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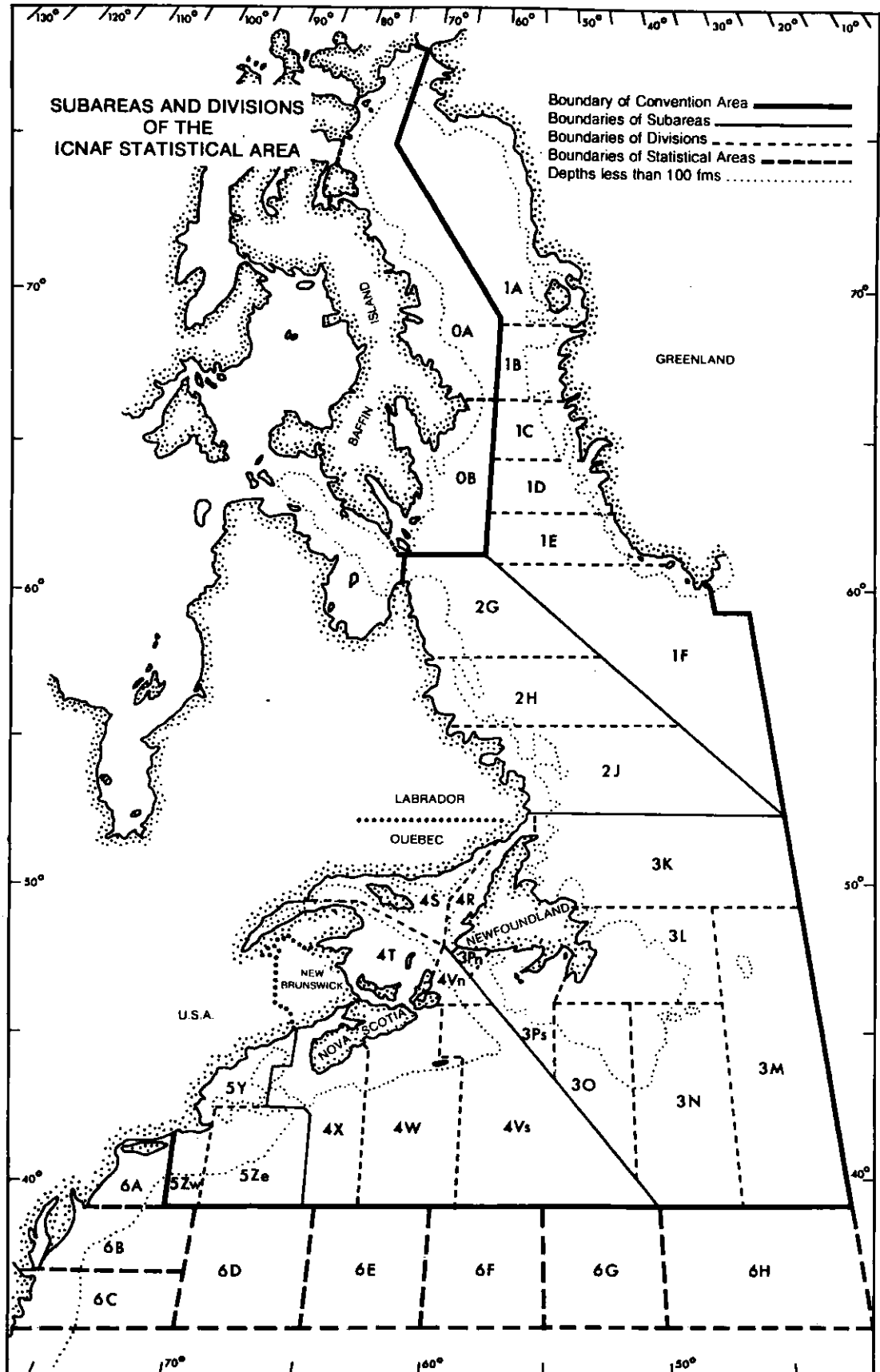

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Foreword

This issue of Selected Papers is the sixth in this series published annually or more frequently, depending on the number of contributions. During the period from 1958 to 1973, selected papers from ICNAF Meetings were published in the Redbook series.

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SUBAREAS AND DIVISIONS
OF THE
ICNAF STATISTICAL AREA

Boundary of Convention Area
Boundaries of Subareas
Boundaries of Divisions
Boundaries of Statistical Areas
Depths less than 100 fms

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Reproduction in the Squid, *Illex Illecebrosus*: First Observations in Captivity and Implications for the Life Cycle[1]

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Abstract

Precocious maturation of male and female *Illex illecebrosus*, induced in the laboratory in about 50 days, was followed by mating and spawning and yielded jelly-like egg masses up to 1 m in diameter containing 100,000 eggs. Fully mature males contained several hundred spermatophores, generally more than were implanted in the mantle of a female. The jelly released by the nidamental glands appears to trigger sperm release from implanted spermatophores. More than one egg mass was produced by single females and eggs remained in the ovary when the females died after spawning. The egg masses were neutrally buoyant and tended to drift with the weak current present in the pool. Larvae hatched in 6–7 days after spawning at about 13° C with mantle length of 1.1 mm. Eight days after hatching (maximum survival time), they had a mantle length of 1.25 mm and were similar to, but younger than, specimens found in plankton collections in late winter.

All stages in the life cycle of *I. illecebrosus* have now been characterized, and the available information is consistent with the hypothesis of a 1-year life cycle with spawning possibly occurring in February. Major gaps in knowledge at present are the spawning time and location. Identification of egg masses and larvae may be useful in determining the time of spawning but the capture of mated females may be the best indicator of spawning sites.

Introduction

Vast numbers of a single year-class of the short-finned squid, *Illex illecebrosus*, appear on the Scotian Shelf and the Grand Banks in May and remain until November when they disappear from coastal waters. Life cycles ranging from 1 to 2 years have been postulated (Squires, 1967; Mesnil, 1977), based principally on the progress of growth and maturity during this period (Mercer, MS 1973; Lu, MS 1973; Amaratunga *et al.*, MS 1978). The only records of fully mature females are in late spring and early summer, but these animals are so rare that they seem more likely to be oddities than the principal breeding stock for such a large population, particularly since rhynchoteuthion larvae, tentatively identified as *I. illecebrosus*, have recently been taken as early as February (Roper and Lu, 1979; Vecchione, 1979). In view of the recent rapid development of the fishery for *I. illecebrosus* in the Newfoundland and Nova Scotia areas, a clearer understanding of the source of the stocks being fished and of the life cycle is needed.

This paper summarizes observations on fertilization, spawning and larval development which followed precocious maturation in a captive population of *I. illecebrosus*, emphasizing those with the greatest potential influence on the natural life cycle.

Materials and Methods

Approximately 300 live *I. illecebrosus* (average mantle length 19.3 cm) were collected from inshore waters (Herring Cove, Nova Scotia) on 18 July 1978 and maintained in captivity on a 15-hour light and 9-hour dark cycle for up to 100 days in the 15-m diameter Aquatron pool at Dalhousie University, Halifax, Nova Scotia. Details of the experimental conditions and the growth of these animals are described by O'Dor *et al* (1980). Additional squid were added on 18 September and 20 October. These could be distinguished from the initial group by their immaturity and skin condition.

The maturity condition of males and females, removed periodically from the pool, was monitored and classified as described by Amaratunga and Durward (1979). The sex ratio of the groups held in the pool was approximately 50:50. A fully mature female with spermatophores attached inside the mantle was removed from the pool after producing an egg mass on 13 September (day 56). Two more egg masses were found on 26 September (day 69), and by 9 October (day 82) three more egg masses had been produced and three more mated females had been found.

Fragments of the egg masses, containing 500 to 2,000 eggs, were removed from the pool for observation and photography. Each fragment was maintained in a 5-liter aquarium and supplied with running sea water at temperature of about 13° C. Randomly selected eggs from each aquarium were examined daily under a dissecting microscope and staged on the basis of Hamabe's (1962) scale of embryological development for *Todarodes pacificus*. Newly hatched larvae were placed in a 500 ml container which was also supplied with running sea water, and larval development was monitored daily.

The early stages of embryological development were observed in artifically fertilized ova. Spermatophores and ova from a mated female were mixed in a beaker of sea water, and the addition of a small amount of jelly from an egg mass resulted in the release of 'clouds' of sperm (as the spermatophores ruptured) and the fertilization of the ova. Ova from an unmated, mature female were fertilized using spermatophores from a mature male by the same technique. Neither set of eggs survived beyond 3 days due to protozoan contamination.

Results

Maturation

Precocious maturation of captive females occurred in about 50 days, as previously described by Durward *et al.* (1979). There was also an acceleration of male maturation. In the field, males begin to show signs of maturation before females, but the maturity condition in the captive males was advanced beyond that observed in the field. The maturation of males which were put in the pool in July advanced from stage 1 to stage 3 [spermatophores present in Needham's sac, as defined by Amaratunga and Durward (1979)] in less than 30 days. By late August (30 days), the captive males weighing 250-280 g contained 100-300 spermatophores, equivalent to the number observed in specimens of similar weight taken offshore during October–November. Similar-sized captive males after spawning (56-82 days following entry to the pool) had 200-700 spermatophores remaining in Needham's sac,

and larger males had even more spermatophores. Since some of these males had mated and used some spermatophores, the higher counts are probably more representative of the total number of spermatophores produced by an individual male.

Mating

The female specimen shown in Fig. 1 contained approximately 1,300 spermatophores, and other mated females examined contained 300–500 spermatophores. Groups of 100-200 were attached in the mantle cavity primarily near or on the oviducal gland. In two cases, however, a spermatophore "bundle" was found on the outside of the mantle. The oral ends of the spermatophores in the bundle are cemented to the tissue, and these attached spermatophores are shorter in length than those found in Needham's sac in males. The retention of sperm in attached spermatophores may provide for some delay between mating and fertilization. Our observation agrees with the report of Hamabe *et al.* (1974) that the use of a buccal pouch for sperm storage, common in squids (Arnold and Williams-Arnold, 1977), does not occur in *I. illecebrosus*.

Spawning and characteristics of the egg mass

The egg masses were of nearly neutrally buoyant jelly, roughly spherical and ranged in size from about 40 to 100 cm in diameter. Although, in most instances, it was uncertain which female had spawned a given egg mass, a mated female was usually found dead a few days after an egg mass appeared. Since only four mated females were found after the six egg masses were produced, it is clear that repeated spawning can occur. *I. illecebrosus* does not appear to be a total spawner, as ova were still present in the oviducts and ovaries of the dead animals. The nidamental and oviducal glands in the spent females were smaller than those in mature (stage 5) females, but morphological distinction from maturing (stage 4) females was difficult.

The largest egg mass (Fig. 2) contained about 100,000 ova spaced about 1-2 cm apart in an apparently uniform mass of jelly. There was no evidence of multiple layers of jelly as seen in the egg mass of *T. pacificus* (Hamabe, 1962), and the tenuous jelly masses broke up easily when handled. The largest egg mass was slightly denser than sea water but drifted with the slight current along the bottom of the pool. Some of the smaller egg masses were neutrally buoyant and remained suspended in mid-water.

Larvae

The fertilized ova are ellipsoid in shape, being approximately 1.0 x 0.8 mm. During embryological development, the egg becomes spherical. The
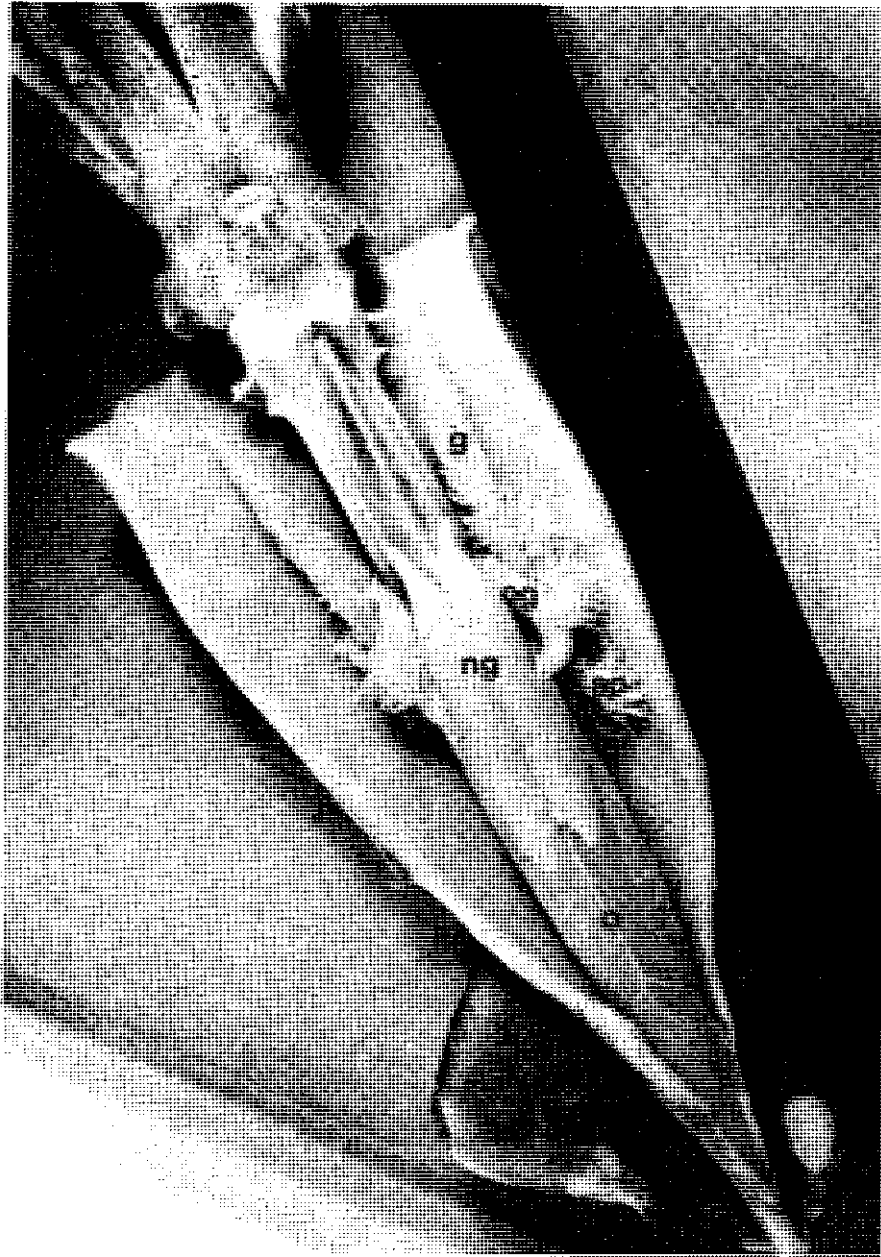
Fig. 1. Mated female *I. illecebrosus*, mantle length 23.0 cm. All organs have shrunk significantly due to fixation. (g = gill; ng = nidamental gland; og = oviducal gland; o = ovary; sp = spermatophore bundle.)

chorionic membrane swells as the embryo develops and the perivitelline space enlarges so that the maximum diameter of the egg is about 1.8 mm just before hatching. The general features of embryological development of *I. illecebrosus* resemble those described by Naef (1923) and Boletzky *et al.* (1973) for *I. coindetii* and by Hamabe (1962) for *T. pacificus.*

Hatching occurred 6–8 days after spawning at about 13° C. This developmental rate for *I. illecebrosus* is similar to that described for some other species: 6–7

days at 20° to 22°C for *I. coindetii* (Boletzky *et al.*, 1973), 10 days at 21° to 23°C for *Loligo pealei* (McMahon and Summers, 1971), and 4–5 days at 15° to 20°C for *T. pacificus* (Hamabe, 1962). Survivorship to hatching in our study was low because of protozoan contamination. From several thousand eggs maintained in the 5-litre tanks, only 13 larvae were hatched, but all of these survived for at least 1 week.

Immediately after hatching a larva had a mantle length of 1.1 mm and a small internal yolk sac. The appearance after 7 days of development (the longest

Fig. 2.   Egg mass of of *I. illecebrosus*, approximately 120 × 70 cm in size. See text for further details.

Fig. 3.   *I. illecebrosus* larva, 7 days after hatching, with mantle length 1.25 mm.

survivor) is shown in Fig. 3. At this stage, the larva has a mantle length of 1.25 mm, two pairs of dorsal arms and and a developing proboscis, which was not evident until 2-3 days after hatching.

The chromatophore pattern of the dorsal and ventral surfaces of a 5-day old larva is shown in Fig. 4.
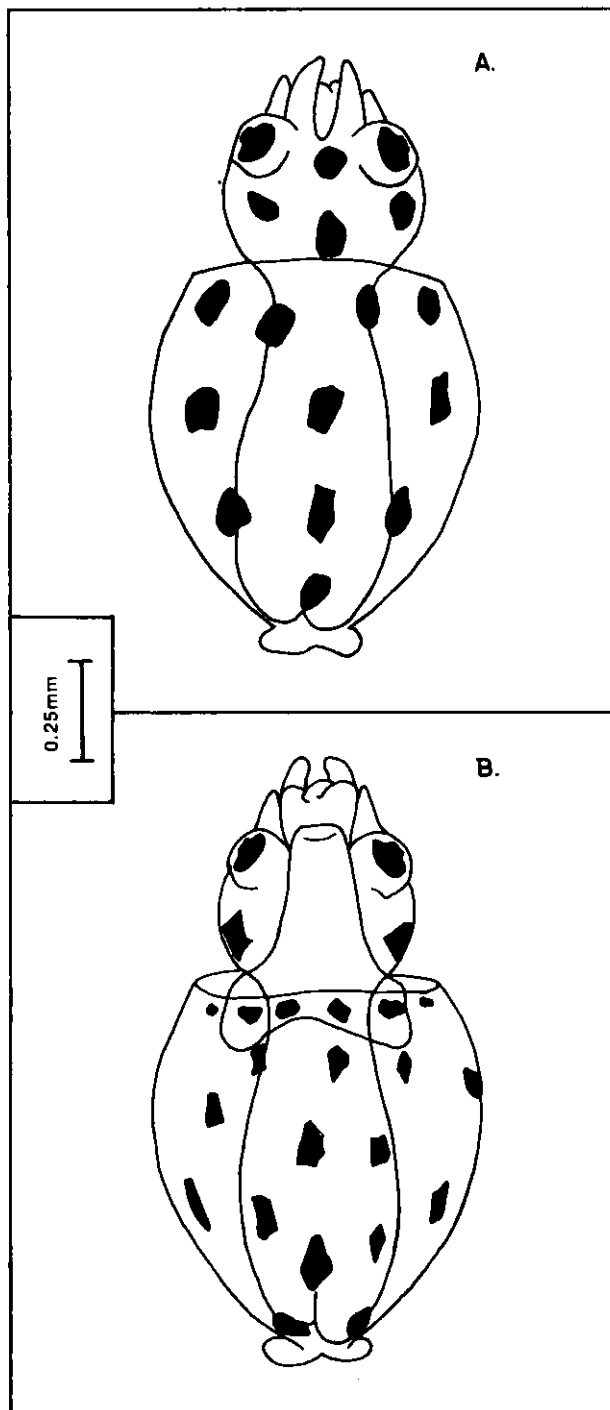

Fig. 4.   Chromatophore pattern of dorsal (A) and ventral (B) surfaces of 5-day-old. *I. illecebrosus* larva.

Living larvae are essentially transparent, but the chromatophores appear black under transmitted light and brownish-red under incident light. Larvae fixed in 10% neutralized formalin for about 2 days and then transferred to 40% 2-propanol in sea water appear opaque and the chromatophores lose some pigment, but the basic pattern is still evident if carefully examined.

Newly-hatched larvae were unable to swim free off the bottom of the aquarium but moved randomly along the bottom. After 4-5 days, the larvae were seen swimming freely in an erratic circular motion. No consistent pattern of phototropism was discerned but intense light (and contact or vibration) induced withdrawal of the head into the mantle cavity, indicating an avoidance reaction to strong light.

During observations on live larvae under a compound microscope, one larva appeared to be feeding on protozoa. Particulate matter and several ciliated protozoans in the water were swept between the dorsal arms and past the mouth in a current which may have been caused by continuous radular movements. On two occasions, protozoans were observed to disappear near the mouth and were probably eaten. Since the early larvae lack a large yolk sac and the means for capturing larger prey, this type of feeding would be valuable, particularly if the larvae remain in or near the egg mass where protozoans living on non-viable eggs are present in high concentrations. In view of the limited swimming ability of newly-hatched larvae and the size and nature of the egg mass, the larvae might remain in the egg mass for some time.

Discussion

The timing and location of spawning are important factors in understanding the population dynamics of *I. illecebrosus*. While it is now possible to describe the morphology and development of the species throughout its life history, the events during the larval and spawning phases of the life cycle still cannot be placed geographically or seasonally. There are two approaches to determining the site and time of spawning, one which traces the events leading to spawning by adults and the second which involves collecting information on the distribution·of larvae. Since studies to date have provided only fragmentary information on these life history phases in nature, future surveys will need to extend the period and area of study. Specimens collected in such surveys can probably be best interpreted in relation to the continuous record available from the laboratory population.

The single aspect of reproduction most critical to the overall life cycle is the timing of spawning, the last

link in a chain of events initiated with the onset of maturation. Current practice is somewhat misleading since it classes males as mature as soon as they begin to produce spermatophores, as early as September in nature (Amaratunga and Durward, 1979). Actually full maturity or spawning readiness probably does not occur until much later. The results from the laboratory studies suggest that male maturation parallels female and that a male can accumulate several hundred spermatophores which are held in reserve until mating is triggered by the presence of mature females. The advanced stages of maturation in males need to be better defined than they are at present, and, although spermatophore counts may be useful for this purpose, further studies are needed. Spawning, in turn, appears to be induced by the mating process or the implantation of spermatophores since females held to maturity in earlier experiments in the absence of males never spawned. The jelly produced during spawning probably causes the release of sperm from the spermatophores upon contact. Some of the spermatophores must become detached from the female, as empty spermatophore cases were common in egg masses. It is possible that fertilization of the ova actually occurs in the egg masses after spawning. The observed pattern of mating and egg mass formation is consistent with the fragmentary data for other species of *Illex*, as reported by Mangold-Wirz (1963) and Boletzky *et al.* (1973) for *I. coindetii*, and by C. Roper (personal communication) for *I. oxygonius.*

Although the rate of maturation of *I. illecebrosus* in captivity was accelerated by conditions (probably photoperiod) in the pool, the pattern observed seems to be consistent with the natural one. In the wild, both sexes could reach spawning readiness by January–February, as predicted by Squires (1967), and this period seems to be the logical time to look for spawning squid. The processes of mating and spawning are probably closely linked, and, although mass matings followed by immediate spawning, as seen in other squids (e.g. *L. opalescens*, Fields, 1965 and *T. pacificus*, Kawahara, 1979), may occur in nature, there was no evidence for them in the laboratory. Even if mass mating and spawning do not occur, the appearance of large homogeneous populations of *I. illecebrosus* on the coastal shelves in May and June still suggests that spawning occurs over a rather limited period possibly related to a photoperiodic cue. The capture of mated females is probably the best indicator of spawning time and site, since mating, spawning and death appear to span only a few days. However, for the same reason such specimens may be difficult to collect.

The characteristics of the larvae bred in captivity are consistent with Rhynchoteuthion type 'C' larvae

collected from the natural population and tentatively identified as *I. illecebrosus* (O'Dor and Durward, 1979; Roper and Lu, 1979; Vecchione, 1979), but further data are required to distinguish *I. illecebrosus* and *I. oxygonius.* Given the southern distribution of *I. oxygonius,* identification of *Illex* larvae, egg masses or even fragments of masses, such as might remain in trawls, should be possible in Canadian waters. However, even extensive larval surveys are unlikely to give any precise localization of spawning if the egg masses drift with the currents, and there may be no specific spawning sites if mass mating does not occur.

Larval surveys could, however, provide information about the time of spawning. If spawning occurs in January–February, growth to a body weight of 50 g is possible by the time that juveniles of this size appear in the fishing areas on the coastal shelves in May–June. Hatching should occur in less than 2 weeks if water temperatures at the time of spawning are greater than 6°C and LaRoe's (1971) data on *Sepioteuthis sepiodiea* indicate that growth from hatching to a size of 50 g is possible in about 3 months at temperatures ranging from 18° to 30°C. The growth rate of adult *I. illecebrosus* at 10° to 15°C is comparable to that of adult *S. sepiodiea* at the higher temperatures and larval *I. illecebrosus* are adapted to colder waters (viz. the rapid embryonic development) so such growth rates are plausible. However, since *I. illecebrosus* growth rates are temperature dependent (O'Dor et al., 1980), any attempts to relate larval size directly to time of spawning will require information on the temperatures to which they have been exposed and on larval growth rates at various temperatures.

Another feature of the species reproductive biology important to its population dynamics is fecundity. The present results suggest that previous values based simply on the number of eggs present in a mature female (Durward *et al*, 1979) are gross overestimates, since spawning was incomplete and the hatch rate of eggs was low. The complexity of the social interactions and mating behaviours which are not yet clearly understood also argue for care in insuring that adequate breeding stocks remain at the end of the season.

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Feeding and Growth in Captive Squid, *Illex Illecebrosus*, and the Influence of Food Availability on Growth in the Natural Population[1]

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Abstract

Feeding and growth rates of tagged individuals and of a captive school of squid, *Illex illecebrosus*, were monitored over a 2-month period on a live fish diet. The daily feeding rate for maintenance is estimated at about 1% of body weight. Average daily feeding rates ranged from 3.6 to 6.7% and average daily growth rates from 1.0 to 1.9% of body weight, both increasing with temperature. Food conversion rates (wet food weight to wet squid weight) ranged from 25 to 36% and conversion efficiency, after allowing for maintenance, ranged from 35 to 51%. These feeding and growth rates are higher than those reported for *Octopus vulgaris* at comparable temperatures. The maintenance requirement was slightly higher for *I. illecebrosus* but the conversion efficiency was much lower.

Growth rates of *I. illecebrosus* from field data are well below those for captive animals, indicating that the food supply of the natural population becomes increasingly limiting as the season progresses. Estimates of food consumption by the natural population are higher before July than in the remaining months of the year, and most of the squid biomass results from early season feeding when crustaceans are the principal prey. Cannibalism may be a major food source for the breeding stock late in the season and during migration from coastal waters.

Introduction

Direct studies on feeding and growth rates and conversion efficiency in large squid of commercial interest have been difficult because of problems of maintaining them in captivity. However, there is some information on juvenile *Loligo opalescens* (Hurley, 1976) and considerable data on small decapods (Choe, 1966; LaRoe, 1971; Boletzky, 1974) and octopods (Nixon, 1966; Wells and Wells, 1970; Mangold and Boletzky, 1973; Joll, 1977). In general, at a constant temperature and unlimited food supply, the weight increase in cephalopods is proportional to their weight, i.e. dw/dt = aw, with the weight doubling in as little as 10 to 20 days (Wells and Wells, 1970; LaRoe, 1971). This pattern seems to hold until sexual maturation which usually leads to decreased feeding, a negative growth rate, and death after a short period of reproductive activity (Van Heukelem, 1973; Wells, 1978). Higher temperatures usually result in increased feeding and growth, although there are some exceptions (Boletzky, 1974).

Growth rates in exploited populations of squid based on sampling are generally lower (Summers, 1971; Ishii, 1977) than those from laboratory studies, and the pattern for *I. illecebrosus* is typical. Squire's (1967) data for *I. illecebrosus* fit well on a von Bertalanffy-type curve which indicate a decline in growth rate well before the squid reach sexual maturity. The experiments described in this paper represent a first attempt at studying growth and feeding rates in a captive school of *I. illecebrosus* under conditions which allow comparison with other studied cephalopods. The results are also compared with available information on feeding and growth in the natural population.

Materials and Methods

On 18 July 1978, 300 squid from a trapnet set at Herring Cove near Halifax, Nova Scotia, were brought to the 15-m diameter pool in the Aquatron Laboratory at Dalhousie University by methods described

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previously (O'Dor et al., 1977; O'Dor, 1978). The mean mantle length (± one standard deviation) for 80 squid from the same trap was 19.3 ± 1.6 cm and the mean body weight was 142 ± 43 g. All of the squid were immature and 43% of this group were male. Feeding and growth studies were conducted until 7 September when both males and females began to reach advanced stages of maturation under the 15-hour light and 9-hour dark regime (O'Dor, 1978). Water temperature in the pool was uncontrolled, ranging from 7 to 17°C during the period. The principal food was live Fundulus sp. ranging from 6 to 11 cm in length and from 2.5 to 17.5 g in weight. This was sometimes supplemented with slices of frozen herring and occasionally with live fish of other species.

Studies on individual squid (Experiment I)

Weight changes in two groups of eleven squid were studied, Group A being fed regularly and Group B being starved. On 19 July, the individuals of each group were measured, weighed, and tagged with anchor tags through the dorsal anterior edge of the mantle (O'Dor et al., MS 1979). Colored tags were used so that the two groups were readily identifiable from the bridge over the pool. The tagging and measuring of the squid required that each animal be out of the water for 30-60 seconds. Weights were taken after the squid were held vertically to empty the mantle cavity. Initially, feeding during this experiment was controlled by threading a knotted line through the backs of the live fish used for food. The knots prevented the escape of fish and allowed the feeder to prevent feeding of Group B individuals without interfering with the feeding of Group A or other squid in the pool. Records were kept of the size of each fish taken by each Group A squid. After 10 days, Group B squid were reweighed and transferred to a 5.5-m diameter outdoor pool (average temperature 13.5°C) where they were starved for an additional 7 days and weighed again. This latter experiment is designated as IC. Squid in the indoor 15-m diameter pool were then fed on free-swimming live fish and records kept for Group A individuals until 1 August.

The weight of food consumed by the squid was calculated from the length of the fish taken, using a standard curve relating length to edible weight. The squid ate only the fleshy portion of the fish leaving the skeleton including head and tail intact. The edible portion was calculated from a length-weight relationship for whole fish and the recovered skeletons to be about 80%. This figure was used as a correction factor for other types of food fish.

