A Personal Perspective on Future Cooperative Research on Lobsters: The International Lobster Recruitment Workshop Held in St. Andrews, N.B.

JOHN F. CADDY
Senior Fishery Resources Officer
Marine Resources Service
Fishery Resources and Environment Division
FAO
Via delle Terme di Caracalla, 00100
Rome, Italy

ABSTRACT

An international workshop on factors related to stock and recruitment of Palinurid and Homarid lobsters was held in July 1986 in St. Andrews, New Brunswick, under the sponsorship of Fisheries and Oceans, Canada, with biologist attendees from around the world. The author was convener for the last session in Research Recommendations, and presents a personal perspective on future lobster research.

His review emphasizes the need to focus lobster research into key areas, and in light of the importance of these fisheries in many countries, research initiatives need coordinating, internationally, to allow poorly coordinated phenomena to be better understood. Areas of focus suggested by the author include:

1. Identification of unit stocks and degrees of stock mingling.
2. Testing and coordinated use of methodologies for recruitment forecasting, especially for Palinurids:
   - widespread use of standard post-larval collector.
   - for Homarids with longer pre-recruit benthic stages, development of 'shelter collectors', or initiation of indices of abundance series for 'short' lobsters.
3. Better understanding of pre-recruit processes using new techniques such as microtags seems feasible, but scanty information on trap performance and catchability still makes direct biomass estimation for lobsters problematical.
4. In support of improved commercial fishing, biodegradable panels avoiding ghost fishing, and improved handling procedures for sublegals, need more widely disseminating. Studies in less intensively fished areas such as the Bahamas, or where management has permitted stock recovery, such as in Cuba, deserve priority.
5. A better understanding of habitat requirements is offered by the possibility of directly mapping relevant habitat features by new technology such as satellite imagery and sidescan sonar, and on the theoretical side, by the fractal concept as it applies to natural surfaces.
6. The progress made with Homarids in understanding the integration of moulting processes with maturation deserves some attention for Palinurids also, and could lead to biologically more soundly based models of exploited populations.

INTRODUCTION

The St. Andrews lobster recruitment workshop held in 1985 was one of an informal series of lobster workshops, of which the last two were held in Australia in 1977 (Phillips and Cobb, 1979) and in Canada (Anthony and Caddy, 1980).

This latest workshop hosted a representative group of lobster workers from both Northern and Southern Hemispheres concerned with both Palinurid and Homarid research, and was particularly successful in showing how progress in a particular research topic can be promoted by the cross fusion and exchange of information between workers on a group of related organisms that a series of conferences is able to foster. Selected papers from the meeting, and an official summary will hopefully be published in 1987 as a Canadian Special Publication of Fisheries and Aquatic Sciences, but the review below represents a personal perspective of the author's prepared after he had served as convener of the conference session on "Research Priorities". As such it does not purport to represent a consensus view of participants, nor does it strictly adhere to the theme of Stock and Recruitment in lobsters, though most of the points raised pertain to this topic.

There are a variety of approaches to preparing a workshop overview: one is to go through all the papers and extract all suggestions by all participants for future work. The second is to record the reviewer's personal sense of the main directions for research that the workshop pointed towards, and this inevitably results in a more individual reaction to the papers and discussion. This review is of the latter kind. Since it had to be prepared in the absence of drafts of papers, reference to individual papers presented has inevitably been kept to a minimum.

In relation to the objective of a workshop overview, namely that of providing joint recommendations, it is suggested that the general criterion should be that these must:

1. Be achievable in 5—10 years, *i.e.*, should not be motherhood statements.
2. Should have a foreseeable practical impact even if not an immediate application.
3. Preferably should be of interest for collaborative work to a significant number of the workshop participants.

There is another subset of criteria that have to be satisfied, particularly for those scientists whose work is aimed to satisfy the information needs of management authorities. Here a real concern of fisheries managers who are approaching a problem such as the management of lobster stocks, is that they need a clear and limited number of research objectives for which they can seek support for with fishermen, industry, and the legislature. When looking at the recommendations that we are discussing, we should bear in mind the severe limitations or budgetary purse strings which still exist, despite the high socioeconomic importance of the lobster fishery and should focus on the questions that merit the most urgent consideration for immediate work. The total amount of funding available in fact may be less vital than attempting to honestly answer the question: Are we focusing our funding, in general, into too many individual small packages to be able to solve the difficult problems, and instead taking the easy way out of spending a small amount of money on every conceivable line of investigation? For those scientists who are not employees of a department of fisheries, the above rationale doesn't necessarily apply in setting their priorities, and independent research groups and universities will continue

to play an important role in what may be regarded as the less applied aspects of crustacean biology.

The following section headings attempt to raise some of the issues that struck the reviewer as being of particular interest, without as noted, attempting to present this as more than an individual perspective.

SAMPLING AND STATISTICS

Given that trapping crustaceans involve active, behavioural responses by the animal, there seems to be a growing suspicion that trap-caught animals are not entirely representative of the whole population.

