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An inventory as part of a feasibility study for passive fisheries on European lobster *Homarus gammarus* in offshore wind farms

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Abstract

Homarus gammarus (European lobster) is a commercially valuable lobster species that is distributed around the European continent and appears to be a viable target species for passive fisheries. In the Win-Wind project, possibilities for passive fishing on *H. gammarus* in offshore wind farms are being investigated. Since *H. gammarus* occurrence at offshore wind farms on the Dutch continental shelf appears uncertain, with few to no specimens found in previous monitoring activities, stocking of lobsters will likely be required to achieve harvestable populations. Accordingly, a demand arose to further investigate the role of *H. gammarus* within its ecosystem to better understand the implications of adding the species to the environment. Hence, a literature review of both the ecology of *H. gammarus* and the (benthic) ecosystem of the North Sea is presented, followed by a comparison of *H. gammarus* with other decapod species for which more work is available, through principal component analysis (PCA). It appears that *H. gammarus* progresses up the food web as it develops from opportunistic larva, to a scavenging juvenile, to an active predator as an adult. Although *H. gammarus* larvae and early benthic settlers are vulnerable to predation, adult *H. gammarus* is not a target species for predators. It is suggested that *H. gammarus* inhabits top-down control on the benthic ecosystem by predation and is controlled bottom-up by food availability. Albeit dependent on the presence of prey and competing species as well as the frequency and intensity of restocking activities, it appears that a sudden increase in *H. gammarus* may have at least temporary inhibitory effects on the benthos population through predation and consequently indirectly on ecologically related species, such as the brown crab. Further investigation is however required as robust data on the dietary diversity of *H. gammarus* as well as comprehensive population monitoring programmes in OWFs on the DCS are currently lacking.

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1 General introduction

1.1 Multi-use of offshore wind farms

The Dutch government has the ambition to produce at least 70% of its countries energy demand from renewable sources by 2030 and aims to completely make the energy supply zero-emission by 2050 (Rijksoverheid, 2019). Offshore wind energy on the Dutch Continental Shelf (DCS) plays an increasing role in the current energy transition in the Netherlands. The North Sea is highly suitable for offshore wind farms (OWFs), due to its relatively shallow water depth, favourable windy climate, ports and industrial energy consumers nearby. Moreover, stagnating and even decreasing technical costs in recent years have resulted in wind energy becoming an increasingly affordable renewable energy source. In the upcoming years the Dutch government aims to further implement OWFs in order to produce a total power of 4.5 gigawatt (GW) by 2023, enabling provision of sustainable energy to approximately 5 million households (Rijksoverheid, 2014). With the development of this "Green North Sea Powerhouse", the area of the DCS that is claimed by the energy sector continues to grow (Rijksoverheid, 2019). This greatly reduces the available area for other users, such as fisheries, oil and gas extraction, sand mining areas, training zones and protected nature reserves.

Whilst the energy transition towards sustainable wind-energy is a positive development regarding climate protection, it results in many professional fishermen getting excluded from an increasing share of the North Sea. Development of OWFs will particularly affect the fishermen using mobile gear, given that current legislations restrict trawl fishing in OWFs. Using mobile fishing gear could damage the energy-infrastructure, such as cables. Mitigating the loss of fishing grounds has recently become a major goal of the Dutch government. Instead of completely excluding the fisheries industry from OWFs, multi-use could be a solution to make the North Sea powerhouse economically profitable for this sector as well. For instance, opportunities for aquaculture (e.g. seaweed production) and passive fisheries (bottomless fishing using passive gear) are imaginable within OWFs.

1.2 Passive fishery of commercial decapod species at OWFs

Recently, a joint venture between Foundation Wageningen Research and the fishery-industry has been set up in the project 'Win-Wind'. The Win-Wind project is financially supported by TKI Wind op Zee (Energy Topsector) and investigates the possibilities for co-use of OWFs. In the project, large-scale and small-scale fishermen, scientists, managers of marine parks and many others work together. In previous research within the Win-Wind project, the possibilities for co-use of OWFs regarding passive fisheries were already explored. In that research brown crab *Cancer pagurus* and European lobster *Homarus gammarus* emerged as viable species (Cramer et al., 2015). Both species belong to the order Decapoda, under the class crustaceans. Decapoda are recognizable by ten pairs of pereiopods (legs) of which the front two are distinctly embellished with huge pinchers, referred to as chelae (claws). Passive fishery on both brown crab and European lobster is commonly achieved by placing pots on the seafloor that trap the specimens. No true technical objections against applying this technique at OWFs were found, since this fishing method is highly selective and low-impact (Vissen voor de Wind, 2015).

The next step is to conduct theoretical and practical research on the ecological, economical and practical aspects of passive brown crab and European lobster fisheries at OWFs. As part of the Win-Wind project, recent studies on the ecology of the European lobster (Rozemeijer & van der Wolfshaar, 2019) and brown crab (Tonk & Rozemeijer, 2019) have been carried out. Moreover, the impact of OWFs on both of the species has already been examined in a study by Skerritt, et al. (2012). Regarding brown crab fisheries, a stable market with reasonable to good prices was observed, thus proves to be very economically attractive (Vissen voor de Wind, 2015). Furthermore, the European lobster is known for its high market values (Pereira & Josupeit, 2017) and wild European lobster stocks seem to be depleting (Rozemeijer & van de Wolfshaar, 2019). Therefore, creating a passive fishery on these species seems profitable, economically and ecologically.

At OWFs, hard substrate can take various shapes such as cables, scouring protection, concrete foundations of the wind turbines, therefore providing a newly inhabitable, varied and complex habitat. The hard substrate created by turbine construction on the previously soft sandy seafloor of the North Sea, may provide suitable habitat for previously absent species to settle on, establishing thriving ecosystems (Skerritt, et al., 2012). Colonization of an artificial reef by epibenthic species has shown to be very rapid, initially by barnacles and worms (Hiscock, et al., 2010; Andersson, et al., 2009) and subsequently by hydroids and tunicates (Andersson, et al., 2009). Currently, the mussel *Mytilus edulis* is known to be the most dominant species within the intertidal zone of the turbines at Dutch OWF Egmond aan Zee. *M. edulis* now covers up to 90-100% of the substrate within the intertidal zone and are known to reach densities over 4200 mussels per m^2 (Bouma & Lengkeek, 2012). Small crustaceans even exceeded mussels in terms of density (>22,000 individuals per m^2 in post-summer season) and high numbers of polychaetes were found (500 individuals per m^2) (Bouma & Lengkeek, 2012). Due to a strong ecological association with rocky habitat for shelter, brown crab and European lobster are also species that are known to be attracted to artificial reefs (Hooper & Austen, 2014). Early studies on recruitment of European lobster to artificial reefs have indeed shown their capacity to cover long distances to inhabit habitats that provide hard-substrate, over 15 kilometres (Jensen, et al. 1994). Altogether, this gives a hopeful picture for the creation of a multi-use OWFs, that not only generate sustainable energy, but also find a concession for loss of fishing grounds on the DCS.

1.3 European lobster

To determine whether a viable fishery can be realised within an OWF, thorough understanding of brown crab and European lobster ecology is required. For example, the mobility of the species within a windfarm, the effects of restocking on the ecosystem and the consequences of subsequent removal of animals from the ecosystem need to be examined. Within this report, a literature review is carried out on the so far unknown trophic position of the European lobster within the North Sea (benthic) ecosystem, indicated as Part I. This knowledge is required to predict the consequences of implementing passive fisheries of European lobster within OWFs.

The European lobster *Homarus gammarus* (occasionally referred to as *Homarus vulgaris*) has a broad geographical distribution, found almost around every European coastline (Prodöhl et al., 2006). However, the species is clearly bound to hard substrates and is not often found on soft sediments. Despite the expectation for *H. gammarus* to settle at offshore windfarms (OWFs) as well, due to the introduction of hard substrates (i.e. scour protection), no clear evidence of (increased) *H. gammarus* populations at OWFs has been found. *H. gammarus* has not been recorded in several monitoring programmes at multiple OWFs throughout the North Sea, including Dutch OWF Egmond at Zee (Hooper & Austen, 2014; Bouma & Lengkeek, 2012; Krone et al., 2017). Although new monitoring programmes are now being planned, to date there have been very few (recent) published observations of *H. gammarus* in OWFs built on North Sea soft sediments, such as the DCS. Lobster sightings by divers have only been mentioned in a study of Belgian OWF (Mesel et al., 2013) and a loose cheliped of a European lobster was found at the scour protection in Dutch OWF Princess Amalia (Vanagt et al., 2014). This lack in monitoring programmes and sightings complicates the assessment of the impact that presence or absence of *H. gammarus* has within these environments.

Nevertheless, off the coast of Brittany, France, concrete mattresses deployed to anchor the submarine power cables appear to provide suitable habitat for lobsters and crabs, including *H. gammarus* (Taormina et al., 2020). Moreover, *H. gammarus* was present at numerous wrecks in the sand-dominated German Bight, which indicates their potential to settle at novel hard substrates (Krone & Schroder, 2011). In the Westermost Rough OWF, located on the north-east coast of the UK, *H. gammarus* was indeed recorded after wind farm construction (Roach et al., 2018). However, this OWF was constructed in Holderness Coast fishing grounds, being the largest lobster fishery in the UK (Roach et al., 2018). Given these *H. gammarus* populations in UK waters and OWFs (Roach et al., 2018), and in Dutch estuarine and coastal waters (namely Grevelingen, see Overmaat et al., 2020), the possibility exists that *H. gammarus* has by now colonised OWFs on the DCS through larval migration.

Restocking of European lobster, i.e. releasing hatchery-reared juveniles at OWFs, has the potential to create a thriving population that could support a stable market (Wickins & Beard, 1991; Vissen voor de Wind, 2015). Given the fact that sustaining a passive fishery therefore requires both extraction of economically valuable lobster (i.e. of a marketable size) and restocking of populations with

juveniles in OFWs, it is necessary to gain more knowledge and insights on the impacts of these actions on the food web.

Currently, the European lobster is considered to be a large, top-end predator that could potentially exhibit a top-down control on the benthic environment it inhabits (Rozemeijer & van de Wolfshaar, 2019). Although several extensive studies on the North Sea foodweb exist, literature on the specific role of European lobster within this ecosystem is lacking (Christensen, et al., 1992; Lynam, et al., 2017). These studies usually focus on the entire North Sea ecosystem, instead of looking closer into the localized ecosystem dynamics, or aim at aggregated groups of benthos instead of specific species. Nevertheless, efforts have been made to study the influence of decapods in general (Boudreau & Worm, 2012). Questions arise on the role *H. gammarus* has on its surrounding ecosystem and furthermore, what the impact is of adding and removing *H. gammarus* from the local communities.

Further research on the role of European lobster within the North Sea food web is required to determine the viability of passive lobster fisheries as being part of co-use of OWFs in the North Sea. *H. gammarus* is known to undergo ontogenetic shifts in diet and habitat during its life, which indicates a lifestyle where morphological development from larva to adult is accompanied by different habitat types and composition of diet. It could therefore exhibit varying environmental influences with increasing age. Another challenge is the scientific uncertainty on its behaviour during early settlement in the seafloor. In literature, *Homarus spp.* are described as opportunistic feeders but also as highly specific predators (Mackie & Shelton, 1972; Hudon & Lamarche, 1989). Clarifying the ontogenetic changes of European lobster and its role as predator and prey, will aid in forecasting the potential ecological consequences of implementing passive fisheries in OWFs.

1.4 Problem definition

In summary, the ecological role of the European lobster within the ecosystem is evaluated in this literature review, since thorough knowledge on its environmental impact is currently unavailable. To start with a broad overview, the complex North Sea ecosystem is reviewed before diving deeper into the ecology of the European lobster. Subsequently, concluding statements are then made about the trophic position of the European lobster. Concludingly, the relevance for potential passive fishery application at OWFs in the North Sea is explained in two parts: the effects of harvesting *H. gammarus* from this ecosystem and the impact of adding *H. gammarus* to the ecosystem.

1.4.1 Objectives

The objective of this literature review is to clarify the potential role of *H. gammarus* in the benthic southern North Sea ecosystem and to predict the impacts of extracting and adding *H. gammarus*:

1. The study will describe the general ecology and life history of the *H. gammarus*.
2. The study will describe the North Sea ecosystem and foodweb, including a specific focus on the environment around OWFs in the Southern Bight.
3. The study analyses literature on the role of *H. gammarus* within its environment, providing additional knowledge by comparing *H. gammarus* to other decapod species, to aid determining its role in the ecosystem.
4. A proposal will be made on the trophic role which *H. gammarus* occupies in the ecosystem.
5. Finally, the relevance of this hypothesis for potential passive fishery at OWFs in the North Sea is analysed, focusing on the expectation of adding and removing *H. gammarus* in and out of the ecosystem.

2 Ecology of *Homarus gammarus*

2.1 Distribution

H. gammarus has a broad geographical distribution, found almost around every European coastline (Prodöhl et al., 2006). This includes the Mediterranean Sea, though being found here in smaller quantities that reach below commercial levels, and does not include the Baltic Sea (Prodöhl et al., 2006). The southern boundary is found around 30° northern latitude, so a substantial proportion of the Moroccan coast is included. This broad geographical range indicates a high tolerance to different conditions (Mercer, et al., 2001) and the availability of wide-spread suitable habitat (Rozemeijer & van de Wolfshaar, 2019). Distribution in depth is determined by a combination of abiotic factors, such as wind and tidal exposure, salinity levels and temperature ranges (after literature analysis in van der Boogaart, et al., 2019).

From the Genetics of the European Lobster (GEL) project, the European lobster populations were found to have limited gene interchange that follows an island model of population structure (Prodöhl et al., 2006). Nonetheless, no major evidence was found for great genetic discontinuities along the European populations, although six or seven clusters could be found that genetically differed slightly (Prodöhl et al., 2006). The American lobster *Homarus americanus* is very similar to *H. gammarus* in terms of ecology and these species are able to produce hybrids when crossed. However, their geographical distribution range differs so much that hybrids of *H. americanus* and *H. gammarus* are very unlikely to exist in nature.

Information on the density of *H. gammarus* in scientific literature appears to be very scarce. Few studies are known, in which densities were found of approx. 0.4 to 5.0 lobster/m^2 in Scottish waters, 0.060 lobster/m^2 in the Oosterschelde and an expected 0.000002 large-lobster/m^2 on the DCS soft sediments (Rozemeijer & van de Wolfshaar, 2019). However, when suitable habitat is available, i.e. crevices, the density could rise up to 1 lobster per 150m^2 (Rozemeijer & van de Wolfshaar, 2019). Suitable habitat will be further discussed in section 3.7.

2.2 Morphology

An overview of the external features of *H. gammarus* is shown in Figure 2. *H. gammarus* has a rigid external skeleton, supporting and protecting the soft tissues of the animal. The exoskeleton is divided in two parts: a foremost part being a solid carapace and a back part covering the abdomen and tail. *H. gammarus* is usually blue to navy colour on their dorsal side and of a lighter more yellow-orange tint underneath. Their two front pereiopods are asymmetrical and large, making them quite distinctive from one another (see Figure 1). The larger pereiopod is used for crushing (blunt rounded nodules) and the smaller pereiopod for cutting (sharp inner edges). The latter is way sharper and smaller and used for holding and tearing apart prey. Male lobsters usually have larger claws than females, yet females usually have wider abdomens, which is expected to be a modification to hold eggs (Beard & McGregor, 1991). *H. gammarus* can reach total body lengths of over 100 cm, yet a maximum of 60 cm is more commonly found (Holthuis, 1991). *H. gammarus* can weigh up to 5 to 6 kilograms (Rozemeijer & van de Wolfshaar, 2019; FAO.org queried on 02-04-2020).

Figure 1   *Homarus gammarus (FAO.org, 2020)*
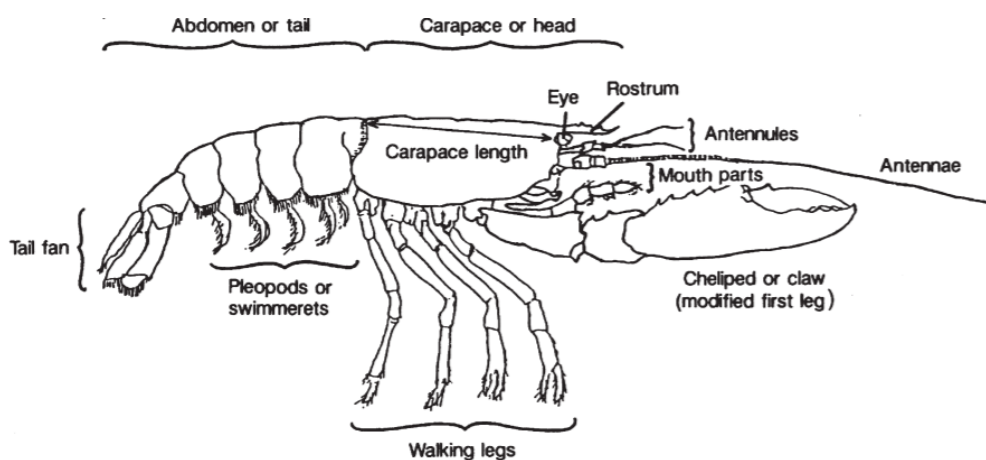
Figure 2   *External features of Homarus gammarus (Beard & McGregor, 1991)*

2.3 Life cycle

The life-span of *H. gammarus* in the wild can exceed 70 years, although an average is given around 31 years for male *H. gammarus* and 54 years for female *H. gammarus* (Sheehy, et al., 1999). Consideration has to be made on the accuracy of age estimation, since very limited sources on longevity and aging of *H. gammarus* can be found. This could result from difficulties in aging of lobsters in general, due to a lack in clear morphological aging characteristics, such as otoliths of fish. Commonly the accumulation of the pigment lipofuscin is used to determine the age, since lipofuscin is produced during cellular metabolism and is known to be quite stable after formation (Sheehy, et al., 1999). Moreover, uncertainty in longevity of the species could arise from low probabilities of big-sized lobsters getting trapped in the fishing methods (mostly pots), since these mechanisms are often too small for bigger animals to enter (Vogt, 2012). When age estimations are solely based on caught lobsters within fisheries, underestimations can be consequence.

