



# **Growth dynamics of juvenile European plaice (*Pleuronectes platessa* L.)**

Elzbieta Baranowska



**Faculty of Life and Environmental Sciences  
University of Iceland  
2016**



# **Growth dynamics of juvenile European plaice (*Pleuronectes platessa* L.)**

Elzbieta Baranowska

90 ECTS thesis submitted in partial fulfillment of a  
*Magister Scientiarum* degree in Biology

Advisor(s)

Björn Gunnarsson

Jónas Páll Jónasson

Prof. Guðrún Marteinsdóttir

Faculty Representative

Guðbjörg Ásta Ólafsdóttir

Faculty of Life and Environmental Sciences

School of Engineering and Natural Sciences

University of Iceland

Reykjavik, May 2016

Growth dynamics of juvenile European plaice (*Pleuronectes platessa* L.)  
Growth dynamics of juvenile plaice  
90 ECTS thesis submitted in partial fulfillment of a *Magister Scientiarum* degree in  
Biology

Copyright © 2016 Elzbieta Baranowska  
All rights reserved

Faculty of Life and Environmental Sciences  
School of Engineering and Natural Sciences  
University of Iceland  
Askja, Sturlugötu 7  
101, Reykjavik  
Iceland

Telephone: 525 4000

Bibliographic information:

Elzbieta Baranowska, 2016, *Growth dynamics of juvenile European plaice (Pleuronectes platessa L.)*, Master's thesis, Faculty of Life and Environmental Sciences, University of Iceland, pp. 79.

Printing: Háskólaprent  
Reykjavik, Iceland, May 2016

# Abstract

The productive nursery areas for many flatfish species are situated on European sandy shores, where both the quality and quantity of the habitat can control the recruitment processes. Juveniles metamorphose and settle at Icelandic nursery areas in early summer to maximize their growth and hide from larger predators during a span of few months before migrating deeper in the autumn. The main objective of the research was to analyse the growth patterns of plaice (*Pleuronectes platessa*) juveniles at the nursery ground in question. Samples of juvenile plaice were obtained bi-weekly from spring to fall at a highly fertile nursery area (Helguvík in Álftanes) from 2005 to present. Newly settled individuals were first observed at the end of May into early June and settlement, with 3 – 4 settling sub-cohorts, lasted until mid-summer with peak densities in June or July. The nursery ground period in Helguvík was short in comparison to European nurseries in general, but proved similar to nurseries at higher latitudes. Densities of settling plaice varied annually, with extremely high peaks observed in comparison to both Icelandic and other nurseries. In view of that, influence of density-dependent processes on growth was evaluated on three different scales; by comparing length measurement data to experimentally established maximum growth models, by otolith microstructure analysis and by evaluation of recent growth by increment width measurements. Maximum growth was visible in several years, at least during the early settlement period. Variability in growth was noticed both on intra- and inter-annual basis, and the influence of density dependent processes on growth was observed by analysis of increment width between two years with highly different settlement densities.

# Útdráttur

Uppeldissvæði margra flatfiskategunda er að finna í evrópskum sandfjörum. Fjörunar eru mikilvægar fyrir afkomu seiða og bæði stærð og gæði svæða geta haft áhrif á nýliðun. Botntaka skarkolaseiða (*Pleuronectes platessa*) hefst snemmsumars á Íslandi þegar sviflægar lirfur ganga í gegnum myndbreytingu og verða að botnlægum seiðum. Þau leita fæðu og skjóls fyrir afræningjum hátt í fjörunni yfir sumarið en fíkra sig dýpra þegar líður að hausti. Markmið rannsóknarinnar var að skoða vaxtarbreytileika hjá skarkolaungviði á uppeldissvæði. Frá árinu 2005 voru sýni tekin árlega með reglulegu millibili í Helguvík á Álftanesi frá vori og fram á haust. Botntakan hófst í lok maí og varði fram á mitt sumar þegar hámarkspéttleika var náð. Lengd þess tímabils sem seiðin dvöldu á uppeldissvæðinu var í samræmi við það sem gerist á hærri breiddargráðum. Botntökutímabilið var breytilegt milli ára, sama gildi um þéttleika skarkolaseiða sem komu á uppeldissvæðið á hverju sumri en þéttleikinn í Helguvík var einn sá mesti sem sést hefur, sé tekið mið af bæði íslenskum og evrópskum uppeldissvæðum. Þrír til fjórir misstórir nýliðunarárhópar voru oftast greinanlegir í fjörunni. Vöxtur var bæði breytilegur innan árs og milli ára. Uppgefinn hámarksvöxtur miðað við hitastig sást á mörgum árunna, aðallega snemma á botntökutímabilinu. Hnignun vaxtar innan ársins var greinanleg þegar leið að hausti. Þéttleikaháð áhrif voru greinanleg með skoðun tveggja samanburðarára þar sem kolar voru aldursgreindir og breiddarhringir mældir.

*Dedykacja*

*Dla moich kochanych babć Nadziei i Czesławy  
oraz dziadka Kazimierza.*

*Udało się!*





# Table of Contents

<b>List of Figures .....</b>	<b>ix</b>
<b>List of Tables.....</b>	<b>xi</b>
<b>Acknowledgements .....</b>	<b>xiii</b>
<b>1 Background .....</b>	<b>1</b>
1.1 Introduction of European plaice .....	1
1.2 Nursery grounds of juvenile flatfish.....	4
1.3 Otolith microstructure and age estimation .....	5
1.4 Fish growth.....	7
1.5 Density-dependent processes .....	8
<b>2 Introduction.....</b>	<b>9</b>
<b>3 Materials and methods .....</b>	<b>13</b>
3.1 Study area and sample collection .....	13
3.2 Sea surface temperature measurements.....	14
3.3 Otolith microstructure examination and analysis .....	16
3.4. Data analysis .....	19
3.3.1 Density .....	19
3.3.2 Growth performance .....	19
3.3.3 Length based instantaneous growth rates .....	19
3.3.4 Annual growth .....	21
3.3.5 Somatic and otolith growth analysis .....	21
3.3.6 Individual instantaneous growth .....	21
3.3.7 Sub-cohort analysis .....	22
<b>4 Results .....</b>	<b>23</b>
4.1 Dynamics of juvenile plaice .....	23
4.1.1 Density .....	23
4.1.2 Average lengths .....	24
4.2 Analysis of length distributions.....	26
4.2.1 Growth performance .....	26
4.2.2 Length based instantaneous growth rate .....	27
4.2.3 Annual growth .....	29
4.3 Growth during high and low density .....	30
4.3.1 Somatic and otolith growth.....	30

4.3.2	Individual instantaneous growth.....	31
4.3.3	Settlement and sub-cohort identification.....	34
4.3.4	Recent growth analysis .....	36
<b>5</b>	<b>DISCUSSION.....</b>	<b>38</b>
	<b>References .....</b>	<b>45</b>
	<b>Appendix A .....</b>	<b>57</b>

# List of Figures

<i>Figure 1.1 Life-cycle of European plaice, adjusted to the Icelandic European plaice population.</i>	4
<i>Figure 1.2 Juvenile plaice otolith.</i>	7
<i>Figure 3.1 Map of Iceland and the study site (Helguvík cove, Álftanes in Faxaflói).</i>	13
<i>Figure 3.2 Helguvík sampling area, beam trawl, sampling and looking for remaining juveniles in the net</i>	14
<i>Figure 3.3 Right otolith with post-rostrum/rostrum axis and accessory growth centres.</i>	17
<i>Figure 4.1 Mean densities of settled 0-group plaice in Helguvík during the years 2005 – 2014.</i>	24
<i>Figure 4.2 Development of mean length (mm) in Helguvík during the years 2005 – 2014.</i>	25
<i>Figure 4.3 Comparison between observed growth of 0-group plaice and predicted growth according to experimentally established models.</i>	26
<i>Figure 4.4 Deviation from the theoretical maximum growth models, Glazenburg (○) and Fonds (Δ).</i>	27
<i>Figure 4.5 Estimations of the instantaneous growth rates (<math>G; d^{-1}</math>) of 0-group plaice in all sampling years (2005 – 2014)</i>	27
<i>Figure 4.6 Annual growth rates in relation to highest density peak for each sampling year.</i>	29
<i>Figure 4.7 Relationship between otolith size and juvenile plaice lengths</i>	30
<i>Figure 4.8 Instantaneous growth rate (<math>G \text{ day}^{-1}</math>) in aged juveniles from June/July and August samples from the years 2005 and 2012.</i>	32
<i>Figure 4.9 Fitted exponential growth curves for the aged June/July and August juveniles</i>	32

<i>Figure 4.10 Plaice lengths histogram with estimated parameters for sampling dates before density peak and during emigration in August. ....</i>	<i>34</i>
<i>Figure 4.11 Back-calculations of settlement date .....</i>	<i>35</i>
<i>Figure 4.12 The mean and the standard error of each sub-cohort are plotted (2005 left and 2012 right). Red dots denote where mean length of the cohort was fixed. Each age reading was also plotted as a thin line between the length at sampling day and the settlement day (12 mm). On each graph, two growth curves are plotted on a given day. In red, the combined growth model of Glazenburg for juveniles between 13-45 mm and Fonds for juveniles between 45-200 mm. In black, exponential growth curve from the same region (Gunnarsson 2010). ....</i>	<i>36</i>
<i>Figure 4.13 Relationship between recent growth (<math>\text{mm d}^{-1}</math>) and total length (mm) .....</i>	<i>37</i>
<i>Figure 4.14 Instantaneous growth rate (<math>G \text{ day}^{-1}</math>) for compared individuals during settlement period in 2005 and 2012. ....</i>	<i>37</i>

# List of Tables

<i>Table 3.1 Overview of mean monthly (Mar. – Sep.) sea surface temperature in Reykjavík harbour during sampling years.....</i>	<i>15</i>
<i>Table 3.2 Numbers of extracted and used otoliths for aging and width measurements from years 2005 and 2012. ....</i>	<i>16</i>
<i>Table 4.1 Summary of fitted regression models: null model (Null<sub>G</sub>) and multiple linear regression (LM<sub>G</sub>) for instantaneous growth model.....</i>	<i>28</i>
<i>Table 4.2 Summary of fitted regression models: null model (Null<sub>AGR</sub>) and multiple linear regression (LM<sub>AGR</sub>) for annual absolute growth model. ....</i>	<i>29</i>
<i>Table 4.3 Summary of growth rates for both settlement and emigration period from aged individuals in years 2005 and 2012. ....</i>	<i>31</i>
<i>Table 4.4 Parameters for exponential growth models in 2005 and 2012 .....</i>	<i>33</i>
<i>Table 4.5 Summary of growth rates for settlement period (June/July) in comparison years.....</i>	<i>37</i>
<i>Table A.1 Summary of sampling dates, number of tows, catch in all tows per sampling date, mean density (+/- SD), mean length of measured individuals (+/- SD) and tide variation for each day. ....</i>	<i>57</i>
<i>Table A.2 Summary of mean length trajectories (length-at-date data) for sampling years 2006 – 2011 and 2013 – 2014 compared to maximum growth models under optimal food conditions; Glazenburg and Fonds. ....</i>	<i>59</i>
<i>Table A.3 Analysis of variance of annual growth variation (mm d<sup>-1</sup>) in years 2005 – 2014, examining the main effects.....</i>	<i>61</i>



# Acknowledgements

First and foremost, I would like to extend my sincere gratitude to my advisors for sharing their knowledge and guiding me through past years. My supervisor, Guðrún Marteinsdóttir, for giving me an opportunity to pursue my field of interest within marine biology and for her guidance along the way, especially at the homestretch. To my advisor at the Marine Research Institute, Björn Gunnarsson, for inspiration and direction through fascinating branches of complex life of plaice juveniles and giving me an opportunity to learn limited fields in marine biology. My advisor at the Marine Research Institute, Jónas Páll Jónasson, for all his guidance, patience and encouragement through the whole statistical and writing process, and especially during times of disorientation. Thank you for always having an open door.

A warmest thank you to everyone at the Marine Research Institute for taking me on this amazing journey and for the opportunity to pursue this dream. To everyone who went to Helguvík and sampled juveniles for all those years before me and later to all my helpers. To my amazing summer co-workers at the MRI, especially Anika, Sigurvin and Viðar, just for being you and for all the breaks. I would like to thank Jónbjörn Pálsson and Jón Sólmundsson for answering all my odd questions regarding flatfishes.

Last but certainly not least I would like to thank my parents for all their support and especially the transport/migration to this amazing island in my childhood. Finally, big and very special thanks to my fiancée Bjarni Gíslason for supporting me, encouraging, listening and reading over many drafts of this thesis and not losing his faith in me during the whole process.





# 1 Background

## 1.1 Introduction of European plaice

European plaice *Pleuronectes platessa* Linnaeus, 1758, (order Pleuronectiformes; Family Pleuronectidae) is the only member of its genus, and one of eight species from its family inhabiting Icelandic waters (Jónsson & Pálsson, 2013). In general, Pleuronectids are characterized as flatfishes with both eyes situated on the right side of the body and having a well-developed lateral line on both of its sides (ICES, 2016; Moyle & Joseph J. Cech, 1982; Thomas A. Munroe, 2004). Biogeographical distribution of plaice stretches from the western Mediterranean Sea, along the European coast, as far north as the White Sea and Iceland (FOA, 2016; Jónsson & Pálsson, 2013). At times, plaice can also be found on the south coast of Greenland (Gunnarsson, Jónsson, & Pálsson, 1998).

Adult European plaice (*Pleuronectes platessa*) is found on the continental shelf and slope around Iceland, with the highest abundance in the south-west and west of the island (Anonymous, 2015). It is mainly found on a sandy or muddy substrate, occurring at depths ranging from the coast down to 200 m, sometimes even deeper (Jónsson & Pálsson, 2013; Sæmundsson, 1926). Small juvenile individuals stay in intertidal areas down to approximately 10 m, while older and larger individuals roam deeper waters (Gunnarsson et al., 1998; Sigurðsson, 1989). Main spawning and feeding grounds of the Icelandic adult plaice population is found in warmer waters to the south and west of the Icelandic coast (Sigurðsson, 1989; Solmundsson, Pálsson, & Karlsson, 2005). However, Gunnarsson, Jonasson, & McAdam, (2010) suggest that spawning locations can be found along the entire Icelandic coast. The Icelandic plaice population to the south and west of Iceland has high fidelity to both its spawning and feeding areas, which demonstrates high structure of Icelandic population (Solmundsson et al., 2005). Plaice has sexual dimorphism in growth, maturation and mortality (Rijnsdorp & Ibelings, 1989; van Walraven, Mollet, van Damme, & Rijnsdorp, 2010). The proportion of females increases with age and size as the females grow faster and reach larger sizes than males (Rijnsdorp & Witthames, 2004). The spawning period in Icelandic waters in the south and south-west ranges from the end of February to early June, peaking in March and April (Gunnarsson et al., 2010; Sigurðsson, 1989; Solmundsson, Karlsson, & Pálsson, 2003; Sæmundsson, 1926). In colder waters in the north, the spawning season starts later, or towards the end of March, and finishes before mid-July, with peaks in May and June (Gunnarsson et al., 2010). Plaice females in the North Sea can stay in spawning condition for approximately 3 – 6 weeks with the duration of this stage increasing with age. Males, however, are in spawning condition for

11 weeks and arrive at the spawning site before the females (Rijnsdorp & Witthames, 2004).

In Icelandic waters spawning takes place at a depth of 50 – 100 m (Jónsson & Pálsson, 2013). Afterwards, pelagic and spherical eggs drift until they hatch (Russell, 1976). Development of eggs and temperature are highly correlated (Hyder & Nash, 1998; van der Veer & Witte, 1999), and the development takes from 10 days at 14°C up to 35 days at 2.8°C (Fuiman & Werner, 2002; Gibson, 1999; Ryland & Nichols, 1975 (seen in Thompson & Riley, 1981)). Plaice is a serial spawner (Nash, Witthames, Pawson, & Alesworth, 2000), with the extended period of batch-spawning and egg size frequently decreasing over successive spawning periods (Fox, Geffen, Blyth, & Nash, 2003; Nash & Geffen, 2014). For female plaice, the term “maternal effects” is in correct use, where the interaction between older age, larger size and better condition produces larger eggs (Fox et al., 2003). Larger eggs produce larger larvae (Chambers & Legget, 1996), and their development time is, therefore, longer than for larvae hatching from smaller eggs (Fox et al., 2003; Geffen, van der Veer, & Nash, 2007). The difference in standard length for larvae from small and large eggs can be up to 2.5 mm (Blaxter & Staines, 1971; Russell, 1976). The vertical dispersal of the eggs in the water column is wide, with occasional clusters at the surface (Coombs, Nichols, & Fosh, 1990; Gibson, 1999). Horizontal dispersal is highly dependent on the characteristics of the waters where the spawning occurs (Fox et al., 2003; Gibson, 1999; van der Veer, Ruardij, van den Berg, & Ridderinkhof, 1998). For Icelandic nursery areas in the south-west of the country, the main dispersal is clockwise and follows the Atlantic water currents from the south and the coastal currents which divide from the warm Atlantic current (see in Gunnarsson et al., 2010).

At hatch, plaice larvae are symmetrical and around 5 – 7.5 mm in length (Blaxter & Staines, 1971; Russell, 1976). During approximately the first two weeks their nourishment is drawn from the yolk sac (Gibson, 1999; Ryland, 1966), but exogenous feeding can occur five days after hatch (Tucker, 1998). The length of the larval development period also differs, with higher temperatures leading to shorter larval periods (Allen, Brophy, McGrath, & King, 2008; Fox, Planque, & Darby, 2000), if no food limitation at high temperatures occurs (van der Veer, Bolle, Geffen, & Witte, 2009). Because of this, the larval period can vary between 31 (Fox et al., 2007) and 100 days (Karakiri & Westernhagen, 1989), considering the otolith increments as a post-hatch day-mark. The larval period in Icelandic waters is around 53 – 61 days (see figure 1.1), with periods reaching the higher range to the north of Iceland (Gunnarsson et al., 2010). At the end of the larval stage, plaice goes through ontogenetic changes, when symmetrical pelagic larva metamorphoses to a benthic flatfish (Geffen, Nash, Dau, & Harwood, 2011; Moyle & Joseph J. Cech, 1982). This dramatic body transformation requires broad dynamic changes, such as flattening of the body, 90° eye migration, development of unpaired fins and reduction of paired fins, accompanied by changes in pigmentation (Christensen &

Korsgaard, 1999; Fuiman, 1997; Geffen et al., 2011; Moyle & Cech, 1982). The onset of metamorphosis in plaice larvae does not seem to be accurately size- or age-related, but rather follows the development of the larvae (Hovenkamp & Witte, 1991). However, the size of metamorphosing larvae can also differ as growth and size at metamorphosis seem fairly disconnected. Thus plaice larvae can grow fast and metamorphose at smaller size or grow slower and metamorphose at larger size (Hovenkamp & Witte, 1991). Brooks & Johnston (1993) observed that metamorphosis occurs between 7 – 10 weeks after hatching at 8°C when larvae are around 10 – 12 mm in total length (TL). Modin, Fagerholm, Gunnarsson, & Pihl (1996), also demonstrated that metamorphosis, in laboratory reared plaice, starts to occur when larvae are around 12 mm. Metamorphosis starts in the pelagic phase (Geffen et al., 2007), when plaice larvae are still off-shore. However, it is not clear if metamorphosing juveniles settle in deeper waters, 6 – 10 m in depth, before they move into the shallower nursery areas (Gibson, Robb, Wennhage, & Burrows, 2002; Lockwood, 1974) or finish the metamorphosis in the shallow water (Creutzberg, Eltink, & Van Noort, 1977, see in Geffen et al., 2011). The metamorphosis and settlement are not necessary fixed events and, therefore, the newly metamorphosed plaice can stay in the water-column even when they have undergone the change (Geffen et al., 2011). However, because their bodies are denser, the larvae at the end of pre-metamorphosis stage increase the time spent on the bottom (Gibson, 1999). Settlement to the nursery areas differs between the seas in Europe, but mainly it lasts through the spring months: February – May in western Wadden Sea (van der Veer, 1986), March – April in the west of Ireland (Allen et al., 2008) and March to late-June in Northern Irish Sea (Geffen et al., 2011). In Icelandic waters the onset of the settlement period has been noted from middle/end of May (Pálsson & Hjörleifsson, 2001).

Settlement or immigration of newly metamorphosed plaice to the nursery areas often takes place in pulses (Al-Hossaini, Liu, & Pitcher, 1989; Rijnsdorp, Stralen, & van der Veer, 1985; van der Veer, 1986). That means the arrival of a large number of individuals in batches to the beach in a short period of time. Those pulses or peaks in settlement are called sub-cohorts (Al-Hossaini et al., 1989) and may be caused by many different reasons, e.g. periodicity in spawning or hatching pulses (Allen et al., 2008), divergent transport from different spawning locations (Al-Hossaini et al., 1989) or selective tidal transport (Rijnsdorp et al., 1985). Following the nursery ground period, plaice juveniles follow the “Heincke’s Law” while emigrating from shallow nursery grounds into deeper waters (Heincke, 1913, see in Nash & Geffen, 2014), when they are approximately between 40 – 55 mm in length (Gibson et al., 2002; Lockwood, 1974). By the time plaice is around 30 cm long and 3 – 4 years old it recruits into the adult spawning population (Anon, 2015; Jón Sólmundsson, personal communication, MRI, 2015). The overview of a typical life-cycle for plaice juvenile in Icelandic waters is illustrated in figure 1.1.

