Population dynamics of the brown shrimp, *Crangon crangon* (L.) at Helguvík bay, Iceland.

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2010

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12 ECTS undergraduate research project of
Baccalaureus Scientiarum degree in biology

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University of Iceland
Reykjavík, Oktober 2010

Líffræði sandrækju *Crangon crangon* (L.) í Helguvík.

Svavar Örn Guðmundsson

12 eininga ritgerð sem er hluti af
Baccalaureus Scientiarum gráðu í líffræði

Leiðbeinandi/endur
Jónas Páll Jónasson
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Líf- og umhverfisvísindadeild
Verkfræði- og náttúruvísindasvið
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Reykjavík, Október 2010

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Skráningarupplýsingar:
Svavar Örn Guðmundsson, 2010, *Population dynamics of the brown shrimp, Crangon crangon (L.) at Helguvík bay, Iceland*, BS ritgerð, Líf- og umhverfisvísindadeild, Háskóli Íslands, 29 bls.

Prentun: Háskólaprent ehf.
Reykjavík, október 2010

Yfirlýsing

Hér með lýsi ég því yfir að ritgerð þessi er samin af mér og að hún hefur hvorki að hluta til né í heild verið lögð fram áður til hærri prófgráðu.

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Svavar Örn Guðmundsson

Abstract

Crangon crangon was first discovered in Iceland in 2003 and now, seven years later, it has become an established species in the marine coastal community. Not much is known about the species in Icelandic waters and here we try to comprehend the population dynamics of the brown shrimp in Helguvík bay, southwest Iceland. Sampling was done at Helguvík bay from May to September in 2008 and from spring of 2009 until early fall of 2010. Individuals from 2008 (n = 652) were weighed, measured and sex was identified. Density and sex ratio were also calculated. Fecundity and reproductive output were calculated from a subsample of 28 shrimps and fitted with a simple linear model. Densities up to 1824 individuals per 100 m2 were observed (Range: 10 - 1824). Sex ratio and density varied a lot between months, which is not unusual in shrimp populations. In contrast to other studies from established populations, no relationship was found between the female size and fecundity or reproductive output. However, reproductive output was similar in Helguvík bay (0.13) and in the Irish Sea (0.12) for the summer brood and the sex ratio was similar to other findings.

Key words: *Crangon crangon*, brown shrimp, fecundity, reproductive output, population dynamics, sex ratio, *appendix masculine*, Iceland.

Úrdráttur

Sandrækjan *(Crangon crangon)* fannst fyrst svo vitað sé á Íslandi árið 2003 og núna sjö árum seinna er hún orðin mikilvægur hluti af grunnsævisfánunni við Íslandsstrendur. Lítið hefur verið fjallað um tegundina við Ísland, en hér verður ljósi varpað á líffræði sandrækjunnar í Helguvík á Álftanesi. Sýnum var safnað frá maí fram í september árið 2008 og frá vori 2009 fram á haust 2010. Þéttleiki var metinn og rækjurnar lengdarmældar. Árið 2008 var þyngd og lengd mæld, og kyngreint úr hlutsýni (n = 652). Frjósemi og hlutfall eggja af þyngd kvendýra var reiknuð út frá smærra hlutsýni er samanstóð af 28 rækjum. Þéttleiki mældist mestur 1824 einstaklingar á hverja 100 m^2 (Spönn: 10 – 1824). Kynhlutfall og þéttleiki voru breytileg á milli mánaða, sem er ekki óalgengt hjá rækjustofnum. En ólíkt öðrum rannsóknum af *C. crangon*, fannst ekkert samband á milli stærðar kvendýra og frjósemi þeirra annars vegar eða stærðar og hlutfalli eggja af heildarþyngd hins vegar. Hlutfall eggja af heildarþyngd sumargots í Helguvík og í Írlandshafi var þó svipað eða 0.13 og 0.12, einnig var kynhlutfallið svipað hér og komið hefur fram í öðrum rannsóknum.

Lykilorð: *Crangon crangon*, sandrækja, frjósemi, stofnstærðarsveiflur, kynhlutfall, *appendix masculine*, Helguvík, Álftanes.

Acknowledgments

I want to thank Dr. Guðrún Marteinsdóttir and the MARICE lab at the University of Iceland for all their support and help during this project. Especially, I want to thank Jónas Páll Jónasson for his assistance and critical reading and Eric dos Santos for his critical reading. Special mention goes to Björn Gunnarsson and Lovísa Ólöf Guðmundssdóttir for their assistance and Dr. Reinhard Saborowski for lending me his figures (Figure 2).

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1 Introduction

The common or brown shrimp *Crangon crangon* is a member of the family Crangonidae, which includes 24 species (Grave et al. 2009). The brown shrimp is one of the few crangonid shrimp that is of commercial value. This species is important in the German Bight where the Germans land annually over 15 000 tons of *C. crangon* and the Dutch and the Danish over 20 000 tons each. North Sea annual landings are 25 000 – 30 000 tons with a market value of about 50 - 70 million Euro (Revill and Holst 2004). *C. crangon* is widely distributed in the coastal areas of the eastern Atlantic (Oh and Hartnoll 2004; Björn Gunnarsson et al. 2007). It lives on sandy or muddy bottom in shallow coastal waters from the White Sea in the north to Morocco in the south. It is also found in the Mediterranean, the Baltic and the Black seas (Oh and Hartnoll 2004).

The brown shrimp is an important species in the coastal marine community. It is regarded to be the most important carnivore of the Wadden Sea tidal zone (Phil and Rosenberg 1984; Kuipers and Dapper 1981). Juvenile brown shrimp mainly prey on meiofaunal species such as ostracods and harpacticoids, but larger shrimps tend to select macrofaunal species like the sand clam (*Mya arenaria)*, cockle (*Cardium edule)*, mud worm (*Nereis spp*.), mud shrimp (*Corophium volutator)* and juvenile plaice (*Pleuronectes platessa)* (Phil and Rosenberg 1984; Agnar Ingólfsson 2010). The shrimp is, in turn, an important prey for many species of fish, for instance cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) (Siegel et al. 2008; Tiews 1970, 1978). Therefore, fluctuations in the stock size of *C. crangon* have an immediate effect on commercial fishing and the coastal marine food web (Siegel et al. 2008). Fluctuations in *C. crangon* population size have been reported. Predation and water temperature are believed to be the main causes (Oh et al. 1999). Oh et al. (1999) found that in the Irish Sea the population size was not significantly different in the years 1995, 1997 and 1998. In 1996, however, there was a significant decrease in the population size and it coincided with colder temperatures recorded that year.