Population studies (Experiments II to V)

By 1 August, it was apparent that the tagged squid of Group A were feeding less than the other squid. The total number of squid in the large pool dropped to 120 and was stabilizing (O'Dor et al., MS 1979). At this time, all of the remaining squid in the pool were captured with a seine, weighed and returned to the pool. This procedure was repeated four times giving the results indicated for experiments II to V in Table 1. By the time of the fourth weighing, the squid had learned to escape the seine, so that a few escapees during the last two weighings prevented measurement of the total population weight.

During all experiments except III, an abundant supply of food was provided by the daily addition of known weights of fish. The pool was vacuumed every second or third day and the recovered waste was weighed. For each experimental period, the weight of food consumed was estimated as the difference between the weight of fish added and the weight of the waste removed. The waste, principally skeletal material, amounted to about 20% of the weight of the fish added, thus indicating agreement with experiment I.

Calculation of growth and feeding rates

Since the data were for short time intervals and for animals in the same size range within each of the intervals, daily growth rates (DGR) of individual squid were calculated as described by Mangold and Boletzky (1973):

$$DGR\ (\%) = \frac{w_f - w_i}{(w_f + w_i)/2} \times \frac{100}{t}$$

where w_i is the initial body weight, w_f is the final body weight, and t is the time interval in days.

The daily feeding rates (DFR) for individuals was calculated as the percentage of food consumed relative to the mean body weight for each period:

$$DFR\ (\%) = \frac{F}{(w_f + w_i)/2} \times \frac{100}{t}$$

where F is the weight of food consumed by each individual.

Because of variation in the number of squid present during each of the population experiments due to the failure to weigh all squid in the pool, to the removal of specimens for study and to natural death, the mean daily feeding rate for each population experiment was calculated from the mean initial weight (w_i) and the mean final weight (w_f) of squid by the relationship

$$DFR\ (\%) = \frac{F}{(w_f + w_i)/2} \times \frac{100}{S}$$

where F is the total amount of food consumed by the population, and S is the number of squid-days (cumulative total of the number of squid present on each day). The use of mean weights should not bias the results significantly as the removals from the population including natural deaths were on the average representative of the live population.

Results

General observations on feeding

Squid in the pool generally remained in a relatively tight school, and those that left the school usually stopped feeding and died in a few days. Squid which behaved oddly (e.g. irregular swimming in tagged animals) were sometimes attacked and driven, at least temporarily, from the school. When live fish were added singly, the largest squid generally fed first, darting across the pool to capture the fish and then returning quickly to the school. Smaller squid approaching the fish often gave way to the larger squid, as failure to do so often resulted in the small squid being attacked and the fish taken away. Observations were difficult when many fish were put in the pool at the same time, but all animals appeared to feed and fighting occurred only when two squid aimed for the same fish.

The squid readily fed on a variety of small live fish, including capelin, *Mallotus villosus*, herring, *Clupea harengus*, mackerel, *Scomber scombrus*, smelt, *Osmerus mordax*, salmon smolts, *Salmo salar*, and *Fundulus* sp., and shrimp, *Crangon* sp., but rejected eels and crabs after capturing them. In one experiment, a small school of herring, ranging in length from 16 to 27 cm (weighing 60-375 g) was added to the pool. All of the herring less than 19 cm were captured, but those greater than 22 cm remained in the pool for the duration of the experiments and were never captured. It appears that there is an upper limit to the size of prey which the squid will attack (roughly equal to the mantle length) and that they are relatively unselective below this limit.

The largest single meal observed was 65 g of herring by a 260 g tagged squid (25% of the body weight) part of which was still present in the gut 24 hours later when the animal rejected its next meal. The next largest meal for this squid was 27 g (10% of body weight) which did not interfere with its subsequent feeding schedule. Similarly, a 118 g squid took 26 g of food (22% of body weight) and skipped its next feeding, but it later took 13% of body weight on 1 day and fed regularly the next. Thus, it appears that, although squid may take quite large meals, they are limited by their digestive capacity to a daily intake of

food equivalent to less than 20% of their body weight. Sustained feeding rates probably do not exceed 10-15% of body weight for animals in the size range studied at temperatures around 10°C.

Feeding and growth rates

Figure 1 shows the daily growth rates (DGR) plotted against daily feeding rates (DFR) for individual animals (Expt. 1A) and the four population experiments (II to V), together with the average daily weight losses for the unfed tagged animals in the pool (Expt. 1B) and in the outside tank (Expt. 1C). The solid line approximates the relationship between feeding rate and growth rate for an 'average' squid. The upper portion (A) is the linear regression for the data for experiments II, IV, V, and all individuals from 1A which did not lose weight. The dashed line (B) is the linear regression for the data for all individuals that did not gain weight from experiments 1A, 1B and III.
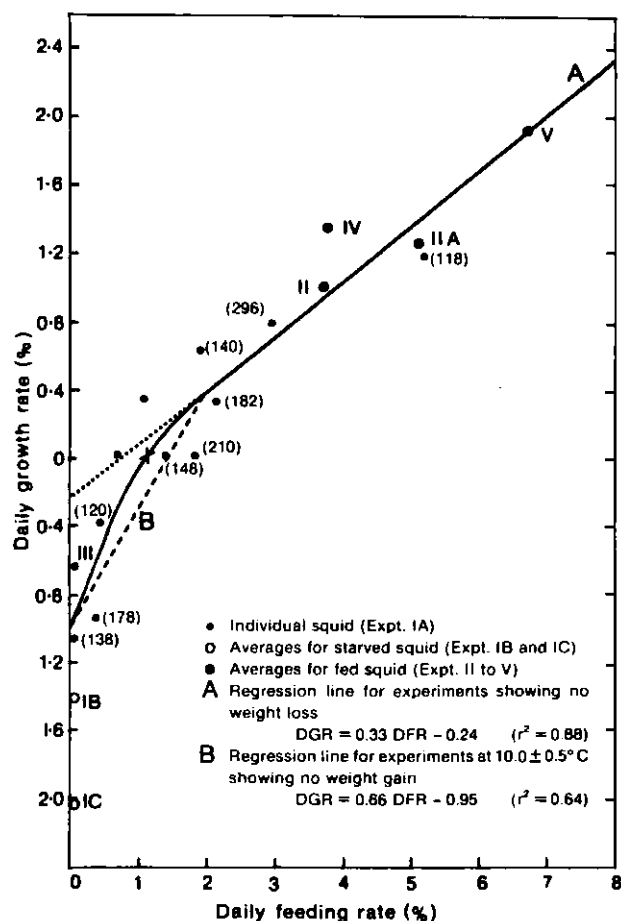

Fig. 1.   Relationship between daily growth rate and daily feeding rate of *Illex illecebrosus*, from laboratory experiments in July–September 1978. (Values in parantheses are initial weights (g) of individual squid from experiment IA. The solid line approximates the overall relation between DGR and DFR.)

A critical value in relating feeding rate and growth rate is the daily feeding rate for maintenance (DFRM), the amount of food required per unit body weight to maintain the animal at a constant weight. Since the feeding rate for the individuals which showed no weight change ranged from 0.7 to 1.8%, the DFRM appears to be quite variable. The daily consumption of food for maintenance is normally approximated by kw^j, where k is the maintenance food coefficient, w is the weight, and j has a value between 0.7 and 0.8 (Beverton and Holt, 1957). Over the weight range of animals in these experiments, weight-related changes were masked by individual variation. The mid-point (X) between the intersects of the two regression lines by a line at DGR = 0 was chosen as the best estimate of DFRM (1.1%) for the weight class of squid. The solid line connects regression line A to the estimated DFRM and continues to the intersect of regression line B at DFR = 0, where DGR = -0.95%, the rate of weight loss during starvation.

Although variation in data for individual squid is high, the solid line (Fig. 1) is probably a reasonable approximation of the relationship between the daily growth rate and the daily feeding rate for a population of squid. Regression line A, in particular, seems robust, because, even with temperature differences (e.g. Expt. V, Table 1) and the systematic errors (see below), variation about the line is small. The additional point (Expt. IIA) recorded in Fig. 1 is the result of a different analysis of the data for experiment II and gives some indication of the reliability of the calculations used for the population experiments. For experiment II, the total initial and final weights of the population and the weights of the dead animals removed were known. Deaths occurred in all experiments at a rate of about 3% per day, and their influence on the results depended on the behaviour of the dying squid. The observations indicated that dying squid did not feed and it is likely that they lost weight at a rate similar to

that of the groups of starved squid. The data for experiment II (Table 2) show that the average weight of the dead squid declined during the experiment, but, if these weights are extrapolated back to day one by assuming a weight loss of 0.95% per day (intercept of line B in Fig. 1), the mean weight on that day is 153.8 g, a value very close to the initial mean weight of 152 g for the whole population at the beginning of the experiment.

If the estimated initial weight of all dead squid is substracted from the initial total weight of the population, the daily growth rate and the daily feeding rate for individual animals are 1.27 and 5.03% respectively (point IIA, Fig. 1). This indicates that the method of calculation based on average weights (point II, Fig. 1) underestimates both the DGR and DFR by about 25%. The values for the other experiments are probably also underestimates, since the dead squid showed similar weight-loss patterns, but not all animals removed in these experiments were dead and the bias should be less. Since the DGR and DFR are both underestimated to a similar degree, these errors should not significantly alter the relationship shown in Fig. 1.

TABLE 2. Observations on number and weight of squid during experiment II in early August 1978.

Day	Live squid weight (g)	Dead squid weight (g)	Number of live squid	Mean weight (g) Live	Mean weight (g) Dead
1	18,237	—	120	152	—
2	...	—	120	...	—
3	...	464	117	...	155
4	...	—	117	...	—
5	...	—	117	...	—
6	...	1,342	108	...	149
7	...	1,618	97	...	147
8	15,229	666	92	166	133

TABLE 1. Summary of experimental conditions and results for laboratory studies on *Illex illecebrosus*, July–September 1978.

Expt.	Dates	Temperature Mean (range) (°C)	Daily Feeding rate (%)	Daily growth rate (%)	Food conversion rate (%)	Conversion efficiency (%)	Initial and final mean weights (g)
IA	19 Jul–1 Aug	8.4 (7.0–8.8)	... [a]	... [a]	—	—	—
IB	19–29 Jul	8.4 (7.0–8.8)	0	-1.4	—	—	—
IC	29 Jul–5 Aug	13.5	0	-2.0	—	—	—
II	1–7 Aug	9.7 (8.7–11.0)	3.6	1.0	29	42	152-166
IIA	1–7 Aug	9.7 (8.7–11.0)	5.0	1.3	25	33	152-166
III	8–10 Aug	9.6 (9.3–9.8)	0	-0.6	—	—	166-165
IV	11–24 Aug	10.3 (9.1–12.5)	3.8	1.4	36	51	165-201
V	25 Aug–7 Sep	15.5 (13.0–17.0)	6.7	1.9	29	35	201-264

[a] Data for individual squid are plotted in Fig. 1.

Discussion

Comparison with other cephalopods

The growth rate of an animal is determined by its feeding rate, its maintenance energy requirement, and its efficiency in food conversion. The maintenance energy requirement is the sum of a variety of physiological demands which are characteristic of an organism and which vary with the activities of the organism. The maintenance energy consumption per unit of body weight usually decreases with increasing weight (typically as a function of $w^{0.7}$) and increases with temperature (typically doubling or trebling with each 10°C rise in temperature). Conversion efficiencies (after deducting maintenance requirements) calculated from wet weight as used in Table 1 vary widely, depending primarily on the composition of the organism and the food. Even for the same food, the efficiency often declines at high feeding rates because digestive efficiency decreases (Beverton and Holt, 1957).

Although the data from the present study are few and are limited to a relatively short portion of the life cycle, they do form a consistent pattern and provide values of feeding and growth parameters for comparison with other cephalopods. For *Octopus vulgaris* (in the same weight range as the squid used in our experiments), average DFR, DGR and food conversion values were 1.6, 0.9 and 56% respectively at 10°C and 3.3, 1.7 and 55% at 15°C (Mangold and Boletzky, 1973). Comparison of these values with those for squid (Table 1) indicates that at a given temperature squid feeding ad *libitum* probably grow slightly faster than octopuses and have a lower food conversion rate. A lower conversion would be expected as a consequence of a higher DFRM for an active animal like squid, but this does not appear to be the only factor. The estimates of conversion efficiency, DGR/(DFR-DFRM) in Table 1, average about 40%, which is less than half of the 83% calculated by Joll (1977) for *Octopus tetricus*. The lower conversion efficiency for squid might be related to the fish diet, as there is some evidence that octopuses grow less efficiently on fish than on crustaceans (Mangold and Boletzky, 1973) which have a composition more similar to that of cephalopods. There is also evidence that the digestive process in *O. vulgaris* is considerably longer than that in *I. illecebrosus* (Boucher-Rodoni, 1975) and may therefore be more efficient.

Boucher-Rodoni (1975) has also shown that digestion rates increase with temperature. Since feeding rates are higher at higher temperatures (Table 1), the digestion rate may be the principal limitation on feeding. Since DGR and DFR increase with temperature, the increase in the digestion rate appears

to exceed the increase in the maintenance requirements. There is evidence for an increase in the maintenance requirement with temperature as indicated by the change in the DGR values for the starved squid (Expt. 1B and 1C).

Comparison with natural populations of squid

Since growth is often temperature-dependent, comparison of growth rates from laboratory studies with those from field studies must be treated with caution. However, the problem may not be a major one in the present studies on squid, because most of the laboratory data were obtained near the 10° to 12°C temperature range in which *I. illecebrosus* are commonly caught (Lu, MS 1973). A second consideration, less easily resolved, is the relative activity levels in captive and wild populations which would influence the DFRM. Squid in the pool swam continuously at speeds of 0.5–1.0 m/sec and exhibited predatory activities similar to those observed in wild populations. They were frequently startled by the observers into 'fast-swimming' which probably created an energy demand similar to that resulting from predators in the wild. These activities seem comparable to those reported from field observations (Bennet, 1978; Merdsoy, 1978). If temperatures and activity levels are comparable, the laboratory data suggest that squid in the wild feed considerably below their ad *libitum* rate in the latter half of the year (Fig. 2B).

Fig. 2A shows the seasonal weight changes for female *I. illecebrosus* in 1977, transformed from lengths given by Amaratunga et al. (MS 1978) using the von Bertalanffy relationship

$$L_t = 254.6 \left[1 - e^{-0.164(t+3.2)} \right]$$

Also shown are the mean weights for squid in the laboratory pool and the weights of the longest lived tagged animal at the indicated dates. The decline in growth rate of this tagged squid in August reflects precocious maturation, the animal being the first to spawn on 9 September. In the wild population, maturation in females is not pronounced until November. The range of temperature during experiments II and IV (Table 1) should be comparable to conditions in the wild, but the growth rates are considerably greater than those calculated for the 1977 population during the same period. The growth rate for experiment V was even higher, but the temperature was probably higher than that prevalent in the field. It seems likely that squid in the wild are not achieving their full growth potential during the last half of the year due possibly to food resource limitation. The dashed line in Fig. 2A indicates the projected growth of an average squid from the 1977 population if growth
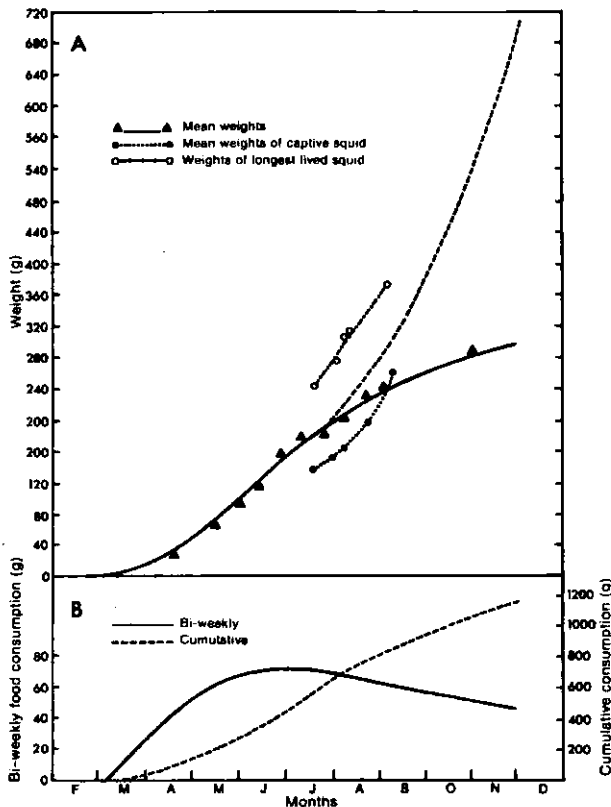
Fig. 2. A. Seasonal weight changes in captive and wild squid, *Illex illecebrosus*. (Data for the wild population are from Amaratunga *et al.*, MS 1978.)

B. Bi-weekly and cumulative food consumption for an average squid estimated from growth data for the wild population in 1977 using the feeding rate-growth rate relationship in Fig. 1.

had continued at the mid-June daily growth rate of 1.05%. Occasional squid weighing 700 g or more do occur in November in the wild population, so that the projection using a DGR of 1.05% is not unreasonable. The presence of both large and small squid late in the season is a predictable consequence of the hierarchic feeding observed in the laboratory.

From the seasonal growth curve in Fig. 2A, a daily growth rate was calculated for each 2-week period, and the corresponding daily feeding rate (DFR) was determined from the relationship in Fig. 1. The product of DFR and the mean weight of squid at the midpoint of the period gives an estimate of food consumption for the period. These estimates are represented by the solid line in Fig. 2B. Even if the entire growth curve were a certainty, the values for food consumption would likely be underestimated during early development, since the DFRM is probably considerably higher in small animals; however, the major food of small squid is crustaceans (Squires, 1957; Ennis and Collins, 1979) which may be digested

more efficiently, resulting in compensating errors. In any case, for the cumulative food consumption curve (Fig. 2B), any errors in the food consumption estimate for very small squid early in the season would have only marginal effects. It is interesting to note that, even with these underestimates nearly 50% of a squid's consumption of food before it leaves the fishing ground in November occurs before mid-June during a period when its predominant prey is planktonic crustaceans (Squires, 1957).

From mid-July onward (Fig. 2B), there is a gradual decline in both weight-specific and absolute food consumption, suggesting depletion of prey species at this time. Increased diversity in the diet also supports this conclusion (Ennis and Collins, 1979). Both the squid and some of their fish prey were fished heavily during this period in 1977. Heavy fishing of squid when food is limiting should result in increased growth of individuals remaining, unless the limiting factor in feeding is spatial distribution rather than abundance, and, since fecundity of squid appears to be proportional to body weight (Durward *et al.*, 1979), an increase in size should compensate to some extent, in terms of reproductive capacity, for decreasing numbers. The decline in the growth rate may indicate overfishing of prey species, and this could potentially affect the squid breeding stock.

From September onward, empty stomachs are common in sampled specimens, and squid becomes an increasingly important component (often the major component) of the diet of *I. illecebrosus* (Ennis and Collins, 1979), presumably due to the scarcity of prey. In one starvation experiment (IC), the smallest squid disappeared and was presumably eaten by a large female which actually gained weight despite the supposed absence of food. Other instances of cannibalism have been observed but only when food had not been provided for several days. The squid eaten were always small males, but it was difficult to identify the cannibals. These observations indicate that the presence of squid remains in squid stomachs is not always the accidental result of fighting for food (Bennet, 1979) or the result of predation of one school on another but is probably due to intra-school cannibalism when other food items are not available. If, as appears likely, a significant portion of the late-season growth of the larger squid, which will become the breeding stock for the next year-class, is based on consumption of other squid, there are several implications: (a) the value of late season squid in terms of the prey they have consumed is not simply their weight multiplied by the conversion rate but some power of this, since cannibalism is equivalent to the insertion of another trophic level; (b) late-season squid that do not themselves spawn may have an important

role as a food reserve for the breeding stock during migration, and, even though fecundity in females is high, a large stock size may still be required for the production of a successful year-class; and (c) the selective removal of smaller squid through cannibalism may affect the size composition of specimens sampled with a consequent effect on the apparent growth rate late in the season.

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Fecundity of Silver Hake on the Scotian Shelf[1]

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Abstract

The fecundity of silver hake, Merluccius bilinearis, on the Scotian Shelf was investigated from 105 specimens collected in July–August 1977. It was found that fecundity increased at a rate proportional to approximately the cube of the total length. With body weight also proportional to the cube of the length, the relationships between fecundity and ovary weight were found to be best described by linear functions. The correlation coefficients for the three relationships ranged from 0.81 to 0.89.

Introduction

The silver hake, Merluccius bilinearis, is among the most important species of the bottom fauna on the Scotian Shelf (ICNAF Div. 4VWX). The population has been continuously studied since 1962 when the trawl fishery for silver hake began. Much research effort has been devoted to studies on the distribution of eggs, larvae and adults and on the spawning season and the fishery (Dannevig, 1919; Kuntz and Radcliffe, 1915; Bigelow and Schroeder, 1953; Serebryakov, 1962; Domanevsky and Nozdrin, 1963; Sauskan, 1966; Sarnits and Sauskan, 1967), but only Sauskan and Serebryankov (1968) have provided some data on the fecundity of the species.

Since the highest catches of silver hake are recorded in the months preceding and during the spawning season, knowledge of fecundity is very important from a practical viewpoint and should be considered in the development of mathematical models for stock assessments. This paper provides additional information on the fecundity of silver hake on the Scotian Shelf based on data collected in 1977.

Materials and Methods

The ovaries from 105 female silver hake were collected from the Scotian Shelf during a cruise of the research vessel Isla de la Juventud in July–August 1977. After the length and weight measurements of the specimens were recorded, the ovaries were carefully extracted, weighed to the nearest gram, slit longitudinally on the side opposite to that containing the large blood vessels, and placed in jars containing Gilson's fluid, as modified by Simpson (1951). The jars were vigorously shaken after 24 hours and 48 hours to facilitate the action of the fluid in breaking down the ovarian connective tissue.

When the eggs appeared to be totally separated, the contents of each jar were strained through 1.0 mm and 0.1 mm mesh bolting cloth. Washing with a jet of water eliminated the residue of ovarian tissue from the meshes leaving the eggs completely clean. After filtering, the eggs from the different ovaries were placed in separate trays to dry. About 3 hours later, the eggs were moved around with the fingertips to avoid clustering when dry.

The dry eggs from each ovary were weighed on a torsion balance with a precision of 1 mg and then stored in a petri dish in a dry place until processed. Before beginning the actual processing of the samples for fecundity estimation, replicate counts of 40 subsamples (3 mg each) from the same ovary were made by two persons and the results compared statistically. There being no significant difference in the counts ($P > 0.50$), the work was speeded up considerably by having two persons do the egg-counting. For fecundity estimation, five subsamples, each weighing 3 mg, were taken from each sample for counting. The number of eggs (F) in each ovary was calculated by the equation $F = nS/s$, where n is the mean number of eggs in the subsamples, S is the weight (mg) of dry eggs in the sample, and s is the subsample weight (3 mg).

In order to determine the accuracy of the gravimetric method used, 15 subsamples with replacement were weighed and counted, giving a coefficient of variation of 7.0%. This value compares favorably with 10.5% obtained in fecundity studies by Bagenal (1957), 9.5% by Simpson (1951) and 6.8% by Alvarez-Lajonchere (1976).

The available fecundity and total weight data for silver hake are summarized by 2-cm length intervals in Table 1.

Results and Discussion

From the scatter diagram of silver hake fecundity against total length (Fig. 1), it is apparent that fecundity

TABLE 1. Summary of silver hake weight and fecundity data for females collected from the Scotian Shelf in July–August 1977.

Length group (cm)	No. of fish	Mean weight (g)	Mean Fecundity (000)
28–29	8	174	103
30–31	9	185	215
32–33	9	246	193
34–35	9	283	234
36–37	6	336	319
38–39	8	417	313
40–41	8	539	393
42–43	10	581	512
44–45	5	728	553
46–47	8	751	483
48–49	6	805	504
50–51	4	933	681
52–53	3	1,100	760
54–55	4	1,095	695
56–57	4	1,225	739
58–59	3	1,400	843
60–61	1	1,800	1,500
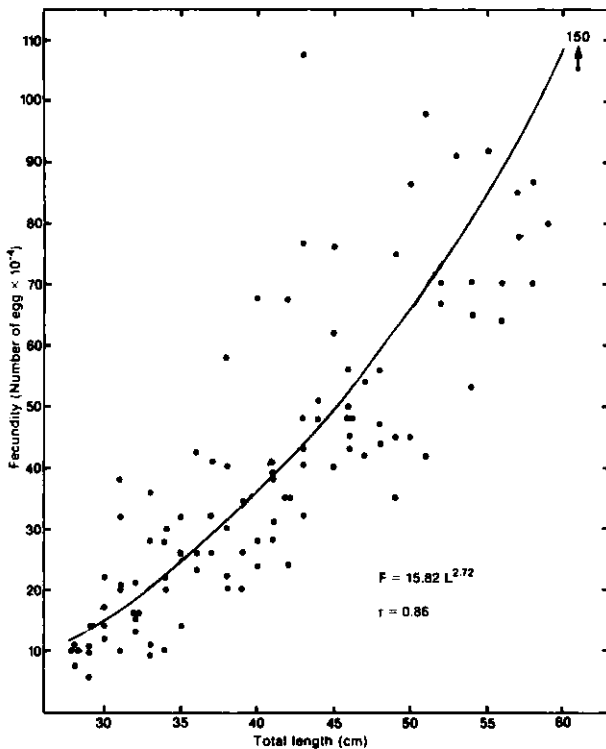
Fig. 1. Relationship between fecundity and total length for silver hake from the Scotian Shelf.

increases at a rate greater than that associated with increase in length. The application of a logarithmic transformation to the two variables resulted in the fecundity-length relationship

$$F = 15.82 \ L^{2.72}$$

where F is fecundity and L is the total length of fish. The data of Fig. 1 indicate that for any one length of fish fecundity varies between wide limits. However, the correlation coefficient ($r = 0.86$) was higher for the log-log regression than for a linear or a semi-log regression of fecundity on length.

It is generally accepted for most species of fish that body weight is approximately proportional to the cube of the length. This fact is confirmed for silver hake by the weight-length relationship (Fig. 2)

$$W = 0.005825 \ L^{3.059}$$

derived from the weighted log-log regression of body weight on total length. Since both fecundity and weight are approximately proportional to the cube of the length, the relationship between fecundity and weight (Fig. 3) is best described by the linear equation

$$F = 560.10 \ W + 92087.05$$

for which the correlation coefficient is 0.81. Similarly the relationship between fecundity and ovary weight (G) (Fig. 4) is best described by the equation

$$F = 25905.94 \ G + 137051.05$$

with a correlation coefficient of 0.88.

The results presented above indicate a lower fecundity for silver hake than that reported by Sauskan
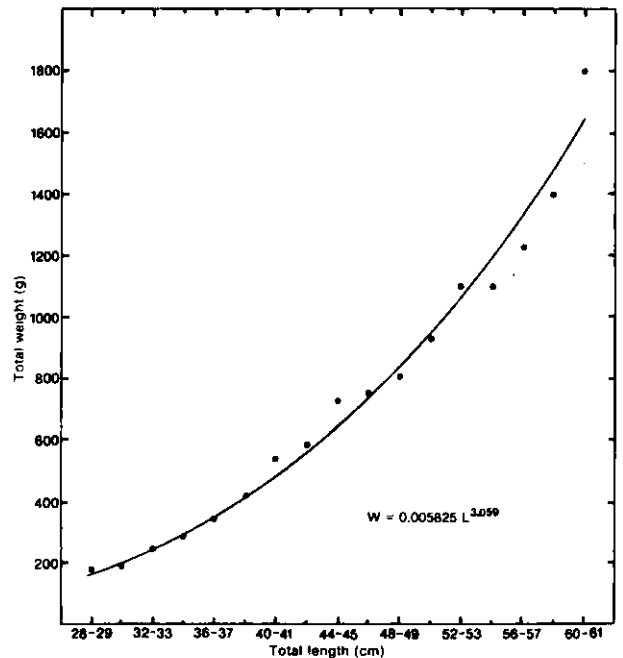
Fig. 2. Length-weight relationship of the female silver hake specimens from the Scotian Sehlf for the fecundity estimations.
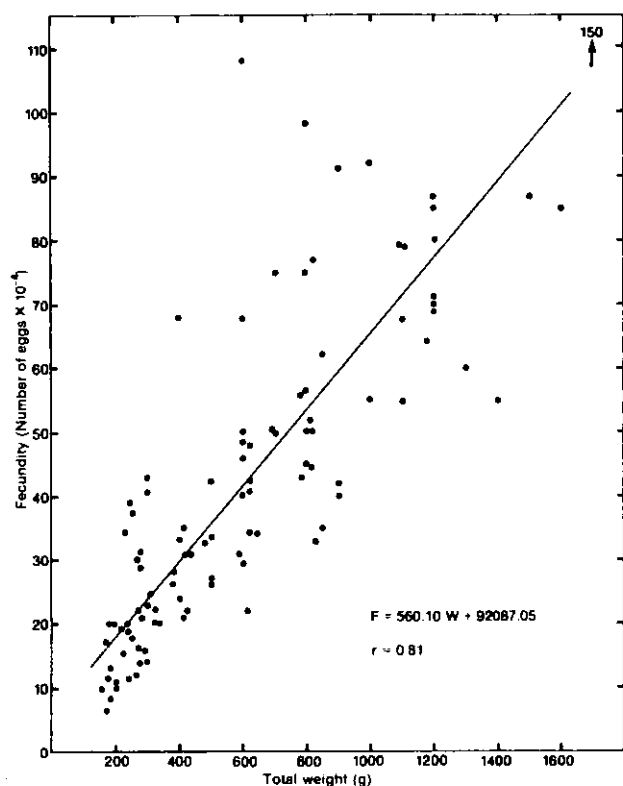
Fig. 3. Relationship between fecundity and total weight for silver hake from the Scotian Shelf.

