Size, age, growth and mortality of the green sea urchin *Strongylocentrotus droebachiensis* in Vega and Hammerfest, Norway.

Sandra Gran Stadniczeñko

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Program for Marine Biology and Limnology

Department of biology

University of Oslo

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[1] UiO
[2] NIVA

SUMMARY

Since the late 1960's the green sea urchin *Strongylocentrotus droebachiensis* (O.F. Müller) has grazed down large areas of kelp forest from the county of Trøndelag to the Russian border. This comprises a coastal area of more than 2000 km^2 with a large proportion of barren areas which are characterized by bare rock, gravel and other earthen material and sparse or no vegetation present. Recent investigations indicate that in the southern areas the kelp forest is returning. This means that the numbers of urchins are likely declining (such as in Vega). On the other hand, the grazing is unaffected in the more northern part of Norway (such as in Hammerfest).

The main goal of this project was to study the size, age, growth and mortality of sea urchins in a region where the population is declining (Vega) and compare this with a region with no evident population reduction (Hammerfest).

Urchins were sampled from three barren stations and three kelp forest stations (200 individuals from each station) in the heavily grazed northern part of the barren ground area (Hammerfest at 71ºN), and from three barren ground stations from the southern part of the barren ground area (Vega 65ºN). In the Vega area, no sea urchins were found inside kelp forests. These samples were shipped alive to the laboratory where size and age (growth rings) of the sea urchins were determined. Further analyses were performed to determine growth and mortality.

The results indicated that the populations on kelp beds reached larger sizes, were younger and had a higher rate of growth than on the barren habitats within Hammerfest. There was also found that between barren grounds *S. droebachiensis* in Hammerfest reached larger sizes, were younger and had a higher rate of growth than on the barren habitats in Vega. However, there was no evidence for mortality to be different between habitats and areas. It was concluded that: 1) size and growth for different populations varied significantly between stations in Hammerfest, 2) age structure was similar between stations in Hammerfest but was significantly different within barren grounds in Hammerfest and Vega, 3) no differences in mortality were observed between habitats and areas.

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1. INTRODUCTION

1.1. Overgrazing on kelp forests

Kelp forests are structurally complex and diverse ecosystems and serve as habitats for diverse flora (Marstein 1997) and fauna (Christie *et al*. 2003; Christie *et al*. 2009). They dominate large areas of shallow rocky coasts of the world's temperate marine habitats, between 40–60° latitude in both hemispheres (Steneck *et al*. 2002).

The total coverage of kelp forests worldwide is known to fluctuate. These fluctuations can result from diseases, physiological stress, herbivore overgrazing or interactions among those processes (Steneck *et al*. 2002). Sea urchins usually occur in low densities, but may have a significant impact on the community structure when the population density increases by overgrazing the kelp (Lawrence 1975; Harrold and Pearse 1987). The worldwide overgrazing effect on kelp forests occurs mainly due to blooms in sea urchin populations in areas where human harvesting impacts have been minimal (Steneck *et al*. 2002). Blooms in sea urchin densities creates fronts that graze all macroalgae and form barren grounds as a result (Sivertsen 2006) (Figure 1.1).

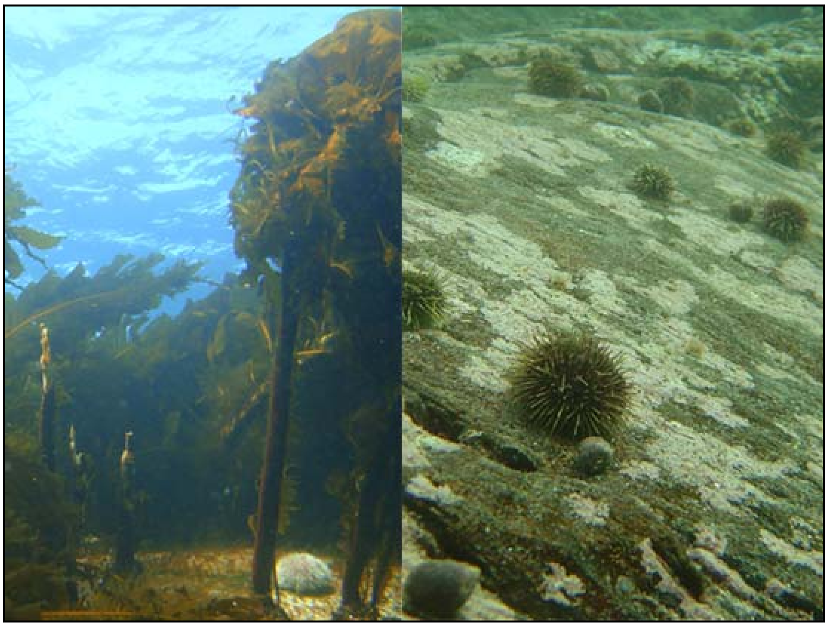


Figure 1.1 Image of Norwegian kelp forest (left) vs. barren ground habitat (right). Photos: Stein Fredriksen.

Several hypotheses on what triggers the dramatic increase in sea urchin densities have been proposed. Some of these hypotheses include: 1) low predation on the sea urchin population (Sivertsen 2006) or 2) high recruitment of sea urchin larvae combined with favourable hydrographical conditions (Foreman 1977; Ebert 1983; Hart and Scheibling 1988; Wing *et al*. 1995).

1.1.1. Overgrazing phenomenon in the Norwegian coasts

Local overgrazing events have been reported in the literature since before 1970 (Mortensen 1943; Vasseur 1952). However, the most extensive and long-lasting over-grazing event reported in the NE Atlantic occurred along from the Trøndelag area and north to the Russian border in the beginning of the 1970s (Norderhaug and Christie 2009). Approximately 2000 km^2 of *Laminaria hyperborea* Gunnerus (Foslie) kelp forest were reported to disappear due to grazing by the green sea urchin *Strongylocentrotus droebachiensis* (O.F. Müller). This event was first reported by fishermen on the Norwegian coast but later documented by a number of studies (e.g. Propp 1977; Hagen 1983; Skadsheim *et al*. 1995; Sivertsen 1997a; Sivertsen 1997b; Sivertsen 2006). The sea urchin dominated barren ground stage has until now, with a few small-scale exceptions, dominated the Norwegian waters for almost 40 years (Christie *et al*. 1998; Levin *et al*. 1998). In addition to this extensive event, small-scale local overgrazing on macrophytes have also been reported from the entire NE Atlantic (Norderhaug and Christie 2009).

This overgrazing activity leads to a partial, or complete, deforestation of the kelp bed resulting in barren grounds that may be dominated by sea urchins for decades (Elner and Vadas 1990). This does not only affect the local area but also the surrounding marine and terrestrial habitats (Steneck *et al*. 2002). Compared to kelp forests, the new barren ground state is structurally simple with low productivity (Chapman 1981) and low biological diversity (Norderhaug and Christie 2009).

Sea urchins from the genus *Strongylocentrotus* have been involved in most reported cases of kelp bed overgrazing (Paine and Vadas 1969; Harrold and Pearse 1987). Species in this genus are capable of surviving starvation periods up to four weeks after the kelp bed is overgrazed without showing apparent harm (Garnick 1978). Once the barrens are formed, sea urchin populations must rely on drift algae and newly settled organisms as a source of food (Chapman 1981), which can prevent the reestablishment of new macroalgal vegetation (Christie and Leinaas Unpublished data).

On a regional scale, re-vegetation of kelp beds in barren areas after the reduction of sea urchin densities is occurring in mid-Norway and was first observed in the late 1980s (Norderhaug and Christie 2009). This event continued northwards along the border between barren grounds and kelp forests from 1990 to 1995, as reported by Skadsheim *et al*. (1995). However, as documented by Hagen (1987) and Christie *et al*. (1995), the re-grown areas can experience new grazing events leading to new barren areas.

Re-growth of kelp forests has occurred in several areas around the world (e.g. California, Nova Scotia and Vega Island (Hawkins and Hartnoll 1983; Scheibling and Hennigar 1997, Norderhaugh and Christie 2009 (Figure 1.2) respectively). In order to allow a shift from the persistent barren ground state back to a new kelp forest state, some sort of perturbation is necessary (Norderhaug and Christie 2009). This perturbation is frequently a mass mortality that reduces the local sea urchin density (Hagen 1987; Christie *et al*. 1995). Mass mortality can be caused by changes in environmental factors that may affect survival, by an increased presence and/or activity of predators, or by increased frequency of diseases and/or parasites (Norderhaug and Christie 2009). However, once the sea urchins density is decimated in the barren area, the substrate is rapidly re-colonized by seaweeds (Mann 1973).

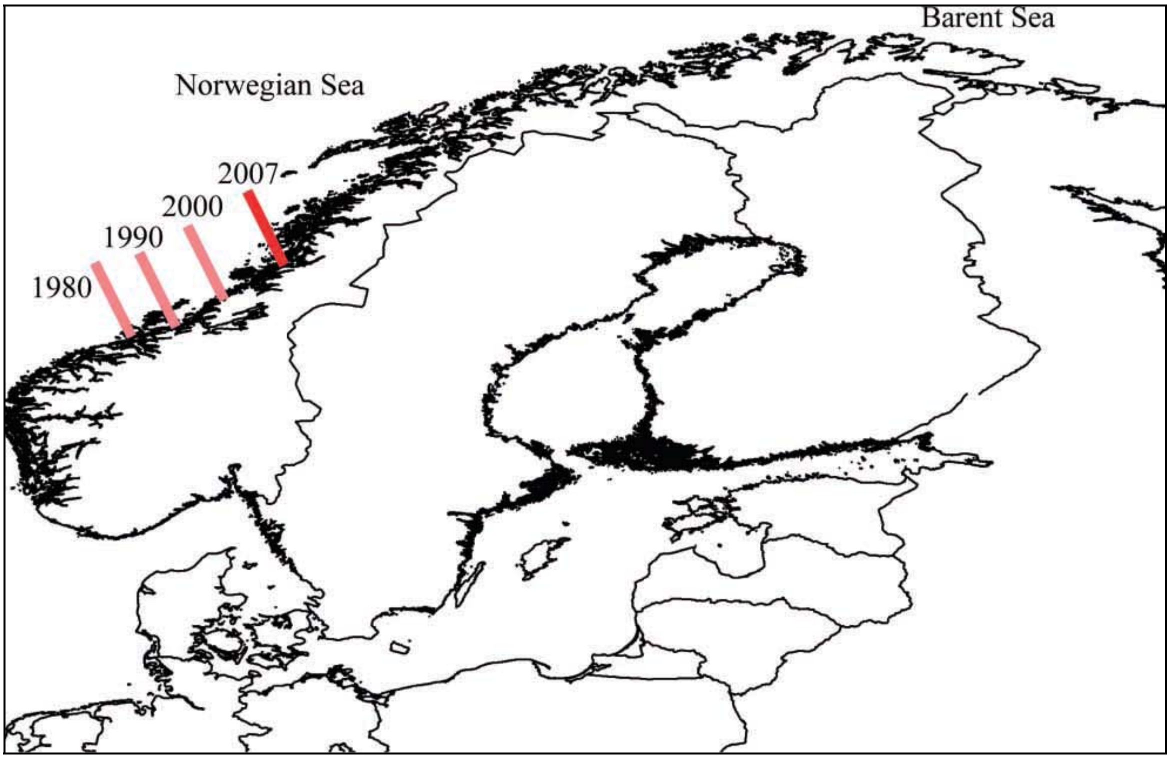


Figure 1.2 Movement of the border between kelp-dominated areas and barren ground in mid-Norway from 1980 until 2007. Barren grounds areas have been reduced northwards. Source: Norderhaug and Christie 2009.

1.2. The green sea urchin *Strongylocentrotus droebachiensis*

The green sea urchin *Strongylocentrotus droebachiensis* (Figure 1.3), is an echinoderm belonging to the class Echinoidea, and is the most widely distributed member of the family Strongylocentrotidae (Mortensen 1943). This species has a broad arctic-boreal distribution (Mortensen 1943; Jensen 1974) and is found over a considerable range of latitudes (Munk 1992). *S. droebachiensis'* distribution and its associated biota are influenced by a set of geographic and environmental factors and parasite prevalence in the urchins (Sivertsen 1997b). In the Northeast Atlantic, it extends across Iceland, the Shetland Islands and northern Scotland, Norway, Denmark, and the west coast of Sweden, occurring also in the Barents Sea, the White Sea, and the Kara Sea (Scheibling and Hatcher 2001). *S. droebachiensis* is commonly present on rocky sublittoral substrata (Himmelman and Steele 1971) such as bedrock outcrops, boulders, and cobbles (Himmelman 1986; Scheibling and Raymond 1990), ranging from 0 to 300 m in depth, but is most commonly present in the shallow subtidal area from 0 to 50 m (Jensen 1974).

Figure 1.3 Photo of the green sea urchin *Strongylocentrotus droebachiensis*. Photo: Stein Fredriksen.

S. droebachiensis has the ability to adjust its metabolism and activity level to compensate for seasonal variations in sea temperature (Percy 1972) which can vary from -1 to 20ºC during the year (Scheibling and Henningar 1997). However, above 10ºC this species is not able to develop normally and this temperature represents an upper limit for larval development (Stephens 1972).

The green sea urchin is an omnivore with food preferences strongly influenced by natural environmental factors such as temperature, seabed topography, wave action, competition and predation (Himmelman and Nedelec 1990; Vadas 1990; Scheibling 1996; Scheibling and Hatcher 2001). Keats *et al.* (1984) reported that *Strongylocentrotus* spp. showed a marked preference for large, dominating kelps species such as *Saccharina longicruris* (Bachelot de la Pylaie) Kuntze and *Laminaria digitata* (Hudson) J.V. Lamouroux, but avoided *Agarum cribrosum* (Bory de Saint-Vicent). When available, *S. droebachiensis* may also ingest animal tissue (Himmelman and Steele 1971; Duggins 1981; Scheibling and Hatcher 2001).

Sea urchins of different age groups use different type of habitats. Juveniles up to 2 years old utilize cryptic behaviour, often dwelling predominantly under a crust of calcareous algae or rock crevices (Propp 1977; Himmelman 1986). In order to maintain high growth rates, these individuals either need adequate supplies of benthic macroalgae or receive enough of the periodically abundant drift algae (Munk 1992) such as kelps from the adjacent kelp beds (Himmelman and Steele 1971; Meidel and Scheibling 1998a). Once they shift their cryptic behaviour to a mobile behaviour and become exposed to predators, they are able to obtain more food (Himmelman 1986) by using chemodetection (Sloan and Campbell 1982; Mann *et al*. 1984). In addition, as mobility increases with increased size, large adults are able to cover larger distances, up to five meters a day in their search for favourable resources (Dumont *et al*. 2004; Dumont *et al*. 2006).

It is this high mobility, together with its preference for kelps, which allows this species to have a marked influence on the distribution and abundance of benthic macroalgae, particularly laminarian kelps (Chapman and Johnson 1990).

S. droebachiensis has one major breeding period in the spring (Miller and Mann 1973) with spawning observed to occur from March through July, usually correlated with the spring phytoplankton bloom period (Himmelman 1975), or up to 6-8 weeks after such a bloom (Munk 1992). According to Hinegardner (1969), the settlement of sea urchins involves both the attachment of a planktonic larva to a suitable substrate and the metamorphosis into a benthic juvenile. Recruitment has been reported to be variable between years and areas (Ebert 1983). For example, other authors (McNaught 1999; Balch and Scheibling 2000) observed annual settlement and recruitment of *S. droebachiensis* in both barren grounds and kelp site populations. The recruitment rate is usually affected by physical factors such as wind driven currents and upwelling (Shanks 1995) and larval supply and mortality (Cameron and Schroeter 1980). In order to increase survival, larvae are able to delay metamorphosis until a suitable substrate is found (Strathman 1978). Once metamorphosis occurs, juveniles increase their diameter by 5 to 17 mm annually (Grieg 1928). However, if juvenile urchin populations are very dense they only grow 1 to 2 mm annually (Himmelman *et al*. 1983a).

