

Stable isotopes as a way to assess the trophic interactions of jellyfish, western Baltic Sea

Master's Thesis

MSc Biological Oceanography:
Helmholtz-Zentrum für Ozeanforschung Kiel
und
der Christian-Albrechts-Universität

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July 25, 2012

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1. Summary

1.1 Abstract

Jellyfish blooms, which occur in many coastal areas, are usually triggered by a shift in the aquatic system (*e.g.*, climate change, eutrophication, and commercial over-fishing). These blooms often result in competition with higher-trophic-level organisms. Because jellyfish are critical drivers of ecosystem change and are ubiquitous in the oceans and many estuaries, it is important to understand their trophic ecology. Stable isotopes (SI) are commonly used to trace marine food webs, and observe how it is affected by changes in the environment. So far, stable isotopes (SI) were applied as tracers of the marine food web in order to gain information about the origin, pathways, and fate of organic matter.

In this study, stable isotope analysis (SIA) was used to assess the trophic ecology of jellyfish, both in the field and in the laboratory. Firstly, a field study in the Kiel Fjord was designed to analyze trophic interactions of the invasive ctenophore, *Mnemiopsis leidyi* A. Agassiz, with the native jellyfish, *Aurelia aurita* and *Cyanea capillata*. Secondly, an experiment was designed to measure for the isotopic turnover rate and fractionation rate for nitrogen (N) and carbon (C) in *M. leidyi* via a food alteration experiment.

For the first time in several years, during the time of the planned field study, *M. leidyi* was not present in the Kiel Fjord; however, samples of *A. aurita* and *C. capillata* were obtained throughout the season from June to October, and C, N, and sulfur (S) isotope compositions were determined. *A. aurita* showed evidence for a change in diet source over time. In particular, $\delta^{13}\text{C}$ values (δ is the measure of the heavy isotope to the light isotope in a given sample) indicated a diet switch; in addition, $\delta^{15}\text{N}$ showed a change in diet trophic position over the season (2011). Additionally, $\delta^{34}\text{S}$ showed a change from a more pelagic based diet to a more benthic based diet.

For the second study (experimental period of 44-days), fractionation rates were estimated by subtracting the δ value of the prey from the δ value of the animal ($\Delta_{\text{ANIMAL-PREY}} = \delta X_{\text{ANIMAL}} - \delta X_{\text{PREY}}$). There was high variance in the prey isotopic values, therefore, the overall mean isotope values for the two prey types were compared with the daily mean values for the consumer. The isotope values for *M. leidyi*, when fed on *Acartia tonsa*, were $\delta^{13}\text{C}$: 0.26‰ and $\delta^{15}\text{N}$: 2.38‰. While the isotope values for *M. leidyi*, when fed on *Artemia salina*, were $\delta^{13}\text{C}$: 2.14‰ and $\delta^{15}\text{N}$: 6.3‰. *A. salina* has a lower nutritional value and does not sustain growth of consumers over a significant period of time, which caused higher $\delta^{15}\text{N}$ fractionation.

Unfortunately, the turnover rate could not be estimated due to several unforeseen factors, such as strong changes in growth and consumption of own tissue due to starvation. Since this is novel work on *M. leidyi*, this study's work should be replicated and verified.

1.2 Zusammenfassung

Starke Quallenvermehrungen, welche in vielen Küstenregionen auftreten, werden meistens durch eine Verschiebung im Aquatischen System ausgelöst (z.B. Klimawandel, Eutrophierung und Über-Fischung). Diese starken Anstiege in den Quallenpopulationen führen oft dazu, dass die entsprechenden Populationen in Konkurrenz mit Organismen höherer Trophie-Ebenen treten. Da Quallen kritische Faktoren im Wandel von Ökosystemen sind und ubiquitär in den Ozeanen und vielen Estuaren vorkommen, ist es wichtig ihre trophische Ökologie zu verstehen. Stabile Isotope (SI) werden gemeinhin genutzt, um marine Nahrungsnetze zu verfolgen und um zu beobachten, wie sie durch Wechsel in der Umwelt beeinflusst werden. Bisher wurden stabile Isotope angewendet um Informationen über die Herkunft, Weitergabe und die Zersetzung organischen Materials in marinen Nahrungsnetzen zu erhalten.

In dieser Studie wurde Stabile Isotopen Analyse (SIA) genutzt, um die trophische Ökologie der Quallen sowohl in freier Natur als auch unter Laborbedingungen zu untersuchen. Eine Feldstudie wurde erstellt, um die trophischen Interaktionen der invasiven Ctenophore, *Mnemiopsis leidyi* A. Agassiz, mit den einheimischen Quallen, *Aurelia aurita* und *Cyanea capillata* zu untersuchen. Im Anschluss wurde ein Experiment durchgeführt, um die Isotopen-Durchsatzrate und Fraktionierung von Stickstoff (N) und Kohlenstoff (C) in *M. leidyi* im Rahmen eines Futteränderungsversuches zu messen.

Zum ersten Mal in mehreren Jahren war *M. leidyi* zur Zeit der geplanten Feldstudie nicht in der Kieler Förde vorhanden; jedoch wurden *A. aurita* und *C. capillata* die Saison hindurch von Juni bis Oktober beprobt und C, N und Schwefel (S) Isotopenzusammensetzungen wurden bestimmt. *A. aurita* zeigte Hinweise auf einen Wechsel der Nahrungsquelle über die Zeit. Besonders die $\delta^{13}\text{C}$ -Werte (δ ist das Verhältnis von schweren Isotopen zu leichten Isotopen in einer gegebenen Probe) deuten auf einen Wechsel hin, außerdem weisen die $\delta^{15}\text{N}$ -Werte auf einen Wechsel der trophischen Position der Nahrung im Laufe der Saison (2011) hin. Zusätzlich zeigen die $\delta^{34}\text{S}$ einen Wechsel von einer hauptsächlich pelagischen zu einer hauptsächlich benthischen Nahrungszusammensetzung an.

Für die zweite Studie (Experimentdauer 44 Tage), wurden Fraktionierungsraten durch Subtrahieren des δ Wertes der Beute vom δ Wert des Tieres ($\Delta_{\text{ANIMAL-PREY}} = \delta X_{\text{ANIMAL}} - \delta X_{\text{PREY}}$) angenähert. Es gab eine hohe Varianz in den isotopischen Werten der Beute, deshalb wurden der Gesamtdurchschnitt der Isotopen Werte der zwei Beute Typen mit den täglichen Mittelwerten der Konsumenten verglichen. Die Isotopen Werte von *M. leidyi* entsprachen $\delta^{13}\text{C}$: 0.26‰ and $\delta^{15}\text{N}$: 2.38‰, wenn sie mit *Acartia tonsa* gefüttert wurde. Bei Fütterung mit *Artemia salina* betrug die Werte $\delta^{13}\text{C}$: 2.14‰ and $\delta^{15}\text{N}$: 6.3‰. *A. salina* hat einen geringeren Nährwert und kann das Wachstum nicht über längere Zeit aufrecht erhalten, was zu einer höheren Fraktionierung von $\delta^{15}\text{N}$ führt.

Auf Grund unvorhergesehener Faktoren wie starken Wechseln in Wachstumsrate und der Aufnahme von eigenem Gewebe durch Hunger, konnte die Durchsatzrate nicht bestimmt werden. Da diese Arbeit die erste auf diesem Gebiet ist, sind weitere Untersuchungen definitiv anzuraten.

2. Introduction

2.1 The Global Importance of Jellyfish for Ecosystem Dynamics

Carnivorous gelatinous zooplankton are known for forming large and dominating population blooms in many coastal areas (Brodeur *et al.*, 1999; Link & Ford, 2006; Lynam *et al.*, 2006; Pitt *et al.*, 2007). This group includes jellyfish (*i.e.*, cnidarian medusa), ctenophore sp. (*i.e.*, comb jellies), and pelagic tunicates. Throughout this thesis, I use the term *jellyfish* to refer to the various jellyfish and ctenophore species.

Blooms in a jellyfish population are usually triggered by a shift in the aquatic system (*e.g.*, climate change, eutrophication, and commercial over-fishing), which can result in competition with higher-trophic-level organisms (Daskalov, 2002). Because jellyfish are critical drivers of ecosystem change (Molinero *et al.*, 2005; Hay, 2006; Lynam *et al.*, 2006) and are ubiquitous in the oceans and many estuaries, it is important to study their trophic ecology in order to understand both the formation and structure of their blooms, role in the transfer of nutrients between benthic and pelagic food webs, and to assess the effects on plankton communities (Pitt *et al.*, 2008).

The influence of jellyfish on the planktonic food web may be significant in environments where jellyfish appear in large densities. A review by Purcell *et al.* (2007) reported increasing problems with jellyfish blooms that may have direct negative impacts on humans by interfering with tourism, aquaculture, and fishing operations, as well as by clogging coastal industrial water intakes (Purcell *et al.*, 2007; Turk *et al.*, 2008). Additionally, studies have shown links between harmful algal blooms, jellyfish, and overfishing (Daskalov, 2002; Turk *et al.* 2008). Moreover, it is known that jellyfish prey on meso- and microzooplankton (Stoecker *et al.*, 1987; Sullivan *et al.*, 1994; Malej *et al.*, 2007; Lo & Chen, 2008; Turk *et al.*, 2008) with selective feeding on slower moving organisms (Williams & Johnson, 2005; Javidpour *et al.*, 2009b), but little is understood about the trophic interaction between the microbial loop and jellyfish predation on different trophic levels (Turk *et al.*, 2008). It has been suggested that jellyfish biomass may stimulate bacterial growth, bacterial production and ectoenzymatic activities in the water column through the release of nutrients and dissolved organic matter (Schneider, 1989; Hansson & Norrman, 1995; Titelman *et al.*, 2006; Turk *et al.*, 2008). This is in contrast to the classical view that jellyfish were a 'dead end' in the food web (Verity & Smetacek, 1996). In order to determine the role of jellyfish in the food web, it is important to gain a thorough understanding of their trophic ecology. One way to trace a food web is through biochemical tracers, such as stable isotopes.

2.2 Applicability of Stable Isotopes for Assessing Trophic Interactions on Jellyfish Ecology

Stable isotopes (SI) are commonly used to elucidate trophic ecology (Pitt *et al.*, 2008). Isotopes are forms of the same element with different numbers of neutrons, resulting in different atomic masses. They are considered stable if they are not known to decay radioactively. For elements with more than one stable isotope—the most important ones for biology being carbon, nitrogen, sulfur, oxygen, and hydrogen (Fry, 2006)—one can measure the isotope ratio, which refers to the ratio of a heavy isotope to a light isotope (*e.g.*, $^{13}\text{C}/^{12}\text{C}$). The SI of the consumer reflect those of its prey—“you are what you eat” (Wada & Hattori, 1990; Fry 2006). Autotrophic SI ratios most directly reflect the SI ratios of the environment and thus are the baseline SI ratios of the food web (Peterson & Fry, 1987). Information about an individual’s trophic ecology (Fry, 2006), migratory patterns (Kelly & Finch, 1998), habitat use (Layman *et al.*, 2007), and other significant characteristics can be inferred by measuring the SI of that individual. For example, the isotopic ratios of C, N, and S in primary producers and in consumers have proven useful in elucidating organic matter flow and trophic relationships in estuaries and coastal benthic communities (Parker, 1964; Peterson & Howarth, 1987; Machás & Santos, 1999; Petersen, 1999).

SI are advantageous for studying compositions of natural materials because SI are commonly occurring (Peterson & Fry, 1987; Savage, 2005) and can act as tracers that provide information about the origin, pathways and fate of organic matter (Lajtha & Michener, 1994; Robinson, 2001; Savage, 2005). Furthermore, these tracers can differentiate between what is assimilated and what is simply ingested, provide an analysis of diet integration over time, and identify source contributions by tracing the chemical compositions within animal tissue of a consumer and its prey.

Finally, excretion, respiration and growth rates affect SI of organisms. For example, *Figure 1* depicts the classical SI conceptual model of trophic enrichment per trophic level in marine food pathways using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Arugto-Muñoz, 2007). In the heavy isotope (^{13}C), some minor enrichment (fractionation) of 0.1-1‰ (France & Peters, 1997) occurs because the consumer preferentially eliminates ^{12}C during respiration (Pitt *et al.*, 2008). In addition, nitrogen isotope values, typically have fractionation differences of 2-4‰ between a consumer and its prey (DeNiro & Epstein, 1981; Owens, 1987; Peterson & Fry, 1987; Vander Zanden *et al.*, 1997; Post, 2002; Vanderkluft & Ponsard, 2003). This enrichment per trophic level makes $\delta^{15}\text{N}$ a good indicator of food web dynamics (McCutchan *et al.*, 2003). Fractionation is the shift in isotopic values from a diet source to the consumer (Pitt *et al.*, 2009).

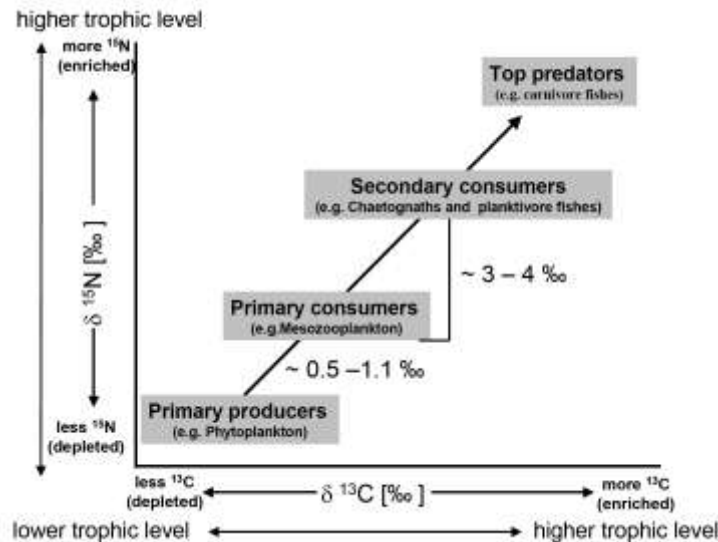


Figure 1: Classical SIA conceptual model of trophic enrichment per trophic level in marine food pathways using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Figure taken from Arugto-Muñoz, 2007). Trophic ecology primarily uses C and N isotopes to assess the diet and trophic position of organisms. C isotope ratios are predictably similar to the isotopic ratios of their diets (varying 0.1-1‰), while N isotopes serve as indicators of trophic position and are enriched in ^{15}N relative to their diets 2-4‰.

Comparisons of the SI values of a consumer over a season can indicate its prey-type and whether it feeds on multiple trophic levels (Kling *et al.*, 1992; Cabana & Rasmussen, 1994; Ponsard & Ardit, 2000). SI values not only represent what an organism has consumed, but can also indicate the mean number of trophic transfers that occurred between the baseline of a food web (i.e. primary producers) and the organism (Ponsard & Ardit, 2000).

SI ratios are altered in predictable ways during transfer to higher trophic levels via fractionation and turnover rates among groups of organisms (Malej *et al.*, 1993). Fractionation rates are important in order to accurately identify dietary sources and to estimate the number of trophic levels in an ecosystem. Changes in SI values are not reflected immediately in the tissue of an organism, as the molecules constituting the organism take time to "turn over". Turnover rates are important to predict the temporal relationship between predator and its prey assimilation and to observe seasonal variations in food webs (Sakano *et al.*, 2005).

For many groups of animals, turnover rates and fractionation rates are already available; however, to date, they are completely lacking for gelatinous zooplankton (Tieszen *et al.*, 1983; Hobson & Clark, 1992; MacAvoy *et al.*, 2001; Bosley *et al.*, 2002; Ayliffe *et al.*, 2004; Philips & Eldridge, 2005).

2.3 *The Biology of Mnemiopsis leidyi*

Due to the recent invasion history of the ctenophore *M. leidyi*, the extent of its impact on trophic pathways is of particular interest. For marine food webs, the ecological impact comes from both direct feeding on fish larvae and eggs and resource competition for mesozooplankton (Javidpour *et al.*, 2008) with higher-trophic-level organisms. In their native habitat, along the east coast of North and South America (41° N - 43° S), *M. leidyi* populations are controlled by predators and competition for food resources (Purcell *et al.*, 2001). This species is an efficient invader because it is a simultaneous hermaphrodite and is able to survive in a wide range of ecological conditions (i.e. temperature (0-32 °C), salinity (<2-38 psu)) (Purcell *et al.*, 2001; Javidpour *et al.*, 2006; Haslob *et al.*, 2007, Kube *et al.*, 2007). It was not until their invasion of the Black Sea, via ballast water tanks in the 1980s, that the magnitude of their predatory potential became clear. This invasion, in addition to over-fishing, was thought to have led to the widespread fisheries collapses and a dramatic change in the food pathways in this area. There is still controversy in the literature about whether *M. leidyi* was a symptom or driver of ecosystem change (Burrell & Van Engel, 1976; Purcell, 1985; Monteleone & Duguay, 1988; Purcell *et al.*, 1994; Shiganova, 1998; Shiganova, 2001; Haslob *et al.*, 2007; Javidpour *et al.*, 2009b; Shiganova, 2010; Hamer *et al.*, 2011)

In 2006, *M. leidyi* was first documented in the Baltic Sea, the North Sea and the European North Atlantic coastal waters (Faasse & Bayha, 2006; Javidpour *et al.*, 2006; Boresma *et al.*, 2007; Tendal *et al.*, 2007). Javidpour *et al.* (2009b) assessed the impacts of *M. leidyi* on plankton communities in the Kiel Fjord (south-western Baltic Sea) and observed clear seasonal differences in food preference. Furthermore, a study done by Javidpour *et al.* (2009b) observed a strong and complex competitive interaction between *A. aurita* (a cnidarian jellyfish native to the Baltic Sea) and *M. leidyi* during the period of co-occurrence (July-September) in the Kiel Fjord (Figure 2).

