

Master's thesis

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Effect of temperature on the settling rate, survival, ingestion rate and biochemical composition of the polyp stages of *A. aurita*

Master's thesis in Ocean Resources

Supervisor: Nicole Aberle-Malzahn

June 2020

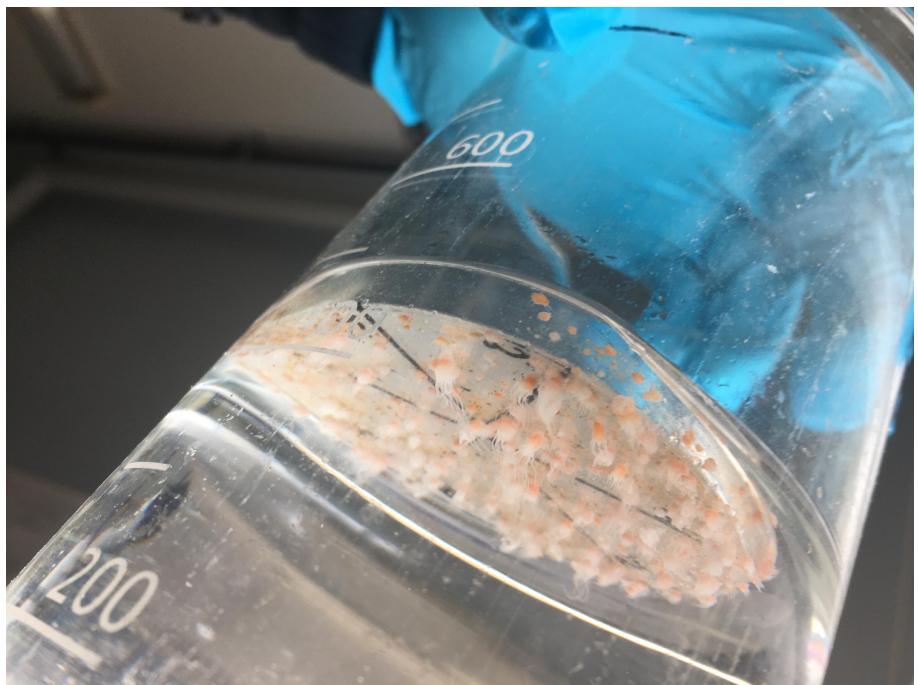


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Tromsø, June 2020

Stian

The picture on the front page depicts an experimental unit, containing polyps hanging from a petri dish.
Photo: S. L. Myrvold

Abstract

Large aggregation of jellyfish known as blooms are expected to increase as a result of anthropogenic influences, these blooms are known to cause economical and potentially ecological harm. The EU Horizon 2002 project GoJelly stems from a need for a deeper understanding for the biotic and abiotic factors promoting bloom formations. The scyphozoan polyp is believed to be one of the driving forces behind formation of jellyfish blooms. The main aim of this thesis was therefore to study the effect of temperature on the settling rate, survival, ingestion rate and biochemical composition of the polyp stages (scyphistoma) of *Aurelia aurita*. A laboratory-based experiment was conducted in order to achieve the goals stated above. Fecund *A. aurita* medusa was collected in the Trondheimfjord and a temperature gradient experiments was conducted on the settlement, survival and ingestion of *A. aurita* polyps. No apparent relationship was observed for the effect of temperature on the settling ability of the *A. aurita* planula and the biochemical composition (carbon and nitrogen) of the polyp. A negative correlation between increasing temperature and the survival of the polyp was detected, and the polyp ingestion rate was observed to increase as a result of increasing temperatures. These observations show that there is an apparent negative relationship between increasing temperatures and survival of the *A. aurita* polyps of the Trondheimfjord, which might result in less frequent *A. aurita* blooms in the Trondheimsfjord as a result of expected increase in the sea surface temperature.

Sammendrag

Store manetansamlinger kjent som manetoppblomstringer er forventet å øke som en følge av menneskeskapte påvirkninger. Oppblomstringene er kjent for å føre til økonomiske, og potensielt økologiske, skader. GoJelly er et EU Horizon 2020 prosjekt startet som en følge av behovet for en dypere forståelse for hvilke biotiske og abiotiske faktorer som fremmer dannelsen av manetoppblomstringer. Polyppen hos Scyphozoa (stormaneter) er antatt å være en av drivkretene bak dannelsen av manetoppblomstringer. Hovedmålet med denne oppgaven var derfor å studere effekten av temperatur på fastsettelsesrate, overlevelse, inntaksrate av mat og biokjemisk komposisjon for polyppstadiet til *Aurelia aurita*. Det ble gjennomført et labforsøk for å oppnå de overnevnte målene. Fruktbare *A. aurita* meduser ble samlet i Trondheimsfjorden og en temperaturgradient ble brukt til å gjennomføre forsøk på fastsettelsesrate, overlevelse og inntaksrate for polyppstadiet til *A. aurita*. Det ble tilsynelatende ikke observert noe forhold mellom temperatur og planulaens evne til å feste seg, samt den biokjemiske komposisjonen (karbon og nitrogen) til polyppen. Det ble observert en negativ sammenheng mellom økende temperatur og polyppens overlevelsesevne, i tillegg til at polyppens inntaksrate økte som et resultat av økende temperatur. Disse observasjonene viser at det er et tilsynelatende negative forhold mellom økende temperatur og overlevelsesevnen hos *A. aurita* polypper i Trondheimsfjorden. Dette indikerer at økt temperatur i havoverflaten som følge av klimaendringer vil kunne føre til mindre hyppige *A. aurita* oppblomstringer i Trondheimsfjorden.

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List of Abbreviations (or Symbols)

<i>A. aurita</i>	<i>Aurelia aurita</i>
ANOVA	Analysis of variance
C	Carbon
DW	Dry weight
EU	Experimental unit
FD	Freeze drying
GFP	Green fluorescent protein
N	Nitrogen
ns	Non significant
OD	Oven dried
R/V	Research Vessel
SD	Standard deviation
sp	species
SST	Sea surface temperatures
TBS	Trondhjem Biological Station
THC	Atlantic Thermohaline Circulation
QQ plot	Quantile quantile plot
WP2	Work Package 2
WW	Wet Weight

1. Introduction

1.1. Jellyfish blooms

Large aggregations of gelatinous plankton in the water masses are known as jellyfish blooms (Lucas and Dawson, 2014). Jellyfish blooms can be divided into true blooms and outbreaks. The true blooms are partly a result of the seasonal life cycles of jellyfish and partly a result of environmental conditions - temperature, light, O₂, food and salinity (Lucas and Dawson, 2014, Purcell et al., 2009). The seasonal biomass normal or abnormal is therefore a result of population increase through reproduction and growth. This may or may not be enhanced by anthropogenic factors.

Outbreaks on the other hand are an unforeseen abrupt increase in the biomass, associated with anthropogenic intrusion on the ecosystem. These outbreaks can be seasonal or unseasonal, and reports have shown that they can vary over a temporal scale, spanning from weekly to decadal. (Graham et al., 2001, Hamner and Dawson, 2009, Lucas and Dawson, 2014, Lucas et al., 2012).

Several anthropogenic influences are suggested to play a role when it comes to higher frequencies and longer durations of jellyfish blooms. Several factors such as climate change, depletion of predators, overfishing and increased habitat availability as a result of increased amounts of artificial substrate are discussed as potential causes. The increased availability of artificial substrate can be a strong factor for increased blooms of jellyfish, specifically for scyphozoa species with benthic life stages (van Walraven et al., 2016, Hamner and Dawson, 2009, Lucas et al., 2012).

There is still a lot that is unknown regarding which biological traits (intrinsic) and which abiotic and biotic environmental characteristics in the ocean (extrinsic) that interact with each other to produce jellyfish blooms (Lucas and Dawson, 2014).

The public opinion about jellyfish is often negative and jellyfish is often considered to be a pest and a nuisance (Condon et al., 2012, Baumann and Schernewski, 2012, Duarte et al., 2014). Jellyfish blooms might have a negative impact on the economy as a result of medusae interfering with fisheries, aquaculture, powerplants, and tourism.

Fisheries are affected when large amounts of jellyfish are caught as bycatch, the jellyfish might damage the net or lower the quality of the caught fish (Lucas et al., 2014).

Jellyfish blooms can have a negative effect on net-based fish aquaculture, either directly or indirectly. These effects can be the result of fish getting stung by the cnidocytes of medusa, either by individuals that are small enough to flow into the sea cage or by fragments of larger individuals (Lucas et al., 2014). Bacterial infections and subsequent fish disease can be a consequence of these stings. Jellyfish blooms can also lead to fish mortality when the jellyfish biomass clog the sea-cages and the gills of the fish. Resulting in hypoxic conditions and subsequent suffocation of the fish (Halsband et al., 2017).

The harm to powerplants is a result of jellyfish aggregation and clogging of the inlets for cooling water (Purcell et al., 2007, Kaneda et al., 2007). The impact on tourism is directly linked to the negative public opinion, since many bathers detest jellyfish. Many jellyfish are also stingers can thus be directly dangerous to the bathers (Baumann and Schernewski, 2012, Purcell et al., 2007).

The negative public opinion regarding jellyfish might be removing focus from the beneficial effects that jellyfish can have (Doyle et al., 2014). Jellyfish are used as a food item in many countries (annual harvest ~750 000 tonnes, 2004-2013 mean) and jellyfish fisheries are present in 23(Brotz, 2016). Collagen stemming from jellyfish has been used experimentally as a treatment for rheumatoid arthritis and may also be of value as a way to rebuild bone, cartilage and muscle in human medicine (Addad et al., 2011).

Novel compounds have been identified and extracted from some jellyfish species, and the green fluorescent protein (GFP) were developed from compounds found in jellyfish. Research based on the GFP have led to a revolution in cell biology and physiology, making it possible to monitor events that takes place inside living cells and organisms (Doyle et al., 2014).

The ecological impact of the jellyfish blooms is often based on interactions between jellyfish and fish. The jellyfish compete with both juvenile and adult stages of planktivorous fish, and it can also act as a predator for fish eggs and larvae(Lynam et al., 2006). Jellyfish are in some instances viewed as food web “dead-ends” for several ecosystems, stopping the transfer of energy between trophic levels. Lynam et al(2006) state that certain ecosystems might shift from fish dominance to jellyfish dominance, this process might be irreversible (Lynam et al., 2006, Sommer et al., 2002, Christopher et al., 2005, Purcell et al., 2007).

Jellyfish are an important part of marine ecosystems. Jellyfish serve as the prey species for approximately 124 fish species, whereas 11 are considered to be jellyfish specialists. There are also 34 species of other animals that are known to prey on jellyfish (Richardson et al., 2009). Juvenile fish in certain ecosystems utilize jellyfish as a refuge from predators, while also feeding on parasitic organisms living on the jellyfish (Richardson et al., 2009).

Benefits obtained by humans through the utilization of the ecosystem are known as ecosystem services. The contribution of jellyfish to ecosystem services is in many cases viewed as more or less non existing (Doyle et al., 2014). Doyle et al. (2014) revise the ecosystem service contribution of jellyfish and place it into these categories: regulation, supporting, provisioning and cultural services. Regulation is the only category that will be explained in detail in this introduction.

Jellyfish can function as a biodiversity regulator (Diaz et al., 2005) and can at low densities perform as a keystone species (Pauly et al., 2009). The jellyfish can serve as the primary predator of abundant fish populations. The top-down control on these populations might increase the fitness of less abundant fish species. This might lead to an enhancement of the ecosystem’s biodiversity (Purcell and Grover, 1990, Boero et al., 2008, Doyle et al., 2014). High abundance of predating jellyfish can affect and control the population size of other zooplankton species, either directly or indirectly (Purcell, 1989)

Jellyfish contribute to climate regulation, through carbon sequestration and the subsequent transport of carbon in the water column. Transport of dead jellyfish to the seabed as particulate organic matter (POM) can play a vital role in the transport of carbon (C) through the water column (Lebrato et al., 2012).

A small but significant amount of nutrients supporting primary production might also stem from the jellyfish. For example, carbon, nitrogen (N) and phosphorous (P) released through mucus production, excretion as well as sloppy feeding (Pitt et al., 2009).

1.1. Scyphozoan lifecycle

Scyphozoa is one of the four classes of Cnidaria, scyphozoa is one of the main taxa responsible for jellyfish blooms. The scyphozoan jellyfish have a complex metagenetic life cycle, alternating between pelagic life stages (medusae) with sexual reproduction and benthic life stages (polyps) with asexual reproduction (*Figure 1*) (Duarte et al., 2014). Asexual reproduction is considered to be an energy efficient and effective method for offspring production (Crow, 1994). The asexual reproduction of scyphozoan polyps (budding) (Purcell et al., 2012, Lucas et al., 2012) and the production of ephyrae (juvenile medusae) through strobilation is seen as one factor that might lead to bloom formation (Lucas and Dawson, 2014, Lesniowski et al., 2015). Strobilation is a transverse division (asexual reproduction), where the upper parts of the polyp mesomorphs into one or several ephyrae which will be released into the water masses from the polyp (Holst and Laakmann, 2013).

Experiments on the budding of *A. aurita* have observed that each polyp may contribute with 0,4-0,6 buds day⁻¹, and that the budding rate is dependent on the temperature as well as the food density (Purcell et al., 2012).

The survival and strobilation of polyps are affected by factors such as temperature, salinity, dissolved oxygen, light, density of feed organisms and predation (e.g. by nudibranchs) (Hoover et al., 2012, Winans and Purcell, 2010, Lesniowski et al., 2015). Purcell et al. (2009) found that strobilation happened during January and February for *Aurelia labiata* as a response to increasing temperature, salinity and light conditions.

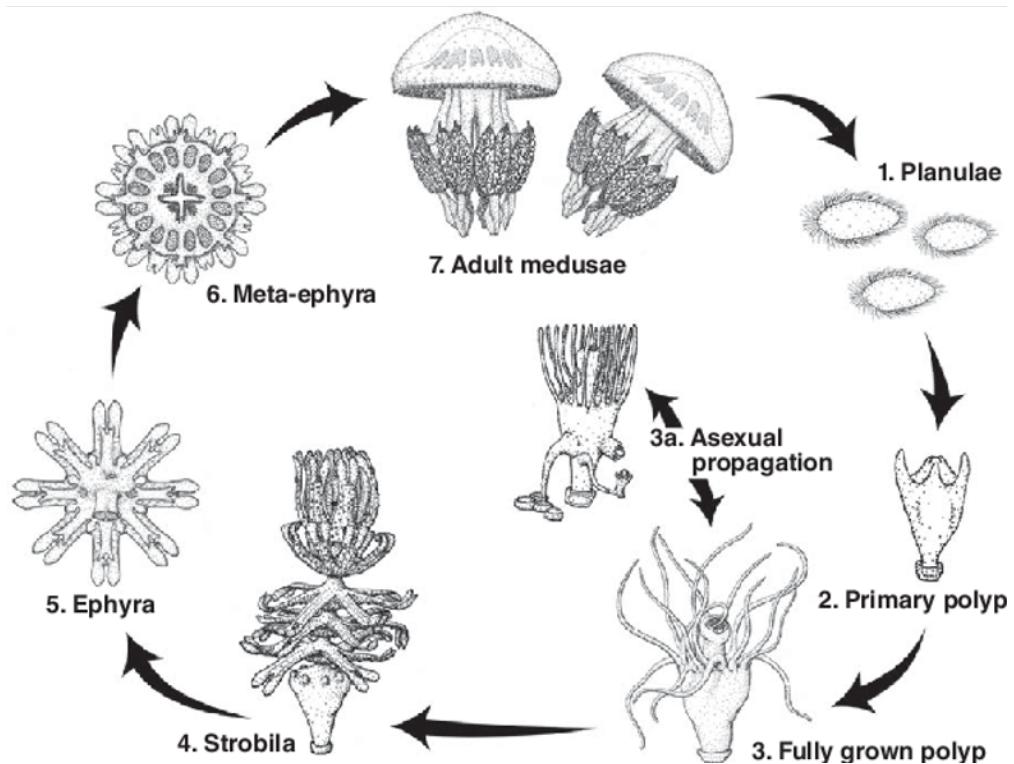


Figure 1: Life cycle of a Scyphozoan jellyfish. Planulae larvae released into the water masses by the adult medusae (1). The larvae will settle onto a suitable substrate and metamorph into a polyp (2-3). The polyp might go through an asexual propagation (3a). The polyp can also metamorph into a strobila (4) when the right temperature conditions are met. The strobila will then release ephyrae (5) into the water masses, which will grow into an adult medusae (6-7). Figure from (Olariaga et al., 2014).

The polyps are typically found in shaded environments, preferring to grow on the underside of horizontal surfaces (Holst and Jarms, 2007). The polyps are able to colonize natural substrates like shells, wood and stones as well as artificial substrates in the form of plastic plates, aluminium, concrete, bricks and glass plates (Holst and Jarms, 2007, van Walraven et al., 2016). Scyphozoan jellyfish are zooplanktivorous and have a diet consisting of a mixture of hard-bodied and soft-bodied prey items (Purcell and Sturdevant, 2001).

The transition from the polyp stage to the medusae stage is a way of asexual reproduction, where immature medusae known as ephyrae are released into the water column through a temperature dependent strobilation. Each polyp can produce up to 40 ephyrae for each strobilation. As a result of the asexual reproduction and the perennial duration of the polyp life stage, the abundance pattern of medusae can be seen as unregular and unpredictable (Boero et al., 2008, Lesniowski et al., 2015, van Walraven et al., 2016).

1.2. Biochemical composition and stoichiometry

The water content of most marine animals is approximately 72% and a carbon content of 8-10% wet weight⁻¹ (Vinogradov et al., 1953). While gelatinous Cnidarian species are composed of 96% water (mean value), with a carbon content of 0,5% (Lucas and

Dawson, 2014), jellyfish consist of low carbon contents, which also require low amounts of energy. The metabolic and gaseous transfers that takes place as diffusion over the body walls, is one of the processes that requires a small input of energy. This makes it possible for the jellyfish to prioritize energy for important functions such as the production of muscle tissue, oral surfaces, gastric surfaces, digestion and gonads (Hamner and Dawson, 2009).

Knowledge about the dry weight (DW) content of carbon and the DW content of nitrogen for jellyfish is important, to get an understanding of the pattern of energy flows and the mass transfer through the food web. Which is reflected in the ratios of C:N between trophic levels (Kogovšek et al., 2014).

The biological processing of materials and energy is known as metabolism. These processes contain the uptake of resources from the environment and the subsequent conversion of resources. As well as allocation of resources for survival, growth and reproduction. Increasing temperature have been found to have an exponential effect on metabolic rates and biochemical rates (Brown et al., 2004). Growth rate, development and lifespans have also shown a temperature dependent relationship (Gillooly et al., 2001, Gillooly et al., 2002).

Stoichiometry is here used to refer to the quantities and ratios of elements in the research organism. The composition of elements in an organism differs from the elemental composition of the environment, it is therefore necessary for the organism to expend energy to acquire needed elements. As well as for the removal of waste products (Brown et al., 2004). Ecological stoichiometry tries to identify the causes and consequences of varying elemental composition between organisms and their local environment, as well as between different organisms (Brown et al., 2004).

1.3. The GoJelly project, aims and hypothesis:

The work done for this master thesis was conducted within the framework of the EU horizon 2020 funded research project GoJelly, as a part of work package 2(WP2). The GoJelly project stem from a call for increasing knowledge concerning jellyfish blooms and their economic and ecological impact. GoJelly's main goal is to gain an increasing understanding of jellyfish bloom formation, and to identify how these blooms might be used as a sustainable ecosystem service. WP2 is called "Driving mechanisms and predictions of jellyfish blooms", the aims of this work package are to identify which abiotic and biotic trigger mechanisms that lead to the formation of jellyfish blooms, as well as the intensity and duration of these blooms.

The main aim of this thesis was to study the effect of temperature on the settling rate, survival, ingestion rate and biochemical composition of the polyp stages (*scyphistoma*) of *A. aurita*. To gain a better understanding on the effect of temperature on the ecology of the *A. aurita* polyp, related to predicted future temperatures.

This study has three hypotheses. The first is that increasing temperatures will have a positive effect on planulae settlement and polyp survival. This hypothesis is based upon the assumption of an increase in bloom formation as a result of increasing temperatures (Lucas and Dawson, 2014, Purcell et al., 2009).

Second, polyp ingestion rate and grazing are expected to increase as a result of increasing temperatures. Former research has showed that there is an exponential relationship between metabolic rates and temperature (Brown et al., 2004). Third, the carbon and nitrogen content of the polyp dry weight is expected to increase as a result of increasing temperatures. This hypothesis is based upon the exponential relationship between metabolic rates and temperature, and therefore the relationship between temperature and biomass.

2. Material and methods

The experimental work for the master thesis was carried out over two separate periods, each involving one *Aurelia aurita* planulae settling and polyp growth experiment.

Experiment 1 lasted for 20 consecutive days and was carried out from the 30th of August 2019 to the 18th of September 2019. Experiment 2 was conducted over 60 consecutive days from the 24th of September 2019 to the 20th of November 2019. The sampling for carbon and nitrogen was done on the 24th of September and 20th of November 2020. The experimental setup for experiment 1 and 2 were close to identical, and specific details regarding experiment 2 will only be given in situations where the experimental setup for experiment 2 differed from the information given about experiment 1.

2.1. Study Area

The study was based on extracted planulae larvae extracted from female fecundate jellyfish in the Trondheimfjord in summer/autumn 2020 (Figure 2), see chapter 2.2.1 (Capture of fecund *A. aurita* medusa) for details about sampling locations.

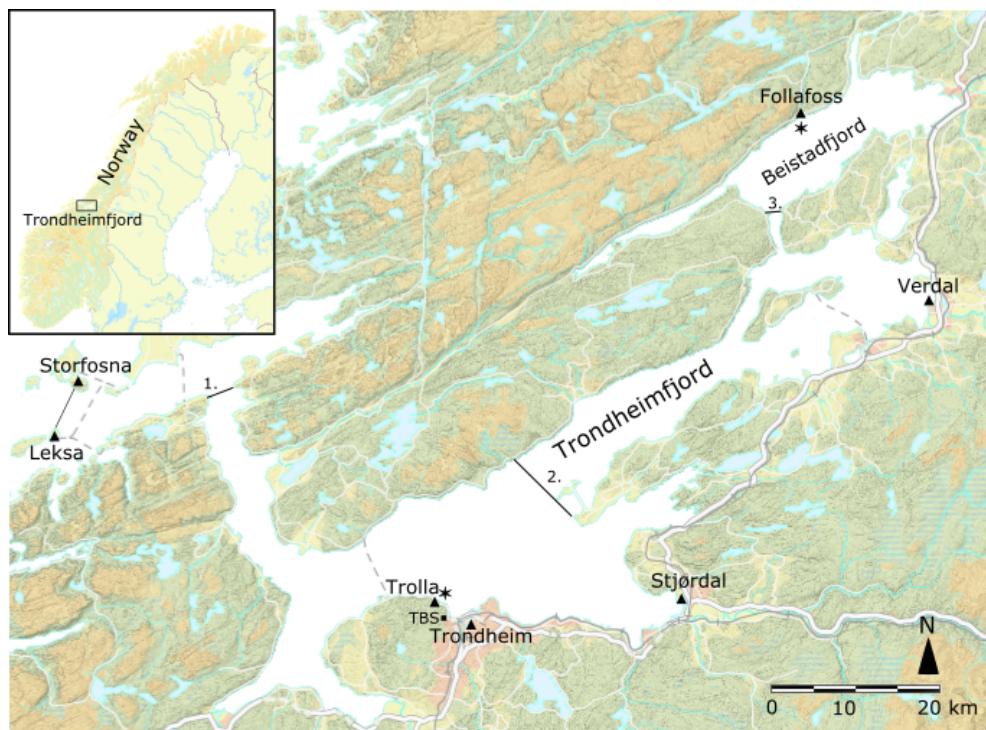


Figure 2: The Trondheimfjord and Beistad fjord. The four black lines represent the sills in the Trondheimsfjord (1: Agdenes sill, 2: Tautra sill, 3: Skarsund sill), as well as the sill between Leksa and Storfosna. Stars represent sampling sites for fecund *A. aurita* medusae, Trolla for experiment 1 and Follafoess for experiment 2. TBS = Trondhjem Biological station. Figure adapted from Kartverket (Kartverket, 2020).

2.1.1. The Trondheimfjord

The Trondheimfjord is ranked as the third largest fjord in Norway, and it is 126 km long when measured from Agdenes in the west to Hjellbotnen near Malm in the east. The volume of the fjord is 235 km³, the surface area is 1420 km² and the average depth is 165 m. The fjord consists of three primary basins, here listed after closeness to the open ocean: Ytterfjorden, Midtfjorden and Beistadfjorden (Figure 2). These basins are separated by three sills, while a fourth sill is separating the fjord from the Norwegian sea. The outermost sill is located between Leksa and Storfosna, while the other three are located at Agdenes, Tautra and Skarsundet respectively. The outer sill between Leksa and Storfosna is a determining factor for the exchange of water between the sea and the fjord (Bakken, 2000). The experimental work for the study was conducted at Trondhjem Biological Station (TBS) (Figure 2).

The mean sea surface temperatures (SST) for the Trondheim area for Sept., Oct. and Nov. was 13,1°C (mean min:11,4°C, mean max: 15,4°C), 10,8°C (mean min:8,8°C, mean max: 12,9°C), and 8,9°C (mean min:6,8°C, mean max: 11,1°C) respectively (Based on satellite readings from National Oceanic and Atmospheric Administration) (Seatemperature.org, 2020).

There is an open connection between the Trondheimsfjord and the Norwegian Sea as a result of the deep sills (Bakken et al., 2000). Atlantic water masses form a thicker layer below the coastal current during the winter, than it does during summer. This leads to an influx of Atlantic water masses during winter, the Atlantic water will in turn sink down behind the sills and replace the lighter water masses occupying the basins. Atlantic water masses are defined as water with a salinity 34,9 or slightly higher (Sakshaug, 2000). The typical salinity for the coast of Trøndelag is 34,5, it is not uncommon for the water masses in the Trondheimfjord to reach a salinity of 34,8 as a result of the inflowing water masses (Bakken et al., 2000, Sakshaug, 2000).

The density of the Atlantic water flowing into the fjord is highest when midsummer is approaching. The density of the Atlantic water is higher than the density of the water in the basins. Atlantic water masses will therefore replace the local water and force it over the sills (Bakken et al., 2000). Water masses in the fjord that are situated at medium depths above the sills, might flow out and get replaced during autumn. The replacement takes place when coastal currents are redirected towards the coast and the density of the coastal water increases. The coastal current will replace the outflowing water in the surface layers. This will over time lead to a turnover of all the local water masses situated above the sills. Convection will lead to a vertical mixing of the masses at medium and deep layers of the fjord. The influx of coastal water during autumn will therefore also affect layers that are situated deeper than the sills (Bakken et al., 2000).