Growth characteristics differ between barren and kelp areas and from one year to another (Pearse and Pearse 1975). These differences have been attributed to food availability (Swan 1961; Himmelman 1986). However, populations of *S. droebachiensis* do not starve and die, or migrate after kelp bed destruction, at least within the first 4 years (Lang and Mann 1976). The populations found in barren grounds are highly dense and consist mainly of smaller sized individuals with low growth rates and high mortality rates (Lang and Mann 1976; Himmelman 1978; Wharton and Mann 1981; Himmelman 1986; Munk 1992; Sivertsen and Hopkins 1995). The persistence of high population densities at barren areas is thought to be maintained by regular recruitment to the adult sea urchin population to compensate for the high mortality (Christie and Leinaas Unpublished data). Conversely, stable sea urchin populations present in kelp forests often consist of larger individuals (Wharton and Mann 1981) and show higher growth rates (10 to 20 mm annually in adults according to Swan 1961) and steady recruitment and mortality (Lang and Mann 1976). Reliable age information for size classes for kelp and barren habitats, however, is lacking (Himmelman 1986), as growth lines are often difficult interpret (Breen and Adkins 1976) and particularly difficult to recognize for slow-growing juveniles (Himmelman 1986).

During the last three decades sea urchins have been harvested because of their highly valuable gonads (Sivertsen *et al*. 2008). The extensive harvesting has lead to overexploitation in some areas of the world, (Keesing and Hall 1998; Botsford *et al*. 2004). In order to protect the decimated populations, a large effort has been devoted to manage sea urchin aquaculture with complete life cycles (Robinson 2004). In Norway, only small scale fisheries has taken place on *S. droebachiensis* (Sivertsen *et al*. 2008).

1.3. Kelp Forests

Kelps in the order Laminariales are the primary species forming the canopy, which provide a three dimensional habitat in the sublittoral (Harrold and Pearse 1987). According to Mann (1973), zonation of kelps seems to be determined by both environmental factors (e.g. light, temperature and wave action) and competitive interactions (e.g. grazing of sea urchins). Along the Norwegian coast the most dominant species is *Laminaria hyperborea* which forms beds distributed from the low tide level down to depths of about 20 m. (Rinde *et al*. 1998).

Kelps have a major impact on local ecology, as they are able to absorb wave action, provide new physical habitat for organisms living above the benthic boundary layer (Steneck *et al*. 2002) and concentrate and magnify secondary production, supporting complex food webs in coastal zones (Duggins *et al*. 1989; Christie *et al*. 2003). These forests are among the most productive biotic assemblages, either marine or terrestrial (Mann 1973) and have rapid growth even at high densities (Mann 1982; Abdullah and Fredriksen 2004). Kelp bed productivity in many coastal areas equals or even exceeds phytoplankton production, supporting diverse benthic communities (Dunton *et al*. 1982). A large part of this production may be transferred to other ecosystems such as beaches (Harrold and Pearse 1987) or deeper water areas (Vetter 1998). However, this enormous production also supports many of the animals within the forest as well, providing the forest with a trophic structure within which different consumers can be found (Harrold and Pearse 1987; Norderhaug *et al*. 2003). Therefore, kelp forests are considered ecologically valuable systems for providing many species with a refuge from predators, a nursery area for juveniles and as a feeding grounds (Keats *et al*. 1987). They are also economically important, as they are harvested worldwide as a source of alginate (Lorentsen *et al*. 2010). *Laminaria hyperborea* has a high economical value in Norway and 160,000 tons (fresh weight/year) are harvested by trawlers as a source of alginate (Fosså and Sjøtun 1993).

1.4. The object of this investigation

This study focus on the size, age, growth and mortality of green urchin populations (*Strongylocentrotus droebachiensis*) in kelp forests and on barren grounds in the southern part of the barren area (Vega) where sea urchins are retreating and kelp forests are recovering and in the northern part of the barren ground area (Hammerfest) where no kelp recovery has been observed. The object of this project was to determine whether there are differences in size, age, growth, and mortality between the green urchin populations in the different stations in kelp and barren habitats in Hammerfest, and in barren habitats in Hammerfest and Vega.

This was done by analyzing the size, age, growth and mortality of the sea urchins at both studied areas and habitats and comparing the results obtained to previous published studies.

2. MATERIALS AND METHODS

2.1. Location

Two areas, Vega and Hammerfest, on the Norwegian coast were selected for this investigation (Figure 2.1). Vega is one of the areas where the overgrazing phenomenon was first observed (Christie and Leinaas Unpublished data). However, currently this region is characterized by a reduced sea urchin population and a re-establishment of kelp forests (Christie *et al*. 1995). Hammerfest, alternatively, is located in the northernmost part of Norway. In this region the sea urchin populations are dense and no re-establishment of kelp forests has been observed so far.

Table 2.1 Date and location of the different sampling stations.

Area	Location	Habitat	Station	Sampling month	Coordinates (WGS 1984)	Densities (ind/m^2) *
Hammerfest	Molvik	kelp	Molvik kelp	May 2010	70°39'10.82"N 23°38'10.69"E	50
		barren	Molvik barren	May 2010	70°39'04.12"N 23°38'25.36"E	25.2
	Rypklubbskjæret	kelp	Rypklubbskjæret kelp	May 2010	70°37'58.29"N 23°35'49.43"E	22
		barren	Rypklubbskjæret barren	May 2010	70°37'52.51"N 23°35'37.72"E	58
	Finnøy	kelp	Finnøy kelp	May 2010	70°37'37.19"N 23°37'51.42"E	2.4
		barren	Finnøy barren	May 2010	70°37'39.14"N 23°38'19.38"E	45.6
Vega	1	barren	Vega 1	May 2010	65°430'7.66"N 11°51'11.02"E	17.2
	2	barren	Vega 2	May 2010	65°44'42.39"N 11°43'24.17"E	11.2
	3	barren	Vega 3	October 2009	65°45'57.79"N 11°41'46.26"E	4.8

* Densities obtained for May 2008.

Figure 2.1 Map showing the stations in Hammerfest (right) and Vega (left). Image: Google Maps.

2.2. Sampling and data collection

In total, 12 stations (3 in kelp forests and 3 in barren grounds in Hammerfest and in Vega) were sampled between the 3rd and 6th of May 2010, with the exception of Vega 3 which was sampled in October 2009 (Table 2.1). However, no sea urchins were found at the 3 kelp stations in Vega and thus data from those stations were not included in this study.

At least 200 individuals were collected in each station by scuba diving using frames of 50 cm x 50 cm (0.25 m^2). In order to sample a representative part of the population, the frames were dropped randomly on the bottom and all urchins inside the frame were collected. This procedure was repeated until a total of at least 200 individuals were obtained in each station, and all sea urchins were collected in the last frame. All individuals were put in polystyrene boxes and transported alive to the laboratory where the measurement and cleaning process took place.

2.3. Size measurement, age, growth and mortality determination

In the laboratory, the diameter of each urchin was measured using vernier calipers to the nearest 1 mm. Age determination was performed by counting growth zones in the interambulacral plates, according to the methodology described by Jensen (1969, with some modification). The individuals were cut in half with pruning shears. One half was cleaned to remove as much organic matter as possible using forceps and brush followed by rinsing with alcohol. The cleaned halves were heated in an oven at 60º for at least 24 hours, and then a small amount of vegetable oil was added in order to make the growth rings visible. Growth zones in the interambulacral plates were observed under a magnifying microscope using reflected light. The growth rings obtained by this method have been described as annual rings (Jensen 1969). As described by Pearse and Pearse (1975) under conditions of reflected light, alternating dark (translucent, representing slower summer growth) and light (opaque, representing faster winter growth) zones can be seen (Figure 2.2). In addition, some plates also exhibited weakly pigmented lines, probably representing periods of food deprivation, but only the clearly detectable bands were recorded for growth analysis. This method is quite reliable for *Strongylocentrotus droebachiensis* between 20 and 50 mm in diameter (Meidel and Scheibling 1998b; Vadas *et al*. 2002), whereas in larger individuals it may lead to an under estimation of their age (Russell and Meredith 2000).

Not all of the sea urchins collected from stations in Hammerfest and Vega showed such natural growth lines in their interambulacral and ambulacral plates. Individuals with growth zones that were not sufficiently visible were considered unsuitable for usage in age determination and discarded in growth distribution.

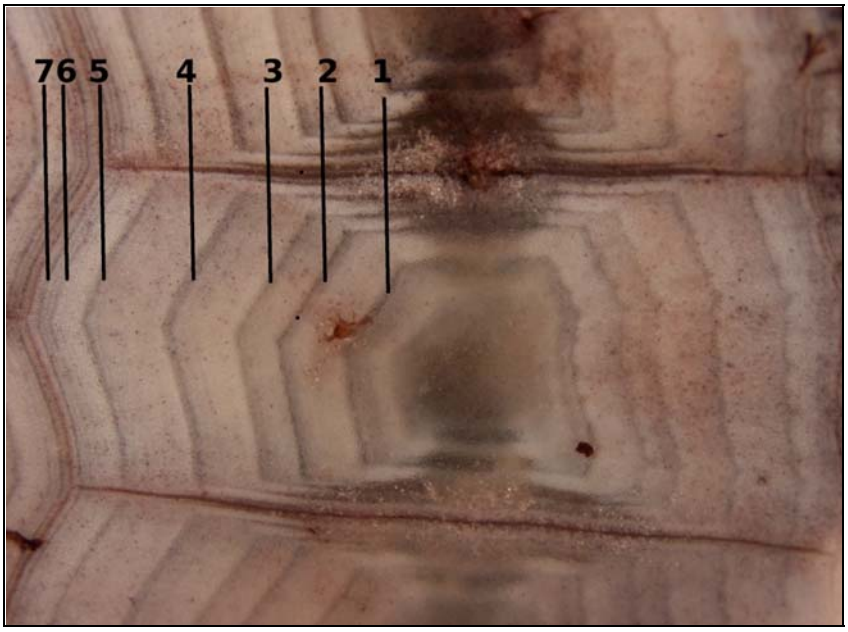


Figure 2.2 A photo of a sea urchins' interambulacral plate. The alternating growth bands (opaque and translucent) can be seen. Numbers indicate translucent bands (7 years old).

Growth curves were obtained by fitting the data of each population to asymptotic (Gompertz) growth curves. The curves were calculated from the Gompertz equation (Winsor 1932),

$$y = L_{\infty}e^{-e^{(k-xt)}}$$

where **L∞** is the upper asymptote, **k** is the lower asymptote, **x** is the growth rate of the population and t is the age of the individuals. The parameters a, b and c were estimated by using SOLVER in EXCEL. The growth rates were calculated from linear regression of individuals between 1 and 5 years old, as those age classes showed linear growth in the fitted Gompertz growth curves.

To calculate mortality rates, catch curves based on distribution among age classes were used. The annual instantaneous mortality rate (Z) is the slope of the line by linear regression of ln n.

2.4. Statistical analyses

Statistical analyses were performed with SPSS software. Nested Analysis of Variance tests (Nested ANOVA, or Hierarchical ANOVA) were used to test differences in size and age structure and upper asymptotes (individuals ≥ 6 years) for individuals between localities and habitats. This statistical analysis was chosen because this experiment has one random factor ("habitat" when comparing stations within Hammerfest, or "area" when comparing barren grounds between Hammerfest and Vega) at the top of the hierarchy and a second one nested within it ("location"). The interaction term; habitat * location (when comparing Hammerfest stations) and area * location (when comparing stations with barren habitats), is referred as "station".

As Nested Analysis of Covariance (Nested ANCOVA) is a method based on linear regression, this was the analysis chosen to test differences in growth (individuals between 1 to 5 years old) and mortality rates (performing analyses on ln at age data for individuals ≥ 1 year) between stations and habitats. When analyzing growth, size was chosen as the response factor and age as the covariant. When analyzing the mortality rate, ln of the number of individuals was chosen as the response factor and age as the covariant.

Tukey's tests were performed following all ANOVA and ANCOVA analyses to identify individual differences among stations.

3. RESULTS

In total 1888 sea urchins were sampled (Table 3.1). The size (measured as the diameter in mm) was measured on all individuals. Selecting the interambulacral plates with visible rings reduced the data to 800 individuals that could be aged and thus used for establishing the growth curve and mortality rates. The number of individuals being aged varied between 104 and 168 at the nine stations.

Table 3.1 Statistical parameters for sizes at the different stations.

Station	N	Mean (mm)	95%CL (mm)	Median (mm)	Variance	SD (mm)	Min (mm)	Max (mm)	Range (mm)
Molvik kelp	214	22.50	1.49	20.00	122.03	11.05	7	72	65
Molvik barren	238	30.87	1.41	30.59	121.53	11.02	4	61	57
Rypklubbskjæret kelp	204	40.52	2.48	46.00	321.33	17.93	8	73	65
Rypklubbskjæret barren	178	43.29	2.59	48.00	305.96	17.43	7	70	63
Finnøy kelp	221	31.05	1.95	30.00	215.49	14.68	6	73	67
Finnøy barren	210	40.67	1.90	39.00	191.53	13.84	8	71	63
Vega 1	205	36.32	1.03	37.00	55.88	7.47	13	54	41
Vega 2	201	32.99	1.28	33.00	83.47	9.13	15	59	44
Vega 3	217	33.44	2.35	29.00	306.69	17.51	9	70	61
Hammerfest kelp	639	31.21	1.28	27.00	270.48	16.45	6	73	67
Hammerfest barren	626	37.68	1.18	37.00	226.38	15.05	4	71	67
Vega barren	623	34.24	0.98	34.00	153.83	12.40	9	70	61
Total	1888								

3.1. Size structure

The main difference in size structure was observed between stations (e.g. similarity between Rypklubbskjæret kelp and Rypklubbskjæret barren and Finnøy kelp and Finnøy barren) rather than between habitats (e.g. Molvik kelp and Molvik barren). Maximum sea urchin sizes (73 mm) were obtained for Rypklubbskjæret kelp and Finnøy kelp. In Hammerfest, the size range was between 6 and 73 mm at kelp stations and from 4 to 71 mm in barren stations. A similar range was observed in the barren habitats of Vega.

Figure 3.1 shows the size-frequencies. At all stations, large size ranges were observed (± 60 mm) with the exception of Vega 1 and Vega 2 that only exhibited a range of ± 40 mm. In Hammerfest, the stations at Molvik and Finnøy had a unimodal distribution (Figure 3.1). However, while the barren stations were more or less symmetric, the kelp stations were skewed to the left. This means that small individuals are more frequent in kelp habitats. On the other hand, both stations in Rypklubbskjæret presented a similar bimodal and symmetrical distribution. Notable differences were also found between the stations in Vega. While Vega 1 and 2 had a unimodal distribution, Vega 3 was bimodal. Further, Vega 2 and 3 had a symmetric distribution, whereas Vega 1 was slightly skewed to the left.

When pooling the data for the different habitats in the 2 areas, it was observed that small individuals (less than 10 mm) were more frequent at the barren habitats in Hammerfest. For the larger individuals (over 10 mm) similar distribution was observed for the barren habitats in Hammerfest and Vega. Those areas were dominated by medium-sized individuals (between 25 and 50 mm). However, kelp habitats in Hammerfest had a different distribution as they were dominated by smaller individuals (between 10 and 25 mm).

There was a clear difference in the mean sizes when comparing all stations (Table 3.2.a). Nested ANOVAs indicated no significant effects of type of habitat and location for size distribution within Hammerfest; however, the station (interaction) term indicated significant differences ($ANOVA_{F= 6.355}$, df = 1259, P < 0.01). 95% C.L. plots (Figure 3.2.a) showed that stations formed three significant different groups: Molvik kelp had the smallest average size, Molvik barren and Finnøy kelp formed an intermediate group and the largest average sizes were found in Rypklubbskjæret kelp, Rypklubbskjæret barren and Finnøy barren. This was confirmed by multiple comparisons Tukey's tests (Table 7.2).

Significantly larger sizes were also found for the station term for *Strongylocentrotus droebachiensis* in barren habitats in Hammerfest and the ones in Vega ($ANOVA_{F= 41.940}$, df = 1243, P < 0.01; Table 3.2.b). 95% C.L. plots (Figure 3.2.b) and multiple comparison Tukey's test (Table 7.3) showed that Molvik barren was significant smaller that Rypklubbskjæret barren, Finnøy barren and Vega 1.

