rochette *et al.,* 2001). Eggs are contained within capsules and laid in masses of between 100 – 140 eggs (Martel *et al.,* 1986, Smith *et al.,* 2013) throughout December and January (Kideys *et al.,* 1993). After 3 – 5 months of embryonic and larval development within the capsules, juveniles hatch between April and early May (Kideys *et al.,* 1993). There has been little scientific research into the juvenile stage of *B. undatum* life history, with studies mainly focussing on the feeding and reproductive behaviour of the species.

B. undatum is both a predatory and scavenging carnivore (Himmelman and Hamel 1993), depending on the availability of local food resources. Although *B. undatum* can only travel a maximum distance of approximately 50 m a day (Himmelman 1988), they still detect, and hunt out, carrion within hours or days (Nickell and Moore 1992, Evans *et al.,* 1996).

Ecological Niche

Habitat & physical environment

*Egg stages**:*** The eggs of *Buccinum undatum* are fertilised internally then laid in capsules attached to hard substrata or algal stipes (Martel *et al.,* 1986, Himmelman and Hamel 1993, Rochette *et al.,* 1999, Valentinsson *et al.,* 1999, Morel and Bossy 2004). Capsules require low energy conditions for development; as laboratory observations have demonstrated that eggs kept in motion (i.e. torn from the substrate) will not develop (Mensink *et al.,* 2000). Larval stages develop inside a capsule rather than being planktonic; which increases the tolerance and survival of early life stages (Valentinsson *et al.,* 1999). Successful hatching occurs between 4 and 18 °C, with 100 % survival between 4 and 10 °C (Smith *et al.,* 2013). Slow development is exhibited at 0 to 2 °C with a high rate of abnormal development, whilst above 22 °C, development ceases (Smith *et al.,* 2013).

Epibenthic life stages: Buccinum undatum is found in a range of habitats including sand, mud, gravel and rock substrates (Himmelman 1988, Himmelman and Hamel 1993, Ager 2008). Feedings rates are higher on sandy substrates (Himmelman and Hamel 1993), most likely due to increased prey availability. It utilises sediment substrates to partially bury themselves to avoid mobile predators such as lobsters (Rochette *et al.,* 1999). Therefore, although *B. undatum* can be found on coarser gravel substrates and exposed rock, it is evident that the species thrives in soft sediment environments.

Whilst it can tolerate the low intertidal zone, it is predominantly found in subtidal habitats down to 1200 m (Ager 2008). Temperature is not a controlling factor in establishing an ecological niche (Morel and Bossy 2004), because the species can tolerate temperatures below freezing, and up to approximately 22 °C, leading to suggestions that it can even survive outside of its ‘natural’ temperature range (Smith *et al.,* 2013). It is a similar case for salinity, with *B. undatum* being tolerant of salinities as low as 20 PSU (de Vooys and van der Meer 2010). The tolerance of *B. undatum* to wide range of habitats and physical environments highlights its broad ‘fundamental’ ecological niche.

Behaviour

Epibenthic life stages: *Buccinum undatum* is considered a solitary epibenthic species, however, it does exhibit some aggregative behaviour around food sources and during reproduction (Hancock 1967, Rochette *et al.,* 2001). There is little interaction with conspecifics (when aggregation is not reproductive), with individuals exhibiting no aggression or territorial behaviour in high densities (Himmelman 1988). The spatial range of *B. undatum* populations is very constrained due to the slow movement of the species; hence it is often referred to as sedentary. Only travelling up to 50 m a day (Himmelman 1988), results in populations being very localised. Any migrations are small scale, and are generally associated with females finding suitable egg-laying sites (Martel *et al.,* 1986). Such movements are often facilitated by currents (Fahy *et al.,* 2000), and are dependent on the quality of egg-laying sites in feeding areas. Therefore migration strategies are considered weak and directionless (Martel *et al.,* 1986).

Reproduction in *B. undatum* causes aggregative behaviour as a result of males gathering around mature females (Martel *et al.,* 1986), and is temperature dependant (Hancock 1967; Martel *et al.,* 1986a; 1986b; Kideys *et al.,* 1993;Valentinsson 2002) . Reproduction is stimulated by cold water; and within the UK, copulation and spawning generally takes place when water temperatures fall below 10°C (Nov- Feb; Smith, 2013). Females can store spermatozoa for up to eight weeks (Martel *et al.,* 1986), during which they go in search of suitable egg-laying areas. Aggregation of females around suitable egg-laying sites is common, and as a result, egg-laying often occurs on top of previous egg masses (Martel *et al.,* 1986). Pheromones are thought to induce simultaneous spawning in groups of females (Martel *et al.,* 1986). Eggs are contained within flexible capsules, with each capsule containing up to 3000 eggs (Fretter and Graham 1985). Each female lays between 80-150 capsules. Only a small proportion of eggs (13 – 14 eggs) within each capsule undergo full development and hatch as fully-formed juveniles. The other eggs are utilised as a food source for the small number of developing embryos (Hancock 1967). Within UK waters, development takes between 2.5 - 5 months (Hancock 1967, Kideys 1993, Nasution 2003). Reproductive activities are equally common in day and night (Martel *et al.,* 1986), and there is no evidence of nocturnal or diurnal cycles in any behaviour of *B. undatum*.

Habitats:
- Eggs – *attached to physical structures*
- Adults – *subtidal zone*
- All substratum – *particularly sandy*

Buccinum undatum is a carnivorous predator and scavenger, which uses chemoreception to detect its prey. Using such mechanisms, they can locate prey at a distance of several tens of metres, but 50 m is thought to be their maximum travel distance per day (Himmelman 1988). Whilst scavenging, *B. undatum* will selectively feed on damaged or dead animals. With crustacean prey, only the muscle, gonad and gut are consumed, whilst the gills and eggs are avoided; with fish prey only the muscle tissue and eyes are consumed (Evans *et al.,* 1996). Detection of carrion via chemoreception is determined predominantly by currents, but seasonal variations in behaviour may play a role (Himmelman 1988). *Buccinum undatum* does not feed in the high temperatures of spring and summer months (Hancock 1967, Himmelman and Hamel 1993) so will not be attracted to carrion; precise reasons for this are unknown.

Buccinum undatum has been observed buried in the sediment, with just the siphon protruding (Hancock, 1967), possibly to avoid predation. Whilst under physical attack from predation, *B. undatum* has been observed to exhibit vigorous escape responses, such as rapid flight, shell rocking and foot contortions (Harvey *et al.,* 1987, Rochette *et al.,* 1996).

Buccinum undatum also exhibits kleptoparasitic behaviour. Kleptoparasitism is a form of feeding in which one species takes prey, or other food, from another species that has caught, collected, or prepared the food. Kleptoparasitism in *B. undatum* is well documented in the Gulf of St. Lawrence, Canada in relation to the starfish, *Leptasterias polaris* (Martel *et al.,* 1986, Himmelman and Hamel 1993), Although *L. polaris* is a predator of *B. undatum*, aggregations of whelks around *L. polaris* feeding on bivalves have been observed. *B. undatum* accumulate in wait either to steal the prey once the valves have been opened by *L. polaris*, or to scavenge the remains (Himmelman and Hamel 1993). This behaviour is more common in pre-laying females due to the increased energy demands of egg production (Rochette *et al.,* 2001), and is absent in juveniles or small individuals due to increased predation risk (Martel *et al.,* 1986). This kleptoparasitic behaviour has also been observed between the common starfish, *Asterias vulgaris* (= *rubens*) and *B. undatum* (Himmelman and Hamel 1993). *Asterias rubens* is a common starfish of UK waters (Budd 2008), however, kleptoparasitism between these two species in UK waters has not yet been documented.

Key behavioural traits:
- Solitary
- Sedentary
- Predatory
- Scavenger
- Kleptoparasitic

Due to the kleptoparasitic relationship with starfish, *B. undatum* does not show a strong reaction in the presence of starfish, even though it is a predator. Even though feeding is reduced in *B. undatum* under such scenarios, it is not as extensive as with other predators (Rochette *et al.,* 1999), and will only display an escape response if directly attacked (Rochette *et al.,* 1999). Lobsters, on the other hand, are known predators of *B. undatum* and are more mobile. Therefore *B. undatum* displays decreased feeding in its presence, and buries itself as an avoidance mechanism before an attack occurs (Rochette *et al.,* 1999). Such responses are magnified in populations where the associated predator is abundant, indicating some inherent or learnt behaviour, although this has yet to be determined (Rochette *et al.,* 1999).

Trophic level, predators & prey

Egg stages: Research has shown the main predator of *B. undatum* eggs to be the green (or Northern) sea urchin, *Strongylocentrotus droebachiensis* (Dumont *et al.,* 2008), which can exert large pressures on populations in areas where it is abundant. However, *S. droebachiensis* is not common in UK waters; currently only being found in coastal waters of the Shetland Isles. Isopod and decapod crustaceans are also known predators of gastropod capsules (Rawlings 1990), although any specific to *B. undatum* are unknown. The starfish, *Leptasterias polaris*, although a major predator of adults, does not actively feed on egg capsules, even when directly upon them (Dumont *et al.,* 2008).