The fjord gets an infusion of freshwater during the spring flood as a result from ice and snow melting, and these water masses will flow towards the outer parts of the fjord. The freshwater current will mix with the topmost layers of seawater and create a "lid" of brackish water on the surface of the fjord. The lid lasts the entire summer or longer. The duration is based on the amount of freshwater flowing into the fjord after the flood (Bakken et al., 2000).

There is a clear transition in temperature and salinity between the brackish water and the water masses below, this transition is called a pycnocline. It is salinity that is the main factor contributing to changes in density between the different layers in a fjord like the Trondheimsfjord (Bakken et al., 2000).

There are several forces that account for the mixing of water masses in a fjord. The topmost layers are strongly affected by currents, especially tidal currents. An open fjord like the Trondheimsfjord is also susceptible to wind, and continuous wind from one direction might transport water masses from one part of the fjord to another. This will lead to upwellings in parts of the fjord, which can be observed through an increase in salinity and reduction in temperature in the surface layers of the fjord. The pycnocline in the Trondheimsfjord is between 5 m and 25 m in the period from May and throughout September. The ratio between seawater and freshwater in these layers might reach a ratio of 1:1 during flooding periods without any wind.

Each of the three basins in the fjord is supplied with freshwater from a greater river, and this results in a pycnocline that covers the entire fjord system. The rivers are therefore creating an estuarine circulation in the fjord, where the brackish water is flowing outwards while there is a compensating flow that is traveling inwards below this layer (Bakken et al., 2000).

The mixing process in the fjord is affected by different currents. The currents in the surface layers are affected by the tides, leading to a variation in the current systems between low and high tide. Which changes approximately four times during a 24-hour period. The currents are also affected by the Coriolis force, the water masses that are flowing into the fjord is forced towards the south eastern parts of the fjord. While the water masses that are flowing out are forced against the Fosen peninsula (Bakken et al., 2000).

2.2. Preparatory work prior the experiments

Subchapter 3.2 covers work that was done prior to the experimental periods. It contains capture of medusae, extraction of planulae, creation of the substrate used to cultivate the polys and setup of the temperature gradient table to create the different temperature treatments.

2.2.1. Capture of fecund *A. aurita* medusae

Fecund medusae of *A. aurita* were collected as part of GoJelly fieldwork onboard R/V Gunnerus. The medusae for experiment 1 was collected near Follafoess (63,97466°N, 11,10959°E) in Beistadfjorden at the 29th of August 2019 (Figure 2). The sea surface temperature at the day of collection was 15°C. The medusae used in experiment 2 were collected near Trolla (63,46305°N, 10,32994°E) in Ytterfjorden on the 23th of September 2019 (Figure 2). The sea surface temperature (SST) was 13 °C. The sampled medusae were collected in the sea surface layers using the Polarcircle 560 workboat out of R/V Gunnerus, and a handheld net. The samples were selected based on availability (in reach with a handheld net), size of the medusae, condition of the medusae and quantities of visible planulae in the gonads. Each collected specimen was then placed in an individual 10 L container, containing seawater filtered through a sieve with a mesh size of 20 µm.

Six medusae were used for experiment 1 and five for experiment 2. The sampled medusae were then transported back to Trondhjem Biological Station (TBS) and kept in darkness overnight at a temperature of 14 °C.

2.2.2. Extraction of planulae and addition of planulae to the experiments

Every medusa was individually weighted using a Camry EK5550 digital scale, and the diameter across the widest part of the bell was measured in cm using a laminated measuring paper (Appendix B. **Sampled medusae and settling rate**). The medusae were transferred to a shallow tray containing seawater pumped from the Trondheimfjord at a depth of 100 m and filtered through a sand filter and a sieving paper with a 20 µm mesh size (This will be referred to as filtered seawater for the rest of the materials and methods chapter). A glass pipette was used to remove the planulae carefully from the outside of the gonads of the medusae, and the planulae that were immersed in the water were also collected.

The planulae collected from the different females in experiment 1 were pooled in an 800 mL beaker containing filtered seawater, before the planulae suspension was filtered through a sieve with a mesh width of 325 microns. This sieving was done to remove any impurities in the form of mucus and detritus from the pipetting process. The planulae suspension consisted of 700 mL after the sieving procedure for experiment 1. Five subsamples (1 mL) were collected in order to calculate the number of planulae in the suspension. The pipetting was done after a thorough stirring, in order to get the planulae dispersed in an even manner. The subsamples were returned to the planulae suspension after all five subsamples had been counted. The counting was done using a Wild Heerbrugg Wild M3 stereomicroscope.

The subsampling for experiment 2 was carried out in the same manner, but only four subsamples were collected and counted from a planulae suspension of 1400 mL prior to the experiment.

The planulae suspension was then pipetted into 25 different 800 mL beakers for both experiments. Each beaker in experiment 1 contained 100 mL of filtrated seawater, before 28 mL of planula suspension were added to each beaker (total volume 128 mL). Each beaker in experiment 2 contained 240 mL of filtered seawater, before 50 mL of planulae suspension were added to each beaker (total volume 290 mL). The pipetting was done in a haphazard pattern. The 25 beakers represent five treatments each consisting of five replicates. Each beaker was in their respective location in the temperature gradient table (Figure 4) during the pipetting. More in-depth information about the temperature gradient table will follow in subchapter 2.2.4. The beakers in experiment 1 were then topped up a total volume of 250 mL per beaker, to fulfill the minimum height requirement for the WTW – Portable conductivity meter ProfiLine Cond 3310.

Every beaker in experiment 1 contained approximately 9 planulae mL⁻¹. Every beaker in experiment 2 contained approximately 11 planulae mL⁻¹. These values were calculated using formula I – IV (Appendix B.).

$$\text{Mean amount of planula } 1 \text{ mL}^{-1} = \frac{(\text{subsample 1} + \text{subsample 2} + \text{subsample 3} + \text{subsample 4})}{4} \quad (\text{I})$$

$$\text{Planulae in solution} = 700 \text{ mL} * \text{mean amount of planula } 1 \text{ mL}^{-1} \quad (\text{II})$$

$$\text{Planulae added to each beaker} = \frac{\text{planulae in solution}}{\text{number of beakers}} \quad (\text{III})$$

$$\text{Planulae } \text{mL}^{-1} \text{ in each beaker} = \frac{\text{added planulae solution}}{\text{mL in beaker}} \quad (\text{IV})$$

2.2.3. Creating the artificial substrate

A. aurita planulae and polyps have shown a preference for attachment and growth on the underside of substrates (Holst and Jarms, 2007). Artificial floating substrates were therefore used for the settling of planulae and cultivation of polyps. The substrates consisted of plastic petri dish lids with a diameter of 5,5cm.

The outside of the lid was scraped with grid paper in order to roughen the surface and make it more suitable for planulae settlement (Figure 3). The artificial substrate was then marked with the treatment number and a replicate number, as represented by 3.1 (treatment 3, replicate 1) in Figure 3. The petri dishes were then divided into 6 different sections. This division was done to make it possible to get a photographic coverage of the entire experimental unit (EU).

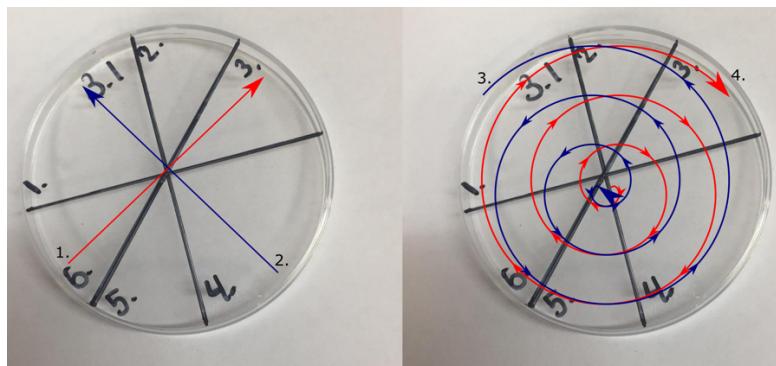


Figure 3: Patterns used for sanding of the petri dishes, the sectioning and treatment markings.

The artificial substrate was then left overnight in filtered seawater, prior to the first day of the experiment to enhance planulae settlement (Webster and Lucas, 2012).

The petri dishes used as the growth substrate, as well as the general usage of the temperature gradient table were adapted from experiments done by Thomas Lesniowski (Lesniowski, 2017).

2.2.4. Temperature gradient table

The five different treatments used for the experiments are temperature based and range from 9°C to 20°C (Table 1). The experiments were carried out in a thermo-regulated laboratory with a mean temperature of 14°C, and a light regime consisting of 16 hours of light and 8 hours of darkness. The temperature gradient used to differentiate the five treatments were created using an aluminium temperature gradient table (Figure 4). The

table consisted of 50 cylindrical holes which each could hold an 800 mL beaker, in a setup of five columns and ten rows. Row 1, 3, 5, 7 and 9 were used for the five treatments, while row 2, 4, 6, 8 and 10 were used for replacement water. The five columns were used for the five different replicates within each treatment.

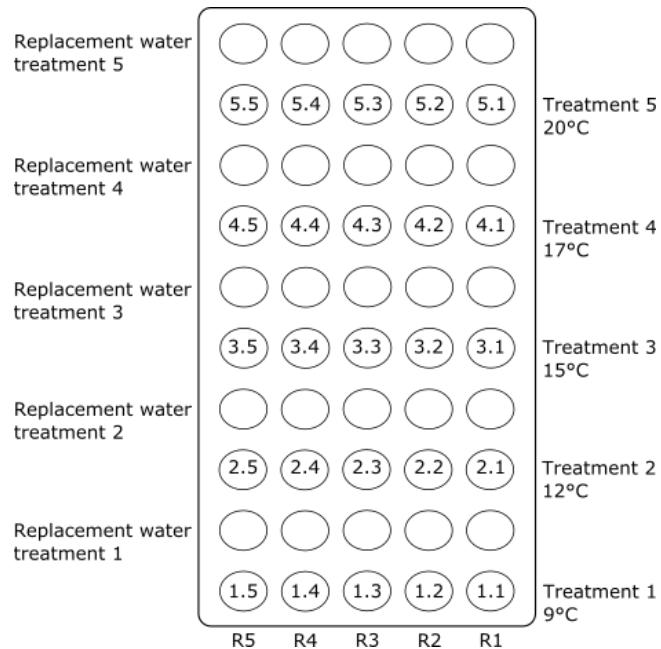


Figure 4: Experimental setup, showing the location of the different replicates and treatments (temperature 9, 12, 15, 17 and 20 °C) in the temperature gradient table.

The temperature gradient was created using two Julabo CORIO CD – 300F Refrigerated – Heating Circulators (temperature stability ± 0.03 °C), one at each side of the aluminium table. Each Julabo CORIO CD – 300F pumped water through a loop at their respective short edge of the table, leading to a heating and cooling of the aluminium and thus creating a reliable temperature gradient ranging from colder temperatures on one side and higher temperature on the opposite side. The temperatures and salinity in the different beakers were measured once every day using the portable conductivity meter (± 0.1 °C) (Appendix. C). Mean temperatures for the complete duration of both experiments was calculated (Table 1).

Table 1: Mean temperature for the complete duration of both experiments given in °C. SD shown in parentheses.

	<i>Experiment 1</i> (°C)	<i>Experiment 2</i> (°C)
Treatment 1	9.5 (± 0.27)	9.4 (± 0.36)
Treatment 2	12.1 (± 0.19)	12.1 (± 0.29)
Treatment 3	14.8 (± 0.27)	14.7 (± 0.47)
Treatment 4	17.2 (± 0.30)	17.1 (± 0.60)
Treatment 5	20.6 (± 0.39)	20.4(± 0.86)

2.2.5. Cultivation of *Artemia* sp.

Artemia sp. cysts produced by INVE Aquaculture was used to cultivate the feed items for the polyps. The cultivation was done at ambient room temperature (14°C), in 275 mL cell culture flasks. Each container had aeration from below to keep the cysts suspended and a ventilation hole in the top to relieve pressure.

The *Artemia* sp. cysts hatched after two days and the nauplii were then kept for two more days, for a total cultivation period of four days. Each batch contained two 275 mL cell culture flasks, and there were always two overlapping batches. This made it possible to feed every other day. The content of the two cell culture flasks was emptied into an 800 mL beaker and a light source from above was used to separate the nauplii from the unhatched cysts. A siphon was used to extract the nauplii and transfer them over to a new 800 mL beaker. Nauplii were then either sub-sampled and counted, or sub-sampled and preserved with Lugol's iodine so that they could be counted later.

The sub sampling was done after a thorough stirring. A sub sample of 1 mL was after a short pause pipetted out of the *Artemia* suspension. The subsample was added to a petri dish and counted using the stereomicroscope. This process was repeated 3 to 5 times and the observed values were used to calculate the concentration of *Artemia* per mL. The concentration was then multiplied with the volume of the original *Artemia* suspension to get the total amount of cultivated *Artemia*.

$$\text{Mean } \textit{Artemia} \text{ } 1 \text{ mL}^{-1} = \frac{(\text{subsample } x + \text{subsample } y + \text{subsample } z)}{3} \quad (\text{V})$$

$$\text{Cultivated } \textit{artemia} = \textit{artemia} \text{ } 1 \text{ mL}^{-1} * V \text{ Artemia solution} \quad (\text{VI})$$

2.3. Polyp experiments

2.3.1. Settling phase

The settling phase for *A. aurita* polyps was induced directly after the planulae had been added to the beakers. The first settling was expected to take place after 2 days, and the settling phase was expected to last 8-10 days (Holst and Jarms, 2007).

The settling phase lasted for 5 days for experiment 1 and 4 days for experiment 2, both settling phases were terminated when no more free-swimming planulae could be detected in the beakers. The planulae were subject to as little disturbance as possible during the settling phase, and the only intrusive operation during this period was the daily measurement of temperature and salinity using the portable conductivity meter.

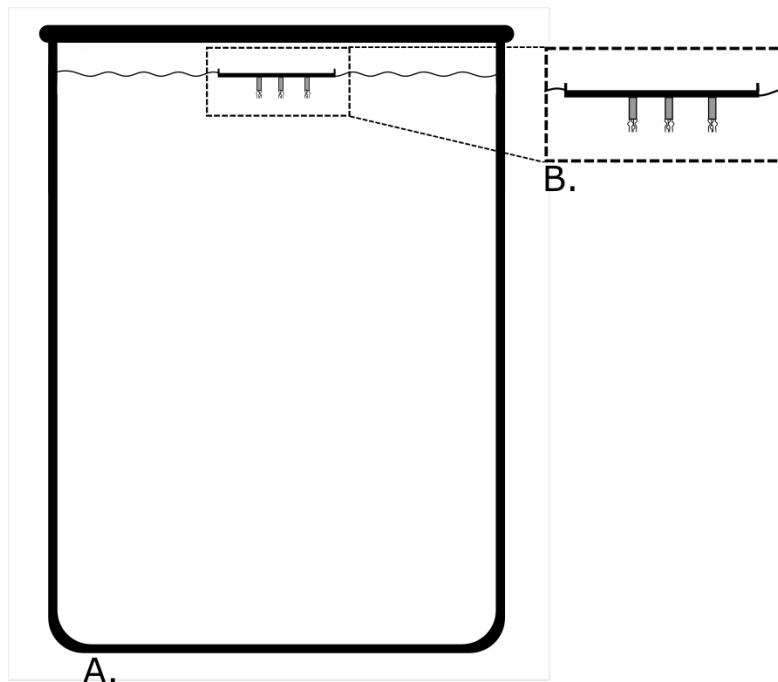


Figure 5: A. An overview of 800 mL beaker, containing one experimental unit, the petri dish substrate, B. *A. aurita* polyps attached to the petri dish.

2.3.2. Feeding and collection of ingestion data

The feeding procedure was the same for both experiments. Uneaten *Artemia* (Ingestion data) were just collected for experiment 1. To reduce handling of the polyps, feeding was not overlapping with the sampling of photographic data. Feeding was done overnight every second day for 16 hours. Feed were removed from the substrates by transporting the petri dishes to the replacement water within the respective temperature treatment. The beaker containing the *Artemia* were then removed from the table, and the beakers (800 mL) now containing the polyps were moved back to the position belonging to its given treatment and replicate.

The amount of fed *Artemia* for experiment 1 was based on the amount of cultivated *Artemia* divided between 28 beakers (800 mL, 25 EUs and 3 controls), and 25 for experiment 2 (25 EUs and 0 controls). Each feeding was done ad libitum (Purcell et al., 2019).

Non-eaten *Artemia* were collected after every feeding period during experiment 1. The content of the beaker was poured through a 20 microns sieve. Uneaten *Artemia* were counted or collected and put into a small glass container to be counted at a later date. One or two drops of Lugol's iodine was added to the sample. The uneaten *Artemia* was counted using a stereomicroscope (Appendix D.).

2.3.3. Photographic data collection

Photographs were used in both experiments to quantify the settling rate and mortality of the polyps. Photographs for experiment 1 were taken every second day starting after the settling period on the 4th of September and ending on the 18th of September. Photographs for experiment 2 were taken every day during the settling phase (25th of

September to 28th of September), then once a week for the rest of the experiment ending on the 20th of November.

The photographs were taken through a Wild Heerbrugg Wild M3 stereomicroscope, using a Canon EOS D1000 with a Canon EF-S 18-55mm f/3.5-5.6 IS lens. Six photographs were taken of each petri dish, one for each section, except for the settling period of experiment 2, where only one photo of each petri dish was taken without the use of the stereomicroscope. This was done to minimize the handling of the planulae and freshly settled polyps. The photographs for experiment 1 were taken with the light source illuminating the EU from below. The setup was changed for experiment 2, with the illumination from above to increase contrast and resolution.

2.3.4. Analysis of photographic data for settling rate and polyp survival

The photographs were manually analyzed using the open source software Inkscape version 0.92.2. Each photograph containing one section of the petri dish was imported into the software and the polyps were marked using colored dots (green or pink) (Figure 6). Each colored dot was recognized as an object by Inkscape and the number was calculated by the software. In cases where it was impossible to determine if an observation was a polyp, *Artemia* cysts, *Artemia* nauplii or an unidentified object, the observation was marked as a polyp and included in the dataset. The number of polyps counted in all six sections of a petri dish was then added together for the final value of that given EU. One picture per EU was analyzed for the settling phase of experiment 2.

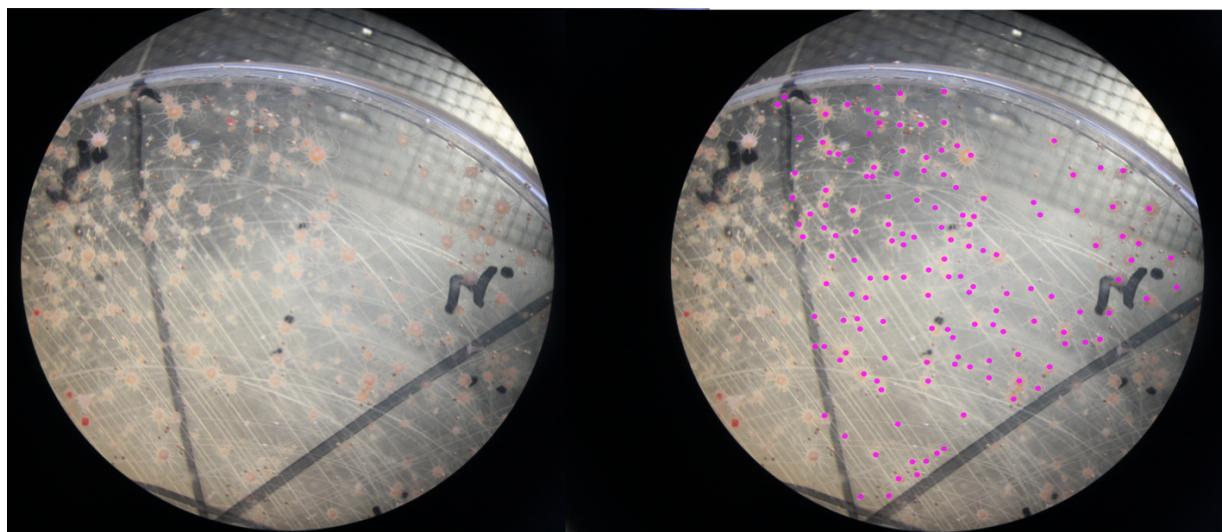


Figure 6: Photograph of section 4 from treatment 3 and replicate 3, showing before and after the polyps were counted.

The analysis of the photos was divided between two people. The photos of the two first days from each experiment were analyzed together to ensure uniformity in the counting procedure. Photographs were analyzed together in cases where the quality of the photograph deviated from the average quality. This was done to ensure that both contributors had the same understanding of which observations to mark as polyps and which observations should be disregarded.

2.3.5. Analysis of carbon and nitrogen content

At the end of each experiment, polyps were collected for carbon and nitrogen content analyses and C:N ratio. The polyps were removed from the petri dishes using scraping needle or forceps. Between four and eight polyps were collected from each replicate in experiment 1, while five polyps were collected from each replicate in experiment 2 (Appendix. E). The polyps from one replicate were put together in a tin capsule containing 40 µL of distilled water. The scraping needle and forceps were washed using alcohol between each replicate. The tin capsules were placed in a 96-well plate and dried at 60°C in an oven for 4-6 days. The samples were then placed in a desiccator to keep them dry until analysis.

A metal plate and a set of two forceps were used to prepare the samples for carbon and nitrogen content analyses analysis. Each tin capsule was removed from its respective slot in the 96-well plate, placed on the metal plate and rolled into a ball using the forceps. The sample were then returned to the 96-well plate. The forceps and metal plate were cleaned with alcohol between each sample.

The two 96 – well plates were then returned to the desiccator and kept there until the analyses were conducted at Trondhjem Biological station. Total content of nitrogen and carbon were analyzed using an Elementar vario EL cube, with acetanilide as the reference substance and the C:N ratio calculated for each replicate sample.

2.4. Statistical analysis of the data

The statistical analysis of the data was conducted using Microsoft® Excel version 16.35 and the open source software RStudio version 1.1.463. Excel was used to compile the data and create tables for all experiments, while RStudio was used for all statistical analysis.

An analysis of variance (ANOVA) followed by a Tukey's HSD pairwise comparison was conducted for all datasets that met the criteria for a parametric test. Datasets that did not meet the criteria were analyzed with the Kruskal-Wallis test, followed by a Wilcoxon signed-rank test.

The assumption criteria that need to be fulfilled before running an ANOVA or other parametric test are a normal distribution of the data, a homogeneity of variance and that the data points for the different treatments are independent of each other.

The assumption of normality was visually tested using a quantile-quantile plot (Q-Q plot) and a Kernel density estimation. The Shapiro-Wilk test of normality was then used as a numerical test of normality. The Levene test was used to test the homogeneity of the variance.

2.4.1. Ingestion experiment

Equations (VII-XII) was used to calculate the ingestion rate (*Artemia* polyp⁻¹ day⁻¹) and the grazing (mL polyp⁻¹ day⁻¹) (Frost, 1972).

k= Growth constant

g= Grazing coefficient (mL h⁻¹)

C₀= *Artemia* concentration (*Artemia* mL⁻¹) at the beginning.

C₁= *Artemia* concentration (*Artemia* mL⁻¹) at the end.

t= Time

$$k = \frac{\ln(\frac{C_1}{C_0})}{t} \quad (\text{VII})$$

$$g = \frac{\ln(\frac{C_1}{C_0})}{t} + k \quad (\text{VIII})$$

F= Grazing(μL polyp⁻¹ h⁻¹)

V= Volume (mL)

$$F = \frac{Vg}{N} \quad (\text{IX})$$

F_{day}= Grazing(mL polyp⁻¹ day⁻¹)

$$F_{day} = F * 24$$

C_{mean}= mean *Artemia* mL⁻¹

$$C_{mean} = \frac{C_1 - C_0}{\ln(C_1/C_0)} \quad (\text{X})$$

$$I=\text{Ingestion rate}(Artemia \text{ polyp}^{-1} \text{ h}^{-1}) \quad I = C_{mean} * F \quad (\text{XI})$$

I_{day}=Ingestion rate(*Artemia* polyp⁻¹ day⁻¹)

$$I_{day} = I * 24 \quad (\text{XII})$$

2.4.2. Settling rate

The data used for the settling rate is based on the number of planulae added to each 800 mL beaker in the beginning of the experiment, compared to the observed amount of polyps on the last day of the settling phase, after the petri dishes were moved from the 800 mL beakers (containing 250 mL in experiment 1 and 290 mL in experiment 2) to new 800 mL beakers containing 800 mL of filtrated seawater (Appendix. B.).

$$\text{Settling rate} = \frac{\text{Planulae added}}{\text{Polyps observed}} \quad (\text{XIII})$$

2.4.3. Polyp survival

The calculation of polyp survival is based on the data collected through the analysis of the photographs (Appendix F.), and the construction of time series datasets showing development in the polyp populations on the EUs.

2.4.4. Carbon and nitrogen analysis

$$C \text{ polyp DW}^{-1}(\%) = \frac{C \text{ capsule}^{-1}}{\text{Polyp DM}} * 100 \quad (\text{XIV})$$

$$N \text{ polyp DW}^{-1}(\%) = \frac{N \text{ capsule}^{-1}}{\text{Polyp DM}} * 100 \quad (\text{XV})$$

M = Molar mass (g mol⁻¹)

n = moles (mol)

m = mass of substance (g)

$$n = \frac{m}{M} \quad (\text{XVI})$$

$$\text{Moles C} = \frac{\text{Carbon g capsule}^{-1}}{\text{Molar mass C}} \quad (\text{XVII})$$

$$\text{Moles N} = \frac{\text{N g capsule}^{-1}}{\text{Molar mass N}} \quad (\text{XVIII})$$

Equations (XIV-XVIII) shows the approach that were used for the calculation of C polyp DW⁻¹(%), N polyp DW⁻¹(Appendix E.).

3. Results

The results for experiment 1 and 2 will be presented together in subchapters representing planulae settling rate, survival analysis and elemental composition. Results for experiment 1 will always be provided first. The ingestion subchapter will only contain results from experiment 1.

3.1. Planulae settling rate

Successful settlement was observed for all temperature treatments, but a high variation was observed for both experiment 1 and experiment 2.