A. aurita, the moon jellyfish, is a scyphomedusae which inhabits coastal waters from 50°N to 50°S (Rackmil, 2009). This species exhibits a bi-phasic life cycle containing both polyp and medusae stages (Arai, 1997). During their medusae stage, *A. aurita*, are opportunistic zooplankton feeders (Ishii & Tanaka, 2001) and are often regarded as top predators (Möller, 1980; Rüsågård *et al.*, 1995; Hansson, 1997). In the Kiel Fjord, *A. aurita* medusae often first appear in May, with peak abundance in July or August and are present until September (Figure 2).

The studies by Hansson (1997) and Javidpour *et al.* (2009b) used gut content analysis, which provides diet information at only a single time point and not about the material that is

actually assimilated by the organism. In order to account for more than the feeding activity, biochemical tracers (stable isotopes and fatty acids) have been employed (Pitt *et al.*, 2008).

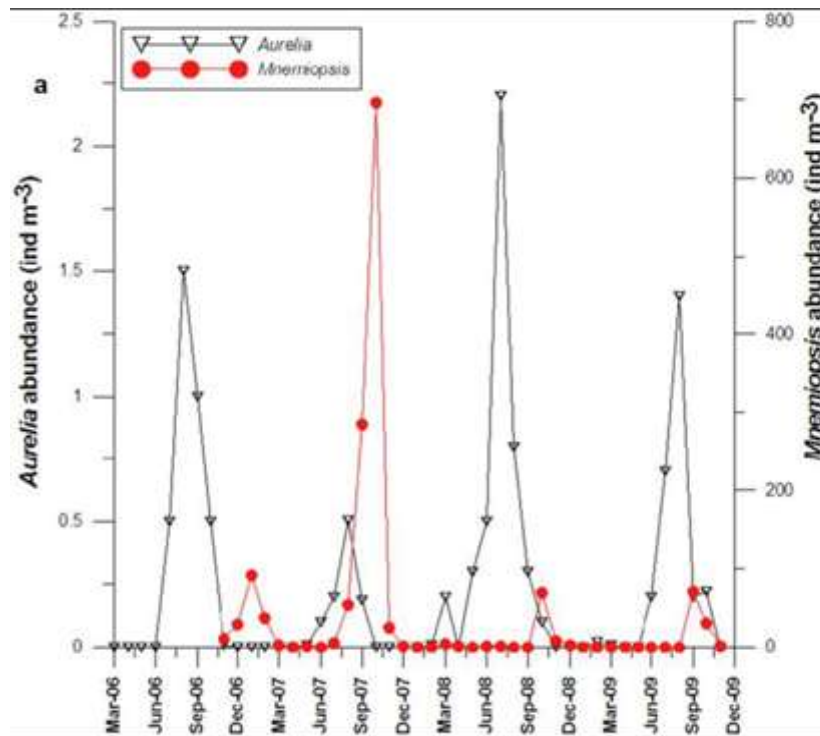


Figure 2: Seasonal distribution of *A. aurita* and *M. leidyi* gained from field observation data during 2007-09 in Kiel Fjord (Javidpour *et al.*, unpublished).

2.4 Study aims

Stable isotope analysis (SIA) was used to assess the trophic ecology of jellyfish in two different studies. Firstly, different jellyfish taxa were sampled over a season (2011) to examine their food spectra and compared to a baseline species, *Mytilus edulis*. Secondly, an experiment was used to measure for the first time the isotopic turnover rate (how long it takes for body tissue to reflect diet) and fractionation rate (the shift in isotopic values from a diet to the consumer) in *M. leidyi* via a food alteration experiment.

3. Materials and Methods

3.2 Times Series Based on Field Sampling

3.1.1 Study Site: The Kiel Fjord

The Kiel Fjord (Figure 3), located in the south-western-Baltic Sea ($54^{\circ} 27' 55''$ N, $10^{\circ} 14' 70''$ E (Javidpour *et al.*, 2009b)), constitutes a small extension of the Kiel Bight in the Belt Sea. The Baltic Sea, a large semi-enclosed brackish-water area, spans from the Belt Seas to the northern part of the Finland Belt Sea (Figure 3.A). The Kiel Fjord's water column in the late autumn and winter is well mixed and has a maximum salinity of 22 psu, while in the spring and summer there is a minimum salinity of 10 psu (Figure 4) (Javidpour *et al.*, 2009a). The annual temperature and salinity variation are strongly influenced by the prevailing atmospheric conditions over the western Baltic Sea (Javidpour *et al.*, 2009a). The Baltic Sea drainage basin is inhabited by over 85 million people (Leppakoski *et al.*, 2002) and therefore is under a variety of threats, including over-fishing, irresponsible shipping practices, exploitation, eutrophication, and species invasions. Within this part of the Baltic Sea, *A. aurita* and *C. capillata* (assumed species) were both present in the Kiel Fjord (2011).

(A)





Figure 3 (A-B): (A) A map of the Baltic Sea. The Kiel Fjord, located in the south western Baltic Sea, is indicated with a yellow star (wikipedia.de). (B) Field sampling site: the Kiel Fjord, indicating the location of the two campuses of the GEOMAR: Helmholtz-Zentrum for Ocean Research, Kiel, Germany (geomar.de).

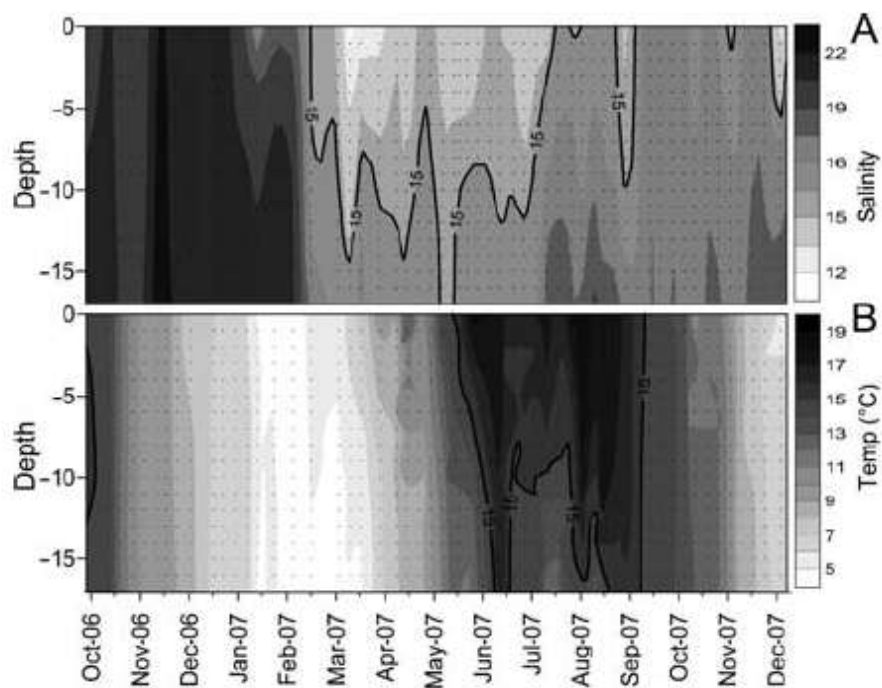


Figure 4: Hydrographic conditions in the Kiel Fjord from October 2006 to December 2007. Salinity (A) and temperature (B) diagram of Kiel Fjord (Figure taken from Javidpour *et al.*, 2009).

3.1.2 Sample Collection and Preparation

Jellyfish samples were taken weekly in the Kiel Fjord (*Witlingskuhle* sampling site, 54° 27' 55" N, 10° 14' 70" E) using a WP3 net hauled from the near bottom (~18 m) to the surface. *M. leidy* were not sampled due to their absence throughout the season. However, samples of *A. aurita* were taken from June to September, and of *C. capillata* from September to October. A minimum of five samples per jellyfish species were collected per sampling time. Specimens were kept for gut evacuation (~1–2 hours) in a collection bucket to clear their stomachs of from undigested food. Nook and round lengths (measured with a standard cm-ruler) (Figure 5) and mass (total wet mass and wet bell mass) of individuals were measured. There was no difference between the nook and round lengths due to nutritional health (Javidpour, *personal communication*). Afterwards, the specimens were washed with filtered seawater to rinse the surrounding water from the body surface. The bell was separated from the rest of the organism and dried in a 50-80 °C oven.

For this study, stable isotopes of C, N, and S were analyzed and compared with a baseline organism, *M. edulis*. Pelagic animals, such as *M. edulis* and jellyfish, are influenced by the autotrophic baseline SI ratio because autotrophs ultimately drive the pelagic food web. As the dominant autotrophs in the ocean, phytoplankton species have great influence on the pelagic food web (Pitt *et al.*, 2009). Therefore, it is important to compare isotope values from a desired organism with that of a baseline organism, such as a filter-feeding mussel (*M. edulis*). Mussels reflect the isotopic values of the pelagic food web which can be used to estimate trophic position or higher trophic level consumers, as well as detecting environmental changes (Post, 2002). *M. edulis* samples were collected from Falckenstein Beach, located in the Kiel Fjord (54° 21' N, 10° 9' E (Mittmayr, *Submitted*), with a Van Veen Grab for baseline comparisons. Samples were rinsed in A.dest and dried for two days at 60 °C.

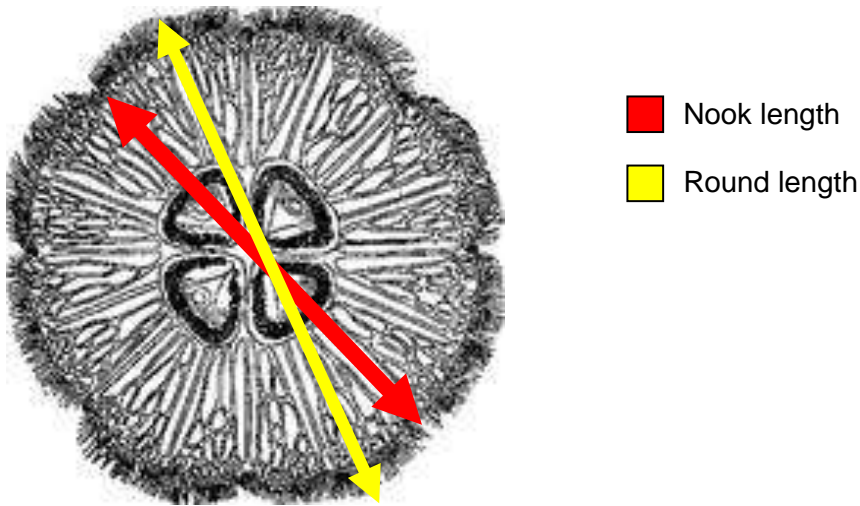


Figure 5: Nook length (red) and round length (yellow) measurements for *A. aurita*. Measurements were taken using standard cm-ruler.

3.1.3 Stable Isotope Analysis Laboratory Methodology

For stable isotope analysis, each dried jellyfish sample was ground to a fine powder with a mortar and pestle, of which $4 \text{ mg} \pm 0.05 \text{ mg}$ were weighed out and sealed in tin capsules (3.2 mm x 4 mm). For *M. edulis*, 0.05 mg of the muscle tissue was weighed out and combined with V2O5 (combustion aide). SIA was then outsourced to the University of California at Davis' stable isotope facility, and followed procedures described in Dierking *et al.* (2011). In particular, carbon ($^{13}\text{C}/^{12}\text{C}$), nitrogen ($^{15}\text{N}/^{14}\text{N}$), and sulfur ($^{34}\text{S}/^{32}\text{S}$) isotope ratios were determined using continuous-flow isotope-ratio mass spectrometry (DeNiro & Epstein, 1978).

In studies using SIA, isotopic compositions are expressed in terms of parts per thousand differences from a standard (δ):

$$\text{Eq. 1} \quad \delta X = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 10^3$$

where X is ^{13}C , ^{15}N , or ^{34}S , and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, or $^{34}\text{S}/^{32}\text{S}$. Standard reference materials for these isotopes are carbon in PeeDee limestone, nitrogen gas from the atmosphere and sulfur from the Cañon Diablo meteorite. The δ values measure the amount of the heavy isotope with respect to the amount of light isotopes in a sample; therefore, increases in these values suggest an increase in the heavy isotope components and vice versa (Peterson and Fry, 1987).

3.1.4 Calculation of Dietary Composition Based on Mixing Models

Values of possible prey items sampled from Falckenstein (outer portion of the Kiel Fjord) where obtained from Mittermayr *et al.* (*submitted*) (Figure 6).

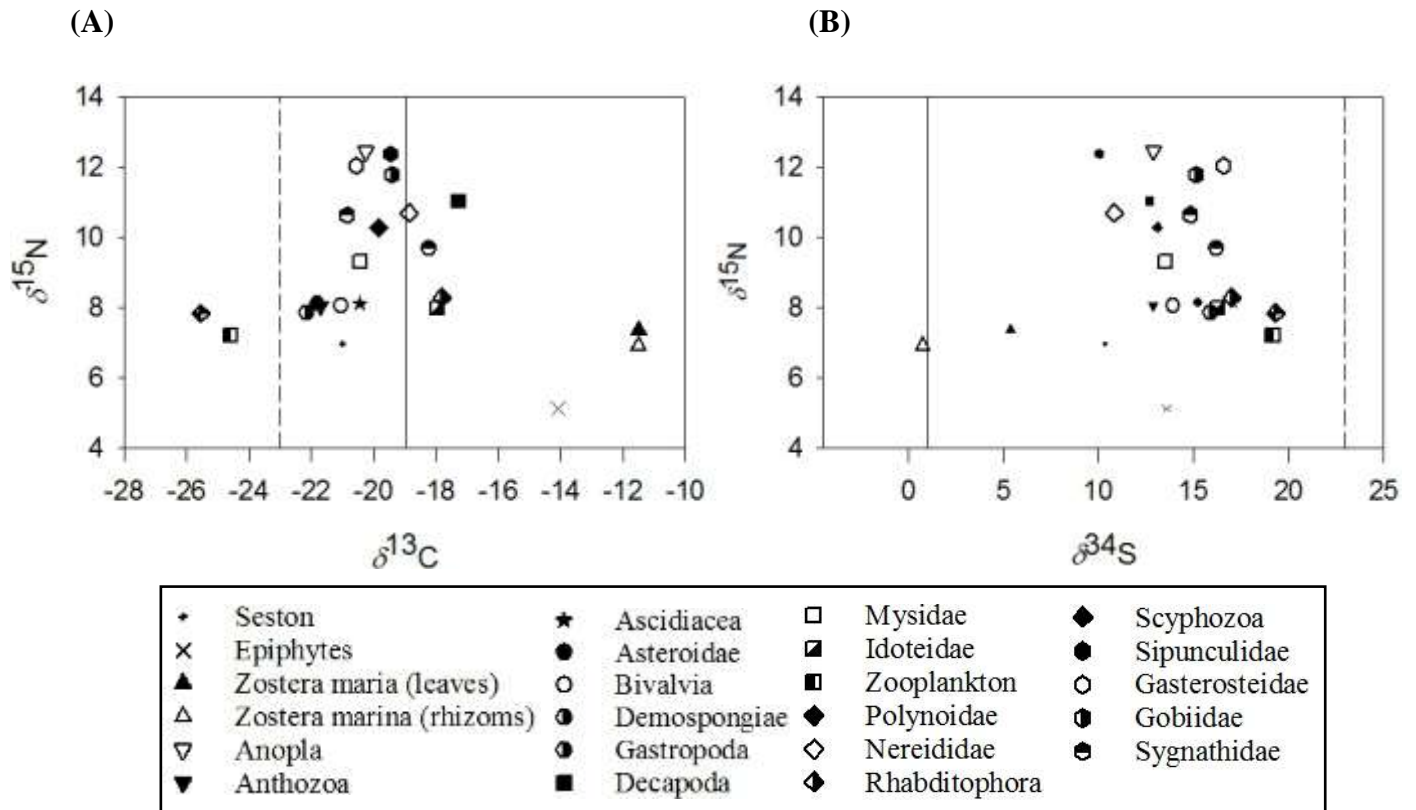


Figure 6: Temporal variation stable isotope values of $\delta^{15}\text{N}$ vs. $\delta^{13}\text{C}$ (A) and $\delta^{15}\text{N}$ vs. $\delta^{34}\text{S}$ (B) with reference lines for $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ of sediment (solid line) and seawater (dashed line). Values are means calculated with results gained from March to September 2011 (Mittermayr *et al.*, *submitted*).

