

Predation pressure on zooplankton communities in the Dutch Wadden Sea

A review



Bachelor thesis

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Predation pressure on zooplankton communities in the Dutch Wadden Sea and methods to investigate gut contents of zooplanktivorous predators

Bachelor Thesis

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Summary

Zooplankton composition and abundance are known to be a fundamental component in the marine food web in both, top down and bottom up processes. However, research on zooplankton composition in the Dutch Wadden Sea has received limited attention during the past decades and is therefore not directly considered in any national and European legislation concerning the protection of this area. In order to sustain and improve the numerous nature values of the Dutch Wadden Sea, additional research on zooplankton communities and its role in the Wadden Sea environment is needed. This knowledge is crucial for the translation into adequate policy and management.

The Dutch research institute, Wageningen Marine Research (WMR) has therefore set up a project to develop knowledge on biodiversity monitoring of zooplankton in the Dutch WS and large freshwater bodies, and to promote its inclusion in relevant policy frameworks. Zooplankton can be ingested by a wide range of higher trophic levels such as small pelagic fish (Chordata), filter-feeding benthos (Mollusca), gelatinous zooplankton (Cnidaria/Ctenophore) and crustaceans (Arthropoda). Top-down predation on zooplankton communities can have strong effect on their composition and development, and impact food webs in the Dutch Wadden Sea.

This review is conducted to give an overview of the current knowledge on which zooplankton groups are eaten by the most dominant predator species in the Dutch Wadden Sea, and how predation on zooplankton can be investigated through gut inspection. By means of existing literature as well as expert interviews, a selection of dominant zooplanktivorous species distributed over various phyla could be determined: herring (*Clupea harengus*), sandeel (*Ammodytes tobianus*), blue mussel (*Mytilus edulis*), cockle (*Cerastoderma edule*), moon jellyfish (*Aurelia aurita*), comb jelly (*Mnemiopsis leidyi*) and brown shrimp (*Crangon crangon*). For each selected species, visual models were created to illustrate abundance/biomass and the predation pressure on different zooplankton groups.

This study shows that the main predation pressure in the Dutch Wadden Sea is found to be on calanoid copepods, being the main prey item of *C. harengus*, *A. tobianus*, *C. edulis*, *A. aurita* and *M. leidyi*. Bivalve veligers are also found to be widely ingested by predator species, with the main predators being *M. edulis*, *C. edule* and *M. leidyi*. This is followed by predation on mysids, mainly by *A. tobianus* and *C. crangon*, as well as harpacticoid copepods preyed by *A. tobianus* and *M. edulis*. In order to investigate zooplankton ingestion by those predator species microscopically, the dissecting method is shown to be the most successful. In addition, the 'flushing' method is another effective way to obtain gut contents of small pelagic fish and ctenophores. For further microscopic as well as DNA analysis of gut contents, the preservation of samples in 96 % ethanol is the preferred method.

The results of this research underpin the important role of zooplankton in the marine trophic food web as well as the need for additional research to eliminate the still existing knowledge gaps on those predator-prey-interactions. Zooplankton needs to be recognized as a key component in the marine ecosystem and should therefore be monitored on a regular basis in order to provide the scientific foundation for adequate management and protection of the Wadden Sea area.

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Abbreviations

WS	Wadden Sea
NS	North Sea
Microzooplankton	Zooplankton size of < 200 µm
Mesozooplankton	Zooplankton size of 0.2 – 2 mm
Meroplankton	Only a part of the life cycle spend as plankton (usually larval or juvenile stage)

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1 Introduction

The Dutch Wadden Sea ecosystem

The Dutch Wadden Sea (WS) is a unique coastal ecosystem and therefore of great natural, scientific, economic and social importance. It is part of one of the last remaining large-scale intertidal ecosystems, stretching along the North Sea (NS) coast of Denmark, Germany and the Netherlands (Marencic, 2009). The Dutch WS consists of an area of 2,500 km² and is separated from the NS by a series of barrier islands (Fig. 1) (Dankers & Zuidema, 1995).

The ecosystem has evolved over the last 8,000 years by complex physical and biological interactions which formed a range of different habitats, such as extended tidal channels, sea-grass meadows, mussel beds, sandbars, mudflats, estuaries, beaches and dunes. These numerous different environments of the WS are basis for a species rich environment, providing habitat and niches for up to 10,000 species of plants and animals (Marencic, 2009; Reise et al., 2010; Wehrmann, 2014). It is one of the most significant breeding areas of birds in western Europe and is also of outstanding importance for migratory birds, as it provides staging and moulting area, accessibility of food, and a low level of disturbance (Marencic, 2009; Reise et al., 2010).



Figure 1: The Dutch Wadden Sea (Elias et al., 2019).

For its outstanding geological, ecological and biodiversity values, the WS was inscribed on the UNESCO World Heritage List. In addition to its ecological value, the WS provides many ecosystem services and is therefore also of economic and social importance. Consequently, the protection and sustainable use of the Dutch WS ecosystem and its biodiversity is of importance. The area is covered by means of several regulations on regional, European and international level, such as the Key Planning Decision Wadden Sea (PKB-Wadden Sea), Natura 2000 (under the Birds - and Habitats Directive), Water Framework Directive, Trilateral Wadden Sea plan (WSP), Ramsar Convention, and OSPAR Convention (CWSS, 2017; Marencic, 2009). In addition, the 2019-2022 Program Plan of the 'Program for a Rich Wadden Sea (PRW)' intends to improve the nature values in the WS with attention to the transition of important knowledge into policy and management on a national and international level (Tjaden et al., 2018). Yet, the ecosystem is facing a number of threats, for example increased human activity, pollution, eutrophication and climate change (Marencic, 2009; Wadden Sea Board - Task Group Climate, 2017). Especially increasing water temperature due to climate change may seriously impact the functions and characteristic biodiversity of the WS ecosystem, as numerous processes of marine organisms are temperature regulated (O'Connor et al., 2007; Wadden Sea Board - Task Group Climate, 2017). This may lead to a shift of zooplankton composition, as well as to a change in seasonal occurrence of certain zooplanktivorous species (Daewel et al., 2014; Frederiksen et al., 2006; van Walraven, 2016).

Zooplankton communities and composition

In order to properly protect the Dutch WS area, more insight is needed in the food web of the ecosystem, including zooplankton and its role in this environment. Zooplankton communities (Greek: Zoon, animal; planktos, wandering) are a fundamental component in the marine food web and are crucial for the proper functioning of aquatic ecosystems (Greve et al., 2001; Heiskanen et al., 2016). It forms a major link between primary production and higher trophic levels, as it transfers organic energy produced by unicellular algae through photosynthesis to higher trophic levels, such as pelagic and benthic communities (Heiskanen et al., 2016). Consequently, the carrying capacity of pelagic and benthic ecosystems, as well as the abundance of marine wildlife is greatly dependent on zooplankton dynamics, composition and abundance (Edwards et al., 2020; Heiskanen et al., 2016).

Despite its importance, zooplankton research in the WS has received limited attention during the past decades. Most knowledge on zooplankton stems from investigations during the late 1970's and start of the 1980's (e.g. Baretta & Malschaert (1988); Colebrook (1984); Fransz & van Arkel (1983)). Due to this lack of knowledge, zooplankton abundance and composition are not directly considered in any national and European legislation concerning the protection of the Dutch WS. The Dutch research institute, Wageningen Marine Research (WMR) has therefore set up a four-year project in order to develop knowledge on biodiversity monitoring of zooplankton in the Dutch WS and large freshwater bodies and to promote its inclusion in relevant policy frameworks. One of the aims is to explore the role of zooplankton in the food web, and to identify how this can be done experimentally, such as microscopic inspections as well as with DNA identification techniques. With a gut content analysis approach, a determination of the importance of different zooplankton prey items will be possible, which henceforth provides the basis for understanding trophic interactions in marine food webs (Manko, 2016).

Predation pressure on zooplankton

Although it is known that the zooplankton communities are structured through bottom-up effects, studies also show that top-down control of zooplankton exerted by predator species is of equal importance (Daewel et al., 2014; Dinasquet et al., 2012; Fauchald et al., 2011; Lynam et al., 2017; McNamara et al., 2013). Several studies confirm that zooplankton can be ingested by a wide range of higher trophic levels, such as small pelagic fish, filter-feeding benthos, gelatinous zooplankton and crustaceans (Davenport et al., 2000; Oh et al., 2001; Raab et al., 2012; van Walraven, 2016). Dense populations and seasonal peaks of these species can thus have a strong effect on the development of zooplankton communities and impact planktonic food webs in the Dutch WS (Ojaveer et al., 2017; van Walraven, 2016; Wong et al., 2003).

For this study, a pre-selection of the species groups pelagic fish (Chordata), filter-feeding benthos (Mollusca), gelatinous zooplankton (Cnidaria/Ctenophore) and crustacea (Arthropoda) was made in accordance with Wageningen Marine Research (WMR). Pelagic fish are highly abundant in the Dutch WS and even exceed the biomass of demersal fish by an order of magnitude (Couperus et al., 2016). They play a critical role in the food web, both as consumer and prey alike, and juveniles of numerous species use the WS area as nursery habitat (Couperus et al., 2016; Dänhardt & Becker, 2011; Kellnreitner, 2012; Munk & Christensen, 1990; Tulp et al., 2008). Also, filter-feeding bivalves are of major importance in terms of biomass, ecological values, as well as for commercial purposes (Beukema & Cadée, 1996; Folmer et al., 2014; Nehls et al., 2009). In addition, gelatinous zooplankton form a significant part of the Dutch WS ecosystem, as they can occur in high numbers and therefore compete

for food with other zooplanktivorous species (van der Veer & Oorthuysen, 1985; van Walraven, 2016). Another key component of the WS trophic web is formed by crustacea, due to their important role as predators as well as food source for numerous species (Beukema, 1991; Campos et al., 2010).

Although these species groups are highly abundant in the Dutch WS, no research in this area has been conducted yet on which species may influence specific zooplankton groups by means of exerted predation pressure. As the project set up by WMR aims to investigate predation pressure on zooplankton experimentally, the most dominant predator species need to be identified first. In this context, dominant species are defined as species that are highly abundant in the Dutch WS and feed on zooplankton. Once determined, methods on their gut extraction and preservation of contents for further microscopic inspection as well as later DNA analysis need to be examined.

In this review, the predation pressure on zooplankton by the most dominant species of the species groups, Chordata, Mollusca, Cnidaria/Ctenophore and Arthropoda has been investigated, as well as methods on how to assess their gut contents.

1.1 Problem statement

In the Dutch WS, the role of zooplankton cannot be fully understood as knowledge on the predation pressure on zooplankton exerted by dominant predator species is missing. For those predator species, methods for further experimental investigations of their gut contents need to be assessed.

1.2 Objective

The aim of this review is to give an overview of current knowledge on which zooplankton groups are eaten by the most dominant predator species in the Dutch WS and to prioritize which species are most relevant for further experimental studies on zooplankton predation by means of gut analysis.

Our research will be a first step towards a more comprehensive study on zooplankton predation in the Dutch WS area. This knowledge is crucial to manage zooplankton communities and to adequately protect the WS and its ecosystem services in future.

1.3 Research questions

Question 1: Which species groups of zooplankton in the Dutch Wadden Sea are consumed by which dominant species in the food chain?

Question 2: And what is a preferred method to extract gut contents to investigate zooplankton ingestion by these dominant predators?

1.4 Reading guide

The following chapter defines the scope of the study as well as methods used for data collection and analysis are elaborated in the methods section.

In Chapter 3, the results are illustrated and explained by means of models in order to provide an overview of the predation pressure exerted on specific zooplankton groups by dominant predator species. This is followed by a step by step description on how to investigate predation on zooplankton of the selected species by means of gut analysis.

The discussion and conclusion are noted in Chapter 4, where findings are concluded and set into wider perspective. A critical consideration on the outcome takes place, as well as on the methods used to answer the research questions. Hereafter, references and appendices are attached.

2 Methods

This research was divided in six different steps, which are elaborated in Figure 2 and explained further below.



Figure 2: Step-by-step illustration of methods used.

For this research, the search engine Google Scholar, as well as databases and online libraries Research Gate, Springer Link, JSTOR, Wiley Online Library, Oxford Academic and World Register of Marine Species (WoRMS) were used. The entire review is based on peer-reviewed papers, and addition of specific expert comments.

2.1 Study scope and species selection

The focus of this study is on the Dutch part of the Wadden Sea (WS). However, if information was scarce the scope was broadened to other parts of the WS and the North Sea (NS). For information on feeding and diet studies, papers from other regions were included as well.

For this study, a pre-selection of the species groups Chordata, Mollusca, Cnidaria/Ctenophore and Arthropoda was made in accordance with Wageningen Marine Research (WMR). Based on this pre-selection, a systematic literature review using the meta-synthesis approach was conducted (Onwuegbuzie & Frels, 2016). By means of this approach, qualitative and quantitative data, such as information from existing studies, papers and interviews, were accumulated, analysed and interpreted.

2.2 Research steps

In this section, the different steps applied are described in more detail:

Step 1. Creating a database (excel table)

In order to make a selection of the most important species in the Dutch WS and accumulate information about its predation pressure on zooplankton, an excel table was created (Appendix I). This table is composed with selective criteria (abundance/biomass; zooplankton predation and feeding behaviour) and informative criteria (occurrence and life cycle; ecological and economical value; life stage predation on zooplankton; species composition in Wadden Sea).

The selective criteria were determined in order to estimate 'dominance' of the species for further selection. For the first selective criterium, both metrics 'Abundance' and 'Biomass' were taken into account depending on the literature available. The informative criteria were included for additional information to be able to create illustrations per selected species in step 5.

In order to get information on the selective and informative criteria, key words were used for searching literature which are noted down below.

- Key words selective criteria:

Most abundant, Most common, Abundance, Biomass, Density, (Dutch) Wadden Sea, North Sea, Chordata, Fish, Pelagic fish, Jellyfish, Medusae, Cnidaria, Ctenophore, Mollusca, Mussel, Bivalve, Crustacea, Arthropoda, Zooplankton, Predation pressure, Diet

- Key words informative criteria:

Life-cycle, Occurrence, Life-stages, Juvenile, Adult, Role/Importance in ecosystem, Seasonality, Ecological importance, Feeding mechanism, Feeding behaviour, Food source, Prey catch, Economical value

For all search terms, the species name was added. These keywords were also used in combination with each other and the Latin names were used over common names (Table 1). In this way, inconsistency in common names may be bypassed and a broader spectrum of literature, including Dutch, German and Danish papers would become available.

Table 1: The Latin and English names of the most abundant species in the Dutch Wadden Sea (based on WoRMS). Also, former names of the species were used (indicated in table with *)

Latin name of species	English name of species
<i>Sprattus sprattus</i>	Sprat
<i>Clupea harengus</i>	Herring
<i>Sardina pilchardus</i>	Pilchard
<i>Engraulis encrasicolus</i>	Anchovy
<i>Aurelia aurita</i>	Moon jellyfish, Common Jellyfish
<i>Cyanea lamarckii</i>	Blue Jellyfish
<i>Cyanea capillata</i>	Lion's mane jellyfish
<i>Chrysaora hysoscella</i>	Compass Jellyfish
<i>Rhizostoma octopus</i>	Barrel Jellyfish
<i>Pleurobrachia pileus</i>	Sea gooseberry
<i>Mnemiopsis leidyi</i>	Comb jelly, Sea walnut
<i>Cerastoderma edule</i>	Common Cockle
<i>Mya arenaria</i>	Sand gaper, Soft-shell clam
<i>Limecola balthica</i> , <i>Macoma balthica</i> *	Baltic tellin, Baltic macoma
<i>Magallana gigas</i> , <i>Crassostrea gigas</i> *	Pacific oyster
<i>Mytilus edulis</i>	Blue mussel, Common mussel
<i>Ensis leei</i> , <i>Ensis directus</i> *	Atlantic razor clam, American jack knife clam
<i>Crangon crangon</i>	Brown shrimp, Common shrimp
<i>Carcinus maenas</i>	Shore crab, Green shore crab, Common shore crab
<i>Austrominius modestus</i> , <i>Elminius modestus</i> *	Australasian barnacle/New Zealand barnacle
<i>Corophium volutator</i>	Mud shrimp, European mud scud

Step 2. Identifying knowledge gaps

Based on the accumulated data, knowledge gaps were identified when information was scarce and/or unavailable. Blind spots in the excel table were concluded if information about criteria was missing or unclear.

Step 3. Interviews

In order to fill knowledge gaps and/or to eliminate uncertainties, the research method was expanded by means of interviews. Experts from the respective fields, which were chosen based on WMR network and authors from literature used, were contacted via email. Prior to the interview, specific questions for each interview were formulated in a way knowledge gaps can be eliminated (see Appendix II). Also, logistics during the interview were planned beforehand, as roles between the authors were divided into interviewer and notetaker. The interviews were conducted via video call. Gained information from the interviews was referenced in the report according APA 7th edition (e.g. Expert A, personal communication, July 15, 2020). Due to policy reasons, the interviewed experts are not cited in the report, but can be contacted via WMR if required.

Step 4. Species selection

In order to select the most dominant predator species, the selective criteria were ranked (see Table 2 as example). Each criterium was weighted with numbers from 3 to 1 (3 = high, 2 = medium and 1 = low) based on its abundance/biomass and feeding behaviour. Then, the sum was taken for all criteria, whereby a high score indicates high dominance and a low score low dominance. Criteria with a high score are coloured green, medium is orange and low is coloured red (for complete table see Appendix I). If a species scored either 'No' or 'Unknown' on the criteria 'Predation on zooplankton', the species was excluded from further analysis. If a species was found to feed besides zooplankton mainly on other species, the criteria was coloured green/red (e.g. see *Magallana gigas* in Appendix I).

Table 2: Example of the ranking method in order to select the most dominant species. The whole database can be found in Appendix I

Species (lat.)	Abundance/Biomass in the Wadden Sea (high/medium/low)	Predation on zooplankton (Yes/ No/Unknown)	Feeding behaviour (zooplanktivorous/opportunistic/unknown)
<i>Aurelia aurita</i>	HIGH – Most abundant Scyphozoan species in Dutch Wadden Sea (van Walraven, 2016)	YES - copepods as main food source; phytoplankton (diatoms and flagellates), ciliates, rotifers, barnacle nauplii and cyprids, copepod nauplii, gastropod and bivalve larvae, polychaete larvae (Stoecker et al., 1987); predator of plaice and flounder larvae (van der Veer, 1985)	Opportunistic - feeds on micro/mesoplankton although able to catch prey the size of small fish larvae (Hay et al., 1990)
<i>Chrysaora hysoscella</i>	LOW - Abundances much lower than <i>A.aurita</i> : in all years, the mean daily number of individuals caught always averaged below 30 and 60 individuals, respectively; commonly found in most Dutch coastal waters (van Walraven et al., 2014)	YES - copepod and other crustacean species, fish larvae, including clupeids; decapod larvae (<i>Brachyura</i> and <i>Caridea</i>); Echinodermata larvae (<i>Brachiolaria</i> and <i>Ophiuroidea</i>). Fish larvae (<i>Syngnathidae</i> , <i>Clupeidae</i> , <i>Trachurus trachurus</i>) (Barz & Hirsche, 2006)	Opportunistic - (Hay et al., 1990; Barz & Hirsche, 2006) Scyphomedusae are efficient, opportunistic predators in the patchy planktonic environment. They grow rapidly and have effective foraging behavior and feeding mechanisms and a wide dietary range (Hay et al., 1990)

<i>Pleurobrachia pileus</i>	MEDIUM - According to Van Walraven (2016) always present from several observations between 1982 and 2012; During 1980s: most abundant gelatinous zooplankton species (van Walraven, 2016). Densities ranged from 1 to 20 individuals per m ³ (Kuipers et al., 1990)	YES - copepods (10 to 20 per day) (Kuipers et al., 1990); predation on plaice and flounder larvae (van der Veer, 1985); large crustacean zooplankton (>1050 µm) were the dominant item, principally calanoid copepods (Frank, 1986)	Opportunistic - Frank (1986) examined fish eggs and <i>Oikopleura</i> sp. in less than 2% of the stomachs examined
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By means of these criteria (Table 2), the most dominant species of each species group in the Dutch WS could be selected for the purpose of our study.

