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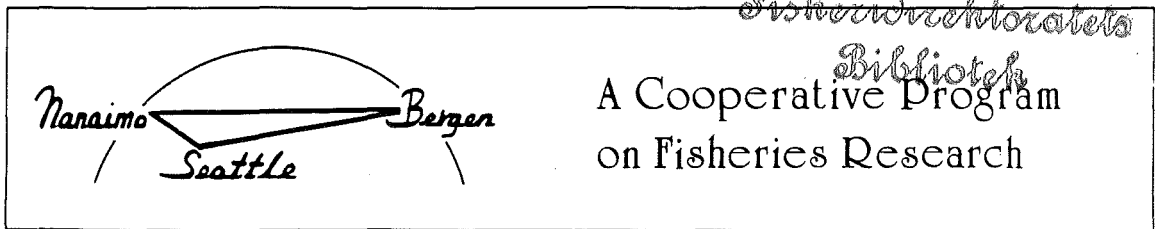
YEAR CLASS VARIATIONS AS DETERMINED
FROM PRE-RECRUIT INVESTIGATIONS

Bergen, Norway, 28-30 September 1988

PART II



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YEAR CLASS VARIATIONS AS DETERMINED FROM

PRE-RECRUIT INVESTIGATIONS

PART II

Proceedings from the second workshop
under the cooperative programme of fisheries research
between the institutions in Seattle, Nanaimo and Bergen,
held in Bergen 28. - 30. September 1988.

Compiled by Svein Sundby.

Institute of Marine Research, Bergen
1989

*"Nothing is so boundless as the sea,
nothing so patient. On its broad back it
bears, like a good-natured elephant, the
tiny mannikins which tread the earth; and
in its vast cool depths it has place for
all mortal woes. It is not true that the
sea is faithless, for it has never
promised anything; without claim, without
obligation, free, pure, and genuine beats
the mighty heart, the last sound one in
an ailing world. And while the mannikins
strain their eyes over it, the sea sings
its old song. Many understand it scarce
at all, but never two understand it in
the same manner, for the sea has
a distinct word for each one that sets
himself face to face with it."*

From "Garman and Worse"

by Alexander L. Kielland (1885)

First workshop under the cooperative programme:

*"Comparative Biology, Assessment, and
Management of Gadoids from
the North Pacific and Atlantic Oceans."*

Proceedings compiled by Miles Alton (1986).

PREFACE

The cooperative programme of fisheries research between institutions in Seattle, Nanaimo and Bergen is based on an agreement between the Northwest and Alaska Fisheries Center in Seattle and the Institute of Marine Research in Bergen. The agreement was signed in November 1983. Since then cooperation has gradually evolved as personal contact between the scientists has increased. Today the cooperation comprises six institutions, and exchange of scientists is an important part of the programme. Working groups have been established on research trawl sampling, multi-species ecological techniques, recruitment studies, acoustic methods, ageing, determination of stock units and aquaculture. The first workshop under the programme was held in Seattle in June 1985. This volume contains the contributions to the second workshop held in Bergen during 28 - 30 September 1988.

Bergen, March 1989

Svein Sundby

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HABITAT SELECTION AND COMPETITION AMONG O-GROUP GADIDAE
OFF MID-NORWAY

by

1 1 2 3
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ABSTRACT

Juvenile gadids and other co-occurring fishes were collected during August in the years 1981 to 1983 at the Møre coast (Mid-Norway). The gears used were pelagic trawl, bottom trawl, Danish seine and beach seine. All species collected were indentified and counted.

Saithe and pollack were never observed in the pelagic hauls. Cod were abundant pelagically in 1981, but had already settled in 1982 and 1983. Haddock and whiting were caught both pelagically and at the bottom during all years. Saithe, pollack and partly cod therefore seem to settle before August, while the other species are settling during this month.

Cod settled mainly in shallow sheltered areas and were absent at the most exposed locations and in deep water. Haddock generally settled at greater depths and in more exposed areas than cod, but were also observed in the fjords. Saithe were caught mainly at exposed littoral locations, and pollack were found in shallow water both in exposed and sheltered areas. Whiting were less abundant than the others, but were found pelagically mostly inshore all over the area studied. Single specimens of settled whiting were found in the sheltered littoral and sublittoral. Although the distribution to some degree overlapped, it seemed that differences in distribution and size reduced competition between the juvenile gadids.

In the beach seine hauls about 30 other species occurred, and some of these may compete with cod for food.

INTRODUCTION

In recent years comprehensive studies have been carried out on the distribution and biology of larval and postlarval stages of cod (Gadus morhua L.) and other gadids in northern Norwegian coastal and offshore waters (e.g. Tilseth 1984, Tilseth and Ellertsen 1984, Bjørke and Sundby 1984). Abundance and distribution of pelagic and settled 0-group gadids in the Barents Sea have also been investigated (e.g. Randa 1984, Ponomarenko 1984). Information on the biology of 0-group gadids from the Norwegian Skagerrak coast are given by Dahl and Dannevig (1906) and Tveite (1971, 1984) and around the British Isles by Hawkins et al. (1986) and Riley and Parnell (1984). Knowledge of the 0-group distribution of gadids settling along the coast of Mid-Norway is, however, sparse.

Year class strength appears to be determined when the fish reach an age of about 6 months (e.g. Hysten and Dragesund 1973, Randa 1984). Recent studies also indicate a direct relationship between postlarvae abundance and subsequent year class strength (Sundby, Bjørke, Soldal and Olsen 1988)

Recently the mechanisms regulating recruitment of gadids in coastal waters have received special attention due to the development of methods for artificial production of cod fry for release in Norwegian inshore areas.

The objective of this paper is to describe the distribution of juvenile gadids occurring at the coast of western Norway (Fig. 1). The distribution is analysed in relation to depth and degree of exposure and compared to the distribution of other fish species. The habitat selection and the possibility of competition and predator-prey relationships between species during settling are discussed.

MATERIAL AND METHODS

Sampling

The investigations were carried out in August of the years 1981 to 1983 with R/V Håkon Mosby, which was equipped with bottom and pelagic trawls as well as a rubber boat from which a beach seine was operated. In 1983 a commercial Danish seiner was hired. The trawl and Danish seine had codends with small meshes. Description of the gears are given in Table 1.

The investigations were carried out at the coast of Møre between 62° N and 64° N. This coastline is permeated by fjords and sheltered by an almost complete row of islands (Fig. 1). Skerries further shelter the islands and the coast. The investigated locations were categorized according to the degree of exposure to the open sea:

- Degree 1, sheltered; including most fjord locations, but also islands locations extremely sheltered by skerries.
- Degree 2, moderately exposed; including most locations between fjord mouths and islands
- Degree 3, exposed; including most locations between the islands or mainland and the outer skerries.
- Degree 4, extremely exposed; including locations off the outer skerries.

The gears and locations were chosen with the aim of getting a reasonable coverage of the various depths in the four categories of exposure. The investigations were primarily designed to map the nursery areas of cod. Based on experience from saithe (Pollachius virens) surveys, beach seine hauls were concentrated in sheltered and moderately exposed areas, and at locations with bottom substrates which permitted safe operation of the seine. Also, a random distribution of the bottom trawl and Danish seine hauls was impossible due to rough bottom. Most of the pelagic trawl hauls were made in the fjords.

The entire catch or a representative subsample was sorted and the catch by numbers was recorded. Total length was measured to the nearest 0.5 cm below (specimen from the Danish seine catches were measured to the nearest cm below).

RESULTS

Variation between years in geographic distribution of the different types of sampling stations are illustrated in Fig. 1 to 3.

Pelagic distribution

In 1981 a considerable number of 0-group cod (maximum 33 specimens per trawl haul) were found pelagically in the fjords, mostly in the upper 50 m (Fig. 4). In the two subsequent years cod were recorded in only one pelagic trawl haul (Figs. 5 and 6). Settling of cod therefore appear to occur in the period July to August.

Haddock (Melanogrammus aeglefinus) and whiting (Merlangius merlangus) were found in all exposure zones (Figs. 7 and 8), haddock having the more offshore distribution. Saithe and pollack (Pollachius pollachius) were not observed in the pelagic trawl catches (Fig. 9, 10).

Demersal distribution

Surface to 10m: The beach seine sampled the zone from the surface to 10 m depth. In the catches cod (Figs. 4-6), saithe (Fig. 9), and pollack (Fig. 10) were frequent. Single specimens of haddock and whiting (Figs. 7 and 8) occurred in 1 and 14 of the hauls respectively.

Saithe were considerably more abundant in 1983 than in the two preceding years (frequently more than 100 specimens per haul). In 1981 and 1982 saithe were most frequent in the areas with degree of exposure 2 to 4. In 1983 the area of distribution had expanded, and the species was also found in sheltered areas (exposure degree 1). Cod were found on the sheltered and moderately exposed locations. The largest catch was 200 specimens per haul, but most catches were below 30. Pollack were found on all types of locations, but the catches seldom exceeded 50 specimens per haul.

20 - 120m (Danish seine grounds): In 1983 coastal and offshore regions with exposure 2 to 4 and with depths ranging from 20 to 120 meters were surveyed with Danish seine (Fig. 3). In the 43 hauls, cod, haddock and whiting were found in 10, 10 and 5 hauls respectively (Figs. 6, 7 and 8). A maximum of about 600 0-group cod were caught per haul. The 0-group haddock and whiting were less numerous in these catches. These species appeared to be settling during the period studied, as they were also caught by pelagic trawl. No 0-group fish were recorded offshore (exposure degree 4). Pollack and saithe were absent in the Danish seine catches.

100 - 300m (bottom trawl grounds): Bottom trawling was done in all exposure zones, but suitable bottom conditions were only found deeper than 100m. No 0-group cod, saithe, pollack or whiting were found in the bottom trawl catches except for a single cod in 1983. Haddock were caught in small numbers mostly offshore. (Fig.7).

Length distributions

Size distribution of the five species were compared based on data from 1983, i.e. the year with most extensive sampling.

The area of investigation was divided in four subareas; subarea 1 being the southmost and subarea 4 the northmost (Fig. 1). The length of cod and saithe caught in the littoral zone differed considerably, saithe being the largest, whereas pollack were smaller than cod. Mean length measurements of cod, saithe and pollack from beach seine catches are shown in Fig. 11 and in the following text table:

	Cod	Saithe	Pollack
Subarea 1	7.3	11.2	5.7
Subarea 2	6.0	9.7	5.2
Subarea 3	7.1	10.3	5.2
Subarea 4	7.1	11.0	6.2

Species specific differences between areas were minor compared with the interspecies differences.

The differences between cod and haddock length distributions in the Danish seine catches were rather pronounced (Fig. 12). More than 80% of the haddock, but only 10% of the cod were 9 cm or more. The haddock in the pelagic trawl catches ($\bar{l}=7.9$) were smaller than haddock caught by Danish seine ($\bar{l}=10.1$ cm) (Fig. 12), which indicated that settling was occurring, the larger fish settling first. The mean length of the pelagic haddock was close to the size of settled cod ($\bar{l}=7.3$ cm in beach seine and $\bar{l}=7.1$ cm in Danish seine catches).

Cod from the Danish seine and the beach seine hauls in the same subarea had approximately the same length distributions (Fig. 11, subarea 1, and Fig. 12).

Other species

In addition to 0-group gadids 35 to 40 other fish species were caught in the beach seine hauls. Most of these occurred only occasionally, but some were of considerable importance (Table 2).

The most regular and also the most abundant species was Gobiculus flavescens occurring at about 90% of all stations with an average catch of almost 80 specimens at each positive station. Pomatoschistus minutus, Gasterosteus aculeatus and Ctenolabrus rupestris occurred at about 25% to 50% of the stations with an average of 10 to 20 specimens per positive haul. In 1983 positive stations of these species were less frequent than positive stations of cod, while they were about equally frequent in 1982. Where they occurred, they were approximately equally abundant.

In the Danish seines about 20 species were caught, but less than 10 were important (Table 3). Out of these, saithe, whiting, hake and also the older age groups of cod are known as predators of 0-group fish, but more knowledge on feeding behavior and habitat selection is needed to assess the importance of the interaction.

DISCUSSION

The five gadids had either settled or were settling in the beginning of August. Saithe and pollack appeared to have finished the settling in August as they were not caught in the pelagic trawl. In 1982 and 1983 cod had also settled at this time, while in 1981 pelagic trawl catches indicated that settling took place somewhat later. Haddock and whiting were settling in the period studied all years. For cod and haddock this is about two months earlier than in the Barents Sea (Hyllen and Dragesund 1973), but similar to what is found in Scottish coastal waters (Hawkins et al. 1985).

Hislop (1985) compared reproductive tactics and strategy of gadids and found considerable species differences. Richards et al. (1978) correlated estimates of abundance through the years 1922 to 1971 of various fish

species in the North Sea. The abundance of the species varied independently. To some extent this is also found for the year classes of abundant species at the Norwegian coast, however, here also strong year classes of several species often co-occurred (Dragesund, 1971). Studies of the diets and feeding behaviour of juvenile gadids in the North Sea indicated a low degree of competition among pelagic 0-group fish (Robb and Hislop 1980, Robb 1981). A general conclusion drawn was that competition among gadids during the pelagic and adult stages is limited or absent.

This study has shown that the degree of exposure and bottom depth are important factors for characterizing the settling areas of the gadids. Cod were found in sheltered areas in the littoral zone, however, the Danish seine catches showed that 0-group cod were also abundant at intermediate depths (20 to 50m) in more exposed locations. This is in accordance with observations from the North-Norway coast and fjords (Strømme, 1977; Soldal and Olsen, 1988), but contrast observation from the Norwegian Skagerrak coast where 0-group cod mostly are found above 20m depth (Dahl and Dannevig, 1906; Flødevigen Biological Station, unpubl. data). Taking into account the greater area with intermediate bottom depths and the occasionally very high abundance observed here, it is plausible that these depths have the major settling areas for 0-group cod.

Saithe mainly settle in the littoral. This species is most abundant in the exposed areas. In years of high abundance, saithe were frequently found in high numbers also in the sheltered littoral locations and co-occurred here with cod and pollack. Similar distribution pattern of 0-group saithe is found by Lie (1961) and Jakobsen (Institute of Marine Research, Bergen, pers. com.).

0-group haddock were settling during the observation period. Based on findings both in the Danish seine and bottom trawl catches, the lack of haddock in the littoral and the offshore recordings of pelagic 0-group haddock, the presumed main settling areas for haddock are at the higher degrees of exposure and at depths below 60m. This is also confirmed by high bottom trawl catches of 1-group haddock offshore at about 100m depth in March (Institute of Marine Research, Bergen, unpubl. data).

A synthesis of the above discussed distribution patterns of the 0-group gadids is suggested in Fig. 13. Pollack are categorized together with saithe as this species co-occurred with saithe and cod in the littoral. Whiting were scarce in the demersal catches but occurred frequently in the pelagic trawl hauls. Compared with the other gadids, this species settle later in the year, and the uncertainty as to the main settling location, prevent us from including it in Fig. 13.

Cod and saithe as well as cod and haddock do co-occur as settled 0-group fish, however, each species also inhabit major areas with no or insignificant occurrence of the others. Further, the length data showed

that when co-occurring both cod/haddock and cod/saithe exhibited pronounced size differences. There is a clear correlation between fish size and prey size among pelagic 0-group gadids (Robb and Hislop 1980), and also for older cod (Ursin 1973, Horbowy 1982). It is therefore likely that the different species of gadids will take different size of prey, and so reduce interspecific competition in the areas where they co-occur. Pollack were found to inhabit the littoral together with saithe and cod. The small size of this species (half the length of saithe) probably minimize competition.

The gadids settle in areas inhabited by a number of other species, and at least in some cases they seem to occupy the same habitats as them (i.e. Gjøsæter 1987 a, b. 1988). Competition from these species, and also predator - prey relationships can, therefore, be expected.

The food of various gadids has been described by many authors (i. e. Wiborg 1948, Lie 1961, Daan 1973, Kislalioglu and Gibson 1977). For other species data are more scarce, but apparently gobids and sticklebacks take food similar to the gadids (Kislalioglu and Gibson 1977). Crenolabrus and other labrids are assumed to take more benthic organisms (Wheeler 1969). Recent studies suggest however that Crenolabrus often look for food at the same places as 0-group cod do (Gjøsæter in prep). Although it seem likely that the species in question partly will take similar food from the same places, it is not known to what extent food is limiting, and how important competition for food may be.

None of the species taken frequently in the beach seine are assumed to be predators on 0-group gadids. In the Danish seines about 20 species were caught, of which less than 10 were abundant (Table 3). Whiting, cod, hake and to some extent saithe are known to be predators of juvenile gadids. Of these cod may be the most important one. It has been shown, however, that 0-group cod avoid habitats with older cod, and hide among benthic algae when older cod approaches (Gjøsæter 1987 b, 1988).

It is, therefore, tentatively concluded that intraspecific competition among 0-group gadids is not important, while competition between 0-group gadids and other fishes from the littoral and sublittoral may be. Further it seem that predation may not be important in the littoral, but it may be at deeper waters, where older gadids probably are the most important predators.

The data presented give a qualitative picture of the distribution of juvenile gadids at the coast of Møre. It is difficult to come to quantitative conclusions because little is known about the efficiency of the different gears, and because the sampling was not random, i.e. the sampling was restricted by topographical factors. Areas with rocks and dense vegetation could not be sampled, and hence fishes preferring open beaches with sand and mud will be overrepresented. Also, the sampling was aimed on cod based on experience from beach seine surveys conducted by T. Jakobsen (Institute of Marine Research, Bergen, pers.

comm.).

Gjøsaeter (1987 a, b) and Keats et al. (1987) indicated that 0-group cod prefer areas with algal vegetation. Other studies have suggested that cod and saithe, and possible also the other 0-group gadids are less attached to the substratum than most of the littoral species caught during this survey (Kislaliogly and Gibson, 1977) and therefore the type of bottom at the sampling locations may be of less importance.

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Table 1. Gear specifications.

Gear size	Mesh-size	Otter boards	Sweep-lines/weight
Pelagic trawl 20 m vertical opening	1600 meshes 200-20 mm	6m ²	80m/300kg
Bottom trawl 6m vertical opening	1800meshes 80-20 mm	6 m ²	40 m
Beach seine 50 m x 4 m	9 mm	-	-
Danish seine 62 m headrope Perepheri mouth 460 meshes	150-35 mm	-	

Table 2. Occurrence of some fish species in the beach seine catches in 1982 and 1983.

Species	1982			1983			Stand div.	
	Occurrence No	% of Sta-tions	Mean No of spec.	Occurrence No	% of Sta-tions	Mean No of spec.		
Cod, (<u>Gadus morhua</u>) Pollack,	12	37,5	20,8	2911	59	68,6	12,4	16.8
<u>Pollacius pollacius</u>)	21	65,6	16,0	423	46	53,5	7,5	16.9
<u>Gobiculus flavescens</u>	28	87,5	79,0	19766	76	88,4	77,3	202.5
<u>Pomatoschistus miuntus</u>	16	50,0	12,4	396	32	37,2	21,8	39.6
<u>Gasterosterus acculatus</u>	14	43,8	16,2	575	22	25,6	12,6	21.6
<u>Ctenolabrus rupestris</u>	9	28,1	14,6	331	33	38,4	8,3	23.2

Table 3. Occurrence of the most abundant fish species in the Danish seine catches.

Species	Occurrence		Mean no of spec.	Stand div.
	No Sta- tions	% of Sta- tions		
Cod, <u>Gadus morhua</u> , all ages	32	74.4	11.3	11.8
Cod, 0-group	10	23.3	88.1	169.8
Haddock, <u>Melanogrammus aeglefinus</u> all ages	37	86.0	31.3	40.1
Haddock, 0-group	10	23.3	20.8	30.2
Saithe, <u>Pollachius virens</u>	19	44.2	6.8	9.5
Plaice, <u>Pleuronectes platessa</u>	31	72.1	20.4	21.5
Whiting, <u>Merlangius merlangus</u>	15	34.9	53.6	87.5
Norway pout, <u>Boreogadus esmarkii</u>	5	11.6	37.0	60.3
Hake, <u>Merluccius merluccius</u>	5	11.6	8.8	8.7

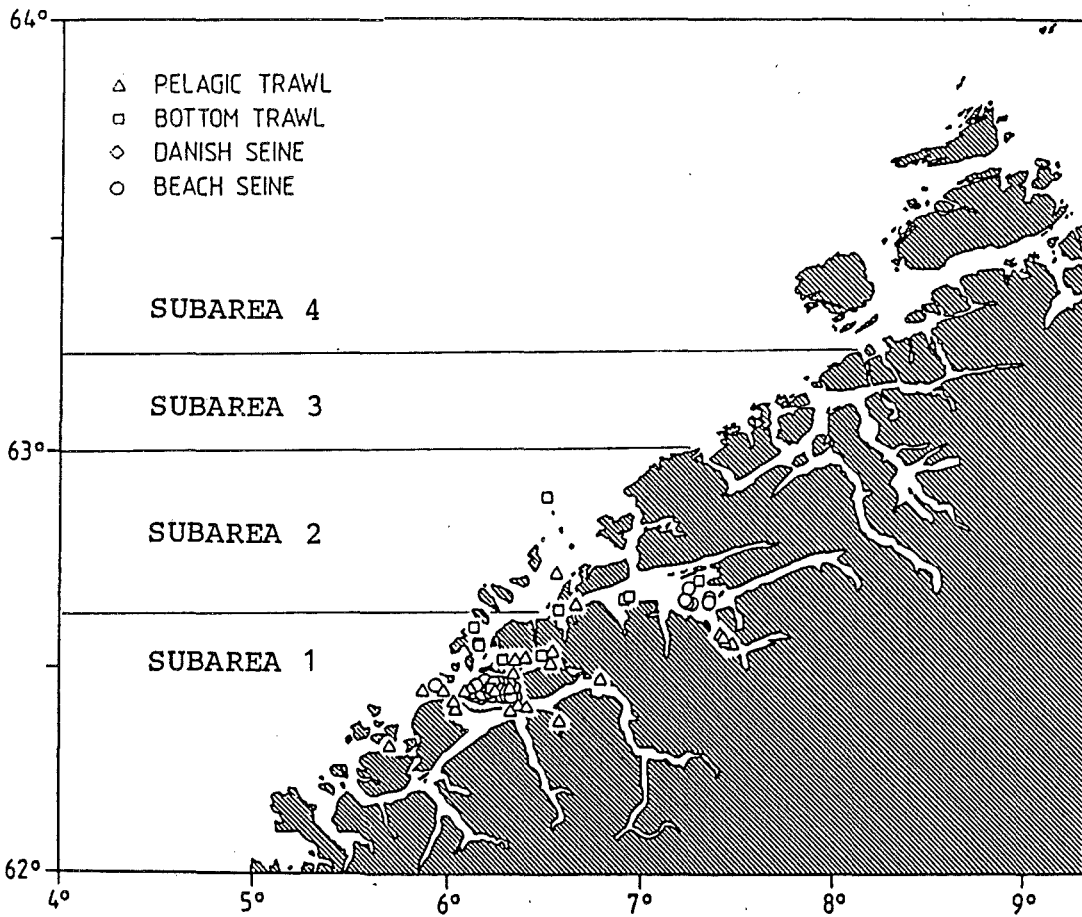


Fig. 1. Sampling stations in 1981 with sub-areas 1-4 indicated.

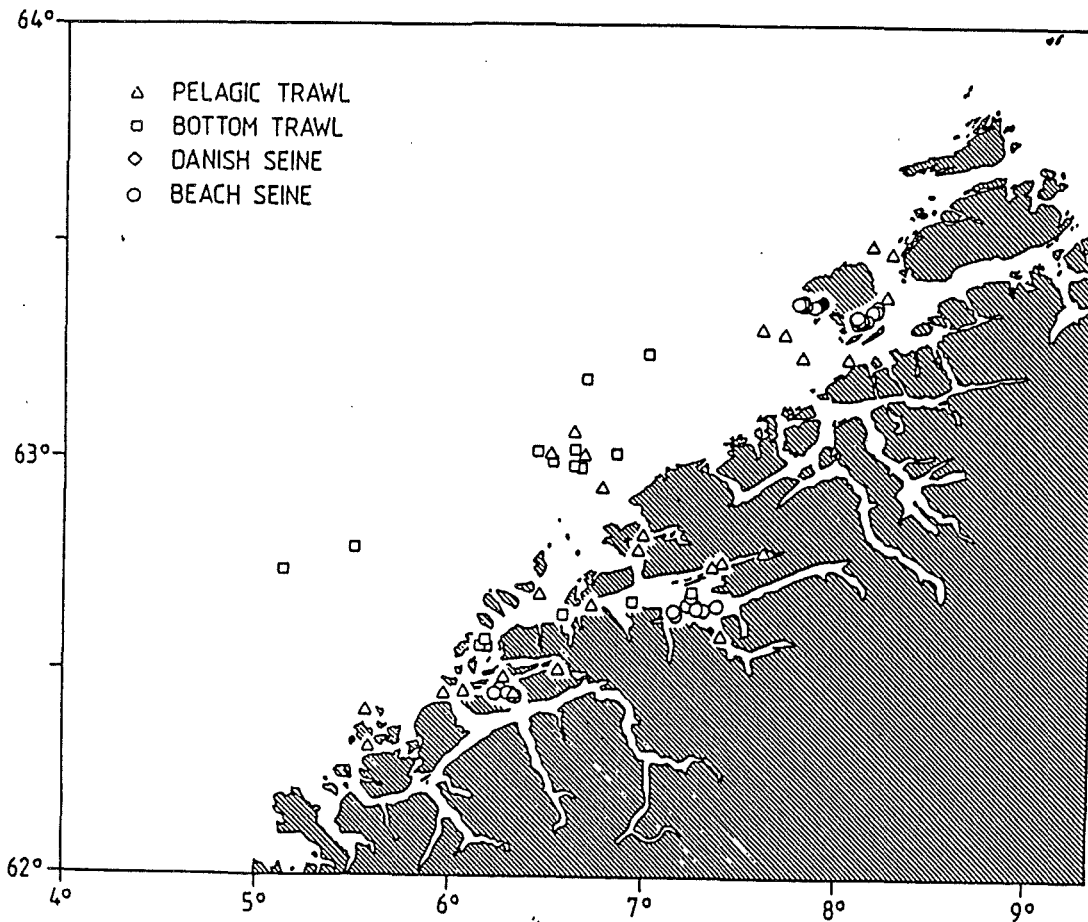


Fig. 2. Sampling stations in 1982.

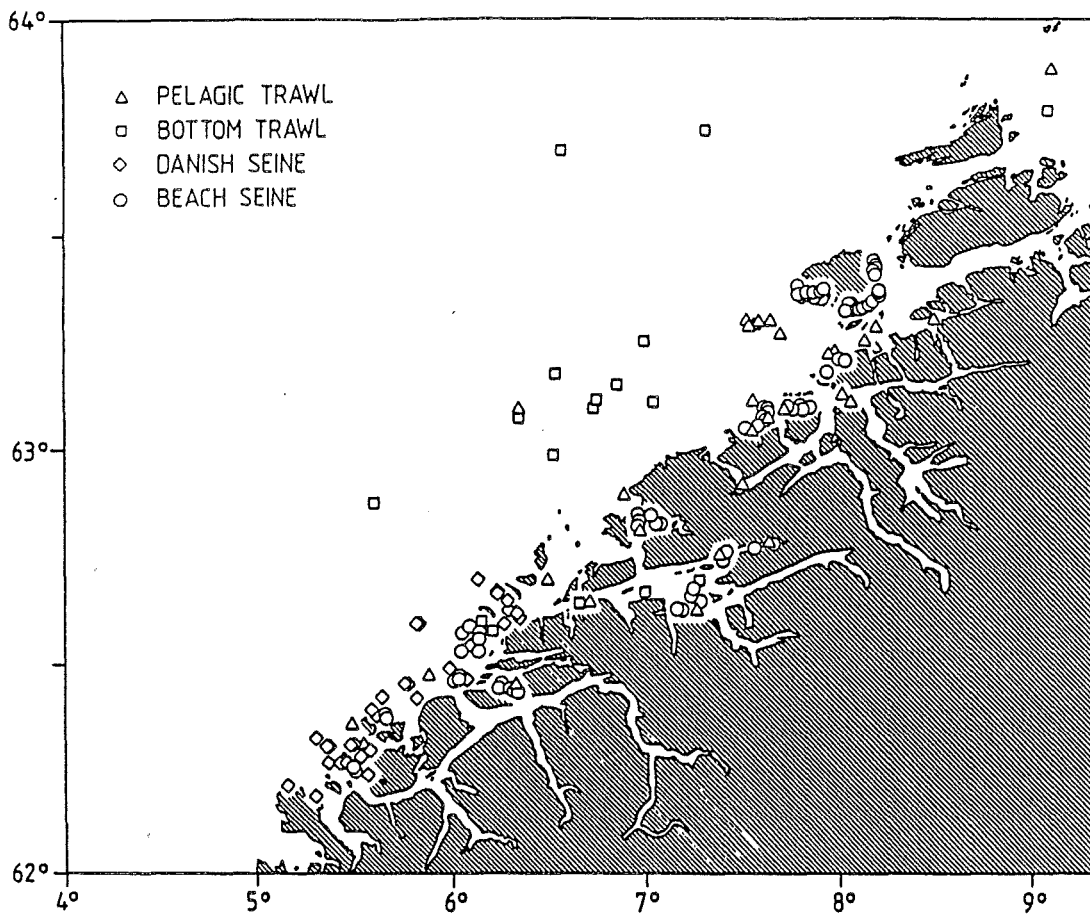


Fig. 3. Sampling stations in 1983.

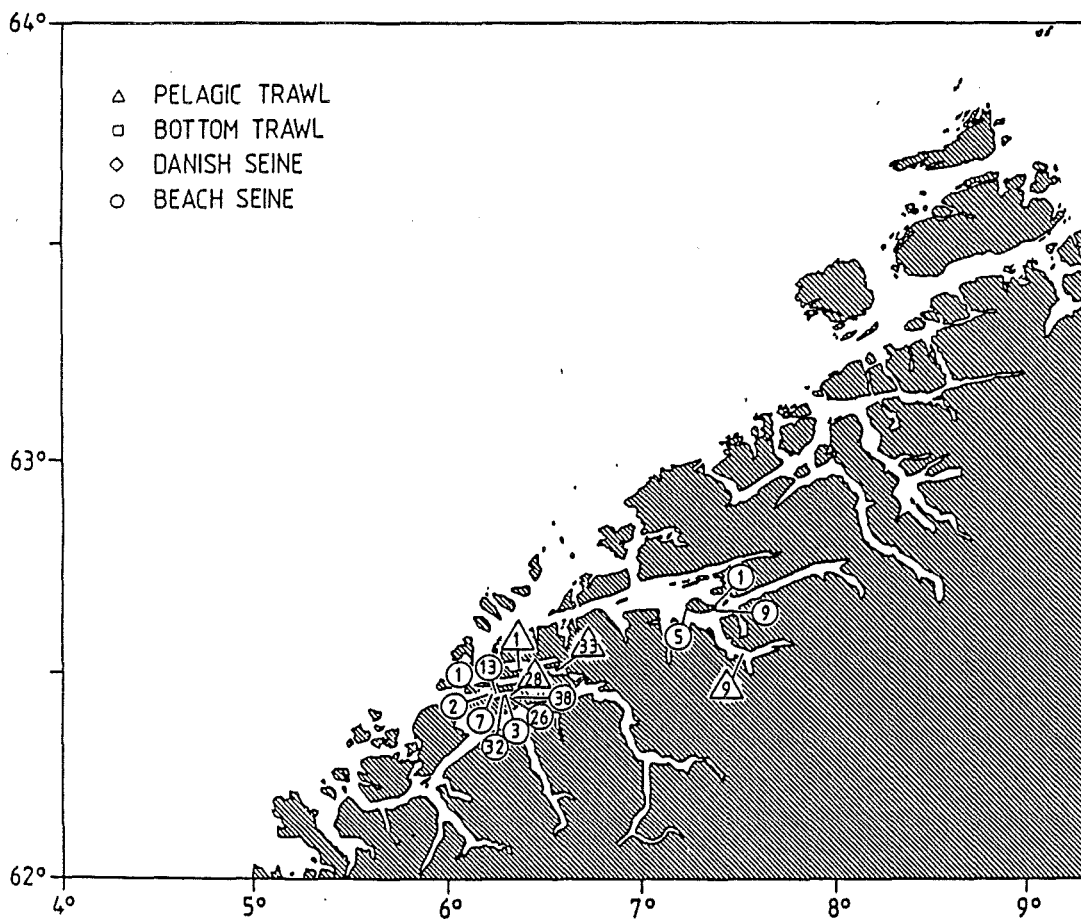


Fig. 4. Catches of cod in numbers taken by the different sampling gears in 1981.

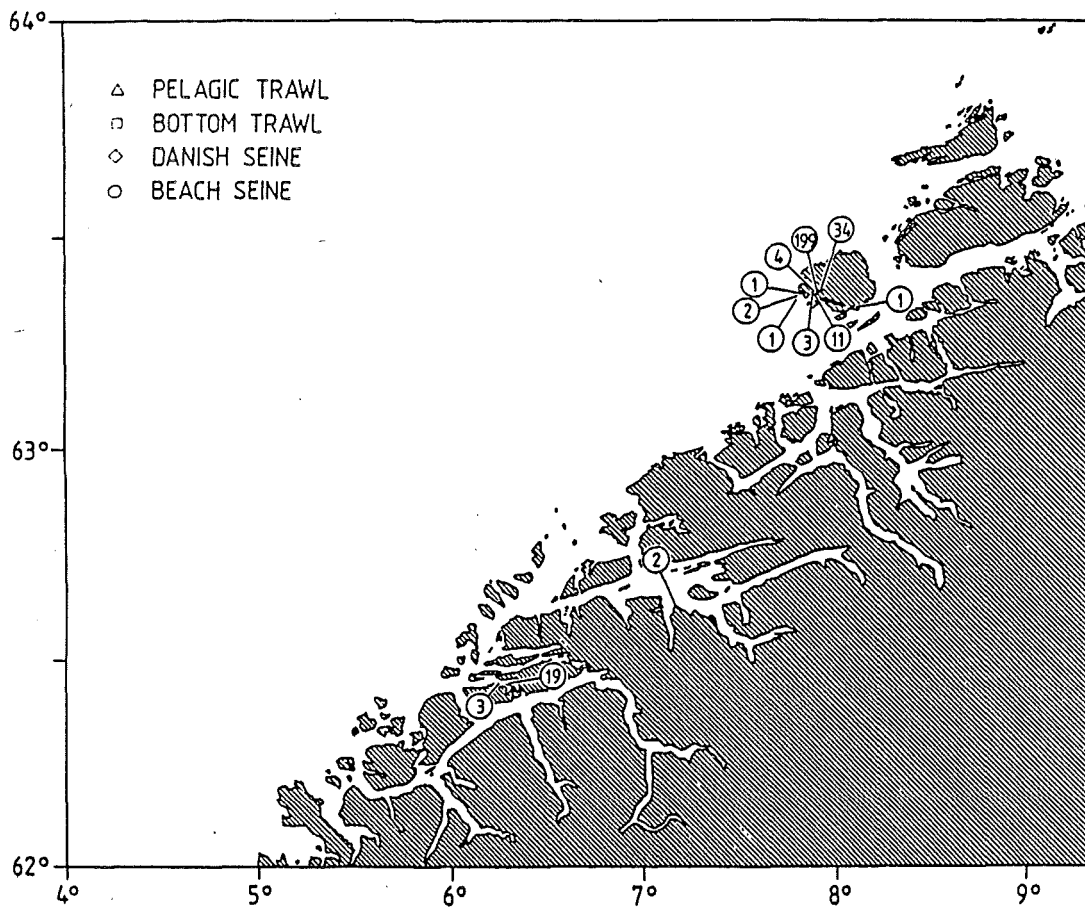


Fig. 5. Catches of cod in numbers taken by the different sampling gears in 1982.

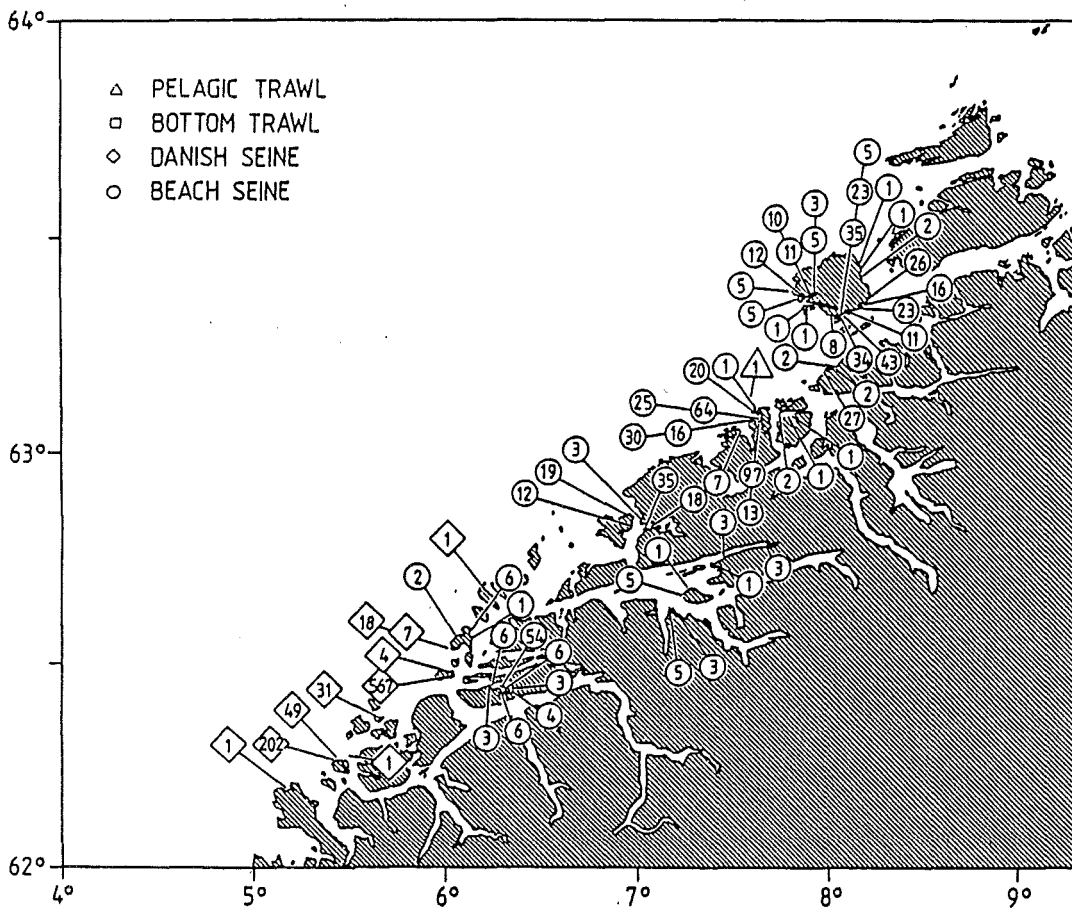


Fig. 6. Catches of cod in numbers taken by the different sampling gears in 1983.

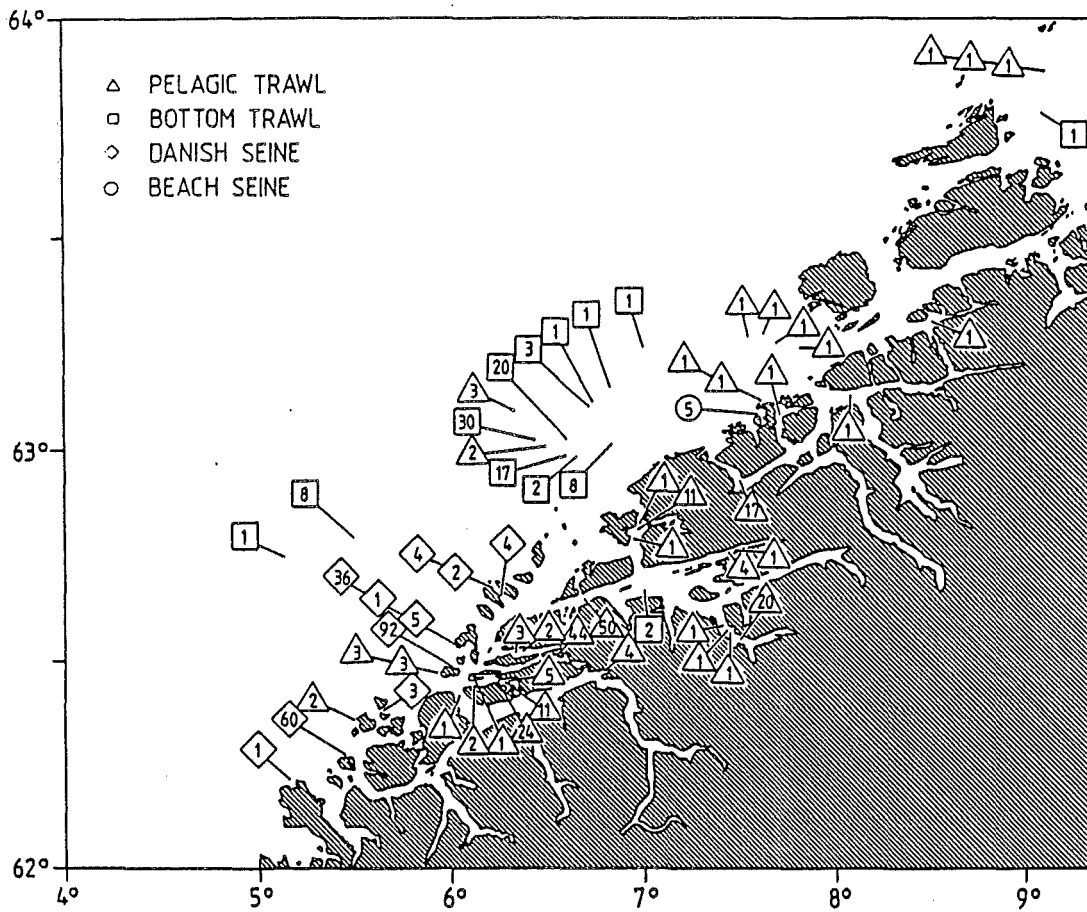


Fig. 7. Catches of haddock in numbers taken by the different sampling gears in 1981 - 1983.

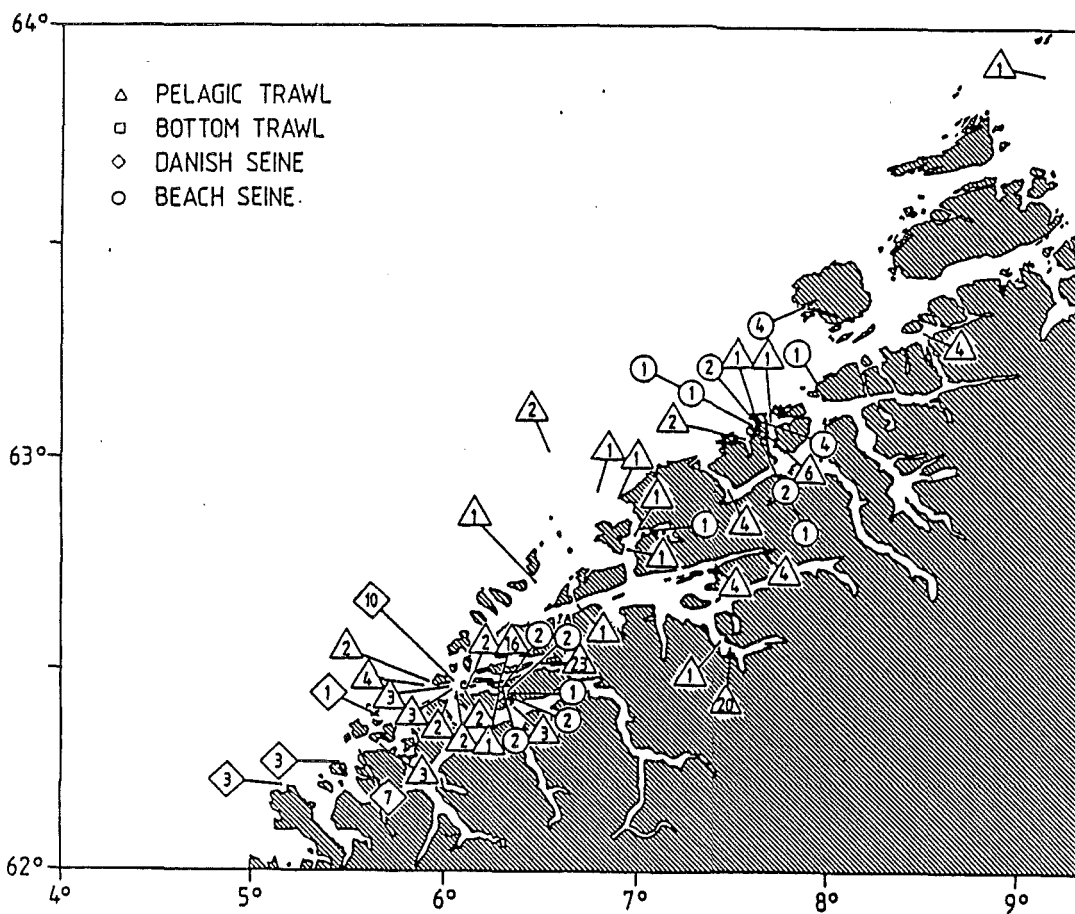


Fig. 8. Catches of whiting in numbers taken by the different sampling gears in 1981 - 1983.

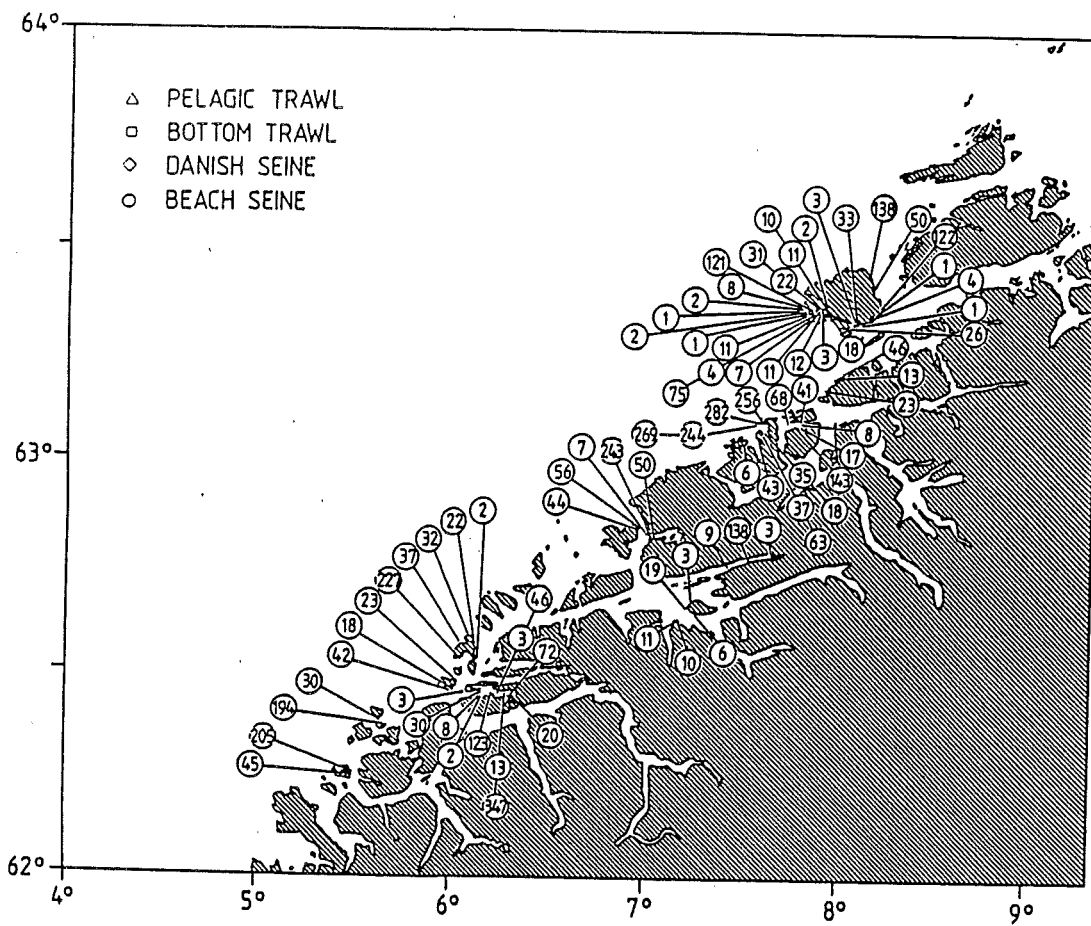


Fig. 9. Catches of saithe in numbers taken by the different sampling gears in 1981 - 1983.

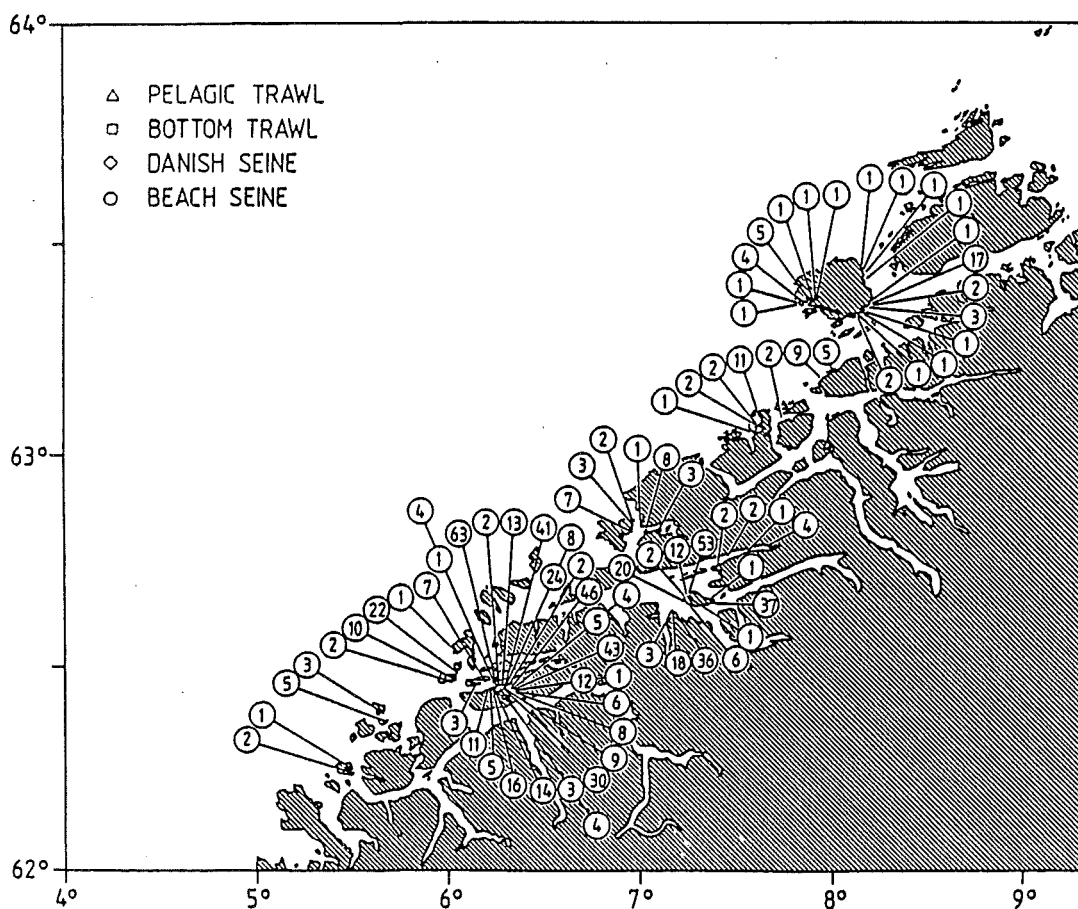
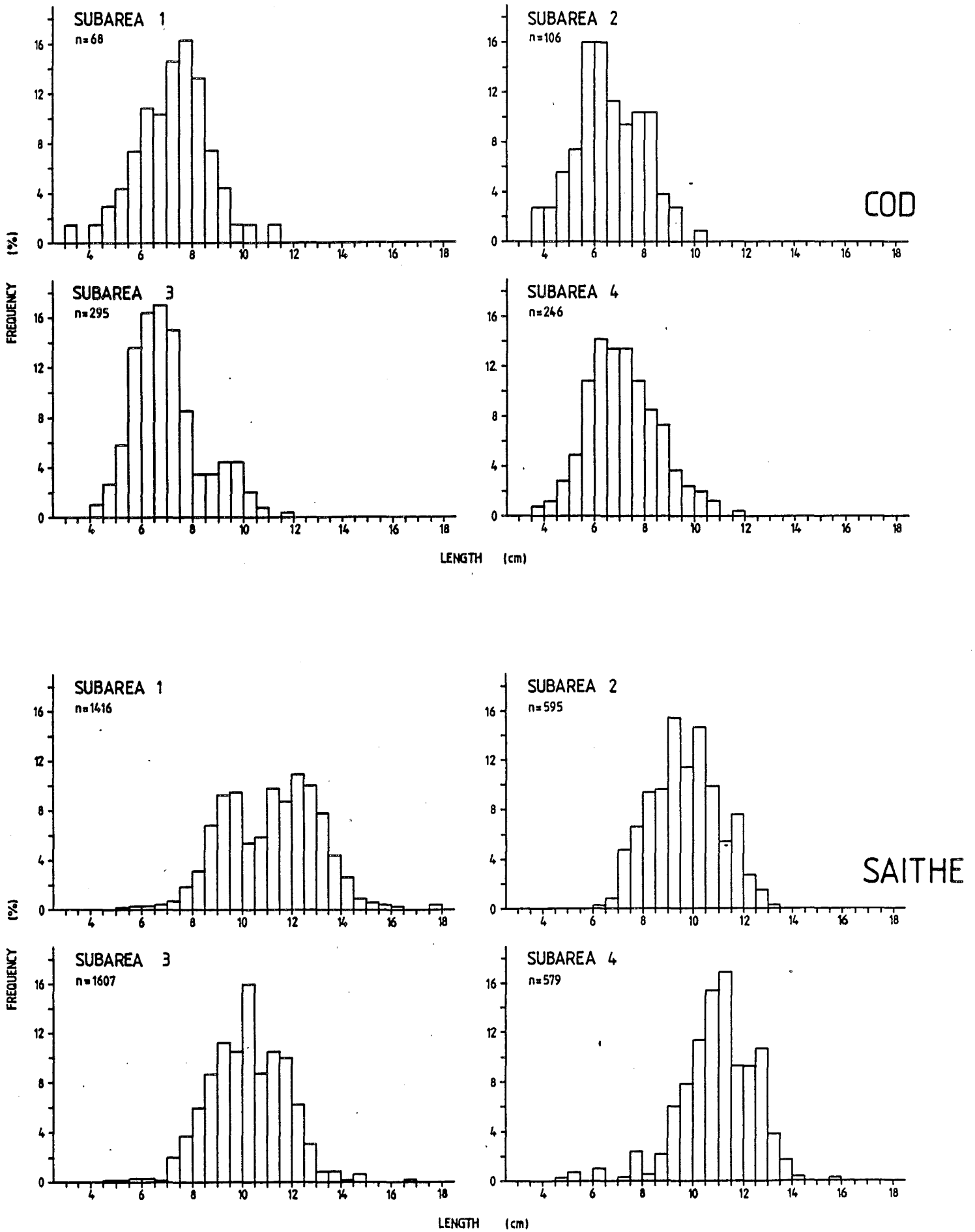
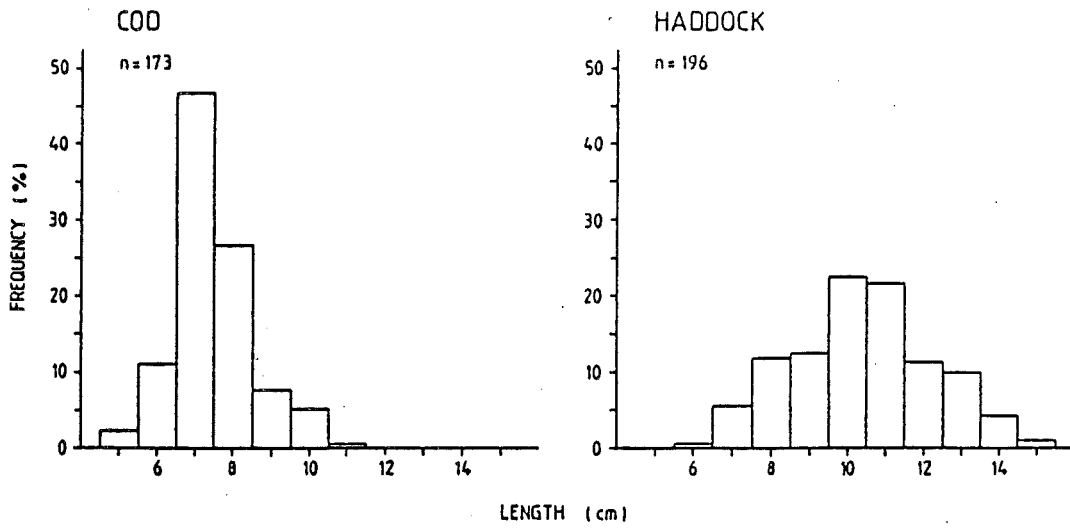


Fig. 10. Catches of pollock in numbers taken by the different sampling gears in 1981 - 1983.



A



B

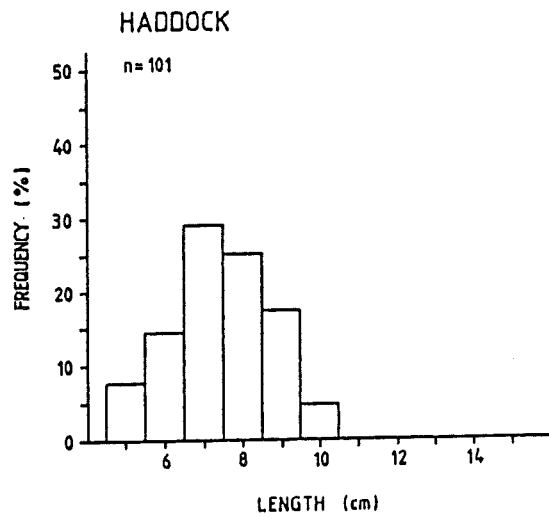


Fig. 12. Length distribution for cod and haddock caught by Danish seine a) and pelagic trawl b) in 1983.

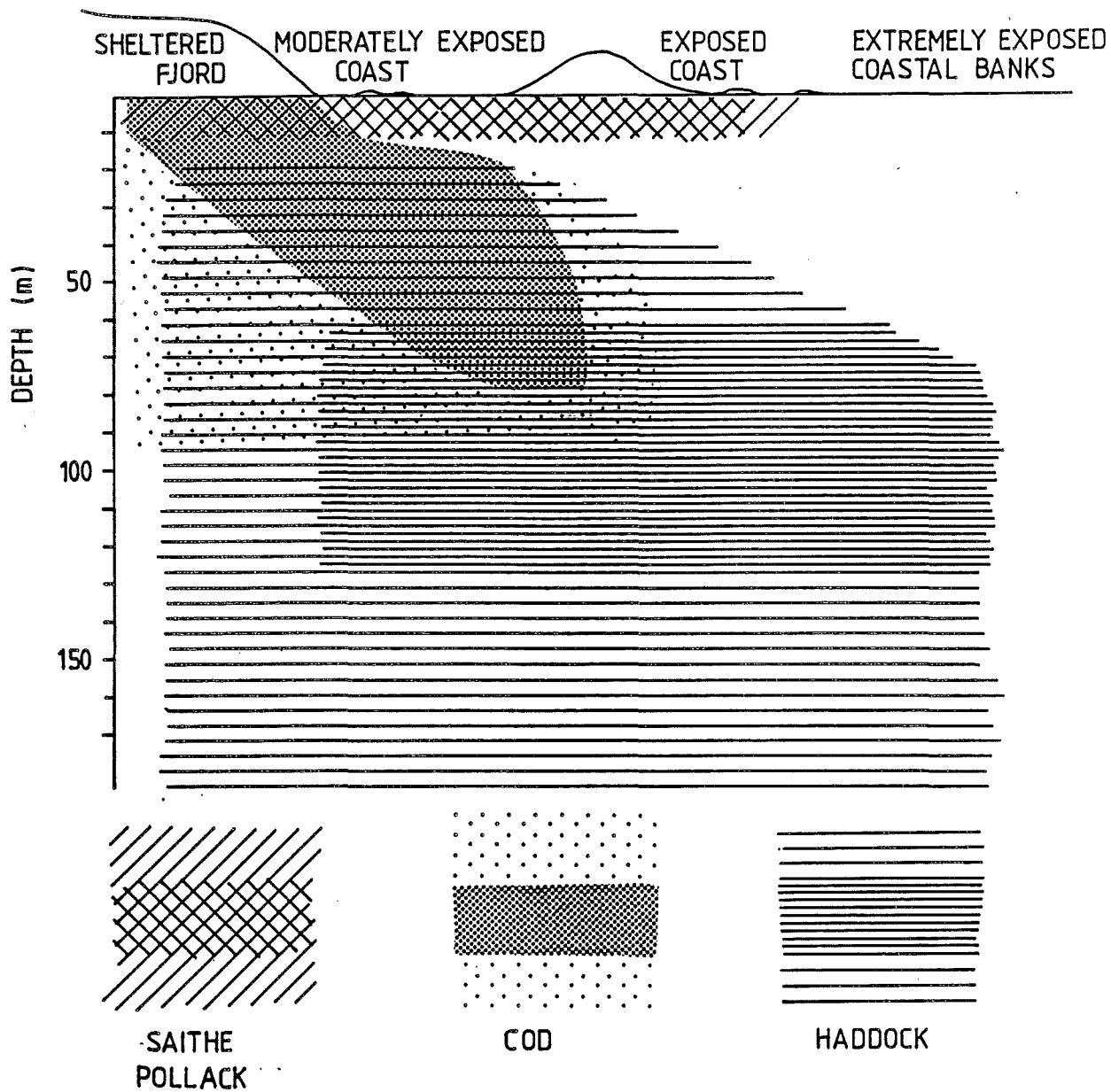


Fig. 13. Schematic presentation of the distribution of 0-group gadids in an exposure to depth coordinate system.

A SECOND FITTING FOR A RECRUITMENT MODEL OF PACIFIC COD
(GADUS MACROCEPHALUS) IN HECATE STRAIT ON THE WEST COAST OF CANADA

by

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EXTENDED ABSTRACT

In an earlier paper we showed that most of the variance in a recruitment time series could be explained by a combination of advection and ambient temperature measured while fish were in egg and larval stages (Tyler and Westrheim 1986). Our present objective is to gain insight into whether biotic, abiotic or fishery factors have been influential in establishing recruitment patterns in Pacific cod.

The model and the data

We developed an improved measure of water advection based on direct current-meter data (Crawford, Huggett and Woodward *et al.*). We compared the current measures with various meteorological and oceanographic time series in order to develop a surrogate series that would serve as an indicator of transport for the period for which we have best fishery data: 1962 to 1981. The best series for the 1962 to 1981 period was adjusted sea level at Prince Rupert in Northern Hecate Strait. Sea level increased directly with increased northward advection, and was significantly correlated.

Our first hypothesis was that stronger northward advection while the fish are in larval stages would transport the young out of Hecate Strait into the open sea, and away from the population. Since the fish are in larval stages during the first quarter of the year, particularly February and March, we used mean adjusted sea level values for the first quarter period as a surrogate measure of transport.

The second physical factor that we examined was sea-surface temperature in the period when most eggs were thought to be hatching—during the month of February. Our hypothesis was that hatch success varies on a dome-shaped

curve with ambient temperature, with percentage hatch optimizing between 5.5 and 6.5°C. This hypothesis was derived from an earlier laboratory study (Alderdice and Forrester 1971) that explored percent hatch as a function of temperature and oxygen concentration. We considered that we could use SST in February because the Strait is mixed by southerly winds from surface to bottom at this time of year, and it is known that SSTs are within one- or two-tenths of a C degree of the bottom temperature.

For our earlier modelling work, we used SST from the McInnes Island Light at the southern edge of Hecate Strait because the records extended back to our earliest fishery recruitment estimations in 1958. We have since found that CPUE at age cannot be well standardized for fishing effort earlier than 1962. Since records of SST from Bonilla Island Light went back to 1962, and since this light is much closer to the cod spawning grounds, this temperature record is considered superior and was used in the present study.

In another published study we reported evidence that Pacific herring fluctuations are related to changes in Pacific cod recruitment in Hecate Strait (Walters et al. 1986). In particular, when two or three year-classes of herring were available to adult cod as prey, then subsequent recruitment was enhanced. We incorporated two hypotheses into the present modelling study regarding herring: hypothesis 3; when young-of-the-year herring are abundant, then survival of young-of-the-year cod is improved because of extra feeding opportunity, and so a stronger cod year-class results; hypothesis 4; when young-of-the-year and 1+ herring are abundant in year t , adult cod have extra feeding opportunity and increase their fecundity so that cod recruitment in the following year ($t+1$) is enhanced.

The fifth hypothesis was that a dome-shaped stock and recruitment relationship existed. In both of the cod recruitment papers cited above, a stock-recruitment relationship improved the fit of the models to the historic time series. The published predation model built a Ricker function into the fitting procedure. In the physical factor model the stock-recruitment relationship was a nearly linear fit showing decreased recruitment with increase in stock size. It was interpreted that the adult stock was never thinned sufficiently in the particular historical series for the recruitment maximum to be evident.

We fit the 20-year time series (1962-1981) by using the response-surface analysis technique of Schnute and McKinnell (1984) that employs the likelihood statistic as an objective function to fit a multi-variate second order equation. The dependent variable was age-3 recruitment index of cod of the Hecate Strait population, from the catch per unit effort (CPUE) time series. These data have been standardized and were the subject of several other reports. It is considered that the data represent well the recruitment and adult stock fluctuations of the Hecate Strait population (Tyler and Westrheim 1986).

We reserved the data for 1982, 1983, 1984, and 1985 to find whether a model fit to 20 years of data ending in 1981 could predict recent events.

Recruitment in 1982 through 1984 was low, but a very strong year-class was formed in 1985. We felt that a test of the model would be prediction of this strong year-class.

Model fitting, prediction, and implications

The series of linear regressions carried out among independent variables showed that SST at Bonilla Island Light was inversely and significantly correlated with transport ($r=0.47$, $0.01 < p < 0.05$), and so these two variables could not be used in the same model. Still, both variables were retained because the variance patterns were different, and each could be investigated in separate models for relative goodness of fit. Similarly, prey of adult cod versus adult cod was inversely and significantly correlated ($r=0.48$, $0.01 < p < 0.05$). It was pointed out by Walters *et al.* that such an inverse relationship was similar to the classical cycling of abundances of predator and prey.

Relationships between recruitment and the five hypothetically controlling factors were initially explored one variable at a time with linear regression. The relationship between recruitment and stock size was vaguely reminiscent on a dome shaped curve, possibly indicating promise for the multivariate fit. Recruitment was negatively related with the transport index. The correlation was significant at the 10% level ($0.05 < p < 0.10$). There was no apparent relationship between recruitment and either SST, prey for juvenile cod, or prey for adult cod.

A series of two factor models was evaluated for goodness of fit to a response surface with the likelihood statistic, and also with the r^2 statistic for the linear relationship between observed and fitted values of recruitment. The pairs of independent variables used in these fittings were as follows: temperature + adult cod, transport + adult cod, temperature + prey for adult cod, transport + prey for adult cod, temperature + prey for juvenile cod, transport + prey for juvenile cod, adult cod + prey for juvenile cod, and prey for adult cod + prey for juvenile cod. Of these, two models stood out in that their fit to the recruitment data was appreciably better than the other models: transport + adults had the highest r^2 , accounting for 60.3% of the observed to fitted variance, with a likelihood statistic of 107×10^3 ; and the other model was temperature + prey for adult cod with an r^2 of 50.0, and likelihood value of 95×10^3 . Likelihood values for other models ranged 124 to 172, with r^2 values of 12.0 to 38.4%. Thus the hypotheses of a relationship between recruitment and temperature, transport, adult stock size and prey for adults seem supported.

It was possible to test four models of three factors each without putting correlated variables together. We added herring as prey for juvenile cod to the two factor models of (1) temperature + adult cod; (2) transport + adult cod model; (3) temperature + prey for adult cod model; and (4) transport + prey for adult cod. For the last model the iterative likelihood fitting did not converge on a unique response surface, and so the model was discarded. The other three models had successful fittings. Adding herring to the temperature + adults model increased r^2 from 12.0% to 54.7%. Models (2) and (3) had r^2 values of 72.0 and 77.9%,

respectively. The corresponding likelihood statistics were 65×10^3 , 61×10^3 , and 48×10^3 . The substantial improvements in the fitting seem to give support to all five of the hypotheses.

Exploration of predictability was the next step in testing of models. For the previous modelling paper we did not at that date have evidence of the extra strong, 1985 year-class as an event against which to test the model. Instead we had only the series of low level, similar year-classes of the late '70s and early '80s. Though the value of the recruitment index (CPUE, number per hour) is not completely finalized at this writing, the '85 year-class was at least three times as strong as anything in the ten previous years. Therefore a good model must be able to predict this year-class. Of the two factor models, the temperature + adults model gave an abundance of only 44% of the observed value of the '85 year-class. The transport + adults model gave a prediction that was 93% of the observed value. For the three factor models, none predicted the '85 year-class. Because of the poor showing of the herring in 1984 and 1985, adding herring as prey gave predictions that were extremely low—all less than 1% of the observed value. Our conclusion was that the transport + adult cod model was the only one that would make predictions.

The response surface of the transport + adult cod model was first examined by looking at cuts through the surface. This was done by plotting the computed values of the age-3 CPUE recruitment against the adult cod CPUE at the mean value of the transport index for the time series. The resulting relationship between the recruitment and spawning stock size indices was dome shaped and skewed to the left (the ascending limb being shorter than the descending). Maximum total recruitment occurred at an adult catch-rate of approximately 500 kg/h. The curve was reminiscent of a Ricker stock-recruitment function. The relationship between recruitment and transport was examined as a cut through the surface at the value of the adult stock index that produced maximum recruitment (500 kg/h). The relationship was a monotonic, decreasing curve reminiscent of a negative exponential function. In addition, the complete response surface was plotted as a series of contours of recruitment CPUE, with the axes of adult cod CPUE and the transport index. The dome shape of the stock recruitment relationship was evident over the range of transport values, but the production rate diminished rapidly with increasing transport values.