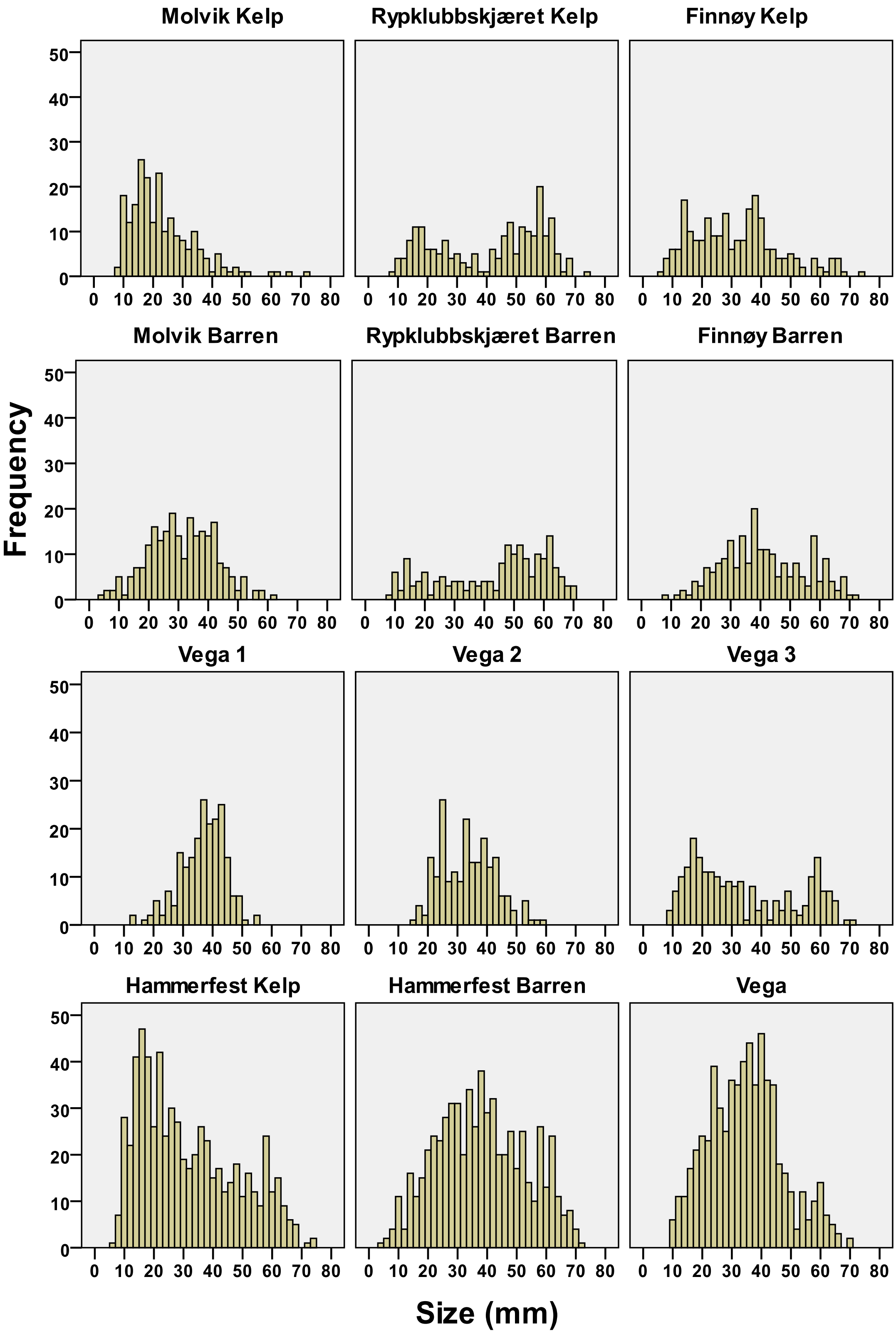


Figure 3.1 Histograms showing size-frequency distributions for all 9 stations in Hammerfest and Vega and for the pooled data in kelp and barren habitats in Hammerfest and barren habitats in Vega.

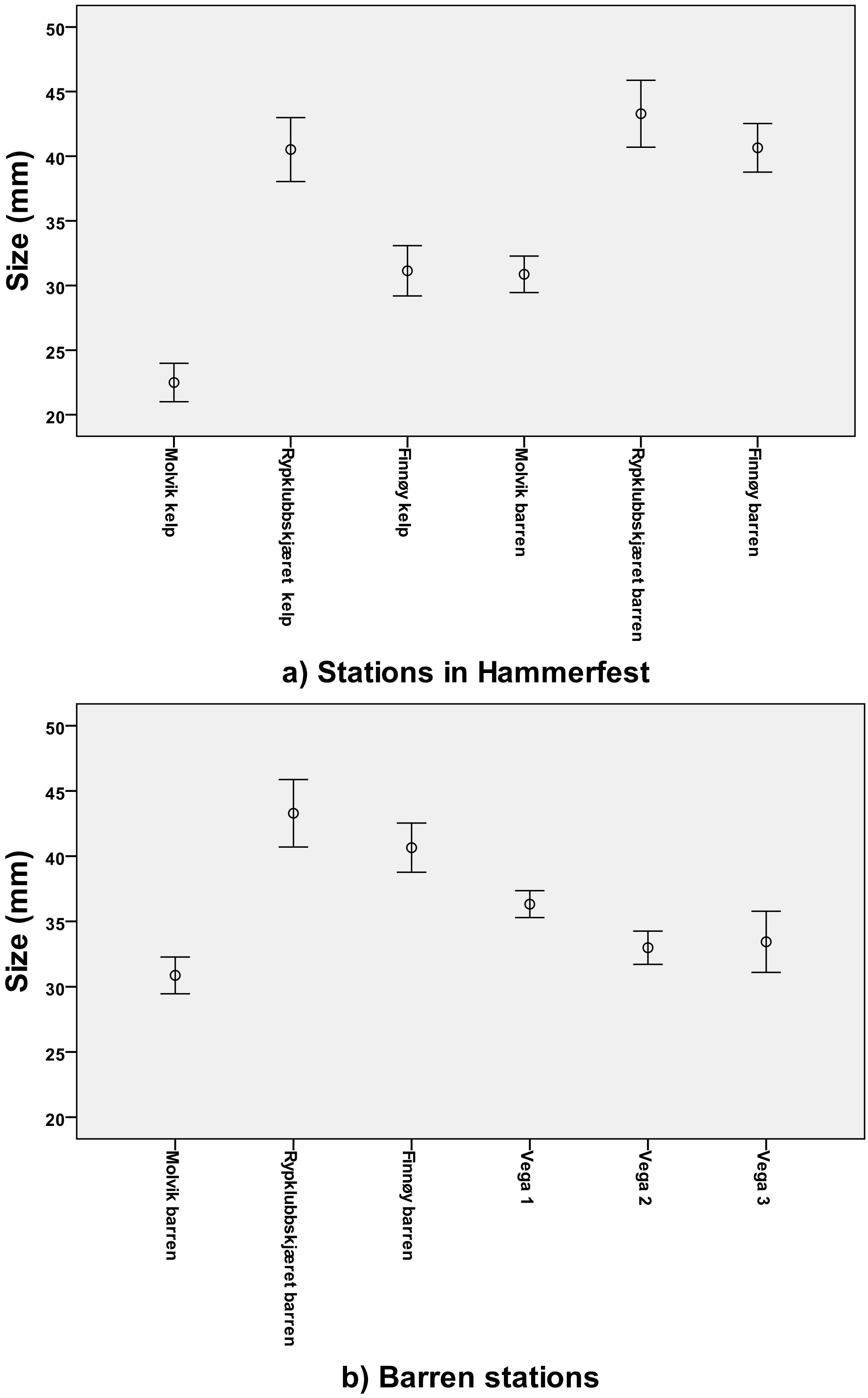


Figure 3.2 Mean size-diameter of sea urchins *S. droebachiensis* for a) all stations at Hammerfest and b) all barren stations in Hammerfest and Vega, plotted with a 95% CL of the mean.

Table 3.2 One-way nested ANOVA test results for size for a) all stations at Hammerfest and b) all barren stations in Hammerfest and Vega.

	Source		Type III SS	df	MS	F	Sig.
a) Hammerfest kelp vs barren	Habitat	Hypothesis	14997,106	1	14997,106	11,383	,078
		Error	2637,254	2,002	1317,515[b]		
	Location	Hypothesis	49171,849	2	24585,924	18,619	,051
		Error	2640,979	2	1320,489[c]		
	Station[b]	Hypothesis	2640,979	2	1320,489	6,355	,002[a]
		Error	261618,578	1259	207,799[d]		
b) Barrens in Vega vs barrens in Hammerfest	Area	Hypothesis	5007,559	1	5007,559	,684	,495
		Error	14634,325	2,000	7316,360[b]		
	Location	Hypothesis	4709,707	2	2354,854	,321	,757
		Error	14665,563	2	7332,781[c]		
	Station[c]	Hypothesis	14665,563	2	7332,781	41,940	,000[a]
		Error	217326,826	1243	174,841[d]		

[a] indicates significance at $\alpha = 0.05$.
[b] Station refers to Habitat * Location interaction
[c] Station refers to Area * Location interaction

3.2. Age structure

Differences in age structure were observed between local areas (e.g. Molvik kelp and Finnøy kelp and between Molvik barren and Finnøy barren) and between the type of habitat (e.g. Finnøy kelp and Finnøy barren) (Table 3.3).

The age of the sea urchins in this investigation varied between 0 and 14 years, and the age distribution varied among the stations. For all the stations except Rypklubbskjæret barren, the age-frequencies were unimodal (Figure 3.3), and skewed to the left indicating dominance of young year classes. On the other hand, Rypklubbskjæret barren did not contain particular dominant year classes during recent years. Half of the individuals (i.e. the median) were less than 4 years among all the aged individuals. At Rypklubbskjæret barren the median was 6, but dropped to 2 at Molvik kelp. Also the maximum age varied among the stations (Table 3.3). A maximum age of 14 years was observed in Rypklubbskjæret barren and Finnøy barren, whereas the lowest maximum age was found in Vega 2 (7 years). Although not very frequent, juvenile individuals (< 2 years) were found at all stations.

When pooling the data for the different areas, it is interesting to note that, although the type of habitat was different, the general population structure and density were very similar. There was a notable dominance in the year classes between 2 and 6 years and a low frequency of older year classes (> 6 years).

Table 3.3 Statistical parameters for age at the different stations.

Station	N	Mean (mm)	95%CL (mm)	Median (mm)	Variance	SD (mm)	Min (mm)	Max (mm)	Range (mm)
Molvik kelp	104	2.42	0.28	2.00	2.05	1.43	0	12	12
Molvik barren	164	3.27	0.20	3.00	1.82	1.35	1	9	8
Rypklubbskjæret kelp	168	4.01	0.38	4.00	6.13	2.47	1	12	11
Rypklubbskjæret barren	137	5.69	0.59	6.00	12.18	3.49	1	14	13
Finnøy kelp	147	3.07	0.27	3.00	2.85	1.69	0	10	10
Finnøy barren	134	4.71	0.37	4.00	4.60	2.14	1	14	13
Vega 1	157	4.16	0.25	4.00	2.43	1.56	1	9	8
Vega 2	153	3.22	0.21	3.00	1.78	1.33	1	7	6
Vega 3	133	5.20	0.58	4.00	11.47	3.39	1	13	13
Hammerfest kelp	419	3.29	0.20	3.00	4.36	2.09	0	12	12
Hammerfest barren	435	4.48	0.25	4.00	6.94	2.63	1	14	13
Vega barren	443	4.15	0.22	4.00	5.52	2.35	1	13	12
Total	1297								

Table 3.4 Nested ANOVA test results for age for a) all stations at Hammerfest and b) all barren stations in Hammerfest and Vega.

	Source		Type III SS	df	MS	F	Sig.
a) Hammerfest kelp vs barren	Habitat	Hypothesis	553.262	2	276.631	18.954	.050
		Error	29.190	2	14.595		
	Area	Hypothesis	402.804	1	402.804	27.643	.034[a]
		Error	29.192	2.003	14.571		
	Station[b]	Hypothesis	29.190	2	14.595	2.936	.054
		Error	4215.981	848	4.972		
b) Barren grounds Vega vs Hammerfest	Area	Hypothesis	28.901	1	28.901	.117	.765
		Error	493.777	2.000	246.858		
	Location	Hypothesis	229.924	2	114.962	.464	.683
		Error	495.067	2	247.534		
	Station[c]	Hypothesis	495.067	2	247.534	45.649	.000[a]
		Error	4728.408	872	5.422		

[a] indicates significance at $\alpha = 0.05$.
[b] Station refers to Habitat * Location interaction.
[c] Station refers to Area * Location interaction.