$F = 560.10 \ W + 92087.05$

$r = 0.81$

and Serebryakov (1968), but no further comparison with their data can be made because equations relating fecundity and length were not given.

The spawning period for silver hake on the Scotian Shelf generally extends from May to October. Sauskan and Serebryakov (1968) noted intense spawning during August and September (1962–65) over Sable Island Bank. During the cruise of the *Isla de la Juventud* in July–August 1977, a high proportion of spent females were found to the south of Sable Island. However, to the west of this area on the Scotian Shelf, the majority of the females caught were in a ripe pre-spawning condition.

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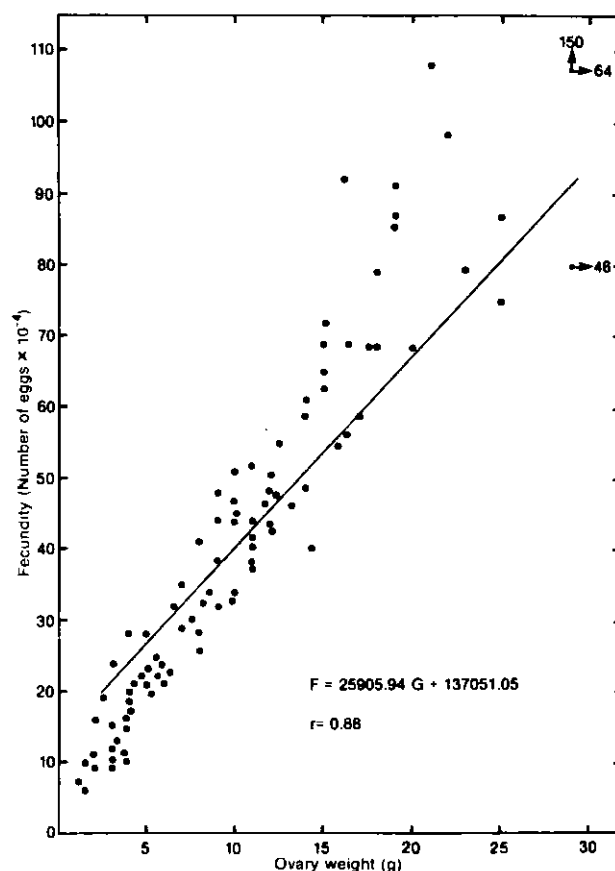
Fig. 4. Relationship between fecundity and ovary weight for silver hake from the Scotian Shelf.

$F = 25905.94 \ G + 137051.05$

$r = 0.88$

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Norwegian Investigations on Shrimp, *Pandalus borealis*, off West Greenland in 1977 and 1978[1]

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Abstract

Investigations on the shrimp fishing grounds off West Greenland in June–July 1977 and July–August 1978 showed that the catches consisted mainly of large shrimp between 18 and 30 mm carapace length. The length compositions of catches on Store Hellefiske Bank were bimodal with peaks at 21–22 and 25 mm, the first being dominant in 1977 and second in 1978. The quentities of discarded shrimp were 21.7% of the observed shrimp catches in 1977 and 10.0% in 1978, the higher value in 1977 being attributed to the occurrence of a larger proportion of soft-shelled shrimp in the 1977 catches which were sampled about a month earlier in 1977 than in 1978. Small redfish (10–20 cm) dominated in the by-catches with small quantities of Greenland halibut and other groundfish species. Analysis of catch per unit of effort data for the Norwegian commercial fishery in 1977 and 1978 indicated that the mean fishable biomass may have declined by about 20% from 1977 to 1978 and by about 33% from 1975–76 to 1978.

Introduction

Norwegian vessels began fishing for shrimp off West Greenland in 1971. By 1976, 26 vessels were involved in the fishery, taking about 11,600 metric tons. Due to quota regulations, only 20 Norwegian vessels participated in the shrimp fishery in 1977. However, the Norwegian quota was increased from 7,000 to 10,300 tons in 1978, and 25 vessels took part in the fishery. The main fishing area in 1977 and 1978 was along the western slope of Store Hellefiske Bank. Fishing gear and techniques were the same as in previous years and are described by Ulltang and Øynes (1978).

Field investigations on the shrimp fishing grounds off West Greenland were initiated in 1976 by the Institute of Marine Research in Bergen, and the results of these studies, together with analyses of commercial fishery data, were reported by Ulltang and Øynes (1978). The results of investigations carried out in 1977 and 1978 are presented in this paper.

Materials and Methods

From 26 June to 12 July 1977, one of the authors was an observer on board the stern trawler *Kap Farvel* (454 gross registered tons and length of 41 m), which used an 1800-mesh Sputnik trawl with groundrope of 51 m and mesh size of 43 mm.

From 20 July to 4 August 1978, Mr E. Moksnes from the University of Bergen was an observer on board the stern trawler *Pero* (575 gross registered tons and

length of 47 m), which used a 2200-mesh Wing trawl with a 62-m groundrope and an 1800-mesh Sputnik trawl with a 51-m groundrope. The mesh size of both trawls was about 41–43 mm.
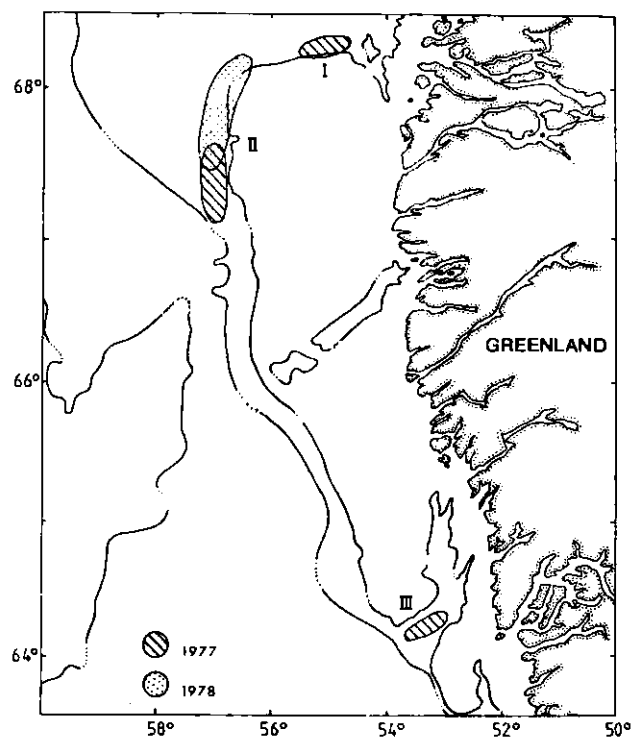

Fig. 1. Fishing areas of *MV Kap Farvel* in June–July 1977 and *MV Pero* in July–August 1978 off West Greenland: (I) south of Disko, (II) Store Hellefiske Bank, and (III) Sukkertoppen Dyb.

On both vessels, sorting machines were used to sort the shrimp into 'large', 'small' and 'discard' categories after they were separated from the fish species in the catch. The routine of processing the catches was the same as that described by Ulltang and Øynes (1978). By-catch quantities were usually determined by counting the number of fish of each species present in the catches, but in some cases the numbers of redfish were estimated in thousands of individuals. Details of the trawl hauls which were examined by the observers in 1977 and 1978 are listed in the Appendix to this paper. The areas of fishing by the two vessels during the period when the observers were on board are shown in Fig. 1.

Random samples of shrimp catches and of discarded shrimp were taken for length measurement (carapace length to nearest mm). In addition some length composition data were obtained for by-catches of redfish and Greenland halibut.

Monthly catch and effort data for 1977 and 1978 were compiled from the logbooks of Norwegian vessels participating in the shrimp fishery off West Greenland. The 1978 data are not complete as some logbook records had not been received at the time of the analysis.

Size Composition of Shrimp

Length compositions of shrimp in samples of total catch and of discards collected on board commercial trawlers in 1977 and 1978 are listed in Tables 1 and 2. The weighted mean length compositions by area (with catch as the weighting factor) for 1977 and 1978, together with the length composition for 1976 (from Ulltang and Oynes, 1978), are shown in Fig. 2. Samples were collected from the slope of Store Hellefiske Bank in each of the three years, but data for the Disko and Sukkertoppen Dyb areas are available only for 1977. Intra-year comparison of length composition data for Store Hellefiske Bank during 1976-78 is enhanced by the fact that the samples were taken at approximately the same time in each year, i.e. late June in 1977 and July in 1976 and 1978.

Two main size groups of shrimp were evident in the catches from Store Hellefiske during 1976-78. In 1976, modal groups were around 21-22 mm and 26 mm with the latter being dominant (Fig. 2). In 1977, the pattern was reversed with the bulk of the shrimp around 22 mm, but there was also a prominant modal group around 25-26 mm. In 1978, the major size groups had modes at 22 mm and 25 mm, with the latter being dominant as in 1976. Considerably more shrimp less than 20 mm in carapace length were caught in 1977 and 1978 than in 1976. Because of the limited sampling over a very short period in each year, no firm conclusions can be drawn about the changes in size composition, but the material indicates that no drastic changes have occurred between 1976 and 1978.

The length composition of shrimp in samples from Sukkertoppen Dyb in 1977 were very similar to that for Store Hellefiske Bank (Fig. 2). The peculiar mean

TABLE 1. Length composition of shrimp catches and discards by MV Kap Farvel off West Greenland in June-July 1977. (Numbers in table heading refer to tow numbers in the first column of Appendix Table I.)

Carapace length (mm)	Random samples of individual catches																			Random samples of discarded shrimp							
	Disko area					Store Hellefiske Bank							Sukkertoppen Dyb														
	1	2	3	4	Total	5	7	12	16	17	19	Total	20	26	33	38	45	Total	5	12	20	26	33	38	45	Total
10	—	—	—	—	—	—	—	—	—	—	3	3	—	—	—	—	—	—	—	1	—	—	—	—	1	2
11	—	—	—	—	—	—	1	1	—	—	—	2	—	—	—	2	—	2	—	—	1	—	—	—	—	1
12	—	—	—	—	—	—	3	2	—	—	2	7	—	—	1	1	—	2	1	8	—	—	1	1	—	11
13	1	—	—	—	1	—	3	2	—	—	—	5	—	1	—	—	—	1	—	4	—	—	—	1	—	5
14	1	—	—	—	1	2	5	4	—	—	—	11	—	—	1	3	—	4	2	4	—	—	2	—	1	9
15	—	2	1	—	3	6	14	2	1	1	2	26	1	1	2	2	1	7	12	7	—	2	5	1	1	28
16	—	3	1	—	4	7	14	4	1	—	2	28	—	1	2	3	9	15	6	6	1	6	5	3	4	31
17	3	5	1	1	10	10	7	2	—	2	5	26	1	2	7	4	9	23	5	7	3	3	11	8	6	43
18	3	14	1	3	21	12	4	5	2	2	2	27	1	2	12	5	7	27	13	10	2	6	9	5	5	50
19	13	11	4	4	32	11	6	3	7	8	3	38	3	3	12	9	8	35	15	16	1	13	16	16	11	88
20	14	20	14	7	55	5	9	5	11	8	9	47	1	5	9	18	9	42	18	12	9	21	20	21	20	121
21	12	8	8	2	30	8	7	5	14	13	10	57	9	7	8	6	5	35	12	13	12	25	18	19	21	120
22	10	11	16	6	43	5	2	7	29	32	18	93	17	16	14	18	10	75	9	4	27	15	8	14	14	91
23	5	4	13	6	28	8	5	6	15	12	18	64	12	19	6	11	5	53	4	5	26	2	6	3	4	50
24	9	7	8	2	26	6	6	5	5	7	8	37	14	10	3	6	2	35	1	1	7	1	—	1	1	12
25	11	6	3	13	33	6	13	18	4	5	4	50	5	9	4	3	12	33	1	1	4	2	—	1	4	13
26	9	2	7	9	27	4	5	19	3	6	4	41	9	7	6	2	7	31	1	1	1	—	—	2	3	8
27	7	2	16	17	42	3	5	13	4	4	7	36	6	12	5	5	7	35	—	—	1	—	—	1	—	2
28	4	4	5	8	21	5	1	7	3	—	5	21	5	6	2	3	3	19	—	1	—	—	—	—	—	1
29	—	1	4	5	10	2	1	4	1	—	2	10	1	1	1	3	4	10	—	—	—	—	—	—	—	—
30	—	—	—	—	—	—	—	—	1	1	—	2	—	2	—	—	—	2	—	1	—	—	—	1	—	2
31	—	—	—	—	—	—	—	1	—	—	—	1	—	—	1	—	—	1	—	—	—	—	—	—	—	—
Total	102	100	102	83	387	100	111	115	101	101	104	632	85	104	98	104	96	487	100	102	95	96	101	98	96	688

TABLE 2. Length composition of shrimp catches and discards by MV Pero off West Greenland (NW slope of Store Hellefiske Bank) in July–August 1978. (Numbers in heading refer to tow numbers in the first column of Appendix Table 2.)

Carapace length (mm)	Random samples of individual catches													Random samples of discarded shrimp												
	1	7	8	15	21	24	26	35	39	44	46	51	Total	1	7	8	15	21	24	26	35	39	44	46	51	Total
10	—	1	—	—	—	—	—	—	—	—	—	1	2	1	—	—	—	—	—	—	—	—	—	—	—	1
11	—	—	—	—	—	—	—	—	—	1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	1
12	—	—	—	1	—	—	—	—	—	—	—	—	1	1	4	—	—	—	—	—	—	—	—	—	2	7
13	—	4	—	1	—	—	—	1	—	1	1	—	8	1	2	1	—	1	—	—	1	—	—	2	—	8
14	1	2	—	—	1	—	—	1	—	—	1	—	6	3	13	3	3	—	1	—	1	1	4	1	3	33
15	2	3	—	6	—	2	—	2	1	2	3	2	23	10	12	3	8	17	4	3	11	9	4	6	7	94
16	8	16	1	5	8	2	1	3	4	2	4	1	55	39	40	28	28	30	16	26	9	24	32	17	27	316
17	4	7	3	6	—	3	1	3	6	10	5	—	48	25	16	28	24	26	28	27	26	25	34	32	28	319
18	3	7	4	11	5	4	6	7	11	6	7	4	75	7	7	13	16	15	26	21	17	16	12	13	16	179
19	—	4	3	6	4	13	6	9	8	3	5	2	63	3	3	6	9	5	12	13	16	11	4	18	12	112
20	3	3	6	11	2	8	7	9	10	4	3	3	69	9	1	5	9	5	7	5	3	5	2	4	4	59
21	6	4	6	7	6	7	12	13	8	4	8	7	88	1	—	5	2	1	1	4	8	6	1	3	1	33
22	9	8	4	3	5	10	9	8	13	6	11	10	96	1	1	4	3	—	4	—	6	2	2	4	2	29
23	6	5	5	5	7	8	11	18	7	2	7	9	88	1	—	4	1	—	1	1	2	—	1	1	2	14
24	7	8	7	9	10	7	8	7	6	14	8	11	102	1	—	1	—	—	—	—	—	—	2	—	1	5
25	25	10	17	10	21	13	11	6	9	14	13	13	162	—	—	—	—	—	—	—	—	—	1	—	—	1
26	12	9	23	12	14	12	10	8	5	14	12	12	143													
27	11	9	12	5	10	6	10	2	8	7	6	15	101													
28	5	5	6	5	6	5	8	3	1	6	5	7	62													
29	1	1	4	2	1	1	—	4	1	6	—	3	24													
30	—	1	—	—	—	1	—	—	—	1	1	—	4													
31	—	—	—	—	—	1	—	—	—	—	—	—	1													
Total	103	107	101	105	100	101	100	104	98	103	100	100	1,222	103	100	101	103	100	100	100	100	102	96	101	105	1,211

length composition for the Disko area in 1977 reflects the rather large variation in the four samples from the area (see Table 1).

The size composition of discarded shrimp in 1977 and 1978 are shown in Fig. 3. In 1977, the discard rate on board the Kap Farvel was found to be 21.7% for Store Hellefiske Bank and 13.1% for Sukkertoppen Dyb. In 1978, the discard rate on board the Pero was found to be 10.0% for Store Hellefiske Bank, a value only slightly greater than the 8.4% reported by Ulltang and Øynes (1978) for the same area from observations on board the Pero in 1976. The observations in 1977 were made a little earlier in the summer than in 1976 and 1978, and this probably explains the differences in discard rate and in length composition of discards between 1977 and 1978. In 1977, a significant proportion of the shrimp were still soft-shelled at the time of sampling, and therefore a greater proportion of larger shrimp were discarded in 1977 than in 1978.

By-catches in the Shrimp Fishery

By-catches of fish species in many of the trawl hauls of Kap Farvel in 1977 and Pero in 1978 are listed in Appendix Tables 1 and 2 respectively. None of the fish were kept except those consumed on board during the trips. Redfish were by far the most numerous, up to 6,500 being taken in a single haul in 1977 and up to 6,000 in 1978. The mean number of fish relative to the mean shrimp catch (retained) per tow, for hauls on which observations were made on board of Pero in

1976 (Ulltang and Øynes, 1978), Kap Farvel in 1977 and Pero in 1978, were as follows:

Species	Mean number per haul		
	1976	1977	1978
Redfish	2,254	1,334	906
Greenland halibut	105	63	67
Cod	6	3	+
Others	21	38	22
Mean by-catch	2,386	1,438	995
No. of hauls observed	71	38	54
Mean shrimp catch (kg)	1,438	862	1,215
No. of fish per kg shrimp	1.66	1.67	0.82

On the average, the rate of by-catch and species composition were essentially the same in 1977 as in 1976, but there was a significant decline in 1978 to about one-half of the 1976–77 level.

Redfish taken as by-catch in the Hellefiske Bank area in 1977 and 1978 were small, ranging in size from 6 to 30 cm with modes at 13 and 14 cm (Fig. 4). At Sukkertoppen Dyb in 1977, redfish up to 60 cm in length were taken, but the bulk of the fish fell in two size-groups with modes at 13 and 24 cm. All of the Greenland halibut taken as by-catch in the Hellefiske Bank area were less than 50 cm in 1977 and 1978, but fish up to 75 cm were taken at Sukkertoppen Dyb in 1977 (Fig. 5).

Very few cod were taken in 1977 and even fewer in 1978. A seal, Pusu hispida, was caught on 30 June 1977 at 67°41′N and 57°25′W.
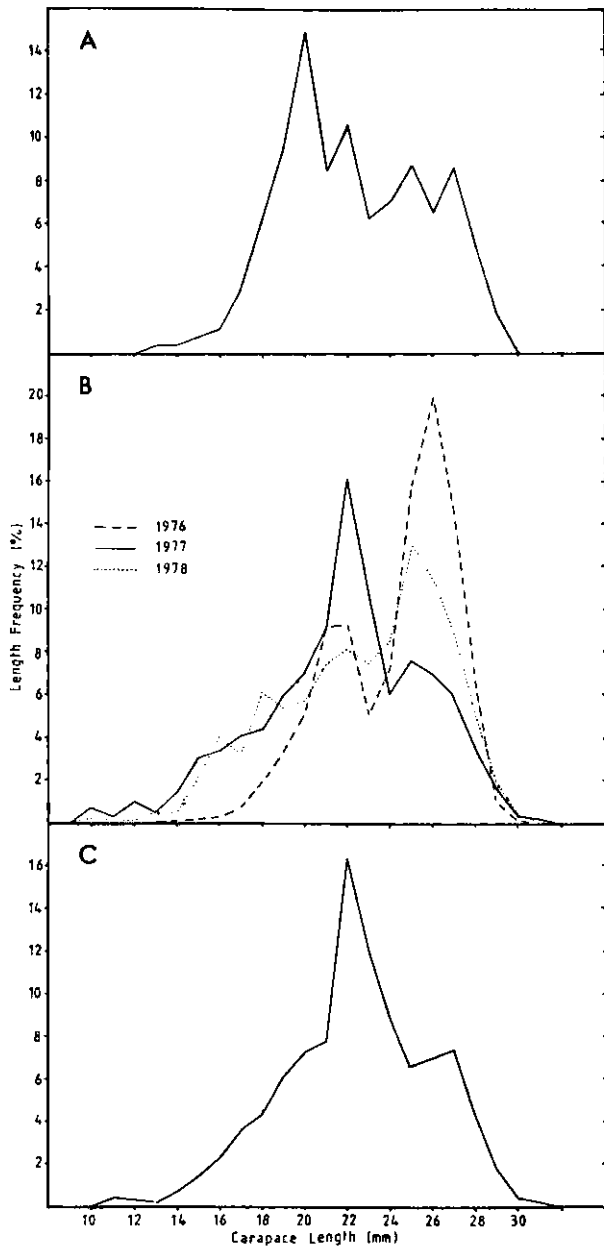
Fig. 2.　Length composition of shrimp weighted from samples taken off West Greenland in 1976-78: (A) south of Disko, (B) Store Hellefiske Bank, and (C) Sukkertoppen Dyb.

Fig. 3.　Length composition of discarded shrimp from samples taken off West Greenland in 1977 and 1978.
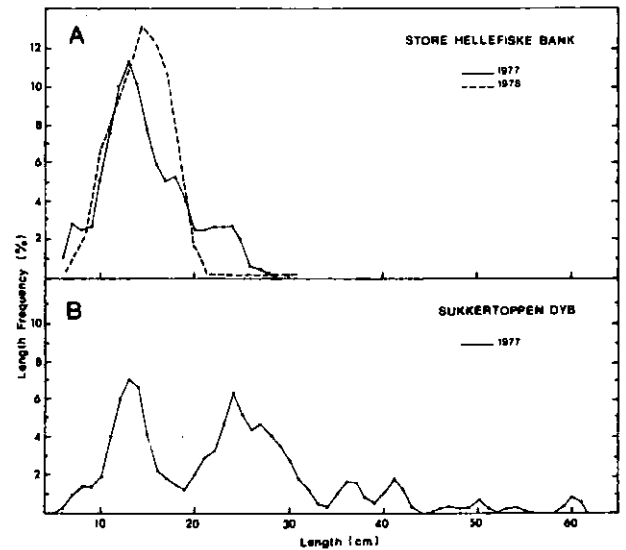
Fig. 4.　Length composition of redfish taken as by-catch with shrimp off West Greenland in 1977 and 1978.
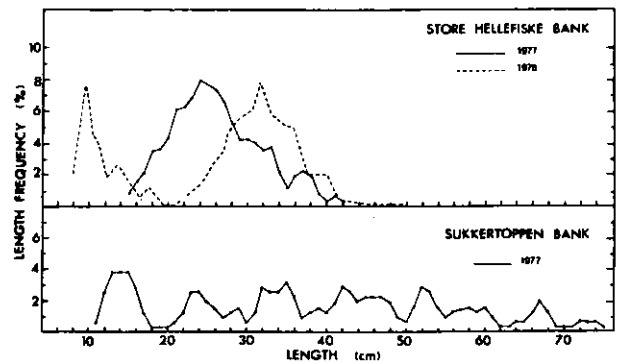
Fig. 5.　Length composition of Greenland halibut taken as by-catch with shrimp off West Greenland in 1977 and 1978.

Catch and Catch per Unit of Effort

Table 3 shows catch and catch per hour trawling (CPUE) by month and division for the Norwegian shrimp fishery off West Greenland in 1977 and 1978. The 1978 data are not complete as some logbooks had not been received and some fishing was still going on at the time of this analysis. The mean CPUE values were calculated as total catch divided by total effort. It is evident that catch rates in the first half of the year were lower in 1978 than in 1977.

TABLE 3.   Catch (metric tons) and catch per hour trawling (CPUE) by month and division in 1977 and 1978. (CPUE is calculated as total catch/total effort; data for 1978 are preliminary.)
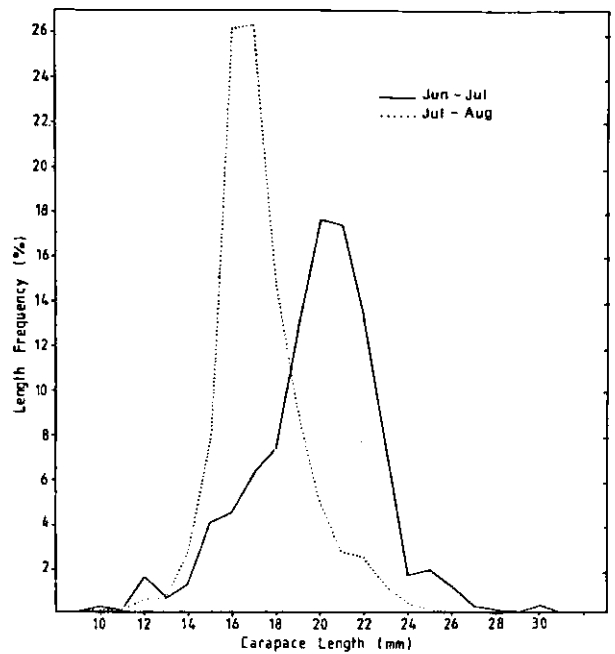
| Year | Month | OA | | 1A | | 1B | | 1C | | 1D | | 1E | | Total catch |
		Catch	CPUE	Catch	CPUE	Catch	CPUE	Catch	CPUE	Catch	CPUE	Catch	CPUE	
1977	Jan	—	—	—	—	471	0.746	8	2.670	5	0.313	10	0.323	494
	Feb	—	—	—	—	805	0.752	—	—	—	—	—	—	805
	Mar	—	—	—	—	230	1.036	—	—	18	0.353	—	—	248
	Apr	—	—	—	—	296	0.441	10	0.250	32	0.274	—	—	338
	May	—	—	—	—	1,799	0.488	2	0.167	—	—	—	—	1,801
	Jun	—	—	—	—	446	0.283	4	0.250	149	0.320	—	—	599
	Jul	—	—	—	—	651	0.396	84	0.225	364	0.256	—	—	1,099
	Aug	—	—	—	—	736	0.348	—	—	13	0.333	—	—	749
	Sep	50	0.212	6	0.200	520	0.265	—	—	—	—	—	—	576
	Oct	99	0.220	11	0.244	250	0.190	—	—	—	—	—	—	360
	Nov	1	0.125	—	—	410	0.330	—	—	—	—	—	—	411
	Dec	—	—	—	—	21	0.212	2	0.054	—	—	—	—	23
	Total	150	0.216	17	0.227	6,635	0.409	110	0.229	581	0.275	10	0.323	7,503
1978	Jan	—	—	—	—	5	0.111	68	0.187	336	0.211	—	—	409
	Feb	—	—	—	—	742	0.206	69	0.158	186	0.146	—	—	997
	Mar	—	—	—	—	317	0.207	113	0.148	56	0.095	—	—	486
	Apr	—	—	—	—	454	0.269	11	0.090	29	0.111	—	—	494
	May	—	—	6	0.462	794	0.250	—	—	1	0.083	—	—	801
	Jun	—	—	5	0.218	337	0.226	72	0.220	193	0.163	—	—	607
	Jul	14	0.269	45	0.313	659	0.248	8	0.131	11	0.092	—	—	737
	Aug	—	—	105	0.420	871	0.280	—	—	14	0.700	—	—	990
	Sep	—	—	—	—	91	0.281	2	0.111	37	0.410	—	—	130
	Total	14	0.269	161	0.374	4,270	0.242	343	0.164	863	0.168	—	—	5,651

TABLE 4. Mean catch per hour trawling (metric tons) for shrimp off West Greenland by Norwegian vessels in 1975 to 1978. (CPUE values based on monthly catches greater than 100 tons.)

Year	OA	1A	1B	1C	1D
1975	—	—	0.510	0.225	0.242
1976	—	—	0.452	0.323	0.239
1977	0.216	—	0.409	0.229	0.275
1978	—	0.374	0.242	0.164	0.168

Annual catch rates by division for 1975–78 are given in Table 4. The mean CPUE values for 1975 and 1976 are based on monthly data given by Ulltang and Øynes (1978). It should be noted that the annual CPUE values presented in that paper were calculated by weighting the monthly CPUE by the monthly catches, which gave slightly higher values than those in Table 4. Ulltang and Øynes (1978) noted that a better weighting factor would be the monthly fishing effort, which is equivalent to dividing annual catch by annual effort to obtain CPUE. The largest difference in the two sets of mean CPUE values occurs for Div. 1B in 1976, giving a decrease in CPUE from 1975 to 1976 (Table 4), whereas Ulltang and Øynes (1978) indicated a slight increase.

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The mean CPUE in Div. 1C and 1D was rather stable during 1975–77, except for a temporary increase in Div. 1C in 1976, but was substantially lower in both divisions in 1978 (Table 4). In Div. 1B, the CPUE has continued to decline since 1975 with the largest decrease from 1977 to 1978. The monthly CPUE values for Div. 1B in 1975–78 are plotted in Fig. 6, which show that CPUE was very high during January–May of 1975–77 but was consistently low in all months of 1978 for which data are available.

Discussion

It is difficult to draw any firm conclusions from annual mean CPUE values, as the means depend on both fluctuations in abundance and the seasonal distribution of fishing effort. Evaluation of the significant decline in commercial catch rates from 1977 to 1978 (Tables 3 and 4; Fig. 6) is difficult without having additional information on shrimp distribution
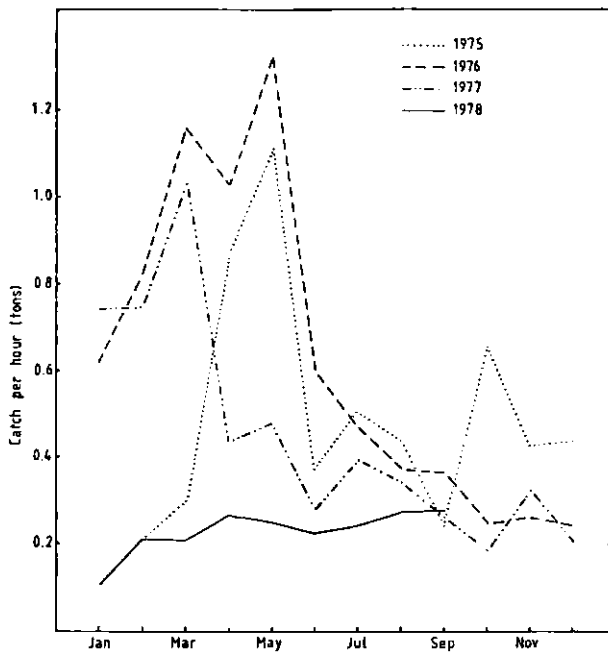
Fig. 6.   Mean shrimp catch per hour trawling by Norwegian vessels in Div. 1B, 1975-78.

from research vessel surveys. It is known that the fishery during the first half of 1978 was severely hampered by ice on the traditional fishing grounds. The effect of ice conditions on CPUE would depend on the distribution of shrimp in relation to the distribution of ice floes, which in turn would affect the area swept by the gear per trawling hour. Generally, unfavourable ice conditions would result in some decrease in CPUE, but it is not possible to quantify it. However, the size of the decrease in CPUE from 1977 to 1978, especially in Div. 1B during the first half of the year gives rise to serious concern. No significant changes are evident in the size composition of shrimp sampled during 1976-78, but these data were not taken in the months when the largest decrease in CPUE was observed. In the absence of more precise information, a conservative approach would be to assume that at least a part of the decline in CPUE is caused by declining stock abundance.