Epibenthic life stages: Buccinum undatum has previously been defined as a predatory carnivorous gastropod mollusc (Himmelman and Hamel 1993), although other studies have categorised it as omnivorous (Garcia *et al.,* 2011) and kleptoparasitic (Morissette and Himmelman 2000). It generally considered to occupy the 3rd tropic level (1st level carnivorous consumers) of the marine ecosystem food web.

Whilst it is acknowledged that adult *B. undatum* feed upon carrion, scavenging is not considered the 'natural' primary method of feeding (Himmelman and Hamel 1993). *B. undatum* is an active predator and commonly feeds on polychaetes (Taylor 1978), urchins, seastars (Himmelman and Hamel 1993) and bivalves (Hancock 1967); the latter being consumed by forcing the valves open with the lip of its own shell (Hancock 1967). In general, feeding rates are lower with the onset of breeding in spring and remain low throughout the summer (Himmelman and Hamel 1993). Spatial variations also occur in relation to substratum, with feeding being highest in sandy sediments (Garcia *et al.,* 2011). Feeding preferences of juvenile *B. undatum* are unknown.

Adult *B. undatum* have been shown to scavenge in areas of high beam trawl damage, with the species actually indicating a preference for prey sources in such conditions (Evans *et al.,* 1996). *B. undatum* moved most rapidly towards swimming crabs (*Liocarcinus depurator*), but also fed on discarded or damaged urchins (*Spatangus purpureus*), gadoid fish and pouting, but not plaice (Evans *et al.,* 1996).

Trophic levels:

- Juveniles – potentially ***Level 3*** (carnivorous consumers)
- Adults - ***Level 3*** (carnivorous consumers)

Common predators of *B. undatum* are asteroid echinoderms such as the common starfish (*Asterias rubens*) (Thomas and Himmelman 1988, Ramsay and Kaiser 1998, Rochette *et al.,* 1999); large crustaceans such as lobsters (Thomas and Himmelman 1988, Rochette *et al.,* 1999) and crabs (e.g. *Cancer pagurus* and *Carcinus maenas*; Hancock 1967); fish (*Gadus morhua*) and elasmobranchs (*Scyliorhinus canicula*) (Hancock 1967).

Niche competitors

Epibenthic life stages: The red whelk (*Neptunea antiqua*) is a taxonomically similar species to *B. undatum*, and both are largely opportunistic feeders (Garcia *et al.,* 2011). Its inhabits the same physical environments as *B. undatum*, however, its abundance is lower and geographical distribution patchier (Avant 2003). Thus niche competition is not common.

Where populations do overlap, with potential niche restriction, examination of gut contents revealed that *N. antiqua* preferentially feeds on bivalves, whilst *B. undatum* targets polychaetes (Taylor 1978). This indicates reduced niche competition due to resource partitioning.

Buccinum undatum exploits disturbed environments, such as recently trawled areas, to scavenge for prey (Evans *et al.,* 1996). Such opportunistic behaviour allows it to fill a temporary niche void, thus reducing interspecies competition (Evans *et al.,* 1996). Although less mobile than many other opportunistic scavengers, such as fish and crustaceans (Evans *et al.,* 1996), *B. undatum* is still able to scavenge in recently disturbed habitats; however, it can take several days for it to arrive (Kaiser and Spencer 1996). It manages to exploit the resource by feeding on remains that other scavengers have missed or rejected, whilst outcompeting even less mobile species such as echinoderms and small crustaceans (Nickell and Moore 1992).

The kleptoparasitic nature of *B. undatum* is an energy efficient solution to the interspecific competition with starfish. In such a relationship, kleptoparasitism occurs in the species most able to displace the other (Hamilton 2002). In the majority of situations, this is not possible for *B. undatum* due to the predation risk on itself, but it does take advantage when the starfish itself is predated upon and therefore preoccupied (Morissette and Himmelman 2000). Where such competition results in the starfish prevailing, such as with *L. polaris* in the Gulf of Lawrence, *B. undatum* has adapted by increasing its feeding rate over winter when the asteroid is brooding and therefore does not feed (Martel *et al.,* 1986).

Role in ecosystem function & stability

Epibenthic life stages: Being a both a scavenger and predator, *B. undatum* plays a large role in energy recycling in ecosystems. With respect to its scavenging and kleptoparasitic behaviour, energy from its prey, which is commonly from fisheries activities (Evans *et al.,* 1996) and other predators (Himmelman and Hamel 1993), is redirected back into the food chain rather than being sequestered in the soft sediments. It should therefore be noted that seasonal variations in feeding of *B. undatum* will influence its role as a bioenergetic consumer and recycler, particularly during reduced feeding activities in summer months (Hancock 1967, Himmelman and Hamel 1993).

In coarse sand sediments such prey sources are more abundant, and *B. undatum* therefore contributes the most to biomass in such environments (Garcia *et al.,* 2011). Whilst *B. undatum* only contributes to the general structuring of webs by having no specialist predators or prey, the kleptoparasitic relationship with starfish may exert pressure on populations where food resources are low. *B. undatum* is not considered a keystone species.

Significant functional roles of *Buccinum undatum*:

- ***Energy flow*** *– High bioenergetic consumer, high source of biomass in coarse sand environments*
- ***Community structuring*** *– Due to scavenging, predatory and kleptoparasitic behaviours*

Potential consequences of removal on ecosystem function & stability

Buccinum undatum is a generalist scavenger and predator, occupying the 3rd trophic level of the marine ecosystem food web. Although there is only one morphologically similar whelk species in UK waters, the red whelk, *Neptunea antiqua*, it is likely that *B. undatum* belongs to a large 'functional' group of species with regards to ecosystem structure and function. There are numerous crustacean echinoderm and fish species of very similar scavenging and predatory natures, thus acting as bioenergetic consumers. Such species could conveniently fill the ecological niche of *B. undatum*, if this species was to be removed (or dramatically decline in abundance) within an ecosystem.

The commercial UK fishery for *B. undatum* represents species removal and/or change in abundance within an ecosystem; however, currently there are no statutory stock assessments to determine the impact of current fishing regimes on species abundance and population sustainability. In addition, to the best of our knowledge, there is no documented evidence on the ecological impacts of *B. undatum* harvesting to the surrounding abiotic and biotic environment. However, *B. undatum* are generally captured in pots and creels, hence indirect ecosystem effects of the physical practice of fishing are likely to be minimal.

The collapse of the once-thriving *B. undatum* fishery in the Wadden Sea, The Netherlands, during the 1970's, may have been able to provide insight into the changes in ecosystem structure and function as a result of species removal. However, there was a distinct lack of fisheries and scientific research at the time of the significant collapse. Subsequent investigations have attempted to determine the factors instigating the *B. undatum* population collapse. Potential candidates were overfishing, pollution (e.g. TBT, nitrogen and phosphorus) and siltation (de Jonge *et al.,* 1993, Cadee *et al.,* 1995, de Vooys and van der Meer, 2010). However, the overall anthropogenic exploitation of the Wadden Sea during this period was so vast that the ecosystem fundamentally changed, both abiotically and biotically (de Jonge *et al.,* 1993), and thus the specific role of the *B. undatum* demise in the ecosystem change was impossible to verify.

Due to the sedentary nature and lack of plankton life stage; dispersal, and hence, population connectivity will be very limited in *B. undatum*. Therefore, if discrete populations were to be lost, it is not likely to affect the overall metapopulation and survival of the species. In contrast, however, recovery of such lost populations may be difficult.

Overview of B. undatum in ecosystem structure & function

The overriding limiting factor in determining the role of *Buccinum undatum* in ecosystem structure, function and stability is the very limited research into tits general biology and ecology. This huge knowledge gaps is consistently referred to in published literature, and as such, is hindering implementation of suitable management strategies for ensuring species sustainability.

Recent research, however, has focused on the species' growth, reproduction, size of sexual maturity (SOM), and population genetics; however the quantity of studies are minimal (Weetham *et al.,* 2006, Smith and Thatje 2013a,b, Smith *et al.,* 2013; Palsson *et al.,* 2014, McIntyre *et al.,* 2015). A recent study by Defra was commissioned to investigate the SOM of *B. undatum* in English waters (Defra report: MF0231; McIntyre *et al.,* 2015), and thus determine whether current minimum landing sizes were suitable for protecting spawning individuals and thus create sustainable fisheries. The study found that SOM was site-specific, with significant differences between discrete populations, as well as between the sexes. Such findings highlight the need for regional research into local *B. undatum* populations (Shelmerdine *et al.,* 2007, McIntyre *et al.,* 2015).

One field of *B. undatum* biology which requires immediate attention is that of juvenile ecology. Information on juvenile habitat, behaviour and ecological niche, is negligible. Lack of knowledge on such a large proportion of a species' life cycle is hugely detrimental to our understanding of the species' role in ecosystem structure, function and stability. Such information is also critical to fishery management strategies. Finally, to best of our knowledge there are no documented studies on *B. undatum* in relation to MPAs and/or trophic cascades.