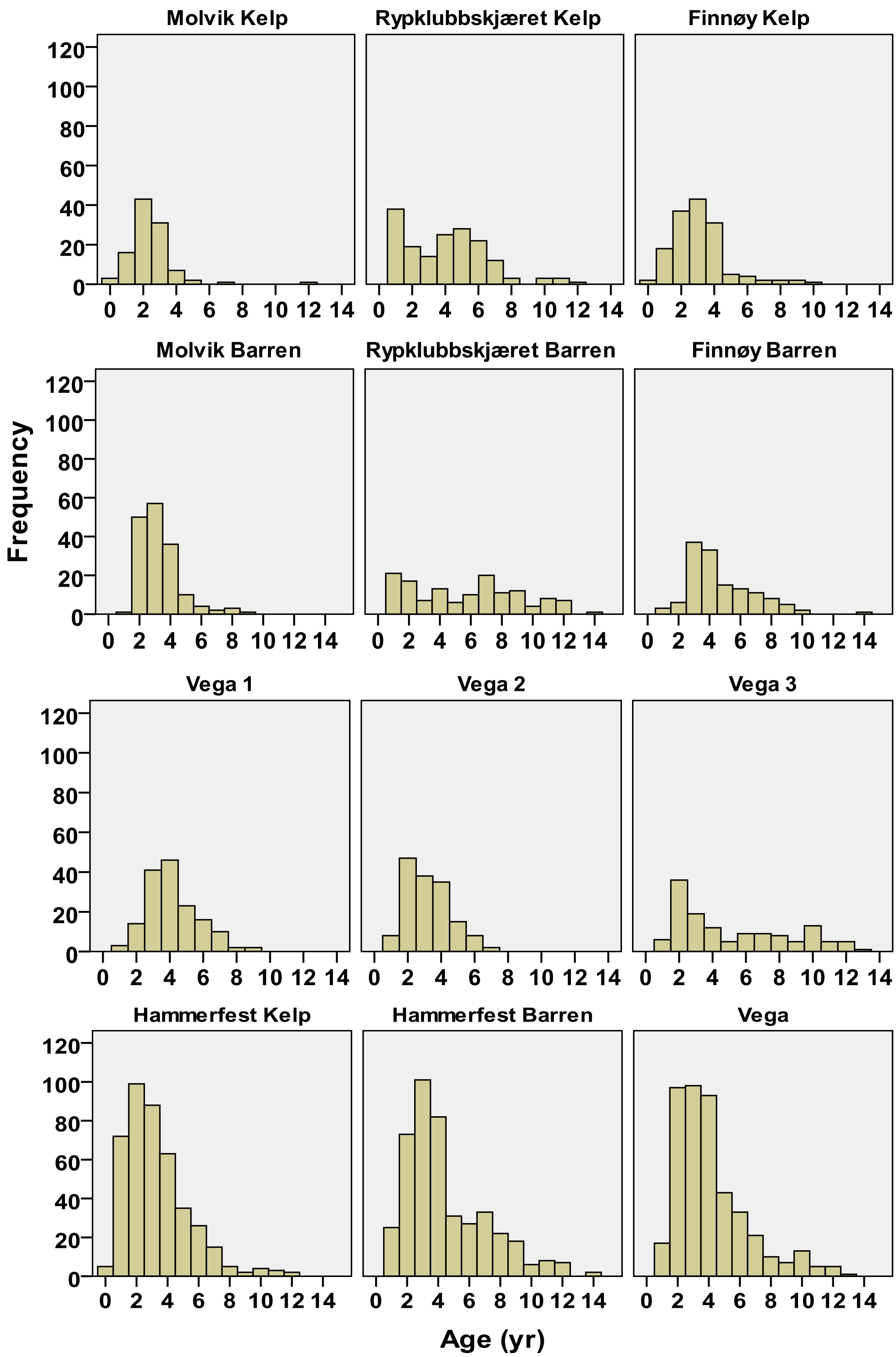
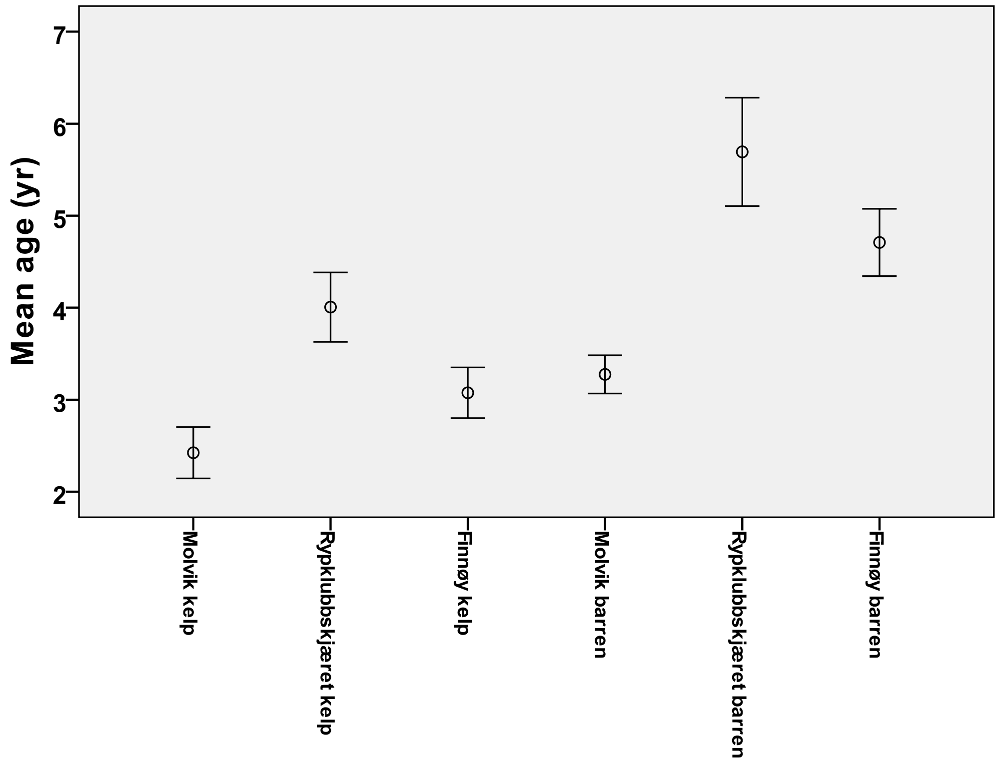
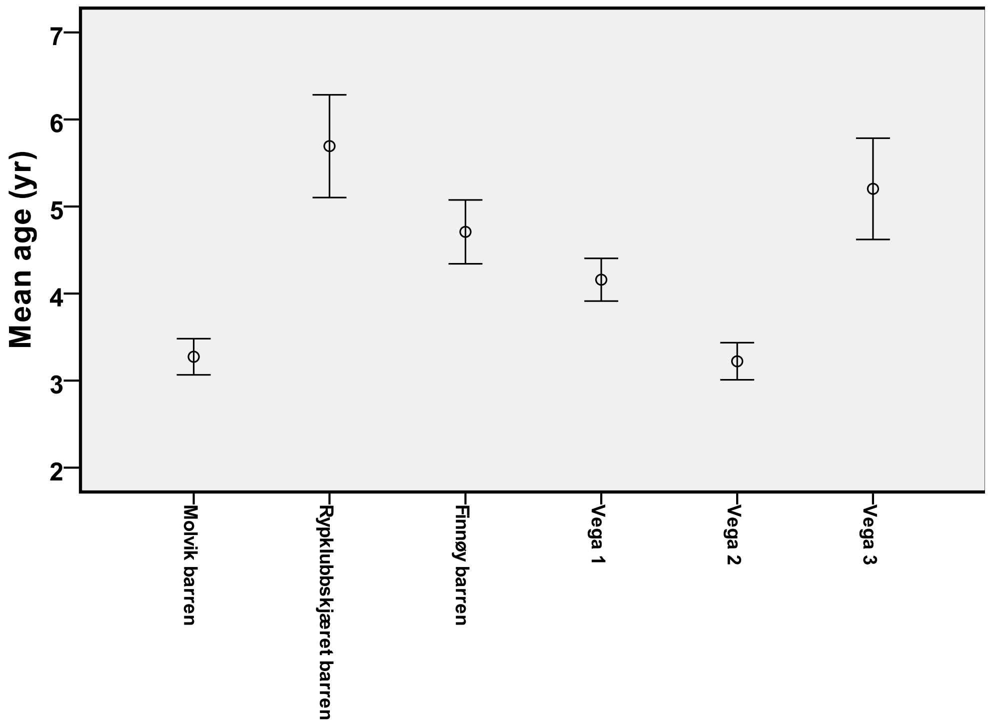


Figure 3.3 Histograms showing age-frequency distributions for all 9 stations in Hammerfest and Vega and for the pooled data in kelps and barren habitats in Hammerfest and barren habitats in Vega.



a) Stations in Hammerfest



b) Barren Stations

Figure 3.4 Mean age of sea urchins *S. droebachiensis* for a) all stations at Hammerfest and b) all barren stations in Hammerfest and Vega, plotted with a 95% CL of the mean.

Table 3.5 Nested ANOVA test results for size at three different year classes (3, 4 and 5) for a) all stations at Hammerfest and b) all barren stations in Hammerfest and Vega.

a) Hammerfest kelp vs barren

Age class	Source		Type III SS	df	MS	F	Sig.
3	Habitat	Hypothesis	36.994	1	36.994	1.075	.489
		Error	34.427	1	34.427		
	Area	Hypothesis	90.429	2	45.214	.995	.612
		Error	34.850	.767	45.423		
	Station[b]	Hypothesis	34.427	1	34.427	2.710	.101
		Error	2337.919	184	12.706		
4	Habitat	Hypothesis	289.434	1	289.434	1.308	.370
		Error	446.286	2.017	221.224		
	Area	Hypothesis	12.170	2	6.085	.026	.975
		Error	474.447	2	237.223		
	Station[b]	Hypothesis	474.447	2	237.223	17.786	.000[a]
		Error	1853.983	139	13.338		
5	Habitat	Hypothesis	152.347	1	152.347	1.088	.402
		Error	292.275	2.088	139.966		
	Area	Hypothesis	105.451	2	52.726	.339	.747
		Error	311.167	2	155.584		
	Station[b]	Hypothesis	311.167	2	155.584	6.226	.003[a]
		Error	1499.324	60	24.989		

b) Barren grounds Hammerfest vs Vega

Age class	Source		Type III SS	df	MS	F	Sig.
3	Area	Hypothesis	46.522	1	46.522	2.749	.211
		Error	43.645	2.579	16.925		
	Location	Hypothesis	66.760	2	33.380	1.900	.345
		Error	35.131	2	17.566		
	Station[c]	Hypothesis	35.131	2	17.566	1.317	.270
		Error	2574.007	193	13.337		
4	Area	Hypothesis	6.103	1	6.103	.063	.825
		Error	197.506	2.037	96.981		
	Location	Hypothesis	342.390	2	171.195	1.691	.372
		Error	202.468	2	101.234		
	Station[c]	Hypothesis	202.468	2	101.234	5.865	.003[a]
		Error	2917.021	169	17.260		
5	Area	Hypothesis	28.657	1	28.657	1.477	.338
		Error	43.119	2.222	19.406		
	Location	Hypothesis	328.066	2	164.033	8.647	.104
		Error	37.938	2	18.969		
	Station[c]	Hypothesis	37.938	2	18.969	.561	.573
		Error	2300.935	68	33.837		

[a] indicates significance at $\alpha = 0.05$.
[b] Station refers to Habitat * Location interaction.
[c] Station refers to Area * Location interaction.

Nested ANOVA indicated significant effects of habitat for age structure within Hammerfest; however, the habitat and the station interaction term were not significant ($ANOVA_{F=2.936}$, df= 848, P = 0.054; Table 3.4.a). The same three groups as obtained for sizes were found: Molvik kelp had the lowest average age, Molvik barren and Finnøy kelp formed an intermediate group and the largest average ages were found in Rypklubbskjæret kelp, Rypklubbskjæret barren and Finnøy barren (Figure 3.4.a; Table 7.4).

However, when comparing the barren stations of Hammerfest and Vega (Figure 3.4.b) a significant difference was found for the station interaction term ($ANOVA_{F=45.649}$, df = 872, P < 0.01; Table 3.4.b). Figure 3.4.b showed that stations formed two significant different groups based on age: Molvik barren and Vega 2 had the lowest average age, and the highest averages were found for Finnøy barren, Rypklubbskjæret barren and Vega 1 and 3. This was confirmed by multiple comparisons Tukey's tests (Table 7.5).

The results of Nested ANOVA for 3, 4 and 5 year classes (Table 3.5) did not indicate significant main effects of habitat and location for sizes for within Hammerfest and within barren stations. For Hammerfest, the station interaction term was significant for the year classes 4 and 5, and not for the 3 year class. However for barren stations significant differences were obtained only for the 4 year class.

3.3. Growth

Growth of *Strongylocentrotus droebachiensis* was higher in kelp forests (9.3 mm $year^{-1}$) than on barren habitats (8.2 mm $year^{-1}$ and 6.6 mm $year^{-1}$ for Hammerfest and Vega respectively). Diameter as a function of number of growth rings (age) for individuals between 1 and 5 years old for pooled samples are shown in Figure 3.5. Nested ANCOVAs indicated no significant effects for habitat and location for growth rate of *S. droebachiensis* within Hammerfest; however, the station (interaction) term indicated the differences were significant ($ANCOVA_{F=21.632}$, df = 662, P < 0.01; Figure 3.5; Table 3.7.a). Individual linear regressions (Table 3.6; Figure 7.1) and Tukey's Multiple Comparison test showed that *S. droebachiensis* from the station Rypklubbskjæret kelp presented the fastest growth within the 6 stations in Hammerfest, whereas the slowest was observed for Finnøy barren (Table 7.8). The same results were observed for growth rates in barren stations at Hammerfest and Vega, where significant differences were observed for the station (interaction) term ($ANCOVA_{F=9.445}$, df = 653, P < 0.01; Figure 3.5; Table 3.7.b). Fastest growth occurred at Vega 3 within all barren grounds while the slowest growth occurred at Vega 1 and 2 (Table 3.6, Figure 7.1; Table 7.9).

Table 3.6 Growth and mortality parameters for all the stations and areas.

Station	**Growth rate (mm/yr)**	**Upper asymptote (L_∞) (mm)**	**Instantaneous Mortality (Z)**
Molvik kelp	8.6	67.85	0.38
Molvik barren	7.9	55.21	0.62
Rypklubbskjæret kelp	9.7	64.55	0.30
Rypklubbskjæret barren	7.9	65.64	0.13
Finnøy kelp	8.5	67.80	0.50
Finnøy barren	7.2	69.73	0.26
Vega 1	6.4	43.74	0.41
Vega 2	6.4	47.76	0.61
Vega 3	8.1	62.52	0.19
Hammerfest kelp	9.3	66.64	0.47
Hammerfest barren	8.2	62.81	0.30
Vega	6.6	63.85	0.37

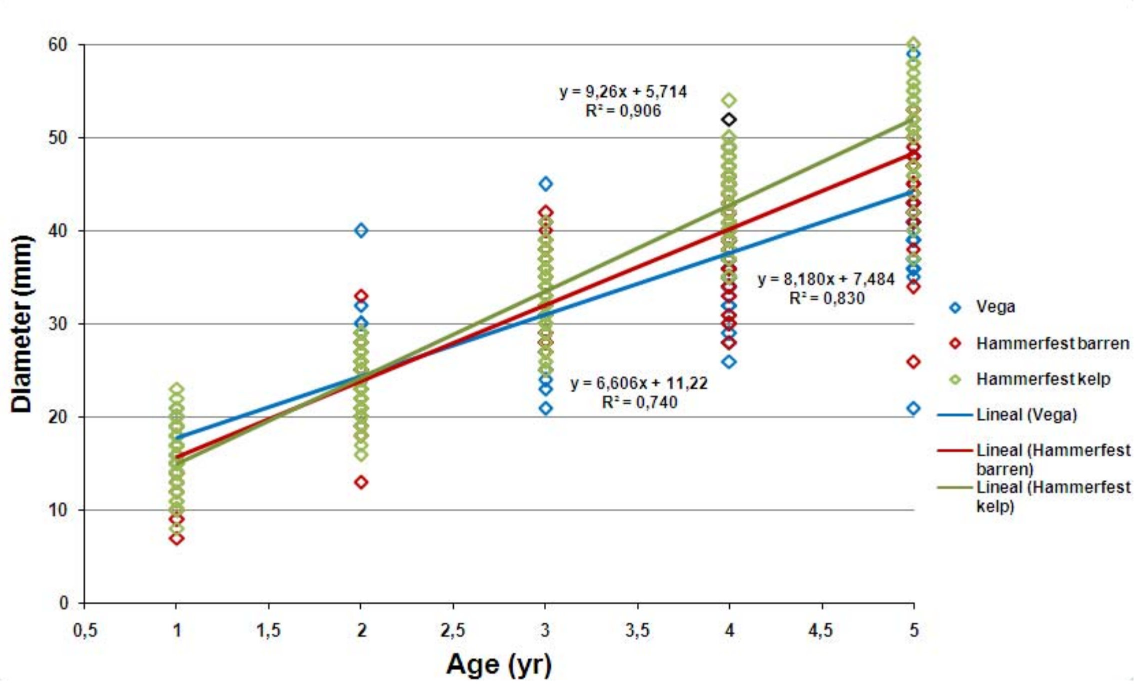


Figure 3.5 Linear regressions (with observed values) of diameter vs. number of growth rings, for *S. droebachiensis* between 1 and 5 years sampled in all areas.

Table 3.7 Nested ANCOVA test results for homogeneity of *S. droebachiensis* individuals between 1 and 5 years old for a) all stations at Hammerfest and b) all barren stations in Hammerfest and Vega.

	Source		Type III SS	df	MS	F	Sig.
a) Hammerfest kelp vs barren	Age	Hypothesis	65282,200	1	65282,200	4465,977	,000[a]
		Error	9676,901	662	14,618[b]		
	Habitat	Hypothesis	344,368	1	344,368	1,103	,404
		Error	625,299	2,002	312,266[c]		
	Location[b]	Hypothesis	28,372	2	14,186	,045	,957
		Error	633,418	2,000	316,762[d]		
	Station	Hypothesis	632,429	2	316,215	21,632	,000[a]
		Error	9676,901	662	14,618[b]		
b) Barren grounds Vega vs Hammerfest	Age	Hypothesis	37329,137	1	37329,137	2210,296	,000[a]
		Error	11028,353	653	16,889[b]		
	Area	Hypothesis	61,878	1	61,878	,382	,600
		Error	322,599	1,993	161,851[c]		
	Locality	Hypothesis	911,780	2	455,890	2,822	,262
		Error	322,180	1,994	161,577[d]		
	Station[c]	Hypothesis	319,032	2	159,516	9,445	,000[a]
		Error	11028,353	653	16,889[b]		

[a] indicates significance at $\alpha = 0.05$.
[b] Station refers to Habitat * Location interaction.
[c] Station refers to Area * Location interaction.

In this study, the maximum observed age was 14 years with a corresponding diameter of 62 and 68 mm (Rypklubbskjæret barren and Finnøy barren respectively). However, the biggest sizes were observed within kelp habitats: 72 mm (Molvik) and 73 mm (Rypklubbskjæret and Finnøy).

The Gompertz growth function provided a good fit (Figure 3.6) and therefore allowed estimation of the asymptotic size. The asymptotic diameter for kelp habitats in Hammerfest (L_∞ = 66.64 mm) was higher to that estimated for the barren stations (L_∞ = 62.81 mm). Whereas significant differences among stations were observed ($ANOVA_{F= 6,277}$, df = 174, P < 0.01; Table 3.8.a), no main effect occurred for the habitat and location terms. The smallest asymptotic diameter was at Molvik barren (55.21 mm) whereas the largest was at Finnøy barren (69.73 mm) (Table 3.6, Figure 7.2; Table 7.6).

