GROWTH OF ICELANDIC CAPELIN (MALLOTUS VILLOSUS) LARVAE

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By

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Abstract

Predicting recruitment is a difficult task and requires solid biological information. Recruitment in capelin is important to the spawning stock biomass due to a short life span. Theory predicts that faster growing, larger individuals will have greater survival. Growth history of two year-classes of Icelandic capelin (*Mallotus villosus*) larvae was examined from hatching until end of summer in their first year of life.

Precision of otolith analysis was independent of larval age and growth estimates were not statistically different between replicates. Estimated growth of 0.37 mm d^{-1} for the 2001 year-class was in the upper end of growth rates while growth of the 2002 year-class, 0.28 mm d^{-1}, was average for capelin larval growth reported in the literature. Increment width models demonstrated a common growth trajectory both within and among year-classes. Environmental conditions were better in 2001 as temperature was higher by roughly 0.7°C and zooplankton biomass was four times greater. This indicates that better environmental conditions facilitated growth of capelin larvae.

The spawning stock biomass was similar between years but abundance of capelin larvae in August was three times higher in 2001 suggesting that survival rate of larvae was higher in 2001. The faster growth and greater abundance of the 2001 year-class suggests that growth of capelin larvae was density independent.

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Chapter 1: Introduction

1.1 General Introduction

Capelin (*Mallotus villosus*) is a pelagic schooling fish with a circumpolar distribution in the northern hemisphere and the most important pelagic fish stock in Icelandic waters (Vilhjálmsson 1994). Studies on the Icelandic capelin stock indicate that the abundance of 0-group capelin larvae in August is related to spawning stock biomass but not to year class strength as 1-group (Jóhannsdóttir and Vilhjálmsson 1999). There was a significant correlation (r^2=0.73, p=0.01) between the abundance of 1-group capelin, measured in autumn and abundance at recruitment to the spawning stock. This suggests that mortality between 0-group and 1-group capelin determines year-class strength (Vilhjálmsson 1994).

For Barents Sea capelin, a significant linear correlation (r^2=0.75 p=0.0001) has been found between the 0-group capelin index and the estimated abundance of 1-group capelin (Gundersen and Gjøsæter 1998). No statistically significant relationship has been found between abundance of capelin larvae and estimated number of 1-group capelin indicating that year class strength of Barents Sea capelin is determined during the larval stage (Gundersen and Gjøsæter 1998). Year class strength of beach spawning capelin in Newfoundland has been correlated to hydrographical and meteorological conditions during emergence of larvae from beaches (Leggett et al. 1984).

Capelin is a keystone species in the food web of the North Atlantic and an important forage species for many fish species, marine birds and whales (Bailey et al. 1977a, Bundy et al. 2000, Vilhjálmsson 1994). The Icelandic capelin stock is heavy exploited by a commercial fishery, with a quota up to 1.6 million tons a year, which is mostly based on

the maturing stock. Current management of the capelin fishery allows approximately 400 000 tons of the maturing stock to spawn each year. Due to a short life span (three years) and a high spawning mortality, the fishable capelin stock is renewed every year based on recruitment (Guðmundsdóttir and Vilhjálmsson 2002). Even though the Icelandic capelin stock is managed to maintain a stable spawning stock biomass, 423 (± SD=157) thousand tons for the years 1981 - 2002 (Anonymous 2003a), there are large annual fluctuations in recruitment to the maturing stock (Guðmundsdóttir and Vilhjálmsson 2002). The estimated biomass of the maturing stock on August 1st has been 1475 (± SD=470) thousand tons for the years 1981 – 2002 (Anonymous 2003a).

1.2 Growth and recruitment of fishes

Growth is a multiplicative process in which cell numbers and cell volume increase (Brett 1979). Both abiotic and biotic factors of the environment affect growth of an organism through metabolic activity (Brett 1979). Temperature has strong effects on growth by controlling both metabolic requirements and digestion rate. Rising temperature increases the standard metabolic cost and increases appetite. When food is in excess growth rate increases linearly with increased temperature up to a peak after which the conversion efficiency starts to decline and growth rate slows (Brett 1979). Food abundance has limiting effects on growth so for growth to be exponential, food has to be in excess. Each species has a preferred range of temperature. Decreasing temperature requires less food for basal metabolic requirements leaving excess food to be used for growth. Fish spawning in temperate zones usually coincides with rising temperature, seasonal abundance of food and increasing day length (Brett 1979).

Growth of fishes is highly variable both within and among species (Houde 1987). The weight of fish increases $10^5 - 10^7$-fold from egg to maturity (Houde 1987). The relatively short larval stage is a period of fast growth with a 10^3 -fold increase in weight that implies a crucial regulation of recruitment via growth rate (Houde 1987). Growth rates of fish larvae affect both their survival and recruitment (Anderson 1988, Houde 1989, Pepin 1991). Recruitment is defined as the numbers of individuals belonging to a year class that survive to enter the reproductive population or to enter the harvested stock (Frank and Leggett 1994). Inter annual variance in recruitment of a fish species can be enormous. Recruitment variability of fish is one of the unsolved puzzles of fisheries science (Anderson 1988). Many theories have been put forward to explain possible connections between stock and recruitment. Stock recruitment theories are based on the idea that density-dependent mechanisms control the relationship between the parent stock and recruitment through feedback (Frank and Leggett 1994). Density dependent factors are believed to be strongest and to have the most influence on population abundance during the larval and juvenile stages when cohort densities are the highest (Frank and Leggett 1994). The oldest theory is Hjort's 'critical period', which states that larval survival is linked to food abundance when larvae start exogenous feeding (Hjort 1914). Theories based on size and development rate connect recruitment to mortality due to predation. The 'bigger is better' theory states that faster growing larvae which gain a larger size at a given age/stage are less susceptible to predation, assuming that risk of predation decreases with size. The 'stage duration' theory links faster growing larvae to lower cumulative mortality due to predation during the larval stage (Leggett and Deblois 1994). Moderate variation in growth rate and its effect on stage duration can be a major

factor affecting recruitment level and need not result from catastrophic or ideal environmental conditions (Houde 1987). Some theories assume density-independent relationships between spawning stock and recruitment like Cushing's 'match-mismatch' hypothesis (Cushing 1990). This theory connects larval survival, and subsequent recruitment, to abundance of food throughout the larval period, assuming fish in temperate waters spawn at a fixed time and that the larvae are released during spring and autumn peaks in plankton production. The degree of overlap in time and space of larval and plankton production explains annual variation in recruitment with a full match, yielding a maximum number of recruits (Cushing 1990). Other density-independent theories are Lasker's 'stable ocean' theory that claims periods of calm weather are essential for development and maintenance of good feeding conditions (Lasker 1987). In the 'member-vagrant' hypothesis, variance in recruitment is believed to be caused by loss during the egg and larval stages due to advection and diffusion (Sinclair and Iles 1989). Feeding success, independent of food abundance, has been connected to mortality of larvae through hydrographical and meteorological conditions, which affect both feeding rate, and capture success of larvae (Leggett and Deblois 1994).

1.3 Biology of capelin

Capelin belong to the suborder *Salmonoidei* – family *Osmeridae*. Capelin is a cold-water species with a circumpolar distribution in the northern hemisphere and consists of several geographically separated and self-contained stocks. The capelin stock distributed around Iceland, over to the Iceland-Greenland ridge and in the area between Iceland, Greenland and Jan Mayan is called the Icelandic capelin stock. Other stocks are the Barents Sea

capelin stock which inhabits the Barents Sea and adjacent waters. The West-Greenland capelin stock is distributed along the west coast of Greenland. Off Atlantic Canada several stocks of capelin can be found. Capelin stocks in the Pacific Ocean have not been comprehensively investigated but are referred to as one stock with different spawning groups (Vilhjálmsson 1994).

Capelin is a pelagic plankton feeder and a keystone species in the boreal ecosystem of the North Atlantic. They are important prey for many fish species, seabirds and whales (Bailey et al. 1977a, Bundy et al. 2000, Pálsson 1997, Vilhjálmsson 1994). The life span of Icelandic capelin is short as most of them die after spawning which usually occurs in the third year. During their short life they undertake extensive feeding and spawning migrations (Vilhjálmsson 1994, 2002).

The main spawning grounds of the Icelandic capelin are the sea beds off the South and West Coast of Iceland (Figure 1.3). Capelin spawn demersally from just below the watermark to 150 m depth, with maximum density of eggs between 30 - 50 m. The bottom type ranges from muddy sand to sandy gravel with grain sizes 0.125 - 4 mm. On average, capelin eggs are 1.12 ± 0.12 mm in diameter and take 20 - 25 days to hatch at temperatures between 5 - 7 °C (Vilhjálmsson 1994). Secondary spawning grounds of capelin are fjords and bays along the north and northwest coasts of Iceland. Capelin found on the secondary spawning grounds, are smaller and in limited numbers compared to the main spawning stock. Spawning starts in late February and ends in April, occasionally continuing until May, with most of the spawning normally taking place in March. Hatching of capelin larvae starts in the middle of March and ends in May or June, with a peak in April. After spawning most males die while a small fraction of females

survives (Vilhjálmsson 1994). Capelin larvae are between 5.0 mm – 7.2 mm in length at hatching (Friðgeirsson 1976, Vilhjálmsson 1994). The larvae are assumed to ascend to surface layers immediately after hatching. With the surface currents, the larvae drift from the spawning grounds to areas northwest, north and east of Iceland (Figure 1.3.). Larval drift is known to be variable among years and has been linked to fluctuations in the intensity of the coastal current and differences in the advance of Atlantic water into the Iceland Sea during spring and early summer (Vilhjálmsson 1994). Capelin larvae are the most abundant fish larvae in the Icelandic waters during spring and summer (Magnússon 1966). Capelin larvae and juveniles from hatching until the first of January the next year are considered as 0-group, after which they are classified as 1-group capelin, etc (Vilhjálmsson 1994).

Distribution and abundance of Icelandic 0-group capelin in August has been recorded annually since 1970. By August, larvae are dispersed over the continental shelf off the west, north and east coast of Iceland and to a varying extent onto the East Greenland plateau. The highest abundance of larvae is usually recorded off the west and north coast (Vilhjálmsson 1994). Juvenile capelin develop in that area until the second or third spring-summer of life. As capelin start to mature at age two, they undertake an extensive feeding migration north into the Iceland Sea between 66°30-72°N and the Denmark Strait. In late autumn, maturing capelin return from the feeding area to the edge of the shelf north of Iceland and in December-January the spawning migration begins clockwise around the Island to the spawning grounds off the south and southwest coast. On rare occasions they migrate counter clockwise around Iceland to the spawning grounds (Vilhjálmsson 1994, 2002).

Capelin larvae mostly feed on copepod nauplii and small copepods (Moksness 1982, Sigurðsson and Ástþórsson 1991, Vesin et al. 1981). Growth of capelin larvae has been correlated to the quantity of zooplankton of a specific size range with the optimal size of prey increasing as larvae grow (Frank and Leggett 1982, Frank and Leggett 1986). By August, the feeding period of 0-group capelin is coming to an end (Sigurðsson and Ástþórsson 1991). Capelin has an extended larval stage duration with metamorphosis occurring at 75 – 80 mm SL (Bailey et al. 1977b, Doyle et al. 2002). The annual average length of 0-group capelin, from 1970 – 2002, measured in August was 45.6 (± SD = 6.2 mm, Sveinbjörnsson & Hjörleifsson 2002) demonstrating that 0-group capelin were still larvae in August. The abundance of capelin larvae in August (0-group) over the shelf around Iceland has been recorded annually since 1970, reported as the average catch per unit effort (CPUE) index calculated over the whole shelf (Sveinbjörnsson & Hjörleifsson 2002). The abundance index of 0-group capelin, from 1970 – 2002, in August was 48 (± SD = 31 individuals nauticalmile^{-1}, Sveinbjörnsson & Hjörleifsson 2002).

1.4 Background on otolith microstructure

Age is an important variable in fisheries science as basic information needed to estimate growth and mortality rate, recruitment, and production of fish stocks (Campana 2001, Jones 1992). Calcified structures in fishes, which encode age information, include bones, scales, fin rays, vertebrae, and otoliths. Otoliths are widely used to determine age, as they provide daily records in larvae and annual marks in late stage of development. Every fish has three pairs of otoliths located in the fish vestibular apparatus (Campana and Neilson 1985, Jones 1992). They consist of the sagittae, lapilli and asterisci (Secor et al. 1992).

Pannella (1971) initiated analysis of daily increment formation in otoliths, and microstructure examination has become an established method to estimate age of most larval and juvenile fish. The sagittae are usually the largest otoliths of the three pairs and most commonly used for microstructure studies (Campana and Neilson 1985).

All otoliths are acellular mineralized structures that are isolated within a semi-permeable inner ear membrane, bathed in an endolymphatic fluid and metabolically inert (Campana 1999). An endocrine driven endogenous circadian rhythm controls daily deposition of growth increments. Additional increments and checks may occur because of environmental masking due to fluctuating variables such as temperature and feeding (Campana and Neilson 1985, Campana 1992). Formation of daily increments is generally continuous during the first six months of life. An increment consists of two bands of distinct deposition of calcium carbonate and protein. Otoliths are the only calcified structures in fish that show no resorption and that keep growing during periods with no somatic growth and thus keep a complete record of a fish growth history (Campana and Neilson 1985).

The key assumption for interpretation of age and growth of fishes from otolith microstructure is that increments are formed at a constant frequency and the distance between successive increments is proportional to fish growth (Campana and Neilson 1985). Before otolith microstructure of a given species can be used for growth estimates the daily increment periodicity has to be verified (Campana 2001). Gjøsæter and Monstad (1985) confirmed daily periodicity of increment formation in capelin larvae.

Accuracy of an age estimate refers to the proximity of the estimated age to the absolute age. Validation experiments of a known age larvae are used to estimate accuracy

for a specified species. Accuracy of an ageing method addresses process error but not interpretation error (Campana 2001).

Ageing precision is the reproducibility of repeated measurements on otolith microstructure. There is no connection between accuracy and precision of ageing. Precision assesses the interpretation error of the otolith analysis (Campana 2001).

Back calculation of growth is a method that estimates length and growth rate of fish at a previous time based on otolith increment width and current fish length. Growth back-calculations assume a linear relationship between fish length and otolith radius length though time (Campana 1990, Campana and Jones 1992). But studies have showed that the relationship between fish and otolith growth is not linear for all species (Campana and Jones 1992).

Errors can be introduced into otolith microstructure studies at many levels. During preparation, the otolith can be mounted tilted on the glue or over grinded. Interpretation errors can cause significant differences in results. Resolution limits of light microscopy pose restriction to the precision of increment width measurement. To reduce measurement errors related to individual increment width a series of evenly spaced widths along a certain radius can be measured (Neilson 1992).

1.5 Study objectives

The objective of this study was to investigate early life history growth of Icelandic capelin based on size-at-age models and micro-otolith increment width models and relate growth to biological measurements of larvae. The effects of biotic and abiotic factors on the growth of capelin larvae were also investigated by comparing two year-classes. The

effects of growth rate on abundance of capelin larvae in August of their first year of life and on recruitment to 1-group capelin were explored.

Chapter 2: Methods

2.1 Study site

Iceland rises from the crest of the Mid-Atlantic Ridge and is part of the system of transversal ridges extending from Scotland through the Faeroes to Greenland. These transversal ridges play an important role in the oceanography around Iceland since they separate the relatively warm waters of the Northeast Atlantic from the cold Arctic waters of the Iceland and the Norwegian Seas (Stefánsson and Ólafsson 1991).

The outer boundary of the continental shelf surrounding Iceland roughly follows the 400 m depth contour. The shelf is narrowest off the south coast where in places it extends only a few miles out. Off the west, north and east coast the shelf is relatively broad and generally extends for 110-170 thousand km out from the coast (Vilhjálmsson 1994).

The sea south and west of Iceland is relatively warm and saline because of the North Atlantic Drift. The Atlantic water flows northwards on both sides of the Reykjanes Ridge and continues clockwise along the south and west coasts. At the Iceland-Greenland Ridge this current splits in two. The larger branch swings towards the west in the Irminger Sea. The smaller North Icelandic Irminger Current rounds the northwest peninsula of Iceland and continues eastward along the north coast (Figure 1.3). The influx of Atlantic water to the north Icelandic shelf area in spring and early summer is highly variable, depending upon weather conditions (Malmberg and Blindheim 1994).

Hydrographical conditions in the sea area north of Iceland (Iceland Sea) are very different from the area west and south of Iceland. There, hydrographical conditions are highly variable due to its location near the boundary between warm and cold currents, i.e. at the oceanic Polar front in the northern North Atlantic. In the Iceland Sea, three water masses of highly different characteristics can be identified (Malmberg and Blindheim 1994). The warmest water mass is Atlantic water derived from the North Atlantic Drift which enters the Iceland Sea via the North Atlantic Drift and the Irminger Current and has a temperature around 7 °C in late spring and a salinity of 35.10 ± 0.05 psu. Polar water from the cold, low salinity upper layer of the East Greenland Current forms another water mass. It may mix to a variable degree into the surface layers of the Iceland Sea, in particular the area north of the Icelandic shelf. It has a temperature < 0°C and salinity < 34.5 psu. The last water mass is made of Arctic bottom water which occupies the deep waters, generally below 300 – 400 m, in the middle and eastern part of the Iceland Sea, but below about 600 m in the western part. It is characterized by a uniform salinity of 34.90 - 34.94 psu and a temperature < 0 °C (Malmberg and Blindheim 1994).

The water circulation around Iceland itself runs in a clockwise direction. Its main components are the coastal current, driven by gravity forces due to water afflux from land, Atlantic water, from the North Atlantic drift, running westward off the south coast and north to the west of Iceland and the North Icelandic Irminger Current, completes the circulation around the island. There are large seasonal variations in the coastal current, with increased coastal circulation in summer, but decreased circulation in winter (Vilhjálmsson 1994).

2.2 Samples from August 2001 and August 2002

Methods description was split into two subchapters because sampling and handling of samples was different between the June and August surveys. The temporal and spatial scale of surveys was different between August and June. The August surveys lasted around a month and covered the shelf around Iceland. The June sampling took place in 24-hours at one location. The June sampling was conducted to capture larvae earlier in the growth season. Unfortunately, the June samples from 2001 got lost in shipping.

2.2.1. Sampling method

Capelin larvae were collected during the annual 0-group fish survey of the Icelandic Marine Research Institute (MRI). In 2001, the survey was conducted from August 8th to September 3rd (Figure 2.2.1). In 2002, the survey was carried out from August 7th to August 25th (Figure 2.2.2). The survey covers the Icelandic shelf area together with deeper waters to 68°N off the north and northwest coasts and the northern Irminger See from approximately 63°N to 66°N (Vilhjálmsson 1994). Sampling was conduced using a Harstad pelagic trawl (18 m * 18 m opening; 0.5 * 0.5 cm cod-end mesh) usually towed at a depth of 20 – 50 meters. The 0-group survey has a fixed survey route. The extent of the survey into the Irminger Sea varies between years. Acoustic techniques were used to track larval distribution and abundance. Sampling stations were not fixed but sampling was conducted when acoustic records indicated changes in the abundance of acoustic targets or approximately every 40 kilometres (Begg and Marteinsdóttir 2000). If capelin larvae were present at the station a sample of fifty capelin was frozen in a small cup (150ml) filled with seawater.

2.2.2. Measurement of larvae

In the laboratory wet weight of larvae was measured to the nearest 0.01 g using a Mettler AE 163 electronic analytical scale (Mettler Instrumente, AG., Zürich Switzerland). The scale was calibrated on a regular basis with a calibration weight. Standard length (SL) of larvae was measured to the nearest 0.1 mm with an Optimas image analysis system (V.4.10) (Media Cybernetics, Inc., Des Moines, Iowa) connected to a CCTV (Hitachi KP-140) camera mounted a top a Heerbrugg Wild M3C dissecting microscope (with S-type mount fitted with a 0.5 x objective). Larvae too long to be measured with the dissecting microscope, approximately above 55 mm SL, were measured on millimetre graph paper to the nearest 0.5 mm.

2.2.3. Handling and measurement of otoliths

Five-larvae from each sample were selected for extraction of otoliths using stratified random sampling. The total standard length range of each sample was split into five parts and one larva chosen at random from each segment. The sagittal otolith pair was extracted from larvae using the teasing method (Secor et al. 1992). The otoliths were cleaned and mounted on a small drop of Crystal Bond® thermoplastic glue on a microscope slide. Each otolith was ground down to the mid plane from one side using hand polishing techniques (Secor et al. 1992) with 3.0 μm and 0.3 μm lapping film. An Olympus BH-2 compound microscope connected to a Pulnix TM-7CN camera was used for otolith measurements using an Optimas image analysis system. A 500x magnification was used for measurement and counting of increments and 100-200x magnification for measurements of the otolith. The setup was calibrated regularly using a 0.1 mm slide

micrometer. Theoretical resolution of the microscope was approximately 0.24 μm (Pepin et al. 2001).

Only one otolith was measured for each larva. The otolith in the better condition of the pair was used for subsequent measurement but if both were in good condition then the left or the right otolith was chosen at random. The number of increments was counted and their width measured along the longest axis of the otolith, which sometimes required refocusing of the image. In addition total radius and first check diameter were measured (Figure 2.2.3.). As either accuracy or the data at the formation of the first increment is known for capelin larvae, I choose to call it a first check but not a hatch check. A number of otoliths were measured for the second time without prior knowledge of results from the first measurements. Otoliths were picked at random for a replicated read.

2.3 Samples from June 2002

2.3.1. Sampling method

Capelin larvae were sampled on June 18th 2002. Seven tows were done at one location at approximately four hour intervals using a Bongo net (61 cm, 335 μm) and a Tucker trawl (1.0 m^2, 333 μm). Each gear was towed for 12 minutes at 1.0 – 1.3 ms^{-1}. Length of tow was 722 m – 870 m and the depth of tow was 0 – 20 m. At sea, sequential fractionations of samples were done using a Matoda splitter until approximately 100 larvae were left in a sub-sample. The sub-samples were preserved in 95% ethanol.

2.3.2. Measurement of larvae

In the laboratory, capelin larvae were identified using Fahay (1983) and measured for standard length (SL). SL was measured to the nearest 0.1 mm with an Optimas image analysis system (V.4.1) (Media Cypernetics, Inc., Des Moines, Iowa) connected to a CCTV (Hitachi KP-140) camera mounted a top a Heerbrugg Wild M3C dissecting microscope (with S-type mount fitted with a 1.0 x objective). SL was corrected for shrinkage using the formula: $SL_{corrected} = 0.940 + 1.036\ SL_{measured}$ (Kruse and Dalley 1990).

2.3.3. Handling and measurement of otoliths

All larvae from survey B6-2002 were measured before any otoliths were extracted. All the measured larvae were pooled together and sorted by SL. Stratified random selection was used to choose 250 larvae for extraction of the sagittae otolith pair. The same method was used for preparing and measuring otoliths as described in chapter 2.2.3. All otoliths were measured three times without prior knowledge about previous measurements.

2.4 Statistical analysis

2.4.1. Standard length and wet weight of larvae

To test for differences in standard length between surveys B10-2001 and B9-2002 the following model was used:

$$SL = \beta_\circ + \beta_S * S + \varepsilon \qquad (2.4.1.1)$$

where SL = standard length (mm), β_0, β_S = parameters which were estimated, S = survey (categorical variable where S = B10-2001 or B9-2002) and ε = error of the model. To test for differences in biomass the following model was used:

$$W = \beta_0 + \beta_S * S + \varepsilon \quad (2.4.1.2)$$

where W = wet weight (g), S = survey, β_0 = parameter which is estimated and ε is the error of the model. To test for differences in wet weight and standard length relationship between year-classes the following model was used:

$$\log W = \beta_0 + \beta_{\log SL} * \log SL + \beta_S * S + \beta_{\log SL * S} * \log SL * S + \varepsilon \quad (2.4.1.3)$$

where logW = logarithm of wet weight (g), logSL = logarithm of standard length (mm), S = survey, β_0, $\beta_{\log S}$, β_S, $\beta_{\log SL * S}$ = parameters which were estimated and ε = error of the model. The relationship between standard length and wet weight of larvae was estimated using a linear model on log transformed data:

$$\log W = \beta_0 + \beta_{\log SL} + \varepsilon \quad (2.4.1.4)$$

where logW = logarithm of wet weight (g), logSL = logarithm of standard length (mm), β_0, $\beta_{\log SL}$ = parameters which were estimated and ε = error of the model.

2.4.2. Replicate readings of increments

The absolute difference in increment number was investigated by plotting the number of increments from first replicate against the second replicate. To test the difference in total number of increments between replicated reads a paired t-test was used.

2.4.3. Diameter of first check

To test if the diameter of first check was different between replicated reads a paired t-test was used. The difference in first check size between surveys was tested using the following model:

$$FC = \beta_{\circ} + \beta_S * S + \beta_{SL} * SL + \beta_{SL*S} * SL * S + \varepsilon \quad (2.4.3.1)$$

where FC = first check diameter (μm), $\beta_{\circ}$, β_S, β_{NI}, β_{NI*S} = parameters which were estimated, SL = standard length (mm), S = survey (categorical variable where S = B10-2001, B9-2002 or B6-2002) and ε is the error of the model. The influence of total number of increments on difference in first check size between surveys was also tested by replacing SL (equation 2.4.3.1) with NI (number increments).