For experiment 1 the lowest mean number of settled planulae was 618(± 62) planulae petri dish $^{-1}$ (28,6 % $\pm 2,9$) out of 2161 in the added planulae suspension $^{-1}$ (100%). This was observed in the 20°C treatment, while the highest mean number of settled planulae was 954(± 244) planulae petri dish $^{-1}$ (43,7% $\pm 13,0$) out of 2161 in the added planulae suspension $^{-1}$ in the 9°C treatment (Table 2, Table 3, Figure 7).

No significant difference was detected between the temperature treatments (Kruskal-Wallis test, p>0,083)(Appendix B.).

For experiment 2 the lowest mean number of settled planulae was 476(± 220) planulae petri dish $^{-1}$ (14,64% $\pm 6,75$) out of 3250 in the added planulae suspension $^{-1}$ (100%) in the 17°C treatment. The highest mean number of settled planulae was 575(± 192) planulae petri dish $^{-1}$ (26,5% $\pm 9,03$) out of 3250 in the added planulae suspension $^{-1}$ in the 9°C treatment (Table 2, Table 3, Figure 8).

No significant difference was detected between the temperature treatments (Anova, p>0,061).

Table 2: Number of *A. aurita* planulae in suspension added to the EUs and settled planulae in different temperature treatments for experiment 1(E1) and 2 (E2). The values are given as mean \pm SD.

Treatment ($^{\circ}$ C)	E1, Planulae in suspension	E1, settled planulae \pm SD	E2, Planulae in suspension	E2, settled planulae \pm SD
9	2162	945 \pm 244	3250	862 \pm 294
12	2162	810 \pm 200	3250	499 \pm 214
15	2162	749 \pm 259	3250	515 \pm 137
17	2162	777 \pm 244	3250	476 \pm 220
20	2162	618 \pm 62	3250	575 \pm 192

Table 3: The settling rate of *A. aurita* planulae in different temperature treatments in percent for experiment 1 (E1) and 2 (E2). The values are given as mean \pm SD.

Treatment ($^{\circ}$ C)	E1, Settling rate \pm SD (%)	E2, Settling rate \pm SD (%)
9	43,7 \pm 13,0	26,5 \pm 9,0
12	37,5 \pm 9,2	15,4 \pm 6,6
15	34,7 \pm 12,0	15,9 \pm 4,2
17	35,9 \pm 11,3	14,6 \pm 6,8
20	28,6 \pm 2,9	17,7 \pm 5,9

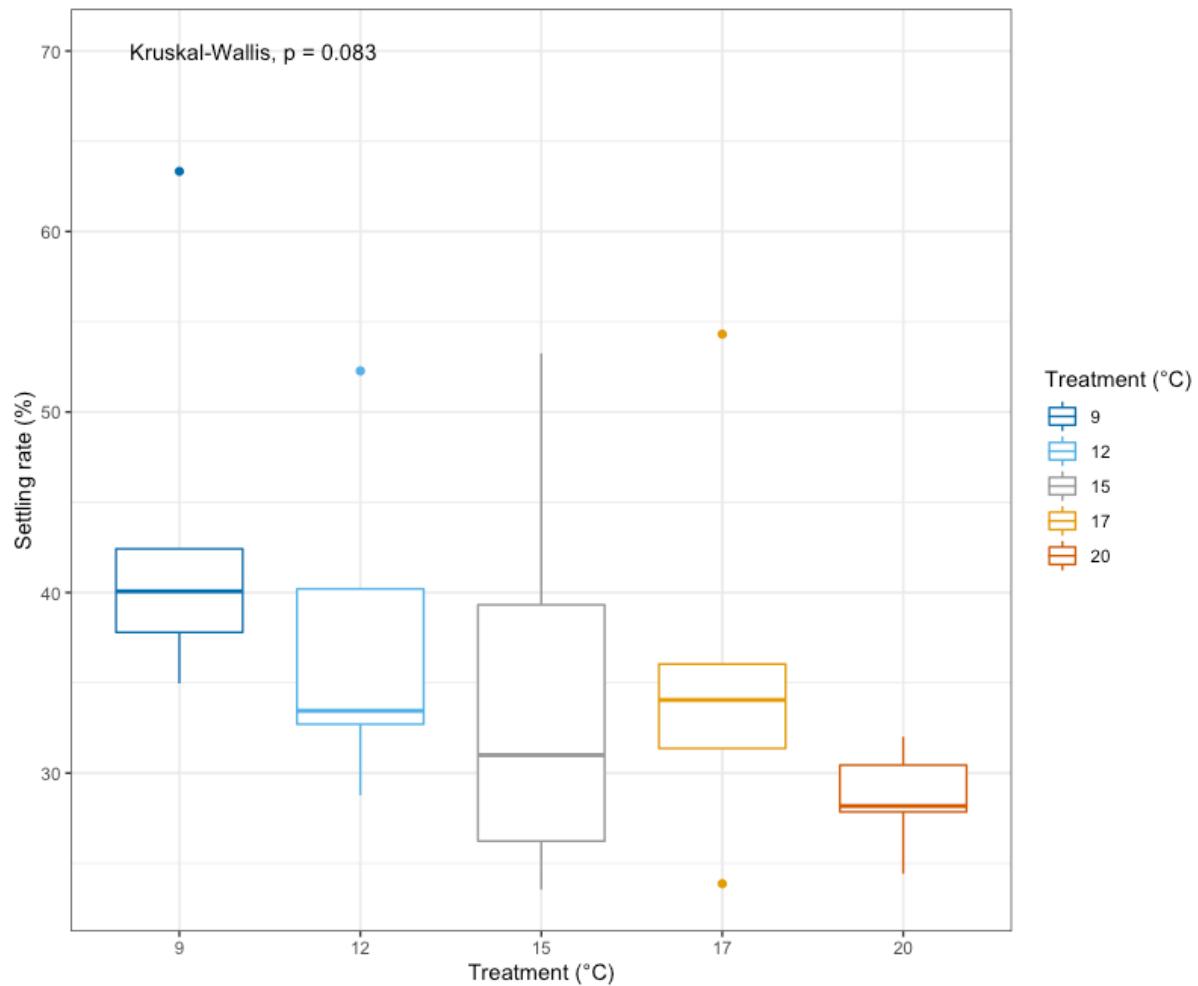


Figure 7: Settling rate (y-axis) of *A. aurita* planulae in different temperature treatments (x-axis) in percent for experiment 1. Treatments are aligned from coldest to warmest (9–20°C) left to right. No significant difference was found as an effect of temperature (Kruskal-Wallis test, $p>0,083$).

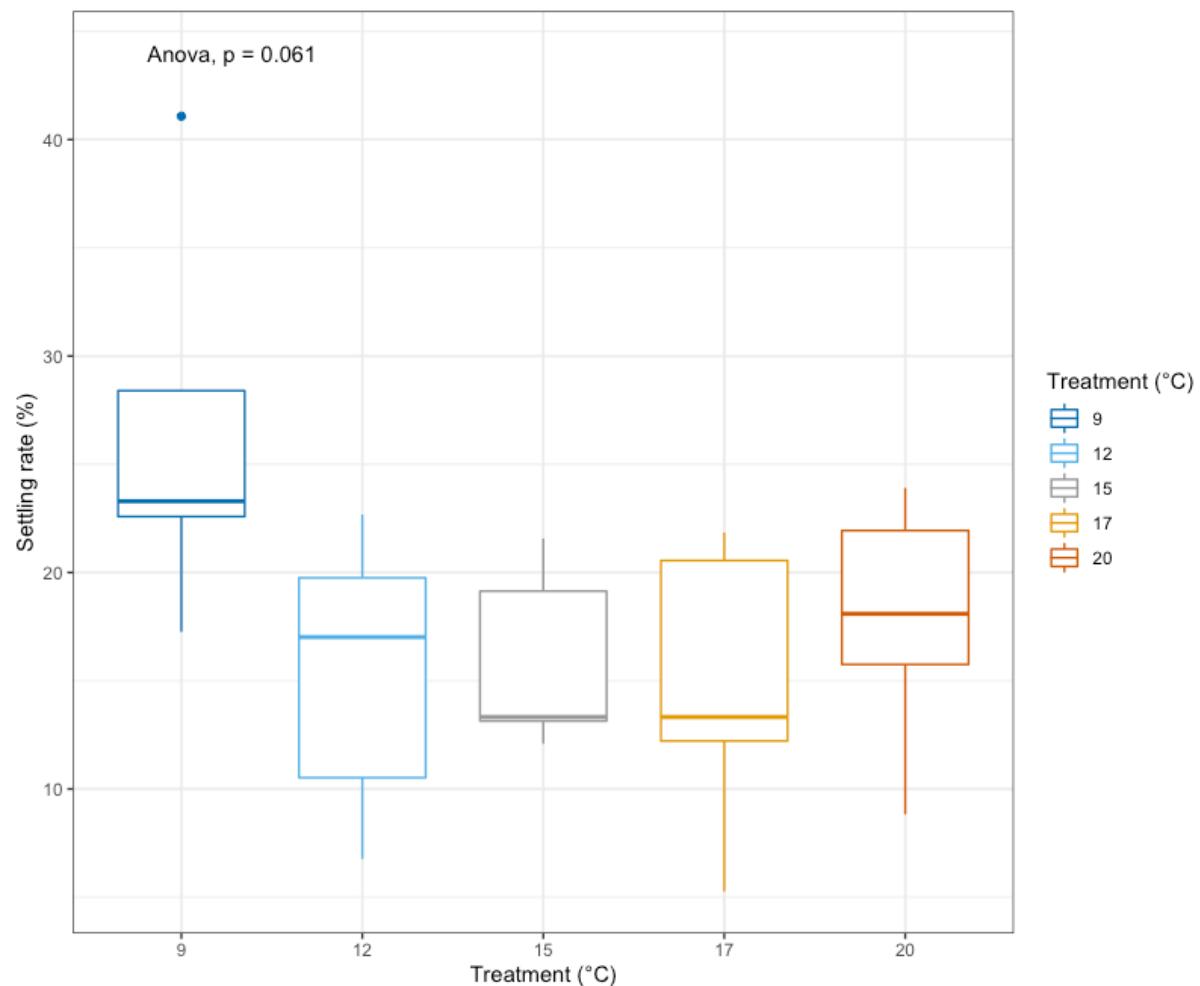


Figure 8: Settling rate(y-axis) of *A. aurita* planulae in different temperature treatments (x-axis) in percent for experiment 2. Treatments are aligned from coldest to warmest (9-20°C) left to right. No significant difference was found as an effect of temperature (Anova, $p>0,061$).

3.2. Survival analysis

Periods of increasing numbers of polyps petri dish⁻¹ was observed for both experiment 1 and experiment 2. Experiment 1 was shown to have an oscillating pattern with several increases and declines for all treatments throughout the experiment (Figure 9). Experiment 2 was shown to have an increase in the number of polyps petri dish⁻¹, followed by a decline (Figure 10).

The lowest number of observed live polyps throughout experiment 1 was in the 20°C treatment, while the highest number was observed in the 9°C treatment. The lowest total mean was 359(±130) polyps petri dish⁻¹ and the lowest observed daily number of was 206(±49) polyps petri dish⁻¹, 15 days after the start of the experiment (18. Sept.). Both these observations stem from the 20°C treatment (Table 4). The highest total mean was 813(±106) polyps petri dish⁻¹ and the highest observed daily was 974(±350) polyps petri dish⁻¹, 5 days after the start of the experiment (08. Sept.). Both observations stem from the 9°C treatment. The 9, 12, 15 and 17 °C treatments all had one replicate with polyp numbers high above the treatment mean in the beginning of the experiment, 1369, 1130, 1151 and 1173 respectively (Appendix F.).

Table 4: Observed live *A. aurita* polyps for each sampling day during the experimental phase of experiment 1. Dates in the first column and temperature treatments (°C) in the first row. The last row contains the total mean for each treatment. Values are given as the mean ± SD.

Treatment (°C)	9	12	15	17	20
04.Sept.	945 ± 244	810 ± 200	749± 259	777 ± 244	618 ± 62
06.Sept.	767 ±320	742 ± 243	482 ± 158	620 ± 237	442 ± 79
08.Sept.	974 ± 350	678 ± 218	714 ± 153	565 ± 96	323 ± 77
10.Sept.	747 ± 265	637 ± 285	690 ± 219	468 ± 78	277 ± 73
12.Sept.	845 ± 317	544 ± 214	580 ± 169	487 ± 164	377 ± 60
14.Sept.	763 ± 259	475 ± 209	590 ± 191	440 ± 191	381 ± 67
16.Sept.	812 ± 245	474 ± 206	535 ± 149	319 ± 126	247 ± 48
18.Sept.	652 ± 210	498 ± 211	387 ± 86	308 ± 121	206 ± 49
Total mean	813 ± 106	607 ±129	591 ±124	498 ± 156	359 ± 130

A significant difference in the number of polyps as a result of temperature was found (Kruskal-Wallis test, $p<5,04e^{-14}$). A pairwise comparison (Wilcoxon signed-rank test) showed that there is a significant difference between the 9°C treatment and all other treatments (12 °C, $p<0,002$; 15 °C, $p<0,000265$; 17 °C, $p<2,73e^{-8}$; 20°C, $p<7.,30e^{-12}$). As well as between the 20°C treatment and all other treatments (12 °C, $p<2,30e^{-6}$; 15 °C, $p<3,76^{-7}$; 17 °C, $p<0,002$).

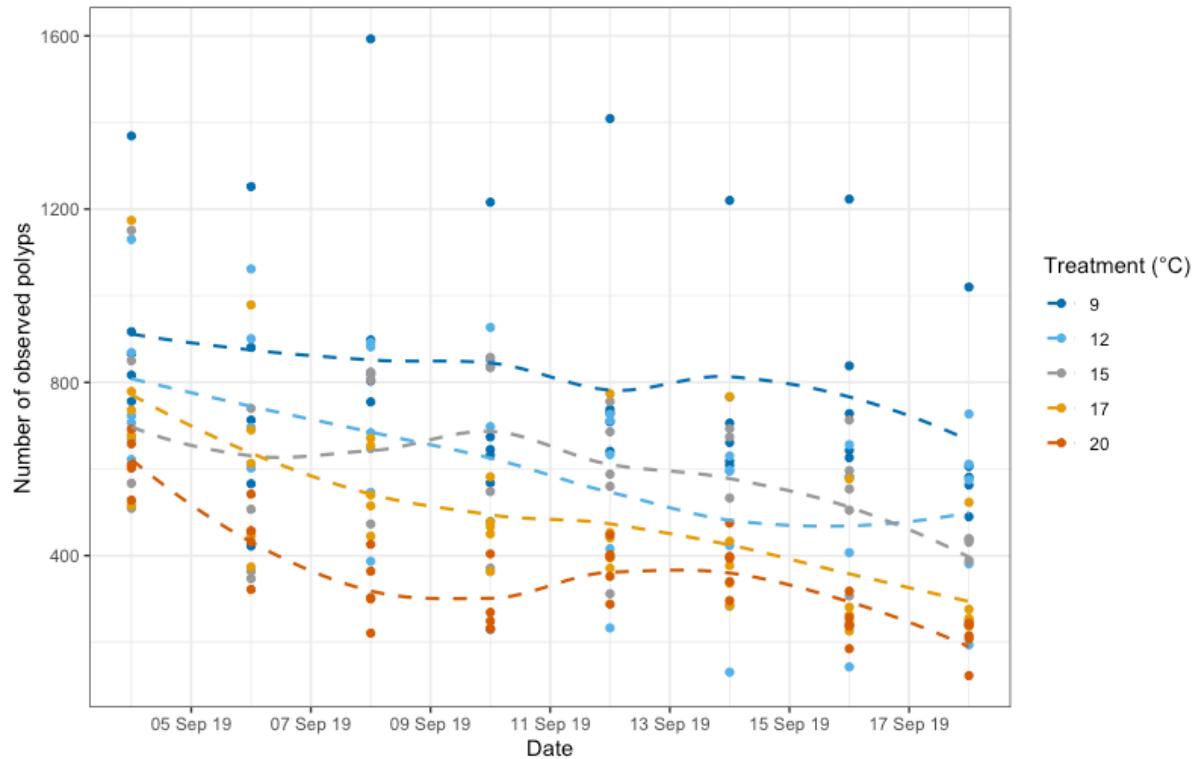


Figure 9: Number of observed *A. aurita* polyps during the duration of the experiment (15 days). Each plotted point represents a replicate, trendlines are constructed using locally estimated scatterplot smoothing (LOESS).

In experiment 2 the lowest number was observed in the 17°C treatment, while the highest number of observed live polyps petri dish⁻¹ was in the 9°C treatment. The lowest total mean was 354(± 143) and the lowest observed daily number of polyps petri dish⁻¹ was 122(± 39), 57 days after the start of the experiment (20.Nov). Both these observations stem from the 17°C treatment. The highest total mean was 911,28($\pm 264,52$) and the highest observed daily number of polyps petri dish⁻¹ was 1406,60($\pm 364,19$), 9 days after the start of the experiment (03.Oct). Both observations stem from the 9°C treatment. (Table 5). The first observation for experiment 2 was done during the settling phase (Day 1-4) and low numbers of observed polyps petri dish⁻¹ was observed for 5 replicates on the first day of the experiment. The observed numbers were 89, 47 and 5 in the 15°C treatment and 88 and 103 in the 20°C treatment (Appendix F.).

Table 5: Observed live *A. aurita* polyps for each sampling day during the experimental phase of experiment 2. Dates in the first column and temperature treatments ($^{\circ}\text{C}$) in the first row. The last row contains the total mean for each treatment. Values are given as the mean \pm SD.

Treatment ($^{\circ}\text{C}$)	9	12	15	17	20
25.Sept.	804 \pm 288	498 \pm 238	186 \pm 203	383 \pm 233	353 \pm 318
26.Sept.	1162 \pm 620	363 \pm 176	449 \pm 95	479 \pm 257	599 \pm 277
27.Sept.	1083 \pm 417	470 \pm 196	565 \pm 272	369 \pm 233	535 \pm 288
28.Sept.	862 \pm 294	499 \pm 214	515 \pm 137	476 \pm 220	575 \pm 192
03.Oct.	1407 \pm 364	680 \pm 176	720 \pm 254	574 \pm 192	751 \pm 163
10.Oct.	1112 \pm 249	572 \pm 132	747 \pm 333	479 \pm 163	507 \pm 145
16.Oct.	1088 \pm 243	496 \pm 49	566 \pm 207	400 \pm 103	448 \pm 114
25.Oct.	856 \pm 162	416 \pm 53	359 \pm 113	349 \pm 139	359 \pm 80
30.Oct.	797 \pm 153	345 \pm 56	317 \pm 75	262 \pm 105	340 \pm 85
06.Nov.	693 \pm 144	328 \pm 46	273 \pm 54	202 \pm 88	257 \pm 57
13.Nov.	558 \pm 65	287 \pm 47	178 \pm 33	149 \pm 46	156 \pm 43
20.Nov.	513 \pm 60	283 \pm 35	144 \pm 24	122 \pm 39	130 \pm 40
Total mean	911 \pm 265	436 \pm 121	418 \pm 208	354 \pm 143	418 \pm 186

A significant difference in the number of polyps as a result of temperature was found (Kruskal-Wallis test, $p < 2,78\text{e}^{-20}$). A pairwise comparison (Wilcoxon signed-rank test) showed that there is a significant difference between the 9°C treatment and all other treatments (12 °C, $p < 9,84\text{e}^{-15}$; 15 °C, $p < 2,93\text{e}^{-13}$; 17 °C, $p < 3,78\text{e}^{-16}$; 20°C, $p < 2,87\text{e}^{-13}$). No significant difference was found between the remaining treatments.

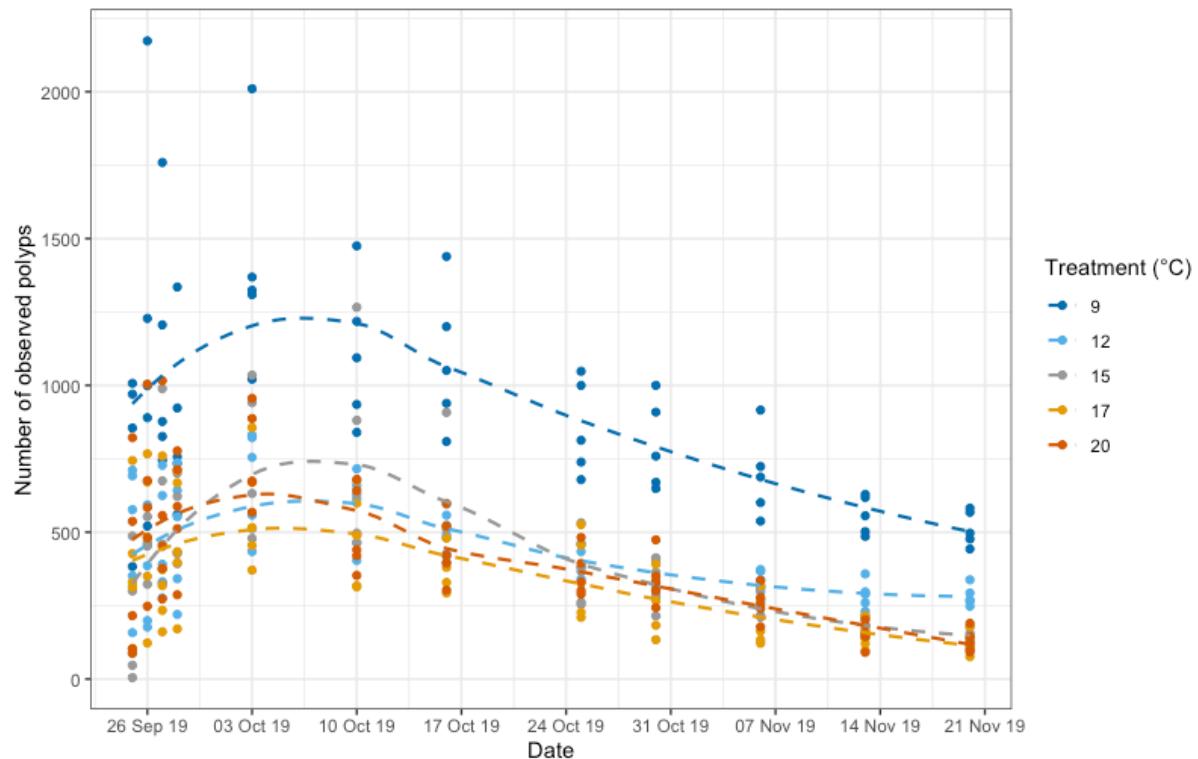


Figure 10: Number of observed *A. aurita* polyps for the period 25. Sept. – 20. Nov. 2019. Each plotted point represents a replicate, trendlines are constructed using locally estimated scatterplot smoothing (LOESS).

3.3. Ingestion rate and grazing

Ingestion rate ($\text{Artemia polyp}^{-1}\text{day}^{-1}$) was observed to increase with higher temperatures for all feeding dates, except for 4 days after the start of the experiment (07.Sept.). The highest mean ingestion rate $24,4(\pm 3,)$ was observed in the 20°C treatment 14 days after the start of the experiment (17.Sept.)(Figure 11, Table 6). The highest observed ingestion rate was $30 \text{ Artemia polyp}^{-1}\text{day}^{-1}$ was in the 20°C treatment 14 days after the start of the experiment (17.Sept.) (Appendix D.).

A significant difference was found as an effect of temperature on the ingestion rate for all feeding dates: (Anova, $p<1,1\text{e}^{-5}$), (Kruskal-Wallis test, $p<0,02$), (Anova, $p<5,0\text{e}^{-4}$), (Anova, $p<1,8\text{e}^{-9}$), (Anova, $p<5\text{e}^{-6}$) and (Kruskal-Wallis test, $p<2,0\text{e}^{-4}$), for 7.Sept., 9.Sept., 11.Sept., 13.Sept., 15.Sept. and 17.Sept. respectively.

Table 6: Ingestion rate (I) calculated for experiment 1. Dates in the first column and temperature treatment ($^{\circ}\text{C}$) in the first row. Values are given as mean $\text{Artemia polyp}^{-1}\text{day}^{-1}\pm \text{SD}$.

Treatment ($^{\circ}\text{C}$)	07. Sept.	09. Sept.	11. Sept.	13. Sept.	15. Sept.	17. Sept.
9	$2,1\pm 1,0$	$3,2\pm 2,4$	$3,5\pm 0,7$	$2,4\pm 1,1$	$0,3\pm 0,5$	$1,0\pm 1,0$
12	$1,1\pm 1,0$	$4,8\pm 3,4$	$4,5\pm 2,8$	$6,2\pm 1,5$	$0,6\pm 1,4$	$5,0\pm 1,0$
15	$0,0\pm 0,0$	$8,4\pm 4,1$	$3,7\pm 1,4$	$6,2\pm 2,26$	$3,0\pm 3,0$	$7,3\pm 1,8$
17	$4,8\pm 1,6$	$7,9\pm 4,9$	$6,5\pm 1,1$	$12,2\pm 2,2$	$6,6\pm 2,4$	$17,3\pm 5,9$
20	$0,9\pm 1,1$	$12,0\pm 6,6$	$10,9\pm 4,2$	$19,7\pm 3,8$	$12,0\pm 4,8$	$24,4\pm 3,8$

Grazing ($\text{mL polyp}^{-1}\text{day}^{-1}$) was also observed to increase with higher temperatures for all feeding dates. The highest mean grazing $6,4(\pm 1,7)$ was observed in the 20°C treatment 14 days after the start of the experiment (17.Sept.)(Table 7). The highest observed grazing rate was $6,5 \text{ mL polyp}^{-1}\text{day}^{-1}$ in the 20°C treatment 14 days after the start of the experiment (17.Sept.) (Appendix D.).

A significant difference was found as an effect of temperature on the grazing for all feeding dates except the 09.Sept. (Kruskal-Wallis test, $p>0.07$): (Anova, $p<3,2\text{e}^{-4}$), (Anova, $p<3,0\text{e}^{-4}$), (Kruskal-Wallis test, $p<2,6\text{e}^{-4}$), (Kruskal-Wallis test, $p<7,0\text{e}^{-4}$) and (Kruskal-Wallis test, $p<1,7\text{e}^{-4}$), for 7.Sept., 11.Sept., 13.Sept., 15.Sept. and 17.Sept. respectively.

Table 7: Grazing ($\text{mL polyp}^{-1}\text{day}^{-1}$) calculated for experiment 1. Dates in the first column and temperature treatment ($^{\circ}\text{C}$) in the first row. Values are given as mean $\mu\text{L polyp}^{-1}\text{day}^{-1}\pm \text{SD}$.