Reproductive strategies of crangonid shrimps are generally quite similar (Oh and Hartnoll 2004). Female *C. crangon* become mature in their second year at about 50 mm long and males mature at about 30 mm in length (Lloyd and Yonge 1947). Age at maturity can differ among regions and there are many reports of smaller shrimps carrying eggs (e.g. Lloyd and Yonge 1947, Wollebaek 1908). The brown shrimp is an ovoviviparous animal that has internal fertilization and carries the eggs under the abdomen on carrying setae until they are ready to hatch. After the female molts from the 'neuter' to the egg carrying condition she is ready for copulation. The male injects a sperm package into the female during copulation and soon after that the female buries herself in the sand. Spawning occurs instantly for the smallest females but about 24 hours later for larger shrimps, and up to 48 hours later for the largest shrimps (Lloyd and Yonge 1947). The reproductive season generally ranges from January to September. The spawning season has two discrete peaks: one in winter/early spring, called the winter brood (ranges from January to June) and the other in the summer, called the summer brood (ranges from July to September) (Oh and Hartnoll 2004; Temming and Damm 2002).

Since there are more mature and ovigerous females that carry larger eggs in the winter brood than in the summer brood, the winter brood is considered to be the main breeding season (Oh and Hartnoll 2004; Kuipers and Dapper 1984; Boddeke 1982). Siegel et al. (2008) observed in the North Sea population that the ratio of females in the smallest size classes was around 50%, then the ratio decreases in the 30 – 45 mm classes and at 60 mm class the population is almost 100% females. Due to those observed changes in the sex ratio in relation to size, speculation about sex change in *C. crangon* has been ripe and many papers have been published on that matter. Boddeke (1962) suggested that *C. crangon* is a protandric hermaphrodite, thus changing sex after reaching a certain size, while others (Meixner 1969; Tiews 1954; Lloyd and Yonge 1947) did not observe any sex changes in their studies.

The brown shrimp was found in Iceland for the first time in 2003, and is believed to have colonized the Icelandic coastal waters between 2001 and 2003 (Björn Gunnarsson et al. 2007). Most likely the brown shrimp was accidentally introduced to Iceland by ballast water since the planktonic larvae is too short lived to reach Iceland by currents (Agnar Ingólfsson 2010). And since it is found in Arctic waters in northern Norway and Russia, colonization is hardly because of temperature increase in recent years (Björn Gunnarson et al. 2007). Nothing is known about the reproductive biology of *C. crangon* in the newly colonized Icelandic waters. Here, first attempts are made to estimate density, sex ratio, fecundity and reproductive output (RO) in Icelandic waters.

2 Materials and methods

2.1 Sampling

Shrimps were caught with a beam trawl in Helguvík bay at Álftanes, southwest Iceland (Figure 1). They were collected twice a month for five months in the summer period from May to September of 2008 - 2010 and once a month in the winter months of 2009 and 2010.

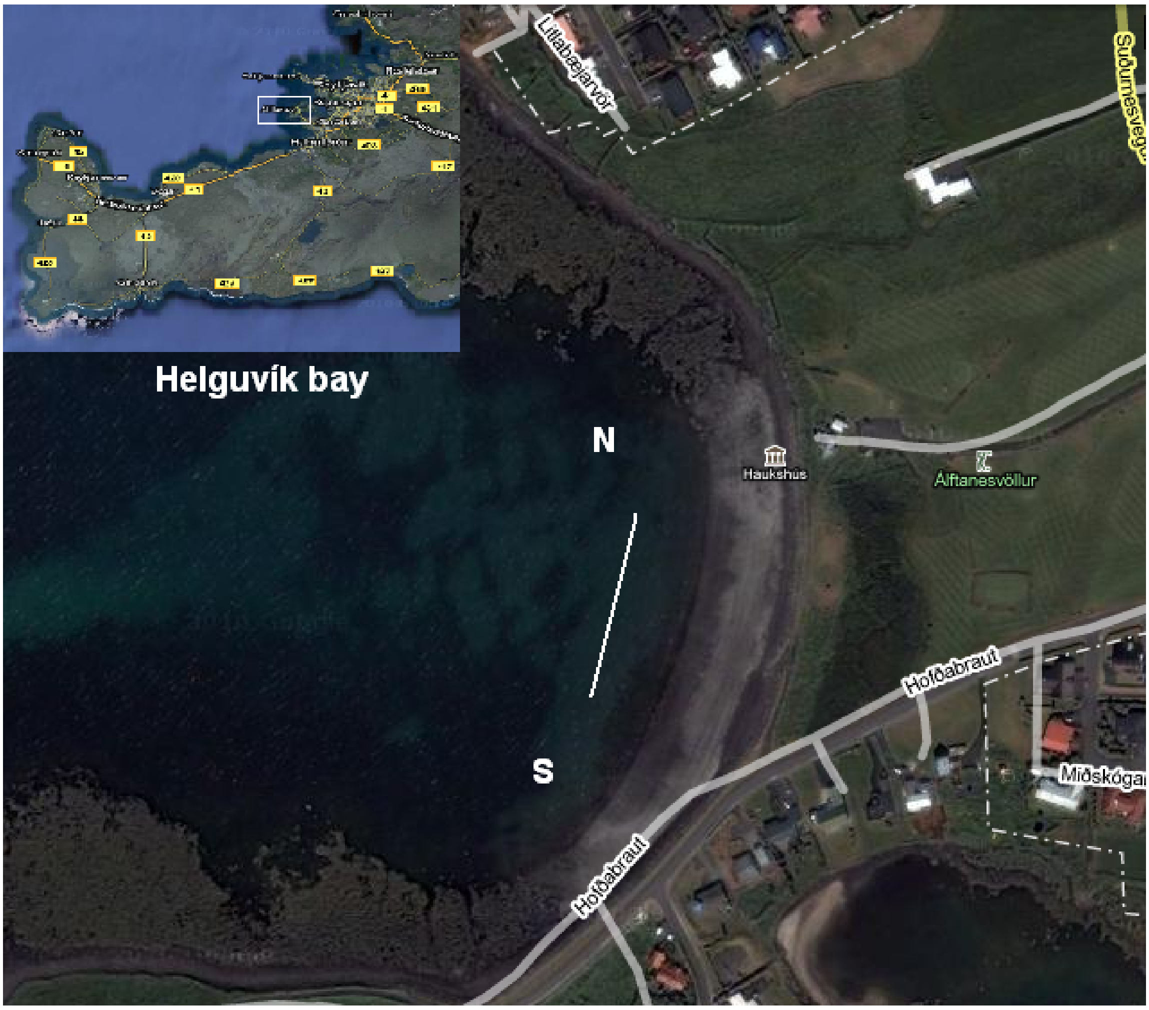

Figure 1: Aerial overview of Helguvík bay at Álftanes, Iceland. The line indicates towing place and direction.