Step 5. Visual model

For each selected species, the predation on different zooplankton species was illustrated by means of a visual model. Within these models, the qualitative as well as quantitative information and data accumulated about abundance/biomass and zooplankton predation was processed and illustrated (see Fig. 3). The abundance of each species was displayed per month, whereby one individual indicates the lowest occurrence and three individuals the highest. The primary zooplankton prey items were illustrated in the middle, surrounded by secondary zooplankton prey ingested by the predator species. Thereafter, a general model was created to give an overall overview of the predation pressure on zooplankton exerted by dominant predator species. For each zooplankton group, the respective predator was included, whereby the main predators were highlighted with a red circle.

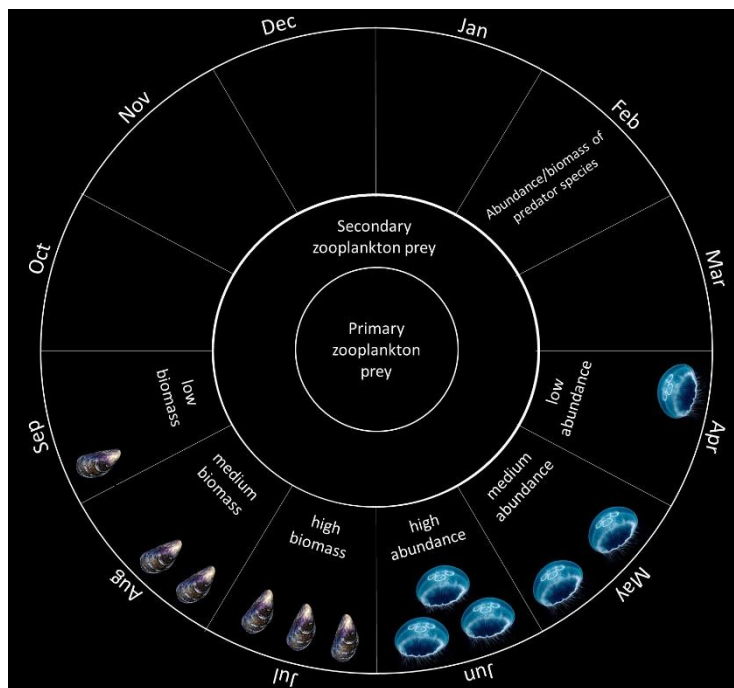


Figure 3: Scheme used for visual models to display occurrence of selected species and its predation pressure on zooplankton.

The results of each predator species were subdivided into two sections, 'Occurrence' and 'Zooplankton predation'. This was done to provide compact and detailed information about what message will be conveyed in the respective visual model.

Step 6. Gut content analysis

For obtaining information about gut extraction, additional literature per species groups was searched and experts were interviewed. Therefore, components of methods were selected based on their feasibility for conducting experimental gut content analysis upon agreement with the problem owner, WMR. The removal and preservation of the gut contents are based on methods which prevent the damage of the intestines, enable microscopic zooplankton identification and allow further DNA analysis. If information was scarce or unclear, recommendations and advices of experts were included (see Step 3: Interviews).

The following key words were used:

Gut content, Diet study, Preserving for DNA analysis, Feeding experiment, Feeding rates

3 Results

For this review, the most dominant species of four different phyla in the Dutch Wadden Sea (WS) were selected based on the excel database (see Appendix I). Within the phyla Chordata, the two pelagic fish herring (*Clupea harengus*) and sandeel (*Ammodytes tobianus*) were selected; for Mollusca, the two bivalves blue mussel (*Mytilus edulis*) and common cockle (*Cerastoderma edule*); for Cnidaria/Ctenophore, the moon jellyfish (*Aurelia aurita*) and comb jelly (*Mnemiopsis leidyi*); and for Arthropoda, the brown shrimp (*Crangon crangon*).

3.1 Overall predation pressure on zooplankton groups

In the Dutch WS, calanoid copepods form a prey item of all selected predator species as shown in Figure 4. In this model, an overall overview of the predation pressure on zooplankton groups for each selected predator species is given.














This study shows that the main predation pressure on calanoid copepods is exerted by *C. harengus*, *A. tobianus*, *M. edulis*, *A. aurita* and *M. leidyi*.







Bivalve veligers are also found to be widely ingested by predator species, with the main predators being *M. edulis*, *C. edule* and *M. leidyi*. This is followed by predation on mysids, mainly by *A. tobianus* and *C. crangon*, as well as harpacticoid copepods predated by *A. tobianus* and *M. edulis*.

Amphipods are also found to be ingested by a variety of predator species, being an important prey item of *C. crangon*. The same is found for crustacean post-larvae and cypris larvae, being mainly predated by *M. edulis*. In addition, nauplius larvae, cladocerans, fish larvae, ctenophores and rotifers are consumed by several predator species, and hydromedusae is found to be an important prey item of *C. edule*.



Figure 4: Predation pressure on zooplankton groups by the selected predator species. The different zooplankton groups are placed in the outermost circle (for detailed description on species groups see legend Figure 5). Per zooplankton group, the respective predator species is visualized in the inner circle. Predators which exert the main predation pressure on a certain zooplankton species are circled in red. This model shows that calanoid copepods are preyed upon by most predator species, followed by bivalve veligers, harpacticoid copepods and mysids.

Crustacea	
	Calanoid copepod 0.2 – 5 mm
	Harpacticoid copepod 0.2 – 2.5 mm
	Cumacean 1 - 10 mm
	Mysid 9 – 22 mm
	Euphausiid 1 -15 cm
	Amphipod 0.5 – 25 mm
	Isopod 0.3 mm – 50 cm
	Cladocera 0.2 – 6.0 mm
	Ostracod 0.1 – 2 mm
Larval stages	
	Cypris 0.6 – 1.2 mm
	Nauplius 0.2 – 1 mm
	Zoea 1.2 - 4.5 mm
	Post-larva (megalopa, parva) 1.2 - 4.5 mm

Mollusca	
	Bivalve veliger 0.5 mm
	Gastropod larva 0.1 – 1 mm
Rotifera	
	Rotifer 50 µm – 2 mm
Annelida	
	Polychaeta larva 70 µm – more than 5 mm
Chordata	
	Fish larva 3 mm – few cm
Tunicata	
	Larvacea < 10 mm






Cnidaria	
	Planula larva 0.5 mm
	Ephyra larva 2 – 10 mm
	Hydromedusa 2 mm – 30 cm
Ctenophora	
	Ctenophore 0.2 mm – 1.5 m
Echinodermata	
	Echinodermata larva 0.3 mm – few cm

Figure 5: Legend of zooplankton groups found to be ingested by selected predator species, arranged in their respective phylum. The larval stages of crustaceans were included as well, as they were found to be an important food item of the selected predator species. Sources of pictures see section ‘References of pictures used in models’.

3.1.1 Pelagic fish in the Wadden Sea

Pelagic fish have an important role in coastal ecosystems, as they form a major link between plankton and higher trophic levels. They are a major food source for predatory fish, sea mammals and birds (Couperus et al., 2016; Dänhardt & Becker, 2011). According to a survey by Couperus et al. (2016) in the western Dutch WS, the abundance of pelagic fish exceeds the biomass of demersal fish by an order of magnitude. The WS provides an important nursery area for juveniles of commercially exploited species such as herring (*Clupea harengus*), sprat (*Sprattus sprattus*) pilchard (*Sarinda pilchardus*), anchovy (*Engraulis encrasicolus*) and sandeel (*Ammodytes sp.*) (Couperus et al., 2016; Dänhardt & Becker, 2011; Munk & Christensen, 1990; Tulp et al., 2008).

3.1.1.1 *Clupea harengus*

Clupea harengus is together with *Sprattus sprattus*, the most dominant pelagic fish in the WS, a major commercial species in the North Sea (NS), as well as a crucial element in the food chain (Couperus et al., 2016; Dänhardt & Becker, 2011; Dickey-Collas et al., 2010).

Occurrence

C. harengus primarily uses the WS as nursery area, and recruits from NS autumn and winter spawning populations. However, local groups of NS herring may be found spawning in almost any months, whereby spawning of herring from February until July is negligible (Bolle et al., 2007; Couperus et al., 2016; Daan et al., 1990; Dänhardt & Becker, 2011). Larval herring arrive in the WS nursery grounds via passive drift in early spring (February/March), where they metamorphose into juvenile herring. After hatching, it typically takes 3- 11 months (typically 6) for the larval stage to be completed and to enter the juvenile stage (Kellnreitner, 2012; Munk & Christensen, 1990).

Due to the high biomass of larvae arriving in spring from their spawning grounds in the NS, high abundance of juvenile herring is found in summer (Dickey-Collas et al., 2010; Kellnreitner, 2012). According to a study in the German WS, abundance in the months of June and July is highest (wet weight $3.0 \pm 1.8 \text{ g m}^{-3}$) (Kellnreitner, 2012). This is followed by a steep decline from August to September (wet weight $0.01 \pm 0.01 \text{ g m}^{-3}$), and even decreases more in October and November (Bleijswijk et al., 2020; Kellnreitner, 2012).

The average length of herring in the WS ranges between 9.1 cm and 12.5 cm, though larger individuals up to 30 cm can be found. Herring leave the nursery grounds when about 2 to 3 years old until they are mature (mostly at 3 years of age), and then join the adult population in the NS (Stroud, 1972).

Zooplankton predation

Once the larvae arrive at the WS nursery grounds, they start to feed on crustacean nauplii and other microzooplankton, moving to small planktonic copepods in the first year. Thereafter the main prey items are calanoid copepods, but also small crustaceans (amphipods, cumaceans, euphausiids, mysids), megalopa larvae, sandeel larvae and ctenophores (FAO, 1985; ICES, 2006; Kellnreitner, 2012; Raab et al., 2012; van Gindereuren et al., 2013). According to a study by Kellnreitner (2012) in the German WS, the predation impact of *C. harengus* on calanoid copepods is highest in June and July. This zooplankton group also forms the main food source in September, followed by cypris and nauplii larvae.

In the NS, the main feeding time of herring is from April to June, whereby calanoid copepods are eaten in large numbers in spring and smaller copepods dominate the diet in summer. Feeding intensity reduces in the build up to spawning and little feeding occurs over winter (ICES, 2006). Herring is known to be a more specialized feeder, with low diversity of food items (Raab et al., 2012). They can switch between filter and particulate feeding, however, they selectively feed on larger zooplankton prey (Kellnreithner, 2012; Sandström, 1980).

It can be concluded that predation pressure of WS herring is mainly exerted on calanoid copepods, followed by other crustaceans, as well as on fish and crustacean larval stages (see Fig. 6).

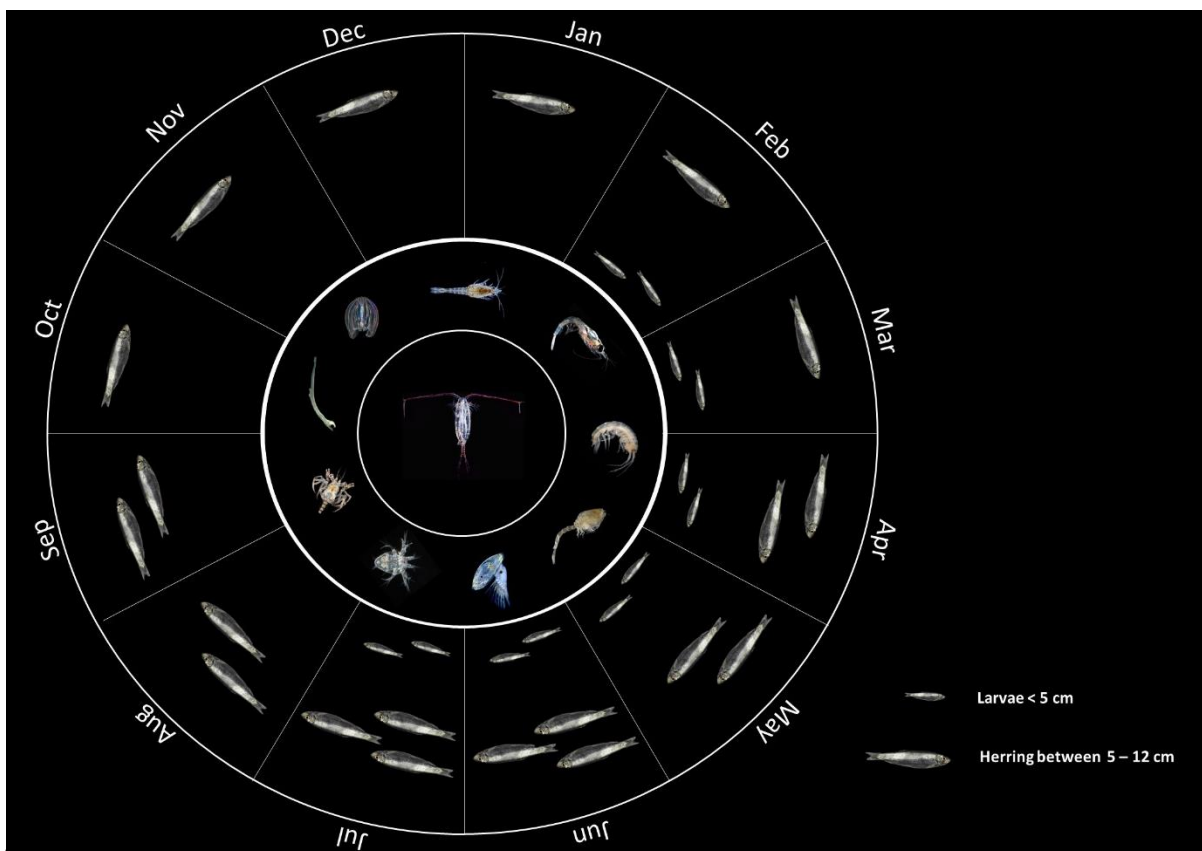


Figure 6: The occurrence of *Clupea harengus* in the Dutch Wadden Sea and its predation pressure on different zooplankton groups. The abundance of *C. harengus* species is displayed per month in the outermost circle, whereby one individual indicates the lowest occurrence and three individuals the highest. The predation on different zooplankton groups is visualised in the inner circles. The primary zooplankton prey items are illustrated in the middle circle, surrounded by secondary zooplankton prey. This model shows that *C. harengus* is most abundant in the summer months (June and July), and that they predominately prey on calanoid copepods, next to other crustacean zooplankton, their larval stages as well as fish larvae and ctenophores.

3.1.1.2 *Ammodytes tobianus*

There are three species of sandeel present in the Dutch coastal waters, *Ammodytes tobianus*, *Ammodytes marinus* and *Hyperoplus lanceolatus* (Tien et al., 2017). *A. tobianus*, however, is the most important sandeel in coastal areas and a resident species in the WS (ICES, 2006; Kellnreitner, 2012; Tulp et al., 2017b). It is a demersal schooling fish and provides an important food resource for many predatory fish, seabirds and marine mammals. Especially seabirds during the breeding season in the NS area feed predominantly on sandeels and are thus strongly impacted by their abundance (Frederiksen et al., 2006; Furness & Tasker, 2000). Frederiksen et al. (2006) suggests a strong bottom-up control of sandeel abundance, as it shows to be determined by the abundance of zoo- and phytoplankton.

Occurrence

Coastal sandeels spend the majority of their lifespan in the WS (Bolle et al., 2007). Data from the NS shows, that sandeel spawn in spring (March, April & May) and in winter (November, December) (Daan et al., 1990). Larvae hatch from February to May and the duration of the larval phase is between 1 to 3 months. Larvae are planktonic until reaching a length around 25 mm (Jensen et al., 2003; Lynam et al., 2013). Information of sandeel spawning in the WS is not available. However, as their preferred spawning substrate is on sandy grounds, this might also be applicable for the WS (Daan et al., 1990; Tien et al., 2017).

In a study in the Sylt-Romo bight, *A. tobianus* is together with *C. harengus*, the most abundant species in bottom trawl catches (Kellnreitner, 2012). Also, a study in the western Dutch WS by Couperus et al. (2016), shows that sandeel is together with sprat and herring, commonly caught in trawl catches and the second most abundant species found in May. Similar observations are made by Bleijswijk et al. (2020), where the pelagic peak in the western WS of *A. tobianus* is found to be in May/June. However, the species abundance is found to diminish in fall and is close to zero in winter, most likely because they stay buried in the seabed during the day from late summer to spring (Couperus et al., 2016; Kellnreitner, 2012). The average size found of *A. tobianus* in the western WS is 10.7 up to 16.1 cm, but they can grow up to 20 cm (Couperus et al., 2016).

Despite its importance as a food item for many prey species, no exact number of sandeel abundance in the WS is available. Sandeel is often not included in trend analyses of fish monitoring programmes, as they are difficult to monitor quantitatively in the deployed gears (Jager et al., 2010; Tulp et al., 2017a).

Zooplankton predation

Sandeels forage in schools on zooplankton, including copepods, amphipods, isopods and their pelagic as well as crustacean larvae, whereas copepods are the dominant food items (Frederiksen et al., 2007; O'Connell & Fives, 1995). A study by O'Connell & Fives (1995) in Galway Bay, Ireland shows that sandeel mainly feed on calanoid copepods followed by harpacticoid copepods. The second most important species are mysids, being even the dominant one in July and August. Peak feeding intensity of sandeels is found to be in April, coinciding with a peak growing period, whereas most stomach contents from November to March are found empty. Sandeel larvae feed mainly on copepod nauplii (Lynam et al., 2013).

It can be concluded, that in the WS *A. tobianus* feeds mainly on calanoid and harpacticoid copepods, followed by copepod nauplii and small crustaceans, such as mysids (Fig. 7).



Figure 7: The occurrence of *Ammodytes tobianus* in the Dutch Wadden Sea and its predation pressure on different zooplankton groups. The abundance of *A. tobianus* species is displayed per month in the outermost circle, whereby one individual indicates the lowest occurrence and three individuals the highest. The predation on different zooplankton groups is visualised in the inner circles. The primary zooplankton prey items are illustrated in the middle circle, surrounded by secondary zooplankton prey. This model shows that *A. tobianus* is most abundant in the months of May and June. *A. tobianus* preys mainly on calanoid copepods, harpacticoid copepods and mysids, next to other crustacean zooplankton groups, crustacean larval stages and their fish larvae.