2.4 Growth by moult

The exoskeleton is very rigid, therefore *H. gammarus* grow by the discrete process of moulting. Initiated water uptake causes the lobster to swell, resulting in rupture of the exoskeleton between the head and

tail (Beard & McGregor, 1991). Subsequently, the lobster can shed its old skeleton, then swell even more and eventually harden the completely new exoskeleton. The inter-moult period increases with age, occurring weekly during the first larval months, while old adults moult annually or biannually (Beard & McGregor, 1991). The preservation and consumption of the divested exoskeleton after moult has been recorded for *H. gammarus* (Howard & Bennett, 1979). Also closely related lobster *H. americanus* is known to consume its old exoskeleton after shedding to provide enough calcium for solidifying the new exoskeleton (Hudon & Lamarche, 1989). After the new exoskeleton has hardened, new body tissue is created, replacing the absorbed water. In research by Agnalt et al. (2007) an average increase of 7mm carapace length (CL) at each moult was observed for *H. gammarus*, independent of previous size. Hepper (1967) found an average moult increment of 9.8mm CL after each moult for male lobsters and 8.4mm CL for female lobsters. During their adulthood, moult becomes part of the mating-spawning-egg hatching cycle (Prodöhl et al., 2006). Limbs and appendages of lobsters are able to regenerate after being lost, yet this takes a few moult cycles (Beard & McGregor, 1991; Rozemeijer & van de Wolfshaar, 2019).

2.5 Reproduction

Females generally reach sexual maturity between the ages of 5-8 years, for which a mean CL of 71mm is found (Prodöhl et al., 2006; Rozemeijer & van de Wolfshaar, 2019). In previous studies a slightly bigger CL at sexual maturity was calculated, estimated at 80mm in length (Beard & McGregor, 1991). Males are marginally smaller than this when they reach sexual maturity (Prodöhl et al., 2006).

Reproduction takes place during summer months after the female has recently moulted (Bennett, 1995). *H. gammarus* is suggested to be iteroparous, which is a reproductive strategy characterized by multiple reproductive cycles during a lifetime (Rozemeijer & van de Wolfshaar, 2019). Furthermore, it is suggested that wild females only mate with one particular male during their lifetime, yet one male may fertilize multiple females in one single season (Prodöhl et al., 2006). Nevertheless, recent research by Sørdalen, et al. (2018) has rejected this prevalent suggestion, showing that several monitored female *H. gammarus* were fertilized by two different males, in natural conditions. Non-specificity in mating partner could reduce impacts of exclusion of male *H. gammarus* from the environment, e.g. by fishing or predation, which results in a more resilient population. Competitively dominant males are expected to be more successful in reproducing due to higher success rates in obtaining shelter for mating and courting of females (Rozemeijer & van de Wolfshaar, 2019).

After the female has ejected the fertilized eggs, they are held attached to her pleopods to be brooded for 6-12 months (Talbot, et al., 1984). After this brooding period, thousands of planktonic larvae hatch during the following summer (Prodöhl et al., 2006). An egg-carrying female is described as 'berried' and takes care of her eggs by cleaning them and providing good circulation of water with her rear legs (Beard & McGregor, 1991). The number of eggs carried by a female *H. gammarus* is partly explained by body size (Lizárraga-Cubedo, et al. 2003), varying between approximately 2400 and 27.700 eggs per female. The number of hatched larvae is positively correlated with the CL of the female parent lobster (Contarini, et al., 2008). Females are able to spawn annually or biannually, the latter only being true for exceptional larger females (>120mm in CL), due to a greater sperm-holding capacity (Prodöhl et al., 2006; Rozemeijer & van de Wolfshaar, 2019).

2.6 Development

As aforementioned, *H. gammarus* go through several stages of development, starting as a pelagic larvae, to adults roaming the seabed. Distinction will be made between the pelagic phase and the benthic phase in the following sections, where development is further discussed.

2.6.1 Pelagic phase

The development through first four larval stages after hatchement take place in the pelagic zone over a period of approximately two to three weeks (Prodöhl et al., 2006). It is hypothesized that planktonic larvae drift along with ocean currents before settling down on the seabed, with drifted distances dependent on the current (Beard & McGregor, 1991). During the moult phase to stage IV, the post-

larval stage, *H. gammarus* take a form that is similar to the final adult morphology (Figure 3). This morphological transformation enables the larvae to swim towards a suitable habitat by using their pleopods (Rozemeijer & van de Wolfshaar, 2019). Settlement appears to be at least partly governed by chemical cues in the water column (Gerlach & Artema, 2012). At this moment, *H. gammarus* measure around 5-7 mm in CL (Prodöhl et al., 2006), although in a more recent study by Skerritt, et al. (2014), CL is argued to exceed 11mm at stage III already.
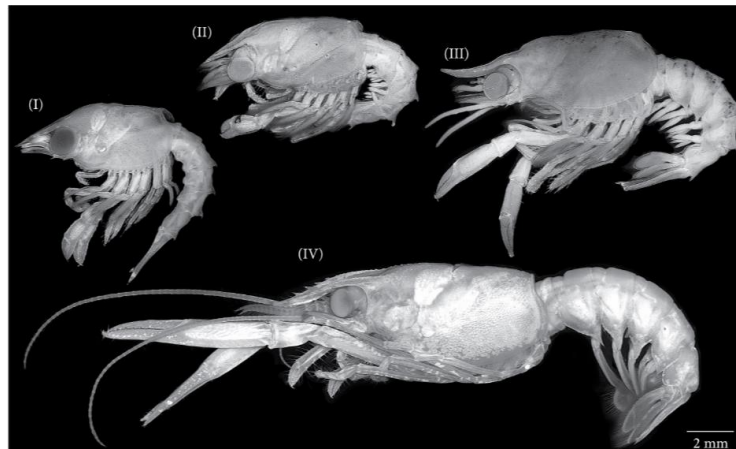

Figure 3   *Homarus gammarus in larval stages I through IV (Rötzer & Haug, 2015)*

2.6.2   Benthic phase

Benthic settlement indicates a noteworthy change in habitat and habits of *H. gammarus*. After settlement of post-larvae onto the benthic habitat, *H. gammarus* become permanent residents of the seafloor. The timing of settlement is dependent on the seawater temperature. This is estimated around 15-35 days after hatching for the British Isles (Beard & McGregor, 1991). Similar rates may be suggested for larvae on the DCS, due to corresponding environmental circumstances (Chapter 3). Settlement of post-larvae is not guaranteed, since predation on lobsters within this phase is generally rapid, especially when suitable habitat is not directly available (Mercer, et al., 2001). It has been estimated that only 0.005% of the hatched larvae survive to this benthic phase (National Lobster Hatchery UK, 2020).

Early benthic phase (EBP) juveniles, bury themselves into the seabed. According to Wickins et al. (1996) they remain in their burrows for approximately 2 to 3 years, but Jensen et al. (2000) argue that *H. gammarus* already tend to exit their burrows after having grown to circa 35 mm, which is approx. after 30 days after hatchment. Subsequently, the benthic lifestyle of *H. gammarus* relocates from burrows to crevices, roaming freely across the sea floor (Wickins, et al., 1996). EBP lobsters barely leave their shelter during their first year and major uncertainty on their behaviour and development during this period of their life exists. The reason for the permanent exit is thought to be depleted food resources in terms of quantity and quality, within and surrounding its inhabited burrow (Rozemeijer & van de Wolfshaar, 2019). A laboratory experiment by Wickins, et al. (1996) has shown that hunger is positively correlated with time spent outside burrows. Relaxed predation pressure and higher metabolic demands could also influence this exit, as has also been described for *H. americanus* (Lawton & Lavalli, 1995) and *J. edwardsii* (Alexander et al., 2014). As aforementioned, it is common that lobsters are not fully matured before reaching the age of 5-8 years (Prodöhl et al., 2006).

2.7 Habitat

The preferred habitat of *H. gammarus* changes several times during development. Observations indicate that during search of inhabitable areas of the seabed individuals face high predation risks, hence making the unavailability of suitable habitat lethal (Ball, et al., 2001). Suitable shelter presence is therefore highly important in early benthic life stages when vulnerability for predation is still high. Juveniles are known to dig burrows in the seabed with extensive tunnel systems, commonly U-shaped and on average

10-15cm in depth (Howard & Bennett, 1979; Beard & McGregor, 1991). Early benthic juveniles appear to prefer coarse to fine sand during this stage in life, although cases of buried juveniles in cohesive mud are also known (Howard & Bennett, 1979). As shown in a study by Ball et al. (2001), the existence of cobble and gravel types of substrata increase the chance of *H. gammarus* post-larvae survival. This reinforced a prior study by Linnane et al. (2000) that showed a preference of EBP lobsters towards pre-existing shelter, such as mussel shells and cobble substrate.

Moreover, as is shown for *H. americanus*, the productiveness of the seabed in terms of available organic matter, is accounted for in habitat preference (Lawton & Lavalli, 1995). A positive correlation between productiveness and habitat preference, is due to a decreasing need for leaving the burrow when food is abundant nearby (Rozemeijer & van de Wolfshaar, 2019). This decreases its exposure to predators and heavy currents. When *H. gammarus* start foraging outside their burrow, they usually stay close to their burrow and seek shelter whenever currents or predators bring them in danger (Rozemeijer & van de Wolfshaar, 2019).

After leaving their burrow, the search for rocky substrate begins, where the lobsters will spend the rest of their adult lives roaming and hiding in crevices. The natural habitat of an adult *H. gammarus* is situated from the sublittoral fringe to up to 150m in depth, usually characterized by hard substrates such as rock or compressed mud (Prodöhl et al., 2006). The most suitable habitat for H. gammarus is argued to be a permeable substrate layer covered by a heterogeneous layer of hard substrate such as boulders, to provide a sufficient amount of shelter for lobsters of wide size ranges (Rozemeijer & van de Wolfshaar, 2019).

Lobsters in general are most abundant when the presence of crevices is high (Beard & McGregor, 1991). Accessibility to shelter seems highly important, since aggressive competition for these habitat types is high, which is noteworthy for this otherwise solitary species (Beard & McGregor, 1991). As Rozemeijer & van de Wolfshaar (2019) have stated in their literature review, the suitability of shelter habitat is mostly determined by oxygen supply, length, size of crevice entrance, number of openings indicating escape possibilities and the size of the shelter. It is assumed that a crevice is only of sufficient size when the lobster can completely disappear into it (Ball, et al., 2001) and that the need for shelter decreases as the lobsters get older (Rozemeijer & van de Wolfshaar, 2019). Nonetheless, European lobsters can also be found in more sandy areas, as long as some stones or rocks are present for shelter (Beard & McGregor, 1991). Soft grounds are also often used as foraging or nursery areas (Rozemeijer & van de Wolfshaar, 2019).

2.8 Mobility

H. gammarus is a mobile decapod, however local horizontal distribution seems to be relatively limited. Its home range is commonly estimated between 2 to 10 kilometres, designating them as a sedentary species (Prodöhl et al., 2006). Movements away from home shelter are general of short lengths, less than 3 kilometres, as shown by a Capture-Mark-Recapture method (Smith, et al. 2001). *H. americanus* showed, using a VEMCO Positioning System (fine scale tracking system), similar averages in terms of home-range bounds to *H. gammarus*: approx. 760 m^2 of *H. americanus,* against 244-7722 m^2 *H. gammarus* (Skerritt, et al. 2015). These home-range bounds showed a clear seasonal patron with a decline to 237-784 m^2 during autumn.

On the contrary, large expeditions have also been observed for *H. americanus*. They were capable of migrating up to hundreds of kilometres (Smith, et al., 2001). Although similar large expeditions for *H. gammarus* have not yet been recorded, large individuals were found tens of kilometres offshore at isolated suitable habitat patches, such as shipwrecks (Smith, et al., 2001). This finding contradicts the aforementioned limited movement by *H. gammarus*.

Multiple studies have shown that *H. gammarus* activity varies seasonally (Smith, et al., 1999; Moland, et al., 2011; Skerritt, et al., 2015). Activity commonly declines in autumn, reaching a minimum in February and March and increasing again around April (Moland, et al., 2011; Skerritt, et al., 2015). Activity of lobsters outside of their shelter was found to be almost completely nocturnal during spring and summer seasons, with a peak in early-night (Smith, et al., 1999). Smith, et al. (1999) argued that timing of this peak and the length of nocturnal active period is correlated to the timing of sunrise and sunset and thus influenced by light levels (Smith, et al., 1999). In research by Moland, et al. (2011) it has been argued that activity is correlated to water temperature as well. Low temperatures in winter were shown to result in overall decrease in activity (Smith, et al., 1999). Lastly, an increase in diurnal

activity was found when turbidity was increased, which could also be related to light-levels (Moland, et al., 2011). Moreover, Skerritt et al. (2015) found that personality traits such as boldness and exploration potentially drive movement of *H. gammarus* and that males use bigger patch sizes than females. The latter is contradicted in research by Smith et al. (2001), where it is indicated that no significant difference between sexes can be found.

2.9 Diet

In order to fully understand the impact *H. gammarus* executes on its surroundings, a detailed review of its diet is required. As *H. gammarus* develops, the type of prey species as well as the amount consumed changes (Holthuis, 1991). It has to be taken into account that when estimating diet composition by examining stomach contents, digestion rates differ for various food resources, making some food items more traceable than other food items (Hudon & Lamarche, 1989). Together with varying calorific value and residence time, stomach contents are not easy to estimate (Hudon & Lamarche, 1989).

2.9.1   Pelagic phase

In the first planktonic larval stages, *H. gammarus* feed on phytoplankton and zooplankton in the pelagic zone (Beard & McGregor, 1991). During this period they are considered to be omnivorous and opportunistic feeders (Beard & McGregor, 1991). Although food encounter is based upon chance during this phase, larvae use chemoreception within the mouthparts to determine whether particles are edible (Kurmaly, et al., 1990). Herewith, Kurmaly et al. (1990) indicate to have found a certain degree of food selectivity. Moreover, their laboratory study on diets of *H. gammarus* larvae has shown that larvae have limited digesting capabilities, while in later stages this efficiency increases (Kurmaly, et al., 1990).

The mouthparts and the gastric mill (grinding stomach) of related species *H. americanus* begin to develop during Stage III and IV, which could indicate a corresponding change in diet during these phases for this lobster species (Lavalli & Barshaw, 1989). However, similar research on *H. gammarus* has been executed by Rötzer & Haug (2015), showing contrasting results. They state that minimal change of the mouthparts over the three stages is observed, indicating stages II through IV, and that mouthparts are developed early on. They conclude that larvae of *H. gammarus* in Stage III are overall more developed (i.e. advanced) than *H. americanus* larvae of the similar stage (Rötzer & Haug, 2015). Therefore a change in diet selectivity can be expected to occur earlier for *H. gammarus* than for *H. americanus*.

2.9.2   Benthic phase

Survival from larvae to the EBP is directly related to the productiveness of the seafloor these juveniles are settled in (Lawton & Lavalli, 1995). Wickins, et al. (1996) agree, stating that overall survival and growth is primarily dependent on the continuity of food availability within the buried environment. It is expected that during the buried period, *H. gammarus* live on consumption of infauna, which are organisms living buried in the sediment (Rozemeijer & van de Wolfshaar, 2019). The infaunal species that EBP *H. gammarus* mostly feed on are worms, but other small animals such as post-larval crabs, urchins and gastropods are consumed as well (National Lobster Hatchery UK, 2020). While chance is believed to be the main factor in food encounter for *H. gammarus* larvae, a more advanced way of chemolocation in juveniles is assumed: antennule chemoreceptors provide a locating mechanism to navigate towards the food source, pereiopod chemoreceptors assist in capturing and moving it towards the mouth-part (Kurmaly, et al., 1990).

For closely related *H. americanus,* pleopod fanning near the burrow entrance is shown to be a manner in which food intake is induced during the buried period of its life (Lavalli & Barshaw, 1989). This method for gathering edible particles by creating a current in the water does not appear to be highly selective. However, selectivity could occur during actual food intake by chemosensitive antennules (Lavalli & Barshaw, 1989; Kurmaly, et al., 1990). A certain extent of combining suspension (small particle collection, e.g. phytoplankton) and raptorial (large particle capture) is indicated for EBP *H. americanus* (Lavalli & Barshaw, 1989). Rötzer & Haug (2015) argue that despite a radical alteration in niche type from the pelagic to the benthic habitat, there is a gradual transition regarding food intake

mechanisms. An overlap in suspension and raptorial feeding may also apply to *H. gammarus*. Nevertheless, uncertainty exists whether pleopod fanning is purely used for feeding, since it could also indicate oxygenation of the burrow (Wickins, et al., 1996).

