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Helminth parasites as biological tags in population studies of Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)), in the north-west Atlantic

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As part of a stock identification study, the parasite fauna of 608 Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum) from six areas in the north-west Atlantic was examined. New records of parasite species for the Greenland area have been added by this study. No significant differences in prevalence were found between sexes or age groups of Greenland halibut. Three digeneans (*Brachyphallus crenatus*, *Steganoderma formosum* and *Stenakron vetustum*) and three nematodes (*Anisakis simplex*, *Ascarophis* sp., and *Contracaecum* sp.) showed irregularities in spatial infestation pattern and were therefore chosen as biological tags. Nonparametric discriminant analyses of the prevalence of these parasites indicated strong similarities between components off Labrador, Davis Strait, and in the fjords of Umanak at West Greenland. Greenland halibut in south-west Greenland fjords appeared to be isolated, as does the component in the Denmark Strait. This general pattern adds further support to previous investigations on stock structure of Greenland halibut in the North-west Atlantic.

Key words: Greenland halibut, helminth parasites, biological tags, north-west Atlantic, stock discrimination.

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Introduction

Parasites have been used successfully as biological "tags" in numerous studies to provide information on fish host populations. The advantage of this method is that it requires little effort in relation to sampling procedures, viz. during routine surveys, and it is independent of fishing activities, unlike conventional tagging for example. In a review of parasites as biological tags, Williams *et al.* (1992) list the commonly stated criteria required for different categories of studies using parasites as biological indicators. In this context, MacKenzie (1987), considered that for fish stock separation studies several different groups of parasites are appropriate for use, although not necessarily parasites with long life spans in the host.

In the north-west Atlantic, Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum) are distributed from Smith Sound, between Greenland and Canada, southward throughout Baffin Bay and Davis Strait to the north-east American coast and eastward along East Greenland to Iceland (Smidt, 1969; Bowering and Brodie, 1995). They have been heavily exploited along the eastern Canadian coast, in Davis Strait, at West and East Greenland and off Iceland, with average annual landings of about 120 000 t during the 1990s (Anon., 1994, 1995). All Greenland halibut stocks throughout the area have declined considerably in recent years (Anon., 1994, 1995) and more detailed knowledge of stock structure has become essential for effective management of the resource. This is especially important considering that the resource extends over several national boundaries and into international waters.

In the north-west Atlantic Greenland halibut reach maturity after 6–11 years (males) and 8–12 years (females) (Smidt, 1969; Bowering, 1982; Serebryakov *et al.*, 1992; Junquera and Zamarro, 1994; Nielsen and Boje, 1995; Anon., 1996). Spawning seems to take place

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in deeper waters (approximately 800–2000 m depth) over an extended area from Davis Strait, south of 67°N (Jensen, 1935; Smidt, 1969) to south of Flemish Pass off Newfoundland (Junquera and Zamarro, 1994). Eggs and larvae are dispersed by the water currents to the western shore of Greenland and the eastern shore of Canada, where they settle on the banks (Templeman, 1973). In the East Greenland/Iceland area, spawning occurs on the continental slopes west of Iceland (Sigurdsson, 1979). From there, eggs and larvae are carried either towards East Greenland by the Irminger Current or north-eastward along the northern Icelandic coast (Sigurdsson, 1979). Although Greenland halibut from Iceland to Newfoundland thus consist of fish derived from at least two spawning stocks, migrations from south-west Greenland fjords to Iceland have been observed (Boje, 1993).

As they grow, fish on the inner continental slopes off West Greenland probably migrate to the deeper parts of the fjords (Smidt, 1969), while those on the outer slopes are believed to migrate to deeper parts of Davis Strait (Riget and Boje, 1989). At the Canadian coast off Newfoundland and Labrador, Bowering (1983, 1984) suggested a prespawning migration of maturing Greenland halibut towards the deep part of the continental slopes in Davis Strait and off Labrador. Similarly, a prespawning migration of Greenland halibut from north-west, north, and east Iceland towards the spawning area west of Iceland in late summer has been described by Chumakov (1969) and Sigurdsson (1979).