Furthermore, in order to determine nutrient sources, the mixing model MixSIR (Semmens & Moore, 2008) was used. MixSIR is a graphical user interface (GUI) built on MATLAB and employs an algorithm based on Bayesian framework to determine the probability distributions for proportional contributions of each source to the mixture (Semmens & Moore, 2008; Mittermayr *et al.*, Submitted). This model allows for the allocation of different fractionation values for each element and source, respectively. The accepted values of 0.5‰ fractionation increase was chosen for $\delta^{13}\text{C}$, while 2.4‰ and 3.4‰ fractionation increase in $\delta^{15}\text{N}$ for the first and following trophic levels, respectively. Fractionation for $\delta^{34}\text{S}$ was assumed to be negligible (Peterson & Fry, 1987;

Currin *et al.*, 1995; Michener & Kaufman, 2007). This methodology taken directly from Mittermayr *et al.* (*submitted*).

3.1.5 Data Analysis

For some of the analyses, weekly sampling points were pooled to represent monthly data. A power regression, which best fit the data and would be comparable to previous literature (Schneider, 1988) was used to evaluate the relationship between weight wet (g) and bell length (cm) with “R” statistical computing software (*Version: R.2.14.1*, R Development Core Team, 2011).

Secondly, due to the differences in C:N, data should be corrected for lipid content. However, due to time constraints, we could not apply them to the data of this thesis. For further information on lipid correction, please refer to Pinnegar and Polunin (1999), Kiljunen *et al.* (2006), and Harrod and Grey (2006).

Lastly, the differences in the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of *A. aurita* and *C. capillata* during the period of co-occurrence were analysed by a non-parametric *Kruskal-wallis* test because the data were not normally distributed and variance was unequal. The two factors were species and sampling date. A pairwise-*wilcox* test was then used with p-values corrected for multiple testing and with a *bonferroni* for any corrections (*Version: R.2.14.1*, R Development Core Team, 2011).

3.2 Turnover Rate and Fractionation Rate Experiment in *M. leidy*

3.2.1 Culturing of *M. leidy* and Potential Prey

This experiment was conducted at the Seven Lovén Centre for Marine Sciences in Fiskebäckskil, Sweden. During maintenance and experiments all cultures were kept at 18 °C, 33 psu.

M. leidy originated from a laboratory culture (33 psu, 18 °C), from ctenophores collected in the Eastern Skagerrak, southwestern Swedish coast (58° 15′ N, 11° 24′ E (Möller, *personal communication*). Experimental animals were raised from a cohort spawned in February 2012. The newly hatched larvae were equally divided into two 50-L buckets with filtered sea water and fed

ad libitum twice a day with *A. tonsa* raised on *Rhodomonas salina* both from laboratory cultures (33 psu, 18 °C) (Figure 8). Until the animals reached a size of 1-2 mm, *A. tonsa nauplii* (~ 200 µm) were used and after that a mixture of copepodites and adult copepods. After week three, the food source was switched to newly hatched *A. salina* in one of the 50-L buckets. The other bucket was continued on the *A. tonsa* diet.

3.2.2 Experimental Sampling Procedure

Starting on day 19, five replicate samples from each bucket were taken every 1-2 days until the end of the experiment 25 days later (Figure 7).

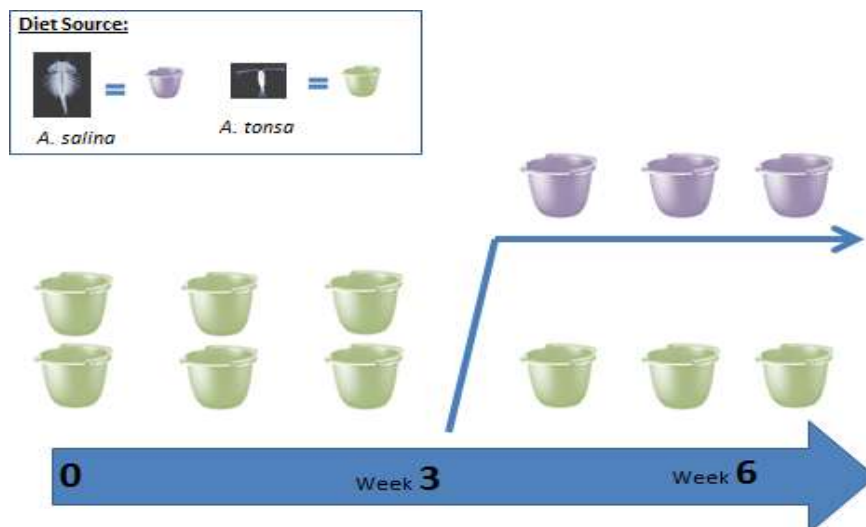


Figure 7: Graphic representation of the fractionation and turnover rate experimental set-up over a 6-week period (44-days). The green 50-L buckets contain *M. leidy* individuals fed on *A. tonsa*. After 3-weeks, the diet source was changed from *A. tonsa* to *A. salina*. The purple 50-L buckets contain *M. leidy* individuals fed on *A. salina*.



Figure 8: Fractionation and turnover rate experimental set-up. There were three 50-L buckets: 1.) *A.tonsa* culture, 2.) *M. leidy* culture fed on *A. tonsa*, and 3.) *M. leidy* culture fed on *A. salina*.

3.2.3 Laboratory Methodology

Total length, oral-aboral length (using an ocular with a graticule) (Figure 9), and mass of *M. leidy* individuals were measured. The graticule was calibrated so that 6.5 units equaled 1 cm. Afterwards, the specimens were washed with filtered seawater to rinse the surrounding water from the body surface. Specimens were kept for gut evacuation (~1–2 hours) in a collection bucket. The organisms were then placed in a glass test tube and freeze-dried overnight (SCANVAC CoolSafe™). For SIA, all dried samples were ground to a fine powder with mortar and pestle and 4 mg \pm 0.05 mg samples was sealed in tin capsules (5 mm x 9 mm). See section 3.1.3 for sample handling.

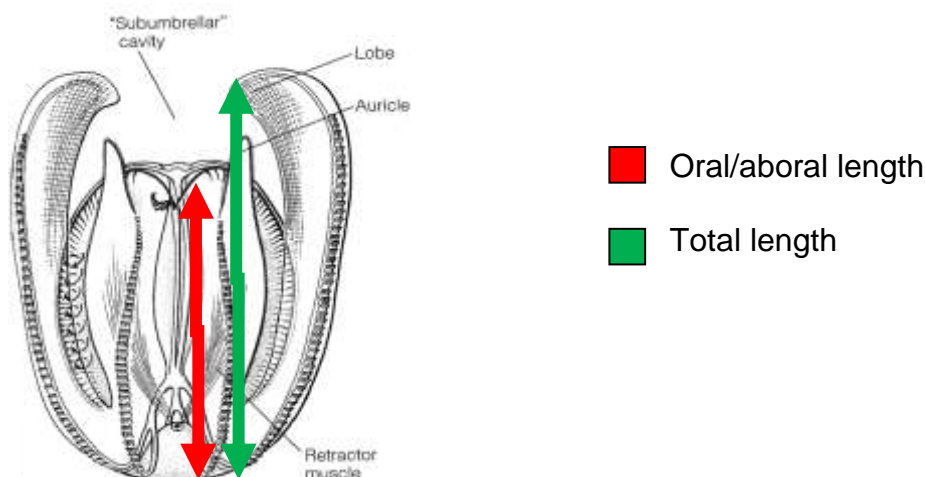


Figure 9: Oral/aboral length (red) and total length (green) measurements for *M. leidy*. Measurements were taken with using an ocular with a graticule.

In parallel to *M. leidyi* sampling, both diet sources were sampled at each time point to control for fluctuations in the isotopic values of dietary sources. After freeze-drying, the SIA ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) was carried out at the UC Davis Stable Isotope Facility. Due to their small size, 75 *A. salina* individuals and 300 *A. tonsa* individuals were pooled for each replicate.

3.2.4 Data Analysis

Turnover Rate

The initial plan was to calculate the turnover rate for *M. leidyi*, using a turnover model composed of growth and metabolism, *shown in detail below* (Hesslein *et al.*, 1993; MacAvoy *et al.*, 2001; Sakano *et al.*, 2005). The model is expressed in Eq. 2:

$$\text{Eq. 2} \quad C = C_n + (C_0 - C_n) \times e^{-(k+m)t}$$

where C is the $\delta^{15}\text{N}$ value of the organism when sampled, C_n is the expected value for the organism in equilibrium with its new diet, C_0 is the initial $\delta^{15}\text{N}$ value of the organism, m and k are the metabolic and growth contributions to isotope turnover, and t is time. Growth rate (k) was calculated using a simple exponential growth model (Eq. 3):

$$\text{Eq. 3} \quad W = W_0 \times e^{kt}$$

where W_0 is the mass of the organism on day 0, W is the mass on days 19, 21, 22, 23, 24, 26, 28, 30, 32, 34, 36, or 44. Metabolic turnover (m) was taken from Grosskopf and Javidpour (*submitted*). Time lags of the $\delta^{15}\text{N}$ shift in tissue were calculated using Eq. 4:

$$\text{Eq. 4} \quad t^* = \ln 5 / (k + m)$$

However, as the growth over the experimental period was erratic, and due to fluctuations in the isotopic values of diet sources over time, calculation of turnover rate was not possible; therefore, no further results on this parameter will be shown.

Fractionation

To calculate fractionation, Eq. 5 was used (DeNiro & Epstein, 1981):

$$\text{Eq. 5} \quad \Delta_{\text{ANIMAL-PREY}} = \delta X_{\text{ANIMAL}} - \delta X_{\text{PREY}}$$

where X can either be ^{13}C or ^{15}N .

4. Results

4.1 Seasonal Observation of Gelatinous Zooplankton, Kiel Fjord

Sampling in the Kiel Fjord occurred between May and October 2011. During this period, *A. aurita* was present in the samples between May and September, whereas, *C. capillata* was found only on four occasions in September and October. *M. leidy*, which was found in the Kiel Fjord in previous summers, surprisingly, was absent in the Kiel Fjord during the entire period.

4.1.1 Biometry

Biometric measurements were used to determine the correlation of an organism's size on the C and N content (Table 1). There was an increase in bell diameter from June, with an average length of $16.5 \text{ cm} \pm 3.64 \text{ cm}$, to July with $22.83 \text{ cm} \pm 6.91 \text{ cm}$. In late summer, there was a decrease in diameter length to $17.05 \text{ cm} \pm 3.15 \text{ cm}$ (September). Wet weight (g) followed the same pattern as length with a maximum value of $530.94 \text{ g} \pm 355.35 \text{ g}$ in July. *A. aurita* disappeared from our net sampling in the beginning of October. Total carbon (μg) and nitrogen (μg) per unit of dry weight showed a peak in August, with $72.66 \mu\text{g} \pm 42.66 \mu\text{g}$ and $18.93 \mu\text{g} \pm 10.94 \mu\text{g}$, respectively.

Table 1: Biometric information for *A. aurita* during the 2011 season (June – September) represented as mean and \pm SD.

Month (2011)	Pooled Sampling Points	Sample Size (n)	Wet Weight (g) (\pm SD)	Length (cm) (\pm SD)	C(μg) (\pm SD)	N(μg) (\pm SD)	C:N Molar Ratio
June	2	9	204.19 (\pm 92.12)	16.5 (\pm 3.64)	26.15 (\pm 9.13)	16.5 (\pm 3.64)	5.37 (\pm 0.87)
July	3	15	530.94 (\pm 355.35)	22.83 (\pm 6.91)	24.59 (\pm 18.7)	6.46 (\pm 5.17)	4.71 (\pm 0.93)
August	4	20	367.55 (\pm 256.27)	19.85 (\pm 5.32)	72.66 (\pm 42.66)	18.93 (\pm 10.94)	4.47 (\pm 0.12)
September	2	10	161.19 (\pm 95.00)	17.05 (\pm 3.15)	28.73 (\pm 13.45)	7.23 (\pm 3.57)	4.72 (\pm 0.67)

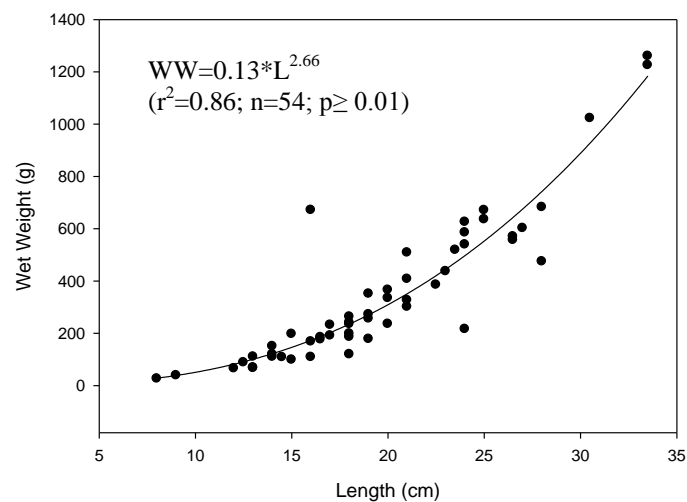


Figure 10: Wet Weight WW (g) plotted versus round length L (cm) for *A. aurita* in the Kiel Fjord (2011).

Figure 10 depicts the relationship between length and wet weight in *A. aurita*. It can be expressed with the following equation:

$$WW = 0.13 * L^{2.66}$$

where L is length in centimetres and WW is wet weight in grams. r^2 was 0.8602 for 54 samples and a p-value of $p \geq 0.01$.

The molar ratio of carbon to nitrogen (C:N) showed a general decrease (Table 1 & Figure 11) with high variability among replicates. In June, the mean of C:N molar ratio was 5.37 ± 0.87 , while September had a mean value of 4.72 ± 0.67 .

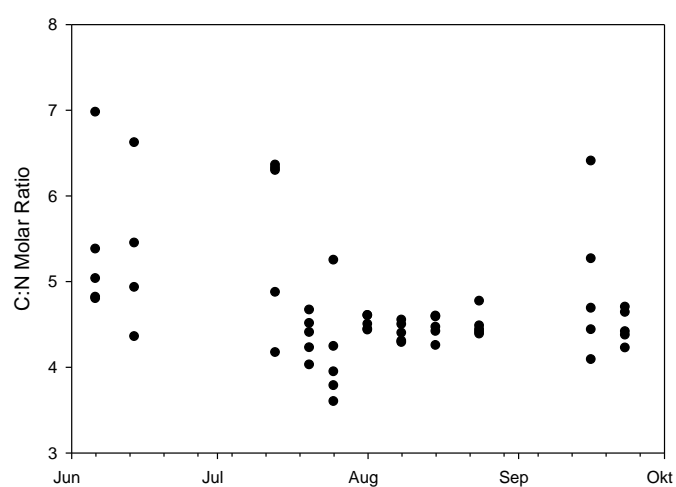


Figure 11: The C:N molar ratio in *A. aurita* over the season in the Kiel Fjord (2011).

4.1.2 Trophic Position and Carbon Transfer in *A. aurita*

The $\delta^{13}\text{C}$ values for *M. edulis* and *A. aurita* during the season (June – September) in the Kiel Fjord (2011) are shown in Figure 12. *A. aurita* showed a positive trend (Figure 12.B). June 6th, 2011 had a depleted value of $-25\text{‰} \pm 0.36\text{‰}$, while September 23 had an enriched value of $-21\text{‰} \pm 0.46\text{‰}$. *M. edulis*, a filter-feeder, was used as a baseline species to assess overall change in the Kiel Fjord in regards to isotope values (Figure 12.A). The $\delta^{13}\text{C}$ values for *M. edulis* showed a positive trend similar to that of *A. aurita* with a mean value of $21.93\text{‰} \pm 1.48\text{‰}$ (Figure 12).