The primarily carnivorous diet of adult *Homarus spp.*, including *H. gammarus* (Prodöhl et al., 2006), usually consists of blue mussels, (hermit) crabs, gastropods starfish, polychaetes and even fish (Cooper & Uzmann, 1980; Beard & McGregor, 1991). Since extensive research on the dietary composition of adult *H. gammarus* seems lacking within literature, a study on *H. americanus* by Sainte-Marie and Chabot (2002) is used to give an indication. This field research at Magdalen Islands on *H. americanus* pointed out that smaller sized lobsters dominantly foraged for food that is considered to be easily acquirable, such as flesh, (juvenile) bivalves, macroalgae, meiobenthic crustaceans and foraminifera's. Bigger sized lobsters fed on a higher quantity of mobile prey usually of higher nutritious value, incl. heavy shelled crayfish and fish. A relationship between main food items of *H. americanus* and CL can be seen in Figure 4, demonstrating an increase in TL with size (from secondary consumers to tertiary consumers). Earlier research on *H. americanus* at Novia Scotia showed similar results, with main prey items being dominated by molluscan, crustacean, echinoderm and polychaetes (Elner & Campbell, 1987). Mussels were found most frequently and in highest volumes (Elner & Campbell, 1987).
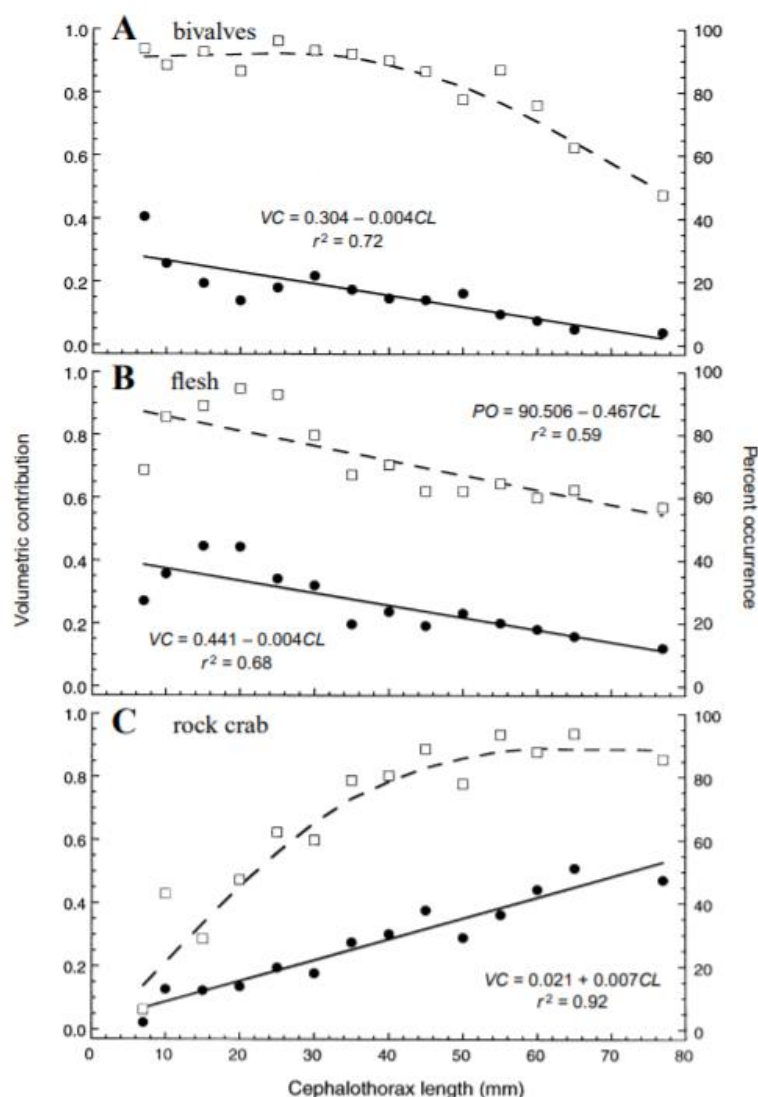

Figure 4 Relation between cephalothorax length and % occurrence (PO; square) or contribution of volume (VC, point), for the main food items (bivalves, flesh bolus and rock crab) of H. americanus, all showing a significant linear regression (P<0.001). Based on research at Magdalen Islands. (Sainte-Marie & Chalot, 2002)

Experimental research by Loo et al. (1993) showed that also adult *H. gammarus* remain capable of filter feeding particles >300-500 µm, showing over 90% particle (*Artemia salina*) reduction after 12 hours of exposure. However, actual consumption of these particles was low, since most of the particles remained on the gills and only a few *A. salina* were found in the gut content (Loo, et al., 1993). Therefore, the actual use of filter feeding and rate of ingestion is still uncertain, although it might be a survival strategy for berried (egg-carrying) females which are usually buried for a period up to 8 months (Loo, et al., 1993).

Whether lobsters are selective feeders remains a discussion in literature, both for *H. gammarus and H. americanus*, differing between truly opportunistic feeders with diets matching the environmental food availability and highly selective foragers showing specific preference towards different resources. Several studies suggested that adult *H. americanus* lobster do in fact show food preference, however because of the variety in the diet based on seasonal availability, maintain in some degree opportunistic feeders (Mackie & Shelton, 1972; Hudon & Lamarche, 1989). For example, Hudon and Lamarche (1989) stated that *H. americanus* shows selectivity for high calory food resources such as mussels when these are available. An experiment by Derby & Atema (1981) show that *H. americanus* shows chemoreceptive plasticity towards food items, i.e. showing improvement in selectivity responses towards prey items they have already experienced before. This plasticity in selectivity is argued to be a manner to increase successful searching of prey items when a certain prey item is abundant (Derby & Atema, 1981).

Furthermore, *Homarus spp.* are known to show cannibalistic behaviour (Hudon & Lamarche, 1989). It has to be taken into account that when gut contents show cannibalistic behaviour, could also indicate ingestion of its own exoskeleton material after moult has taken place (Hudon & Lamarche, 1989). Moreover, Wickins, et al. (1996) showed that buried *H. gammarus* show behaviour of hiding left-over food to be eaten at a later time. Another interesting and noteworthy finding by Wickins et al. (1996) is that when food is buried, numerous other organisms were attracted towards the area. This included copepods, nemerteans and amphipods, potentially increasing the overall fertility and thus food availability for the buried lobster (Wickins et al., 1996). This could indicate a regulatory role of *H. gammarus* in the environment it inhabits.

2.10　Summary of ecology

Table 1 is given to summarize sections 3.1 to 3.9, showing size, age, habitat, feeding and general behaviour for *H. gammarus* throughout several life stages.

Table 1
Summary of the ecology of the European lobster (H. gammarus) for size, age, habitat, feeding and general behaviour for five different life stages ranging from larvae to the adult phase.

Life stage	Carapace length	Age	Habitat	Feeding	Behaviour
Larval phase I-III	1-7 mm (Prodöhl et al., 2006)	0-2 weeks (Prodöhl et al., 2006)	Pelagic zone (Prodöhl et al., 2006)	Filter-feeding on plankton (Beard & McGregor, 1991)	Passively drifting with currents (Beard & McGregor, 1991)
Larval phase IV / post-larval phase	7-11mm (Prodöhl et al., 2006; Skerritt, 2014)	2-3 weeks (Beard & McGregor, 1991; Prodöhl et al., 2006)	Shifting from pelagic to benthic zone (Rozemeijer & van de Wolfshaar, 2019)	Shifting from filter-feeding towards scavenging of infauna (Rötzer & Haug, 2015)	Swimming with pleopods, settling onto benthic habitat by burrowing (Rozemeijer & van de Wolfshaar, 2019)
Buried juvenile phase	Up to 15mm (Wickins, et al., 1996; Jensen, 2000)	Ranging from 30 days (Jensen et al., 2000) to 2-3 years (Wickins, et al., 1996)	Buried in seafloor , only exiting occasionally to forage or when oxygen gets depleted (Wickins, et al., 1996)	Harvesting walls of their burrow for infauna (National Lobster Hatchery UK, 2020), occasionally scavenging of surrounding habitat	Barely leaving burrow, only leaving for scavenging (Wickins, et al., 1996)

Non-buried juvenile phase	15-70 mm (Jensen, 2000; Rozemeijer & van de Wolfshaar, 2019)	Up to 5-8 years (Prodöhl et al., 2006)	Rocky substrate seabed, crevices (Wickins, et al., 1996; Prodöhl et al., 2006)	Active scavenging and foraging on smaller and less-mobile species (Sainte-Marie & Chabot, 2002)	Roaming freely across seafloor, hiding in crevices (Wickins, et al., 1996)
Adult phase	From 7-8 cm up to 60-100 mm (Holthuis, 1991; Beard & McGregor, 1991; Rozemeijer & van de Wolfshaar, 2019)	Sexually mature at 5-8 years, may live up to 30-100 years (Sheehy, et al, 1999; Prodöhl et al., 2006)	Rocky substrate seabed, crevices (Wickins, et al., 1996; Prodöhl et al., 2006)	Mainly carnivorous, active nocturnal foraging on more mobile and competitive species (Sainte-Marie & Chabot, 2002; Prodöhl et al., 2006)	Roaming freely across seafloor, actively foraging, competing and mating (Wickins, et al., 1996)

2.11 Fisheries and farming

European lobsters *H. gammarus* are globally known to have high market value, up to twice as valuable as the American lobster *H. americanus* (Pereira & Josupeit, 2017). Global lobster stocks undergo increasing fishing pressure, recreational and professional, especially in Norway (Kleiven, et al., 2019). Nevertheless, *Homarus gammarus* is not yet considered as threatened, and of '*least concern*' according to the IUCN red list (Butler, et al., 2001). Landings of H. gammarus are shown in

Figure 5.

     According Pereira & Josupeit (2017), the main producing countries of lobsters in general within the EU are the United Kingdom, Ireland and France, and the main consuming countries within the EU are France, Spain and Italy. *H. gammarus* fisheries have always been unregulated or lightly regulated, however, few regulations exist: the prohibition on landing of berried females within the Mediterranean (European Commission, 2006) and UK (Bridges, 2017), prohibition on V-notched animals in the UK (Bridges, 2017) and overall minimum landing sizes of 87mm. V-notching is a technique that aims at conserving egg-bearing females when caught, by notching the tail of the lobster before putting them back in the ocean (Acheson & Gardner, 2011).

     H. gammarus farming is beginning to emerge (Prodöhl et al., 2006). Drivers of this growth are decline in lobster landings from fisheries and increasing market value for *H. gammarus* (Prodöhl et al., 2006). Lobster aquaculture can be carried out for different goals: product enhancement (catching of wild lobsters and fed in captivity to improve quality and/or size), resource enhancement (hatching of eggs and releasing early stage larvae to improve wild stocks) or full grow-out (cultivation of lobsters from egg to market size).

     According to Beard & McGregor (1991) the marketable size of *H. Gammarus* is reached around the age of 5-7 years in nature, which is after approximately 26 to 30 moult cycles. Under farming conditions, *H. gammarus* is found to be able to reach 210mm total length, 75mm in CL and 250-800 gr weight within 24-30 months (Wickins & Beard, 1991). This means that marketable sizes are reached more than two times faster under aquacultural conditions. *H. gammarus* reproduction cycle is relatively simple, they feed on natural and artificial feed and are able to reach fast growth when conditions such as habitat size, water quality, temperature and stock density are optimal (Prodöhl et al., 2006). However, problems arising in *H. gammarus* farming are high variability in growth rates, partly due to genetic differences (Wickins & Beard, 1991) and cannibalism, which requires high maintenance effort and placement in separate tanks (Prodöhl et al., 2006). Another negative side of cultivation of lobster in artificial circumstances is the increased likelihood for disease outbreak due to high temperatures, physiological stressors and inadequate nutrition (Waddy, 1988).
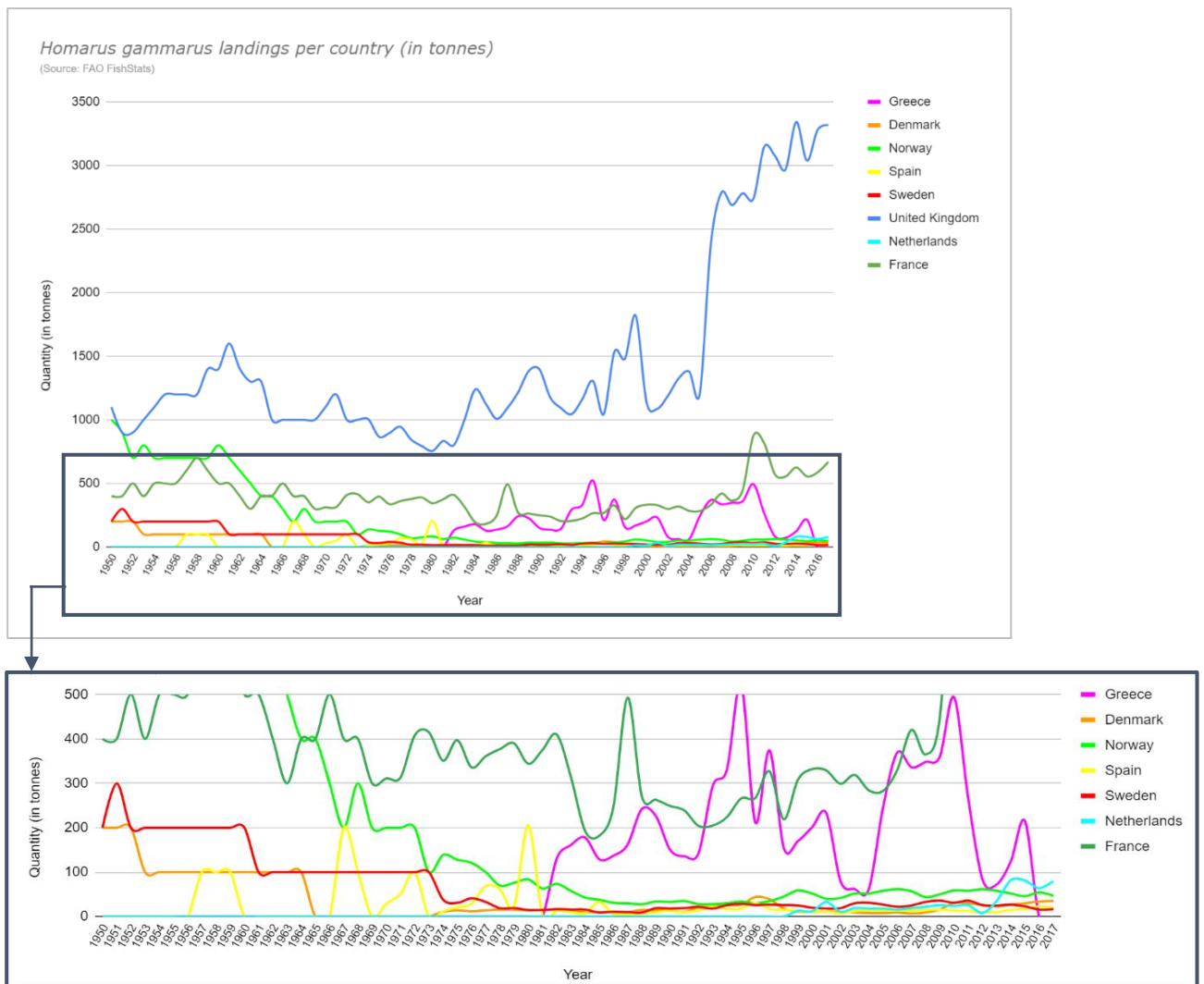
Figure 5   *Yearly landings in tonnes of Homarus gammarus per country (based on data from FAO, 2020)*

3 The North Sea ecosystem

The North Sea is considered to be one of the most productive seas on our planet (Vanaverbeke, et al., 2007; Capuzzo, et al., 2018). A discontinuous habitat and high species diversity and abundance can be found, despite the seemingly small area and continuity of water masses (Vanaverbeke, et al., 2007). By describing ecological principles that are found within regional ecosystems, e.g. ecosystem controls, dominant biomass flows and differences in species interaction between habitat types, ideas can be generated on how *H. gammarus* interacts with its local environment. In this chapter, the North Sea dynamics and the North Sea foodweb are reviewed before zooming in on the benthic habitat (as *H. gammarus* inhabits the seafloor for the majority of its lifecycle). As aforementioned, the geographical distribution of *H. gammarus* almost covers the entire North Sea. Since the Win-Wind project focusses on OWFs within the Dutch Continental Shelf (DCS), this study however focuses on the southern parts of the North Sea.

3.1 The North Sea dynamics

The North Sea covers approximately 570,000 km^2 and is connected to the Atlantic Ocean with the English Channel in the south, and the Norwegian sea in the north. Circa 57,065 km^2 is part of the DCS (ICONA, 1992). The majority of the North Sea has a relatively shallow depth of 90 meters, due to its location on the European continental shelf (Stäbler, 2018). Northern parts are overall reaching deeper than southern regions. Especially the Southern Bight is quite shallow, a depth of approximately 20-30m. Due to strong impacts of tidal action in the shallower southern parts of the North Sea, the water body in this region is always vertically mixed, while the northern parts show strong stratification in summer (Hal et al., 2011).