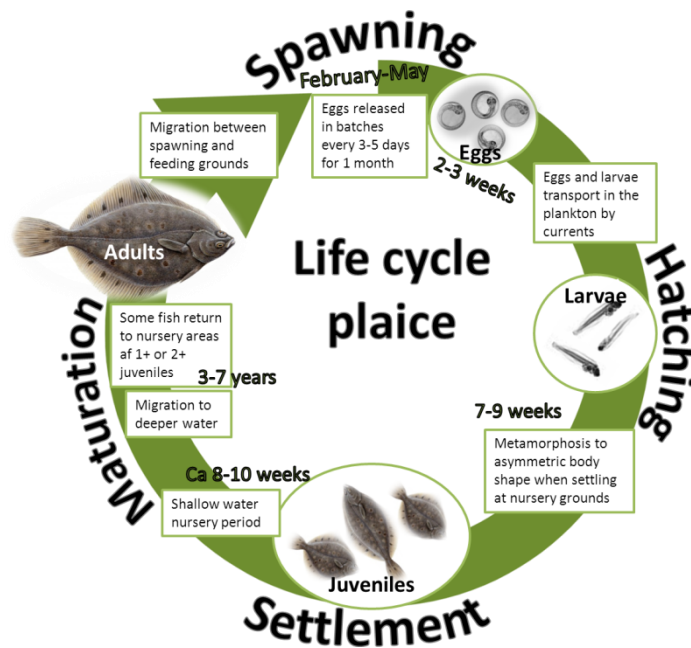


Figure 1.1 Life-cycle of European plaice, adjusted to the Icelandic European plaice population.

## 1.2 Nursery grounds of juvenile flatfish

Shallow coastal zones are considered to be hard ecosystems, with great variations in abiotic factors that can fairly limit species diversity in such habitats (Moyle & Cech, 1982). Nevertheless, sheltered beaches can play a major role as essential nursery areas for divergent epibenthic fish and crustacean species (Amara, 2003; van der Veer, Freitas, Koot, Witte, & Zuur, 2010). Various flatfish species, i.e. plaice, European flounder (*Platichthys flesus*) and Common dab (*Limanda limanda*) (Amara & Paul, 2003; Amara, 2003; Freitas, Cardoso, Skreslet, & van der Veer, 2010) aggregate in large numbers in those relatively sheltered, soft-bottomed beaches to enhance growth and survival during the summer period (Able, Neuman, & Wennhage, 2005; Gibson, 1994). Thus, when contemplating the functioning of nursery grounds it is important to look both at the quantity and quality of those habitats (Gibson, 1994).

The amount of suitable habitats is referred to as habitat quantity which seems to have explicit impact on flatfish population size (Gibson, 1994; Rijnsdorp et al., 1992; van der Veer, Berghahn, Miller, & Rijnsdorp, 2000). However, the influence of biotic (i.e. larval supply, food, predators) and abiotic (i.e. temperature, salinity, oxygen, hydrodynamic processes, habitat structure, depth) factors on juveniles in nursery can be defined as habitat quality (Gibson, 1994; Wennhage, Pihl, & Stål, 2007). While the quantity of suitable nursery areas can be measured directly, to measure the quality of nurseries can be complex and is almost always done on a comparative basis (Wennhage et al., 2007). The quantity and quality of ideal nursery habitats can vary both spatially and temporally. Exposure of the nursery can contribute to the settling behaviour of plaice, by affecting sediment and

vegetation (Pihl & van der Veer, 1992). The presence of predators such as brown shrimp (*Crangon crangon*) and shore crab (*Carcinus maenas*) can also have influence on the settling behaviour (Wennhage & Gibson, 1998). It has been shown that the year-class strength of plaice is determined early; during egg and larval stage (Leggett & Deblois, 1994), before metamorphosis in the North Sea (van der Veer, 1986) or just shortly after for the Irish Sea (Nash & Geffen, 2000). The nursery ground period, however dampens the variability in recruitment with the quantity and quality of nursery habitats (Beverton & Iles, 1992; Gibson, 1994; Nash & Geffen, 2000; Rijnsdorp, Berghahn, Miller, & van der Veer, 1995), as high-quality nurseries will contribute more juveniles into the adult population than sub-optimal nursery areas and larger nursery sites can give rise to a greater number of juveniles into adult stock (Dahlgren et al., 2006; van der Veer et al., 2000).

In Icelandic waters, plaice nursery areas have been found all around the Icelandic coast, with the highest abundance on spatially restricted beaches in the south and west (Gunnarsson et al., 2010). There are not many predators of plaice juveniles around Iceland, except the main two, brown shrimp and shore crab. Shrimp is mainly predator on small plaice juveniles (under 30 mm) (van der Veer & Bergman, 1987), but is also one of the main interspecific competitor for larger individuals in late summer (Evans, 1983, seen in Link, Fogarty, & Langton, 2004). The brown shrimp has recently colonised Iceland as the first individuals were found between 2001 and 2003 on tidal flats in Southwestern part of the country in Faxaflói (Gunnarsson, Ásgeirsson, & Ingólfsson, 2007). Since then the shrimp has colonized quickly with northward expansion along west Icelandic coast (Gunnarsson et al., 2010) and has been observed in high numbers on sandy beaches in the northern part of Westfjords as far as Bolungarvík (Koberstein, 2013).

### **1.3 Otolith microstructure and age estimation**

The inner ear in fish lies adjacent to the brain on either side of the head (Helfman, Collette, Facey, & Bowen, 2009) and is responsible for the detection of sound and movement of the head relative to gravity (Farrell, 2011). The labyrinth is a peripheral sensory compartment within the inner ear that includes orthogonally arranged semi-circular canals and three otolith end organs (Farrell, 2011). The otolith organs are the saccule, the lagena and the utricle. Each has a sensory epithelium and white calcareous structures of characteristic shapes called otoliths or “earstones”. The sagitta is situated in the sacculus, the lapillus in the utricle and the asteriscus in the lagena (Helfman et al., 2009). Typically the two largest pairs, i.e., the sagittae and the lapilli, are present at hatch and therefore, they are used for age estimation in larvae and juveniles (Fuiman & Werner, 2002). Crystallized calcium carbonate, usually in the form of aragonite and collagenous fibrous protein otolin form the otoliths (Degens, Deuser, & Haedrich, 1969; Fuiman & Werner, 2002). Shortly after the onset of the crystallization, the otolith growth occurs through the accretion of new

material over its surface. The otolith growth is cyclic, and a unit that forms due to a daily calcium metabolism rhythm and amino acid synthesis is called growth increment (Campana & Neilson, 1985). The daily growth increment is bipartite and divided into the incremental zone, deposited during the active period of the calcium metabolism, and discontinuous zone. In a compound microscope, the incremental zone appears broad and translucent and the discontinuous zone, narrow and opaque (Campana & Neilson, 1985). During active growth, broad daily incremental units are laid down but during slow growth increment units are narrower and with solid aragonite microcrystals (Watabe, Tanaka, Yamada, & Dean, 1982). Formation of daily increments is driven by endocrine-driven endogenous circadian rhythm and occurs within 24-hours (Al-Hossaini & Pitcher, 1988). This inner formation system is entrained at an early age by photoperiod or other daily environmental cues (Campana & Neilson, 1985). In 1971, Greog Pannella discovered the phenomena of daily growth increment in the otoliths of larval fishes (Pannella, 1971, see in Fuiman & Werner, 2002). This phenomenon opened the window to explore deeper and with more accuracy the hatch and early life cycle of larval and juvenile fish. Estimating age in young fishes was of vital importance for fish ecology, where the survival and growth could be investigated more thoroughly at this crucial a stage when year classes for coming adult populations were being established (Fuiman & Werner, 2002). Age estimation studies of larval flatfish expanded rapidly from the 1980s, through application of otolith analysis techniques that enabled the estimation of larval age, especially for recruitment studies (Nash & Geffen, 2014). Karakiri & Westernhagen, (1989) confirmed the daily increment formation in otoliths in larval and juvenile plaice and the response of increment formation to different abiotic (temperature and salinity) changes. In otoliths of plaice larvae and juveniles, important life events are often noted as the approximate time of hatch (Karakiri & Westernhagen, 1989) and also the time of metamorphosis and settlement (Modin et al., 1996). Many factors, for example, changes in temperature, food intake or composition, can attribute to the formation of extra increments between the daily increments or decrease the clearness of growth increments which can disturb the accuracy of age-reading (Al-Hossaini & Pitcher, 1988; Campana, 1992; Karakiri & Westernhagen, 1989; Lagardère, 1989). However, the daily growth increments still stand out and have a rhythmical pattern.

When the symmetrical flatfish larvae go through metamorphosis the orientation of the otoliths changes, from begin vertically positioned to being horizontally placed (Sogard, 1991). At this point, the cyclic formation shifts and accessory growth centres are established on the external part of the otolith and these tend to shape the growing otolith into the prone rectangular shape found in adult individuals (Al-Hossaini et al., 1989). In plaice, metamorphosis is marked on otoliths with the formation of accessory growth centres (Karakiri, Berghahn, & van der Veer, 1991; Modin et al., 1996) and wide and fairly distinct increments in post-metamorphosed juveniles (Karakiri, Berghahn, & Westernhagen, 1989; Modin & Pihl, 1994). This occurs when the body is already flattened,

and the eye has completed migration (Fox et al., 2007; Modin et al., 1996). Nevertheless, age estimation within the accessory growth centres is often difficult and it is not known for sure if the increments there reflect the daily growth. However, when the increment zones once again collide into unbroken rings, it is almost certain that these show daily growth increments (Nash & Geffen, 2014).

Otoliths grow as the fish grows (also defined as somatic growth of the fish) and they follow the general pattern in accordance with slower growth when the organism gets larger and after its maturation (Fuiman & Werner, 2002; Helfman et al., 2009). Many environmental factors, such as temperature, starvation, stress, etc., which influences the growth rate of the fish, can also affect the width of the daily increments however solely under extreme conditions (Morales-Nin, 2000; Selleslagh & Amara, 2012). Examination of the increment width has been applied for the studies of changes in daily or recent growth in both larvae and juvenile flatfishes (Geffen et al., 2011; Karakiri et al., 1989; Lagardère, 1989; Modin & Pihl, 1994; Raedemaeker, 2011; Sogard, 1991).



*Figure 1.2 Juvenile plaice otolith.*

## **1.4 Fish growth**

Growth of marine organisms can be defined as physiological response to exogenous biotic (food availability and quality, interaction with other species) and abiotic (temperature, oxygen, salinity and light) environmental factors and endogenous physiological factors (such as genetics, maternal factors, health, stress and reproductive state) (Al-Hossaini & Pitcher, 1988; Fuiman & Werner, 2002; Nash & Geffen, 2014). Lower vertebrates, for example, fish, exhibit indeterminate growth, which is when growth continues throughout the lifespan of an individual, although at a continually decelerating rate (Fuiman & Werner, 2002; Helfman et al., 2009). As mentioned earlier genetics can influence growth, for example; larger females produce larger eggs which eventuate in larger larvae hatching (Fox et al., 2003). However, aside from the size at hatch, the body mass and the growth of the fish during first year is considered critical. Faster growing juveniles reach larger size

sooner, swim faster, and therefore, have increased immunity to predators (Modin & Pihl, 1994). The enhanced body condition and the ability to deal with variable food supply also adds to their competitive ability (for example regarding food selection). Growth, therefore, can often be found to correlate with the survival of juveniles in the nursery area and, therefore, have an impact on recruitment (Beverton & Iles, 1992; van der Veer, Pihl, & Bergman, 1990).

Growth during larval stage until metamorphosis is considered rapid in larval plaice (Hovenkamp & Witte, 1991). It, however, ceases during ontogenetic changes at metamorphosis (Christensen & Korsgaard, 1999). Variation in individual growth, during nursery ground period, annually and on spatial scale, is known in plaice and is a topic of many studies (reviewed in Ciotti, Targett, Nash, & Geffen, 2014). Influential factors that have received the most attention concerning the variability in growth, both on the intra-annual and annual basis, are temperature, prey conditions, intraspecific competition and interspecific competition (reviewed in Ciotti et al., 2014). The growth of plaice juveniles in nursery areas can also be one of the general indicators of individual fitness, habitat quality and ecosystem status (Gibson, 1994).

## **1.5 Density-dependent processes**

In studies of fish population dynamics, density dependence is one of the fundamental concepts (Rose, Cowan Jr, Winemiller, Myers, & Hilborn, 2001). If population gain and loss rates, i.e. growth or primary demographic rates (such as survival, movement and reproduction), are influenced by variation in population size or density, then the density dependent processes operate (Hixon & Johnson, 2009). Density dependent processes are said to be compensatory if their proportional (per capita) gain rate decreases or the loss rate increases as density increases. However, density dependent processes are said to be depensatory if they slow population gain rates (especially population growth) at low densities (Hixon & Johnson, 2009; Rose et al., 2001). This kind of pattern is also defined as Allee effect (see in Hixon & Johnson, 2009). Compensatory density dependence can be caused by competition and, occasionally, by predation. It has a negative feedback on population size and, therefore, acts towards stabilization of a population (Hixon & Johnson, 2009; Rose et al., 2001). Influence from compensatory density dependent processes has been noted during the nursery ground phase in juvenile flatfish (Rijnsdorp et al., 1995), where the processes dampen the inter-annual variability in year-class strength (Nash & Geffen, 2000). During the juvenile plaice nursery ground period, mortality is primarily density-dependent, and it occurs predominately during settlement and shortly after density peak (Nash & Geffen, 2012). Juvenile plaice mortality during nursery ground phase is mainly regulated by predation by brown shrimp and shore crab (Nash & Geffen, 2012; van der Veer & Bergman, 1987) but high settlement densities have also been observed as contributing factor (Pihl, Modin, & Wennhage, 2000). Nevertheless, very high densities have also been associated with lower juvenile growth (Ciotti, Targett, &



Burrows, 2013; Fox et al., 2014; Modin & Pihl, 1994; Nash, Geffen, Burrows, & Gibson, 2007; Nash & Geffen, 2012; Pihl et al., 2000; Teal, de Leeuw, van der Veer, & Rijnsdorp, 2008). As density-dependant growth could result not strictly from food limitation but by reduction of feeding rate of individuals when other members of same population are present. That is intra-specific competition could increase with increasing density of individuals (Heath, 1992) and result in possible limitations of food resources (Le Pape & Bonhommeau, 2015).

## 2 Introduction

In terms of survival and successful recruitment, growth in the early life stages is exceptionally important for fish populations (Anderson, 1988). Consequentially growth can be a good determinant for individual fitness and survival (Sogard, 1997), but overall population growth can also identify influential environmental factors and quality of the habitat (Able, 1999; Beck et al., 2001). Numerous fish species have a structural bipartite life cycle, where their particular developmental periods are highly dependent on specific type of habitats (Moyle & Joseph J. Cech, 1982). Multiple flatfish species, for example, are attached to shallow inshore habitats during their first summer, where they accumulate and thrive in a limited geographical environment (van der Veer et al., 1990). Those nursery zones very rarely provide ideal circumstances throughout a whole summer, leading to maximum possible growth of juveniles (Nash & Geffen, 2014). Nevertheless, the nursery areas are normally highly productive (Gibson, 1994), without drastic environmental changes influencing the growth of the juveniles. Growth conditions, however, can invariably shift during this first crucial year and both intra- and inter-annual variations can be observed (Ciotti et al., 2014). Many variables, both biotic (larval supply, food, predators) and abiotic (temperature, salinity, oxygen, hydrodynamic processes, habitat structure, depth) can impact growth (Fuiman & Werner, 2002). Thus, patterns, causes and effects of variability in growth during first year of fish life can be difficult to grasp.

European plaice (*Pleuronectes platessa* L.), is a commercially exploited temperate flatfish species, which geographical distribution ranges widely in European coastal waters (FOA, 2016). Its general accessibility and economical importance pushed European researchers into intensive studies of this flatfish species, especially with regards to its early life history in the North Sea and the Irish Sea. Adult plaice populations spawn offshore where they reproduce by broadcast spawning, which can span a 100 day period (Ellis & Nash, 1997; ICES, 2016; Sigurðsson, 1989). Eggs and larvae are pelagic and their drift and dispersal are mainly controlled by hydrodynamics of the surrounding waters (Fox, McCloghrie, & Nash, 2009; Gibson, 1999; Rijnsdorp et al., 1985; van der Veer et al., 1998). When plaice larvae have reached a certain developmental stage, they undergo ontogenetic changes,

called metamorphosis, to start a demersal life (Geffen et al., 2007; Moyle & Joseph J. Cech, 1982). Metamorphosed larvae settle in pulses (Al-Hossaini et al., 1989; Geffen et al., 2011) and concentrate at shallow, sandy-bottomed beaches in spring or early summer, known as nursery areas (Able et al., 2005; Gibson, 1994). Juveniles spend their first summer at shallow depths (Gibson, Burrows, & Robb, 2011), where they maximize their growth and thus likelihood of survival. In European waters, the abundance of settling plaice is primarily determined at early egg and larval stages, mostly by controlling abiotic factors such as temperature (Fox et al., 2000; van der Veer et al., 1990; van der Veer & Witte, 1999), predation (Nash & Geffen, 2012; van der Veer & Bergman, 1987), hydrodynamics (Bolle et al., 2009III; Nielsen, Bagge, & Mackenzie, 1998; van der Veer et al., 1998) and connectivity between the spawning sites and nursery areas (Bolle et al., 2009III; Fox, McCloghrie, & Young, 2006). During first summer, 0-group plaice assemble at low depths in the beach, at this stage the abundance can be very high at limited area (Modin & Pihl, 1994). As mentioned before, the settling abundance is determined at early life stages, however the year class strength is fixed during the nursery ground period, because of dampening effects due to density dependent processes (Nash & Geffen, 2000). Those dampening processes operate mainly through density-dependant mortality during settlement phase, however, they influence also juvenile growth at some point. Although growth has been widely studied for juvenile European plaice (Ciotti et al., 2014), even in the case of such well researched species the overall understanding of growth variations is still somewhat incomplete.

Variability in juvenile plaice growth rate on temporal and inter-annual basis has been observed on many occasions in various nursery grounds in European shallow sandy areas (Ciotti et al., 2014). Primarily, the influence of ambient water temperature was considered the main determinant for maximum growth (Gibson, 1994; van der Veer et al., 1990; van der Veer, 1986) as “maximum growth – optimal food” hypothesis (Karakiri et al., 1991; van der Veer & Witte, 1993) assumed optimal food conditions in nursery areas and therefore no competition for food. However, the intra-annual variability in juvenile plaice growth has been widely reported, especially the decline in growth rate late in the nursery ground period which deviates from experimentally established maximum growth models with large thermal range (Freitas et al., 2010; Jager, Kleef, & Tydeman, 1995; Nash et al., 2007; Nash, Geffen, & Hughes, 1994; Teal et al., 2008; van der Veer et al., 1990; van der Veer & Witte, 1993). Some studies have observed a steady decline in growth rate during whole nursery ground period (Freitas, Kooijman, & van der Veer, 2012; van der Veer et al., 2010), other have shown a decline late in the summer (Amara, 2004; Ciotti, Targett, Burrows, & Jech, 2013; Freitas et al., 2010; Hjörleifsson & Palsson, 2001; Nash et al., 2007; van der Veer et al., 1990; van der Veer & Witte, 1993) and yet others did not identify any declining growth pattern (van der Veer et al., 1990). Many influencing factors for temporal growth variation have been identified; factors such as size-selective migration, food limitations or intake (Amara & Paul, 2003; Freitas et al., 2010), inter-

specific competition (Freitas et al., 2010), have all been proposed as potential influences. However, some contradiction has also been seen considering those as influencing factors, pointing to opposite patterns. Intra-specific competition has not been identified as influencing factor for intra-annual growth variations (Amara & Paul, 2003; Freitas et al., 2010; Nash et al., 2007, 1994a). However, mortality due to density dependant processes including intra-specific competition has been widely seen during nursery ground period (Nash & Geffen, 2012).

Inter-annual growth variation has also received much attention and has been widely reported in European nursery areas (Fox et al., 2007; Haynes, Brophy, & McGrath, 2012; Modin & Pihl, 1994; Teal et al., 2008; van der Veer et al., 2010). The interest of ecologists on this variability in growth has been driven by deeper understanding in inter-annual recruitment variability. Factors mentioned earlier that influence the intra-annual variabilities have also been contributed to inter-annual variations and the annual changes in temperature (Teal et al., 2008; van der Veer et al., 1990; van der Veer, 1986) have been considered as important variable. However, it is often very difficult to untangle thermal variations from other environmental factors influenced by change in temperature (Nash et al., 2007). Variations in prey condition have also been proposed as effecting variable (Karakiri et al., 1989), however intra-specific competition is probably most intriguing factor. Effects of plaice density on inter-annual growth variation have been analysed on several occasions, however the conclusions were equivocal. Some studies found negative (Teal et al., 2008) or none (Haynes et al., 2012) relationship between plaice density and growth rate, but others found that growth rate was lower in years with high plaice density (Ciotti et al., 2013a; Geffen et al., 2011; Modin & Pihl, 1994; Nash et al., 2007).