Implications for fisheries stock assessments are that the Hecate Strait stock is likely to experience recruitment overfishing at standardized catch rates of less than 500 k/h regardless of the degree of transport to the north. High transport will interfere with recruitment. Recruitment rate is apparently density dependent, and supported by herring as a forage fish, though in the absence of herring, strong recruitment still occurs, possibly supported by alternative predation on sand lance (Ammodytes hexapterus), as observed in yet unpublished stomach content data.

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RELATIONSHIP BETWEEN SPAWNING STOCK BIOMASS AND RECRUITMENT INDICES FOR NORWEGIAN SPRING SPAWNING HERRING

by

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INTRODUCTION

The Norwegian spring spawning herring spawns on the Norwegian west coast in February-March. The benthic eggs hatch after 6-8 weeks and the larvae and 0-group herring are carried northwards by the major water currents and in late autumn they are distributed in Norwegian coastal waters and occasionally in the Barents Sea.

Prior to 1960, the size of the adult herring stock ranged between 5 and 10 million tonnes, but it was almost completely fished out by 1970. In the period 1975-1982 the spawning stock increased from about 100 thousand tonnes to 500 thousand tonnes and the geographical distribution of both juveniles and adult herring was restricted to the Norwegian coastal areas.

An investigation series on 0-group herring has been carried out by the Institute of Marine Research since 1975. The aim of this investigation series, which has remained unchanged during this period, has been to produce a series of comparable measurements of year class strength. This is done by carrying out an acoustic survey of the Norwegian coastal areas, and in some years also in the Barents Sea. It was planned that these measurements could be applied to foresee the long term development of the spawning stock.

METHODS AND RESULTS

0-group herring

Acoustic abundance estimates of 0-group herring have been calculated on the basis of the results from an acoustic survey which has been carried out in November-December in the fjord and coastal areas of western and northern Norway since 1975. In the years 1983-1985, when the results from the international 0-group surveys in the Barents sea showed that the 0-group herring distribution area also included wide areas in the Barents Sea (Anon 1983, 1984, 1985) there were also conducted acoustic surveys in that area at the same time as the investigation in the fjord and coastal areas. The 0-group estimates from November-December are taken to be representative of 1-group estimates 1 January the following year.

The results from this survey programme are given in the text table below:

Year	Abundance of 0-group herring (millions)	
	Norwegian coast	Barents Sea
1975	538	
1976	1888	
1977	206	
1978	603	
1979	1729	
1980	117	
1981	133	
1982	1468	
1983	6865	17850
1984	701	3806
1985	502	2670
1986	204	
1987	410	

A target strength of $TS=20.0-71.9$ dB has been applied (Foote 1987, Anon 1988). The methodology of these surveys have been discussed by Røttingen (1987). Due to uncertainties in target strength, sampling etc, these estimates, although presented as million individuals, should be regarded as abundance indices rather than absolute estimates.

Estimates of 3 year old herring

The estimates for the 3 year old herring for the year classes 1975-1981 are from Anon 1988. They are derived from a VPA run from 1987 backwards and tuned against the 1984 stock estimate obtained by tagging. The method is therefore not valid for year classes recruited to the spawning stock after 1984 (ie year classes after 1981). The results are given in the text table below:

Year class	:	1975	1976	1977	1978	1979	1980	1981
Abundance (millions):		127	580	422	392	630	97	64

The estimates of 3 year old herring for the year classes 1982 to 1985 are calculated on the basis of the results from an acousting survey on the coastal areas in the spawning season in February-March 1988. These yearclass estimates are taken as representative for the abundance of 1 January 1988 and are backcalculated by VPA to 3 years old fish. The results are given in the text table below:

Year class:	:	1982	1983	1984	1985
Abundance (millions):		126	10030	176	255

Relation between abundance indices of 0-group and absolute estimates of 3 year old herring

As pointed out earlier the 0-group estimates should not be regarded as absolute estimates, but as abundance indices. It is therefore not appropriate to calculate instantaneous mortality coefficients to relate the 0-group indices with the absolute estimates as 3 year old fish.

In the years 1975-1982 the great majority of the 0-group was distributed on the Norwegian coast. Although in some years (especially in 1976 and 1979) the main part of the 0-group were distributed in fjords south of 68° N, and in other years (1982) the main part was distributed north of 68° N, it would be natural to believe that the conditions for growth and survival should in principle not differ to any great extent.

In Fig 1 the 0-group abundance indices for the years 1975-1982 are plotted against the absolute estimates of this year class as 3 years old, and a linear regression is calculated. Two data points, for 1977 and 1982 are omitted in the calculation of the regression coefficient. For some unknown reason the 0-group of the 1977 year class has been underestimated. For the 1982 year class the situation is the opposite. This year class seems to be much weaker than the 0-group abundance indicates. This year class had an extreme northerly distribution (fjords of Finnmark), but it is at present unknown if this should result in a decreased survival.

The relation shown in Fig 1 is valid when the nursery area of the herring is limited to the Norwegian coastal areas. However, in the years 1983-1985 the main component of the 0-group herring was distributed in the off shore areas in the Barents Sea. In the text table below are given the calculated abundance of 3 year old herring for the year classes 1983 to 1985, according to the relation given in Fig 1 (the combined 0-group index for the Barents Sea and coastal areas has been used in the calculations), and corresponding estimates derived from a VPA tuned against the acoustic estimate in winter 1988:

Year class	Abundance	
	Calculated from 0-group ($N_3 = 0.3045N_0 + 60.8 \times 10^6$)	Measured as adults and backcalculated by VPA
1983	7630	10030
1984	1225	176
1985	875	255

The 1983 year class shows up as 3 years old as more abundant than than calculated from the 0-group index, while the two following year classes, 1984 and 1985, seem to be much weaker.

DISCUSSION

During the acoustic 0-group survey, herring of the 1983 year class was often encountered in dense schools, and this may have resulted in an underestimation of this year class as 0-group (Røttingen 1984, 1987).

Taking into account the different methods used in calculating the abundance of adult herring (tagging and acoustic), the results indicate that the survival of the 1983 year class has been on the same level as observed in the coastal component in the years 1975-1981. For the year classes 1984 and 1985 the mortality has obviously increased dramatically.

Satersdal and Loeng (1987) indicate that in periods with increased heat transport in the Atlantic component of the Norwegian current, the environmental conditions which result in year classes of high abundance are present.

The period 1983-1985 was characterized by such a heat inflow, and in August-September these years large amounts of both 0-group cod and herring were distributed over wide areas in the Barents Sea. (Anon 1983, 1984, 1985). However, the 1984 and 1985 year classes of herring were strongly reduced due to the predation pressure from the growing stock of young cod, the 1983 year class was less exposed to this predation pressure. This is illustrated by the consumption figures given in the text table below (modified from Mehl 1987):

Year class of herring	Age group of herring	Number (billions) consumed by cod (north of 67° N)
1983	0	(measurements of consumption started in 1984)
	1	7.0
	2	5.4
	3	1.8
	Total	14.2
1984	0	12.0
	1	9.5
	2	0.6
	Total	22.1
1985	0	35.2
	1	10.3
	Total	45.5
1986	0	Total 0

It should be noted that a major part of the 0-group herring of the year classes 1984-1985 are consumed prior to the time of the 0-group survey.

The present analysis thus indicates that the natural mortality rate from late 0-group stage to 3 year old fish varies for the different year classes. This variation is caused by changes in abundance and distribution of both 0-group herring and of the main predator stock.

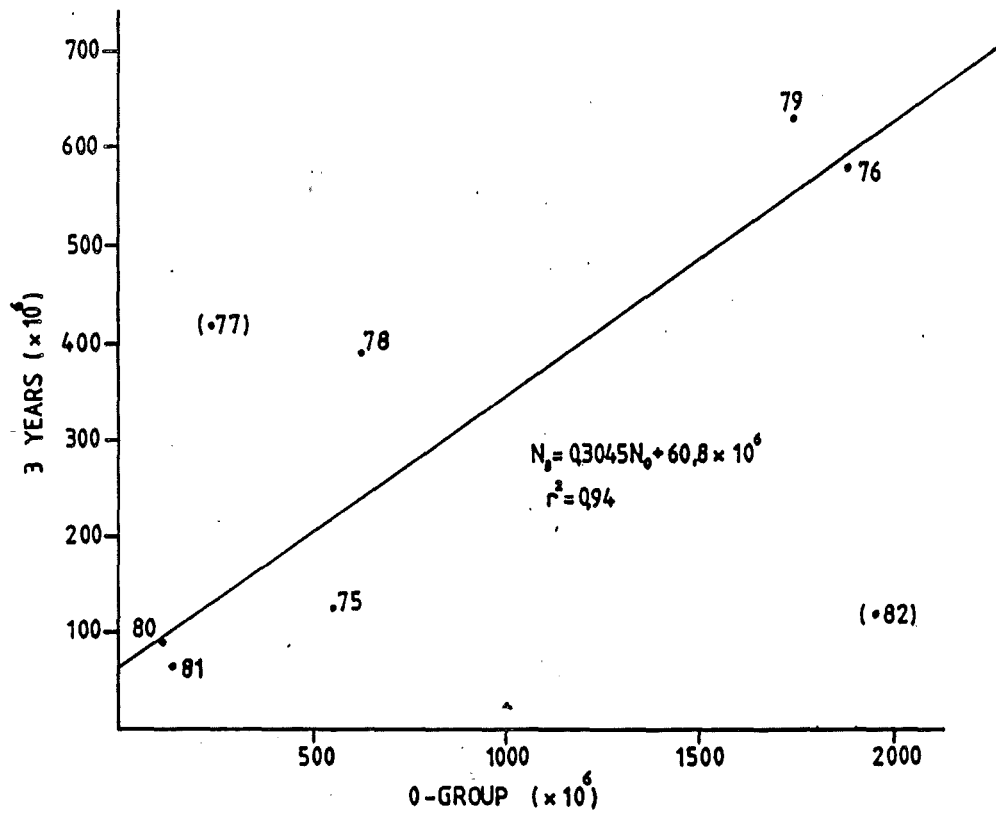


Fig 1 Relationship between age 3 numbers from VPA and 0-group indices from acoustic survey

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Variable Growth of Recruits and the Stock-Recruit
Relationship for Bristol Bay (Alaska) King Crabs

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ABSTRACT

The stock-recruit relationship estimated for Bristol Bay red king crabs provides information needed for management regarding the appropriate level of harvest given the current state of the spawning stock. This study examines the effect of potential inaccuracies in the recruit data on the estimation of the spawner-recruit relationship. Errors of concern may stem from age mis-classification, or from assuming a constant time lag when growth of recruits may be variable due to a variable temperature regime. Results indicate that variations in recruitment and mortality will bias estimates of recruits calculated indirectly from growth curves, and corrections are introduced based on a knowledge of the extent and direction of the bias. Similarly, the data are adjusted for hypothesized variations in the time lag. Effects of aging bias on the spawner-recruit data set have been minor, but the assumption of temperature-dependent growth could lead to differing management implications.

INTRODUCTION

The crab fisheries of Alaska form a significant part of the fisheries of the north Pacific, as well as contributing considerably to world crab landings (Otto 1981). The

southeastern Bering Sea, which includes Bristol Bay, has historically been a top producer of the red king crab, Paralithodes camtschatica, which is the predominant commercial king crab in Alaska. The Bristol Bay fishery for red king crabs typically occurs in the fall of the year, when the crabs are approaching maximum meat fullness, and is prosecuted with large modern vessels using individually-bouyed pots (traps). Several management measures are used to ensure the reproductive viability of the stock: female crabs are not landed, but returned to the sea when encountered; sublegal males, smaller than the minimum carapace width limit of 6.5" (165mm), are likewise returned to the sea; seasons are set to avoid the spring molting and mating period; and quotas are set based on stock abundance and desired exploitation rates.

Regarding the establishment of quotas, abundance estimates for the Bristol Bay stock of red king crabs are provided by an annual summer trawl survey (Stevens, MacIntosh and Stahl-Johnson 1987). Area-swept estimates (Alverson and Pereyra 1969) of legal males, as well as other stock components, are used to make annual quota determinations. In addition, estimates of spawner and recruit abundance from the survey data go back to 1968, and were first fit by stock-recruit models in Reeves and Marasco (1980). Stock-recruit models hold potential for providing guidance in the adjustment of exploitation rates as the spawning stock fluctuates with reference to its optimum level. The time series of abundance estimates available for the Bristol Bay stock has permitted an estimation of S_{max} for the Ricker model, to which the current level of S_{max} spawners may be compared. The result of this comparison can provide guidance on adjustment of the rate of exploitation. If the current level of spawners is below S_{max} , a lower rate may be most prudent; at higher spawner S_{max} levels more liberal rates of exploitation may be allowed.

The spawner-recruit relationship for Bristol Bay red king crabs relates five-year old male recruits to the female spawning stock. Although the fishery harvests only males, the rate of exploitation may impact females through reduced clutch size or handling mortality. Annual spawning abundance and population fecundity, which is expressed in terms of an average population clutch size, is assessed following the mating period. Abundance of mature females is adjusted for clutch size thereby implicitly accounting for the effect of changing sex ratios, to the extent that less-than-full clutches are the result of low abundance of mating male crabs. External fertilized clutches are carried for approximately one year before hatching. Male recruits are considered adequately recruited to the survey trawl gear

(Incze, Otto and McDowell 1986) rather than to the fishing gear, such recruitment occurring several years later. They are further considered to be age 5 and are related to the spawning stock six years earlier, due to delayed hatching.

The purpose of this paper is to assess the effects of errors due to variable growth of recruits on the form and parameters of the stock-recruit curve. Two types of errors are considered: (1) bias related to the inability to age crabs accurately because there are no known hard parts to record growth history annually, and (2) bias in the time lag between spawners and recruits caused by variable growth of recruits prior to entering the fishery. In the first situation, error arises when a growth equation determined from tagging is solved for t (age) but does not account for error around the curve. The effect of variation in length at age on these indirect estimates of "age 5" recruits is assessed by simulation of crab growth characteristics. In the second case, The hypothesis proposed by Stevens (1988) relating growth of sublegal male crabs to their temperature environment is evaluated. If growth is temperature dependent as proposed, then the lag between spawners and resulting recruitment is larger and more variable than growth based on earlier tagging studies.

BIAS DUE TO INDIRECT AGE ESTIMATION

In this section, the procedure for estimating age 5 recruits from a von Bertalanffy growth curve is given, as well as an evaluation of the resulting estimates based on a model of king crab growth. Corrected recruit data resulting from this evaluation are then used to re-estimate the spawner-recruit relationship. The current spawner-recruit relationships for Bristol Bay red king crabs, employing indirect estimates of age 5 male recruits, is shown in figure 1 (years of recruit estimates shown), with the plotted data given in table 1. It should be noted that the solid curve of figure 1 represents an improved nonlinear fit to the data compared to log-transformed fit, based on R-squared values of table 2. Although transformed data have been used in earlier analyses (Reeves and Marasco 1980; Reeves 1982; Jamieson 1986), untransformed fits of the Ricker model will be used for comparisons in this study.

Recruit estimation

Indirect estimates of recruits are based on the study by Weber (1967), who utilized modal analysis to derive a growth curve for immature crabs, and Balsiger's (1974) analysis of

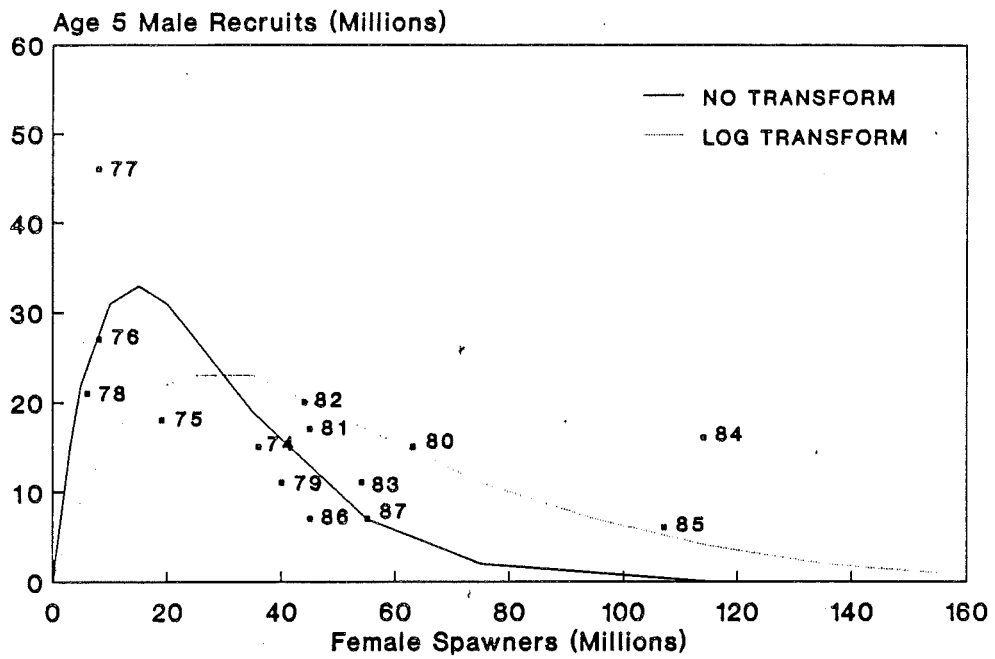


Figure 1. Uncorrected spawner-recruit relationships for red king crabs.

Table 1. Spawner-recruit data for Bristol Bay red king crabs.

Year i	Female spawners (millions)			Age 5 male recruits (millions) in year i+6 (1)		
	>89mm	Percent full clutch	Adjusted for clutch size	Un-corrected	Corrected for year class changes	Corrected for temp. dep. growth
1968 (2	53.7	67%	36.0	15	15	24
1969 (2	28.5	67%	19.1	18	18	29
1970	13.0	62%	8.1	27	24	12
1971(2,3	12.6	67%	8.4	46	55	5
1972	12.1	49%	5.9	21	14	13
1973	76.8	52%	39.9	11	11	7
1974	72.0	88%	63.4	15	15	24
1975	58.9	77%	45.4	17	17	13
1976	71.8	61%	43.8	20	20	14
1977	150.1	36%	54.0	11	11	5
1978	128.4	89%	114.3	16	16	5
1979	110.9	96%	106.5	6	2	0
1980	67.6	67%	45.3	7	9	
1981	67.3	81%	54.5	7	7	

- (1 Lag is variable for data corrected for temperature-dependent growth
- (2 Missing clutch size value replaced with average for the series (67%)
- (3 Missing abundance estimate replaced with average of adjacent years

Table 2. Nonlinear regression estimates for four red king crab spawner-recruit data sets.

Parameter estimates	Log transform	No transform	Year class corrected	Growth corrected
b	0.036	0.070	0.069	0.042
Smax (1/b)	28	14	14	24
95% CI(Smax)	10-38	11-18	9-19	14-34
var(Smax)*	24.5	3.7	5.5	26.6
var(b)	4.11E-05	8.86E-05	1.24E-04	8.26E-05
a	2.27	6.29	6.19	2.26
var(a)	0.660	2.053	2.900	0.587
R sq.	-0.46	0.25	0.25	0.36

* Approximated by the delta method

tagging data for mature male king crabs. The latter utilized information on molting frequency and growth increment per molt to construct growth curves for tagging periods in the 1950's and 1960's. Carapace length-at-age data for these two studies were combined and fit with a von Bertalanffy growth curve having the following parameter estimates: $k=0.16$, $L_{inf}=190\text{mm}$, $t_0=0$. The growth function is then solved for t as a function of carapace length in mm, and approximate (rounded to the nearest 5-mm) equidistant intervals around each whole age value are established. This process is shown diagrammatically for age 5 recruits in figure 2, indicating a 95-109mm interval for this age group.

Evaluation of recruit estimates

A growth simulation model developed by Somerton (1981) was used to evaluate estimates of age 5 recruits. The GROW model incorporates estimates of molting probabilities, growth per molt and survival to compute size distributions by age for given cohorts of crabs. Size distributions of initial cohorts are computed from input values for mean size and variance and initial number in the cohort. In successive simulation years the number of crabs within each 1-mm size interval is determined by molting probabilities, growth increment and survival for that interval. Growth increments are determined by means of Hiatt plots relating postmolt size to premolt size. Simulation output includes annual size distributions, specified by molting history, of a cohort over its lifespan, as well as the number alive and mean size for each simulation year.

Base parameters for evaluation of recruit estimates are given in table 3, with the exception of molting probabilities which were calculated as the average of the two sets of molting probability functions in Balsiger (1974). Mean size represents age 3 determined from the von Bertalanffy growth curve, its variance having been calculated from data given by Stevens (1988) for crabs of that size. Annual survival is based on an average value calculated from survey age compositions derived from the growth curve. Hiatt parameters were selected to reflect the growth curve, and represent the situation where the increment per molt (year) changes from 15 to 13mm at a size of 100mm. Figure 3 shows distributions for ages 3 through 8 generated by the basic parameter set. During simulations, such "actual" size-at-age distributions were generated and then age groups were estimated from them by taking sections of the overall length range corresponding to growth curve size-at-age intervals, and summing crabs of all ages in each section. As an example, the age 5 recruit length interval estimated from the von Bertalanffy curve is superimposed on the distributions in figure 3.

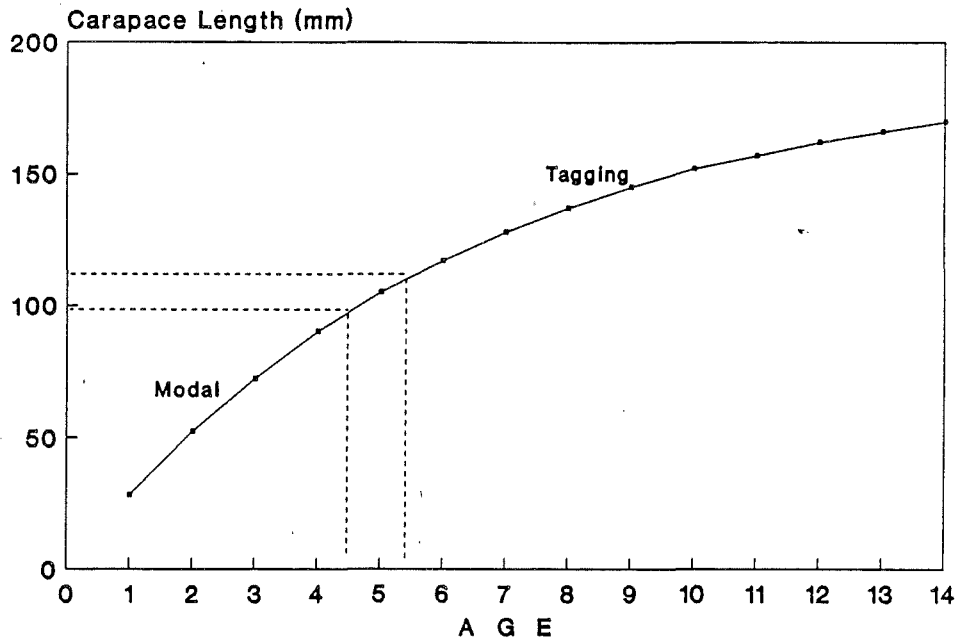


Figure 2. Von Bertalanffy growth curve for red king crab males.

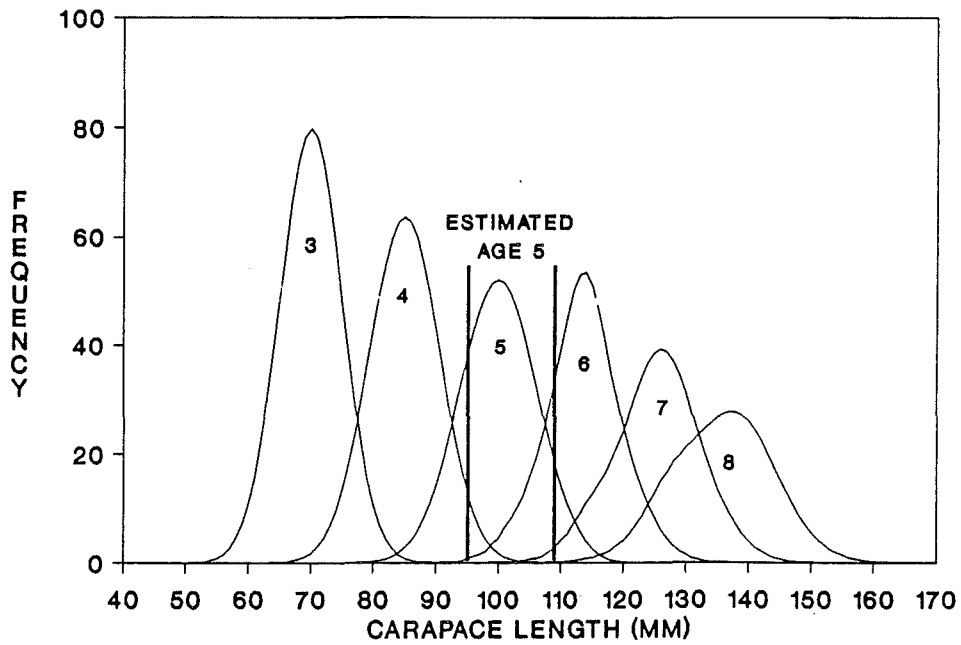


Figure 3. Simulated size distributions for age 3-8 crabs, with estimation interval.

Table 3. Base parameters for GROW model simulations.

Initial cohort numbers	1000
Mean size (mm)	70
Variance (mm)	25
Annual survival	0.9
Hiatt parameters:	
Intersection point (mm)	100
Lower intercept (mm)	15.0
Lower slope	1.0
Upper intercept (mm)	13.0
Upper slope	1.0
Variance	6.9

Simulated actual and estimated numbers at age are shown in figure 4 for the case of constant recruitment. Bias, indicated by the ratio of estimated to actual values, increases with age. It is relatively minor through age 8 and insignificant for ages 4 and 5, but increases at age 9 and above, leading to a tendency of increasing underestimation with age. This tendency is caused by the increasing overlap of size distributions with increasing age. The age of interest in this study is age 5, but it should be noted in passing that age 3-13 Z is overestimated, being .14 for the estimated data set compared to .10 for the actual data. The approximate 95% confidence interval on the estimate includes the actual value, however.

The effect of fluctuating recruitment on the estimates of age 5 males was examined by inducing changes in year class strength similar to those observed, as indicated by the uncorrected age 5 index of table 1. The average for this data series is 17 million crabs, with a range of 6-46 million. Thus, simulated year classes were followed through the population at levels of 3 times and .3 times the constant recruitment level to assess the effect on the estimate of age 5 males. These effects are shown in figure 5 where strong and weak recruitment is compared to the constant R case for age 5. When the strong year class is age 4, age 5 recruits are overestimated; the next year age 5 recruits are underestimated; and in the following year when the strong year class is age 6, recruitment is again overestimated. Slight overestimation occurs the next year but the bias goes to zero thereafter. This pattern is caused by contamination of the estimation interval when the year class is at ages 4 and 6, and exclusion from the interval of significant numbers of age 5 recruits in the intervening year. The pattern is reversed during years of a weak year class. When it is age 5, adjacent age groups are over-represented. The age 6 individuals provide less compensation for the excluded tails of the actual age 5 distribution, causing underestimation. This occurs to a lesser degree with the age 4 year class because its size distribution overlaps less with the estimation interval.

The effect of increased mortality on the estimates of age 5 recruits under variable recruitment is depicted in figure 6. The effect of a strong year class on the estimate is dampened considerably when survival is reduced to 0.5. Conversely, the effect of a weak year class is increased substantially by increased mortality. Weak recruitment combined with increasing mortality approaches the missing year class situation. The performance of the age 5 recruitment estimate based on the growth curve is probably approaching a "worst

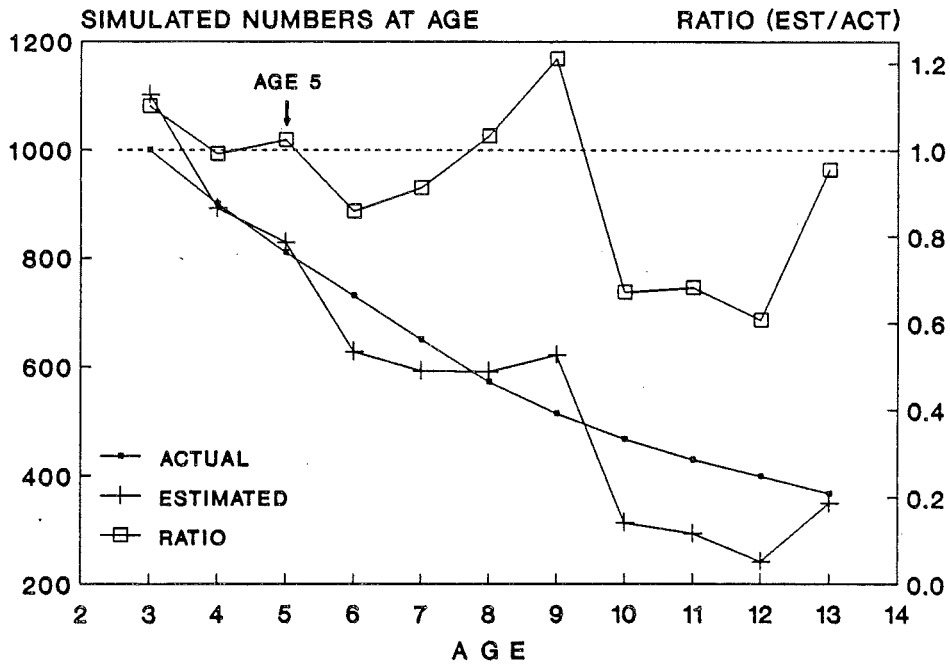


Figure 4. Bias in age estimated from Von Bertalanffy growth.

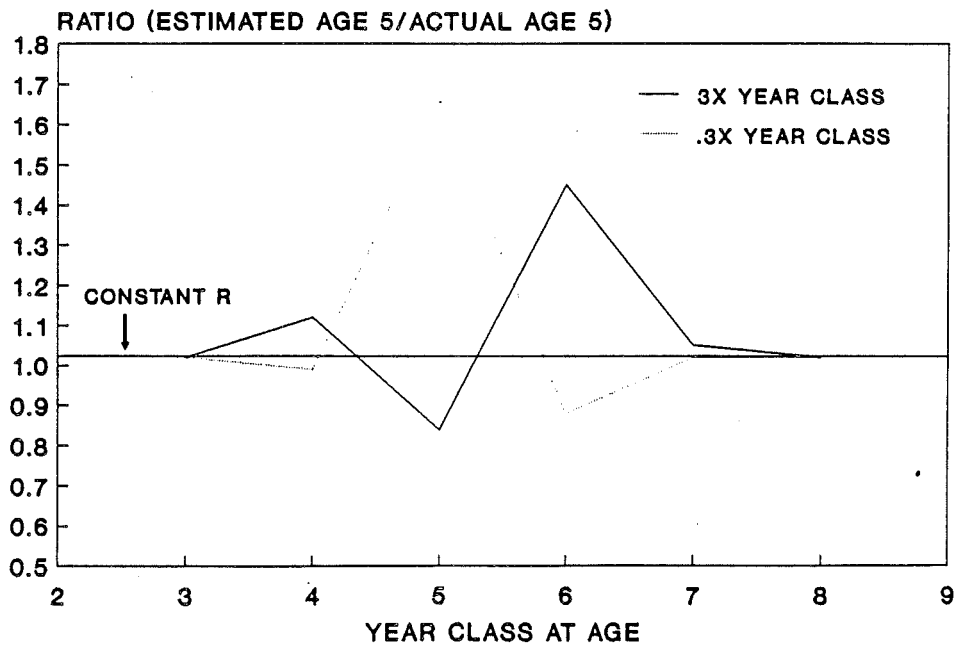


Figure 5. Changes in age 5 bias related to strong and weak recruitment.

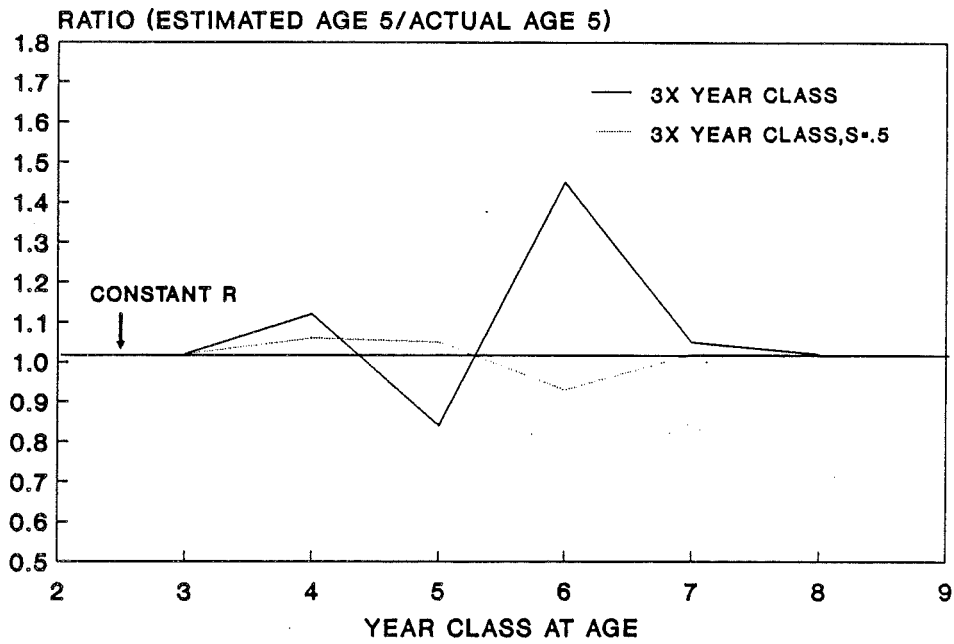


Figure 6a. Effect of higher mortality on age 5 bias related to strong recruitment.

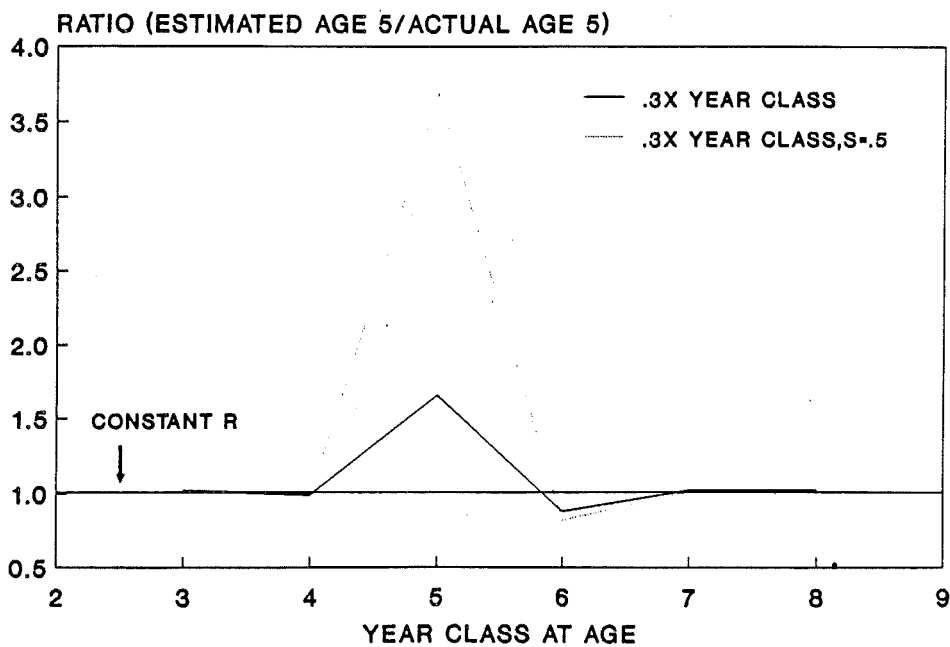


Figure 6b. Effect of higher mortality on age 5 bias related to weak recruitment.

case" under these conditions.

In order to examine the effect of biased recruit estimates on the spawner-recruit relationship, corrections to the time series were made based on the foregoing analysis of bias. The largest departures from average recruitment occurred in 1977 (+2.7x) and in 1985 (-.35x). The values for the years 1976-78 were divided by the ratios 1.12,.84 and 1.45, respectively (figure 5). Values for 1984-86 were corrected using the ratios .99,3.70 and .82 of figure 6b, since mortality was relatively high during those years. The corrected series is given in table 1. Results of fitting the Ricker model to the corrected scatterplot are shown in figure 7. While variance is increased somewhat, parameter estimates remain essentially unchanged (table 2). Further, a non-parametric classification of both data sets according to the methodology of Rothschild and Mullen (1985) gives quite similar results (figure 8). Both sets exhibit a preponderance of states two (S2,low stock/high recruitment) and four (S2,high stock/low recruitment), leading to classification as a type III stock which suggests the presence of compensatory mechanisms.

EFFECTS OF TEMPERATURE-DEPENDENT GROWTH VARIABILITY

Stevens (1988) has proposed that temperature is a fundamental determinate of the rate of growth of juvenile red king crabs in Bristol Bay. Under this condition, the time required for a given cohort to reach a given recruit interval will vary according to variation in the temperature regime to which the cohort is exposed. In order to relate progeny to spawning stock in this situation, either the estimated recruit interval specified for a particular age must vary, or the lag time for a given recruitment to reached a fixed interval must vary. The latter approach has been adopted here to re-estimate the spawner-recruit relationship under the hypothesis of temperature-dependent growth. New recruit values which can be related to a given spawning year were estimated by allocating the original values (95-109mm) to year classes based on the Stevens' growth model. A Ricker fit to the new data points was computed, as well as a non-parametric classification. Results were then compared to the original data set.

Table 6 of Stevens gives the number of each estimated year class recruiting to the 95-109mm interval by year. Summing over year classes by year, proportions were calculated to allocate the value of the recruit interval to year classes for each year. Then for each year class, allocated values

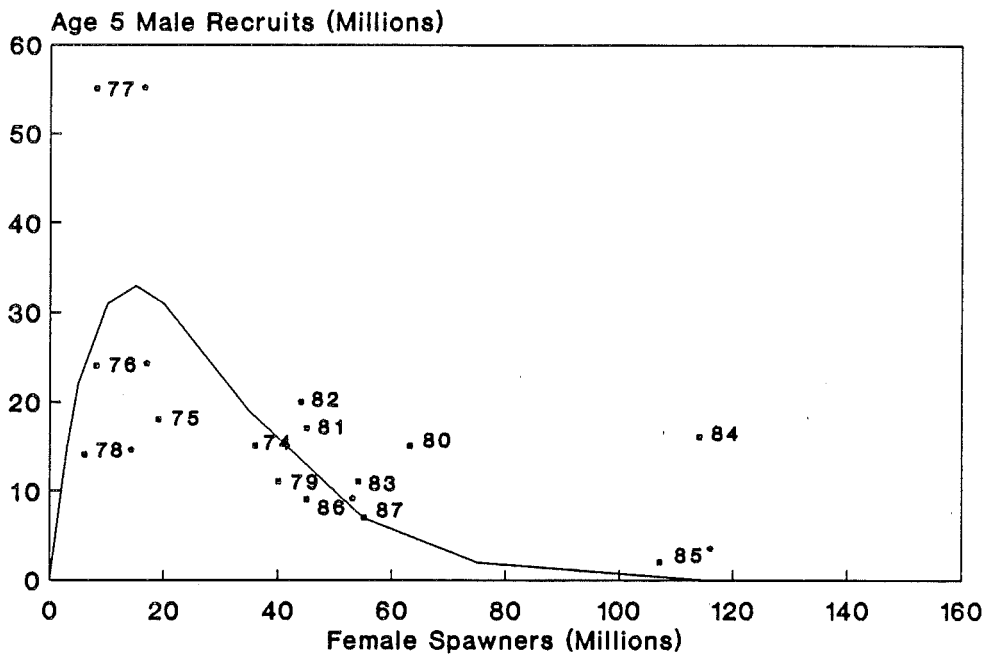


Figure 7. Recruit values corrected for year class strength, indicated by asterisks.

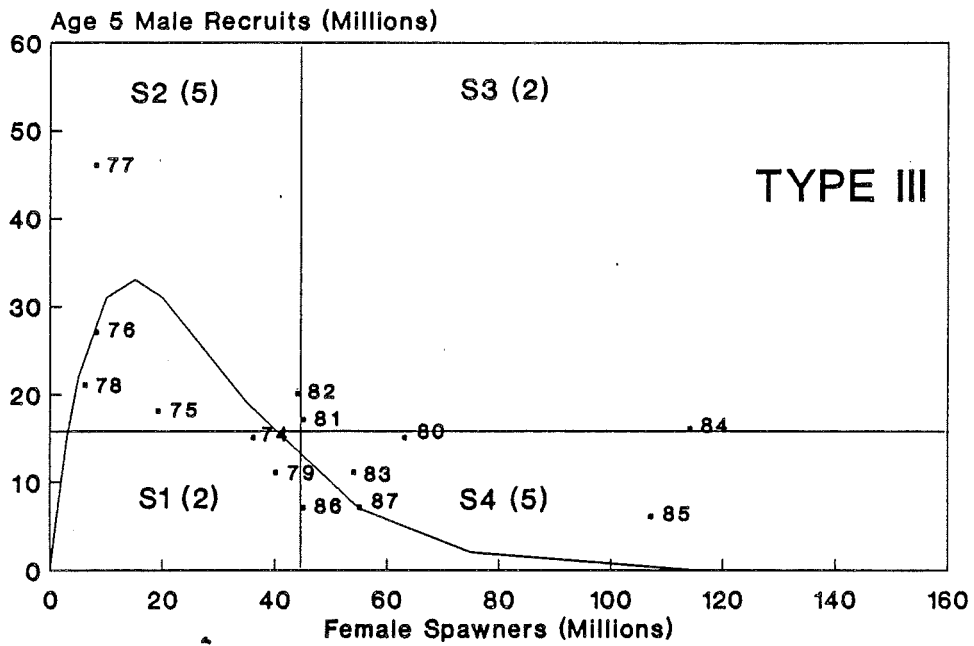


Figure 8a. Non-parametric classification of uncorrected spawner-recruit data.

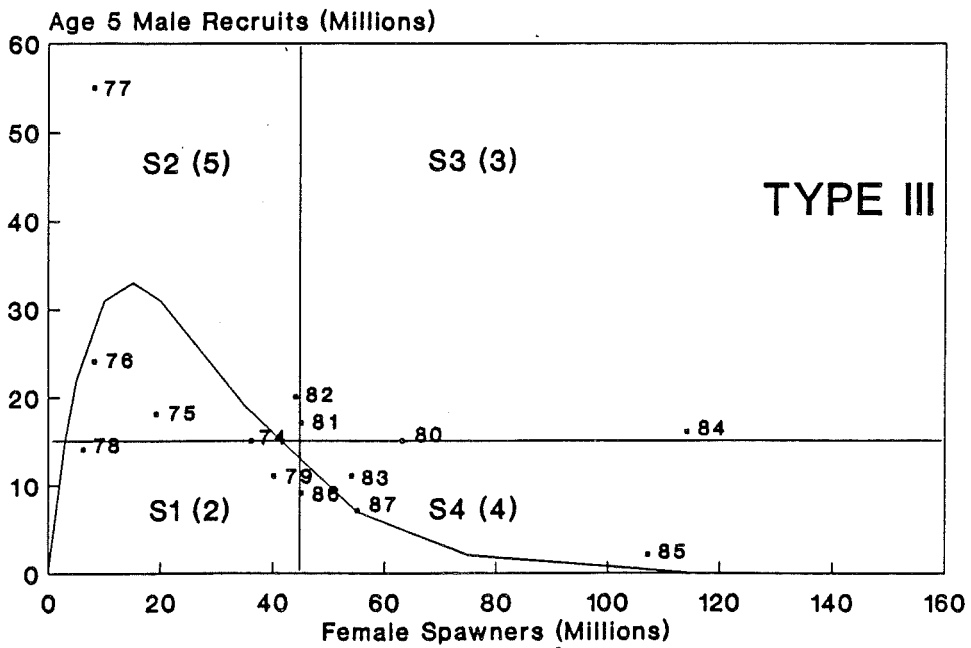


Figure 8b. Non-parametric classification of data corrected for year class strength.

were summed over years to give the total recruitment contribution. These calculations were done for each of the five recruitment scenarios examined by Stevens and each data set was fit by the Ricker model. Parameter estimates were similar for each scenario so an average of all was computed to simplify comparisons. The average values are given in table 1, associated with the appropriate spawning stock. The time lags implicit in this data set vary from 8-10 years from mating year to recruitment to the 95-109mm interval, compared to a 6-year lag for the original data set

A fit of the Ricker model to the data is shown in figure 9a, where years of spawning stock estimates are indicated. The associated parameter estimates are given in the last column of table 2. These data indicate a higher S_{max} , although the approximate 95% confidence interval includes the estimates for the other data sets. The value of R-squared is somewhat improved over the other fits. It should be noted that the points for 1978 and 1979 are underestimated due to incomplete recruitment to the survey, but were included because they are associated with high spawning stocks. Their actual values should not change the parameter estimates substantially in subsequent years, based on the pattern of recruitment in earlier years. Non-parametric classification of the data (figure 9b) indicates a more uniform distribution of points among states, which suggest a Type I stock where no particular form of stock-recruitment control is evident. This is at odds with the parametric analysis, which indicates a better fit to the temperature-dependent data, and suggests that at higher spawner levels recruitment is not related to stock.

DISCUSSION

This study indicates that bias caused by an indirect method of age determination for recruits has not materially affected parameter estimates for the Ricker model, or substantially changed the distribution of data points according to the non-parametric classification of Rothschild and Mullen (1985). Only the largest departures from average recruitment have been corrected, and the correction factors used are approximate. The need for a more accurate method of dealing with future annual fluctuations in recruitment is apparent. The interaction involved in estimating recruitment and age-specific mortality from survey abundance estimates prescribes that some iterative scheme be developed, whereby recruits and mortality are estimated alternately in successive iterations until a predetermined level of stability is achieved. Iterative solutions of this type

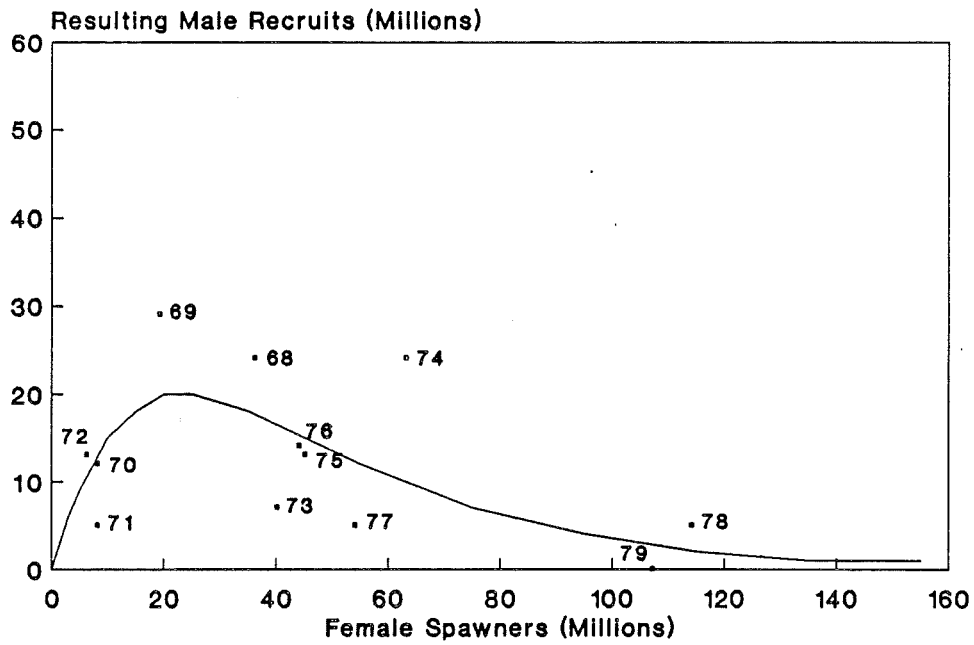


Figure 9a. Recruit values based on temperature-dependent growth (Stevens 1988).

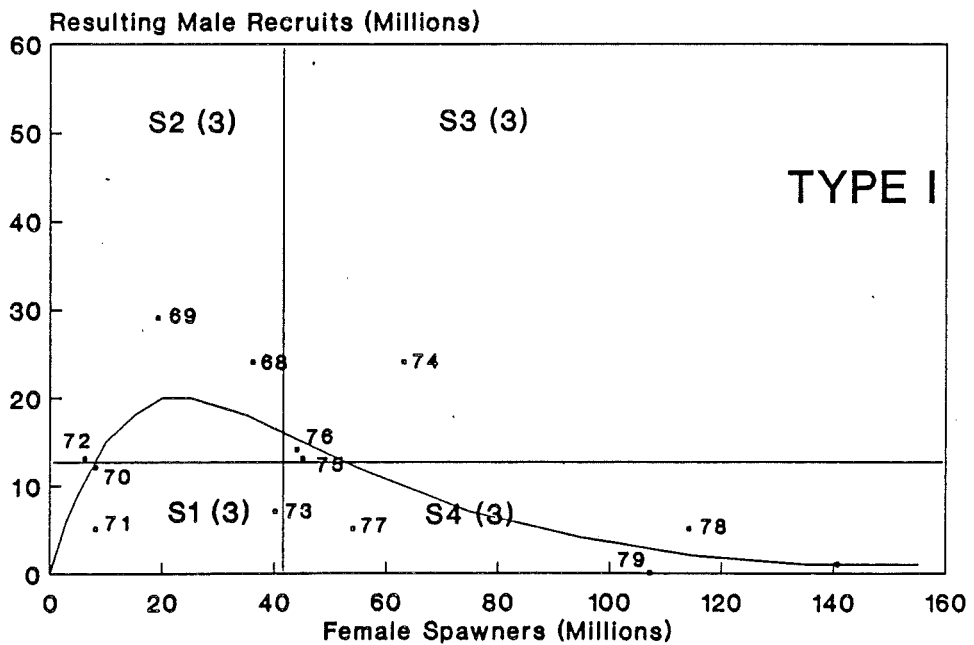


Figure 9b. Non-parametric classification of data based on temperature-dependent growth.

would be required for adjacent age groups, as well as the recruit age group. A starting point for such computations might come from a matrix of correction factors relating R to Z, estimated by simulations similar to those described in this study.

Growth parameter inputs to simulations of king crab growth may be out of date, since the last complete analysis was carried out on data from the 1950's and 1960's (Balsiger 1974). cursory examination of more recent tagging data suggests that growth increments and molting probabilities have not changed. However, a more thorough review of the data is required in order to confirm that conclusion for this study.

The hypothesis of temperature-dependent growth (Stevens 1988) appears to have more impact on the the spawner-recruit relationship. Results from this model, which estimates a slower rate of growth for immature male crabs, lead to a higher estimate of S_{max} . This in turn would presumably lead to a somewhat more conservative mode of management in terms of setting exploitation rates. The results of the non-parametric analysis of these data, suggesting that compensatory mechanisms may be lacking, has further implications for management. The depressive effect of high stock sizes on recruitment may not be occurring, making management decisions less critical when stocks are at high levels.

As mentioned earlier, the temperature-dependent hypothesis results in a generally slower rate of growth than that estimated from previous studies (see figure 10). Thus, as with the results from the analysis of aging bias, an examination of tagging data since Balsiger's work should be useful in resolving these differences.

Persuant to resolving these difficulties in the estimation of recruitment, examination of residuals and other statistical studies should be undertaken to improve the spawner-recruit analysis. Of course, further work on the spawning stock data series would also be desirable, including the "errors in variables" and other estimation problems.

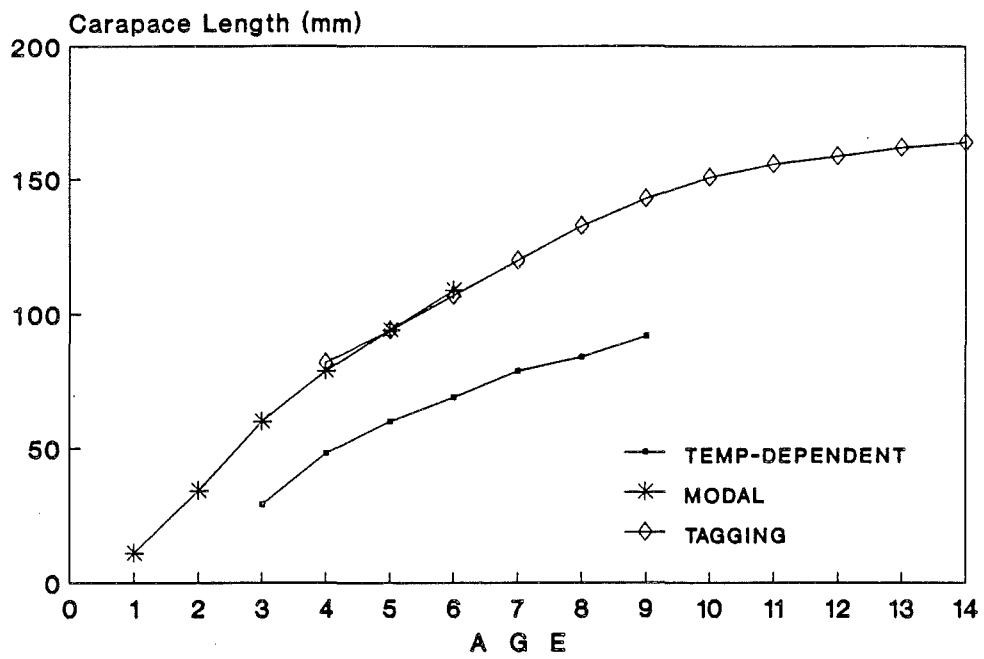


Figure 10. Comparison of growth analyses for red king crab males.

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Effects of ocean variability on the abundance
of Dungeness crab megalopae - 1985 to 1988.

by

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Abstract

The longshore and cross-shelf abundance of Cancer crab megalopae have been studied off the south coast of Vancouver Island since 1985. Megalopae occur in abundance from about 28 km to at least 170 km offshore, well beyond the general location (70 km offshore) of the continental shelf break (200 m depth). Intermolt staging of megalopae indicates that later stage megalopae are found progressively closer inshore, but in the study area, megalopae may not always reach the coast, which they must do in order to survive as settled juveniles. From at least 1985 to 1987, no substantive settlement occurred in the commercial Dungeness crab (C. magister) fishing areas immediately around Tofino, British Columbia. Since Dungeness crab recruit to the fishery at 3-4 yr of age, a significant decrease in annual landing from this fishery is predicted over the next few years.

Environmental factors influencing the movement of megalopae have been investigated by documenting surface current patterns in the study area by means of drifters, estimating geostrophic flow patterns from STD data, and analyzing meteorological events as contributors to onshore larval movement. Results indicate that the patterns of currents and their relative velocities in the study areas differ on an annual basis. It appears that these current patterns affect where crab megalopae are concentrated in abundance and their subsequent ability to move onshore.

Introduction

Fisheries for Dungeness crab (Cancer magister) occur from Kodiak, Alaska, to central California, with landed value at \$CDN 40 million in 1986. Canadian landings are the composite of a number of geographically distinct fisheries (Jamieson 1985), with the major one on the west coast of Vancouver Island near Tofino. Study of factors affecting recruitment to this fishery was initiated in 1985, with focus on megalopal abundance and distribution, juvenile growth and survival after settlement, and adult population dynamics. The seasonal and cross-shelf occurrences of larval Dungeness crab megalopae have been described for 1985 along a transect extending 185 km off Tofino (Jamieson and Phillips 1988) and long-shelf megalopal occurrence coupled with simultaneous oceanographic monitoring, have been described off both Vancouver Island and the State of Washington for 1986 and 1987 by Jamieson et al. (in press). This study expands these latter observations by including data for 1988. From 1985 to 1987, C. magister megalopae were abundant from about 36-148 km offshore off Tofino, but there was little nearshore settlement of C. magister.

A number of studies (Lough 1976; Reilly 1983; Jamieson and Phillips 1988) have shown that while C. magister larvae are hatched nearshore, some larvae then move a considerable distance offshore. The extent to which these offshore larvae return to nearshore waters is uncertain, and it may be that most nearshore settlement results from those larvae which remained shoreward of as yet undetermined

oceanographic boundaries. The degree to which larvae move onshore or offshore may vary with latitude, since current patterns vary considerably over the range of the species. The oceanography of the west coast of Vancouver Island and Washington has been described by a number of recent reports, including Thomson (1981, 1984, in press), Freeland et al. (1984), Leblond et al. (1986), Freeland and Denman (1982), Hickey (1979), Denman et al. (1981), and Ikeda et al. (1984a,b). Of particular interest to this study is the significance of the change that occurs at Cape Flattery. Surface current direction south of Cape Flattery is largely determined by the prevailing wind direction (northwards in winter and southwards in summer). To the north, along the west coast of Vancouver Island, the 30-50 km wide, northward-flowing Vancouver Island Coastal Current hugs the coast and is generally present throughout the year, with the broader Shelf-break Current, a reversing, wind-driven current, extending seaward to at least the continental slope. This latter current is an extension of the continental shelf currents found south of Cape Flattery.

The objectives of this study were to investigate the cross-shelf and long-shelf distributions of C. magister megalopae in relation to the strength and direction of surface currents, and to evaluate possible oceanographic and meteorological mechanisms which might influence onshore or offshore movement of megalopae.

Dungeness crab larval biology

Dungeness crab larvae are planktonic and pass through five zoeal stages and one megalopal stage before settling to the bottom. Total larval period is about 110 days (Poole 1966; Lough 1976; Reilly 1983), with about 28 days spent as megalopae (Hatfield 1983). Late stage zoea tend to be found progressively further offshore (Reilly 1983). If significant onshore transport occurs, it seems to be the megalopal stage which returns inshore. Late-intermoult stage megalopae tend to be found progressively closer inshore (Hatfield 1983; Jamieson and Phillips 1988; Jamieson et al. in press).

Megalopae are the strongest swimming stage (Jacoby 1982), although there is no evidence to date that horizontal navigation occurs. Swimming is rheotropic and megalopae show a pronounced diel vertical migration, being concentrated in the top few metres of the water column at night (Booth et al. 1985, Jamieson et al. in press). There is relatively little data on their depth preference during daylight hours, and while megalopae have on occasion been found at the surface during daylight (Wickham 1979; Reilly 1983; Jamieson and Phillips, submitted), they are not observed regularly at the surface during the day in abundance comparable to nighttime observations.

Methods and Materials

Biological Sampling:

In 1986, megalopal sampling was widespread but was conducted

along essentially five transects extending from 10 km offshore to about 120 km offshore, with one of the transects extending to about 170 km offshore (Fig. 1). Individual stations were at about 10 km intervals inshore and at about 30 km intervals furthest offshore. Sampling was conducted from June 9-July 3 on the R/V Parizeau.

In 1987, sampling was conducted on two separate cruises, from May 4-15 on the R/V W.E. Ricker and from June 15-26 on the R/V Parizeau. On each cruise, sampling was carried out in two broad geographical areas, off Tofino on the west coast of Vancouver Island, as in 1985 and 1986, and off Grays Harbor, Washington. In each area, sampling was conducted along 2-4 transects, about 35 km apart, extending from 9-140 km offshore (Figs. 2, 3). The distance between transects in all surveys was arbitrarily established and primarily reflected a compromise between staying within the broadcast range of the drifters and surveying the broadest area possible. While surveying along each transect, the duration of darkness was the limiting factor, and both transect lengths and number of stations sampled were a compromise between the need to complete each transect in a single night and to take as many samples as possible. Individual stations were 10-20 km apart.

In 1988, sampling was again conducted on two cruises, from May 23 - June 2 and from June 13-24, both on the R/V Parizeau, but the only geographical area sampled was off the west coast of Vancouver Island. Survey design was the same as in 1987.

Nighttime sampling of megalopal occurrence at each station was

done with a neuston sampler, 45 cm on each side, which sampled the top 35 cm of the water column under calm sea conditions (Mason and Phillips 1986). A General Oceanics flowmeter in the mouth of the net was used to establish distance travelled and sea surface area filtered. Tow duration was typically 10 min and sampled 500-600 m² of sea surface, but at times of high megalopal abundance (>100 m⁻²), tow duration was shortened to 5 min. The net was 1 mm (0.5 mm in 1986), black Nitex, and the sampler was towed at 4 kn, parallel to and at a distance of approximately 10 m from the side of the vessel.

All plankton samples were preserved initially in a 4% formaldehyde in saltwater solution. In the laboratory, settled volume was determined and general composition of the plankton noted. Samples were then sieved and C. magister larvae, readily identifiable by their larger size (Trask 1970; Lough 1975), picked out, counted, and further preserved in a 2% formaldehyde solution. Intermoult staging used the criteria described by Hatfield (1983), and stages were grouped according to Jamieson and Phillips (1988).

Abundance data in time were weighted by time of capture at night, with the product reflecting the maximal abundance estimated to be present during the night between 2130 and 0500 hr at that location in that month (Jamieson et al. in press). Scaling factors ranged from 1.0-20.0, with an upper limit set because accurate value estimation becomes impossible at the times when a majority of megalopae are ascending or descending. In May, data collected between 2100 and 0515 hr

was used and the scaling factor used was 1.0, since linear regression slopes were not significantly different from zero (Jamieson et al. in press).

Oceanographic Sampling:

Salinity-temperature-depth (STD) profiles of the water column were collected with a Guildline System, and processing of the data from 1985-87 and from 1988 to give geostrophic flow values was conducted by Dr. R. Thomson and Dr. H. Freeland, respectively, Institute of Ocean Sciences, Sidney, B.C. Current patterns were determined empirically by the simultaneous deployment of up to 8 Lagrangian drifters at selected distances offshore. Each drifter consisted of a 1.0 m diameter, 0.6 m deep fibreglass buoy containing a Loran C receiver and a radio transmitter with a range of about 90 km (Greisman and Crawford 1985, Crawford and Greisman 1987). Suspended from the buoy was a 1 m diameter, 5 m long, "holey sock" fabric drogue, whose depth was controlled by varying the length of the cable suspending it from the buoy. Drogues were centered at a depth of 7.5 m. The location (Loran C time differences) of each drifter was transmitted every 30 min, allowing the relative locations of each drifter to be monitored simultaneously from the supporting survey vessel. The drifters were generally allowed to drift for 4-5 days before retrieval and transport to the next study area.

Three distinct geographical deployments of drifters, spread over 3 years and over the months of May and June, are presented.

Locations and dates are: in the Juan de Fuca Gyre off the mouth of Juan de Fuca Strait (June, 1985 and 1986), along a cross-shelf transect off Tofino, B.C. (May, 1987, and June, 1987 and 1988), and along another cross-shelf transect off Grays Harbor, Washington (June 1987).

Results

Geostrophic flow:

Mid-June geostrophic surface currents, relative to 100-m depth, determined for mid-June off southern Vancouver Island are presented for 1986 and 1987 (Fig. 4a-b), and off Washington for 1987 (Fig. 4b). Boxed areas indicate the outer boundaries of the spatial pattern of STD casts for the specified time period which provided the data used in current determinations. Geopotential heights at the surface, relative to 70 m depth, determined monthly from April to June, 1988, off Vancouver Island are shown in Figure 5.

The basic surface current pattern shown off Vancouver Island in May and June from 1985-1987 was a counter-clockwise gyre (Juan de Fuca Gyre) off the mouth of Juan de Fuca Strait, a north-flowing current (Vancouver Island Coastal Current) of variable strength centered about 20-30 km offshore from Barkley Sound to Estevan Point, a south-flowing current of again variable strength 50-70 km offshore (Shelf-break Current), and furthest offshore, an area of negligible or north-flowing current. The north-flowing Vancouver Island Coastal Current appeared to extend seaward over La Perouse Bank, perhaps because of bottom

topography, and then moved shoreward until near Estevan Point. Off Washington, there was a broad, south-flowing current (Shelf-break, or California, Current) across the entire shelf, with no particularly strong long-shore currents nearshore. The current pattern seemed to contain ephemeral eddies or gyres. There was little difference between estimated currents at the surface and at 50 m, relative to that at 100 m, off either Vancouver Island or Washington.

In 1988, the Vancouver Island Coastal Current was present at the surface in April but was absent in May and June, presumably because of the relatively poorer weather (storms with associated southerly winds) which occurred in late April and early May in comparison to the 3 previous years.

Lagrangian current measurements (drifters):

The deployment of drifters across the counter-clockwise Juan de Fuca Gyre is useful in establishing whether crab larvae entrained in the gyre, after drifting south in the southward-flowing Shelf-break Current seaward of the Vancouver Island Coastal Current, are likely to 1) leave the Gyre on its seaward side and continue moving southward, or conversely, 2) circle around in it and leave the Gyre on its shoreward side, to move northwards, closer inshore and entrained in the seaward side of the Vancouver Island Coastal Current. In 1985, all drifters released across the Gyre spun out on the seaward side of the Gyre and moved rapidly southwards at an oblique angle towards the Washington coast

(Fig. 6a). In 1986, the opposite occurred, with drifters either circling around within the Gyre or spinning out on its inshore side to move northwards (Fig. 6b). During the periods of observations in both years, winds were consistently light to moderate and primarily from a northerly direction, as would be expected during the month of June. It thus appears that from a transport perspective, dramatically different results can occur between different times during the year or between years, even though the basic geostrophic current pattern may appear similar (Jamieson et al. in press).

Along the transect off Tofino, drifters were deployed 10-25 km apart, thereby allowing determination of the relative directions and strengths of the surface currents across and beyond the continental shelf. The basic pattern evident (Fig. 7a-b) was an inshore, northward-flowing surface current of variable strength (strong in 1986, weak in 1987, and absent in 1988), and a southward-flowing surface current centered slightly seaward of the shelf break (200 m depth). In 1986, the drifter deployed seaward of this latter current (90 km offshore) was essentially stationary while the drifter deployed 100 km offshore moved strongly northwards (Fig. 7a). This outer-most, northward-flowing current was not evident in later years (Fig. 7b-d).

The relative stability of regions in the observed currents off Tofino were established in June, 1986 (Fig. 7a), when about 30 hr after deploying the drifters in moderate westerly 22 kn winds, wind direction shifted to the southeast, but stayed at similar strength. The two

drifters on the coastal side of the Shelf-break Current quickly began moving northwards and obliquely towards the coast, whereas all other drifters continued moving at a similar rate and direction as before the change in weather.

The main features pertinent to movement of larvae either onshore or offshore off Tofino, then, are:

- 1) the presence of generally stable long-shore surface currents, although moderate-to-large meteorological events may significantly influence current strength and direction in at least some areas;
- 2) when the Vancouver Island Coastal Current is present, the occurrence of at least one, and possibly two, relatively stable zones of little long-shore and cross-shelf transport, which appear to be at the boundary between opposing surface currents;
- 3) significant potential monthly and annual differences in the current velocity of the Vancouver Island Coastal Current;
- 4) when there is no outward surface flow through Juan de Fuca Strait, and hence temporal cessation of the Vancouver Island Coastal Current, there is no Juan de Fuca Eddy. Nearshore surface currents show little long-shore flow, but there does appear to be an outflow extending seaward from the mouth of Barkley Sound to the Shelf-break current.
- 5) general southeasterly long-shore transport at the surface in the Shelf-break Current, presumably because of the seasonal northwesterly winds prevalent off Vancouver Island (it should be noted there was little evidence of cross-shelf, offshore transport, as would be expected from Ekman theory);

6) periodic onshore cross-shelf transport in surface waters in some regions of the Shelf-break Current with the southerly or southeasterly winds associated with summer storms.

As expected, the current pattern off Grays Harbor, Washington, was significantly different from that observed off Vancouver Island. In 1987, all deployed drifters moved southwards (Fig. 8), regardless of their distance offshore. However, there was variation in longshore current strength across the continental shelf, with maximal velocity (about 15 cm sec^{-1}) 50-75 km off the coast.

Off Washington, then, zones of little or no long-shore current flow appear less structured and relatively little long-shore variability in current flow and strength existed over most of the survey area during the study period in 1987. With northerly winds, all currents were to the south and maximum current strength was just seaward of the shelf break. Current direction and velocity were influenced by moderate wind events which, if from a southerly direction, can result in onshore, cross-shelf transport of surface waters. With the prevalent seasonal northerly winds, southerly long-shore transport of surface water predominated.

Megalopal cross-shelf abundance and distribution:

General results (Fig. 9) obtained in both 1986 and 1987 confirm the observations made in 1985 that when the Vancouver Island Coastal Current is present, crab megalopae were only regularly abundant off the west coast of Vancouver Island in water >40 km offshore, i.e., beyond the

probable outer boundary of the Vancouver Island Coastal Current (Figs. 1, 4). Extensive searching in 1985-87 for newly settled juvenile crabs near the coast, using beam trawls and methods described by Jamieson and Phillips (1988), yielded few 0-year class crabs in each years (Smith 1988; G. Jamieson, unpub. data), supporting the absence of significant megalopal settlement in the Tofino area from 1985 to 1987. Settlement in 1987 appeared slightly greater than in either 1985 or 1986, but megalopae were observed in greatest abundance in both coastal and inlet waters around Tofino in early May, 1988. Megalopal settlement was apparently substantial as recently as 1983 or 1984, since crabs are considered to largely recruit to the fishery at age 3 (Smith 1988) and landings in 1986 and 1987 in Tofino (Statistical Area 24: 365 and 488 t, respectively) were high (1966-1985 average = 160 ± 69 t).

Megalopae were caught on the seaward ends of all transects, indicating their distribution extended beyond the maximum distances surveyed offshore (about 140 km on average). In 1986, greatest abundance off Tofino was at about 100 km, nearly twice as far offshore as in 1985 and 1987 (Fig. 9) and at a location where little longshore drifter movement occurred (Fig. 7a). Megalopal abundance was low at the mouth of Juan de Fuca Strait (Fig. 1). In both 1986 and 1987, maximum megalopal abundance was in the regions indicated by drifter movements to be between major currents moving in opposite directions, with relatively few megalopae (Fig. 9) collected at stations in the Vancouver Island Coastal Current.

In late May, 1988, megalopal abundance was the lowest observed in the 4 years of survey, but again, maximum abundance was on the shoreward side of the Shelf-break Current.

Off Washington, the spatial distribution of megalopae differed substantially from that observed off Vancouver Island (Fig. 9). While megalopae were again collected along the entire length of each transect, megalopae were on occasion in highest abundance <20 km from shore. North of Grays Harbour in June, 1987, there was a zone of relatively low megalopal abundance near the shelf break, 70-90 km offshore. The presence of megalopae in nearshore waters suggests that relatively greater megalopal settlement was occurring off the central Washington coast than along the west coast of Vancouver Island in both May and June, 1987.

