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Les stades juvéniles :
le chaînon manquant en
recherche sur les pêches

Juvenile Stages:
The Missing Link in
Fisheries Research

Rapport d'atelier de travail / Report of a Workshop

Octobre 1-3 October, 1991

Bedford Institute of Oceanography

Dartmouth, Nova Scotia

Éditeurs / Editors

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Mont-Joli (Québec) G5H 3Z4

1992

Rapport technique canadien
des sciences halieutiques et
aquatiques 1890

Canadian Technical Report
of Fisheries and Aquatic
Sciences 1890



Pêches
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Fisheries
and Oceans

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Mont-Joli (Québec)
G5H 3Z4

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1992

Cat. No. Fs 97-6/1890
ISSN 0706-6457

Correct citation for this publication:

de Lafontaine, Y., T. Lambert, G.R. Lilly,
W.D. McKone, and R.J. Miller. (ed.).
1992. Juvenile Stages: The Missing Link
in Fisheries Research. Report of a
Workshop. Can. Tech. Rep. Fish. Aquat.
Sci. 1890: vii + 139 p.

© Ministre des Approvisionnements et
Services Canada 1992

No de cat. Fs 97-6/1890
ISSN 0706-6457

On devra citer la référence comme suit :

de Lafontaine, Y., T. Lambert, G.R. Lilly,
W.D. McKone, et R.J. Miller. (éd.). 1992.
Les stades juveniles : le chaînon
manquant en recherche sur les pêches.
Rapport d'atelier de travail. Rapp. tech.
can. sci. halieut. aquat. 1890 : vii +
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REMERCIEMENTS

Au nom de tous les membres du comité organisateur, j'aimerais remercier tous les participants pour leur dynamisme et leur intérêt soutenu lors de la tenue de l'atelier de travail. Cette participation active a contribué largement à créer un climat stimulant et bénéfique en terme de discussion et d'échanges scientifiques. Mes remerciements s'adressent aussi au comité directeur du CSCPCA ainsi qu'à son directeur, M. Jean-Jacques Maguire, pour avoir encouragé la tenue de cet atelier. Je désire remercier sincèrement la direction et le personnel de l'OPANO à Dartmouth, N.É., pour nous avoir permis d'utiliser gracieusement, et avec un très court préavis, leurs locaux de conférence. Leur disponibilité et leur accueil chaleureux ont facilité la bonne marche de notre atelier. J'aimerais aussi souligner l'excellent travail d'organisation accompli par Mme Jackie Dale et M. Timothy Lambert. Je tiens également à remercier tous les membres du comité directeur de cet atelier pour leur collaboration et leur support continu. Finalement, ma sincère gratitude va aussi à Mme Manon Laflamme pour sa précieuse collaboration dans la préparation de l'atelier.

ACKNOWLEDGEMENTS

On behalf of all members of the organizing committee, I wish to thank all participants for their interest and their dynamic participation during the workshop. This contributed to create a stimulating and favourable ambience for scientific exchange and discussion. My thanks are also expressed to the CAFSAC steering committee and its chairman, Mr. Jean-Jacques Maguire, for supporting the workshop. I sincerely thank the NAFO secretariat and personnel in Dartmouth, N.S. for kindly providing us, on a very short notice, the opportunity to use their conference room facilities. Their hospitality and availability have facilitated the venue of our workshop. I also wish to acknowledge the excellent work by Mrs Jackie Dale and Mr. Timothy Lambert during the organization of the workshop. I also thank all members of the workshop steering committee for their collaboration and continuous support. Finally, I express my sincere gratitude to Mrs. Manon Laflamme for her dedicated collaboration in preparing the workshop.

Yves de Lafontaine
Président d'atelier

RÉSUMÉ

Organisé sous les auspices du Sous-comité des écosystèmes et de l'environnement marin (SÉEM) du Comité scientifique consultatif des pêches canadiennes dans l'Atlantique (CSCPCA), un atelier de travail d'une durée de 3 jours et portant sur les stades juvéniles des poissons et invertébrés marins s'est tenu à Dartmouth, N.É. en octobre 1991. Les objectifs de cet atelier étaient de faire le point sur la recherche menée sur les stades juvéniles en appui à la gestion des ressources halieutiques et de fournir des recommandations pour de futures recherches afin d'obtenir des indices de recrutement à partir des stades juvéniles. La première partie de l'atelier fut dédiée à une revue des activités de recherche par la présentation de résultats inédits ou non-publiés ou de recherche en cours portant sur l'écologie des stades juvéniles. Le présent rapport fournit sous forme de notes ou résumés le contenu des contributions couvrant les études tant sur les vertébrés et invertébrés. Durant la seconde partie de l'atelier, les participants furent divisés en quatre groupes de travail afin de formuler des recommandations de recherche sur quatre sujets de discussion préalablement définis. Les recommandations de chaque groupe de travail furent révisées par tous les participants réunis en assemblée générale. Les rapports de discussion de chaque groupe de travail sont présentés ici. Les recommandations finales ainsi que les généralisations du comité organisateur de l'atelier sont aussi incluses dans le présent rapport.

ABSTRACT

Under the auspices of the Marine Environment and Ecosystems Subcommittee (MEES) of the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC), a 3-day workshop on the juvenile stages of commercially important marine fish and invertebrates was held in Dartmouth, N.S., in October 1991. The objectives of the workshop were to review the present status of research on juvenile stages for fisheries management and to provide recommendations for future research on juvenile stages as an index of recruitment. The first part of the workshop was dedicated to an overview of research activities through the presentation of new or unreported results on the ecology of juvenile stages. This report presents the extended abstracts of the contributed papers which embraced both vertebrate and invertebrate research studies. During the second part of the workshop, participants were divided into four working groups to formulate recommendations on four discussion topics previously defined. Recommendations of each working group were reviewed by all participants during a general discussion. The discussion reports of each working group are presented here. The final recommendations and the generalizations of the steering committee are also included.

INTRODUCTION

Increasing our knowledge on the ecology, life history and populations dynamics of juvenile stages of marine species is part of the Department of Fisheries and Oceans (DFO) mandate of assessing, managing and protecting marine biological resources. The need for a workshop on juvenile stages was expressed during the 1990 fall meeting of the Marine Environment and Ecosystems Subcommittee (MEES) of the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC). Recognizing the importance of juvenile stages for fisheries population dynamics and the potential for predicting recruitment levels, the present workshop centered on the idea that the rationale for studying juvenile stages is to develop an index of recruitment. The major objectives of the workshop were: 1) to review the present status of studies on juvenile stages for fisheries management; and 2) to provide recommendations for future research on juvenile stages as indices of recruitment.

The organization of the workshop was entrusted to a six-member steering group: Doug Clay of the Gulf Region, George Lilly of the Newfoundland Region, Tim Lambert and Robert Miller of the Scotia-Fundy Region, Doug McKone from the DFO headquarters in Ottawa and Yves de Lafontaine from the Québec Region who acted as chairman. The steering group met twice to define the scope and structure of the workshop.

To avoid confusion in terminology due to the variable degree of complexity in the ontogeny of different species, the steering committee adopted the following definitions for the purposes of the workshop:

Juvenile stage: "The part of the life cycle from the time or size of metamorphosis until the species enters the commercial fishery".

Recruitment: "The age or size at which a species enters the fishery".

Here, recruitment and recruits are defined solely on fisheries aspects without reference to biological characteristics. It follows that "juveniles" is synonymous with "pre-recruits".

The workshop took place at the Bedford Institute of Oceanography (BIO) and at the Northwest Atlantic Fisheries Organization (NAFO) headquarters in Dartmouth, N.S., on October 1-3, 1991. The workshop was open to all interested scientists from governmental laboratories and Canadian universities. A total of 50 scientists attended, including experts from both the vertebrate and invertebrate fields of study and the list of participants is provided at the end of the report. To meet the workshop objectives, the steering committee decided to divide the meeting into two parts. First, the review of information available on juvenile stages and of current research in this field was achieved by a series of contributed papers. A total of 22 oral presentations (20 min. duration including question period) and 6 posters were presented. These covered the following topics: sampling techniques for juveniles, distribution aspects, characterization of juvenile habitats, feeding studies, investigations of life history strategies and of growth patterns and their implications for management. Extended abstracts of these

contributions are included in this report.

The second part of the workshop was dedicated to group discussion dealing with 4 specific subjects in order to provide recommendations for research on juvenile stages. Each group produced a report of its deliberations and research recommendations. These were summarized by the chairpersons during a plenary session where the recommendations were further commented on and criticized prior to seeking final agreement by general consensus. The list of recommendations and generalizations from the workshop are presented hereafter.

A WORKSHOP ON JUVENILE STAGES: SEARCHING FOR THE MISSING LINK IN FISHERIES RESEARCH

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Recruitment variability and prediction are probably among the most long-standing problems in fisheries research (Sinclair 1988). The majority of aquatic exploited species have relatively complex life-cycles and it is commonly admitted that recruitment is established at some time period during the early-life stages of development. However, the demonstration that year-class strength is regulated during a particular or "critical" stage (*sensu* Gulland 1965) remains to be done and many consider that recruitment could be determined over all the pre-recruit life stages, including the juvenile stages (Rothschild 1986; Houde 1987; Beyer 1989). This shift toward an emphasis on the juvenile stages was recognized a few years ago at the National Workshop on Recruitment held in St. John's, Newfoundland (Sinclair *et al.* 1988) and was explicitly stated among the generalizations issued at that workshop:

"It is apparent from the papers that were presented at the workshop, and the resulting discussions, that there has been a shift in emphasis, in the last year, from the critical period concept to the view that recruitment is also affected by significant events and processes in the adult and juvenile life history stages. The current approach to solving the recruitment problem, therefore, has become more balanced since it also places some emphasis on other life history stages. ...The paucity of knowledge of the biology of many species means that critical gaps are encountered when attempts are made to study the influence on recruitment of events affecting juvenile fish."

In this context, increasing the present knowledge on the ecology and dynamics of juvenile stages is viewed as an integral part and sometimes even a necessity of the mandate of assessing, managing and protecting marine resources. Despite this recognition, and in comparison with the large research effort dedicated to both adult and the very early life stages (i.e. eggs and larvae) during the last two decades, it is generally considered that too little is known and done on the juvenile stages of many important species (Rothschild 1986; Houde 1987). It is therefore tempting to regard the juvenile stage as the missing link in our understanding of fisheries dynamics.

In many instances, the term "juveniles" is almost synonymous to "pre-recruits", thus the study of juveniles appears to be closely linked to that of recruitment forecast and of year-class strength indices. Presently many commercially exploited fish stocks in Eastern Canada are

assessed through sequential population analysis (SPA) which allows projections of the future stock abundance on the basis of actual abundance of recruits. In most cases however, recruit abundance is not a direct and independent measure, but is rather calculated as the geometric mean of abundance estimates of the previous years as back-calculated from the SPA of adult populations. Therefore, if one admits that recruitment is established prior to or very early in the juvenile stage, the use of juvenile abundance as an independent index of recruitment would certainly improve the assessment of many stocks and contribute to better projections of stock abundance. This appealing idea has received much hearing and has gained more interest in recent years both at the national and international level (Koslow 1992).

One could legitimately question the reason for interest in juvenile stages or the necessity for holding a workshop on this topic. The present workshop was indeed the third one dealing with the "juvenile" issue in Canada within 1991, and all three were sponsored by the Department of Fisheries and Oceans. In March 1991, a workshop on cod juveniles was held in St. John's, Newfoundland, as part of a broad research proposal on Northern cod (see abstract by Lilly, this volume). At the end of June 1991, the International Symposium on the Production of Juvenile Atlantic Salmon in Natural Waters was also hosted in St. John's. The objective was to examine the ecology and population dynamics of juvenile salmon with a view of assessing natural stocks. The proceedings of these two meetings will be published in the near future. While the two workshops were very much species-oriented, the present workshop was aimed at reviewing and discussing more general aspects without being too species-specific.

Concern about the importance of the juvenile stages to fisheries is not necessarily something new or due to a sudden awakening that occurred over the past year. The Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC), which has the responsibility of assessing the marine resources in Eastern Canadian waters, considered the "juveniles" question in internal reports from the early 1980's.

"Juvenile abundance estimates for the major groundfish stocks are generated from the various research vessel trawl surveys. Generally only several stations within each stratum are sampled, and the standard survey is carried out once a year. Large year-to-year fluctuations in a given year-class abundance estimate are common due to "availability" changes. Thus single estimates of juvenile abundance using Research Vessel surveys have very large confidence limits. It seems safe to conclude that it would not be possible to statistically detect anything smaller than one order of magnitude mortality effects at the juvenile stage using our present monitoring program. For greater precision in juvenile abundance, stock specific surveys would need to be considered."

(CAFSAC MEES Report, 1981)

At that time, the possibility of using juvenile abundance to forecast year-class strength was already proposed and avenues to solve this problem were sought. The proposal was based on the assumption that mechanisms contributing to year-class formation and variability operate during the egg and larval stages and that juvenile mortality rate is relatively "stable" between

years and close to estimates of adults natural mortality.

The "availability" of juvenile stages for estimating their abundance was, and still is, problematic. Changes in juvenile abundance may, in some instances, be caused by true "availability" changes due to interannual variation in distribution patterns (see abstract by Frank, this volume), but in several other cases the relatively low abundance of juvenile stages have been attributed to inadequate sampling. The poor knowledge of the general ecology and distribution of juveniles, and the difficulty of finding and efficiently sampling juvenile stages were perceived as the two sides of a same coin. While the large-scale distribution and movement of adult fish have been relatively well described from fisheries operations, research surveys and tagging studies, the development of plankton sampling programs during the mid-sixties and the seventies shed light on the distribution and dynamics of eggs and larvae. However, it was soon recognized that catchability of post-larval stages by plankton gears was rather poor (Lenarz 1972; Barkley 1972; Murphy and Clutter 1972; Colton *et al.* 1980; Dalley and Anderson, this volume), a situation which largely impeded progress on the study of juvenile stages. Moreover, the now-classic fish migration triangle as formulated by Harden-Jones (1968) explicitly included a "juvenile nursery area" which eggs and larvae would drift into. In many cases, the nursery zone was considered to be spatially distinct from spawning sites (where eggs and early larvae are found) or adult feeding areas (where fishing operations normally take place). Despite the caveat of gear limitation, the difficulty of finding juveniles in regular adult and plankton surveys has often been interpreted as evidence for the existence of separate "juvenile" distribution areas. The example of the North Sea plaice using small estuarine habitats as juvenile nurseries (Creutzberg *et al.* 1978) and the direct or visual observations of juvenile fish in shallow/coastal regions (Riley *et al.* 1981; Methven, this volume; Steele and Keats, this volume; Tupper and Boutilier, this volume) and estuarine systems (McHugh 1967; Graham 1972; Weinstein 1979; Cunjack and Chin, this volume) contributed to the argument that inshore environments would represent important areas for juvenile stages of many "offshore" species.

Progress in solving the juvenile "availability" problem will probably necessitate new sampling approaches (methods and designs) (see Hudon, this volume). The difficulty of employing the same sampling methods in various environments (for example: nearshore vs offshore) often precluded comparative studies and has perpetuated the speculative debate on the most appropriate habitat for a particular juvenile species. The challenge is to verify that zero values in juvenile abundance can be interpreted with confidence as evidence for the absence of individuals and not the result of gear avoidance. Once this is correctly evaluated, juvenile monitoring programs can be set in place.

Although it may be argued that, for predictive purposes, there is no need to debate and understand the ecological concepts linking the juvenile stages and recruitment, the fundamental question concerning the role of juveniles in the regulation of year-class strength and recruitment levels must be addressed and eventually resolved.

Perhaps, the most stimulating, and almost provocative, statement in support of the study of juveniles came from Sissenwine (1984) who, in his paper entitled "Why do fish populations

vary?", made a plea for studying recruitment processes at the post-larval stages:

"Recruitment is likely to be a multiplicative function of highly variable processes occurring throughout the first year of life, including the post-larval stage. ...It is ironic that post-larvae (*sensu* juveniles) have been nearly ignored since there is an obvious clue that year-class strength may not be established until this stage."

The obvious "clue" as stated by Sissenwine was based on the concept that year-class strength is determined by the product of the mortality rate (M) and the duration (t) of the life stage during which this mortality rate is acting. The calculated product of $M \cdot t$ for late-larval stages and juveniles was either equal to or even higher than that for eggs and early-larval stages. He concluded that there was a potential that year-class strength would not be established until the juvenile stage. Assuming that predation is the principal cause of this juvenile mortality, he also implied that predation probably affects and regulates recruitment.

Foreseeing the important role of predator-prey interactions at the juvenile level for fisheries dynamics, Shepherd (1984) wrote:

"Although assessment of many species together (*multi-species management*) is still in its infancy, it is clear that the main effects of biological interactions are due to predation on juvenile fish and, therefore fully apparent on the long term. They may, however, be of great importance, particularly as they may influence the desirability of various management options."

Shepherd's concern was primarily related to multi-species management where species interactions have to be taken into account. So the importance for a better understanding of juvenile ecology and biological interactions was therefore clearly stressed, especially for cases where the fishing pressure on one species (predator) may influence the abundance of other species, specially those for which juveniles are used as prey (Gulland and Garcia 1984). Given the relatively minor importance of the multi-species view in marine fisheries and in management models developed for northern temperate stocks in particular (Gulland 1977; Sugihara 1984), it is, therefore, not surprising that predator-prey interactions have not been fully described nor properly quantified for most species. However, the nature of specific data to collect is not so obvious and may rapidly become unaffordable for complete multi-species solution (Gulland and Garcia 1984).

Qualitative evidence for fish predation on juveniles exists (for example: large cod feeding on redfish juveniles - Lilly and Gavaris 1982; cod feeding on juvenile shrimps - Lilly, this volume; see also Bailey and Houde 1989), but the impact of these interactions on year-class strength and recruitment variability remains speculative and not adequately estimated. In addition, cannibalism, which was recognized very early by Ricker (1954) as potentially the most powerful mechanism for regulating recruitment, has also been documented for some species but only rarely quantified (see examples of cannibalism for cod and redfish - Konstantinov *et al.* 1985). Despite this evidence and the repeated suggestion (Sissenwine 1984; Shepherd 1984;

Anderson 1988; Bailey and Houde 1989; Beyer 1989) that predation is the main source of juvenile mortality, the role of predators, including cannibalism, on year-to-year variability in recruitment has not been fully embedded in theoretical concepts yielding testable hypotheses. At the present time, the most current hypothesis linking juveniles and recruitment is essentially that the abundance of predators preying upon juveniles determines juvenile survival and recruitment. However, factors controlling predation at sea are still largely unknown. The refinement of our concepts and hypotheses concerning the impact of predation on juveniles and recruitment will await the accumulation of additional information on these biological interactions.

Having postulated that predation was certainly the major source of death during the juvenile stage, Houde (1987) concluded, based on a modelling exercise, that growth rate variability and its effect on the duration of the different life stanza can be a major factor affecting subsequent recruitment. But Houde was quick to point out that growth rate and stage duration do vary largely among species and therefore that the greatest potential for regulation of year-class size may lie in the larval stage for some species and in the juvenile stage for others. The same concept was further developed by Beyer (1989) who mathematically expressed recruitment processes upon the principles of size-based theory. His basic premise is that "predation, the single most important known cause of natural mortality in juvenile life, bears a decreasing relationship to body size" (Beyer 1989). In consequence, it can be derived that survival to a recruiting size is essentially determined by the rate-ratio of mortality to growth, which led Beyer to conclude that year-class strength would be fixed during the early-life stages corresponding to the largest gain in individual weight. Interannual variability in recruitment would therefore be related to variability in growth rate controlled by food and its interplay with mortality rate due to predation.

This brief overview demonstrates that, during the last 15 years, there has been a shift in our conceptualization of the recruitment process for marine species. One consequence of this is a change in the nature and the precision of important variables to be measured, which have switched from precision in mortality rate to precision in growth rate. The change is important because 1) it is generally felt that it would be more feasible to measure and detect variation in growth rate than in mortality rate (Houde 1987) and 2) growth rates do not necessarily covary among the different life stanza during development (Bertram *et al.*, this volume). Moreover, apart from its probable influence on immediate survival, growth rate may also affect other life history traits which contribute to reproductive success of a population. The suggestion that juvenile growth influences maturation and timing of spawning (McQuinn, this volume) or migration timing (D'Amours, this volume) calls for a better understanding of growth processes during the juvenile phase.

The juvenile stages are part of a complex life cycle for most invertebrate and vertebrate marine species. Because of the variable degree of complexity in the ontogeny of different species and because of possible difference in the terminology used by different people interested in particular species, research effort and studies have been largely conducted by experts from the two main groups of species in a somewhat independent way and without much interaction. Without denying that many ecological differences exist between invertebrate and vertebrate

species, the life cycles of many species of the two groups do have similarities. The great majority of these species are characterized by a larval dispersal stage which will eventually metamorphose into a juvenile stage prior to becoming part of the reproductive adult stock. Many species have a pelagic larval dispersal stage followed by a benthic settlement or juvenile phase. However, for an unknown reason, existing theories on recruitment processes and recruitment regulation differ between invertebrate and vertebrate groups. The point was clearly made by Roughgarden *et al.* (1984):

"The stock-recruitment theory usually identified with fishery science seems inappropriate to sessile invertebrates because it does not revolve around space as a resource and does not deal with open systems."

Population dynamics studies of some unexploited benthic invertebrate species have shown that settlement rate corresponding to the transition between the pelagic larval stage to the benthic juvenile stage was the primary source of variation in population abundance (Roughgarden *et al.* 1984; Caffey, 1985). Survival was essentially controlled by the amount of free space or adequate habitat (Miller *et al.*, this volume) available to new settlers. It is interesting to note that this concept of "space" has been echoed in coral reef fish literature (Doherty 1982; Shulman *et al.* 1983; Victor 1983, 1986; Sale *et al.* 1984), but does not seem to have any correspondence or equivalent in northern temperate groundfish studies.

Thus, is there some parallel that can be drawn from the various but still not numerous studies on juveniles of both invertebrate and vertebrate groups? Can research in one taxonomic group benefit from the research efforts of the other group? Can the failure or the success achieved in one field of research be applicable to the other one? I personally believe so. The exchange of ideas and information from different fields of expertise may prompt a reexamination of classical concepts. It can also favour the emergence of some ecological ideas and concepts with regards to the juvenile stages that would be fundamental to several taxonomic groups, and not only valid for invertebrate or fish species.

It is with this philosophy in mind that the present workshop was put forward with the challenge to avoid falling into species specific debate or discussion. While it may be premature to evaluate the progress achieved during those three days, the number of participants and the variety of contributed papers and posters presented surely reflect the level of activity and enthusiasm of the present research on juvenile stages and would indicate that the decision of holding the workshop was highly justified.

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GENERALIZATIONS FROM THE WORKSHOP

Papers presented and discussed during the workshop addressed many aspects of the research on juvenile stages. The principal points of these deliberations are summarized as follows:

- The overall consensus emerging from the workshop was that the life cycles of marine species presently under exploitation are still not fully understood. Descriptive data on the distribution and behaviour of the juvenile stages of many commercial species are lacking and important gaps in our knowledge of the ecology of juvenile stages still persist.
- Completing our understanding of the life cycle is a necessary step for explaining the relationships between environmental and ecological processes during the juvenile phases. Knowledge of the life cycle is also a requirement for describing and defining juvenile habitats.
- Research studies have indicated that juveniles are distributed in a variety of habitats, in both offshore and inshore environments, in pelagic as well as in benthic realms. The distribution of all life stages both in space and time must be adequately described.
- Although specific differences exist among species, there are some parallels between invertebrate and vertebrate life history strategies of juveniles (i.e. after metamorphosis) which can be categorized into three major types: 1) entirely pelagic (herring, mackerel, capelin, squid); 2) juvenile pelagic phase followed by settlement to a benthic phase (cod, haddock, hake, molluscs); 3) entirely benthic (flatfish, most crustaceans).
- In many cases, the inadequacy of sampling methods has often been, and still is, a major impediment to the collection of information on all developmental stages prior to recruitment. Such knowledge is a prerequisite for developing predictive models of recruitment and for habitat protection.
- Finally, until basic information on the biology and ecology of the juvenile stages is acquired, hypotheses concerning the role of juvenile stages in recruitment and population dynamics will remain untested.

RELATIONSHIP BETWEEN JUVENILE ABUNDANCE AND RECRUITMENT INDICES

"The main rationale for studying juvenile stages is to develop an index of recruitment."

- There was a general consensus on the necessity and the feasibility of developing a recruitment index based on independent juvenile surveys. A measure of juvenile abundance will improve our chance of providing a reliable index of recruitment and, by extension, providing a better projection of future stock size.

- It was generally agreed that recruitment and year-class strength are determined during or by the juvenile stage, but direct and conclusive evidence on the age or size at which recruitment is established is still lacking for the majority of species of interest. It was acknowledged that juvenile surveys are presently used as recruitment indices in other parts of the world (gadoid in Barents sea) as well as in Canadian waters (silver hake on Scotian shelf, plaice and yellowtail on Grand Banks), and seem to be useful. Juvenile surveys recently initiated for other eastern Canadian stocks have not yet been validated.
- A consensus was reached that sampling techniques and designs will always be species specific and may also vary between areas or habitats under investigation. Developing a useful index for recruitment based upon juvenile surveys is a function of appropriate sampling and of the extent of knowledge of life history of the target species. Both failures and successes in gear development and sampling designs for monitoring juvenile stages should further be documented properly to avoid repetition. Technology and sampling in offshore juveniles have progressed considerably through electronics and acoustics development while sampling in coastal/shallow waters still relies on conventional gears and requires improvement.
- It was recognized that a juvenile index should be developed at the earliest age possible to maximize the lead time for prediction of stock abundance estimates, but it was noted that precision and accuracy will probably diminish with increasing time between the age surveyed and age at entry into the fishery.
- Due to ontogenetic variability in distribution both in space and in time, it would be useful to sample several pre-recruit ages to maximize predictive capabilities.
- The use of existing research surveys for recruited ("adult") ages and modifications to gears designed for adult sampling are not recommended for juvenile abundance estimates unless the possibility of bias in estimating adult abundance indices is properly and fully investigated and found to be negligible.
- There was no consensus on the level of precision acceptable for a recruitment index. Standardization in sampling protocols and abundance measurements is highly desirable to facilitate comparison of abundance indices among stocks and areas. However, it should be recognized that standardization can stifle improvements and perpetuate biases. Existing and future recruitment indices must be validated. Variation in the index must reflect variation in recruitment, and measurement error on the abundance of a juvenile year-class must be less than the interannual variation of the recruit year-classes to be predicted.

IMPORTANCE OF JUVENILE HABITATS

- Juvenile habitats can be characterized for only a few species or populations at the present time. Habitat definition for each developmental stage during the life cycle of a particular species

must draw upon all evidence available on the distribution of that species in a variety of areas.

- The definition of habitat quality for juvenile stages is necessary for enhancement of natural populations.
- Preferred habitats for juveniles must be defined in terms of abiotic and biotic factors so that they can be protected or replaced if destroyed in compliance to the Fisheries Act and according to the "no net loss" principle of the habitat management policy.
- Presence or absence of a species cannot alone indicate habitat preference, unless distribution and movements of juveniles are followed over time. Distinction between movements of individuals and differential survival needs to be investigated.
- Technologies for identification of juvenile habitats and quantification of juvenile abundance in various habitats must be examined to assess the relative importance of different habitats for juveniles.
- Evidence was presented that inshore environments are important nursery areas for juveniles of many invertebrate species and some fish species, notably herring and pollock.
- Predation pressure was considered to be of prime importance in habitat utilization by juvenile stages.
- In theory, juvenile abundance can be affected by habitat availability, but conclusive evidence is presently nonexistent. A given habitat must have a carrying capacity for a particular species. Therefore habitat quantity can be one factor limiting the abundance of a particular species or population.

REGULATION OF GROWTH AND MORTALITY DURING JUVENILE STAGES

- For predictive purposes only, it was argued there is no need to study juvenile survival after the earliest age or size at which recruitment is determined. The study of processes affecting mortality and growth during the entire pre-recruit period is however highly justifiable for defining and protecting the aquatic habitat and in the broader context of process-oriented research.
- Juvenile mortality cannot be quantified unless reliable indices of abundance can be obtained. Given the present lack of adequate measures, a relative estimate of mortality rate would however be considered as "progress".
- Cumulative mortality over the entire juvenile period may be more important to recruitment variability than short-term mortality variation.

- Predation was considered to be the main cause of mortality during the juvenile stages, but potential predators remain to be identified for specific habitats and stocks. Abundance and consumption rates of potential predators must be measured in order to evaluate their impact on juveniles used as prey. Understanding predator-prey interactions at the juvenile level is necessary for the development of analytical (*sensu* comprehensive) models of recruitment and for multi-species management.
- Although it was recognized that density-dependent growth would have implications for stock-recruitment relationships, irrefutable evidence for this phenomenon was not presented and most supporting examples are primarily derived from analysis of adult populations.
- Research studies presented during the workshop indicated that juvenile growth can also affect other life history parameters, such as maturity, time or age at first spawning or migratory behaviour. Implications of these effects on subsequent availability of recruits to the fishery should be explored.

RECOMMENDATIONS OF THE STEERING COMMITTEE

Through consensus obtained at the plenary session, workshop participants proposed the following recommendations to improve research on the juvenile stages:

1. It is unanimously recommended that research be actively supported to describe and document the complete life cycle of exploited species.
2. It is recommended that independent surveys for juvenile stages be developed as indices of recruitment for exploited species.
3. It is recommended that existing data sets from DFO research surveys for groundfish, pelagic and invertebrate species and commercial fisheries be investigated for gathering information on juvenile stages of different species and for evaluating promising candidates for a pre-recruit index.
4. It is recommended that existing juvenile surveys for some eastern Canadian stocks be continued for a number of years and that their validation as recruitment indices be evaluated in the near future.
5. Having reached consensus on the feasibility of predicting year-class strength from juvenile abundance, the group recommended that the optimal developmental stage and stocks to be assessed for a predictive index be determined according to a number of criteria:
 - abundance estimate obtained at the longest feasible time (earliest age) prior to entry into the fishery;
 - a pre-recruit index developed for stocks or populations characterized by large recruitment variability;
 - partial recruitment be considered so that accuracy of prediction may be weighted against cumulative natural mortality and overlap in cohorts due to growth variability;
 - contribution of recruitment in terms of numbers or biomass of recruits should be considered in regards to the fishable biomass and stocks with a high fraction of recruits in the landings should be chosen;
 - a relative abundance index as opposed to an absolute index should be developed, but the index must be validated and reflect inter-annual changes in juvenile abundance;
 - measurement error of the index should not be more variable than reported recruitment variability of the stock;
 - juvenile surveys for recruitment index should cover all habitats where juvenile stages occur;
 - juvenile surveys for recruitment indices must incorporate environmental and physiological correlates.

6. It is recommended that special research effort be directed at improving sampling efficiency in coastal and shallow waters. The possibility for standardization in sampling techniques and protocols for a given species should be investigated to facilitate comparison of indices among stocks and to achieve uniformity in abundance measurements.
7. It is recommended that juvenile habitats be characterized on the basis of all evidence available on the distribution of all life stages and that limits set by abiotic factors, including physical and chemical water properties, substrate, accessibility and availability of required space, be defined.
8. Predation being thought to be the dominant source of mortality during the juvenile stage, it is recommended that research into predation, specially identification and impact of potential predators, and its interaction with growth should be strongly supported.
9. It is recommended that the effect of cumulative juvenile mortality on recruitment should be investigated through process-oriented studies.

REPORTS OF WORKING GROUPS

As part of the general objectives of the workshop, participants were invited to participate in working group discussions dealing with selected topics and to provide specific research recommendations. In order to stimulate discussion and scientific debate and to ensure effective communication, the participants were divided into four discussion groups, each one consisting of a maximum of 12 people including a chairperson selected by the steering committee. Group membership was determined on the basis of expertise and scientific interest as indicated by participants on their registration forms.

The discussion program was planned to allow scientific exchange on the three following headings:

- evaluate the relationship between juvenile abundance and recruitment indices;
- examine the role of juvenile ecology in relation to population dynamics;
- identify the importance of juvenile habitats.

In this context, the steering committee had previously identified four discussion topics:

1. sampling techniques (methods & designs) for juvenile stages;
2. regulation of growth/mortality during the juvenile stages;
3. juvenile stages and recruitment indices;
4. juvenile habitats: definition, characterization and availability.

Each group was asked to discuss and make recommendations on two of the four topics. Thus, each topic was addressed by two groups. Each topic was presented as questions to the participants. With the exception of the chairpersons, none of the participants was informed of the discussion topics before the discussion began.

QUESTIONS ADDRESSED BY DISCUSSION GROUPS

Topic 1 – Sampling techniques for juvenile stages:

- Is there one gear or more than one to adequately sample juveniles for a particular species?
- What are the most appropriate gears & designs to sample pelagic juveniles? Same, but for benthic juveniles?
 - Should sampling protocols be standardized?
 - Are sampling method strategies developed for adults applicable to juveniles?
 - Are research surveys for juveniles possible? Applicable?

Topic 2 – Growth/Mortality during the juvenile stages:

In the context of recruitment variability and potential use of juveniles as recruitment predictor, what are the main biotic and abiotic factors affecting growth and mortality during the juvenile stages?

- Can mortality be quantified during the juvenile phase? If so, how?
- What are the main causes of mortality during the juveniles phases?
- Is juvenile growth density-dependent? Is there irrefutable evidence? Implications for stock assessment and management?
- Is juvenile mortality sufficiently variable to generate year-class variability?

Topic 3 – Juvenile stages and recruitment indices:

Are recruitment and year-class strength determined during the juvenile stage?

- How successful are current or past juvenile surveys, and recruitment indices?
- What is the earliest age at which year-class is determined? Is year-class strength determined before or after metamorphosis (corresponding to the beginning of the juvenile phase)?
- Are research surveys for juveniles necessary for stock assessment and management ?
- What would be the acceptable (or target) level of accuracy for a juvenile recruitment index?

Topic 4 – Preferred habitats for juvenile stages:

In the context of recruitment generation and control, why are juveniles often or sometimes distributed in different habitats from adults?

- Can we define juvenile habitats? How?
- What defines the most appropriate habitat for juveniles?
- Is habitat quality or quantity limiting for juveniles?
- Does habitat availability affect juvenile abundance?

DISCUSSION REPORT: GROUP A

Chair: John Anderson

Rapporteur: John Anderson

Participants: Julian Addison, Douglas Bertram, Joseph Brown, Denis D'Amours, Earl Dawe, H       Dupuis, Tim Lambert, Dave Methven, Shawn Robinson, John Tremblay.

TOPIC 1: Sampling Techniques for Juvenile Stages

The group agreed that the discussion be focused on sampling strategies aimed at developing and maintaining pre-recruit indices for marine species, and presumes that such an index is necessary for the management of a given fishery. It was apparent that sampling strategies for marine juveniles would always be species specific and also may vary for some species among areas or stocks. With this in mind the life histories of different marine species for juveniles, i.e. the period from metamorphosis to recruitment by the commercial fishery, were characterized to fall into one of 3 types: 1) entirely pelagic; 2) pelagic initially and then demersal (*sensu* on or near the bottom); 3) entirely demersal. The discussion subsequently focused on deriving a set of guidelines which would be important criteria for pre-recruit indices and, secondly, on a list of recommended approaches to meet these criteria.