Treatment ($^{\circ}\text{C}$)	07. Sept.	09. Sept.	11. Sept.	13. Sept.	15. Sept.	17. Sept.
9	$0,6\pm 0,3$	$0,7\pm 0,6$	$1,0\pm 0,2$	$0,3\pm 0,2$	$0,04\pm 0,07$	$0,2\pm 0,2$
12	$0,3\pm 2,95$	$1,2\pm 1,0$	$1,2\pm 0,7$	$0,9\pm 0,2$	$0,09\pm 0,2$	$0,9\pm 0,3$
15	$0,0\pm 0$	$3,1\pm 3,6$	$1,0\pm 0,4$	$1,0\pm 0,4$	$0,5\pm 0,5$	$1,5\pm 0,4$
17	$1,4\pm 0,9$	$3,1\pm 4,1$	$2,0\pm 0,6$	$2,3\pm 0,4$	$1,1\pm 0,4$	$4,0\pm 1,6$
20	$1,6\pm 0,6$	$5,7\pm 7,8$	$3,5\pm 1,5$	$4,6\pm 1,2$	$2,3\pm 1,0$	$6,4\pm 1,7$

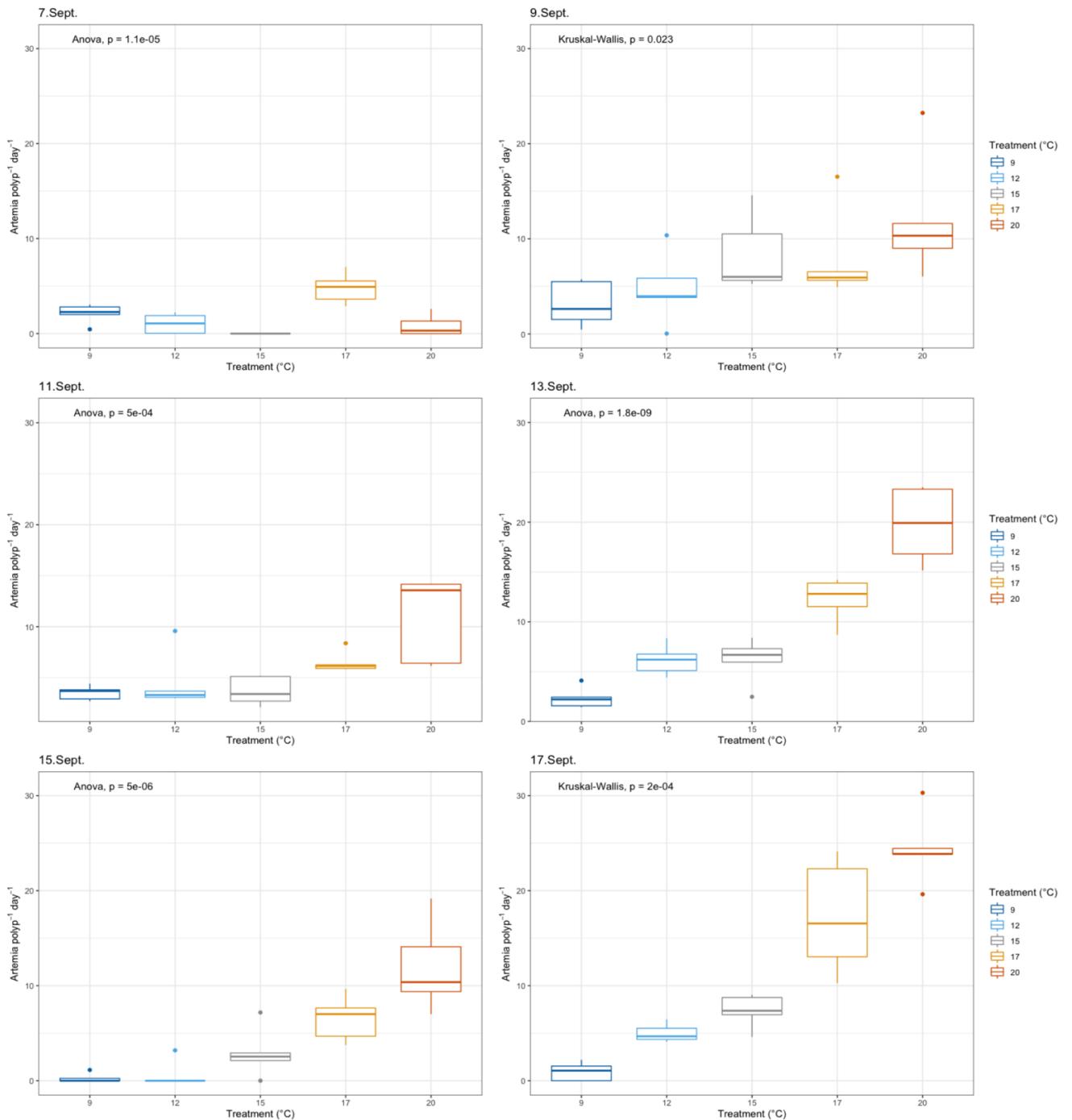


Figure 11: Ingestion rate (I) calculated for the different feeding dates of experiment 1. $\text{Artemia polyp}^{-1}\text{day}^{-1}$ (y-axis) in the different temperature treatments (x-axis). Treatments are aligned from coldest to warmest (9-20°C) left to right. A significant difference was found as an effect of temperature for all feeding dates: (Anova, $p < 1,1\text{e}^{-5}$), (Kruskal-Wallis test, $p < 0,023$), (Anova, $p < 5\text{e}^{-4}$), (Anova, $p < 1,8\text{e}^{-9}$), (Anova, $p < 5\text{e}^{-6}$) and (Kruskal-Wallis test, $p < 2\text{e}^{-4}$), for 7.Sept., 9.Sept., 11.Sept., 13.Sept., 15.Sept. and 17.Sept. respectively.

3.4. Elemental composition

The mean carbon (C) content given in C polyp⁻¹ (μg) for experiment 1 ranged from 2,0($\pm 1,1$) to 16,7($\pm 8,8$). The lowest content was found in the 9°C treatment and the highest content was found in the 20°C treatment (Table 8). A significant difference in carbon content was observed for the different treatments (Kruskal-Wallis test, $p<0,0039$).

The mean carbon C share (%) for the polyps from experiment 1 ranged from 0,5($\pm 0,3$) to 4,3($\pm 2,0$). The lowest share was found in the 9°C treatment and the highest share was found in the 20°C treatment. A significant difference in C share (%) was observed for the different treatments (Kruskal-Wallis test, $p<0,000323$).

The mean nitrogen (N) content given in N polyp⁻¹ (μg) for experiment 1 ranged from 0,5($\pm 0,2$) to 3,4($\pm 1,8$). The lowest content was found in the 9°C treatment and the highest content was found in the 20°C treatment (Table 8). A significant difference in nitrogen content was observed for the different treatments (Kruskal-Wallis test, $p<0,0048$).

The mean N share (%) for the polyps from experiment 1 ranged from 0,1($\pm 0,05$) to 0,9($\pm 0,4$). The lowest share was found in the 9°C treatment and the highest share was found in the 20°C treatment (Table 8). A significant difference in N share (%) was observed for the different treatments (Kruskal-Wallis test, $p<0,00873$).

Table 8: C content (μg), N content (μg), C share (%), N share (%) for the five temperature treatments and the C/N molar ratio for the respective treatments in experiment 1. The values are given as mean \pm SD. Pairwise comparison (Wilcoxon signed-rank test) showed no significance between the treatments for C polyp⁻¹ (μg), C(%), N polyp⁻¹ (μg) and N(%). Significant difference between the C/N molar for the treatments (Tukey's HSD test), showing a significant difference between treatment 9°C and treatment 15 °C (* = $p < 0,05$; ns = non significant).

Treatment (°C)	C polyp ⁻¹ (μg)	C (%)	N polyp ⁻¹ (μg)	N (%)	C/N ratio (mol)
9	2,0 $\pm 1,1$	0,5 \pm 0,3 ns	0,5 $\pm 0,2$	0,1 \pm 0,05 ns	4,7 \pm 0,8*
12	3,0 $\pm 1,0$	0,7 \pm 0,3 ns	0,6 $\pm 0,2$	0,2 \pm 0,06 ns	5,7 \pm 0,7ns
15	3,6 $\pm 1,2$	1,9 \pm 0,2 ns	0,7 $\pm 0,3$	0,2 \pm 0,06 ns	6,4 \pm 1,1*
17	6,7 $\pm 4,4$	1,8 \pm 1,5 ns	1,4 $\pm 0,9$	0,4 \pm 0,3 ns	5,6 \pm 0,7ns
20	16,7 $\pm 8,8$	4,3 \pm 2,0 ns	3,4 $\pm 1,8$	0,9 \pm 0,4 ns	5,7 \pm 0,1ns

The molar carbon to nitrogen ratio for experiment 1 ranged from 4,7($\pm 0,8$) to 6,4($\pm 1,1$). The lowest value was found in the 9°C treatment. The highest value was found in the 15°C treatment (Table 8, Figure 12). A significant difference was observed between the treatments as a result of temperature (Anova, $p<0,024$). A pairwise comparison showed that the 9°C treatment and the 15°C treatment were the only treatments that were significantly different from each other (Tukey's HSD test, $p<0,0102$).

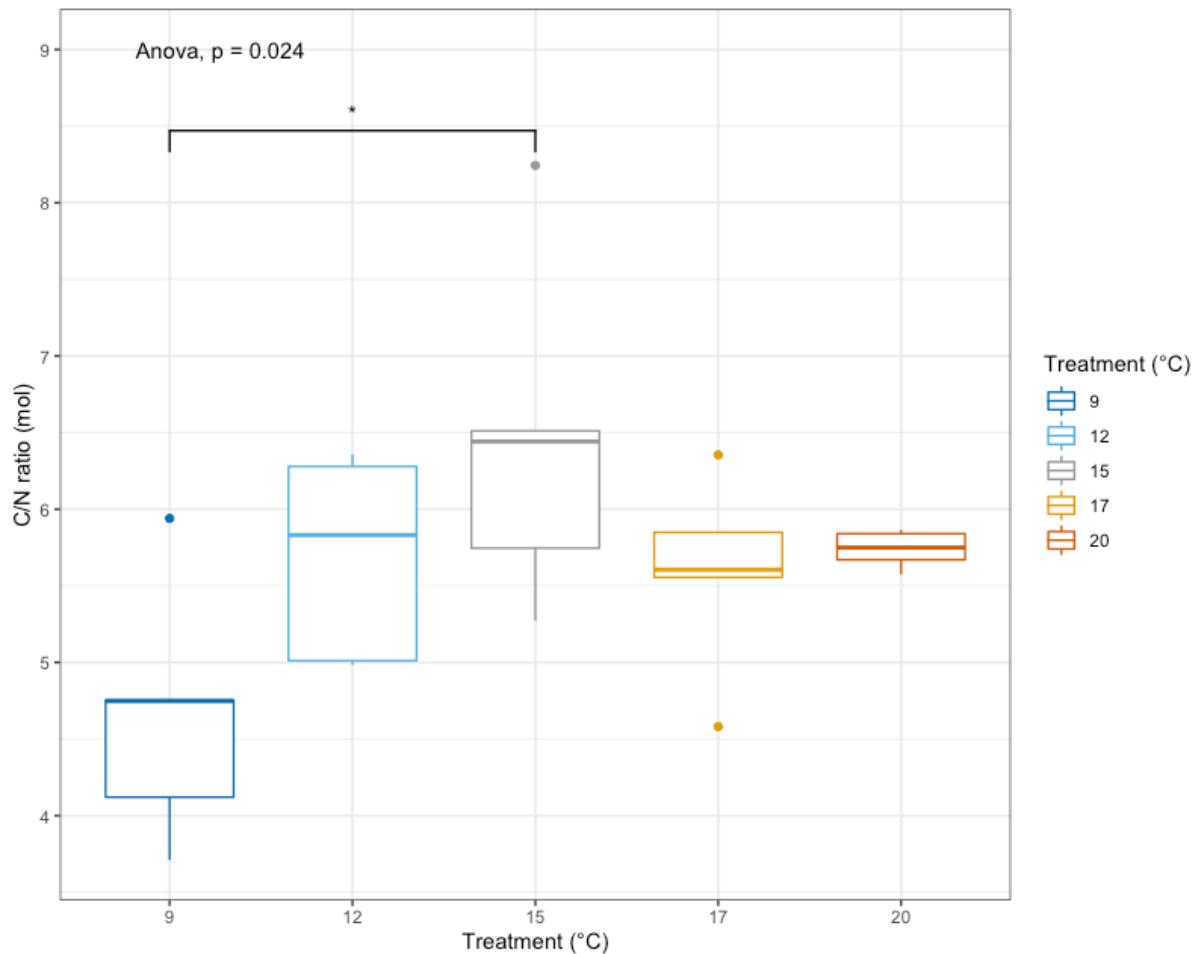


Figure 12: Molar ratio of carbon to nitrogen for the five given temperature treatments in experiment 1. Treatments are aligned from coldest to warmest (9–20 °C) left to right. A significant difference was observed between the treatments (Anova test, $p < 0,024$). A pairwise comparison showed that the 9°C treatment and the 15°C treatment were the only treatments that were significantly different from each other (Tukey's HSD test, $p < 0,0102$).

The mean C content given in $C \text{ polyp}^{-1}$ (μg) for experiment 2 ranged from $4,2(\pm 2,6)$ to $95,1(\pm 39,6)$. The lowest content was found in the 15°C treatment and the highest content was found in the 12°C treatment (Table 9). A significant difference in carbon content was observed for the different treatments (Kruskal-Wallis test, $p < 0,00068$).

The mean C share (%) for the polyps from experiment 2 ranged from 0,9 ($\pm 0,6$) to 13,3($\pm 4,2$), the lowest share was found in the 15°C treatment and the highest share was observed in the 12°C treatment. A significant difference in C share (%) were observed for the different treatments (Kruskal-Wallis test, $p < 0,00068$). Replicate 1 from the 17°C treatment was removed as an outlier, the value was 2 magnitudes larger than the mean of the treatment (18,6).

The mean N content given in $N \text{ polyp}^{-1}$ (μg) for experiment 2 ranged from $2,0(\pm 1,1)$ to $16,7(\pm 8,8)$. The lowest content was found in the 15°C treatment and the highest content was found in the 12°C treatment (Table 9). A significant difference in nitrogen content was observed for the different treatments (Kruskal-Wallis test, $p < 0,00065$).

The mean N share (%) for the polyps from experiment 2 ranged from 0,2($\pm 0,2$) to 3,0($\pm 0,9$), the lowest share was found in the 15°C treatment and the share highest was observed in the 12°C treatment. A significant difference in N share (%) was observed for the different treatments (Kruskal-Wallis test, $p < 0,0067$). Replicate 1 from the 17°C treatment was removed as an outlier.

Table 9: C content (μg), N content (μg), C share (%), N share (%) for the five temperature treatments and the C/N molar ratio for the respective treatments in experiment 2. The values are given as mean \pm SD. Significant difference between the C/N molar for the treatments (Wilcoxon signed-rank test), showing no significant difference between any treatments. ns = non-significant.

Treatment (°C)	C polyp $^{-1}$ (μg)	C (%)	N polyp $^{-1}$ (μg)	N (%)	C/N ratio (mol)
9	41,3 \pm 5,3	7,0 \pm 2,7	9,3 \pm 1,3	1,6 \pm 0,6	5,2 \pm 0,1 ^{ns}
12	95,1 \pm 39,6	13,3 \pm 4,2	21,4 \pm 8,8	3,0 \pm 0,9	5,2 \pm 0,09 ^{ns}
15	3,4 \pm 1,3	0,9 \pm 0,6	0,8 \pm 0,3	0,2 \pm 0,2	4,9 \pm 0,2 ^{ns}
17	4,2 \pm 2,6	0,6 \pm 0,2	0,5 \pm 0,2	0,1 \pm 0,4	4,9 \pm 0,5 ^{ns}
20	21,6 \pm 17,0	4,9 \pm 2,6	5,0 \pm 4,1	1,1 \pm 0,6	5,1 \pm 0,1 ^{ns}

The molar carbon to nitrogen ratio for experiment 2 ranged from 4,92($\pm 0,51$) to 5,19($\pm 0,10$). The lowest value was found in the 9°C treatment. The highest value was found in the 17°C treatment (Table 9, Figure 13). No significant difference was found for the C/N molar values in experiment 2 (Kruskal-Wallis test, $p > 0,1$). The pairwise comparison (Wilcoxon signed-rank test) showed that there was no significant difference between any of the treatments within the experiment.

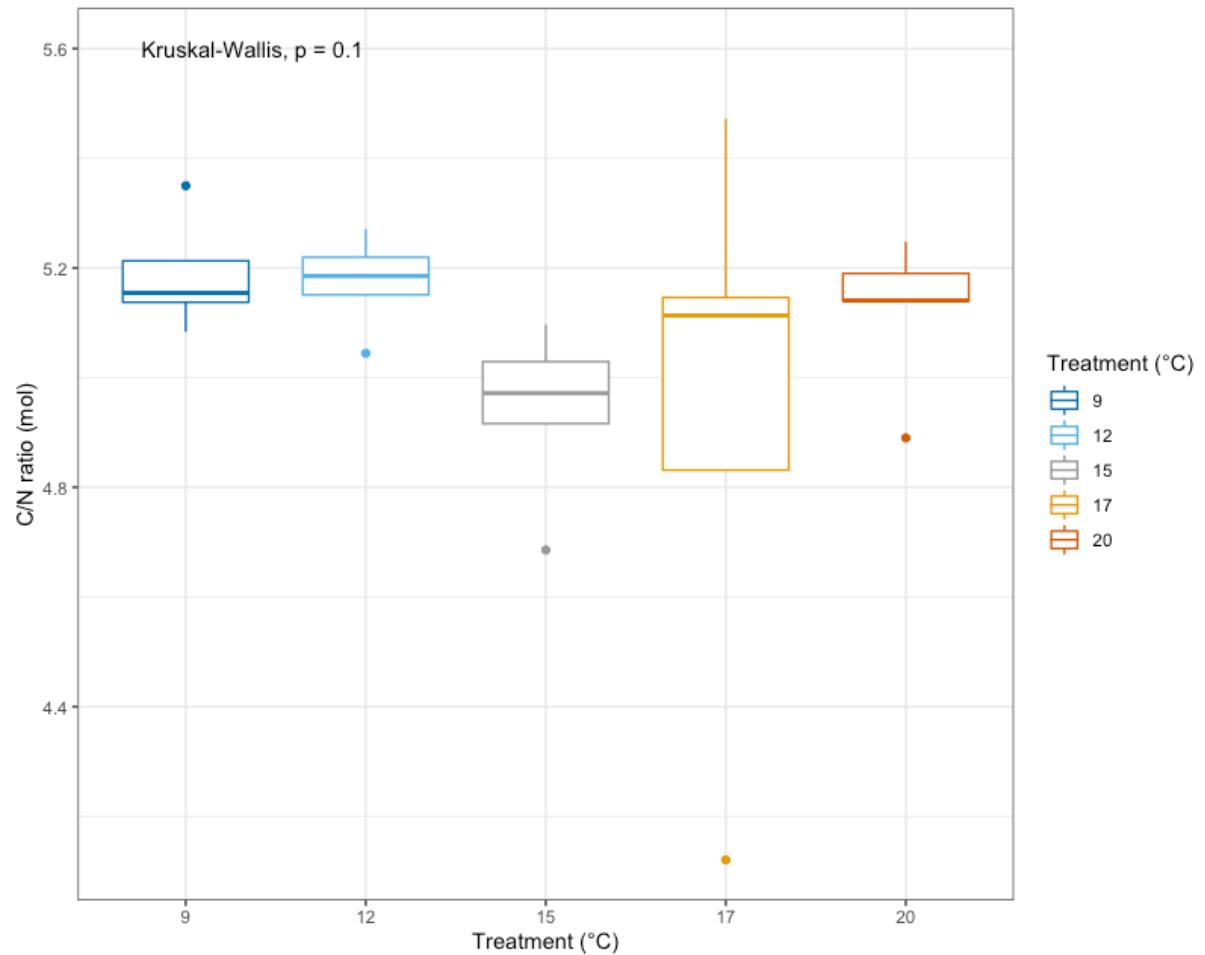


Figure 13: Molar ratio of carbon to nitrogen for the five given temperature treatments in experiment 2. Treatments are aligned from coldest to warmest (9-20°C) left to right. No significant difference was observed between the treatments (Kruskal-Wallis test, $p>0,1$).

4. Discussion

4.1. Planulae settling rate

Scyphozoan planulae larvae are lecithotrophic (First feeding takes place after metamorphosis), a rapid settlement is therefore crucial after they have been suspended into the water masses (Lucas et al., 2012, Lucas, 2001). The planulae are the connection between the planktonic medusae stages and the benthic polyps. A better understanding of how increasing temperatures might affect the settlement of planulae from the Trondheimfjord, is therefore important to gain a better insight in the causation of local jellyfish blooms.

No apparent effects of temperature on the planula larvae's ability to settle on the substrate were found for both experiments. Hypotheses one stating that an increase in temperature will have a positive effect on the planulae's ability to settle, can be rejected for this study.

The observations regarding the effect of temperature on planulae settling found in this study does not concur with previous observations (Webster and Lucas, 2012, Prieto et al., 2010). In the experiment conducted by Webster and Lucas (2012), *A. aurita* planulae were observed in the water column until day 14 at 6°C, day 10 at 12°C and day 5 for the 18°C treatment, whereas *A. aurita* planulae were observed in the water column until day 8 at 18°C for Holst and Jarms (2007).

The previous findings are in contrast to this study where planulae were observed in the water until day 5 for experiment 1 and day 4 for experiment 2. Planulae were observed to travel upwards in a close proximity to the sides of the beaker, which concurs with observations of *A. aurita* planulae done by Holst and Jarms (2007). In this study the mentioned behavior led to planulae settling on the sides of the beakers, before metamorphosis into polyps. Leading to a formation of polyp populations on other surfaces than the experimental units. Which might have skewed the data for the settling experiment, leading to lower numbers of settled planulae on the intended plates and additional settling on surfaces at the edge of the beakers that were not taken into consideration.

The conditions during the two settling experiments were similar and it is therefore possible to do a comparison between experiment 1 and experiment 2. When comparing the effect of temperature on the settling rate (%) for both experiments, a significant difference was observed. This might be a product of the number of planulae added initially to the two different experiments (E1:2162 planulae, E2:3250 planulae). A comparison between the number of observed polyps for experiment 1 and experiment 2 were conducted to see if the difference in settling rate (%) could be a result of several factors and not just temperature. An analysis of observed numbers of settled planulae for all treatments in experiment 1 and 2 showed a significant difference, while a comparison of the mean values for experiment 1 and experiment 2 showed no significant difference. Based on this, it can be speculated that there are other factors affecting the settling success of *A. aurita* planulae, e.g. a density dependent threshold. Evidence has been provided for the relationship between planulae density and settling rates (gregarious settlement) (Brewer, 1978, Gröndahl, 1989). It has also been found that there might not

be a density dependent factor affecting settling and that the settlement is rather dependent on locations with low shear stress as well as the boundary layer thickness (Keen, 1987). Gröndahl (1989) revised the results displayed by Keen (1987) and suggests that hydrodynamic processes are a stronger factor than conspecific density in locations with substantial water movements. It is possible to assume that conspecific density is one of the major factors affecting the settling rate in this study, based on the findings when taking the number of added planulae into account during the comparison of experiment 1 and experiment 2.

4.2. Survival analysis

An understanding of how temperature affects the survival of *A. aurita* polyps is crucial for a better understanding of how climate change might affect the frequency and duration of future scyphozoan jellyfish blooms in the Trondheimfjord.

Temperature was proven to have an apparent impact on the survival of the polyps in experiment 1, the number of observed live polyps decrease with warmer temperature and the highest number of observed live polyps was observed in the coldest temperature treatment. Temperature was also proven to have an apparent impact on the survival of the polyps in experiment 2. The trend observed in experiment 2 followed a similar pattern to the observations in experiment 1, where the number of observed live polyps decreased with increasing temperature with the highest number of observed polyps in the 9°C temperature treatment. These findings contradict hypothesis two, stating that an increase in temperature will have a positive effect on the survivability of the polyps. The relationship between temperature and polyp survival observed in experiment 1 and 2 concurs with observations done by Purcell et al. (2012), where the survival of *A. aurita* polyps differed significantly between 14°C and 21°C. Purcell et al. (2012) found that the polyp survival over a 70 days period was 94,4% at 14°C and 75% at 21 °C.

An experiment done by Purcell et al. (2012) found that polyps of *A. aurita* might contribute with 0,1-0,6 buds polyp⁻¹ day⁻¹, the budding was observed to be dependent on both food density and temperature. They had the lowest numbers of buds polyp⁻¹ day⁻¹ in their coldest temperature (14°C), with an increase in budding activity as a function of higher temperature.

The increase in observed polyps after the settling phase in experiment 1 and 2 are assumed to be a result of budding. The observed budding is assumed to be within expected values based on (Purcell et al., 2012). Purcell et al. (2012) found that the amount of buds polyp⁻¹ increased with temperature between three temperature treatments (14, 21 and 28°C).

Polyp budding have been proven to be a density dependent reaction, Schiariti et al. (2015) observed a significantly higher budding rate at lower polyp densities compared to treatments with a high density. Population growth in polyp populations and budding have been suggested to be a response to intra- and interspecific competition for food items and space (Willcox et al., 2008). Budding can be assumed to be a beneficial trait when competing with other species for space (Schiariti et al., 2015). *A. aurita* have also been observed to have a motile bud-like tissue particle, produced at higher densities with the ability to disperse and colonize new locations, this is believed to reduce the negative density dependent factors of intraspecific competition on the original polyp population (Schiariti et al., 2015, Schiariti et al., 2014).

Data collected during this study does not go into detail on the effect of temperature as a factor on budding and it is therefore not possible to make any assumptions regarding the correlation between temperature and the budding response of polyps from the Trondheimfjord.

When assessing the negative effect of increasing temperature on polyp survival found in experiment 1 and 2, one might suspect that the survivability might decrease for polyps adapted to low or moderate temperature conditions. Global warming and the predicted global mean temperature increase of 1,5 or 2°C (compared to pre-industrial times)(Hoegh-Guldberg et al., 2018), might therefore counteract the predicted temperature based increase in jellyfish bloom formation for *A. aurita* adapted to low or moderate temperature conditions.

On the other hand, a potential decrease in the Atlantic thermohaline circulation (THC) and a subsequent drop in SST might have an opposite effect on the formation of jellyfish blooms (Levermann et al., 2012). Based on the observations of higher polyp survivability at 9°C treatment.