The seafloor of the North Sea is dominantly covered with soft and mobile sediments (Figure 6). While sandy soils dominate in the shallow southern part, the soil in the northern half shows a more clayey character (Hal et al., 2011). This is due to the continuous exposure to tidal forces and wave action. Muddy areas occur as patches, for example the Oystergrounds on the DCS (Hal et al., 2011). The only widespread natural hard substrate in the North Sea can be found near Helgoland (Germany) and near the UK coast. Gravel is the hardest natural substrate that can be found on the DCS, located at the Cleaverbank and Borkum Reef ground (Lengkeek, et al., 2013).
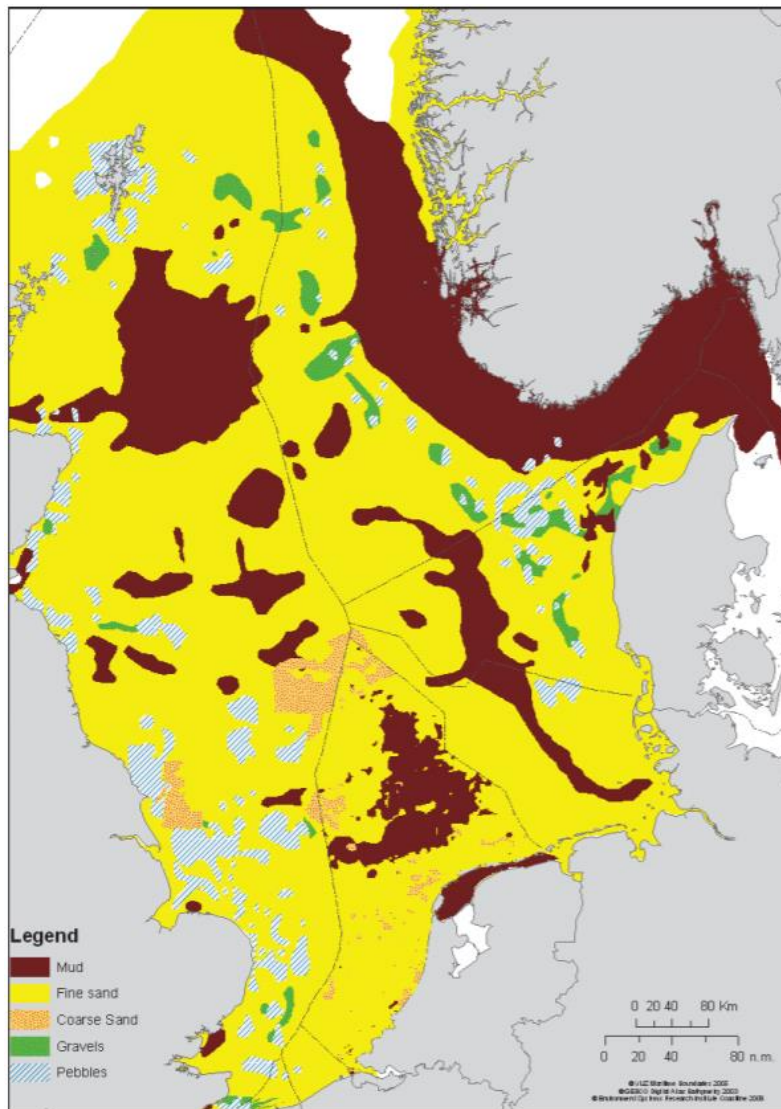
Figure 6 *North Sea sediment map (Paramor, et al., 2009)*

3.2 The North Sea foodweb

A food web is a composition of multiple integrated food chains that are connected by trophic links. In a food web as well as in an individual food chain, different levels can be allocated based on consumer-resource interactions, called trophic levels (TL). In marine ecosystems, primary production (PP) and detritus are considered to be the foundation of the food web, while apex predators are on the highest ranks (Christensen, 1992). In Annex 1 a more comprehensive description is provided of foodweb functioning in general, as well as an analysis of the different conceptions of the type of ecosystem controls exercised in the North Sea.

Early research has shown that northern and southern parts of the North Sea show different food web systems (Hannon & Joiris, 1989). In the northern North Sea, the majority of phytoplankton is taken up by zooplankton. The southern regions seem to show a pattern that is more typical for coastal regions: planktonic bacteria (40% of PP) and benthic habitats (40% of PP) dominate consumption of phytoplankton; and zooplankton play a less dominant role (20% of PP) (Hannon & Joiris, 1989). A recent study by Stäbler et al. (2018) has further examined the transfer of energy within the southern North Sea food web, shown in Table 2. Stäbler et al. (2018) showed that the transfer of biomass from phytoplankton to the benthic community occurs mainly via detritus, which is considered the most important energy flow within the southern North Sea ecosystem (Table 2). A huge part of phytoplankton ends up as detritus (approx. 2423 tonnes/km^2/year). Subsequently, the major part of the biomass received by benthos originates from detritus and discards (approx. 2177.58 tonnes/km^2).

This data by Stäbler et al., (2018) therefore support the coastal pattern as aforementioned, indicating that the majority of phytoplankton production in the southern North Sea ends up as detritus and hence remains within the benthic community. This clearly shows the key role benthos have within the southern North Sea foodweb. The food web structure as seen in southern regions, is known to result in higher abundances of demersal fish (Hannon & Joiris, 1989; Stäbler et al., 2018). This could indicate a dominant role of benthos in terms of food web control.

Stäbler et al. (2018) also examined the trophic levels of the main species groups within the southern North Sea (Figure 7). The mean trophic level in which benthic organisms are organized are approx. TL 2.5 (benthic microflora) up to TL 4.1 (commercial sized crangon). Large crabs, which could be compared to some extent with lobsters, are classified in this group of benthos at TL ~3.8 (Stäbler et al., 2018). This TL is higher than fish, which are mostly ranked approx. between TL 3 and TL 4.75.

Table 2

Consumption by aggregated groups in the southern North Sea in tonnes/km²/year. The source of biomass or prey are indicated in rows, the recipient groups of biomass or predator are indicated in columns. Most important flows are indicated in red, the least important in green. This matrix has used 68 functional groups that were aggregated into 7 groups for the sake of a general overview (Stäbler et al., 2018). Stäbler et al. (2018) defined the southern North Sea as the area between 51° and 56° Northern latitude (half-way Scotland to the southern border of the North Sea).

		Recipient group of biomass							
		Upper TL	Fish	Zooplankton	Benthos	Detritus & Discards	Key commercial species	Planktonic microflora	Total
Source group of biomass	Upper TL	0.0017	0.00073			0.88	0.0007		0.88
	Fish	1.32	8.54		0.0025	40.99	4.72		55.57
	Zooplankton	0.01	60.79	35.66	0.74	255.11	54.88		407.19
	Benthos	0.84	49.96	3.96	1302.7	1132.15	22.06	33.35	2545.02
	Detritus & Discards	0.11		24	2177.58	0.28		1467.24	3669.21
	Key commercial species	1.01	4.56		0.00056	30.03	2.26		37.86
	Phytoplankton		5.31	461.16	426.98	2423.67	5.19	166.73	3489.04
	Total	3.2917	129.16073	524.78	3908.00306	3883.11	89.1107	1667.32	10204.78
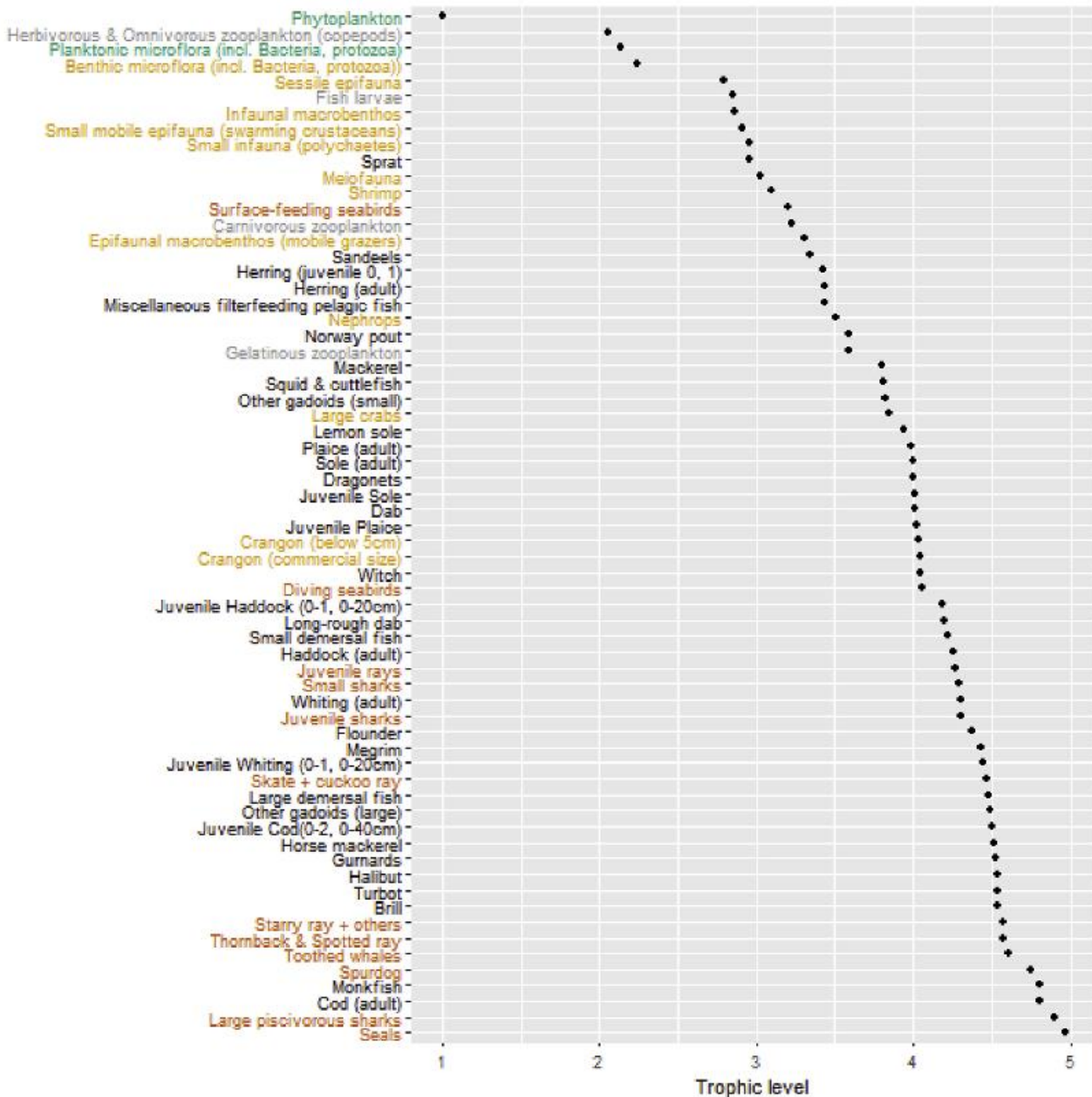
Figure 7 *Trophic levels of the southern North Sea. Upper trophic levels are indicated in dark brown, fish in black, benthos in yellow, zooplankton in grey and phytoplankton in green (Stäbler, et al., 2018).*

3.3 The benthic environment

Due to environmental variables such as substrate type, depth, temperature, stratification, salinity and tidal exposure, benthic communities vary throughout the North Sea (Rees, et al., 2007; Stäbler, et al., 2018). In general, marine benthic communities exist of nonpredatory infaunal species such as suspension feeders (straining of particles from water), deposit feeders (ingestion of sediment particles), epifaunal predators and infaunal predators. It has been argued that a latitudinal gradient exists in density, diversity and biomass of benthic macrofauna (Heip & Craeymeersch, 1995; Rees, et al., 2007). When moving northwards, the higher the species richness and diversity become, but the lower the individual weight gets. The southern-most parts are dominated by mobile epibenthos, in contrast to sessile organisms dominating the benthos in the north (Stäbler, et al., 2018).

Leewis, et al. (2017) has examined the species presence and distribution of benthos across the DCS, including the macrozoobenthos (Table 3). The area with highest total species richness appears to be the Oysterground, while the Doggersbank shows a higher diversity in terms of mean amount of

species per monster taken. Although having a lower species richness, a higher total biomass is observed in the coastal zone and offshore area. The overall mean density is approximately 1330 individuals per m^2, with Polychaeta being the most abundant group in every area, followed by bivalves and crustacea. In offshore areas, the total biomass is dominated by Echinodermata, almost accounting for 50% (Leewis, et al., 2017).

Variations between spatial scales on top-down and bottom-up interactions can be found for benthic ecosystems (Seitz et al., 2001). At local scale, benthic ecosystems are predominantly governed by top-down factors, while bottom-up interactions are more important for a large areal scale (Seitz et al., 2001). Therefore, when studying the role of *H. gammarus* in its environment, primary focus should be on the local benthic environment. Fauchald et al. (2011) argue that top-down forces control benthic food webs through predatory pressures, while bottom-up forces dominantly control the pelagic food webs through primary and secondary production. This can also be seen as a loop: bottom-up control of pelagic populations that subsequently conduct top-down control through predation of benthos (Heath, 2005).

Table 3

*Characteristics of benthos on the Dutch continental shelf, based on 164 stations. Four areas are distinguished: Doggersbank, Oystergrounds (Oestergronden), offshore areas and the coastal zone. *Means are calculated by dividing the amount of individuals or biomass by the amount of monitoring stations within the area. This table is based on 100 original MWTL (Monitoring Waterstaatkundige Toestand des Lands) locations and new stations based on Natura 2000 and KRM (Kaderrichtlijn Mariene Strategie) areas. (translated from Dutch to English, data from Leewis, et al., 2017).*

All stations	Total	Doggers Bank	Oyster grounds	Offshore area	North sea coastal zone
Number of stations	164	19	55	37	53
Median of grainsize (µm)	225	197	134	313	267
Fraction of silt (fr < 63 µm)	4,18	1,03	9,87	0,83	1,52
Diversity					
Total number of species	262	119	172	114	117
Mean number of species	21	31	28	15	14
Shannon & Wiener diversity	2,30	2,85	2,61	2,14	1,90
Simpson's dominance	0,18	0,10	0,14	0,19	0,25
Number of individual (ind./m^2)					
Bivalvia	316,5	282,7	496,3	92,9	298,3
Crustacea	277,0	381,9	191,8	384,6	252,5
Echinodermata	166,6	319,2	352,0	22,9	19,8
Gastropoda	27,8	40,5	63,9	3,8	2,7
Other	102,5	129,6	135,0	90,1	91,7
Polychaeta	438,4	561,4	421,0	379,8	453,3
Mean density*	**1328,8**	**1715,2**	**1659,1**	**974,0**	**1118,3**
Biomass (g AFDW/m^2)					
Bivalvia	14,4	3,0	2,5	4,7	37,5
Crustacea	1,9	0,2	4,2	0,4	1,2
Echinodermata	6,2	4,8	4,6	10,5	5,3
Gastropoda	0,1	0,1	0,1	0,0	0,3
Other	0,4	0,7	0,6	0,1	0,1
Polychaeta	2,6	2,5	3,1	2,0	2,4
Mean biomass*	**25,5**	**11,3**	**15,1**	**17,8**	**46,8**

3.3.1 Soft substrates

Soft-sediment communities dominate the Southern Bight of the North Sea, including the DCS (Figure 6). Sedimentary species that are adapted to this continuously evolving habitat can be found here, such as burrowing organisms. In areas where currents are stronger, interface and suspension feeders (organisms that use organic matter from water column) dominate (Kröncke, 2006) dominate, which is applicable to the south-eastern North Sea. Deposit feeders are commonly unabundant or absent due to low deposition rates (Kröncke, 2006). Where deposit rates are low, macrofauna are highly important for the connection between the infaunal population and the benthic boundary layer, e.g. through their excretion (Kröncke, 2006). Also in areas where less PP is found, such as the Oyster Grounds, microbes are found that dominantly use organic matter originating from macrofaunal activity or excretion (Kröncke, 2006).

Not only physical oceanographic aspects alter the ecosystem within a soft-sediment habitat. Infaunal species affect the environment they live in, for example by increased porosity and erodibility resulting from their extensive burrow systems (Wilson, 1990). Wilson (1990) mentions that bioturbating organisms might positively effect suspension feeders on the benthic habitat, such as bivalves. Also Kröncke (2006) found that bioturbation due to the presence of burrowing macrofauna was significantly increasing decomposition, which caused benthic life to thrive.

3.3.2 Hard substrates

The only widespread natural hard substrate in the North Sea can be found near Helgoland (Germany) and near the UK coast. Gravel is the hardest substrate that can be found on the DCS, located at the Cleaverbank and Borkum Reef ground (Lengkeek, et al., 2013). Artificial hard substrate can also be provided in various artificial ways, for instance by wrecks, boardwalks, dykes, platforms of oil- or gas extraction and offshore wind turbines. Where coarse to hard substrata is present, benthic communities are found to get increasingly species-rich compared to soft-sediment habitats (Rees, et al., 2007; Lengkeek, et al., 2013; Reubens et al., 2013). Especially species of whom the first life stages are spent as planktonic larvae, e.g. sessile invertebrates such as molluscs, need hard substrate to settle and survive in the marine environment. Logically, complexity in a habitat increases the availability of shelter, therefore limiting the success rate of predators (Wilson, 1990; Alexander, et al., 2014). Nevertheless, a higher abundance of refuges appears not only to result in higher prey densities but also a higher abundance in predator species (Thrush, 1999; Reubens et al., 2013).

On the DCS, hard substrate communities are considered important for sustaining increased biodiversity levels of native species, such as cod, goldsinny wrasse (*Ctenolabrus rupestris*), leopard spotted goby (*Thorogobius ephippiatus*), squid (*Alloteuthis subulate*), ghost shrimp (*Caprella linearis*) and brown crab (*Cancer pagurus*) (Lengkeek, et al., 2013). In a study on the Belgian part of the North Sea, numerous fish species have been observed to roam along shipwrecks and OWF foundations, such as pouting, cod, sea bass, mackerel and horse mackerel (Reubens, et al., 2013). This increase of fish species might be explained by provision of shelter, nursery grounds and recruitment sites, yet improved food provisioning might be an at least equally important factor. Especially mussel larvae of *M. edulis* appear to be great competitors for space, resulting in rapid recruitment of mussel populations on novel hard substrate in the North Sea (Joschko, et al., 2008; Bouma & Lengkeek, 2012).