Common cuttlefish (*Sepia officinalis*)

General biology & ecology

The Common cuttlefish (*Sepia officinalis*) is a cephalopod native to UK coastlines, but is commonly found on southern and western coasts (Wilson and Bilewitch 2009). It is a bottom-dwelling species, commonly over soft sediments, in waters up to 200 m deep. Between 150-4000 eggs are laid by each female (Pierce *et al.,* 2010) on inshore grounds between March and July, attached to sheltered substrates. Upon hatching, juveniles morphologically resemble adults (Guerra 2006) and therefore do not have a distinguishable juvenile stage. They are active, opportunistic predators from hatching (Blanc *et al.,* 1998, Blanc and Daguzan 2000, Pinczon du Sel *et al.,* 2000), with approximately 40 prey species documented (Castro and Guerra 1990). *S. officinalis*, itself, prey to approximately 30 different fish and marine mammal species (Guerra 2006). The cuttlefish is usually solitary in nature; however, they do aggregate for reproduction at the end of their life (Wilson and Bilewitch 2009). In these high density aggregations, larger individuals can become aggressive and cannibalistic towards smaller conspecifics

S. officinalis experiences short (10-100 km) ontogenetic migrations in its lifetime (Rodhouse *et al.,* 2014), moving from offshore overwintering grounds to shallower coastal areas in search of suitable spawning and nursery grounds (Pierce *et al.,* 2010). The inshore migration coincides with sexual maturity, which varies between 6-14 cm mantle length (Wilson and Bilewitch 2009, Pierce *et al.,* 2010). *S. officinalis* are intermittent terminal spawners (Guerra 2006, Pierce *et al.,* 2010, Bloor *et al.,* 2013); they have a lifespan of approximately two years, after which they return to inshore waters to reproduce, and subsequently die (Wilson and Bilewitch 2009).

Ecological Niche

Habitat & physical environment

*Egg stages***:** *S. officinalis* attaches its eggs to many different structures that can provide shelter, including plants and algae, sessile animals such as tube worms, drowned trees (Guerra 2006, Neves *et al.,* 2009, Bloor *et al.,* 2013, Robin *et al.,* 2014), and anthropogenic structures such as cables, nets and traps (Blanc and Daguzan 1998, Cabanellas-Reboredo *et al.,* 2014). Furthermore, spawning grounds are commonly in coastal, low energy environments with sandy substrates (Bloor *et al.,* 2013). Although the eggs are white, the female camouflages them during laying by injecting a small amount of ink into the outer envelope of each egg (Robin *et al.,* 2014). Eggs are rarely deposited below a depth of 30-40 m (Guerra 2006, Guerra and González 2011) and development is temperature dependent (Boletzky 1983 in Guerra 2006). Salinity is also a limiting factor in the hatching of *S. officinalis*, with no hatching occurring below 23.9 PSU (Paulij *et al.,* 1990).

Nektobenthic life stages: Once hatched, *S. officinalis* is a bottom-dwelling (nektobenthic) species (Guerra 2006), being able to actively swim near the seabed. There are two hypotheses surrounding the habitat preferences of the early life stages (ELS) of *S. officinalis*. It is unknown whether sexually mature *S. officinalis* actively select suitable habitats for egg laying, thereby causing just the ELS to search for suitable habitat, or whether they select laying sites for improved development of their young, therefore allowing the ELS to remain in their natal habitat (Bloor *et al.,* 2013). Nevertheless, in many cases the egg placement provides an optimal habitat for both embryonic and ELS development. The vertical structures that eggs are attached to will provide anchors for ELS in strong currents (Guerra 2006), whilst the sandy substrate will allow burying for predator avoidance (Blanc *et al.,* 1998, Poirier *et al.,* 2004, Guerra 2006).

Habitats:
- Eggs – ***attached to structures***
- Juveniles & adults –*Subtidal zone*
- Substratum – *sandy*

In their adult stage, *S. officinalis* will inhabit various substrates throughout its life due to migration, and are found in a range of substrates from sandy and muddy bottoms (Guerra 2006) to stone and shell debris (Blanc *et al.,* 1998). Dependency on specific substrates or structural habitat decreases with size, as predation risk is decreased, negating the need to bury (Guerra 2006). Therefore *S. officinalis* becomes more mobile and habitat preference becomes increasing influenced by environmental conditions such as temperature, which will ultimately influence migrations between inshore and offshore habitats (Bloor *et al.,* 2013).

Sepia officinalis is highly tolerant of environmental variations throughout both the ELS and adult stage, exhibiting high physiological flexibility (Sobrino *et al.,* 2002). Therefore it has also been found to thrive in disturbed environments (Rodhouse *et al.,* 2014), although whether it is due to a reduction in predators or increased abundance of prey is undetermined. The species can be found in sublittoral waters and offshore down to 200 m but is more common within depths of 100 m (Wilson and Bilewitch 2009), as below 150 – 200 m, adults risk implosion from pressure on the buoyancy chambers (Guerra 2006). Growth is not influenced by salinity (Paulij *et al.,* 1990, Guerra 2006), but is dependent on temperature (Blanc *et al.,* 1998, Koueta and Boucaud-Camou 2003, Bloor *et al.,* 2013). Within 10-30 °C, *S. officinalis* will exhibit normal feeding behaviour, but outside these ranges, activity will decrease and death occurs after 2 days (Guerra 2006). Temperature also influences seasonal habitat preferences to some extent; hence, affecting migration patterns (Bloor *et al.,* 2013).

Behaviour

Nektobenthic life stages: Sepia officinalis is a nocturnal species, actively feeding at night close to the seabed. It is a highly motile species and it uses it strong swimming behaviour to capture prey, reproduce and fight with conspecifics. During the day individuals are commonly found buried in sandy sediments. *S. officinalis* is a solitary species except during mating, when males and females migrate and coalesce in shallow waters. In common with other cephalopods, *S. officinalis* can rapidly change the colour and texture of its skin. This behaviour has numerous roles, including camouflage and anti-predation; as well as communication between conspecifics, particularly during courtship and reproduction. *S. officinalis* has a range of defensive strategies, involving a large number of chromatic, textural and postural components (Hanlon and Messenger, 1996).

Key behavioural traits:
- Nocturnal
- Motile
- Ambush predator
- Solitary
- Migratory

All European populations of *S. officinalis* have documented offshore migrations during winter months, returning inshore in spring and summer to reproduce in warmer waters (Blanc and Daguzan 1999, Royer *et al.,* 2006, Pierce *et al.,* 2010, Bloor *et al.,* 2013, Cabanellas-Reboredo *et al.,* 2014, Keller *et al.,* 2014). Such behaviour has been linked to seasonal changes in temperature and photo-period (Bloor 2012, Keller *et al.,* 2014, Rodhouse *et al.,* 2014), although it should be noted that the role of temperature in spring migrations is not yet clear (Bloor *et al.,* 2013).

The behaviour of *S. officinalis* is highly influenced by learning throughout all life stages (Bloor *et al.,* 2013). Prey selection is learnt from within the egg, with preference being due to visual exposure (Guibé *et al.,* 2012). After hatching, preference is still based heavily on previous visual exposure (Darmaillacq *et al.,* 2006). Such learning continues into adult life, with lab-reared individuals remembering distasteful prey sources for up to 72 hours, selecting instead a non-preferred prey source as a result (Darmaillacq *et al.,* 2004). This is also the case for predation techniques, with adult *S. officinalis* learning to successfully attack crabs from behind after just one failed attempt from the front (Boal *et al.,* 2000). This learning behaviour has been suggested to be from olfactory responses of prey, as the behaviour cannot be learned from conspecifics (Boal *et al.,* 2000)

Such learning also affects the susceptibility of *S. officinalis* to predation. Field observations have suggested that embryonic *S. officinalis* can recognise potential predators in the late stages of development and subsequently avoid them after hatching (Guerra and González 2011), although experimental evidence is needed to test this hypothesis. Newly-hatched juveniles have also been observed improve upon avoidance behaviour, such as burial in the sediment (Poirier *et al.,* 2004). In adult life, *S. officinalis* selectively uses startle displays only on predators posing an indirect threat, resorting immediately to escape responses with larger predators (Langridge 2009). This has been identified as an innate response as it has even been exhibited in naïve juveniles (Langridge *et al.,* 2007).

Trophic level, predators & prey

Egg stages: In general there are few predators, specialist or opportunistic, of *S. officinalis* eggs, so it is not considered a major source of mortality in the egg stage (Guerra 2006). The only documented cases of direct predation were by the tompot blenny (*Parablennius gattorugine*) (Guerra and González 2011) and grey triggerfish (*Balistes carolinensis*) (Blanc and Daguzan 1999).

Nektobenthic life stages: S. officinalis is a prey source to numerous predators at both the ELS and adult stage; including elasmobranchs (Clarke and Stevens 1974, Langridge 2009, Bloor *et al.,* 2013), fish (Morte *et al.,* 1997, Blanc and Daguzan 1999, Velasco *et al.,* 2001, Langridge *et al.,* 2007, Langridge 2009), crustaceans (Bloor *et al.,* 2013) and marine mammals (Clarke and Pascoe 1985, Salman *et al.,* 2001). There are approximately 30 recorded predators of *S. officinalis* throughout its geographical range, of which extensive review can be found in

Trophic levels:
- All life stages - ≥ ***Level 3*** (carnivorous consumers)
- Occupies wide range of trophic levels
- Possible apex predator

Guerra (2006). Whilst predation mortality has not yet been quantified for *S. officinalis*, it is suggested that no fishes are specialist cephalopod predators and therefore feed opportunistically on this species (Guerra 2006).

