Experimental Evaluation of the Impact of Macrozooplankton Predation on Mortality in Larval Capelin (*Mallotus villosus* Müller)

by

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A thesis presented to the Faculty of Graduate Studies and Research of McGill University in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy.

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ISBN 0-315-38137-X

Seule l'intuition, appuyée sur une compréhension viscérale de l'expérience, peut permettre l'établissement de lois universelles. Seul le monde des phénomenes détermine le systeme théorique.

Albert Einstein

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ABSTRACT

Large *in-situ* enclosures were designed, evaluated, and used to study the impact of jellyfish predation on mortality of larval fish at near natural scales. These enclosures accurately reproduced ambient conditions for both prey and predators and allowed the natural migratory behavior of prey to be expressed. The mortality rate of larval capelin (*Mallotus villosus*) due to jellyfish predation increased exponentially as the size of containers declined. This showed that previously published mortality rates, obtained in experiments involving small laboratory containers, were overestimated by one order of magnitude. Contrary to the findings of these laboratory studies, I found that mortality rates of larval capelin imposed by four jellyfish species were independent of larval density and unaffected by the presence of alternate prey for predators. These differences were attributed to the physical scales of my experiments which more closely approximate the *in-situ* predator-prey interactions. Mortality rates due to jellyfish predation varied between 3% and 35% per day. This variance was primarily determined by the dome-shape relationship between larval mortality rate and predator size and by higher mortality due to predation at the transition from endogenous to exogenous feeding for larval capelin. The absence of predator satiation and the linear relationship between larval mortality and predator density supports the hypothesis that predation pressure on larval fish is reduced by the selection of "safe sites" at the onset of larval drift.

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RESUME

Le développement, l'évaluation et l'utilisation de larges enclos in-situ a permis d'étudier l'impact de la prédation par les méduses sur la mortalité des larves de poissons à une échelle spatiale plus naturelle. Ces enclos reproduisent efficacement les conditions du milieu ambient pour les larves et prédateurs et permettent l'établissement du comportement migratoire des proies. La mortalité des larves de capelan (Mallotus villosus) induite par les méduses est inversement reliée à la dimension des contenants expérimentaux utilisés. Ce résultat démontre que les taux de mortalité préalablement publiés à partir de d'expériences réalisées de petits contenants de laboratoire ont été surestimés par une ordre de grandeur. Contrairement aux résultats déjà publiés, cette étude a révélé que les taux de mortalité larvaire induite par quatre espèces de méduses sont indépendants de la densité des larves et demeurent inchangés en présence de nourriture alternée pour les prédateurs. Ces différences sont attribuées aux échelles spatiales de mes expériences qui se rapprochent des interactions naturelles entre prédateurs et proies. Les taux de mortalité due à la prédation ont variés entre 3% et 35% par jour. Cette variabilité est principalement déterminée par les différences dans la taille des prédateurs et des proies. Une relation en cloche entre la mortalité larvaire et la taille des prédateurs a été mise en évidence. La susceptibilité des larves de capelan à la prédation par les méduses est plus élevée lors de la transition d'une alimentation endogène à une

alimentation exogène. L'absence de saturation du taux de prédation chez ces prédateurs ainsi que la relation linéaire entre la mortalité larvaire et la densité des prédateurs supportent l'hypothèse que la pression de prédation sur les larves de poissons est significativement réduite par la sélection de "sites sûrs" par les larves au début de la période de dérive larvaire.

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STATEMENT OF CONTRIBUTION TO ORIGINAL KNOWLEDGE

This study has made original contributions to scientific knowledge in the following ways:

1) Through successful development and evaluation of large experimental enclosures which accurately and instantaneously track the physical properties of the surrounding environment and allow the behavioral characteristics of the enclosed organisms to be expressed. This facilitates in-situ experimental studies of predator-prey and feeding studies of larval fishes at scales approximating those occurring in nature.

2) By demonstrating that the mortality rates of larval fish imposed by jellyfish predators increased exponentially as the size of the experimental containers employed declined below approximately 3 m^3, and consequently that previously published estimates of mortality rates derived from experiments that used small laboratory containers were positively biased by at least one order of magnitude.

3) By demonstrating that the predation rate of jellyfish predators is linearly related to larval density within the range of densities typically encountered in nature (Type I functional response). Previous laboratory studies had indicated that a Type II response (predator satiation) would occur in nature.

4) By providing the first experimental evidence that the relationship between larval mortality and jellyfish density is linear.

5) By demonstrating that the presence of alternate prey for jellyfish predators neither alters the shape of the functional response

nor reduces the total mortality experienced by larval fish due to predation.

6) By providing the first evidence of a dome-shape relationship between larval mortality and jellyfish size.

7) By providing the most reliable estimates to date of in-situ predation rates of jellyfish predators on larval fishes, and thereby confirming that macrozooplankton predation alone is capable of inducing the rates of mortality observed in nature.

7) By conducting the first experimental test of Frank and Leggett's (1982a) safe site hypothesis which demonstrated that the selection of safe sites by fish larvae at the onset of their larval drift significantly reduces the predation pressure imposed by macrozooplankton predators, as predicted by the hypothesis.