4.3. Ingestion rate and grazing

Increasing knowledge of how temperature affects the ingestion rate and grazing rate in the *A. aurita* polyp is important for a better understanding of how the individual energetic balance of a polyp might affect population dynamics (Ikeda et al., 2017). The relationship between temperature ingestion rate and grazing is also important when assessing the effect on increasing sea temperatures on bloom formations, since this information can give insight into the pace of the polyp lifecycle and the demands the polyp population place upon the environment (Brown et al., 2004).

A significant difference in the Ingestion rate ($\text{Artemia polyp}^{-1}\text{day}^{-1}$) as a result of temperature was observed for all sampling dates for the feed experiment. The 20°C treatment was observed to have the highest ingestion rate for all days except the first sampling date, 4 days after the start of the experiment (07.Sept.). A clear trend showing increasing ingestion rates as a result of increasing temperature was observed for all sampling days except for 4 days after the start of the experiment (07.Sept.).

A significant difference in grazing ($\text{mL polyp}^{-1}\text{day}^{-1}$) was observed for all sampling dates for the feed experiment. The 20°C treatment was observed to have the highest ingestion rate for all days of the experiment. A clear trend showing increasing grazing as a result of increasing temperature was observed for all sampling days.

The increase in ingestion rate ($\text{Artemia polyp}^{-1}\text{day}^{-1}$) and grazing ($\text{mL polyp}^{-1}\text{day}^{-1}$) as an effect of temperature, concurs with previously proven relationships between temperature and metabolic rates (Brown et al., 2004). This also shows that the 20°C treatment is within the temperature range of normal activity for the polyp (Brown et al., 2004).

The results from the Ingestion rate and grazing data collected in this study, confirms hypothesis two: stating that the polyp ingestion rate and grazing will increase as a result of increasing temperatures.

4.4. Elemental composition

A significant difference in the content of C polyp⁻¹ (μg) was observed as a result of temperature in experiment 1. The C polyp⁻¹ (μg) content increased with increasing temperature, and the highest value for experiment 1 was observed at the 20°C temperature treatment.

A significant difference in the content of C polyp⁻¹ (μg) was observed as a result of temperature in experiment 2. The highest C polyp⁻¹ (μg) content observed for experiment 2 were found in the two coldest treatments (9 and 12 °C), while the lowest value was observed in the 15 °C treatment.

A significant difference in the content of N polyp⁻¹ (μg) was observed as a result of temperature in experiment 1. The N polyp⁻¹ (μg) content increased with increasing temperature, and the highest value for experiment 1 was observed at the 20°C temperature treatment.

A significant difference in the amount of N polyp⁻¹ (μg) as a result of temperature was also observed for experiment 2. The highest N polyp⁻¹ (μg) content observed for experiment 2 were found in the two coldest treatments (9 and 12 °C), while the lowest value was observed in the 15 °C treatment.

An apparent relationship was detected between C:N ratio (mol) and temperature for experiment 1, with a significant difference between the C:N ratio (mol) for the 9 °C treatment and the 15 °C treatment.

There was observed no significant effect of temperature on the C:N ratio (mol) for experiment 2.

Based on the observations for ingestion rate, C polyp⁻¹ (μg) and N polyp⁻¹ (μg) in experiment 1, one might assume that the polyps follows the exponential relationship between temperature and metabolic rates (Brown et al., 2004). The increase in C polyp⁻¹ (μg) and N polyp⁻¹ (μg) might therefore be explained by the temperature dependent relationship of growth rate and lifespan (Gillooly et al., 2001, Gillooly et al., 2002).

A significant difference as a result of temperature was observed for both C polyp⁻¹ (μg) and N polyp⁻¹ (μg) in experiment 2 but experiment 2 does not follow the exponential pattern observed in experiment 1. One might expect that the difference between experiment 1 and experiment 2 in this regard is a result of the duration of the experiments. The duration of experiment 1 was 20 days, while the duration of experiment 2 was 58 days. Experiment 2 might have had the same growth rate as experiment 1 during the first 20 days of the experiment, and the difference might be a result of the effect of temperature on the lifespan of the polyps (Gillooly et al., 2001, Gillooly et al., 2002). The polyps showed the highest survival for both experiment 1 and experiment 2 at the 9°C treatment, showing that the 20°C treatment might lead to a quick growth followed by a lower survivability and lifespan.

Hypothesis three: stating that the carbon and nitrogen content of the polyp dry weight will increase as a result of increasing temperatures were, confirmed for experiment 1 of the study but rejected for experiment 2.

A better understanding of how temperature affects the biochemical composition of the polyps will also give an insight into how a great increase in the polyp population, followed by a subsequent decrease in the population might affect benthic bacterial communities. Through a release of organic matter into the water masses, during decomposing of dead polyps which might lead to a food web dominated by microbial organisms (Condon et al., 2011, Tinta et al., 2012) and an alteration to the diversity and function of the ecosystem (Kogovšek et al., 2014). The experiments conducted by Tinta et al. (2012), Condon et al. (2011) and Kogovšek et al. (2014) did only focus on the scyphozoan medusae. One might speculate that the polyps will have a similar effect, only to a lesser degree.

4.5. Methodology and further work

4.5.1. Methodology

The temperature gradient table worked as intended and made it possible to sustain a fairly reliable temperature regime, with a temperature gradient ranging from approximately 10°C to approximately 20°C. The mean values for all treatments were within the chosen temperatures except for the 20°C treatment of experiment 1 (mean temperature of 21°C) and the 10°C of experiment 2 (mean temperature of 9°C) (Appendix C.). 15°C was used to represent the temperature conditions in the field at the time of medusae sampling.

Rising salinity values were observed for the 17 and 20°C temperature treatments, as a result of evaporation. The salinity levels did not reach values that would be considered harmful to the polyps (Winans and Purcell, 2010, Lucas et al., 2012), but a better water replenishment regime (daily or flow-through) could have eliminated this problem and therefore salinity as a potential confounding variable.

The methods used for the photography were created as an attempt to minimize the handling of the polyps, and as an adaptation to the equipment that was available to use in the temperature regulated lab. Photographs for experiment 1 (Figure 14) were taken with illumination from below, leading to variation in the photo quality. Resulting in several photos where it was hard to distinguish between *A. aurita* polyps, *Artemia* cysts, uneaten *Artemia* and unidentified detritus. Unidentifiable objects were recorded as live polyps, it is advised to remove unidentified object from the calculations in future experiments to avoid misrepresentation and overestimation of the polyp population.

This might account for a certain misrepresentation in the data for the survival of experiment 1, resulting in an overestimation of the number of observed polyps petri dish¹. A revision of the method was done after termination of experiment 1 and alterations were done to the experimental setup for experiment 2. The photography for experiment 2 was done using the same equipment, but with illumination from above. Figure 14 illustrates the change in photo quality between the two experiments, experiment 2 had fewer instances of unidentifiable objects. Providing a higher accuracy for the estimated number of polyps in experiment 2.

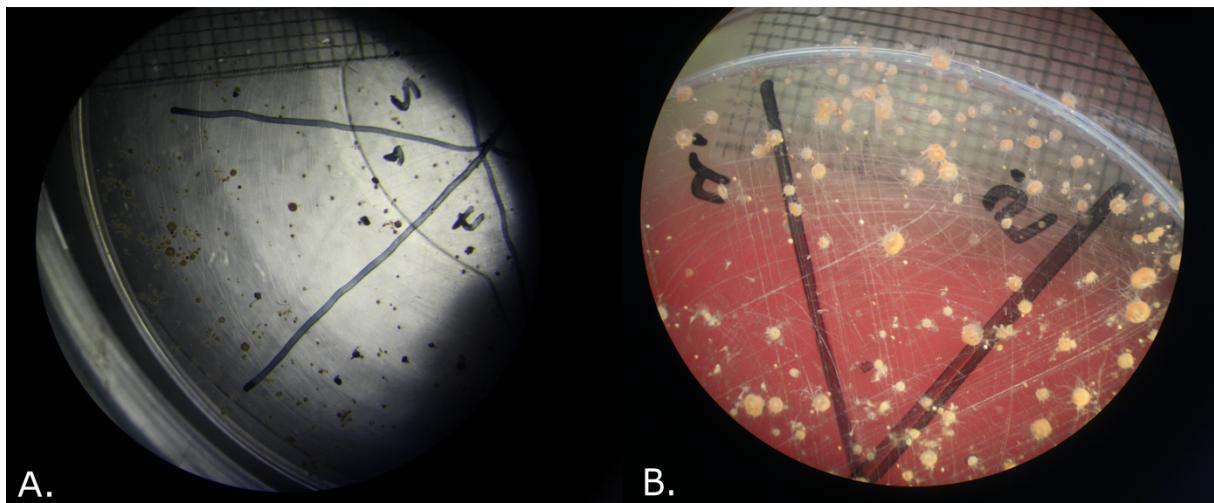


Figure 14: A comparison of a picture from experiment 1(A.) and a picture from experiment 2(B.) illustrating the change in quality after revision of the method.

A biofilm consisting of organic matter presumed to be *A. aurita* polyp carcasses, uneaten *Artemia*, *Artemia* cysts and bacteria were observed to form near the end of experiment 2 (Figure 15).



Figure 15: Biofilm and detritus observed in one of the replicates for the 17°C treatment near the end of experiment 2. Artemia cysts are observed as brown and light brown spheres, biofilm and detritus are assumed to be *A. aurita* carcasses, uneaten *Artemia* and microbial biofilm.

The experiment was conducted without any water movement and this might be the explanation for the formation of biofilm. The formation of biofilm is assumed to increase with elevating temperature conditions, as biofilm was mainly observed in the 17 and 20°C treatments. A trial period using aeration was conducted to observe the effect of aeration on the petri dishes and on the amount of *Artemia* in close proximity to the polyps in the surface layer of the beaker. The precision of the airflow through the system were deemed to be too low, no impact was observed on *Artemia* and sudden outbursts of large air bubbles from the aeration tubes were assumed to have a negative impact on

the polyp survival and growth. The use of aeration was therefore terminated, and the water exchange after feeding (Every second day) were the only process leading to higher water quality. An improvement of the water quality regime is advised for future experiments, by more frequent water exchange or through the use of a precise aeration system. It can be speculated that the biofilm discovered at later stages of the experiment had a negative impact on the survival of the polyps near the end of experiment 2. Either by covering live polyps or by changing the environment. The decay of uneaten food items either in the gastric cavity of the polyps or on the substrate around the polyps have in other experiments been shown to increase polyp mortality (Holst and Jarms, 2007).

Polyp wet weight (WW) and the weight of each individual capsule was not calculated or recorded during sampling for C and N analysis for neither experiment 1 nor experiment 2. Estimated values for polyp dry weight (DW) used for calculation of C, N and C:N ratio was therefore calculated after the samples had been oven dried. The estimated values were calculated using the mean value of 10 blank capsules selected at random (Table 10), the mean blank value (mg) was then subtracted from the value (mg) of the capsules containing polyp DW.

Table 10: Capsules used for calculation of mean capsule weight (mg), and mean value used to calculate approximately *A. aurita* polyp DW (mg).

Capsule number	1	2	3	4	5	6	7	8	9	10
Capsule weight (mg)	31,55	31,11	31,12	31,65	30,94	31,68	31,05	32,31	31,37	31,03
Mean (mg) ± SD	31,38 ± 0,42									

It can therefore be assumed that the data sampled for elemental analysis for both experiment 1 and experiment 2 will contain a slight inaccuracy.

All samples used in this study were oven dried (OD). An experiment conducted by Kogovšek et al. (2014) shows that one could suspect more realistic representation of elemental composition by freezedrying (FD) the samples. Kogovšek et al. (2014) had higher values for C (%) and N (%) in their FD samples when compared to the OD samples, but they did not detect any significant difference in the C/N ratio (Kogovšek et al., 2014). It is also suspected that a dialysis before the quantification of the organic matter will give a more realistic representation, because biomass for gelatinous organisms is affected by the ambient salinity. Leading to an inaccurate analysis affected by salt ions bound to the biomass (Kogovšek et al., 2014, Engel and Händel, 2011).

4.5.2. Further work

Based on the current observations done in this study, it would be valuable to conduct another experiment with an improved experimental setup. Removing several of the assumed confounding factors, and thus creating a deeper understanding of the relationship between temperature, planulae settling rate, polyp survival and biochemical composition of the *A. aurita* polyp. A second study should also contain several measurements that weren't included in this study.

Samples for polyp size (weight or length) should also be included together with the C content (DW), to gain a better understanding of the relationship between polyp abundance and biomass as a result of temperature. These measurements should also be done throughout the experimental period to form a clearer picture of the changes in the polyp population.

It would also be advised to run this experiment until strobilation, to assess if there is a relationship between temperature, polyp fitness and medusae populations.

One of the aims of experiment 2 was investigate the effect of temperature on strobilation, to get a better understanding of the factors that are responsible for triggering strobilation in *A. aurita* polyps. The strobilation was attempted induced through a temperature shift, with a 5°C decrease over 5 days followed by a 5 day increase to the original temperature. The chosen temperature was based on research done by Holst (2012), but the chosen time period was assumed to have been too short to induce strobilation. A mellower temperature change would be beneficial for a future experiment, e.g. a decrease of 5°C over a period of 60 days, followed by an increase of 5°C over a period of 60 days (Holst, 2012).

4.6. Conclusion

This work has investigated the effect of temperature on settling, survival, ingestion, grazing and C/N content of *A. aurita* from the Trondheimfjord. The hypothesis stated that temperature would have a positive effect on planulae settlement, polyp survival, ingestion rate, grazing and C/N content.

The results show no apparent relationship between temperature and the settling ability of the planula larvae. This contradict the first hypothesis of this study stating that higher temperatures can be expected to have a positive effect on the settling rate of the *A. aurita* planulae larvae. Density did however seem to affect settling, as there was a higher settling rate in experiment X compared to Z. Increased access to substrate can therefore have a positive effect on settling, independently of temperature.

The first hypothesis was also contradicted regards to survival. A negative correlation between increasing temperatures and polyp survival was observed, indicating that higher temperatures will not have a positive effect on the survivability of the *A. aurita* polyps.

The second hypothesis stated that increasing temperature will increase polyp ingestion rate and grazing. This was confirmed, as an apparent effect of temperature on the ingestion rate and grazing of the polyps was observed.

An increase in carbon and nitrogen content of the polyp dry weight was observed in experiment 1, but not experiment 2. It is therefore not possible to determine the relationship between temperature and elemental composition of the polyps. The third hypothesis stating that the carbon and nitrogen content of the polyp dry weight will increase as a result of increasing temperatures must be rejected.

To conclude, this study shows that there is an apparent negative relationship between increasing temperatures and survival of the *A. aurita* polyps local to the Trondheimfjord. This might lead to less frequent blooms of *A. aurita* in the Trondheimfjord, as a result of expected increase in the sea surface temperatures in the region.

Whether temperature affects strobilation and ephyrae survivability and further effect on local blooms in the Trondheimfjord is not known. Further studies on this topic would be beneficial for future estimations of *A. aurita* blooms in the Trondheimfjord.

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Appendices

<i>Appendix A. Project plan</i>	<i>a</i>
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Polyp survival experiment 1	<i>jj</i>
Polyp survival experiment 2	<i>ll</i>

Appendix A. Project plan

A project plan was created in the beginning of this master project (Table). The project plan has been revised several times and it was used as a tool during the planning of the lab work. It was also used for parts of the discussion.

Table A: Project plan describing the main aim and aims. As well as issues connected to each aim and the solutions to said issues. The project plan was used to plan and conduct parts of the study.

Main aim	Aims	Issues	Solution
Effects of temperature on the settling rate, mortality, feeding rate and biochemical composition of the polyp stages (Scyphozoa) of <i>Aurelia aurita</i>.	How will the change in ocean temperature affect <i>A. aurita</i> .	What are the expected changes?	Find temperature predictions for the Trondheim fjord. Describe how increasing water temperatures will affect life in the oceans.
		At which temperatures does the polyps thrive.	Identify at which temperatures the planulae are released into the water masses. Identify at which temperatures the polyps are expected to strobilate in nature.
	Describe the lifecycle of <i>A. aurita</i> .	Importance of the polyp stages.	Describe role in the reproduction of <i>A. aurita</i> . Describe the scyphozoan benthic life stages.
	Establish a research design.	How should the experimental setup be done to make it viable.	Test the suspension of prey with and without aeration. Find the least intrusive way of doing the measurements.
		Develop a method for cultivation of <i>Artemia sp.</i>	Gather information about how this have been done in other studies. Make an estimate for the required feed amount.

	<p>Test methods for measurements.</p>	<p>Poking the polyps for measurements of size.</p> <p>Identify how to best utilize the camera and the stereomicroscope.</p> <p>Identify suitable software for counting.</p>
Mortality rate.	<p>Which ecological theories and statistical models will fit the species?</p> <p>How does the change in temperature affect mortality?</p> <p>Is there a significant difference between experiment one and two?</p>	<p>Describe relevant ecological theories.</p> <p>Identify the most relevant statistical models.</p> <p>Analyse the data and compare the treatments.</p> <p>Identify any temperature-based thresholds.</p> <p>Identify if there is any statistical value in comparing the two experiments.</p>
Ingestion rate.	<p>Effect of temperature on ingestion rate?</p> <p>How should the data be analysed in R?</p>	<p>The effect of temperature on chemical processes.</p> <p>Analyse the data using FROST.</p> <p>Identify potential outliers.</p> <p>Identify the best way to visualize the data.</p>
C and N analysis.	<p>How does changing temperatures affect the elemental composition of <i>A. aurita</i> polyps?</p>	<p>Analyse the C and N content of polyp DW post experiment.</p> <p>Compare the data both in terms of % and mol.</p>

Settling rate.	How does increasing temperatures affect planulae settling? Is there a correlation between settling rate and mortality?	Analyse the number of settled planulae per treatment. Gather information about the transformation from pelagic to benthic life stages. Compare the effect of temperature on settling and mortality.
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Appendix B. Sampled medusae and settling rate

Sampled medusae for experiment 1 and 2

Table K contains the measurements for the fecund medusae sampled for experiment 1 on the 30.aug and experiment 2 on the 24.sep. These measurements were conducted prior to the collection of planulae.

Table K: Weight (g) and bell diameter (cm) of fecund medusae collected for experiment 1 and experiment 2.

Medusae	Experiment 1 (30.aug)		Experiment 2 (24.sep)	
	Weight (g)	Bell diameter(cm)	Weight (g)	Bell diameter(cm)
1	64	12	100	11
2	56	10	161	12
3	123	10	244	15
4	96	12	411	19
5	77	16	284	14
6	53	12	NA	NA

Calculation of planulae suspension for experiment 1 and experiment 2

An approximate number for the planulae added to the beakers (Planulae $\text{mL}^{-1}\text{beaker}^{-1}$) in the beginning of experiment 1 and 2 were calculated using equations (I-IV)(Table L).

$$\text{Mean planulae } \text{mL}^{-1} = \frac{44+94+66+89+93}{5} = 77,2 \text{ planulae } \text{mL}^{-1} \quad (\text{I})$$

$$\text{Total planula} = 77,2 \text{ planulae } \text{mL}^{-1} * 700\text{mL} = 54050 \text{ planulae} \quad (\text{II})$$

$$\text{Planulae beaker}^{-1} = \frac{54040 \text{ planulae}}{25 \text{ beakers}} = 2161,6 \text{ planulae beaker}^{-1} \quad (\text{III})$$

$$\text{Planulae } \text{mL}^{-1} \text{ beaker}^{-1} = \frac{2161,6 \text{ planulae beaker}^{-1}}{250\text{mL}} = 8,65 \text{ planulae } \text{mL}^{-1} \text{ beaker}^{-1} \quad (\text{IV})$$

Table L: Planulae counted in 1mL subsamples (SS) for experiment 1 and experiment 2. Calculated values for mean planula mL^{-1} , total number of planulae, number of planulae beaker^{-1} and planulae $\text{mL}^{-1}\text{beaker}^{-1}$ for experiment 1 and experiment 2. Calculations are performed as shown in equations (I-IV).

	SS1	SS2	SS3	SS4	SS5	Mean planulae mL^{-1}	Total planulae	Planulae beaker^{-1}	Planulae $\text{mL}^{-1}\text{beaker}^{-1}$
Experiment 1	44	94	66	89	93	77,2	54040	2161,6	8,65
Experiment2	61	72	72	55	NA	65	91000	3250	11,2

Settling rate experiment 1

The settling rate for experiment 1 and experiment 2 were based on the number of observed polyps after termination of the settling period, divided by the number of planulae in the suspension added to the beakers in the beginning of the settling phase.

Table M: Number of planulae in the suspension added to each beaker at the beginning of the settling period in experiment 1 and the number of observed settled polyps after termination of the settling period. Settling rate (Observed polyps/planulae beaker⁻¹) and settled planulae (%) out of 2161,6(100%).

Treatment(C°)	Replicate	Planulae beaker ⁻¹	Observed polyps	Settling rate	Settled planulae (%)	Mean Settled planulae (%) ± SD
9	1	2161,6	756	0,3497	34,97 %	43,72 %±13,03
	2	2161,6	866	0,4006	40,06 %	
	3	2161,6	817	0,3780	37,80 %	
	4	2161,6	1369	0,6333	63,33 %	
	5	2161,6	917	0,4242	42,42 %	
12	1	2161,6	723	0,3345	33,45 %	37,48 %±9,24
	2	2161,6	622	0,2877	28,77 %	
	3	2161,6	1130	0,5228	52,28 %	
	4	2161,6	707	0,3271	32,71 %	
	5	2161,6	869	0,4020	40,20 %	
15	1	2161,6	509	0,2355	23,55 %	34,67 %±11,99
	2	2161,6	670	0,3100	31,00 %	
	3	2161,6	567	0,2623	26,23 %	
	4	2161,6	850	0,3932	39,32 %	
	5	2161,6	1151	0,5325	53,25 %	
17	1	2161,6	779	0,3604	36,04 %	35,93 %±11,27
	2	2161,6	516	0,2387	23,87 %	
	3	2161,6	736	0,3405	34,05 %	
	4	2161,6	678	0,3137	31,37 %	
	5	2161,6	1174	0,5431	54,31 %	
20	1	2161,6	658	0,3044	30,44 %	28,58 % ±2,88
	2	2161,6	528	0,2443	24,43 %	
	3	2161,6	609	0,2817	28,17 %	
	4	2161,6	692	0,3201	32,01 %	
	5	2161,6	602	0,2785	27,85 %	

h

Settling rate experiment 2

Table N: Number of planulae in the suspension added to each beaker at the beginning of the settling period in experiment 2 and the number of observed settled polyps after termination of the settling period. Settling rate (Observed polyps/planulae beaker⁻¹) and settled planulae (%) out of 3250(100%).

Treatment(C°)	Replicate	Planulae beaker ⁻¹	Settled polyps	Settling rate	Settled planulae (%)	Mean Settled planulae (%) ± SD
9	1	3250	734	0,22584615	22,58 %	26,52 % ±0,09042438
	2	3250	757	0,23292308	23,29 %	
	3	3250	561	0,17261538	17,26 %	
	4	3250	923	0,284	28,40 %	
	5	3250	1335	0,41076923	41,08 %	
12	1	3250	642	0,19753846	19,75 %	15,35 % ±0,06572289
	2	3250	220	0,06769231	6,77 %	
	3	3250	342	0,10523077	10,52 %	
	4	3250	737	0,22676923	22,68 %	
	5	3250	553	0,17015385	17,02 %	
15	1	3250	433	0,13323077	13,32 %	15,85 % ±0,04224381
	2	3250	427	0,13138462	13,14 %	
	3	3250	701	0,21569231	21,57 %	
	4	3250	622	0,19138462	19,14 %	
	5	3250	393	0,12092308	12,09 %	
17	1	3250	433	0,13323077	13,32 %	14,64 % ±0,06754088
	2	3250	171	0,05261538	5,26 %	
	3	3250	397	0,12215385	12,22 %	
	4	3250	710	0,21846154	21,85 %	
	5	3250	668	0,20553846	20,55 %	
20	1	3250	713	0,21938462	21,94 %	17,70 % ±0,0589713
	2	3250	287	0,08830769	8,83 %	
	3	3250	777	0,23907692	23,91 %	
	4	3250	588	0,18092308	18,09 %	
	5	3250	512	0,15753846	15,75 %	

Appendix C. Temperature and salinity measurements

This appendix contains measurements of temperature and salinity for experiment 1 and 2. These measurements were conducted on a daily basis, using the WTW – Portable conductivity meter ProfiLine Cond 3310.

Experiment 1

Table O: Temperatures measured for experiment 1 (30.aug–18.sep). All temperatures are given in °C ($\pm 0,1^{\circ}\text{C}$). Mean temperature with SD is given at the bottom of the table.