2.4.4. Size-at-age models

The larvae in this study were of an unknown age and thus it was impossible to estimate the accuracy of larval ageing. When the accuracy of ageing is unknown, the exact age in days cannot be estimated (Campana and Moksness 1991). Timing of formation of the first check is also unknown. For that reason, the number of increments was used unaltered as an estimate for age of larvae. Size-at-age was compared between replicates within a survey using the model:

$$SL = \beta_{\circ} + \beta_{NI} * NI + \beta_R * R + \beta_{NI*R} * NI * R + \varepsilon \quad (2.4.4.1)$$

where SL = standard length (mm) of larvae, $\beta_{\circ}$, β_{NI}, β_R, β_{NI*R} = parameters which were estimated, NI = number of increments (days), R = read number (categorical variable where R = 1, 2 or 3) and ε = error of the model. The linear relationship of size-at-age was

compared between the two 0-group surveys and between the two surveys conducted in 2002 using the following model:

$$SL = \beta_{\cdot} + \beta_{NI}*NI + \beta_S*S + \beta_{NI*S}*NI*S + \varepsilon \quad (2.4.4.2)$$

where SL = standard length (mm) of larvae, $\beta_{\cdot}$, β_{NI}, β_S, β_{NI*S} = parameters which were estimated, NI = number of increments (days), S = survey (categorical variable where S = B10-2001 or B9-2002) and ε = error of the model. It is not appropriate to compare surveys B10-2001 and B6-2002 as the size range of their larvae neither overlapped nor were the larvae from the same cohort. To test if the radius length was different between replicated reads a paired t-test was used. To test the linear relationship between radius and number of increments between surveys the following model was used:

$$R = \beta_{\cdot} + \beta_{NI}*NI + \beta_S*S + \beta_{NI*S}*NI*S + \varepsilon \quad (2.4.4.3)$$

where R = radius (μm) of otolith, $\beta_{\cdot}$, β_{NI}, β_S, β_{NI*S} = parameters which were estimated, NI = number of increments (days), S = survey and ε = error of the model.

Hatch dates of larvae were estimated by subtracting the number of increments from the capture date.

2.4.5. Increment width

Results from the first read from surveys B10-2001 and B9-2002 were used to test for differences in increment widths. For survey B6-2002 the mean of all three measurements was used. When widths of more than one increment were measured together the total width was divided by number of increments to determine the width of an individual increment. The increment width data were analysed directly as the date at formation of the first check was unknown and the relationship between somatic growth and otolith

growth was also unknown. A growth trajectory based on increment width, by age and day-of-year, was constructed for each fish. For presentation, an average growth trajectory was calculated for each cohort with 95% confidence limits.

Sequential growth increments in the otolith of an individual fish are correlated and interdependent (Campana 1996). Measurements of the width of individual increments of an otolith form a longitudinal record of growth for each fish. Multivariate analysis of variance is the proper method to test for differences between cohorts when data are drawn both from within and among individuals (Chambers and Miller 1995). A multivariate analysis was executed on individual growth trajectories to test for differences in growth rate between years and to determine if the difference was dependent on survey, age (total number of increments), day-of-year (DOY) or defined a to limited age range. Statistical analysis of growth data was restricted to the age range of 1 - 110 days to assure equivalent coverage across surveys B10-2001 and B9-2002. Analysis of growth for DOY was restricted to increment widths of increment 40 and higher to minimize influence of age on average increment width. The DOY range from 150 - 230 days was used to assure equivalent coverage across surveys B10-2001 and B9-2002. For comparison of growth between the two surveys conducted in 2002 the statistical analysis was restricted to the first 25 days of life. Increment width for DOY was not compared between the two surveys conducted in 2002 due to different age structure of larvae between surveys. To compare growth trajectories within and among surveys the following model was used:

$$R_{ij} = \beta_{\circ} + \beta_S * S + \beta_{IW} * IW + \beta_{S*IW} * S * IW + \varepsilon \qquad (2.4.5.1)$$

where R_{ij} is the otolith radius (μm) of fish j at age i (days) / day-of-year, $\beta_{\circ}$, β_S, β_{IW}, β_{S*IW} = parameters which were estimated, S = survey (categorical variable where S = B10-

2001, B9-2002 or B6-2002), IW = increment width (μm) and ε = error of the model. Partial correlation analysis of increment width was used to investigate where the age range should be split into separate segments. Partial correlation considers the correlation between each pairs of variables while holding constant the value of each of the other variables (Zar 1999). The last analysis was to fit a non-linear model to the mean increment width for surveys B10-2001 and B9-2002 using the model:

$$MIW = A + ((B*(NI^C))*(10000 + NI^C)^{-1}) \quad (2.4.5.2)$$

where MIW = mean increment width (μm), NI = number of increments (days), A, B and C = parameters whose values were estimated.

All analyses were preformed using SAS (1999-2000). All models were based on a general linear model with normal error structure. Tolerance for type I error was $\alpha = 0.05$. Residuals were examined for homogeneity, normality and independence. If there was a significant difference in variance between surveys, a non-parametric test was executed.

2.5. Temperature and zooplankton data

Temperature data was collected with a CTD-sonde during the four annual hydrographical surveys, conducted in February, May, August and November, by the Icelandic Marine Institute. These data were used to construct the average temperature experience of capelin larvae based on age. There are 13 standard transects with a total of 76 stations sampled in the annual hydrographical and plankton research in Icelandic waters (Anonymous 2003b). The average temperature data from stations one to five for the Siglunes standard section (Figure 1.3) that extends northwards from the north coast of Iceland were used as it has been shown that conditions at the Siglunes section represent the overall conditions

on the shelf in the north of Iceland (Malmberg and Kristmannsson 1992). This area is the main nursery ground for capelin larvae (Vilhjálmsson 1994). Data from depths of five meters, 20 m and 50 m were used as capelin larvae are distributed in the surface layers of the ocean (Vilhjálmsson 1994). The temperature history of each year-class was estimated by taking the average of the temperatures experienced by individual larva at each day during its life. First, temperature was estimated for every day of the year by simple regression between pairs of measured temperatures. Next, the temperature experience of individual larvae for each day of its life was constructed based on hatch date and age of larvae. This meant every individual larva having a temperature estimate assigned to every single day of its life. Finally, the average temperature experienced by larvae in their first day of life was calculated and then at day two, and so on. The average temperature experienced at each age of larvae was constructed for each year-class.

The temperature estimates may not give a detailed picture of the temperature conditions experienced by larvae for several reasons. First, only three data points are used to calculate temperature for day of the year. Secondly, larvae hatch in the south and drift north. The time it takes larvae to drift from the spawning area to the nursery ground in the north was ignored. The environmental conditions on the spawning grounds in the south are usually constant between years (Vilhjálmsson 1994). The temperature experienced by larvae at the spawning area was assumed to be identical between years. Finally, the drift rate of larvae from the south into the north is not known and was assumed to be identical between years.

During the annual hydrographical survey in May information on zooplankton abundances have also been collected. A WP-2 net with a diameter of 57 cm and a mesh

size of 200 μm was used for sampling. The samples were taken in vertical hauls from 50 m to the surface. Displaced volume measurements of zooplankton were converted to biomass as dry weight per m^2 (Ástþórsson and Gíslason. 1995). The annual peak in zooplankton abundance in the area in the north of Iceland is in late May (Gíslason and Ástþórsson 1998). The zooplankton abundance in May give an indication of how feeding conditions for capelin larvae will be in the summer, assuming that higher peak abundance of zooplankton results in better feeding conditions for larvae. The average zooplankton abundance in May each year for Siglunes section station 1-5 was used to estimate the feeding conditions experienced by capelin larvae at their nursery ground in the north.

Chapter 3: Results

The abundance index (individuals nauticalmile^{-1}) of capelin larvae in August was 82 in 2001 and 26 in 2002 (Sveinbjörnsson & Hjörleifsson 2002). The abundance of larvae in 2001 was among the highest ever reported and the abundance in 2002 was one of the lowest ever measured. The spawning stock biomass was similar between years, 450 thousand tons in 2001 and 475 thousand tons in 2002 (Anonymous 2003a).

3.1. Relationship between length and weight of larvae

In the 0-group survey in August and September 2001 (B10-2001), capelin larvae were collected at 88 stations of 212 pelagic tows. The number of measured larvae at a station ranged from 25 - 75. A total of 4189 larvae were measured from survey B10-2001. In June 2002 (B6-2002) seven station tows were done at one location. Number of measured larvae at a station ranged from 21 - 116 larvae. A total of 1010 larvae were measured

from survey B6-2002. In the 0-group survey in August 2002 (B9-2002), capelin larvae were collected at 50 stations of 152 pelagic tow stations. Number of measured larvae at a station ranged from 19 - 58. A total of 2387 larvae were measured from survey B9-2002.

Standard length (SL) of larvae sampled in the 0-group surveys ranged from 19.6 mm to 64.0 mm in 2001 and from 11.8 mm to 62.5 mm in 2002 (Figure 3.1.1.). The mean SL was 36.1 mm for both years (Table 3.1.1.). Wet weight of larvae from the 0-group survey 2001 ranged from 0.02 g to 1.53 g with an average of 0.26 g. Wet weight of larvae in 2002 ranged from 0.01 g to 1.35 g with an average of 0.24 g (Figure 3.1.2., Table 3.1.2.). Average SL for larvae sampled in June 2002 was 15.3 mm, ranging from 7.7 mm – 28.0 mm. There was no significant difference ($F_{[1, 6574]} = 0.15$, $p=0.6946$) between mean standard length of larvae from surveys B10-2001 and B9-2002. However, there was a significant difference in mean wet weight ($F_{[1, 6574]} = 13.35$, $p=0.0003$).

The linear relationship between the log of standard length and log of wet weight was different between years. Smaller larvae weighed less in 2002 but the gap decreased to zero as larval length increased (Figures 3.1.3). The interaction term for the linear relationship $\beta_{logSL*S}$*logSL*S was significant ($F_{[1, 6572]} = 182.86$, $p < 0.0001$) demonstrating a difference in slopes. As slopes of the regressions lines were significantly different, comparison of the intercepts was not possible.

3.2. Replicate readings of increments

The assumptions that difference in number of increments between replicates was independent of total number of increments was met as the confidence interval (CI: 0.988 ± 0.012) for the slope of the regression, for replicates (Figure 3.2.1.), included one.

3.2.1. Survey B10-2001 (August)

Otoliths were extracted from 256 larvae sampled in August 2001 and 83 otoliths were measured for the second time. The number of increments ranged from 50 – 143 with the average of 91 increments for the first read and 90 increments for the second read (Figure 3.2.2, Table 3.2.1.). There was no statistical difference ($t=1.76$, $df=82$, $p=0.0825$) in numbers of increments between replicated reads. The precision of age estimates from the otolith analysis was good. The independence of difference in number of increments on total number of increments and a good precision of the ageing method support the assumption that otolith analysis is a valid tool to estimated age of capelin larvae.

3.2.2. Survey B6-2002 (June)

Otoliths were extracted from 252 larvae but due to difficulties in handling the small otoliths their number was reduced to 163 by the third read. Only the 163 otoliths read three times were used for statistical analysis. Number of increments ranged from 5 – 46 with the average of 17 increments for the first read and 18 increments for the second and third replicate (Figure 3.2.3, Table 3.2.2.1.). The number of increments increased significantly with each replicated read with the third read having the greatest number of increments (Table 3.2.2.2.). The precision of otolith analysis was not as good for smaller larvae. The same absolute difference between replicates has more profound influence on younger larvae causing lower precision in age estimates of young larvae.

3.2.3. Survey B9-2002 (August)

Otoliths were extracted from 216 larvae sampled in August 2002 and 64 otoliths were measured for the second time. Number of increments ranged from 32 – 219 with the average of 85 increments for the first read and 87 increments for the second replicate (Figure 3.2.4, Table 3.2.3.). The number of increments was significantly greater for the second read ($t=-2.65$, $df=63$, $p=0.0101$). That the precision for age estimates in August 2002 was not as good as the precision for August 2001 was a surprise as the larvae were sampled at the same time of year and were of similar age but greater range.

3.3. Diameter of first check

Diameter of first check ranged from 6.7 to 29.5 μm (Figure 3.3.1., Table 3.3.1.). There was no statistical difference in the diameter of the first check between replicated reads for survey B10-2001 ($t=1.48$, $df=81$, $p=0.1416$) and B9-2002 ($t=-0.50$, $df=58$, $p=0.6193$). There was a statistical difference between the first read and later replicates for B6-2002, with average diameter of first check decreasing with each replicate (Table 3.3.2.) suggesting that interpretation of first check is harder for smaller larvae.

The mean diameter of the first check for all surveys, ranged from 15.4 μm – 18.3 μm (Table 3.3.3.). The linear relationship between diameter of first check and total number of increments for the two 0-group surveys was investigated using the first read because there was no significant difference between replicates, and only a fraction of the total number of otliths had replicated reads. The linear relationship between diameter of first check and total number of increments were parallel between surveys as the interaction term β_{NI*S}*NI*S was not statistically significant ($F_{[1, 461]}=0.35$, $p=0.5549$).

There was no statistical difference ($F_{[1, 461]}$=0.02, p=0.8967) in the slope of the linear relationship between surveys. The total number of increments had no significant ($F_{[1, 461]}$=0.90, p=0.3422) influence on the slope of the linear relationship. The linear relationship between diameter of first check and SL were parallel between survey as the interaction term β_{NI*S}*NI*S was not statistically significant ($F_{[1, 461]}$=0.37, p=0.5417). There was no statistical difference ($F_{[1, 461]}$=1.36, p=0.8967) in the slope of the linear relationship between surveys. The SL had significant ($F_{[1, 461]}$=4.44, p=0.0357) influence on the slope of the linear relationship. The diameter of first check size increased significantly with increased size of larvae. This increase in first check size with size (SL) of larvae suggests that faster growing larvae have bigger first check size. When comparing the diameter of first check for the two surveys in 2002 the average diameter of all three reads was used for B6-2002 because all otoliths had replicated reads. The difference in diameter of the first check between the two surveys in 2002 was also statistically different (χ^2=58.58, df=1, p<0.0001). A χ^2-test was used because there was a difference in variance between surveys. Result of this study suggests that the hatch check diameter of capelin larvae could be some where between 15 μm – 18 μm.

3.4. Size-at-age model

The difference between replicated reads within a survey was tested before differences between surveys were investigated. The linear relationship of the size-at-age models were parallel within each survey as the interaction term β_{NI*R}*NI*R was not statistically significant (Figures 3.4.1, 3.4.2. and 3.4.3, Table 3.4.1.). Neither was there any significant difference in intercepts between replicated reads within surveys B10-2001 and

B9-2002. For survey B6-2002 there was a statistical difference in intercepts only between the first read and the third read (Table 3.4.2.). For tests of differences between surveys, results from the first reads were used for B10-2001 and B9-2002 because there was no significant difference between replicates and only a part of the total number of otoliths had replicated reads. However, for B6-2002 the average size-at-age from all replicates was calculated and used for comparison because all otoliths had replicated reads.

The slopes of the regression of size-at-age ranged from 0.278 mm day^{-1} in 2002 to 0.371 mm day^{-1} in 2001. The intercepts ranged from 2.690 mm – 10.661 mm (Figure 3.4.4.). Comparison of slopes for the two 0-group surveys revealed that the interaction term for the linear size-at-age relationship β_{NI*S}*NI*S was significant ($F_{[1, 468]}$=41.02, $p<0.0001$) demonstrating difference in slopes. As slopes of the regressions lines were statistically different, comparison of the intercepts was not possible. There was no statistical difference (slopes: $F_{[1, 376]}$=2.48, p=0.1158; intercepts: $F_{[1, 376]}$=0.18, p=0.6724) between the linear size-at-age relationship of the two surveys conducted in 2002. This indicates a very similar growth within the 2002 cohort over a wide range of larval sizes.

There was no significant difference in total mineral growth (radius length) between replicated reads within surveys B10-2001 (df=82, t=-1.02, p=0.3087) and B9-2002 (df=63, t=-0.31, p=0.7544). The total growth of larvae ranged from 43.2 μm – 375.4 μm for the August surveys and the average was 155.4 μm and 179 μm (Table 3.4.3.). The average total mineral growth for the June survey was 19.6 μm and ranged from 4.6 μm – 58.7 μm.

Comparison of the relationship between total growth and number of increments for two 0-group surveys revealed that the interaction term for the linear relationship

β_{NI*S}*NI*S was significant ($F_{[1, 468]}$=19.09, p<0.0001) demonstrating a difference in slopes making comparison of intercepts impossible (Figure 3.4.5.). When comparing the two surveys conducted in 2002, the interaction term for the linear relationship β_{NI*S}*NI*S was significant ($F_{[1,376]}$=22.81, p<0.0001) indicating a difference in slopes. As slopes of the regressions lines were statistically different, assessment of the intercepts was not possible. Regression of total growth on number of increments for all surveys gave a negative value for intercepts for all surveys. Regression of total growth on standard length of larvae also gave a negative value for intercepts of all surveys (Figure 3.4.6.).

Estimated hatch dates were stretched out over a similar time span between years (Figure 3.4.7.). Hatching started in the middle of March and ended in early July. The mean hatch date was May 17th in 2001 and May 22nd in 2002. Larvae sampled in June 2002 hatched during the period from May 7th to June 14th and the mean hatch data was on June 1st. The hatch times estimated, in this study, were within the known hatch season of Icelandic capelin (Vilhjálmson 1994).

3.5. Increment width

The width of increments ranged from 0.6 μm – 4.8 μm for the August surveys and 0.9 μm – 2.1 μm for the June survey (Figur 3.5.1, 3.5.2, 3.5.3., Table 3.5.1.). Auto-correlation analysis of increment width, relative to age for the two 0-group surveys, showed high correlation in width of increments over a range of ten days (Figures 3.5.4., 3.5.5.). Therefore, when comparing growth trajectories between the two 0-group surveys the age span from 0-110 days was split into eleven parts each consisting of ten days. Auto-

correlation analysis was not carried out for survey B6-2002 as the age range of larvae was limited and there were few larvae available with more than ten increments.

It was assumed that increment width represents growth rate and therefore that increased increment width indicated faster growth of larvae. The average increment width was ≈ 1.4 μm from first check until the larvae reached the age of about fifteen days when growth started to increase (Figure 3.5.6.). The growth increased steadily until the larvae were circa 40 days old then the growth levelled off at the increment width of ≈ 2.1 μm for the 2001 cohort and at ≈ 1.9 μm for the 2002 cohort. Comparison of the average growth trajectories between the 0-group surveys revealed a very similar pattern in growth between years as the interaction term β_{S*IW}*S*IW was not significant ($p<0.05$) (Table 3.5.2.).

There was a significant difference in width of increments for the first forty days in larval life. After the larvae reached the age of 40 days, there was no significant difference in width of increments over the age range investigated. Growth was significantly different between surveys for larvae aged 20 – 100 days, excluding the age period 51 – 60 days, with larvae growing faster in 2001. The year-classes both followed a similar growth trajectory but after the first twenty days of life growth of the two year-classes diverged and the 2001 year-class started to show faster growth.

Comparison of growth between the two surveys in 2002 showed that the larvae sampled during the 0-group survey had significantly wider increments than the larvae sampled in June (Figure 3.5.7., Table 3.5.3.). However, the growth patterns were similar as the interaction term β_{S*IW}*S*IW was not significant ($p<0.05$) with the larvae sampled

in August always showing faster growth than larvae sampled in June. There was a significant increase in increment width after the larvae reached the age of ten days.

Auto-correlation analysis of increment width, for day-of-year for the two 0-group surveys, showed high correlation in width of increments over a range of ten days (Figures 3.5.8., 3.5.9.). Therefore, when comparing growth trajectories between the two 0-group surveys the day-of-year range from 150 - 230 days was divided into eight parts each consisting of ten days. The DOY range of 150 – 230 covers the period from May 30th to August the 18th. In the beginning, the average increment width was ≈ 2.0 μm and fluctuated between 2.0 μm and 2.0 μm over the period from late May until middle of July. Between July 19th and July 28th, there was a significant decrease in increment width. This was the only period with significant changes in increment width (Figure 3.5.10., Table 3.5.4.). Comparison of the average growth trajectories between surveys revealed a very similar pattern in growth between years as the interaction term β_{S*IW}*S*IW was not significant ($p<0.05$). Larvae from the 2001 cohort grew significantly faster over the period from July 9th to August 7th but before and after that time there was no significant difference in growth between years. Growth for DOY did not show significant changes except for a short period of decrease in July. This indicates that growth of capelin larvae was strongly related to age but not to time of year.

A non-linear model with three parameters had the best fit to the average increment width at age for surveys B10-2001 and B9-2002 (Figure 3.5.11). A model with four parameters was tested but as the confidence limits for the fourth parameter included zero it was rejected. The non-linear model explains 99.9% of the variance for both surveys but there was a pattern in the residuals of the model as expected when looking at the original

data. After increment width reaches the high plateau there were small fluctuations that cannot be modelled with a reasonable number of parameters and the small scale of residuals justify using the model (Appendices 1). There was no significant difference between the parameters A (intercept) and C (slope) but parameter B (inflection point) was statistically different between surveys (Table 3.5.5.).

3.6. Temperature and zooplankton data

Temperature on the nursery ground in the north increased from approximately 4°C in February – May to 7.4°C. In 2002 temperatures increased from 2.3°C in February – May to 6.7°C in August (Table 3.6.). Larvae from the 2001 year-class experienced higher temperature than the 2002 year-class. The average temperature experienced by larvae sampled in August 2001 (Figure 3.6.) increased from ≈ 4.2 °C at hatch to ≈ 6.8 °C for 110 days old larvae. For larvae sampled in August 2002 the average temperature at hatch, was ≈ 3.0 °C and increased to ≈ 5.7°C for larvae 110 days old.

The average biomass of zooplankton in the north in May was 4.6 g dry weight m^{-2} in 2001 and 1.2 g dry weight m^{-2} in 2002 (Anonymous 2003b).

Chapter 4: Discussion

This study investigated growth of two year-classes of Icelandic capelin larvae using otolith microstructure. The precision of otolith analysis increased as larvae got older. The absolute difference between replicates was independent of age. Size-at-age models revealed a faster growth of larvae in 2001 than in 2002. Investigation of individual increment widths showed that growth started to increase when larvae were about fifteen

days old. Growth increased steadily until the larvae were about 40 days old when growth reached a plateau. The mean increment width at the plateau was significantly greater for the 2001 year-class than the 2002 year-class. Growth trajectories were similar both within and among year-classes. Results of both size-at-age models and increment widths demonstrated that capelin larvae from the 2001 year-class grew faster than capelin larvae in 2002.

The spawning stock biomass was similar between years but abundance of capelin larvae in August was three times higher in 2001 than 2002. This supports the theory that faster growth facilitates better survival. Faster growth of the more abundant 2001 year-class suggests that growth was density independent. Temperature was higher and zooplankton abundance greater in 2001 than 2002 indicating that favourable environmental conditions facilitated growth.

The precision of otolith analysis was better for larvae sampled in August than in June. This increase in precision as larvae get older was expected, as the larvae sampled in June were on average 68 days younger than larvae sampled in August. A difference of one increment between replicates has more influence on the age estimate precision of 18 days old larva than 86 days old larva. This trend of increasing precision of age estimates as larvae get older has been reported for herring larvae (Moksness 1992).

The difference in precision of replicated age estimates between the two 0-group surveys was a surprise. The mean increment width was significantly smaller in 2002 than in 2001. Smaller increments are harder to interpret and this could be the cause for the lower precision of replicates in 2002 than in 2002. Growth estimated from the size-at-age models was not significantly ($p<0.05$) different between replicates. The precision of the

ageing method support the assumption that otolith analysis was a valid tool to estimate growth of capelin larvae.

The scale of the difference between the absolute age of larvae and the estimated age can be investigated by comparing hatch and spawning times calculated for the otolith analysis to the spawning time of Icelandic capelin. Estimated egg development times based on temperature at the spawning ground in spring that ranges from 5 – 7 °C (Anonymous 2003b), is 19 – 23 days based on Frank and Leggett (1981). The estimated spawning season, in both years, ranged from the middle of February to the middle of June. There is no information on the absolute spawning times of capelin in 2001 and 2002. However, the estimated timing of the spawning seasons is within the time range of spawning known from the literature (Vilhjálmsson 1994).

This indicates that there was not a great difference between age estimated from otolith analysis and the absolute age of larvae. Studies on herring larvae have showed that micro-otolith analysis underestimates absolute age of herring larvae by ten days (Moksness 1992). However, the accuracy of the ageing method for capelin and time of hatch check formation have to be investigated before the difference between estimated age from otoliths and the absolute age of capelin larvae can be quantified.

The growth rates estimated from the size-at-age models, 0.37 mm day^{-1} in 2001 and 0.28 mm day^{-1} in 2002, were within the growth range, 0.1 mm day^{-1} - 0.4 mm day^{-1}, which has been reported for capelin larvae (Doyle et al. 2002, Frank and Carcadden 1989, Frank and Leggett 1986, Jacquaz et al. 1977, Moksness 1982, Moksness and Øiestad 1979). The only information on growth on Icelandic capelin was from length frequency distributions. The estimated daily growth, from May to August, ranged from 0.06 mm

day^{-1} to 0.38 mm day^{-1} (Magnússon 1966). The growth of the 2001 year-class was in the higher end of the scale of growth rates that have been reported for capelin larvae while growth of the 2002 year-class was average.

Width of increments give a more detailed picture of growth then size-at-age models as they reveal how growth rate changes with age (Campana and Neilson 1985). The individual growth trajectories differed relatively little within a year-class, suggesting that individual larvae shared a common growth history. The identical pattern of growth trajectories between years presented in the good fit of the non-linear model and the fact that two of three parameters were not statistically different ($p<0.05$) demonstrated that capelin larvae shared a common growth trajectory each year. It appears the factors that influenced growth of larval capelin were consistent between years. Capelin larvae finish their yolk sack absorption in 8 – 10 days and at the size of about 8 mm (Friðgeirsson 1976). The width of increments starts to increase around age 15 days, which may have occurred with the onset of exogenous feeding. Growth rate increased steadily until the larvae were about 40 days old when growth reached a plateau. The estimated size of 40 days old larvae, using the size-at-age model, was about 22 mm. After the yolk sack is absorbed, the notochord flexion begins and ends at larval size (SL) of about 25.5 mm, which is when ossification of vertebrae and fin rays begin in capelin larvae (Doyle et al. 2002). The ossification is not finished until larvae reach the size (SL) of 60.0 mm. This suggests that onset of ossification stabilizes growth.

