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Growth and Survival of Larval Fishes in Relation to the Trophodynamics of Georges Bank Cod and Haddock

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FOREWORD

A paramount problem in fisheries science is understanding the causes of natural variability in fish production and resultant stock size. This variability is thought to be fixed by the time fishes are recruited to the fishery and is believed to be determined by factors influencing survival and growth in the early life stages (egg, larval and juvenile). These determining factors are both biological and physical. Predator-prey relationships are the important biological mechanisms with early life stage success linked to capture of prey (food) and avoidance of predators. Physical factors directly affect physiological mechanism and developmental rates as well as the transport and distribution of the early life stages and their predators and prey.

The Marine Ecosystems Division of the National Marine Fisheries Service, Northeast Fisheries Center, has been especially cognizant of the need to understand recruitment variability for potential use in management strategies. As a result, the Division has focused on research designed to understand the possible controlling factors mentioned above. The Larval Dynamics Investigation within the Division has concentrated its research on the role of food sources and successful feeding in the larval stage. The three papers of this NOAA Technical Memorandum (two of which have been presented elsewhere) present a detailed description of this research. The first paper on nutrition and trophodynamics explores the present state of knowledge of larval feeding as it relates to success (growth and survival) or failure (starvation and death) with special emphasis on experimental research. The second paper describes the at-sea sampling strategy of process-oriented, multi-discipline studies of fine and micro-scale distributions of cod and haddock larvae and prey on Georges Bank in relation to physical factors. The operational plan, sampling gear & instrumentation, and special techniques employed are discussed in terms of results and usefulness of the parameters measured. The third paper documents the evolution and development of stochastic models simulating processes associated with feeding, growth, and survival of larval cod and haddock as individuals and populations. This modelling synthesizes much of the laboratory experimental and field empirical data bases collected by the Division.

Interim conclusions from this compendium of continuing research indicate that starvation mortality in the larval stage is one of the largest components of total mortality and is most prominent in the first weeks after hatching. However, its magnitude is such that it does not appear to be population limiting under most conditions observed in the field thus far. There is normally enough food in the sea to allow an ecologically significant portion of larval populations to grow and survive. Thus, the implication is that predation and/or factors affecting the juvenile stage may be keys to variable recruitment.

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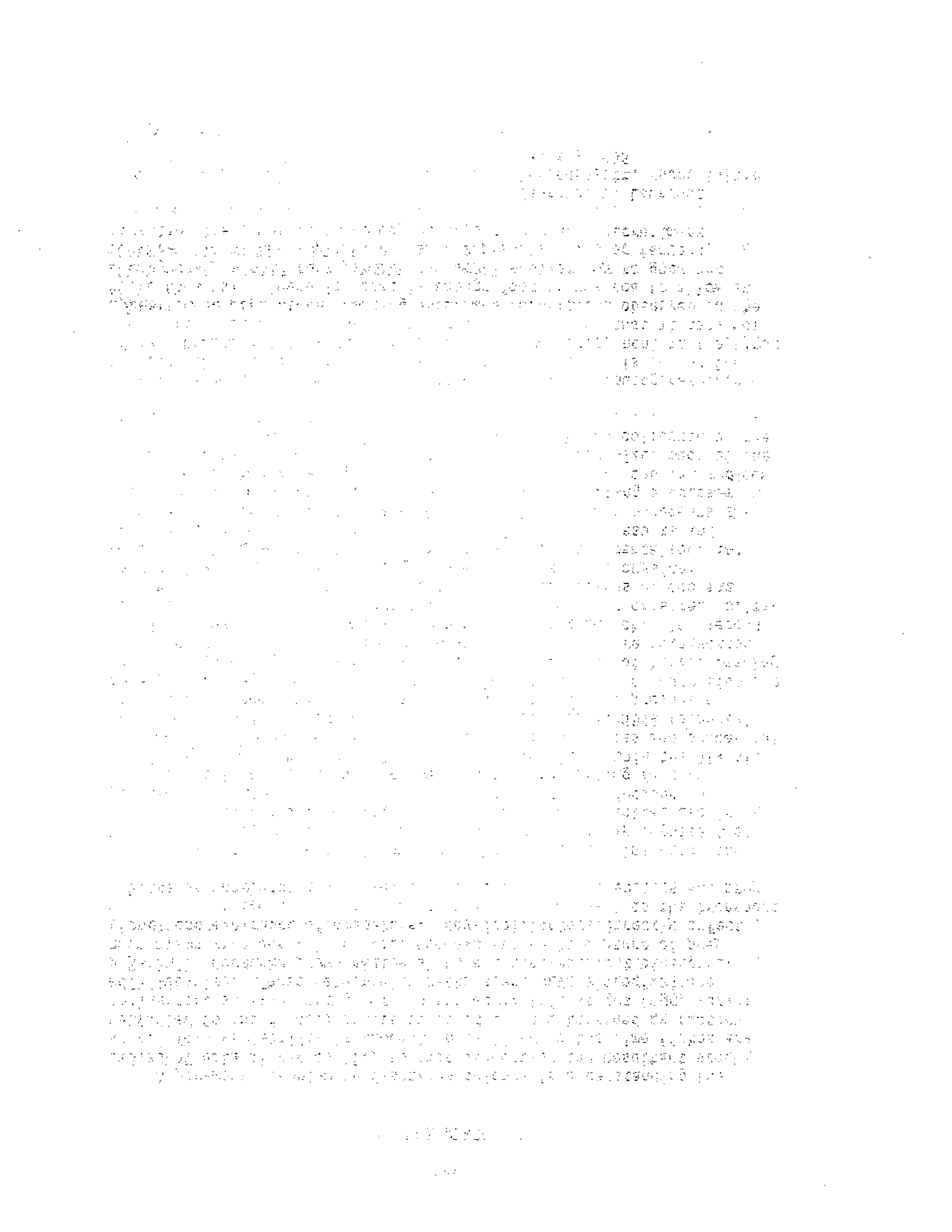

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Figure 44. A graphic illustration of the parameters and calculations involved in assessing food limitation and impact on prey for larval gadids on Georges Bank.

NUTRITION AND TROPHODYNAMICS OF LARVAL FISH--REVIEW, CONCEPTS, STRATEGIC RECOMMENDATIONS AND OPINIONS[1,2,3]

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I INTRODUCTION

A significant proportion of the natural variability in fish production and resultant stock size is believed to be the result of changing recruitment to a fishery. Recruitment is, in turn, thought to be directly related to the survival success of the early life stages. The ability to understand the causative factors and predict early life survival and relate it to recruitment would be a paramount step toward effective fishery management schemes.

In a consideration of the early stages, particularly the larval, it has almost become axiomatic that the trophic (feeding) relationships of predation and starvation with their inherent biological components modified by environmental physical factors are the basic controlling principles of survival. It is the purpose of this document to explore the state of knowledge of larval feeding as it relates to success (growth and survival) or failure (starvation and death) under the general heading of larval fish nutrition.

II STATE OF KNOWLEDGE AND REVIEW

Because of the length restriction of this paper and the desire to use a good portion of it for concepts, opinions, and recommendations, I will highlight our present state of knowledge concerning larval feeding with reference to a number of recent review or workshop contributions for more detail. A workshop on approaches to larval fish feeding studies (G. Laurence and E. Houde, convenors) was held at this year's 6th Annual Larval Fish Conference, CBL, Solomons, MD. The appended outline (Appendix) used to prepare the program for that workshop gives a reasonably detailed presentation of factors involved in larval feeding. Additionally, 2 recent review publications (Hunter, 1981, and Theilacker and Dorsey, 1980) as well as the original larval fish review by Blaxter (1969) serve as a compendium from which much of the review part of this paper is drawn.

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[1]A contribution to: Fish Ecology III, Cooperative Institute of Marine and Atmospheric Studies, University of Miami; September 6-10, 1982; Brian J. Rothschild, University of Maryland, and Claes G. H. Rooth, University of Miami, Convenors.

[2]This is MARMAP Contribution No. MED/NEFC 82-50.

[3]This is a University of Miami Technical Report No. 82008.

There are a number of factors related to food and feeding which directly affect larval survival. They are: 1) duration of development from the embryo stage to the time when the first feeding responses occur, 2) the preferred food species and its abundance and distribution, 3) the behavioral relation between the larva and its prey, 4) the success of feeding responses, 5) the swimming ability of larvae in search of food, and 6) the required food ration for growth and metabolic expenditure.

Maternal inheritance and temperature control the initial amount of endogenous yolk reserves and the developmental rate, respectively, prior to external feeding. The efficiency with which yolk is utilized probably is an important determinent of early survival since size and condition of larvae will affect their ability to begin feeding. Presumably, larger larvae produced by more efficient use of endogenous reserves will have an advantage over smaller larvae in foraging ability. Blaxter (1969) noted for a number of species that development at different temperatures can produce larvae with morphological differences as well as different percentages of yolk and larval tissue at hatching and the initiation of feeding. Furthermore, a number of authors (Gray, 1926; Smith, 1947; Lasker, 1962; Toetz, 1966; Laurence, 1969, 1973) reported potential energy deficits with not enough yolk to provide for normal requirements before the ability to feed on external prey organisms. Another aspect is the ability to withstand starvation during the period when feeding commences if food is initially unavailable. This has been termed "point of no return" or delayed feeding. Table 1 from Theilacker and Dorsey (1980) presents an extensive summary of the known information about these early developmental factors.

Preference for certain food organisms by larvae has been indicated in numerous field studies (Ogilvie, 1938; Marak, 1960; Last, 1978a,b). This selective feeding is influenced by the size of the larva and its mouth in relation to prey size (Hempel, 1965; Sherman et al., 1981). Figure 1 from Last (1978b) and Figure 2 from Hunter (1981) illustrate these points. Hunter (1981) summarizes by stating that marine larvae select foods of increasingly larger size as they grow, but that the average and range of sizes selected differ greatly among species and may be diagnostic of specific ecological roles.

Prey concentration or abundance has been directly correlated with larval growth (Laurence, 1974; Houde, 1975). Many larval fish researchers feel that the contagious distribution of larvae and their prey in patches and the chance meeting of these patches is a prime determinent of larval feeding success (Jones, 1973; Lasker, 1975; Laurence, 1977). This has been demonstrated experimentally in the laboratory by Houde and Schekter (1978) who showed that larval sea bream subjected to simulated patches of copepods for short periods of time could equal results from constant exposure to similar concentrations. Summary Tables 2 and 3 from Theilacker and Dorsey (1980) and Table 4 from Houde (19780 present relevant aspects of prey concentration.

Behavioral relationships between larvae and prey determine the effectiveness of prey capture. Larval behavior usually consists of perception, recognition and directed, definite responses to a food organism. Hunter (1972, 1977, 1981) has discussed and described the ethological basis of these activities in detail. Most larvae are daylight feeders and perceptive distances generally increase

with increasing body length. There is some indication that older larvae may feed in reduced light (Blaxter, 1969).

The swimming ability of larvae directly determines the amount of water searched for prey as well as metabolic expenditures of energy. When food is scarce, weaker-swimming larvae would be subject to starvation because of the lowered frequency of contact with prey organisms. Swimming capability as measured in speed tests are summarized in Table 5 from Theilacker and Dorsey (1980) showing species specific results for burst and cruising measurements.

The combination of swimming ability as measured by linear speed and perception as measured by visual field produce a functional measure of the actual volume of water a larva is capable of searching. The volumes are small in the range of 0.1's to 10.0's of liters per hour as indicated by the compilation in Table 6.

Success or failure of feeding responses has been observed by some researchers to influence larval mortality. Blaxter (1962) reported a failure of some herring larvae to feed at all. Schulmann (1965) attributed failure of Pacific sardine larvae to feed to a "non-feeding behavior" in which the larvae would "give up" if initially unsuccessful. First feeding success is typically lower than for success of older, larger larvae within a given species, although there can be a significant difference between species that are approximately the same age. As examples: larval anchovy captured food successfully 10% of the time at first feeding increasing to 90% in 3 weeks (Hunter, 1972); initial feeding success of herring larvae was 2-6% and 32-62% for plaice (Blaxter and Staines, 1971). These differences are attributed to swimming abilities by the researchers.

The required food ration of larvae for growth is of prime importance in survival and successful development. All physiological and developmental processes require energy in the form of food. The processes involved include growth, metabolism, digestion, assimilation, excretion and osmoregulation. The bioenergetic relationships of these processes for early life stages have only recently been studied and quantitated in a holistic way (Vlymen, 1974; Laurence, 1977; Beyer and Laurence, 1980; Houde and Schekter, 1982). The review by Theilacker and Dorsey (1980) presents summaries of research results for many of the individual factors involved in larval energetics. Clearly, most of the processes are species specific and/or temperature dependent and generalizations are difficult with the present state of knowledge. Table 7 from Theilacker and Dorsey for growth efficiencies and associated parameters gives, perhaps, the most valid general comparison of known information between larval marine species.

Absolute nutritional requirements for fish larvae, especially non-salmonids, are virtually unknown. For fishes in general, proteins are the largest single class of natural dietary component. Twenty-three amino acids occur in natural fish foods, 10 of which are incapable of being synthesized by fish and are therefore essential. Tests in feeding young salmonids and freshwater species show that gross protein requirements as a percent of diet are highest in initial feeding stages and decrease as size increases (National Research Council, Subcommittee on Cold Water Fish Nutrition, 1981). For maximum growth, young fish must ingest a diet nearly half of which is digestable protein containing at least the

10 required amino acids. Lipid requirements for fishes are not adequately described (NRC, 1981). Polyunsaturated lipids are found in the natural diets of fishes including essential fatty acids. These are used for energy, for cellular structure, and for maintenance of the integrity of biomembranes. Little carbohydrate is found in the natural diet or body of fishes, and they can grow on diets devoid of carbohydrates. However, hexoses are of natural nutritional significance to fishes, and all fishes studied have the ability to utilize carbohydrate as an energy source (NRC, 1981). Nutritional constituent composition of larval fish food organisms is virtually unknown, although gross energetic equivalents have been measured for some crustacean prey (Table 8).

III CONCEPTS, STRATEGIES AND RECOMMENDATIONS

It is clear from the review that we have a great deal of specific knowledge regarding component parts of larval feeding relationships and associated processes. Nevertheless, we have thus far been unable to relate this knowledge to conditions in the sea that pinpoint functional causal mechanisms controlling survival in a reliable, quantitative way for predictive management purposes. The following discussion presents a conceptualization of larval trophodynamics as well as recommendations for sampling schemes and rationale, integration into appropriate management systems, and some personal opinions about persistent problems.

A Concept

My conception of larval trophodynamics and related survival is that it is most likely a probabilistic process. Given the fact that fish have evolved over millions of years to respond reproductively (spawn) to environmental cues, primarily temperature and photoperiod, within a certain finite range (temperatures usually have a range of 1-3°C), they are not likely to be affected by productivity (primary-secondary) disynchrony for the entire spawning period. Match-mismatch is not apt to occur on a large scale. More plausible is the situation where larval survival is controlled stochastically within a range of population levels affected by chance encounter with "patchy" food and fine tuned by predation. Catastrophic events such as major meteorological occurrences, advective currents, anoxias, or man's fishing could also cause fortuitous major negative impact.

The basic functional aspect of this in terms of trophic encounter-interactions can be explained within the framework of Hutchinson's (1961) "paradox of the plankton." Plankton systems support a diversity of organisms in similar niches unlike most systems where competitive exclusion sets up. Physical mixing in the planktonic environment prevents dominance and contagion caused by gradations of this mixing causes a probabilistic environment. Chance trophic encounter resulting in success or failure could easily happen in this type system.

Progressing from the more general picture of Hutchinson's "paradox" to the specifics of predator-prey interactions, it can be argued that it doesn't really matter if you're a proponent of the so-called Cushing (predation) or Jones (starvation) hypotheses regarding larval survival because they are both the same thing. They can be expressed together in a triotrophic relationship (Laurence,

1981; Figure 3). A key point in this triotrophus is a redefinition of or clarified interpretation of density independence/dependence. If larvae function as predators, they are essentially density independent of each other because the order of magnitude of their own spatial density distribution in nature is so much greater than that of the density of the food they feed and grow on that they are unlikely to directly compete with each other but are more affected by the density of their food as it affects starvation. Conversely, if a larva functions as a prey organism, its mortality is most likely density dependent because its spatial distribution is much denser than its predators and the more larvae there are, the more chances for predation mortality.

The overall interpretation of this is that at normal adult stock and larval population levels, larval survival and growth is mainly density independent and controlled by the varying encounter with patchy prey. This is a probabilistic process and results in varying recruitment. At extremely abundant levels of larvae, density dependent predation on larvae may operate to prevent abnormally large populations in most instances or to reduce levels produced from large adult stock size. This is mainly a correlative process associated with abundances. At very low adult stock levels, egg production and subsequent larval survival may be inherently so low as not to produce any recruitment. All this is affected by adult stock size and physical oceanographic process. The physical processes have, in general, a random influence and the adult stock level has a more direct or abundance-cause and effect at low population levels and can be influenced greatly by fishing effort.

Strategy Relating Larval Trophodynamics to Applied Fishery Management

As previously stated, the ability to understand larval fish trophodynamics and resultant survival and relate this to fishery production would be a major advancement in resource management capabilities. Three main components are needed: 1) abundance estimates or indices of egg and larval stages, 2) quantitative estimates of larval growth and feeding parameters, and 3) predictive models. Two of these three requirements are currently available as well as portions of the third. Ichthyoplankton surveys conducted routinely as in the MARMAP mode, for example, provide abundance estimates. A variety of larval fish growth and survival models exist (Laurence, 1977; Beyer and Laurence, 1980, 1981; Beyer, 1980), some of which have population predictive capabilities. Larval trophodynamics, physiology and behavior have been studied extensively in the laboratory and field, as indicated in the review portion of this paper. The only area of incomplete knowledge is in the physical-mathematical description of the spatial-temporal bounds of larval predator-prey organisms from the natural environment and associated production factors. Several laboratories have or are attempting multidiscipline process-oriented field programs to study these problems (Lasker, 1975, 1981; Tilseth and Ellertsen, 1981; Lough and Laurence, 1981). Once these are known, prey encounter rate functions in the existing models can be used to predict larval individual and population growth and survival based on the abundance estimates of the eggs or early larvae from ichthyoplankton surveys as an initial starting point. Predicted estimates of larval survival can then

be correlated with data from subsequent fall juvenile survey estimates conducted for a number of species as a validation test. The final step is to integrate the results into the recruitment functions of appropriate ecosystem or management models.

Sampling Rationale and Strategy for Field Verification-- Georges Bank Haddock as an Example

The above cited experimental and descriptive field results of larval trophodynamics from the first half of this paper, the proposed conceptualization of functional mechanisms of larval trophodynamics, and the proposed strategy relating to fishery management needs provide the basis for formulating sampling rationale and strategy for appropriate field research. Particular emphasis should be given to the "arena of predation" within which larvae succeed or fail including: 1) a description of spatial and temporal variability of larval prey and predators, 2) confirmation of linkages and factors affecting production of the 3 trophic levels, 3) identification and understanding of the operating function of physical processes causing or mediating biological consequences. Since fish larvae are small, and short time and small space scales need to be considered, the proposed sampling presents unique and challenging problems for a field program and the technology currently available to support it.

Quantitative Rationale

The prey field of a larval fish is defined by the larva's physical abilities of locomotion, behavior, and physiological limitations. Actual quantification of these aspects can provide discrete dimensions relative to a feasible ship board sampling scheme. The following presentation defines the problem in quantified terms for Georges Bank haddock based on empirical observations from experimental research similar to that reviewed in the first part of this paper and model application extended to the current field program operated by the Larval Fish Dynamics Investigation of the Northeast Fisheries Center.

Constant, Variable and Parameter Definitions

ΔG = change in growth day^{-1}. Lab experiments (Laurence, 1974, 1978) and field data have shown a maximum rate of approximately 6% day^{-1} on a weight basis and about 2% day^{-1} as a minimum, viable rate.

$R\omega$ = food ingested day^{-1}. Where: R = # ingested and ω = food weight which is a variable function of larval size (Beyer, 1980; Beyer and Laurence, 1981).

β = coefficient of digestion, a variable changing with larval size based on nitrogen budget data (Buckley and Dillman, 1982) and from Beyer and Laurence (1981).

so:

$\beta R\omega$ = Ingested food that is digested

and

$(1-\beta)R\omega$ = Defecated portion of ingested food

α = Fraction of digested food lost in chemical and physiological processing; a constant 0.40.

Thus:

$$(1-\alpha)\beta R\omega \tag{1}$$

is available for growth and metabolism

where

KW^n = Metabolism day^{-1} with

K = Coefficient of metabolism (a variable changing with larval activity level (Beyer and Laurence, 1980, 1981)

n = 0.671 (a constant exponent, Laurence, 1978), and W is larval weight.

Thus:

$$(1-\alpha)\beta R\omega = \Delta G + KW^n \tag{2}$$

is the mass balance equation

and

$$R = \frac{\Delta G + KW^n}{(1-\alpha)\beta\omega} \tag{3}$$

is the solution for the number of food organisms required day^{-1}.

Miscellaneous

The above relationships need to be converted into a standard unit of measurement for calculation purposes. The calorie is that unit and conversion factors are as follows:

Larval haddock tissue = 0.0046 calμg^{-1} (Unpublished Narragansett Lab data)

Copepods (larval prey) = 0.0052 calμg^{-1} (Laurence, 1976)

Metabolism ($\mu \ell O_2$) = 0.005 cal (standard oxycaloric equivalent)

The larval haddock weight-length equation is:

$$W = 0.044 \ell^{4.476} \quad \text{(Laurence, 1979)}$$

Larval Haddock Feeding Requirements

Table 9 presents upper and lower limit values of feeding related parameters for haddock larvae of three different sizes. The most important parameter from this Table is R the required number of ingested prey day^{-1}. The absolute value of the range decreases with larval size because the preferred prey size increases.

Larval Haddock Swimming Abilities and Searching Behavior

The visual field and perception distance for larval haddock is important in the calculation of prey encounter rates.

Visual Field = $2/3 \pi \delta^2$

where δ is the perception distance which is approximately 0.5-1.0 times the body length (BL) of the larva (Beyer and Laurence, 1981).

Larval swiming speed is also a determinent of prey encounter rate.

Larval linear sustained swim speed ≈ 1.0-2.0 BL sec^{-1} (Laurence, 1972).

The total volume of water searched day^{-1} by a larval haddock then becomes the product of the visual field times the linear distance swam = $2/3 \pi \delta^2 \cdot$Distance swam unit $time^{-1}$.

Larval Haddock Food Encounter

All the above parameters and relationships have been used to calculate the important factors in larval food encounter and searching capabilities. These are presented in Table 10 for three larval haddock sizes.

The linear distance swam, if a larva decided to swim in a straight line, at the sustained swim speed is in the order of hundreds of meters day^{-1}. This assumes a 12 h swimming day because larvae are visual feeders and become relatively inactive at night.

The swimming speed transformed to cm sec^{-1} is for a comparison to current velocities. Most larvae would be actively transported by prevailing tidal or other currents.

The volumes of water searched day^{-1} are relatively small because of the short perception distances. However, they can be over long vertical or horizontal distances (hundreds of meters).

The number of required prey captures per linear swimming distance shows that larvae need to be successful in the order of meters to tens of meters.

The required number of prey $liter^{-1}$ for larval feeding at a 10% capture rate is in the order of 1000-100,000 m^{-3} which has often been observed in zooplankton surveys.

Sampling Strategy

If we relate the above calculations to a potential sampling strategy for process-oriented field cruises we can assess feasibility, compatibility and appropriateness. The core of the sampling scheme is to conduct on station vertical profiling of T, S, chlorophyll, and zooplankton organisms with plankton pumps and electronic sensors (CTD, fluorometer and HIAC particle counter) at selected stations within a mesoscale survey (25 km^2 grid) of larval distribution and abundance (Appendix II). This will provide the capability of continuous, instantaneous (real time) measurements in the vertical. Since we know that even the smallest fish larva is capable of swimming up and down the vertical extent of the water column in the Georges Bank study area (40-100 m), the instrument measurement capabilities are more than adequate in this dimension.

The horizontal mensuration aspects present some problems. Unlike the vertical (bounded by the water surface and the bottom), the horizontal boundaries of critical factors may far exceed the larva's ability to encounter them. A larva can swim hundreds of meters day^{-1} in the horizontal plane, while prey encounter related to patch or inter-patch distance could conceivably be on the order of kilometers. Also, larvae and their food are transported by horizontal currents, thus compounding the picture. From a sampling strategy, the horizontal current speed and the vertical sheer can be measured with profiling current meters strung at depths, or a cyclosonde. This gives transport. Temperature and salinity changes most likely will not differ significantly enough in the horizontal to affect larvae and/or their food except, perhaps, in frontal zones. Discrete measurements to the hundreds of meters in the horizontal can be made for T, S, chlorophyll and zooplanktors with instruments such as U.O.R., other fluorometers and particle counters. This does not approach the ability to make these measurements in meters as in the vertical; but, nevertheless, it approaches the scale (hundreds of meters) that fish larvae are able to travel and encounter prey in a day's time.

The above estimates of feeding parameters are apt to be conservative, and haddock larvae are likely to have powers of locomotion and/or transport and encounter rates of prey greater than discussed. Three factors contribute to this: 1) Delayed feeding ("point of no return") or the ability to withstand

starvation, keep actively searching for food, and be able to still feed successfully is in the order of 4-7 days for haddock larvae (Laurence 1974, 1978). So searching parameters could be expanded by a factor of 4-7. 2) Larval fishes have the behavioral ability to remain in concentrations of prey once located. This strategy might allow successful existence in a contagious prey environment with small scale patches or considerable distances between patches. 3) Since larvae and their prey are transported by currents of greater velocity than their own swimming power and since the prey swim with a certain velocity relative to the larvae, larval searching parameters could be expanded if prey were moving in a direction opposed to the larvae or if the larvae swam against the prevailing current direction for any length of time. This expansion would be by a factor of the prey or current velocity. These factors have been or are quantifiable.

This sampling strategy and the measurement capabilities of available sensors exceed requirements necessary to relate to fish larvae on the vertical and approach those necessary for horizontal determinations. The discrete and continuous measurements of the aforementioned physical and biological factors will allow a physical and statistical description of the heterogeneity (or lack of) of the prey environment of larval haddock as well as describe and understand functional trophic linkages and production aspects.

Results to date (Lough and Laurence, 1981, and unpublished) indicate that larval food is contagiously distributed on a small scale (Table 11), that the absolute abundance of food organisms can approach the calculated requirements based on experimental results (Fig. 4 and Table 11), that larvae and prey do co-occur vertically in the water column and that these distributions and occurrences can be both maintained and disrupted by meteorological and physical forces (Figs. 4 and 5), and that conditions can be quite variable from year to year (Figs. 4-7) and in different areas of bottom depth on the bank (Figs. 6 and 7).

IV OPINIONS--TWO PERSISTENT PROBLEMS

Without a doubt the single most significant drawback to understanding larval trophodynamics in the natural environment is a lack of available technological means for making fine scale measurements of small organisms. There is a particular need to be able to count and size planktonic organisms "in situ" in real time without disturbing their behavior or distribution. There have been some small advances in particle counting technology as spin-off from other applications, however, it has been minimal. There is little doubt that the acoustic, optical and laser technologies currently available to the defense, space and oil industries could be applied to fishery problems. But, until society places living resource problems above defense, space and oil, there is little chance that engineers, etc. associated with developmental technological systems will cooperate with living resource programs in other than a trickle down manner, or that living resource programs will receive enough money to devote to specific developmental engineering research.

Another significant problem is a general failure of physical oceanographers and biologists to communicate and interact in the area of early life survival and recruitment studies. Most biologists feel that physical factors are extremely important in influencing biological events. Circulation patterns on the macroscale level and such processes as boundary or frontal exchange, thermal inversion and double diffusion on meso and microscales could be prime factors affecting broad scale distribution of fish larvae as well as the small scale heterogeneity involved in individual larvae meeting contagiously distributed prey.

Differences in training and background may cause some of the dichotomy. Nevertheless, with few exceptions that I can see, biologists dealing with early life stage research have apparently failed to convey the essence of their problems and importance of physical factors to oceanographers even when they work in the same organization; while, at the same time, oceanographers generally have treated these particular biological problems as lower priority, especially those dealing with small scale phenomena. The best solution for this communication problem is for astute program managers to use a big club.

A second aspect to the problem is available instrumentation and technology. Current means to measure and record physical parameters are more advanced than those used for biological. It's basically nets vs. electronics. This gap is narrowing, however, as biologists become more sophisticated in their needs. It should become a non-problem provided funds are allocated to the necessary technological development.

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APPENDIX

Approaches to Laboratory Studies of Feeding of Fish Larvae

I. Logistics
   A. Food Collection or Propagation
      1. Techniques
      2. Systems
      3. Cost-Effort
   B. Rearing System Design and Development
      1. Open vs. Closed
      2. Freshwater vs. Marine
      3. Tank or Wall Effects
   C. System Hygiene
      1. Physical (vacuum, scraping, filtering, etc.)
      2. Chemical (antibiotics, etc.)

II. General Food Requirements
   A. Preferred Foods
      1. Natural (trophic level) foods
      2. Atypical Natural Foods (i.e. brine shrimp, rotifers, etc.)
      3. Artificial Foods
         a. Microencapsulation
   B. Food Densities
      1. Naturally Occurring
      2. Critical
      3. Optimal
      4. Fluctuating
      5. Measurement (#'s, calories)

C. Timing

1. Critical

2. Diurnal

III. General Experimental Studies

A. Endogenous Nourishment

1. Chemical Constituents

2. Sequence of Utilization

B. First Exogenous Feeding

1. Timing

2. Food Size Preference and Absolute Requirements

C. Delayed Feeding

1. Delayed First Feeding

2. Delayed Feeding of Older Larvae

3. Temperature Effects on Timing

4. Comparisons Between Species

D. Growth and Mortality vs. Food Density and/or Physical Factors

1. T, Sal, Pollutants, etc.

2. Age and Growth (otoliths, chemical indicators)

3. Competition

a. interspecific, intraspecific, cannabalism

E. Starvation

1. Initial Post Hatch Starvation

2. Condition of Older Larvae and Starvation

3. Size and Condition @ Starvation

4. Sequence of Events During Starvation Process (behavioral, physiological, chemical)

5. Bioassays

1. Feeding levels in Assays Interpreted in Relation to Toxic Insult Effects and Interactions

IV. Energetics

A. Gross Metabolic Requirements

1. Techniques for Measurement

2. Reconciliation of Standard, Routine and Active Metabolic Levels and Activity

B. Digestion Rate

1. Techniques

2. Mathematical Formulations

3. Digestion vs. Feeding activity, Prey Level, Prey Type

C. Assimilation

1. Definitions

2. Measurements and Techniques

D. Consumption Estimates

1. Direct and Indirect Determinations

E. Budgets

1. Theory

2. Types (Caloric, Nitrogen, Carbon)

3. Current Models

V. Biochemistry

A. Condition Indices (organo-cpds, nucleic)

1. Comparisons with Morphological and Histological Indices

2. Relation to Feeding Level and Diet

B. Digestive Enzyme Kinetics

1. Identification, Inervation and Sequence

2. Relations to Food Type and/or Level

3. Temperature Kinetics

VI. Morphology, Histology and Development

A. Developmental Sequence, Inhibitors, Enhancers of:

1. Mouthparts

2. Eye

3. Digestive Organs

4. Musculature and Locomotor Skeletal Components

VII. Behavior

A. Ethological Reactions and Interactions

1. Predator-prey Responses

a. detection, reaction, attack, flight

B. Swimming Abilities

1. Activity Levels

2. Sustained and Short Term "burst" levels

3. Changes with Age/Size

4. Changes with Prey Level

C. Visual Fields

1. Phototaxis

2. Perception

VIII. Nutrition

A. Palatability - Acceptability

B. Nutritional Values

C. Organic (Energy) Components

D. Inorganic (Essential) Components

E. Non Essential Fillers, Binders, Matrices, Encapsulators, etc.

IX. Aquaculture

A. Differences in Concepts and Goals of Laboratory Experimental Research and Culture Optimization

GENERAL SCHEDULE

HADDOCK PROCESS-ORIENTED LARVAL SURVIVAL STUDIES

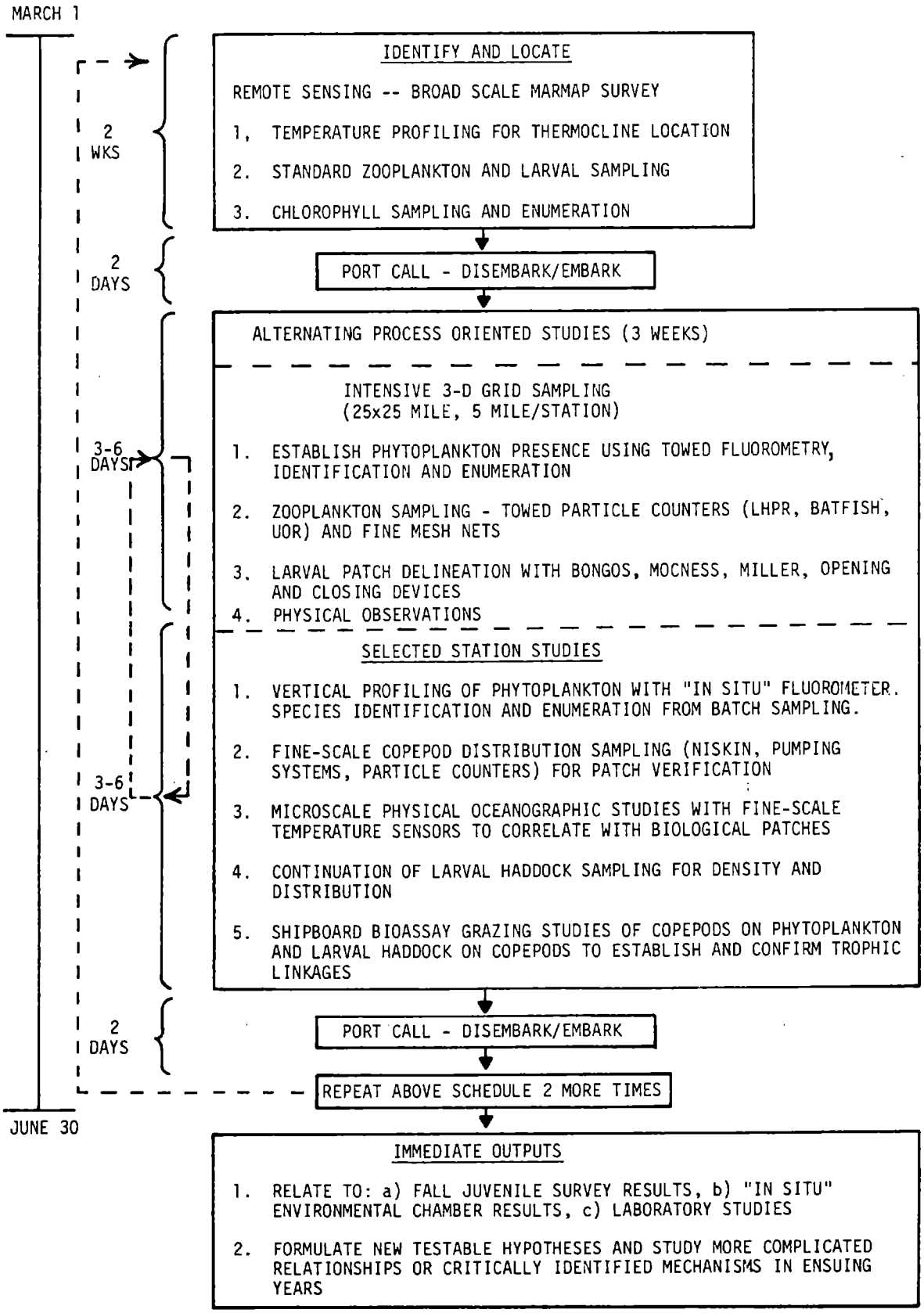

Table 1. Species specific early life history parameters. (Table 1 from Theilacker and Dorsey, 1980.)

Species	Range	Spawning season (peak)	Egg Type	Egg diameter (mm) range	Incubation days	Incubation °C	Hatching Size mm	Hatching dry wt µg
Limanda ferruginea (Yellowtail flounder) 1.	Gulf of St. Lawrence to Virginia	March-Aug.	Pelagic	0.88 0.79-1.01	5-7	10	2.0-3.5	16
Limanda limanda (Dab) 2.	North Sea English Channel	March-June (Feb.-April)	Pelagic	0.65-0.95			2.6	
Pleuronectes platessa (Plaice) 3.	North Sea English Channel to Norwegian Rinne Skagarrate	Dec.-April	Pelagic	2.0 1.7-2.2	18	7-11	5.0-6.7	151
Pseudo-pleuronectes americanus (Winter flounder) 4.	Northern Labrador to Georgia	Dec.-May	Demersal	0.80 0.71-0.96	17-25	3	2.3-3.5	10-30
Paralichthys dentatus (Summer flounder) 5.	Maine to Florida	Oct.-April	Pelagic	1.04 0.90-1.13	3	17	2.4-2.8	
Solea solea (Sole) 6.	North Sea English Channel	April-June	Pelagic	1.0-1.5	8	10-12	3.2-3.7	
Achirus lineatus (Lined sole) 7.	Florida and Gulf of Mexico to Uruguay		Pelagic		1	28		21.8
Stenotomus chrysops (Scup) 8.	Nova Scotia to Eastern Florida	May-July	Pelagic	0.94 0.85-1.15	1.5	22	2.0	
Archosargus rhomboidalis (Seabream) 9.	New Jersey to Rio de Janeiro	Sept.-May	Pelagic		1	26	1.8-3.2	27.8
Gadus morhua (Cod) 10.	North Atlantic Coastal Waters	Dec.-April	Pelagic	1.52 1.10-1.72	12	5.5	3.3-5.7	
Melanogrammus aeglefinus (Haddock) 11.	North Atlantic Biscay to Barents Sea Newfoundland to Cape Cod	Feb.-June	Pelagic	1.46 1.10-1.67	17	5.5	2.0-4.1	
Clupea harengus (Atlantic herring) 12.	Greenland-Cape Hatteras Iceland-Gibraltar	July-Nov.; May (Sept. & May)	Demersal	1.0-1.4 0.36-3.0	15 (Maine, Downs)	8	4.0-10.0	90 (50-220)
Sardinops sagax (Pacific sardine) 13.	Southern Alaska to Gulf of California	Feb.-July (May-June)	Pelagic	1.7	2.8	15	3.75	36
Engraulis mordax (Northern anchovy) 14.	Northern Baja California to Arctic Alaska and Japan	Jan.-July (March-May)	Pelagic	0.66-1.35	2-3	16	2.9-3.2	21
Engraulis ringens (Anchoveta) 15.	Coasts of Peru and Chile	July-March (Sept. & Feb.)	Pelagic	0.71-1.42	2-2.25	14-16	2.19-2.72	
Scomber japonicus (Pacific mackerel) 16.	Southeast Alaska to Banderas Bay, Mexico	April-August (May-July)	Pelagic	1.06-1.14	3.6	16	3.1	40
Trachurus symmetricus (Jack mackerel) 17.	Magdalena Bay, Baja California to Southeast Alaska	Feb.-August (May-June)	Pelagic	1.0 0.90-1.02	2-3	15	2.1[c] 2.8[d]	34[e]

Table 1. (continued)

Yolk absorption		Onset of feeding		Irreversible starvation		Metamorphosis		Length
Days from hatching	°C	Days from hatching	°C	(a) Days from hatching (b) Days from Yolk Abs.	°C	Days from hatching	°C	(mmSL)
4-5	10	4-5	10				14	
		Yolk absorption						
6-10	7-11	4-6	7-10	6-8[b]	8-11	40-75	7-11	9-13
9	8	5	8	5-7[b]	8	58	8	6.5-9
3-4	16	4	16	6-7	16	47-56	16	15
7						42-56	10-12	9-10
3	28	2	28	3-3.5	28	16	28	4-5
3	22	3						10
2	28	1.5	28	2.5	28	9-11	23-29	7-9
6	7.2	~5	7	5[b]	7	52	7	10
7	7	~5	7	5[b]	7	42-49	7	10
6 (Firth of Clyde) 15-20 (W. Baltic)	8	2-6 (Firth of Clyde) 15-20 (Baltic)	8	6[b] (Firth of Clyde) 12-22[a]	8-12 8	112-168	8-12	30-40
		4-5	16			45-50		31-35
4	16	4	15-16	2.5[b] 4.5[b]	16.5 15	50-60		34-40
3	18	4.5 (3.5-6.8)	18	4.5	18			32
3	19	2-2.5 4	19 16	2[b] 3.5	19 16	25		15
		5	15	2.5[b]	15	40		11-16

Table 2. Critical prey densities for fish larvae. (Table 4 from Theilacker and Dorsey, 1980).

Species and common name	Container volume (liters)	Duration (days)	Food type	Stock density No./L	Survival at various food densities: Density No./L	Survival at various food densities: Percent survival	Reference
PLAICE							
Pleuronectes platessa	5	14	*Artemia* nauplii	50 (larvae)	1,000	72[1]	Wyatt 1972
5					500	72	
					200	54	
					100	32	
NORTHERN ANCHOVY							
Engraulis mordax	10.8	12	Wild zooplankton (nauplii)	10 (eggs)	4,000	51	O'Connell & Raymond 1970
5					900	12	
					90	0.5	
					9	0	
BAY ANCHOVY							
Anchoa mitchilli	76	16	Wild zooplankton (nauplii-copepodites)[3]	0.5-2 (eggs)	5,000	64	Houde 1978
5					1,000	48	
					100	5	
					50	0-12	
SEA BREAM							
Archosaurgus rhomboidalis	76	16	"	0.5-2 (eggs)	500	72	" "
5					100	37	
					50	13	
					25	7	
					10	4	
LINED SOLE							
Achirus lineatus	38	16	"	0.5-2 (eggs)	1,000	54	" "
5					100	13	
					50	1	
HADDOCK							
Melanogrammus aeglefinus	37.8	42	Wild zooplankton (nauplii)	9[4] (larvae)	3,000	39	Laurence 1974
5					1,000	22	
					500	3	
					100	0	
					10	0	
HERRING							
Clupea harengus	20	21-63 58-84	*Artemia*	8	3,000	4-8	Werner & Blaxter 1980
					1,000	3-12	
					300	0-8	
					100	0-12	
					30	0-1	
WINTER FLOUNDER							
Pseudopleurontectes americanus	64	49	Wild zooplankton (nauplii)	9[4] (larvae)	3,000	34	Laurence 1977
					1,000	4	
					500	3	
					100	1	
					10	0	

[1]Survival was 100% at 50/L for first 7 days without a decrement in length; see also Riley (1966).

[2]Estimated food density for indicated survival levels.

[3]Plankton blooms of *Chlorella* sp. and *Anacystis* sp. maintained in rearing tanks.

[4]Estimated by adjusting for hatching success.

[5]Hunter, in press.

Table 3. Average densities of microcopepods in the sea. (Table 5 from Theilacker and Dorsey, 1980).

	Average density of microcopepods (number per liter)				
	nauplii	copepodites	total	Location	Reference
OPEN SEA	13	2	15	Southeast Coast of Kyoshu	Yokota et al. 1961
	22	36	58[2]	California Current	Beers and Stewart 1967
	40	5	45[2]	Southern California near shore	Beers and Steward 1970
	27	7	34[3]	Eastern Topical Pacific	Beers and Steward 1971
	36	1	37	California Current	Arthur 1977
PARTLY CLOSED	76	19	95	Azov Sea	Duka 1969
	-	-	223[4]	Gulf of Taganrog	Mikhman 1969
	40	-	40	North Sea (0-10 m)	Ellertsen et al. 1980
	20-30	-	25	North Sea (10-20 m)	" "

[1]Mean for all stations and years given in publication listed in table (Hunter, in press).

[2]Includes all copepods passing 202 µm mesh net.

[3]Includes all copepods passing 202 µm mesh net and caught on 35 µm mesh.

[4]Defined as food of Clupeonella delicatula; microcopepods account for over 90% of items eaten (Mikhman 1969).

Table 4. Field concentrations of larval fish food organisms. (Table 10 from Houde, 1978).

Reference	Place	Organisms	Concentration
Purdick (1969, cited in May, 1974	Kaneohe Bay, Hawaii	copepod nauplii	59-100/l common 200/l sometimes present
Duka (1969)	Sea of Azov	Acartia clausi nauplii	62-65/l
		Other copepod nauplii and copepodites	>30/l
		Total	>90/l
Mikhman (1969)	Gulf of Taganrog, Sea of Azov	Early stages of copepoda	39-546/l
Hargrave and Green (1970)	Two eastern Canada estuaries	Copepod nauplii and copepodites	>60/l
Reeve and Cosper (1973)	Card Sound, South Florida	Copepod stages 20-200 µm in breadth	range 23-209/l mean for 28 collections 72/l
		Tintinnids	range 40-369/l
Heinle and Flemer (1975)	Patuxent River estuary	Eurytemora affinis nauplii and copepodites	>100/l frequently >2,000/l occasionally
Houde (unpublished data)	Biscayne Bay, South Florida	Copepod nauplii and copepodids <100 µm in breadth	usually 50-100/l
		Tintinnids	frequently >100/l

Table 5. Swimming performance of larval fishes. (Table 2 from Theilacker and Dorsey, 1980).

Species	°C	Age (d; mm; ng)	Cruising[1] cm/s	Cruising[1] BL/s	Burst cm/s	Burst BL/s	Duration of burst or distance traveled per burst	Reference
Sardine	15-18	yolk; 3-5 mm	0.2					Blaxter & Staines
Sardina pilchardus	"	3 wks.	0.3					1971
Herring	8-12	yolk; 6-11 mm	0.4					Blaxter & Staines
Clupea harengus	"	8 wks.	1.4					1971
				2.3	8-10			Blaxter 1969
Northern anchovy	13	3 mm	0.1	.2				Hunter 1972
Engraulis mordax	19	3 mm	0.2	.6				Hunter (in press)
	13	5 mm	0.3	.5				
	19	5 mm	0.5	.9				
	17	15 mm	1.5	1.0				
" "	17	35 mm[2]	3.5	1.0				
	17	80 mm	12.0	1.5				Theilacker (unpubl.)
	17	150 mm	50.0	3.3				
	17	8 mm[3]			3		8-16 ms	Hunter 1972
	17	13 mm[3]			8		8-16 ms	
" "	17	3 mm			7.3[4]	24	1.3 cm/176 ms	Webb & Carolla (MS)
	17	8 mm			11.4[4]	14	3.1 cm/272 ms	
	17	13 mm			15.5[4]	12	5.0 cm/323 ms	
Whitefish[5]	7-15	15 mm	1.5	1.0				Hoagman 1974
Coregonus clupeaformis								
Jack mackerel	16	6.0-6.5 mm	.36-.72	0.8 (0.6-1.2)		4-6	2-8 cm; 2 s	Devonald (pers.comm.)
Trachurus symmetricus								
Pacific mackerel	19	3.6 mm	0.46	1.3				Hunter & Kimbrell
Scomber japonicus	"	15.0 mm[2]	5.6	3.8				1980
Large mouth bass	19	2-7 d; 6-7 mm	3-4[6]	4-5				Laurence 1971
Micropterus salmoides								
Plaice[7]	10-12	yolk; 5-7 mm	0.2					Blaxter & Staines
Pleuronectes platessa	"	9-10 mm	1.0					1971
	"	5-7 mm	1.5[8]		4-9[1]	~10	9-15 cm	Ryland 1963
	"	9-10 mm	2.2[8]		9-15[1]	~13	12-36 cm	
	"	25 mm	6.5[8]					
Sole[7]	10-12	yolk; 3-5 mm	0.1					Blaxter & Staines
Solea solea		9-10 mm	0.7					1971
Walleye perch[9]	13	7.5 mm	0.5	0.6				Houde 1969
Stizostedion vitreum vitreum	13	11.0 mm	3.5	3.0				
Yellow perch[9]	13	7.5 mm	1.5	1.8				Houde 1969
Perca flavescens	"	11.0 mm	3.5	3.0				

[1]voluntary swimming.

[2]metamorphosis.

[3]attacking prey.

[4]mean burst speed = 8.18 L + 4.89; maximum distance traveled = 3.79 + 0.08.

[5]no effect of temp. or age.

[6]forced swimming; speed sustained for 30 m.

[7]90% decrease in activity at metamorphosis.

[8]forced swimming; speed sustained 4-20 s.

[9]forced swimming; speed sustained for 1 h.

Table 6. Searching ability of larval fishes. (Table XIII from Blaxter, 1969).

Volume Searched during Feeding

Species	Size (mm)	Volume searched (liter/hr)	Author
Coregonus wartmanni (whitefish)	(?)10	14.6	Braum (1964)
Clupea harengus (herring)	8-16	0.3-2.0	Blaxter (1966), Blaxter and Staines (1969a)
Clupea harengus (herring)	10 13-14	1.5-2 6-8	Rosenthal and Hempel (1968)
Sardina pilchardus (pilchard)	5-7	0.1-0.2	Blaxter and Staines (1969a)
Pleuronectes platessa	6-10	0.1-1.8	Blaxter and Staines (1969a)

Table 7. Growth efficiencies of larval fishes. (Table 9 from Theilacker and Dorsey, 1980).

