Variation in abundance, diet, otolith zone patterns and black spot disease (*Cryptocotyle lingua*) of 0-group coastal cod (*Gadus morhua* L.) in northern Norway

Master Thesis in Marine Ecology
60 ECTS.

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November 2006

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TAKK TIL

Tromsø, 15.11.06

Så var to års arbeid over, og en rekke personer har på hver sin måte bidratt til at jeg ble ferdig. Først vil jeg takke Torstein Pedersen som hadde ideene til problemstillingene i denne oppgaven. Takk for din hjelp med innsamling av torsk, veiledning under opparbeiding av materialet og ved skriving av oppgaven. Takk til Roar Kristoffersen for generell veiledning om sortprikksyke og "bibelsk" lesning av oppgaven.

Takk til Marte Kanck, Ragni Olsson, Nina Henriksen, Charles Aas for hjelp ved innsamlingen av torsk. Håper dere hadde det like fint som meg.

Stor takk til alle "biologijentene" for en utrolig artig, spennende og lærerik studietid.
Vi møtes i Mexico i 2015!

Min familie og venner i trønderlag for støtte og oppmuntrende ord. Nå kommer jeg oftere hjem på besøk. Takk til min samboer for tålmodighet, støtte og photoshop ekspertise.

Elida Sandneseng

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ABSTRACT: Knowledge of the early life-history and habitat requirements of coastal cod is very sparse. Young of the year cod juveniles from three different locations in northern Norway were collected monthly from August to November 2005 using beach seine. Diet analyses based on stomach contents showed that 0-group cod mainly ate copepods, gammarids, polychaetes, mysids, shrimps and isopods. The three locations differed with regard to prey composition, and copepods were generally most abundant, but benthic (polychaetes) and hyperbenthic species (decapods) had the highest weight proportion. To investigate when the first hyaline (winter) zone is formed, length and width of 122 pairs of otoliths were measured and assessed into four zone pattern categories. The proportion of cod with a hyaline otolith zone increased from 20.5% in October to 67.9% in November. There were clear differences between the locations with regard to the otolith-width fish length relation, and this relation was lowest at the location with the highest cod abundance (Jøvik). Abundance and seasonal infection of the digenean parasite *Cryptocotyle lingua* differed between the three samplings locations, most likely due to differences in abundance of the intermediate host (the snail *Littorina littorea*). Cod from Njosken exhibited the heaviest infections, whereas fish from Makkjosen had some and those from Jøvik had almost no parasites. It is suggested that infection of this parasite can be used as a habitat indicator of the cod during summer and autumn.

INTRODUCTION

The cod in Norwegian waters north of 62ºN are divided in two main groups, Norwegian coastal cod and Northeast Arctic cod. The coastal cod is important for several predators, for instance harbour seal (*Phoca vitulina*), Great Cormorant (*Phalacrocorax carbo*) and Pollack (*Pollachius pollachius*) (Bergstad *et al.* 1987, Salvanes 1995, Berg *et al.* 2002). In addition, coastal cod is an important commercial species for the economy of small coastal villages in Norway. The main criteria for splitting these two groups have been different otoliths patterns between individuals of the two groups (Rollefsen 1934). For both groups the classification of otoliths is based on difference in form and size of the two inner opaque (summer) and hyaline (winter) zones. For Norwegian coastal cod the first hyaline zone is more elliptically formed than in Northeast Arctic cod, and the distance between the first and second hyaline zone is

greater for Norwegian coastal cod than for Northeast Arctic cod (Rollefsen 1934). Genetic surveys with the pantophysin gene (PANI) as a marker shows that the difference between Norwegian coastal cod and Northeast Arctic cod coincide well with surveys of otolith patterns (Fevolden and Pogson 1997, Berg *et al.* 2005). Further, the differences in number of vertebra also coincide with otolith and PANI patterns (Løken *et al*. 1994). Based on surveys of vertebra number and PANI, it looks like offspring from Norwegian coastal cod and Northeast Arctic cod can be mixed in the pelagic waters during summer, whereas Norwegian coastal cod offspring settles in the summer and early fall at shallow water depths (Løken *et al.* 1994).

LIFE HISTORY

Coastal cod can be found in the sublittoral zone and towards deeper water in nearby coastal banks. The spawning grounds used by coastal cod are at numerous locations inside fjords and partly in the same areas used by the Northeast Arctic cod (Jakobsen 1987). Tagging experiments have showed that the coastal cod is stationary (Jakobsen 1987). In contrast, the Northeast Arctic cod migrate over long distances, from their feeding area in the Barents Sea to the spawning area at the Norwegian coast (Bergstad *et al*. 1987). Average age at sexual maturity has been lower in coastal cod than in Northeast Arctic cod, but the fish length at maturity may vary between different areas (Berg and Pedersen 2001) due to environmental factors. Berg and Albert (2003) showed that there is only a small difference in length at age between coastal cod and Northeast Arctic cod, especially before maturation. However, average age maturity differed by more than 1 year, and Northeast Arctic cod was therefore 10% longer than coastal cod at age at 50% maturity. It has been suggested that there are differences in bottom settling strategies between coastal cod and Northeast Arctic juvenile cod. Løken *et al.* (1994) discussed settling strategies for coastal cod, and suggested that the macroalgae belt in the fjords provide refuge for juvenile cod from the large cannibalistic cod. The Northeast Arctic cod, on the other hand, settles in deeper waters, and juveniles that settles at deeper waters in the fjords may be exposed to a higher predation rate (Løken *et al.* 1994).

ZONING IN OTOLITHS OF JUVENILE COD

Although the distribution pattern of 0-group coastal cod seems to be different from Northeast Artic cod, there is very sparse knowledge about which factors that influences life history and otolith zone patterns during the first two years. Since otoliths are used as an individual record of size and growth, it is important to acquire knowledge about when the first zones are formed

and which factors that influence the zoning. Factors that might affect the relationship of otolith growth and somatic growth are also important due to the assumption of proportionality for back-calculation (Hare and Cowen 1995).

The interpretation of annual zones has been based upon subjective human interpretation. The otolith zone pattern in fish is influenced by biotic and abiotic factors such as temperature, light, growth, food supply and sexual maturity (Hopkins *et al.* 1986, Otterlei *et al.* 1999). The presence of larger otoliths in specimens, populations or species with lower somatic growth rates has been recognized as uncoupling, in which otolith grow independently of somatic growth rate. Although there are studies in which uncoupling were tested and did not occur (i.e. Dickey *et al.* 1997), it has been documented that at a given temperature, slower growing individuals has larger otoliths than fast growing individuals (Wright *et al*. 1990, Francis *et al.* 1993). The importance of phylogenetic and environmental influences varies depending on the life phase of the fish and their ontogenetic development (Lombarte *et al*. 2003). Based on the assumption that somatic growth is reflected in the growth of the otolith, a period with a shift in diet with reduced food intake can hypothetically cause physiological stress and formation of hyaline zones in the otoliths.

Secondary growth structures are defined as otolith structures that do not conform to hyaline and opaque zones of a yearly increment (Panfili *et al.* 2002). When ageing fish based on otolith macrostructure, the secondary growth structures are a substantial source of error. Little is known about the causes of these secondary structures, although feeding, spawning, temperature and developmental changes have been suggested to play a role (Wright *et al.* 2002). The identification of the first growth increment is an important component in age determination of fish. If the first increment in otoliths is not correctly defined, age determination will be consistently wrong by a constant amount. Reliable identification of the first increment can increase the precision of any individual age determination of young fish.

In the period of settling from July to December, coastal cod probably forms its first hyaline zone. In this period, there are great changes in biotic and abiotic factors in their environment, for instance a decline in temperature and day length. The otoliths zone pattern can give information about conditions that the juvenile cod grow up in, e.g. food supply and temperature.

DIET OF JUVENILE COASTAL COD

The cod diet has been studied for over a hundred years in various areas of the North Atlantic Ocean, due to its importance for fisheries and considerable influence on the ecosystem.

Early studies provided qualitative information on the food of cod, while later analysis of diet has been quantitative, assessing the interactions between fish species, competition or mortality by predation on commercially important stocks (Daan 1973, Fjøsne *et al.* 1996). There have been several diet studies conducted in the North Sea on 0-group cod (Daan 1973, Robb and Hislop 1980, Pobb 1981, Bromley *et al.* 1997), and on I-II group cod in Norwegian coastal waters (Kanapathippillai *et al.* 1994). Wiborg (1948, 1949) studied the food of 0-, I-, and II-group cod in a wide range of coastal and fjord localities in northern Norway, including Ullsfjord where two of the localities in this study are situated. Because earlier results from Ullsfjord were sparse (Wiborg 1949) and only from deep water an update and more extensive studies were needed from the fjord. Ecosystem-based models and investigations have become more and more important the last decades. In order to describe predator-prey and competitive interactions in the ecosystem, these models rely on detailed diet information. Even though 0-group cod, in comparison with larger cod, does not consume as much as the latter, they do play an important role in the ecosystem. Diet information from juvenile cod is therefore also important, including any significant annual variation within years.

Many different prey groups have been found in the stomach of the juvenile cod, but only a few prey groups dominate the diet composition (Wiborg 1949, Bromley *et al*. 1997). Small 0-group cod have previously been found to mainly feed upon large amounts of copepods (Bromley *et al*. 1997), while larger 0-group cod tends to eat fewer and bigger preys (Robb and Hislop 1980).

INFECTION OF *CRYPTOCOTYLE LINGUA* METACERCARIA

Naturally occurring parasites can be utilised in tagging programmes to provide information on various aspects of host biology. One of the first attempts to employ parasite indicators in a study of fish biology was that of Dogiel and Bychovsky (1939) to distinguish between stocks of sturgeon (*Acipenser* spp., Acipenseridae) in the Caspian Sea (Williams *et al.* 1992). Protozoans and nematodes have been used to separate stocks of cod in northern Norway, while digeneans has been suggested for tracing seasonal migration of cod (Hemmingsen *et al.* 1991).

The earliest record of the digenean *Cryptocotyle lingua* as a parasite was done by Creplin (1825), where he found the adult stage in gull *Larus marinus* (L.). Stunkard (1930) showed that the periwinkle *Littorina littorea* (L.) is the first intermediate host of this parasite on the Atlantic coast of North America. He also described the cercaria of *C. lingua* which measured 0.12-0.2 mm in length, and as adult *C. lingua* is 0.5-2 mm long. The parasite eggs

enter sea water or brackish water with the faeces from birds. The periwinkle *Littorina littorea* eats these eggs that sink to the bottom. Asexual reproduction inside the infected periwinkles enables cercaria to emerge in high numbers out of these hosts when the conditions regulating the reproduction are positive. For instance, Sindermann and Rosenfield (1954) noted that up to 15.000 cercaria emerged from a single snail during a 24 hour period. The temperature was found to be important to cercaria emergence, and it declined below 12°C, and ceased below 10 °C. The cercaria drills its way out of the periwinkle before it swims vertically in the water to find its second intermediate host; fish. With the help of enzymes, the cercaria drills through the skin, gills and cornea of the fish, where it encysts as a metacercariae (Køie 1977).

The digenean can cause muscle degeneration in addition to infections of eye and nervous tissue which can be quite damaging, and even mortal to juvenile fish (Sindermann and Rosenfield 1954). MacKenzie (1968) identified massive infestation of young plaice with *C. lingua* metacercaria as the possible cause of mortality. Lauckner (1984) showed that a single metacercaria of *C. lingua* is sufficient to kill a larval fish. The parasite may also represent a problem by reducing the market value of fish from the marine farming industry due to the unappealing black spots in the skin (Kristoffersen 1991).

It has been shown that fish can develop a temperature dependent immunity against this parasite, and at temperatures below 5°C the fish are not able to react against the parasite (Paperna 1995). Möller (1978) found that at temperature of 0°C and salinity of 0 and 2‰, no infection of metacercariae was found in flounders (*Platichthyes flesus*). He also found that *C. lingua* proved to be infective to fish at salinities down to 4‰.

OBJECTIVES OF THIS STUDY

This study was conducted in northern Norway during fall 2005, where factors affecting abundance, diet, growth and condition of coastal cod have been the subject of a study. Despite the importance of coastal cod in Norway, only limited diet information of 0-group coastal cod in northern Norway is available since Wiborgs studies in 1948 and 1949. The aim of this study was to investigate;

i) if prey composition in the 0-group cod's diet, and the relative importance of the different prey differ between the three locations from August to November.

ii) when the first hyaline zone in the otoliths is formed, and factors that may affect this formation.

iii) the possibility of using *Cryptocotyle lingua* as a biological tag and indicator for habitat choice of 0-group cod during summer and autumn. This study investigates the parasites infecting the cod caught at three locations: one in Kvalsundet (Makkjosen) and two in Ullsfjord (Njosken and Jøvik).

MATERIAL AND METHODS

STUDY AREA AND SAMPLING

The material for this study was sampled from three different locations; Jøvik and Njosken in Ullsfjorden and Makkjosen in Kvalsundet, Norway, monthly from August to November 2005 (Fig. 1). 11 locations around Tromsø were tested in August, and the three locations previously mentioned were chosen because of their accessibility and the large catches of cod juveniles. These three locations are different with regard to flora and bottom habitat.