The difference in growth, after the plateau was reached, between year-classes was probably caused by more favourable environmental conditions in 2001. The zooplankton abundance on the nursery ground is measured annually in late May (Anonymous 2003b)

which coincides with the annual peak in zooplankton abundance (Gíslason and Ástþórsson 1998). Zooplankton abundance in spring indicates how the feeding condition of capelin larvae during their first few months of life is going to be. The zooplankton abundance was almost four times higher in 2001 than 2002 (Anonymous 2003b). Temperature in spring on the nursery ground was also higher in 2001 than 2002 (Anonymous 2003b). Studies on growth of capelin larvae have shown that abundance of food has a significant influence on growth with larvae growing faster when food is more abundant (Frank and Leggett 1982, Frank and Leggett 1986, Moksness and Øiestad 1979). Temperature does not influence growth of larvae as strongly as food abundance (Moksness and Øiestad 1979). This suggests that faster growth of the 2001 year-class was mostly facilitated by higher zooplankton abundance in 2001. While temperature in August only differed by 0.7°C, zooplankton abundance was approximately four times higher in 2001.

The larvae sampled in August have been subjected to selective mortality over a period of at least 45 days to around 150 days. The growth calculations show the estimated growth of survivors. Survival of capelin larvae raised in a predator free environment has been correlated with food abundance with higher survival rate of larvae when food is more abundant (Frank and Leggett 1986, Moksness and Øiestad 1979). The larvae in this study were, of course, subjected to predation but the scale of mortality due to predation is impossible to quantify due to lack of information. The lower abundance of food in 2002 and slower growth of larvae the same year both suggest poorer conditions for survival.

The spawning stock biomass was 450 thousand tons in 2001 and 475 thousand tons in 2002 suggesting that the abundance of larval production was similar between

years. The catch per unit effort abundance index of capelin larvae measured in the annual 0-group survey in August was 82 in 2001 and 26 in 2002 (Sveinbjörnsson & Hjörleifsson 2002). The abundance of capelin larvae in August was three times higher in 2001 than 2002 but the spawning stock biomass was the same between years, which supports the interpretation that survival of larvae was higher in 2001 than 2002.

The increment width of larvae collected in June 2002 was significantly smaller than for larvae collected in August of the same year. The majority of the larvae collected in June were under the age of 25 days and therefore had been subjected to selective mortality for a short period compared to the larvae sampled in August. This indicates that survival of faster growing larvae was higher than survival of slower growing larvae. This supports the suggestion that growth effects survival with faster growing larvae having higher survival rate (Baumann et al. 2003).

The effect of capelin larval growth on year-class strength as 1-group was impossible to estimate as the 1-group estimate failed for both year-classes (Anonymous 2004). The annual estimate of 1-group capelin failed for both year-classes as no 1-group capelin were found in their usual distribution area in autumn (Vilhjálmsson personal communications). There are preliminary abundance estimates of the 2001 year-class as 2-group capelin but the year-class strength of the 2002 cohort is still unknown (Anonymous 2004). This lack of information of about abundance of the two year-classes at a later life history stages preludes drawing conclusions about relative year-class strength for 2001 and 2002 at this time.

The mean length (SL) of larvae was not significantly different between year-classes ($p<0.05$) but the mean weight of the 2001 year-class was significantly greater than

the mean weight of the 2002 year-class. This indicates that the biomass of larvae is a better indicator of growth than length. Better conditions and faster growth of the more abundant 2001 year-class suggest that growth of capelin larvae was density independent.

The results of this study suggest that higher food abundance on the nursery ground increased survival rate of capelin larvae. However, this suggestion was not supported by long-time data series. An exploration of the long-time data of zooplankton abundance on the nursery ground and abundance of 0-group capelin in August revealed a poor linear correlation, r^2=0.24 (Figure 4.0.). This suggests that survival of larvae depends of not only food abundance but that other variables influence survival. Possible variables are predation pressure, drift out of the nursery ground and size composition of the zooplankton community. An effect of predation on survival is unknown. The effect of drift out of the nursery ground on survival on larvae is unknown.

Diet of capelin larvae changes as they grow with the edible size range of food particles increasing as size of capelin increase (Moksness 1982). Larvae grow slower when overlap in capelin size and preferred size rages of zooplankton is low (Frank and Leggett 1986). Knowledge on the size composition of the zooplankton community on the nursery ground is very limited. The effects of predation, drift and size composition of food on survival of larvae will remain nothing but mere speculations and need further studies.

Chapter 5: Conclusion

1. Hatch date distributions were the same between years and within the known hatch time of Icelandic capelin from the literature. These results support Gjøsæter and Monstad (1985) that increment formation is daily in capelin larvae.

2. Precision of otolith analysis was independent of age. Growth estimates were not different between replicates demonstrating that micro-otolith analysis can be used to estimate age of capelin larvae.

3. Growth estimated both from size-at-age models and micro-otolith width of increments showed that the 2001 year-class grew faster than the 2002 year-class. Higher growth rates and better biological condition of capelin larvae in 2001 were correlated with higher water temperature and greater zooplankton abundance.

4. Common growth trajectories both within and among years demonstrate a consistency in factors affecting the growth pattern of capelin larvae.

5. Abundance of capelin larvae in August was four times higher for the faster growing 2001 year-class. Results suggest that survival rate was higher for faster growing larvae and that growth was not density-dependant.

Tables

Table 3.1.1: Summary of standard length (mm) for all surveys.

Survey	N	Mean	Max	Min	Std. dev.
B10-2001	4189	36.1	64.0	19.6	6.8
B9-2002	2387	36.1	62.5	11.8	6.9
B6-2002	1010	15.3	28.0	7.7	2.9

Table 3.1.2: Summary of wet weight (g) for 0-group surveys.

Survey	N	Mean	Max	Min	Std. dev.
B10-2001	4189	0.26	1.53	0.02	0.17
B9-2002	2387	0.24	1.35	0.01	0.19

Table 3.2.1: Summary of results for number of increments of replicated reads for survey B10-2001. Diff = results of paired difference in number of increments (diff=replicate 1- replicate 2).

Read	N	Mean	Max	Min	Std. dev.
Read 1	83	91	140	51	24
Read 2	83	90	143	50	24
Diff	83	1	14	-17	5

Table 3.2.2.1: Summary of results for number of increments of replicated reads for survey B6-2002. Diff = results of paired difference in number of increments (diff 1-2 =replicate 1 - replicate 2).

Read	N	Mean	Max	Min	Std. dev.
Read 1	163	17	42	5	6
Read 2	163	18	43	5	6
Read 2	163	18	46	5	7
Diff 1 - 2	163	-1	5	-8	2
Diff 1 - 3	163	-2	3	-11	3
Diff 2 - 3	163	-1	6	-8	2

Table 3.2.2.2: Comparison of number of increments for replicated reads for survey B6-2002.

Replicate	df	t-value	p-value
read 1-read 2	162	-5.17	<0.0001
read 2-read 3	162	-3.64	<0.0001
read 1-read 3	162	-8.19	<0.0001

Table 3.2.3: Summary of results for number of increments of replicated reads for survey B9-2002. Diff = results of paired difference in number of increments (diff=replicate 1-replicate 2).

Replicate	N	Mean	Max	Min	Std. dev.
Read 1	64	85	219	32	37
Read 2	64	87	214	34	37
Diff	64	-2	15	-15	6

Table 3.3.1: Summary of diameter (µm) of first check for all replicates for all surveys. N is number of otoliths, R is read number.

Survey	N	R	Mean	Max	Min	Std. dev.
B10-2001*	81	1	18.8	29.5	12.6	2.2
B10-2001*	81	2	18.5	25.5	12.5	2.1
B6-2002	163	1	16.5	22.0	6.7	2.9
B6-2002	163	2	15.1	23.1	6.8	3.7
B6-2002	163	3	15.0	21.1	6.5	3.2
B9-2002**	59	1	17.4	28.0	11.5	2.5
B9-2002**	59	2	17.6	25.2	10.5	2.3

*Diameter of FC was missing for 1 otoliths.
** Diameter of FC was missing for 5 otoliths.

Table 3.3.2: Comparison of diameter of first check of replicated reads for survey B6-2002.

Reads	df	t-value	p-value
read 1-read 2	162	23,878*	0.0012
read 2-read 3	162	0.48	0.6346
read 1-read 3	162	6.43	<0.0001

*Wilcoxon statistic

Table 3.3.3: Diameter (µm) of first check for all surveys. N is number of otoliths.

Survey	N	Mean	Max	Min	Std. dev.
B10-2001*	254	18.3	29.5	10.6	2.4
B6-2002**	163	15.4	21.5	6.8	2.8
B9-2002***	211	17.7	28.0	11.5	2.4

* Measurements from first read, diameter of FC was missing for 2 otoliths.
** Mean of measurements from all three reads.
*** Measurements from first read, diameter of FC was missing for 5 otoliths.

Table 3.4.1: Statistical values for difference in slopes of the linear size-at-age models within surveys. N is number of otoliths.

Survey	df	N	F-value	p-value
B10-2001	1	83	0.07	0.7850
B6-2002	2	163	0.15	0.8569
B9-2002	1	64	0.01	0.9207

Table 3.4.2: Statistical values for difference in intercept of the linear size-at-age models within surveys. N is number of otoliths.

Survey	df	N	Read #	F-value	p-value
B10-2001	1	83	read 1- read 2	0.44	0.5101
B6-2002	1	163	read 1- read 2	2.18	0.1406
B6-2002	1	163	read 2- read 3	1.03	0.3117
B6-2002	1	163	read 1- read 3	5.62	0.0184
B9-2002	1	64	read 1- read 2	0.76	0.3865

Table 3.4.3: Summary of total growth measured as radius length (µm). N is number of otoliths.

Survey	N	Mean	Max	Min	Std. dev.
B10-2001*	256	179.0	375.4	60.3	61.9
B6-2002**	163	19.6	58.7	4.6	8.1
B9-2002*	216	155.4	372.6	43.2	57.0

*Results from measurements of first read.
**Average of all three reads.

Table 3.5.1: Summary for width of increments (µm). NI is the total number of measured increments.

Survey	NI	Mean	Max	Min	Std. dev.
B10-2001	24,278	1.9	4.8	0.6	0.5
B6-2002	18,687	1.8	4.8	0.9	0.5
B9-2002	2,885	1.1	2.1	0.6	0.2

Table 3.5.2: Statistical results for comparison of growth trajectories, for age, between the two 0-group surveys. N is number of larvae included in the analysis.

Range of increments (days)	N	Increment (β_{IW}*IW) F-value [df_{num}, df_{den}] p-value	Increment * Survey (β_{S*IW}*S*IW) F-value [df_{num}, df_{den}] p-value	Survey (β_S*S) F-value [df_{num}, df_{den}] p-value
1 - 10	472	2.95 [9, 462] $p = 0.0021$	0.99 [9, 462] $p = 0.4467$	2.28 [1, 470] $p = 0.1321$
11 - 20	472	24.06 [9, 462] $p < 0.0001$	0.67 [9, 462] $p = 0.7331$	0.88 [1, 470] $p = 0.3492$
21 - 30	472	26.84 [9, 462] $p < 0.0001$	1.03 [9, 462] $p = 0.4120$	3.98 [1, 470] $p = 0.0465$
31 - 40	466	2.94 [9, 456] $p = 0.0021$	0.28 [9, 456]) $p = 0.9809$	4.63 [1, 464] $p = 0.0319$
41 - 50	458	1.04 [9, 448] $p = 0.4103$	0.28 [9, 448] $p = 0.3651$	4.63 [1, 456] $p = 0.0488$
51 - 60	423	1.93 [9, 413] $p = 0.0462$	1.69 [9, 413] $p = 0.0892$	1.58 [1, 421] $p = 0.2102$
61 - 70	368	0.79 [9, 358] $p = 0.6221$	0.80 [9, 358] $p = 0.6178$	8.28 [1, 366] $p = 0.0043$
71 - 80	306	0.23 [9, 296] $p = 0.9906$	0.83 [9, 296] $p = 0.5876$	8.92 [1, 304] $p = 0.0030$
81 - 90	236	1.44 [9, 226] $p = 0.1728$	1.24 [9, 226] $p = 0.2741$	6.72 [1, 234] $p = 0.0102$
91 - 100	156	1.22 [9, 146] $p = 0.2867$	1.03 [9, 146] $p = 0.4162$	6.33 [1, 1540] $p = 0.0129$
101 - 110	121	1.03 [9, 111] $p = 0.4235$	1.62 [9, 111] $p = 0.1184$	0.88 [1, 119] $p = 0.3510$

Table 3.5.3: Statistical results for comparison of growth trajectories, for age, between the two surveys conducted in 2002. N is number of larvae included in the analysis.

Range of increments (days)	N	Increment (β_{IW}*IW) F-value[df_{num}, df_{den}] p-value	Increment * Survey (β_{S*IW}*S*IW) F-value [df_{num}, df_{den}] p-value	Survey (β_S*S) F-value [df_{num}, df_{den}] p-value
1 - 10	361	1.56 [9, 351] $p = 0.1257$	0.61 [9, 351] $p = 0.7871$	141.89 [1, 359] $p < 0.0001$
11 - 20	274	7.52 [9, 264] $p < 0.0001$	1.45 [9, 264] $p = 0.1687$	97.22 [1, 272] $p < 0.0001$
21 - 25	241	2.44 [4, 236] $p = 0.0478$	1.56 [4, 236] $p = 0.1870$	48.25 [1, 239] $p < 0.0001$

Table 3.5.4: Statistical results of comparison of growth trajectories, for DOY, between the two 0-group surveys. N is number of larvae included in the analysis.

Day-of-year range	N	Increment (β_{IW}*IW) F-value[df_{num}, df_{den}] p-value	Increment * Survey (β_{S*IW}*S*IW) F-value[df_{num}, df_{den}] p-value	Survey (β_S*S) F-value[df_{num}, df_{den}] p-value
150 – 159	67	0.64 [9, 57] p = 0.7556	0.71 [9, 57] p = 0.6956	0.31 [1, 65] p = 0.5805
160 – 169	114	0.46 [9, 104] p = 0.8983	0.79 [9, 104] p = 0.6255	0.83 [1, 112] p = 0.3629
170 – 179	159	0.59 [9, 149] p = 0.8010	1.69 [9, 149] p = 0.0967	0.08 [1, 157] p = 0.7820
180 – 189	220	0.50 [9, 210] p = 0.8743	0.63 [9, 210] p = 0.7695	0.2.31 [1, 218] p = 0.1304
190 – 199	297	0.67 [9, 287] p = 0.7319	0.82 [9, 287] p = 0.5943	4.63 [1, 295] p = 0.0322
200 – 209	359	2.28 [9, 349] p = 0.0172	1.14 [9, 349] p = 0.3364	9.54 [1, 357] p = 0.0022
210 – 219	404	1.42 [9, 394] p = 0.1754	0.15 [9, 394] p = 0.9981	12.40 [1, 402] p = 0.0005
220 – 229	228	1.26 [9, 218] p = 0.2578	0.71 [9, 218] p = 0.6970	0.24 [1, 226] p = 0.6239

Table 3.5.5: Summary of parameters results for non-linear model of increment width for survey B10-2001 and B9-2002. App. std. error = approximate standard error, app. 95% con. lim. = approximate 95% confidence limits.

Parameter	Estimate		App. std. error		App. 95% con. lim.	
	B10-2001	B9-2002	B10-2001	B9-2002	B10-2001	B9-2002
A (μm)	1.29	1.27	0.01	0.02	1.26 - 1.32	1.23 - 1.30
B ($\mu m*day^{-1}$)	0.81	0.71	0.02	0.02	0.78 - 0.84	0.68 - 0.75
C (μm)	2.99	3.04	0.02	0.03	2.94 - 3.04	2.97 - 3.10

Table 3.6: Average temperature at station one to five, depth surface to 50 m, for Siglunes section for years 2001 and 2002. Date is the time of measurement.

2001		2002	
Date	Temperature (°C)	Date	Temperature (°C)
February 18th	4.0	February 11th	2.3
May 23rd	3.9	May 21st	2.3
August 22nd	7.4	August 15th	6.7
November 19th	5.8	November 18th	5.2

Figures

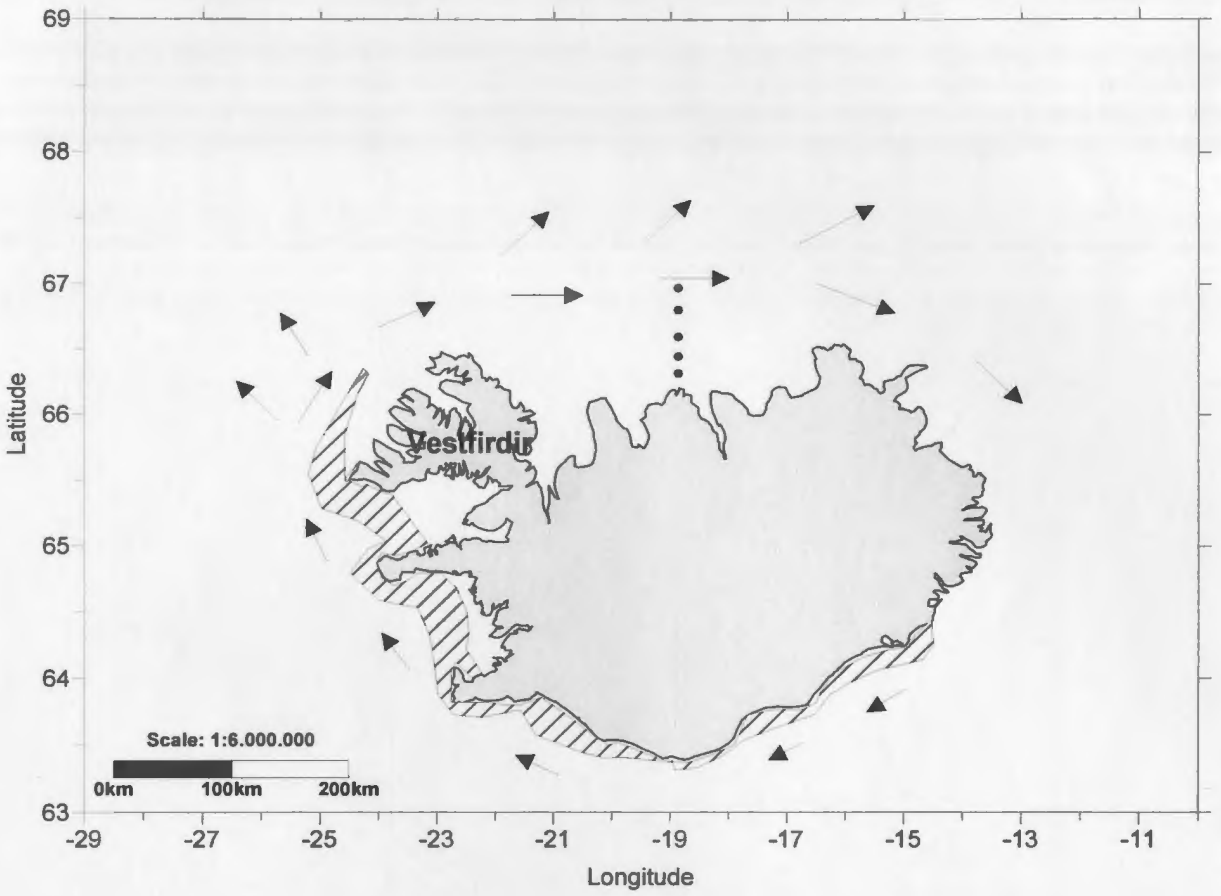

Figure 1.3: Spawning grounds (striped area) of Icelandic capelin and direction of larval drift (arrows), from Vilhjálmsson (1994). Hydrographic stations of the Siglunes standard section (filled dots).

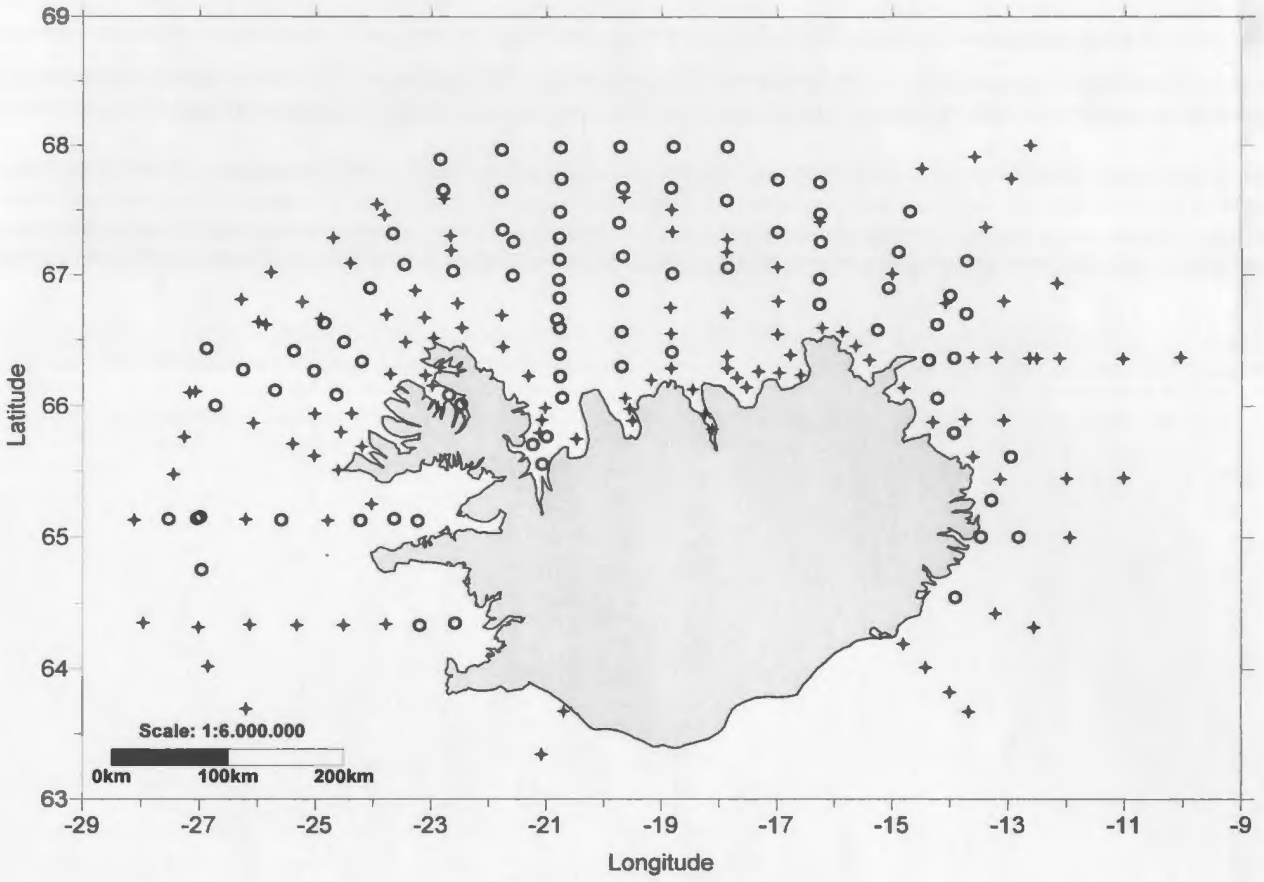

Figure 2.2.1: Pelagic sampling stations during the 0-group survey of the Icelandic Marine Research Institute in August 2001 (B10-2001). Capelin larvae were captured at 88 stations (open circles) out of 212 stations. Crosses represent stations without capelin larvae.