The beam troll was 1 m wide and 5.5 m long with a tickler chain and trawl opening of 1 m^2. It had 8 mm mesh size in the main body and 5.5 mm mesh size in the cod end. Towing speed was kept as constant as possible at 35 m/min. and pulled by two people for 50 m at 0.5 - 1m depth parallel to the shore (Figure 1). Usually there were 3 tows taken each catch day, but severe currents and/or weather occasionally limited the number of tows. The first tow was from south to north, the second was from north to south, and the third tow the same as the first.

2.2 Sample analysis

From every tow all shrimps were length measured unless the catch numbers were very high (75 or more individuals), then a subsample was taken. Specimens were length measured from the posterior margin of the orbit and to the tip of the telson to the nearest 0.01 millimeter. Furthermore, shrimps were picked randomly from the total sample in the summer of 2008 for further analysis; those shrimps were fixed in formalin for at least 48 hours and then transferred to alcohol. Length was measured again to the nearest millimeter, wet weight was measured to the nearest 0.01 gram and sex identified (n = 652).

Sex was classified by the size and shape of the endopodite. One major morphological difference between the sexes is a much smaller endopodite of the first pleopods on mature males in relation to that on mature females. Endopodites on males are spine-like, round, pointed, lie close to or behind the exopodite, and are without hair (Schatte and Saborowski 2006; Tiews 1954; Dornheim 1969). Female endopodites are modified to carry eggs and are larger than male's, they are flat and spatula-shaped, they bare setae and are never concealed by the exopodite (Schatte and Saborowski 2006). On the second pair of pleopods, which is of the same size on both sexes, the male endopod has the *appendix masculine*, which is not visible to the naked eye (Figure 2). Individuals less than 20 mm in length are difficult to sex, since the endopodite of the first pleopod is of similar size in both sexes and they were therefore classified as juveniles (Lloyd and Yonge 1947).

Density (individuals per 100 m^2) was calculated per each individual tow, and mean density for every month according to the following equation:

$$Density = (C / D) / W * 100 \quad \text{(Eq: 1).}$$

Where D is the tow length, C is the total catch of shrimp and W is the width of the trawl (1 m). No corrections where made for gear efficiency.

2.3 Fecundity and reproductive output

Fecundity was estimated from the June, July, and August catches of 2008. In total, 28 egg carrying females were used to calculate fecundity and reproductive output. Eggs were cleaned off the females' egg carrying setae with forceps. A subsample of 200 - 500 eggs was counted, egg number in the subsample depended on the total number of eggs the female was carrying. The subsample, the remaining eggs along with the body of the female was dried at 60°C for 48 hours and dry weight was measured to the nearest 0.01 milligram (mg).

Fecundity was calculated by the total amount of eggs that the female produces. Total number of eggs was estimated from the proportion of eggs in the subsample to the total sample, according to the following equation:

Fecundity = *(total weight of sample/weight of subsample)*nr. eggs in subsample* (Eq: 2)

Reproductive output (RO) was calculated, with the following equation:

RO = *dry weight of the female/total dry weight of the brood.* (Eq: 3)

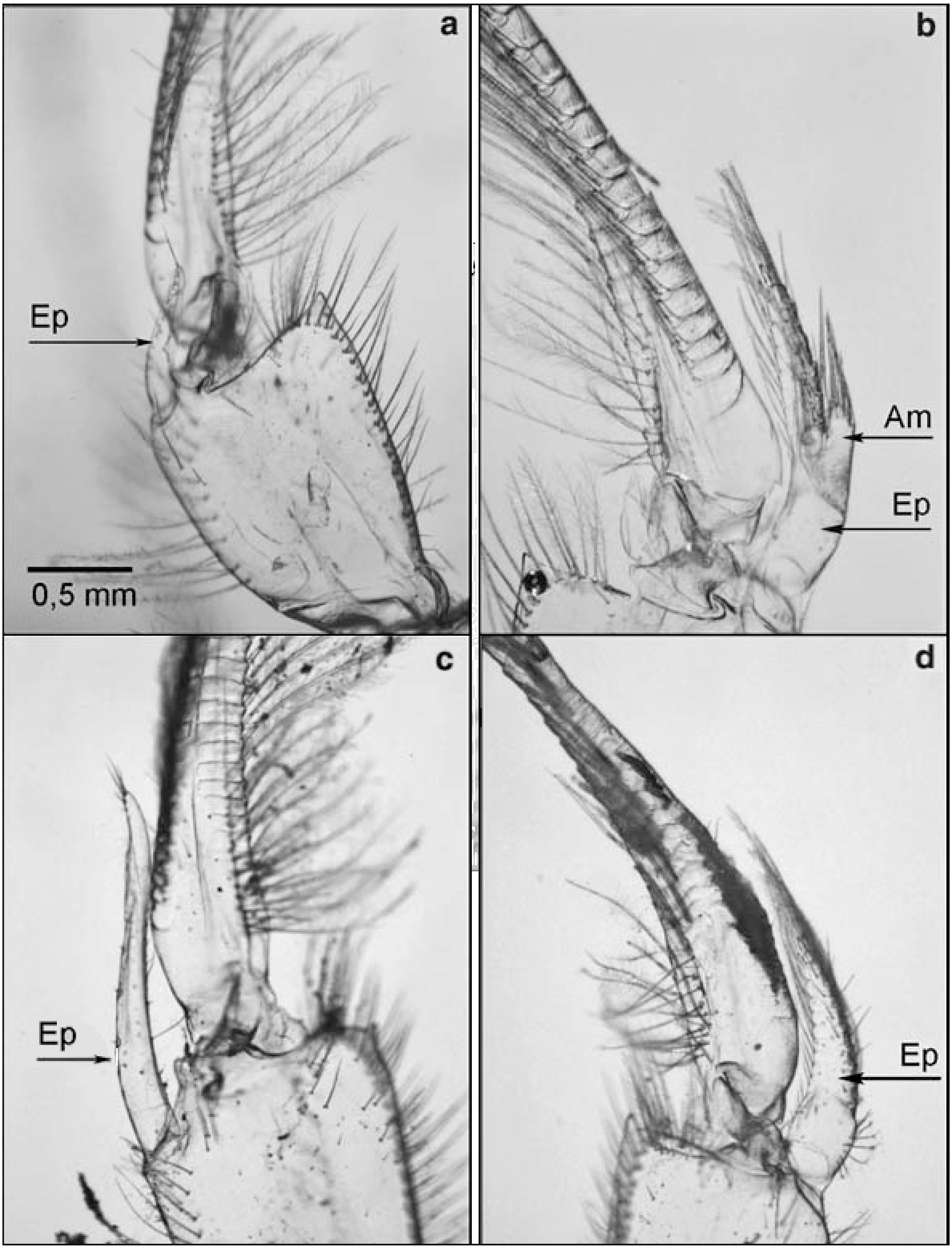

Figure 2: External reproductive organs of brown shrimp (*C. crangon*). First pleopod (A) and second pleopod (B) of a male and first pleopod (C) and second pleopod (D) of a female brown shrimp. Endopodites (EP) and *appendix masculine* (AM) (Schatte and Saborowski 2006).