Several studies on stock identification of Greenland halibut in the north-west Atlantic have been carried out, using meristic characters (Templeman, 1970; Misra and Bowering, 1984; Riget *et al*., 1992), morphometric characters (Bowering, 1988), genetic differentiation (Fairbairn, 1981; Riget *et al*., 1992), parasite infestation as biological tags (Khan *et al*., 1982; Reimer and Ernst, 1989; Arthur and Albert, 1993) and external tagging (Bowering, 1984; Boje, 1993). These studies indicate that Greenland halibut form a single homogeneous stock throughout the East Canadian–West Greenland area, except for components in Gulf of St Lawrence and Fortune Bay (Templeman, 1970; Fairbairn, 1981; Misra and Bowering, 1984; Arthur and Albert, 1993) and in fjords of West Greenland (Riget *et al*., 1992; Boje, 1993). Furthermore, tagging experiments indicate that the spawning stock west of Iceland and the fjord components in south-west Greenland are related (Smidt, 1969; Riget *et al*., 1992; Boje, 1993).

In view of the present stock decline of Greenland halibut observed in the whole north-west Atlantic, and the associated requirement for a better understanding of stock affinities to improve management, this study contributes new information on the discreteness of Greenland halibut stock components in the Iceland–Greenland–Canada area based on regional differences in parasite fauna. The study is part of an integrated study using meristics, genetic variation, and parasites (Riget *et al*., 1992) to complement conventional tagging (Boje, 1993).

Materials and methods

Approximately 100 Greenland halibut, ranging from 46–87 cm in total length, were sampled in each of six localities: off eastern Newfoundland, Davis Strait, Umanak fjord, Godthaabsfjord, Julianehaab district, and Denmark Strait (see Fig. 1 and Table 1). The fish were caught by research vessels using bottom trawl and long-line from several hauls/line settings at each locality. Sex of all specimens was determined, total length, and weight were measured and otoliths were taken for age determination. The alimentary tract of all fish (i.e. stomach including lower part of oesophagus, pyloric caeca, and intestine) and the right fillet including the napes, i.e. the hypaxial musculature surrounding the body cavity, were removed and frozen immediately for later examination. A thin smear of blood from the heart was prepared from each fish dried at room temperature, fixed with 96% ethanol and stained with Giemsa stain. However, no blood smears or fillets were sampled from Godthaabsfjord, as this locality was sampled before the sampling program was fully developed.

Smears of 20 fish from each locality were examined microscopically with 40 × and 100 × magnification for periods of 10 min each. The exterior of the alimentary tract was examined by eye for nematodes, while the lumen was examined microscopically. Fillets were skinned and cut into thin slices, and were then candled to observe for nematodes.

All parasites were stored in 70% ethanol and cleared in lactophenol to determine classification. Where necessary, parasites were mounted in glycerol jelly for microscopic examination.

In order to use prevalence as a dependent variable, each fish was assigned a value of 0 (absence of parasite) or 1 (parasite present). In order to investigate age and sex effects on prevalence, data were analysed with a logistic regression model with age as continuous independent variable and sex as another independent variable (Hosmer and Lemeshow, 1989). A nonparametric discriminant analysis (SAS, 1988), based on estimates of group-specific probability densities, was executed on prevalence data of selected parasite species to achieve classification estimates for the six localities. The nonparametric density estimates were calculated by a normal kernel method using a radius (r) value of 1.0. To avoid a reduction in sample size by dividing the data in a ''training'' data set and an evaluation data set, cross-validation on the entire data set was used. All calculations in present study were done using the statistical software SAS (SAS, 1988).