Mean catch per hour trawling in Div. 1B in July–September decreased by 20% from 1977 to 1978 and by 33% from 1976 to 1978, the CPUE value for 1976 being derived from data presented by Ulltang and Øynes (1978). Since ice conditions should not influence fishing activity during late summer, these percentages may therefore indicate the decrease in the abundance of commercial-sized shrimp from 1976-77 to 1978. A similar decline in abundance of shrimp in Div. 1C and 1D is indicated by the annual mean CPUE values given in Table 4 for 1977 and 1978. Ulltang and

Øynes (1978) gave stock size estimates for 1975-76, based on the 'swept area' method. If the above-noted decrease in CPUE is assumed to reflect the change in abundance, these stock size estimates should be reduced by approximately one-third to give an estimate of the mean fishable biomass in 1978.

The recommended total allowable catch (TAC) of 40,000 tons for 1977 and 1978 was based on an estimated mean annual biomass of 100,000 tons and a fishing mortality (F) of 0.4. From the model presented by Ulltang (1978), it was estimated that F = 0.4 would reduce the spawning potential by about 50% (in number) relative to the size of the unexploited stock, assuming that no change occurred in recruitment to the fishable stock.

The same model may be used to predict the mean annual fishable biomass after a new equilibrium corresponding to F = 0.4 has been established. Using the same notation as in Ulltang (1978) (i.e. R shrimp recruit to the fishery at age r, shrimp produce larvae for the first time at age r+t, and natural mortality is M before age r+t and M_1 thereafter), the equilibrium mean annual fishable biomass is

$$B = \frac{R\overline{W}_1}{F+M}(1 - e^{-(F+M)t}) + \frac{R\overline{W}^2}{F+M_1} e^{-(F+M)t}$$

where $\overline{W}_1$ is the mean weight of shrimp between ages r and r+t, and $\overline{W}_2$ is the mean weight of shrimp older than age r+t. $\overline{W}_1$ and $\overline{W}_2$ depend to some extent on F.

If $\overline{W}_1$ and $\overline{W}_2$ are assumed to correspond roughly to the weight of shrimp of carapace length around 21–22 and 25–26 mm respectively (Fig. 2B), the length-weight relationship given by Minet et al. (1978) for Statistical Area 0 indicates that $\overline{W}_2 \simeq 2\overline{W}_1$. If it is further assumed that $M_1 = 1.5$ and $t = 1.5$ (ICNAF, 1977), and that M = 0.8 (i.e. approximately half the value of M_1), the equation given above predicts a decrease in equilibrium mean annual fishable biomass (B) of approximately 25% with an increase in F from 0.1 to 0.4. Comparison of this figure with the observed decrease in CPUE of about one-third indicates that the development in the West Greenland shrimp fishery is in good agreement with what could be predicted from the model, using the various assumptions of the Working Group on Shrimp in 1976 (ICNAF, 1977). However, there is great uncertainty in the values of the parameters used in the model and also in the estimates of decrease in abundance. Furthermore, even if a new equilibrium corresponding to F = 0.4 according to the model were established by 1978-79, fluctuations in biomass from year to year could be expected due to recruitment variations.

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Appendix

TABLE 1.   Catches of shrimp and by-catches of fish in some trawl hauls by MV Kap Farvel off West Greenland in June-July 1977.

Tow no.	Date	Time	Position N lat.	Position W long.	Towing time (hr)	Shrimp catch (kg) Small	Shrimp catch (kg) Large	Shrimp catch (kg) Total	Shrimp catch (kg) Discard	By-catches (numbers) Redfish	By-catches (numbers) Cod	By-catches (numbers) G. hal.	By-catches (numbers) Other
1	Jun 26	0820	68°13'	55°06'	2.00	66	308	374		145	—	75	34
2	Jun 26	1110	68°13'	55°06'	2.00	66	264	330		240	16	70	20
3	Jun 26	1350	68°15'	54°40'	1.00	22	132	154		114	4	21	7
4	Jun 26	1620	68°09'	55°33'	1.00	22	132	154		114	5	18	40
5	Jun 27	0655	67°42'	57°04'	2.42	240	780	1,020	122	4,000	—	220	120
6	Jun 27	0944	67°42'	57°04'	2.56	240	530	770	100	...	...	...	...
7	Jun 27	1335	67°42'	57°04'	2.50	130	300	430	200	2,500	—	107	Few
8	Jun 27	1845	67°42'	57°04'	2.50	290	600	890	400	...	...	...	...
9	Jun 28	0510	67°13'	57°21'	2.33	220	950	1,170		3,500	3	159	50
10	Jun 28	1020	67°13'	57°21'	2.17	250	750	1,000		...	...	...	...
11	Jun 28	1300	67°13'	57°21'	2.25	...	...	800		5,500	—	92	20
12	Jun 29	0635	67°13'	57°21'	2.25	230	970	1,200	300	5,500	3	378	131
13	Jun 29	0935	67°13'	57°21'	2.25	250	950	1,200		...	...	...	...
14	Jun 29	1220	67°13'	57°21'	2.17	220	770	990		6,500	2	135	63
15	Jun 29	1510	67°13'	57°21'	2.17	250	750	1,000		...	...	...	...
16	Jun 30	0845	67°41'	57°25'	1.67	175	220	395	180	281	—	36	1
17	Jun 30	1050	67°41'	57°25'	2.17	810	640	1,450		344	—	112	1 seal
18	Jun 30	1325	67°41'	57°25'	2.06	725	615	1,340		361	—	109	7
19	Jun 30	1840	67°41'	57°25'	2.00	660	640	1,300		...	...	...	...
20	Jul 2	0755	64°15'	53°17'	3.17	460	900	1,360	220	178	2	118	1
21	Jul 2	1200	64°15'	53°17'	3.00	310	925	1,235		361	3	98	46
22	Jul 2	1545	64°15'	53°17'	3.33	290	840	1,130		127	1	77	3
23	Jul 4	0745	64°15'	53°17'	3.17	150	530	680		66	2	32	13
24	Jul 4	1140	64°10'	53°15'	3.33	240	725	965		173	5	31	19
25	Jul 4	1535	64°10'	53°25'	3.50	90	330	420		38	1	14	—
26	Jul 5	0645	64°05'	53°10'	3.25	250	750	1,000	150	155	6	34	53
27	Jul 5	1030	64°05'	53°10'	3.17	220	640	860		161	4	23	17
28	Jul 5	1420	64°05'	53°10'	3.50	220	680	900		231	3	19	27
29	Jul 6	0545	64°25'	53°10'	1.50	—	1,200	1,200		321	6	17	10
30	Jul 6	0855	64°25'	53°10'	1.92	110	350	460		410	1	7	17
31	Jul 6	1125	64°25'	53°10'	2.00	220	750	970		...	...	...	...
32	Jul 6	1410	64°25'	53°10'	2.00	130	440	570		1,500	—	9	2
33	Jul 7	0815	64°15'	53°10'	2.17	150	530	680	100	231	4	18	Few
34	Jul 7	1105	64°21'	53°15'	2.33	370	1,060	1,430	200	200	2	77	4
35	Jul 7	1410	64°21'	53°15'	2.50	200	500	700	150	...	...	...	...
36	Jul 8	0345	64°21'	53°15'	3.67	200	810	1,010	200	300	7	18	32
37	Jul 8	0750	64°21'	53°15'	3.17	220	660	880	150	150	—	8	27
38	Jul 8	1135	64°21'	53°15'	2.67	220	620	840		110	—	9	5
39	Jul 8	1450	64°21'	53°15'	3.42	310	620	930	150	123	—	9	Few
40	Jul 9	0615	64°20'	53°15'	3.00	160	920	1,100	200	5,000	2	22	49
41	Jul 9	0950	64°20'	53°15'	3.17	220	840	1,060		4,000	7	79	164
42	Jul 9	1335	64°20'	53°15'	3.33	260	730	990		...	...	...	...
43	Jul 10	0330	64°19'	53°17'	3.00	220	900	1,120		...	...	...	...
44	Jul 10	0705	64°19'	53°17'	3.00	150	620	770		2,000	20	34	138
45	Jul 10	1030	64°19'	53°17'	3.17	90	480	570		...	...	...	...
46	Jul 10	1415	64°19'	53°17'	3.00	180	620	800		1,000	8	11	116
47	Jul 11	0515	64°20'	55°19'	2.50	286	726	1,012		800	3	22	60
48	Jul 11	0845	64°20'	55°19'	3.00	245	1,320	1,565	250	...	...	...	...
49	Jul 11	1235	64°20'	55°19'	3.00	310	840	1,150	150	2,000	2	54	104
50	Jul 12	0720	64°20'	55°19'	3.00	110	480	590		2,000	2	29	41
51	Jul 12	1055	64°20'	55°19'	3.00	220	680	900		...	...	...	...

TABLE 2.   Catches of shrimp and by-catches of fish in some trawl hauls by MV Pero off West Greenland in July–August 1978.

Tow no.	Date	Time	Position N lat.	Position W long.	Towing time (hr)	Shrimp catch (kg) Small	Shrimp catch (kg) Large	Shrimp catch (kg) Total	Shrimp catch (kg) Discard	By-catches (numbers) Redfish	By-catches (numbers) Cod	By-catches (numbers) G. hal.	By-catches (numbers) Other
1	Jul 22	0755	67°31'	57°02'	3.08	270	630	900	90	75	—	155	99
2	Jul 22	1310	67°32'	56°43'	3.00	150	350	500		110	4	70	44
3	Jul 22	1650	67°34'	56°58'	3.00	300	800	1,100		10	—	45	44
4	Jul 23	0445	67°30'	56°42'	3.00	360	760	1,120	187	600	—	110	55
7	Jul 23	1830	67°36'	56°56'	3.00	308	572	880	136	110	—	76	60
6	Jul 24	0355	67°57'	56°56'	3.00	154	308	462	50	500	—	185	50
9	Jul 24	0830	68°09'	56°59'	2.83	730	1,970	2,700	330	3,000	1	23	2
10	Jul 24	1310	68°06'	57°01'	2.00	560	600	1,360	115	2,300	—	12	3
11	Jul 24	1800	68°11'	56°54'	2.25	560	800	1,360	87	43	—	15	5
12	Jul 24	1920	68°13'	56°47'	2.50	420	980	1,400	116	240	—	12	—
13	Jul 25	0330	68°08'	57°02'	3.00	418	1,002	1,420	200	300	—	15	1
14	Jul 25	0720	68°12'	56°48'	3.00	548	1,277	1,825	168	95	—	26	2
15	Jul 25	1100	68°08'	57°01'	2.83	700	1,150	1,850	263	670	—	80	3
16	Jul 25	1450	68°12'	56°40'	3.00	660	990	1,650	163	385	—	45	—
17	Jul 25	1650	67°56'	56°57'	1.58	352	616	968	97	300	—	15	—
18	Jul 26	0550	68°14'	56°38'	3.00	316	740	1,056	132	105	—	32	—
19	Jul 26	1055	68°11'	56°56'	2.50	484	814	1,298	130	150	—	30	4
20	Jul 26	1305	68°12'	56°40'	3.17	440	814	1,254	156	1,200	—	151	10
21	Jul 26	1705	68°08'	57°02'	3.00	480	900	1,380	153	1,500	—	85	13
22	Jul 26	2050	68°13'	56°44'	3.50	220	480	700	70	150	—	150	50
23	Jul 27	0515	68°14'	56°39'	2.75	540	520	1,060	155	140	—	35	5
24	Jul 27	0840	68°15'	56°20'	3.00	528	1,276	1,804	164	650	—	55	10
26	Jul 27	1745	68°14'	56°13'	3.00	282	1,056	1,338	300	350	—	40	10
27	Jul 27	2120	68°13'	56°34'	2.83	385	915	1,300	130	1,500	—	85	15
28	Jul 28	0530	68°13'	56°35'	3.00	555	924	1,479	145	1,100	—	160	30
29	Jul 28	0920	68°14'	56°14'	3.17	660	902	1,562	223	1,000	—	68	11
30	Jul 28	1330	68°14'	56°29'	3.00	735	840	1,575	225	1,000	—	125	18
31	Jul 28	1740	68°15'	56°11'	3.00	462	660	1,122	110	1,000	—	90	21
32	Jul 28	2210	68°13'	56°29'	3.00	572	946	1,518	213	4,000	—	110	18
33	Jul 29	0815	68°13'	56°31'	2.75	500	750	1,250	170	400	1	65	14
34	Jul 29	0945	68°13'	56°12'	3.00	460	1,240	1,700	178	1,400	1	100	58
35	Jul 29	1345	68°13'	56°14'	2.17	352	682	1,034	148	1,000	3	42	63
36	Jul 29	1710	68°14'	56°09'	3.00	352	726	1,078	100	6,000	—	32	18
37	Jul 29	2215	68°12'	56°31'	3.00	290	610	900		...	...	...	...
38	Jul 30	0710	68°13'	56°28'	3.00	374	594	968	100	107	—	57	29
39	Jul 30	1115	68°15'	56°03'	3.08	440	660	1,100	138	700	—	55	26
40	Jul 30	1500	68°13'	56°24'	2.83	260	570	630	80	750	1	35	17
41	Jul 30	1920	68°15'	56°02'	1.00	30	70	100		95	—	8	—
42	Jul 31	0810	68°02'	57°10'	3.00	242	594	836	70	800	—	38	10
43	Jul 31	1230	67°57'	56°53'	3.00	330	1,232	1,562		1,000	—	105	38
44	Jul 31	1700	68°03'	56°58'	3.00	176	616	792	72	5,000	—	93	25
45	Jul 31	2110	67°56'	57°01'	2.00	110	330	440		400	—	21	11
46	Aug 1	0645	68°01'	56°53'	3.00	198	770	968	80	150	—	43	13
47	Aug 1	1130	67°59'	56°56'	3.00	132	616	746	62	73	4	115	38
48	Aug 1	1445	68°01'	57°04'	3.00	176	780	936	76	3,000	—	104	18
49	Aug 1	1850	67°53'	56°56'	3.00	325	1,000	1,325	100	1,000	—	132	38
50	Aug 2	0220	67°57'	56°56'	2.75	396	1,174	1,570	170	425	3	42	26
51	Aug 2	0915	67°53'	56°51'	3.00	792	2,134	2,926		560	—	49	8
52	Aug 2	1310	67°46'	57°05'	3.00	352	1,276	1,628	100	100	—	31	17
53	Aug 2	1705	67°51'	56°59'	3.00	396	1,296	1,694	130	1,000	—	35	13
54	Aug 2	2050	67°46'	57°08'	2.67	320	660	1,000	70	1,000	—	135	36
55	Aug 3	0525	67°46'	57°06'	3.00	231	781	1,012	100	450	—	64	32
56	Aug 3	0855	67°52'	56°56'	3.00	308	1,100	1,408	110	210	2	. 47	18
57	Aug 3	1240	67°46'	57°10'	3.00	175	410	585	52	800	·	64	41
58	Aug 3	1620	67°41'	57°22'	1.00	50	150	200		105	—	3	11

Year-Class Strength of Redfish and Growth of Cod on Flemish Cap[1]

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Abstract

The Flemish Cap lacks large resident populations of fish species whose adults are of a size suitable as prey for adult cod. The growth rate of adult cod on the bank had been slow compared to that on adjacent areas of the Grand Bank, but has increased in recent years. This increase coincides with the appearance of highly successful year-classes of redfish. Intermediate-sized redfish appear to provide the energetically-favourable forage needed for continued growth of adult cod.

Introduction

The Flemish Cap, an isolated bank east of the Grand Bank, lacks large resident populations of fish species whose adults are of a size suitable as prey for adult cod, *Gadus morhua*, (Popova, 1962; Templeman, 1976). Capelin, *Mallotus villosus*, and sand lance, *Ammodytes* sp., the two major prey species on the Grand Bank (Popova, 1962), appear to be only occasional visitors to the Flemish Cap. White barracudina, *Paralepis rissoi*, and lanternfishes, Myctophidae, have been reported from cod stomachs but seldom in large numbers (Kashintsev, 1962; Popova, 1962; Turuk, 1968). The Flemish Cap also has a low biomass of benthos (Nesis, 1965), and this is reflected in the relative unimportance of benthic organisms in the stomachs of the cod (Popova, 1962; Lilly, MS 1979). Popova (1962) concluded that the food supply on the Flemish Cap was poor. This poor food supply was reflected in the growth rate of cod. Postolakii (1962) reported that the growth rate was lower on the Flemish Cap than on the Grand Bank, and Stanek (MS 1967) found in 1965 that young cod grew as fast as cod on the Grand Bank but that older cod grew more slowly.

Bishop (MS 1977) reported that the growth rate of cod has increased considerably in recent years. The average length-at-age of cod of intermediate ages (5-12 years) is now higher on the Flemish Cap than on the northern and central Grand Bank (Lear *et al.*, MS 1979). This increase in growth rate might have resulted from a decrease in the population size of cod, but data for assessing this possibility are not yet available. Wells (MS 1973) estimated the numbers at each age during each year of the period 1959-68, and S. Gavaris (MS 1979) provided catch per unit effort for the period 1960-77, but information back to about 1950 is required for examination of the change in growth rate shown by Bishop (MS 1977). A second factor which might have affected growth rate is temperature, but, to the author's knowledge, there is no evidence of a significant change in the average temperature on the Flemish Cap during the 1950-75 period. A third factor which might affect growth is a change in the food supply. Templeman (1976) has shown that very successful year-classes of redfish, *Sebastes* sp., in 1959 and 1963 followed at least 17 years without highly successful recruitment. The purpose of this paper is to show that the increase in the growth rate of cod may be due to the improved recruitment of redfish.

Size-selective Predation by Cod on Redfish

An increase in size of redfish prey with increasing body size of cod was found in a sample of cod caught on the Flemish Cap in the winter of 1978 (Lilly, MS 1979). Size-selective predation appears to be of general occurrence in predaceous fish, especially piscivores, and has often been demonstrated in cod (Daan, 1973; Ursin, 1973; Edwards and Bowman, 1979). The importance of prey size as a major determinant of growth rate in predators is well documented (Paloheimo and Dickie, 1966; Hall *et al.*, 1970; Kerr, 1971b; Wankowski and Thorpe, 1979).

The cod sample from the Flemish Cap was too small to define accurately the relationship between prey size and body size, but approximate upper and lower limits may be estimated. The maximum sizes of redfish consumed by cod were 34-36% of the length of the cod. If very large prey are difficult to handle, the optimum prey size, defined as that size which yields maximum net energy per unit of handling time, may be a little smaller than the maximum prey size. Kerr

(1971a) showed that the growth efficiency of fish declines as prey size declines. This suggests that there is a threshold size of prey below which the predator can no longer grow. It is not known if such a critical size exists for cod preying on redfish, but large cod tended not to eat the smallest size-class of redfish (Lilly, MS 1979). Data presented by Parsons (1971) and Kakuda and Matsumoto (1978) show that the minimum prey length taken is roughly 25–50% of the maximum prey length. Thus, as estimate of the minimum size of redfish that will provide good growth for cod is 15% of the cod's length. These values for maximum and minimum size of redfish prey are used to demonstrate the possible influence of successful year-classes of redfish on the growth of cod on the Flemish Cap.

Relationship between year-classes of cod and redfish

There appear to be no growth curves available for individual year-classes of cod and redfish on the

Flemish Cap. A composite growth curve was obtained for cod by using length-at-age for ages 1–4 from research catches in February 1977 (Wells, MS 1977) and length-at-age for ages 5–13 from commercial catches in June 1975 (Bishop, MS 1977). A curve for redfish was obtained by averaging the mean length-at-age for males and females of *Sebastes mentella* from research catches in January–February 1978. The actual values for both curves are not critical, as the curves are merely illustrative.

Growth curves for a single year-class of cod and four year-classes of redfish are shown in Fig. 1. The time scale of this figure does not refer to any specific series of years. The cod year-class was spawned in year 12, and the redfish larvae were released in years 1, 9, 12 and 14. The stippled area represents the size range of redfish on which cod can feed and maintain good growth (i.e. redfish lengths between 15 and 35% of the lengths of cod). The relationship between the
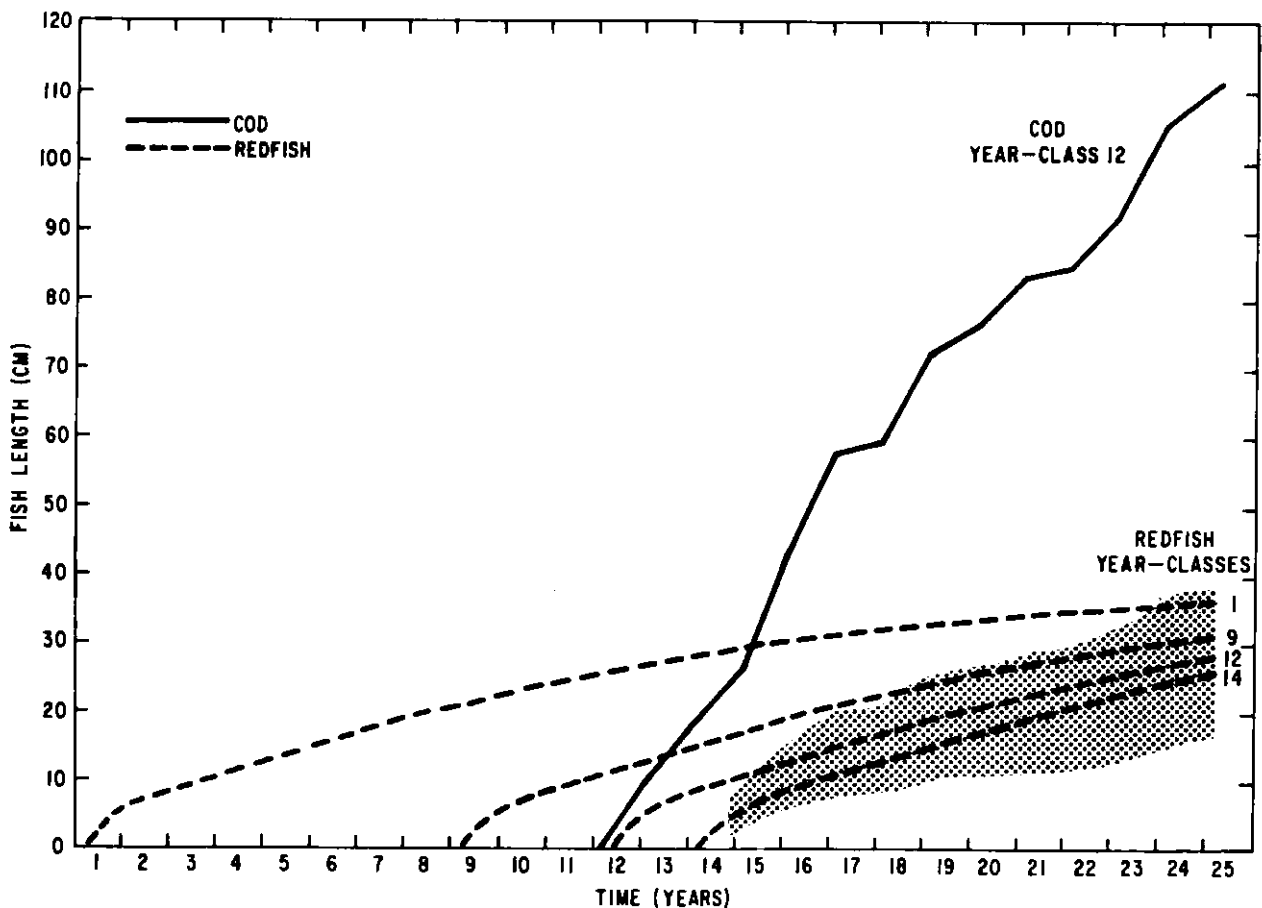
Fig. 1.   Growth curves of one year-class of cod and four year-classes of redfish. The time scale does not refer to any specific series of years. The stippled area is the size spectrum of redfish on which the cod can feed and maintain good growth.

two species during the first three years of the life of the cod is uncertain because of the lack of information on the feeding of juvenile cod and some uncertainty regarding the growth rate of redfish during the first two years of its life. From age 3 or 4 onwards, cod can prey on successively older year-classes of redfish, starting with 1-year-old redfish (year-class 14 in Fig. 1). By the time cod are 12–13 years old, they may be feeding on redfish 11 years older than themselves (year class 1 in Fig. 1). A single successful year-class of redfish from age 1 onwards should provide forage for successively younger year-classes of cod.

The timing of events shown in Fig. 1 is dependent on the growth rates of the various year-classes of redfish and especially on the growth rate of cod. However, from this type of analysis, it should be possible to predict, from knowledge of the abundance and size distribution of redfish, whether a year-class of cod will grow rapidly or slowly.

History of redfish recruitment and predation by cod

The history of redfish recruitment on the Flemish Cap has been reviewed by Templeman (1976). A schematic picture of the lengths of redfish present from 1940 to 1976, adapted from Templeman's review, is given in Fig. 2. It is assumed that redfish of approximately 28–42 cm have been present throughout this period. There is no evidence of a highly successful year-class of redfish for at least 14–18 years prior to 1959. Three small year-classes (1952, 1953 and 1957) preceded the very successful year-class in 1959 or the pair of year-classes in 1959–60. Another pair of highly successful year-classes appeared in 1963–64. Data provided by C. Gavaris (MS 1979) show a further series of successful year-classes centred around 1970.

The pattern of redfish occurrences in cod stomachs matches the above interpretation of size-frequency distributions. Popova (1962) did not
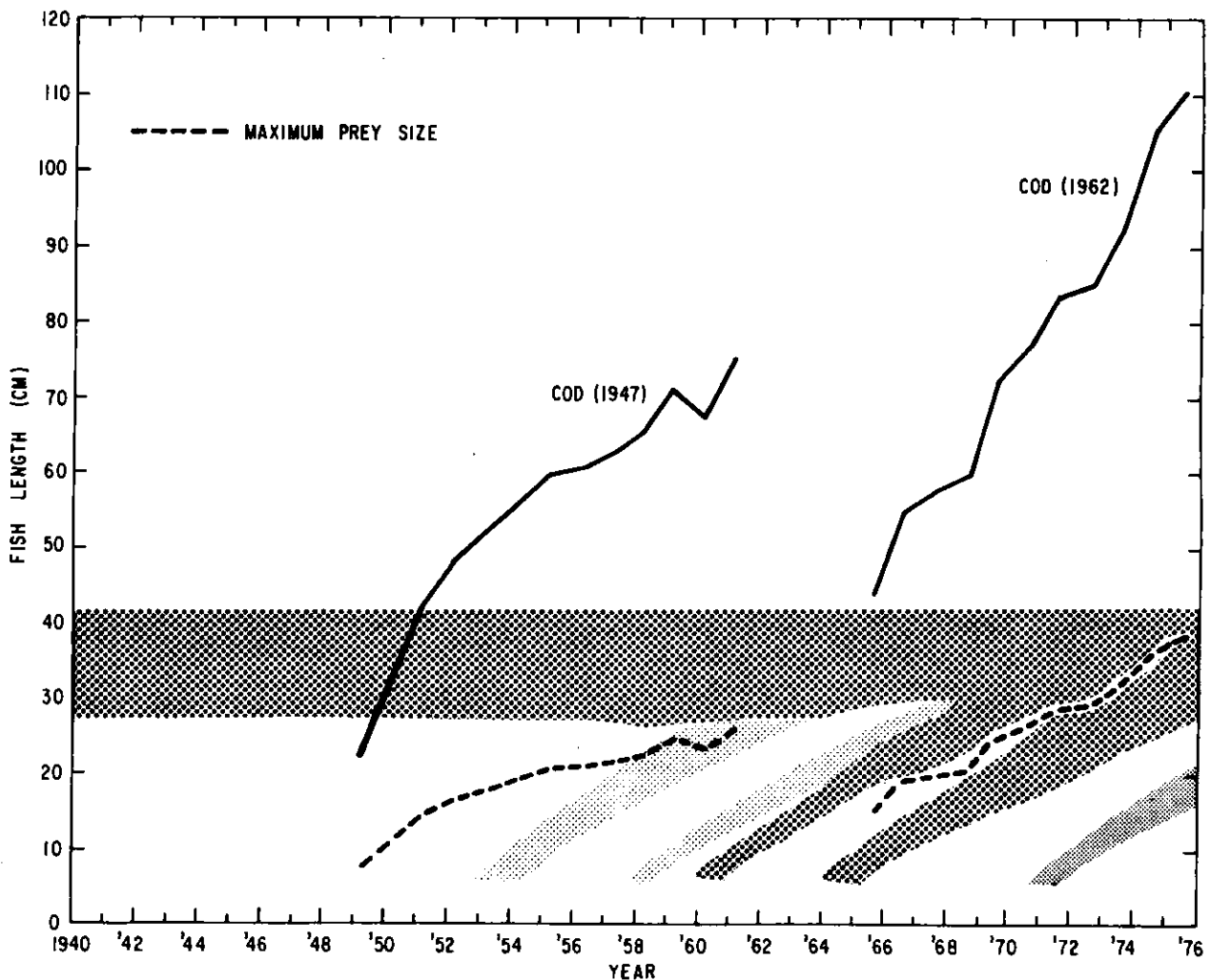
Fig. 2.   Presumed size distribution of redfish on the Flemish Cap, 1940–76, and composite growth curves for cod (solid lines) during two different periods. The broken lines show the maximum size of redfish which the two year-classes of cod could consume.

mention redfish as a significant food of cod in July–August 1959, but did state that redfish fry were more abundant in stomachs in July–August 1960. Kashintsev (1962) found young redfish in stomachs in December 1960, and Templeman (1976) reported small redfish (7.5–12.0 cm) occurring frequently in cod in certain areas of the Flemish Cap in March 1961. All of these reports point to a low level of feeding on redfish immediately prior to the appearance of the 1959–60 year-classes but to intensive feeding on these year-classes by 1961. Templeman (1976) also stated that cod were feeding heavily on small (18 cm) redfish in September 1964. These again would be the 1959–60 year-class group. Turuk (1968) found that cod (35–40 cm in length) were feeding intensively on young redfish in November–December 1964. The size of these redfish was not stated, but it can be assumed from the above discussion of predator-prey lengths that they were no more than 10–11 cm and thus belonged to the large 1963 year-class. It appears that published information on the food of cod on the Flemish Cap is limited to the years 1959–64.