3 Results

3.1 Size distribution

The length of the brown shrimp in the summer of 2008 ranged from 7.92 mm to 58.06 mm with a mean length of 32.92 mm, and the weight ranged from 0.00 g (was lighter than the scale permitted) to 2.16 g, with a mean weight of 0.5 grams (Table 1).

Table 1: Size distribution of *C. cragnon* during the five month study period of 2008.

date	Min. length (mm)	Max. length (mm)	Mean length (mm)	Min. wet weight (g)	Max. wet weight (g)	Mean wet weight (g)	N
May	17.06	51.80	32.80	0.05	1.90	0.39	152
June	23.73	47.95	36.62	0.15	1.30	0.56	100
July	7.92	55.18	37.89	0.00	1.76	0.78	100
Aug.	8.06	56.35	31.23	0.01	2.16	0.54	100
Sept.	9.41	58.06	26.08	0.01	2.14	0.30	200

According to the length frequency distribution we observed two distinct recruitment peaks per year. In June and July (Julian day 191-209) of 2008 through to 2010 we observed a great influx of juveniles coming into the population (Figure 3 and 4). Those juveniles came from the winter brood that ranges from January to June. In January 2010 (Julian day 14) we also had a distinct peak in recruitment originating from the summer brood of the previous year that ranges from July to September (Figure 4).

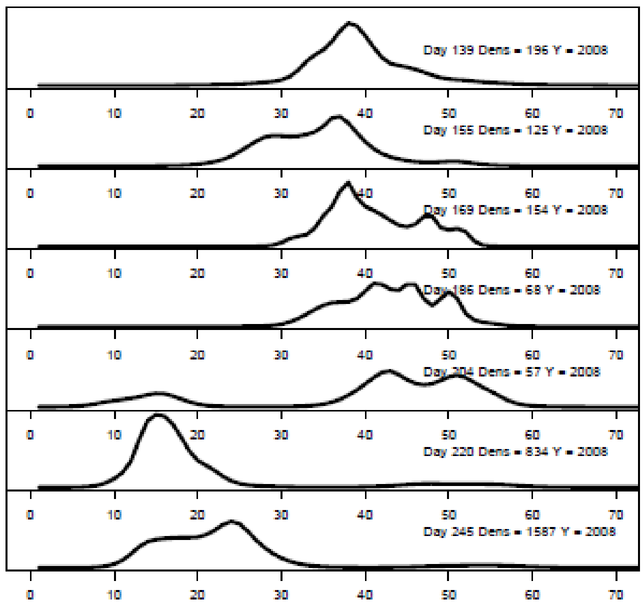

Figure 3: Length frequency distribution of *C. crangon* in Helguvík bay, Álftanes in the summer of 2008. Day refers to a julian day. Densities are in number of individuals per 100 m^2.

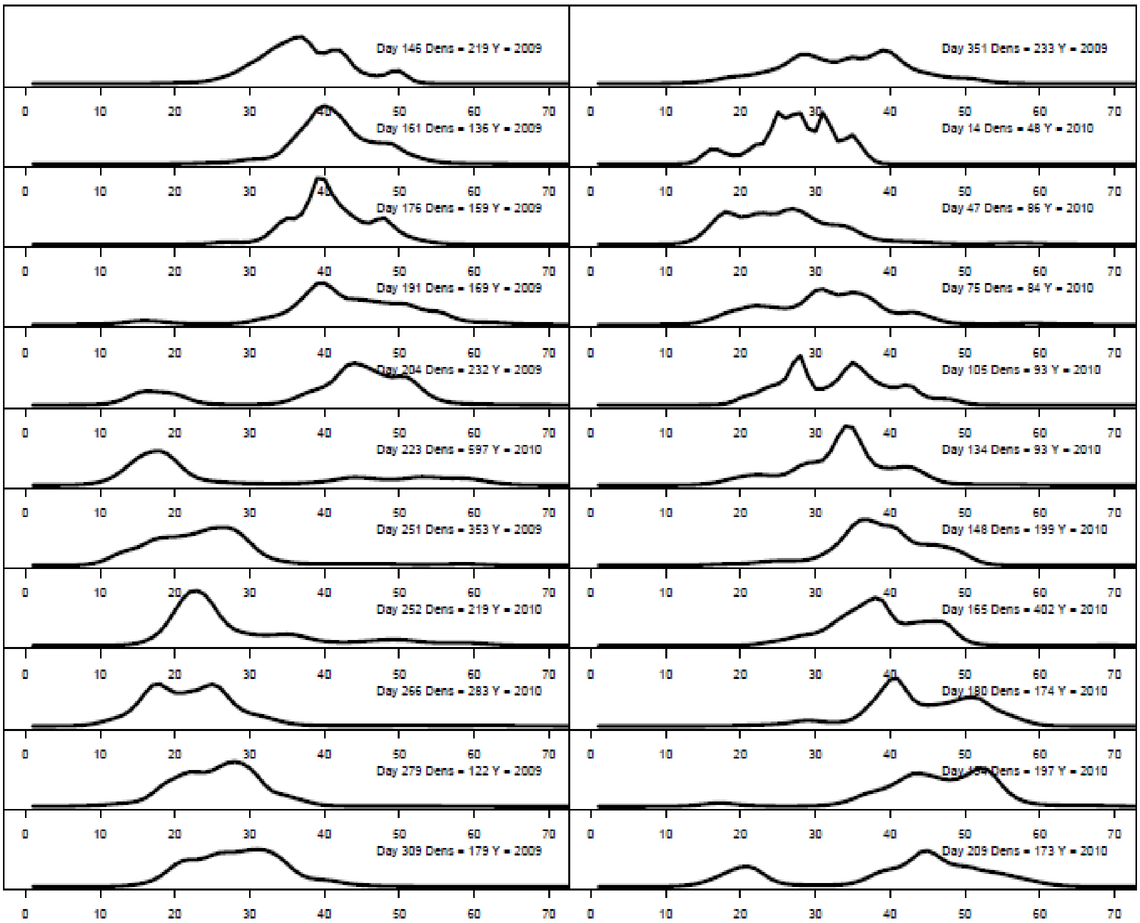

Figure 4: Length frequency distribution of *C. crangon* in Helguvík bay, Álftanes from 2009 – 2010. Day refers to a julian day. Densities are in number of individuals per 100 m^2.