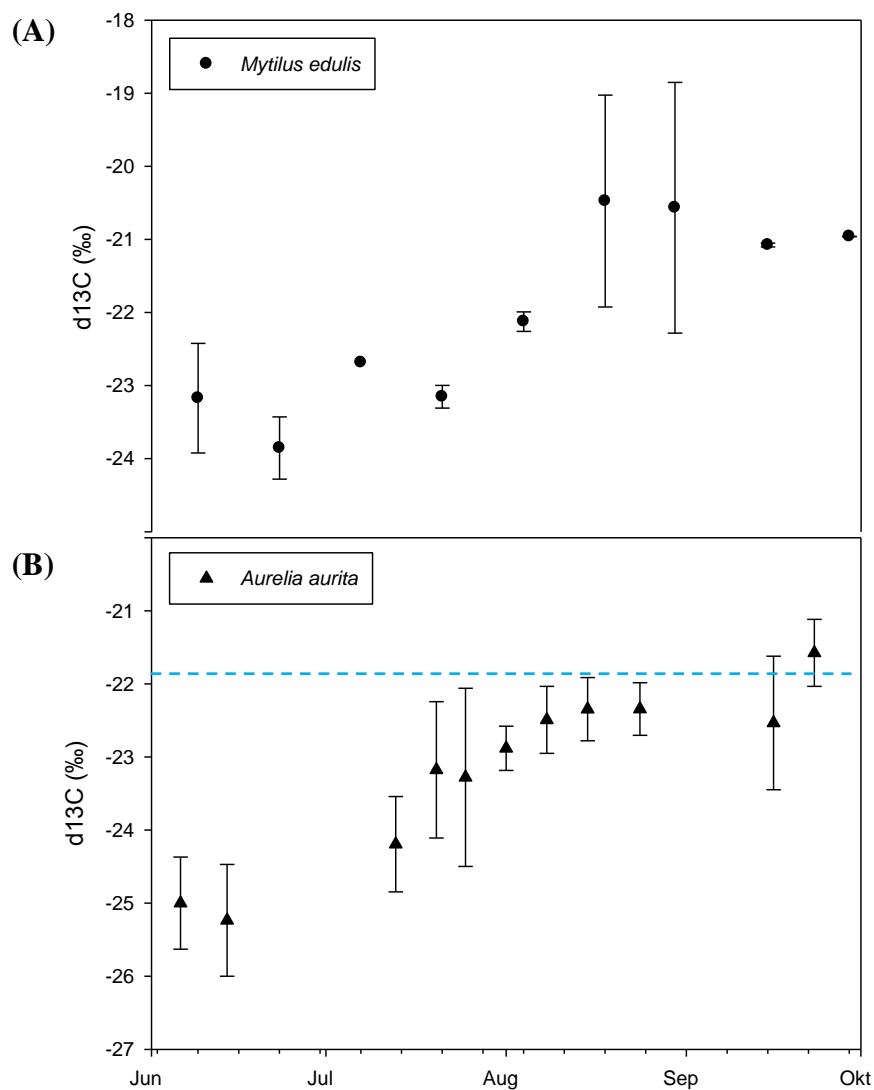


Figure 12: The $\delta^{13}\text{C}$ values for *M. edulis* (A) and *A. aurita* (B) during the season (June – September) in the Kiel Fjord (2011). (B) The blue-dashed line is the mean value of *M. edulis* from (A).

The $\delta^{15}\text{N}$ values for *M. edulis* and *A. aurita* during the season (June – September) in the Kiel Fjord (2011) are shown in Figure 13. *A. aurita* showed high variance in June and July and then reached an equilibrium of $\sim 11\text{‰}$ (Figure 13.B). *M. edulis* $\delta^{15}\text{N}$ values had a plateau with a mean value of $7.76\text{‰} \pm 1.62\text{‰}$ (Figure 13.A). There was some variance observed at two sampling points in late July.

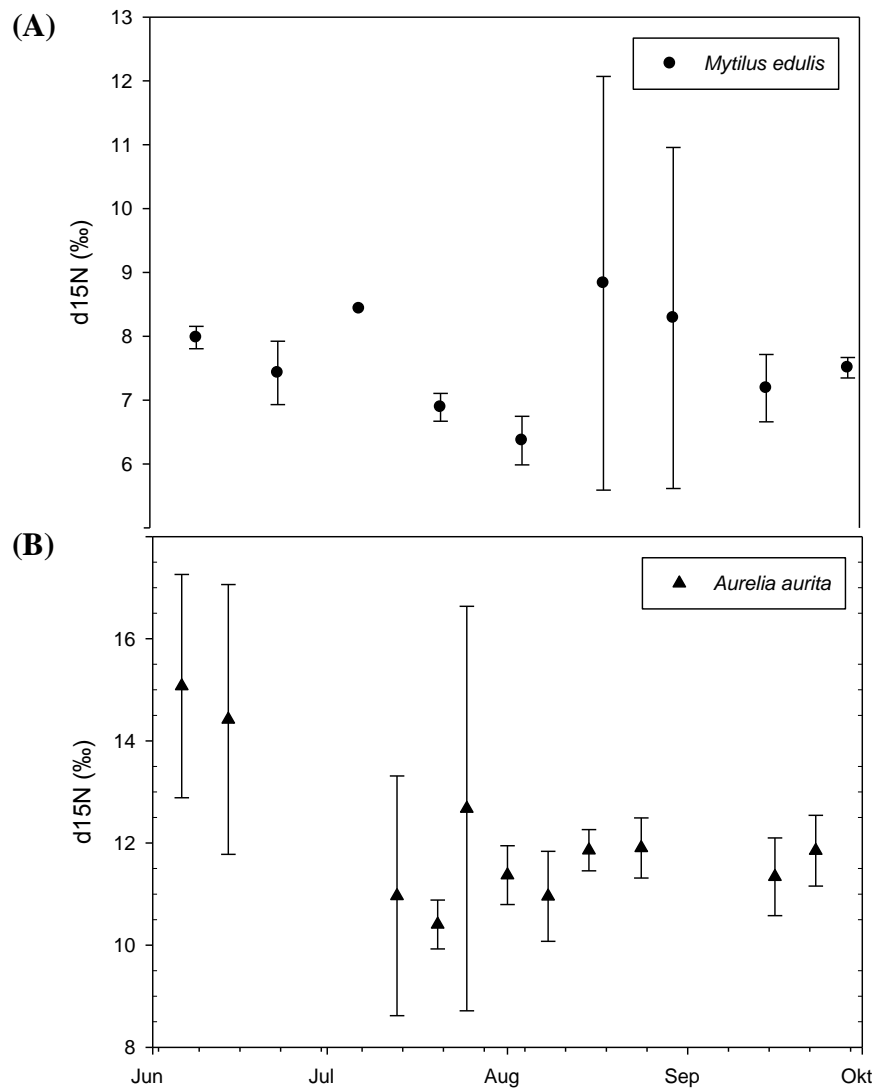


Figure 13: The $\delta^{15}\text{N}$ values for *M. edulis* (A) and *A. aurita* (B) during the season (June – September) in the Kiel Fjord (2011).

The average $\delta^{34}\text{S}$ values for *M. edulis* and *A. aurita* during the season (June – September) in the Kiel Fjord (2011) are shown in Figure 14. The *A. aurita* values showed a negative trend (Figure 14.B). June 6th, 2011 had an enriched value of $17.686\text{‰} \pm 1.84\text{‰}$, while September 23 had a more depleted value of $9.806\text{‰} \pm 0.67\text{‰}$. *M. edulis* $\delta^{34}\text{S}$ values had a plateau with a mean value of $15.80\text{‰} \pm 2.61\text{‰}$ (Figure 14.A). There was some variance observed at two sampling points in late July.

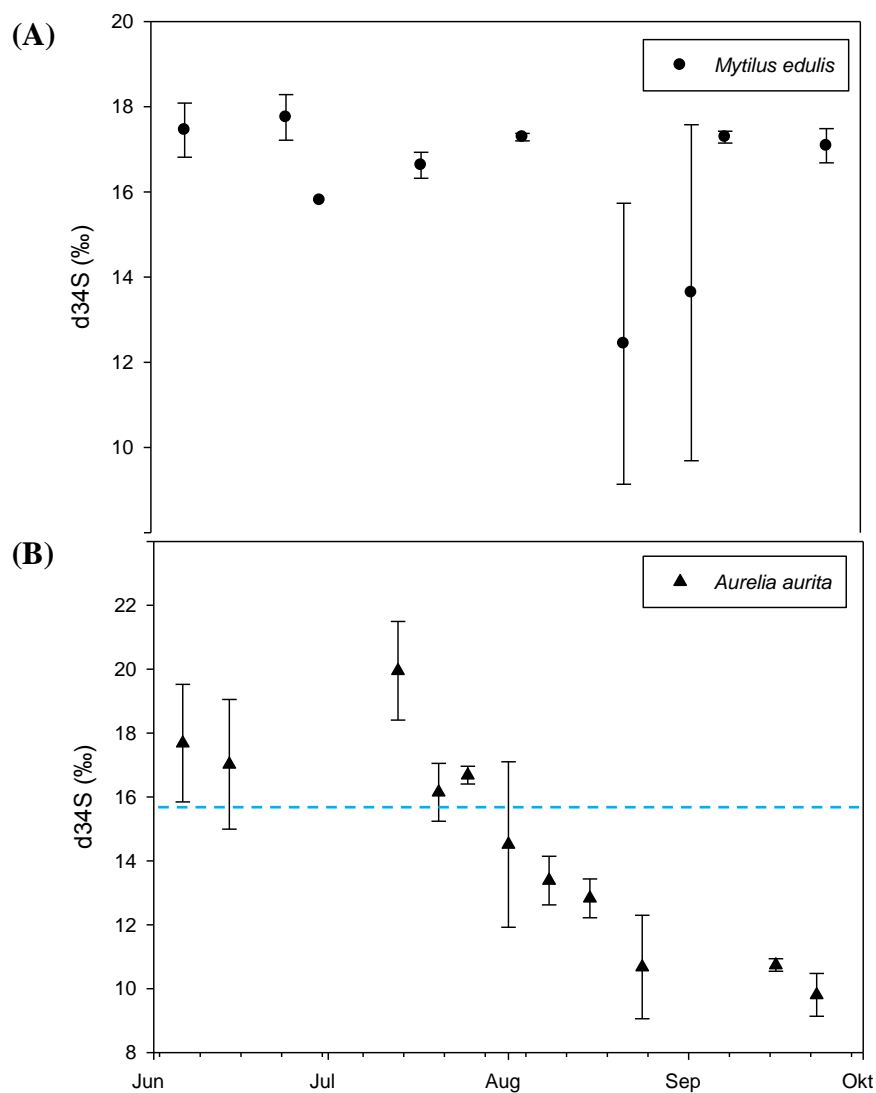


Figure 14: The $\delta^{34}\text{S}$ values for *M. edulis* (A) and *A. aurita* (B) during the season (June – September) in the Kiel Fjord (2011). (B) The blue-dashed line is the mean value of *M. edulis* from (A).

Average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures from *A. aurita* (Figure 15) showed significant differences between sampling points. The general trend shows that with an enriched $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ also has enriched values.

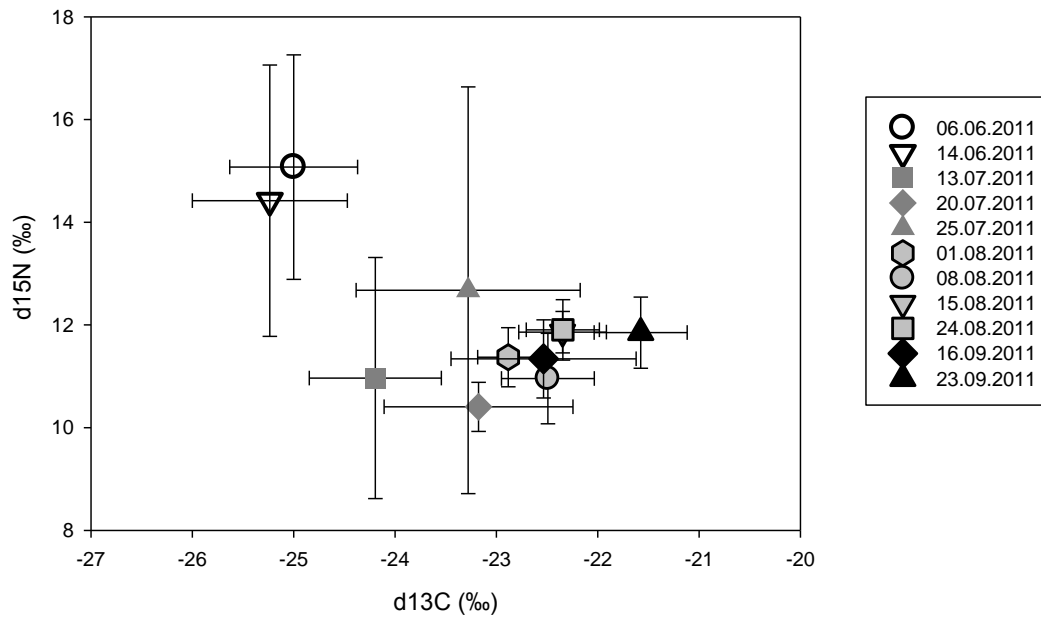


Figure 15: General dual isotope diagram of (mean \pm SD) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of *A. aurita* in the Kiel Fjord. The different shapes represent different sampling months 2011 (June – September).

4.1.3 Trophic Relationship between *A. aurita* and *C. capillata*

C. capillata was sampled four times beginning at the first appearance (September) until the end of the sampling period in the Kiel Fjord (October). In order to evaluate the trophic interaction between this species and *A. aurita*, $\delta^{13}\text{C}$ (Figure 16), $\delta^{15}\text{N}$ (Figure 17), and $\delta^{34}\text{S}$ (Figure 18) values were compared on sampling dates where both individuals were present (September 16th and 23rd).

For $\delta^{13}\text{C}$ (Figure 16), both species showed an increased value from September 16th to September 23rd. *C. capillata*, however, has an enriched $\delta^{13}\text{C}$ values ($21.45\text{‰} \pm 0.71\text{‰}$) than *A. aurita* ($-22.06\text{‰} \pm 0.85\text{‰}$).

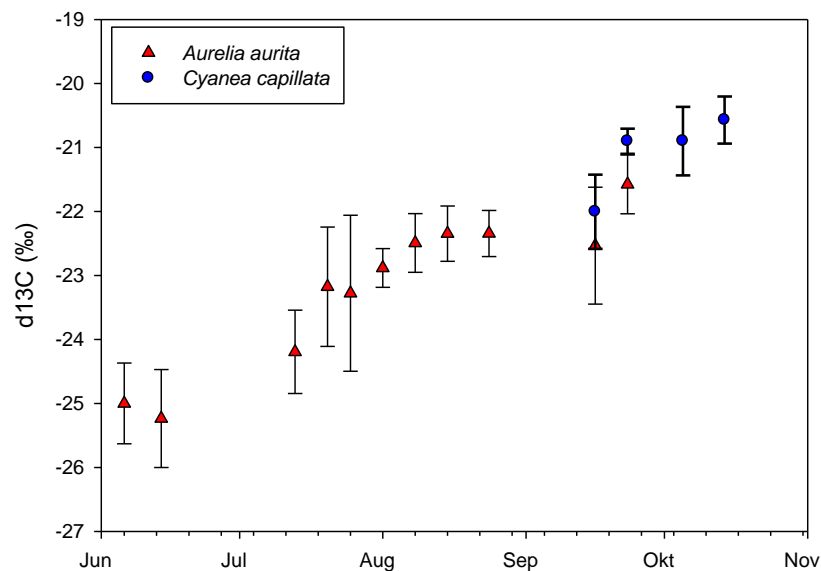


Figure 16: $\delta^{13}\text{C}$ values for the annual 2011 season for *A. aurita* (red) and *C. capillata* (blue).

For $\delta^{15}\text{N}$ (Figure 17), *A. aurita* had a steady value of $11.6\text{‰} \pm 0.74\text{‰}$, while *C. capillata* showed a decrease between sampling points from $15.93\text{‰} \pm 2.97\text{‰}$ to $12.37\text{‰} \pm 0.51\text{‰}$. *C. capillata*, however, still had an enriched $\delta^{15}\text{N}$ value ($14.15\text{‰} \pm 2.75\text{‰}$) than *A. aurita* ($11.6\text{‰} \pm 0.74\text{‰}$).

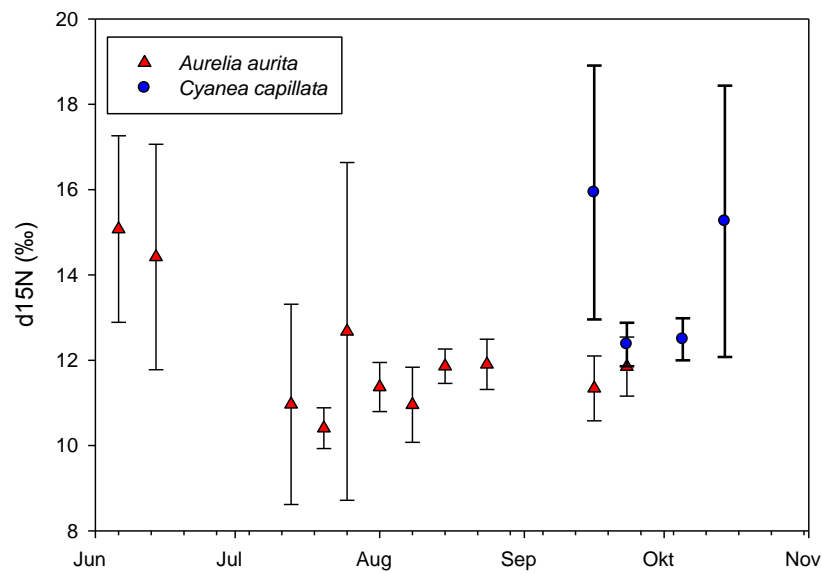


Figure 17: $\delta^{15}\text{N}$ values for the annual 2011 season for *A. aurita* (red) and *C. capillata* (blue).

For $\delta^{34}\text{S}$ (Figure 18), *A. aurita* had a steady value of $10.27\text{‰} \pm 0.68\text{‰}$, while *C. capillata* also showed a steady value of $18.13\text{‰} \pm 0.72\text{‰}$.