3.1.2 Filter-feeding benthos in the Wadden Sea

A long-term study (46 years) of macrozoobenthos in the WS tidal flats reveals that the most abundant bivalve species in terms of biomass have been the cockle (*Cerastoderma edule*), the blue mussel (*Mytilus edulis*), the sand gaper (*Mya arenaria*), and the baltic clam (*Limecola balthica*) (Beukema & Dekker, 2019).

However, successful invaders such as the razor clam (*Ensis leei*) and the pacific oyster (*Magallana gigas*) are now found in high numbers throughout the WS (Diederich et al., 2005; Nehls et al., 2009; Reise et al., 2005). *E. leei* successfully inhabited an empty niche and forms an important prey item for flatfish and bird species. Currently *E. leei* is the most common shellfish species in the WS coastal zone, leading to an increasing trend in total zoobenthic biomass (Dekker & Beukema, 2012; Tulp et al., 2010). The rapid spread of *M. gigas*, however, is leading to a noticeable change in habitat structure of WS mussel beds and is considered to be a potential risk to the blue mussel population due to competition for food and space (Nehls et al., 2009).

Bivalves species were considered to mainly feed on phytoplankton for a long time. Several studies, however, pointed out that zooplankton actually can be an important food source for bivalve molluscs (Davenport et al., 2000; Lehane & Davenport, 2002, 2004, 2006). Stomach content analyses show that bivalves are able to ingest a variety of zooplankton organisms (Lehane & Davenport, 2002, 2004, 2006).

3.1.2.1 *Mytilus edulis*

The bivalve *Mytilus edulis* is a key species of the Dutch WS ecosystem and is found in intertidal beds as well as subtidal beds and culture plots (Baer et al., 2017; Dankers & Zuidema, 1995). Through its high suspension-feeding and filtering activity, it forms an important link between the primary producers and higher trophic levels, as well as between the benthic and pelagic zone (Beukema & Cadée, 1996; Kamermans, 1994; Lüskow & Riisgård, 2018). The mussel beds of *M. edulis* serve as habitat and food source for many other species, and thus facilitate biodiversity (Folmer et al., 2014; van der Zee et al., 2012). *M. edulis* is a commercial fished species in the Dutch WS. Due to heavy exploitation of natural intertidal mussel bed, mussel cultivation is since 1991 restricted to subtidal areas, where young or half-grown mussels ('seed mussels') are collected on wild mussel beds to stock bottom culture lots and suspended seed mussel collectors (ropes and nets) (Baer et al., 2017; Nehls et al., 2009).

Occurrence

Peak settlement of spat occurs around June, leading to the appearance of young mussels by the end of June and beginning of July. This suggests that the main spawning event of mussels in the WS occurs between April and June, followed by smaller spawning events along the summer (Cardoso et al., 2007; de Vooys, 1999). The duration of the total larval period ranges from 3 to more than 5 weeks before metamorphosis and settlement (Figueira et al., 2015).

In a stock assessment in spring 2018, the biomass of *M. edulis* in the Dutch WS was estimated to be about 55,5 million kg wet weight, whereby more than 60 % are located in the western part. From the total biomass, 95 % consist of adult and older mussels (> 25 mm, up to 20 years, and sexually mature), and only 5 % of young mussels (< 25 mm, < 1 year, and sexually immature) (van den Ende et al., 2018). According to a study in the western Dutch WS by Cardoso et al. (2007), growth in terms of body mass of *M. edulis* increases from January to July. Peak body mass occurs in July while the period with lowest mass is between December and February. A study by Dankers & Zuidema (1995), shows similar growth

patterns, where mussel weight increases from spring on, and decreases again from August on, whereby 50 % of the weight is lost by December. According to a study in the Danish WS, mussels will attain on average a size of up to 15 mm in the period between spat fall beginning of July and winter but may even reach a size of up to around 30 mm if spat fall occurs early (Munch-Petersen & Kristensen, 2001).

Zooplankton predation

While mussels are known to ingest phytoplankton, they also take up large numbers of micro- and mesozooplankton. Although they are able to ingest zooplankton prey up to and larger than the mesozooplankton size range ($> 200 \mu\text{m}$), studies show that *M. edulis* selectively consume smaller zooplankton categories (Davenport et al., 2000; Horsted et al., 1988; Lehane & Davenport, 2002; Wong et al., 2003). A study by Mavraki et al. (2020), in the NS, shows that most of the diet of *M. edulis* consists of various zooplankton groups – mainly crab larvae and copepods. According to studies by Lehane & Davenport (2002, 2004, 2006) in bays in Scotland and Ireland, the main groups ingested by mussels are calanoid and harpacticoid copepods, crustacean nauplii, barnacle cyprids, and bivalve larvae. Also, amphipods, ostracods, cladocerans, hydromedusae and rotifers are ingested (Davenport et al., 2000; Lehane & Davenport, 2002; Wong et al., 2003; Wong & Levinton, 2004, 2006). Pelagic larval stages ($< 1.5 \text{ mm}$) feed predominately on small phytoplankton (Bos et al., 2006). Smaller *M. edulis* ($< 25 \text{ mm}$) have the capacity to filter out mesozooplankton from the water column shown by a study of Lehane & Davenport (2002). However, they may be more opportunistic than larger bivalves ($> 25 \text{ mm}$), as the smaller mussels generally filter on smaller particles in higher rates than adults (Jacobs et al., 2015). Davenport et al. (2000) and Lehane & Davenport (2002) suggest that the ingestion of zooplankton size and species does not differ between benthic and pelagic *M. edulis*. According to numerous studies, filtration activity of *M. edulis* is attributed to changes in particle concentrations, phytoplankton composition and temperature (Cranford & Hill, 1999; Prins et al., 1994; Widdows et al., 1979).

No studies were found on the feeding of mussels on zooplankton in the WS. However, according to Lehane & Davenport (2002, 2004, 2006), next to phytoplankton, *M. edulis* are likely to feed mainly on micro- and mesozooplankton, such as smaller sized copepods and other invertebrate larvae (Fig. 8).

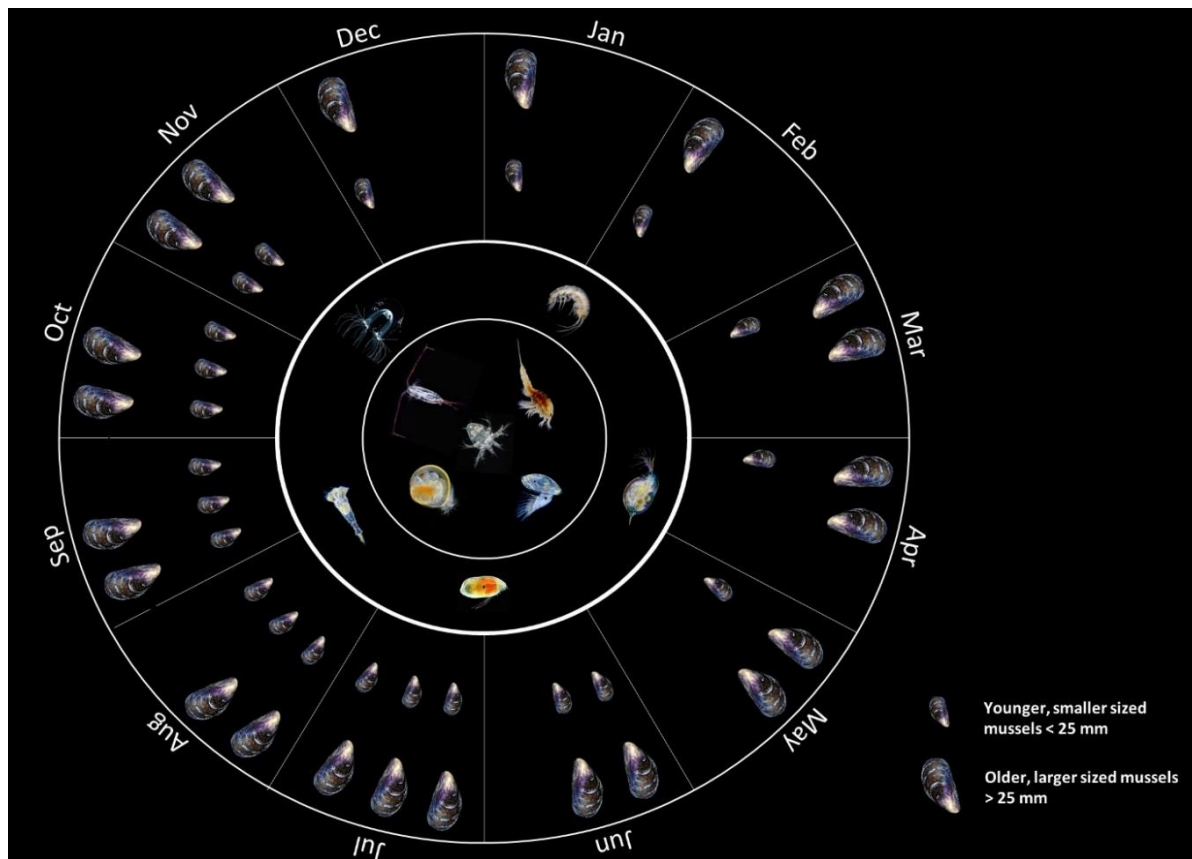


Figure 8: The occurrence of *Mytilus edulis* in the Dutch Wadden Sea and its predation pressure on different zooplankton groups. The abundance of *M. edulis* is displayed per month in the outermost circle, whereby one individual indicates the lowest occurrence and three individuals the highest. It is to be noted here that in this model the biomass of the species is displayed. The predation on different zooplankton groups is visualised in the inner circles. The primary zooplankton prey items are illustrated in the middle circle, surrounded by secondary zooplankton prey. This model shows that the biomass of *M. edulis* is highest in summer and autumn. Within the zooplankton, *M. edulis* preys on a variety of groups, mainly compiled of calanoid copepods, harpacticoid copepods, crustacean larval stages and bivalves veligers.

3.1.2.2 *Cerastoderma edule*

The cockle (*Cerastoderma edule*) is common in both, intertidal and subtidal areas, in the Dutch WS, where they play an important role in terms of biomass, productivity and suspension-feeding activity (Cardoso et al., 2009; Dekker, 1989). In the past, cockle fishery removed a substantial part of the available cockle stocks. Low cockle stocks have caused ecological problems, including declines in bird species such as the oystercatcher (*Haematopus ostralegus*) and eider (*Somateria mollissima*) (Beukema & Dekker, 2006). In the present, manual cockle fishery is taking place in designated areas with restricted annual harvest (Baer et al., 2017).

Occurrence

According to a study by Compton et al. (2013), *C. edule* contributes the largest share of the benthic biomass in the eastern part of the Dutch WS and contributes a large share of biomass with two other bivalve species (*Mya arenaria* and *Ensis leei*) in the western part of the system. The overall biomass of *C. edule* in the Dutch WS was estimated to be 196,4 million kg in spring 2019, and 308,1 million kg in autumn 2019 (van Asch et al., 2019).

For cockle populations in the WS, annual recruitment varies widely from year to year and experience high fluctuations in annual biomass on WS tidal flats. *C. edule* is sensitive to extreme climate conditions, and mortality increases with strong winters and hot summers. After high mortality of cockle, larvae recruitment is usually high (Beukema & Dekker, 2020; Beukema & Dekker, 2006; Beukema et al., 2001). Settlement of *C. edule* spat starts end of April and peak numbers are reached in the beginning of June (van der Veer et al., 1998). According to Cardoso et al. (2009), *C. edule* reaches a shell length of 4.3 cm and rarely exceed 6 years of age in the WS.

Studies by Zwarts (1991) and Honkoop & Beukema (1997), observed decreasing body mass in autumn and winter (November – March) due to low food supply. According to Honkoop & Beukema (1997), body mass increases again prior to spawning in the second half of May, and Zwarts (1991) observed a peak in May/June. In the western WS, maximal biomass values are observed in August around the end of the second growing season (about 1.3 years after their settlement) (Beukema & Dekker, 2006).

Zooplankton predation

Cockles are known to be generalist, opportunistic feeders, which feed on phytoplankton, detritus and also zooplankton (Kang et al., 1999; Malham et al., 2012; Rossi et al., 2004). Numerous studies show that adult *C. edule* can ingest a variety of zooplankton species, but selectively consume smaller categories of zooplankton (Lehane & Davenport, 2002, 2004; Malham et al., 2012). Stomach content analysis shows the ingestion of calanoid copepods, harpacticoid copepods, crustacean nauplii, barnacle cypris, bivalve larvae, cladocerans, euphausiids and hydromedusae (Lehane & Davenport, 2002, 2004). Another study by André & Rosenberg (1991) observes the depletion of bivalve larvae up to 40 % around adult *C. edule*.

Pelagic larval stages of *C. edule*, like other bivalves, feed mainly on small phytoplankton (Bos et al., 2006). In comparison with *M. edulis*, *C. edule* ingested significantly shorter prey items but can ingest three to four times more food per hour, which indicates a shorter gut passage time than in *M. edulis* (Hawkins et al., 1990; Lehane & Davenport, 2002). This is confirmed in a study by Lehane & Davenport (2002), which shows that *C. edule* consumes the greatest number of zooplankton, primarily in the form of small hydromedusae. Beukema et al. (2001) and Troost et al. (2009), also observe larviphagy in cockles, as dense adult stocks of *C. edule* suppress their own recruitment. Several studies point out

that zooplankton is especially an important food source for bivalves during periods of low phytoplankton biomass (Cranford & Grant, 1990; Ezgeta-Balić et al., 2012).

Based on these studies, it can be concluded that *C. edule* in the WS are likely to feed, besides phytoplankton, on a variety of micro- and mesozooplankton compiled of copepod crustaceans, crustacean larval stages and invertebrate larvae, but mainly ingests bivalve veligers and hydromedusae (see Fig. 9).

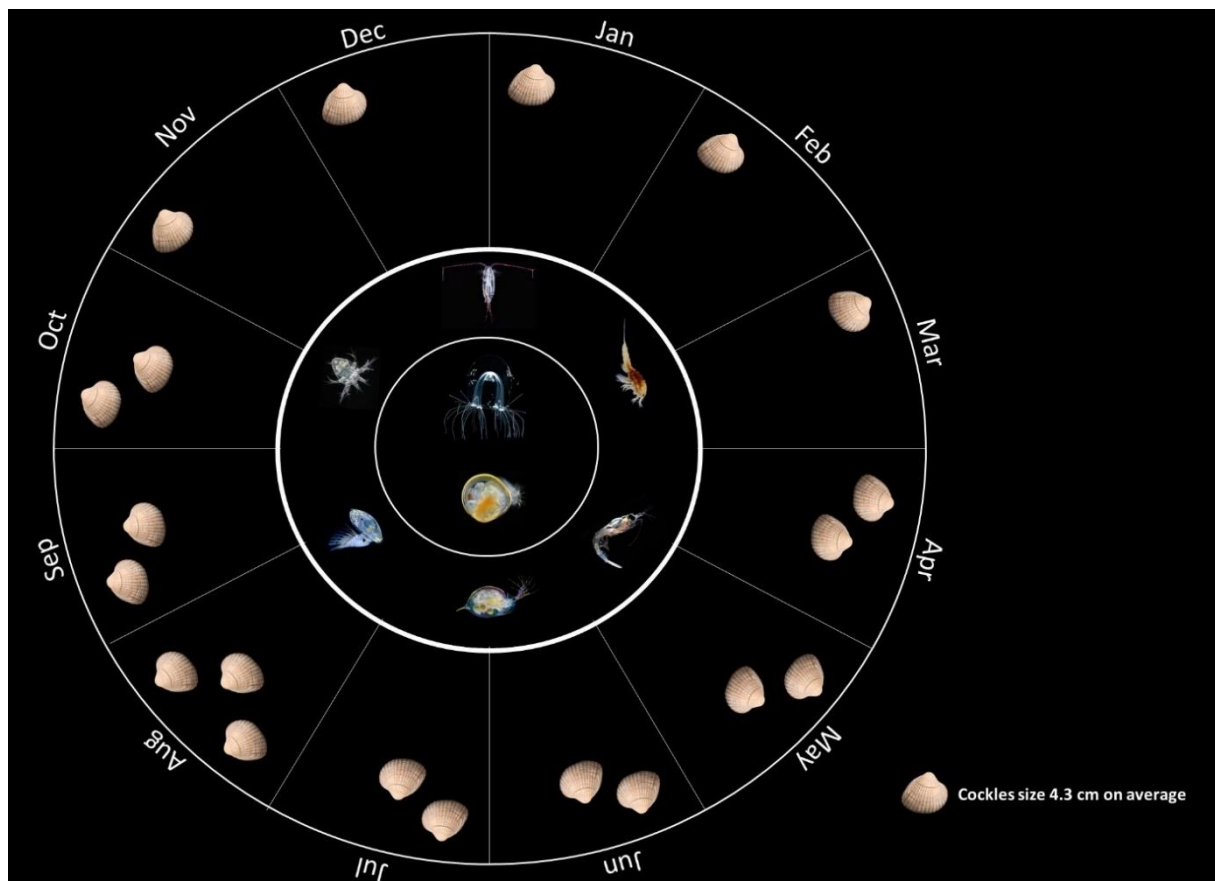


Figure 9: The occurrence of *Cerastoderma edule* in the Dutch Wadden Sea and its predation pressure on different zooplankton groups. The abundance of *C. edule* is displayed per month in the outermost circle, whereby one individual indicates the lowest occurrence and three individuals the highest. It is to be noted here that in this model the biomass of the species is displayed. The predation on different zooplankton groups is visualised in the inner circles. The primary zooplankton prey items are illustrated in the middle circle, surrounded by secondary zooplankton prey. This model shows that the biomass of *C. edule* is highest in August. Within the zooplankton, *C. edule* preys predominately on bivalve veligers and hydromedusae, next to a range of other crustacean zooplankton groups and their larval stages.

3.1.3 Gelatinous zooplankton in the Wadden Sea

Gelatinous zooplankton are very important members of the marine ecosystem where they have major implications for the structure and function of the food web through top-down and bottom-up control mechanism (Archdale & Anraku, 2005; Dinasquet et al., 2012). The WS ecosystem is mainly influenced by jellyfish through competition for food with other zooplanktivorous species and the predation impact on fish larvae (van der Veer & Oorthuysen, 1985; van Walraven, 2016).

According to Van Walraven (2016), five scyphomedusae (*Aurelia aurita*, *Chrysaora hysoscella*, *Cyanea capillata*, *Cyanea lamarckii*, *Rhizostoma octopus*) and two ctenophores (*Mnemiopsis leidyi*, *Pleurobrachia pileus*) are commonly found in Dutch coastal waters and can occur in high numbers in the Dutch WS.

3.1.3.1 *Aurelia Aurita*

The common moon jellyfish, *Aurelia aurita*, is the most abundant scyphomedusae in the Dutch WS and has a worldwide distribution in temperate and tropical coastal waters (Lucas, 2001; Stoecker et al., 1987; van Walraven, 2016). In dense aggregations during spring and summer, medusae can have considerable impact on coastal ecosystems through their high predation rate and competition with other species for food (Lesniewski et al., 2015; Möller, 1980; Stoecker et al., 1987). Medusae blooms can also have industrial consequences such as clogging of power station sea water inlets and economic damage through affecting aquaculture, fishery and tourism (Hay et al., 1990; Lesniewski et al., 2015).