Criteria for Pre-Recruit Indices:

- It is sufficient to develop a relative abundance index, as opposed to an absolute measure of population abundance. The index may be a biased estimator as long as it is consistently biased. Validation of the abundance index is necessary.
- It is necessary to incorporate the possibility of changing conditions into the sampling strategy for pre-recruit indices. This approach acknowledges that population distributions and behaviours may vary over time.
- It is desirable to sample a number of pre-recruit ages simultaneously in order to maximize the predictive capabilities of the index. Sampling more than one age/stage prior to recruitment will increase confidence in the index. This method acknowledges that the age at which recruitment is determined for a given stock may vary over time.
- Sampling protocols have to be standardized to facilitate comparison of relative abundance indices among stocks.
- When possible, it is desirable to standardize abundance measurements (i.e. CPUE) during the pre-recruit period. Standardized abundance measurements will assure a wider application of

abundance data, particularly when process oriented research can also be carried out.

Approaches for Meeting Index Criteria:

- Estimate the earliest age at which recruitment is determined. This should begin first by analyses of existing data, working backwards in age from the oldest pre-recruit ages to the youngest.
- When multiple ages cannot be sampled simultaneously then it is recommended that the earliest age after which recruitment is determined be sampled.
- Initial development of a pre-recruit index for a given stock should begin with a major effort (pilot program) designed to fully describe the age specific abundance distributions and associated habitat characteristics. The pilot program should incorporate, and evaluate, a variety of gear types which simultaneously sample different ages and habitats.
- Validation of an index can be done by comparing the index to measured recruitment over many years. Validation can also be achieved by developing several indices simultaneously and comparing estimates among indices over a smaller number of years.
- Passive sampling gears are probably more cost effective than active sampling gears and should be evaluated first, when cost and effort is considered to be limiting.
- Assess the precision required for a pre-recruit index relative to recruitment variation for a given stock. Assess recruitment variation in particular for the exploited period, but also incorporate in the sampling strategy the possible, or measured, magnitude of low frequency oscillations in recruitment.
- Utilization of fully recruited or adult sampling strategies currently in use is not recommended due to: a) juveniles often occupy different habitats and, therefore, would not be adequately sampled; b) pre-recruit stages will not be adequately sampled due to their smaller size; c) modifying existing gear designed to capture adults may result in estimation problems for adult abundance indices.

TOPIC 2: Growth/Mortality during the Juvenile Stages

The study of growth and mortality rates for juvenile stages was regarded in the broader context of process oriented research. The group considers that the study of the processes affecting survival during the pre-recruit period of marine species is fully justifiable. In particular, it was recognized that population distributions and behaviour may change over time in response to various factors such as climate change and ecological dynamics of marine systems. In

addition, proxy measures of survival, such as growth or physiological condition, may serve as practical measures of pre-recruit abundance. Finally, the process of developing predictive models of recruitment, which incorporate environmental and/or multi-species interactions depends on understanding the processes controlling population abundance.

The group emphasized that the determination of the earliest age at which recruitment is established is an important prerequisite to the initiation of research on processes affecting survival during pre-recruit stages. Obviously, if recruitment has been determined by the earliest pre-recruit age then the study of survival processes during the juvenile period cannot be justified. If this was the case, process oriented research should be directed at egg and larval stages.

Determining the degree to which density dependence occurs, in particular density dependent growth, is important in the development of pre-recruit indices. The occurrence of density dependent growth would demonstrate that stock-recruitment relationships must be incorporated into predictive models of recruitment.

Cumulative mortality resulting from processes which occur throughout the juvenile period is expected to be more important in determining eventual recruitment than single, isolated events. Therefore, research must be directed at all juvenile ages. Predation is likely to be the main source of mortality for juveniles. However, abiotic factors, such as freezing, food limitation and possible physiological stress associated with pre-recruit migration may all be important sources of mortality.

DISCUSSION REPORT: GROUP B

Chair: Christiane Hudon

Rapporteur: Christiane Hudon

Participants: Bernard Boudreau, Rodney Bradford, Edgar Dalley, Réjean Dufour, Ken Frank, Tom Hurlburt.

TOPIC 1: Sampling Techniques for the Juvenile Stages

The group felt that sampling techniques for the juvenile stages needed to be adapted to specific sampling questions, species, specific stocks, habitats, life history stages, and the purpose of each study. In all cases, fundamental knowledge of the biology of the species and of its habitat, particularly for the demersal stages, is an absolute prerequisite for efficient sampling.

Sampling gears currently available for the offshore environment were thought to be adequate for juvenile studies, provided that a certain amount of modifications be made to adapt them to specific purposes/species. The performance and sampling characteristics of offshore gears (i.e. BIONESS, IYGPT trawl, RMT trawl) operated from large ships also tend to be more standardized and better known than traditional plankton gear. With this information the pitfall of being in the right place at the wrong time or vice-versa can be avoided.

Sampling juveniles in coastal and shallow waters is often more problematic, relying on gear of unknown and/or poor efficiency over rocky or heterogeneous bottoms. In coastal waters, the possibility of direct observations by SCUBA and video or photographic techniques facilitates the understanding of species behaviour and sampling deficiencies, also making possible visual estimates of juvenile abundance.

As a result, given the generally poor knowledge of juvenile life history, distribution and habitat characteristics, present sampling programs must go through an initial phase of experimentation and exploration, allowing to optimize the sampling gear and the sampling strategy. Consideration should be given to define how representative samples are, either in terms of volume filtered or available surface of habitats, and the degree to which abundance estimates can be extrapolated. Whenever possible, there should be an effort at standardizing abundance measurements.

There are several species or stocks for which juveniles are captured concurrently with the adults during biomass assessment sampling and/or fishery operations, which would not incur major additional costs. However, in the cases in which juveniles are sampled simultaneously with the adults, additional considerations apply:

- With minimal gear alteration, juvenile captures could be improved and integrated to the current assessment. However, specific problems such as behavioral interactions that influence catchability (i.e. crabs, lobsters) and catch efficiency of small individuals in large mesh gear (i.e. groundfish) must be considered.
- Differences in distribution and catchability through time should be investigated.
- Analysis of the currently available data on pre-recruit abundance gathered from samples at sea and research surveys for adult biomass assessment would be advisable.
- Information gathered from the fishery itself via log-books and index fishermen program could also be used or modified for that purpose.

TOPIC 3: Juvenile Stages and Recruitment Indices

There was a general consensus that recruitment and year-class strength were determined during or by the juvenile stage. There was no consensus on the level of precision deemed acceptable for a predictive index. The traits of the survivors might provide a useful information on selective pressure during the juvenile stage.

The group considered that the effects of stochastic or unpredictable processes on early larval survival could in some cases drive the survival of the year class (i.e. Thames estuary herring and Bryants Cove capelin), but were thought to be hard to quantify and verify in other cases, such as lobsters. Sutcliffe's model relating freshwater outflow of the St. Lawrence river and subsequent lobster landings was initially very appealing, but did not provide any insights on the mechanisms explaining its early success and subsequent failure. A better handle on species life history and of ecosystems are required before such large scale, generalized and undoubtedly elegant approach can be used with any degree of certainty. This suggests that studies of large scale processes and mechanisms may be useful in the long run, but should be combined in the mean time with baseline descriptive data.

Early investigations aiming at developing recruitment indices from juvenile stages should focus on quantifying the stage immediately prior to the entry in the fishery, since data is often currently gathered and chances of success are better than with earlier stages. The determination of the optimal life history stage and stocks to be assessed for a predictive index has to be determined according to a number of criteria:

- determination should be done at the earliest feasible time prior to the entry in the fishery.
- the accuracy of the prediction must be weighted against cumulative natural mortality and overlap in cohorts due to growth variability. The effect of partial recruitment on year to year estimates of recruitment variability in the stock should be examined.

- the percentage contribution of the recruiting year-class to the total fishable biomass. For instance, stocks of species relying primarily on yearly recruits (i.e. lobster, crab, capelin, haddock on the Scotian Shelf) would be most likely to benefit from an index forecasting recruitment. At the other end of the life history/fisheries mortality spectrum, fisheries relying on a multi-age distribution of catches targeting a strong year class would not be so tied to recruitment indices since a successful year class could be followed over several years.
- the relative age/size at entry in the fishery against longevity of the species.

DISCUSSION REPORT: GROUP C

<u>Chair:</u>	Jacques A. Gagné
<u>Rapporteurs:</u>	George Lilly, Robert Miller
<u>Participants:</u>	Vytenis Gotceitas, Bruce Hatcher, Pierre Pepin, Angel Perez, Donald H. Steele

Acquiescing to a suggestion from the chair, the group began its activities by addressing three additional questions:

1. Why does the Department of Fisheries and Oceans (DFO) need to conduct research on the juvenile phase?

DFO has the mandate to protect the Canadian renewable marine resources and manage their exploitation. Its ability to meet this challenge would be greatly enhanced if it could provide reliable indices of the strength of a year-class as early as possible before commercial exploitation. Despite considerable efforts worldwide, such indices have yet to be obtained from estimates of larval abundance and survival. We concluded that chances of success should improve using the juvenile phase, provided it can be surveyed properly.

DFO is also responsible for protecting fish habitats. To avoid compromising the survival of entire populations because of insufficient protection provided to any part of their life cycle, the habitats occupied by each life history stage must be described. This is essential to appraise, for instance, the multispecific impacts of management decisions on prey and predator species or of proposed habitat uses and modifications.

To fully accomplish its role as the custodian of the Canadian aquatic resources, DFO must better understand the dynamics of underlying systems; sustained exploitation of adult populations cannot be guaranteed if early life history stages are ignored.

2. To meet these objectives, do we need to concentrate on all stages of the juvenile phase or only on part of it (e.g. pelagic, demersal, pre-recruits)?

To provide the industry with as much lead time as possible for planning its operations before a year-class influences a fishery, a recruitment index must be obtained early in the life cycle. Concentrating on that early stage would suffice for predictive purposes. Protecting the aquatic habitat however requires that the dynamics of all stages of the juvenile phase be better understood.

3. In the context outlined by our answers to questions 1 and 2, is the existing theoretical framework sufficient?

The group agreed that there was little need to concern ourselves with theories and hypotheses to obtain a "working" recruitment index, as long as the index features can be quantified with sufficient precision. In the context of habitat protection and ecosystem dynamics studies however, it was concluded that it is difficult to ask for more theory when even basic distribution patterns are still unknown.

TOPIC 4: Preferred Habitats for Juvenile Stages

The fundamental factors that determine habitat suitability are probably the same throughout the life cycle. The differences observed between stages would result from varying degrees of importance taken by each factor during the ontogenetic development of the organisms. In general, abiotic factors related to spatial adequacy and availability such as shelter from predation, bottom type for settlement or feeding diet probably set the initial boundaries. Biotic factors mainly associated with resource adequacy (e.g. food availability or predation) would further reduce these initial boundaries.

Overall, the group felt 1) that juvenile habitats can be defined, but only for a few species or populations at the present time, 2) that the most appropriate habitat is that in which survival is optimized, and 3) that juvenile abundance can be affected by habitat availability. The group noted that actual juvenile distribution may not necessarily reflect habitat suitability because it depends on the availability of the preceding stages. For instance, colonization of acceptable juvenile habitats may be prevented by events occurring during the egg and the larval phases.

The group concluded by formulating three recommendations:

- To define a habitat for any stage in a life cycle, the distribution of the earlier life stages must be examined, and changes in distribution of a group (cohort) followed over time. It is essential to distinguish between movement of individuals and differential survival.
- Research on limiting factors should define limits set by physical (abiotic) factors, but should concentrate on biological interactions, particularly predation.
- Shallow areas are preferred habitats of juveniles of several commercially important invertebrate species and may deserve more attention as potentially important nursery grounds for juvenile finfish.

TOPIC 2: Growth/Mortality during the Juvenile Stages

Growth and mortality during the juvenile phase are modulated by shelter, food availability, predation, and temperature. Juvenile mortality cannot be measured unless reliable indices of abundance are obtained. Although juvenile mortality rates cannot yet be properly quantified, it was agreed that they could fluctuate enough to generate year-class variability. Evidence provided included the great gadoid outburst of the 70's in the North Atlantic, cod in NAFO Subdivision 4X and mussels in general. Members of our group could not provide irrefutable evidence of density-dependent juvenile growth although examples derived from adult populations were mentioned i.e. some cod stocks assessed by CAFSAC and sea urchin populations on the Scotian Shelf.

To sum up, the following recommendation was proposed:

- On the basis of the evidence available to the group, predation on juveniles is identified as a dominant source of subsequent year-class variability. Research into predation and its interaction with growth should be strongly supported. However, the implementation of the results will have to await the development of estimates of juvenile abundance which are more proximal for some benthic invertebrates than for most pelagic species.

DISCUSSION REPORT: GROUP D

Chair: Simon Courtenay

Rapporteurs: Lyse Godbout, Ian McQuinn

Participants: Jean-Claude Brêthes, Ben Davis, Garth Fletcher, Mark Hanson, Peter Lawton, Doug McKone, Douglas Pezzack, Mark Tupper, Stephen Walsh.

TOPIC 3: Juvenile Stages and Recruitment Indices

Members of the group felt that, in some species, juvenile recruitment indices have been helpful. Examples cited were: yellowtail flounder on the Grand Banks, American plaice on the Grand Banks, silver hake off Nova Scotia, haddock, cod stocks in the Barents Sea, salmon in Western Arm brook, Newfoundland. For other stocks or species, such as Gulf of St. Lawrence herring, insufficient data exist to determine whether juvenile abundances are a useful indicator of subsequent recruitment to the adult fishery. It was agreed that data on the distribution in time and space of all life stages are required in order to identify production-limiting periods and to understand the mechanisms of population regulation. It was noted that while managers would prefer an index as many years as possible ahead of recruitment, precision and accuracy of the index will improve as recruitment is approached. The survey should initially cover the whole of the suspected geographic range of the stock in question, but may later be restricted to certain areas of the range shown to reflect the dynamics of the stock as a whole. The group suspected that such "index" areas would be areas of low interannual variation in physical parameters. The group noted that in cases of conspecific stocks that overlap in range, management might best be carried out on the stock complex. It was concluded that the probability of developing a useful index of recruitment is a function of the extent of knowledge of life history, and appropriate sampling design and technique.

The group was reluctant to broaden discussion from the juvenile to the egg and larval stages, but noted that data were available with which to address the question of the earliest age at recruitment for some species (e.g. herring). It was noted that age of recruitment may be influenced by events in more than one stage of life. In one species showing variability in age of recruitment (e.g. Atlantic salmon), temperature and growth rate during the juvenile stage have been shown to be influential.

Opinion was unanimous and strong in stating that research surveys for juvenile stages are necessary for stock assessment and management. Given the lack of predictive power of present environmental models, there is no alternative for projections of future stock size. This comment was not intended to belittle the potential value of environmental models; consideration of biological and environmental information together may provide stronger predictive power than either alone.

The group judged the ability to detect a halving or doubling of the stock to be a minimum acceptable level of accuracy. The optimal level should be decided on a stock by stock basis, in the context of the management strategy being utilized.

The group made the following recommendations:

- Emphasis should be placed on juvenile research surveys. If long term advice on a stock is desired and sought, an understanding of its basic biology is crucial. Priority should be given to delimiting the distribution in space and time of all life stages, but particularly of juveniles and recruits. These surveys must be continued for a number of years which will vary with species, but never be less than 3.
- Concurrent with determining abundance over time and space, data should be collected on potential environmental correlates and potential physiological indices. Inclusion of these data in predictive models may improve projections of recruitment, as has been shown for Atlantic salmon.
- Full use should be made of existing research surveys and commercial fisheries to gather data. For example, bycatch of herring, striped bass, silver hake, flounder species, and tomcod in winter estuarine smelt fisheries may provide economic indices of recruitment for these species.
- Explore possibilities of modifying gear and surveyed areas on regular groundfish and other research surveys in order to catch juveniles.
- Continue exploration of acoustic techniques for the identification and enumeration of juveniles.
- Continue exploration of other techniques for assessing abundance of juveniles, such as, examination of diet of predators, beach-seining, and measurements of incidence of settlement (see Hudon, this volume).

TOPIC 4: Preferred Habitats for Juvenile Stages

The group found the general question of the topic to be rather uninspiring. It was concluded that juveniles and adults are often found in different habitats because their needs differ. The primary needs of juvenile stages are thought to be conditions which facilitate growth and avoidance of predation. Needs for juveniles habitats were identified: food, shelter from predators, presence and/or density of conspecifics, depth, light, temperature, habitat access, retention mechanism. A number of points concerning these requirements were noted:

- interactions of requirements (e.g. the substrate chosen by lobsters is affected by the presence of predators - see Gotceitas and Brown, this volume);
- an otherwise suitable rearing area may be rendered unusable by the absence of any one requirement;

- presence or absence of juveniles in a particular habitat is not necessarily evidence of preference or suitability;
- habitats may vary temporally in suitability, as may access to them;
- laboratory studies may be useful in determining preferences and ranges of tolerance;
- it is difficult to measure prey availability to juveniles;
- in some species, there is a good understanding of what constitutes a good rearing habitat.

The group noted that it is an ecological truism that a given habitat will have a certain carrying capacity for a particular animal. In some cases the carrying capacity is met. For example, in some small Pacific coast streams, coho salmon fry are unable to establish feeding territories because other conspecifics have already occupied all of the available space. Therefore, latecomers are carried downriver and out to sea where presumably they perish. This represents evidence that habitat quantity limits coho salmon. Habitat quality may also limit production. For example, data have indicated that the number of feeding territories that can be established in a stream is a function of the abundance of food, and cover.

In other cases, the carrying capacity of the juvenile rearing area appears to be well above the density of juveniles observed there (e.g. lobsters in Nova Scotian coastal waters - see Miller *et al.* this volume). This is often a difficult assessment to make however, as the requirements of the species in question may be partially or completely unknown.

The group recommendations were as follows:

- Identify and characterize juvenile rearing habitats. In association with juvenile surveys, collect data on potential environmental correlates. Support laboratory investigations of juvenile preferences and tolerances among the range of conditions found in the juvenile distribution.
- Determine survival rates in each habitat.
- Examine new technologies for identifying juvenile habitats (e.g. ROXANN sounder to provide information on substrate type and presence of bivalves). This recommendation encompasses work on gear calibration.
- Review existing data on habitat from non-traditional sources.
- Explore modelling approaches which include both biological and environmental factors.

EXTENDED ABSTRACTS
OF CONTRIBUTED PAPERS

Critical Factors for the Development of a Collector for Postlarval and Juvenile Lobsters (*Homarus americanus*)¹

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As with other fisheries, prediction of lobster landings relies on knowledge of ecology and habitat requirements during each life history stage and on the understanding the processes determining year-class strength. The early life history of the American lobster comprises three free swimming planktonic larval stages (Stages I-II-III), during which larvae make vertical migrations (Hudon *et al.* 1986) and can likely be dispersed over a wide area by advective processes. Attempts to predict landings from planktonic stages have met with limited success (see the review by Ennis 1986), presumably due to our limited understanding of the complex environmental factors determining larval survival and advection.

Stage IV postlarvae are neustonic until they start exploratory dives to the bottom in search of an appropriate shelter for settlement (Cobb *et al.* 1983). The process of substrate selection in nature is poorly known, since it takes place over a brief period in late summer or early fall. After settlement, postlarvae hide in crevices between stones, becoming highly cryptic until they reach a size of about 30 mm carapace length (CL) (Hudon 1987). Estimates of abundance of this life stages remain difficult, especially since natural densities are typically very low [maximum concentrations of 13.2 Stage IV $\cdot 1000 \text{ m}^{-3}$ (Hudon *et al.* 1986), 0.18 stage V $\cdot \text{m}^{-2}$ and 3.8 juveniles $\cdot \text{m}^{-2}$ (Hudon 1987)]. However, quantitative collection of early benthic stages requires labour-intensive SCUBA diving surveys, and would be greatly facilitated by the development of an efficient collector for yearly monitoring of postlarval settlement.

Although they are generally shelter-bound during daytime, lobsters >30 mm CL become increasingly active in the open for night-time foraging, and start to be captured in small numbers in commercial lobster traps. Sublegal lobsters (>30 mm CL) can be selectively trapped using a small ring entrance (Duggan and Pringle 1988). Regression relationships between a pre-recruit juvenile abundance index and the recruit yield one to two fishing seasons later were significantly correlated for 8-9 years of data in lower Argyle, Nova Scotia (Campbell 1990). For the western rock lobster (*Panulirus cygnus*) a similar type of relationship, using the relative abundances of both settling larvae and juveniles 1-2 molts before legal size has succeeded in predicting landings with > 90% accuracy (Caputi *et al.* 1991).

This paper examines the operational requirements for the development of a predictive

relationship between early life stages and subsequent lobster landings, to determine the optimal life history stage to be assessed for this purpose. I then focus on the characteristics of a collector for benthic postlarvae and juveniles.

Critical operational characteristics of lobster recruitment monitoring programs

Optimize the ratio between predictive span versus accuracy – Although planktonic larval surveys could provide a long prediction span, their accuracy and forecasting ability are severely limited. The opposite is true of estimates of pre-recruit abundance, only one molt before entry in the fishery. At best, the optimal life stage to monitor should be determined from information on the relative importance of natural mortality and animal dispersal intervening between the time of the assessment and the recruitment into the fishery. For the American lobster, limited available information suggests that recruitment pulses could be determined by the time of benthic settlement.

Integrate the benthic settlement period – The timing and duration of postlarval settlement is quite variable from year to year and among regions, since egg hatching and larval growth are strongly temperature dependent (Aiken and Waddy 1986). An extended period of sampling would be required to adequately estimate the abundance of the planktonic stages, whereas a benthic collector would integrate the season's events regardless of the timing of planktonic larval occurrence.

Standardizable across a variety of sites – The physiography, i.e. water circulation, temperature regime, exposure to prevailing winds, bottom types, etc., of lobster grounds is extremely variable among the fishing districts of the Canadian Atlantic seaboard. Census of later life history stages might provide more accurate indication of interannual variability in fisheries recruitment within each region. Depending on their characteristic physiography, different quantitative relationships between early life stages and recruit into the fishery could be found.

Account for partial recruitment – The long duration of settlement results in a large span of sizes within the cohort by the time lobsters reach its first winter (Hudon 1987). In addition, the individual growth rate of lobsters is highly variable (Roach 1983; Aiken and Waddy 1986), the recruits into the fishery on a given year could belong to several overlapping cohorts, which could presumably dampen the year-to-year variability in recruitment. The estimate of pre-recruits one or two molts before entry in the fishery is the most effective way to by-pass this problem.

Cost-effectiveness – A realistic monitoring program would require a non-labour intensive technique that is simple enough for local contracting, using fairly cheap and re-usable material. Standardized trapping surveys and benthic collectors fit those pre-requisite.

Potential to expand to a large-scale monitoring network – The question of selecting the number and the location of sites to monitor will require a better knowledge of stock identity than is currently available. The extent of and the mechanisms regulating the exchanges of larvae and

migrating adults between adjacent lobster fishing districts which are at present equated with distinct stocks (Ennis 1986; Elner and Campbell 1991) are key issues in determining the distribution and intensity of the monitoring effort.

The above considerations suggest that estimates of early benthic settlement and of pre-recruits one or two molts before recruitment are the life history stages that offer the most potential for lobsters landing forecasts. Both life history stages are successfully used for the predictions of recruitment in the Western Rock lobster fishery (Caputi *et al.* 1991): early settlement allows a rough but long-term forecast which can be "fine-tuned" one year ahead of the fishery using pre-recruit abundance. However, for the American lobster, monitoring of early benthic settlement relies on the development of an efficient collector (Elner and Campbell 1991).

Previous attempts at collecting benthic postlarvae

Several unsuccessful attempts at developing postlarval and juvenile lobster collectors were made in the past, many of which remained unpublished. In the best of conditions, prototypes were "recycled" for the collection of more common and less selective larval species, such as *Cancer irroratus* (Beninger *et al.* 1986).

Various collectors were tested by Vézina (1980): a plastic coated wire frame, plastic frame, Witham habitat, nylon net bag, artificial seaweed and hatbox (Fig. 1a-f). The frames, hatboxes and bags were filled with either oyster or mussel shells, plastic spacers used in oyster spat collectors, or kelp, and baited with salted herring. The Witham habitats (Witham *et al.* 1968) consisted of half rolled polypropylene indoor-outdoor carpeting, attached together under a plastic coated wire screen. The artificial seaweed were made of teased sections of hemp ropes 0.25 m long. Series of collectors were deployed in the summer months near the surface, in mid-water and on the bottom. None of these collectors were successful in attracting lobster larvae, either due to lack of resistance to field conditions (net bag), possible lobster escapement at retrieval (all except hatboxes), the decay of bait and seaweed, or lack of attractiveness to the postlarvae.

Other prototypes of juvenile lobster collectors were tested in Iles-de-la-Madeleine in 1984 (Hudon unpubl. data) (Fig. 2a-e): miniature lobster traps (5 cm ring), PVC tubes with funnels at each end, wooden blocks with 2.5 and 4.0 cm diameter drilled holes in the sides, a pocket made of two layers of shaggy carpet face to face, and a clear plexiglass ichthyoplankton trap. All collectors were baited with rock crabs or herring and were set on a favourable juvenile lobster bottom for 24 h. Underwater inspection prior to retrieval showed juvenile lobsters on the bottom and inside the miniature traps, which was the only gear capturing lobsters (30-39 mm CL). The size of captures corresponds with the onset of open foraging. The lack of success of the other collectors could result from several factors: high light intensity (ichthyoplankton trap), inadequate or unstable shelter (carpet, PVC tubing, wooden blocks) or foreign chemical scent (carpet, PVC, wooden blocks).

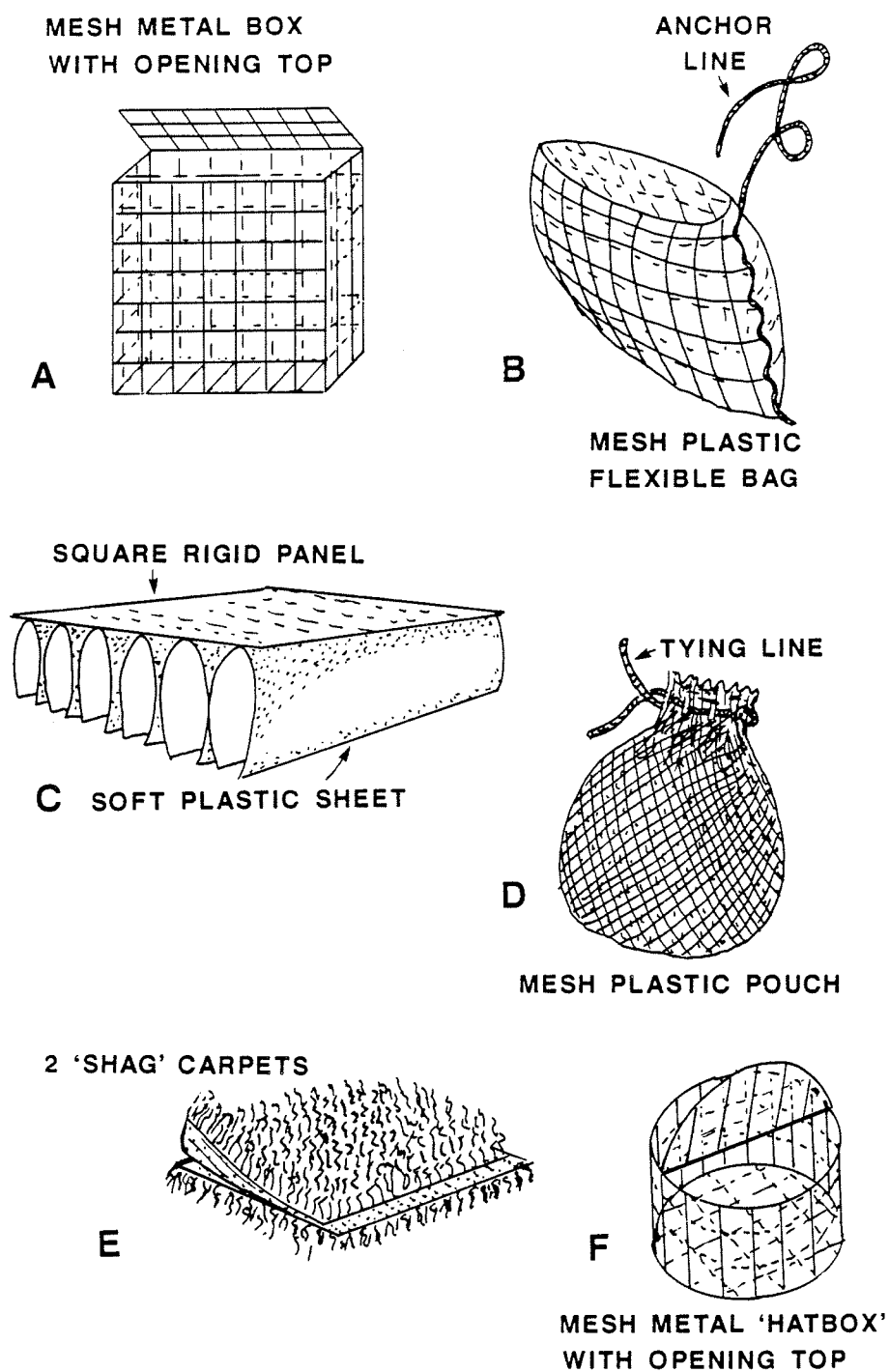


Figure 1. Various collectors for post-larval and juvenile lobsters as tested by Vézina (1980).

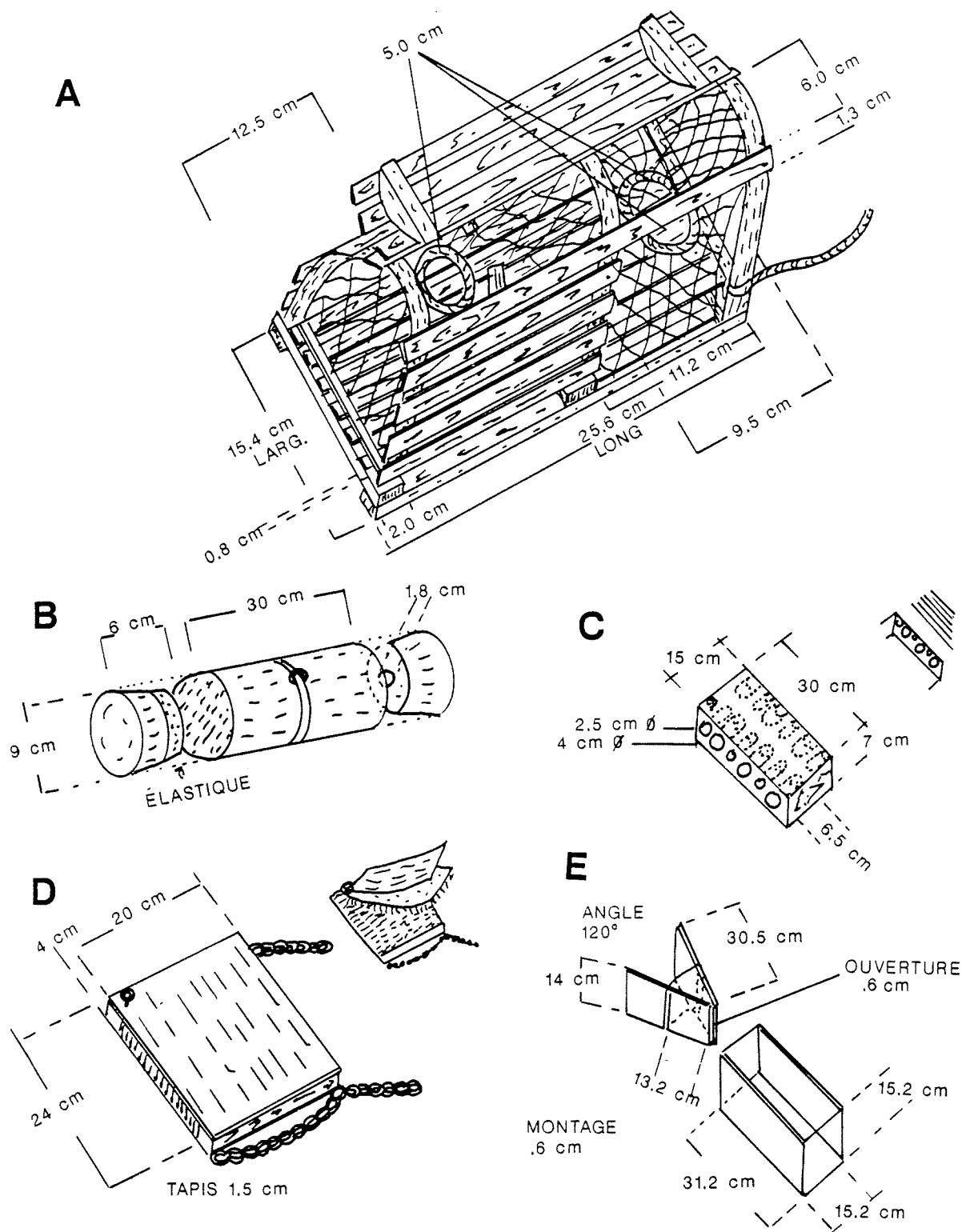


Figure 2. Prototypes of juvenile lobster collectors tested in Iles-de-la-Madeleine during 1984 (Hudon unpubl. data).

Other trials deployed a variety of shelter types: concrete blocks with underside grooves opening on the sides with a clear plexiglass floor were deployed on cobble bottoms for several weeks and periodically surveyed by SCUBA divers (G. Sharp, pers. comm.); trays were filled with layers of black plastic vexar (G. Sharp, pers. comm.) or with rock-cobble substrate taken from an underwater site to mimic the natural habitat of benthic juvenile lobsters (G. Ennis, pers. comm.). The low natural density of juvenile lobsters, the lack of clearly attractive feature and the widespread availability of suitable bottom in the vicinity could explain their lack of success.

An unexpected improvement to the tray technique was brought by the fortuitous capture of postlarval lobsters in a 2 m high stack of plastic trays (1m x 1m x 15 cm) in a Magdalen Island lagoon (P. Fradette, pers. comm.). The trays were divided in 4 compartment for the storage and growth of adult lobsters under semi-natural conditions. The stacks of trays were set on the bottom in late summer and were retrieved the next spring, during which interval postlarval lobsters had entered through the holes on the sides of the trays and grown to a size which prevented their escapement. Several factors could account for their selection: the presence of a complex shelter in an environment largely devoid of cobble substrate, the abundance of epizooic food organisms colonizing the trays, the exclusion of most predators, the presence of adult lobsters.