Acknowledgements

The realization of the field work described in this study was achieved by considerable effort of several people who assisted me and to whom I am sincerely grateful. I particularly thank Kathleen Tallon for her professional expertise at both field and laboratory work, and Carolyn Gravel, Gary Maillet, Joshua Korman, Gilles Kerhuel, Don Webb and Michael Dolan for their help in the field. I am also grateful to Tony Brisa for his workshop skill, to Robert Lamarche and Guy L´Heureux for their care at the photography.

I would also like to thank Dr. Jim Carscadden and the Department of Fisheries and Oceans Canada, St.John´s, Newfoundland and Jean-Yves Anctil and Groupe Interuniversitaire de Recherches Oceanographiques du Québec (GIROQ) for their valuable logistic support during the field work.

Financial support for this study was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC) and by the Department of Fisheries and Oceans of Canada. Personal support was provided by NSERC post-graduate scholarship and by scholarship from Fonds pour l´Aide et le Soutien à la Recherche du Québec (FCAC).

I also wish to thank my supervisory committe, Drs. W.C. Leggett, J. Kalff and D. Roff, and also Drs. R. Peters and K. Frank for their suggestions, advice and criticisms during the course of my research. My sincere thanks are also expressed to my friend and colleague Christopher Taggart whose enthusiasm for larval fish ecology has been very stimulating.

I express my sincere gratitude to my thesis supervisor, Dr. W.C. Leggett, who continously supported me financially, academically and personally.

Je voudrais aussi exprimer mes sincères remerciements à ma femme, Lucie, pour son encouragement continuel, sa patience et son amour. Cette thèse lui est tout particulièrement dédiée.

GENERAL INTRODUCTION

The relationship between interannual variability in the size of fish populations and variability in the recruiting year-classes was first established by Hjort (1914,1926). Theoretical models (Ricker 1954; Beverton and Holt 1957) originally developed to answer the question "how is recruitment related to the abundance of the spawning population?" have been shown to be unreliable management tools (Gulland 1973). The lack of clear relationship between parental stock size and recruiting year-class size in most fish populations has led to the general concensus that factors other than spawning stock size affect recruitment (Hempel 1963; Jones 1973; Lett and Kohler 1976; Gulland 1977; Sharp 1980; Ware 1980). It is now widely believed, but not yet proved, that temporal variability in recruitment is due to environmental factors which induce year to year variability in the survival of the early life stages of fish, primarily between the egg and juvenile stages (Murphy 1961; Hempel 1963; Gulland 1965; Jones 1973; Cushing 1972,1975; Ware 1975,1980; Lasker 1981; Jones 1984; Sissenwine 1984; Victor 1986).

Among the several potential causes of mortality during the early life stages of fish, starvation and predation are generally considered the major sources of death (see Ricker 1954). Although Ricker (1954) correctly noted that death cannot be ascribed to a single cause, and that more than one cause could act at the same time, researchers have consistently sought to isolate the main cause of larval mortality.

Hjort (1914,1926) proposed that mortality in larval fish was controlled by the availability of food during the "critical period" when feeding is initiated. This hypothesis has served as the basis for more

developed hypotheses such as the "match/mismatch" hypothesis (Cushing 1972,1975) and the "transport hypothesis" (Nelson et al. 1977; Bailey 1981). Despite a great deal of research dedicated to the starvation hypothesis, the supporting evidence linking starvation to interannual variability in larval mortality remains suspect (Sissenwine 1984, Leggett 1986).

The hypothesis that larval mortality could arise from predation was first investigated by Lebour (1922,1923,1925). Although her qualitative experimental work clearly indicated that several members of the planktonic community could act as potential predators of larval fish, and despite the fact that predation has been repeatedly postulated as the major cause of death at sea (Ricker 1954; Murphy 1961; Cushing and Harris 1973; Cushing 1983; Ware 1975,1980; Lett and Kohler 1976; Johannes 1978; Hunter 1984; Sissenwine 1984), this hypothesis remained largely ignored until very recently.

The hypothesis that predation is the principal agent of larval mortality derives primarily from two lines of evidence. The first is the widespread observation that numbers of pelagic fish eggs decline during incubation. As an example, the mortality of North Sea plaice eggs over eleven years (Harding et al. 1978) was shown to be highly variable, ranging from 1.8 to 12.6% per day. This resulted in survival rates which ranged from 15 to 55% over a time period of 20 days. These high and variable losses are very consistant with the predation hypothesis. Predator exclusion experiments provide the second line of evidence. Very high survival has been reported for winter flounder (78% after 20 days), dace (46% after 20 weeks), herring (96% after 30 days) and capelin larvae (65% after 20 days) stocked in in-situ enclosures or

large basins which restricted the access of large predators (Laurence et al. 1979; Mills 1982, Oiestad and Moksness 1981; Moksness 1982). These survival rates are far superior to any reported in nature. Recently Hewitt et al. (1985) attempted to partition the relative importance of starvation and predation on the mortality of jack mackerel based on the determination of sea caught larvae. They concluded that, in terms of numbers removed, predation was the most important source of death and that predation was most severe during the yolk sac phase.

During the last 15 years, both quantitative and qualitative laboratory studies and field evidence have identified the principal predators of larval fish (see reviews in Hunter 1981, 1984 and Purcell 1985). Large pelagic invertebrates (macrozooplankton) such as carnivorous copepods, euphausiids, amphipods, chaetognaths, ctenophores and coelenterates have all been shown to be voracious predators capable of killing and ingesting larval fish.