	°C	Age (d; µg)	Prey density (#/L)	Container volume (liters)	Daily ration µg	Daily ration % body wt	Gross efficiency (%)	Reference
Bay anchovy[1]	26	17 d; 200 µg	50	10	19	31	57	Houde & Schekter 1980
Anchoa mitchilli	"	15 d; 200 µg	100		37	51	32	
	"	11 d; 200 µg	1000 nauplii wild plankton)		115	140	14	
Herring	-	12-22 d;	14,000-	8			71	Eldridge *et al.* 1977
Clupea harengus pallasi		100-150 µg	20,000 rotifers					
Sea bream[1]	26	17 d; 200 µg	50	10	12	-	83	Houde & Schekter 1980
Archosargus rhomboidalis	"	15 d; 200 µg	100		31	42	38	
	"	10 d; 200 µg	500 nauplii (wild)		45	-	38	
" "	23-26	2-3 d	1000	75	14	68-147	33	Stepien 1976
	29	2-3 d	1000		32	199	16	
	23	10 d	1000		-	69	31	
Pacific mackerel[2]	19	3 d; 38 µg	157,000	200	27	70	20	Hunter & Kimbrell
Scomber japonicus	"	4 d; 43 µg	47,000		38	89	37	1980
	"	5 d; 85 µg	198,000 rotifers		86	102	44	
Striped bass	18	15 d; 400 µ	10				13	Eldridge (unpubl.)
Morona saxatilis	"		100				15	
	"		500				20	
	"		1000				21	
			5000 *Artemia*				50	
	18	29 d	10				20	
	"		100				14	
	"		500				17	
	"		1000				19	
	"		5000 *Artemia*				32	
Lined sole	26	21 d; 200 µg	50	10	14	-	63	Houde & Schekter
Achirus lineatus	"	17 d; 200 µg	100		20	29	52	1980
	"	12 d; 200 µg	1000 nauplii (wild)		74	~90	20	
Winter flounder[3,4]	8	2 wks.	500				10	Laurence 1977
Pseudopleuronectes americanus	8	7 wks.					20	
	8	2 wks.	nauplii-copepods			300	15	
	8	7 wks.	3000			30	33	

[1]Daily ration estimated from grazing experiments; dry weights determined with preserved larvae; wild plankton nauplii 0.15 µg, fresh dry wt.

[2]Ration from stomach contents and evacuation rate (discontinuous feeding).

[3]Ration from stomach contents and evacuation rate (active feeding).

[4]Net growth efficiencies.

Table 8. Caloric and ash values for some North Atlantic copepods. Species are recorded in order from largest to smallest mean value under each category. Those species side-scored have similar means (Duncan's New Multiple Range Test, P=0.05). (Table 1 from Laurence, 1976)

Species	Mean	Standard Deviation
	cal/g dry weight	
Calanus finmarchicus	6425.1	±187.0
Tortanus discaudatus	5398.3	± 14.6
Centropages typicus	5244.7	±183.3
Acartia tonsa	5160.0	± 78.8
Pseudocalanus minutus	5070.9	±181.7
Centropages hamatus	4998.6	±246.3
Temora longicornis	4466.3	± 92.8
	cal/g ash-free dry weight	
Calanus finmarchicus	6835.2	±191.2
Acartia tonsa	5664.1	± 86.6
Tortanus discaudatus	5642.0	± 15.3
Pseudocalanus minutus	5541.9	±198.6
Centropages typicus	5503.4	±192.3
Centropages hamatus	5212.3	±256.9
Temora longicornis	4984.7	±103.6
	% ash	
Temora longicornis	10.40	± 0.16
Acartia tonsa	8.90	± 0.16
Pseudocalanus minutus	8.50	± 0.11
Calanus finmarchicus	6.00	± 1.82
Centropages typicus	4.70	± 0.28
Tortanus discaudatus	4.32	± 0.07
Centropages hamatus	4.10	± 0.13

Table 9. Larval haddock daily feeding requirements and calculation parameters.

Parameter	Larval Haddock Std. Length (mm)		
	5	10	15
Dry Wgt (µg)	59.2	1316.0	8084.2
Δ G 6% day^{-1} (µg)	3.6	79.0	485.0
Δ G 2% day^{-1} (µg)	1.2	26.3	161.7
Daily Metabolism - Upper Limit (µℓO_2)	41.4	347.6	1203.3
Daily Metabolism - Lower Limit (µℓO_2)	18.3	152.8	529.4
β	0.290	0.769	0.800
ω - Preferred Prey Size (µg)	1.0	7.9	23.0
Range of R, # of Prey Ingested day^{-1}, Calculated from Eq. 3 with Upper and Lower Values of above Parameters	107-248	47-111	57-143

Table 10. Larval haddock swimming, searching and food encounter.

Parameter	Larval Haddock Size, Std. Length (mm) 5	10	15
Daily Linear Distance Swam @ 1.5 BL sec^{-1} and 12 h Activity (meters)	324	648	972
CM Sec^{-1}	0.75	1.5	2.25
Volume Water Searched in 12 h Day (liters)	9.5	76.2	257.2
Range of Required Prey Captures (R) day^{-1}	107-248	47-111	59-143
Range of Required Linear Swimming Distance $Capture^{-1}$ (meters)	3.0-1.3	13.7-5.8	16.5-6.8
Range Required # Prey $Liter^{-1}$ if 100% Capture Rate	11.2-26.1	0.6-1.5	0.2-0.6
Range 10% Capture Rate	112-261	6.2-15.0	2.0-6.0

Table 11. Small scale discrete plankton sampling on Georges Bank.
Twelve replicates each of 1.7, 8.0 and 30 l collected simultaneously in same area. Morisita index 1.0 or greater denotes statistically significant contagion between replicates. Evrika 80-02, Station 47, May 21, 1980, 1610 GMT, 41°00'N, 67°51'W, bottom depth 44 m. Water temperature 7.4 isothermal. Gadoid larvae present.

PLANKTON CATEGORY	SAMPLE SIZE (l)	MEAN COUNT (12 REPLICATES)		NUMBER PER LITER		VARIANCE TO MEAN RATIO		MORISITA CONTAGION INDEX		NUMERICAL DOMINANT		MOST CONTAGIOUS	
		DEPTH (M)											
		10	40	10	40	10	40	10	40	10	40	10	40
Phytoplankton	1.7	327.67	308.33	192.75	181.37	34.01	5.16	1.09	1.01	Ceratium	Ceratium	Unident. Phyto.	Pennate Diatom
	8	1991.00	Missing	248.88	Missing	58.14	Missing	1.03	Missing	Chain Diatom	Missing	Unident. Phyto	Missing
	30	4590.18	5620.00	153.01	187.33	564.00	410.38	1.11	1.07	Ceratium	Ceratium	Pennate Diatom	Pennate Diatom
Non-Crustacea Zooplankton	1.7	10.17	10.50	5.98	6.18	2.36	2.85	1.12	1.16	Echinodern Lar.	Polychaete Lar.	Sagitta	Medusae
	8	47.00	50.09	5.86	6.26	1.42	2.07	1.01	1.02	Polychaete Lar.	Polychaete Lar.	Protozoa	Medusae
	30	128.64	158.70	4.29	5.29	15.94	3.00	1.11	1.01	Polychaete Lar.	Echinoderm Lar.	Bryozoa Lar.	Bryozoa Lar.
Copepod Eggs	1.7	9.50	13.92	5.58	8.19	14.36	4.77	2.30	1.25	--	--	--	--
	8	37.58	26.18	4.70	3.27	6.65	5.84	1.14	1.17	--	--	--	--
	30	114.00	107.30	3.80	3.58	20.50	6.23	1.16	1.04	--	--	--	--
Non-Copepoda Crustacea	1.7	0	0	0	0	0	0	0	0	0	0	0	0
	8	0.25	0.36	0.03	0.05	0.82	0.70	0	0	Zoea	Euphausid Lar.	0	0
	30	0.27	1.00	0.01	0.03	0.80	1.11	0	1.11	Zoea	Barnacle Lar.	0	Zoea
Copepoda Nauplii	1.7	15.42	12.08	9.07	7.11	3.30	1.53	1.14	1.04	Oithona I,III	Oithona I	Pseudocalanus II	Pseudocalanus III
	8	69.17	55.73	8.65	6.97	1.78	0.82	1.01	1.00	Oithona V	Oithona VI	Centropages II	Cal.III, Cent. IV
	30	206.82	164.00	6.89	5.47	23.73	2.16	1.10	1.01	Oithona I	Oithona I	Pseudocalanus VI	Centropages VI
Older Stage Copepoda	1.7	5.75	4.00	3.38	2.35	1.52	1.68	1.08	1.16	Oithona II	Oithona II,V	Misc. Copepoda	Oithona III
	8	21.33	13.73	2.67	1.72	2.18	0.96	1.05	1.00	Oithona I	Oithona II	Centropages III	Pseudocalanus III
	30	61.36	49.90	2.05	1.66	9.01	1.18	1.12	1.00	Oithona II	Oithona II	Centropages IV	Microsetella
TOTAL Zooplankton	1.7	40.83	40.50	24.02	23.82	8.52	3.45	1.17	1.06	*Echinoderm Lar.	*Polychaete Lar.	*Misc. Copepoda	*Sagitta
	8	175.33	146.09	21.92	18.26	5.74	1.46	1.02	1.00	*Polychaete Lar.	*Polychaete Lar.	*Centropages III	*Medusae
	30	510.00	480.00	17.00	16.03	59.99	7.34	1.11	1.01	*Polychaete Lar.	*Polychaete Lar.	*Pseudocalanus VI	*Centropages VI

* Does not include eggs

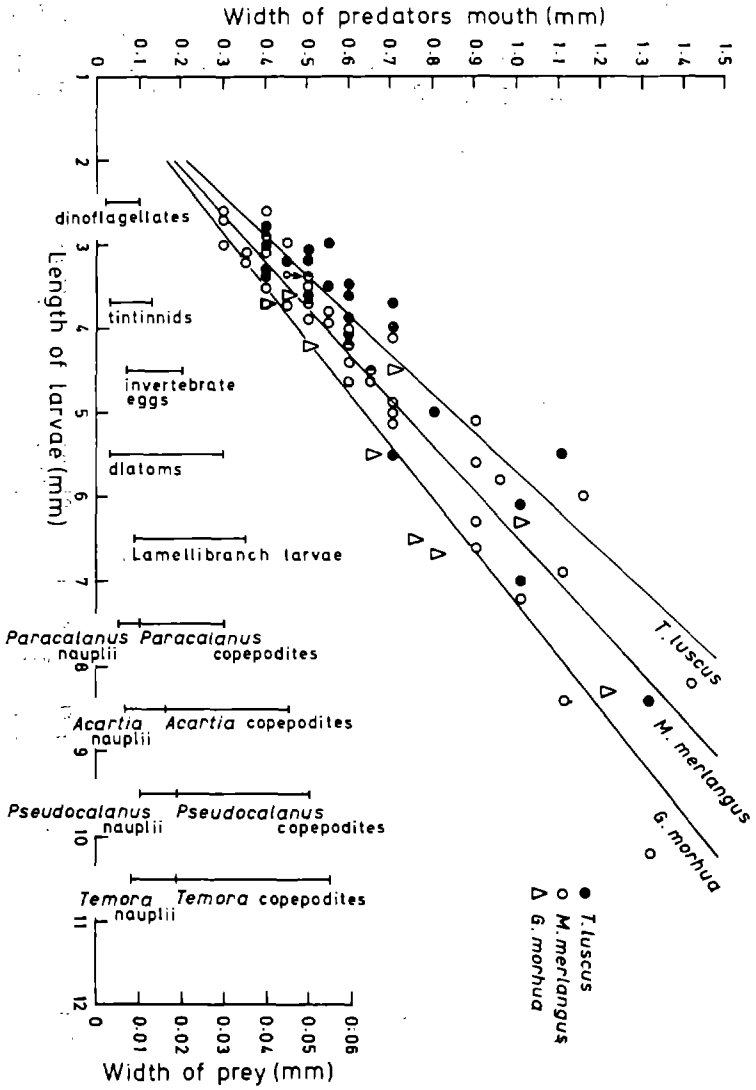

Fig. 3. *Gadus morhua*, *Merlangius merlangus* and *Trisopterus luscus*. Relationship of width of larval mouth to width of prey. For full specific names please refer to Tables 2–4

Figure 1. Relationship of larval and prey sizes. (Figure 3 from Last, 1978b).

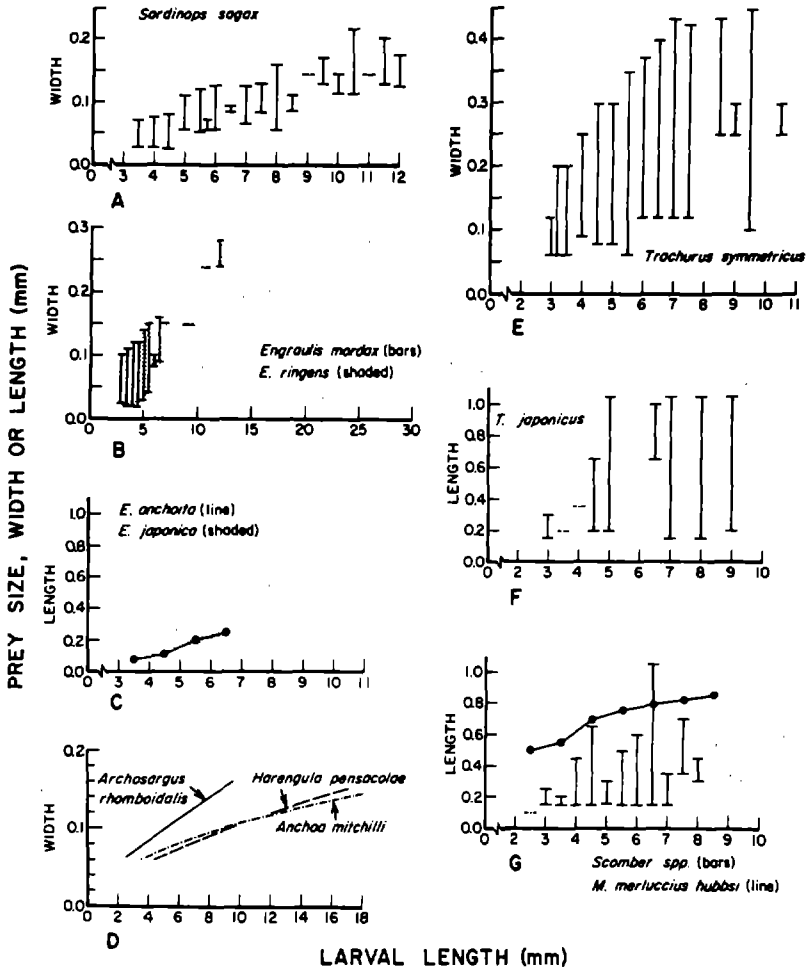

Figure 3. Relation between prey size and larval length for 12 species of marine fishes; label on ordinate indicates whether prey width or prey length were measured; vertical bars and shaded areas represent range of prey sizes; and straight lines connecting dots indicate average prey sizes. Plots were redrawn from Arthur (1976) for *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*; from Rojas de Mendiola (1974) for *Engraulis ringens*; from Detwyler and Houde (1970) for *Harengula pensacolae* and *Anchoa mitchilli*; from Stepien (1976) for *Archosargus rhomboidalis*; from Ciechomski and Weiss (1974) for *Engraulis anchoita* and *Merluccius merluccius*; and from Yokota et al. (1961) for *Engraulis japonica*, *Trachurus japonicus*, and *Scomber* spp. Data were for sea-caught larvae except panel D, which were laboratory reared.

Figure 2. Relationship between prey size and larval size. (Figure 3 from Hunter, 1981).

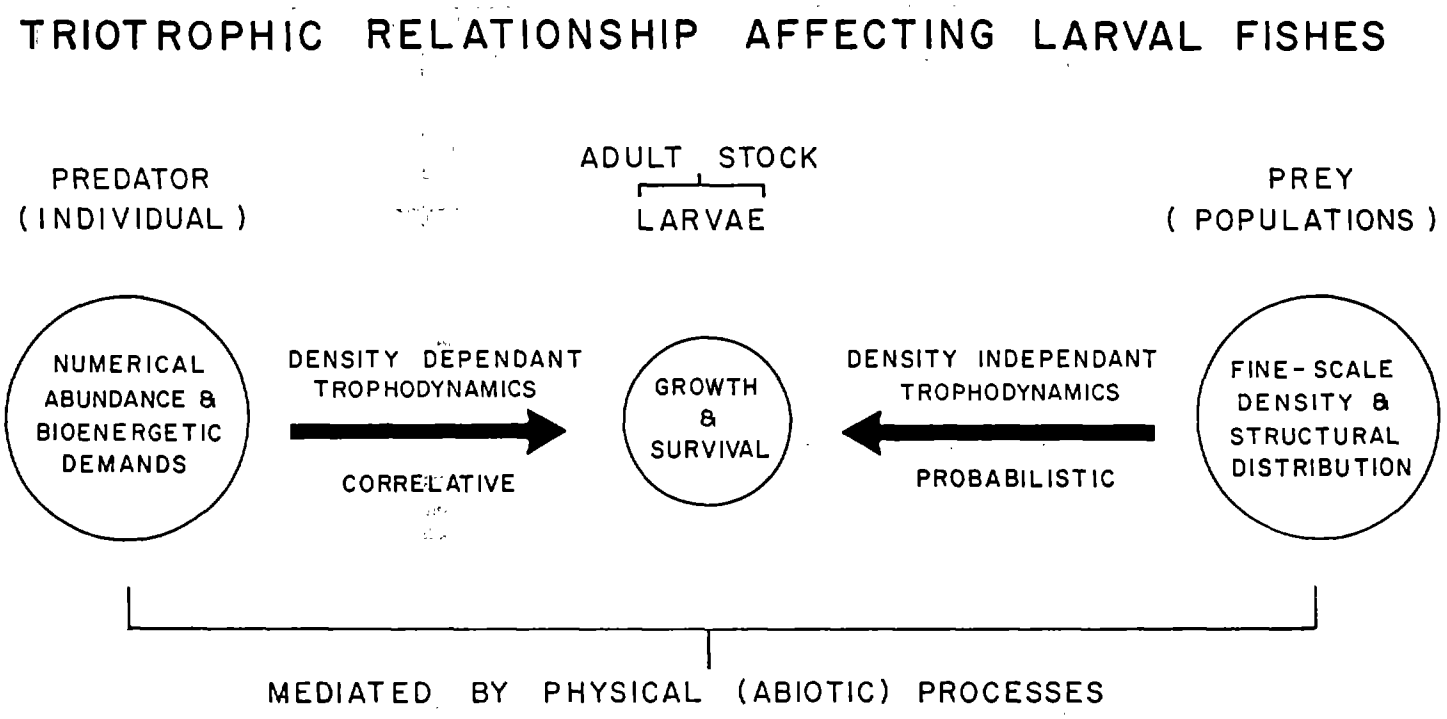

Figure 3. Triotrophic relationship affecting larval fishes.

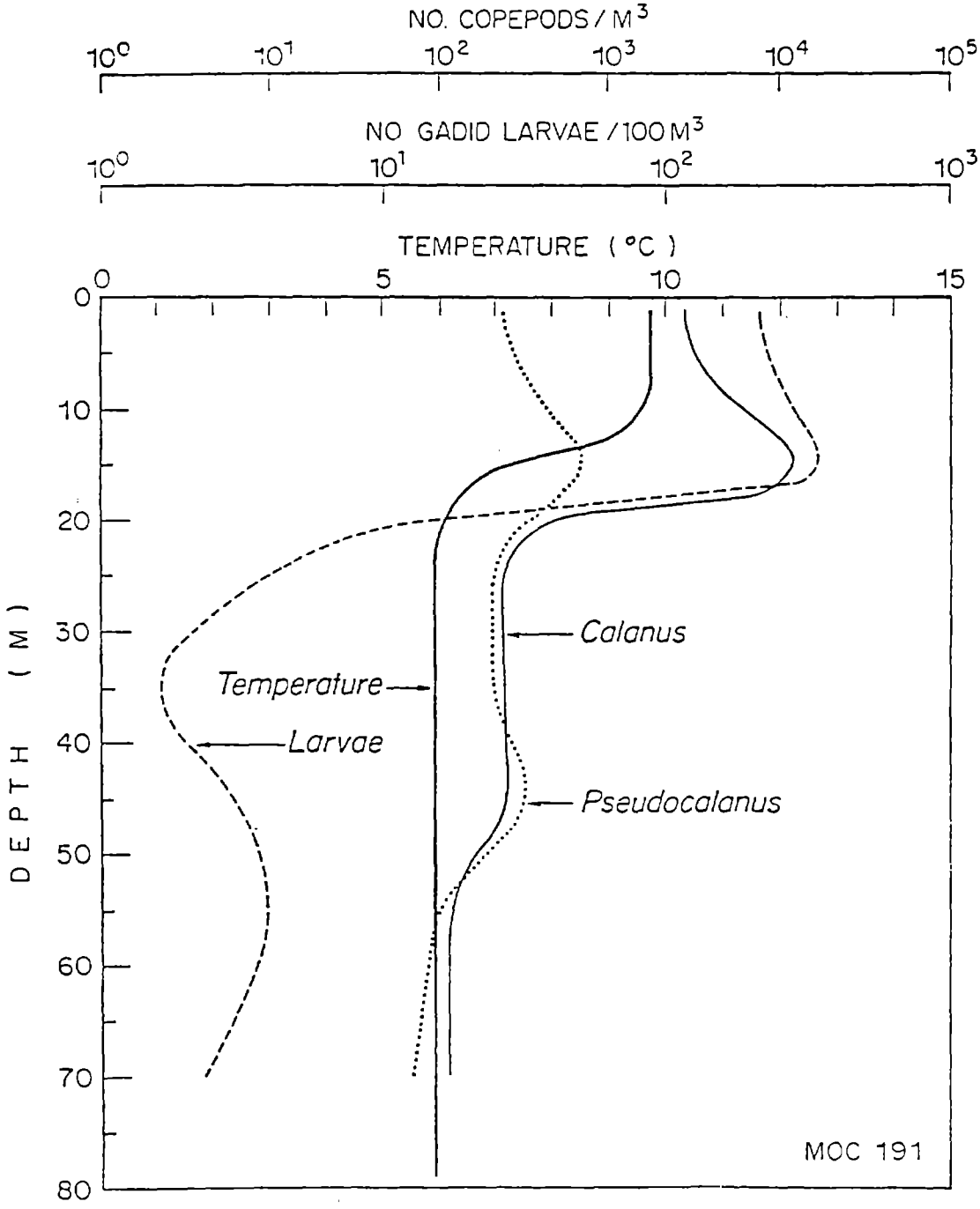

Figure 4. Vertical distribution of gadid (haddock and cod) larvae and dominant copepods (Calanus finmarchicus, Pseudocalanus sp.) in relation to thermocline on the Southeast Part of Georges Bank before storm. (MOCNESS-1m, 0.333-mm mesh, 21 May 1981, 2303-2358 D.S.T. 40°55'N, 67°16'W. Bottom depth: 78-80 m). Note different log-scales used for copepods and gadid larvae.

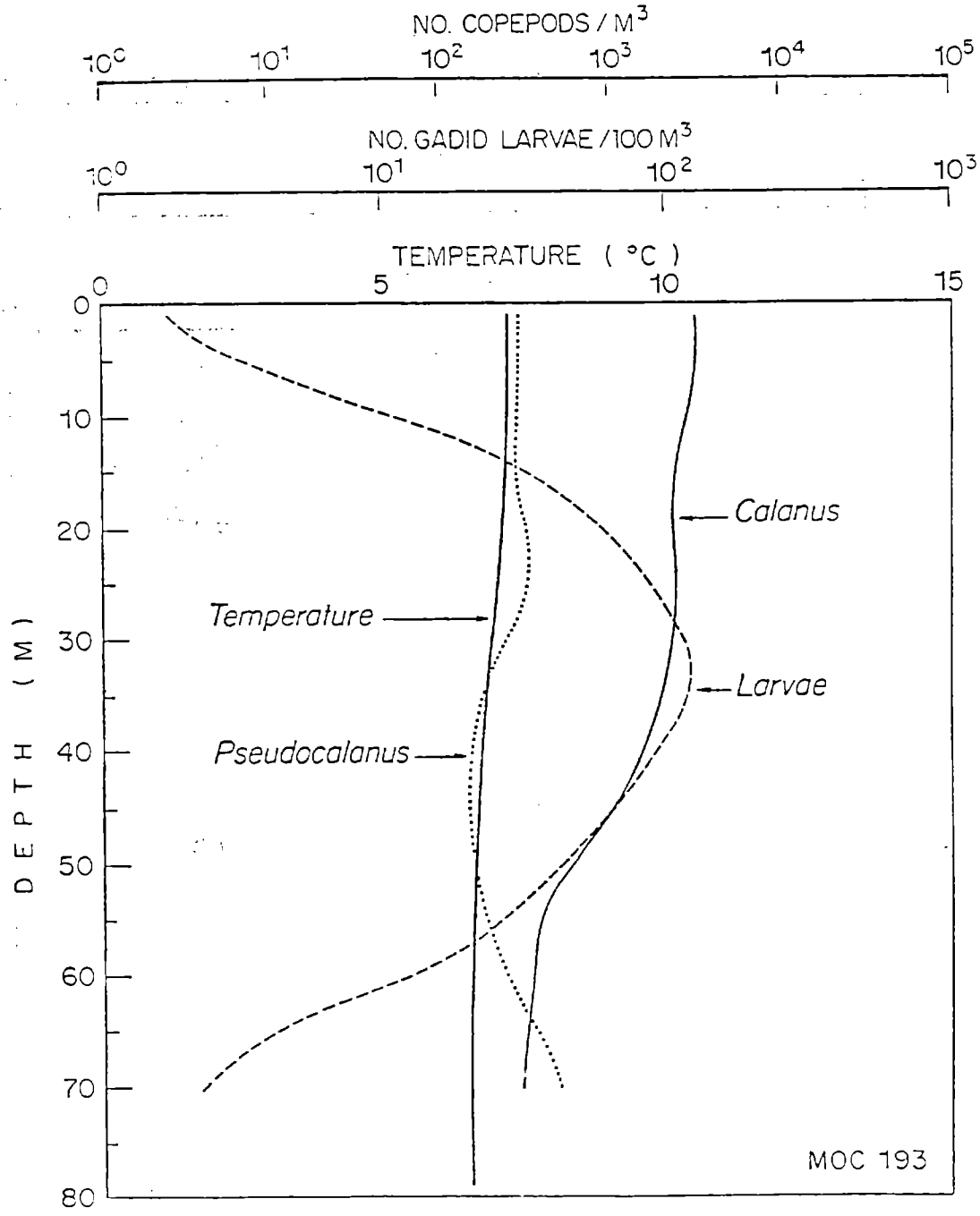

Figure 5. Vertical distribution of gadid (haddock and cod) larvae and dominant copepods (Calanus finmarchicus, Pseudocalanus sp.) on the Southeast Part of Georges Bank after storm. (MOCNESS-1m, 0.333-mm mesh. 24 May 1981, 1835-1920 D.S.T. 40°55'N, 67°13'W. Bottom depth: 80 m). Note different log-scales used for copepods and gadid larvae.

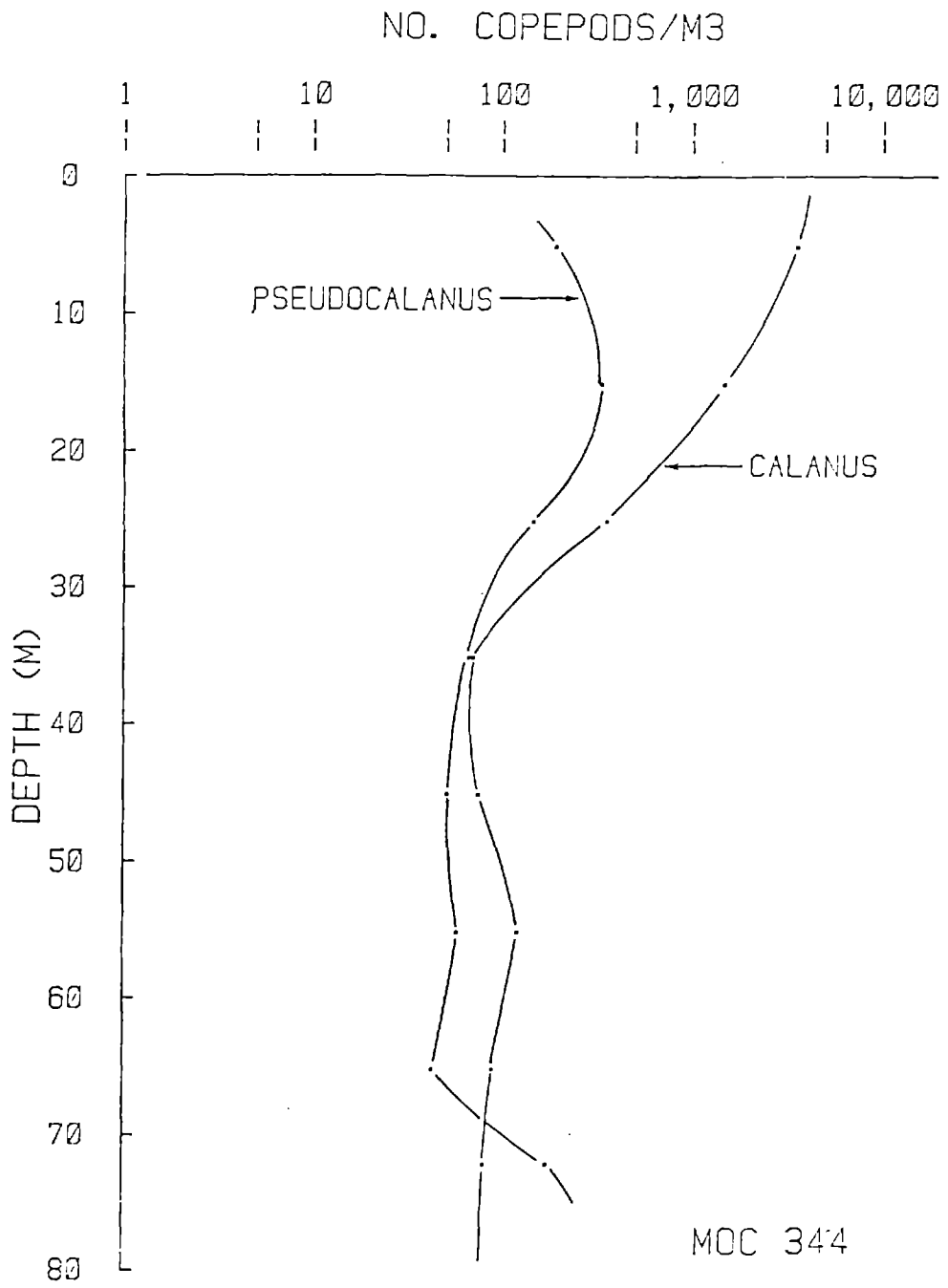

Figure 6. Vertical distribution of dominant copepods on Georges Bank. (Albatross 82-05, May 17, 1982, 1830-1920 D.S.T. MOCNESS-1 m, 0.333 mm mesh, 40°55'N, 67°17'W. Bottom depth: 75.9 m). No gadoid larvae present. Temperature Ca. 5-6° C isothermal.

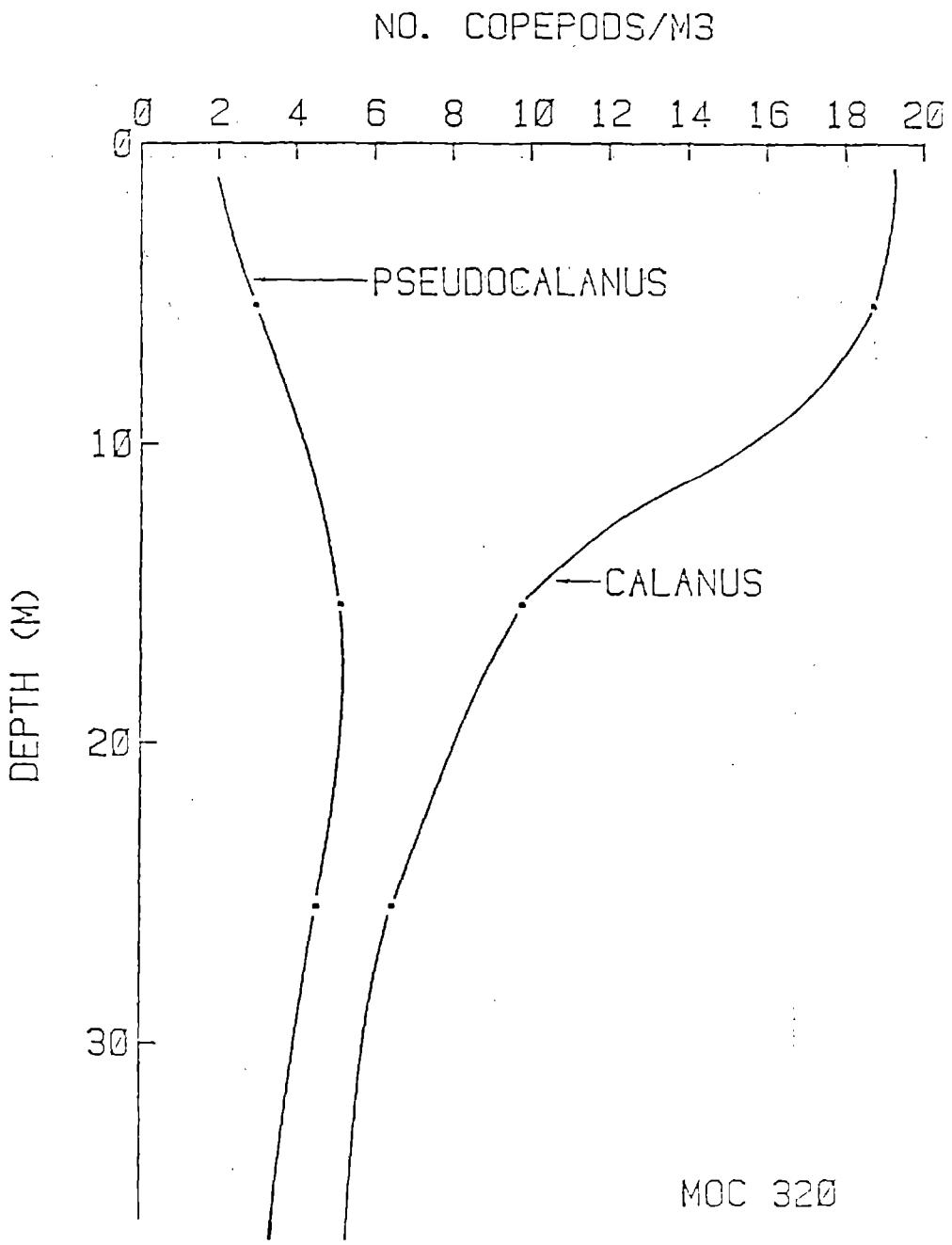

Figure 7. Vertical distribution of dominant copepods on Georges Bank. (Albatross 82-05, May 15, 1982, 1831-1844 D.S.T. MOCNESS-1 m, 0.333 mesh, 41°14'N, 67°37'W. Bottom depth: 36 m). No gadoid larvae present. Temperature 6.7°C isothermal.

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The Propagation of Cod *Gadus morhua* L.

LARVAL FISH TROPHODYNAMIC STUDIES ON GEORGES BANK: SAMPLING STRATEGY AND INITIAL RESULTS

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ABSTRACT

Lough, R. G., 1984. Larval fish trophodynamic studies on Georges Bank: Sampling strategy and initial results. In: E. Dahl, D.S. Danielssen, E. Moksness and P. Solemdal (Editors), The Propagation of Cod *Gadus morhua* L., Flødevigen rapportser., 1, 1984:

A sampling strategy is outlined to serve as a framework for determining the fine- to micro-scale vertical distribution or fish larvae and their prey on Georges Bank in a single vessel, interdisciplinary mode of operation. A major objective of this sampling program is to characterize the development and temporal-spatial variability of these distributions to evaluate growth and survival of larval populations. The operational plan, sampling gear and instrumentation, as well as special techniques employed are discussed in terms of the usefulness of the parameters measured. Initial results are presented from a two-part study conducted in April-May 1981, focused on haddock (*Melanogrammus aeglefinus* L.) and Cod (*Gadus morhua* L.) larvae.

In April, a gadid egg patch with recently-hatched larvae (c. 91% haddock) was located on the southeastern part of Georges Bank, between the tidally-well-mixed front (c. 60-m isobath) and the shelf/slope-water front (c. 100 m). The water column along the southern flank was still well-mixed in April and the larvae were broadly distributed with a weighted mean depth between 30 and 40 m. Density of their dominant copepod prey was relatively low near the surface (<3 prey/l) but increased with depth (5-10 prey/l).

When the same larval population was surveyed again in May it had moved to the southwest at a rate consistent with the residual currents. By May the water column was stratified along the southern flank. A seasonal thermocline was observed between 10 and 20 m and fish larvae and their prey (50 prey/l) were concentrated in this zone. A storm swept the region and dispersed the larvae and prey (5-10 prey/l) throughout the water column. On the crest of the bank in the well-mixed waters (<60 m), larvae and their prey (10-25 prey/l) were broadly distributed vertically, but the mean depth of the larvae coincided with the highest density of prey at middepth. The implication of these observations to haddock and cod survival are discussed.

INTRODUCTION

Other than catastrophic losses, trophic (feeding) interrelationships involving both growth and predation are considered to be the basic factors controlling larval mortality. The mortality process at the individual level is thought to be a function of chance encounters by larvae with their predators and zooplankton prey which (like the larvae themselves) are distributed contagiously or in patches (Lasker, 1975; Vlymen, 1977; Beyer, 1980). It is believed that the degree to which larvae are able to grow rapidly through a succession of decreasing predatory fields, thereby reducing mortality, determines their potential population size. However, this process is a complex function of the density distribution (patchiness) of the larvae, their prey and predators, and possible competitors or other forms which may be alternative prey of larval predators. Since prey abundance below some level will be a critical factor influencing larval survival, it is necessary to know how feeding of larvae in the field is affected by the fine-scale (patchy) distribution of plankton communities and to understand the biological and physical processes which lead to the formation and dissipation of such patches.

At the Northeast Fisheries Center (NEFC), the Marine Ecosystems Division is conducting a broad-based research program (MARMAP) on the Continental Shelf, involving both monitoring and process-oriented studies, directed towards a better understanding of the recruitment process (Grosslein et al., 1979; Sherman, 1980). In the last decade, process-oriented studies have been carried out by the NEFC in the Georges Bank area addressing the recruitment problem. The first major study is represented by the autumn 1978 Larval Herring Patch Study which was conducted as an international, multi-ship, multi-disciplinary experiment (Lough, 1979). The primary objective was to define and follow a patch (homologous cohort) of herring larvae as a dissipative feature to gain a better understanding of the physical processes affecting its dispersal. The sampling strategy was designed to provide short-term estimates of larval growth and mortality in relation to the prey-predator field as the patch advected. More recent studies have been conducted on haddock and cod larvae since spring 1980 in a single vessel, inter-disciplinary mode of operation. Most of the sampling effort in this mode is to determine the fine- to micro-scale vertical distribution of larvae and their prey (copepods) in well-mixed and stratified waters. A major objective in this case is to characterize the development and temporal variability of these distributions for use in simulation models. These studies require different sampling strategies within the constraints of available resources to meet the desired objectives.

Each sampling strategy must be uniquely designed for the specific objectives and hypotheses investigated, taking into account the peculiarities of the target species and its biological and physical environment. However, as an investigation of larval fish growth and mortality is inherently complex, involving the intimate interaction of three trophic levels simultaneously (Shepherd and Cushing, 1980; Laurence, 1981), a multi-faceted sampling strategy is required to

resolve patterns and interactions occurring on the overlapping time-space scales (Haury et al., 1978). In this paper our sampling strategy is presented on the haddock-cod study which has evolved in part from the results of the Larval Herring Patch Study. The experimental objectives, sampling gear and instrumentation employed are discussed in terms of the usefulness of the parameters measured and highlighted with data analyzed to-date.

Target Species

Haddock (*Melanogrammus aeglefinus* L.) was chosen as the main target species, followed by cod (*Gadus morhua* L.), because of its commercial and ecological importance and the best overall base of life history data. This data base includes extensive laboratory experimental data, an index of year-class strength at the '0-group' stage, and fecundity and spawning population biomass data. The northeastern part of Georges Bank is a principal spawning ground for haddock and cod and their early life histories are similar in many respects. Their spawning seasons overlap, but for cod it is considerably longer and also its spawning distribution appears to extend further south than the haddock's (Colton et al., 1979). Cod spawn from late autumn into April-May, whereas haddock spawn from February to June. Peak spawning for both cod and haddock occurs in the spring with cod spawning about a month earlier than haddock. The onset and duration of haddock spawning appears to be associated with increasing water temperature (Marak and Livingstone, 1970).

Fertilized cod and haddock eggs hatch in about 2-3 weeks at average spring temperatures (Marak and Colton, 1961; Laurence and Rogers, 1976), and the larvae are planktonic for several months thereafter. The larvae hatch at c. 4 mm SL (Colton and Marak, 1969) and yolksac resorption is

completed 6-7 days post-hatch at 7°C (Laurence, 1974). Lab-reared larvae were considered metamorphosed (c. 10 mm, 1000 µg dry wt) in 30 days at 9°C and 40-50 days at 7°C. Fig. 1 depicts the principal haddock spawning time and area on Georges Bank, the generalized egg and larval drift, and areas where demersal 0-group fish are most abundant 6-8 months later (Grosslein and Hennemuth, 1973). The distribution of late stage eggs and recently-hatched larvae indicate that dispersion from the spawning center on northeast Georges follows the general pattern of drift, predominantly to the southwest at 1-4 miles/d (2-7 km/d) (Walford, 1938; Marak and Colton, 1961; Colton, 1965; Smith et al., 1979). During April-May, high concentrations of larvae (>0.1/m^3) can be found along the southern flank of Georges between the 60 and 100 m isobaths. Some

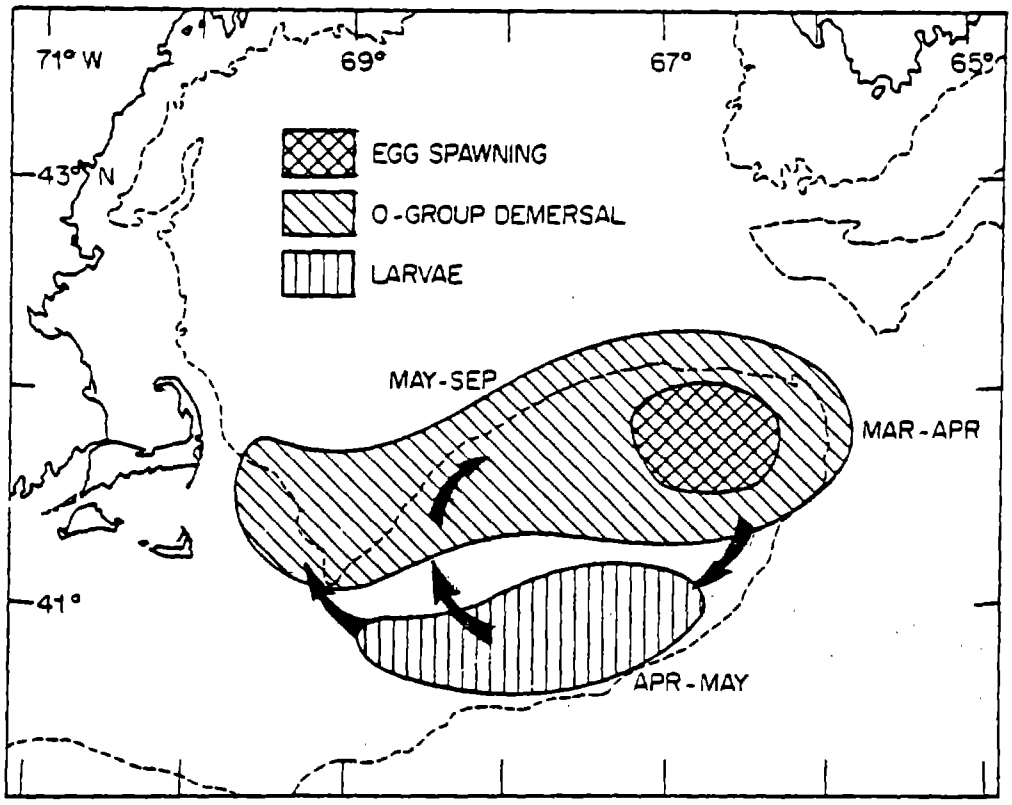

Fig. 1. Principal haddock spawning area on Georges Bank and generalized larval drift (indicated by arrows) and areas where demersal 0-group haddock are most abundant 6-8 months later.

portion of the larvae apparently are transported north on the western side of Georges Bank, but little is known about possible losses of larvae off the bank. The 0-group fish tend to be concentrated on the northern part of the bank indicating a favorable environment for their survival.

Hydrography of Georges Bank

The residual drift of Georges Bank is described as a semi-enclosed clockwise circulation with a mean speed of approximately 10 cm/s or 5 km/d (Fig. 2). A counter-clockwise circulation develops in the Gulf of Maine and both gyres intensify in the summer (Bumpus and Lauzier, 1965). In winter the

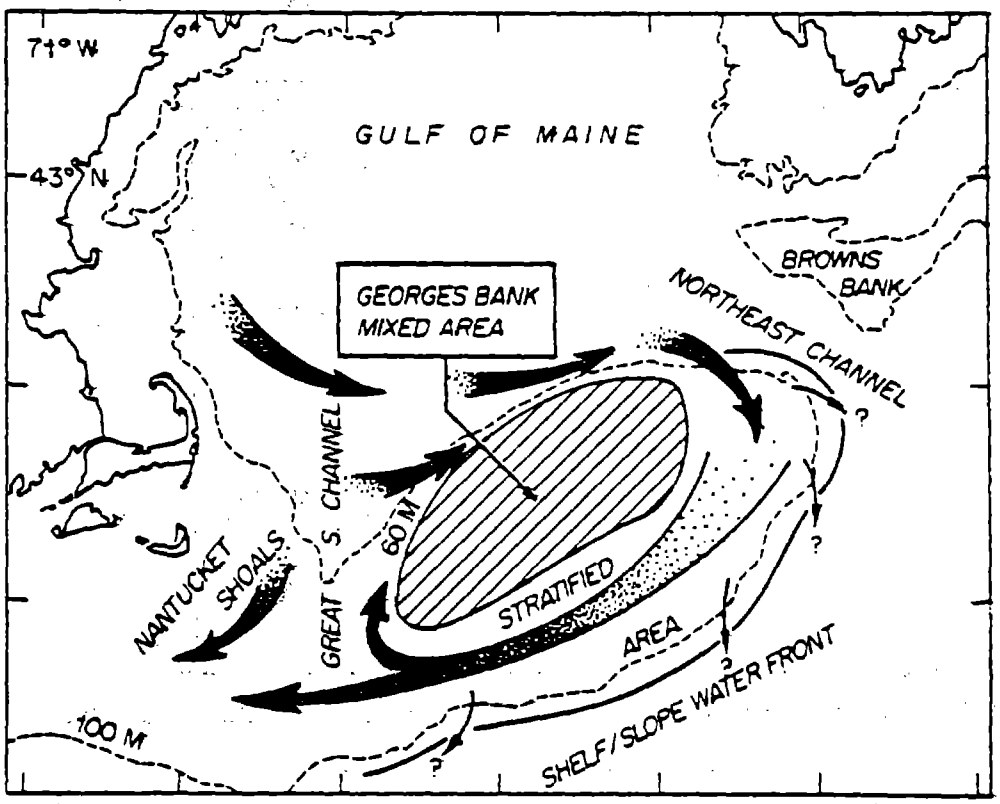

Fig. 2. Schematic representation of the well-mixed and stratified waters on Georges Bank and mean circulation flow (arrows) during spring and summer.

near surface flow is generally driven by the winds; the mean transport is offshore. Recent studies summarized by Butman et al. (1982) concluded that the observed mean flow at 10 m has a permanent clockwise circulation around Georges Bank with a mean circuit time of c. 2 months for a parcel moving along the 60 m isobath. Despite the considerable variability that could occur in the trajectory of such a parcel, they inferred that the clockwise circulation around the crest of the bank may provide a mechanism for partial retention of plankton.

The water on Georges Bank shoaler than 60 m is vertically well-mixed throughout the year by the semi-diurnal, rotary tidal currents that have speeds up to >2 knots (103 cm/s) (Bumpus, 1976). Progressive vector diagrams of the tidal elipses are oriented NW-SE on the crest with their long axes ranging 4-8 miles (7-15 km) in length. Summing the hourly speeds over a 12 h period, an approximation of the distance travelled by a parcel of water ranged 10-20 miles (19-37 km) over the shoals and 5-6 miles (9-11 km) over the deeper parts.

Besides the dominant tidal energy on the shelf, storms at 4-5 d intervals have an important role in shelf water dynamics (Beardsley et al., 1976).

In winter the well-mixed water is separated from adjacent water masses by two fronts. On the southern flank, the shelf/slope-water front intersects the bottom at about 80 m and separates the cooler, fresher shelf water from the warmer, more saline slope water. On the northern side, a subsurface front separates the Georges Bank water from the Gulf of Maine water. In late spring-summer a seasonal thermocline (20-30 m) develops in waters greater than 60 m. A subsurface band of cool winter water is found along the southern flank between the 60 and 100 m isobaths.

Gulf Stream warm-core eddies moving near the southern edge of the bank may play an important role in the movement of shelf/slope-water, both on and off the shelf, and the entrainment of organisms residing there (Lough, 1982; Joyce and Wiebe, 1983).