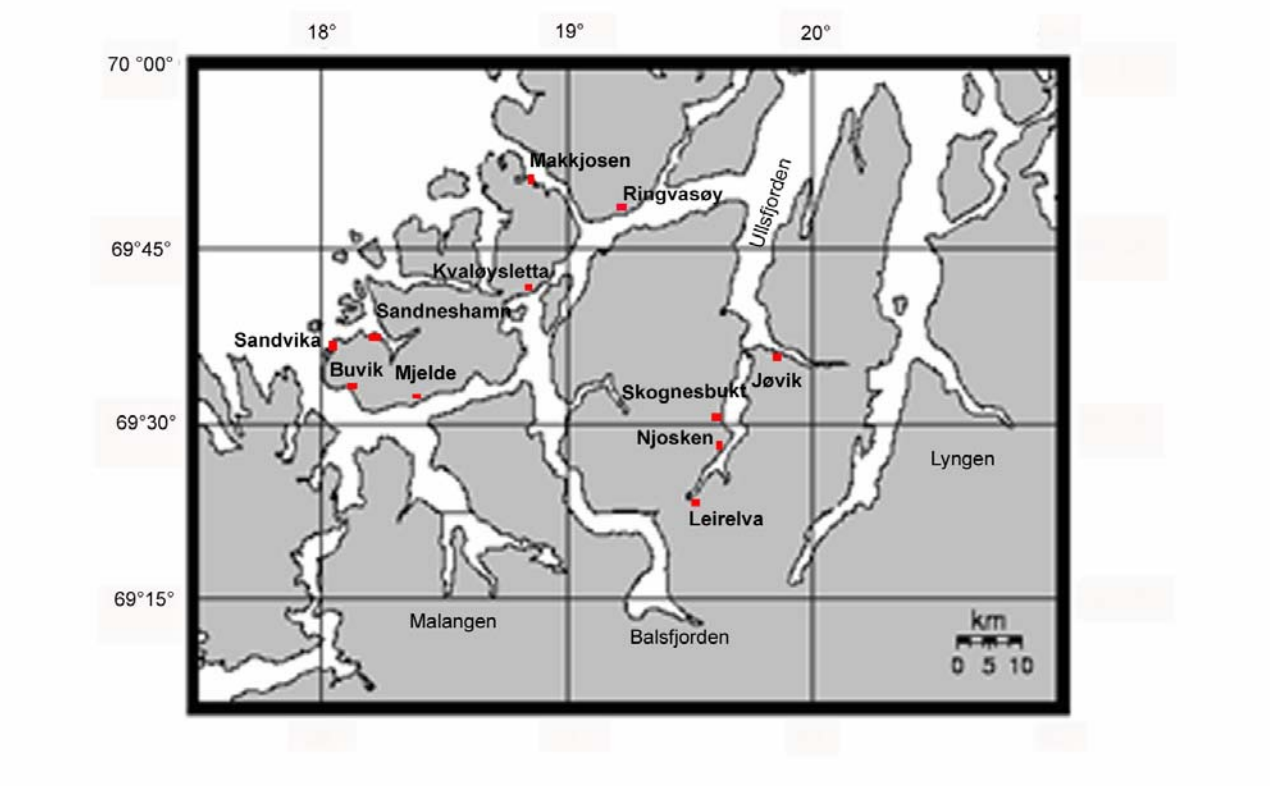


Fig 1. Map over Tromsø with the eleven sampling locations indicated by a red square.

Jøvik had a pebble and cobble covered rocky beach with a relative large freshwater runoff (Appendix table A1). Two kelp types were abundant; *Laminaria saccharina* and *Laminaria hyperborean*. The rocks were partly covered by one year old algae. The beach had a weak slope far out (ca. 25 m) before it dropped in depth. Makkjosen had coarse-grained sandy bottom with patchy distribution of alga. Juvenile saithe (*Pollachius virens*) was abundant in this area. Njosken had the most macroalgae, and the most abundant species were Knotted wrack (*Ascophyllum nodosum*), Toothed wrack (*Fucus serratus*) in addition to some Dead man's rope (*Chorda filum*).

Surface water temperature was measured at every location with a 76 mm Immersion thermometer. The average water temperature at the three locations declined from August to

November. Generally the lowest water temperature was found in Jøvik, probably due to a strong influence of fresh water runoff.

Collection of cod was carried out with a beach seine 1.5 meter deep, 30 meter long, with an inner 5.2 mm stretch mesh. The beach seine was set in a semicircle from shore using a small boat, and three persons participated in the sampling process. If the seine got stock in stones, it was released using a long rod with a hook. At least two hauls were taken at each location, but at several occasions the number was higher due to few cod caught in each haul. All cod collected were put in small plastic vessels with ethanol (96%) for later identification. If many cod (>12) were caught, a minimum of 12 cod were put in plastic vessels and the rest was put in plastic bags and stored at ice during transportation. The seine hauls were taken at the same location every month, but the different hauls at each date were taken side by side. The collection was carried out during day time when the tide was high.

DIETARY COMPOSITION

The cod was opened before the stomach was taken out by using a scalpel to cut over the oesophagus and the base of the pyloric caeca. The stomach was placed on a small piece of overhead-sheet. Under a binocular microscope, the stomach was gently opened with a dissecting needle. The content was carefully scratched out, and the prey items were identified to the lowest possible taxonomic level. For some prey items, species, genus or even family characteristics could not be determined due to heavy digestion. In cases for decapods and mysids where food items were fragmented or partly digested, the number of specimen was estimated by counting number of eyes and dividing by two.

All prey items were measured in length, except when very abundant samples of one prey category occurred. In such cases a sub sample of minimum ten individuals were measured. If the taxonomical status of a prey item was uncertain, a picture was taken using a Canon Power Shot G2 camera, and later studied and identified to nearest possible taxa.

All crustaceans were identified by the help of keys in Enckells (1980) book *Kräftdjur*, and polychaetes and one fish were identified by the help of descriptions in Moen and Svensen (2003).

The stomach content was dried on an overhead-sheet at ~ 60°C in a Termaks oven for 24 hours. A Mettler MT5 with accuracy of 0.001 mg was used to weigh the dry stomach content. Before weighting, the content was cooled down for a few minutes. During the procedure of weighing of the content there was no contact between hands and the material in order to avoid fat or other substances to affect the weighing. A pincette was therefore used to

move the different objects during the weighting. The stomach content was weighted before and after a short time (maximum 10 minutes) in an exicator. The plastic sheet that the content was placed on was only weighted after the time in the exicator.

Small rocks, Cladocera, Bivalvia and Gastropoda were underestimated in biomass because some were lost during weighing. At two weightings in October for Jøvik, Cyclopoida and Harpacopida were weighted as diverse copepods due to very high abundance, and later calculated as the two groups, with the assumption that they had the same individual weight.

FISH LENGTH AND –DRY WEIGHT MEASUREMENTS

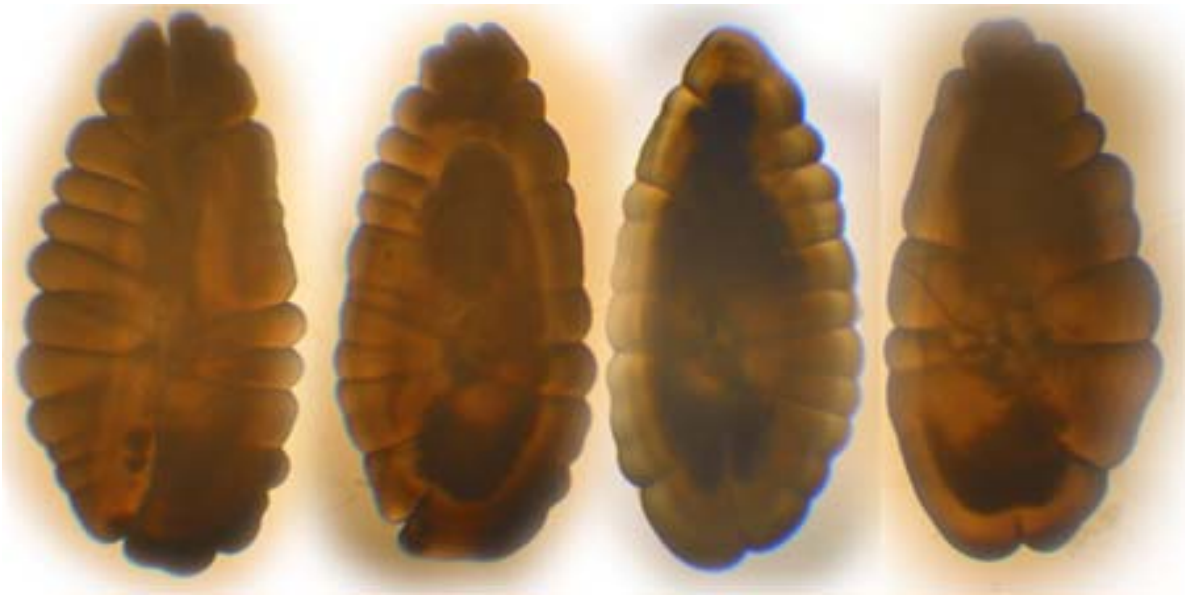
Because the tailfin was cut off for possible genetic examination, length of cod was measured from snout to base of tail fin, and dry weight of cod did not include the tail fin. In addition total fish length from snout to end of tail fin was measured. The cod was dried for six days at ~ 60°C. A test with 18 cod showed only an average 0.26% decline in weight from day six to seven.

Table 1. Length data (total length) for cod in each period in each location. Total length (cm) given as minimum (Min), maximum (Max), average (Av) and standard deviation (sd.).Number of fish collected/examined for diet composition, otolith patterns and *Cryptocotyle lingua* are given. (*) indicate average values for only August and September. (-) indicate no values. Sea temperature is given for each month and location.

		Number of seine	Total length (cm)				Number of fish	Number of fishes examined in			Sea temp.
Date	Location	hauls	Min	Max	Av	sd.	collected	Diet	Otolith	Parasite	(°C)
15.08.2005	Jøvik	2	4.1	8.0	5.9	1.1	62	24	24	24	-
18.08.2005	Njosken	4	4.5	8.5	5.8	1.5	9	9	9	9	10.8
19.08.2005	Makkjosen	2	5.5	8.1	7.1	1.3	39	12	11	12	10.5
22.09.2005	Jøvik	2	6.1	9.4	7.9	0.9	168	24	23	24	7.8
21.09.2005	Njosken	4	6.5	9.0	7.4	1.0	16	16	16	16	8.0
06.09.2005	Makkjosen	3	5.5	9.4	6.9	1.3	20	12	12	12	10.7
30.09.2005	Makkjosen	4	-	-	-	-	0	-	-	-	8.7
13.10.2005	Jøvik	3	4.9	9.6	7.2	1.5	25	25	26	26	7.2
14.10.2005	Njosken	4	6.2	9.1	7.1	0.9	13	13	13	13	6.4
20.10.2005	Makkjosen	3	-	-	-	-	0	-	-	-	6.1
14.11.2005	Jøvik	3	-	-	-	-	4	-	-	-	6.7
16.11.2005	Njosken	4	6.6	9.9	8.1	1.0	19	19	19	19	6.8
24.11.2005	Jøvik	2	5.2	9.9	8.0	1.1	31	21	21	21	4.9
Total	Jøvik	12	4.1	9.9	7.2	1.4	286	94	94	95	
	Njosken	16	4.5	9.9	7.3	1.3	57	57	57	57	
	Makkjosen	9	5.5*	9.4*	7.0*	1.3*	59	24	23	24	

OTOLITHS

122 pairs of otoliths were dissected from the cod using a blade pincette and a dissecting needle. All otoliths were preserved on small glass jars (1 ml.) on 96% ethanol and a few drops of glycerol. Ten otoliths were first studied by two persons, and four zone pattern categories were decided; 0, 1, 2 and 3 (Fig. 2). All otoliths were placed in a precise order when examined; posterior end and inside faced up. Category 0 has no sign of a hyaline zone, where as category 2 have a clear hyaline zone around the whole otolith (Fig. 2). A hyaline zone with an opaque area further away from the core was interpreted as a bottom-settling zone. The width of the opaque area inside the bottom-settling zone was measured. There was found 19 pairs of otoliths with bottom-settling zone, but there was not conducted any separate analysis on these otoliths. Category 1 has either a hyaline settling ring or has a hyaline zone from posterior to the anterior end of the otolith (Fig. 2). Category 3 has a dark posterior tip and only a clear hyaline zone on one side of the otolith (Fig. 2).



Category 0 Category 1 Category 2 Category 3

Fig. 2. Picture of the four zone pattern categories in 0-group coastal cod used as a template in the paper.

After the initial category assessment, the ten otoliths were mixed in with the rest of the otoliths, and all were coded randomly so that it was not possible for the otolith-reader to identify from which station or time period they originated. Thirty random otoliths were analysed by two persons using two different binocular microscopes with regard to length, width and zone pattern. All otoliths were studied in a Petri dish with a few drops of glycerol. The length and widths of the rest of the otoliths were measured at 25x magnification by one person, but the zone pattern categories were determined separately by two persons.

INFECTION OF *CRYPTOCOTYLE LINGUA* METACERCARIA

The same cod analysed for diet composition were examined for *Cryptocotyle lingua* infection.