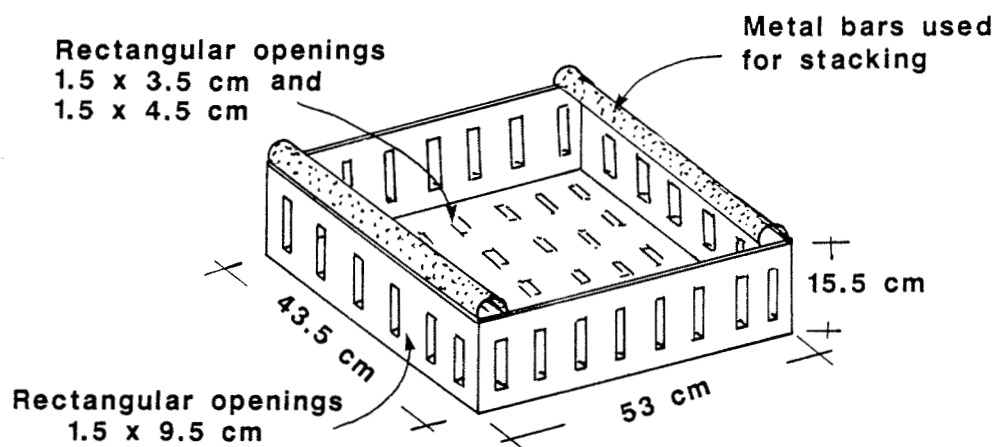
The above observations prompted an experiment (Hudon, unpubl. data) using similar stacks of trays (Fig. 3) set in Baie de Plaisance, Iles-de-la-Madeleine, between June and early October 1991. Each tray was filled with rocks from the subtidal zone complemented with 2-4 L of live mussels and byssal material, providing an initiator to epizooic colonization. Ten stacks of three trays were set on a cobble bottom where juvenile lobsters were abundant, in an area where planktonic postlarvae occurred (Hudon *et al.* 1986). Collectors were retrieved after wrapping into a 3 mm mesh net by a SCUBA diver. A preliminary total of 14 lobsters (6-42 mm CL) were captured ($2 \text{ juveniles} \cdot \text{m}^{-2}$ and of $0.29 \text{ postlarva} \cdot \text{m}^{-2}$), consistent with natural density estimates. The wide range of sizes and the higher abundance in bottom trays indicate that older juveniles had entered the collectors in addition to settling postlarvae. Lobsters < 40 mm escaped in the seine during retrieval whereas larger ones were trapped in.

Critical biological characteristics of lobster collectors

Substrate coarseness and potential shelter – A growing number of field studies report that highest densities of postlarval and juvenile lobsters are found on coarse bottoms (Hudon 1987; Wahle and Steneck 1991). The availability and size of hiding spaces in crevices and under stones likely determines the carrying capacity of various habitat and the resulting population size structure of lobsters.

Stability and darkness – Adult and juvenile lobsters are negatively phototactic, tend to forage at night and avoid unstable shelters. Escape reaction is well developed for small lobsters, as most animals captured were found in the fine-meshed seine surrounding the collectors during retrieval.

A. Individual Tray



B. Collector

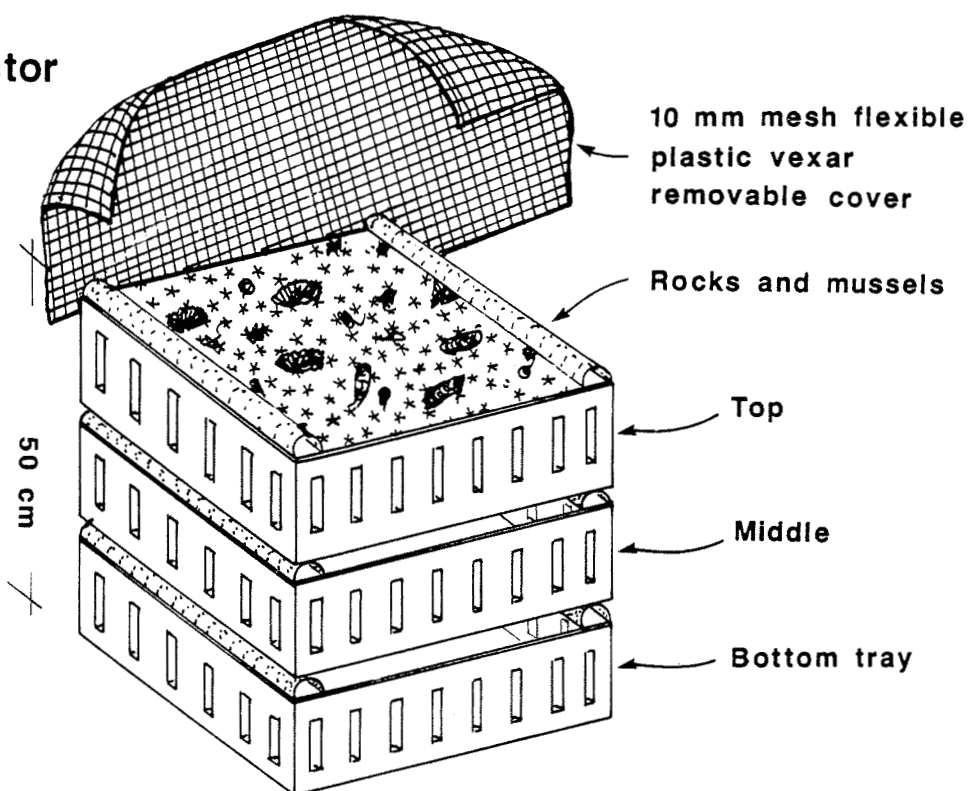


Figure 3. Juvenile lobster collectors used in Iles-de-la-Madeleine during 1991.

Eating without being eaten – The cryptic behaviour and predominantly nocturnal activity regime postlarvae and juvenile lobsters adopt for the early part of their benthic life has been attributed to the interaction of predator avoidance and food requirements (Lawton 1987). Epizootic colonization and the addition of living organisms (mussels) to the collector would enhance its attractiveness through a self sustaining food supply to postlarvae. Small lobsters fall prey to a wide variety of small and large fish and crustacean species, the largest of which can easily be excluded from the collector.

Location and surface area – In order to maximize the chances of successfully collecting postlarvae, the collectors should be located in areas where planktonic stage IV and benthic juveniles and adults are known to occur. Since postlarval concentrations in the plankton and on the bottom are naturally very low, the minimal collecting surface area should be 5-10 m². Much work needs to be done in this area, since collectors efficiency in detecting year to year variability in recruitment relies on their representative sampling of key habitats.

Relative availability of favourable habitat surface area – As suggested by earlier attempts, collecting performance could vary with the relative availability of suitable bottom types for benthic settlement. For instance, shallow rocky bottoms favourable to juveniles comprise only 10% of the total surface area of the Iles-de-la-Madeleine, whereas they equal 36% (see Miller *et al.* this volume) of coastal Nova Scotia. To evaluate the importance of this factor, simultaneous experiments should be conducted in physiographically different areas where lobsters are present.

Water circulation vs sanding up – The immersion of any structure on the bottom changes the small-scale water circulation and eventually become sanded in. The appropriate amount of sediment deposition adequate for lobster is unknown and is difficult (or impossible) to control/predict in a field setting. The stacking of individual trays is one way to ensure that at least one of the trays of each collector will provide suitable conditions at any given time during the immersion period.

Ground truthing – Before the catches of the collectors can be used for predictive purposes, their performance must be calibrated against natural densities on the bottom and related to subsequent pre-recruit catches in traps over several years. Introduction and monitoring of tagged lobsters offer potential for study of residency and escapement. Laboratory studies are also required for direct observation of colonizing behaviour at different sizes and establishing the carrying capacity/saturation level of the collectors.

As seen above, the characteristics of an efficient collector comprise a number of components, the significance of which are still being explored. Further field and laboratory work will likely improve the present prototype. Whether or not postlarval collectors can be successfully used for the prediction of subsequent landings remains unknown at this stage. Nevertheless, they represent a powerful tool to improve our understanding of postlarval and juvenile lobster ecology, growth and habitat requirements.

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Dynamique de la structure démographique du crabe des neiges (*Chionoecetes opilio*) sur la rive nord de l'estuaire maritime du Saint-Laurent et ses implications sur le recrutement à la pêche.

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Le crabe des neiges (*Chionoecetes opilio*) est un crustacé de grande importance commerciale dont les principaux sites de pêche sur la côte Atlantique sont situés dans l'estuaire et le golfe du Saint-Laurent, autour de l'île du Cap-Breton et sur la côte est de Terre-Neuve (Dufour 1988). Seuls les mâles présentant une largeur de carapace supérieure à 95 mm sont exploités. La stratégie de gestion de la pêcherie du crabe des neiges est de viser un taux d'exploitation de 50 à 60% de la biomasse exploitable. L'évaluation du statut de la ressource est généralement faite en utilisant la méthode de Leslie-De Lury d'analyse des prises et effort (Ricker 1975).

Un récent atelier sur la biologie du crabe des neiges recommandait l'étude de la distribution, de l'abondance et de la croissance des stades pré-recrutés à la pêche afin de réaliser des modèles de prédiction (Jamieson et McKone 1988). A cette fin, une étude a été entreprise en 1989 sur la rive nord de l'estuaire maritime du Saint-Laurent afin de mieux connaître les variations à court terme de la distribution et l'abondance du crabe des neiges dans ce secteur.

MATÉRIEL ET MÉTHODES

ÉCHANTILLONNAGE

L'étude a été réalisée au large de Forestville sur la rive nord de l'estuaire maritime du Saint-Laurent (48° 43' N-68° 57' W), sur une zone d'environ 160 km² (Fig. 4). Sur la base des caractéristiques sédimentaires favorables à l'espèce, le secteur a été divisé en trois strates de profondeur : (1) 50-89 m, (2) 90-119 m, (3) 120-160 m. Le nombre de stations par strate a été pondéré par la surface de chacune d'elle et la répartition des échantillons a été établie au hasard à l'intérieur de chacune des strates. L'échantillonnage s'est déroulé au cours de six sorties mensuelles, du 27 avril au 12 septembre 1989 (Tableau 1). Les crabes ont été capturés à l'aide d'un chalut à perche d'une ouverture horizontale de 3 m et de maille étirée de 45 mm doublée

d'un maillage intérieur de 25 mm dans le cul (Miller et O'Keefe 1981). Quatre chaînes racleuses ont été disposées entre les patins et à l'entrée de la poche afin de mieux pénétrer le sédiment. Les traits de chalut exécutés à une vitesse de $1 \text{ à } 1.5 \text{ m} \cdot \text{s}^{-1}$ duraient environ 20 min. La position du début et de la fin de chaque trait, ainsi que la profondeur moyenne ont été notées. La température et la salinité près du fond ont été mesurées à l'aide d'un enregistreur STD. La capture était triée sur un tamis de 2 mm de maille à l'aide d'un jet d'eau et pesée par espèce. L'abondance de *Chionoecetes opilio* fut calculée et exprimée en $\text{ind} \cdot \text{km}^{-2}$. Les mesures suivantes ont été également effectuées sur les mâles : largeur maximale de la carapace (Lc), hauteur (Hp) et largeur (Lp) de la pince droite. Bien que des données sur l'ensemble de la population aient été récoltées, nous ne considérons ici que l'information sur les individus mâles à cause de leur plus grande importance dans le contexte de l'exploitation.

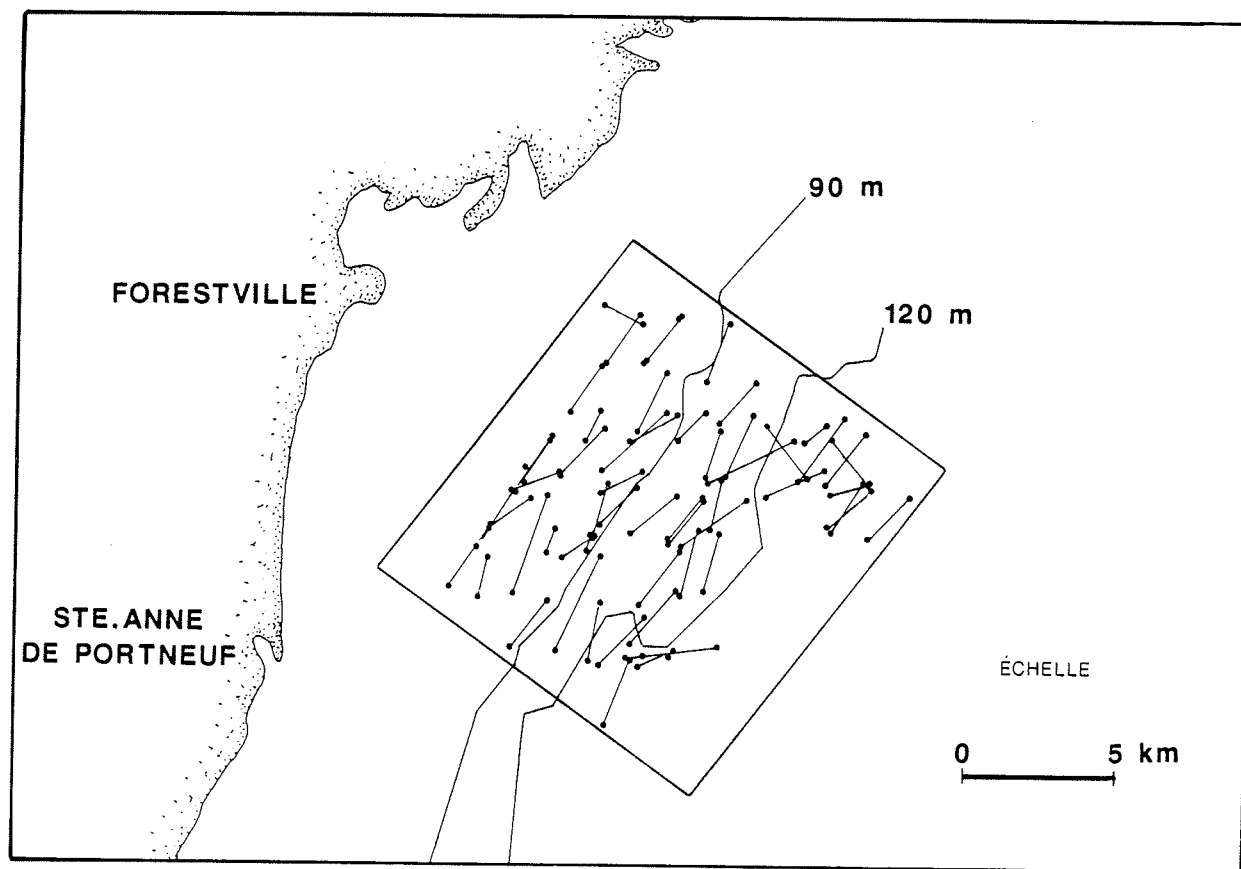


Figure 4. Stations d'échantillonnage.

Tableau 1. Sommaire des activités d'échantillonnage réalisées en 1989.

Dates des sorties en mer	Nombre de traits effectués	Durée moyenne de chalutage (min)	Surface moyenne des traits de chalut (m ²)
27-29 avril	5	21	3892
15-17 mai	6	20	3892
16-18 juin	11	21	5330
3 & 17-20 juillet	15	21	6531
2-4 août	12	20	4856
8-12 septembre	14	21	6027

ANALYSES

Le degré d'agrégation des crabes par sortie a été évalué selon l'approche proposée par Elliott (1977) en regroupant toutes les strates de profondeur. Les individus ont été séparés en deux classes de taille ($L_c < 70$ mm et $L_c \geq 70$ mm) auxquelles un test de χ^2 a été appliqué pour comparer la distribution des densités observées à une distribution de Poisson, selon l'hypothèse nulle d'une distribution aléatoire. Lorsqu'une distribution contagieuse était notée, le coefficient de Green (1966) était calculé selon l'équation :

$$G = \frac{VARIANCE - MOYENNE}{MOYENNE \times ((\Sigma DENSITÉS) - 1)}$$

Cet indice, indépendant des variations du nombre d'observations, de la moyenne et de la somme des densités, était calculé afin de préciser un peu plus le degré d'agrégation présent. Cet indice varie de : $-(1 / \Sigma \text{ densités})$, pour une distribution régulière, à 1 lors d'une agrégation maximum; 0 représentant une dispersion au hasard des individus.

Selon les recommandations de Conan et Comeau (1986), la maturité morphométrique a été déterminée à partir d'une analyse en composante principale (programme Princomp du logiciel SAS) des variables morphologiques (L_c , H_p , L_p) pour les individus capturés en août. Une analyse discriminante de Fisher à partir de L_c et H_p a ensuite permis de séparer, avec une précision de 95 %, les mâles en deux groupes, morphométriquement matures ou non, à partir de l'équation de séparation :

$$\text{Log}_e H_p = -3,0808 + 1,3304 \text{ Log}_e L_c$$

Les distributions de fréquence de taille mensuelles, toutes profondeurs confondues, ont été décomposées, séparément pour les crabes matures et pour les immatures, à l'aide de la technique de Bhattacharya (logiciel ELEFAN, Gayanilo *et al.* 1989). Les résultats ont fait ressortir trois modes chez les individus immatures (56-67 mm, 78-82 mm et 91-95 mm) et un mode additionnel, moins important, chez les matures (107-115 mm). On a ainsi défini trois groupes empiriques correspondant aux tailles prérecrutées suivantes : (1) 55-69 mm ; (2) 70-84 mm ; (3) 85-99 mm. Les variations d'abondance de chacun de ces 3 groupes d'immatures pré-recrutés ont été suivies mensuellement à chacune des strates de profondeur et testées par l'analyse non paramétrique de Kruskal-Wallis (logiciel SYSTAT).

RÉSULTATS

TEMPÉRATURE

La température près du fond dans la strate supérieure (50-89 m) s'est maintenue toujours très froide (-0.5°C à 0.6°C) tout au long de l'échantillonnage. La strate intermédiaire (90-119 m) était baignée par des eaux plus chaudes (1.3°C à 2.4°C) en avril. En mai, le régime de température des trois strates s'est individualisé et les températures les plus basses (<0°C) ont été observées dans la strate supérieure. Par la suite, l'ensemble des températures a augmenté progressivement.

Tableau 2. Résultats du test du χ^2 afin de déterminer la dispersion spatiale des mâles de taille ≥ 70 mm et < 70 mm à différentes périodes d'échantillonnage. Les valeurs entre parenthèses indiquent le degré de liberté du test (n-1). Cont. = contagieuse, Has = hasard; * = $P > 0.05$.

Taille	Avril	Mai	Juin	Juillet	Août	Sept.
≥ 70 mm	20,72 (4) Cont.*	288,29 (5) Cont.*	28,57 (9) Cont.*	23,20 (14) Has.*	5,69 (11) Has.*	25,23 (13) Cont.*
< 70 mm	11,79 (4) Cont.*	309,46 (5) Cont.*	51,74 (7) Cont.*	66,03 (14) Cont.*	33,70 (11) Cont.*	74,42 (9) Cont.*

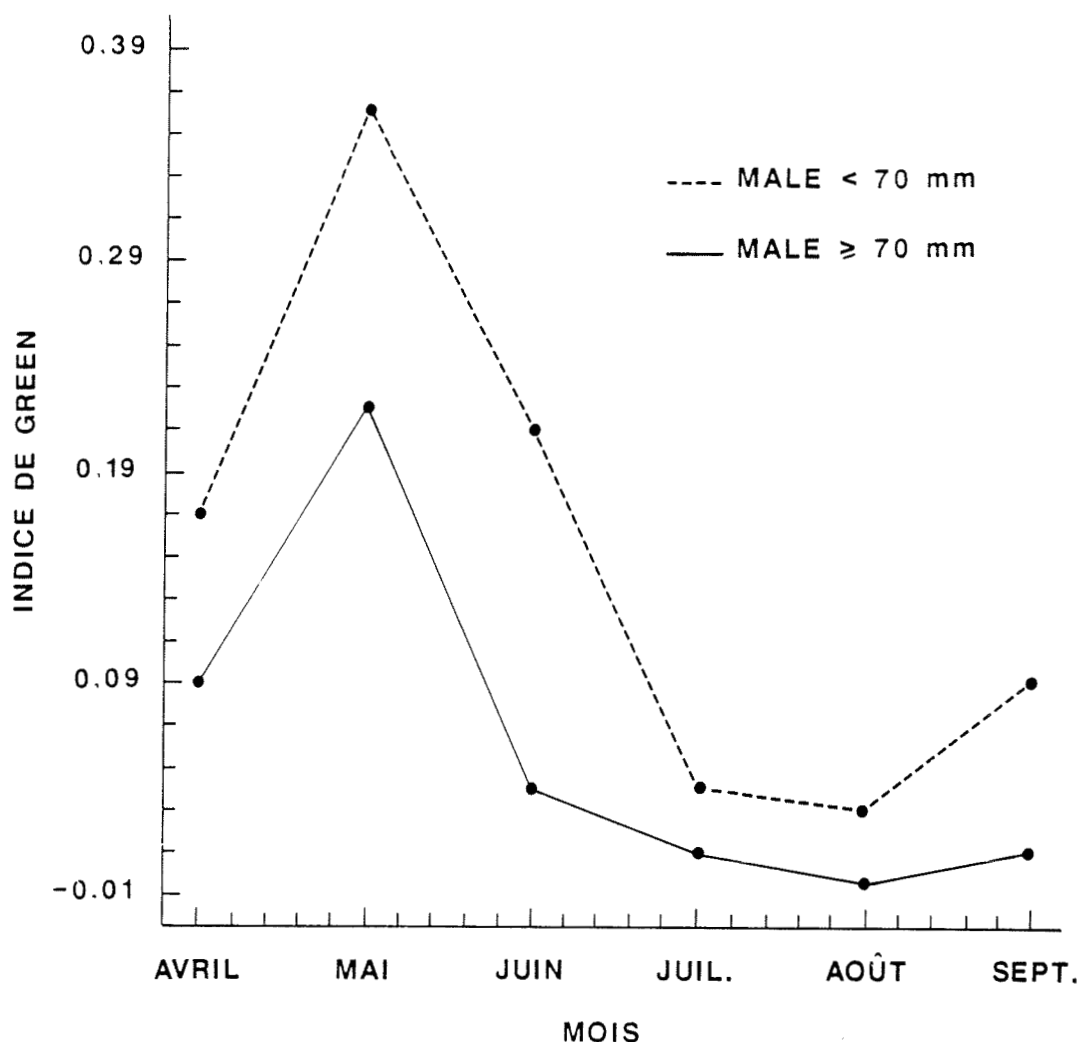


Figure 5. Fluctuations mensuelles de l'indice de Green.

RÉPARTITION SPATIALE

L'analyse du χ^2 montre l'existence d'une distribution au hasard uniquement pour les gros crabes mâles ($L_c \geq 70$ mm) durant les mois de juillet et août (Tableau 2). De façon générale, les deux groupes de taille tendaient à former des agrégats bien définis durant les autres mois d'échantillonnage, particulièrement en mai, où la valeur du χ^2 et du coefficient de Green étaient très élevées (Fig. 5).

DYNAMIQUE DÉMOGRAPHIQUE SUR LES FONDS

Les variations mensuelles d'abondance des trois groupes de taille des individus matures (Fig. 6) ne sont pas apparues significatives aux différentes profondeurs échantillonnées (Kruskal-

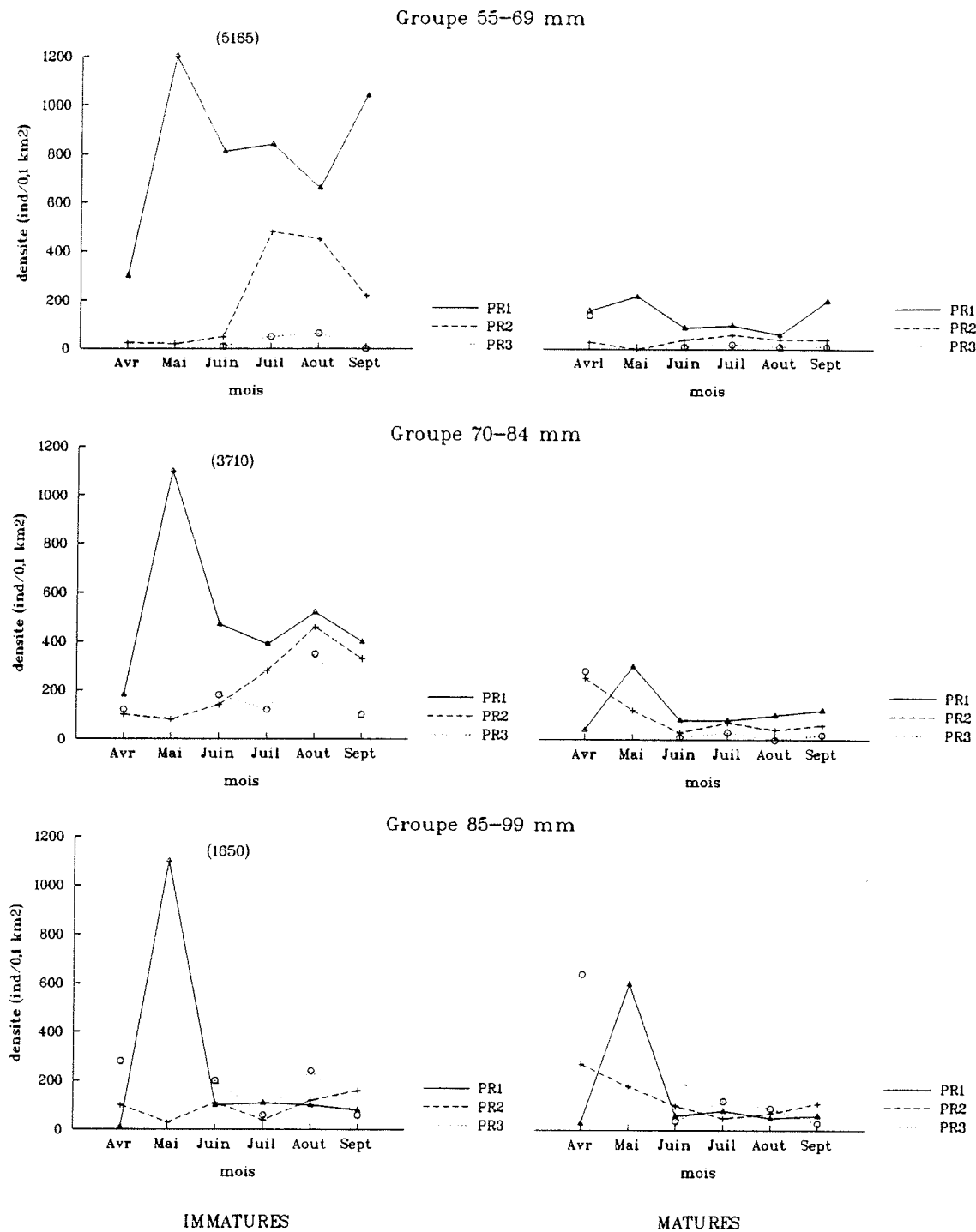


Figure 6. Variations mensuelles des densités de crabes mâles immatures et matures selon les 3 groupes de taille à trois strates de profondeur (PR1=50-89m; PR2=90-119m; PR3=120-160m).

Wallis, $P > 0.05$). Les valeurs étaient relativement faibles pour les trois groupes de taille et généralement inférieures à $2000 \text{ ind} \cdot \text{km}^{-2}$ sauf entre 50 et 89 m en mai où environ $6000 \text{ ind} \cdot \text{km}^{-2}$ avaient été recensés. De façon générale, les captures d'individus matures furent maximales en avril et mai à toutes les profondeurs. De plus, l'abondance des individus des trois groupes de taille tendaient à diminuer d'avril à juin entre 90 et 119 m et entre 120 et 160 m.

Les tendances sont mieux définies chez les individus immatures (Fig. 6) bien que les différences d'abondance entre les strates de profondeur soient faiblement significatives entre elles ($P < 0.05$). Pour les groupes de taille de 55-69 mm et 70-84 mm, les abondances variaient de $200 \text{ ind} \cdot \text{km}^{-2}$ à $51650 \text{ ind} \cdot \text{km}^{-2}$ et étaient maximales entre 50 et 89 m durant toute la période échantillonnée. A cette profondeur, tous les groupes d'immatures ont montré un accroissement marqué de leur abondance en mai, suivi d'une diminution en juin-juillet. Un accroissement a également été perçu plus tard en saison (juillet-août) aux profondeurs $> 90 \text{ m}$, mais leur nombre a diminué en septembre.

DISCUSSION

L'ensemble des résultats montre une très grande variabilité, aussi bien spatiale que temporelle, dans la dynamique de distribution des mâles. Cette variabilité peut être attribuable en partie à des biais d'échantillonnage liés au nombre d'échantillons prélevés mensuellement et à l'engin utilisé (Miller and O'Keefe 1981; Robichaud *et al.* 1989). Nos résultats sont toutefois similaires à ceux rencontrés dans d'autres secteurs du Golfe du Saint-Laurent et les tendances observées sont cohérentes sur l'ensemble de l'échantillonnage. En considérant que les valeurs obtenues s'échelonnent sur quelques ordres de grandeur, il est donc possible de définir certaines tendances marquées pour cette population de *Chionoecetes opilio*.

Les abondances de crabes, variant de 200 à $51650 \text{ ind} \cdot \text{km}^{-2}$ pour les tailles échantillonnées, recourent l'intervalle d'abondance de 700 à $2400 \text{ ind} \cdot \text{km}^{-2}$ au Cap-Breton (Robichaud *et al.* 1989) mais sont inférieures aux fortes abondances (10400 à $18400 \text{ ind} \cdot \text{km}^{-2}$) notées à Terre-Neuve par Miller (1975). Ces variations apparaissent liées à la profondeur des stations, à la taille et à la maturité des individus et aussi, tel que mis en évidence par notre type d'échantillonnage, à la période de l'année durant les récoltes sont effectuées.

D'une façon générale, les mâles semblent fortement agrégés sur le fond, quelle que soit leur taille (Miller 1975; Conan and Maynard 1987). Nos résultats montrent que la période de l'année influence fortement le type et l'intensité de la distribution rencontrée. Une distribution aléatoire des gros individus ($L_c \geq 70 \text{ mm}$) n'a été notée qu'en juillet et août, conséquence probable des effets de l'exploitation par la pêche qui dure d'avril au début juillet dans cette région. La forte agrégation et les fortes abondances observées en mai, pour toutes les catégories de taille sont des phénomènes importants et peu mentionnés dans la littérature. Nos résultats, bien que préliminaires, montrent que cette forte agrégation des mâles en mai ne se retrouve qu'en faible profondeur (50-89 m). Sainte-Marie *et al.* (1988) ont rencontré un phénomène de forte agrégation similaire à la fin avril dans la Baie Sainte-Marguerite près de Sept-îles, mais à de plus

faibles profondeurs, soit 4-6 m. Les prochaines études permettront de connaître plus précisément la nature de ces agrégations de même que les causes exactes et le degré de persistance de ce phénomène d'une année à l'autre. Le mois de mai marque une modification importante dans la structure hydrologique de la colonne d'eau. Il correspond également à la fin de la période de reproduction et de mue dans le golfe. Il pourrait donc s'agir d'une période charnière dans le cycle biologique de cette population.

L'augmentation d'abondance des trois groupes d'individus de taille différente en mai sur les niveaux bathymétriques supérieurs est suivie d'une part d'une diminution dans les mois subséquents, mais aussi par une augmentation plus tardive sur les niveaux inférieurs. Le décalage temporel des pics d'abondance en fonction de la profondeur pourrait être relié à des phénomènes migratoires, où les niveaux superficiels pourraient approvisionner les niveaux plus profonds, corroborant les idées émises par Coulombe *et al.* (1985) et Bouchard *et al.* (1986). De tels déplacements selon le gradient de pente ont également été notés par Brêthes and Coulombe (1990) et Lefebvre and Brêthes (1991).

L'évolution générale des tendances observées semble indiquer trois grandes périodes marquant la dynamique de distribution spatiale des crabes mâles de cette région : une première période, soit la fin du printemps, est caractérisée par une distribution plus agrégative des individus sur le fond et correspond à la fin de deux grandes phases du cycle vital des mâles que sont la mue et la reproduction et à des modifications hydrologiques importantes, soit la fin de la crue printanière du Saint-Laurent et la modification de la stratification des masses d'eau. La période estivale montre un réajustement des distributions, avec des mouvements migratoires probablement induits par la pêche, et une certaine re-dispersion au hasard des individus sur les fonds. Enfin la troisième période correspondant au début de l'automne est marquée par un retour à une dispersion moins aléatoire des crabes et souligne le passage de la population aux conditions hivernales.

D'un point de vue pratique, ce travail a permis de déterminer les bases sur lesquelles s'appuieront les prochains relevés de recherche portant sur le recrutement à la pêche qui devraient débuter en 1992 dans cette région. L'engin utilisé, dont la sélectivité sera examinée plus en détail en 1992, s'est montré très fiable sur les fonds échantillonnés et facile d'utilisation avec des bateaux de faible tonnage. L'étendue des tailles échantillonnées permet d'entrevoir des possibilités de prédiction des biomasses exploitables à partir des stades pré-recrutés, s'appuyant sur deux cohortes théoriques dont les modes se situeraient aux environs de 55-65 mm et 70-80 mm, correspondant à une période d'environ deux ans avant l'entrée dans la pêche. De plus la biomasse d'une certaine fraction de la population commercialisable, disponible à la pêche la saison suivante pourra également être évaluée. Notre travail montre que ces relevés devraient être réalisés préférentiellement durant la période estivale, alors que les plus gros individus pré-recrutés (≥ 70 mm) se distribuent au hasard sur les fonds. L'échantillonnage devrait couvrir les profondeurs de 50 à 160 mètres, puisque toutes les tailles recherchées y sont représentées.

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Lobster Juvenile Recruitment and Adult Landings: Influence of Larval Behaviour, Temperature Stratification and Strong Wind Events.

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The behavioural responses of the truly planktonic stages (I-III) and the settling stage (IV) of the American lobster (*Homarus americanus*) to a thermal gradient were studied using an experimental approach in the laboratory. The thermocline markedly influence the vertical distribution of all larval stages, which were limited to the upper part of the water column (Boudreau *et al.* 1991). Both in absence or in presence of a thermocline, older individuals (stages III & IV) were observed deeper in the water column than younger individuals (stages I & II). The percentage of post-larvae (stage IV) settled after 24 h was two times less in the presence of a thermocline than in the corresponding controlled situation (Boudreau *et al.* submitted). Gradients from 18.5 to 13.5°C and from 16.5 to 12°C were sufficient to significantly reduce the proportion of settled post-larvae, even though these temperatures were well within the range encountered on natural nursery grounds during settlement period (Boudreau *et al.* submitted). The proportion of post-larvae crossing the thermocline increased with a decrease in stratification, going from 13% for a thermocline of 6°C to 15% and 28% for gradients of 4.5 and 2.5°C respectively. Conversely, settled post-larvae left the bottom when the ambient temperature was reduced. The vertical distribution of both planktonic and settling larvae was unaffected by the day/night light regime (Boudreau *et al.* 1991; submitted). The ecological significance of this temperature-driven behaviour of the larvae/post-larvae relative to the recruitment dynamics of the adult stock was analyzed. We hypothesize that this temperature-driven behaviour was related to the larval and post-larval success in the field. The validity of this hypothesis was explored for the lobster stock of Iles-de-la-Madeleine, Gulf of St. Lawrence. Significant negative correlations obtained between the frequency of strong winds ($> 30 \text{ km}\cdot\text{h}^{-1}$) during dispersal and settlement periods, and subsequent lobster landings (with an 8-yr lag) in this region over a 15-year interval support the hypothesis (Boudreau *et al.* 1991).