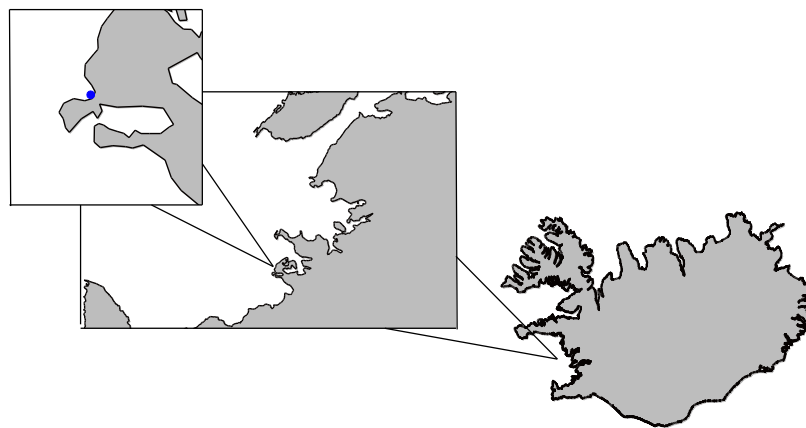
Plaice is commercially exploited flatfish species in Icelandic waters and has been for many decades. Adult population in Icelandic waters reached a historical low around the year 2000, where the population and recruitment were noticeably small (Anonymous, 2015). While the early life history of plaice has received considerable attention in the North Sea, the Dutch Wadden Sea and the Irish Sea, information for Icelandic waters is lacking. In 1926, Bjarni Sæmundsson, was the first to mention plaice juveniles in Icelandic shore waters, in his paper (1926) he revealed that juveniles stay in shallow waters in Faxaflói and Breiðafjörður but also in brackish waters in the south of Iceland near Hornafjörður, Hamarsfjörður and Álftafjörður. Little is known about nursery grounds of the juvenile plaice in Icelandic shores, even though one of the oldest sources for the processes of the juveniles comes from Icelandic shores (Tåning, 1929). Since Tåning, (1929), two studies have been published on growth and nursery ground processes of juvenile plaice, by Hjörleifsson & Pálsson, (2001) in the northern part of Faxaflói and Gunnarsson et al., (2010) around Iceland. However, these studies cover solely one year and cannot verify the repeated patterns and processes of juvenile nursery areas. Gunnarsson et al., (2010) observed very high density numbers, possible existence of spawning areas in northern Icelandic waters and spatial variability in growth.

The objectives of the current study were to investigate patterns and processes of juvenile plaice in Icelandic inshore waters. Ten year sampling data was used to observe the settling pattern and density variations during nursery ground period. Growth pattern was investigated both on intra- and inter-annual basis, where length-at-date data was compared to experimentally establish maximum growth models and seasonal growth was calculated between the samplings and on annual basis. Two years with variable population density were chosen from this data to examine closer by ageing juveniles and comparing growth of individuals on particular dates during the settlement period and later in the summer. Length-frequency data, finite mixture distribution and otoliths were used to analyse the number of sub-cohorts migrating to the nursery in these two years. Furthermore, width of otolith increments in those two years was measured during settlement period (June/July) to investigate recent growth and if density variation has an effect on growth rate. The null-hypothesis was that there is no difference in recent growth between comparison years.

## 3 Materials and methods

### 3.1 Study area and sample collection

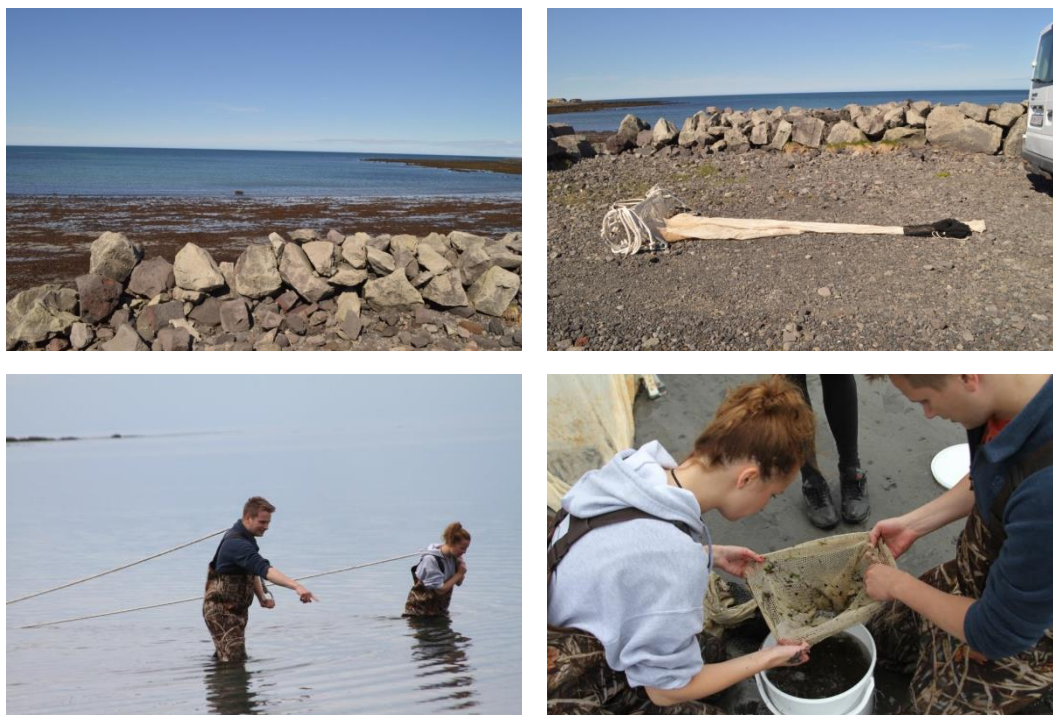
The study area was located in Faxaflói bay, more specifically in Helguvík cove in Álfanes (Fig. 3.1) ( $64^{\circ}05'54.5''\text{N}$   $22^{\circ}01'55.9''\text{W}$ ). It has a non-vegetated sandy substrate, is readily accessible and considered exposed with moderate sloping shore. The sampling period in Helguvík started in the end of May of 2005 and has been ongoing through the summer months (May – September) annually until 2014. It was scheduled to start sampling around late-May, early-June, if circumstances allowed it. In the years 2006 and 2007 sampling started earlier, or mid-May, to examine if 0-group juveniles were already present. Due to poor or non-existing catch numbers it was decided to start sampling from now on later that month. During 2009 and 2010 the sampling went on for roughly one year, from end of May 2009 until end of October 2010. In that year sampling was done biweekly in the summertime but once a month before and after the summer period.



*Figure 3.1 Map of Iceland and the study site (Helguvík cove, Álfanes in Faxaflói) with indication of sampling station.*

A one meter wide beam trawl (Fig. 3.2) was used as a sampling instrument. 5.5 m long, the trawl, equipped with one tickler chain, had 8 mm mesh size in its main body and 7 mm mesh size at cod end. The trawl was pulled by two people, parallel to the beach, 3 – 6 times at low tide ( $-0.32 - 1.05$  m). Sampling was undertaken during daytime and around neap tide, since the newly settled plaice juveniles are concentrated near the surf-line at these times (Gibson et al., 2002). The number of tows depended on weather conditions as well as algae and sand consistency accumulated in the trawl. The trawl was pulled for approximately 3 min and the towing speed was kept as constant as possible at around  $35 \text{ m min}^{-1}$ . Tow length varied between 40 – 100 meters, but after 2008, if nothing disrupted the tow (i.e. sand or algae in the trawl net), 50 m tow length was standard. The tow length was measured with a hand held GPS device (Garmin). The average depth at each sampling

varied between 0.3 – 1 meter as this is the optimal depth for highest plaice density (Gibson et al., 2002) and variation of the depth was used so that the trawl would not pass through the same path as the previous tow. The trawl catch was put carefully into sampling buckets with seawater and the net was checked for any left behind flatfish juveniles. In the laboratory, individuals were collected out of the buckets, counted and measured from snout to tail (i.e. total length, TL) along with other fish and large crustacean species collected. Numbers of juveniles that were length measured from each tow varied depending on the count of individuals in the tow; from larger samples (>100 ind. per tow) normally only a subsample was length measured. Samples were preserved in 96% ethanol until extraction of otoliths. No corrections for gear efficiency were made nor for size-selective gear efficiency.



*Figure 3.2 Helguvík sampling area (upper left), 1 m beam trawl (upper right), handtowing the trawl (lower left) and looking for remaining juveniles in the net (lower right).*

## **3.2 Sea surface temperature measurements**

Sea surface temperature (SST) records were obtained from dataset extracted from the Marine Research Institute website (<http://www.hafro.is/Sjora/>). The thermometer, type MS-110SH produced by HUGRUN, is situated in the nearby (~13 km) Reykjavík harbour (64°09'10.3"N 21°55'55.5"W) and the mean temperature is recorded on a daily basis. There was a malfunction of the thermometer in 2006, from 24 of July until 14 of August and during that period interpolated temperature values were used, based on the average between the last available values. Monthly mean values were calculated from April to October (Fig 3.3).

Table 3.1 Overview of mean monthly (Mar. – Sep.) sea surface temperature in Reykjavik harbour during sampling years.

Month/Year	Temperature (°C)									
	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
March	3.13	3.60	2.45	2.75	2.97	2.80	2.91	3.75	3.78	2.37
April	4.43	3.51	4.89	3.81	4.28	3.34	4.81	5.57	4.31	4.97
May	6.81	6.33	7.43	6.69	6.98	7.30	7.27	7.38	5.76	7.72
June	10.05	8.33	10.05	10.46	10.04	11.41	9.08	11.27	8.94	11.10
July	11.51	10.63	13.13	11.81	12.68	12.89	11.50	12.30	11.00	11.38
August	11.49	11.94	11.55	12.93	12.07	13.19	12.25	12.86	10.37	11.54
September	9.22	10.64	10.20	11.12	10.53	11.10	10.54	9.90	9.17	10.82

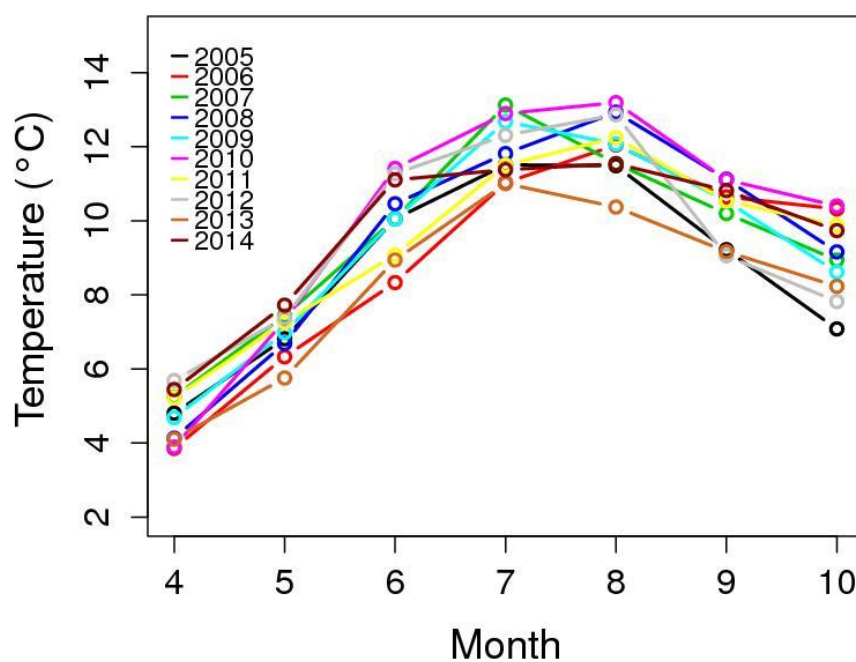


Figure 3.3 Mean monthly seawater temperature (°C) observed in Reykjavík harbour from April to October 2005 through 2014.



### 3.3 Otolith microstructure examination and analysis

Two years were randomly picked out as indicators of low juvenile density (2005) and high juvenile density (2012) years in Helguvík (See table A1 in Appendix A, for accurate density numbers). Afterwards, right and left sagittal otoliths were extracted from randomly picked plaice juveniles from 2005 and 2012, around day 60 from first settlement (27 June 2005 and 4 July 2012) and again around day 85 (17 August 2005 and 20 August 2012).

*Table 3.2 Numbers of extracted and used otoliths for aging and width measurements from years 2005 and 2012.*

Year	Sampling date (calendar day)	<i>n</i> of otoliths extracted	<i>n</i> of aged otoliths	<i>n</i> of used (readable) otoliths	Otoliths used for somatic growth/otolith growth	<i>n</i> of otoliths used for width measurement
2005	June 27th (178)	68	64 (98%)	54 (84%)	41	18
2005	August 17th (229)	50	46 (92%)	40 (87%)	-	-
2012	July 4th (186)	84	69 (82%)	59 (86%)	43	19
2012	August 20th (233)	50	44 (88%)	38 (86%)	-	-

Total length of the juveniles, which the otoliths were extracted from, was measured to the nearest mm and correction was made for shrinkage due to dehydration caused by ethanol preservation. The relationship between TL before ( $TL_b$ ) and TL after ( $TL_a$ ) the preservation in ethanol (96%) for approximately two months was obtained by simple linear regression model from samples collected in 2005 where the overall shrinkage of juveniles from ethanol was around 6% ( $n = 267$ , range = 13.42–68.08 mm and  $R^2 = 0.9985$ ):

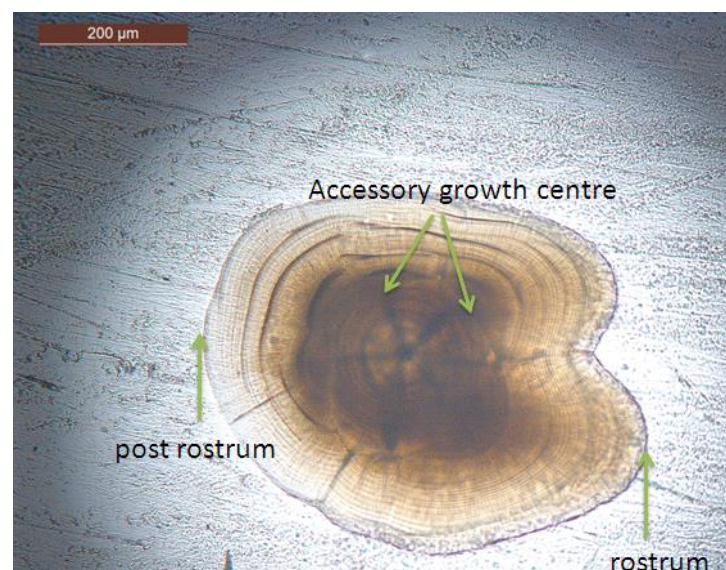
$$TL_b = 1.0373TL_a + 0.4361 \text{ (Eq. 1)}$$

Otoliths were cleaned, dried and mounted with convex side up on a standard microscopic slide and covered with quick-dry glue (containing: etyl-2-cyanoacrylate). As soon as the glue had fully dried (after approximately 24 hours) the otoliths were handground to the core with lapping film. Some larger otoliths from individuals approximately larger than 40 mm TL were too thick for polishing only on one side, therefore they had to be turned around and polished from both sides to get a clear view of daily increments from the hatch ring to the end of the otolith. This was done by polishing first the side which turned upwards on the microscope slide until outer daily increments appeared clearly. The microscope slide was then immersed in water and left until the glued area had peeled off



from the glass. Next the glued surface was cut as close to the otolith as possible, turned and glued again to the microscope slide. Afterwards, the otolith was polished down to the nuclear plane with lapping film. The number of daily increments was counted using 1000x magnification (Campana & Neilson, 1985). Each otolith was counted three to six times and if a consistent age was not obtained due to poor otolith preparation (counts differed by more than 10%), the otolith was discarded (see table 3.2). The secondary growth centres were used as indicator of the end of metamorphosis (Al-Hossaini & Pitcher, 1988; Karakiri & Westernhagen, 1989; Modin et al., 1996). Even though the juveniles can stay in the water column for period of time after the secondary growth centres form (Geffen et al., 2011), we assumed that settlement and metamorphosis go together for settlement date calculations. The dates of settlement for the aged 0-group plaice juveniles were calculated for each individual based on the post-metamorphic age. Individuals were grouped into three-day classes and settlement date identified.

For recent growth analysis from the settlement period (June/July, Table 3.2) in years 2005 and 2012, the 37 otoliths were extracted from juveniles who ranged between 15.96 – 21.66 mm TL. Right sagittal otolith was chosen for diameter and recent growth analysis because of anterior-dorsal/posterior-ventral axis which allows the maximum growth axis due to nucleus off-centering (Gilliers, Amara, Bergeron, & Le, 2004). A picture of a usable right sagitta was captured using a Microscope Camera (Leica DFC320), using 200x or 400x magnification and afterwards the daily increments were enhanced with a software (Adobe Photoshop). Shortly after metamorphosis the flatfish otoliths are asymmetric, both in size and shape (Sogard, 1991). Therefore, a rostrum to post-rostrum axis was identified in sectioned sagittae (Fig. 3.3). Image analysis system (ImageJ) was used to measure the longest diameter along the core rostrum axis and the width of the 10 most recently deposited daily increments where they are the widest for more accurate comparison (Modin & Pihl, 1994).



*Figure 3.3 Right otolith with post-rostrum/rostrum axis and accessory growth centres.*

The diameter in micrometres ( $\mu\text{m}$ ) was recorded as otolith size at catch. The relationship between the sagittal size (from the otoliths used in recent growth analysis and aged usable otoliths from June/July samplings) and size of the juveniles was identified as linear with strong correlation between the variables ( $R^2 = 0.8965$ ) (Fuiman & Werner, 2002). Thence, the mean daily increment width over the last 10 days before capture was calculated as an index of recent growth. Total length at 10 d before capture (TL10) was back-calculated from the otolith using the biological intercept method (Campana & Jones, 1992; Campana, 1990; seen in Suthers & Sundby, 1996):

$$TL10 = TL_c - [10d \text{ width } (TL_c - 6.5) / radius] \quad (\text{Eq. 2})$$

Where the TL10 is total length 10 days before capture,  $TL_c$  is total length at capture and 6.5 was the chosen standard length of plaice larvae at hatch in Icelandic waters (Blaxter & Staines, 1971).

## 3.4. Data analysis

### 3.3.1 Density

The density of juvenile plaice in Helguvík bay was calculated as the number of individuals per 100 m<sup>2</sup> for every single tow using the following equation:

$$Density = (C / TM) / W * 100 \quad (Eq. 3)$$

Where C is total catch of juvenile plaice, TM is tow length in meters and W is the width of the trawl in meters. Mean density was calculated for every sampling date (Table A1 in appendix.)

### 3.3.2 Growth performance

Analysis of growth performance was made for all sampling years by comparing the observed field mean lengths with simple model predictions on maximum growth. Such models were established under unlimited food supply at various temperatures, in case of plaice two such models were available (Fonds, Cronie, Vethaak, & Van Der Puyl, 1992; Glazenburg, 1983, see in Freitas et al., 2010). These models were obtained by monitoring plaice originated from populations in the Dutch Wadden Sea. The given temperature range varies from 2-20°C which fits with expected temperature at Helguvík Bay (Fig. 3.3, Table 3.1). In both studies, maximum growth rate ( $dL/dt$ ) was expressed in terms of increase in length per time (mm d<sup>-1</sup>):

$$Glazenburg \text{ model: } dL/dt = (1.3T + 1.7)/30 \quad (T = 2 - 20^\circ C) \quad (Eq. 4)$$

$$Fonds \text{ model: } dL/dt = 0.0136T^{1.5} - 6 \cdot 10^{-9} * T^6 \quad (T = 2 - 22^\circ C) \quad (Eq. 5)$$

Glazenburg model was based on small 0-group plaice juveniles (13 to 40 mm TL), but Fonds used larger 0-group plaice juveniles (50 to 200 mm TL).

### 3.3.3 Length based instantaneous growth rates

Mean lengths were used to determine the instantaneous growth rate of the population ( $G$ , d<sup>-1</sup>) in all sampling years, between two successive samplings:

$$G = \frac{\ln L_{i+1} - \ln L_i}{\Delta t} \quad (Eq. 6)$$

Where  $L_i$  were mean length at respectively sampling  $i$  and the subsequent sampling  $i+1$  and  $t$  is the time differences in days between the two samplings.  $G$  is considered to represent the growth rate at the midpoint between two successive samplings. After calculations values growth rate ( $G$ ,  $n = 59$ ) were divided into periods before and after observed annual peak in density.

Loess (Cleveland, 1979), a nonparametric smoothing method was used to draw a smoothing curve through data points for instantaneous growth rate to visualize the trend of intra-annual growth variation before and after the density peaks. Smoothing parameter  $\alpha = 0.75$  and polynomial degree  $p = 2$  (quadratic) were visually selected as estimators by most plausible fit.

Multiple regression was used to analyse the effect of juvenile density (D) and mean total length (TL) in each sampling date and the mean SST between the adjacent samplings on the instantaneous growth (G) for all sampling years. Prior to analysis the density of juveniles were log-transformed to establish linearity.

The starting model was:

$$G_t = \alpha + \beta_1 \log D_t + \beta_2 SST_t + \beta_3 TL_t + \varepsilon$$

Where G is instantaneous growth rate, D is density and TL is mean total length for each sampling date and SST is mean sea surface temperature in Reykjavík harbour,  $\alpha$  is intercept,  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are regression coefficients and  $\varepsilon$  is the error term.

Predictor variables from a stepwise model selection were included in the models if they were significant at  $p < 0.1$ , which led to the following models used in this study,

Instantaneous growth model,

$$G_t = \alpha \quad (\text{Null})$$

$$G_t = \alpha + \beta_2 SST_t + \beta_3 TL_t + \varepsilon \quad (\text{LM})$$

$\alpha$  is intercept,  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are regression coefficients and  $\varepsilon$  is the error term.

All regression models in length based instantaneous growth and later in annual growth (chapter 3.3.4) were fitted by minimizing the negative log-likelihood,

$$-\log L = 0.5n \log(2\pi) + n \log \hat{\sigma} + \frac{\sum (Y_i - \hat{Y}_i)^2}{\hat{\sigma}^2} \quad (\text{Eq. 7})$$

Where n is the sample size and  $\sigma$  is the maximum-likelihood standard deviation of the error term:

$$\hat{\sigma}_{MLE} = \sqrt{\frac{\sum (Y_i - \hat{Y}_i)^2}{n}} \quad (\text{Eq. 8})$$

Models were compared by second-order Akaike's information criterion ( $AIC_c$ ) for small samples (when  $n / K < 40$ ) (Burnham & Anderson, 1998).

$$AIC_c = -2\log L + 2K \left( \frac{n}{n-K-1} \right) \quad (\text{Eq. 9})$$

Where  $K$  is the number of estimated parameters.