Objectives and Sampling Strategy

The main focus of the haddock-cod study to-date is to describe the spatial-temporal variability of larvae and their prey (copepods) during their first month of life on Georges Bank. Observations also are made to better understand factors governing their production and to survey post-larvae and potential predators of larval fish by sampling the macro-plankton and micro-nekton components on the same cruise. Our sampling program is presently designed to investigate the following hypotheses which we feel are important in order to understand the feeding dynamics and survival of larvae retained on Georges Bank:

1. Growth of larvae is related to the density of micro-zooplankton prey.
2. Micro-zooplankton are concentrated in areas of relatively high phytoplankton biomass.
3. Micro-zooplankton are contagiously distributed (clumped).
4. Stratification of the water column along the southern flank of Georges Bank in late spring serves to concentrate zooplankton and fish larvae vertically.
5. Feeding success is a stochastic process of random encounters with 'patchy' prey.

Supportive evidence for the first four hypotheses can be made by field observations; the fifth hypothesis must be investigated through probabilistic food encounter models or quasi-realistic laboratory experiments. The thermocline is potentially important because biological productivity appears concentrated near this layer and larval and juvenile haddock appear to be uniquely associated with it (Miller et al., 1963; Colton, 1965, 1972; Houghton and Marra, 1983). During spring when recently-hatched larvae are present, the seasonal thermocline is beginning to form, vertically stratifying the water column (>60 m bottom depth). The presence of a discontinuity layer resulting in a greater degree of structure and patchiness of the plankton may be critical to the survival of larvae in this region. There is a need to measure prey availability prior to, during, and after thermocline formation in order to evaluate the importance of this phenomenon.

A field program addressing these hypotheses requires sampling on spatial scales ranging from centimeters to kilometers and temporal scales from minutes to weeks. Considerable emphasis is given to the smaller scales of pattern as individual larvae encounter their prey on the micro-scale level (1 cm to 1 m); however, a larva's swimming capabilities soon develop to where it can migrate vertically 10's of meters in a matter of hours. Sampling larvae at the population level requires discrete samples at the fine-scale level (1 m to 1 km), for example, to resolve vertical migration patterns. To define a coherent patch of larvae, or to sample post-larvae or larger predators, requires sampling on a coarse scale (1 to 100 km). Synoptic, three-dimensional sampling of the variable fields is needed, but our present technology and sampling techniques usually only permit quasi-synoptic sampling of the parameters or organisms of interest (Kelley, 1976). The sampling gear used should be directed towards collecting discrete samples of the target organism

as synoptically as possible at the population level. However, since populations of larvae, their prey and predators usually occur at different scales, an array of sampling gear is required which tends to negate simultaneous sampling, unless more than one research vessel is used. Nevertheless, we can approach near synopticity for some elements of the sampling program utilizing just one vessel.

The rotary tides (12.4 h period) are the dominant forcing function on the bank so that experiments should be nested within its space-time domain. According to the Nyquist theorem, which states that a function can be detected if its period is at least twice the sampling frequency, station sampling on a grid would have to be taken at least once every 6 h at a sampling distance between 5 and 20 miles (9 and 37 km) depending on bottom depth. And in order to encompass a before and after storm event, observations should be repeated every 2 d over at least an 8-10 d period. Sameoto (1975, 1978) found that zooplankton variability was similar over a broad area of the Scotian Shelf so that an accurate and efficient estimate of population means could be made by taking 2 net samples 6 h apart at a fixed station.

Our basic field strategy is to locate and characterize a population of larvae and their prey, and then to compare and contrast their fine- to micro-scale distribution within stratified and well-mixed waters on Georges Bank. Previous experience from the 1978 Larval Herring Patch Study indicated that relatively coherent and stable patches of larvae and zooplankton could be defined with conventional sampling techniques (bongo-net samples) and followed for a number of days to weeks at a spatial scale somewhat greater than the tidal excursion (>5 miles or >10 km). It was assumed for sampling purposes that variability within the tidal regime was similar as mixing processes dominate on this scale. Also, by following a drogue for station time-series observations, one assumed the same parcel of water was being sampled with the

same larvae-prey population. Thus, by reducing horizontal variability, aliasing of observations vertically would be reduced in order to conduct time-series observations over a minimum of two tidal cycles. The limitations of time-series analyses in marine ecosystems are discussed by Denman and Platt (1978).

The deployment of moored current meter arrays can provide a truly synoptic three-dimensional picture of the horizontal current field within the study area. Coarse to meso-scale MARMAP plankton-hydrography surveys conducted on Georges Bank and contiguous waters during the same time provide a broader background in which to compare our more intensive fine-scale studies. Remote sensing offers the potential of regional synopticity for a number of near-surface parameters such as ocean temperature and color (Chamberlin, 1982; Gower, 1982).

METHODS

Gear, Instrumentation, and Special Techniques

Bongo-net sampler

Standard MARMAP bongo-type samplers are used to make integrated water-column hauls from 5 m above the bottom to the surface to collect zooplankton (Posgay and Marak, 1980). A 61-cm bongo sampler (505 and 333 µm mesh nets) and 20 cm bongo sampler (253 and 165 µm nets) array are towed obliquely at 1 1/2 knots (78 cm/s) and lowered at a wire speed of 50 m/min and retrieved at 20 m/min. Water filtered through each net is measured by a flowmeter and the tow depth profile is measured with a time-depth recorder.

MOCNESS

A Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al., 1976; 1982) with three separate underwater sampling units (1/4 m, 1 m, 10 m) provides us with wide spectrum capabilities of sampling discrete vertical strata encompassing three trophic levels from micro-plankton, fish larvae-zooplankton, to micro-nektonic organisms. MOCNESS is a rectangular sampler whose nine serially linked nets can be opened and closed sequentially by commands through a conducting cable from the surface vessel, thus permitting sampling of up to nine discrete depth levels or horizontal series in a single haul. The three underwater samplers are designed to be hauled at 1 1/2 knots (78 cm/s), 45° net angle, for an effective mouth area of 1/4 m^2, 1 m^2, and 10 m^2. Standard net mesh size for the underwater units are 64 µm, 333 µm, and 3 mm, respectively. On-deck, real-time monitoring includes depth (pressure), net angle, number of the net presently filtering water, volume of water filtered, temperature and chlorophyll fluorescence (Aiken, 1981). Parameter data are stored on an HP-85 computer system for real-time X-Y plots of temperature and fluorescence vs. depth, which are useful in selecting sampling depths (see Fig. 3). A Northstar Loran C unit with plotter also is integrated with the MOCNESS for recording the position at each net release. Other sensors such as salinity, light, and oxygen will be integrated with MOCNESS.

Plankton pump

In 1981 a 1-hp submersible well pump was used to sample micro-zooplankton at depth. The pump is typically deployed attached to 1/4" (6.4 mm) wire with a 45 kg lead ball. Delivery of water from depth to a deck manifold fitted with fine-mesh nets (20 and 53 µm mesh) is by a 7.5 cm diameter PVC discharge hose. Water is typically pumped from five

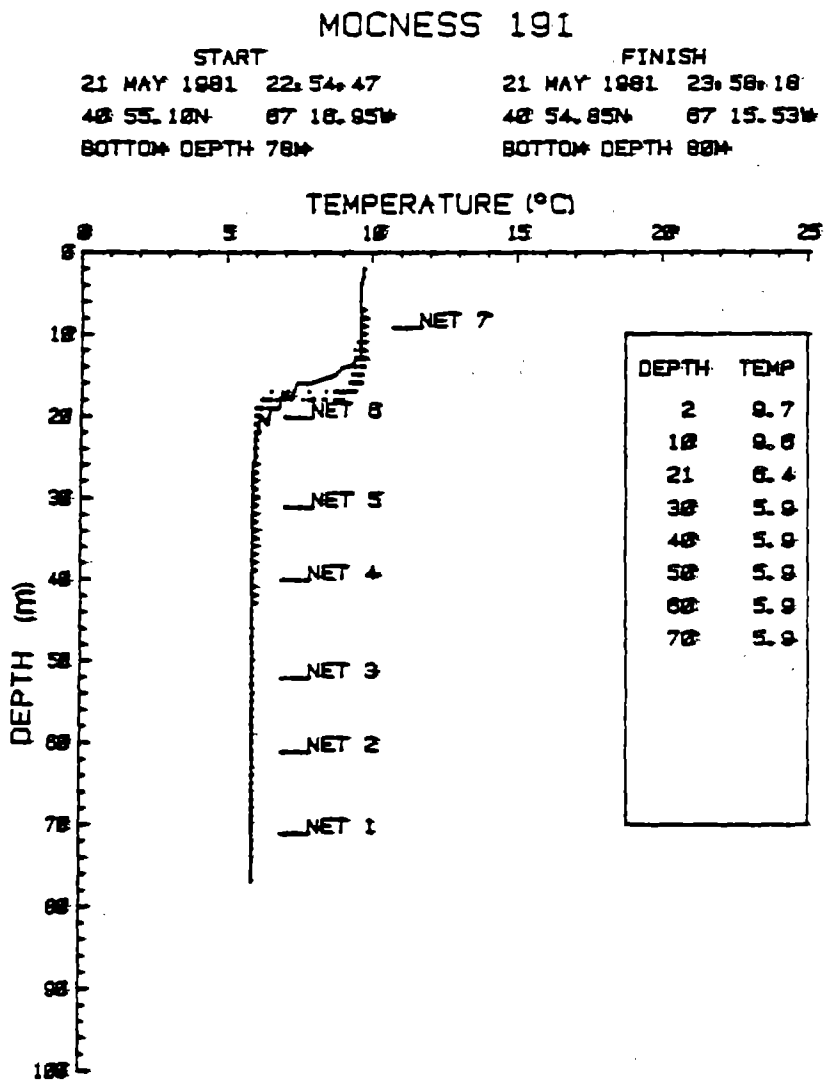

Fig. 3. Real-time temperature-depth plot of 1 m MOCNESS haul 191. A solid temperature line is drawn as net is set to maximum depth and dotted after first net is opened and sampling sequence begins.

depth levels in the upper 50 m of water for 10 min each depth to filter 1 m^3 of water. Since the 1982 season, a larger submersible pump has been used to filter 1 m^3 of water in 1 min.

CTD-fluorometer

A Neil Brown CTD micro-profiling system with a General Oceanics Niskin bottle rosette is used for rapid continuous profiling of temperature and salinity with depth. The water

bottle collections also are used to make discrete observations of micro-zooplankton, nutrients, and phytoplankton biomass measures by conventional methods. Continuous *in-situ* fluorescence is measured at the same time by deploying an ENDECO submersible fluorometer (Turner Designs Model) with on-deck recording of depth, fluorescence, and temperature via conducting cable. A recently acquired Variosens *in-situ* fluorometer will be interfaced with the CTD.

Real-time zooplankton processing

In process-oriented studies there is need for real-time results so that decisions can be made to optimize the experimental operations. A method we employ at sea to make routine, quantitative analyses of plankton-net samples using silhouette photography techniques coupled with a microfiche reader, an electronic digitizer, and a small personal computer is described by Lough and Potter (1983). More than 90% of the organisms can be identified to species level and life stage, and a subsample enumerated within 20 min after collecting by this method.

A HIAC Criterion PC320 12-channel particle counting and sizing system (Pugh, 1978; Tungate and Reynolds, 1980) has been acquired for development as a real-time tool for the quantification of marine plankton. Three sensors (CMH-150, CMH-600, E-2500) are used to count particles in the range of 5-2500 µm. However, at present we process Niskin bottle water samples only in a batch mode. The HIAC unit has been interfaced with a Canberra Multi-Channel Analyzer and an HP-85 computer system to control all settings and functions. The instrument is being modified for *in-situ* particle profiling along the lines reported by Tilseth and Ellertsen (1984).

Larval condition and growth indices

Special collections of larvae, preserved throughout the cruise, are analyzed in the laboratory for biochemical content, histological and morphological assessment, and otolith increment deposition. Laboratory studies by Buckley (1979, 1981) have demonstrated relations between food availability and larval RNA/DNA ratios and growth rate. A regression model has been developed recently (Buckley, 1982) between temperature, RNA-DNA ratio, and mean daily protein growth rate which accounts for short-term growth over the previous 2-4 days. This sensitive technique is now being used to study the relations between environmental conditions and larval growth and survival in the field. From the same samples larvae are being analyzed histologically (O'Connell, 1976) and morphometrically (Theilacker, 1981) to evaluate their condition and develop criteria for detecting starved and weakened larvae. Population mean age and long-term average growth of larvae can be estimated by relating otolith growth increments to larval size (Bolz and Lough, 1983). An individual larva's past environmental growth history also may be revealed with proper laboratory verification of their otoliths (Radtke, 1984).

Prey selection

Larvae from selected MOCNESS hauls are processed for gut contents by the methods described in Cohen and Lough (1983) and Kane (in press).

Field Operational Plan

A concentration of larvae (or eggs) on Georges Bank is located from a previous MARMAP broad-scale survey, or at the time of the cruise by exploratory transects using standard bongo-net gear in likely areas. Then a grid of

40-50 stations, 5 miles apart, is occupied within a 2 d period to characterize the larval fish, plankton, and temperature-salinity field in an area sufficiently large (c. 30 x 50 miles [56 x 93 km]) to encompass the anticipated dispersal of plankton having a residual drift of 4 miles/d (7 km/d) in which the fine-scale station studies will be carried out over 4-6 d. The survey grid usually is situated so that stations overlap the shoal front of the well-mixed waters (<60 m) and the southern shelf/slope-water front (c. 100 m) bounding the stratified waters on the bank. A bongo haul and XBT drop are made on each grid station, and surface temperature, salinity and fluorescence are monitored continuously.

Based upon real-time sample analyses made during the grid survey, a station is selected for the fine-scale time-series observations and a drogue is deployed at the depth corresponding, ideally, to the weighted center of gravity of the larval population. On one occasion, a drogue was deployed with an array of vector-averaging current meters (VACM) positioned to measure current velocity and temperature at selected depths to determine shear in the water column. On station, the sampling scheme used is a combination of fine- to micro-scale observations in order to sample fish larvae and their prey, and other environmental parameters. This scheme allows 2-4 observations of each kind during a tidal period (12.4 h). On each drogue-follower station, time-series observations are made for a minimum of 30 h and sometimes as long as 50 h encompassing 2-4 tidal periods. A complete series of observations is made every 6 h in the following sequence: CTD-fluorometer cast, MOCNESS 1 m haul, plankton pump cast, CTD-fluorometer cast, and MOCNESS 1/4 m haul.

CTD-fluorometer cast

The objective of this operation is to obtain a vertical profile (and variability) of temperature, salinity, and chlorophyll *a* fluorescence on a micro-scale level. Casts may be repeated for short-term variability. Niskin water bottle samples are collected at selected depths for calibration purposes and particle size analysis using the HIAC PC320 system. Ancillary observations include a light-meter cast to define the light extinction curve, and a bottom-trip Niskin bottle cast to collect a phytoplankton sample within a meter of bottom.

MOCNESS 1 m haul

The objective of this haul is to determine the vertical distribution and abundance of fish larvae and larger zooplankton from near bottom (<5 m) to surface with 10 or 5 m resolution. An adequate sample of larvae (30-100 individuals) is usually obtained by filtering 250 m^3 of water which takes about 5 min for each net. During this 5 min the net travels a horizontal distance of c. 235 m.

Plankton pump cast

Micro-zooplankton samples are collected at 4-6 discrete depth levels based upon the vertical distribution of the fish larvae and environmental conditions. At each depth level, 1 m^3 of water is pumped on deck and filtered through 20 and 53 µm mesh nets. Sampling resolution is 1-2 m vertically and 10's of meters horizontally, depending on the rate of pumping and ship's drift.

MOCNESS 1/4 m² haul

The objective of this haul is to determine the vertical distribution and abundance of micro-zooplankton retained by 64-µm mesh nets over the vertical distribution range of fish larvae. About 20-36 m^3 of water is filtered by each net (1-3 min) within an integrated strata of 10, 5, or 2-m resolution (94-170 m horizontal distance traveled).

Following the fine-scale station observations, the grid of stations may be resurveyed and new transects added in the direction of the residual current, or MOCNESS 10-m² hauls may be made on a transect of stations in the study area. The 10 m² MOCNESS is used to determine the vertical distribution and abundance of potential micro-nektonic predators and post-larvae with 15 or 25 m resolution, each net filtering 7000-14000 m^3 of water in 15-30 min (705-1410 horizontal distance traveled). A 1 m² MOCNESS haul usually is made immediately before or after to collect larval fish or other food prey.

RESULTS AND DISCUSSION

Some of the initial results are presented here from a two-part study conducted aboard R/V ALBATROSS IV, 15-30 April 1981 and 18-30 May 1981. On the April cruise a well-defined concentration of gadid eggs was located on the southeast part of Georges Bank between the 60 and 100 m isobaths by the bongo sampling grid of stations (Figs. 4-8). Recently-hatched haddock and cod larvae (3-5 mm SL) were found most abundantly towards the southeastern part of the grid and a ratio of their abundance indicated that about 91% of the gadid eggs were haddock, the other 9% cod. The majority of eggs were at a late stage of development (Colton and Marak, 1962) and were estimated to have been spawned 8-10 d previously in the 6°C water. Early stage eggs were more abundant to the northeast near the

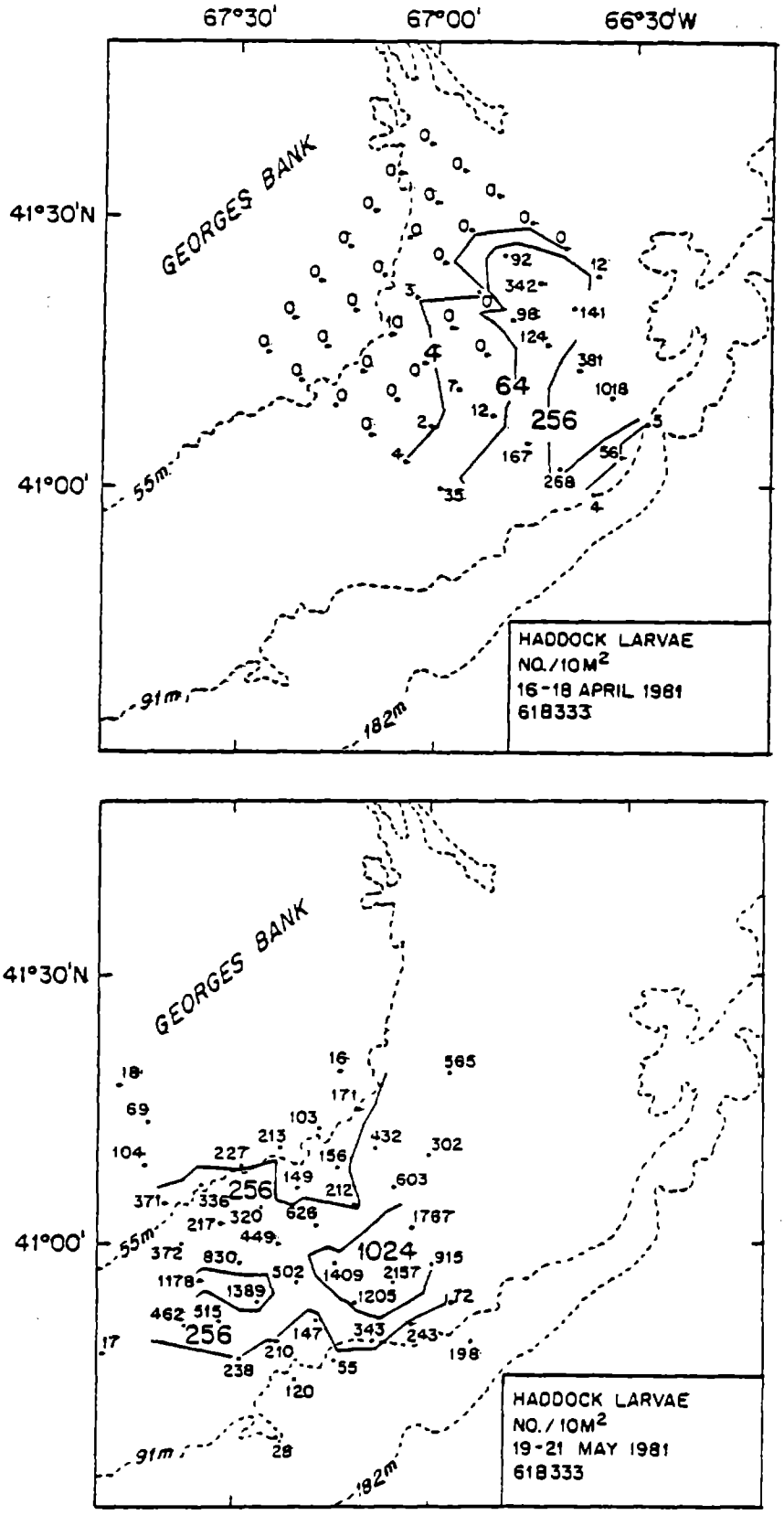

Fig. 4. Haddock larval distributions from April and May 1981 grid surveys. Densities contoured by factor level of 4.

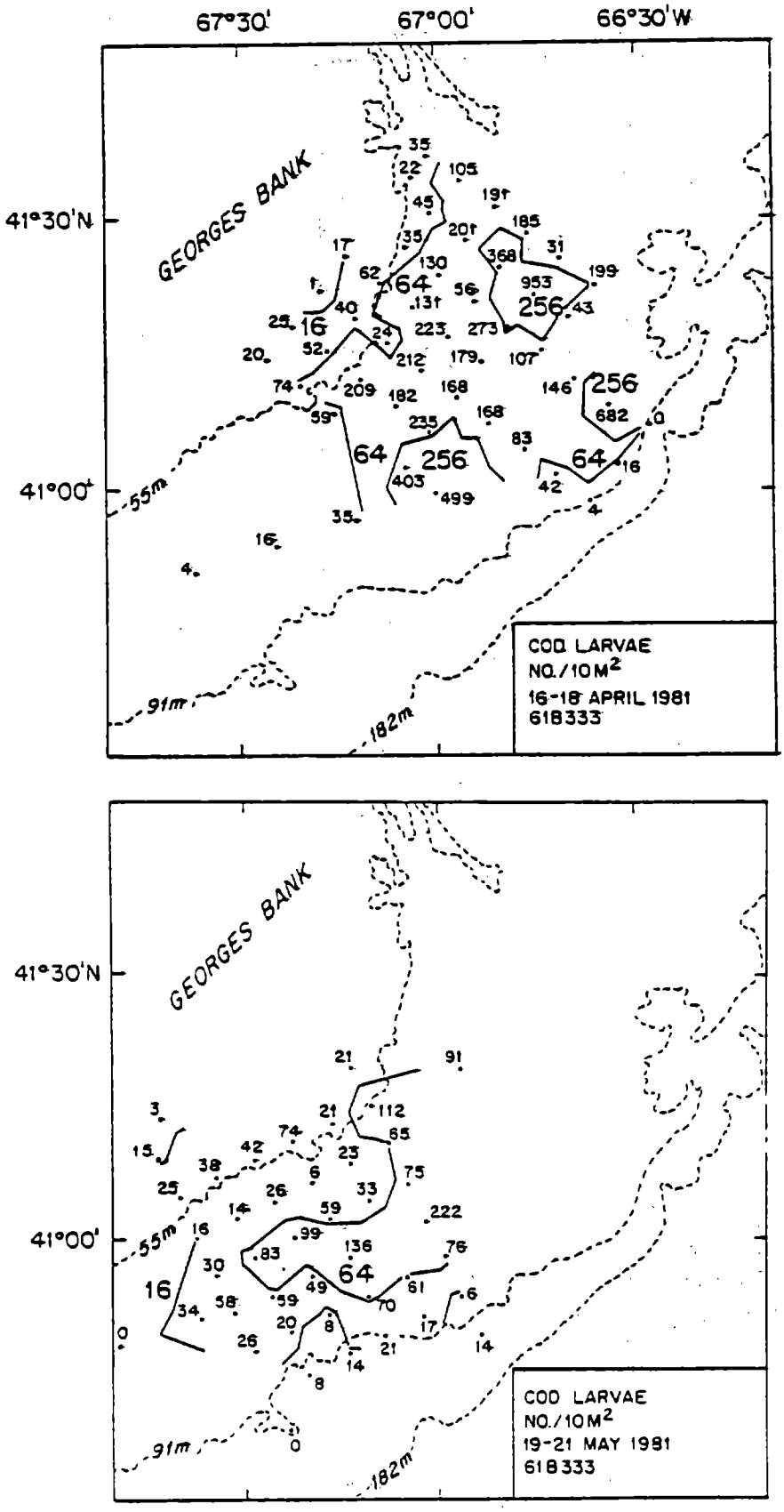

Fig. 5. Cod larval distributions from April and May 1981 grid surveys. Densities contoured by factor level of 4.

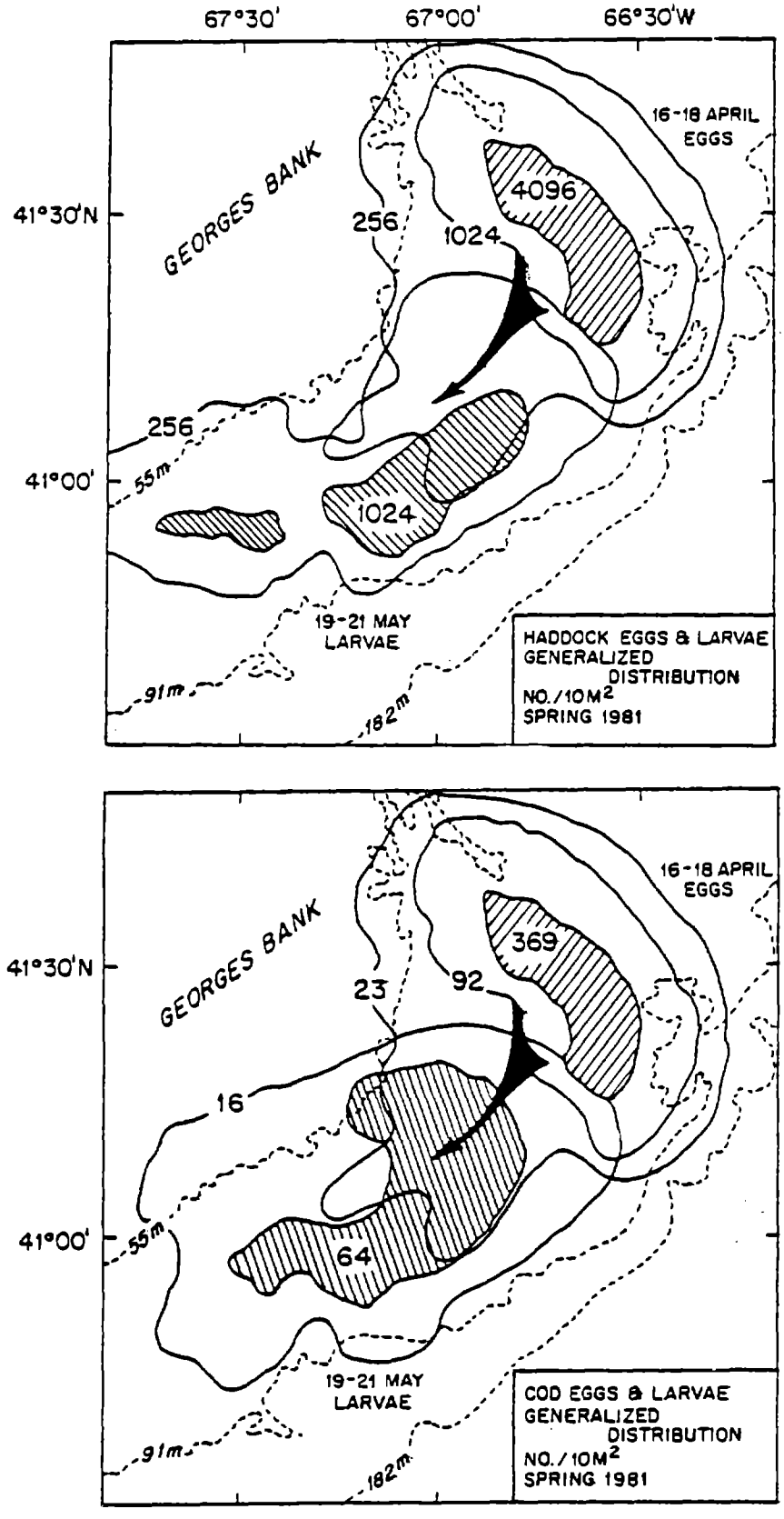

Fig. 6. Haddock and cod egg and larval distributions generalized from the April and May 1981 grid surveys.

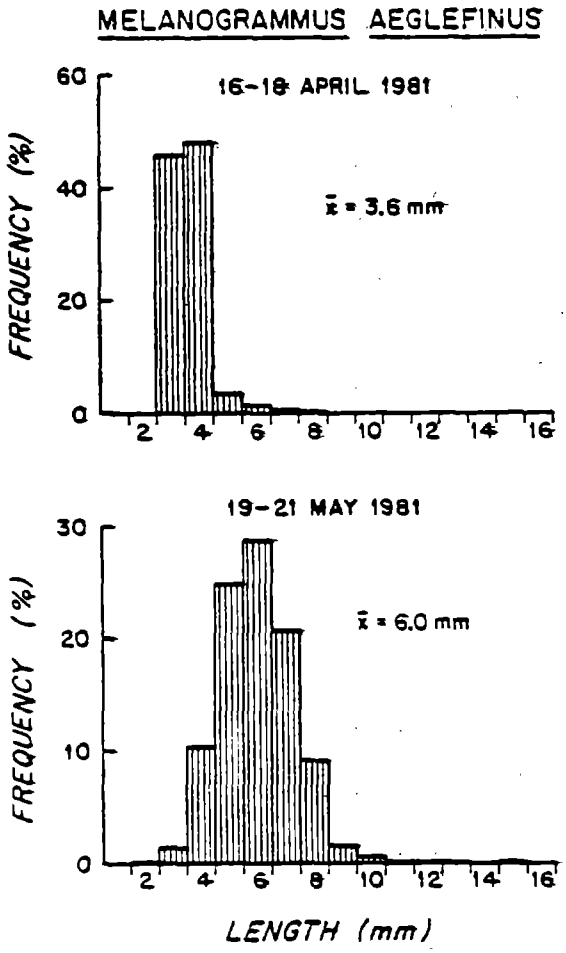

Fig. 7. Length-frequency distributions of haddock larvae collected on the April and May 1981 grid surveys.

historical spawning grounds. Cod larvae were more widespread than haddock and their greater size range was indicative of their earlier spawning in February-March.

By May, a concentration of larval haddock and cod was located along the southern flank of Georges to the southwest of the April distribution, situated between the shoal tidal front and the deeper shelf/slope-water front. The mean length of both larval populations sampled on the grid was 6 mm and is consistent with laboratory growth rates over the period of time between hatching in April and the May survey (Laurence, 1978; Bolz and Lough, 1983). Also, an estimated transport of 1-2 miles/d, which is consistent with the long-term residual currents reported for this area, would account

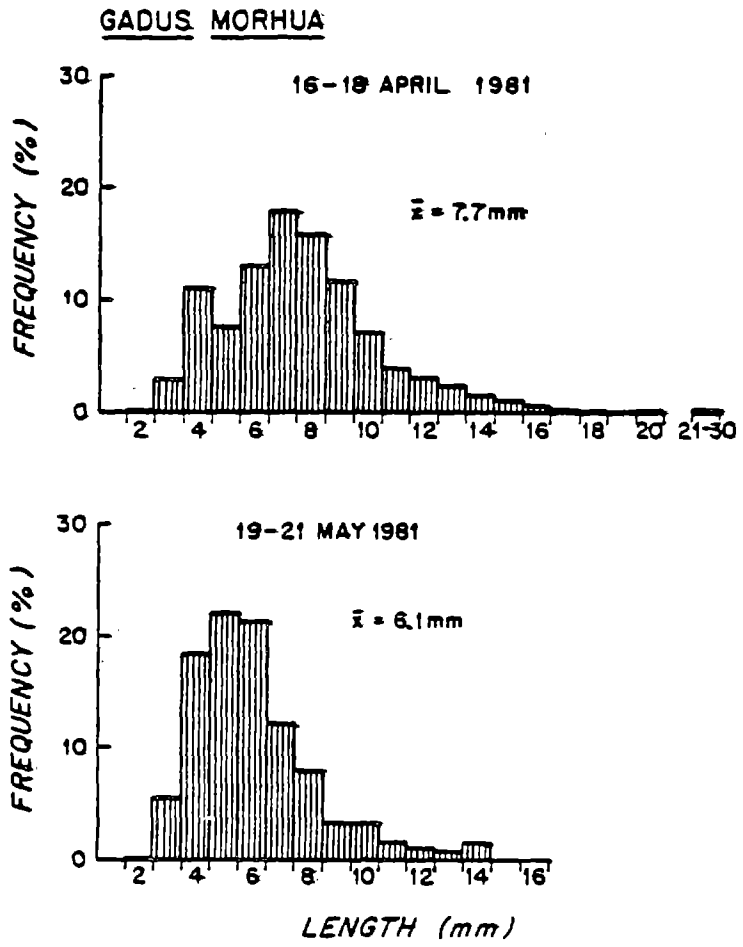

Fig. 8. Length-frequency distributions of cod larvae collected on the April and May 1981 grid surveys.

for the displacement between the highest concentration of eggs in April and larvae in May. Coupled with the fact that no other egg or larval concentrations were found in the area, these observations support the view that the egg and larval concentrations defined belonged to the same spawning population.

An important feature of these egg and larval concentrations is their coherence and stability which provide continuity in the sampling program. The grid station densities have been contoured by a factor of 4 as the coefficient of variation of a single plankton haul typically is in the range of 22-44% (Cassie, 1963). Note the internal consistency of the station values within the contoured areas. Resampling a grid transect once on the April survey and again in May 4-7 d later

produced egg and larval concentrations nearly identical to the previous station values (within a factor of 4). Using all available information, the haddock and cod egg and larval concentrations have been generalized in Fig. 6 to show their size, shape, and dispersal between surveys. The highest concentrations of eggs and larvae contoured were elliptical in shape with major and minor axes of about 30 x 15 miles (56 x 28 km). The smallest patch resolved is about 10 x 5 miles (19 x 9 km), which is on the scale of the tidal excursions and the sampled grid of stations. The lowest concentration of larvae defined and contoured as a patch was about 60 miles (111 km) long between the shelf/slope-water front and the tidal front. If one assumes that the patch dimensions are reasonably accurate, an estimate of mortality can be made between the eggs in April and the larvae in May. Using methods similar to those described in Lough et al. (1980), mortality of haddock and cod from their hatching midpoint through the 6-mm size class (18-24 d post-hatch) was estimated to be 6-8%/d. These loss rates are consistent with the range of rates (5-15%/d) reported by Saville (1956) for Faroe haddock larvae.

It also is of interest to note that the largest and presumably oldest larvae collected on the grid survey were found to the extreme southwest and on the shoals (<60 m). This past May 1983, using the 10 m MOCNESS, relatively high densities (70-450/10 000 m^3) of cod post-larvae (15-50 mm) and sand eel, *Ammodytes* sp. (45-80 mm), were collected throughout the shoaler parts of western Georges Bank, both of which have been observed to prey upon young fish larvae.

In April, winter conditions still prevailed; the water column was well-mixed throughout the study area, isothermal (6°C) from surface to bottom. Only during the final days of the cruise was a slight warming of surface waters observed, indicating the onset of spring thermal stratification on the flank of the bank. Net-phytoplankton (>20 µm) biomass increased with depth from 1-2 mg chl *a*/m^3 near the surface to 5-

10 mg chl a/m^3 near the bottom, apparently due to sinking of larger diatoms and dinoflagellates (Busch and Mountain, 1982). Nanno-phytoplankton (<20 µm) biomass was evenly distributed throughout the water column at 1-2 mg chl a/m^3. The vertical distribution of gadid eggs was low at the surface and also generally increased in density with depth to a maximum at the bottom (Fig. 9). The cod larvae were separated into two size groups for analysis (3-8 mm and >8 mm)

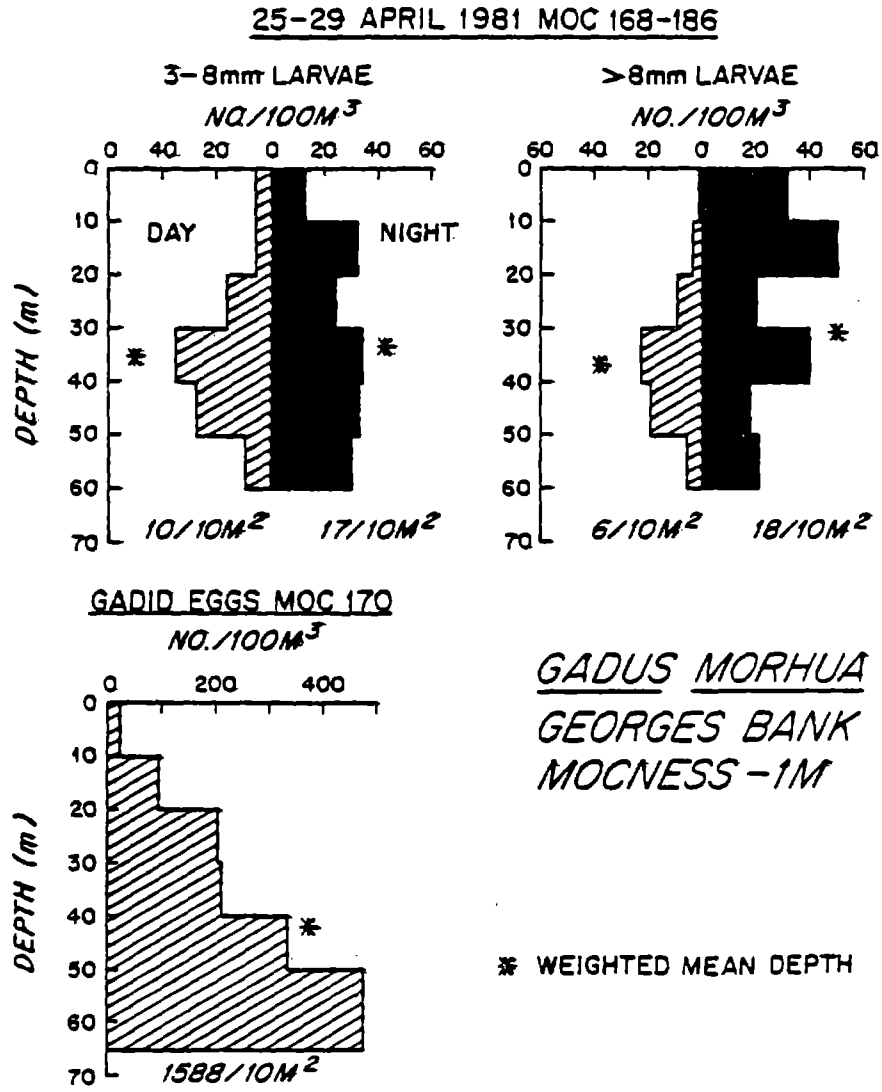

Fig. 9. Vertical distribution of cod larvae and gadid eggs collected by 1 m MOCNESS (333 µm mesh) on the southeast part of Georges Bank (41°20'N 66°53'W), 25-29 April 1981.

because of reported differences in behavior of the larger larvae (Wiborg, 1960; Miller et al., 1963). Their mean day and night abundances within 10 m sampling strata over a 54 h period are shown in Fig. 9. The size range of larvae collected by the 1 m MOCNESS are essentially the same as that collected by the 61 cm bongo net shown in Figs. 7 and 8. Both size groups of cod larvae are broadly distributed throughout the water column with weighted mean population depths between 30 and 40 m in water 66-70 m bottom depth. More cod larvae are usually caught by night than day, especially in the upper 20 m. A significant vertical displacement between day and night is shown by the larger size group. Night mean abundance of these larvae in the upper 20 m of the water column (mean length of 11 mm) was greater by a factor of 14-26 than that of the mean day abundance.

By mid-May, the water column was well-stratified at bottom depths greater than 60 m. At the first time-series station (80 m), 21 May, the surface temperature approached 10°C, a strong thermal gradient (0.75°C/m) was evident between 15 and 20 m, and below the thermocline the water was 5.9°C to bottom (refer Fig. 3). Both net- and nanno-phytoplankton biomass were reduced to <1 mg chl a/m^3, but showed a slight increase in the nanno-phytoplankton biomass above 20 m. Both haddock and cod larvae were almost exclusively confined to the upper 20 m of the water column with maximum abundance within the thermocline (Figs. 10 and 11A, MOC 191). An intense storm swept the area with high northeasterly winds, 35-40 knots (18-21 m/s), and upon resuming operations at the same site several days later on 24 May, it was evident that the water column was well-mixed, c. 7°C isothermal. Phytoplankton biomass was uniformly dispersed from top to bottom. Haddock and cod larvae now were broadly distributed throughout the water column with a weighted mean depth between 30 and 42 m, although there was a suggestion of an upper shift in the vertical distribution of larvae during the night (Figs. 10 and 11A, MOC 193-207). On 28 May, a single MOCNESS haul

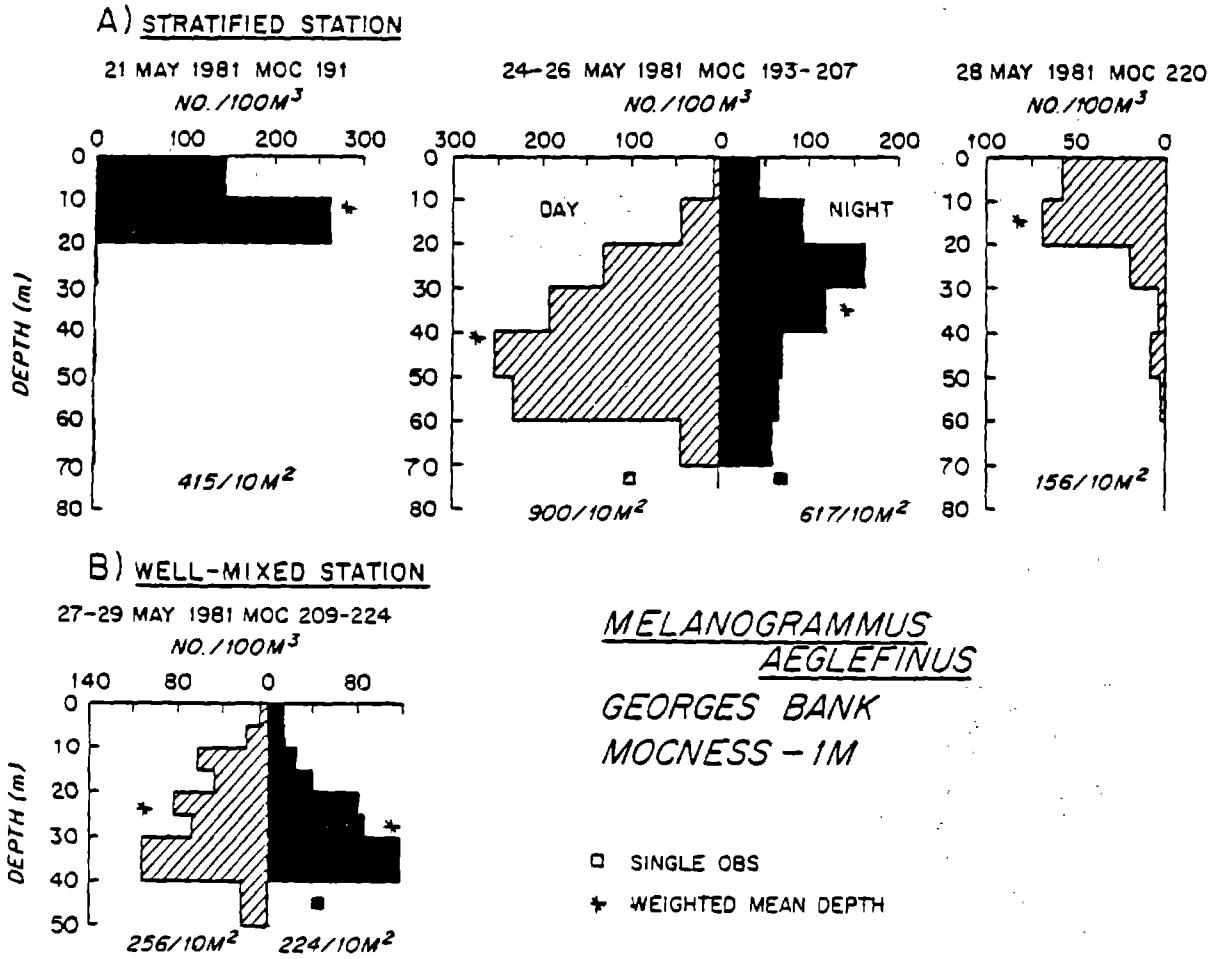

Fig. 10. Vertical distribution of haddock larvae on (A) stratified station (40°55'N 67°16'W) before and after storm, 22-24 May 1981, and on (B) shoal, well-mixed station (41°07'N 67°35'W), 27-29 May 1981.

(220) showed that a shallow thermocline had formed and the larvae were reaggregating in the upper 20 m associated with the restratification. By plotting water column density (sigma-t) values during this period in Fig. 12, one can see the process of restratification between the time the storm abated sufficiently to resume sampling on 24 May (MOC 193) and the last haul on 28 May (MOC 220). At this rate it would take a total of about 7-10 d for the water column and fish larvae to restructure to the same degree observed prior to the storm. Miller et al. (1963), in a mid-May 1958 vertical distribution study of larval haddock around the flank

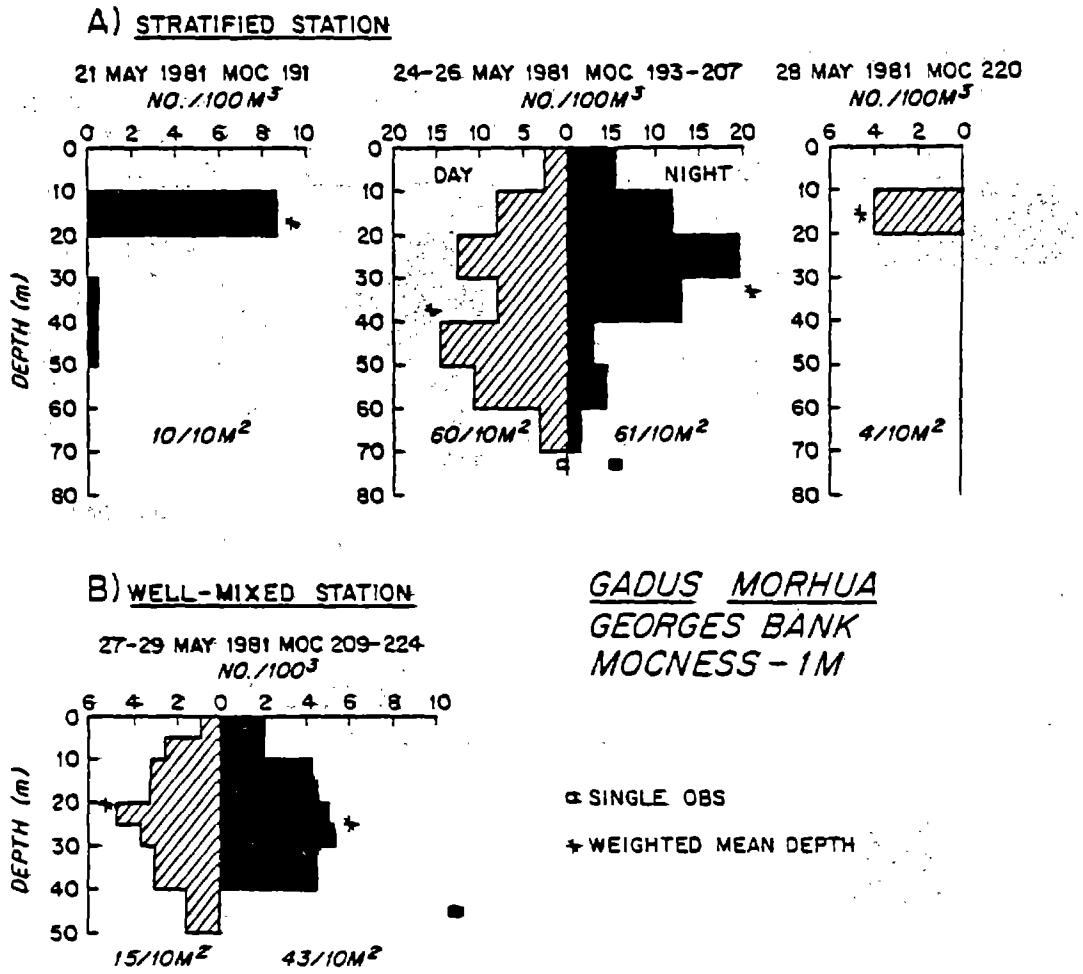

Fig. 11. Vertical distribution of cod larvae on (A) stratified station (40°55'N 67°16'W) before and after storm, 22-24 May 1981, and on (B) shoal, well-mixed station (41°07'N 67°35'W), 27-29 May 1981.

of Georges Bank, found that 84% of the larval population occurred within the discontinuity layer, the confines of a thermocline, which occupied about 25% of the water column.

A shoal-water station (50 m bottom depth) was occupied for 25 h, 27-29 May, where the water column was well-mixed, 8-9°C. Haddock and cod larvae were broadly distributed through the water column with weighted mean depths between 20 and 30 m (Figs. 10 and 11B). There was no significant difference between their day and night vertical distribution.