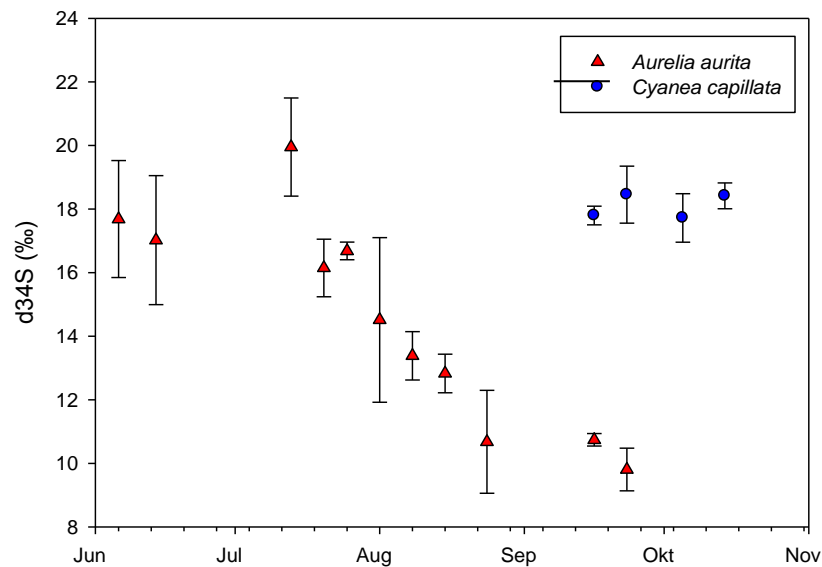


Figure 18: $\delta^{34}\text{S}$ signatures for the annual 2011 season for *A. aurita* (red) and *C. capillata* (blue).

A non-parametric *Kruskal-wallis* test was run to test for significance between the means of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ for *A. aurita* and *C. capillata* during the period of co-occurrence (Table 2). The degrees of freedom were $df = 1$ for each test. $\delta^{13}\text{C}$ values was found to be non-significant ($p=0.096$), while $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ values were found to be significant between species ($p=0.002$ and $p<0.001$, respectively).

Table 2: Statistical analysis (*Kruskal-wallis*) of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ results during the period of co-occurrence (16.09.2011 and 23.09.2011) of *A. aurita* and *C. capillata*.

SI	df	χ^2	P-value
$\delta^{13}\text{C}$	1	2.77	0.096
$\delta^{15}\text{N}$	1	9.14	0.002
$\delta^{34}\text{S}$	1	14.29	<0.001

Due to the factors of the *Kruskal-wallis* test being species and sampling date, a pairwise-*wilcox* test was then applied. Results are shown in Table 3.

Table 3: Significance comparisons of the two factors, species and sample dates, from the *Kruskal-wallis* test via a pairwise-*wilcox* test.

	Day 1	Day 2
$\delta^{15}\text{N}$		
<i>A. aurita</i>	Significantly different	Significantly different
<i>C. capillata</i>	Not significantly different	Not significantly different
$\delta^{34}\text{S}$		
<i>A. aurita</i>	Significantly different	Significantly different
<i>C. capillata</i>	Significantly different	Significantly different

4.1.4 Diet Source Contribution for *A. aurita* and *C. capillata* using C, N, & S

A Bayesian mixing model was run as a useful means to allocate the contribution of the potential dietary sources of seston and zooplankton (data from Mittermayr *et al.*, *submitted*) for *A. aurita*, using $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ data. The sampling points of *A. aurita* were run by month (June-September) with monthly data of seston and zooplankton from the same annual 2011 season (Mittermayr *et al.*, *submitted*) but a month prior to account for metabolic rates. The mixing models for *A. aurita* (Figure 19) and *C. capillata* (Figure 20) showed a dietary shift over the season from zooplankton to seston.

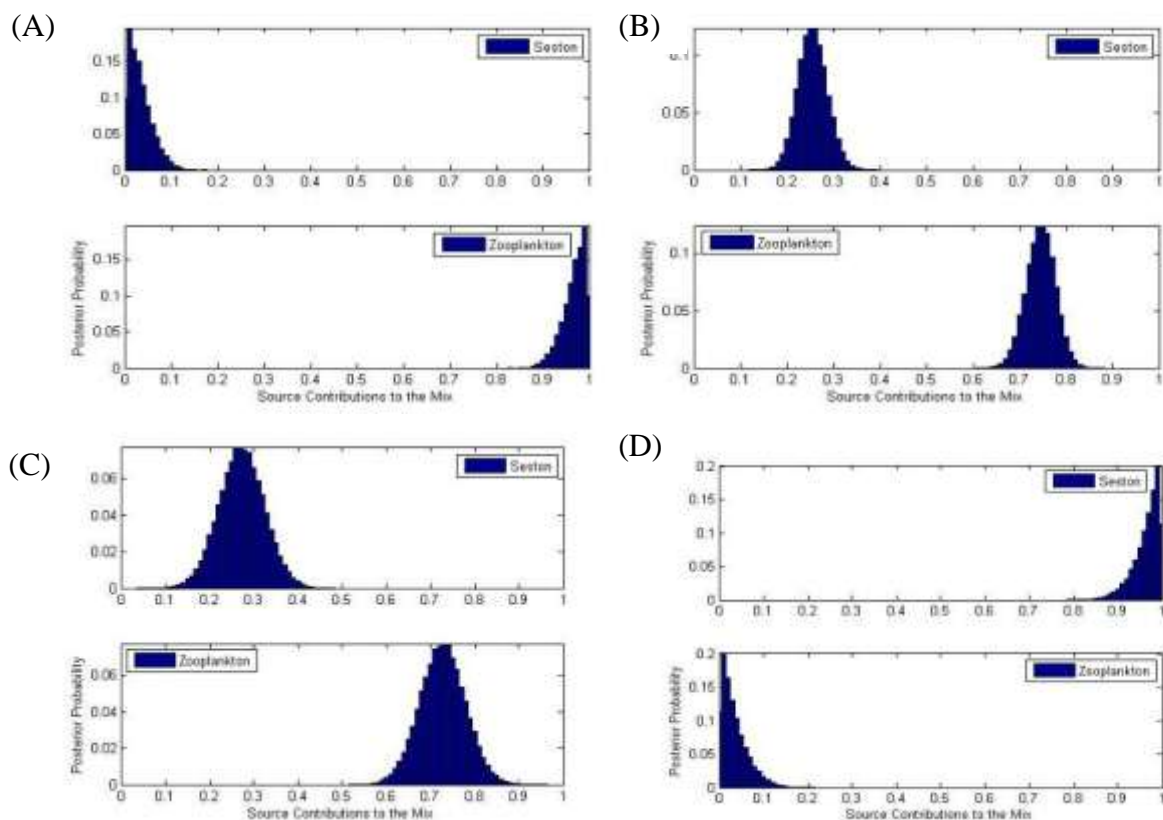


Figure 19 (A-D): In June (A), *A. aurita* fed almost entirely on zooplankton (>90%). During July (B) and August (C), there is a shift towards feeding on more seston (~25%) and less on zooplankton (~75%). At the end of the season (2011), *A. aurita* was feeding almost entirely on seston (>90%) (D).

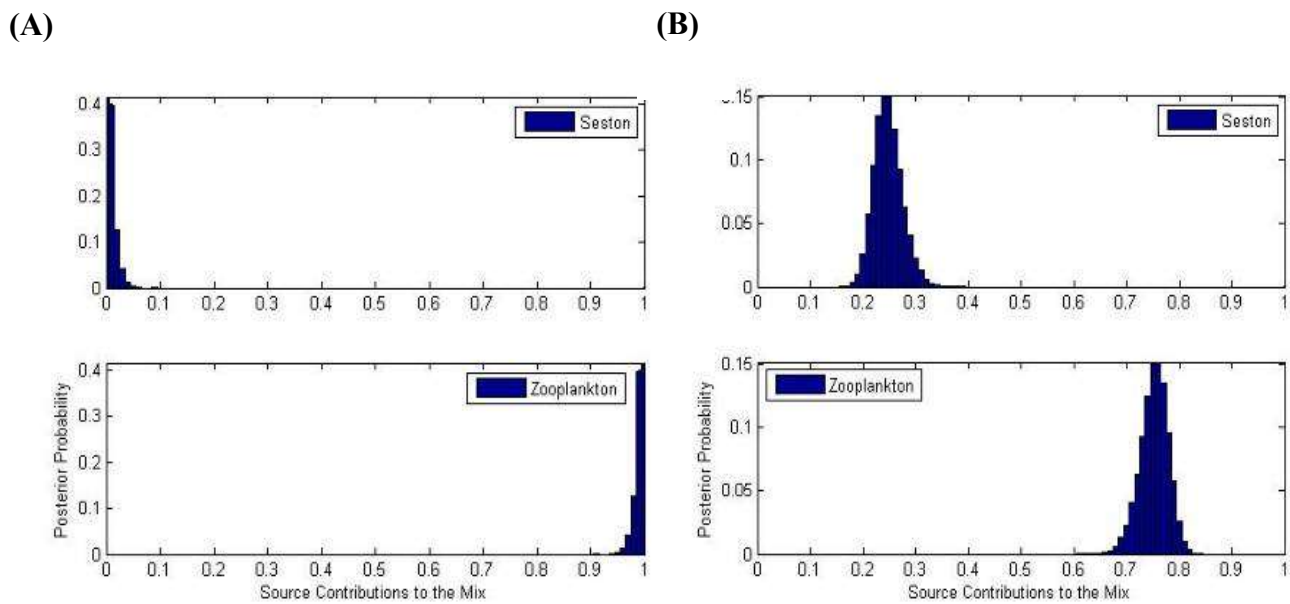


Figure 20 (A-B): Mixing models for *C. capillata* to determine contribution of seston and zooplankton to diet. In September (15.A), zooplankton is almost the sole food source (>95%). In October (15.B), there is a shift in food contributions as more seston (~25%) and less zooplankton (~75%) is consumed.

4.2 Experimental Determination of Fractionation and Turnover Rate in the Ctenophore, *M. leidy*

A food alteration experiment, over 6-weeks (44-days), was used to measure for the first time the fractionation rates in gelatinous zooplankton, specifically *M. leidy*. The diet of *M. leidy* was switched from *A. tonsa* to *A. salina*.

4.2.1 Biometry

The total length (cm) over the 6-week experimental period was recorded for *M. leidy* fed on *A. tonsa* and *M. leidy* fed on *A. salina*. Both groups experience varied, but increasing, growth; however, there is a clear separation between groups on day 44. The mean total length on day 44 for *M. leidy* fed on *A. tonsa* was $1.44\text{cm} \pm 0.19\text{cm}$, while $0.66\text{cm} \pm 0.1\text{cm}$ for *M. leidy* fed on *A. salina*.

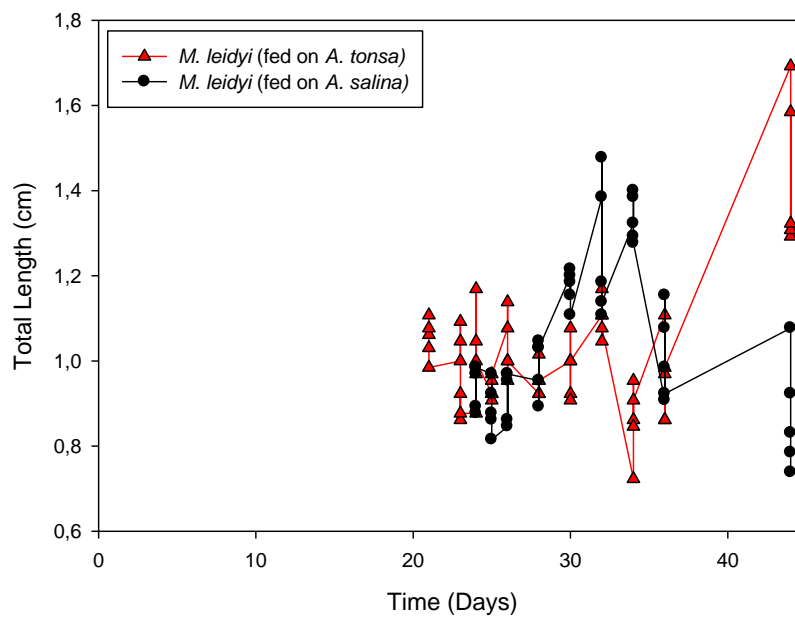


Figure 21: Total Length (cm) over the 6-weeks experimental period (44-days). *M. leidy* fed on *A. tonsa* is depicted with a red line and *M. leidy* fed on *A. salina* has a black line. There was no data collected until the 19th day of the experimental period.

4.2.2 Fractionation between *M. leidy* and Its Prey

Fractionation is the difference in isotopic values between a predator and its prey, in this case, *M. leidy* and either *A. tonsa* or *A. salina* (Figure 22). In group 1, *M. leidy* was fed on *A. tonsa* for the entirety of the experiment (Figure 22.A, B). Group 2 was fed for the first 3-weeks on *A. tonsa* and then for the last 3-weeks on *A. salina* (Figure 22.C, D). In all figures, isotope values are presented as daily mean (\pm SD). The black line represents the prey type and the red line represents *M. leidy*. The $\delta^{15}\text{N}$ values for *M. leidy* show a general increase in isotopic values when compared to those of its prey (Figure 22. B, D). The $\delta^{13}\text{C}$ values for *M. leidy* have varied results and differ from those of its prey (Figure 19.A, C). All isotope values for *A. tonsa* and *A. salina* showed high variance between sampling days, therefore, fractionation was difficult to calculate.

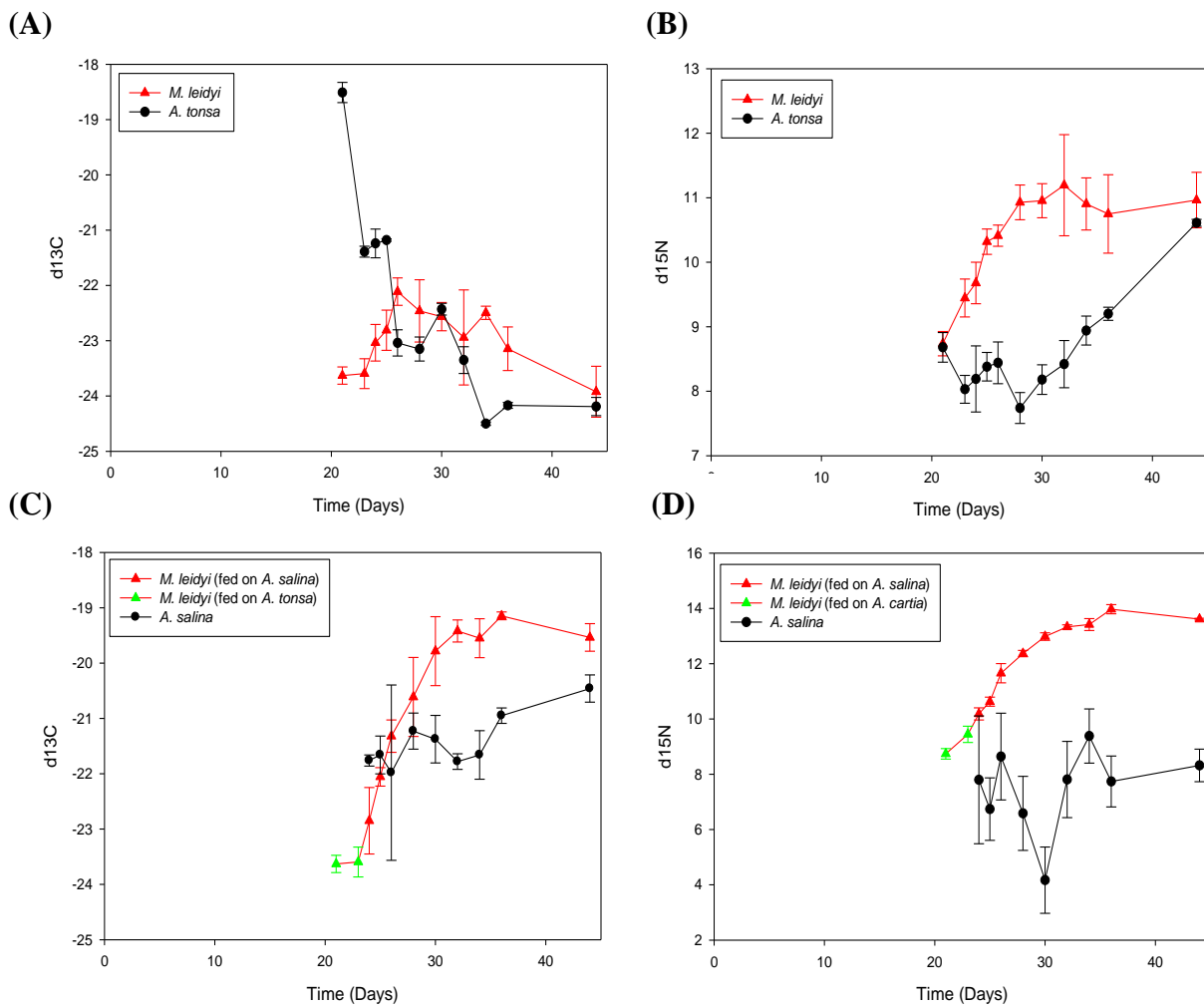


Figure 22: Isotopic composition of *M. leidy* and its prey over the 44-day fractionation rate experiment. Group 1 was fed on *A. tonsa* for the entirety of the experiment and group 2 was fed for the first 3-weeks on *A. tonsa* and then for the last 3-weeks on *A. salina*. (A) The daily mean (\pm SD) for the $\delta^{13}\text{C}$ values of *M. leidy* and *A. tonsa*. (B) The daily mean (\pm SD) for the $\delta^{15}\text{N}$ values of *M. leidy* and *A. salina*. (C) The daily mean (\pm SD) for the $\delta^{13}\text{C}$ values of *M. leidy* and *A. salina*. (D) The daily mean (\pm SD) for the $\delta^{15}\text{N}$ values of *M. leidy* and *A. salina*. For graphs (C) and (D), the green data points represent the sampling days before the diet switch. There was no data collected until the 19th day of the experimental period.