Megalopal long-shore abundance and distribution:

Along a transect 83-141 km offshore, megalopal density ranged from 8-60 $10m^{-2}$ of sea surface (Fig. 10). Considering the latitudinal distance covered (about 100 km), average megalopal density was consistently within one order of magnitude at stations along the transect, which is considered to be relatively constant. Patchiness in plankton abundance is expected (e.g., Hardy 1936; Wiebe 1970; Booth et al. 1985), and while megalopal patch sizes were not determined in this study, megalopae were continuously present at all stations.

Intermoult stage distribution:

Late intermoult stage megalopae in 1986 were most abundant nearest shore whereas early and mid-intermoult stage megalopae were most abundant further offshore (Fig. 11). However, because total megalopal abundance was relatively low overall close to shore (Fig. 9), late intermoult stage megalopae comprised a relatively small proportion of the total megalopal population present (Fig. 12), similar to observations in 1985 (Jamieson and Phillips 1988).

Discussion

A problem common to both oceanographic and biological sampling at sea is the compromise between covering a sufficiently large area to develop an understanding of broad-scale events or processes and taking a sufficient number of samples in any specific area to account for microscale patchiness in the parameter being investigated. Until either rapid movement between stations is possible or inexpensive, deployable, automatic samplers are developed, the only practical approach currently available is the sampling of stations along a grid or transect survey design in as short a time frame as possible, coupled with stationary, repetitive sampling at a few locations to try and establish an estimate of local variability. Any compromise is always open to criticism that more samples of either type should have been taken, but the logistic constraints associated with the simultaneous collection of both oceanographic and biological data over the same time period are facts

which have to be recognized. Interpretation of our results should be considered in the context of these limitations.

Quantitative sampling of megalopae was primarily conducted with neuston gear because of the relatively large sea surface area sampled in comparison to the integrated area obtained from bongo and Tucker trawl gear. The distribution of plankton is known to be patchy (e.g., Hardy 1946; Wiebe 1920; Booth et al. 1985) and while our ability to establish macroscale (kilometer) variation was limited, as described above, maximizing sea surface area sampled per tow at least tended to minimize microscale (meter) variation. A 10-min neuston tow samples about 500-600 m² of sea surface whereas a 20-min Tucker trawl tow to 50-m depth, assuming 2 min down for the first net and 9 min each for the remaining 2 nets coming up over 2, 25-m depth ranges, samples 540 m³, or 22 m² of integrated sea surface area, for each of the last two nets. There is about a 25 fold difference in relative sea surface areas sampled per unit tow time period in this comparison, and while the ratio decreases by sampling a smaller depth range with the Tucker trawl, the greater awkwardness of using a Tucker trawl relative to neuston gear discourages this for logistical reasons.

Cross-shelf movement of megalopae:

Our work off the west coast of Vancouver Island suggests that although relatively little crab settlement occurred between 1985 and 1987, Dungeness crab megalopae occur annually in abundance over at least

the continental shelf and, for much of the coast, such abundance probably extends many kilometres further offshore. We did not investigate the movement of zoeal stages, which occur earlier in the year, and so the mechanisms whereby larvae from nearshore areas move offshore remain uncertain. Presumably, movement is mostly passive and is affected by Ekman transport, but because the total larval period of C. magister is relatively long (about 4 mo) and extends over a time period of major seasonal change in regional oceanography (January-July), estimating long-term movement patterns for any group of larvae is considered impractical with available data. Nichols et al. (1982) had some success attempting this for C. paguras, but that species has only a 23-30 d pelagic larval period (Edwards 1979). It was for this reason that our studies have focused on megalopae and on the relatively simpler question of trying to establish which megalopae are potentially able to settle inshore. They must do this if they are to survive as settled juveniles and, therefore, it is useful to resolve what mechanisms or processes influence their potential onshore movement. Few Dungeness crab juveniles can be found in quantity at depths >64 m (Carrasco et al. 1985) which means that for most of the coast, megalopae must settle within 10-15 km of shore to survive as juveniles.

Evidence for onshore movement: Dungeness crab megalopae, along with the megalopae of C. oregonensis (Lough 1976; Jamieson and Phillips 1988), another inshore crab species, are often the dominant organisms at the

surface at night in the spring in offshore waters (Jamieson and Phillips, submitted). Since other Cancer species (eg. C. productus) abundant along the coast have larvae which are not abundant in offshore waters, offshore dispersal is apparently not an essential nor automatic occurrence arising from nearshore hatching of eggs in the spring.

For species indigenous to a region, it would seem likely that a dispersal strategy would evolve which would tend to maximize larval survival to the juvenile stage. It seems unlikely that many, if not most, C. magister and C. oregonensis larvae would move offshore if there was no mechanism to result in their ultimately returning inshore, at least in most years. Dispersal mortality arising from being in an unfavourable place for survival at settlement can be termed larval wastage, and although partially unavoidable, the two Cancer species are the only inshore crustacean species found regularly in abundance in offshore waters off Washington and Vancouver Island. Some onshore transport process or mechanism thus seems likely to exist.

Onshore movement of megalopae is suggested by the observation that late intermoult stage megalopae tend to be found progressively closer inshore (Hatfield 1983; Jamieson and Phillips 1988; Jamieson et al. in press). Megalopae are relatively strong swimmers (Jacoby 1982), yet apart from a nocturnal migration to the water surface, no directed geographical movement has yet been determined. When abundant in surface waters during daylight hours, megalopae were usually found clinging to floating objects (Velella velella: Reilly 1983; Wickham 1979; Jamieson

and Phillips 1988; dead salps and floating debris: Jamieson and Phillips, submitted). These observations suggest that being at the water surface may be important to the onshore movement of megalopae.

Evidence against onshore movement: Jamieson and Phillips (1988) point out that while earlier studies by Reilly (1983) off northern California and Lough (1976) off Oregon established the occurrence of megalopae in offshore waters, their sampling was primarily during the day with gear not optimal for rapid, accurate estimation of relative areal megalopal abundance. The only other data available are ours off British Columbia (1985-88) and Washington (1987); for the years and locations monitored, no substantial movement of a specific larval concentration was evident and significant Dungeness crab settlement occurred in inshore waters only in 1988. Substantial crab settlement at any specific location has yet to be correlated with the movement of megalopae from offshore areas to the coast. While it can be argued that monitoring of both settlement and potential transport has been limited, available data nevertheless fail to show that major transport to shore can or does occur. A major settlement apparently occurred at Tofino in 1983 or 1984 (Smith 1988), and major settlements were reported off the Washington coast in 1984 and 1985 (Armstrong et al. 1987), but from 1986-88, during the course of our studies which might have detected larval movement through correlation with Lagrangian drifters, no major crab settlement occurred at these location (1986: Armstrong et al. 1987; 1987: D. Armstrong, Univ. of

Washington, Seattle, Wa., pers. comm.). It cannot be proven that previous major settlements involved larvae which had left the nearshore environment.

In the absence of data to refute either argument, only additional observations will resolve this issue. C. magister megalopae are probably always abundant off Washington and southern British Columbia in May and June within about 140 km of shore, and the potential for substantial settlement to occur somewhere along the coast is likely high. Study of factors which prevent major inshore settlement may be more relevant than trying to establish where successful onshore settlement would be permitted. If settlement in the area of a particular fishery is very poor, later recruitment to the fishery will be low, even with high subsequent juvenile survival. Survival of juveniles in the few months immediately after settlement can be quite variable (Armstrong et al. 1987), so a high settlement of megalopae does not necessarily mean high recruitment at a later date.

The probable settlement locations of progeny hatched in a specific region and the degree of intermixing of larvae originating from different coastal regions are issues relevant to both fishermen and managers. Factors affecting both the magnitude of Dungeness crab recruitment, and the timing of major fluctuations are still speculative. The cyclical fluctuation in crab abundance is well documented from northern California to Washington (see Botsford 1986) but, to date, no satisfactory explanation has been developed. The Tofino fishery does not

fluctuate in a similar cyclical manner, but its fluctuations are nevertheless substantial (Jamieson 1985).

Currents and the Spatial Distribution of Megalopae:

The geostrophic method of estimating current flows and patterns utilizes information on the distribution of density in the ocean, and while it ignores the effect of wind, it is easier to obtain density information than it is to measure currents directly over a large survey area. Currents estimated by this method express the balance between the pressure force and the Coriolis force, and give the relative velocity component between two depths, i.e., the velocity shear. It assumes no friction (and hence is less useful close to shore or in shallow water) and assumes that there is no motion at some specified depth level. With all these assumptions, results are perhaps more qualitative than quantitative, but they are nevertheless useful because they do indicate probable current patterns in surface waters when winds are relaxed. However, this is not always the case, particularly in surface waters, and while geostrophic currents may partially indicate a region's currents, only by direct measurement of the movement of water masses can the interplay of all oceanographic and meteorological variables be established. This can only be done for a few locations at any specific time because of resource and logistic constraints, so geostrophic and direct current measurements should be complementary.

Oceanographic events, excluding the effects of wind, account for long-shore movement of megalopae but do not appear to explain

offshore or onshore movement in the study area, except in the vicinity of the Juan de Fuca Gyre and perhaps Barkley Sound. The concentration of megalopae at distances offshore which seem to coincide with the boundaries between long-shore currents flowing in opposite directions suggests that while oceanographic processes may not usually facilitate onshore megalopal movement, they can impede it, and it is perhaps this aspect which is most important to cross-shelf megalopal movement, at least off British Columbia.

The substantial Lagrangian drifter movement observed supports earlier suggestions (Gaumer 1971; Reilly 1983; Jamieson and Phillips 1988) that over the estimated 4-mo larval period of Dungeness crab, larvae can move considerable distances long-shore.

Meteorological Considerations:

The only pronounced onshore movement of drifters observed prior to 1988 was in association with meteorological change. This suggests that southerly winds, typically indicative of a passing storm front, may serve as a mechanism to rapidly move megalopae at the surface at specific locations onshore. This process may be facilitated if the Vancouver Island Coastal Current is absent, as lighter winds may initiate more onshore movement.

The only extensive time series of hourly wind data for the west coast of Vancouver Island are those from lighthouses. It is recognized that wind data from lighthouses are only partially reflective of

meteorological conditions which might occur on the continental shelf or beyond, both because of regional variability in wind patterns and because of the influence of land on coastal winds. Nevertheless, these data are presented because while it might be argued that the relative magnitude and direction of winds at any specific time is not representative of conditions somewhere else, the relative frequency of storms, their relative strengths, and the general wind pattern in the region are all considered. These data are not presented here to explain microscale events but are rather used to suggest both the importance of meteorological events and the need to obtain more accurate wind data from moored weather-monitoring buoys located on the continental shelf.

Wind data are presented here for both Amphitrite and Estevan Points, which are located 37 km south and 50 km north of Tofino, respectively (Fig. 13). Wind direction was analyzed in terms of its vector orientation to the coast, with positive ordinate values indicating onshore movement and negative ordinate values indicating offshore movement (Fig. 14). Because megalopae are primarily present off Tofino in May and June (Jamieson and Phillips 1988) and the megalopal stage is of about 28 d duration, wind data from April 1-July 31 each year were analyzed.

Preliminary study of megalopae at night with a series of 0.01 m² Miller nets suspended at 1 m intervals over a depth range of 0-4 m indicated that in calm sea conditions at least, megalopae were concentrated in the top metre of the water column (in 3, 20 m³ per

depth interval tows, the total number of megalopae caught between 2100-0005 hr, June 23, 1987, at 0, 1, 2, 3 and 4-m depths were 11, 0, 1, 1, and 0, respectively). It was therefore assumed that movement of megalopae by winds was comparable to that of oil slicks, ie. with a velocity 3% that of the wind and in the direction of the wind. Ekman theory, which suggests surface transport is at a direction 15° to the right of the the wind, does not seem to apply to oil slicks (A. Ages, Inst. of Ocean Sciences, Sidney, B.C., pers. comm.), but since megalopae, unlike oil, are not in the top few millimeters of the water column, additional analyses where Ekman transport does occur are also presented. Analyses in both cases are presented with the assumption that megalopae are either continuously, ie. both day and night, at the water surface or are only present at the surface at night. In the latter case, the change in number of hours of darkness over the course of the season was considered, with night defined as the hours between civil twilight in the evening and morning (rounded to the nearest hour).

Finally, onshore-offshore transport was measured in two ways:

- 1) where, relative to a location on any date, would a megalopae end up 28 days (i.e., the duration of the megalopal stage) later and
- 2) what were the relative frequencies of days at each site when the maximum net onshore transport over the next 28 days was greater than the following specified distances between April 1 and June 30: 10, 15, 20, and 25 km.

Results indicate that average maximum onshore transport at

Estevan Point (31.4 km) is greater than twice that at Amphitrite Point (14.4 km) and that the frequency of days with stronger onshore transport is also greater at Estevan Point (Table 1). Comparison of average onshore transport (Tables 1c, 2) for dates arbitrarily selected as the first 6 yr of each of the 1970s and 1980s, indicated that for onshore transport >10 km and >20 km at Amphitrite and Estevan Points, respectively, onshore transport in the 1980s was considerably lower. Different threshold transport levels are used for the two sites since because average transport is relatively high at Estevan Point, little observed difference in transport between the two time intervals occurred if the Estevan Point data were considered at the >10 km level. This difference between the two time periods may be biased by the presence of a particularly strong El Nino in 1983 (Wooster and Fluharty 1985), but exactly how this might be correlated with meteorological change and might have influenced crab settlement is uncertain. Crab settlement appears to have been high at Tofino in 1983 or 1984 on the basis of recent fishery performance (Smith 1988).

Future Direction:

On the basis of biological, oceanographic, and meteorological observations to date, some general hypotheses can be established which are capable of being evaluated by monitoring future events:

- 1) Onshore movement of megalopae is facilitated by diel vertical migration.

Moderate winds from the southeast or south noticeably affect drifter movements and cause them to move shorewards. The timing and magnitude of such events seems important, and transport to a barrier, such as the coast or a frontal zone, should be correlatable with storm event scale and frequency. Location of megalopae at depth during the day may be more to avoid predation than to benefit from transport by subsurface currents.

2) The Vancouver Island Coastal Current is normally an effective barrier to onshore surface movement.

The absence of megalopae in abundance in the current when it is evident suggests both an absence of megalopae in the current's source, Juan de Fuca Strait, and little entrainment of continental shelf water and megalopae during its progression along the coast.

3) Relaxation of the Vancouver Island Coastal Current allows onshore surface movement to the coast.

Annual and seasonal variability in Coastal Current strength can be expected to occur because of variation in prevailing winds, coastal runoff and outer shelf/slope circulation, thus explaining its absence in May and June, 1988. The relation between current strength, wind strength, and onshore movement of megalopae needs to be further investigated.

4) Southeasterly or southerly winds enhance onshore movement of megalopae.

Wind alone in the spring appears insufficient to move neuston particles more than about 30 km onshore on average during a 28-day

developmental period (Table 5a). Megalopal behaviour and the significance of the relatively strong swimming ability of megalopae need to be established before the location of offshore concentrations of megalopae can be related to inshore settlement patterns. The relatively strong swimming ability of megalopae may primarily allow megalopae to remain as close to the surface as possible in the turbulent waters associated with storms, and so benefit maximally from wind-induced transport.

In conclusion, while our studies partially explain megalopal crab dynamics and have enabled us to advise both fishermen and managers on why landings in the Tofino Dungeness crab fishery should be relatively low for the next few years, many basic questions relating to the potential movement of larvae over sometimes considerable distances remain to be answered. What has become obvious is that the problem is not a biological one alone, and that collaboration between biologists and oceanographers is essential if answers are to be determined. Both biotic and abiotic factors are involved, and it is the result of this mix that seems to largely determine the magnitude of Dungeness crab movement and, presumably, recruitment.

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Figure Legends

- Figure 1. Sample locations (dots) and isopleths of relative megalopal abundance (shaded areas) during June, 1986, off the west coast of Vancouver Island. Stars = location at beginning and end of the 3-day time series of nocturnal neuston sampling.
- Figure 2. Sample station locations (dots) during May, 1987, off southern Vancouver Island and Washington. The large dots indicate locations where a concentration of megalopae was monitored continuously through the night. Cross-shelf transects are referred to in later figures by the 2-letter codes indicated.
- Figure 3. Sample station locations (dots) during June, 1987, off southern Vancouver Island and Washington. Cross-shelf transects are referred to in later figures by the 2-letter codes indicated.
- Figure 4. Objectively smoothed near-surface water property maps of currents for a depth of 0 m relative to 100 m. Assumed cross-shore and longshore correlation scales are 25 and 50 km, respectively. A. for June 12-20, 1986. B. for June 15-26, 1987.
- Figure 5. Objectively smoothed near-surface water property maps of geopotential heights for a depth of 0 m relative to 70 m, using the isotropic covariance function recommended by Denman and Freeland (1985).

Figure 6. Tracks of drifters deployed across the Juan de Fuca Gyre: A. 3 drifters in June, 1985. B. 4 drifters in June, 1986. Marks along each track indicate the position of each drifter at noon on the day (the adjacent 1 or 2-digit number) indicated. Four-digit numbers refer to the hour the drifter was deployed and/or retrieved.

Figure 7. Tracks of deployed along a transect off Tofino, B.C.: A. 9 drifters in June, 1986. The 2 drifters closest inshore were retrieved after 8 hr since because they were moving northwards so fast, they were approaching the maximum broadcast range of their radio transmitters. B. 6 drifters in June, 1987. Marks along each track indicate the position of each drifter at noon on the day (the adjacent 1 or 2-digit number) indicated. Four-digit numbers refer to the hour the drifter was deployed and/or retrieved.

Figure 8. Tracks of drifters deployed along a transect off Grays Hbr., Washington: 7 drifters in June, 1987. The end drifter on the right was picked up by a fisherman in the afternoon on June 17, but was recovered and redeployed about 30 km north of the initial deployment at 1607 hr, June 18. Marks along each track indicate the position of each drifter at noon on the day (the adjacent 1 or 2-digit number) indicated. Four-digit numbers refer to the hour the drifter was deployed and/or retrieved.

- Figure 9. Abundance of megalopae found along the transects off Vancouver Island and Washington from 1985-1988. The arrow indicates the distance from shore of the shelf break (200 m depth isopleth). Locations of each transect are given in Figs. 2 and 3, respectively, referenced by the two-letter codes indicated.
- Figure 10. Abundance of megalopae found along the offshore, longshore transect off Washington in May, 1987. The arrows indicate the latitudes of significant geographical features, and the times at night that sampling began or terminated are shown. Location of the transect is given in Fig. 2.
- Figure 11. Percentage of the three C. magister megalopal intermoult groups observed at each station on the transect off Tofino, B.C. in June, 1986 (Fig.1). The intermoult stages comprising each group, early (1-4), middle (5-8), and late (9-13), are those of Hatfield (1983).
- Figure 12. Scaled abundance of C. magister megalopae by intermoult group (see Fig. 13) at each station along the Tofino, B.C., transect in June, 1986.
- Figure 13. Geographical locations of Amphitrite and Estevan Points relative to Tofino. The "feathered circles" off each lighthouse on the west coast of Vancouver Island illustrate the average direction (location of arrow), average force

(Beaufort scale: number of feathers) and maximum winds observed over the previous 7-10 years. Thus, off Amphitrite Point., NW winds blew 45% of the time (measure the length of the arrow against the scale) at Force 3, with calms 1% of the time (values in circle). [Source: Sailing Directions - British Columbia Coast (South Portion). Vol. 1, 14th ed., 1987, Department of Fisheries and Oceans, Institute of Ocean Sciences, Sidney, B.C.].

Figure 14. An example of analysis of the wind data for each year for each of the two lighthouse locations. Data presented is for Amphitrite Point, April 1-June 30, 1986. Vector directions have been rotated by 45° because of the angle of the coast to magnetic north, allowing onshore and offshore movements to be indicated by positive and negative values, respectively. Values are averages for each 6 hr time interval, but in this analysis, only wind data between civil twilight in the evening and morning is included. This therefore assumes that megalopal transport is only affected by winds at night. A. Wind strength (km hr^{-1}) and direction. B. Onshore (+) and offshore (-) wind movement (km) at each time interval. C. Relative accumulative positioning onshore or offshore (km) of a particle starting at any specified location, commencing April 1 and ending June 30. Here it is assumed movement is at 3% of the wind speed and at an angle 15° to the right of the

wind. D. Maximum onshore movement (km) over the next 28 days (= duration of megalopal stage) for a particle starting at any specified location on each date, assuming movement relative to the wind as in (C).

Table 1. Estimated onshore transport of neuston between April 1 and June 30, assuming transport is at a direction of 15° to the right of the wind for 28-day periods commencing during this time frame. A. Average minimum and maximum transport (km) by location over a 15-yr period (1969/70-1986). B. Average number of days (maximum possible is 91) during which onshore transport of neuston exceeded selected distances over a 15-yr period (April-June, 1969/70-1986). C. Average number of days during which onshore transport of neuston exceeded selected distances over two, 7-yr periods (April-June). Day = day and night presence in neuston; night = night only presence in neuston.

A.		Average 28-d onshore transport (km): 1969/70-1986			
		Estevan Point		Amphitrite Point	
		Min.	Max.	Min.	Max.
Night	x	-0.5	31.4	-1.5	14.4
	S.D.	6.4	8.8	2.5	7.4
Day	x	-9.6	78.4	-9.9	32.5
	S.D.	13.8	42.2	4.7	25.4

B.		Average number of days (April-June, 1969/70-1986)							
		Estevan Pt. - onshore transport (km)				Amphitrite Pt. - onshore transport (km)			
		>10	>15	>20	>25	>10	>15	>20	>35
Night	x	60.4	41.9	26.6	14.2	20.4	7.3	2.6	0.6
	S.D.	21.5	22.5	19.4	17.7	21.6	15.7	8.5	2.3
Day	x	54.9	50.2	40.1	43.4	37.3	22.9	22.5	17.1
	S.D.	24.7	25.8	27.9	25.1	30.0	28.2	22.7	19.3

C.		Average number of days (April-June)							
		Estevan Pt. - onshore transport (km)				Amphitrite Pt. - onshore transport (km)			
		>10	>15	>20	>25	>10	>15	>20	>35
Time period		>10	>15	>20	>25	>10	>15	>20	>35
	1970-76	55.9	35.4	29.4	23.3	27.4	13.6	5.4	1.3
	1980-86	53.6	37.1	21.3	11.7	9.9	2.4	0.1	0

Table 2. Number of days between April 1 and June 30 in which net wind transport off Amphitrite Point exceeded four specified distances (10, 15, 20, and 25 km) over the subsequent 28 days. A. Transport is in the direction of the wind. B. Transport is at a direction of 15° to the right of the wind.

Year	Days of onshore transport > specified distances (km)							
	A. 0° to wind				B. 15° to wind			
	10	15	20	25	10	15	20	25
1970	54	20	13	0	83	61	33	9
1971	16	10	2	0	28	9	3	0
1972	7	1	0	0	13	5	0	0
1973	0	0	0	0	23	0	0	0
1974	4	0	0	0	13	0	0	0
1975	11	3	0	0	38	18	2	0
1976	8	1	0	0	24	2	0	0
1977	0	0	0	0	25	0	0	0
1978 ^a	-	-	-	-	-	-	-	-
1979 ^a	-	-	-	-	-	-	-	-
1980	0	0	0	0	0	0	0	0
1981	0	0	0	0	0	0	0	0
1982	0	0	0	0	0	0	0	0
1983	5	0	0	0	8	0	0	0
1984	24	12	8	3	19	8	1	0
1985	0	0	0	0	32	6	0	0
1986	11	0	0	0	10	0	0	0
Mean	9.3	3.1	1.5	0.2	20.4	7.3	2.6	0.6
SD	14.2	6.0	3.8	0.8	21.6	15.7	8.5	2.3

^aNo wind data available.

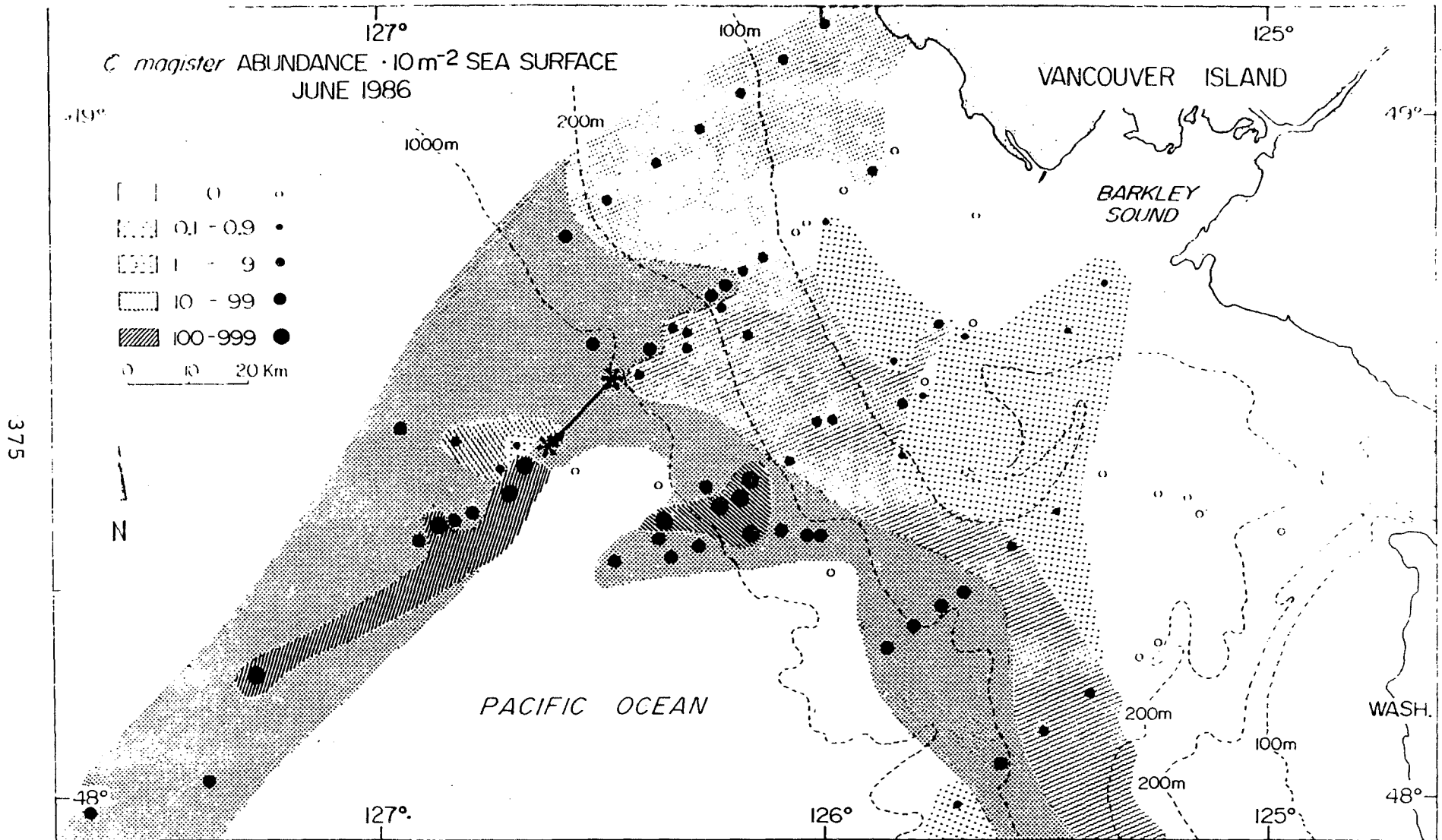


Figure 1.

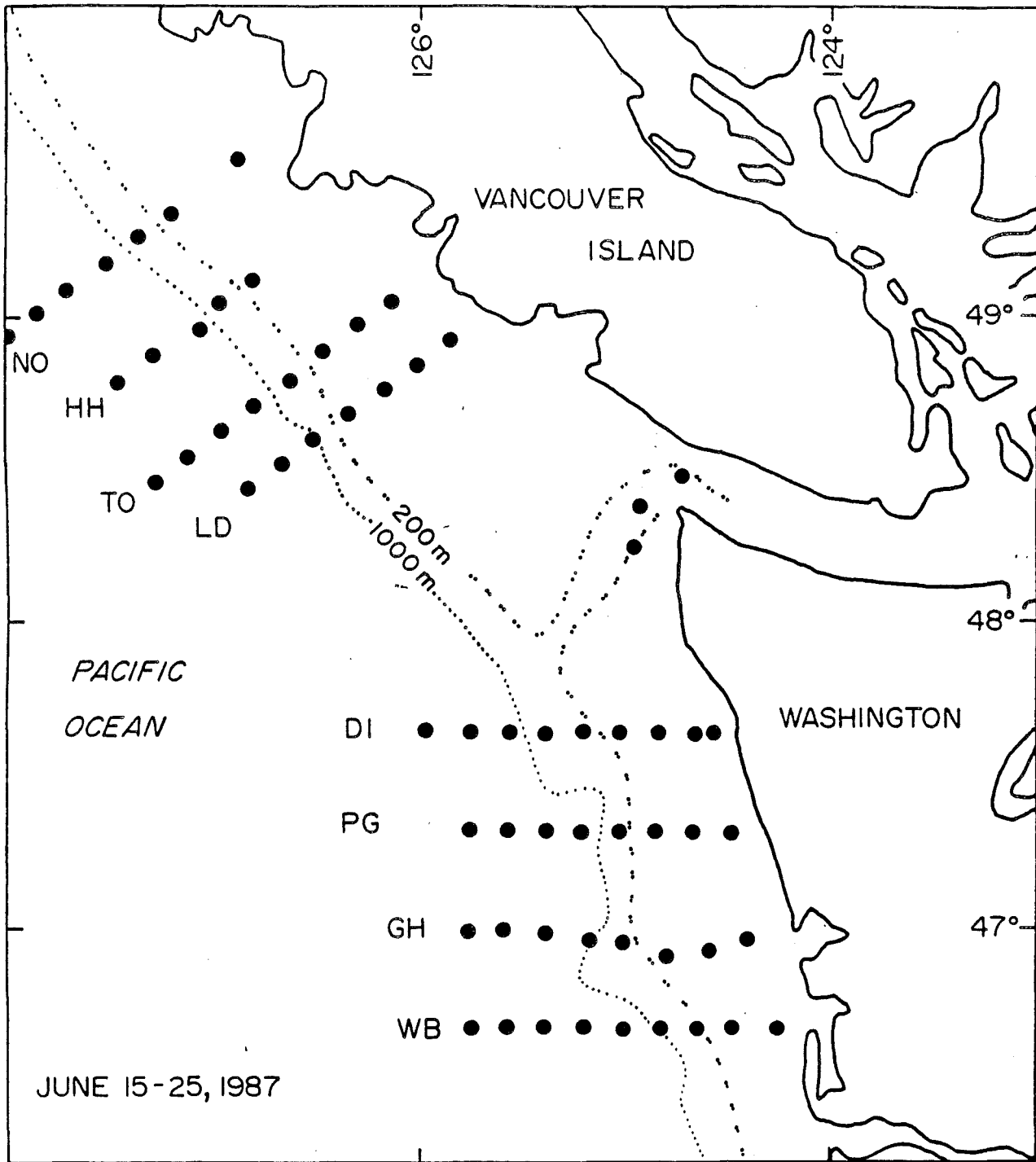


Figure 2.

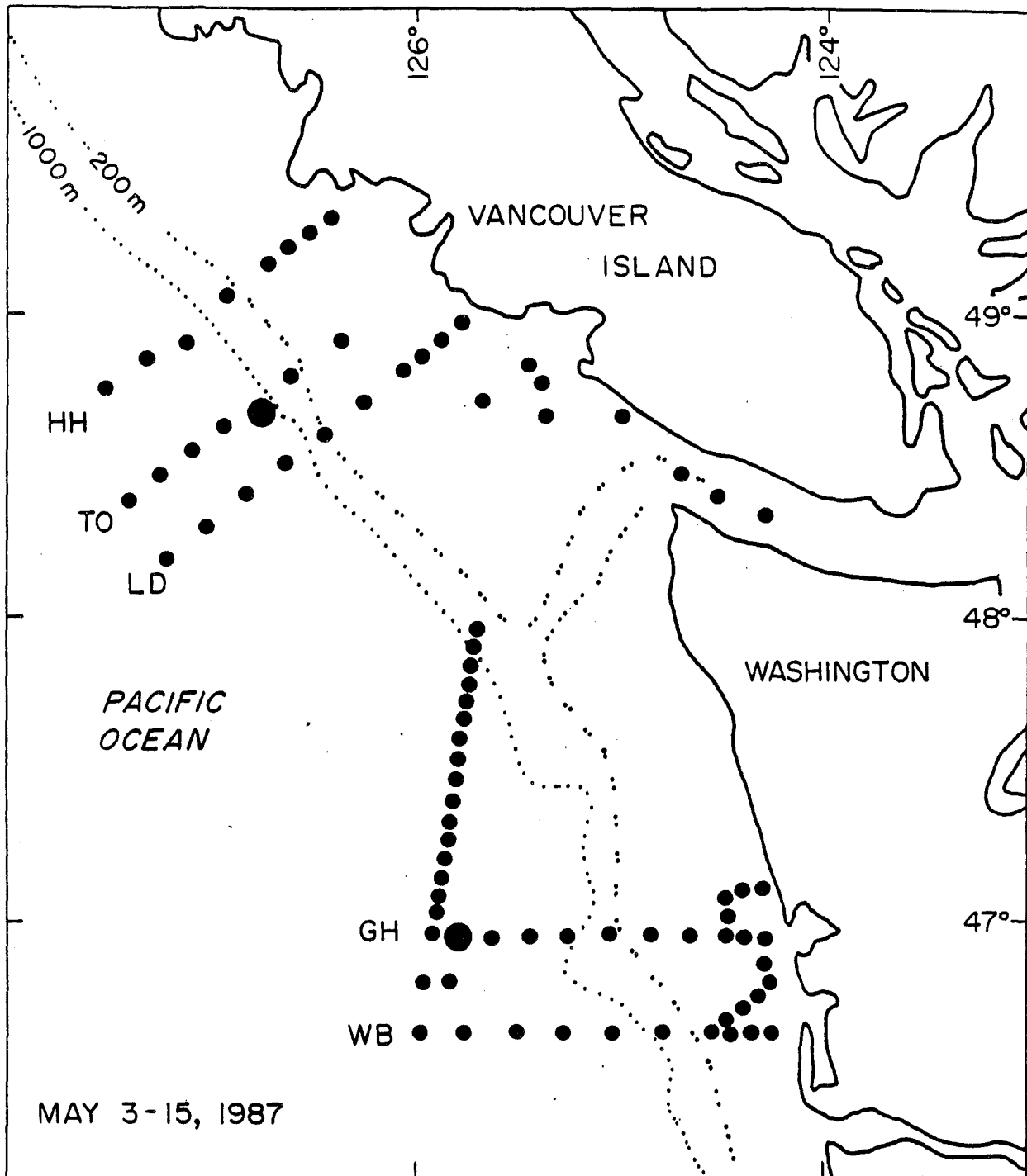


Figure 3.

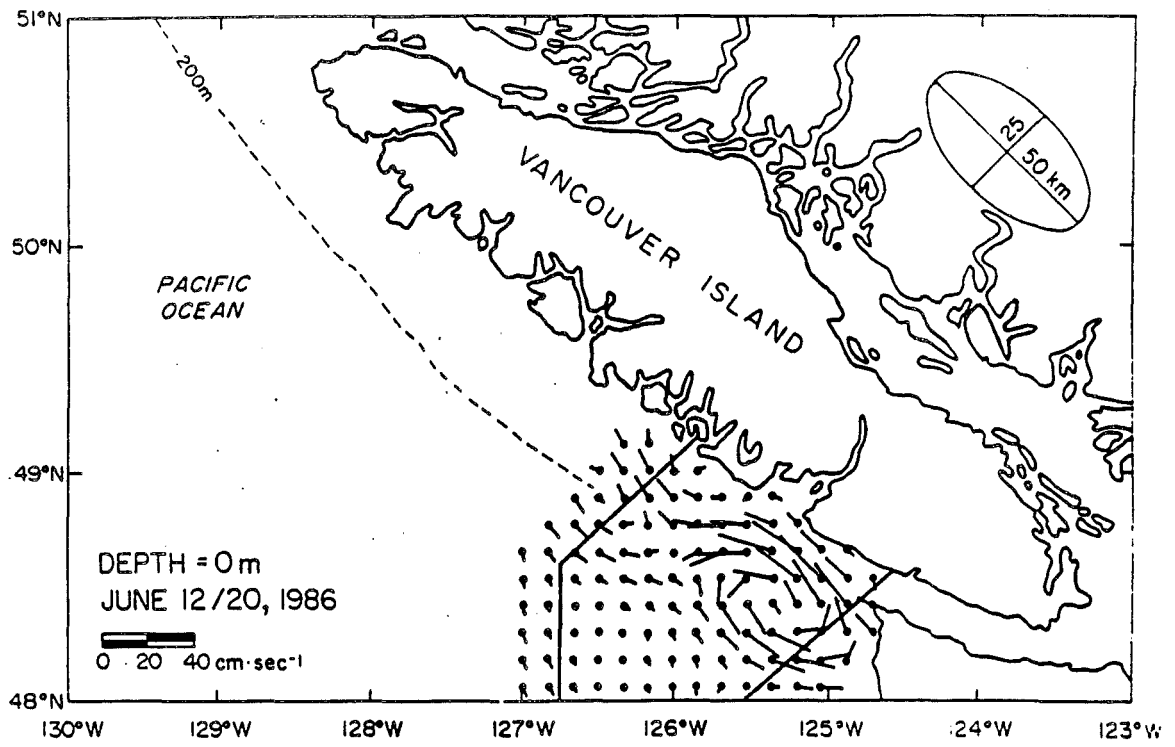


Figure 4a.

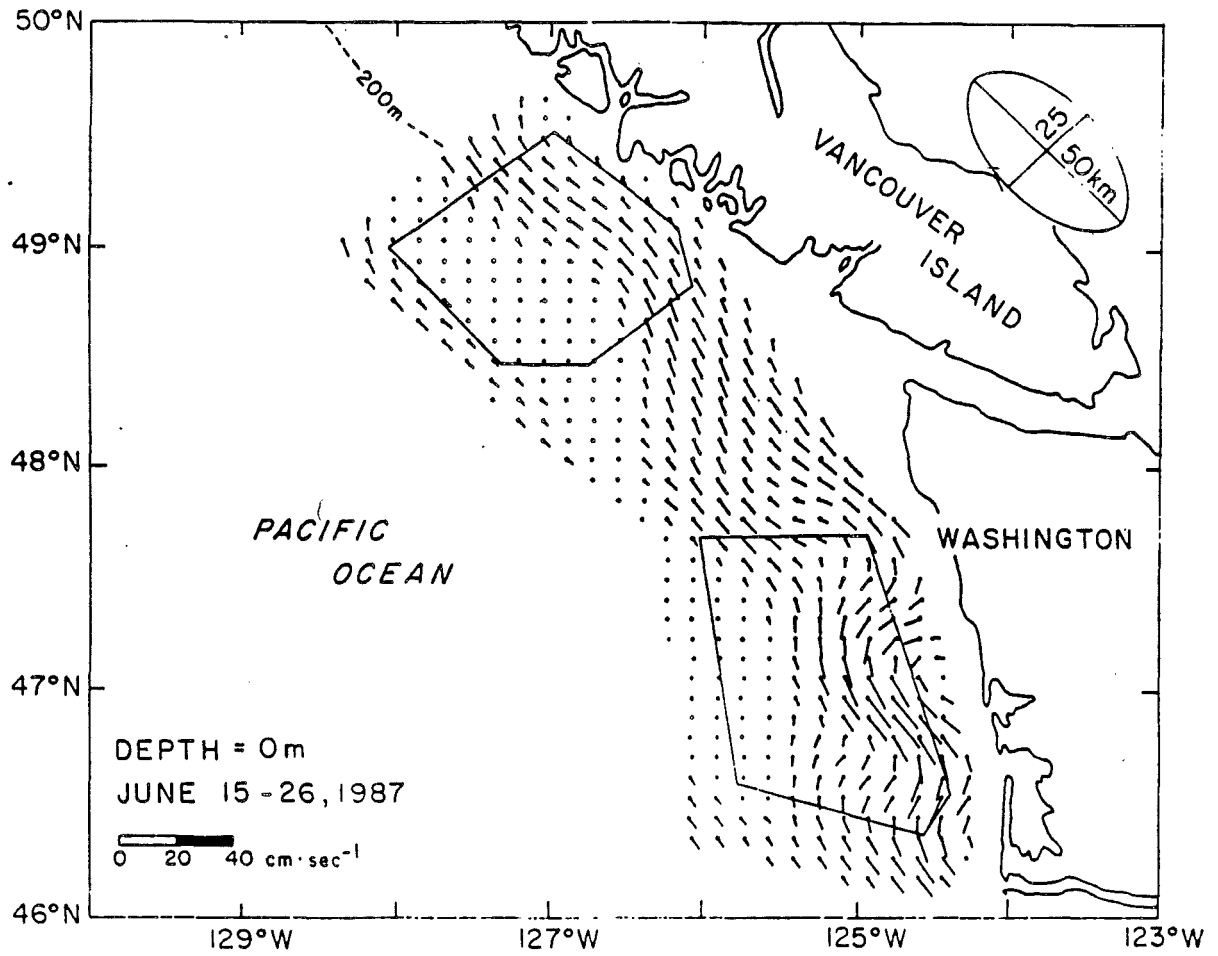


Figure 4b.

Cont. Int. = .05
 Solid Cont. = 2.18
 # of data pts. = 97
 Max. Hgt = 150.000
 Ex. Err. < .4
 $C_p = (1-\alpha) J_0 (h/\sigma) \exp(-h^2/\sigma^2)$
 $\sigma = .1$
 $\sigma = 18000.$
 $\sigma = 10.300.$
 Upslope integration used

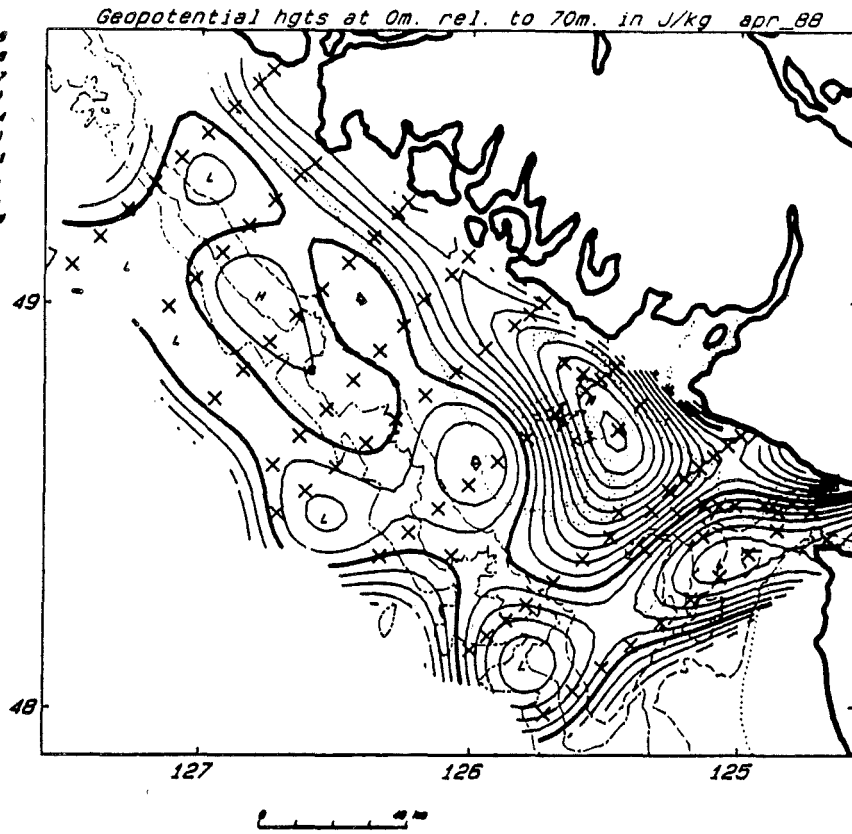


Figure 5a.

Cont. Int. = .05
 Solid Cont. = 2.50
 # of data pts. = 78
 Max. Hgt = 100.000
 Ex. Err. < .4
 $C_p = (1-\alpha) J_0 (h/\sigma) \exp(-h^2/\sigma^2)$
 $\sigma = .1$
 $\sigma = 18000.$
 $\sigma = 10.300.$
 Upslope integration used

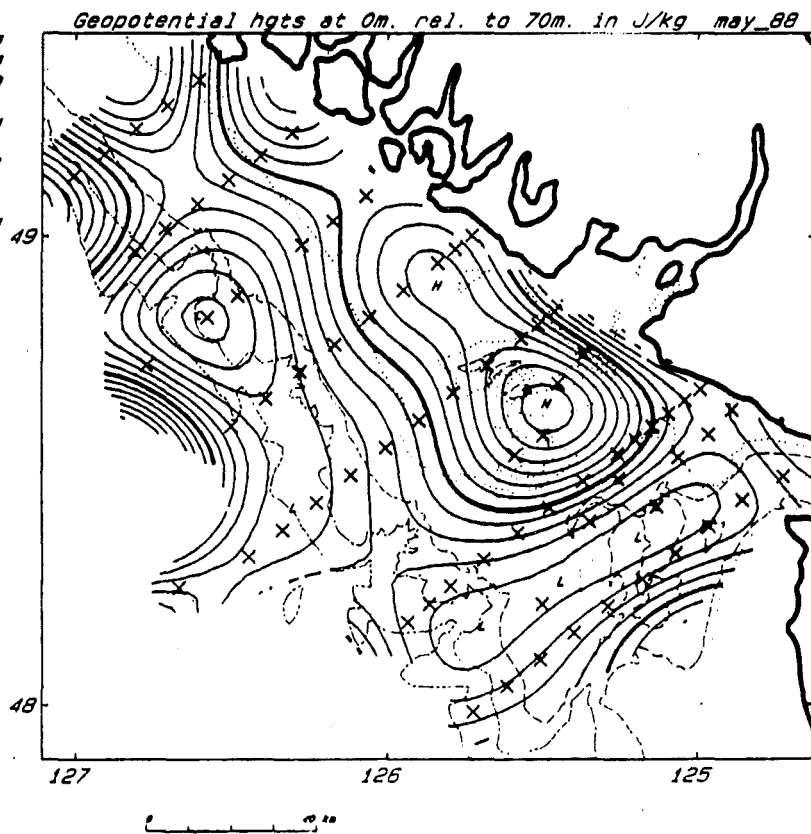


Figure 5b.

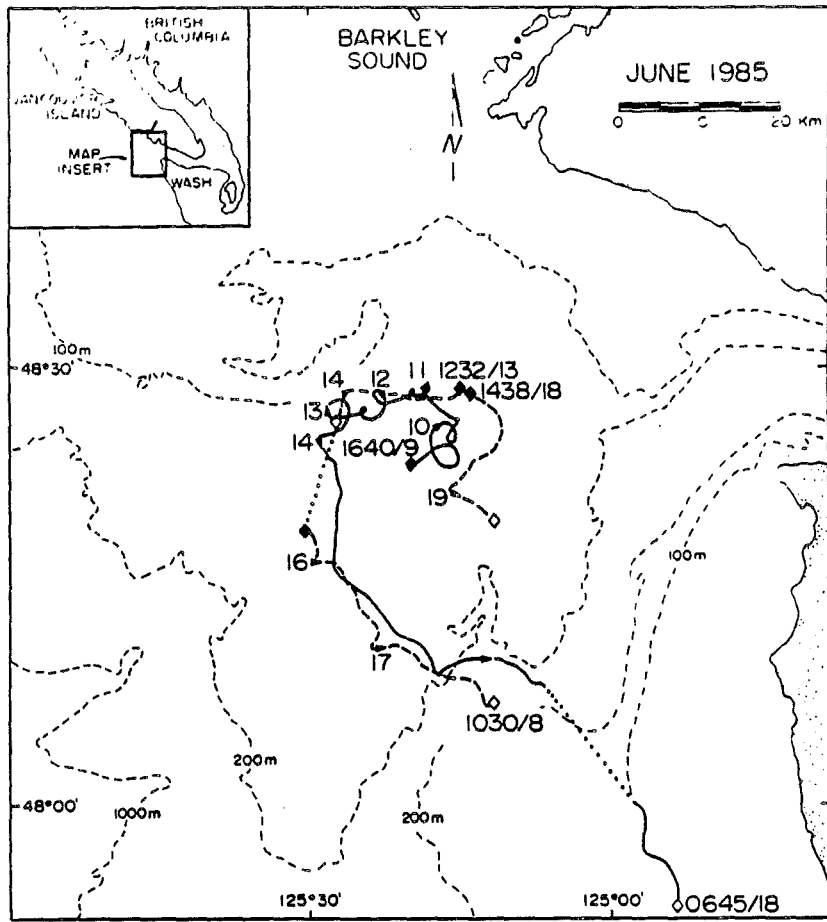


Figure 6a..

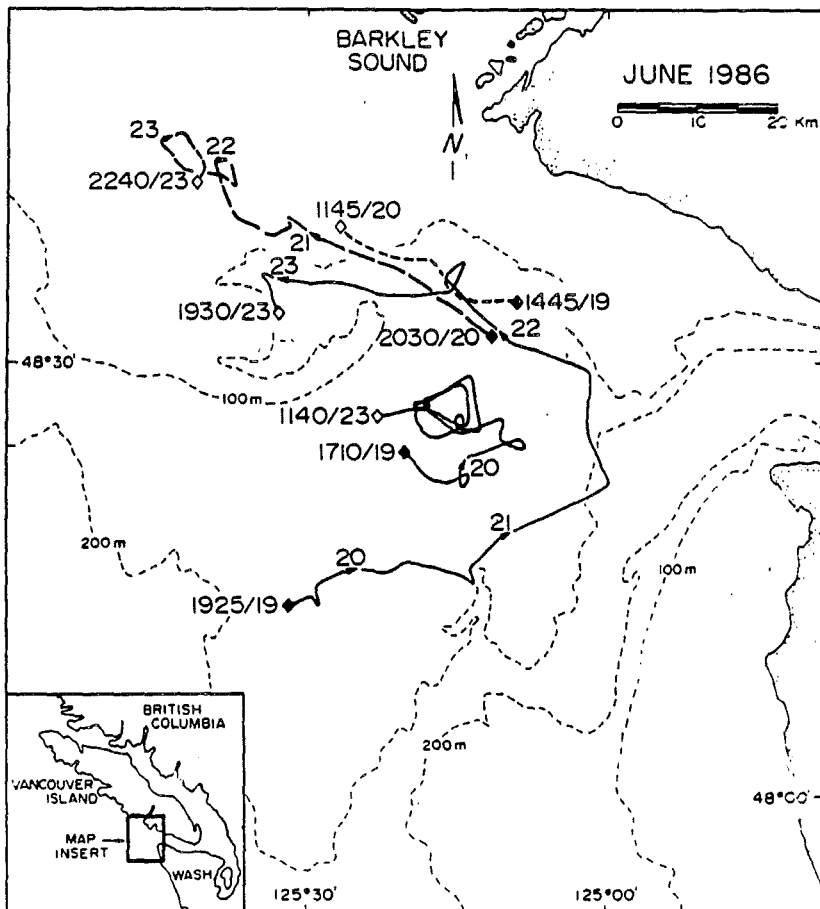


Figure 6b.

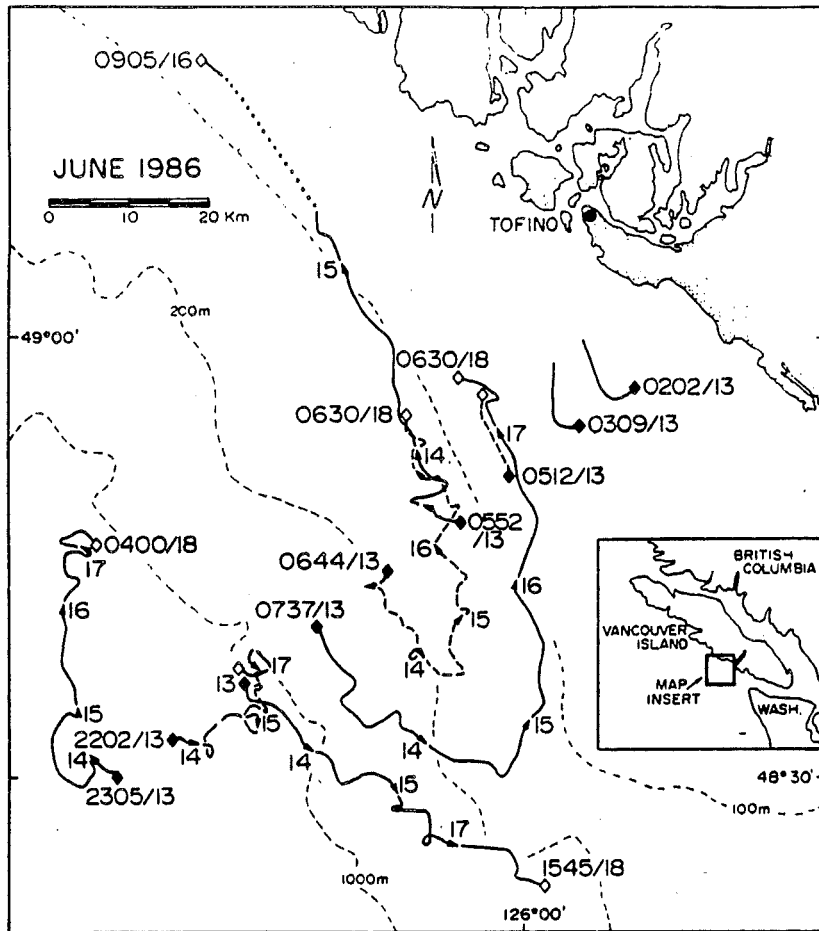


Figure 7a.

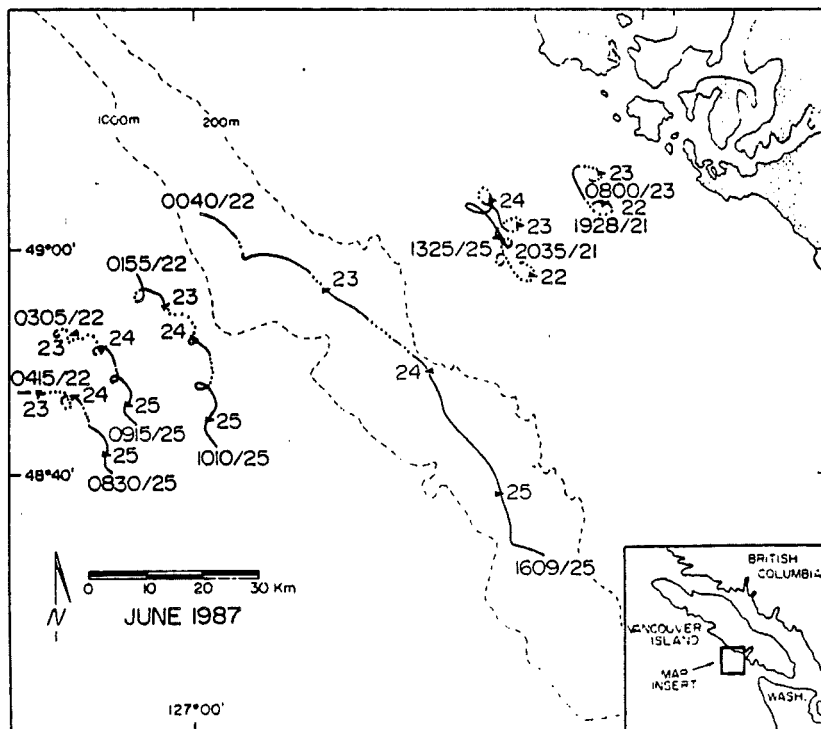


Figure 7b.

June 1988

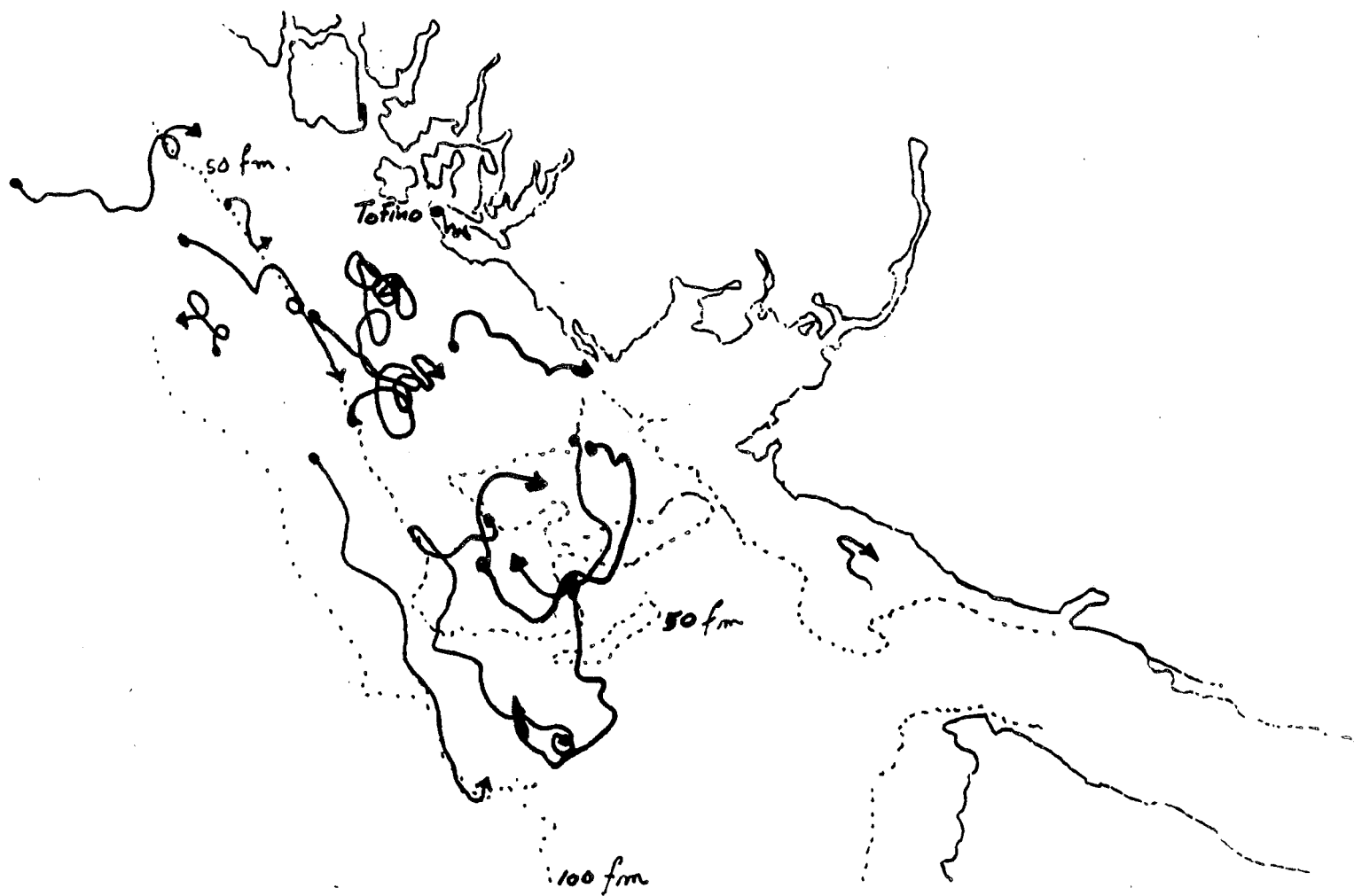


Figure 7c.

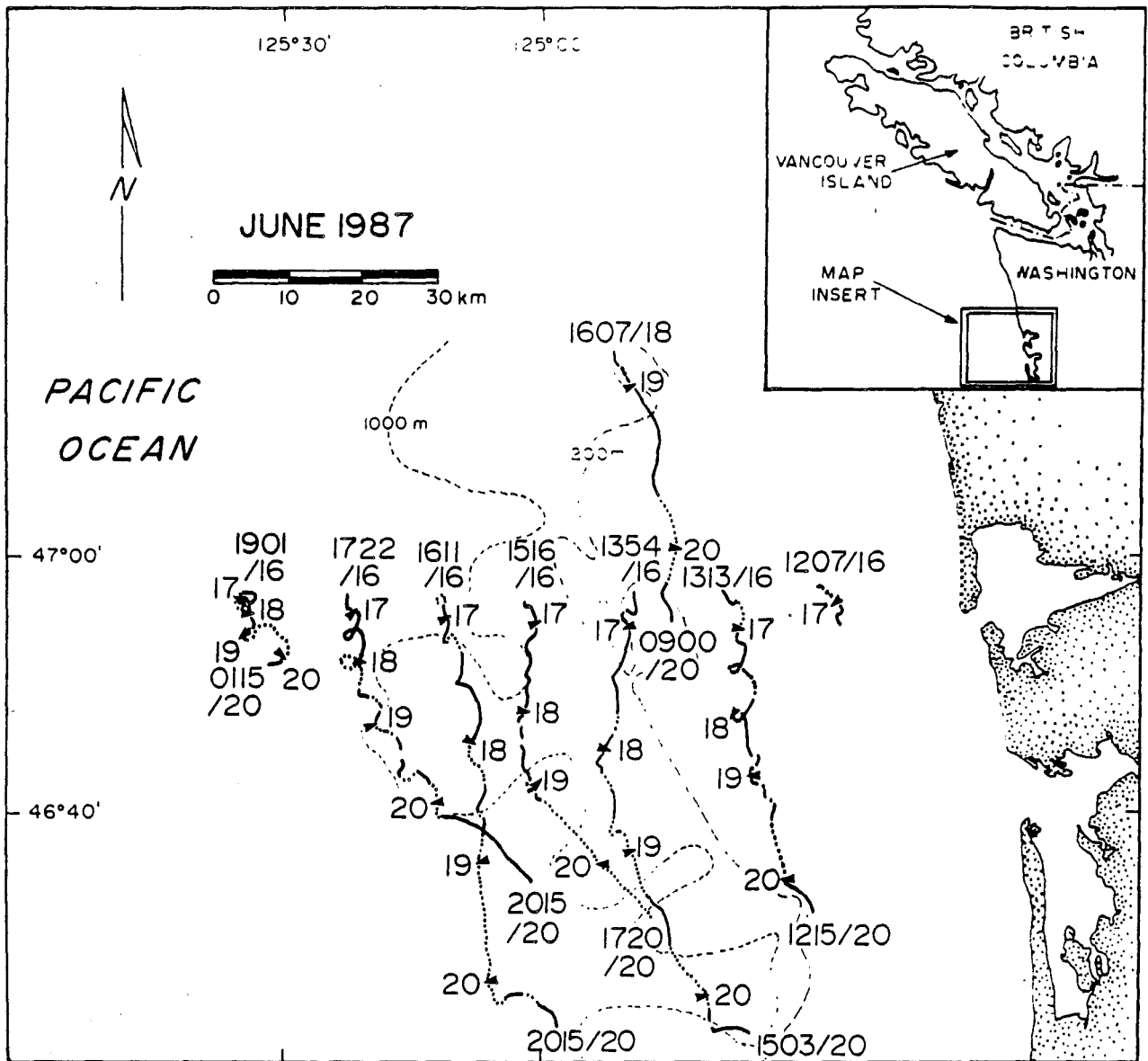
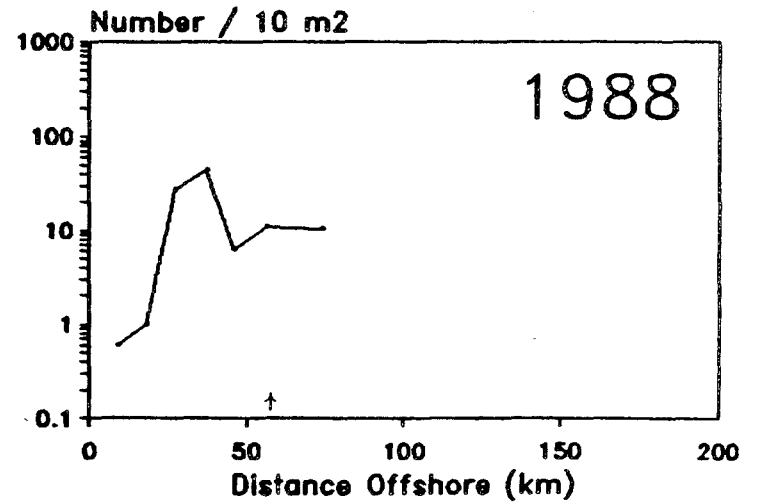
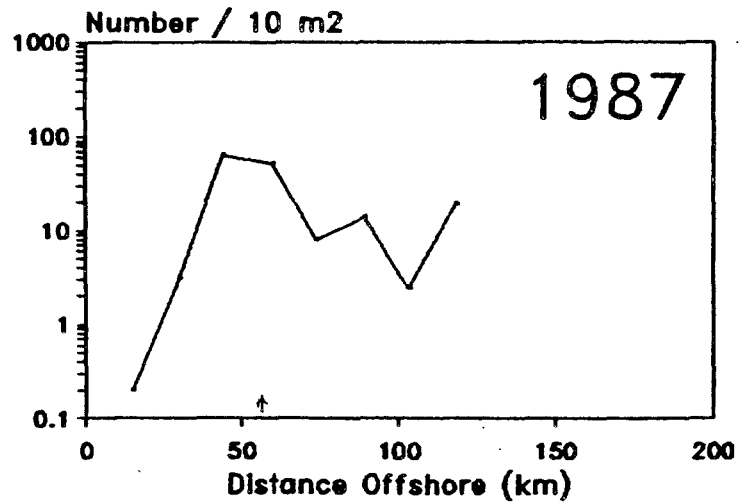
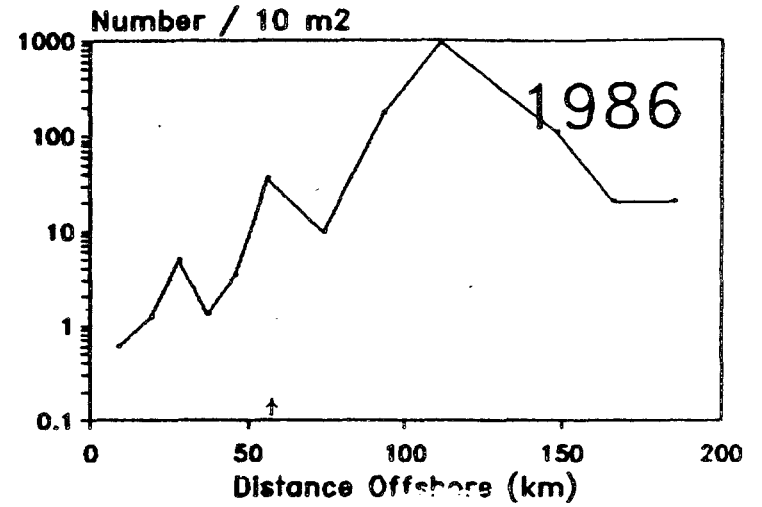
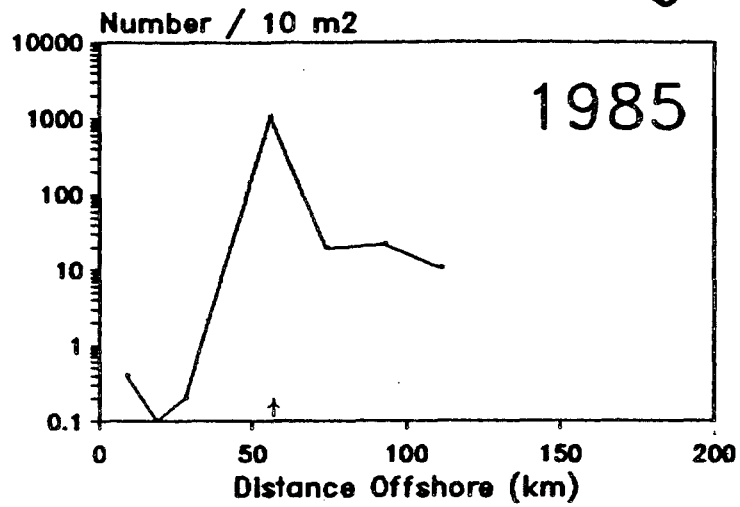


Figure 8.

Scaled Megalopal Abundance



384

Figure 9.

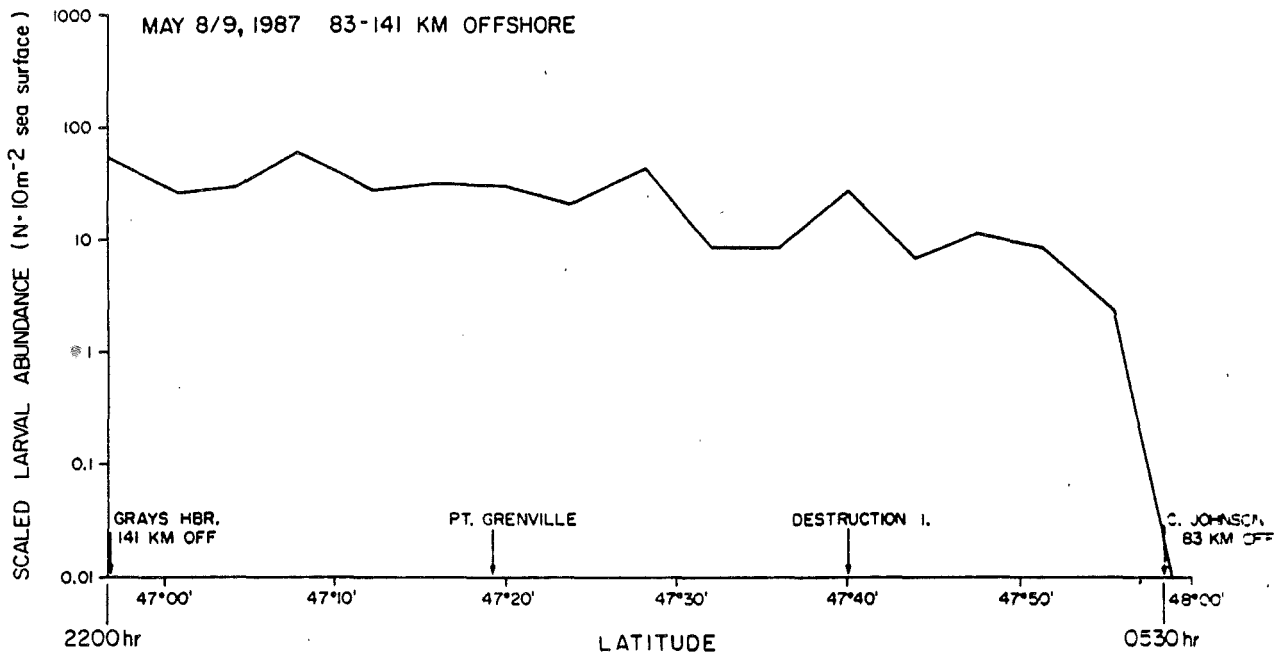


Figure 10.