On the other hand, the asymptotic diameter (L_∞ = 63.85 mm) was significantly different in the barren stations in Hammerfest and those in Vega ($ANOVA_{F= 10,954}$, df = 211, P<0.01; Table 3.8.b). Within the barren stations, smallest asymptotic diameter was obtained at Vega 1 (43.74 mm) and the largest was obtained at Finnøy barren (69.73 mm) (Table 3.6, Figure 7.2; Table 7.7).

Table 3.8 Nested ANOVA test results for homogeneity of *S. droebachiensis* individuals older than 5 years (asymptotes) for a) all stations at Hammerfest and b) all barren stations in Hammerfest and Vega.

	Source		**Type III SS**	**df**	**MS**	**F**	**Sig.**
a) Hammerfest kelp vs barren	Habitat	Hypothesis	574,142	1	574,142	4,992	,123
		Error	306,792	2,667	115,014		
	Location	Hypothesis	119,358	2	59,679	,304	,767
		Error	392,942	2	196,471		
	Station[b]	Hypothesis	392,942	2	196,471	6,277	,002[a]
		Error	5446,443	174	31,301		
b) Barren grounds Vega vs Hammerfest	Area	Hypothesis	1066,462	1	1066,462	3,449	,202
		Error	628,390	2,032	309,204		
	Location	Hypothesis	3635,367	2	1817,683	5,446	,155
		Error	667,496	2	333,748		
	Station[c]	Hypothesis	667,496	2	333,748	10,954	,000[a]
		Error	6428,602	211	30,467		

[a] indicates significance at α = 0.05.
[b] Station refers to Habitat * Location interaction.
[c] Station refers to Area * Location interaction.

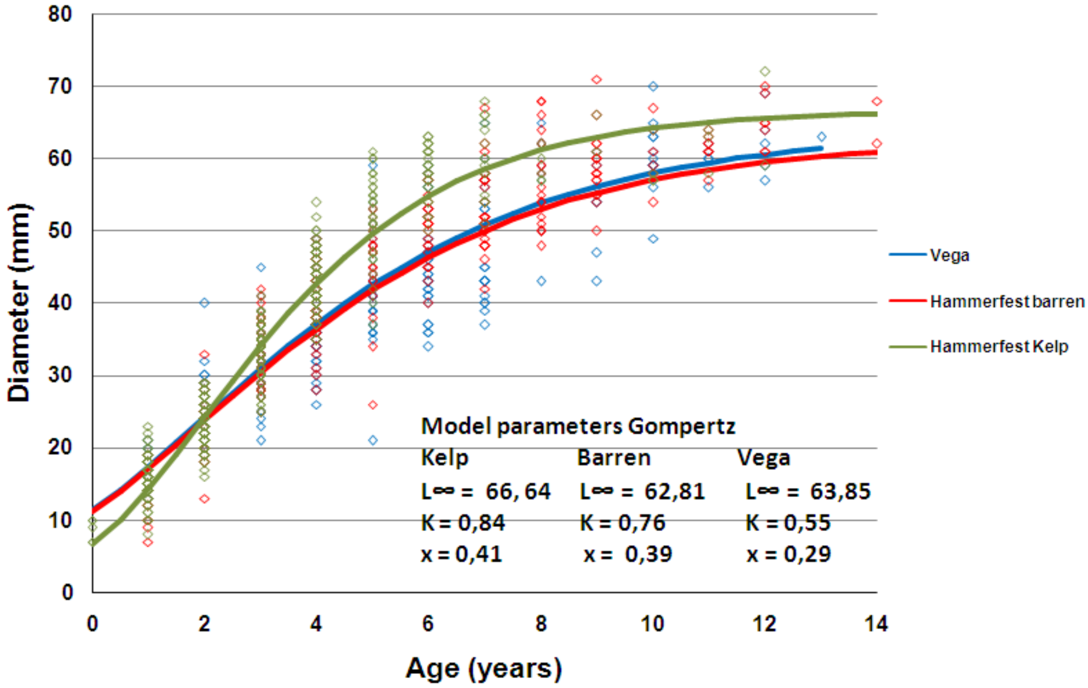


Figure 3.6 Gompertz growth functions (with observed values) fitted to size-at-age data for individuals from Hammerfest and Vega. L_∞ is the upper asymptote, k is the lower asymptote, x is the growth rate of the population.

3.4. Mortality

There were no differences in sea urchin mortality between kelp forests and barrens and between Hammerfest and Vega. The estimated catch curves for the three areas (data from all habitats pooled) are shown in Figure 3.7. Estimated instantaneous mortality rates (Z) are presented in Table 3.6. This shows that instantaneous mortality for all sites and habitats varied from 0.13 to 0.62. Although a similar recruitment to the adult population was observed for the 2 areas, urchins in kelp habitats in Hammerfest suffered a higher mortality (Z = 0.47) compared to urchins in barren areas in Hammerfest (Z = 0.30) and the ones in Vega (Z = 0.37) (Table 3.6; Figure 3.7). However, no significant differences were found between stations ($ANCOVA_{F=0{,}088}$, df = 48, p = 0,916; Table 3.9.a). For barren habitats, higher mortalities were observed in Vega (Z = 0.37) than those in Hammerfest, but again no significant statistically difference was observed between stations ($ANCOVA_{F=1{,}802}$, df = 49, P = 0,176; Table 3.9.b). Those assumptions were confirmed with the multiple comparisons Tukey's test

(Tables 7.10 and 7.11) where all individual comparisons indicated that there is no significant difference in survival between areas and habitats.

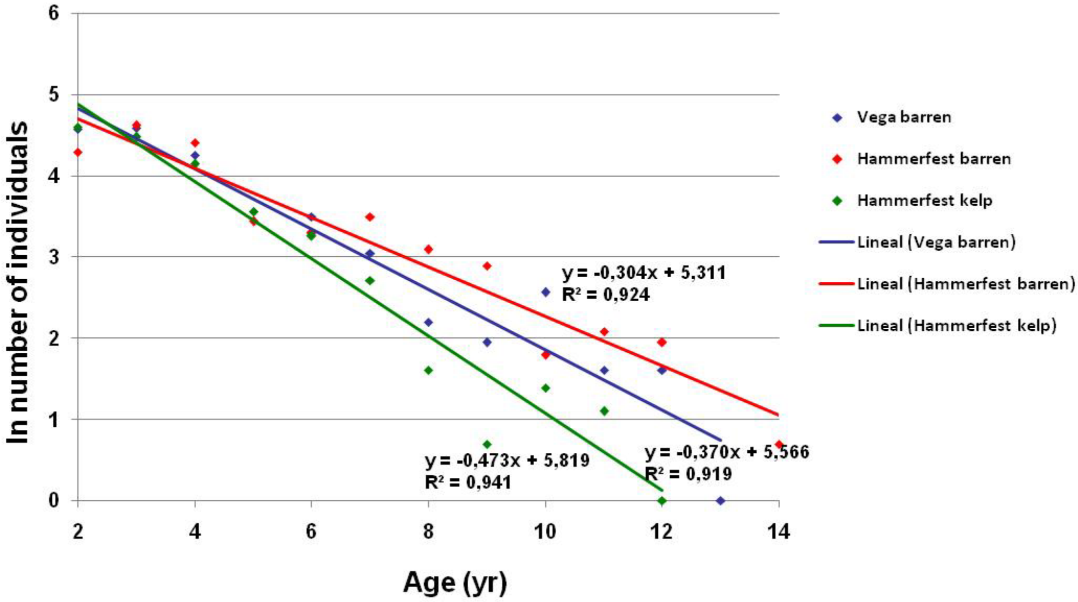


Figure 3.7 Catch curve for *S. droebachiensis* sampled in all habitats.

Table 3.9 Nested ANCOVA test results for homogeneity of *S. droebachiensis* catch curves for individuals from a) all stations at Hammerfest and b) all barren stations in Hammerfest and Vega.

	Source		Type III SS	df	MS	F	Sig.
a) Hammerfest kelp vs barren	Age	Hypothesis	48,866	1	48,866	78,166	,000[a]
		Error	30,008	48	,625		
	Habitat	Hypothesis	,356	1	,356	5,104	,100
		Error	,233	3,347	,070		
	Locality	Hypothesis	1,984	2	,992	14,966	,028[a]
		Error	,199	2,995	,066		
	Station[b]	Hypothesis	,110	2	,055	,088	,916
		Error	30,008	48	,625		
b) Barren grounds Vega vs Hammerfest	Age	Hypothesis	33,783	1	33,783	56,241	,000[a]
		Error	29,434	49	,601		
	Area	Hypothesis	,528	1	,528	,486	,558
		Error	2,155	1,985	1,085		
	Locality	Hypothesis	1,513	2	,756	,697	,590
		Error	2,157	1,989	1,085		
	Station[c]	Hypothesis	2,164	2	1,082	1,802	,176
		Error	29,434	49	,601		

[a] indicates significance at $\alpha = 0.05$.
[b] Station refers to Habitat * Location interaction.
[c] Station refers to Area * Location interaction.

According to the hypothesis:

- There were significant differences in size among stations in Hammerfest and among barren ground stations (Hammerfest and Vega).
- No differences were found in age among stations in Hammerfest. However, significant differences in age were found among barren ground stations (in Hammerfest and Vega).
- Significant differences were obtained in growth for both Hammerfest stations and barren grounds (in Hammerfest and Vega).
- No significant differences were found in mortality rates within Hammerfest and within barren grounds (in Hammerfest and Vega).

4. DISCUSSION:

Two specific issues must be addressed before discussing the results obtained in this study. The first issue concerns the sampling of small individuals. Usually small individuals (<20 mm) cannot be counted and collected in proportion to their true abundance. Newly settled juveniles up to 2 years old tend to hide in cracks, crevices and kelps holdfast. Those habitats possibly act as refuges against predation by certain species of decapods, echinoderms, fish and birds (Himmelman and Steele 1971). In addition small individuals are hardly visible and therefore hard to find during collection. A third factor could be that the sampling period may have fallen between recruitment events. However, data for all stations were collected similarly and all individuals less than 20 mm were included in analyses while acknowledging this issue.

A second important issue relates to aging individuals. Growth lines in urchins are often difficult to interpret (Pearse and Pearse 1975) and therefore it is likely that annual growth lines are difficult to recognize for slow-growing juveniles (Himmelman 1986). Some authors (e.g. Meidel and Scheibling 1998b) have also emphasized that the method of counting growth rings is most reliable for *Strongylocentrotus droebachiensis* between 20 and 50 mm in diameter (between 2 and 6 years old). Thus, the results for individuals older than 6 years should be interpreted cautiously.

4.1. Size structure

There was a considerable variation in the size distribution among stations in both areas. Compared to the barren grounds, sea urchins in kelp habitats at Hammerfest reached the maximum sizes (73 mm). Presence of larger sea urchins in kelp habitats may be due to higher amounts of food compared to the barren areas, which support lower growth rates in such food limited areas (Lang and Mann 1976; Wharton and Mann 1981). Such results could lead to a higher grazing activity from the larger individuals, which, at the same time, could lead to a new barren habitat.

When comparing barren stations in Hammerfest and Vega, similar results between both areas were obtained. Mean urchin sizes in barren stations at Hammerfest (37.68 mm) were more similar to those found in the barren ones in Vega (34.24 mm) than to kelp habitats in Hammerfest (31.21 mm). This could indicate that there is a difference in sizes due to the type of habitat. However, the results of nested ANOVA indicated the opposite ($p = 0.078$). Reasons for finding smaller average sizes in kelp habitats are due to the fact that size-frequencies were highest for smaller individuals. This pattern is opposite to what Vadas *et al*. (2002) described.

Sea urchins of less than 4 mm were not recorded at all, but individuals between 4 and 20 mm were occasionally found at all stations in both types of habitats. Small individuals (< 20 mm) of *Strongylocentrotus droebachiensis* are known to settle in macroalgal beds, in crevices of rocks and within the matrix formed by calcareous algae (Propp 1977; Vadas and Steneck 1988). Therefore sea urchins with diameters smaller than 20 mm are most likely under-represented in the data due to bias in sampling.

Both unimodal and bimodal populations were observed in the two habitats. Whereas bimodal distribution can be explained by several strong recruitments of young sea urchins or size-specific predation on juveniles (such as Rypklubbskjæret and Vega 3) (Himmelman *et al*. 1983b), the unimodal distributions are probably a consequence of stable conditions characterized by a high individual variability in growth (such as Molvik, Finnøy and Vega 1 and 2) (Bluhm *et al*. 1998). Nested ANOVA for all stations showed that the mean size differs significantly among stations within Hammerfest ($p < 0.01$). A dominance of small size classes in kelp beds may be the result of a higher density in the population. Data obtained in May 2008 indicated that Finnøy kelp had the highest density (50 individuals /m^2) compared to the other stations, while the lowest was obtained for Molvik kelp (2.4 individuals /m^2) (Table 2.1). However, in this investigation, higher frequencies of small individuals were found at Molvik kelp. It seems then that density has a minor impact on the magnitude of the small size classes. Thus, strong recruitment in sea urchin populations or other local factors (such as absence of predators or favourable hydrological conditions) can be the reason why there were smaller urchins in kelp beds compared to barren grounds.

As stated by Sivertsen and Hopkins (1995) *S. droebachiensis* juveniles rarely occur together with adults on shallow rocky bottoms. They proposed that larvae settle in loose substrata, usually at 8 to 30 m depth. As juvenile individuals grow they migrate from these areas to join adult populations on the shallow rocky ones. As our samples were obtained at 5 m depth, it can be suggested that this migration to upper areas could be the reason why higher frequencies of larger individuals were found on the barren areas compared to the kelp ones. Other proposed explanation is that even though larvae could settle on hard bottoms, juveniles may be very susceptible to predation or cannibalism (e.g. Himmelman *et al.* 1983a). Himmelman and Steele (1971) also indicated that cannibalism is frequently observed between sea urchins, and Sivertsen (1997b) stated that due to this interaction some forms of competition occur between large and small sea urchins. Therefore, such cannibalism could also explain why there were lower frequencies of sea urchins in barren habitats.

Compared to previous studies done at Vega (Figure 4.1) no sea urchins were found in kelp habitats in the present study. Thus no comparisons in sea urchin populations were done between the two habitats in Vega. *S. droebachiensis* are seldom found in this habitats in Vega because pristine kelp beds, not affected by grazing, are only located in wave exposed areas (Kain and Jones 1971) where sea urchins, due to several factors (e.g. swapping away or even death due to water motion), cannot survive (Cowen *et al.* 1982). However, the fact that no sea urchins were found in this area during 2009 could indicate a strong influence of local factors affecting this species during previous years.

On the other hand, comparing the overall picture of barren grounds in Vega in 1993 (Figure 4.1) to the ones obtained in 2009 (Figure 3.1), larger individuals were found in

2009. Similar frequencies were observed for young individuals (<20 mm). However, urchins larger than 40 mm were less common in 1993.

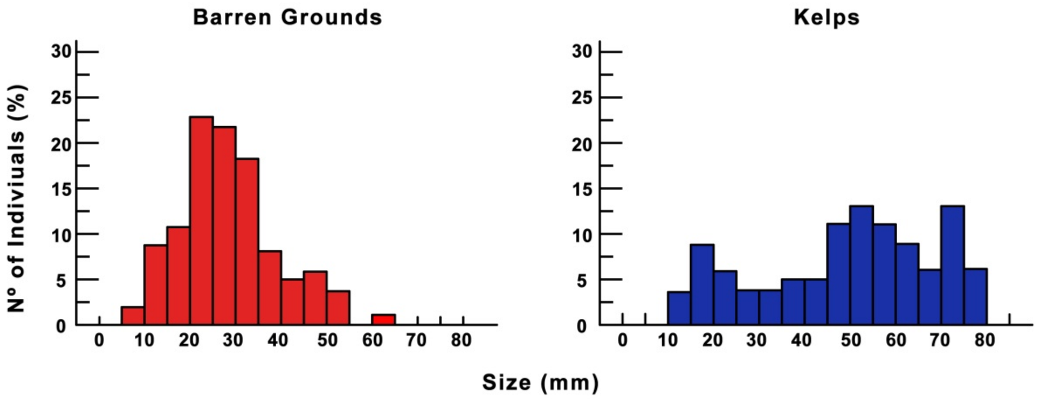


Figure 4.1 Size-frequency distributions of *S. droebachiensis* from the two habitat types in Vega in 1993 (left: barren grounds and right: kelp beds). Source: (Rinde *et al*. 1998).