To facilitate the assessment of general patterns over the experimental period, I also plotted *M. leidyi* isotopic values together with the mean values of its diet (Figure 23).

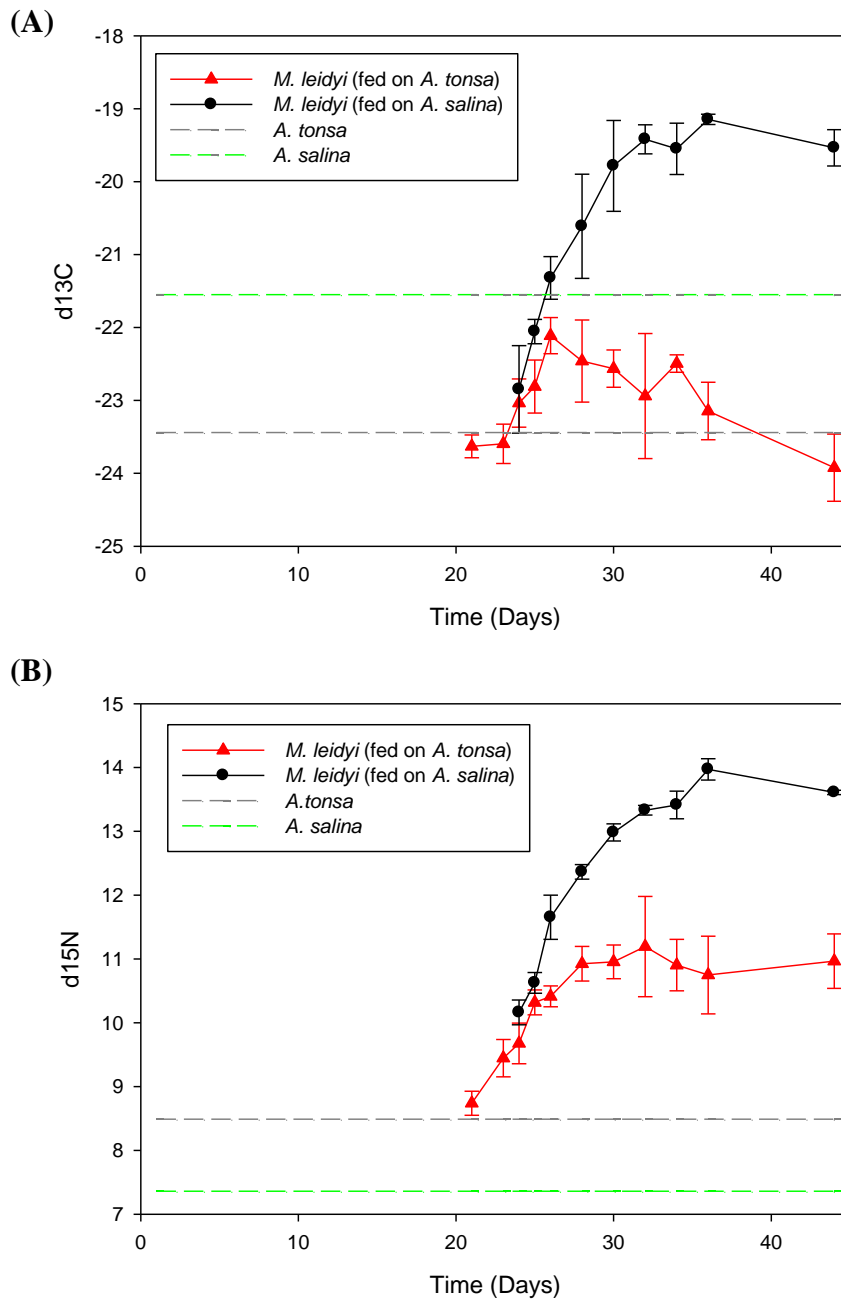


Figure 23: Isotopic composition of *M. leidyi* and its prey over the 44-day fractionation rate experiment. Group 1 was fed on *A. tonsa* for the entirety of the experiment (red) and group 2 was fed for the first 3-weeks on *A. tonsa* and then for the last 3-weeks on *A. salina* (black). There was no data collected until the 19th day of the experimental period. The mean $\delta^{13}\text{C}$ (A) and $\delta^{15}\text{N}$ (B) values for *A. tonsa* (grey) and *A. salina* (green) are depicted.

Fractionation was measured once *M. leidy* reached equilibrium with its prey. For this experiment, equilibrium was assumed for the last three time points, days 34, 36, and 44 (Table 4).

Table 4: Estimation of isotopic fractionation for *M. leidy* fed on *A. tonsa* and *A. salina*. The overall mean value of *A. tonsa* and *A. salina* were subtracted from the daily means of *A. aurita* on days 34, 36, and 44. The mean fractionation rates for the days 34, 36, and 44 are displayed in the last column.

Stable Isotope	Diet Source				Mean
		Day 34 (‰)	Day 36 (‰)	Day 44 (‰)	fractionation (‰)
$\delta^{13}\text{C}$	<i>A. tonsa</i>	0.95	0.3	-0.48	0.26
	<i>A. salina</i>	2.0	2.4	2.01	2.14
$\delta^{15}\text{N}$	<i>A. tonsa</i>	2.41	2.26	2.48	2.38
	<i>A. salina</i>	6.05	6.61	6.25	6.30

5. Discussion

5.1 Field Study of Jellyfish in the Kiel Fjord

5.1.1 Absence of *M. leidyi* in the Kiel Fjord (2011)

A field study in the Kiel Fjord was done to analyze trophic interactions of the invasive ctenophore, *M. leidyi*, with the native jellyfish, *A. aurita* and *C. capillata*. However, *M. leidyi*, surprisingly, was absent during the season (2011).

There are several possible explanations for the absence of *M. leidyi* in 2011. The first explanation accounts for the harsh winter, prior to the 2011 jellyfish appearance, in the Kiel Fjord (Javidpour, *personal communication*). *M. leidyi* populations often overwinter in the fjord; therefore, they might not have survived (Javidpour *et al.*, 2009a). Secondly, it has previously been reported that some jellyfish species are flushed into the Baltic Sea from the North Sea via wind and water currents (Javidpour, *personal communication*). Additionally, there may be several other unforeseen explanations; therefore, no conclusions can be made about their absence.

However, samples of the *A. aurita* and *C. capillata* were taken. *A. aurita* was observed in the Kiel Fjord from May until late September, while *C. capillata* was present in September and October.

5.1.2 Comparison of Jellyfish Studies in the Kiel Fjord from Previous Years

There are few studies done on *A. aurita* (Hammer & Jenssen, 1974; Stoecker *et al.*, 1987; Schneider, 1988; Schneider & Behrends, 1994; Sullivan *et al.*, 1994; Båmstedt *et al.*, 1994; Hansson & Norrman, 1995; Hansson, 1997; Fukuda & Naganuma, 2001; Ishii & Tanaka, 2001; Malej *et al.*, 2007; Lo & Chen, 2008; Turk *et al.*, 2008; Rackmil *et al.*, 2009; Kamiyama, 2011), and even fewer on *C. capillata* (Seravin, 1991; Hansson, 1997). Furthermore, there are only a couple of studies conducted on these species in the Kiel Fjord (Kerstan, 1977; Schneider, 1988, Mittermayr *et al.*, *submitted*).

In this study, the significant correlation of bell length and wet weight observed in *A. aurita* coincides with previous findings by Kerstan (1977) and Schneider (1988) with similar results, indicating individuals with larger bell lengths are also heavier.

Throughout the season (2011), the WW of *A. aurita* had a peak in July followed by a decrease in August- September. Schneider and Behrends (1994) reported a peak in WW in May and June with decreases in July and August. Size decrease, late in the summer, is often contributed to reproduction which occurs in July and August, and has a high energy cost. However, further research is needed to verify whether size decrease is due to starvation as a result of reproduction or because larger animals die earlier than smaller individuals (Schneider & Behrends, 1994).

C and N showed similar trends; a peak in August followed by a decrease in September. The peak occurs during the time of reproduction and when degradation and starvation begin (Schneider & Behrends, 1994). C and N are essential elements for synthesizing carbohydrates, peptides, and proteins, as well as for the storage and conservation of energy (LaRoche, *presentation*). The amounts of C and N in a sample are used to track energy flow and trophic position in an ecosystem (Fry & Sherr, 1984; Peterson *et al.*, 1986; Peterson & Fry, 1987; Post, 2002). Carbon content measures the amount of biomass and energy transfer in a system, while nitrogen measures source contribution (*i.e.*, diet or environmental). For example, Schneider and Behrends (1994) observed *A. aurita* individuals were smaller and lighter (200-400 mg C ind⁻¹) in seasons with higher abundances, while larger and heavier individuals (750 - 1050 mg C ind⁻¹) were found in periods of lower abundances. During periods of low abundance, it was observed that more larvae are produced per individual (~500,000 larvae) when compared to periods of high abundance (~120,000 larvae). These density dependent relationships were suggested to be due to food limitation and starvation (Hamner & Jenssen, 1974; Schneider & Behrends, 1994), reflected in the C and N content. Taking this into consideration, the generally small sizes of the individuals sampled in the 2011 season would be consistent with a season of high abundance with smaller and lighter individuals (50-500 mg C ind⁻¹).

5.1.3 Seasonal Trends in the Isotopic Composition of Jellyfish in the Kiel Fjord

The use of C, N, and S isotopes as natural tracers in trophic ecology has become increasingly widespread (Fry, 1988; Rau *et al.*, 1990) in order to identify different food

sources and trophic linkages (Malej *et al.*, 1993; Post, 2002). The elucidation of food pathways is based on the observation that consumers possess an isotopic and biochemical composition similar to that of their food. SIA is beneficial because it combines trophic-level ($\delta^{15}\text{N}$), food web paradigms ($\delta^{13}\text{C}$), and spatial position ($\delta^{34}\text{S}$) in trophic ecology (Post, 2002). Past studies have shown that the dominant prey of *A. aurita* is mesozooplankton (Malej *et al.*, 2007; Turk *et al.*, 2008). Fukuda and Naganuma (2001) also reported these dietary traits with the use of fatty acid composition. However, the results of this field study showed that the isotopic values of *A. aurita* changed from a zooplankton-based or pelagic signature to a more seston-based or benthic signature.

The $\delta^{13}\text{C}$ values of *A. aurita* in the Kiel Fjord (2011) showed a $\sim 3\text{‰}$ shift from June to September. According to work done by Mittermayr *et al.* (*submitted*) and the Bayesian mixing models, the isotope range of *A. aurita* suggests a diet change from a primarily zooplankton-based diet to more seston-based diet. Furthermore, the $\delta^{34}\text{S}$ values show a shift (of 7-10‰) from a more pelagic isotopic value to a more benthic value over the season. This conclusion was reached by the isotope values for seawater in the form of sulfate, +21‰ (Rees *et al.*, 1978; Grey & Deines, 2005), and the reduced, depleted sulfur derived from sediment pore water, +1‰ (Hansen *et al.*, 2009). $\delta^{15}\text{N}$ values showed a high variance in June and July, but steadied to an isotopic equilibrium in August and September. From information about trophic steps, it can be said that there was a trophic level change during June and July, but it stayed on one trophic level for August and September.

There are several possible reasons for this inter-annual diet shift and the variance observed in the beginning of the season. The first possibility suggests that the degradation of an *A. aurita* individual may affect that individual's ability to migrate through the water column (Malej *et al.*, 2007; Turk *et al.*, 2008). If unable to migrate, the animal could possibly get trapped in a stratified layer of the water column with limited or no prey selection; therefore, causing a shift isotope composition via diet change or starvation.

Secondly, a shift in food sources caused by seasonal variations, such as fish spawning or migration, could result in a possible contribution to jellyfish diets and a shift in SI values (Brodeur *et al.*, 2002; Hamer *et al.*, 2011). Hamer *et al.* (2011) found that fish eggs in the North Sea had $\delta^{15}\text{N}$ values with an approximate mean of 16‰ in June and July (2008). Additionally, this study, although on *M. leidyi*, said that fish eggs account for <10% of the diet. Therefore, further research is needed to determine if fish eggs are a significant diet source for *A. aurita*.

Thirdly, in the late summer, the water column of the fjord becomes well-mixed, due to both increasing water temperature and ship traffic, compared to early summer when the water column is stratified (Javidpour, *personal communication*). Mixing of the water column would mix benthic and pelagic organic matter; therefore, creating an isotopic shift in consumers.

Additionally, the influence of environmental factors such as rain, sewage and agriculture can also influence SI values. In late spring and early summer of 2011, there was a lot of rainfall (*personal observation*) which would increase agricultural runoff and pollution in the Kiel Fjord from fresh water inputs. In the literature, it has been shown for several species that additional nutrients from sewage are reflected at different rates determined by physiological characteristics (Littler & Arnold, 1982; Wallentinus, 1984; Padilla & Allen, 2000; Gartner *et al.*, 2002). Gartner *et al.* (2002) reported a range of $\delta^{15}\text{N}$ sewage values of 13.5 to 25.3‰, which marginally extends the values reported in past literature (Aravena *et al.*, 1993; Paerl & Fogel, 1994; McClelland & Valiela, 1998). Currently, $\delta^{15}\text{N}$ values for sewage input from the Baltic Sea region are missing, so we can only speculate the influence of these inputs on our sample values. Another difficulty in acquiring these values is that seawater has low nitrogen concentrations as a limiting nutrient (Gartner *et al.*, 2002).

Lastly, *A. aurita* and other jellyfish species are transported into the western Baltic Sea from the North Sea via wind direction and water movement (Javidpour, *personal communication*) and the isotope values adjust to reflect the settlement of the organisms into the Fjord (a.k.a. suspension subsidizing, Harrod *et al.*, *personal communication*). More simply, the isotope values take time, hence the gradual shift over the season, to reflect the environment of the open deeper sea to the shallower closed fjord.

In order to find out whether the cause of the shift over the season is caused by one or more, or even none of these possible explanations are correct, more research is needed.

5.1.4 Trophic Interaction between *A. aurita* and *C. capillata*

Another native species to the Kiel Fjord is *C. capillata*, the lion's mane jellyfish, another scyphomedusae species known to be a top predator (Hansson, 1997).

The $\delta^{34}\text{S}$ values for *C. capillata* were significant when compared to the values of *A. aurita*. There are two possible explanations for this observation. Firstly, *C. capillata* feeds purely on a zooplankton-based diet (*i.e.*, copepods). This observation is generally reported in the literature; however, other studies suggest that there is a strong trophic interaction of *C.*

capillata preying on the medusa stage of *A. aurita* (Plotnikova, 1961; Loginova & Perzova, 1967; Seravin, 1991; Båmstedt *et al.*, 1994; Hansson, 1997). Furthermore, if you look at the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of both species in this study, you can see a slight enrichment in the $\delta^{13}\text{C}$ value and a higher expected enrichment in $\delta^{15}\text{N}$ values between *A. aurita* and *C. capillata*, respectively. Secondly, because there are only four sampling dates for *C. capillata* at the end of the summer, the isotopic values might not yet reflect settlement of the population into the Fjord. When taken together, the isotopic values show that *C. capillata* and *A. aurita* have similar feeding habits. This study is the first to provide data for trophic interactions between *A. aurita* and *C. capillata* in the Kiel Fjord; therefore, further investigation is warranted.

5.1.5 Benthic vs. Pelagic Organic Matter Sources in the Kiel Fjord

In order to interpret isotopic values, a comparison to the environment must be made. Here, I present three such comparisons.

The first comparison is from a gut content analysis study of *A. aurita* in the Kiel Bight (2008) by Javidpour *et al.* (*unpublished*) (Figure 24). Although this data has a temporal limitation, it provides evidence for a decrease in zooplankton and an increase in planula larvae as a diet source. A possible explanation for this observation is that in July and August, *A. aurita* is at its height of reproductive potential (Schneider & Behrends, 1994; Javidpour, *personal communication*); therefore, there are more larvae present in the environment than zooplankton.

The second comparison is with a percent composition study of zooplankton in the Kiel Fjord (Mittermayr *et al.*, *unpublished*) (Figure 24). The percent composition of zooplankton shows a general decrease in July and August followed by a peak in September and October. This could explain why we see a decrease in this isotope values in *A. aurita*. However, more research is needed to determine if the values of *A. aurita* follow this pattern.