### 3.3.4 Annual growth

Absolute growth rate (AGR, mm d<sup>-1</sup>) calculation is slightly simpler approach than the instantaneous growth rate calculations, however as AGR has been used frequently in literature and for comparison it was also calculated for each sampling year. AGR calculation was used to calculate growth rate for whole nursery ground period, from settlement date to mid-August. AGR values were calculated as:

$$AGR = \frac{L_e - L_s}{\Delta t} \quad (\text{Eq.10})$$

Where the  $L_s$  is mean length of juveniles at the start of sampling period,  $L_e$  was mean length around mid-August and  $\Delta t$  was a duration of sampling period in days.

Multiple regression analysis was used to examine which factors might have influenced the absolute growth rates. The external predictors in the starting linear regression model were highest density peak (DP) for each year and the mean sea surface temperature in May ( $SST_M$ ) from Reykjavík harbour (SST) as the plaice juveniles are metamorphosing and settling to the nurseries. Prior to analysis the density peak of juveniles was log-transformed to establish linearity.

Absolute growth model,

$$AGR_t = \alpha \quad (\text{Null})$$

$$AGR = \alpha + \beta_1 \log DP + \beta_2 SST_M + \varepsilon \quad (\text{LM})$$

$\alpha$  is intercept,  $\beta_1$ , and  $\beta_2$  are regression coefficients and  $\varepsilon$  is the error term.

### 3.3.5 Somatic and otolith growth analysis

Analysis of covariance (ANCOVA), with total fish length as a covariate, was used to investigate if otolith diameter differed between plaice from different years (2005 and 2012) during settlement period and check if juvenile and otolith growth had linear relationship.

### 3.3.6 Individual instantaneous growth

Analysis of individual instantaneous growth was done with two comparison years 2005 and 2012, at peak of settlement period (June/July) and start of emigration (August), was back-calculated from the otoliths as instantaneous growth rate ( $G$ , d<sup>-1</sup>). Equation 6 was

used here as well where  $L_{t+1}$  is length at catch  $t$ ,  $L_t$  is length at settlement here 12 mm according to (Modin et al., 1996) and  $\Delta t$  is post-settlement age.

Generalized linear model (GLM) with log-linked Gamma distribution from exponential family was used to analyse the relationship between the length ( $L$ ) of aged individuals and post-settlement age between the years, during settlement period (June/July), emigration period (late August) and whole nursery ground period. The regression coefficients ( $g$ ) from the models were thereafter used to fit an exponential model for nursery ground growth period after metamorphosis through the seasons.

$$L_t = L_0 e^{gt} \quad (\text{Eq. 11})$$

Where  $L_t$  is length (mm total length) at time  $t$ ,  $L_0$  is estimated length at settlement,  $g$  is growth coefficient, and  $t$  is estimated age (days after settlement).

Models were compared by Akaike's information criterion, AIC (Akaike, 1974),

$$\text{AIC} = -2\log L + 2K \quad (\text{Eq. 12})$$

Where  $K$  is the number of estimated parameters.

Student's t-test was also used for comparison of the individual instantaneous growth rates between the comparison years (2005 and 2012) and also the recent instantaneous growth rates (calculated from biological intercept method, equation 2 mentioned in chapter 3.3). Data was first tested for equality of variances with F-tests. Two sampled t-test was used when variances were equal and Welch t-test when variances were unequal.

### 3.3.7 Sub-cohort analysis

Sub-cohort analysis for each sampling date in years 2005 and 2012 was done using modal analysis ("mixdist" in R environment), by fitting finite mixture distribution models to the length frequency histograms. The finite mixture model is a convex combination of two or more probability density functions. The length-frequency data in all sampling dates was compressed into bins of 3 mm. The number of sub-cohorts or means ( $\mu$ ), mixing proportions ( $\pi$ ) and standard deviation ( $\sigma$ ), at each separate sampling date was estimated visually before fitting the distribution with MIX software. Constant coefficient of variation (CCV) constrain was set on standard deviation, as this constrain assumes that standard deviation ( $\sigma$ ) increases with means ( $\mu$ ). The curves were fitted by the least squares and iterations, and chi-squared value gave the goodness of fit.

All model residuals were tested for normality using normal probability plots and Shapiro-Wilk test for small-sized data set. Homogeneity of variances was tested using Bartlett's test.

Statistical work was carried out with the aid of R i386 3.0.1, using "geo", "MuMIn" and "mixdist" packages designed for R environment.

## 4 Results

### 4.1 Dynamics of juvenile plaice

Newly settled 0-group plaice (10 – 17 mm) were first observed in the catches in Helguvík at the end of May in 2010, after the sampling was continued monthly through winter from fall of 2009. This observation was also noted in other sampling years, 2006 and 2007, which started earlier than usual. The sampling data showed a clear pattern of new individuals immigrating to the shallow nursery area at the beginning of Icelandic summer (end of May) with a peak in 0-group plaice numbers around mid-summer and decrease towards the fall (Fig. 4.1 and Table A.1 in Appendix A).

#### 4.1.1 Density

A total of 32,895 0-group plaice were captured in Helguvík over the ten year period 2005 – 2014, inclusive. The peak densities of 0-group plaice varied over the years and ranged from  $62 (\pm 2.55) 100 \text{ m}^{-2}$  on August 8<sup>th</sup> in the year 2008 to  $1910 (\pm 299.25)$  on June 25<sup>th</sup> in year the 2014 (Fig. 4.1 and Table 1 in Appendix A). There was a significant difference in density between high-density years, 2012 and 2014, and low-density years 2008 and 2013 ( $p < 0.05$ ), and also between growth comparison years 2005 and 2012 ( $p < 0.05$ ) (Fig. 4.1). The duration of settlement period, i.e. period when sub-cohorts arrive at the nursery area before reaching the density peak, varied over the years. In years 2006, 2010 and 2014 the settlement period was short with a peak in density at the end of June (around ordinal day 180). In the other seven years, the settlement period was longer and reached density peak in mid-July (around ordinal day 200). In years with high density (2012 and 2014), the decrease in abundance was steep after the peak and reached similar density numbers as other years around mid-August. In years 2010 and 2012 a small increase in density was visible in late August, which indicates a pulse of small individuals still coming to the nursery area (Fig. 4.1).

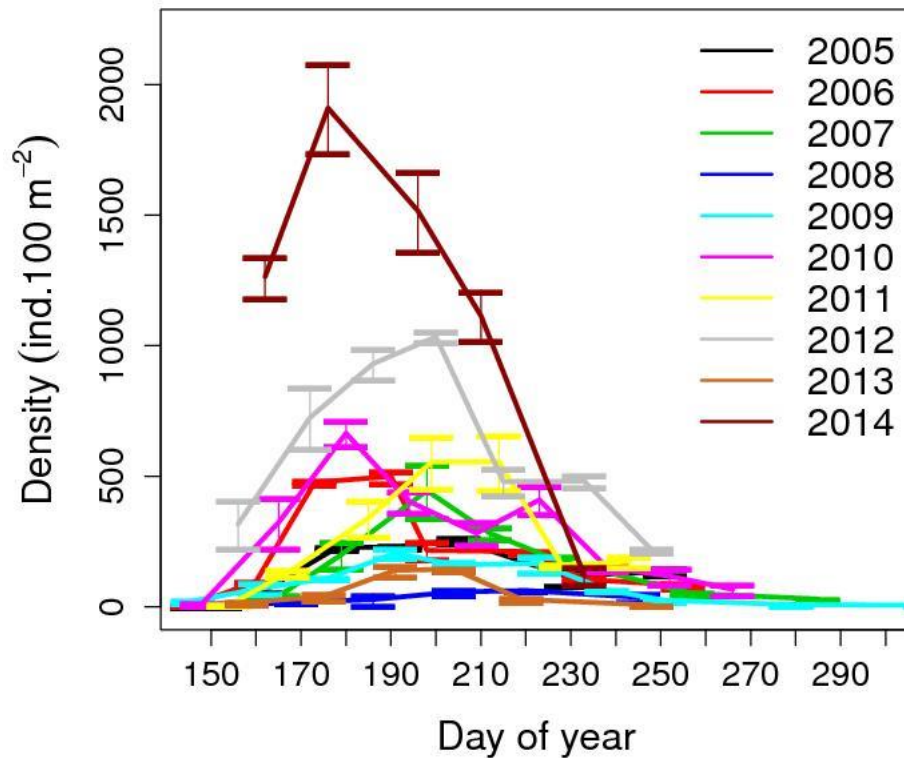


Figure 4.1 Mean densities ( $\pm$  standard error) of settled 0-group plaice (ind. 100 m<sup>-2</sup>) in Helguvík, SW Iceland, during the years 2005–2014.

#### 4.1.2 Average lengths

The development of mean lengths of 0-group plaice in Helguvík varied inter-annually (Fig. 4.2). Mean lengths at the onset of sampling ranged between the years from 11.00 ( $\pm 1.08$ ) mm in the end of May 2007 to 16.12 ( $\pm 3.24$ ) mm on June 11<sup>th</sup>, 2014. Sampling in 2014 started almost two weeks later than in previous years. On average the mean length of 0-group plaice at the beginning of settlement period did not vary significantly between the sampling years ( $p > 0.05$ ). The mean length at the end of the nursery ground period (sampling period), or at the beginning of September, ranged from 41.72 ( $\pm 13.38$ ) mm at September 5<sup>th</sup>, 2013 to 68.32 ( $\pm 14.04$ ) mm at September 1<sup>st</sup>, 2008 (see Table A1 in the Appendix A). The range in mean length between the years got larger at the end of summer. Two years stood out, 2006 and 2013, as mean length trajectories were notably lower than in other years, after ordinal day 190.



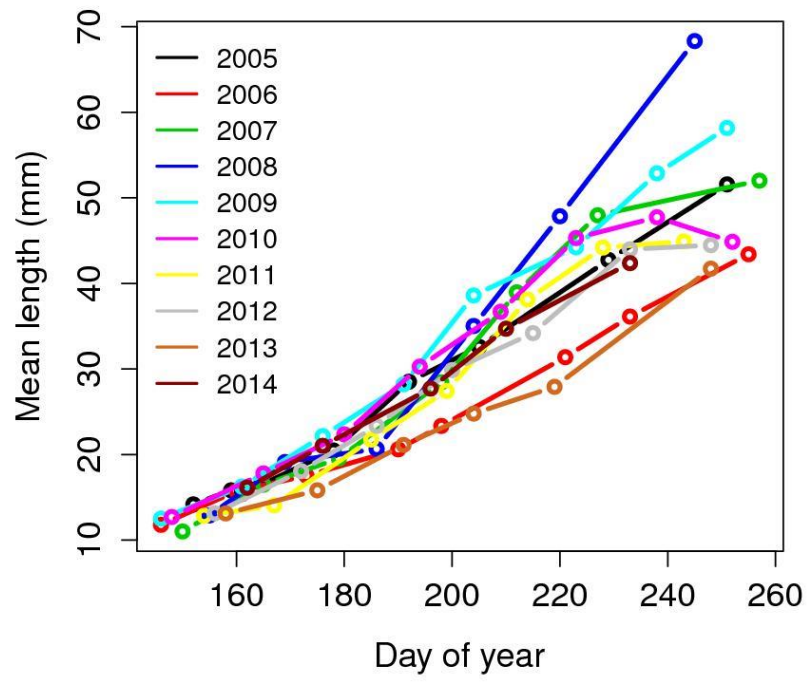


Figure 4.2 Development of mean length (mm) of juvenile plaice in Helguvík during the years 2005 – 2014.

## 4.2 Analysis of length distributions

### 4.2.1 Growth performance

Observed changes in the average length trajectories, for the comparison years (2005 and 2012), corresponded with model predictions on maximum growth until approximately the mid-July, thereafter deviating slightly from predictions (Fig. 4.3). Decline from maximum growth was visible late in the summer in 2012, but not in 2005. Average length-at-date trajectories fitted more closely to the Fonds model through whole nursery ground period for both years, nevertheless, both models corresponded closely to the changes in mean lengths at the beginning of the nursery ground period (Fig. 4.3). Comparison of average length-at-date trajectories to both models for all sampling years are found in Appendix A, table A.2.

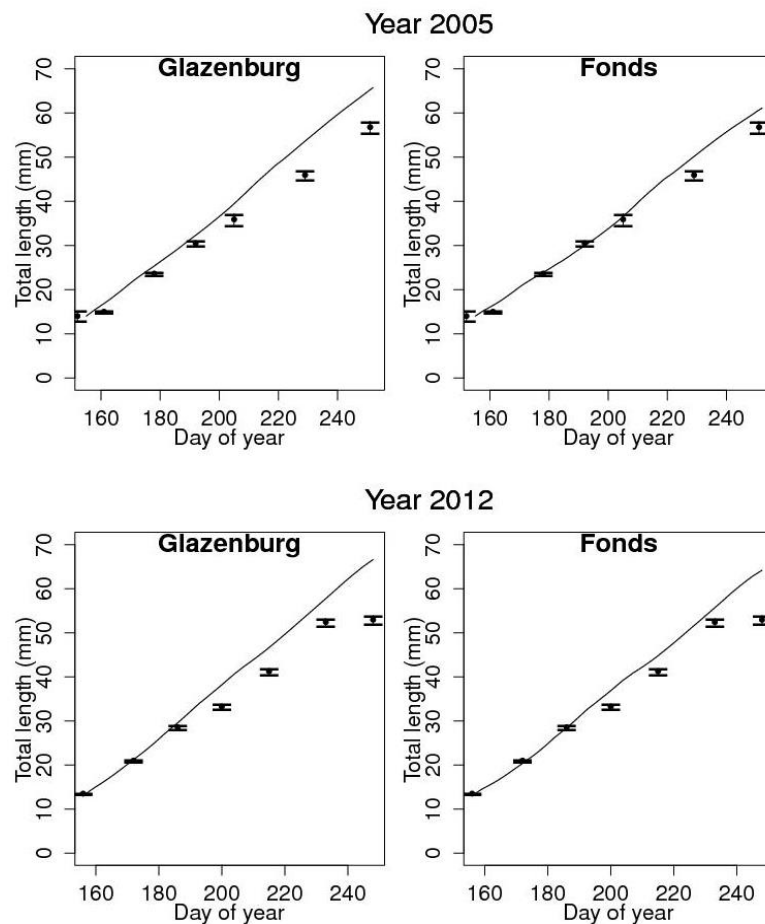


Figure 4.3 Comparison between observed growth of 0-group plaice in Helguvík and predicted growth according to experimentally established models. Mean total lengths ( $\pm$ SE) of 0-group plaice points and predicted maximum length (mm) lines according to Glazenburg's (1983) left and Fonds et al.'s (1992) right, growth models.

The deviation of mean lengths during nursery ground period, in years 2005 and 2012, from the maximum growth models established unlimited food supply were estimated and shown in figure 4.4. Deviations for almost each sampling date were negative for both models (Glazenbug and Fonds), except for one sampling date in 2012, ordinal date 176, where the mean lengths reached over the Fonds maximum growth model. Fonds model corresponded better to our average lengths in both years than the Glazenbug model.

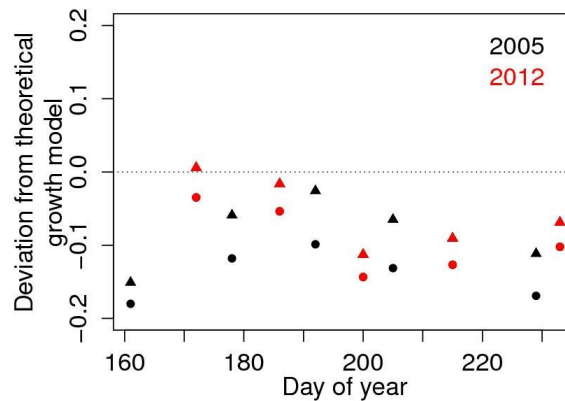


Figure 4.4 Deviation from the theoretical maximum growth models, Glazenburg ( $\circ$ ) and Fonds ( $\Delta$ ).

#### 4.2.2 Length based instantaneous growth rate

Instantaneous growth rates estimated from change in mean lengths was generally between 0.005 – 0.03 ( $G, d^{-1}$ ) (Fig. 4.5). The maximum growth rate was around 0.029 ( $G, d^{-1}$ ) at a mean length of approximately 35 mm. After the peak in abundance, instantaneous growth rates decreased with length as autumn and emigration drew nearer, displayed by Loess smoother (Fig. 4.5).

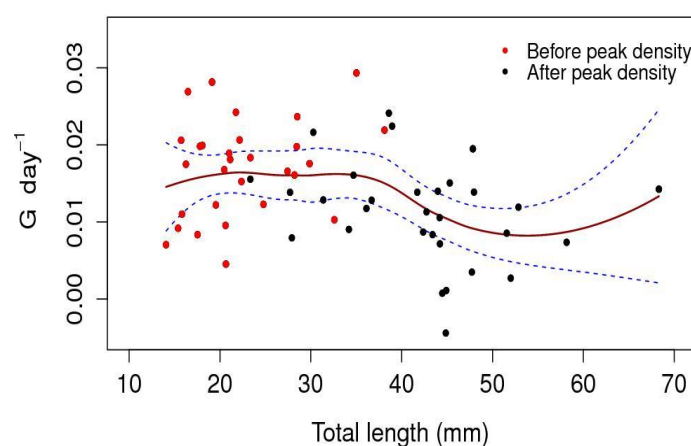


Figure 4.5 Estimations of the instantaneous growth rates ( $G; d^{-1}$ ) of O-group plaice in all sampling years (2005-2014). Red: during larval immigration; black: from peak densities and onwards. Dark red line: Loess smoother with 95% confidence intervals (blue dotted lines).

An examination with multiple regression model was carried out to determine which factors influenced the intra-annual growth variability in Helguvík. A stepwise linear model selection suggested the total length (TL) and mean SST between adjacent samplings as two significant ( $p < 0.1$ ) explanatory variables (Table 4.1). Together those variables explained 17.6% of the variation in instantaneous growth between the sampling dates for each year. No clear relationship pattern was, however, visible between the instantaneous growth rate and juvenile plaice density in each sampling date for all years sampled (2005 – 2014) ( $p > 0.05$ ).

*Table 4.1 Summary of fitted regression models: null model (Null<sub>G</sub>) and multiple linear regression (LM<sub>G</sub>) for instantaneous growth model. The significant external factor was mean total length (TL<sub>G</sub>) of juveniles in each sampling date for each year.  $\alpha$  is the regression intercept,  $\beta_2$  is regression coefficient for mean SST between the adjacent samplings and  $\beta_3$  is regression coefficient of plaice mean total length in each sampling (TL<sub>G</sub>).  $K$  is the number of estimated parameters, and  $AIC_C$  is Akaike's information criterion for small samples.*

Model	$\alpha$	$B_2$	$\beta_3$	$K$	$AIC_C$
Null <sub>G</sub>	0.0141			2	-414.38
LM <sub>G</sub>	0.0086	0.0013	-0.00029	4	-421.3

### 4.2.3 Annual growth

The annual absolute growth rate was between 0.28 and 0.53 (mm d<sup>-1</sup>), with highest growth rate in 2008 and lowest in the cold year of 2006 (Fig. 4.7). Stepwise linear model selection from the null model indicated two significant ( $p < 0.001$ ) explanatory variables, density peak (DP) and mean SST in May (Table 3.1). Together those variables explained 92% of the variation in annual absolute growth (mm d<sup>-1</sup>) in Helguvík and the SST in May contributed most to the regression sum of squares (Table A.3 in Appendix A). Correlation between the two regression terms was insignificant ( $p < 0.05$ ) and no autocorrelation was detected in the residuals ( $p < 0.1$ ).

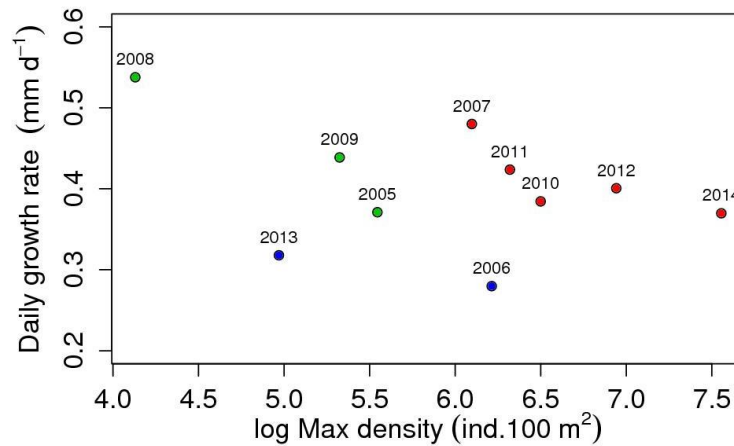


Figure 4.6 Annual growth rates in relation to (log) highest density peak for each sampling year (2005 – 2014). Colours indicate mean temperature in May. Blue range: 5.76 – 6.33°C, green range: 6.81 – 6.98°C and red range: 7.27 – 7.72°C.

Table 4.2 Summary of fitted regression models: null model (Null AGR) and multiple linear regression (LM<sub>AGR</sub>) for annual absolute growth model. The external factors were (log) mean density peak for each year (DP) and mean sea surface temperature in May (SST<sub>M</sub>).  $\alpha$  is the regression intercept,  $\beta_1$  and  $\beta_2$  are regression coefficients of plaice density peak (DP) and mean sea surface temperature in Reykjavík harbour in May (SST<sub>M</sub>),  $K$  is the number of estimated parameters, and AIC<sub>C</sub> is Akaike's information criterion for small samples.