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Are Small Juvenile Lobsters Habitat Limited?

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Fogarty and Idoine (1986) and Caddy (1986) postulated that lobster recruitment to the fishery is resource limited during the benthic phase. Using a 15 yr time series of lobster larval collections in Northumberland Strait, Scarratt (1973) found a weak correlation between stage IV production and size of the resulting year-class recruited to the fishery. But, Fogarty and Idoine (1986) interpreted the same data as more or less constant recruitment, a three fold range, over a very large, 100 fold range, variability in larval production. They further concluded that this would result in a stable fishery even when subjected to variable exploitation rates, and hence variable spawning stock size. Thus, the size of the recruit year-class is limited during the benthic rather than larval phase. Caddy (1986) also proposed that year class size is determined after larval settlement because he could find few instances in the literature where spawning stock size and recruitment to the fishery were correlated for decapods. Both Fogarty and Idoine and Caddy suggested that shelters which allow small lobsters to escape predation might be the limiting resource.

Wahle and Steneck (1991) surveyed the substrate types bordering 60 km of shoreline in central Maine. Because only 11% was shelter-providing cobble and boulder habitat they also advocated this as being a limiting resource for lobsters. Thus, the hypothesis that habitat available for juvenile lobster controls recruit year class size is gathering momentum and deserves consideration. The following discussion gives our thoughts on the topic. We will focus on lobsters <40 mm carapace length (CL) because these sizes spend little time outside their shelters (Cooper and Uzmann 1980; Lawton 1987) and are obviously shelter dependent.

The Atlantic coast of Nova Scotia from Cape Sable Island to Bay St. Lawrence has 4915 km of shoreline (Fig. 7), 50% of which is bordered by rocky subtidal, and 50% by mud, sand, or gravel (Table 3). Divers surveyed the rocky portion at 2088 stations on 140 transects (Moore and Miller 1983; Moore *et al.* 1986). The transects ran perpendicular to shore to a depth of 15 m, or until the substrate became <50% bedrock, boulders, or cobble. Twenty-eight percent of the area surveyed by divers was bedrock or scattered boulders on bedrock. The remaining 72%, or 682 km² consisted of boulders and cobble bottom and was considered habitat most suitable for small juvenile lobsters (<40 mm CL).

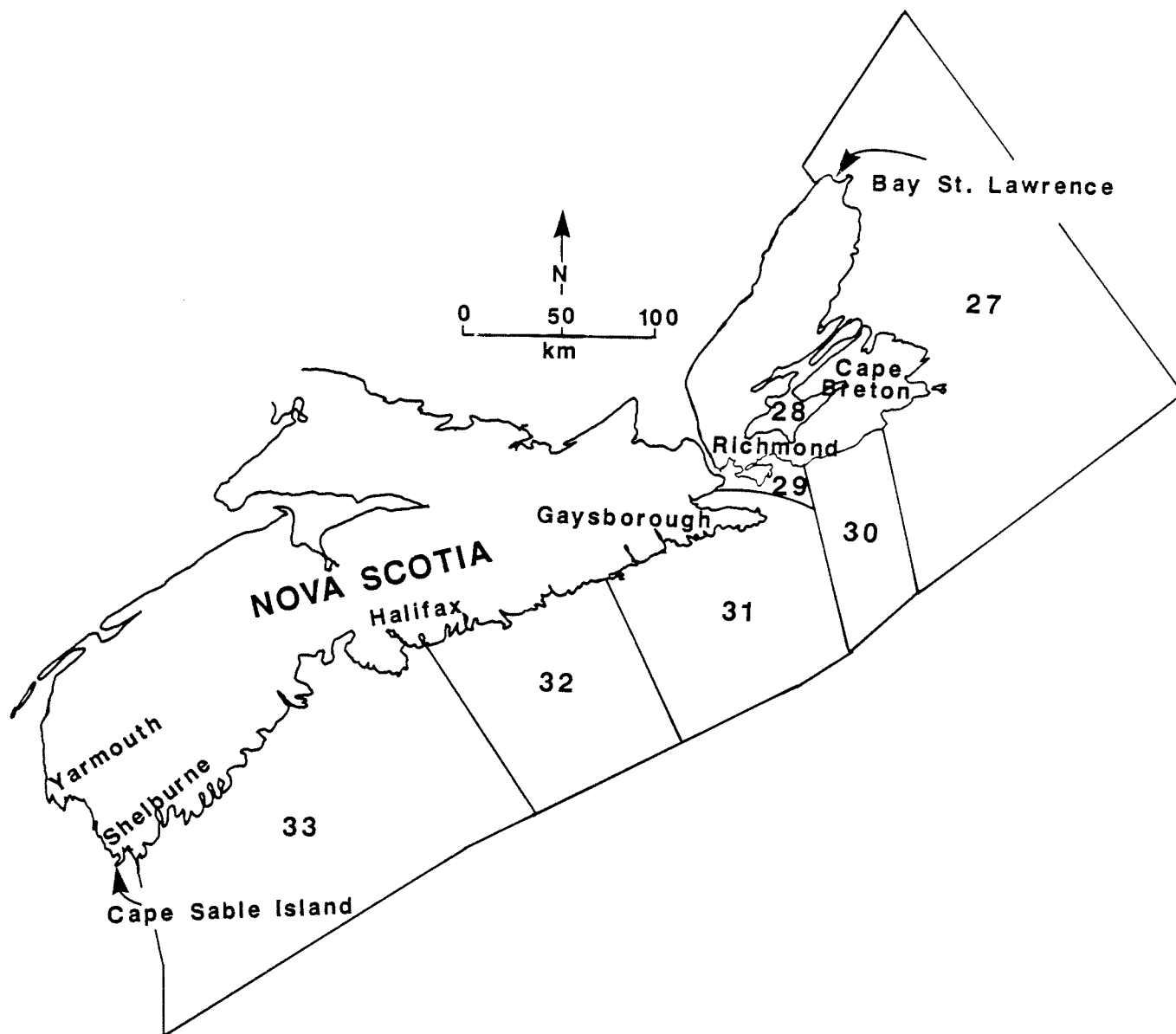


Figure 7. The numbered areas include the shoreline surveyed. Area 27 is referred to as eastern Cape Breton.

This definition of most suitable habitat was based on field studies in Nova Scotia, Iles-de-la-Madeleine, and central Maine, as summarized in Table 4. The 682 km² represents a minimum estimate because juvenile lobsters have been also found in low densities on bedrock and in sea grass beds. Moreover we have no reason to expect that juvenile distribution stops at 15 m, the depth limit of the habitat survey and the surveys referenced in Table 4.

Table 3. Juvenile lobster habitat to 15 m depth on the Atlantic coast of Nova Scotia.

Bottom type	Shoreline length (km)	Bottom area (km ²)
soft bottom	2479	
hard bottom	2436 (50%)	941
bedrock		259 (28%)
cobble,boulder,etc. (juvenile lobster habitat)		682 (72%)

Averaged over 1986-90, lobster landings for eastern Cape Breton (Area 27 in Fig. 7) were 7.5×10^6 lobsters. Because annual exploitation rates are about 80% (Miller *et al.* 1987), lobster landings are a reasonable proxy to annual recruitment, and to the size of a single year-class. According to the diving survey for eastern Cape Breton there were 73 km² of habitat suitable for small juvenile lobsters, and thus about 10 m² per lobster in a recruit year-class (Table 5). Eastern Cape Breton landings exceeded the previous 100 yr record in 1986, and by 1990 were three-fold higher than at any time prior to the 1980's. Assuming constancy of habitat and a reasonably high exploitation rate over the history of the fishery, one can argue that carrying capacity must not have been limiting to any previous year class.

Using the suitable habitat area and 1986-90 lobster landings for the remainder of the survey area gives a result of 110 m² per lobster per year class (Table 5). If habitat carrying capacity is at least 1 per 10 m² as in eastern Cape Breton, then habitat cannot have been limiting in these areas. For both areas this line of reasoning is valid only if lobster predators present now are as numerous and as effective at penetrating shelters as lobster predators were in the past. Although not explicitly considered here, food can also limit carrying capacity. We cannot say whether food or predators of juvenile lobsters have changed over the history of the fishery.

There is other evidence on habitat carrying capacity. Roach (1983) stocked rock filled containers (75 X 75 X 45 cm deep) with 25 stage IV larvae and followed their survival with and without predators added. After 4 weeks 50-60%, or about 25 ind · m⁻², survived with or without starfish or crab predators. In another experiment 74% survived for 4 weeks without predators and 50% for 4 weeks with fish predators. In another experiment without predators, survivorship did not change from 2 to 4 to 6 weeks using stocking densities of 27 to 178 ind · m⁻², suggesting that mortality occurred soon after introduction of lobsters and was independent of density. Barshaw and Lavalli (1988) stocked rock substrate with juvenile lobsters at a density of 30 ind · m⁻². About 75% survived 4 d exposure to fish (cunner) and mud crab predators, although during one series only 4% survived crab predators. The authors of this paper have spent many hours peering at cobble and boulder covered habitats, and are of the opinion that a great labyrinth of small interstitial spaces exist in these areas. Enough spaces to accommodate 30 juvenile lobsters · m⁻² would not seem unreasonable.

Table 4. Density of small lobsters (<40 mm CL) as measured by diver collections at several sites.

Location	Habitat depth (m)	Bottom type	Lobster size (mm)	Lobster density (# m ⁻²)	Source
SW Nova Scotia	3-9	small boulders	20-40	0.08	Bernstein and Campbell (1983)
			20-40	0.16	A. Campbell (unpubl. data)
			20-40	0.10	
			20-40	0.10	
			20-40	0	
SW Nova Scotia	4-10	boulders on sand	20-40	0.26	G.J. Sharp (unpubl. data)
		boulder	20-40	0.01	
		bedrock	20-40	0	
Iles-de-la-Madeleine	2-5	stones on sand	15-39	1.17 (0.5-2.4)	Hudon (1987)
	2-5	boulders on sand	15-39	1.88 (0.9-2.9)	
	7	bedrock	15-39	0.29 (0.2-0.4)	
	2-5	sand & eelgrass	15-39	0.01	
	2-5	sand	15-39	0	
Central Maine	5	cobble or boulder	9-40	2.37 (0.1-6.9)	Wahle and Steneck (1991)
	10	cobble or boulder	9-40	2.1 (1.0-6.7)	
	5	mud or sand with eelgrass	20-40	0.2	
	5 or 10	mud or sand	20-40	0	
	5 or 10	bedrock	<40	0.06	
	5 or 10	bedrock with kelp	<40	1.05	

Table 5. Habitat area per lobster per year-class.

	Eastern Cape Breton	Remaining area
no. lobster/year-class	7.5×10^6	5.4×10^6
juvenile lobster habitat (m^2)	73×10^6	609×10^6
$\text{m}^2/\text{lobster}/\text{year-class}$	~ 10	~ 110

Another approach to deciding how much juvenile habitat is enough to support the fishery is to back-calculate the density of small juveniles from the density of a recruit year-class. The population <40 mm CL present at one time would consist of two year-classes (Wilder 1953; Hughes and Matthiessen 1962; Hudon 1987) if one considers that the third year class would grow past 40 mm CL by the time of settlement of the first year class in August-September. If natural mortality between 40 mm CL and recruit size reduced population numbers by 90% (this would result from natural mortality of 37% per yr for 5 years and is probably an overestimate.), then for eastern Cape Breton the density of lobsters <40 mm CL would need to be $2 \text{ ind} \cdot \text{m}^{-2}$ ($0.1 \text{ ind} \cdot \text{m}^{-2} \times 2 \text{ year-classes} \times 10$). For the remainder of the survey area the density <40 mm would need to be only $0.18 \text{ ind} \cdot \text{m}^{-2}$ ($0.009 \cdot \text{m}^{-2} \times 2 \text{ year-classes} \times 10$). Hudon (1987) and Wahle and Steneck (1991) recorded maximum densities of 3.8 and $6.9 \text{ ind} \cdot \text{m}^{-2}$ respectively. These are certain to be minimum estimates because of the difficulty of capturing the smallest lobsters. Thus, we have some indication that the maximum densities of juveniles found in nature underutilize the spaces available, and that these maximum densities are in turn greater than necessary to support the fishery.

Empirical tests of the hypothesis that juvenile shelters limit year class size would be useful. Caddy (1986) suggested stocking natural lobster habitats with shelters of a variety of sizes. Any size that was near fully occupied might then be limiting. One could also increase the size scale and duration of Roach's (1983) and Barshaw and Lavalli's (1988) experiments by stocking natural substrates with lobsters and predators as a measure of the habitat carrying capacity. A sharp decrease in survival of a size or age class of juveniles would identify a point in the life history worthy of focus on causes of the mortality. Estimating mortality among the older age classes of juveniles might be a good place to start because larger shelters will likely be scarcer than small ones (Caddy 1986; Caddy and Stamatopoulos 1990), and because more agonistic interactions among larger lobsters will result in larger space requirements (Lawton 1987).

In summary, we have a definition of juvenile lobster habitat, and for the Atlantic coast of Nova Scotia, a minimum estimate of habitat area. Assuming constancy of physical habitat and constancy of predatory pressure, the recent record high landings indicate that the carrying capacity of the physical habitat has not previously been exceeded. Short term tests also suggest

a potential carrying capacity higher than that observed. Finally, rough calculations of the carrying capacity of small juveniles necessary to support large recruit year-classes suggest underutilization of habitat space. Experimental field measurements of habitat carrying capacity in presence of predators, and a measure of the depth limits of juvenile habitat would be useful additions to this discussion.

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Mortality and Dispersion of Juvenile Giant Sea Scallop (*Placopecten magellanicus*) in a Tidal Channel

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Hatchery-reared giant sea scallops ranging in size from 10 to 30 mm were used to experimentally assess juvenile mortality and dispersion as a function of size, tidal currents and season over an annual cycle in a 7 m deep channel in Lunenburg Bay, Nova Scotia. Size-specific mortality rates were measured from multiple arrays of 30 juveniles tethered to the seabed with 15 cm monofilament allowing an escape response, and monitored by divers over periods of up to 90 days. High mortality (20 - 75% after 10 days) resulted primarily from feeding by the sea star *Asterias forbesi*. Mortality rates were inversely related to scallop size, and were reduced greatly between February and April, when sea temperatures fell below 6°C. A release of 10,220 scallops within a 40 m² area has been monitored by quadrat census since November 1990. The mean density decreased rapidly from ~255 ind · m⁻² to ~4 ind · m⁻² during the first two weeks, remained stable for the next four months, and then decreased to ~1 ind · m⁻² during the summer. This approximates the natural density of scallops in the area. Mortality during the first two weeks reduced the seeded population by >60%. Dispersion into an area >1200 m² occurred during this period, with a further expansion into an area of ~2500 m² during the following summer. The pattern of dispersion is not fully explained by the near bottom velocity field as measured with current meters. The swimming behaviour of juveniles which moves them out of the benthic log-layer is an important process linking predation and advection in dispersing juvenile scallops after seeding.

Estuaries as Rearing Environments for Atlantic Salmon (*Salmo salar*) Parr

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The rearing habitat of young, pre-smolt Atlantic salmon (*Salmo salar*) is typically found in freshwater, specifically the fast flowing reaches of streams and rivers. Research carried out in two river systems in Newfoundland (Chadwick and Green 1985; Hutchings 1985) has also demonstrated the importance of ponds and lakes for the rearing and production of riverine stages of wild Atlantic salmon. Recent studies in estuaries in Newfoundland and in Nova Scotia (Shears 1984; Cunjak *et al.* 1989,1990) have found substantial numbers of Atlantic salmon parr in habitats with measured salinities as high as 20 ppt.

If the use of estuarine habitats by young Atlantic salmon is indeed a common phenomenon in Atlantic river systems, there could be important implications for current salmon management practices. For example, production units would need to be extended further downstream than previously anticipated (i.e. into brackish water). The purpose of this paper is to summarize the results of preliminary surveys of habitat use and abundance of salmon parr in different Atlantic estuaries.

MATERIALS AND METHODS

Sampling for young salmon was carried out between May and November in the estuaries of the following river systems (Fig. 8): Western Arm Brook, Newfoundland (1983, 1987, 1989); Western Brook, Newfoundland (1988); Margaree River, Nova Scotia (1988); South River, Nova Scotia (1987, 1988); Black River, New Brunswick (1987); and the Miramichi River, New Brunswick (1991). To facilitate temporal comparisons of fish abundance, the data were separated into seasonal categories of spring (May-June), summer (July-August), and autumn (October and November). The number of sampling sites and the frequency of sampling varied among the locations. Generally, 6-12 sites were chosen which represented a variety of substrate types and a salinity gradient from river mouth seaward. A 30 m long, 2 m deep beach seine (6mm mesh) was used to capture fish. From 1 to 3 seine hauls were made per sampling site approximately twice per month except as Western Brook which was sampled only in July, 1988. To standardize sampling effort among the locations, the catch per unit effort (CPUE) was defined as the number of fish captured per single seine haul.

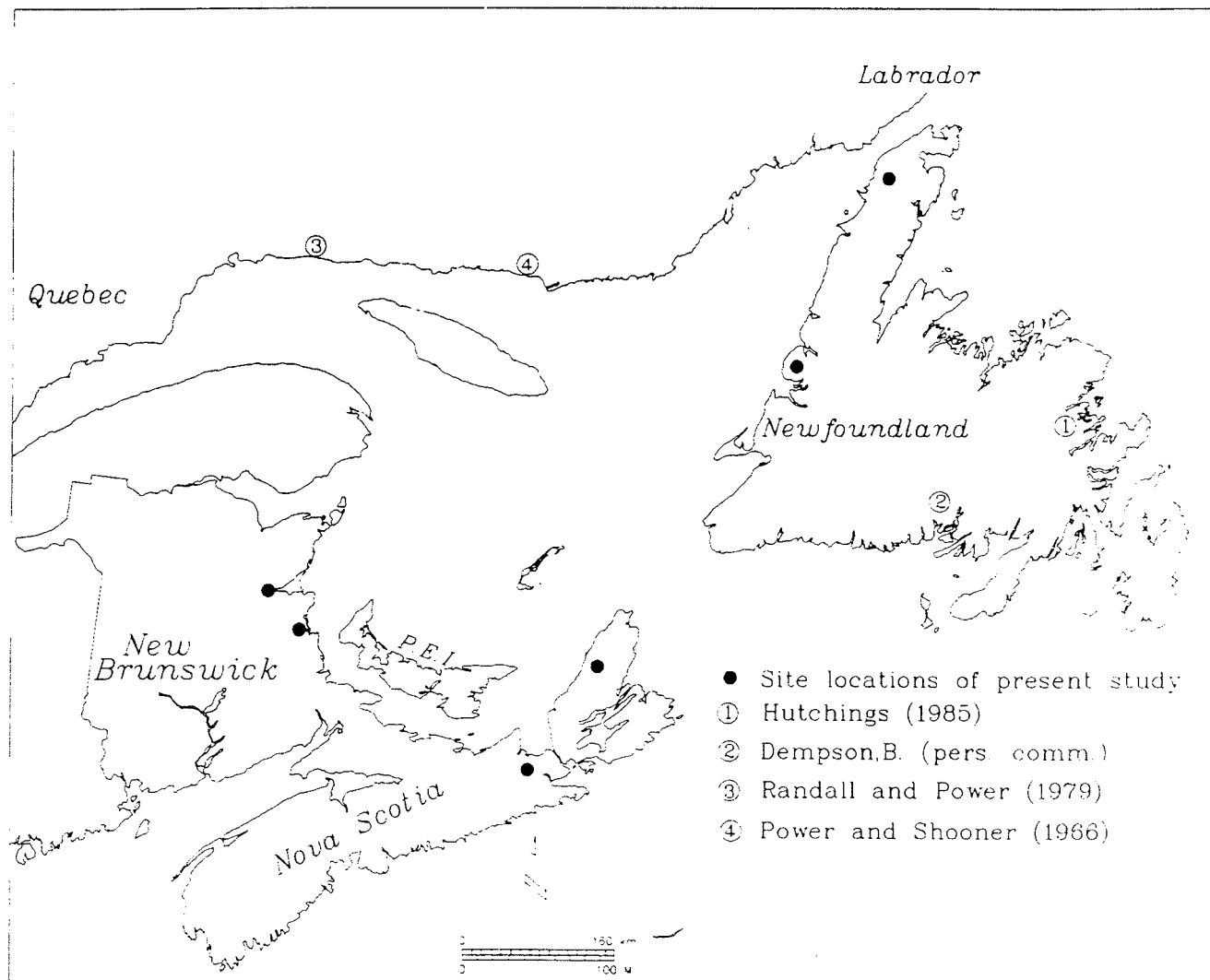


Figure 8. Map of Atlantic Canada showing estuarine sampling locations for this study as well as other estuaries where juvenile Atlantic salmon have been found. For the present study, locations were (moving clockwise from Northern Newfoundland): Western Arm Brook, Western Brook, Margaree River, South River, Black River, and Miramichi River.

Water salinity and temperature were measured, using a YSI meter, at the surface, at the substrate, and at 25 cm increments within the water column at each site immediately after fish collections. Fork length (cm) of all captured salmon parr was measured. At Western Arm Brook, in 1987 and in 1988, many parr were tagged to monitor their movements within the estuary over the spring to autumn period. A subsample of parr from each site was taken for sex and age determination and for diet analysis.

RESULTS

Young Atlantic salmon (ages 0+ to 4+) were found in substantial numbers in the estuaries of Western Arm Brook, Margaree River, and South River. Very few parr were found in the Miramichi estuary and then only in May and where salinities were low (< 5 ppt). No salmon parr were found in the estuaries of Western Brook or Black River; the former has a poorly defined estuary with an abrupt entry to the sea whereas the latter is a sandy-bottomed, macrophyte-choked lagoon through which runs a narrow channel.

The CPUE data (Table 6) indicated a spatial and a seasonal component to the use of estuarine habitats by young Atlantic salmon. At all three sites, regardless of year or season, salmon were most abundant at the inner estuarine sites where salinities were lowest but still measurable to as high as 16 ppt during high tides (Fig. 9). Movement of the tagged parr showed a similar concentration in the inner estuary close to the river mouth. At Western Arm Brook, salmon parr were most common throughout the spring and summer (Table 6). By autumn, it appeared that the largest parr had emigrated seaward whereas the smaller parr likely re-entered the river to overwinter (Cunjak *et al.* 1989).

Table 6. Seasonal CPUE (mean number of parr captured per seine haul) of juvenile Atlantic salmon in the inner and outer parts of the estuaries of Western Arm Brook (Nlfd), South River (N.S.), and Margaree River (N.S.).

LOCATION	YEAR		SPRING	SUMMER	AUTUMN
Western Arm Brook	1983	Inner	13.5	42.5	1.5
		Outer	5.7	8.2	0.0
	1987	Inner	48.8	18.6	1.8
		Outer	4.2	5.2	0.0
	1988	Inner	10.9	18.8	7.1
		Outer	1.0	2.4	0.1
Margaree River	1988	Inner	9.7	4.6	1.8
		Outer	0.7	0.1	0.1
South River	1987	Inner	44.8	1.8	4.0
		Outer	0.1	0.0	--

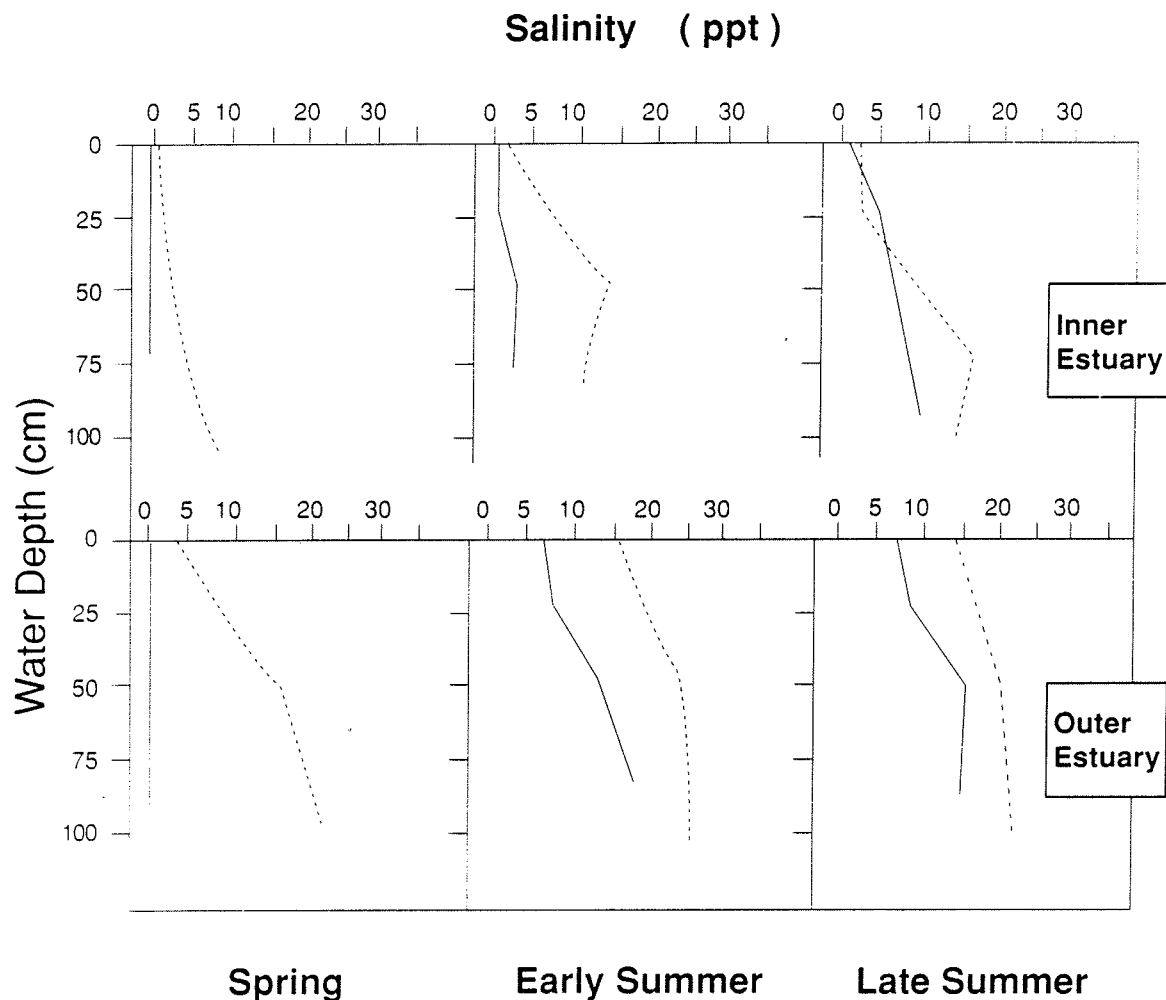


Figure 9. Mean seasonal salinity profiles at inner and outer parts of Western Arm Brook estuary as measured at high (dashed line) and low (solid line) tide. Measurements were on 12 sampling dates in 1983 and 10 sampling dates in 1987.

At Margaree and South Rivers, parr abundance declined markedly after the spring (Table 6) and was believed to be linked to the presence of very warm water temperatures and higher salinities typical of summer conditions (Fig. 9) when freshwater discharge was reduced. For example, in the South River estuary, daytime surface water temperatures of $> 25^{\circ}\text{C}$ were measured in mid-July on several occasions. Similarly warm water temperatures ($> 20^{\circ}\text{C}$) during summer in the Miramichi estuary may be part of the reason that so few salmon parr were found there. In the estuary of Western Arm Brook, where parr were most common, surface water temperatures rarely reached 20°C .

Based on recaptures of individually marked parr, movement in the estuary as predominantly along the shoreline and concentrated near the river mouth where the parr fed on

prey items often of riverine origin, especially in the spring of the year.

DISCUSSION

Estuaries have generally been considered to be environments of limited importance to pre-smolt stages of salmon. However, in the past decade, research along the West Coast (Healey 1982; Simenstad *et al.* 1982) has clearly demonstrated the importance of estuaries as rearing environments of juvenile Pacific salmonids.

On the Atlantic Coast, although Atlantic salmon parr have been documented from various estuaries (Fig. 8) in the early 1940's (Huntsman 1945), their occurrence has generally been dismissed as being of little significance to the general population (Hutchings 1985), was likely the result of displacement from upriver (Power and Shooner 1966), or remained largely unexplained (Randall and Power 1979). Our results strongly suggest that the phenomenon is more widespread than previously believed and may represent an alternative life history strategy by Atlantic salmon. Certainly more research is warranted to test this hypothesis and to ultimately determine what contribution estuarine-reared parr make to the returning adult run of mature fish. For example, do estuarine parr have higher marine survival after rearing in brackish water compared with their riverine counterparts?

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Identification of Redfish Juveniles in the Gulf of St. Lawrence Using Genotypic Specific Variations

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The commercial stock of redfish in the Gulf of St. Lawrence comprises two species, *Sebastes mentella* and *S. fasciatus*. The two sympatric species are primarily found in the deep zones of the Laurentian and Esquiman channels at depths exceeding 150 m. Species distinction is not possible on the basis of external morphology. However evidence for the existence of two genetic groups in the Gulf of St. Lawrence is based mainly on the variability observed at liver MDH^{*} locus (Rubec *et al.* 1991 and references therein). Because the actual proportion of the two species in the exploited stock is unknown, redfish are presently managed as a single population.

Redfish recruitment is characterized by periodic impulses of very strong year-classes (Laberge 1988). Given the presence of the two species at the adult stage, it is commonly assumed that the life cycle of both species is completed inside the Gulf and that the recruiting population represents a mixture of the two species ensuring their coexistence in the area. However, the species composition of the pre-recruit population has never been investigated. In order to bring some insight into this problem, a study of the genotypic composition of redfish juveniles distributed in the Gulf of St. Lawrence was initiated. The objectives of our study are 1) to determine the specific composition of redfish juveniles in using genotypic variations and 2) to describe the spatial distribution of these juveniles in relation to their taxonomic status. Preliminary results of this ongoing study are presented here.

MATERIALS AND METHODS

Juvenile redfish ranging from 5 to 20 cm in length were collected at various locations in the Gulf of St. Lawrence during the annual research groundfish surveys conducted in August 1990 and 1991. A total of 488 fish were collected at 5 different sampling sites in 1990 while the 1991 survey provided 566 juvenile fish from 11 different locations (Fig. 10). Upon collection, fish were rapidly frozen at -20°C. At the laboratory, specimens were thawed and measured for total length and total weight. Samples of liver tissue were taken and analysed for genetic variation at the malate dehydrogenase (MDH^{*}) locus according to the methods described by Hebert and Beaton (1989). Biochemical analyses were performed within one month after specimens collection.

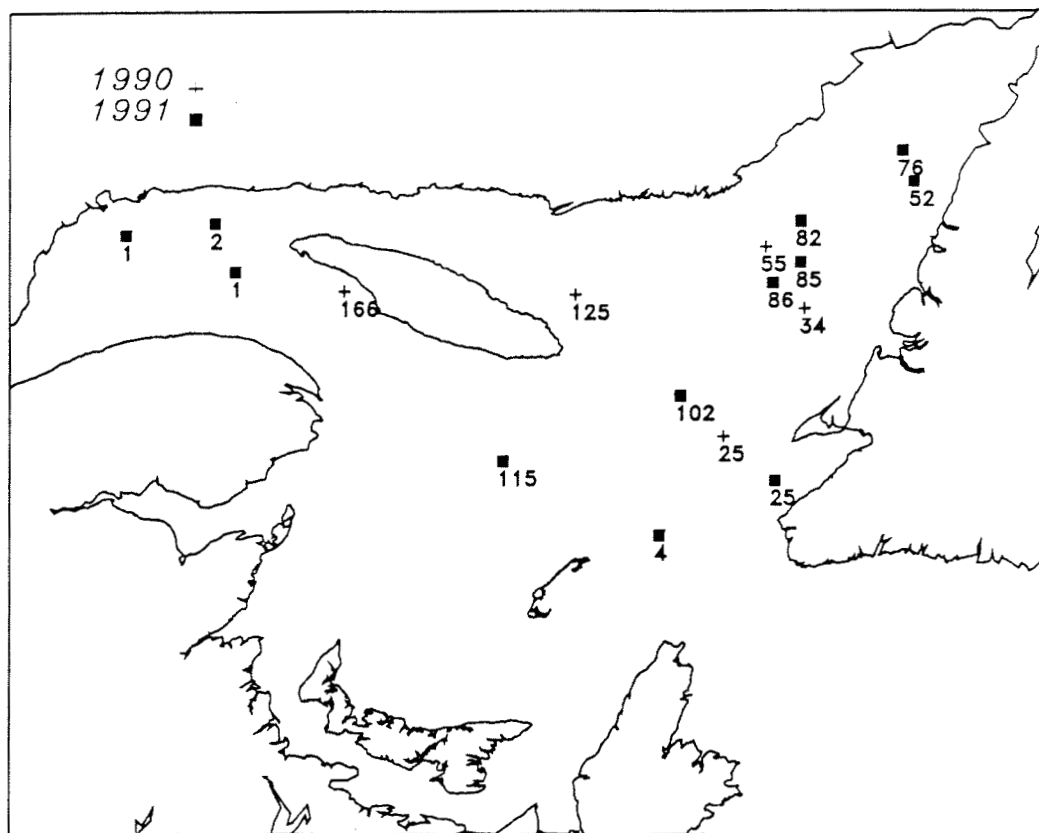


Figure 10. Sampling locations where juvenile redfish were caught during the annual groundfish surveys in 1990 and 1991.

Two alleles segregate at the MDH* locus resulting in the presence of three genotypes. Homozygotes for the slowest allele (allele* a2) were considered to be *S. fasciatus* while the homozygotes for the fastest allele (allele* a1) were classified as *S. mentella*. The identification of heterozygote individuals remained undefined (see Rubec *et al.* 1991 for a discussion).

RESULTS

The three genotypes were detected in our samples. Their relative proportion in the overall sampled population for the Gulf differed significantly (G-test, $P < 0.001$) from that expected under the assumption that all fish belonged to a single panmictic population (Table 7).

Results from 1991 clearly demonstrate geographic variations in the distribution of the redfish juvenile genotypes within the Gulf of St. Lawrence (Table 7). All stations located on the eastern side of Anticosti island were dominated by one genotypic group corresponding to *S. fasciatus*. Only 2 fish out of 328 collected east of Anticosti were identified as *S. mentella*.

because they were homozygote for the alternate allele. It is interesting to note that only one heterozygote was detected in this part of the Gulf.

Analyses performed on fish collected in 1990 showed very similar results to those obtained in 1991. All but 3 fish were homozygotes for the *S. fasciatus* type. The size frequency distribution of fish was unimodal in both years and the average length was 3 cm smaller in 1990 than in 1991 which corresponds to the annual growth rate of redfish juveniles (data not included). This indicates that the same cohort was sampled during the two consecutive years. These results demonstrate that the genotypic pattern observed for a given cohort is stable over time and consistent between years.