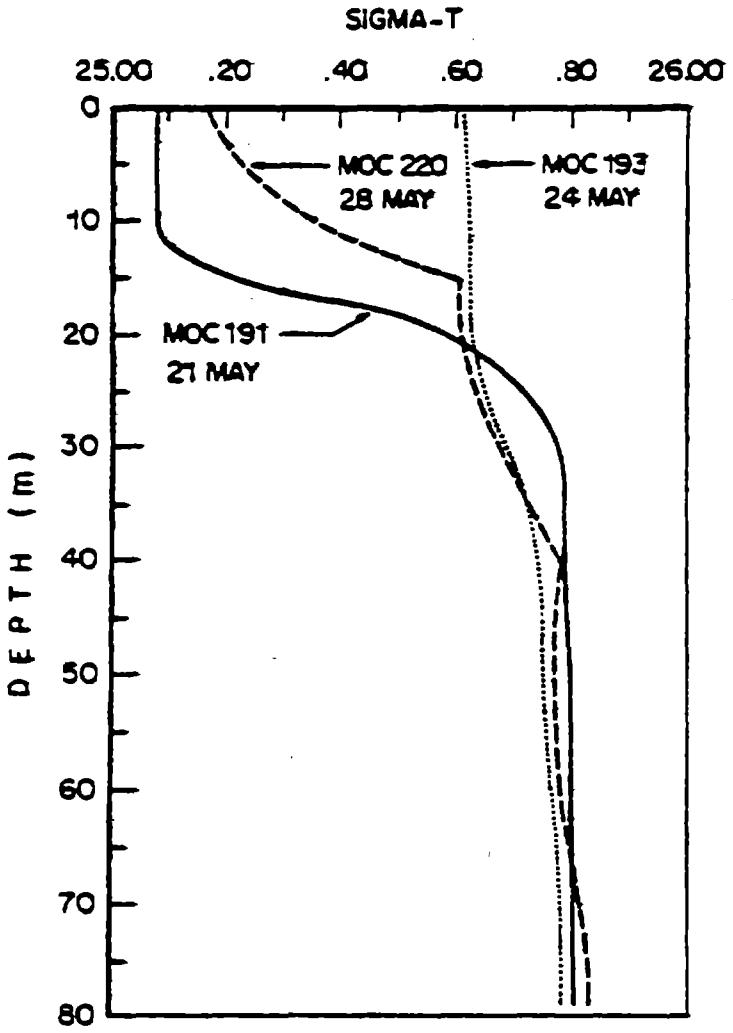

Fig. 12. Water-column density (sigma-t) profiles on stratified station (40°55'N 67°16'W) before and after storm, 22-24 May 1981. Corresponding MOCNESS haul numbers shown.

Phytoplankton biomass was uniformly low throughout the water column with a noticeable increase in the bottom few meters, but slightly higher (1-2 mg chl a/m^3) than the deeper station (80 m).

The dominant copepods on Georges Bank in late-winter and spring are *Pseudocalanus* sp., *Calanus finmarchicus*, and *Oithona similis*. *Pseudocalanus* tends to be more abundant on the shoal area of Georges while *Calanus* develops high abundance in the near-surface waters of the stratified zone along the southern flank. *Oithona*, a small copepod, is widespread in its distribution. Prey selection studies of larval

haddock and cod show that the naupliar and copepodite stages of *Pseudocalanus* and *Calanus* are their most important prey (Sherman et al., 1981; Kane, in press). Eggs of these two species can sometimes comprise a significant number of prey items for the smallest larvae (<6 mm), especially for the more passively feeding haddock larvae. The preferred prey size of four length groups of larvae is depicted in Fig. 13. Note that cod feed upon larger prey at a smaller size than haddock. Both species of larvae (<10 mm) select 50-80% of their prey in the 0.10-0.19 mm width class. Recently-hatched larvae, 3.5-5.9 mm, are particularly dependent on this size class of prey which encompasses the nauplius III through copepodite II stages of *Pseudocalanus* and the nauplius II-V stages of *Calanus*.

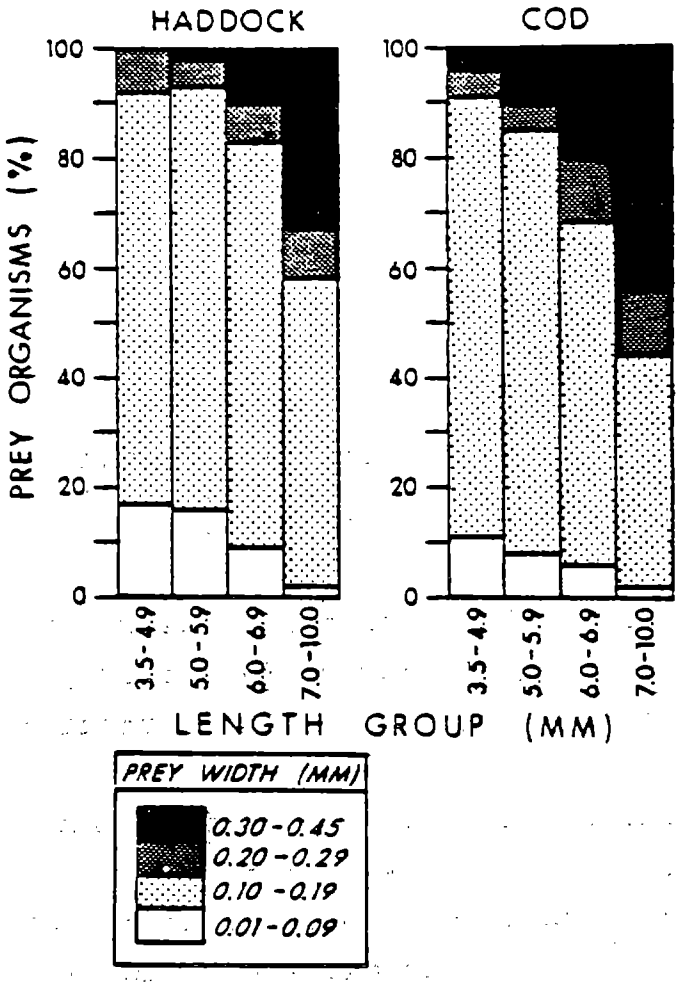

Fig. 13. Preferred prey size of larval haddock and cod length groups from May 1980 Georges Bank study (Kane, in press).

A conservative estimate of prey density in the field has been made by summing the appropriate life stages of *Pseudocalanus* and *Calanus* in the same prey size classes used above in Fig. 13 from the 1/4 m MOCNESS hauls made during the April and May station time-series. A comparison of various sampling gear and net mesh sizes indicated that the naupliar and copepodite stages of these two species were quantitatively sampled by the 1/4 m MOCNESS. In well-mixed waters, a coefficient of variation of 26% was estimated for the total copepod nauplii count from net samples within a selected stratum. In Figs. 14 and 15 the mean number of prey per liter within each depth stratum is plotted by width class. In April (Fig. 14), the vertical distribution of prey was low near the surface and increased with depth. The dominant and most important size class of prey, <0.19 mm, had <3 prey/l above 20 m depth and 5-10 prey/l at greater depths. The weighted mean depth of the small cod larvae in this same series of hauls was between 30 and 40 m. In May (Fig. 15A), the single 1/4 m MOCNESS haul

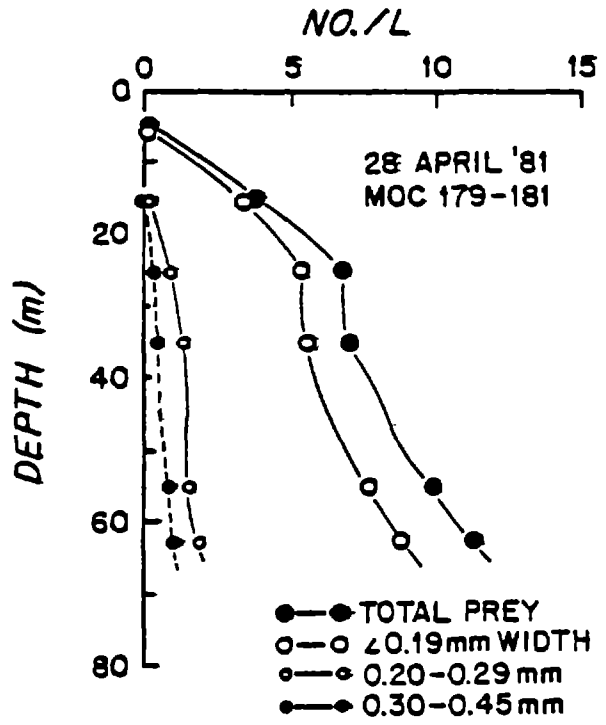

Fig. 14. Vertical distribution of larval prey field collected by 1/4 m MOCNESS (64 µm mesh) on the southeast part of Georges Bank, 28 April 1981.

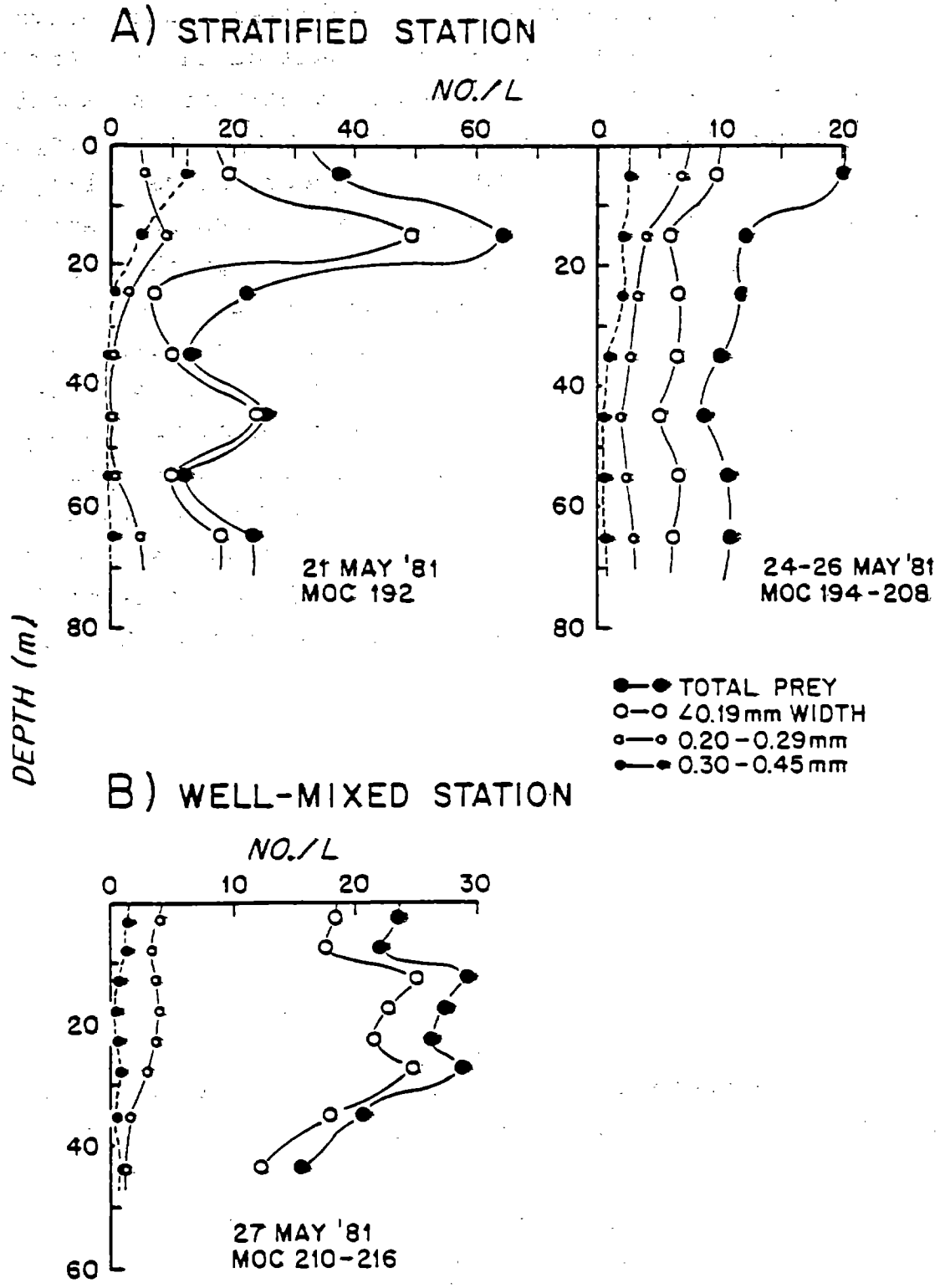

Fig. 15. Vertical distribution of larval prey field on (A) stratified station before and after storm, 22-24 May 1981, and on (B) shoal, well-mixed station, 27 May 1981.

(192), 21 May, made in the well-stratified waters showed a peak concentration of c. 50 prey/l for the <0.19 mm prey size class at 10-20 m depth where the thermocline layer resided, as well as the peak concentration of both haddock and cod larvae. A range of 5-25 prey/l was observed at other strata sampled. During 22-24 May, the storm which mixed the water column, also throughly redistributed the zooplankton. The important size class of prey now were uniformly distributed from top to bottom with a range of 5-10 prey/l. On the shoal, well-mixed station, 27 May (Fig. 15B), the <0.19 mm size class of prey ranged from 12-25 prey/l with peak densities between 15 and 30 m depth. The weighted mean depth of larvae at this station was between 20 and 30 m.

Probabilistic larval prey encounter models, similar to that developed by Beyer and Laurence (1980, 1981), are being used to assess the degree of food limitation on Georges Bank. The most recent empirical results from laboratory experiments and field studies have been incorporated into the model and preliminary simulation runs provide some interesting contrasts in the survival capabilities of larval haddock and cod. One model run (Laurence, 1983) shows that haddock larvae need 20 prey/l for minimal survival, and about 50 prey/l for 50% survival through 42 days. On the other hand, cod larvae only require about 5 prey/l for minimal survival, and 20 prey/l for 50% survival. These kinds of relatively high prey densities for larval survival have been observed in the Georges Bank area for the first time. Our field methods and modeling techniques now appear sufficiently sophisticated to produce an accurate picture of the environment in which the larvae grow and survive. Although haddock larvae hatch at a somewhat larger size than cod and remain larger, cod are more efficient behaviorally and metabolically and consequently, require lower prey densities for the same percentage survival. Cod larvae appear to be more adapted as a winter species when prey densities are generally lower. Haddock larvae, more

adapted to spring conditions, require higher prey densities which appear to be concentrated by spring stratification. Prey densities tend to be uniformly higher in the shoal, well-mixed waters, but stratification along the southern flank of Georges offers a greater potential for higher than average prey densities on which an opportunistic species like haddock can capitalize. The recruitment pattern of haddock also tends to be a 'boom or bust' type with 3-4 good years out of 20, whereas cod recruitment tends to be relatively low but with less variation (Hennemuth et al., 1980).

Further evaluation of population growth and survival in the sea may best be made through a comparison of biochemical condition indices derived from larvae reared in laboratory experiments. The RNA/DNA ratios of haddock and cod larvae collected in spring 1981 are plotted against size in Fig. 16. A minimum laboratory-determined RNA/DNA ratio of 3.2 has been established for cod, below which starvation and death occur (Buckley, 1979). However, very few (<2%) of the larvae analyzed from the field had ratios <4, indicating recent high population growth rates. Nevertheless, differences in station mean ratios occur which may be related to short-term variations in prey density, and may in turn be related to predation of the slower growing individuals. Perhaps in future simulation studies, population growth rates can be associated with discrete predation proabilities.

In conclusion, our sampling scheme is similar in many aspects to other multidisciplinary studies of larval growth and survival (Report of the Working Group on Larval Fish Ecology, 1982), but specifically designed to be carried out within the spawning season of haddock-cod and the physical regime of the Georges Bank region. Our sampling strategy is unique for a single vessel operation in its attempt to allocate a suitable balance of sampling effort among the various spatial and temporal scales needed to estimate the abundance and distribution of fish larvae, their prey, and predators in order to achieve the proper integration of

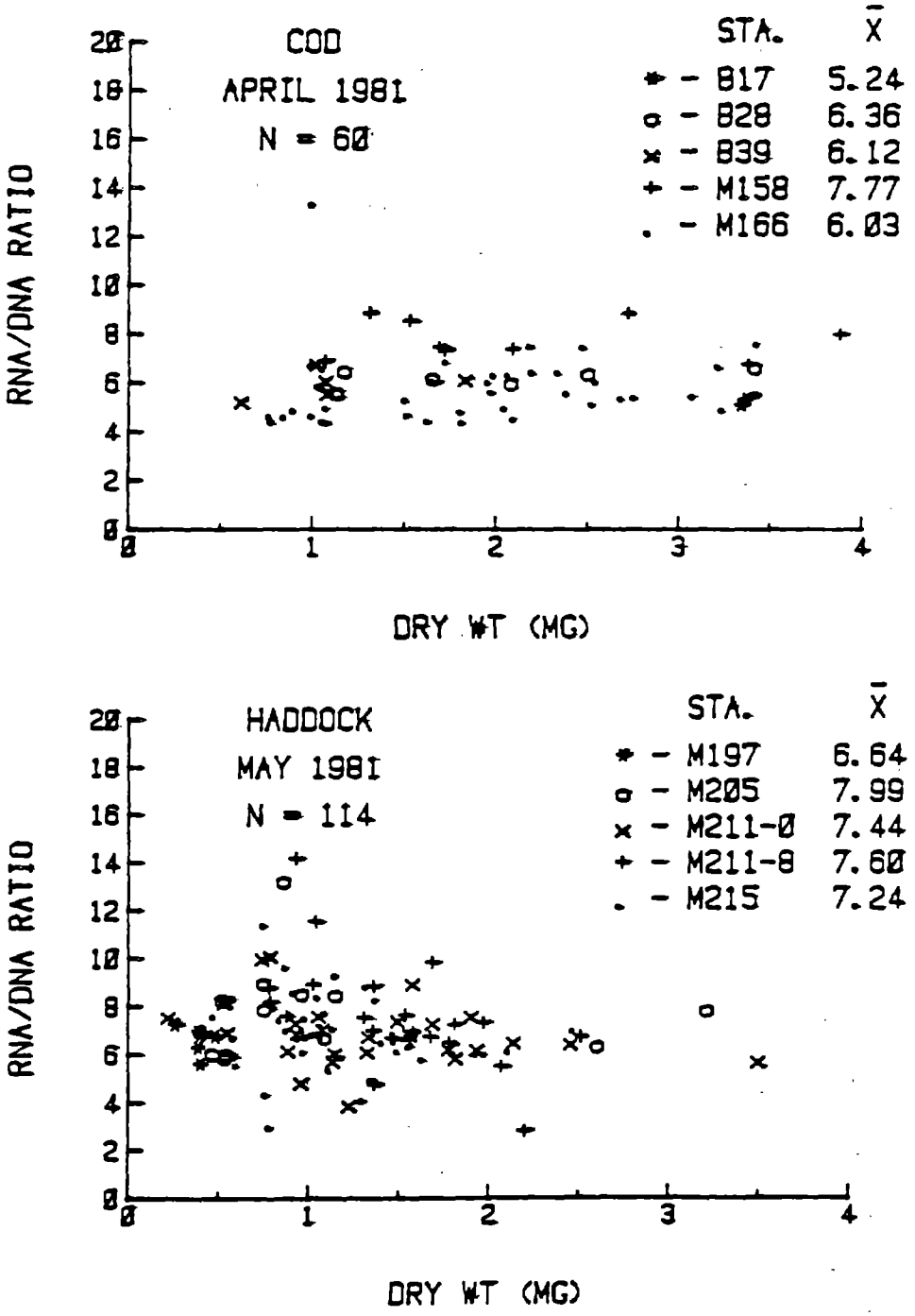

Fig. 16. RNA/DNA ratio values versus size of individual cod and haddock larvae (denoted by station) collected during April-May 1981 on Georges Bank.

observations for evaluating the causes of mortality. Special effort is made to make our program truly interdisciplinary by linking laboratory studies and model simulations with field observations.

ACKNOWLEDGEMENTS

The core of our research program described in this report is based on staff biologists and oceanographers from various investigations within the Marine Ecosystem Division of the Northeast Fisheries Center. Other individuals intimately involved in the planning, execution, or data analysis are: Geoffrey C. Laurence, John R. Green, Laurence J. Buckley, Donna S. Busch, David G. Mountain, Ronald J. Schlitz, David C. Potter, George R. Bolz, Rosalind E. Cohen, Joseph Kane, Philip R. LeBlanc, Peter J. Auditore, Bruce Burns, Jacquelyn Anderson, and Harold G. Merry. This report is MARMAP Contribution MED/NEFC 83-31. Reference to trade names does not imply endorsement by NMFS, NOAA. Special thanks to Cheryl D. Windsor for typing the manuscript.

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A REPORT ON THE DEVELOPMENT OF STOCHASTIC MODELS OF FOOD LIMITED GROWTH AND SURVIVAL OF COD AND HADDOCK LARVAE ON GEORGES BANK

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MARMAP Contribution MED/NEFC 83-34

INTRODUCTION

This report documents the evolution and development of stochastic models simulating the processes associated with feeding, growth and survival of larval cod and haddock both as individuals and populations. The predecessors to this research were an initial deterministic energetic model approach by Laurence (1977) and subsequent stochastic models by Beyer and Laurence (1980, 1981). This exercise is an extension of the Beyer and Laurence model (1981) with the addition of more stochastic elements because of new empirical information now available for both species. Data sources used are principally from published and unpublished studies conducted in the Marine Ecosystems Division of the National Marine Fisheries Service, Northeast Fisheries Center, although all available sources from the published literature were used when applicable. The ultimate goal of the modelling is to assess aspects of food-limited larval starvation and predation pressure of the larvae on their food sources in the Georges Bank spawning and nursery areas.

BASIC DETERMINISTIC ELEMENTS

Interconversion between length and weight are given from the research of Laurence (1978a) as:

$$L = 1.935\ W^{0.247} \qquad (1) \text{ for cod}$$

and

$$L = 2.026 W^{0.222} \qquad (1a) \text{ for haddock}$$

where L = standard length in mm and W = dry weight in µg.

Metabolism was derived from empirical laboratory respirometer measurements (Laurence, 1978b). Coefficients from that research were adjusted for active periods in daylight and resting periods in darkness and prorated over 24 hours with 13 light - 11 dark for cod and 14 light - 10 dark for haddock corresponding to the amount of ambient light at the peak of larval abundance for each species. Equations for daily metabolism (Fig. 1) are:

$$M = 24\ (0.010\ W^{0.775}) \qquad (2) \text{ for cod}$$

and

$$M = 24\ (0.038\ W^{0.684}) \qquad (2a) \text{ for haddock}$$

where M = metabolism in µg day^{-1} (1 $\mu\ell O_2$ = 1 µg larval tissue by caloric conversion), W = weight in µg.

Preferred prey size for given size larvae was calculated from the data and relationships reported by Kane (1984). Regressions (Fig. 2) are:

$$P = -0.073 + 0.043\ L \qquad (3) \text{ for cod}$$

and

$$P = -0.046 + 0.032\ L \qquad (3a) \text{ for haddock}$$

where P = prey width in mm and L = larval standard length in mm.

Conversions of prey width to prey wet weight were done according to the generalized equation from Pearre (1980):

$$P1 = 1000\ (1.557\ P^{2.878}) \qquad (4)$$

where P1 = prey wet weight in µg and P = prey width in mm.

Conversion of prey wet weight to prey dry weight is:

$$P2 = 0.277\ P1 \qquad (5)$$

where P2 = prey dry weight in µg.

The fraction of food ingested that is actually digested by larvae has been measured in nitrogen budget studies by Buckley and Dillmann (1982). Beyer and Laurence (1981) reworked these data (Fig. 3) as:

$$\beta = 0.8\ (1-0.625\ e^{-0.002(W - W_{min})}) \qquad (6)$$

where β = fraction of ingested food digested, W = larval dry weight in µg and W_{min} = minimum larval dry weight in µg.

The cost of processing and utilization of the digested food is put to $\alpha = 0.4$ (Andersen and Ursin, 1977).

Daily growth increment is expressed as:

$$G1 = G \cdot W \qquad (7)$$

where G1 = daily growth increment in µg, G = % growth day^{-1} and W larval dry weight in µg.

Daily ration is calculated from:

$$R1 = \frac{G1 + M}{(1 - \alpha) \cdot \beta \cdot P2} \qquad (8)$$

where R1 = daily ration as # prey, and G1, M, α, β and P2 are as previously defined.

Tables 1 and 2 present examples of the deterministic parameters and output variables at a constant growth rate for both species.

STOCHASTIC EXTENSION

Two major steps were taken in stochastizing the basic deterministic model. These were adding additional model variables based on empirical data and generating probability distributions about a number of these variables to form stochastic elements.

One of the additional variables is larval searching capacity. Searching capacity equals the swimming speed multiplied by the cross-sectional area of the perception field (Blaxter and Staines, 1971). Swimming speed and perceptive field defined in terms of larval body length are converted to terms of larval dry weight by the weight length equations yielding searching capacity as a function of weight (Fig. 4) as:

$$S = 0.737\ W^{0.741} \qquad (9) \text{ for cod}$$

and

$$S = 0.846\ W^{0.666} \qquad (9a) \text{ for haddock}$$

where S = searching capacity in liters day^{-1} and W = dry weight in µg.

The probability of a larva capturing and swallowing an encountered and perceived prey organism was determined from unpublished behavioral observation at the Narragansett Laboratory for haddock and from observations by Ellertsen et al. (1980) for cod. The probability increased asymptotically with larval size (Fig. 5) and is described by the following empirical equations:

$$Sl = 0.9\ (1 - 0.667\ e^{-0.004\ (W - W_{min})}) \qquad (10) \text{ for cod}$$

and

$$Sl = 0.9\ (1 - 0.778\ e^{-0.0045\ (W - W_{min})}) \qquad (10a) \text{ for haddock}$$

where Sl = swallowing probability, W = larval dry weight in µg and W_{min} = minimum larval dry weight in µg.

At a given prey density, D, in number of organisms $liter^{-1}$, the mean daily ration for a larva would be:

$$R = S \cdot Sl \cdot D \cdot L1 \qquad (11)$$

where R = mean daily ration in number of organisms, S, Sl, and D are defined as immediately above and L1 is the percentage of daylight hours in 24 h.

Larval growth can then be defined as:

$$G = (1 - \alpha) \cdot \beta \cdot R \cdot P2 - M \quad (12)$$

where G = larval daily growth increment in μg dry weight and α, β (Equation 6), R (Equation 11), P2 (Equation 5), and M (Equation 2) are previously defined.

Maximum and minimum rations which produce growth rates of +15% and -10% of body weight day^{-1} respectively are calculated as:

$$R2\ (+15\%) = \frac{0.15 \cdot W + M}{(1 - \alpha) \cdot \beta \cdot P2} \quad (13)$$

and

$$R0\ (-10\%) = \frac{M - 0.1W}{(1 - \alpha) \cdot \beta \cdot P2} \quad (14)$$

where R2 and R0 are the rations in μg dry weight and all other parameters are previously defined. The maximum and minimum figures are based on empirical results of field estimated growth rates from daily growth increments of otoliths (Bolz and Lough, 1983) and results of laboratory starvation studies (Beyer and Laurence, 1980).

A "minimum barrier" or death size has been calculated for both species. This barrier corresponds to the smallest sizes of live larvae of known age ever recorded in all the various laboratory studies conducted at Narragansett over the years. The rationale is that any fish smaller than these were dead and thus, the minimum live size.

Regression relationships describing the barriers for each species (Fig. 6) are:

$$W_b = W_{min}\, e^{0.0282T} \quad (15) \text{ for cod}$$

and

$$W_b = W_{min}\, e^{0.0226T} \quad (16) \text{ for haddock}$$

where W_b = larval barrier dry weight in μg, W_{min} = larval initial, minimal hatching weight in μg, and T = age in days. During model runs, larvae of given size and age are compared with the minimum barrier at each time step (day) and judged to be alive and growing or dead and eliminated from the simulation. Examples of this process are depicted in Figure 7 which shows the weight trajectory (size) on a daily basis for 3 haddock larvae feeding on variable daily rations. Larva #1 did not grow well and reached the minimum barrier and died on day 12. Larvae #2 barely maintained its weight for the first 4 1/2 weeks at which time it increased its growth rate. Larvae #3 is an example of a fast growing individual.

METHOD FOR TRANSFERRING A NORMAL PROBABILITY DISTRIBUTION TO A DISTRIBUTION WITH KNOWN MEAN AND VARIANCE

A number of variables in this model development were transformed into stochastic elements from empirically derived laboratory and field data. Basically, the process was to use the known mean and variance or the relationship of mean and variance of the empirical data and transfer these to a known normalized probability distribution from statistical tables.

The steps in the method are:

1. Generate 21 random numbers between 0 and 20.

2. Calculate the mean (≈10) and variance of the random number sample or assign the variance of the required distribution (i.e. poisson where mean = variance).

3. Normalize the random number distribution to a distribution with mean = 0 and variance = 1 and with known probability distribution by calculating the Z-statistic as $Z = \bar{x} - 10/s$ (Steele and Torrie, 1960).

4. Multiply calculated Z-statistic by the known standard deviation of the empirical population and add or subtract (depending on sign of Z-statistic) to known mean from empirical population to get a normalized stochastic parameter.

STOCHASTIC MODEL EVOLUTION

Figure 8 is an abbreviated flow chart of the stochastic model that illustrates basic routines, stochastic elements, chronology of operation and flow. The model was developed by adding one stochastic element at a time and noting parameter responses. The first stochastic element incorporated was prey encounter which was a random process. At this point the model was essentially like the one of Beyer and Laurence (1980). In this version (#1) all larvae started out the same initial size, the prey density was constant, and the prey size was the preferred size according to equations (3) and (3a). Random prey encounter was chosen because analyses of relevant prey organisms from field studies (Laurence et al., 1984) showed the prey to be randomly distributed at small scales on Georges Bank. This was approximated by estimating a poisson distribution about the mean daily ration R from equation (11) and transferring it to a normalized probability distribution with ±2 standard errors. Examples of two of these derived distributions about the mean number of prey consumed day^{-1} for newly hatched cod and haddock are shown in Figures 9 and 10. Results from this version (#1) of the model proved to be somewhat deterministic with the larvae either all living or dying in a narrow range of prey densities (45 to 50 prey $liter^{-1}$ for haddock and 5 to 10 for cod). A population of cod that survived 100% until day 42 after hatching and attained large body weights is shown in the frequency histogram of larval weight in

Figure 11. This type of population simulation is derived by making repetitive runs for individual larvae like the ones illustrated in Figure 7 and simply noting sizes and numbers alive at given times.

Version #2 of the model included a second stochastic element which was varying the size of prey about the preferred prey size. The procedure was to compute the preferred size from equations (3) and (3a) through (5) and (5a) and compute a normalized probability distribution based on a poisson (random) distribution about the preferred size. The computed distribution was arbitrarily truncated on both ends based on biological considerations. The upper prey size was truncated at +2 standard errors. If a larvae encountered a prey larger than this it did not eat the prey since it was too big to handle. The lower end of the prey size distribution was at a prey size of 0.1 μg. Any encounters of prey smaller than this were considered to be 0.1 μg and were calculated to be consumed rather than truncated and not consumed. The rationale behind this was that there are many more smaller and available prey in the natural environment than larger so the encounter of numbers of smaller prey should be greater. Figures 12 through 17 show the frequency histograms of prey size about the preferred size encountered by cod and haddock larvae at 3 different body weights.

This model version (#2) with its addition of stochastic prey size to stochastic prey encounter was more robust and somewhat less deterministic than model 1. A simulation of survival and size (growth) for cod similar to Figure 11 is shown in Figure 18. It can be easily seen that survival and growth has been reduced to more realistic levels with the addition of stochastic prey size.

The third stochastic element added to the model (version #3) was a distribution of different initial larval weights at hatching. Until this version, all larvae started out at the same size. Empirical data from laboratory studies of known age larvae from known hatching times and known date spawnings showed the distribution of hatching sizes to be essentially normal about the mean size. A normal probability distribution of initial larval sizes ±2 standard errors about the mean size was calculated based on the known empirical mean and standard errors. Examples of generated frequency distributions for cod and haddock initial sizes are presented in Figures 19 and 20.

An additional element of model version #3 was a calculated delay of any weight loss due to unsuccessful food encounter for 3 days after hatching. This was to compensate for energy available from yolk still present, and was based on empirical laboratory observations and experiments.

This model version (#3) proved to be even more robust and intuitively as well as actually more realistic. Simulations at different constant prey densities with this #3 stochastic element version pinpointed the ranges of population survival as a function of prey density for each species. This relationship is shown in Figure 21 where it can be seen that cod survive a lower prey density than haddock.

This model version also proved useful in simulating a variety of different situations. Population growth and survival can be simultaneously followed for any time frame at a given prey density. Growth (distribution of sizes at time) and survival percentages for populations of cod and haddock larvae at constant prey densities of 6 and 30 liter^{-1}, respectively, every 7 days after hatching until day 42 are presented in Figures 22 to 35. One can follow the population progress up the weight axis and down the survival axis noting the intermittent mean size and distribution about this mean. These figures graphically show that most of the mortality takes place in the first 2-3 weeks after hatching.

Another type exercise is to make runs of relatively large populations of individuals ($\simeq$ 10,000) at the lower prey densities supporting population survival (as indicated in Figure 21) to try and simulate and elucidate conditions approaching the empirically observed low survival measurements from field survey estimation. Figures 36 and 37, respectively, depict the sizes of the 0.37% cod and 0.61% haddock that survived at the marginal densities of 3 and 15 prey liter^{-1}. The initial size distribution of these very same surviving larvae are given in Figures 38 and 39.

The fourth and final stochastic element added to derive model version 4 was varying the prey density encountered on a daily basis. This tends to create a somewhat patchy food environment in terms of time and may not be far from the real situation. The day can be considered a discrete feeding state for larvae which can change from state to state. Larvae are known to be visual feeders that cease feeding and become passive in darkness. During the dark, non-feeding time the larvae could be transported by physical factors to a new and different feeding regime where the density of prey is different. The likelihood of this seems quite high at the small spatial scales in which larvae interact with their physical and biological environment.

Empirical data on small scale spatial variability and absolute densities of prey are available from process-oriented cruises on Georges Bank (Laurence et al., 1984; Lough, 1984). These data give mean-variance parameters with which to generate probability distributions for daily varying prey density. They showed that prey were distributed in a uniform manner and likely to be in a range of 1 to 50 prey liter^{-1} on a small scale (30 liters or less) relative to larvae. A uniform distribution for daily varying prey density was used as the stochastic element; that is, larvae would have an equal probability of encountering any one of the prey densities within the range.

Frequency histograms of survivors at 42 days show the differences between cod and haddock in this #4 stochastic element simulation with 86% of the cod surviving (Fig. 40) and 15% of the haddock surviving (Fig. 41).

A further look at the surviving haddock revealed some insight as to why they might have survived. The initial weight frequency distribution of the actual individual survivors at time 0 is shown in Figure 42. If this is matched up with the initial weight distribution of the whole

population (Fig. 43), it can be seen that the survivors definitely come from the upper range of weights of the whole population. The implication is that larger initial larvae have a higher probability of initial growth and subsequent or consequential survival.

ASPECTS OF FOOD LIMITATION OF LARVAE AND PREDATION PRESSURE BY LARVAE ON THEIR FOOD RESOURCE

A primary goal of this modelling effort was to assess food-limited growth and survival of cod and haddock larvae on Georges Bank. A combination of model simulations and empirical field data from Georges Bank research cruises allowed this to be done. The method was to use MARMAP field data on seasonal abundances and production of cod and haddock larvae (Table 3) (Smith et al., 1979, 1981), fine-scale estimates of relevant larval fish prey abundance from process-oriented research cruises (Table 4) (Lough, 1984; Laurence et al., 1984), and model simulations to calculate the required food intake of the indicated amount of larvae from the individual amount of prey organisms.

The following results of this approach are based on the use of conservative parameters from the field data. The total volume of water on Georges Bank within the 100 m contour (where cod and haddock larvae mainly reside) is 2.96×10^{12} m^3 (Green, J. R. pers. comm.) (Fig. 44). The highest abundance of cod or haddock larvae from the MARMAP data base (Table 3) was for haddock in 1980 at 743.8×10^9. This would give a peak haddock abundance of 0.25 larvae per m^3 (Fig. 44). The mean relevant larval prey density from the process-oriented research bottle samples (Table 4) is approximately 14 organisms $liter^{-1}$ or 14×10^3 per m^3. This gives an overwhelming ratio of instantaneous abundances of 55,000 to 1 prey organisms over larvae in a m^3 within the 100 m contour (Fig. 44). A model simulation was used to assess the more dynamic aspects of larvae grazing the prey. The model subroutine dealing with feeding and growth parameters (equations 1-14) was used to deterministically calculate the prey consumption of preferred prey size for an average of cod and haddock larvae at a growth rate of 8% day^{-1}, at 7° C, and from hatching - yolk absorption until a dry weight of 1000 µg. The calculated consumption was ≈ 1700 prey (Fig. 44). This was conservatively matched with total annual larval production for the entire peak season of 110×10^{12} larvae (Table 3) to derive a seasonal (not instantaneous) grazing requirement of 188×10^{15} organisms (Fig. 44) for the entire larval population produced. A comparison of the larval population's seasonal requirement with the instantaneous estimate of prey abundance shows a ratio of 1 to 4.5. This means that the instantaneous (not even considering any food production aspects) estimate of prey should be enough to allow 22% of the entire annual production of larvae to survive and grow at 8% day^{-1}.

Of course the larvae must encounter the food and capture it after encounter, and this is what the modelling is all about. But, in general, it would appear that food is not the single limiting, catastrophically critical factor.

The following points serve as interim conclusions in this continuing research:

1. Starvation mortality is undoubtedly one of the largest, if not the largest, components of total mortality in the early life stages.

2. Starvation mortality is most significant in the first 2-3 weeks after hatching.

3. Haddock are considerably more food limited than cod.

4. However, starvation mortality does not appear to be population limiting or the single controlling mortality factor under the normal range of prey densities.

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Table 1. Deterministic parameters and output variables at three constant daily growth rates for cod larvae. Each iteration represents a specific weight in the range from the initial weight at hatching-yolk absorption until 10,000 µg.

			4% Growth Rate			
Length (mm)	Dry Weight (µg)	Daily Growth Increment (µg)	Preferred Prey Size (µg)	Metabolism (µg)	Digestion-Utilization Coefficient	# Prey Required
5.1	50	2.0	1.69	5.0	.32	20.8
5.6	75	3.0	2.57	6.8	.34	17.9
6.0	100	4.0	3.43	8.5	.36	16.0
6.7	150	6.0	5.09	11.7	.40	13.7
7.2	200	8.0	6.68	14.6	.44	12.2
7.6	250	10.0	8.20	17.3	.48	11.1
7.9	300	12.0	9.69	20.0	.51	10.4
8.2	350	14.0	11.13	22.5	.53	9.7
8.5	400	16.0	12.54	24.9	.56	9.3
8.8	450	18.0	13.91	27.3	.58	8.9
9.0	500	20.0	15.26	29.6	.60	8.6
9.4	600	24.0	17.90	34.1	.64	8.1
9.8	700	28.0	20.44	38.5	.67	7.7
10.1	800	32.0	22.93	42.7	.69	7.5
10.4	900	36.0	25.35	46.7	.71	7.3
10.7	1000	40.0	27.71	50.7	.73	7.1
10.9	1100	44.0	30.03	54.6	.74	7.0
11.1	1200	48.0	32.31	58.4	.75	7.0
11.4	1300	52.0	34.55	62.2	.76	6.9
11.6	1400	56.0	36.76	65.8	.77	6.9
11.8	1500	60.0	38.93	69.5	.77	6.8
12.0	1600	64.0	41.07	73.0	.78	6.8
12.2	1700	68.0	43.18	76.5	.78	6.8
12.3	1800	72.0	45.26	80.0	.79	6.8
12.5	1900	76.0	47.33	83.4	.79	6.8
12.6	2000	80.0	49.36	86.8	.79	6.8
12.8	2100	84.0	51.38	90.1	.79	6.8
12.9	2200	88.0	53.37	93.5	.79	6.8
13.1	2300	92.0	55.35	96.7	.79	6.8
13.2	2400	96.0	57.31	100.0	.80	6.8
13.4	2500	100.0	59.24	103.2	.80	6.8
13.5	2600	104.0	61.17	106.4	.80	6.8
13.6	2700	108.0	63.07	109.5	.80	6.9
13.7	2800	112.0	64.96	112.7	.80	6.9
13.9	2900	116.0	66.83	115.8	.80	6.9
14.0	3000	120.0	68.69	118.8	.80	6.9
14.1	3100	124.0	70.54	121.9	.80	6.9
14.2	3200	128.0	72.37	124.9	.80	6.9
14.3	3300	132.0	74.19	128.0	.80	7.0
14.4	3400	136.0	76.00	131.0	.80	7.0
14.5	3500	140.0	77.79	133.9	.80	7.0
14.6	3600	144.0	79.58	136.9	.80	7.0
14.7	3700	148.0	81.35	139.8	.80	7.0
14.8	3800	152.0	83.11	142.7	.80	7.0
14.9	3900	156.0	84.86	145.6	.80	7.0
15.0	4000	160.0	86.60	148.5	.80	7.1
15.1	4100	164.0	88.33	151.4	.80	7.1
15.2	4200	168.0	90.05	154.3	.80	7.1
15.3	4300	172.0	91.76	157.1	.80	7.1
15.4	4400	176.0	93.47	159.9	.80	7.1
15.5	4500	180.0	95.16	162.7	.80	7.1
15.5	4600	184.0	96.84	165.5	.80	7.2
15.6	4700	188.0	98.52	168.3	.80	7.2
15.7	4800	192.0	100.19	171.1	.80	7.2
15.8	4900	196.0	101.85	173.8	.80	7.2
15.9	5000	200.0	103.50	176.6	.80	7.2
15.9	5100	204.0	105.14	179.3	.80	7.2
16.0	5200	208.0	106.78	182.0	.80	7.2
16.1	5300	212.0	108.41	184.7	.80	7.3
16.2	5400	216.0	110.03	187.4	.80	7.3
16.2	5500	220.0	111.64	190.1	.80	7.3
16.3	5600	224.0	113.25	192.8	.80	7.3
16.4	5700	228.0	114.85	195.4	.80	7.3
16.5	5800	232.0	116.45	198.1	.80	7.3
16.5	5900	236.0	118.04	200.7	.80	7.3
16.6	6000	240.0	119.62	203.4	.80	7.3
16.7	6100	244.0	121.19	206.0	.80	7.4

16.7	6200	248.0	122.76	208.6	.80	7.4
16.8	6300	252.0	124.33	211.2	.80	7.4
16.9	6400	256.0	125.89	213.8	.80	7.4
16.9	6500	260.0	127.44	216.4	.80	7.4
17.0	6600	264.0	128.98	219.0	.80	7.4
17.0	6700	268.0	130.52	221.5	.80	7.4
17.1	6800	272.0	132.06	224.1	.80	7.4
17.2	6900	276.0	133.59	226.6	.80	7.5
17.2	7000	280.0	135.11	229.2	.80	7.5
17.3	7100	284.0	136.63	231.7	.80	7.5
17.4	7200	288.0	138.15	234.2	.80	7.5
17.4	7300	292.0	139.66	236.7	.80	7.5
17.5	7400	296.0	141.16	239.3	.80	7.5
17.5	7500	300.0	142.66	241.8	.80	7.5
17.6	7600	304.0	144.16	244.3	.80	7.5
17.6	7700	308.0	145.65	246.7	.80	7.5
17.7	7800	312.0	147.13	249.2	.80	7.6
17.8	7900	316.0	148.61	251.7	.80	7.6
17.8	8000	320.0	150.09	254.2	.80	7.6
17.9	8100	324.0	151.56	256.6	.80	7.6
17.9	8200	328.0	153.03	259.1	.80	7.6
18.0	8300	332.0	154.49	261.5	.80	7.6
18.0	8400	336.0	155.95	264.0	.80	7.6
18.1	8500	340.0	157.41	266.4	.80	7.6
18.1	8600	344.0	158.86	268.8	.80	7.6
18.2	8700	348.0	160.30	271.2	.80	7.7
18.2	8800	352.0	161.75	273.6	.80	7.7
18.3	8900	356.0	163.18	276.1	.80	7.7
18.3	9000	360.0	164.62	278.5	.80	7.7
18.4	9100	364.0	166.05	280.8	.80	7.7
18.4	9200	368.0	167.48	283.2	.80	7.7
18.5	9300	372.0	168.90	285.6	.80	7.7
18.5	9400	376.0	170.32	288.0	.80	7.7
18.6	9500	380.0	171.74	290.4	.80	7.7
18.6	9600	384.0	173.15	292.7	.80	7.7
18.7	9700	388.0	174.56	295.1	.80	7.8
18.7	9800	392.0	175.96	297.4	.80	7.8
18.8	9900	396.0	177.36	299.8	.80	7.8
18.8	10000	400.0	178.76	302.1	.80	7.8

8% Growth

5.1	50	4.0	1.69	5.0	.32	26.7
5.6	75	6.0	2.57	6.8	.34	23.2
6.0	100	8.0	3.43	8.5	.36	21.0
6.7	150	12.0	5.09	11.7	.40	18.2
7.2	200	16.0	6.68	14.6	.44	16.4
7.6	250	20.0	8.20	17.3	.48	15.1
7.9	300	24.0	9.69	20.0	.51	14.2
8.2	350	28.0	11.13	22.5	.53	13.4
8.5	400	32.0	12.54	24.9	.56	12.9
8.8	450	36.0	13.91	27.3	.58	12.4
9.0	500	40.0	15.26	29.6	.60	12.0
9.4	600	48.0	17.90	34.1	.64	11.4
9.8	700	56.0	20.44	38.5	.67	10.9
10.1	800	64.0	22.93	42.7	.69	10.6
10.4	900	72.0	25.35	46.7	.71	10.4
10.7	1000	80.0	27.71	50.7	.73	10.3
10.9	1100	88.0	30.03	54.6	.74	10.1
11.1	1200	96.0	32.31	58.4	.75	10.1
11.4	1300	104.0	34.55	62.2	.76	10.0
11.6	1400	112.0	36.76	65.8	.77	10.0
11.8	1500	120.0	38.93	69.5	.77	10.0
12.0	1600	128.0	41.07	73.0	.78	10.0
12.2	1700	136.0	43.18	76.5	.78	10.0
12.3	1800	144.0	45.26	80.0	.79	10.0
12.5	1900	152.0	47.33	83.4	.79	10.0
12.6	2000	160.0	49.36	86.8	.79	10.0
12.8	2100	168.0	51.38	90.1	.79	10.0
12.9	2200	176.0	53.37	93.5	.79	10.1
13.1	2300	184.0	55.35	96.7	.79	10.1
13.2	2400	192.0	57.31	100.0	.80	10.1
13.4	2500	200.0	59.24	103.2	.80	10.2
13.5	2600	208.0	61.17	106.4	.80	10.2
13.6	2700	216.0	63.07	109.5	.80	10.2
13.7	2800	224.0	64.96	112.7	.80	10.3
13.9	2900	232.0	66.83	115.8	.80	10.3

14.0	3000	240.0	68.69	118.8	.80	10.3
14.1	3100	248.0	70.54	121.9	.80	10.4
14.2	3200	256.0	72.37	124.9	.80	10.4
14.3	3300	264.0	74.19	128.0	.80	10.4
14.4	3400	272.0	76.00	131.0	.80	10.5
14.5	3500	280.0	77.79	133.9	.80	10.5
14.6	3600	288.0	79.58	136.9	.80	10.6
14.7	3700	296.0	81.35	139.8	.80	10.6
14.8	3800	304.0	83.11	142.7	.80	10.6
14.9	3900	312.0	84.86	145.6	.80	10.7
15.0	4000	320.0	86.60	148.5	.80	10.7
15.1	4100	328.0	88.33	151.4	.80	10.7
15.2	4200	336.0	90.05	154.3	.80	10.8
15.3	4300	344.0	91.76	157.1	.80	10.8
15.4	4400	352.0	93.47	159.9	.80	10.8
15.5	4500	360.0	95.16	162.7	.80	10.9
15.5	4600	368.0	96.84	165.5	.80	10.9
15.6	4700	376.0	98.52	168.3	.80	10.9
15.7	4800	384.0	100.19	171.1	.80	10.9
15.8	4900	392.0	101.85	173.8	.80	11.0
15.9	5000	400.0	103.50	176.6	.80	11.0
15.9	5100	408.0	105.14	179.3	.80	11.0
16.0	5200	416.0	106.78	182.0	.80	11.1
16.1	5300	424.0	108.41	184.7	.80	11.1
16.2	5400	432.0	110.03	187.4	.80	11.1
16.2	5500	440.0	111.64	190.1	.80	11.1
16.3	5600	448.0	113.25	192.8	.80	11.2
16.4	5700	456.0	114.85	195.4	.80	11.2
16.5	4800	464.0	116.45	198.1	.80	11.2
16.5	5900	472.0	118.04	200.7	.80	11.3
16.6	6000	480.0	119.62	203.4	.80	11.3
16.7	6100	488.0	121.19	206.0	.80	11.3
16.7	6200	496.0	122.76	208.6	.80	11.3
16.8	6300	504.0	124.33	211.2	.80	11.4
16.9	6400	512.0	125.89	213.8	.80	11.4
16.9	6500	520.0	127.44	216.4	.80	11.4
17.0	6600	528.0	128.98	219.0	.80	11.4
17.0	6700	536.0	130.52	221.5	.80	11.5
17.1	6800	544.0	132.06	224.1	.80	11.5
17.2	6900	552.0	133.59	226.6	.80	11.5
17.2	7000	560.0	135.11	229.2	.80	11.5
17.3	7100	568.0	136.63	231.7	.80	11.6
17.4	7200	576.0	138.15	234.2	.80	11.6
17.4	7300	584.0	139.66	236.7	.80	11.6
17.5	7400	592.0	141.16	239.3	.80	11.6
17.5	7500	600.0	142.66	241.8	.80	11.7
17.6	7600	608.0	144.16	244.3	.80	11.7
17.6	7700	616.0	145.65	246.7	.80	11.7
17.7	7800	624.0	147.13	249.2	.80	11.7
17.8	7900	632.0	148.61	251.7	.80	11.7
17.8	8000	640.0	150.09	254.2	.80	11.8
17.9	8100	648.0	151.56	256.6	.80	11.8
17.9	8200	656.0	153.03	259.1	.80	11.8
18.0	8300	664.0	154.49	261.5	.80	11.8
18.0	8400	672.0	155.95	264.0	.80	11.8
18.1	8500	680.0	157.41	266.4	.80	11.9
18.1	8600	688.0	158.86	268.8	.80	11.9
18.2	8700	696.0	160.30	271.2	.80	11.9
18.2	8800	704.0	161.75	273.6	.80	11.9
18.3	8900	712.0	163.18	276.1	.80	12.0
18.3	9000	720.0	164.62	278.5	.80	12.0
18.4	9100	728.0	166.05	280.8	.80	12.0
18.4	9200	736.0	167.48	283.2	.80	12.0
18.5	9300	744.0	168.90	285.6	.80	12.0
18.5	9400	752.0	170.32	288.0	.80	12.1
18.6	9500	760.0	171.74	290.4	.80	12.1
18.6	9600	768.0	173.15	292.7	.80	12.1
18.7	9700	776.0	174.56	295.1	.80	12.1
18.7	9800	784.0	175.96	297.4	.80	12.1
18.8	9900	792.0	177.36	299.8	.80	12.2
18.8	10000	800.0	178.76	302.1	.80	12.2