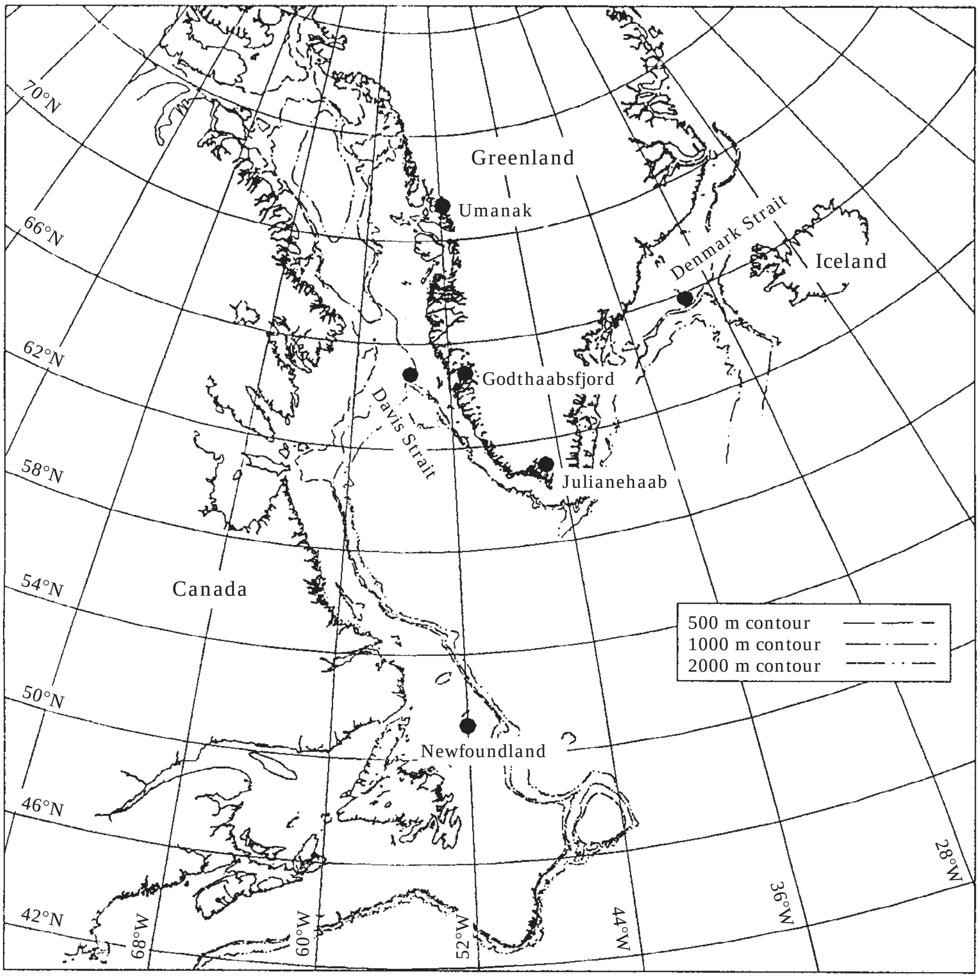

Figure 1. Map of the area investigated and sample localities.

The quantitative terms intensity (I) and prevalence (P) are defined as mean number of parasites per infested fish and percentage fish infested in a sample, respectively, according to Margolis *et al.* (1982). The term component is often used when describing Greenland halibut populations in certain areas, intimating that spawning origin is poorly known and that the component may be part of a larger (unknown) spawning complex.

Results

Twenty-one species of parasite (1 Monogenea, 12 Digenea, 1 Cestoda, 2 Acanthocephala and 6 Nematoda) were found (Table 2). No blood protozoa were observed from smears. Due to inadequate fixation, *Ascarophis* could not be identified to species, but all specimens appeared to belong to the same species. *Contracaecum* sp. could not be identified to the species level, but specimens found were identical to those described by Smith and Wootten (1984).

Six parasite species were selected for further statistical analyses of fish stock affinities, based on the criterion that the parasite be relatively abundant in at least one of the samples. They were *Brachyphallus crenatus*, *Steganoderma formosum*, *Stenakron vetustum*, *Anisakis simplex* larvae (in body cavity and fillets), *Ascarophis* sp., and *Contracaecum* sp. larvae.

The sex ratio (no. males/no. females) in the samples varied from 0.29 (Julianehaab) to 2.54 (Davis Strait). Results of the logistic regression model for each of the six selected parasite species and each locality, showed that in only one case (*Ascarophis* sp. in Godthaabsfjord) a significant (5% level) model was found (likelihood ratio test). In that case a significant difference was found between sexes (Wald test). The presence of a single case with a relationship between both age and sex, and prevalence was regarded a coincidence that was not

Table 1. Data for samples of Greenland halibut from six areas in the Northwest Atlantic. For length, weight and age are given mean values, ranges and standard error of the means.