Fish from the western side of Anticosti island were genetically more variable. The three genotypes were detected in various proportions at these stations. Comparisons of the observed number of genotypes to those expected from Hardy-Weinberg equilibrium show that the individuals sampled at stations 1 and 2 are issued from a randomly mating population of *S. mentella*. However, the statistically significant deficit in heterozygotes observed at station 3 (Table 7) implies the cooccurrence of both *S. mentella* and *S. fasciatus*. If results from the three western sampling sites are pooled, *S. mentella* electrophoretic types are proportionally more abundant than *S. fasciatus* in this part of the Gulf. Indeed the frequency of allele* a_2 decreases drastically from 0.992 in the eastern Gulf to 0.340 in the western Gulf (Table 7).

DISCUSSION

The present study demonstrates that the specific composition of juvenile redfish can be determined in using genotypic specific variations at the liver MDH* locus and that there is no difference in the electrophoretic patterns of adults and juveniles. A similar conclusion was recently reached by Nedreaas and Naevdal (1991) for redfish populations along the Norwegian coast.

Recruiting redfish enters the fishery at around 20 cm in length, but juveniles (5-20 cm) are currently sampled during annual research surveys conducted by DFO. Given the average juvenile growth rate of about 3 cm per year (MS in preparation), this sampling survey would provide an excellent opportunity for predicting the strength and specific composition of in-coming year-classes of redfish at least 4-5 years before their entry into the fishery. Our results, although still preliminary, indicate that the species composition of redfish juveniles in the Gulf of St. Lawrence is spatially variable. *S. fasciatus* was found both in the eastern and the western sectors of the Gulf while *S. mentella* was numerically important only in the Western Gulf. Such a division is consistent with the idea that the Gulf of St. Lawrence is not an homogeneous unit but may consist of distinct pelagic ecosystems, where the eastern sector and the western sector are considered to be different (de Lafontaine *et al.* 1991). Although the average size of juveniles was similar among stations (Table 7), the larger variability (CV in Table 7) in size noted at the western stations may be due to multiple cohorts. The analysis of genotypic variation as a function of size will be presented elsewhere (de Lafontaine and Sévigny, in prep.).

Table 7. Observed and expected genotypic frequencies and allelic frequency for redfish juveniles from different sampling sites in the western (W) or eastern (E) sector in the Gulf of St. Lawrence during 1991. Expected numbers of genotypes were not calculated for eastern (E) stations because of the fixation of the allele* a_2 in the majority of these stations. The values of the test for goodness-of-fit (G-test, $**=P<0.001$) for comparing the observed and expected genotypic frequencies are presented. The average length of juveniles and the coefficient of variation (CV%) in size are given for each sampling site.

SAMPLING SITES	GENOTYPES						ALLELIC FREQUENCY		N	G-test	FISH LENGTH (cm)	
	A2A2*		A1A2*		A1A1*						MEAN	CV(%)
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	A2	A1				
1 (W)	2	2.2	29	28.6	93	93.2	0.133	0.867	124	0.025	10.2	26.6
2 (W)	4	2.0	9	13.1	24	21.9	0.230	0.770	37	3.183	15.1	13.8
3 (W)	53	40.7	6	30.6	18	5.7	0.727	0.273	77	49.840**	10.9	19.4
4 (E)	40		0		1		0.976	0.024	41		11.7	8.2
25 (E)	29		0		0		1	0	29		10.1	19.0
52 (E)	30		0		0		1	0	30		11.1	6.7
76 (E)	45		0		0		1	0	45		11.7	6.8
82 (E)	32		0		0		1	0	32		11.3	6.4
85 (E)	42		0		0		1	0	42		10.8	7.0
86 (E)	41		0		0		1	0	41		11.2	6.2
102 (E)	39		1		0		0.988	0.012	40		10.8	6.7
115 (E)	27		0		1		0.964	0.036	28		11.2	17.7
WEST STAT.	59	27.5	44	106.8	135	103.7	0.340	0.660	238	83.26**	11.2	26.5
EAST STAT.	325	322.8	1	5.2	2	0.02	0.992	0.008	328		11.1	10.4
ALL	384	292.6	45	228.7	137	44.7	0.719	0.281	566	369.34**	11.1	19.0

Mechanisms to explain the geographic variability in the species composition of redfish juveniles are presently unknown, but work is presently under way for the determination of genetic variation at the larval stage in order to investigate the spawning location and subsequent larval drift of the two species within the Gulf.

The relative proportion of the two species in the present study does not take into account their relative importance in terms of numbers or biomass between the two areas. Therefore, the exact proportion of the two species in the juvenile population could not be calculated for the current sampling year. This aspect is presently under investigation.

ACKNOWLEDGEMENTS

We wish to thank Geneviève Ross, Eric Parent and Jean-François St-Pierre for technical assistance during analyses and Louise Savard and Dominique Gascon for samples collection.

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Juvenile Yellowtail Flounder (*Limanda ferruginea*) Distribution on the Grand Bank of Newfoundland¹

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On the Grand Bank (NAFO Divisions 3L, 3N and 3O), yellowtail flounder (*Limanda ferruginea*) is at its northern limit in commercial fishery concentrations. This species is a short-lived one, reaching a maximum age of 10 years (~50 cm). Yellowtail flounder begin to sexually mature at 5 and 6 years old (31-34 cm) and spawning has been reported to take place on the Grand Bank from May to September peaking in mid- to late-June at depths less than 100 m and temperatures above 2°C. There is no evidence of a spawning migration or spawning aggregations and the Grand Bank population is considered to be sedentary.

There has been no ichthyoplankton program directed towards studying early life history stages of yellowtail flounder on the Grand Bank. However, ancillary data on eggs and larvae are available from other research studies on the Grand Bank fish populations. Since 1985 annual bottom trawl juvenile surveys have been directed towards estimating yellowtail flounder recruitment indices on the Grand Bank using a modified Yankee 41(80/104) shrimp trawl with a mesh size of 38 mm throughout and a 12 mm stretched mesh liner in the codend. These surveys, carried out from mid-August to mid-September, followed a stratified random design which covered the entire Grand Bank within the 100 m isobath during 1985-88 and the 200 m isobath since 1989.

Using data collected from juvenile flatfish surveys during the period of 1985-89 and incorporating historical information on eggs and larvae, a composite picture of the distribution of yellowtail flounder and environmental factors on the Grand Bank can be obtained. Any attempt to understand factors which influence distribution of early history stages of a species may provide some insight in understanding recruitment variability.

During the 5 survey years in late-summer, both juveniles (ages 1 to 4) and adult yellowtail flounder were concentrated on the southern Grand Bank in NAFO Divisions 3N and 3O in the area of the Southeast Shoal. The adult distribution was very similar to that derived from regular spring groundfish surveys carried out during the same years. Juvenile and adult yellowtail were found at depths ranging from 55 to 62 m and in temperatures ranging from -1.2° to 5.8°C, averaging 3.7°C for juveniles and 1.9°C for adults. Thus, both juveniles and adults maintained their shallow water depth distribution despite wide fluctuations in temperature.

Based on the analyses of the distribution of age -1 group and older juveniles, up to 4 yr,

and incorporating historical information from egg and larval surveys, physical oceanography and substrate type in the region it was found that all early life history stages were distributed in the same geographic area, on and adjacent to the Southeast Shoal on the southern Grand Bank. It is suggested that eggs and larvae are passively retained due to a weak current regime on the southern Grand Bank. Age -1 group and older juveniles were consistently found on a sandy substrate in the same area indicating that sediment size may also be an important factor affecting the distribution.

These observed egg, larval, and juvenile distribution patterns indicate that the Southeast Shoal area is an oceanic nursery area for Grand Bank yellowtail flounder. But unlike the well-published North Sea coastal nurseries, this oceanic nursery also contains newly settled juveniles, older juveniles, and adults.

¹A complete version of this paper will appear in a 1992 edition of the Netherlands Journal of Sea Research.

Distribution of Spring- and Fall-spawned Juvenile Herring (*Clupea harengus harengus*) in the Southern Gulf of St. Lawrence

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Herring in the southern Gulf of St. Lawrence spawn either in the spring (May and June) or in the fall (August and September). The larger spawning aggregations are found in the fall. The major fishery relies on inshore gillnets to harvest spawners on or near their spawning beds, while the offshore purse-seiners harvest migrating schools in late fall.

The youngest herring caught in significant numbers in the herring fisheries of the southern Gulf are 3 yr old. Between 1978 and 1990, the proportion of total annual catch consisting of recruiting 3 yr-old fish varied between 1-40% of all fall-spawned herring, and between 3-74% of all spring-spawned herring landed (Claytor *et al.* 1991). Given the wide fluctuations in annual recruitment, a measure of the strength of a year-class before it recruits to the fisheries would be highly desirable. Unfortunately, there is no fishery on juvenile herring in the southern Gulf of St. Lawrence so pre-recruits are not easily monitored from the commercial catch. Because there is presently no index of recruitment, projections for the fisheries rely on the average of previous years' observed recruitment.

The goals of our research is 1) to determine the distribution and migration timing of juvenile herring, particularly the 1- and 2 yr-old fish, and 2) to identify good sampling locations and times for measuring the abundance of each year-class separately for each of the two spawning groups. This paper summarizes our recent sampling program on juvenile herring.

WINTER SURVEYS

In December 1988, a juvenile herring survey was initiated using hydro-acoustics and a midwater trawl in western Baie-des-Chaleurs, where juveniles had been found earlier in the fall during annual acoustic surveys. By December, adult herring had moved out of Baie-des-Chaleurs, and the only herring-like schools (which appear on the sounder as dense smears or bands) were found to be capelin (*Mallotus villosus*). Over the muddy bottom in western Baie-des-Chaleurs, however, traces in the form of small specks were uniformly spread out near the bottom in a layer 2-6 m thick. Individual sets with a midwater trawl towed very close to the bottom in this area yielded both smelt (*Osmerus mordax*) and juvenile herring, and the proportion of each species varied considerably from tow to tow. Almost all herring caught during this survey were 9-13 cm long, corresponding to young-of-the-year (YOY) from the previous spring

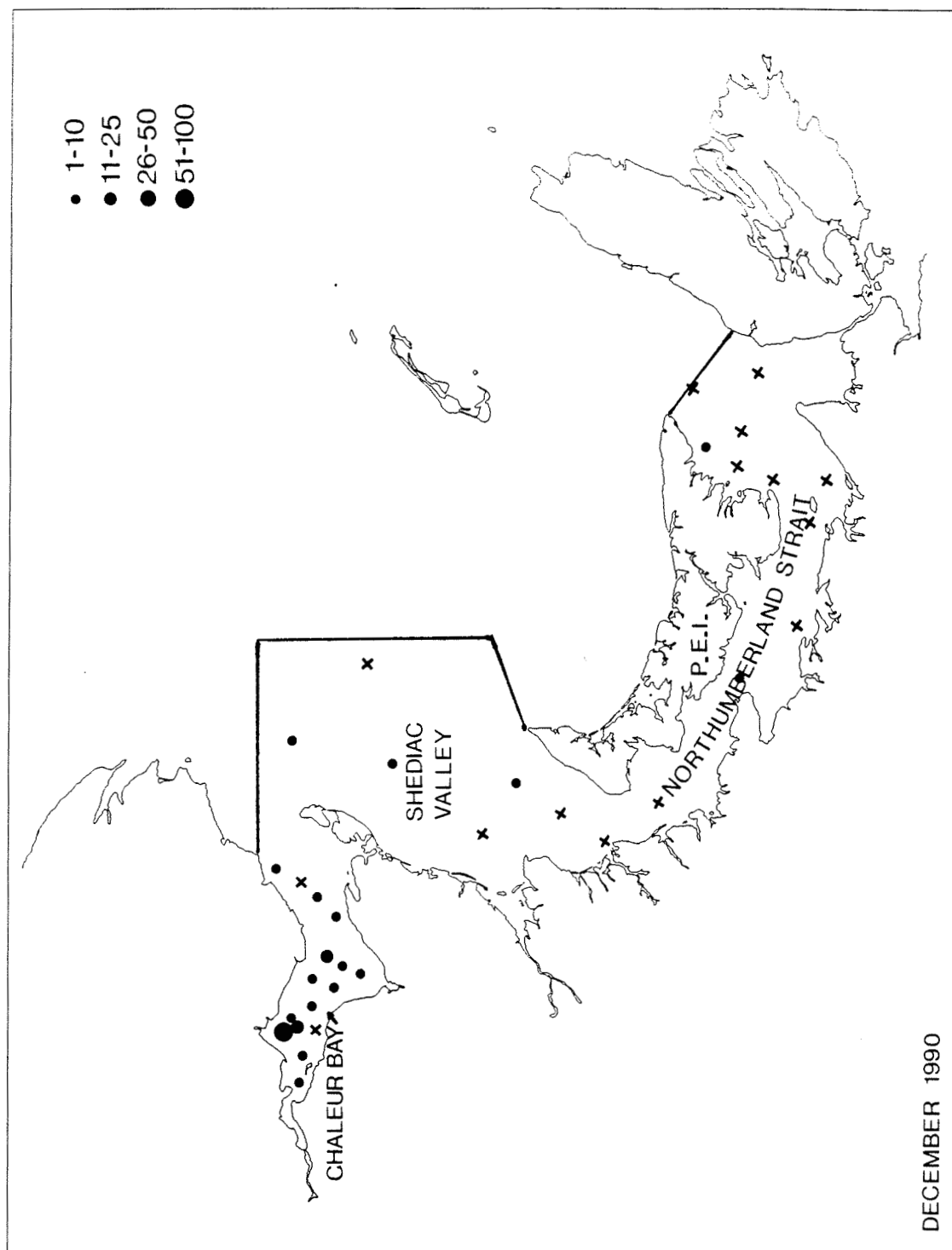


Figure 11. Juvenile herring survey aboard the R/V *EE Prince* in December 1990. Black lines delimit the searched area. Dots size is proportional to the number of juvenile (<25 cm) herring caught during 30 min with a Yankee 36 bottom trawl towed at 3.5 kts. X indicates tow without juvenile herring.

(Table 8). There were very few 1-yr-old fall-spawned juveniles (season of birth is determined from otolith characteristics).

In December 1990, a similar survey covered the same area and as much of the nearshore southwestern Gulf as possible (Fig. 11). Very few traces were detected on the sounder and mostly adult herring were caught with the midwater trawl. Yet a simultaneous groundfish survey of Baie-des-Chaleurs was collecting many juvenile herring with a bottom trawl. Switching to a bottom trawl as well, we repeated our survey of the Bay, still searching with the echosounder. Fishing through the bottom specks yielded, as in December 1988, some sets containing both smelt and juvenile herring, or smelt only. Some successful tows (with herring) were also made in areas devoid of fish traces. These observations suggest that the specks appearing near the bottom in December are either echoes from both smelt and herring and frequent fishing is required to determine the specific ratio, or only smelt produce such specks and the herring are not visible at all. In any case, the abundance estimates derived from hydroacoustics are unreliable.

In the western part of Baie-des-Chaleurs, the bottom trawl collected hardly any spring-spawned YOY (unlike the December 1988 survey), but some 1-yr-old spring-spawned fish and a substantial amount of fall-spawned 1- and 2-yr-old juveniles were caught (Table 8). Samples also contained adults. All few fish caught in Shediac Valley were spring-spawned YOY.

The two December surveys therefore failed to locate large concentrations of fall-spawned juveniles (which were expected to outnumber the spring-spawned fish, having been spawned by the larger of the two components in the southern Gulf). The observed geographic distribution suggests that spring-spawned juveniles aggregate in Baie-des-Chaleurs before the winter instead of leaving it as adults do. Chadwick *et al.* (1990) found that juvenile herring collected within Baie-des-Chaleurs in early winter had higher levels of blood antifreeze proteins than found in adults suggesting that juveniles may be able to tolerate colder water.

The presence of juveniles in Baie-des-Chaleurs was monitored throughout winter as part of the smelt fishery at the mouth of the Restigouche River emptying into the western end of Baie-des-Chaleurs. Box- and bagnet smelt fishermen were asked to report the occurrence of 'sardines' (i.e. juvenile herring) in their bycatch during February and March. Some 2.3 cm mesh gillnets were also set for 24 h under the ice in February in Nepisiguit Bay (on the southern side of Baie-des-Chaleurs). These two sampling approaches yielded predominantly spring-spawned YOY herring (under Age-Group 1 in Table 8). Smelt fishermen fishing in the middle of the Restigouche channel caught juvenile herring regularly throughout winter. The bagnets fish tidally in 15-18 m of water, at about 1 m off the muddy bottom. Temperatures as low as -1.5°C were recorded at these depths in March 1990. In 1992 a new program was implemented by asking smelt bagnets fishermen to fill out a simple logbook and keep weekly samples of juvenile herring. We expected this program to be very useful for monitoring the spring-spawned pre-recruits but the market for smelts suddenly collapsed in early 1992.

Table 8. Number of juvenile herring (<25 cm TL) sampled during surveys in 1988-1990 falling under each age- and spawning-group. P: spring-spawned fish; A: fall-spawned fish. Note that YOY are classified as age 0 when caught in December but as 1-yr old if caught later because the "birthdate" is set to January 1. See Figures 11-13 for corresponding total catches.

SURVEY / AREA	AGE / SPAWNING GROUP									
	0		1		2		3		4+	
	P	A	P	A	P	A	P	A	P	A
<i>December 1988</i>										
Baie-des-Chaleurs	786	6	1	4	0	0	0	0	0	0
<i>December 1990</i>										
Baie-des-Chaleurs	6	0	50	25	40	13	19	10	12	3
Shediac Valley	4	0	0	0	0	0	0	0	0	0
<i>February-March 1990</i>										
Baie-des-Chaleurs	0	0	221	0	4	1	0	0	0	0
<i>July 1989</i>										
Baie-des-Chaleurs	8	0	25	0	1	6	1	0	1	0
Shediac Valley	0	0	5	0	8	21	0	0	0	0
Northumberland	1	0	8	85	0	0	0	0	0	0
<i>July 1990</i>										
Baie-des-Chaleurs	0	0	20	0	49	13	13	12	5	13
Shediac Valley	0	0	0	0	20	1	12	10	16	32
Northumberland	0	0	20	0	6	5	2	11	3	30
East P.E.I.	0	0	3	0	11	19	1	16	5	20

In April 1990, Baie-des-Chaleurs was surveyed as soon as possible after ice breakup. Water temperature ranged from slightly above 0°C at the surface to as low as -1.4°C near the bottom. Very few juvenile herring were caught with a 50-ft flounder drag at that time, which suggests that juvenile herring were no longer on the bottom. The species composition of fish schools visible on the sonar could not be verified because no midwater gear was available. Antifreeze activity was slightly lower in the blood of juveniles captured in April than in midwinter samples (Ewart, unpubl. data). This observation, in conjunction with the low abundance of juveniles on the bottom, may be explained by the availability of a relatively warm layer of water off the bottom.

SUMMER SURVEYS

In July 1989 and 1990, the southern Gulf was surveyed using midwater trawl because juveniles are known to be usually pelagic in warmer waters. As observed in adults, they tend to form dense schools which might be located anywhere in the water column at night.

During the 1989 survey (July 23-August 1, Fig. 12), the ratios of smelt to herring within individual sets were again variable and unpredictable. YOY and 1-yr-old spring-spawned juveniles were present in Baie-des-Chaleurs, whereas fall-spawned juveniles outnumbered the spring-spawned fish in Shediac Valley and Northumberland Strait (Table 8).

During the 1990 survey (July 11-19, Fig. 13), more spring- than fall-spawned juveniles were collected in Baie-des-Chaleurs, as well as in Shediac Valley and Northumberland Strait (Table 8). Mostly fall-spawned juveniles were found along eastern Prince Edward Island making this area the most promising one for surveying fall fish.

Juvenile herring were more widely dispersed throughout the southern Gulf in July than in December. Fewer YOY were caught in July surveys, which can be due to some trawl escapement or to a much shallower water distribution. In July and August 1991, a 5-m wide bottom trawl and a Boston whaler were used to fish in water 2-12 m deep along shore to ascertain whether or not juveniles occupied shallow waters during the summer. No herring (but other small pelagic species like smelt) were found at the head of Baie-des-Chaleurs (the Québec shore, the Restigouche estuary and around Heron Island), nor along Prince Edward Island's eastern coast and Malpeque Bay, on its north shore. Juvenile herring therefore do not seem to occupy very shallow water in these areas, at least not during the day, in the summer.

DISCUSSION

Either because we caught few YOY, or because juveniles were less clumped, or else because the commercial fishing gear is pervasive during the summer, December seems a more appropriate time of year to sample juvenile herring aboard a research vessel. In consequence, we have abandoned the July juvenile survey. We have also dropped transects and hydroacoustics in favour of standardised bottom-trawl sets for the December survey. We feel that the echo sounder is not a reliable estimator of herring juvenile biomass at that time of year and locations. The use of bottom-trawl seems preferable in December, as juveniles apparently stay close to the bottom, both day and night. It allows us to fish successfully during daytime as well, which is improbable when using a midwater trawl on pelagic schools. The search for fall-spawned juveniles will continue via the vessel survey, and inshore trawling will be attempted at night during summer 1992. Both approaches will concentrate on eastern Prince Edward Island.

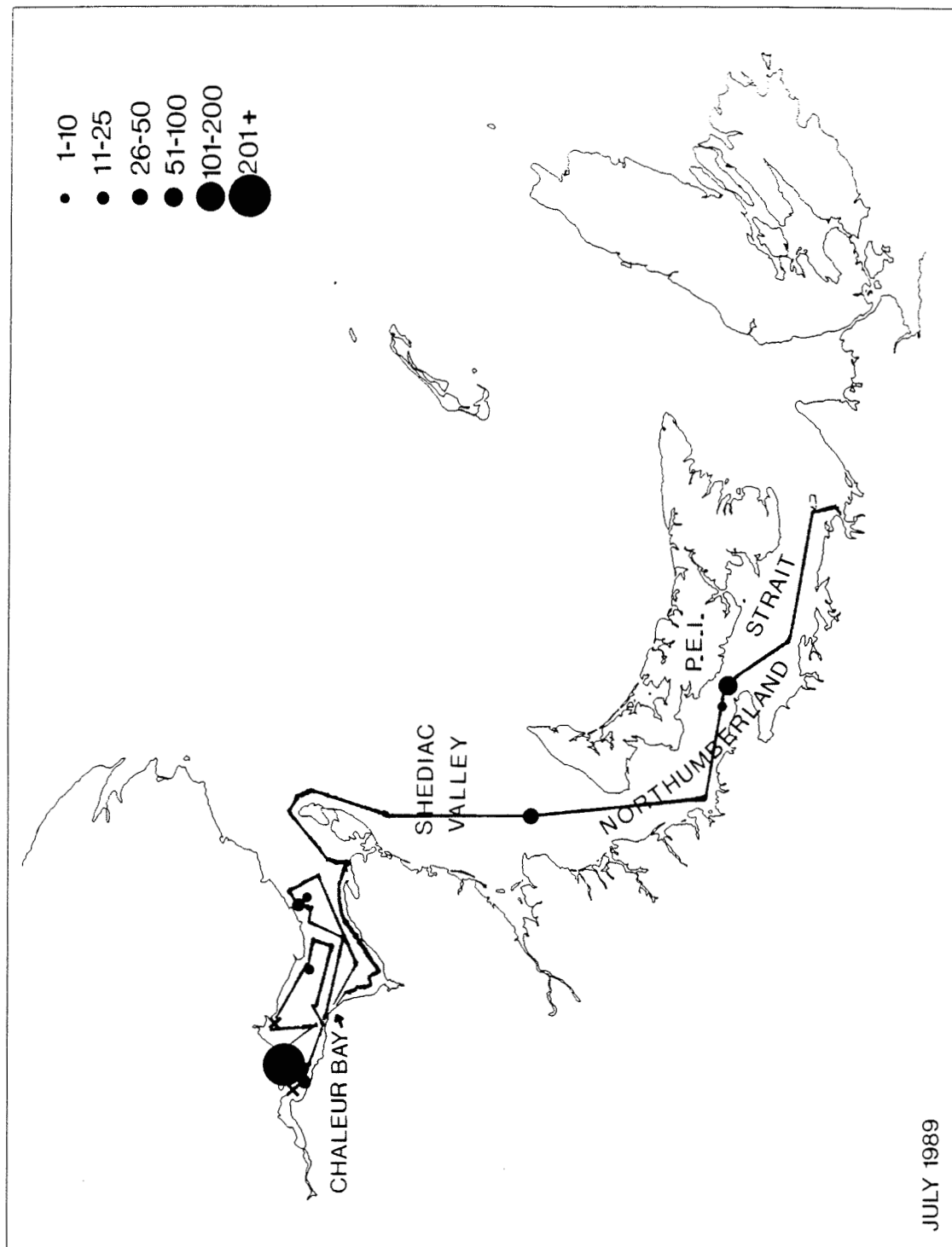


Figure 12. Juvenile herring survey aboard the R/V *Navicula* in July 1989. Black lines show the vessel's route. Dots size is proportional to the number of juvenile herring caught during 30 min with a Boris midwater trawl. X indicates tow without juvenile herring.

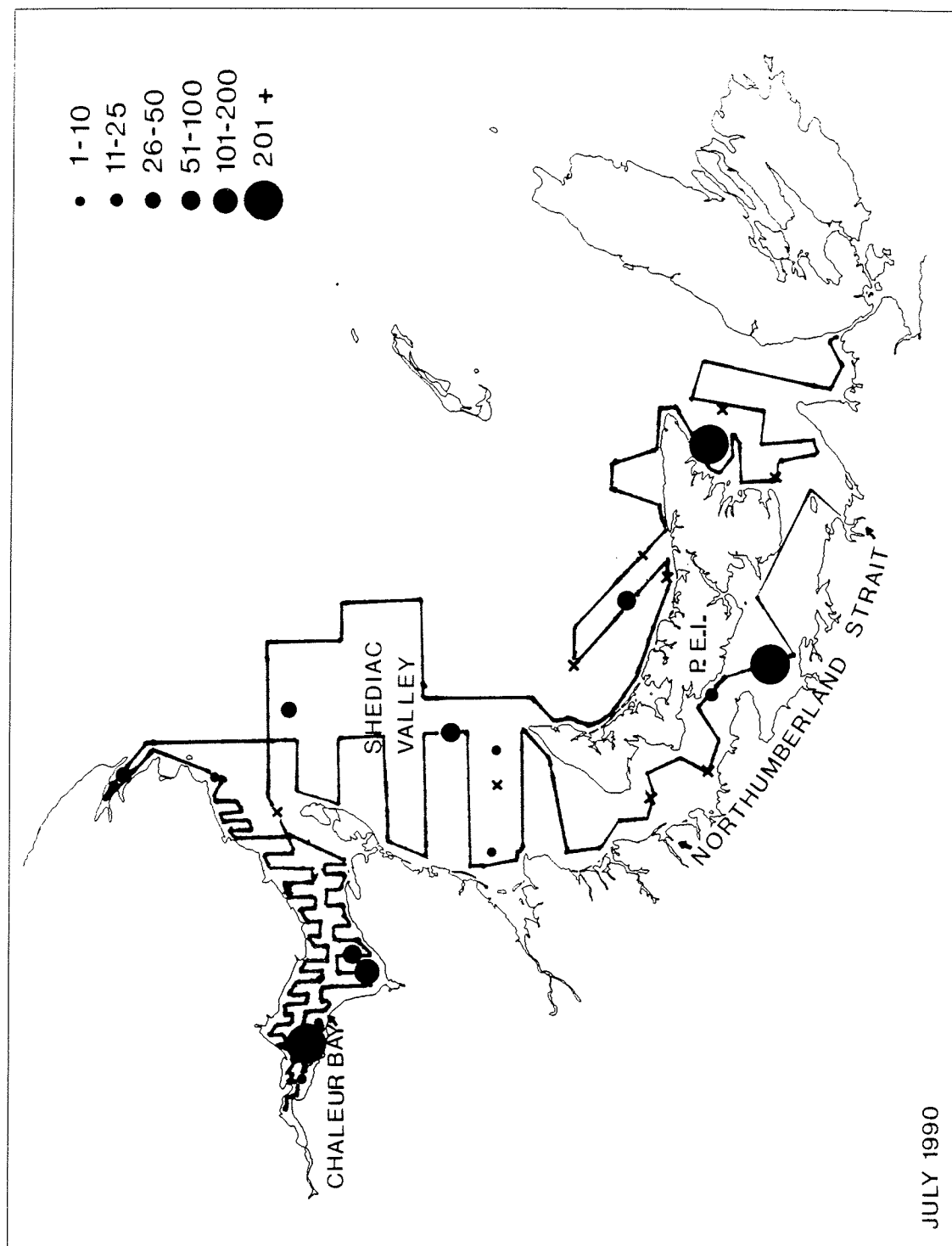


Figure 13. Juvenile herring survey aboard the R/V *EE Prince* in July 1990. Black lines show survey transects. Dots size is proportional to the number of juvenile herring caught per 30 min with an Engel midwater trawl. X indicates tow without juvenile herring.

ACKNOWLEDGEMENTS

Many people contributed to the collection of the information presented here: C. Bourque, R. Bradford, R. Brown, D. Cairns, M. Chadwick, R. Claytor, G. Comeau, D. Daigle, T. Hurlbut, C. LeBlanc, C. MacDougall, P. Westcott, and of course the many fishermen who provided their wisdom, fishing boat, gear or herring samples.

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The Range of Winter Habitats Available to Juvenile Cod (*Gadus morhua*) may be extended by their Ability to Produce Antifreeze

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In the coastal waters off Newfoundland and Labrador, winter water temperatures usually fall below -1.0°C , and frequently reach the freezing point of seawater ($\sim -1.8^{\circ}\text{C}$). Fish die if cooled below the freezing point of their blood plasma in the presence of ice (Fletcher *et al.* 1986). The blood plasma of most teleost fish freezes at between -0.7 and -0.8°C (Holmes and Donaldson 1969; Fletcher *et al.* 1992). Thus, fish residing in areas where the temperature falls below their plasma freezing point are in acute danger of freezing if ice crystals form in the water. In the Newfoundland region, this factor would appear to be winter habitat limiting for some fish species, and the Atlantic cod (*Gadus morhua* L.) has developed strategies to avoid freezing in such an environment.

Before the arrival of winter, the majority of adult northern cod migrate into deep, comparatively warm water offshore, where they overwinter and spawn in the spring (Templeman 1979; Lear and Green 1984). Adult cod can also produce plasma antifreeze glycoproteins in response to exposure to cold water (Fletcher *et al.* 1982, 1987). However, adult cod must be exposed to temperatures near 0°C for some time before plasma antifreeze levels become significant. Therefore, in nature, freeze-protection would not be achieved before the arrival of sub-zero winter temperatures. Also, the levels of plasma antifreeze produced by adult cod do not generally protect them from freezing at temperatures below -1.2°C . Thus, it seems likely that migration into deep, relatively warm water out of the reach of ice is the main strategy used by adult cod to avoid adverse winter conditions.

While winter behaviour patterns of adult cod are quite well documented, considerably less information is available as to the whereabouts of juvenile cod over the winter months. Juvenile cod are found in the bays around Newfoundland during the summer months, and are present until late in the year. There would appear to be certain advantages to small cod in remaining inshore rather than migrating with the adults (Keats *et al.* 1987; Brown *et al.* 1989). However, to utilize these inshore habitats over winter, juvenile cod must be able to survive in icy water at very low temperatures.

The ability of juvenile cod to tolerate low temperatures via the production of plasma antifreeze was experimentally investigated in laboratory. Four size groups of cod, <15 cm, 15-25

cm, 26-40 cm, and adults >50 cm, were maintained at ambient temperature and photoperiod over a winter cycle. At monthly intervals between November and June, blood plasma samples were taken from all fish groups and examined for the presence of antifreeze using the method of Kao *et al.* (1986). Using this technique, the freezing and melting behaviour of a single ice crystal within each plasma sample is examined using a nanolitre osmometer (Clifton Technical Physics, Hartford, New York). The difference between the melting and freezing temperature of the crystal is termed thermal hysteresis, and is a direct measure of antifreeze activity.

The results of these experiments are reported in full in Goddard *et al.* 1992, and can be summarized as follows (Fig. 14):

- all juvenile groups started to produce antifreeze earlier in the winter, and at higher ambient temperatures than did the adults;
- all juvenile groups produced higher winter levels of plasma antifreeze than the adults;
- highest winter plasma antifreeze levels, and lowest plasma freezing temperatures were consistently found in the 15-25cm group.

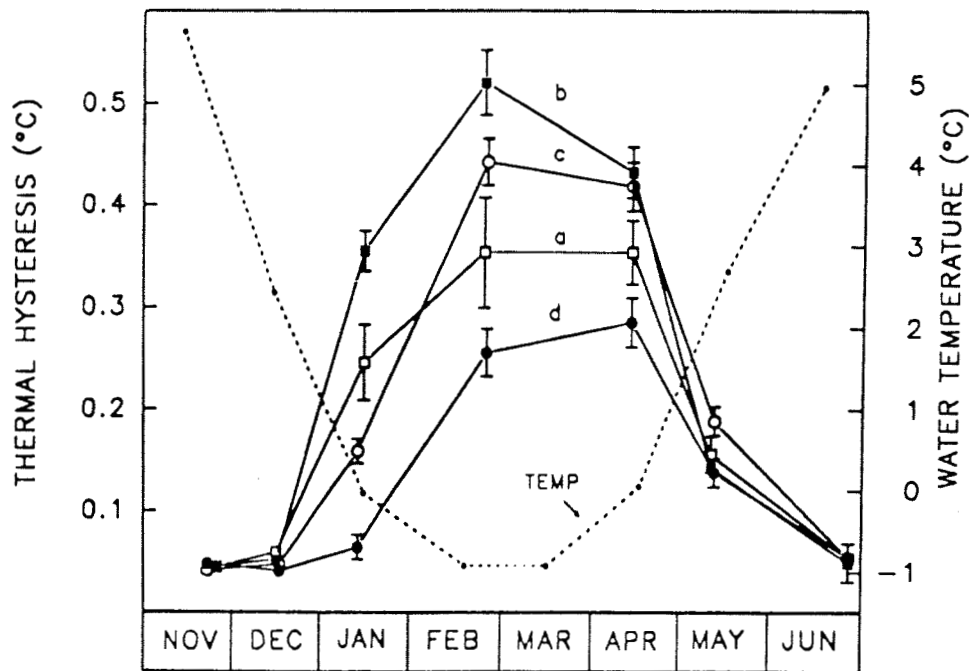


Figure 14. Seasonal changes in the plasma thermal hysteresis in four size groups of Atlantic cod, a = <15cm, b = 15-25cm, c = 26-40cm, d = >50cm. Values of thermal hysteresis are plotted as means \pm one standard error. Water temperatures are the monthly means of values recorded several times each week.

The difference in antifreeze levels produced by the smallest fish and the 15-25 cm group could be the result of selection pressure during the first winter spent in the wild. It may also be the result of a change in physiology with age.