Fig. 3. Juvenile cod with visible black spots caused by *Cryptocotyle lingua* metacercaria.

Each cod were macroscopically examined, and every clear visible black spot was counted as one metacercarie. If there was any uncertainty with regard to whether a black spot was caused by natural pigmentation in the skin or a metacercarie caused by *C. lingua*, then these were not counted as a metacercarie.

SOFTWARE AND STATISTICAL ANALYSIS OF DATA

According to Hyslop (1980), no method gives a complete picture of diet, and it is therefore recommended to use methods measuring both the numbers and the bulk of food material. Consequently, three different measurements for analysing the stomach contents were used:

1) the frequency of occurrence (FO) of every prey type:

$$FO_i\ (\%) = (C_i/C_t) \times 100$$

where C_i is the number of cod with prey type *i*, and C_t is the total number of cod;

2) the relative frequency (N_i), which is the numeric proportion of each prey type in the diet expressed as the total number of each prey type (n_i) relative to the total number of all prey (n_t):

$$N_i\ (\%) = (n_i/n_t) \times 100$$

3) the relative proportion of each prey type in terms of biomass (dry weight) (B_i):

$$B_i\ (\%) = (b_i/b_t) \times 100$$

where b_i is the total biomass of prey type *i*, and b_t is the total biomass of all prey types.

Microsoft ® Exel, R 2.3.0 and SYSTAT 10.2 were used for exploratory and inferential statistics. Statistical significance level was set at $\alpha \leq 0.05$.

To model diet composition as a function of sample location, time and temperature, a Constrained Correspondence Analysis (CCA) was carried out on the dry weight of prey groups. A CCA is sensitive to species occurring in a low abundance; hence all rare prey taxa except for seven main prey groups (Polychaetes, amphipods, decapods, isopods, calanoid and cyclopoid copepods, mysids and Harpacticoida) was not included in this analysis if they had total B% lower than 18. The three locations, month, fish length and body and dry weight of the main prey groups were set as the depended variables. For testing the significance of the CCA model a Monte Carlo permutation test was applied, which do not require the assumption of normality (ter Braak and Verdonschot 1995).

A linear regression was carried out to investigate if there were a linear relationship between fish length and otolith length. A chi-square test was applied to test if the four different zone pattern categories differed between months.

Four different Generalized Linear Models (GLM) were run with otolith width (Ow) of cod as the dependent variable to analyze for effects of the independent variables; fish length, month, location, water temperature and a interaction between month and location;

Model I $Ow = \beta_1$ Fish length + β_2 month

Model II $Ow = \beta_1$ Fish length + β_2 temperature

Model IV $Ow = \beta_1$ Fish length + β_2 location

Model V $Ow = \beta_1$ Fish length + β_2 month$*$location

All these models were used for; i) the complete dataset, ii) all locations in August and September, and iii) for all months in Njosken and Jøvik. This was done to minimize bias in model coefficient estimates due to the lack of otoliths from Makkjosen in October and November, and the variation in number of measurements between locations and months. Based on the estimated standard errors (SE), a 95% confidence interval (CI) was calculated for all derived coefficient estimates from the models. Analysis of variance was applied on all four models to test for significant effects of the independent variables on the dependent variable.

Abundance of black spot disease for each month and location was calculated as the total number of spots in all the examined cod divided with the number of cod examined. Prevalence was calculated as number of fish infected divided by the number of fish examined. A chi-square test was applied to test for significance between parasite infections in the three locations, and for the increase and decrease of parasite infection between months.

RESULTS

The numbers of fish collected and examined are given in table 1 page 12. The cod increased 2.3 cm and 2.1 cm in average length from August to November, for Njosken and Jøvik, respectively. In October and November there was no cod collected in the beach seine hauls in Makkjosen.

DIET COMPOSITION

A total of 7776 items were identified from the stomach analysis and assigned to 20 diet groups or taxa (Table 2). Only one of the 172 cod examined had no prey remains in its stomach. A total of 3 copepod prey types were identified (Table 2); 3 to order and one to genus, and these orders were very common with a high frequency of occurrence (FO_i %). Two genus of Ostracoda were identified, and Branchiopoda were not taxonomically identified further than cohort (Table 2). A total of 6 orders of Malacostraca were identified, 3 to suborder, 2 to infraorder, 3 to genus and 8 to species (Table 2). In addition, remains of polychaetes were found in some cod, but only one specie were identified (Table 2). Various fragments of algae and insects, small Bivalva and Gastropoda, rocks/sand and a one fish (Table 2) were considered to be secondary prey groups and were not included in further analyses. Small parasites was found in a few stomachs but were not included in the analysis of diet composition.

Most of the prey types were found in small numbers. A total of 73% of the various prey types had a frequency of occurrence (FO_i) of less than 10%, and only three prey groups had a relative frequency (N_i) over 10 %(Table 2). Maxillopoda was by far the most important prey in terms of numbers of individuals and frequency of occurrence (Table 2). Malacostraca, like Maxillopoda, had a frequency of occurrence of 100%, but was not as important in terms of number of individuals as Maxillopoda was.

The smallest measured prey item was a Harpacticoida with a length of 0.28 mm, and the largest was a Polycheatea indet. with a length of 26.67 mm. In general, Harpacticoida, Cyclopoida, Cladocera, Ostracoda, Bivalvia and Gastropoda were the smallest preys, and Isopoda and polychaetes the longest.

Most prey was active and benthic (B) or hyperbenthic (HB) (Table 2). In general, the pelagic maxilliopods were by far the most important prey type for the newly settled cod, in terms of number and frequency, occurring in all fish (Table 2). Calanoida was the most numerous group, and Harpacticoida were more numerous than Cyclopoida. All cod had also some species of Malacostraca, and of this cohort the most numerous groups were *gammarus* sp. and Cumacea (Table 2).

Table 2. Taxonomic grouping of stomach content from 172 0-group coastal cod from Northern Norway. FO_i (%) - frequency of occurrence, N_i (%) - relative numerical frequency. P - pelagic, HB – hyperbenthic and B - benthic.

Prey item			**Prey group**	**Number of prey**	**FO_i(%)**	**N_i (%)**
Crustaceans						
Maxillopoda	Copepoda	Calanoida	P	2701	60.47	34.78
		Calanoida fragments		18	4.07	0.23
		Cyclopoida	P	1268	41.86	16.33
		Oithona sp.	P	139	1.16	1.79
		Harpacticoida	B	2100	46.51	27.04
Branchiopoda	Cladocera	*Podon* sp.	P	84	13.95	1.08
		Evadne sp.	P	30	4.65	0.38
		Cladocera unspes.	P	14	0.58	0.18
Ostracoda unspes				32	9.88	0.41
Malacostraca	Mysidacea	Mysidacea unspes.		18	3.49	0.12
		Mysis litoralis	HB	90	16.28	1.16
		Mysis oculata	HB	2	1.16	0.03
		Mysis sp.	HB	50	12.79	0.64
		Erythrops sp.	HB	1	0.58	0.01
		Mysidacea fragments		13	4.07	0.23
	Cumacea unspes.		B	220	4.65	2.83
	Isopoda	*Idoeta baltica*	B	6	1.74	0.08
		Idoeta neglecta	B	4	1.16	0.05
		Isopoda unspes.		29	2.33	0.37
	Amphipoda	Gammeridea	HB	5	1.74	0.06
		Gammarus locusta	HB	1	0.58	0.01
		Gammarus spp.	HB	252	23.26	3.25
		Gammaridea fragments		39	6.98	0.50
		Hyperiidea	P	73	7.56	0.94
		Hyperiidea fragments		2	1.16	0.03
		Caprellidea uspes.	HB	2	1.16	0.03
		Phtisica marina	HB	1	0.58	0.01
		Corophium crassicorne	HB	74	12.21	0.95
		Amphipoda fragments		28	1.74	0.36
	Decapoda	*Pandalus borealis*	HB	2	0.58	0.03
		Pandalus sp.	HB	3	5.23	0.04
		Caridea uspes.	HB	12	4.65	0.15
		Anomura	B	1	0.58	0.01
		Decapoda fragments		9	2.91	0.12
Polychaeta		*Aphrodita aculeata*	B	1	0.58	0.01
		Eunicidae uspes.	B	1	0.58	0.01
		Polychaeta fragments	B	64	10.47	0.82
Others:	Bivalvia		B	19	5.81	0.24
	Gastropoda		B	40	1.74	0.52
	Teleostei	*Pholis gunnellus*	HB	1	0.58	0.01
	Insect			5	1.16	0.06
	Plantae	Plantae fragments		8	1.74	0.10
	Rocks/sand			212	23.26	2.73
Unidentified		Fragments		91	27.91	1.17
Sum:	**Maxillopoda**			6226	100.00	80.07
	Malacostraca			948	100.00	12.19
	Branchiopoda			160	28.90	2.06
	Polychaeta			66	11.56	0.85
	All prey			**7776**		

There was a clear difference in diet composition between the three locations (Fig. 4, appendix table A1). Makkjosen was dominated by Cumacea and amphipods in August. In September there was a shift to a dominance of polychaetes (Fig. 4). In Jøvik, mysids and decapods were the most important prey groups in terms of biomass in September, October and November. In August amphipods, calanoid and cyclopoid copepods were the most dominant prey groups at this location (Fig. 4). In Njosken the diet was more diverse, but polychaetes were most important in terms of biomass in every month except for September (Fig. 4).

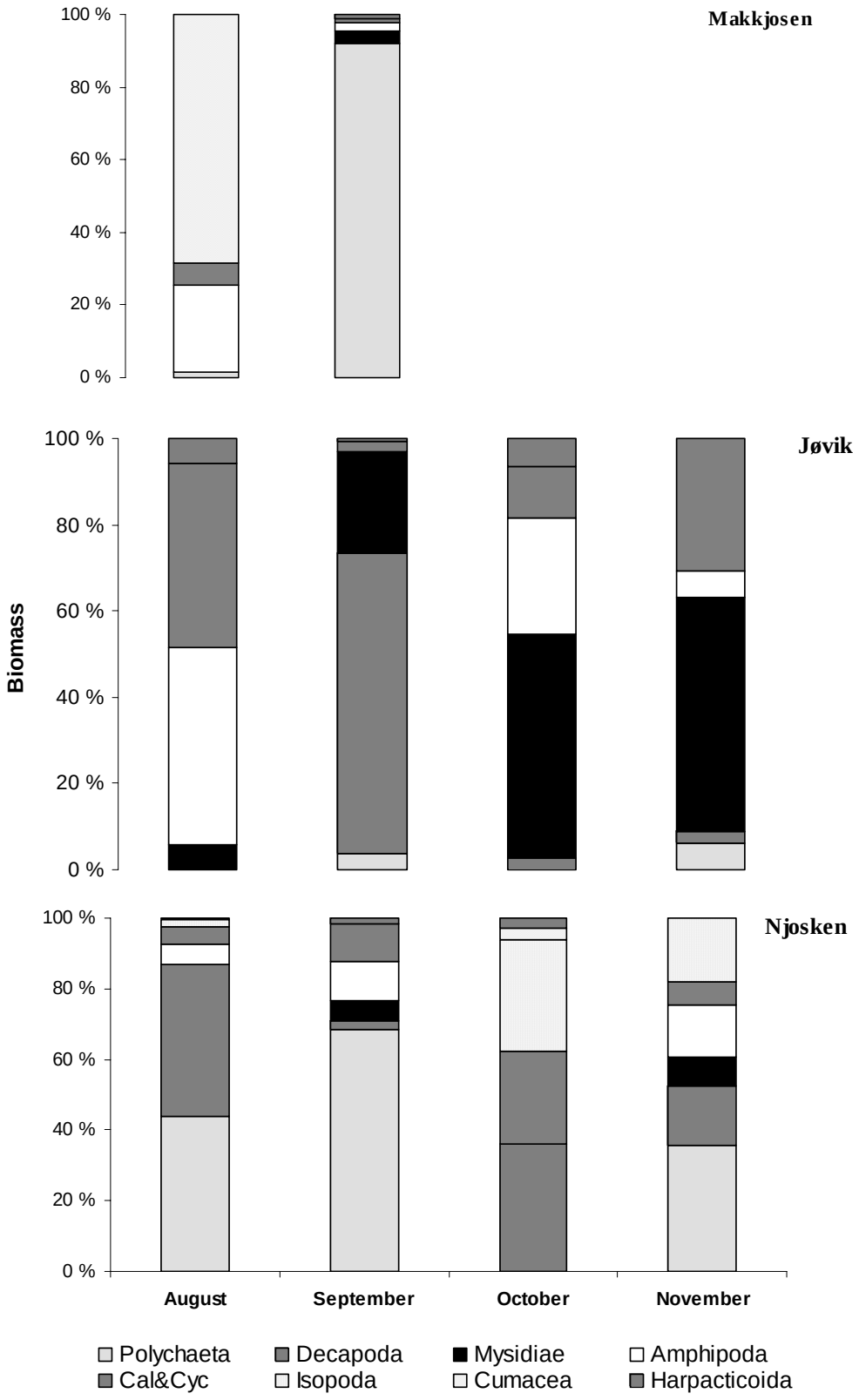


Fig. 4. Biomass (%) of the eight dominant prey groups for newly settled cod, sampled at Makkjosen, Jøvik and Njosken during fall 2005. Cal&Cyc = Calanoida & Cyclopoida copepods.