3.4 Sub-conclusion

In conclusion, the North Sea ecosystem is highly diverse, showing latitudinal differences in terms of bathymetry, substrate types, stratification and exposure to ocean currents. Various types of ecosystem controls, such as top-down, bottom-up and wasp-waist, can be distinguished and substantiated in the North Sea ecosystem. Bottom-up controlled ecosystems are mainly governed by abiotic factors that influence primary production, while top-down controlled ecosystems show high impact of predation of top-predators on lower trophic levels. Wasp-waist ecosystems are governed by an intermediate trophic level that executes control on both upper and lower trophic levels and therefore influencing the ecosystem both bottom-up and top-down, such as the lesser sandeel. These controls also apply to local ecosystems and can be used to investigate the role of *H. gammarus* within the environment. It appears that mainly top-down controls affect local ecosystems and that the benthic ecosystem plays a very

important role in the biomass flow in the North Sea. Moreover, species diversity and abundance differ, with hard-substrates showing the highest benthic-species richness. However, hard-substrate in the southern North Sea is rare. Artificial substrates, such as shipwrecks and windmill foundations, seem to attract high numbers of species.

4 Trophic position of *Homarus gammarus* in the food web

In ecology it has always been a grand challenge to understand in which way specific species influence an ecosystem (Wilson, 1990). Few literature is found on the specific diet of *H. gammarus,* which complicates suggesting its influence on abundance and distribution of other species. Additionally, *H. gammarus* is often grouped within a general label of "*other crustaceans*" in research, therefore excluding its individual influence on the environment (Christensen, 1992). To partially overcome this lack in research, knowledge on species that have similar diets, habitats and behaviour can be used for determining the potential trophic interactions of *H. gammarus*. Several similarities and suggestions have already been made for the diet of *H. americanus* in the Chapter 3.

4.1 Decapods within the benthic environment

Environmental influences by decapod crustaceans can be both consumptive (predator-prey) and non-consumptive (habitat provision or alteration, interference, competition). Exoskeletons may provide habitat for invertebrates such as barnacles, bivalves, gastropods and polychaetas. However, significant provisioning of habitat for populations is only relevant when decapod densities are very high and other suitable habitat is not highly abundant.

      Predation and competition by decapod crustaceans can have significant influences on the benthic ecosystem (Boudreau & Worm, 2012). Although decapods are likely to be generalists, they do show a certain degree of selectivity linked to habitat differences (Boudreau & Worm, 2012). Exclusion experiments where decapod predators were deliberately removed from a habitat showed a significant effect on benthic infauna and epifauna species abundance (increase in density) and species composition habitat (Quijon & Snelgrove, 2005). Several species are even considered as keystone predators, such as *H. americanus* through sea urchin predations (Boudreau & Worm, 2012). However, Boudreau & Worm (2012) state that uncertainty exist on the extent that this finding is applicable across other decapod species, such as *H. gammarus*. Decapod crustaceans are influenced by top-down interactions as well, such as predation on larvae or anthropogenic influences, such as exploitation or establishment of protected reserves (Boudreau & Worm, 2012).

      Within the extensive review on multiple decapod species done by Boudreau & Worm (2012), a conceptual synthesis was established (Figure 8). A differentiation between clawed and clawless lobsters is made, since their morphological differences result in different interactions within the environment. For instance, clawed lobsters can tackle a different range of prey items and will be involved in more successful defensive or aggressive behaviour (Boudreau & Worm, 2012). 'Clawless' lobsters include spiny lobsters and spiny rock lobsters. Boudreau & Worm (2012) indicate that clawed lobsters (*Astacidea*), to which *H. gammarus belongs,* execute predatory and competitive influences on crabs, while only predatory influences are executed on mussels (Figure 8). However, it can be noticed that no relation between clawed lobsters and polychaetes is drawn, even though *H. gammarus* is known to consume species within this group during their juveniles phase. The missing link between clawed lobsters and polychaetes within the scheme could occur because of lower consumed densities of polychaetes or a chosen focus by the authors on the adult phase of lobsters. Both anthropogenic factors and predation by predatory fish influence clawed lobsters top-down.
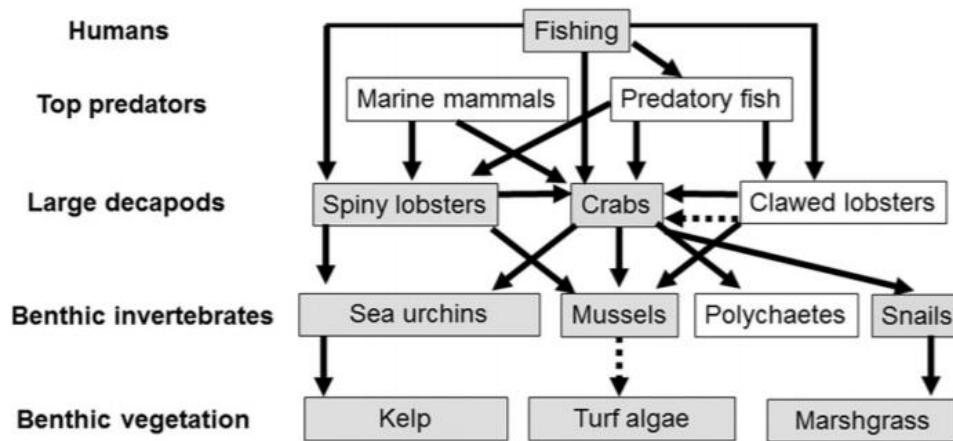
Figure 8 *Simplified scheme of ecosystem interactions of large decapod species. Dotted arrows indicate competitive interactions, while solid arrows indicated predation. Note: cannibalism is not displayed, yet occurs for both crabs and lobsters. The species in grey have strong implications in trophic cascades (Boudreau & Worm, 2012).*

Field- and laboratory research on soft-sediment benthic ecosystems in Newfoundland by Quijon & Snelgrove (2005) has ascertained the interaction between predatory epibenthos and polychaetes by predation, namely the influence of both snow crab and rock crab predation on bristle worms. Exclusion of snow crab resulted in an increased density of bristle worms and clams. Similar results were noticed when excluding rock crab from the environment. However, no specific research on the relationship between adult clawed lobster and polychaetes was found, yet similar interactions could be expected for *H. gammarus* and polychaetes. The role of *H. gammarus* as predator is further discussed in 4.2.1.

A decline of top predators, such as Atlantic cod, caused by overexploitations is seen to be followed by an increase of large decapod crustaceans (Boudreau & Worm, 2012). Nevertheless the correlation is vague, since impacts by predation on adult decapod species is considered to be relatively low, due to their hard exoskeleton and large size (Boudreau & Worm, 2012). Furthermore, Boudreau and Worm (2012) argue that despite a wide variety of species consume decapods, 1) most of these interactions seem to be a result from opportunistic feeding behaviour and 2) little evidence was found that any predator is greatly dependent on a decapod species for their consumption. Moreover, most decapods are found to behave nocturnally while hiding in shelter during the day, possibly to avoid competition or predation (Boudreau & Worm, 2012). Therefore, top-down control on adult decapod crustaceans is assumed to be limited. Nonetheless, the abundance of decapod crustaceans, such as *H. gammarus*, seems to be governed by predation on their larval and juvenile stage individuals (Ambrose, 1984; Mercer, et al., 2001), which will be discussed in further detail in 4.2.2.

4.2 Trophic interactions of *H. gammarus*

In the following sections some tentative ideas are generated what the possible role and functioning of *H. gammarus* in the southern North Sea food web could be. Any mentioned TLs are derived from Figure 7 (Stäbler, et al., 2018).

Life phase	Main prey groups	Main predator groups
Larval phase	Phytoplankton and zooplankton that drift in the pelagic.	Schooling fish e.g. cod and herring and filter feeders (although expected to be non-selective but random).
Early benthic phase (EBP) phase	Mostly small and easily edible organisms, such as bivalves, macroalgae, meiobenthic crustaceans and foraminifera's, harvesting the walls of their	High predation during early benthic settlement by small benthic fish, shore crabs, sand goby and cuttlefish.

	burrow. Potentially remain the ability to filter-feed in early benthic phase.	
Adult phase	Prey of higher mobility and bigger size, such as heavy shelled crayfish and fish. Also discards and bait are expected to be consumed during this phase.	Commercial and recreative fisheries, other decapods.

Table 4 is established to summarize the findings on the diet of *H. gammarus* and its role as predator.

Table 4 *Summary of main prey and predator groups for Homarus gammarus throughout life stages. Derived from multiple sources as mentioned in previous chapters and 4.2.2.*

Life phase	Main prey groups	Main predator groups
Larval phase	Phytoplankton and zooplankton that drift in the pelagic.	Schooling fish e.g. cod and herring and filter feeders (although expected to be non-selective but random).
Early benthic phase (EBP) phase	Mostly small and easily edible organisms, such as bivalves, macroalgae, meiobenthic crustaceans and foraminifera's, harvesting the walls of their burrow. Potentially remain the ability to filter-feed in early benthic phase.	High predation during early benthic settlement by small benthic fish, shore crabs, sand goby and cuttlefish.
Adult phase	Prey of higher mobility and bigger size, such as heavy shelled crayfish and fish. Also discards and bait are expected to be consumed during this phase.	Commercial and recreative fisheries, other decapods.

4.2.1 Role as predator

The diet of *H. gammarus* is already extensively discussed in section 3.9. Firstly, it is clear that ontogenetic changes of *H. gammarus* involve alteration in diet (see Chapter 2 and Table 1). It can be stated that a relationship between age of *H. gammarus* and TL of prey exists. *H. gammarus* larvae feed on phytoplankton and zooplankton, TL1-2. After settling in the habitat, buried juveniles mostly harvest the benthic habitat surrounding them. The majority of their diet consists of small and easily edible organisms, such as bivalves, macroalgae, meiobenthic crustaceans and foraminifera's, TL2—3. After growing to an adult sized lobster, the individuals leave their burrows for good to forage on the seafloor for prey of higher mobility and bigger size, such as heavy shelled crayfish and fish (Sainte-Marie & Chabot, 2002), TL2-3.5 or even higher. However, due to its omnivoric diet, assigning one TL to *H. gammarus* is difficult.

4.2.2 Function as prey

As larvae, the most common predators are schooling fish such as cod and herring or pelagic filter feeders, (National Lobster Hatchery UK, 2020), TL approx. >3.4 up to 4.8. However, the abundance of larvae is considered very low compared to the size of the marine environment, which means the larvae will make up only a very small part of the diet of these predators.

EBP *H. gammarus* remain very vulnerable to predation, especially recently moulted individuals (National Lobster Hatchery UK, 2020). Small benthic fish are thought to be highly efficient predators of early benthic phase *H. gammarus* (Ball, et al., 2001). According to Ball, et al. (2001), the dominant predator of juvenile *H. gammarus* in the intertidal habitat are shore crabs *Carcinus maenas* (TL 3.7 for large crabs), yet fish were observed to attack early benthic juveniles more frequently and quicker. Also the sand goby *Pomatoschistus minutus* is mentioned as being a common predator of juveniles (Hooper & Austen, 2014). To make the effect of predation on *H. gammarus* more quantitative, extensive research by Mercer et al. (2001) on *H. gammarus* populations throughout Europe is further discussed. Mercer et al. (2001) showed that when cover was provided, survival of *H. gammarus* increased from 0% (when no cover was provided) to 45% in the subtidal zone and 15% in the intertidal zone. Since the control group with all caged lobsters, showed survival rates of 100%, the driver for mortality was highly confidently assigned to predation (Mercer et al., 2001). Specifically, smaller fish and cuttlefish were the main predators of early benthic *H. gammarus* as observed by divers, yet no similar result were found when examining stomach contents of these species (Mercer et al., 2001). Additionally, EBP lobsters (<20 mm) were not found in soil-suction samples, therefore uncertainty on its prey-predator interactions during this period remains (Mercer, et al., 2000). It may be hypothesized, as mentioned by Hooper & Austen (2014), that benthic juveniles may be limited from areas where species diversity is high due to predation. Predation during adult stages of *H. gammarus* seems to be unclear, although the protection of *H. gammarus* removal by humans has shown to rapidly increase abundance and size of the individual in the UK (Boudreau & Worm, 2012).

4.3 Comparison to other decapod species

Using other decapod species as model species for *H. gammarus* is useful to examine potential trophic influences. As aforementioned, clawless lobsters and crabs seem to differ with clawed lobster, e.g. *H. gammarus*, in terms of general trophic interactions (Figure 8). Despite these apparent differences, decapods other than clawed lobsters can still act as inspiration for species-environment engagements, when similarities in prey and predator interactions are observed. Therefore, the diets and predators of several decapod species were investigated and subsequently compared using a principal component analysis (PCA). PCA is a statistical technique in which a linear relation between the variables is assumed, in this case the species and its prey or predators. The decapod species that were examined on their prey-predator interactions are: *H. americanus, Nephrops norvegicus, Panulirus cygnus, Panulirus argus, Panulirus marginatus, Jasus edwardsii, C. pagurus, Carcinus maenas, Callinectes sapidus* and *Cancer irroratus* (

Annex 2 PCA analysis

Table 7, Annex 2). To compile the PCA plot, the consumed species were examined and ordered to functional group: macroalgae; molluscs (bivalves, chepalopoda, gastropoda); echinoderms; polychaetes; small crustaceans; big crustaceans (incl. decapods) and fish (Table 8, Annex 2). Similar methods were used for predator interactions, in terms of species preying on the concerned decapod species. For this analysis, the functional groups macroalgae and polychaetes were excluded (highly unlikely to prey on decapods), and only taking the group cephalopods of the functional group molluscs into account. Since we are mainly interested in the benthic phase of *H. gammarus*, the larval pelagic phases were excluded in this review. Moreover, human induced impacts were also excluded, thus excluding discards and fisheries. Lastly, since the available data on diets often vary greatly per species and per area, this PCA is based on unbalanced and incomplete data. Nevertheless, this analysis can be used to provide a quick, but simplified, overview of how a species differs from other species.

Based on the PCA of prey groups (Figure 9A), three decapod species were further examined: American lobster *H. americanus,* brown crab *C. pagurus* and Australian spiny lobster *Panulirus cygnus*. The PCA based on predator groups did not show any apparent comparable species of *H. gammarus* and was therefore not taken into account. In summary, Table 5 is composed to compare the four decapod crustaceans with further explanation on each species (excluding *H. gammarus*) below.
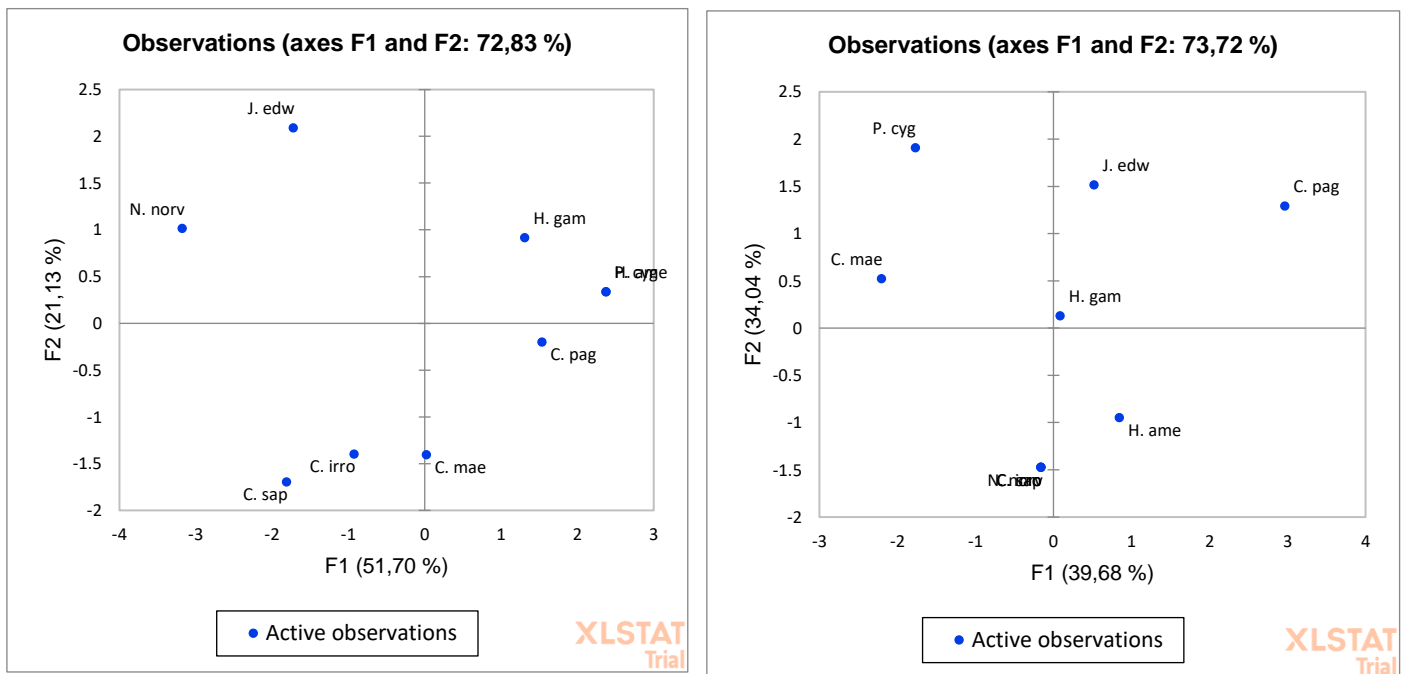

Figure 9A and B *PCA plots based on presence-absence of prey groups (left) and predator groups (right). In the left plot H. americanus and P. cygnus are overlapping, in the right plot N. norvegicus and C. irroratus and C. sapidus are overlapping*

Table 5

Overview of environmental relations of H. gammarus, H. americanus, C. pagurus and P. cygnus in terms of habitat, mobility, main prey groups (orange), main predator groups (green) and non-trophic interactions. Filled boxes within prey and predator sections indicate similarities with H. gammarus. Statements found about their overall trophic relationship to the food web are listed in the last column. Used sources are mentioned in 4.3.1, 4.3.2 and 4.3.3.