By the time the water temperature had fallen to 0°C (in early January) all juvenile groups had developed considerable freeze protection while the adults had produced little, if any, antifreeze. This observation, and the difference in levels of antifreeze present in the four groups suggest a physiological readiness to cope with low temperatures in cod juveniles which diminishes as the fish reach maturity.

These findings support the hypothesis that, at least during their first two winters, juvenile cod do not migrate offshore into deeper water with the adults. Rather, they remain in their nursery areas, and the high levels of antifreeze produced before the onset of sub-zero temperatures enable them to survive in the inshore environment over winter. Such behaviour would be consistent with reports that juvenile cod are relatively site-attached in their early years, but that with increasing size, they undertake seasonal migrations of increasing magnitude (Trout 1957; Jean 1964; Clarke and Green 1990; Tupper and Boutilier, this volume). Decreasing levels of antifreeze coupled with late onset of antifreeze production in fish of increasing size, could be of functional significance in prompting different levels of migratory behaviour out of cold water in the winter.

We suggest that the difference in ability of adult and juvenile groups to produce antifreeze reflects differences in the overwintering strategies adopted by these animals.

ACKNOWLEDGEMENTS

This work was supported by grants from the Natural Sciences and Engineering Research Council of Canada, and by the National Centres of Excellence Program (Ocean Production Enhancement Network - OPEN).

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Temporal Variation in Size and Abundance of Juvenile Cod (*Gadus morhua*), at Bellevue, Trinity Bay, Newfoundland

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Diel, seasonal and annual variability in abundance and size of juvenile cod (*Gadus morhua*) were studied at a single sampling site at Bellevue, Trinity Bay, Newfoundland from July 1982 to September 1983 and July 1989 to September 1990. Cod were collected at low tide by a small seine, four times a month, twice during the night and twice during the day. Two age groups, 0+ and 1+, predominated. Cod was significantly more abundant and larger during night time catches than during day time catches. This difference was due, in part, to the presence of large 1+ cod which were only collected at night. 1+ cod were not collected when water temperature was $< 0^{\circ}\text{C}$ and when ice was present. Catches of both age groups peaked in August-November and April-June. Pelagic juvenile cod arrived nearshore in August and September and were easily distinguished from the more settled 0+ cod by their small size ($< 45\text{-}50\text{ mm SL}$), pelagic coloration and lack of *Cryptocotyle lingua*, a skin parasite common to fishes of inshore waters. The arrival of pelagic juvenile cod was usually associated with high temperature ($> 12^{\circ}\text{C}$) and high salinity water (28 ppt or more). Settled 0+ cod were collected at temperatures and salinities ranging from -2 to 17°C and from 18 to 32 ppt. One year old (1+) cod were taken at a slightly narrower range, $1\text{-}16^{\circ}\text{C}$ and 18-31 ppt.

Juvenile cod catches were significantly higher in 1989-1990 than in 1982-1983. The 0+ age group represented 91.6% and 92.3% of all the cod collected in 1982-1983 and 1989-1990 respectively. Mean lengths and weights of 0+ cod (but not 1+) differed significantly between 1982-1983 and 1989-1990. The modal length of 0+ cod increased by $0.56\text{-}0.57\text{ mm}\cdot\text{d}^{-1}$ from August to November 1989. This was almost twice the growth rate ($0.29\text{-}0.34\text{ mm}\cdot\text{d}^{-1}$) for the same period in 1982. A general conclusion of this study is that 0+ and 1+ cod occur in the nearshore and shallow environment throughout most of the year. Sampling by large seines and gill nets, in addition to observations by Scuba divers and regular day-night sampling with a small seine support the hypothesis that benthic juvenile cod undergo an inshore migration at night and that differences between day and night catches and size of cod are not due to net avoidance. The difference in catch rates between 1982-1983 and 1989-1990 suggests that the abundance of juvenile cod varies from year to year at Bellevue. Regular sampling of the nearshore environment for juvenile cod may be promising for estimating year-class strength prior to recruitment into the fishery.

Settlement and Growth of Juvenile Atlantic Cod (*Gadus morhua*) in St.Margaret's Bay, Nova Scotia

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Variability in the survival of early life history stages of fish is currently assumed to be a major factor limiting the size of adult populations. While studies of recruitment variability have largely focused on planktonic larval survivorship, recent evidence has pointed to early juvenile survivorship as an important contributor to year-class strength.

The abundance of newly settled cod on Back Cove Reef in St.Margaret's Bay was estimated by visual census at roughly biweekly intervals from June through December, 1991. Water temperature at each census was recorded to the nearest 0.1°C with a mercury thermometer. Visual censuses were conducted while snorkelling a 50 m transect line running parallel to the shore, at a depth of 1.5 to 2.5 m. Juvenile cod within 1 m of either side of the transect line were counted and their lengths estimated to the nearest 0.5 cm using a clear plastic ruler fastened to the end of a 50 cm length of wood. Newly settled fish were captured using anaesthetic and marked by a specific pattern of fin clipping, allowing individual fish to be recognized and measured by visual estimation in subsequent censuses.

Settlement of 0+ cod occurred in two pulses, the first in late June and the second in mid August. Newly settled cod inhabited crevices in the reef substrate and remained site-attached, defending territories around their home site. The growth in length of 10 individual 0+ cod from Back Cove is illustrated in Figure 15. Individuals settling in late June, during period of rising temperature, grew faster and remained larger than individuals settling in late August during a falling temperature period. In addition, within cohorts, there was a tendency for individuals that were larger at settlement to remain larger throughout the study period, while individuals that were smaller at settlement tended to remain smaller. Post-settlement growth rates of individual cod ranged from 0 to 1.75 mm·d⁻¹ (mean = 0.71 mm·d⁻¹), increasing with temperature to a maximum of 0.9-1.5 mm·d⁻¹ (mean = 1.06 mm·d⁻¹) at a temperature of about 18°C, above which growth rates appeared to decline. Maximum growth occurred in early August, coinciding with the peak of settlement. Settlement of fish during a period of enhanced growth may reduce the amount of time spent in the smaller and possibly more vulnerable early juvenile stages. After early August, growth rate declined steadily until December (mean = 0.33 mm·d⁻¹ for december). As

temperatures decreased, cod became more active and were observed swimming farther offshore from their home sites. By late December, all cod had left the study area, presumably migrating to deeper water. At this point, 0+ cod ranged from 13-20 cm in total length and may have been less dependent on the reef for shelter. Temperature might then have become a more significant factor influencing habitat selection of these fish.

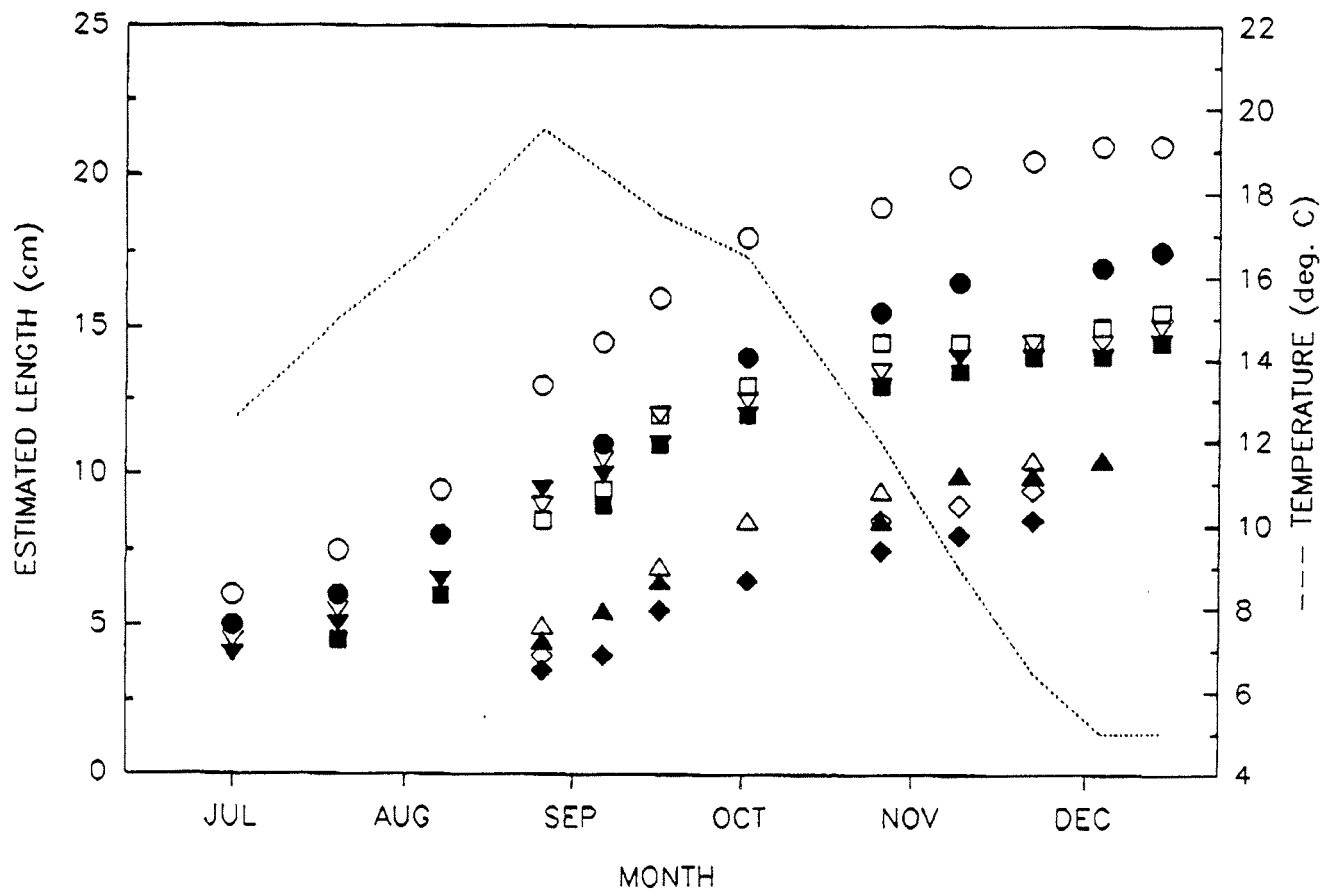


Figure 15. Temporal increase in estimated total length (cm) of 6 individual 0+ cod (*Gadus morhua*) from Back Cove, St. Margaret's Bay. The dotted line represents water temperature measured at each census.

Distribution of Pelagic 2J3KL 0-group Cod (*Gadus morhua*) in Inshore and Offshore Areas

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This study examines data collected during September surveys, using an 8 m² rectangular midwater trawl, to test the hypothesis that pelagic 0-group cod occur abundantly in inshore waters and not in offshore waters of NAFO Subarea 3L, consistent with existing early life history theory. Pelagic cod were widely distributed offshore ranging from 0 to 56.7 per 100m² with a mean of 6.6 per 100m². Mean length was 38.1 mm (range = 17-70). Pelagic cod were caught at 38 and 57 stations in Trinity Bay in 1984 and 1985 respectively, and at 15 stations in Conception Bay in 1989 with mean abundances of 4.3, 3.4, and 6.2 per 100m², and ranges from 0 to 8.9, 0 to 27.1 and 0 to 130.7 respectively. Mean lengths from inshore were 34.1 mm (range = 12-69), 36.9 mm (range = 7-124), and 28.3 mm (range = 4-65), respectively. These data lead us to conclude that there were no differences between inshore and offshore abundance and mean size of pelagic cod, contrary to expectations. Simulation estimates of egg abundance for 1981 based on pelagic 0-group abundance offshore, incorporating a range of stage dependent growth/development and survival rates indicate that the pelagic juvenile cod sampled in September 1981 could account for the majority of cod eggs spawned that year. Based on these results we hypothesize that the majority of cod eggs and larvae of the 2J3KL stock do not drift into inshore areas along the NE Newfoundland following spawning on offshore banks.

Juvenile Atlantic Cod (*Gadus morhua*) in the Northern Gulf of St. Lawrence

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Preliminary results are reported for research designed to elucidate the biological, physiological, and hydrographic variables that are important to survival for juvenile Atlantic cod (ages: 6 months-2 years) in the northern Gulf of St. Lawrence. The available distribution data (west coast of Newfoundland bottom-trawl survey, November 1990; cod by-catch from northern Gulf shrimp surveys, September-October, years 1982-1988, 1990) indicate that juvenile cod are concentrated in at least three regions: 1) southwestern Newfoundland, 2) Strait of Belle-Isle, and 3) the western portion of Jacques Cartier Passage. The coverage of the shelf area along the Quebec lower north shore during these surveys was poor because the bathymetry of this region is too rough to allow for spatially representative sampling with bottom-trawls.

Analysis of length (both data sets) and age (November 1990 survey only) frequency distributions showed that the abundance of demersal 0+ cod was very low in all regions. During the 1990 survey 0+ cod (total catch=6) were only captured in the southern approaches to the Strait of Belle-Isle. Additional survey information for southwestern Newfoundland was gathered during September, 1991, which included nearshore (within 1 km of shoreland), shallow water (<50 m depth) stations not usually sampled from large research vessels. The results show that the previous surveys had probably undersampled 0+ cod as a consequence of minimum depth - minimum distance from shore constraints on their operation. Kelp beds appeared to be the preferred habitat of demersal 0+ cod. In general, size and age of fish increased with increasing depth and distance from shore.

Distribution and Feeding of Juvenile Cod (*Gadus morhua*) in the Principal Nursery Area of the Southern Gulf of St. Lawrence

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Current practice for fish management is to project the impact of various management options on the size of a specific stock one or more years into the future. Estimates of the size of the recruiting year-classes are a critical part of this process. Average values are presently used because indices of abundance of the younger age-groups are unreliable or lacking. For practical purposes, the earlier the size of a year-class recruiting to a fishery is estimated, the better the stock can be managed. Since the early 1900's, many studies have stated that better knowledge of the biology or abundance of fish eggs and larvae will improve the ability to estimate recruitment to marine fisheries. To our knowledge, there are presently no indices of fish eggs or larval abundance that can be used to estimate numbers of recruits to a fishery.

For most Atlantic cod stocks in Canadian waters, areas of consistently high abundance of juvenile cod are not known (one exception is the Georges Bank stock). Data analyses of cod distribution between 1971 and 1981 in the southern Gulf of St. Lawrence permitted to identify three areas where large numbers of juvenile cod are consistently found: (1) the Miramichi Bay - Shediac Valley area; (2) near the Magdalen Islands; and (3) in Baie-des-Chaleurs (Tremblay and Sinclair 1985). Subsequent work confirmed these findings and showed that the densities of young cod were consistently highest in the Miramichi Bay - Shediac Valley area (subsequently referred to as 4Tl) followed by the area near the Magdalen Islands (Chouinard *et al.* 1990, 1991). Therefore, the 4Tl area was chosen as the site for studies to develop indices of abundance of prerecruits and recruiting age-classes for the 4T-Vn (Jan.-Apr.) cod stock and to study factors affecting the abundance, growth, and distribution of these age-groups.

This paper summarizes results of analyses completed to date on research surveys designed to examine seasonal distributions of groundfish in the southern Gulf of St. Lawrence (conducted during 1990 and 1991) and two research surveys directed at estimating juvenile cod abundance and studying selected aspects of cod biology in 4Tl (conducted during August 1990 and 1991). In particular, cod diets are being examined for evidence consistent with the hypothesis that recent changes in growth of 4T cod are due to the effects of inter- and intraspecific competition for food (Hanson and Chouinard, in press). A second purpose of the diet analysis is to calculate the degree of population regulation attributable to cannibalism.

METHODS

Research surveys were conducted in the area west of the Magdalen Islands and western-most tip of Prince Edward Island during July 1990, November 1990, and April 1991 to document the seasonal variation in the distribution of juvenile cod. The annual research survey conducted during September 1990 (Hanson *et al.* 1991) was used to represent the autumn 1990 period. The southern Gulf of St. Lawrence being usually ice-covered from late December to early April, surveys are not possible during this period. Stratified random surveys have been the standard design used to monitor groundfish abundance in the Northwest Atlantic since 1971 (Doubleday 1981; Halliday and Koeller 1981).

Surveys to determine juvenile cod abundance and distribution and to study various aspects of cod biology (e.g., diets, fine-scale distribution, predation) were conducted in subdivision 4Tl during the first week of August of both 1990 and 1991. The survey area was divided into four depth strata (originally measured in fathoms): 14.5 to 29.0 m (810 square nautical miles); 29.1 to 43.5 m (720 square nautical miles); 43.6 to 58.0 m (330 square nautical miles); and 58.1 to 73.0 m (150 square nautical miles). Sampling sites were established by dividing the area into 3 by 3 nautical mile grid and stations sampled within each stratum were chosen at random. The number of stations chosen within each stratum was proportional to stratum area in both years. Sampling consisted of towing a 286 Rockhopper trawl with a 6 mm mesh liner in the cod end for 30 minutes at an average speed of 3.5 nautical miles per hour. The distance towed was determined from the LORAN-C bearings recorded at the beginning and end of each tow. Standard survey protocols were followed for both the seasonal and juvenile cod research surveys (Hurlbut and Clay 1990). Catch-per-tow data were determined by means of the Research Survey Analysis computer program (RVAN; Clay 1989).

RESULTS AND DISCUSSION

In July 1990, the largest numbers of juvenile cod (< 30 cm) were caught in 4Tl and near the Magdalen Islands (Fig. 16a). In September 1990, the largest numbers of young cod were caught in area 4Tl and along the north shore of Prince Edward Island (Fig. 16b). Due to time constraints, coverage within area 4Tl was incomplete and areas where large numbers of small cod were caught in previous years (i.e. near the Miramichi Estuary and at the west end of Prince Edward Island) were not well sampled. In November 1990, the largest numbers of small cod were caught along the Laurentian Channel (Fig. 16c) although low numbers (< 5 per tow) of very small cod (< 20 cm) were caught in nearly every set taken in 4Tl. The observation that very few and small cod remained in the western Gulf at the end of November is consistent with Clay's (1991) observations that only a few, small, cod were caught in the eastern Gulf in a survey done during January 1987. During April 1991, the largest numbers of small cod were taken along the Laurentian Channel but there was also one large set taken at the mouth of the Baie-des-Chaleurs (Fig. 16d) and some small cod were present in 4Tl. These data suggest that young cod spend summer months in the nursery areas but overwinter in deeper, warmer, water along the Laurentian Channel; moving back into summer feeding areas during late April and early May.

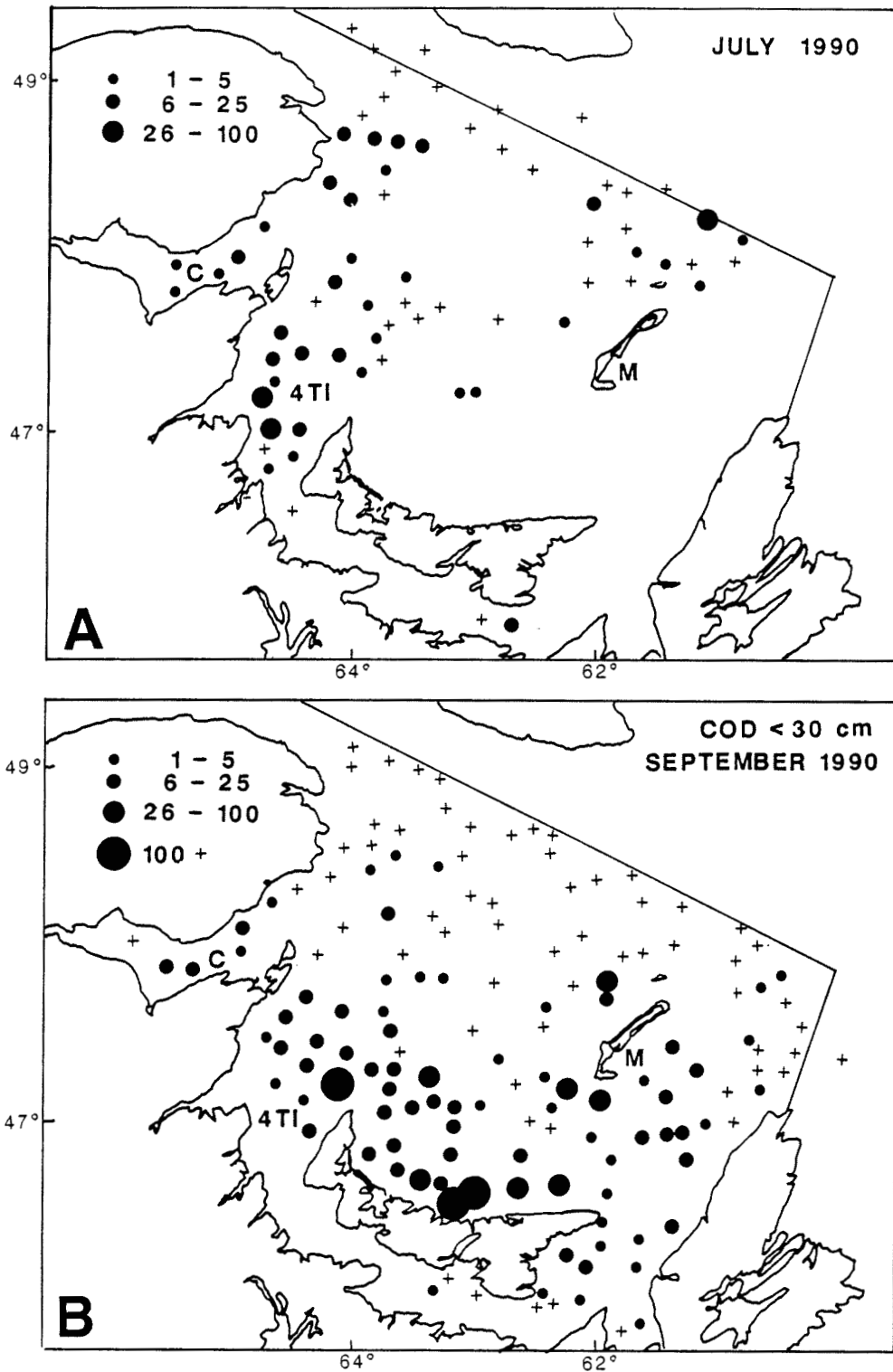


Figure 16. Seasonal distribution of juvenile cod (<30 cm long) in the southwestern Gulf of St. Lawrence. M=Magdalen Islands, C=Baie-des-Chaleurs, 4TI=Miramichi-Shediac valley.

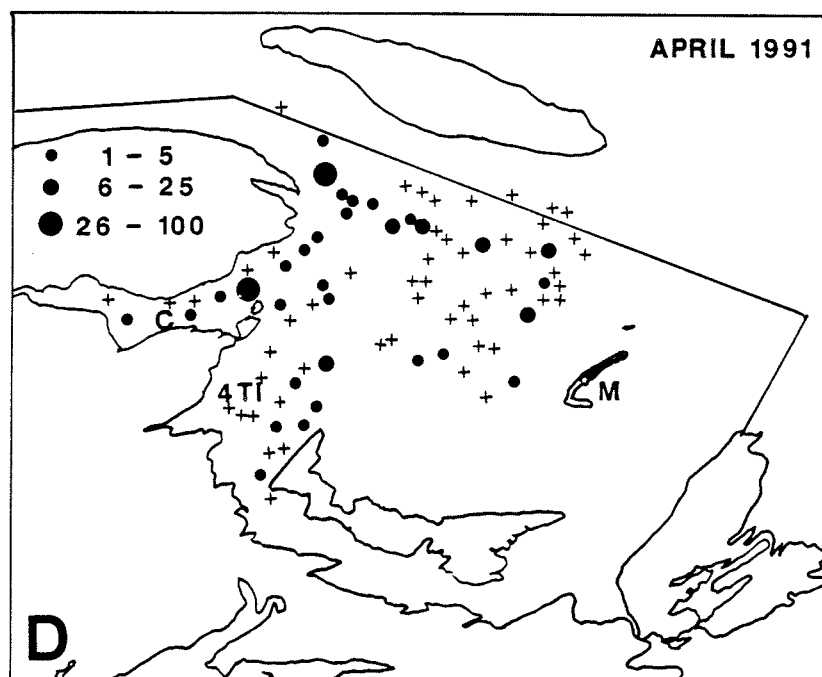
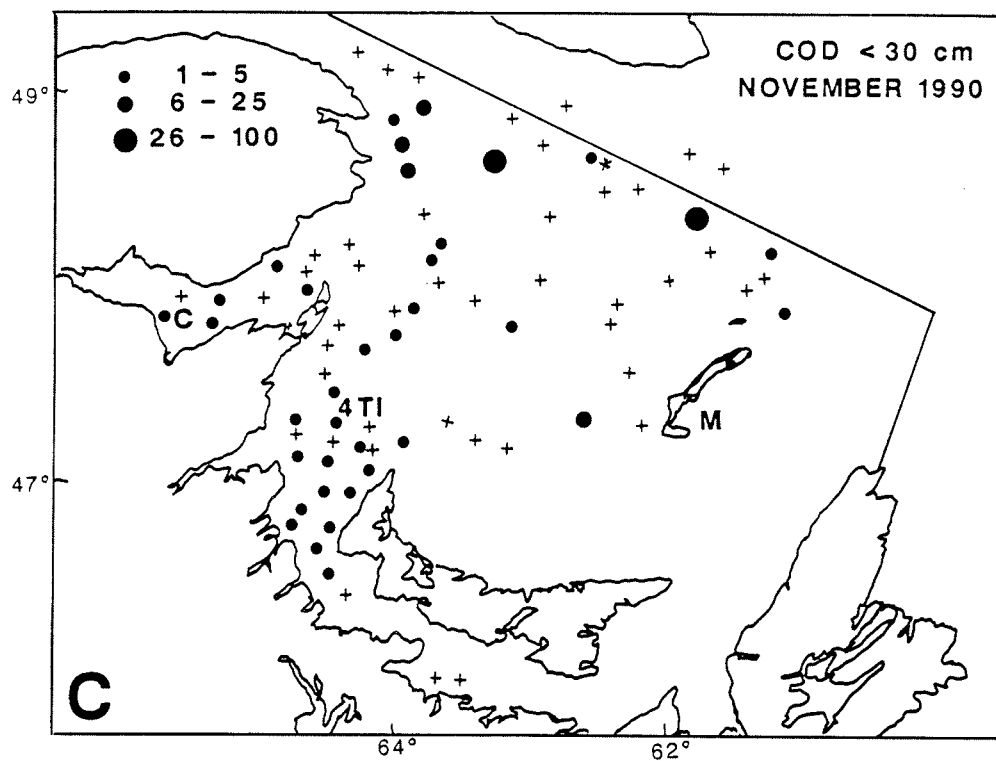


Figure 16. (continued)

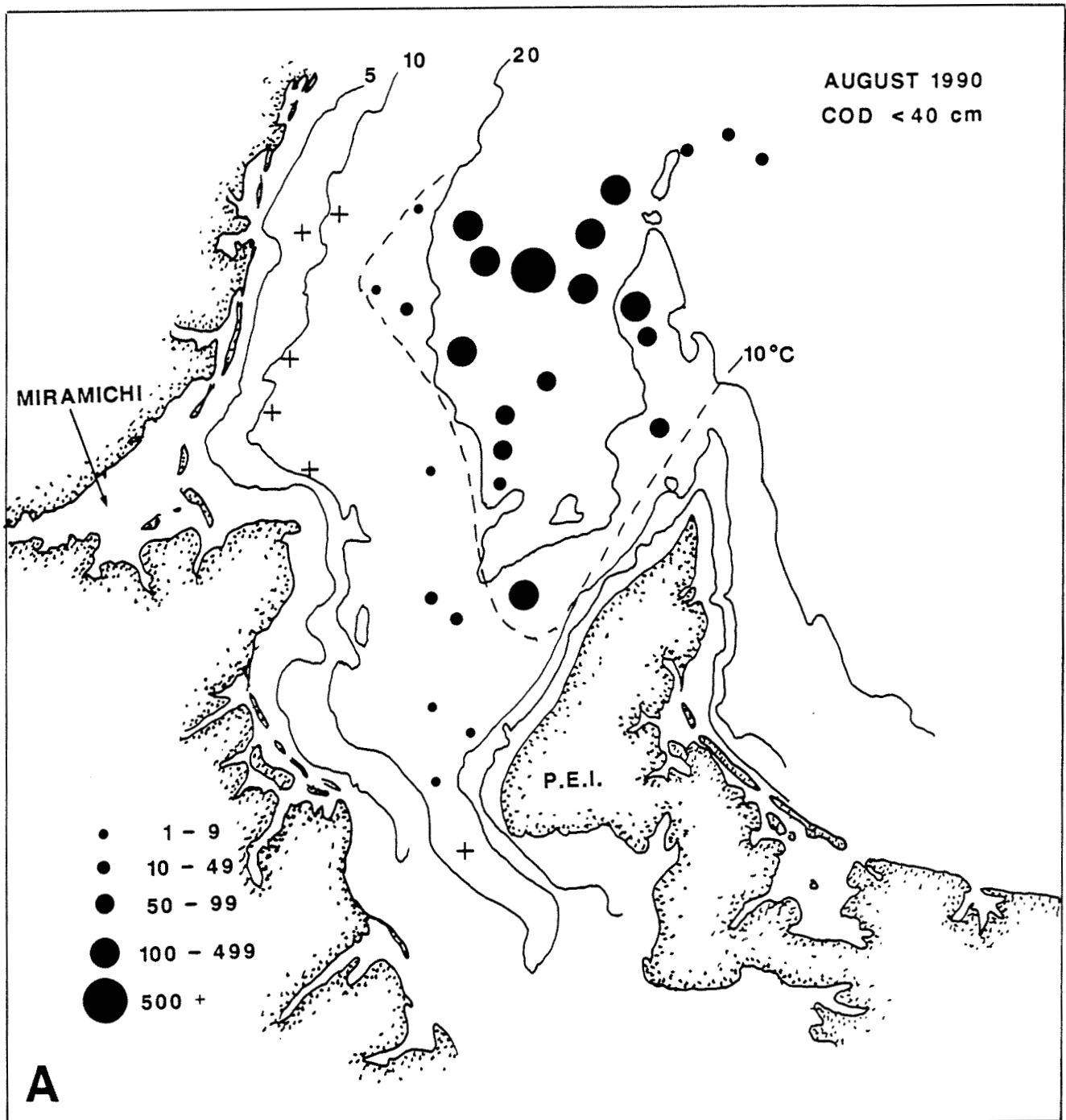


Figure 17. Distribution of juvenile cod (<40 cm long) in subdivision 4T1 during August 1990 and 1991. The dashed line represents the 10°C isotherm.

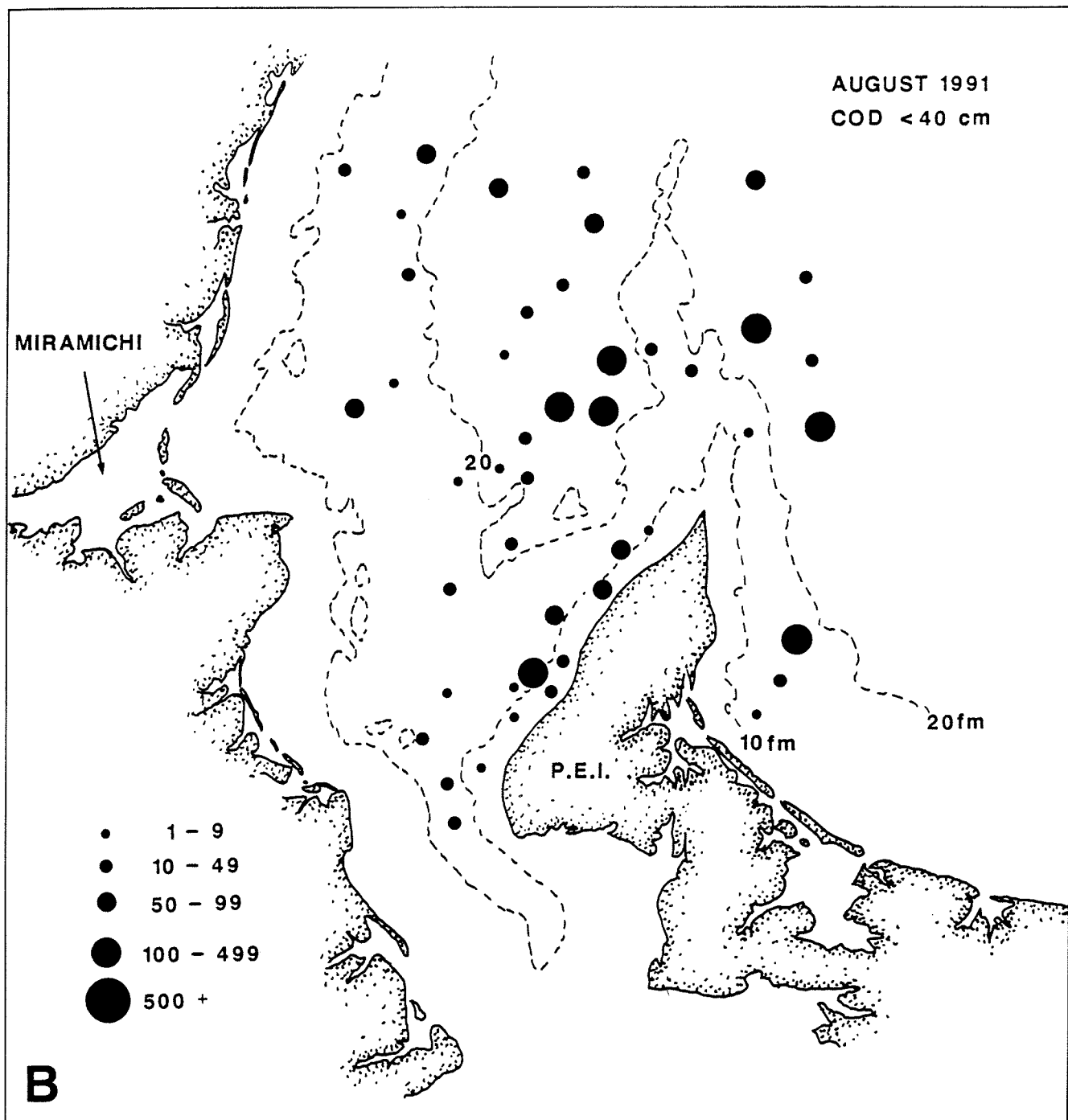


Figure 17. (continued)

Table 9. Average number per tow of juvenile cod in 4Tl during August 1990 and 1991. Stratum depths are in meters and age in years.

STRATUM DEPTH (m)	AGE GROUPS					TEMP. (°C)
	0	1	2	3	4	
<i>August 1990</i>						
14-29	0.9	0.7	1.9	6.8	4.2	12.0
29-44	0	1.1	16.2	65.4	31.2	5.6
44-58	0	0.4	6.5	107.4	79.5	5.4
58-73	0	0.4	1.3	54.7	69.8	2.5
<i>August 1991</i>						
14-29	3.8	7.2	5.4	4.8	1.8	6.3
29-44	0	1.1	13.8	19.4	13.2	3.4
44-58	0	0	1.9	38.9	99.5	2.1
58-73	0	0	0.2	12.6	56.4	-0.4

During July and September, there were virtually no young cod near the Laurentian Channel except in the nursery area near the Magdalen Islands. This hypothesis needs further study (e.g., tagging studies) to determine whether the apparent migration is real and whether young cod return to the same juvenile area each year. If so, the migration of juvenile cod would differ markedly from that of adult 4T cod, which migrate out of the southern Gulf during the fall to overwinter near Sidney Bight, and return to the southern Gulf during April and May (Jean 1964; Martin and Jean 1964; Clay 1991).