Biases in size captured may apparently occur due to:

1. State of maturity.
2. Individual vulnerability (some individuals are apparently more trappable than others). Homarids may show foraging behaviour at particular states of the tide.
3. Trap characteristics, bait etc.

Catch rate may also be affected by pheromones, social interactions, species interactions, and temperature.

Despite the above, we need to use traps in the absence of any other cost-effective sampling device and, therefore need to know more about their mode of operation and likely biases.

Other methods of direct sampling and observation of lobster populations have been used in the past and have considerable potential application. Thus, diving, submersibles, underwater photography, sonic tags, shelter samplers or juvenile trapping were all quoted as actual or potential techniques of investigation. Despite their obvious potential for fisheries forecasting, little progress has yet been made in the development of benthic, early stage collectors. A question that appears to need addressing here, is whether this lack of success with small mesh traps is just a function of low catch rate: will spending more money on research and development solve this particular problem?

It became obvious at the workshop that better information is needed on the abundance and distribution of small lobsters ("shorts") and on discarding practices in lobster fisheries, such as has been well documented by the Western Australian State Fishery Agency for their rock lobster fishery. Good cooperation from the fishermen is obviously essential in both cases, if at-sea observations are to be carried out.

One aspect of a field sampling programme would be to capitalize on the gains already made in the understanding of lobster biology in the laboratory. If these are to be fully exploited by field workers, simple and fool-proof methods of field sampling for state of maturity and stage of moult cycle will be essential. This type of data will help greatly in the interpretation of size frequency and catch rate information, particularly if taken in conjunction with environmental data series such as bottom water temperatures, etc.

All types of statistical information will need to be integrated over stock units in order to be helpful in management predictions and will need to be interpreted also from what we suspect about the functional aspects of the life history.

SURVEYS

Although lobster stocks in a number of parts of the world are among the most valuable marine resources being exploited by man, there are obviously problems met, in implementing survey methodology for lobster stocks for a number of reasons. Part of the problem is that although larval studies are well adapted to research vessel cruises, trapping studies are not particularly well adapted for execution from research vessels. The lack of a clear rationale and economic justification for obtaining research vessel time for field studies of lobsters is also an important reason for the lack of success in this area.

Some research vessel operations that appear not to have been carried out so far in North America or the Caribbean to any great extent are those that parallel U.K. studies with side side scan sonar: namely to produce a definitive "one-off" mapping of habitat types in terms of frequency and size structure of outcroppings, ledges, and bottom roughness features at different scales. Such maps would be extremely useful in designing sampling programmes, in migration studies, and in siting artificial reefs.

With the excellent geological maps and mapping procedures now available in Canada for example, and the convergence of interest by marine biologists in the area of surface relief, cooperative work could be effected to produce a map that could conceivably be used to facilitate future survey work, particularly for stratified sampling by means of traps, or directly by underwater observation. Such a map would also, I believe, help in understanding migration routes of lobsters, particularly if combined with information on bottom current direction and speed, and might also be helpful in elucidating stock structure and improving the reality of spatial models of lobster populations.

For Palinurids, the use of satellite photographs, would be a suitable alternative basis for such a habitat mapping. These surveys should also include the major biologically related habitats such as grass beds, mangroves, and other lobster juvenile habitat and illustrate how these types of habitats may vary with time and space.

A further development that seems relevant to potential new survey methodologies for both Homarids and Palinurids, is the growing use of innovative types of shelter samplers, and those used in the commercial fisheries for spiny lobsters in the Yucatan Peninsula might be suitable for field survey purposes and might show less bias for size and state of maturity than is evident from some trapping performance studies.

In relation to the question of research strategy, if it is decided that the large amount of funding required for research vessel operations is not to be allocated for lobster research, equivalent funding in proportion to the relative value of the resource and its fragility to overexploitation should be made available for large-scale field experiments such as those involving habitat manipulation or controlled fishing or stocking of comparable areas. Such large-scale experiments may result in a more tightly focussed lobster research programme around a limited number of objectives as we have discussed earlier. I am convinced that despite tighter fiscal conditions, one of the features that has held back progress in lobster research has been our inability to mobilize enough effort in one or more promising areas, and demonstrate real effects of scientific projections on a meso-scale (thousand of square metres, as opposed to tens of square metres, in the case for example of artificial reef construction).

This question of intensive versus extensive research strategies was raised at the workshop and seems appropriate to raise here since some problems cannot be resolved on the small scale, and call for coordinated efforts. This would seem to be particularly appropriate for example, in the Gulf of Maine for *Homarus americanus* and in the Caribbean for *Panulirus argus* in relation to stock identification and fisheries forecasting. International, as well as national, strategies for developing such programmes need to be discussed.