Locality	NAFO/ ICES Divisions	Latitude (N)	Longitude (W)	Date	Depth (m)	N	Length (cm)			Weight (g)			Age (yrs)			Sex ratio (m:f)
							Mean	Range	SE	Mean	Range	SE	Mean	Range	SE	
Newfoundland	3K	49°21′0–50°01′5	51°45′8–50°18′9	27 Nov.–8 Dec. 1987	220–835	100	52.56	49–66	0.280	1273	800–2800	26.1	8.07	7–10	0.056	38:59
Davis Strait	1C	64°17′0–65°46′0	55°02′0–57°31′0	12–28 Sept. 1988	603–869	100	54.32	46–68	0.786	1444	810–3300	51.1	8.91	7–12	0.109	71:28
Denmark Strait	XIVb	64°24′0–66°26′0	35°23′0–28°49′0	10–19 Oct. 1987	180–930	100	57.45	49–79	0.722	1983	940–5200	84.9	9.35	7–13	0.143	47:53
West Greenland fjords																
Umanak	1A	70°37′1–70°39′7	52°03′8–50°53′0	17–30 Aug. 1987	210–1080	107	59.80	50–73	0.647	2125	880–4360	82.3	9.74	8–13	0.133	47:60
Godthaabsfjord	1D	63°44′7–64°25′3	52°08′0–51°16′2	9–14 Jan. 1987	140–600	101	57.52	40–87	0.847	1857	600–5660	98.4	8.79	6–15	0.177	30:71
Julianehaab	1F	60°45′2–60°34′0	45°51′2–44°50′0	22–27 Jan. 1988	330–430	101	59.02	50–83	0.584	2007	1020–5400	69.5	10.17	8–15	0.141	23:78

Table 2. Parasites from Greenland halibut in six samples from the Northwest Atlantic. P: prevalence (%), I: mean intensity of infestation ± SE of the mean followed by numbers of observations in parentheses.

Locality	Newfoundland 3K P	Newfoundland 3K I ± SE (n)	Davis Strait 1C P	Davis Strait 1C I ± SE (n)	Umanak 1A P	Umanak 1A I ± SE (n)	Godthaabsfjord 1D P	Godthaabsfjord 1D I ± SE (n)	Julianehaab 1F P	Julianehaab 1F I ± SE (n)	Denmark Strait XIVb P	Denmark Strait XIVb I ± SE (n)
MONOGENEA:												
Entobdella hippoglossi (skin)	0		0		1	1.00 (1)	0		0		0	
DIGENEA: (all a)												
Anomalotrema koiae	0		1	3.00 (1)	0		0		0		0	
Brachyphallus crenatus	0		0		0		0		19	1.68 ± 0.351 (19)	0	
Derogenes varicus	22	2.68 ± 0.929 (22)	51	5.53 ± 1.248 (51)	84	10.20 ± 1.300 (90)	41	1.71 ± 0.198 (41)	58	2.69 ± 0.261 (59)	20	1.76 ± 0.316 (21)
Genolinea laticauda	0		0		0		0		0		1	1.00 (1)
Gonocerca phycidis	0		1	4.00 (1)	0		0		0		0	0
Hemiurus levinseni	0		1	2.00 (1)	2	1.00 ± 0.000 (2)	0		0		0	
Lecithaster sp.	33	3.24 ± 0.498 (33)	21	2.38 ± 0.455 (21)	2	1.00 ± 0.000 (2)	22	4.23 ± 0.738 (22)	35	2.63 ± 0.619 (35)	3	1.00 ± 0.000 (3)
Lecithophyllum sp.	0		0		1	1.00 (1)	0		0		0	
Steganoderma formosum	24	2.46 ± 0.500 (24)	3	1.33 ± 0.333 (3)	1	1.00 (1)	1	2.00 (1)	0		0	
Stenakron vetustum	29	2.93 ± 0.626 (29)	3	2.00 ± 0.577 (3)	1	1.00 (1)	2	3.50 ± 1.500 (2)	1	3.00 (1)	0	
Stephanostomum sp.	0		0		1	1.00 (1)	0		0		0	
Steringophorus furciger	10	3.80 ± 1.632 (10)	40	8.78 ± 2.017 (40)	15	8.38 ± 6.088 (16)	21	11.24 ± 6.386 (21)	15	7.13 ± 3.028 (15)	8	2.00 ± 0.567 (8)
CESTODA:												
Cestoda larvae sp. (a)	0		0		0		0		0		1	1.00 (1)
ACANTHOCEPHALA:												
Echinorhynchus sp. (a)	11	3.36 ± 1.344 (11)	7	3.14 ± 0.670 (7)	0		18	1.50 ± 0.246 (18)	10	4.20 ± 1.153 (10)	15	2.00 ± 0.793 (15)
Corynosoma sp. (a)	2	1.00 ± 0.000 (2)	1	2.00 (1)	18	1.58 ± 0.221 (19)	0		0		4	1.00 ± 0.000 (4)
NEMATODA:												
Anisakis simplex, larvae (a)	4	1.25 ± 0.250 (4)	7	1.57 ± 0.297 (7)	3	1.67 ± 0.333 (3)	19	1.42 ± 0.139 (19)	14	2.20 ± 0.509 (15)	16	4.06 ± 2.409 (16)
Anisakis simplex, larvae (f+b)	26	1.76 ± 0.237 (26)	20	1.95 ± 0.654 (20)	15	1.19 ± 0.100 (16)	50	2.20 ± 0.271 (51)	76	3.21 ± 0.320 (77)	72	4.22 ± 2.850 (72)
Ascarophis sp., adults (a)	1	4.00 (1)	2	4.00 ± 3.000 (2)	7	4.29 ± 2.652 (7)	68	30.78 ± 3.422 (69)	84	51.76 ± 3.721 (8)	0	
Capillaria sp. (a)	0		0	1.00 ± 0.000 (2)	1	1.00 (1)	3	7.00 ± 6.000 (3)	7	9.43 ± 4.908 (7)	0	
Contracaecum sp., larvae (a)	90	9.389 ± 0.806 (90)	53	2.75 ± 0.393 (53)	49	2.00 ± 0.234 (52)	6	1.00 ± 0.000 (6)	27	1.52 ± 0.172 (27)	49	2.43 ± 0.459 (49)
Hysterothylacium aduncum (L3+4) (a)	6	4.17 ± 1.833 (6)	7	1.14 ± 0.143 (7)	0		1	1.00 (1)	2	1.00 ± 0.000 (2)	15	9.07 ± 4.186 (15)
Pseudoterranova decipiens, larvae (a)	0		0		3	1.00 ± 0.000 (3)	0		1	2.00 (1)	3	6.00 ± 3.215 (3)
Pseudoterranova decipiens, larvae (f)	0		1	1.00 (1)	1	1.00 (1)	0		7	1.43 ± 0.297 (7)	4	1.00 ± 0.000 (4)
Nematoda sp. (a)	6	1.67 ± 0.167 (6)	3	1.00 ± 0.000 (3)	0		5	1.00 ± 0.000 (5)	5	1.00 ± 0.000 (5)	2	1.50 ± 0.500 (2)