Species		Homarus gammarus	Homarus americanus	Cancer pagurus	Panulirus cygnus
Habitat and mobility	**Ocean/sea**	North-eastern Atlantic	North-western Atlantic	North-eastern Atlantic	Sub-tropical Indian Ocean
	Substrate type	Mostly hard-sediment of sublittoral	Shallow intertidal and subtidal rocky areas	Hard-substrate	Shallow reefs, hard-substrate
	Mobility	Low	High	High	High
Main prey groups	Macroalgae	X			X
	Molluscs: bivalves, cephalopoda	X	X	X	X
	Molluscs: echinoderms		X	X	X
	Polychaetes				
	Small crustaceans	X	X	X	X
	Big crustaceans (incl. decapods)	X	X	X	x
	Fish	X			
Main predator groups	Macroalgae				
	Molluscs: bivalves and cephalopoda				
	Small crustaceans				
	Big crustaceans: incl. decapods	X	X	X	X
	Benthic fish	X			
	Pelagic fish	X	X	X	
Trophic interactions		To be discussed further	Food limitation controls *H. americanus* bottom-up. Potential keystone predators through sea urchin predation.	No keystone interactions known, although crabs in general were shown to show intertrophical regulatory functions.	First-order predator. No evidence of keystone role.
Non-trophic interactions		Habitat alteration?	Habitat alteration, usually successful in competition for habitat compared to crab species	Habitat alteration	Unknown
TL		To be discussed further	3.2 (Steneck et al., 2004)	3.1 (Schaal et al., 2010)	2.7 (Phillips et al., 2013)

4.3.1 American lobster (*Homarus americanus*)

The American lobster *Homarus americanus* is a clawed lobster species and inhabits shallow rocky habitats, avoiding muddy and sandy habitats (Hanson, 2009). As aforementioned, *H. americanus* is known to be highly mobile compared to *H. gammarus*. *H. americanus* is considered a secondary consumer and is largely carnivorous (Hanson, 2009). There are clear indications that food availability can play a role as bottom-up control in population dynamics (Grabowski, et al., 2009). The diet of *H. americanus* is mainly composed of rock crab, sea stars and lobster, of which mostly moulted carapaces (Hanson, 2009). Studies have shown that *Cancer spp.* are contributing to the majority of the diet of *H. americanus* (Hanson, 2009; Grabowski et al., 2009). Especially rock crab *Cancer productus* appears to be an important prey item (Sainte-Marie & Chabot 2002; Hanson, 2009). Polychaetes and fish were also found, but did not contribute a significant portion of their diet (Hanson, 2009). Stable isotope ratios in diets of distinct *H. americanus* populations have shown that the mean trophic level of their prey species differs across populations, sometimes mainly consisting out of molluscs which are positioned lower in the foodweb, others mainly consuming *Cancer* spp. (Grabowski, et al., 2009). All in all, decapod crustaceans account for the majority of *H. americanus* its diet (Hanson, 2009).

H. americanus has been described as keystone predator through sea urchin predation by Boudreau & Worm (2012). Predation on sea urchins consequently reduces the grazing on kelp, which avoids kelp forest degeneration to barrens (Boudreau & Worm, 2012). However, the selectivity of *H. americanus* for sea urchins remains questionable, since molluscs remained the main prey item in this particular study (Boudreau & Worms, 2012). Additionally, research by Elner & Campbell (1987) has found that other prey species, such as mussels, surpasses the importance of sea urchin in the diet of *H. americanus*, despite sea urchins being the most dominant macrofaunal organism within the examined ecosystem.

The predators of *H. americanus* include fish species, such as sculpins, although Hanson (2009) has shown that this proportion was incredibly low compared to cannibalism. Increases in *H. americanus* populations in the Gulf of Maine were thought to arise due to the fisheries induced decline in cod populations, an important predator of *H. americanus* (Grabowski et al., 2009), indicating at top-down control of the *H. americanus* population. Nevertheless, Hanson (2009) argues that insufficient data has been gathered to indicate pelagic fishes, such as cod, as important predators of *H. americanus*.

4.3.2 Brown crab (*Cancer pagurus*)

C. pagurus is a mobile species, yet male crabs being more sedentary than their female counterparts (Tonk & Rozemeijer, 2019). Its carnivorous diet consists out of a wide variety of organisms (molluscs, crustaceans and echinoderms) (Neal & Wilson, 2008). Due to its heavy clawed morphology it is able to crush hard-shelled species relatively easy (Tonk & Rozemeijer, 2019). Moreover, Tonk & Rozemeijer (2019) mentioned its potential role as keystone species, as several crab species are known to structure benthic communities by predation, e.g. limiting urchins or snails populations so that their grazing on algae gets decreased. An example that is given, is the blue crab and its predation on gastropods. However, for *C. pagurus* this regulatory role has not sufficiently been examined yet, thus remains highly uncertain (Tonk & Rozemeijer, 2019).

Its role as prey alters throughout its lifetime. Smaller crabs remain vulnerable for predation by benthic fish species, other decapods and birds, whereas larger crabs are not very vulnerable to predation at all (Tonk & Rozemeijer, 2019). Yet, top-predators such as octopus, wolf fish (strong jaws can crush decapods, molluscs and echinoderms easily), seals and cod (Tonk & Rozemeijer, 2019).

4.3.3 Australian spiny lobster (*Panulirus cygnus*)

The family of spiny lobsters, also called rock lobster, crayfish, or langoustes, consists out of tens of lobster species that sustain multiple important fisheries worldwide (Phillips et al., 2013). They differ greatly from 'true lobsters', since they lack the distinctive chelae (claws), therefore referred to as clawless. *Panulirus cygnus*, referred to as Australian spiny lobster or western rock lobster, inhabits rocky reefs and is highly mobile (Phillips et al., 2013).

P. cygnus is described as a first-order predator species (Waddington, et al., 2008). Stable isotope analyses showed that *P. cygnus* is a highly omnivorous lobster, with bait (4 to 79%), crabs (up to 76%) and amphipods or isopods (up to 54%) being the main contributors to their diet (Waddington et al. 2008). Laboratory experiments showed that *P. cygnus* might interact strongly with crab species through predation, since crabs were consumed by both smaller and bigger *P. cygnus* individuals (Dumas, et al., 2013). Moreover, larger specimens moreover showed strong preference in mussels, while smaller individuals also included gastropods and sea urchins in their preferred diet (Dumas, et al., 2013). In a study Phillips et al. (2013) also cannibalistic behaviour was mentioned, additionally to small crustaceans, algae and invertebrates. The diet composition of *P. cygnus* is highly correlated to available food items, indicating a certain degree of non-selectivity (Waddington, et al., 2008). This could also indicate a relative low or even absent top-down control, since they are not dependent on a certain type of food.

Spiny lobsters are often considered a link between their smaller prey items and larger species that prey on spiny lobsters (Briones-Fourzán, et al., 2019). The main predators of *P. cygnus* are marine predators such as sea lions and seabirds, cephalopods and other rock lobster (Phillips et al., 2013). Predation on *P. cygnus* by fish species appeared to be quite low. In an early study by Howard (1988), six fish species were recorded to predate on *P. cygnus*, but only one species had >5% of their diet volume consisting out of *P. cygnus*. The majority of consumed *P. cygnus* were early benthic juveniles (8-15 mm CL) (Howard, 1988).

However, for other spiny lobster species observations may differ. For example, the spotted spiny lobster (*Panulirus guttatus)* is a relatively small decapod which is commonly sedentary, yet executes a higher trophic function compared to *P. cygnus* (Briones-Fourzán, 2019). Moreover, the diet of *P. guttatus* has been shown to correlate with habitat complexity: the more complex its ecosystem, the lower the trophic level of its prey. This can be explained by the relatively high abundance of molluscs within complex habitats, while crustaceans are more abundant in less complex habitats (Biones-Fourzán, 2019).

4.4 Discussion

In contrast to sub-arctic environments that *H. americanus, C. pagurus* and *H. gammarus* inhibit, *P. cygnus* occurs in sub-tropical habitats. Moreover, a distinct difference between *P. cygnus* and the other three decapods is the lack of large claws, what one might expect to be of importance in relation to prey-potential. This could explain the relatively low trophic level of *P. cygnus*, namely 2.7, in contrast to the TL of *H. americanus* (TL 3.2) and *C. pagurus* (TL 3.1), as indicated by Phillips et al. (2013). Therefore, *P. cygnus* is not suitable as an example species for *H. gammarus*, despite the similarities in prey groups according to the PCA plot and Table 5.

On the contrary, *H. gammarus* and *H. americanus* do inhibit similar substrates and are highly conform in terms of morphology and taxonomy. Based on their similarities, *H. americanus* could be a fitting example species for *H. gammarus*. Thus far based on available knowledge, *H. gammarus* does not show specific preference for decapod crustaceans within its diet, while the majority of *H. americanus* its diet contains crabs and moulted carapaces. Similar feeding behaviour for *H. gammarus* is imaginable. Moreover, *H. americanus* is discussed as a potential keystone predatory species, which could also account for *H. gammarus*.

Similarities between *C. pagurus* and *H. gammarus* are its distribution (north-eastern Atlantic, including North Sea), substrate-preference and diet (Table 5). In terms of prey species, also *C. pagurus* and *H. americanus* are quite similar, however a lower trophic level is estimated, namely 3.1 and 3.2 respectively. This is highly likely due to the diet of *C. pagurus* consisting of a higher degree of molluscs compared to *H. americanus*, which diet mostly consist out of crustaceans. Both *C. pagurus* as the *Homarus spp.* are able to crush and consume a wide range of prey. However, dissimilarities are found in species that predate on the decapods, namely much more varied for *C. pagurus* than for *H. gammarus*, according to currently available literature. This might indicate a different degree of potential top-down control on *C. pagurus*, than what could be expected for *H. gammarus*. Nevertheless, crabs are overall more flexible than lobster species, and therefore having the advantage in terms of their speed of digging burrows and hiding for predators (Boudreau & Worm, 2012). Concludingly, *C. pagurus* could be considered an example species for *H. gammarus* only when focussing on their top-down control on the environment.

From this discussion and previous chapters and subchapters, several hypotheses and observations can be compiled, as shown in table Table 6. Accompanied are suggestions for its trophic position within the North Sea benthic ecosystem.

Table 6
Findings on H. gammarus in relation to its trophic position, accompanied by the chapter in which the finding has been previously explained and discussed.

Finding on *H. gammarus*	Discussed in section	Indication on trophic position
Dietary composition: algae consumption only during early benthic phase and larval phase, preying only on primary consumers in later stages. Main prey items are molluscs and other decapods.	2.9	At least secondary consumers. The trophic position of *H. gammarus* appears to be at least higher than TL 2.7 and possibly exceeding 3.8 (based on Figure 9).
Low expected densities on the DCS, absent in monitored OWFs. Modelled calculations based on mussel consumption show resource depletion after 10 years of introduction of *H. gammarus* to OWF ecosystem.	2.1	Currently no to little environmental impact at OWFs, but may be expected after introduction.
High vulnerability to predation in EBP. Uncertainty exists on the degree of *H. gammarus* consumption by predators. Provisioning of shelter shows increases survival rate of juveniles.	Mentioned in 2.7 and further discussed in 4.2.2	Early benthic phase is controlled top-down by predation, but potential bottom-up control is highly uncertain.
Vulnerability of *H. gammarus* to predation decreases with size. Relatively low predation on adult lobster species is expected due to their hard exoskeleton.	Mentioned in 2.7 and 4.1, and further discussed in 4.2.2	Stronger position within the ecosystem during adult phase, may indicate increased competitive abilities towards other species. Minimal top-down control on adult *H. gammarus* expected.
For several lobster species, a keystone role has been found, e.g. trophic cascades with lobster removal.	4.1	Top-down control by *H. gammarus* highly plausible.
Increased capability of consuming larger and more mobile prey with age, that are likely to be secondary consumers.	2.9.2	Trophic position increases with age.
Uncertainty exists on selectivity in diet. Feeds on lower trophic levels, such as infauna, and higher trophic levels, such as crab. *P. guttatus*, a spiny lobster, is known to consume prey of lower TLs within complex habitats (mostly molluscs), compared to less complex habitats (mostly crustaceans)	Selectivity discussed in 2.9.2 and *P. guttatus* mentioned in 4.3.3	Its trophic level may differ with alterations in food availability. Trophic position might differ with habitat type, consuming prey of higher trophic levels when the habitat is less complex.
H. gammarus is closely related to *H. americanus,* not only morphological but also in terms of habitat preferences. However, *H. gammarus* may consume prey species lower down the food web in comparison to *H. americanus,* based on available knowledge on *H. gammarus* diet.	Similarities mentioned in 2.1, 2.4, 2.6.2, 2.7 and 2.9, further discussed in 4.3 and 4.4	TL of *H. gammarus* could be similar or lower to the estimated TL of *H. americanus*, namely 3.2 (Steneck et al., 2004).
H. gammarus is considered to be far less mobile than *H. americanus*, which indicates a smaller niche. Potential balance exists between being an omnivore, yet being restricted to whatever food it can find close to its shelter.	Mobility discussed in 2.8 and diet discussed in 2.9	The scale and level of trophical interactions may differ from that of *H. americanus*. TL may differ with alterations in food availability.
Sedentary behaviour of *H. gammarus* limits its beneficial outputs by bioturbation of suspension feeders to a highly local bound.	4.1	Due to low densities likely to be a limited impact.

Finding on *H. gammarus*	Discussed in section	Indication on trophic position
H. gammarus and *P. cygnus* share many prey species groups, yet *H. gammarus* consumes prey species higher in the food web compared to *P. cygnus.*	4.3	TL of *H. gammarus* is higher than the estimated TL of *P. cygnus* (>2.7).
An overlap between diets and habitat of *H. gammarus* and *C. pagurus* is found.	4.3	Highly likely to lead to competition for food between species when inhabiting similar habitats, e.g. when implementing passive fisheries on these species in OWFs.

5 Potential impact of *Homarus gammarus* introduction to and removal from an ecosystem

As aforementioned, restocking of *H. gammarus* is likely needed to realize fishable and sustainable populations at OWFs. Removing or adding a species to an ecosystem could have significant ecological effects (Boudreau & Worm, 2012). Whether this could be true for *H. gammarus* is discussed in the following sections.

5.1 Potential effects of introduction to an ecosystem

Calculations by Rozemeijer & van de Wolfshaar (2019) show that top-down effects on the local ecosystem may be expected when introducing *H. gammarus* into an environment. They argue that it might lead to decreased populations of their prey species, such as molluscs, in which only prey species that have high reproduction capacities will not get depleted. To make this assumption more quantitative, the exact intake of *H. gammarus* per time unit and area should be investigated, for instance by gut content examination, preferably in relation to local communities at OWFs.

As has been shown for various lobster species, an increase in lobster abundance may have impacts on the ecosystem and may even be able to result in trophic cascades (Boudreau & Worm, 2012). It seems that these effects are mainly felt lower in the food web, and less so in the higher trophic levels. An example is that of *J. edwardsii* within marine reserves. Boudreau & Worm (2012) argued that after fisheries were abolished, an increase in *J. edwardsii* resulted in a reduction of sea urchin abundance. The decline of sea urchin consequently led to decreased predation on kelp, which caused an increase in kelp abundance in the reserve (Boudreau & Worm, 2012). As aforementioned, similar results have been monitored for *H. americanus* (Boudreau & Worm, 2012).

Additionally, although not specific for lobster, Seitz & Lipcius (2001) argue that the presence of benthic predators results in a shift from epifauna to infauna due to high levels of epifaunal predation. This could influence other species that predate on epifauna as well. Additionally, Alexander et al. (2014) have shown that habitat-prey relationships strengthen when predation pressure increases. This means that when predators are added to the ecosystem or increasing in abundance, their prey items start utilizing refuges in a higher degree. Although this might not sound trivial, potential effects of an increased relationship with the seabed could result in significant decreases in abundance and size of prey species when habitat complexity is lacking (Alexander, et al., 2014). On the long run, this decrease in prey species could influence predator populations as well.

5.2 Potential effects of removing out of an ecosystem

An ecosystem that is controlled bottom-up, is expected to stay intact when top-predators are harvested (Fauchald, 2011). In contrast, benthic ecosystems are expected to be controlled top-down, which appear to be less resilient to perturbations on top of a food chain (Fauchald, 2011). Therefore, removal of top-predators, such as *H. gammarus* could result in alternation of dynamics within a benthic community. This is substantiated by Quijon and Snelgrove (2005), arguing that the removal of decapod predators from the ecosystem could result in significant ecosystem changes. This statement by Quijon and Snelgrove (2005) is partially based on a model proposed by Ambrose (1984) that presumes top-down regulation of the benthic environment, as shown in Figure 10.

From previous chapters, the predation on adult *H. gammarus* appears to be limited. However, more information should be gathered on the predation on *H. gammarus* of lengths between 5cm (recommended restocking size, Rozemeijer & van de Wolfshaar, 2019) and adult lobsters. By collecting

knowledge on potential *H. gammarus* predators, the interaction between the lobster and higher trophic levels can be better understood and the consequences of removing the lobster can be better estimated. However, thus far the predation on adult *H. gammarus* seems limited and *H. gammarus* does not appear to be a specific prey species in any animals diet. Hence, removal of *H. gammarus* from the ecosystem does not seem to have (major) consequences up the food chain.