STOCK IDENTITY AND GENETICS

The problem of identifying "unit stocks" and genetically distinct populations (these are not necessarily always the same thing), seem more intractable for coastal lobsters than for those with an oceanic larval cycle. Using one definition of a coastal resource, namely where the adults and larvae do not go more than several hundred kilometers offshore, the coastal lobster resources would seem to include most *Nephrops* and *Homarus* stocks, and possibly some Palinurids where discrete stock boundaries seem still largely hypothetical. Many Palinurid stocks however, such as those found off southern Africa, western Australia and California, seem to be associated with large-scale oceanographic systems, and the impact of large-scale fluctuations such as the El Niño type of phenomenon appear to be indicated by recent work. An interesting suggestion from the workshop is that although both northern Homarid and tropical Palinurid lobsters are, in evolutionary terms, ancient organisms, the Palinurids may well be occupying a much older habitat than many northern Homarid stocks, reflecting the generally greater age of many tropical ecosystems than those in northern boreal waters which suffered major disruptions by glacial processes fifteen to twenty thousand years ago. Perhaps we may expect more discrete stock units for Palinurids than Homarids?

Oceanographic and biological work should ideally be extended to other zoogeographical zones, particularly, for example, the Indian Ocean where a number of developing countries are exploiting their spiny lobster resources.

On the other end of the scale, it was noted for estuarine crab populations that larval recruitment processes appear to be better understood than for coastal shelf stocks: presumably a given estuary has its own unit stock? One interesting research question asked here, however, is what is the impact of the flushing characteristics of the different estuaries on the unit stocks and to what extent is there an interchange between different estuarine stocks?

Stock units for other organisms, particularly fish, have tended to be associated with identified spawning loci, and for Penaeid shrimp the unit stocks tend to be associated with particular coastal nursery areas, even if in both cases mixing occurs in the adult (feeding) phase. Is this true for example, for Gulf of Maine lobster stocks, or are we looking at gene drift and mixing along a coastal fringe population with no zoogeographic boundaries? Not being able to answer this question makes for serious difficulties in stock management. Can we seriously discuss managing the Gulf of Maine or Caribbean lobster stocks as separate national units with the tagging data presently available? In the absence of good stock differentiation, obviously the conservative answer is yes; we should attempt to manage in terms of those adult populations which seem to be spatially discrete. However, for eastern Canadian lobster stocks it seems from morphometric and genetic data that there is more than one stock unit involved, but it is not clear, despite promising tagging results, that there is any fixed

geographical delineation between the different fisheries for inshore and offshore stocks in the Gulf of Maine/Bay of Fundy complex. We should remember that lobsters do not always stick to one side or other of Maritime boundaries and concerted action may be needed, the first step of which could be to pool data for the whole major zoogeographical province involved.

The difficulties that have been outlined in the last paragraph should emphasize the need and the value of detailed studies on discrete, self reproducing stock units such as the Magdalen Island *Homarus* stock, the Hawaiian stocks of Palinurids, and the Irish Sea *Nephrops* population.

Do we have enough evidence to postulate the existence of reproductive units (cells) or whatever terminology you wish to use to describe them for both Homarids and Palinurids? The New Zealand experience with *Jasus* suggests an affirmative answer, and the concept of a contranatant movement of adults is shown in a less idealized fashion by several other Palinurid stocks. It is less clear whether this type of process occurs for Homarid stocks, although extensive horizontal and vertical migrations on a seasonal basis are well established.

The separation of a Maritime *Homarus* stock by blocking of the Straits of Canso was an important opportunity lost to carry out some "big biology" studies on the impacts of blocking the flow of reproductive material from one major zoogeographic province to another. Clearly being able to take advantage of major perturbations of this kind is one way in which "big biology" can be implemented in the absence of the large amounts of funding necessary for realistic scales of environmental manipulation.

Returning to the main theme of the meeting, the lack of resolution of the stock units in many areas, makes solving the spawner-recruit relationships very difficult, and the isolated stocks referred to earlier play a key role in resolving the nature of these types of relationships for Homarids. Since fitting of any regression relationship requires that the independent variable shows major variation during the time period under consideration in order that a proper linear or nonlinear fit may be effected, it is obviously important to make the best use of existing historical data where it exists. Since, as I noted in a review paper at the workshop, many lobster stocks are being exploited intensively, resulting in spawning stock size remaining relatively low for long periods of recent time. We might therefore look to those resources which have been exploited at a low intensity or relatively low intensity for further information on the stock recruit relationship. The data series emerging from Cuban stocks is of great interest and we would expect that more intensive investigation of the stocks on the Bahamas Banks which are at present lightly fished should yield valuable information on this relationship, although noting that for both of these resources it is not entirely clear whether they are independent or not from adjacent spiny lobster "stocks". The problem of determining the proportion of intermixing between local and long-distance recruits is particularly severe in the Caribbean and will require better information on their genetic structure in order to solve this issue. Some work is being done on this aspect and needs promoting.

In general, however, the workshop tended to support the idea that any stock recruitment relationship for lobsters would tend to resemble an asymptotic stock recruit curve such as the Beverton and Holt curve rather than a dome-shaped relationship such as the Ricker curve. Exceptions to this might occur (*e.g.*, in the case of density-dependent parasitic infections of egg masses), but in general it was felt that the impacts of environmental perturbations and year-to-year

fluctuations in predation on juveniles and in some cases, variable rates of parasitism on egg masses by (*e.g.*) Nemertean worms, would override any stock recruitment relationship and make it very difficult to determine. More emphasis seems to be needed in elucidating current functional interactions between recruitment and biotic and abiotic factors, rather than further work being confined to searching for nebulous statistical correlations between number of recruits and spawning stock size, both of which are notoriously difficult to measure for lobsters.