Growth rate of cod

Evidence for an increase in the growth rate of cod over the 1960-75 period was presented by Bishop (MS 1977). Average length-at-age for cod caught by USSR otter trawl, averaged over the 1960–62 period, are plotted in Fig. 2 as though they represent the growth of the 1947 year-class. Similarly, length-at-age from Canadian commercial landings in 1975 are plotted as though they represent the growth of the 1962 year-class. Also plotted are the maximum sizes of redfish which these year-classes of cod could consume, assuming the maximum prey length to be 35% of predator length.

From the early 1940's to the late 1950's there were few juvenile redfish on the Flemish Cap (Fig. 2), so that all year-classes of cod had few prey of near-optimal size. In contrast, redfish less than 28 cm in length have been relatively abundant since 1959. The size distribution of these juvenile redfish varied from year to year, and it is likely that particular size classes of cod feeding on these juveniles varied similarly. However, the probability is high that every year-class of cod since about 1956 or 1957 has been able to prey on juvenile redfish of near optimal size for at least a part of its lifetime and thus has grown faster than cod spawned in the earlier period.

Of particular importance is the presence of redfish of intermediate size (about 15–20 cm). These redfish should enable cod to bridge the large gap in prey size between small crustaceans (hyperiid amphipods and shrimp) and the larger redfish. In the absence of these intermediate-sized redfish, cod may virtually stop

growing at about 60–70 cm. However, it would be expected that some cod would have attained a size sufficient to prey on large redfish and that these individuals would then have grown rapidly and attained a size in excess of 100 cm. In the recent years of rapid growth in cod, the large redfish remain essentially in a size refuge from cod predation, because the fishery removes most cod before they reach 90 cm.

The postulated heavy dependence by cod on juvenile redfish would, of course, be reduced by any large influx of appropriately-sized prey, such as capelin, sand lance, barracudina and lanternfishes. The frequency of occurrence of white barracudina in cod stomachs increases in years when the water on the Flemish Cap is cool (Popova, 1962) and the frequency of occurrence of lanternfishes increases when the water is warmer (Turuk, 1968). There is also one report of cod feeding extensively on younger cod in the shallow part of the bank (Templeman, 1976). A strong year-class of cod could provide an excellent source of food for larger cod, but the juvenile cod grow so rapidly that they would be of value as food for any older year-class of cod for only a short period, perhaps 1 or 2 years.

As mentioned above, at least two major factors other than size of prey may have influenced the growth rate of cod on the Flemish Cap. Both stock size and temperature fluctuate, and any trend toward a lower stock size or higher temperature could have promoted more rapid growth. The relative importance and interaction of these three factors remain to be elucidated.

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Parasitic Fauna of Anarhichadidae and Pleuronectidae Families of Fish in the Northwest Atlantic [1]

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Abstract

The parasitic fauna of two species of wolffish (Anarhichadidae) and four species of flatfish (Pleuronectidae) in the Northwest Atlantic revealed 47 species of parasites of which only seven were common to the two families of fishes. There was evidence of distinction in parasite composition and ecology among closely related fishes, a particular example being the high incidence of the trematode *Fellodistomum fellis*, associated with feeding on the echinoderm *Ophiura sarsi*, in the Atlantic wolffish, *Anarhichas lupus*, and the absence of this parasite in the spotted wolffish, *A. minor*. The parasitic fauna of *A. minor* consisted largely of parasites specific for Anarhichadidae, whereas *A. lupus* had a greater variety of non-specific parasites.

Comparison of the parasitic faunas of the species examined from the Northwest Atlantic with analogous species in the Northeast Atlantic indicates a greater degree of similarity within families from different regions of the North Atlantic than between the two groups of fish inhabiting the same region.

Introduction

Investigation of the parasitic fauna of fishes provides valuable information on the ecological aspects of the species studied, particularly in respect to their feeding behaviour and the role they play in the 'parasite-host' cycle. There is a considerable body of evidence in the literature which indicates that the parasitic faunas of fishes inhabiting the same general areas under various hydrological conditions differ greatly. In this paper, the ecological peculiarities of six species of bottom-dwelling fish of the families Anarhichadidae and Pleuronectidae are considered on the basis of their parasitic faunas.

Materials and Methods

Collections of parasites from two species of wolffish and four species of flatfish were obtained during 1975–78 from different parts of the continental shelf and slope extending from northeastern Newfoundland to Baffin Island (50°00'–63°00'N). Ninety-nine specimens (*Anarhichas lupus* 15, *A. minor* 12, *Reinhardtius hippoglossoides* 20, *Hippoglossus hippoglossus* 10, *Hippoglossoides platessoides* 27, and *Glyptocephalus cynoglossus* 15) were examined by the method of complete parasitological dissection (Dogel, 1933; Bykhovskaya-Pavlovskaya, 1969). Species identification of parasites was made from examination of fresh material and preserved specimens.

Results

In the six host species of fish examined, 47 species of parasites related to seven taxonomic groups were found: Myxosporidia 6, Cestoda 4, Trematoda 24, Nematoda 6, Acanthocephala 2, Hirudinea 1, and Crustacea 4.

Wolffishes (*Anarhichas lupus* and *A. minor*)

Fourteen species of parasites were found in the 15 species of Atlantic wolffishes, *A. lupus*, examined (Table 1). The trematode *Acanthopsolus anarrhichae* was the most common parasite (1,364 specimens in one fish) with infection incidence of 47% and average infection intensity of 180.5 specimens. Next in importance were *Fellodistomum fellis* and *F. agnotum*, with incidences of 67 and 53% and average infection intensities of 22.6 and 11.9 specimens respectively. Some other parasites of significance were *Lepidophyllum steenstrupii* (80% and 6.7 specimens), *Plagioporus idoneus* (40% and 7.9 specimens), and *Platybdella anarhichae* (40% and 1.0 specimens). The rather weak infection of *A. lupus* by nematodes (*Ascarophis morrhuae*, *Capillaris kabatai*, and *Terranova decipiens* l.) is perhaps connected with feeding on decapods (*Pagurus pubescens*, *Eualus gaimardi*, *Hetairus polaris*, *Spirontocaris spinus*, *Pandalus borealis*, and *Sclerocrangon boreas*) (Uspenskaya, 1963). On the other hand, wolffish are very much infected by parasites whose development cycle is connected with benthic organisms. Infection of wolffishes by *A. anarhichae* may be the result of their

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TABLE 1. Parasitic fauna of Atlantic wolffish and spotted wolffish in the Northwest Atlantic.

| Parasite | Atlantic wolffish (15 spec.) | | | | | Spotted wolffish (12 spec.) | | | | |
| | Specimens infected | | Intensity of infection | | | Specimens infected | | Intensity of infection | | |
	No.	%	Min	Max	Mean	No.	%	Min	Max	Mean
Myxosporidia										
Myxidium sphaericum	3	20.0	+	+	+	1	8.3	+	+	+
Cestoda										
Pseudophyllidea gen. sp.	—	—	—	—	—	1	8.3	1	1	0.1
Trematoda										
Acanthopsolus anarhichae	7	46.7	4	1,364	180.5	6	50.0	3	764	88.4
Diphterostomum microacetabulum	—	—	—	—	—	5	41.7	16	5,000	449.3
Fellodistomum agnotum	8	53.3	1	117	11.9	8	66.7	1	82	18.9
Fellodistomum fellis	10	66.7	1	90	22.6	—	—	—	—	—
Genolinea laticauda	1	6.7	1	1	0.1	—	—	—	—	—
Lepidophyllum steenstrupii	12	80.0	1	44	6.7	6	50.0	1	16	2.9
Plagioporus idoneus	6	40.0	1	42	7.9	12	100.0	1	28	9.8
Rodotrema ovacutum	1	6.7	1	1	0.1	—	—	—	—	—
Steganoderma spinosa	—	—	—	—	—	5	41.7	3	183	17.7
Steringophorus furciger	3	20.0	1	19	1.5	1	6.7	2	2	0.2
Nematoda										
Ascarophis morrhuae	1	6.7	1	1	0.1	—	—	—	—	—
Capillaria kabatai	2	13.3	1	2	0.2	—	—	—	—	—
Terranova decipiens l.	1	6.7	2	2	0.1	—	—	—	—	—
Hirudinea										
Platybdella anarhichae	6	40.0	1	8	1.0	4	33.3	1	4	0.8
Crustacea										
Clavellodes rugosa	2	13.3	4	5	0.6	1	6.7	1	1	0.1

feeding on the snails Buccinum undatum (Lebour, 1911, 1918) and B. groenlandicum (Zelikman, 1966), and infection by F. fellis the result of feeding on the sublittoral echinoderm Ophiura sarsi, which is the second intermediate host (Chubrik, 1952, 1966). The development cycle of F. agnotum may also be connected with the same animal group. The first intermediate host of the trematode Steringophorus furciger is a bivalve mollusc Nuculana pernula (Chubrik, 1966), and it is supposed that wolffish become infected by eating N. pernula.

Eleven species of parasites were found in the 12 specimens of spotted wolffish, A. minor, examined (Table 1). The degree of infection by most of the trematodes was quite high, with infection by Diphterostomum microacetabulum reaching 5,000 specimens (average intensity of 449.3 specimens), by Acanthopsolus anarhichae reaching 764 specimens (average 88.4), and by Steganoderma spinosa reaching 183 specimens (average 17.7). Other parasites of significance were Fellodistomum agnotum, Plagioporus idoneus, and Lepidophyllum steenstrupii.

Although eight of the parasites found in the wolffish examined were common to both species (Table 1), the parasitic fauna of Atlantic wolffish and spotted wolffish differed greatly by the absence of F. fellis in A. minor and of D. microacetabulum and S. spinosa in A. lupus. The absence of F. fellis in A. minor is quite surprising in that the second intermediate host (Ophiura sarsi) is found both in coastal waters and at depths to 3,000 m. On the other hand, the high degree of infection of both wolffish species by other trematodes indicates that many animals which serve as intermediate hosts of the parasites form a major part of the diet of wolffishes. It is apparent that both species of wolffish migrate to coastal regions where they become infected by A. anarhichae, whose intermediate host (Buccinum undatum) is only found in depths less than 150 m. The high intensity of infection by this trematode indicates that wolffish feed actively on B. undatum.

Greenland halibut (Reinhardtius hippoglossoides)

Fifteen species of parasites were found in the 20 specimens of Greenland halibut examined (Table 2). Six of the parasites (Hatschekia hippoglossi and five

TABLE 2. Parasitic fauna of Greenland halibut, Atlantic halibut, American plaice, and witch flounder in the Northwest Atlantic.

Parasite	Greenland halibut (20 spec.) Specimens infected No.	%	Intensity of infection Min	Max	Mean	Atlantic halibut (10 spec.) Specimens infected No.	%	Intensity of infection Min	Max	Mean	American plaice (27 spec.) Specimens infected No.	%	Intensity of infection Min	Max	Mean	Witch flounder (15 spec.) Specimens infected No.	%	Intensity of infection Min	Max	Mean
Myxosporidia																				
Ceratomyxa drepanopsettae	15	75.0	+	+	+	6	60.0	+	+	+	17	63.0	+	+	+	7	46.7	+	+	+
Ceratomyxa ramosa	1	5.0	+	+	+	1	10.0	+	+	+	—	—	—	—	—	—	—	—	—	—
Leptotheca sp.	—	—	—	—	—	1	10.0	+	+	+	—	—	—	—	—	—	—	—	—	—
Myxidium sphaericum	2	10.0	+	+	+	2	20.0	+	+	+	12	44.4	+	+	+	2	13.3	+	+	+
Myxoproteus sp.	7	35.0	+	+	+	—	—	—	—	—	4	14.8	+	+	+	—	—	—	—	—
Ortholinea divergens	5	25.0	+	+	+	—	—	—	—	—	2	7.4	+	+	+	—	—	—	—	—
Cestoda																				
Grillotia erinaceus l.	1	5.0	2	2	0.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phyllobothrium tridax l.	1	5.0	1	1	0.1	1	10.0	1	1	0.1	—	—	—	—	—	—	—	—	—	—
Scolex pleuronectis l	13	65.0	1	37	8.0	7	70.0	4	37	12.6	10	37.0	1	29	3.6	3	20.0	2	4	0.5
Trematoda																				
Aporocotyle simplex	—	—	—	—	—	—	—	—	—	—	3	11.1	1	1	0.1	1	6.7	1	1	0.1
Brachyphallus crenatus	—	—	—	—	—	—	—	—	—	—	1	3.7	1	1	+	—	—	—	—	—
Derogenes crassus	—	—	—	—	—	2	20.0	2	2	0.2	—	—	—	—	—	—	—	—	—	—
Derogenes varicus	14	70.0	1	23	4.7	9	90.0	2	23	9.1	5	18.5	1	2	0.2	4	26.7	1	3	0.5
Genolinea laticauda	—	—	—	—	—	—	—	—	—	—	2	7.4	1	3	0.2	5	33.3	1	2	0.5
Gonocerca phycidis	—	—	—	—	—	4	40.0	1	1	0.4	—	—	—	—	—	—	—	—	—	—
Hemiurus levinseni	—	—	—	—	—	2	20.0	1	4	0.5	—	—	—	—	—	—	—	—	—	—
Lecithaster confusus	—	—	—	—	—	1	10.0	1	1	0.1	—	—	—	—	—	—	—	—	—	—
Lecithaster gibbosus	7	35.0	1	16	1.6	1	10.0	1	1	0.1	6	22.2	1	2	0.3	—	—	—	—	—
Podocotyle reflexa	—	—	—	—	—	1	10.0	1	1	0.1	—	—	—	—	—	—	—	—	—	—
Rodotrema ovacutum	—	—	—	—	—	—	—	—	—	—	12	44.4	1	84	6.9	—	—	—	—	—
Steganoderma formosum	—	—	—	—	—	2	20.0	1	2	0.3	—	—	—	—	—	—	—	—	—	—
Stenakron vetustum	—	—	—	—	—	4	40.0	1	13	2.2	1	3.7	1	1	+	10	66.7	1	20	4.5
Stephanochasmus baccatus	—	—	—	—	—	4	40.0	2	8	1.8	—	—	—	—	—	—	—	—	—	—
Steringophorus furciger	6	30.0	1	10	1.1	1	10.0	1	1	0.1	14	51.9	1	136	10.5	2	13.3	8	45	3.5
Zoogonoides viviparus	—	—	—	—	—	—	—	—	—	—	3	11.1	1	5	0.4	—	—	—	—	—
Trematoda gen. sp.	—	—	—	—	—	—	—	—	—	—	1	3.7	18	18	0.7	—	—	—	—	—
Nematoda																				
Anisakis sp. l.	5	25.0	1	3	0.4	1	10.0	1	1	0.1	7	25.9	1	5	0.5	1	6.7	3	3	0.2
Ascarophis morrhuae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	6.7	1	1	0.1
Capillaria kabatai	—	—	—	—	—	1	10.0	1	1	0.1	3	11.1	2	4	0.3	—	—	—	—	—
Contracaecum aduncum	11	55.0	1	5	1.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Contracaecum aduncum l.	4	20.0	1	2	0.3	5	50.0	1	2	0.6	12	44.4	1	87	4.4	1	6.7	2	2	0.1
Terranova decipiens l.	—	—	—	—	—	—	—	—	—	—	2	7.4	1	1	0.1	—	—	—	—	—
Nematoda gen. sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	6.7	1	1	0.1
Acanthocephala																				
Corynosoma strumosum	2	10.0	1	1	0.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Echinorhynchus gadi	—	—	—	—	—	6	60.0	1	35	4.9	12	44.4	3	42	4.0	6	40.0	1	24	2.8
Crustacea																				
Acanthochondria cornuta	—	—	—	—	—	—	—	—	—	—	8	29.6	1	1	0.3	—	—	—	—	—
Hatschekia hippoglossi	1	5.0	3	3	0.2	5	50.0	1	5	1.5	—	—	—	—	—	—	—	—	—	—
Lepeophtheirus hippoglossi	—	—	—	—	—	1	10.0	2	2	0.2	—	—	—	—	—	—	—	—	—	—

species of *Myxosporidia*) have a direct development cycle. Qualitatively, Myxosporidia was represented by five species, Cestoda and Trematoda by three species each, and Nematoda by two species. Quantitatively, the incidence of infection was high for *Ceratomyxa drepanopsettae* (75%), *Contracaecum aduncum* (55%), *Scolex pleuronectis* (65%), and *Derogenes varicus* (70%), with average infection intensities by the last two being 8.0 and 4.7 specimens respectively. Among the parasites found in Greenland halibut, those typically found in flounders include *Ortholinea divergens*, *C. drepanopsettae*, *C. ramosa*, and *Steringophorus furciger*, and those characteristic of Atlantic halibut include *Myxoproteus* sp. and *Hatschekia hippoglossi*, the remainder being relatively common to many fish species.

Nine of the 15 parasites found in Greenland halibut have a complex development cycle. These include *Derogenes varicus*, *Contracaecum aduncum*, and *Anisakis* sp. l., whose intermediate hosts are planktonic copepods, euphausiids, coelenterates, and chaetognaths (Daves, 1959; Lebour, 1918, 1935; Dollfus, 1923, 1927; Dollfus et al., 1954; Wülker, 1930; Markowsky, 1937; Myers, 1956; Hanumantha-Rao, 1958; Anantharaman, 1959; Uspenskaya, 1963; Zelikman, 1966; Smith, 1971), and also benthic amphipods, decapods, and molluscs (Wülker, 1930; Uspenskaya, 1963; Shiraki et al., 1976). Infection of Greenland halibut by *Steringophorus furciger*, *Corynosoma strumosum* and *Contracaecum aduncum* probably occurs from feeding on benthos (*Gammarus* sp., and bivalve molluscs) (Zelikman, 1966; Chubrik,

1966) and fishes. According to Konstantinov (1976), decapods and fish form a major part of the diet of Greenland halibut, and this probably accounts for the high degree of infection by *D. varicus, C. aduncum* and *Anisakis* sp. I. It is possible that infection of Greenland halibut by *Scolex pleuronectis* I. and *Lecithaster gibbosus*, whose development cycles is connected with plankton, results from eating small fish which became infected by feeding on plankton. This, of course, does not exclude the possibility of incidental infection by some of these parasites through the swallowing of plankton with other food components. Although five of the six species of Myxosporidia were found in Greenland halibut, the parasitic fauna lacks many species, especially trematodes, which are typically found in flounders.

Atlantic halibut (*Hippoglossus hippoglossus*)

The parasitic fauna of Atlantic halibut is considerably richer than that of Greenland halibut, in that 23 species of parasites were found in 10 specimens of Atlantic halibut examined (Table 2). Of the six species with a direct development cycle (*Hatschekia hippoglossi, Lepeophteirus hippoglossi,* and four species of Myxosporidia), the incidence of infection was relatively high for *Ceratomyxa drepanopsettae* (60%) and *H. hippoglossi* (50%). Among the remaining parasites with a complex development cycle, the incidence of infection by *Scolex pleuronectis* I. (70%), *Derogenes varicus* (90%), *Echinorhynchus gadi* (60%) and *Contracaecum aduncum* (50%) stand out. The parasitic fauna of Atlantic halibut differs from that of Greenland halibut by the greater number of trematodes in the former (11 *versus* 3 species). The development cycle of most of them (*Podocotyle reflexa, Steganoderma formosum, Stenakron vetustum, Steringophorus furciger, Stephanochasmus baccatus, D. varicus, Gonocerca phycidis*) is connected with benthic molluscs, amphipods and decapods (Zelikman, 1966; Chubrik, 1966; Uspenskaya, 1963), which result in infection upon being eaten by Atlantic halibut. Infection by *Anisakis* sp. I. and *E. gadi* is also connected with eating amphipods and decapods (Uspenskaya, 1963; Shiraki *et al.*, 1976, Shulman and Shulman-Albowa, 1953). Fish species seem to play a lesser role in the diet of Atlantic halibut than the intermediate hosts noted above, as evidenced from the slight infection by *Lecithaster gibbosus* and *L. confusus,* whose intermediate hosts are planktonic copepods. It is possible that Atlantic halibut eat such pelagic animals as medusae, ctenophores, chaetognaths and cephalopods, which are the intermediate hosts of *Hemiurus levinseni, Derogenes varicus* and *Contracaecum aduncum* (Lebour, 1918, 1935; Dollfus, 1923, 1927; Anantharaman, 1959; Wülker, 1930; Myers, 1956; Markowsky, 1937; Hanumantha-Rao, 1958; Daves,

1959; Uspenskaya, 1963; Zelikman, 1966), but the infection of Atlantic halibut by these parasites may also result from feeding on certain fish species which are the hosts for these parasites.

American plaice (*Hippoglossoides platessoides*)

The parasitic fauna of American plaice, also commonly known as long rough dab, consisted of 21 species (Table 2). Parasites having a direct development cycle are represented by five species (*Acanthochondria cornuta* and four species of Myxosporidia). The incidence of infection was especially high for *Ceratomyxa drepanopsettae* (63%), *Myxidium sphaericum* (44%), *Rodotrema ovacutum* (44%), *Steringophorus furciger* (52%), *Contracaecum aduncum* I. (44%) and *Echinorhynchus gadi* (44%). The average intensity of infection was also relatively high for some of these parasites: *S. furciger* (10.5 specimens), *R. ovacutum* (6.9), *C. aduncum* I. (4.4) and *E. gadi* (4.0). According to the composition of parasites, benthic animals form a major part of the food of American plaice. Such animals include gastropod and bivalve molluscs, which are intermediate hosts of *R. ovacutum, Stenakron vetustum, Zoogonoides viviparus* and *S. furciger* (Chubrik, 1966; Zelikman, 1966), and also amphipods and decapods, with which the development cycle of *Derogenes varicus, C. aduncum* I., *Terranova decipiens* I., *Anisakis* sp. I., and *E. gadi* is connected (Shulman and Shulman-Albowa, 1953; Uspenskaya, 1963; Shiraki *et al.*, 1976). The development cycle of *Scolex pleuronectis* I., *Lecithaster gibbosdus* and also the above-mentioned *D. varicus, C. aduncum* I. and *Anisakis* sp. I. is connected with planktonic organisms, which seem to occur in the food of flounders. These observations agree with Pitt's (1973) data on feeding of American plaice on the Grand Bank. American plaice is a typical bottom-feeding fish, which probably accounts for the great variety of, and relatively high infection by, trematodes as well as the rather high infection by Myxosporidia.

Witch flounder (*Glyptocephalus cynoglossus*)

In contrast to the composition of the parasitic fauna of the three flatfish species noted above, only 13 species of parasites were found in the 15 specimens of witch flounder examined (Table 2). The highest incidences of infection were recorded for *Ceratomyxa drepanopsettae* (47%), *Stenakron vetustum* (67%) and *Echinorhynchus gadi* (40%), with infection intensities of 4.5 and 2.8 for the last two species respectively. Witch flounder presumably become infected by *S. vetustum* and *E. gadi* from eating amphipods and gastropods, which are the intermediate hosts of these parasites and perhaps serve as the main components in the diet of witch flounder. Decapods and plankton do not seem to be very important in the diet of this

flounder, as indicated by finding only single specimens of Scolex pleuronectis l., Derogenes varicus, Contracaecum aduncum l, Anisakis sp. l., and Ascarophis morrhuae.

Discussion

Comparison of the parasitic faunas of the two groups of typical bottom fishes of the families Anarhichadidae and Pleuronectidae (Tables 1 and 2) indicates that only seven species were common to both groups (Genolinea laticauda, Rodotrema ovacutum, Steringophorus furciger, Myxidium sphaericum, Capillaria kabatai, Ascarophis morrhuae, and Terranova decipiens). The first three are specific flounder parasites, the next three are characteristic parasites of Gadidae, and the last is generally found in a wide variety of fishes. The relatively low degree of infection by these common parasites and the diversity of the remaining parasitic fauna of the wolffishes and flatfishes, despite some common food components and similarity of living conditions, indicate that the ecology of these groups of fishes differ greatly. This suggests that most of the parasites of the species concerned are rather specific to the two groups of fishes, although such parasites as Scolex pleuronectis l., Derogenes varicus, Lecithaster gibbosus and Contracaecum aduncum, which were found in flatfishes, are generally present in a wide variety of fishes.

There are signs of distinction in parasite composition and ecology even among closely related fishes. For example, the absence of Fellodistomum fellis in spotted wolffish is indicative of the absence of Ophiura sarsi, the intermediate host of F. fellis, in their food, whereas O. sarsi is a major component of the food of Atlantic wolffish. Parasitic fauna of spotted wolffish consisted almost entirely of parasites for Anarhichadidae, except for M. sphaericum and S. furciger which are peculiar to cod and flounder, whereas Atlantic wolffish had more non-specific parasites (M. sphaericum, R. ovacutum, S. furciger, G. laticauda, T. decipiens, C. kabatai, and A. morrhuae) which suggests that they eat a greater variety of food organisms.

There are even more signs of distinction in parasite composition and consequently in the ecology of the flatfishes. The parasitic fauna of a typical predator (Greenland halibut) is characterized by a small number of trematodes and high infection by parasites acquired by eating various species of fish. The other three flatfish species are characterized by a greater variety of trematodes which indicates that benthic animals form a major part of their diet. However, the greater number of non-specific parasites in American plaice and Atlantic halibut than in witch

flounder indicates that the trophic relationships of the first two species are wider and that their activity in searching for food is greater than for witch flounder. The slight degree of infection of Atlantic halibut by S. furciger and the absence of R. ovacutum indicate that molluscs, the main food component of American plaice and witch flounder, are not important in the diet of Atlantic halibut.

Comparison of the parasitic faunas of the species examined from the Northwest Atlantic with the same species from the Barents and White Seas presents an interesting picture. Polyansky (1955) noted 21 species of parasites (we have 17) in two wolffish species from the White Sea, 11 of which were found in Northwest Atlantic wolffish. This extent of similarity is very high, considering that only those species characteristic for wolffishes were included in the list of common parasites, even though some of the species not included, because they were considered peculiar to other fishes, could possibly be characteristic for wolffishes. Shulman and Shulman-Albowa (1953) also found 21 species of parasites in White Sea catfishes, of which seven were common to the parasitic fauna of wolffishes in the Northwest Atlantic, but in this case also the majority of the species excluded from the list were considered to be more peculiar to other species of fish examined.

Parasitic fauna of the flatfish species is also characterized by quite a number of species common to the Northwest and Northeast Atlantic. Of the 18 species of parasites found to be peculiar to the Atlantic halibut in the Barents Sea (Polyansky, 1955), 13 of them were found in Atlantic halibut of the Northwest Atlantic, and, of the 16 parasites noted by the same author in the long rough dab (American plaice), 12 appeared to be common. Thus, despite the great extent of geographic separation, the similarity of the parasitic faunas of wolffishes in one case and flatfishes in the other case from different regions of the North Atlantic is much greater than for the two groups of fish inhabiting the same region.

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Results of USSR Oceanographic Observations on Flemish Cap, 1977-78[1]

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Abstract

The analysis of geostrophic circulation charts based on hydrological data from seven surveys by USSR research vessels from December 1977 to July 1978 confirmed the existence of a quasi-stationary water circulation system in the Flemish Cap area, the main element of which is the anticyclonic gyre over the central part of the bank, composed predominantly of mixed water from the Flemish Cap Current. Variation in the intensity or horizontal and vertical water movements within the gyre was observed, and the most probable factors causing this variability are discussed, with particular reference to its influence on the ichthyofauna of the area.

Introduction

At a meeting of the ICNAF Environmental Working Group in Murmansk, USSR, in May 1977, attended by representatives from Canada, Poland, USA and USSR, a coordinated international research program was developed with a view to elucidating the influence of biotic and abiotic factors on reproduction and year-class success of the major commercial fish stocks on Flemish Cap (ICNAF Division 3M). The program was approved by the Standing Committee on Research and Statistics at the 1977 Annual Meeting and recommended for execution by member countries (ICNAF, 1977). The Polar Research Institute of Marine Fisheries and Oceanography (PINRO) began to make oceanological observations according to the program late in 1977, with emphasis on studying the peculiarities of horizontal water circulation in the area. Before elaborating on the results of the investigations carried out in 1977 and 1978, it seems appropriate to provide some background information on previous studies of the current system in the Flemish Cap area.

On the basis of observations from the *Scotia* Expedition in 1913 (Matthews, 1914), it was shown that the Labrador Current, near the northern extremity of the Grand Bank, divided into three branches, one flowing southwestward in the Avalon Channel off southeastern Newfoundland, another flowing southward along the eastern slope of the Grand Bank, and the third flowing eastward along the northern slope of Flemish Cap. Systematic observations by the US Coast Guard during International Ice Patrol activities provided the opportunity for further elucidation of the currents surrounding Flemish Cap, and at an early stage it was shown that the water off the southern slope of the bank was of North Atlantic Current origin (Smith *et al.*, 1937).