12.5% Growth

5.1	50	6.3	1.69	5.0	.32	33.3
5.6	75	9.4	2.57	6.8	.34	29.3
6.0	100	12.5	3.43	8.5	.36	26.7

6.7	150	18.8	5.09	11.7	.40	23.4
7.2	200	25.0	6.68	14.6	.44	21.2
7.6	250	31.3	8.20	17.3	.48	19.7
7.9	300	37.5	9.69	20.0	.51	18.5
8.2	350	43.8	11.13	22.5	.53	17.6
8.5	400	50.0	12.54	24.9	.56	16.9
8.8	450	56.3	13.91	27.3	.58	16.3
9.0	500	62.5	15.26	29.6	.60	15.8
9.4	600	75.0	17.90	34.1	.64	15.1
9.8	700	87.5	20.44	38.5	.67	14.6
10.1	800	100.0	22.93	42.7	.69	14.2
10.4	900	112.5	25.35	46.7	.71	13.9
10.7	1000	125.0	27.71	50.7	.73	13.8
10.9	1100	137.5	30.03	54.6	.74	13.6
11.1	1200	150.0	32.31	58.4	.75	13.6
11.4	1300	162.5	34.55	62.2	.76	13.5
11.6	1400	175.0	36.76	65.8	.77	13.5
11.8	1500	187.5	38.93	69.5	.77	13.5
12.0	1600	200.0	41.07	73.0	.78	13.5
12.2	1700	212.5	43.18	76.5	.78	13.5
12.3	1800	225.0	45.26	80.0	.79	13.5
12.5	1900	237.5	47.33	83.4	.79	13.6
12.6	2000	250.0	49.36	86.8	.79	13.6
12.8	2100	262.5	51.38	90.1	.79	13.7
12.9	2200	275.0	53.37	93.5	.79	13.7
13.1	2300	287.5	55.35	96.7	.79	13.8
13.2	2400	300.0	57.31	100.0	.80	13.8
13.4	2500	312.5	59.24	103.2	.80	13.9
13.5	2600	325.0	61.17	106.4	.80	14.0
13.6	2700	337.5	63.07	109.5	.80	14.0
13.7	2800	350.0	64.96	112.7	.80	14.1
13.9	2900	362.5	66.83	115.8	.80	14.1
14.0	3000	375.0	68.69	118.8	.80	14.2
14.1	3100	387.5	70.54	121.9	.80	14.3
14.2	3200	400.0	72.37	124.9	.80	14.3
14.3	3300	412.5	74.19	128.0	.80	14.4
14.4	3400	425.0	76.00	131.0	.80	14.4
14.5	3500	437.5	77.79	133.9	.80	14.5
14.6	3600	450.0	79.58	136.9	.80	14.6
14.7	3700	462.5	81.35	139.8	.80	14.6
14.8	3800	475.0	83.11	142.7	.80	14.7
14.9	3900	487.5	84.86	145.6	.80	14.7
15.0	4000	500.0	86.60	148.5	.80	14.8
15.1	4100	512.5	88.33	151.4	.80	14.8
15.2	4200	525.0	90.05	154.3	.80	14.9
15.3	4300	537.5	91.76	157.1	.80	14.9
15.4	4400	550.0	93.47	159.9	.80	15.0
15.5	4500	562.5	95.16	162.7	.80	15.0
15.5	4600	575.0	96.84	165.5	.80	15.1
15.6	4700	587.5	98.52	168.3	.80	15.1
15.7	4800	600.0	100.19	171.1	.80	15.2
15.8	4900	612.5	101.85	173.8	.80	15.2
15.9	5000	625.0	103.50	176.6	.80	15.3
15.9	5100	637.5	105.14	179.3	.80	15.3
16.0	5200	650.0	106.78	182.0	.80	15.4
16.1	5300	662.5	108.41	184.7	.80	15.4
16.2	5400	675.0	110.03	187.4	.80	15.5
16.2	5500	687.5	111.64	190.1	.80	15.5
16.3	5600	700.0	113.25	192.8	.80	15.5
16.4	5700	712.5	114.85	195.4	.80	15.6
16.5	5800	725.0	116.45	198.1	.80	15.6
16.5	5900	737.5	118.04	200.7	.80	15.7
16.6	6000	750.0	119.62	203.4	.80	15.7
16.7	6100	762.5	121.19	206.0	.80	15.8
16.7	6200	775.0	122.76	208.6	.80	15.8
16.8	6300	787.5	124.33	211.2	.80	15.8
16.9	6400	800.0	125.89	213.8	.80	15.9
16.9	6500	812.5	127.44	216.4	.80	15.9
17.0	6600	825.0	128.98	219.0	.80	16.0
17.0	6700	837.5	130.52	221.5	.80	16.0
17.1	6800	850.0	132.06	224.1	.80	16.0
17.2	6900	862.5	133.59	226.6	.80	16.1
17.2	7000	875.0	135.11	229.2	.80	16.1
17.3	7100	887.5	136.63	231.7	.80	16.1
17.4	7200	900.0	138.15	234.2	.80	16.2
17.4	7300	912.5	139.66	236.7	.80	16.2
17.5	7400	925.0	141.16	239.3	.80	16.3
17.5	7500	937.5	142.66	241.8	.80	16.3

17.6	7600	950.0	144.16	244.3	.80	16.3
17.6	7700	962.5	145.65	246.7	.80	16.4
17.7	7800	975.0	147.13	249.2	.80	16.4
17.8	7900	987.5	148.61	251.7	.80	16.4
17.8	8000	1000.0	150.09	254.2	.80	16.5
17.9	8100	1012.5	151.56	256.6	.80	16.5
17.9	8200	1025.0	153.03	259.1	.80	16.5
18.0	8300	1037.5	154.49	261.5	.80	16.6
18.0	8400	1050.0	155.95	264.0	.80	16.6
18.1	8500	1062.5	157.41	266.4	.80	16.6
18.1	8600	1075.0	158.86	268.8	.80	16.7
18.2	8700	1087.5	160.30	271.2	.80	16.7
18.2	8800	1100.0	161.75	273.6	.80	16.7
18.3	8900	1112.5	163.18	276.1	.80	16.8
18.3	9000	1125.0	164.62	278.5	.80	16.8
18.4	9100	1137.5	166.05	280.8	.80	16.8
18.4	9200	1150.0	167.48	283.2	.80	16.9
18.5	9300	1162.5	168.90	285.6	.80	16.9
18.5	9400	1175.0	170.32	288.0	.80	16.9
18.6	9500	1187.5	171.74	290.4	.80	17.0
18.6	9600	1200.0	173.15	292.7	.80	17.0
18.7	9700	1212.5	174.56	295.1	.80	17.0
18.7	9800	1225.0	175.96	297.4	.80	17.1
18.8	9900	1237.5	177.36	299.8	.80	17.1
18.8	10000	1250.0	178.76	302.1	.80	17.1

Table 2. Deterministic parameters and output variables at three constant daily growth rates for haddock larvae. Each iteration represents a specific weight in the range from the initial weight at hatching-yolk absorption until 10,000 µg.

			12.5% Growth Rate			
Length (mm)	Dry Weight (µg)	Daily Growth Increment (µg)	Preferred Prey Size (µg)	Metabolism (µg)	Digestion-Utilization Coefficient	# Prey Required
4.8	50	6.3	.72	13.2	.30	140.4
5.3	75	9.4	1.04	17.5	.32	124.3
5.6	100	12.5	1.33	21.3	.35	113.5
6.2	150	18.8	1.88	28.1	.39	99.1
6.6	200	25.0	2.38	34.2	.43	89.6
6.9	250	31.3	2.85	39.8	.46	82.9
7.2	300	37.5	3.30	45.1	.50	77.8
7.4	350	43.8	3.73	50.1	.53	73.8
7.7	400	50.0	4.15	54.9	.55	70.7
7.9	450	56.3	4.55	59.5	.58	68.1
8.1	500	62.5	4.94	64.0	.60	66.1
8.4	600	75.0	5.69	72.5	.63	62.9
8.7	700	87.5	6.40	80.5	.66	60.7
8.9	800	100.0	7.09	88.2	.69	59.2
9.2	900	112.5	7.75	95.7	.71	58.1
9.4	1000	125.0	8.40	102.8	.73	57.3
9.6	1100	137.5	9.02	109.7	.74	56.8
9.8	1200	150.0	9.63	116.5	.75	56.5
10.0	1300	162.5	10.23	123.0	.76	56.3
10.1	1400	175.0	10.81	129.4	.77	56.2
10.3	1500	187.5	11.38	135.7	.77	56.2
10.4	1600	200.0	11.93	141.8	.78	56.3
10.6	1700	212.5	12.48	147.8	.78	56.4
10.7	1800	225.0	13.02	153.7	.78	56.6
10.8	1900	237.5	13.55	159.5	.79	56.8
11.0	2000	250.0	14.07	165.2	.79	57.0
11.1	2100	262.5	14.58	170.8	.79	57.2
11.2	2200	275.0	15.09	176.3	.79	57.5
11.3	2300	287.5	15.59	181.7	.79	57.7
11.4	2400	300.0	16.08	187.1	.80	58.0
11.5	2500	312.5	16.57	192.4	.80	58.3
11.6	2600	325.0	17.05	197.6	.80	58.6
11.7	2700	337.5	17.53	202.8	.80	58.9
11.8	2800	350.0	18.00	207.9	.80	59.1
11.9	2900	362.5	18.46	212.9	.80	59.4
12.0	3000	375.0	18.92	217.9	.80	59.7
12.1	3100	387.5	19.38	222.9	.80	60.0
12.2	3200	400.0	19.83	227.8	.80	60.3
12.2	3300	412.5	20.28	232.6	.80	60.5
12.3	3400	425.0	20.72	237.4	.80	60.8
12.4	3500	437.5	21.16	242.2	.80	61.1
12.5	3600	450.0	21.59	246.9	.80	61.3
12.6	3700	462.5	22.02	251.6	.80	61.6
12.6	3800	475.0	22.45	256.2	.80	61.9
12.7	3900	487.5	22.88	260.8	.80	62.1
12.8	4000	500.0	23.30	265.3	.80	62.4
12.8	4100	512.5	23.71	269.9	.80	62.6
12.9	4200	525.0	24.13	274.3	.80	62.9
13.0	4300	537.5	24.54	278.8	.80	63.1
13.0	4400	550.0	24.95	283.2	.80	63.4
13.1	4500	562.5	25.35	287.6	.80	63.6
13.2	4600	575.0	25.76	292.0	.80	63.9
13.2	4700	587.5	26.16	296.3	.80	64.1
13.3	4800	600.0	26.55	300.6	.80	64.3
13.4	4900	612.5	26.95	304.9	.80	64.5
13.4	5000	625.0	27.34	309.1	.80	64.8
13.5	5100	637.5	27.73	313.3	.80	65.0
13.5	5200	650.0	28.12	317.5	.80	65.2
13.6	5300	662.5	28.51	321.7	.80	65.4
13.7	5400	675.0	28.89	325.8	.80	65.7
13.7	5500	687.5	29.27	329.9	.80	65.9
13.8	5600	700.0	29.65	334.0	.80	66.1
13.8	5700	712.5	30.03	338.1	.80	66.3
13.9	5800	725.0	30.40	342.1	.80	66.5
13.9	5900	737.5	30.77	346.1	.80	66.7
14.0	6000	750.0	31.14	350.1	.80	66.9
14.0	6100	762.5	31.51	354.1	.80	67.1

14.1	6200	775.0	31.88	358.1	.80	67.3
14.1	6300	787.5	32.24	362.0	.80	67.5
14.2	6400	800.0	32.61	366.0	.80	67.7
14.2	6500	812.5	32.97	369.9	.80	67.9
14.3	6600	825.0	33.33	373.7	.80	68.1
14.3	6700	837.5	33.69	377.6	.80	68.3
14.4	6800	850.0	34.04	381.4	.80	68.5
14.4	6900	862.5	34.40	385.3	.80	68.7
14.5	7000	875.0	34.75	389.1	.80	68.8
14.5	7100	887.5	35.10	392.9	.80	69.0
14.6	7200	900.0	35.45	396.7	.80	69.2
14.6	7300	912.5	35.80	400.4	.80	69.4
14.6	7400	925.0	36.15	404.2	.80	69.6
14.7	7500	937.5	36.49	407.9	.80	69.7
14.7	7600	950.0	36.83	411.6	.80	69.9
14.8	7700	962.5	37.18	415.3	.80	70.1
14.8	7800	975.0	37.52	419.0	.80	70.3
14.9	7900	987.5	37.86	422.6	.80	70.4
14.9	8000	1000.0	38.20	426.3	.80	70.6
14.9	8100	1012.5	38.53	429.9	.80	70.8
15.0	8200	1025.0	38.87	433.6	.80	70.9
15.0	8300	1037.5	39.20	437.2	.80	71.1
15.1	8400	1050.0	39.54	440.8	.80	71.3
15.1	8500	1062.5	39.87	444.3	.80	71.4
15.1	8600	1075.0	40.20	447.9	.80	71.6
15.2	8700	1087.5	40.53	541.5	.80	71.8
15.2	8800	1100.0	40.86	455.0	.80	71.9
15.3	8900	1112.5	41.18	458.5	.80	72.1
15.3	9000	1125.0	41.51	462.1	.80	72.2
15.3	9100	1137.5	41.83	465.6	.80	72.4
15.4	9200	1150.0	42.16	469.1	.80	72.6
15.4	9300	1162.5	42.48	472.5	.80	72.7
15.4	9400	1175.0	42.80	476.0	.80	72.9
15.5	9500	1187.5	43.12	479.5	.80	73.0
15.5	9600	1200.0	43.44	482.9	.80	73.2
15.5	9700	1212.5	43.76	486.3	.80	73.3
15.6	9800	1225.0	44.08	489.8	.80	73.5
15.6	9900	1237.5	44.39	493.2	.80	73.6
15.7	10000	1250.0	44.71	496.6	.80	73.8

4% Growth

4.8	50	2.0	.72	13.2	.30	111.5
5.3	75	3.0	1.04	17.5	.32	96.3
5.6	100	4.0	1.33	21.3	.35	86.4
6.2	150	6.0	1.88	28.1	.39	73.5
6.6	200	8.0	2.38	34.2	.43	65.1
6.9	250	10.0	2.85	39.8	.46	59.2
7.2	300	12.0	3.30	45.1	.50	54.9
7.4	350	14.0	3.73	50.1	.53	51.5
7.7	400	16.0	4.15	54.9	.55	48.8
7.9	450	18.0	4.55	59.5	.58	46.6
8.1	500	20.0	4.94	64.0	.60	44.8
8.4	600	24.0	5.69	72.5	.63	42.1
8.7	700	28.0	6.40	80.5	.66	40.1
8.9	800	32.0	7.09	88.2	.69	38.6
9.2	900	36.0	7.75	95.7	.71	37.6
9.4	1000	40.0	8.40	102.8	.73	36.7
9.6	1100	44.0	9.02	109.7	.74	36.1
9.8	1200	48.0	9.63	116.5	.75	35.6
10.0	1300	52.0	10.23	123.0	.76	35.3
10.1	1400	56.0	10.81	129.4	.77	35.0
10.3	1500	60.0	11.38	135.7	.77	34.8
10.4	1600	64.0	11.93	141.8	.78	34.7
10.6	1700	68.0	12.48	147.8	.78	34.6
10.7	1800	72.0	13.02	153.7	.78	34.5
10.8	1900	76.0	13.55	159.5	.79	34.4
11.0	2000	80.0	14.07	165.2	.79	34.4
11.1	2100	84.0	14.58	170.8	.79	34.4
11.2	2200	88.0	15.09	176.3	.79	34.4
11.3	2300	92.0	15.59	181.7	.79	34.5
11.4	2400	96.0	16.08	187.1	.80	34.5
11.5	2500	100.0	16.57	192.4	.80	34.5
11.6	2600	104.0	17.05	197.6	.80	34.6
11.7	2700	108.0	17.53	202.8	.80	34.6
11.8	2800	112.0	18.00	207.9	.80	34.7
11.9	2900	116.0	18.46	212.9	.80	34.8

12.0	3000	120.0	18.92	217.9	.80	34.8
12.1	3100	124.0	19.38	222.9	.80	34.9
12.2	3200	128.0	19.83	227.8	.80	34.9
12.2	3300	132.0	20.28	232.6	.80	35.0
12.3	3400	136.0	20.72	237.4	.80	35.1
12.4	3500	140.0	21.16	242.2	.80	35.1
12.5	3600	144.0	21.59	246.9	.80	35.2
12.6	3700	148.0	22.02	251.6	.80	35.3
12.6	3800	152.0	22.45	256.2	.80	35.3
12.7	3900	156.0	22.88	260.8	.80	35.4
12.8	4000	160.0	23.30	265.3	.80	35.5
12.8	4100	164.0	23.71	269.9	.80	35.5
12.9	4200	168.0	24.13	274.3	.80	35.6
13.0	4300	172.0	24.54	278.8	.80	35.7
13.0	4400	176.0	24.95	283.2	.80	35.7
13.1	4500	180.0	25.35	287.6	.80	35.8
13.2	4600	184.0	25.76	292.0	.80	35.9
13.2	4700	188.0	26.16	296.3	.80	35.9
13.3	4800	192.0	26.55	300.6	.80	36.0
13.4	4900	196.0	26.95	304.9	.80	36.1
13.4	5000	200.0	27.34	309.1	.80	36.1
13.5	5100	204.0	27.73	313.3	.80	36.2
13.5	5200	208.0	28.12	317.5	.80	36.3
13.6	5300	212.0	28.51	321.7	.80	36.3
13.7	5400	216.0	28.89	325.8	.80	36.4
13.7	5500	220.0	29.27	329.9	.80	36.4
13.8	5600	224.0	29.65	334.0	.80	36.5
13.8	5700	228.0	30.03	338.1	.80	36.6
13.9	5800	232.0	30.40	342.1	.80	36.6
13.9	5900	236.0	30.77	346.1	.80	36.7
14.0	6000	240.0	31.14	350.1	.80	36.7
14.0	6100	244.0	31.51	354.1	.80	36.8
14.1	6200	248.0	31.88	358.1	.80	36.8
14.1	6300	252.0	32.24	362.0	.80	36.9
14.2	6400	256.0	32.61	366.0	.80	37.0
14.2	6500	260.0	32.97	369.9	.80	37.0
14.3	6600	264.0	33.33	373.7	.80	37.1
14.3	6700	268.0	33.69	377.6	.80	37.1
14.4	6800	272.0	34.04	381.4	.80	37.2
14.4	6900	276.0	34.40	385.3	.80	37.2
14.5	7000	280.0	34.75	389.1	.80	37.3
14.5	7100	284.0	35.10	392.9	.80	37.3
14.6	7200	288.0	35.45	396.7	.80	37.4
14.6	7300	292.0	35.80	400.4	.80	37.4
14.6	7400	296.0	36.15	404.2	.80	37.5
14.7	7500	300.0	36.49	407.9	.80	37.5
14.7	7600	304.0	36.83	411.6	.80	37.6
14.8	7700	308.0	37.18	415.3	.80	37.6
14.8	7800	312.0	37.52	419.0	.80	37.7
14.9	7900	316.0	37.86	422.6	.80	37.7
14.9	8000	320.0	38.20	426.3	.80	37.8
14.9	8100	324.0	38.53	429.9	.80	37.8
15.0	8200	328.0	38.87	433.6	.80	37.9
15.0	8300	332.0	39.20	437.2	.80	37.9
15.1	8400	336.0	39.54	440.8	.80	38.0
15.1	8500	340.0	39.87	444.3	.80	38.0
15.1	8600	344.0	40.20	447.9	.80	38.1
15.2	8700	348.0	40.53	451.5	.80	38.1
15.2	8800	352.0	40.86	455.0	.80	38.2
15.3	8900	356.0	41.18	458.5	.80	38.2
15.3	9000	360.0	41.51	462.1	.80	38.3
15.3	9100	364.0	41.83	465.6	.80	38.3
15.4	9200	368.0	42.16	469.1	.80	38.4
15.4	9300	372.0	42.48	472.5	.80	38.4
15.4	9400	376.0	42.80	476.0	.80	38.5
15.5	9500	380.0	43.12	479.5	.80	38.5
15.5	9600	384.0	43.44	482.9	.80	38.6
15.5	9700	388.0	43.76	486.3	.80	38.6
15.6	9800	392.0	44.08	489.8	.80	38.7
15.6	9900	396.0	44.39	493.2	.80	38.7
15.7	10000	400.0	44.71	496.6	.80	38.7

8% Growth

4.8	50	4.0	.72	13.2	.30	125.1
5.3	75	6.0	1.04	17.5	.32	109.5
5.6	100	8.0	1.33	21.3	.35	99.1

6.2	150	12.0	1.88	28.1	.39	85.5
6.6	200	16.0	2.38	34.2	.43	76.7
6.9	250	20.0	2.85	39.8	.46	70.4
7.2	300	24.0	3.30	45.1	.50	65.6
7.4	350	28.0	3.73	50.1	.53	62.0
7.7	400	32.0	4.15	54.9	.55	59.1
7.9	450	36.0	4.55	59.5	.58	56.7
8.1	500	40.0	4.94	64.0	.60	54.8
8.4	600	48.0	5.69	72.5	.63	51.9
8.7	700	56.0	6.40	80.5	.66	49.8
8.9	800	64.0	7.09	88.2	.69	48.3
9.2	900	72.0	7.75	95.7	.71	47.2
9.4	1000	80.0	8.40	102.8	.73	46.4
9.6	1100	88.0	9.02	109.7	.74	45.8
9.8	1200	96.0	9.63	116.5	.75	45.4
10.0	1300	104.0	10.23	123.0	.76	45.2
10.1	1400	112.0	10.81	129.4	.77	45.0
10.3	1500	120.0	11.38	135.7	.77	44.9
10.4	1600	128.0	11.93	141.8	.78	44.8
10.6	1700	136.0	12.48	147.8	.78	44.8
10.7	1800	144.0	13.02	153.7	.78	44.9
10.8	1900	152.0	13.55	159.5	.79	44.9
11.0	2000	160.0	14.07	165.2	.79	45.0
11.1	2100	168.0	14.58	170.8	.79	45.2
11.2	2200	176.0	15.09	176.3	.79	45.3
11.3	2300	184.0	15.59	181.7	.79	45.4
11.4	2400	192.0	16.08	187.1	.80	45.6
11.5	2500	200.0	16.57	192.4	.80	45.7
11.6	2600	208.0	17.05	197.6	.80	45.9
11.7	2700	216.0	17.53	202.8	.80	46.0
11.8	2800	224.0	18.00	207.9	.80	46.2
11.9	2900	232.0	18.46	212.9	.80	46.4
12.0	3000	240.0	18.92	217.9	.80	46.5
12.1	3100	248.0	19.38	222.9	.80	46.7
12.2	3200	256.0	19.83	227.8	.80	46.9
12.2	3300	264.0	20.28	232.6	.80	47.0
12.3	3400	272.0	20.72	237.4	.80	47.2
12.4	3500	280.0	21.16	242.2	.80	47.4
12.5	3600	288.0	21.59	246.9	.80	47.5
12.6	3700	296.0	22.02	251.6	.80	47.7
12.6	3800	304.0	22.45	256.2	.80	47.8
12.7	3900	312.0	22.88	260.8	.80	48.0
12.8	4000	320.0	23.30	265.3	.80	48.1
12.8	4100	328.0	23.71	269.9	.80	48.3
12.9	4200	336.0	24.13	274.3	.80	48.4
13.0	4300	344.0	24.54	278.8	.80	48.6
13.0	4400	352.0	24.95	283.2	.80	48.7
13.1	4500	360.0	25.35	287.6	.80	48.9
13.2	4600	368.0	25.76	292.0	.80	49.0
13.2	4700	376.0	26.16	296.3	.80	49.2
13.3	4800	384.0	26.55	300.6	.80	49.3
13.4	4900	392.0	26.95	304.9	.80	49.5
13.4	5000	400.0	27.34	309.1	.80	49.6
13.5	5100	408.0	27.73	313.3	.80	49.7
13.5	5200	416.0	28.12	317.5	.80	49.9
13.6	5300	424.0	28.51	321.7	.80	50.0
13.7	5400	432.0	28.89	325.8	.80	50.2
13.7	5500	440.0	29.27	329.9	.80	50.3
13.8	5600	448.0	29.65	334.0	.80	50.4
13.8	5700	456.0	30.03	338.1	.80	50.5
13.9	5800	464.0	30.40	342.1	.80	50.7
13.9	5900	472.0	30.77	346.1	.80	50.8
14.0	6000	480.0	31.14	350.1	.80	50.9
14.0	6100	488.0	31.51	354.1	.80	51.1
14.1	6200	496.0	31.88	358.1	.80	51.2
14.1	6300	504.0	32.24	362.0	.80	51.3
14.2	6400	512.0	32.61	366.0	.80	51.4
14.2	6500	520.0	32.97	369.9	.80	51.5
14.3	6600	528.0	33.33	373.7	.80	51.7
14.3	6700	536.0	33.69	377.6	.80	51.8
14.4	6800	544.0	34.04	381.4	.80	51.9
14.4	6900	552.0	34.40	385.3	.80	52.0
14.5	7000	560.0	34.75	389.1	.80	52.1
14.5	7100	568.0	35.10	392.9	.80	52.2
14.6	7200	576.0	35.45	396.7	.80	52.4
14.6	7300	584.0	35.80	400.4	.80	52.5
14.6	7400	592.0	36.15	404.2	.80	52.6
14.7	7500	600.0	36.49	407.9	.80	52.7

14.7	7600	608.0	36.83	411.6	.80	52.8
14.8	7700	616.0	37.18	415.3	.80	52.9
14.8	7800	624.0	37.52	419.0	.80	53.0
14.9	7900	632.0	37.86	422.6	.80	53.1
14.9	8000	640.0	38.20	426.3	.80	53.2
14.9	8100	648.0	38.53	429.9	.80	53.3
15.0	8200	656.0	38.87	433.6	.80	53.4
15.0	8300	664.0	39.20	437.2	.80	53.6
15.1	8400	672.0	39.54	440.8	.80	53.7
15.1	8500	680.0	39.87	444.3	.80	53.8
15.1	8600	688.0	40.20	447.9	.80	53.9
15.2	8700	696.0	40.53	451.5	.80	54.0
15.2	8800	704.0	40.86	455.0	.80	54.1
15.3	8900	712.0	41.18	458.5	.80	54.2
15.3	9000	720.0	41.51	462.1	.80	54.3
15.3	9100	728.0	41.83	465.6	.80	54.4
15.4	9200	736.0	42.16	469.1	.80	54.5
15.4	9300	744.0	42.48	472.5	.80	54.6
15.4	9400	752.0	42.80	476.0	.80	54.7
15.5	9500	760.0	43.12	479.5	.80	54.8
15.5	9600	768.0	43.44	482.9	.80	54.9
15.5	9700	776.0	43.76	486.3	.80	54.9
15.6	9800	784.0	44.08	489.8	.80	55.0
15.6	9900	792.0	44.39	493.2	.80	55.1
15.7	10000	800.0	44.71	496.6	.80	55.2

Table 3. Relevant larval gadid parameters for Georges Bank (from Smith et al. 1979, 1981 and Sherman et al. 1983).

Year	Species	Maximum Larval Abundance (# x 10^9)	#/m^3	Annual Production (# x 10^{12})
1974	Cod	157.5	0.05	
	Haddock	54.1	0.02	
1975	Cod	121.8	0.04	
	Haddock	138.9	0.05	
1976	Cod	16.1	0.01	
	Haddock	76.5	0.03	
1977	Cod	459.6	0.15	
	Haddock	431.6	0.15	
1978	Cod	71.1	0.02	
	Haddock	313.2	0.11	
1979	Cod	122.1	0.04	39.1
	Haddock	408.3	0.14	64.3
1980	Cod	227.8	0.08	102.8
	Haddock	743.8	0.25	110.4
1981	Cod	311.2	0.11	
	Haddock	405.8	0.14	
1982	Cod	10.4	0.003	
	Haddock	6.5	0.002	

Table 4. Summary of bottle samples (all sampler sizes, depths, stations) -- EVRIKA-80-02 relevant larval cod and haddock prey organisms.

Prey Category	No. Per Liter Mean	Range	%
Lamellibranch Larvae	1.21	0.30 - 3.34	8.8
Copepod Eggs (0.1 - 0.2 mm diam)	2.14	0.23 - 5.29	15.6
Copepod Nauplii	7.55	4.10 - 14.28	55.0
Older Stage Copepods	2.82	1.08 - 8.66	20.6

$\bar{X}$ for all sampler sizes, depths and stations = 13.72 $\pm$ 4.04.
Range 8.63 - 24.17.

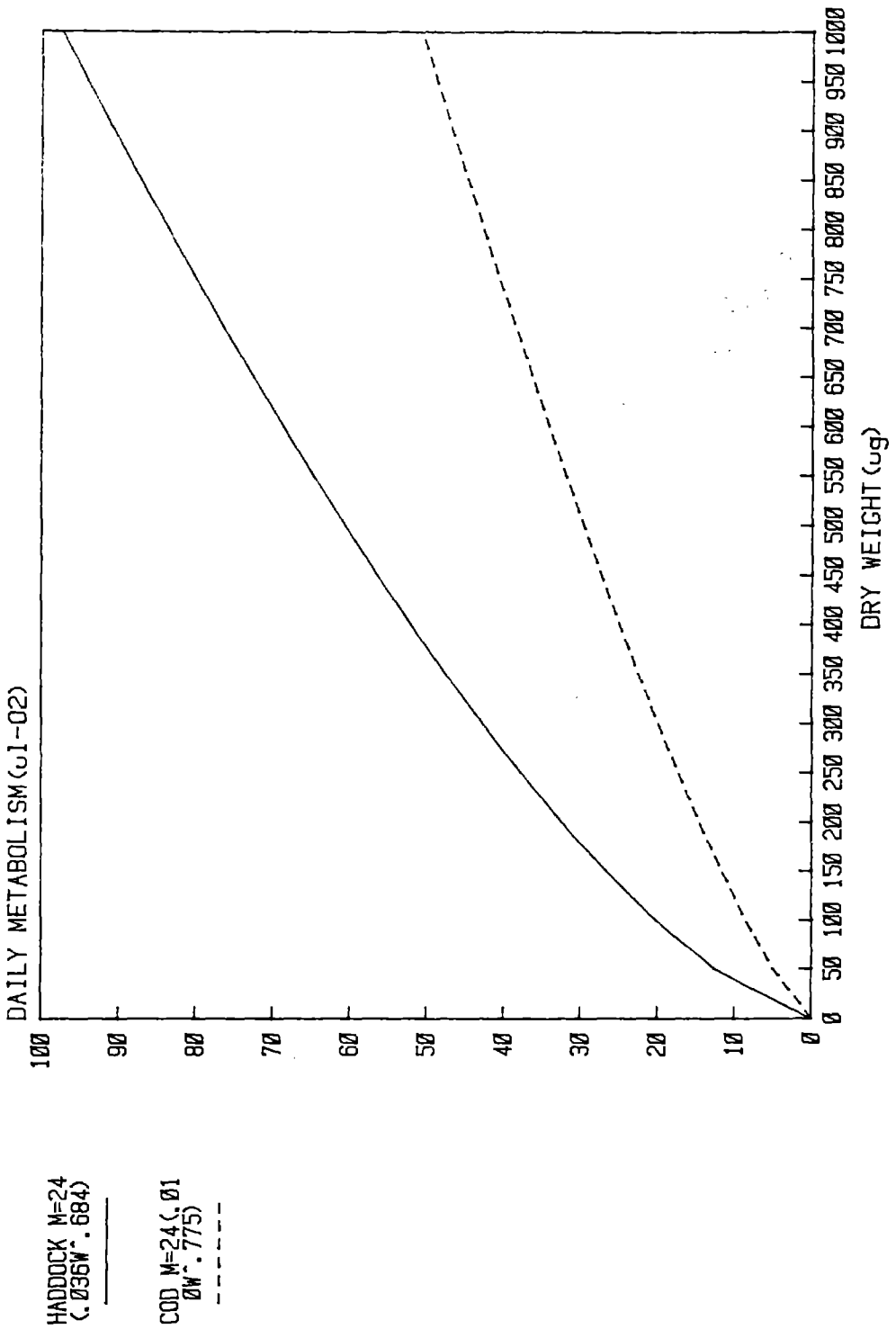

Figure 1. Daily (24-hr) metabolic expenditure of cod and haddock larvae as a function of body size. Based on empirical respirometer measurements from Laurence (1978).

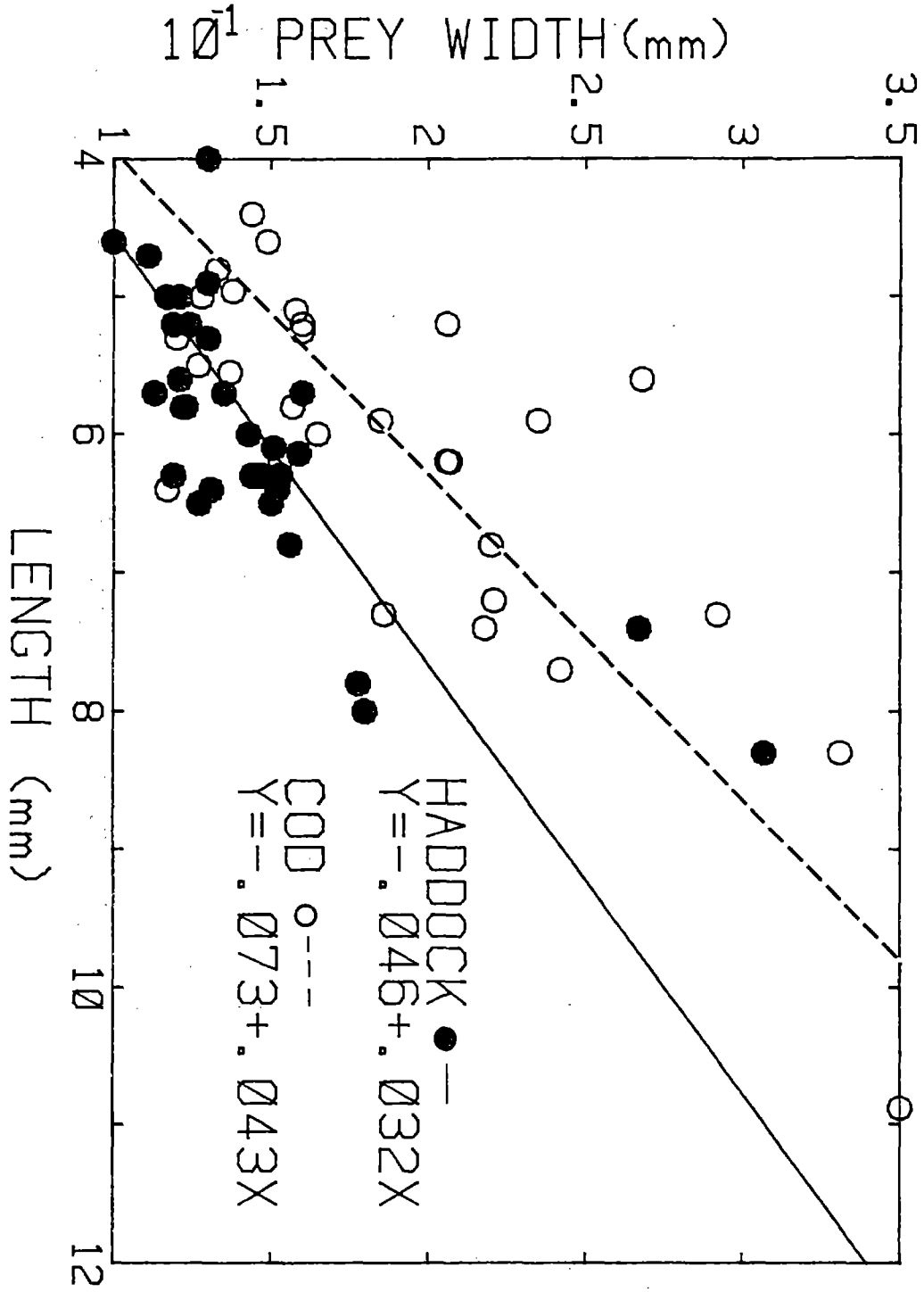

Figure 2. Relationship of mean preferred prey size and larval size for cod and haddock larvae. Based on empirical data from Kane (1983).

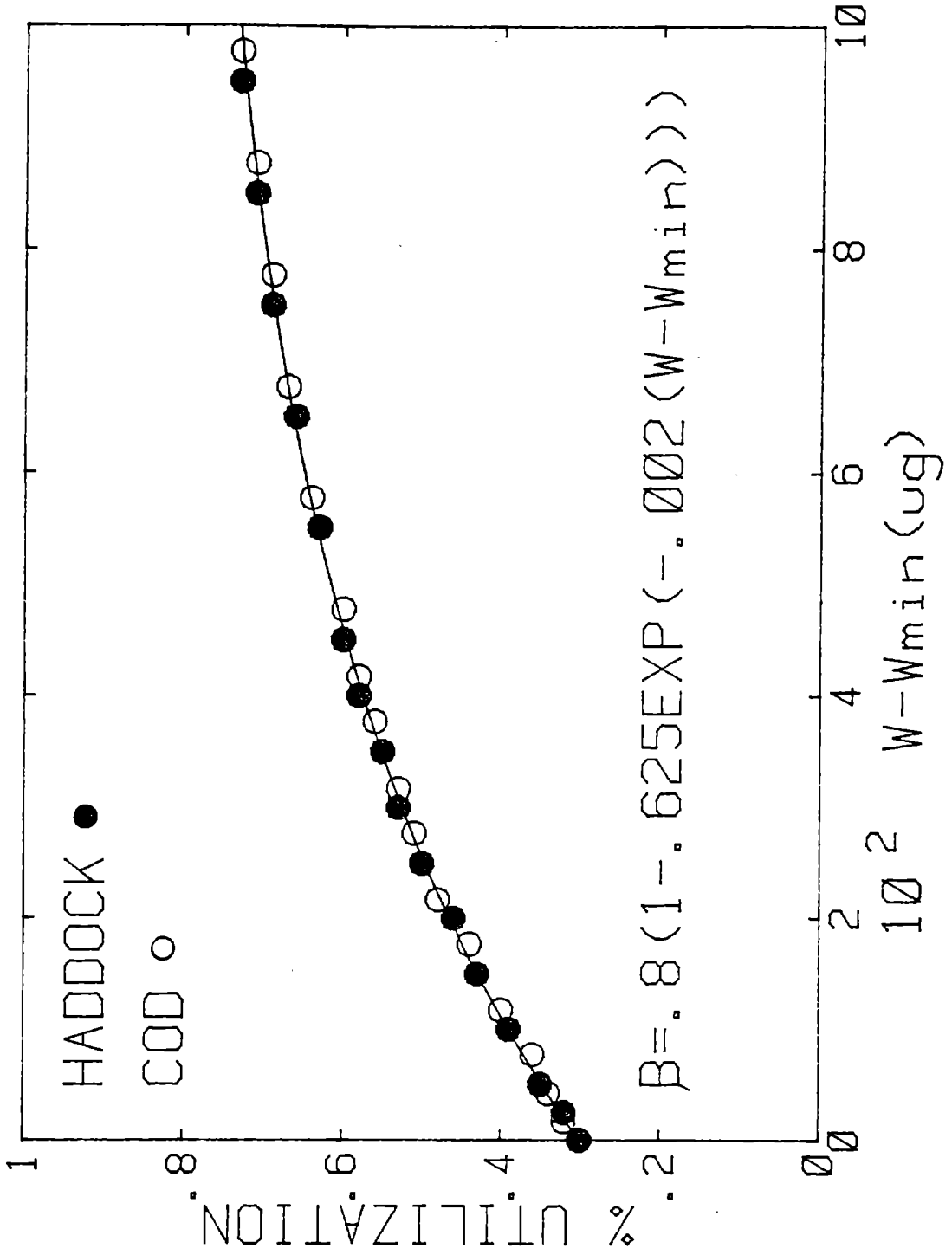

Figure 3. Relationship of the fraction of food ingested that is utilized in the digestion process and larval size for cod and haddock larvae. From Beyer and Laurence (1981) based on nitrogen budget research of Buckley and Dillmann (1982).

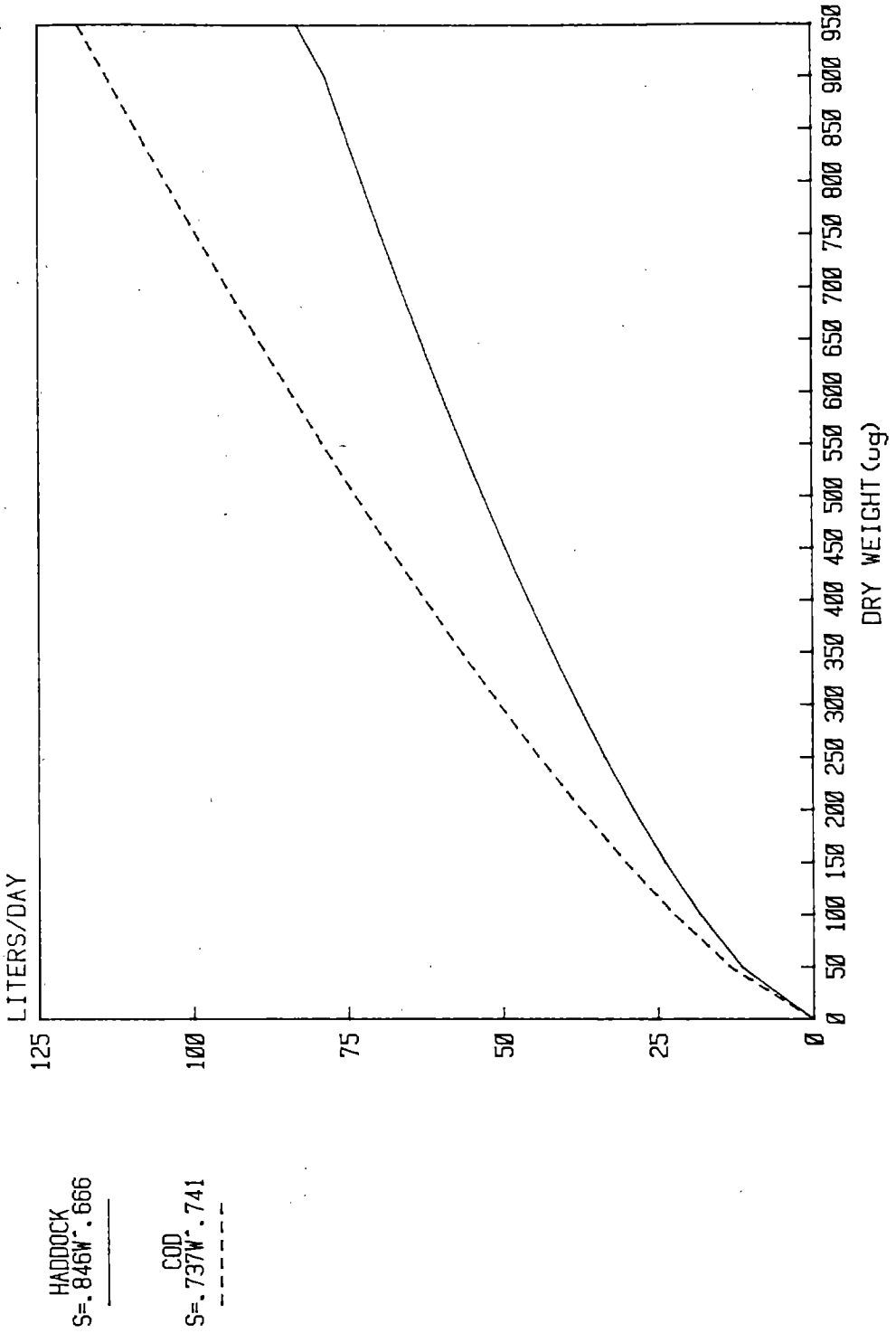

Figure 4. Daily visual searching capacity of cod and haddock larvae.

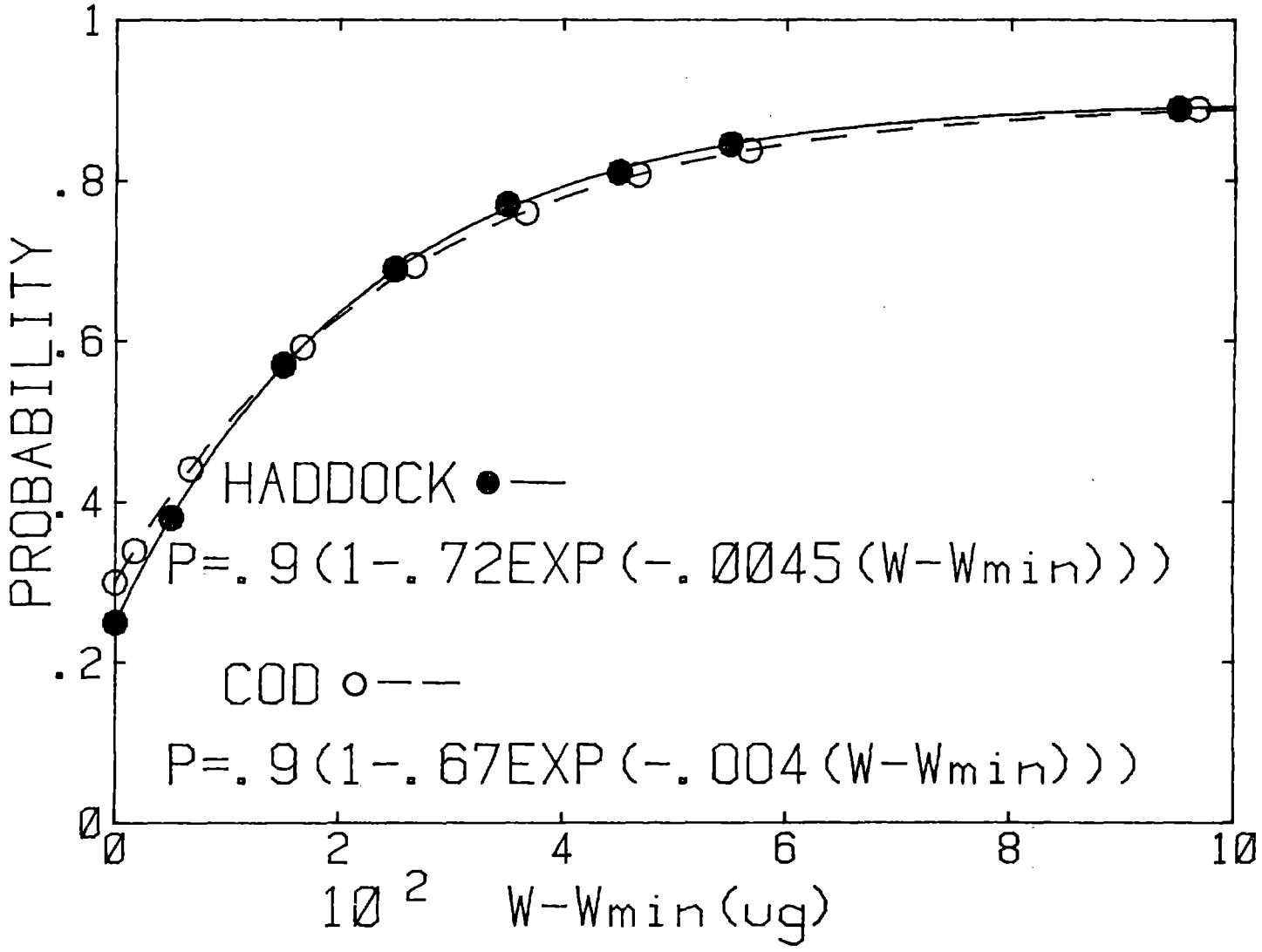

Figure 5. Relationship of the probability of capturing an encountered prey organism and larval size of cod and haddock.