The last comparison is with the baseline filter-feeder, *M. edulis*. When comparing *A. aurita* $\delta^{13}\text{C}$ isotope values to the $\delta^{13}\text{C}$ baseline values of *M. edulis*, similar patterns were observed in the seasonal trends. The $\delta^{15}\text{N}$ isotope values, when compared to the $\delta^{15}\text{N}$ baseline values of *M. edulis*, show a clear trophic level difference for the two species of 1-2 trophic levels. Additionally, *M. edulis* $\delta^{34}\text{S}$ isotope values show an isotopic equilibrium at $\sim 17\text{‰}$, representing a pelagic- based diet, while there is a clear change from a more pelagic to a more benthic- based diet for *A. aurita*. This could be explained by a general shift in dominant prey

type in the Kiel Fjord over the season (i.e. zooplankton to seston). The trophic level difference could be *M. edulis* feeding primarily on seston and *A. aurita* feeding on seston and planula larvae.

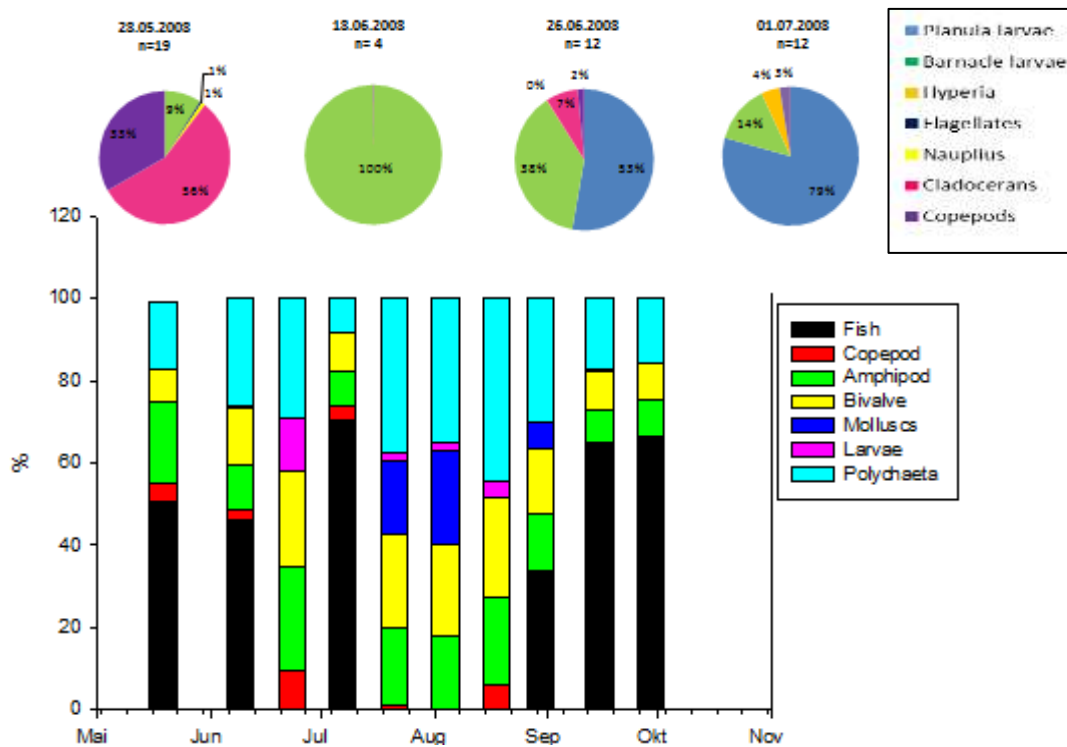


Figure 24: The pie-charts are representative of a gut content analysis study of *A. aurita* in the Kiel Bight (2008) (Javidpour et al., *unpublished*). The stacked bar chart is representative of a percent composition study of zooplankton in the Kiel Fjord (2011) (Mittermayr et al., *submitted*).

5.1.6 Comparison of Jellyfish Values in the Kiel Fjord with Other Locations

In addition to this work, a review of the literature allowed for a comparison of isotopic values of different jellyfish species from different parts of the world at various life stages (

Table 5). When compared to other studies of *A. aurita* and jellyfish species, this study's results have depleted $\delta^{13}\text{C}$ values and fit within the range of $\delta^{15}\text{N}$ values. However, there are few studies that have examined $\delta^{34}\text{S}$ values in the marine environment (Peterson, 1999; Moncreiff & Sullivan, 2001; Mittermayr *et al.*, *submitted*). Moncreiff & Sullivan (2001) observed $\delta^{34}\text{S}$ values in *A. aurita* of 19.6‰ in Hom Island, Queensland suggesting a pelagic

diet. Mittermayr *et al.* (*submitted*) also reported $\delta^{34}\text{S}$ values of 19.30 for *A. aurita*. The $\delta^{34}\text{S}$ values obtained from this study show similar results to the aforementioned studies but only in the beginning of the season. Values later in the season show a benthic signature. To my knowledge, these are the first such results obtained for *A. aurita*. Therefore, further research is strongly encouraged to verify these results.

5.1.7 Conclusions

Although *M. leidyi* was not present during the 2011 field study, interesting observations were made for *A. aurita* and *C. capillata* in the Kiel Fjord. The isotope values (C, N, and S) for *A. aurita* show evidence for a change in diet source. $\delta^{13}\text{C}$ suggested either a change in a diet or a shift in the entire Kiel Fjord baseline from the early-summer to late-summer. $\delta^{34}\text{S}$ added additional detail to this picture, as it revealed a strong shift from a isotopic value typical for a pelagic food web to one of a (at least partially) benthic food web. *M. edulis* also provides evidence for this picture by showing a general shift in diet source ($\delta^{34}\text{S}$) but in their stationary pelagic environment ($\delta^{34}\text{S}$). Mixing models, gut content analysis, and zooplankton percent composition also provide evidence for the change from a zooplankton-based diet to a more seston-based diet for both *A. aurita*. These patterns, combined with other biological and environmental factors (i.e. biometry, diet source, size, and weather), provide a picture of jellyfish activity in the Kiel Fjord. This is novel work for these two species in Kiel Fjord and deserves further investigation.

Table 5: Literature review of isotopic signatures of different jellyfish species from different parts of the world at various life stages.

Species	Location	Size (cm)	$\delta^{13}\text{C}$ ‰ (SD)	$\delta^{15}\text{N}$ ‰ (SD)	$\delta^{34}\text{S}$ ‰ (SD)	Diet Source (mean $\delta^{13}\text{C} \pm \text{SD}$)	Study
<i>Aurelia</i> sp.	Northern Baltic Proper	40	-20.0(0.40)	5.8 (0.85)	--	Zooplankton (-21.64 \pm 1.68)	Rolff, 2000
<i>Aurelia aurita</i>	Horn Island, Queensland	--	-19.5	15.0	19.6	--	Moncreiff & Sullivan, 2001
<i>Aurelia aurita</i>	Kiel Fjord, Baltic Sea	--	-25.56	7.83	19.30	Zooplankton (-24.5)	Mittermayr, submitted
<i>Aurelia aurita</i>	Kiel Fjord, Baltic Sea (June 2011)	16.5	-25 (0.66)	14.78 (2.26)	17.39 (1.83)	--	This Study
<i>Aurelia aurita</i>	Kiel Fjord, Baltic Sea (September)	17.05	-22 (0.85)	11.6 (0.74)	10.3 (0.68)	--	This Study
<i>Aurelia</i> sp. Polyps	Lab	0.12	--	5.5 (0.43)	--	Planktonic ciliates (--)	Kamiyama 2011
Rhizostoma/ <i>Aurelia</i>	French Guiana	--	-15.8 (1)	9.3 (1.4)	--	--	Fossette <i>et al.</i> , 2006
<i>Hydromedusae</i>	E. Bering Sea	5-50	-21 to -19	9 to 12	--	Amiphipods and Copepods (-24)	Brodeur <i>et al.</i> 2002
<i>Hydromedusae</i>	Bering Sea	5-50	~20	~11	--	Amiphipods and Copepods (-24)	Brodeur <i>et al.</i> , 2002
<i>Pelagia noctiluca</i>	Gulf of Trieste	> 4	-18.8	--	--	Zooplankton (-20.9 \pm 2)	Malej 1993
<i>C. mosaicus</i>	Smiths Lake, Australia	> 15	~22	--	--	Copepods (-22.2 to -25.75)	Pitt <i>et al</i> 2008
<i>P. camtschatica</i>	--	--	-25.7 (1.2)	--	--	--	Pitt <i>et al</i> 2009
<i>E. indicansm</i>	Central North Sea	--	-22.5	~7	--	Mesozooplankton (-22 to -21)	Frost <i>et al.</i> , 2011
<i>Tima bairdi</i>	Central North Sea	--	-20.5	9.5	--	Mesozooplankton (-22 to -21)	Frost <i>et al.</i> , 2011
<i>P. pileus</i>	Central North Sea	--	-21	8	--	Mesozooplankton (-22 to -21)	Frost <i>et al.</i> , 2011
<i>P. pileus</i>	Eastern North Sea	--	~ -19.5	~13.5	--	Mesozooplankton (-22 to -21)	Frost <i>et al.</i> , 2011
<i>P. pileus</i>	North Sea	--	~20	~15	--	Fish eggs (-18.5)	Hamer <i>et al.</i> , 2011
<i>Beroe</i> sp	Central North Sea	--	~20.5	~9.5	--	Mesozooplankton (-22 to -21)	Frost <i>et al.</i> , 2011
<i>Chrysaora melanaster</i>	Eastern Bering Sea	5-50	-18 to -22	11 to 15	--	Amiphipods and Copepods (-24)	Brodeur <i>et al.</i> , 2002
<i>Mnemiopsis leidyi</i>	North Sea	>0.05	~-19	~14	--	Zookplankton (-22 to -16)	Hamer <i>et al.</i> , 2011
<i>Bolinopsis infundibulum</i>	North Sea	--	~-21	~12.5	--	Zookplankton (-22 to -16)	Hamer <i>et al.</i> , 2011
<i>C. capillata</i>	Kiel Fjord, Baltic Sea	>8	-21 (0.7)	14(2.6)	18 (0.7)	--	This Study

5.2 Experimental Determination of Fractionation in the Ctenophore, *M. leidy*

Knowledge of species specific, or at least organism specific, fractionation rates are essential for understanding trophic relationships within a system. When animals undergo rapid dietary shifts due to migration, metamorphosis, or habitat change, the isotopic composition of their tissues begins changing to reflect that of the diet (Philips and Eldridge, 2006; Malpica-Cruz *et al.*, 2011). The use of SIA is based on the idea that there is a fixed isotopic enrichment (fractionation) between animals and their diets (Yokoyama *et al.*, 2005).

This study was designed to measure the fractionation rates in *M. leidy* when fed upon two different diet sources. The values presented here are the first reported values for *M. leidy* to my knowledge.

The $\delta^{13}\text{C}$ fractionation between *M. leidy* and *A. tonsa* was 0.26‰. Alternatively, *M. leidy* fed *A. salina* had fractionation of 2.14. This last value is relatively high and might be explained by the high variation in the prey values. However, DeNiro & Epstein (1978) reported $\delta^{13}\text{C}$ values up to 3‰ of whole-body tissue of individuals. The 3‰ fractionation can occur because the relationship between the consumer and its prey depends on the type of tissue and the diet source, and on the preservation of the lipids, carbohydrates, and proteins from the diet. Additionally, a study done by Malej *et al.* (1993) found that *Pelagia noctiluca*, a warm-water holoplanktonic scyphomedusa, was enriched 2‰ relative to its zooplankton-based diet.

The $\delta^{15}\text{N}$ fractionation between *M. leidy* and *A. tonsa* was 2.38‰. This value is relatively low quality; however, since it is the first such value for any ctenophore, it is valuable as a first proxy mixing models of ctenophore diet. The $\delta^{15}\text{N}$ fractionation between *M. leidy* and *A. salina* was 6.3‰. This could be related to the less nutritional value of *A. salina* and the starvation of *M. leidy* on this diet (Moller, *personal communication*). There is still much debate in the literature about nutritional stress (diet quality and starvation) affecting $\delta^{15}\text{N}$ fractionation (Hobson *et al.*, 1993; Fantle *et al.*, 1999; Adams & Sterner, 2000; Vanderklift & Ponsard, 2003). Additionally, the difference between 2.34‰ and 6.19‰ is also representative of a trophic step (3.4‰) (McCutchan *et al.*, 2003; Nordstrom *et al.*, 2009).

There are several factors influencing the fractionation of $\delta^{15}\text{N}$, including excretion, diet, taxon, environment, tissue type, and turnover rates (Vanderklift & Ponsard, 2003). Literature on fractionation values vary widely, but Table 4 provides a few examples of studies done on different marine organisms. For more listed studies on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of

freshwater and terrestrial organisms, please refer to McCutchan *et al.*, 2003, Vanderklift & Ponsard, 2003, and Yokoyama *et al.*, 2005.

Following a dietary shift to a diet differing in isotopic composition, the SI of a consumer's tissues will change over time to reflect the isotopic value of the new diet. Isotopic turnover rates vary as a function of metabolic turnover and growth rates (Fry & Arnold, 1982; Hesslein *et al.*, 1993; Carleton & Martínez del Rio, 2010). No studies, to my knowledge, have assessed the isotopic turnover rates for gelatinous zooplankton under fully controlled conditions. In this experiment, the ctenophore, *M. leidy*, was observed under a controlled dietary shift from *A. tonsa* ($\delta^{13}\text{C}$: $-22.66 \pm 1.97\text{‰}$, $\delta^{15}\text{N}$: $8.62 \pm 0.79\text{‰}$) to *A. salina*. ($\delta^{13}\text{C}$: $-21.82 \pm 1.55\text{‰}$, $\delta^{15}\text{N}$: $7.42 \pm 1.95\text{‰}$). From the literature, it was known that the metabolic carbon turnover rate for *M. leidy* was approximately 8.9 days at 20°C and 32.7 days at 10°C (Grosskopf & Javidpour, *Submitted*). Therefore, for this study, three weeks was allotted for adequate turnover at 18°C. Turnover was observed almost immediately (Figure 23), but the actual turnover rate could not be calculated due to unforeseen factors and complications. The first complication was the strong changes in growth rate throughout the experimental period. Secondly, if starvation occurred, then consumption of own body tissue would have occurred and altered the isotope value to reflect that of the consumer plus fractionation (no equalization). Lastly, during the last week of the experiment, there was a ~80% die-off in the *A. salina* culture. A sample was taken on the last day of the experiment after the survivors were allowed to grow to the required 4.0 mg. However, the die-off might bias the estimated turnover rate due to remaining individuals.

Conclusions and Recommendations

This was the first study to report C and N isotope trophic fractionation rates for gelatinous zooplankton, specifically *M. leidy*, based on a laboratory controlled feeding experiment. Although fractionation was estimated, there was high variance in the prey isotopic values. The turnover rate could not be estimated due to several unforeseen factors. For future research in this area, it would be better to have a larger experimental set up that would provide true replicates and protect against die-offs, to have a more controlled food concentration, and to have less animals per bucket. Since this is novel work on *M. leidy*, this study's results should be replicated and verified.

Table 6: Previous $\delta^{15}\text{N}$ fractionation studies compiled on marine organisms.

Consumer Species	Prey Species	$\delta^{15}\text{N}$ Fractionation Value (‰)	$\delta^{13}\text{C}$ Fractionation Value (‰)	Study
Amphipod	<i>Ulva</i> detritus	2.2 to 2.7	-1.3 to -0.4	Macko <i>et al.</i> , 1982
Prawn	Zooplankton	2.7	0.4	Dittel <i>et al.</i> , 1997
Crab	Meiobenthos	0.1 to 3.1	-3.4 to 1.0	Fantle <i>et al.</i> , 1999
Copepods	Phytoplankton	5.8	2.8	Checkley & Entzeroth, 1985
Fish	Zooplankton	5.6	3.7	Gaston & Suthers, 2004
Bivalves	Microalga	3.4 to 3.6	0.6 to 0.9	Yokoyama <i>et al.</i> , 2005
Ghost Shrimp	Microalga	3.6 to 4.0	2.0 to 2.2	Yokoyama <i>et al.</i> , 2005
Fish	Fish	2.6 to 3	0.8	Owens, 1987
Copepod	Flounder (parasitic)	-0.8 to 1.2	-1.6	Pinnegar <i>et al.</i> ,
Seal	Herring	+2.4	+1.3	Hobson <i>et al.</i> , 1996
<i>Artemia salina</i>	Algae	+9.2	+1.3	DeNiro & Epstein, 1978
<i>Artemia salina</i>	Yeast	+4.9	-	Minagawa & Wada, 1984

6. Supplementary Material

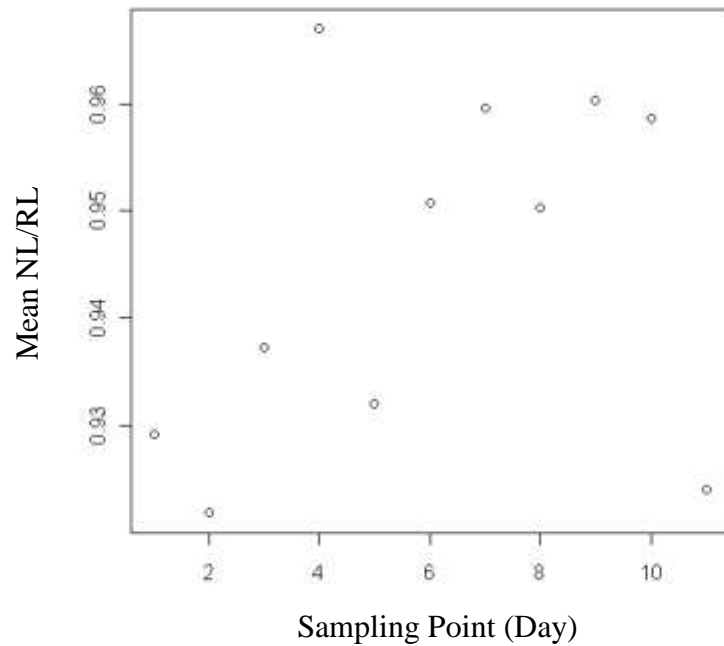


Figure 25: The mean nook length (cm) to round length (cm) of *A. aurita* over the sampling season (June – September) in the Kiel Fjord (2011).

