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A Review of the Population Dynamics of American Lobster in the Northeast

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A Review of the Population Dynamics of American Lobster in the Northeast

PREPARED FOR

The Northeast Stock Assessment Review Committee

BY

The Office of the Senior Scientist
National Marine Fisheries Service

AND

The Atlantic States Marine Fisheries Commission

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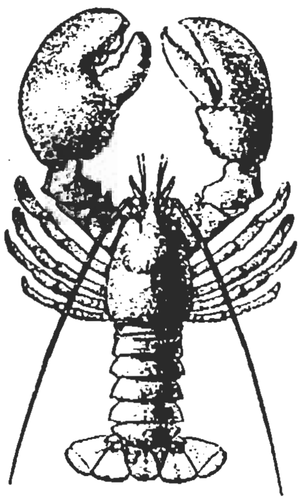

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Executive Summary

This report presents the conclusions and recommendations of an independent panel of experts convened to review the population dynamics of American lobster (*Homarus americanus*) in the Northeast United States. The review was jointly sponsored by the National Marine Fisheries Service (NMFS), Office of the Senior Scientist, and the Atlantic States Marine Fisheries Commission. The Review Panel meet from 25-29 March 1996 in Warwick, Rhode Island.

The goal of the review was to provide managers of American lobster and scientists conducting research on American lobster with a set of testable hypotheses that could resolve some of the fundamental questions concerning productivity and recruitment of the species. In addition, the overfishing definition for lobster was to be re-examined in light of other findings of the review. The review focused on the population dynamics and ecological factors affecting productivity of lobster.

The conclusions and recommendations were drawn from the individual expertise of the panel members, from information presented to the Review Panel by academic, state, and federal research scientists, as well as by individuals from the fishing industry, and from background papers provided to the Panel in advance of the review. The sections below are summaries of the Panel's key findings; more extensive discussions may be found in the complete report under the same section titles.

Section 2. Stock Structure

Decisions about the identity or definition of assessment units depend on the knowledge available, but also on balancing the advantage of having uniform regulations against the need to allow for meaningful genetic, population structure, or jurisdictional differences between sub-areas. For the American lobster the Panel reviewed the information available from fisheries data, NMFS bottom trawl surveys, extensive tagging results, and some larval investigations. It concluded that there is a good understanding of the broad picture of North American lobster distribution, abundance, migration, and larval distribution, but that the detailed relationships are not clear, especially those between the inshore and offshore areas. On the other hand, genetic and morphometric data, though not complete, show little evidence of clear cut stock separation. The Panel therefore endorsed the practicality of the decision by the 16th Stock Assessment Workshop (SAW 16) to divide the lobster population into only three units, the Gulf of Maine (GOM), Georges Bank and Offshore (GBS-O) and South of Cape Cod to Long Island Sound (SCCLIS).

The Panel viewed the lobster population as a metapopulation, i.e. a number of sub-populations linked by dispersal. It is concerned that if the very heavily fished inshore part of the population depends critically on larval subsidy from the offshore and canyon areas, as some data indicate, the recent expansion of fishing into the offshore area could be a significant threat to population persistence. The metapopulation aspect is worth further detailed study. The contribution of different areas to overall egg production could be quantified, and the patterns of larval dispersal and transport described and modelled more precisely. Past tagging data should also be re-analysed to calculate area-specific transfer rates which take into account how recapture data may have been affected by different spatial patterns and levels of fishing mortality. The role of genetic analysis should also be extended.

The sensitivity of the assessment to the weighting of data from different sub-areas may be worth further study. This should include examining whether the precision of the assessment would benefit from treating Long Island Sound as a separate stratum, although the Panel felt that the justification for treating this area as a separate management unit needs to be evaluated carefully.

Section 3 Stock Assessment

Increased lobster landings on the east coast of the USA (and Canada) since the mid-1970's have occurred despite the historical evidence that the level of fishing mortality on the stocks has been very high. The Panel therefore carefully reviewed the present SAW 16 assessment, based on the DeLury model of Conser and Idoine (1992). The model uses annual landings, and NMFS bottom trawl survey data, to calculate the abundance of pre-recruits and post-recruits, defined by specific size ranges, and thence calculates the mortality between these two stages. The SAW 16 assessment also reviewed results from the more traditional length cohort analysis (LCA) model based on landings and size frequency data.

<u>The DeLury model.</u>
The advantage of the DeLury model is that it incorporates relative abundance data from a fairly comprehensive trawl survey, and SAW 16 made preliminary investigations of the sensitivity of the results to the spatial combinations of the data, and to assumptions about the relative selectivity of the trawl survey gear to pre- and post-recruits. The Panel recommended that sensitivity analyses and simulations could be extended to investigate in more detail the effect of all the basic assumptions, and of different spatial combinations of the data. The degree of uncertainty associated with the results should be measured routinely. The effect of the absence of inshore stations in the NMFS trawl survey should be investigated further, and consideration given to adapting the model to use multiple survey indices, so that data from the NMFS and State surveys could be used together. Nevertheless, the Panel accepted that the DeLury results give an adequate description of the overall trends in abundance and fishing mortality based on a major fishery-independent data set, and found no obvious grounds for disputing the findings. These findings are that fishing mortality in the GOM area has increased from 0.44 in 1983 to 0.65 in 1989/91; that it reached 1.47 for SCCLIS in 1989/91; and that for GBS-O, where effort is known to have increased, it ranged form 0.24 to 0.51 depending on the assumptions made about selectivity.

<u>Length cohort analysis.</u>
The lobster size distributions for the Maine and Massachusetts fisheries contain only a very small proportion of lobsters above the immediate recruit size range, and length cohort analysis results give very high values of fishing mortality, ranging from 1.2 to 1.5. Given the availability of historical data on size distribution, and that spatially explicit catch-rate and size frequency data must be available from at-sea sampling programmes, the LCA method has the potential to provide a long time series of fishing mortality estimates from a variety of sub-areas, and also to facilitate comparison between the North American lobster fishery and lobster fisheries elsewhere. These comparisons are open to error, however, because size distribution data can be affected by so many factors other than fishing effort. Also, it is not quite clear theoretically how the LCA results map to the DeLury results. The Panel therefore recommends that work on LCA should continue in order to evaluate its utility and accuracy; to facilitate a

rigorous comparison with the DeLury results; and to develop a long term historical analysis of how fishing mortality on American lobster has changed in relation to changes in fishing effort.

Landings per effort.

The DeLury results represent the position at the end of a period of substantial change in the US lobster fishery. The main elements have been an increase in fishing effort, and later an increase in recruitment. Data on fishing effort and landings per unit effort (LPUE) from Maine and Massachusetts show that on the historical scale, lobster fishing effort has risen slowly since the 1900's, but since the 1970's trap numbers have risen dramatically (at least fourfold), and efficiency has also increased. The recent increase in landings has been strongly influenced by the increase in effort, and even crude aggregated landings per trap haul, uncorrected for efficiency changes, declined by 67% after 1970 in Maine, and by 50% in Massachusetts. Since the mid-1980's, however, LPUE, although low overall, has remained stable in Maine, and increased in Massachusetts, and bottom trawl survey indices also increased in this recent period. An increase in recruitment has therefore also occurred. The Panel recommends that the spatial distribution of the change in abundance could be examined in more detail using spatially explicit LPUE data, standardised to allow for changes in trap design and in set-over times.

Stock and recruitment.

Given the high fishing mortality values in this fishery, the Panel considered what is known about the relationship between stock and recruitment in the American lobster. Data from two localities, the Northumberland Strait in the Gulf of St. Lawrence, and Arnold's Cove in Newfoundland, give very similar results which provide qualitative guidelines to managers. They show that recruitment is independent over a wide range of egg production. The slope of the recruitment curve at low levels of egg production will therefore be very steep, so that stock collapse could come quickly and without warning, particularly given the six year time lag between egg production and recruitment. The proximity of the slope can only be assessed from data by allowing fishing mortality to reach dangerously high levels, and this illustrates why it is prudent and necessary to have a specific definition of overfishing which precipitates management action before such a point is reached. The Panel therefore supports the adoption of an overfishing definition. It stresses that this is not a target level for management, but a danger level which the fishery should move away from on a precautionary basis.

Egg per recruit and the overfishing definition.

For lobster, the overfishing reference point is defined by the egg per recruit model of Fogarty and Idoine (1988). The benchmark, based on experience with other crustacean fisheries, is $F_{10\%}$EPR. For this assessment the egg per recruit model was modified to include new growth data, and to allow for an assumed 50% compliance in the voluntary v-notching scheme operated in Maine. The Panel suggested that the model could usefully be modified to take into account individual variability in growth or reproduction, and that error analysis should be conducted. It would also be helpful to define the degree of risk that could be accepted in estimating the probability that F exceeds $F_{10\%}$EPR. For practical purposes, however, the Panel accepts the present definition overfishing, and the results from the current egg per recruit model.

The Panel were also shown results from a version of the egg per recruit model applied to data for Long Island Sound. This takes into account egg production derived from the significant number of mature undersized lobsters present in that area. The Panel felt that the importance of an undersized subsidy should be evaluated further, but points out that at present the Long Island Sound model is incompatible with the DeLury estimate of fishing mortality, since the two models are currently using different definitions of recruitment.

Stock status.
The Panel accepted the description of stock status for the American lobster derived from the DeLury and the egg per recruit models. In all three assessment areas fishing mortality is well in excess of F_{max} on the yield per recruit curve, so that the stocks are growth overfished, i.e the same average yield, or greater, could be obtained from a substantially reduced fishing mortality, and hence much lower cost. In terms of recruitment overfishing, average $F_{1989\text{-}91}$ was much higher than the $F_{10\%}$EPR biological reference point for SCCLIS, moderately higher for the GOM, and approximately equal for GBS-O. Overall, and taking account of concern about the GBS-O as a source of recruits to the inshore area, the Panel found no substantive grounds for disputing the SAW 16 findings that the U.S. lobster stock is, by definition, overfished. Egg production is predominantly dependent on very small animals inshore, and the critical larger lobsters offshore, and practically speaking, the risk is high that recruitment is vulnerable to further increases in fishing mortality.

Section 4. Changes in abundance

Since the 1970's and the 1980's lobster landings increased markedly. This does not of itself indicate that stock abundance has increased, since there has also been a substantial increase in fishing effort (fourfold) and efficiency. Landings might also be influenced in part by the increased amount of fishing taking place in offshore waters. U.S. bottom trawl survey data show that in the 1980's a real increase in abundance occurred in all survey areas, however, and fishery LPUE for the GOM, although low compared to the 1960's and earlier, has recently been stable. Data presented by Drinkwater showed that the landings increase is synchronous over a very wide geographical range. Correlations between trends increasing distances apart persist over a scale of 2000 km, covering a wide range of different habitats, fisheries and management regimes, and suggesting a global cause. For the 1960's, temperature was shown to influence lobster landings, but comparable correlations between temperature trends increasing distances apart decay beyond a spatial scale of 800 km, and Drinkwater was unable to show that temperature predicted the recent increase in landings in the various parts of the geographical range. On the other hand, Fogarty showed that for the Gulf of Maine, landings in any year were predicted by a model comprising landings the previous year, temperature lagged by 6 years, and temperature lagged zero years. It seems likely that the increase in landings is due to a combination of fishing effort and temperature, the latter affecting lagged recruitment through either increased survival or growth, but also catchability or availability in any given year. The Panel recommends a careful re-analysis of the magnitude and timing of abundance changes using spatially explicit bottom trawl survey and standardised LPUE data, coupled with a search for temperature-related effects on population size or age structure. The Panel was not able to examine the effect of changes in larval transport, changes in predation, or the likely effect of regime shifts, but noted that in both the latter cases other species in addition to lobster might be expected to show comparable changes, which could be looked for. It would also be useful to compare data from Canada, where because of the nominal control of fishing effort the balance between effort and recruitment is likely to have been different. The fact that in both USA and Canada landings increased at a similar rate, but that fishing effort changes in each areas are likely to have been very different, could serve to exclude the hypothesis that the recruitment increase was caused by an increase in the amount of bait on the sea bed.

Section 5. Management.

The increase in the United States lobster landings is most likely to be due to a combination of increased fishing effort, and increased recruitment. Fishing mortality is now high enough for the lobster fishery to be considered overfished by definition, and irrespective of the recent increase in abundance, fishing is still removing an unacceptably high proportion of each recruitment. Even if the abundance increase is due to an increase in recruitment, for whatever reason, it is a critical fact that the stock and fishery are vulnerable to any reversal of the factor causing the abundance change. Such a reversal could move the fishery beyond the replacement point on the stock and recruitment curve. On this basis a risk-averse management policy should continue to use the overfishing definition based on a per-recruit model, and the conclusion of SAW16, that the U.S. lobster stocks are overfished, should not be challenged. The risk of stock collapse would be contained or reduced if fishing effort were capped or reduced, and legal size increased. It would also be prudent to assume that the offshore stocks provide a larval subsidy, necessitating that the level and pattern of offshore exploitation should be controlled. In the absence of data for the relationship between fishing effort and fishing mortality, a pragmatic first step would be to set an effort ceiling.

Section 6. Benthic ecology

The Panel spent some time considering the details and implications of results emerging from ecological studies of the early benthic and adolescent phases of the lobster. In the Gulf of Maine, benthic abundance can critically depend on the delivery of larvae to suitable sites. Off New England it is clear that the delivery process involves passive transport, wind effects, active larval swimming, and vertical behaviour aimed at searching for suitable habitat. Although settlement may involve choice, however, juveniles in the Gulf of Maine do occur on less preferred habitat. In the northern Gulf it is hypothesised that the absence of juveniles in suitable habitat may be correlated with the presence of water below 15°C. Once settled, early benthic stage lobsters can be subject to high predation rates, which encourages lobsters to remain in their refuges. Although mortality in the early benthic phase is high, the results of manipulation experiments presented to the Panel do not provide evidence that mortality depends on lobster density. Such lobsters do not necessarily stay at the settlement site, but may redistribute themselves through time. Later, as adolescents, they may experience agonistic interactions, which could also create distributional changes.