Occurrence

Medusae of *A. aurita* are present in the Dutch WS from around March and strongly increase in numbers in April. From May to July, the medusae occurs in peak densities with maximum numbers of 250 to 500 individuals 1000 m⁻³. Hereafter, the numbers decrease again and is almost complete absent in August (van der Veer, 1985; van Walraven, 2016; van Walraven et al., 2017). According to Van Walraven (2016) in some years, the medusae were present after the summer as well, the latest in October.

A. aurita has an annual life cycle involving a pelagic medusa and a benthic polyp stage. In early spring until the end of May, the polyps, reproduce asexually and release tiny pelagic medusae (ephyrae) of 2 mm in size into the water column, which transform into a new generation of medusae (Riisgård et al., 2012; van der Veer & Oorthuysen, 1985; van Walraven, 2016). Polyps (2.0 mm in mean diameter including tentacles) can live for several years attached on various hard substrata e.g. artificial substrates or natural substrates such as bivalve shells (Gröndahl, 1988; van Walraven, 2016; van Walraven et al., 2020). Within a few months, the medusae reach a mean bell diameter of 10 to 15 cm and continuous to increase till July – August, when individuals with a diameter of 25 cm or more can be found (Båmstedt et al., 2001; van der Veer & Oorthuysen, 1985). In summer (July and August), the spawning of adult medusae occurs, whereafter the medusae degrow and usually die in autumn (Schneider & Behrends, 1994; van Walraven, 2016). From the fertilized eggs, free-swimming planula larvae hatch which settle on a suitable surface and develop into polyps (van Walraven, 2016). In September, a decrease of individual size and number can be observed (Schneider & Behrends, 1994).

Zooplankton predation

A. aurita is an opportunistic planktonic predator which feeds on micro- and mesozooplankton and is able to catch prey size of small fish larvae of e.g. plaice and flounder (Hay et al., 1990; van der Veer, 1985). In areas such as the Scottish east coast, dense swarms of *A. aurita* can consume 29-89 % of the daily mesoplankton production (Hay et al., 1990).

Gröndahl (1988) described the polyps of *A. aurita* as opportunistic which occasionally prey on planula larvae of the scyphozoa *C. capillata* and their own species. Besides, a variety of other organisms were captured and eaten by the polyps such as mussel larvae, gastropod larvae, fish larvae (herring) and calanoid copepods (Gröndahl, 1988).

The ephyra larvae feeds on a large variety of prey types which range in length from 0.1 to 5.0 mm, such as rotifers, copepods nauplii and barnacle nauplii (Båmstedt et al., 1994, 2001; Sullivan et al., 1994). Hansson (2006) & Båmstedt et al. (1994, 2001) prove additionally the ingestion of calanoid copepods and hydromedusae by the ephyra larva.

According to Sullivan et al. (1994) and Hansson (2006), the patterns of prey selection change with increasing size of the medusae. Smaller individuals (< 12 mm) ingest mostly hydromedusae while larger individuals (up to 3 cm diameter) feed more on barnacle nauplii, and great numbers of calanoid copepods (Sullivan et al., 1994). Stoecker et al. (1987) shows that small < 6 cm as well as large > 6 cm medusae predate on microplankton including rotifer, polychaete larvae and copepod nauplii, whereby copepod nauplii are selected over rotifers and polychaete larvae. Through the potential fast growth of *A. aurita*, a high food demand is expected, resulting in a possible heavy predation pressure on zooplankton (Möller, 1980; Stoecker et al., 1987). However, after spawning, a deformation of the medusae, and hence a decrease of diameter size occurs, which leads to a decreased ability to feed (Schneider & Behrends, 1994; Stoecker et al., 1987). According to Schneider & Behrends (1994), 80 % of the ingested prey biomass in the Kiel Bight consists of calanoid copepods, 15 % of other organisms such as mysids, polychaetae, isopods and amphipods and 5 % of bivalve larvae. Hansson (2006) shows selectively feeding behaviour on cladocerans and calanoid copepods and that *A. aurita* also feeds on tunicate and echinoderm larvae. Also, cannibalism on other gelatinous zooplankton such as small ctenophores (*Mnemiopsis leidyi* < 1 cm) and the ephyrae larvae of *A. aurita* is observed (Purcell, 1991; Weisse & Gomoiu, 2000).

In conclusion, *A. aurita* in the WS has shown to feed on a wide range of micro- and mesozooplankton (see Fig. 10), whereby the predation pressure exerted on zooplankton depends on life stage and size of the medusae. *A. aurita* mainly feeds on calanoid copepods followed by copepods nauplii, bivalve larvae, polychaete larvae, crustaceans such as mysids, isopods and amphipods, and is likely to consume other zooplankton present in the WS as well.

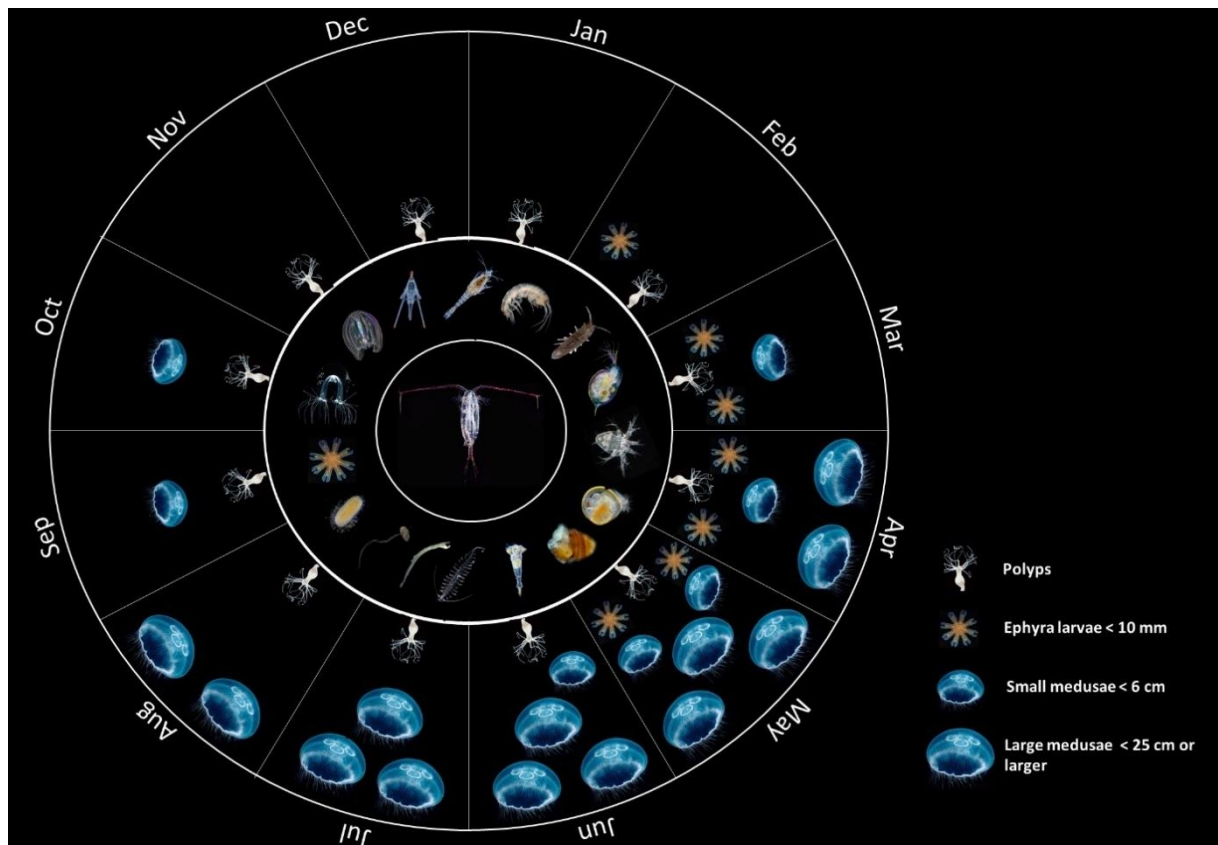


Figure 10: The occurrence of *Aurelia aurita* in the Dutch Wadden Sea and its predation pressure on different zooplankton groups. The abundance of *A. aurita* species is displayed per month in the outermost circle, whereby one individual indicates the lowest occurrence and three individuals the highest. The predation on different zooplankton groups is visualised in the inner circles. The primary zooplankton prey items are illustrated in the middle circle, surrounded by secondary zooplankton prey. This model shows that *A. aurita* is most abundant from April to July and completely absent in the winter months. Only the polyps are present all year around. *A. aurita* has a wide range of zooplankton prey but predominantly feeds on calanoid copepods.

3.1.3.2 *Mnemiopsis leidyi*

The invasive ctenophore *Mnemiopsis leidyi* counts as major zooplanktivorous predator in the WS pelagic ecosystem (van Walraven, 2016). Originated from estuaries of the Atlantic coast of North and South America, *M. leidyi* successfully invaded European coastal waters and was primarily confirmed in the Dutch WS in 2006 where it occurs in substantial numbers (Faasse & Bayha, 2006; Shiganova, 1998; van Walraven, 2016). *M. leidyi* is one of the most common species in the Dutch WS and responsible for most of the predation pressure on mesozooplankton in this area (van Walraven et al., 2017).

Occurrence

According to Van Walraven et al. (2013), the ctenophore *Mnemiopsis leidyi*, is all year around present in the Dutch WS, with lowest numbers in February. In winter and spring, from December until mid-May, the density is at or below 1 individual m⁻³ and the population consist of ctenophores between 5 and 20 mm in length or even larger. In May, when spawning starts, the first small ctenophores < 5 mm in length can be observed. The first density peak of *M. leidyi* occurs in June with the highest mean density of 360 individuals m⁻³, while juveniles of < 5 mm length dominate. Hereafter, the population of mainly smaller individuals (< 20 mm) decline rapidly (minimum of 0.7 individuals m⁻³) which might be due to predation by adult *M. leidyi* and other jellyfish such *A. aurita*, *C. hysoscella*. In mid-August, when almost the entire population comprises larvae and juveniles, another bloom takes place, resulting in a second peak of 921 ind. m⁻³ as its highest. From begin September on, a rapid decrease of the population occurs, similar to that of July. Afterwards, a last increase takes place with a stable population until end of October/begin of November, when the population decreases again with wintertime (van Walraven et al., 2013)

Zooplankton predation

M. leidyi is an opportunistic planktonic predator, feeding on a wide range of prey such as calanoid copepods and their nauplii, bivalve veligers, barnacle nauplii, cladocerans, rotifers and fish larvae (Cowan & Houde, 1992; Granhag et al., 2011; Javidpour et al., 2009; McNamara et al., 2010; Purcell et al., 2001; Sullivan & Gifford, 2004, 2007). Also, meroplankton such as crab zoea, mysid shrimp, gastropod larvae, larvacea, polychaeta larvae and cyprids were consumed by the ctenophore (Granhag et al., 2011; McNamara et al., 2010). Javidpour et al. (2009) even suggests cannibalism and predation of other gelatinous zooplankton as high concentrations of jellyfish planula larvae were found in the gut content of *M. leidyi*.

Larvae and smaller individuals < 10 mm of *M. leidyi* mainly feed on microplankton, but can also feed on larger prey such as mesozooplankton (Stanlaw et al., 1981; Sullivan & Gifford, 2004, 2007). With increasing size of the ctenophore, the proportion of microplankton in the diet decreases (Rapoza et al., 2005). According to McNamara et al. (2013), adults of *M. leidyi* primarily feed on mesozooplankton. Kellnreitner (2012) shows that the ctenophore selectively feeds on harpacticoid and calanoid copepods in June, July and September, followed by balanid cypris and nauplii larvae. In August and September, the bivalve larvae of the Pacific oyster (*Magallana gigas*) dominated as prey item, resulting in a consumption of the complete standing stock of bivalve larvae (Kellnreitner, 2012). According to Van Walraven et al. (2017) the period of clearance rate by *M. leidyi* and thus predation rates on zooplankton is high in summer (June and July) and autumn (October and November), with peak in

September. Studies of McNamara et al. (2010) and Riisgård et al. (2007) show that *M. leidy* can remove up to 89 % of bivalve veligers, calanoid copepods and other zooplankton taxa.

In conclusion, the reviewed information shows that *M. leidy* in the WS is dependent on zooplankton as its main food source and feeds on a variety of zooplankton species (see Fig. 11). The ctenophore is able to remove almost 90 % of the zooplankton whereby the most predation pressure is exerted on calanoid copepods and bivalve larvae.

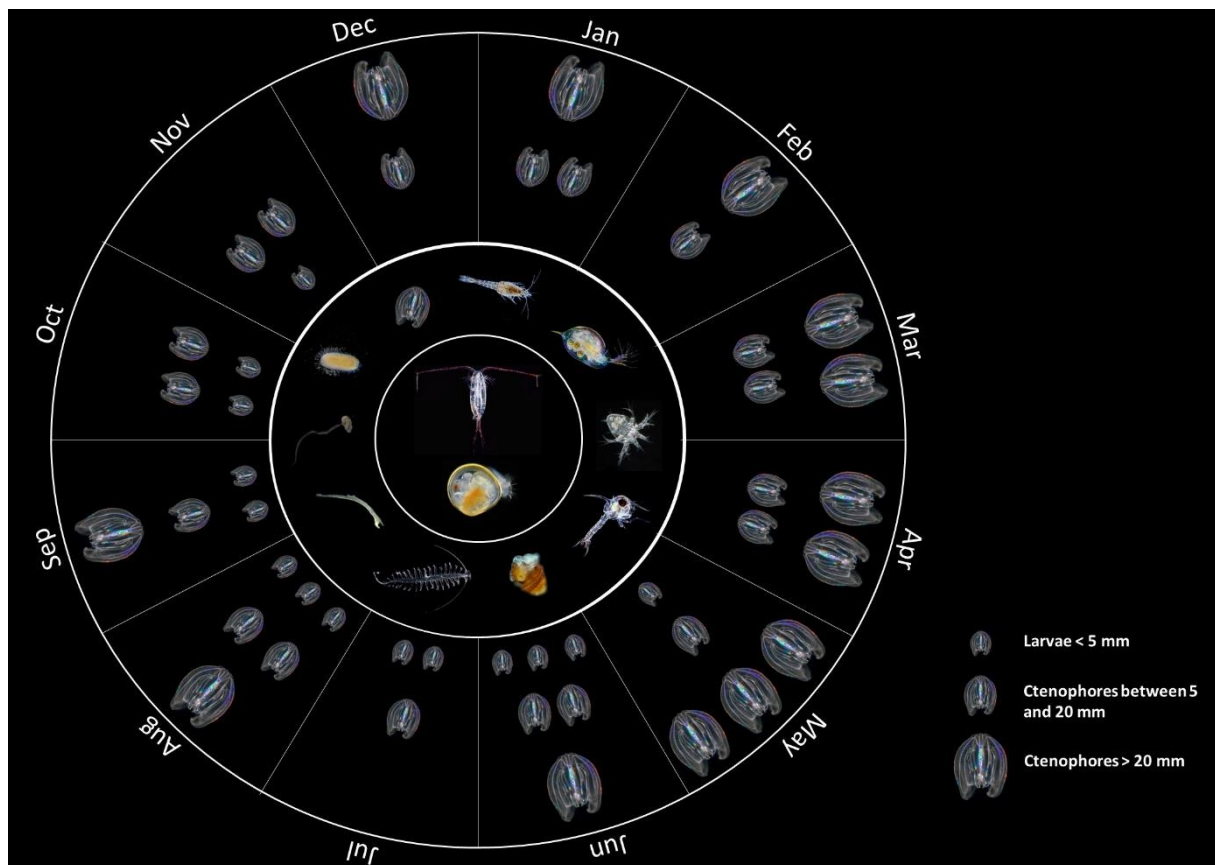


Figure 11: The occurrence of *Mnemiopsis leidy* in the Dutch Wadden Sea and its predation pressure on different zooplankton groups. The abundance of *M. leidy* is displayed per month in the outermost circle, whereby one individual indicates the lowest occurrence and three individuals the highest. The predation on different zooplankton groups is visualised in the inner circles. The primary zooplankton prey items are illustrated in the middle circle, surrounded by secondary zooplankton prey. This model shows that *M. leidy* is present whole year around with two peak occurrences in June and August whereby small ctenophores (< 5 mm) dominate. *M. leidy* feeds on a variety of zooplankton but predominantly preys on calanoid copepods and bivalve veligers.

3.1.4 Crustacea in the Wadden Sea

Crustacea are key components of the trophic web where they play an important role as predators as well as food source for several species including fish, crustaceans and shorebirds (Beukema, 1991; Campos et al., 2010). In the Dutch WS, brown shrimp (*Crangon crangon*), shore crab (*Carcinus maenas*), the invasive Australasian barnacle (*Elminius/Austrominius modestus*) and mud shrimp (*Corophium volutator*) are very abundant and occur in high densities (Campos et al., 2010; Dekker, 1989; Flach, 1992; Gittenberger et al., 2010).

3.1.4.1 *Crangon crangon*

The brown or common shrimp (*Crangon crangon*) is one of the most abundant and important benthic carnivore in shallow soft bottom areas along the European coast, including the WS tidal zone (Campos et al., 2010; Kuipers & Dapper, 1984). *C. crangon* exerts major predation pressure on the infauna community and serves as food source for several predators including crustaceans, shorebirds and commercially exploit fish such as plaice and flounder (Campos et al., 2010; Criales & Anger, 1986; Pihl & Rosenberg, 1984). In the NS, the shrimp is intensively fished and therefore of great economical value (Criales & Anger, 1986).

Occurrence

Crangon crangon can be found all year around in the Dutch WS with five times greater abundance in autumn than in spring (Campos et al., 2010). Reproduction takes place throughout the entire year with spawning peaks in spring to summer and winter (Campos et al., 2010; Kuipers & Dapper, 1984). Larvae originating from winter eggs migrate into shallow nursery grounds and can be found over almost the entire year with highest numbers from May to September (Campos et al., 2010). Juveniles (< 3.5 cm) enter the shallow tidal zone in May, where their numbers steadily increase with peak density of 70 individuals m⁻² in July and remain in the shallow area till October-November (Kuipers & Dapper, 1981). During these months there is a constant shift of shrimps of 30 – 35 mm length that leave the shallow nursery habitats and migrate to deeper, sublittoral areas where they contribute to high numbers in autumn (Daewel et al., 2011; Kuipers & Dapper, 1981). Campos et al. (2010) studied the abundance of *C. crangon* in the Dutch WS using a 34-year time series of fyke net catches which shows highest daily abundance of 220 individuals on average in autumn. These high numbers of *C. crangon* represent emigration of mature shrimps towards overwintering grounds in the NS. High numbers in spring correspond to the immigration of adult shrimps returning to the shallow waters of the WS after the winter (Campos et al., 2010). However, according to Campos et al. (2010), spring abundance was in general rather low with daily catches of average 6.1 individuals which might be due to heavy predation pressure resulting in high mortality (Campos et al., 2010; Kuipers & Dapper, 1984).