ECOLOGICAL PERSPECTIVES

Evolutionary Concepts

Two questions that I found interesting arose from the United Kingdom presentations on *Homarus gammarus*. The first was the question raised by Colin Bannister as to why western Atlantic stocks are larger (individually and in population size) than the *Homarus americanus* resources. The resolution of this problem, it seems to me, may stem from the more recent and extensive glaciation periods suffered by the Canadian Atlantic Provinces and the more recently submerged parts of the shallow shelf since the last glacial fringes receded from this area some 10—20 thousands of years ago. The nearshore areas of Nova Scotia for example, consisting of submerged land dominated by glacial till, have been eroded and the finer sediments washed out to the edge of the Continental Shelf and beyond (King, pers. comm.). The remaining substrate is heavily dominated by boulders which provide ample habitat for lobsters, although we have no quantitative estimates of the size and type of such habitat. Even on the Canadian shelf area, recent work has identified abundances of boulders of half a metre and more in diameter that are of the order of 200—300 per km^2. Even in the North Sea, terminal moraines or boulder piles were identified as important habitats for juvenile *Homarus gammarus* and have been used as sites for tagging and recapture experiments recently. Consisting as they do of boulders some tens of centimeters across, they may exert a limiting influence on lobster abundance, although the importance of low ledges is also identified for *H. gammarus* as a key habitat, permitting these crustacea to save energy during flood tide in areas of high tidal currents. Similarly, surficial cobbles and flint nodules in this area are also apparently an important feature of the environment for small lobsters, but apparently rarely exceed a foot or so in length. This would seem to impose some kind of limit to the maximum size that lobsters in such an area could attain. Such limitations on Canadian lobster grounds only come into affect at sizes of boulders approaching half a metre or so in diameter, and this would seem to be one of the factors that permits lobsters to attain a much larger maximum size in the northwestern Atlantic.

Glaciers as a lobster habitat enhancement mechanism have obviously had some impact in the past and the subsidence of Georges Bank in fairly recent geological time changed the dominant fauna of the bank from mammoths to herring, and the subsistence eventually produced the deepest spawning herring stock in the North Atlantic on the northeastern peak of the bank before that resource followed the mammoth to apparent extinction in the early 1970s. Did the same processes also lead to genetic isolation of the deepwater component of the lobster stock? Mike Fogarty suggested that some of the underwater canyons at the edge of Georges may perhaps be the oldest lobster habitat in the region since they were presumably being used by lobsters before the wholesale

submergence of much of the present coastal habitat that now forms the sublittoral zone fringing the Gulf of Maine. Possibly similar events occurred around that period in relation to the isolation to the Gulf of St. Lawrence from the Bay of Fundy, and these may be reflected in genetic analyses of the substocks of *Homarus* around the Maritime Provinces of Canada. Some further investigations of the timing of these events would seem justified.

As indicated above, an interesting speculation is to ask whether the prevalence of big boulders, ledges, and crevices in an area rather than just the prevailing physiological conditions experienced, leads in geological time to a higher L_∞ and a later maturing lobster than in areas where such subhabitats are more limiting as in the southern North Sea and possibly the southern Gulf of St. Lawrence, where (relatively speaking) "dwarf" lobster growth rates predominate.

LONG-TERM GENETIC IMPACTS OF SIZE SELECTIVITY BY FISHERIES

One question that continues to intrigue Homarid lobster biologists in areas where size limits have been in force for many years, is whether the lobster fishery is selecting for small, early-breeding animals? This seems at least theoretically a possibility, given that much harvesting is occurring at or below the size at 50 percent maturity for many of the western Atlantic *H. americanus* stocks. How fast will this process occur at present fishing rates given the genetic structure of the population?

It was a bit disappointing that there were not more papers dealing with the problem of the genetics of lobster stocks presented at the workshop. The selection pressures being imposed by an intensive fishery with strictly enforced size limits needs to be looked at. This problem could, and should, be modeled by geneticists and poses uncomfortable management questions. The freshwater crayfish experience is a way of testing this and may give some clues as to the likely answers to be attained.

LOBSTER BIOLOGY

Reproduction

Important advances have been made in our knowledge of the ovarian cycle and how it interacts with the molting cycles, especially in Homarid lobsters. Similar work seems not to have reached the same stage in relation to Palinurids and the importance of the investigation of these processes, particularly in tropical and subtropical lobsters of the Palinurid type, seems indicated. One aspect here of direct practical and theoretical importance is to study the perturbations caused by the fishing and discarding process on the moulting and ovarian cycles, and eventually to incorporate physiological events into population and yield models.

The role of "refugia" which was a "buzz" word at the last lobster meeting in St. Andrews on lobsters, but was not mentioned at this one, still seems an important concept in explaining how large berried females may survive. Their importance for *Homarus* is highlighted in the light of the now-proven role of multiple extrusion in *Homarus* populations in the Canadian Maritimes. The relative impact of small/large berried females on population fecundity for most areas seems still not to be finally resolved, and must have some priority involving pooling of data and experience by workers on lobster reproduction.