The rapid development of the fishery on Flemish Cap in the 1950's was accompanied by increased interest in the oceanological regime of the area, and a substantial amount of information on current patterns was obtained from the analyses of data from USSR investigations of 1958–60 (Elizarov and Prokhorov, 1958; Buzdalin and Elizarov, 1962). From these studies, the eastern branch of the Labrador Current transporting water of relatively low temperature and salinity was observed over the northern and eastern slopes of Flemish Cap. Elizarov and Prokhorov (1958) called this current the Flemish Cap Current, the name used in this paper when referring to the eastern branch of the Labrador Current. The Flemish Cap Current merges with the warmer and relatively high saline water of the North Atlantic Current over the southeastern slope of Flemish Cap and flows in a northeasterly direction away from the bank. It was also shown that an anticyclonic gyre which is in direct contact with the Flemish Cap Current exists in the central shallow area of the bank.

The main elements of the current field in the Flemish Cap area were repeatedly indicated from the results of subsequent PINRO investigations (Kudlo and Burmakin, 1972; Kudlo and Borovkov, MS 1975; Kudlo *et al.*, MS 1976; Kudlo and Boytsov, MS 1977), and it was supposed that the current system over the bank, which formed the basis of hypotheses concerning the causes of fluctuations in the strength of cod year-classes on Flemish Cap, was of quasi-stationary character (Kudlo and Borovkov, 1977; Kudlo and Boytsov, 1979). They hypothesized that the size of

cod year-classes depends mainly on the dynamic state of the anticyclonic gyre in the early stages of cod ontogenesis, with strong year-classes occurring in years of strengthened water circulation and vice versa. Variation in gyre intensity causes changes in water convergence over the central part of the bank, which in turn influences the retention on the bank of the pelagic eggs, larvae and fry, together with phytoplankton and zooplankton. The provision of an adequate food supply for the larvae and fry over the shallow part of the bank is probably the most important factor that controls directly the strength of cod year-classes in the Flemish Cap area.

Further consideration of the hypotheses relating year-class abundance of the major species to water circulation requires more detailed study of the oceanography of the area. The main purpose of the investigations reported in this paper was to determine the nature of the water masses contributing to the circulation pattern with some indication of the variability associated with the main elements of the system.

Materials and Methods

Existing views on horizontal water circulation in the Flemish Cap area were formed on the basis of analysis of dynamic topography fields. Available data from direct instrumental measurements of currents over the bank (Hill et al., 1975) were insufficient to confirm or disprove these views, and, in any case, the conducting of continuous measurements of currents over a large area is a very time-consuming and complex operation. Consequently, the most tested and practical indirect method of current determination, namely the dynamic method, was used in the present study.

The materials used for analysis of water circulation were temperature and salinity measurements from about 300 hydrographic stations in the Flemish Cap area during cruises 16 and 17 of the Protsion and cruise 20 of the Persey III from December 1977 to July 1978. During cruise 16 of the Protsion, four bathymetric surveys were carried out. The first two surveys (6-26 December 1977 and 12-22 January 1978) were of a reconnoitring character and were mainly conducted on two perpendicular sections across the bank, one at 47°N latitude and the other at 45°W longitude. The next two surveys (3-12 February and 20-27 February 1978) were undertaken in an area bounded by 46°20' and 48°20'N and by 44°00' and 46°30'W longitude, consisting of a grid of stations at intervals of 20' latitude and 30' longitude. The grid of stations was again surveyed twice during cruise 17 of

the Protsion (24 May-2 June and 17-29 July 1978) and also in part during cruise 20 of the Persey III (26 July-1August 1978).

Data from the above-mentioned surveys were used to construct a series of charts of dynamic sea surface topography relative to the 200 decibar level taking into account the long-term experience which showed that this level was reasonable to use in studying currents over shallow bank areas. In addition, estimates of current velocities at the surface and at 100 m were made by the method suggested by Belyayeva (1964). According to this method, the components of current velocities were estimated by assuming no movement near the bottom. Dynamic heights of stations taken in pairs were brought to the same level by Somov's method (Zubov and Mamayev, 1956). The components of current velocities for points within the grid area were calculated by the three-point method, for points at the corners of the grid by the two-point method and for the remainder of the stations in contour by the complex method. The resulting vectors of current velocity enabled the compilation of charts of geostrophic currents for different depths and time periods.

Results and Discussion

Such well-known elements of circulation as the Flemish Cap Current, which flows around the northwest, north and northeast slopes, and the North Atlantic Current, which flows over the southern slope of the bank, are clearly indicated in Fig. 1 and 2. Although the velocities, directions and locations of the main currents vary considerably in space and time, there seems to be no doubt about the constancy of their presence in the Flemish Cap area.

Another distinct feature of the current pattern on Flemish Cap from the dynamic topography charts is the anticyclonic gyre, which was usually located over the central part of the bank and appeared to vary in intensity during the course of the winter surveys. The circulation field in December 1977 (Fig. 1) is characterized by a well-developed gyre, which declined in intensity in January, disappeared in early February and showed signs of developing again in late February. Thus, over the 3-month period of the four surveys, the gyre was evident over the central part of the bank for all but a period of about 2 weeks in early February. The course of development of the gyre during the spring and summer of 1978 is difficult to determine due to the irregularity of observations. However, it is evident from Fig. 2 that the anticyclonic current field existed during all three summer surveys
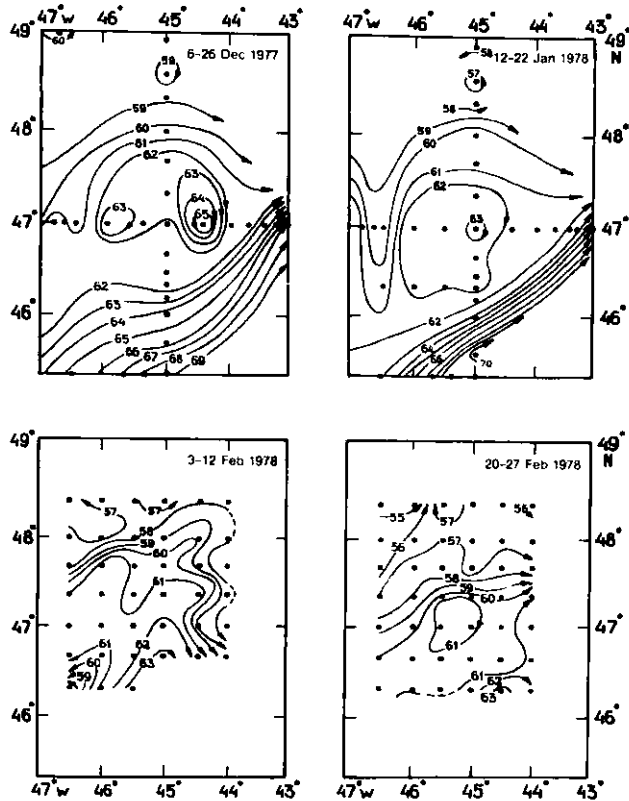
Fig. 1.   Dynmaic topography of the sea surface relative to the 200 dbar level in the Flemish Cap in the winter of 1977/78. (Dynamic heights are given in dyn. cm.)
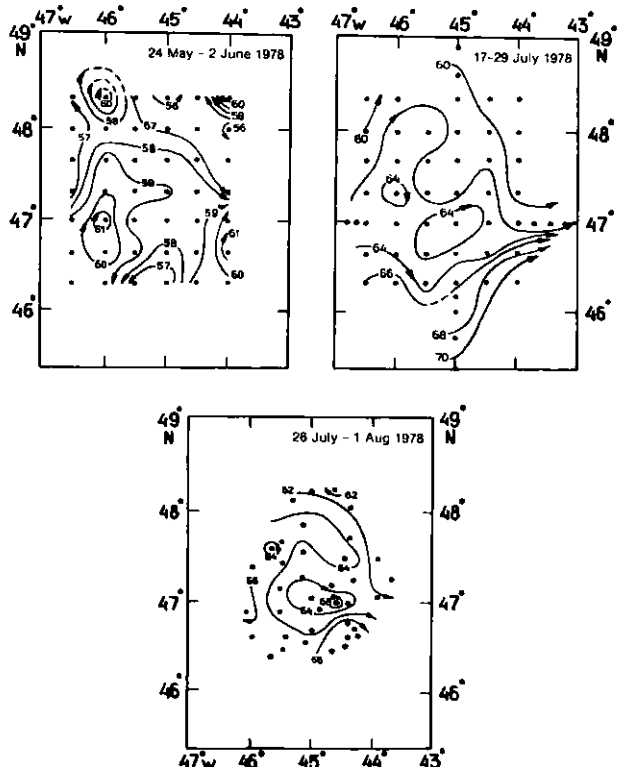

Fig. 2.   Dynamic topography of the sea surface relative to the 200 dbar level in the Flemish Cap area in the summer of 1978. (Dynamic heights are given in dyn. cm.)

with only slight changes in its position from late May to late July. Therefore, on the basis of the analyses presented in Fig. 1 and 2, and taking into account the results of previous analyses of geostrophic circulation over the bank as noted in the Introduction, it is reasonable to conclude that the main current system in the Flemish Cap is quasi-stationary (i.e. it exists almost constantly in the area).

Data from the two grid surveys in February 1978 enabled an analysis of the vertical structure of the currents over the bank through the estimation of current vectors at the surface and at 100 m (Fig. 3). In nearly every situation, current direction is the same at the surface and at 100 m, and, in general, the current velocity at 100 m is less than that at the surface. This regularity was not only characteristic of the upper 100-m layer but was also evident from analyses of the circulation fields at greater depths. It appears, therefore, that the main elements of circulation over the bank, including the anticyclonic gyre, are distributed from the surface to the bottom and are influenced by the bottom topography of the area, an important consideration that is discussed later.

To qualitatively verify conformity of the geostrophic circulation to the current system, the matter of the origin and distribution of water masses in
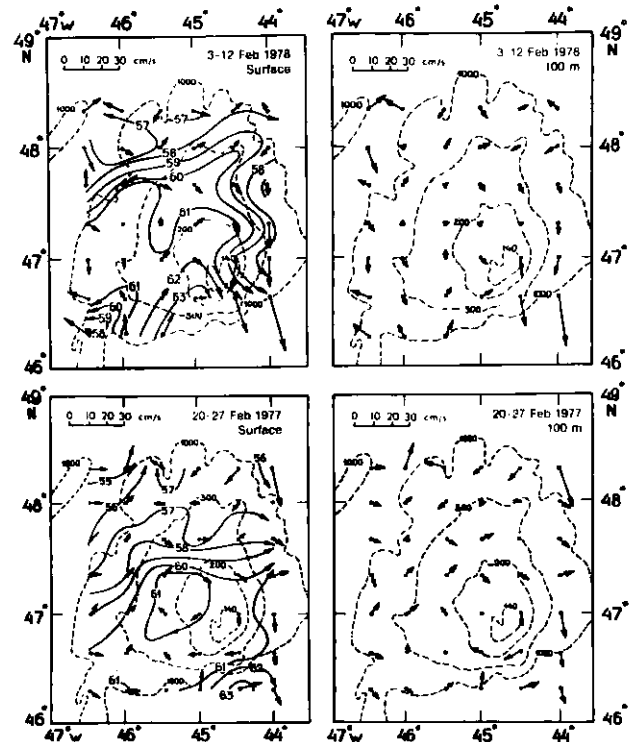
Fig. 3.   Geostrophic water circulation over the Flemish Cap in February 1978. (Vectors indicate direction and velocity of currents calculated from near-bottom depths. Solid lines on the surface diagrams represent dynamic heights (dyn. cm) of the surface relative to the 200 d bar level. Depth contours in meters.)

the area surveyed is considered from Fig. 4, which shows the mean temperature and salinity distribution in the upper quasi-homogeneous 100-m layer based on observations from the two surveys in February 1978. Water temperature from 3.0° to 4.5°C and salinities from 34.1 to 34.3‰ prevailed over the bank during the period, and warmer, more saline water was observed over the southeast slope. According to its thermohaline characteristics, the water mass on the bank resulted from a mixture of Arctic and North Atlantic water, but the contribution of each to the mixture varied over different parts of the bank. Arctic water prevailed in the mixture over the greatest part of the bank, with Atlantic water being the main component only over the southeastern slope. These results are consistent with views about the horizontal water movements in the area, based on the analysis of geostrophic current patterns.

As noted above, the gyre is formed mostly of mixed water of the eastern branch of the Labrador Current which flows around the northern slopes of the bank as the Flemish Cap Current, and it is unlikely that the water mass within the gyre is affected by outside masses of less dense water. It is also unlikely that the water mass is influenced by meteorological factors which result in raising the temperature or making the

water less saline, because the spatial scale of the effects produced by them is not comparable with the scale of the anticyclonic gyre, the maximum horizontal diameter of the latter being only 150–180 km. Therefore, it is believed that the negative anomaly of water density in the central part of the gyre is the result of pure dynamic factors, namely the convergence of currents which results in the sinking of the upper, less dense water. The distinctive flexure of the isohalines seen in Fig. 5 provides qualitative evidence of the presence of descending water movement within the gyre.

The results of the investigations carried out in 1977/78 confirm earlier suppositions about the existence of the quasi-stationary anticyclonic gyre over the Flemish Cap, with a zone of sinking water in its center. From a scientific point of view, it is interesting to explore the reasons for the existence and changeability of the gyre. All synoptic oceanic eddies reported in the literature (see Anon, 1978, for summary), analogous to the Flemish Cap gyre by
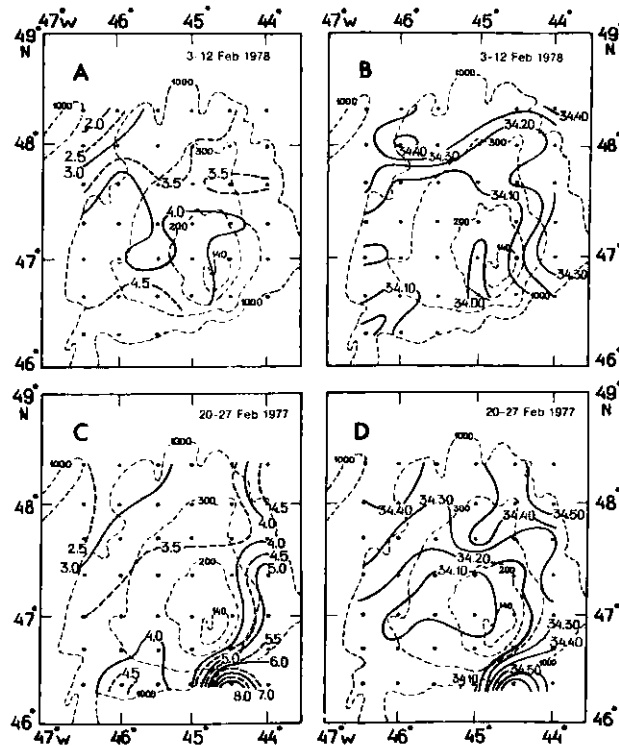

Fig. 4. · Horizontal distribution of mean temperature (a,c) and mean salinity (b,d) in the upper 100 m layer over the Flemish Cap in February 1978. (Isotherms are in °C, isohalines in °/oo, and depth contours in m.)
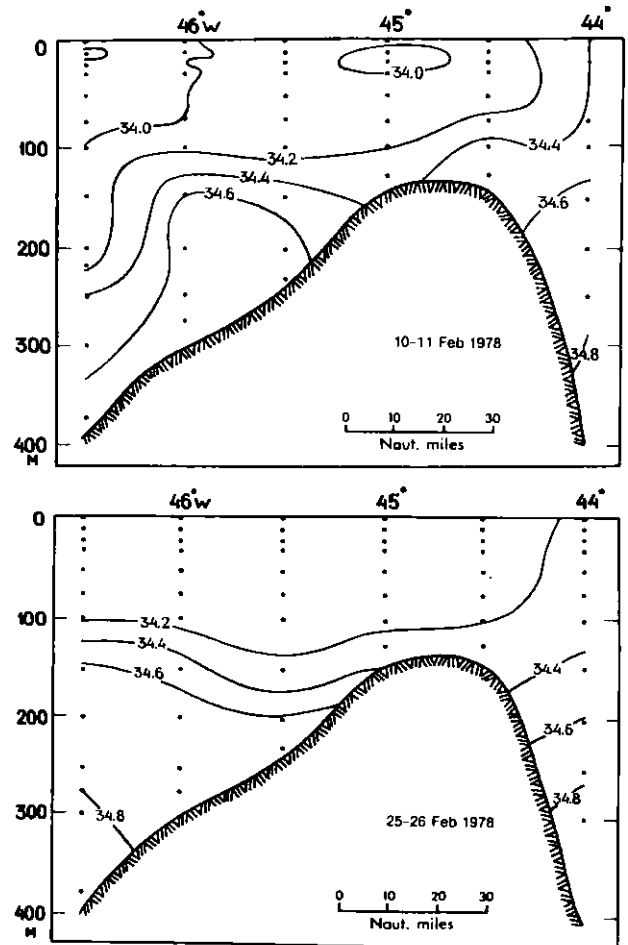

Fig. 5.   Vertical distribution of salinity along the 47°N section during two surveys in February 1978. (Isohalines are in °/oo .)

several features (rotatory movement, horizontal and vertical dimensions), differ radically from it by their spatial movements over great distances. The quasi-stationary nature of the Flemish Cap gyre suggests the existence of a powerful factor which tends to stabilize the water circulation over the bank. It is possible that the morphological features of the bank itself may be the factor which influences the flow of the Flemish Cap Current, resulting in the peculiar pattern of water circulation over the bank.

The observed temporal variation in the dimension, form and intensity of the gyre indicates that the influence of bottom configuration on the flow of the Flemish Cap Current is not constant. This inconsistency may be related to variation in intensity of the Flemish Cap Current and deviation from its normal flow path, the occasional weakening and disappearance of the gyre being due to a decrease in velocity of the current or the moving away of the current from the bank periphery. Sarkisyan (1977) indicated that the influence of bottom topography on currents in the upper layers of the ocean decreases with increasing distance from the surface to the bottom.

A major factor in the periodic destruction of the gyre may be its interaction with one or more successive atmospheric disturbances (cyclones) passing over the bank area. Examination of daily weather charts for the winter of 1978 showed that the most frequent occurrence of cyclones over the bank (31 January, 5 and 9 February) coincided with the apparent disappearance of the gyre over the central part of the bank in early February, as shown in Fig. 1. In this connection, variation in the circulation pattern on the bank, particularly the changes in the anticyclonic gyre, is likely to be greater in the autumn-winter period, when atmospheric disturbances are more frequent and have a greater effect on surface currents, than in summer when the disturbances are weaker and less frequent.

Seasonal variation in the intensity of the anticyclonic gyre of the Flemish Cap may be the reason for the pronounced anomaly in the composition of the ichthyofauna in the area. Capelin and sand lance, which together predominate in abundance among the commercial fish species on the adjacent Grand Bank, are seldom found on the Flemish Cap. In fact, the only species of major commercial importance on Flemish Cap are cod and redfish, and the existence of these populations indicates the availability of favorable environmental conditions for the development of the pelagic eggs, larvae and fry during the period from spawning in the spring to the settling of the juveniles on or near the bottom in late autumn.

Survival of young during this critical phase depends on their accumulation in the zone of converging currents, which acts as a hydrodynamic trap in retaining the larvae over the bank area. This suggests that the anticyclonic gyre exists almost constantly, disappearing perhaps only for very short intervals. Since capelin and sand lance tend to spawn later in the season and the juveniles are pelagically-oriented for a longer period, the almost complete absence of these species on Flemish Cap is probably a consequence of the instability of the anticyclonic gyre in winter, thus preventing the establishment of large resident populations.

The role of water circulation on Flemish Cap as a regulating factor in determining year-class of cod and redfish is a very complex one, since it affects not only the distribution of adults during spawning in the spring but also the distribution of young for several months during the early pelagic phase of their life and the distribution and abundance of food organisms. It is common knowledge that definite distinctions exist in the location and size of the areas where cod and redfish spawn, and the influence of the anticyclonic gyre, depending on its size and intensity and its location over the bank, on the distribution and abundance of cod and redfish would not be expected to be the same. This might be a possible explanation for the lack of coincidence of the peak years of relative abundance of cod (1958 and 1962) and redfish (1959 and 1963) year-classes, as indicated by Templeman (1976).

In conclusion, the investigations carried out during the winter and summer of 1978 confirm the important role of water dynamics in the reproduction of the major species inhabiting the Flemish Cap area. In this connection, the need to further investigate the variability in water circulation in relation to ichthyoplankton distribution and survival is justified. Such investigations would undoubtedly enhance the development of better models of the Flemish Cap ecosystem.

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Geostrophic Circulation of Northwest Atlantic Waters from Davis Strait to Newfoundland, Generalized from 1962 to 1978 Data[1]

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Abstract

New schemes of geostrophic circulation in the Northwest Atlantic from Davis Strait to the Newfoundland banks are presented, based on the generalization of dynamic topography charts from some hydrological surveys carried out by USSR research vessels during 1962-78.

Introduction

One of the first charts of dynamic topography of the surface water layers in the Northwest Atlantic was drawn up by Smith *et al.* (1937). In subsequent years, many such charts covering the area of the International Ice Patrol activities of the U.S. Coast Guard have been published (e.g. Kollmeyer (1967)). Data from the ICNAF NORWESTLANT Environmental Surveys in the spring and summer of 1963 were used to construct charts of dynamic topography of sea surface relative to the pressure surface at 1,000 m for the Labrador and Irminger Seas (Lee, 1968). Mean charts on a monthly basis for April-July were constructed by Scobie and Schultz (1976) for the area southeast of Grand Bank and south of Flemish Cap. However, the incomplete coverage of the Northwest Atlantic in space and time and the relatively small number of observations for most areas, except the Newfoundland banks and Flemish Cap, have made it difficult to construct reliable long-term mean charts of water circulation by month or season.

The purpose of this paper is to present a probable scheme of mean geostrophic water circulation in the surface layer of the Northwest Atlantic from Davis Strait to the Newfoundland banks for the warm period of the year, and a mean long-term chart of the dynamic topography of water in the Newfoundland banks and Flemish Cap areas for the spring-summer period.

Materials and Methods

More than 40 charts of dynamic topography for separate parts of the Northwest Atlantic, based on data from hydrological surveys by USSR vessels in 1962-78 (Alekseev *et al.*, 1972; Kudlo and Burmakin, 1972;

Kudlo, 1975; Kudlo and Boytsov, MS 1978), were used in drawing up a probable scheme of geostrophic circulation for this area. The observations covered the warm period of the year from April to October. A series of 'mean' charts, i.e. those considered closest to a mean pattern of circulation, were composed by visual examination of the available charts for each subarea, and these were used to construct the scheme of mean geostrophic water circulation presented in Fig. 1. Data from the mean chart by Scobie and Schultz (1976) for June were used for the deep-sea area southeast of the Grand Bank.

Hydrological data from USSR research vessel trawl surveys in 1972-76 were used to construct the mean dynamic topography chart for the Newfoundland banks and Flemish Cap (Subarea 3). The observations were made from March to September, but most of them were in the summer months of June-August. Averaging of the data was carried out for groups of stations (330 groups in all) in which the maximum distance between stations in different years was not more than 5 miles. Coordinates of the mean geometric position of each group of stations were taken as the coordinates of the 'mean' station, shown by dots in Fig. 2. Dynamic heights of the sea surface relative to the 200 decibar level were calculated (Zubov and Mamayev, 1956) for each station of each hydrological survey and were then averaged for each group of stations (i.e. for 5 years). These mean dynamic heights were the basis for the circulation patterns shown in Fig. 2.

Conclusions

The mean charts of geostrophic circulation providing details of water movements especially on the
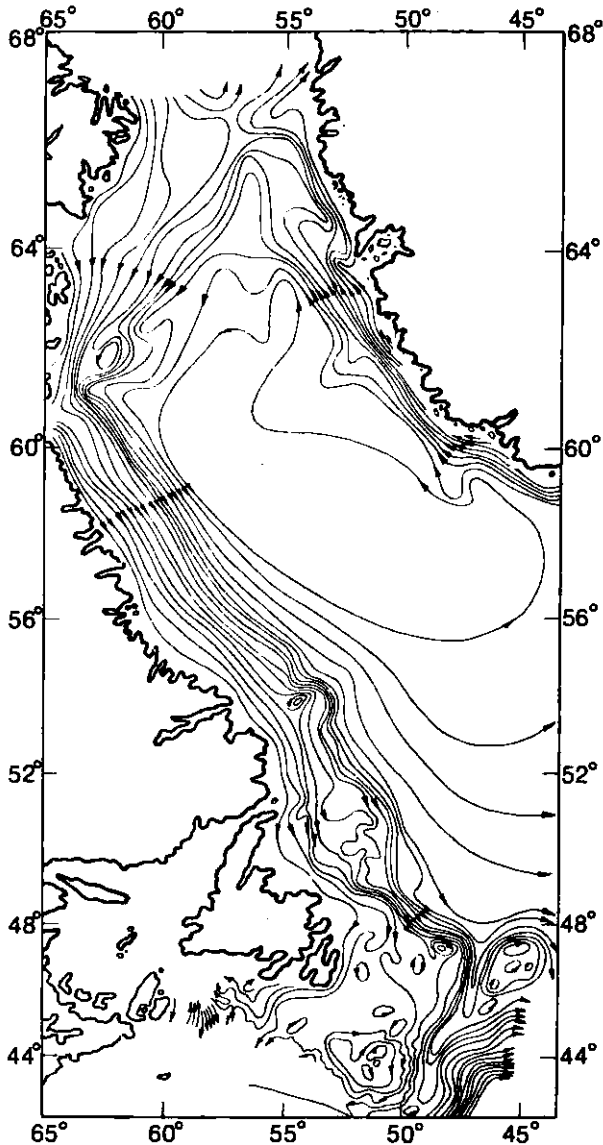
Fig. 1.   Probable mean geostrophic water circulation in the surface layer of the Northwest Atlantic from Davis Strait to Newfoundland banks during the warm period of the year, based on observations in 1962-78.
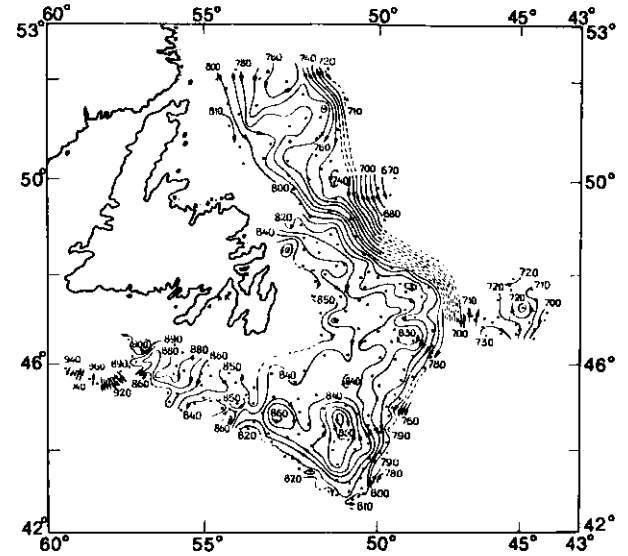

Fig. 2.   Mean geostrophic water circulation in the surface layer of the Newfoundland area and Flemish Cap for the spring-summer period, based on observations in 1972-76.

relates to the subjectivity of the method used in constructing the chart for the area as a whole from an arbitrary selection of charts considered to be representative of the 'average' circulation, whereas in the second case (Fig. 2) it is the relatively short time series of observation used in the averaging. The charts may be more accurate as new data are accumulated and incorporated into them.

Newfoundland banks and Flemish Cap differ significantly from existing diagrams of current patterns based on short-term observations, in that they represent the 'average' circulation based on several years of observations in the warm months of the year. Such charts may serve as the basis for investigating the influence of variation in abiotic conditions on reproduction and development during the early life history stages of the major fish species.

It is recognized that both charts have some defects. A major problem in the first case (Fig. 1)

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The 1977 Census of Northwest Atlantic Harp Seals, *Pagophilus groenlandicus* [1]

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Abstract

An aerial census of whelping 'patches' is one of several available techniques which has been used to assess the number of harp seals in the Northwest Atlantic. In March 1977, aerial surveys, incorporating black and white photography in the visible spectrum and in the ultraviolet, were conducted over concentrations of whelping harp seals in the Gulf of St. Lawrence and at the Front off eastern Newfoundland and Labrador.

Photographic coverage of the main whelping concentrations on the Front was judged to be reasonably complete and the number of pups accounted for by the census in this region was in the order of 200,000 animals. The survey in the Gulf of St. Lawrence was incomplete and the census accounted for fewer than 30,000 pups. No attempt was made to estimate the number of pups produced in areas not covered by the aerial survey.

Introduction

Although harp seals have been exploited for centuries, efforts to estimate their numbers and to manage the stocks are relatively recent developments. Aerial photographic surveys were first employed by Russian biologists working on harp seals in the White Sea about 50 years ago (Sergeant, 1976). In the western Atlantic, aerial surveys using conventional black and white photography have been conducted at irregular intervals since the early 1950's (Fisher, 1952, 1955; Sergeant, 1975). In general, these aerial censuses have not produced 'satisfactory' absolute estimates of pup production or population size (Sergeant, 1975) which are necessary for the development of adequate management strategies. Conventional black and white photography, used prior to 1974, accurately detects only adult seals on the surface of the ice (Lavigne, 1976). On whelping patches the assumption has often been made that all adults on the ice are breeding females, each of which gives birth to a single pup. In reality, adult males have been observed on the ice at the time of parturition and during the nursing period. In addition, the number of adult seals on the ice varies with the time of day, and it is difficult to estimate the number of animals in the water at any given time. Aerial surveys of moulting patches are plagued by similar problems because it is impossible to discriminate adult seals from immature seals, and male seals from female seals. Thus, although it is relatively easy to obtain photographs of large concentrations of animals, it is extremely difficult to know which components of the total population these seals represent.