There is substantial interest in this work. Much of it is based on small samples collected at a local scale, and the data have a high variance, but there is clearly scope to use the results to develop more intensive and extensive programmes for testing hypotheses about those factors which affect distribution, and about the possible ecological determinants of the stock-recruitment relationship. The behaviour of mature, reproductive animals is also important for investigating how density, sex ratios, and abundance, may affect egg production and determine the effective minimum spawning stock size. The Panel therefore strongly recommends the continuation of benthic studies. It also supports the suggestion that fishers could be invited to assist in a large-scale long-term programme to deploy settlement collectors and test their usefulness in predicting lobster recruitment. This is still a long way off, and it should be stressed that this would supplement, not substitute for, existing assessments.

Section 7. Conclusions and Recommendations

Based on this evaluation of the results and methods presented at the Review, the Panel recommendations for additional studies are listed in section 7 of the main report.

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Report of the Peer Review of Population Dynamics of the American Lobster in the Northeast

Preface

This review was jointly sponsored by the National Marine Fisheries Service (NMFS), Office of the Senior Scientist, and the Atlantic States Marine Fisheries Commission (ASMFC). We thank all who participated in this review, especially the members of the Review Panel who contributed their time and expertise to this review and the scientists who presented information from their own research to the Panel. Except for the brief Background to the Review below and the Annexes at the end of the report, this report was written in its entirety by the Review Panel.

Background to the Review

The principal fishery for American lobster (*Homarus americanus*) in the United States extends from coastal Maine through southern New England and Long Island Sound. Landings increased from about 15 thousand mt in 1964 to more than 30 thousand mt in 1994. More than 85 percent of the landings in 1993 were from the territorial waters of individual states, with the remainder from the U.S. Exclusive Economic Zone. In 1993, 97 percent of the landings were taken in traditional lobster pots or traps, with the remaining 3 percent by trawls or in fisheries directed toward other species. The portion of the catch by trawls declined from more than 12 percent of the total landings in the 1960s and early 1970s to less than 1 percent in 1992 and about 2 percent in 1993.

Some scientists and fishery managers are concerned about the health of the lobster resource despite the increases in landings over the last three decades and the record high catch in 1994 (30,126 mt). These concerns focus on the intense fishing pressure applied to the resource and its potential long-term effect on recruitment. The record catches may be attributable to a variety of interacting factors, such as increased recruitment and increased fishing effort coupled with an expansion of fishing areas and favorable environmental factors. If environmental factors favoring high lobster production and recruitment become less favorable or even unfavorable, the potential exists for the fishery to collapse with a severe economic impact on the region.

Others, both scientists and the fishing industry, argue that the fishery is essentially healthy and that the major problem is one of increased competition for catch within the fishing industry itself. One theory, proposed to explain the increases in landings, is that the large number of traps (between 2.5 and 3.3 million) constitute an expansion of lobster habitat and provide protection for young, undersized lobsters. In addition, the great quantities of bait used in the traps may provide a food subsidy for young lobsters.

A number of management measures have been implemented since adoption of the American Lobster Fishery Management Plan in 1983 that were intended to improve lobster recruitment and survival. These measures included requirements for escape vents in lobster pots, increases in minimum size, and protection of v-notched females. However, due to the relatively long period of time between larval settlement and recruitment to the fishery (6-8 years), the impact of many management measures is not immediately observable and their effect on the fishery may not be seen for several years after implementation. In addition, confounding effects of multiple management measures, environmental changes, and changes in the fishery over time may make it difficult to determine the effectiveness of particular management decisions.

The most recent lobster stock assessment conducted in 1993 concluded that the lobster fishery, as a whole, was overfished. Amendment 5 to the American Lobster Fisheries Management Plan published in June 1994 revised the definition of overfishing for the species to specifically include the issue of recruitment overfishing. The current definition is: "The resource is recruitment overfished when, throughout its range, the fishing mortality rate (F), given the regulations in place at that time under the suite of regional management measures, results in a reduction in estimated egg production per recruit to 10 percent or less of a non-fished population [$F_{10\%}$]." This definition was adopted as a precautionary measure and means that fishing mortality (F) above the $F_{10\%}$ rate does not necessarily imply that a stock collapse is imminent, but rather that fishing mortality rates below $F_{10\%}$ maintain a spawning biomass with a low risk of collapse. However, under U.S. law, Fishery Management Councils cannot operate a fishery with an F above the overfishing definition over the long term. Fishing mortality rates for the Gulf of Maine and Southern Cape Cod to Long Island Sound stocks were estimated to be 0.65 and 1.47, respectively. Corresponding F_{max} or $F_{10\%}$ estimates for these two stocks are 0.62 and 0.68, respectively, and thus, by definition, are overfished, the latter one particularly so. The Georges Bank and Offshore stock has an estimated F between 0.24 and 0.51 and is considered to be at least fully exploited.

Decades of overfishing, according to the existing definition, accompanied by continued increases in landings without recruitment failure has been perceived by many to be a contradiction. Thus, alternate hypotheses are needed to attempt to explain why Northeast lobster stocks have not experienced recruitment failure despite continued high fishing mortality rates and record high fishing effort.

Goal of the Review

The goal of the review was to provide managers of American lobster and scientists conducting research on American lobster with a set of testable hypotheses that could resolve some of the fundamental questions concerning productivity and recruitment of the species. In addition, the overfishing definition for lobster was to be re-examined in light of other findings of the review.

Scope of the Review

The review focused on population dynamics and ecological factors affecting productivity of lobster. The overriding theme of the review was to determine whether or not existing information and analyses supported the current interpretation of lobster productivity. The review considered fishery-dependent and fishery-independent data and biological and ecological information.

The Review Panel

Nominations for membership on the Review Panel were submitted to the Atlantic States Marine Fisheries Commission and the National Marine Fisheries Service by representatives of the lobster fishing industry. In addition, geographic distribution was considered so that the Panel would include experience as broad as possible with population dynamics, crustacean biology and ecology, and assessment and survey methodologies.

Report of the Peer Review of Population Dynamics of the American Lobster in the Northeast

Section 1. Introduction

This report describes the activities, views and conclusions of an independent Peer Review Panel convened to investigate the Population Dynamics of the American Lobster in the Northeast. The Review was convened by the Office of the Senior Scientist for the National Marine Fisheries Service, at the request of the Steering Committee for the Northeast Regional Stock Assessment Workshops (SAW).

The Panel comprised:

Dr. R.C.A. Bannister (Chairman)
Directorate of Fisheries Research, Fisheries Laboratory, Lowestoft, United Kingdom
Dr. L. Botsford
Deptartment of Wildlife, Fish and Conservation, University of California, Davis, USA
Dr. R. Mohn
Deptartment of Fisheries and Oceans, Dartmouth, Nova Scotia, Canada
Dr. V. Restrepo
Rosenstiel School of Marine and Atmospheric Science, University of Miami, USA
Dr. P. Sale
Department of Biology, University of Windsor, Ontario, Canada

The credentials of the Panel members are presented in Annex 1, but briefly they are scientists experienced in the assessment and management of crustacea, other shellfish, and finfish stocks; the biology and ecology of the lobster; the ecology of finfish; and the development of overfishing definitions. The members are independent of the American lobster stock assessment and fisheries management processes.

The Peer Review

The Review was held from 25-29 March, 1996. It comprised a two day Open Session at Warwick, Rhode Island, a three day Closed Session at the Northeast Fisheries Center, Narragansett Laboratory, and subsequent correspondence. During the Open Session, scientists from the National Marine Fisheries Service, individual State agencies, and from Ocean Science Centres, presented review papers on lobster population dynamics, biology and ecology, and on the results of the 1993 assessments carried out using fishery dependent and fishery independent data. Presenters were questioned by the Panel and the audience after each paper. On the second afternoon, representatives of the fishers gave their views on the state of the fisheries and on conservation priorities, and the day ended with a short open discussion between the Panel, presenters and audience members. Panel members were provided with a portfolio of key science papers and reports (listed in Annex 2), copies of the presentations (listed in Annex 3), and also with some additional data requested following the Open Session. Annex 4 lists those who attended the Review.

Acknowledgements.

The Panel records the following thanks:

1. To all presenters, for their talks and their open handed approach.
2. To NMFS, Woods Hole, and in particular Dr. M. J. Fogarty, for cooperation throughout.
3. To Dr. M. Sissenwine, Dr. J. Witzig, L. Lauck and B. Rootes of the NMFS Office of the Senior Scientist, Silver Spring, for their detailed work in organising the Review and assisting the Panel.

4. To Dr. K. Sherman and staff for accommodation and help during the Closed Session at the NMFS Narragansett Laboratory.

Goals and working methods.

The Panel identified the following goals:

1. Review the validity and utility of the current assessment, and its implications for management advice, having regard to the underlying biology and life history of lobster, the available assessment and biological data, and the current definition of overfishing. The assessment was that outlined in the Report of the 16th Northeast Regional Stock Assessment Workshop (16th SAW), Stock Assessment Review Committee (SARC) Consensus Summary of Assessments. The Panel refers to this as SAW 16. The conclusion from SAW 16 was that the lobster stock is overfished, and the overarching question for the Review is whether the Panel supports this conclusion.

2. Examine the temporal and spatial scale of the increased lobster landings; evaluate evidence available for interpreting the most likely causative factors; and assess the relevance of the phenomenon to the present assessment.

3. Consider whether any revision of the overfishing definition is needed.

4. Summarise the present state of studies on the early benthic phase, and assess their implications for understanding lobster population processes and predicting population trends.

5. Consider the questions put to the panel by the Commissions, and fishermen, including in particular the question of whether managers should still be concerned about the possibility of future recruitment failure.

6. Consider the need for additional scientific studies.

The Panel discussed a wide range of issues, and scrutinised the data available in the reports and presentations. It did not have the resources, nor the mandate, to make any individual reassessments, or quantitative reviews of data. Therefore, many aspects of the presentations had to be accepted as they were presented, and our conclusions must be interpreted in this light. In relation to the increase in lobster landings, the Panel reviewed all materials presented, some additional background documentation, and performed limited data evaluations. It formed opinions on the principal issues and causes, but the main concern was to determine how this influenced the interpretation of the status of the stock, rather than to provide a definitive statement about the underlying cause.

In order to comment effectively on what has been done, and to make clear the basis of the Panel's views, this Report refers to the key findings of SAW 16, and some of the presented papers, but it must be read in conjunction with the background reports and literature as there was simply not enough time to provide a completely stand-alone summary of all of the material available.

In the text of the Report, sections which are underlined represent conclusions which the Panel wish to emphasise, and sections in italics represent suggestions and recommendations for further work which are particularly noteworthy. Most of these are included again in the specific section dealing with Recommendations.

linked by dispersal. The subpopulations run together continuously, but dispersal scales are probably smaller than the spatial extent of the population, and so mixing is probably incomplete. The spatial structure has implications for assessment, but also for the risk of collapse due to overfishing. On the first point, the population is heterogeneous in terms of life history characteristics such as growth rates and maturity schedules, which vary over space, and which influence estimates of egg production. Harvest mortality rates also vary spatially. They were initially highest in the near shore area, before effort expanded to the offshore canyons in the 1970s, but anecdotal evidence indicates that in the last ten years or so high harvest rates have extended much further from shore, from say 10 nm to 40 nm. Secondly, from the overfishing viewpoint, the metapopulation structure is likely to be an important factor contributing to the ability of lobster populations to persist while enduring high localised harvest mortality rates. Intuitively it is sensible to suppose that metapopulations are inherently more persistent because extinction of local subpopulations can be compensated by either migration or larval subsidy from other subpopulations (Pulliam 1988, Quinn and Hastings 1987). A mechanism whereby a single subpopulation supplies the necessary recruits to other subpopulations which are no longer self-sustaining because of intense harvest, could lead to a false sense of security. If effort shifts to the "source" population, the whole metapopulation could collapse with little warning. For the lobster, where offshore areas were not intensively fished historically, but have been increasingly exploited over the past 10 years, it is important to consider this possibility. A preliminary theoretical model of two subpopulations, which mimics the inshore-offshore links in the lobster (Fogarty, pers. comm.), illustrates quite clearly how, "a larval subsidy from offshore to inshore at even low levels can permit persistence under intense exploitation and could explain, in part, the apparent resilience of coastal stocks to very high fishing mortality rates". Further, "contribution of larvae from the offshore to inshore groups results in a reduction in the resilience of offshore stocks to exploitation, particularly for the case of little or no return migration from inshore." Given the increase in offshore effort as the nearshore fishery has moved seaward, there may well have been a decline in eggs-per-recruit and in actual egg production over the past 10 years. *It would obviously be helpful if the contribution of different areas to egg production could be assessed, and the whole question of metapopulations reviewed in depth. In discussing this, the Panel noted that on the basis of hydrography it could be sensible to explore the benefit of extending the Gulf of Maine assessment area to include the Bay of Fundy and Southern Nova Scotia.*

During the presentations the Panel was specifically asked to consider the justification for treating the relatively small Long Island Sound fishery separately, on the grounds that the area is heavily fished, there is little out-migration, and lobsters there mature at a relatively low size (Review presentation by Blake). The Panel noted that the absence of out-migration could be strongly influenced by the heavy exploitation level, and that the larvae data shown for Long Island Sound do not distinguish between larvae from local and more distant sources. *Even so, it concluded that the benefits of incorporating Long Island Sound as an individual stratum in the assessment should be examined. These benefits would likely be in terms of precision and understanding. It does not necessarily follow that there is also a case for extending this stratification to the management level, an aspect which would need to be examined carefully. The question of the identity of lobsters in Southern New England could usefully be explored using genetic methods.*

In conclusion the Panel noted that whilst the tagging and migration data have previously been analysed and presented to describe the broad biological picture, a more spatially explicit subpopulation model would make considerably more demands on such data. *Further analyses by biologists and assessment scientists would be required in order to assess the scope for calculating area-specific transfer rates. To make the most of the available tagging data it could be fruitful to model the sensitivity of recapture data to different stock and migration scenarios, and different fishery distributions and fishing mortality levels. It could be beneficial to attempt to integrate this approach across the American-Canadian boundary.*

Whilst the Panel has noted a number of problems associated with stock definitions, and with the metapopulation question, and has indicated several topics for further consideration, it accepted that SAW 16 scientists had a realistic perspective on the stock structure question, and had made justifiable decisions about how best to handle the data presently available. <u>The Panel found no grounds for disputing this aspect of the 1993 assessment.</u>

Section 3. Stock Assessment

The Panel evaluated the lobster assessment carried out by SAW 16 using data representing the period from 1980. The results were examined in the context of

a. conclusions about the overfished state of the stocks, as presented by National Marine Fisheries Service and individual State scientists;

b. comparable concerns expressed by a majority of the fishers present about the large amount of fishing gear being used and deployed over an increasingly wide area of the stock;

c. queries raised by some fishers, scientists and legislators, as to whether recent increases in landings and in stock abundance data, are grounds for challenging the validity of the assessments and its management implications.