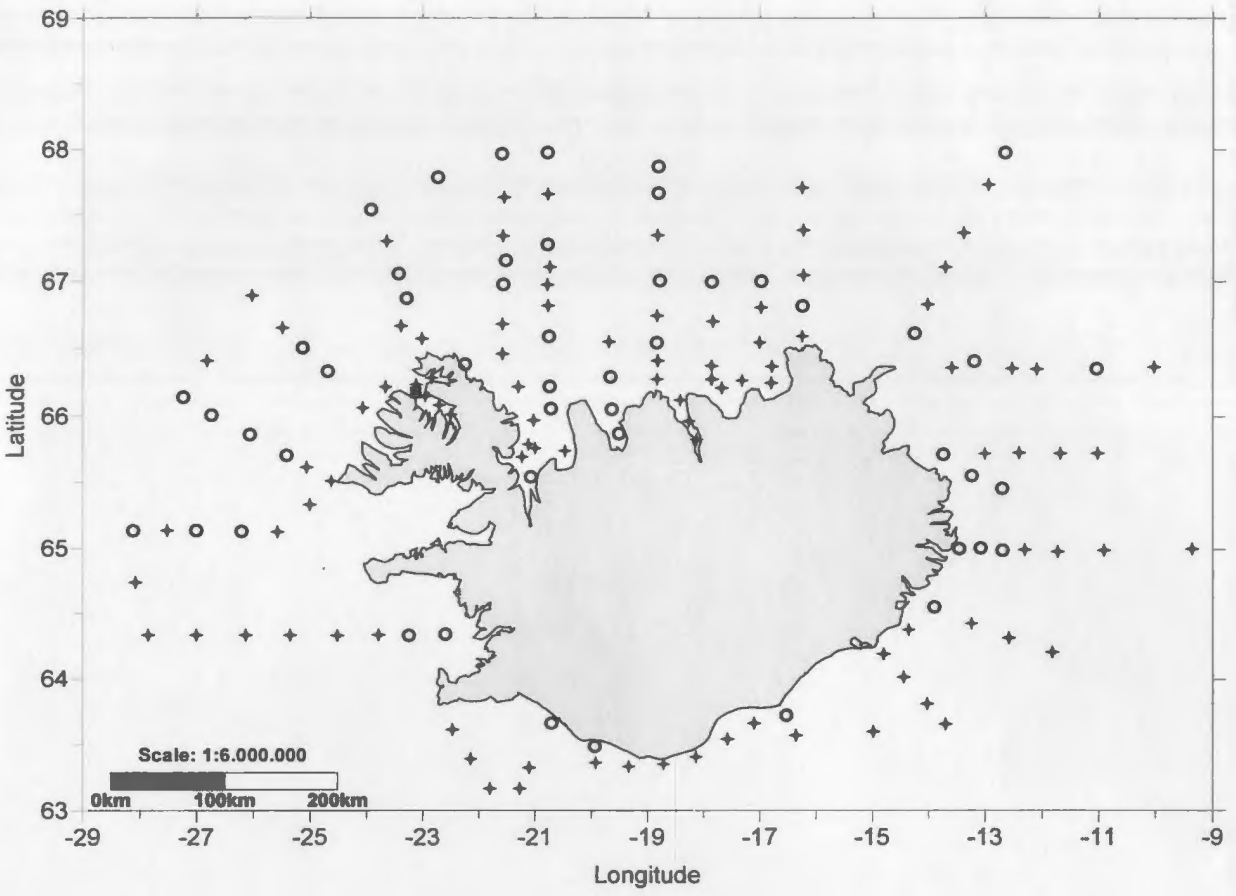

Figure 2.2.2: Pelagic sampling stations during the 0-group survey of the Icelandic Marine Research Institute in August 2002 (B9-2002) and sampling from June 2002 (B6-2002). In August 152 stations were sampled and capelin larvae were captured at 50 stations (open circles). Crosses represent stations without capelin larvae. The box shows the sampling position for June 2002.

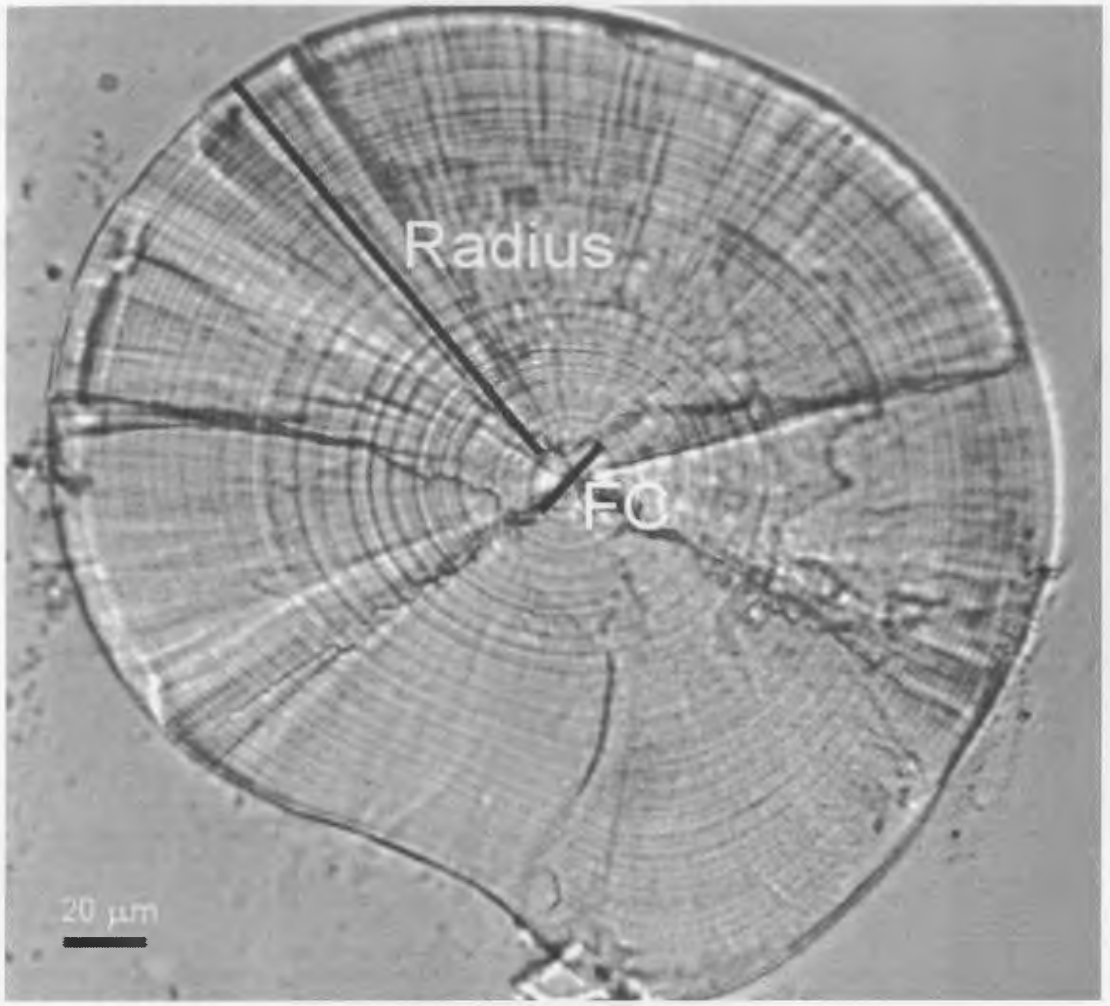

Figure 2.2.3: Picture of an otolith. FC is diameter of the first check. Radius is the axis used for counting and measuring of increments.

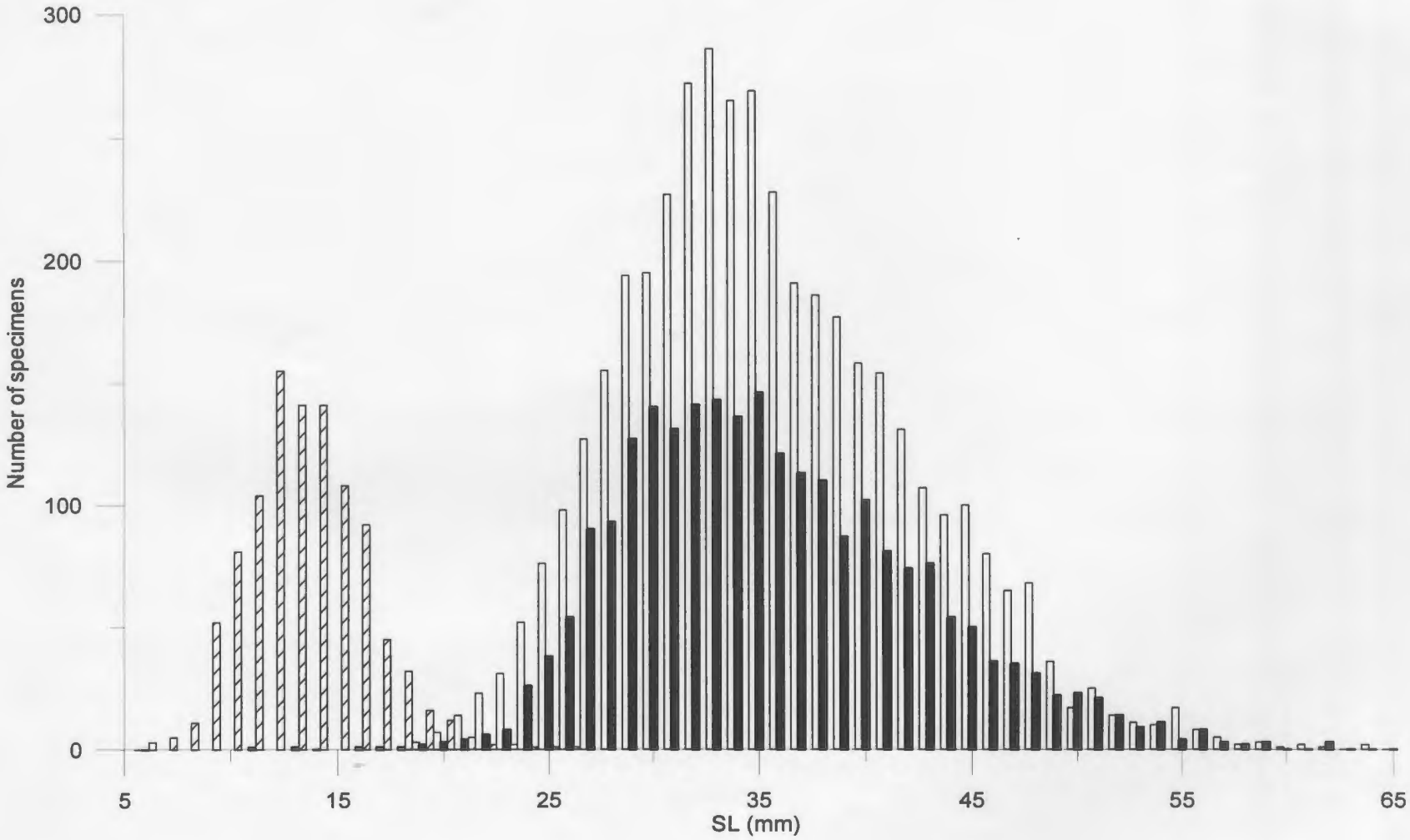

Figure 3.1.1: Standard length (SL, mm) of all measured larvae. 4189 larvae were measured from B10-2001 (open bars), 2387 larvae from B9-2002 (solid bars) and 1010 larvae from B6-2002 (striped bars).

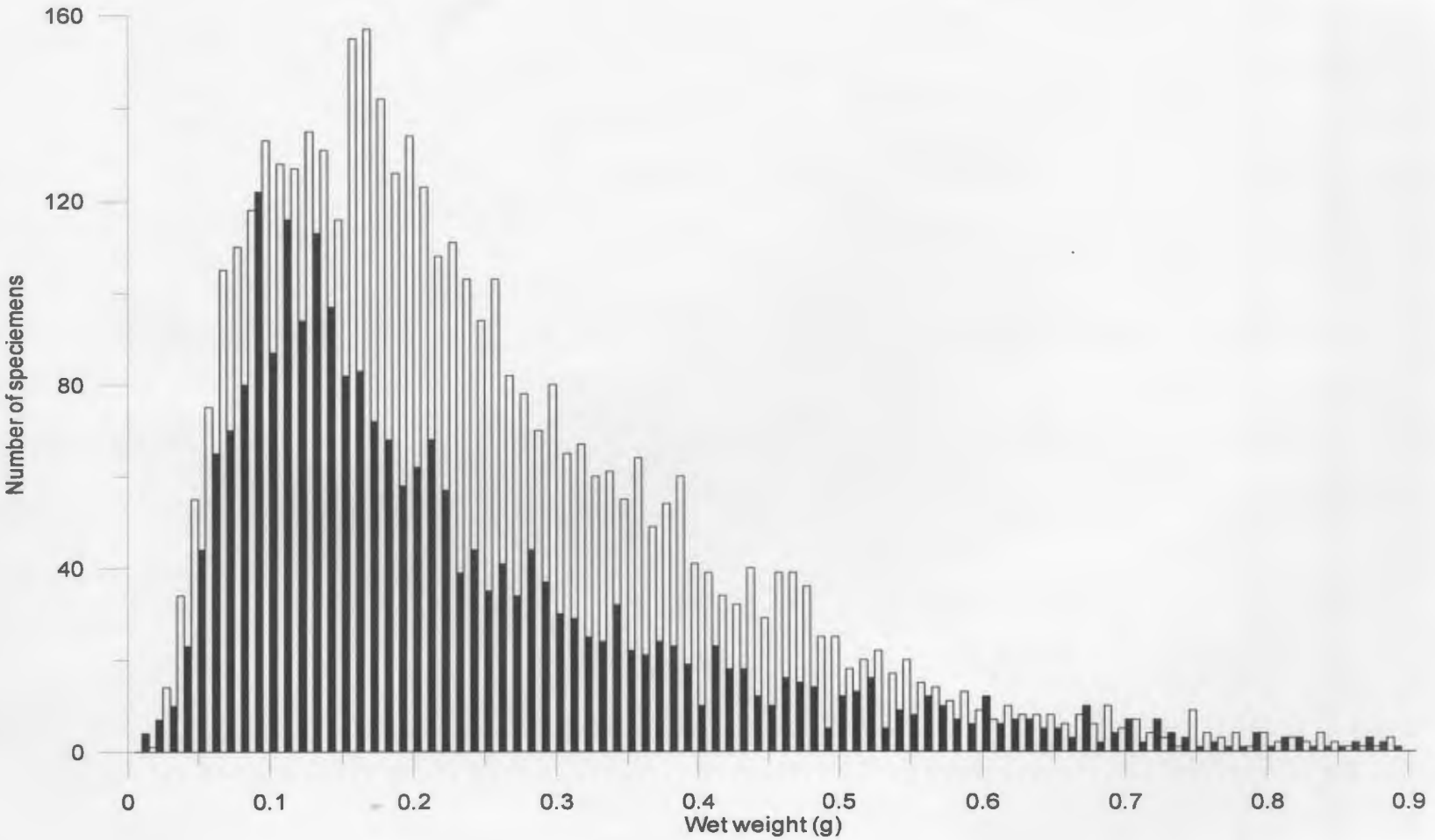

Figure 3.1.2: Wet weight (g) of measured larvae from B10-2001 and B9-2002. 4189 larvae were measured from B10-2001 (open bars) and 2387 larvae from B9-2002 (solid bars). For presentation, larvae weighing more than 0.9g were omitted from the graph. B10-2001 33 larvae are not showed and for B9-2002 30 larvae are not on the graph.

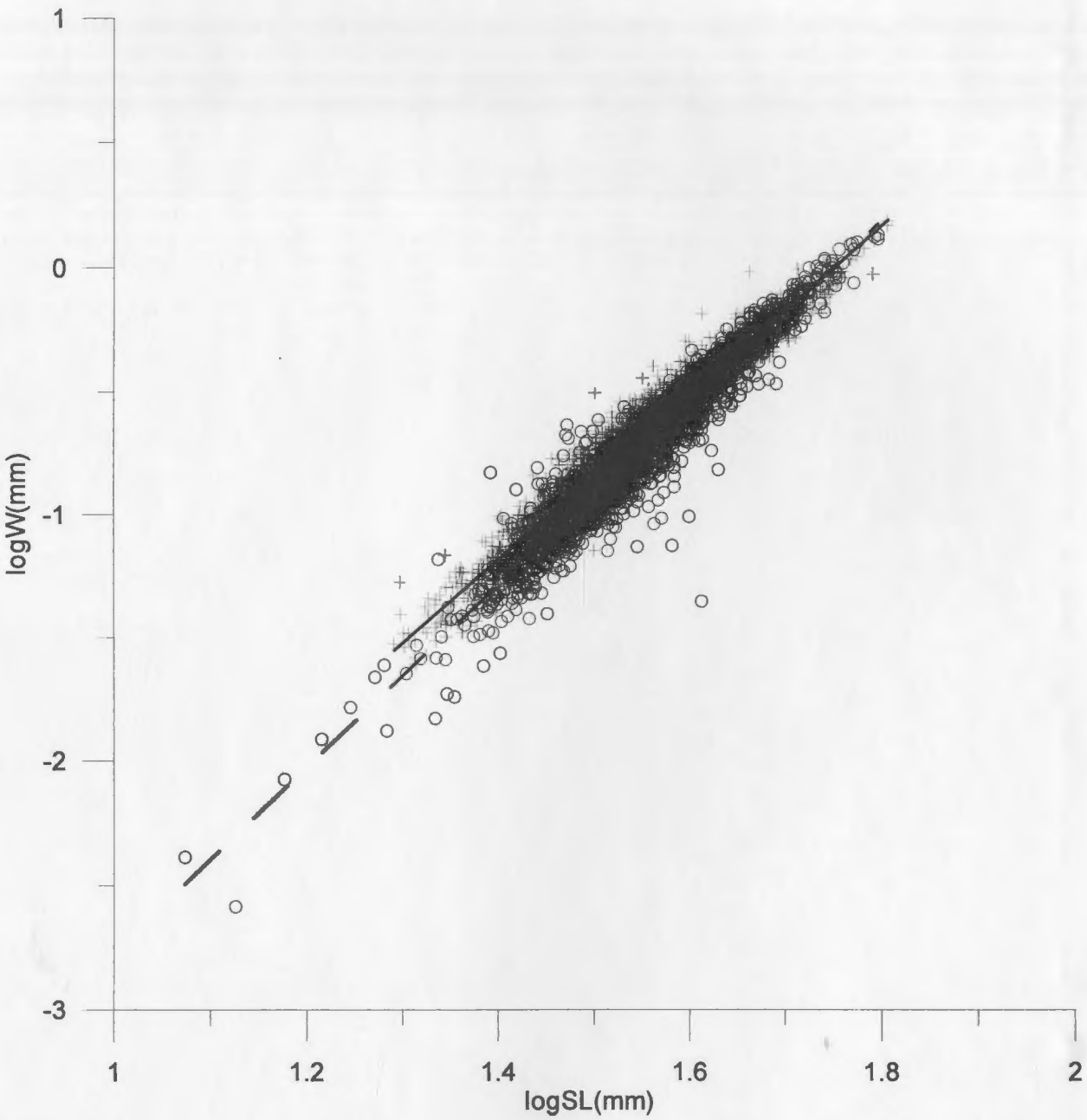

Figure 3.1.3: Log-log plot of standard length (SL, mm) and wet weight (g) for measured larvae from surveys B10-2001 (n=4189, crosses and solid line) and B9-2002 (n=2387, open circles and dashed line). Formula B10-2001: logW = 3.388*logSL – 5.929, r^2 = 0.95. Formula B9-2002: logW = 3.694*logSL – 6.460, r^2 = 0.93.

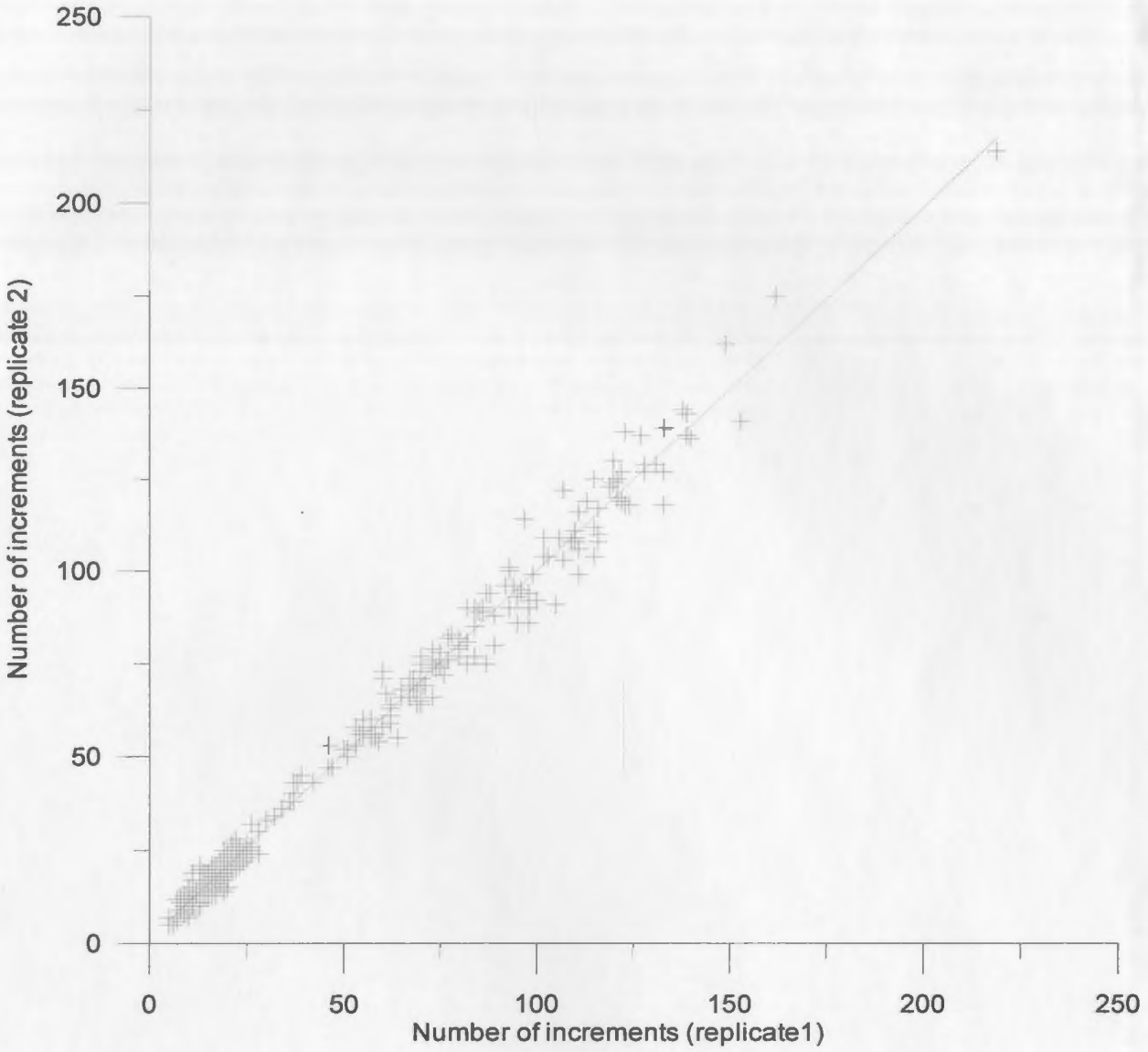

Figure 3.2.1: Absolute difference among replicates of increments counts for all surveys, 310 larvae. Formula regression: number of increments (replicate 2) = 0.988* number of increments (replicate 1) + 1.299, $r^2 = 0.99$.

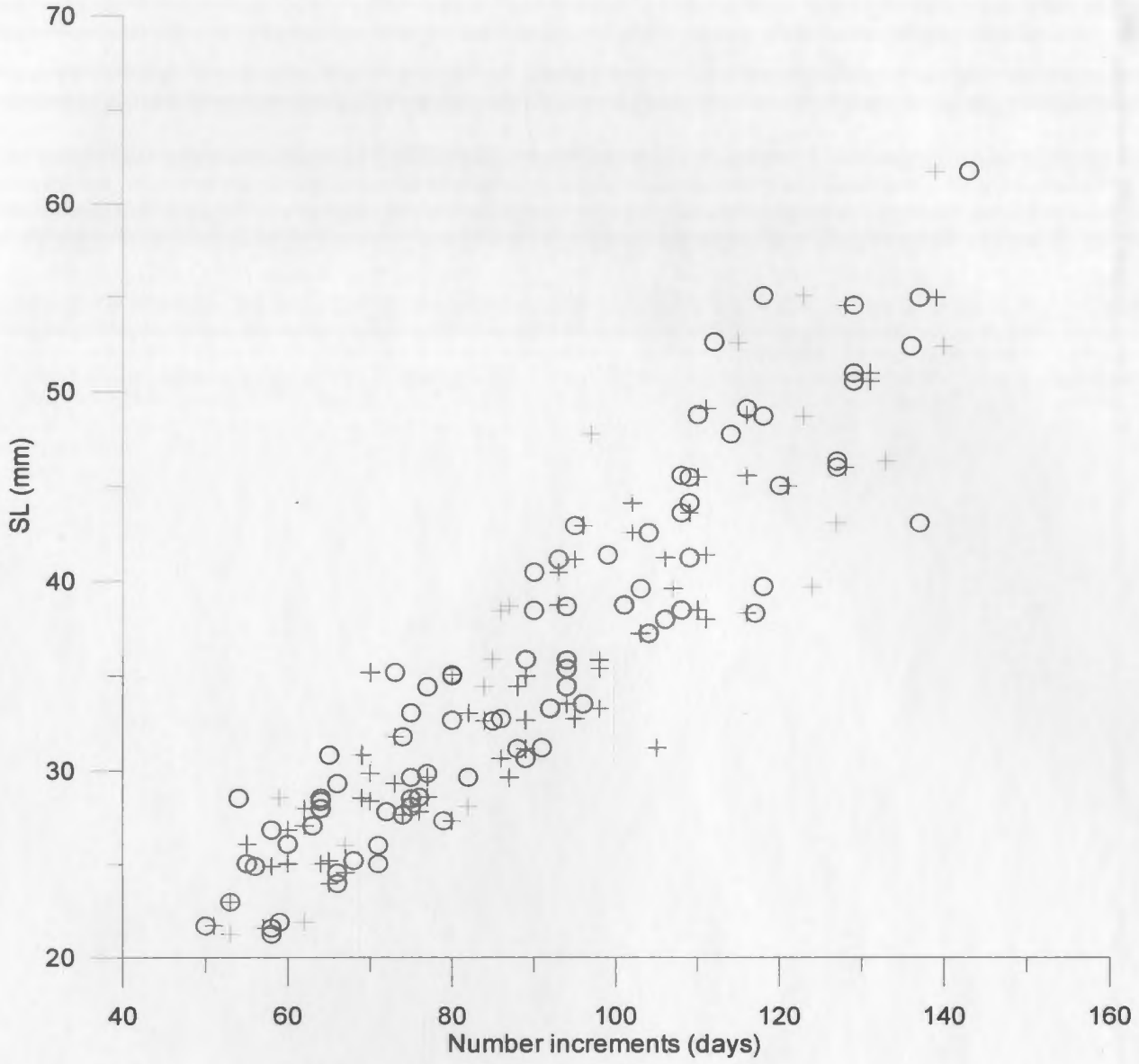

Figure 3.2.2: Results from replicated reads from B10-2001. This graph only shows otoliths with replicated reads (n=83). Crosses represent first read and circles represent second read.