Treatment($^{\circ}\text{C}$)	9					12					15					17					20				
Replicate	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
30.aug	10,2	9,8	9,8	9,9	10,0	12,2	12,3	12,3	12,3	12,1	15,0	15,1	15,2	15,1	14,8	17,3	17,3	17,2	17,2	17,2	20,1	20,1	20,5	20,4	20,0
31.aug	10,2	9,7	9,7	9,7	9,8	11,9	12,1	12,1	12,2	12,3	14,6	15,1	15,2	15,1	15,1	17,3	17,5	17,5	17,5	17,5	20,3	20,5	20,9	20,8	20,7
01.sep	10,1	9,6	9,6	9,8	9,8	12,0	12,2	12,2	12,3	12,4	14,6	14,9	15,0	15,0	15,0	17,2	17,2	17,2	17,0	17,2	20,1	20,3	20,7	20,5	20,5
02.sep	10,3	9,7	9,6	9,6	9,6	11,8	12,0	12,0	12,1	12,1	14,5	14,8	14,9	14,9	14,9	17,2	17,2	17,3	17,2	17,3	20,2	20,5	20,8	20,8	20,7
03.sep	10,1	9,7	9,5	9,4	9,5	11,7	11,9	11,9	12,0	12,1	14,5	14,8	14,8	14,8	14,9	17,2	17,3	17,4	17,1	17,3	20,1	20,5	20,7	20,8	20,7
04.sep	9,4	9,1	9,1	9,1	9,1	11,7	11,8	11,9	11,9	11,9	14,1	14,4	14,4	14,5	14,4	16,4	16,5	16,6	16,6	16,5	19,7	19,9	19,9	20,0	20,2
05.sep	9,3	9,1	9,2	9,1	9,2	11,9	12,0	12,1	12,1	12,2	14,6	14,8	14,8	14,9	14,9	17,3	17,5	17,4	17,4	17,4	20,8	20,9	20,9	21,1	21,2
06.sep	9,9	9,7	9,7	9,4	9,5	12,0	12,1	12,3	12,3	12,1	14,4	14,7	14,7	14,7	14,7	17,0	17,2	17,3	17,1	17,1	20,1	20,5	20,7	20,7	20,7
07.sep	9,4	9,4	9,5	9,5	9,5	12,1	12,1	12,2	12,3	12,3	14,4	14,7	14,8	15,0	15,0	17,1	17,2	17,2	17,0	17,2	20,7	20,9	20,9	20,9	21,0
08.sep	9,6	9,5	9,7	9,7	9,7	11,7	12,1	12,2	12,2	12,3	14,3	14,7	14,7	14,7	14,7	16,8	17,2	17,1	17,1	17,2	20,6	21,0	21,3	21,3	21,6
09.sep	9,3	9,3	9,6	9,6	9,7	11,5	11,8	11,9	11,8	12,0	14,0	14,1	14,2	14,2	14,2	16,5	16,3	16,3	16,4	16,5	19,6	20,1	20,1	20,3	20,4
10.sep	9,2	9,5	9,6	9,3	9,3	12,0	12,2	12,2	12,2	12,2	14,6	14,8	14,9	14,9	14,9	17,3	17,3	17,3	17,3	17,2	20,6	20,7	20,8	21,0	21,0
11.sep	9,3	9,3	9,4	9,7	9,4	12,0	12,1	12,2	12,1	12,1	14,8	14,8	15,0	14,9	14,9	17,5	17,4	17,4	17,3	17,2	20,7	20,9	21,0	21,0	21,0
12.sep	9,5	9,6	9,6	9,6	9,5	11,7	12,0	12,1	12,2	12,3	14,9	14,9	15,0	15,0	15,0	17,3	17,6	17,4	17,3	17,3	20,4	20,8	20,6	21,0	20,7
13.sep	9,5	9,6	9,6	9,6	9,8	12,1	12,2	12,2	12,3	12,3	14,8	14,9	15,1	15,1	15,0	17,1	17,3	17,3	17,2	17,2	19,9	20,2	20,2	20,3	20,3
14.sep	10,1	9,6	10,0	9,9	9,7	12,3	12,5	12,4	12,5	12,5	14,8	15,0	15,1	15,2	15,2	17,5	17,7	17,4	17,3	17,6	20,1	20,3	20,9	21,1	20,8
15.sep	9,5	9,3	9,3	9,4	9,5	12,1	12,2	12,3	12,3	12,4	15,0	15,1	15,2	15,2	15,2	17,6	17,7	17,6	17,5	17,6	20,5	20,7	21,2	21,2	21,1
16.sep	9,3	9,5	9,3	9,4	9,4	12,1	12,2	12,2	12,2	12,2	14,9	15,0	15,1	15,0	15,0	17,5	17,5	17,5	17,5	17,5	20,4	20,8	20,9	21,0	21,1
17.sep	9,3	9,2	9,4	9,3	9,2	11,9	12,1	12,1	12,0	12,1	14,6	14,8	14,9	14,8	14,8	17,2	17,3	17,3	17,3	17,2	20,4	20,7	20,7	21,0	21,0
18.sep	9,2	9,3	9,2	9,1	9,3	11,9	12,0	12,1	12,0	12,1	14,7	14,9	15,0	14,9	15,0	17,4	17,5	17,5	17,4	17,4	20,7	20,6	20,7	21,0	21,1
Mean	9,5±0,3					12,1±0,2					14,8±0,3					17,2±0,3					20,6±0,4				

Table P: Salinities measured for experiment 1 (30.aug–18.sep). Mean salinity with SD is given at the bottom of the table.

Treatment(C°)	9					12					15					17					20				
Replicate	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
30.aug	33,2	33,4	33,4	33,4	32,9	33,7	33,6	33,6	33,6	33,6	33,9	33,8	33,8	33,8	33,9	34,3	34,2	34,1	34,3	34,2	34,4	34,4	34,3	34,3	34,2
31.aug	32,9	33,1	33,1	33,1	33,5	33,4	33,4	33,4	33,4	33,4	33,7	33,7	33,7	33,6	33,7	34,3	34,4	34,1	34,1	34,3	34,7	34,6	34,6	34,6	34,7
01.sep	32,6	32,9	33,0	32,9	32,3	33,4	33,4	33,4	33,4	33,4	33,9	33,9	33,9	33,8	33,9	34,9	35,0	34,7	34,9	34,9	35,9	35,8	36,0	35,8	35,9
02.sep	32,5	32,8	32,9	32,7	32,2	33,4	33,5	33,5	33,5	33,5	34,1	34,1	34,1	34,0	34,1	32,8	32,8	32,9	32,4	32,7	34,0	34,5	34,2	34,5	34,1
03.sep	32,3	32,7	32,9	32,7	33,2	33,5	33,5	33,6	33,5	33,6	34,4	34,3	34,3	34,3	34,5	33,4	33,5	33,0	33,0	33,2	35,0	35,7	35,5	35,6	35,1
04.sep	32,9	33,1	33,2	33,1	33,2	33,7	33,7	33,5	33,7	33,6	33,9	33,9	33,8	33,9	33,9	34,3	34,2	34,2	34,2	34,1	34,8	35,0	34,8	34,8	34,8
05.sep	33,0	33,2	33,2	33,2	33,2	33,7	33,6	33,7	33,6	33,5	34,0	34,0	34,0	34,0	33,9	34,5	34,5	34,4	34,4	34,5	34,8	35,1	34,9	35,0	34,8
06.sep	32,9	33,3	33,2	33,5	33,3	33,5	33,5	33,4	33,4	33,5	33,7	33,7	33,7	33,7	33,9	33,9	33,9	33,9	33,9	33,8	34,1	34,2	34,1	34,2	34,0
07.sep	33,1	33,6	33,5	33,4	33,5	33,5	33,5	33,5	33,5	33,6	33,9	33,8	33,7	33,7	33,8	34,0	34,1	34,1	34,0	34,0	34,4	34,6	34,6	34,6	34,4
08.sep	33,0	33,0	33,3	32,9	32,9	33,6	33,4	33,2	33,1	33,0	33,5	33,6	33,7	33,6	33,4	33,9	33,7	33,6	33,7	33,7	33,7	33,8	33,7	33,6	33,6
09.sep	33,3	33,1	33,3	32,9	33,1	33,5	33,3	33,3	33,3	33,2	33,5	33,6	33,6	33,6	33,4	33,8	33,9	33,7	33,8	33,8	34,3	34,1	34,0	34,2	33,8
10.sep	33,3	33,4	33,4	33,6	33,5	33,7	33,6	33,6	33,6	33,6	33,9	33,8	33,9	33,9	33,9	34,3	34,2	34,0	34,1	34,1	34,8	34,9	34,8	34,7	34,6
11.sep	33,3,	33,4	33,4	33,4	33,4	33,8	33,7	33,6	33,7	33,7	34,0	33,9	34,0	34,0	34,0	34,4	34,3	34,2	34,2	34,3	35,1	35,2	35,0	35,1	34,9
12.sep	33,7	33,6	33,5	33,5	33,7	33,8	33,8	33,8	33,6	33,6	33,7	33,9	34,0	34,0	34,0	34,3	34,3	34,3	34,2	34,3	34,9	34,9	34,8	34,9	34,7
13.sep	33,3	33,4	33,5	33,6	33,6	33,9	33,8	33,8	33,8	33,8	34,2	34,1	34,1	34,1	34,1	34,6	34,6	34,6	34,5	34,5	35,3	35,3	35,3	35,4	35,1
14.sep	33,5	33,6	33,6	33,7	33,8	34,0	34,0	33,8	33,8	33,8	34,1	34,1	34,1	34,1	34,1	34,5	34,4	34,4	34,5	34,5	35,1	35,1	34,9	34,8	34,8
15.sep	33,6	33,5	33,8	33,9	33,9	34,1	34,0	33,9	33,9	33,8	34,2	34,2	34,2	34,2	34,2	34,7	34,7	34,7	34,6	34,7	35,0	35,0	35,1	35,1	34,9
16.sep	33,3	33,3	33,3	33,4	33,3	33,6	33,4	33,5	33,4	33,6	33,9	33,9	33,7	33,8	33,6	34,2	34,1	34,1	34,0	34,0	34,7	34,7	34,7	34,9	34,6
17.sep	33,3	33,4	33,2	33,3	33,5	33,7	33,6	33,4	33,5	33,5	34,1	34,1	34,0	34,0	33,8	34,6	34,5	34,4	34,4	34,3	35,3	35,2	35,3	35,5	35,2
18.sep	32,9	33,1	33,1	33,2	33,0	33,5	33,4	33,3	33,3	33,4	33,6	33,6	33,5	33,5	33,5	33,8	33,8	33,9	33,8	33,9	34,5	34,4	34,5	34,5	34,4
Mean	33,2±0,3					33,6±0,2					33,9±0,2					34,1±0,5					34,8±0,5				

Experiment 2

Table Q: Temperatures measured for experiment 1 (24.sep–20.nov). All temperatures are given in °C ($\pm 0,1^{\circ}\text{C}$). Mean temperature with SD is given at the bottom of the table.

Treatment (°C)	9					12					15					17					20					
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
Replicate																										
24.sep	9,7	9,4	9,5	9,7	10,0	12,1	12,2	12,2	12,1	12,1	14,6	14,7	14,9	14,9	15,0	17,1	17,4	17,2	17,2	17,2	20,2	20,4	20,5	20,3	20,5	
25.sep	9,4	9,1	9,1	9,2	9,5	12,0	11,9	11,9	12,0	11,9	14,5	14,7	14,8	14,9	14,9	17,1	17,3	17,3	17,1	17,2	20,0	20,5	20,7	20,8	20,6	
26.sep	9,3	9,3	9,3	9,3	9,1	11,6	11,4	11,4	11,5	11,5	14	14	14	14,1	14,1	16,5	16,5	16,4	16,1	16,2	19,5	19,5	19,9	19,9	20,1	
27.sep	9,2	9,0	9,0	9,1	9,2	11,7	11,8	11,9	11,9	11,9	14,6	14,6	14,8	14,8	14,8	17,1	17,3	17,2	17,0	16,9	20,0	20,3	20,7	20,5	20,5	
28.sep	9,4	9,4	9,0	4,3	9,9	12,0	12,1	12,4	12,4	12,4	14,3	14,8	14,8	14,8	14,8	17,1	17,1	17,0	16,8	16,5	19,8	20,0	20,2	20,1	19,7	
29.sep	9,7	9,8	9,8	9,6	9,7	12,4	12,5	12,4	12,6	12,6	15,2	15,3	15,3	15,4	15,3	17,9	18,1	18,0	17,7	17,9	21,1	21,3	21,3	21,4	21,3	
30.sep	9,4	9,3	9,0	9,1	9,3	11,7	11,8	11,7	11,8	11,9	14,0	14,3	14,3	14,4	14,3	16,4	16,5	16,5	16,1	16,3	19,3	19,7	19,7	19,8	19,8	
01.okt	9,6	9,5	9,1	9,3	9,4	11,6	12,1	12,2	12,2	12,2	14,4	14,8	14,9	14,9	14,9	17,2	17,6	17,5	17,4	17,5	20,5	20,6	20,8	20,9	20,8	
02.okt	9,5	9,6	9,2	9,4	9,3	11,6	11,9	12,0	12,1	12,0	13,9	14,1	14,2	14,2	14,1	16,2	16,4	16,3	16,2	16,3	19,5	19,7	20,1	20,2	20,2	
03.okt	9,7	9,7	9,7	9,3	9,6	12,0	12,2	12,3	12,4	12,5	15,0	15,0	15,1	15,3	15,2	17,7	17,6	17,7	17,7	17,7	20,4	20,8	21,1	21,1	21,1	
04.okt	9,4	9,5	9,3	9,1	9,4	11,8	12,0	12,1	12,1	12,2	14,5	14,5	14,7	14,9	14,9	17,6	17,5	17,4	17,4	17,4	20,5	20,7	20,9	21,1	32,0	
05.okt	9,6	9,9	9,8	9,5	9,7	12,5	12,5	12,6	12,7	12,6	14,1	14,2	14,2	14,2	14,2	16,1	16,0	15,9	15,8	15,8	19,4	19,5	19,5	19,4	19,5	
06.okt	9,4	9,4	9,4	9,1	9,3	11,6	11,7	11,8	11,9	11,9	14,0	14,3	14,3	14,3	14,2	16,2	16,4	16,3	16,3	16,2	19,6	19,9	20,0	20,2	20,1	
07.okt	9,3	9,5	9,4	9,3	9,4	12,1	12,1	12,1	12,2	12,3	14,8	15,0	15,1	15,1	15,0	17,7	17,8	17,6	17,6	17,6	20,4	21,0	21,0	21,2	21,0	
08.okt	9,3	9,4	9,2	9,3	9,4	11,7	11,7	11,7	11,8	11,8	14,0	14,2	14,3	14,2	14,2	16,9	16,9	16,8	16,8	16,7	19,9	20,3	20,4	20,4	20,5	
09.okt	9,9	9,9	9,9	9,9	9,8	12,5	12,5	12,6	12,6	12,6	15,1	15,3	15,3	15,3	15,3	17,7	17,9	17,9	17,9	17,8	20,9	21,1	21,4	21,3	21,4	
10.okt	9,6	9,3	9,4	9,2	9,3	11,3	11,5	11,7	11,7	11,8	14,0	14,1	14,0	14,0	14,0	15,9	16,3	16,2	16,1	16,0	19,5	19,7	19,8	19,8	19,7	
11.okt	9,6	9,3	9,4	9,3	9,4	12,2	12,4	12,3	12,4	12,5	15,1	15,1	15,2	15,2	15,2	17,9	17,8	17,8	17,8	17,8	20,6	20,9	21,1	21,3	21,2	
12.okt	9,3	9,4	9,0	9,2	9,2	12,0	12,1	12,0	12,1	12,2	14,9	14,9	15,0	15,0	15,0	17,6	17,7	17,7	17,6	17,6	20,5	20,6	20,8	21,1	21,0	

13.okt	9,5	9,4	9,4	9,4	9,5	12,2	12,3	12,2	12,3	12,4	14,8	15,0	15,0	15,0	15,0	17,8	17,7	17,7	17,7	17,6	20,8	20,8	21,0	21,0	21,0
14.okt	9,3	9,2	9,2	9,3	9,3	11,4	11,5	11,6	11,7	11,7	13,8	13,9	13,9	13,9	14,0	16,3	16,6	16,5	16,5	16,5	19,7	20,1	20,2	20,3	20,5
15.okt	9,5	9,5	9,4	9,4	9,4	12,1	12,3	12,4	12,4	12,5	15,1	15,3	15,1	15,2	15,2	17,8	17,9	17,7	17,7	17,6	20,6	20,8	20,8	20,9	20,7
16.okt	9,3	9,2	9,2	9,3	9,3	11,4	11,5	11,5	11,7	11,7	13,8	13,9	13,9	13,9	14,0	16,6	16,5	16,5	16,5	16,5	19,7	20,1	20,2	20,3	20,5
17.okt	9,7	9,5	9,4	9,6	9,4	12,1	12,3	12,3	12,3	12,5	15,1	15,3	15,3	15,3	15,2	17,8	17,9	17,9	17,9	17,9	20,4	20,6	21,1	21,2	21,1
18.okt	9,4	9,5	9,5	9,5	9,4	11,7	11,8	11,6	11,7	11,8	13,7	14,0	14,0	14,0	14,0	16,5	16,5	16,5	16,5	16,3	19,8	19,8	20,4	20,4	20,4
19.okt	9,5	9,5	9,5	9,4	9,4	11,9	12,0	12,1	12,1	12,2	14,7	14,7	14,7	14,8	14,8	17,4	17,5	17,4	17,3	17,3	20,7	20,6	21,0	21,0	21,0
20.okt	9,5	9,7	9,5	9,4	9,5	11,8	11,9	12,1	12,1	12,1	14,0	14,2	14,3	14,3	14,2	16,2	16,1	16,2	16,1	16,0	19,2	19,3	19,7	19,6	19,7
21.okt	9,7	9,5	9,5	9,7	9,5	12,3	12,4	12,3	12,4	12,4	15,0	15,1	15,2	15,3	15,2	17,6	17,5	17,6	17,6	17,6	20,1	20,5	20,6	20,9	20,8
22.okt	9,8	9,6	9,7	9,9	9,8	12,3	12,3	12,3	12,4	12,3	14,3	14,5	14,5	14,5	14,5	16,7	16,6	16,6	16,5	16,4	19,3	19,6	19,9	20,0	20,1
23.okt	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
24.okt	9,3	9,1	9,1	9,4	9,4	11,9	11,9	11,9	11,9	12,2	14,1	14,2	14,2	14,3	14,2	16,1	16,3	16,2	16,2	16,3	19,4	19,8	20,0	20,0	20,2
25.okt	9,4	9,5	9,4	9,3	9,3	12,0	12,2	12,2	12,2	12,3	14,8	14,9	14,9	14,9	14,9	17,3	17,6	17,5	17,4	17,3	20,6	20,6	20,7	20,5	20,7
26.okt	9,4	9,5	9,3	9,3	9,4	11,5	11,7	11,7	11,8	11,9	14,1	14,2	14,2	14,2	14,2	16,7	16,7	16,7	16,6	16,6	20,2	20,2	20,2	20,5	20,5
27.okt	9,9	9,4	9,4	9,3	9,7	12,3	12,5	12,5	12,6	12,7	15,0	15,3	15,3	15,3	15,3	17,8	17,8	17,9	17,8	17,7	20,3	20,9	21,0	21,0	21,0
28.okt	9,5	9,3	9,3	9,2	9,4	11,7	11,6	11,7	11,8	11,9	14,0	14,1	14,2	14,2	14,1	16,8	16,7	16,8	16,7	16,8	20,1	20,4	20,5	20,5	20,5
29.okt	9,7	9,3	9,2	9,5	9,4	12,2	12,3	12,4	12,4	12,5	15,0	15,0	15,0	15,1	14,9	17,6	17,5	17,5	17,5	17,7	20,3	20,7	20,9	21,0	20,9
30.okt	9,4	9,5	9,2	9,4	9,2	11,8	12,0	12,1	12,0	12,2	14,5	14,6	14,6	14,6	14,5	17,0	17,0	17,1	17,0	17,1	20,3	20,7	20,6	20,6	20,6
31.okt	9,5	9,6	9,5	9,5	9,5	12,0	12,1	12,0	12,1	12,1	14,8	14,8	14,8	14,8	14,8	17,5	17,4	17,4	17,3	17,2	20,6	20,8	20,9	20,8	
01.nov	9,3	9,4	9,5	9,4	9,4	12,0	12,2	12,1	12,1	12,2	14,8	14,8	15,0	14,9	14,9	17,5	17,5	17,6	17,4	17,4	20,6	20,7	20,9	21,0	20,9
02.nov	9,5	9,5	9,5	9,5	9,6	12,4	12,5	12,5	12,6	12,6	15,1	15,1	15,2	15,3	15,3	17,7	17,8	17,8	17,8	17,7	20,9	20,9	20,9	21,0	21,0
03.nov	9,4	9,5	9,5	9,5	9,4	12,0	12,1	12,2	12,2	12,3	14,7	14,8	14,8	14,8	14,9	16,9	17,0	17,0	17,0	16,9	19,7	19,8	20,0	20,2	20,2
04.nov	9,5	9,3	9,2	9,2	9,5	12,1	12,2	12,2	12,2	12,3	15,0	15,1	15,1	15,1	15,1	17,7	17,7	17,6	17,6	17,5	20,9	20,8	20,8	21,0	20,9
05.nov	9,5	9,5	9,4	9,4	9,6	12,1	12,1	12,2	12,2	12,2	14,4	14,4	14,3	14,3	14,3	16,3	16,4	16,4	16,4	16,4	20,0	20,0	20,0	20,3	20,3
06.nov	9,1	9,3	9,3	9,6	9,4	12,1	12,1	12,2	12,2	12,2	14,8	15,0	15,0	15,0	15,0	17,4	17,5	17,6	17,6	17,5	20,4	20,6	20,9	21,0	21,0
07.nov	9,3	9,3	9,4	9,4	9,4	11,7	11,6	11,8	11,8	11,7	13,8	13,9	13,9	14,0	14,0	16,1	16,1	16,1	16,1	16,1	19,7	19,8	20,0	20,1	20,1

<i>08.nov</i>	9,5	9,5	9,4	9,5	9,5	12,2	12,3	12,3	12,4	12,4	15,0	15,2	15,2	15,2	15,2	17,7	17,7	17,6	17,6	20,4	20,6	20,8	20,8	20,9	
<i>09.nov</i>	9,7	9,5	9,4	9,5	9,4	11,7	12,0	12,1	12,1	12,1	14,5	14,8	14,8	14,9	14,9	17,2	17,3	17,3	17,3	20,0	20,4	20,7	20,7	20,7	
<i>10.nov</i>	9,4	9,5	9,6	9,6	9,5	12,1	12,2	12,2	12,3	12,3	15,1	15,1	15,1	15,0	15,1	17,7	17,6	17,7	17,7	20,8	21,0	21,1	21,2	21,2	
<i>11.nov</i>	9,4	9,4	9,3	9,3	9,3	11,8	11,9	11,9	12,0	12,0	14,3	14,3	14,4	14,4	14,4	16,3	16,3	16,4	16,3	19,2	19,3	19,6	19,8	19,9	
<i>12.nov</i>	9,9	9,6	9,6	9,7	9,6	12,2	12,3	12,3	12,4	12,5	14,9	15,2	15,2	15,2	15,2	17,7	17,7	17,6	17,6	20,5	20,9	20,8	21,0	21,0	
<i>13.nov</i>	9,7	9,4	9,5	9,6	9,6	12,0	12,2	12,1	12,1	12,2	14,5	14,5	14,6	14,6	14,5	16,6	16,7	16,6	16,5	16,6	19,8	19,9	20,0	20,1	20,1
<i>14.nov</i>	9,6	9,5	9,2	9,4	9,5	12,4	12,4	12,4	12,5	12,6	15,3	15,3	15,4	15,4	15,4	17,8	17,9	17,8	17,7	20,5	20,7	20,9	21,1	21,0	
<i>15.nov</i>	9,5	9,4	9,3	9,4	9,5	12,2	12,2	12,2	12,3	12,4	14,9	15,1	15,1	15,1	15,1	17,3	17,4	17,3	17,2	17,2	19,8	19,9	20,1	20,4	20,4
<i>16.nov</i>	9,3	9,4	9,3	9,4	9,3	12,1	12,3	12,3	12,3	12,3	15,0	15,1	15,2	15,1	15,1	17,7	17,7	17,6	17,6	20,7	20,8	21,0	21,0	21,0	
<i>17.nov</i>	9,7	9,6	9,7	9,7	9,9	12,4	12,4	12,5	12,6	12,7	14,9	15,1	15,2	15,2	15,2	17,4	17,5	17,4	17,3	17,3	19,9	20,2	20,3	20,4	20,5
<i>18.nov</i>	9,3	9,4	9,3	9,4	9,3	12,1	12,3	12,3	12,3	12,3	15,0	15,1	15,2	15,1	15,1	17,7	17,7	17,6	17,6	20,7	20,8	21,0	21,0	21,0	
<i>19.nov</i>	9,5	9,4	9,3	9,4	9,3	12,0	12,0	12,0	12,0	12,0	14,5	14,5	14,5	14,5	14,4	16,5	16,6	16,6	16,5	16,3	19,7	19,6	20,0	20,0	20,0
<i>20.nov</i>	9,4	9,3	9,3	9,4	9,5	12,2	12,3	12,3	12,3	12,4	14,4	14,9	15,0	15,1	15,1	17,8	17,7	17,7	17,6	17,5	20,4	20,5	20,9	20,8	20,9
<i>Mean</i>	9,4±0,36				12,1±0,29				14,7±0,45				17,1±0,60				20,5±0,86								

Table R: Salinities measured for experiment 2 (24.sep–20.nov). Mean salinity with SD is given at the bottom of the table.