4.2. Age structure and growth

According to Propp (1977) *Strongylocentrotus droebachiensis* is able to migrate several hundred meters in shallow waters. Therefore different areas may contain quite different age frequencies. This phenomenon is also represented in the present study data set (Table 3.1). Sea urchins between 1 and 12 years were found in all stations, while individuals younger than 1 year old were only found in kelp beds and urchins older than 12 years were only found in barren grounds. However, as mentioned previously, growth rings in individuals older than 6 years can be hard to interpret.

The age-structure (Figure 3.3) was similar at barren and kelp stations in Molvik and Finnøy. At both locations, there was a high frequency of young individuals (< 4 years) and a low frequency of older individuals. This likely indicates high recruitment with subsequent high mortality. On the other hand, it is interesting to note that although the age distribution in Rypklubbskjæret kelp and Rypklubbskjæret barren is different, both locations had a high frequency of 6-7 year old individuals. A possible explanation for this pattern is that there was a recruitment event and subsequent high survival of *S. droebachiensis* in the seasons 2002 and 2003 in Rypklubbskjæret (back calculation).

The 3 stations in Vega also had a strong recruitment during recent years (between 2005 and 2007) as very high frequencies of young age classes were observed.

Almost all stations had similar age distributions with a very high frequency of young age groups. There was no significant difference in the average age at stations within Hammerfest ($p = 0.054$). However, significant differences were obtained when comparing barren stations ($p < 0.01$). Therefore, such results indicate that the type of habitat is not the factor influencing the population age structure**.**

According to the study conducted by Lang and Mann (1976) in St. Margaret´s Bay in Nova Scotia, growth rates in natural populations are often lower in barren areas than in kelp habitats. Sivertsen (1997b) found similar results in his study along the Norwegian coast. The same pattern can be observed in the present study (Figure 3.5), where sea urchins grew faster in the kelp beds than in barren grounds in Hammerfest during the first 5 years. Higher availability of food (as it is the case in kelp habitats) could be the reason for high growth rates, which would lead to a short generation time and to a high productivity (Sivertsen 1997a).

Under optimal conditions, Himmelman (1986) found that *S. droebachiensis* younger than 2 years grow at a rate of 17 mm annually. When the food is scarce, as is the case in barren grounds, growth rates may drop to 1 to 2 mm annually. He stated that two year old individuals range from 6 to 26 mm. In the present investigation the average size at the age of 2 years was 24 mm for all stations (Figure 3.5). Further, the range for 2 year old individuals was from 13 to 40 mm. However, juvenile individuals were smaller at age 1in kelp beds than in barren grounds both in Vega and Hammerfest. This is contrary to what is expected, as kelp habitats often have higher food availability. But as urchins in the kelp beds grow faster, they reached the same size as urchins from barren grounds at the age of 2 years.

There are disagreements among authors about the growth rate of older age groups. While some report growth rates up to 27.5 mm yr^{-1} (e.g. Swan 1961; Miller and Mann 1973; Meidel and Scheibling 1999), others (e.g. Lang and Mann 1976; Propp 1977; Himmelman *et al*. 1983b; Sivertsen and Hopkins 1995) propose 12 mm yr^{-1} to be more realistic for natural populations. In the present investigation, the growth rates were even lower: 9.3 mm yr^{-1} (kelp beds in Hammerfest), 8.2 mm yr^{-1} (barren areas in

Hammerfest) and 6.6 mm yr^{-1} (barrens in Vega) (Table 3.6). It has been argued that such differences are caused by a large sensitivity to the type and quantity of available food (Swan 1961; Keats *et al*. 1984). From the Gompertz growth curves (Figure 3.6) the annual increments are estimated to be over 1 cm during the first year and substantially less for older age groups. Kelp beds provided the fastest growth rate and largest body size. This was also reported by Sivertsen and Hopkins (1995). The asymptotic growth varied significantly between the stations in Hammerfest ($p < 0.01$) and within barren stations ($p < 0.01$), although the differences were minimal as seen in Figures 3.5 and 3.6. However, it is possible for urchins to survive in barren grounds because they can utilize carbon from broken kelp fragments and whole, loose kelp from adjacent kelp beds (Himmelman and Steele 1971; Munk 1992; Meidel and Scheibling 1998a).

Figure 4.2 shows the growth curve for Vega barren grounds obtained in the present investigation (Gompertz growth curve) relative to the barren grounds growth curve obtained in 1993 (von Bertalanffy growth curve). When comparing both curves, it was observed that sea urchins in Vega (barren) grew faster and reached larger sizes in 2009. Possible reasons for this include higher temperatures or higher food input. However older sea urchins were found in 1993. This could be a result of lack of predators, bias in sampling or absence of parasites.

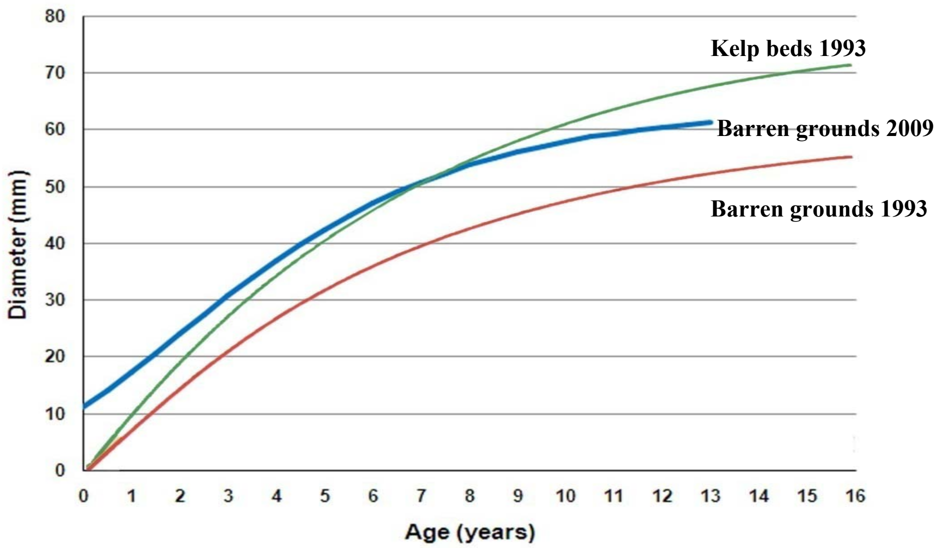


Figure 4.2 Von Bertalanffy growth curves for kelp beds and barren grounds in Vega in 1993 (Source: Rinde *et al*. 1998), and superimposed Gompertz curve for barren grounds in Vega in 2009.

4.3. Mortality

Several authors (e.g. Pauly 1984; Ebert 1985) have stated that growth rates tend to be inversely linked with longevity and mortality. In the present study, recruitment was found to be similar in both habitats and areas. On the other hand, although not different ($p = 0.916$ and $p = 0.176$ for Hammerfest and barren grounds respectively), there was a tendency for mortality of sea urchins to be higher in the kelp-beds. Those results are contrary to Christie and Leinaas observations between 1990 and 1994 (unpublished data, Norway). They found higher recruitment, higher frequencies of young individuals and higher mortalities in barren areas compared to kelp-beds. However, the data in the present investigation are consistent with the hypothesis that the number of adult individuals is lower in kelp beds because of higher mortality in such habitats (Ebert 1982; Himmelman *et al*. 1983a; Bluhm *et al*. 1998). This could be due to the presence of parasites (e.g. *Echinomermella matsi* (Jones and Hagen)) or sea urchin predators (such as wolfish, plaice, lobster or crabs, among others). Other reasons could be high food availability and/or higher temperatures as they contribute to high individual growth rates. That would result in earlier age at maturity and elevated mortality rates (Sivertsen 1997b).

5. CONCLUSIONS

From the present study it can be concluded that interactions between habitats and location result in:

1) Differences in size and growth within Hammerfest.
2) Similarities in age and mortality within Hammerfest
3) Differences in size, age and growth within barren grounds in Hammerfest and in Vega.
4) Similarities in mortality within barren grounds in Hammerfest and in Vega.

The results indicated that the populations on kelp beds reached larger sizes, were younger, had a higher rate of growth, and suffered higher mortality than on barren habitats in Hammerfest. Within barren grounds, it was found that *S. droebachiensis* in Hammerfest reached larger sizes, were older, grew faster and had lower mortality rate than in Vega.

Factors suggested for such results include presence/absence of food, and/or sea urchin predators, strong recruitment, favourable hydrological conditions, cannibalism behaviour, and migration ability. However, there is no consensus on the ecological causal mechanisms for the decimation of the kelp forests and further studies are needed.

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APPENDIX

APPENDIX I

Table 7.1 Size-at-age cross-tabs for *S. droebachiensis* at all stations.

Molvik kelp		Size (mm)								Total
		0-10	11-20	21-30	31-40	41-50	51-60	61-70	71- 80	
Age (yr)	0	3	0	0	0	0	0	0	0	3
	1	0	16	0	0	0	0	0	0	16
	2	0	5	38	0	0	0	0	0	43
	3	0	0	9	21	1	0	0	0	31
	4	0	0	0	0	7	0	0	0	7
	5	0	0	0	0	1	1	0	0	2
	6	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	1	0	1
	8	0	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	1	1
Total		3	21	47	21	9	1	1	1	104

Molvik barren		Size (mm)								Total
		0-10	11-20	21-30	31-40	41-50	51-60	61-70	71- 80	
Age (yr)	0	0	0	0	0	0	0	0	0	0
	1	0	1	0	0	0	0	0	0	1
	2	0	10	40	0	0	0	0	0	50
	3	0	0	19	36	2	0	0	0	57
	4	0	0	1	13	22	0	0	0	36
	5	0	0	1	1	7	1	0	0	10
	6	0	0	0	1	1	2	0	0	4
	7	0	0	0	0	0	1	1	0	2
	8	0	0	0	0	1	2	0	0	3
	9	0	0	0	0	0	1	0	0	1
Total		0	11	61	51	33	7	1	0	164

Rypklubbskjæret kelp		Size (mm)								Total
		0-10	11-20	21-30	31-40	41-50	51-60	61-70	71- 80	
Age (yr)	0	0	0	0	0	0	0	0	0	0
	1	4	30	4	0	0	0	0	0	38
	2	0	4	15	0	0	0	0	0	19
	3	0	0	3	11	0	0	0	0	14
	4	0	0	0	0	23	2	0	0	25
	5	0	0	0	0	5	22	1	0	28
	6	0	0	0	0	1	12	9	0	22
	7	0	0	0	0	0	8	4	0	12
	8	0	0	0	0	0	2	1	0	3
	9	0	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	3	0	0	3
	11	0	0	0	0	0	1	2	0	3
	12	0	0	0	0	0	1	0	0	1
Total		4	34	22	11	29	51	17	0	168

Rypklubbskjæret barren		Size (mm)								Total
		0-10	11-20	21-30	31-40	41-50	51-60	61-70	71- 80	
Age (yr)	0	0	0	0	0	0	0	0	0	0
	1	6	15	0	0	0	0	0	0	21
	2	0	6	11	0	0	0	0	0	17
	3	0	0	4	3	0	0	0	0	7
	4	0	0	1	9	3	0	0	0	13
	5	0	0	0	1	4	1	0	0	6
	6	0	0	0	0	7	3	0	0	10
	7	0	0	0	0	9	11	0	0	20
	8	0	0	0	0	3	8	0	0	11
	9	0	0	0	0	1	9	0	0	12
	10	0	0	0	0	0	2	0	0	4
	11	0	0	0	0	0	1	0	0	8
	12	0	0	0	0	0	0	7	0	7
	13	0	0	0	0	0	0	0	0	0
	14	0	0	0	0	0	0	1	0	1
Total		6	21	16	13	27	35	19	0	137

Finnøy kelp		Size (mm)								Total
		0-10	11-20	21-30	31-40	41-50	51-60	61-70	71- 80	
Age (yr)	0	2	0	0	0	0	0	0	0	2
	1	0	18	0	0	0	0	0	0	18
	2	0	7	30	0	0	0	0	0	37
	3	0	0	9	34	0	0	0	0	43
	4	0	0	0	16	15	0	0	0	31
	5	0	0	0	2	2	1	0	0	5
	6	0	0	0	0	0	4	0	0	4
	7	0	0	0	0	0	1	1	0	2
	8	0	0	0	0	0	2	0	0	2
	9	0	0	0	0	0	0	2	0	2
	10	0	0	0	0	0	0	1	0	1
Total		2	25	39	52	17	8	4	0	147

Finnøy barren		Size (mm)								Total
		0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	
Age (yr)	0	0	0	0	0	0	0	0	0	3
	1	0	3	0	0	0	0	0	0	0
	2	0	0	5	1	0	0	0	0	6
	3	0	0	4	33	0	0	0	0	37
	4	0	0	0	14	19	0	0	0	33
	5	0	0	0	0	13	2	0	0	15
	6	0	0	0	0	1	12	0	0	13
	7	0	0	0	0	0	9	2	0	11
	8	0	0	0	0	0	1	7	0	8
	9	0	0	0	0	0	2	2	1	5
	10	0	0	0	0	0	1	1	0	2
	11	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0
	14	0	0	0	0	0	0	1	0	1
Total		0	3	9	48	33	27	13	1	134

Vega 1		Size (mm)								
		0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	Total
Age (yr)	0	0	0	0	0	0	0	0	0	0
	1	0	3	0	0	0	0	0	0	3
	2	0	2	12	0	0	0	0	0	14
	3	0	0	19	22	0	0	0	0	41
	4	0	0	4	25	17	0	0	0	46
	5	0	0	0	12	9	2	0	0	23
	6	0	0	0	6	10	0	0	0	16
	7	0	0	0	4	6	0	0	0	10
	8	0	0	0	0	1	0	0	0	1
	9	0	0	0	0	2	0	0	0	2
Total		0	5	35	69	45	2	0	0	156

Vega 2		Size (mm)								
		0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	Total
Age (yr)	0	0	0	0	0	0	0	0	0	0
	1	0	8	0	0	0	0	0	0	8
	2	0	7	39	1	0	0	0	0	47
	3	0	0	13	25	0	0	0	0	38
	4	0	0	0	31	4	0	0	0	35
	5	0	0	1	1	12	1	0	0	15
	6	0	0	0	0	6	2	0	0	8
	7	0	0	0	0	1	1	0	0	2
Total		0	15	53	58	23	4	0	0	153

Vega 3		Size (mm)								
		0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	Total
Age (yr)	0	0	0	0	0	0	0	0	0	0
	1	0	5	1	0	0	0	0	0	6
	2	0	3	32	1	0	0	0	0	36
	3	0	0	7	10	2	0	0	0	19
	4	0	0	1	3	8	0	0	0	12
	5	0	0	0	1	2	2	0	0	5
	6	0	0	0	0	3	6	0	0	9
	7	0	0	0	0	0	8	1	0	9
	8	0	0	0	0	1	4	3	0	8
	9	0	0	0	0	0	4	1	0	5
	10	0	0	0	0	1	6	6	0	13
	11	0	0	0	0	0	3	2	0	5
	12	0	0	0	0	0	2	3	0	5
	13	0	0	0	0	0	0	1	0	1
Total		0	8	41	15	17	35	17	0	133