In the case of the harp seal, the only factor that seems to remain constant for any time during the whelping season is the number of white-coated pups. They remain on the ice for the first 2 or 3 weeks of life and tend not to enter the water in significant numbers. Consequently, once pupping is completed there is a brief period when virtually all of the young of the year are on the surface of the ice together. However, young harp seal pups, being white animals on a white background of ice and snow have not been accurately detected in the past using conventional photographic techniques (Sergeant, 1975). This problem was overcome with the introduction of ultraviolet photography as an appropriate sensor for detecting certain white animals, such as white-coated seal pups and polar bears in white environments (Lavigne and Øritsland, 1974a, b; Lavigne, 1976). Although the white coat of the harp seal pup reflects all wavelengths in the visible spectrum, and appears white to the human eye, it absorbs much of the ultraviolet component in incident solar radiation. Snow not only reflects visible light and appears white to the eye, but also reflects much of the invisible (to the human eye) ultraviolet radiation. Thus, an ultraviolet photograph of a white harp seal pup on snow results in a black image of the

animal against a grey-white background (Lavigne, 1976).

Ultraviolet photography was initially tested in the field in March 1974 (Lavigne et al., MS 1974). In the following year, a preliminary aerial survey was conducted over all known whelping patches in the Gulf of St. Lawrence and at the 'Front', the latter area including the waters of the Strait of Belle Isle and off the east coasts of Labrador and Newfoundland. The results of this census indicated that pup production was somewhat lower than generally expected, perhaps less than 200,000 animals, implying that the number of animals age 1 or older in the stock might be less than one million seals (Lavigne et al., MS 1975a, b; Lavigne, 1976).

Further development of the ultraviolet aerial census technique was recognized as a priority for further research by the Scientific Advisors to the International Commission for the Northwest Atlantic Fisheries (ICNAF) at their meetings in late 1975 (ICNAF, 1976) and plans for a full scale census were made for March 1976. This survey was not completed because of unsuitable ice conditions in the Gulf of St. Lawrence and inclement weather at the Front. Nevertheless, the need for a complete census of Northwest Atlantic harp seals was reiterated at the October 1976 Meeting of ICNAF Scientific Advisers (Benjaminsen and Lett, MS 1976; Capstick et al., MS 1976; ICNAF, 1977).

A census was subsequently completed in March 1977. The present paper outlines the design of the aerial survey, the field operations, data analyses, and the resulting estimates of pup production for Northwest Atlantic harp seals in March 1977.

Methods

The design of the aerial survey was based on the results of the preliminary census in 1975 (Lavigne et al., MS 1975a, b). Discussion among various collaborators, in preparation for the proposed 1976 census and prior to the 1977 census, resulted in further refinements and modifications in the survey design. Aerial surveys were conducted through the facilities of the Canada Centre for Remote Sensing, using a DC-3 (Dakota) aircraft operated by Innotech Aviation Ltd. in conjunction with Intera Environmental Consultants Ltd., Ottawa.

For each survey flight, the following general procedure was employed, with minor modification as necessitated by field conditions. Whelping patches were initially located and delineated as to approximate

area and orientation by helicopter or small fixed-wing aircraft. Once pupping was judged to be virtually complete (by the absence of newborn seals and placentas on the ice) and suitable weather conditions were obtained, the DC-3 flew to a position designated by one of the support aircraft as one corner of an imaginary rectangular grid superimposed over the entire whelping patch (Fig. 1). The position (A) was then entered into the inertial navigation system (INS) on board the DC-3. The support aircraft (usually a helicopter) then flew a straight course along the apparent boundry of the whelping patch (Fig. 1, line AB). The DC-3 followed and entered a second position (B) into the INS. In this way, one side (AB) of the imaginary rectangle (ABCD) oriented in the direction of the long axis was established to provide a basis for constructing a grid over the entire whelping patch (Fig. 1). This grid was subsequently flown and photographed at 1,220 m with 20 to 30% forward overlap between adjacent frames within each line. Attempts were made to obtain 20% overlap between adjacent lines to ensure complete coverage and to aid in mosaicing the imagery and in reconstructing the whelping patch on film in the laboratory. For the 1,220 m flights (scale 1:8,000) the primary sensor was a Wild Heerbrugg RC-10, 23 cm × 23 cm format aerial survey camera with a 15.2 cm lens, a NAV filter, and Kodak Double-X (2405) Aerographic Film.
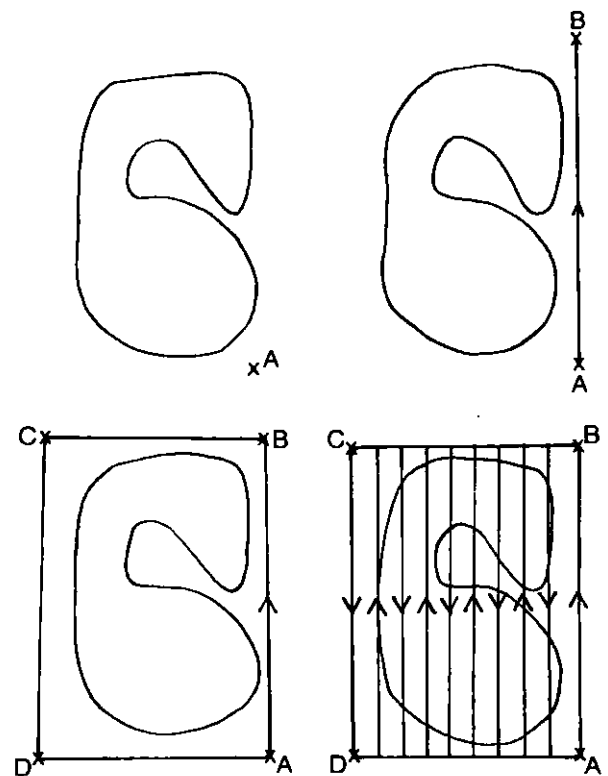

Fig. 1. General procedure used to establish a survey grid over a whelping patch of harp seals.

While flying the survey at 1,220 m, observers in the DC-3 continually viewed the ice. If, upon completing the full programmed length of a line, there were still seals on the line of flight, the line was continued beyond the point where seals were last sighted. Similarly, although the width of the grid was initially estimated by observers in the support aircraft, observers in the DC-3 ultimately determined this when seals could no longer be detected.

Once the 1,220 m coverage was completed, lower altitude samples were obtained at 305 m using ultraviolet photography as the primary sensor. A Hasselblad camera, equipped with a 105 mm UV-Sonnar lens, a Kodak Wratten 18A filter (Lavigne and Øritsland, 1974a) and Kodak Double-X (2405) Aerographic film, produced imagery in 70 mm format at a scale of 1:2,900.

The dimensions of the grid obtained at 1,220 m defined the total number of possible sample lines which could be flown at 305 m, given unlimited time, fuel and film. A single sample was then defined as one 305 m flight line running the complete length of the grid. For the purpose of stratification, the grid was divided into a number of zones, the number being dependent on the width of the grid and the available flying time which remained.

Aerial survey flights were tentatively scheduled to begin at 1100 h (local time) and to finish about 1500 h to take advantage of favorable sun angles and suitable radiation intensities for photography and the fact that the largest proportion of adult seals appears to congregate on the surface of the ice during this time (Lavigne, 1976). Available flying time for obtaining the sample imagery was determined by the time of day when the 1,220 m imagery was completed, by the amount of fuel remaining, and the transit time required for the DC-3 to return to base. Acordingly, the average time taken to fly each 1,220 m flight line, including positioning times, was then used to estimate the maximum number of 305 m sample lines which could be flown in the time remaining. This in turn dictated the number of sampling zones to be used in the stratification of the grid. Two 305 m flight lines were then selected from each zone using a random number table.

The resulting imagery was later processed and annotated by the Canada Centre for Remote Sensing before being shipped to the University of Guelph. After the field work was completed, participants from the University of Guelph and the Canadian Department of Environment independently assessed the apparent completeness of the aerial surveys in the Gulf of St. Lawrence and at the Front prior to examination of the processed imagery.

Survey Results

Extent of photographic coverage

The remote sensing aircraft was positioned in Summerside, Prince Edward Island, on 4 March 1977. By this time, two concentrations of whelping harp seals had been located in the Gulf of St. Lawrence, one to the west of Magdalen Islands and the other to the east of Bird Rocks. However, inclement weather and low cloud cover prevented any survey work during 5–8 March.

Suitable weather finally prevailed on 9 March and a survey was conducted over the whelping patch northwest of the Grindstone Beacon on the Magdalen Islands. Twelve overlapping 1,220 m flight lines were flown over this patch and six 305 m samples were obtained using 70 mm ultraviolet photography. On 10 March, an additional survey was conducted in the same general region, the objective being to obtain coverage of whelping seals to the west and northeast of the area flown on the previous day. Details of the 1,220 m flight lines and the 305 m sample lines flown on 9 and 10 March are given in Appendix Tables A and B.

On 11 March, an attempt was made to photograph the whelping patch near the Bird Rocks. The support helicopter was not able to locate this patch, but after a systematic search the DC-3 remote sensing aircraft located and surveyed a whelping patch running east-west just north of Bird Rocks (Appendix Table C).

Having surveyed all reported whelping concentrations in the Gulf of St. Lawrence, the DC-3 moved its base of operations to St. John's, Newfoundland, on 12 March. On 13 March, a reconaissance flight by the support aircraft located and delineated the Front herd. The herd was essentially divided into two adjacent patches located to the east of Belle Isle (Fig. 2). The larger (A) of the two patches was surveyed and sampled on 14 March and the remainder (B) was surveyed on 15 March (Appendix Tables D and E).

The Mecatina patch in the northern Gulf of St. Lawrence apparently did not form up in 1977, and plans to survey this patch were cancelled. Since all known concentrations of whelping harp seals in the western Atlantic off eastern Canada had been surveyed, the field work was terminated on 15 March 1977.

Preliminary evaluation of the census

Two large concentrations of whelping harp seals in the Gulf of St. Lawrence, one to the west of the Magdalen Islands and another off Bird Rocks, were

A — 14 March
B — 15 March

Labrador

Belle Isle

B

A

52°

1220 m

51°
30'

Newfoundland

Labrador

Belle Isle

B

A

52°

305 m

51°
30'

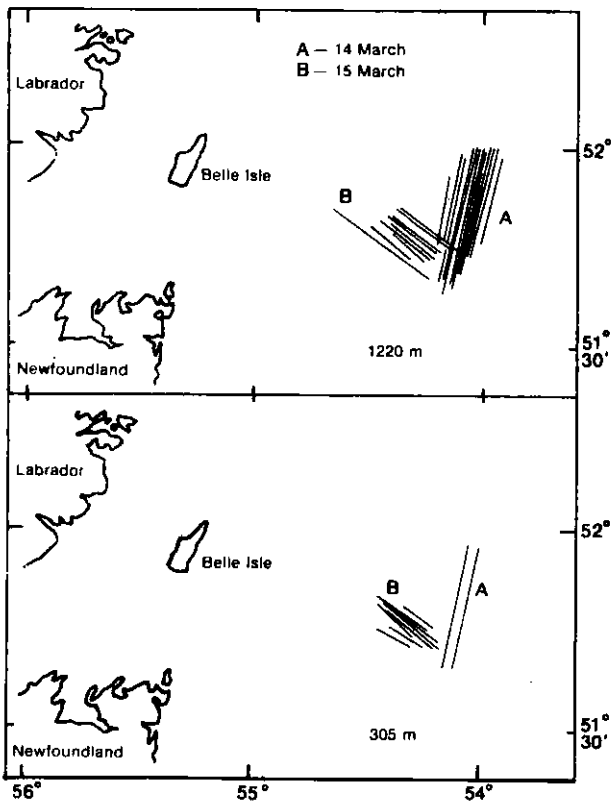Newfoundland

56°   55°   54°

Fig. 2.   Survey lines flown at 1,220 m (above) and sample lines flown
at 305 m (below) for the aerial census of harp seals at the
Front in March 1977.

located by 4 March 1977 and remained in their respective positions, aside from relatively insignificant ice movements, until they were photographed. The large concentration to the west of Magdalen Islands was surveyed on 9 and 10 March. Using the sealing vessel *Nadine*, dye markers and recognizable leads as markers, an attempt was made to obtain overlapping coverage between the two days, and to extend coverage on 10 March to seals not photographed on 9 March. The smaller patch off Bird Rocks was surveyed on 11 March.

A small group of seals was observed to the southwest of Bird Rocks and this group of seals may not have been photographed as part of the main Bird Rocks patch. A report of harp seals to the west of Deadman's Island was investigated but no seals were located.

At the Front, systematic and thorough searching for seals from Cape St. Anthony to beyond Hamilton Inlet resulted in the location of only one major concentration of seals. The herd was photographed on 14 and 15 March, and it was subsequently concluded that coverage of the Front herd was virtually complete with only scattered seals being missed. It was later suggested that a source of error may have been introducted by flying the Front herd on successive days. This approach was necessitated because of the extensive area of the patch, but ice movements during 14–15 March made it difficult to evaluate whether total coverage was, in fact, obtained. It was noted that the surveys did not cover a small group of seals (perhaps 1,000 pups) south of the main Front patch, and the historical Mecatina patch in the north Gulf (about 30 seals).

It was generally agreed by all participants involved in the program that the major concentrations of whelping harp seals had been surveyed.

Analysis of Photographic Imagery

Preliminary assessment of the quality of the imagery was made by the Canada Centre for Remote Sensing. The 70 mm ultraviolet imagery from the 305 m surveys appeared to be of good quality. However, an apparent malfunction of the motor drive noted in the field, attributed in part to the power pack, resulted in erratic movement of the film through the camera. When this occurred, less than 20% forward overlap was obtained on adjacent frames, and in some instances there were small gaps between adjacent frames of the sample line recorded on film. This did not cause major problems during the subsequent quantitative assessment of the imagery.

The Canada Centre for Remote Sensing also reported that the imagery obtained from the 1,220 m surveys with the RC-10 camera was somewhat overexposed, and steps were taken to compensate for this during production of contact transparencies used in the counting procedure. Subsequently, when this imagery was being counted, it became obvious that image quality was much inferior to that obtained in 1974 and 1975 (Lavigne et al., MS 1974; MS 1975a). A distinct lack of resolution, especially near the edges of each frame, was noted. The centre of the frame was in better focus but not to the extent obtained in previous years. A comparison of ultraviolet imagery (305 m) and black and white imagery (1,220 m) from identical areas on the ice confirmed that many adult seals detected at 305 m were present on the 1,220 m imagery, but that they would not have been positively identified because of the lack of focus on the 1,220 m imagery.

The malfunctioning of the RC-10 camera which resulted in the poor quality imagery may have been due

in part to a loss of vacuum in the camera, but the results are not totally consistent with imagery problems associated with a loss of vacuum, and other unknown factors may have been involved. The limited usefulness of the 1,220 m black and white imagery necessitated consideration of various estimation methods other than the ratio estimation technique proposed previously (Lavigne et al., MS 1975a, b).

Ultraviolet imagery from 305 m survey

The ultraviolet imagery obtained from the Gulf of St. Lawrence and the Front areas in March 1977 represents samples obtained at 305 m altitude, to detect adult harp seals and their pups, including whitecoats (Lavigne et al., MS 1975a), which were selected using a random or stratified random sampling procedure. All of the imagery was assessed and the animals counted by two or three photo-interpreters. A variety of approaches was undertaken in order to determine the most effective and efficient procedure for use in future surveys.

Initially the photo-interpreters spent about 2 weeks learning to recognize seals and to interpret correctly various types of imagery at different scales. The first two rolls of film taken on 9 March were analyzed by all three photo-interpreters to provide information on between-observer variation in seal counts. The remaining six rolls of film taken in the Gulf on 10-11 March and at the Front on 14-15 March were assessed by two interpreters. During the initial count, frames in each roll were analyzed separately and in random order by each interpreter. For the first two rolls, adult and pups were counted on separate occasions without reference to previous counts. For all other rolls, adults and pups were counted simultaneously on each frame in random order by each interpreter. This procedure was adopted to test whether counts of pups were more precise when made in reference to adult counts (adults are easier to detect) on the same frame.

The results of all counts were tabulated by individuals not involved in counting, so that the counts by the photo-interpreters were made independently and without reference to counts by others. Preliminary assessment of these initial counts involved separating the frames into two categories: (a) frames which all interpreters reported to be devoid of both adults and pups, and (b) frames on which at least one interpreter reported seals. This latter category was further subdivided into categories representing frames on which all interpreters reported indentical numbers of adults seals and pups, and frames on which the counts of seals differed between interpreters.

After the initial examination of all the ultraviolet imagery, replicate counts were carried out in order to quantify within-observer variation and to verify previous counts. Replicate counts were made on every frame in which a seal (adult or pup) had previously been detected. In addition, a number of frames with no seals, equal to or in excess of the number of frames with seals on which total agreement had been obtained, were selected at random and included in the replicate counts. These counts were made in chronological order by frame number within each roll. Adults and pups were counted simultaneously. The interpreters did not have access to their previous counts or to the counts of others.

The data were compiled so that the initial counts and the replicates by each interpreter for each frame could be compared. Means and standard deviations for adult and pup counts from each frame were determined, and obvious 'outliers' (Snedecor and Cochran, 1969) were rejected (i.e. if one out of six counts for the two rolls examined by three interpreters and one of four counts from the rolls examined by two interpreters were significantly different from the remaining counts, that count was rejected).

Additional counts were subsequently made to confirm earlier interpretations; the area of each frame was measured using a digital planimeter, and the final data matrix for the ultraviolet samples was tabulated. Statistical analysis of the data indicated no significant differences ($p > 0.05$) within or between interpreters, regardless of the counting procedure employed.

Black and white imagery from 1,220 m surveys

Initially the black and white transparencies for each flight were mosaiced together. In this way the area covered on the ice by the survey was reconstructed in the laboratory. At this time areas of overlap were marked on adjacent frames to prevent duplicate counts. This imagery was obtained to provide a good estimate of the area of the patch, or the area surveyed on a particular day, and to provide a count of adult seals on the ice at the time of the survey (Lavigne et al., MS 1975a).

In the original design, counting of adult seals on 1,220 m imagery was to be as rigorous as the counting of ultraviolet imagery outlined above. However, after a number of frames had been counted in duplicate, considerable variation was observed both between and within counters. At this point, comparison of the 1977 imagery with similar imagery from previous flights in 1974 and 1975 revealed the resolution problems noted above. As a result, all frames were counted a minimum of two times each and no attempt was made to resolve differences between or within counters. Areas on the
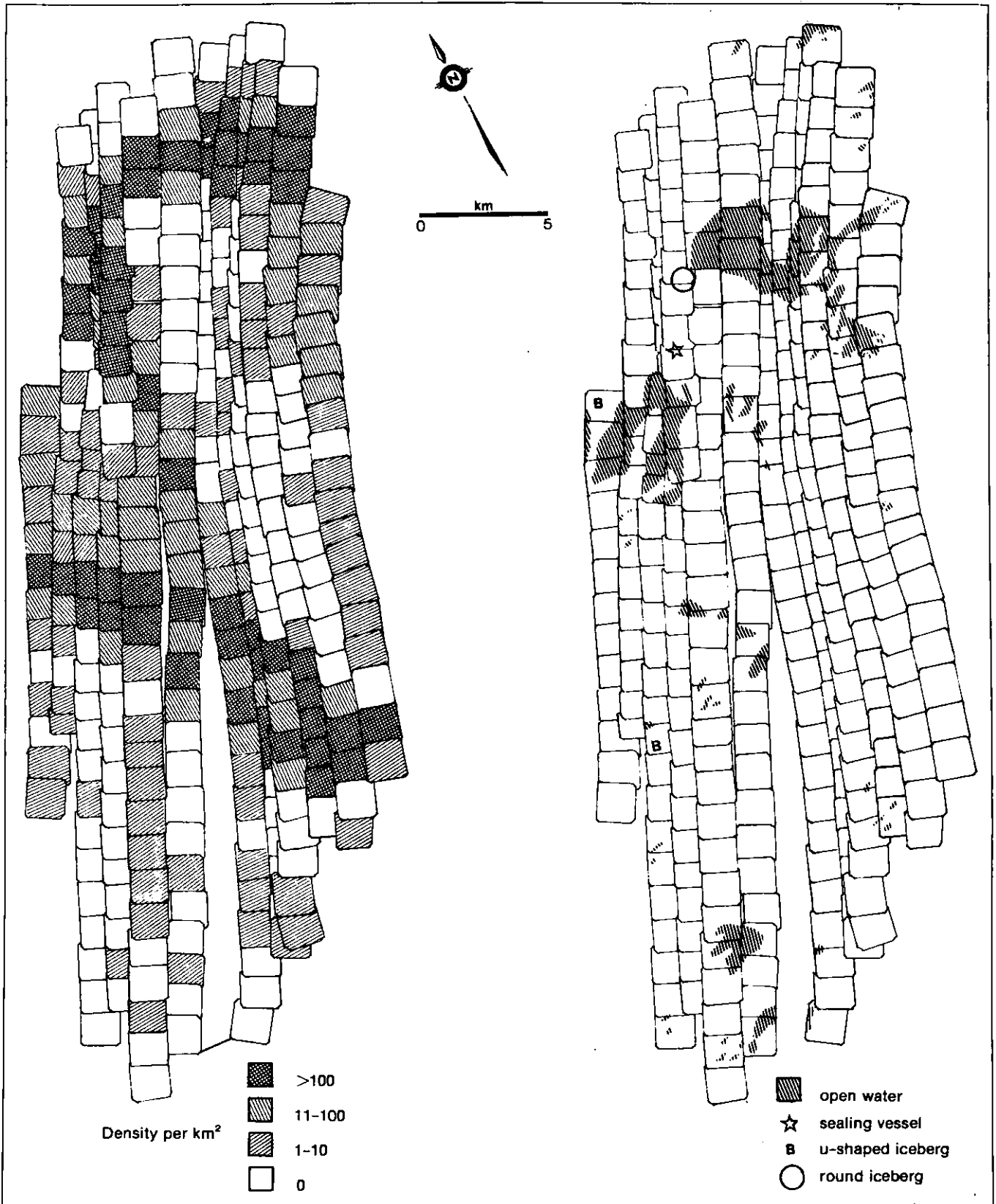
Fig. 3.   Mosaic of imagery obtained at an altitude of 1,220 m on 14 March 1977 at the Front, showing densities of adult harp seals in the whelping
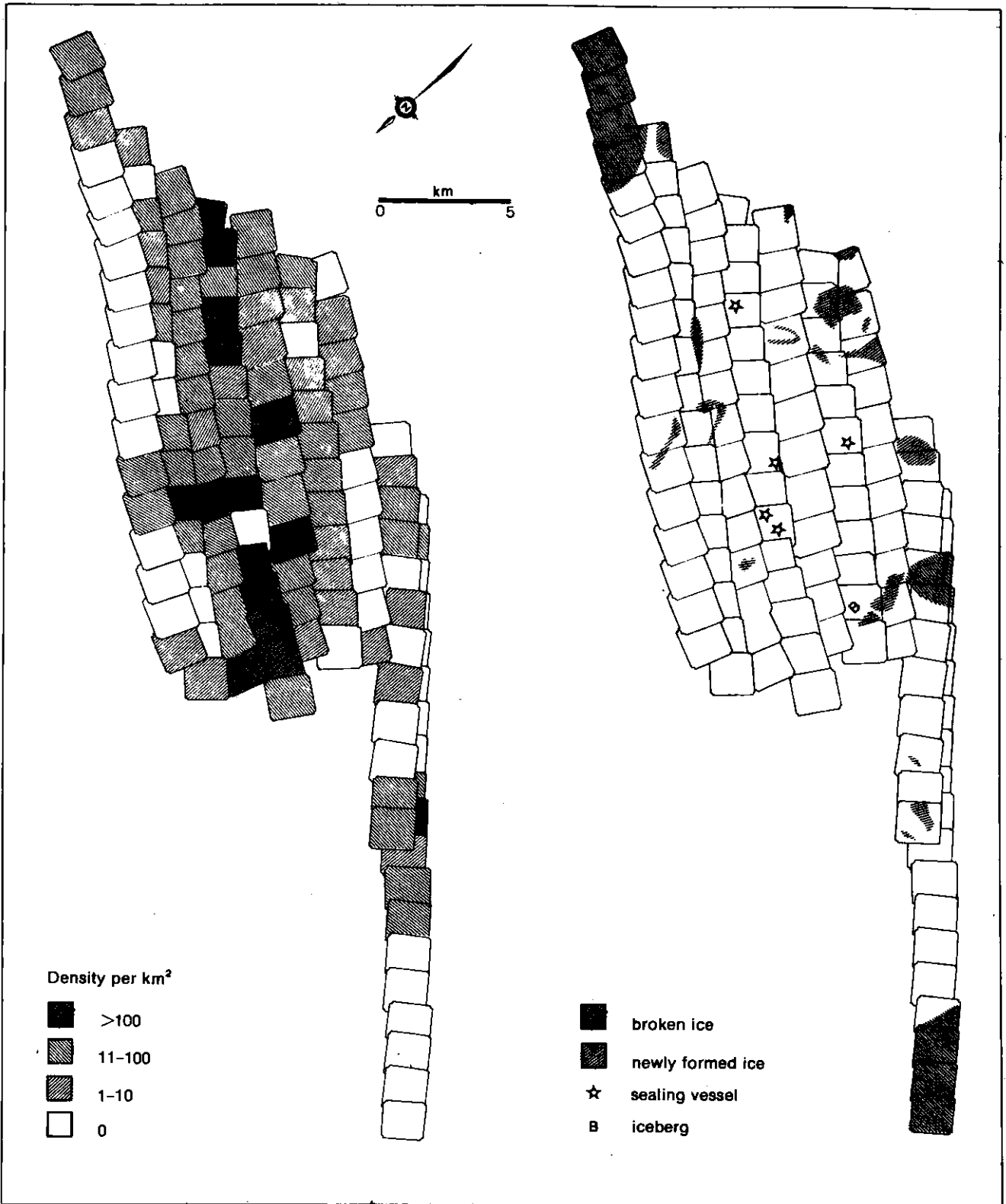patch (left), and major 'landmarks' (right).

km

0 _____ 5

Density per km²

■   >100

▨   11–100

▨   1–10

□   0

■   broken ice

▨   newly formed ice

☆   sealing vessel

B   iceberg

Fig. 4.   Mosaic of imagery obtained at an altitude of 1,220 m on 15 March 1977 at the Front, showing densities of adult harp seals in the whelping patch (left), and major 'landmarks' (right).

ice covered by each frame were again measured using a planimeter.

Maps of each of the aerial survey flights were then constructed from the mosaiced transparencies (see Fig. 3 and 4). It was known that some areas of the whelping patch west of the Magdalen Islands had been covered on both 9 and 10 March. When the imagery from these two surveys was mosaiced, it became obvious that little additional coverage had been obtained on 10 March. As a result, total coverage of this patch was not obtained. Because of this previously unrecognized problem, further detailed analyses were confined to the imagery obtained at the Front. Only preliminary calculations were completed for the Gulf of St. Lawrence whelping herds, since any estimate of pup production would include only those seals photographed, and estimates of the area not covered by the aerial survey would be highly speculative at best.

Analysis of Data

Aerial survey coverage of harp seal whelping patches in the Gulf and Front areas is summarized in Table 1. Preliminary estimates of the number of harp seal pups accounted for by the surveys, based on a simple random sampling procedure for flight lines, are summarized in Table 2. For these calculations each flight line at 305 m was treated as a sample with equal weight. Since not all flight lines were of equal length, the samples were effectively weighed in inverse proportion to the area within the herd they represented (Som, 1973). The results of these calculations were characterized by wide confidence intervals commonly encountered in harp seal census results for various reasons (Lavigne et al., MS 1975a). Since this estimator does not make the most efficient or complete use of all available data, a variety of other estimates was subsequently investigated using data from the Front surveys only.

Post-stratification was carried out with respect to

the apparent density of adult seals on the 1,220 m imagery (Fig. 3 and 4). Four strata were identified: >100 seals/km^2, 11–100 seals/km^2, 1–10 seals/km^2, and 0 seals/km^2. Ultraviolet frames were then matched to the 1,220 m imagery and separated into samples. All ultraviolet imagery from one flight line within a single 1,220 m frame was considered a sample. The number of pups in the area covered by the survey was then estimated (Table 3) using varying probability, stratified sampling estimators (Som, 1973).

For 14 March survey, an additional stratum was added to account for an area within the patch not photographed on the 1,220 m imagery, but sampled at

TABLE 1. Aerial survey coverage of harp seal whelping patches in the Northwest Atlantic in March 1977.

Area	Date	Area surveyed (km^2)	Area sampled (km^2)	Area sampled (%)
Gulf	9 Mar[a]	453.5	24.4	5.4
	10 Mar[b]	188.8	9.3	4.9
	11 Mar[c]	252.0	14.8	5.9
Front	14 Mar	571.7	11.7	2.0
	15 Mar	261.1	16.3	6.2

[a] Lines 1–5 (209.0 km^2) not included in area sampled due to absence of seals; total area flown was 662.5 km^2.

[b] Much of imagery from 10 March overlapped imagery from 9 March.

[c] Line 5 (3.29 km^2) not included in area sampled, as it was not randomly selected and it overlapped sample line 3.

TABLE 2. Estimates of the number of harp seal pups in whelping patches surveyed during March 1977. (Estimates are based on simple random sampling procedure.)

Area	Date	Mean number	Standard deviation
Gulf (NW of Magdalen I.)	9 March	19,421	7,709
(Bird Rocks)	11 March	6,909	2,769
Front (E of Belle Isle)	14 March	115,818	4,601
	15 March	69,341	18,823
Total		211,489	

TABLE 3. Estimates of the number of harp seal pups accounted for by the aerial survey at the Front off Newfoundland on 14–15 March 1977.