On the other hand, removal of a certain top-predator could support the establishment of another top-predator within the food web (Quijon & Snelgrove, 2005) as an alternative stable state gets established (Fauchald, 2011). For example, as *H. americanus* predates on crabs, it consequently reduces crab predation on their main prey species, such as mussels, therefore preventing overgrazing of the mussel population (Boudreau & Worm, 2012). Removing *H. gammarus* out of the habitat by harvesting may also lead to increased mussel consumption by crabs. Nonetheless, *H. gammarus* is expected to eat a more diverse variety of prey than *H. americanus,* including mussels as a part of its diet. Removing of *H. gammarus* could therefore result in a balance: the mussels that were previously eaten by *H. gammarus* will now be eaten by crabs instead.
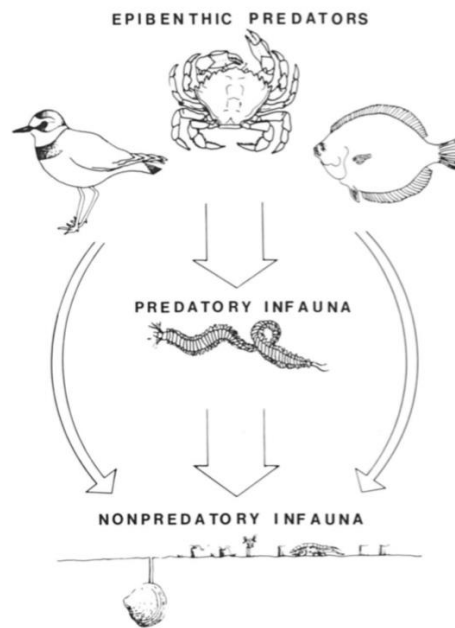

Figure 10   *3-level interactive model between epibenthic predators, infaunal predators and non-predatory infauna. The arrows indicate importance of relationships, with broader arrows being more important (by Ambrose, 1984).*

5.3 In relation to artificial substrate of OWFs

Typically, a windmill that is placed on the DCS, is surrounded by 2,000 m² scour-protection (to prevent sediment erosion by tides and waves) (Coolen, et al., 2019). Epibenthic biomass around an offshore windmill turbine is known to rise 24 times in comparison to soft-sediment (Coolen, et al., 2019). This means, that when 5,000 turbines will eventually be built on the DCS, the benthic biomass will be increased with 0.43% (4,300 tonnes) (Coolen, et al., 2019). At the Dutch OWFs Egmond aan Zee, up to 55 species were found between 2008 and 2011 on the monopiles, 35 species on the scour protection layers and 55 benthos species in the sediment cores (Bouma & Lengkeek, 2012). Bouma and Lengkeek (2012) also found that the soft sediment between scour protection does not only contain soft-substrate species, but also several hard-substrate species, e.g. *Ectopleura larynx,* several crustacean species (*Abludomelita obtusata* and *Phtisica marina*) and worms (*Arenicola defodiens*). These species found at the OWFs provide a valuable food source for birds and fish, in specific the high density of mussels (Bouma & Lengkeek, 2012).

H. gammarus is present in the estuarine and coastal areas in the Netherlands, which has relatively high epifaunal biodiversity in comparison to the soft sediment habitats (Didderen et al., 2019; Overmaat et al., 2020). While this may indicate that their presence does not hinder the development of rich benthic biodiversity per se, these natural populations of *H. gammarus* are often quite low in density. In general, 0.002 individuals/m^2 are found for *H. gammarus* populations, and their density could rise up to 0.27 lobster per m^2 when artificial reefs with crevices especially designed to support lobsters are present (Jensen et al., 1994). The active release of large numbers of the species into an environment, and consequent higher densities, may therefore lead to effects that do not usually occur in natural conditions.

In theory, the environmental effects of introduction and removal of *H. gammarus* from the environment as described in sections 5.1 and 5.2 can be expected when actively stocking *H. gammarus* into OWFs, such as trophic cascades, limited food availability and increased competition. However, uncertainty about the specifics of this environment makes it difficult to predict how this will play out in practice. Calculations of Rozemeijer & van de Wolfshaar (2019) show that the scouring-protection, that provides lobster habitat at monopiles of OWFs, is able to support 1 lobster per 364m^2 (Rozemeijer & van de Wolfshaar, 2019). A linear relation between resource productivity and lobster growth was found, thus the more lobsters are introduced, the smaller the maximum size that is reached will get (Rozemeijer & van de Wolfshaar, 2019). They showed with modelling that when one lobster is put in an ecosystem, resource depletion is visible after 10 years. When two lobsters of 5 cm CL are introduced, the timing of resource depletion seems to coincide with the timing of maturation, after which they will not be able to grow any further. The moment maturation is expected is after three years, based on the model (Rozemeijer & van de Wolfshaar, 2019). However, the lobsters are not expected to starve, since they are able to survive on low resource densities (Rozemeijer & van de Wolfshaar, 2019). However, the size at maturation (calculated in the model at 8.2 cm) has not yet reached the minimum landing size yet. The calculations by Rozemeijer & van de Wolfshaar (2019) show that restocking *H. gammarus* within an OWF could dramatically cumulate the effect on the environment. Improvements for their calculations could however be sought in adding more hard substrate prey species to the population model, instead of only including mussel, and in adding soft substrate areas as potential feeding habitats for *H. gammarus*.

As discussed, Seitz et al. (2001) argue that benthic ecosystems are governed locally mainly by top-down factors. As the main prey of *H. gammarus* are molluscs, molluscs populations might be reduced in abundance after lobster introduction. Moreover, as aforementioned, crab species have similarities with lobster in terms of prey type, are already present in large numbers in OWFs and could become competitors for that reason. This may lead to an even greater reduction in prey numbers, displace or decline the crab population, and/or inhibit or low down the growth of the lobster population. Although the degree in which this will for instance alter the filtering of water by molluscs is expected to be minor, the reduction of (a certain type of) prey species, and/or increasing competition for a single prey species, may have effects on similar species to *H. gammarus* and the upper local food web and in a greater degree.

Beyond that, it might be of more concern if lobsters were to heavily prey on other species, such as the benthic species found in sandy habitats, that were present in local environment before the construction of the OWFs, i.e. before the introduction of hard substrates. This would put additional pressure on species already under pressure from the introduction of the OWFs and alter these soft sediment food webs. Although analysis of the diet of adult *H. gammarus* shows that this effect is unlikely to arise, juvenile *H. gammarus* do prey on small and easily edible organisms, such as meiobenthic crustaceans and foraminifera's, which they harvest from the walls of their burrow. Therefore this relationship should need better understanding before their impacts on soft sediment ecosystems can be ruled out.

6 Conclusion and recommendations

6.1 Conclusions

Most of the DCS consists of soft substrates, where the density of *H. gammarus* is expected to be very low. Research has shown that decapod crustaceans are attracted to newly constructed hard substrate, such as artificial reefs and OWFs. This could provide an interesting opportunity for passive fishing for this species in OWFs, possibly through the introduction and restocking of individuals. To understand the role of *H. gammarus* in the ecosystem, and more specifically the impact of passive fishing on this species in OWFs, this literature review examined the role of *H. gammarus* in the North Sea food web, more specifically in the benthic environment of the southern North Sea, thereby comparing *H. gammarus* with other decapod species. Although extensive monitoring programmes are now being planned, to date there have been very few (recent) published observations of *H. gammarus* in OWFs built on North Sea soft sediments, such as the DCS. Given the *H. gammarus* populations in UK waters and OWFs (Roach et al., 2018), and in Dutch estuarine and coastal waters (for example the Grevelingen lake, as described in Overmaat et al., 2020), the possibility exists that *H. gammarus* has by now colonised OWFs on the DCS through larval migration. Lobster sightings by divers have only been mentioned in a study of Belgian OWF (Mesel et al., 2013) and a loose cheliped of a European lobster was found at the scour protection in Dutch OWF Princess Amalia (Vanagt et al., 2014). This lack in monitoring programmes and sightings complicates the assessment of the impact that presence or absence of *H. gammarus* has within these environments. Therefore, this study is based on available knowledge and theoretical assumptions to try to predict the role of *H. gammarus* in this environment.

The majority of PP within the southern North Sea ends up as detritus, sinking towards the benthic habitat. Benthic species therefore play a major role in the energy flow of biomass. The dominating food web control acting upon the local benthic environment appears to be top-down control by predation. Since *H. gammarus* goes through multiple ontogenetic changes throughout its life, trophic interactions within this North Sea food web are likely to differ through time. As pelagic larvae, a negligible impact on the environment is expected, since the larvae are expected to be opportunistic feeders and predation on these larvae is highly based on chance. When settling onto the benthic habitat, predation on *H. gammarus* juveniles increases significantly. During this period, sufficient supply of suitable habitat, i.e. sediment or crevices in which juveniles can burrow themselves in, is directly correlated to survival rates. This might indicate top-down control on the species population by predation during EBP and juvenile life phases. Furthermore, their hard exoskeleton and increased size result in low vulnerability for predators, other than human impacts. It is therefore expected that top-down control decreases with age. However, previous research has not found significant high numbers of *H. gammarus* in gut contents of their predators, thus *H. gammarus* is likely to be just a small share of their diets. This indicates limited bottom-up control by *H. gammarus*.

Depleted food resources in terms of quantity and quality, within and surrounding its inhabited burrow, result in permanent exit of burrows by juvenile *H. gammarus*, indicating localized top-down control. Moreover, previous studies have argued that removal of decapod crustaceans did increase the levels of infauna significantly. Furthermore, after exiting their burrows, *H. gammarus* become active scavengers and hunters. It is known that during this life stage, larger and more mobile prey are consumed, since their size and chelae enable them to combat a wider range of species. Lastly, calculations have shown that resources density can deplete after introduction of *H. gammarus* to the anti-scouring habitat of OWFs. Concluding from this, top-down control of *H. gammarus* on its environment is expected, growing from local impacts as a juvenile to wider impacts as an adult.

However, detailed information on prey consumption and degree of diversity in diet of *H. gammarus* is still lacking. Moreover, extensive monitoring programmes of species present as well as habitats currently established in OWFs, including those in the DCS, are required prior to incorporating the findings identified in this research into this specific environmental regime. For example, the presence of competing species, such as edible crab, and prey species, such as the blue mussel, greatly influences the behaviour and subsequent impacts of the introduction of *H. gammarus* into the environment.

6.2 Suggestions for further research

Firstly, the abundance of *H. gammarus* in OWFs should be further monitored. It appears logical that with the expected density of lobster in OWFs (1 lobster in circa 300m^2), noticing that one lobster is very difficult for divers, despite systematic monitoring of a habitat. Moreover, research by Skerritt et al. (2012) did appoint that not all samples were equally precise and of high quality (lack of baseline studies, small samples sizes, no repeated surveys, not focussed on *C. pagurus* nor *H. gammarus*) and monitoring of scour protection was not always included, despite the likely possibility of lobsters being present due to a high occurrence of crevices (Hooper & Austen, 2014). Additionally, the productiveness of the seabed within and close to the OWFs should be investigated, considering that this is a prerequisite of survival of juvenile *H. gammarus*.

Secondly, previous calculations show that one *H. gammarus* individual is expected to require an area of 300m^2 in an OWF to sustain its dietary needs (Rozemeijer & van de Wolfshaar, 2019). In order to increase the population to fishable sizes, the habitat around OWFs needs to be further adapted to sustain elevated population levels. Adapting the environment could be done by increasing shelter and food availability.

Thirdly, quantifying dietary preferences of *H. gammarus* could enable profound research on the ecosystem dynamics. Increasing population levels of a previous (almost) absent species, could have cumulative ecological effects that seem negligible per individual. To make this assumption more quantitative, the exact intake of prey species by *H. gammarus* per time unit and area should be investigated, for instance by gut content examination.

Furthermore, predation on *H. gammarus* should be further investigated, although current literature shows low possibility of top-down control by predation on the species. For other lobster species, such as the Caribbean spiny lobster *Panulirus argus,* top-down control by predation of fish, cephalopods, sharks and octopuses has been observed (Boudreau & Worm, 2012). To rule out whether similar interactions are true for *H. gammarus*, more thorough research should be conducted on its predator-prey interactions. However, there a difference in predation per life stage , i.e. between juvenile lobsters and large adult lobsters. This knowledge is especially required to implement a passive *H. gammarus* fishery, without risking great losses of individuals. This could be realized by observing gut contents of potential predators of *H. gammarus*, before and after lobster introduction.

Although exclusion experiments seem highly valuable for understanding ecological impacts of certain decapod species on their environment, no exclusion experiments have been conducted for *H. gammarus* as far as the author is aware. This could be useful in examining its role within the ecosystem, top-down and bottom-up, potentially together with exclusion experiments on *C. pagurus* considering the Win-Wind project.

Lastly, studies on the mobility of *H. gammarus* should be extended, since there exists disagreement on the contrast between sedentary *H. gammarus* and highly mobile *H. americanus*. This contrast could have arisen due to other types of monitoring systems per species. When implementing a passive fishery, exact knowledge on the species mobility is indispensable knowledge.

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8 Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system. The organisation has been certified since 27 February 2001. The certification was issued by DNV.

Justification

Report C070/22
Project Number: 4316100149

The scientific quality of this report has been peer reviewed by a colleague scientist and a member of the Management Team of Wageningen Marine Research

Approved: Ralf van Hal
                 Researcher

Signature:

Date: 16 November 2022

Approved: Jakob Asjes
                 Management team Integration and Science

Signature:

Date: 16 November 2022

Annex 1   North Sea food web dynamics

A simplified schematic overview of the North-Sea food web is shown in
Figure *11* (Heath, 2005). A food web is a composition of multiple integrated food chains that are connected by trophic links. In a food web as well as in an individual food chain, different levels can be allocated based on consumer-resource interactions, called trophic levels (TL). In marine ecosystems, primary production (PP) and detritus are considered to be the foundation of the food web, while apex predators are on the highest ranks (Christensen, 1992). Determining TLs and the accompanied consumer-diet composition can aid the understanding of important ecological linkages between different groups of species within an ecosystem (Fath, 2018). However, also habitat differences and other environmental factors influence a TL of certain species through space and time. Because of this high complexity of food webs, food web models are usually simplified systems compared to natural conditions, e.g. due to necessary aggregation of species into groups, a lack of detail in energy flows or an overemphasis on the role of individual (commercial) species groups.
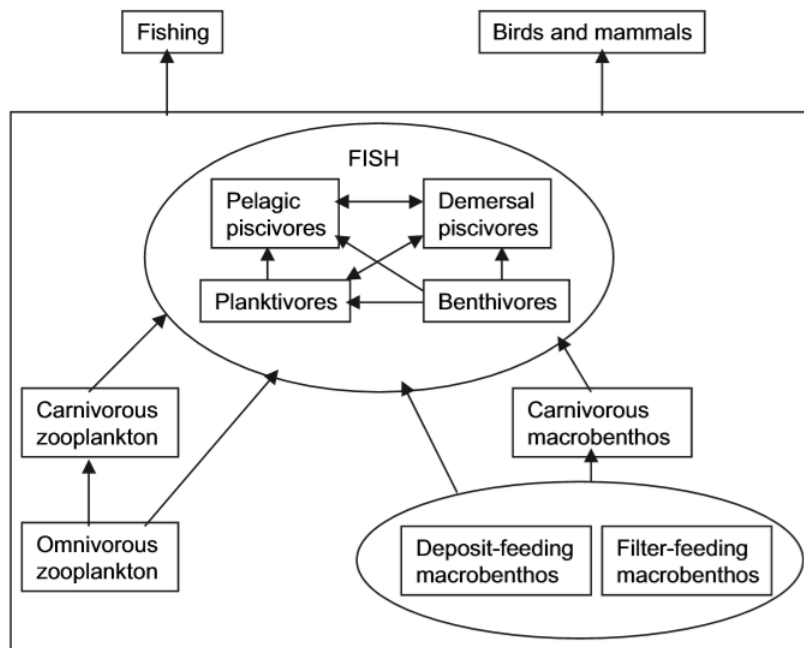

Figure 11   *Schematic overview of the North Sea food-web between trophic levels, showing predator-prey links (prey to predator) although the connection between both birds and mammals with the rest of the system is oversimplified. The higher the trophic level, the more upward the species is illustrated in the figure. Secondary producers are omnivorous zooplankton, deposit-feeders and filter-feeders. (from Heath, 2005). Primary production is not included within this overview, though are the input of biomass for many species groups within the system, e.g. zooplankton and filter-feeding macrobenthos. Abiotic influences are not included within the foodweb either.*

TLs are controlled by species interaction and abiotic influences. Recognition can be made between top-down (e.g. predation) and bottom-up (e.g. prey availability) control (Lynam, et al., 2017). Additionally, a 'wasp-waist control' may be present, which indicates control by an intermediate trophic level that executes control on both upper and lower trophic levels. Although these controls are not mutually exclusive, whether one of these types of controls dominates in an ecosystem, is a frequently asked question within ecological studies (Lynam, et al., 2017). Disruptions in the food web, and hence the controls, can namely lead to cascading effects on distinct trophic levels (Christensen, 1992).