Zooplankton predation

C. crangon is an opportunistic predator with a very varied diet, mainly composed of benthic species such as bivalve spat and juvenile flatfish (Campos et al., 2010; Pihl & Rosenberg, 1984). However, also zooplankton is a dominate food source of shrimp which starts to prey on rotifers already in the larvae stage (Criales & Anger, 1986). Juvenile shrimp mainly feed on ostracods and harpacticoid copepods (Pihl & Rosenberg, 1984). The dominant prey of larger shrimp (> 3.5 cm) is constituted by mysids and amphipods which comprise > 40 % of the diet in spring, around 50 % in summer and 60 % in autumn (Oh et al., 2001; Pihl & Rosenberg, 1984). Other prey items are isopods and crustaceans such as copepods, cumaceans, megalopa larvae and cypris larvae of barnacles (Janssen, 1980; Oh et al., 2001).

Also, cannibalism of larger sized shrimp on post-larvae of *C. crangon* (parva) was observed. Shrimp selects its prey according to its size. Thus, with increasing length, *C. crangon* switches to macrofauna and larger crustacea such as amphipods, young bivalves and mysids (Pihl & Rosenberg, 1984).

In conclusion, besides other macrofauna prey, *C. crangon* in the WS feeds mainly on crustacean zooplankton (see Fig. 12). Ostracods and harpacticoid copepods are mainly predated by smaller-sized shrimp, whereas mysids and amphipods are important prey items for larger-sized shrimp.

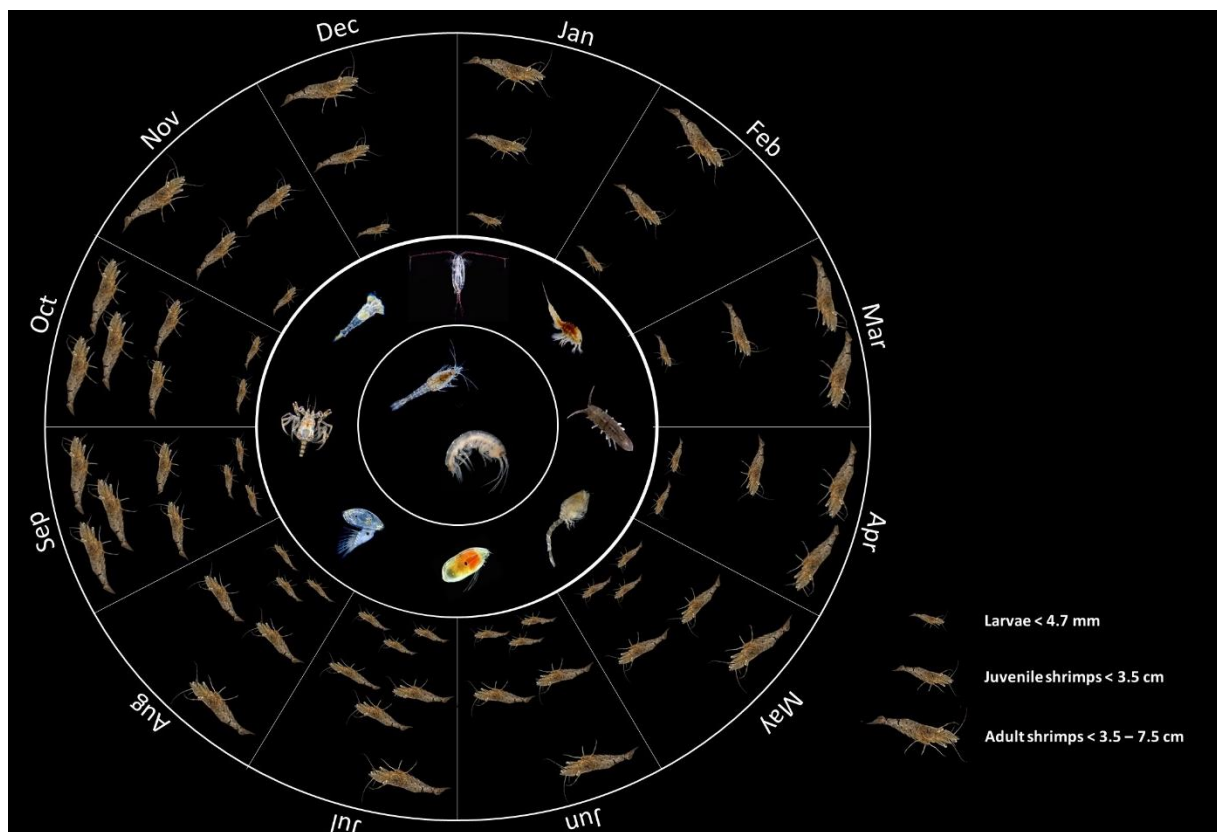


Figure 12: The occurrence of *Crangon crangon* in the Dutch Wadden Sea and its predation pressure on different zooplankton groups is illustrated. The abundance of *C. crangon* species is displayed per month in the outermost circle, whereby one species indicates the lowest occurrence and three species the highest. The predation on different zooplankton groups is visualised in the inner circles. The primary zooplankton prey items are illustrated in the middle circle, surrounded by secondary zooplankton prey. This model shows that *C. crangon* is present whole year around with highest number of adult shrimp in autumn. *C. crangon* preys besides rotifers only on crustacean zooplankton whereby the main predation is exerted on mysids and amphipods.

3.2 Gut content analysis

This section provides a step-by-step description of gut content analysis per selected species group. These methods are essential in order to visually identify prey items under microscopic conditions and to conduct further DNA analysis.

3.2.1 Pelagic fish

There are several techniques to collect stomach contents of fish, such as dissection, stomach flushing, tubes, gastroscopes, and many more. The most effective and precise results for small fish, such as herring and sandeel, are obtained with the dissection method. In addition, for obtaining the stomach contents of live fish, stomach flushing has also been widely used (Kamler & Pope, 2001; Manko, 2016). However, most studies investigating stomach contents of fish are choosing gut removal (e.g. Jakubavičiūtė et al. (2017); Kellnreitner (2012); Ojaveer et al. (2017, 2018); Raab et al. (2012)). After the feeding experiment or field collection, stomachs should be extracted immediately to avoid continued digestion. If immediate stomach extraction is not possible, individuals can be stored by shock freezing or by fixing in formalin to avoid continued digestion of food contents (Manko, 2016; Ojaveer et al., 2017; Sagar et al., 2018; Expert A, personal communication, July 15, 2020). The following step by step protocol is compiled from several studies (mainly Manko (2016), but also Raab et al. (2012), Kellnreitner (2012), and Jakubavičiūtė et al. (2017)), and provides a description for fish gut extraction and analysis:

1. Make a longitudinal cut on the ventral side of the fish from the gills to the anal fin with appropriately sized scissors or scalpel (Fig. 13).
2. At each end of the first cut, make two transverse cuts to open the coelom and expose the viscera (Fig. 14).
3. Separate the digestive tract (oesophagus, stomach, and intestine) from other visceral organs.
4. Open the stomach with fine scissors or scalpel, making a lengthwise shallow slit and extract contents (Fig. 15).
5. Preserve contents in 4 % buffered formaldehyde for microscopic inspection or if DNA analysis is required in 96 % ethanol solution. When samples were previously preserved in formalin, keep contents in water for at least 5 minutes (better for several hours or even a day) to remove excess formalin.

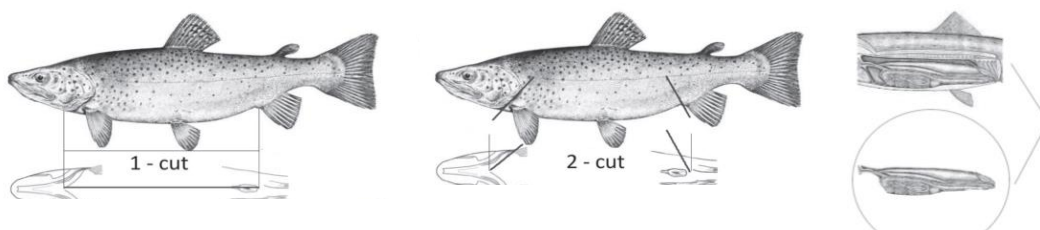


Figure 13 – 15: Illustrations of appropriate method to extract the stomach of a fish (step 1 -3) (Manko, 2016).

A non-lethal approach for stomach content collection of small fish, is described by Kamler & Pope (2001) and Manko (2016), whereby the stomach is flushed out using syringes and pumps. This method has been proved to be effective, removing up to 100 % of the stomach contents. However, it can be also harmful damaging swim bladders and causing internal injuries associated with exerted water pressure while flushing. The following step-by-step description shows how to actively flush fish stomachs using syringes and pumps:

1. Depending on the fish, select the largest diameter tube that easily passes the oesophagus without injuring the fish. Alternatively, select appropriate tubes for anal backwashing.
2. Wet the end of the tube before inserting it into the fish.
3. One person holds the fish with its head and dorsal side upwards, and another person inserts the wet tube into the stomach. Alternatively, for anal backwashing, insert the tube into the anus.
4. Water is injected by means of a hand pump or syringe and carefully directing water pulses into the gut.
5. Hold the tube and fish mouth over a container and allow the contents to flush through the tube.
6. Repeat the steps 4 and 5 until no additional contents are flushed.
7. Preserve samples in 4 % buffered formaldehyde for later microscopic inspection or 96 % ethanol solution for further DNA analysis and store in labelled plastic bags or containers.

3.2.2 Bivalves

After the feeding period or collection in the field, each mussel is injected with 8 ml 96 % alcohol into the mantle cavity to kill the mussel immediately and stop the digestive processes (Lehane & Davenport, 2004, 2006). Stomach contents are preserved and extracted followed by studies of Lehane & Davenport (2002, 2004, 2006) and Zeldis et al. (2004):

For extracting the stomach contents of *M. edulis*:

1. Cut the anterior and posterior adductor muscles (see Fig. 16).
2. Cut away the labial palps of *M. edulis* and the membrane directly above the stomach.
3. Pick away carefully the digestive gland using forceps, revealing the stomach with the crystalline style.
4. Make a slit through the digestive gland into the stomach and remove the contents with a glass pipette.
5. Preserve contents in 4 % formaldehyde for microscopic analysis or in 96 % ethanol if further DNA analysis is required.

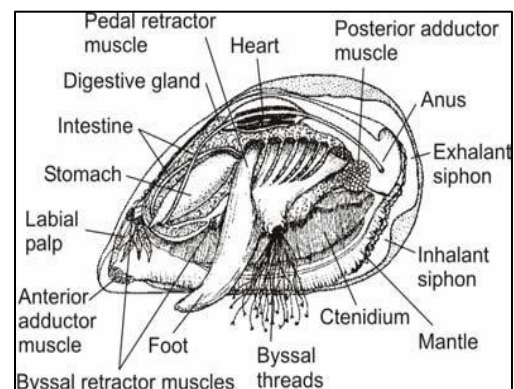


Figure 16: Schematic drawing of anatomy of *M. edulis* (Gendron et al., 2003).

For obtaining stomach contents of *C. edule*:

1. Cut the adductor mussels (see Fig. 17).
2. Pass a fine bore glass pipette into the mouth, down the oesophagus and into the stomach and remove contents with the pipette.
3. Preserve contents in 4 % formaldehyde for later microscopic inspection or in 96 % ethanol for later DNA analysis and label samples.

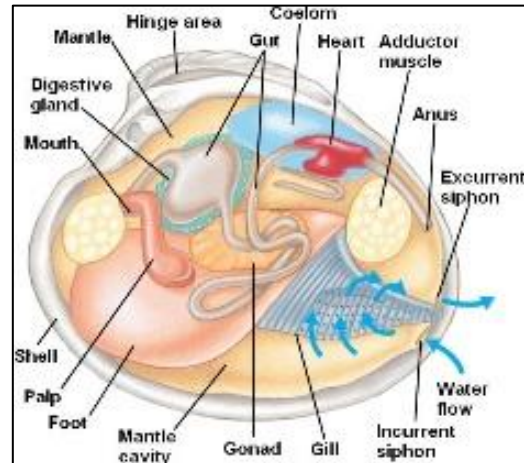


Figure 17: Schematic picture of anatomy of *C. edule* (Campbell & Reece, 2005).

3.2.3 Jellyfish

Species will be preserved and gut content will be extracted followed by studies of Barz & Hirche (2005); Granhag et al. (2011); Ishii & Tanaka (2001); Javidpour et al. (2009); Shao et al. (2006); van Walraven (2016) and personal communication (Expert B, personal communication, July 1, 2020). If immediate extracting of the gut contents is not possible, samples of *A. aurita* and *M. leidyi* can be preserved by shock freezing using liquid nitrogen (-196°C) or dry ice (-78°C). With this treatment, the digestion of the species immediately stops and additionally prevents disintegration which would occur with all types of fixation solutions (Dawson et al., 1998; Javidpour et al., 2009).

For obtaining gut contents of *A. aurita*:

1. Dissect medusa immediately after collecting and examine canals, stomach and gastric pouches for prey organisms (see Fig. 18).
2. Open the gastric pouches of the medusa using a scalpel.
3. Remove stomach content using a pipette.
4. Preserve species and stomach content in 96 % ethanol and label samples for later microscopic analysis and further DNA study.

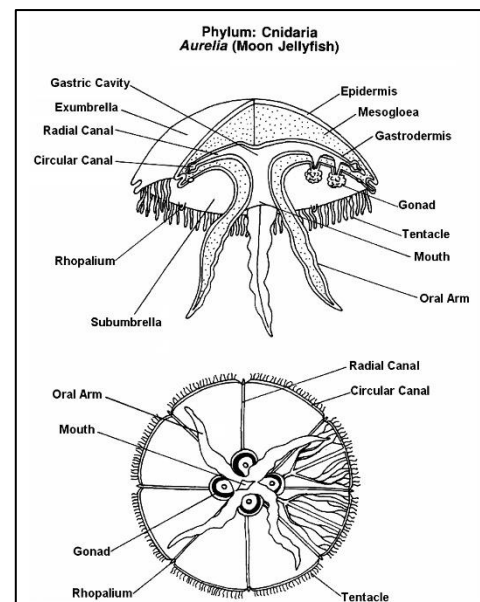


Figure 18: Schematic drawing of the body of *A. aurita* (Cronodon, 2019).

For extracting the stomach content of *M. leidy*:

1. Extract gut with surrounding tissues (if needed under dissecting microscope).
2. In case, freezing gears are not available, extract the stomach content of *M. leidy* through a flushing method by injecting 10 ml of sterile filtered seawater into the stomach cavity (van Walraven, 2016) (see Fig. 19).
3. Fix ctenophore as well the gut contents in 96 % ethanol and label samples for later microscopic and DNA analysis.

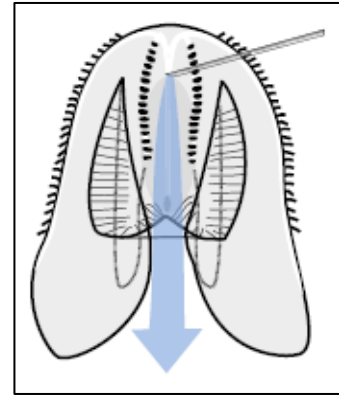


Figure 19: Flushing method of *M. leidy* with a syringe needle (van Walraven, 2016).

3.2.4 Crustacea

The following step-by-step description of *C. crangon* is based on personal communication (Expert D, personal communication, July 31, 2020) as no exact method on the gut removal is described in published articles. Stomach content analysis of freshly caught shrimp can be difficult as *C. crangon* has a very fast digesting time, resulting in empty stomach for 40 to 60 % of catches. Also, egg bearing females are mostly found with an empty stomach. Besides, stomachs of shrimps are often filled with sand which literally crush the prey items, making visual inspection almost impossible. However, small zooplankton may be possible to detect as the shrimp ingest smaller prey wholly, whereas large prey is consumed through small bites. If immediate extraction of stomach contents is not possible, *C. crangon* can be stored in 96 % ethanol or by freezing at -20 °C (Expert D, personal communication, July 31, 2020, Siegenthaler et al., 2018).

For obtaining stomach content of *C. crangon*, following steps should be conducted:

1. Remove carapace of freshly collected shrimp (round body beneath).
2. Cut into oesophagus (see Fig. 20) with small scissors and remove stomach with tweezers.
3. Preserve gut content in 96% ethanol and label for further microscopic investigation and DNA analysis.

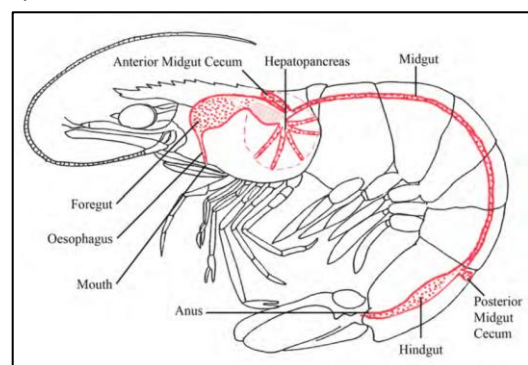


Figure 20: Schematic drawing of the digestive system of *C. crangon* (Corteel, 2013).

4 Discussion and Conclusion

The aim of this review was to give an overview on which zooplankton species are consumed by which dominant predator species in the Dutch Wadden Sea (WS). In addition, methods on the extraction of gut contents of predator species were investigated in order to provide a step-by-step description for experimentally studying zooplankton ingestion.

Based on literature, the herring (*C. harengus*), sandeel (*A. tobianus*), blue mussel (*M. edulis*), cockle (*C. edule*), moon jellyfish (*A. aurita*), comb jelly (*M. leidy*), and brown shrimp (*C. crangon*) were determined as the most dominant species in the Dutch WS in terms of abundance/biomass and predation on zooplankton. The review shows that the main predation pressure on zooplankton is exerted on the crustacean group calanoid copepods, which forms a prey item of each selected predator species. This is followed by bivalve veligers, mysids and harpacticoid copepods. Also amphipods, different crustacean larval stages, cladocerans, fish larvae, ctenophores, rotifers and hydromedusae are found to be frequently ingested. For the extraction of gut contents of predator species, the dissection and the 'flushing' method have been investigated due to their effectiveness and precision as shown in several studies and confirmed by expert interviews (e.g. Lehane & Davenport (2002, 2004, 2006); Manko (2016); van Walraven (2016); Expert A, personal communication (July 15, 2020); Expert B, personal communication (July 1, 2020); Expert D, personal communication (July 31, 2020)).

Predation pressure on zooplankton

In general, most of the predation pressure on zooplankton is found to be within the crustacean group and its' larval stages, followed by bivalve larvae, hydromedusae, fish larvae, ctenophores and rotifers. This finding is supported by a study of Fransz & van Arkel (1983), which showed that the zooplankton in the western WS is dominated by calanoid copepods. Also, in the neighbouring North Sea (NS), most zooplankton species found were crustacean, with calanoid copepods being the most prevalent one (van Gindereuren et al., 2013). After crustacean zooplankton, meroplankton such as larval stages of invertebrates, fish and Echinodermata, forms also a dominant component of the marine food web (Hickel, 1975; van Gindereuren et al., 2013). Martens (1980), observed high densities of meroplanktonic larvae in the German WS, that could even exceed the biomass of copepods, which was also supported by a study of Fransz & van Arkel (1983).