TOFINO TRANSECT, JUNE 11/12, 1986

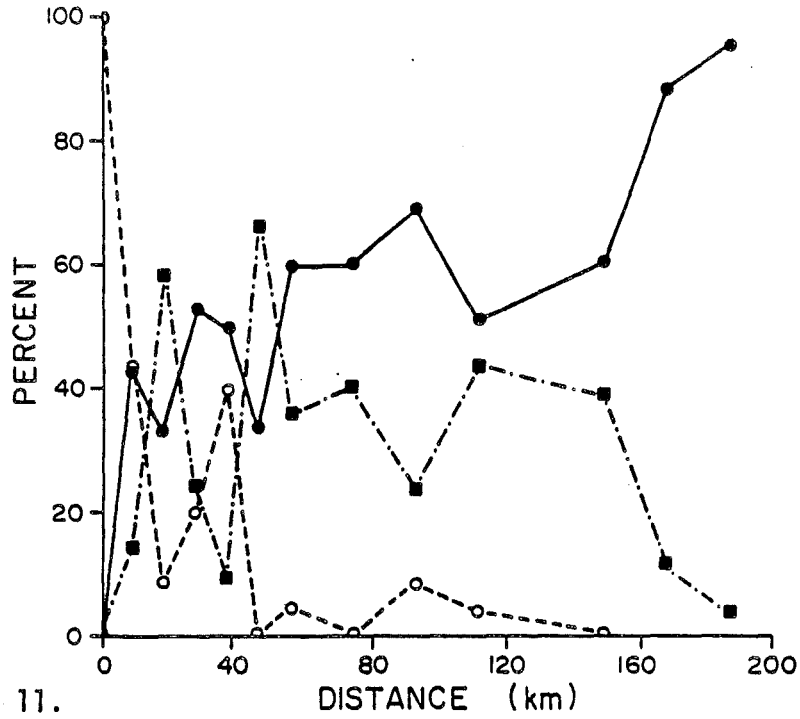


Figure 11.

C. magister
INTERMOLT STAGES
 ●—● 1-4
 ○- - -○ 5-8
 ■- · - · ■ 9-13

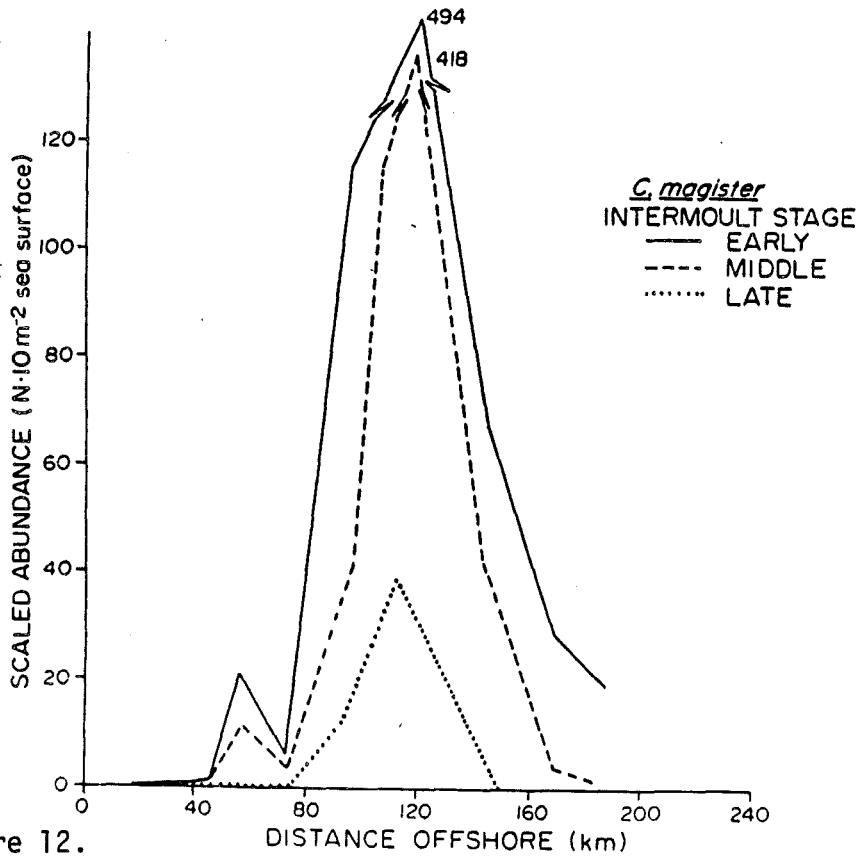


Figure 12.

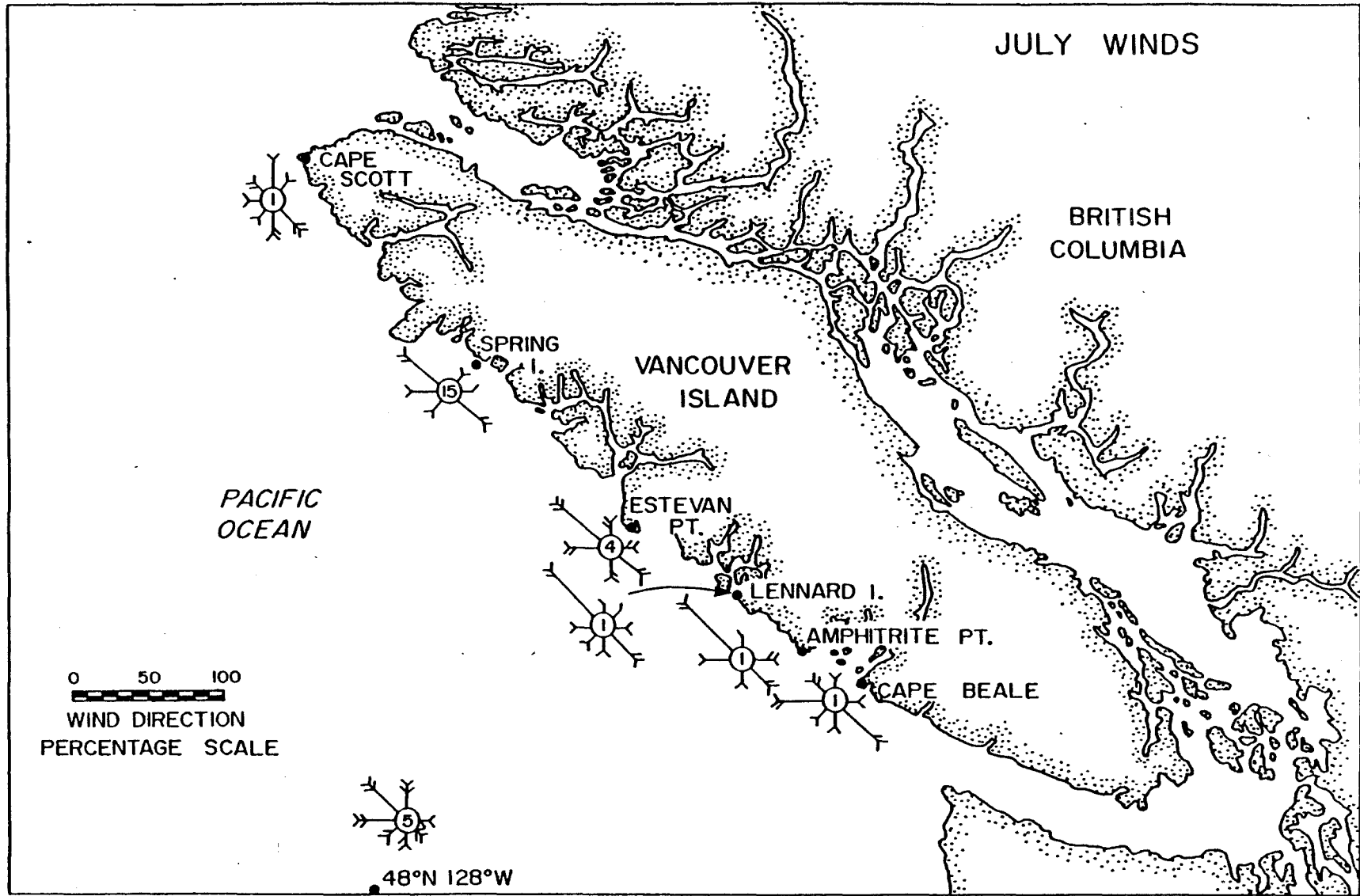


Figure 13.

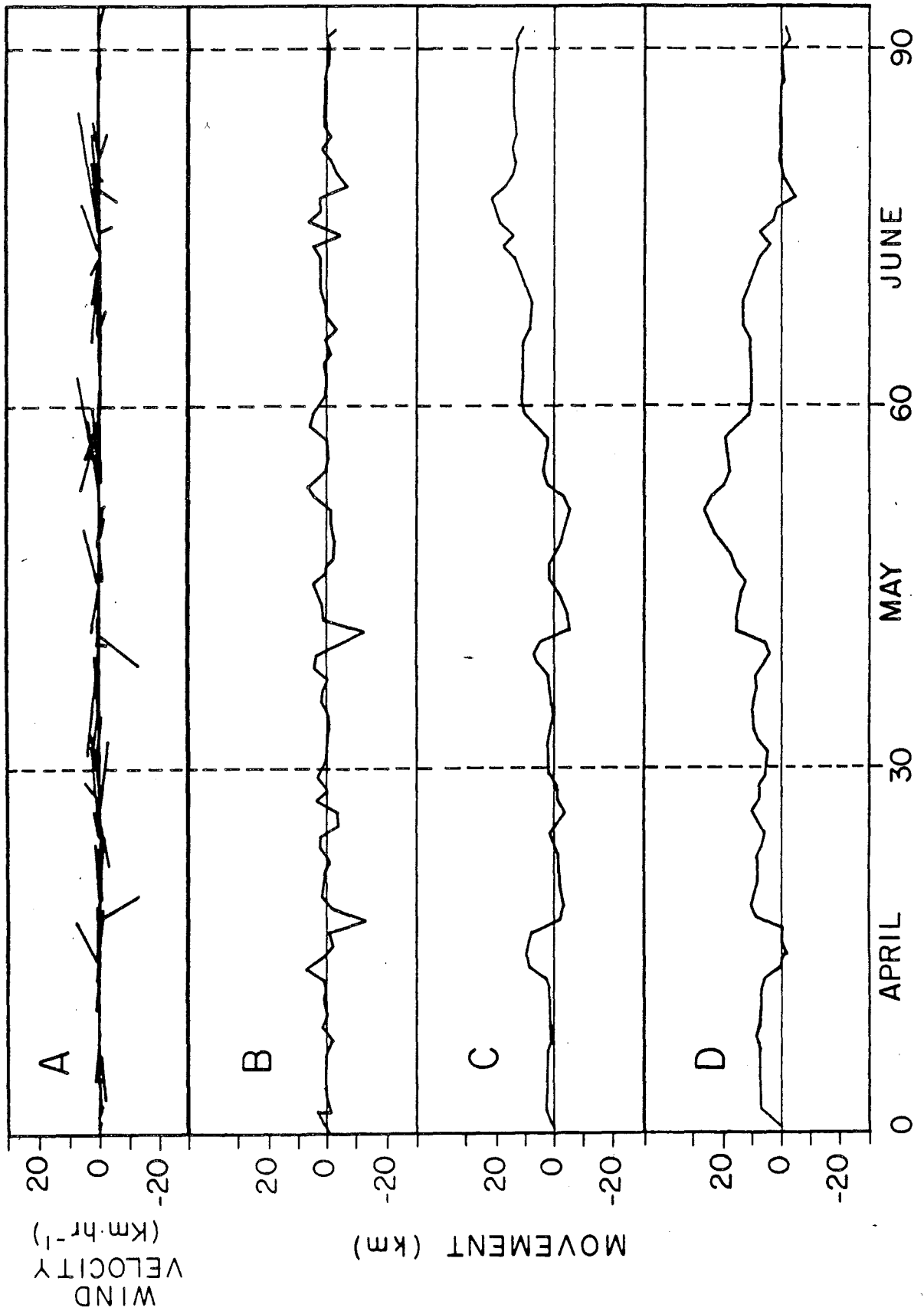


Figure 14.

THE EFFECT OF TEMPERATURE-DEPENDENT GROWTH
ON SIZE-AT-AGE AND SUBSEQUENT RECRUITMENT
OF EASTERN BERING SEA RED KING CRAB
(Paralithodes camtschatica)

By

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ABSTRACT

Stock recruitment studies of exploited fishery resources require estimates of the age at recruitment, but the age of crustaceans cannot be estimated precisely due to the lack of permanent hard body parts. Crustacean growth is a function of ambient temperature, and knowledge of this relationship can allow their age to be estimated. A temperature-based growth relationship was derived for juvenile red king crab from published data. Long-term water temperature observations were used to construct a time-by-area temperature matrix for Bristol Bay, AK. Growth of a cohort of crabs was simulated at various locations, and the resulting mean sizes compared to those observed by the annual NMFS eastern Bering Sea crab survey. Results indicate that age-at-recruitment is 3 to 5 years greater than previously estimated, and has decreased by 2 years over the past decade as a result of climatic change. Single year-classes require 3-5 years for complete recruitment to a given size interval, and recruitment in any year may consist of crabs from 4-5 yearclasses. Future stock-recruitment studies should account for the effects of multi-year recruitment and yearclass overlap.

INTRODUCTION

The management of fishery resources requires an understanding of the factors allowing successful recruitment to an exploited population. A common technique is to examine the relationship between the abundance of reproductively mature adults and the abundance of recruits produced by them. This stock-recruitment relationship has been described in various forms, the most functional being those of Ricker (1954), and Beverton and Holt (1957). Both models have certain characteristics in common (Ricker, 1975): 1) when there are no parents, no juveniles are produced; 2) recruitment must exceed spawner abundance over some part of their range, and does not fall to zero at higher levels of spawner abundance; 3) both assume constant growth rates and mortality of juveniles until recruitment; 4) both require essentially knife-edge recruitment, i.e., that the majority, if not all, of the offspring of the parent stock existing in a given year recruit in a single season; 5) both require that the age of recruits be known. Neither model takes environmental variation into account. Although both models work reasonably well for fish species such as salmon and cod (Ricker, 1975), attempts to apply them to crustacean populations (Reeves and Marasco, 1980; Reeves, 1985; Stevens, unpublished) have met with limited success, perhaps because the required assumptions are usually not met.

The red king crab, Paralithodes camtschatica, comprises one of the most valuable fisheries in the United States. In 1980, it was the most valuable single-species fishery in the U.S., with landings of 84,400 metric tons (mt), valued at \$168.7 million (U.S. Dept. of Commerce, 1982). Since 1971, the Bristol Bay king crab stock, in the eastern Bering Sea, has produced the majority of the landings (Alaska Dept. Fish and Game (ADFG), 1987). After foreign vessels were excluded from this fishery, U.S. landings increased steadily to a peak in 1980, after which they declined precipitously (Fig. 1). The Bristol Bay fishery was closed in 1983; since 1984, landings have gradually increased to 5,600 mt, valued at \$49 million in 1987 (ADFG, 1987).

The National Marine Fisheries Service (NMFS) has conducted annual surveys of the fish and crab resources of the eastern Bering Sea (EBS) since the late 1960's, providing estimates of population abundance for king crabs and other exploited species (Stevens, Macintosh, and Stahl-Johnson, 1987). Using this data, Reeves and Marasco (1980) analyzed the dynamics of the Bristol Bay king crab population with a Ricker-type model, by defining recruits as the estimated number of males in the size range 95-109 mm carapace length (CL) and assigning them an age of 5 years. They concluded that a stock-recruitment relationship existed, and that recruitment of male crabs would be maximized by maintaining the abundance of fertilized females in the range of 24-47 million crabs (a level that has not occurred since 1982, Stevens et al., 1987). Current management strategies for the Bristol Bay king crab fishery are based in part on Reeves and Marasco's findings.

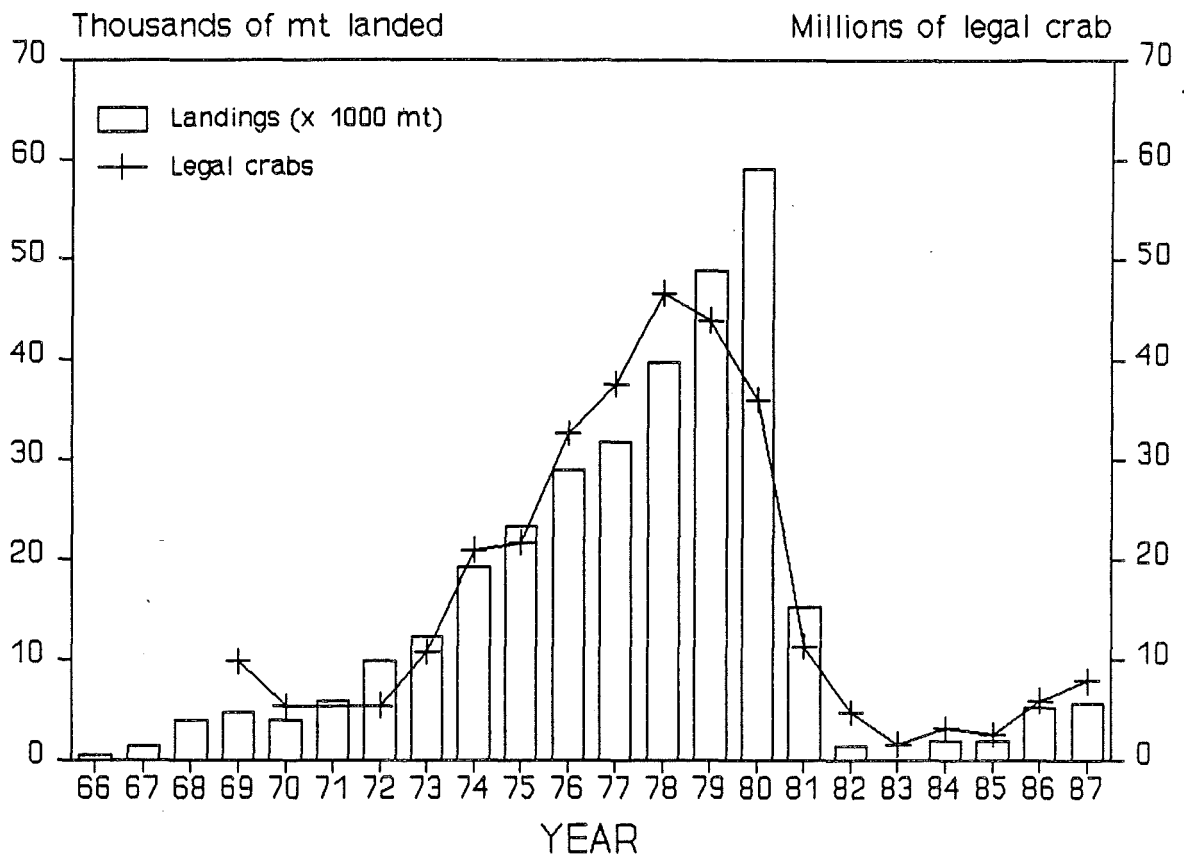


Fig. 1. Commercial landings of Bristol Bay king crab by U.S. fishermen (thousands of metric tons), and abundance of legal sized male crabs (millions) estimated by the NMFS EBS surveys.

Certain problems exist with this type of analysis due to fundamental differences in the biology of crabs and fish. Age of crustaceans is difficult to estimate due to the lack of permanent hard body parts. Ecdysis prevents long-term retention of externally applied tags by most crustaceans other than king crabs. Consequently, most studies of the age of crustaceans have relied on length-frequency analysis (Mauchline, 1977). Studies on red king crab at Unalaska, AK (Weber, 1967), and Kodiak, AK (McCaughran and Powell, 1977) indicate the size of 5-year-old male crabs to be in the range of 86-105 mm CL (Table 1). Careful re-examination of Weber's (1967) data supports his conclusions regarding age and growth for crabs up to about 60 mm at that location. However, he expected that growth of king crabs in Bristol Bay would be similar to Unalaska crabs, despite an acknowledged temperature difference

Table 1. Age-length relationships proposed for red king crab by various authors. M=male, F=female. Same is same as value to left. Values are carapace length (mm), except those of Vinogradov, but at small sizes length and width are similar. nd= no data.

Age	Weber (1967) Unalaska		McCaughran & Powell (1977) Kodiak		Kawasaki (1959) Bering Sea	Vinogradov (1968) Kamchatka
	M	F	M	F	All	All ¹
1	<23.0	same	same	same	4.0	8.0
2	23.1- 47.5	same	23.1- 45.6	23.1-45.4	9.0	14.0
3	47.6- 69.0	same	45.7- 68.4	45.5-67.4	17.0	22.0
4	69.1- 86.0	69.1- 84.0	68.5- 87.2	67.5-84.2	nd	30.0
5	86.1-101.5	84.1- 94.0	87.3-104.6	84.3-97.3	nd	44.0
6	>101.5	>94.1	>104.7	>97.4	nd	58.0

of about 3 °C. In contrast, Kawasaki (1959) showed four years of king crab length frequency data from Bristol Bay which indicate much slower growth than was postulated for Kodiak and Unalaska crabs, with mean sizes of about 4, 9, and 17 mm CL at ages 1, 2 and 3. Studies by Vinogradov (1968) in the eastern Sea of Okhotsk indicate growth rates between those apparent from Kawasaki's data and those reported by other authors. Evidently, growth rate of red king crabs is not a constant, but seems to vary spatially, and perhaps temporally as well.

Crustacean growth can be shown to be a function of temperature. Kurata (1960, 1961) established a linear relationship between instar number and the logarithm of cumulative degree-days (dC) for larval and early postlarval red king crab, and estimated the entire period of larval development from hatching to first instar postlarva to require 460 dC. Nakanishi (1987) demonstrated a linear relationship between log CL and instar number, thus implying a linear relationship between log CL and log dC. The phenomenon of temperature-dependent growth can probably be generalized to most crustacea (Hartnoll, 1982). Increasing temperature usually causes a decrease in the intermolt period, with little effect on the molt increment (Ibid). Thus, because of inter-annual variation in temperature, crabs do not meet the requirement of a constant growth rate.

This study was conducted to examine the relationship between growth of red king crab and water temperature in Bristol Bay, with the goal of estimating more precisely the age of crabs captured in the NMFS surveys of the EBS, and predicting their age at recruitment to the mature adult population.

¹ Carapace width instead of carapace length.

MATERIALS AND METHODS

This investigation consisted of four phases: 1) the examination of previously collected growth data for juvenile red king crab from Unalaska, AK (Weber, 1967), and the establishment of a temperature-based growth equation for those data; 2) the creation of a chronological temperature matrix for inner Bristol Bay, AK, and simulated growth of crabs at gridpoints of the temperature matrix via a computer model employing the above equation; 3) analysis of data from the NMFS EBS crab-groundfish survey for the appearance of large catches of small red king crabs in Bristol Bay, and 4) comparison of estimated mean sizes at matrix gridpoints to modes observed at those locations by the NMFS crab survey, in order to back-calculate the probable year of hatching and estimate the age of captured crabs.

Derivation of temperature-growth equation

Weber (1967) conducted a study of juvenile king crab growth at Unalaska, AK in the period 1958-1959. Mean carapace lengths of modes depicted in that paper (primarily from his figures 20 and 21) were estimated by eye, and corresponding dates were noted. Only clearly distinct modes with mean lengths up to 60 mm were used. A date of July 1 was assigned by Weber for the mean time of metamorphosis from glaucothoe to first benthic instar, and the age in days of each mode was determined from that date. Since his sampling periods covered 1-2 weeks, and since mean water temperatures were available only on a monthly basis, the first day of the month nearest to the sampling date was used.

Monthly mean water temperatures of Unalaska harbor for the period 1955-1985 were obtained from the NOAA National Ocean Survey, but due to intermittent data collection, were missing 19 months (not all consecutive) in the period 1957 to 1960, i.e. the time period during which Weber's observations were made. The missing water temperature data were estimated by establishment of a multiple regression equation relating monthly mean Unalaska water temperature to monthly mean air temperature at Cold Bay, AK, for the period January 1956 to December 1962. The two predictor variables were mean air temperature during the month of interest, and mean air temperature for the previous month i.e., lagged 0 and 1 months.

Degree-days (dC) for each month in this period were calculated by multiplying the number of days in the month by the mean monthly Unalaska water temperature. Estimated water temperatures were used only for the 19 months in which an observed temperature was not available. Total degree-days were accumulated from presumed settling dates of 1 July 1957 or 1958 to the dates each length-frequency mode was observed by Weber (1967). An additional 460 dC were added to account for the estimated requirement of larval development, according to Kurata (1960), and a mean length of 1.75 mm was assigned to the first instar, which

was not observed by Weber². A temperature-based growth equation was calculated by regression of the natural log (ln) of mean length against the natural log of cumulative degree-days for each mode observed.

Creation of the Growth Model

Bering Sea water temperature data were obtained from Ingraham (1983). These data were collected at various random and selected stations by research vessels and ships of opportunity during the period 1953 to 1982. To standardize them for use in numerical modeling, Ingraham created a 24 by 24 gridpoint matrix covering the eastern Bering Sea, and integrated all temperature records to the nearest gridpoint, weighted by the inverse square of their distance from that point. Long-term (30 years) mean surface and bottom water temperatures were presented for each month; deviations from those means for each month of the 30 year period were given at each gridpoint where data were available. A 7:6 sub-matrix³ of these gridpoints which lay within Bristol Bay was utilized for the present study, containing 28 ocean locations (the remaining points occurring over land; Fig. 2).

Due to the infrequency of observations, data were incomplete or unavailable for many of the months in that period, the majority of observations occurring from May to October. Therefore, multiple regression equations were established relating the mean monthly surface and bottom water temperature of the 21 easternmost gridpoints of the submatrix to mean monthly Cold Bay air temperature lagged 0 and 1 months, as was done for Unalaska water temperatures. The selection of only 21 instead of all 28 points occurred because Ingraham had previously defined those 21 points as a geographic subregion of interest and calculated the means in each month. Only those months were used in which data was available for at least 16 of the 21 gridpoints. Months which fit that criterion included 45 with surface temperature observations, and 33 with bottom temperatures.

My temperature model for Bristol Bay consisted of two 3-dimensional matrices (MMSTEMP and MMBTEMP, each 12:7:6) containing the 12 long-term monthly mean surface or bottom temperatures, respectively, for each of the 28 gridpoints of Ingraham's model which occur in Bristol Bay. A vector of 360 mean monthly air

² Mean carapace length of first instar provided by T. Shirley, College of Fisheries and Science, University of Alaska, Juneau, AK, 99801, pers. commun., March 1988.

³ Dimensions of matrices and vectors are given as Z:Y:X or Y:X, respectively, corresponding to the number of elements in each of the Z, Y, or X dimensions. Similarly, gridpoints of the geographic temperature matrix were given 2-digit labels corresponding to their row and column (Y and X) coordinates in the matrix; gridpoint 11 is at the upper left corner (Fig. 2).

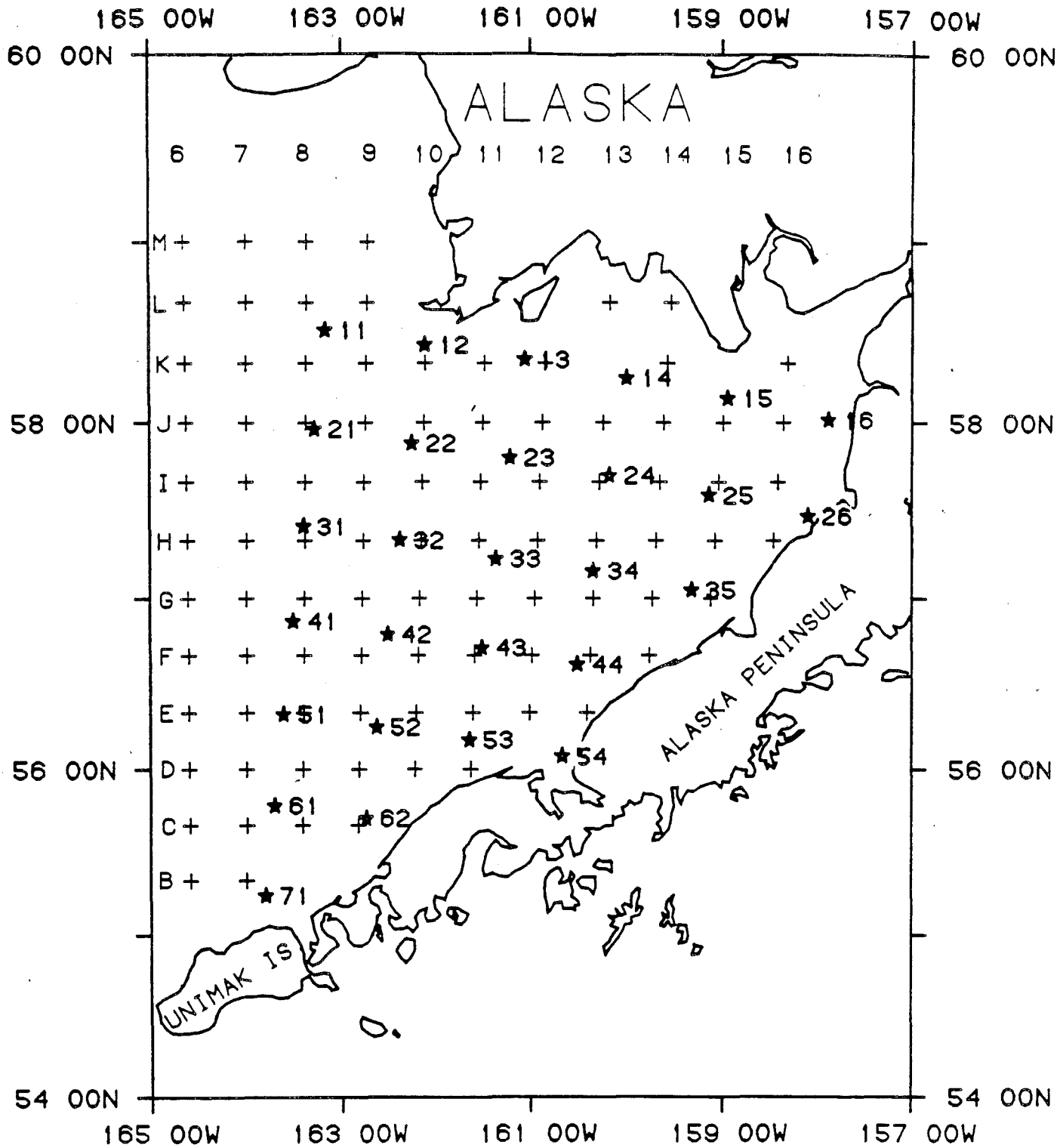


Fig. 2. Chart of Bristol Bay, Alaska, showing the NMFS survey station pattern (crosses), and the temperature matrix gridpoints (stars) within that region. Both grid patterns extend west and north beyond the Bristol Bay region. See text for explanation of grid labels.

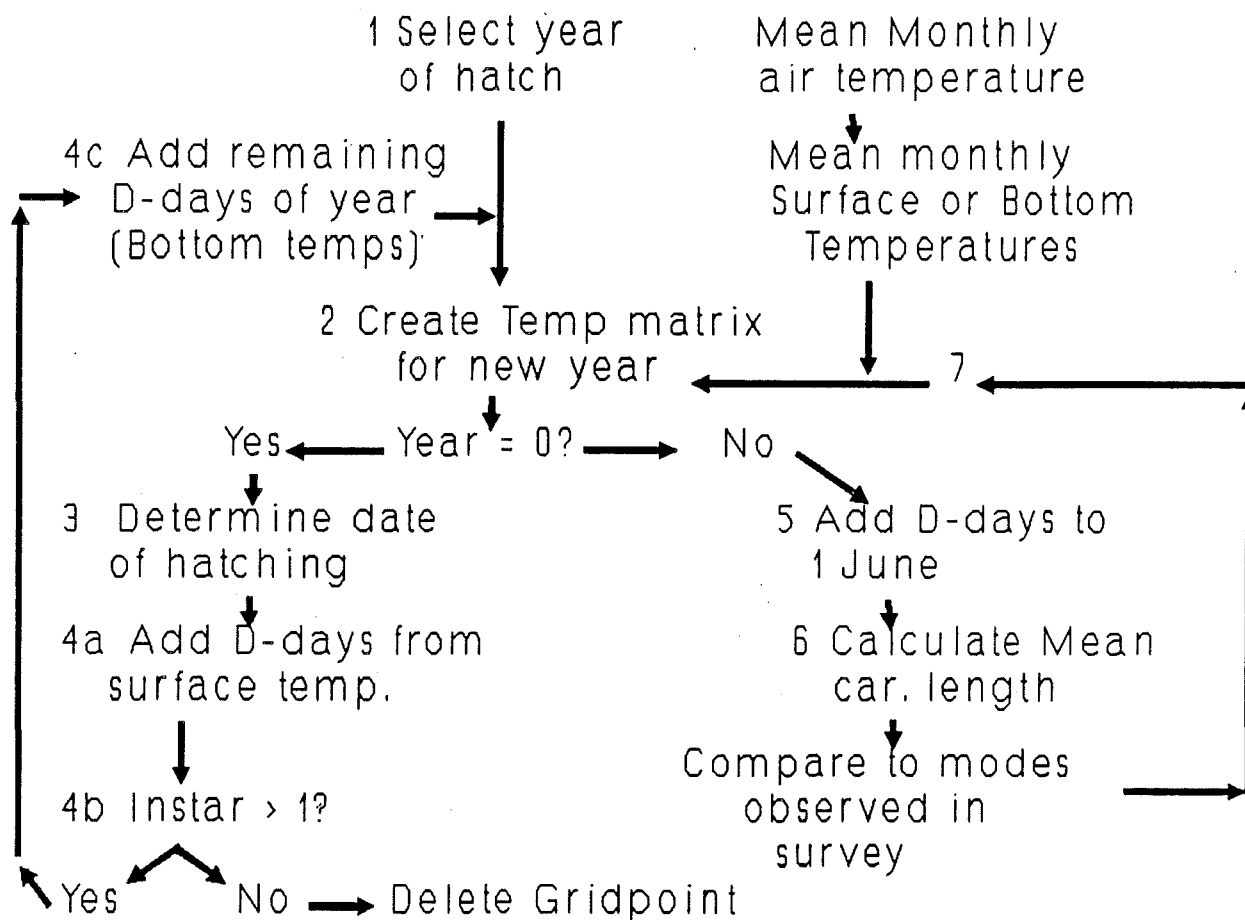


Fig. 3. Flowchart of GROW model. Program was written in APL to facilitate handling of multidimensional matrices. Input data (Cold Bay air temperatures) were converted to seawater temperatures via regression equations based on long-term data series.

temperatures at Cold Bay (CBAIR) representing the years 1955-1987, was used to generate a single mean temperature anomaly for surface or bottom water in each month (STANOM and BTANOM) via the multiple regression equations. Due to the sparsity of observed water temperature data, only calculated anomalies were used.

The growth model (GROW) was written in APL, and operated in the following manner (Fig. 3): 1) A hatching year (1967-1983), was selected and designated as year 0. 2) STANOM and BTANOM (each vectors of dimension 1:12) were calculated for each year, and added to MMSTEMP or MMBTEMP to create two 12:7:6 matrices of the estimated monthly surface or bottom temperatures (EMST and EMBT)

for the year selected (year 0). Kurata (1961) concluded that red king crabs had a biological zero temperature at which no further growth occurred, and estimated this to be approximately 0° C. To account for this, all estimated water temperatures below 0° C were converted to 0, such that accumulated degree-days actually represent growing-degree-days, i.e., growth presumably stopped at 0 degrees, and was not allowed to reverse at lower temperatures.

3) A normal hatch date of 1 May was employed. However, NMFS unpublished data on red king crab embryo conditions (eyed vs uneyed) in Bristol Bay suggest that hatching occurs later in cold years. For this reason, an earlier hatching date of 1 April was selected in warm years (STANOM for June >1.0° C), and a later hatching date of 1 June was selected in cold years (STANOM for June < -1.0° C).

4a) At each gridpoint, degree-days were accumulated from the hatching date, on a monthly basis, using the surface temperature matrix (EMST) until accumulating 460 dC, at which time crabs were assumed to change from a planktonic existence to a benthic one.

4b) Those gridpoints which had not accumulated the minimum number of degree days (460) required for metamorphosis from glaucothoe to first instar crab (C1) by October 1 were dropped from the matrix.

4c) Degree-days for the remaining months of the year were then added to the total from the bottom temperature matrix (EMBT), which was used for all further growth.

5) A new temperature matrix for the year following hatching (year 1) was then created as above, and degree-days were further accumulated from the bottom temperature matrix (EMBT) until 1 June, approximately the date at which the annual NMFS survey usually began.

6) The accumulated degree-days were plugged into the temperature-based growth equation, and mean carapace length was calculated for all gridpoints remaining in the sub-matrix.

7) The remaining degree-days in the year were added to the total, a new matrix was calculated for year 2, and degree-days accumulated to 1 June, at which point they were again plugged into the growth equation, and mean carapace lengths calculated and displayed. Growth up to 60 mm CL was assumed to follow the regression on cumulative dC. Beyond this size, crabs tend to molt annually, and growth stabilizes at approximately 15 mm per molt (Weber, 1967; Weber and Miyahara, 1962), and this increment is also predicted by the growth equation at a size of 60 mm as well. For these reasons, further growth in the model was accomplished simply by adding 15 mm per year. This step was repeated through year 10.

8) A new hatching year was selected and the entire process repeated.

Analysis of King Crab recruitment in Bristol Bay

The NMFS has conducted a trawl survey of commercially exploited crab and groundfish resources in the EBS annually since the late 1960's. Organisms were collected with a 400-mesh eastern otter trawl, until 1981 when an 83-112 eastern trawl became the standard gear. Tows were made for one half hour at predesignated stations at intervals of 20 n.mi (Fig. 2). All crabs were removed from the catch, sorted by species and sex, and weighed in aggregate. King crabs were measured to the nearest 1.0 mm with a

steel vernier caliper from the rear of the right eyesocket to the center of the rear margin of the carapace (carapace length, CL).

Population abundance was calculated by the area-swept method (Alverson and Pereyra, 1969). The cumulative square root of frequencies (CSRF) technique (Cochran, 1963) was used to separate the stations into high and low density strata based on the abundance of male crabs <110 mm CL in each year. Total abundance was calculated by 5 mm length categories for each sex separately, using a stratified systematic technique (Ibid). Male and female king crabs mature at lengths of 103 and 102 mm CL respectively, Somerton, 1980. For this reason, and for consistency with Reeves and Marasco (1980), the abundance of male crabs in the size interval 95-109 mm CL was used as an index of recruitment to the adult population. This index will subsequently be referred to as the Reeves-Marasco index of recruitment, or RMI. Another reason for selecting this particular size group is that king crab appear to be less than fully recruited to the survey sampling gear at smaller sizes. Evidence for this is that abundance estimates typically increase with size up to this interval, then decline at larger sizes.

Original data from surveys prior to 1972 are not currently available for analysis. Therefore, only data collected from 1972 to 1987 were examined for the presence of small crabs. In each year, individual stations were again stratified by the CSRF method and stations were selected for examination if they fell into the high density stratum for crabs of 0-50 mm CL ('small'), or 51-75 mm CL ('medium'). This division of sizes was necessary because larger crabs were almost always more abundant and tended to mask smaller ones. Data from each station thus selected was analyzed with a mode separation technique (program NORMSEP; adapted from MacDonald and Pitcher, 1979) to determine the mean carapace length, standard deviation, and number of crabs in the primary mode, and were plotted for visual verification. The selection of survey station/modes for analysis was a conservative process. By stratifying for high density in each year, years of lower abundance were not masked by years of higher abundance, although in years of high abundance, station/modes which would have been considered high density in low abundance years were classified as low density. For this reason, additional station/modes were added to those selected in high abundance years if the difference between the density of the highest low density stations and the lowest high density station was no greater than the density between the two lowest high density stations. For practical purposes this amounted to adding 1 to 3 stations in each of 6 years.

Comparison of Observed and Estimated Carapace Lengths

Crab growth was simulated at the 28 temperature matrix gridpoints under several assumptions. The first of these was that the crabs were essentially non-migratory up to 60 mm CL. Both larval development and settling occurred at a given sampling

Table 2. Cross-reference list for comparison of temperature model gridpoints used to determine growth and stations where small crab were encountered by NMFS survey tows. Only stations classified as high density by CSRF stratification are shown. Stations located more-or-less equidistant from 2 or more gridpoints were referenced to mean estimated lengths for the gridpoints shown.

Survey Station	Gridpoint ⁴
B09,C09	62
B07,B08	71
D09	Mean of 52, 62
D10	Mean of 53, 62
D11,E11	53
E10	52
E11	53
E12	Mean of 44, 53
E13	Mean of 44, 54
F12	Mean of 43, 44
F13	44
G12	Mean of 34, 43
G13,H13	34
G15	35
H11	33
H14	Mean of 24, 25, 34, 35
I11	23
I12	Mean of 23, 24
I13	24
I14	Mean of 24, 25
I15	25
J15,J16,K17	16

station, actually a 400 n.mi.² square. After settlement, the mode at each station was considered to remain in place until a size of about 60 mm CL, and was subject to the bottom temperature field at that station only. Since growth apparently stabilizes at that size, movement from that location, and subsequent temperature changes, were assumed to have no further effect upon growth rates. Carapace lengths estimated by model GROW were considered to represent the mean length of crabs grown at each of the 28 gridpoints. Since the NMFS survey includes 92 stations in this region, each gridpoint represented growth at 3 or 4 adjacent trawl stations. A standard cross-reference table (Table 2) was used to select those gridpoints which represented each station.

Determining the probable age of observed strong recruitment modes was an iterative process. The mean carapace length of each observed mode was compared to the mean length estimated by the GROW model for the year observed, comparing different possible hatching years until the best match was obtained. Each mode was then further 'grown' either according to the regression on dC, or by adding 15 mm per year to modes with mean lengths >60 mm CL. 'Growth' of each mode occurred until the mean size 'recruited' into

⁴ Gridpoint labels are given as (rc), where r indicates row, and c indicates column. Gridpoint 11 is in upper left hand corner of Fig 2.

the mature size interval (95-109 mm CL), and the age at which it did so was determined. The year of recruitment was designated year R.

The relationship between carapace length and its standard deviation was determined from the modal statistics analysis, and each mode (defined as a group of crabs with a distinctly quasi-normal distribution, observed at a given station and date) was assigned an appropriate variance at the size and time of 'recruitment'. Starting in year R-1, and continuing through year R+1, a period of three years, the proportion of each mode recruiting in any given year was determined by calculating the position of the predicted mean length relative to the recruitment size interval (95-109 mm CL), translating the difference into units of standard deviation, and determining the proportion of a normal curve having the predicted mean and standard deviation lying within the interval. This value was then multiplied by the estimated number of crabs in each mode to determine the number recruiting in each year. All crabs recruiting in a given year from different modes were summed up and plotted, to give a crude index of potential recruitment as predicted from early juvenile mode abundance. Initially, no effort was made to incorporate mortality. However, since smaller crabs required several years longer than larger ones to recruit, several different scenarios incorporating mortality were prepared.

RESULTS

Temperature-Growth Relationship

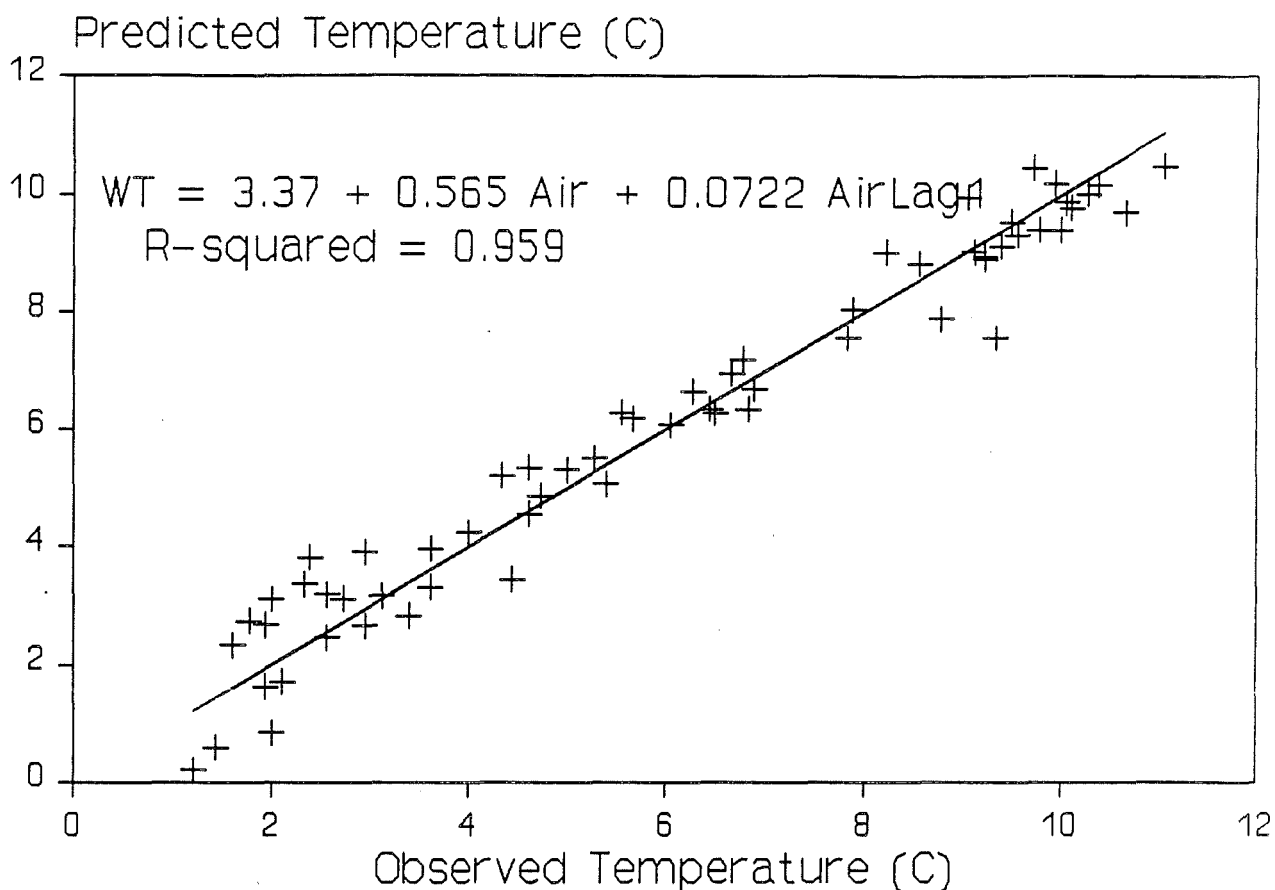
The regression of Unalaska water temperatures on Cold Bay air temperatures (lagged 0 and 1 months) included 64 data points and gave an R^2 value of 0.959 (Fig. 4). Significant results were also obtained for the regressions on Cold Bay air temperatures (also lagged 0 and 1 months) of mean monthly Bristol Bay surface temperatures ($n=45$, $R^2=0.904$, Fig. 5a) and bottom temperatures ($n=33$, $R^2=0.855$, Fig. 5b). Regression equations are given below:

$$(1) \quad UST_i = 3.37 + 0.565(CBA_i) + 0.0722(CBA_{i-1}) \quad (R^2=0.959, n=64)$$

$$(2) \quad BBST_i = 0.0687 + 0.246(CBA_i) + 0.6541(CBA_{i-1}) \quad (R^2=0.904, n=45)$$

$$(3) \quad BBST_i = 0.6144 - 0.0114(CBA_i) + 0.6266(CBA_{i-1}) \quad (R^2=0.855, n=33)$$

where UST_i = mean Unalaska Surface Temperature, °C, month i.
 $BBST_i$ = mean Bristol Bay Surface Temp, °C, month i.
 $BBBT_i$ = mean Bristol Bay Bottom Temp, °C, month i.
 CBA_i = mean Cold Bay Air temperature, °C, month i.
 CBA_{i-1} = mean Cold Bay Air temperature, °C, month i-1.



Line defines perfect correlation

Fig. 4. Predicted vs observed mean monthly water temperature at Unalaska Harbor, Unalaska Island, AK, 1956-1962. Seawater temperatures provided by NOAA National Ocean Survey were regressed against air temperature at Cold Bay, AK, lagged 0 and 1 months. The diagonal line defines perfect correlation. Vertical distances between line and points are essentially residuals.

Long term records of temperature show that both air and sea surface temperatures were above average in the late 1960's, dropped well below average from 1971 through 1976, and have been above average ever since (Fig. 6).

Including the estimated size, date of appearance, and required degree-days of first instar crab as an index variable, a total of 11 modes of carapace length were available for analysis from Weber (1967). Only mean sizes up to 61 mm were included in the regression. Regression of \ln length (mm CL) on the natural log (\ln) of cumulative degree days was significant (Fig. 7; Eqn. 4).

$$(4) \quad \ln(\text{CL}) = -8.58 + 1.44[\ln(\text{dC})] \quad (R^2=0.97, n=11)$$

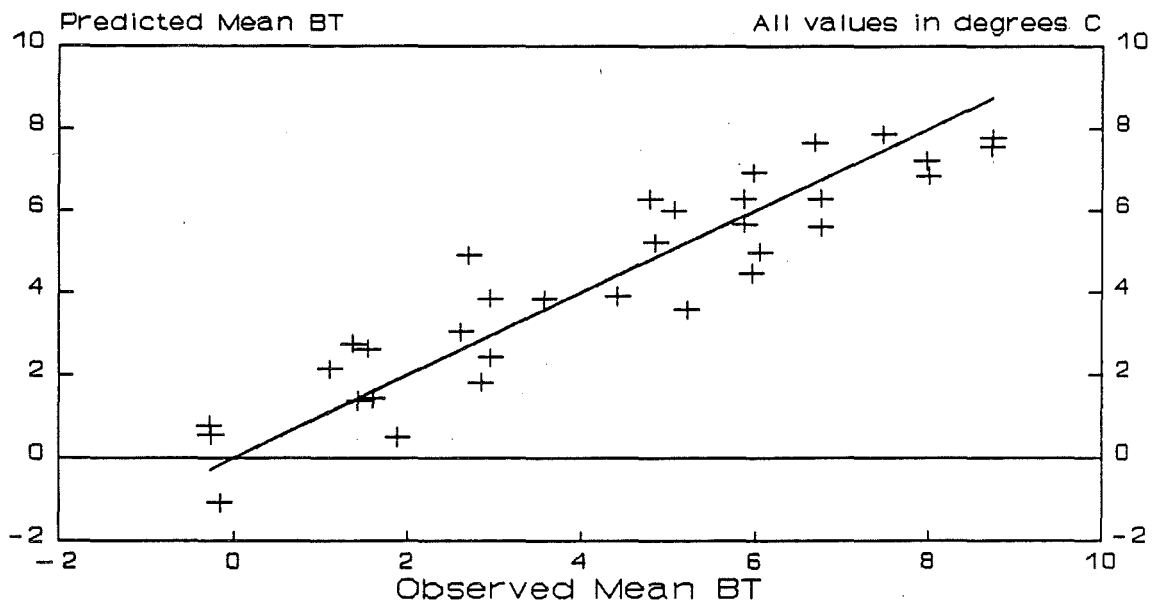
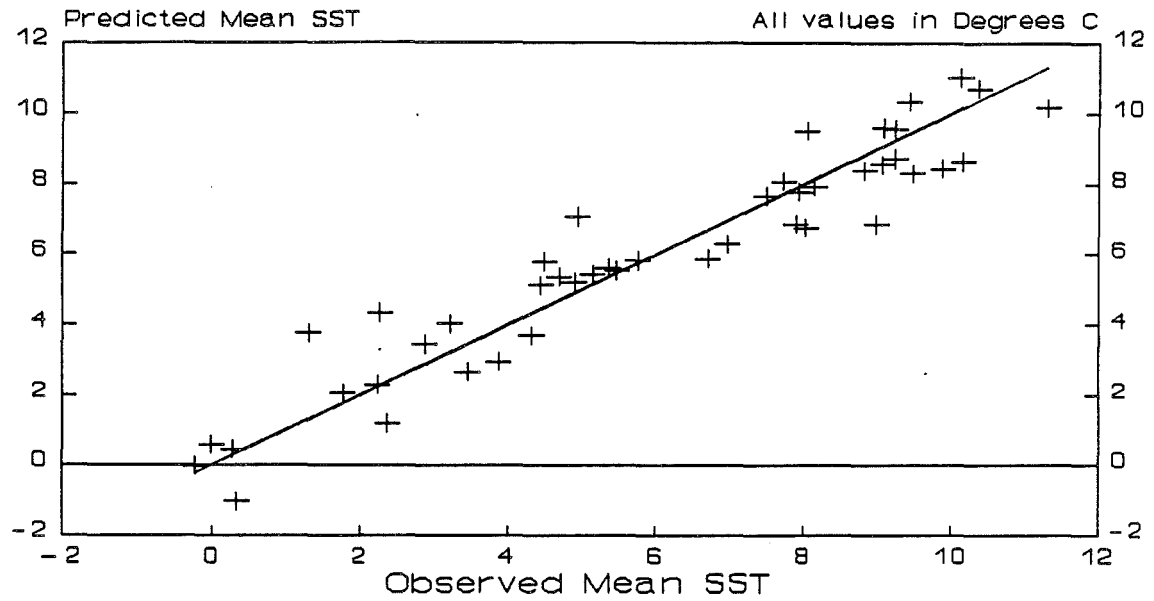


Fig. 5. Predicted vs observed mean monthly sea temperature for 21 of the 28 Bristol Bay gridpoints (columns 2-5). Figure covers the period 1953-1982, but includes only the months for which sufficient data were available, primarily June-October. Data were regressed against Cold Bay air temperatures as described in text. See Table 2 for regression parameters. A(Top): Sea surface temperatures. B(Bottom): Bottom temperatures.

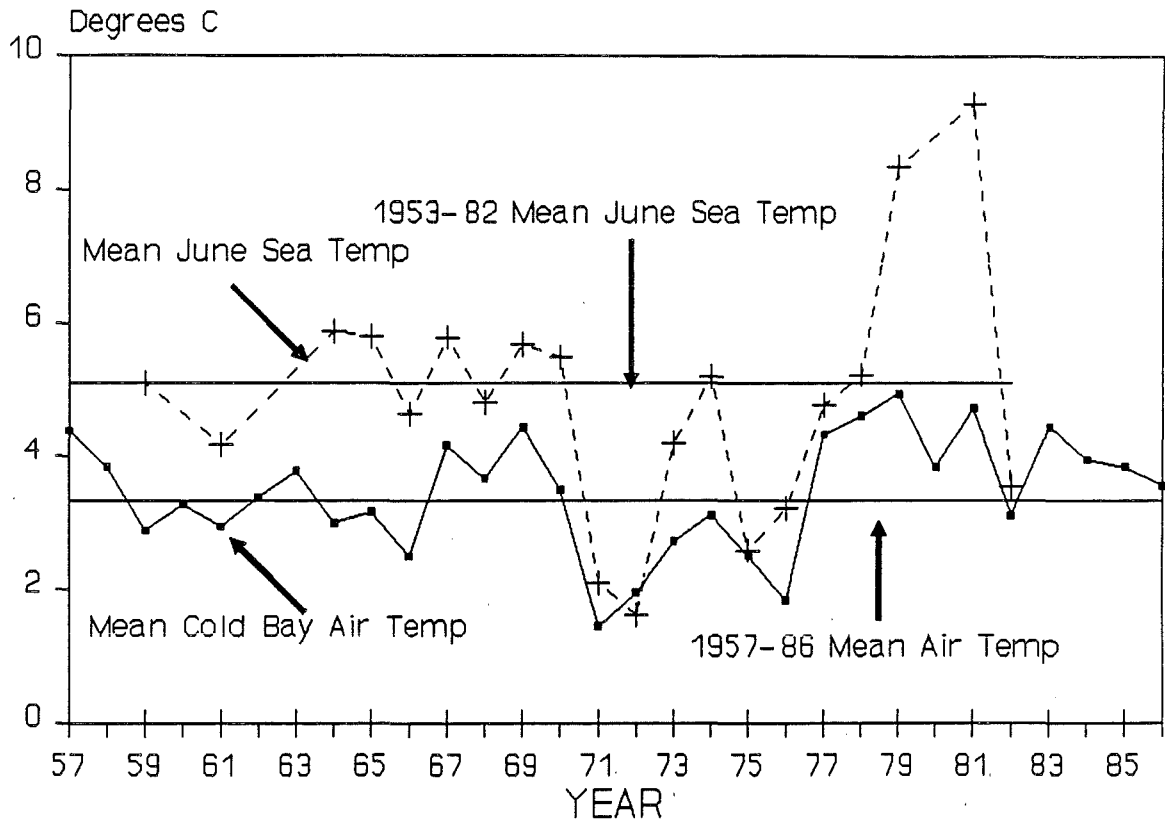


Fig. 6. Annual and long term (1957-1986) mean air temperature (°C) at Cold Bay, AK, and mean sea surface temperature of Bristol Bay in June (annual and long term). Sea surface temperatures are means for the 21 eastern-most gridpoints in Fig. 2 (columns 2-5).

Appearance of modes in the NMFS survey data

A total of 82 stations with high densities of crabs were identified from 13 years of data (Tables 3 and 4). Fig. 8 shows four examples covering a range from the least to the most abundant mode selected by stratification. Because each year was examined independently, some modes were much smaller than others, and could not be adequately defined. Those containing fewer than 25 crabs were considered negligible, and are identified in Table 3 as ndm (no definitive mode). Sixty one of these 82 stations had modes which were statistically discernible. Differences between observed mean carapace lengths (as determined by NORMSEP) and mean carapace lengths estimated by the GROW model were usually less than 10% (Fig. 9). There appeared to be a slight negative bias in the model, i.e. estimated mean lengths were generally slightly smaller than observed lengths. The best fit between mean lengths

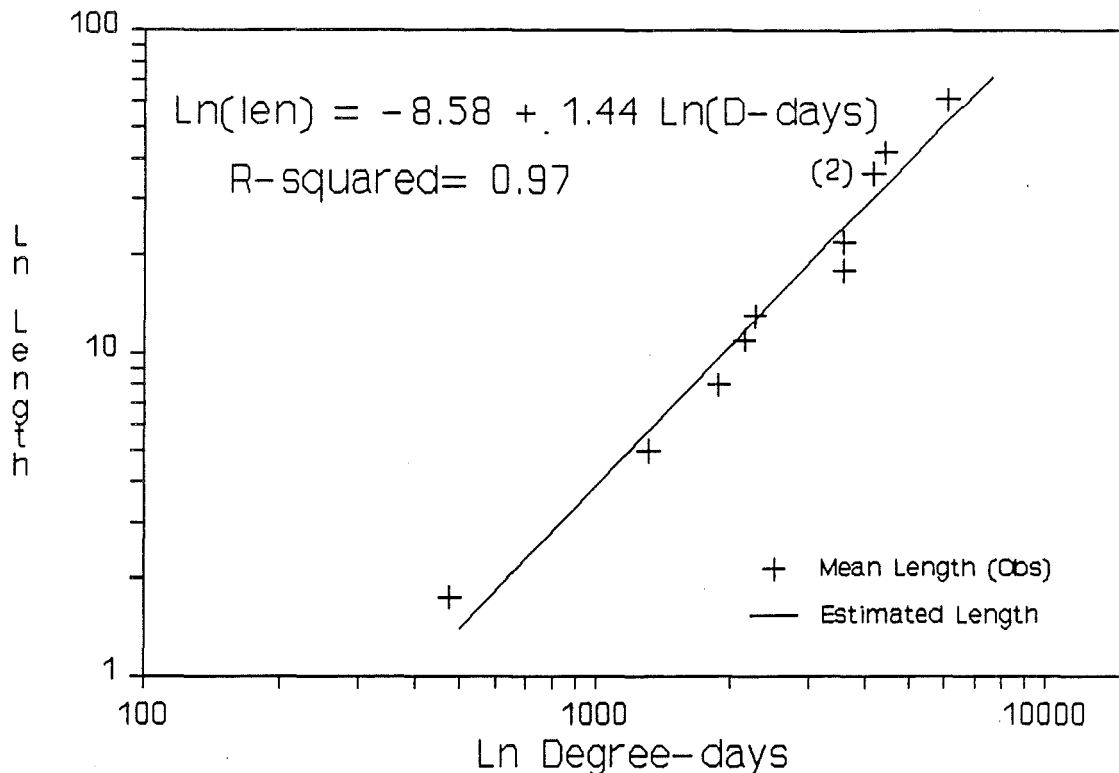


Fig. 7. Regression of log of mean carapace length (CL) on log of cumulative degree-days (dC) for 10 modes of crab length frequency observed by Weber (1967), and estimated length of first instar.

estimated from the survey data and their standard deviations (sd) was obtained by a simple least squares regression (Fig. 10):

$$(5) \quad sd = 0.04 + 0.075(CL) \quad (n=37, R^2 = 0.38, p < 0.05)$$

as opposed to regressions in which one or both variables were log-transformed. The estimated sd of a mode with mean length equal to 100 mm CL is 7.54 mm. Thus, one would expect 95% of the crabs in a mode at this size to lie between 85 and 115 mm (i.e., ± 2 sd's), a range of 30 mm.

Certain stations occur repeatedly as locations of high abundance of small crabs. These locations occur in disjunct geographic subgroups of adjacent stations: B07-08/C09 (7 years); D10-11/E11-12/F12 (8 years); G15 (3 years); and J15-16 (6 years). These four subgroups have several characteristics in common: they are within 30 nmi of shore, all except for the first group are less than 25 fm in depth, and all are within 30 miles of a major

Table 3. Mean size, standard deviation, and number of red king crabs in observed modes, and predicted yearclass (YC), age, and mean size of crabs from GROW model. Each mode is identified by the year of observation and the station where captured. Modes designated as ndm (no definable mode) were too small to be estimated precisely, so were ignored.

Year	Station	Predicted			Observed		No.
		YC	Age	Mean CL	Mean CL	St.dev.	
1972	C08				ndm		
1973	C09				ndm		
	D10				ndm		
	I13				ndm		
	I14				ndm		
	I15	1968	5	44.3	47.0	2.43	75.8
	"	1966	7	73.0	71.1	6.45	143.0
1974	B08	1969	5	66.5	68.2	4.16	28.9
	"	1969	5	66.5	75.7	2.37	36.2
	C09	1969	5	65.3	59.8	3.31	42.7
	G13	1967	7	68.0	76.2	4.53	70.6
	"	1966	8	83.1	87.7	3.59	20.3
	I14	1968	6	55.8	60.4	4.20	174.4
	J16	1969	5	58.4	52.7	4.09	135.6
1975	B07	1970	5	61.9	60.3	3.86	302.0
	"	1970	5	61.9	70.3	4.44	724.8
	D11	1969	6	67.6	70.5	5.62	1062.4
	E12	1968	7	78.8	73.4	5.08	574.3
	"	1968	7	78.8	83.7	5.72	166.7
	J16	1970	5	56.3	56.9	4.12	430.0
1976	G13	1968	8	82.4	78.5	6.80	146.3
	"	1967	9	98.0	93.8	7.49	101.7
	H11	1967	9	86.0	84.3	7.53	1258.0
1977	B07	1970	7	91.9	84.8	8.11	887.0
	C09			ndm			
	D10			ndm			
	D11	1971	6	57.2	52.9	1.76	207.9
	"	1971	6	57.2	60.7	7.71	339.1
	E11			ndm			
	F12			ndm			
1978	B08	1973	5	68.0	72.3	4.97	177.0
	E12	1973	5	47.8	53.2	4.62	117.5
	F09	1967	11	79.7	80.6	6.23	266.2
	G15	1973	5	44.4	45.2	3.40	674.0
1979	B09	1975	4	54.6	56.8	3.95	1260.0
	D10	1974	5	63.0	62.9	6.11	453.0
	E13	1975	4	50.6	56.2	4.33	103.0
	G15	1976	3	26.7	30.2	2.53	83.0
	H11	1971	8	67.7	72.2	4.62	50.0
	J16	1975	4	47.5	57.9	4.94	208.0
	K17	1975	4	47.5	42.8	5.05	154.6
1980	E11			ndm			
	G13	1972	8	82.6	82.0	6.64	318.7
	G15	1977	3	30.5	33.7	3.59	680.0
	I12	1974	6	70.6	70.9	4.00	42.0
	I13	1974	6	70.8	71.1	4.44	37.0
	J16	1976	4	49.7	50.3	3.26	156.0
1981	G12	1975	6	58.6	66.8	5.10	116.0
	G13	1975	6	61.7	61.7	6.57	111.0
	G14			ndm			
	H13			ndm			
	I11	1975	6	71.2	64.4	3.87	1164.1

Table 3 (Continued)

I12	1975	6	70.6	65.9	4.72	79.2
"	1974	7	85.6	81.9	4.36	52.8
I13			ndm			
I14			ndm			
1982 E11	1977	5	70.8	70.4	5.50	1046.4
"	1976	6	82.3	86.4	10.80	1133.6
F13	1977	5	63.8	70.5	6.04	694.1
H11	1975	7	71.5	70.5	5.96	984.0
"	1974	8	84.6	89.7	6.40	246.0
J15			ndm			
1983 E12	1979	4	41.8	44.1	2.69	49.7
"	1979	4	41.8	51.7	3.19	92.3
F12	1976	7	81.1	78.9	6.41	332.5
"	1975	8	94.2	93.4	5.08	161.5
H14	1978	5	53.9	60.4	5.18	97.0
I11	1977	6	72.7	73.3	7.59	123.8
J16	1979	4	46.9	53.6	4.44	100.0
1984 F12	1978	6	66.7	73.2	5.37	808.4
"	1976	8	96.1	96.1	8.63	1412.6
G13	1977	7	83.4	75.2	6.77	212.5
H13	1977	7	83.4	80.0	5.77	7547.0
1985 D09	1979	6	73.1	77.3	4.43	77.4
F12			ndm			
I12			ndm			
1986 D10			ndm			
I11	1979	6	84.7	78.3	6.70	168.0
1987 G12	1980	7	75.6	80.7	5.07	420.0
H15			ndm			
I13			ndm			
E10	1979	6	86.5	89.3	8.49	141.0

estuary. A fifth subgroup, including stations I11-15 and H11-14, appears in a total of 8 years, but usually at larger sizes (50-80 mm CL). This group is also in shallow water, but is not close to shore or a major estuary.

At least 4 modes appear to be trackable over 2 consecutive years. Three of these remained in place for two years (yearclass 1970, station B07; 1973/G15; and 1976/F12; Table 4). The fourth, which appeared to have hatched in 1968, appeared first at station I15 at age 5, then at station I14 at age 6, a distance of 20 nmi.

Recruitment of modes to the adult size interval

The predicted ages at recruitment to the 95-109 mm CL size interval (Table 4) are greater than the value of 5 or 6 suggested by previous authors (Weber, 1967; McCaughran and Powell, 1977; Incze et al, 1986; Table 1), and appear to vary from 7 to 10 years. Over the period of this study it appears to have steadily declined from a mean of 9.5 (for the 1966-68 year-classes) to a mean of about 7.6 years (1977-80).

The hatching year, age, length and year of recruitment to the 95-109 mm CL size interval were estimated for each selected mode (Table 4). The 'recruitment year' (year R) specified in table 4 indicates the year in which the mean size of crabs in each

Table 4. Estimated age at observed sizes (mm, CL) of red king crab, and predicted length, age and year in which each mode would recruit to the 95-109 mm CL interval. Observed data from the NMFS survey; predicted data from GROW model. Dashed lines indicate growth of an individual mode.