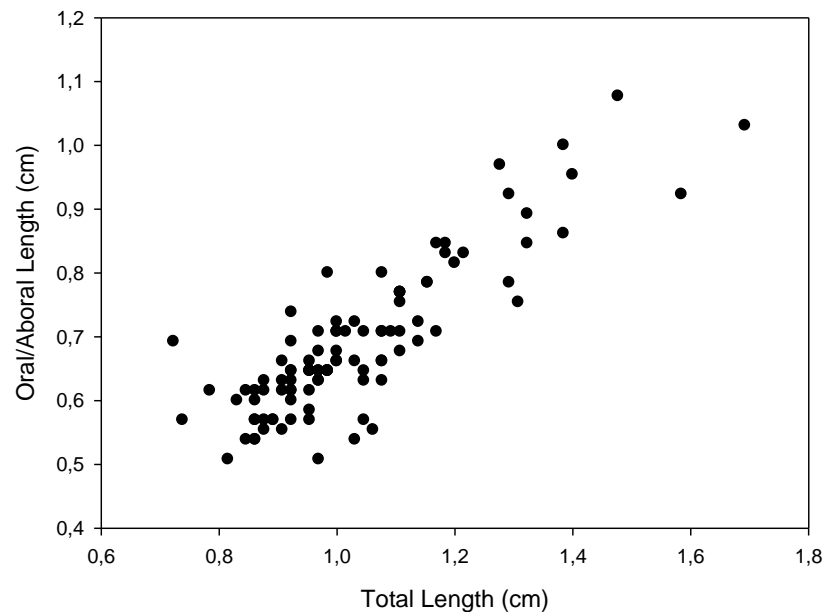


Figure 26: The ratio of oral length (cm) to aboral length (cm) vs. the total length (cm) of *M. leidy*.

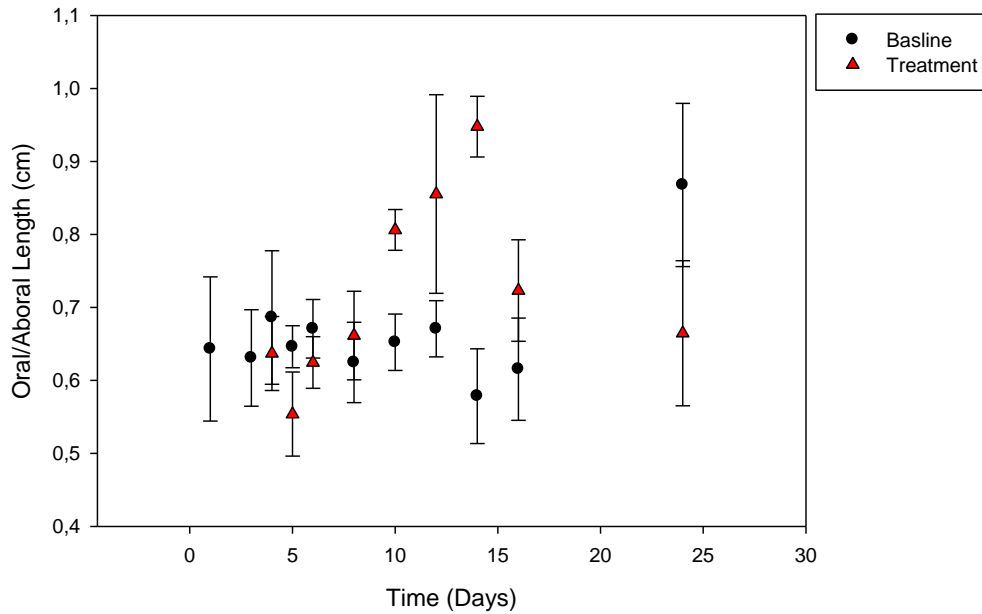


Figure 27: The ratio of oral length (cm) to aboral length (cm) of *M. leidyi* over the six week experimental period. *M. leidyi* was fed on two different diet sources. The baseline food source (black) was *A. tonsa*. The Treatment food source (red) was *A. salina*.

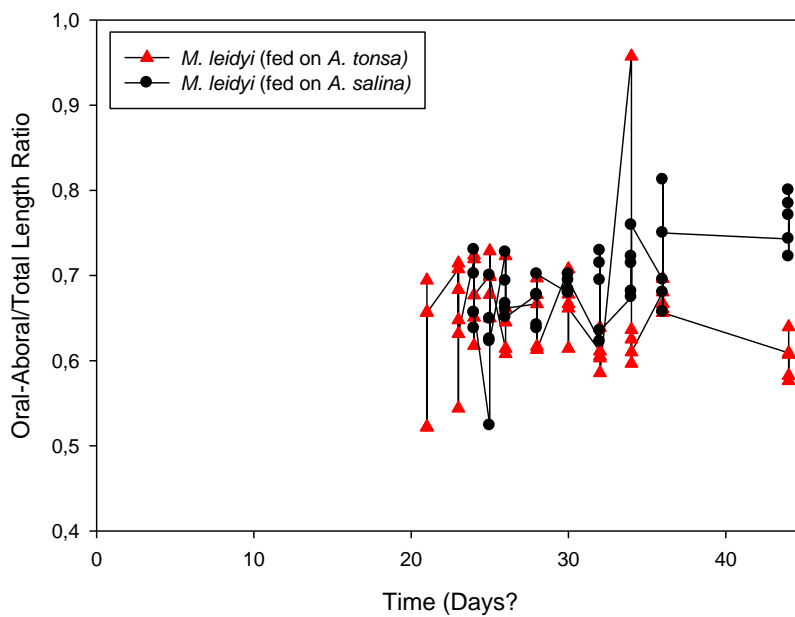


Figure 28: The ratio of oral length (cm)/aboral length (cm) to total length (cm) over the six week experimental period (44-days). *M. leidyi* was fed on two different diet sources. *M. leidyi* fed on *A. tonsa* is in red. *M. leidyi* fed on *A. salina* is in black.

7. Acknowledgements

To the best supervisors ever, Dr. Jamileh Javidpour, Dr. Jan Dierking and Prof. Dr. Ulrich Sommer, I owe you everything! Thank you so much for everything you have helped me achieve and the opportunities you presented me with.

To my friends, here in Europe and those in the U.S., you know who you are and you know that I couldn't have done this without you.

To all the supervisors, professors, and other scientists who offered their support, experience, and, especially, time to helping become a better scientist. Especially Charlotte Rafaluk, Christine Røllike Ditlefsen, Jessica Garzke, Agnes Mittermayr, Lene Friis-Moller and Thomas Hansen.

And...

To my family for their love and support, their grammar corrections and critiques, and their insane insurances that I have made them proud even before my thesis was finished.

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WILLIAMS, R. L., & JOHNSON, K. B. (2005). SEASONAL VARIATION, DIET AND PREY SELECTION OF THE CTENOPHORE *MNEMIOPSIS LEIDYI* IN A SUBTROPICAL ESTUARY. *INTEGRATIVE AND COMPARATIVE BIOLOGY*, 45(6), 1098. JOURNALS DEPT, 2001 EVANS RD, CARY, NC 27513 USA: OXFORD UNIV PRESS INC.

YOKOYAMA, H., TAMAKI, A., HARADA, K., SHIMODA, K., KOYAMA, K., & ISHIHI, Y. (2005). VARIABILITY OF DIET-TISSUE ISOTOPIC FRACTIONATION IN ESTUARINE MACROBENTHOS. *MARINE ECOLOGY-PROGRESS SERIES*, 296, 115-128. NORDBUNTE 23, D-21385 OLDENDORF LUHE, GERMANY: INTER-RESEARCH. DOI:10.3354/MEPS296115

IMAGES: 1. Figure3 (A-B): (A) Wikipedia.com, and (B) geomar.de
2. Figure 25: worldatlas.com
3. Cover Pages: <http://img.fotocommunity.com> (front) and <http://farm2.static.flickr.com> (Back)

9. Curriculum vitae

Ashlie Nicole Cipriano

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EDUCATION

University of Kiel, IFM-GEOMAR: Leibniz Institute of Marine Sciences, Kiel, Germany **July**
2012

- *Master of Science, Biological Oceanography*
- *Title: Biochemical tracers as a way to assess the trophic interactions of jellyfish, Baltic Sea*

American University, College of Arts and Sciences, Washington, D.C. **May**
2010

- Bachelor of Science, Marine Science and Biology (Dual Degree)
- GPA: 3.24 (4.0 scale)

GRANTS AND SCHOLARSHIPS

DAAD, Scientific Exchange, Co-collaborator **October 2011-2013**

Project Title and Amount, contract pending

Supervisors: Dr. Jamileh Javidpour (Post-doc at the Leibniz Institute of Marine Sciences (IFM-GEOMAR), Department of Food Web Ecology in Kiel, Germany) and Dr. Mark Martindale (Director of the Kewalo Marine Laboratory, Professor of Organismal Biology, and Principle Investigator at the University of Hawai'i).

ACADEMIC PUBLICATIONS

Cipriano AN, Moller LF, Javidpour J, Dierking J. Experimental determination of discrimination factors and turnover rates of the ctenophore *Mnemiopsis leidyi*. *Manuscript in preparation.*

RESEARCH EXPERIENCE

Harbour Propoise Bycatch, Iceland **06-2011-Present**

Seven Lovén Centre for Marine Sciences, Fiskebäckskil, Sweden **02/2012-Present**
Stable Isotope Analysis Experiment: fractionation and turnover rates in M. leidyi

Development of Ctenophores, IFM-GEOMAR Aquarium, Kiel, Germany **10/2010-09/2011**
Intern

- Developed Ctenophores as a model organism for the aquarium
 - Maintained breeding environment, while researching new breeding in captivity methods
 - Studied the development of Ctenophore larvae
 - Went on expeditions to collect organisms from the Baltic Sea and Kiel Fjord
-

Effects of Oceanic Acidification on Marine Organisms, Kiel/Sylt, Germany
07/2010

- Studied developmental response to different pCO_2 levels in Cephalopods
- Studied at the IFM-GEOMAR and Alfred-Wegener Institutes
- Cared for over 400 Cephalopod hatchlings, while maintaining their aquatic environments

Sea Urchin Development (National Institute of Health), Maryland USA
12/2009- 05/2010

- Designed and conducted different methodologies that look at specific genes that are involved in the signaling pathways between the ectoderm and primary mesenchyme cells (PMCs) of sea urchin larvae
- Studied the effects of different environmental cues on Sea Urchin development (i.e. food, predation)

Personal Care Product Effects on the Development of Zebrafish Larvae, American University,
 Washington, D.C.

2008-2010

- Designed and conducted experiments to determine the effects of sunscreen on development
- Designed and implemented all aspects of experiments (obtaining eggs/larvae, culture maintenance, data analysis)

Enrichment and Behavior in Cephalopods (Smithsonian National Zoo)

2007-2008

- Participated in Cuttlefish and Octopod behavioral studies
- Prepared enrichment sources for experiments
- Studied nervous systems involved with certain behaviors (recognition and movement)
- Prepared a paper summarizing evolutionary relationships and behavior

RELEVANT WORK EXPERIENCE

Harbour Porpoise Dissection Course, Husavik, Iceland
Assistant lecturer

06/2012 & 06/2013

Department of Experimental Ecology, Kiel, Germany
Hilfswissenschaftler (Laboratory Assistant)

09/2011-Present

- MesoAQUA, Conference. *Planning committee.*
- Weekly sampling on the Polarfuchs research vessel
- Narrator of published MesoAqua documentary film

Physiology Department, Kiel University, Kiel, Germany
Hilfswissenschaftler (Laboratory Assistant)

10/2010-09/2011

- Observed developmental response to different pCO_2 levels in Cephalopods and Sea Urchins
- Studied at the IFM-GEOMAR and Physiology Department at Kiel University
- Cared for Cephalopod hatchlings and Sea Urchins, while maintaining their aquatic environments

General Education Faculty Assistance Program, American University
Teaching Assistant, General Biology II

01/2010 -05/2010

National Institute of Health
Intern

12/2009-05/2010

- Studied the effects of different environmental cues on Sea Urchin development (i.e. food, predation)
- Conducted experiments and developed laboratory skills (i.e. immunostaining, PCR, etc.)

EnvironMentors
Mentor

08/2009-05/2010

- Mentored a high school student in two semester science program
- Helped high school student submit a project into research competition

National Smithsonian Zoo, Washington, D.C.

Keeper's Aide

2007-2009

- Acted as a source of guidance and education for visitors to the exhibits
- Assisted in food preparation, feeding, upkeep of habitats, and animal enrichment

ACADEMIC PRESENTATIONS, DOCUMENTARIES AND CONFERENCES

Stable Isotopes as a way to assess the trophic interactions in jellyfish, Baltic Sea

Oral Presentation, Current Topics in Marine Ecology, GEOMAR. Presented Winter 2012.

Geomar's mesocosm facilities and the last MESOAQUA PhD conference in mesocosm ecology

Narrator of published documentary film on mesoaqua.eu, December 2011

Mnemiopsis leidyi in European Waters: Where are they and what do we know?

Conference, 2nd Technical University of Denmark (DTU) Jelly Day, National Institute of Aquatic Resources, Kavalegåden 6, 2920 Charlottenlund, Denmark, October 2011

Mineralization in Vertebrates

Oral Presentation, Mechanisms of Biomineralization, IFM-GEOMAR: Leibniz Institute of Marine Sciences, presented Spring 2011.

Chemical Compounds of Sunscreen

Poster Presentation, Robyn Rafferty Matthias Student Research Conference, College of Arts and Sciences, American University, Spring 2009. Co-presented with Kimberly Fitzgibbons.

The Effects of Sunscreen on Zebrafish Embryonic Development

Oral Presentation, Robyn Rafferty Matthias Student Research Conference, College of Arts and Sciences, American University, Spring 2009.

RECENT & UPCOMING SEA TIME

2011. Culturing of *Mnemiopsis leidyi*. Sweden. IFM-Geomar. August 23-25.

2011. Marine Mammals in the Wild. Iceland. University of Iceland. July 1-10.

2011. Net Sampling. Cruise Ship Polarfuchs. Kiel Fjord. Weekly from February 2011-Present.

2010. Marine Biogeochemistry. Cruise ship RV Heincke. Kiel Fjord/Baltic Sea. December 1.

2010. Benthos Ecology. Cruise ship RV Heincke. Kiel Fjord/Baltic Sea. November 29.

RELEVANT SKILLS

- Skilled research images in Image J
- Skilled in Statistical Databases MATLAB, MixSIR, SigmaPlot, and the "R" program
- Skilled in Microsoft Office (Word, Excel, PowerPoint)
- Scuba Certified (PADI and CMAS)

MEMBERSHIP AND EXTRACURRICULAR ACTIVITIES

Verband Deutscher Sporttaucher E.V. (VDST)- CMAS (Scuba diving sports club)

2010- Present

10. Statement (Erklärung)

Herewith, I certify that the present thesis, apart from the consultation of my supervisors, was independently prepared by me. No other than the indicated resources and references were used. This thesis was presented to no other place within the scope of an examination procedure. The written thesis is identical with the electronic one.

I agree on including this thesis in the library of the Helmholtz –Zentrum für Ozeanforschung Kiel as well as in the library of the Christian-Albrechts-Universität zu Kiel.

Hiermit erkläre ich, dass ich die vorliegende Arbeit, abgesehen von der Beratung meiner Betreuer, selbstständig angefertigt und keine anderen als die angegebenen Hilfsmittel und Quellen verwendet habe. Sie wurde keiner anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Die schriftliche Arbeit ist mit der elektronischen identisch.

Mit der Aufnahme dieser Arbeit in die Fachbibliothek des Helmholtz –Zentrum für Ozeanforschung Kiel sowie in die Universitätsbibliothek der Christian-Albrechts-Universität zu Kiel bin ich einverstanden.

Kiel, den 25.07.2012

Ashlie Nicole Cipriano