(L3+4): larvae stages 3 and 4.
(a): in alimentary tract.
(f): in fillets.
(b): in body cavity.
*No fillets were sampled at Godthaabsfjord.

Table 3. Results of a nonparametric discriminant analysis including all localities as categories.

From locality	Number of observations (and percent) classified into locality						
	Newfoundland	Davis Strait	Umanak	Godthaabsfjord	Julianehaab	Denmark Strait	Total
Newfoundland	82 (82.0)	0 (0.0)	4 (4.0)	0 (0.0)	0 (0.0)	14 (14.0)	100 (100.0)
Davis Strait	40 (40.0)	0 (0.0)	41 (41.0)	0 (0.0)	2 (2.0)	17 (17.0)	100 (100.0)
Umanak	39 (36.5)	0 (0.0)	45 (42.1)	3 (2.8)	4 (3.7)	16 (15.0)	107 (100.0)
Godthaabsfjord	2 (2.0)	0 (0.0)	20 (19.8)	28 (27.7)	40 (39.6)	11 (10.9)	101 (100.0)
Julianehaab	3 (3.0)	1 (1.0)	4 (4.0)	11 (10.9)	73 (72.3)	9 (8.9)	101 (100.0)
Denmark Strait	12 (12.1)	0 (0.0)	16 (16.2)	0 (0.0)	0 (0.0)	71 (71.7)	99 (100.0)
Total	178 (29.3)	1 (0.2)	130 (21.4)	42 (6.9)	119 (19.6)	138 (22.7)	608 (100.0)
Prior probability for classification	0.167	0.167	0.167	0.167	0.167	0.167	
	Error count estimates for localities						
Rate	0.18	1.00	0.58	0.72	0.28	0.28	0.51

representative for the total material. The data were therefore pooled for each locality in subsequent analyses.