From a related management perspective, it still seems desirable to use caution in exploiting large mature deepwater components of lobster populations. It should be noted that these resources were not fished commercially for *H. americanus* to any extent prior to the 1960s, and it will take 7+ years before any major impact of this exploitation will begin to work through the system in terms of significant changes in recruitment. There seems some interest in the use of sanctuaries in areas of high abundance of large berried females, and some kinds of gear regulation could act as a refugium for these particular spawning stocks until we have a better idea of what their real role in the breeding system is. Comparable questions for Palinurid lobsters still seem to await answers for most populations.

The relationship between molt cycle and reproduction has been rather exhaustively worked out for *Homarus*, and what seems to be required now is for the physiologists and ecologists to work closely with mathematical modelers to incorporate their results into a predictive framework. Also, there seems a need to incorporate the physiological tests developed in the laboratory for extensive use in the field to improve our criteria for diagnosing the state of individuals sampled in terms of their reproductive and molt condition. Here the distinction between physiological and functional maturity must be considered in sampling. Although there seems no obvious reason why large lobsters should not be reproductively functional, this may not be the case for small mature lobsters which may need a certain minimum size, and size relationship between the males and females for successful mating. Something similar has been suggested also for snow crabs (*Chionoecetes*) recently (Conan and Comeau, 1986). The possibility of reproductive senility of large Palinurid females in the Caribbean was raised but there seems little reason why such individuals should not be reproductively capable if mates of sufficient size are available.

Parasitism and Population Fecundity

The potentially major role of parasitism on *H. americanus* suggested by Dr. James Stewart and its implied impact on spawner-recruit relationships, was noted by several participants, and it was felt that this could conceivably lead to dome-shaped spawning recruitment curves and host-parasite oscillations. Further investigations of this phenomenon in relation to *H. americanus* seem indicated. The high figures given for percent egg loss also appear to make it desirable to revise downwards the larval mortality rates needed to make quantitative life tables balance themselves.

LARVAL DISTRIBUTION DYNAMICS AND OCEANOGRAPHY

Much discussion of lobster larval dynamics seems to resemble the Anthropomorphic Principle, or what we may call here the Decapomorphic Principle; namely that the existence of a 9 month larval life history in Palinurids means that the ocean currents have to have a 9 month periodicity or vice-versa! Despite the potential tautologies and circular reasonings that can develop if sufficient caution is not used, the connection for Palinurids between the oceanic gyres and the larval stages of Palinurids seems somewhat clearer now as a result of pioneering Australian work, although there still appears to be a shortage of information on two main aspects:

1. What is the purpose of the long life history duration - does it reflect some periodicity of the system or is it simply a safety factor in that a

given larva has more than one opportunity of being carried past a suitable settlement area?

2. What are these animals feeding on - is it reasonable to conceive of an animal finding enough food in clear oceanic water to allow it to swim several hundred kilometers to shore? Is it sufficient simply to use vertical migration between wind-driven surface currents and deeper countercurrent systems to allow for homing? What is the wastage of larvae as a result of whatever strategy they are following?

I believe that the debate between the enthusiasts for directed migration versus stochastic dispersal processes will continue to rage at least until the next workshop, but no one can fault the excellent western Australian work done in developing larval collectors and using them in fishery management. Judging from the western Australian success, it would seem desirable to try and develop similar larval collectors for Homarids, especially since only after 15 years or so of steady use are they valuable for prediction purposes. Some questions remain in my mind as to the potential success and use of this type of collector in a direct, predictive mode for other areas and species, given that a number of workers believe that the bottleneck in recruitment may be occurring at the postlarval or later stages. Several reanalyses of Dave Scarratt's (1973) valuable work on the abundance of different stages of larvae in the southern Gulf of St. Lawrence would seem to cast doubt on whether the abundance of Stage IV Homarid larvae, for example, could be very predictive in terms of the numbers of recruits entering the fishery some years later. Discussion on this question does, however, outline the tenuous nature of our information on the age of recruitment of Homarid lobsters, which largely seems to stem from lag correlation studies and has little basis of support in terms of field experimentation to date.

Postlarval Processes

Crevices were identified in the workshop as important for a variety of reasons:

1. As mating loci and for social interactions.
2. For protection of post-molt lobsters.
3. For saving energy in areas of high tidal currents.
4. For growing food on, particularly in areas where hard substrates are not common.

The critical nature of crevices in lobster ecology does not seem to relate to just providing more crevices, but also to providing the appropriate size spectrum of crevices allowing movement through the molt stages to commercial size without undue competition and predation. The density-dependent or crevice-dependent mortality and growth effects would seem to be worthy of further investigation under experimental conditions. The Fractal Concept, I believe, provides a useful "field theory" for looking at niche size spectra, even though departures from a fractal expectation could be very important (Caddy, in press), particularly in relation to identifying possible bottlenecks in the recruitment process. They could also perhaps have an evolutionary importance as well as an ecological one, in that the onset of migration may well be related to some reduced expectation of local crevices that will support lobsters above pre-migration sizes.