To investigate if the environmental variables could explain any of the variation in diet a CCA was used. The CCA explained 22.7% of the total variation in the model (Monte Carlo permutation test, df = 7, P < 0.005). Thereby the CCA confirms that location explains a large part of the observed variation in prey type composition (Fig. 5).

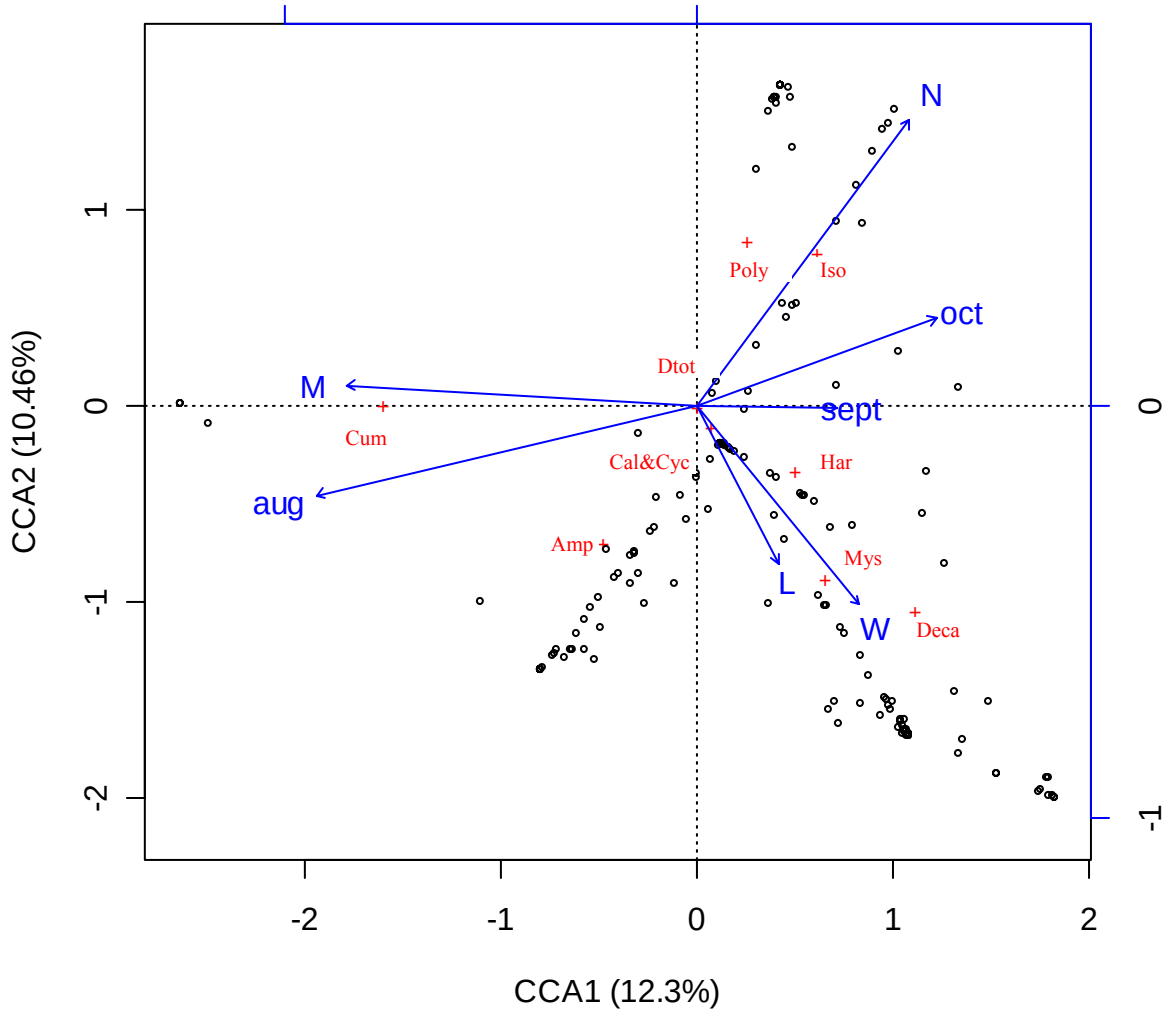


Fig. 5. A plot of the Constrained Correspondence Analysis (CCA) on dry weight of prey in 172 juvenile cod from Jøvik, Njosken (N) and Makkjosen (M) related to location, month (aug - August, sept - September, oct – October), fish length (L) and weight (W). The selected prey types (Amp - Amphipods, Poly - Polycheatea, Har – Harpacticoida, Mys – Mysidia, Deca – Decapods, Iso – Isopoda, Cum – Cumacea, Cal&Cyc – Calanoida & Cyclopoida copepods, Dtot – total amount of preys digested in each fish are marked by red crosses. The percentage of total variation explained by the two first axes are indicated respectively on Axis 1 and 2. Center of arrows represent Jøvik and November.

From the CCA there seemed to be a correlation with prey size and fish length, with larger preys like mysids and decapods pointing in the same direction as fish weight/length (Fig. 5).

NUMBER OF PREY PER FISH

The mean number of organisms present in the stomach can be related to length (Fig. 6). In Njosken there is a peak value, while in Jøvik the number of organisms per stomach decreases with length (Fig. 6). The peak value in Njosken for fish length 5 and 6 cm only represents 8% of the cod at this location. Two cod with a very high number of preys pulled the average value up for fish with a length of 5 and 6 cm in Jøvik. The small number of cod examined (n = 24) in Makkjosen, may be the reason for lack of a clear trend between the average numbers of preys related to fish length. In general, small cod seems to eat a high number of preys, and longer cod tend to eat fewer prey.

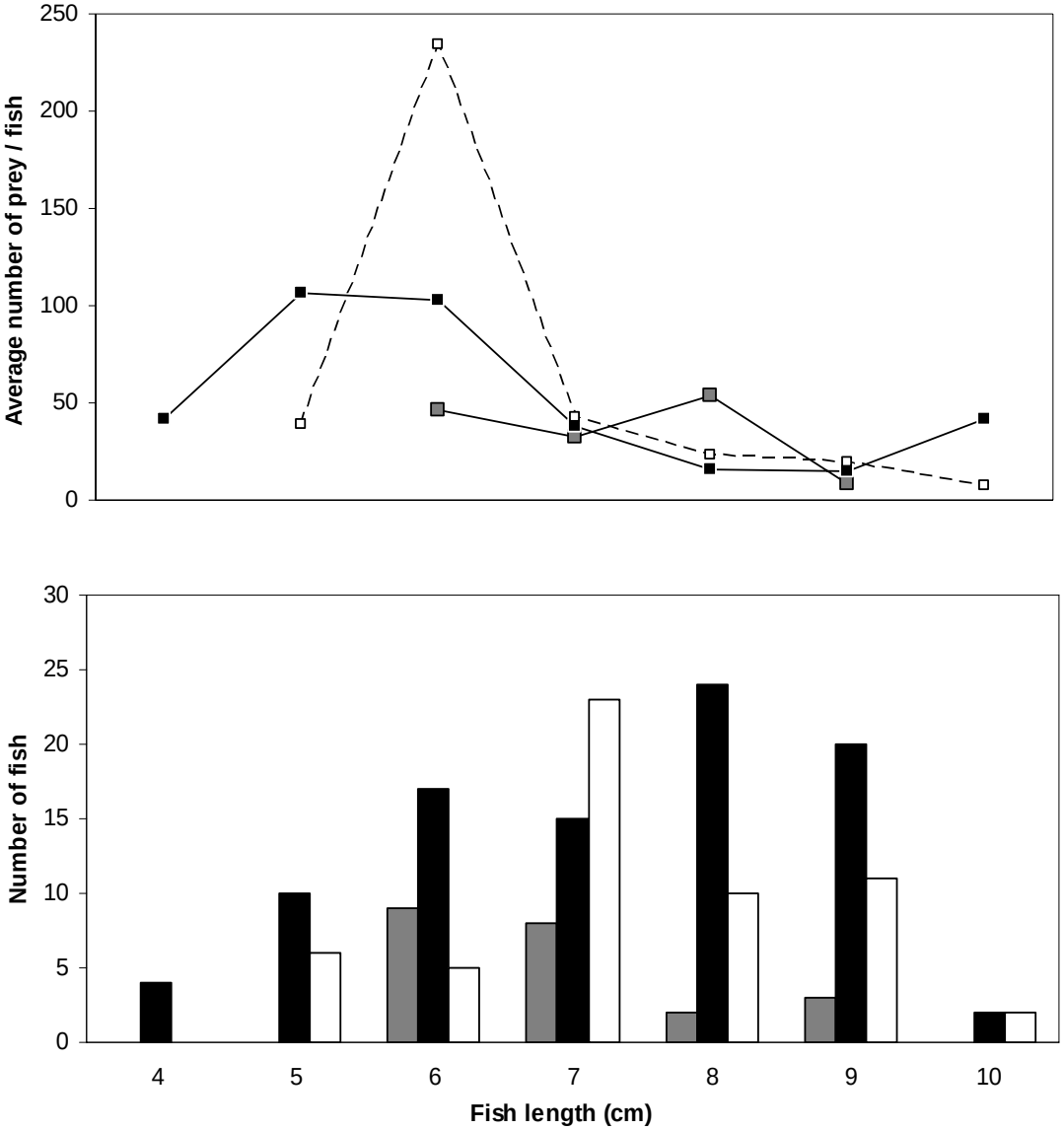


Fig. 6. Mean number of organisms per stomach in relation to length of cod (top figure), and number of fish in relation to fish length (bottom figure) in Makkjosen (□), Jøvik (■) and Njosken (□). Length at x-scale refer to midpoint of length intervals.

LENGTH AND TIME FOR FORMING OF THE FIRST HYALINE ZONE

To determine when the first hyaline zone in coastal cod is formed, the results of the reading on the sagitta from two persons where considered as two separate data sets. There was however no significant difference ($\chi^2 = 0.765$, df = 3, P > 0.25) with regard to total number of otoliths in the four categories between the two persons who determined the stage zone patterns. A clear trend with an increase in zone pattern category 2 and decline in category 0 was found towards November for both persons (Fig. 7). The frequency of category 0 and the three other category zone patterns categories differed between months for both persons a and b ($\chi^2 = 71.42$, df = 3, P< 0.001 & $\chi^2 = 59.02$, df = 3, P < 0.001, respectively). When compared, the left and right otolith shows very little differences between zone pattern categories (Fig. 7). Otoliths from two fish were not included in the statistic, because the left and right otoliths were very different in size and shape. In October 20.5 % of the cod had otolith category 2, and had increased to 67.9 % in November.

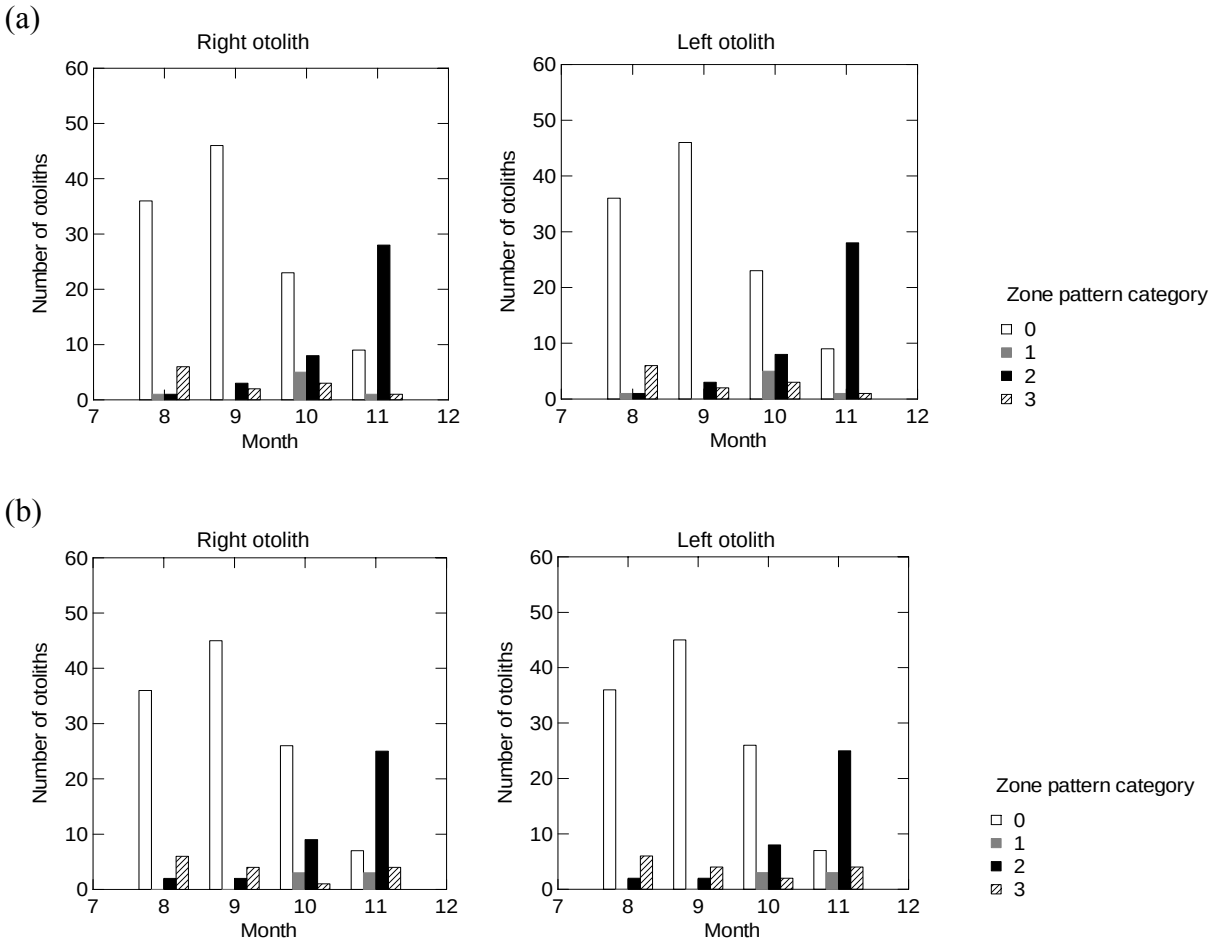


Fig. 7: Monthly distributions of the four zone pattern categories (0, 1, 2 and 3) in the right and left otolith of newly settled cod for person *a* and *b*.