3.2 Density

Monthly mean density calculations (Eq: 1) showed fluctuations during the study period (Table 2). Mean densities increased during the summer months in 2010 and decreased again in the winter months (2009 and 2010). The density was high in spring and early summer (May – June) and decreased generally in July. The recruitment period in late June and July corresponded to an increase in density in August and September, with strong recruitment in 2008 compared to 2009 and 2010. The lowest density was 48 individuals per 100 m^2 in January 2010 and the highest density was found in September of 2008 with 1573 individuals (Table 2 and 3).

Table 2: Summary of density calculations during sampling, sampling was made from 2008 – 2010.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Okt.	Nov.	Dec.	Mean annual density
2008	x	x	x	x	196	140	58	834	1573	x	x	x	560,2
2009	x	x	x	x	214	147	201	387	353	122	179	233	229,5
2010	48	86	85	93	146	288	185	244	257	x	x	x	159,1

3.3 Sex

Sex ratio tends to vary a lot in *C. crangon* populations. In Helguvík bay the female ratio varied, both between months and also in relation to size. Of all the individuals that were sexed, 17 % were juveniles, 35 % males and 48 % females. The sex ratio was even in May and June, but juveniles start to enter the population in July (Figure 5). In August 45 % the population are juveniles. Females were 62 % of the population in September with both fewer juveniles and fewer males than in the previous month.

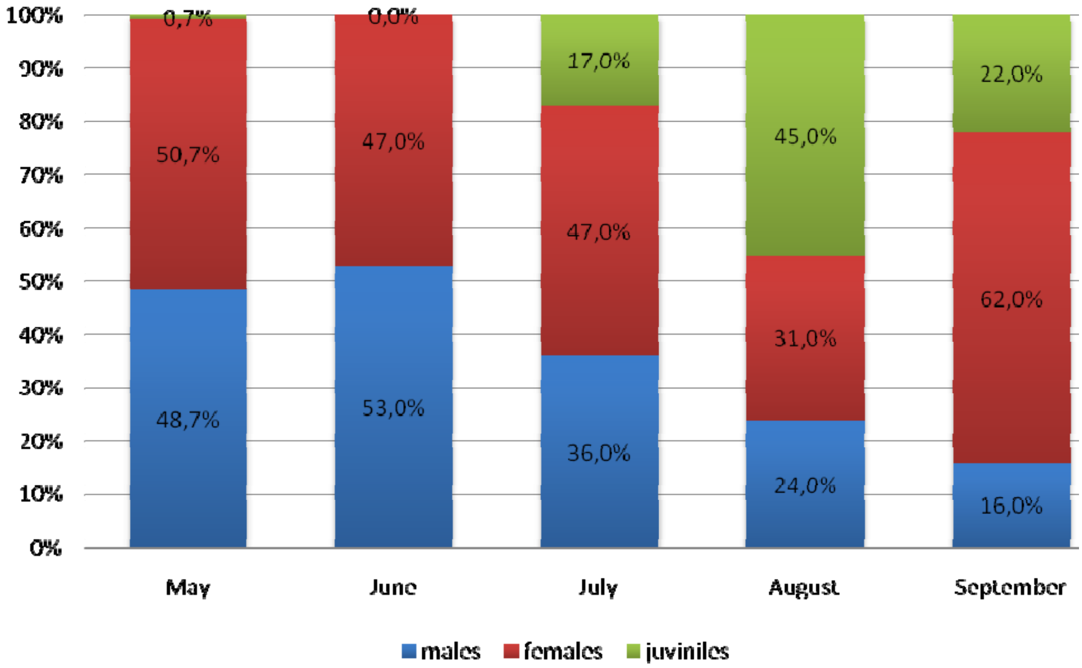

Figure 5: Monthly sex ratio during the study period in 2008.

Females were divided up into four size classes. The female sex ratio in Helguvík bay fluctuated a lot and ranged from 75 % in the smallest size class, down to 33 % in the second smallest size class and up to 100 % in the largest size class (range: 33 % - 100 %). A variation in the sex ratio is also apparent when it is distributed between months (Figure 6), but the 100% female ratio in the largest size classes persists.

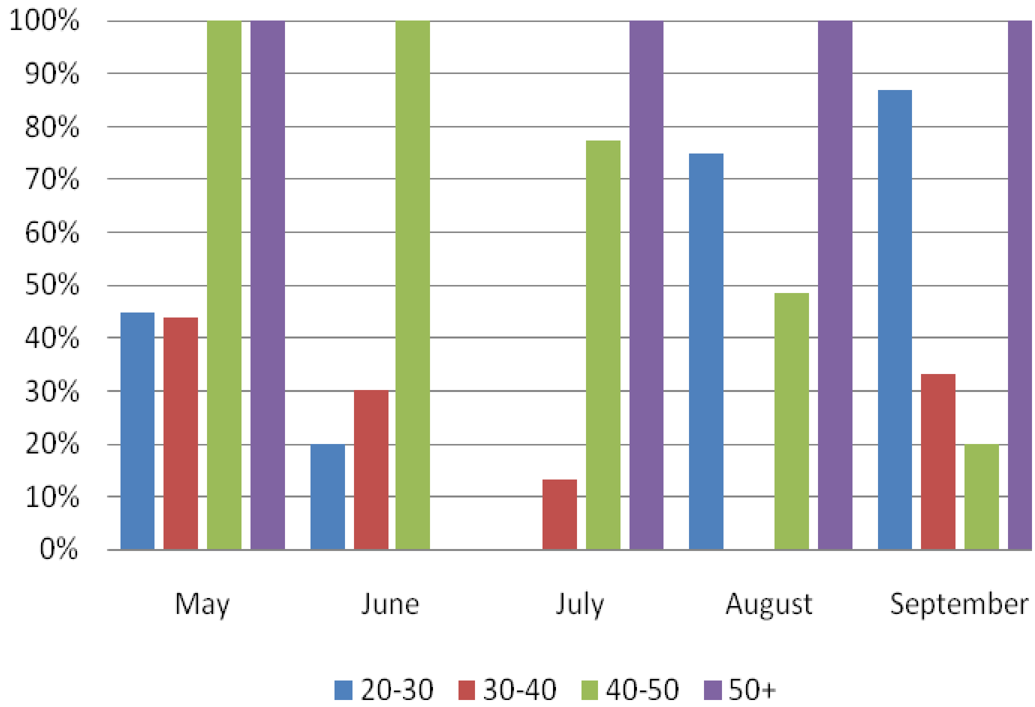

Figure 6: Female frequency distribution per size class and month in Helguvík bay.