Other types of habitat are also critical, but many questions remain. Thus we may ask what is the difference, ecologically, between a ledge and a loose boulder from a lobster's perspective? Seaweeds and other epiflora and fauna also are part of the niche creation system, and the significance of recent changes in southwest Nova Scotia in kelp abundance merit further study. Given the high production of kelp bed areas and the wide range of food items of Homarid lobsters, a general relationship between lobster production and seaweed abundance from a trophic viewpoint may occur; however, studies comparing trophic relationships of lobsters in barren and kelp areas would seem to suggest that the importance of kelp as shelter may be greater than its obligate relationship as a source or substrate for food organisms of lobsters.

For many Palinurids, grass beds and mangroves play key roles in recruitment and feeding, and the former has been adversely impacted in recent years in many areas by man. Mangroves also have been subjected to clear cutting in South America and parts of southeast Asia, and this may have had an important real or potential impact on lobster nursery habitat and could give rise to biases in potential stock recruitment relationships unless taken into account.

FORECASTING

The successful use of larval collectors in forecasting abundance of western Australian rock lobsters has been alluded to earlier. The use of pre-recruit indices for the same purpose in Western Australia, New Zealand and other areas also looks promising and possibly more cost-effective, and could lead to their use in models with autocorrelation terms. The use of a "shorts" index in the Northwest Atlantic fisheries for *H. americanus* seems not to have been tried yet and should be attempted. What is not clear with current forecast models in use, for example in New Zealand, is how the time series becomes biased once the industry starts to believe the forecasts! Certainly, moving to a quota system or changing the management system in other small ways may radically compromise the validity of autocorrelated studies of time series of catch and effort, a fact that is rarely appreciated and could lead to the need for more costly, regular biomass surveys of lobster stocks.

Density-Dependent Processes

One apparent conflict is that between the good predictive powers of Palinurid post-larval collectors several years later, and the fact that for some other populations (*e.g.*, some freshwater crayfish stocks), niche availability and other energetic bottlenecks seem the limiting factor in the postlarval stages, and would be expected to degrade the effectiveness of a predictive scheme based on larval collectors. Clearly there is a range of responses here for different lobsters in different environments that need looking at before putting too many eggs in one basket. This type of study, however, needs to be started as soon as possible in view of the long period of time before such recruitment predictors can be validated.

STOCK ENHANCEMENT

We seem to be in a transitional phase for Homarid stocks that have a protracted larval life history, from:

1. Unrestrained harvesting of wild stocks.
2. Licence limitation schemes.

3. TURF (Territorial User Rights in Fisheries).
4. Some form of stock enhancement/brood stock protection involving artificial habitats and exclusive harvesting rights, and the use of sanctuaries.

However, until recently, the concepts and practical tools available for tackling stock enhancement problems were missing.

Although nursery areas are not always saturated by recruits, a number of papers suggested that a degree of niche limitation occurs. Limited experience with artificial shelters, for example, on the Yucatan Peninsula of Mexico, looks promising in exploring this phenomenon. Here, although the placement of shelters may reduce mortality as well as allowing protection from predators during migration, they may also increase vulnerability. The use of individual, disposable shelters in the French mode looks like a good idea and these might also make good sampling devices for juvenile lobsters.

It is noted that the widespread use of fishable shelters can lead to TURF's and even avoidance of juvenile areas by fishermen. It was also suggested that natural nursery areas may be used for release of lobsters in tagging experiments. This would not be so effective however if niche limitation for natural stocks were the case. Also interestingly, at the other end of the niche spectrum, it was noted that *Homarus gammarus* may avoid large boulders since there are too many predators present in those types of habitats. The possible importance of adult borrows as habitat for juvenile lobsters was referred to both for *Homarus gammarus* and for *Homarus americanus*. Does aggregation of lobsters in artificial shelters increase vulnerability to fishing as much as it increases lobster production?

It is clear that the interests of those concerned with habitat enhancement, stocking and wild fisheries coincide in this respect, particularly in relation to the pressing need to investigate possible bottlenecks in recruitment. Personally, I find it difficult to believe that the main bottleneck occurs for *Homarus* at settlement, and it would appear from Japanese experience with Homarids, that introducing larger animals to the habitat is likely to be a more effective stocking approach. The fact emerges from paper after paper that lobsters are crevice dwelling for a wide range of reasons discussed earlier, that crevice availability will be limited in the wild, and especially for larger lobsters. There seems no point then in dumping post-recruits, whatever their size, in the natural habitat if the available spectrum of crevice sizes does not allow many to reach commercial size.

We may ask, then, that if increasing numbers of crevices is the critical factor, why not enhance the habitat for natural recruitment rather than expensive laboratory rearing? A number of fascinating research questions seems indicated, and some new techniques are now available to address them. This, I must say, seems to me the most exciting field of possibilities this workshop has opened up. Among such techniques are:

1. Microtags for evaluating post-recruit survival mortality and the cost effectiveness of stocking juveniles.
2. Settlement collectors and the possibility that at a larger scale they could be a stock enhancement device.
3. The large-scale use of benthic shelters based on the Cuban shelter/trap may lead to improved stock enhancement techniques and an understanding of post-recruitment limitation processes.