Est. Sta- YC tion	Observed Mean Length at age							Predicted Recruitment To 95-109 mm interval		
	3	4	5	6	7	8	9	CL	Age	Year
1966 I15					71			101	9	1975
G13						88		103	9	1975
1967 G13					76		94	109	10	1977
H11							84	99	10	1977
F09						(80 at 11)		95	12	1979
1968 E12					73			103	9	1977
E12					84			99	8	1976
G13						78		108	10	1978
I15/114			47---	60				105	9	1977
1969 B08			72					102	7	1976
C09			60					105	8	1977
D11				71				101	8	1977
J16			53					98	8	1977
1970 B07			60-----	85				100	8	1978
B07			70					100	7	1977
J16			57					102	8	1978
1971 D11				58				103	9	1980
H11							72	102	10	1981
1972 G13							82	97	9	1981
1973 B08			72					102	7	1980
E12			54					99	8	1981
G15			45---	64				109	9	1982
1974 D10			63					108	8	1982
I12				71				101	8	1982
I13				71				101	8	1982
H11							90	105	9	1983
1975 B09		57						102	7	1982
E13		56						101	7	1982
F12							93	108	9	1984
G12				67				97	8	1983
G13				62				107	9	1984
H11					70			100	9	1984
I11				64				109	9	1984
I12				66				96	8	1983
J16		58						103	7	1982
K17		43						102	7	1982
1976 G15	30							103	8	1984
J16		50						103	7	1983
E11				86				101	7	1983
F12					79---	96		96	8	1984
1977 E11			70					103	7	1984
F13			70					100	7	1984
G13					75			105	9	1986
G15	34							95	7	1984
I11				73				103	8	1985
H13					80			95	8	1985
1978 H14			60					105	8	1986
F12				73				103	8	1986
1979 D09				77				107	8	1987
E10				89				104	7	1986
E12		49						98	7	1986
I11				78				108	8	1986
J16		54						103	7	1986
1980 G12					81			96	8	1988

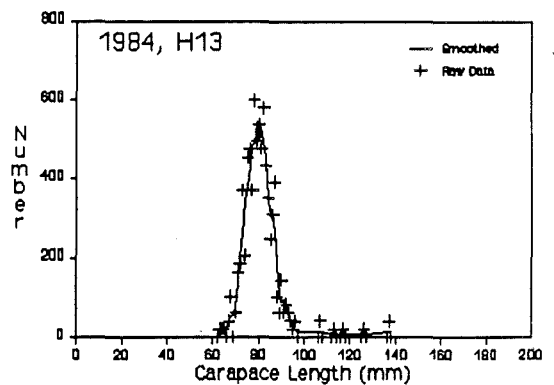
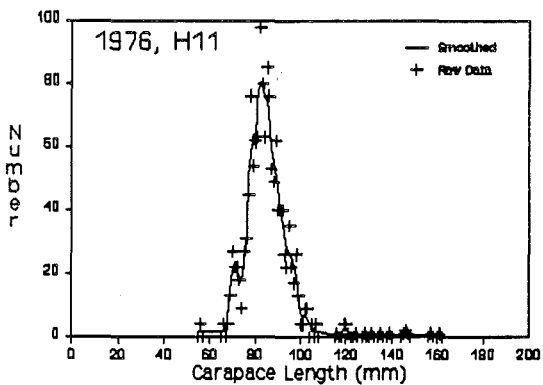
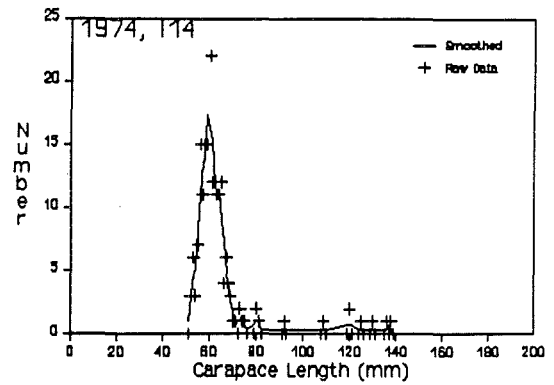
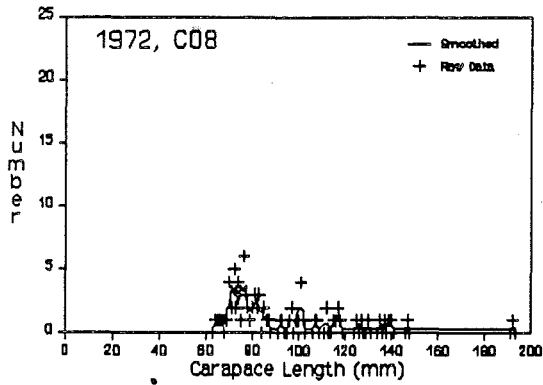


Fig. 8. Examples of red king crab length frequency modes observed at individual sampling stations of the NMFS eastern Bering Sea crab survey. Each is identified by the year observed and the station name. Mode 1972/C08 was the smallest identified by the stratification method, and was excluded from analysis. Mode 1984/H13 was the largest identified, containing over 7500 crabs. Crosses indicate actual frequencies at 1 mm intervals; solid line is a moving average of 3 intervals. Note different vertical scales.

mode was predicted to reach the interval of 95-109 mm CL, previously identified as the size at which both sexes are physiologically mature, and have largely completed recruitment to the trawl gear. However, the spread of each mode (at least 30 mm, as indicated above) is such that the entire mode cannot recruit in a single year. The leading edge of the mode (the right tail of a normal distribution) reaches this interval 1 or 2 years earlier than the mean (in year R-1 or R-2), and the trailing edge (the left tail) reaches it 1 or 2 years later (year R+1 or R+2). Because of the relatively small sd determined above, I only examined the range of years from R-1 to R+1. In each of these three years, modes were grouped together according to the estimated hatching and recruiting

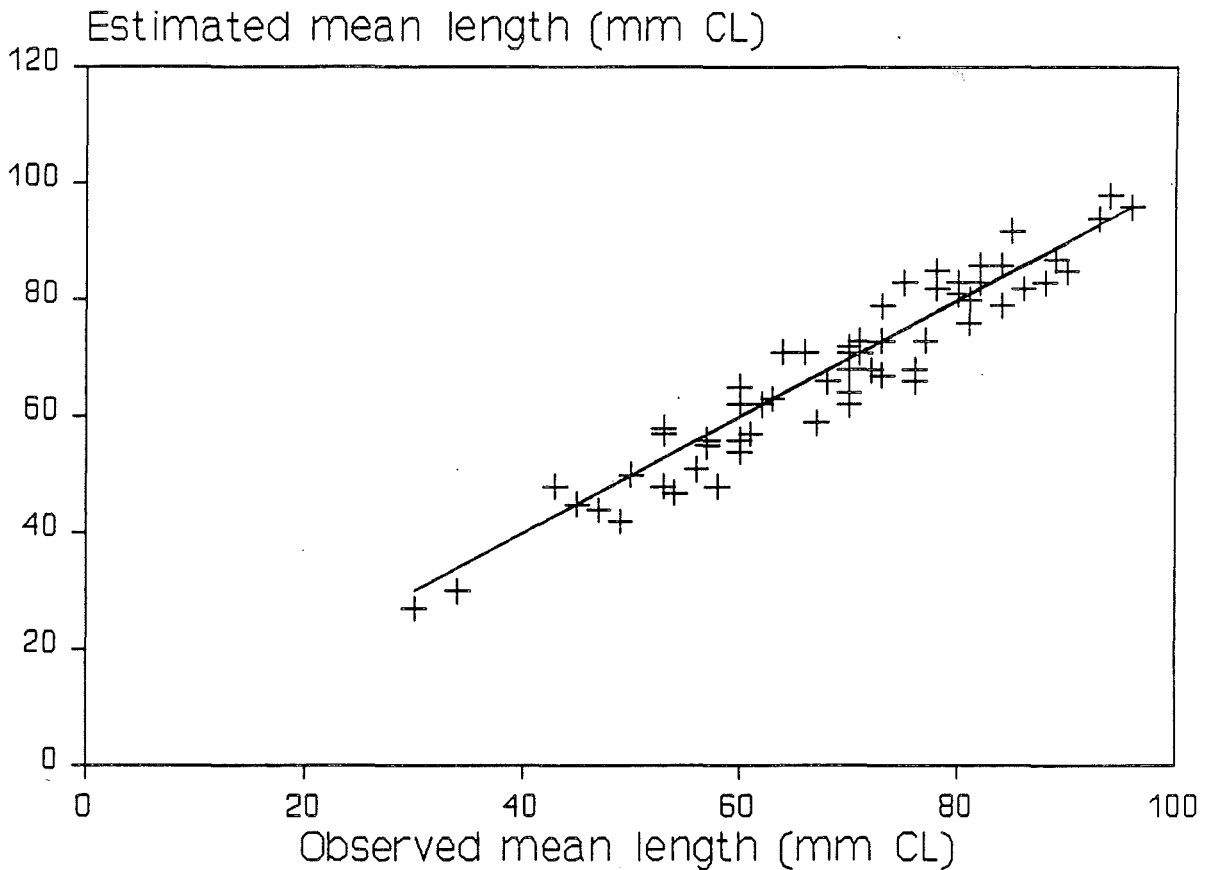


Fig. 9. Comparison of observed and estimated mean sizes of crab length-frequency modes for Bristol Bay red king crab. Observed data are from the NMFS survey (cf. Fig. 8), and estimated sizes are from the GROW model. Line indicates region of equality.

years, and the number of crabs recruiting in each year was summed (Table 5A). Averaging over all modes, 97.5% of the observed crabs 'recruited' over a 3-year period.

Table 5A shows that recruitment in any single year, e.g. 1976, may consist of crabs from up to 5 different year-classes (YC), 1966 through 1970, in this case. A corollary result is that crabs from a single YC, e.g. 1967, incorporating multiple locations, may recruit to the adult size over 4-5 years or more. In some years recruitment was essentially nonexistent or negligible. Vertical summation of crabs recruiting in each year provides a crude "modal recruitment index". Table 5B indicates the proportion of total recruits observed in each survey year examined which originated in each year-class. Table 5C shows the proportion of total recruits produced by a given year-class which recruit in each survey year.

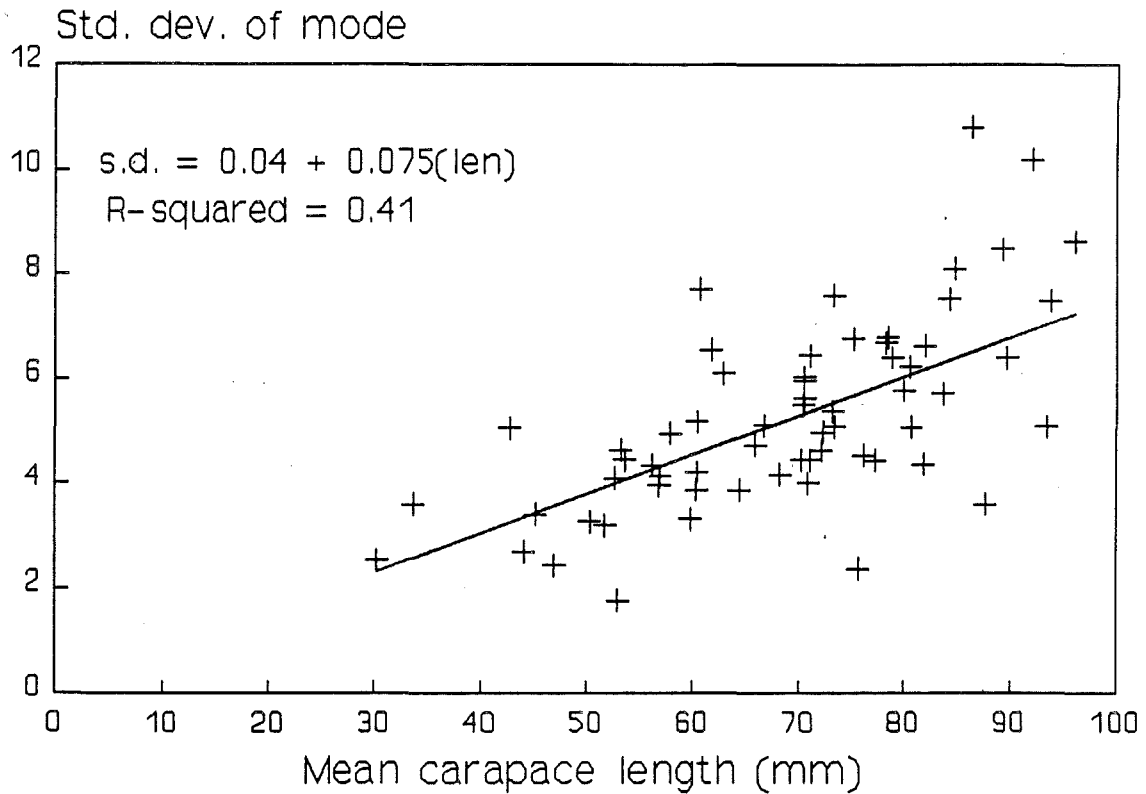


Fig. 10. Regression of standard deviation (s.d.) on mean size of red king crab length frequency modes observed by the NMFS survey. Data were used to estimate variance of modes after several years of additional projected growth.

An extremely large mode of crabs was observed at station H13 in 1984, consisting of over 7500 crabs with a mean size of 80 mm CL. These crabs contribute substantially to recruitment over the period 1984-1986. This mode was not observed in the previous or following years, suggesting that sampling (or subsampling) error may have occurred, crabs were highly aggregated, that mortality increased substantially in that time period, or some combination of factors. For this reason, several alternative scenarios were prepared in which the abundance of this mode was reduced from its estimated value of 7547, by the subsampling factor of 21 employed at that station, to a value of 365, i.e., the number of crabs actually counted and measured.

Five scenarios covering a range of mortality conditions were examined: 1) No mortality, or mortality balanced by increasing recruitment of larger crabs to the sampling gear (Tables 5A-5C). 2) No mortality, but with abundance of mode 1984/H13 (see Table 3)

Table 5A. Results of recruitment scenario 1, as described in text. Values are numbers of crab from each yearclass (YC) recruiting to the 95-109 mm CL interval in each survey year. Vertical sums are cumulative numbers of observed crabs from all year-classes surviving to recruitment in a given year and constitute a modal recruitment index. Horizontal sums are numbers of crabs from each YC which survive to recruitment, i.e., an index of YC success. No mortality applied in this scenario.

YC	Year of Observation (Survey)																YC Sum
	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	
1966	15	108	38														161
1967			83	830	396	128	123										1560
1968		7	229	599	206	12											1053
1969		7	147	828	308												1290
1970			44	575	1064	332											2015
1971						80	369	132	10								591
1972							6	181	123								310
1973						20	123	402	375	45							965
1974								180	354	210	33						777
1975								199	1157	1125	1457	371					4309
1976									118	884	1098	620					2720
1977										200	1543	4463	3659	28			9893
1978												141	598	160			899
1979												109	359	146	7		621
1980														5	220	180	405
	15	122	541	2832	1974	572	621	1094	2137	2464	4131	5704	4616	339	227	180	27569

Table 5B. Results of Scenario 1: Proportion of total recruits (95-109 mm CL) observed in each survey year (bottom row of Table 5A) originating from each yearclass (left column). No mortality applied. Values sum vertically to 100%.

YC	Year of Observation (Survey)															
	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
1966	1.000	0.885	0.070													
1967			0.153	0.293	0.201	0.244	0.198									
1968		0.057	0.423	0.212	0.104	0.021										
1969		0.057	0.272	0.292	0.156											
1970			0.081	0.203	0.539	0.580										
1971						0.140	0.594	0.121	0.005							
1972							0.010	0.165	0.058							
1973						0.035	0.198	0.367	0.175	0.018						
1974								0.165	0.166	0.085	0.008					
1975								0.182	0.541	0.457	0.353	0.065				
1976									0.055	0.359	0.266	0.109				
1977										0.081	0.374	0.782	0.793	0.083		
1978												0.025	0.130	0.472		
1979												0.019	0.078	0.431	0.031	
1980														0.015	0.969	1.000
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 5C. Results of Scenario 1: Proportion of yearclass production recruiting to 95-109 mm CI interval in each year. Total production equivalent to rightmost column ('YC Sum') of Table 5A, and includes only those crabs surviving to recruitment size. Values sum horizontally to 1.00

YC	Year of Observation (Survey)																
	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	
1966	0.093	0.671	0.236														
1967			0.053	0.532	0.254	0.082	0.079										
1968		0.007	0.217	0.569	0.196	0.111											
1969		0.005	0.114	0.642	0.239												
1970			0.022	0.285	0.528	0.165											
1971						0.135	0.624	0.223	0.017								
1972							0.019	0.584	0.397								
1973						0.021	0.127	0.417	0.389	0.047							
1974								0.232	0.456	0.270	0.042						
1975								0.046	0.269	0.261	0.338	0.086					
1976									0.043	0.325	0.404	0.228					
1977										0.020	0.156	0.451	0.370	0.003			
1978												0.157	0.665	0.178			
1979												0.176	0.578	0.235	0.111		
1980															0.012	0.543	0.444

reduced from 7547 to 365. 3) Equal annual mortality (A) of 0.1 (as per Balsiger, 1974) applied to all modes in all years. 4) Differential annual mortality applied. A = 0.1 for all modes in all years except 1983-1986, when A = 0.5. 5) Differential annual mortality, as in scenario 4, but abundance of mode 1984/H13 reduced as in scenario 2. Results similar to Tables 5A-5C were produced for each of the five scenarios described, but the differences were minor so complete tables are not given. Figure 11 compares the total recruitment produced by each yearclass, as estimated by Scenarios 1-5 (essentially the column labeled 'YC Sum' of Table 5A, and its equivalents from each scenario). Reduction of mode 1984/H13 significantly reduces the predicted recruitment in 1977. Application of constant mortality reduces all values by 13-32%, whereas higher mortality in the years 1983-1986 reduces the contribution of 5 YC's, from 1974 to 1979.

Although it was not intended for such use, comparison of the modal recruitment index with the adult recruitment index (numbers of crab in the 95-109 mm CL interval; Fig. 11) reveals that a dominant group of crabs (1977 recruits) is reasonably represented by both techniques. Scenario 5 gave the best fit between the observed data (adult index) and the predicted recruitment (modal index). Over the period of this analysis, three periods of strong recruitment are detectable, occurring in 1975-77, 1981-82, and 1984. In the first two cases, the modal index predicts both the timing and magnitude of recruitment relatively well, although that was not its intended purpose. The three outstanding recruitment years (1977, 1982, and 1984) all consist of multiple YC's, each of which was relatively successful. In the case of 1977, four relatively strong, adjacent YC's (1967-1970) appeared to recruit simultaneously, and none contribute more than 30% of the total recruitment. The 1982 and 1984 recruitment years consist primarily of crabs from the 1975 and 1976 YC's, but in neither case does the predominant YC contribute more than 56% of the total recruitment. In fact, no single YC stands out above the others over the period considered (Fig. 12), except perhaps 1975, if mortality is assumed constant (Scenarios 1-3), and 1977, if the high value at station H13 is retained (Scenarios 1, 3, and 4).

The estimated recruitment contributed by each YC ranges from (an index value of) 161 to 9893 in scenario 1, covering 1.8 orders of magnitude, or from 131 to 1755 in scenario 5, covering 1.1 orders of magnitude. The modal indices of summed recruitment in each survey year also lie within this range, but with slightly less variance. Over this same period, the Reeves-Marasco recruitment index has varied from about 6 to 40 million, i.e., 0.8 orders of magnitude, and the estimates of legal-sized male crabs from 1.5 to 46.6 million, or 1.49 orders of magnitude. There appears to be a 'basement' level of recruitment of 7-8 million crabs occurring in years other than those identified as years of strong recruitment. This basement level may be representative of low level recruitment actually occurring in those years, or it may represent the overlapping of the extreme tail ends of strong modes which occur

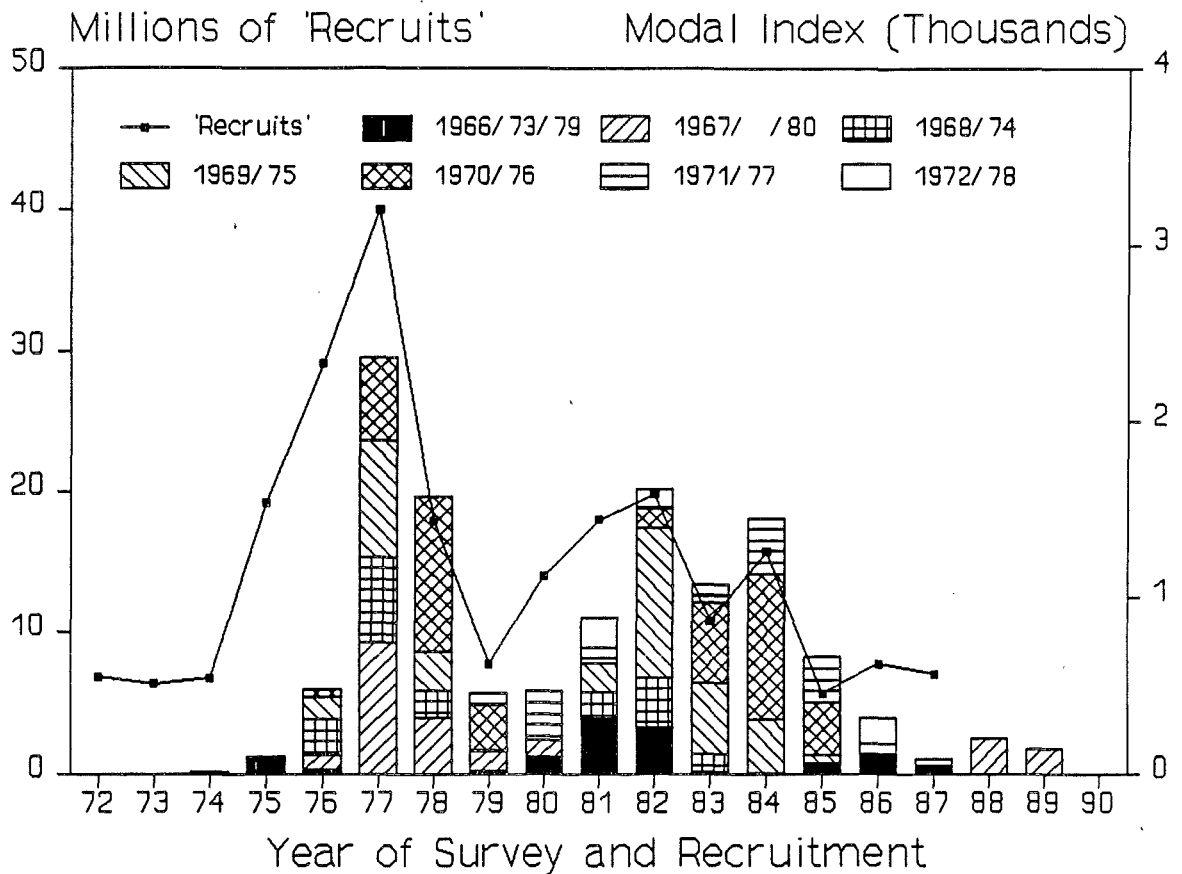
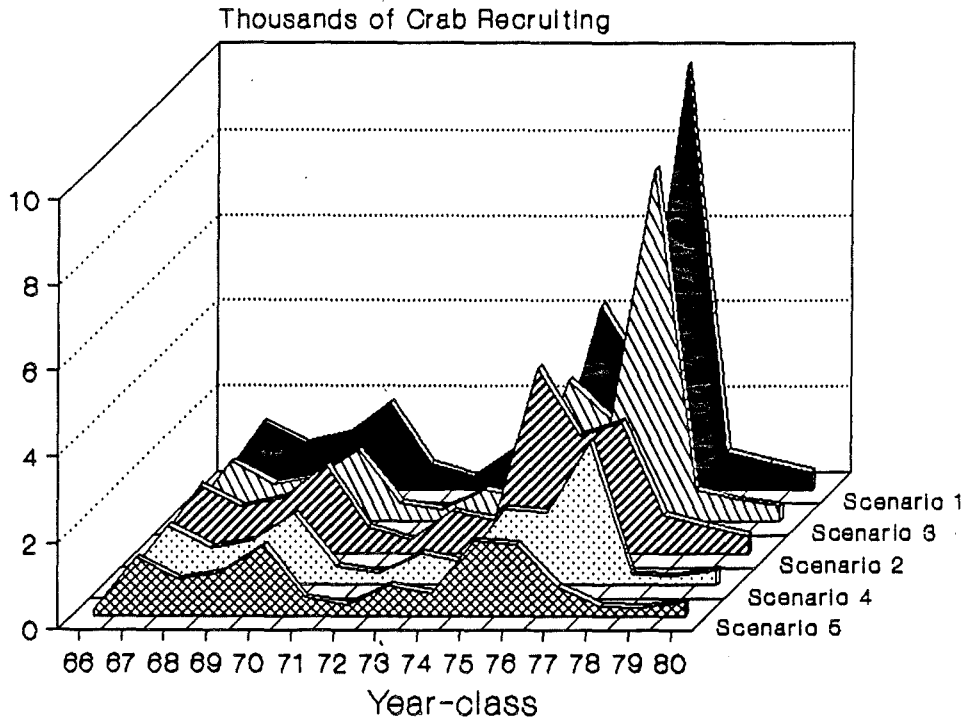


Fig. 11. Recruitment scenario 5: Comparison of Reeves-Marasco recruitment index (observed numbers of crab in 95-109 mm CL interval; solid line) with modal recruitment index (predicted numbers of crab surviving from initial observation to entry into the 95-109 mm CL interval; vertical bars). Modal index shows the number of crabs recruiting from individual year-classes. This scenario incorporates annual mortality of 0.5 in 1983-1986, and 0.1 in all other years. Station H13 (1977 YC) has been reduced to a value of 365 (see text for explanation).

at intervals of 3-5 years. Over the period of analysis, there has not been a long enough gap between strong modes to determine if this basement level would approach 0 in the absence of adjacent strong peaks.

The years 1974-76 lack proper representation in this analysis because of the 3-5 year lag times required between first observation of the modes (1973) and subsequent recruitment (1977). Although analysis included the 1987 survey data, essentially no significant numbers of small crabs have been observed since 1983, implying either that no detectable year-classes have been produced since about 1980, or that year-classes produced since that time have gone undetected by the survey.



Note: Scenarios not in numerical order

Fig. 12. Comparison of results of recruitment scenarios 1-5. Values are number of crabs surviving to recruitment to the 95-109 mm CL interval from yearclass shown. Scenario 1 values represent the rightmost column of Table 5A ('YC Sum'). All other scenarios follow same form as Tables 5A-5C.

DISCUSSION

One assumption implicit in stock-recruitment analysis is that of constant lag times, i.e. that recruitment in consecutive years is the result of successive yearclasses of successful offspring hatched in consecutive years and recruiting at the same age in consecutive years. A corollary assumption is that a one-to-one relationship exists between the parent stock index (P) and a subsequent recruitment index (R), such that for each estimate of P, only one R exists, and vice versa. These assumptions are apparently invalid for Bristol Bay king crab. According to the model, eight modes, collectively spanning 4 hatching years (1967 to 1970, with the majority originating in 1969), recruited to the RMI in 1977. Also, at least 9 modes appear to have originated in 1975, and these recruited over a period of 3 years (1982-1984). Even though the strong recruitment modes of 1975-77 were composed of multiple year-classes, their recruitment was essentially simultaneous, and required at least 3 (and probably more) years to

complete. They may be considered to comprise a single 'functional' cohort with respect to recruitment to the mature adult size interval, or RMI. Thus the gradual rise in recruitment over the period 1975-77, rather than representing several increasingly successful consecutive year-classes, probably represents the successive sampling of a strong functional cohort as it first entered, then passed through, and finally left a given 'window' of size, as though a series of photographs were taken of a mountain through the window of a passing automobile. Values employed by Reeves and Marasco (1980; Fig. 13) as indicators of recruitment in 1976-78 are probably the result of this same phenomenon of sequential partial sampling of a single functional cohort. For a geographically dispersed crustacean population such as the red king crab, the simultaneous recruitment of crabs from multiple year-classes and nursery areas seriously inhibits the capacity to distinguish year-class modes in the combined length frequency data.

Marine organisms with pelagic young typically produce large numbers of larvae. Fecundity of red king crab varies from about 50,000 to 400,000 (Haynes, 1968; also footnote⁵). Survival of red king crab from larvae to adult appears to vary greatly between years, perhaps by factors up to 60 (Table 5). If the data for station 1984/H13 is accepted, one could draw the conclusion that Paralithodes camtschatica has the capacity to rebuild a diminished population with a single strong year-class. Thus, the high reproductive rate could be viewed not as an adaptation to overcome constant high mortality by survival of a small but constant portion of each YC, but rather as a mechanism to provide a large reserve of larvae in each year, in case the environmental conditions are unusually good. From most year-classes, only a very small proportion of these larvae survive to adulthood, perhaps only enough to provide a low-level background of noise-like recruitment. However, occasionally a large enough proportion would survive to replenish the stock many times over, and temperature variation over the geographic range of the stock would insure that growth rates vary enough to spread recruitment over a period of 4-5 years.

If the value for 1984/H13 is dismissed as an unreliable outlier, an alternative conclusion can be drawn. Scenario 5 indicates that two or more adjacent strong, i.e., better than average, YC's may be required in order to boost recruitment of adults to an outstanding level. In this case the booster effect is produced not by a single YC, but by the overlap in size of crabs from each YC as they recruit to the adult population, and this effect is augmented by temperature-induced variation in growth rates, smoothing the differences between recruits from each YC.

In fact both mechanisms may be at work. The increase in recruitment during the mid-1970's, which produced the high landings during the latter part of that decade, was primarily the result of overlapping adjacent strong YC's. But the two periods of increased

⁵ MacIntosh, R., NMFS, P.O. Box 1638, Kodiak, AK. Unpublished data.

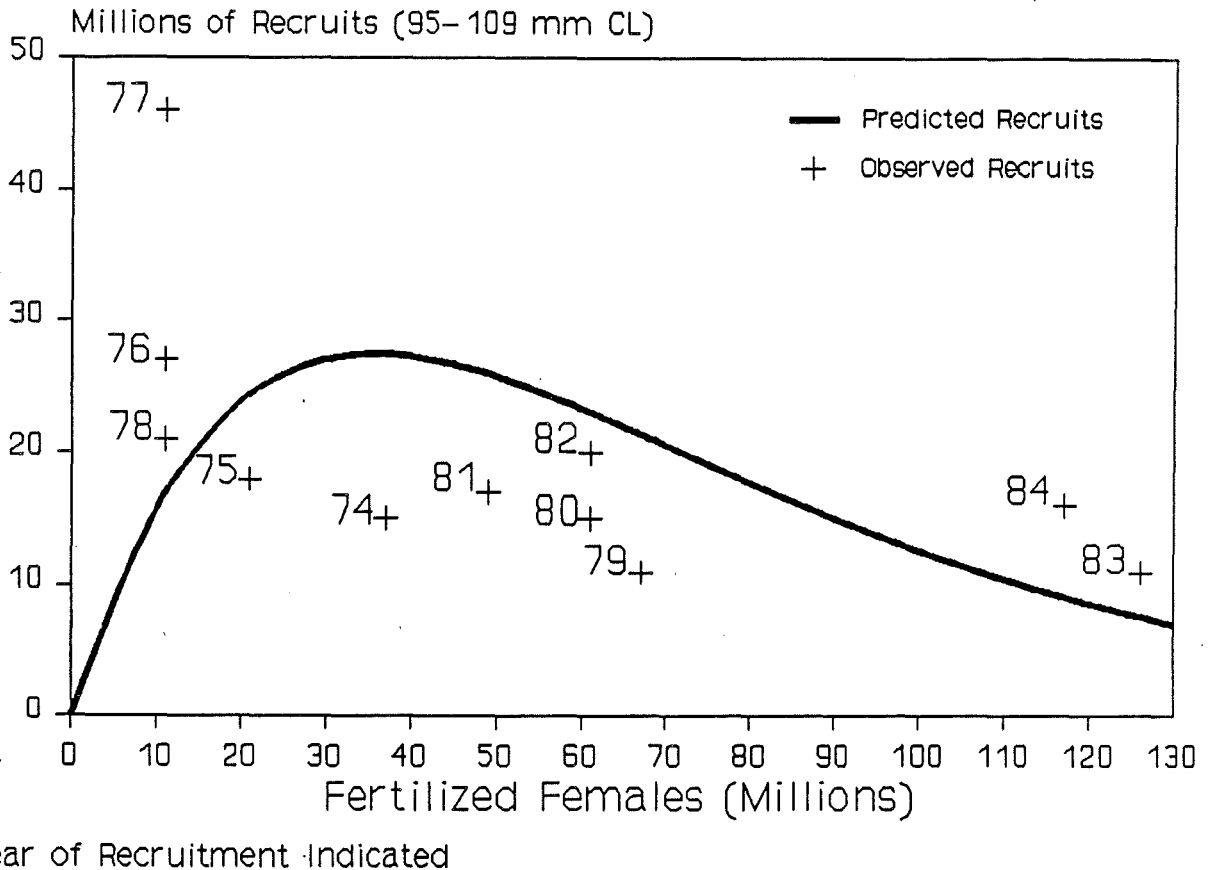


Fig. 13. Stock-recruitment model of Reeves (1985) for Bristol Bay red king crab. Each point is designated by the year of the recruitment estimate. Values are similar to the adult recruitment index of Fig. 12, with minor differences due to the standardized recalculation procedure used for the present study.

recruitment in the early 1980's, while comprised of adjacent YC's as well, may have been more the result of an individual strong YC.

Although the selection of modes for analysis was done by stratifying on small and medium sized crabs (<75 mm CL), some stations with modes having mean sizes above this limit (eg. station 84/H13) were selected by this process if they were composed of a large number of crabs, but the left tail was below the stratification limit, i.e., the high density group identified by stratification was only the tail end of a much more abundant group which was slightly out of the 'frame' of the size window. This provides some justification for deleting this particular mode from later analysis, but it does not explain the mysterious appearance-disappearance of this same group of crabs.

The ultimate use and test of these results will be to allocate the survey estimates of abundance of crabs in the RMI size group to the most probable YC according to the proportionate distribution implied by Tables 5a-5c. This will provide an index of recruitment from each YC that is similar in nature and magnitude (millions of

crab), but not value, to the RMI index, and which can then be applied to further analysis of stock-recruitment relationships.

The assumption that crabs remain non-migratory until reaching a size of 60 mm CL is perhaps questionable, but has several origins. Crabs below this size are usually not caught by the EBS survey trawl except in years of apparently high abundance. Although this might suggest that smaller crabs are not physically retained by the gear, that conclusion is not supportable because small king crabs are occasionally captured, and Tanner crabs (*Chionoecetes* spp.) are commonly caught in high abundance down to sizes of 20 mm CL or less (Stevens and MacIntosh, 1986). Thus, there may be a behavioral change which occurs at about 60 mm CL which causes king crabs to become vulnerable to the trawl gear at larger sizes.

This conclusion is supported by two observations. The first is that the smallest king crabs (<50 mm CL) were routinely found in shallow water within 20-30 miles of shore. This same observation was made by McMurray et al. (1984), who found higher abundances of very small king crabs (<30 mm CL) in nearshore habitats dominated by bivalve shell debris and bryozoans. The highest density of such crabs found by them occurred in Kvichak Bay (close to NMFS station K17). The second is that king crabs have been observed to aggregate into pods of several hundred to several thousand individuals, which remain essentially localized for long periods of time (Powell and Nickerson, 1965). One such pod has been continuously observed in a small area of a bay near Kodiak for over 6 months (Dew, 1988).

In contrast, the assumption of non-migratory larvae is questionable. King crab larvae are not strong swimmers, although they can swim vertically, and do so in response to certain environmental factors (footnote 1). Such behavior could allow them to take advantage of different current regimes at different levels of the water column, which could just as easily result in transport of larvae over long distances as it could in retention of larvae in a given region. Haynes (1974) showed that king crab larvae could be transported over distances of 100 miles or more during larval development, by longshore currents flowing eastward along the north side of the Alaska Peninsula. This argument has also been developed by Armstrong et al (1981). While short-period tidal currents often approach several knots in this region, the net transport is on the order of only about 1-5 cm/sec, or about 0.02-0.10 kt (Kinder and Schumacher, 1981). Thus net current flow is enough to transport larvae from 30 to 150 nmi from their origin over a 40-60 day period of development, if they remained stationary relative to the water mass. On the other hand, by selective vertical migration between surface and bottom water masses, they could reduce or constrain their horizontal transport.

Regardless of how king crab larvae arrive at their location of settlement, certain locations seem to be more productive of juvenile crabs. It is currently unknown whether this is the result of localized hatching and retention of larvae, or whether it is due to a scarcity of good habitat, such that only those larvae which

settle and become benthic postlarvae in habitats which provide adequate shelter and food survive their first year. The latter conclusion was considered most probable by McMurray et al (1984).

It is interesting to note that the four areas where the smallest crabs have been collected by the NMFS survey are all near estuaries. Although generally considered to be a fairly straight, continuous coastline, the Alaska Peninsula is punctuated by Izembek Lagoon, Port Moller/Herendeen Bay, Port Heiden, and several other smaller river outlets. Stations J16 and K17 are within the influence of Kvichak Bay, to which freshwater is contributed by the Egegik, Naknek, Kvichak, and Nushagak rivers as well as others. It is tempting to postulate that the presence of these estuaries may somehow contribute to survival or settlement of king crab postlarvae, perhaps as sources of gravel and glacial deposits and/or localized water currents which might create good benthic habitat for crabs or their prey/cover species, or by providing a source of lower-salinity water which may have some positive physiological or behavioral effect on the settling crabs.

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ON THE CONTRIBUTION OF DENSITY-DEPENDENT
FACTORS TO YEAR CLASS VARIATIONS
IN ALASKAN WALLEYE POLLOCK

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ABSTRACT

This paper presents evidence that density-dependent factors may be playing a role in determining year class variations in Alaskan walleye pollock (*Theragra chalcogramma*). Results from analysis of commercial fisheries statistics and information collected from juvenile and hydroacoustic research surveys are used to look at interannual differences in maturity, to examine the relationship between spawners and recruits and also to investigate the likelihood of a density-dependent catchability fishing mortality model.

Results indicate that size at 50% maturity shows substantial interannual variation. Comparisons to trends in population abundance hint at an indication of density-dependent growth. Results from a spawner-recruit analysis and also from application of an alternative statistical test for density-dependence suggest that strong compensatory density-dependent regulatory mechanisms may be an attribute of the pollock population. Finally, analysis of a catch-at-age and standardized effort data set show a clear and well defined relationship between catchability and population size demonstrating that catchability is density-dependent for this pelagic stock.

The relationship of these features to year class fluctuations are discussed. The paper also discusses what is known regarding recruitment processes in the Gulf pollock stock and the relationship of recruitment to overall stock population dynamics. The significance of environmental effects in determining year class success are discussed in light of considering density-dependent influences.

INTRODUCTION

One of the most important factors that influences changes in fish stock abundance is the number of fish that recruit to the population from a year class. Variations in year class strength are of interest to fisheries biologists because their study may potentially shed some light on the biotic and abiotic factors that influence the recruitment process. With respect to fisheries management, the study of recruitment or year class variation is particularly important since it is this feature of fish population dynamics that largely determines annual abundance levels of commercially exploited fish stocks.

Recruitment as a biological process is very complex since many different facets of a species reproductive biology come into play. It is important however to draw a distinction between two different aspects of recruitment: recruitment to the stock (i.e. the introduction of eggs and larvae into the population) vs. recruitment to the exploitable population (the movement of juveniles into a size range or locale that makes them vulnerable to a fishery). The former is usually referred to as the pre-recruit phase.

It is generally believed that most fluctuations in recruitment are due to interannual variations in pre-recruit survival and that year class strength is primarily determined at some time during the pre-recruit stage. In addition to the factors that affect pre-recruit survival, there are other factors that influence trends in recruitment. Factors such as the abundance and biological/reproductive characteristics (growth, fecundity, maturity, and sex ratio) of the spawning stock influence recruitment directly by affecting the number of eggs and larvae produced by the stock. Moreover, the intensity of any commercial fishery can also contribute to variations in year class strength by affecting the biological characteristics of the spawning population. The fishery has the potential to alter the size and age composition of the exploitable stock through selective removals, either by size or sex. Indirectly this could affect growth and ultimately the maturity or fecundity characteristics of the stock. When the fishery is operating during the time of spawning as it does in the Bering Sea and Gulf of Alaska pollock roe fishery, reproductive products that would normally contribute to the population are removed through directed harvest of fecund females.

The objectives of this paper are to present three pieces of evidence that density-dependent factors may be playing a role in the population dynamics of walleye pollock (*Theragra chalcogramma*) stocks in the Gulf of Alaska. Results from analysis of commercial fisheries statistics and information collected from juvenile and hydroacoustic research surveys are used to look at (1) interannual differences in maturity, (2) the relationship between spawners and recruits, and (3) the relationship between fishing mortality and population abundance.

DATA SOURCES

Maturity analysis

Data used in the maturity analysis were collected during hydroacoustic surveys of the walleye pollock spawning stock in the Shelikof Strait region of the Gulf of Alaska (Fig. 1) during March, 1983-1988. A data set collected as part of routine U.S. Observer sampling of the commercial joint venture fishing fleet in March of 1984 was also analyzed. This latter data set was also used to estimate maturity schedules for three reasons. First, the timing of the joint venture fishery and the taking of biological samples from that fishery corresponds to the spring spawning period of walleye pollock in the Gulf of Alaska (Nunnallee, Williamson and Nelson 1982; Nelson and Nunnallee 1985, 1986, 1987). Secondly, the population was well sampled by the joint venture fishery in 1984. The total catch of pollock in the Gulf of Alaska reached its peak of 306,700 t in 1984 and the catch from joint venture fisheries, 207,100 t, was the second highest on record (Megrey 1988a). In addition, observer coverage of the Shelikof Strait joint venture fishing fleet in 1984 was very complete (87.1%) relative to earlier years (Alton 1986). Third, analysis of the commercial fisheries length/maturity data would provide a check against results derived from analysis of the research data sets.

Raw data consisted of length measurements by sex and a coded indication of maturity condition. A simple five-point maturity scale (Table 1) was used to determine maturity of male and female pollock. More complex maturity classification schemes have been proposed by Kesteven (1960) but these are typically needed only in special studies. The raw data used in this analysis are tabulated elsewhere (Megrey and Nunnallee 1988)

For the purposes of this study, a fish was classified mature if the maturity code was three or greater. The decision to use maturity code three as the cutoff for maturity classification is based on direct histological examination of female pollock ovaries. After examining ovaries from pollock classified with a maturity code of two, no sign of vitellogenesis was apparent (Sarah Hinckley, Pers. Commun., Northwest and Alaska Fisheries Center, Seattle, WA).

Spawner-recruit analysis

Results from the Gulf of Alaska pollock stock assessment (Megrey 1988a) furnish the necessary information to perform a spawner-recruit analysis. The input data set consisted of estimates of pollock catch-at-age, ages 3-10, aggregated over all nations, vessel classes and statistical reporting areas of the western and central Gulf of Alaska for calendar years 1976-1987. This will be referred to as the all-nation catch-at-age data set. Also fishery-independent data, consisting of hydroacoustic biomass estimates of the Shelikof Strait spawning pollock population for calendar years 1981, 1983, 1984, 1985 and 1986 (Nunnallee 1988) were incorporated into the stock assessment in order to calibrate

abundance estimates. No hydroacoustic survey was conducted in 1982.

The CAGEAN separable non-linear log catch model of Deriso, Quinn and Neal (1985) was applied to the catch-at-age data in order to estimate age-specific selectivities, fishing mortalities and absolute estimates of population abundance. The assumptions of the stock assessment model are as follows: 1) Catch-at-age is modeled by a stochastic Baranov catch equation that incorporates a lognormal error random variable (Doubleday 1976); 2) Catch is aged without error; 3) M is assumed to be equal to a constant 0.4 per year for all ages and years; 4) Selectivity-at-age trends are modeled with the selectivity model described in Megrey (1988a); 5) Fishing mortality can be separable into an age-dependent factor and a year-dependent factor; 6) Full recruitment fishing mortality parameters from the log catch model can differ from fishery-independent estimates of the same quantity by a lognormally distributed random variable; 7) Catchability is constrained to be equal to an assumed value of 1.0; 8) The effort sum of squares weighting factor (see equation 9, Deriso *et al.* 1985) is fixed at an assumed value of 0.6; 9) The catch sum of squares weighting factor is fixed at an assumed value of 1.0; and 10) Average weight-at-age does not change significantly over the 1976-1987 time period.

The information from the stock assessment that serves as the basis of the spawner-recruit analysis is presented in Table 2. Provided are annual trends in year-class strength of age 3 recruits and total spawning population abundance. A single set of average weight-at-age values (Table 2) were used to convert numerical estimates of absolute abundance and recruitment to weight. These data are presented in units of numbers and biomass.

Density-dependent catchability analysis

The input data set for the density-dependent catchability analysis consisted of estimates of pollock catch-at-age, ages 3-10, and annual estimates of standardized effort from the Japanese foreign fleet in the Gulf of Alaska for years 1973-1983. Normally effort statistics are not collected in the Gulf pollock fisheries, therefore this data set is the only one available for analysis with catch/effort stock assessment models. Japan, which began its operations in the early 1960's, has the longest history of continuous fishing for pollock in the Gulf of Alaska. As a member of the International North Pacific Fisheries Commission (INPFC), Japan provides detailed catch and effort statistics to the U.S. according to the standard INPFC format. Since 1983 Japanese catch of pollock has diminished as the U.S. domestic fishery has expanded.

Effort was standardized based on applying a fishing power model to a reconstructed set of Japanese catch and effort data for 1973-1983 (Megrey 1986) using methodology described by Kimura (1981). The log-linear fishing power model attempted to relate variability in CPUE to factors affecting underlying population density (year, quarter, and INPFC statistical area) and factors that affect vessel efficiency (trawler type (surimi trawler vs. freezer trawler) and vessel size (gross tons)). Nominal effort was standardized to a 2505-

3504 gross ton surimi trawler operating in the INPFC Chirikof statistical area during the third quarter of the year.

The stochastic nonlinear log catch ratio stock assessment model of Fournier and Archibald (1982) was applied to the Japanese catch-at-age and standardized effort data. The assumptions of the catch/effort stock assessment model are as follows: 1) Effort is supplied to the model; 2) The average level of fishing mortality in each year could deviate from the level of effort determined from the model. A variance of 0.02 in the log effort-F relationship is assumed; 3) The oldest age group is assumed to be completely fished out; 4) Fishing mortality is separable and described by the VB parameterization (see Fournier and Archibald 1982); 5) Catch is aged without error; 6) No stock-recruitment relationship is assumed; 7) Catchability is density-dependent; 8) No age class grouping in the input data is assumed; 9) Variance of the total catch estimate is assumed to be 0.0025; and 10) M is assumed to be equal to a constant 0.4 per year for all ages and year.

ANALYTICAL PROCEDURES

Maturity analysis

A logistic response function was used to describe the relationship between maturity and size. Data consisted of different levels of the independent variable X (length cm), the number of observations at each 1 cm length interval, denoted N, and the number of successes (number of mature animals) at X, denoted S. With these definitions, the logistic function is written

$$Y = \frac{\exp(\alpha + \beta * X)}{1 + \exp(\alpha + \beta * X)} \quad [1]$$

where Y is the proportion mature ($Y=S/N$) in a size interval, X is the midpoint of the size interval, and α and β are parameters to be estimated. The range of the dependent variable is $0 \leq Y \leq 1$. Normally parameters of equation [1] are estimated with linear regression.

In this study the method of maximum likelihood was used to estimate the parameters of the logistic function. Fortunately, the problem of estimating percent maturity can be easily cast into a framework of maximum likelihood estimation (Cox 1970). Parameters of the likelihood equation were estimated via nonlinear least squares regression (Jennrich and Moore 1975).

The data are slightly different in the maximum likelihood approach than those used to estimate parameters of the logistic function with linear regression as described above. The dependent variable submitted to the maximum likelihood method, Q, is binary and takes on only values of 0 (is not mature) and 1 (is mature). Successes ($Q=1$) and failures

($Q=0$) occur with frequency N at each of K intervals of the independent variable. Because Q is distributed as a binomial random variable the likelihood equation for the sample observations is expressed as

$$L(Q_1, \dots, Q_K) = \prod_{i=1}^K p^{Q_i} q^{1-Q_i} \quad [2]$$

where p is the probability of success and $q=(1-p)$ is the probability of failure.

Equation [2] is simplified (i.e. the multiplicative terms are made additive) by taking natural logs giving the log likelihood equation

$$\ln[L(Q_i | \alpha, \beta)] = \sum_{i=1}^K \left[Q_i * \ln(\theta_i) + (1-Q_i) * \ln(1-\theta_i) \right] \quad [3]$$

where

$$\theta_i = \frac{\exp(\alpha + \beta * X_i)}{1 + \exp(\alpha + \beta * X_i)} \quad [4]$$

The objective function for estimating the two parameters α and β by maximum likelihood becomes (ignoring subscripts) the negative of the log likelihood function weighted by the frequency of the likelihood

$$\ln[L(Q | \alpha, \beta)] = - N \left[Q * \ln(\theta) + (1-Q) * \ln(1-\theta) \right] \quad [5]$$

Parameter estimates from [4] were obtained by submitting [5] to a nonlinear least squares procedure. Parameter values used to initialize the nonlinear least squares procedure were obtained by applying least squares regression techniques to a linearized form of equation [1].

Once final parameter values are obtained, the linearized form of [1] can be rearranged to solve for the estimated size when the proportion mature is equal to 50% giving

$$\hat{X}_{0.5} = - \frac{\alpha}{\beta} \quad [6]$$

An expression for the variance associated with the estimated size of 50% maturity can be approximated by the Delta method (Seber 1982).

The logistic function was fit to the length and maturity data using length as the

independent variable. Size at 50% maturity was estimated directly by applying equation [6]. All linear and nonlinear least squares regression procedures used in the maturity analysis were performed on an IBM PC compatible microcomputer with the SYSTAT interactive software package, Version 3.0 (Wilkinson 1987).

Spawner-recruit analysis

The appearance of Ricker's classic paper (Ricker 1954) formally started the modeling of stock/recruitment relationships in fisheries biology. Ricker's spawner-recruit model (Ricker 1975, p. 282) assumes that recruitment is generated from adult stock by density-dependent and density-independent mortality. The model is usually written

$$R(y+\delta) = \alpha S(y) \exp^{-\beta S(y)} \quad [7]$$

where the symbols R and S denote recruitment and stock, respectively, α is the coefficient of density-independent mortality and β is the coefficient of density-dependent mortality. Time in years is symbolized by y and δ is the number of years it takes for the young to reach recruitment age. The assumption behind [7] are 1) the number of eggs hatched is proportional to the parent stock, 2) the number of predators is proportional to the parent stock, and 3) the mortality at some immature stage is proportional to the number of predators (i.e. number in the parent stock).

Parameters from equation [7] can be estimated with linear regression but only after linearizing [7] by taking natural logs of both sides, which gives

$$\ln \left[\frac{R(y+\delta)}{S(y)} \right] = \ln(\alpha) - \beta S(y) \quad [8]$$

Equation [7] describes a family of unimodal curves that predict, because of strong density-dependent mechanisms, low recruitment levels at high adult stock densities. The density-dependence increases geometrically over a certain range of stock densities. The density-dependence is related directly to initial adult abundance and only operates at the beginning of the interval between generations. Also the curve predicts that a certain stock density will produce a maximum number of recruits. Ricker (1975, p. 281) lists possible regulatory mechanisms that may underlie this relationship. These may include cannibalism of young by adults or when an increase in the density of larvae increases the time it takes a young fish to grow through a particularly vulnerable life stage. A final regulatory mechanism would be when there is a lag in response of a predator to its prey abundance, with overcompensation for higher initial prey densities.

Recently Shepherd (1982) has proposed a flexible three parameter model that includes as

special cases the models of Cushing (1971) as well as those of Ricker (1975) and Beverton-Holt (1957). Shepherd's model is written

$$R(y+\delta) = \frac{\alpha S(y)}{\left[1 + \left[\frac{S(y)}{\beta} \right]^\tau \right]} \quad [9]$$

where the parameters R , S , y and δ are as defined earlier. The slope at the origin, described by α , is the density-independent parameter describing maximum recruitment at low stock densities, β is the threshold biomass which quantifies the level of stock biomass below which density-dependence is weak, and τ measures the nature of the density-dependent process. The τ parameter is proportional to the magnitude of the density dependent effect and the β parameter provides an estimate of the population level where the likelihood of stock collapse increases because of increasing stock vulnerability. If $\tau < 1$, recruitment will increase indefinitely as stock biomass increases, and [9] imitates the Cushing model. If $\tau = 1$, recruitment increases to some asymptotic level with increasing levels of stock biomass, and [9] describes the Beverton-Holt model. If $\tau > 1$, then density-dependent compensation is strong and increased stock biomass will lead to decreased recruitment, and [9] mimics the Ricker model. Hassell (1974) and Deriso (1978) proposed a three parameter model that incorporates much of the same behavior as the Shepherd's model.

Recruitment estimates were used directly from the stock assessment in the numbers-based analysis. In the biomass-based analysis recruits in numbers were converted to biomass equivalents with the average weight-at-age values reported in Table 2. Spawners in the numbers-based analysis were represented as potential eggs. These numbers were generated with the relationship

$$S(y) = \sum_{a=3}^{10} N(a,y) \text{ fec}(a) m(a) \quad [10]$$

where $N(a,y)$ is the number of age a individuals in the population in year y estimated from the stock assessment, $\text{fec}(a)$ is the fecundity at age a , and $m(a)$ is the proportion of age a females that are mature. A sex ratio of 1:1 is assumed. Fecundity was calculated as a function of average weight-at-age (from Table 2) from (Miller *et al.* 1986) using the equation

$$\text{fec}(a) = 387.4551 w(a)^{1.016} \quad [11]$$

where $w(a)$ is the average weight-at-age. Maturity was indirectly calculated as a function of weight-at-age using equation [1] as follows. First, length-at-age was calculated from average weight-at-age by rearranging the allometric weight-length equation to give

$$l(a) = \left[\frac{w(a)}{0.0059} \right]^{\frac{1}{3.0273}} \quad [12]$$

where the weight-length parameter values are from Miller *et al.* (1986). This was substituted into [1] giving maturity as a function of length

$$m(a) = \frac{\exp[-16.01 + 0.44 l(a)]}{1 + \exp[-16.01 + 0.44 l(a)]} \quad [13]$$

Spawners in the biomass-based analysis were calculated by multiplying [10] (without the fecundity term) by the average weight-at-age values. The data used in the spawner-recruit analysis, expressed in units of numbers and biomass, are presented in Table 2. Also presented are weight-at-age and estimates of length, fecundity, and maturity calculated from equations [11], [12], and [13]. One maturity-at-age vector was used, based on parameter estimates from the 1984 commercial fisheries maturity-length data set.

Both the Ricker and Shepherd spawner-recruit models were applied to the data. Parameter values used to initialize the nonlinear least squares procedure for the Ricker model were obtained by applying least squares regression techniques to the linearized form of the equation. All parameters were unconstrained in both the biomass and numbers-based analyses using the Ricker model. Initial values for fitting the Shepherd model were approximated as described in Shepherd (1982). As he suggested, values for τ were determined by regressing $\ln(R)$ on $\ln(S)$ using linear regression and using the slope estimate as the value of τ . In the nonlinear regression the shape parameter of the Shepherd spawner-recruit model (τ) was constrained to be equal to the linear regression estimate, while α and β were unconstrained. All linear and nonlinear least squares regression procedures used in the spawner-recruit analysis were performed on an IBM PC compatible microcomputer with the SYSTAT interactive software package, Version 3.0 (Wilkinson 1987).

The existence of density-dependence in the stock abundance and recruitment data was investigated further by a statistical method first proposed by Bulmer (1975). This approach does not rely on a presumed spawner-recruit model. In terms of the spawner-recruit data for Gulf of Alaska pollock Bulmer (1975) suggests the statistic

$$V = \frac{\sum_{y=1}^n [N(y) - \bar{N}]^2}{\sum_{y=1}^{n-\delta} [N(y+\delta) - N(y)]} \quad [14]$$

where $N(y)$ is the population abundance in year y , \bar{N} is the average population abundance, n is the sample size and δ is the recruitment lag time. The year index is adjusted so that the first year of population abundance data corresponds to an index value of one. When abundance observations are subject to measurement error Bulmer (1975) suggests

$$V^* = \frac{\sum_{y=1}^{n-\delta-1} [N(y+\delta+1) - N(y+1)] [N(y) - \bar{N}]}{\sum_{y=1}^n [N(y) - \bar{N}]^2} \quad [15]$$

Significant density-dependence is demonstrated when V or V^* is less than tabular values provided in Bulmer (1975).

Density-dependent catchability analysis

The usual assumption regarding the relationship between fishing mortality (F) and effort (f) is that fishing mortality is proportional to the effort or fishing intensity exerted by the fishing gear (Beverton and Holt 1957). The constant of proportionality is often referred to as the catchability coefficient (q), or the degree to which the fish are vulnerable to the gear. If catchability is considered a constant or average, then the fishing mortality model is written

$$F = q f \quad [16]$$

Fishing mortality is seldom constant from year to year and often within any one year there is a significant age effect. To accommodate these features, the stock assessment model of Fournier and Archibald (1982) permits further structure to be added to equation [16] by considering the catchability and effort parameters as separate submodels. The model is fairly generalized and flexible. Ultimately the level of complexity depends on what contingencies are appropriate to the fishery being analyzed. A fully developed fishing mortality model might have to account for an age effect such as age-specific selectivity of the gear, an age and/or year effect such as changes in catchability with age and/or time, a population density effect such as a density-dependent catchability coefficient (Fox 1974; Schaaf 1975; MacCall 1976; Ulltang 1976, 1980; Garrod 1977; Peterman and Steer 1981;

Bannerot and Austin 1983) or a gear saturation effect (Bannerot and Austin 1983). To accommodate all of these features substitute

$$q = q(y) s(a) N(a,y)^\theta f(y)^\Phi \quad [17]$$

into [16] which gives the generalized fishing mortality model

$$F(a,y) = q(y) s(a) N(a,y)^\theta f(y)^{1+\Phi} \quad [18]$$

where $F(a,y)$ is the fishing mortality at age a in year y , $q(y)$ is the catchability in year y , $s(a)$ is the age-specific selectivity of the gear, $N(a,y)$ is the population at age a in year y , $f(y)$ is fishing effort in year y , θ is a density-dependent catchability coefficient, and Φ is a gear saturation coefficient.

If we define $C(a,y)$ as the catch of a -year-old's in year y , then the catch equation

$$C(a,y) = F(a,y) N(a,y) \quad [19]$$

would be modified to

$$C(a,y) = q(y) s(a) N(a,y)^{1+\theta} f(y)^{1+\Phi} \quad [20]$$

Even though equation [20] is highly nonlinear, it is useful because it represents a very general expression from which numerous different expression of fishing mortality can result. Unfortunately it is extremely difficult to predict what effect these nonlinearities will have on the total estimation process when [20] is used in a stock assessment framework. Paloheimo and Dickie (1964) and more recently Cooke (1985) provide a good discussion of the problems introduced by nonlinearities in the catch effort relationship. The Fournier and Archibald stock assessment model used in this analysis is based on [20] but omits the gear saturation effect on the effort variable.

RESULTS

Interannual variations in maturity-at-size

Results from fitting the logistic response function to the pollock maturity data are given in Table 3. Tabulated for each calendar year and sex are the logistic function parameter estimates, their standard errors, sample size and the estimated length at 50% maturity.

The logistic model fit the data well. In all cases, over 90% of the variation in maturity of

walleye pollock was explained by length. Figure 2 shows the logistic curve fit to the male and female maturity data from the 1984 commercial fishery data set. This plot is typical of the fits from other years. Data for male pollock were more consistent with the logistic model over the entire observed length range. Female pollock showed more variation in maturity over the pre-mature length interval (20-35 cm) compared to males. A few data points in Figure 2 show large departures from the logistic model for both sexes of fish lengths between 50 and 60 cm. Animals in this size range have in all likelihood already spawned so these data points probably reflect maturity misclassification error. Maturity codes 1 and 5 are the maturity conditions most easy to confuse. It is very easy to misclassify an animal as immature (maturity code 1) instead of spent (maturity code 5) since gonads look similar from male or female animals in either maturity condition. Another interesting feature of Figure 2 is the apparent knife-edged maturity as indicated by few points on the steeply rising portion of the logistic curve. This feature is undoubtedly related to the fact that the data used in the analysis were collected at the time pollock were spawning. During the time spawning aggregations take place there are few fish of intermediate maturity condition; either they will not spawn at all, they are ripe and will spawn soon, or they have already spawned.

Comparisons of estimates of size at 50% maturity from the 1984 hydroacoustic survey and commercial fisheries data sets compare well. Even though estimates from the commercial fisheries data set were consistently lower than the corresponding hydroacoustic survey estimates, statistical tests indicated no significant ($P < 0.05$) difference. The maturity analysis indicates considerable interannual variation in maturity-at-size. Size at 50% maturity has been increasing for both male and female pollock (Table 3). Between 1983 and 1988 this difference is 4.64 cm and 7.60 cm for male and female pollock, respectively. Over the same annual period, the increase in size of 50% maturity (Fig. 3, panel A) has been accompanied by a decrease in population abundance (Fig. 3, panel B). These data suggest that pollock may be growing faster in recent years, perhaps in response to decreased competition due to reduced abundance levels.

Estimates of the size at 50% maturity from this study correspond well with results reported in earlier studies. Based on research surveys conducted in the Gulf of Alaska from May through September in 1973-1975, Hughes and Hirschhorn (1979) estimate length at first maturity occurred at 29-32 cm for males and 30-35 cm for females. The only other example of estimates of size at 50% maturity was reported by Smith (1981) for pollock in the Bering Sea. Direct comparison of parameter estimates from this study with Smith's are not possible because Smith used a logistic model of slightly different mathematical form. Smith (1981) estimated that the size of 50% sexual maturity for pollock in the Bering Sea was 31.0 cm for males and 34.2 cm for females. These values are lower than those estimated for the Gulf of Alaska pollock by 11% and 6% for males and females respectively.

Other information on aspects of reproductive biology of pollock in the Bering Sea

(Hinckley 1987) and Gulf of Alaska suggest that there is also a difference in the fecundity-size relationship (Miller *et al.* 1986) with pollock from the Gulf being more fecund at size in lengths above 45 cm. Perhaps these differences reflect either dissimilar productivity characteristics between the two pollock stocks or between the Bering Sea and Gulf of Alaska ecosystems.

Spawner-recruit analysis

Results from the stock assessment indicate that the population increased from about 1,000,000 t in 1976-1977 to a peak of a little over 2,000,000 t in 1981 or 1982 and then has been in a declining phase (Fig. 4, panel A). The rise in population biomass during 1982-1983 was primarily the result of five strong consecutive year classes (1975-1979) moving through the population (Fig. 4, panel B). The post 1982 decline in abundance was a result of poor recruitment during 1980-1983. Population abundance estimates from the stock assessment agree well with independent estimates from the hydroacoustic surveys (Fig. 4, panel A).

Figure 4 also suggests an apparent inverse relationship between the magnitude of the spawning biomass and subsequent recruits arising from that spawning biomass. For example, the four strong year classes 1976-1979 were all produced from a spawning biomass between 780,000 and 1,660,00 t. The poor 1980-1983 year classes were all produced from a spawning biomass that was close to 2,000,000 t. Because fish do not recruit to the fishery until they are three years old, the first three years of data provide recruitment estimates for years 1973-1975 but there are no corresponding spawner estimates (Table 2). Also, the last three years of spawning biomass estimates (1984-1986) do not have a corresponding recruitment estimate.

Spawner-recruit parameter estimates from the two spawner-recruit models, their variances, and a measure of the variability in recruitment explained by the model are presented in Table 4. The units of measurement did not affect the results very much. When comparing results from the numbers and biomass-based analyses, each model did about equally well at predicting recruitment. Only the results from the biomass-based analysis will be described in subsequent discussions.

A comparison of the fitted spawner-recruit curves plotted against the raw data are presented in Figure 5. The correspondence between predicted estimates of recruitment from the spawner-recruit models are surprisingly close to the raw data. The Ricker spawner-recruit relationship accounted for about 82% of the variation in pollock recruitment while the Shepherd model accounted for slightly less, or about 75% of the variation. Both models resulted in a statistically significant fit to the data ($P < 0.05$). Also conspicuous is the apparent lack of variability characteristic of many exploited marine species. This is probably due to the limited time series of spawner-recruit data points.

The Ricker and Shepherd models describe well the situation that as spawning levels have been increasing, recruitment levels have been declining. This suggests that strong compensatory density-dependent processes may be playing an important role in the population dynamics of this species. Even though the Ricker and Shepherd spawner-recruit models appear to fit the data very well, the results should be interpreted with some caution. There are many weaknesses with the spawner-recruit modeling approach described above. There are only eight data points available to fit two and three parameter nonlinear equations. Also the range of spawning biomass is limited, resulting in a lack of data points to the left of the hump in the spawner-recruit curve. The Ricker and Shepherd models essentially fit a relationship to two conditions--high recruitment at low to intermediate spawning levels and low recruitment at high levels of spawning.

Estimation of Minimum Spawning Biomass

One of the advantages of the Shepherd spawner-recruit model is that a threshold population level can be estimated directly. Recall that in the Shepherd model β is defined as the threshold biomass. This parameter quantifies the level of stock biomass below which density-dependence is weak and provides an estimate of the population level where the likelihood of stock collapse increases because of increasing stock vulnerability. The estimated value for β from the Shepherd model using units of biomass is 580,000 t (Table 4). This parameter was estimated with moderate precision, having a coefficient of variation of 31%. The 95% confidence interval for β in biomass units ($227,000 < \beta < 930,000$).

Over the time period that fishery statistics have been collected on Gulf of Alaska pollock, population abundance levels have been at high levels. Furthermore the range of spawning biomass is fairly narrow. Note that levels of spawning biomass have never fallen below about 750,000 t so we do not have any recruitment observations that correspond to low levels of spawning biomass. Consequently, there are relatively few data on which to base an estimation of what constitutes a minimum spawning biomass. The year class strength estimates and the annual trend in estimated population biomass from the catch-at-age analysis however can be used to indirectly infer an approximation. From Figure 4 we can see that the population biomass levels in calendar years 1976 to 1979 produced strong year classes and years of peak population biomass (1980 to 1983) produced poor year classes. Even though catch-at-age analysis cannot provided estimates of the abundance of the 1984 or 1985 year classes, preliminary estimates from the hydroacoustic surveys indicate that the 1984 year class (seen as 2-year-olds in 1986 and 3-year-olds in 1987) may be above average in abundance and the 1985 year class (measured as 2-year-olds in 1987) appears to be average (Nunnallee 1988). The population biomass levels in 1983 (1.7 million t) is very close in magnitude to the biomass levels in 1979 (1.5 million t). Similarly, levels in 1984 (1.2 million t) are very close to the 1978 levels (1.0 million t). Since we know that biomass levels in 1978 and 1979 produced strong year classes it is not unreasonable to expect that moderate biomass levels in 1983 and 1984 might once again

give rise to average or strong year classes. To provide a value for minimum spawning biomass, it seems reasonable to use the lowest observed population biomass level that produced a strong year class. This value is the population biomass estimate for 1977, or about 752,000 t and is included in the confidence interval of the minimum spawning biomass estimate provided above.

In addition to the results from the spawner-recruit analysis, statistically significant ($P < 0.01$) compensatory density-dependence was confirmed by Bulmer's test when equations [14] and [15] were applied to the abundance data in Table 2.

Density-dependent catchability

Application of the Fournier and Archibald stock assessment model to the Japanese catch-at-age and standardized effort data demonstrated that including the density-dependent catchability coefficient in the model resulted in a significant improvement in the fit (lowered the value of the log likelihood function). A likelihood ratio test was performed (Schute 1983) to determine if reductions in the value of the log likelihood function achieved by including the density-dependent catchability feature were statistically significant. Performing this test resulted in a value of the log likelihood function of 95.4 using the Fournier and Archibald model without the density-dependent catchability parameter and a value of 74.4 with the density-dependent catchability parameter. This reduction (approximately 22%) in the log likelihood function due to including one extra parameter in the model (the density-dependent catchability parameter) was highly significant ($P < 0.01$) based on the likelihood ratio test.

Two relationships between the catchability coefficient and population abundance from the Fournier and Archibald model are shown in Figure 6. Panel A shows clearly that q varies in an inverse fashion with stock size over time. Panel B shows a highly statistically significant relationship between the catchability coefficient and population abundance. From this figure the estimated density-dependent coefficient is -1.298. This value compares well with other values reported in the literature: -0.3 for Pacific sardine (Fox 1974); -0.74 for Atlantic menhaden (Schaaf 1975); -0.611 for Pacific sardine (MacCall 1976); -1.375 for Atlanto-scandian herring (Ulltang 1976, 1980), -0.72, -1.56, and -1.10 for chinook salmon (Peterman and Steer 1981); and -0.5065 for yellowtail snapper (Bannerot and Austin 1983).

DISCUSSION

Results from the maturity analysis are critically linked to the assumption that all pollock from the entire western and central Gulf of Alaska return to Shelikof Strait during the spring of the year and are assessed by the spring hydroacoustic survey. No other major spawning aggregations have been located in the Gulf of Alaska. Maturity results suggest that pollock growth may be density-dependent. In order to draw this conclusion with

confidence, we need to demonstrate that size-at-age has been changing in accordance with the observed shift in estimated size at 50% maturity. Unfortunately, no firm conclusions can be drawn from this study because there were too few years of data with which to carry out a growth study. A more detailed analysis of the commercial fisheries statistics will have to be performed so that the observed changes in size can be related to changes in age. Many other studies have shown that size at maturity in fishes can be variable (Templeman and Bishop 1979; Beacham 1983; Stearns and Crandall 1984; Echeverria 1987; Overholtz 1987). Overholtz (1987) has demonstrated that size at 50% maturity is density-dependent in haddock. Another factor that could affect conclusions from the maturity analysis is whether the onset of maturity is triggered by attaining a certain size/weight or is more related to the fishes age (Roff 1982).

Results from the spawner-recruit analysis suggest that strong compensatory density-dependent processes may be playing an important role in the population dynamics of this species. The lack of large fluctuations in recruitment and population size, which are common in many exploited marine species, implies that strong density-dependent regulatory mechanisms may be important. Ricker proposed that cannibalism could lead to a dome-shaped spawner-recruit curve. It is well documented that walleye pollock are cannibalistic in the Bering Sea (Dwyer, Bailey and Livingston 1987) however cannibalism has rarely been observed in the Gulf of Alaska pollock stocks. Speculations regarding possible sources of the density-dependence in the Gulf of Alaska ecosystem are described in Alton, Nelson and Megrey (1987).

If pollock stock dynamics are largely regulated by strong compensatory density-dependent mechanisms, as indicated by the apparently well defined relationship between spawners and recruits, then environmental influences appear to play only a minor role in determining year class strength. Since the spawner-recruit models seem to explain a large amount of recruitment variability then these models leave little unexplained variation in recruitment that could be due to an environmental variable. Alternatively, the apparent inverse relationship between spawners and recruits could be due entirely to an unknown environmental factor. For instance, an environmental variable that exhibits a negative influence on recruitment could have produced the observed time series of spawners and recruits if the environmental variable had an decreasing temporal trend up to 1979 and an increasing temporal trend since 1979. Moreover Maelzer (1970) and Amant (1970) have pointed out that under certain conditions, even random density-independent population trends can give spurious statistical indications of density-dependence.

Despite these caveats, the fitted spawner recruit models describe the data well and in terms of predictive capacity are consistent with early indications of year classes strength from the spring 1987 hydroacoustic cruise (Nunnallee 1988). Evaluating the Ricker spawner-recruit model at spawning biomass levels observed in 1984-1986 (Table 2) suggest that the 1984, 1985 and possibly the 1986 year classes will all be average to above average in abundance. Nunnallee (1988) shows that abundance of 2 and 3 year old pollock in 1987

(the 1984 and 1985 year classes) made up over 90% of the total assessed population biomass. Also preliminary data from the 1987-1988 commercial fishery (Megrey 1988b) indicates that pollock from age groups 2, 3 and 4 (1984, 1985 and 1986 year classes) are very abundant.

When the stock dynamics of a population are not well understood fisheries management should be conservative; seeking to minimize the risk of stock collapse. One way to achieve this goal is to attempt to manage a population so as to maintain some minimum level of stock abundance. Another approach is to preserve a level of reproductive stock that will produce good year classes. Tacitly assumed in each of these approaches is that there is a relationship between spawners and recruits. Results of the spawner-recruit analysis presented here allow both a direct and indirect estimate of minimum spawning biomass thresholds.