Field evidence of predation on larval fish is scarce, but Möller (1984) suggested that the impact of predation should be demonstrable in three contexts. Negative correlations between the relative abundance of predators and fish larvae should be found 1) spatially within a sampled area 2) temporally within a given area in a given year and 3) between years in a given surveyed area. Inverse relationships between various macrozooplankters and ichthyoplankton have frequently been reported (Pearcy 1962; Ali Khan and Hempel 1974; Theilacker and Lasker 1974; Möller 1980,1984; Alvarino 1981; Arai and Hay 1982; van der Veer 1985). However, the validity of this evidence has recently been questionned by Frank and Leggett (1985) who argued that reciprocal oscillations in relative densities may occur because predators and prey occupy distinct

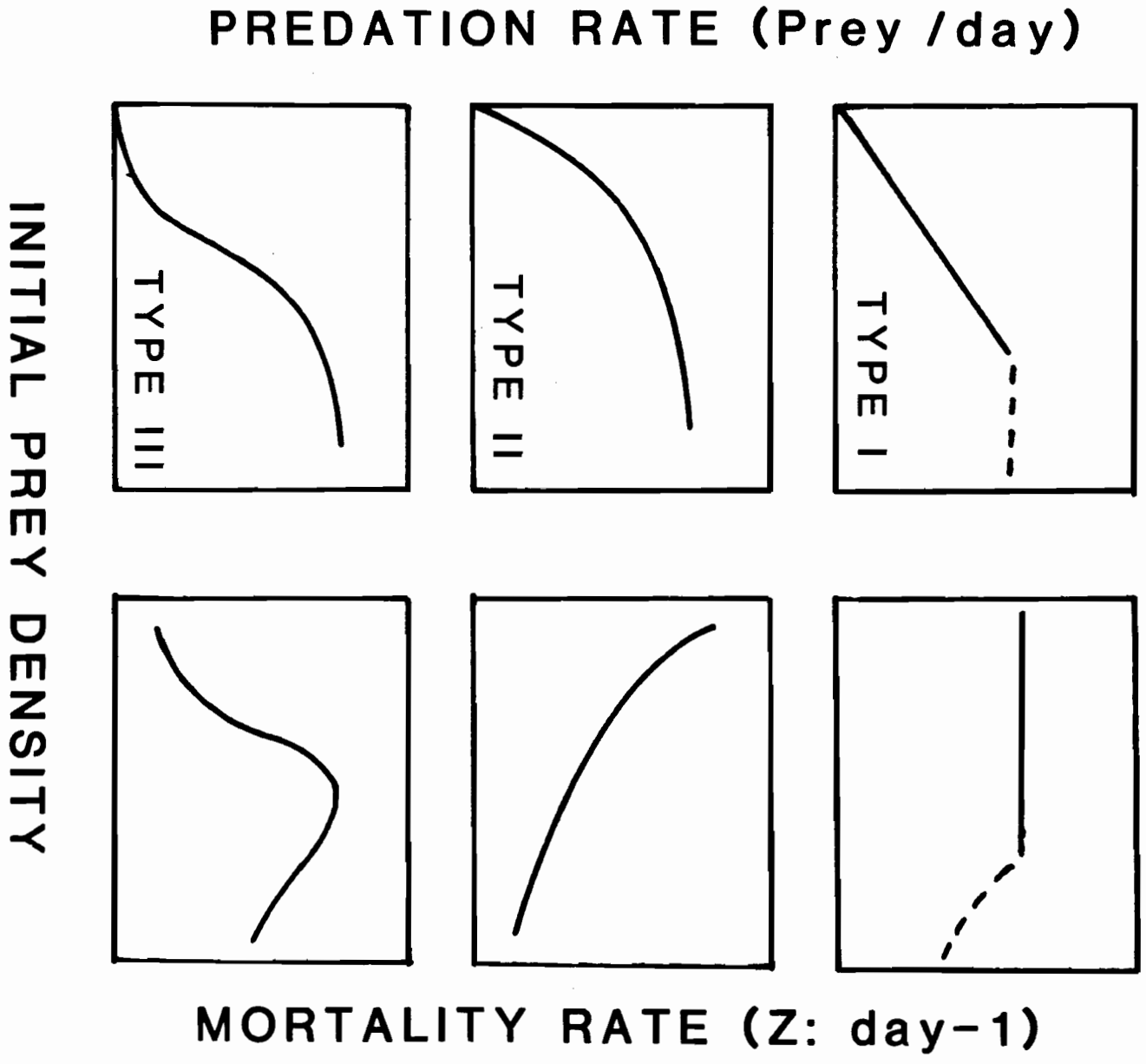
water masses which vary spatially and temporally. Frank and Leggett (1985) further suggested that these negative correlations between predators and prey may reflect an adaptive response of spawning adults or larvae to historical patterns of predation. Frank and Leggett (1982a,1983) had previously shown that larvae of several fish species responded to reliable environmental signals in ways which synchronized the onset of larval drift with the occurrence of specific water masses in which the density of predators was greatly reduced. These water masses, which are typically rich in potential food items for larvae, were designated "safe sites" for larval fish (Frank and Leggett 1982a,1985). The synchronous emergence of larval fish into such water masses in order to minimize the impact of predation mortality has also been observed in coral reef fish (Johannes 1978).