Model	$\alpha$	$\beta_1$	$\beta_2$	$K$	AIC <sub>C</sub>
Null <sub>AGR</sub>	0.4			2	-18.77
LM <sub>AGR</sub>	-0.13	-0.089	0.152	4	-33.46

## 4.3 Growth during high and low density

### 4.3.1 Somatic and otolith growth

Otolith diameter from juveniles in settlement period (June/July) increased linearly with fish length ( $F = 190.2, p < 0.0001$ ) (Fig 4.7), confirming that otolith growth reflects somatic growth. There was a significant difference in otolith diameter between the two comparison years ( $F = 48.641, p < 0.0001$ ), with larger otoliths in juveniles from the high-density year of 2012.

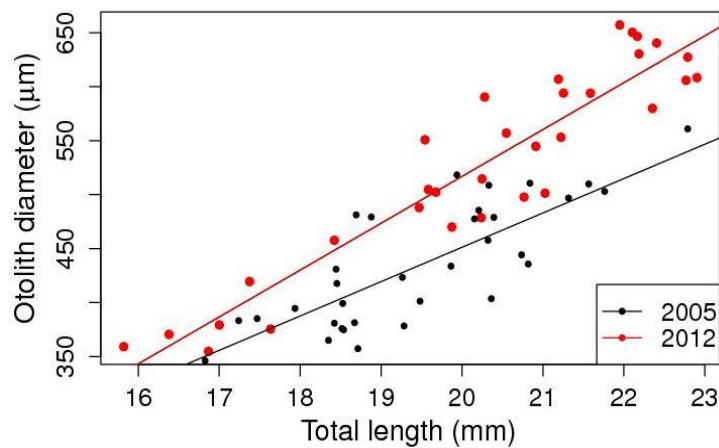


Figure 4.7 Relationship between otolith size and juvenile plaice lengths. Black: 2005, red: 2012.

### 4.3.2 Individual instantaneous growth

Growth rates of 0-group plaice were calculated during the settlement period in the mid-summer (27. June 2005 and 4. July 2012) and the emigration period at the end of the nursery ground phase (17. August 2005 and 20. August 2012) (see table 4.3).

The individual instantaneous growth rate ( $G \text{ day}^{-1}$ ) comparison showed a significant difference in means (Student's t-Test,  $p < 0.01$ ) between the years during settlement period where the juveniles from early-July 2012 grew a little faster than juveniles from 2005 (Fig. 4.8). There was also a significant difference between the means of total length in aged individuals during the settlement period (Student's t-Test,  $p < 0.01$ ), as the range of the total length in settlement period individuals was 15.61 – 28.94 mm in 2005 and 15.82 – 42.08 mm in 2012. However, when fish from the same size range were compared there was no significant difference between the years in growth during settlement period (Student's t-Test,  $p = 0.9$ ). The mean SST two weeks before sampling dates was 10.3°C in 2005 and 12.5°C in 2012.

The instantaneous growth rate ( $G \text{ day}^{-1}$ ) comparison during emigration period showed a significant variation in  $G$  between the years (Student's t-Test,  $p < 0.0001$ ), with juveniles in 2005 growing a little faster than 2012 juveniles (Fig. 4.8). During emigration period the difference in means of total length of individuals did not vary significantly between the years (Student's t-Test,  $p = 0.7$ ), however, juveniles in 2012 span larger range. The range of a total length during emigration period in 2005 was 37.09 – 54.93 and in 2012 was 27.99 – 60.01 mm. The mean temperature two weeks before the sampling date was 11.7°C in 2005 and 13.1°C in 2012, respectively.

Table 4.3 Summary of growth rates for both settlement and emigration period from aged individuals in years 2005 and 2012.

Date	<i>n</i>	Growth rate ( $\text{mmd}^{-1}$ )	Instantaneous growth rate ( $G, \text{m}^{-1}$ )
27.6.2005	54	0.1 – 0.41	0.00735 – 0.024
4.7.2012	59	0.13 – 0.69	0.0095 – 0.033
17.8.2005	40	0.47 – 0.85	0.02 – 0.31
20.8.2012	38	0.35 – 0.74	0.018 – 0.028

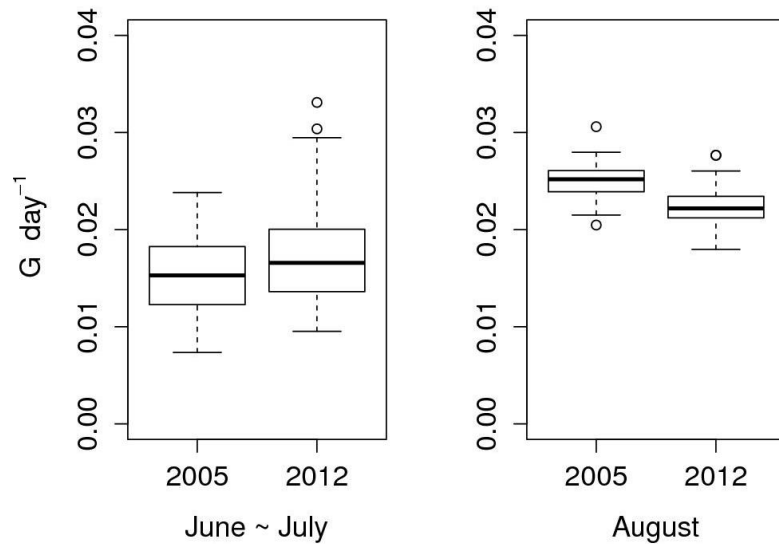


Figure 4.8 Instantaneous growth rate ( $G \text{ day}^{-1}$ ) in aged juveniles from June/July and August samples from the years 2005 and 2012.

Growth during the whole nursery ground period was estimated by fitting exponential growth curves to the length-at-age plot (see parameters in Table 4.4). There was significant difference between the years when settlement and emigration periods were investigated separately, June/July individuals ( $p < 0.001$ ) and August ( $p < 0.01$ ) (Fig. 4.9). However, the whole period exponential growth curves show no significant difference between the years ( $p = 0.4$ ).

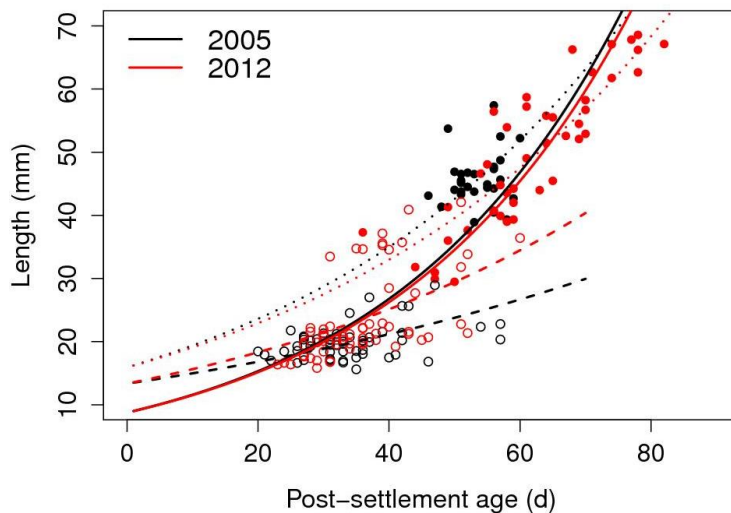


Figure 4.9 Fitted exponential growth curves for the aged June/July and August juveniles. Only earlier sampling date (June/July) shows significant difference in growth. Exponential growth lines; June/July line (---), August line (····) and whole season line (—).



Table 4.4 Parameters for exponential growth models in 2005 and 2012

Parameters	Estimate	SE	p-value
<i>a). Exponential growth model of juvenile plaice lengths against age for whole season between the years</i>			
Intercept	2.16	0.051	< 0.0001
Age	0.028	0.0013	< 0.0001
Age:2012	-0.0005	0.0007	0.441
AIC: 1188.3			
<i>b). Exponential growth model of juvenile plaice lengths against age for settlement period between years</i>			
Intercept	2.59	0.081	< 0.0001
Age	0.012	0.0024	< 0.0001
Age:2012	0.0043	0.001	< 0.0001
AIC: 634.42			
<i>c). Exponential growth model of juvenile plaice lengths against age for emigration period between years</i>			
Intercept	2.72	0.104	< 0.0001
Age	0.021	0.002	< 0.0001
Age:2012	-0.0016	0.0006	< 0.01
AIC: 445.53			

### 4.3.3 Settlement and sub-cohort identification

Estimation of the sub-cohorts for two sampling years, 2005 (low density) and 2012 (high density), was made by fitting a mixture model to the length frequency data (Fig. 4.10). During settlement period in 2005 (Fig. 4.10a), a clear, single large “pulse” with mean length around 18 mm, was identified and two older smaller ones, approximately 24 and 29 mm in length. The last one to settle is a small peak around 13 mm, signifying very newly settled individuals. In 2012 (Fig. 4.10b) four “pulses” more equal in size and with the less clear pattern were observed. The largest had the mean length around 22 mm, and the earlier two were around 27 and 35 mm in length. The newest pulse was 15 mm in length. At the start of the emigration period in August, there were no small settling individuals identified and in both years (Fig. 4.10c d), the newest sub-cohort to be seen had a mean length around 33 mm. In August 2005, was a slightly older sub-cohort which was similar in size with mean length around 44 mm. There were also two smaller sub-cohorts with mean lengths around, 50 and 59 mm (Fig. 4.10c). During emigration in August 2012, the identified sub-cohorts were four, with largest one having mean length around 33 mm and the older and smaller ones with mean lengths 42, 53 and 66 mm (Fig. 4.10d).

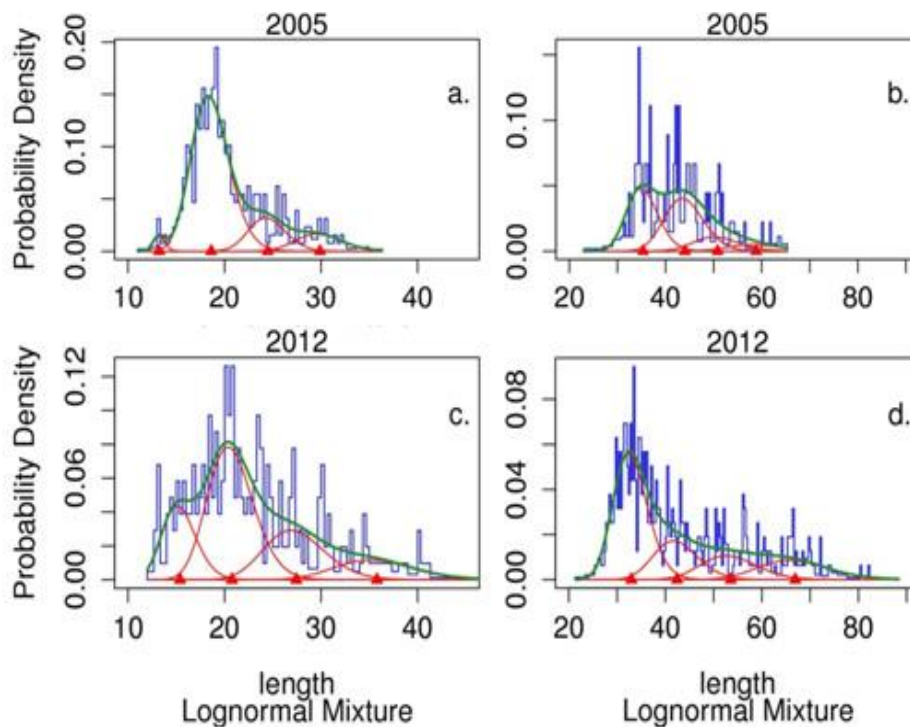


Figure 4.10 Placice lengths histogram with estimated parameters for sampling dates before density peak (a. and c.) and during emigration in August (b. and d.) in years 2005 (a,b) and 2012 (c,d).

Back-calculation of the settlement date (Fig. 4.11) revealed that the aged individuals during the settlement period and at the end of it came from different sub-cohorts as there was no overlap in settlement dates during the year 2005 and little overlap in 2012.

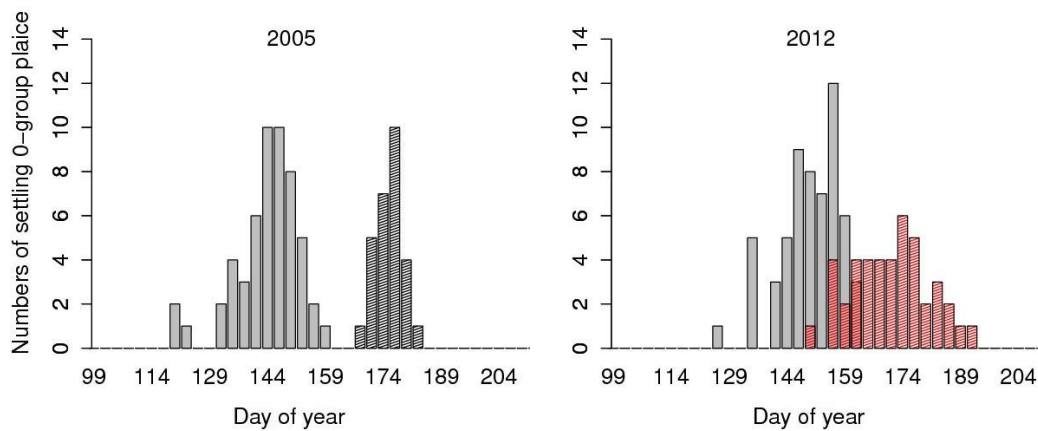


Figure 4.11 Back-calculations of settlement date during settlement period June/July (grey) and emigration period mid-August (stripes / red stripes) in aged 0-group juveniles

A summary of the general results of this chapter has been set together in two figures (Fig. 4.12). Back-calculated settlement dates from periods during settlement and early emigration from years 2005 and 2012 are visible. Estimated sub-cohorts from the mixture models analysis were also included, with exponential growth curve from Gunnarsson et al. (2010) for this particular area and the combined maximum growth model under unlimited food conditions from Glazenburg and Fonds. The number of identified sub-cohorts in 2005 varied through the summer. After the four sub-cohorts on the sampling day chosen for ageing (ordinal day 178), three sub-cohorts were identified on the next three sampling dates. The exponential growth curve was set to start at first cohort of sampling day 161 and fitted well to identified sub-cohorts on three successive sampling dates. The exponential model seemed to fit better to the data then the combined growth model of Glazenburg and Fonds. We could also see some late-settlers emerge at the nursery late in the summer of 2005. In 2012, the sub-cohorts were better identified by the mixture model and four sub-cohorts were visible after ordinal day 186. Again the exponential model seems to follow the sub-cohorts better than the combined growth model (set to start at ordinal day 172), but it deviates from observed sub-cohorts at ordinal day 218. On the last day of sampling in 2012 (ordinal day 248) a new sub-cohort is visible and the largest sub-cohort has disappeared.

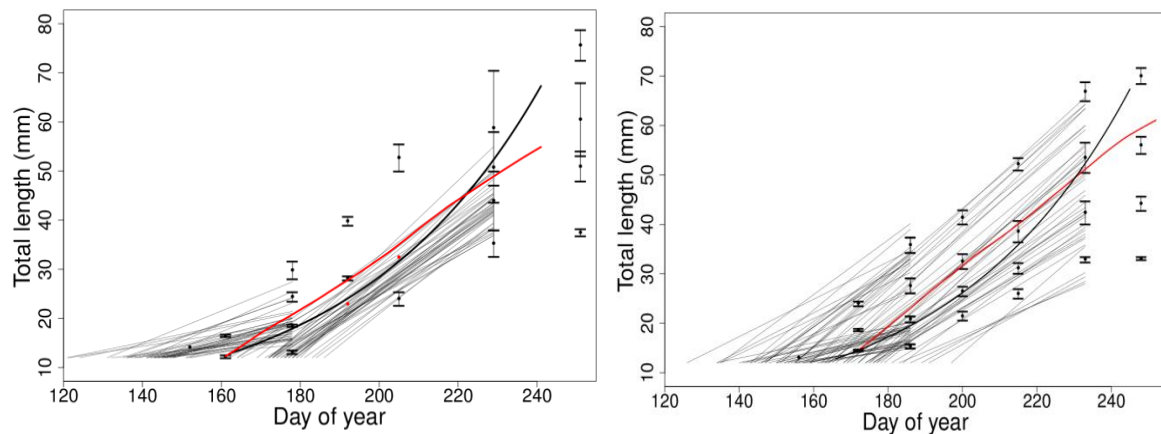


Figure 4.12 The mean and the standard error of each sub-cohort are plotted (2005 left and 2012 right). Red dots denote where mean length of the cohort was fixed. Each age reading was also plotted as a thin line between the length at sampling day and the settlement day (12 mm). On each graph, two growth curves are plotted on a given day. In red, the combined growth model of Glazenburg for juveniles between 13 – 45 mm and Fonds for juveniles between 45 – 200 mm. In black, exponential growth curve from the same region (Gunnarsson 2010).

#### 4.3.4 Recent growth analysis

There was no significant difference in mean peripheral increment width between the two years in June/July settlement period, which ranged between 7.26 – 10.25  $\mu\text{m}$  in 2005 and 7.31 – 11.4  $\mu\text{m}$  in 2012 (Student's t-Test,  $p = 0.452$ ). However, there was a significant difference in the post-metamorphic age (Student's t-Test,  $p < 0.0001$ ), which confirms that the 2012 juveniles have been longer on the nursery ground than the juveniles from 2005 (8 days difference between the samplings). Also, the juveniles from settlement period in 2012 were larger than the 2005 juveniles (Student's t-Test,  $p < 0.0001$ ).

The biological intercept method assumes a linear relationship between fish length and otolith length for individual fish (Campana & Jones, 1992). Biological intercept equation was used to back-calculate total lengths of juveniles 10 days before capture. The individual absolute growth rate in those ten days was between 0.42 – 0.62 ( $\text{mm d}^{-1}$ ) in 2005 and 0.36 – 0.57 ( $\text{mm d}^{-1}$ ) in 2012. There was a significant difference both in absolute and instantaneous growth rate (Student's t-Test and ANOVA,  $p < 0.001$ ) between the comparison years, as individuals during settlement period in 2005 grew faster than individuals in 2012 (Fig. 4.14 and 4.15). Growth rates for settlement period (June/July) in years 2005 and 2012 from different approaches were summarized in table 4.4.

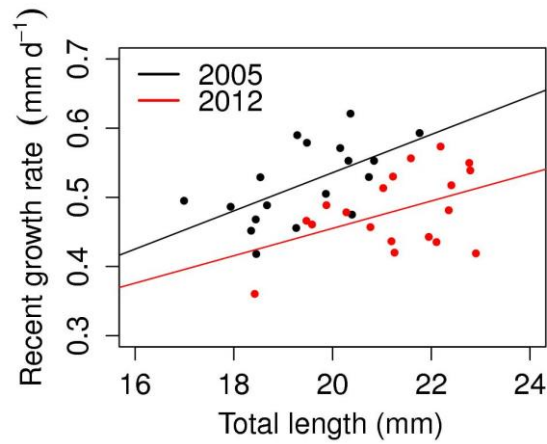


Figure 4.13 Relationship between recent growth ( $\text{mm d}^{-1}$ ) and total length (mm) in comparison years 2005 and 2012. Regression lines are also showed for both years.

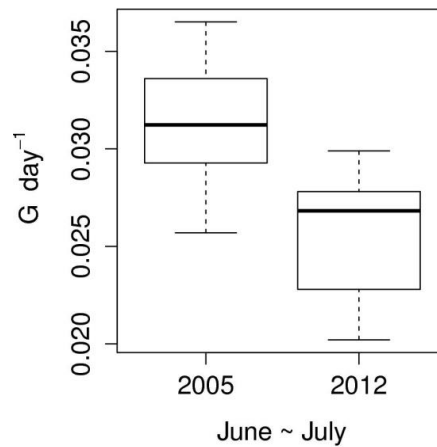


Figure 4.14 Instantaneous growth rate ( $G \text{ day}^{-1}$ ) for compared individuals during settlement period in 2005 and 2012. Median values are showed for each box (bold horizontal line) and the 25 and 75 percentiles upper and lower limit of the box, respectively.

Table 4.5 Summary of growth rates for settlement period (June/July) in comparison years.

Date	<i>n</i>	SST 10d b. capture	Growth 10 days b. capture, $\text{mmd}^{-1}$ ( $G, \text{m}^{-1}$ )	Length-at-age, $\text{mmd}^{-1}$ ( $G, \text{m}^{-1}$ )	Glazenburg, $\text{mmd}^{-1}$
<b>27.6.2005</b>	18	11.21	0.42 – 0.62 (0.026 – 0.037)	0.1 – 0.41 (0.00735 – 0.024)	0.49
<b>4.7.2012</b>	19	12.86	0.36 – 0.57 (0.02 – 0.03)	0.13 – 0.69 (0.0095 – 0.033)	0.61

## 5 DISCUSSION

An indication of density-dependent growth pattern was observed, at Helguvík cove when comparing the high and low density years. The arrival pattern of juveniles entering the nursery each year followed a trend similar to the other European nursery areas; with newly settled individuals at the end of May, a density peak during mid-summer, followed by a decline in numbers. However, the settlement pattern and the duration of the nursery ground period were more similar to nurseries at higher than lower latitudes. Investigation of the overall growth pattern for all years showed higher growth rates before the density peak and lower rates after the peak with increasing mean lengths and in late-summer, which is in agreement with earlier findings in European nursery areas.