Evaluation of the Success of Stock Enhancement and Sanctuaries

It was noted that any attempt to carry out just stock or habitat improvement schemes should attempt to determine if:

1. Catch value of tagged animals exceeds operating costs.
2. An evaluation of the success of stock enhancement should take into account the potential reproductive impact of the introduced animals after successful introduction.

This needs a well planned, large-scale experiment to hope for any degree of proof using a controlled approach to the experimental design. In general, large-scale studies with proper control seem essential for any validation of this type of methodology which will, of course, be extremely expensive.

In terms of their potential payoff in the field of studies on post-recruit stages of lobsters, it looks probable that predator niche competition studies may pay more dividends in the medium term than feeding studies, although possibly density-dependent effects such as those noted for *Nephrops* and for spiny lobster will depend to some extent on the size of individual forage areas. On the other hand, it seems that successive "waves" of Palinurid recruits passing through an area may "open up" the habitat for later recruits to the population and food-limited situations in general, seem less obviously to apply to large crustaceans. In fact, dominance, hierarchy, and competition for niches may be more responsible for reduced growth rates and higher natural mortality with density effects than the availability of food itself.

STOCK ASSESSMENT AND MODELING

As noted in Caddy (in press), the early phase or application of finfish stock assessment models to crustaceans seems equivalent to the wholesale forcing of a square peg into a round hole. To some extent these simple stock assessment models are useful at the coarse level that most management is currently operating at, but are not very satisfactory from a biological point of view, particularly in relation to the effects of fishing on recruitment.

Length-Weight Relationships

Problems with interpreting morphometric interrelationships of essentially allometric growth processes were raised in the workshop. Are typically-inflected Hiatt diagrams a statistical artifact of fitting a logarithmic relationship as two or more linear segments? There seem some grounds for believing this may be the case.

Growth

Von Bertalanffy fits to growth data are still currently used and found to be useful, although they appear often redundant given that the raw data on increment and frequency can readily be used directly. Von Bertalanffy is also a limited growth model for crustacea in other ways:

1. It does not fit too well (not at all if there is a terminal molt to maturity as in some crabs eg. Conan and Comeau 1986).
2. It does not illustrate very well the impact of changes in size at maturity on inflection of the growth curve.
3. It lacks flexibility to combine fecundity and yield modeling information.

The alternative approach of using actual moult information or Mauchline's fits of molt increment versus size, lead directly to yield-per-recruit and

egg-per-recruit calculations as I demonstrated in 1977—79. This is, I feel, the appropriate way to proceed if increment/frequency data are available. However, this whole area looks ripe for further development as was illustrated by several papers presented at the workshop. More biologically realistic models will biologically affect how we perceive the optimal harvesting strategy. So far as I know, these models have not been widely used for Palinurid stocks or for crab stocks; although in the latter case, they would seem to be the appropriate way to proceed.

Some evidence presented suggested that, given the variable physiological "moult window", size at maturity can be very variable, suggesting the need for stochastic modeling. Models may also have to be modified to take into account that for crustacea, the impression is growing that 50 percent maturity occurs at a given age and is not just size-based.

If this is true, and several papers suggested it at the workshop, this provides for the exciting possibility (at least for north temperate stocks spawned at discrete times of the year), that we should be able to use this as the reference point for aging and not base aging on the time since some arbitrary (unknown) age at first entry to the fishery. The situation may not be so complicated in some populations, and there were also suggestions of more or less synchronous molting in early stages and discrete size modes for example, early in *Nephrops* recruitment. Although there seems to be a theoretical problem in assuming that these modes are necessarily age-groups, the possibility of synchronous molting may make it possible to identify age-groups from length frequencies. The differential migration of immature and mature individuals of the same size as in the squat lobster, *Pleuroncodes*, if it occurs in other lobsters, could make it rather difficult to interpret size frequencies unless the individuals are pooled over appropriate stock units.

Just what is the true variation of size at age in lobster populations? It seems we still do not know. We need to answer this in order to model lobster populations stochastically. Perhaps microtagging or keeping lobsters of known age in bottom cages will help answer this question?

Stock and Recruitment

The meeting focussed on classical approaches to stock and recruitment studies, especially the Ricker and Beverton and Holt models. Apart from the lack of data on spawning stock size and recruitment, a common problem in most crustacean fisheries is the narrow range of biomass in the population since exploitation is usually going on at or beyond MSY levels. At low biomasses we cannot distinguish an asymptotic and dome-shaped curve. Hopefully, the relatively moderate exploitation rates in Cuba and the Bahamas would allow a sufficient range of biomass figures for us to test the two major hypotheses.