3.1 Historical Perspective

The present assessment has to be seen in the context of the long term trend in U.S. lobster fishery landings, as described in for example Figure 2b of Fogarty (1995). This illustrates

a. the long downward trend in landings from 1880 to the 1930's as the early fishery developed,

b. an upward step in the 1940's followed by a very slow rise to the early 1970's,

c. the recent phase in which landings increased progressively from the mid-1970's to reach a historical high point in 1990.

Landings in Maine, the principal fishery, show broadly the same pattern but with a more convex trend prior to 1970. The trend in Canadian landings (Figure 2a of Fogarty 1995) is also similar, albeit more variable in the intermediate phase from 1930 to 1970. Despite the inception of an offshore trawl fishery since 1950 (whose landings are probably under-recorded in recent years) and of an offshore pot fishery since 1970, the principal source of U.S. lobster landings (SAW 16, Figure D3) is still the inshore pot fishery, but as already noted landings from offshore have undoubtedly increased in recent years.

Scientifically, the U.S. lobster stock has been considered to be very heavily exploited for many years. No assessment data seem to be available for the early phase of the fishery, but Fogarty (1995) cites evidence from Gould (1841) and Goode (1887) that at that time the average weight of lobster being caught was 4 lbs and that lobsters of 8 to 12 lbs were common. Data for the 1970's show that by then, however, a very substantial deterioration in the available size range had occurred. Thus Anthony (1980) showed that the coefficient of total mortality, Z, estimated by length frequency analysis for seven coastal and one offshore area, averaged the very high value of 2. Fogarty (1980) showed that this value was well beyond the maximum of the yield per recruit curve, so that the stock was considered to be growth overfished. This is not the same definition of overfishing used today, and in any case such estimates may have been biased by well known problems attributable to the estimation of growth rate, the influence of selection and behavioural interactions on length frequency data from traps, and the possible effects of emigration from inshore to offshore areas. They nevertheless illustrate that there was a very high level of exploitation, and they set a yardstick against which to judge the most recent results.

3.2 Stock Assessment Methods and Results

The data routinely collected for the U.S. lobster comprise landings and effort, port-based size frequency data, and also in some areas LPUE and size frequency data from sea-sampling. Data are collected by individual States, and collated nationally for assessment purposes. In addition, the National Marine Fisheries Service, and some States, carry out a bottom trawl survey for groundfish, which also obtains catches of lobster. These are used to derive fishery-independent lobster abundance indices. Using landings data and the bottom trawl survey data, SAW 16 calculated up-to-date estimates of fishing mortality using a DeLury (so-called) population model introduced at SAW 14 (Conser and Idoine, 1992). SAW 16 also evaluated published length cohort analysis results calculated from length frequency data. The Panel discussed these methods and their results in some detail in order to evaluate the conclusions reached by SAW 16.

3.2.1 The DeLury Model

In the DeLury model of Conser and Idoine, input data are annual landings, and relative abundance indices from the bottom trawl survey. These are used to calculate the abundance of pre-recruits and post-recruits, defined by specific size ranges, and thence to estimate the mortality between these two stages. This is analogous to an age structured model with only two 'age' classes. Advantages are that the model avoids some of the bias associated with trap data, it uses fishery-independent data, and it makes no assumptions about growth, age or size of lobsters after recruitment. Further, it allows for both process errors (in survival) and observation errors (in relative abundance). The latter can be particularly advantageous when there are inter-annual fluctuations in natural mortality. On the other hand, results depend on what assumption is made about the selectivity of the bottom trawl for pre-recruits relative to post-recruits. Also, in relation to the overfishing definition, it suffers by considering all fully-recruited animals as a lumped group, which cannot be disaggregated accurately into length classes, so that the relative contribution of different length groups to reproduction cannot be ascertained. Consequently, fishing mortality rates in the the egg-per-recruit model, which is length structured, do not map directly to those calculated by the DeLury model. *At current levels of exploitation, such difficulties may be minor, and have little effect on the present assessment,* but at low exploitation rates, the distribution of abundance-at-length would be expected to spread out, and the computation of adult egg production from a single size class could be problematical. *Long term it would therefore be helpful to explore alternative methods that better account for size and age stages.*

SAW 16 shows that the current stock assessment is still exploring the likely robustness of the DeLury results to problems posed by the quality and representativeness of the bottom trawl survey data, the spatial structure of the population, and the assumption about survey gear selectivity for the pre-recruit size group. Results are affected by the spatial distribution of the survey data, and by the present inability of the current model to accommodate multiple survey indices. The present assessment uses Northeast Fisheries Science Center (NEFSC) survey data for Maine and for Georges Bank, plus a Rhode Island State survey for the SCC-LIS area. For Maine, the NEFSC survey is a consistent long-term series, but SAW 16 acknowledged that because of the rough bottom, survey stations were located in 'relatively deep water' (not defined specifically) and it also conceded that although the Massachusetts State survey data were not used they were collected by a gear which might well catch lobsters more efficiently than the NEFSC gear. Similarly the SCC-LIS assessment did not incorporate data from the Connecticut survey. The Panel could not evaluate whether exclusion of the inshore grounds in Maine is likely to have caused bias, *but suggests that this be investigated in the future*, particularly as the abundance trend in the Massachusetts survey data (SAW 16, Figure D6) appears to show none of the increase found in the NEFSC Maine data (SAW 16, Figure D5). *If the DeLury model could be adapted to include multiple indices*, some of these problems could recede, although the additional difficulty would then arise of determining the relative selectivities and weightings for the different indices. In the short term it might be possible to explore this problem by comparing results for smaller assessment areas based on the State surveys, and subs-sets of the NEFSC data, but this would be complicated by the question of migration, and the difficulty of interpreting how results for smaller areas relate to the level of exploitation overall. The problems posed by spatial structure are illustrated by the way different data inputs affected the GBS-O assessment. Different results were obtained from the different spatial combinations used in the SAW 14 and SAW 16 assessments, and also when SAW 16 attempted to make an integrated inshore/offshore assessment based on different combinations of landings, selectivities for the two size groups, and the NEFSC and Rhode Island survey data.

The SAW 16 assessment examined the effect of two assumptions about the relative trawl selectivity of the pre-recruit and recruit size groups, and final results for the Gulf of Maine were obtained using bootstrap methods. The Panel considers that these sensitivity analyses are a useful tool which could be extended to, for example, the sensitivity of DeLury results to the effects of changes in compliance with catch reports through time, or the choice of natural mortality, keeping in mind that M should then also be changed in the eggs-per-recruit model, so that a fair comparison is made against the overfishing definition. More insight can be obtained from simulation experiments. Assessment conclusions would obviously be strengthened if DeLury model estimates were found to be robust for departures from both implicit and explicit assumptions. The following lists some issues that the Panel considered, with annotations on priority and a time horizon:

a. Uneven lobster and effort distribution within a stock unit (inshore-offshore) over time. High priority, 1 year. This may help elucidate whether more accuracy can be gained from further dividing stock subunits.

b. Distribution of the fishery-independent sampling gear over time, relative to (b). Medium priority, 2-3 years. Examine the pros and cons of random sampling versus fixed stations.

c. Movement in and out of stock units. Medium priority, 2-3 years. The impact of movement between broadly-defined stock units may be larger when fishing mortality rates are lower. At current F levels, the fishery depends largely on recruiting cohorts and transfer may be negligible.

d. Trends in the relative selectivities of the survey gear over time and space. Medium priority, 2-3 years. The relative selectivities are not necessarily fixed through time and it would be interesting to understand the consequences of hypothesised systematic changes.

3.2.2 Estimates of Fishing Mortality from the DeLury Model

For the period from 1980, the DeLury model was used to estimate the mortality of pre-recruit and fully recruited size groups defined on p 81 of the SAW 16 Report, based on the bottom trawl survey indices described on pp 81-82 of the SAW 16 report. For female lobsters in the Gulf of Maine, the NEFSC trawl survey indices of pre-recruit and fully recruited lobster abundance increased but the estimated fishing mortality rate also increased, from 0.44 in 1983 to a mean of 0.65 for 1989-1991. For the SCC-LIS area the trawl survey indices of female lobster abundance increased, especially for pre-recruits after 1986, but estimated female fishing mortality was very high, averaging 1.47 for 1989-1991. This was a new analysis. For the GBS-O area, the trawl survey index for pre-recruit females increased, but the index for fully recruited lobsters fluctuated without trend. GBS-O fishing mortality on females increased then decreased. Mortality for 1988-90 ranged from 0.24 to 0.51 for two assumptions about pre-recruit selectivity. SAW 16 considered the latter assessment to be somewhat tentative, because of sensitivity to the spatial combination of the input data. Overall, stock biomass has been increasing, but so also has fishing mortality, which is extremely high in coastal southern New England, high in the Gulf of Maine, and moderate in the GBS-O area. *The Panel considered that in future the degree of uncertainty associated with the DeLury results should be measured as a matter of routine*, but it accepted the present results as an adequate description of the overall trends in abundance and fishing mortality, and found no obvious grounds for disputing the findings.

3.2.3 Length Cohort Analysis and its Results

When representative length frequency data are available, length cohort analysis (LCA) has traditionally been used widely in crustacean assessments. LCA results are sensitive to the growth estimates, however, and size distributions obtained from trap data may be biased by recruitment fluctuations, emigration, and trap selectivity. Size frequency data may also be biased by size-specific shelter availability, and behavioural interactions affecting entry and escape at the trap. Intuitively, the method appears to be attractive for investigating fishing mortality trends over long historical time periods, and for comparing the state of exploitation on lobster between different stocks where fishery independent data are not collected, but in practice these potential uses tend to be qualified by the fact that it is not always clear whether size distribution data from fishery sampling are sensitive to changes in exploitation over time. Simulation results quoted by the SAW 16 report showed that very large numbers of measurements would be needed to demonstrate small significant differences in size distribution.

The Panel were presented with results from the continuing use of the LCA method by the Lobster Technical Committee of the Atlantic States Marine Fisheries Commission. The Committee estimated F for the Gulf of Maine using length frequency data derived from a combination of port based sampling and at-sea sampling for inshore waters, and a limited amount of at-sea sampling from offshore waters. These results were presented to the Review by Estrella and Cadrin. A sensitivity analysis undertaken in 1992 confirmed existing knowledge that F estimates are fairly robust to assumptions about M and terminal F, but sensitive to von Bertalanffy growth parameters, especially K, hence the incorporation in 1993 of a molt-increment, molt probability growth curve. The Panel accepted the use of the three year moving average to smooth the input length frequencies, and approved the modification of the difference equation to model the catch removal in late summer rather than mid-year.

Based on this analysis, estimated F in the Gulf of Maine increased from 1981 to 1986, then stabilised. The absolute values are in the range 1.2 to1.5 (Figure D 15, SAW 16). Given that new recruits comprise up to 90% of most U.S. lobster landings, and that the size distribution of landings from all areas, especially the most inshore areas, comprises very few size and molt groups, a high F value from this analysis is intuitively reasonable, but the estimated F values are substantially higher than the DeLury values, and do not correlate with them, showing that it is difficult to use the LCA results to calibrate those from the DeLury method. The SAW 16 Report (p97) noted that there is greater concordance between LCA and DeLury results for size 2+, and based on a pre-recruit/fully recruited ratio of 0.5, but it is not yet evident that there is any real understanding of how the two methods and sets of results relate to one another. Since LCA estimates of F are also lower than the length frequency analysis results for the 1970's (Anthony, 1980), there may also be some difficulty in establishing trends across historical periods.

Given that length frequency sampling is relatively easy, and that sea-sampling can target specific fleets, areas, and seasons, stratified sampling should in principle provide an excellent data base for understanding how exploitation has changed among areas, through time, assuming that the LCA can be relied upon. *The Panel therefore feels that work on the use of LCA should continue, but in a structured way, with the specific aim of resolving the utility of the method for analysing time-space differences in fishing mortality, and in particular for resolving differences between the LCA and the DeLury results. In the short term, it may be possible to investigate similarities and differences between area-specific length frequency and catch-rate data, sampled on lobster boats at sea, with the results for sets of stations in the bottom trawl survey, and to assess how these are interpreted by the two methods. In the long term, perhaps, simulation modelling of spatial structure, based on the analysis of transfer rates from tagging recommended in Section 2, could be coupled with simulated effort-related changes in size distribution through time, to provide a basis for testing the validity and compatibility of the LCA and DeLury analyses.*

As discussed, there are advantages and disadvantages to both the length cohort analysis and the DeLury model, and some difficulty in reconciling how these results can be compared. On balance, however, the Panel concluded that because the DeLury method uses fishery-independent survey data, and calculates both fishing mortality and stock size, it gives the most useful results for current assessment purposes. The Panel therefore supports the decision made by SAW 16 to assess the U.S. lobster stocks using this method, but as noted above it also encourages the continuation of research on the utility of the LCA approach.