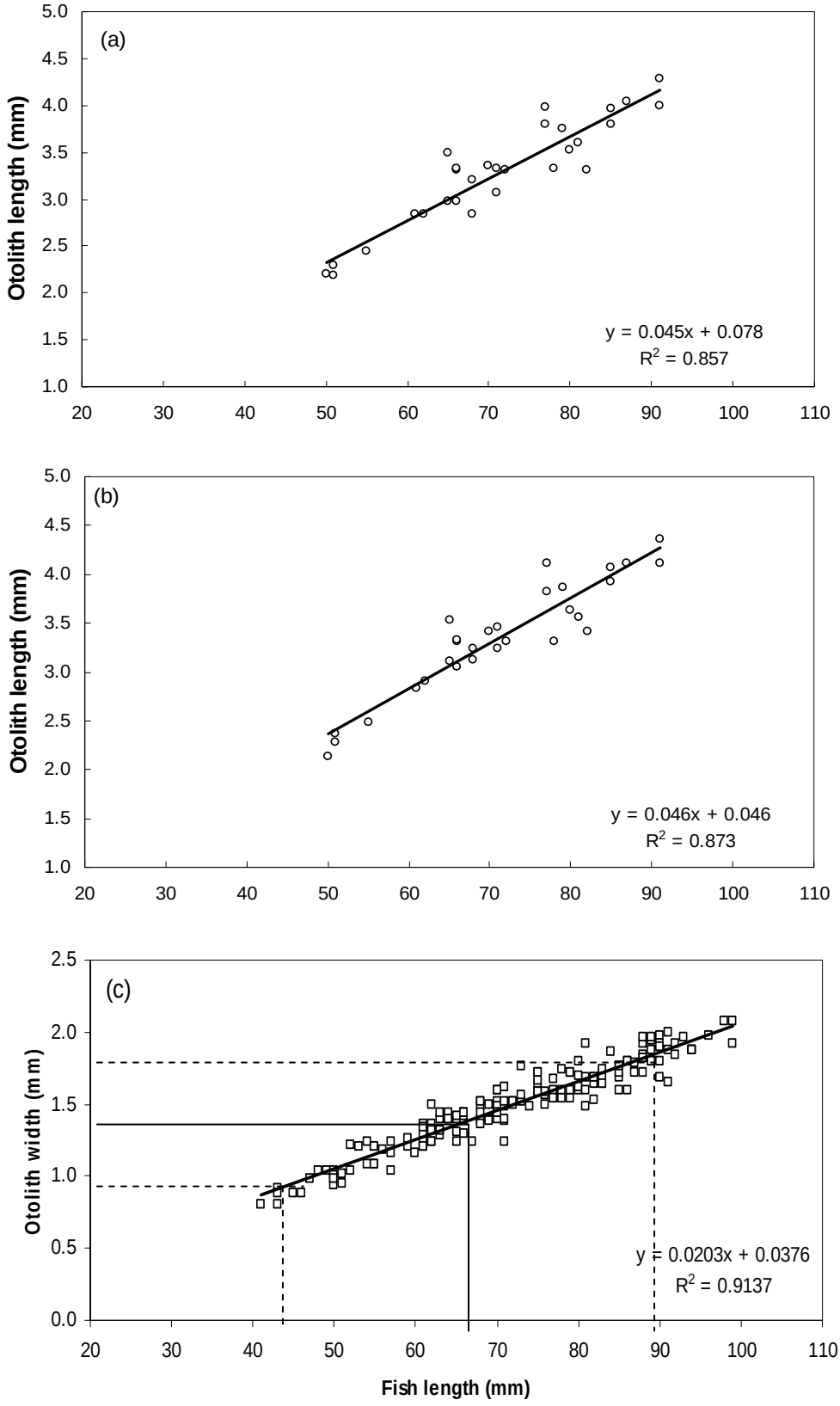


Fig. 8. Correlation between fish length (mm) and otolith length (mm) for 28 cod, for person (a) and (b). Correlation between otolith width and fish length for 173 otoliths (c). A linear regression model was fitted to the data, R-squared value and equation is given in the figures, stippled lines are minimum and maximum opaque width, line is mean opaque with for cod reached zone pattern 2.

As expected, larger cod had larger otoliths than smaller cod. Since there was only one person measuring the otolith width for all otoliths, these values were plotted in a single figure and not separated in two dataset as for otolith length. There is a slightly higher correlation ($R^2 = 0.91$) for otolith as a function of fish length than for otolith length ($R^2 = 0.86$ and 0.87) (Fig. 8).

FACTORS AFFECTING ZONING IN THE FIRST HYALINE ZONE

It was investigated if; fish length, month, water temperature and location had any effect on either zone pattern category or otolith width.

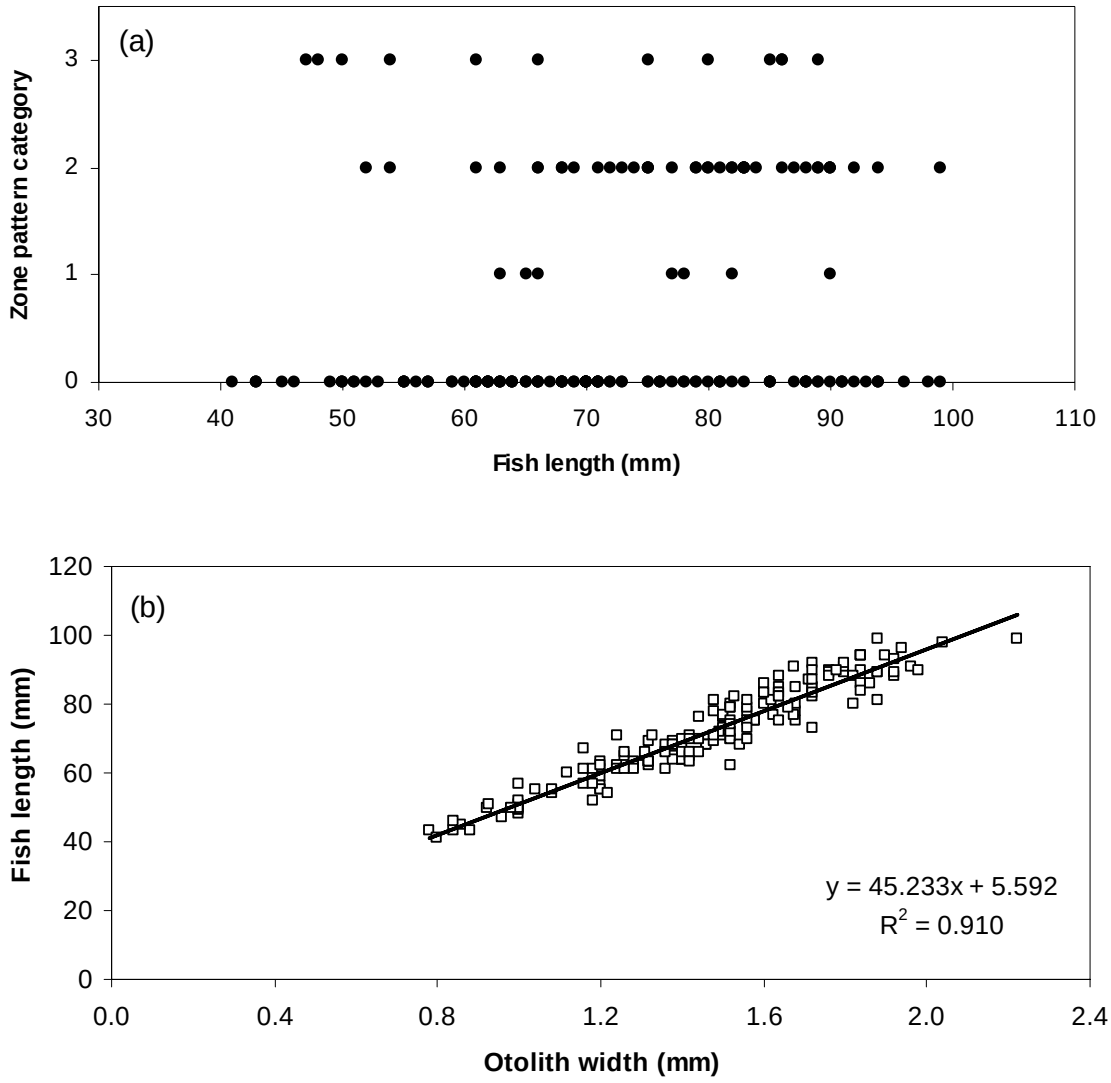


Fig. 9. Relationship between fish length and zone pattern category (0-3) in 173 juvenile cod in northern Norway (a), and relationship between fish length and otolith width in 173 juvenile cod (b). A linear regression model was fitted to the data, R-square and equation is given in the figure (b).

There was no strong relationship between fish length and zone pattern category, and fish size of commencement of the hyaline zone were estimated to range in length from 48-99 mm (Fig. 9). Mean width of the opaque zone for the cod that had reached zone pattern category 2 was 1.37 mm (SD = 0.22). This mean value and the values (a and b) from the regression equation in figure 9b was used in the following equation:

$$\text{Fish length} = 5.592 + 45.233 * \text{opaque zone width}$$

to estimate the average length of cod when the hyaline zone is formed. This length was found to be 69.6 mm (SD = 10.0).

Because of a few outliers found in a linear regression for right otolith length/width as a function of fish length, data from the left otolith was used for further analysis as the dependent variable used in the GLMs presented below. It was also found that otolith width had a higher R^2 value in a GLM than otolith length. Since only one person had measured the width and length of all otoliths there was not performed two separate GLMs for each persons readings.

Table 3. Summary table of Generalized Linear Models used to analyze the effects of fish length, month, location, water temperature and interaction of month and location on otolith width (Ow) (mm) in 0-group cod. Highest R-square value is given in bold. Fish length (mm);"FL".

Model	Dataset / equation	term	P-value	R^2
	All months and locations			
IA	Ow = a+b*FL+c*mnd	mnd	*	0.948
IB	Ow = a+b*FL+c*temp	temp	*	0.942
IC	Ow = a+b*FL+c*loc	loc	NS	0.940
ID	Ow = a+b*FL+c*(mnd*loc)	mnd*loc	*	**0.949**
	August & September, all locations			
IIA	Ow = a+b*FL+c*mnd	mnd	***	0.962
IIB	Ow = a+b*FL+c*temp	temp	***	0.927
IIC	Ow = a+b*FL+c*loc	loc	***	**0.964**
IID	Ow = a+b*FL+c*(mnd*loc)	mnd*loc	NS	0.962
	Jøvik & Njosken, all months			
IIIA	Ow = a+b*FL+c*mnd	mnd	*	**0.960**
IIIB	Ow = a+b*FL+c*temp	temp	*	0.958
IIIC	Ow = a+b*FL+c*loc	loc	NS	0.950
IIID	Ow = a+b*FL+c*(mnd*loc)	mnd*loc	**	0.953

*; $0.001 < P \leq 0.025$, **; $0.025 < P \leq 0.10$, ***; $0.10 < P \leq 0.25$, NS; not significant.
In all models the fish length term were significant.

The analysis of variance applied to the models IA-D, showed a significant ($0.001 < P \leq 0.025$) effect of all the variables except for location (Table 3). Model ID had an interaction term for

month and location accounted for 95% of the variance in the otolith width. In model IIA-D, where only otoliths of cod from August and September at all locations were included, the sample size declined from 172 to 95 cod, and three of the variables was slightly significant ($0.10 < P \leq 0.25$) (Table 3). In model IIIA-D, where only Jøvik and Njosken was included, a significant effect was found of month ($0.001 < P \leq 0.025$) and temperature ($0.001 < P \leq 0.025$) on otolith width, and both accounted each for 96 % of the variance in the scores (Table 3).