3.4 Fecundity and reproductive output

Fecundity was highly variable and not correlated to female size. Maximum fecundity was about 4177 eggs for a 46.58 mm long female, the minimum fecundity was 214 eggs for a 47.23 mm long female and mean fecundity was 1687 eggs with the mean size of the female at 47.22 mm (Table 4). Our results indicate that there was no correlation between fecundity and female length ($\rho > 0.05$), nor with the female dry weight ($\rho > 0.5$). Also the relationship between the dry weight of the female and the dry weight of the brood was not significant ($\rho > 0.5$, Figure 7).

Mean reproductive output (RO) for the summer brood was 0.13 (range 0.01 - 0.28), where the mean length of the females was 47.22 mm (range: 41.01 – 51.94 mm, Table 4). There was no correlation between reproductive output and the length of the females ($\rho > 0.05$, Figure 7).

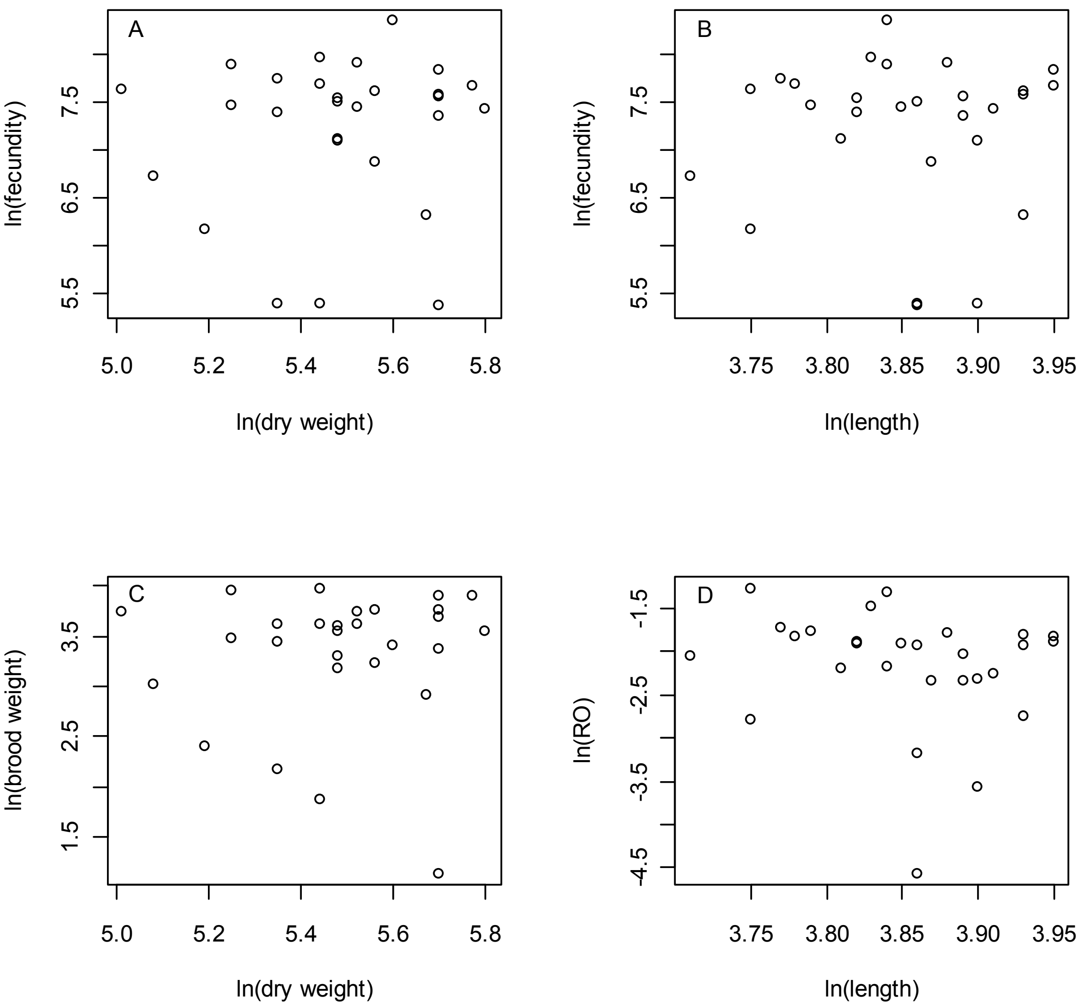

Figure 7: Fecundity and reproductive output (RO) of brown shrimp. Fecundity of brown shrimp in relation to dry weight (A) and length (B). Brood weight of brown shrimp in relation to dry weight (C) and reproductive output in relations to length (D).

4 Discussion

In the Helguvík population, the recruitment of the winter brood is a month later than in the North Sea population (Temming and Damm 2002). According to Temming and Damm (2002) the winter egg production followed by the recruitment of juveniles (10 – 20 mm) in May/June is what makes up the autumn commercial catch. Juveniles enter the Helguvík bay population in July (day 191 – 204) from the winter brood and with a small peak in January from the summer brood. This difference in recruitment time could be due to latitudinal variation. Oh and Hartnoll (2004) and Kuipers and Dapper (1984) found that breeding seasons differ between latitudes. In Øresund, the breeding season ranges from June to September but in Bergen, Norway it ranges from August to November (Kuipers and Dapper 1984). Weather conditions can also affect recruitment. Temmings and Damms (2002) showed that after cold winters the recruitment peak was more definite and occurred weeks later. According to our data, the female *C. crangon* grow to be larger than the males. That is not uncommon for shrimp populations. Usually the number of large females is much higher than that of large males (Schatte and Saborowski 2006; Boddeke 1976; Oh et al. 1999) and large males are almost absent in commercial shrimp catches (Schatte and Saborowski 2006; Martens and Redant 1986; Tiews 1987). We observed in Helguvík bay, that female brown shrimps become almost completely dominant in the largest size class (> 50 mm). Siegel et al. (2008) observed the same trend in the North Sea population, where the ratio of females in the smallest size classes (less than 30 mm) was around 50%, the ratio decreased in the 30 – 45 mm classes, and at size classes larger than 50 mm the female ratio regularly increases to 100%. In Helguvík bay we had a similar trend, where the sex ratio fluctuated in the smaller size classes but over 50 mm the population was almost exclusively females. Many factors can affect sex ratio, such as sex change, mortality, gender-linked growth rates, and migration. Faster growth rate has been reported in studies made by Meixner (1970) and Tiews (1954) and mortality is higher for males since the sex ratio is almost the same at the beginning but as mentioned above, females sex ratio is much higher in the bigger size classes (Siegel et al. 2008).