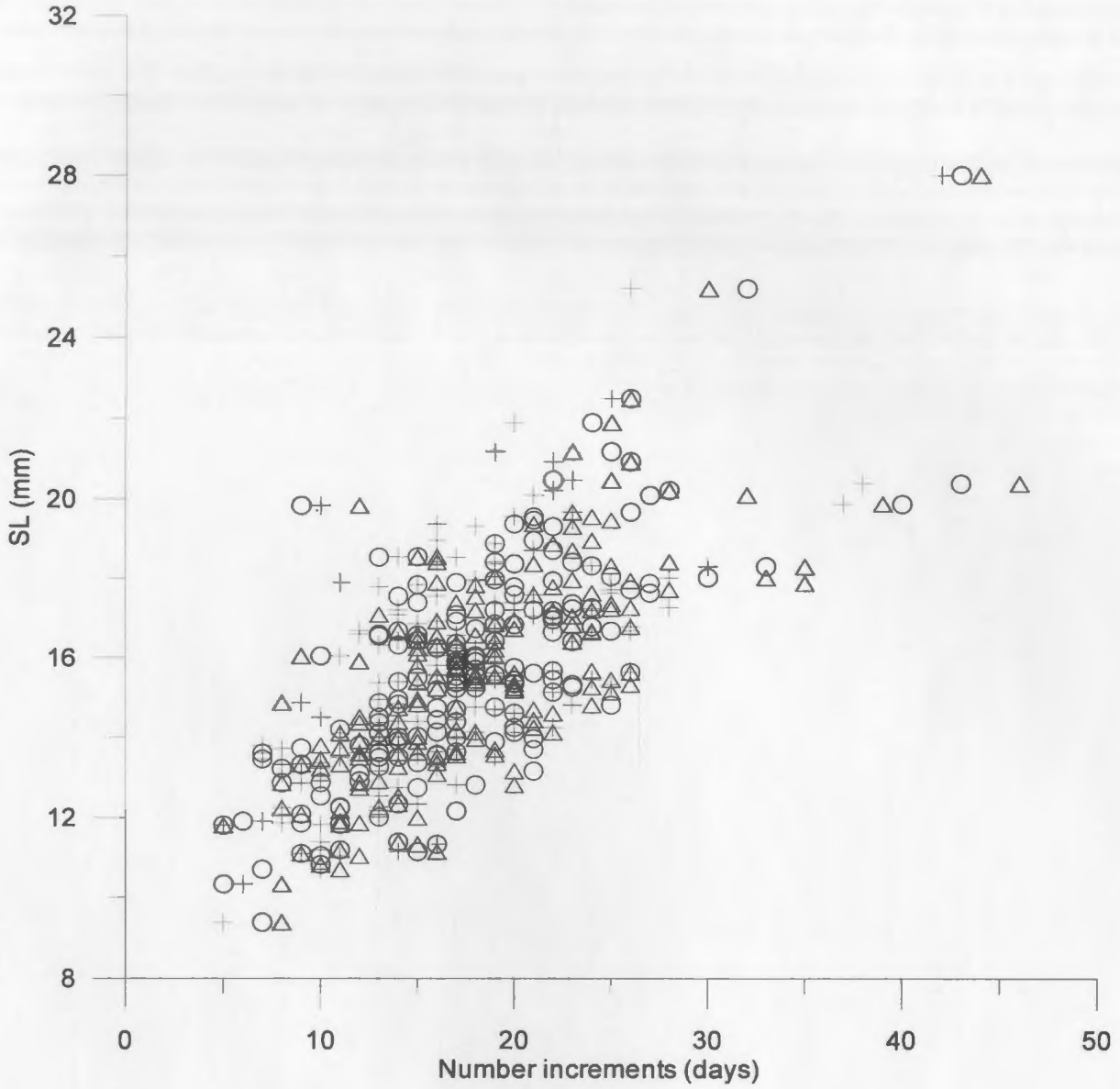

Figure 3.2.3: Results from replicated reads from B6-2002. This graph only shows otoliths with replicated reads (n=163). Crosses represent first read, circles represent second read and triangles represent third read.

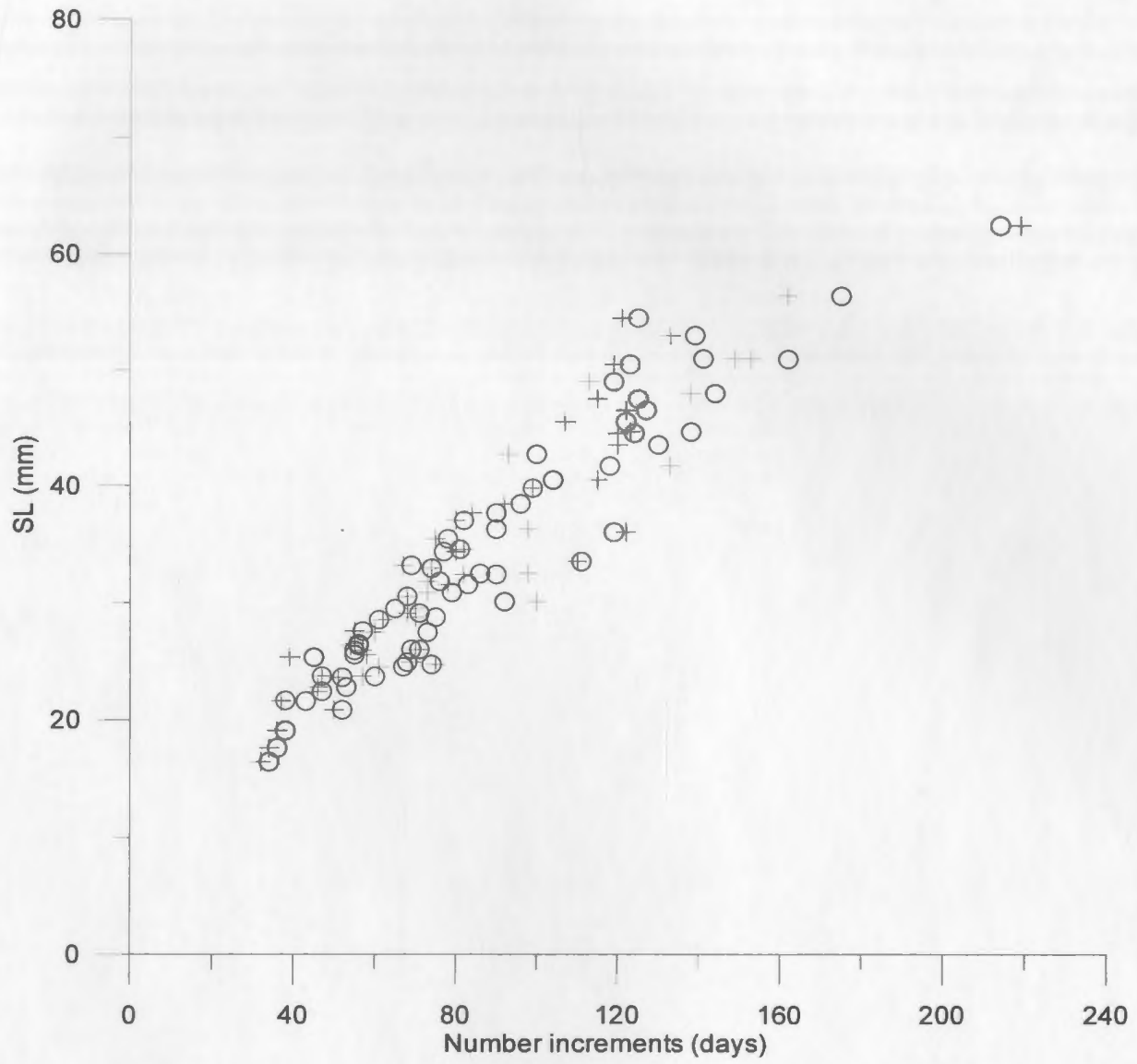

Figure 3.2.4: Results from replicated reads from B9-2002. This graph only shows otoliths with replicated reads (n=64). Crosses represent first read and circles represent second read.

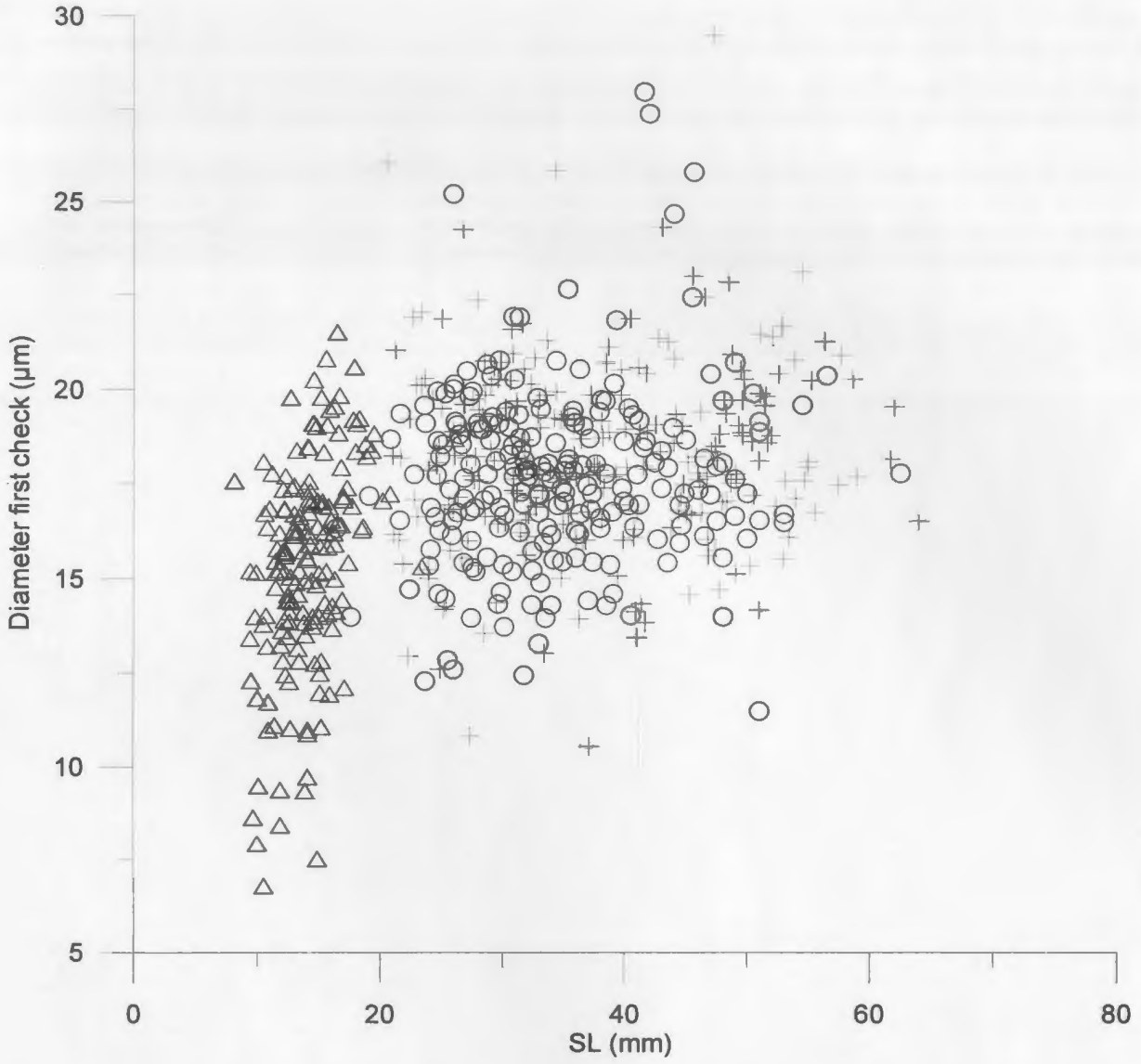

Figure 3.3.1: Standard length (SL, mm) and diameter of first check for all surveys. For surveys B10-2001 (n=256, crosses) and B9-2002 (n=216, open circles) measurement of first check from the first read was used. For B6-2002 (n=163, open triangles) mean from all reads was used.

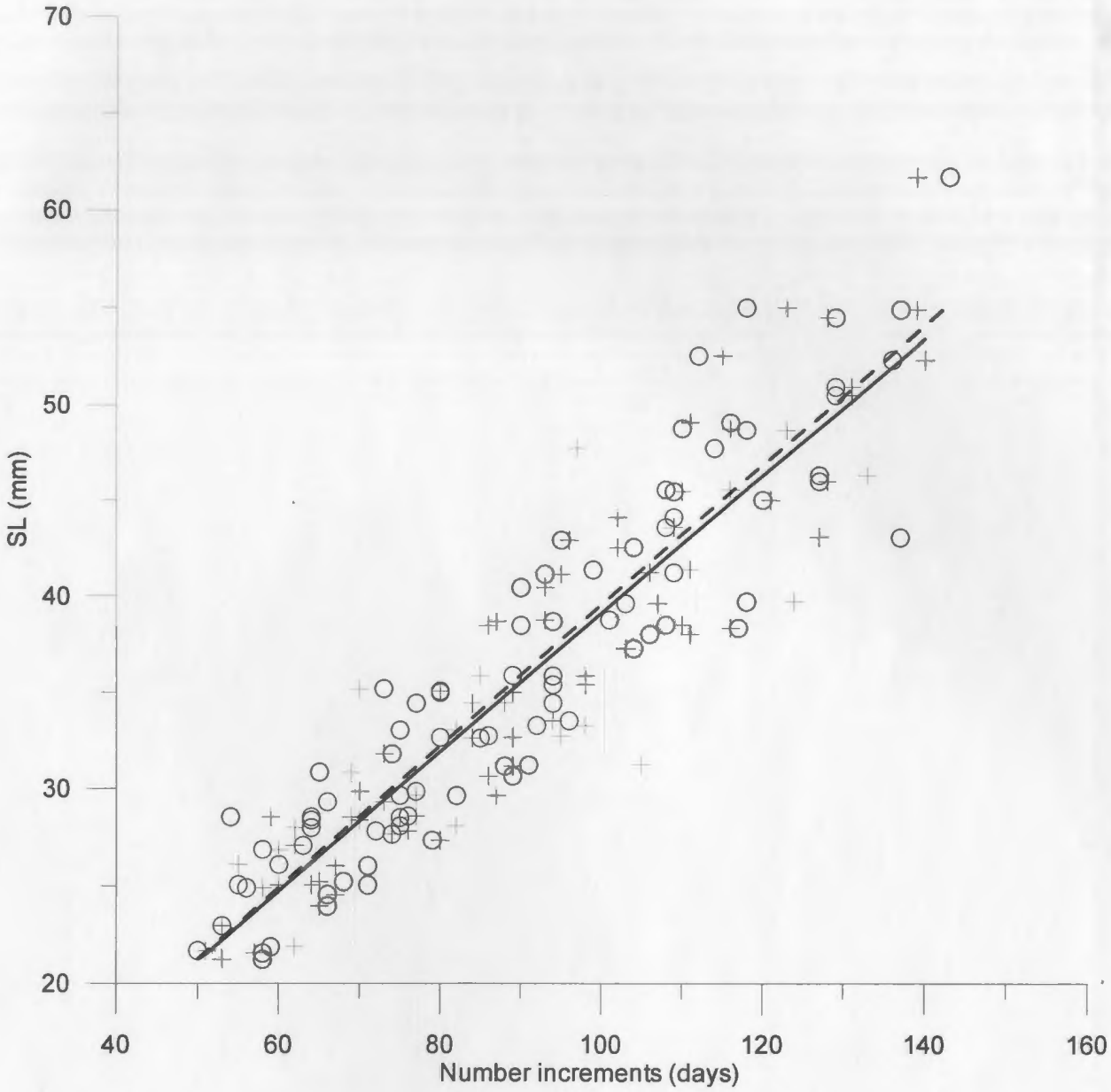

Figure 3.4.1: Replicated reads for B10-2001 (n=83). Crosses and a solid line represent first read and open circles and a dashed line represent second read. A linear model was fitted to the data. Formula Read 1: SL = 0.359*Number increments + 3.210, r^2 = 0.84. Formula Read 2: SL = 0.366*Number increments + 2.991, r^2 = 0.86.

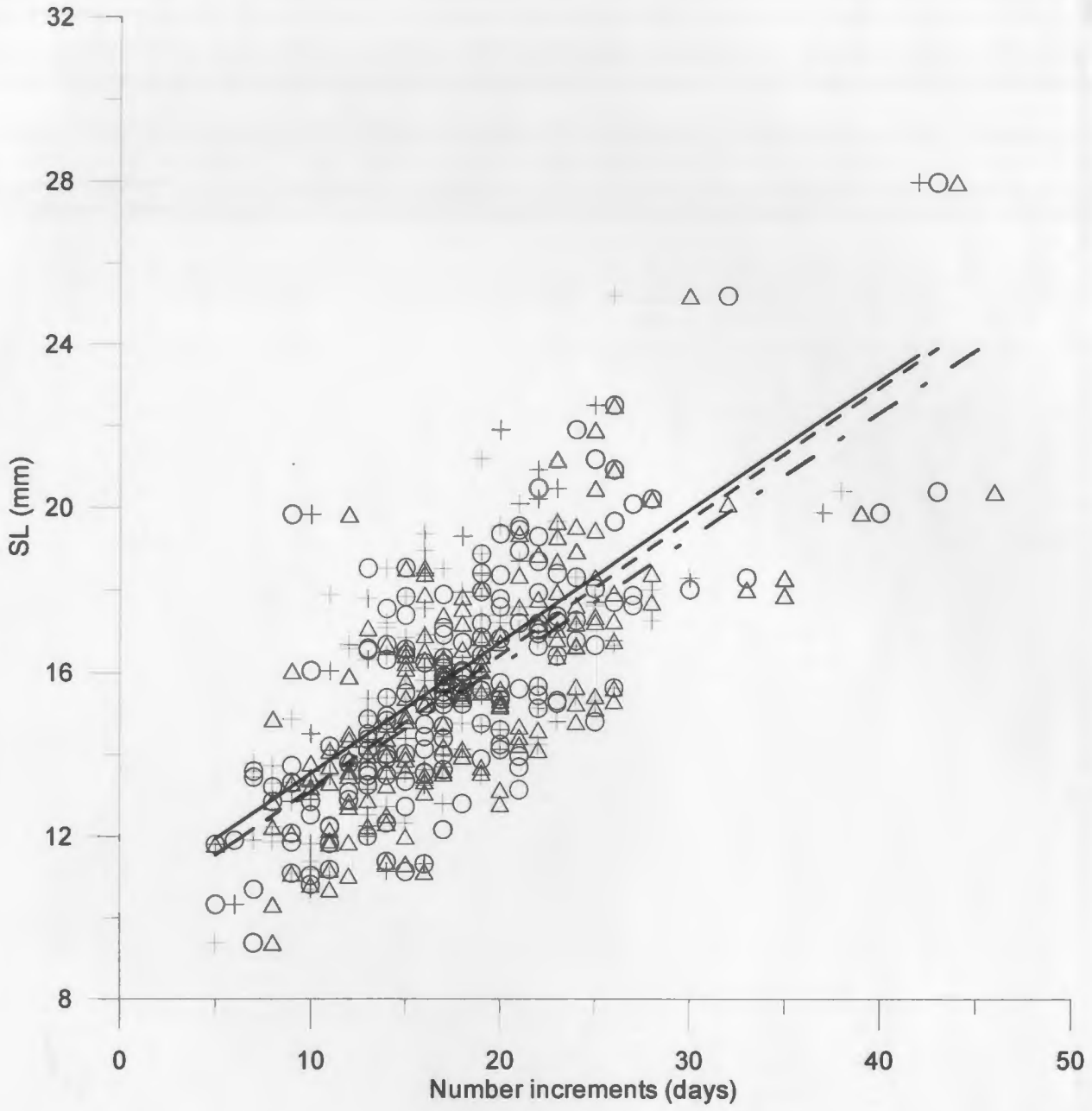

Figure 3.4.2: Replicated reads for B6-2002 (n=163). Solid line and crosses represent first read, dashed line and open circles represent second read and dot dashed line and open triangle represent third read. A linear model was fitted to the data. Formula Read 1: SL = 0.320*Number increments + 10.352, r^2 = 0.48. Formula Read 2: SL = 0.326*Number increments + 9.910, r^2 = 0.55. Formula Read 3: SL = 0.308*Number increments + 10.021, r^2 = 0.53.

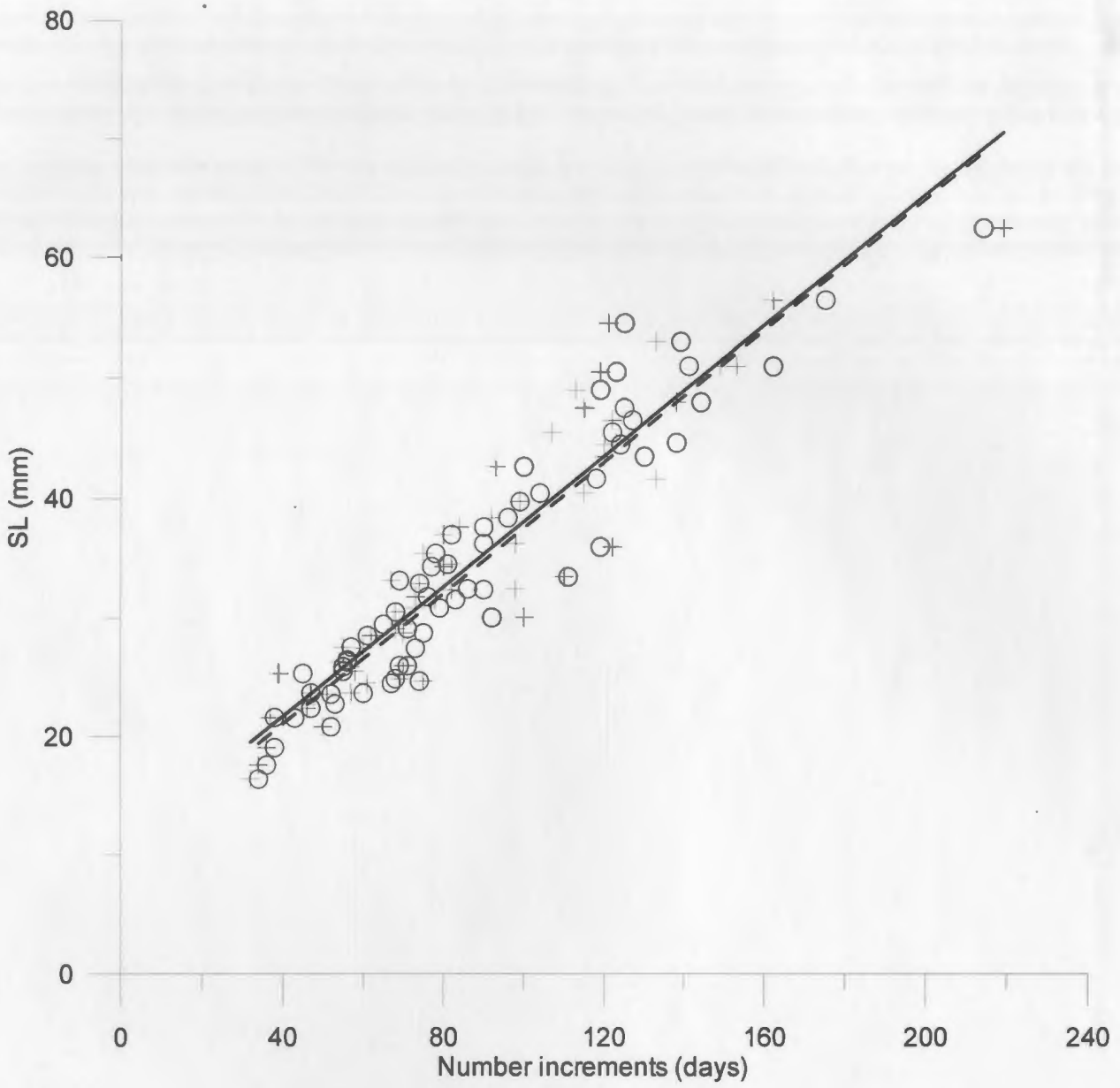

Figure 3.4.3: Replicated reads for B9-2002 (n=64). Crosses and a solid line represent first read and a dashed line and open circles represent second read. A linear model was fitted to the data. Formula Read 1: SL = 0.273*Number increments + 10.812, r^2 = 0.87. Formula Read 2: SL = 0.275*Number increments + 10.104, r^2 = 0.90.