Method of estimation[a]	14 March Number of pups	14 March 95% conf. interval	15 March Number of pups	15 March 95% conf. interval	Front total Number of pups	Front total 95% conf. interval
Simple random sampling	115,818	58,433	69,341	48,394	185,159	84,260
Stratified random sampling	131,865	59,500	50,412	12,686	182,277	60,837
Ratio estimation	72,281[b]	11,785	29,312	3,510	101,593[b]	12,297
Regression estimation	44,955[b]	2,546	13,891	1,555	58,846[b]	2,983
Geometric mean regression	54,170[b]	—	22,408	—	76,578[b]	—

[a] Estimates from simple random sampling and stratified random sampling are not independent of each other, and the same applies to the estimates from ratio estimation and regression estimation, but the first two estimators are independent of the latter two estimators.

[b] As noted in the text, these three estimates do not include pups in a small area covered by the 1,220 imagery; the number of pups in this area estimated by stratified random sampling procedure was 3,805 ± 1,958 (one standard error); this raises the estimates from the last three methods to 105,398, 62,651 and 80,383 respectively.

305 m with ultraviolet photography. These ultraviolet frames were separated into samples in units of 10 frames for analysis. The results of this analysis are given in a footnote to Table 3.

The original experimental design proposed using the ratio of pups to adults counted on the ultraviolet imagery and the total count of adults on the 1,220 m imagery to obtain an estimate of the total number of pups in the area surveyed (Lavigne et al., MS 1975a; Lavigne and Ronald, MS 1975). From a March 1975 survey in the Gulf of St. Lawrence, this relationship was linear with a correlation coefficient of r = 0.99 (Lavigne et al., MS 1975a). However, in 1977, the poor quality black and white imagery from the 1,220 m survey and the resulting variation in counts of adult seals precluded use of this analysis.

As an alternative method, use of a ratio of pup counts on the ultra-violet imagery to the corresponding adult counts on the 1,220 m imagery, in combination with the total count from the 1,220 m imagery, was examined. This assumes that the relative number of seals in the compared areas not detected from 1,220 m because of poor quality imagery is similar to the whole area surveyed (i.e. that the compared areas are random samples of the whole.) As a first approximation, the relationship between pup counts at 305 m and adult counts at 1,220 m from corresponding areas on the ice might be considered linear through the origin (Fig. 5), with variance increasing with mean count especially for 14 March samples. According to Cochran (1963), in the situation where the variance is proportional to the mean, the ratio estimator should be the best linear unbiased estimator of the total number of pups.

For 14 March survey, a mean pup count of 3.6234 from ultraviolet imagery, a mean adult count of 1.5014 from 1,220 m imagery, and the total adult count of 29,950 results in an overall estimate of 72,281 pups. If the variance of the total adult count is estimated from repeated counting, the coefficient of variation of the estimator is approximately 0.083. This value was obtained by substituting sample estimates of covariances in equation 6.7 of Cochran (1963, p. 158), ignoring the finite population correction factor and adding the relative variances of the ratio and the estimated adult count. Since the relationship between the pup and adult counts used in this calculation is not precisely linear, the ratio estimator is biased. According to Cochran (1963, eq. 6.14), this bias is approximately 0.82% with the total pup count underestimated. The estimate of 72,281 pups for the region of the Front surveyed on 14 March does not include an area not photographed in the 1,220 m mosaic (see Table 3 footnote).
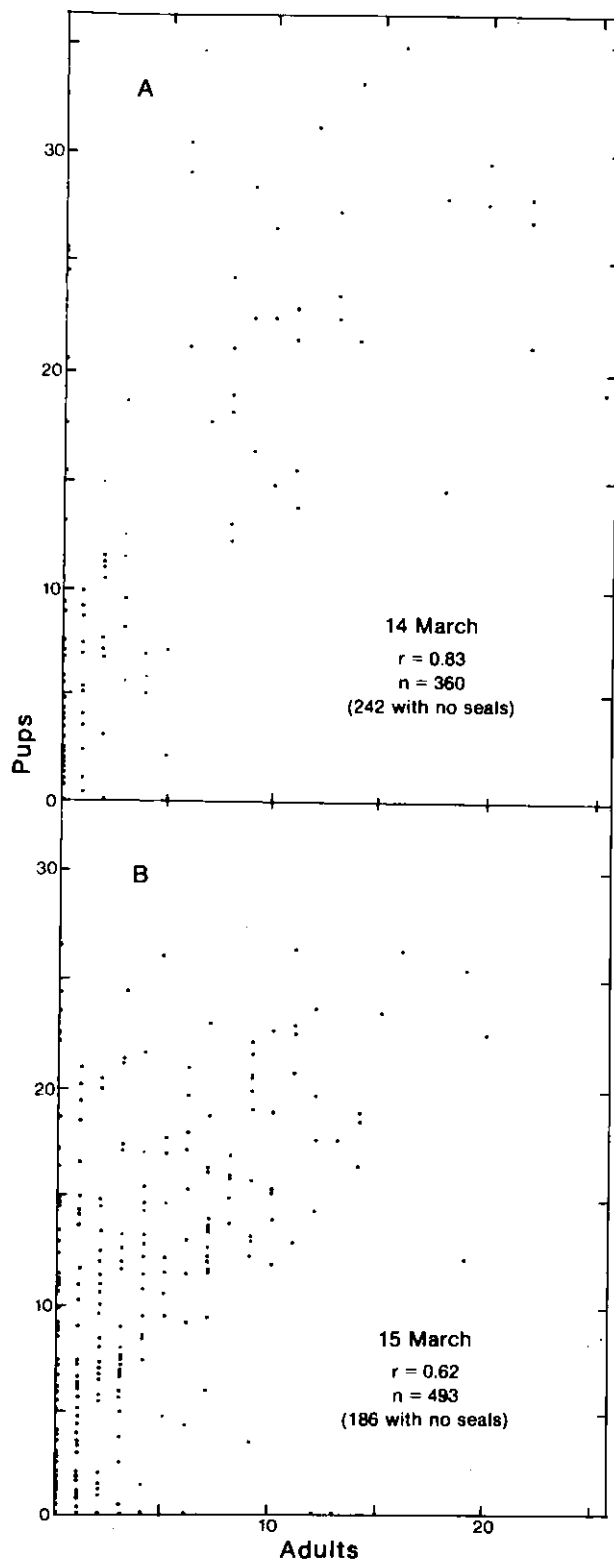

Fig. 5.   Relationship between number of pups counted on 305 m ultraviolet imagery and number of adult harp seals counted in the same area on 1,220 m black and white imagery at the Front in March 1977. (r = correlation coefficient and n = number of observations.)

Similar calculations were made for the area on the Front surveyed on 15 March. A mean pup count of 5.6114 from the 305 m survey, a mean adult count of 2.1278 from the 1,220 m survey, and the total adult count of 11,115 resulted in an overall estimate of 29,312 pups (Table 3). The coefficient of variation calculated as described above was 0.061 and the estimation of bias was less than 0.3%.

Regression estimators [y(pups) predicted from x (adults)] were also calculated from data for the 14 and 15 March surveys on the Front. These estimates may also be biased due to the nonlinearity of the regressions between pups counted on the 305 m ultraviolet imagery and corresponding adults on the 1,220 m imagery (Fig. 5). The estimated number of pups for the 14 and 15 March surveys were 44,955 and 13,891 (Table 3) with coefficients of variation of 0.029 and 0.057 respectively. For these data some ICNAF scientists suggested that, the geometric mean (GM) regression was probably more appropriate (Ricker, 1973), since variability in pup to adult ratios appears to be a natural consequence of movements of adult seals. Predictions of the number of pups surveyed on 14 and 15 March using the GM regression estimator were 54,170 and 22,408 respectively (Table 3).

Discussion

It would appear that reasonably complete photographic coverage was obtained for the main whelping concentration of harp seals in the Front area off Newfoundland in March 1977. Five estimates of the number of pups accounted for by the census ranged from 58,846 to 185,159 (Table 3). Estimates based on simple random sampling and stratified random sampling procedures had relatively large variances. Estimates obtained from ratio estimation and regression analyses were more efficient (i.e. narrower confidence limits) but they were lower than the estimates obtained from simple random and stratified random sampling (Table 3).

The use of any remote sensing technique to obtain scientific data requires confirmation that the subject under study is reliably detected by the sensor. This necessitates first hand observation of the subject and the exercise is usually termed 'ground-truthing' or ground-verification. In conjunction with the present census, an attempt was made to design and test a new ground-truth procedure for use in future surveys (Capstick et al., MS 1977). At the Front, however, ice conditions were such that a back-up procedure had to be employed. Two observers were asked to classify pups on the ice into three groups: pups in the open

which would be in a direct line with a camera overhead, pups which would obviously be hidden from view, and pups which might or might not be photographed. This qualitative assessment of the detectability of pups on the Front in March 1977 suggested that a correction factor of about 10% would be appropriate to account for seal pups not photogaphed by the sensor (Capstick et al., MS 1977). Application of this correction factor resulted in estimates of pup production in the area censused at the Front ranging from 68,916 to 203,675 (Table 4).

The question remains as to which of the five methods of estimation produced the most reliable estimate of the number of pups surveyed at the Front in 1977. The simple random sampling procedure did not utilize all sources of information but was based on good quality photographic imagery. A bias may be incorporated into the area estimates used in this procedure depending on the accuracy and precision of the altimeter in the aircraft, but this was not considered to be a serious problem. However, analysis of the low level line samples was complicated by the fact that while the two samples of 14 March were nearly equal, two observations are a poor basis for estimating a variance. Thus the confidence limits for 14 March in Table 3 are wider than for 14 March. Prior to combining the estimates for 14 and 15 March, an F test was carried out to determine whether the variance observed on 14 March could be equal to that of the 15th. F was 50.25, much less than $F_{0.05,5,1} = 230.2$. Since it seems unlikely, a priori, that sampling variance on 14 March should be less than that on the 15th in a smaller patch of seals, variance estimates from the 2 days were pooled giving a single variance estimate with six degrees of freedom. Thus the combined estimate for the 2 days has 95% confidence of $\pm 84,260$ (Table 3).

Simple random sampling and stratified random sampling methods produced similar estimates of the total number of pups accounted for by the survey (Table 3). Where an adequate number of samples was obtained (15 March) post-stratification increased the efficiency of estimation (Table 3).

TABLE 4. Summary of estimates of pup production at the Front in March 1977. (These estimates include the small group of 3,805 seals not covered by the 1,220 imagery and a 10% correction factor to account for seals not detected by the remote sensors.)

Method of estimation	Number of pups
Simple random sampling	203,675
Stratified random sampling	200,504
Ratio estimation	115,938
Regression estimation	68,916
Geometric mean regression	88,421

Estimates obtained using ratio estimation and the two regression estimators utilized more information, incorporating counts from the 1,220 m black and white imagery. Normally, estimators obtained by these methods are more efficient and avoid the possible bias in area estimation, and would thus be favoured over simple and stratified random sampling procedures. However, in 1977, the 1,220 m imagery was of poor quality and the resulting counts were subject to considerable variability. Comparison of 305 m ultraviolet imagery and similar areas on the 1,220 m imagery confirmed that adult seals present were not counted because of the poor resolution. Error may have also been introduced since resolution deteriorated more towards the edges of each frame, and the position of each 70 mm frame on the corresponding 1,220 m image could thus bias the results obtained. Most important, however, is the fact that the 1977 survey apparently took place relatively later in the whelping season than the 1975 census in the Gulf (Lavigne et al., MS 1975a). This is reflected in the more variable relationship between adult and pups (Fig. 5), i.e. adult females were less likely to be on the ice nursing pups, as they frequently do shortly after parturition. Furthermore, the results of the two regression estimates (Table 4) were not consistent with the number of pups subsequently killed (108,632) in the seal hunt shortly after the census.

In conclusion, the estimate of pups surveyed at the Front in 1977 based on stratified random sampling is the best estimate from the available data. This estimate easily accounts for the number of pups subsequently killed by sealers at the Front, but the relatively wide confidence intervals nevertheless place bounds on the attendant uncertainty in the estimate.

The census in the Gulf of St. Lawrence was incomplete and the survey accounted for less than 30,000 seals (Table 2). A portion of the whelping patch to the west of the Magdalen Islands was not surveyed. This was recognized only when the imagery was mosaiced and extensive overlap was found between imagery obtained on 10 March with that obtained on the previous day. This problem resulted in part from temporary difficulties with the inertial navigation system in the remote sensing aircraft. In addition, another large whelping patch was reported to have been seen in the Gulf of St. Lawrence on or about 21 March, but this was not reported to us until mid-August. Consequently, it is not reasonable to even speculate on the percentage of coverage obtained in the Gulf of St. Lawrence by the March survey, and thus no estimate of pup production was made for harp seals whelping there in 1977.

It is nevertheless desirable, to obtain an estimate of pup production in the Northwest Atlantic from aerial census techniques to compare with independent estimates made using other techniques (e.g. Sergeant, 1975; Benjaminsen and Lett, MS 1976; Capstick et al., MS 1976). In 1975, pup production in the Gulf was estimated to be 46,300 ± 5,158 (Lavigne et al., MS 1975b; Lavigne, 1976). If it is assumed that female harp seals return to the same place to whelp each year, an approximation of pup production in the Northwest Atlantic in recent years can be made. Using the maximum corrected estimates for the Front in 1977 (Table 4) and the estimate from the Gulf of St. Lawrence in 1975 (46,300), pup production estimated by aerial census techniques in recent years may be in the order of 250,000 animals. This assumes no difference in the proportion of harp seals in the Front and Gulf areas between 1975 and 1977 and does not account for any changes in the number of seals whelping in the Gulf which may have occurred since 1975. If the foregoing assumptions are correct, the total estimate must be low since 48,748 young of the year were taken in the Gulf in 1978, and more than 4,000 tagged pups escaped the hunt (Bowen, personal communication).

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Appendix

TABLE A. Gulf of St. Lawrence survey and sample line positions on 9 March 1977 (northwest of Magdalen Islands).

Survey altitude	Line no.	Displacement[a] (nm)	Position		Time (GMT)		Random no.	Zone	No. of frames
			Start	Finish	Start	Finish			
305 m	1	8.1	47°51.1'N 62°21.6'W	47°29.8'N 62°38.7'W	1816	1832	90	10	177
	2	7.7	47°38.6'N 62°31.0'W	47°23.1'N 62°43.5'W	1847	1859	86	10	236
	3	6.7	47°40.0'N 62°28.1'W	47°28.1'N 62°38.0'W	1913	1922	75	9	190
	4	6.5	47°38.1'N 62°29.5'W	47°28.9'N 62°36.8'W	1930	1937	73	9	140
	5	6.3	47°36.7'N 62°30.1'W	47°29.6'N 62°35.9'W	1945	1950	70	8[b]	109
	6	3.7	47°38.1'N 62°24.6'W	47°30.7'N 62°30.7'W	2000	2006	41	6[b]	127
1,220 m		No records were made of positions of the 12 survey lines flown							

[a] Displacement (nautical miles) from line 1 of the 1,220 m survey.

[b] Only one sample line was obtained from zones 6 and 8 due to lack of time and low sun angle. No samples were obtained from zone 7 for the same reason. Zones 1–5, defined from the 1,220 m data (see text), were not sampled because of the absence of seals, i. e. this area was outside the boundaries of the whelping patch.

TABLE 8. Gulf of St. Lawrence survey and sample line positions on 10 March 1977 (northwest of Magdalen Islands).

Survey altitude	Line no.	Displacement[a] (nm)	Position Start	Position Finish	Time (GMT) Start	Time (GMT) Finish	Random no.	Zone	No. of frames
1,220 m	1	0	47°40.9'N 62°20.7'W	47°34.8'N 62°29.5'W	1556	1602	—	—	14
	2	0.7	47°35.4'N 62°28.9'W	47°41.0'N 62°21.1'W	1606	1609	—	—	11
	3	1.4	47°42.0'N 62°22.4'W	47°34.9'N 62°32.3'W	1613	1620	—	—	13
	4	2.1	47°35.3'N 62°32.2'W	47°42.9'N 62°21.3'W	1625	1629	—	—	15
	5	2.8	47°42.8'N 62°24.1'W	47°35.7'N 62°33.9'W	1635	1641	—	—	13
	6	3.5	47°37.0'N 62°32.3'W	47°43.7'N 62°23.0'W	1645	1648	—	—	13
	7[b]	—	—	—	1701	1704	—	—	—
	8	4.2	47°38.1'N 62°32.2'W	47°44.3'N 62°23.7'W	1720	1723	—	—	11
	9	4.9	47°45.1'N 62°23.7'W	47°38.1'N 62°33.3'W	1728	1733	—	—	12
305 m	1	1.1	47°40.9'N 62°22.9'W	47°34.9'N 62°31.4'W	1814	1821	13	1	126
	2	1.5	47°41.0'N 62°24.0'W	47°35.4'N 62°31.3'W	1828	1834	17	1	79
	3	2.0	47°41.1'N 62°24.4'W	47°35.7'N 62°32.1'W	1841	1846	23	2	73
	4	2.7	47°41.6'N 62°25.4'W	47°36.9'N 62°31.8'W	1853	1857	30	2	65
	5	3.0	47°41.3'N 62°26.3'W	47°37.6'N 62°31.4'W	1904	1917	34	3	47
	6	3.8	47°41.6'N 62°27.3'W	47°38.9'N 62°31.2'W	1916	1918	43	4	35

[a] Displacement (nautical miles) from line 1 of the 1,220 m survey.
[b] Line aborted due to navigational malfunction.

TABLE C. Gulf of St. Lawrence survey and sample line positions on 11 March 1977 (north of Bird Rocks).

Survey altitude	Line no.	Displacement[a] (nm)	Position Start	Position Finish	Time (GMT) Start	Time (GMT) Finish	Random no.	Zone	No. of frames
1,220 m	1	0	47°51.9'N 61°22.5'W	47°49.3'N 61°10.7'W	1641	1644	—	—	11
	2	0.7	47°49.7'N 61°08.2'W	47°53.0'N 61°25.4'W	1646	1653	—	—	18
	3	1.4	47°53.7'N 61°24.8'W	47°50.0'N 61°05.6'W	1656	1701	—	—	17
	4	2.1	47°50.6'N 61°05.9'W	47°54.7'N 61°26.3'W	1704	1712	—	—	19
	5	2.8	47°55.5'N 61°26.6'W	47°51.4'N 61°06.7'W	1719	1724	—	—	19
	6	3.5	47°51.7'N 61°03.8'W	47°55.7'N 61°23.6'W	1727	1735	—	—	18
	7	4.2	47°56.5'N 61°24.4'W	47°52.7'N 61°05.7'W	1737	1742	—	—	17
	8	4.9	47°46.2'N 60°57.5'W	47°50.3'N 61°05.0'W	1924	1928	—	—	10
305 m	1	0.9	47°50.2'N 61°09.8'W	47°53.1'N 61°24.6'W	1752	1758	10	1	125
	2	1.3	47°49.9'N 61°06.3'W	47°53.3'N 61°23.2'W	1808	1815	15	1	158
	3	2.4	47°51.1'N 61°07.1'W	47°54.5'N 61°23.8'W	1825	1832	27	2	155
	4	3.2	47°51.8'N 61°06.1'W	47°53.3'N 61°23.6'W	1842	1849	36	2	162
	5[b]	2.5	47°51.1'N 61°06.3'W	47°54.5'N 61°23.0'W	1859	1906	—	2	155
	6[c]	—	47°45.9'N 60°58.0'W	47°49.2'N 61°03.8'W	1934	1938	—	—	76

[a] Displacement (nautical miles) from line 1 of the 1,220 m survey.
[b] Sample not random but chosen to fall in seal concentrations.
[c] No displacement recorded; sample was taken by line of sight from center of line 8 of 1,220 m survey.

TABLE D. Front survey and sample line positions on 14 March 1977 (see Fig. 2).

Survey altitude	Line no.	Displacement[a] (nm)	Position		Time (GMT)		Random no.	Zone	No. of frames
			Start	Finish	Start	Finish			
1,220 m	1	0	51°52.0'N 54°02.6'W	51°39.0'N 54°08.0'W	1501	1506	—	—	19
	2	0.7	51°37.6'N 54°10.0'W	51°55.1'N 54°02.5'W	1509	1520	—	—	25
	3	1.4	51°55.1'N 54°03.5'W	51°37.9'N 54°10.8'W	1523	1529	—	—	25
	4	2.1	51°35.9'N 54°13.0'W	51°55.7'N 54°04.7'W	1532	1544	—	—	29
	5	2.8	51°54.5'N 54°05.9'W	51°35.6'N 54°14.2'W	1547	1555	—	—	30
	6	3.5	51°33.8'N 54°16.3'W	51°55.8'N 54°06.8'W	1558	1611	—	—	31
	7	4.2	51°55.7'N 54°06.1'W	51°33.2'N 54°17.6'W	1619	1628	—	—	31
	8	4.9	51°32.3'N 54°19.0'W	51°55.1'N 54°09.7'W	1631	1645	—	—	29
	9	5.6	51°55.1'N 54°10.5'W	51°34.8'N 54°19.1'W	1647	1655	—	—	29
	10	6.3	51°34.0'N 54°20.7'W	51°54.8'N 54°12.1'W	1659	1711	—	—	30
	11	7.0	51°54.6'N 54°13.2'W	51°40.8'N 54°18.9'W	1713	1719	—	—	20
	12	7.7	51°39.5'N 54°20.5'W	51°48.4'N 54°17.0'W	1722	1727	—	—	13
305 m[b]	1	3.6	51°53.2'N 54°08.0'W	51°34.1'N 54°16.1'W	1735	1744	40	1	256
	2	5.7	51°34.9'N 54°19.1'W	51°54.7'N 54°10.9'W	1748	1801	64	2	255

[a] Displacement (nautical miles) from line 1 of the 1,220 m survey.
[b] Lack of fuel prevented flying more sample lines.

TABLE E. Front survey and sample line positions on 15 March 1977 (see Fig. 2).

Survey altitude	Line no.	Displacement[a] (nm)	Position Start	Position Finish	Time (GMT) Start	Time (GMT) Finish	Random no.	Zone	No. of frames
1,220 m	1	0	51°44.3'N 54°48.3'W	51°37.7'N 54°30.0'W	1424	1430	—	—	19
	2	0.7	51°42.1'N 54°39.4'W	51°37.9'N 54°28.2'W	1509	1511	—	—	12
	3	1.4	51°37.9'N 54°25.7'W	51°41.1'N 54°34.8'W	1513	1517	—	—	10
	4	2.1	51°42.3'N 54°36.0'W	51°38.1'N 54°24.3'W	1520	1523	—	—	12
	5	2.8	51°37.9'N 54°21.3'W	51°42.8'N 54°34.9'W	1526	1531	—	—	13
	6	3.5	51°43.5'N 54°34.7'W	51°38.1'N 54°20.2'W	1533	1538	—	—	15
	7	4.2	51°38.3'N 54°18.4'W	51°43.7'N 54°33.2'W	1540	1546	—	—	13
	8	4.9	51°44.4'N 54°32.8'W	51°38.4'N 54°16.5'W	1550	1555	—	—	16
	9	5.6	51°38.1'N 54°13.2'W	51°44.8'N 54°31.6'W	1558	1605	—	—	18
305 m	1	0.5	51°40.7'N 54°36.6'W	51°37.6'N 54°27.9'W	1611	1614	5	1	78
	2	1.0	51°37.6'N 54°27.0'W	51°40.7'N 54°34.9'W	1617	1621	10	1	83
	3	2.8	51°42.5'N 54°34.6'W	51°37.6'N 54°21.1'W	1623	1628	31	2	125
	4	3.5	51°37.9'N 54°19.3'W	51°43.5'N 54°34.2'W	1632	1638	39	2	144
	5	3.6	51°43.8'N 54°35.5'W	51°39.3'N 54°23.0'W	1641	1645	41	3	117
	6	4.6	51°40.1'N 54°21.9'W	51°43.2'N 54°30.5'W	1648	1653	51	3	91
	7[b]	2.3	51°43.4'N 54°37.5'W	51°38.9'N 54°26.0'W	1701	1705	—	2	112
	8[b]	4.0	51°38.7'N 54°20.2'W	51°44.8'N 54°37.3'W	1709	1716	—	3	168

[a] Displacement (nautical miles) from line 1 of the 1,220 m survey.
[b] Samples not random but chosen to fall in seal concentrations.

Instructions to Authors for the Preparation of Manuscripts Intended for Publication in the ICNAF Research Bulletin and Selected Papers

Text

a)   Manuscript should be type-written, *double-spaced,* and on one side only of good quality white bond paper, size 8½ × 11 inches (220 × 280 mm).

b)   Leave all margins 1 inch (25 mm) to 1½ inches (38 mm) for editorial marks and queries.

c)   Prepare and submit the original and one copy of the text and two sets of illustrations.

d)   Number all pages of the manuscript consecutively with Arabic numerals in the centre of the top margin space.

e)   Start a new page for each of the following sections with appropriate headings and sub-headings: (1) title, name and address of author, list of contents (if applicable); (2) abstract of the paper; (3) text; (4) references to literature; (5) tables; (6) legends for figures and (7) figures.

f)   Please *double-space everything* — Text, quotations, footnotes, tables and table headings, legends, references to literature, and use even greater spacing where helpful (particularly around equations and formulate).

g)   Wherever practical the text should be subheaded into Abstract, Introduction, Materials and Methods, Results, Discussion and Acknowledgements. If authors wish to provide a summary of the conclusions, it should follow the Discussion.

h)   All measurements, linear, weight, and time, should be given in numerals (not words) in the metric system. The Celsius scale should be used as a standard. When other units of measure are preferred, authors should include equivalents in metric units.

i)   Footnotes should be avoided as far as possible, but if necessary they must be numbered consecutively in the text and typed under a horizontal line at the bottom of the page concerned.

j)   Only those words to be printed in italics should be underlined.

Abstract

Each Manuscript should have an abstract not to exceed 3% of the length of the text or 200 words whichever is the smaller. For position of the abstract in the manuscript see (e) above. The abstract should summarize the contents and conclusions of the paper, point to new information in the paper and indicate the relevance of the work.

Tables

a)   Tables should be carefully constructed so that the data presented may be easily understood.

b)   Tables should be set out on separate sheets following the references.

c)   Position of the tables in the text should be indicated clearly.

d)   Each table should be provided with a descriptive heading which, together with the column headings, makes the table intelligble without reference to the text.

e)   Tables should be numbered consecutively with Arabic numerals, e.g. Table 1, 2, 3, etc.

Figures

a)   All illustrations, whether black-and-white drawings, graphs, photographs, or tone drawings, are to be considered as figures.

b)   Each figure should be mentioned and described in the text.

c)   A legend should be provided for each figure; the legends should all be typed together on a separate sheet or sheets attached to the manuscript following the tables.

d)   Figures should be numbered consecutively with Arabic numerals, as Fig. 1, 2, 3, etc.

e)   Figures should be set out on sheets preferably the same size as the text pages and in any case should not require a printer's reduction to less than one-third. Small figures can be arranged in groups on sheets the same size as the text pages.

f)   For guidance in preparing figures, the size of the printed area of the page is 21 × 17 cm. The publications have a two-column format, each column 8 cm wide.

g)   Photographs presented as figures should be high contrast, glossy prints, about 5 × 7 inches (125 × 175 mm) in size and should be shipped flat protected by stout cardboard.

h)   Each illustration should be identified by marking the figure number and the author's name on the back lightly in soft pencil.

Bibliographic Style

a)   References to literature in the text should be by the author-date system, for example

It was reported that (Collins, 1960) the...;
In examining the situation, Rossini (1959) felt that...

Where more than one paper by the same author(s) have appeared in one year, reference should be given as follows:

Osborne and Mendel (1914a); Osborne and Mendal (1914b)

or   Osborne and Mendel (1914a and b); (Barnet and Robinson, 1942; King and Pierce 1943a, 1954)

Reference to material not yet submitted for publication should be written into the text e.g. "Harvey, in an unpublished manuscript,..." or "Harvey, in a letter,..."

b)   All references cited by the author-name system in the text should be listed alphabetically by the surname of the first *author* at the end of the paper. *Year* of publication follows the authorship. Then give the full *title* of the paper. This should be followed by the abbreviated name of the *periodical* with the *volume and pages* in Arabic numbers (e.g.:2: 120-136). For abbreviations of periodicals follow the "Word List of Scientific Periodicals"[1] An issue, number supplement or other part within a volume is shown in parentheses only when paged independently (e.g.:2(4):1-56; 34 (Suppl. 2):1-26). Any special Series (Ser 3, III or C) precedes the volume number. In *book citations* after the title, there appears the edition, the publisher's name, place of publication, and the number of pages if one volume, but the number of *volumes* if more. Reference to material submitted but not yet published should be referred to in the list of references as "in press" or "Submitted for publication" followed by the date of submission.

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[1] The following abbreviations *(in italics)* should be used when citing ICNAF publications and documents:

(ICNAF Res. Bull.) International Commission for the Northwest Atlantic Fisheries Research Bulletin
(ICNAF Sel. Papers) International Commission for the Northwest Atlantic Fisheries Selected Papers
(ICNAF Stat. Bull.) International Commission for the Northwest Atlantic Fisheries Statistical Bulletin
(ICNAF Redbook) International Commission for the Northwest Atlantic Fisheries Redbook
(ICNAF Annu. Rept.) International Commission for the Northwest Atlantic Fisheries Annual Report
(ICNAF Samp. Yearb.) International Commission for the Northwest Atlantic Fisheries Sampling Yearbook
(ICNAF Spec. Publ.) International Commission for the Northwest Atlantic Fisheries Special Publication
(ICNAF Meet. Proc.) International Commission for the Northwest Atlantic Fisheries Meeting Proceedings
(ICNAF List Fish. Vessels) International Commission for the Northwest Atlantic Fisheries List of Fishing Vessels
(ICNAF Res. Doc.) International Commission for the Northwest Atlantic Fisheries Research Document
(ICNAF Sum. Doc.) International Commission for the Northwest Atlantic Fisheries Summary Document
(ICNAF Com. Doc.) International Commission for the Northwest Atlantic Fisheries Commissioner Document