APPENDIX II

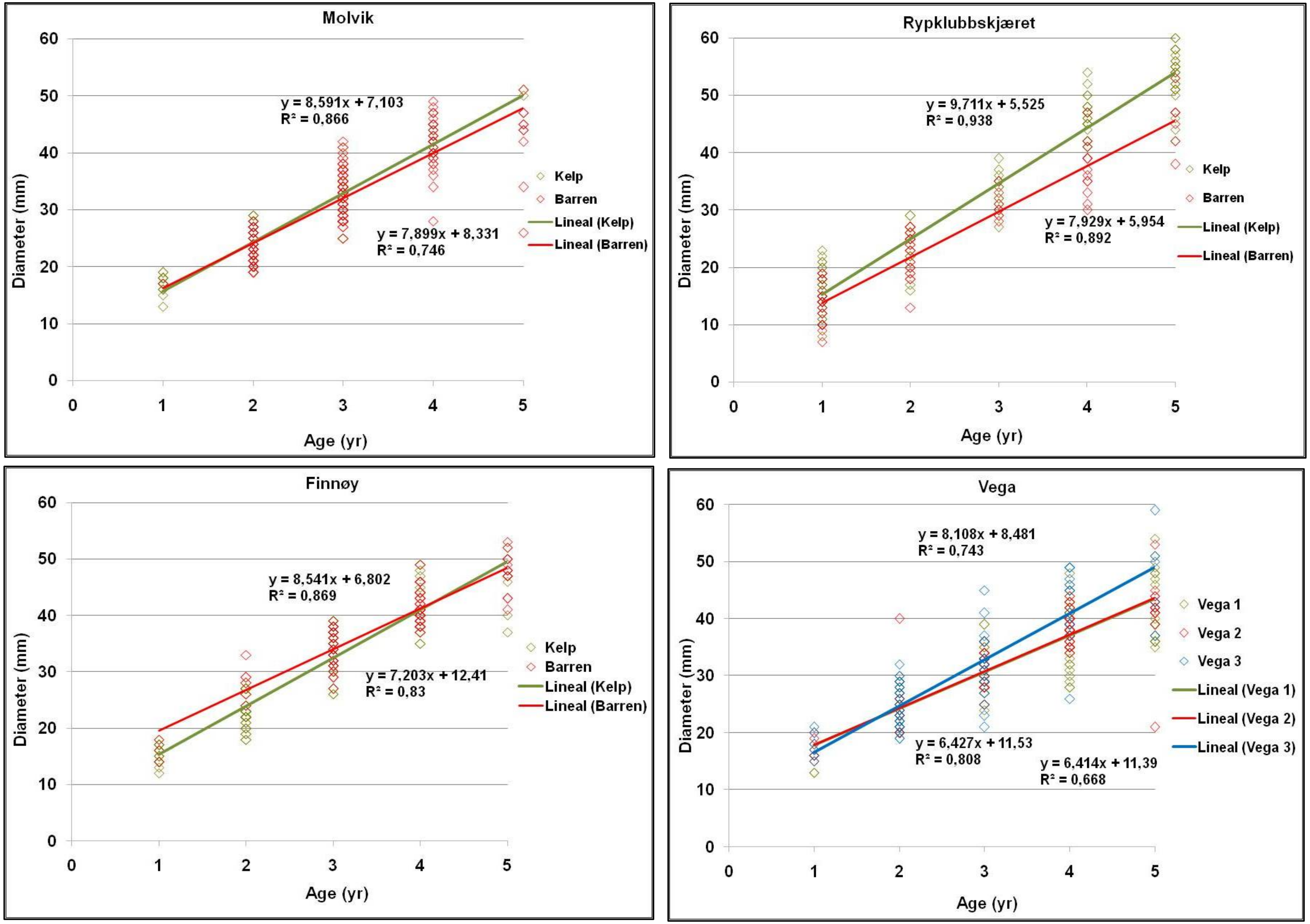

Figure 7.1 Linear regressions (with observed values) of diameter vs. number of growth rings for *S. Droebachiensis* between 1 and 5 years for all sampled stations.

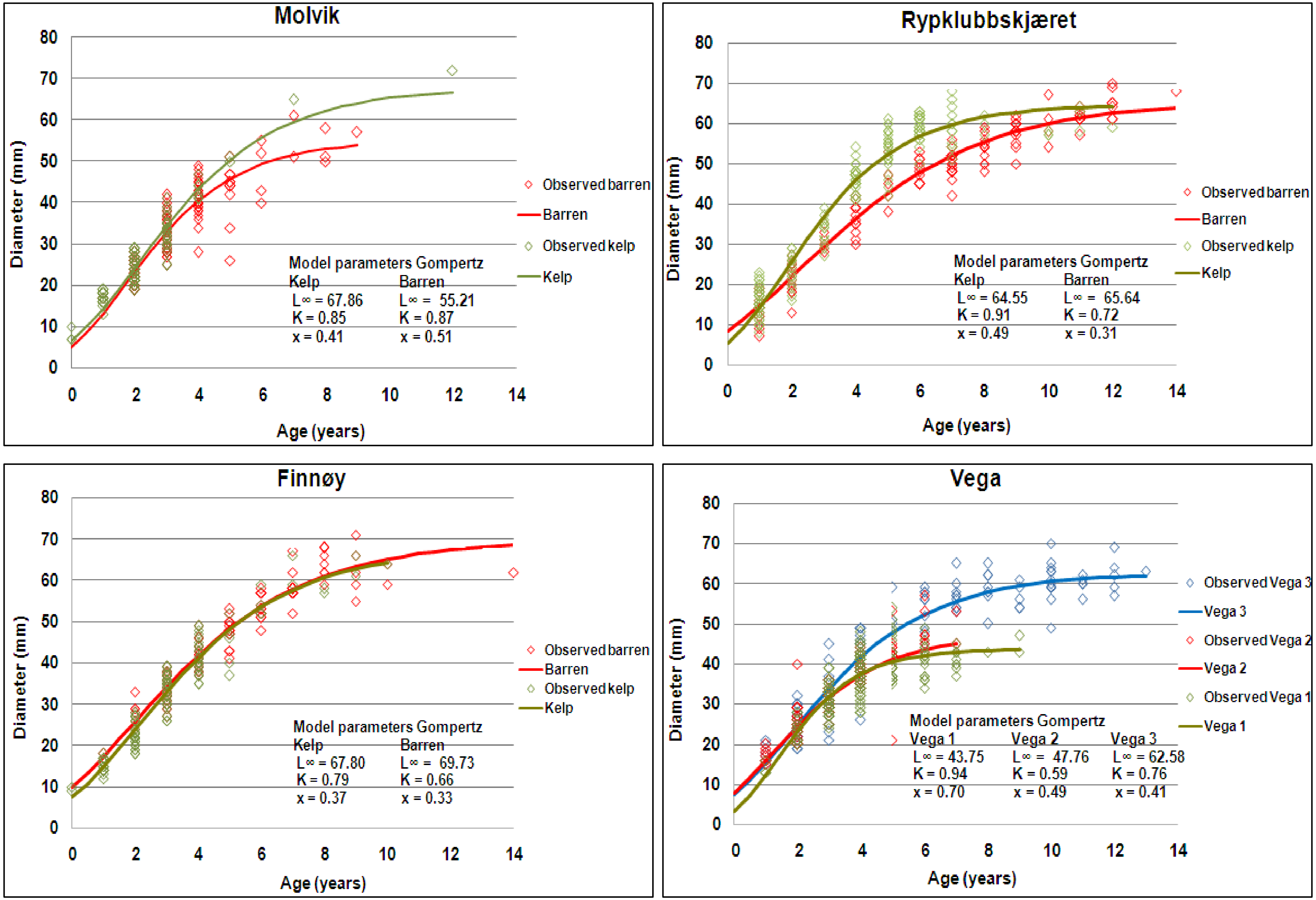

Figure 7.2 Gompertz growth functions fitted to size-at-age data (with observed values) for all sampled stations. L_∞ is the upper asymptote, k is the lower asymptote, x is the growth rate of the population.

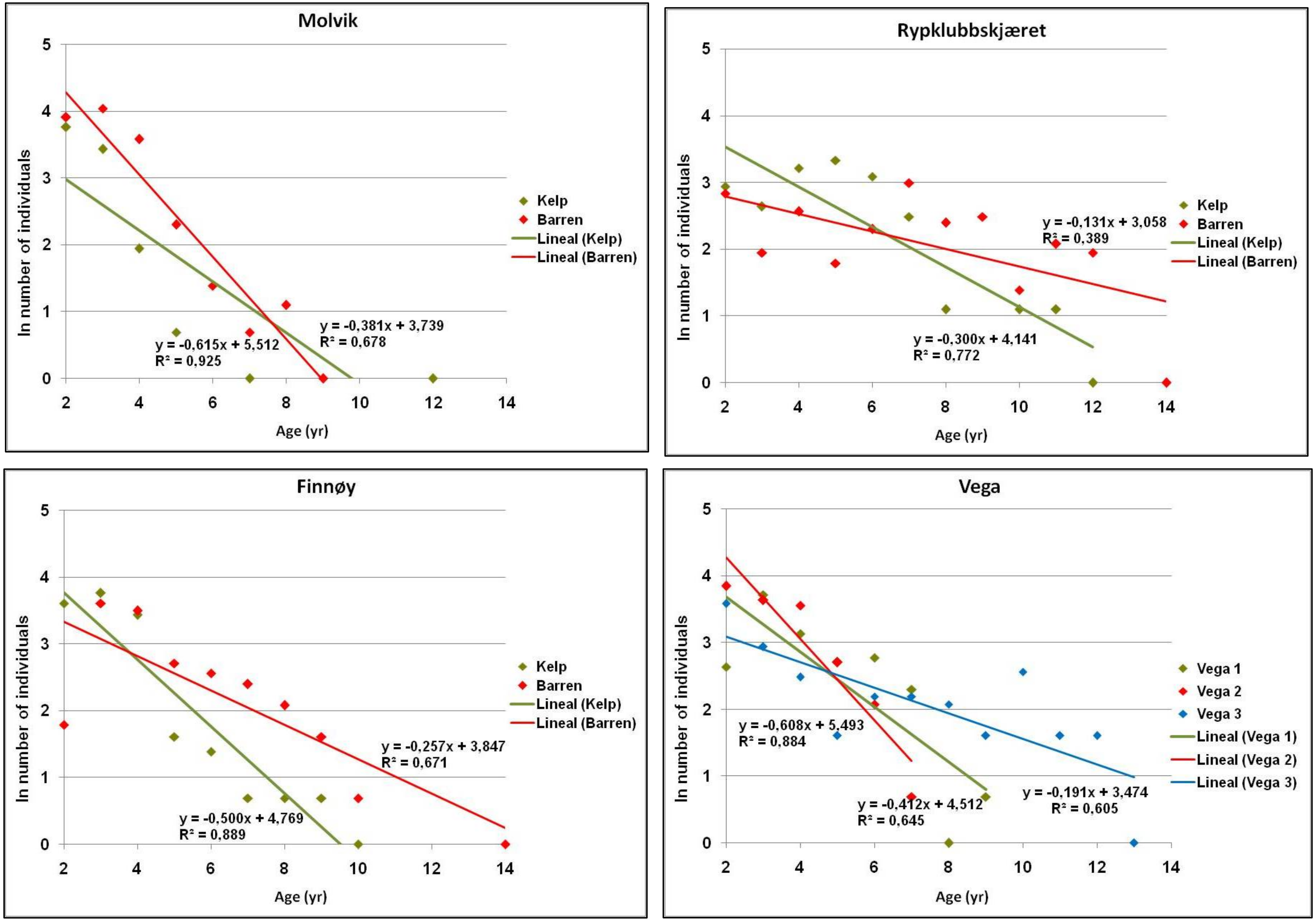

Figure 7.3 Catch curves for *S. droebachiensis* in all sampled stations

APPENDIX III

Table 7.2 Multiple comparisons Tukey's test results for ANOVA for *S. droebachiensis'* size within all stations in Hammerfest.

(I) Station	(J) Station	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Molvik kelp	Molvik barren	-8,370*	1.354	.000	-12.23	-4.51
	Rypklubbskjæret kelp	-21.982*	1.458	.000	-26.14	-17.82
	Rypklubbskjæret barren	-16.985*	1.406	.000	-21.00	-12.97
	Finnøy kelp	-8.554*	1.378	.000	-12.49	-4.62
	Finnøy barren	-18.157*	1.396	.000	-22.14	-14.17
Molvik barren	Molvik kelp	8.370*	1.354	.000	4.51	12.23
	Rypklubbskjæret kelp	-13.612*	1.424	.000	-17.68	-9.55
	Rypklubbskjæret barren	-8.615*	1.371	.000	-12.53	-4.70
	Finnøy kelp	-.184	1.342	1.000	-4.02	3.65
	Finnøy barren	-9.787*	1.360	.000	-13.67	-5.90
Rypklubbskjæret kelp	Molvik kelp	21.982*	1.458	.000	17.82	26.14
	Molvik barren	13.612*	1.424	.000	9.55	17.68
	Rypklubbskjæret barren	4.997*	1.474	.009	.79	9.20
	Finnøy kelp	13.428*	1.447	.000	9.30	17.56
	Finnøy barren	3.825	1.464	.095	-.35	8.00
Rypklubbskjæret barren	Molvik kelp	16.985*	1.406	.000	12.97	21.00
	Molvik barren	8.615*	1.371	.000	4.70	12.53
	Rypklubbskjæret kelp	-4.997*	1.474	.009	-9.20	-.79
	Finnøy kelp	8.431*	1.395	.000	4.45	12.41
	Finnøy barren	-1.172	1.413	.962	-5.20	2.86
Finnøy kelp	Molvik kelp	8.554*	1.378	.000	4.62	12.49
	Molvik barren	.184	1.342	1.000	-3.65	4.02
	Rypklubbskjæret kelp	-13.428*	1.447	.000	-17.56	-9.30
	Rypklubbskjæret barren	-8.431*	1.395	.000	-12.41	-4.45
	Finnøy barren	-9.603*	1.385	.000	-13.55	-5.65
Finnøy barren	Molvik kelp	18.157*	1.396	.000	14.17	22.14
	Molvik barren	9.787*	1.360	.000	5.90	13.67
	Rypklubbskjæret kelp	-3.825	1.464	.095	-8.00	.35
	Rypklubbskjæret barren	1.172	1.413	.962	-2.86	5.20
	Finnøy kelp	9.603*	1.385	.000	5.65	13.55

*. The mean difference is significant at the 0.05 level.

Table 7.3 Multiple comparisons Tukey's test results for ANOVA for *S. droebachiensis'* size within all barren stations at Hammerfest and Vega.

(I) Station	(J) Station	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Molvik barren	Rypklubbskjæret barren	-8.615*	1.305	.000	-12.34	-4.89
	Finnøy barren	-9.656*	1.296	.000	-13.36	-5.96
	Vega 1	-5.456*	1.303	.000	-9.17	-1.74
	Vega 2	-2.120	1.310	.587	-5.86	1.62
	Vega 3	-2.572	1.283	.340	-6.23	1.09
Rypklubbskjæret barren	Molvik barren	8.615*	1.305	.000	4.89	12.34
	Finnøy barren	-1.041	1.346	.972	-4.88	2.80
	Vega 1	3.158	1.352	.180	-.70	7.02
	Vega 2	6.495*	1.359	.000	2.62	10.37
	Vega 3	6.043*	1.333	.000	2.24	9.85
Finnøy barren	Molvik barren	9.656*	1.296	.000	5.96	13.36
	Rypklubbskjæret barren	1.041	1.346	.972	-2.80	4.88
	Vega 1	4.200*	1.344	.022	.36	8.04
	Vega 2	7.536*	1.351	.000	3.68	11.39
	Vega 3	7.084*	1.325	.000	3.30	10.87
Vega 1	Molvik barren	5.456*	1.303	.000	1.74	9.17
	Rypklubbskjæret barren	-3.158	1.352	.180	-7.02	.70
	Finnøy barren	-4.200*	1.344	.022	-8.04	-.36
	Vega 2	3.337	1.357	.137	-.54	7.21
	Vega 3	2.884	1.332	.255	-.92	6.68
Vega 2	Molvik barren	2.120	1.310	.587	-1.62	5.86
	Rypklubbskjæret barren	-6.495*	1.359	.000	-10.37	-2.62
	Finnøy barren	-7.536*	1.351	.000	-11.39	-3.68
	Vega 1	-3.337	1.357	.137	-7.21	.54
	Vega 3	-.453	1.338	.999	-4.27	3.37
Vega 3	Molvik barren	2.572	1.283	.340	-1.09	6.23
	Rypklubbskjæret barren	-6.043*	1.333	.000	-9.85	-2.24
	Finnøy barren	-7.084*	1.325	.000	-10.87	-3.30
	Vega 1	-2.884	1.332	.255	-6.68	.92
	Vega 2	.453	1.338	.999	-3.37	4.27

*. The mean difference is significant at the 0.05 level.