Settlement of the juvenile plaice in Helguvík started at the end of May or in the beginning of June in all ten sampling years (2005 – 2014). It followed a similar seasonal occurrence pattern as seen in other nurseries in Europe (Geffen et al., 2011; van der Veer, 1986), where plaice numbers increased during settlement period, reached a density peak during early/mid-summer, which was followed by a continuous decline after the density peak. However, the later timing and shorter duration of the settlement period in Helguvík was more similar to nurseries at a higher latitude in north-west Norway (Freitas et al., 2010), than to the other nurseries in continental Europe (Geffen et al., 2011; Modin & Pihl, 1994; van der Veer, 1986). Hjörleifsson & Pálsson, (2001) also observed similar pattern among juvenile plaice in the northern region of Faxaflói. The current study and Hjörleifsson & Pálsson, (2001) indicate a shift in settlement of juvenile plaice a month earlier than previously reported by Tåning, (1929). Also, the start of the settlement in Helguvík at the end of May or early in June corresponds to the spawning season in south-west of Iceland, which starts at the end of February and is finished by the end of May (Sigurðsson, 1989; Solmundsson et al., 2003; Sæmundsson, 1926).

Annual variation in settlement duration was observed in Helguvík, where the settlement period was shorter for some years (2006, 2010 and 2014) with a density peak in late-June and longer in other (2011, 2012) with a peak in late-July. In species with serial spawning, such as plaice, the annual variations in numbers of arriving individuals, settlement pattern and duration of settlement period have been observed (Hyder & Nash, 1998). The length of the settlement period has been connected with duration of egg production during the spawning season (Geffen et al., 2011), therefore, the variability in duration of the settlement period in Helguvík may possibly reflect variation linked with the spawning season in the south and south-west of Iceland, which may range over 100 days (Gunnarsson et al., 2010; Sigurðsson, 1989; Solmundsson et al., 2003). The temperature during the pelagic stage can also influence the duration of the settlement period because temperature and development of both eggs and larvae are highly correlated (Hyder & Nash, 1998; van der Veer & Witte, 1999). Therefore, in colder years temperature can

extend the development period (Allen et al., 2008; Fox et al., 2000) and prolong the timing of metamorphosis and settlement, such that duration of the settlement period becomes extended. However, in Helguvík the interplay between the variability in temperature during pelagic stage and variability in settlement duration is not clear and needs more complex investigation.

Plaice density in Helguvík-bay varied between years over the ten year sampling period and the two highest density peaks occurred in years 2012 and 2014 with 1034 ind. 100 m<sup>-2</sup> and 1910 ind. 100m<sup>-2</sup> (not corrected for gear efficiency), respectively. These are the highest densities observed in Icelandic nursery areas so far. Other studies have reported on densities ranging from 1022 to 1034.5 ind. 100 m<sup>-2</sup> in the north-west and south-east of Iceland (Gunnarsson et al., 2010). Such high density numbers have rarely been seen in European nurseries which are generally characterized by much lower numbers or rarely higher than 50 ind. 100 m<sup>-2</sup> (Amara, 2004; Amara et al., 2001; Freitas et al., 2010; Jager et al., 1995; van der Veer et al., 1990). However, few exceptions of high density in nursery areas have been observed in the northern part of Swedish west coast, with a drop trap (almost 100% efficiency), when peaks reached around 800 – 1000 ind. 100 m<sup>-2</sup> (Modin & Pihl, 1994; Wennhage, Pihl, & Stål, 2007) and highest density recorded of 2200 ind. 100 m<sup>-2</sup> (Pihl et al., 2000). The high density areas in north-west Swedish nurseries were considered to be in a good geographical position to the main spawning areas in North Sea-Skagerrak-Kattegat system, even with a complex archipelago possibly restricting larvae influx to those nurseries (Wennhage et al., 2007). Nursery area in Helguvík was considered exposed and larvae influx from the main spawning areas should therefore, not be much hindered. Also the moderate steep in Helguvík could influence the aggregation of the juveniles high in the shore as this is considered to be optimal habitat for 0-group plaice juveniles (Gibson et al., 2002; Pihl et al., 2000), and therefore, can eventuate in very high densities. Gunnarsson et al., (2010) investigated suitable nursery areas for plaice juveniles around Iceland and their conclusions were that there were few suitable nursery sites but with high juvenile densities. Therefore, the high densities in Icelandic nursery areas could result from spatial restrictions.

The inter-annual variability in numbers of settling plaice has been observed in Helguvík and has also been recorded in European nurseries (Bergman, van der Veer, & Zijlstra, 1988; Modin & Pihl, 1994; Nash & Geffen, 2000; van der Veer et al., 1990). This variability in settlement abundance is driven by variability in larval supply to the nursery ground (Wennhage et al., 2007) and has been connected to variations in exogenous factors such as hydrodynamics (Bolle et al., 2009; Nielsen et al., 1998; van der Veer et al., 1998), temperature (Fox et al., 2006; van der Veer et al., 2009; van der Veer et al., 1990; van der Veer & Witte, 1999) and predation (Nash & Geffen, 2012; van der Veer & Bergman, 1987) in European waters. Strong connection between variability in hydrodynamics and variations in settling plaice has been shown in European waters (Bolle et al., 2009; Nielsen et al., 1998; van der Veer et al., 1998). As variations in a combination of both passive

transport and selective tidal transport of egg and larvae to nursery areas may contribute to variability in settling plaice densities. Plaice egg and larvae drift most likely with coastal water currents, developed from warm Atlantic current (see in Gunnarsson et al., 2010) into Faxaflói from spawning grounds west of Reykjanes (on Hafnaleir, or in Miðnessjór) and Selvogsbanki south of Iceland (Sigurðsson, 1989; Solmundsson et al., 2005). Therefore, all variations in hydrodynamics on this long way can highly contribute to variability in numbers of settling juveniles to nursery grounds many kilometres away. Temperature variations during pelagic stage have also been connected to year-class strength in European waters, where colder winters produce stronger year-classes (Fox et al., 2000; van der Veer & Witte, 1999). However, this relationship could be exact the opposite for year-class strength in Icelandic waters considering the geographical and thermal distributional range of the species. As high temperature events were associated with poor year-classes for warm plaice stocks (Fox et al., 2000; van der Veer et al., 1990). This pattern could be reversed for cold stocks, around Iceland, with year-class strength being positively affected in warmer temperatures (Mantzouni & MacKenzie, 2010; Myers, 1998). In Helguvík during high density years mean temperatures in April and May have been slightly higher than the previous years, however no significant pattern between temperature and variability in settlement abundance was observed and thus, more thorough examinations are needed regarding this relationship. There has also been observed a positive connection between lower predation on plaice eggs and larvae and low sea temperature during pelagic stage in European waters (Bailey, 1989; reviewed in Nash & Geffen, 2012). However this topic was not investigated in this study and with previously mentioned thermal range differences for plaice between Icelandic and European waters a completely different pattern could be occurring here. Ultimately, the interplay of the previously mentioned topics could be the cause of variation in settlement density in Icelandic nurseries and in this study we acknowledge the existence of variability in settlement to Helguvík's nursery area, however more thorough studies are needed in this regard.

For European plaice a number of experiments have been done to evaluate the effects of temperature on growth (Fonds, Cronie, Vethaak, & Van Der Puyl, 1992; (Glazenburg, 1983) see in Freitas et al., 2010). Those growth models were established under wide ambient thermal regime and with optimal food conditions to promote maximum growth at different temperatures. A number of studies, which have compared field growth to those maximum growth models, observed a maximum field growth in early settlement period with temperature as controlling factor (Amara & Paul, 2003; Freitas et al., 2010; Hjörleifsson & Palsson, 2001; Jager et al., 1995; Karakiri et al., 1991; Nash, Geffen, & Hughes, 1994b; Teal et al., 2008). It can be assumed that as field growth correspond to experimental maximum growth models, then the „Maximum Growth/Optimal Food Conditions“ hypothesis (Karakiri et al., 1991) is accepted for the juvenile growth in early nursery ground period. The „MG/OFC“ hypothesis states that during juvenile plaice's nursery ground period the food is never limited and that ambient water temperature alone



controls the growth (Karakiri et al., 1991; van der Veer & Witte, 1993). In Helguvík, juvenile population growth follows the trajectories of the maximum growth models, however rarely reaches the maximum possible growth through whole nursery ground period. Decline in growth has been observed both after the density peaks and in early-autumn. Growth declines from the maximum growth models seem to be temperature-independent. However, comparison of the length-at-date data can be problematic due to size-selective processes (reviewed in Ciotti et al., 2014), such as immigration and emigration of individuals to the nursery. More accurate size-selective migration analysis is needed to confirm the migration patterns in Helguvík. Therefore, observed length based population growth can not be taken as an ultimate proxy for growth rate but can illustrate the growth variation at some level. Similar growth decline patterns have been observed at other nurseries (Amara, 2004; Freitas et al., 2010; Jager et al., 1995; Nash et al., 1994b; Teal et al., 2008) and the deviation could not be considered completely due to emigration of fast growing individuals (Ciotti et al., 2013b). The growth decline in the end of summer could therefore proceed from growth-limitations due to other controlling factors, such as possible food-limitations due to density-dependent processes such as intra- or inter-specific competition or changes in food quality or quantity (Freitas et al., 2010). In this study, no information was available on food abundance, quality or composition in Helguvík, therefore it is difficult to conclude their potential effects on growth. The influence of inter-specific competition on growth decline has been evaluated on two occasions (Ciotti et al., 2013b; Freitas et al., 2010) and no clear conclusions were visible. Brown shrimp (*Crangon crangon*), a principle inter-specific competitor (Evans, 1983, seen in Link, Fogarty, & Langton, 2004) has colonized in south and south-west Icelandic intertidal areas approximately since year 2003 (Gunnarsson et al., 2007), and is presumably the only inter-specific competitor which can be considered influential because of high numbers in nurseries. The effect of shrimp densities on growth variation in Helguvík was not investigated in this study. However by comparing the shrimp densities in Helguvík from Jónsdóttir et al., (2016 in review) to our data, there could be some inter-specific competition as the density of larger shrimp was still quite high late in the summer.

The influence of intra-specific competition on within-year growth variabilities in European nurseries have also been addressed in number of studies (Amara, 2003; Ciotti et al., 2014; Freitas et al., 2010; Geffen & Nash, 1994; Nash et al., 2007; van der Veer et al., 2010). In all those various nurseries in Europe the overall conclusion was that there was no relationship between the plaice densities and intra-annual growth variations. However, none of those nurseries has experience as high densities as there have been seen in Helguvík. Therefore the small deviation from the maximum growth models around the density peak in high density years (for example 2012) could, thus be influenced by reduction in feeding rate due to intraspecific competition. Intra-annual growth was also investigated more thoroughly by comparing individual length-at-age (post-metamorphosis age) in two separate years. Intra-annual growth trend followed the exponential growth

curve, with individual growth rate being faster in both years in late August in comparison to growth rate in June/July. Growth rates were in range of those in other nurseries (Al-Hossaini et al., 1989; Amara & Paul, 2003; Berghahn, Lüdemann, & Ruth, 1995; Geffen et al., 2011; Modin & Pihl, 1994; van der Veer et al., 2010), however they varied from the maximum growth models and were lower than expected (Fonds et al., 1992; (Glazenburg, 1983) see in Freitas et al., 2010). This could indicate some density-dependant processes during settlement period. The variation in individual growth has been seen (Berghahn et al., 1995) and also between the settling sub-cohorts (Al-Hossaini et al., 1989; Geffen et al., 2011), thus it can be difficult to disentangle those factors from density induced influences. Considering that the maximum growth period is shorter in higher latitudes (Freitas et al., 2010) and the ambient water temperature experienced by the juveniles in August was higher than in June, thus it was still too early to observe the decline in aged individuals as it appears to occur in early autumn in Helguvík.

Inter-annual growth rate variations have been observed in Helguvík, when both looked at length-at-date, length-at-age and recent growth data. This kind of growth variabilities have also been experienced in diverse plaice nurseries in Europe (Ciotti et al., 2013a; Fox et al., 2014; Geffen et al., 2011; Modin & Pihl, 1994; Nash et al., 2007; Teal et al., 2008; van der Veer et al., 2010) and the exogenous factors which could have most influenced those variabilities have been defined as variations in temperature, prey condition, and intra- and inter-specific competition. In Helguvík the inter-annual variations have been observed in trajectories of average size at date as two years 2006 and 2013 had noticeably lower growth rate through most part of nursery ground period in comparison to other years. In both those years the average temperature in Helguvík was also noticeably lower in early summer than in other years, which could highly influence the lower growth increase. Positive relationship between growth rate and temperature has been observed (Teal et al., 2008), which implies an influence of low temperature on lower growth in both years. However, growth was not at its maximum compared to maximum growth models with wide temperature regime and unlimited food supply. Long term growth potential has been linked with initial larval growth in cod (Steinarsson, 2013), but others have concluded that it is mainly the post-settlement habitat quality which controls growth in plaice during nursery ground period (Fox et al., 2014). Low temperature could also possible influence the food quality or quantity at nursery in those years. The influence of variability in prey conditions (Karakiri et al., 1989) and nutrient condition (Teal et al., 2008) has been linked to inter-annual variability in growth rate, thus this could also be the case in those years in Helguvík. At the same time brown shrimp density was considered low (Jónsdóttir et al., 2016), thus the effect of interspecific competition is considered minimal. In our studies a strong relationship was found between both density maximum peak and spring temperature (May) on summer growth. Therefore the interplay between those variables is likely controlling the growth during the summer. However, there are still relatively few data

available and information is missing on the food abundance at the site which warrants deeper studies regarding those matters.

Effects of plaice density on inter-annual growth variability has been investigated in various studies in plaice nursery areas (Fox et al., 2014; Geffen et al., 2011; Haynes et al., 2012; Modin & Pihl, 1994; Nash et al., 2007; Raedemaecker, 2011; Teal et al., 2008). The conclusions were somewhat indecisive, however the influence of variations in plaice density on growth have been reported on numerous occasions and when more thorough methods, such as otolith microstructure analysis or RNA-based index, were used growth rate was lower with higher plaice density (Geffen et al., 2011; Modin & Pihl, 1994). In this study, two years with highly different density pattern were compared by otolith microstructure analysis. The conclusions were complex with higher growth during settlement period in high density year and exact opposite in late August. Complex settlement pattern in high density year could influence the higher growth during the settlement period as growth variations have been found between different sub-cohorts (Al-Hossaini et al., 1989; Geffen et al., 2011; Modin & Pihl, 1994) and by growth compensation after metamorphosis of newly settled juveniles (Geffen et al., 2007). This change in growth pattern could indicate density-dependant processes after the peak, as the growth was higher later in the nursery ground period in low density year. Very high numbers of juveniles in settlement period could have influence the food supply which individuals later in the season experienced. Those processes could influence this shift in growth between those two years as food limitation (Pihl et al., 2000; Wennhage et al., 2007), intra-specific competition (Geffen et al., 2011; Modin & Pihl, 1994; Nash et al., 2007, 1994b) or just disturbance in capturing and handling the prey (Heath, 1992) have been suggested as possible influencing factors. Effects of inter-specific competition on growth in those two years was also not investigated, but in comparison to Jónsdóttir et al., 2016, in review) the shrimp densities did not vary greatly between the years. Thus the effect of brown shrimp on feeding patterns of plaice and therefore growth variations could not be determined. Also, as mentioned earlier the lack of information on food quality and quantity in Helguvík prevent more accurate analysis of both intra- and interspecific processes on juvenile plaice growth.

The increments widths in comparison years were considered wide in comparison to previous studies (Karakiri et al., 1991, 1989; Modin & Pihl, 1994; Raedemaecker, 2011; Selleslagh & Amara, 2012), however they were in range for high growth period Al-Hossaini et al., (1989) noted during July-August in Red Wharf Bay in North Wales. As mentioned before, the growth period at higher latitudes is shorter and starts later in comparison to European nurseries (Freitas et al., 2010; Hjörleifsson & Palsson, 2001, this study). Therefore, our wide increments could correspond to a high growth period starting earlier in the nursery ground period in Helguvík. Also the increment widths in juvenile plaice have not been measured before in Icelandic waters (or in higher latitude nurseries), as in higher latitudes the day is longer during summer and more visibility and longer

feeding period during day could influence larger widths (Al-Hossaini & Pitcher, 1988; Karakiri & Westernhagen, 1989; Suthers & Sundby, 1996). There was no significant difference in increment width between the years, however otolith diameters in 2012 juveniles were larger, which could indicate a slower growth in 2012, as the increments widths can increase with otoliths size, even under constant (or decreasing) growth rates (Campana & Jones, 1992). Selleslagh & Amara, (2012) showed clear response in the recent otolith growth, the Fulton's condition index and the RNA/DNA ratio to the starvation and that those biological factors should hence detect stress endured by juveniles in natural environment. In Helguvík's juveniles the otoliths recent increment widths were similar in both years, and much larger than 3.99 micrometres which indicates that the fish was not starving during the settlement period (Selleslagh & Amara, 2012). When growth rate of those individuals was back-calculated using the biological intercept equation, the significantly higher growth rate was noted in 2005 individuals in comparison to 2012 individuals. This indicates density-dependent effects on growth. The size-selective mortality can also have an influence on individual growth, especially in high density years. This is linked to observational bias, where if the individuals have been affected by size-selective mortality due to food-limitations, the remaining survivors are those which growth is close to optimal and therefore had higher chances of survival (reviewed in Le Pape & Bonhommeau, 2015). This could mean that the individuals that are compared from the high density year are the "lucky" ones, in comparison to all the others in low density years (Le Pape & Bonhommeau, 2015). Density-dependent growth has previously been observed in nurseries; (Ciotti et al., 2013a; Geffen et al., 2011; Modin & Pihl, 1994; Nash et al., 2007) and Pihl et al., (2000) noted that density-dependent processes reduced growth at high juvenile densities ( $> 5 \text{ ind. m}^{-2}$ ). Therefore, as observed densities in Helguvík can be regarded as extremely high on several occasions the influence of density-dependent processes on juvenile plaice growth could be considered as an influencing factor for growth variability.

# References

- Able, K. W. (1999). Measures of juvenile fish habitat quality: examples from a National Estuarine Research Reserve. *American Fisheries Society Symposium*, 22, 134–147.
- Able, K. W., Neuman, M. J., & Wennhage, H. (2005). Ecology of juvenile and adult stages of flatfishes: distribution and dynamics of habitat associations. In *Flatfishes: Biology and Exploitation* (pp. 164–184).
- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19(6), 716–723.
- Al-Hossaini, M., Liu, Q., & Pitcher, T. J. (1989). Otolith microstructure indicating growth and mortality among plaice, *Pleuronectes platessa* L., post-larval sub-cohorts. *Journal of Fish Biology*, 35(Supplement A), 81–90.
- Al-Hossaini, M., & Pitcher, T. J. (1988). The relation between daily rings, body growth and environmental factors in plaice, *Pleuronectes platessa* L., juvenile otoliths. *Journal of Fish Biology*, 33, 409–418.
- Allen, B. M., Brophy, D., McGrath, D., & King, P. a. (2008). Hatching times, larval duration, settlement and larval growth of plaice (*Pleuronectes platessa* L.) in Galway bay determined using otolith microstructure. *Biology & Environment: Proceedings of the Royal Irish Academy*, 108(3)
- Amara, R. (2003). Seasonal ichthyodiversity and growth patterns of juvenile flatfish on a nursery ground in the Southern Bight of the North Sea (France). *Environmental Biology of Fishes*, 67, 191–201.
- Amara, R. (2004). 0-group flatfish growth conditions on a nursery ground (Bay of Canche, Eastern English Channel). *Hydrobiologia*, 518(1-3), 23–32.
- Amara, R., Laffargue, P., Dewarumez, J. M., Maryniak, C., Lagardere, F., & Luczac, C. (2001). Feeding ecology and growth of O-group flatfish (sole, dab and plaice) on a nursery ground (Southern Bight of the North Sea). *Journal of Fish Biology*, 58(3).
- Amara, R., & Paul, C. (2003). Seasonal patterns in the fish and epibenthic crustaceans community of an intertidal zone with particular reference to the population dynamics of plaice and brown shrimp. *Estuarine, Coastal and Shelf Science*, 56(3-4), 807–818.
- Anderson, J. T. (1988). A Review of Size Dependent Survival During Pre-Recruit Stages of Fishes in Relation to Recruitment. *Journal Northwest Atlantic Fishery Science*, 8, 55–66.

Anonymous. (2015). Nytjastofnar sjávar 2014/2015 og aflahorfur fiskveiðiárið 2015/2016. *Hafrannsóknir*, 182, 54–56.

Bailey, K. M. (1989). Predation on Eggs and Larvae of Marine Fishes and the Recruitment Problem. *Advances in Marine Biology*, 25, 1–83.

Beck, M. W., Heck Jr., K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., ... Weinstein, M. P. (2001). The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. *BioScience*, 51(8), 633–641.

Berghahn, R., Lüdemann, K., & Ruth, M. (1995). Difference in individual growth of newly settled 0-group plaice (*Pleuronectes platessa* L.) in the intertidal of neighbouring Wadden Sea areas. *Netherlands Journal of Sea Research*, 34, 131–138.

Bergman, M. J. N., van der Veer, H. W., & Zijlstra, J. J. (1988). Plaice nurseries: effects on recruitment. *Journal of Fish Biology*, 33, 201–218.

Beverton, R. J. H., & Iles, T. C. (1992). Mortality rates of 0-group plaice (*Pleuronectes platessa* L.), dab (*Limanda limanda* L.) and turbot (*Scophthalmus maximus* L.) in European waters. Density-dependence of mortality rates of 0-group plaice and some demographic implications. *Netherlands Journal of Sea Research*, 29(1-3), 61–79.

Blaxter, J. H. S., & Staines, M. E. (1971). Food searching potential in marine fish larvae. *Proceedings. 4th European Marine Biology Symposium*, 467–481.

