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Prospects for the Development of Color Phases for Lobster Population Studies

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Abstract

Virtually nothing is known about the survival and distribution of wild lobsters from hatching to recruitment, as techniques have not been available for marking eggs or larvae in such a way that they can be identified for recovery from the fishery 5-12 yr later. One possibility that has been considered is the development of distinctive color phases (red, yellow, blue) for release under "natural" conditions. Such a variant could easily be identified years later in the commercial catch, and might be further marked with biochemical or genetic information that would identify date and location of release.

Previous attempts to develop distinctive color strains have failed primarily because the biological information needed for successful husbandry was not available. However, the required techniques have been developed, and larvae could be released in as little as 5 yr from the time the necessary brood stock are acquired.

If a decision is made to attempt large scale release of distinctive color variants, immediate effort should be applied in four areas: (a) acquisition of brood stock for the preferred color phase, (b) assessment of natural incidence of various color phases in Canadian and Gulf of Maine inshore and offshore waters, (c) development of biochemical or genetic markers for the identification of released progeny, and (d) an in-depth study of lobster stocks, leading to the selection of the most appropriate site for release of color variants.

Résumé

On ne connaît à peu près rien de la survie et de la distribution des homards dans la nature depuis l'éclosion jusqu'au moment où ils sont recrutés, parce qu'on ne disposait pas de techniques de marquage des oeufs et des larves qui auraient permis de les identifier dans les prises, 5 à 10 ans plus tard. On a étudié une possibilité, celle de l'établissement de phases de coloration distincte (rouge, jaune, bleue) à être mises en liberté dans des conditions "naturelles". Un tel mutant pourrait être facilement identifié plusieurs années plus tard dans les prises commerciales. On pourrait le marquer de nouveau en faisant appel à une information biochimique ou génétique qui permettrait de reconnaître la date et l'endroit de la mise en liberté.

Les efforts passés en vue de l'établissement de lignées de couleur différente ont échoué, en grande partie à cause de l'insuffisance d'information biologique nécessaire à une bonne gestion. Cependant, les techniques nécessaires ont été mises au point, et des larves peuvent être libérées dès 5 ans à partir du moment de l'acquisition du stock reproducteur.

Si l'on décidait d'entreprendre la libération à grande échelle de mutants de coloration distinctive, on devrait dès maintenant axer l'effort sur quatre domaines: (a) acquisition d'un stock reproducteur de la phase désirée, (b) évaluation de l'occurrence naturelle des diverses phases dans les eaux côtières et du large du Canada et du golfe du Maine, (c) définition de marqueurs biochimiques ou génétiques qui permettront d'identifier la progéniture libérée et (d) étude approfondie des stocks de homards en vue d'un choix judicieux du site de libération des mutants.

Introduction

The literature contains little empirical information on the mortality and distribution of American lobsters from hatching to recruitment several years later. Survival through the larval stages to settlement is often quoted as less than one percent, and estimates of survival from hatching to maturity vary from 1:1000 to 1:100,000.

Distribution patterns are equally speculative. The planktonic larvae may or may not drift in the surface waters, and time spent in the planktonic stages (and, therefore, potential distance travelled) is dramatically affected by temperature. Whether hatches from one site routinely populate another highly specific site is not known. The profound technical difficulties in tagging or marking eggs or larvae for future identification have deterred the accumulation of any firm data on survival and distribution from hatching to recruitment.

To be recovered from among the thousands of lobsters landed each year, a marked lobster must be highly visible. One obvious solution to this is the release of distinct color phases. Although it has long been recognized that a true-breeding stock of red, yellow or blue lobsters could be used as biological tags to study lobster population dynamics, little progress has been made in the development of such color phases. This paper summarizes the history of, present technical basis for, and problems likely to be encountered in the development of color variants for the study of survival and distribution of American lobsters.

History and Present Status

John T. Hughes has been collecting and breeding color variants at the Massachusetts State Lobster Hatchery since 1964, trying to develop distinct color phases that could be used to assess the effectiveness of the State lobster stocking progam. Although they obtained their first hatch of color variants in 1969, they have never had progeny available in sufficient numbers to be used in their stocking program, and have never released color variants in the wild.

At the St. Andrews Biological Station, color variants have been gradually incorporated into a breeding program that includes eight hatches of larvae from female color variants mated with normal males over the last 6 years. The present stock at St. Andrews includes red, orange, white, blue and grey females and males, as well as several mottled and variegated patterns.

Although blue is the color phase preferred by the Massachusetts State Lobster Hatchery, red seems to be the most common, most easily recognized, and most inclined to breed true. The stock at St. Andrews includes 13 red lobsters, four of which are female, and 12 individuals of the F_1 generation from a red female x normal male (six red, six normal) which are approaching maturity. In addition, there are 20 normal colored progeny from a blue female x normal male, and more than a hundred from a white female x normal male, all being maintained for future breeding studies.