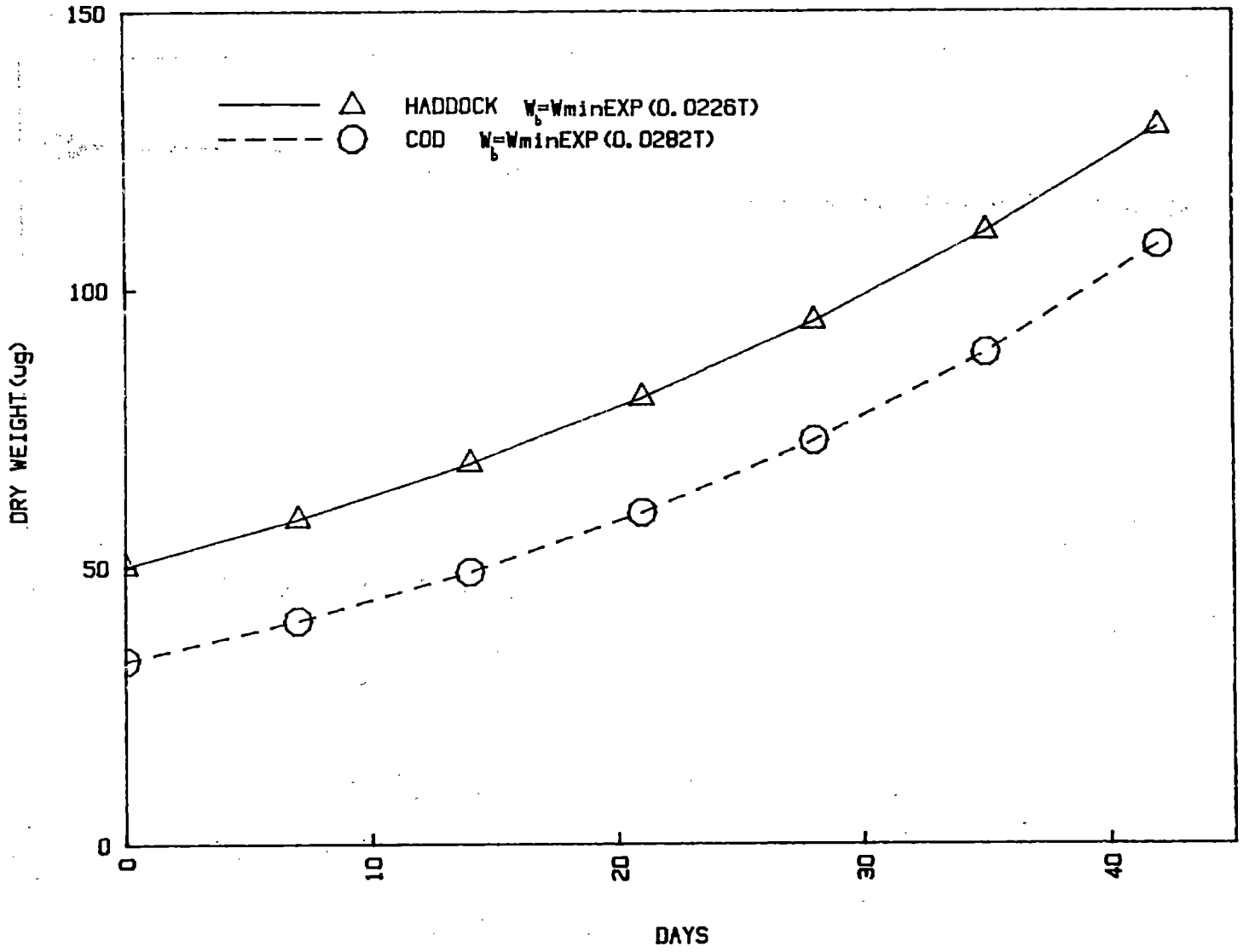

Figure 6. Minimum barrier or the smallest size larvae alive at a given time for cod and haddock larvae in laboratory experiments.

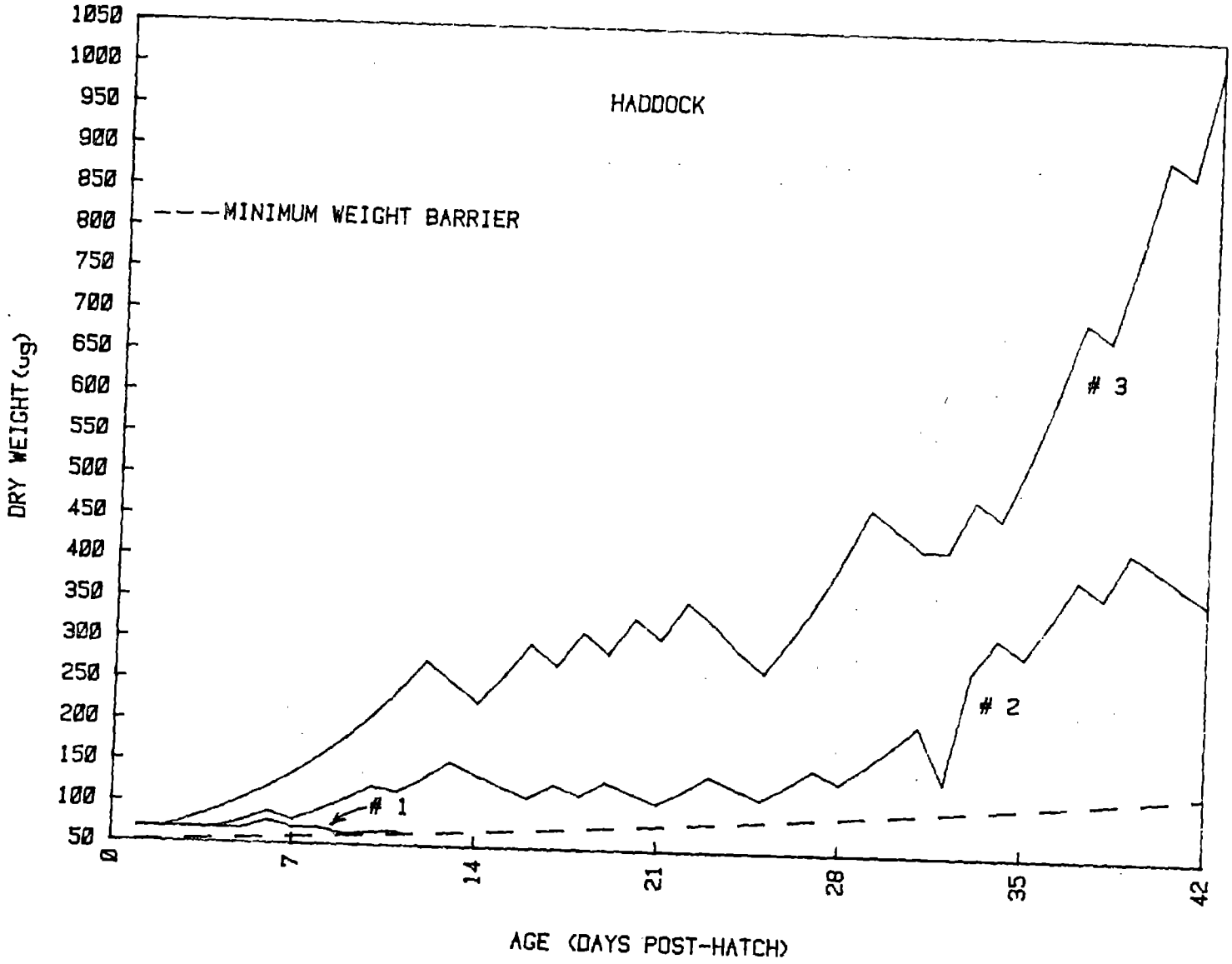

Figure 7. Daily weight gain or loss of 3 haddock larvae feeding on variable daily rations.

ABBREVIATED FLOW CHART OF STOCHASTIC MODEL

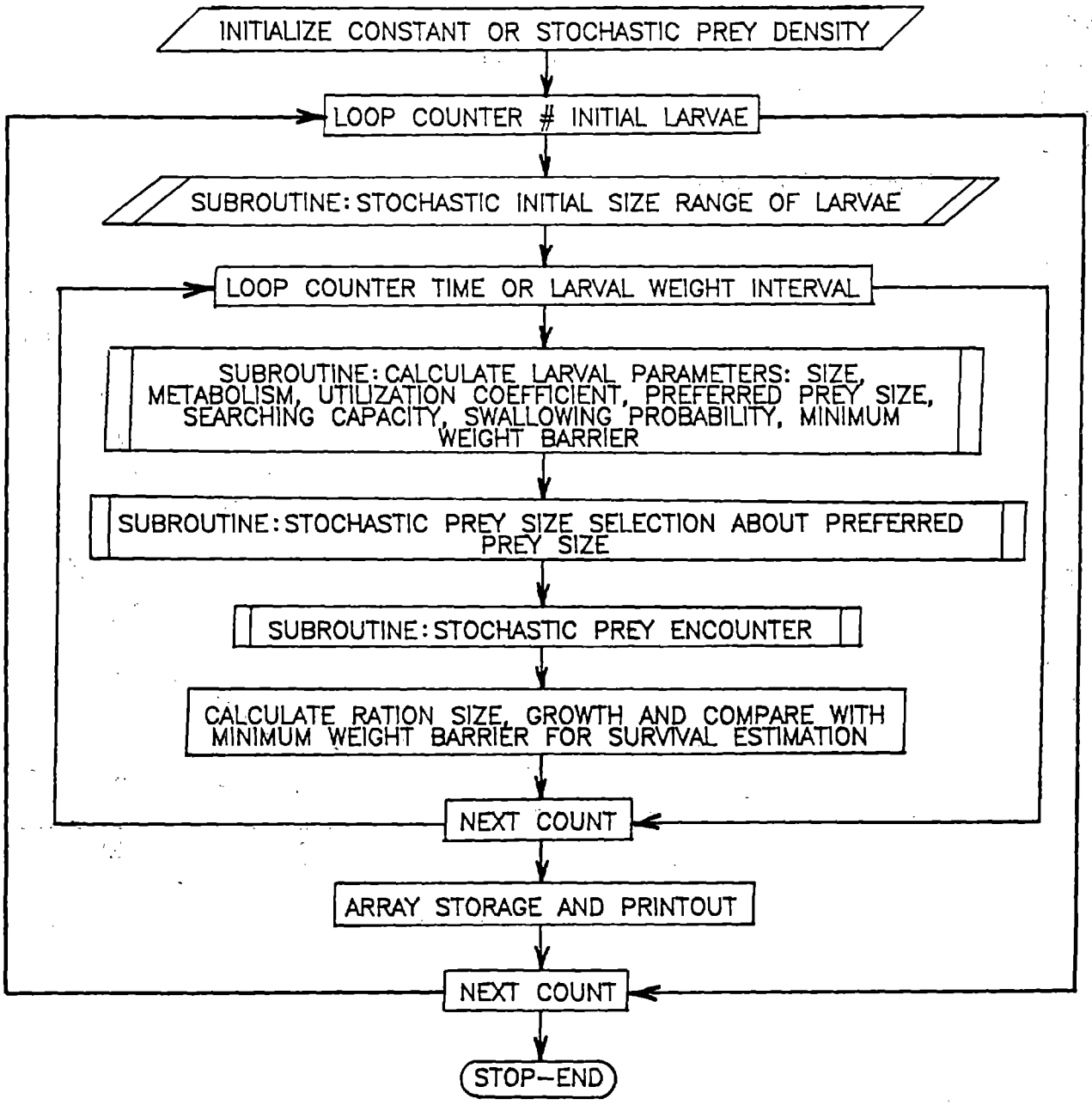

Figure 8. An abbreviated flow chart of the basic 4 element stochastic computer model.

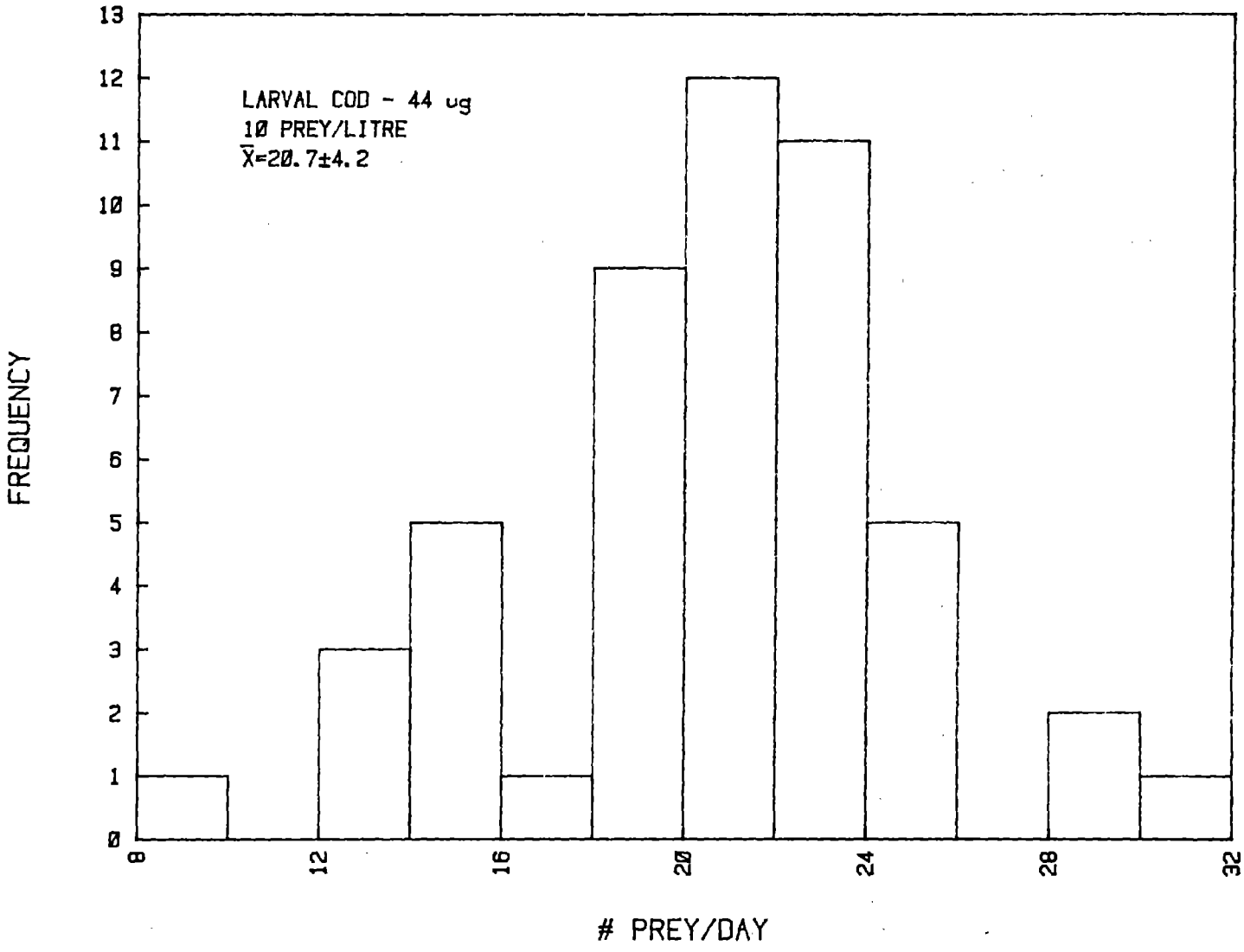

Figure 9. Frequency histograms of the normalized distribution of # of prey of preferred size consumed day^{-1} for a newly hatched 44 µg cod larva at a prey density of 10 liter^{-1}.

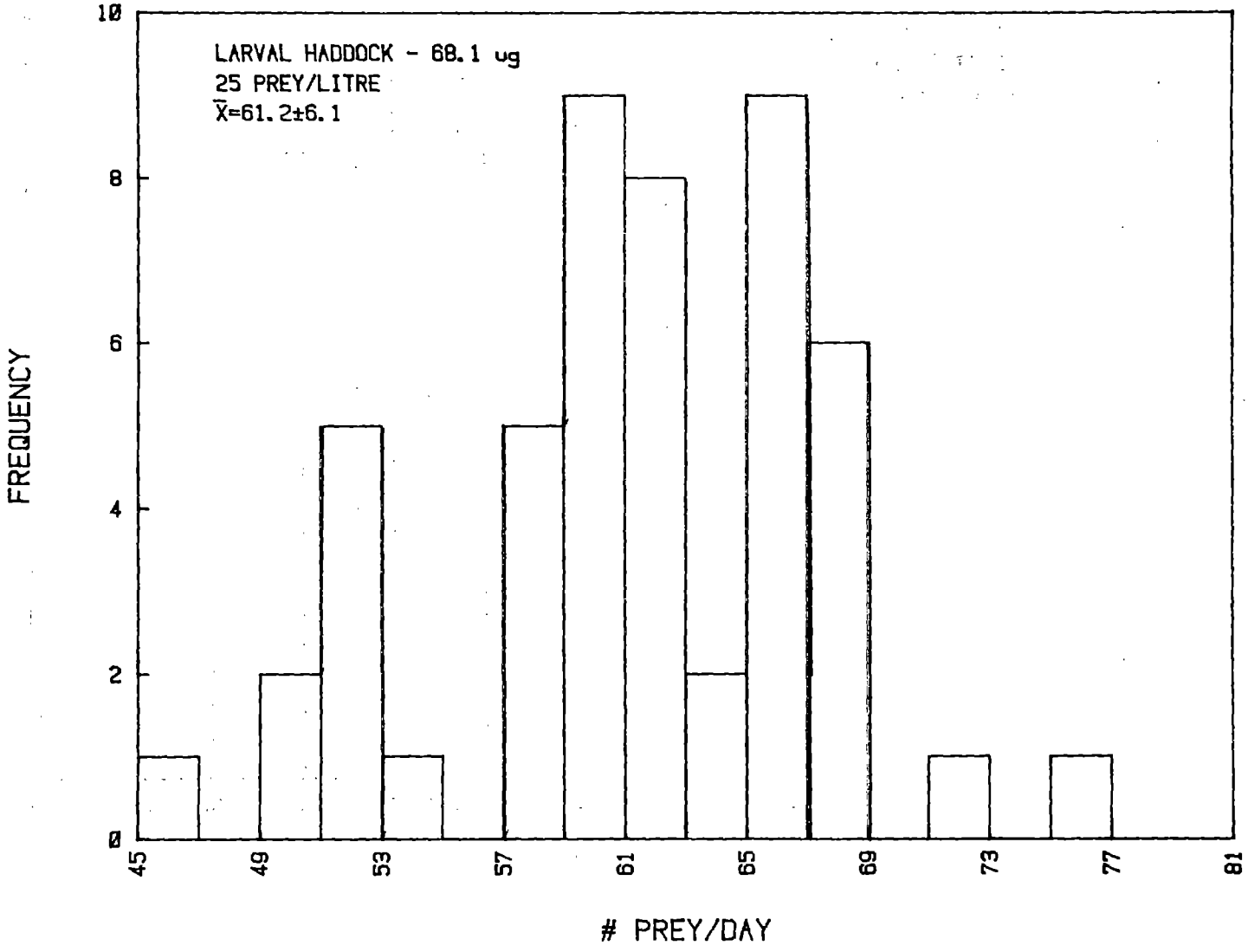

Figure 10. Frequency histograms of the normalized distribution of # of prey of preferred size consumed day^{-1} for a newly hatched 68.1 µg haddock larva at a prey density of 25 liter^{-1}

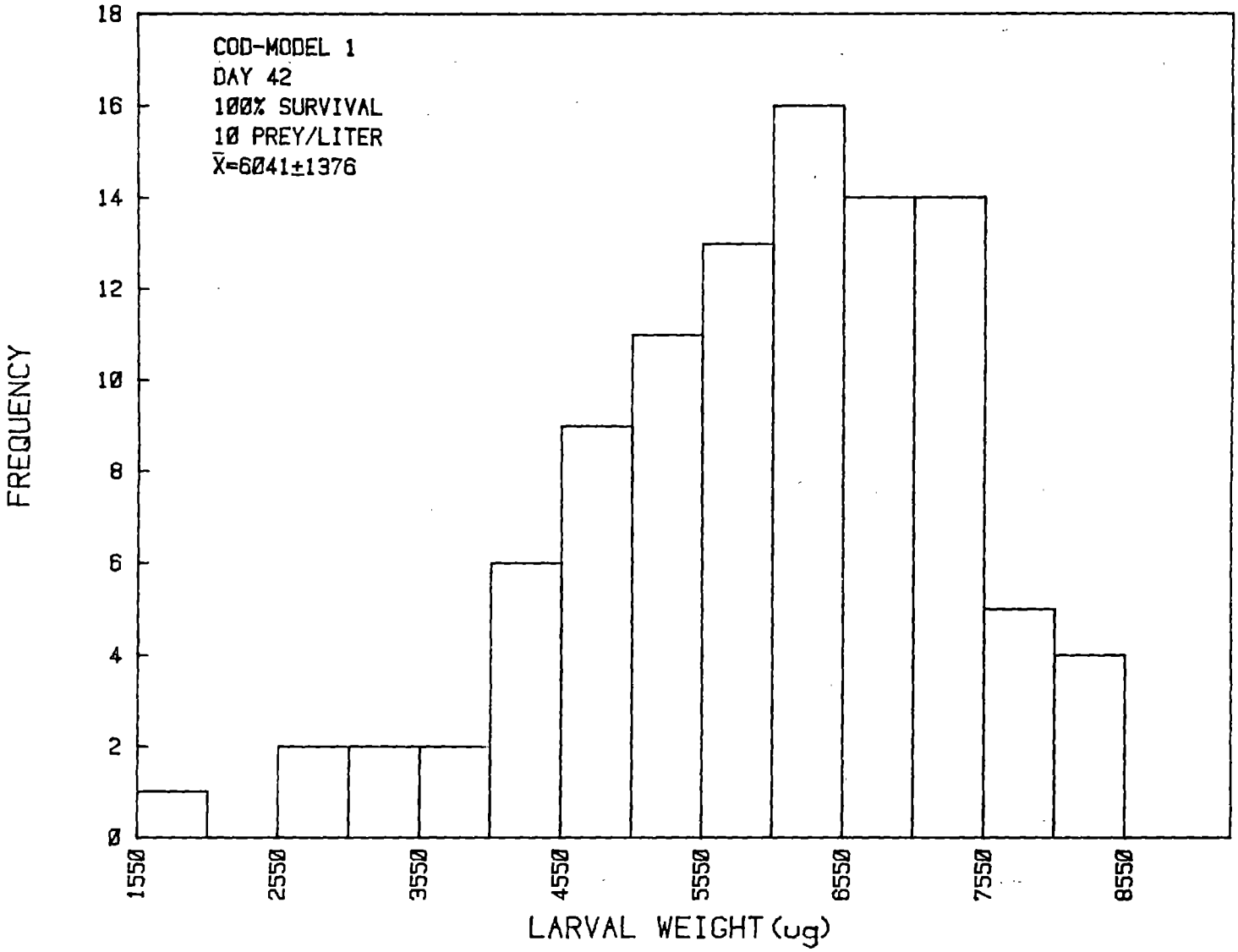

Figure 11. Frequency histogram of the distribution of larval weights of survivors at 42 days after hatching. Cod model 1 at 10 prey liter $^{-1}$.

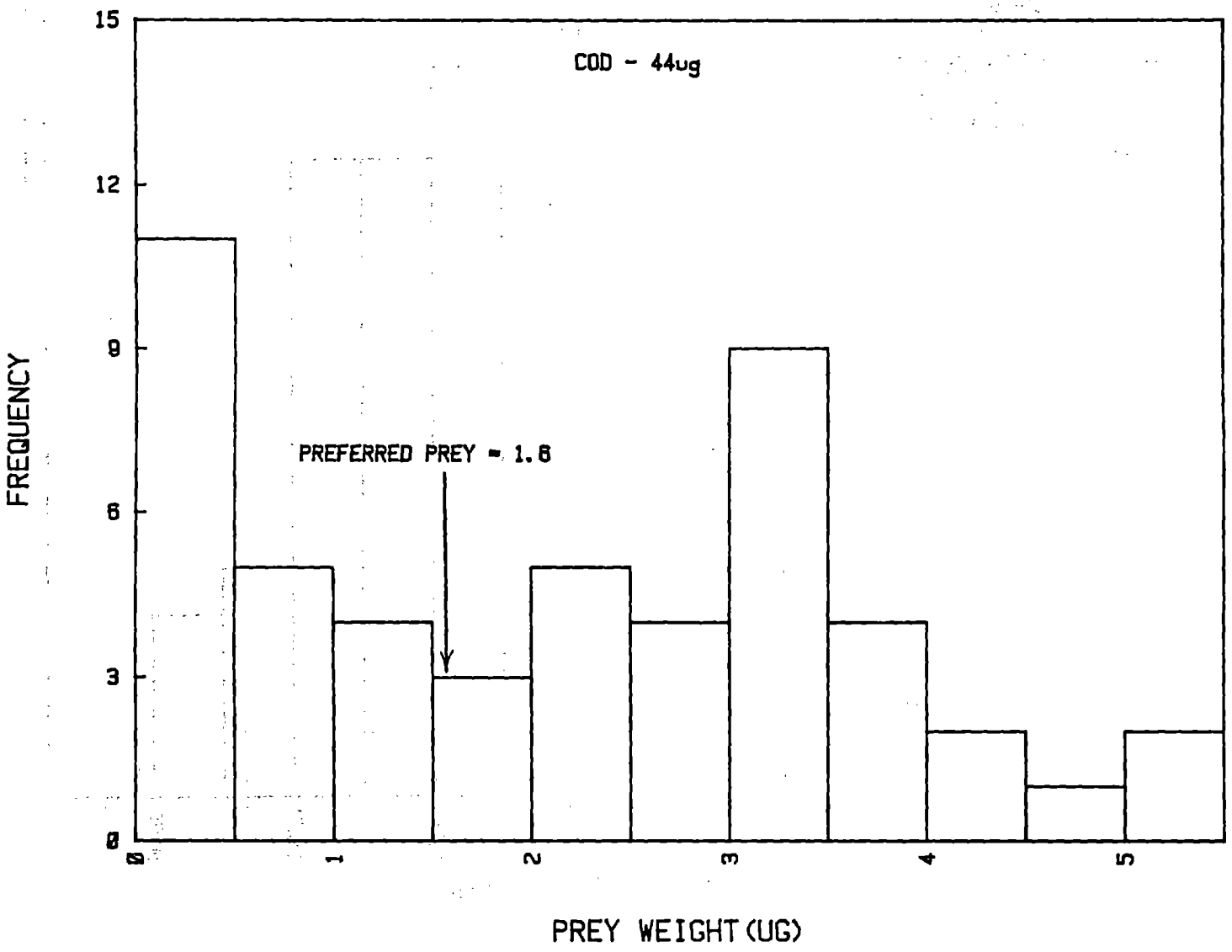

Figure 12. Frequency histogram of the distribution of prey size about the preferred prey size for a 44 µg cod larva.

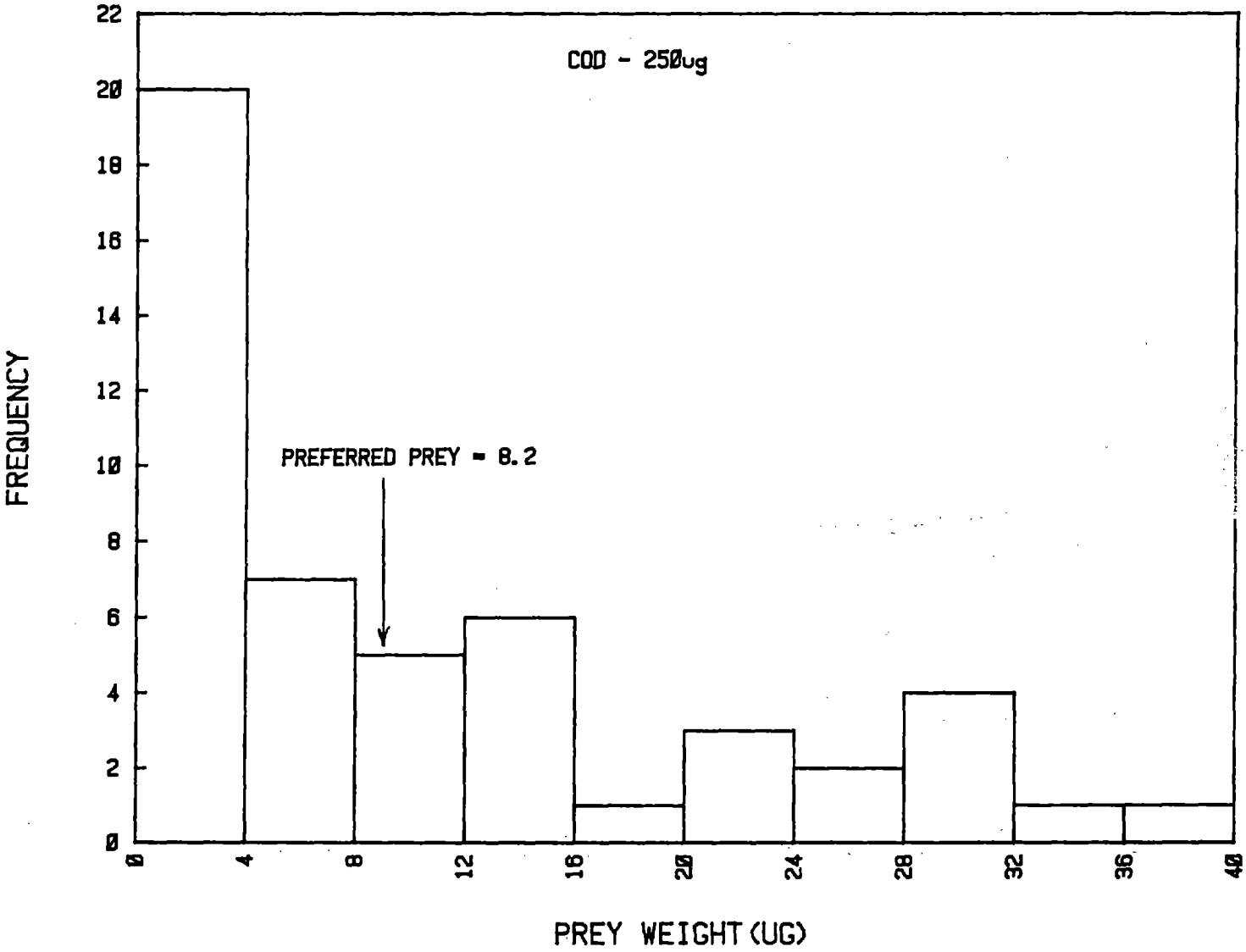

Figure 13. Frequency histogram of the distribution of prey size about the preferred prey size for a 250 µg cod larva.

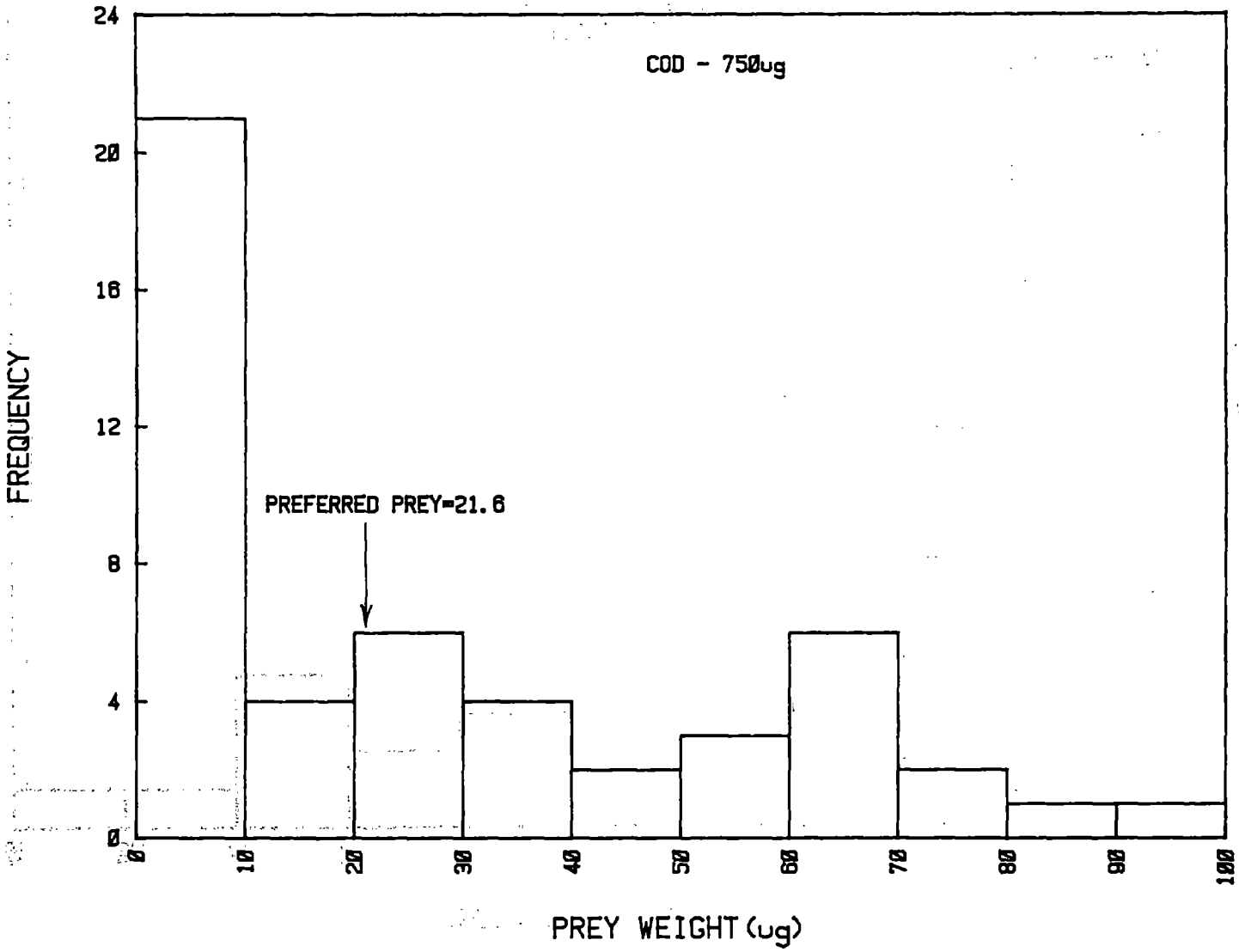

Figure 14. Frequency histogram of the distribution of prey size about the preferred prey size for a 750 µg cod larva.

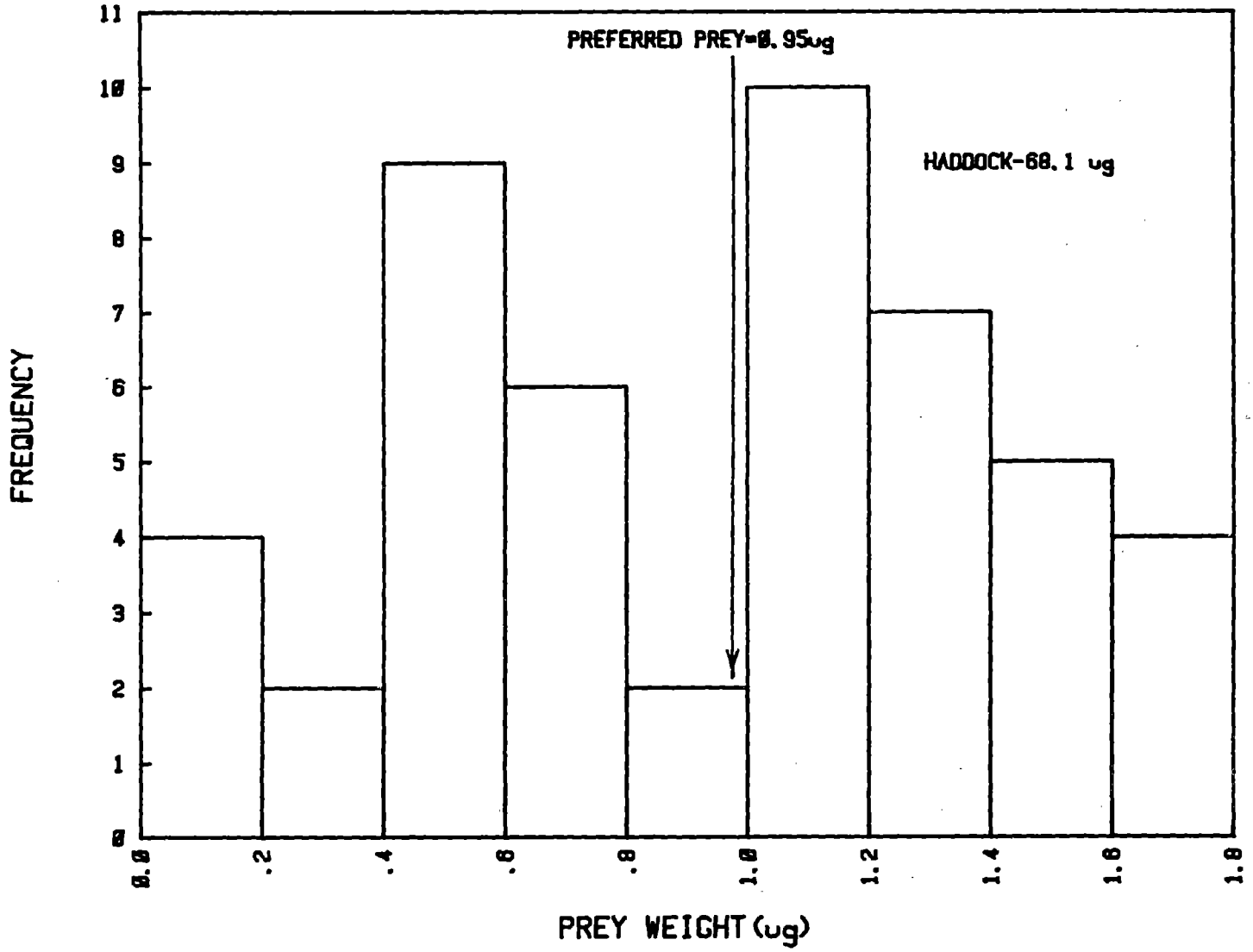

Figure 15. Frequency histogram of the distribution of prey size about the preferred prey size for a 68.1 µg haddock larva.

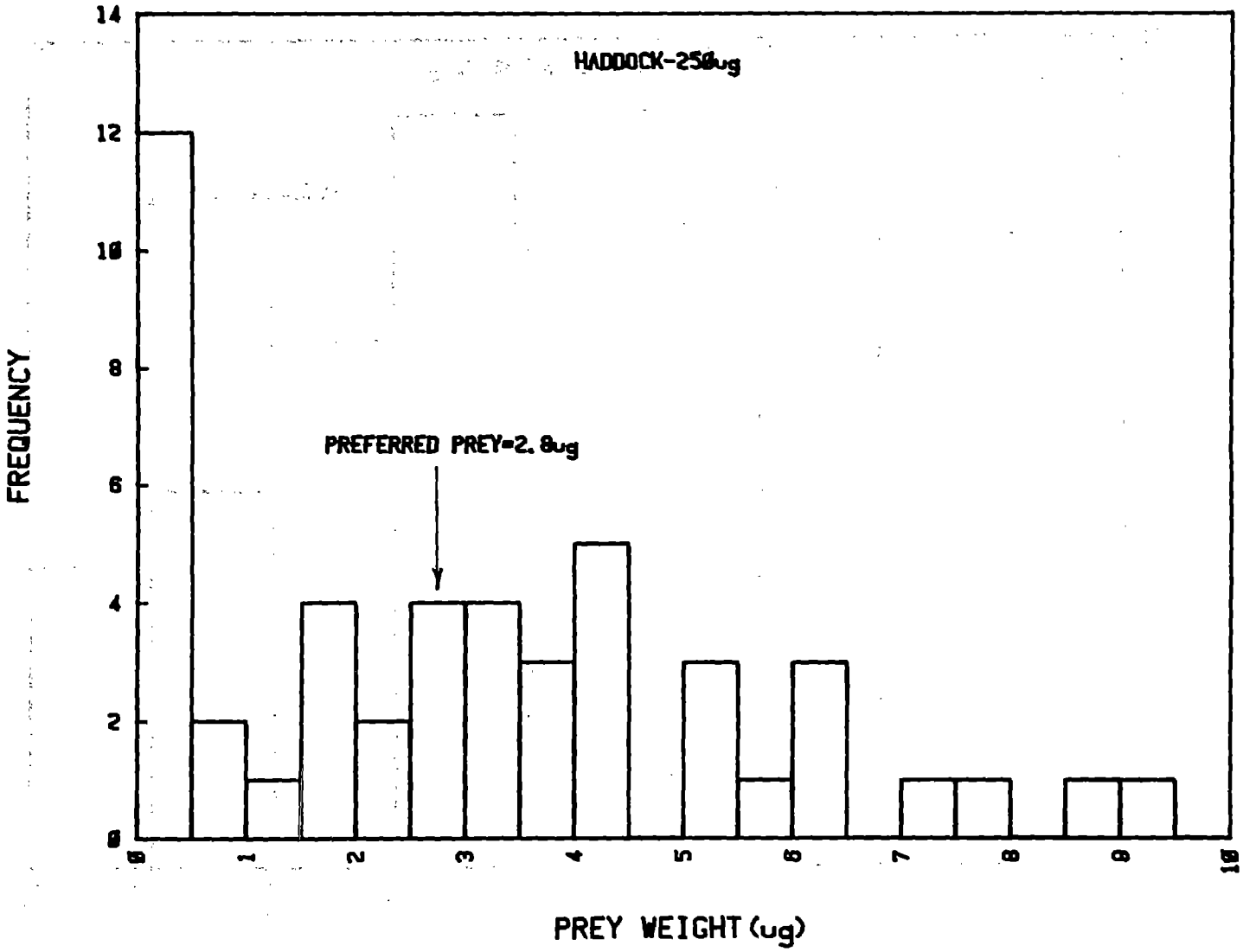

Figure 16. Frequency histogram of the distribution of prey size about the preferred prey size for a 250 µg haddock larva.

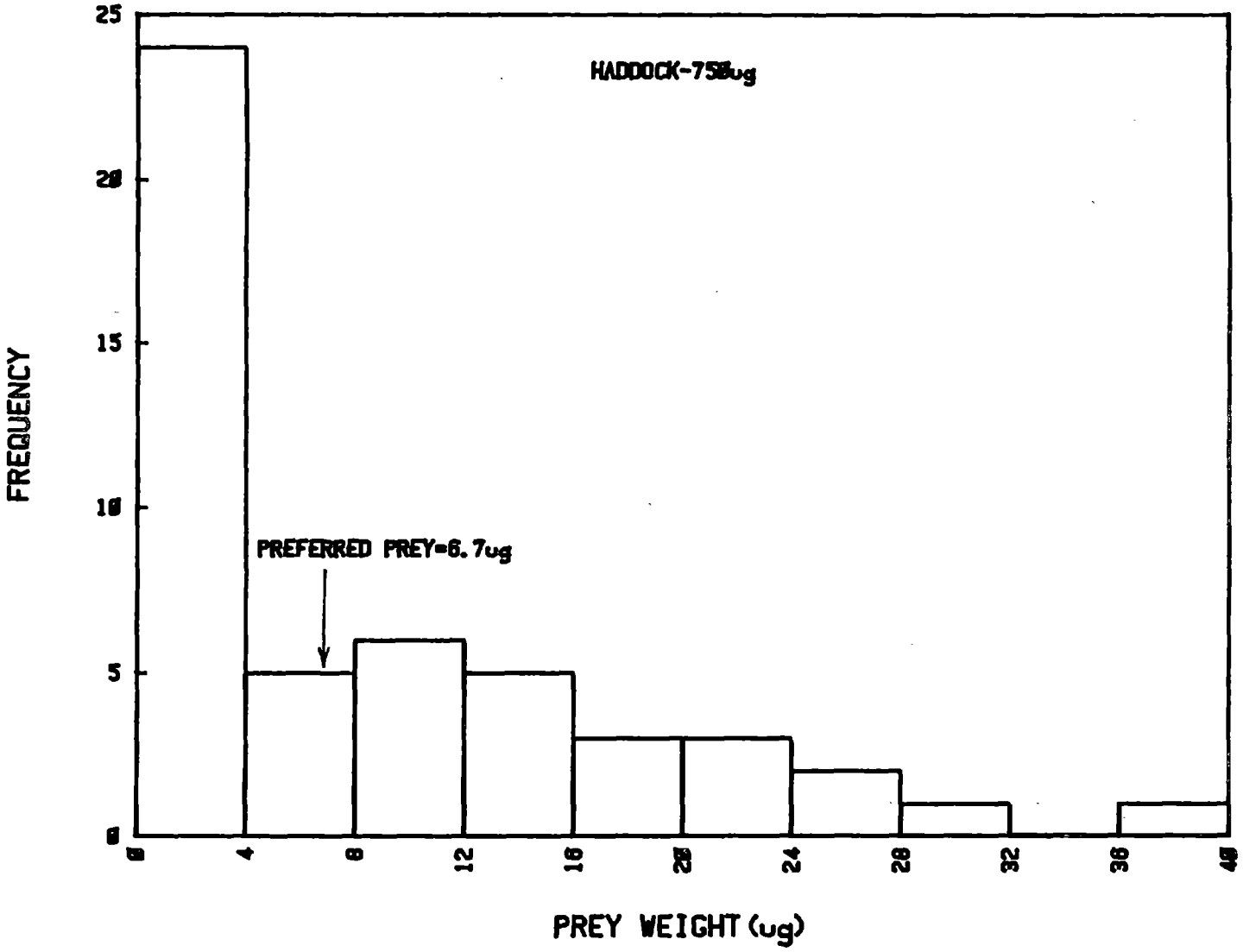

Figure 17. Frequency histogram of the distribution of prey size about the preferred prey size for a 750 µg haddock larva.

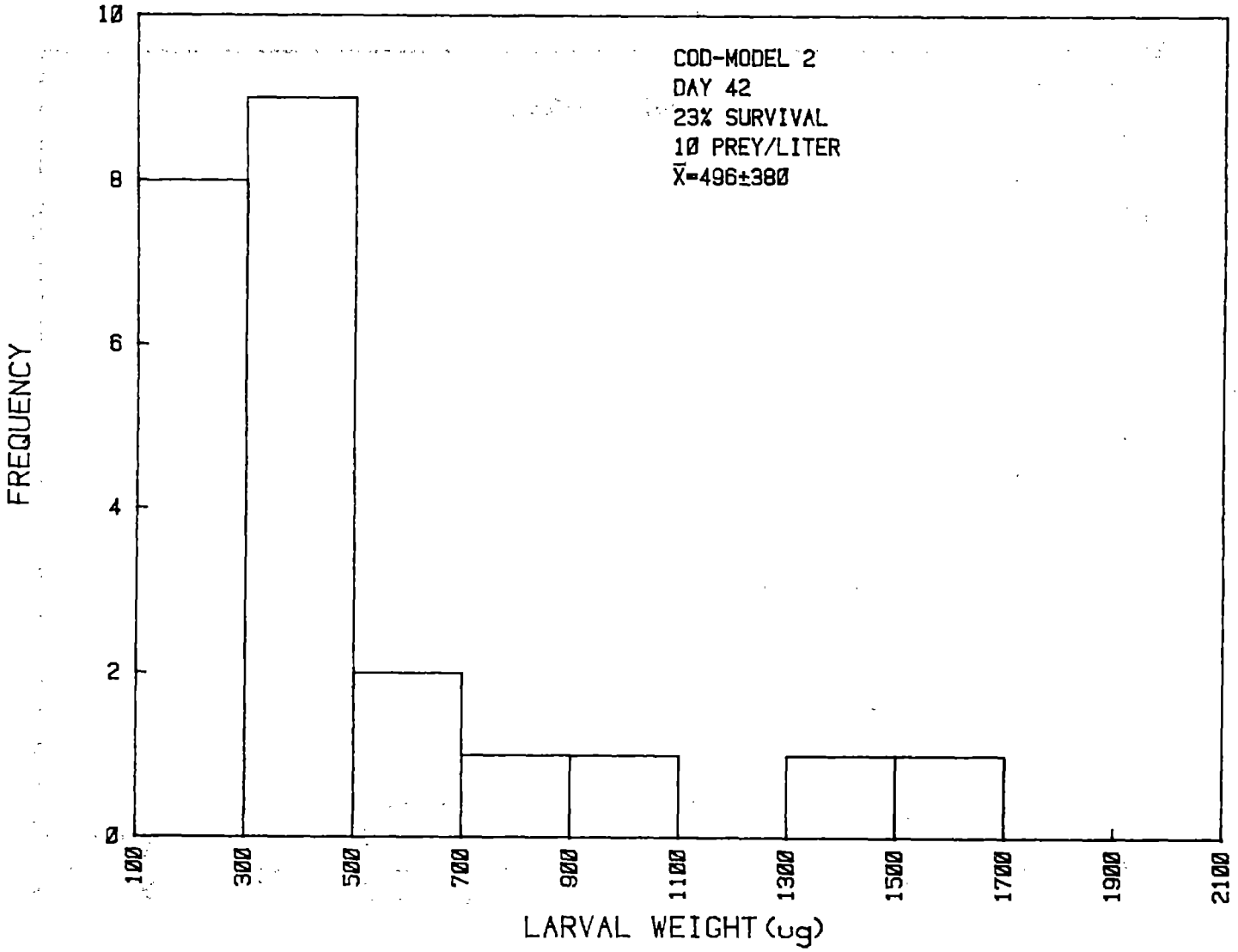

Figure 18. Frequency histogram of the distribution of larval weights of survivors at 42 days after hatching. Cod model 2 at 10 prey liter^{-1}.