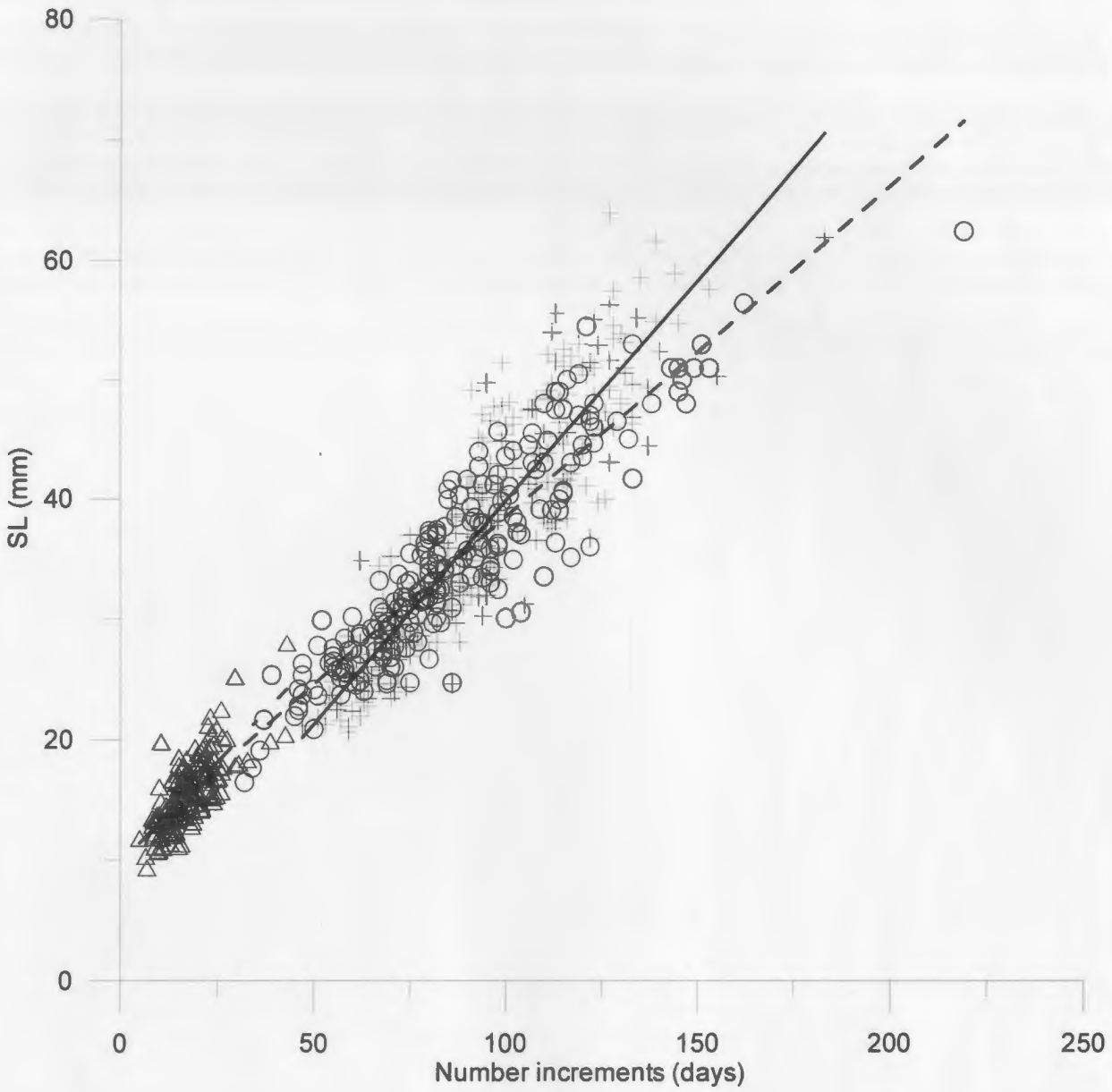

Figure 3.4.4: Linear size-at-age model for all surveys. For B10-2001 (n=256, crosses and solid line) and B9-2002 (n=216, open circles and dashed line) results from the first read were used. For B6-2002 (n=163, open triangles and dot dashed line) mean of all three reads was used. Formula B10-2001: SL = 0.371*number increments + 2.690, r^2 = 0.80. Formula B6-2002: SL = 0.336*number increments + 9.723, r^2 = 0.55. Formula B9-2002: SL = 0.278*number increments + 10.661, r^2 = 0.83.

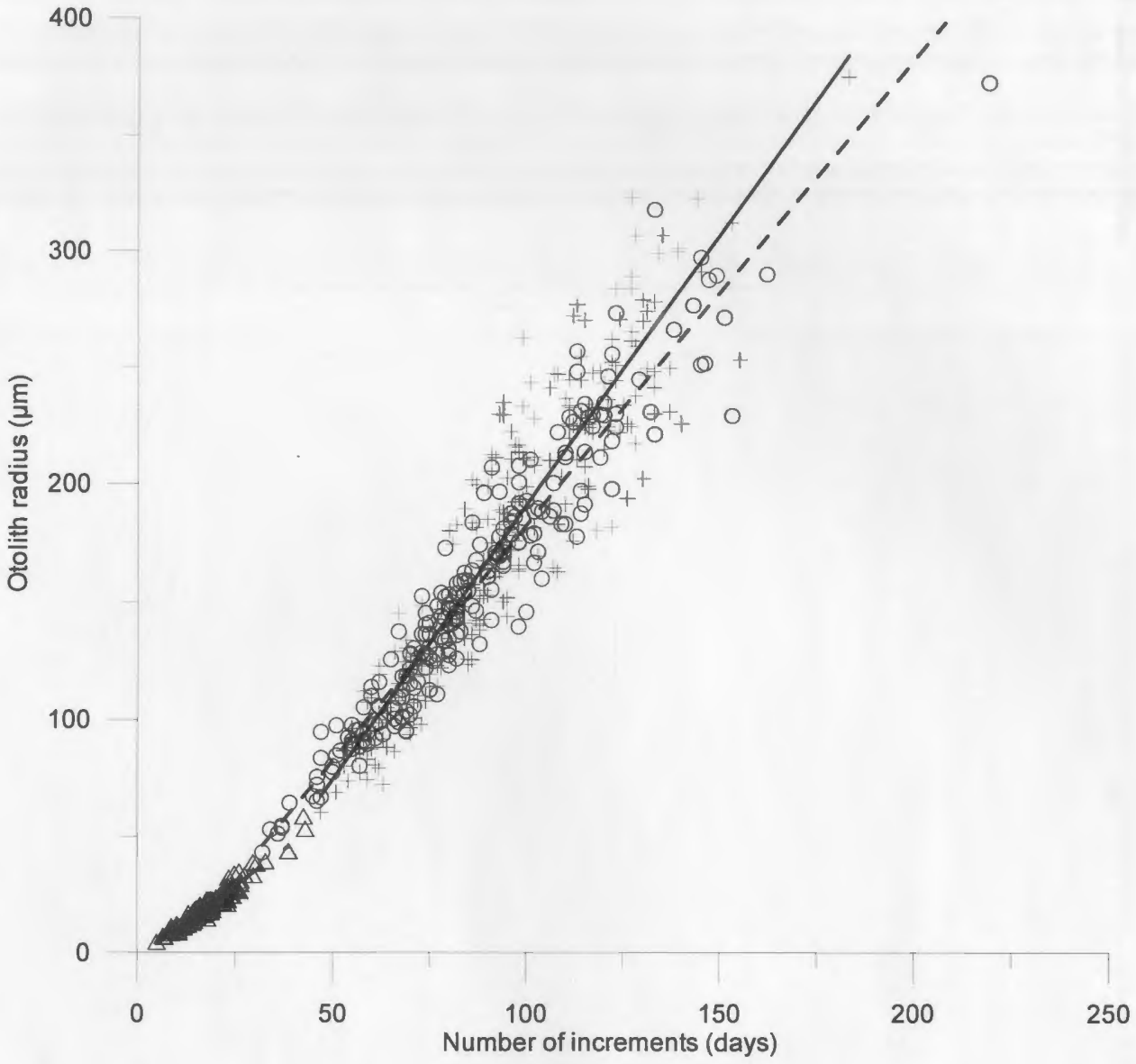

Figure 3.4.5: Relationship between otolith radius and number of increments for all three surveys. For B10-2001 (n=256, crosses and solid line) and B9-2002 (n=216, open circles and dashed line) results from the first read were used. For B6-2002 (n=163, open triangles and dot dashed line) mean of all three reads was used. Formula B10-2001: Radius = 2.332*NI – 42.323, r^2 = 0.85. Formula B6-2002: Radius = 1.251* NI – 2.601, r^2 = 0.94. Formula B9-2002: Radius = 2.003* NI – 17.911, r^2 = 0.92.

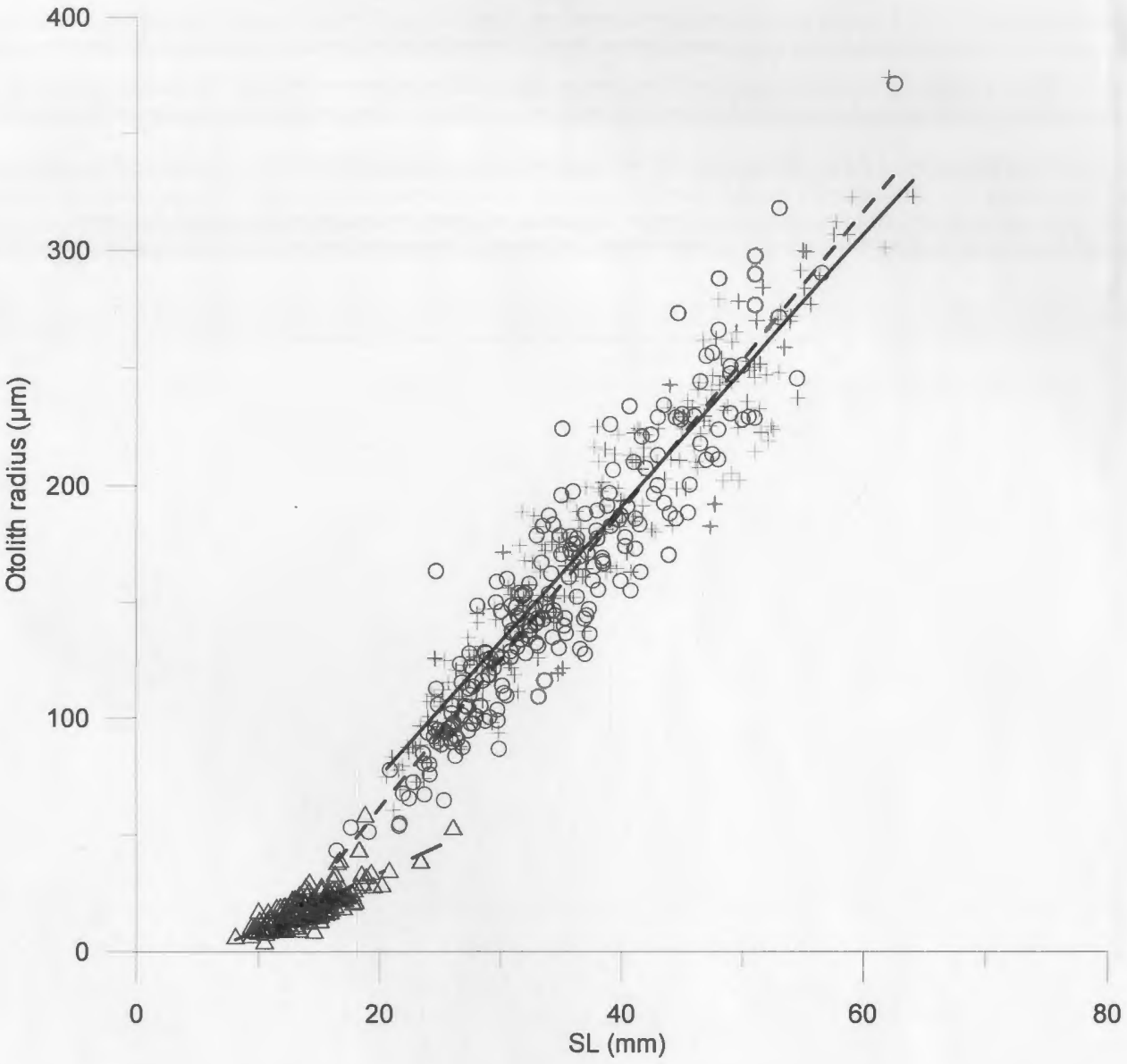

Figure 3.4.6: Relationship between otolith radius and standard length (SL, mm) for all surveys. For B10-2001 (n=256, crosses and solid line) and B9-2002 (n=216, open circles and dashed line) results from the first read were used. For B6-2002 (n=163, open triangles and dot dashed line) mean of all three reads was used. Formula B10-2001: Radius = 5.821*SL – 41.774, r^2 = 0.91. Formula B6-2002: Radius = 2.383*SL – 14.777, r^2 = 0.64. Formula B9-2002: Radius = 6.407*SL – 66.993, r^2 = 0.87.

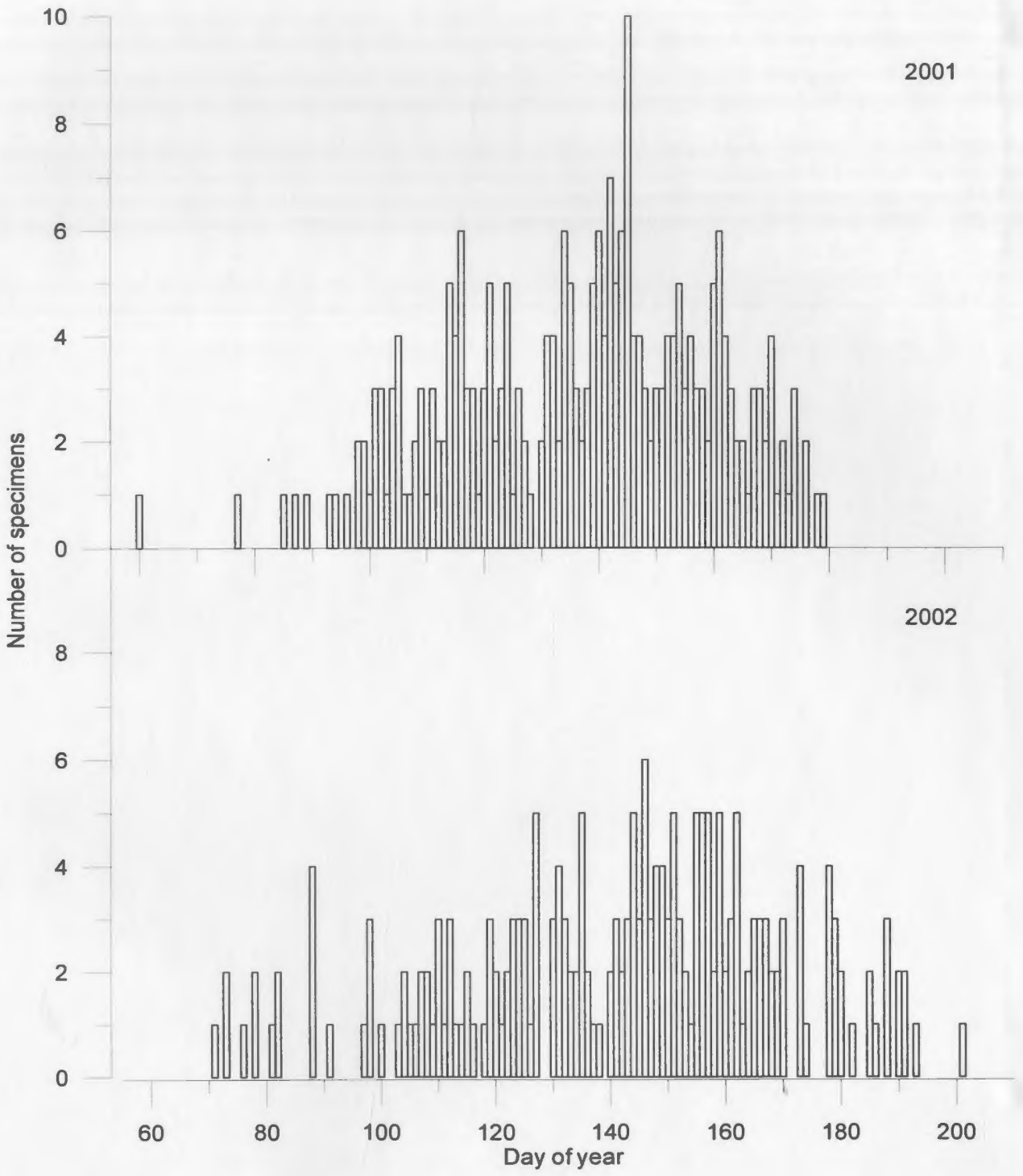

Figure 3.4.7: Estimated hatch dates of larvae from the two August surveys B10-2001 and B9-2002.

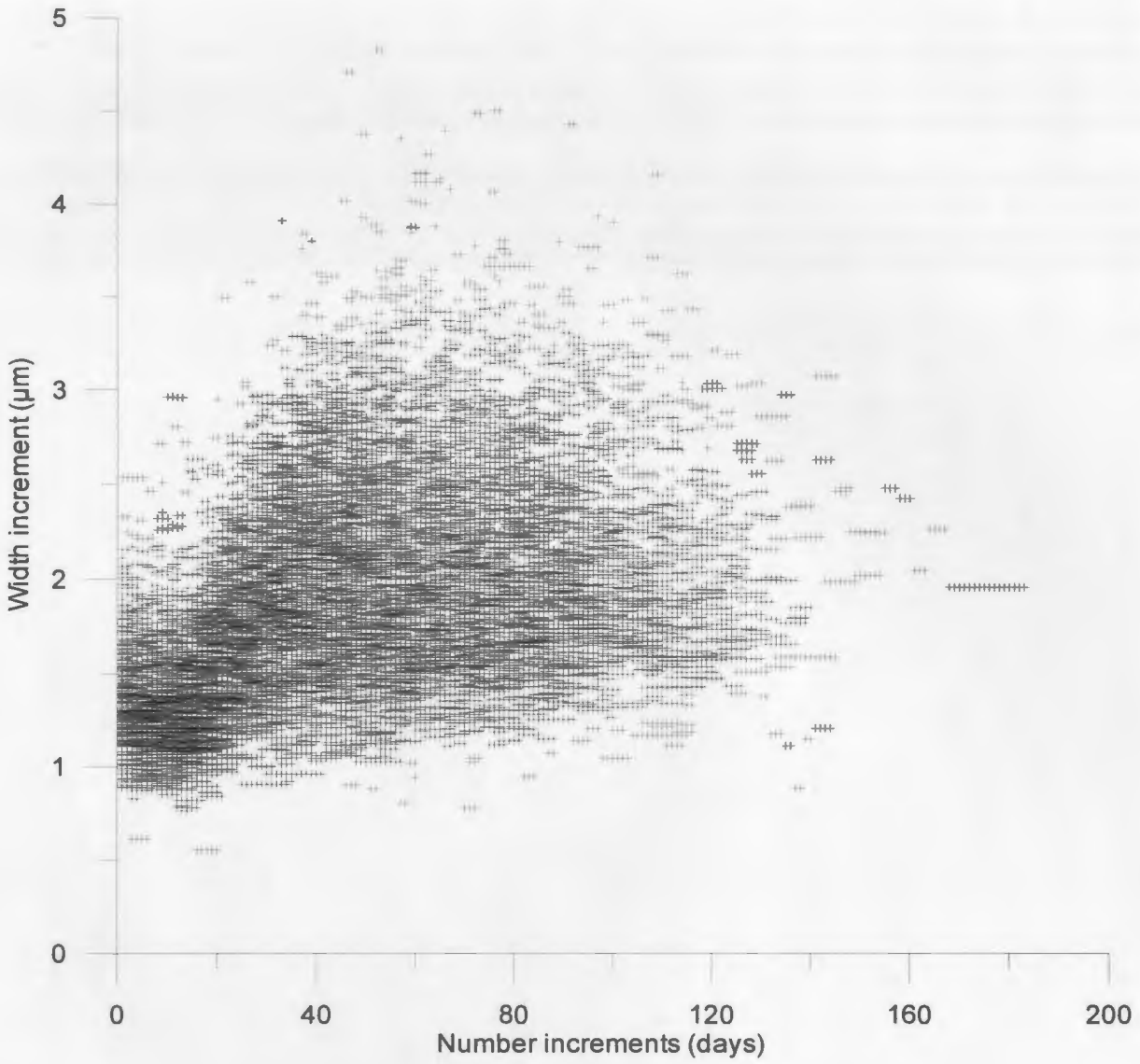

Figure 3.5.1: Measured increment width from the first read for survey B10-2001, 256 otoliths.

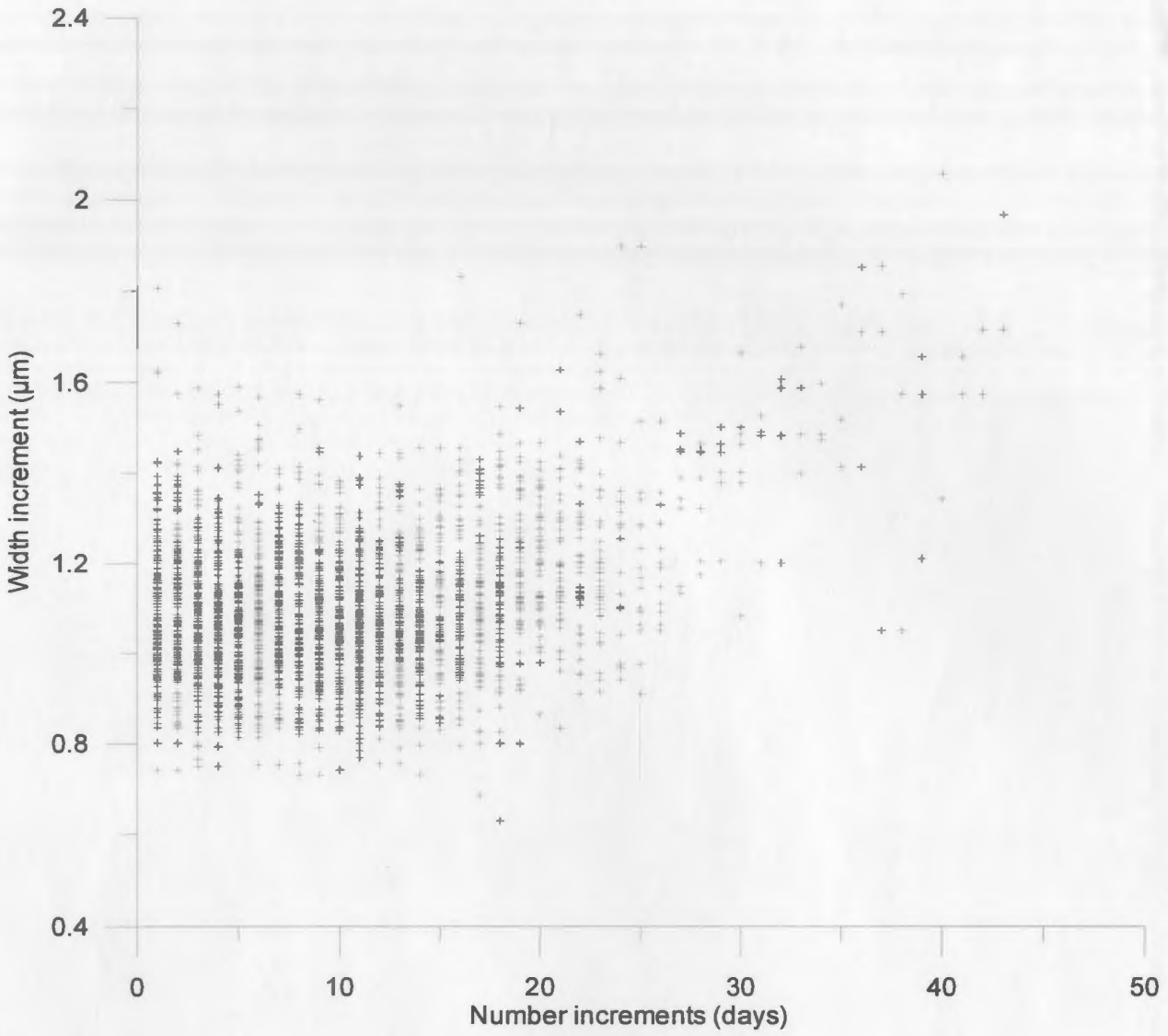

Figure 3.5.2: Measured increment width from all reads for survey B6-2002, 163 otoliths.

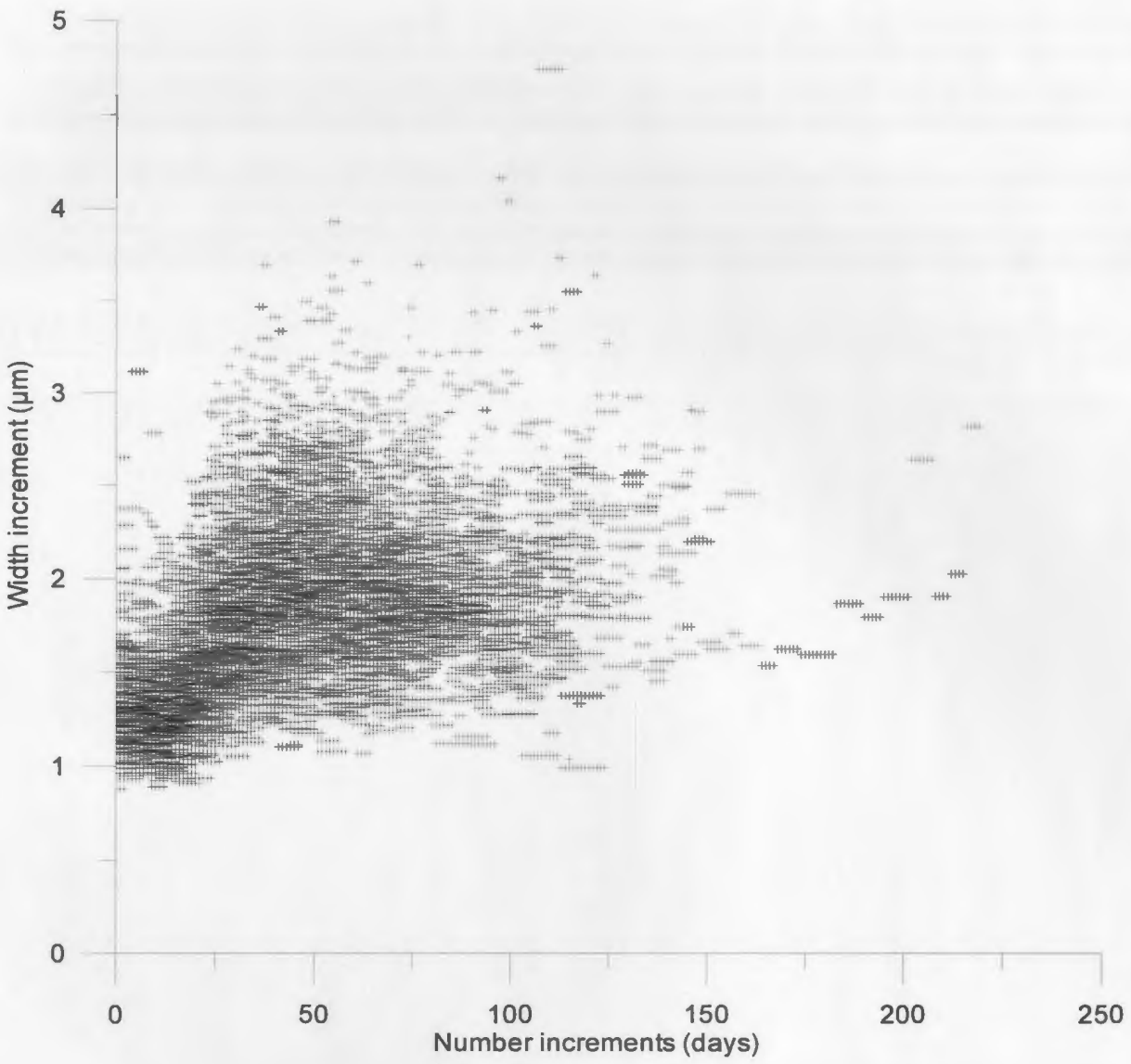

Figure 3.5.3: Measured increment width from the first read for survey B9-2002, 216 otoliths.