Small stocks of color variants are also maintained at the Ellerslie Station in Prince Edward Island and at the Halifax Laboratory in Nova Scotia, but no long-term breeding programs have been attempted with these lobsters. The principal impediment at all of the above institutions has been lack of a sufficiently large pool of mature monochromatic variants of any color phase. As a result, most of the crosses that have been attempted so far have been between color variants and normal lobsters. The Massachusetts State Lobster Hatchery is now holding approximately a dozen females that are scheduled to produce eggs during 1981, and some of these represent monochromatic blue x blue crosses.

Biochemistry and Genetics of Shell Color

Shell coloration in lobsters is due to the presence or absence of carotenoids, pigments that occur widely in nature but are synthesized only in plant tissues. Therefore, lobsters must either obtain carotenoids directly from their diet or produce them by oxidation of dietary carotenoids. Astaxanthin (red), which is the major carotenoid in crustaceans, undergoes remarkable spectral shifts upon binding with protein. In the shell it is only found in the conjugated form and, depending on the nature of the protein, may appear yellow, red, orange, dark green, blue or brown. Although the shell displays a number of basic colors, the only integumentary carotenoprotein identified to date seems to be crustacyanin, a blue pigment (Zagalsky 1976), although the literature is far from clear on this point (Salares et al. 1978).

Unfortunately, there is very little information on the heritability of shell colors and color patterns. The metabolic pathway for conversion of β-carotene to astaxanthin involves five intermediates (Katayama et al. 1973), and since the final color depends not only on the carotenoid but on the nature of the binding protein as well, a number of genes or enzymes may be involved.

Development of a Breeding Program

One of the major impediments to lobster breeding programs has been an inadequate understanding of the female reproductive cycle. Over the years a great deal has been written about the lobster reproductive cycle, but much of it has been inaccurate. We have recently provided a comprehensive description of the female cycle (Aiken and Waddy 1976, 1980a, b; Waddy and Aiken 1979), and have developed or improved techniques for determining the state of maturity, predicting egg extrusion (Waddy and Aiken 1980a, b), and controlling mating, brooding success and hatching time (Aiken and Waddy 1980c). As a result, the technology is now available for the production of large numbers of larvae from crosses of color variants.

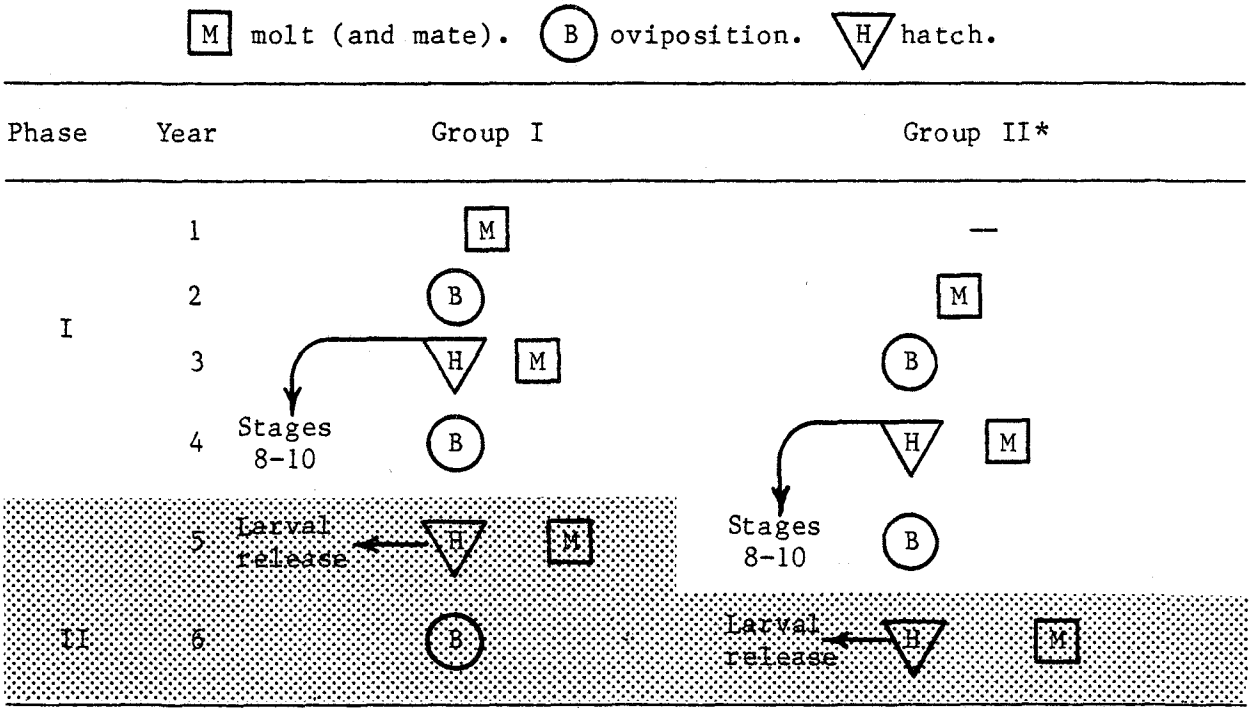
Unfortunately, little is known about the results to be expected from various crosses, and available information can be misleading. For example, the progeny of a cross between a red male and a red female were described as 50% red, 25% normal color, and 25% albino (Anon. 1969). Actually, the male was yellow, not red (J. T. Hughes, pers. comm.), a fact that explains the color distribution of progeny and provides some insight into the heritability of shell color. Unfortunately, the color of an egg or a larva is not a reliable indication of what the shell color will be when the lobster reaches stage 15, 20 or 30, several years after release. White