The density-dependent catchability coefficient reported here has never before been demonstrated in pollock. The result is not surprising considering that pollock school heavily and fleets that exploit them use highly sophisticated fish-locating techniques. This has been suggested in a theoretical model by Paloheimo and Dickie (1964). Density-dependent catchability is a prominent feature in pelagic species that school heavily. The mechanism behind a density-dependent catchability is as follows: As density declines the school size may stay constant and fishing success on schools remains constant. However as abundance declines, each unit of effort removes a larger proportion of the total population. This finding has serious fisheries management implications. Ulltang (1980) has shown that when the catchability coefficient is density-dependent, any increases in fishing effort accompanied by decreasing recruitment may lead to exponential increase in fishing mortality.

The three pieces of evidence presented here all suggest that density-dependence is a feature of pollock population dynamics. Unfortunately the problem of ascertaining how all of these factors simultaneously affect stock dynamics is extremely complex. The only effective way to quantitatively deal with each of these features is to use age-structured simulation modelling to investigate the simultaneous effects of each density-dependent factor on the yield and the stocks response to exploitation.

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Table 1. The five-point maturity scale used to determine maturity condition for male and female walleye pollock in the Gulf of Alaska.

MALES		
CODE	CONDITION	DESCRIPTION
1	Immature	Testes thread-like, contained within a transparent membrane.
2	Developing	Testes uniformly ribbon-like. Surface of testes appear smooth and uniformly textured.
3	Mature	Testes large and highly convoluted; sperm cannot be extruded. Body wall incision causes gonads to be expelled from opening.
4	Spawning	Testes milk freely or extrude sperm when compressed.
5	Spent	Testes large but flaccid, watery, and bloodshot.
FEMALES		
CODE	CONDITION	DESCRIPTION
1	Immature	Ovaries small, transparent and tapered.
2	Developing	Ovaries tapered, forming two distinct lobes having well developed red blood vessels. Ovaries may be partially granular (some distinct ova).
3	Mature	Ova distinctly visible but cannot be extruded when ovaries are compressed. Ovaries are two large, distinct lobes. Body wall incision causes gonads to be expelled from opening.
4	Spawning	Ova extruded when gonads are compressed or ova are loose in ovaries.
5	Spent	Ovaries large but flaccid and watery. Ovaries may contain remnants of disintegrated ova and associated structures.

Table 2. Data from the Gulf of Alaska walleye pollock stock assessment (Megrey 1988a) used in the spawner-recruit analysis.

Spawn Year (y)	Recruit Year (y+ δ)	Biomass		Numbers	
		Spawning Population (million t)	Age 3 Recruits (million t)	Spawners as Eggs (trillions)	Age 3 Recruits (billions)
1973	1976		0.176		0.421
1974	1977		0.146		0.351
1975	1978		0.583		1.398
1976	1979	0.869	0.821	372	1.971
1977	1980	0.752	0.683	323	1.637
1978	1981	1.008	0.955	432	2.291
1979	1982	1.501	0.541	646	1.296
1980	1983	1.824	0.130	782	0.312
1981	1984	2.236	0.124	958	0.298
1982	1985	2.258	0.024	968	0.058
1983	1986	1.765	0.098	758	0.234
1984		1.217		523	
1985		0.676		291	
1986		0.356		153	

Age	Weight (kg)	Length (cm)	Maturity	Fecundity
3	0.417	39.98	0.82	177942
4	0.565	44.20	0.97	242272
5	0.637	45.99	0.98	273670
6	0.686	47.13	0.99	295071
7	0.760	48.75	1.00	327437
8	0.839	50.37	1.00	362046
9	0.872	51.01	1.00	376518
10	0.855	50.68	1.00	369062

Table 3. Results from fitting the logistic response function to Gulf of Alaska walleye pollock length-maturity data, 1983-1988 by the method of maximum likelihood.

Data Source	Year	α	SE(α)	β	SE(β)	Sample Size	Length at 50% Maturity
MALES							
Hydroacoustic	1983	-16.17	2.32	0.48	0.06	3641	33.70
Hydroacoustic	1984	-22.90	3.09	0.65	0.08	2867	35.44
Commercial	1984	-18.29	0.48	0.52	0.01	9521	34.91
Hydroacoustic	1985	-16.04	3.31	0.41	0.08	1805	38.81
Hydroacoustic	1986	-17.32	2.13	0.44	0.05	1175	39.13
Hydroacoustic	1987	-12.43	1.53	0.31	0.03	677	39.44
Hydroacoustic	1988	-11.94	1.41	0.31	0.04	975	38.34
FEMALES							
Hydroacoustic	1983	-14.57	2.78	0.40	0.07	2460	36.81
Hydroacoustic	1984	-22.58	2.73	0.60	0.07	2889	37.41
Commercial	1984	-16.01	0.64	0.44	0.02	8673	36.58
Hydroacoustic	1985	-19.08	3.91	0.46	0.09	2091	41.67
Hydroacoustic	1986	-19.94	2.78	0.47	0.06	1178	42.21
Hydroacoustic	1987	-15.35	2.04	0.34	0.04	733	44.59
Hydroacoustic	1988	-10.96	0.99	0.25	0.03	946	44.41

Table 4. Results of the spawner-recruit nonlinear regression analysis. Presented are the parameter estimates, their standard errors, residual sum of squares (RSS) and the r-squared value.

Model	Parameters	Spawner-recruit Units	
		Biomass	Numbers
Ricker	α	5.35	0.030
	SE(α)	1.50	0.009
	β	2.02	0.005
	SE(β)	0.27	0.001
	RSS	0.18	1.03
	R^2	82.4	83.5
Shepherd	α	3.38	0.02
	SE(α)	2.13	0.01
	β	0.58	248.52
	SE(β)	0.18	82.94
	τ^*	2.621479	2.627812
	RSS	0.26	1.51
	R^2	74.8	75.7

* - parameter constrained to a constant value.

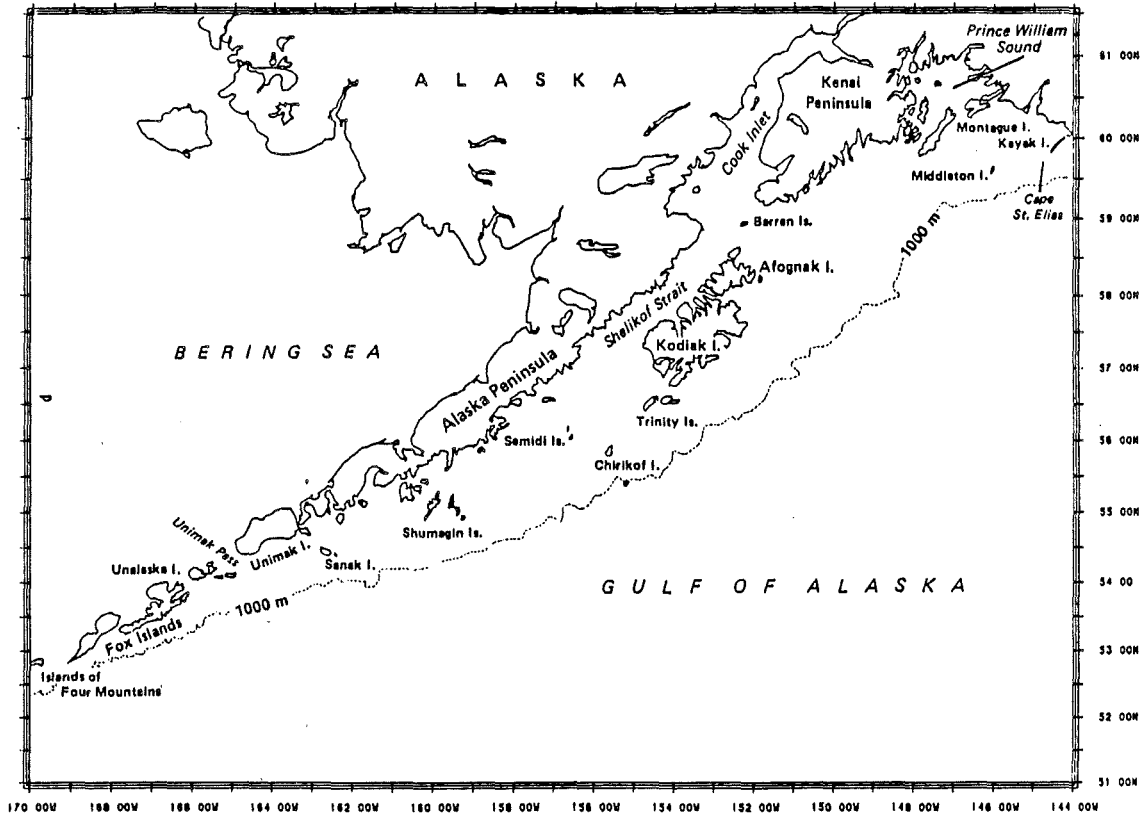


Figure 1. Geographical areas of the central and western Gulf of Alaska.

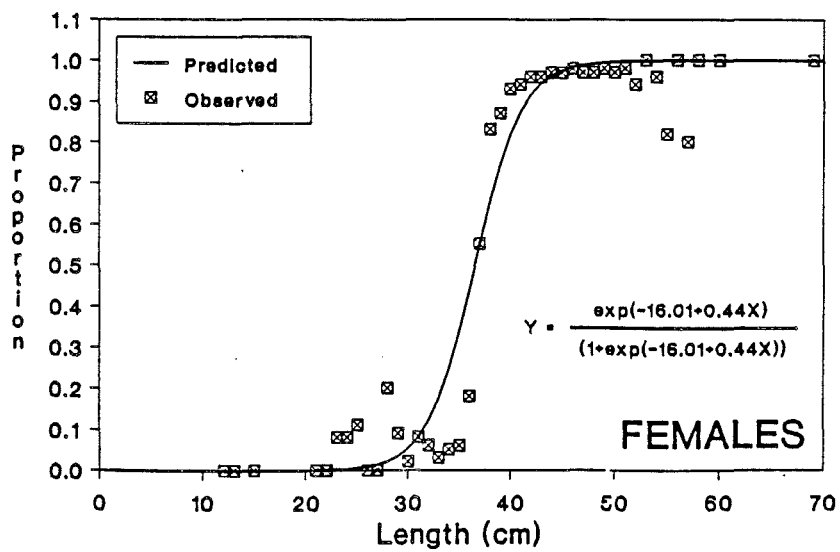
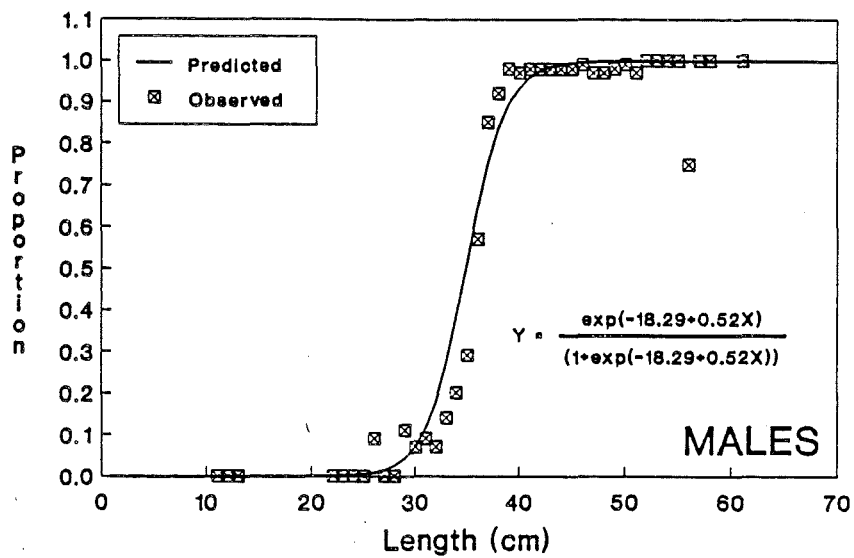


Figure 2. Maturity ogives and length-maturity relationship for male and female Gulf of Alaska walleye pollock as estimated with maximum likelihood procedures. Data collected during the spring 1984 joint venture fishery.

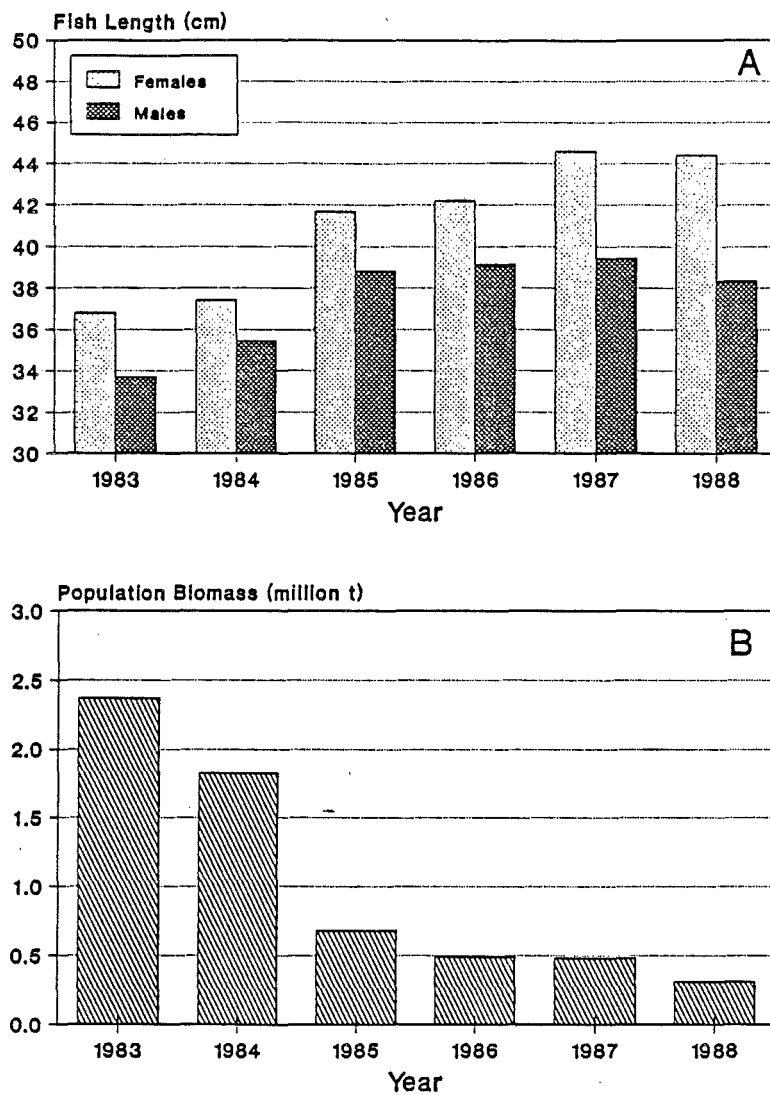


Figure 3. Annual trends in estimates of size at 50% maturity for male and female walleye pollock (panel A) and total population abundance (panel B) from Gulf of Alaska hydroacoustic surveys, 1983-1988.

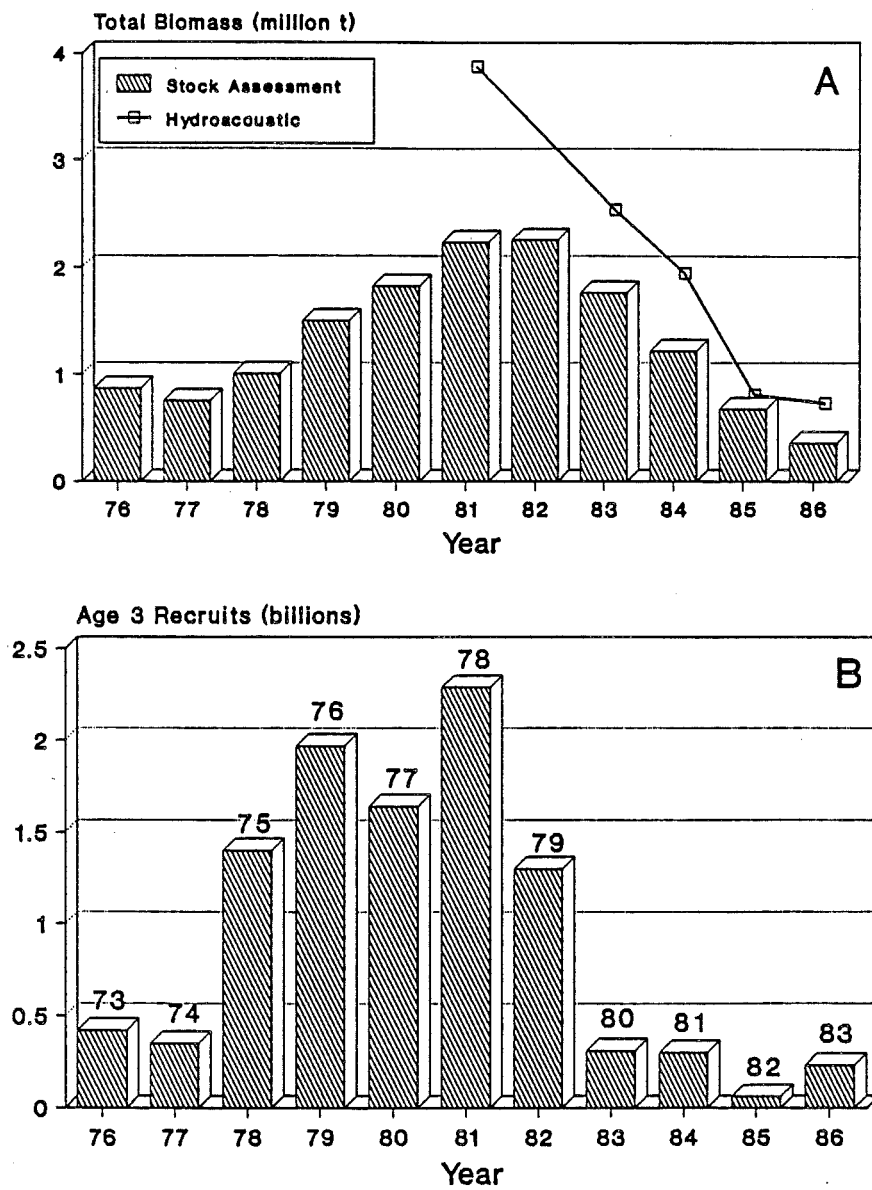


Figure 4. Trends in population biomass (panel A) and age 3 recruit abundance (panel B) of Gulf of Alaska walleye pollock as estimated from an application of the CAGEAN stock assessment model to the all-nation catch-at-age data set. Year classes are labeled above each bar in the lower figure.

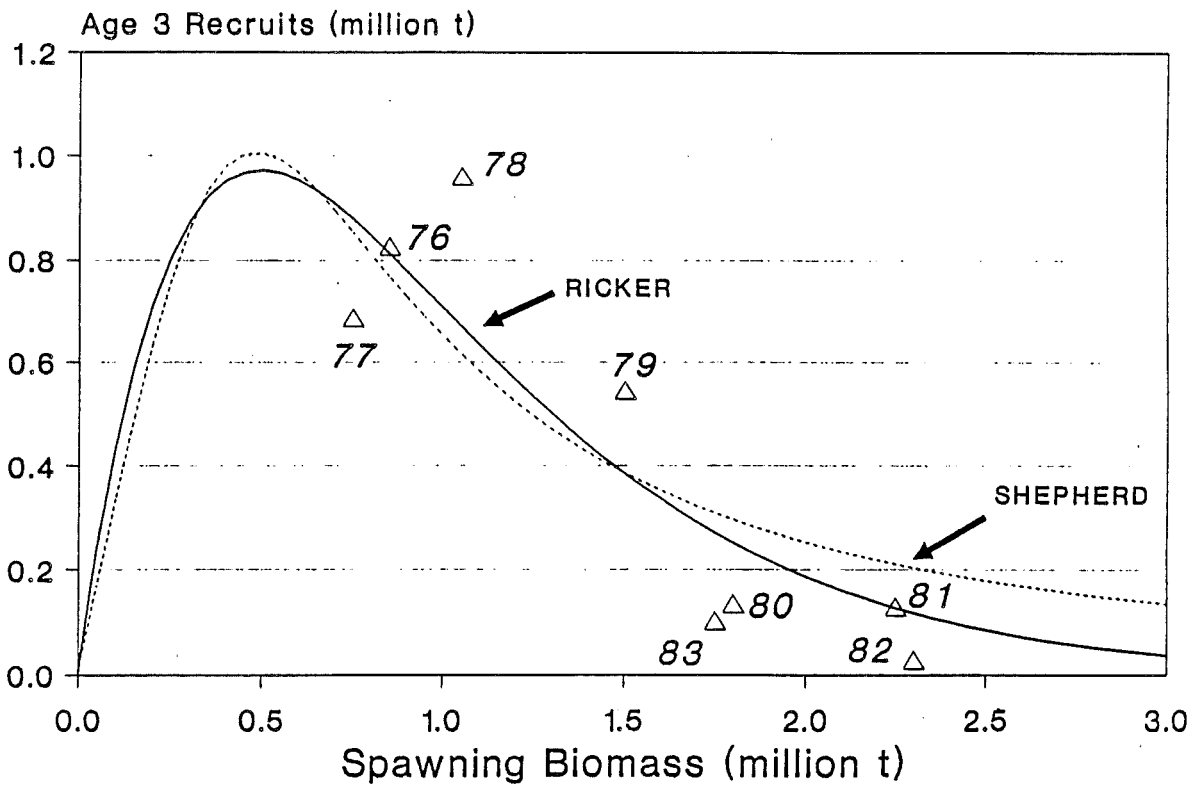


Figure 5. Comparison of two Gulf of Alaska walleye pollock spawner-recruit relationships plotted against the raw data from the biomass-based analyses. Observed data points are labeled by calendar year.

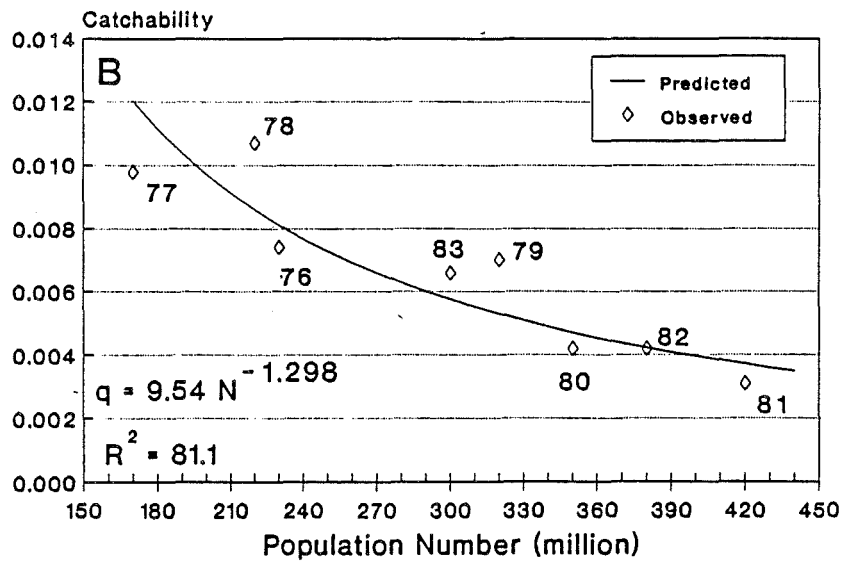
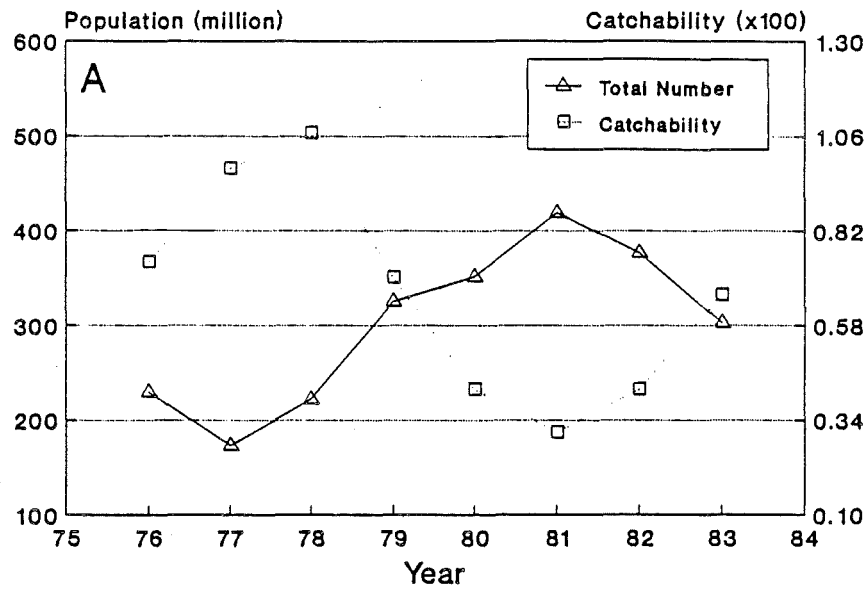


Figure 6. The association between the catchability coefficient and stock size plotted against calendar year (panel A) and the estimated relationship between catchability and stock size (panel B) of Gulf of Alaska walleye pollock, as estimated from application of the Fournier and Archibald stock assessment model to the Japanese catch-at-age and standardized effort data set.

NATURAL MORTALITY AND FISHING MORTALITY OF REARED JUVENILE
COD (Gadus morhua L) RELEASED IN THE SEA

by

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ABSTRACT

An enhancement study of coastal cod was started in Austevoll in western Norway in 1983. Important objectives of the study were investigation of mortality patterns of the released fish. Natural mortality (M) and fishing mortality (F) were estimated using Rickers two-release method, and Virtual population analysis (VPA).

The released cod recruited to the local fishery as II-group. The results show a low survival (12-34 %) in the pre-recruit period. The high pre-recruit mortality was attributed to predation and cannibalism, and both size and density dependent effects were suggested. Natural mortality of cod larger than 30 cm was estimated to 0.11 year⁻¹. After recruitment to the fishery, the mean fish mortality was estimated to 0.49 year⁻¹.

INTRODUCTION

An enhancement experiment with reared juvenile cod was started in Austevoll in western Norway in 1983 (Svåsand, 1985). The objectives of the project were to study mortality and migration pattern of released cod, and investigate possible biological, behavioural, and genetic differences between reared and wild cod. The results from studies of migration pattern of released reared cod (Svåsand and Godø, 1987), recruitment patterns of reared and wild cod to a local spawning stock (Svåsand, Jørstad and Kristiansen, in press), comparisons of growth and prey preferences between wild and released cod (Svåsand and Kristiansen, 1985; Kristiansen, 1987), and evaluation of different tagging and release methods (Svåsand, Kristiansen and Næss, 1987) have been reported earlier.

This paper presents the results of investigations on natural and fishing mortality of different size groups of reared cod released as 0 and I-group. Effects of fish size, age at release and 0-group density on pre-recruit survival are discussed.

MATERIAL AND METHODS

Tagging and release

Most of the cod juveniles in this experiment were reared in Hyltøpollen, a dammed seawater pond at Austevoll (Øiestad, Kvenseth and Folkvord, 1985). Some of the juveniles released in 1984 were reared in a seawater basin (Øiestad, Kvenseth, and Pedersen, 1984). The released fish were tagged with Floy FD-67C anchor tags, and after tagging, the cod were kept for at least four hours to remove fish dead or injured due to tagging. The cod were then transported to the release sites in Heimarkspollen (Fig. 1) in 1 m³ tanks with oxygen supply, and the fish were set free in shallow near shore waters.

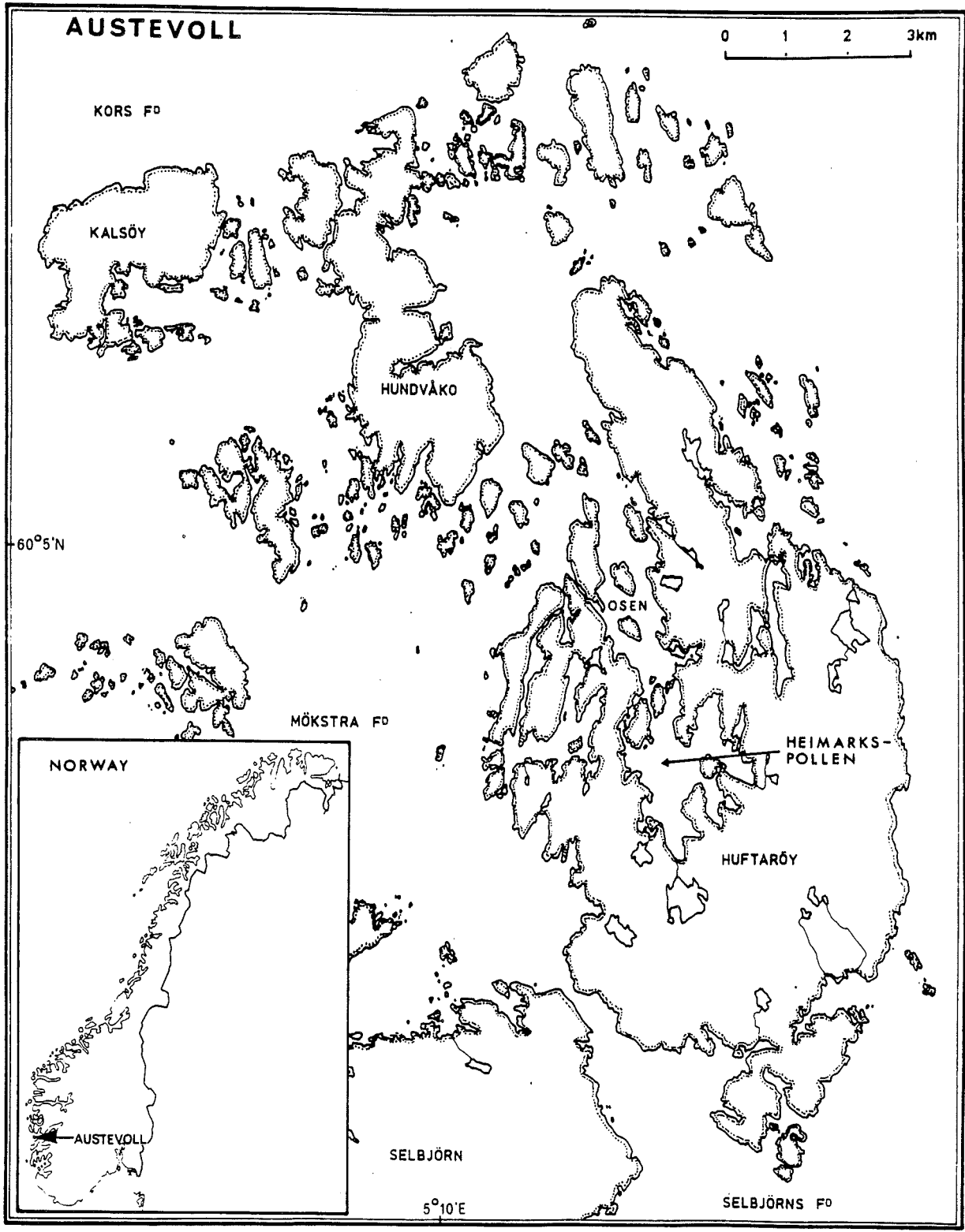


Fig. 1. Map showing the location of Heimarkspollen, the release area of juvenile cod at Austevoll.

Groups of wild and recaptured reared cod (> 30 cm) have also been tagged and released in Heimarkspollen. These groups were prior to tagging, caught in Heimarkspollen.

The releases of Floy tagged cod in Heimarkspollen are summarized in Table 1.

In 1983 reared cod were also released at other areas than Heimarkspollen (Svåsand and Godø, 1987). In 1984, groups of reared cod, tagged with Internal steel tags were in addition to the Floy tagged fish, released in Heimarkspollen (Svåsand et al., 1987). Recaptures from these groups were not used in this report.

Table 1. Number and fish size (no. measured and mean length with SD) of eight groups of reared cod (83-85 yearclass) and two groups of wild and recaptured reared cod (W1 and W2) released in Heimarkspollen.

GROUP	RELEASE** PERIOD	NO. RELEASED	L E N G T H			W E I G H T		
			N	Mean (cm)	SD	N	Mean (g)	SD
A83	Sep-Nov 83	2,923	569	17.6	1.5	*		
A84-1	Nov-Dec 84	1,575	581	15.9	1.4	578	39.5	11.6
A84-2	Nov-Dec 84	1,585	535	18.6	1.7	534	65.1	19.9
A84-3	Nov-Dec 84	594	194	21.2	1.3	194	97.1	17.2
S84****	Apr 85	449	440	21.4	2.4	440	104.0	35.8
A85	Sep-Oct 85	7,790	376	16.2	1.6	376	47.1	16.0
S85-1	Apr 86	840	99	18.1	1.4	99	57.7	12.8
S85-2	Apr 86	2,144	98	21.5	1.4	98	101.0	23.3
W1	Nov 86-Febr 87	86	86	36.9	6.2	*		
W2	Nov 87-Febr 88	505	505	40.5	9.4	*		

* Not measured

** The release date were set as the middle of the release period

**** Length and weight were measured 13-14 February 1985

Release area

Heimarkspollen is an almost landlocked fjord (2,9 km²) at Huftarøy, the largest island of the Austevoll archipelago (Fig. 1). The maximum depth is 120 m, and more than 1/3 of the fjord is shallower than 40 m. The bottom consists mainly of rock and boulders, but there are also areas with sandy or muddy bottom. The connection to the outside fjord is through three narrow inlets, where the largest is about 3 m deep and 30 m wide. The salinity below 5 m varies between 30-32.5 ppt, and is slightly lower than in the outside fjord.

Tag returns and fishing surveys

The tagging experiments were announced in newspapers, and a pamphlet including registration forms (Svåsand, 1985) on which to record information on recaptured cod (tag. no., place, depth, and time of recapture, length, weight, fishing gear, and no. untagged cod in the catch) was sent to local fishermen and households near the release sites. A reward of 25 NOK. was offered for every returned tag.

Periodic fishing in Heimarkspollen began in May 1984 (Svåsand and Kristiansen, 1985; Kristiansen, 1987; Svåsand et al., 1987). As the rocky bottom prohibits trawling or seining, trammel nets, with small meshed (45-104 mm) loosely hung inner nets were used. To catch cod smaller than 20 cm, we used small meshed gill nets (39 mm mesh length). The nets were placed randomly in the shallow part (2-30 m depth) of the fjord.

Tagged fish liberated in the sea after recapture were not included in the tag returns. After February 1988, no cod were set free after recapture.

Methods for estimating of natural and fishing mortality

Total mortality (or survival) for given periods was estimated using Rickers two-release method (Ricker, 1958). This method gives an estimate of survival for a period of time, by making a release (of marked individuals) at the beginning and at the end of the period, followed by sampling after the last release. Using this method, it must be assumed that every marked individual alive just after the second release has the same probability of surviving to the time of the sampling and being caught in the sample. Ricker (1958) gives following estimators:

$$S = [m_1(R_2+1)] / [(m_2+1)R_1]$$

$$\text{Var}(S) = S^2 - [m_1(m_1-1)(R_2+1)(R_2+2)] / [R_1(R_1-1)(m_2+1)(m_2+2)]$$

where

- S = probability of survival between releases
- R₁ = number released at the beginning of the period
- R₂ = number released at the end of the period
- m₁ = number from the R₁ group, caught in the sample
- m₂ = number from the R₂ group, caught in the sample

Virtual population analysis (VPA) was used to back calculate numbers alive, and fishing mortality in time intervals (quarter years) according to the following equations (Sims, 1985):

$$C_i/N_{i+1} = F_i(\exp(Z_i)-1)/Z_i$$

$$N_i = N_{i+1}\exp(Z_i)$$

where

- C_i = catch in the time period i
- M_i = instantaneous natural mortality in time period i
- F_i = instantaneous fishing mortality in time period i
- N_i = stock size at the beginning of time period i
- $Z_i = F_i + M_i$ = total instantaneous mortality in time period i

All mortality rates are given per year. One time period (i) was set to a quarter year, and the catch equation was solved for F_i using the bi-section method (Burden and Faires, 1985).

Estimation of mortality rates

Survival of the released groups to January 1988 were estimated by Rickers two-release method, by using the released number of each group as R_1 , and the 505 newly released cod (W_2) as R_2 . The W_2 group consisted of both wild and recaptured reared cod (> 30 cm), caught alive in Heimarkspollen. Subsequent recaptures after the release of group W_2 were used as samples (m_1 and m_2).

VPA was used to back calculate numbers alive (N) and fishing mortality (F) at age intervals from January 1988 to the beginning of quarter 8 (age = 21 months). The tag returns were used as catch data (C), and natural mortality (M) was assumed to be equal and constant for all groups from age II (age > 21 months).

Natural mortality (M) used in the VPA was estimated by releasing two groups of large tagged cod (length > 30 cm) with an interval of one year between the releases (W_1 , January 87 and W_2 , January 88). Survival between the two releases was estimated by Rickers two-release method, and natural mortality in the period was estimated by trying different values of M in the VPA until the back calculated number at the time of release of W_1 was the same as the number released.

Mortality the first six months after release was estimated for the group released in the autumn 1985 (A_{85}) by releasing two groups of reared tagged cod in April 1986 (S_{85-1} , S_{85-2}). After the last releases, a fishing survey in the area was conducted in the period 22 April - 6 May 1986. In this survey a total of 142 trammel nets (45-48 mm mesh lengths) and 71

gill nets (39 mm mesh length) were set, randomly distributed in the shallow part (2-30 m depth) of Heimarkspollen. In this experiment, the two groups released in April were treated as one group. The groups released in April had been kept in a net cage during the winter and had been fed dry pellets.

RESULTS

Tag returns

To 1 October 1988, 3,261 tags were recovered from the released groups. Of the total tag returns, 426 (13.1 %) were recovered in the fishing surveys in Heimarkspollen, and 2,835 (86.9 %) were reported by local fishermen and leisure anglers in Heimarkspollen and other areas. Place of recapture were reported for 2,875 (88.2 %) cod. Most cod were recaptured in Heimarkspollen (2,538), 264 were recaptured in Osen (Fig. 1), and 73 in other areas. The percentage emigrants from Heimarkspollen in the released groups varied between 8 and 18 % (Fig. 2).

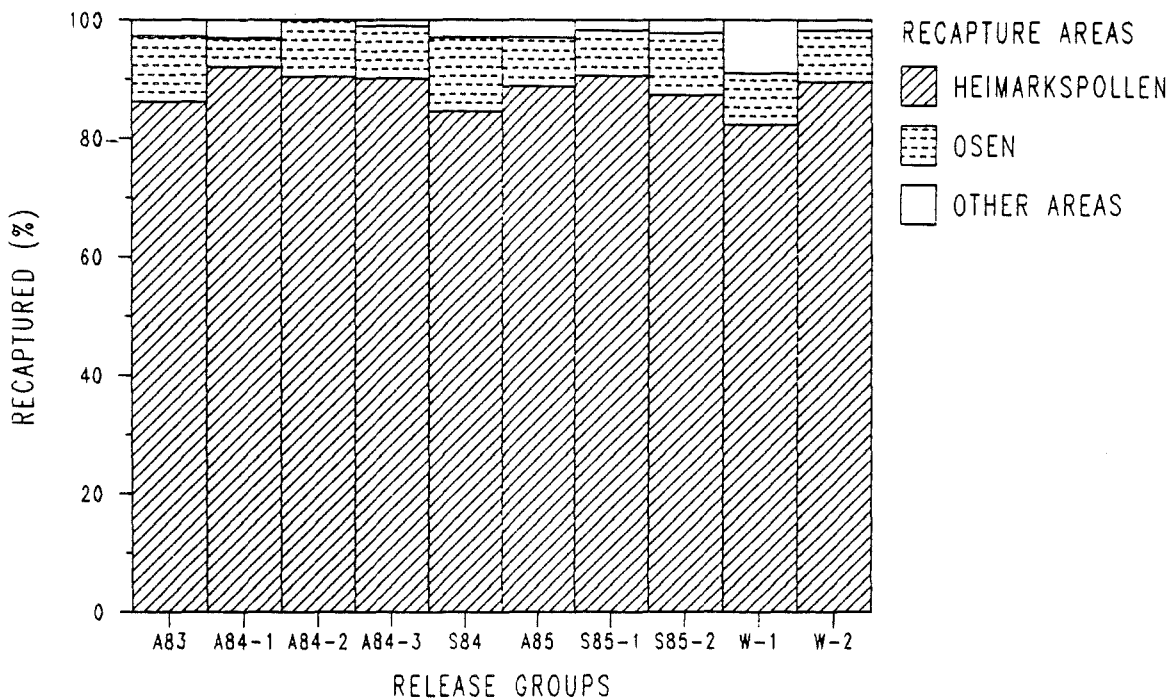


Fig. 2. Distribution of recapture areas of the released groups in Heimarkspollen.

From the reared groups the recapture rates increased after release to a maximum when the cod were about 2 years old (Table 2). Between 11.4-25.5 % were recaptured, and the mean age at recapture varied between 2 and 2.5 years. From most of the groups there was a marked decline in recapture rates of fish older than three years.

Table 2. Tag returns to 1 October 1988 in age intervals (quarter years), and total number and percentage recovered tags of the reared groups released in Heimarkspollen.

AGE IN QUARTER YEARS	AGE GROUP	R E L A S E G R O U P S							
		A83	A84-1	A84-2	A84-3	S84	A85	S85-1	S85-2
?"		8	6	6	0	1	48	1	12
3	0	4	0	2	2	0	63	0	0
4	I	2	7	9	5	0	48	0	0
5	I	35	13	29	8	17	196	18	110
6	I	88	16	27	16	21	169	17	95
7	I	66	13	21	13	9	113	11	36
8	II	52	14	31	13	13	53	5	25
9	II	72	20	27	17	15	112	13	64
10	II	101	24	41	11	13	100	22	63
11	II	48	12	6	8	3	50	13	27
12	III	31	14	6	2	1	33	6	36
13	III	37	14	18	5	7	59	10	52
14	III	43	9	19	12	3	38	8	26
15	III	20	4	9	4	1			
16	IV	10	5	9	4	0			
17	IV	15	5	6	6	5			
18	IV	17	3	3	2	1			
19	IV	12							
20	V	7							
21	V	9							
22	V	4							
All Age groups		681	179	269	128	110	1,082	124	546
% Rec.		23.3	11.4	17.0	21.6	24.5	13.9	14.8	25.5

* Date of recapture not given

From the two groups of large cod, 46.5 % were recaptured 21 months after release of W1 and 20.2 % were recovered 9 months after release of W2 (Table 3). Larger fish were released in these groups (length > 30 cm), and high recapture rates were found already in the first quarters after liberation.

Table 3. Tag returns to 1 October 1988 in time intervals (quarter years), and total number and percentage recovered tags of the two groups of large cod released in Heimarkspollen.

TIME INTERVAL	RELEASE GROUPS	
	W1	W2
IN QUARTER YEARS		
Jan 87 - Mar 87	1	
Apr 87 - Jun 87	18	
Jul 87 - Sept 87	7	
Oct 87 - Dec 87	4	
Jan 88 - Mar 88	0	23
Apr 88 - Jun 88	9	49
Jul 88 - Sept 88	1	30
Total	40	102
% Rec.	46.5	20.2

Recruitment to the local fishery

The fishery in Heimarkspollen is mainly a leisure fishery by locals, and weekend and holiday visitors, fishing with hooks, lines, and trammel nets. As shown in Fig. 3, the released fish recruited to the fishery the first summer after release. Highest recapture rates were reached between quarter 6 and 10 (of age), indicating full recruitment to the fishery already as II-group, when the mean lengths in most of the groups were > 30 cm (Fig. 4).

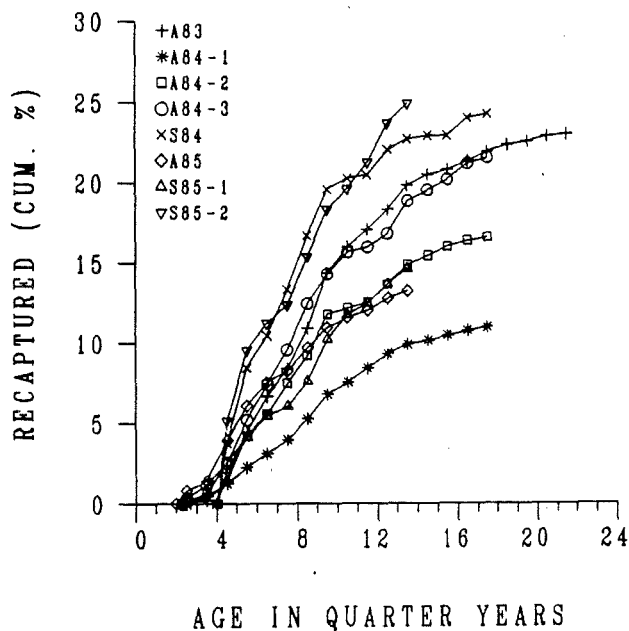


Fig. 3. Cumulative percentage recovered tags in age intervals from the reared groups released in Heimarkspollen.

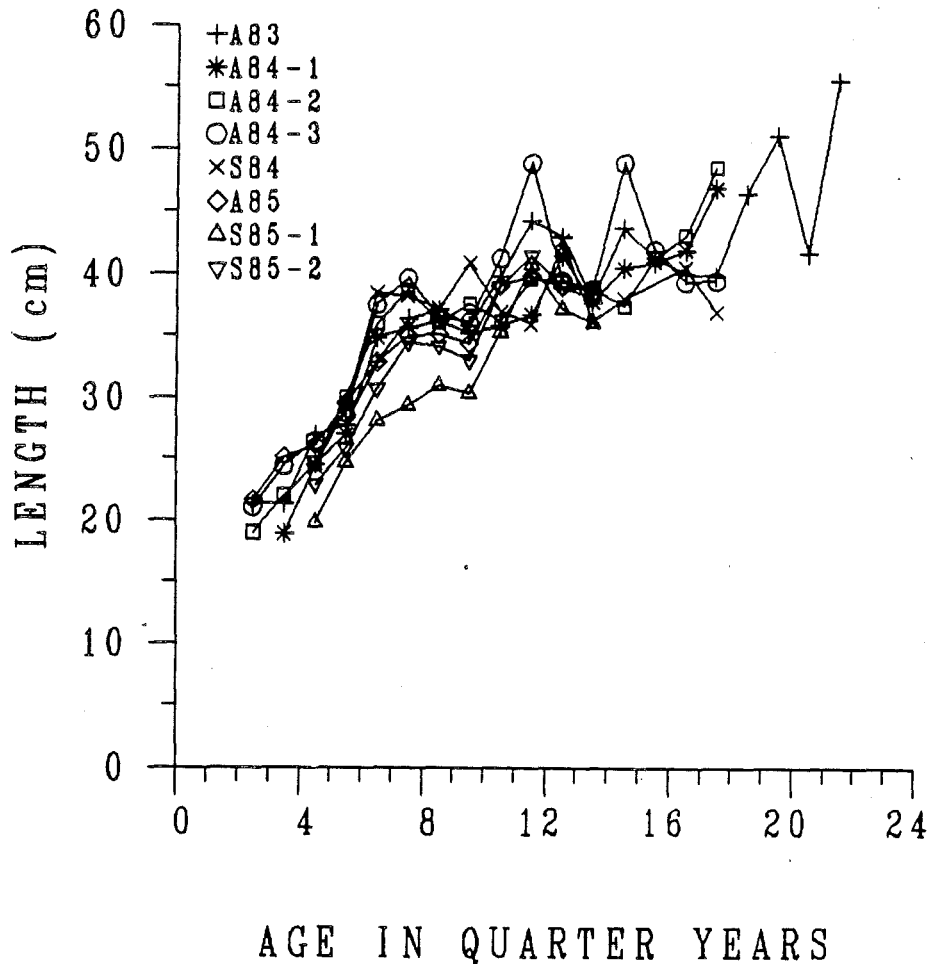


Fig. 4. Mean length at age at recapture of the reared groups released in Heimakspollen.

Mortality of cod in Heimakspollen

The upper limit of the 95 % confidence intervals of S ($S+2SD$; Table 4) shows that less than 12.5 % and 4.5 % survived to the IV and V-group stages, respectively. E.g., of the 2,923 cod released in 1983, less than 120 were alive in January 1988.

Survival 12 months after release of group W1 (large cod) was estimated to 57.1 % ($SD = 17.7 \%$), or 49 fish (Table 4). During 1987, 30 cod were recaptured from W1 (Table 3). These results were used in a VPA to estimate natural mortality of cod larger than 30 cm. An estimated value of $M = 0.11$ was found (Table 5).

Table 4. Estimates of survival (S with SD, and 95 % confidence interval of N) between release and January 1988 of the released groups in Heimarkspollen. The estimates are based on Rickers-two release method.

R1 : No. cod liberated in the first release (Table 1); m1: No. cod recaptured from the first release after February 1988. In the second release (W2), 505 fish (R2) were tagged and 102 fish (m2) were recaptured after February 1988.

RELEASE GROUP	R1	m1	ESTIMATED SURVIVAL				
			S %	SD(S) %	$N_{(-2SD)}$	N	$N_{(+2SD)}$
A83	2,923	16	2.7	.7	37	79	120
A84-1	1,575	14	4.4	1.2	30	69	107
A84-2	1,585	11	3.4	1.1	20	54	88
A84-3	594	9	7.4	2.5	14	44	74
S84	449	6	6.6	2.7	5	30	54
A85	7,790	108	6.8	.9	393	531	668
S85-1	840	22	12.9	2.9	59	108	157
S85-2	2,144	97	22.2	2.9	351	477	602
W1	86	10	57.1	17.7	19	49	56*

* Number released - number recaptured

Table 5. Results from the VPA on recaptured cod from release group W1. Estimate of N_{i+1} in the last interval (Oct-Dec) are given in Table 4. VPA was executed with different values of natural mortality (M_i) until the calculated value of N_i in the first interval (Jan-Mar) corresponded to the number released (86). An estimated value of $M_i = 0.11$ was found.

TIME INTERVAL IN QUARTER YEARS (i)	N_i	N_{i+1}	C_i	F_i
Oct 87 - Dec 87	54	49	4	.31
Jul 87 - Sept 87	63	54	7	.48
Apr 87 - Jun 87	83	63	18	.99
Jan 87 - Mar 87	86	83	1	.05

The estimated value of natural mortality, the estimated numbers alive January 1988 (Table 4), and the reported tag returns (Table 2) were used as input in a VPA (Table 6). The resulting mortality curves are shown in Fig. 5, and estimates of number and percentage surviving to the II-group stage (age 21 months) are summarized in Table 7. These results show that only 11.9-33.7 % of the released fish survived to the II-group stage (pre-recruit survival).

Table 6. Results from the VPA on recaptured cod older than 21 months. Estimates of N_{t+1} in the last interval are given in Table 4, and the C_t values are given in Table 2. An estimated value of $M_t = 0.11$ of recruited cod were used (Table 5).

i	N_t	N_{t+1}	C_t	F_t	i	N_t	N_{t+1}	C_t	F_t
GROUP A83					GROUP S84				
19	93	79	12	.56	15	32	30	1	.13
18	113	93	17	.66	14	36	32	3	.36
17	132	113	15	.49	13	44	36	7	.71
16	145	132	10	.29	12	46	44	1	.09
15	170	145	20	.51	11	50	46	3	.25
14	218	170	43	.89	10	65	50	13	.91
13	262	218	37	.62	9	82	65	15	.82
12	300	262	31	.44	8	97	82	13	.58
11	357	300	48	.59					
10	470	357	101	.98					
9	556	470	72	.56					
8	624	556	52	.35					
GROUP A84-1					GROUP A85				
15	75	69	4	.22	11	596	531	50	.36
14	86	75	9	.45	10	714	596	100	.61
13	103	86	14	.59	9	848	714	112	.58
12	120	103	14	.50	8	925	848	53	.24
11	135	120	12	.38					
10	163	135	24	.65					
9	188	163	20	.46					
8	208	188	14	.28					
GROUP A84-2					GROUP S85-1				
15	65	54	9	.61	11	124	108	13	.45
14	86	65	19	1.02	10	150	124	22	.64
13	106	86	18	.75	9	167	150	13	.33
12	115	106	6	.22	8	177	167	5	.12
11	125	115	6	.20					
10	170	125	41	1.12					
9	202	170	27	.58					
8	239	202	31	.56					
GROUP A84-3					GROUP S85-2				
15	49	44	4	.36	11	518	477	27	.22
14	63	49	12	.86	10	596	518	63	.45
13	70	63	5	.30	9	677	596	64	.40
12	74	70	2	.11	8	722	677	25	.14
11	84	74	8	.41					
10	97	84	11	.49					
9	117	97	17	.64					
8	134	117	13	.42					

The pre-recruit survival of groups of different mean size (length) at release, liberated the same year (A84-1, A84-2, A84-3, and S85-1, S85-2) increased with increasing size at release, indicating a size selective mortality. The increase in survival was most clear for fish larger than 20 cm at release.

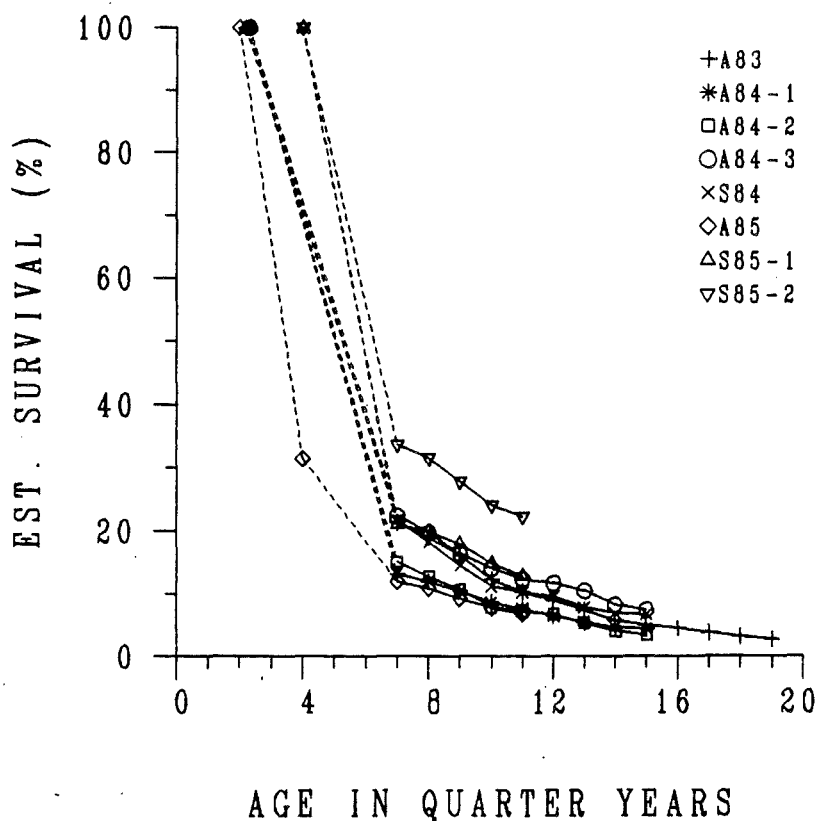


Fig. 5. Estimated survival of the reared groups from release to January 1988. The figure are based on Tables 1&6. The first six months survival of group A85, is based on Table 8.

The pre-recruit survival of groups of similar fish size, released in years with different yearclass abundance (A83, A84-1, A85) indicated a density dependent mortality on the 0 and I-group stages (Table 7). The highest pre-recruit survival was found in group A83 (21.3 %), and the lowest in A85 (11.9 %). The estimated 0-group abundances in September-November increased from 4,500-5,900 in 1983, via 11,000-13,400 in 1984, to 17,200-23,600 in 1985 (Table 7).

Table 7. Estimates of pre-recruit survival (from release to II - group) compared to mean length at release and 95 % confidence intervals of the 0-group abundance of wild and released cod in September-November.

RELEASE GROUP	No.	MEAN LENGTH AT RELEASE (cm)	0-GROUP ABUNDANCE*		PRE-REC. SURV.	
				(x 1,000)	N _a	%
A83	2,923	17.6	4.5	5.9	624	21.3
A84-1	1,575	15.9	11.0	13.4	208	13.2
A84-2	1,585	18.6	11.0	13.4	239	15.1
A84-3	594	21.2	11.0	13.4	134	22.6
S84	449	21.4	11.0	13.4	97	21.6
A85	7,790	16.2	17.2	23.6	925	11.9
S85-1	840	18.1	17.2	23.6	177	21.1
S85-2	2,144	21.5	17.2	23.6	722	33.7

* From Kristiansen (1987)

For II-group and older cod, fishing mortality was the most important cause of death (Table 6). Assuming equal and constant natural mortality of all groups ($M = 0.11$), the mean annual fishing mortality was 40 % (mean F of all groups 0.49). Highest values of F were found in the summer season (April-September).

For younger cod (0 and I-group), natural mortality was by far most important. The estimate of the survival the first six months after release of group A85, was 45.6 % (Table 8) or $Z = 1.57$. The fishing mortality in this period was insignificant ($F < 0.03$).

Using estimated number alive at age 12 months (Table 8) and the back calculated number alive at age 21 months (Table 4), the mortality from April 1986 to January 1987 was 74 % ($Z = 1.79$). The fishing mortality in this period had increased ($F = 0.36$), but the mean natural mortality was similar to the first period ($M = 1.43$).

Table 8. Estimates of survival (S with SD, and 95 % confidence interval of N) six months after release of group A85 (October 1985 - April 1986). The estimates are based on Rickers two-release method.

R1 : No. cod liberated in the first release (A85, Table 1),
R2 : No. cod liberated in the second release (S85, Table 1),
m1 : number of cod recaptured from R1, and
m2: number of cod recaptured from R2, in the fishing survey in April-May 1986.

RELEASE GROUP	Sample	ESTIMATED SURVIVAL		SURVIVAL		
		S %	SD(S) %	N _(-2SD)	N	N _(+2SD)
R1 (A85):	7,790; m1: 88	45.6	7.1	2,448	3,550	4,651
R2 (S85):	2,984; m2: 73					

DISCUSSION

The mortality patterns of the released reared cod, showed high natural mortality and low fishing mortality on young cod (0 and I-groups), and low natural mortality and high fishing mortality on older cod (II+ groups). The mortality patterns were estimated using Rickers two-release method and VPA, which both are subjected to errors.

The pre-recruit survival (to age 21 months) were underestimated, if the starting values of N in the VPA, the estimated natural mortality of II+ cod, or the reported tag returns were underestimated.

Rickers two-release method, used to estimate the starting N, assumes equal catchability of all groups after the release of the last group. This assumption may be violated in case of increased distribution with time after release, to areas with lower fishing intensity. As shown earlier less than 3 % of the recaptures were caught more than 5 km from the release sites, meaning that this source of error had probably small influence on the results.

Size selective fishing mortality may also cause errors if the size distribution of the groups are different. Comparisons of size distributions of recaptured II+ cod between fishing surveys and other tag returns showed no significant difference (Svåsand et al., 1987). This indicates that size selection of II+ cod in the local fishery was low.

If the assumptions in the Rickers two-release method are followed, the accuracy is dependent on sample size and number released in the groups (Seber, 1982). In this study the 95 % confidence intervals of survival (S) to January 1988 were in the range $\pm 26-52$ % of the estimates. This may influence the differences in survival between the groups, but as these errors are supposed to be random, the trend in survival of the groups were probably not influenced.

Estimates of natural mortality of coastal cod in western Norway have not previously been made. In the multispecies VPA used in the North Sea, $M = 0.35$ (II-group), $M = 0.25$ (III-group) and $M = 0.2$ (IV+ groups) were used (Anon., 1988). Compared to these results, the natural mortality estimated in Heimarkspollen (II+ groups) is low ($M = 0.11$). However, an increase in M to North Sea level ($M = 0.3$), will only give a minor increase of the survival estimates.

Different exposure time to errors in the VPA parameters (N,M,C) may change the relative difference in survival between groups, compared to the true values. E.g, the effect of wrong starting values of N in the VPA decreases with accumulated fishing mortality (Ulltang, 1977). However, within probable error limits the range of the groups will not be altered.

To illustrate this, a 20 % increase in the starting value for

N (1.2N) in the VPA, will increase the pre-recruit survival of the group with highest estimated survival (S85-2) from 33.7 % to 38.6 %, a 20 % increase in the catch data (1.2C) will increase the pre-recruit survival to 36.3 %, while increase in M from 0.11 to 0.3 increases the survival to 39.8 %. Similar values for the group with lowest survival (A85) give increases in pre-recruit survival from 11.6 % to 13.6 % (1.2N), 12.7 % (1.2C), and 13.9 % (M = 0.3), respectively.

The difference in pre-recruit survival of different size groups released the same year, indicated size dependent mortality. The most probable reasons for the pre-recruit mortality of cod in this area are cannibalism and predation from pollack (Pollachius pollachius) (Svåsand and Kristiansen, 1985; Salvanes, 1986). As the cod grow in size, there will be fewer and fewer potential predators in the area, and the risk of predation will decrease. Stomach contents analysis of cod (E.g. Daan, 1973; Edwards and Bowman, 1979) showed that number of fish (10-30 cm) decreased with increased prey size, and that fish larger than 30 cm were seldom eaten. This indicates that size at release and time spent to grow through the "predation field" will affect the survival of released cod, and may explain the observed size dependent mortality.

The results indicate a negative correspondence between survival and 0-group abundance. Indices of density dependent mortality have been observed on wild juvenile cod in the Belt Seas (Cushing, 1974), and in several studies on reared salmonids (E.g. Petermen, 1978, 1983; Carl, 1984). A study of the Georges Bank ecosystem have shown that if the production is food limited, the fish community may modify their own abundance by predation (Sissenwine, Overholtz and Clark, 1984). Density dependent mortality may be explained by stronger competition and slower growth rates, leading to increased vulnerability to predation and cannibalism. Because of the high size selective natural mortality, possible decreases in growth rates attributed to increased abundance are difficult to detect. In this study, no clear trends in growth rates between the released groups were found. Further studies will, however, be needed before these density dependent mechanisms are clarified for coastal cod in western Norway.

CONCLUDING REMARKS

In this report we have shown that the survival of released cod were probably both size and density dependent. With regard to future large scale enhancement programmes on cod, the results suggest that the cod should be reared to a size of at least 20 cm before release to reduce the risk of predation or cannibalism. Due to density dependent effects on growth and mortality the wild 0-group abundance ought to be monitored before deciding the number to be released. The size of the release should further be adjusted to the production of prey and abundance of competitors and predators. This aspects are now being investigated in a fjord in western Norway (Salvanes,

1986). These results, will together with the results from the Austevoll project, give important information on the future prospects of enhancements of coastal populations of cod.

The output from an enhancement program will also depend on management routines (Ulltang, 1984). The results in this report showed that the released groups were growth overfished. Before starting larger enhancement programmes, it will therefore be of great importance to investigate how the fishing pattern (no. gears and gear types) effects the yield.

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MORTALITY RATES DURING THE EARLY LIFE STAGES AND YEAR CLASS STRENGTH
OF THE ARCTO-NORWEGIAN COD (GADUS MORHUA L.)

by

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ABSTRACT

Abundance indices of Arcto-Norwegian cod based on trawl surveys at the 0-group stage (4 - 5 months old fish) and at the postlarval stage (2 - 3 months old fish) are converted to absolute numbers by evaluating the catch efficiencies of the survey trawls. Together with estimates of the egg production and virtual population analysis of fish at age 3 years, these data have been used to compute the instantaneous natural mortality rates during three pre-recruit periods: 1) egg/hatching larvae - post larvae, 2) post larvae - 0-group fish and 3) 0-group fish - 3 years old fish. The instantaneous natural mortality coefficient, m , decreases much from the period egg/hatching larvae - post larvae stage ($m=42 \text{ year}^{-1}$, or 10.9 per cent per day) to the period post larvae - 0-group stage (average $m=8 \text{ year}^{-1}$, or 2.2 per cent per day). Also the variation of mortality between years is considerably larger for the period before the time of the post larvae stage than for the period between the post larvae and the 0-group stage. In addition the larger part of the mortality variation in the period from post larvae to 0-group stage is correlated with the abundance at the postlarval stage (density dependent mortality). Consequently, the year class strength is mainly determined before the postlarvae stage, and therefore, reliable assessments of postlarvae abundance will have a prognostic value. The relation between the abundance of postlarvae and 0-group fish and the abundance at age 3 years, assessed from virtual population analysis, are discussed in the light of large ecological changes which occurred in the Barents Sea in 1984-1987. Even though the mortality rate is considerably lower after the 0-group stage, such large ecological changes may influence the year class strength after the 0-group stage.

INTRODUCTION

Since the start of the international 0-group surveys in the Barents Sea and the eastern Norwegian Sea, increasing effort has been put into distribution measurements of the early stages of fish in this region. In particular the Arcto-Norwegian cod has been subjected to a variety of field studies from the egg stage to the 0-group stage (See Bergstad, Jørgensen and Dragesund 1987 for a review). The main objectives of the larger part of these investigations have been to study conditions for larval survival and typical features of distribution, transport and spreading. Only a fraction of the studies allows quantitative abundance estimates. In general, the lack of such estimates has mainly two reasons: Firstly, during the egg and early larval stage it is a problem to measure the rapidly changing production and mortality of eggs/larvae. Secondly, for the late larval stages and the early juvenile stages no assessments of the catching efficiency of the gear have so far been reported.

Recruitment studies often concentrate on qualitative processes related to larval survival. A major impact towards the understanding of the variations of the year class strength, is to quantify growth and mortality of the stock. To quantify larval mortality subsequent quantitative abundance estimates from the egg stage to the juvenile stage should be made.

Stock abundance estimates based on surveys exist at three stages for the early period of the Arcto-Norwegian cod: From the international 0-group surveys in August-September, abundance estimates of 4 - 5 months old juveniles have been made each year since 1965 (Anon. 1981a-1987). Since 1979 abundance estimates of 2 - 3 months old fish have been made based on the post larvae surveys (Bjørke and Sundby 1986, Bjørke and Sundby 1987). In the period 1983 - 1985 the egg production was estimated based on egg surveys (Sundby and Solemdal 1984, Sundby and Bratland 1987). The abundance estimates are given as relative indices for the 0-group and the postlarval stage, while the egg production is reported in absolute numbers. Figure 1 shows the spatial distribution of post larvae and 0-group fish for each year. The average time difference between the two distributions is 53 days.

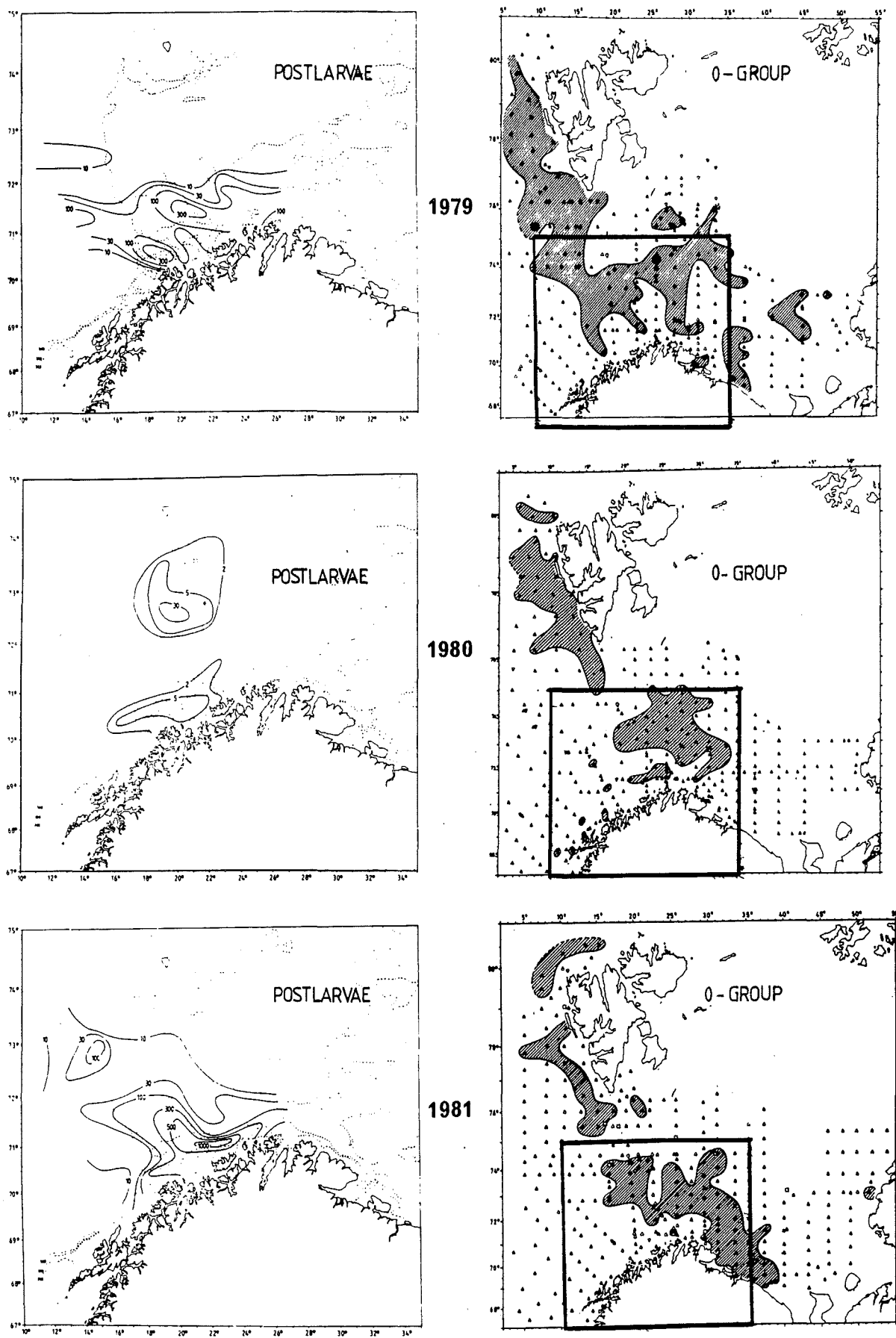


Fig. 1a. Distribution of postlarvae and 0-group cod in 1978 - 1981. Frames indicate sampled area during post larvae surveys.