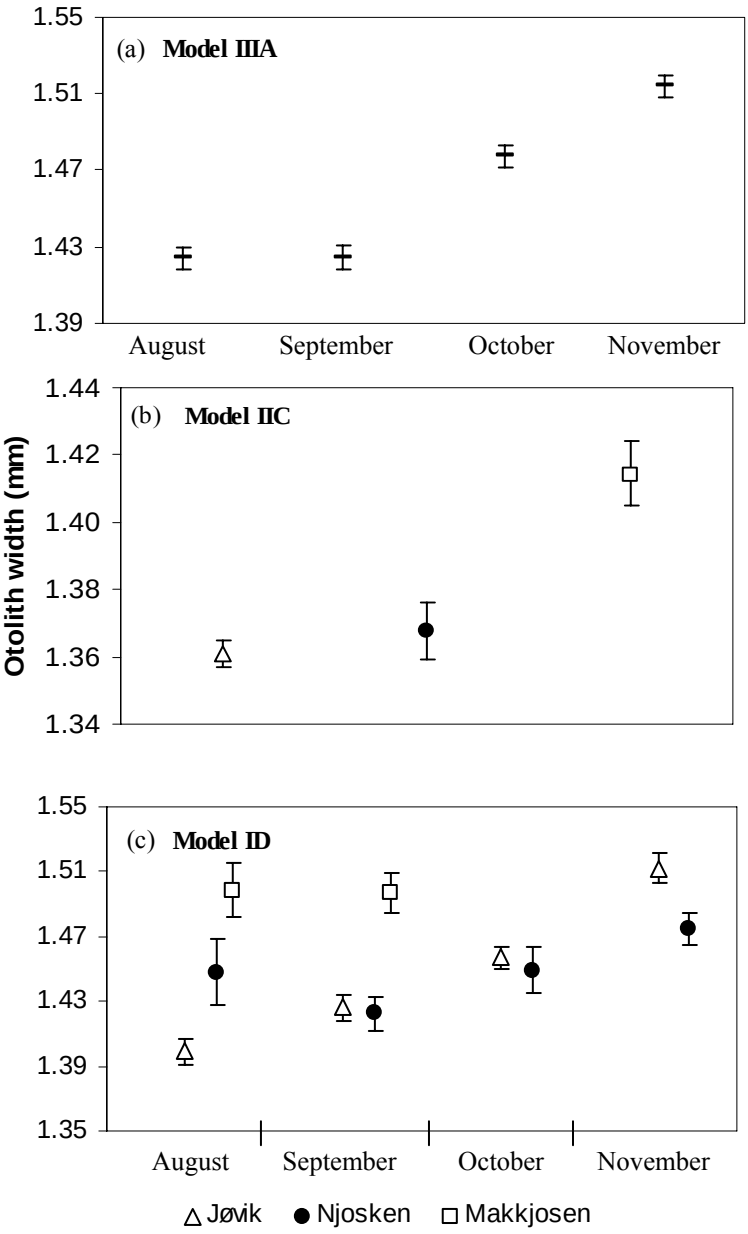


Fig. 10. Least square means and confidence intervals (95%) for the estimated models for otolith width. Model versions refer to table 3.

For further analysis the least square means and 95% confidence intervals from the models with highest R^2 value were derived and presented in figure 10. Generally, there was an increase in

otolith width relative to fish length, from August towards November (Fig. 10a). However, when the locations were separated it became clear that Makkjosen had no clear differences between the two months, while Jøvik had an increase of otolith width towards November, and Njosken had the same progression except for a higher value in August (Fig. 10c). In August and September, cod from Makkjosen had much broader otolith widths compared to the other two locations, and Njosken had a similar least square means as Jøvik (Fig. 10b). However, otolith width of cod from Jøvik increased more than for cod from Njosken from September towards November (Fig. 10c).

INFECTION OF *CRYPTOCOTYLE LINGUA* METACERCARIA

In general, the infection with *Cryptocotyle lingua* metacercaria in cod was markedly lower in Jøvik than at the two other locations (Fig. 11), and differences in total prevalence were statistically significant between Jøvik (13%) and both Njosken (72%) and Makkjosen (67%) ($\chi^2 = 54.52$, df = 1, $P < 0.001$, $\chi^2 = 30.69$, d f= 1, $P < 0.001$ respectively). However, the total prevalence was not significantly different between Njosken and Makkjosen ($\chi^2 = 0.22$, df = 1, $P > 0.05$).

Furthermore, there was little variation in the infection throughout the season in Jøvik, although there was a slight tendency towards an increase (Fig. 11). In Njosken, the prevalence of *C. lingua* increased steadily from about 33% in August to almost 95% in November, and the difference between these two months was significant ($\chi^2 = 12.28$, df = 1, $P < 0.001$) (Fig. 11). Similarly, the parasite abundance at this location increased with time and was more than twice as high in November (16.6) as in August (6.9). In Makkjosen, on the other hand, both prevalence and abundance of *C. lingua* apparently declined between the two only sampling occasions in August and September (Fig. 11), but the difference in prevalence was not significant ($\chi^2 = 3.00$, df = 1, $P > 0.05$).

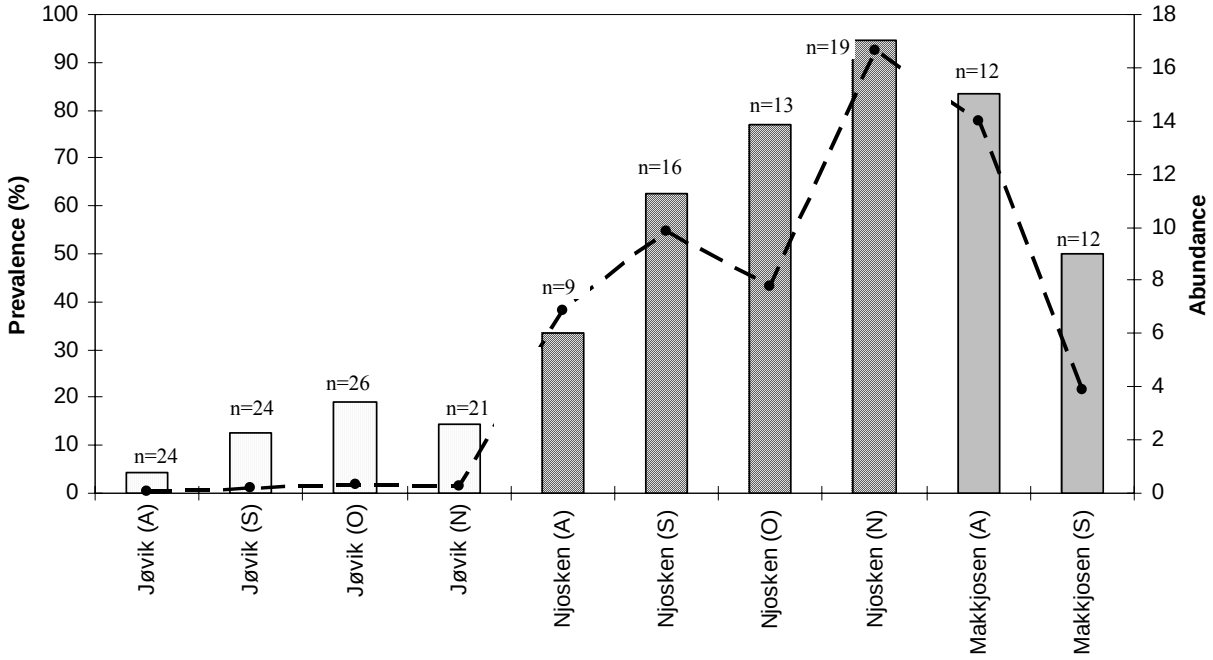


Fig. 12. Prevalence (%) (bars) and abundance (stippled line) of *Cryptocotyle lingua* at three locations; Jøvik, Njosken and Makkjosen in August (A), September (S), October (O) and November (N). Number of fish examined for each location at every month is given at the top of each columns.

In accordance with the results above, there were also differences in the frequency distributions of the number of *C. lingua* metacercaria found in the cod from the three locations (Fig. 13). Most of the cod in Jøvik was not infected, and only a few had 1-10 black spots (Fig. 13). The maximum number of metacercaria recorded in one fish at this location was only five, in contrast to 65 in both Njosken and Makkjosen. These two locations had both a tail shaped distribution pattern (Fig. 13). Njosken had a wide range of distribution, while Makkjosen had higher rates for 1-10 and 61-65 metacercaria (Fig. 13). The variance to mean ratio showed that these two locations had a strong over dispersed distribution of *C. lingua* metacercaria. The variation in number of parasites in each fish was much lower in Jøvik. The total abundance of parasites also confirm that the highest infection was in Njosken with a value of 9.9, Makkjosen follows with 8.8, and Jøvik had only 0.2.

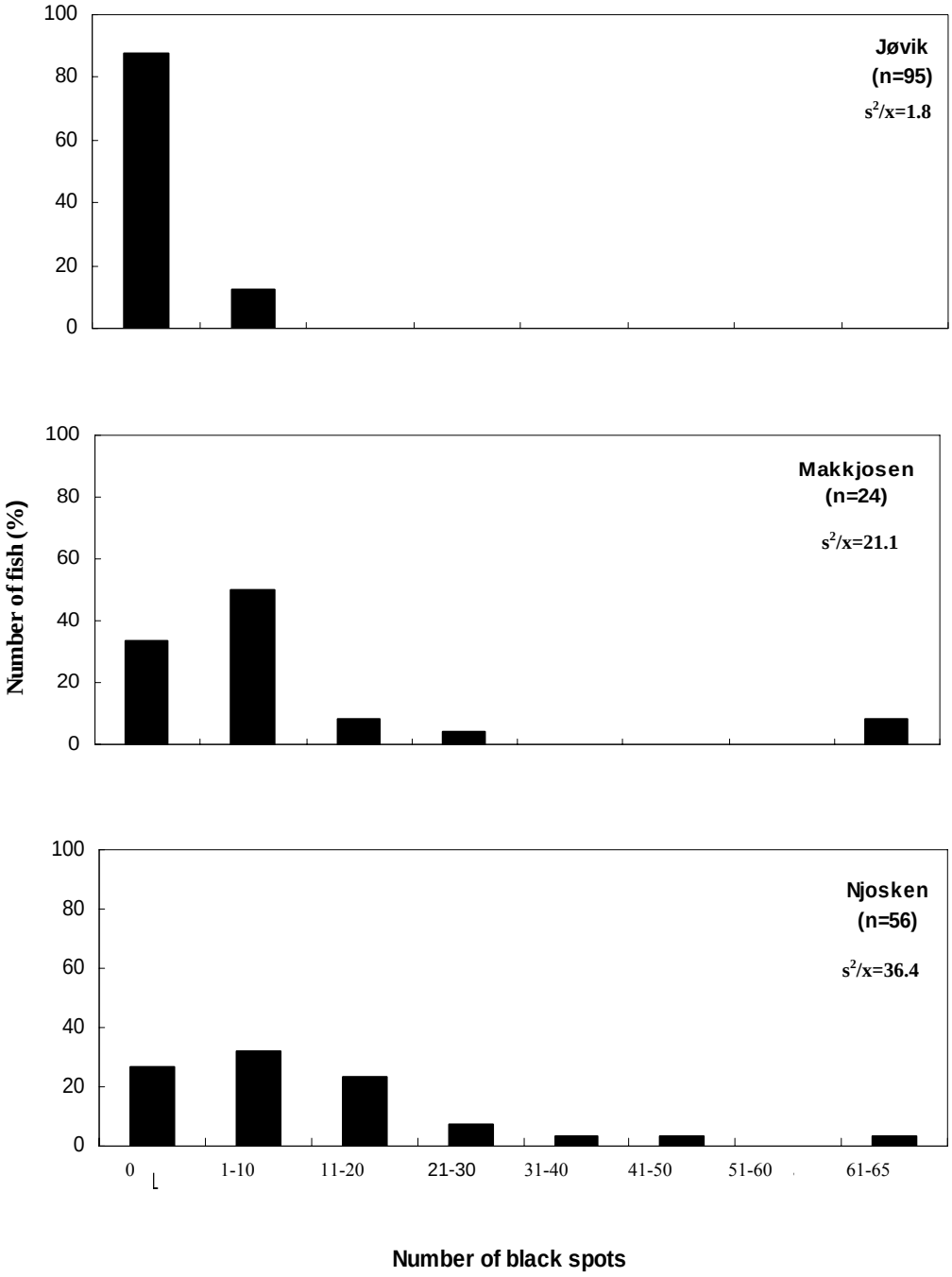


Fig. 13. Frequency distribution (%) of *Cryptocotyle lingua* in cod from Jøvik, Makkjosen and Njosken. Number of fish examined and variance to mean ratio (s^2/x) at each location is given in the plots.

DISCUSSION

DIET

METHODS

Depending on the quantitative method used in a study, the relative importance of different prey groups may differ (Hyslop 1980), as it also is observed in this study. Small prey like copepods contributed more in percentage of relative frequency (N_i%) than relative biomass (B_i%), and larger prey like polychaetes made up more in relative biomass (B_i%) than N_i%. As Hyslop (1980) suggested, prey numbers may therefore emphasise the importance of large amounts of small prey, and therefore the analyses of dietary composition in this study also included biomass and frequency of occurrence.