Although parasitic crustaceans and egg disease might lead to a dome-shaped stock recruitment curve, the general separation of pre-recruits and spawners geographically does not, on theoretical grounds, favor dome-shaped models in which cannibalism is often a crucial factor. Asymptotic models look more likely, but here also, impacts of other variables (salinity, rainfall, other predators and competitors) which vary annually, could lead to misleading two-factor relationships.

This problem appears not to apply however, for pre-recruit-recruit relationships, which seem to show considerable promise for forecasting, or for

lagged autoregressive models incorporating recruitment information, so long as the data collection and fishery management systems do not change radically.

Basically, however, most progress is being made with biologically, geographically, and oceanographically based approaches to recruitment prediction rather than worrying exclusively about stock recruitment relationships, and this appears to be the right way to go. At the same time, the importance of maintaining population fecundity at some high level is evident, and the effects on net fecundity are being documented, including the impact of egg loss in handling.

MODELING

In general, the conclusions of the workshop in this area would seem to be that it is very desirable that the model keeps as close to reality as possible in terms of its basic biological assumptions. Such studies as the recent work on freshwater crayfish illustrate the potential dangers of making too many assumptions without underlying data. Mathematicians should structure their models along the functional lines demonstrated by biologists, and in fact close collaboration is needed between both disciplines to avoid erroneous hypotheses entering the literature. Such models might ideally combine reproductive and moult cycles with the effects of temperature on catchability and gear selectivity, and might, after suitable experimentation, also incorporate impacts of culling at sea and by-catch mortality as well as the availability of niche sizes at different stages in the life history. These approaches might individually be best described by a series of smaller models or subroutines than one big one. Simple cohort models seem less attractive for multi-stage life histories within complex regulatory and environmental regimes and, as was seen in the meeting, using simple population indices without considering how these observations might be generated by different biological underlying assumptions is also likely to be misleading. Co-operation of biologists in modeling with oceanographers, economists, fishery managers and, possibly also, marine geologists seems useful here.

I believe, in conclusion, that proper consideration of spatial factors in the mapping to modeling transition is essential to realistic modeling. Mapping resources and substrates will contribute to a likely realism in the resulting model.

Management Measures

It is clear from southern hemisphere experience that we are in the era where information on recruitment can be built directly into the fisheries management process, and with the high mortality rates caused by high unit values of lobsters, the recruits of the year play a dominant role in most fisheries. The fact that other variables also affect recruitment, so that a simple relationship with stock size is not usually apparent, does not affect the general feeling that although for a number, especially Homarid species, yield-per-recruit is suboptimal, the main concern with low size limits is that in a number of fisheries size at first capture is below the size at 50 percent maturity of the stock.

Improving the yield from a given number of recruits is important given limited recruitment and high unit value: measures to reduce incidental mortality of shorts and discards look very promising and will increase the yield from a given number of recruits. Future work might focus on the stress caused by

handling, displacement, and behaviour of the post-recruits as well as on the function and impact of escape gaps in traps.

The new promising area with management implications is in habitat manipulation, which theoretically could lead to increased recruitment and possibly reduced natural mortality. Research in this area by developed countries, though expensive, could prove to be a good investment for the future of severely resource-limited lobster fisheries.

Possible Future Workshops

The workshop considered what might be the special topics of future lobster meetings. Although there was no general agreement that there was a need for a follow-up meeting to be held in the near future, it appeared desirable to have some objective to which work could be directed in order that the next meeting might address a relevant topic. Some possible topics were discussed such as: "Habitat and ecological and fishery interactions", " modeling lobster populations from biological and bioeconomic perspectives" and, in general, it was felt that future workshops should be restricted to lobster populations in order to encourage a small but key group of people to attend.

The other aspect that seemed critical for further lobster research, is the need to maintain good communication between workers in the immediate future. An updated list of lobster workers currently in the field would be useful in arranging exchange of information. In general, it was felt that the next meeting should ideally be in the Caribbean region, in order to promote discussion of some of the Palinurid problems of the northern hemisphere.

REFERENCES

Anthony V.G. and J.F. Caddy. 1980. Proceedings of the Canada-US workshop on status of assessment science for N.W. Atlantic lobster (*Homarus americanus*) stocks, St. Andrews N.B. October 24-26, 1978. *Can. Tech. Rep. Fish. Aquat. Sci.* 932:186 pp.

Caddy, J.F. (in press). Modeling stock-recruitment processes in crustacea: some practical and theoretical perspectives. In: "International Workshop on lobster recruitment" to appear as a Canadian special Publication of Fisheries and Aquatic Sciences.

Conan, G.Y. and M. Comeau. 1986. Functional maturity and terminal molt of male snow crab, *Chionoecetes opilio*. *Can. J. Fish. Aquat. Sci.* 43:1710-1719.

Phillips, R.F. and J.S. Cobb. 1979. Workshop on lobster and rock lobster ecology and physiology. CSIRO Publication of the Division of Fisheries and Oceanography, Circular No. 7 Melbourne, Australia, 300 pp.

Scarratt, D.J. 1973. Abundance, survival, and vertical and diurnal distribution of lobster larvae in Northumberland Strait, 1962-63, and their relationship with commercial stocks. *J. Fish. Res. Bd. Can.* 30:1819-24.