Bottom-up controlled North Sea
Although not included in

Figure *11*, phytoplanktonic PP is the base of the North Sea foodweb (Capuzzo, et al., 2018). The main primary producers in the North Sea are phytoplankton, such as diatoms and dinoflagellates (Mackinson & Daskalov, 2007; Lynam, et al. 2017). When approaching the North Sea ecosystem as a bottom-up controlled ecosystem, the main regulatory role is therefore designated to abiotic influences that influence PP (Lynam, et al., 2017). These drivers include temperature, nutrients and light availability (Capuzzo, et al., 2018; Lynam et al., 2017; Lessin, et al., 2018). In the North Sea PP is highest in terrigenous coastal regions, accounting for 9% of total PP, due to nutrient input from rivers (ICONA, 1992; Capuzzo, et al., 2018; Stäbler, et al., 2018). The Southern Bight is proposed to have the highest estimated annual PP compared to the rest of the North Sea (Rees, et al., 2007).

Just a minority of organic matter produced in PP is directly consumed by higher trophic levels within the pelagic zone, while the majority sinks to the seafloor as detritus and is subsequently consumed by benthic organisms (Mackinson & Daskalov, 2007; Stäbler, 2018). The consequence of this supply of organic matter to the benthic environment is thought to be the main driver of benthic production, abundance and species richness, having a great impact on the benthic-pelagic coupling (Lessin, et al., 2019). It has been found that suspension feeders and deposit feeders respond near-instantaneously to pelagic changes in phytoplankton biomass (Lessin, et al., 2018). A large fraction of PP is also unavailable for zooplankton, since it is lost as dissolved organic matter (e.g. excretion by phytoplankton or not grazed phytoplankton) (Mackinson & Daskalov, 2007). This part of PP is made available again for higher trophic levels via microbiota groups through the microbial loop, a concept first mentioned by Azam et al. (1983).

Moreover, Kröncke (2006) argue that the food availability for macrofauna in the North Sea is highly controlled by regional hydrodynamics, and that the spatial distribution of species is correlated to food availability. Lessin, et al. (2019) argue that macrofauna subsequently play a key role in sustaining fish populations in upper TL. Lastly, although seabirds are top-predators, they are known to be very vulnerable for changes in their prey abundance, mostly planktivorous fish such as sprat (Lynam, 2017). Therefore it seems as if these top-predators are controlled bottom-up instead of governing the ecosystem top-down.

Top-down controlled North Sea

In contrast to the widely recognized assumption that marine ecosystems are controlled bottom-up, a more recent study has shown that the North Sea ecosystem may be controlled top-down (Lynam, et al., 2017). As species on top of the food-chains are removed in large quantities from the aquatic environment by fisheries, the governing role of highest trophic levels becomes clearer (Lynam, et al., 2017). Overfishing of pelagic top-predators, such as whiting and cod, is considered to show top-down control of marine ecosystems (Fauchald, et al., 2011). A schematic overview of these and other pelagic ecosystem interactions is shown in Figure 12. Although Link et al. (2009) question the degree of top-down control cod has due to its low abundance compared to other piscivorous fish, in the Baltic Sea intensive cod fisheries did already result in increased pelagic forage fish abundance (Fauchald et al., 2011). Moreover, apart from pelagic ecosystems, demersal fish abundances are also decreasing due to fisheries (Heath, 2005). The resulting reduced predatory pressure on benthic communities induced growth of crustacean communities (Heath, 2005), indicating a top-down controlled relationship between top-predator abundance and benthic populations. Also direct anthropogenic impact by bottom disturbing fisheries have affected the benthic ecosystem through physical damage and removal of target and non-target species (Gislason, 1994; Groenewold & Fonds, 2000).
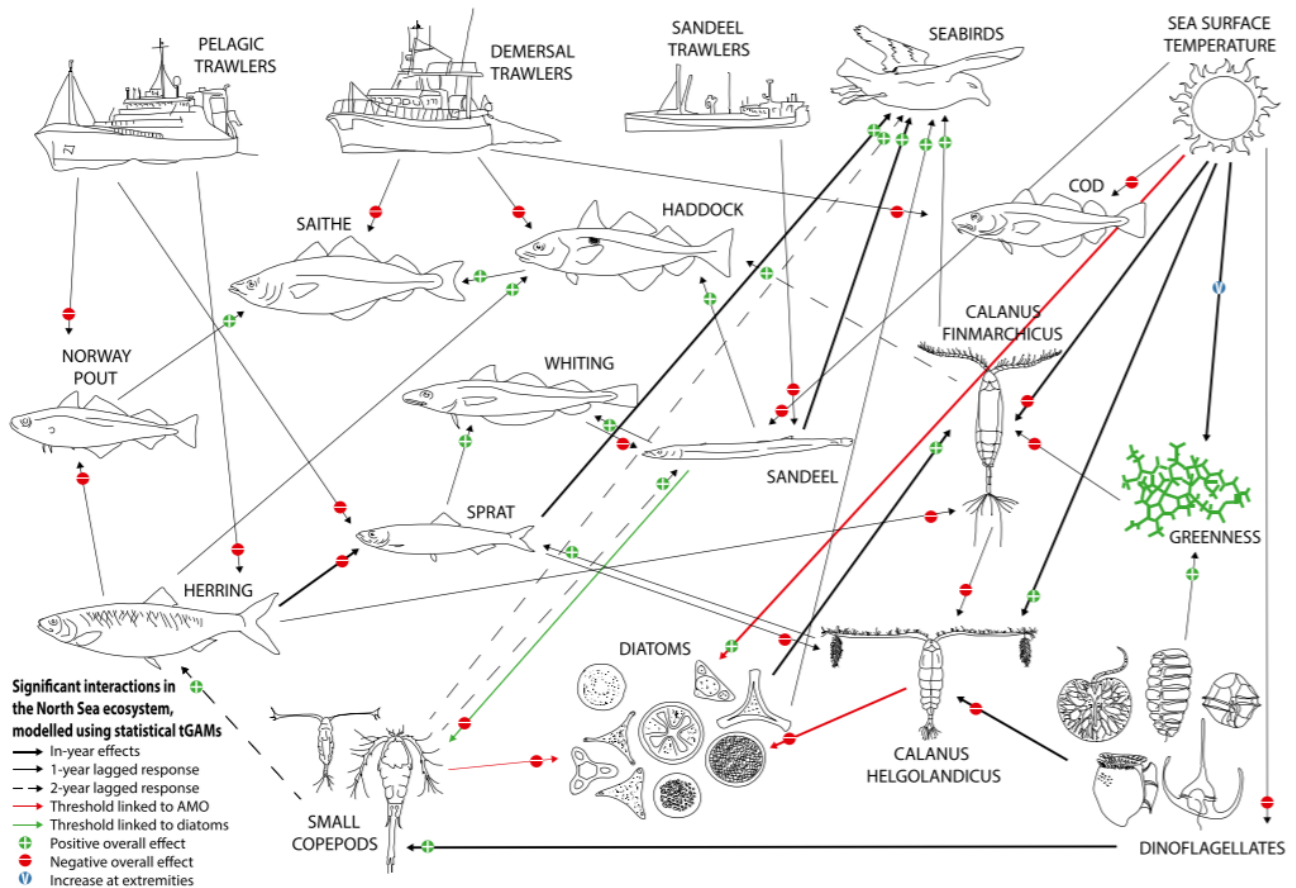
Figure 12 Schematic overview of pelagic North Sea food web with functional groups and drivers (taken from Lynam, et al., 2017)

Wasp-waist controlled North Sea

Wasp-waist controlled ecosystems are governed by an intermediate trophic level that executes control on both upper and lower trophic levels and therefore influencing the ecosystem both bottom-up and top-down. For example, Fauchald et al. (2011) showed that herring was an important regulator of both bottom-up (through predation by seabirds) and top-down (through predation on zooplankton) interactions. Also the mid-trophic level lesser sand-eel (*Ammodytes marinus*) has been described as "*critically important*" within the North Sea ecosystem by Fredriksen et al. (2007). Sand-eels have been recognized as key species within the southern North Sea in other studies as well, exceeding herring and sprat in terms of interconnectedness with other species or species groups (Otto et al., 2019). Its connection with other trophic levels is shown in Figure 13. From this figure it is clearly visible that sand-eels (TL 3) govern the ecosystem by a top-down and bottom-up control. Otto et al. (2019) state that they found an above-average number of species that are dependent on sand-eels within their diets, indicating a bottom-up control. Furthermore, top-down control was explained by the high degree of zooplankton consumption by the species. Compared to all other trophic levels, sand-eels were found to consume the most zooplankton (in g C/m^2/year) (Otto et al., 2019). The control on benthic macrofauna is considered to be highly important as well, potentially through sinks in deceased fish towards the benthic habitat (Otto et al., 2019).
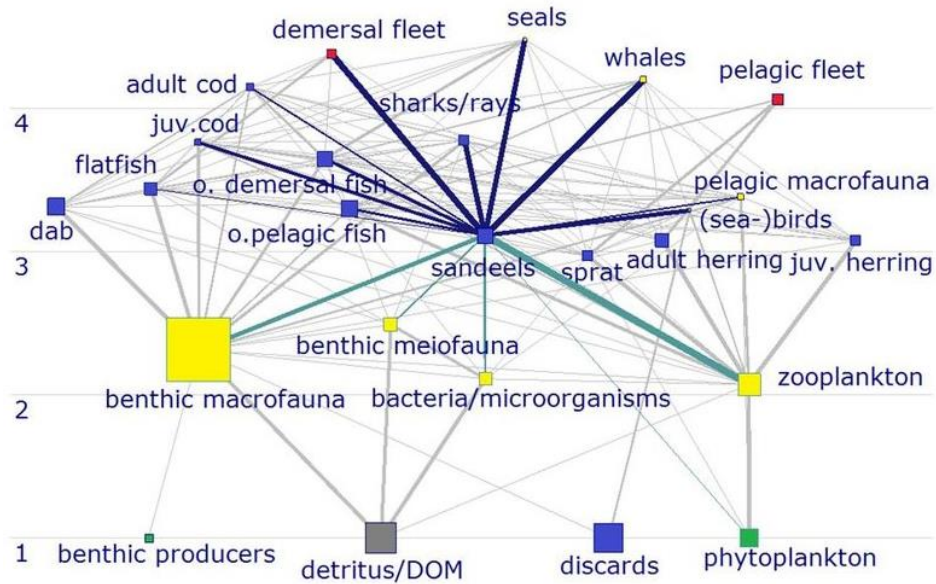
Figure 13 *The key role of sand-eels within a southern North Sea food web showing a wasp-waist control of the ecosystem. Lines show trophic flows. The bolder the line, the bigger the energy flow. Dark blue lines indicate bottom-up control, green lines indicate top-down control. The size of squares is proportional to the biomass of the species group. Green squares indicate primary production, blue squares indicate fish groups, red square indicate anthropogenic influences, yellow squares indicate marine organisms other than fish groups, grey squares are detritus (taken from Otto et al., 2019).*

Annex 2   PCA analysis

Table 7

Data used for PCA analysis per species. Human interactions are excluded (fisheries, bait and bottom disturbance)

Species	Main prey groups	Main predator groups
Homarus gammarus	Larvae: phytoplankton and zooplankton. EBP: small and easily edible organisms, such as bivalves, macroalgae, meiobenthic crustaceans and foraminifera's. Larger lobster: heavy shelled crayfish and fish. (Cooper & Uzmann, 1980; Beard & McGregor, 1991; Loo, et al., 1993; Hudon & Lamarche, 1989; Prodöhl et al., 2006).	During larval stages by pelagic fishes and filter-feeders. During benthic phases consumed by bony fish and elasmobranchs (Phillips et al., 2013; National Lobster Hatchery UK, 2020; Ball, et al., 2001; Hooper & Austen, 2014).
Homarus americanus	Mostly rock crab, mollusks, polychaetas and fish, also sea stars and other lobster species. Diet of smaller lobsters consists mostly of mussels and fewer crab, while the opposite is true for larger individuals. Also shows consumption of algae (Sainte-Marie & Chabot, 2002; Elner & Campbell, 1987; Hudon & Lamarche, 1989; Lavalli & Barshaw, 1989).	During larval stages by pelagic fishes such as shad, rainbow smelt and herring. Early benthic settlers vulnerable for green crab predation. Benthic lobsters consumed by sculpins, various bony fish and elasmobranches (Hanson, 2009; Grabowski et al., 2009; Sainte-Marie & Chabot 2002)
Nephrops norvegicus	Worms, fish and jellyfish (Wikipedia)	*Not included*
Panulirus cygnus	Primarily carnivorous, diet mostly consistent of small crustaceans (crabs and amphipods or isopods). Also considered omnivorous due to foliose red algae and sponges in their diet, although in lower amounts. Invertebrates and rock lobster were also found (Waddington, et al., 2008; Dumas, et al., 2013; Phillips et al., 2013)	Sea lions, seabirds, cephalopods, rock lobster (Dumas, et al., 2013; Phillips et al., 2013; Howard; 1988)
Panulirus argus	*Uncertain, not included*	Fish (Nassau grouper Epinephelus striatus and grey triggerfish Balistes capriscus), the Caribbean reef octopus Octopus briareus, oupers Epinephelus striatus (Boudreau & Worm, 2012).
Panulirus marginatus	*Uncertain, not included*	Large top-predators such as Hawaiian monk seal *Monachus schauinslandi* and fish white ulua *Caranx ignobilis* (Boudreau & Worm, 2012; Phillips et al., 2013)
Panulirus interruptus	Mussels and algae, other bivalves, and limpets (Phillips et al., 2013)	*Uncertain, not included*
Jasus edwardsii	Algae, sea urchin, abalone (Phillips et al., 2013)	Wrasse – fish, octopus, crabs, and large lobsters (Phillips et al., 2013)
Cancer pagurus	Carnivorous diet: molluscs, crustaceans and echinoderms (Neal & Wilson, 2008; Tonk & Rozemeijer, 2019).	Bony fish and elasmobranchs, top-predators, such as seal, cod and wolf fish (Neal & Wilson, 2008; Tonk & Rozemeijer, 2019)
Carcinus maenas	Mussels, clams, snails (Elner, 1981)	Lobster (*H. americanus*) and Asian shore crabs (Lord & Dalvano, 2015)
Callinectes sapidus	Clams, amphipods, polychaetes, crustaceans and algae (Seitz, 2011)	Bony fish and top-predators, e.g. birds and elasmobranchs (Woodbury, 1986)
Cancer irroratus	Polychaete Pholoetecta and the clam Macoma calcarean (Quijon & Snelgrove, 2005)	Cod, herring gull Larus agentatus and ring-billed gull (Boudreau & Worm, 2012)

Table 8

Presence-absence table of prey species per decapod based on Table 5. Presence is indicated by 1, absence by 0.

Prey	Macroalgae	Molluscs: bivalves, chepalopoda, gastropoda	Echinoderms	Polychaetes	Small crustaceans	Big crustaceans (incl. decapoda)	Fish
H. gam	1	1	0	0	1	1	1
H. ame	1	1	1	0	1	1	0
N. norv	0	0	0	1	0	0	1
P. cyg	1	1	1	0	1	1	0
J. edw	0	0	1	0	0	0	1
C. pag	0	1	1	0	1	1	0
C. sap	0	1	0	1	0	0	0
C. mae	0	1	0	0	1	0	0
C. irro	0	1	0	0	0	0	0

Table 9

Presence/absence table of predator groups per decapod based on Table 5. Presence is indicated by 1, absence by 0.

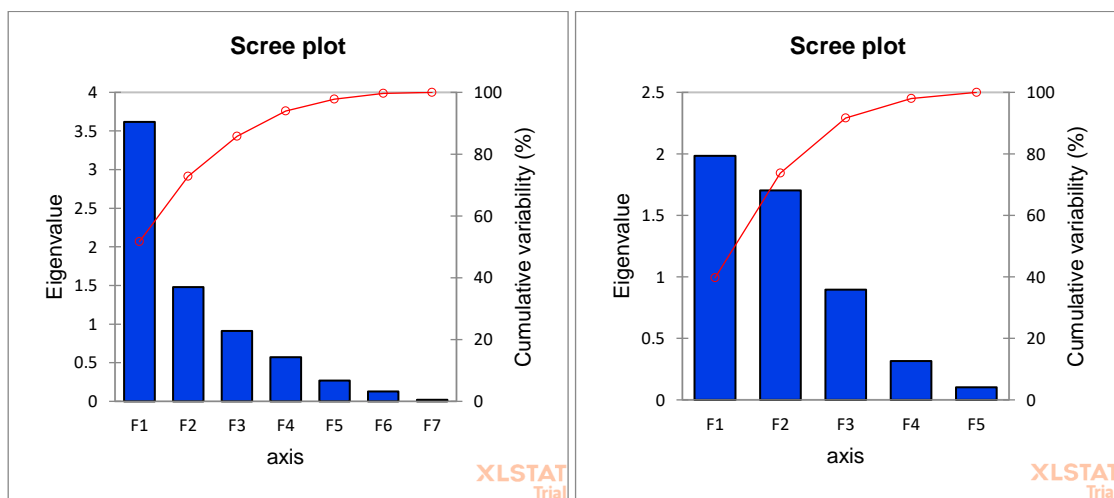| Predator	Cephalopods	Small crustaceans	Big crustaceans (incl. decapoda)	Fish
H. gam	0	1	1	1
H. ame	0	1	0	1
N. norv	0	0	0	1
P. cyg	1	0	1	0
J. edw	1	1	1	1
C. pag	1	1	0	1
C. sap	0	0	0	1
C. mae	0	0	1	0
C. irro	0	0	0	1

Figure 14 *Scree plot for prey species accompanying PCA plot in Figure 9A (on the left) and scree plot of predator groups accompanying PCA plot in Figure 12B (on the right)*

With knowledge, independent scientific research and advice, **Wageningen Marine Research** substantially contributes to more sustainable and more careful management, use and protection of natural riches in marine, coastal and freshwater areas.

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