Treatment (C°)	9					12					15					17					20					
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
24.sep	32,8	33,5	33,1	33,7	32,9	33,1	32,8	33,0	33,2	33,2	33,4	33,2	33,2	33,2	32,9	33,2	33,2	33,3	33,3	33,3	33,7	33,5	33,5	33,8	33,8	
25.sep	32,7	33,7	33,2	33,8	33,0	33,2	33,3	33,3	33,2	33,3	33,5	33,5	33,5	33,5	33,2	33,7	33,8	33,7	33,8	33,8	34,5	34,5	34,5	34,9	34,6	
26.sep	33,0	33,8	33,3	33,3	33,3	33,1	33,2	33,3	32,9	33,2	33,6	33,5	33,8	33,6	33,3	34,1	34,1	34,0	34,2	34,1	35,0	34,9	35,2	35,5	35,0	
27.sep	33,1	33,7	33,2	33,7	33,0	33,3	33,5	33,5	33,1	33,4	34,0	34,0	34,1	34,0	33,7	34,9	34,7	34,9	34,9	34,8	34,7	34,7	35,3	35,4	35,1	
28.sep	34,0	34,2	34,1	34,1	34,2	34,4	34,2	34,3	34,3	34,4	34,6	34,6	34,6	34,6	34,6	34,8	34,8	34,9	34,9	35,7	35,6	35,6	35,7	35,5	35,5	
29.sep	33,6	33,8	33,8	33,8	33,9	34,2	34,1	34,1	34,2	34,0	34,3	34,2	34,4	34,2	34,2	34,9	34,7	34,6	34,6	34,7	35,6	35,3	35,6	35,6	35,2	
30.sep	33,7	34,0	34,0	34,0	34,0	34,2	34,2	34,2	34,3	34,1	34,4	34,4	34,6	34,3	34,3	35,1	35,0	35,0	35,0	35,0	36,0	35,4	35,4	35,5	35,3	
01.okt	33,9	34,1	34,1	34,2	34,1	34,6	34,5	34,4	34,4	34,4	34,8	34,7	34,8	34,7	34,7	35,2	35,2	35,1	35,0	35,5	35,6	35,8	35,8	35,6	35,7	
02.okt	34,0	34,0	34,0	34,1	34,2	34,6	34,5	34,5	34,5	34,3	34,9	34,9	35,0	34,9	34,9	35,1	35,0	35,1	34,7	35,0	36,0	36,3	35,9	36,0	36,0	36,0
03.okt	34,1	33,8	33,9	34,0	34,2	34,3	34,2	34,3	34,2	34,5	34,6	34,6	34,5	34,2	34,3	34,5	34,8	34,8	34,6	34,8	35,0	35,5	35,4	35,4	35,0	35,0
04.okt	34,3	33,8	34,1	34,1	34,1	34,3	34,3	34,3	34,3	34,6	34,8	34,8	34,6	34,6	34,5	34,5	35,1	35,1	35,1	35,1	35,6	36,1	36,1	60,0	35,6	35,6
05.okt	34,0	33,4	34,5	34,5	34,6	34,7	34,7	34,7	34,7	34,7	34,9	34,9	34,9	34,9	34,9	35,1	35,1	35,1	35,1	35,0	35,0	35,3	35,3	35,2	35,4	35,4
06.okt	34,5	34,4	34,5	34,5	34,6	34,8	34,7	34,8	34,8	34,7	35,1	35,1	35,2	35,2	35,1	35,6	35,6	35,5	35,4	36,1	36,2	36,2	36,0	36,0	36,0	36,0
07.okt	34,1	34,5	34,2	34,2	34,2	34,4	34,7	34,4	34,3	34,3	34,8	35,0	34,7	34,8	34,9	35,2	35,0	34,8	34,8	34,9	35,3	35,5	35,4	35,4	35,5	35,5
08.okt	34,0	5,0	34,9	34,6	34,6	34,5	34,9	34,6	34,6	34,5	35,1	35,1	35,0	35,1	35,2	35,2	35,1	34,9	35,0	35,0	35,6	36,0	35,8	35,9	35,9	35,9
09.okt	34,4	34,4	34,4	34,5	34,5	34,8	34,7	34,8	34,8	34,8	35,1	35,1	35,1	35,1	35,1	35,4	35,4	35,4	35,4	36,1	36,1	36,0	35,9	35,9	35,8	35,8
10.okt	34,4	34,4	34,4	34,5	34,5	35,0	34,9	34,9	34,9	35,0	35,4	35,3	35,3	35,4	35,4	35,6	35,5	35,3	35,5	35,4	36,6	36,4	36,5	36,2	36,2	36,2
11.okt	34,3	34,4	34,5	34,5	34,6	34,8	34,8	34,6	34,8	34,8	35,1	35,1	35,0	35,0	34,9	35,5	35,4	35,5	35,5	36,2	36,0	36,0	35,8	35,8	35,8	
12.okt	34,4	34,5	34,6	34,6	34,6	35,0	35,0	34,8	34,9	35,0	35,4	35,4	35,3	35,4	35,5	35,7	35,5	35,6	35,7	35,6	36,7	36,6	36,6	36,4	36,4	36,4
13.okt	33,9	34,0	34,1	34,4	34,5	34,6	34,6	34,6	34,4	34,5	34,9	34,8	34,7	34,8	34,8	35,1	35,0	35,1	34,8	35,0	35,0	35,4	35,4	35,3	35,3	35,3
14.okt	34,3	34,4	34,2	34,4	34,4	34,9	34,8	34,9	34,0	34,7	35,4	35,4	35,4	35,4	35,4	35,6	35,5	35,3	35,5	35,3	36,1	36,3	36,4	36,1	36,1	36,1
15.okt	34,2	34,2	34,3	34,4	34,4	34,9	34,7	34,8	34,7	34,6	35,1	35,1	35,1	35,1	35,1	35,6	35,6	35,5	35,5	35,4	36,0	36,2	36,1	35,9	36,2	36,2
16.okt	34,3	34,4	34,2	34,4	34,4	34,9	34,8	34,9	34,9	34,7	35,4	35,4	35,4	35,4	35,4	35,5	35,5	35,3	35,5	35,4	36,1	36,1	36,4	26,1	36,1	36,1
17.okt	34,1	34,2	34,3	34,4	34,2	34,6	34,5	34,3	34,6	34,6	34,7	34,7	34,8	34,5	34,7	34,6	35,1	34,9	35,1	35,2	35,5	35,7	35,8	35,7	35,7	35,7

<i>15.nov</i>	34,4	34,3	34,5	34,6	34,6	34,8	34,8	34,9	34,9	35,0	35,1	35,4	35,4	35,4	35,4	35,8	35,5	35,8	35,7	35,8	36,0	36,2	36,3	36,2	36,1
<i>16.nov</i>	34,2	34,1	34,3	34,3	34,5	34,5	34,5	34,5	34,6	34,8	34,8	34,8	34,8	34,8	34,8	34,8	35,1	35,1	35,1	35,1	35,5	35,5	35,5	35,5	35,5
<i>17.nov</i>	34,3	34,3	34,3	34,3	34,3	34,8	34,7	34,8	34,8	34,9	35,3	35,3	35,4	35,4	35,4	36,1	36,0	35,9	36,0	35,9	36,5	36,7	36,5	36,4	36,5
<i>18.nov</i>	34,2	34,1	34,3	34,3	34,5	34,5	34,5	34,5	34,6	34,8	34,8	34,8	34,8	34,8	34,8	34,8	35,1	35,1	35,1	35,1	35,5	35,5	35,5	35,5	35,5
<i>19.nov</i>	34,1	34,1	34,2	34,2	34,2	34,6	34,6	34,5	34,7	34,6	35,0	35,0	35,0	35,0	35,1	35,6	35,7	35,5	35,6	35,5	35,9	35,8	35,7	35,8	35,5
<i>20.nov</i>	34,1	34,1	34,2	34,2	34,2	34,5	34,4	34,4	34,5	34,5	34,3	34,7	34,8	34,7	34,8	34,8	35,2	35,1	35,1	35,1	35,7	35,7	35,6	35,5	35,5
<i>Mean</i>	$34,0 \pm 1,76$				$34,4 \pm 0,45$				$34,8 \pm 0,49$				$35,2 \pm 0,51$				$35,8 \pm 1,64$								

Appendix D. Ingestion rate and Grazing

Appendix D contains the raw data for the ingestion rate and grazing calculations.

Table J: 07.Sept. Data and calculations for ingestion rate and grazing.

Treatment (°C)	Replicate	beginning	end	no of ind.	t1-t0	volume of	Algal growth	Grazing	Average cell	The	Ingestion	Ingestion	grazing		
		cells/µl	cells/µl			bottle (µl)	constant (k)	coefficient (g)	concentration / bottle (C)	volume swept clear (F) (grazing rate)	rate (cells eaten /copepod /hour) I	rate (cells eaten /copepod /day) I			
		c1/*c1	c2/*c2	N	t	V	k	ave k	g (µl/h)	C (cells / µl)	F (µl / ind / h)	I (cells / ind / h)	I (cells / ind / day)	F (µl ind.-1 day-1)	I (ug C / ind / day)
9	1	0,00546	0,00225	713,0	16,0	837000,0		0,01969	0,00362	23,11736	0,08369	2,00858	554,81663	0,00004	
	2	0,00546	0,00167	881,0	16,0	837000,0		0,03845	0,00320	36,52883	0,11675	2,80204	876,69191	0,00006	
	3	0,00546	0,00233	422,0	16,0	837000,0		0,01742	0,00368	34,55022	0,12705	3,04909	829,20540	0,00006	
	4	0,00546	0,00275	1252,0	16,0	837000,0		0,00715	0,00395	4,78042	0,01889	0,45326	114,73019	0,00001	
	5	0,00546	0,00233	566,0	16,0	837000,0		0,01742	0,00368	25,76006	0,09472	2,27335	618,24148	0,00005	
12	1	0,00546	0,00307	696,0	16,0	837000,0		0,00034	0,00415	0,40738	0,00169	0,04056	9,77715	0,000001	
	2	0,00546	0,00342	447,0	16,0	837000,0		-0,00642	0,00436	-	-0,05236	-1,25655	-288,32727	-0,00003	
	3	0,00546	0,00242	1062,0	16,0	837000,0		0,01523	0,00373	12,01364	12,00045	0,04480	1,07521	288,01085	0,00002
	4	0,00546	0,00242	602,0	16,0	837000,0		0,01523	0,00373	21,17023	0,07903	1,89680	508,08559	0,00004	
	5	0,00546	0,00192	901,0	16,0	837000,0		0,02971	0,00338	27,60333	0,09341	2,24190	662,47997	0,00005	
15	1	0,00546	0,00373	364,0	16,0	837000,0		-0,01196	0,00454	-	-0,12485	-2,99635	-659,79363	-0,00006	
	2	0,00546	0,00467	507,0	16,0	837000,0		-0,02590	0,00505	42,76147	-	-0,21604	-5,18490	-	-0,0001
	3	0,00546	0,00433	347,0	16,0	837000,0		-0,02127	0,00487	-	-0,25008	-6,00186	-	1231,35173	-0,0001
	4	0,00546	0,00413	454,0	16,0	837000,0		-0,01832	0,00477	51,30632	-	-0,16092	-3,86201	-810,46928	-0,00008
	5	0,00546	0,00325	740,0	16,0	837000,0		-0,00329	0,00426	33,76955	-3,72152	-0,01585	-0,38041	-89,31650	-
17	1	0,00546	0,00158	374,0	16,0	837000,0		0,04165	0,00313	93,22240	0,29188	7,00515	2237,33770	0,00008	
	2	0,00546	0,00233	446,0	16,0	837000,0		0,01742	0,00368	32,69102	0,12021	2,88502	784,58448	0,00006	
	3	0,00546	0,00117	613,0	16,0	837000,0		0,06074	0,00278	82,93712	0,23068	5,53632	1990,49097	0,0001	
	4	0,00546	0,00117	690,0	16,0	837000,0		0,06074	0,00278	73,68182	0,20494	4,91849	1768,36371	0,0001	
	5	0,00546	0,00108	979,0	16,0	837000,0		0,06537	0,00271	55,89094	0,15121	3,62904	1341,38255	0,00008	
20	1	0,00546	0,00239	457,0	16,0	837000,0		0,01595	0,00371	29,20490	0,10849	2,60369	700,91761	0,000058	
	2	0,00546	0,00283	322,0	16,0	837000,0		0,00528	0,00400	13,73729	0,05500	1,31990	329,69503	0,00003	

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3	0,00546	0,00383	432,0	16,0	837000,0		-0,01361	0,00460	-	-0,12123	-2,90946	-632,75887	-0,00006	
4	0,00546	0,00333	542,0	16,0	837000,0		-0,00487	0,00431	26,36495	-7,52466	-0,03242	-0,77814	-180,59173	-0,00002
5	0,00546	0,0030	457,0	16,0	837000,0		0,00171	0,00411	3,13634	0,01288	0,30916	75,27224	0,00001	
Control1	0,00546	0,00308	na	16,0	837000,0	-0,0357	-0,0357					0,0		
Control2	0,00000		na		837000,0	na						0,0		
Control3	0,00000		na		837000,0	na						0,0		

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Table K: 09.Sept. Data and calculations for ingestion rate and grazing.

Treatment	Replicate	beginning cells/µl	end cells/µl				Grazing coefficient (g)	Average cell concentration / bottle (C)	The volume swept clear (F) (grazing rate)	Ingestion rate (cells eaten /copepod /hour) I	Ingestion rate (cells eaten /copepod /day) I	grazing F (ml ind.-1 day-1)	I (ug C / ind /day)
		c1/*c1	c2/*c2	no of ind.	t1-t0	volume of bottle (µl)	Algal growth constant (k)	k	ave k	g	C	F	I
		N	t	V									
9	1	0,00603	0,00606	713,0	16,0	824000,0				0,00276	0,00605	3,19123	0,01929
	2	0,00603	0,00230	881,0	16,0	824000,0				0,06327	0,00387	59,17366	0,22911
	3	0,00603	0,00432	422,0	16,0	824000,0				0,02389	0,00513	46,64992	0,23928
	4	0,00603	0,00475	1252,0	16,0	824000,0				0,01800	0,00536	11,84539	0,06355
	5	0,00603	0,00510	566,0	16,0	824000,0				0,01356	0,00555	19,73866	0,10959
12	1	0,00603	0,00631	696,0	16,0	824000,0				0,00021	0,00617	0,24858	0,00153
	2	0,00603	0,00248	447,0	16,0	824000,0				0,05869	0,00399	108,19243	0,43210
	3	0,00603	0,00114	1062,0	16,0	824000,0				0,10712	0,00294	83,11254	0,24414
	4	0,00603	0,00435	602,0	16,0	824000,0				0,02347	0,00515	32,12664	0,16531
	5	0,00603	0,00347	901,0	16,0	824000,0				0,03766	0,00463	34,44362	0,15953
15	1	0,00603	0,00463	364,0	16,0	824000,0				0,01955	0,00530	44,25822	0,23463
	2	0,00603	0,00013	507,0	16,0	824000,0				0,24305	0,00154	395,01774	0,60722
	3	0,00603	0,00482	347,0	16,0	824000,0				0,01711	0,00540	40,62948	0,21946
	4	0,00603	0,00236	454,0	16,0	824000,0				0,06170	0,00391	111,99213	0,43821
	5	0,00603	0,00264	740,0	16,0	824000,0				0,05466	0,00411	60,86255	0,24990
17	1	0,00603	0,00458	374,0	16,0	824000,0				0,02021	0,00527	44,52586	0,23486
	2	0,00603	0,00015	446,0	16,0	824000,0				0,23577	0,00158	435,58858	0,68867
	3	0,00603	0,00300	613,0	16,0	824000,0				0,04669	0,00434	62,75696	0,27246
	4	0,00603	0,00293	690,0	16,0	824000,0				0,04812	0,00430	57,46391	0,24697
	5	0,00603	0,00231	979,0	16,0	824000,0				0,06300	0,00388	53,02875	0,20568
20	1	0,00603	0,00191	457,0	16,0	824000,0				0,07482	0,00359	134,90612	0,48389
	2	0,00603	0,00004	322,0	16,0	824000,0				0,31838	0,00119	814,72960	0,96792
	3	0,00603	0,00262	432,0	16,0	824000,0				0,05512	0,00409	105,13509	0,43032
	4	0,00603	0,00361	542,0	16,0	824000,0				0,03509	0,00472	53,34697	0,25176

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5	0,00603	<u>0,00291</u>	457,0	16,0	824000,0	-	0,04853	0,00429	87,51049	0,37500	9,00002	2100,25171	0,000189
<i>Control 1</i>	0,00603	0,00578	na	16,0	824000,0	0,00272	0,00302	-	-	-	-	0,0	
<i>Control 2</i>	0,00603	0,00503	na	16,0	824000,0	0,01134	-	-	-	-	-	0,0	
<i>Control 3</i>	0,00603	0,00873	na	16,0	824000,0	0,02311	-	-	-	-	-	0,0	
<i>sal6</i>	0,00003	0,00001	30,0	16,0	500000,0	-	-	0,00002	0,0	0,0	0,0	0,0	0,0
<i>f1</i>	0,00003	0,00001	30,0	16,0	500000,0	0,04208	0,02699	-	-	-	-	0,0	
<i>f2</i>	0,00003	0,00002	30,0	16,0	500000,0	0,03636	-	-	-	-	-	0,0	
<i>f3</i>	0,00003	0,00003	30,0	16,0	500000,0	0,00251	-	-	-	-	-	0,0	

Table L: 11.Sept. Data and calculations for ingestion rate and grazing.

Treatment	Replicate	beginning cells/ μ l		end cells/ μ l		volume of bottle (μ l)	Algal growth constant (k)	Grazing coefficient (g)	Average cell concentration / bottle (C)	The volume swept clear (F) (grazing rate)	Ingestion rate (cells eaten /copepod /hour) I	Ingestion rate (cells eaten /copepod /day) I	grazing F (ml ind.-1 day-1)	I (ug C / ind / day)
		$c1/*c1$	$c2/*c2$	no of ind.	$t1-t0$									
9	1	0,00401	0,00368	568,0	16,0	824000,0		0,02756	0,00384	39,97969	0,15371	3,68902	959,51264	0,000077
	2	0,00401	0,00337	632,0	16,0	824000,00		0,03307	0,00368	43,11923	0,15878	3,81071	1034,86155	0,000080
	3	0,00401	0,00389	645,0	16,0	824000,0		0,02403	0,00395	30,70165	0,12138	2,91317	736,83970	0,000061
	4	0,00401	0,00250	1216,0	16,0	824000,0		0,05184	0,00319	35,12678	0,11223	2,69342	843,04267	0,000057
	5	0,00401	0,00280	674,0	16,0	824000,0		0,04472	0,00337	54,67228	0,18418	4,42021	1312,13468	0,000093
12	1	0,00401	0,00358	229,0	16,0	824000,0		0,02923	0,00379	105,17709	0,39909	9,57819	2524,25012	0,000201
	2	0,00401	0,00418	479,0	16,0	824000,0		0,01952	0,00410	33,58458	0,13766	3,30388	806,02992	0,000069
	3	0,00401	0,00324	851,0	16,0	824000,0		0,03546	0,00361	34,33351	0,12411	2,97873	824,00430	0,000063
	4	0,00401	0,00363	698,0	16,0	824000,0		0,02839	0,00382	33,51348	0,12801	3,07222	804,32345	0,000065
	5	0,00401	0,00235	927,0	16,0	824000,0		0,05560	0,00311	49,41886	0,15360	3,68635	1186,05275	0,000077
15	1	0,00401	0,00396	858,0	16,0	824000,0		0,02295	0,00399	22,04117	0,08790	2,10951	528,98800	0,000044
	2	0,00401	0,00293	837,0	16,0	824000,0		0,04175	0,00345	41,10465	0,14161	3,39855	986,51151	0,000071
	3	0,00401	0,00387	371,0	16,0	824000,0		0,02434	0,00394	54,07026	0,21324	5,11779	1297,68630	0,000107
	4	0,00401	0,00293	548,0	16,0	824000,0		0,04175	0,00345	62,78210	0,21629	5,19086	1506,77032	0,000109
	5	0,00401	0,00352	834,0	16,0	824000,0		0,03025	0,00376	29,89189	0,11252	2,70040	717,40531	0,000057
17	1	0,00401	0,00183	467,0	16,0	824000,0		0,07105	0,00278	125,35676	0,34899	8,37585	3008,56235	0,000176
	2	0,00401	0,00363	363,0	16,0	824000,0		0,02839	0,00382	64,44189	0,24614	5,90746	1546,60541	0,000124
	3	0,00401	0,00296	450,0	16,0	824000,0		0,04114	0,00346	75,32339	0,26071	6,25704	1807,76128	0,000131
	4	0,00401	0,00299	478,0	16,0	824000,0		0,04052	0,00348	69,85657	0,24292	5,82997	1676,55774	0,000122
	5	0,00401	0,00219	582,0	16,0	824000,0		0,06011	0,00301	85,10963	0,25601	6,14432	2042,63120	0,000129
20	1	0,00401	0,00194	269,0	16,0	824000,0		0,06751	0,00285	206,79642	0,59016	14,16374	4963,11400	0,000297
	2	0,00401	0,00239	249,0	16,0	824000,0		0,05457	0,00313	180,59039	0,56550	13,57208	4334,16928	0,000285
	3	0,00401	0,00248	232,0	16,0	824000,0		0,05233	0,00318	185,84702	0,59163	14,19909	4460,32840	0,000298
	4	0,00401	0,00318	404,0	16,0	824000,0		0,03659	0,00358	74,63213	0,26745	6,41871	1791,17107	0,000135

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	0,00401	0,00149	231,0	16,0	824000,0		0,06011	0,00301	85,10963	0,25601	6,14432	2042,63120	0,000129
<i>Control 1</i>	0,00401	0,00480	na	16,0	824000,0	0,01112	0,02211	0,00285	0,00000	0,00000	0,00000	0,00000	0,000000
<i>Control 2</i>	0,00401	0,00574	na	16,0	824000,0	0,02232		0,00313	0,00000	0,00000	0,00000	0,00000	0,000000
<i>Control 3</i>	0,00401	0,00680	na	16,0	824000,0	0,03290		0,00318	0,00000	0,00000	0,00000	0,00000	0,000000

Table M: 13.Sept. Data and calculations for ingestion rate and grazing.

Treatment	Replicate	beginning cells/ μ l	end cells/ μ l	no of ind.	t1-t0	volume of bottle (μ l)	Algal growth constant (k)	Grazing coefficient (g)	Average cell concentration / bottle (C)	The volume swept clear (F) (grazing rate)	Ingestion rate (cells eaten /copepod /hour)	Ingestion rate (cells eaten /copepod /day) I	grazing F (ml ind.-1 day-1)	I (ug C / ind./day)
		c1/*c1	c2/*c2								I (cells / ind / day)	I (cells / ind / day)		
9	1	0,00772	0,00732	641,0	16,0	824000,0		0,00956	0,00752	12,28764	0,09237	2,21687	294,90339	0,000047
	2	0,00772	0,00605	709,0	16,0	824000,0		0,02149	0,00685	24,97171	0,17104	4,10490	599,32093	0,000086
	3	0,00772	0,00701	730,0	16,0	824000,0		0,01225	0,00736	13,82949	0,10177	2,44252	331,90771	0,000051
	4	0,00772	0,00681	1410,0	16,0	824000,0		0,01411	0,00725	8,24818	0,05982	1,43562	197,95623	0,000030
	5	0,00772	0,00754	738,0	16,0	824000,0		0,00768	0,00763	8,57575	0,06544	1,57047	205,81811	0,000033
12	1	0,00772	0,00687	233,0	16,0	824000,0		0,01349	0,00729	47,71766	0,34775	8,34593	1145,22376	0,000175
	2	0,00772	0,00633	416,0	16,0	824000,0		0,01864	0,00700	36,92738	0,25853	6,20468	886,25711	0,000130
	3	0,00772	0,00442	712,0	16,0	824000,0		0,04113	0,00591	47,59658	0,28153	6,75673	1142,31802	0,000142
	4	0,00772	0,00615	633,0	16,0	824000,0		0,02049	0,00690	26,67434	0,18410	4,41845	640,18419	0,000093
	5	0,00772	0,00537	726,0	16,0	824000,0		0,02894	0,00647	32,84180	0,21257	5,10160	788,20323	0,000107
15	1	0,00772	0,00504	560,0	16,0	824000,0		0,03290	0,00628	48,41256	0,30419	7,30066	1161,90149	0,000153
	2	0,00772	0,00461	686,0	16,0	824000,0		0,03844	0,00603	46,17110	0,27850	6,68407	1108,10633	0,000140
	3	0,00772	0,00787	312,0	16,0	824000,0		0,00500	0,00780	13,21564	0,10302	2,47253	317,17539	0,000052
	4	0,00772	0,00431	588,0	16,0	824000,0		0,04266	0,00585	59,77741	0,34968	8,39239	1434,65796	0,000176
	5	0,00772	0,00468	756,0	16,0	824000,0		0,03752	0,00607	40,89942	0,24836	5,96069	981,58613	0,000125
17	1	0,00772	0,00418	441,0	16,0	824000,0		0,04451	0,00577	83,17351	0,48007	11,52178	1996,16426	0,000242
	2	0,00772	0,00402	371,0	16,0	824000,0		0,04703	0,00567	104,45280	0,59213	14,21120	2506,86710	0,000298
	3	0,00772	0,00314	453,0	16,0	824000,0		0,06254	0,00509	113,76378	0,57877	13,89058	2730,33061	0,000292
	4	0,00772	0,00420	395,0	16,0	824000,0		0,04422	0,00578	92,25593	0,53361	12,80656	2214,14229	0,000269
	5	0,00772	0,00275	774,0	16,0	824000,0		0,07081	0,00481	75,37929	0,36275	8,70592	1809,10293	0,000183
20	1	0,00772	0,00272	288,0	16,0	824000,0		0,07147	0,00479	204,48757	0,97971	23,51304	4907,70169	0,000494
	2	0,00772	0,00273	402,0	16,0	824000,0		0,07125	0,00480	146,04184	0,70073	16,81750	3505,00414	0,000353
	3	0,00772	0,00172	397,0	16,0	824000,0		0,10014	0,00399	207,83973	0,83009	19,92228	4988,15357	0,000418
	4	0,00772	0,00270	448,0	16,0	824000,0		0,07192	0,00478	132,28035	0,63188	15,16518	3174,72844	0,000318
	5	0,00772	0,00146	352,0	16,0	824000,0		0,11048	0,00375	258,62604	0,97106	23,30555	6207,02504	0,000489
Control	1	0,00772	0,00771	0,0	16,0	824000,0	0,00007	0,00626					0,00000	
	2	0,00772	0,00855	0,0	16,0	824000,0	0,00643						0,00000	

<i>Control</i>											
3	0,00491	0,00599	0,0	16,0	824000,0	0,01241				0,0	
<i>sal6</i>	0,00002	0,00001	30,0	16,0	824000,0	-	0,05351	0,00001	1469,71951	0,01759	0,4 35273,26816 0,000009
<i>f1</i>	0,00002	0,00001	30,0	16,0	824000,0	0,04208	0,02699				0,0
<i>f2</i>	0,00002	0,00001	30,0	16,0	824000,0	0,03636	-				0,0
<i>f3</i>	0,00002	0,00002	30,0	16,0	824000,0	0,00251	-				0,0

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Table N: 15.Sept. Data and calculations for ingestion rate and grazing.