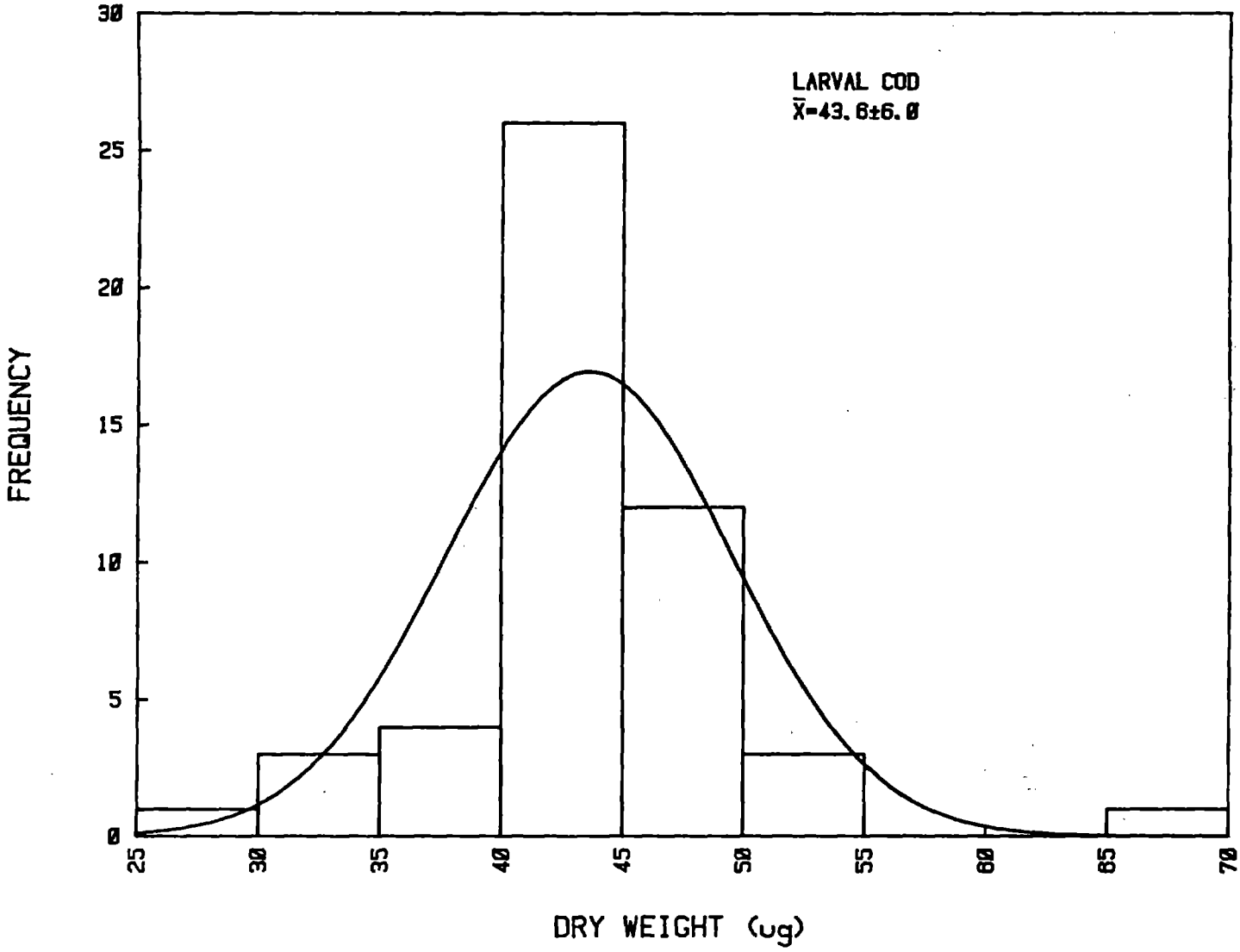

Figure 19. Frequency histogram of a generated normal distribution of larval initial hatching weights based on empirical laboratory measurements for cod.

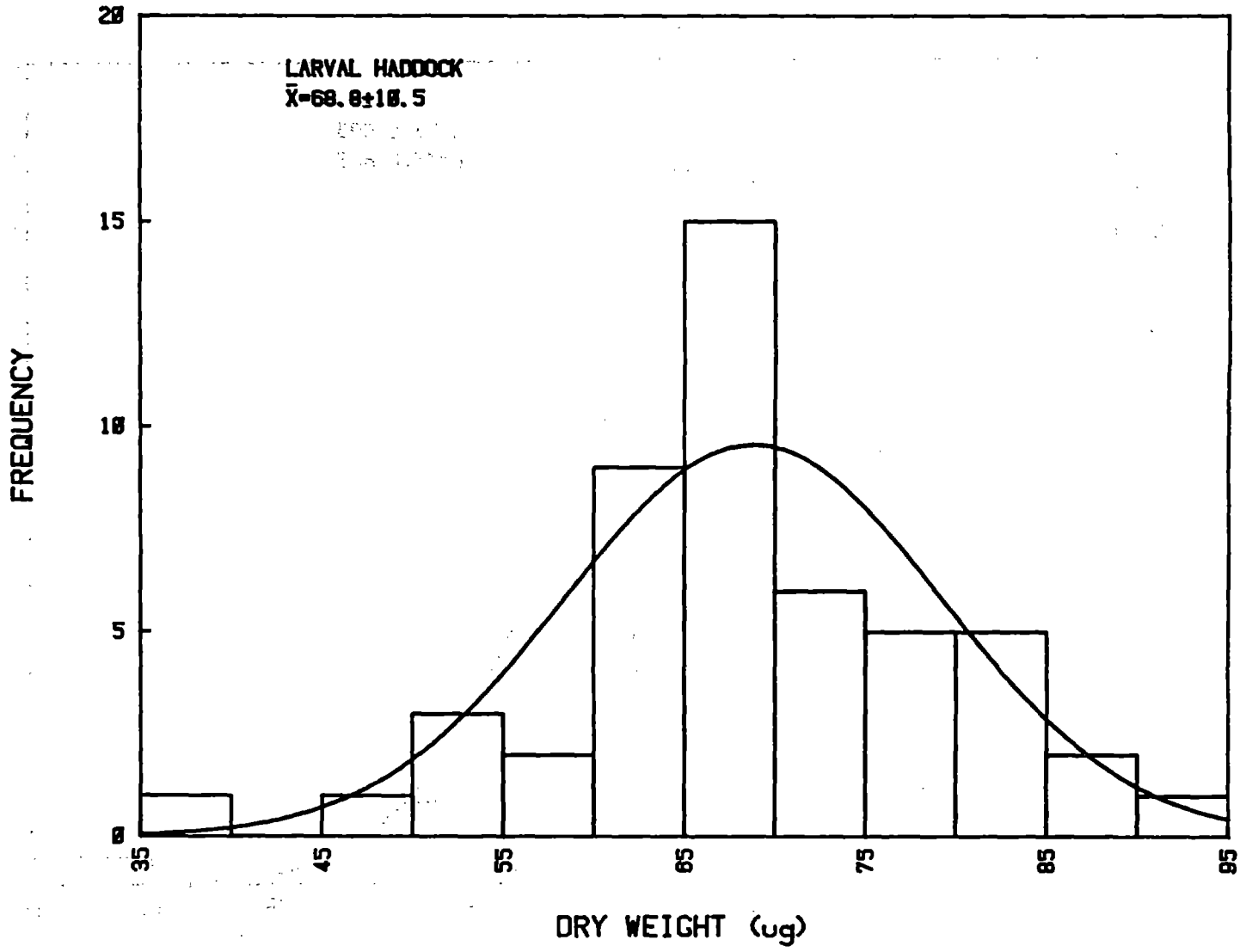

Figure 20. Frequency histogram of a generated normal distribution of larval initial hatching weights based on empirical laboratory measurements for haddock.

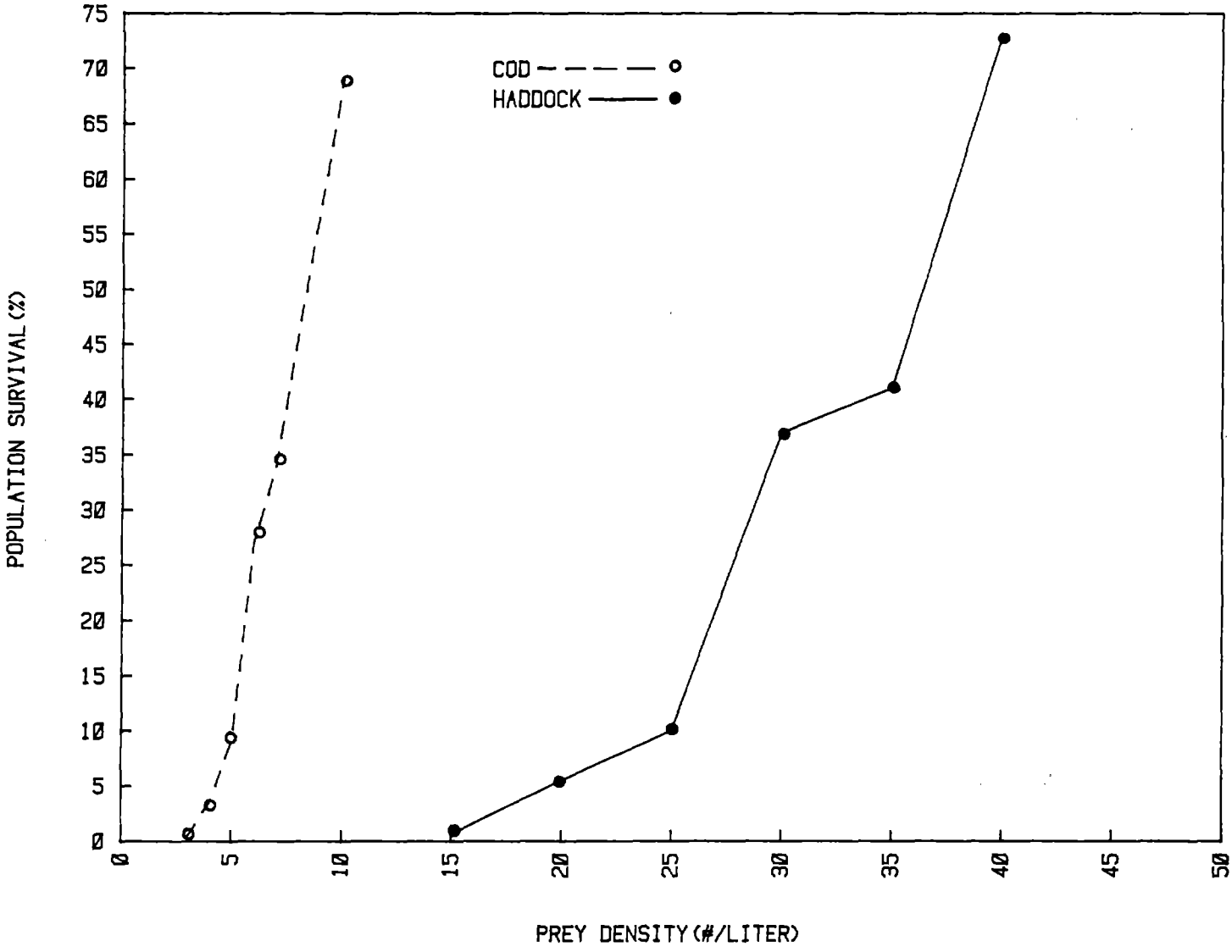

Figure 21. Simulated population survival at different constant prey densities for larval cod and haddock. Based on the 3 stochastic element model (version 3).

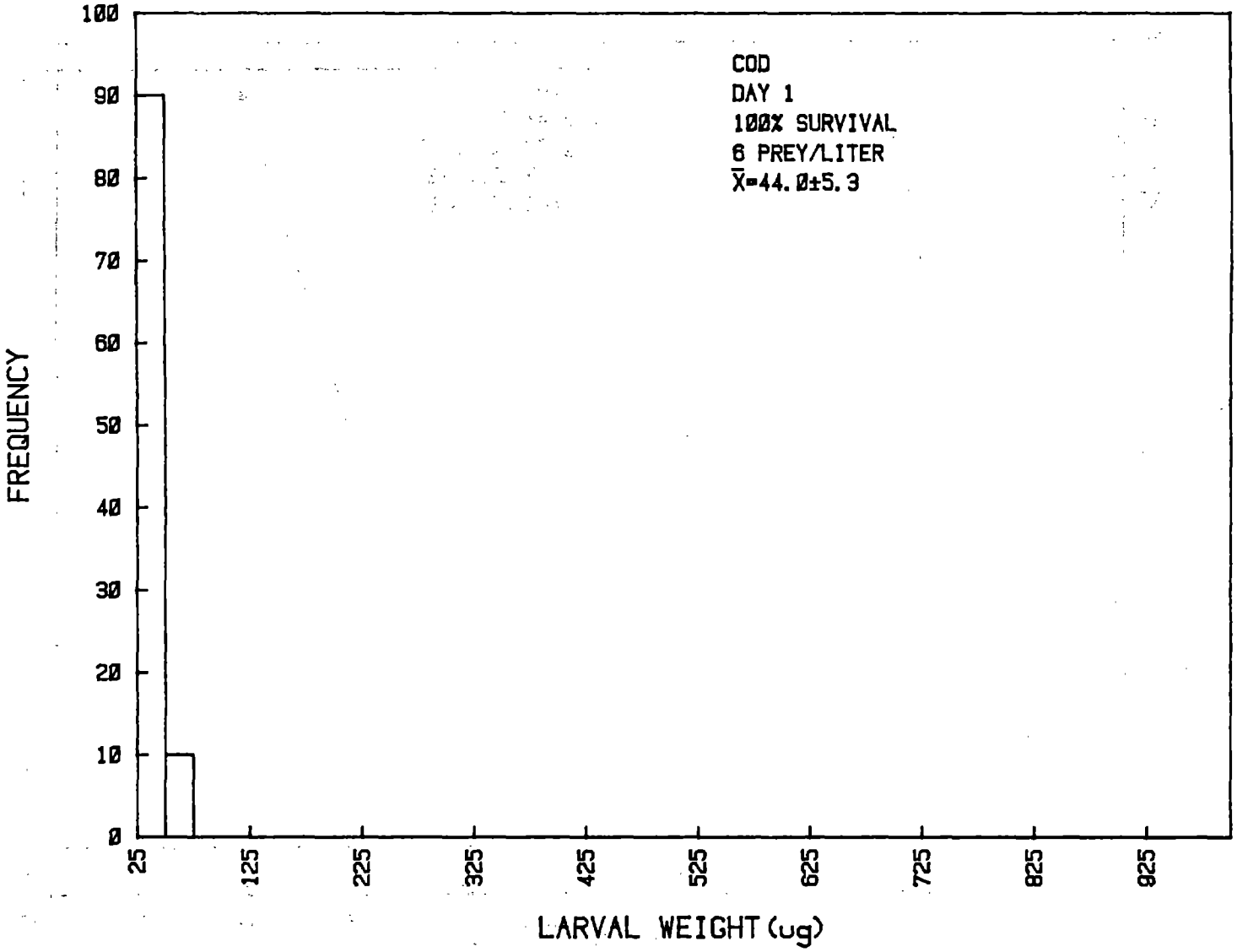

Figure 22. Frequency histogram of an initial weight distribution from a 3 stochastic element model run at a prey density of 6 liter^{-1} for cod larvae.

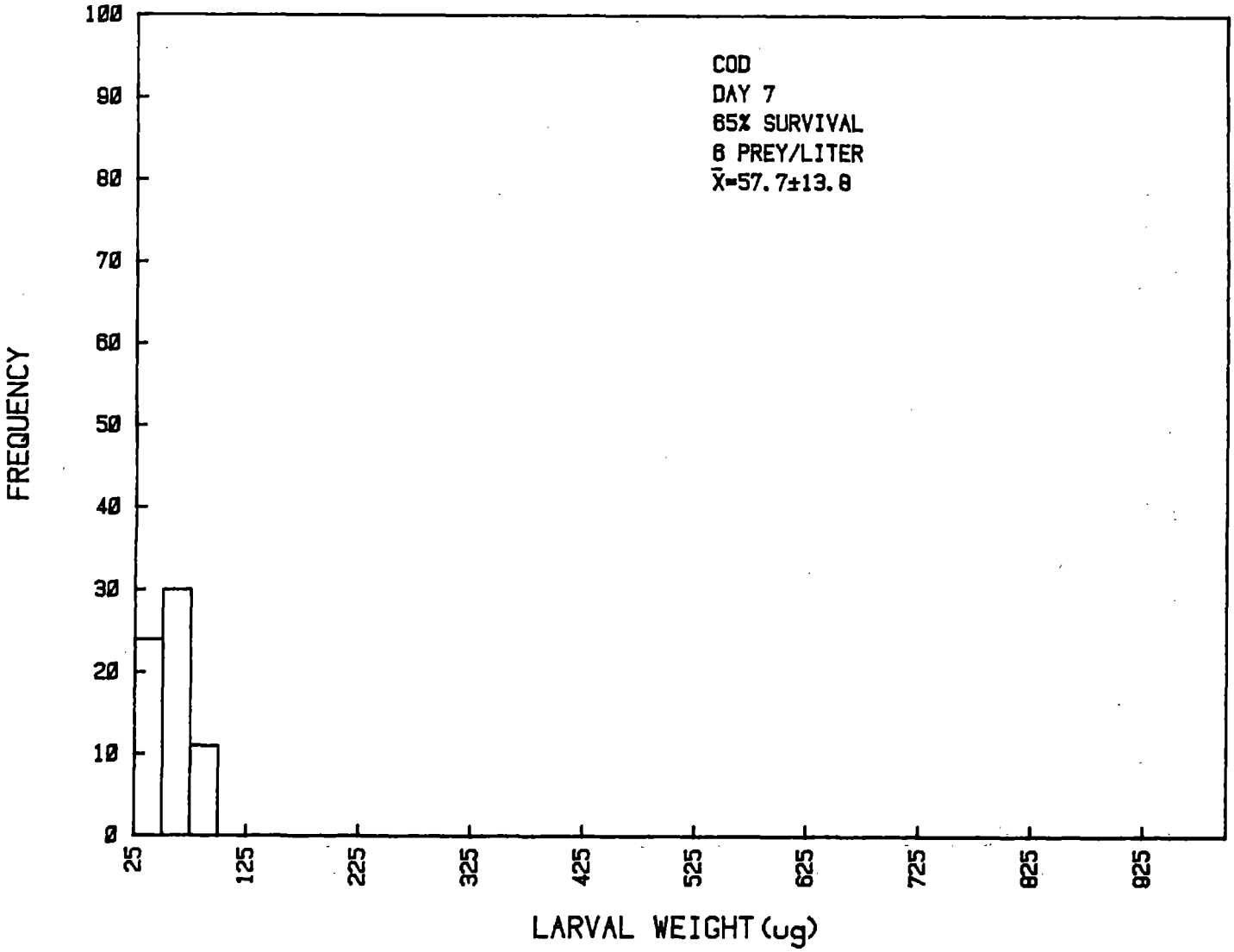

Figure 23. Frequency histogram of the weight distribution from a 3 stochastic element model run at a prey density of 6 liter^{-1} for cod larvae at 7 days after hatching.

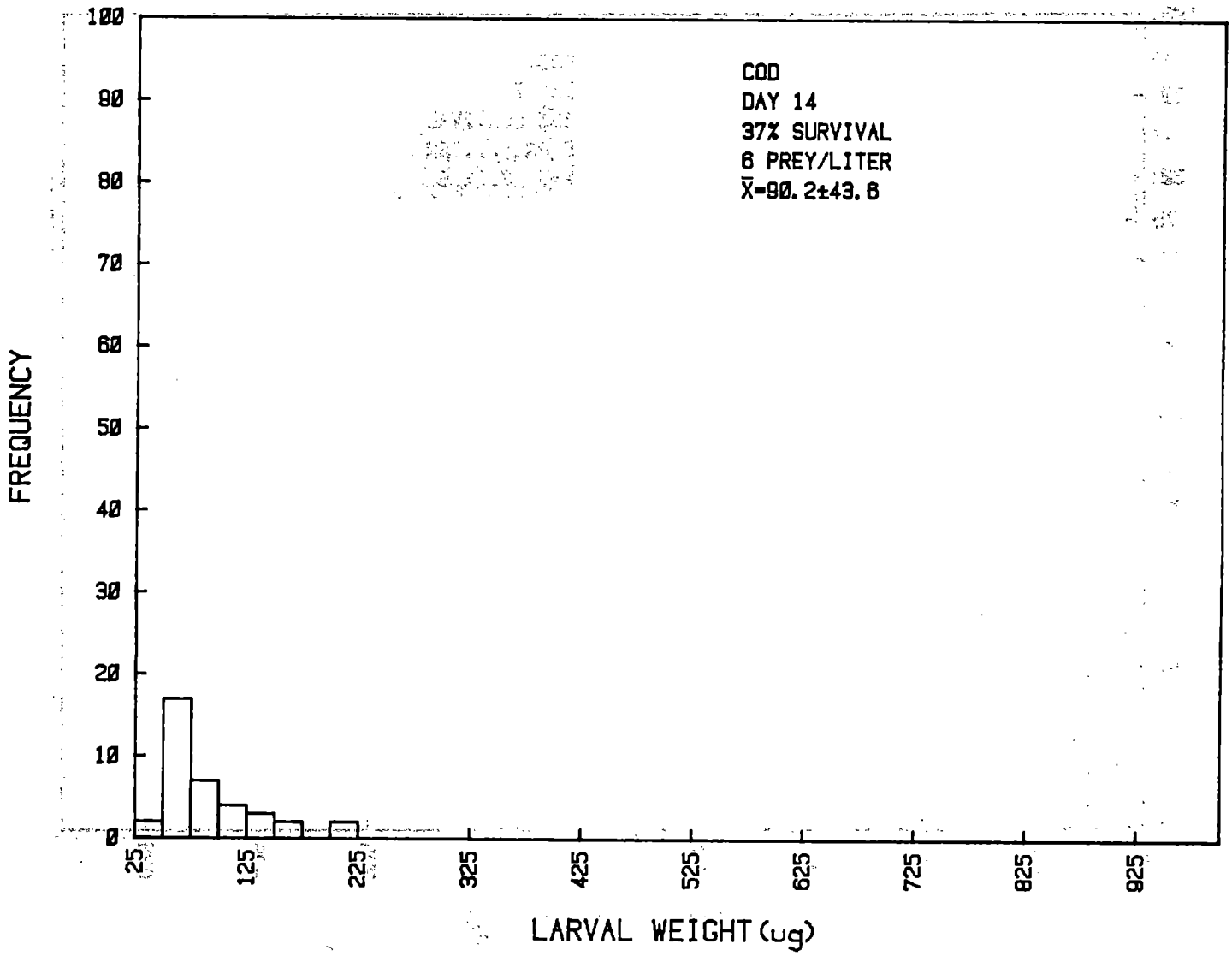

Figure 24. Frequency histogram of the weight distribution from a 3 stochastic element model run at a prey density of 6 liter^{-1} for cod larvae at 14 days after hatching.

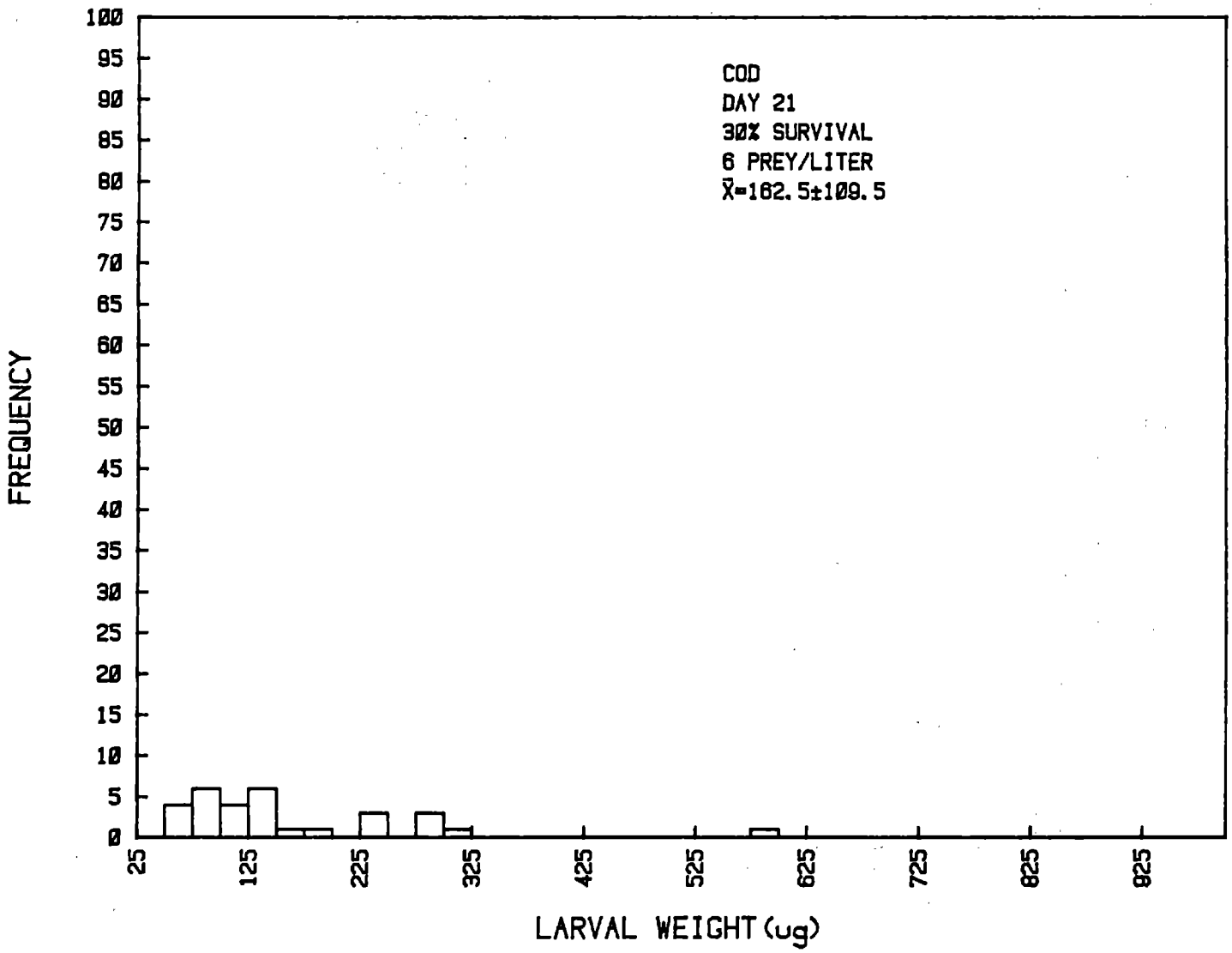

Figure 25. Frequency histogram of the weight distribution from a 3 stochastic element model run at a prey density of 6 liter^{-1} for cod larvae at 21 days after hatching.

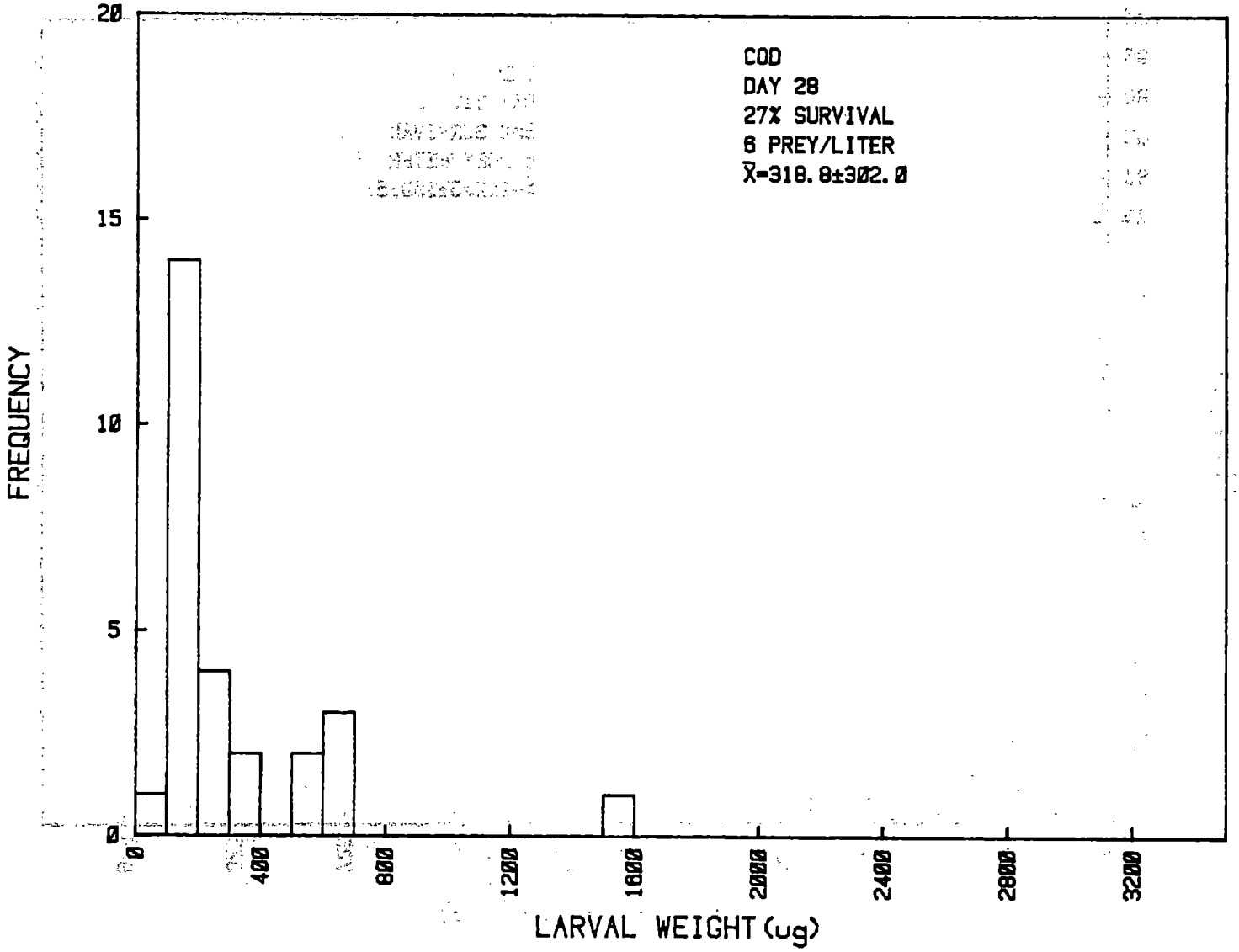

Figure 26. Frequency histogram of the weight distribution from a 3 stochastic element model run at a prey density of 6 liter^{-1} for cod larvae at 28 days after hatching.

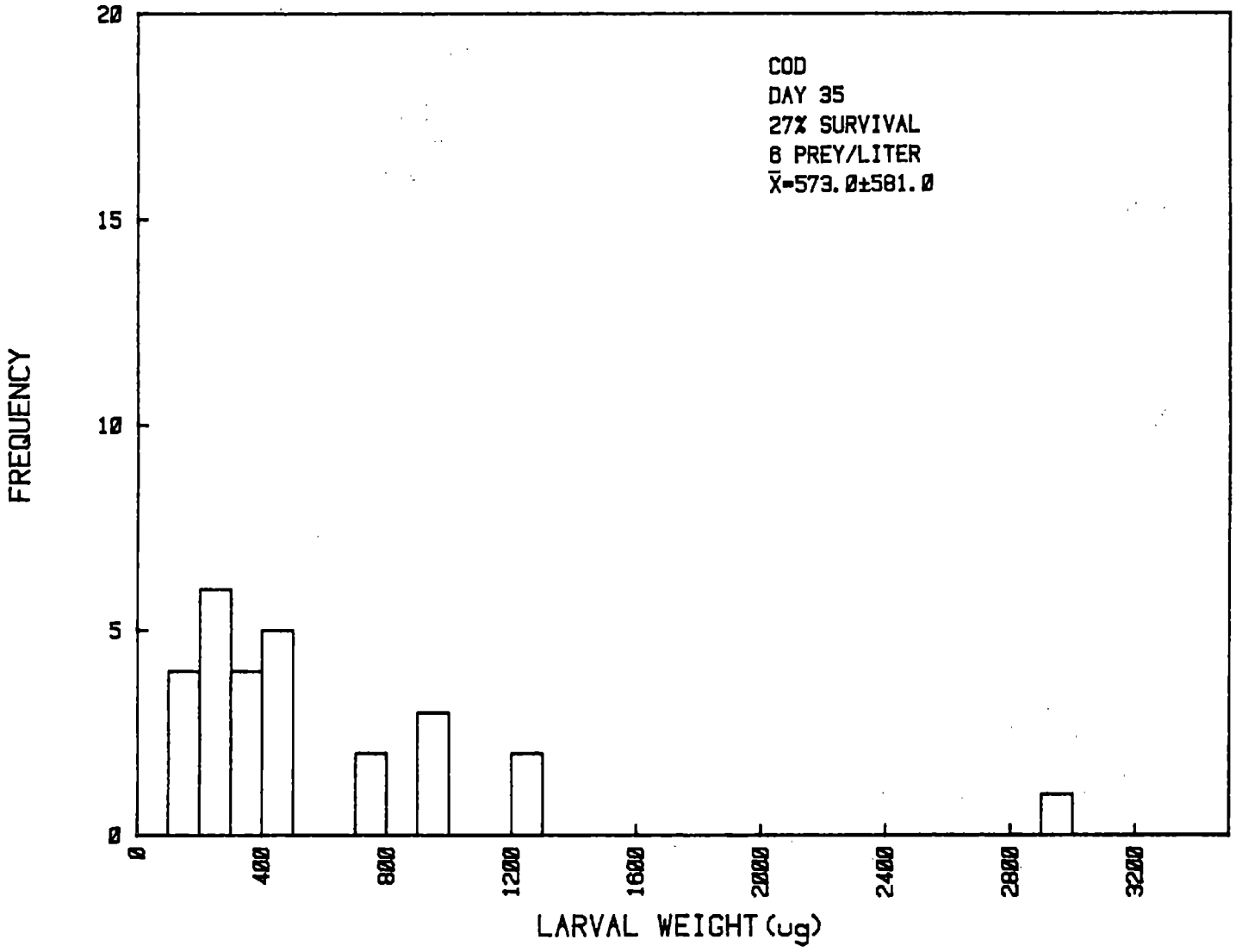

Figure 27. Frequency histogram of the weight distribution from a 3 stochastic element model run at a prey density of 6 liter^{-1} for cod larvae at 35 days after hatching.

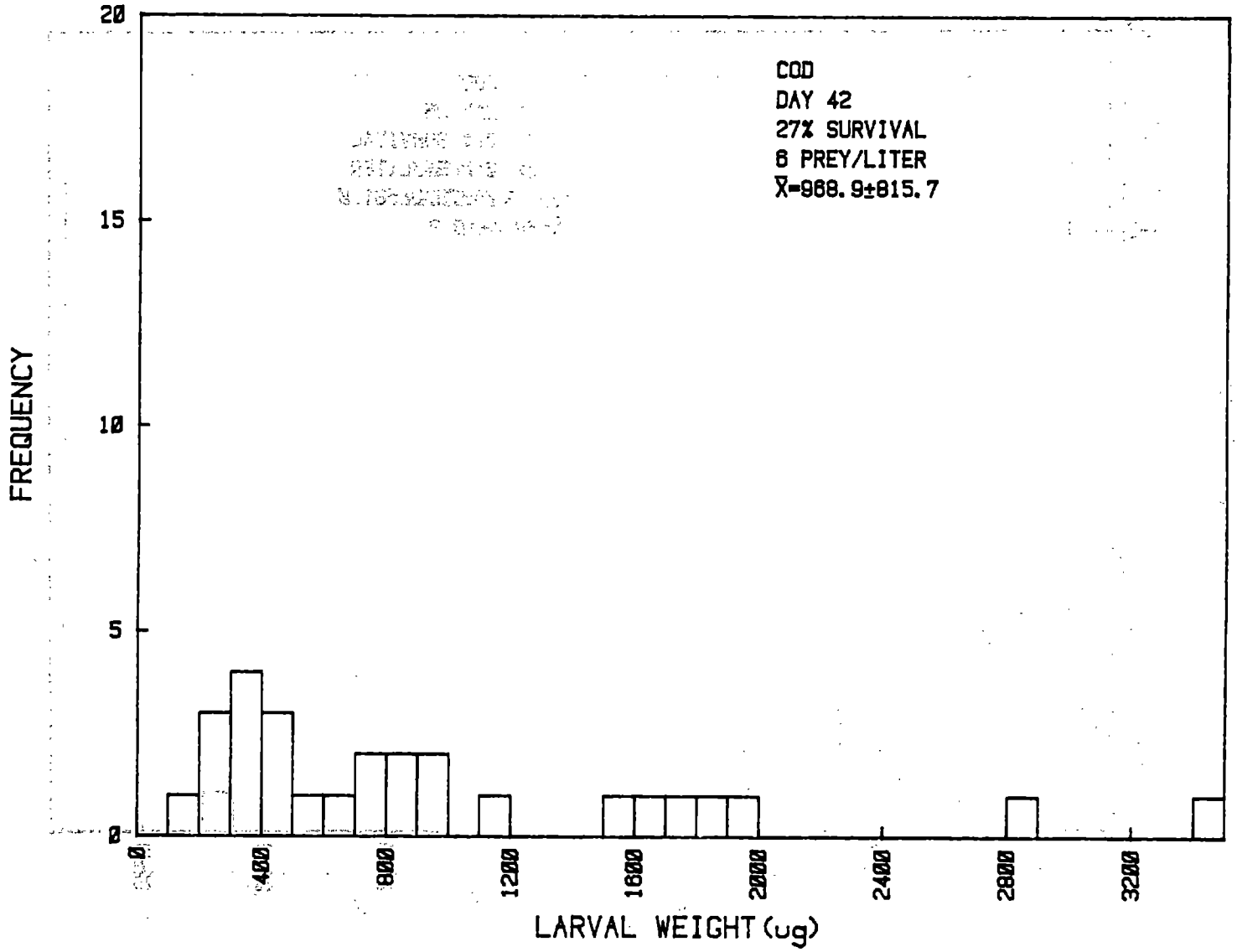

Figure 28. Frequency histogram of the weight distribution from a 3 stochastic element model run at a prey density of 6 liter^{-1} for cod larvae at 42 days after hatching.

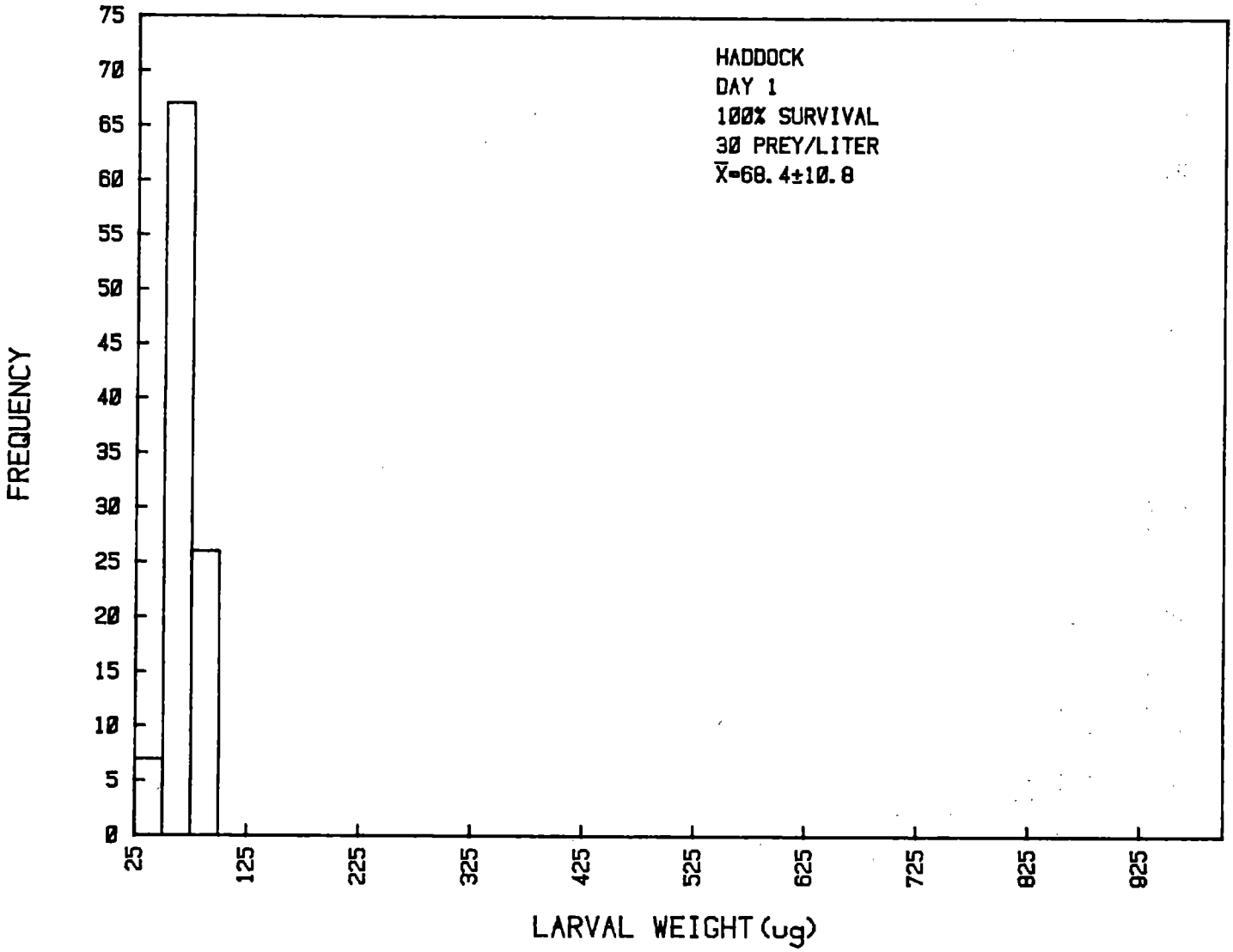

Figure 29. Frequency histogram of an initial weight distribution from a 3 stochastic element model run at a prey density of 30 liter^{-1} for haddock larvae.

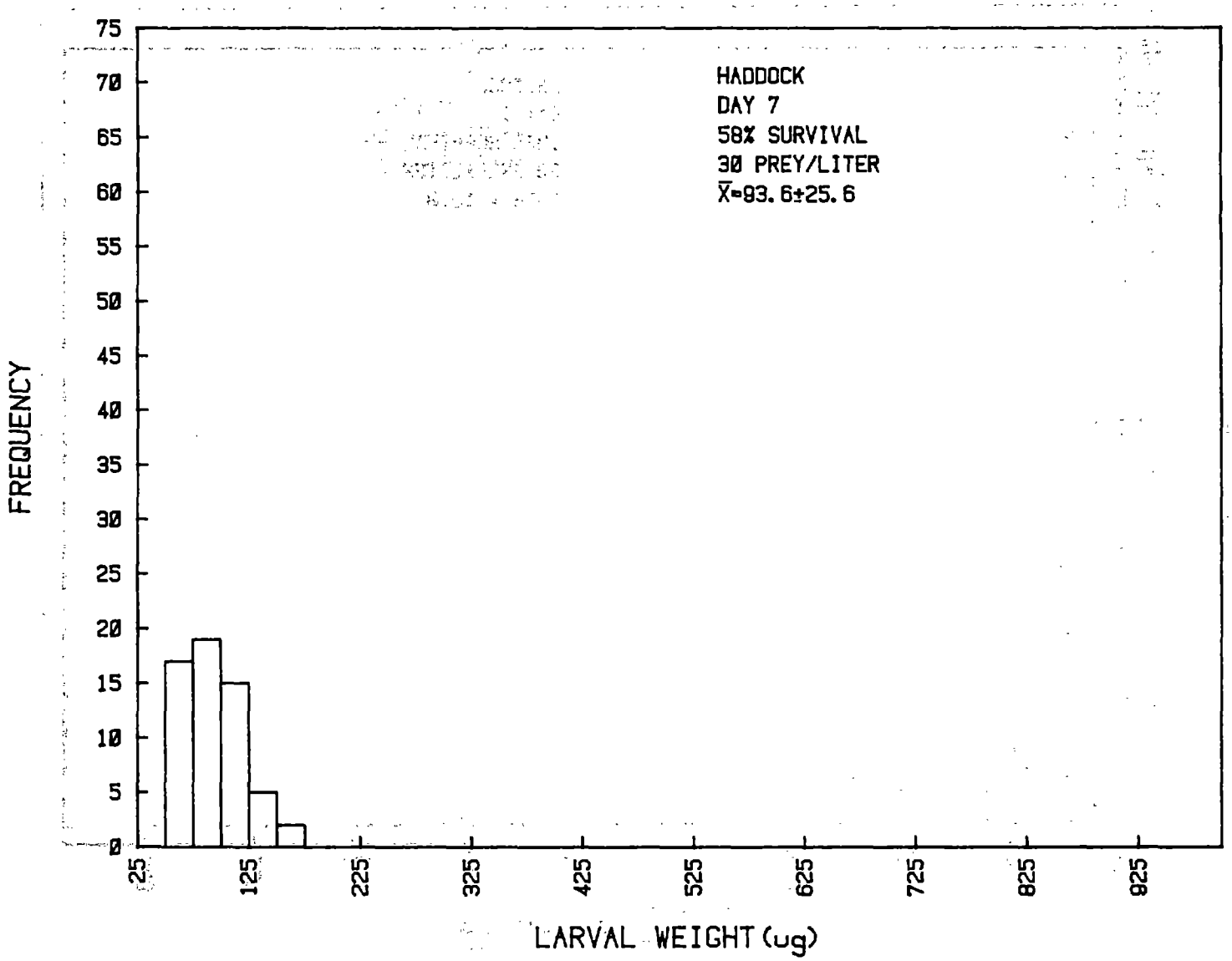

Figure 30. Frequency histogram of the weight distribution from a 3 stochastic element model run at a prey density of 30 liter^{-1} for haddock larvae at 7 days after hatching.

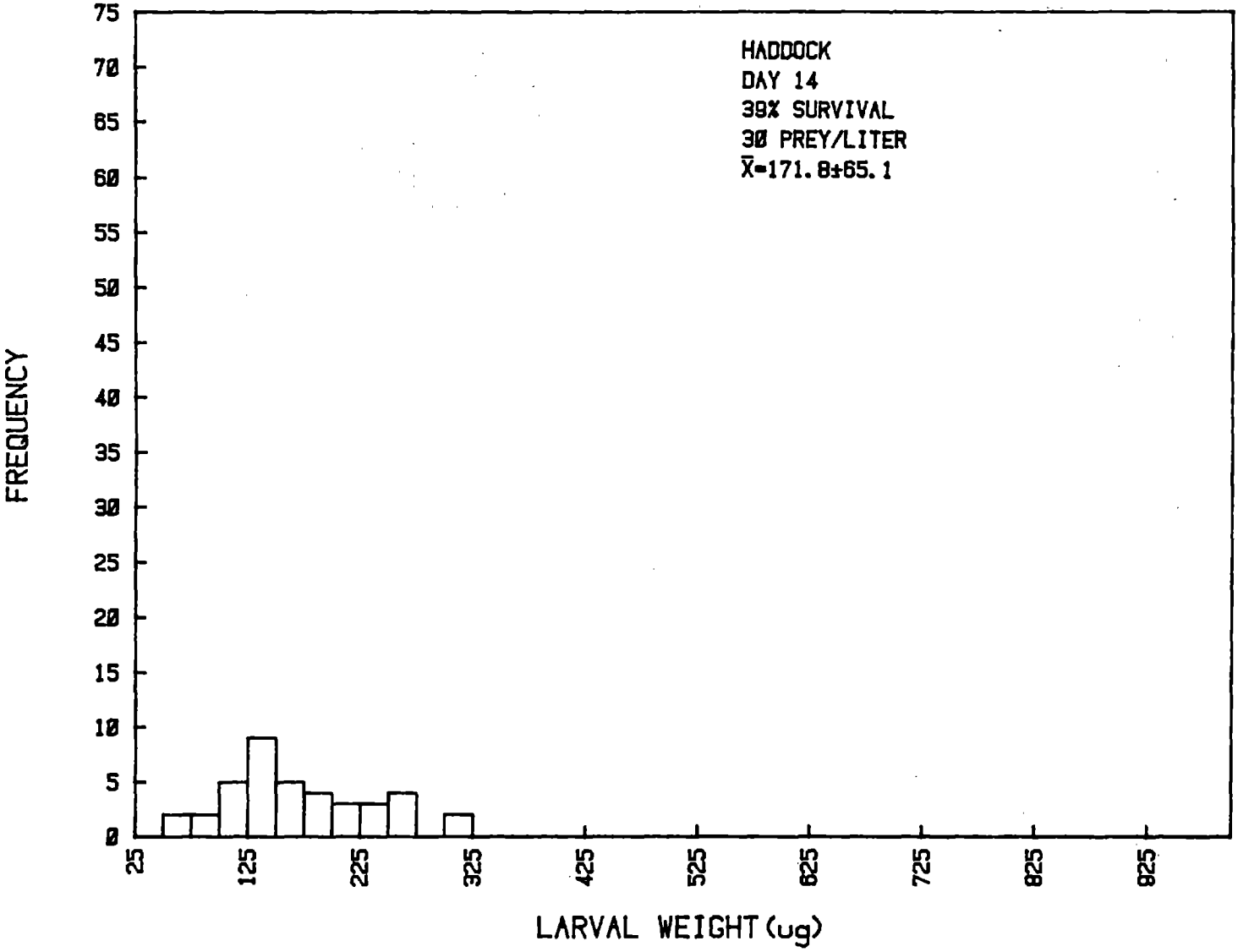

Figure 31. Frequency histogram of the weight distribution from a 3 stochastic element model run at a prey density of 30 liter^{-1} for haddock larvae at 14 days after hatching.