Field estimates of mortality to larval fish based upon gut content analyses of potential predators suggest relatively high removal rates. Hartig et al. (1982) found that up to 16% of alewife larvae in-situ were attacked by cyclopoid copepods. The estimated daily loss of sand eel larvae due to predation by hyperiid amphipods varied between 0.1 and 45% per day depending on the degree of overlap in the distribution (Yamashita et al. 1985). The jellyfish Aurelia aurita was estimated remove between 2 and 5% of a larval herring stock (Møller 1980) and larval removal rates of 28 and 60% per day were calculated for two other species of medusae (Purcell 1981,1984). However, these estimates assumed constant feeding rates and are strongly dependent on estimated digestion rates. Moreover, the impact of spatial and temporal variability in the distribution and size of both predators and prey are rarely accounted for in these calculations. With the exception of studies of individually

collected jellyfish (Purcell 1981,1984), estimates of predation may be positively biased by "net feeding" during collection (Nicol 1984).

The most direct approach to estimating larval mortality due to predation has been to quantify the predation rate under experimental conditions. The relationship between the number of prey taken by a predator and prey density defines the functional response of a predator. Holling (1959,1961,1965,1966) proposed three basic types of functional responses (Figure 1). These have been experimentally observed in various animals species (reviews in Murdoch and Oaten 1975 and in Arditi 1982). The predation rates of large invertebrate predators fed on larval fish were found to increase with prey density in a manner characteristic of a type II functional response in all cases studied to date. However, the extrapolation of these laboratory results to field situations has been questionned because the majority of the experiments upon which these observations were drawn were conducted in relatively small (0.2 to 5 liter) containers (Solemdal 1981; Hunter 1984; Purcell 1985). Moreover, the larval densities at which maximum predation rates were observed consistently exceeded those reported in nature. Finally, the small size of laboratory containers used to date precludes the use of large predators and makes use of delicate gelatinous predators difficult. The majority of the laboratory studies conducted to date have thus used the smallest forms of potential predators (copepods, euphausiids, amphipods, chaetognaths and relatively small medusae). It has been repeatedly recommended that studies of the effect of predators on survival of larval fish should be investigated at larger scales and preferably under controlled in-situ conditions (Solemdal 1981; Hunter 1984; Purcell 1985).

Figure 1. Three types of functional response relating predation rate to prey density as described by Holling (1959). The prey mortality rate as a function of prey density is also presented for each type.


PREDATION RATE (Prey /day)
INITIAL PREY DENSITY
TYPE III
TYPE II
TYPE I
MORTALITY RATE (Z: day-1)

When properly investigated, quantitative knowledge of the functional response could be linked with data on the numerical response, which relates the variation in predator density as a function of prey density, thereby leading to a comprehensive evaluation of the interaction between predators and prey (Murdoch and Oaten 1975, Hassell et al. 1976; Hassell 1978; Murdoch et al. 1984).

Preliminary experimental investigations of the mortality experienced by capelin larvae due to predation by ctenophores were conducted by Frank and Leggett (1982a) who used large (3.2 cubic meters) in-situ enclosures. Their results indicated that mortality was inversely related to the initial density of larvae offered. Frank and Leggett (1982a) suggested that the mass release of capelin larvae in open waters could be an adaptation which served to satiate the predators present in the "safe" water mass. Predator satiation by means of synchronous release of numerous reproductive products has been frequently suggested for other predator prey systems (Janzen 1978; Johannes 1978; Sweeney and Vannote 1982; Forward et al. 1986). The "safe-site" hypothesis implicitly suggests that the impact of predation on larval survival is very important. Although the lines of evidence presented above tend to support this view, the role of predation as a regulator of larval survival remains controversial due to the problems inherent to all approaches used to study the problem to date.

Fish larvae are rapidly dispersed in the marine environment. It has therefore been suggested that their low densities should elicit little or no aggregative (numerical) response from predator populations (Murphy 1961; Hempel 1965; Harding and Talbot 1973; Cushing 1983). If true, larval fish would be subject to the same predation rates as are

other organisms in the plankton. These rates would thus be proportional to predator numbers (Hempel 1963; Jones 1973; Ware 1975,1980).

Due to their great abundance and their wide distribution in marine ecosystems, macrozooplankton predators are often cited as the most important "potential" predators of fish eggs and larvae (Harding and Talbot 1973; Möller 1980,1984; Purcell 1985). Modelling studies conducted by Cushing and Harris (1973) indicated that the densities of carnivorous zooplankton required to yield larval mortality rates of 5% per day were one or two orders of magnitude higher than those normally observed in nature. They concluded that the "true" predators of larval fish were other fish rather than carnivorous zooplankton. At that time, the lack of knowledge on the feeding of the potential predators precluded the evaluation of the assumptions concerning searching and ingestion rates used in their model. More recent estimates of larval mortality based on laboratory studies of predation rates and on estimated densities of both predators and prey in-situ suggest that high mortality rates could be caused by macroinvertebrate predators (euphausiids - Theilacker and Lasker 1974; copepods - Bailey and Yen 1983; amphipods - von Westernhagen and Rosenthal 1976) even at natural densities. However the impact and the role of predation by macrozooplankton on larval fish survival remains a matter of debate principally because of uncertainty concerning the wisdom of extrapolating laboratory results to natural situations. The influence of predator density, predator size and the presence of alternate food on larval mortality due to predation have been also largely neglected in most previous studies.