Bolle, L. J., Dickey-Collas, M., van Beek, J., Erftemeijer, P., Witte, J. I. J., van der Veer, H. W., & Rijnsdorp, A. D. (2009). Variability in transport of fish eggs and larvae. III. Effects of hydrodynamics and larval behaviour on recruitment in plaice. *Marine Ecology Progress Series*, 390, 195–211.

Brooks, S., & Johnston, I. A. (1993). Influence of development and rearing temperature on the distribution, ultrastructure and myosin sub-unit composition of myotomal muscle-fibre types in the plaice *Pleuronectes platessa*. *Marine Biology*, 117(3), 501–513.

Burnham, K., & Anderson, D. (1998). *Model Selection and Multimodel Inference: a practical information-theoretic approach*. (Second edi.). Springer, New York.

Campana, S. E. (1990). How Reliable are Growth Back-Calculations Based on Otoliths? *Canadian Journal of Fisheries and Aquatic Sciences*, 47(11), 2219–2227.

Campana, S. E. (1992). Measurement and interpretation of the microstructure of fish otoliths,. In D. K. Stevenson & S. E. Campana (Eds.), *Otolith microstructure examination and analysis*. (pp. 59–71). Can. Spec. Publ. Fish. Aquat. Sci.

Campana, S. E., & Jones, C. M. (1992). Analysis of Otolith Microstructur Data. In D. K. Stevenson & S. E. Campana (Eds.), *Otolith Microstructure and Analysis* (pp. 73–100). Canadian Special Publication of Fisheries and Aquatic Science.

- Campana, S. E., & Neilson, J. D. (1985). Microstructure of Fish Otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*, 42, 1014–1032.
- Chambers, R. C., & Legget, W. C. (1996). Maternal Influences on Variation in Egg Sizes in Temperate Marine Fishes. *American Zoologist*, 36, 180–196.
- Christensen, M. N., & Korsgaard, B. (1999). Protein metabolism, growth and pigmentation patterns during metamorphosis of plaice (*Pleuronectes platessa*) larvae. *Journal of Experimental Marine Biology and Ecology*, 237(2), 225–241.
- Ciotti, B. J., Targett, T., & Burrows, M. (2013a). Spatial variation in growth rate of early juvenile European plaice *Pleuronectes platessa*. *Marine Ecology Progress Series*, 475, 213–232.
- Ciotti, B. J., Targett, T. E., Burrows, M. T., & Jech, J. M. (2013b). Decline in growth rate of juvenile European plaice ( *Pleuronectes platessa* ) during summer at nursery beaches along the west coast of Scotland. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(5), 720–734.
- Ciotti, B. J., Targett, T. E., Nash, R. D. M., & Geffen, A. J. (2014). Growth dynamics of European plaice *Pleuronectes platessa* L. in nursery areas: A review. *Journal of Sea Research*, 90, 64–82.
- Cleveland, W. S. (1979). Robust Locally Weighted Regression and Smoothing Scatterplots. *Journal of the American Statistical Association*, 74(368), 829–836.
- Coombs, S. H., Nichols, J. H., & Fosh, C. A. (1990). Plaice eggs (*Pleuronectes platessa* L.) in the southern North Sea : abundance, spawning area, vertical distribution, and buoyancy. *J. Cons.Int.Explor.Mer.*, 47, 133–139.
- Creutzberg, F., Eltink, A. T. G. W., & Van Noort, G. (1977). The migration of plaice larvae *Pleuronectes platessa* into the western Wadden Sea. In D. S. McLusky & A. J. Berry (Eds.), *Proceedings of the 12th European Symposium on Marine Biology*. Stirling, Scotland.
- Dahlgren, C., Kellison, G., Adams, A., Gillanders, B., Kendall, M., Layman, C., ... Serafy, J. (2006). Marine nurseries and effective juvenile habitats: concepts and applications. *Marine Ecology Progress Series*, 312(April), 291–295.
- Degens, E. T., Deuser, W. G., & Haedrich, R. L. (1969). Molecular structure and composition of fish otoliths \*. *Marine Biology*, 2, 105–113.
- Ellis, T., & Nash, R. D. M. (1997). Spawning of plaice *Pleuronectes platessa* L. around the Isle of Man , Irish Sea. *ICES Journal of Marine Science*, 54, 84–92.
- Evans, S. (1983). Production, predation and food niche segregation in a marine shallow soft-bottom community. *Marine Ecology Progress Series*, 10, 147–157.

- Farrell, A. P. (Ed.). (2011). *Encyclopedia of Fish Physiology. From Geonome to Environment*. Elsevier.
- FOA. (2016). Species Fact Sheets: *Pleuronectes platessa*. FOA: Fisheries and Aquaculture Department. Retrieved March 16, 2016, from <http://www.fao.org/fishery/species/3354/en>
- Fonds, M., Cronie, R., Vethaak, a. D., & Van Der Puyl, P. (1992). Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. *Netherlands Journal of Sea Research*, 29(1-3), 127–143.
- Fox, C. J., Geffen, A. J., Blyth, R., & Nash, R. D. M. (2003). Temperature-dependent development rates of plaice (*Pleuronectes platessa* L.) eggs from the Irish Sea. *Journal of Plankton Research*, 25(11), 1319–1329.
- Fox, C. J., Geffen, A. J., Taylor, N., Davison, P., Rossetti, H., & Nash, R. D. M. (2007). Birth-date selection in early life stages of plaice *Pleuronectes platessa* in the eastern Irish Sea ( British Isles ). *Marine Ecology Progress Series*, 345, 255–269.
- Fox, C. J., McCloghrie, P., & Nash, R. D. M. (2009). Potential transport of plaice eggs and larvae between two apparently self-contained populations in the Irish Sea. *Estuarine, Coastal and Shelf Science*, 81(3), 381–389.
- Fox, C. J., McCloghrie, P., & Young, E. F. (2006). The importance of individual behaviour for successful settlement of juvenile plaice (*Pleuronectes platessa* L.): a modelling and field study in the eastern Irish Sea. *Fisheries Oceanography*, 15 (4), 301–313.
- Fox, C. J., Planque, B. ., & Darby, C. (2000). Synchrony in the recruitment time-series of plaice (*Pleuronectes platessa* L.) around the United Kingdom and the influence of sea temperature. *Journal of Sea Research*, 44(1-2), 159–168.
- Fox, C. J., Targett, T. E., Ciotti, B. J., de Kroon, K., Hortsmeier, L., & T. Burrows, M. (2014). Size variation of 0-group plaice: Are earlier influences on growth potential a contributing factor? *Journal of Sea Research*, 88, 59–66.
- Freitas, V., Cardoso, J. F. M. F., Skreslet, S., & van der Veer, H. W. (2010). Habitat quality of a subarctic nursery ground for 0-group plaice (*Pleuronectes platessa* L.). *Journal of Sea Research*, 64(1-2), 26–33.
- Freitas, V., Kooijman, S. A. L. M., & van der Veer, H. W. (2012). Latitudinal trends in habitat quality of shallow-water flatfish nurseries. *Marine Ecology Progress Series*, 471, 203–214.
- Fuiman, L. A. (1997). What can flatfish ontogenies tell us about pelagic and benthic lifestyles? *Journal of Sea Research*, 37(3-4), 257–267.
- Fuiman, L. A., & Werner, R. G. (Eds.). (2002). *Fishery Science: The Unique Contributions of Early Life Stages* (p. 304). Wiley-Blackwell.



- Geffen, A. J., & Nash, R. D. M. (1994). Periodicity of Otolith Check Formation in the Juvenile Plaice *Pleuronectes platessa* L. *Recent Developments in Fish Otolith Research*, (19), 65–73.
- Geffen, A. J., Nash, R. D. M., Dau, K., & Harwood, A. J. P. (2011). Sub-cohort dynamics of 0-group plaice, *Pleuronectes platessa* L., in the Northern Irish Sea : Settlement , growth and mortality. *Journal of Experimental Marine Biology and Ecology*, 400(1-2), 108–119.
- Geffen, A. J., van der Veer, H. W., & Nash, R. D. M. (2007). The cost of metamorphosis in flatfishes. *Journal of Sea Research*, 58(1), 35–45.
- Gibson, R. N. (1994). Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research*, 32(2), 191–206.
- Gibson, R. N. (1999). The ecology of the early life stages of the plaice, *Pleuronectes platessa* L.: a review. *Bulletin of Tohoku National Fisheries Research Institute*, 62, 17–50.
- Gibson, R. N., Burrows, M. T., & Robb, L. (2011). Field experiments on depth selection by juvenile plaice *Pleuronectes platessa*. *Marine Ecology Progress Series*, 430, 197–205.
- Gibson, R. N., Robb, L., Wennhage, H., & Burrows, M. T. (2002). Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground. *Marine Ecology Progress Series*, 229, 233–244.
- Gilliers, C., Amara, R., Bergeron, J., & Le, O. (2004). Comparison of growth and condition indices of juvenile flatfish in different coastal nursery grounds. *Environmental Biology of Fishes*, 71, 189–198.
- Glazenburg, B. (1983). Een experimenteel onderzoek naar de groei van 0-groep schol en bot in relatie tot de watertemperatuur. *Internal Reports NIOZ*, 5, 1–19.
- Gunnarsson, B., Ásgeirsson, Þ. H., & Ingólfsson, A. (2007). The rapid colonization by *Crangon Crangon* (Linnaeus, 1758) (Eucarida, Caridea, Crangonidae) of Icelandic Coastal Waters. *Crustaceana*, 80(6), 747–753.
- Gunnarsson, B., Jonasson, J. P., & McAdam, B. J. (2010). Variation in hatch date distributions, settlement and growth of juvenile plaice (*Pleuronectes platessa* L.) in Icelandic waters. *Journal of Sea Research*, 64(1-2), 61–67.
- Gunnarsson, K., Jónsson, G., & Pálsson, Ó. K. (1998). Skarkoli. In *Sjávarnytjar við Ísland* (pp. 236–239).
- Haynes, P. S., Brophy, D., & McGrath, D. (2012). Variability in the early life stages of juvenile plaice (*Pleuronectes platessa*) on west of Ireland nursery grounds: 2000–2007. *Journal of the Marine Biological Association of the United Kingdom*, 92(02), 395–406.
- Heath, M. R. (1992). Field Investigations of the Early Life Stages of Marine Fish. *Advances in Marine Biology*, 28.

- Heincke, F. (1913). Investigations on the plaice. 1. Plaice fishery and protective measures. *Rap- Ports et Procès-Verbaux Des Réunions Du Conseil International Pour l'Exploration de La Mer*, 17, 1–153.
- Helfman, G. S., Collette, B. B., Facey, D. E., & Bowen, B. W. (2009). *The Diversity of Fishes. Biology, Evolution, and Ecology* (Second Edi.). Wiley-Blackwell.
- Hixon, M. A., & Johnson, D. W. (2009). Density Dependence and Independence. In *Encyclopedia of Life Science*. Chichester, UK: John Wiley & Sons, Ltd.
- Hjörleifsson, E., & Pálsson, J. (2001). Settlement, growth and mortality of 0-group plaice (*Pleuronectes platessa*) in Icelandic waters. *Journal of Sea Research*, 45, 321–324.
- Hovenkamp, F., & Witte, J. I. J. (1991). Growth, otolith growth and RNA/DNA ratios of larval plaice *Pleuronectes platessa* in the North Sea 1987 to 1989. *Marine Ecology Progress Series*, 70, 105–116.
- Hyder, K., & Nash, R. D. M. (1998). Variations in settlement pattern of Irish Sea plaice (*Pleuronectes platessa* L.) as determined from a simulation model. *Journal of Sea Research*, 40, 59–71.
- ICES. (2016). Plaice. *ICES-FishMap*. Retrieved March 16, 2016, from [http://www.ices.dk/explore-us/projects/EU-RFP/EU\\_Repository/ICES\\_FishMap/ICES\\_FishMap\\_species\\_factsheet-plaice.pdf](http://www.ices.dk/explore-us/projects/EU-RFP/EU_Repository/ICES_FishMap/ICES_FishMap_species_factsheet-plaice.pdf)
- Jager, Z., Kleef, H. L., & Tydeman, P. (1995). Mortality and growth of 0-group flatfish in the brackish dollard (Ems Estuary, Wadden Sea). *Netherlands Journal of Sea Research*, 34(1-3), 119–129.
- Jónsdóttir, I. G., Jónasson, J. P., Guðmundsson, S. Ö., Puro, H., Marteinsdottir, G., & Gunnarsson, B. (2016). Population dynamics of the brown shrimp (*Crangon crangon*) in a newly colonized area. *Journal of Sea Research*. In review.
- Jónsson, G., & Pálsson, J. (2013). *Íslenskir fiskar* (2nd ed., p. 493). Mál og menning.
- Karakiri, M., Berghahn, R., & van der Veer, H. W. (1991). Variations in settlement and growth of 0-group plaice (*Pleuronectes platessa* L.) in the dutch Wadden Sea as determined by otolith microstructure analysis\*. *Netherlands Journal of Sea Research*, 27(3/4), 345–351.
- Karakiri, M., Berghahn, R., & Westernhagen, H. von. (1989). Growth differences in 0-group plaice *Pleuronectes platessa* as revealed by otolith microstructure analysis. *Marine Ecology Progress Series*, 55(1), 0–5.
- Karakiri, M., & Westernhagen, H. von. (1989). Daily growth patterns in otoliths of larval and juvenile plaice (*Pleuronectes platessa* L.): influence of temperature, salinity and light conditions. *Rapp. Proc.-V.Réun. Cons. Int.Explor.Mer.*, 191, 376–382.

- Koberstein, M. J. (2013). Expansion of the brown shrimp *Crangon crangon* L. onto juvenile plaice *Pleuronectes platessa* L. nursery habitat in the Westfjords of Iceland. University of Akureyri.
- Lagardère, F. (1989). Influence of feeding conditions and temperature on the growth rate and otolith-increment deposition of larval Dover sole (*Solea solea* (L.)). *Rapp. Proc.-V.Réun. Cons. Int.Explor.Mer.*, 191, 390–399.
- Le Pape, O., & Bonhommeau, S. (2015). The food limitation hypothesis for juvenile marine fish, *Fish and Fisheries*, 16(3), 373–398.
- Leggett, W. C., & Deblois, E. (1994). Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research*, 32(2), 119–134.
- Link, J. S., Fogarty, M. J., & Langton, R. W. (2004). The trophic ecology of flatfishes. In *Flatfishes: Biology and Exploitation* (pp. 185–212).
- Mantzouni, I., & MacKenzie, B. R. (2010). Productivity responses of a widespread marine piscivore, *Gadus morhua*, to oceanic thermal extremes and trends. *Proceedings. Biological Sciences / The Royal Society*, 277(1689), 1867–74.
- Modin, J., Fagerholm, B., Gunnarsson, B., & Pihl, L. (1996). Short communication Changes in otolith microstructure at metamorphosis of plaice, *Pleuronectes platessa* L. *ICES Journal of Marine Science*, 53, 745–748.
- Modin, J., & Pihl, L. (1994). Differences in growth and mortality of juvenile plaice (*Pleuronectes platessa* L.), following normal and extremely high settlement. *Netherlands Journal of Sea Research*, 32(3/4), 331–341.
- Morales-Nin, B. (2000). Review of the growth regulation processes of otolith daily increment formation. *Fisheries Research*, 46(1-3), 53–67.
- Moyle, P. B., & Joseph J. Cech, J. (1982). *Fishes: an introduction to ichthyology*. (R. Herion, Ed.) (p. 593). Prentice-Hall, Inc.
- Myers, R. A. (1998). When do environment  $\pm$  recruitment correlations work? *Reviews in Fish Biology and Fisheries*, 8, 285–305.
- Nash, R. D. M., & Geffen, A. J. (2000). The influence of nursery ground processes in the determination of year-class strength in juvenile plaice *Pleuronectes platessa* L. in Port Erin Bay, Irish Sea. *Journal of Sea Research*, 44, 101–110.
- Nash, R. D. M., & Geffen, A. J. (2012). Mortality through the early life-history of fish: What can we learn from European plaice (*Pleuronectes platessa* L.)? *Journal of Marine Systems*, 93, 58–68.

- Nash, R. D. M., & Geffen, A. J. (2014). Age and growth. In R. N. Gibson, R. D. M. Nash, A. J. Geffen, & H. W. van der Veer (Eds.), *Flatfishes: Biology and Exploitation* (pp. 207–241). John Wiley & Sons, Ltd, Chichester, UK.
- Nash, R. D. M., Geffen, A. J., Burrows, M. T., & Gibson, R. N. (2007). Dynamics of shallow-water juvenile flatfish nursery grounds : application of the self-thinning rule. *Marine Ecology Progress Series*, 344, 231–244.
- Nash, R. D. M., Geffen, A. J., & Hughes, G. (1994). Individual growth of juvenile plaice (*Pleuronectes platessa* L.) on a small Irish Sea nursery ground (Port Erin Bay, Isle of Man, UK). *Netherlands Journal of Sea Research*, 32(3/4), 369–378.
- Nash, R. D. M., Witthames, P. ., Pawson, M., & Alesworth, E. (2000). Regional variability in the dynamics of reproduction and growth of Irish Sea plaice, *Pleuronectes platessa* L. *Journal of Sea Research*, 44(1-2), 55–64.
- Nielsen, E., Bagge, O., & Mackenzie, B. R. (1998). Wind-induced transport of plaice (*Pleuronectes platessa*) early life-history stages in the Skagerrak-Kattegat. *Journal of Sea Research*, 39, 11–28.
- Pannella, G. (1971). Fish otoliths: daily growth layers and periodical patterns. *Science*, 173, 1124–1127.
- Pálsson, J., & Hjörleifsson, E. (2001). Skarkoli á fyrsta aldursári rannsakaður. *Hafrannsóknir*, 56, 86–89.
- Pihl, L., Modin, J., & Wennhage, H. (2000). Spatial distribution patterns of newly settled plaice (*Pleuronectes platessa* L.) along the Swedish Skagerrak archipelago. *Journal of Sea Research*, 44(1-2), 65–80.
- Pihl, L., & van der Veer, H. W. (1992). Importance of exposure and habitat structure density of 0-group plaice,. *Netherlands Journal of Sea Research*, 29(1-3), 145–152.
- Raedemaeker, F. De. (2011). Spatial variability in diet, condition and growth of juvenile plaice (*Pleuronectes platessa*) at sandy beach nursery grounds on the south-west coast of Ireland. *Journal of the Marine Biological Association of the United Kingdom*, 91(6), 1215–1223.
- Rijnsdorp, A. D., Beek, F. A. Van, Flatman, S., Millner, R. M., Riley, J. D., Giret, M., & De Clerck, R. (1992). Recruitment of sole stocks, *Solea solea* (L.), in the Northeast Atlantic. *Neth. J. Sea Res.* 29: 173–192. *Netherlands Journal of Sea Research*, 29, 173–192.
- Rijnsdorp, A. D., Berghahn, R., Miller, J. M., & van der Veer, H. W. (1995). Recruitment mechanisms in flatfish: What did we learn and where do we go? *Netherlands Journal of Sea Research*, 34(1-3), 237–242.

- Rijnsdorp, A. D., & Ibelings, B. (1989). Sexual dimorphism in the energetics of reproduction and growth of North Sea plaice, *Pleuronectes platessa* L. *Journal of Fish Biology*, 35(3), 401–415.
- Rijnsdorp, A. D., Stralen, M. van, & van der Veer, H. W. (1985). Selective Tidal Transport of North Sea Plaice Larvae *Pleuronectes platessa* in Coastal Nursery Areas. *Transactions of the American Fisheries Society*, 114, 461–470.
- Rijnsdorp, A. D., & Witthames, P. R. (2004). Ecology of reproduction. In *Flatfishes: Biology and Exploitation* (pp. 68–93).
- Rose, K. A., Cowan Jr, J. H., Winemiller, K. O., Myers, R. A., & Hilborn, R. (2001). Compensatory density dependence in fish populations: importance , controversy , understanding and prognosis. *Fish and Fisheries*, 2, 293–327.
- Russell, F. (1976). The eggs and planktonic stages of British marine fishes. Academic Press, London, (pp.524).
- Ryland, J. S. (1966). Observations on the Development of Larvae of the Plaice, *Pleuronectes platessa* L., in Auquaria. *J. Cons. Perm. Int. Explor. Mer.*, 30(2), 177–195.
- Ryland, J. S., & Nichols, J. H. (1975). The effect of temperature on the embryonic development of the plaice *Pleuronectes platessa* L. (Teleostei). *Journal of Experimental Marine Biology and Ecology*, 18, 121–137.
- Selleslagh, J., & Amara, R. (2012). Effect of starvation on condition and growth of juvenile plaice *Pleuronectes platessa*: nursery habitat quality assessment during the settlement period. *Journal of the Marine Biological Association of the United Kingdom*, 93(02), 479–488.
- Aðalsteinn Sigurðsson (1989). Skarkolamerkingar við Ísland árin 1953-1965. *Hafrannsóknir*, 39, 5–24.
- Sogard, S. M. (1991). Interpretation of Otolith Microstructure in Juvenile Winter Flounder (*Pseudopleuronectes americanus*): Ontogenetic Development, Daily Increment Validation, and Somatic Growth Relationships. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 1862–1871.
- Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: A review. *Bulletin of Marine Science*, 60(3), 1129–1157.
- Solmundsson, J., Karlsson, H., & Palsson, J. (2003). Sexual differences in spawning behaviour and catchability of plaice (*Pleuronectes platessa*) west of Iceland. *Fisheries Research*, 61(1-3), 57–71.
- Solmundsson, J., Palsson, J., & Karlsson, H. (2005). Fidelity of mature Icelandic plaice () to spawning and feeding grounds. *ICES Journal of Marine Science*, 62(2), 189–200.

Steinarsson, A. (2013). Growth curve modelling (GCM) and possible application in fish stock assessment. In *ICES Conference paper*.