The gastric evacuation rate is also dependent on prey size and species and the occurrence of ingestible or slowly digestible parts such as shell or exoskeletons (e.g. Berg 1979, Hyslop 1980). Thus, the prey composition of the diet will be somewhat different from the observed prey composition in the stomachs, because there was not made any adjustments for the fact that digestion rate differ between prey types. By reducing the diet analysis to only consider material from the oesophagus and stomach, the bias was probably reduced (Pillay 1952, Berg 1979). In addition, the cod caught were killed immediately after capture and conserved on ethanol, thus stopping the stomach-evacuation. Digestion and stomach-evacuation rate also depend on temperature (dos Santos and Jobling 1995). An experimental study by dos Santos and Jobling (1995) has showed that the stomach evacuation rate and consumption increases by 10–15% when temperature increases by only 1°C.

Canonical Correspondence Analysis (CCA) was used as a statistical method to investigate associations between the environmental variables (area, month, cod length and body weight) and prey weight composition from stomachs. By classifying the stomach data into higher-order groups, the geographical analysis becomes easier to comprehend. However, there will be a loss of detailed niches information (Graham and Vrijenhoek 1988).

DIETARY COMPOSITION

That many different prey groups were found in the stomach of the sampled juvenile cod, but only a few prey groups dominated the diet composition is similar to other studies (Wiborg 1949, Klemetsen 1982, Bromley *et al*. 1997). Copepods were found to be the most important prey group in terms of frequency of occurrence and relative numerical frequency, which is also consistent with previous studies of juvenile cod (Daan 1973, Robb and Hislop 1980,

Bromley *et al.* 1997). Copepods and krill (*Thysanoessa* spp.) are very abundant in the coastal regions and are regarded as key groups in the coastal ecosystem in northern Norway. They are important not only for cod but for a wide range of other marine fish and marine mammals around the world (Albert 1995, Whisner *et al.* 1995, Fjøsne and Gjøsæter 1996, Bromley *et al.* 1997, Nilssen *et al.* 2001). The reason that cod consumed more harpacticoids than cyclopids might be their differences in locomotion patterns. Their unbroken swimming path makes them easier to catch than the jumping calanoids, and their relatively rapid movements may trigger a feeding reaction in the cod. In addition, harpacticoids are associated with bottom and/or macroalgae. Polychaetes were found to be an important prey group for the cod in terms of biomass, which is also consistent with previous studies (Kanapathippillai *et al.* 1994). Mysids and decapods are hyperbenthic prey which also was important for the juvenile cod diet in the study of Wiborg (1949). Gammaridae is very common in the tidal zone among brown alga and below rocks. Many of these species (e.g. *Gammarus locusta*) can cope with brackish water and are thus common in areas with freshwater runoff. This prey group had high numerical frequency and also with high biomass. Decapods were found to be an important in terms prey group in terms of biomass for the juvenile cod.

BETWEEN AREA DIFFERENCES

The majority of the cod from Jøvik had a mixture of pelagic and hyperbenthic prey groups in their stomach. Copepods were clearly most important in terms of FO_i%, N_i% (Table 3) and also important in terms of B_i% (Fig. 3) at this location. The very high B_i% value of amphipods in August could be expected due to the fact that many gammarids (which was the dominant group of amphipods) is commonly found in areas with freshwater runoff, which this location had. The only study that enables comparison for this location is again that of Wiborg from 1949. He found that the most dominant prey groups in material collected from Svendsby 16 October with a prawn trawl at deep waters, were Mysidacea (FO%:76), Euphausiacea (FO%: 52), Copepoda (FO%:28) and Amphipoda (FO%: 35.2). He does not give any information about what exact depth his samples were collected at. Svendsby is situated cross over the fjord from Jøvik. The results of Wiborg investigation is similar to the present study were Mysidiacea (*Mysis litoralis* FO_i%:54, Mysis sp. FO_i%:23) and copepods (Calanoida FO_i%:62, Cyclopoida FO_i%:50) also were very important in the cods diet in October. The reason for the high values of mysids in the cod stomachs at this location might be explained by the preys habitat preferences. *Mysis litoralis* is as it name indicate an littoral specie, and

can be found in water with changing salinity. Most species of mysids form aggregations which result in many coastal mysids occurring at high densities, especially in estuarine or sandy beach habitats. There decreasing trend in number of prey per fish with increasing fish length at this location is most likely due to size of the preys. Smaller preys were eaten in August when the fish was small and with increasing fish length the prey size also increased. Contrary to the study of Wiborg (1949), decapods were not important in the cod diet in October, but rather in September. The small B_i% eaten of this prey group in the other months and a decreasing abundance of copepods may have forced the cod to change their diet. These possible explanations might be the reason for the transition from a pelagic diet in August and September with copepods and decapods, towards more hyperbenthic prey groups such as mysids and amphipods in October and November.

The diet in Njosken seems to consist of relative many prey groups compared with the two other locations examined in this study (Fig. 2). The benthic and hyperbenthic prey groups that dominate the diet in October at this location were Calanoida, Cyclopoida and Harpacoptida (FO_i%:85, 54 and 46 respectively). In contrast, Wiborg (1949) found that diet of 0-group cod in the inner part of Sørfjord was dominated by Mysidacea (FO%:70.5), Amphipoda (FO%: 35.2) and Euphausiacea (FO%: 35.2) in October. He does not show where

exactly in Sørfjorden this location is, but this is still the only study available to compare the current one with. The reason for these differences might be that Wiborg collected his material with a prawn trawl at deep waters, whereas material for this study was collected with a beach seine in the sub-littoral zone. Isopods were very important in October and November in Njosken, and isopods are commonly found at alga in shallow water, where they feed upon epiphytic algae. In August, decapods and polychaetes contributed the most in terms of biomass, while polychaetes had a biomass of 42% in September (Table 3). The CCA plot confirmed that polychaetes and isopods were the prey groups that were most characteristic for Njosken (Fig. 3).

In Makkjosen, cod ate relatively few but large preys compared with the other two locations (Fig. 5), and only a few prey groups dominated the diet of the cod (Fig. 2). In Kvalsundet in August the far most important prey group in Makkjosen were Cumacea (B_i%:48) followed by amphipods (B_i%:23). Generally however, cumaceans can not be considered as an important prey group for the juvenile cod, since only two of twelve individuals ate this prey group, indicating that some cod are specialists. In September, polychaetes totally dominated the diet with 84% (B_i), and polychaetes were found in more than half of the cod examined at this location (Tabel 3). The feeding strategy at this location

might be more opportunistic rather than generalistic compared with the other two locations. The results observed at this location may also be a result of small-scale patchiness in the occurrence of suitable prey or aggregation of the predator. There has not been conducted any analysis of whether each haul tended to collect cod that were feeding on the same "prey patch" or belonged to the same feeding shoal. There was a very high abundance of juvenile saithe at Makkjosen, and this may have forced the cod to specialize at certain prey groups as a response of the competition. However, there is no evidence available from this study to asses whether food supply was scarce or abundant for either cod or saithe. A fact that may support the hypothesis that there was a strong competition between saithe and cod, is that there was not any cod caught here after September. The competition of food by saithe, might have forced the cod to immigrate to other habitats elsewhere. Another explanation can be that the cod present belonged to a very local abundance and might have been caught during the two first months of sampling. As discussed later, the black spot disease infection at this location may also be a reason for the low abundance of cod.

Kanapathippillai *et al.* (1994) have demonstrated differences in the food of cod between fairly close stations, due to habitat differences. Euphausiacea has been found important in larger cod diet in several previous studies (Wiborg 1948, Kanapathippillai *et al.* 1994). The aggregation of krill in deeper waters (Falk-Petersen and Kristiansen 1985) may be the reason as to why there is not observed any krill in the cod diet from the sublittoral zone in this study.

In summary, the prey composition and relative importance differ between location and between months. The habitat differences at the locations may have caused different prey species to dominate at the different locations. In the inner part of Ullsfjord (Jøvik) where a strong tidal current through the nearby fjord sill area, the hyper-benthic prey groups mysids, decapods and amphipods were most important. In the inner part of the Sørfjord (Njosken), the water masses were less turbulent, and bentho-pelagic preys such decapods and isopods become more important. In Kvalsundet, there is a strong tidal water movement and the bottom in Makkjosen is shallow far out. Cumacea and polychaetes seem to be most important in the 0-group cod diet, which may be a response to the competition by juvenile saithe.

OTOLITH

OTOLITH ANALYSIS

Precision in measurements of otolith width may influence the calculation of fish length and otolith width for cod reaching zone pattern category 2 (hyaline zone). Since there was no significant difference in readings between person a and b, a more advanced method like picture analysis would most likely not have given a different result regarding the otolith zone patterns observed at this study. Use of picture analysis may minimize measurement errors. On the other hand, pictures will have less resolution than visual observation of otoliths.

ROLE OF DAY-LENGTH, TEMPERATURE AND PREY ABUNDANCE

This study showed that most 0-group coastal cod deposits the inner edge of the first hyaline zone in the otolith between October and November (Fig. 6). There are several possible factors that may trigger the deposition of the hyaline zone, and these are many and complex. Suthers and Sundby (1996) found a large difference in growth rate of pelagic juvenile cod sampled from populations at 43 and 70°N. They suggested that the 6-8 hour additional daylight per day at 70°N could almost double the size of pelagic juvenile cod by mid-summer. At 70°N, the daylength decreases towards November (Appendix figure A1), and the deposition of the hyaline zone might be a result of this decrease. Cod juveniles are visual predators and the availability of prey is not simply a function of prey biomass, but also light and turbulence (for cod larvae Sundby *et al*. 1994). The decrease in day-length from September (average 13h) to November (average 4h) may have decreased food-consumption, and hence triggered deposition of the hyaline zone. Since average otolith width differed between the locations, daylength could not have been the main factor affecting the otolith growth, since daylength would have the same effect on all locations. However, it is likely to be the main factor affecting the timing of the zoning.

Individual growth in fish depends on food supply, and physiological stress related to dietary change may have induced deposition of the hyaline zone. When fishes experience periods of poor food supply, they react to an extended period of food shortage by reducing superfluous activity, both metabolic and locomotory (Beamish 1964). When food supply increase again, some fish species show marked growth spurts, a phenomenon termed compensatory growth (Ali *et al*. 2003). The stomach data revealed that the cod had relatively similar diet in October and November, and that the diet in September differs from the other

months by having only one dominating prey group in terms of biomass. The diet transition from September to October could possibly have induced the zoning of the hyaline zone in the cod otoliths.

Other than food availability, temperature is the most important influence on growth rate of cod (Suthers and Sundby 1996), and has been suggested to influence otolith growth increments in juvenile fish (Lombarte *et al.* 2003). Temperature may have an influence directly through the distribution, growth, metabolism and excretion (Nakken and Raknes 1987), and indirect through the advection of plankton and by influencing the growth and abundance of other prey groups in the cod diet. The optimum temperature for small cod when given food excess is 11-15°C and for large cod 9-12°C (Pedersen and Jobling 1989), and occurs at lower temperatures at lower food rations as in the wild. It is rare that the water temperatures exceed these temperatures for the areas in this study. It has been documented that at a given temperature, slower growing individuals has larger otoliths than fast growing individuals (Wright *et al*. 1990, Hare and Cowen 1995, Otterlei *et al*. 2002). Temperature was found to have a significant effect on the relationship between otolith width and fish length in this study. The large otoliths for cod in Makkjosen might be a result of higher temperatures than at the two other locations. Water temperatures at Makkjosen were higher (10.7°C) in September compared with temperatures from Jøvik (7.8°C) and Njosken (8.0°C).

SOMATIC GROWTH

Factors that might affect the relationship of otolith growth and somatic growth are important due to the proportionality assumption for back-calculation (Hare and Cowen 1995). That there was not found any relationship between fish length and zone pattern category, indicates that fish length has a minor effect for the hyaline zone deposition in the otoliths. Due to the lack of cod from October and November at Makkjosen, and the low numbers caught, it is difficult to conclude whether cod from this location had an overall slower growth than cod from the other locations.

In summary, the deposition of the inner edge of the hyaline zone in 0-group coastal cod takes place between October and November, and the average fish length at this formation was calculated to be 69.7 mm, with an average otolith width of 1.37 mm. Timing for the formation of the first hyaline zone in 0-group cod seems not to be controlled by fish length, but rather an interaction of daylength, diet and sea temperature. More investigations are needed in order to learn more about the factors that influence the timing of the zoning.

CRYPTOCOTYLE LINGUA INFECTION

This study shows that *Cryptocotyle lingua* appears to be a common parasite in cod populations at the two locations Njosken and Makkjosen, and thus also in periwinkles in these areas. Other studies have also showed that *C. lingua* is commonly found in the coastal waters in northern Norway (Kristoffersen, 1991). There was a large difference between all locations in the seasonal progression of the parasite infection. Cod from Njosken and Makkjosen exhibited the heaviest infections, whereas fish from Jøvik had almost no parasites (Fig. 12).