eggs have hatched into normal colored larvae, white lobsters taken from the wild at canner sizes have turned pale blue within a couple of years, and pale green wild adults have gradually acquired a normal coloration after a molt or two in captivity.

The first step in propagation is the acquisition of significant numbers of mature lobsters displaying "strong" and uniform color variance. "Strong" in this sense refers to color saturation, whether it be red, yellow, blue or white, because experience indicates the weak or insipid colors are the least stable. Uniformity of color also appears to be important. However striking the calico, marbled or variegated patterns may be, they complicate a breeding program designed to produce predictable results in the shortest possible time.

The minimum breeding stock would consist of six adult males and twelve adult females of a given color. The first phase in the program would be the determination of heritability, and would require the rearing of progeny to approximately Tenth Stage to assess color stability. This phase would require approximately 5 yr for completion. Phase II, the production of larvae for population studies, could actually commence before the completion of Phase I, assuming some of the initial crosses produced stable monochromatic progeny. Thus, larvae might be available for release as early as years 5 and 6 of the program. This is summarized diagrammatically in Table 1.

Table 1. Schedule for production of confirmed color variants for release within 5-6 years of acquisition of mature brood stock.



*Reproductive cycles of approximately half of females will be 180 degrees out of phase.

In this program, all breeding stock would be held under normal environmental conditions on a 12-mo cycle. In theory the annual cycle be compressed to 9 mo, thus reducing the 6-yr program to 4.5 yr, but the effects of such an accelerated cycle have not been adequately assessed.

Phase II can commence on year-5 if a sufficient number of stable color types can be identified from the initial crosses in Phase I. The same parents would be used on the second breeding cycle, and those that initially produced stable monochromatic progeny would then be available for release at year-5. If no stable monochromatic progeny result, or if it seems desirable to use F_1 progeny as breeding stock, then the schedule would be protracted by as much as 3 yr.

Natural Incidence of Color Phases

The primary objective of large scale releases of color variants would be to obtain information on natural mortality and distribution, information that cannot be obtained with conventional methods. Such information would accrue as a result of recaptures, presumably 4-12 yr after release. To ensure that recaptures are reported, the program would have to be extensively publicized and an adequate monetary incentive offered. A motivated industry could return large numbers of color variants, an undetermined but possibly significant number of which would be those that occur naturally and which have always been processed without fanfare. On the few occasions where color variants have been actively solicited from the fishing industry, they have been available in surprising numbers.

Therefore, the first step in the development of color phases for population studies would be the determination of natural incidence of the different color phases in inshore and offshore Canadian and Gulf of Maine waters. If this were started immediately, it would have the added benefit of producing the color phases needed for a breeding program. Since we cannot predetermine where released larvae will turn up 4-12 yr hence (and since this information could be one of the major products of the program), it will be necessary to have an adequate picture of natural incidence in all areas. Of course, this assumes that statistical means will be used to identify variants released through the program. If X-Ray spectroscopic, electrophoretic, immunologic or other biochemical means (see Hedgecock et al. 1974, 1977) can be developed to identify individuals that originated from released families, the importance of natural incidence would be diminished. The color phase then becomes the visual messenger that ensures the lobster will be returned for analysis to determine whether the specimen was part of the release program. This approach holds considerable promise, and should be included as a primary element in any program to release color variants.

Methods of Release

A great deal of thought must be given to the method and site of release, as the success of the program in producing meaningful mortality and distribution data will be affected by this. Color variants may be released as: (a) First Stage larvae hatching from females contained in cages on the bottom; (b) Fifth Stage lobsters released on the bottom according to standard techniques; or (c) juvenile lobsters (Eighth or Tenth Stage) released as they are in France. Each of these methods would yield different types of information. The most meaningful data on mortality and

distribution would be expected with a natural hatch of larvae from females caged on the bottom. However, we know nothing about possible effects of genetic programming on larval behavior and distribution. For example, if a female is genetically programmed to be at a specific geographical location when her eggs hatch, and the behavior of her larvae after hatching is genetically programmed to take best advantage of tides and currents in that specific release area, then mortality and distribution data would be inordinately biased for larvae hatched and released at the wrong location.[1] Release of juvenile lobsters on the bottom avoids this bias, but fails to account for two very significant aspects of the planktonic stages - natural larval drift, and natural mortality.