Given the importance of larval mortality in determining the

dynamics of fish populations and the inadequate state of knowledge of the importance of predation as a regulator of this mortality, I designed this study to answer questions regarding the impact of macrozooplankton predation on the survival of early life stages of fish. Specifically, the goals of my research were:

1) to develop large in-situ enclosures suitable for studies of larval fish at scales larger than had previously been realized.

2) to evaluate the effect of experimental container size larval fish mortality induced by macrozooplankton predators.

3) to measure and compare the larval mortality rates induced by different species of macrozooplankton predators in these large-scale in-situ enclosures.

4) to evaluate the effect of larval density, predator density, presence or absence of alternate prey, and predator size on the larval mortality imposed by macrozooplankton predation.

5) to identify the principal variables controlling the predator/prey interactions between macrozooplankton and larval fish.

The research was conducted at Bryants Cove, Newfoundland. Capelin (Mallotus villosus Muller) larvae were selected as prey. Capelin are an excellent choice for this type of study because:

1) The species is commercially important along the east coast of Canada and exhibits large interannual recruitment variability (Leggett et al. 1984).

2) Spawning occurs on beaches. The larvae hatch after an incubation period of 10-20 days, and remain in the beach sediments for various times before emergence and the onset of drift (Frank and Leggett 1981). Larvae are therefore readily available for experimental use for 4-6

weeks each year. This eliminates the costly and difficult task of artificially rearing larvae.

The predator species selected were Catablema vesicarium, Cyanea capillata, Staurophora mertensi and Aurelia aurita. These Coelenterate species have been identified as potential predators of larval fish (Lebour 1922,1923; Fraser 1969; Purcell 1985). They are ubiquitous in temperate marine coastal waters and are commonly observed along the east coast of Canada (Shih 1977). They occur in surface waters and single individuals can be easily captured by scuba diving, without damage or stress.

The results of this study are presented in three chapters each prepared as an original manuscript for submission to a scientific journal. This is in accord with section 7 of the Guidelines Concerning Thesis Preparation, Faculty of Graduate Studies, McGill University, which states:

> "The candidate has the option, subject to the approval of the department, of including as part of the thesis the text of an original paper, or papers, suitable for submission to learned journals for publication. In this case the thesis must still conform to all other requirements explained in the Guidelines Concerning Thesis Preparation. Additional material (experimental and design data as well as descriptions of equipment) must be provided in sufficient detail to allow a clear and precise judgement to be made of the importance and originality of the research reported. Abstract, full introduction and conclusion must be included, and where more than one manuscript appears, connecting texts and common abstracts, introduction and conclusions are required. A mere collection of manuscripts is not acceptable; nor can reprints of published papers be accepted.
>
> While the inclusion of manuscripts co-authored by the candidate and others is not prohibited by McGill, the candidate is warned to make explicit statement on who contributed to such work and to what extent, and supervisors and others will have to bear witness to the accuracy of such claims before the oral committee. It should also be noted that the task of the External Examiner is made much more difficult in such cases, and it is in the candidate's interest to make authorship responsabilities perfectly clear."

A general introduction and conclusion have been added and figures and tables have been inserted as part of the text to facilitate readability.

Chapter 1 has been accepted for publication by the Canadian Journal of Fisheries and Aquatic Sciences (de Lafontaine, Y. and W.C. Leggett. 1987. Evaluation of in-situ enclosures for larval fish studies). Chapter 2 has been submitted to the same journal and is presently under review (de Lafontaine, Y. and W.C. Leggett. Effect of container size on mortality rate and predation rate by macrozooplankton on larval fish). Chapter 3 will be submitted for publication in the near future. An Appendix "Changes in umbrella dimensions and weight of planktonic coelenterates during formalin preservation" (de Lafontaine and Leggett) detailing the results of a study undertaken to resolve a methodological problem relative to preservation effects has recently been submitted to the Journal of Plankton Research.

This study was developed and executed by the author of this thesis. My supervisor contributed in an advisory and editorial capacity, participated in some phases of the field work, and provided the funds necessary to realize the work.

The results of this research have been presented in annual seminars at the Department of Biology, McGill University. Portions of this material have also been presented at the scientific meetings listed below:

de Lafontaine, Y. 1986. Predation mortality in larval fish: a look at different scales. Presented at the Hunstman Marine Laboratory Marine Science Symposium, St.Andrews, N.B. June 3-5, 1986. (Contributed paper; publ. abstr.).

de Lafontaine, Y. 1983. Macrozooplankton predation on larval fish: the effect of larval density. Presented at the 46th Annual Meeting of the American Society of Limnology and Oceanography, St.John's, Nfld. June 13-16, 1986. (Contributed paper; publ. abstr.).

CHAPTER 1

Evaluation of *in-situ* enclosures for larval fish studies.

INTRODUCTION

In-situ estimation of mortality during the early larval stages of fish is made difficult by the sampling effort necessary to cover both spatial and temporal fluctuations in distribution and abundance of natural populations. Even when successful, such approaches yield only averaged results and cannot account for short-term variability resulting from the dynamic nature of the physical environment (Taggart 1986). An alternative approach, the tracking of distinct cohorts of larvae while monitoring their abundance over time, may provide more accurate estimates (Shelton and Hutchings 1982; Fortier and Leggett 1985), but the method is not yet well proven. Neither approach yields much in the way of concrete knowledge of the causes of mortality observed. Direct knowledge of the relationships between physical and biological events and larval mortality is best developed through manipulative experiments. Extending the results of small-scale laboratory experiments to field situations has been difficult, however, and larger-scale experiments have been recommended as a possible solution (Solemdal 1981; Oiestad 1982, Houde and Berkeley 1982). The growing use of in-situ enclosures to study the early life history of fishes (Table 1) reflects this reality.