3.3 Fishing Effort, LPUE, and Stock Abundance

Before discussing the management implications of the present level of fishing mortality, the Panel examined the other information available on the underlying trends in the fishery and the stock. The 1981-1992 DeLury estimates of fishing mortality represent the position at the end of a period of substantial change in the U.S. lobster fishery. In Maine, recorded post-war trap numbers actually increased four-fold, from half a million in the mid 1950's to over 2 million by the late 1980's (Fogarty, 1995, Figure 3, and Krouse, this review). Data presented for Massachusetts (Estrella and McKiernan, 1989) and for New York show a similar proportional increase. In addition the presentation by Krouse for Maine showed that since the late 1960's, immersion time has increased from 2.5 to 3.5 days, mean trap number per boat has risen from 250 to 500, and the proportions of wire traps and parlour traps have increased to 90% and 40% respectively. The presentation by Fogarty also highlighted that various technological innovations (haulers, GPS/Loran, colour sounders) must have increased fishing power, coupled with the advent in some districts of much larger boats capable of fishing more gear and further offshore. These factors were all acknowledged in the presentations made by the fishers speaking in the Open Session. The Panel were left in no doubt that a major increase in effective fishing effort has occurred during the same period as the increase in landings. Even landings per trap haul, a crude landings per unit effort (LPUE) statistic uncorrected for fishing power changes, shows that since1970, LPUE in Maine declined 67% compared to the fluctuating but stable level between 1930 and 1960 (data from Krouse). In Massachusetts, LPUE declined by 50 %, before beginning to increase again (Estrella and McKiernan, 1989, Figure 5).

On the historical scale, lobster fishing effort has risen slowly since the 1900's, then dramatically since the 1970's, and landings per trap haul have fallen in consequence. On the scale of the recent decade, however, LPUE , although low overall, has either remained stable (as in Maine), or increased (as in Massachusetts), at a time of rising effort and high or increasing fishing mortality. This implies that the increase in landings is not solely effort dependent, but must include an additional component, presumably recruitment. This is corroborated by the results of the fishery-independent bottom trawl survey data, and the estimates of pre-recruit and recruit abundance used in the DeLury assessment. Although not originally designed for catching lobster, and although not carried out over the rougher grounds, the Panel accepted the survey results as an unbiased estimate of abundance. Figure 1a shows the trawl survey pre-recruit indices for female lobster for the three stock assessment areas re-plotted on the same scale, and Figure 1b similarly shows the recruitment estimates from the DeLury assessment. Both show a consistent increasing trend from 1979 to 1992, although the trend for GBS-O is less marked than for the other areas. It is important to note that in Maine and Massachusetts, the increase in abundance which started in the late 1970's may have come later than the initial increase in effort, which started in the mid 1970's. The increase in recruitment has therefore contributed to stabilising or increasing LPUE from its otherwise low level.

The Panel recommended that serious consideration be given to the task of investigating how to get more out of lobster LPUE data. At this review it was not possible to calibrate or standardise the various LPUE U.S. fishery, and the effects of increased immersion time, and this should be done. Although the fishers present drew attention to the increased fishing offshore, it was not possible to quantify this using fishery data, which were not disaggregated down to a finer spatial scale. During the presentations, reference was made to several sea-sampling programmes carried out in the individual

Figure 1a. ***Trends in the bottom trawl survey index of pre-recruit American lobster in three stock assessment areas plotted on the same scale, 1979 - 1992.***

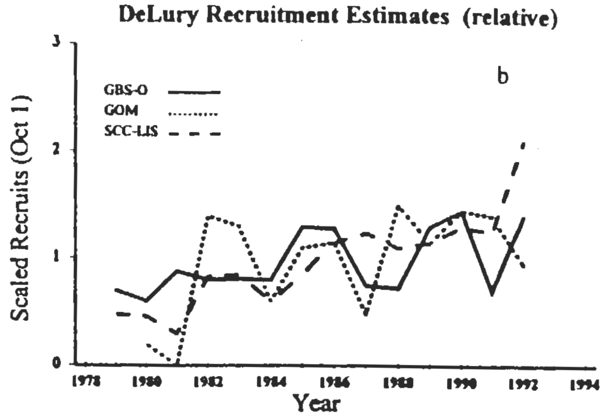

Figure 1b. ***Trends in DeLury estimates of recruitment for the American lobster in three stock assessment areas plotted on the same scale, 1979 - 1992.***

GBS-O is Georges Bank South and Offshore; GOM is Gulf of Maine; SCCLIS is South of Cape Code to Long Island Sound.

States. If standardised area and season specific LPUE data could be obtained from these programmes it may be possible to quantify local trends, and develop some form of Leslie analysis.

The Panel concluded that the available LPUE data for Maine and Massachusetts are consistent with three important trends, namely a long term decrease in stock abundance as fishing effort rose from the developing years of the fishery; a further decrease in stock abundance as fishing effort rose dramatically after the mid 1970's; and then a stabilisation or increase in abundance as recruitment in the most recent decade increased, as measured by bottom trawl survey data. It appears that landings have responded first to the increase in effort, and then to the increase in recruitment. These conclusions refer to aggregated data for the Maine and Massachusetts areas. This interpretation, arrived at independently by the Panel, appears to be almost identical to that contained in NOAA Technical Memorandum NMFS-NE-108, January 1995.

3.4 Stock and Recruitment

For the fisheries scientist and the manager, the critical problem when effort expands is to achieve realistic safeguards against the occurrence of a stock collapse, without curtailing the socio-economic activity of the fishery unnecessarily early. The point is illustrated by considering how the stock-recruitment and the recruitment-spawning stock relationships interact. As presented to the panel by Fogarty, the stock-recruit relationship shows the degree to which declining stock affects the number of recruits produced (Figure 2a). As exploitation increases, these recruits replace less and less spawning stock (Figure 2b). Taken together, the replacement point, where the two relationships intersect, moves steadily towards the collapse point, determined by the slope of the stock-recruitment curve near the origin (Figure 2c). Figures 2a-c are copied from the presentation by Fogarty.

The difficulty is to establish the likely form of these relationships from real data. As with most species,

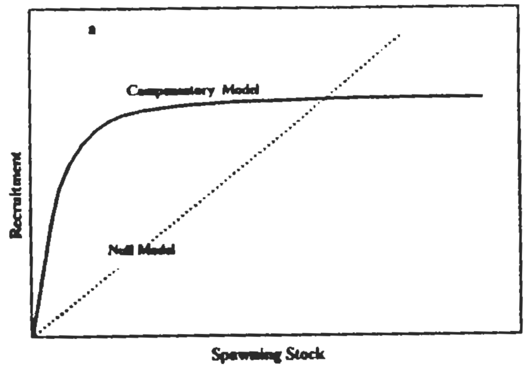

Figure 2a. *Hypothetical curve showing the effect on recruitment of changes in spawning*

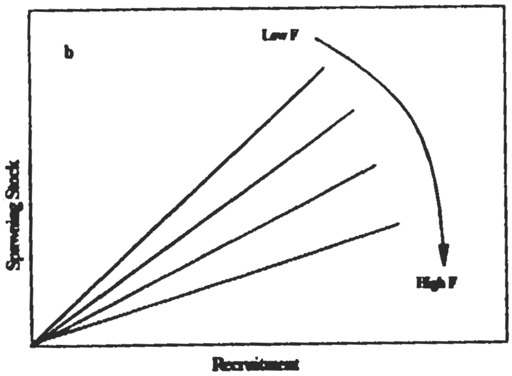

Figure 2b. *Hypothetical curves showing how the spawning stock derived from each recruitment changes with the level of fishing mortality.*

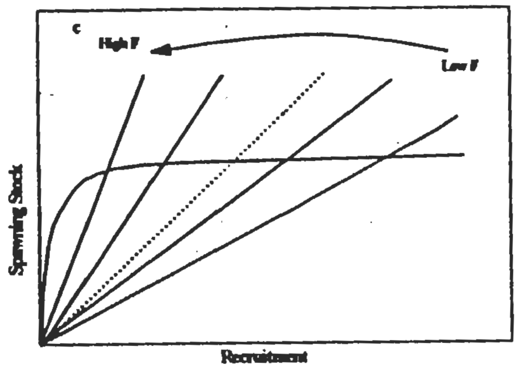

Figure 2c. *Hypothetical curves of the interaction between Figures 2a and 2b, showing how fishing mortalith affects the replacement point.*

Figure 2a-c is from presentation by M. Fogarty, March 25, 1996.

definitive stock-recruitment information is not available for lobsters in US waters, but two sets of data from Canadian waters provide information to show that the relation is likely to be non-linear, involving some form of density-dependence. In one case, data on late stage larvae and subsequent stock size for the Northumberland State, Canada, were analysed by Fogarty and Idoine (1986). They showed that over a wide range the amount of input (stage IV larvae) had very little influence on the resultant stock size, but that very near the origin, when the abundance of stage IV larvae was reduced to about a tenth of the average for the eleven year period, the 6 year lagged stock was suppressed by about a half. A process operating from settlement to recruitment that involves density-dependence is stabilising, in that exploitation can increase substantially before affecting recruitment, but on the other hand if the descending limb of the curve is very close to the origin, and very steep, the effect on recruitment could occur suddenly and without warning, and lead to a rapid collapse.

At the Review, the Panel were given preliminary evidence of a similar relationship, using data on lobster egg production and recruitment for Arnold's Cove, Newfoundland (Ennis and Pezzak, pers. comm., as presented by Fogarty). In these data, recruitment is independent over a wide range of egg production, with the potential for a very steep slope near the origin at an exploitation level of F=2.0, indicating that collapse could occur suddenly. Data for the Bristol Bay Red Crab were also presented to illustrate an actual collapse, which occurred within two years, after a 15 year trend of increasing landings.

Although these examples for the Northumberland Strait and Arnold's Cove areas do not provide a predictive solution for management of the U.S. lobster, their pattern is similar and may well illustrate the likely general form of the lobster stock-recruitment relationship. They serve to focus the mind on the inherent dangers of high exploitation rates. For the U.S. lobster the position is further compounded by the metapopulation problem discussed in section 2, where the possible critical role of an offshore subsidy was postulated.

3.5 The Overfishing Definition

The previous paragraphs illustrate just why an overfishing definition is necessary. For the lobster, it is likely that the threshold where egg production falls so low as to affect recruitment, can only be investigated with real data by allowing the level of exploitation to reach very high levels near the collapse point. Even then a collapse would only be detectable five or six years later because of the time taken for lobsters to reach legal size. Further, detection in real data will be masked by natural fluctuations in recruitment resulting from environmental variation. The justification for an overfishing definition is that it is just too dangerous and costly to wait until recruitment collapses, then try to reduce effort and rebuild the stock. It is much more prudent to estimate a safe level of fishing mortality on a pragmatic basis, and then avoid going below that level. Although there is a well developed theory underlying the setting of overfishing thresholds, the essential basis for these thresholds is comparison with other fisheries or similar stocks. Comparisons among similar species have shown that an F level that results in 30-40 % EPR (i.e. egg production per recruit which is 30-40 % of that at zero fishing mortality) is an appropriate level for finfish, and that F values corresponding to 5% or 10% EPR ($F_{5\%}$EPR, or $F_{10\%}$EPR) are appropriate for many crustaceans. Such definitions are widely applied in the management of fisheries in the U.S., and the Panel supports the adoption of such an overfishing definition for the lobster.

We stress that the overfishing F threshold is not the target level at which a fishery should be managed. It is specifically identified as the 'danger' level which, when approached or reached, should give rise to management action to move the fishery away from the danger area. The benefit of taking such action is not necessarily any overt benefit in yield, particularly in the lobster fishery, where the mortality rate is so far in excess of the maximum on the yield per recruit curve. The benefit is the reduction or avoidance of the risk of collapse, and the preservation of the existing social and economic order.

3.6 Egg Per Recruit Model

For lobster the overfishing reference point is defined by the egg per recruit model. The Panel supports this approach since when there is no egg production, all can agree that there will be no recruitment. Calculation on a per recruit basis makes sense since this is more akin to a per capita growth rate, and removes the problem caused by recruitment variation occurring independently of exploitation. Expressing the overfishing definition as a percentage of unfished egg production allows us to compare in a standard way different species with different growth, maturity and fecundity schedules, or different stocks of the same species.

The specific model used for the American lobster is that of Fogarty and Idoine (1988). The model calculates the egg production which would be obtained at different levels of fishing mortality, taking into account discontinuous size-specific growth, and the interactions between growth and reproduction. The model has been in use for some years and is adopted for crustacean fisheries assessments throughout the world. The SAW 16 Report indicates that the model was modified for the recent assessment to include new growth data, and, in the case of the Gulf of Maine assessment, to convert results from nominal F to realised F. This latter adjustment makes the model more realistic for this fishery. Nominal F is used to calculate a catch, which is then decremented to take account of berried female protection, an assumed compliance rate for the discarding of v-notched females, and the maximum size limit. The decremented catch is then used to calculate the realised F. The level of compliance with the voluntary v-notching measure is not known, and this needs further information, but a sensitivity analysis showed that the $F_{10\%}$ EPR reference point is relatively insensitive to this factor, although in the actual assessment a 50% compliance was assumed.

3.6.1 Variability and Error

For a given lobster substock, considerable individual variability exists in growth and reproduction, and it is important to account for variability in the estimation of the overfishing benchmark because of the interactions between these two processes. The present model accounts for variability only partially, by means of annual length-specific molt probabilities. Some aspects of natural variability such as multiple egg extrusions are not accounted for, and it is not known how much this would affect the estimation of the overfishing threshold. Several means of better accounting for process errors are plausible (e.g. individual-based models). The Panel did not discuss this in sufficient detail to make a specific recommendation, but *it suggests that lobster assessment scientists should certainly discuss the need to incorporate variability, and the best way of achieving this.*

The other important component of variability is assessment error. As with the DeLury stock assessment model, the Panel considered that it was important to conduct error analyses for the EPR model, since some of the growth and reproduction relationships used for the various substocks were derived from limited data sets. Bootstraps or Monte Carlo simulations would be useful to infer the precision of the EPR estimates corresponding to a particular fishing mortality rate.