Site and Timing of Releases

Unless sophisticated techniques can be developed for differentiating between wild and released lobsters, and between families of released individuals, the release sites will have to be concentrated at a single location so that long-term distribution data will be meaningful. The selection of this release site therefore requires a great deal of thought, and the primary criterion should be the potential for demonstrating a principle (not political expediency).

Consideration must also be given to the timing of releases, since they should correspond to the natural hatching time for lobsters in the selected areas. Hatching in some locations in the Bay of Fundy, for example, occurs in September-October. The survival and distribution of larvae released at those sites in June or July probably would not be representative of the normal situation. As previously noted, techniques now available permit the control of embryo development rate so that hatching can be obtained when required.

Validity of Returns

There is some question whether the mortality and distribution of color variants released by any of the above means will be representative of the mortality and distribution of wild lobsters. If not, then the use of color variants to study population dynamics is questionable. The problem of genetically programmed maternal and larval behavior has already been mentioned. If distribution patterns are influenced by genetics, then the study of distribution through release of cultured larvae is even more complicated.

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[1] Ovigerous females, for example, are found in large numbers in certain areas prior to hatching, and some larvae demonstrate depth-regulatory capability (Ennis 1975). Larvae are assumed to drift in the upper few mm of the water column, but if this is so, why do they have depth-regulatory capability, why has it been so difficult to collect a continuous series of larval stages in the surface waters of areas other than the Gulf of St. Lawrence, and why are some larvae in the Bay of Fundy released so late in the year that declining surface temperature virtually assures their destruction? Are these larvae programmed to depths where favorable currents will ensure their survival and distribution? Until these questions can be answered, a genetic component should be assumed and the release of larvae handled accordingly.

Another problem concerns the relative mortality of color variants. All other things being equal, is the natural mortality of a red, white or a blue lobster comparable to that of a normal colored one? Intuitively, one would say no, but there are no empirical data to corroborate the assumption, and the relative survival of different color phases has never been assessed scientifically. The concept of natural selection suggests that color variants compete less successfully than normal colored lobsters, and that the most common phase (red?) has relatively better survival than the less common phases, but this may be an oversimplification. An appropriate analogy might be the current use of internally tagged lobsters to study growth. When the internal ("sphyrion") tag was first developed, it was assumed that a lobster bearing an external tag anchored in the thoracic musculature would grow at a slower rate than an untagged lobster.[2] Nevertheless, internal tags were accepted as an important tool for field studies on the pragmatic assumption that some indication of growth rate is better than no indication at all. If the same reasoning is applied to the use of color phases to study natural mortality and distribution, most of the objections become academic.

Summary and Conclusions

There are no serious biological or technological impediments to the development of distinct color phases for lobster population studies. The reproductive cycle is now sufficiently understood, and the techniques required for a selective breeding program have been in practical use for the last few years. There are, however, some philosophical questions concerning the value of mortality and distribution data derived from such a program.

No single color phase stands out as the obvious choice, but blue and red seem to offer the most promise. The red phase seems to be the most common, and since there are a number of these now in captivity in various places, a reasonable supply of breeding animals could be obtained with a minimum of trouble. Furthermore, red should be the preferred color for Canadian work if present emphasis on the blue phase continues at the Massachusetts State Lobster Hatchery.

Immediate effort should be applied in four areas: (1) acquisition of brood stock for the preferred color phase; (2) assessment of natural incidence of various color phases throughout Canadian inshore-offshore waters and the Gulf of Maine; (3) development of biochemical techniques for the identification of released progeny; and (4) in-depth study of lobster stocks, leading to the selection of the most appropriate site for (and method of) release of color variants. Items (1) and (2) can be accomplished concurrently.

From the time of acquisition of necessary brood stock to the earliest possible time of release, approximately 5 yr would be required. Results from such releases could not be expected for at least 4-5 yr after release. Therefore, the period of productive returns from a program begun in 1981 would be the years 1990-95, depending on breeding success, area of release, and subsequent growth rate (i.e., temperature experience) of released lobsters. Costs would be relatively insignificant, occurring primarily

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[2] It now appears this is not the case. Measurements of postmolt lobsters in their burrows with their cast shells indicated that growth of internally tagged lobsters is no different from untagged lobsters (R. A. Cooper, pers. comm.).

during the initial acquisition period and then again during the recapture period.

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