The enclosures used to date in various studies on plankton dynamics and pollution have varied in size, volume, wall material and porosity (Grice and Reeve 1982), but they can be classified into three main types: 1) "non porous" plastic enclosures which eliminate virtually all water exchange with the surrounding environment, 2) "low porosity" enclosures which permit limited water exchange with surrounding medium

(sailcloth bags), 3) "high porosity" enclosures, typically constructed of nylon mesh material, which allow rapid water exchange and selective exchange of plankton.

Any enclosure design will introduce artificialities in the physical and chemical conditions and the biological dynamics of the water column (Banse 1982; Gamble and Davies 1982; Mullin 1982). Non-porous plastic enclosures are particularly prone to create differences in the physical (temperature, salinity, stratification) and chemical (oxygen levels, pH) properties of the enclosed water relative to the outside conditions through impedence of diffusion (Takahashi et al. 1975; Takahashi and Whitney 1977; Steele et al. 1977; Gieskes and Kraay 1982; LeCohu 1982). Most enclosures, regardless of their porosity, significantly reduce horizontal patchiness (Grice et al. 1977,1980; Oviatt et al. 1977; Stephenson et al. 1984) and restrict the evolution of populations to the vertical dimension. Vertical patchiness varies with enclosure type and plankton species (Takahashi et al. 1975; Grice et al. 1977; Brockmann et al. 1977; Laurence et al. 1979; LeCohu 1982; Harris et al. 1982). The distribution of larval fish in enclosures is poorly described. Gamble and Houde (1984) found that cod larvae were mainly concentrated in the top 7 m of a 20 m deep non-porous enclosure, but the vertical distribution of fish larvae in relation to diel changes or to different bag size remains unknown.

The characteristics of the "ideal" enclosure should allow 1) good replication among enclosures, 2) good reproducibility of the natural environment 3) the ability to establish a representative community and 4) observation of predator-prey relations at natural densities and ratios (Walde and Davies 1984). Replicability and reproducibility have

often been inversely related in enclosure work (Kuiper et al. 1983, Hulbert 1984). Researchers who have been interested in studying interactions between trophic levels or in the behavior of larger but scarcer organisms have typically employed large scale enclosures whose high cost and logistic demands have precluded the use of replicates (Gamble and Davies 1982), and which frequently failed to accurately reproduce the surrounding physical and chemical environment. These workers have justified this approach by arguing that the important consideration is how enclosures duplicate each other and not how closely they duplicate the outside environment (Menzel 1977; Menzel and Steele 1978). However, the mounting evidence of the potential effect of short term physical and biological events on larval growth and survival (Lasker 1975; Frank and Leggett 1982a; Fortier and Leggett 1984,1985) strongly suggests that an ideal enclosure for larval fish studies should accurately reproduce the dynamics of the physical and chemical characteristics of seawater and, at the same time, act as a barrier to biological material for manipulation purposes. Careful evaluation of the effect of enclosure design on the characteristics of the physical and biological systems enclosed, and on the behavior of enclosed organisms is thus required if results from trophic studies using enclosures are to be applied to natural systems (Solemdal 1981; Hulbert 1984).

In this chapter I describe and evaluate an enclosure specifically designed for the study of the growth and mortality of larval fish in-situ. I first report the capability of this enclosure to track and reproduce natural variations in the physical properties of the surrounding seawater. I then evaluate the behavioural characteristics of organisms inside the enclosure, relative to their behavior at liberty.

Table 1. Summary of enclosure types and uses for larval fish study

Enclosure description: Wall Material	Z: depth(m) D: diameter(m) V: volume(m^3)	Duration (days)	Study objectives	Species	Reference
Non-porous bags					
Black polyethylene	Z: 2.5 D: 0.95 V: 1.8	10-32	Growth,mortality	Herring	Oiestad and Moksness 1981
		26	Growth	Turbot	Rosenberg and Haugen 1982
		18-42	Survival	Capelin	Oiestad 1985
Transparent PVC bags (Loch Ewe)	Z: 19.5 D: 4.75 V: 310	50-60	Growth,feeding	Herring	Gamble et al. 1981
		60-80	Growth,feeding	Herring	Gamble et al. 1985
		86	Lipids content	Herring	Gatten et al. 1983
		56	Otolith growth	Herring	Geffen 1982
		30	Growth,feeding	Cod	Gamble and Houde 1984
Transparent polyethylene (CEPEX)	Z: 23.5 D: 10 V: 1300	31	Growth,feeding	Herring	Houde and Berkeley 1982
		45	Growth,	Salmon	Koeller and Parsons 1977
Porous bags					
White polyester	Z: 3.0 D: 2.0 V: 6.0	76	Survival	Herring	Schnack 1981
White dacron	Z: 5.0 D: 1.0 V: 3.2	7-10	Growth,survival	Capelin	Leggett 1986