Sepia officinalis is a voracious predator and ambusher; and as an opportunistic, carnivorous feeder, *S. officinalis* adapts its feeding to the local environment (Guerra 2006). Both ELS and adults using ambush tactics to capture approximately 40 different prey sources over 4 taxonomic groups (Polychaeta, Cephalopoda, Crustacea and bony fish) (Castro and Guerra 1990, Blanc *et al.,* 1998, Guerra 2006). An ontogenetic shift of prey preference from crustaceans to fish occurs throughout its growth (Castro and Guerra 1990, Pierce *et al.,* 2010). The ELS actively feeds predominantly on isopods and amphipods (Blanc *et al.,* 1998, Pinczon du Sel *et al.,* 2000, Darmaillacq *et al.,* 2006) within hours of hatching (Blanc *et al.,* 1998), but can, however, adapt to very low levels of prey availability and maintain normal growth rates by living of the yoke sack in the first 3-5 days (Blanc *et al.,* 1998, Guerra 2006). The shift to an increasingly fish-based diet with growth is linked to increased energy demands, as larger fish species will provide a more substantial source of energy (Castro and Guerra 1990).

Variety of prey species decreases with size of *S. officinalis* (Castro and Guerra 1990), which has been linked to the development of individual prey preference from learnt behaviour throughout the ELS (Darmaillacq *et al.,* 2006, Guibé *et al.,* 2012). *Sepia officinalis* is known to be cannibalistic, with large individuals eating smaller conspecifics in high density populations (Pinczon du Sel *et al.,* 2000, Guerra 2006, Ibáñez and Keyl 2010). This is assumed to be an energy storage strategy commonly used by cephalopod populations to react to altering conditions by increasing or reducing their abundance (Ibáñez and Keyl 2010).

Whilst there is evidence of an ontogenetic diet shift towards fish and larger crustaceans (raising it to the 4th trophic level), stable isotopic analysis could not identify any size-related differences in trophic level (Filgueira and Castro 2002 in Guerra 2006). This is because *S. officinalis* is an opportunistic predator (Guerra 2006), adapting to the abundances of prey in local environments, and so does not exert pressure on any specific food source. This, together with their voracity and complex sensory system, allows them to inhabit a range of different ecosystems. *S. officinalis* can occupy all carnivorous trophic levels throughout its life stages (levels 3 – 5). Occupation of the apex predator role in food webs is confined to specific food webs where diurnal vertical migrations occur. As *Sepia officinalis* is less energetically expensive with depth than the fish species it competes with (Guerra 2006), it allows them to exploit the migrations and occupy the top trophic level. Conversely, large individuals have been found to revert to lower trophic levels through cannibalism, although this is not common (Ibáñez and Keyl 2010).

Niche competitors

Nektobenthic life stages: Competition appears more intraspecific than interspecific in *S. officinalis*, with the solitary lifestyle and density-dependent cannibalism in the species reinforcing this (Ibáñez and Keyl 2010). In other environments, small fish have the potential to compete with *S. officinalis* for food resources (Langridge 2009). Population expansions in *S. officinalis* on the Sahara Bank (West Africa) have been linked to the overexploitation of Sparidae fisheries in the area (Balguerías *et al.,* 2000), indicating potential for niche competition where such species interact. However, the very limited number of documented cases of interspecific competition could be associated with the broad diet and high mobility of *S. officinalis*, thus allowing it to avoid such circumstances.

In UK waters, *S. officinalis* shares an identical distribution to the closely related elegant squid (*Sepia elegans*) (Wilson 2007, Wilson and Bilewitch 2009) and also shares a very similar diet, suggesting potential for niche competition (Castro and Guerra 1990). However, the two species differ in their variety and proportions of prey types diet (Castro and Guerra 1990), suggesting that the two species occupy restricted ecological niches within their fundamental niche, in order to avoid direct competition for resources. This hypothesis is supported by the theory that spatial segregation of the two species avoids competition (Guerra 1985).

Role in ecosystem function & stability

Nektobenthic life stages: According to a large scale review of cuttlefish (Rodhouse *et al.,* 2014), Sepiidae were ranked as having the highest potential for ecological importance of all cuttlefish. However, there was little elaboration on the factors influencing that rank, as there is a distinct lack of knowledge regarding the ecological and functional roles of *S. officinalis*. The species does not exhibit any influence on habitat structure or engineering as it predominantly lives in the water column. Although *S. officinalis* can occupy the role of apex predator in a food web, this is restricted to shallow water environments where diurnal migrations occur (Guerra 2006).

S. officinalis has no specialist predators, and there is no direct evidence of top-down control in cephalopods in general (Rodhouse *et al.,* 2014). This is probably related to their intricate anti-predatory mechanisms (i.e. camouflage and ink secretion) However, in other cephalopod species, population stability has been linked to fluctuations in predators (Rodhouse *et al.,* 2014). In South Australia, the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) has learnt specialist techniques to predate giant cuttlefish (*Sepia apama*), including specific herding and the extraction of toxic ink and calcareous cuttlebone before consumption (Finn *et al.,* 2009). Such well-evolved feeding behaviour indicates that *T. aduncus* is reliant upon *S. apama* as a regular food source and therefore experiences bottom-up control. Although dolphins are known predators of *S. officinalis* in UK waters (Clarke and Pascoe 1985), there are no documented cases of specialist feeding behaviour.

The *S. officinalis* population expansion on the Saharan Bank (Balguerías *et al.,* 2000) may shed some light on the potential for bottom-up control on *S. officinalis* populations. The fisheries expansion in the area led to a high level of discards, including that of *S. officinalis*. As cephalopods are known to have a high discard survival rate, then it is possible that *S. officinalis* could exploit the scavengers feeding on surrounding discards. Balguerías *et al.,* (2000) determined that, in fact, increased discard rates did play an important role in the population expansion of *S. officinalis*; hence this may provide evidence of *S. officinalis* populations being limited by the abundance of their prey. In summary, change in the faunal composition of the Sahara Bank communities show that major ecological perturbations, such environmental shifts or imposed effects such as commercial fishing, may have a significant impact on *S. officinalis* and other cephalopod populations (Boyle and Boletzky 1996).

Currently, the primary functional role of *S. officinalis* in ecosystem function and structure is considered to be energy flow and transfer. The species is highly active, grows rapidly and expends high amounts of energy per reproductive effort. It also has a very short life span. In order to meet its energetic needs, *S. officinalis* is a voracious opportunistic predator, consuming a wide variety of prey species. It, therefore, fulfils the significant functional role of major bioenergetic consumer (Guerra, 2006), which in turn contributes to the general overall structuring of food webs (Denis and Robin 2001).

Although, *S. officinalis* belongs to a small taxonomic group (Order: Sepiida) of UK representatives, it's broad opportunistic carnivorous feeding behaviour over a wide range of prey species, habitats and trophic levels (Levels 3-5), lends itself to belonging to a large ' functional' group of organisms. Other organisms in this functional group may include numerous carnivorous crustaceans, fish and mammals. There is also no documented evidence of *S. officinalis* being classified as a 'keystone' species, hence supporting the hypothesis that the species belongs to a large functional group of organisms.

Significant functional roles of *Sepia officinalis*:

- ***Energy flow****: High bioenergetic consumers*
- ***Community structuring****: Food web structuring via wide variety of prey species*

Potential consequences of removal on ecosystem function & stability

S. officinalis is a short-lived species (2 year lifespan), and as such, may be susceptible to large inter-annual fluctuations in abundance (Piatkowski *et al.,* 2001, Rodhouse *et al.,* 2014). However, there is no documented information on the knock-on effects of such variations in abundance on ecosystem function and stability. As mentioned above, it is likely that *S. officinalis* belongs to a large functional group of organisms; hence it is probable that species within the group, such as fish, could rapidly fill the vacant ecological niche of *S. officinalis*, thus offsetting any potential detrimental effects to ecological structure and function due to diminished *S. officinalis* populations.

There are extensive knowledge gaps in all aspects of *S. officinalis* biology and ecology, hence detailed valid discussions on the potential consequences of *S. officinalis* removal on ecosystem structure and function are not possible. Such knowledge gaps and research priorities are discussed in the section below.