Many studies and speculations have been made on sex change in *C. crangon* with conflicting results. Boddeke (1965) reported sex change in the brown shrimp but Siegel et al. (2008) and Lloyd and Yonge (1946) did not observe any sex reversals in their studies. Schatte and Saborowski (2006) did observe sex reversals and they reported males changing their external sexual characteristics during a single molt cycle. However, due to low number of reversals they concluded that the brown shrimp is a facultative protandric hermaphrodite. This conclusion differs from Boddeke's (1962) research where he concluded that *C. crangon* was an obligate protantric hermaphrodite and thus changing sex after reaching a certain size.

Fecundity is considered a good indication of the reproductive fitness of a crustacean population (Bilgin and Samsun 2006; Nazari et al. 2003), and it is directly influenced by natural selection (Bilgin and Samsun 2006; Stearns 1977). In malacostracan crustaceans, fecundity is often positively correlated with the female body size (Bilgin and Samsun 2006; Chockley and Mary 2003). Bilgin and Samsun (2006) calculated fecundity for the brown shrimp population in the Black Sea (n = 35). Their mean shrimp size was 59 mm and mean fecundity was 2297 eggs per female. They found that fecundity was positively correlated to the size of the female. Earlier studies have also found that fecundity was the same for both summer and winter brood but the eggs of the winter brood are larger in size and are heavier than the eggs of the summer brood (Oh and Hartnoll 2004). Here we got lower fecundity values and, while our average shrimp size was also lower, we did not find a correlation with size.

Difference in reproductive output in crustacean species is mostly due to differences in female body size. Factors such as egg size and latitudinal variation can also have an effect (Boddeke 1982). Oh and Hartnoll (2004) calculated reproductive output (RO) for the brown shrimp in the central Irish Sea and found that their winter brood females had on average RO = 0.20 (n = 126) and in the summer brood RO was on average 0.12 (n = 55). Our study only had data from the summer brood so that Oh's and Hartnolls' (2004) findings are similar to our findings of RO = 0.13 (n = 28). According to the Helguvík data, there was not a positive relationship between fecundity and body size or between reproductive output and body length. These findings might be due to the small sample size and/or small population size as well as a narrow length distribution of the shrimp.

The brown shrimp was found in Iceland for the first time in 2003 (Björn Gunnarsson et al. 2007), therefore, it can be considered an established species in the Icelandic coastal community. With the introduction of *C. crangon* the coastal community probably will have to adapt accordingly considering that the shrimp is usually regarded as one of the most important carnivores of the coastal community where their populations have a longer history (Phil and Rosenberg 1984; Kuipers and Dapper 1981). Direct effects on the community are not known but common garden experiments have been made to simulate the introduction of the brown shrimp into a coastal population. As mentioned before, *C. crangon* feeds mostly on meiofaunal and macrofaunal species including juvenile plaice (*Pleuronectes platessa)* (Phil and Rosenberg 1984; Agnar Ingólfsson 2010). Nilsson et al. (1993) observed no significant differences in either meiofaunal and macrofaunal communities with the introduction of *C. crangon* into the new system. Although the brown shrimp is an important prey for many commercially important fish species (Siegel et al. 2008; Tiews 1970, 1978), the effect of an increased brown shrimp population size in Iceland is unknown. Densities varied a lot during the study period with distinct increases in the summer months compared to the winter months. Oh et al. (1999) observed annual fluctuations in their estimated population size. Their study had distinct peaks in population size in July, August and September, sometimes starting in June. Those seasonal fluctuations occurred at the same time as the seasonal change in sea temperature. There was a positive relationship between the population estimate and the ambient seawater temperature. The Helguvik bay population seemed to have a distinct peak in density in May – June and then again in August – September with the recruitment of the winter brood. With longer sample series we could observe more distinct trends in density after months and compare it more effectively with environmental parameters.

For future studies of the *C. crangon* population in Iceland it would be good to have fecundity data that ranges for at least a whole year so we could cover both the summer and the winter brood. Egg size and weight measurements would benefit the study.

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Appendix 1

Table 3: Tow information, catch numbers and density for Helguvík bay.

Cruise	Tow nr.	Date	Julian	Depth	Tow length	Tow direction	Number	Nr. 100m^2*	Mean nr.100 m^2 per month**
27	1	18.5.2008	139	0.50	40	N	85	213	
28	2	18.5.2008	139	0.75	40	S	72	180	196
29	1	3.6.2008	155	0.25	60	N	67	112	
30	2	3.6.2008	155	0.75	60	S	55	92	
31	3	3.6.2008	155	0.50	50	N	86	172	
32	1	17.6.2008	169	0.50	60	N	59	98	
33	2	17.6.2008	169	0.75	60	S	144	240	
34	3	17.6.2008	169	0.75	60	N	75	125	140
35	1	4.7.2008	186	1.0	65	N	25	38	
36	2	4.7.2008	186	0.80	60	S	33	55	
37	2	4.7.2008	186	0.50	60	N	46	77	
38	4	4.7.2008	186	0.30	60	S	43	72	
39	1	22.7.2008	204	1.0	55	N	18	33	
40	2	22.7.2008	204	1.0	50	S	5	10	
41	3	22.7.2008	204	0.70	50	N	18	36	
42	4	22.7.2008	204	0.70	50	S	21	42	
43	5	22.7.2008	204	0.30	50	N	68	136	
44	6	22.7.2008	204	0.30	50	N	43	86	58
45	1	7.8.2008	220	0.60	60	N	398	663	
46	2	7.8.2008	220	0.70	60	N	457	762	
47	3	7.8.2008	220	0.70	60	S	646	1077	834
48	1	1.9.2008	245	0.75	50	N	752	1504	
49	2	1.9.2008	245	0.50	50	S	912	1824	
50	3	1.9.2008	245	0.75	50	N	696	1392	1573
51	1	25.5.2009	146	0.75	50	N	76	152	
52	2	25.5.2009	146	0.75	50	S	70	140	
53	3	25.5.2009	146	0.50	50	N	175	350	214
54	1	10.6.2009	161	0.50	50	N	62	124	
55	2	10.6.2009	161	0.25	50	S	50	100	
56	3	10.6.2009	161	0.50	50	N	92	184	
57	1	25.6.2009	176	0.50	50	N	78	156	
58	2	25.6.2009	161	0.50	50	S	86	172	
59	3	25.6.2009	161	0.50	50	N	73	146	147
60	1	10.7.2009	191	0.70	50	-	88	176	