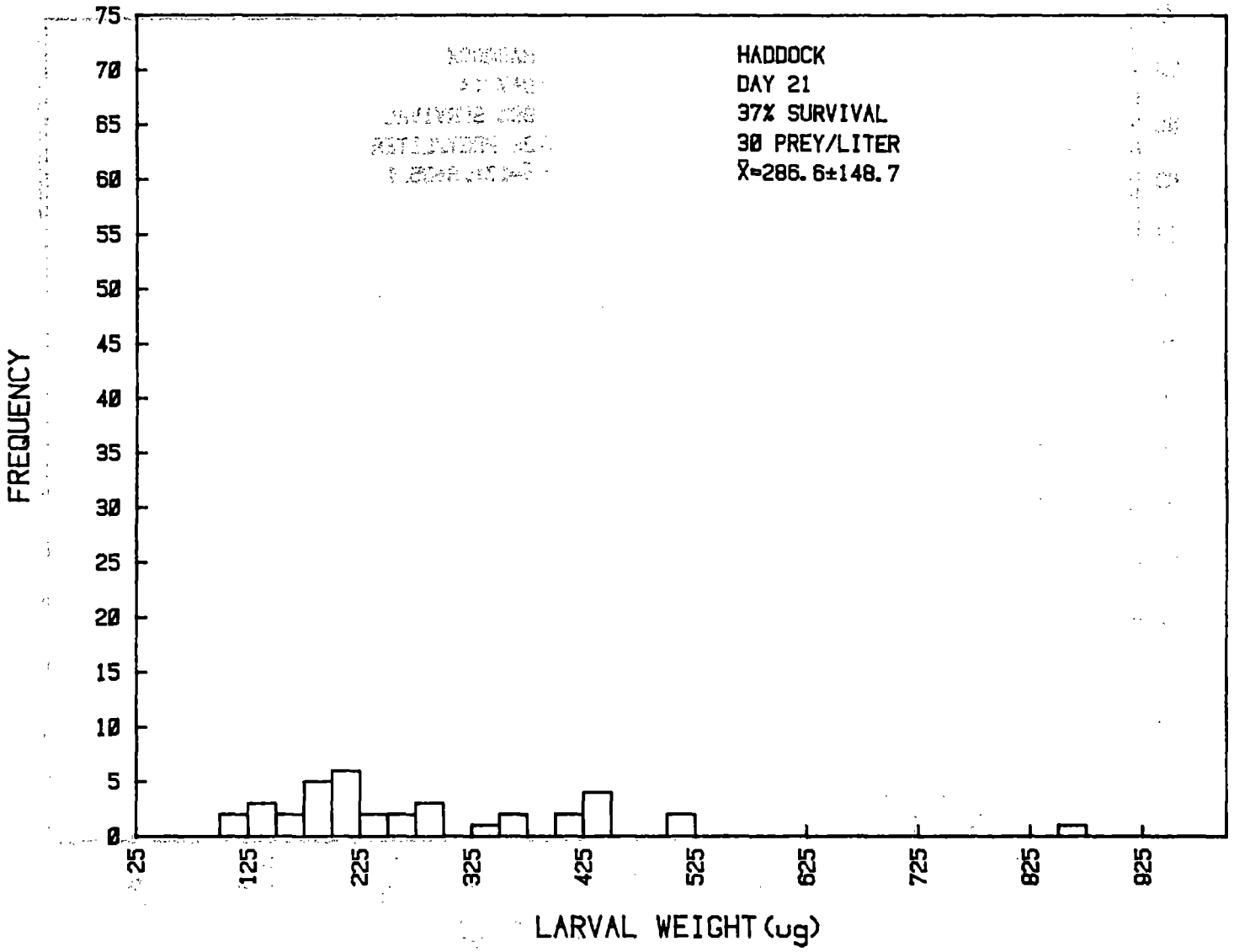

Figure 32. Frequency histogram of the weight distribution from a 3 stochastic element model run at a prey density of 30 liter^{-1} for haddock larvae at 21 days after hatching.

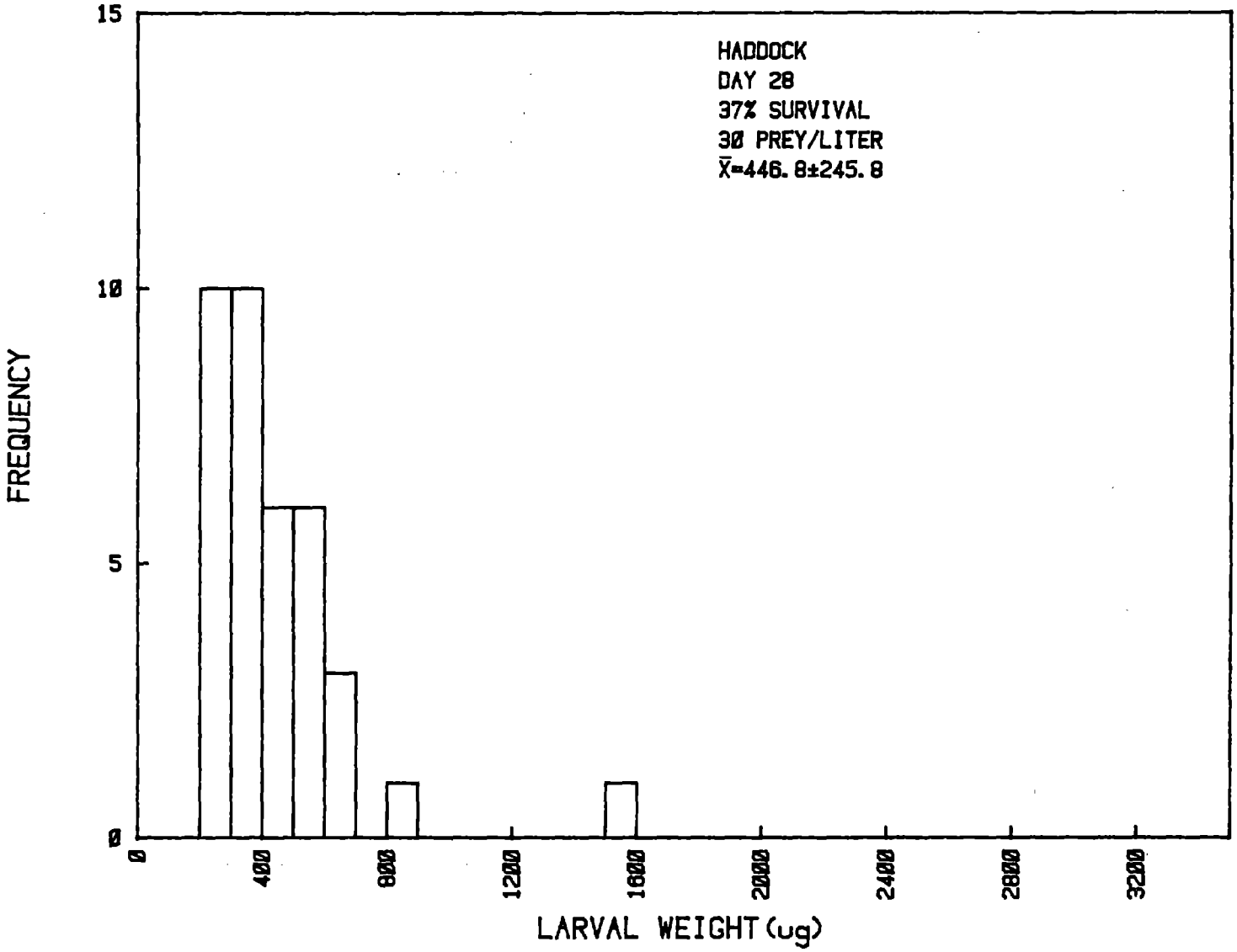

Figure 33. Frequency histogram of the weight distribution from a 3 stochastic element model run at a prey density of 30 liter^{-1} for haddock larvae at 28 days after hatching.

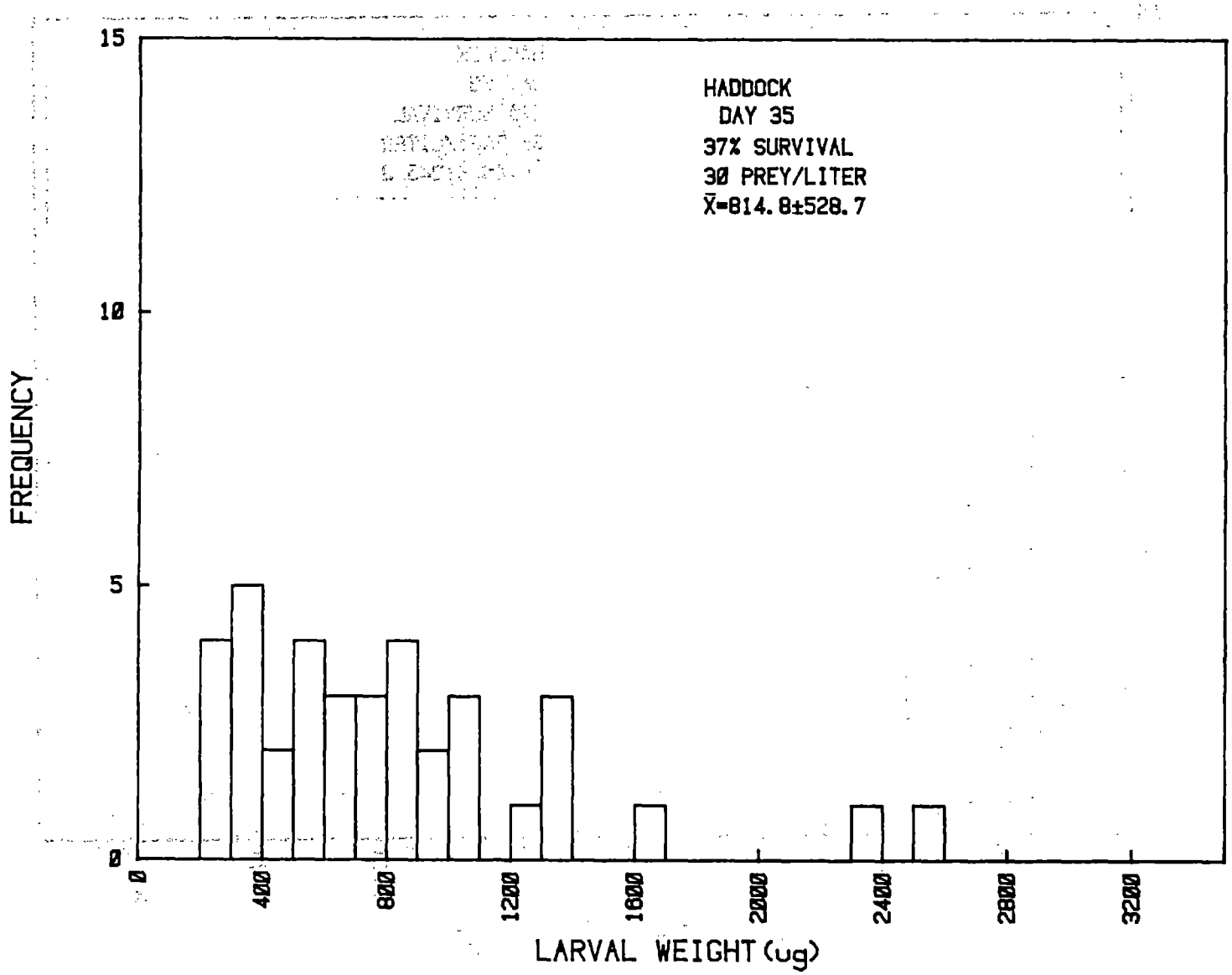

Figure 34. Frequency histogram of the weight distribution from a 3 stochastic element model run at a prey density of 30 liter^{-1} for haddock larvae at 35 days after hatching.

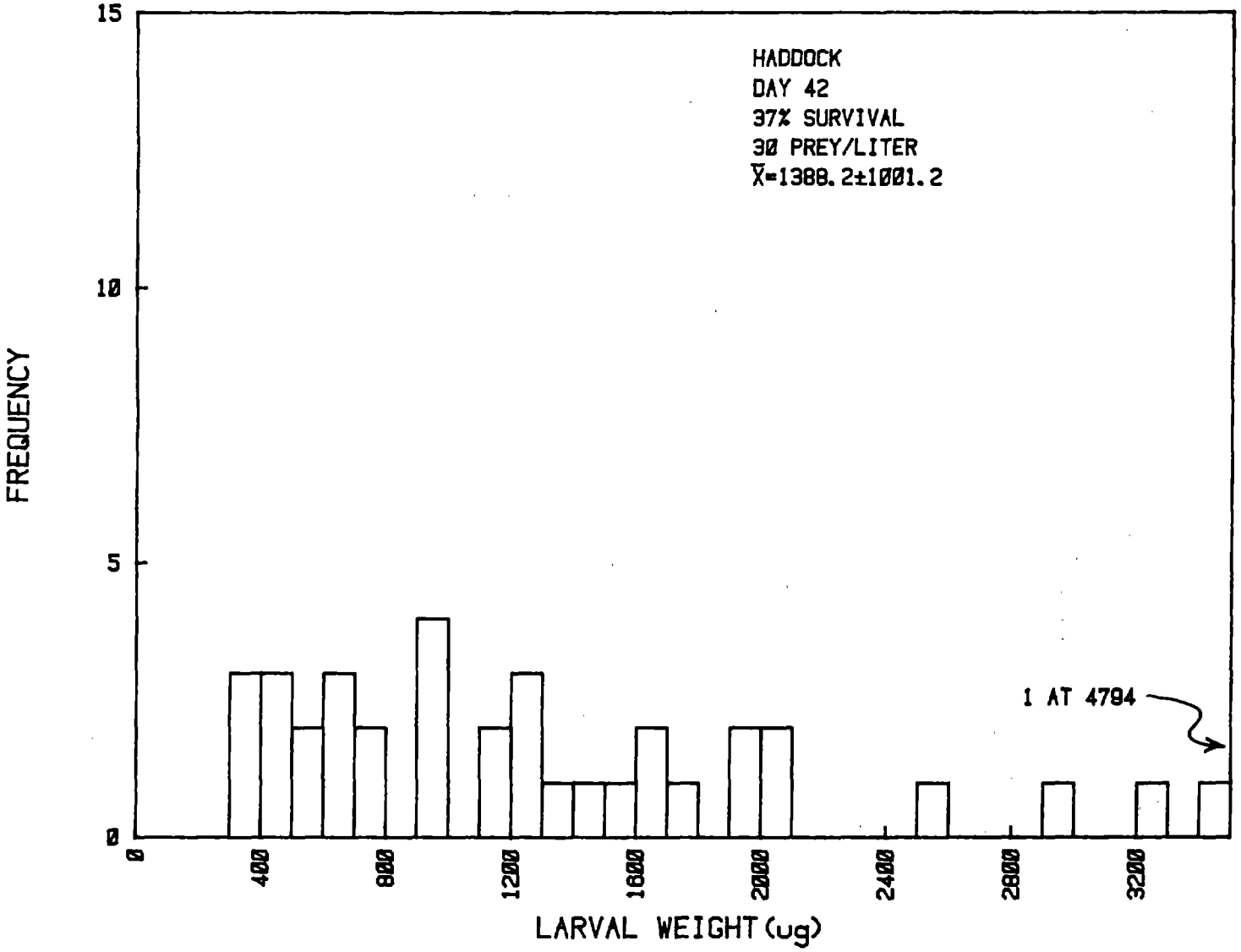

Figure 35. Frequency histogram of the weight distribution from a 3 stochastic element model run at a prey density of 30 liter^{-1} for haddock larvae at 42 days after hatching.

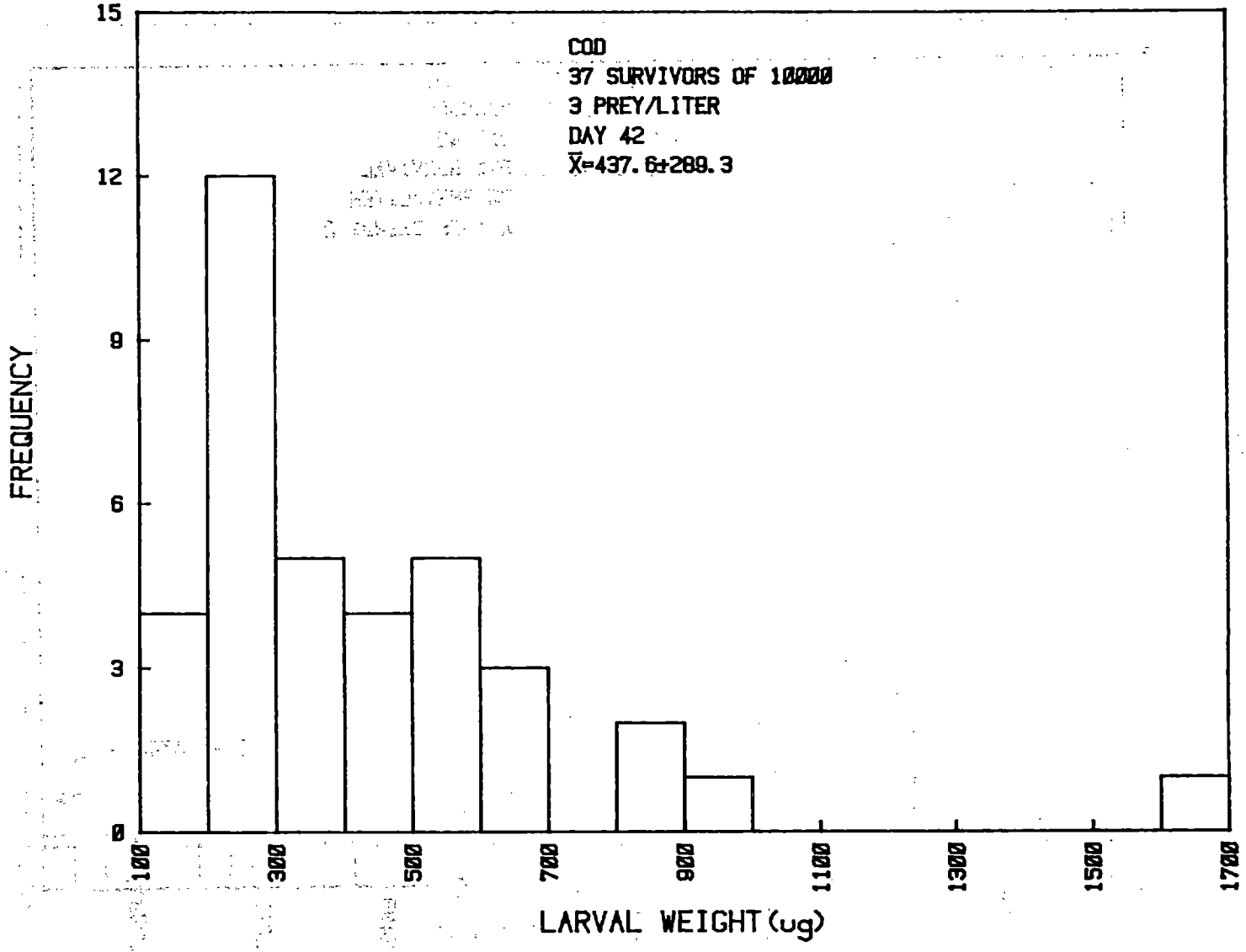

Figure 36. Frequency histogram of the distribution of weights of larval cod survivors on day 42 from a large population run (10,000 initially) with the 3 stochastic element model at a prey density of 3 liter^{-1}.

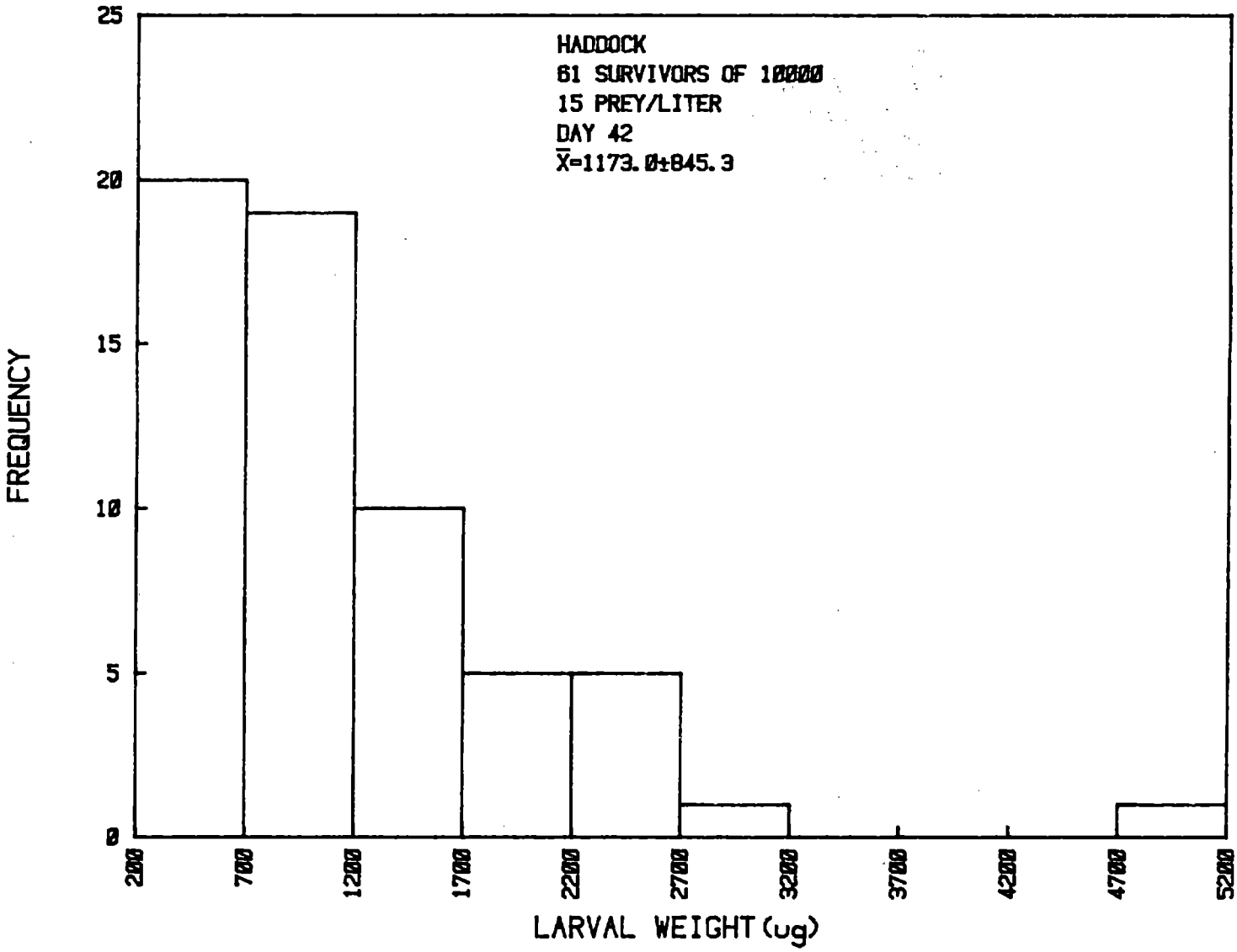

Figure 37. Frequency histogram of the distribution of weights or larval haddock survivors on day 42 from a large population run (10,000 initially) with the 3 stochastic element model at a prey density of 15 liter^{-1}.

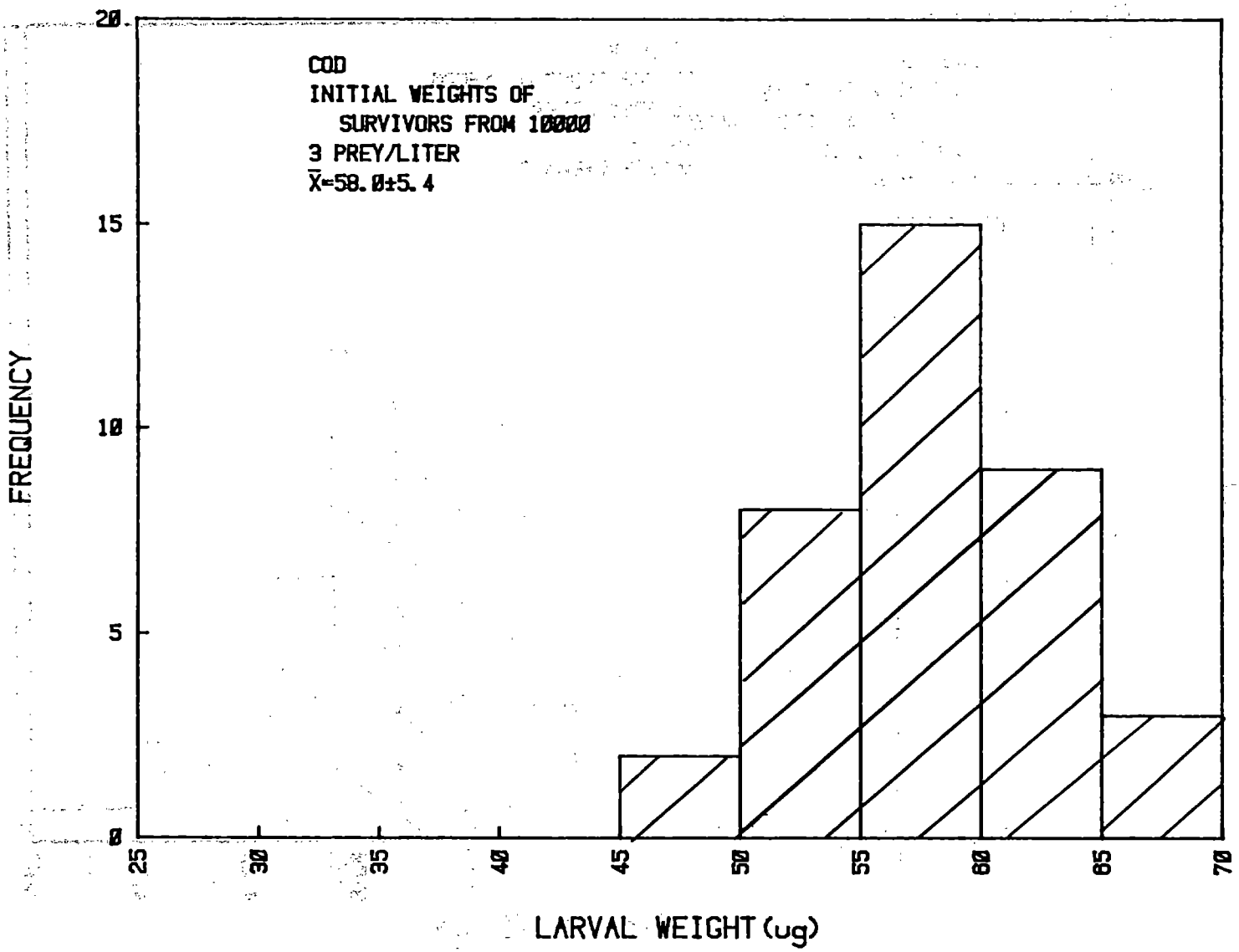

Figure 38. Frequency histogram of the distribution of initial weights of the surviving cod larvae from Figure 36.

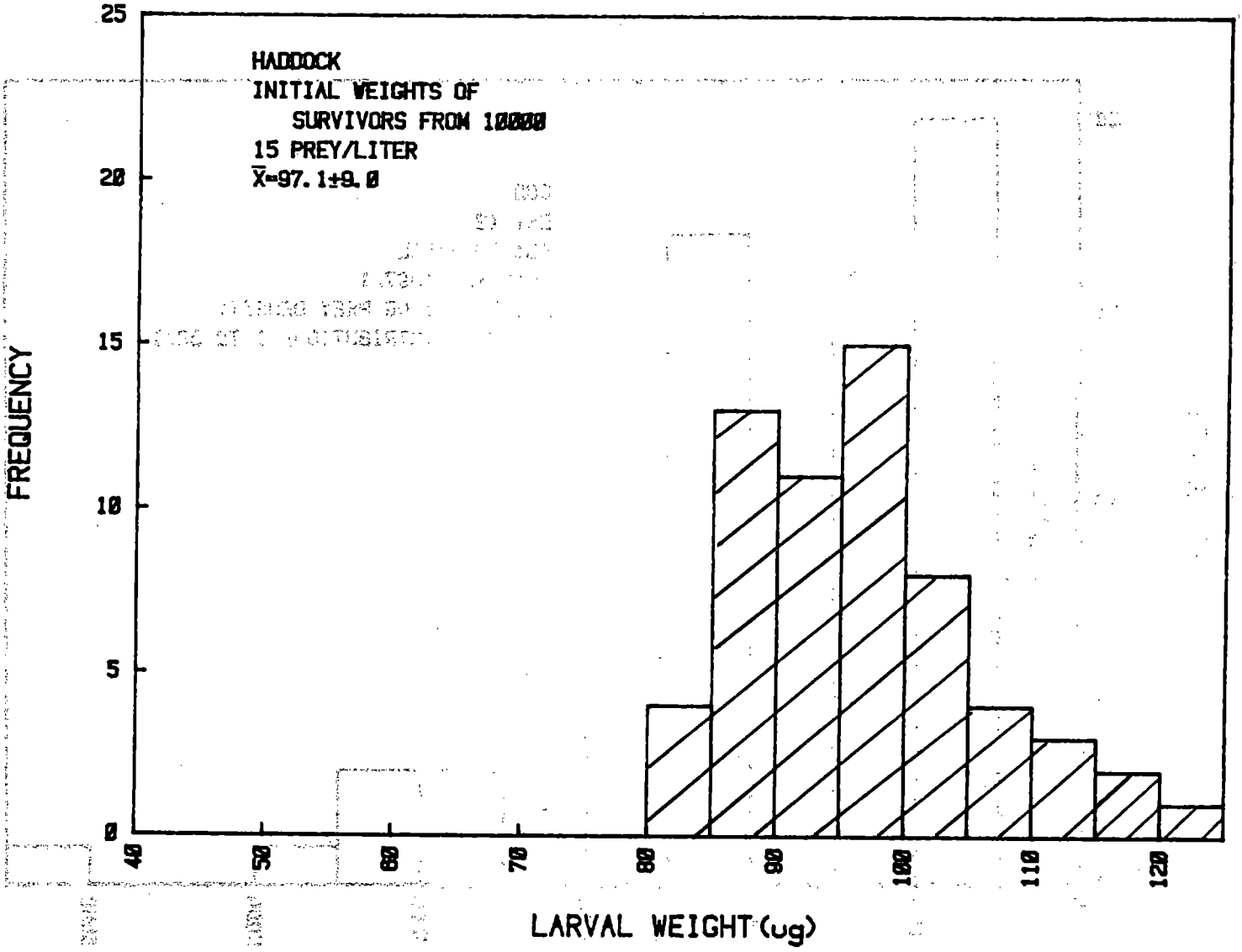

Figure 39. Frequency histogram of the distribution of initial weights of the surviving haddock larvae from Figure 37.

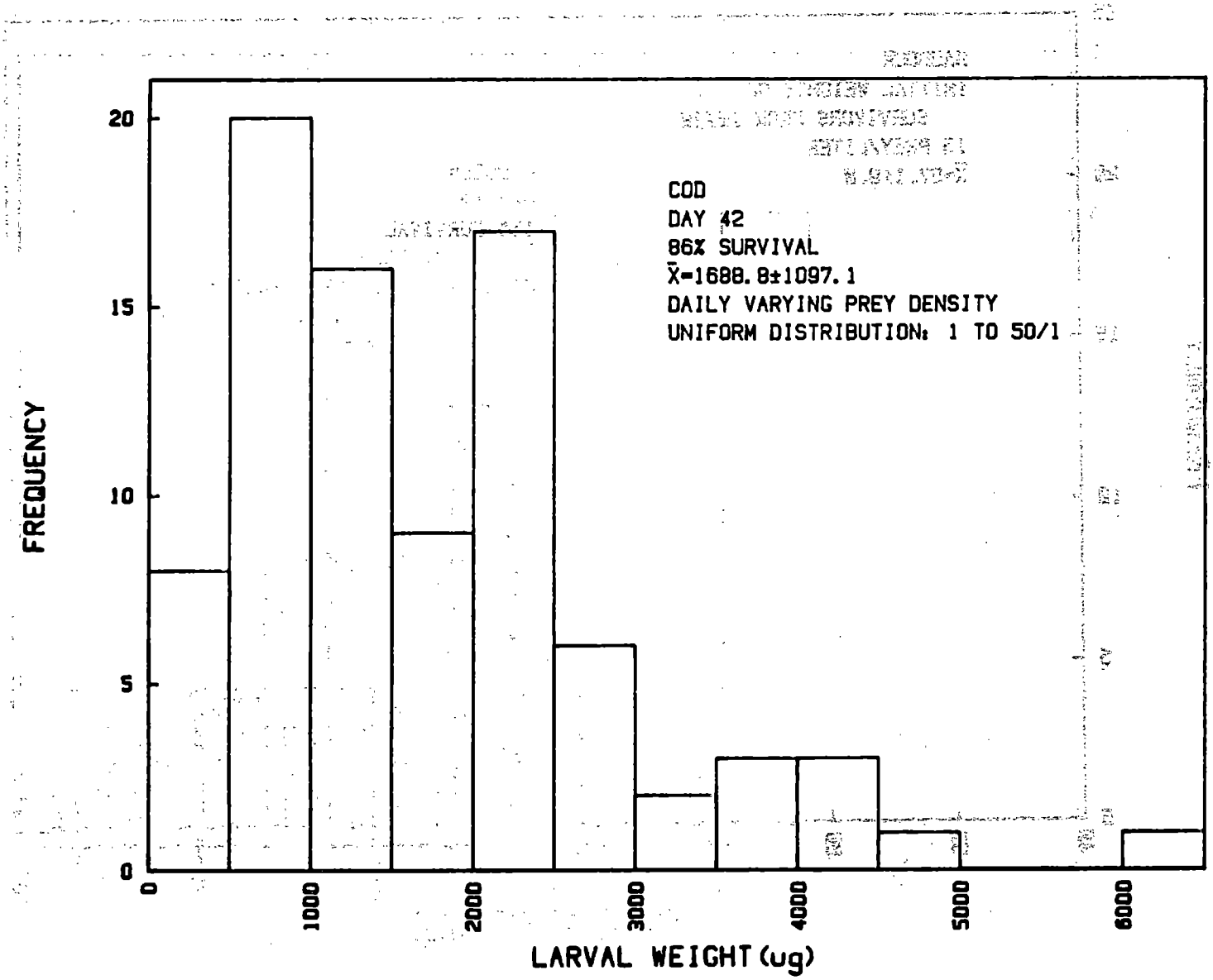

Figure 40. Frequency histogram of the distribution of weights of surviving cod larvae on day 42 from the 4 stochastic element model with a daily varying prey density.

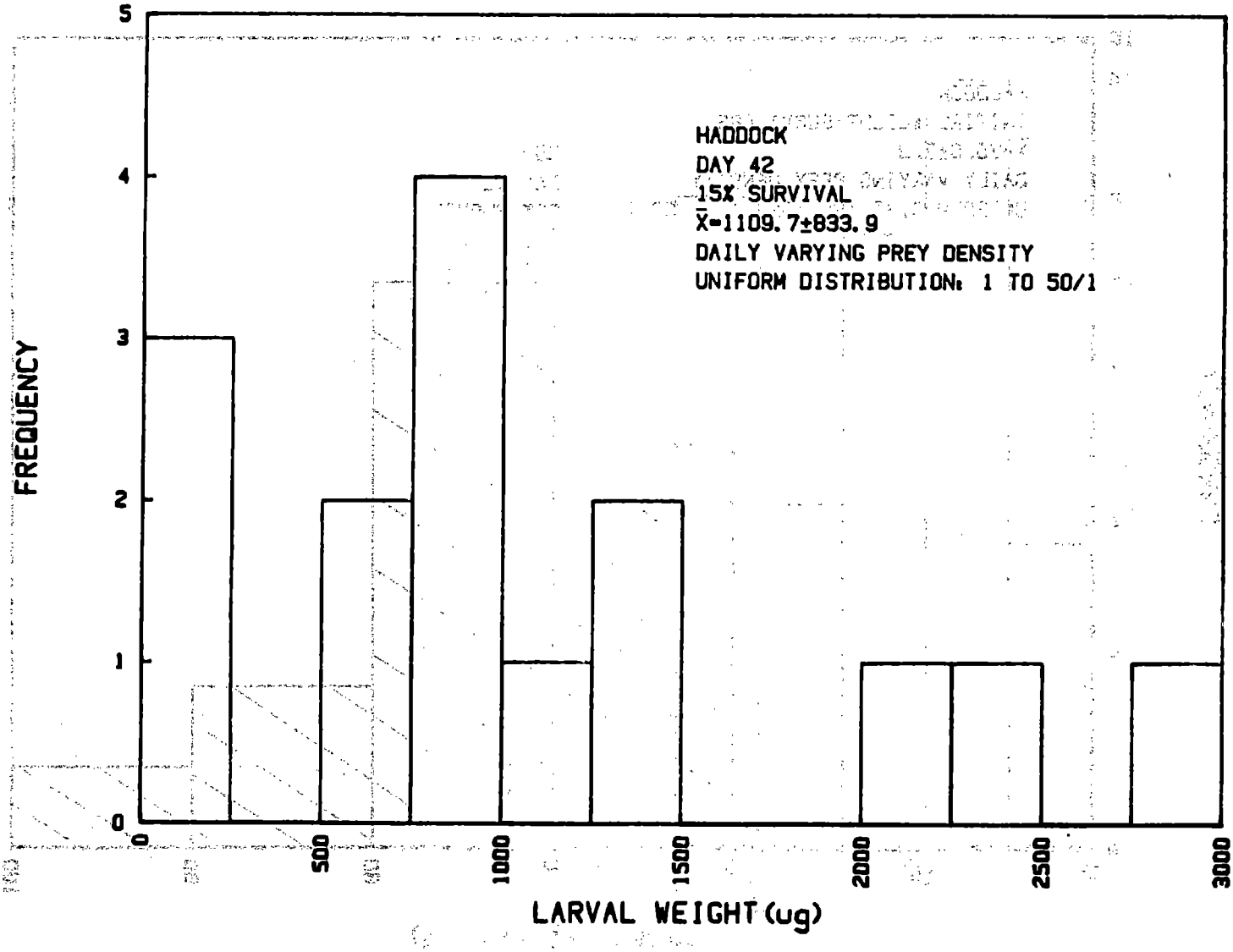

Figure 41. Frequency histogram of the distribution of weights of surviving haddock larvae on day 42 from the 4 stochastic element model with a daily varying prey density.

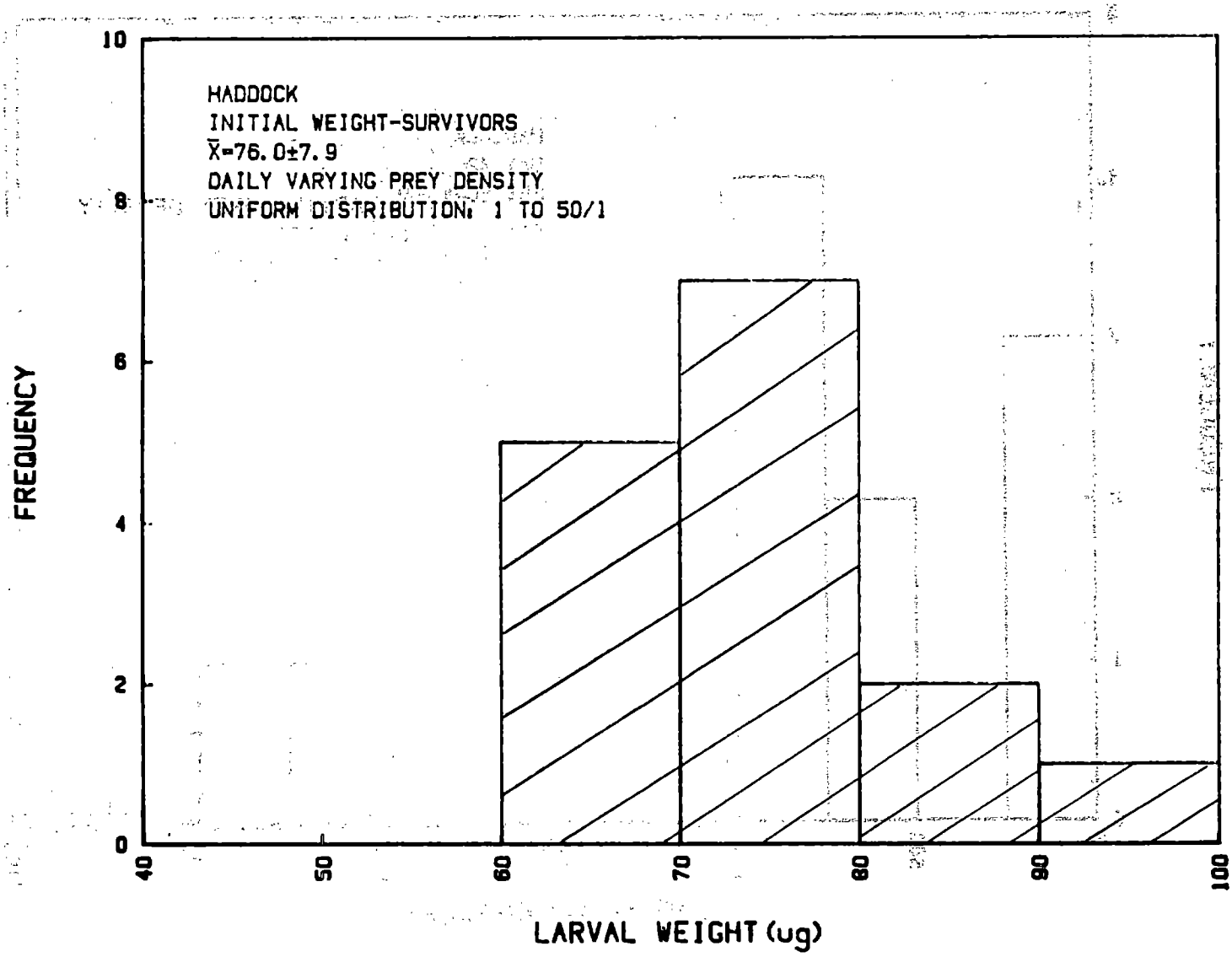

Figure 42. Frequency histogram of the distribution of initial weights of the survivors from Figure 41.

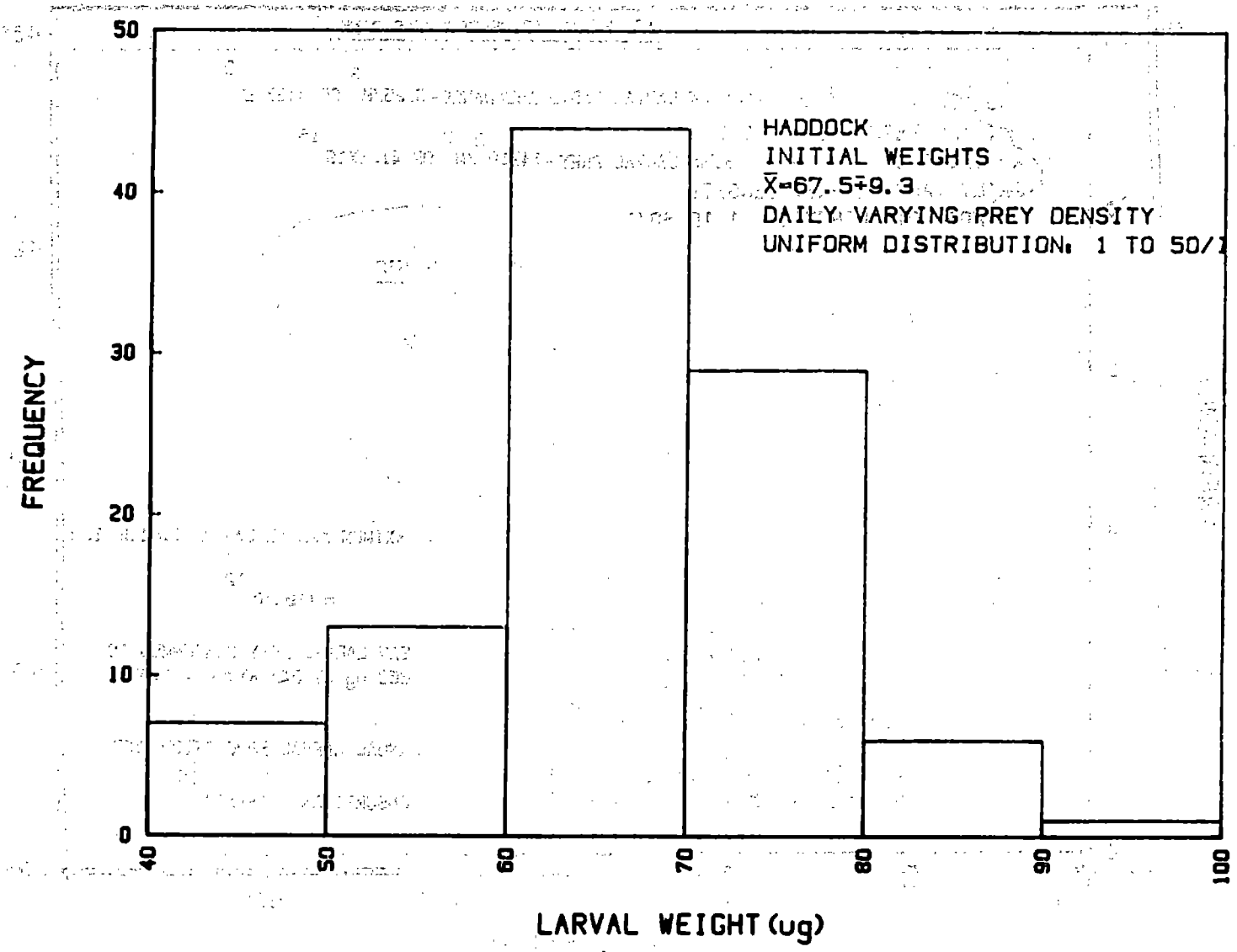

Figure 43. Frequency histogram of the distribution of initial weights of the entire population for the runs depicted in Figures 41 and 42.

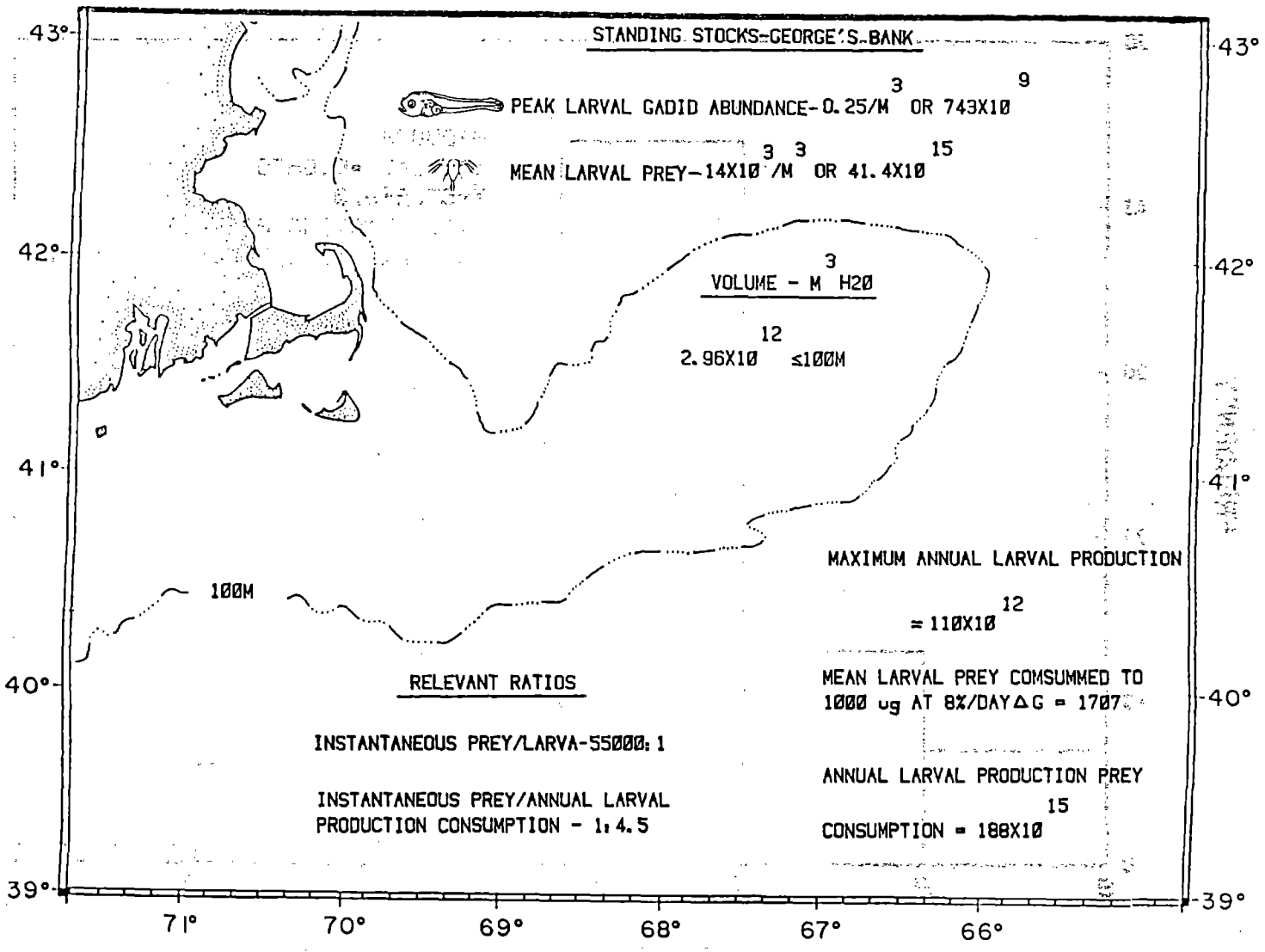

Figure 44. A graphic illustration of the parameters and calculations involved in assessing food limitation and impact on prey for larval gadids on Georges Bank.

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