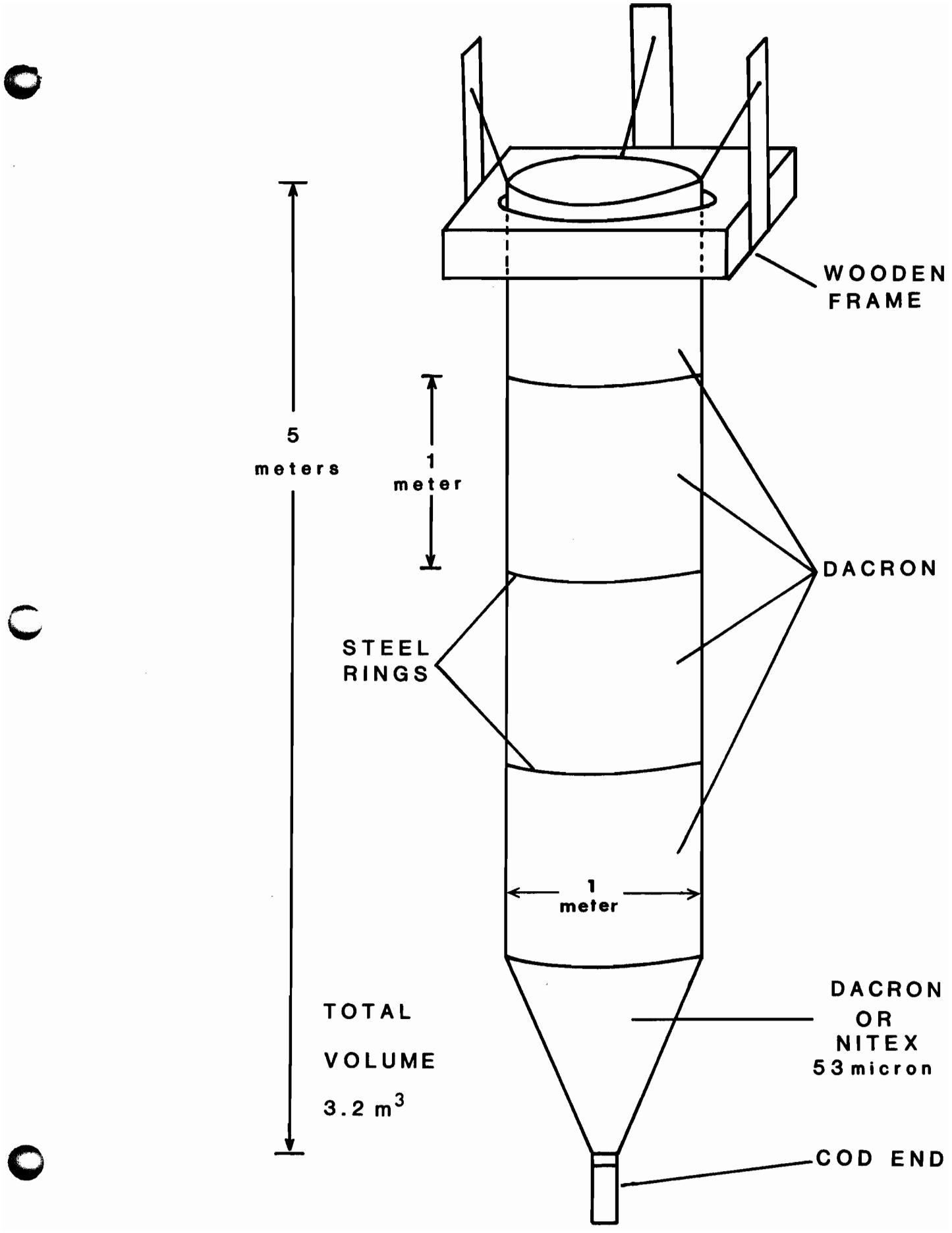
Table 1. (suite)

Enclosure description: Wall Material	Z: depth(m) D: diameter(m) V: volume(m^3)	Duration (days)	Study objectives	Species	Reference
Nitex 153 µm mesh	Z: 5.0 D: 1.0 V: 3.2	3	Predation mortality	Capelin	Frank and Leggett 1982a
Nitex 505 µm mesh	Z: 6.0 D: 1.7 V: 11.5	14	Survival	Winter flounder	Laurence et al. 1979
Green knotless mesh, 9 & 19mm	Z: 12.0 D: 3.1 V: 90.0	41	Feeding	Salmon	English 1983
Basins					
Norwegian concrete basin	Z: 4.5 V: 4400	130-180	Growth, survival	Cod	Ellertsen et al. 1981
		73	Growth, survival	Herring	Oiestad and Moksness 1981
		89	Otolith growth	Herring	Geffen 1982
		15-20	Condition factor	Cod	Oiestad 1984
		100	Multispecies interaction	Capelin-Herring	Oiestad 1985
same as above	Z: 5.0 V: 2200	11	Growth, survival	Turbot	Rosenberg and Haugen 1982
		127	Growth, survival	Capelin	Moksness 1982