Uncertainty is an important consideration when it comes to the practical use of the $F_{10\%}$ EPR benchmark. The perception of the degree of overfishing depends not only on the point estimates of realised and benchmark fishing mortality rates, but also on the variance associated with those estimates. Whether a 50%, 75%, or 99% probability of overfishing is "acceptable" depends on the acceptable level of "risk" to be taken, above and beyond the basic nature of the overfishing definition itself. Such a level of risk is not defined explicitly for American lobsters and *the Panel considers that it would be advantageous to define one. This possibility should be looked at by managers in consultation with scientists.*

3.6.2 Larval Subsidies

An understanding of the nature and degree of the sub-population linkages is required to model this resource optimally. It has already been noted that offshore spawners may provide a recruitment subsidy which sustains the high level of exploitation inshore (Harding and Trites, 1988), although SAW 16 suggests that the apparent high inshore mortality could be in part an artefact of the migration of recruits away from the fishing grounds, so that exploitation is not really as high as indicated by LCA or the examination of length frequency data. The picture is further confounded by the distribution of larvae, which may be non-local. The two-subpopulation model of Fogarty, which explored aspects of these relationships, was already noted in Section 2. *Until the resolution of the metapopulation dynamics is accomplished, it is difficult to take these concepts into account in the EPR model, but thought should obviously be given to these aspects.*

In current practice, the word "recruit" is interpreted as a lobster that enters the fishable population (above the minimum size) each year. Both the EPR computations and the stock assessment models use this definition, so that the realised fishing mortality rates in the fishery map directly to the benchmark EPR computations. There is, however, evidence that particularly in warmer waters some females below this recruitment size produce eggs, and as currently computed the egg-per-recruit model ignores their contribution to reproduction. If all recruits into the fishery came from a single year class, this would imply that the current computation of eggs per recruit is conservative for measuring overfishing with respect to the threshold. In other words, EPR values resulting from a given fishing mortality rate are lower than if the computations allowed for reproduction at smaller sizes. This does not imply that the risk of overfishing would be removed, but rather that this risk would be somewhat less than estimated.

The role of this sub-legal subsidy was identified by Graulich in a presentation on the Long Island Sound EPR model. Lowering the size at which recruits are defined should be carried out carefully, however, because the size corresponding to "recruits" should be the same in both the EPR and the assessment model. Care would therefore be needed when comparing results from different areas where the definitions of recruitment are distinct. An additional problem is that of not being able to estimate accurately the reproductive output from a single year class, given the variability in growth which results in recruitment spreading out over several years.

For practical purposes, the Panel accepts the present definition of overfishing, and the current egg per recruit model, *but recommends that careful thought should be given to how the various points raised above may influence the measurement of overfishing. In particular, it is important to include the reproductive output from sub-legal females in future computations for areas where this is clearly warranted by the population structure, growth, and maturity schedules. The incorporation of such change into the EPR model must be carried over to the assessment model as well, however, so that the models are compatible.*

3.7 Stock Status

The state of the U.S. lobster stocks was assessed by SAW 16 in July 1993. Fishing mortality rates calculated from the DeLury model (as described in Section 3.2.2) were compared to the $F_{10\%}$EPR threshold, and to F_{max} from the yield per recruit curve. For the Gulf of Maine the benchmarks are the realised F values assuming 50% compliance for v-notching. These results (SAW 16 table D 23) are listed in Table 1.

For the Gulf of Maine the SAW 16 assessment used a bootstrap method to estimate that there was roughly an 80% chance that the rate of overfishing was being exceeded. As noted previously these confidence bounds could be investigated further for all the areas.

The nominal results show that in all three stock areas F is well in excess of F_{max} and hence the stocks are technically growth overfished. In relation to recruitment overfishing, the average F for 1989-91 was much higher than the $F_{10\%}$ biological reference point for the South of Cape Cod-Long Island Sound area, moderately higher in the Gulf of Maine, and approximately equal for Georges Bank South and Offshore. SAW 16 notes that 'the Gulf of Maine stock currently generates about 71% of annual landings, while the SCCLIS area contributes about 14%. Since both of these stock components (contributing 85% of the landings) are determined to have fishing mortality rates in excess of the overfishing level, and the Georges Bank-Southern New England offshore area is near the overfishing level, the aggregate resource is determined to exceed the reference overfishing level'. It should be noted that for the Gulf of Maine, the degree of overfishing defined by using the DeLury results is less than that indicated if the

Table 1. Benchmark fishing mortality rates for three stocks assessessed by SAW 16.

Area	$F_{10\%}$EPR	F_{max}	Mean F '89-'91
GulfofMaine	0.52	0.29	0.65
Georges Bank S-O	0.44	0.15	0.24-.051
S. Cape Cod-LIS	0.68	0.38	1.47

length cohort analysis results are used (F=1.36, compared to the $F_{10\%}$ EPR of 0.52).

The Gulf of Maine and the SCCLIS assessments can be considered to be reasonably definitive, and only the Georges Bank S-O assessment to be somewhat tentative. The Panel found no substantive grounds for disputing the SAW 16 findings, from which it follows that according to the current definition the U.S. lobster stock is overfished. This result was obtained against the background of the dramatic increase in fishing effort which has taken place since the 1970's. Fishing mortality estimates from the DeLury assessment model indicate that over a wide area of stock, fishing is removing a large proportion of each recruit group as it enters the fishery. Even in the area of Georges Bank South and Offshore, where fishing mortality is more moderate, exploitation has increased and is affecting a part of the stock which is conceivably a source of recruitment subsidy to the hard pressed inshore area. The seriousness of the EPR results is underlined by data presented to the Panel on the size distribution of lobsters in Maine, Massachusetts, Long Island Sound, and New Hampshire. In all cases the size distribution is clustered closely on either side of the legal size limit, and a very large proportion of the landed size range occurs within one or two molt groups of the minimum size, which is itself very close to the mean size of first maturity. Except in the offshore areas, egg production is therefore still predominantly dependent on small animals, and the risks from overfishing, identified on numerous previous occasions, remain. The Panel recognises that, as discussed in Section 3.3, LPUE and stock survey data show that over the last decade stock abundance has increased from its previous low level, and this aspect is discussed in the next section, but irrespective of this, the present fishery is still removing a high proportion of each recruitment.

Section 4. Changes in Abundance

Three types of observation represent the principal evidence that there has been an increase in lobster abundance, namely the improved landings in the 1980's and the 1990's, the stable LPUE at a time of increasing effort, and the increase in the survey index, especially for pre-recruits. In order to explain the changes, at least three factors need to be disentangled. Firstly, as shown in Section 3.2, fishing effort in the U.S. has increased substantially, and a substantial component of the landings increase in the U.S. must be effort-related. This could be confounded, at least partly, by changes in the spatial distribution of stock and the fishery. Fishers have stated that the fishery has expanded into offshore areas, and the DeLury estimates show that fishing mortality for the GBS-O area has increased. If effort has spread into a relatively unexplored region landings could improve while the actual resource is being depleted. As noted previously, testing this possibility using landings and LPUE data is compromised by the lack of standardised data, and by the lack of historical information on the spatial distribution of the fishery. Finally, however, the bottom trawl survey for U.S. waters does seem to show that in the 1980's a real increase in abundance is taking place in all the survey areas, and it is desirable to explain the cause of this increase, and how much it has contributed to the landings increase.

A critical observation is that the increase in lobster landings, as shown by aggregated national data, is common to both the United States and Canada. The widespread geographical nature of this trend was illustrated in more detail in the presentation at this Review by Drinkwater et al, using principal component analysis. For 34 statistical landing areas an upward trend in landings since 1980 explained 59% of the combined variance, representing areas across the geographical range from Southern New England to the Magdalen Islands. A further 9% of the variance was explained by landings which increased in the mid 1980's, but less dramatically, as in the Gulf of Maine and the coastal waters of Rhode Island. Finally, 16% of the variance was explained by landings from eastern Nova Scotia and Northumberland Strait, where lobster landings have, unusually, declined since the 1980's, but still showed a late increase in the late 1980's. Correlations between landings trends increasing distances apart persisted over a scale of 2000 km.(Figure 12, Drinkwater et al.), covering a range of different habitats, fisheries, and management regimes.

Given the very complex ecology of an animal like the lobster, it is perhaps simplistic to assume that one single factor could be responsible for population trends which occur in a wide range of coastal habitats. It might be more likely that a spectrum of factors determines abundance across the various pre-recruit life history stages, that the balance between these differs between regions and areas, and that changes in abundance in the different areas are unlikely to be synchronous. The fact that the landings increase is synchronous over such a broad area does therefore place a significant constraint on any causal explanation, hence the consideration given to the possible effect of some large scale environmental or ecological change. Temperature is an obvious contender, and Drinkwater noted that several studies previously showed a strong relation between temperature and lagged lobster landings for Maine (Dow 1969, Flowers and Saila 1972) and Nova Scotia (Flowers and Saila 1972). He therefore developed models to test whether temperature alone predicted the recent landings increase, but this prediction failed. In fact correlations between temperature trends across increasing distances decayed beyond a spatial scale of 800 km, so that the scales of variability of landings and temperature are therefore different. Temperature did not rise in a consistent way throughout the range of the lobster, and it could not therefore be expected to explain the recent changes in all areas. Further, where temperature did increase in the last decade, the change was no greater than previous changes which occurred in the 1950's and 1960's, when no comparable increase in landings occurred.

For Nova Scotia, however, Drinkwater also made predictions using both temperature and landings the previous year, and a good prediction was achieved. This recapitulates the result for Maine shown in Figure 13 of Fogarty 1995, whose model includes landings, a temperature lagged 6 years to represent the effect of temperature in early life, and a zero temperature lag to account for an increase in catchability as water temperature changes. This temperature-landings model can be compared with the analysis of fishing effort, landings, and stock abundance for Maine described in Section 3.2. This showed that in Maine and Southern New England, fishing effort quadrupled in the period running into the increase in landings, at the same time as recruitment, measured by the bottom trawl survey, increased. If landings in the Fogarty and Drinkwater projections are a proxy for effort, a feasible explanation of the overall landings increase in the United States could be the combination of fishing effort and temperature, as illustrated in Figure 9 of Fogarty 1995.

Temperature could affect several aspects of lobster biology and ecology, such as larval survival (Caddy, 1979), growth rate and age of maturation, and also perhaps the extent of habitat which is suitable for survival at settlement, as postulated by Steneck at this review. These biological and ecological effects would require detailed study. For example, the question whether the area of settlement has increased due to a warming of areas hitherto too cold for larval survival and or settlement, could presumably be investigated further using the bottom trawl survey data, and also perhaps historical data, since such a phenomenon should presumably have occurred on past occasions when temperature increased. For the present *it could be helpful to examine carefully the timing of the effort increases, the temperature change, and the abundance change, and then to attempt to model their combined effects on size and age structure, for comparison with the available data, especially that available from sea-sampling. This is important because of the need to distinguish between an effort change per se, an increase in recruitment, and any effort increase which occurred in response to the increase in recruitment.*

An important consideration with an effort-temperature hypothesis is the apparent difference between the United States, where effort is uncontrolled, and Canada, where effort is in principle controlled by a combination of TAC, licence and trap limit. The Canadian offshore fleet has been limited by these means since its inception, while the inshore fleet has been limited by licence and trap limit, although to what extent this has controlled effective effort is not clear. It could be worthwhile to investigate whether there are any important differences between the United States and Canada in the relative contribution of fishing effort and recruitment to the increase in landings in each country. It is therefore desirable to find fishery-independent estimates for the increase in lobster abundance in Canada, and to continue to search for a substantial environmental and or ecological factor which could have affected Canadian stocks. *The Panel recommends that if possible an effort-temperature-recruitment hypothesis should be tested for all the lobster areas, and accompanied by an all-area analysis based on, say, LPUE, in order to investigate the bounds of areas where effort is a contributory factor, and areas where increased landings may be more dependent on an abundance change. Comparing U.S. and Canadian data would be a cornerstone of this approach.*

Interest centres not just on the possible explanation of the changes, but on their implication for management thus a situation where the landings increase is predominantly due to effort increase, compensated to some extent by recruitment, is potentially much more threatening than one where landings increased mainly because of recruitment so that there is no implied additional threat to the stock. On the other hand in neither case is it desirable to allow effort to increase further.

The difference between the U.S. and Canadian management regimes also bears on the hypothesis by some fishers, that increased effort has increased the productivity of the resource by providing shelter or food (bait). Such a hypothesis would have to operate in all areas of the fishery, and so the fact that it could not account for Canada, where effort is limited, appears to be a strong counter argument. Dr. Fogarty (pers. comm.) has suggested that if the increase in landings were due to the direct effect of fishing taking lobsters out of the stock, there should be a correlation between landings and effort with minimal lag, whereas with a productivity change it would take several years for survival to work through to recruitment, and the lag would be longer. His preliminary findings suggest that it may be possible to exclude the hypothesis of there being a substantial lag, but the statistical nature of the analysis is complicated by the non-stationary nature of the time series, and must be considered tentative at this stage (Fogarty, pers. comm.).

The Panel noted that a reduction in predation, particularly on early life history stages, could result in improved abundance. Ctenophores, sculpins and sea bass are reported to prey upon larvae, juvenile and adult lobster respectively. Although not reported at the Review, data may exist to investigate whether changes have occurred in the predator field, but as with temperature, these changes would have to occur across the whole geographical range if they are to explain the observed effect on lobster landings. An alternative question is whether or not an increase in lobster recruitment implies that lobster carrying capacity has increased, or was not previously limiting. This depends on how much of the change has been effort led, how much is due to increased survival, and whether the increase relates predominantly to the known areas of stock, or involves the settlement of juveniles in new areas. In Maine, where LPUE data show that abundance was low prior to the increase in the bottom trawl survey index of recruitment, new recruits may not have encountered a carrying capacity limit. In Canada, where effort may have been less important than recruitment, the increase in landings might imply that carrying capacity is not limiting at current population levels (Miller, 1993). Clearly, the interaction between lobster abundance and carrying capacity is complex, and regional differences may throw light on the processes involved.