Table 7.4 Multiple comparisons Tukey's test results for ANOVA for of *S. droebachiensis'* age within all stations in Hammerfest.

(I) Station	(J) Station	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Molvik kelp	Rypklubbskjæret kelp	-1.583*	.278	.000	-2.38	-.79
	Finnøy kelp	-.652	.286	.203	-1.47	.16
	Molvik barren	-.851*	.279	.029	-1.65	-.05
	Rypklubbskjæret barren	-3.270*	.290	.000	-4.10	-2.44
	Finnøy barren	-2.286*	.291	.000	-3.12	-1.45
Rypklubbskjæret kelp	Molvik Kelp	1.583*	.278	.000	.79	2.38
	Finnøy Kelp	.931*	.252	.003	.21	1.65
	Molvik barren	.732*	.245	.034	.03	1.43
	Rypklubbskjæret barren	-1.687*	.257	.000	-2.42	-.95
	Finnøy barren	-.703	.258	.072	-1.44	.03
Finnøy kelp	Molvik kelp	.652	.286	.203	-.16	1.47
	Rypklubbskjæret kelp	-.931*	.252	.003	-1.65	-.21
	Molvik barren	-.200	.253	.970	-.92	.52
	Rypklubbskjæret barren	-2.619*	.265	.000	-3.37	-1.86
	Finnøy barren	-1.634*	.266	.000	-2.39	-.87
Molvik barren	Molvik kelp	.851*	.279	.029	.05	1.65
	Rypklubbskjæret kelp	-.732*	.245	.034	-1.43	-.03
	Finnøy kelp	.200	.253	.970	-.52	.92
	Rypklubbskjæret barren	-2.419*	.258	.000	-3.16	-1.68
	Finnøy barren	-1.435*	.260	.000	-2.18	-.69
Rypklubbskjæretbarren	Molvik kelp	3.270*	.290	.000	2.44	4.10
	Rypklubbskjæret kelp	1.687*	.257	.000	.95	2.42
	Finnøy kelp	2.619*	.265	.000	1.86	3.37
	Molvik barren	2.419*	.258	.000	1.68	3.16
	Finnøy barren	.984*	.271	.004	.21	1.76
Finnøy barren	Molvik kelp	2.286*	.291	.000	1.45	3.12
	Rypklubbskjæret kelp	.703	.258	.072	-.03	1.44
	Finnøy kelp	1.634*	.266	.000	.87	2.39
	Molvik barren	1.435*	.260	.000	.69	2.18
	Rypklubbskjæret barren	-.984*	.271	.004	-1.76	-.21

*. The mean difference is significant at the 0.05 level.

Table 7.5 Multiple comparisons Tukey's test results for ANOVA for *S. droebachiensis'* age within all barren stations at Hammerfest and Vega.

(I) Station	(J) Station	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Molvik barren	Rypklubbskjæret barren	-2.419*	.270	.000	-3.19	-1.65
	Finnøy barren	-1.435*	.271	.000	-2.21	-.66
	Vega 1	-.885*	.260	.009	-1.63	-.14
	Vega 2	.052	.262	1.000	-.70	.80
	Vega 3	-1.929*	.272	.000	-2.70	-1.15
Rypklubbskjæret barren	Molvik barren	2.419*	.270	.000	1.65	3.19
	Finnøy barren	.984*	.283	.007	.18	1.79
	Vega 1	1.534*	.272	.000	.76	2.31
	Vega 2	2.471*	.274	.000	1.69	3.25
	Vega 3	.490	.283	.512	-.32	1.30
Finnøy barren	Molvik barren	1.435*	.271	.000	.66	2.21
	Rypklubbskjæret barren	-.984*	.283	.007	-1.79	-.18
	Vega 1	.550	.274	.339	-.23	1.33
	Vega 2	1.487*	.276	.000	.70	2.27
	Vega 3	-.494	.285	.510	-1.31	.32
Vega 1	Molvik barren	.885*	.260	.009	.14	1.63
	Rypklubbskjæret barren	-1.534*	.272	.000	-2.31	-.76
	Finnøy barren	-.550	.274	.339	-1.33	.23
	Vega 2	.937*	.265	.006	.18	1.69
	Vega 3	-1.044*	.274	.002	-1.83	-.26
Vega 2	Molvik barren	-.052	.262	1.000	-.80	.70
	Rypklubbskjæret barren	-2.471*	.274	.000	-3.25	-1.69
	Finnøy barren	-1.487*	.276	.000	-2.27	-.70
	Vega 1	-.937*	.265	.006	-1.69	-.18
	Vega 3	-1.981*	.276	.000	-2.77	-1.19
Vega 3	Molvik barren	1.929*	.272	.000	1.15	2.70
	Rypklubbskjæret barren	-.490	.283	.512	-1.30	.32
	Finnøy barren	.494	.285	.510	-.32	1.31
	Vega 1	1.044*	.274	.002	.26	1.83
	Vega 2	1.981*	.276	.000	1.19	2.77

*. The mean difference is significant at the 0.05 level.

Table 7.6 Multiple comparisons Tukey's test results for ANOVA for asymptotes (individuals ≥ 6 years) for *S. droebachiensis* within all stations in Hammerfest.

(I) Station	(J) Station	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Molvik kelp	Molvik barren	16.700*	4.334	.002	4.21	29.19
	Rypklubbskjæret kelp	9.386	4.045	.191	-2.27	21.04
	Rypklubbskjæret barren	13.336*	4.010	.014	1.78	24.89
	Finnøy kelp	9.591	4.301	.229	-2.80	21.98
	Finnøy barren	9.725	4.054	.162	-1.96	21.41
Molvik barren	Molvik kelp	-16.700*	4.334	.002	-29.19	-4.21
	Rypklubbskjæret kelp	-7.314*	1.960	.003	-12.96	-1.67
	Rypklubbskjæret barren	-3.364	1.887	.479	-8.80	2.07
	Finnøy kelp	-7.109*	2.445	.047	-14.15	-.06
	Finnøy barren	-6.975*	1.978	.007	-12.68	-1.27
Rypklubbskjæret kelp	Molvik kelp	-9.386	4.045	.191	-21.04	2.27
	Molvik barren	7.314*	1.960	.003	1.67	12.96
	Rypklubbskjæret barren	3.949*	1.068	.004	.87	7.03
	Finnøy kelp	.205	1.886	1.000	-5.23	5.64
	Finnøy barren	.339	1.222	1.000	-3.18	3.86
Rypklubbskjæret barren	Molvik kelp	-13.336*	4.010	.014	-24.89	-1.78
	Molvik barren	3.364	1.887	.479	-2.07	8.80
	Rypklubbskjæret kelp	-3.949*	1.068	.004	-7.03	-.87
	Finnøy kelp	-3.745	1.810	.308	-8.96	1.47
	Finnøy barren	-3.611*	1.101	.016	-6.78	-.44
Finnøy kelp	Molvik kelp	-9.591	4.301	.229	-21.98	2.80
	Molvik barren	7.109*	2.445	.047	.06	14.15
	Rypklubbskjæret kelp	-.205	1.886	1.000	-5.64	5.23
	Rypklubbskjæret barren	3.745	1.810	.308	-1.47	8.96
	Finnøy barren	.134	1.905	1.000	-5.35	5.62
Finnøy barren	Molvik kelp	-9.725	4.054	.162	-21.41	1.96
	Molvik barren	6.975*	1.978	.007	1.27	12.68
	Rypklubbskjæret kelp	-.339	1.222	1.000	-3.86	3.18
	Rypklubbskjæret barren	3.611*	1.101	.016	.44	6.78
	Finnøy kelp	-.134	1.905	1.000	-5.62	5.35

*. The mean difference is significant at the 0.05 level.

Table 7.7 Multiple comparisons Tukey's test results for ANOVA for asymptotes (individuals ≥ 6 years) for *S. droebachiensis* within all barren stations at Hammerfest and Vega.

(I) Station	(J) Station	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Molvik barren	Rypklubbskjæret barren	-3.364	1.861	.463	-8.72	1.99
	Finnøy barren	-6.975*	1.952	.006	-12.59	-1.36
	Vega 1	10.352*	2.024	.000	4.53	16.17
	Vega 2	3.500	2.468	.716	-3.60	10.60
	Vega 3	-6.564*	1.898	.008	-12.02	-1.11
Rypklubbskjæret barren	Molvik barren	3.364	1.861	.463	-1.99	8.72
	Finnøy barren	-3.611*	1.086	.013	-6.73	-.49
	Vega 1	13.716*	1.212	.000	10.23	17.20
	Vega 2	6.864*	1.861	.004	1.51	12.22
	Vega 3	-3.199*	.986	.017	-6.03	-.36
Finnøy barren	Molvik barren	6.975*	1.952	.006	1.36	12.59
	Rypklubbskjæret barren	3.611*	1.086	.013	.49	6.73
	Vega 1	17.327*	1.346	.000	13.45	21.20
	Vega 2	10.475*	1.952	.000	4.86	16.09
	Vega 3	.411	1.147	.999	-2.89	3.71
Vega 1	Molvik barren	-10.352*	2.024	.000	-16.17	-4.53
	Rypklubbskjæret barren	-13.716*	1.212	.000	-17.20	-10.23
	Finnøy barren	-17.327*	1.346	.000	-21.20	-13.45
	Vega 2	-6.852*	2.024	.011	-12.67	-1.03
	Vega 3	-16.915*	1.267	.000	-20.56	-13.27
Vega 2	Molvik barren	-3.500	2.468	.716	-10.60	3.60
	Rypklubbskjæret barren	-6.864*	1.861	.004	-12.22	-1.51
	Finnøy barren	-10.475*	1.952	.000	-16.09	-4.86
	Vega 1	6.852*	2.024	.011	1.03	12.67
	Vega 3	-10.064*	1.898	.000	-15.52	-4.61
Vega 3	Molvik barren	6.564*	1.898	.008	1.11	12.02
	Rypklubbskjæret barren	3.199*	.986	.017	.36	6.03
	Finnøy barren	-.411	1.147	.999	-3.71	2.89
	Vega 1	16.915*	1.267	.000	13.27	20.56
	Vega 2	10.064*	1.898	.000	4.61	15.52

*. The mean difference is significant at the 0.05 level.

Table 7.8 Multiple comparisons Tukey's test results for ANCOVA for growth rates (individuals from 2 to 5 years) for *S. droebachiensis* within all stations at Hammerfest.

TUKEY'S TEST Comparison	Std. Error	q	$q_{0.05.6.\infty}$	Conclusion
Finnøy barren-Finnøy kelp	0.37	3.634	4.030	Not different
Finnøy barren - Molvik barren	0.38	1.834	4.030	Not different
Finnøy barren - Molvik kelp	0.42	3.286	4.030	Not different
Finnøy barren-Rypklubbskjæret barren	0.39	1.884	4.030	Not different
Finnøy barren-Rypklubbskjæret kelp	0.33	7.510	4.030	Different
Finnøy kelp - Molvik kelp	0.37	0.133	4.030	Not different
Finnøy kelp-Rypklubbskjæret kelp	0.27	4.366	4.030	Different
Molvik barren- Finnøy kelp	0.32	1.991	4.030	Not different
Molvik barren - Molvik kelp	0.38	1.806	4.030	Not different
Molvik barren-Rypklubbskjæret barren	0.34	0.089	4.030	Not different
Molvik barren-Rypklubbskjæret kelp	0.28	6.404	4.030	Different
Molvik kelp-Rypklubbskjæret kelp	0.34	3.311	4.030	Not different
Rypklubbskjæret barren- Finnøy kelp	0.33	1.855	4.030	Not different
Rypklubbskjæret barren - Molvik kelp	0.39	0.127	4.030	Not different
Rypklubbskjæret barren -Rypklubbskjæret kelp	0.29	6.120	4.030	Different

Table 7.9 Multiple comparisons Tukey's test results for ANCOVA for growth rates (individuals from 2 to 5 years) for *S. droebachiensis* within all barren stations at Hammerfest and Vega.

TUKEY'S TEST Comparison	Std. error	q	$q_{0.05.6.\infty}$	Conclusion
Finnøy barren- Molvik barren	0.41	1.706	4.030	Not different
Finnøy barren-Rypklubbskjæret barren	0.41	1.753	4.030	Not different
Finnøy barren- Vega 1	0.41	1.914	4.030	Not different
Finnøy barren- Vega 2	0.39	2.004	4.030	Not different
Finnøy barren- Vega 3	0.45	2.009	4.030	Not different
Molvik barren-Rypklubbskjæret barren	0.41	0.074	4.030	Not different
Molvik barren- Vega 1	0.37	4.062	4.030	Different
Molvik barren- Vega 2	0.45	3.269	4.030	Not different
Molvik barren- Vega 3	0.41	0.512	4.030	Not different
Rypklubbskjæret barren- Vega 1	0.37	4.064	4.030	Different
Rypklubbskjæret barren- Vega 3	0.41	0.430	4.030	Not different
Rypklubbskjæret barren- Vega2	0.34	4.356	4.030	Different
Vega 1- Vega 2	0.34	0.037	4.030	Not different
Vega 1- Vega 3	0.41	4.108	4.030	Different
Vega 2 - Vega 3	0.39	4.341	4.030	Not different

Table 7.10 Multiple comparisons Tukey's test results for ANCOVA for mortality rates (individuals ≥ 2 years) for *S. droebachiensis* within all stations at Hammerfest.

TUKEY'S TEST Comparison	Std. Error	q	$q_{0.05.6.\infty}$	Conclusion
Finnøy barren - Molvik barren	0.064	0.606	4.03	Not different
Finnøy barren - Rypklubbskjæret barren	0.047	1.141	4.03	Not different
Finnøy barren - Finnøy kelp	0.058	0.449	4.03	Not different
Finnøy barren - Molvik kelp	0.072	0.682	4.03	Not different
Finnøy barren - Rypklubbskjæret kelp	0.052	0.067	4.03	Not different
Molvik barren - Rypklubbskjæret barren	0.060	1.107	4.03	Not different
Molvik barren - Finnøy kelp	0.069	0.000	4.03	Not different
Molvik barren - Molvik kelp	0.077	0.134	4.03	Not different
Molvik barren - Rypklubbskjæret kelp	0.064	0.550	4.03	Not different
Rypklubbskjæret barren - Finnøy kelp	0.054	1.000	4.03	Not different
Rypklubbskjæret barren - Molvik kelp	0.064	0.851	4.03	Not different
Rypklubbskjæret barren - Rypklubbskjæret kelp	0.048	0.663	4.03	Not different
Finnøy kelp - Molvik kelp	0.072	0.320	4.03	Not different
Finnøy kelp - Rypklubbskjæret kelp	0.058	0.387	4.03	Not different
Molvik kelp - Rypklubbskjæret kelp	0.067	0.678	4.03	Not different

Table 7.11 Multiple comparisons Tukey's test results for ANCOVA for mortality rates (individuals ≥ 2 years) for *S. droebachiensis* within all barren stations at Hammerfest and Vega.

TUKEY'S TEST Comparison	Std. error	q	$q_{0.05.6.\infty}$	Conclusion
Finnøy barren - Molvik barren	0.057	0.680	4.030	Not different
Finnøy barren - Rypklubbskjæret barren	0.042	0.665	4.030	Not different
Finnøy barren - Vega 1	0.057	0.153	4.030	Not different
Finnøy barren - Vega 2	0.074	0.329	4.030	Not different
Finnøy barren - Vega 3	0.043	0.442	4.030	Not different
Molvik barren - Rypklubbskjæret barren	0.054	1.241	4.030	Not different
Molvik barren - Vega 1	0.066	0.455	4.030	Not different
Molvik barren - Vega 2	0.081	0.176	4.030	Not different
Molvik barren - Vega 3	0.054	1.063	4.030	Not different
Rypklubbskjæret barren - Vega 1	0.054	0.684	4.030	Not different
Rypklubbskjæret barren - Vega2	0.072	0.731	4.030	Not different
Rypklubbskjæret barren - Vega 3	0.039	0.243	4.030	Not different
Vega 1 - Vega 2	0.081	0.193	4.030	Not different
Vega 1 - Vega 3	0.054	0.509	4.030	Not different
Vega 2 - Vega 3	0.072	0.600	4.030	Not different