COMPARISON OF LOCALITIES

The three locations differ with regard to topography, macroalgae species and abundance, in addition to freshwater input. During low tides, brown algae in the littoral zone are frequently exposed to air. This is usually also the time when gull congregate in the littoral and where trematode eggs would get contact with seawater in droppings from the gulls. In Jøvik there were a limited numbers of algae exposed to air during low tides, which led to a scarce abundance of gull aggregation here. This might be one cause for the low infection rate seen at Jøvik. However, there was not recorded how many or which bird species were present at the different locations. The main reason for the low infection rate and small changes in seasonal development of the parasite infection in Jøvik might be the small numbers of periwinkles here (visual assessment). Sindermann and Farrin (1962) found that production of *C. lingua* cercariae ceases when the temperature drops below 8 to 10°C. Möller (1978) also found that low temperatures in addition to low salinities have a negative effect upon the development, infectivity and survival of eggs and cercaria of *C. lingua*. The relatively large freshwater runoff at this location (see Appendix table A1), low water temperatures and a relatively large exchange of water due to strong tidal currents may all contributed to low infection rates at this location. Thus, a combination of these four factors is most likely the reason for the low values of infection in Jøvik. Further, the relatively stable parasite infection recorded at this location indicates that there is not any significant immigration of cod into this area, and that the cod present retains itself here, hence the conclusion that 0-group cod from Jøvik are probably stationary in this area during summer and fall.

The seasonal development in Njosken, with an increase with time, has also been documented in previous studies (van den Broek 1979). This seasonal pattern is an indication that cod has been relatively stationary at this location during summer and fall. In Njosken and Makkjosen, the brown algae are exposed to air during low tide, which increases the possibility

of infection of *C. lingua* to the periwinkles and thus also to the fish. These two locations received a relatively small amount of freshwater runoff, had higher average water temperatures than Jøvik, and also exhibited larger densities of periwinkles and macroalgae. These are the most likely explanations as to why cod from Njosken and Makkjosen had higher numbers of *C. lingua* metacercaria than those from Jøvik.

There are three possible explanations for the apparent decrease, in both prevalence and abundance in Makkjosen. One is that the black spots had disappeared between the sampling dates. This did most likely not occur, since the black spots caused by *C. lingua* infections are known to remain for long periods of time, perhaps years (Stunkard 1930). A second explanation may be that the most heavily infected cod became weakened and thus an easier target for predators, and bringing the prevalence and abundance of *C. lingua* down at the last sampling occasion. About 10 % of the fish at Makkjosen had more than 60 parasites in August, and because of the method employed in this study, this represent a minimum estimate, since some metacercaria may not have reached the stage for causing black spots in the skin. However, a cyst in the eye or nervous tissue is likely to do more damage than a cyst in the fins of the fish. The two most heavily infected cod at this location did in fact have several cysts in their eyes, but it is difficult to conclude whether they became blind because of this infection. Most previous studies concerning this parasite have been conducted on larva or juvenile fish, and have shown that the infection must be massive in order to kill the fish (Sindermann and Rosenfield 1954, MacKenzie 1968). A third explanation is that uninfected fish have immigrated into the area, or that the most heavily infected individuals migrated out. Seasonal levels of parasitic infections have provided mush useful information in determining the migrations patterns of individual fish populations in the past (van den Broek 1977). The fact that the average fish length decreased from August to September at Makkjosen, might indicate that larger cod has migrated out of the area, or that smaller cod has immigrated into the area. It is difficult to conclude what happened at this location, and the decline in prevalence and abundance of *C. lingua* might just be a coincidence due to small sample sizes.

CRYPTOCOTYLE LINGUA AS HABITAT INDICATOR

There seems to be a correlation between the variation in the habitat and abiotic factors inflecting the three locations and the infection rate of *C. lingua*. The infection of *C. lingua* at the three locations indicates that juvenile cod from Jøvik and Njosken are relatively stationary, and that there is little emigration and immigration in these areas. The infection rate

of *C. lingua* in Makkjosen indicate that the cod is relatively stationary during the summer and fall, but there is a degree of uncertainty of whether heavily infected cod migrated out of the area, or less infected cod immigrated to the area. If a parasite is to be used as a biological tag, the parasite should have a life span, or remain in an identifiable form, in the subject host long enough to cover the time scale of the investigation. Sindermann (1983) suggested that the prevalence of a good parasite tag should remain relatively stable from season to season and from year to year. On the other hand, seasonal variations can determine seasonal migrations of the subject host. With this in mind, the conclusion of the present study is that infection of *C. lingua* can be used as a habitat indicator of 0-group cod during the summer and fall, but that the sampling must be sufficiently high to rule out any coincidence in the parasite progression.

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APPENDIX

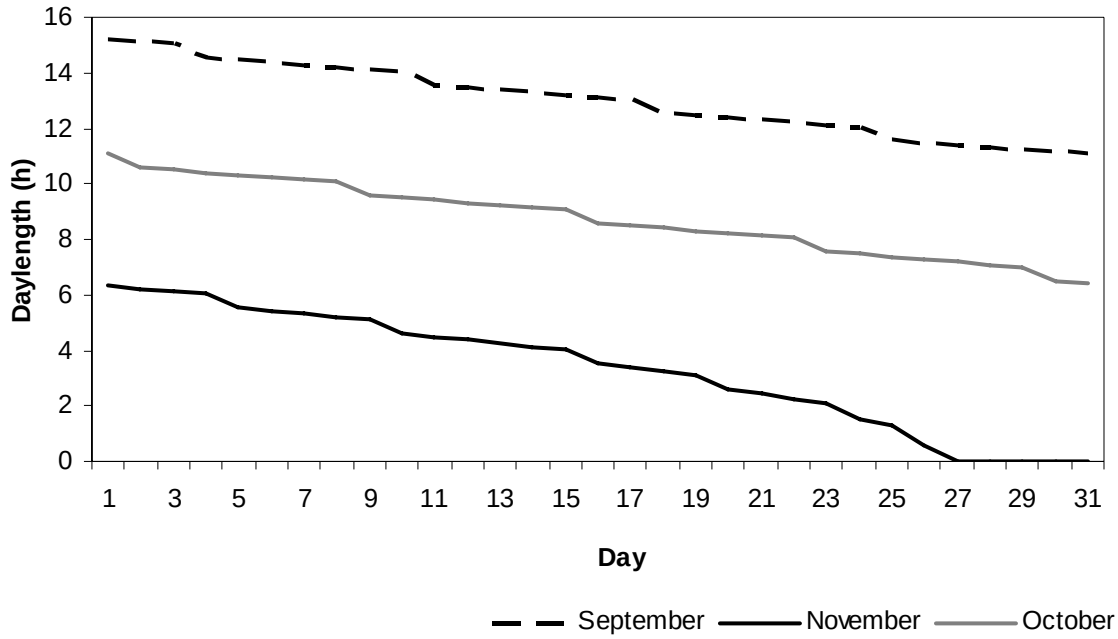

Fig A1. Daylength (sun rise-sun set) in September, October and November in Tromsø 2005.

Table A1. Water runoff from NVEs (Norges vassdrag - og energidirektorat) water runoff map 2001.

Location	**(water runoff l/s * km^2)**
Makkjosen	35-40
Njosken	25-30
Jøvik	50

Table A2. Results from stomach content from 175 Coastal Cod from Jøvik (J), Njosken (N) and Makkjosen (M). Ni (%) - relative numerical frequency, FOi (%) - frequency of occurrence, Bi (%) - relative biomass. <0.5; "0", not detected; "-".

	AUGUST									**September**									**October**						**November**					
	N_i (%)			**Fo_i (%)**			**B_i (%)**			**N_i (%)**			**Fo_i (%)**			**B_i (%)**			**N_i (%)**		**Fo_i (%)**		**B_i (%)**		**N_i (%)**		**Fo_i (%)**		**B_i (%)**	
Prey item	J	N	M	J	N	M	J	N	M	J	N	M	J	N	M	J	N	M	J	N	J	N	J	N	J	N	J	N	J	N
Calanoida spp.	19	1	7	96	22	30	3	0	4	38	51	40	33	81	50	1	7	1	18	85	62	85	6	8	37	3	76	42	13	0
Calanoida fragments	0	-	-	5	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	23	-	62	-	12	3
Cyclopida spp.	40	42		59	67	-	1	2	-	14		0	50		8	1	-	0	18	5	50	46	4	1	21	13	67	37	1	2
Oithona sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	27	-	11	-	0
Harpacticoida spp.	18	2	0	27	11	10	1	0	0	28	37	26	50	69	33	1	10	1	52	4	77	62	6	1	3	12	19	68	0	0
Cladocera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	11	-	0
Podon sp.	2	10	2	9	44	30	0	0	0	4	1	1	29	31	8	0	0	0	-	0	-	15	-	0	-	-	-	-	-	-
Evedane sp.	0	10	1	5	33	20	0	0	0	0	-	-	4	-	-	0	-	-	-	0	-	8	-	0	-	-	-	-	-	-
Ostracoda	0	5	2	18	33	50	0	0	0	0	-	1	4	-	25	0	-	0	0	-	4	-	0	-	-	-	-	-	-	-
Mysidiae spp.	-	-	-	-	-	-	-	-	-	2	-	-	21	-	-	4	-	-	0	-	4	-	7	-	-	0	-	5	-	1
Mysis sp.	0	-	-	5	-	-	1	-	-	6	-	0	25	-	8	17	-	3	0	0	23	8	4	8	2	-	29	-	2	-
Mysis litoralis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	54	-	32	-	7	0	62	5	39	1
Mysis oculata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	4	-	1	-	-	0	-	5	-	6
Erythrops sp.	-	-	-	-	-	-	-	-	-	0	-	-	4	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mysidiae fragments	-	-	-	-	-	-	-	-	-	1	0	-	8	6	-	1	4	-	-	-	-	-	-	-	2	0	29	5	5	0
Cumacea	-	0	56	-	11	30	-	0	48	-	0	-	-	6	-	-	0	-	-	0	-	15	-	1	-	0	-	5		0
Idoeta sp.	-	1	-	-	22	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Idotea baltica	-	2	-	-	22	-	-	0	-	-	-	-	-	-	-	-	-	-		0	-	8	-	12	-	-	-	-	-	-
Idotea neglecta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	11	-	14
Gammarus.spp	8	0	9	41	11	60	3	0	3	1	1	6	8	19	25	0	4	2	5	-	38	-	23	-	1	1	14	16	2	4
Gammarus locusta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	5	-	0	-
Gammaridae fragments	2	-	0	18	-	10	5	-	14	-	-	0	-	-	8	-	-	0	0	-	4	-	1	-	1	1	14	11	3	2

Table A2, continuing. Results from stomach content from 175 Coastal Cod from Jøvik (J), Njosken (N) and Makkjosen (M). Ni (%) - relative numerical frequency, FOi (%) - frequency of occurrence, Bi (%) - relative biomass. <0.5; "0", not detected; "-".

	AUGUST									September									Oktober						November					
	N_i (%)			Fo_i (%)			B_i (%)			N_i (%)			Fo_i (%)			B_i (%)			Ni (%)		Foi (%)		Bi (%)		N_i (%)		Fo_i (%)		B_i (%)	
Prey item	J	N	M	J	N	M	J	N	M	J	N	M	J	N	M	J	N	M	J	N	J	N	J	N	J	N	J	N	J	N
Hyperiidae	-	3	11	-	22	30	-	2	7	1	-	1	8	-	17	0	-	0	-	-	-	-	-	-	-	3	-	21	-	1
Corophium crassicorne	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	8	-	0	-	-	-	-	-	-
Hyperiidae fragment	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	11	-	1
Caprellidea	-	-	0	-	-	10	-	-	0	0	-	-	4	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phtisica marina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	8	-	0	-	-	-	-	-	-
Amphipoda fragments	-	1	-	-	11	-	-	0	-	1	1	3	4	13	8	2	3	2	-	-	-	-	-	-	-	8	-	47	-	4
Caridea	-	-	-	-	-	-	-	-	-	1	-	-	8	-	-	17	-	-	0	0	4	15	2	13	-	1	-	11	-	5
Pandalus sp.	-	-	-	-	-	-	-	-	-	0	0	-	25	6	-	38	1	-	-	-	-	-	-	-	0	0	5	5	2	8
Pandalus borelais	-	-	-	-	-	-	-	-	-	0	-	-	4	-	-	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Decapoda fragments	-	0	-	-	11	-	-	14	-	2	-	-	13	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polychaeta fragments	-	0	-	-	11	-	-	14	1	-	0	11	4	13	58	4	42	84	-	-	-	-	-	-	0	3	5	42	5	28
Aphrodita aculeata	-	-	0	-	-	10	-	-	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eunicidae n.det	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	5	-	0
Bivalvia	-	-	1	-	-	13	-	-	0	-	0	1	-	13	8	-	0	0	0	-	15	-	0	-	-	-	-	-	-	-
Gastropoda	-	-	0	-	-	10	-	-	-	0	-	8	4	-	17	0	-	0	0	0	4	8	0	0	-	-	-	-	-	-
Insect	0	1	1	5	22	10	0	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rocks	6	0	-	48	11	-	75	13	-	-	4	-	-	31	-	-	3	-	2	1	39	15	5	1	0	12	5	53	-	4
Pholis gunnelus	-	0	-	-	11	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plantae fragments	-	0	-	-	11	-	-	1	-	0	-	-	4	-	-	0	-	-	-	-	-	-	-	-	-	1	-	15	-	4
Unidentified fragments	4	5	8	63	22	50	7	22	26	0	1	4	8	13	25	3	25	8	-	-	42	31	7	3	1	1	14	11	16	12