The change in lobster recruitment must be compared with other world-wide changes in the abundance of harvested stocks. Several populations throughout the world have shifted between low and high levels on time scales of 20 to 50 years. This has happened to populations of clupeids (anchovy, herring, sardine and pilchard) in several regions (California, Japan and Peru). In some cases these have been associated with shifts in global meteorological and oceanographic conditions. A recent example is the strengthening and shift in position of the Aleutian Low Pressure System in 1977, which has been associated with a shift in salmon production in the North Pacific. The possible North Atlantic implications of this shift have not been explored in detail for the lobster. Clearly, if such a shift were to have been involved, the possibility of its reversal at some future stage must be considered.

The Panel has not been able to reach a definite conclusions about the cause of the change in landings throughout the geographical range of the American lobster, but it does feel that it has clarified some of the options. *For U.S. waters, a combination of increased effort and temperature change could offer a feasible explanation which should be tested further, alongside investigations to identify any component arising from spatial changes in the distribution of effort. If temperature is a factor, it is conceivable that the relevant biological and ecological processes (e.g. molt frequency and or increment, age of maturity, larval survival, habitat extension) could be postulated in detail and tested. A simulation of how effort and recruitment would change the size and age structure of the stock, for testing against observed data, may also be feasible, paying careful attention to timing and spatial aspects, and to the likely asymptotic stock-recruit relationship. It seems important to develop, now, detailed hypotheses about postulated controlling variables, since if these were to reverse, there should be an opportunity to collect additional data over the next decade to test for the reverse trends. The account for U.S. waters must be seen, however, in the context of the situation in Canada, where change in effort may be less important, and an increase in abundance more influential. This needs to be clarified further, and attention given to a* *co-ordinated U.S.-Canadian investigation. The Canadian situation does suggest however that an effort-related productivity change associated with bait seems unlikely. The Panel did not have enough information to comment authoritatively on hypotheses about predation, regime shifts, or larval delivery. It notes in passing, however, that these factors, together with temperature, are very unlikely to affect just the lobster, and that it could be very worthwhile to investigate which other species would be likely to benefit from their effect, and to seek information on those.*

Section 5. Management

For United States waters, the present Review indicates that the most reasonable working hypothesis for mangers is that fishery landings have benefited from the combination of a proven increase in effort, including a component directed to previously lightly exploited offshore stocks, and an increase in recruitment. The relative contribution of the causes has not been calculated explicitly, but the increase in nominal effort was substantial, and compounded by fishing power changes driven by technological factors whose full effects have yet to be assessed. The increase in recruitment may be due to temperature, but the precise effects (i.e. whether on for example growth, age of maturity, larval survival, or extent of settlement) have not been elaborated.

The implication of the fishing mortality estimates measured by the DeLury model, that fishing is removing a major proportion of the lobsters reaching legal size each season, is consistent with all previous assessments, and with the effort increase. Size distribution data also show quite clearly why, at the current level of exploitation, egg production per recruit is low, since except in the offshore area there are very few large females to contribute to egg production. Consequently, present estimates of F exceed the $F_{10\%}$ EPR threshold in the Gulf of Maine, and the SCCLIS area. Given these findings, it is reasonable to take the precautionary view that the GBS-O area could be an important source of larval subsidy to the inshore area, so the fact that F for GBS-O is quite close to the $F_{10\%}$ EPR level for that area is also a cause for concern.

Reduced stock abundance due to the effort increase has been partially offset by recent recruitment, but this does not remove the concern about recruitment. The likely asymptotic nature of the lobster stock-recruitment curve suggests that the recruitment change is unlikely to be an inherent result of lobster demography, and must therefore be environmental or ecological in origin, in which case it can clearly reverse. It would therefore be foolhardy to rely on its continuation to offset effort changes in perpetuity. As Fogarty discussed at the Review, it is easy to conceive of a stock-recruit diagram for a high recruitment regime which sustains a level of exploitation that, when the recruitment regime falls to a lower level, is to the left of the replacement point (Figure 3), and therefore leads in the long term to stock collapse. On this basis a risk-averse management policy should continue to use an overfishing definition based on a per-recruit model, in which case the conclusion of SAW 16, that the U.S. lobster stocks are overfished, remains unchallenged. As already noted in Section 3, fishing mortality is well beyond F_{max} and from this viewpoint the fishery is also making sub-optimal use of both biological and capital resources.

Giving particular weight to the increase in effort which has already occurred, and also to the views expressed at the Review by the fishers present, the above conclusions imply that the risk of stock collapse would be contained or reduced if fishing effort were capped, and legal size increased. It would be prudent to assume that the offshore stocks provide a larval subsidy, and to control the level and pattern of offshore exploitation.

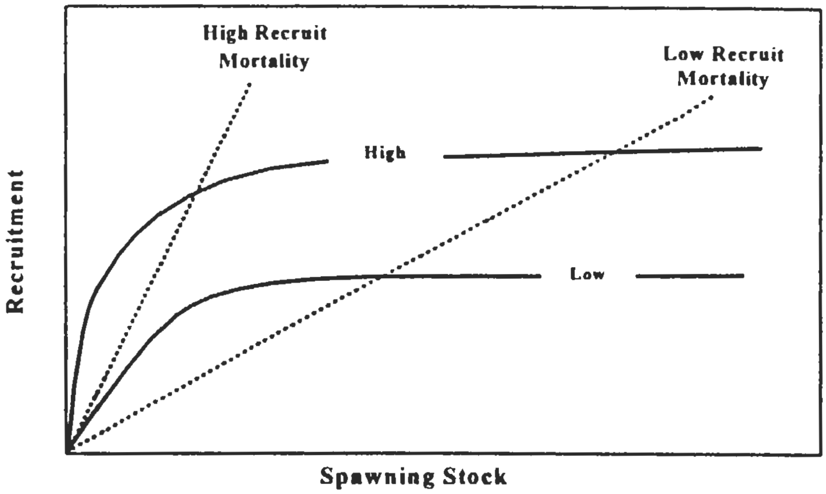

Figure 3. ***Hypothetical curves showing the interaction between the stock-recruitment curve and the replacement point at high and low levels of fishing mortality, for high and low recruitment regimes (from presentation by M. Fogarty, March 25, 1996).***

The Panel notes the current absence of a valid relationship between fishing mortality and standardised fishing effort data, which may well be non-linear. The definition of an effort target required to achieve a specific fishing mortality may therefore be difficult to achieve, except on a rule of thumb basis, and in the first instance the most practicable first step may be to establish an effort ceiling. That ceiling must incorporate a real trap limit, however, and not a number so far above the mean number of traps worked as to allow a large subsequent increase in 'latent effort'.

If the U.S. had been, like Canada, an area where effort was capped, it is suggested that the recruitment increase would still give no grounds for increasing the effort limit, given the possibility that the recruitment regime could reverse at some future time.

Section 6. Benthic Ecology

The likely asymptotic form of the lobster stock-recruitment relationship (Fogarty and Idoine, 1986, Ennis and Pezzak, this Review) shows that density-dependent mortality must occur at some stage in the pre-recruit life history, and the question of how the recent recruitment change interacts with such a mechanism has already been raised. Wahle, Stennek and Cobb at this Review presented the results of field studies on the pelagic, early benthic and adolescent phases, and discussed numerous ideas and hypotheses highly relevant to the topic of population regulation in the lobster. The overview contained in this section was stimulated by these presentations.

The lobster life cycle includes an approximately 40 day pelagic phase followed by a 6-7 year benthic phase prior to recruitment to the fishery. This provides many opportunities for environmental factors to impinge on recruitment success by modifying survival or growth rates at particular developmental stages. These factors may include physical characteristics of the water mass (particularly temperature), patterns of water transport, and the density of plankton food sources, each of which may affect larval growth, survival, or distribution. Water temperature may also directly affect the readiness of Stage IV larvae to settle to the benthic habitat. Other environmental factors, such as benthic habitat type, abundance of conspecific competitors for refuge space, availability of benthic food sources, and presence of predatory fish, will affect growth or survivorship of juvenile lobsters in the benthic environment. Each of these factors could act locally, or on broader scales, and either continuously or at critical times, to determine the rate of, or time to recruitment to the fishery. The pattern of water movement, which is itself determined by meteorological and oceanographic factors, will determine the spatial distribution of particular life stages through its effects on the transport of larval lobsters. It may aggregate young lobsters in certain places and leave others sparsely supplied. Occasionally, this factor will directly affect recruitment success when larval lobsters are expatriated from the region.

The summed effects of this suite of factors must determine the relationship between egg production and recruitment to the fishery 6-7 years later. Understanding how they act, and on what scale, will be necessary if we are to understand (rather than estimate) the stock-recruitment relationship for the lobster population. This is a major task. Because of the nature of the life cycle with its more dispersive larval and its more sedentary benthic phase, as well as the varying spatial scales of the different factors, the overall stock-recruitment relationship will be a temporally shifting summation of a set of spatially discrete formulations. A better understanding of these processes should enhance our ability to anticipate the consequences of future perturbations to this system, whether caused by changes in fishing effort, environmental or weather conditions, or exploitation of other components of the ecosystem. Recent ecological research is beginning to identify some patterns and processes during the pelagic larval phases and the early benthic phase (20-40mm CL), but relatively little is known of the later parts of the pre-recruitment phase.

6.1. Pelagic Phase

Larval development comprises four pelagic instars. In New England, hatching occurs primarily from late May to mid-June, and larvae are present in the water column as late as early September depending on location. Larval duration is 26 days at 18 to 21°C, but is strongly temperature dependent and can be 40 days in parts of the region. Katz et al. (1994) report that the first three stages (10 of 26 days) are passive drifters, while Stage IV larvae are active directional swimmers. Stages I and II may exhibit vertical diel migration, and Stages I-III are within the water column. Stage IV larvae are predominantly within the upper 1m, and will be subject to wind-driven surface drift rather than geostrophic movements of the water mass. Rooney and Cobb (1991) report that Stage IV larvae swim at a mean velocity of 18 cm sec^{-1}, with the majority of larvae swimming in a northerly direction. Towards the end of larval life, Stage IV larvae make vertical excursions, apparently to search for suitable benthic habitat.

Though preliminary, present data suggest that the behaviour of larvae at different developmental stages is sufficiently complex that estimating the path and extent of transport will not be straightforward. The duration of larval life, and the current regime into which larvae are placed clearly allow for substantial transport during the larval phase. The general direction of transport is likely to be northward, into the Gulf of Maine for eggs hatched anywhere east of the Rhode Island shore.

6.2 Settlement

Stage IV larvae that find suitable benthic habitat settle and remain demersal. Wahle and Steneck (1991) defined "early benthic phase" (EBP) lobsters as those living demersally and of <40 mm CL in size. For sites near Damariscove Island, Incze & Wahle (1991) demonstrated that abundance of EBP lobsters in cobble habitat in September was correlated with abundance of

Stage IV larvae in plankton tows in August. The island appeared to act as a barrier to wind-driven dispersal of larvae, and both larvae and EBP juveniles were less common in sites in the down-wind "recruitment shadow". Wahle and Steneck (1991) also demonstrated significant preferences by EBP lobsters among benthic habitats although they do not know how much of this is due to selection by Stage IV settlers and how much is due to differential predation on EBP animals in the first few days after settlement.

EBP animals consistently preferred cobble habitat, but this preference might be overstated, since substantial numbers were also found in boulder habitat and somewhat smaller numbers occur on rocky ledge or on soft sediment locations. EBP lobsters are also found on extensive mud flat substrata in Long Island Sound, and certainly occur in eelgrass beds, kelp beds, and peat reefs as well. Particularly with the recent reduction in sea urchin numbers in the coastal region of the Gulf of Maine, and the resulting expansion of kelp beds, it is now even less easy to argue that juvenile lobsters are limited by the availability of suitable settlement habitat.

In an extensive survey of suitable cobble habitat at a number of coastal sites in Maine in 1988-89, Steneck obtained data suggesting that settlement did not occur where surface water in August was colder than 15°C. In these years, several sites in far eastern Maine, and more seaward sites near Mt. Desert Island received no EBP lobsters, while more inshore sites, as well as all sites further southwest, where water in August was warmer, were colonised by EBP lobsters. This implies that water temperature could determine both the rate of development (and therefore the time available for larval dispersal), and the decision whether or not to settle, even when suitable habitat for juveniles is present. This latter effect of temperature on settlement behaviour may account for the finding that EBP lobsters are limited to relatively shallow sites on the Maine coast.

6.3. Survivorship of EBP Lobsters

Steneck and Wahle confirm that EBP lobsters are subject to intense predation by benthic fish and crabs, and remain confined to refuges. Estimates of predation rates in different habitats have been obtained by tethering small lobsters, and by releasing known numbers of laboratory-reared lobsters onto experimental plots. Survival of 42% after one day and 20% after nine days for oyster shell on sand, or 17% after 4 weeks in rocks and vegetation are typical. They demonstrate that substantial numbers of EBP lobsters die, and that rates of predation are probably markedly higher during the first few days in habitat. In this respect lobsters appear remarkably similar to coral reef fish, that also show marked habitat preferences and substantial mortality due to predation in the first few days after settling from the planktonic phase (Jones 1991).

Although the mortality of EBP lobsters is high, the field studies do not provide evidence that it is dependent on lobster density. Steneck (this Review) reported that experimental manipulation of EBP lobster densities in cobble, raising some to several times average natural density (16 individuals m^{-2} vs 0.4 to 1.4 individuals m^{-2} in cobble sites at five coastal Maine locations) resulted in no increase in per capita mortality rate. Furthermore, densities of EBP lobsters at these five coastal Maine locations were correlated (r^2=0.49) with densities of larger "adolescent phase" (AP) lobsters in nearby boulder habitat 1-2 years later. These results need further testing because if they were to be generalised they would substantially change our view on this aspect of population regulation.