A number of patterns were evident from the two August surveys in 4Tl. There was evidence of segregation by depth between the various size and age groups and evidence of temperature control at the shallowest stations occupied. In 1990, the average bottom temperature for the shallowest stratum was 12°C and cod <40 cm long were rarely found at stations having bottom temperatures > 10°C (Fig. 17a). During the 1991 survey, bottom temperatures > 8.2°C were not recorded in the surveyed area and cod <40 cm long were collected at every station (Fig. 17b). Besides temperature effects, there were clear age, and presumably size, dependent differences in depths inhabited by young cod (Table 9). In both years, the youngest, smallest, fish were most abundant in water <44 m deep whereas older and larger cod were most abundant

in water >44 m deep.

DIET ANALYSIS

Diet analysis has only been completed for about 250 cod <50 cm long captured in August 1990 (Fig. 17). To examine the hypothesis that observed changes in growth of 4T cod might be due to the effects of competition for food, we compared our results with studies conducted in about the same area and during the same season for the late 1950s, early 1960s, and 1980 (Powles 1958; Kohler and Fitzgerald 1969; Waiwood and Majkowski 1984).

During 1990, the smallest cod (< 20 cm long) fed primarily on mysids, crabs, and shrimps (especially *Crangon* sp.). This contrasts with the observations by Powles (1958) who found that proportionately more euphausiids and mysids and fewer shrimps and crabs were eaten by cod of the same size-class during 1955-56 (Table 10). Juvenile 4T cod 21-30 cm long also consumed proportionately more shrimps, mysids and crabs during 1990 than cod of the same size during 1955-56 and 1958-63 (Powles 1958; Kohler and Fitzgerald 1969). The dominant prey during the two earlier studies was euphausiids, which were absent from the diet in 1990. Fish were also absent from the diet during 1990 but comprised about 10% of the diets described in the two earlier studies.

For cod 30 to 49 cm long, brittle stars comprised 23% of the diet during 1990 compared with about 5% of the diets in earlier studies. In contrast, fish comprised < 10% of the diet of 4T cod in 1990 compared with 24 to 58% in the earlier studies. This difference suggests that a significant diet shift has occurred for juvenile 4T cod if brittle stars are assumed to be an energetically inferior food type compared to fish. The diet change is consistent with the hypothesis of competition for food (Hanson and Leggett 1986; Persson and Greenberg 1990; Parrish and Margraf 1990). Further work will be conducted to evaluate this hypothesis.

No young cod have been found in the stomachs of the larger cod examined for 1990 and 1991. This is not surprising because young cod are seldom eaten by cod <60 cm long (Powles 1958; Kohler and Fitzgerald 1969; Waiwood and Majkowski 1984) and the stomachs of cod >50 cm long collected during this study remain to be analysed.

Table 10. Diets (% biomass or volume) of juvenile 4T cod caught in, or near, subdivision 4T1 during 1955-56 (Powles 1958), 1958-63 (Kohler and Fitzgerald 1969), 1980 (Waiwood and Majkowski 1984), and 1990 (this study). Minor dietary items were ignored, therefore, totals do not equal 100% (n.d. = no data).

PREY	1955-56	1958-63	1980	1990
10-20 cm Cod				
Mysids	45	n.d.	n.d.	25
Shrimps	4	n.d.	n.d.	28
Euphausiids	31	n.d.	n.d.	0
Brittle stars	0	n.d.	n.d.	0
Crabs	1	n.d.	n.d.	25
Fish	7	n.d.	n.d.	0
21-30 cm Cod				
Mysids	15	2	n.d.	25
Shrimps	20	12	n.d.	27
Euphausiids	22	35	n.d.	0
Brittle stars	0	0	n.d.	0
Crabs	4	14	n.d.	35
Fish	10	9	n.d.	0
31-49 cm Cod				
Mysids	15	0	5	12
Shrimps	15	1	2	20
Euphausiids	15	6	8	0
Brittle stars	5	6	4	24
Crabs	13	3	10	5
Fish	25	58	24	7

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Comparison of Size and Abundance of Larval and Pelagic Juvenile Capelin (*Mallotus villosus*) and Cod (*Gadus morhua*) caught in Bongos and the RMT-8

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From 1982-1985 eight surveys consisting of comparative tows using 61 cm paired Bongo nets and an 8 m² rectangular midwater trawl (RMT-8) were carried out during August to December in Trinity Bay, Newfoundland. In general larval and juvenile capelin were encountered more frequently than cod. The proportion of tows that captured capelin was similar for both gears, but cod were more frequently caught by the RMT-8. Mean standardized abundance (numbers per m²) was always higher in the Bongos for both species even in cases where actual catch (i.e. actual number of organisms caught) was higher in the RMT-8, indicating the Bongo nets may be more efficient. Abundance indices calculated for each gear during each survey were significantly correlated, ($P=0.0128$ for capelin, 0.0002 for cod) indicating the utility of both gears in monitoring abundance of the 2 species. The ratio of catch in the Bongo nets relative to that in the RMT-8 was calculated to compare the relative catchability efficiency of the gears for each species. For capelin the ratio gradually decreased as season progressed. A similar decreasing trend was also noted for cod from August to September but this did not continue into October when the ratio had reached its minimum value. These results illustrate the decreasing efficiency of the Bongo gear relative to the RMT-8 with increasing fish size. During all surveys, the mean length of larvae and juveniles caught in the RMT-8 was significantly larger than those caught in the Bongo nets. The mean length of capelin during these surveys ranged from 8.6 to 20.7 mm in the Bongo nets and from 11.4 to 24.7 mm in the RMT-8 while cod ranged from 6.5 to 26.6 mm and from 18.7 to 47.5 mm respectively. Mean length differences between the 2 gears were significantly larger for cod (ranging from 5.0 mm to 31.5 mm) than for capelin (from 1.5 mm to 5.9 mm). Mean length of individuals in each gear were highly correlated for capelin, but not for cod, despite the fact that the RMT-8 sampled significantly larger fish of both species. This species difference in gear avoidance will have implications to 1) survival and growth estimates using data collected by the Bongo nets and 2) the selection of an optimal sampling gear which will depend on target species, size ranges of larvae and juveniles in the population, and the objectives of the survey.

Analysis of Research Survey Catch at Age Data Using a Multiplicative Model

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Stratified random bottom trawl surveys (RV) have been used to monitor groundfish abundance in the northwest Atlantic for over 20 years (Doubleday 1981; Halliday and Koeller 1981). The results of these surveys are currently used in stock assessments to calibrate virtual population analysis or cohort analysis, hereafter referred to as sequential population analysis (SPA). The RV estimates are treated as indices of abundance while absolute abundance, stock biomass, and fishing mortality estimates are derived from SPA which is an age structured model based on commercial catches of cohorts from the same populations. At times SPA is not possible due to misreporting of catches, incomplete information on landings, low fishing mortalities, or uncertain stock identification. Alternatively, the RV data represent sequential estimates of year-class strength at different ages and are thus also suitable for age-structured analyses. In addition, surveys using a spatially stratified design may also provide useful information on the distribution of the populations.

In this paper, we investigate the use of age-structured analysis for obtaining robust estimates of year-class strength at an early age as well as to investigate the spatial distribution of different age groups. Both applications are important in studying juvenile fish. First, the earlier one can get an index of recruitment, the better the stock management advice will be. Secondly, the approach may be useful in identifying juvenile habitat. The southern Gulf of St. Lawrence cod stock (Div. 4TVn (J-A)) (Fig. 18) was used as an example. Results of our model are compared to those of SPA used for the assessment of this stock since the mid-1970's. However, the method can also be used for populations for which SPA has not been used.

METHODS

Shepherd and Nicholson (1991) describe the use of multiplicative models for analyzing these types of data. They expressed catch at age as a multiplicative function of year-class strength, age, and cumulative total mortality to that age. The latter is a combination of fishing mortality and selection at age. It was pointed out several times in their paper that the model is

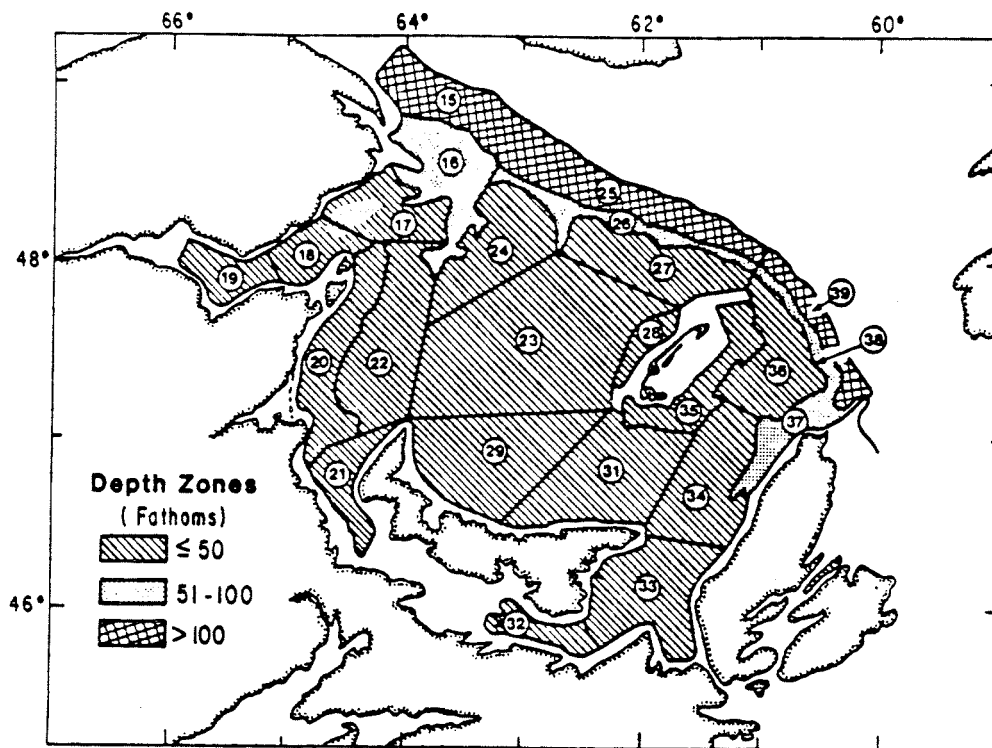


Figure 18. Stratification scheme for the southern Gulf of St. Lawrence groundfish survey.

true only if total fishing mortality and the exploitation pattern are constant through time. However, minor violations of this assumption did not seriously affect the results. They fitted parameters for age, year-class and year effects. Since these parameters are linearly related, the problem is indeterminate. They suggested the application of reasonable constraints to one of the effects, in their case the year effect was constrained to the observed trend in fishing effort.

The RV surveys in the southern Gulf have been conducted in a standard manner since 1971. Thus, it is reasonable to expect that there has been no trend in vessel fishing effort that could confound the RV results. This is in contrast to the commercial fishery catch at age where annual variation in fishing effort is common and needs to be accounted for in the analysis of data. Consequently, we elected not to include year effects in our model. Abnormal survey years could be detected by residual analysis. However, being interested in the spatial distribution at age of the cod in the area, we tested the hypothesis that the age groups were spatially segregated, by adding parameters for stratum effects and age*stratum interactions. Our overall model was

$$\ln(0.5 + C_{akn}) = \alpha + E_a + R_k + S_n + (E_a * S_n)$$

where C_{akn} is the catch at age a of year-class k and in stratum n ; E , R , and S are the overall age, year-class and stratum effects; and α is the model intercept.

The RV data for the period 1971 to 1988 were obtained from the Canadian Department of Fisheries and Oceans, Gulf Fisheries Center, Moncton, New Brunswick. Catch at age of cod was calculated on a tow by tow basis according to a two stage sampling scheme described by Halliday and Koeller (1981). Catch per tow in numbers was adjusted to a standard tow length of 1.75 nm and the mean catch per tow at age by stratum was calculated for input to the model. The catches were transformed as $\ln(C+.5)$ to allow parameter estimation using linear regression and to take care of null values. Strata with large numbers of sets without cod (i.e. strata 15, 25, and 39) and age groups 0, 1, and 8+ were not included in the analysis to reduce the number of null observations to less than 10%.

It is well accepted that SPA provides fairly robust estimates of population size for the historical part of the time series, however the estimates for the most recent period are susceptible to change with the addition of new data (Sinclair *et al.*, 1991). Our RV time series (1971-1988) covered the 1968-1986 year-classes. SPA estimates using RV and commercial data for the same period were taken from Chouinard and Sinclair (1989). In this case, only estimates for the 1968-84 year-classes were available due to the lack, at that time, of a reliable index for the 1985 and 1986 year-classes. SPA estimates for the 1968-86 year-classes were also obtained from a more recent assessment (Hanson *et al.* 1991).

Statistical analysis was performed using the general linear models procedure (PROC GLM) of SAS version 6.06 (Anon. 1990). When parameter estimates were retransformed to the linear scale, no bias adjustment was applied. In one trial, retransformation of parameter estimates to the linear scale was carried out using the methods described by Gavaris (1980) and Bradu and Mundlak (1970) and the adjustment was found to be strictly proportional. Moreover, because the results are used here as indices, there is no need to apply the bias adjustment. The log residual distribution was near normal and there was no evidence of heteroscedasticity.

RESULTS

The model parameters for the age effects are presented in Figure 19. These were obtained from two separate analyses, one for the years 1971-79, the second for 1980-88. The results indicate a change in the total mortality pattern for cod between the two periods. The two series are scaled differently, which represents a lower abundance of cod during the 1970's. However, the pattern is also different. The age effects peak at age 4 in the 1970's while the modal age is age 5 in the 1980's. This is likely to be the result of reduced fishing mortality, increased mesh size, and slower cod growth in the latter period. We were unable at this time to determine the effect of this violation of model assumptions on the estimated parameters, and this deserves further study. However, we suspect that the effect will be minor given the strong relationships that are evident between the year-class parameters and SPA estimates described below.

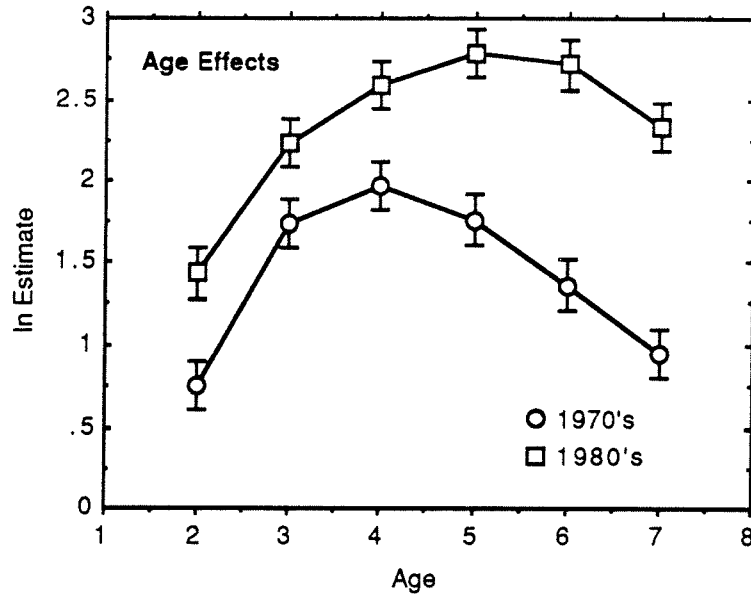


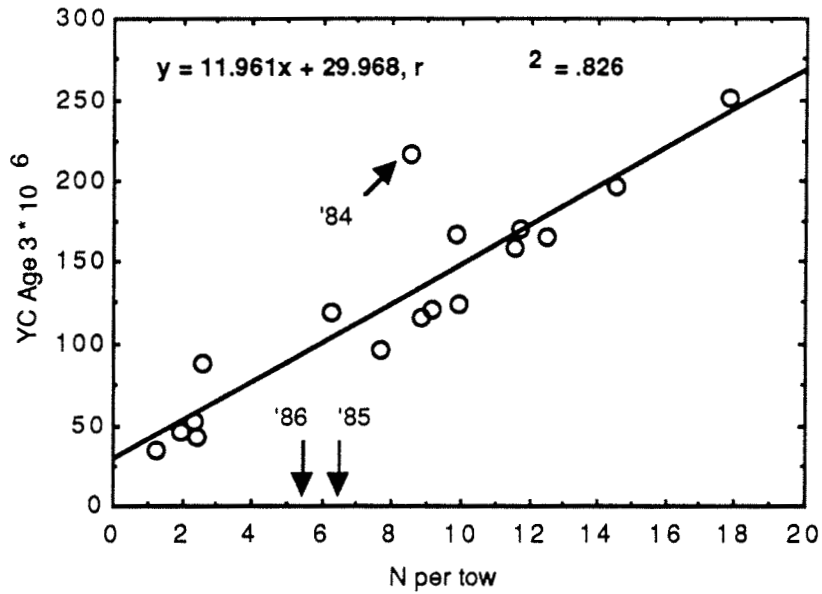
Figure 19. Least squares means of the age effects estimated from the RV catch at age data using a multiplicative model.

The analysis of variance of the overall model (Table 11) indicated all terms were significant and the model explained 60% of total variance. The stratum effect was relatively strong and this indicates an important spatial component in the distribution of cod in the area. While the stratum*age interaction term was weak, it was statistically significant ($p < .0001$) thus indicating spatial segregation of age groups.

Estimates from our model were highly and significantly correlated ($R^2 = .826$, $p < .0001$) with earlier SPA estimates (Fig. 20a). However, the 1984 year-class appeared as a high residual value. The model estimates for the 1985 and 1986 year-classes are shown on the X-axis. The comparison was repeated using the SPA year-class estimates from the more recent assessment (Fig. 20b). The model estimates of the 1985 and 1986 year-classes compared well with the more recent SPA. The SPA estimate of the 1984 year-class was revised downward and it is now more in line with the model estimate.

We interpreted the stratum*age parameters as an indication of the mean age composition in each stratum. Least squares means were calculated along with their standard errors and these are presented for selected strata in Figure 21. The modal age in strata 22 and 28 was age 3, while in strata 16 and 36 it was 5, and in strata 26 and 38 the modal age was 6. It was also noted that strata 36 had relatively fewer cod than the other strata. The general pattern of distribution at age was that the shallow strata close to land had younger fish than the deeper strata. The strata 22 and 28 had the highest catches of juvenile fish and these have been identified elsewhere as important juvenile habitats (Tremblay and Sinclair 1985, Chouinard *et al.* 1991).

a.



b.

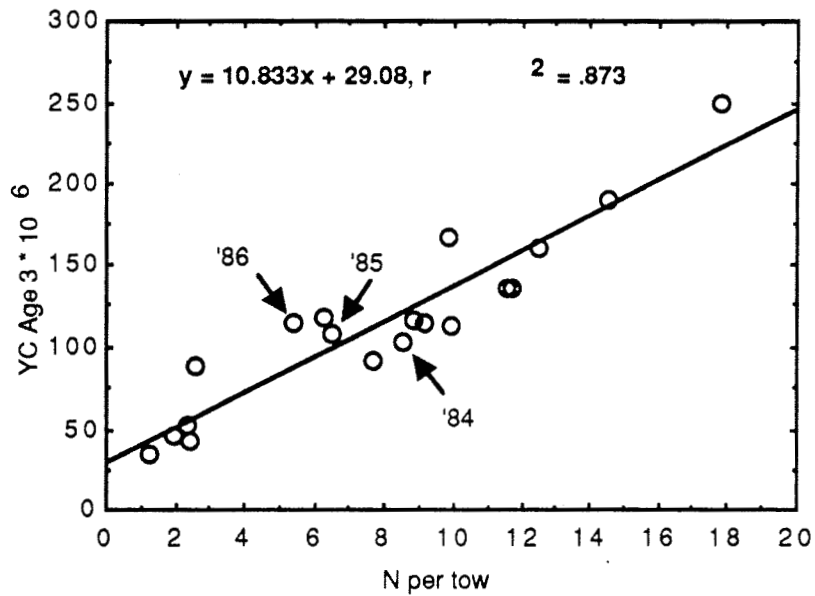


Figure 20. Comparison of SPA age 3 year-class estimates and those obtained from a multiplicative analysis of RV catch at age, a) for SPA including the 1968-1984 year-classes, b) for SPA including the 1968-1986 year-classes.

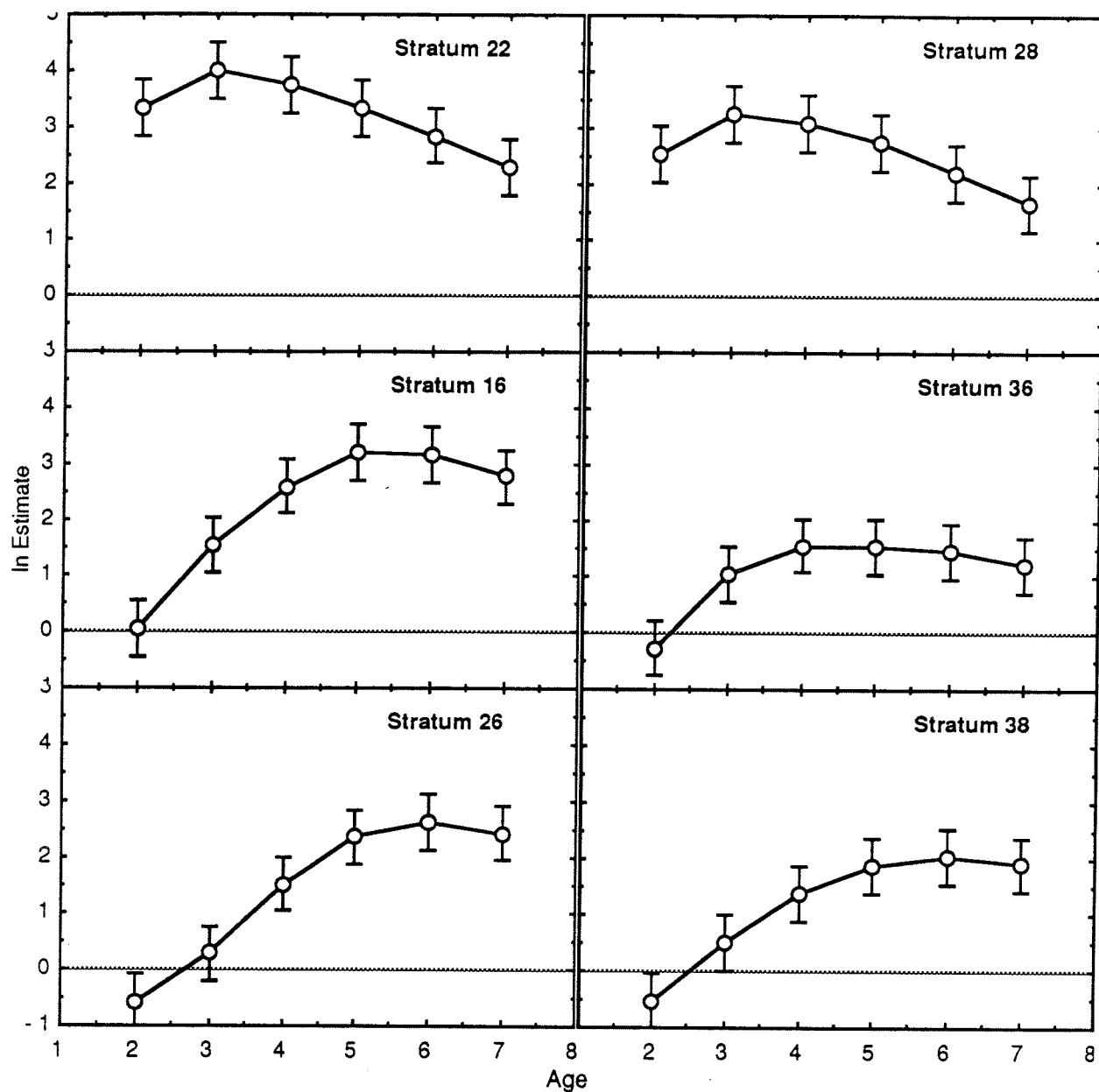


Figure 21. Least squares means estimates of the mean catch per tow at age and per stratum from a multiplicative model analysis of RV data. Vertical bars give two standard errors of the estimates.

Table 11. ANOVA results from a multiplicative model of year-class, stratum, age and age*stratum effects on the mean catch per tow for 4T cod stock.

Source	DF	Sum of Squares	Mean Square	F-value	P > F	R ²
Model	147	3291.36	22.39	20.96	0.0001	0.598
Year-class	22	1152.81	52.40	49.06	0.0001	
Stratum	20	1268.20	63.41	59.37	0.0001	
Age	5	371.23	74.24	69.52	0.0001	
Age*Stratum	100	510.06	5.10	4.78	0.0001	
Error	2072	2213.00	1.06			
Total	2219	5504.36				

DISCUSSION

The multiplicative analysis described by Shepherd and Nicholson (1991) is useful in analyzing abundance-at-age data from stratified random groundfish surveys. The addition of parameters on strata and strata-age interactions can provide information on the spatial distribution of the fish. Our results showed that estimates of year-class strength from the model compared favorably to those from SPA. In fact, it was found that in the case of the 1984 year-class, the model gave a more consistent estimate than the SPA. Thus, for stocks for which RV surveys are conducted and age determination is accomplished, such an age-structured model can provide important stock assessment parameters (i.e. a recruitment index). Even in the case of 4TVn cod, where an SPA is used for stock assessment purposes, the multiplicative analysis provided reliable estimates of two additional year-classes, the 1985-1986, that were not available from the SPA.

The change in the age specific mortality pattern between the 1970's and 1980's is consistent with changes in the fishery associated with different management measures. Fishing mortality in the 1980's was less than in the 1970's and larger mesh sizes have been used recently. The analysis assumes that this pattern was fixed throughout the period and while we have not attempted to investigate the effect of such a violation of the assumption on the results such additional work is warranted. It is likely that the estimates of the earlier year-classes are biased downward in this analysis because they probably experienced higher exploitation rates than the more recent year-classes.

Overall, we find that such models provide a relatively simple method for obtaining stock assessment parameters and information on spatial distribution from research surveys catch-at-age

data. We recommend their use along with SPA, and certainly when commercial data are insufficient to perform SPA.

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Geographic Response of Haddock to Changing Abundance

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Haddock (*Melanogrammus aeglefinus*) year-classes on the Scotian Shelf exhibit characteristic spatial distributions. Analysis of research vessel survey data has revealed that strong year-classes (estimated at age 2) tend to be more widely distributed than weak ones. The question as to whether or not haddock year-classes can be diagnosed from their spatial distribution at ages < 2 yr was examined from data collected during the Fisheries Ecology Program (FEP). Egg and larval surveys conducted monthly from February to June and a pelagic juvenile survey conducted in June during 1983-1985 were assessed for patterns in spatial distribution by determining the proportion of zero sets (PZ). PZ was used to make comparisons of the strength of developing year-classes from collections based on different gear types over a common grid of stations. The results showed an unusual reversal in PZ from an extremely high value at the larval stage (i.e. low abundance) to a relative low value during the pelagic juvenile stage (i.e. high abundance) for the 1983 year-class. This situation was not evident in 1984 and 1985. The results suggest that the pelagic juvenile stage of the 1983 year-class may have originated from outside the census area. The fact that a strong 1983 year-class occurred in an adjacent haddock stock positioned "upstream" from the FEP census area supports the hypothesis that immigrants made a significant contribution to the 1983 haddock year-class off southwestern Nova Scotia.

**Distribution of Juvenile Shrimp (*Pandalus borealis*)
off southern Labrador and eastern Newfoundland
as Inferred from Stomach Contents of Cod (*Gadus morhua*)**

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Predators may be viewed as sampling devices. Examination of their stomachs can provide relatively inexpensive information on the distribution, relative abundance and size distribution of juvenile fish and invertebrates. For example, examination of stomachs of cod (*Gadus morhua*) collected during autumn bottom-trawl surveys off southern Labrador and northeastern Newfoundland (NAFO Divisions 2J3K) revealed the presence of many juvenile shrimp (*Pandalus borealis*). Prominent modes at 3-5 mm and 8-11 mm carapace length (C.L.) are thought to represent young of the year and age 1 shrimp respectively (Lilly 1984; Parsons *et al.* 1986).

There appears to be ontogenetic variability in distribution. Large shrimp (>16 mm C.L.) occurred in highest numbers in cod collected from those relatively discrete areas where the commercial fishery has operated, *viz.*, in Cartwright Channel, in northwestern Hawke Channel, on the flanks of St. Anthony Basin and Funk Island Deep, and in the saddle between Belle Isle Bank and Funk Island Bank (Fig. 22). There were a few additional high occurrences, most notably on the southern side of Hawke Channel. A modal group at 13-16 mm C.L. also was broadly distributed, but tended to be in shallower water than larger shrimp. The modal group at 8-11 mm C.L. occurred primarily to the west of Funk Island Deep (Fig. 23). Moderate densities were found in Cartwright Channel, west of St. Anthony Basin, and to the east and south of Funk Island Deep. Densities in Hawke Channel were low. The smallest modal group (3-5 mm C.L.) occurred primarily to the south of St. Anthony Basin, on the flanks of Funk Island Deep, and south of Funk Island Bank (Lilly and Parsons 1991). Very few shrimps were found in Div. 2J.

The use of predators as sampling devices for juveniles has several advantages. It is relatively inexpensive if the catching of predators is already conducted as part of an ongoing program (eg. annual groundfish surveys). The examination of stomachs may provide individuals of smaller size than are taken by other collection methods, and may provide information at times and places not covered by species-specific surveys, including areas where other sampling tools cannot be deployed. The examination of predator stomachs may provide information on the juveniles of several prey species simultaneously.

There are, of course, potential disadvantages to the use of predators. Prey may be

misidentified because of partial digestion. The number of individuals collected may be small compared to many other collection methods. The predator distribution may not completely overlap the prey distribution. The prey may have been ingested at a location other than where the predator was captured. The rate of consumption of the prey of interest may vary with the relative sizes of the predator and the prey, and may be affected by the availability of other prey.

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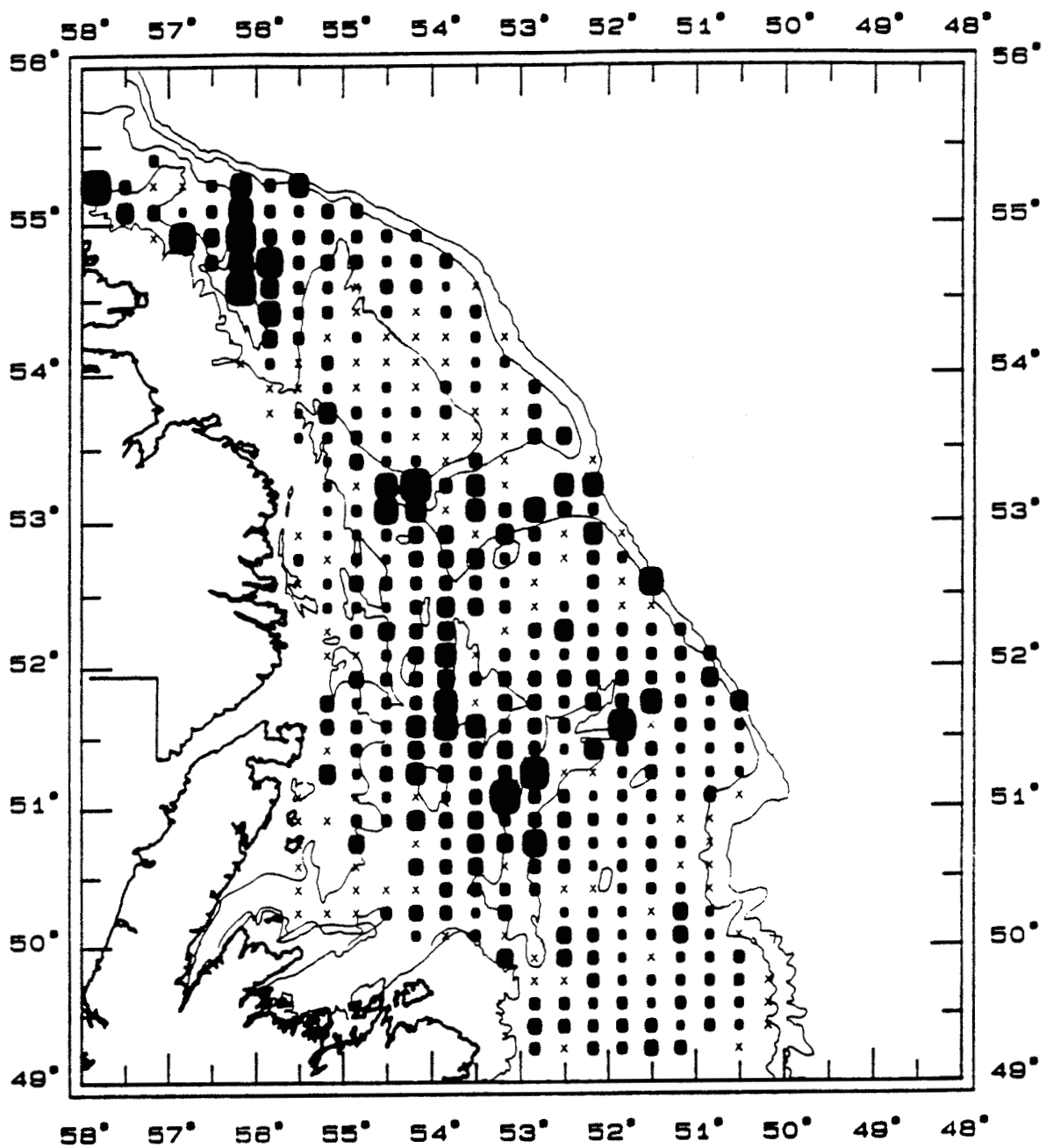


Figure 22. Geographic variation in mean number of large (>16 mm CL) shrimps found in cod stomachs (all sizes pooled) collected in the autumns 1980-1990 in areas of 10' latitude and 20' longitude in NAFO Divisions 2J3K. Areas represented by < 6 stomachs analysed are not plotted. Symbol size is proportional to the mean. Maximum symbol size represents mean ≥ 1 and $x=0$.