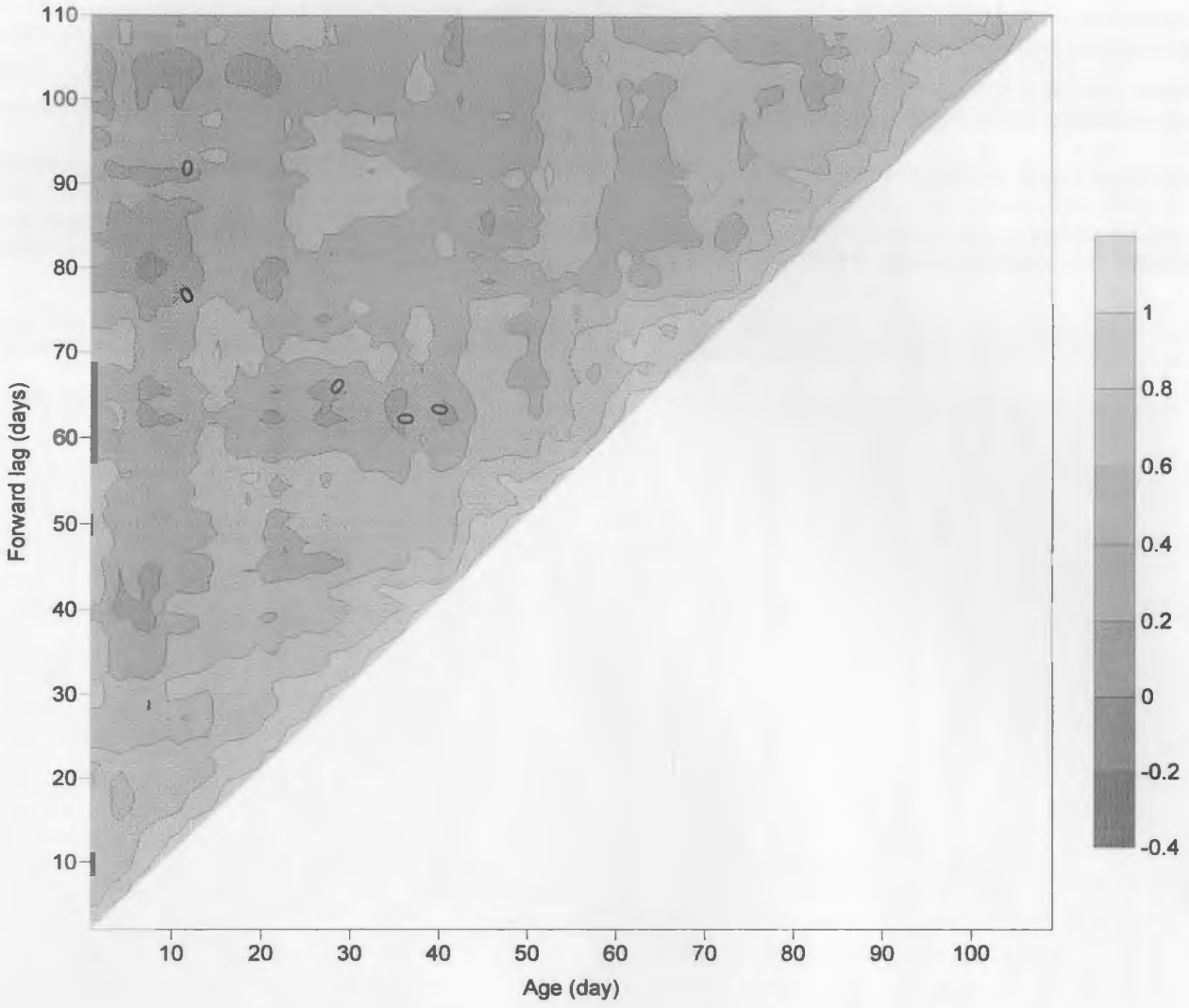

Figure 3.5.4: Forward lag partial correlation between increment widths for age, survey B10-2001 (n=78). The bar shows the scale of correlation in width of increments with one presenting the maximum correlation and zero presenting the minimum. Negative values present negative correlation.

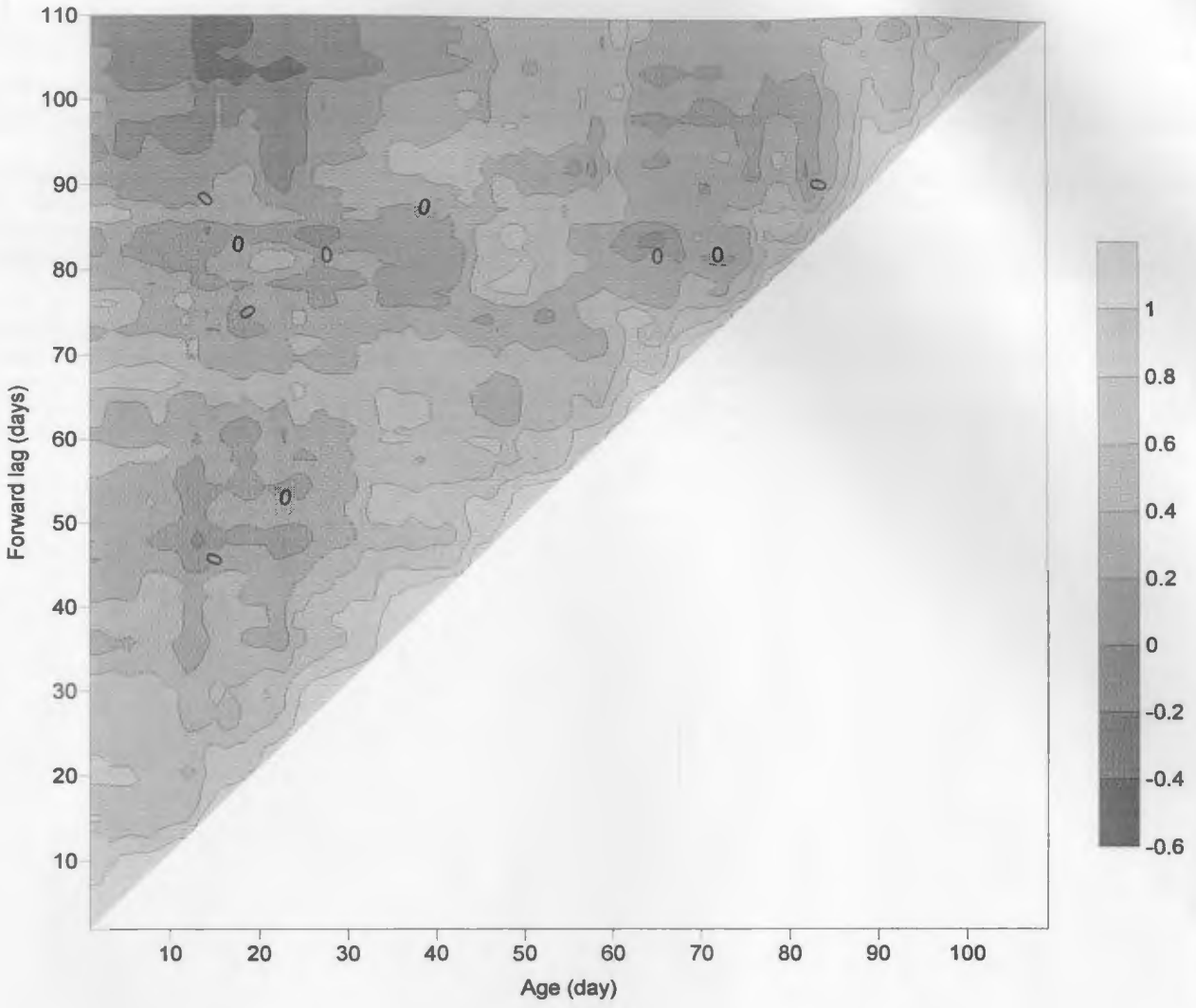

Figure 3.5.5: Forward lag partial correlation between increment widths for age, survey B9-2002 (n=43). The bar shows the scale of correlation in width of increments. The bar shows the scale of correlation in width of increments with one presenting the maximum correlation and zero presenting the minimum. Negative values present negative correlation.

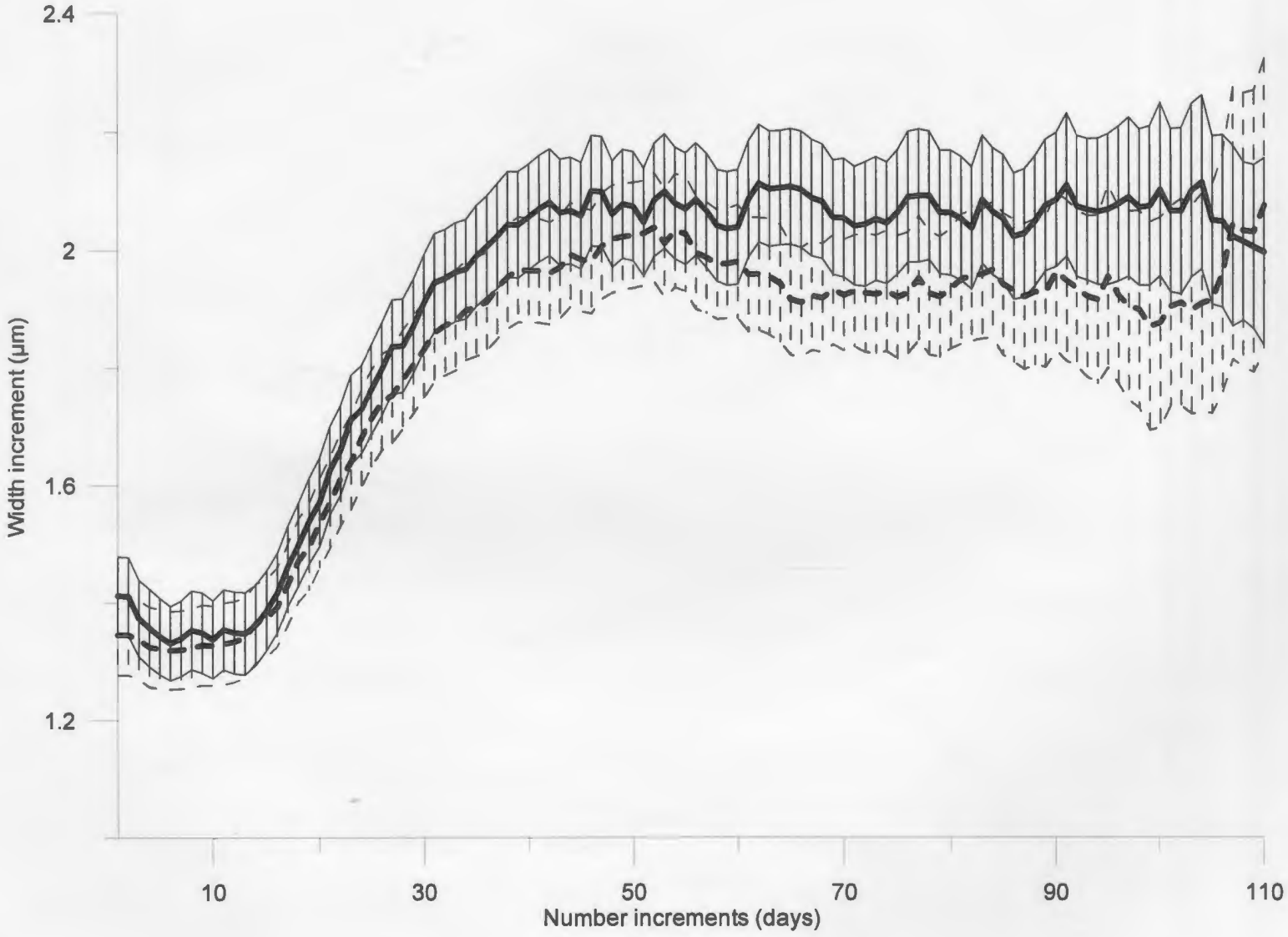

Figure 3.5.6: Mean increment width for age and 95% confidence limits for B10-2001 (solid lines) and B9-2002 (dashed lines).

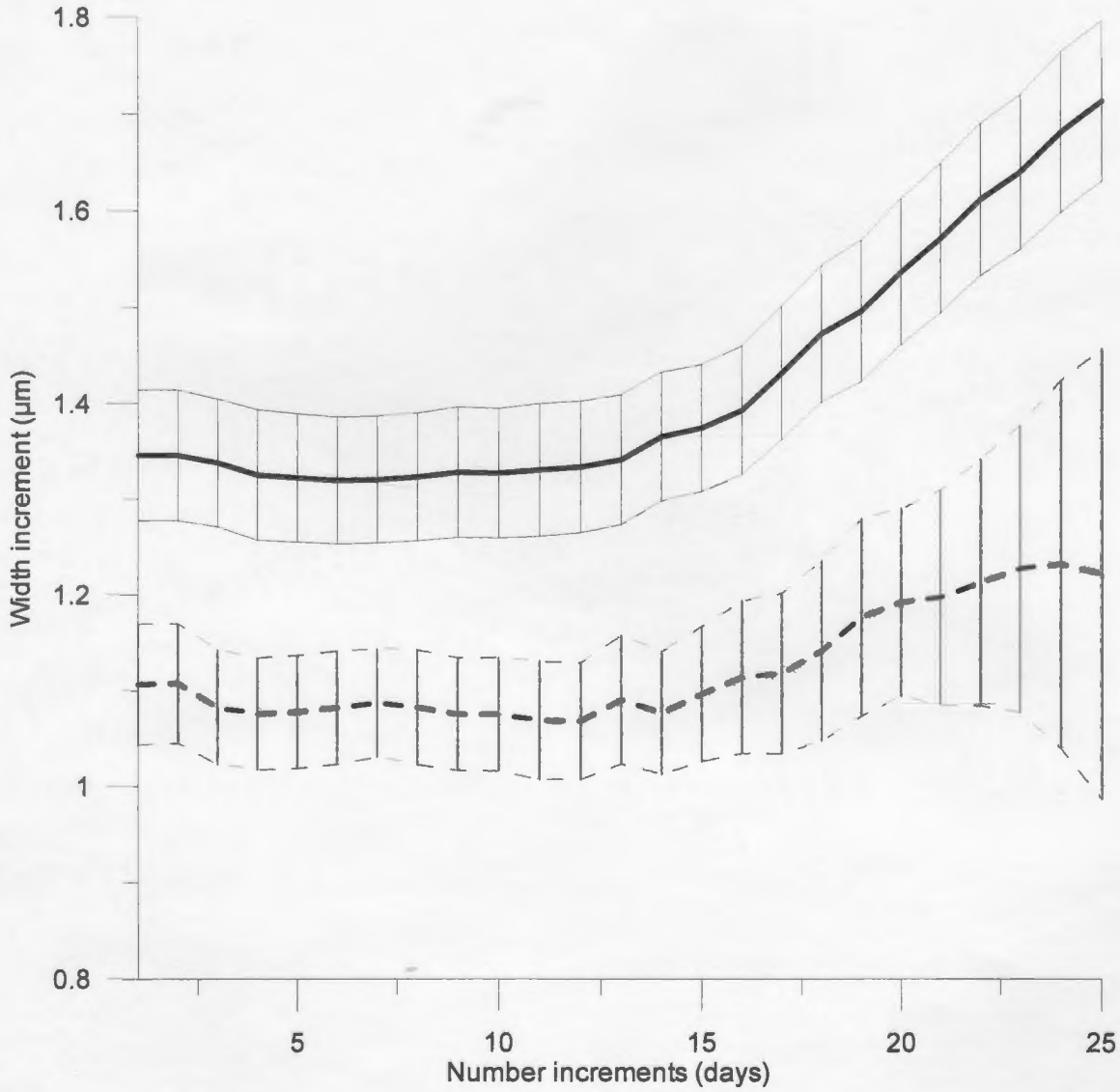

Figure 3.5.7: Mean increment width for age and 95% confidence limits for B9-2002 (solid lines) and B6-2002 (dashed lines).

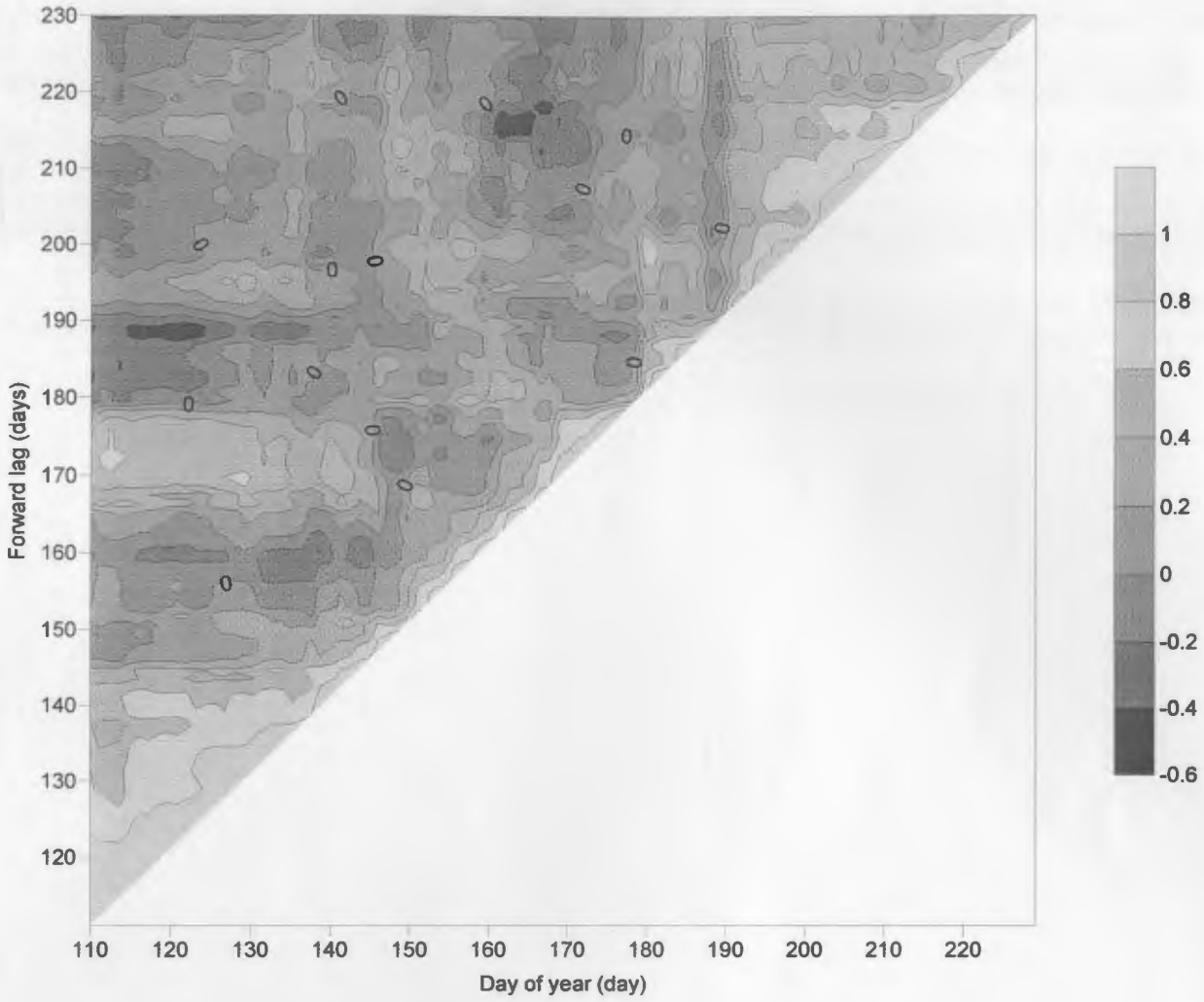

Figure 3.5.8: Forward lag partial correlation between increment widths for day-of-year, survey B10-2001 (n=22). The bar shows the scale of correlation in width of increments with one presenting the maximum correlation and zero presenting the minimum. Negative values present negative correlation.

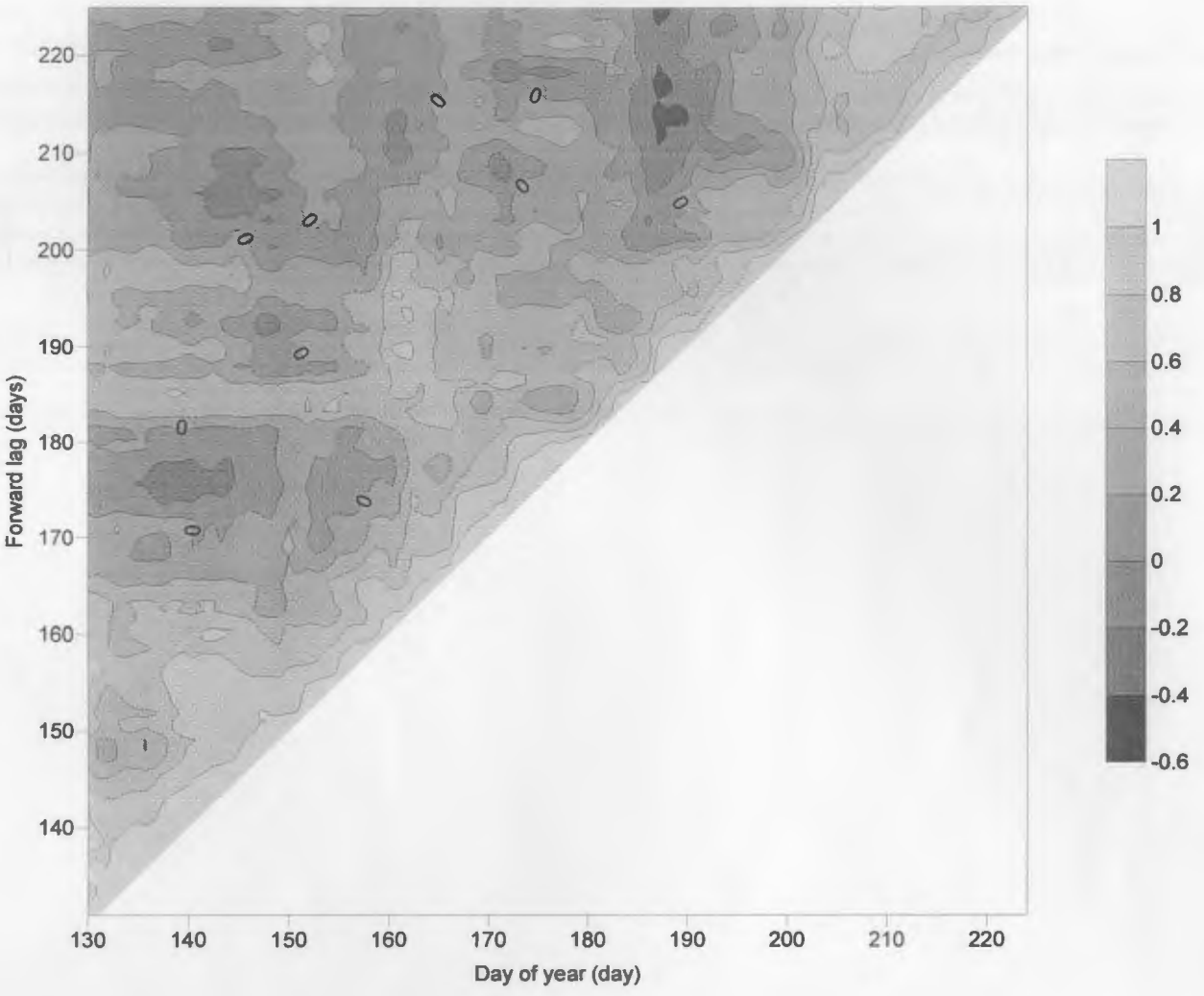

Figure 3.5.9: Forward lag partial correlation between increment widths for day-of-year, survey B9-2002 (n=28). The bar shows the scale of correlation in width of increments with one presenting the maximum correlation and zero presenting the minimum. Negative values present negative correlation.