Stephen J. Lockwood. (1974). The settlement, distribution and movements of 0-group plaice *Pleuronectes platessa* (L.) in Filey Bay, Yorkshire. *Journal of Fish Biology* 1, 6(4), 465–477.

Suthers, I. M., & Sundby, S. (1996). Role of the midnight sun : comparative growth of pelagic juvenile cod ( *Gadus morhua* ) from the Arcto-Norwegian and a Nova Scotian stock. *ICES Journal of Marine Science*, 53, 827–836.

Sæmundsson, B. (1926). *Fiskarnir (Pisces Islandiæ)*. Bókaverslun Sigfúsar Eymundssonar, Reykjavík, (pp. 579).

Tåning, Å. V. (1929). Plaice investigations in Icelandic waters. In *Rapp. Proc.-V.Réun. Cons. Int.Explor.Mer.* 57, (pp. 1–134).

Teal, L., de Leeuw, J., van der Veer, H. W., & Rijnsdorp, A. D. (2008). Effects of climate change on growth of 0-group sole and plaice. *Marine Ecology Progress Series*, 358, 219–230.

Thomas A. Munroe. (2004). Systematic diversity of the Pleuronectiformes. In R. N. Gibson (Ed.), *Flatfishes: Biology and Exploitation* (1st editio., pp. 10–36). Blackwell Science Ltd.

Thompson, B. M., & Riley, J. D. (1981). Egg and larval development studies in the North Sea cod (*Gadus Morhua* L.). *Rapp. Proc.-V.Réun. Cons. Int.Explor.Mer.*, (178), 553–559.

Tucker, J. E. (1998). *Marine Fish Culture. Marine Fish Culture* (p. 750). Springer US.

Van der Veer, H. W. (1986). Immigration, settlement, and density-dependent mortality of a larval and early postlarval 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. *Marine Ecology Progress Series*, 29, 223–236.

Van der Veer, H. W., Berghahn, R., Miller, J. M., & Rijnsdorp, A. D. (2000). Recruitment in flatfish, with special emphasis on North Atlantic species: Progress made by the Flatfish Symposia. *ICES Journal of Marine Science*, 57(2), 202–215.

Van der Veer, H. W., & Bergman, M. J. N. (1987). Predation by crustaceans on a newly settled 0-group plaice *Pleuronectes platessa* population in the western Wadden Sea. *Marine Ecology Progress Series*, 35, 203–215.

Van der Veer, H. W., Bolle, L. J., Geffen, A. J., & Witte, J. I. J. (2009). Variability in transport of fish eggs and larvae. IV. Interannual variability in larval stage duration of immigrating plaice in the Dutch Wadden Sea. *Marine Ecology Progress Series*, 390, 213–223.

- Van der Veer, H. W., Freitas, V., Koot, J., Witte, J. I. J., & Zuur, A. (2010). Food limitation in epibenthic species in temperate intertidal systems in summer: analysis of 0-group plaice *Pleuronectes platessa*. *Marine Ecology Progress Series*, 416, 215–227.
- Van der Veer, H. W., Pihl, L., & Bergman, M. J. N. (1990). Recruitment mechanism in North Sea plaice *Pleuronectes platessa*. *Marine Ecology Progress Series*, 64, 1–12.
- Van der Veer, H. W., Ruardij, P., van den Berg, A. J., & Ridderinkhof, H. (1998). Impact of interannual variability in hydrodynamics circulation on egg and larval transport of plaice *Pleuronectes platessa* L. in the southern North Sea. *Journal of Sea Research*, 39, 29–40.
- Van der Veer, H. W., & Witte, J. I. J. (1993). The 'maximum growth/optimal food condition' hypothesis : a test for 0-group plaice *Pleuronectes platessa* in the Dutch Wadden Sea. *Marine Ecology Progress Series*, 101, 81–90.
- Van der Veer, H. W., & Witte, J. I. J. (1999). Year-class strength of plaice *Pleuronectes platessa* in the Southern Bight of the North Sea : a validation. *Marine Ecology Progress Series*, 184, 245–257.
- Van Walraven, L., Mollet, F. M., van Damme, C. J. G., & Rijnsdorp, A. D. (2010). Fisheries-induced evolution in growth, maturation and reproductive investment of the sexually dimorphic North Sea plaice (*Pleuronectes platessa* L.). *Journal of Sea Research*, 64(1-2), 85–93.
- Watabe, N., Tanaka, K., Yamada, J., & Dean, J. M. (1982). Scanning electron microscope observations of the organic matrix in the otolith of the teleost fish *Fundulus heteroclitus* (Linnaeus) and *Tilapia nilotica* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, 58(1), 127–134.
- Wennhage, H., & Gibson, R. N. (1998). Influence of food supply and a potential predator (Crangon crangon) on settling behaviour of plaice (*Pleuronectes platessa* ). *Journal of Sea Research*, 39, 103–112.
- Wennhage, H., Pihl, L., & Stål, J. (2007). Distribution and quality of plaice (*Pleuronectes platessa*) nursery grounds on the Swedish west coast. *Journal of Sea Research*, 57(2-3), 218–229.





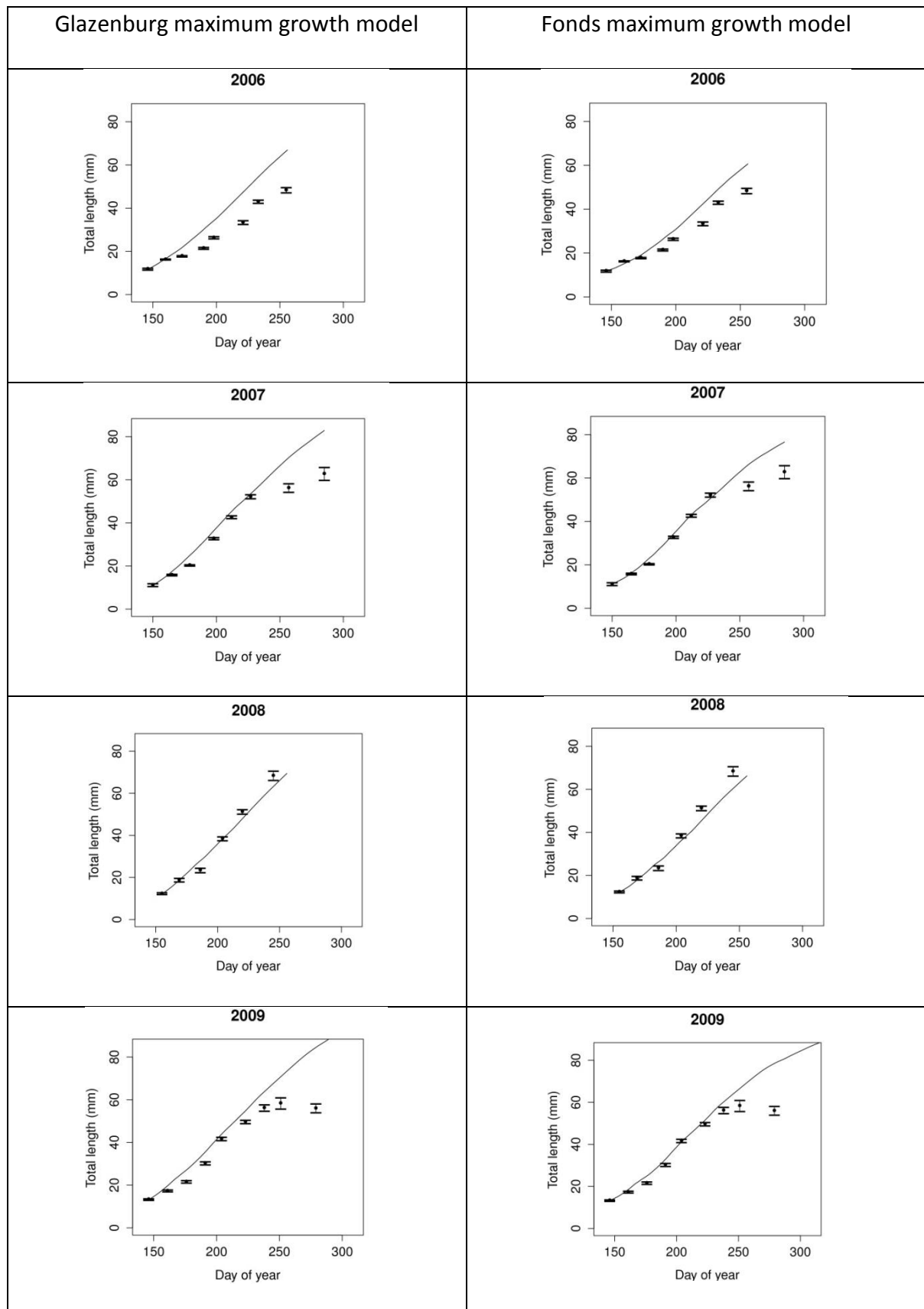
# Appendix A

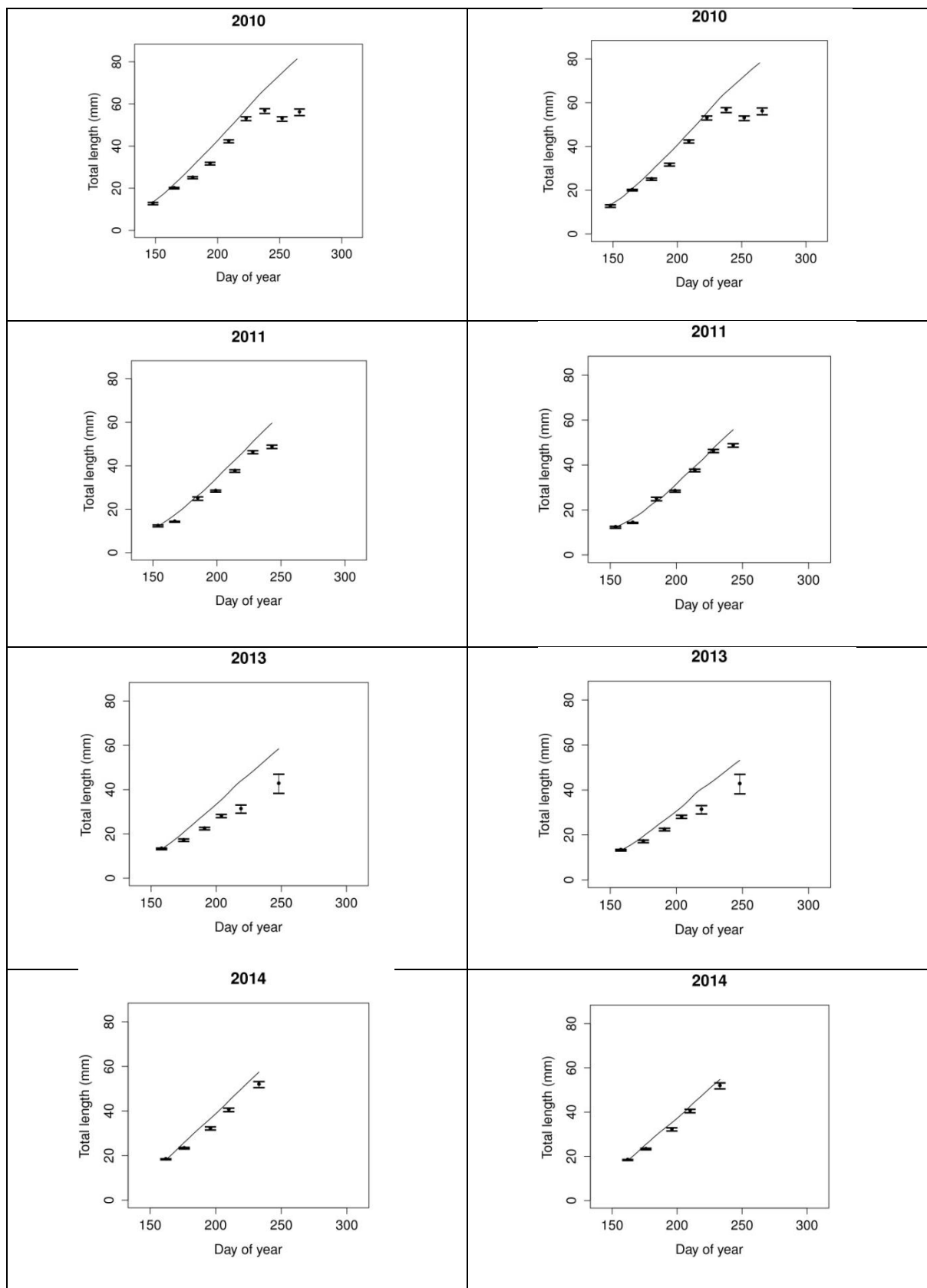
*Table A.1 Summary of sampling dates, number of tows, catch in all tows per sampling date, mean density (+/- SD), mean length of measured individuals (+/- SD) and tide variation for each day.*

Year	Sampling date (ordinal day)	<i>n</i> tows per sampling	<i>n</i> YOY plaice in all hauls	<i>n</i> measured plaice	Density (ind. 100 m <sup>-2</sup> ) ± SD	Mean length (mm) ± SD	Tide variation
2005	May 26 (146)	2	0	0	0	0	0.37
	June 1 (152)	2	3	3	2.25 ± 0.34	14.17 ± 2.00	0.91
	June 8 (159)	1	1	1	2 ± NA	15.81 ± NA	0.67
	June 10 (161)	2	106	106	54.79 ± 1.64	15.39 ± 2.40	0.88
	June 27 (178)	3	681	360	227 ± 7.54	20.47 ± 4.32	0.64
	July 11 (192)	2	459	199	229.5 ± 4.95	28.51 ± 5.37	0.86
	July 24 (205)	2	512	100	256 ± 15.56	32.59 ± 8.56	0.06
	August 17 (229)	2	211	135	117.2 ± 46.36	42.74 ± 8.20	0.84
	September 8 (251)	2	270	149	135 ± 19.8	51.57 ± 13.87	0.59
2006	May 26 (146)	2	14	14	7.75 ± 0.35	11.78 ± 1.18	0.30
	June 9 (160)	3	291	291	97 ± 3.6	15.72 ± 1.92	0.90
	June 22 (173)	3	1429	301	476.3 ± 12.66	17.52 ± 3.44	0.76
	July 9 (190)	3	1444	210	499.3 ± 39.1	20.61 ± 5.27	0.89
	July 17 (198)	3	649	221	216.3 ± 57	23.34 ± 5.49	0.73
	August 9 (221)	3	634	162	211.3 ± 9.1	31.37 ± 6.87	0.37
	August 21 (233)	3	314	314	104.67 ± 10.6	36.12 ± 8.02	0.95
	September 12 (255)	3	227	227	82.58 ± 20	43.40 ± 11.22	0.35
2007	May 30 (150)	2	6	6	6.5 ± 2.12	11.00 ± 1.08	0.84
	June 14 (165)	4	103	103	40.54 ± 14.16	16.47 ± 1.87	0.35
	June 28 (179)	3	341	341	199.85 ± 91.71	19.54 ± 3.86	1.06
	July 17 (198)	3	735	615	444.56 ± 179.8	28.45 ± 7.97	0.40
	July 31 (212)	3	507	507	281.67 ± 39.41	38.95 ± 9.03	0.27
	August 15 (227)	3	283	283	178.56 ± 24.6	47.96 ± 11.12	0.29
	September 14 (257)	3	70	70	51.06 ± 11.4	52.01 ± 14.07	0.36
	October 12 (285)	2	27	27	29.5 ± 6.36	60.95 ± 15.33	0.39
2008	June 3 (155)	1	3	3	5 ± NA	12.89 ± 0.78	0.22
	June 17 (169)	3	32	32	17.78 ± 3.85	19.12 ± 3.46	0.93
	July 4 (186)	4	12	12	27.82 ± 42.59	20.65 ± 8.84	0.14
	July 22 (204)	6	174	174	56.85 ± 25.61	35.02 ± 11.06	0.50
	August 7 (220)	3	112	112	62.22 ± 2.55	47.84 ± 10.11	0.85
	September 1 (245)	3	55	55	36.67 ± 23.86	68.32 ± 14.04	0.03
2009	May 26 (146)	3	34	34	22.67 ± 9.02	12.50 ± 1.27	0.21
	June 10 (161)	3	106	106	70.67 ± 35.23	16.25 ± 2.59	0.79
	June 25 (176)	3	164	164	109.33 ± 6.43	22.15 ± 4.59	0.11
	July 10 (191)	3	308	162	205.33 ± 30.55	28.20 ± 7.15	0.65
	July 23 (204)	3	232	232	160.82 ± 20.68	38.59 ± 8.97	-0.05
	August 11 (223)	3	249	249	166 ± 52.92	44.21 ± 10.51	0.70

2010	August 26 (238)	3	96	96	$64 \pm 3.46$	$52.86 \pm 12.65$	0.89
	September 8 (251)	3	34	34	$24.5 \pm 2.78$	$58.16 \pm 15.03$	0.42
	October 6 (279)	3	13	13	$8.67 \pm 6.43$	$55.50 \pm 11.12$	0.29
	November 5 (309)	3	8	8	$5.33 \pm 3.06$	$76.70 \pm 24.90$	0.41
	December 17 (351)	3	8	8	$5.33 \pm 2.31$	$52.30 \pm 11.34$	0.78
	May 28 (148)	3	19	19	$12.67 \pm 9.45$	$12.70 \pm 1.97$	0.42
	June 14 (165)	3	480	272	$322.68 \pm 168.93$	$17.79 \pm 3.14$	0.29
	June 29 (180)	3	997	232	$664.67 \pm 84.67$	$22.36 \pm 6.21$	0.64
	July 13 (194)	3	606	259	$404 \pm 68.09$	$30.27 \pm 7.82$	0.05
	July 28 (209)	3	423	221	$282 \pm 75.02$	$36.69 \pm 8.95$	0.50
2011	August 11 (223)	3	614	289	$409.33 \pm 93.52$	$45.30 \pm 13.87$	-0.17
	August 26 (238)	3	226	226	$150.67 \pm 25.17$	$47.73 \pm 13.11$	0.38
	September 9 (252)	3	170	170	$117.26 \pm 51$	$44.86 \pm 10.37$	-0.27
	September 23 (266)	3	100	100	$66.67 \pm 33.01$	$50.36 \pm 12.96$	0.43
	June 3 (154)	3	10	10	$6.67 \pm 4.16$	$12.83 \pm 0.98$	0.57
	June 16 (167)	3	195	195	$130 \pm 22.27$	$14.06 \pm 2.01$	0.30
	july 4 (185)	3	510	510	$340 \pm 121.84$	$21.75 \pm 8.67$	0.30
	July 18 (199)	3	831	415	$554 \pm 174.22$	$27.43 \pm 6.63$	0.43
	August 2 (214)	3	532	333	$555.33 \pm 181.93$	$38.11 \pm 8.75$	0.00
	August 16 (228)	3	239	239	$159.33 \pm 12.22$	$44.18 \pm 9.82$	0.35
2012	August 31 (243)	3	260	260	$173.33 \pm 35.8$	$44.91 \pm 10.12$	-0.20
	June 4 (156)	3	475	266	$316.67 \pm 156.07$	$13.13 \pm 1.36$	0.10
	June 20 (172)	3	1087	406	$724.67 \pm 202.08$	$18.06 \pm 3.74$	0.65
	July 4 (186)	3	1396	303	$930.67 \pm 99.95$	$23.35 \pm 6.76$	0.12
	July 18 (200)	3	1551	295	$1034 \pm 35.04$	$29.86 \pm 6.73$	0.70
	August 2 (215)	3	719	334	$479.33 \pm 91.24$	$34.19 \pm 8.97$	0.16
	August 20 (233)	3	722	476	$481.33 \pm 40.17$	$43.98 \pm 13.67$	0.08
	September 4 (248)	3	326	326	$217.33 \pm 15.14$	$44.47 \pm 14.20$	0.43
	June 7 (158)	3	25	25	$16.67 \pm 7.024$	$13.11 \pm 1.56$	0.71
	June 24 (175)	3	59	59	$39.33 \pm 23.18$	$15.81 \pm 3.01$	-0.01
2013	July 10 (191)	3	210	210	$140 \pm 34.18$	$21.12 \pm 4.80$	0.56
	July 23 (204)	3	216	213	$144 \pm 8.72$	$24.78 \pm 6.73$	-0.05
	August 7 (219)	3	43	43	$28.67 \pm 13.32$	$27.91 \pm 8.47$	0.47
	September 5 (248)	3	10	10	$6.67 \pm 2.31$	$41.72 \pm 13.38$	0.37
	June 11 (162)	3	1896	356	$1264 \pm 135.54$	$16.12 \pm 3.24$	0.54
	June 25 (176)	3	2865	417	$1910 \pm 299.25$	$21.01 \pm 5.40$	0.73
	July 15 (196)	3	2274	303	$1516 \pm 265.1$	$27.71 \pm 8.01$	-0.04
	July 29 (210)	3	1672	318	$1114.67 \pm 167.16$	$34.70 \pm 11.07$	0.49
	August 21 (233)	3	180	180	$120 \pm 57.26$	$42.37 \pm 14.93$	1.18

Table A.2 Summary of mean length trajectories (length-at-date data) for sampling years 2006 – 2011 and 2013 – 2014 compared to maximum growth models under optimal food conditions; Glazenburg and Fonds.





*Table A.3 Analysis of variance of annual growth variation ( $\text{mm d}^{-1}$ ) in years 2005 – 2014, examining the main effects.*

<b>Source</b>	<b>d.f.</b>	<b>Sum of</b>	<b>Mean square</b>	<b><i>F</i></b>	<b><i>p</i>-value</b>
log(DP)	1	0.00702	0.00702	11.81	<0.05
SST <sub>M</sub>	1	0.03942	0.03942	66.30	<0.0001
Residuals	7	0.00416	0.00416	-	-