Juvenile American lobsters do not necessarily stay at their initial settlement location. Wahle deduced that immigration of juvenile lobsters occurred at his study sites, presumably as a result of redistribution, and Steneck proposed that lobsters would move to deeper water as they grew older.

A shift from cobble to boulder habitat might be a consequence of a juvenile lobster becoming less sensitive to predation, and able to forage more actively, coupled with a need for larger refuge spaces and a tendency to interact more agonistically with other lobsters. These behavioural changes with growth may act to space out lobsters in denser populations, and may continue to cause movement apart as the juvenile lobsters grow in size. By the time juvenile lobsters are 60 cm CL they are virtually immune to the predators currently available in the Gulf of Maine.

6.4 Later Stage Pre-recruit Lobsters

Information on adolescent phase (AP) lobsters is far more limited. Steneck has demonstrated the need for increasing space due to agonistic interactions. Numerous tagging studies of AP and adult lobsters have disclosed considerable capacity for movement, particularly as an annual onshore-offshore migration. Interpreting the tagging studies is made difficult by the undue influence of the high fishing effort : few tagged lobster are at sea for very long without being recaptured, and few adult lobster are recaptured more than once. It may be possible to study space-use patterns more precisely by reworking the numerous tagging studies, and by using new sonar technology on pre-recruit lobsters.

For AP lobsters the greatest need is for information on survivorship and growth rates. Results obtained to date with EBP lobsters suggest that standard manipulative ecological approaches, including diver census and mark-recapture studies, can be effective in providing such data for local coastal populations of these animals.

6.5. Summary and Conclusions

The information available on the ecology of larval and juvenile lobsters is clearly limited. It provides tantalising hints rather than precise documentation of these important life history phases. Complex larval behaviour will interact with water temperature and patterns of water movement to determine where and when settlement to the benthic habitat will occur. These will be complex interactions. Data on EBP lobsters show clear evidence of habitat preferences, perhaps mediated directly by predation, but more likely due to explicit choices made at the time of settlement. Some data on rates of mortality during this first benthic phase, suggest that mortality will be habitat dependent but, at least at current levels of density, they may be density independent. This needs further work before it can be considered to be general result, but it is potentially a very important finding. There is also evidence that density of AP lobsters can be estimated from density of EBP lobsters at nearby sites 1-2 years earlier.

To date, the field results, while far from sufficient, do not show any density-dependent compensatory mortality during the benthic phases of the life history prior to recruitment to the fishery. This may be in part because of the large coefficients of variation in some data sets, but it is unexpected. Perhaps density dependence did occur in the past when populations were more dense, whereas current densities of, for example EBP lobsters, may be below those at which density-dependent increases in per capita mortality rate occur. If further work confirmed that mortality is generally density independent in this phase, the lobster population would be designated as "recruitment limited" (sensu Doherty and Fowler 1994), in that the sizes of successive cohorts added to the fished stock are determined by largely extrinsic processes determining survivorship from eggs to that stage, rather than by a regulated relationship of stock and recruitment. It is far too early to draw this as a firm conclusion, but lobster ecologists, should keep

d. trends in selectivity of the survey gear over time.

7.3.7 Examine the pros and cons of random sampling versus fixed stations in the bottom trawl survey

7.3.8 Investigate how the DeLury model can be modified to take into account multiple survey indices, and whether there is bias in the use of lumped recruit and post-recruit groups

7. 4 The Length-Cohort Analysis

Work on the use of LCA should continue in a structured way, in order to resolve whether the method is valid for analysing time-space differences in fishing mortality, and in particular for resolving differences between the LCA and the DeLury results.

7.4.1 In the short term, it may be possible to investigate similarities and differences between area-specific length frequency and catch-rate data, sampled on lobster boats at sea, with results for sets of stations in the bottom trawl survey, and to assess how these are interpreted by the two methods.

7.4.2 In the long term, simulation modelling of spatial structure, based on the analysis of transfer rates from tagging recommended in Section 2, could be coupled with simulated effort-related changes in size distribution through time, to provide a basis for testing the validity and compatibility of the LCA and DeLury analyses.

7.5 Fishing Mortality and Fishing Effort

7.5.1 Develop a long time series of standardised effort and fishing mortality data to quantify this relationship for management purposes.

7.6 Egg Production per Recruit

7.6.1 Examine the sensitivity of $F_{10\%}$ EPR estimates to changes in assumed inputs such as M

7.6.2 Analyse the effect of measurement errors, using bootstraps

7.6.3 Consider setting an acceptable level of risk associated with measuring stock status relative to the overfishing definition

7.6.4 Contrast how estimates of $F_{10\%}$ EPR may differ between small areas with distinct life history characteristics, and the wider regions used for stock assessment purposes, and assess any implications

7.6.5 Include the reproductive output from sub-legal females into future computations for areas where this is clearly warranted by the population structure and its growth and maturity schedules, and carry over to the assessment model as well, so that the models are compatible.

7.6.6 Investigate the effect of incorporating into the EPR model natural individual variability in growth and reproduction, including variability in moult increment, and multiple egg extrusions

7.6.7 Consider how reproductive behaviour, mating hierarchies, sex and size ratios etc. at low stock abundance, may affect egg production. This implies that analyses should also be conducted for male lobsters.

7.7 Future Assessment Methods

The DeLury model is not capable of tracking changes in abundance by length-age stages. Traditional age or length structured fisheries models would be inappropriate because of the life history characteristics of lobsters and the regulations in place to manage them. The opportunity exists for a new, state-of-the-art assessment model to be used for American lobster (and other crustacea), since the egg-per-recruit model is also set up as a population projection matrix. In principle, it should be simple (in the short term) to embed this projection model within a non-linear minimisation algorithm to estimate recruitment and fishing mortality rates given data on catches and relative indices of abundance. An even more fruitful approach would be to generalise this into a maximum likelihood estimation procedure (see Fournier and Archibald 1982) that would incorporate multiple sets of information: landings, length frequencies in the catches, relative abundance, tagging, and environmental data.The Panel strongly recommends that such a model be developed and implemented in the near future. However, considering the importance of continuity and model testing, the Panel also recommends that the DeLury and LCA models continue to be used in parallel, at least for several assessments.

7.8 Changes in Abundance and Recruitment

7.8.1 Examine in detail the timing and scale of increases in effort, temperature and abundance and then attempt to model their combined effects on size and age structure, for comparison with the available data, especially that available from sea-sampling.

7.8.2 The effort-temperature-recruitment hypothesis should be tested for all lobster areas, and accompanied by an all-area analysis based on, say, the LPUE of small lobsters, in order to identify the relative contribution of effort, temperature and abundance in different areas. Comparison between U.S. and Canadian data would be central to this approach, incorporating a test of Canadian compliance with effort and catch restrictions, plus any fishery independent survey data for the Canadian area.

7.8.3 Identify areas with similar or different thermal regimes, or larval drift regimes, and test for similarities or differences.

7.8.4 Conduct analyses of the lags between effort and landings, to test hypotheses about the possible role of bait as a contributor to productivity changes.

7.8.5 Investigate the likely effect on biomass of temperature-related changes in molt frequency and or increment, age of maturity, larval survival, habitat extension.

7.8.6 Search for additional data on predation effects, regime shifts, and on the abundance of other species likely to show co-related changes.

7.8.7 Identify data to be collected in the future to monitor for a reversal of recruitment in order distinguish between competing hypotheses about causative factors.

7.8.8 Promote a co-ordinated U.S.-Canadian investigation of these issues.

7. 9 Benthic Ecology

7.9.1 Establish field studies to confirm that EBP and AP mortality are not density dependent. This will involve much larger sample sizes than historically obtained so as to increase statistical power.

7.9.2 Test the hypothesis that water temperatures below 15 °C are unsuitable for settlement or survival of post larval lobster.

7.9.3 Establish a wide scale collector survey and recruitment prediction network.

7.10 Collaboration

SAW 16 and this Review have stressed the importance of understanding fishery and population processes at a variety of ecological and geographical scales.The development of new analyses and new research programmes should pay particular attention to maintaining and developing scientific collaboration and co-ordination between State, Federal and Canadian researchers and programmes.

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Annexes

Annex 1

Panel Credentials

Bannister, R.C.A.

Dr. Bannister has been the head of the Shellfish Research Group for the Ministry of Agriculture, Fisheries and Food for the United Kingdom since 1981. He has over 30 years of experience in conducting assessments of important fishery resources including North Sea demersal flatfish and roundfish, European lobster, and other shellfish. He is currently responsible for initiating and developing monitoring, assessment and research programmes on crustacea and mollusca, and pursuing individual research on lobster fisheries studies and on lobster stock enhancement for the United Kingdom. He collaborates closely with industry and managers in developing policy level, limited entry management recommendations.

Dr. Bannister received a Ph.D. in Fisheries from the University of East Anglia in 1971. He was the fisheries advisor to the European Commission during the early development of the Common Fisheries Policy. During his career he has served on numerous international scientific committees including serving as Chairman of the Shellfish Committee of the International Council for the Exploration of the Sea (ICES). Dr. Bannister is currently the Chairman of the ICES Consultative Committee which coordinates the ICES science progammes, sets research priorities and conducts scientific reviews. Dr. Bannister has authored numerous scientific articles, research reports, and educational articles.

Selected Publications:

Bannister, R.C.A.1986. Assessment and population dynamics of commercially exploited shellfish in England and Wales. pp. 182-194. *In* G.S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Canadian Special Publication in Fisheries and Aquatic Sciences 92.

Bannister, R.C.A., and J.T. Addison. 1986. Effect of assumptions about the stock-recruitment relationship on a lobster (*Homarus gammarus*) stock assessment. Canadian Journal of Fisheries and Aquatic Sciences 43:2353-2359.

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Addison, J. T., R. C. A. Bannister, and S. R. J. Lovewell. 1995. Variation and persistence of pre-recruit catch rates of *Homarus gammarus* in Bridlington Bay, England. Crustaceana 68: 267-279.

Botsford, Louis W.

Dr. Botsford has been on the faculty of the University of California, Davis in the Department of Wildlife, Fish and Conservation Biology since 1980 and is currently a professor in the Department. He has also been associated with Bodega Marine Laboratory where he conducted economic analysis of fisheries and aquaculture. In 1992, Dr. Botsford was a member of a team which conducted a special study for the New England Fishery Management Council entitled "Lobster Market Study with Analysis for Management." He has also conducted research for the State of Maine and the Canadian Department of Fisheries and Oceans on impacts of increasing minimum size for lobsters.

Dr. Botsford received a Ph.D. in electrical engineering from the University of California, Davis in 1978. Since then he his research has focused on quantitative fisheries research of invertebrates and age and size structured population models. In addition to his own research, he has supervised the research of numerous graduate students and served on many scientific review committees. Dr. Botsford has published over 60 papers in scientific Journals, reviews and scientific reports.

Selected Publications:

Botsford, L.W., C.L. Moloney, J.L. Largier, and A. Hastings. 1996. Metapopulation dynamics of meroplanktonic invertebrates: the Dungeness crab as an example. In press, Canadian Journal of Fisheries and Aquatic Sciences.

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Hobbs, R.C., L.W. Botsford and A. Thomas. 1992. Influence of hydrographic conditions and wind forcing on the distribution and abundance of Dungeness crab, *Cancer magister*, larvae. Canadian Journal of Fisheries and Aquatic Sciences 49:1379-1388.

Mohn, Robert K.

Dr. Mohn is a Research Scientist in the Marine Fish Division of the Department of Fisheries and Oceans in Halifax, Nova Scotia. He has over two decades of experience in conducting and analyzing stock assessments and has extensive knowledge of the marine fisheries of the North Atlantic. His current responsibilities include fishery systems modeling and the development of assessment methods. Previously, Dr. Mohn headed the Modeling and Statistics Group of the Department of Fisheries and Oceans and served as a Research Scientist in the Division of Benthic Fisheries and Aquaculture and the Division of Invertebrates and Marine Plants. Dr. Mohn has served as Biomathematics editor of the Journal of the Northwest Atlantic Fisheries Organization. He also chaired the working group to assess the impact of Canadian fisheries for the International Court of Justice decision in the Gulf of Maine. In 1992 Dr. Mohn co-convened the North Atlantic Fisheries Organization Special Session of Fish Stock Assessment Calibration Methods.

Dr. Mohn received a Ph.D. in Physiology/Biophysics from Dalhousie University in 1974. He also holds advanced degrees in Physics and Mathematics. Dr. Mohn is currently on the faculty of Dalhousie University and has lectured internationally on population modeling and assessment methodology. Dr. Mohn has authored numerous scientific articles, research reports and educational articles.

Selected Publications:

Mohn, R. and W.D. Bowen. 1996. Grey seal predation on the Eastern Scotian Shelf: modeling the impact on Atlantic cod. Canadian Journal of Fisheries and Aquatic Science. (in press).

Campana, S., R.K. Mohn, S.J. Smith and G. Chouinard. 1995. Spatial implications of temperature-based growth model for Atlantic cod (*Gadus morhua*) off the eastern coast of Canada. Canadian Journal of Fisheries and Aquatic Science 52:2445-2456.

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Mohn, R.K. 1993. Bootstrap estimates of ADAPT parameters, their projection in risk analysis and their retrospective patterns. pp. 173-184 *In* S.J. Smith, J.J. Hunt, and D. Rivard [eds.]. Risk evaluation and biological reference points for fisheries management. Canadian Special Publication in Fisheries and Aquatic Sciences 120.

Mohn, R.K. and R. Cook. 1993. Introduction to Sequential Population Analysis. NAFO Sci. Conc. Studies. No. 17. P. 110.

RESTREPO, VICTOR R.

Dr. Restrepo is a research assistant professor at the University of Miami, Rosenstiel School of Marine and Atmospheric Science. He is also the Associate Director of the Cooperative Unit for Fisheries Education and Research at the University. Dr. Restrepo is responsible for developing and implementing research programs on analytical methods for stock assessment. His current research interests are in fishery stock assessment and management applications, population dynamics model development, and Monte Carlo and deterministic simulation modeling. He has conducted assessment research on many fish and invertebrate stocks in the Atlantic including stone crabs, king and Spanish mackerel, swordfish, bluefin and yellowfin tuna, and tropical shrimp fisheries.