Feeding selectivity and future changes

The results of this study show, that the pelagic fish species *C. harengus* and *A. tobianus* predominately prey on crustacean zooplankton. The main prey item for both species are calanoid copepods, while *A. tobianus* also feeds mainly on harpacticoid copepods and mysids.

Shifts in planktonic species composition due to changing environmental factors (e.g. climate and salinity), are likely to affect fish populations (Daewel et al., 2014; Frederiksen et al., 2006; Möllmann, 2000). In the NS, a shift towards warmer-water zooplankton species was observed after 1980. Key zooplankton species, such larger copepods generally declined and shifted towards smaller copepods (Alvarez-Fernandez et al., 2012; Daewel et al., 2014; Pitois & Fox, 2006). It is known that *C. harengus* has a rather specialized diet with low diversity of food items, which depends on prey size, visibility and particle concentration (Kellnreithner, 2012; Raab et al., 2012). Also, Sandström (1980) observed that *C. harengus* selectively feeds on larger zooplankton prey. This is supported by Corten (2000) and Van Deurs et al. (2014), which show that *C. harengus* redistributes according to food density. There, a northwards shift in the NS of herring feeding grounds was observed due to a climate-driven change in copepod distribution. The sandeel however, may be more sensitive to changes in copepod abundance

than herring, as they are a resident species and unable to move between areas (Jensen et al., 2011; van Deurs et al., 2014).

The bivalve species *M. edulis* and *C. edule* are filter feeders that feed on a variety of food particles, including phytoplankton, detritus, and zooplankton. Within the zooplankton they are found to prey primarily on crustacean zooplankton and bivalve veligers, but also ingest hydromedusae. The role of zooplankton in bivalve nutrition has been overlooked for a long time, which could be due to their fast digestion rate (e.g. 40 min at 15-20°C for *Mytilus edulis*) (Arapov et al., 2010; Davenport et al., 2000). Numerous studies have pointed out that bivalves are able to ingest a wide range of planktonic organisms and are capable of selective particle feeding, and thus also selectively feed on zooplankton (e.g. Davenport et al. (2000); Lehane & Davenport (2002, 2004, 2006); Troost et al. (2009)). Bivalves may even decrease recruitment of new bivalve stocks, as due to grazing pressure on bivalve larvae, their settlement success can be influenced significantly (André & Rosenberg, 1991; Arapov et al., 2010; Lehane & Davenport, 2004). The size of bivalves, position in the water column, turbidity of water and filtration rate have been suggested factors that might affect the selectivity on size of the zooplankton ingested (Lehane & Davenport, 2006; Troost et al., 2009). Filgueira et al. (2016), suggests that increased temperatures due to climate change could critically influence bivalve metabolism and increase exerted top-down predation pressure. However, he also points out that temperature increase could influence recruitment negatively and may lead to an increased bivalve mortality, as bivalves are highly vulnerability to temperature and salinity changes.

There has been a concern that oceans will increasingly be dominated by gelatinous zooplankton, as they may benefit from changing environmental conditions, such as warmer water temperatures. In general, water temperature influences numerous processes of marine organisms, affecting life cycles, reproductive periods, and metabolic rates (O'Connor et al., 2007; Rossi et al., 2019; van Walraven, 2016). Jellyfish are known to be adaptable to new conditions and to be able to increase their abundance rapidly (Lynam et al., 2011; van Walraven, 2016). In the western Dutch WS, it has been observed that seasonal occurrence of *A. aurita* has changed with climate change and the species is now occurring significantly earlier in the year. However, a change in abundance in relation to changing climate has not been observed (van Walraven, 2016). Also, the reproduction of *M. leidy* has shown to be influenced by temperature, resulting in earlier blooms which leads to an increased overlap with the zooplankton spring bloom and spawning periods of bivalves (Robinson & Graham, 2014; van Walraven, 2016).

In this study found, it is noticeable that *A. aurita* and *M. leidy* prey on a wide variety of zooplankton occurrent in the Dutch WS. Both species predate mainly on calanoid copepods and *M. leidy* additionally on bivalve veligers. *A. aurita* as well as *M. leidy*, have been observed to prey selectively on crustacean zooplankton, such as calanoid and harpacticoid copepods, cladocerans, different crustacean larvae stages and bivalve larvae (Hansson, 2006; Kellnreitner, 2012). A study by Hansson (2006) shows, that *A. aurita* selects its prey according to the prey size. Graham & Kroutil (2001) also observed that a higher diversity of prey was found in larger medusae, whereby larger crustacean zooplankton (copepods and cladocerans) were selected over smaller-sized zooplankton (echinoderm larvae and copepod nauplii). Also, the ctenophore *M. leidy* preys on larger zooplankton with increasing size (Granhag et al., 2011; Rapoza et al., 2005). In general, according to Van Walraven (2016), *M. leidy* is responsible for most of the predation pressure on mesozooplankton in the Dutch WS. Hence, larger medusae and ctenophores contribute the most to predation pressure on zooplankton, as the predation rate of jellyfish increases with its size (Granhag et al., 2011; Hansson, 2006; van Walraven, 2016).

Consequently, this can result in food competition with other zooplanktivorous species and influence their recruitment as observed with *C. harengus* in a study by Lynam et al. (2005) in the North Sea. Also, Van Walraven (2016) concluded that *M. leidy* could influence the WS ecosystem significantly through food competition, as the ctenophore is able to remove an extensive amount of zooplankton (Riisgård et al., 2007). As suggested in a study by Lynam et al. (2011) in the Irish Sea, an overlap of numerous zooplanktivorous species together with a decline in copepod biomass, might not be sustained by marine systems and may lead to ecosystem instability.

The crustacean species, *C. crangon* was found to prey mostly on crustacea zooplankton groups, with mysids and amphipods being the main prey item for larger-sized shrimps, and ostracods and harpacticoid copepods for juveniles (Campos et al., 2010; Pihl & Rosenberg, 1984). However, as its diet is predominately compiled of other benthic species, such as bivalve spat and juvenile flatfish, its predation pressure on zooplankton groups may be of minor importance. No studies regarding its prey selectivity and influence on zooplankton have been found.

Species selection and table evaluation

Information on the species composition and feeding behaviour of pelagic fish, gelatinous zooplankton as well as crustacea in the WS, was accessible and available. However, information on zooplankton ingestion by some bivalve species appeared to be scarce (e.g. *Ensis leei*, *Limecola balthica*). This could be due to the fact that for a long time, bivalves were not considered to actually consume zooplankton, but only indirectly influence zooplankton community through grazing on phytoplankton.

In order to define dominant species, both metrics 'Abundance' and 'Biomass' were taken into account as indicator for 'dominance' of the species. While the high abundance of a species may not inevitably be an indicator for high predation pressure, the biomass of a species alternately may provide a better representation of exerted predation pressure, as body mass is positively correlated with metabolism (Saint-Germain et al., 2007). However, we included both metrics in this study, depending on the studies and papers available. Data of pelagic fish, gelatinous zooplankton and crustacea are based on abundance, whereas bivalves are based on biomass. Monitoring data on biomass and abundance of each zooplanktivorous species was well obtainable, but not always available for the whole year. Other values such as consumption rate, chemical composition of nutritional requirements and the biomass ingested, were not included in the ranking to determine the 'dominance' of a species, but may as well influence predation pressure on zooplankton exerted by predator species. Additionally, it was found that all selected species undergo strong yearly fluctuations in abundance and biomass, due to variations in environmental factors (e.g. temperature) as well as pressures induced through human activities (e.g. fisheries) (Beukema & Dekker, 2006; Kuipers & Dapper, 1984; Philippart et al., 1996; Selleslagh & Amara, 2008; van den Ende et al., 2012; van Walraven, 2016) (see Fig. 21 & Fig. 22). Thus, even research results of the most recent years may not be fully representative of the current species composition. Hence, the lack of information on seasonal dynamics about certain species, as well as the recency of research may have influenced the species selection. However, regarding the results of this review, we think that the lack of information about seasonal species dynamics has no to minor consequences, as all selected species are either found to be highly zooplanktivorous and/or influence zooplankton composition through predation. To determine which zooplankton groups are predated mainly, the predation per species was split in primary and secondary prey. This was based on information available of diet studies.

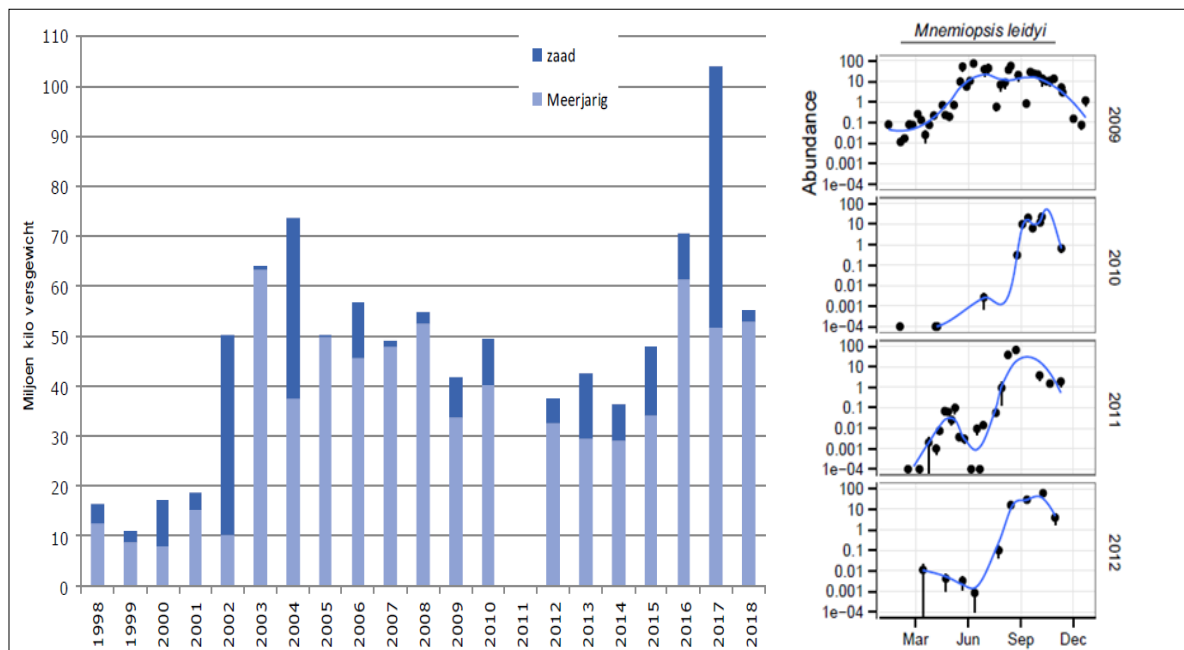


Figure 21 & 22: Yearly fluctuations of *Mytilus edulis* and *Mnemiopsis leidyi*. Fig. 21 (left) shows the stock and composition of *M. edulis* in the littoral zone of the Dutch Wadden Sea from spring 1998 until 2018. The mussels are classified into mussel seeds and multiannual mussels. There is no stock estimation available for 2011 (van den Ende et al., 2012). Fig. 22 (right) shows the yearly fluctuations *M. leidyi* from mean weekly densities from 2009 until 2012 in the Dutch Wadden Sea (van Walraven, 2016).

Gut content analysis

The two methods chosen, dissection and ‘flushing’, are based on papers, studies and/or on expert advices, and can therefore be expected as effective for displaying successful results to obtain, preserve and investigate gut contents. With the dissection method, analyses of other parts of the species can be used in addition to retrieve information for additional research. However, this approach requires to kill the species which is controversial in term of ethical, protection and economic issues. This can be prevented with the alternative non-lethal ‘flushing’ method, though this approach might entail higher costs and time consumption, as well damage of intestines of the species can occur (Manko, 2016). According to Kamler & Pope (2001), the flushing method with syringes is the preferred approach for young and small fishes. Also, Van Walraven (2016) refers to this gut content extraction method for ctenophores. For larger fishes (> 10 cm), it is recommended to use a hand pump or mechanized pressure as devices to ‘flush’ out the stomach contents (Kamler & Pope, 2001).

Other possible methodologies for gut content analysis such as radioisotopes, stable isotope analysis or fatty acid analysis benefit by precision and reveal items which cannot be identified by microscopic analysis. Yet, direct gut content analysis through dissecting or ‘flushing’ the species are the easiest methods with great potential for ecological studies (Manko, 2016).

As this research asks for gut extraction methods to enable further DNA analysis, 96 % ethanol was chosen as suitable preservation method. Ethanol allows a long storage time and keeps both, the physical structure and the DNA of the species in good condition (Dawson et al., 1998). For a mere microscopical inspection, formalin solution is the most common storage approach (Manko, 2016). However, the toxin solution brings high health risks for scientists and laboratory personal (Wetzel et al., 2005). Also, for the fixation of vertebrates it can have disadvantages as bones and otoliths possibly dissolve (Manko, 2016). Likewise, for studying the gut contents of *A. aurita* and *M. leidyi*, most studies

preserve the species in formaldehyde (Hansson, 2006; Kellnreiter, 2012). However, this methods can lead to disintegration of the jellyfish, especially of smaller individuals (Expert B, personal communication, 1 July, 2020; Javidpour et al., 2009). As the structure of preserved species can easily damage with formalin fixation, further DNA analysis is difficult or even impossible (Quach et al., 2004; Wetzel et al., 2005). Hence, ethanol is the preferred preservation method to store the samples for further microscopical inspection and DNA analysis. Some studies refer to the pre-freezing storage approach if immediate extracting of the gut contents is not possible. Thereby, the species is stored by freezing in -20 °C, in dry ice (-78 °C) or in liquid nitrogen (-196 °C) (Dawson et al., 1998; Javidpour et al., 2009; Sagar et al., 2019; Siegenthaler et al., 2018). Deep freezing allows further DNA analysis, however, careful handling, special equipment and strict regulations for transporting should be considered (Dawson et al., 1998).

Conclusions and recommendations

Our study aimed to give an overall overview of which zooplankton groups are eaten by which dominant predator species in the Dutch WS, and how this can be investigated by means of gut content analysis. Species from the phyla Chordata, Mollusca, Ctenophore/Cnidaria and Arthropoda were investigated. We show that zooplankton is predated amongst different species groups, with herring (*C. harengus*), sandeel (*A. tobianus*), blue mussel (*M. edulis*), cockle (*C. edule*), moon jellyfish (*A. aurita*), comb jelly (*M. leidy*), and brown shrimp (*C. crangon*) being the most dominant predator species. The majority of the predated zooplankton is found to be within the crustacean group, mainly calanoid copepods and crustacean larval stages, followed by other zooplankton groups, such as bivalve larvae, hydromedusae, fish larvae, ctenophores and rotifers. For studying zooplankton predation experimentally by means of gut analysis, the dissection as well as the ‘flushing’ approach have been shown to be effective.

The findings of this study underpin the important role of zooplankton communities in the WS marine food web and the need for understanding the trophic interactions between predator species and zooplankton prey. A shift in abundance and composition of key zooplankton groups due to changing environmental factors, might affect various species and higher trophic levels and may result in a reduced carrying capacity of marine ecosystems (Alvarez-Fernandez et al., 2012; Daewel et al., 2014; Lynam et al., 2011; Martens & van Beusekom, 2008). Particularly species that selectively feed on certain zooplankton groups, e.g. herring, may be thus more vulnerable to shifts in planktonic composition, than more opportunistic species, such as the invasive comb jelly. Hence, a change in seasonality of various zooplankton groups may have a cascading effect on the WS marine ecosystem, as it may result in a potential food competition between zooplanktivorous species.

Based on this knowledge it can be concluded that in order to preserve the nature values of the WS area, the role of zooplankton in the trophic food web needs to be understood and investigated further. Especially in times of human induced pressure and climate change, the comprehension of trophic interactions, as well as their strengths and weaknesses are crucial for sustaining a healthy ecosystem. Additional research is thus necessary to examine those predator-prey-interactions in order to get an understanding of the importance of certain zooplankton groups for predator species. Frameworks and legislations regarding the conservation, use and management of the Dutch WS area, as well as monitoring programmes have been neglecting the importance of zooplankton as a key element in the food web. Therefore, the potential cascading effects on the WS ecosystem resulting from a change in zooplankton dynamics remain unknown. Consequently, programmes and directives in the Dutch WS need to include regular monitoring of zooplankton composition and abundance in order to provide the

scientific foundation for a consideration in policy-making relevant for management and conservation. For example, the joint programme 'Trilateral Monitoring and Assessment Programme' (TMAP) carried out by the Netherlands, Germany and Denmark, covers many research topics and is the common monitoring programme for the entire WS area (CWSS, 2014). Although several subjects are tackled by this programme, zooplankton is not mentioned in any of their monitor objectives. The EU Water Framework Directive (WFD), implemented as 'Kaderrichtlijn Water' (KRW) in the Netherlands, have to monitor the ecological status of surface waters, including coastal waters (Ministerie van Infrastructuur en Waterstaat, 2015). Whereas the abundance and composition of phytoplankton is one of the key tools, zooplankton monitoring is not included. Only with tackling zooplankton as a key component in the food web and accordingly including it in future monitoring and management programmes, potential threats can be anticipated, and a healthy ecosystem will be sustained.

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Appendix I – Species database

The following excel table shows the database created in order to identify the most dominant predator species of zooplankton in the Dutch Wadden Sea.