Prevalence is considered to be a more useful parameter than intensity since it is less variable and represents the entire data set (intensity only comprises infested fish), and was therefore used as the variable in the following analyses. Significant differences in prevalence were noted between localities for all selected species (99% confidence limits, Chi-square tests). *Brachyphallus crenatus* was found only in the Julianehaab area. The prevalence of *Steganoderma formosum* and *Stenakron vetustum* decreased from Newfoundland to Davis Strait and among the remaining sample localities, was observed only in Umanak. *Anisakis simplex* (larvae found in fillets and body cavity) generally has a high prevalence, especially in Julianehaab, Godthaabsfjord, and Denmark Strait. *Ascarophis* sp. was frequent at Julianehaab and in Godthaabsfjord, but was sparse in the remaining localities. The occurrence of *Contracaecum* sp. was widespread, with highest prevalence at Newfoundland and lowest in Godthaabsfjord.

To determine whether the data on prevalence of selected parasite species could be used to correctly assign Greenland halibut to the localities where they were caught, nonparametric discriminant analyses (SAS, 1988) were carried out. The results of an analysis where all six sampled localities are included as categories are shown in Table 3. The overall rate of misclassificaiton is 0.51, i.e. only half of the specimens are classified in accordance to their origin. Newfoundland, Julianehaab and Denmark Strait showed high levels of correct classification, with misclassification rates of 0.18, 0.28, and 0.28, respectively. Fish from Newfoundland are well separated from all localities apart from Denmark Strait, where 14% of the fish from Newfoundland were assigned. Davis Strait fish were totally misclassified, mainly to Newfoundland and Umanak with classification rates of 40% and 41%, respectively. Most fish from Denmark Strait are correctly classified (72%), but some are classified to Umanak and Newfoundland (16% and 12%, respectively). Of the West Greenland inshore samples, some specimens from Umanak were assigned to Newfoundland and Denmark Strait (37% and 15%, respectively), but to a lesser extent also to Godthaabsfjord and Julianehaab. Most Greenland halibut from Godthaabsfjord are assigned to either Julianehaab, Umanak or Denmark Strait (40%, 20%, and 11%, respectively). Fish from Julianehaab are in most cases correctly assigned (73%), but some are misclassified mainly to Godthaabsfjord (11%) and Denmark Strait (9%).

In order to simplify relationships between areas and to minimize the total rate of misclassification as much as possible, the number of categories was reduced to three in a subsequent analysis, each comprised of localities which most closely associated in the former analysis. Newfoundland, Davis Strait, and Umanak were considered one area, Godthaabsfjord and Julianehaab were considered another area, and Denmark Strait was kept separate as the third area (Table 4). The overall rate of misclassification was lowered to 0.23. The western area, Newfoundland/Davis Strait/Umanak, is most correctly

Table 4. Results of a nonparametric discriminant analysis with areas consisting of joined localities as categories.

From area	Number of observations (and percent) classified into area Newfoundland/ Davis Strait/ Umanak	Godthaabsfjord/ Julianehaab	Denmark Strait	Total
Newfoundland/Davis Strait/Umanak	252 (82.1)	8 (2.6)	47 (15.3)	307 (100.0)
Godthaabsfjord/Julianehaab	25 (12.4)	157 (77.7)	20 (9.9)	202 (100.0)
Denmark Strait	28 (28.3)	0 (0.00)	71 (71.7)	99 (100.0)
Total	305 (50.2)	165 (27.1)	138 (22.7)	608 (100.0)
Prior probability for classification	0.33	0.33	0.33	
	Error count estimates for area			
Rate	0.18	0.22	0.28	0.23

classified (82%), with some misclassification mainly to Denmark Strait (15%). Specimens from the area including south-west Greenland fjord samples from Godthaabsfjord and Julianehaab are also mostly well assigned (78%), with equal misclassification to both other areas. Of specimens from Denmark Strait, 72% are correctly assigned and the remaining 28% are assigned to the area Newfoundland/Davis Strait/Umanak.

In summary, fish from the south-west Greenland fjords, Godthaabsfjord and Julianehaab harboured a unique combination of parasite species, characterised by high prevalence of *Anisakis simplex* and *Ascarophis* sp. (Table 2). Greenland halibut from Denmark Strait are characterised by the absence of most of the selected parasite species, while all localities in the western area, Newfoundland/Davis Strait/Umanak was identified by high prevalence of *Brachyphallus crenatus*, *Steganoderma formosum*, and *Contracaecum* sp.