Dr. Restrepo received his Ph.D. in fisheries science from the University of Miami in 1989. His dissertation research focused the population dynamics and yield-per-recruit assessment of southwest Florida stone crabs. Dr. Restrepo has served on the editorial board for the North American Journal of Fisheries Management and Frente Maritimo. He has published numerous articles in scientific journals in the last 8 years.

SELECTED PUBLICATIONS

Rosenberg, A.A., and V.R. Restrepo. In press. Uncertainty and risk evaluation in stock assessment advice for U.S. marine fisheries. Canadian Journal of Fisheries and Aquatic Sciences 51:.

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Watson, R.A., D.J. Die, and V.R. Restrepo. 1993. Closed seasons and tropical penaeid fisheries: A simulation including fleet dynamics and uncertainty. North American Journal of Fisheries Management 13: 326-336.

Restrepo, V.R. 1992. A mortality model for a population in which harvested individuals do not necessarily die: The stone crab. Fisheries Bulletin 90: 412-416.

Restrepo, V.R., and R.A. Watson. 1991. An approach to modeling crustacean egg-bearing fractions as a function of size and season. Canadian Journal of Fisheries and Aquatic Sciences 48:1431-1436.

SALE, PETER F.

Dr. Sale is widely known for his research on reef fish communities and marine fisheries research conducted over almost 30 years. He has been the Chairman of the Department of Biology at the University of Windsor since 1994. Dr. Sale has also held academic posts at the University of New Hampshire and the University of Sydney. His main research interests are in community structure and dynamics, particularly for coral fishes, management of coral reef fishes and reef fisheries. Dr. Sale's current research focuses on recruitment dynamics in coral reefs and temperate lake systems.

Dr. Sale received his Ph.D. in Zoology from the University of Hawaii in 1968. In addition to his own research, he has supervised the research of 17 Ph.D. students since 1971. Dr. Sale has published over 90 articles in scientific journals and books.

SELECTED PUBLICATIONS

Sale, P.F., G.E. Forrester, and P.S. Levin, 1994. The fishes of coral reefs — ecology and management. National Geographic Research and Exploration 10:224-235.

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Annex 2

Papers in Review Portfolio

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Drinkwater, K.F., and R.A. Myers 1987. Testing predictions of marine fish and shellfish landings from environmental variables. Canadian Journal of Fisheries and Aquatic Sciences 44:1568-1573.

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Idoine, J. 1995. American Lobster. pp. 114-116. *In*. NMFS, Status of the Fishery Resources off the Northeastern United States for 1994. NOAA Technical Memorandum NMFS-NE-108.

Keser, M., D.F. Landers, Jr., and J.D. Morris. 1983. Population characteristics of the American lobster, *Homarus americanus*, in eastern Long Island Sound, Connecticut. U.S. Department of Commerce, NOAA Tech. Rep. NMFS SSRF-770.

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LaPointe, George. 1995. Memorandum to Helen Mustafa, Stock Assessment Workshop Coordinator from George LaPointe, Atlantic States Marine Fisheries Commission (October 16, 1995).

Lawton, P., and K.L. Lavalli. 1995. Postlarval, juvenile, adolescent, and adult ecology. Chapter 4. pp. 47-88. *In*. J.R. Factor [ed] Biology of the American lobster, *Homarus americanus*. Academic Press, New York

Mercaldo-Allen, R., and C.A. Kuropat. 1994. Review of American lobster *(Homarus americanus)* habitat requirements and responses to contaminant exposures. NOAA Technical Memorandum NMFS-NE-105.

Miller, R.J. 1995. Fishery regulations and methods. Chapter 5. pp. 89-109. *In* J.R. Factor [ed] Biology of the American lobster, *Homarus americanus*. Academic Press, New York

National Marine Fisheries Service. 1993. Report of the 16th Northeast Regional Stock Assessment Workshop (16th SAW). Stock Assessment Review Committee (SARC) Consensus Summary of Assessments. Northeast Fisheries Science Center Reference Document 93-18.

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Rosenberg, A., P. Mace, G. Thompson, G. Darcy, W. Clark, J. Collie, W. Gabriel, A. MacCall, R. Methot, J. Powers, V. Restrepo, T. Wainwright, L. Botsford, J. Hoenig, and K. Stokes. 1994. Scientific Review of Definitions of Overfishing in U.S. Fishery Management Plans. American Lobster, pp 46-46. NOAA Technical Memorandum NMFS-F/SPO-17.

Smith Terry. 1995. Memorandum to John Witzig, NMFS, from Terry Smith, Stock Assessment Workshops Chairman (October 23, 1995).

Annex 3

Review of the Population Dynamics of American Lobster in the Northeast United States

Presentations

Blake, Mark. (*Connecticut Department of Environmental Protection, Old Lyme, CT*). Long Island Sound lobster biology and parameterization for egg production model. *Review information on the fishery, distribution and abundance, habitat, tag-recapture studies, maturity, growth, and larvae production with respect to stock assessment.*

Cobb, Stanley. (*Department of Biological Sciences University of Rhode Island, Narragansett, RI*). Lobster Ecology. *Larval behavior, hydrodynamic transport, and potential offshore-to-inshore recruitment in the American lobster, Homarus americanus.*

Drinkwater, Ken. (*Department of Fisheries and Oceans Halifax, Nova Scotia*). Temperature and Environmental Factors Affecting Lobster Production: Did temperature play a role in the recent Rise in lobster landings?

Estrella, Bruce. (*Division of Marine Fisheries, Sandwich, MA*). Surveys in Massachusetts. *A review of data collection programs, regulatory changes, and trends in resource and fishery related data.*

Fogarty, Michael. (*National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA*). Overview of Lobster Fisheries, Population Dynamics, and Overfishing Definitions. *A review of trends in American lobster fisheries with emphasis on historical trends in yield and factors affecting catch rates, key aspects of recruitment dynamics, and their implications for the development of a proactive, precautionary approach to defining overfishing levels.*

Graulich, Karen. (*New York Department of Environmental Conservation, East Setauket, NY*). Assessing the biological reference point for Long Island Sound lobsters. *Describe a model for calculating the biological reference point (F_{10}) based on total egg production in Long Island Sound lobster.*

Howell, Hunt. (*University of New Hampshire, Durham, NH*). Lobster Research in New Hampshire. *A review of lobster research in New Hampshire coastal and estuarine waters with particular emphasis on population size composition, relative abundance and habitat preference. Study methods included SCUBA surveys, sea sampling and ventless traps.*

Idoine, Josef. (*National Marine Fisheries Service, Northeast Fisheries Science Center Woods Hole, MA.*). Egg Production Models and Biological Reference Points. *A description of lobster autecology and the mathematical basis of the eggs per recruit model. Additional topics include: present application to stock regions, sensitivity analysis to key assumptions and extensions to non-equilibrium projections.*

Krouse, Jay. (*Maine Department of Marine Resource, West Boothbay Harbor, ME*). Maine's lobster fishery, its management and research. *The characteristics of Maine's lobster fishery, along with a review of important management practices, monitoring programs and research findings will be presented.*

Murawski, Steve, and Steve Cardin. (*National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA and Massachusetts Department of Marine Fisheries*). Assessment Methodology and Status of Stock. *A review of the methodology in previous assessments including sources of data, DeLury model, other indicators of stock status, and sources of uncertainty.*

Pezzack, Doug. (*Department of Fisheries and Oceans Halifax, Nova Scotia*). Migration

Pezzack, Doug. (*Department of Fisheries and Oceans, Halifax, Nova Scotia*). Conservation Framework for Atlantic Lobster - Canada's Approach.

Steneck, Robert. (*Darling Marine Center, Walpole, ME*). Ecological and Oceanographic Approach to Lobster Production (Introduction). *We approach the question of lobster productivity over a range of scales considering patterns in time, space and ontogeny. Spacial scales range from substrate habitat selection to Gulf of Maine ecosystem and New England wide scales. Temporal scales range from over a century to seasonal.*

Steneck, Robert. (*Darling Marine Center, Walpole, ME*). Patterns of Distribution and Abundance of Lobsters at scales ranging from the Gulf of Maine to local habitats. *Discuss and show results of experiments that indicate particular processes that are consistent with the patterns observed. Demonstrate ecological linkages in patterns and processes leading to patterns in stock size and landings. Report on newly developed post larval collectors that offer considerable promise for predicting future stocks and landings.*

Wahle, Rick, and Louis Incze. (*Bigelow Laboratory of Ocean Science West Boothbay Harbor, ME*). Patterns and processes in benthic recruitment. *Quantifying spatial and temporal correlations between postlarval abundance and benthic recruitment of 0 year class lobsters in New England. Environmental determinants of larval supply and benthic recruitment. Nursery habitat and processes operating during the "early benthic phase", the most habitat-restricted segment of the life history. Challenges of following cohorts after settlement and the transition from sedentary to nomadic behavior. The relative importance of post-settlement mortality and dispersal to local and regional differences in abundance and implications to lobster production.*

Annex 4

Review of the Population Dynamics of American Lobster in the Northeast United States

Participants, Presenters and Observers

Names	Address	Phone/FAX
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their minds open to this possibility, and test it rigorously.

The ecological data also suggest that the demography of the lobster may be spatially variable depending, as it does, on spatially varying conditions for growth and survival, and spatially varying extent of suitable habitat for specific life stages. Data are again far from adequate, but are possibly more definitive than for the question of recruitment limitation. If the existence of spatially variable demographic conditions is to be taken into account in stock assessments, sampling to obtain such data should be properly stratified with respect to area and location.

The current paucity of information should not be taken as evidence that an ecological approach to the demography of this species is unfruitful. On the contrary, the results presented at this Review as a consequnece of a relatively short period of investigation by relatively few dedicated researchers, are very encouraging, and strongly support a continuation and strengthening of co-ordinated, manipulative ecological studies, especially as the lobster is clearly amenable to such approaches.

6.6 Predictive Indices of Recruitment

Ecological research on EBP lobsters has led to the development of efficient techniques for sampling lobsters in this critical early phase of the benthic life cycle. Collectors designed to quantify the local success of settlement now exist, and could be incorporated into a large scale survey plan. An annual survey in August-September, properly stratified with respect to location and season, and adequately replicated, could provide an "early warning" of settlement failure. Such an early warning would come 6-7 years before a fishery decline allowing time to make corrections to fishing effort. Involvement of the industry in deployment and retrieval of collectors would introduce "stake-holders" to this stock monitoring process. While we recommend that implementation of such an annual settlement survey should be seriously considered, we are not proposing that this would replace current stock assessment procedures. We see it merely as a useful addition to ways for gathering information about this resource

7. Research Recommendations

The previous text includes a number of comments and suggestions about further investigations and this section provides a collated summary.

7.1 Stock structure

The Panel recommends that the metapopulation status of the American lobster be studied in more detail in order to a) resolve the question of how the offshore stocks relate to the inshore stocks, and in particular whether there is a larval subsidy from offshore, and b) assess whether regional or area differences in demographic parameters are likely to be of genotypic rather than phenotypic significance.

Work should include:

7.1.1 the SAW 16 recommendation to compile existing tagging results. This should involve assessing the scope for calculating area-specific transfer rates, taking into account the sensitivity of recapture data to different stock and migration scenarios, and trends in the distribution of the fishery

7.1.2 the SAW 16 recommendation for genetic studies (particularly in relation to the Southern New England area)

7.1.3 an assessment of the contribution of different areas to total egg production

7.1.4 a compilation from larval data of the main characteristics of the dispersal and transport of larvae.

7.1.5 further investigation of spatial differences in demographic parameters, and their significance for assessment and management.

7.2 Landings, Effort and LPUE

Serious consideration should be given to getting more out of lobster LPUE data, as standardised catch rate information can still be very useful. Suggestions are :

7.2.1 Historical data should be investigated to see whether disaggegated data can be obtained for inshore and other areas with bottom types where the fishery-independent trawl sampling has not been conducted. In a simplified scenario, such data could come from the catch rate of small recruits realised by similar boats using the same type of traps and soak time in a particular area and during a particular time of the year, such as the months of recruitment. Any such information available from sea sampling programs should be carefully analysed.

7.2.2 Disaggregated historical data should be used to quantify the offshore spread of effort, and also time-space differences in effort relevant to testing the effort-temperature hypothesis.

7.2.3 In future, area-specific data should be obtained on catch, effort, LPUE, and size distribution, from port based and sea-sampling sources, as a matter of routine. Sea sampling on board commercial boats for a number of years should provide valuable information on catches and length frequency data, as well as effort and gear (trap type, soak time, location, time, etc.). This would provide an opportunity for standardisation, or estimation of relative fishing power, and for investigation of subpopulation differences and trends. If standardised area- / season-specific LPUE data can be obtained it may be possible to quantify local trends, and develop some form of Leslie analysis.

7.2.4 Sampling should be enhanced in offshore waters as recommended by SAW 16.

7.2.5 The willingness of fishers to participate in research could be used to conduct experiments on catchability, the alleged increase in efficiency of wire traps, the benefit of using parlour traps, and investigation of the relationship between catch rates and trap density.

7.3 DeLury Asessments

Future DeLury assessments should:

7.3.1 Evaluate whether DeLury estimates are biased by poor representation of the rocky and inshore stations in the bottom trawl survey data.

7.3.2 Complete analysis of the effect of different spatial combinations of survey stations.

7.3.3 Extend the use of sensitivity analysis to evaluate the robustness of the DeLury results to departures from both implicit and explicit assumptions, including M.

7.3.4 Introduce routine estimates of the degree of uncertainty.

7.3.5 Verify assumptions about the selectivity of the survey gear for the prerecruit and recruit groups.

7.3.6 Investigate the effect of

a. uneven lobster and effort distribution within a stock unit (inshore-offshore) over time;
b. changes in the distribution of the bottom trawl survey with time;
c. the movement of lobsters in and out of stock units;