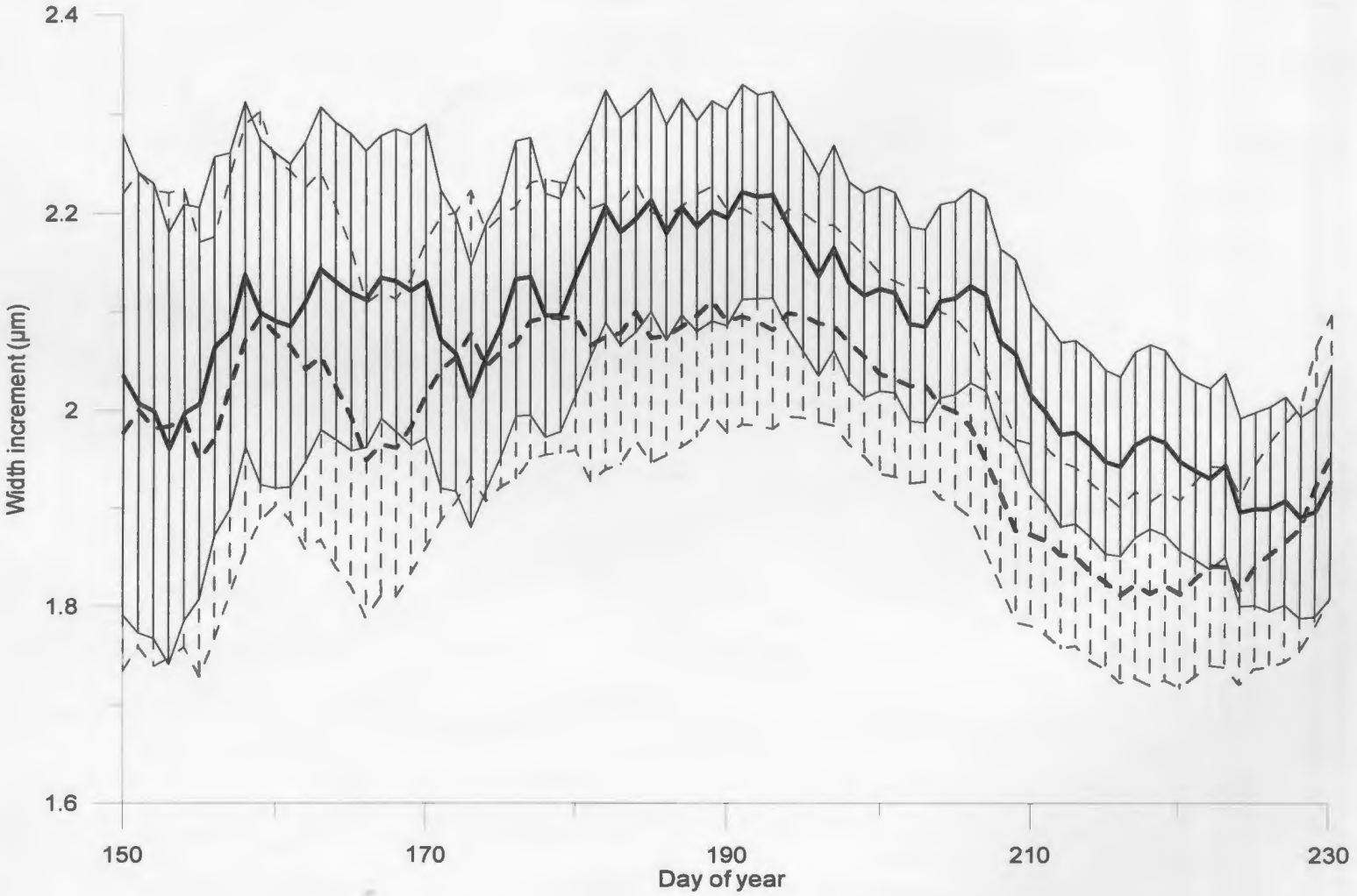

Figure 3.5.10: Mean increment width for day-of-year and 95% confidence limits for B10-2001 (solid lines) and B9-2002 (dashed lines).

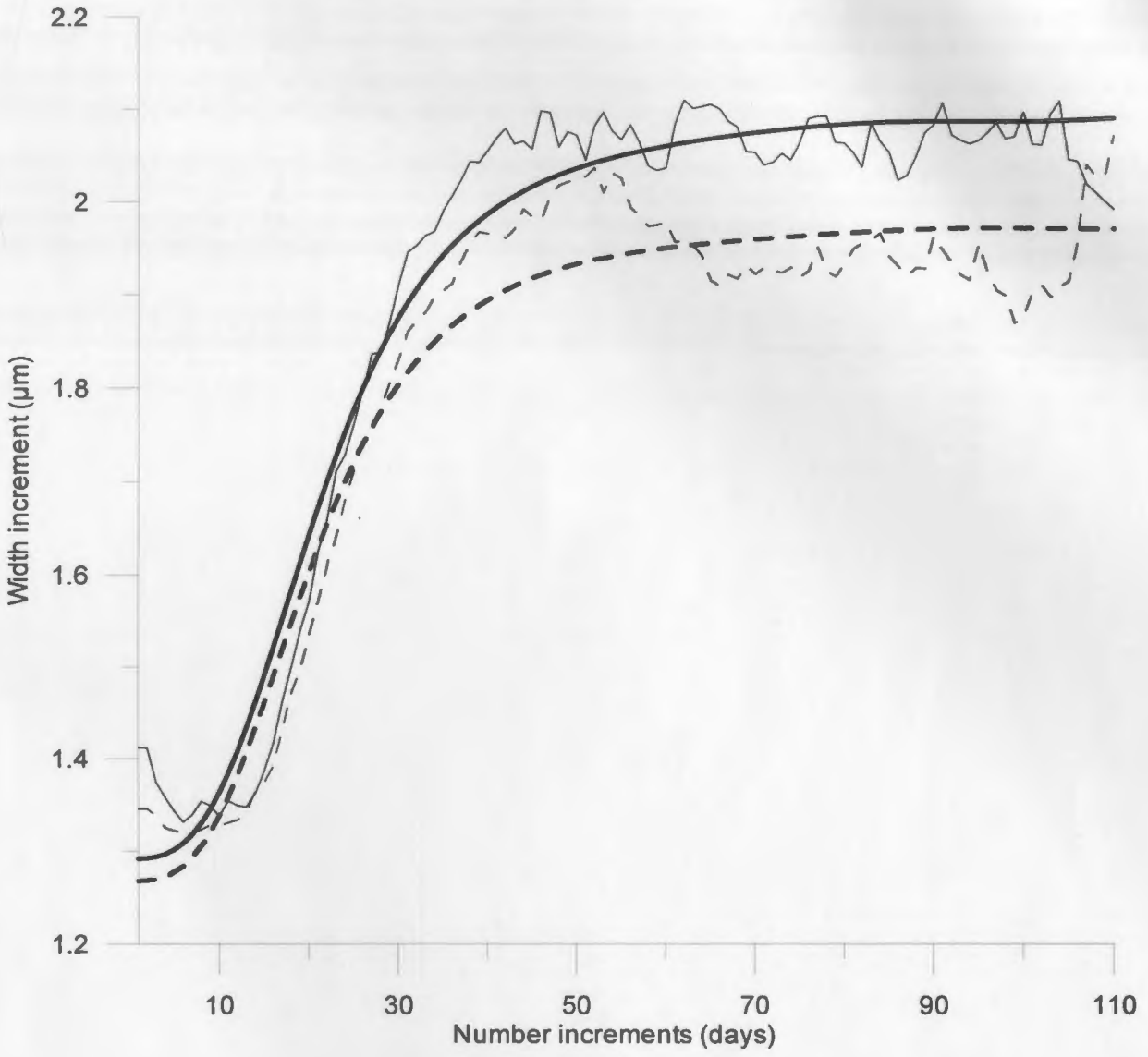

Figure 3.5.11: A non-linear model (wide lines) was fitted to mean increment width (thin line) for B10-2001 (solid line) and B9-2002 (dashed line). WI = width increment (µm) and NI = number increments. Model B10-2001: $WI = 1.2918 + (0.8085*NI^{2.9886} * (10{,}000 + NI^{2.9886})^{-1})$. Model B9-2002: $WI = 1.2683 + (0.7110*NI^{3.0372} * (10{,}000 + NI^{3.0372})^{-1})$.

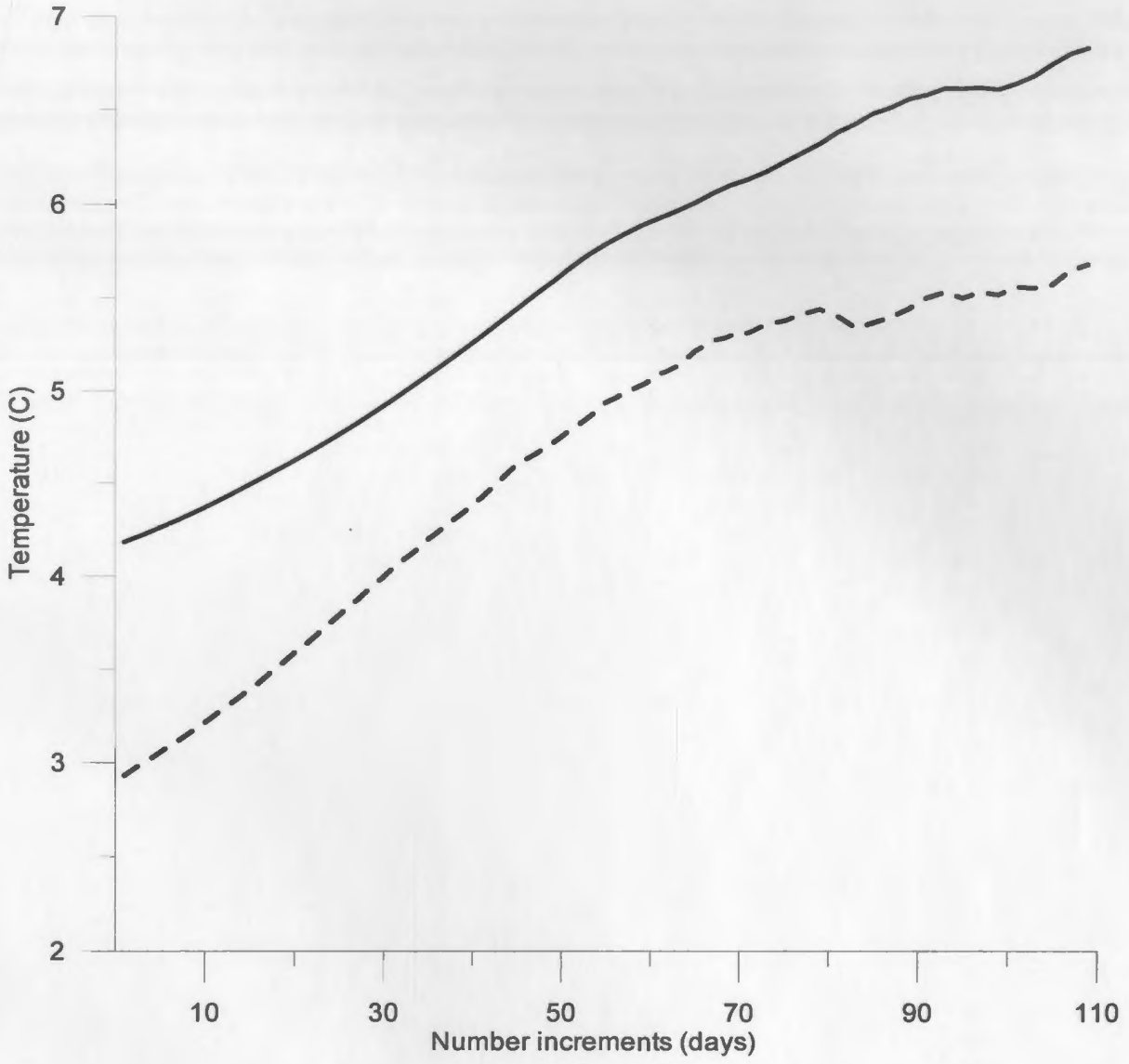

Figure 3.6: Estimated temperature for age of larvae from the two August surveys B10-2001 (solid line) and B9-2002 (dashed line). Temperature was calculated as the average of measurements at stations one to five at Siglunes section at depth of five meters to 50 meters for surveys in February, May and August.

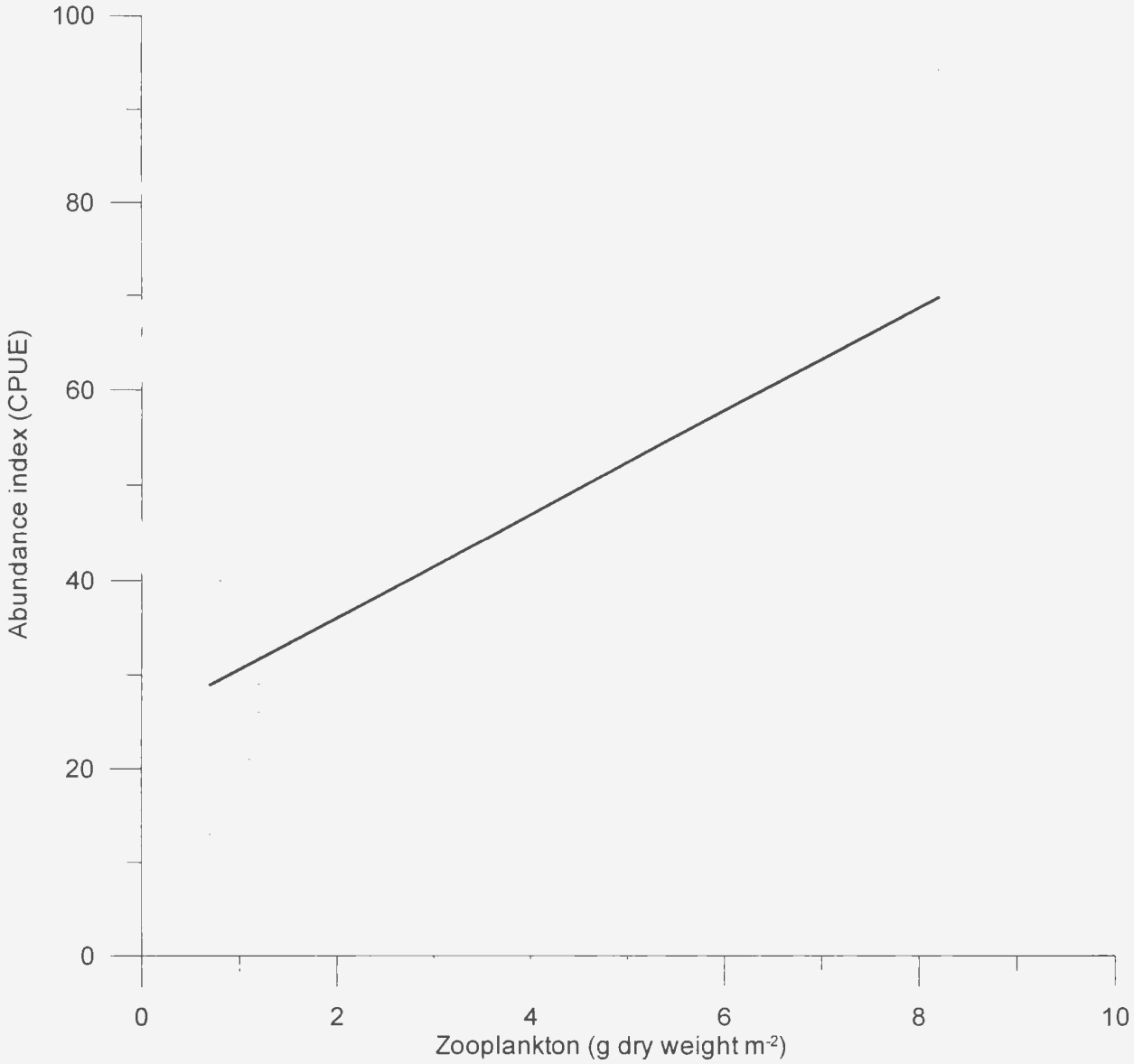

Figure 4.0: The relationship between August estimates of capelin larvae abundance measured as catch per unit effort (CPUE) (Sveinbjörnsson and Hjörleifsson 2002) and zooplankton abundance measured in May (Anonymous 2003b) on the nursery ground of capelin in the north. (Siglunes standard section). Data from the capelin year-classes 1980 – 2002 are used. The regression line explains 24% of the varianc

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Appendices

Appendix 1: Non-linear model of increment width for surveys B10-2001 and B9-2002.

B10-2001:

Model:
$MIW = A + ((B*(NI^C))*(10000 + NI^C)^{-1})$

Symbols:
MIW = mean increment width (μm)
NI = number of increments (days)
A, B and C = parameters whose values were estimated.

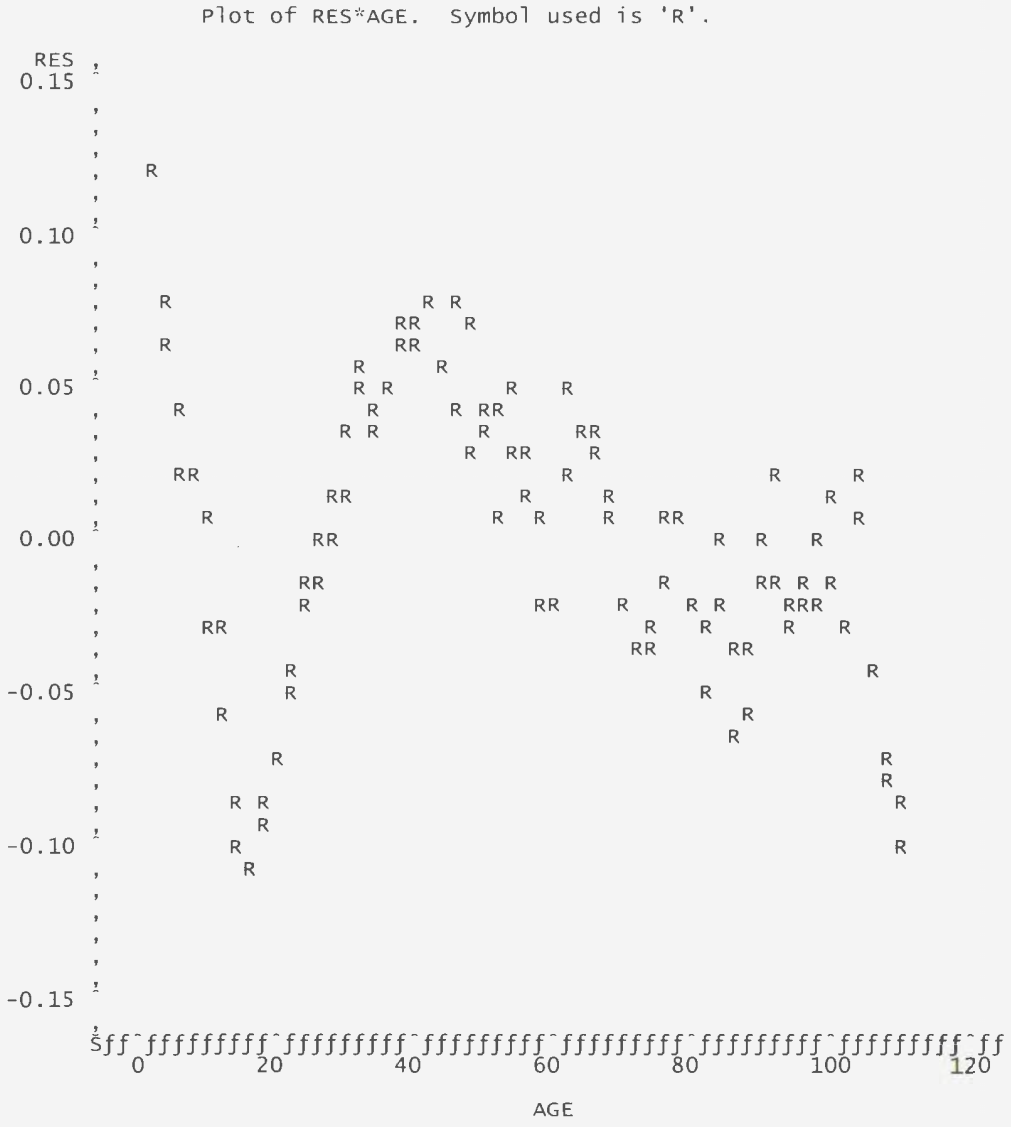
Results:
Method: Gauss-Newton
Iterations: 18
Number of observations: 110
Dependant variable: mean increment width

Source	DF	Sum of Squares	Mean Square	F Value	Approx Pr > F
Regression	3	409.9	136.6	1502.68	<.0001
Residual	107	0.2599	0.00243		
Uncorrected Total	110	410.2			
Corrected Total	109	7.5606			

Parameter	Estimate	Approx Std Error	Approximate 95% Confidence limits	
A	1.2918	0.0148	1.2626	1.3210
B	0.8085	0.0152	0.7783	0.8387
C	2.9886	0.0249	2.9392	3.0379

Therefore the non-linear model is:

Model B10-2001: $WI = 1.2918 + (0.8085*NI^{2.9886} * (10.000 + NI^{2.9886})^{-1})$.


Plot of RES*AGE. Symbol used is 'R'.
RES
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
0
20
40
60
80
100
120
AGE

B9-2002:

Model:
$MIW = A + ((B*(NI^C))*(10000 + NI^C)^{-1})$

Symbols:
MIW = mean increment width (μm)
NI = number of increments (days)
A, B and C = parameters whose values were estimated.

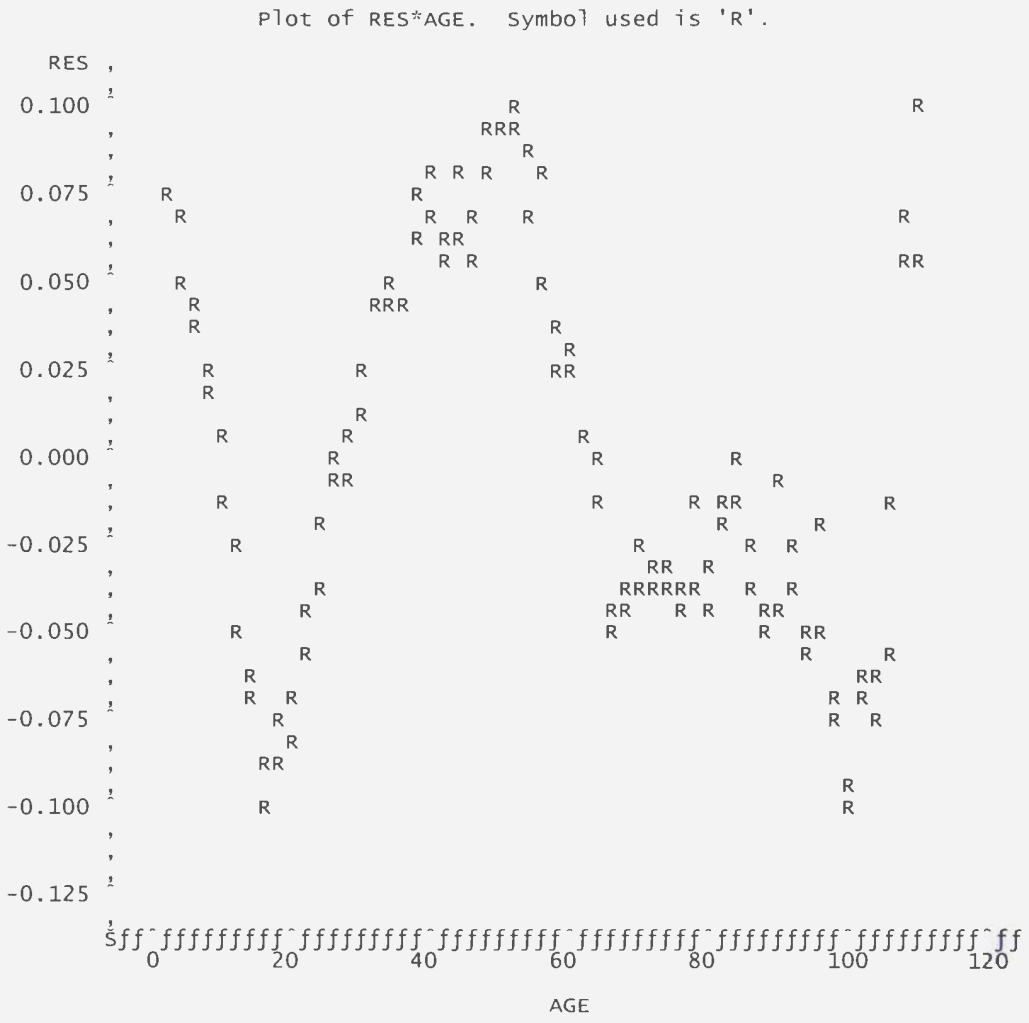
Results:
Method: Gauss-Newton
Iterations: 21
Number of observations: 110
Dependant variable: mean increment width

Source	DF	Sum of Squares	Mean Square	F Value	Approx Pr > F
Regression	3	371.2	123.7	883.02	<.0001
Residual	107	0.3355	0.00314		
Uncorrected Total	110	371.6			
Corrected Total	109	5.8723			

Parameter	Estimate	Approx Std Error	Approximate 95% Confidence Limits	
A	1.2683	0.0171	1.2344	1.3022
B	0.7110	0.0176	0.6761	0.7459
C	3.0372	0.0330	2.9717	3.1027

Therefore the non-linear model is:

Model B9-2002: $WI = 1.2683 + (0.7110*NI^{3.0372} * (10.000 + NI^{3.0372})^{-1})$.


Plot of RES*AGE. Symbol used is 'R'.
RES
0.100
0.075
0.050
0.025
0.000
-0.025
-0.050
-0.075
-0.100
-0.125
0
20
40
60
80
100
120
AGE