Discussion

All parasite species found are new records for Greenland halibut in the Greenland area, except for *Derogenes varicus*, *Steringophorus furciger*, and *Entobdella hippoglossi*, which have been found previously by Brinkmann (1975).

The observed differences in infestations may reflect the variability in the underlying ecosystem within the area studied, i.e. the distribution limits of parasites and their other hosts, as well as different feeding habits of Greenland halibut.

A. simplex is considered to be the most suitable species to use as a biological ''tag'' to provide information on fish stock discreteness because of its longevity in the intermediate hosts (Smith, 1983). The pronounced variation in infestation rate of *Anisakis simplex* between areas (Table 2) is assumed to be partly related to variation in Greenland halibut prey items. Pedersen and Riget (1993) found that Greenland halibut feeding reflects the abundance of surrounding fish and pelagic crustacean fauna, i.e. Greenland halibut probably feed on what is available within these prey-groups. This suggestion is in accordance with previous studies on feeding habits of Greenland halibut and the distribution of prey items. The main prey items in Davis Strait are northern shrimp (*Pandalus borealis*), redfish (*Sebastes* sp.), roundnose grenadier (*Coryphaenoides rupestris*) and Greenland halibut (Jørgensen, 1995; Pedersen and Riget, 1993). The main fish prey off Newfoundland and in the south-west Greenland fjords is capelin (*Mallotus villosus*) (Smidt, 1969; Chumakov and Podrazhanskaya, 1986; Bowering and Lilly, 1992). Capelin have not been found as a prey item of Greenland halibut in the Umanak area (Smidt, 1969), which is believed to be the northernmost limit of this species (Vilhjálmsson, 1994).

All major fish prey of Greenland halibut have been recorded as intermediate or paratenic hosts for *A. simplex* or *Anisakis* sp. (Margolis and Arthur, 1979; Køie, 1993). Northern shrimp have also been reported as being infected with larval *A. simplex*, although not in the present area, and with insignificant prevalence rates (Smith, 1983). *A. simplex* has been recorded from all the cetaceans most common in the area (Davey, 1971; Gibson and Harris, 1979). Information on distribution patterns of cetaceans is sparse. However, the most common whale, the minke whale (*Balaenoptera acutorostrata*), is primarily found close to shore (Larsen, 1995) and may therefore be a source of the high infestation rate in the south-west Greenland fjords. The absence of capelin as a prey item in Umanak may partly explain the low prevalence of *A. simplex* in that area.

Nevertheless, the variation in infestation rate of *A. simplex* remains enigmatic. Arthur and Albert (1993) in their study of Greenland halibut stock discreteness in the Canadian north-west Atlantic also found high infestation rates of *A. simplex* in inshore waters and related this to high densities of whales in the area.

The occurrence of the digenean, *Brachyphallus crenatus*, in fish (final host) is closely related to the distribution of its molluscan host, the opisthobranch snail *Retusa obtusa* (Montagu) (Køie, 1992). *R. obtusa* has an arctic-boreal distribution and occurs around Nova Scotia in Canada, in the southernmost part of Greenland and Iceland, and in the north-west Atlantic (Thompson, 1988). This coincides well with the distribution of *B. crenatus* in the present study, where the digenean was only found in Julianehaab. The life span of digeneans is usually relatively short in the fish host, so the occurrence of *B. crenatus* in Greenland halibut in the southernmost fjords of Greenland cannot be taken conclusive that fish in these fjords are resident.

The life-cycles and distribution of the digeneans *Steganoderma formosum* and *Stenakron vetustum* are poorly known. They have been previously recorded from several fish species in Canadian Pacific and Atlantic waters (Margolis and Arthur, 1979). They are commonly found in fish from the Scotian shelf (Scott and Bray, 1989). There are no previous records of these species from Greenland halibut along the continental slope and shelf from north-eastern Newfoundland to Baffin Island (Zubchenko, 1980). This is in accordance with present data where a distinct decline in prevalence of the two species was observed from Newfoundland to Greenland (Table 2).