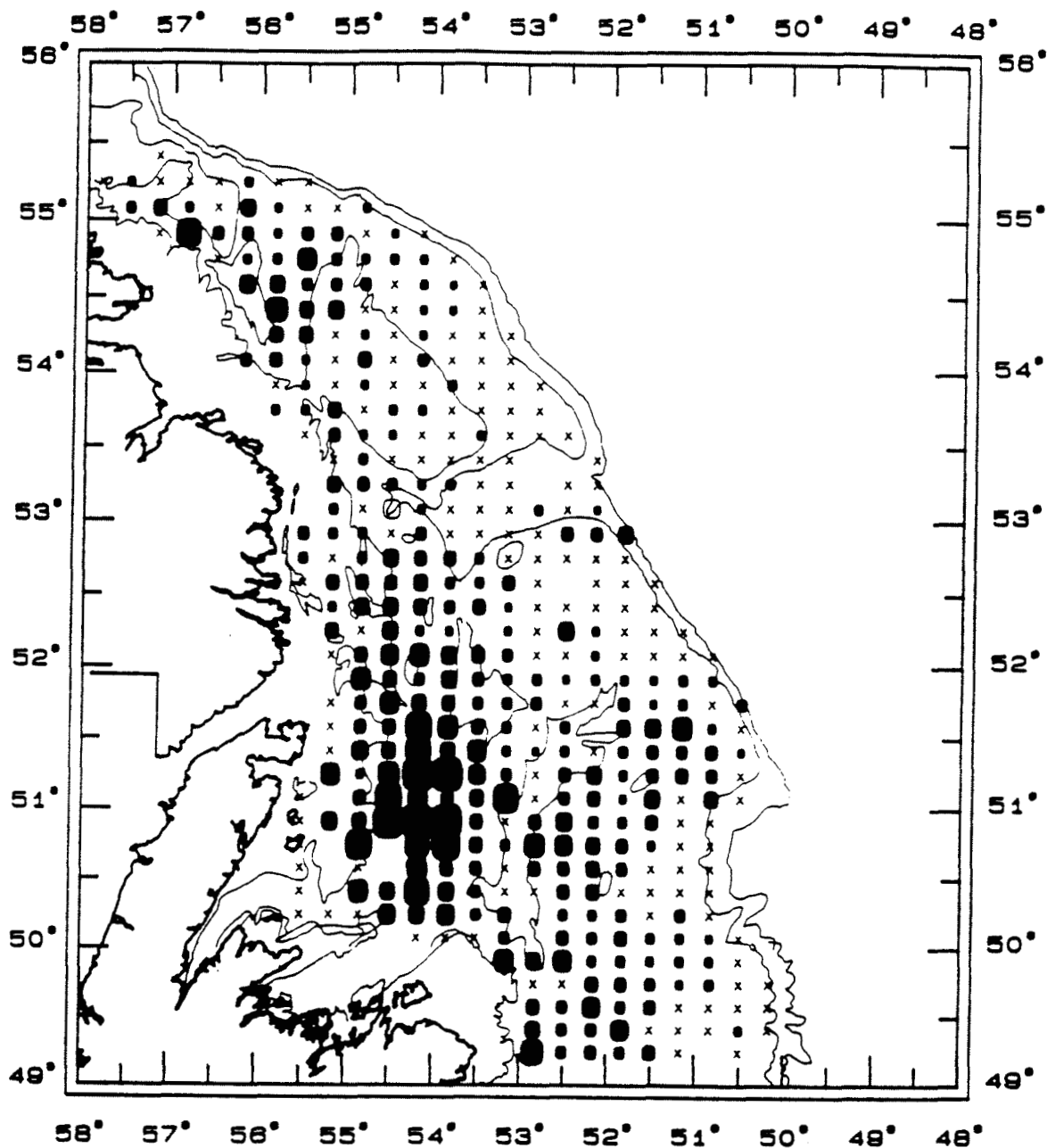


Figure 23. Geographic variation in mean number of shrimps at age 1 (8-11 mm CL) found in cod stomachs collected in the autumns 1980-1990 in areas of 10' latitude and 20' longitude in NAFO Divisions 2J3K. Symbols as in Figure 22.

The Importance of Harpacticoid Copepods (Meiofauna) in the Diet of Juvenile Fish

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One of the constraints on the type of food ingested by fish is the size of their mouth (gape limitation). However, because the size of gape increases with body size within a given species, the same size of mouth occurs in various species of fish at different body sizes. For comparative purposes therefore it seems preferable to analyze fish with the same size of mouth rather than of similar body length. Benthic juvenile (0+ group) fish of 10 different species that comprise the inshore subtidal fish community in eastern Newfoundland were compared to determine the types of food consumed and to evaluate how mouth size limits the size of the food items ingested.

Mouth size was measured (mm^2) as the product of the length and the width of the mouth. Stomach analysis was restricted to specimens having mouth size $< 30 \text{ mm}^2$. Fish diet was determined as 1) the frequency of occurrence of food items in those specimens containing food in their stomach, and 2) the relative importance of prey items. Importance was estimated as the relative volume of each type of food (estimated on a scale of 1 to 10) X stomach fullness (ranked on a scale of 0 (empty) to 4 (distended)). The importance values for each food type were summed for all fish sampled and expressed as a percentage of the total. Diameters of the food items were measured with an eyepiece micrometer installed on a dissecting microscope.

The data obtained confirm that the juveniles of all the species studied were constrained to small food items. Moreover, they appeared to consume predominantly items that were much smaller than what they are physically capable of consuming. Capability was determined from the largest items found in any stomach for a given species. Among all the food types observed, harpacticoid copepods seemed most predominant, being found in a high proportion of the stomachs (Table 12) despite their very small size ($< 0.5 \text{ mm}$ in diameter). Harpacticoid copepods also formed a significant portion of the total volume of food ingested by most fish species. The only exception was juvenile cod (*Gadus morhua*) which fed more on pelagic calanoid copepods (85% occurrence, 70% importance) even though juvenile cod had settled on the bottom and were associated with benthic algae.

Although harpacticoid copepods are found on all types of benthic substrates, those found in the stomachs of subtidal juvenile fish were morphologically similar to epiphytic harpacticoids. This would emphasize the importance of subtidal macroalgae as preferred habitats for newly settled juvenile of numerous fish species in temperate regions.

Table 12. Harpacticoid copepods in the stomachs of subtidal juvenile fish having mouth gape < 30 mm².

Fish species	Frequency of Occurrence (%)	Relative Importance (%)
<i>Gadus morhua</i>	30	13
<i>Liparis atlanticus</i>	67	18
<i>Pseudopleuronectes americanus</i>	69	26
<i>Ulvaria subbifurcata</i>	77	32
<i>Cyclopterus lumpus</i>	83	52
<i>Tautogolabrus adspersus</i>	100	8
<i>Stichaeus punctatus</i>	100	48
<i>Pholis gunnellus</i>	100	59
<i>Lumpenus fabicii</i>	100	69
<i>Macrozoarces americanus</i>	100	82

Covariation in Larval and Juvenile Growth Rates in Winter Flounder

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Many fish species have discrete larval and juvenile phases separated by metamorphosis. Scientists, in their attempts to understand fish population dynamics, have primarily focused their attention on larval (pre-metamorphic) fish (see Bailey and Houde 1989 for a review). In contrast, the juvenile stages (post metamorphic) have received comparatively little attention (but see Smith 1985; Peterman and Bradford 1987). The difficulties inherent in accurately estimating mortality rates of larval fishes (Taggart and Leggett 1987) and the biological and abiotic factors influencing these rates are motivating attempts to identify those characteristics of larval fish that may influence survivorship to metamorphosis, and perhaps, recruitment to the fishery. These approaches have focused primarily on factors that are known to influence the duration of the larval period (time to metamorphosis; e.g., Houde 1987; Chambers and Leggett 1987). For example, Houde (1987) has demonstrated how growth rate variability, through its effect on life stage duration, may act as a major factor affecting recruitment levels. However, Houde's review is based on an analysis of population mean values for the traits in question whereas survival, and the effects of growth rates or other variables influencing survival operate at the level of the individual. The difficulties inherent in generalizing from population means to individual survival trajectories have recently been highlighted by Chambers and Leggett (1991) and Chambers *et al.* (1989).

Studies of fish early life history dynamics have recently revealed among individual variation in phenotypic traits such as size and growth rate and have commented on their survival consequences. Rice *et al.* (1987) argue that the study of characteristics of individual survivors would permit identification of "which of the many mechanisms potentially influencing survival are important and at what times or ontogenetic stages they have their effect". Chambers *et al.* (1989) have demonstrated how analyses based on individual observations can reveal features of life history organization that might otherwise be obscured by averaged data. These views have been echoed in recent reviews on recruitment processes (Miller *et al.* 1988; Pepin 1991).

While the importance of this focus on phenotypic variability and individual traits has now been recognized, knowledge of the magnitude of variation in larval stage duration, its relationship to size at metamorphosis, and their survival consequences for individual larvae remains scant and inadequate. Chambers and Leggett (1987) in their review of this question have emphasized that, despite the potentially pervasive effects of changes in larval stage duration and size at metamorphosis on fish population dynamics, the ecological consequences of such changes are virtually unknown. In a further assessment, Chambers *et al.* (1988) demonstrated that patterns

of variation in life history traits established during the larval period appear to propagate into early juvenile life and, moreover, that these associations could have important population consequences.

In this paper we extend these findings by focusing on two conceptual issues: 1) the covariance between growth rates of juveniles and the growth experienced during their larval period, and 2) the implications of covariation between larval and juvenile growth for the study of the mechanisms underlying recruitment variation in marine fishes. We have employed laboratory-reared winter flounder (*Pseudopleuronectes americanus*) in our experimental studies of these questions. This species expresses a rapid and distinct metamorphosis which clearly separates the larval and juvenile life stages and thereby allows us to precisely identify the timing of this transition.

Winter flounder exhibit considerable variation in the duration of the larval period (age at metamorphosis) even when reared under constant environments (Chambers and Leggett 1987; Bertram unpubl. data). We found that growth ($\text{mm}\cdot\text{d}^{-1}$) and development rates (the inverse of age at metamorphosis) of individuals were positively correlated indicating that larvae which grow most rapidly metamorphosed earliest, and not infrequently, at smaller sizes than their slower growing counterparts. Moreover, among similar-sized metamorphs, those fish which metamorphosed later (60 d) grew significantly faster in the 10 d following metamorphosis than did those which metamorphosed earlier (48 d; Chambers *et al.* 1988). When viewed in terms of length at a common age since hatching, juveniles which metamorphosed late achieved sizes equivalent to those which metamorphosed early. This accelerated growth of late metamorphs appears to compensate for relatively slow larval growth. We have confirmed that fish which metamorphose at older ages exhibit accelerated growth as juveniles.

This phenotypic variation in larval and juvenile growth has several important implications. First, if as commonly hypothesized mortality rates due to predation decrease with size (Folkvord and Hunter 1986; Fuiman 1989), the total mortality experienced by faster growing larvae will be less than that experienced by slower growing counterparts, because they spend less time in the vulnerable sizes and thereby suffer lower cumulative mortality. The same argument may also apply to juveniles. In several studies (Victor 1986; van der Veer and Bergman 1987) juveniles have been shown to suffer high predation mortality shortly after metamorphosis when they are small and vulnerable. Laboratory experimentation on European plaice (*Pleuronectes platessa*) has demonstrated that the smallest juveniles were most vulnerable to predation by the brown shrimp, *Crangon crangon*. Predation rate declined as the size of plaice increased and reached zero when juveniles exceeded 30 mm (approximately 120 d old). In that system, which has many similarities to winter flounder, fast growth through this "predation window" could enhance survival.

Second, if the ranking of individual growth rates in the juvenile stage is consistent with that of the larval growth rates (i.e. positive covariance of growth rates) faster growing larvae would also be expected to grow fast as juveniles. Further, assuming that fast growing fish have higher survival, higher survival should be expected in both stages. However, our data suggest that growth dynamics are not so simple; juveniles which metamorphose at older ages grow faster

after metamorphosis than do members of their cohort that grew faster as larvae. Thus, fish which grow fastest in the juvenile phase and therefore experience enhanced survival probabilities may have experienced low survival as larvae. Hence, given that individual growth trajectories can differ in successive life stages it is not correct to assume that fish which experience the highest survival of members of their cohort as larvae will also have the highest survival as juveniles. Juveniles experiencing accelerated growth may also increase their survival prospects if: 1) the growing season is limited, as it is for winter flounder (Pearcy 1962); and 2) there is a minimum size below which overwintering survival is improbable (e.g., for smallmouth bass, MacLean *et al.* 1981; for smelt, Henderson *et al.* 1988; for perch, Post and Evans 1989; Johnson and Evans 1990).

We conclude that each juvenile has had a unique growth history, which is likely to have been influenced by its growth trajectory as a larva. Variation in growth and development during larval life will lead to different ages, sizes, and dates of entry into the juvenile stage and this variation is likely to affect survival not only prior to and during that period but also after metamorphosis. Therefore a greater knowledge of the dynamics of growth in both the larval and the juvenile stages, of the nature of their covariation, and of the interaction of these growth rates with survival probabilities of larvae and juveniles, is likely to be required to more fully understand the basis of variation in survival to recruitment.

ACKNOWLEDGEMENTS

This work was made possible through an N.S.E.R.C. postgraduate scholarship to D.F.B. and N.S.E.R.C. grants to W.C.L.

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Determination of Seasonal Spawning Type in Atlantic Herring (*Clupea harengus*) via the Effects of Juvenile Growth

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The standard theory relating sympatric communities of seasonal spawning types in Atlantic herring (*Clupea harengus*) describes these as discrete unit stocks or populations, with independent life histories. This concept has largely been based on studies which noted significant differences in meristic and morphometric measurements with special emphasis given to otolith characteristics and fecundities, and homing to spawning grounds as revealed by tagging studies. Identifiable larval retention areas based on hydrographic features have been hypothesized as the mechanism responsible for sustaining discrete seasonal-spawning populations. However, several observations are difficult if not impossible to reconcile with the notion of discrete spawning populations: (a) typical spring-type otoliths are often found in autumn-spawning herring and vice versa, (b) "twinning" of recruitment strength between spring- and fall-spawning year-classes, i.e. a strong spring-spawner year-class of a given year often coincides with a strong autumn-spawner cohort of the previous year, (c) a lack of genetic divergence has been demonstrated in numerous electrophoretic and mitochondrial DNA studies.

In light of the paradoxical evidence for stock discreteness, a new stock concept has recently been proposed whereby seasonal spawning stocks are seen as subunits of a larger population in "dynamic balance", and extensive gene flow is the rule rather than the exception. However, a limited stock structure must remain in order to explain the differences in the stock parameters observed in earlier studies. I therefore hypothesize that sympatric spring and autumn spawners form reproductively isolated groups as adults, but that the progeny of a given seasonal group do not necessarily recruit to the parental stock, and may indeed contribute to a group of another reproductive season. This implies that spawning season is determined at the time of first maturation, and is then fixed for the remainder of the adult phase. Evidence from other teleosts suggests that density-dependent, or environmentally induced variability in growth and condition in the juvenile phase can regulate the onset of first maturation. The analysis of data from Gulf of St. Lawrence where both spring- and fall-spawning herring co-occur does suggest that the juvenile growth influences the determination of the season of first spawning in herring stocks. When the length distribution of three year-old spring-hatched herring was unimodal with a relatively small variance, the vast majority subsequently spawned in the spring. However, when the three-year-old length distribution was bimodal with a relatively large variance, the larger individuals became spring spawners, while the smaller individuals became autumn spawners. Data also showed that this length difference observed during the juvenile phase was maintained throughout the adult phase.

It is further hypothesized that seasonal spawning groups are sustained through behavioural isolation, as homing to spawning areas is a learned response through the social transmission of migration patterns from adults to recruiting individuals in the year preceding first spawning. Spawning group integrity is therefore maintained through repeat rather than a natal homing.

A Test of the Adaptive Value of Growth for Juvenile (0-group) Atlantic Mackerel (*Scomber scombrus*)

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The success of recruitment of fishes is believed to be determined primarily in the first year of life (Rothschild 1986). For the juvenile stage (0-group), the success of recruitment is often discussed alongside the theory of size-dependent mortality. This long-standing theory states that fast growth will result in low mortality, since duration of exposure to size-selective predation will vary inversely with growth rate (Ricker and Foester 1948; Shepherd and Cushing 1980). However, the existence of a generalized link between early growth and survival of fishes remains to be demonstrated (as reviewed by Anderson 1988). In the present study, the link between growth and survival of 0-group Atlantic mackerel was studied using the 1988 year-class from the Gulf of St. Lawrence (GSL).

METHODS

Juvenile Atlantic mackerel 10 to 80 days old were caught in 1988 with beach-seines and gill-nets (as described by D'Amours and Landry 1989). The frequency of daily ring deposition was validated on the sagittal otoliths of the fish (D'Amours *et al.* 1990); the growth of the otolith was considered an appropriate proxy for the somatic growth. A Gompertz curve (e.g. D'Amours *et al.* 1990) was used to describe the growth of the otoliths, and the model was:

$$L_t = L_{\infty} e^{-e^{-k(t-t_0)}}$$

where L_t = radius at time t , L_{∞} = asymptotic radius, k = rate constant, and t_0 = point of inflection. Computed radius-at-age from the growth curve of the otoliths of 0-group fish was subtracted from the radius at corresponding age observed on the otoliths of 2 yr-old fish of the same 1988 year-class. This subtraction yielded differences ("deltas" in Fig. 25) in radius between 0-group and 2 yr-old fish. The hypothesis tested was that size-selective mortality acted between the ages. Evidence for a directional selection (Endler 1986) on the growth phenotypes was sought in the patterns of a plot of the differences in otolith size between age 0 and age 2. If faster growing fish survived better, a positive slope should be detected in the plot of those differences. This expectation is based on the observation of a divergence of growth trajectories between fast and slow growing fish in the nearly linear segment of the growth curves (D. D'Amours, unpublished

data). The slope of the differences versus age was computed for each 2 yr-old fish, and the resulting 30 slope estimates were used to test the hypothesis that the mean of the 30 slope estimates would be greater than 0 (one-tailed t -test).

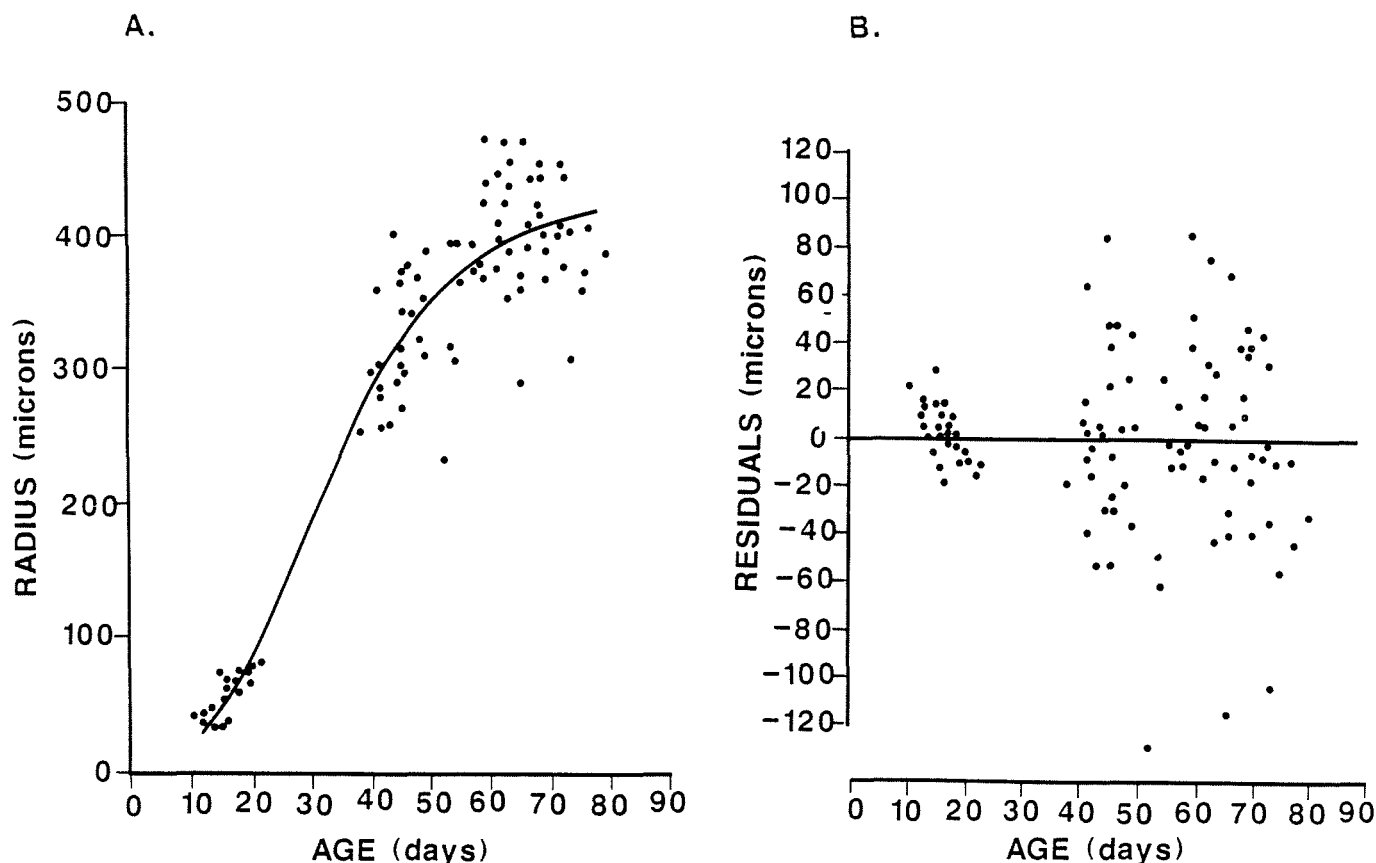


Figure 24. A) One-cycle Gompertz curve of sagittal otolith fitted to total-radius at age from 0-group Atlantic mackerel of the 1988 year-class from the Gulf of St. Lawrence; B) plot of residual values thereof.

RESULTS

The daily growth of the otolith of 0-group mackerel was described with one-cycle Gompertz curve (Fig. 24a) with parameters as in Table 13. The residuals about this growth curve (Fig. 24b) increased with age. To accommodate this increasing variability, a weighing factor equal to the inverse of age was introduced in the least-squares analysis. Total radius-at-age was measured along a defined reading axis on the otolith, for fish ranging in age from 10 to 80 days. Micro-rings were also visible on the otoliths of 2 yr-old mackerel after proper grinding; total radius at each consecutive ring was measured from the 20th to the 50th nominal ring. Total radius

at the 20th nominal ring on the otoliths of 2 yr-old fish was identical to total radius at the 17th day of age from the growth curve of 0-group fish. Sub-daily rings must have been included in the count of the first 20 nominal rings; after the 20th nominal ring, the preparation was clear enough to distinguish between daily and sub-daily rings as per D'Amours *et al.* (1990). Age represented by ring number on otoliths of 2 yr-old fish was thus equal to nominal ring number minus 3. The radius-at-age as computed from the 0-group otolith growth curve was subtracted from corresponding radius-at-age for daily ring 17 to 47 on the otoliths of 2 yr-old fish, and plotted against age (Fig. 25). The mean of the 30 slope estimates of the deltas was not significantly different from 0 ($0.25 > p > 0.2$).

Table 13. 95% confidence intervals of the parameters of a one-cycle Gompertz growth curve fitted to radius-at-age of 0-group mackerel otolith from the 1988 year-class in the Gulf of St. Lawrence.

PARAMETER	VALUE (with 95% confidence intervals)
L (asymptotic radius)	438 μm (411-454)
k (rate constant)	0.065 d^{-1} (0.058-0.078)
t_0 (point of inflection)	27.2 d (25-29)

DISCUSSION

The null hypothesis of no positive trends in the deltas could not be rejected. Consequently, the different growth phenotypes, acting over the period 17 days to 47 days, cannot be said to have resulted in a differential survival from age 0 to age 2. At least two scenarios could explain why no evidence was found of a higher survivorship of faster growing fish.

First, the analysis assumes that size-selective death occurs sometime between age 0 and age 2. For growth to be an adaptation to predation during this period, predation must be acting simultaneously on growth phenotypes. Investigations of the gut contents of the most abundant potentially predator fish in the GSL, adult mackerel, did not reveal any predatory mortality of juvenile mackerel (D. D'Amours, unpubl. data). However, juvenile mackerel could suffer most of their predation outside the GSL along the continental shelf (Overholtz *et al.* 1991) where they emigrate to spend their first winter (as reviewed by MacKay 1979). Differential growth rates inside the GSL would not necessarily result in differential size outside the GSL, if fish migrate when they reached a certain size, in which case predation by various fish species outside the GSL (Overholtz *et al.* 1991) could not be size-selective.

Alternatively, fast growth could be an adaptation to complete an extensive migration, since juvenile mackerel must exit the GSL before winter. To complete the migration, a minimal size would need to be attained before a certain time in autumn. Fish growing fast enough to attain at least this size threshold at the right time would be equally favoured; fish not attaining this size would all have a low or zero probability of survival (threshold selection; see Falconer 1981). In this case, the relationship between growth and survival would not be monotonic, but a step function. Of two groups of fish, the one with the highest mean growth would have the higher viability only if the two groups bracket the size threshold at the time of selection. If for the year-class 1988, most of the 0-group fish had a growth phenotype resulting in a size above the threshold at the time of selection, no directional selection could be expected on this phenotype between age 0 and age 2.

The simple monotonic relationship usually implied between growth and survival (Shepherd and Cushing 1980) may not reflect the complexity of the constraints faced by juvenile mackerel, and by juvenile fishes in general.

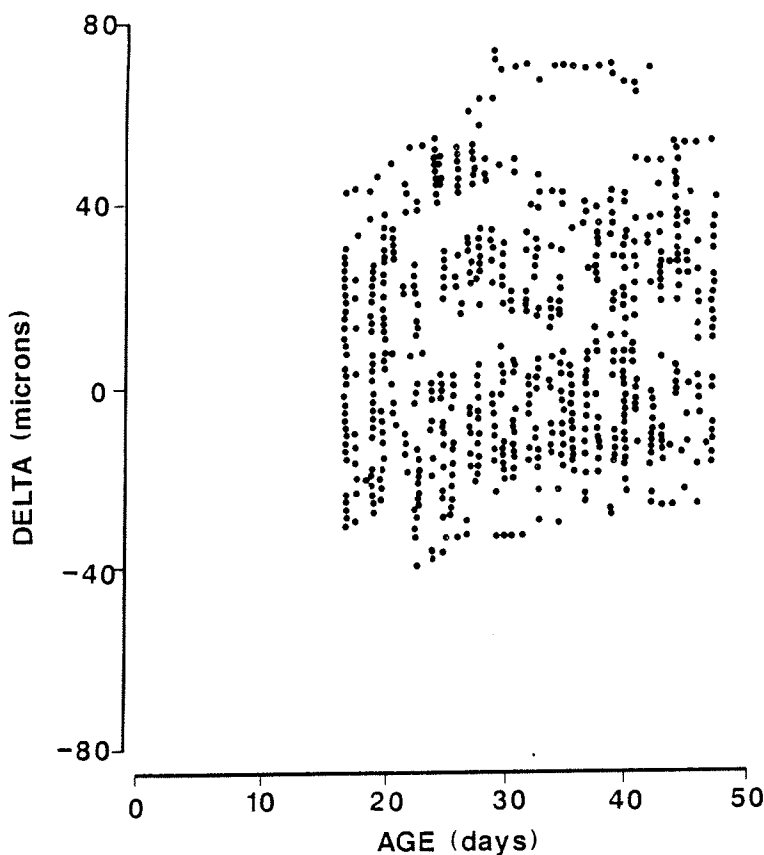


Figure 25. Difference ("delta") between observed radius-at-age on otoliths of 2 year-old mackerel, and radius-at-age computed from otoliths of 0-group mackerel; both age groups from the 1988 year-class from the Gulf of St. Lawrence. Deltas were measured for daily rings 17 to 47, 30 fish (30 measurements per fish, on 30 fish = 900 measurements; one symbol may represent several measurements).

ACKNOWLEDGEMENTS

I thank J.G. Landry for his technical support at every stage of this study, and Steve Campana and an anonymous referee for helpful comments.

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Substrate Selection by Juvenile Cod (*Gadus morhua*) in the Absence and Presence of a Predator

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Various biotic (e.g. predators, food) and abiotic (e.g. substrate type, temperature) factors are known to affect the spatial distribution, and survival, of fish and other animals. Evidence exists that substrate type and risk of predation may affect the distribution of juvenile cod. Therefore, the purpose of this study was to investigate substrate selection by juvenile cod in the absence and presence of predation risk. Experiments presented a group (n=5) of juvenile cod with a choice between two different substrates (sand and gravel/pebble, sand and cobble, and gravel/pebble and cobble) in the absence or presence of a predator. With no threat of predation, juvenile cod preferred finer substrate types. In contrast, the presence of a predator resulted in selection for the coarse substrate by the juveniles. In those trials where one of the substrates was cobble, juvenile cod sought shelter in among, and under the larger stones. The presence of cobble resulted in fewer juveniles being captured by the predator. Our results indicate that substrate selection and the absence or presence of predators affects the survival and distribution of juvenile cod.

Effects of Tidal Current Speed on Settlement of Reef Fish in the Exuma Cays, Bahamas

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Reef fish larvae are transported from offshore waters of Exuma Sound through tidal channels to the shallow Bahama Bank, where they settle onto hard bottom. At Lee Stocking Island, small artificial reefs were deployed along a gradient of distance from the channel mouth, in order to investigate the effects of tidal current speed and proximity to larval source on the settlement of reef fish. Mean current speed at mid-flood tide decreased with distance from the channel mouth. Settlement was inversely related to current speed and proximity to the channel mouth. This suggests that high current speeds may prevent reef fish larvae from settling onto the nearest suitable habitat, and that competent larvae are more able to settle in areas of relatively slack water.

100
50
0
0
50
100

A Study on the Early-life Growth of the Short-finned Squid, *Illex illecebrosus*

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The short-finned squid, *Illex illecebrosus*, is an annual species that sustains a valuable but unstable seasonal fishery on the East coast of Canada. The bulk of this fishery is based on a single cohort originated from a winter spawning group that uses the Nova Scotia and Newfoundland continental shelves as feeding grounds during the spring and summer. During the autumn, maturing animals migrate southward to the spawning grounds which are presumed to be in the Gulf Stream waters south of Cape Hatteras, USA. Juveniles are recruited to this fishery during the spring, about four months after hatching. During this time, hatchlings go through the transition from larvae to juvenile stages and begin their early predatory life style in the plankton. Critical periods during the squid life are related to the individual feeding success during this early predatory phase and are reflected by changes in growth rate. Samples from the 1991 fishing season on the Scotian shelf were used to reconstruct the early growth histories of individual squid by measuring the diel growth increments deposited on the gladius, a chitinous internal shell. The variability of individual growth rate changes have been studied in an attempt to develop a model relating growth to feeding success and larval mortality.

**Report of the Workshop on Juveniles of Northern (Division 2J3KL)
Cod (*Gadus morhua*), 20-22 March, 1991, St. John's**

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A workshop on juveniles of northern (Division 2J3KL) cod was held during 20-22 March 1991 at the Northwest Atlantic Fisheries Centre, St. John's, Newfoundland. The workshop was sponsored by the Northern Cod Science Program - Early Life History Initiative. The prime objective was to recommend a monitoring programme which will provide a reliable index of year-class strength for one or more age-groups younger than age 3.

The purpose of the workshop was to formulate a 4-year pilot project which will: (i) identify and delineate the habitats of juvenile cod, from the 0-group pelagic stage to age 3, for each of the various components of the Div. 2J3KL stock; (ii) identify or develop gears for quantitative sampling of cod of specific ages or sizes in specific habitats; and (iii) describe the behaviour of young cod, with emphasis on how behavioural patterns and external factors create spatial and temporal variation in abundance and catchability. Field studies on factors influencing survival of juveniles may be incorporated into the programme.

Approximately 32 participants attended the workshop. The first day was devoted to an overview of the early life history of northern cod. This consisted of a review of published data, including Soviet reports, and 18 presentations of new analyses of unpublished data. These included analyses of archived DFO data on the time and location of spawning of 2J3KL cod, the distribution of pelagic juvenile cod, and the distribution of catches of demersal juvenile cod during various Canadian offshore bottom-trawl surveys. The second day started with a review of discontinued, existing and proposed studies of juveniles in other cod stocks. Both research and monitoring programmes were discussed. The remainder of the workshop was devoted to the consideration of new research.

Juvenile cod, of ages 0 and 1, are abundant in shallow water along the coast of Div. 2J3KL. These juveniles have already received some study with respect to growth, broad-scale distribution, seasonal variability in relative abundance at a single site, diel movement, and association with specific types of substratum. It was concluded that there was excellent potential for monitoring of these age-groups in shallow coastal waters. It will be necessary to determine the advantages and disadvantages of employing SCUBA, acoustics, seines, trawls, gillnets, traps, and so on, in various habitats. The most promising gears should be used to determine variability in distribution and catchability on various temporal and spatial scales. Consideration should be given to diel, tidal, seasonal and annual variability. On fine spatial scales there should be an

investigation of the influence of physical factors such as currents, temperature, depth, exposure, distance from shore, bottom type, and vegetation. There must also be consideration of broad scale spatial variability.

There was concern that the high visibility of young cod in shallow coastal waters might be giving a false impression of the importance of the inshore as a habitat for juvenile cod. Very few age 0 and age 1 cod have been caught offshore during standard research surveys, but it is known that the trawls used for these surveys are very inefficient at catching small cod. It was recommended that a more efficient trawl be designed (possibly a shrimp trawl with rockhopper foot gear), that the trawl be tested on the southern Grand Bank where small cod have been caught during juvenile flatfish surveys, and that exploratory surveys be conducted in those areas where the smallest juveniles have been found with standard gears. The most promising areas are the plateau of the northern Grand Bank, and the coastal shelf from the Grey Islands to just north of Belle Isle.

The distribution of pelagic juvenile cod has not been extensively studied. Exploratory surveys for juvenile capelin have revealed the presence of pelagic cod over much of the offshore area off eastern Newfoundland as well as within southeastern bays. It was recommended that surveys for pelagic juveniles be conducted over the whole shelf and adjacent inshore areas, from the northern Grand Bank to southern Labrador, to provide a link between the distribution of eggs and larvae (being studied under another initiative) and the distribution of demersal juveniles.

It is important to know what happens to the pelagic juveniles offshore. Do they migrate to the inshore, or do they settle to the bottom offshore? If they settle offshore, is their survival different from juveniles which settle inshore? It may be difficult to address these questions unless there is a series of pelagic surveys during the late summer and autumn, concurrent surveying of demersal juveniles, and examination of stomachs of potential predators.

Because it is suspected that the northern cod stock comprises several spawning components, it will be advantageous to identify the parent "stock" for the juveniles found at each specific time and place. Methods which may be useful in linking parents and progeny include patterns in egg and larval drift, the distribution of pelagic juveniles, meristics, otolith characteristics, genetics, parasites and tag returns.

Most of the new research should be directed toward obtaining the information required for recommending a specific monitoring programme, targeted at a certain age-group, time of year, geographic area and depth, and employing a specific survey method, sampling design, and level of effort. Additional studies may be more process-oriented. These include study of the role of substratum type and predators in site selection, the relationship between antifreeze production and survival, the influence of temporal and spatial variability in feeding on growth and survival, and the extent to which predators (eg. squid, larger cod) can effect annual variability in mortality rate.

A report of the workshop will be published in the technical report series of the Canadian Fisheries and Aquatic Sciences.

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