Overview of *S. officinalis* in ecosystem structure & function

The increasing importance of *S. officinalis* as a commercial fishery in the UK raises concerns that limited knowledge of its functional roles in ecosystem structure, function and stability, may impede implementation of suitable management strategies for the sustainability of this species, including MPA designation. The UK fishery in the English Channel targets both offshore and inshore populations. Inshore populations are composed of reproducing and spawning *S. officinalis* hence removal of these individuals may substantially impact *S. officinalis* populations, which in turn may influence ecosystem structure and function. Currently, there are no routine stock assessments of the *S. officinalis* fishery in the UK; therefore our knowledge of the impact of such a fishery, and change in *S. officinalis* abundance, on ecosystem stability is non-existent. Particular issues arising in relation to assessment and management include stock identification, variability in abundance (and how to predict it) and prevention of damage to spawning areas (Rodhouse *et al.,* 2014). From a general perspective, however, it can be noted that humans are acting as apex predators, and thus, exerting significant top-down control on a species which has few natural predators. The ‘sliding baseline’ phenomenon in marine ecosystems means that any present day conclusions on the ecological impact of the *S. officinalis* fishery (hence, removal of the species) will be anecdotal, and not scientifically robust. As such, new studies utilising present-day information as baseline data need to be implemented.

However, scientists and fisheries stakeholders are realising the requirement to expand our knowledge of cephalopod ecology, in general, within ecosystems, and this is discussed in detail in the recent reviews of Robin *et al.,* (2014), Rodhouse *et al.,* (2014) and Vidal *et al.,* (2014). Recent developments on *S. officinalis* ecology, however, include biomass modelling for stock assessments (Gras *et al.,* 2014), study of home range data and species distribution models for MPA assessment (in Portuguese waters; Abecasis *et al.,* 2014), microsatellite markers for population genetics (McKeown and Shaw 2014), requirements of hatchlings and juveniles in *S. officinalis* aquaculture (Sykes *et al.,* 2014), mitigation of egg loss due to fishing activities (Melli *et al.,* 2014), and tracking via acoustic telemetry (Bloor *et al*., 2013). All such studies contribute to further enhancing our knowledge of the functional roles of *S. officinalis* in ecosystem structure, function and stability.

Table 2. Summary of species' significant 'Functional roles' within ecosystems

Species	Effect of Removal on Ecosystem Function & Stability								
	Keystone species	Bottom-up regulator	Top-down regulator	Apex predator	Bioturbator	Biogenic engineer	Community structuring	Ecosystem connectivity	Energy flow
Langoustine *Nephrops norvegicus*	●	●			●	●	●		●
European lobster *Homarus gammarus*	●		●	●			●		
European spiny lobster *Palinurus elephas*			● ★				● ★	● ★	
Velvet swimming crab *Necora puber*		●	●				●	●	●
Spider crab *Maja squinado*			●	●				●	
Cuttlefish *Sepia officinalis*							●		●
Whelk *Buccinum undatum*							●		●

★ ; Potential functional roles - low population levels restricting current ecological impacts; lack of research

Table 3. Summary of the potential effects of species removal on ecosystem function and stability

Species	**Effect of Removal on Ecosystem Function & Stability**								
	Keystone species	Bottom-up regulator	Top-down regulator	Apex predator	Bioturbator	Biogenic engineer	Community structuring	Ecosystem connectivity	Energy flow
Brown crab *Cancer pagurus*	?	~	~	✓	N/A	~	~	~	N/A
Langoustine *Nephrops norvegicus*	✓	~	?	~	✓	✓	✓	N/A	✓
European lobster *Homarus gammarus*	✓	~	✓	✓	N/A	N/A	✓	~	N/A
European spiny lobster *Palinurus elephas*	?	?	?	?	N/A	N/A	?	?	~
Velvet swimming crab *Necora puber*	?	~	✓	?	N/A	N/A	✓	~	~
Spider crab *Maja squinado*	?	?	?	?	N/A	N/A	~	~	?
Cuttlefish *Sepia officinalis*	?	~	?	?	N/A	N/A	~	?	~
Whelk *Buccinum undatum*	~	?	?	?	N/A	N/A	~	N/A	✓

Key	**Risk of effect**
~	Low Risk
?	Unknown or Undescribed Role
✓	Potential Risk **(Refer to text)**
N/A	Not Applicable

Gap analysis

Successful management and conservation of the marine environment is challenging; due to the often opposing forces of provision of ecosystem goods and services, and that of restoring and protecting ecosystem structure and function. Lack of robust scientific evidence is a common discourse when addressing policy and management strategies; hence this ‘Gap Analysis’ section highlights the significant voids in our current understanding of the ecological niche, and subsequent role in ecosystem function and stability, of the 8 commercial shellfish species targeted in this review. Emphasis will be placed on the potential impact of species’ removal from ecosystems; and, where relevant, the role of marine protected areas (MPAs)

Brown crab (Cancer pagurus)

Cancer pagurus is one of the better-studied decapod crustaceans; with knowledge of various ecological and functional traits; including reproduction, predators and prey, niche competitors, migrations, parasites and disease, and population genetics. However, knowledge gaps do exist that may be hindering management and preservation of UK brown crab populations. For example, little information exists on the larval dispersal and population connectivity of *C. pagurus*. A spatio-temporal understanding of larval dispersal is fundamental to effective MPA implementation, but currently is scientifically very limited (Sale *et al*., 2005; Pelc *et al*., 2010). This is probably due to the difficulty in obtaining empirical field data on larval distribution transportation. Field sampling for species-specific planktonic larvae can be extremely expensive and time-consuming

Furthermore, to the best of our knowledge there are no documented studies that assess the consequences of adult *C. pagurus* removal from ecosystems. This aspect of ecological knowledge is not only pertinent for evaluating ecosystem function, but also for evaluating fisheries impact and sustainability. The fact that adult *C. pagurus* may be able to assume the role of apex predator suggests that trophic cascades and detriments to ecosystem function and stability are feasible. A critical question to answer is: what level of *C. pagurus* removal can ecosystems withstand before detrimental impacts on ecosystem function and stability are instigated? In concurrence with red deer acting as apex predators in terrestrial environments, it may be necessary to manage and restrict apex marine predator populations in order to enhance species biodiversity and ecosystem stability.

Another important factor to consider when assessing the ecological niche and functional roles of marine species is the high degree of spatio-temporal variation within marine ecosystems. For example, *C. pagurus* populations in the English Channel are unlikely to function in the same way as those located on the north east coast of England. Population genetics have, in fact, confirmed a distinction between these two areas (Bannister, 2009). In addition, the populations will vary from year-to-year. This highlights the requirement for local and regional scientific assessments and investigations, with longevity of several years, in order to obtain robust data and knowledge. Such information is pivotal to successful marine management.

The Lundy Island No-take zone (NTZ) highlights the intricacies of marine ecosystem structure and function. In the NTZ, where human fishing activities are prohibited, several studies have found *C. pagurus* not to increase in abundance since implementation of the fishing ban (*per obs*; Hoskin *et al.,* 2011, Davies *et al., in prep*). There appears to be a negative relationship between the abundance of *C. pagurus* and the abundance of European lobster, *Homarus gammarus* within the NTZ. The *H. gammarus* population boom has coincided with a decrease in the *C. pagurus* population, possibly due to ecological niche competition. This scenario highlights the complexity of ecosystem functioning and subsequent management strategies; and thus reiterates the need for robust scientific research within the MPAs.

European lobster (*Homarus gammarus*)

The principle outcome of this review on the ecological niche and functional role of *H. gammarus* is that the species appears to be the dominant decapod crustacean in UK waters. Adult H. gammarus can out-compete potentially co-existing species, such the Brown crab, *C. pagurus* and the Velvet swimming crab, *N. puber*; and as a result, *H. gammarus* is commonly the apex predator in UK benthic marine ecosystems.

However, our in-depth understanding of such functional roles of this species is very limited, and the majority of information is inferred from the well-studied (but closely-related) American lobster, *H. americanus*. There are currently significant gaps in our general ecological knowledge of *H. gammarus* which are hindering interpretation of present day observations and findings. The key knowledge deficits are larval dispersal and settlement processes, the ecology of early-benthic phase (EBP) and juvenile lobsters, and the accurate status of adult *H. gammarus* populations.

Similar to the Brown crab, *C. pagurus*, understanding larval dispersal and settlement in *H. gammarus* is an important factor in deciphering population connectivity and location of nursery grounds. In addition, improving our knowledge on the ecology of EBP and juvenile lobsters is imperative, because successful settlement and recruitment of EBP lobsters is thought to drive the demography of adult lobster populations. We currently have no documented evidence on sightings of EBP and juvenile lobsters, and as such, nursery habitats remain elusive. This is despite the dedicated LEAR (Lobster Ecology And Recruitment) project during 1998-1999 to locate such nursery sites. Whether it is because EBP and juvenile lobsters are so scarce or, in fact, studies have been looking in the wrong place, is unknown. Future research effort should be dedicated to filling this important knowledge gap.

Furthermore, data on the status of adult *H. gammarus* populations should be treated with caution, particularly within MPAs, because as both scientists and fisheries stakeholders are aware, passive sampling via capture in pots is very discriminate (i.e. pot-bias); with catchability being influenced by numerous internal and external stimuli; and hence, not truly reflecting the population status. This predicament is common to all pot-caught shellfish species, including those within the present review.