It is suggested that Greenland halibut stock components in the south-west Greenland fjords are isolated, based on infestations of *Anisakis simplex* and *Ascarophis* sp. in particular and the lack of *Steganoderma formosum* and *Stenakron vetustum* (Table 2), and based on the results of the discriminant analyses (Tables 3 and 4). The isolation of populations in West Greenland fjords has previously been shown by comprehensive tagging experiments (Smidt, 1969; Riget and Boje, 1989; Boje, 1993), where tagging–recapture data indicate little mixing among the fjord populations. Meristic studies based on numbers of vertebrae (Riget *et al*., 1992) support the residency hypothesis of the various fjord stock components with a significant difference both among themselves and fish from the offshore areas. Studies on sexual maturity (Riget and Boje, 1989; Jørgensen and Boje, 1994; Nielsen and Boje, 1995) suggest that Greenland halibut in the West Greenland fjords do not develop their gonads to a ripe stage but usually reabsorb their products, probably due to low bottom temperatures (Nielsen and Boje, 1995). This implies that the fjord stock components do not perform spawning migrations to the offshore stock complex in Davis Strait but remain resident and mainly recruited by juveniles from the Davis Strait spawning complex.

In spite of the fact that the discriminant analysis of parasite prevalence (Tables 3 and 4) showed considerable differences between Greenland halibut in Denmark Strait and the south-west Greenland fjords, connections between the two components cannot be excluded. The dilution effect of any numbers of migrating Greenland halibut from the south-west Greenland fjords mixing with the Icelandic spawning stock is not assumed to be detectable to any measurable degree because the Icelandic stock size is expected to be considerably larger than inshore components at south-west Greenland (Anon., 1995, 1996). Occasional migrations from the south-west Greenland fjords to Denmark Strait (Smidt, 1969; Riget and Boje, 1989; Boje, 1993) suggest that Greenland halibut in the south-west Greenland fjords are recruited to some extent from the spawning stock west of Iceland, and that some prespawners in south-west Greenland do return to these spawning grounds.

Although the present analyses reveal marked similarities between Umanak and Davis Strait/Newfoundland (Tables 3 and 4), the adult component in Umanak is considered to be resident, as determined from tagging experiments (Boje, 1993) and meristic studies (Riget *et al*., 1992). However, the lack of recaptures in Davis Strait from tagging in West Greenland fjords have not been considered to be conclusive enough to reject possible migrations between inshore and offshore areas, due to low fishing effort in Davis Strait (Anon., 1995). Although there have been no recorded migrations from the fjords of Umanak to Baffin Bay (Boje, 1993), the fjord stock component in Umanak is believed to be recruited by juveniles from the stock complex in the Davis Strait (Riget and Boje, 1989).

A strong connection between the Greenland halibut components off Newfoundland and in the Davis Strait as outlined in the present study (Table 3) has previously been demonstrated by means of tagging studies off Newfoundland (Bowering, 1984), where migrations in a northerly and easterly direction towards deeper waters were reported. Investigations of biological characteristics such as age, growth, and sexual maturity (Bowering, 1983), showed that size of onset of maturity of female Greenland halibut increased progressively northward, suggesting that mature fish migrate toward spawning grounds as growth rates were found to be similar over the entire area. Studies on meristics, genetic differentiation and previous studies using parasites as natural tags in Atlantic Canada and the Davis Strait (Templeman, 1970; Fairbairn, 1981; Misra and Bowering, 1984) revealed no significant differences throughout the range apart from fish in Gulf of St Lawrence. Khan *et al*. (1982) and Arthur and Albert (1993), however, found that Greenland halibut at

Hamilton Bank, off Labrador, and off Newfoundland north of Grand Bank, differed notably in their parasite infestations, and suggested that these stock components mainly remained resident or represented a cline between areas.

Conclusion

In summary, our results generally support previously published data on the stock delineation of Greenland halibut in the western Atlantic and provide additional evidence on the stock structure especially in the West Greenland fjords and East Greenland. Based on our analyses we have reached the following conclusions:

(1) The adult stock components of Greenland halibut in the south-west Greenland fjords appeared isolated from offshore components in the western Atlantic, as well as from inshore components in north-west Greenland fjords. They are, however, believed to have their spawning origin from the Icelandic spawning stock.

(2) Greenland halibut stock components off Newfoundland and in the Davis Strait seem to have common origin from a spawning stock complex in the Davis Strait and hence mix while performing spawning migrations to this area.

(3) The component sampled in Denmark Strait appeared isolated from other components in the Western Atlantic and is believed to belong to the Icelandic spawning stock.

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