Species (engl.)	Species (lat.)	Abundance/Biomass in the Wadden Sea (high/medium/low)	Predation on zooplankton (Yes/No/Unknown)	Feeding behaviour (zooplanktivorous/opportunistic/unknown)	Occurrence and life cycle	Ecological value	Economical value	Life stage of zooplankton predation (juvenile/adult/ juvenile & adult/ unknown)	Species composition in Wadden Sea (juv. / ad. / juv. & ad./ unknown)	Feeding mechanism
Sprat	<i>Sprattus sprattus</i>	HIGH - Together with herring most abundant pelagic fish in Wadden Sea (Programma naar een rijke Waddenzee, n.d.; Couperus et al., 2016)	YES - dominated by calanoid copepods (van Ginderdeuren et al., 2013).	Zooplanktivorous - Mainly zooplanktivorous but also opportunistic; feeds on a broad diversity of prey types, including copepods, phytoplankton and meroplankton depending on area, season, and zooplankton community composition (Falkenhaus & Dalpadado, 2013; (Solberg et al., 2015). During its preflexion stage, consumes mostly copepod nauplii (Rossi et al., 2005).	PRESENCE: April-Oct (Programma naar een rijke Waddenzee, n.d.; Couperus et al., 2016) PEAK: June - August (van Bleijswijk et al., 2020) SPAWNING: Between March and August (offshore) (Dänhardt & Becker, 2011)	plays an important role in the trophic structure of pelagic ecosystems being a major predator on zooplankton and an abundant prey for piscivorous fish like cod and whiting (Solberg et al., 2015). Key species (together with herring) for common terns in the WS; due to high abundance and high energy content (Dänhardt & Becker, 2011).	Sprat is landed commercially in the North Sea, although large part is used in the fishmeal industry. Human consumption only exists locally (Heessen et al., 2015)	Juvenile & Adult (Van Ginderdeuren, 2013).	Juvenile & Adult (Van Ginderdeuren, 2013) Species composition WS: marine seasonal (Bolle et al., 2007) Sprat living in the WS originate from various spawning grounds in the southern NS. Sprat also spawn in the WS, but more importantly, the area is inundated by juveniles from the broader NS region (Dänhardt & Becker, 2011).	Filter & particulate feeding (Möhlmann et al., 2004)
Herring	<i>Clupea harengus</i>	HIGH - Together with sprat most abundant species in the Wadden Sea (Programma naar een rijke Waddenzee, n.d.; Couperus et al., 2016). Although herring is outnumbering sprat in a majority of years (Dänhardt & Becker, 2011).	YES - Copepods formed an important prey taxon for herring, followed by mysids, megalopa larvae of decapods and amphipods (Van Ginderdeuren, 2013). Predation impact on calanoid copepods was highest in June and July (Kellnreithner, 2012).	Zooplanktivorous - Mainly zooplanktivorous but also opportunistic - small planktonic copepods in the first year, and thereafter mainly copepods (especially <i>Calanus finmarchicus</i> and <i>Temora longicornis</i>), but also hyperid amphipods, euphausiids, mysid shrimps, small fishes, arrow-worms, ctenophores and pteropods) (FAO, 1985)	PRESENCE: April - Oct (Programma naar een rijke Waddenzee, n.d.) PEAK: June - August (van Bleijswijk, et al., 2020). High biomass of <i>C. harengus</i> was found in June and July followed by a steep decline from August to September (Kellnreithner et al., 2013); high numbers of juveniles in the summer months (5-10 cm) (van Bleijswijk et al., 2020) SPAWNING: in autumn and winter in NS (Kellnreithner, 2012)	Herring is a critical element in the food web as consumer and prey alike. Together with sprat, key prey resources of common terns (<i>Sterna hirundo</i>) breeding in the Wadden Sea (Dänhardt & Becker, 2011)	Herring is one of the main commercial species of the North Sea and has suffered low recruitment since 2000, likely due to environmental changes (Raab et al., 2012)	Juvenile & Adult (Dänhardt & Becker, 2011; ICES, 2006)	Juvenile (Dänhardt & Becker, 2011) Species composition in WS: marine juvenile (Bolle et al., 2007) Herring in WS area are primarily recruiting from NS autumn and winter spawning using WS waters as a nursery (Kellnreithner, 2012).	Filter & particulate feeding (Möhlmann et al., 2004; Kellnreithner, 2012)

Sandeel	<i>Ammodytes sp</i>	HIGH - After sprat and herring, the most abundant pelagic species in Wadden Sea (Programma naar een rijke Waddenzee, n.d.; Couperus et al., 2016).	YES - feed largely on copepods, but also on mysids, crangonids, gammarid amphipods, their pelagic and crustacean larvae, polychaetes, and fish (Programma naar een rijke Waddenzee, n.d.; Frederiksen et al., 2007; O'Connell & Fives, 1995).	Zooplanktivorous (ICES, 2006; Frederiksen et al., 2007). According to O'Connell & Fives (1995), Copepods were the dominant food items. The copepods species <i>Calanus sp</i> & <i>Temora sp</i> were mostly ingested, followed by the more demersal harpacticoids and mysids (mysids being the dominant one in July and August).	PRESENCE: year round (Kellnreitner, 2012; Bolle et al., 2007); In May, sandeel was the second most abundant species after sprat, whereas in October absent in the trawl catches, most likely because they stayed buried in the seabed during the day from late summer to spring (Couperus et al., 2016). PEAK: Pelagic peak in May/June (van Bleijswijk et al., 2020). In WS, present in summer in large swarms to feed (Kellnreitner, 2012). Peak feeding intensity coincided with a peak growing period in April (O'Connell & Fives, 1995). SPAWNING: mid-winter; pelagic larvae hatch in early spring (Frederiksen et al., 2007).	Major food resource for fish, marine mammals and seabirds (Programma naar een rijke Waddenzee, n.d.; Couperus et al., 2016). Of particular importance in the diet of many bird species during breeding season and often represents a major food for growing chicks. Breeding success of some seabirds can be reduced dramatically when sandeel abundance decreases (Furness & Tasker, 2000).	Commercial fishery in NS. Large-scale fishery in NS closed since 2000 (Frederiksen, et al., 2007). Not used for human consumption, but industrial fishery for fishmeal and fish oil. Industrial fishery fleets. Seasonal fishery - mostly spring/summer (FIN, 2008).	Juvenile & Adult (Frederiksen, et al., 2007)	Juvenile & Adult Species composition in Wadden Sea: resident (spend the majority of their lifespan in the WS) (Bolle et al., 2007).	Particulate (Deurs et al., 2014)
Pilchard	<i>Sardina pilchardus</i>	MEDIUM - In October, second most abundant species caught after sprat in Marsdiep area (Couperus et al., 2016).	YES - feeds on copepods, ostracods, euphausiids, juvenile stage of many other groups of crustaceans, and diatoms (Heessen et al., 2015; Camphuysen & Henderson, 2016).	Zooplanktivorous - feeds mainly on zooplanktonic organisms, specialising in crustaceans including copepods, amphipods and mysids; but also phytoplankton and larger prey (Camphuysen & Henderson, 2016; FAO, 1985; Heessen et al., 2015).	PRESENCE: predominantly April - October (Annual western Wadden Sea NIOZ fyke catches) (Camphuysen & Henderson, 2016). In Marsdiep, pilchard was caught in October surveys, but not in May surveys (Couperus et al., 2016). PEAK: October (Couperus et al., 2016) SPAWNING: spawn offshore during spring and summer (May/June) (Camphuysen & Henderson, 2016; Couperus, et al., 2016).	food source for a range of fish and marine mammal species (Heessen et al., 2015).	In North Sea, pilchard seldom appear in sufficient quantity to be of economic importance (Heessen et al., 2015)	Juvenile & Adult (Dickmann, 2005; Costalago & Palomera, 2014)	Juvenile & Adult (Couperus et al., 2016)	Filter & particulate feeding Dominate feeding mode appears to be non-selective filter feeding, although they may also feed selectively on larger prey (Heessen et al., 2015).
Anchovy	<i>Engraulis encrasicolus</i>	HIGH - Together with sprat, herring, sandeel & pilchard the most abundant pelagic fish in Marsdiep area (Couperus et al., 2016).	YES - feeds mainly on copepods, malacostracan larvae and fish larvae, with other items like fish, chaetognaths, larvaceans, gastropods and cephalopods also being found (Heessen et al., 2015; Raab et al., 2011). During preflexion stage, Anchovy mainly consumes copepod nauplii (similar to sprat), although there is some evidence that anchovy larvae are opportunistic feeders that can consume protozoans (Rossi et al., 2006)	Opportunistic - found to be more generalist, consuming a higher diversity of prey items. anchovy is likely to be the least affected by changing plankton communities (Raab et al., 2012; Petitgas et al., 2012)	PRESENCE: found May-Oct in pelagic sampling net in Marsdiep (Programma naar een rijke Waddenzee, n.d.) PEAK: June (van Bleijswijk, et al., 2020). SPAWNING: April - October (inshore) (Camphuysen & Henderson, 2016)	Important food fish for marine wildlife and predatory fish around the world, but only fairly recently of significance within the North Sea (Camphuysen & Henderson, 2016).	Popular consumption fish; also used extensively for fishmeal; have supported large coastal fisheries in Europe (Camphuysen & Henderson, 2016).	Juvenile & Adult (Kanstinger & Peck, 2009)	Juvenile - After moving into inshore water to spawn, the migrate offshore (Heessen et al., 2015).	Filter-feeders, but can switch to particulate feeding (Louw et al., 1998).

Moon jellyfish	<i>Aurelia aurita</i>	HIGH – Most abundant Scyphozoan species in Dutch Wadden Sea (van Walraven, 2016)	YES - copepods as main food source; phytoplankton (diatoms and flagellates), ciliates, rotifers, barnacle nauplii and cyprids, copepod nauplii, gastropod and bivalve larvae, polychaete larvae (Stoecker et al., 1987); predator of plaice and flounder larvae (van der Veer, 1985)	Opportunistic - feeds on micro/mesoplankton although able to catch prey the size of small fish larvae (Hay et al., 1990)	Presence: April - August (Van der Veer & Oorthuysen, 1985; van Walraven, 2016); Ephyrae present: early March - May, sometimes earlier; Medusae peak: April - June (Walraven, 2016); Spawning: Summer (Van der Veer & Oorthuysen, 1985)	Medusae can have considerable impact on coastal ecosystems through high predation rate and competition with other species for food (Stoecker et al., 1987; Möller 1980; Lesniewski et al., 2015).	Economical damage: Scyphomedusae (blooms) affect aquaculture, fishery, tourism and the operation of power plants through clogging of sea water inlets (Hay et al., 1990; Lesniewski et al., 2015); Food source: In some Asian countries exploited as a valuable fisheries resource for food (Archdale & Anraku, 2005)	Juvenile & adult (Van der Veer & Oorthuysen, 1985); Ephyra larva feeds on copepods, phytoplankton & POM (Bämstedt et al., 2001) Polyps fed on planula larvae of <i>A. aurita</i> and <i>C. capillata</i> (Gröndahl, 1988)	Juvenile & adult (Van der Veer & Oorthuysen, 1985)	Suspension feeder (Stoecker et al., 1987); Tentacles on umbrella margin stick to the prey and contract, bringing it close to the margin; can discriminate a prey according to its taste; prey selection takes place after transfer to the oral arms; generates feeding current (Archdale & Anraku, 2005)
Blue Jellyfish	<i>Cyanea lamarckii</i>	LOW - Much lower than <i>A. aurita</i> ; Mean daily number of individuals caught always averaged below 30 and 60 individuals (van Walraven, 2016); Was the most frequently encountered species in study of Barz & Hirsche (2006); More offshore distribution (Hay et al., 1990)	YES - copepod and other crustacean species, fish eggs & larvae, including clupeids; decapod larvae (<i>Brachyura</i> and <i>Caridea</i>); Echinodermata larvae (<i>Brachiolaria</i> and <i>Ophiuroidea</i>). Fish larvae (<i>Syngnathidae</i> , <i>Clupeidae</i> , <i>Trachurus trachurus</i>) (Barz & Hirsche, 2006)	Opportunistic - (Hay et al., 1990; Barz & Hirsche, 2006) Scyphomedusae are efficient, opportunistic predators in the patchy planktonic environment. They grow rapidly and have effective foraging behavior and feeding mechanisms and a wide dietary range (Hay et al., 1990)	Presence: end of May - Aug; Ephyrae present: usually Nov - May; Medusae peak: two peaks, Dec-Feb & Jun-Aug. (van Walraven, 2016); Occurrence southern North Sea: February – August Most abundant in June, thereafter abundance dropped until August, and completely disappeared by September (Barz & Hirsche, 2006)	Medusae can have considerable impact on coastal ecosystems through high predation rate and competition with other species for food (Stoecker et al., 1987; Möller 1980; Lesniewski et al., 2015).	Economical damage: Scyphomedusae (blooms) affect aquaculture, fishery, tourism and the operation of power plants through clogging of sea water inlets (Hay et al., 1990; Lesniewski et al., 2015); Food source: In some Asian countries exploited as a valuable fisheries resource for food (Archdale & Anraku, 2005)	Adult: prey contained several copepod and other crustacean species (Barz & Hirsche, 2006); Juvenile: unknown	Adult (van Walraven, 2016); Juvenile unknown	Tactile predation - Banks of nematocysts in tentacles for capturing planktonic prey (Lilley et al., 2008)
Lion's mane jellyfish	<i>Cyanea capillata</i>	LOW - Much lower than <i>A. aurita</i> ; Mean daily number of individuals caught always averaged below 30 and 60 individuals (van Walraven, 2016); occur en masse during the summer months in the North Sea; more offshore distributed (Hay et al. 1990; Barz & Hirsche, 2006)	YES - copepod and other crustacean species, fish larvae, including clupeids; decapod larvae (<i>Brachyura</i> and <i>Caridea</i>); Echinodermata larvae (<i>Brachiolaria</i> and <i>Ophiuroidea</i>). Fish larvae (<i>Syngnathidae</i> , <i>Clupeidae</i> , <i>Trachurus trachurus</i>) (Barz & Hirsche, 2006)	Opportunistic - (Hay et al., 1990; Barz & Hirsche, 2006) Scyphomedusae are efficient, opportunistic predators in the patchy planktonic environment. They grow rapidly and have effective foraging behavior and feeding mechanisms and a wide dietary range (Hay et al., 1990)	Presence: beginning of June - August; Ephyrae present: unknown; Medusae peak: very rare, later than <i>C. lamarckii</i> (Walraven, 2016); Months with highest catches were May-July; <i>Cyanea spp.</i> was present for 100 days on average (van Walraven, 2016); Occurrence in southern North Sea: Most abundant in June, thereafter abundance dropped until August, and completely disappeared by September (Barz & Hirsche, 2006)	Medusae can have considerable impact on coastal ecosystems through high predation rate and competition with other species for food (Stoecker et al., 1987; Möller 1980; Lesniewski et al., 2015).	Economical damage: Scyphomedusae (blooms) affect aquaculture, fishery, tourism and the operation of power plants through clogging of sea water inlets (Hay et al., 1990; Lesniewski et al., 2015); Food source: In some Asian countries exploited as a valuable fisheries resource for food (Archdale & Anraku, 2005)	Juvenile & adult Adult: prey contained several copepod and other crustacean species (Barz & Hirsche, 2006) Polyps: fed with hatched nauplii of the brine shrimp, <i>Artemia franciscana</i> & living <i>Artemia nauplii</i> (copepod nauplii) (Lesniewski et al., 2015)	Adult (van Walraven, 2016); Juvenile unknown	Tactile predation - Banks of nematocysts in tentacles for capturing planktonic prey (Lilley et al., 2008)

Compass Jellyfish	<i>Chrysaora hysoscella</i>	LOW - Abundances much lower than <i>A. aurita</i> : in all years, the mean daily number of individuals caught always averaged below 30 and 60 individuals, respectively; commonly found in most Dutch coastal waters (Walraven et al., 2014)	YES - copepod and other crustacean species, fish larvae, including clupeids; decapod larvae (<i>Brachyura</i> and <i>Caridea</i>); Echinodermata larvae (<i>Brachiolaria</i> and <i>Ophiuroidea</i>). Fish larvae (<i>Syngnathidae</i> , <i>Clupeidae</i> , <i>Trachurus trachurus</i>) (Barz & Hirsche, 2006)	Opportunistic - (Hay et al., 1990); (Barz & Hirsche, 2006) Scyphomedusae are efficient, opportunistic predators in the patchy planktonic environment. They grow rapidly and have effective foraging behavior and feeding mechanisms and a wide dietary range (Hay et al., 1990)	Presence: June - Sept; for 95 days on average Ephyrae present: scarce, May - Aug, sometimes later; Medusae peak: August/September (van Walraven, 2016)	Medusae can have considerable impact on coastal ecosystems through high predation rate and competition with other species for food (Stoecker et al., 1987; Möller 1980; Lesniewski et al., 2015).	Economical damage: Scyphomedusae (blooms) affect aquaculture, fishery, tourism and the operation of power plants through clogging of sea water inlets (Hay et al., 1990; Lesniewski et al., 2015); Food source: In some Asian countries exploited as a valuable fisheries resource for food (Archdale & Anraku, 2005)	Juvenile & adult Adult: prey contained several copepod and other crustacean species (Barz & Hirsche, 2006) Polyps: fed with hatched nauplii of the brine shrimp, <i>Artemia franciscana</i> & living <i>Artemia nauplii</i> (copepod nauplii) (Lesniewski et al., 2015)	Adult (van Walraven, 2016); Juvenile unknown	Tactile predation - Banks of nematocysts in tentacles for capturing planktonic prey (Lilley et al., 2008)	Pelagic – adult, juvenile Benthic – polyp
Barrel Jellyfish	<i>Rhizostoma octopus</i>	MEDIUM - Abundance of <i>R. octopus</i> was intermediate between that of <i>A. aurita</i> and the other Scyphozoans (van Walraven, 2016)	YES - copepods (3%); predominant species preyed upon were diatoms <i>Asterionella</i> and <i>Coscinodiscus</i> <200µm (Perez-Ruzafa et al., 2002);	Opportunistic - (Hay et al., 1990); Scyphomedusae are efficient, opportunistic predators in the patchy planktonic environment. They grow rapidly and have effective foraging behavior and feeding mechanisms and a wide dietary range (Hay et al., 1990)	Presence: mid- July - Oct; First appearance: <i>R. octopus</i> from mid-July (van Walraven, 2016) Ephyrae present: never; Medusae peak: Low numbers in autumn (van Walraven, 2016); peak abundances in August/September and September/October (Hay et al., 1990)	Medusae can have considerable impact on coastal ecosystems through high predation rate and competition with other species for food (Stoecker et al., 1987; Möller 1980; Lesniewski et al., 2015).	Economical damage: Scyphomedusae (blooms) affect aquaculture, fishery, tourism and the operation of power plants through clogging of sea water inlets (Hay et al., 1990; Lesniewski et al., 2015); Food source: In some Asian countries exploited as a valuable fisheries resource for food (Archdale & Anraku, 2005) In Wales: commercially harvested to produce high-value medical grade collagen (Elliott et al., 2016)	Adult (Perez-Ruzafa et al., 2002), Juvenile unknown	Adult (van Walraven, 2016); Juvenile/ polyp unknown	Filter feeder - filters prey through a mass of eight oral arms hanging below the bell (Lilley et al., 2008)	Pelagic – adult, juvenile Benthic – polyp
Sea gooseberry	<i>Pleurobrachia pileus</i>	MEDIUM - According to van Walraven (2016) always present from several observations between 1982 and 2012; During 1980s: most abundant gelatinous zooplankton species (van Walraven, 2016). Densities ranged from 1 to 20 individuals per m3 (Kuipers et al., 1990)	YES - copepods (10 to 20 per day) (Kuipers et al., 1990); predation on plaice and flounder larvae (van der Veer, 1985); large crustacean zooplankton (>1050 µm) were the dominant item, principally calanoid copepods (Frank, 1986)	Opportunistic - Frank (1986) examined fish eggs and <i>Oikopleura</i> sp. in less than 2% of the stomachs examined	Presence: March - August; Increasing at end of March; First peak mid-May; Decreasing until beginning of June; Increasing again end of June (first peak of <i>M. leidyi</i>); Decrease, only few left in August (van Walraven, 2016)	Competition for crustacean zooplankton with pelagic fish and planktonic larval stages of most fish (Frank, 1986).		Adult & Juvenile?	Adult & Juvenile? (<5mm) (Kuipers et al., 1990)	Sit-and-wait predators and use long, branched tentacles containing colloblasts, sticky adhesive cells to which the prey adheres (van Walraven, 2016)	Pelagic – adult, juvenile Benthic – polyp
Comb jelly/Sea walnut	<i>Mnemiopsis leidyi</i>	HIGH - Most common species in Dutch coastal waters; Occurs year-round in substantial numbers (van Walraven, 2016)	YES - wide range of different zooplankton prey such as copepods and their nauplii, bivalve veligers, barnacle nauplii fish larvae and eggs (van Walraven, 2016). Responsible for most of the predation pressure on mesozooplankton in the Dutch Wadden Sea (van Walraven, 2016)	Zooplanktivorous - but also opportunistic planktonic predator (van Walraven, 2016)	Presence: whole year round with multiple peaks. Spawning: May; First peak: mid-June (highest mean density 360 ind m-3). Second peak mid-August; At peak densities: 912 ind m-3. population almost entirely small (<20 mm), remain high until October, decreasing to low levels in November (van Walraven, 2016)	Potential to cause ecological damage and cascading consequences through the food web (van Walraven, 2016).		Juvenile & Adult (Granhag et al., 2011; Purcell et al., 1994; Javidpour et al., 2009); Juv.: microzooplankton, 2010; van Walraven, 2016). Adult: mesozooplankton (van Walraven, 2016)	Juvenile & Adult: Winter/spring: mixture of small individuals between 5 and 20 mm & larger than 20 mm. In May first wave of juveniles (<5mm) (van Walraven, 2016)	Filter feeder (van Walraven, 2016)	Pelagic – adult, juvenile Benthic – polyp