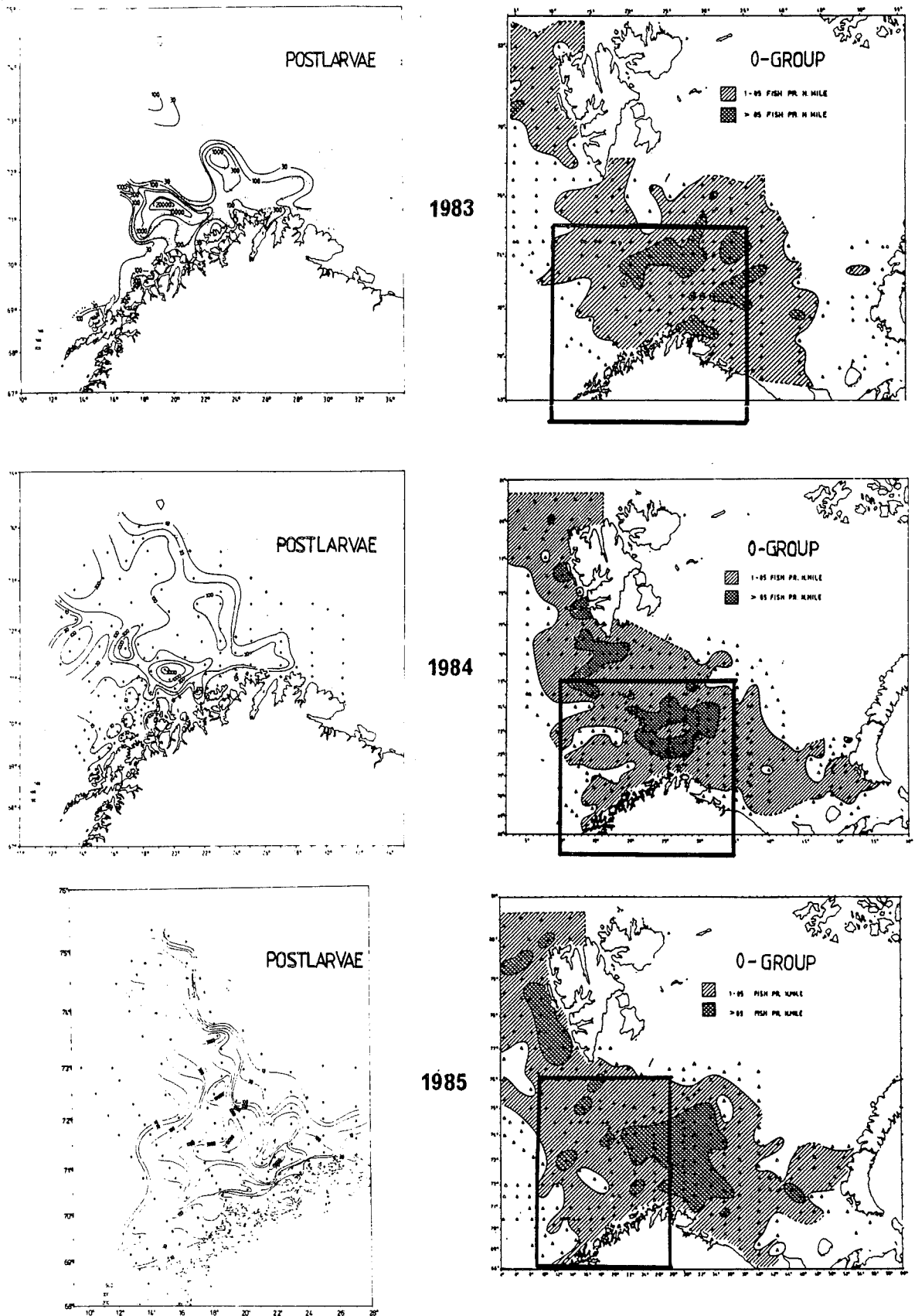


Fig. 1b. Distribution of postlarvae and 0-group cod in 1983-1985. Frames indicate sampled area during post larvae surveys.

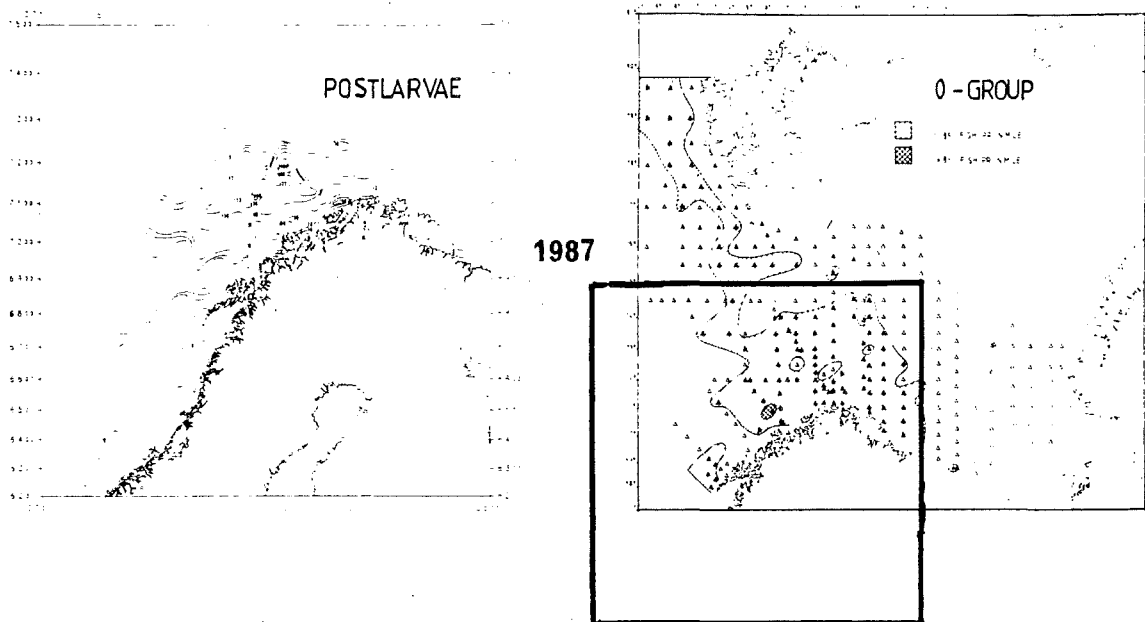


Fig. 1c. Distribution of postlarvae and 0-group cod in 1987. Frame indicate sampled area during post larvae surveys.

In this paper the catching efficiency of the trawls used during the 0-group and post larvae surveys is discussed and 0-group and post larval indices have been converted into absolute numbers. The instantaneous mortality rates from eggs to post larvae and from post larvae to 0-group are calculated. The year class strength, in number of fish at age 3, is compared to the abundance and the distribution of different early stages.

MATERIALS AND METHODS

General information about the types of surveys is given in Table 1.

Egg and larvae.

Egg surveys were conducted during the period 1983 - 1985 at the spawning areas in North Norway (Sundby and Solemdal 1984, Sundby and Bratland 1987). The egg production at the Møre coast, off Mid Norway, was very small these years, and were not covered by the surveys. An egg net, vertically towed from 75 m depth, were used to sample the eggs. The filtering efficiency of the net was 0.5 - 0.7 (Solemdal and Ellertsen 1984) and in the estimates of the egg production a mean value of 0.6 was used.

Postlarvae.

The postlarvae have been surveyed each year since 1977 (Bjørke and Sundby 1987). However, abundance indices were not estimated in the years 1977, 1978 and 1982 due to insufficient number of stations in the most important areas, and in 1986 due to an extreme easterly distribution of the postlarvae.

The geographical distribution of the postlarvae was found by fishing with a midwater trawl. A trawl with an opening of 18 x 18 m was used from 1978 until 1985. In 1985 a trawl with an opening of 29 x 29 m was introduced. The measured opening of this trawl is 20 x 20 m² during standard tows with the head-line at the surface and at 20 m depth (Nedreaas and Smedstad 1986). Both trawls were lined with 4 m long net of 8 mm mesh size (stretched) at the inner part of the cod end. To adjust for the bigger opening of the larger trawl a ratio of 2.8:1 for fishing capacities between the largest and the smallest trawl was used.

The postlarval abundance index, I_p , presented by Bjørke and Sundby (1986, 1987) has the unit:

$$\text{Nos. of postlarvae/trawlh hour} \times \text{km}^2 \times 10^6$$

During the period 1978-1981 two hauls were made on each station, one with the headline at 40 and at 20 m depth and with a towing time of 15 minutes in each depth interval. The other haul was made at the surface with five big floats on the headline. Towing time was 30 minutes.

Only one kind of haul was made at each station from 1982 onwards. From 1982 until 1985 the depths and towing time were the same as the previous years and five big floats were used on the headline during the haul. The same procedure was followed in 1985 but the towing time at each depth interval was halved. Towing speed during all years was 2,5 knots on the average.

The total number of postlarval cod, N_p , is expressed:

$$N_p = I_p \times 10^{12} / (A/60 \times D \times q)$$

where A is the area of the trawl opening, D is the distance towed per hour and q is the catching efficiency of the trawl.

0-group fish.

Each year since 1965 a 0-group cod abundance index, I_0 , has been estimated based on the The International 0-group Fish Investigations in the Barents Sea (Anon. 1981a-1987). It is a logarithmic index expressing the mean number of fish caught per nautical mile (Randa 1984). The trawl is identical to the postlarval trawl, i.e. with an opening of $29 \times 29 \text{ m}^2$. Until 1980 the fishing depth of the trawl was selected based on acoustic observations. From 1980 a standard trawling procedure, recommended by the International Council for the Exploration of the Sea (Anon. 1981b) has been used. The trawl is towed 0.5 nautical mile with the head line at three different depths: 0, 20 and 40 m. If acoustic observations show deeper distribution of fish, the trawl is also towed at 60 m. The total number of 0-group cod, N_0 , is expressed:

$$N_0 = \text{antiln}(I_0) \times VT / (VH \times q)$$

where VT is the total volume of 0-group cod spatial distribution which equals the survey area times the maximum depth of distribution, (60 m). VH is the water volume filtered of one nautical mile trawling, which equals $1852 \text{ m} \times 400 \text{ m}^2 = 74.08 \times 10^4 \text{ m}^3$, and q is the catching efficiency of the trawl.

The major problem in estimating the total number of post larvae and 0-group fish is to assess the catching efficiency, q, of the trawl. Based on some preliminary investigation on the comparison of the mid water trawl and the Mocness 10 m^2 plankton trawl, and on cited literature on the catching efficiency of mid water trawls for 0-group capelin, the catching efficiency of post larval and 0-group cod is assumed to be within the range 0.1 - 0.25. Both values are used in the subsequent calculations.

Table 1. Survey of the data used to calculate the instantaneous natural mortality coefficient.

STAGE	YEAR	AREA COVERED	SAMPLING GEAR	REFERENCE
Egg	1983 1984 1985	Spawning areas off the coast of North Norway.	Vertically hailed egg net	Sundby and Bratland 1987
Post larvae	1979-81 1983-85 1987-88	The coast of North and the western Barents Sea.	Mid water trawl	Bjørke and Sundby 1987
0-group fish	1979- 1988	The Barents Sea and the coast of Spitsbergen.	Mid water trawl	Anon. 1988
Fish at age 3 years	1979- 1983	The Barents Sea and the coasts of Norway and Spitsbergen	Commercial gear V.P.A.	Anon. 1987

RESULTS

Abundance estimates

Table 2 shows the abundance indices and the abundance in numbers for the three stages: egg, post larvae and 0-group fish. For postlarvae and 0-group fish two abundance numbers are given corresponding to a catching efficiency of 0.1 and 0.25 respectively. The filtering efficiency for the egg net is 0.60 (Sundby and Bratland 1987). The egg numbers in brackets are not based on egg surveys but on indirect measurements: The spawning stock biomass, given by the ICES Working Group on Arctic Fisheries (Anon. 1988), is applied together with fecundity measurements (Kjesbu 1988). His measurements show that the average spawner contains 0.37 mill. eggs per kilo fish. The fraction of female spawners is supposed to be 40 percent (Sundby and Bratland 1987).

The post larvae abundances in Table 2 shows four years of poor year classes (1979, 1980, 1987, 1988) and four years of average or strong year classes (1981, 1983, 1984, 1985). The following additional information is given to the abundance estimates in Table 2:

In 1980 an extremely poor year class was produced. The virtual population analysis (V.P.A.) estimate gave only 96 mill. fish at age three (Table 4), which is the poorest year class in 45 years. Large uncer-

tainties are to be expected from the estimates this year, and the the table also shows the contradicting result of a larger number of 0-group fish than post larvae.

In 1981 the 0-group index was 0.10. Later measurements show that the year class must have been underestimated. V.P.A. at age three gave approximately four times the number deduced from the 0-group index.

Table 2. Abundance indices and abundance in numbers of eggs, post larvae and 0-group fish for the years 1979-1981, 1983-1985 and 1987-1988. Abundance numbers for post larvae and 0-group fish correspond to $q=0.1$ and $q=0.25$. The egg numbers in brackets are based on spawning stock biomass assessments, fecundity measurements and the fraction of female spawners as outlined in the text below. The two 0-group indices marked with a "*" have been shown by later investigations to have significantly erroneous values. Corrected values are underlined. (Egg numbers are in 10^{-12} . Numbers for post larvae and 0-group fish are in 10^{-9} .)

YEAR	STAGE	ABUNDANCE	ABUNDANCE NUMBERS		
		INDEX	q=0.1	q=0.25	eggs
1979	Egg	-			- (34)
	Post larvae	7.2	2.880	1.152	
	0-group	0.4	1.320	0.528	
1980	Egg	-			- (25)
	Post larvae	0.4	0.160	0.064	
	0-group	0.13	1.010	0.404	
1981	Egg	-			- (23)
	Post larvae	15.4	6.160	2.464	
	0-group *	0.10	0.983	0.393	
	0-group corr.	<u>~1.0</u>	<u>2.5</u>	<u>1.0</u>	
1983	Egg	27.3			45,4 (49)
	Post larvae	74.7	29.880	11.952	
	0-group	1.69	4.803	1.921	
1984	Egg	18.7			31.2 (43)
	Post larvae	23.5	9.400	3.760	
	0-group	1.55	4.175	1.670	
1985	Egg	21.4			35.7 (47)
	Post larvae	56.5	22.600	9.040	
	0-group *	2.46	10.370	4.148	
	0-group corr.	<u>~1.6</u>	<u>4.3</u>	<u>1.7</u>	
1987	Egg	-			- (52)
	Post larvae	10.7	4.280	1.712	
	0-group	0.17	1.050	0.420	
1988	Egg	-			- (81)
	Post larvae	6.0	2.400	0.960	
	0-group	0.33	1.250	0.500	

In 1984 the abundance of postlarvae was underestimated due to a west-ernly distribution. The area to the west and partly to the north in the Norwegian Current was not properly covered (Bjørke and Sundby 1987). The post larvae estimate should probably be at least 10 per cent larger than the estimate shown in Table 2.

In 1985 the abundance estimates from the 0-group surveys showed a year class more than twice as large as the very strong 1983. Data from all subsequent stages of this year class do not indicate such a large year class (Anon 1987). It is probably overestimated by at least a factor of 2. Young fish survey results (see part C of Table 5) indicate that the 1985 year class at age 1 year was considerably smaller than the 1983 year class.

Mortality estimates

Table 3 shows the computed instantaneous natural mortality coefficients,

$$m = -(t_1 - t_0)^{-1} \ln (Nt_1 / Nt_0)$$

where Nt_0 is the abundance at time t_0 , and Nt_1 is the abundance at time t_1 . Time is given in years.

Results from Ellertsen et al. (1988) on mortality from newly spawned egg to hatching larvae are included in Table 3. They found that 10 per cent of the eggs reached hatching in the years 1983, 1984 and 1985. This corresponds to a instantaneous mortality coefficient of 42. The results were based on abundance estimates of hatching larval cohorts and on the egg production estimates by Sundby and Bratland (1987). The numbers in brackets are based on the indirect measurements of the egg production by spawning stock biomass, fecundity measurements and fraction of female spawners as outlined in the text above. For the years 1979-1981 and 1987-1988, when data from egg surveys are missing, an egg mortality of 42 is assumed in the calculation of the mortality coefficient for the period between hatching larvae and post larvae.

The table shows rapidly decreasing values of the instantaneous mortality coefficient from the egg stage to the 0-group stage. The mortality coefficients from hatching larvae to postlarvae, m_p , show, as to be expected, a natural logarithmic relation to the post larval index, I_p

Table 3. Instantaneous natural mortality coefficient, m , during four periods: From newly spawned eggs to hatching larvae, from hatching larvae to post larvae, from postlarvae to 0-group fish and from 0-group to three years old fish. The results from newly spawned eggs to hatching larvae are based on Ellertsen *et al.* (1988). Mortality coefficients based on abundance estimates with catch efficiencies, q , using both $q = 0.1$ and $q = 0.25$ are given. The numbers marked with a "*" are due to erroneous 0-group estimates as outlined in Table 2 and in the text above. Corrected values are underlined. Numbers in brackets are based on data from spawning stock biomass. The other numbers from 1983-1985 are based on egg surveys.

YEAR	EGG-HATCH LARVAE	HATCH LARVAE-POST LARVAE		POST LARVAE-O-GROUP FISH		O-GROUP-AGE THREE	
		$qp=0.1$	$qp=0.25$	$qp=q_0$	$qp=0.1$ $q_0=0.25$	$q_0=0.1$	$q_0=0.25$
1979	-	(39.1)	(44.2)	4.5	9.8	1.0	0.6
1980	-	(51.1)	(55.9)	*	*	1.0	0.6
1981	-	(27.7)	(32.0)	*13.7 <u>6.7</u>	*20.5 <u>13.5</u>	0.8	0.4
1983	42.0	25.1 (25.5)	29.7 (30.1)	12.1	18.2	0.5	0.1
1984	42.0	28.6 (30.2)	33.2 (34.7)	6.0	12.9	-	-
1985	42.0	26.4 (27.8)	31.2 (32.6)	* 5.3 <u>12.4</u>	*11.5 <u>19.3</u>	-	-
1987	-	(36.0)	(40.7)	10.3	16.9	-	-
1988	-	(40.0)	(44.5)	4.9	11.7	-	-

(Upper part of Figure 2a). The mortality calculations are based on the catching efficiency, $qp=0.1$. A regression can be expressed

$$m_p = 48.06 + 5.50 \ln I_p \quad \text{where } r^2 = 0.92 \quad \text{and } P < 0.001$$

The lower part of Figure 2a. shows the relation between the mortality between the post larval and the 0-group stages, m_0 , and the post larval index, I_p . The mortality calculations are based on a catch efficiency of $qp=q_0$. The mortalities for 1981 and 1985 are corrected for errors of the 0-group estimates. The figure shows that the mortality is correlated with the abundance of post larvae. A linear regression gives

$$m_0 = 5.31 + 0.102 I_p \quad \text{where } r^2 = 0.65 \quad \text{and } P < 0.03$$

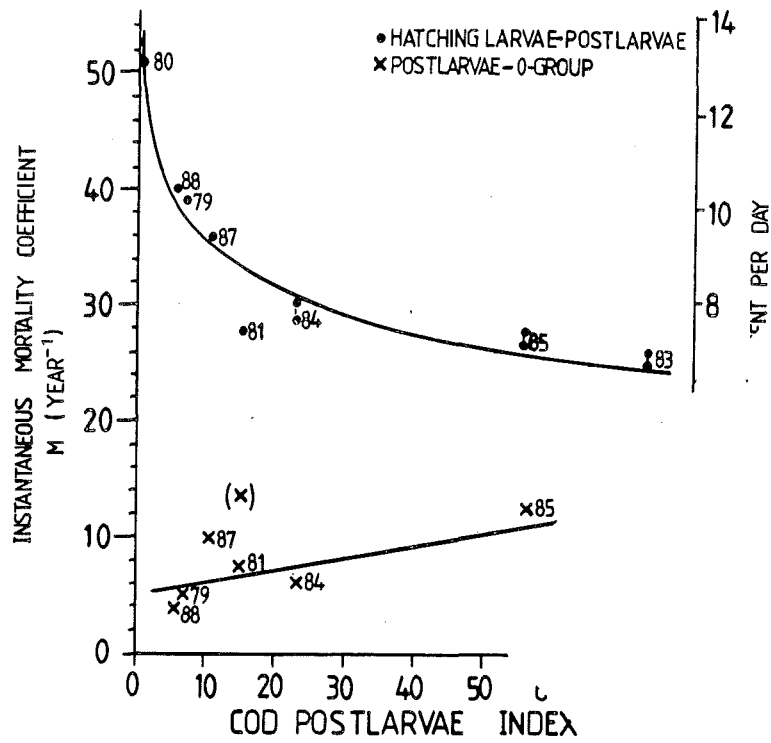


Fig. 2a. Instantaneous natural mortality, m (years^{-1}) for the periods hatching larvae - post larvae (dots and upper line), $q_p=0.1$, and post larvae - 0-group (crosses and lower line), $q_0=q_p$. Crosses in brackets are based on uncorrected 0-group estimates for 1981 and 1985.

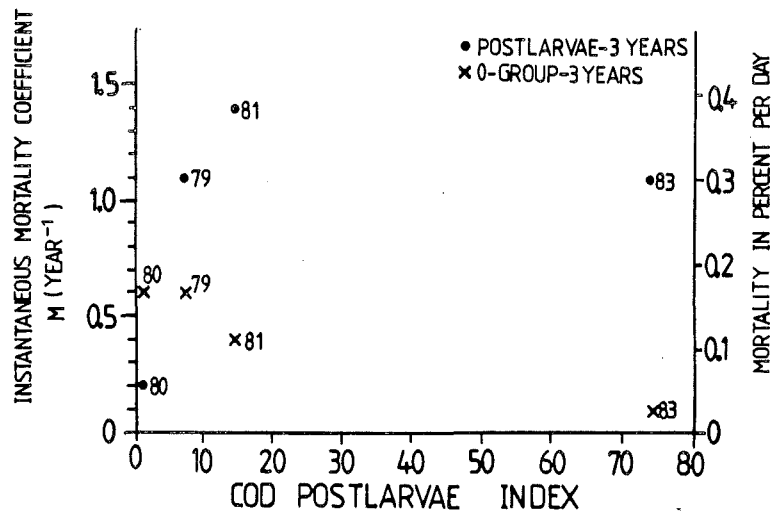


Fig. 2b. Instantaneous natural mortality, m (years^{-1}) for the periods post larvae - 3 years old cod (dots), $q_p=0.1$, and 0-group - 3 years old cod (crosses), $q_0=0.25$.

Virtual population analysis at age three gives year class abundances of 133 mill., 96 mill., 144 mill. and 1500 mill. for the years 1979, 1980, 1981 and 1983 (Anon. 1986). This corresponds to m -values between 0-group stage and 3 years old stage ranging from 0.6 to 0.1 (for $q_0=0.25$) and m -value ranging from 0.2 to 1.4 between the post larval stage and the 3 years old stage ($qp=0.1$) (Figure 2b). No correlation between the between year class strength and the mortality rate is found at these stages. A large fraction of the variation of the mortality coefficient can as well be caused by inaccuracies of the abundance estimates.

Table 4 shows the range of variation of the mortality in each of the periods from hatching larvae to 3 years fish. The extreme low post larvae index for 1980 is not used as the minimum value, since it may be underestimated. Instead, an average of the two lowest indices (1980 and 1988) is used as the minimum value.

Table 4. Range of instantaneous mortality and the total mortality for the periods hatching larvae - post larvae ($qp=0.1$), post larvae - 0-group ($qp=q_0$) and 0-group - 3 years old fish ($q_0=0.25$). N_h is the number of hatching larvae, N_p is the number of post larvae, N_0 is the number of 0-group fish and N_3 is the number of three years old fish.

HATCH. LARVAE-POST LARVAE	POST LARVAE-0-GROUP	0-GROUP-3 YEARS
$m(\max) = 48$	$m(\max) = 12.4$	$m(\max) = 0.15$
$m(\min) = 25$	$m(\min) = 4.5$	$m(\min) = 0.59$
$N_p(\max) = 67.4 \times 10^{-4} N_h$	$N_0(\max) = 0.52 N_p$	$N_3(\max) = 0.70 N_0$
$N_p(\min) = 1.0 \times 10^{-4} N_h$	$N_0(\min) = 0.17 N_p$	$N_3(\max) = 0.25 N_0$
Range of variation: 67.4	Range of variation: 3	Range of variation: 2.8

Relations between postlarvae, 0-group, and 3-group abundance

Table 5 shows the post larval and 0-group indices together with estimates of the year class at later stages. Abundance estimates of 3-group fish in part B are based on a linear regression between the 0-group indices and the virtual population analysis of 3-group fish (Anon. 1987). Separate estimates are given of 1-group, 2-group and 3-group fish based on trawl and acoustic young fish surveys (Hysten and Nakken 1982-1985), and the data are found in part C. In part D the virtual population analysis from the Arctic Fisheries Working Group in 1983, 1984 and 1985 is shown, and in part E the assessments of the

Arctic Fisheries Working Group in 1985-1987 are shown (Anon. 1986-1988). The assessments are based on virtual population analysis, Norwegian and Soviet young fish investigations, on the 0-group surveys, but not yet on the postlarval survey.

In Figure 3 the postlarval indices are plotted versus the 0-group indices. Figure 4 shows the postlarval indices versus the number of fish at age 3 years (in mill.) from the assessments and the virtual population analysis by the Arctic Fisheries Working Group. The assessment of the 1981 year class at age 3 years has been increased from 144 mill. ind. by the 1985-Working Group to 393 mill. ind. by the 1987-Working Group. This indicates that the 0-group estimate was too low. The estimates by the WG of the 1984 and 1985 year class have been drastically reduced from 1985 to 1987. The reason for this reduction has been ascribed to cannibalism at the 1-group and 2-group stage from the strong 1983 year class (Mehl 1988), and the general lack of food after the break down of the capelin stock in 1986 (Tjelmeland 1988). Mehl (1988) estimated that approximately 1.7×10^9 juvenile cod of the 1985 year class were consumed by the older cod. The 1985 year class was assessed by the 1987-Working Group to be approximately 0.35×10^9 fish at age three years.

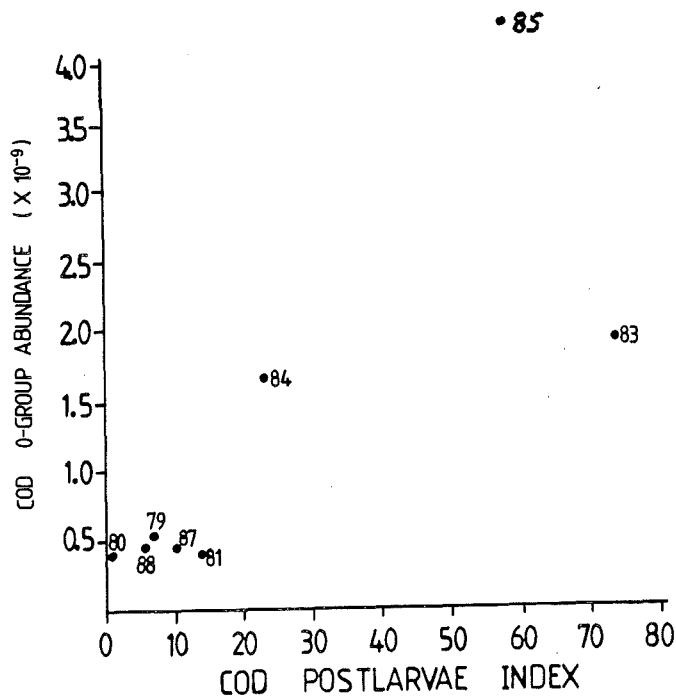


Fig. 3. Relation between post larvae index and 0-group abundance for cod. The 0-group values for 1981 and 1985 are not corrected.

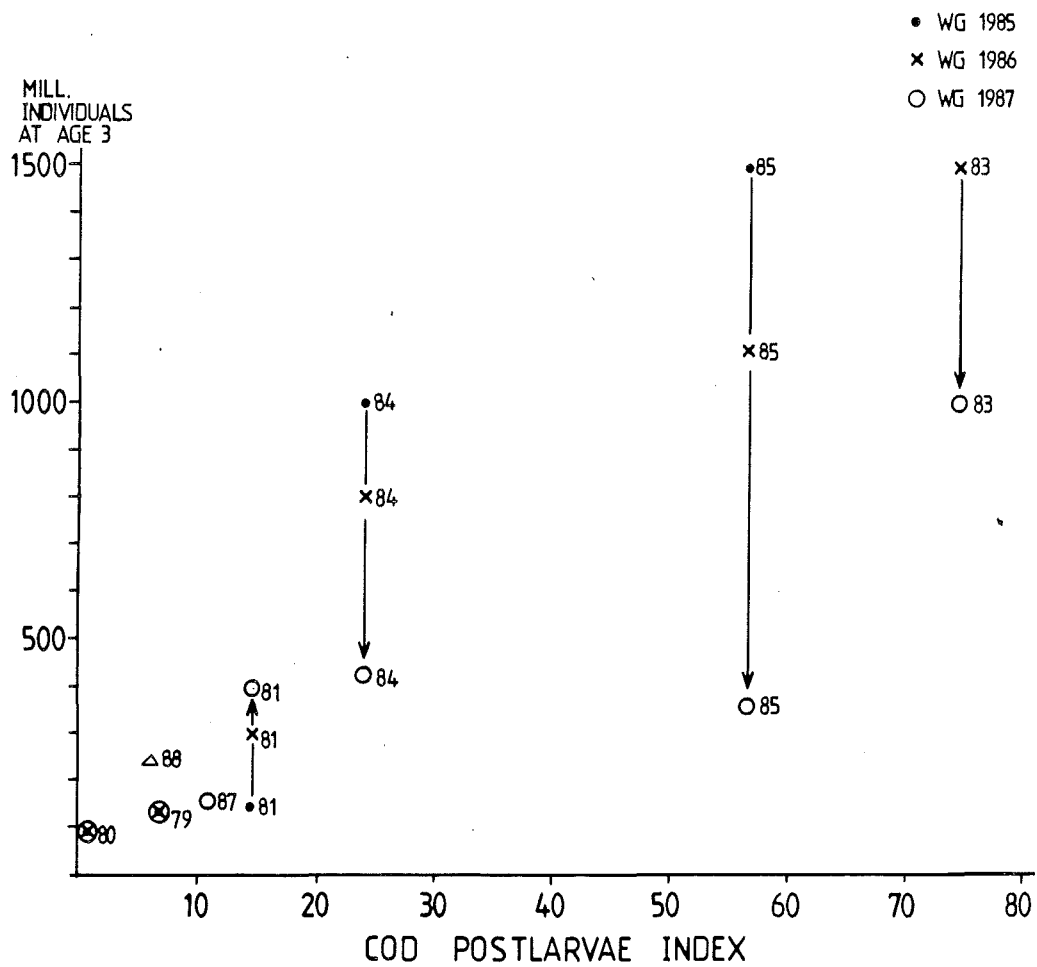


Fig. 4. Relation between the post larvae indices and year class strength at age 3 years from the assessments of the Working Group on Arctic Fisheries in 1985 (•), 1986 (×) and 1987 (○). The estimate for the 1988-year class is based on the 0-group index.

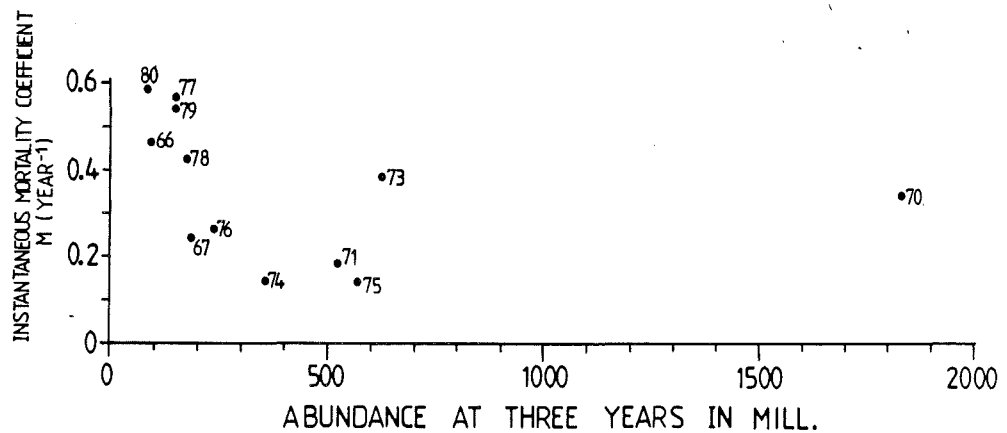


Fig. 5. Relation between the abundance of cod at age 3 years and the instantaneous mortality coefficient for the period 0-group - 3 years old cod, $q_0=0,25$.

Table 5. Abundance of year classes during the period 1978-1988. Part A: Postlarval index. Part B: 0-group index and the number of fish (in mill.) at age 3 based on a linear regression between the 0-group index and the abundance at age 3. Part C: Number of fish (in mill.) at age 1, 2, and 3 years based on young fish surveys by Hysten and Nakken 1982-1985. Part D: Virtual population analysis at age 3 years (numbers in mill.) from the Arctic Fisheries Working Group in 1983-1985 (Anon. 1984-1986). The instantaneous natural mortality coefficient, m used is 0.2. Part E: Assessments of year classes at age 3 years by the Arctic Fisheries Working Group 1985-1987 (Anon. 1986-1988). The assessments are based on a combination of the virtual population analysis, Norwegian and Soviet young fish surveys and the 0-group survey.

		YEAR CLASS										
		1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
A	Postlarvae index	-	7.2	0.4	15.4	-	74.7	23.5	56.5	-	10.7	6.0
B	0-group index	0.22	0.40	0.13	0.13	0.59	1.69	1.55	2.46	1.37	0.17	
B	3years based on 0-gr. ind.	180	290	120	120	400	1100	1000	1600	900	145	
C	1 years				1	-	2382	118	435	1		
C	2 years			4	27	506	1534	361	62			
C	3 years		81	29	121	817	1717	197				
D	3years VPA, $M=0,2$ WG 83	180	108	30								
D	3years VPA, $M=0,2$ WG 84	169	137	69	66							
D	3years VPA, $M=0,2$ WG 85	168	133	96	144							
E	3years WG 85					800	1500	1000	1500			
E	3years WG 86				303	677	1500	800	1100	900		
E	3years WG 87				393	636	1000	430	346	391	155	

DISCUSSION

In general there is little information on the catching efficiency of pelagic trawls. However, Larsen (1984) investigated the midwater trawl with respect to 0-group capelin by mounting "bags" outside the trawl. He found that the catching efficiency varied between 0.27 and 0.98. Isaksen (1979) used a different trawl and found a catching efficiency for capelin of 0.28. In a preliminary experiment during the 1988 post larvae survey the midwater trawl was compared to a 10 m² Mocness plankton sampler with 3 mm mesh size. The catching efficiency of the midwater trawl was found to be 0.24 of the Mocness sampler. Wiebe et al. (1985) assumed that the deviation from a 100 percent filtering capacity of the Mocness is small compared to the effect of gear avoidance. The average length of the sampled cod postlarvae was 25 mm. The largest postlarvae, > 40 mm, was better sampled by the midwater trawl than the Mocness, while the smallest postlarvae, < 15 mm, was better sampled by the Mocness (Bjørke et al. in prep.). Since there are no measurements of the avoidance by this size cod larvae on the 10 m² Mocness, we have to assume a rather wide range of catching efficiency. If this is in the range 0.4 - 1.0, the catching efficiency of the midwater trawl becomes 0.1 - 0.25. It is to be expected that the 0-group fish (approximately 60 - 80 mm) is subjected to a greater influence of sweeping by the trawl ropes than the postlarvae (approximately 20 - 50 mm). Ona (1988) indicate that the propellers noise will generate avoidance behind the path of the vessel. At present neither of these processes have been satisfactorily quantified, and it leaves us with the suggestion that the catching efficiency is within the rather wide range mentioned above, and that the catching efficiency is higher for the 0-group fish than for the post larvae. However, it must be mentioned that the question of catching efficiency does not influence on the variation between years of the mortality estimates.

After spawning in March and April the cod eggs/larvae are advected northwards and dispersed in the Norwegian coastal current. The bottom topography exerts a strong influence on the circulation and, in consequence, the egg and larval distribution (Sundby 1984). The year class reaches its maximum extension just prior to when the juveniles settles towards the bottom in the autumn. The spatial distribution of post larvae has been studied by Bjørke and Sundby (1984, 1987). They found that the circulation above the large bank Tromsøflaket in the southwestern Barents Sea has an important influence of the postlarval

cod distribution. From 40 to 90 percent of the year class is concentrated above this bank during the postlarval stage. The water masses above another bank, the western part of the North Cape Bank, usually also contain high concentrations of post larvae. In consequence, the survey strategy is adapted to this knowledge. The influence of the bottom topography on the distribution of juvenile is not considered in the 0-group survey strategy. The effect of schooling and near bottom distribution can be neglected during the post larvae survey. However, those effects may to some extent bias the 0-group estimate. Finally, the total area of postlarval distribution is smaller than the area of 0-group fish distribution. We expect therefore that the postlarval cod abundance estimate should be more precise than the 0-group estimate.

The magnitude of the mortality in the period between hatching larvae and post larvae emphasize the importance of recruitment processes during this early period. However, talking about determination of the year class strength, more important is the variation between years of the mortality. Also here, the period before the post larval stage is the most important. The range of variation of year class strength at the postlarval stage varies by a factor of ~70 (between the 1983 year class and the 1980 year class). From the post larval stage to the 0-group stage the range of variation of mortality is only 3 (Table 4). However, since most of this variation is correlated to the abundance of the year class, as shown in Figure 2a (density dependent mortality), it only contributes to reduce the differences of the year class strengths, and will not alter the rank of the year classes. Density dependent mortality has also been reported by Bergman, van der Veer and Zijlstra (1988) who investigated the juvenile plaice of the Wadden Sea.

Less conclusive are the results on mortality in the period from the 0-group stage to three years old fish. At present, dependable virtual population analysis at age three years only exists on to the 1983 year class. The data in Figure 2b show no significant correlation between the the mortality and the abundance indices. Neither do data on 0-group abundance and virtual population analysis at age three years for the period 1965 to 1981, given by the ICES Working Group on Arctic Fisheries (Anon. 1987), show any correlation between abundance and mortality, but the instantaneous mortality coefficient for both time series ranges from 0.1 to 0.6 (Figure 5). This corresponds to a range of variation in mortality for the period from 0-group stage to three

years old fish of 2.8. Since this variation apparently is not density dependent, the mortality in this period may contribute to change the year class strength determined at the post larvae stage. However, Ponomarenko (1984) found that one important factor for the mortality for 1 and 2 years old fish is low winter temperatures. When there are periods of low temperatures in the Barents Sea, strong year classes are never produced (Sætersdal and Loeng 1987, Ellertsen et al. 1988). Hence, the extreme high mortality rates seem to be connected to poor year classes. This also seems evident from Figure 5. Based on this the mortality may have two components opposing each other, one density dependent component and one component related to low temperatures.

Figure 4 shows that the post larvae index may to some extent have a prognostic value with respect to the assessment of year classes. However, the dramatic ecological changes of the Barents Sea, related to the break-down of the capelin stock (Tjelmeland 1988) which occurred in 1984 have influenced the mortality rate of the 1984 and 1985 year classes. Mehl (1988) showed that cannibalism from the 1983 year class has reduced the 1984 and 1985 year classes considerably. At present the Arctic Fisheries Working Group still considers the year class estimates for 1984 and 1985 at age three years to be uncertain (Anon 1987).

The working hypothesis of the Norwegian Cod Larvae Project (Ellertsen et al. 1979) conducted during the years 1975-1984, was that the year class strength mainly was determined during the first feeding period, which is just at the time of, and after, yolk sac adsorption, and that it was caused by starvation, the so-called Hjort hypothesis (Hjort 1914). Ellertsen et al. (1988) document that the starvation during first feeding is an important factor on determining year class strength, partly because early larvae are found in regions with prey concentrations both below and above the critical concentration for survival, and partly because strong match/mismatch, induced by the temperature, occur between years with respect to the timing of the cod larvae and nauplii production. However, the high egg mortality indicate that the determination of year class strength is not only a question of starvation during the first feeding period. This is also concluded by Ellertsen et al. (1988). During the egg surveys in the years 1983-1985 (Sundby and Bratland 1987) identical cohorts of eggs were mapped from spawning to 7 days old, and they concluded that the egg mortality during the first week was less than 20 percent. This

implies that the instantaneous egg mortality coefficient for the subsequent two weeks should be even higher (about 54 years⁻¹ corresponding to 13.8 per cent per day), than the average of 42 years⁻¹ from Ellertsen et al. (1988) given in Table 3. On this background it is unlikely that other processes than starvation should be unimportant during subsequent the early larval stages, as long as eggs and larvae have approximately the same size, concentration and spatial distribution.

The present investigations emphasize the importance of the recruitment processes during the first 2 - 3 months after hatching for the determination of the year class strength. Leggett (1986) reviewing investigations on prey concentrations and predation, concluded that recruitment investigations still lack evidence of whether predation or starvation is the important recruitment process. He concluded that neither food nor predators can be eliminated to significantly alter survival rates in larval fishes. The Norwegian recruitment investigations on cod fit well into this description. Most probably are both processes important for the Norwegian cod. Only more quantitative stock abundance investigations on predator, cod larvae and prey during the first 2 - 3 months after hatching can bring us new steps towards the answer.

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An Age- and Temperature-Mediated Growth Model for Cod
(Gadus morhua) and Haddock (Melanogrammus aeglefinus)
Larvae in the Gulf of Maine

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While field studies of larval fish growth require an easily-parameterized growth model, simple relationships between size and age are seldom applicable to other populations and/or environments. The model presented here attempts to bridge the gap between simple age-length regressions and more sophisticated experiment-based models by incorporating a temperature term as a function of absolute growth rate. Growth is assumed to be logistic, with temperature influencing growth rate parabolically on a daily basis. The integrated form of the model provides an estimate of length-at-age of the larva. When fitted to a variety of independent cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) data sets collected in the Gulf of Maine, the model performed with minimal bias despite the absence of a food availability term. Larval age data were generated through validated otolith microstructure examinations, although the resolution limits of light microscopy introduced a small degree of bias (2-3 d) into the estimates. The daily temperature record was generated from a sinusoidal model using monthly mean temperatures. Since otolith microstructure examination and remote sensing of temperature are established techniques, this model may prove useful in other larval studies.

Introduction

Predictive growth models for larval gadids span the range from simple linear regression of length on age (Anderson 1982; Yin and Blaxter 1986) to sophisticated environment-mediated foraging calculations (Beyer and Laurence 1981; Ellertsen et al. 1981). The degree of sophistication and predictive power in these studies is often inversely related to the level of the experimenter's control: complex models are not easily parameterized in field situations, nor are they necessarily intended to be. Yet realistic growth models of wild fish larvae often form the basis for models of higher-order processes such as recruitment and survival (e.g. Jones 1973; Leak and Houde 1987). The realities of monitoring the growth and environment of marine larvae in situ have constrained previous workers to the fitting of imprecise and/or point specific length-at-age curves. For this reason, we see the need for an easily-parameterized growth model of intermediate complexity, with powers of prediction for wild larvae, and the flexibility necessary for application to a broad range of environmental conditions and/or populations. Such a model is presented here in application to larval cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) in the Gulf of Maine.

Current models of the growth of larval cod and haddock are largely based upon the results of laboratory (Laurence 1974, 1978; Beyer and Laurence 1981; Laurence et al. 1981; Gamble and Houde 1984; Yin and Blaxter 1986) and enclosure (Ellertsen et al. 1981; Gamble and Houde 1984; Kvenseth 1984) studies. Growth data were modelled primarily as a function of age, with prey availability, temperature, and other variables incorporated as accessory variables into the more complex models. While age data are intrinsic to controlled experiments, they have (until recently) been difficult to obtain in field studies. Therefore, earlier field studies of larval cod and haddock growth necessarily adopted length-frequency analysis as a proxy for age, despite the confounding effects of immigration/emigration, size-selective mortality and an extended spawning period (Graham 1934; Saville 1956; Anderson 1982). All of these effects can skew a length-frequency mode, thus making it difficult or impossible to track a larval cohort and/or assess its rate of growth. With the advent of otolith microstructure examination as a more precise age determination tool (Pannella 1971; Brothers et al. 1976;

reviewed by Campana and Neilson 1985), direct age measurements of field-collected larvae became possible. Such measurements have been used to advantage in other field studies of larval gadoids (Nishimura and Yamada 1984; Walline 1985; Kendall et al. 1987), as well as in the only other field study of larval gadid age structure in the Gulf of Maine (Bolz and Lough 1983). It is also the approach adopted here.

In this paper, we wish to reassess the results of Bolz and Lough (1983) in light of recent findings concerning apparent bias in otolith microstructure studies (Geffen 1982; Campana et al. 1987), as well as extend the scope of their study beyond that of a point estimate. Accordingly, we shall evaluate the spatio-temporal variation in larval growth rate over a broad region and sequence of surveys, encompassing the waters in and around Browns and Georges Bank in 1984 and 1985. A third objective is to develop a generalized growth model to fit these data, with the view towards making it broadly applicable to other areas and times. Finally, we use the model to test competing hypotheses concerning the relative growth of cod and haddock larvae under a variety of environmental regimes (Laurence 1978; Laurence et al. 1981).

Materials and Methods

Cod and haddock larvae were collected in 7 different cruises over a fixed survey grid as part of the Fisheries Ecology Program ichthyoplankton survey. The survey encompassed 97 stations to the south, east, and west of Nova Scotia, down to and including portions of Georges Bank (Figure 1). Surveys represented in this study were conducted in March and April of 1984 and monthly between January and June of 1985, although weather restricted grid coverage on some cruises (Table 1). Each station was sampled with paired bongo nets fitted with 61-cm frames, 333 μ m Nitex mesh, and mouth-mounted flowmeters. Tows were made obliquely to within 5 m of the bottom (to a maximum of 200 m) and immediately replicated. Full sampling details and cruise-by-cruise station locations are documented elsewhere (Hurley and Campana, unpublished).

Upon collection, unsorted samples were preserved in 5% Formalin/saltwater made basic to a pH of 8.0-9.0 with sodium carbonate; the latter retarded acidic degradation of the otoliths until the samples could be preserved in 95% ethanol. Samples were transferred to 95% ethanol for storage within 3 weeks of collection. Prior to otolith removal, larvae were measured to the nearest 0.1 mm. Both pairs of sagittal and lapillar otoliths were removed, cleansed of adhering tissue, and mounted individually on microscope slides with Krazy Glue according to standard techniques (Campana and Neilson 1985). All otoliths with diameters exceeding 40 μm were polished with lapping film prior to microscopic examination. Otoliths showing evidence of formalin degradation (brown discolouration, pitting) were not considered further. Degraded otoliths constituted approximately 20% of the total number (primarily in Cruise H135), although the proportion degraded within a sample varied substantially among samples. Microstructural examinations were made with a research quality compound microscope at 1250x; the functional resolution limit of this system was previously estimated to be 0.25 μm (Campana et al. 1987). Measurements of otolith and hatch check diameter were made with an ocular micrometer to the nearest μm , with the difference between the two measurements hereafter defined as the growth diameter. Criteria for definition of the hatch check were those of Bolz and Lough (1983), Bergstad (1984), and Dale (1984). All daily increment counts were replicated by the same reader. Unless stated otherwise, the mean measurement and count values for each otolith type within a larva were used in all analyses.

Indices of potential resolution loss during increment counts were generated through the increment width estimation procedure described in Campana et al. (1987). Briefly, this involved the fitting of a logistic curve to the increment count data associated with each otolith growth diameter (OGD = otolith diameter - hatch check diameter), and then using the fitted model to estimate increment width in the first few days post-hatch. Specifically, otolith growth diameter (OGD) was related to increment count (C) in the logistic equation:

$$\text{OGD} = a + b(1 + \exp(-c(C-d)))^{-1}$$

where a, b, c, and d are model parameters. Increment width on Day i was then calculated as $(OGD_i - OGD_{i-1}) \div 2$ for each of the samples.

To determine the frequency of increment formation in newly-hatched cod larvae, samples of known-age larvae were obtained incidentally from two separate experiments conducted by J.D. Neilson and K.G. Waiwood of the St. Andrews Biological Station, N.B. In both experiments, larvae were reared from the egg stage under a diel light cycle (12 h light:12 h dark) and ambient temperatures of 5-6° C (Expt 1: 29 April-13 May 1983, N = 42; Expt 2: February 7-March 4, 1984, N = 8). Larvae were fed twice daily with rotifers. Sampled larvae were preserved in 95% ethanol prior to otolith removal. Microstructural examinations were made as described above without knowledge of true larval age or sampling frequency.

Vertical temperature profiles were made at each cruise station. However, retrospective analysis of larval growth required a daily sequence of water temperatures. Daily temperature series for 1984 and 1985 were generated from mean monthly temperatures (NOAA 1984, 1985) in two areas: Browns and Georges Banks. Sinusoidal least-squares regressions were fit to the monthly data, with the resulting equations used to predict the daily sea surface temperature (SST) record for each region (Table 2). The predicted temperature values were consistent with those actually observed during each cruise.

Parameters for larval and otolith growth models were generated for two regions — Browns Bank/Southwest Nova Scotia, and Georges Bank — based upon presumed stock boundaries (Bowen 1987) and hydrographic regimes (Smith 1983; Perry and Hurley 1986). All linear and nonlinear regression parameters were estimated by least-squares methods. Residuals from the models were given careful examination, particularly near the origin. Models were accepted only in the absence of patterns in the residuals. The significance level was set at 0.05 for all tests.

Results and Discussion

Estimation of Age, Resolution Loss, and Length

The otolith microstructure of the cod and haddock larvae was largely unambiguous in its interpretation. Intralarval increment counts were highly correlated both within an otolith type and between lapillae and sagittae (slope = 1.0 ± 0.05 ; $R^2 > 0.95$) in both species. However, the intercept term for the regression of sagittal counts on lapillar counts was highly significant, and indicated that the latter exceeded the former by an average of 2.6 and 1.6 for cod and haddock respectively. Given the smaller size of the sagittae at hatch and the very narrow ($< 0.5 \mu\text{m}$) increments encircling the nucleus (Bolz and Lough 1983; Campana, unpublished), resolution limitations associated with the use of light microscopy were suspected to be the source of the inter-otolith discrepancy (Campana et al. 1987). The significance of this suspicion is that increment counts would underestimate the number actually present if increments were too narrow to resolve as individual units. In the case of larval herring (*Clupea harengus*), resolution-limited increment counts resulted in serious underestimates of age (15-20 d) (Campana et al. 1987). The existence of a significant, within-larva correlation ($P < 0.01$) between the intersagittal differences in growth radius and increment count, confirmed the presence of resolution-limited increment visibility in all large samples of cod and haddock larvae. Since a significant relationship was also observed among the lapillae, estimates of the magnitude of the resolution loss were deemed necessary.

Increment widths at age from each of the cruise collections were compared both with the functional resolution limit of our microscope system, and among themselves, in order to assess the relative magnitude of the potential count bias. Increment widths at Day 1 were close to the resolution limit of our system for sagittae and lapillae in both cod and haddock in all cruises (Table 3). However, the increment widths increased rapidly with age, suggesting that unresolved increments, if they existed, were associated only with the youngest larvae. Haddock increment widths at Day 1 tended to be larger than those of cod.

The validity of using increment counts to estimate the age of cod and haddock larvae was assessed in the first validation experiment. Increment counts were highly correlated with age in both sagittae and lapillae (Table 4). In addition, a daily frequency of increment formation in the lapillae was indicated by a regression of increment count on age not significantly different from 1.0. However, the regression slope was significantly less than 1.0 for the sagittae, and indeed, increment counts tended to underestimate age in both otolith types. Since the age-increment discrepancy stabilized in both otolith types before Day 10 (asymptotic discrepancy = 2-3 and 5-6 for lapillae and sagittae respectively), resolution limitations induced by light microscopy were again suspected. The generally good fit between the ages and increment counts in Experiment 2 (see below) was also consistent with resolution-limited visibility, since the one poorly-predicted age was associated with a very slow-growing larva.

Validation Experiment 2

<u>Sample</u>	<u>N</u>	<u>Age (d)</u>	<u>Mean Count</u>
1	3	14	17
2	2	16	15
3	2	4	7
4	1	26	16

In a procedure analogous to that applied to the wild larvae, increment width at Day 1 was estimated for the known-age larvae in Experiment 1. The resultant values (lapillae - 0.31 μm ; sagittae - 0.36 μm) fell within the lower range observed among the wild larvae (Table 3), and were probably not different from our functional resolution limit. Accordingly, we have assumed that increment counts in the wild larvae underestimated larval age to an extent similar to that observed in the laboratory. Given hatch check formation in larval cod on Day 1 (Bergstad 1984; Dale 1984), and the close similarity of haddock otolith microstructure to that of cod (Bolz and Lough 1983; Campana, unpublished), our daily increment counts appear to have underestimated age in these two species by 1-2 and 4-5 days for the lapillae and sagittae respectively; this level of bias was considered both acceptable and unavoidable. Therefore, estimates of larval age were calculated by

adding one (corresponding to the age at hatch check formation) to the mean count in the lapillae (or sagittae, if larger).

Variability is introduced into measurements of larval length through factors such as net handling time, preservation schedule, etc. (Radtke and Waiwood 1980; Fowler and Smith 1983), all of which may deform the soft tissues of a larva and vary in magnitude from sample to sample. This variability was reduced through use of sagitta length as a correlate of total length in cod larvae. The rigid sagittae can be precisely measured, are unaffected by factors other than those that cause dissolution, and were linearly related to larval length after ln-ln transformation (Figure 2), as in:

$$\ln L = 0.5996 \cdot \ln \text{Sag} - 0.6199 \quad N = 507; R^2 = 0.95$$

where L = total length of the larvae (mm) and Sag = maximum sagittal length (μm). Tests for a variety of factor effects indicated that the assumption of a common slope and intercept was justified across regions, cruises and years (ANOCOVA, $P > 0.1$) (Campana, unpublished). Accordingly, sagittal measurements were used to more precisely estimate cod larval length in the growth models that follow. While at first glance similar relationships could have been generated for haddock larvae, and for lapillae of both species, consistent (albeit minor) patterns in the residuals among cruises suggested that they not be applied (Campana, unpublished).

Growth as a Function of Age

On a cruise-by-cruise basis, cod (Figure 3) and haddock (Figure 4) larval length was successfully modelled as a function of age, using the exponential equation:

$$L = \exp(a + b \cdot \text{age})$$

where a and b are regression parameters. All model fits were unbiased and highly correlated, with the correlation coefficients for cod generally exceeding those for haddock (Table 5). While specific growth rates for cod and haddock did not differ significantly within a cruise and region, such an

analysis is of little value without reference to the range of ages present in the data; this fact is also at least partially responsible for the differing magnitudes of the correlation coefficients between species.

Attempts to fit the exponential model of larval growth to data aggregated on a regional (Browns vs Georges banks) and/or yearly basis were unsuccessful; the residuals formed a clear pattern across ages and cruises. While use of the log-transformed logistic model

$$\ln L = \ln (a + b \div (1 + \exp(-cx(\text{age}-d))))$$

where a, b, c, and d are model parameters, improved the overall model fit, strong trends in the residuals persisted when examined on a cruise-by-cruise basis.

Development of an Age- and Temperature-Mediated Growth Model

Given the inadequacy of the simple age-based models in application to the aggregated regional data sets, more complex models were developed which incorporated temperature as an accessory variable. Temperature is widely recognized as a significant modifier of the growth rate of fishes. Justification for the inclusion of temperature in this study was based upon laboratory demonstrations of temperature-mediated growth rates in gadid larvae (Laurence 1978; Buckley 1984). Further justification was derived from this study in the form of a significant relationship between mean SST during each cruise and the calculated specific growth rate of cod larvae less than 30 d old in each cruise collection ($P = 0.02$, $R^2 = 0.64$). While the relationship was not significant for haddock larvae, the haddock data exhibited a similar trend. Established principles concerning temperature effects on growth processes (Brett 1979; Ricker 1979) suggested the need for a logistic growth model where temperature influenced absolute growth rate in a parabolic fashion. However, in keeping with the principle of parsimony, model development began with the simplest possible formulation, progressing to more complex designs only if the statistical criteria for the simpler model were not met.

The heterogeneity of larval ages evident in all of the samples implies that the history of temperature exposure will have differed for most larvae. Because the growth response to temperature is seldom constant across all ages/sizes (Ricker 1979), any calculations for a daily growth-temperature interaction would have to be estimated for each individual larva. The simplest form of such an interaction is that of a linear relationship between absolute growth rate and temperature, or equivalently, the hyperbolic or degree-day relationship of salmonid egg development models (Ricker 1979). This form of interaction assumes a growth response to temperature analogous to that of metabolic rate, but is formulated to deal with the changes in absolute growth rate that often occur as a fish ages. Because it is virtually impossible to monitor the growth rate of individual wild fish on a daily basis, the model was integrated to reflect larval length-at-age upon sampling, as in:

$$L_{\text{age}} = L_{\text{hatch}} + \int_{t=0}^{\text{age}} (\text{Absolute growth rate} \times \text{Temperature}) dt \quad (1)$$

The form of the absolute growth rate term (dL/dt) depends on the model selected, but since the exponential model described earlier was applied successfully on a cruise-by-cruise basis, it was also the initial choice here. This results in:

$$L_{\text{age}} = L_{\text{hatch}} + \int_{t=0}^{\text{age}} (aGe^{Gt} \cdot T_t) dt \quad (2)$$

and the discrete approximation:

$$L_{\text{age}} = L_{\text{hatch}} + \sum_{t=0}^{\text{age}} (aGe^{Gt} \cdot T_t) \quad (3)$$

where L_{hatch} , a , and G are model parameters, G is the instantaneous (or specific) growth rate, T_t is temperature on the appropriate Julian day, and t is time (days). The term aGe^{Gt} is the derivative of the exponential growth model, or equivalently, the absolute growth rate at age t . Using the daily

temperature record (Table 2) and the age of each larva, model (3) was fit to the data from Browns Bank in 1985. The Browns Bank data were selected since they represented the largest regional data set (N = 507 for cod; N = 545 for haddock) and the broadest temperature range through the time series: 3-11° C.

The fit of the model initially appeared to be quite good ($R^2 = 0.93$ and 0.81 for cod and haddock, respectively), but examination of the residuals as a function of age indicated that the model seriously overestimated the length of larvae older than 90 days. Accordingly, the model was altered to reflect a more realistic growth form — the logistic equation — in conjunction with a linear temperature interaction. The fit of this model was better than that of (3), but persistent patterns in the residuals were identified among the older larvae of the February cruise (H130) and the younger larvae of the June cruise (H137). Since these two sets of larvae would have experienced the highest temperatures of the sampling season ($> 10^\circ \text{C}$), it is likely that such temperatures would have exceeded the larval growth optimum. Temperature optima are well documented in temperate fishes (see review by Brett (1979)) and would be expected in cod and haddock stocks nearing the southern limit of their range. Growth-temperature optima were modelled in this study through use of a quadratic parabola, which has been used successfully in many other studies of fish growth (Ricker 1979). The parabolic temperature term was initially incorporated into a modification of Model (3), allying exponential growth (the most parsimonious model) with an inverse parabolic temperature term; the latter served to increase absolute growth rate parabolically to a temperature-based optimum, after which growth rate decreased.

The fit of this model was again good for both species, but it produced trends in the residuals for the oldest larvae. These results suggested that the temperature parabola was effective, but that exponential growth could not be assumed in older fish. Accordingly, the latter two models were merged to incorporate both logistic growth and a parabolic temperature interaction, resulting in:

$$L_{\text{age}} = L_{\text{hatch}} + K \int_{t=0}^{\text{age}} \frac{d(\text{logistic})}{dt} \cdot (c - (T_t - T_{\text{opt}})^2) dt$$

and the numerical approximation:

$$L_{\text{age}} = L_{\text{hatch}} + K \sum_{t=0}^{\text{age}} (G l_t - G l_t L_{\infty}^{-1}) (c - (T_t - T_{\text{opt}})^2) \quad (4)$$

where $l_t = L_{\infty}(1 + \exp(-G(t-t_0)))^{-1}$; G , L_{∞} , t_0 , c , and T_{opt} (= temperature optimum) are model parameters; and L_{hatch} and K are fixed at 3.0 and 0.2, respectively. While the fixed value of L_{hatch} was somewhat arbitrary, model results were insensitive to the specific value within the range of 2-5 mm. The fit of this model to the aggregated Browns Bank data was excellent ($R^2 = 0.96$ and 0.83 for cod and haddock, respectively) and appeared to be unbiased across all combinations of cruise, length, and age (Figure 5, Table 6). The fit was particularly good for the cod larvae, and given the range of months, temperatures, ages, and lengths present in the data, would appear to be a robust predictor of larval length. Use of five different cruise collections in the test data set precluded any collinearity between temperature and age. Of course, the predictive power of any model decreases near the extremes of the data range, and this effect is to be particularly expected for the largest cod larvae; the potential for avoidance of the bongo gear is almost certainly present in larvae >10 mm (I. Suthers, Dept. of Biology, Dalhousie University, Halifax, N.S., pers. comm.) and would be expected to result in preferential capture of the slower-growing individuals. It is unlikely that gear avoidance had a significant effect upon the size-at-age estimates of the much smaller haddock larvae. However, the restricted ranges of the haddock age, length, and temperature data constrained the utility of the growth model to larvae less than 35-40 days old.

The predictive capability of the model was assessed through tests with independent data sets. Growth projections for cod and haddock on Browns and Georges banks in 1984, and on Georges Bank in 1985, were made using the parameters in Table 6, resulting in predictions similar to those actually observed; in all cases, the mean residual was approximately 0. Slight trends were observed in the residual patterns of cod from cruises H116 (1984 - Browns) and H135 (1985 - Georges), and in haddock from H114 (1984 - Georges), but the source of the discrepancy was difficult to pinpoint. There is no

question that imprecision in the estimated temperature record could have resulted in the predicted growth anomalies; simulations with the temperature data verified this. An equally viable explanation is the absence of food availability/consumption as a term in the growth model. Since food consumption is known to influence the growth of larval cod and haddock (Laurence 1974; Laurence et al. 1981; Ellertsen et al. 1981), food availability may differ enough spatially and temporally to introduce error into the model projections. It is important to note however, that the model residuals from 5 independent data sets were invariably small, and equally explicable in terms of prey concentration or temperature anomalies. Given the level of precision required here, and the close correspondence between temperature and prey abundance in many ecosystems, the distinction between these latter two factors may be irrelevant in the context of this model.

Comparative Growth of Cod and Haddock Larvae

The logistic form of the growth equation used here has been fitted to length-at-age data from a wide variety of other species (Bailey 1982; Nishimura and Yamada 1984; Boehlert and Yoklavich 1985; Crecco and Savoy 1985; Warlen and Chester 1985). With the incorporation of the temperature term as a function of absolute growth rate, temperature becomes a significant modifier of growth rate. Growth was optimized at a specific temperature in both species, in keeping with the parabolic form of the temperature terms (Figure 6). The greater optimal temperature for (T_{opt}) haddock (6.7° C) over that of cod (5.9° C) is consistent with the distribution of each species along the eastern coast of North America.

Temperature exerted its most significant effect upon growth at the inflection point of the growth curve, where the rate of growth was most rapid. In the case of haddock, this occurred at an age of 20-30 d; the inflection point for cod was somewhat later (40-50 d). The influence of an age-structured temperature-growth rate relationship was demonstrated in growth projections where temperature was held constant at 3° C until Age 30 d, after which it was shifted to 7° C until Age 60 d; the converse temperature shift did not result in a comparable length at Age 60 d, despite the equivalent number of degree-days in each 30-d interval, because of the higher size-structured growth rates in the older larvae (Figure 7).

A comparison of the growth projections for each species indicates that neither has a substantial growth advantage within the temperature range of 3-7° C, at least until the age of 30 d (Figure 5). After that age, haddock growth rate was reduced relative to that of cod, resulting in significant differences in size at age 50 at all temperatures. The inter-specific comparability of the growth curves noted here for young larvae is similar to that reported on Georges Bank (Bolz and Lough 1983; Buckley and Lough 1987) and in the laboratory (Laurence 1978). However, the divergence of the growth curves after approximately age 30 d is inconsistent both with Bolz and Lough's (1983) field study and with Laurence's (1978) laboratory work. Interestingly, a later study by Laurence (1981), in which cod and haddock larvae were forced to compete for food resources, produced an inter-specific growth divergence nearly identical to that reported here. Laurence (1981) discussed possible mechanisms for the divergence, including cannibalism, predation on haddock by cod, and prey size selectivity. Neither of our studies were designed to test among these hypotheses, but the similarity in results between his laboratory experiment and our field study is striking.

Predicted length-at-age values from our model are 30-40% less than those reported for Georges Bank by Bolz and Lough (1983). While the latter did not test for potential resolution losses in their interpretation of the otolith microstructure, our results indicate that these losses would have introduced little error into either of our estimates of age. The remaining procedural difference between the two studies was that associated with the measurement of larval length: Bolz and Lough (1983) applied Theilacker's (1980) shrinkage correction equation to all of their length data, while we did not. On the assumption that the observed cod lapillus diameter: larval length relationship was similar in both studies (Campana, unpublished), and given the resistance of lapillae to deformation/shrinkage, the observed lapillus diameters were used to calculate a common frame of reference for length between the studies. When Theilacker's (1980) equation was then applied to the standardized data, our prediction of cod larval length at the temperatures reported by Bolz and Lough (1983) fall within 3% of their estimates. While the consistency between the two independent growth estimates is remarkable, the question remains of whether or not to calculate growth on the basis of preserved or adjusted lengths. An unbiased estimate

of live length would certainly be preferable. However, Theilacker's (1980) equation was designed for use with anchovy (Engraulis mordax) larvae, whose shape differs substantially from that of cod and haddock. It also results in cod shrinkage estimates on the order of 30%, which appears to be unreasonably high compared to the ~10% reported for silver hake (Merluccius bilinearis) larvae (Fowler and Smith 1983). Given the morphological similarity between larval silver hake and cod/haddock, we feel that a shrinkage estimate of ~10% is more representative of gadids. However, in the absence of a valid predictive equation for shrinkage, we have left our growth predictions uncorrected, in the knowledge that adjustments can always be made after the appropriate calibrations have been conducted.

Aside from the study of Bolz and Lough (1983), there are few studies with which to test the generality of our growth model. Anderson's (1982) growth rate calculations for cod were length- rather than age-structured, but our estimates of growth rate from his data were consistent with those that he estimated for Flemish Cap. Laboratory estimates of growth rate do not necessarily reflect those obtained in the field, but in the case of Laurence's (1981) cod and haddock data, they do. Similarly, using the temperatures and ages reported by Ellertsen et al. (1981), our predictions of cod length at ages of 30-50 d were consistent with those ($\pm 10\%$) actually measured in two of their three enclosures; their third, high-food density enclosure supported growth rates considerably higher than those predicted by our model. Therefore, we conclude that the age- and temperature-based growth model developed here accurately reflects the growth of larval cod and haddock over a broad range of environmental conditions, but requires modification if it is to deal with extended, anomalous food conditions. Such conditions were not encountered in seven independent larval collections in the Gulf of Maine.

General Discussion

Process-oriented growth models derived from experimental results serve a useful function as vehicles for hypothesis testing. However, studies reporting the growth of wild marine larvae have made almost exclusive use of

simple age-length regressions, in apparent disregard of the more sophisticated models developed elsewhere (Bolz and Lough 1983; Beckman and Dean 1984; Nishimura and Yamada 1984; Walline 1985; Leak and Houde 1987). This situation reflects not so much the inapplicability of the alternative models, as the difficulty associated with their parameterization. Parameters are particularly difficult to estimate for terms associated with feeding and behaviour. Yet, in addition to age, feeding and temperature are the two variables most influential in determining larval growth (Vlymen 1977; Laurence 1978; Ellertsen et al. 1981; Laurence et al. 1981; Taniguchi 1981; Buckley 1984; Crecco and Savoy 1985). As a result, age-length regressions perform well as growth descriptors for a specific study, but lack applicability to other water masses, seasons, and populations.

In this paper, we hope to have bridged some of the gap between theory and application, through presentation of a generic larval growth model with a number of advantages over existing formulations. The advantages include: 1) conceptual soundness — the influence of age and temperature upon growth rate is well documented in both the theoretical and the empirical literature; 2) ease of parameterization — age-structured data can now be routinely collected through otolith microstructure techniques in a wide variety of species. Temperature data are easy to collect, either through hydrographic sampling or remote sensing observations. Since foraging data are difficult both to collect and to interpret, a feeding term has intentionally been omitted from the model; and 3) the potential for application of the model to a wide variety of environmental regimes, populations, and even species.

The robustness of any model will inevitably depend upon the nature of the inherent assumptions, and how well they are met. In this study, the assumption that otolith microstructure examination provided an accurate index of age was tested both through validation experiments and tests for inadequate resolution of narrow increments. The former were consistent with previous reports of daily increment formation in larval cod (Radtke and Waiwood 1980; Bergstad 1984; Dale 1984) in that increments formed daily in all but the early larval stage; the resolution limitations of light microscopy were almost certainly responsible for the poorer increment-age correlation among the youngest larvae. Age underestimation of the Gulf of

Maine larvae was less than or equal to the magnitude of that in the laboratory, implying a minimal bias. However, the bias would be expected to be more severe in slower-growing populations (Campana et al. 1987).

A second model assumption was that sea surface temperature (SST) adequately characterized the temperature environment of the larvae. Cod and haddock larvae are generally concentrated in the upper 30 m of the water column, above the thermocline (Tilseth and Ellertsen 1984; Ellertsen et al. 1984; Fridgeirsson 1984), where SST adequately reflects the temperature regime. Of course, neither day-to-day temperature anomalies nor small-scale spatial variations are reflected in the smoothed temperature record used here. However, given the fact that the drift path of individual larvae was also unknown, the temperature model provided a useful integration of temperature at the daily level.

The final assumption concerned the validity of the model formulation. Yet the empirical basis for a growth-temperature interaction in cod and haddock larvae is so strong that only the omission of such a term should have to be justified. The advantage of incorporating the temperature term at the daily level was the elimination of the need for broad estimates of the mean temperature experienced by a sample of larvae. While a posteriori tests for temperature effects have been successful in some instances (Crecco and Savoy 1985), there have been other studies where the explicit incorporation of a temperature term in the growth model may have proven more effective (Methot and Kramer 1979; Jones 1985; Walline 1985; Leak and Houde 1987). A secondary benefit of the temperature term was the apparently-reduced requirement for a feeding term. While an explanation for this is not yet clear, feeding effects upon growth should become evident in the model residuals, thus providing an index of relative food availability through the study period.

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Table 1. Summary of cruises represented in this study.