Treatment	Replicat e	beginning cells/ μ l		end cells/ μ l		volume of bottle (μ l)	Algal growth constant (k)	Grazing coefficient (g)	Average cell concentration / bottle (C)	The volume swept clear (F) (grazing rate)	Ingestion rate (cells eaten / copepod /hour) I	Ingestion rate (cells eaten / copepod /day) I	grazing F (ml ind.-1 day-1)	I (ug C / ind / day)
		$c1/*c1$	$c2/*c2$	no of ind.	$t1-t0$									
9	1	0,0089	0,00754	4	706,0	16,0	824000,0000	-0,00928	0,00822	-10,83565	-0,08906	-2,13741	-260,05553	0,00004
	2	0,0075	0,00754	7	661,0	16,0	824000,0000	0,00110	0,00755	1,37305	0,01037	0,24895	32,95327	0,00000
	3	0,0085	0,00754	5	618,0	16,0	824000,0000	-0,00651	0,00803	-8,67839	-0,06972	-1,67337	-208,28127	0,00003
	4	0,0079	0,00754	1	1220,0	16,0	824000,0000	-0,00164	0,00772	-1,10899	-0,00856	-0,20555	-26,61566	0,00000
	5	0,0071	0,00754	5	608,0	16,0	824000,0000	0,00473	0,00734	6,41098	0,04705	1,12925	153,86344	0,00002
12	1	0,0092	0,00754	8	131,0	16,0	824000,0000	-0,01162	0,00838	-73,05960	-0,61215	14,69149	1753,4303	0,00030
	2	0,0096	0,00754	0	423,0	16,0	824000,0000	-0,01374	0,00853	-26,75776	-0,22818	-5,47626	-642,18628	0,00011
	3	0,0077	0,00754	8	595,0	16,0	824000,0000	-0,00056	0,00766	-0,77414	-0,00593	-0,14224	-18,57938	0,00000
	4	0,0082	0,00754	4	597,0	16,0	824000,0000	-0,00420	0,00788	-5,79200	-0,04567	-1,09598	-139,00797	0,00002
	5	0,0060	0,00754	6	630,0	16,0	824000,0000	0,01505	0,00677	19,68172	0,13325	3,19810	472,36118	0,00006
15	1	0,0061	0,00754	2	766,0	16,0	824000,0000	0,01445	0,00680	15,54394	0,10573	2,53743	373,05444	0,00005
	2	0,0061	0,00754	0	674,0	16,0	824000,0000	0,01465	0,00679	17,90861	0,12162	2,91897	429,80676	0,00006
	3	0,0093	0,00754	7	283,0	16,0	824000,0000	-0,01220	0,00842	-35,52428	-0,29910	-7,17829	-852,58281	0,00015
	4	0,0045	0,00754	7	533,0	16,0	824000,0000	0,03263	0,00593	50,44284	0,29921	7,18112	1210,6281	0,00015
	5	0,0065	0,00754	0	693,0	16,0	824000,0000	0,01060	0,00701	12,60667	0,08835	2,12034	302,56010	0,00004
17	1	0,0062	0,00754	6	377,0	16,0	824000,0000	0,01298	0,00688	28,36826	0,19516	4,68390	680,83822	0,00009
	2	0,0059	0,00754	2	285,0	16,0	824000,0000	0,01647	0,00670	47,60733	0,31883	7,65181	1142,5758	0,00016

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3	0,00754	0,00638	433,0	16,0	824000,00000		0,01183	0,00694	22,50692	0,15623	3,74953	540,16617	0,000079			
4	0,00754	0,00505	336,0	16,0	824000,0		0,02644	0,00621	64,84834	0,40268	9,66443	1556,36000	0,00020			
5	0,00754	0,00330					0,05300	0,00513	56,93680	0,29212	7,01084	1366,4832	0,00014			
20	1	0,00754	0,00300	767,0	16,0	824000,0		0,05777	0,00497	160,8234	3	0,79853	19,16463	0	7	
	2	0,00754	0,00316	296,0	16,0	824000,0		0,05582	0,00503	116,7366	2	0,58741	14,09792	2	2	
	3	0,00754	0,00516	394,0	16,0	824000,0		0,02584	0,00624	62,63592	0,39069	9,37653	2801,6788	0,00029		
	4	0,00754	0,00360	340,0	16,0	824000,0		0,04638	0,00537	80,45089	0,43228	10,37484	1503,2622	0,00019		
	5	0,00754	0,00467	475,0	16,0	824000,0		0,05300	0,00513	56,93680	0,29212	7,01084	1930,8214	0,00021		
		<u>0,00754</u>	<u>0</u>	<u>398,0</u>	<u>16,0</u>	<u>824000,0</u>							1366,4832	0,00014		
													0	7		
<i>Control</i>	<i>1</i>	0,00754	0,00656	0,0	16,0	824000,0	0,00864	0,00140	160,8234	3	0,79853	19,16463	3859,7622	0,00040		
<i>Control</i>	<i>2</i>	0,00754	0,00970	0,0	16,0	824000,0	0,01577	0,05777	0,00497	116,7366	2	0,58741	14,09792	2801,6788	0,00029	
<i>Control</i>	<i>3</i>	0,00577	0,00550	0,0	16,0	824000,0	0,00292	0,02584	0,00624	62,63592	0,39069	9,37653	1503,2622	0,00019		
													0	7		

aa

Table O: 17.Sept. Data and calculations for ingestion rate and grazing.

Treatment	Replicate	beginning cells/ μ l	end cells/ μ l	no of ind.	t_{1-t_0}	volume of bottle (μ l)	Algal growth constant (k)	Grazing coefficient (g)	Average cell concentration / bottle (C)	The volume swept clear (F) (grazing rate)	Ingestion rate (cells eaten /copepod /hour) I	Ingestion rate (cells eaten /copepod /day) I	grazing F (ml ind.-1 day-1)	I (ug C / ind./day)
		$c1/*c1$	$c2/*c2$											
9	1	0,00663	0,00707	728,0	16,0	824000,0		-0,00260	0,00685	-2,94557	-0,02017	-0,48399	-70,69376	0,000010
	2	0,00663	0,00691	838,0	16,0	824000,0		-0,00121	0,00677	-1,19318	-0,00808	-0,19387	-28,63635	0,000004
	3	0,00663	0,00599	626,0	16,0	824000,0		0,00774	0,00630	10,18430	0,06421	1,54094	244,42321	0,000032
	4	0,00663	0,00572	1223,0	16,0	824000,0		0,01064	0,00616	7,16858	0,04418	1,06026	172,04602	0,000022
	5	0,00663	0,00562	643,0	16,0	824000,0		0,01171	0,00611	15,00630	0,09171	2,20105	360,15113	0,000046
12	1	0,00663	0,00630	143,0	16,0	824000,0		0,00458	0,00646	26,37302	0,17047	4,09123	632,95247	0,000086
	2	0,00663	0,00533	407,0	16,0	824000,0		0,01504	0,00596	30,43994	0,18130	4,35126	730,55864	0,000091
	3	0,00663	0,00382	656,0	16,0	824000,0		0,03593	0,00509	45,12947	0,22987	5,51683	1083,10726	0,000116
	4	0,00663	0,00455	582,0	16,0	824000,0		0,02488	0,00553	35,22351	0,19466	4,67190	845,36429	0,000098
	5	0,00663	0,00370	582,0	16,0	824000,0		0,03787	0,00502	53,61161	0,26926	6,46231	1286,67872	0,000136
15	1	0,00663	0,00410	713,0	16,0	824000,0		0,03148	0,00526	36,37918	0,19143	4,59427	873,10024	0,000096
	2	0,00663	0,00339	596,0	16,0	824000,0		0,04335	0,00483	59,93276	0,28941	6,94580	1438,38615	0,000146
	3	0,00663	0,00450	307,0	16,0	824000,0		0,02555	0,00550	68,57353	0,37707	9,04977	1645,76461	0,000190
	4	0,00663	0,00316	505,0	16,0	824000,0		0,04780	0,00468	77,99828	0,36498	8,75950	1871,95864	0,000184
	5	0,00663	0,00344	554,0	16,0	824000,0		0,04246	0,00486	63,15404	0,30690	7,36561	1515,69685	0,000155
17	1	0,00663	0,00378	281,0	16,0	824000,0		0,03657	0,00507	107,23057	0,54365	13,04763	2573,53371	0,000274
	2	0,00663	0,00321	263,0	16,0	824000,0		0,04666	0,00472	146,18643	0,68957	16,54980	3508,47425	0,000348
	3	0,00663	0,00231	226,0	16,0	824000,0		0,06727	0,00410	245,28401	1,00505	24,12128	5886,81632	0,000507
	4	0,00663	0,00228	246,0	16,0	824000,0		0,06807	0,00408	227,99786	0,92934	22,30413	5471,94856	0,000468
	5	0,00663	0,00192	577,0	16,0	824000,0		0,07877	0,00380	112,49632	0,42773	10,26554	2699,91160	0,000216
20	1	0,00663	0,00218	185,0	16,0	824000,0		0,07079	0,00400	315,28084	1,26235	30,29628	7566,74023	0,000636
	2	0,00663	0,00203	237,0	16,0	824000,0		0,07540	0,00389	262,13465	1,01855	24,44528	6291,23167	0,000513
	3	0,00663	0,00211	239,0	16,0	824000,0		0,07305	0,00395	251,84692	0,99358	23,84596	6044,32599	0,000501
	4	0,00663	0,00166	318,0	16,0	824000,0		0,08794	0,00359	227,86306	0,81778	19,62674	5468,71347	0,000412
	5	0,00663	0,00175	257,0	16,0	824000,0		0,08473	0,00366	271,66867	0,99470	23,87282	6520,04814	0,000501
Control 1		0,00663	0,00762	0,0	16,0	824000,0	0,00872	0,00576				0,0		
Control 2		0,00663	0,00742	0,0	16,0	824000,0	0,00702					0,0		

bb

<i>Control 3</i>	0,00530	0,00544	0,0	16,0	824000,0	0,00155					0,0
<i>sal6</i>	0,00035	0,00017	30,0	16,0	40000,0	-	0,01156	0,00025	15,41105	0,00380	0,09120 369,86524 0,000002
<i>f1</i>	0,00035	0,00018	30,0	16,0	40000,0	0,04208	0,02699	-			0,0
<i>f2</i>	0,00035	0,00020	30,0	16,0	40000,0	0,03636	-				0,0
<i>f3</i>	0,00034	0,00033	30,0	16,0	40000,0	0,00251	-				0,0

Appendix E. Elemental composition

Appendix E contains all data sampled for calculations of elemental composition.

Table S: Randomly sampled blank capsules used to create a mean value, used in the estimation of the weight of polyps sampled for the analysis of elemental composition.

<i>Capsule number</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>	<i>9</i>	<i>10</i>
<i>Capsule weight (mg)</i>	31,55	31,11	31,12	31,65	30,94	31,68	31,05	32,31	31,37	31,03
<i>Mean (mg) ± SD</i>	31,38±0,42									

Experiment 1

Table T: Polyps used for the analysis of elemental composition from experiment 1. Polyp DM (mg) is based on the capsule weight (mg) with the mean (mg) (Table S) subtracted.

Treatment(C°)	Replicate	Polyps capsule $^{-1}$	Capsule weight (mg)	Poplyp DM (mg)	Polyp DM (μ g)
9	1,00	5,00	33,50	2,12	2122,90
	3,00	6,00	33,65	2,27	2272,90
	5,00	5,00	33,30	1,92	1919,90
	2,00	6,00	33,34	1,96	1959,90
	4,00	5,00	33,14	1,76	1759,90
12	1,00	5,00	33,56	2,18	2179,90
	3,00	5,00	33,70	2,32	2316,90
	5,00	5,00	33,61	2,23	2231,90
	2,00	5,00	33,04	1,66	1656,90
	4,00	6,00	33,80	2,42	2421,90
15	1,00	5,00	33,78	2,40	2402,90
	3,00	4,00	32,17	0,79	787,90
	5,00	6,00	33,93	2,55	2552,90
	2,00	5,00	33,32	1,94	1940,90
	4,00	5,00	33,09	1,71	1705,90
17	1,00	6,00	33,70	2,32	2322,90
	3,00	5,00	33,55	2,17	2172,90
	5,00	5,00	33,70	2,32	2316,90
	2,00	8,00	33,73	2,35	2349,90
	4,00	6,00	34,11	2,73	2733,90
20	1,00	5,00	33,79	2,41	2413,90
	3,00	5,00	33,84	2,46	2455,90
	5,00	7,00	33,80	2,42	2419,90
	2,00	5,00	33,56	2,18	2177,90
	4,00	6,00	32,86	1,48	1479,90

Table U: C and N values from the elemental analysis for experiment 1. Calculations of C polyp DM⁻¹(%) and N polyp DM⁻¹(%) are based on the C capsule⁻¹ (µg) and N capsule⁻¹(µg) values given in this table, and the polyp DM (µg) in Table T. Calculations for C polyp ⁻¹ (µg) and N polyp ⁻¹ (µg) are based upon the C capsule⁻¹ (µg) and N capsule⁻¹(µg) and the polyps capsule⁻¹ in Table T.

Treatment(C°)	Replicate	Polyp DM (µg)	C capsule ⁻¹ (µg)	C polyp ⁻¹ (µg)	Mean C polyp ⁻¹ (µg)	C polyp DM ⁻¹ (%)	Mean C polyp DM ⁻¹ (%)	N capsule ⁻¹ (µg)	N polyp ⁻¹ (µg)	Mean N polyp ⁻¹ (µg)	N polyp DM ⁻¹ (%)	Mean N polyp DM ⁻¹ (%)	Moles C (10 ⁻⁷)	Moles N (10 ⁻⁷)	C/N ratio(mol)	Mean C/N (mol)
9	1	2122,9	16,3	3,3	2,0±1,1	0,8	0,5±0,3	3,2	0,6	0,5±0,2	0,2	0,1±0,1	13,6	2,3	5,9	4,7±0,8
	3	2272,9	15,9	2,7		0,7		3,9	0,7		0,2		13,2	2,8	4,8	
	5	1919,9	11,4	2,3		0,6		2,8	0,6		0,2		9,5	2,0	4,8	
	2	1959,9	5,3	0,9		0,3		1,5	0,3		0,1		4,4	1,1	4,1	
	4	1759,9	3,5	0,7		0,2		1,1	0,2		0,1		2,9	0,8	3,7	
	1	2179,9	7,0	1,4	3,0±1,0	0,3	0,7±0,3	1,3	0,3	0,6±0,2	0,1	0,2±0,1	5,8	0,9	6,3	5,7±0,7
12	3	2316,9	18,0	3,6		0,8		3,6	0,7		0,2		15,0	2,6	5,8	
	5	2231,9	14,1	2,8		0,6		3,3	0,7		0,2		11,7	2,4	5,0	
	2	1655,9	15,9	3,2		1,0		3,7	0,7		0,2		13,2	2,6	5,0	
	4	2421,9	22,9	3,8		1,0		4,2	0,7		0,2		19,1	3,0	6,4	
	1	2402,9	23,2	4,6	3,6±1,2	1,0	1,0±0,2	4,2	0,8	0,7±0,3	0,2	0,2±0,1	19,3	3,0	6,4	6,4±1,1
	3	787,9	6,7	1,7		0,9		1,2	0,3		0,2		5,6	0,9	6,5	
15	5	2552,9	20,2	3,4		0,8		4,1	0,7		0,2		16,8	2,9	5,8	
	2	1940,9	20,5	4,1		1,1		2,9	0,6		0,2		17,1	2,1	8,2	
	4	1705,9	21,7	4,3		1,3		4,8	1,0		0,3		18,1	3,4	5,3	
	1	2322,9	26,7	4,5	6,7±4,4	1,2	1,8±1,5	4,9	0,8	1,4±0,9	0,2	0,4±0,3	22,2	3,5	6,4	5,6±0,7
	3	2172,9	32,6	6,5		1,5		6,5	1,3		0,3		27,1	4,6	5,9	
	5	2316,9	5,5	1,1		0,2		1,4	0,3		0,1		4,6	1,0	4,6	
17	2	2349,9	101,9	12,7		4,3		21,2	2,7		0,9		84,8	15,1	5,6	
	4	2733,9	52,4	8,7		1,9		11,0	1,8		0,4		43,6	7,9	5,6	
	1	2413,9	116,2	23,2	16,7±8,8	4,8	4,3±2,0	23,9	4,8	3,4±1,8	1,0	0,9±0,4	96,8	17,1	5,7	5,7±4,1
	3	2455,9	28,2	5,6		1,2		5,9	1,2		0,24		23,5	4,2	5,6	
	5	2419,9	148,9	21,3		6,2		30,2	4,3		1,3		124,0	21,6	5,8	
	2	2177,9	123,2	24,6		5,7		24,6	4,9		1,1		102,6	17,6	5,8	
20	4	1479,9	52,3	8,7		3,5		10,4	1,7		0,7		43,5	7,4	5,9	

Experiment 2

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Table V: Polyps used for the analysis of elemental composition from experiment 2. Polyp DM (mg) is based on the capsule weight (mg) with the mean (mg) (Table S) subtracted.

Treatment (C°)	Replicate	Polyps capsule ⁻¹	Capsule weight (mg)	Polyp weight (mg)	Polyp DM (µg)
9	1,00	5,00	32,89	1,51	1505,90
	3,00	5,00	34,04	2,66	2655,90
	5,00	5,00	35,87	4,48	4484,90
	2,00	5,00	35,83	4,45	4445,90
	4,00	5,00	34,91	3,53	3533,90
	1,00	5,00	35,00	3,62	3618,90
12	3,00	5,00	35,79	4,41	4408,90
	5,00	5,00	35,06	3,68	3683,90
	2,00	5,00	34,30	2,92	2922,90
	4,00	5,00	34,15	2,76	2764,90
	1,00	5,00	33,51	2,13	2127,90
	3,00	5,00	33,56	2,18	2181,90
15	5,00	5,00	33,77	2,39	2390,90
	2,00	5,00	34,03	2,65	2646,90
	4,00	5,00	32,63	1,25	1250,90
	1,00	5,00	37,30	5,92	5918,90
	3,00	5,00	33,22	1,84	1836,90
	5,00	5,00	33,68	2,30	2296,90
17	2,00	5,00	33,09	1,71	1713,90
	4,00	5,00	32,80	1,42	1415,90
	1,00	5,00	33,23	1,85	1850,90
	3,00	5,00	33,07	1,68	1684,90
	5,00	5,00	34,29	2,91	2912,90
	2,00	5,00	34,67	3,29	3287,90
20	4,00	5,00	32,63	1,25	1251,90

Table W: C and N values from the elemental analysis for experiment 2. Calculations of C polyp DM⁻¹(%) and N polyp DM⁻¹(%) are based on the C capsule⁻¹(µg) and N capsule⁻¹(µg) values given in this table, and the polyp DM (µg) in Table V. Calculations for C polyp⁻¹(µg) and N polyp⁻¹(µg) are based upon the C capsule⁻¹(µg) and N capsule⁻¹(µg) and the polyps capsule⁻¹ in Table V.

Treatment (C°)	Replicate	Polyp DM (µg)	C capsule ⁻¹ (µg)	C polyp ⁻¹ (µg)	Mean C polyp ⁻¹ (µg)	C polyp DM ⁻¹ (%)	Mean C polyp DM ⁻¹ (%)	N capsule ⁻¹ (µg)	N polyp ⁻¹ (µg)	Mean N polyp ⁻¹ (µg)	N polyp DM ⁻¹ (%)	Mean N polyp DM ⁻¹ (%)	Moles C (10 ⁻⁷)	Moles N (10 ⁻⁷)	C:N ratio(mol)	mean C:N ratio (mol)
9	1	1505,9	172,1	34,4	41,3±5,3	11,4	7,0±2,7	38,5	7,7	9,3±1,3	2,6	1,6±0,6	143,3	27,5	5,2	5,2±0,1
	3	2655,9	190,5	38,1		7,2		43,1	8,6		1,6		158,6	30,8	5,2	
	5	4484,9	204,6	40,9		4,6		44,6	8,9		1,0		170,4	31,8	5,4	
	2	4445,9	234,8	47,0		5,3		53,3	10,7		1,2		195,5	38,1	5,1	
	4	3533,9	230,6	46,1		6,5		52,9	10,6		1,5		192,0	37,8	5,1	
12	1	3618,9	485,9	97,2	95,1±39,6	13,4	13,3±4,2	107,5	21,5	21,4±8,8	3,0	3,0±0,9	404,6	76,8	5,3	5,2±0,1
	3	4408,9	691,5	138,3		15,7		154,5	30,9		3,5		0,0	0,0	5,2	
	5	3683,9	590,1	118,0		16,0		133,6	26,7		3,6		491,3	95,4	5,2	
	2	2922,9	444,2	88,8		15,2		99,9	20,0		3,4		369,8	71,3	5,2	
	4	2764,9	166,1	33,2		6,0		38,4	7,7		1,4		138,3	27,4	5,0	
15	1	2127,9	20,7	4,1	3,4±1,3	1,0	0,9±0,6	4,8	1,0	0,8±0,3	0,2	0,2±0,2	17,2	3,4	5,0	4,9±0,2
	3	2181,9	21,5	4,3		1,0		5,1	1,0		0,2		17,9	3,6	4,9	
	5	2390,9	11,8	2,4		0,5		2,7	0,5		0,1		9,8	1,9	5,1	
	2	2646,9	8,1	1,6		0,3		1,9	0,4		0,1		6,7	1,4	5,0	
	4	1250,9	22,5	4,5		1,8		5,6	1,1		0,5		18,7	4,0	4,7	
17	1	5918,9	1097,9	219,6	45,7±97,2	18,6	4,2±8,0	248,8	49,8	10,4±22,0	4,2	1,0±1,8	914,1	177,6	5,2	4,9±0,5
	3	1836,9	5,3	1,1		0,3		1,5	0,3		0,1		4,41	1,1	4,1	
	5	2296,9	14,5	2,9		0,6		3,5	0,7		0,2		12,1	2,5	4,8	
	2	1713,9	11,4	2,3		0,7		2,6	0,5		0,2		9,5	1,9	5,1	
	4	1415,9	12,2	2,4		0,9		2,6	0,5		0,2		10,2	1,9	5,5	
20	1	1850,9	59,5	11,9	21,6±17,0	3,2	4,9±2,6	13,5	2,7	5,0±4,1	0,7	1,1±0,6	49,5	9,6	5,1	5,1±0,1
	3	1684,9	90,9	18,2		5,4		20,2	4,0		1,2		75,7	14,4	5,3	
	5	2912,9	258,3	51,7		8,9		61,6	12,3		2,1		215,1	44,0	4,9	
	2	3287,9	67,2	13,4		2,0		15,1	3,0		0,5		56,0	10,8	5,2	
	4	1251,9	64,8	13,0		5,2		14,7	2,9		1,2		54,0	10,5	5,1	

Appendix F. Polyp survival

Appendix F contains the number of observed live polyps petri dish^{-1} for all sampled days of experiment 1 and experiment 2.

Polyp survival experiment 1

Table X: Observed number of live polyps for experiment 1 (4.sep-18.sep). Data was collected every second day, after termination of the settling phase.

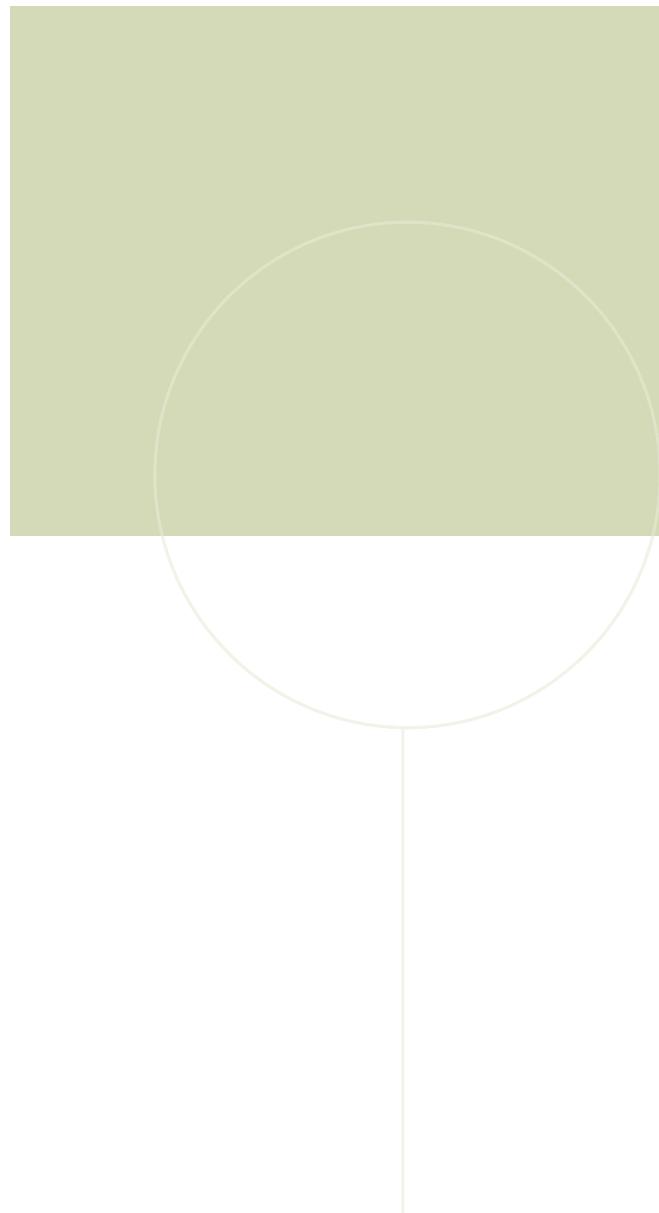
Treatment(C°)	9					12					15					17					20				
	Replicate	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4
4.sep	756	866	817	1369	917	723	622	1130	707	869	509	670	567	850	1151	779	516	736	678	1174	658	528	609	692	602
6.sep	713	881	422	1252	566	696	447	1062	602	901	364	507	347	454	740	374	446	613	690	979	457	322	432	542	457
8.sep	820	898	803	1593	755	387	546	892	684	882	824	819	473	647	805	515	445	540	654	671	221	300	303	426	364
10.sep	568	632	645	1216	674	229	479	851	698	927	858	837	371	548	834	467	363	450	478	582	269	249	232	404	231
12.sep	641	709	730	1409	738	233	416	712	633	726	560	686	312	588	756	441	371	453	395	774	288	402	397	448	352
14.sep	706	661	618	1220	608	131	423	595	597	630	766	674	283	533	693	377	285	433	336	767	296	394	340	475	398
16.sep	728	838	626	1223	643	143	407	656	582	582	713	596	307	505	554	281	263	226	246	577	185	237	239	318	257
18.sep	581	606	563	1020	490	194	381	611	575	727	439	431	238	438	389	255	276	250	237	523	123	240	208	244	215

Polyp survival experiment 2

Table Y: Observed number of live polyps for experiment 2 (25.sep-20.nov). Data was collected once a week, except for (25.sep-28sep) representing the settling phase where data collection was done daily.

Treatment(C°)	9					12					15					17					20				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Replicate	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
25.sep	855	1007	NA	970	383	351	692	158	711	577	89	487	47	5	300	104	313	427	744	329	537	88	822	103	216
26.sep	521	999	1228	890	2173	593	458	199	177	386	553	466	453	NA	323	123	484	350	767	671	481	676	1004	248	584
27.sep	826	745	1206	877	1759	625	276	331	391	728	989	460	675	375	325	234	161	373	760	318	377	273	1016	557	452
28.sep	734	757	561	923	1335	642	220	342	737	553	433	427	701	622	393	433	171	397	710	668	713	287	777	588	512
03.okt	1309	1021	1324	1369	2010	822	558	434	831	755	1035	512	941	632	479	455	371	516	671	856	956	568	671	887	674
10.okt	1218	840	935	1094	1475	614	465	404	716	659	1266	497	881	629	464	314	318	489	599	676	680	353	420	642	440
16.okt	1200	809	939	1051	1439	492	481	427	523	558	908	417	596	511	397	329	293	380	480	520	598	303	395	521	422
25.okt	1000	679	739	813	1048	462	381	341	434	460	532	254	367	381	262	210	227	456	327	526	394	289	301	482	331
30.okt	909	649	670	759	1000	408	315	279	323	398	307	215	413	364	288	183	134	267	334	391	474	243	301	350	330
06.nov	688	538	601	724	916	367	297	267	338	373	217	211	308	316	315	163	122	134	272	318	336	178	255	278	240
13.nov	618	486	502	556	629	289	231	260	297	358	143	154	208	218	166	174	97	138	121	214	202	91	155	185	145
20.nov	568	443	477	497	582	265	248	269	293	338	117	138	156	178	130	141	76	106	111	178	190	99	92	145	123

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