The Lundy Island NTZ has provided insight into the repercussions of prohibiting *H. gammarus* fishing activities. The boom in *H. gammarus* abundance within the NTZ may have significant implications for ecosystem structure, function and stability, due to the overriding presence of *H. gammarus* as apex predator. Initial studies suggest that there may be detrimental consequences to the co-existing species in the NTZ, such as to the Brown crab, *C. pagurus*, and the Velvet Swimming crab, *N. puber*. This highlights the potential for trophic cascades within the NTZ; and, as such, corresponding indirect detrimental impacts on ecosystem function and stability. However, at present, such hypotheses have not been fully tested. Similar to terrestrial ecosystems, marine ecosystem dominance by a single apex predator, such as *H. gammarus,* may not always be beneficial to species biodiversity and preservation of ecosystem function and stability. Deleterious trophic cascades may diminish the value of MPAs as a conservation tool; therefore research into this field of ecology must be treated as a priority. Determining the *H. gammarus* population level at which an ecosystem remains stable and resilient should be the primary focus of study.

Fortunately, there is ongoing research interest into *H. gammarus* biology and ecology. For example, in-depth research into the abundance, interaction and movement of a *H. gammarus* population has been carried out by Skerritt (2014), in conjunction with Newcastle University, Northumberland IFCA, Natural England and the MMO. Key findings included observations of high site fidelity; catchability differences between sexes (leading to female-skewed density estimates); the presence of *H. gammarus* significantly lowering the catchability of crab species; and male *H. gammarus* exhibiting significantly larger home-ranges than female *H. gammarus*, potentially leading to increased catchability of males in baited pots. The fundamental ecological research carried out as part of this study has furthered our understanding of *H. gammarus* population dynamics and of the species' behaviour.

Norway lobster (Nephrops norvegicus)

Despite significant knowledge on the general ecology of *Nephrops norvegicus*, there are still extensive knowledge gaps in our understanding of the role of *N. norvegicus* in ecosystem structure and function. This is of concern given that *N. norvegicus* is classified as a '*keystone*' species. The predominant limiting factor in such research is the lack of unexploited *N. norvegicus* populations to act as control sites for study. Without robust comparisons between control (i.e. unfished) and experimental (i.e. fished) populations, hypotheses cannot be rigorously tested. Some studies have attempted such comparisons by using un-fished wrecks as control sites (Hall *et al.,* 1993; Ball *et al.,* 2000), but doubt has been cast over the validity of such research. Significant effort must therefore be invested into determining appropriate experimental and control sites for studying the role of *N. norvegicus* in ecosystem function and stability.

Research on *N. norvegicus* is also hampered by the fact that the species' behaviour under laboratory conditions is not always comparable to that of it in its natural environment; particularly with regard to burrow construction (Farmer 1974b). Furthermore, attempts to understand the role of *N. norvegicus* burrows in sediment-water fluxes of ecosystems have concluded that it is a highly complex and variable process to measure and quantify (Aller

1980; Hughes and Atkinson 1997; Gilbert *et al.,* 2003); and as such, extensive replication in space and time is required to fully understand the ecological implications (Hughes *et al.,* 2000).

The closest example of a using a MPA reference area to study *N. norvegicus* is the annual spatio-temporal closure (3 months per year) of a section of the Porcupine Bank *N. norvegicus* fishery ground in the Irish Sea (Stokes and Lordan 2011). The area is primarily closed and surveyed each year to gain data on the residing *N. norvegicus* stock. The closure is not implemented to investigate the effects of fishing cessation on *N. norvegicus* population structure and ecosystem function; hence, the annual surveys do not encompass comparisons between the fished and unfished areas. Nonetheless, the 2012 survey did include underwater video surveys to gather ecological data on *N. norvegicus* burrow density, and coexisting macro-benthic species (Lordan *et al.,* 2012). This limited spatio-temporal closure and survey of *N. norvegicus* fishery stocks highlights the potential of MPAs and/or references areas in gaining valuable information on the ecology of *N. norvegicus*.

Spiny lobster (*Palinurus elephas*)

In summary, there are vast knowledge gaps in not only the general biology and ecology of the species, but also the role of *Palinurus elephas* in ecosystem structure and function. This is mainly a result of the scarcity of individuals for study. Such scarcity is thought to be a consequence of overexploitation and environmental change. Knowledge gaps that are particularly pertinent are those associated with the spatio-temporal location of wild populations or individuals (especially in the UK), as well as overall knowledge of early benthic phase (EBP) and juvenile ecology. In order to facilitate population recovery and discover the role of *P. elephas* in ecosystem structure and function, knowledge of suitable nursery grounds is vital. There is ongoing research into *P. elephas* biology, ecology and aquaculture; however, it is primarily focused on Mediterranean, not UK, populations. The only current UK research project appears to be the tagging of *P. elephas* within the Isles of Scilly MCZ, in order to monitor local populations. The project is being managed by the Isles of Scilly IFCA, and is currently in its 3rd year (2015).

Despite the now limited *P. elephas* fishery in UK waters, the population does not appear to be recovering. This may be due to lack of research and data, or possibly the population size being below the effective threshold required for net growth. In addition, it is possible that *P. elephas* is currently subordinate to co-existing clawed decapods crustaceans (e.g. *C. pagurus* and *H. gammarus*), and unable to establish its own ecological niche. Research into assessing the interspecies competition endured by *P. elephas*, would not only help determine factors inhibiting population revival, but also gain insight into the species' role in ecosystem structure and function. It is acceptable to assume that the majority of UK benthic ecosystems are currently functioning without (i.e. removal) of *P. elephas*, therefore establishment of a sustainable un-fished population for comparison studies is pivotal to robust research into the ecology of this species.

MPA designation within the Mediterranean Sea has reported increases in abundance, biomass and size of *P. elephas* within protected areas (e.g. Goni *et al.,* 2010, Follesa *et al.,* 2008, 2009). However, the effect of MPA designation on the long-term recovery of *P. elephas* populations is currently unknown, and is hindered by lack of knowledge on larval dispersal, subsequent nursery grounds, and thus population connectivity. Furthermore, there is has been no research conducted on the indirect effects of increased *P. elephas* abundance within MPAs, such trophic cascades and changes in functional (and bio) diversity, which may ultimately affect ecosystem structure, function and resilience. A study by Diaz *et al* (2005), however, recorded increased levels of juvenile *P. elephas* predation within the reserve, probably as a result of the simultaneous protection afforded to the predatory fish within the MPA. Such findings highlight the necessity for thorough and long-term monitoring of MPAs for determining the role of *P. elephas*, in ecosystem function and stability.

Spider crab (*Maja squinado*)

Similar to the spiny lobster, *Palinurus elephas*, the limiting factor in determining the ecological roles of the spider crab, *M. squinado,* is lack of documented evidence and research on the species as a whole. There are significant knowledge gaps in the species' general biology; ecology and abundance; particularly with regard to UK populations of *M. squinado* (now classified as *M. brachydactyla*). There is insufficient knowledge on the ecology of all life stages; larval, juvenile and adults. Current research is, in fact, is focussed on Mediterranean populations, due to the species' protected status in these waters, and the subsequent incentive for Mediterranean re-stocking programmes.

With regard to establishing the species' functional role in UK waters, the principle areas to study, and thus understand, are the impacts of large aggregations of *M. squinado* individuals (both juveniles and adults) on the local ecosystem, and the corresponding implications of their intense macroalgal grazing on community structure and function.

M. squinado is considered a warm water, temperate species, with a similar biogeographic range to that of the velvet swimming crab, *Necora puber*. Therefore, there are suggestions that rising sea temperatures are extending the range of both species northwards, further into UK waters. Hence, *M squinado* may become a more widespread and common species; and thus understanding their roles in ecosystem function, structure and resilience is imperative.

Velvet swimming crab (*Necora puber*)

N. puber fulfils functional roles similar to that of other UK decapod crustaceans in ecosystem structure function and stability. However, it's highly aggressive nature may allow it to dominate over co-existing crab species, and thus occupy a slightly higher trophic level. This is evident in Loch Hyne marine reserve, Northern Ireland, where there has been a significant increase in the *N. puber* population, but not in the shore crab, *Carcinus maenus* population (O'Sullivan and Emmerson 2011). As a consequence, increased *N. puber* abundance appears to have induced a deleterious trophic cascade within the ecosystem. Therefore, although *N. puber* has not been classified as a keystone species, it has the potential to influence ecosystem structure and function. This is further highlighted by Silva *et al.,* (2008; 2010), who revealed that 94% of the limpet, *Patella vulgata,* population on rocky shores is vulnerable to *N. puber* predation. The limpet, *P. vulgata,* is a keystone species; therefore, *N. puber* can indirectly impose significant impact on community assemblages, and subsequent ecosystem function and stability.

Research on the ecology of *N. puber* is less than that on other decapod crustaceans, and this may be unjustified given the potential for this decapod to influence ecosystem structure and function. Further research into all aspects of the ecology of this species, including larval dispersal, EBP and juvenile ecology, population genetics, and parasites and pathogens, will promote our ecological understanding of this decapod crustacean, and possibly reveal additional roles of *N. puber* in ecosystem function and stability. Subsequent studies on the effects of the species' removal from ecosystems are also pivotal to further understanding the ecology of *N. puber*.