Year	Cruise	Date	Number of Stations Sampled	Number of Larvae Examined	
				Cod	Haddock
1984	H114	March 12-30	54	7	67
	H116	April 16-27	59	100	-
1985	H130	Feb. 4-22	93	15	-
	H132	March 11-29	49	42	7
	H133	April 2-17	90	202	40
	H135	May 6-16	57	95	136
	H137	June 3-14	59	35	372

Table 2. Sinusoidal model used to generate a daily sea surface temperature record from mean monthly temperatures. Separate models were developed for Browns and Georges Bank in each of 1984 and 1985. DOY = day of year.

$$\text{Model: Temp}(\text{°C}) = (a\text{Sin}(\frac{2\pi}{365}(\text{DOY} + b))) + c$$

Region	Year	Parameter Estimate			R ²	Estimated Temperature		
		a	b	c		Jan. 1	Mar. 1	June 1
Browns	1984	5.350	-158.5	8.417	0.98	6.2	3.1	7.7
	1985	5.301	-161.1	8.355	0.99	6.4	3.1	7.4
Georges	1984	5.088	-156.9	9.616	0.99	7.4	4.6	9.1
	1985	5.187	-159.5	9.290	0.97	7.2	4.2	8.5

Table 3. Increment width at Age 1 day in the otoliths of cod and haddock larvae collected on several cruises. The 1984 larvae were collected on Georges Bank while the 1985 samples were from the vicinity of Browns Bank. Widths were estimated for each otolith type from the logistic model relating increment count to otolith growth radius in each larva (see text for details).

Cruise Date	Increment Width (μm) at Age 1 day			
	Cod		Haddock	
	Lapillus	Sagitta	Lapillus	Sagitta
1984 : March 12-30	0.33	0.40	0.54	0.33
1985 : March 11-29	0.42	0.42	-	-
April 2-17	0.37	0.43	0.45	-
May 6-16	0.39	0.37	0.44	-
June 3-14	0.25	0.19	0.53	0.63

- = poor fit of model (pattern in residuals), rendering width estimation inappropriate

Table 4. Results of the first experiment reporting the frequency of increment formation in newly-hatched cod larvae.

EXPERIMENT 1

Model: Increment Count = a + b (Age)

Range of Ages = 0 - 14

; N = 42

P < 0.001

R² = 0.80

Parameters:	<u>Estimate</u>	<u>SE</u>	<u>Significance</u>
Intercept	-0.45	0.63	0.48
Slope	0.89	0.069	< 0.001

Table 5. Parameters and diagnostics of an exponential growth model $TL = \exp -(a + b \cdot \text{age})$ fitted to cod and haddock larvae (Figure 3) on a cruise-by-cruise and regional basis. All models were highly significant. Specific growth rates (% day⁻¹) for each cruise, region, and species are also presented.

Species	Region	Year	Cruise Date	Intercept (a)		Slope (b)		N	R ²	Specific Growth Rate	
				Estimate	SE	Estimate	SE				
Cod	Browns	1984	April 16-17	1.24	0.13	0.0133	0.0011	7	0.97	1.33	
			1985	Feb. 4-22	1.04	0.03	0.0217	0.0001	14	0.99	2.18
			March 11-29	1.02	0.02	0.0230	0.0012	39	0.91	2.30	
			April 2-17	1.13	0.01	0.0161	0.0002	184	0.97	1.61	
			May 6-16	1.02	0.02	0.0278	0.0009	69	0.94	2.78	
			June 3-14	1.01	0.04	0.0275	0.0011	24	0.96	2.75	
		Georges	1984	March 12-30	1.04	0.03	0.0186	0.00179	100	0.52	1.86
	1985		April 2-17	1.00	0.04	0.0272	0.0033	16	0.83	2.72	
			May 6-16	1.45	0.14	0.0225	0.0020	24	0.85	2.25	
Haddock	Browns	1984	March 12-30	0.828	0.044	0.0234	0.0023	67	0.61	2.34	
			1985	April 2-17	0.920	0.070	0.0258	0.0053	38	0.40	2.58
			May 6-16	0.905	0.034	0.0266	0.0028	130	0.41	2.66	
			June 3-14	0.941	0.017	0.0284	0.0007	370	0.79	2.84	

Table 6. Parameter estimates, associated error terms, and ANOVAs for a model integrating logistic growth and a parabolic temperature term in the estimation of larval length (see Model (6) in text). The model was fit to both cod (ln-transformed) and haddock (untransformed) data collected on and around Browns Bank in 1985.

Species	Source of Error	Sum of Squares	df	Mean Square	R ²	Parameter	Coefficient	SE
Cod	Model	875.81	5	175.16	0.96	G	0.05016	0.00274
	Error	3.2169	357	.00901		L _∞	59.18	13.44
						t ₀	60.57	2.33
						c	22.77	4.44
						T _{opt}	5.925	0.195
Haddock	Model	11047	5	2209.5	0.83	G	0.1571	0.0110
	Error	158.02	539	0.29318		L _∞	5.467	5.081
						t ₀	24.44	0.89
						c	44.00	39.79
						T _{opt}	6.701	0.936

List of Figures

- Figure 1. The location of sampling stations relevant to this study during the ichthyoplankton survey of southwest Nova Scotia in 1984 and 1985. Coverage of the survey grid varied slightly among cruises (Table 1).
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- Figure 4. Exponential growth models for haddock larvae collected on each of 4 cruises on Browns and Georges banks in 1984 and 1985. Model statistics are presented in Table 5.
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temperature (3° or 7° - second digit in label) for the remaining 30 d. Temperature had the most sustained effect on growth when absolute growth rate was greatest.

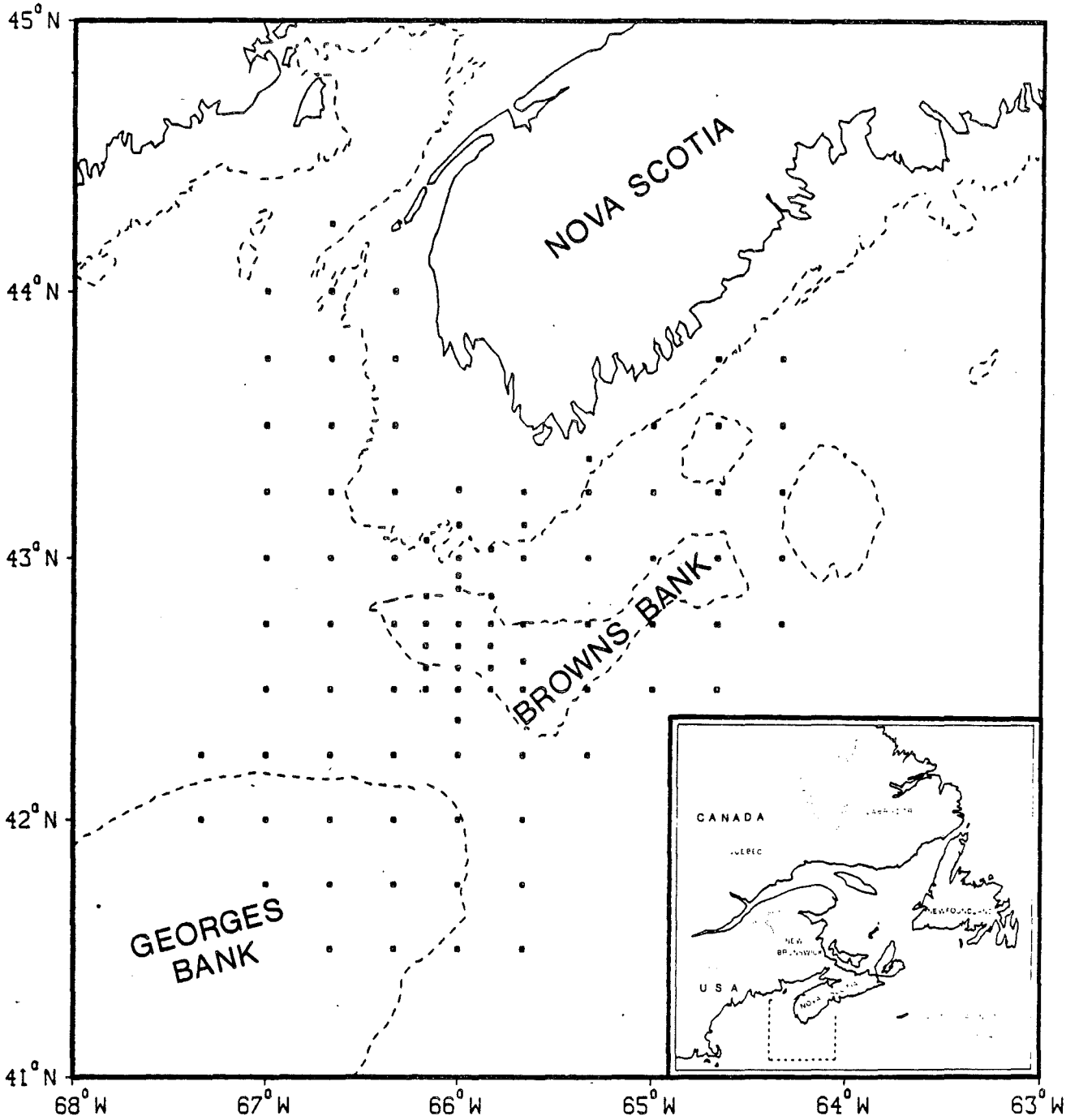


Figure 1. Map of study area. Points represent collection stations.

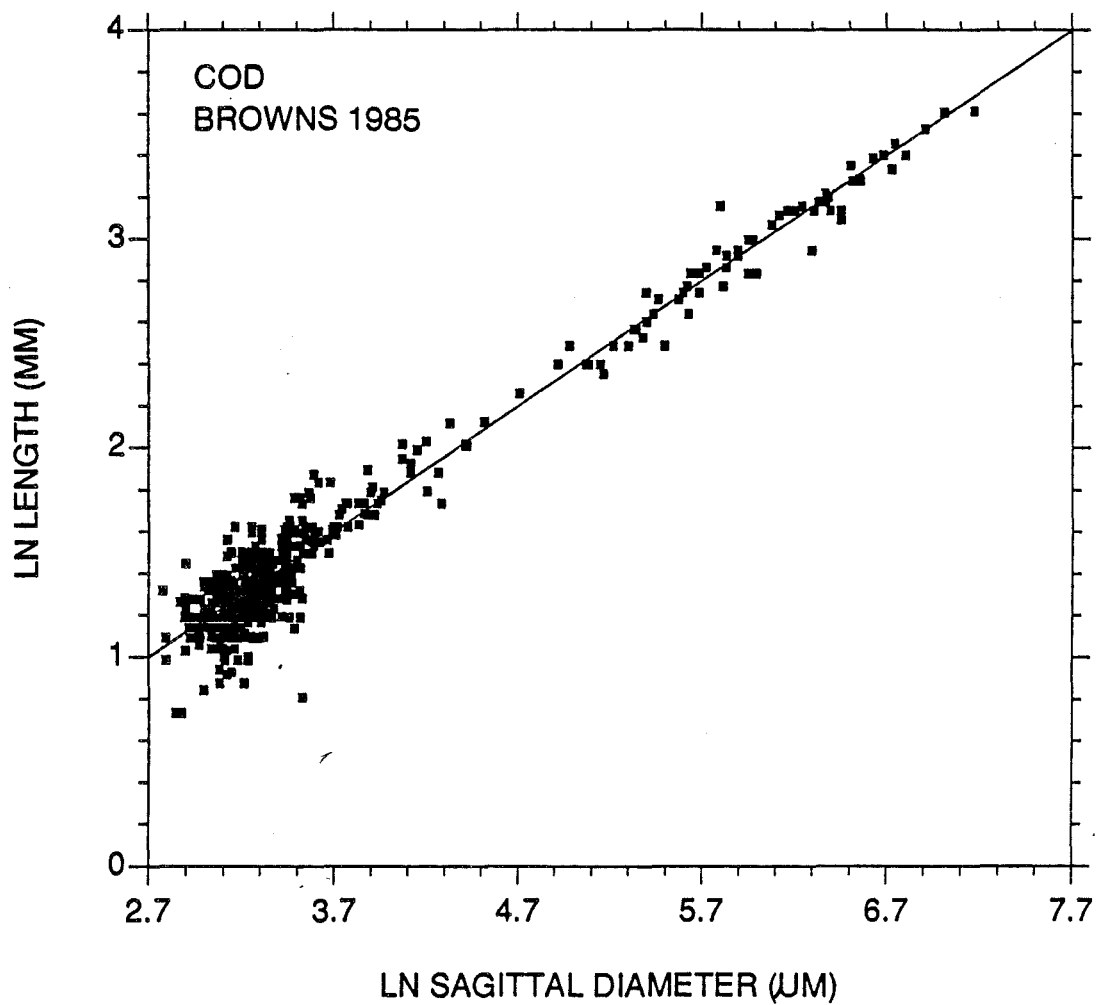


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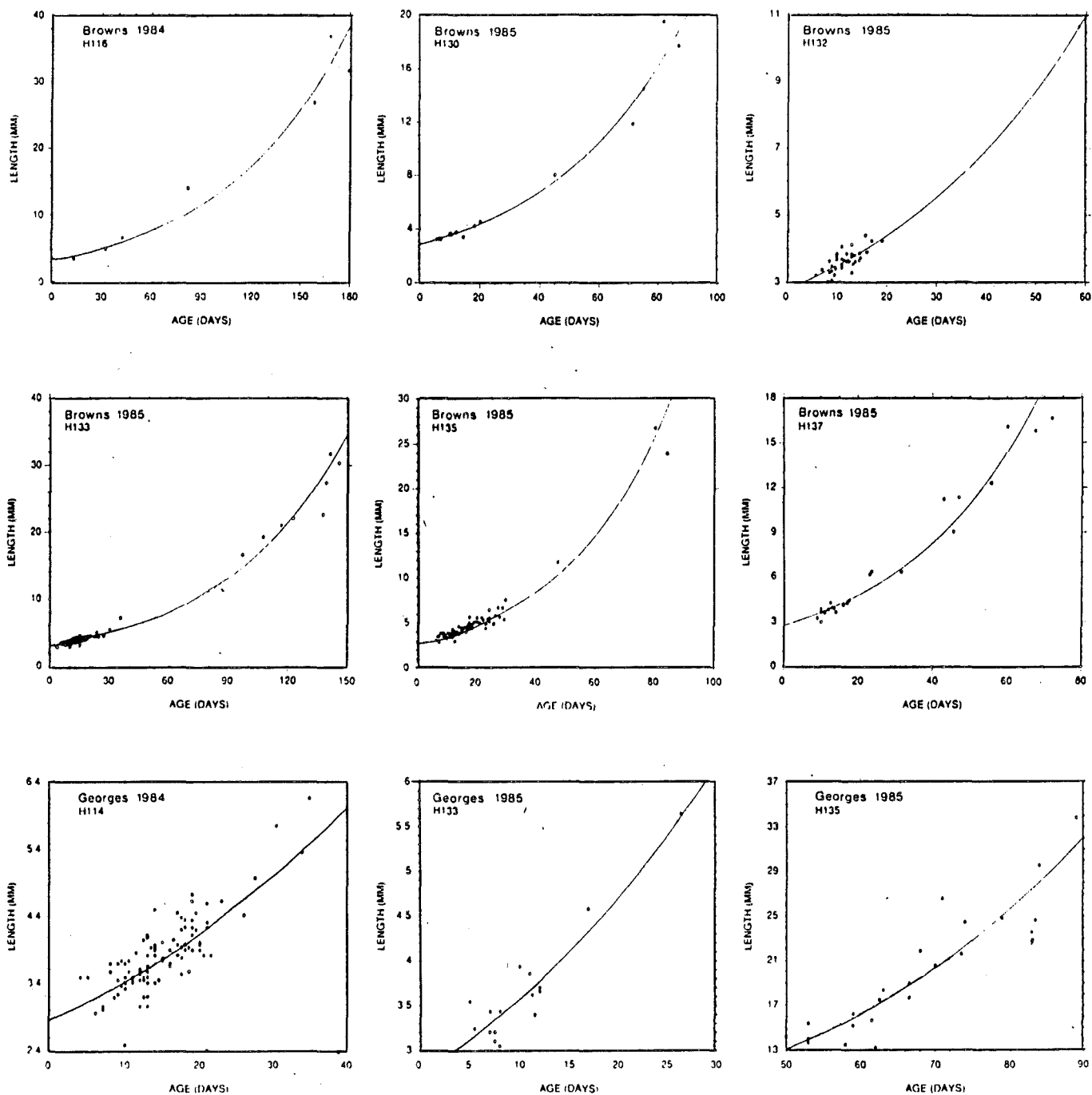


Figure 3. Exponential growth models for cod larvae collected on each of 7 cruises on Browns and Georges banks in 1984 and 1985.

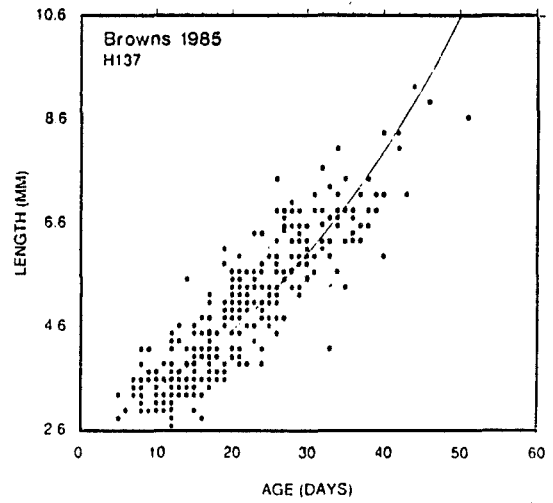
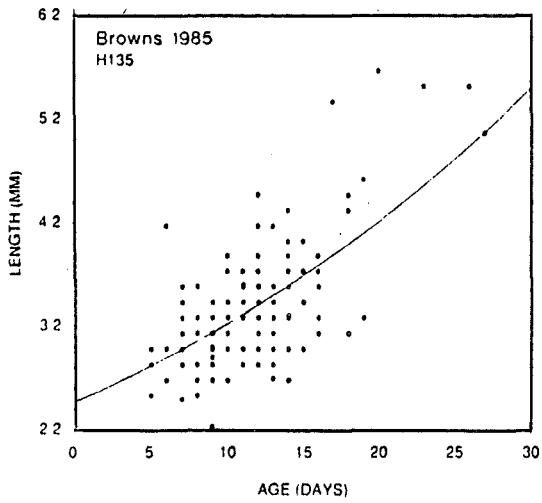
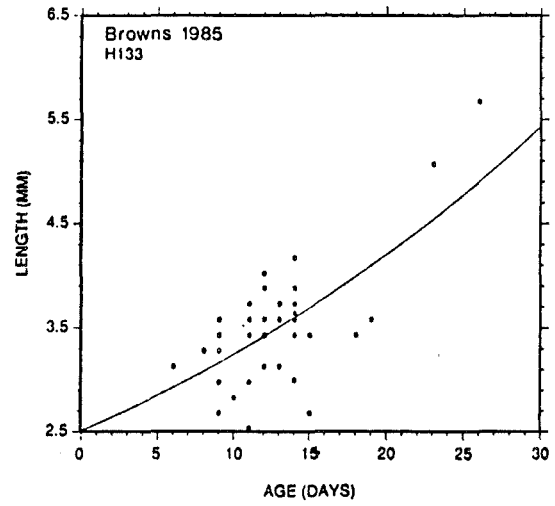
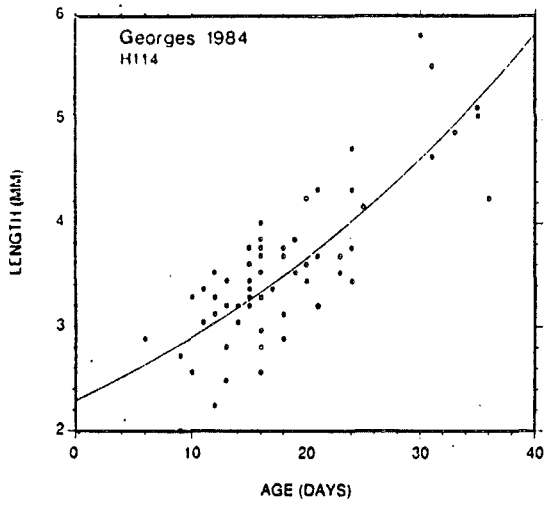


Figure 4. Exponential growth models for haddock larvae collected on each of 4 cruises on Browns and Georges banks in 1984 and 1985. Model statistics are presented in Table 5.

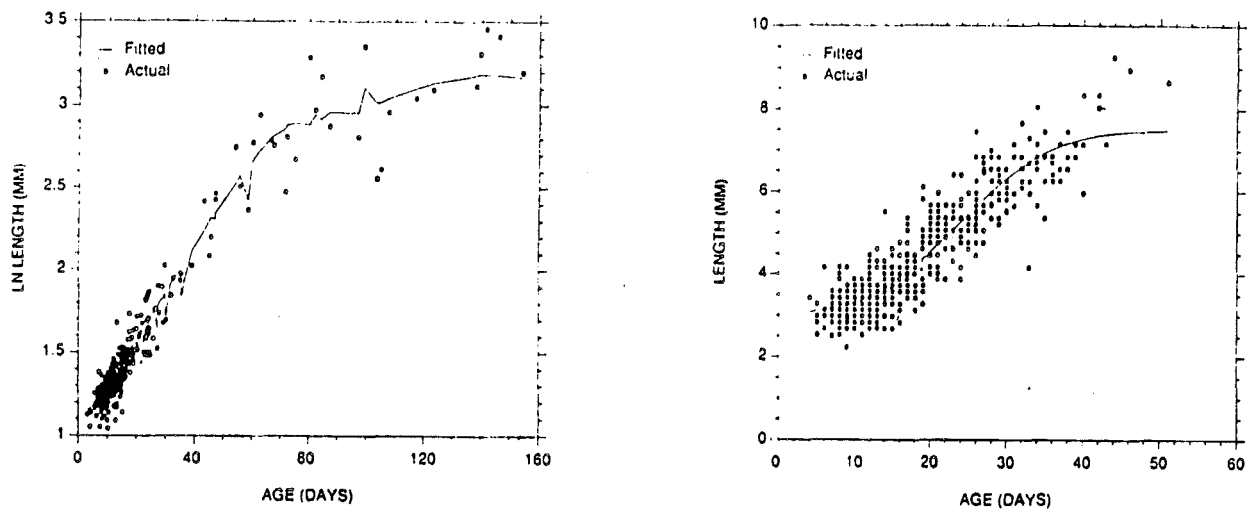


Figure 5. Fit of an age- and temperature-mediated growth model (Equation 6, described in text) to cod (left) and haddock (right) larvae on Browns Bank in 1985. Data were aggregated across cruises. The model assumes logistic growth and a parabolic relationship between temperature and absolute growth rate on a daily basis. The fitted line appears irregular since only one of the two independent variables is plotted. Model results are summarized in Table 6.

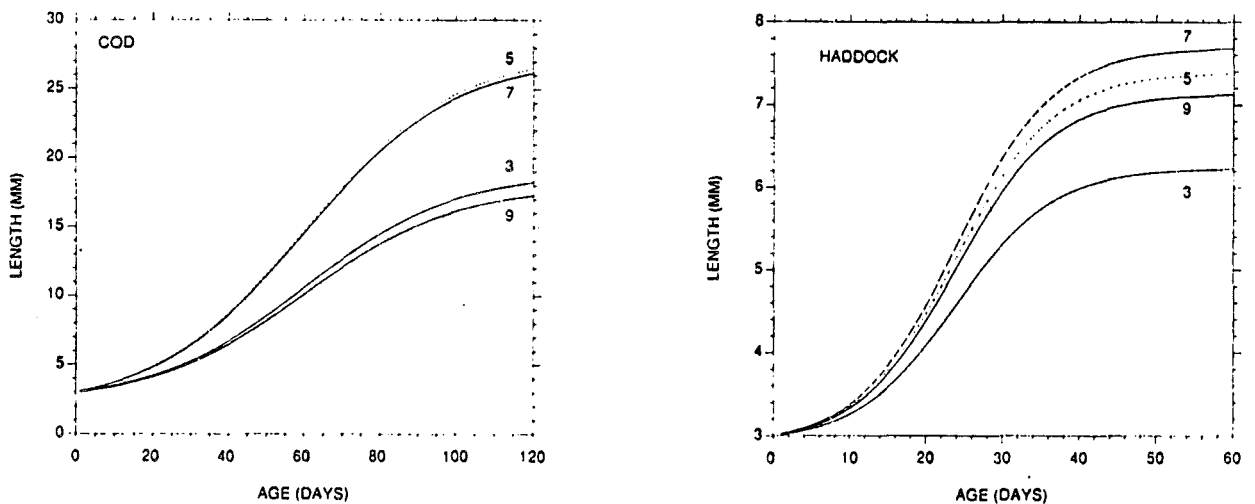


Figure 6. Growth projections for cod and haddock larvae at various constant temperatures as predicted from Model 6 (described in text). Digits refer to the temperature in $^{\circ}\text{C}$.

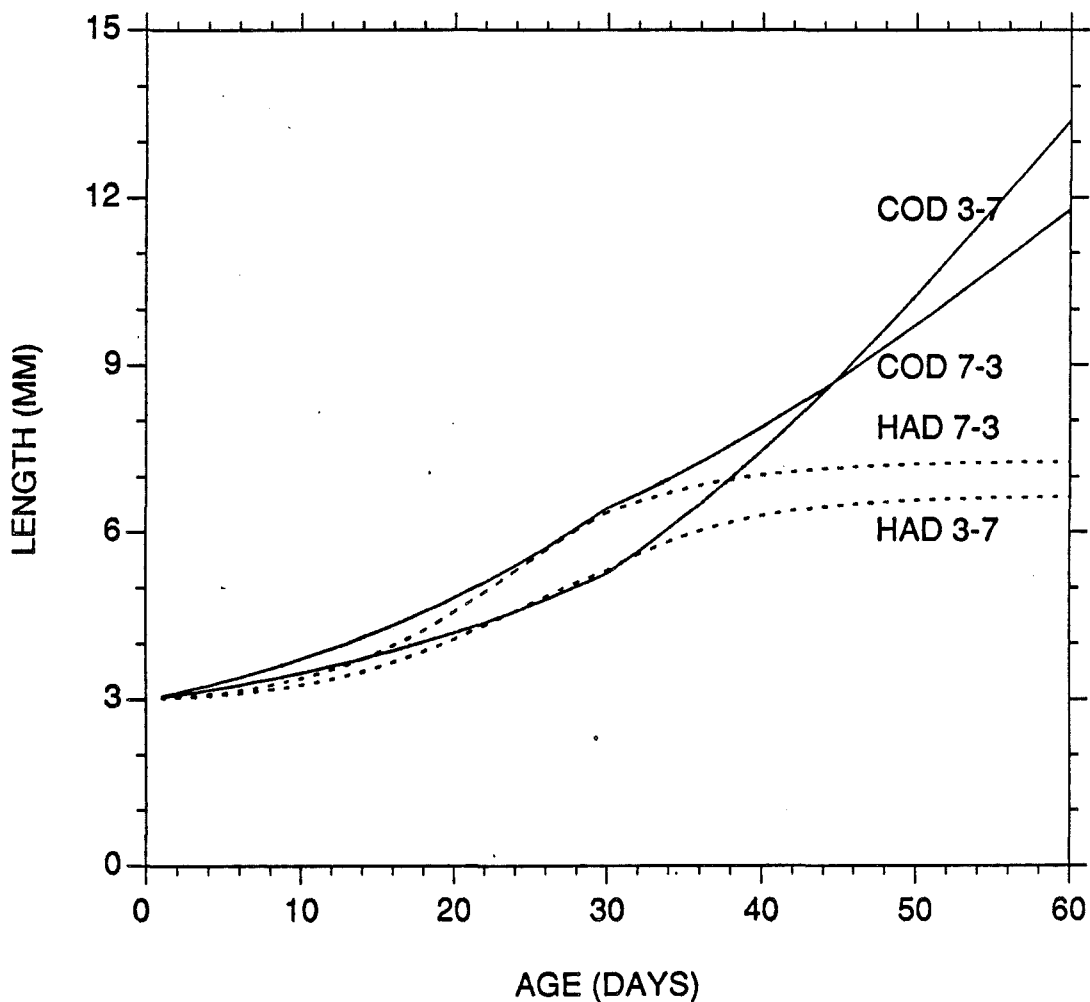


Figure 7. Growth projections from Model 6 (described in text) for cod and haddock larvae under interrupted temperature regimes. Temperature was held constant at one temperature (3° or 7° - first digit in label) for 30 d, following which it was shifted to a second temperature (3° or 7° - second digit in label) for the remaining 30 d. Temperature had the most sustained effect on growth when absolute growth rate was greatest.

AGEING AND BACK-CALCULATING GROWTH RATE OF PACIFIC
HERRING (*Clupea harengus pallasii*) LARVAE BY READING DAILY
OTOLITH INCREMENTS

By

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ABSTRACT

Newly hatched Pacific herring (*Clupea harengus pallasii*) from eastern Bering Sea were released into an outdoor concrete basin and raised on natural plankton. The larvae were sampled frequently during the first two months and an growth curve for that period has been established. Otoliths from 52 herring larvae in the whole experimental period were examined for daily increments. Increments were formed on daily bases from the end of the yolk sac stage (age 8 days) and independent of the growth rate of the herring larvae. The increment widths reflected the growth rate of the larvae.

INTRODUCTION

Otoliths have been used to estimate daily age and growth since Pannella (1971) reported that the number of primary increments in otoliths approximated daily deposition. Brothers et al. (1976) raised northern anchovy (*Engraulis mordax*) and California grunion (*Leuresthes tenuis*) from eggs in the laboratory and verified that increment formation was daily. Jones (1986) found that daily increment analysis has been applied to at least 29 species of larval fish to estimate age, but validation of the technique was based on laboratory observations which may not be valid for wild populations. Atlantic herring (*Clupea harengus*) have been investigated for daily increment formation (Gjøsæter and Øiestad 1981, Geffen 1982, Jones 1985, Lough et al. 1982 and Messieh et al. 1987). The results of validation studies are inconclusive for Atlantic herring (Jones 1986). Gjøsæter and Øiestad (1981) found 99 increments in 97 d.-old herring grown in a large outdoor enclosure, however their sample size was too small to be conclusive (Jones 1986).

The early life history of Pacific herring (Clupea harengus pallasii) from the eastern Bering Sea was studied in the same enclosure as Gjørseter and Øiestad (1981). The herring were all spawned on the same day and larvae hatched over a 3 day period. Otoliths were examined periodically through the experiment and from surviving individuals at the termination of the experiment.

MATERIAL AND METHODS

Herring eggs for the experiment were collected from the spawning grounds in Bristol Bay at low tide on 24 May 1986. The eggs collected had been deposited between 22 May and 23 May on intertidal rockweed (Fucus sp.). Water temperature at the time of spawning was 4.5 °C and salinity was 30 ‰. Spawning did not occur before or after this one spawning event in the area the eggs were collected. Fucus fronds with light egg coverage (1-2 egg layers) were collected at random within the spawning area. The Fucus fronds with eggs attached were packed into half liter plastic bags, filled with seawater and sealed. A total of 25 bags were filled with about 2000 eggs/bag. The bags were placed in insulated shipping containers with gel ice. The containers were shipped via air to the Flødevigen Biological Station in Arendal. Upon arrival at Flødevigen the eggs were unpacked and placed in hatching boxes which were supplied with flowing seawater at 7.7 °C and salinity of 32 ‰.

The eggs began hatching on 10 June 1986 and was complete by 12 June 1986. 50 % hatching (11 June) were defined as day 0 (age = 0) in the experiment. Newly hatched larvae were collected from incubation boxes in white plastic cups in groups of 5 - 25, counted, and transferred to 5 L cylinders placed in a 8.1 °C water bath. A total of 25,200 larvae hatched from an estimated total of 50,000. The eggs were not treated during incubation and heavy fungus growth developed which caused most of the egg mortality.

On 13 June (age 2 days) 24,840 larvae were released into a large artificial outdoor basin 2000 m³ in volume, 600 m² surface area and a maximum depth of 3.5 m. The basin had been filled with sea water pumped from a depth of 19 m. At the time the larvae were introduced phytoplankton and zooplankton production was high. The basin were drained the 12. August and the remained herring larvae in the basin collected (age = 62 days).

The larvae in the basin were sampled daily using a two chambered plankton net of 500 µm mesh and a total sampling area of 0.3 m². The net was drawn diagonally across the basin at a depth of 2 m. The total volume sampled was 7.5 m³. All the larvae were preserved in 80% buffered ethanol. A more detailed description of the basin experiment is given in Weststad and Moksness (1988). The standard length (snout to the tip of the notochord or hypural plate) of the larvae/juveniles were measured to the nearest 1.0 mm. The largest otolith, the sagittae, were removed and mounted on a glass plate and as mounting medium clear nail polish was used. The dry weight of each individual was measured to the nearest ± 1 µg, after drying at 60°C for 24 hours. Otoliths of herring

juveniles over 30 mm had to be ground to expose growth rings. This was done by grading with fine grain paper (0.3 and 30 μm). The Maximum magnification that could be used to read the growth rings in the microscope was 400, due to insufficient light penetrating through the microscope. Table 1 gives an overview of the number of larvae used in otolith analyzes. A more detailed description of the otolith analyzing system and the method used are given in Andersen and Moksness (1988).

Table 1. The number of larvae examined for daily increments in each age-group.

Date	Age	Number examined
25. June	14	1
3. July	22	2
10. July	29	5
14. July	33	5
18. July	37	5
21. July	40	5
27. July	46	10
12. August	62	19

RESULTS

The relationship between the estimated age (estimated number of rings) and the actual age of the herring larvae is shown in Fig. 1. The residuals are shown in the same figure. The relationship was linear and the deposition rate was not significantly different from one increment per day from age 8 days of the larvae (t-test; $t=0.08$, d.f.=50). The residuals were equally distributed around the zero indicating no trend in the data. The relationship between the discrepancy (real age minus estimated age) and actual age of the herring larvae is shown in Fig. 2. The discrepancy did not tend to change sign or range with the age of the larvae, indicating that the frequency of daily increments in the otoliths did not change with the age of the larvae. The standard deviation of estimated age from real age was ± 4.2 days with a range from -12 to + 11 days. At hatching the range was -1 to + 1 days with a standard deviation close to ± 1 day. In Figs. 3 and 4 are shown the estimated age to the standard length of the larvae at age groups 46 and 62 days respectively. The results shown in figures 3 and 4 indicate that there is little correlation between estimated age and length which signify that there is no relationship between the rate of otolith ring deposition and larval growth.

Three different relationships between larval standard length and otolith radius are presented in figure 5. All three relationships exhibited a high degree of correlation ($r>0.96$), but equation 5a provided the best fit to the initial length of the larvae.

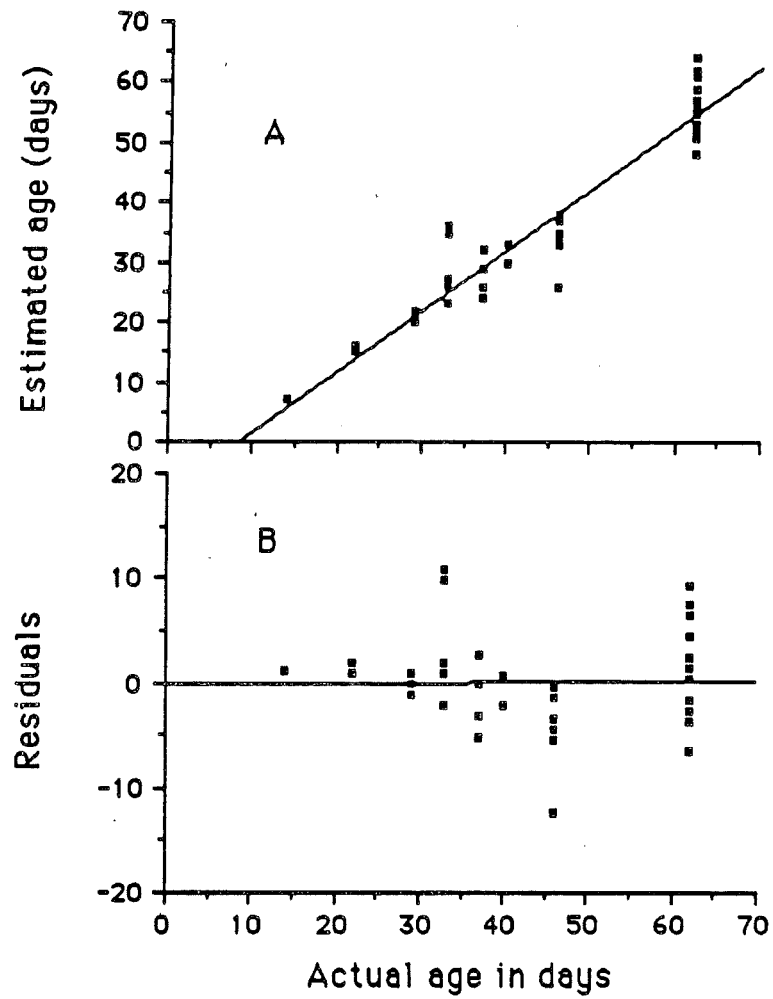


Figure 1. Relationship between estimated and actual age in days (A), $y = -8.3 + 1.0144 * x$, $r = 0.96$ and the pattern of the residuals (B).

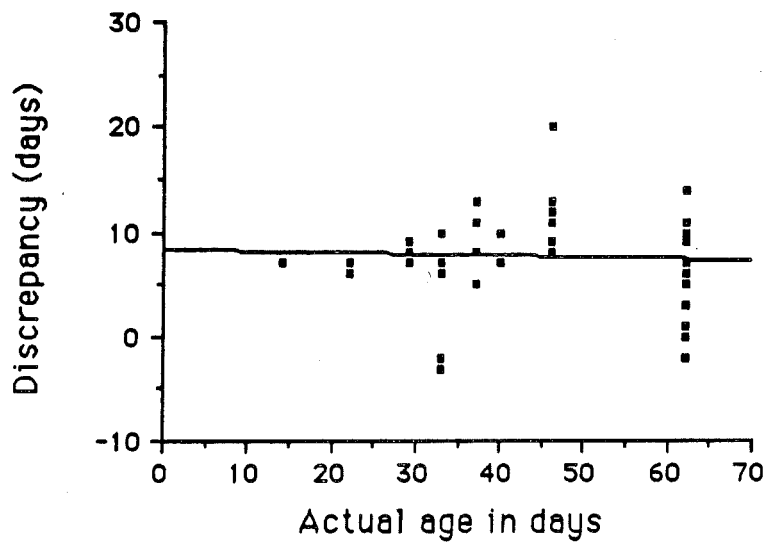


Figure 2. Discrepancy between estimated age (real age minus estimated age) and actual age as a function of actual age. $y = 8.3 - 0.014 x$, $r = 0.05$.

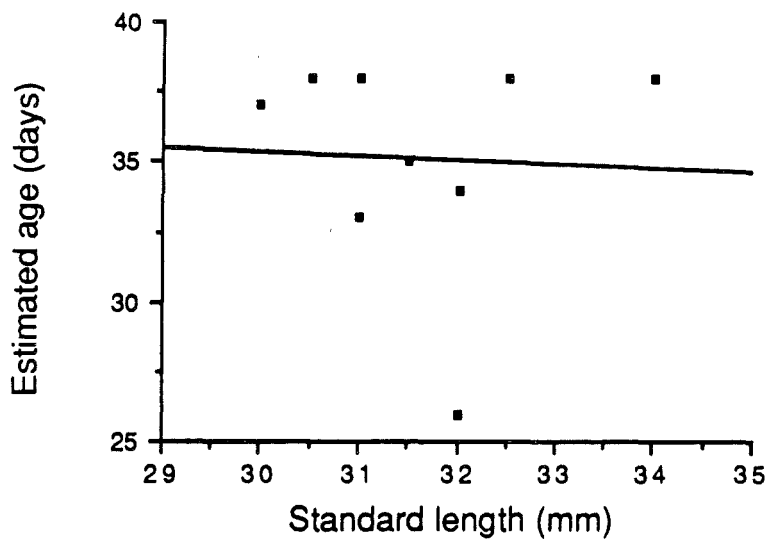


Figure 3. Relationship between estimated age and standard length in larvae of same age. Age 46 days. $y = 39.63 - 0.14x$, $r = 0.04$.

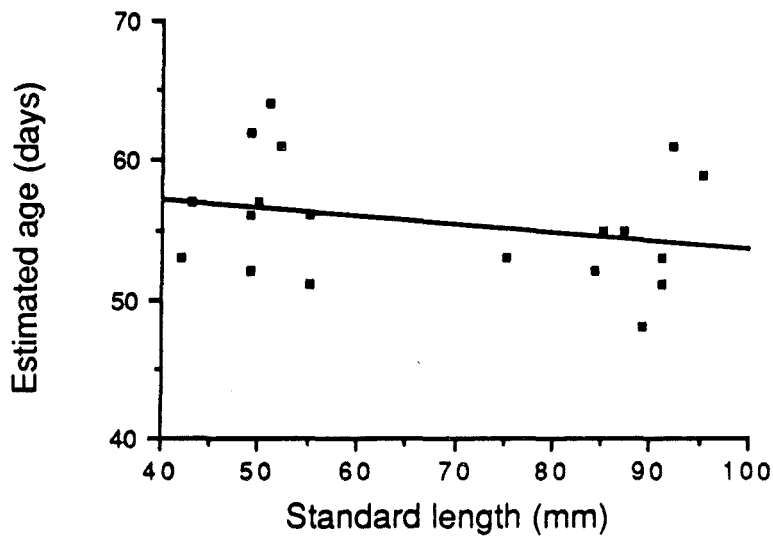


Figure 4. Relationship between estimated age and standard length in larvae of same age. Age 62 days. $y = 59.53 - 0.06x$, $r = 0.27$.

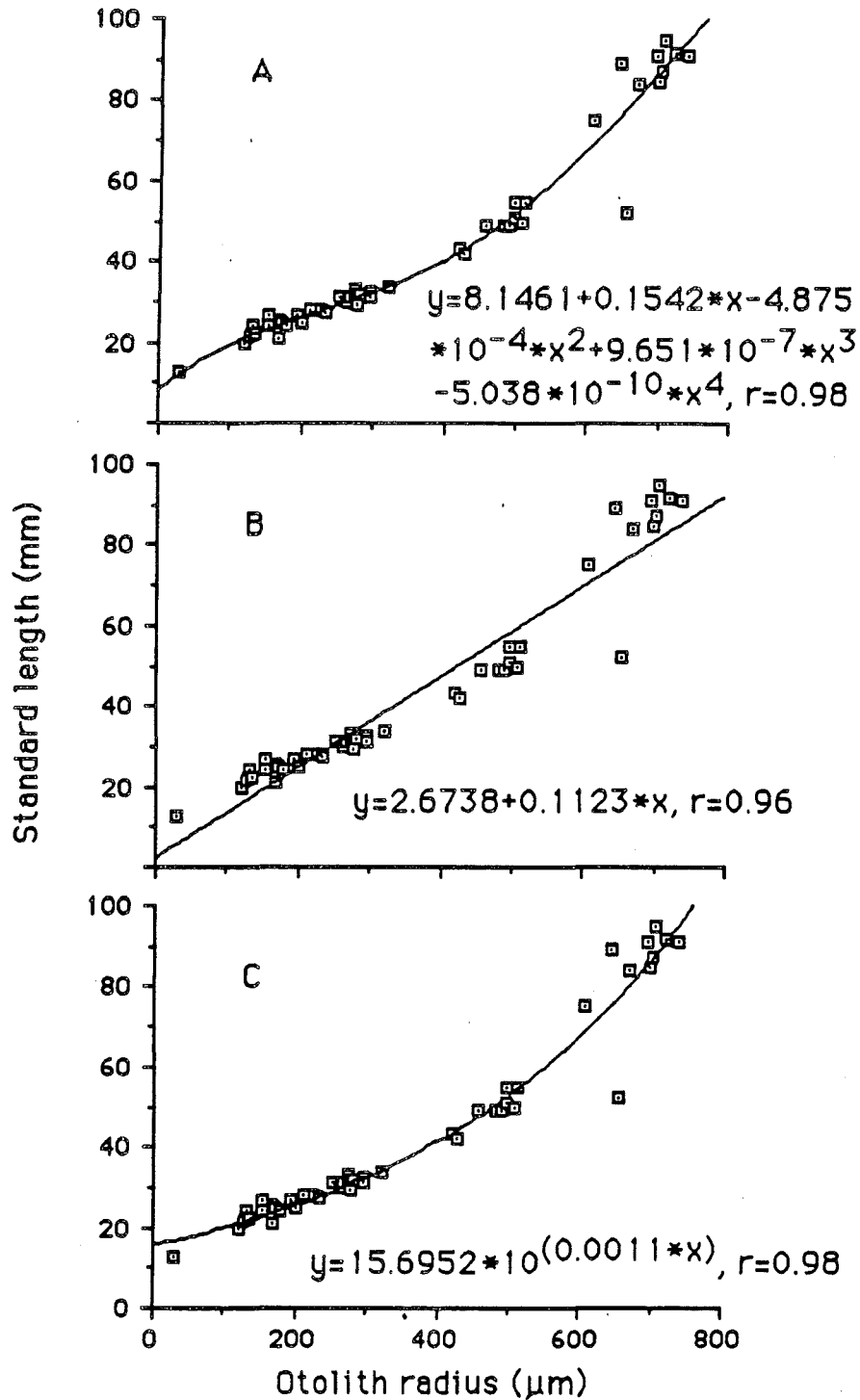


Figure 5. Relationship between otolith radius (x) and standard length (y) of the larvae.

The estimated growth oncrements (mm/day) based on equation A are shown in figures 6 - 8 for all the otoliths examined. The average daily growth rate and +/- 1 standard deviation calculated from all otoliths with equation A is presented in figure 10 along with the estimated minimum, maximum and average growth rate obtained from the herring measured at termination. The figure shows that there is a high similarity in the

trends of the growth curves between the different age groups (Figs. 6, 7 and 8). The daily growth rate calculated from the standard length of the larvae at termination of the experiment shown an average of 0.66 mm/day, a minimum of 0.31 and a maximum of 1.48 mm/day. Estimation of the average growth rate using the results in Fig. 9 gives a average growth rate of 0.73 mm/day.

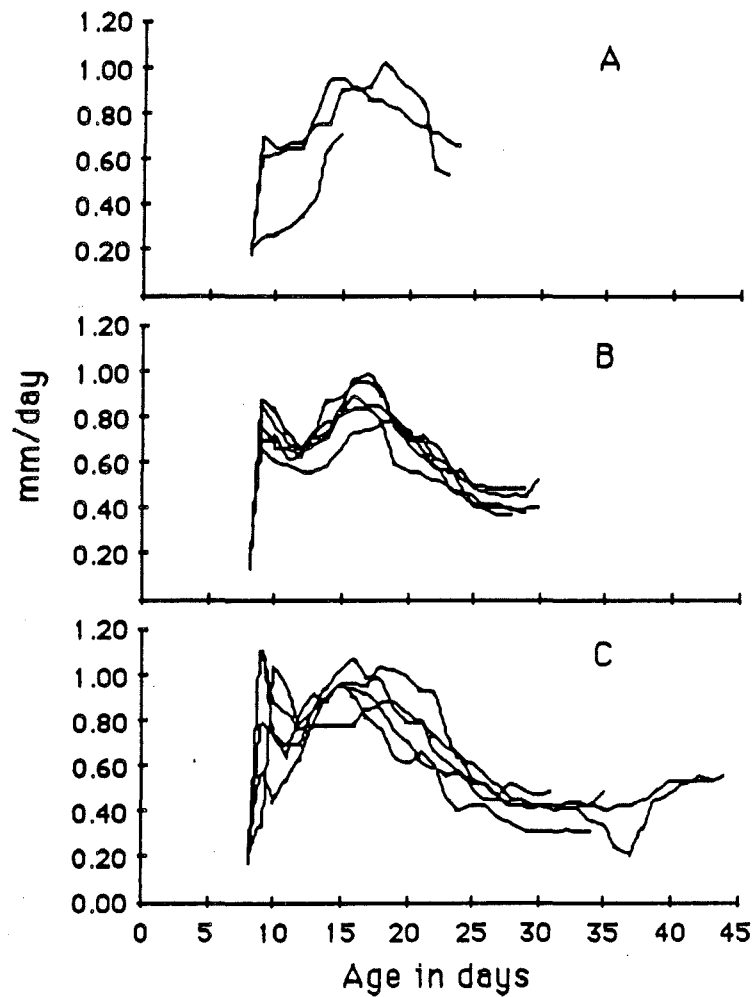


Figure 6. Daily length increment (DLI) estimated from otoliths in 14 and 22 days (A), 29 days (B) and 33 days (C) old herring larvae.

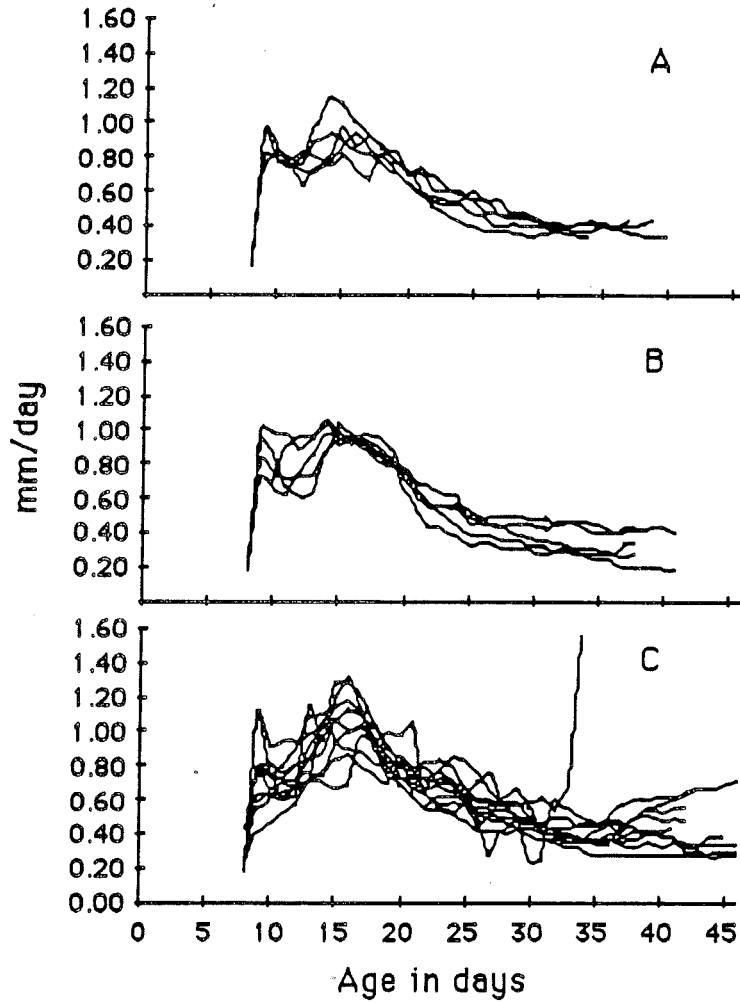


Figure 7. Daily length increment (DLI) estimated from daily increments in otoliths of 37 days (A), 40 days (B) and 46 days (C) old herring larvae.

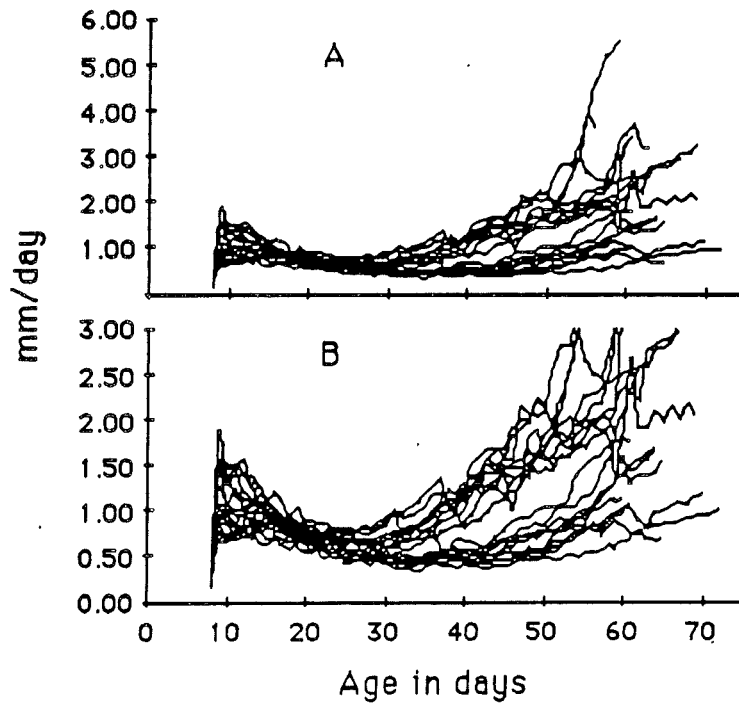


Figure 8. Daily length increment (DLI) estimated from daily increments in otoliths from 62 days old herring larvae. The estimated daily length increment (A) and enlargement (B) of the same data.

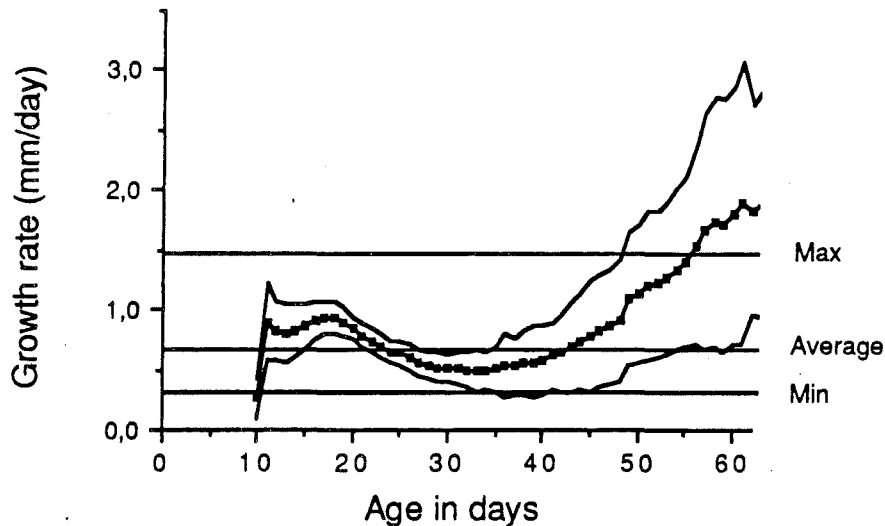


Figure 9. The average daily growth rate (mm/day) estimated from otolith analyzes (•) with ± 1 standard deviation. The minimum (min), average and Maximum (Max) growth rate (mm/day) calculated from herring surviving to the termination of the experiment (day 62) are indicated.

DISCUSSION

The present paper gives evidence of daily increments in the otoliths of Pacific herring, which are in accordance with earlier investigations in the same species (McGurk 1984a). A difference of 8 days was observed between the estimated age in days and the actual age in days of the larvae. This corresponds well with the end of yolk sac stage of the same larvae given in Wespestad and Moksness (1988) which is three days later compared to the observations by McGurk (1984b) on Pacific herring larvae at the same temperature (8.0 °C). This results also confirm that mesocosms are a method for studying of marine fish larvae and juveniles. It confirms earlier investigations with Norwegian spring spawning herring in mesocosms (Gjørseter and Øiestad 1981) with one increment per day. It confirm the tendency reported by Geffen (1982), of an increasing growth coefficient from the small laboratory tanks up to mesocosms in the size from 2500 to 4400 m³. These results strongly indicate that laboratory experiments produce the phenomenon that increments are not formed daily in the otoliths initially due to low growth rate as reported by Moksness et al (1987). The use of mesocosms has also been successful with other species such as the capelin (*Mallotus villosus*) reported by Gjørseter and Monstad (1985).

The range in the residuals and deviations reported in this paper are belived due to the use of low power microscope equipment. The maximum magnification available was 400 x, which later has been shown

too low to give good resolution of the otoliths. Unfortunately, the otoliths used in this study had been ground and could not be fully read again. Campana et al. (1987) concluded that light microscopes have limits in indentifying small increments. In this study, a 400 x magnification probably resulted in the production of a poor image of the otolith which lead to an range of erroneous readings around the actual age.

The lack of correlation between growth rate of the larvae and the number of increments in the otoliths are counter to the results of Geffen (1982) on Atlantic herring and McGurk (1984a) on Pacific herring. A possible explanation of the above discrepancy between this paper and results from Geffen (1982) and McGurk (1984a) might be an observed minimum growth rate on average of 0.31 mm/day in this study. The results reported here is important when age in days is to be estimated and also when one want to distinguish between a spring and autumn spawned herring as reported by Fossum and Moksness (1988).

Otolith increment size was well correlated with the measured growth in standard length of the larvae. The choosen equation in this paper is probably not the right one, but gave a good fit with the observed values. The number of observation are to small and specially the smallest larvae are lacking in the samples. An exponential fit might be a better one with more data available. When fitting the data on dry weight of the larvae to then radius of the otolith a very good fit was observed for the exponential equation.

The resulting daily length increment from the choosen equition gave a good description of the calculated daily length increment reported by Wespestad and Moksness (1988). This indicates that by estimating the relationship between the standard length of the larvae and the radius of the otolith, this relationship will give a good description of the daily length increment of the fish.

ACKNOWLEDGEMENT

We would like to thank Technical Assistant Inger Henriksen at Flødevigen Biological Station for reading the otoliths. Partial funding for this study was provided by NFFR grant.

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IDENTIFICATION OF 0- AND I-GROUP REDFISH BY ELECTROPHORESIS

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ABSTRACT

The aim of the present study is to develop and utilize electrophoretic methods on north-east Atlantic redfish (Genus Sebastes) for identification of individual specimens or groups of specimens when morphological traits are insufficient for proper classification. This is especially the case for 0-and I-group fish of these species. Hemoglobins and totally 17 enzymes in white muscle, heart, eye and liver were analysed. In adult specimens only some of these enzymes turned out to be useful for the separation of the species. For 0- and I-group fish, therefore, only 4 enzymes were analysed. The enzymes were identified by histochemical staining procedures. S. viviparus was identified by phenotypes of malate dehydrogenase (MDH) in all tissues, isocitrate dehydrogenase (IDH) in eye and malic enzyme (ME) in liver. To identify individual specimens of S. mentella blood samples are needed because only the hemoglobin patterns are diagnostic for this species relative to S. viviparus and S. marinus. All species could be group identified by use of frequency distributions of IDH (liver) and ME (all tissues) phenotypes.

INTRODUCTION

Three species of Sebastes are known from the Norwegian waters, Barents Sea and Svalbard area: Sebastes marinus, Sebastes mentella, and Sebastes viviparus. Several attempts have been made to distinguish these species from each other. It may even be difficult to distinguish adults in some areas, but the problems increase with smaller size of the specimens. Morphological (e.g. preopercular spines, body shape, beak, colour) and morphometric characters (e.g. eye diameter) as well as other attributes have mostly been used (Einarsson 1960, Barsukov 1973, Magnusson and Magnusson 1977). Such characters may often be difficult to use because of different development of the young depending on different areas and time of release, and also the possibility of having been influenced by the environment. We also feel that morphological and meristic criteria for distinguishing these species need a very well trained and experienced eye.

Twenty-three annual international 0-group fish surveys have been made in the Barents Sea and adjacent waters since 1965. These surveys have never been able to identify the different redfish species, neither have the following years' young fish surveys on I-group fish. Consequently, we have so far not been able to produce an index of the yearclass strength of each species at an important early 0- or I-group stage.

Recent electroforetic works on adult specimens of S. marinus, S. mentella, and S. viviparus have shown that these species can be identified by use of hemoglobin and/or tissue enzymes (Nedreaas and Nævdal, in press). In the present paper we have discussed to what degree it is possible to transfer our genetic knowledge on adult redfish down to the 0- and I-group stage.

MATERIAL AND METHODS

Material for the present study was collected onboard research vessels belonging to the Institute of Marine Research. A total number of 425 0-group and 64 early I-group redfish were collected and analysed onboard R/V "Eldjarn" 17.8.- 3.9.87 and R/V "G.O.Sars" 23.2.- 8.3.88, respectively. Figure 1 shows the distribution of 0-group redfish during the international 0-group survey in 1987. Figure 2 show an identical map with the sampling sites of the analysed 0-group redfish being indicated.

The fish were sampled immediately after the catch had come on deck. Under field conditions it may be very difficult to have blood samples from individuals less than 50 mm. The mean length of the 0-group redfish in the surveyed area in 1987 was 30 mm. However, we succeeded in collecting hemoglobin samples from individuals between 30 and 50 mm by sucking up small quantities of blood with a pipette when the fish were bled in the gill region, or by sucking up the blood by use of a piece of filter paper. The agar gel had in advance been prepared so either was the blood sample placed directly into small wells in the gel, or the gel was sliced vertically and the filter papers placed in the slit. In either case the blood was used whole, and the cells ruptured during the electrophoretic process.

Experience from our previous electrophoretic work on adult Sebastes spp. (Nedreaas and Nævdal, in press) made us decide which enzymes and tissues from 0- and I-group fish it was worth while to analyse. Muscle, liver, eye, and whole fish were used. Trawl catches of adult specimens gave us control samples. Electrophoresis of the tissue samples was made immediately or not later than 24 h after first freezing the samples.

The hemoglobins were subjected to agar gel electrophoresis at pH 8.0. The concentration of the TRIS-HCl gel buffer was 1/10 of the buffer for the electrodes. A 2% agar concentration was used, and the samples were run at 90 mV for half an hour.

The tissue enzymes were analysed by horizontal starch-gel

electrophoresis followed by selective staining of the enzymes (Allendorf et al. 1977, Aebersold et al. 1987). In this study we concentrated our effort on the enzymes Isocitrate dehydrogenase (IDH), Malate dehydrogenase (MDH) and Malic enzyme (ME). We also looked upon Lactate dehydrogenase (LDH). Only one buffer system was used, namely Citric acid/morpholine buffer (AM), pH 6.1 (Allendorf et al. 1977), which according to earlier experience gave the best resolution for adult redfish.

RESULTS

HEMOGLOBINS

The results of the hemoglobin analyses seem to be in good accordance with our previous studies, but we noticed a slight difference in the migration on the gel compared with the adult controls. Since we most probably did not catch 0-group S.marinus or S.viviparus we were not able to compare 0-group of all three species on the same gel. Nevertheless, the slightly different migration distance of hemoglobins between 0-group and adult mentella did not interfere or overlap with the adult marinus or viviparus controls.

TISSUE ENZYMES

The results of the tissue analyses were in accordance with the results obtained in the studies on adult Sebastes spp. (Nedreaas and Nævdal, in press).

Isocitrate dehydrogenase (IDH) - Strong patterns of activity were seen in both muscle and liver, especially in muscle. The very clear intraspecific variation in liver IDH in older marinus and viviparus did never occur in the 0-group samples. In the analysed I-group redfish this specific variation occurred and corresponded to the morphological criteria we used. On four 0-group stations outside

Bellsund, Spitsbergen, we observed a weak but probably true polymorphism in liver from mentella. This enzyme seemed to have a dimer structure with the rare faster-moving allele identical to the rare allele in liver IDH reported by Nedreaas and Nævdal (in press).

Lactate dehydrogenase (LDH) - The observed patterns in muscle, liver, eye and whole fish (O-group) were the same as those reported from older redfish. However, LDH did not seem to give any useful information for separating the Sebastes spp.. The pattern was especially strong in muscle but there were no indications of polymorphism.

Malate dehydrogenase (MDH) - Also here strong patterns of activity were observed in both muscle, liver, eye and whole fish (O-group). The observed bands were in complete accordance with the observations described by Nedreaas and Nævdal (in press). The MDH component found in

liver was also the stronger band in extracts from muscle and whole fish. A variant described by Nedreaas and Nævdal as a rare heterozygote in liver of S.mentella was found once in the O-group samples.

Malic enzyme (ME) - Possible variations of this enzyme is often difficult to display because of low activity. Fresh samples improve the interpretation considerably. The ME pattern in liver is diagnostic for older viviparus versus the other two species (Nedreaas and Nævdal in press). This diagnostic viviparus pattern did never occur in the present study of O-group fish, but in the analysis of I-group fish this pattern occurred as expected.

In the earlier referred analysis of older redfish intraspecific variation was only seen in muscle for S.mentella where five alleles seem to be involved. In this study only three of these alleles were observed. Because of this intraspecific variation only found in mentella, ME in muscle is helpful in separating mentella from the other two species. This intraspecific variation in muscle ME occurred in all samples of O-group fish which in addition to the hemoglobin analyses made us conclude that all O-group redfish analysed were S.mentella. This conclusion is further supported by the fact that the

common IDH polymorphism of S. viviparus and S. marinus was not observed.

DISCUSSION

This work must be considered as preliminary since the results show that we most probably only managed to sample and analyse S. mentella. Although we did not get any contradictory results compared to our previous work, we are not able at this stage to draw too firm conclusions since we most probably have not yet seen a marinus or a viviparus pattern from 0-group specimens less than 60 mm. Based on the few samples we have on early I-group redfish (January-February) these fishes show the adult electrophoretic pattern both in hemoglobin and in the analysed tissue enzymes. At this stage the specific morphological traits for each species are also more pronounced.

For many mammals, including man, the fetal hemoglobin is slightly different from the maternal hemoglobin. This is in part due to a difference in the organic phosphate within the red cells (Schmidt-Nielsen 1979). This gradually disappears after birth and by twenty weeks has been replaced by the adult type (Villem 1977). All species of Sebastes are ovoviviparous. The observed slight difference in migration distance of hemoglobins between 0-group and adult mentella may be a result of a fetal hemoglobin type present in 3-4 months old 0-group.

More data are needed. However, the present results of 0- and I-group redfish show that we most probably can transfer results obtained on adult fish down to these youngest stages and thereby use the same criteria for identifying 0-group fish.

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Vessel station	and lat	Location long	Sample size
O-group:			
14439	7053	1857	24
14441	7114	1759	12
14443	7200	1559	8
14448	7331	1411	28
14455	7900	0500	12
14456	7937	0501	4
14457	7937	0736	4
14463	7859	0729	24
14474	7730	0858	23
14475	7730	0702	31
14477	7700	0900	24
14478	7659	1104	48
14486	7629	0901	24
14490	7530	0901	6
14491	7500	1003	28
14493	7500	1223	48
14509	7329	1919	12
14510	7259	1928	12
14511	7229	1934	24
14513	7129	1946	18
14514	7059	1953	11
I-group:			
15140	7253	2050	2
15149	7315	2003	26
15162	7157	1705	16
15167	7033	1719	20

Table 1. Account of material and sampling localities of O-group and I-group redfish.

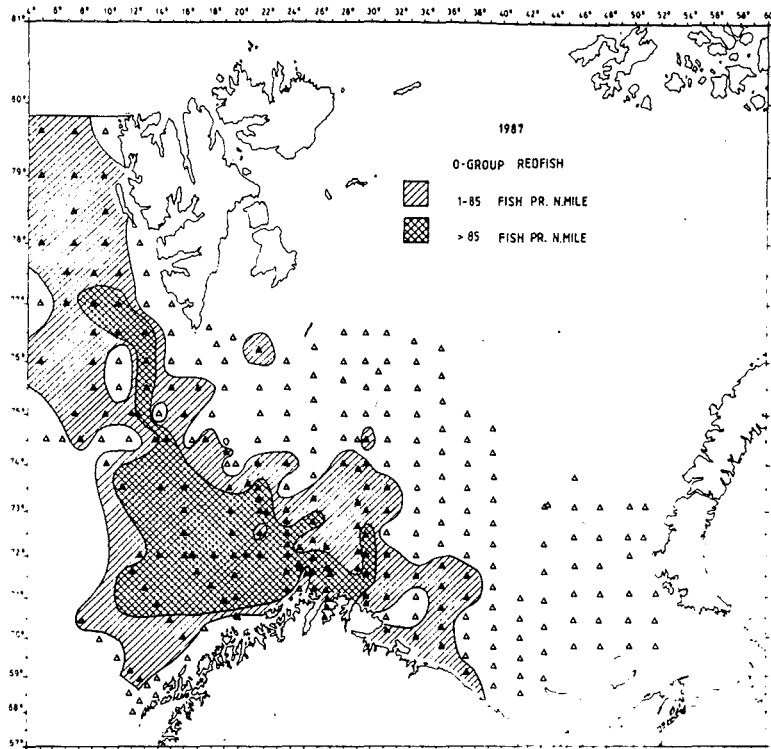


Figure 1. Distribution of O-group redfish in autumn 1987. Pelagic trawl stations are marked by a triangle.

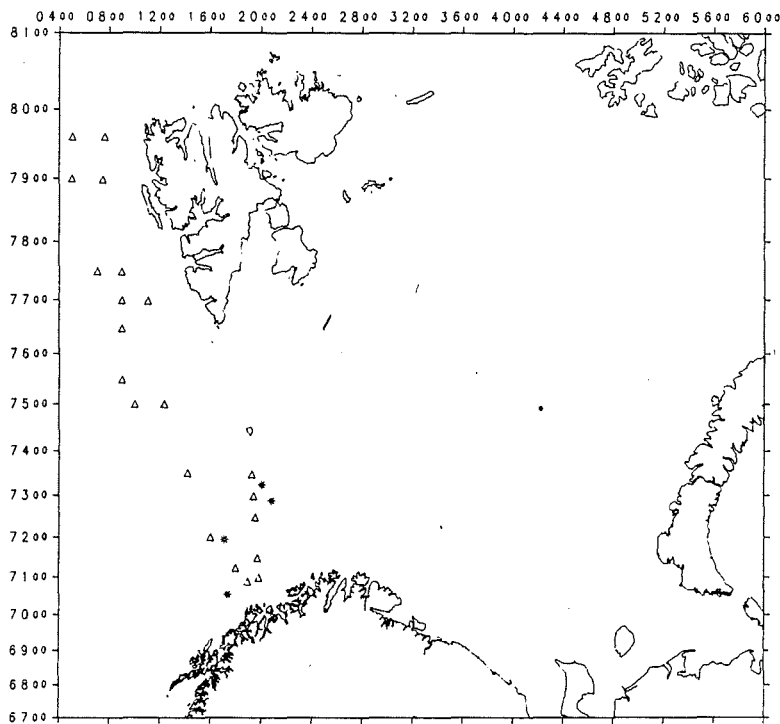


Figure 2. Sample locations of O-group (triangle) and 1-group redfish (star).