61	2	10.7.2009	191	0.70	50	-	74	148	
62	3	10.7.2009	191	0.50	50	-	92	184	
63	1	23.7.2009	204	0.50	50	N	74	148	
64	2	23.7.2009	204	0.50	50	S	96	192	
65	3	23.7.2009	204	0.40	45	N	160	356	201
66	1	11.8.2009	223	0.50	50	-	146	292	
67	2	11.8.2009	223	0.75	50	-	174	348	
68	3	11.8.2009	223	0.50	50	-	224	448	
69	1	26.8.2009	238	0.75	50	N	264	528	
70	2	26.8.2009	238	0.75	50	S	116	232	
71	3	26.8.2009	238	1.0	50	N	238	476	387
72	1	8.9.2009	251	0.75	50	N	190	380	
73	2	8.9.2009	251	0.75	50	S	182	364	
74	3	8.9.2009	251	0.75	40	N	126	315	353
75	1	6.10.2009	279	0.75	50	N	59	118	
76	2	6.10.2009	279	1.0	50	S	51	102	
77	3	6.10.2009	279	0.75	50	N	73	146	122
78	1	5.11.2009	309	1.0	50	N	101	202	
79	2	5.11.2009	309	1.0	50	S	67	134	
80	3	5.11.2009	309	1.0	50	N	101	202	179
81	1	17.12.2009	351	1.0	50	N	180	360	
82	2	17.12.2009	351	1.0	50	S	104	208	
83	3	17.12.2009	351	1.0	50	N	66	132	233
84	1	14.1.2010	14	1.0	40	N	26	65	
85	2	14.1.2010	14	1.0	30	S	9	30	48
86	1	16.2.2010	47	0.75	50	N	15	30	
87	2	16.2.2010	47	0.75	50	S	61	122	
88	3	16.2.2010	47	0.75	50	N	53	106	86
89	1	16.3.2010	75	0.75	50	S	32	64	
90	2	16.3.2010	75	0.50	40	N	42	105	85
91	1	15.4.2010	105	0.50	20	N	8	40	
92	2	15.4.2010	105	0.50	30	N	44	147	93
93	1	14.5.2010	134	0.50	50	N	60	120	
94	2	14.5.2010	134	0.75	50	S	25	50	
95	3	14.5.2010	134	0.75	50	N	54	108	
96	1	25.5.2010	148	0.75	50	N	75	150	
97	2	25.5.2010	148	0.50	50	S	105	210	
98	3	25.5.2010	148	0.50	50	N	119	238	146
99	1	14.6.2010	165	0.75	47	N	100	213	
100	2	14.6.2010	165	0.50	50	S	206	412	
101	3	14.6.2010	165	0.40	50	N	290	580	
102	1	29.6.2010	180	0.50	50	N	90	180	
103	2	29.6.2010	180	0.50	50	S	89	178	

104	3	29.6.2010	180	0.50	50	N	82	164	288
109	1	13.7.2010	194	0.50	50	N	79	158	
110	2	13.7.2010	194	0.50	50	S	115	230	
111	3	13.7.2010	194	0.40	50	N	83	166	
112	1	28.7.2010	209	0.50	50	N	116	232	
113	2	28.7.2010	209	0.75	50	S	96	192	
114	3	28.7.2010	209	0.50	50	N	67	134	185
115	1	11.8.2010	223	0.50	50	N	171	342	
116	2	11.8.2010	223	0.60	50	S	85	170	
117	3	11.8.2010	223	0.40	50	N	96	192	
118	1	26.8.2010	238	0.50	50	N	152	304	
119	2	28.8.2010	238	0.75	50	S	122	244	
120	3	28.8.2010	238	0.40	50	N	106	212	244
121	1	9.9.2010	252	0.65	45	N	81	180	
122	2	9.9.2010	252	0.65	50	S	168	336	
123	3	9.9.2010	252	0.65	50	S	90	180	
124	1	23.9.2010	266	0.60	50	N	138	276	
125	2	23.9.2010	266	1.0	50	S	153	306	
126	3	23.9.2010	266	0.50	50	N	133	266	257

* Number of individuals per 100m^2
** Average number of individuals per 100m^2 in every month.

Appendix 2

Table 4 Fecundity and reproductive output data (n = 28).

Id	Length (mm)	Wet weight (g)	Dry weight (g)	Nr. eggs total	RO
0808_1	46.58	1.48	0.27	4176.51	0.11
0808_2	49.43	1.58	0.24	1207.87	0.10
0808_3	51.94	1.91	0.30	2526.94	0.16
0808_4	51.94	1.92	0.32	2123.98	0.15
0808_5	47.31	1.23	0.21	221.71	0.04
0808_6	49.58	1.46	0.23	222.27	0.03
0808_7	50.87	1.71	0.26	2006.57	0.16
0808_8	49.91	1.78	0.33	1686.61	0.10
0808_9	51.16	1.69	0.30	1937.04	0.14
0808_10	50.89	1.63	0.29	547.34	0.06
0808_11	49.10	1.49	0.30	1544.75	0.10
0808_12	48.02	1.45	0.26	963.40	0.10
0708_1	48.64	1.67	0.25	2728.18	0.17
0708_2	47.23	1.29	0.30	214.00	0.01
0708_3	46.37	1.54	0.19	2654.19	0.27
0708_4	47.61	1.53	0.24	1796.50	0.14
0708_5	44.12	1.22	0.19	1734.68	0.17
0708_6	45.02	1.37	0.24	1218.42	0.11
0608_1	48.95	1.57	0.30	1911.56	0.13
0608_2	42.48	1.11	0.18	476.49	0.06
0608_3	43.59	1.26	0.21	2293.62	0.18
0608_4	45.42	1.43	0.24	1858.49	0.15
0608_5	45.98	1.45	0.23	2828.28	0.23
0608_6	43.73	1.25	0.23	2168.37	0.16
0608_7	46.90	1.46	0.25	1716.83	0.15
0608_8	41.01	0.93	0.16	837.71	0.13
0608_9	42.72	1.15	0.15	2048.67	0.28
0608_10	45.68	1.41	0.21	1598.81	0.15
Mean	47.22	1.46	0.25	1687.49	0.13
Maximum	51.94	1.92	0.33	4176.51	0.28
Minimum	41.01	0.93	0.15	214.00	0.01