Common whelk (*Buccinum undatum*)

The overriding limiting factor in determining the role of *Buccinum undatum* in ecosystem structure, function and stability is the very limited research into its general biology and ecology. This huge knowledge gap is consistently referred to in published literature, and as such, is hindering implementation of suitable management strategies for ensuring species sustainability.

Any recent research has focused on the fisheries science aspect of *B. undatum*; and as such there are published articles and reports on the species' growth, reproduction, size of sexual maturity (SOM), and population genetics; however the quantity of studies are minimal (Weetham *et al.,* 2006, Smith and Thatje 2013a,b, Smith *et al.,* 2013; Palsson *et al.,* 2014, McIntyre *et al.,* 2015). A recent study by Defra was commissioned to investigate the SOM of *B. undatum* in English waters (Defra report: MF0231; McIntyre *et al.,* 2015), and thus determine whether current minimum landing sizes were suitable for protecting spawning individuals and thus create sustainable fisheries. The study found that SOM was site-specific, with significant differences between discrete populations, as well as between the sexes. Such findings highlight the need for regional research into local *B. undatum* populations (Shelmerdine *et al.,* 2007, McIntyre *et al.,* 2015).

One field of *B. undatum* biology which requires immediate attention is that of juvenile ecology. Information on juvenile habitat, behaviour and ecological niche, is negligible. Lack of knowledge on such a large proportion of a species' life cycle is hugely detrimental to our understanding of the species' role in ecosystem structure, function and stability. Such information is also critical to fishery management strategies. Finally, to best of our knowledge there are no documented studies on *B. undatum* in relation to MPAs and/or trophic cascades.

Common cuttlefish (*Sepia officinalis*)

The increasing importance of *S. officinalis* as a commercial fishery in the UK raises concerns that the current limited knowledge of its functional roles in ecosystem structure and stability may impede implementation of suitable management strategies for the sustainability of this species. The UK fishery in the English Channel targets both offshore and inshore populations. Inshore populations are composed of reproducing and spawning *S. officinalis*, hence removal of these individuals may substantially impact the overall *S. officinalis* stock. Currently, there are no routine stock assessments of the *S. officinalis* fishery in the UK; therefore our knowledge of the impact of such a fishery, and subsequent change in *S. officinalis* abundance, on ecosystem function and stability is non-existent. Particular issues arising in relation to assessment and management of *S. officinalis* include stock identification, variability in abundance (and how to predict it) and prevention of damage to spawning areas (Rodhouse *et al.,* 2014).

However, scientists and fisheries stakeholders are recognising the need to expand our knowledge of general cephalopod ecology, and this is discussed in detail in the recent reviews of Robin *et al.,* (2014), Rodhouse *et al.,* (2014) and Vidal *et al.,* (2014). There is ongoing research into *S. officinalis*, and recent developments in its ecology include biomass modelling for stock assessments (Gras *et al.,* 2014), study of home range data and species distribution models for MPA assessment (in Portuguese waters; Abecasis *et al.,* 2014), microsatellite markers for population genetics (McKeown and Shaw 2014), requirements of hatchlings and juveniles in *S. officinalis* aquaculture (Sykes *et al.,* 2014), mitigation of egg loss due to fishing activities (Melli *et al.,* 2014), and tracking via acoustic telemetry (Bloor *et al*., 2013). All such studies are vital in enhancing our knowledge of the functional roles of *S. officinalis* in ecosystem structure, function and stability. In contrast to the sedentary nature of benthic decapod crustaceans, the mobility of *S. officinalis* creates additional hurdles to overcome when studying and evaluating its role in ecosystem structure and function.

Summary of common knowledge gaps

All species targeted in this review would benefit from increased research effort into their roles in ecosystem function and stability. The most common areas of requiring dedicated study are those of larval and juvenile ecology. Knowledge gaps in the ecology of these life stages may be bottlenecks in managing the species as whole. This is pertinent in decapod crustaceans, where planktonic larval life stages are responsible for dispersal, gene flow and population connectivity within species who exhibit sedentary behaviour in the adult life stages. Understanding population connectivity is pivotal in optimising management strategies and subsequent sustainability of a species. The difficulty in field sampling larval and juvenile crustaceans, as well as young cuttlefish, is most likely responsible for the lack of research in this aspect of ecology.

Another factor hindering our enhancement of understanding benthic ecosystem function and stability is the ‘unnatural’ behaviour commonly expressed by species under laboratory conditions. Therefore, research effort is required to reassess the potential of using *in situ* field sampling sites for such studies. Advances in technology, as well as implementation of MPA reference areas, may provide solutions to this research dilemma.

Addressing the Knowledge Gaps

There are a number of common themes which can be used to address the ecological knowledge gaps of the species identified. Firstly, there is the potential use of MPAs and/or experimental areas for scientific research. Such areas overcome the problems associated with ‘unnatural’ laboratory studies, but at the same allow for species manipulation. To study the potential effects of removing particular species on ecosystem structure and function, control and experimental sites will be required for comparison; and in some scenarios may require a manual reduction in a species’ abundance. Furthermore, MPAs and experimental areas allow for study over numerous trophic levels within an ecosystem, and this is fundamental for studying overall ecosystem structure and function. Indirect effects of species removal (or significant change in abundance), such as trophic cascades, are often inconspicuous and therefore require robust monitoring strategies to elucidate their presence.

Successful implementation of MPAs and experimental areas for research purposes requires careful and thorough consideration. The primary objective is to determine clear and testable research hypotheses. For example, is the intention to investigate particular species or overall ecosystem function? Overall ecosystem function will require a multi-species approach spanning several trophic levels. It will also overcome monitoring bias and prejudice towards particular species or trophic levels. The agreed upon research hypotheses will influence MPA location, size and subsequent monitoring strategies. Monitoring strategies are critical in collecting robust scientific data.

A commonly overlooked aspect of monitoring strategy design is assessment of ‘experimental power’. Experimental (or statistical) power analysis determines the number of samples (and sampling sites) required to statistically detect significant change. For example, if the sample size is too low, the experiment will lack the precision to provide reliable answers to the questions it is investigating. If sample size is too large, time and resources will be wasted, often for minimal gain. Experimental power analysis can be carried out by experienced statisticians and/or computational software programs. It is highly recommended to incorporate this analysis into monitoring strategy designs in order to gather robust scientific data.

Furthermore, the general design approach should be given careful consideration. MPA-type assessments, which aim to investigate site-specific effects, are typically model-based (Osenberg *et al.,* 2011). Variations on the BACI model approach are thought to be most appropriate. BACI (Before- After-Control-Impact) experiments utilise Control and Impact (’experimental’) sites which are sampled both before and after MPA establishment (or hypothesis testing). Many previous MPA monitoring programmes have neglected ‘Before’ sampling, and this has reduced the robustness and validity of data. Unfortunately, research on the Lundy Island NTZ falls into this category. ‘Before’ sampling is pivotal to monitoring programmes in the marine environment due to the phenomenon of ‘sliding baselines’.

Longevity of MPA monitoring programmes is also a highly- debated topic, but in general, 5 years should be considered the minimum. Direct effects, such as changes in species abundance, size and biomass may be observed with a few years; however, indirect effects such as trophic cascades, and overall ecosystem function and stability, are more inconspicuous and can take up to several decades to materialise (Shears and Babcock 2003, Edgar *et al.,* 2009, Babcock *et al.,* 2010). Therefore, monitoring programmes are idiosyncratic to the specific hypothesis being tested, but should be always be considered as long term commitments.

Addressing the knowledge gaps in the ecology, and subsequent ecological role of individual species, may appear daunting; particularly with regard to the larval and juvenile life stages. Field sampling and experimentation can be extremely expensive and time-consuming. However, numerous advances in technology can help overcome such hurdles. For example, with regard to larval dispersal, oceanographic modelling can simulate larval dispersal and population connectivity. Biophysical models, incorporating both physical and biological parameters, can be applied to 'real-world' systems, providing detailed information on both temporal and spatial scales (e.g. Cowen 2006, North *et al.,* 2008, Metaxas and Saunders 2009, Robins *et al.,* 2012). Sophisticated biophysical models can even generate data based on past, present and future hydrodynamic and biological conditions. The data can identify potential settlement sites, and hence nursery grounds, for decapod crustaceans. As a consequence, *in situ* field sampling effort could be focussed on such sites of interest in order to validate modelling results and gain valuable empirical data. This would significantly reduce the cost (both time and monetary) of otherwise extensive field studies. Biophysical modelling has been successfully used to locate nursery grounds of the American lobster, *Homarus gammarus* (e.g. Incze and Naimie 2000, Harding *et al.,* 2005, Xue *et al.,* 2008, Chasse and Millar 2010; Incze *et al.,* 2010), and more specifically, to model larval dispersal from MPAs (Cudney – Bueno *et al.,* 2009, Corell *et al.,* 2012)

Population genetics is another expanding field of expanding research and technology, and as such can provide valuable information on larval settlement, parentage, migrations and population connectivity. Studies on gene flow and genetic variation may also help identify physical barriers in the marine environment, which lead to population isolation. Continuing development of sensitive probes and techniques can discern population segregation and/or connectivity on local and regional scales; which can help overcome problems associated with the spatiotemporal variations in marine communities and ecosystems.