Common Cockle	<i>Cerastoderma edule</i>	HIGH - <i>C. edule</i> contributed together with <i>M. arenaria</i> most to total-bivalve biomass (in the Balgzand area) (Beukema & Dekker, 2019). In the east of the Wadden Sea, <i>C. edule</i> contributed the sole largest share of the total biomass (Compton, et al., 2013). Total biomass in Dutch WS in spring 2019: 196,4 million kg, and autumn 2019 308,1 million kg wet weight (van Asch et al., 2019).	YES - consume a wide range of zooplankton species, but selectively consumed smaller categories of zooplankton. According to a diet study by Lehane & Davenport (2002), <i>C. edule</i> consumed mostly hydromedusae (followed by Crustacea nauplii & Cladocerans). Bivalve larvae are also depleted around adult <i>C. edule</i> (André & Rosenberg, 1991; Lehane & Davenport, 2004).	Opportunistic - feed on a combination of both, suspended particulate organic matter and phytoplankton, but also a wide range of zooplankton (Malham et al., 2012; Lehane & Davenport, 2002)	PRESENCE: all year around (large year-to-year fluctuations in annual biomass) (Beukema & Dekker, 2001, 2006). PEAK BIOMASS: August (max biomass around the end of the second growing season - 1.3 yr after their settlement (Beukema & Dekker, 2006). Generally high in May/June and low in February/March (Zwarts, 1991). SPAWNING: April - October (Cardoso et al., 2009)	Together with blue mussels <i>Mytilus edulis</i> , they constitute the main food item of the 2 (quantitatively) most important bird species of the Wadden Sea: oystercatcher <i>Haematopus ostralegus</i> and eider <i>Somateria mollissima</i> (Beukema & Dekker, 2006).	Manual cockle fishery in the WS in designated areas. Annual harvest should not exceed 5 % of the overall stock (Baer et al., 2017).	Adult (>12mm) (Lehane & Davenport, 2002); pelagic larval stages, spat (≤5mm) & juveniles (5mm up to ≤12mm) feed predominately on small phytoplankton, including dinoflagellates, diatoms, ciliates and bacteria (Bos et al., 2006; Kang et al., 1999)	Juvenile & Adult (Bos et al., 2006)	Filter feeders (Malham et al., 2012) (Suspension - feeder (Beukema & Dekker, 2019).
Sand gaper	<i>Mya arenaria</i>	MEDIUM - <i>M. arenaria</i> contributed together with <i>C. edule</i> most to total-bivalve biomass (in the Balgzand area) (Beukema & Dekker, 2019). In the western WS, <i>M. arenaria</i> , <i>C. edule</i> and <i>E. directus</i> contributed the largest share of the total biomass (Compton et al., 2013).	YES - prey on bivalve larvae. According to a study by André & Rosenberg (1991), settlement of bivalve larvae was reduced by 20% in the presence of <i>M. arenaria</i> .	Opportunistic - important grazer of phytoplankton such as dinoflagellates, but also filters out ciliates and copepod eggs and nauplii (Lonsdale et al., 2009).	PRESENCE: all year around (large year-to-year fluctuations in annual biomass) (Beukema & Dekker, 2001). PEAK BIOMASS: Generally high in May/June and low in February/March (Zwarts, 1991). SPAWNING: April - Novmeber (Cardoso et al., 2009).	play an important role in Dutch WS in terms of biomass as well as in terms of productivity (Cardoso et al., 2009)		Unknown	Juvenile & Adult	Filter-feeders (Suspension - feeder (Beukema & Dekker, 2019).
Baltic tellin, Baltic macoma	<i>Limecola balthica</i>	MEDIUM - Among the most abundant bivalves in WS, together with <i>C. edule</i> , <i>M. arenaria</i> & <i>M. edulis</i> (Beukema et al., 1978; Beukema et al., 1993).	Unknown	Unknown - feed mostly on algae from the sediment (facultative deposit feeder) and the water column (Rossi et al., 2004).	PRESENCE: all year around (large year-to-year fluctuations in annual biomass) (Beukema et al., 2001). PEAK BIOMASS: Generally high in May/June and low in February/March (Zwarts, 1991). SPAWNING: end of March or the beginning of April (Honkoop, 1998)	Prey - Waders and ducks, as well as epibenthic crustaceans and fish exert a strong predation pressure on <i>L. balthica</i> (Hiddink, et al., 2002).			Juvenile & Adult (Hiddink et al., 2002)	Suspension/deposit-feeder (Beukema & Dekker, 2019).
Pacific oyster	<i>Magallana gigas</i>	HIGH - Since 2000, <i>C. gigas</i> is found in all parts of the Dutch Wadden Sea, although in most places in small numbers (Nehls et al., 2009). Total biomass in Dutch WS in 2018: 63,8 million kg wet weight & total area of 1475 ha (Ende et al., 2018).	YES - but feeds mainly on phytoplankton, such as flagellates, microphytoplankton, dinoflagellates, ciliates, but also clears out larger zooplankton (<i>Appendicularia</i> & bivalvia veligers, but also Copepoda nauplii) as shown in a diet study by Dupuy et. al (2000). According to Xu and Yang (2007) phytoplankton is the most important food source for intertidal oyster <i>C. gigas</i> .	Opportunistic (Dupuy et al., 2000)	PRESENCE: all year around (Brandt et. al, 2008) PEAK BIOMASS: highest growth in the first spring after settlement until November (Diederich, et. al, 2004) SPAWNING: July & August (Diederich et al., 2005)	As an ecosystem engineer , oysters are replacing and enhancing the ecological function of intertidal blue mussel beds in the Wadden Sea (Nehls et al., 2009).	Human consumption; in Dutch WS, collection of <i>M. gigas</i> by hand and only smaller specimens are individually collected (Fey et al., 2010).	Adult (Dupuy et al., 2000) Juvenile unknown?	Juvenile & Adult (Brandt et al., 2008)	Suspension-feeder (Nehls et al., 2009).

Blue mussel	<i>Mytilus edulis</i>	HIGH - Among the most abundant bivalves in WS, together with <i>C. edule</i> , <i>M. arenaria</i> & <i>M. balthica</i> (Beukema et al, 1978; Beukema et al, 1993). Total biomass in Dutch WS in 2018: about 55,5 million kg wet weight. Total size of mussel beds: 2672 ha in 2018 (Ende et al., 2018)	YES - feed on phyto- and zooplankton; they can take up large numbers of micro- and mesozooplankton, including crustaceans. Studies show that <i>M. edulis</i> selectively consume smaller zooplankton categories (Davenport et al., 2000; Horsted et al., 1988; Lehane & Davenport, 2002; Wong et al., 2003).	Opportunistic (Davenport et al., 2000; Lehane & Davenport, 2002)	PRESENCE: all year around (large year-to-year fluctuations in annual biomass) (Beukema et al., 2001). PEAK BIOMASS: growth in body mass from Jan to Jul; with peak in July (de Vooy, 1999; Cardoso et al., 2007). SPAWNING: April - June (main spawning event); larval peak in May, followed by smaller peaks until Sept (de Vooy, 1999; Cardoso et al., 2007).	Key components of the Wadden Sea ecosystem; important role in the food web - link between primary producers and the higher trophic levels. Prey for numerous birds, crabs, shrimp & fish (Baer et al., 2017).	Mussel cultivation and fishery: heavily exploited by mussel farmers, collecting young or half-grown mussels ('seed mussels') to stock their culture lots (Nehls et al., 2009).	Juvenile (up to 25mm; <1yr) & Adult (>25mm) (Davenport et al., 2000; Lehane & Davenport, 2002); pelagic larval stages (up to 1.5mm) feed predominately on small phytoplankton, including dinoflagellates, diatoms, ciliates and bacteria (Bos et al., 2006); Juvenile <i>M. edulis</i> generally filter on smaller particles in higher rates than adults, and therefore may be more opportunistic than adult bivalves (Jacobs et al., 2015).	Juvenile & Adult (Cardoso et al., 2007)	Suspension - feeder (Beukema & Dekker, 2019).
American razor-clam; Jack-knife clam	<i>Ensis leei</i>	HIGH - Since 2002, <i>E. directus</i> has been the most common mollusc species in the Dutch coastal zone (Tulp et al., 2010). According to Compton et al. (2013), <i>E. directus</i> contributes, together with <i>M. arenaria</i> and <i>C. edule</i> , the largest share of the total biomass in the western Dutch WS. High biomass in the transition area (between subtidal and intertidal), as it occupies an empty niche - resulted in significant increasing trend in total zoobenthic biomass (Dekker & Beukema, 2012).	NO - typically feeds on suspended organic detritus and phytoplankton (Hill, 2006; Kamermans & Dedert, 2012)	Opportunistic - broad diet or opportunistic feeding strategy (Dannheim & Rumohr, 2012); feed on phytoplankton, diatoms and flagellates; in diet study by Kamermans & Dedert (2012)	PRESENCE: all year around (Tulp, 2010) PEAK BIOMASS: highest growth rate in first year mussels (peak in August) (Dannheim & Rumohr, 2012) SPAWNING: March/April (Dannheim & Rumohr, 2012).	Significant prey for fish, such as plaice, sole, dab, flounder and dragonet; also important food for eider and common scoter. <i>E. leei</i> is an alternative prey to native species such as trough shells, blue mussels and cockle (Tulp, 2010).			Juvenile & Adult (Dannheim & Rumohr, 2012)	Filter-feeder (Kamermans & Dedert, 2012)

Brown shrimp, comm on shrimp, bay shrimp, sand shrimp	<i>Crangon crangon</i>	HIGH - most numerous & important macrobenthic carnivore in the Wadden Sea tidal zone; One of the most abundant benthic species in shallow soft bottom areas along the European coast (Campos et al., 2010)	YES – Juvenile shrimps mainly feed on ostracods and harpacticoids (Pihl & Rosenberg, 1984). Feeds on mysids, amphipods, isopods and crustaceans such as copepods, crab post larvae and cypris larvae of barnacle (Pihl & Rosenberg, 1984; Oh et al., 2001; Criales & Anger, 1986)	Opportunistic - very varied diet, mainly composed of demersal, in- and epifaunal organisms during its juvenile and adult life (Campos et al., 2010)	Presence: All year around; In autumn, abundance 5 times greater than in spring; Spawning: egg-bearing females can be found all year round, mainly in summer and winter (Campos et al. 2010);	Key component of the trophic web as important food source for several predators including fish, crustaceans and shorebirds (Campos et al., 2010); Key predator of benthic animals; One of most Frequent prey items for commercially exploited fish populations such as plaice, flounder, and cod (Criales & Anger, 1986)	Intensively exploited by coastal fisheries in the North Sea, and thus plays an important economic role in this region (Criales & Anger, 1986)	Juvenile & adult (Pihl & Rosenberg, 1984; Janssen, 1980)	Juvenile & Adult - Extensive tidal flats: population consists of juvenile shrimps (< 35 mm) : Subtidal: Shrimps of length > 3.5 cm, average length of roughly 3,5 to 4.5 cm; Juvenile enter in May, remain till Oct/Nov in considerable numbers (Kuipers and Dapper, 1981)	
Shore crab, green shore crab	<i>Carcinus maenas</i>	HIGH - Dominating biomass of macrozoobenthos (Dekker, 1989); Occurred in high numbers at the Danish Wadden Sea in 1982 (Jensen & Jensen, 1985); Abundance varies significantly from year to year, partly in response to winter temperatures (Beukema, 1991)	YES – but only larvae feeds on zooplankton (copepods); Adults: wide variety of benthic organisms (Meyer-Harms & Anger, (1994)	Opportunistic - omnivorous animal with raptorial feeding abilities (Klein Breteler, 1976)	Presence: All year around; Larvae are found in the plankton from spring to autumn; High abundance from June to July, forming up to 70 % of the total mesozooplankton (Meyer-Harms & Anger,1994) Juvenile & adult crabs inhabit the flats in summer and autumn at low tide (Klein Breteler, 1976)	Key role in structuring the benthic community in the Wadden Sea (Jensen & Jensen, 1985); Important role as predators on the benthos in shallow coastal waters (Beukema, 1991);		Larvae (Meyer-Harms & Anger, 1994)	Juvenile & adult (Beukema, 1991, Klein Breteler, 1976) Juvenile: tidal flats Adults: lower intertidal and subtidal areas	
Australasian barnacle; New Zealand barnacle	<i>Austrominius modestus</i>	HIGH - According to the survey of Gittenberger et al., (2010), <i>A. modestus</i> is the most abundant barnacle in the Dutch Wadden Sea, inhabiting a wide range of littoral and sublittoral habitats	YES - but mainly phytoplankton (2 diatoms, a dinoflagellate, a prasinophyte and a chlorophyte); zooplankton (the copepod <i>Acartia spinicauda</i>) (Rainbow & Wang, 2010) The nauplii probably feed mainly on particles less than 10µm in size, as the diameter of the oesophagus is of this magnitude (Crisp, 1958)	Opportunistic - feed by filtering suspended matter in large quantities; feed on phyto- & zooplankton (Rainbow & Wang, 2010); wide range of particle sizes and taking in both animal and plant material (Crisp, 1958)	Presence: All year around; Spawning: under optimum conditions broods may be liberated every 10 days; larvae are extremely abundant, often forming the dominant component of the plankton in May, June and July (in estuaries of south-east England); <i>A. modestus</i> rapidly converts the food into nauplii which enter the plankton during summer (Crisp, 1958)	Competition for space with native species (Gittenberg et al., 2010)		Adult – Stone (1988) shows that there is mechanistic selection of larger sized particles as the larvae become larger, which supports the idea of feeding using filtering appendages; juvenile feed on phytoplankton	Juvenile & adult (De Wolf, 1973; Gittenberger et al., 2010)	Suspended filter feeders (Rainbow & Wang, 2010)
Mud shrimp	<i>Corophium volutator</i>	HIGH - can be found in high densities (up to 100 000 per m 2) in the muddy upper tidal flats along the coast line, where it numerically dominates the macrozoobenthic community (Flach, 1992)	NO – diatoms & bacteria (Gerdol & Hughes, 1994; Fenchel et al., 1975)	Opportunistic - diet is indirect and inconclusive; ingest particles within the size range 4 to 63 µm (Gerdol & Hughes, 1994)	Presence: All year around (Whales); Overwintering group (mature >7mm, Immature <7mm); newly hatched max April - Oct (Watkin, 1941) Spawning: Mature breed in February, died off in March, April; Immature breed March-July, died off August; New brood breed October (Watkin, 1941)	Increase bioturbation rate through behavioral activities in sediment. Bioturbation is one of the major processes influencing ecosystem functioning (de Backer et al., 2011) Predated extensively by strand piper and other shorebirds (Hamilton et al., 2006)			Juvenile & adult (Regarding Watkin (1941) studied <i>C. voluator</i> in Whales)	Suspension & deposit feeder (Gerdol & Hughes, 1994; Jensen, 1985)

Appendix II – Interview questions for experts

Expert	Species	Knowledge gaps	Questions
A	Chordata		
Date: 15.07.2020		Gut content analysis	<ol style="list-style-type: none"> 1. Do you know an appropriate method for collecting stomach content of small fish? 2. Do you know an appropriate preservation method of fish stomach contents for later gut analysis?
B	Cnidaria/ Ctenophore		
Date: 01.07.2020		Life stage of zooplankton predation	<ol style="list-style-type: none"> 1. Do you know if the planula larvae feeds on zooplankton? 2. Do you know if ephyra (tiny pelagic medusa which forms after polyp stage) feeds on zooplankton? 3. <i>R. octopus/ P. pileus</i>: Do you know if juvenile also predate on zooplankton & live in the WS?
		Occurrence and life cycle	<ol style="list-style-type: none"> 4. Do you know if planula is the only larva stage or is there a second larva stage after the polyp detachment? 5. The benthic stages of all species except <i>Aurelia aurita</i> have seldom to never been found in the NS or other Dutch coastal waters (van Walraven, 2016) → Does this mean that planula probably migrate out of WS (to hard substrate) and come back in ephyra stage to feed?)
		Species composition Wadden Sea	<ol style="list-style-type: none"> 6. Larvae of ctenophores are 2- 5mm: → Thus juveniles are > 5 mm? Do you know from which size adult? 7. Do you know from which size on, is scyphozoa adult?
		Gut content analysis	<ol style="list-style-type: none"> 8. In order to analyse the gut content would you rather suggest to do it as Michiel van Harten with a needle to flush out stomach content or preserving it immediately in 70% ethanol. for later gut content analyses? -> better for later DNA analysis? 9. Fixation method using Trichloroacetic Acid allows fixation and preservation of <i>M. leidy</i> and storage of samples for longer periods (van Walraven, 2016) → Which method would you suggest for gut content analysis & later DNA analysis? → TCA method? But then gut analysis is difficult. Maybe combining "flush-method" and TCA?
C	Mollusca		
Date: 01.07.2020		Predation on zooplankton	<ol style="list-style-type: none"> 1. Do you know if <i>M. balthica</i> and <i>E. directus</i> feed on zooplankton? If yes, on what zooplankton species?
		Life stage of zooplankton predation	<ol style="list-style-type: none"> 2. Diet shift of bivalves during different life stages: → Do you know if bivalve larvae feed on zooplankton? → Do you know if diet of juvenile bivalves differs from adults?
		Gut content analysis	<ol style="list-style-type: none"> 3. Have you been involved with conducting feeding experiments/gut analysis on bivalves? Or do you know of someone who conducted these experiments? 4. Do you know if methods with <i>M. edulis</i> similar to other bivalves?
D	Crustacea		
Date: 31.07.2020		Feeding mechanism	<ol style="list-style-type: none"> 1. Do you know how <i>C. crangon</i> feeds?
		Species composition in Wadden Sea	<ol style="list-style-type: none"> 2. Do you know if shrimps migrate from WS to North Sea and back?
		Gut content analysis	<ol style="list-style-type: none"> 3. Which method would you suggest to conduct gut content analysis?

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