Underwater video is another technique coming to the forefront of marine research. Static underwater video can provide useful information on numerous biotic and abiotic factors, such species presence/absence, population levels, intra and inter-species behaviour and physical habitat. Such *in-situ* recording of observations is highly valuable for multispecies assessments, particularly at the level of ecosystem structure, function and stability. In addition, it overcomes the problem of the 'unnatural' behaviour commonly observed by species under laboratory conditions. Long-life batteries now allow for remote time-lapse photography of more than 1 month; therefore, underwater video (both baited and unbaited) is a very cost-effective method of gathering ecological data over seasonal and annual time scales. Mobile underwater video is also a very cost-effective technique of assimilating data on larger spatial scales. Towed underwater cameras can provide valuable information on the physical habitat, and thus identify potential areas of interest, such as larval settlement sites and juvenile nursery grounds.

The research field of biotelemetry is also rapidly developing. Such tagging studies are increasing in popularity due to technological improvements. Reductions in tag size and cost are allowing more individual organisms to be tagged; whilst improvements in remote tag recording methods are reducing the need for physical recapture of individuals. Both radio and acoustic transmitters can be attached as tags to individuals, and their movements recorded. Such tags are very useful for evaluating the movement and migration of organisms, particularly of highly mobile species such as the cuttlefish, *Sepia officinalis* (Bloor *et al.,* 2013) and but also of less mobile decapod crustaceans such as the European lobster, *Homarus gammarus* (Skerritt 2014). A species' home range can be determined using biotelemetry, and this is important factor in MPA design and subsequent species removal studies. Furthermore, insight into potential spawning and nursery grounds may also be gained using this technology. Sophisticated data logger-type tags are proving popular due to their ability to record and store data on both internal and external parameters, such as behaviour, spatial ecology, energetics and physiology; however, the disadvantage of this method is that the tags must be retrieved from individuals in order to download the data. Finally, a forthcoming research project by 'South and West Wales Fishing Communities Ltd' is developing and trialling an automated GPS lobster tracking methodology. Radio Frequency Identification (RFID) tags will be attached to lobsters, which will then be automatically recorded by inshore Vessel Monitoring Systems (iVMS) onboard fishing vessels. Scanning of RFID tags (with unique ID numbers) allows for tracking of individual lobsters, and logs both GPS location and time. Logged data is automatically transmitted to a database, which allows for remote data monitoring and analysis. Such a set-up produces continuous, real-time, data collection from tagged lobsters captured in pots. It also allows for automatic scanning of lobsters as part of the normal fishing operation, with minimal impediment to the fisherman. It is perceived that this new tracking technology will provide valuable ecological data, including that of lobster movement, behaviour, population structure and density.

Another current relevant research project is being undertaken in Lyme Bay Marine Protected Area (MPA), Dorset, to assess the impact of potting density on seabed biodiversity and target species within the Lyme Bay MPA. This study is being carried out by the Marine Institute Plymouth University in partnership with the Blue Marine Foundation and members of the local fishing industry. The study is gathering a wide range of data, including video images of seabed habitats and species; quantitative data on mobile species utilizing the MPA; data on target species under standardised fishing conditions; and finally an assessment of potential spill-over from control areas. *H. gammarus* is one of the project's target species. Ultimately, the study will provide valuable insight into the ecological functioning of the Lyme Bay MPA, with emphasis on shellfish potting activity and biodiversity. If this project proves successful, this collaborative research approach should be extended to other MPAs and marine ecosystems.

Evaluating ecosystem structure and function is considered integral to the ecosystem-based management (EBM) approach of the marine environment. As a consequence, there is an increasing interest in studying the functional diversity of ecosystems, and the functional roles of particular species. This allows us to determine whether species loss or gain will fundamentally change ecosystem structure, function and stability. If a species belongs to a large 'functional group' of organisms, it is unlikely that ecosystem function will significantly alter if such a species is lost, due to the fact there are numerous other species within the 'functional group' which can expand their ecological niche and absorb the niche and functional role of the absent species. The present report has highlighted that there are significant knowledge gaps in the ecological and functional roles of the 8 species included in this review, and as such we are currently unsure of the implications of such species' loss on ecosystem function and stability. Fortunately, there are numerous approaches to studying both ecosystem and species function, however, in reality community ecology is highly complex subject (Byrne *et al.,* 2014). Hence, only the approaches which are of relevance to the present review will be highlighted below.

Functional diversity is a commonly measured ecological parameter, and can be calculated using empirical data from field –based experiments (e.g. Griffin *et al* 2008, Martins *et al.,* 2012, Reiss *et al*., 2014), or broader-scale meta-analyses based on simple biological trait categorisations such as habitat, feeding method, reproductive method, life span and mobility (e.g. Bremner *et al.,* 2003, Van der Linden *et al.,* 2012, Bolam and Eggleton 2014, Darr *et al.,* 2014, Törnroos *et al.,* 2014). This relatively straight forward approach of evaluating the functional diversity is known as Biological Traits Analysis (BTA), and may provide a useful first step in preliminary assessment, and/or for novice community ecologists. Ecosystem modelling using the free 'Ecopath' software package is also an approach with increasing popularity. The package is designed to address general ecological questions as well as explore the impact and placement of MPAs (www.ecopath.org; Araújo *et al*., 2008, Guo *et al.,* 2013; Guenette *et al.,* 2014, Cornwall and Eddy 2015, Valls *et al.,* 2015).

Modelling more specific to ecological niches, known as 'environmental niche modelling' and 'species distribution modelling' is also common place and is based around computer algorithms. A relevant recent review by Reiss *et al.,* (2015) reviews the various methods and value of distribution modelling marine benthic ecosystems, and discusses its significance in marine ecosystem management.

A final research approach to consider is that of stable isotope analysis. It is considered a powerful approach for determining the specific trophic level of an organism (Jennings *et al*., 2008), as well as its position and role in ecosystem function (e.g. Friere *et al.,* 2009, Oakley *et al.,* 2014, Sokolowski *et al*., 2014, Kopp *et al.,* 2015). Naturally-occurring stable isotopes, commonly carbon and nitrogen, are quantified in organisms tissues, with subsequent analyses providing a wealth of useful ecological information. Nitrogen stable isotope data, for example, can provide information on intra- and inter-specific variation in trophic level, predator-prey size ratios, food chain length, relationships between predator and prey species diversity, and the dynamics of energy use (Chikaraishi *et al*., 2014). All of these parameters are extremely important in determining an organism's ecological niche and functional role.

Key Approaches for Addressing Knowledge Gaps:

- ***Targeted MPA Monitoring***: *Existing MPAs offer the opportunity to study changes to communities and site function*
- ***Establishment of Experimental Sites***: *Well-designed field study sites and BACI designs offer the potential to establish effects of removal and establishment of thresholds*
- ***Statistical Design and Power***: *Monitoring programmes and experiments should employ a robust statistical design and clear hypothesis testing*
- ***Appropriate Time-Series:*** *Experiments and monitoring programmes need to have appropriate longevity in order to detect change*
- ***Modelling:*** *The use of modelling techniques may assist in prediction and locating ecologically important habitats such as nursery grounds*
- ***Molecular Tools:*** *Population genetics can provide valuable information on larval settlement, parentage, migrations and population connectivity*
- ***New technologies***: *Remote sensing and video technologies may offer cost-effective methodologies to collect in-situ time-series information*
- ***Tagging Studies***: *Telemetry and data logging tag technologies offer the opportunity to study habitat use and distributions and migrations of mobile species*
- ***Collaborative Projects***: *There is much to be gained by establishing collaborative programmes of work with the fishing industry both in terms of practical expertise and local ecological knowledge*
- ***Functional Diversity Analysis***: *Establishing the functional diversity within sites enables more complex analysis and modelling of scenarios*

Summary

In summary, even though there are numerous knowledge gaps in our understanding of the ecological niche and functional roles of the shellfish species targeted in this review, there are various approaches and methodologies which can be effectively used to fill these voids. By doing so we will significantly improve our understanding of ecosystem function and stability, and thus determine whether the removal of particular species will induce detrimental impacts.

Within the UK, there already an established MPA at Lundy Island, where numerous studies have highlighted both direct and indirect effects of MPA designation, including changes in species size and abundance, as well as in levels of injury and disease (e.g. Hoskin *et al.,* 2011, Wootton *et al.,* 2012, Davies *et al*., 2014). A further study by Coleman *et al.,* (2013) in the Lundy Island NTZ found no significant changes in sessile epibenthic community structure after that exclusion of commercial static potting gear; thus highlighting that highly-protected NTZs may not always be required to protect ecosystem structure, function and stability. It, therefore, appears that the Lundy Island NTZ is an ideal candidate for future studies on ecosystem function, and as such should be liberally used as a research reference area.

Furthermore, the studies in the Lundy Island NTZ and the Lyme bay MPA were all based on collaborative research, with participation from fisheries stakeholders, scientists, IFCAs, Natural England and other NGOs. Such multidisciplinary approaches are fundamental in successfully applying ecosystem-based management strategies to the future protection and conservation of our marine resources.

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