MATERIALS and METHODS

The enclosures employed were 1 m in diameter, 5 m deep, and consisted of four cylindrical sections and a conical bottom section, giving a total internal volume of 3.2 cubic meters (Figure 1). The cylindrical sections were constructed from white Dacron sailcloth which mesh aperture varies between 15 and 34 µm (average 25 µm) giving a porosity of 0.017. Two types of conical sections were used: one was constructed of Dacron and the second of 53 µm Nitex having a porosity of 0.265. A 10 cm band of raw (untreated) canvas was sewn to the external side of the enclosures at 1 m intervals. A 6 mm solid steel ring was lashed to each canvas band to support the enclosure walls. The enclosures were supported at sea in pairs by a floating wooden frame anchored to the sea bottom. The frames were joined in pairs thereby creating a four enclosure platform on which two persons could stand and work with ease. A 10 cm diameter PVC cod-end collector with a side window of desired mesh size, was attached to the bottom of the enclosure to facilitate recovery of the experimental organisms at the end of the experiment. To prevent the organisms from becoming trapped in the cod-end during the experiment, a tight fitting plug was installed over the cod-end from the inside of the enclosure before deployment. Prior to lifting the enclosure at the end of an experiment, the plug was pulled using a line running to the surface. I allowed the enclosures to fill by diffusion of water through the walls. This required about 1.5 h for the full Dacron type, and less than 5 min for the Nitex cone type.

Figure 1. Specifications of the experimental enclosure.


WOODEN
FRAME
5
meters
1
meter
DACRON
STEEL
RINGS
1
meter
TOTAL
VOLUME
3.2 m3
DACRON
OR
NITEX
53 micron
COD END

The Dacron/Nitex enclosures were hauled by hand with two persons holding one section at a time and a third rinsing the inside walls. Rinsing seawater was continuously pumped from the surrounding waters and passed through a series of 3 filters of 153, 53 and 20 μm. The hauling procedure was completed in 15 min. The Dacron enclosures were lifted with block and tackle fixed to a portable wooden A-frame installed on the floating platform. Once one section was out of the water and rinsed, the block and tackle was attached to the next steel ring and the rinsed section was folded down. This process was repeated until the conical section holding the 20 μm cod-end was out of the water. The hauling operation required about 1.5 h per enclosure. The cost for one complete enclosure of either design was approximately $Can. 1500.

Diffusibility experiment

Two enclosures of each design were moored in the nearshore waters at Bryant's Cove, Newfoundland (47°40'36"N, 53°11'24"W) on June 20th, 1983, at 15:00 local time (11:00 GMT). Sampling was initiated at 18:00 EAT and was repeated every three hours for 24 h and then on a daily basis (at approximately 9:00 local time) for 6 consecutive days. Temperature, salinity and dissolved oxygen were measured at depths of 0, 1, 2, 3, 4 and 5m both inside and outside the enclosures. A Parr diaphragm pump (flowrate of 3 L/min) was used to collect 500 ml water samples at 0.5, 2.5 and 4.5 m depths inside and outside the enclosures. These samples were used to construct vertical profiles of fluorescence, chlorophyll *a* and particulate matter. Relative fluorescence was measured with a Turner Design model 10 fluorometer and chlorophyll *a* was

determined by fluorometric techniques (Parsons et al. 1984). Replicate (250 mL) subsamples were preserved with 2% unbuffered formaldehyde seawater solution for subsequent particulate matter analysis. Particle concentrations in 20 size classes ranging from 2.0 to 161 μm equivalent spherical diameter (e.s.d.), were determined with a Coulter model TA-II counter fitted with 100 and 400 μm aperture tubes. Prior to counting the preserved sample was gently but thoroughly mixed, filtered through a 153 μm filter, and split into two equal fractions. One fraction was processed on the 400 μm tube at a flowrate of 0.56 mL/s, until 2.0 mL of the sample had been counted. The second fraction was sieved again on a 43 μm filter and counted with the 100 μm aperture tube using the manometer (0.5 mL) mode of operation (Sheldon and Parsons 1967a). Replicate counts were made on each sample and the resulting counts were averaged. Total particle biomass expressed in ppm/vol was estimated from the sum of volumes of each size class.

Behavior experiment

The diel vertical distribution of yolk-sac capelin (Mallotus villosus) larvae was examined in three experiments conducted in 1982, 1983 and 1984. Four full-Dacron enclosures were used in 1982. Four Dacron/Nitex enclosures were employed in 1983 and one in 1984.

Larvae were collected from the capelin spawning beach at Bryant's Cove and stocked into each enclosure (1500/enclosure in 1982 and 1984; 2500 in 1983). A separate sample of not less than 100 larvae was collected at the same time and these larvae were measured to the nearest 0.1 mm total length (TL) to determine the initial size of the stocked

larvae. In 1984, wild zooplankton collected from the surrounding seawater with a large-volume plankton pump (Taggart and Leggett 1984) and filtered on 1 mm screen filter was added to the enclosures with the larvae.

Vertical distribution of larvae and plankton was assessed by pump sampling within pre-determined layers: surface (0-1m), mid-depth (2-3m) and bottom (4-5m). All samples (74 L) were collected with a Jabsco submersible pump having a mean flowrate of 37 L/min, and were preserved immediately in a 4% formaldehyde seawater solution buffered with sodium borate. Zooplankton counts were made with a Coulter model TA-II particle counter using a 2000 μm aperture tube. This yielded counts for plankters of 10 size classes ranging from 80 to 520 μm equivalent spherical diameter.

Data on the vertical distribution of both zooplankton and fish larvae were expressed as the proportion taken at depth for each sampling session. Arc-sine transformation (Sokal and Rohlf 1981) was applied on proportion data prior to an analysis of variance of differences between years and enclosures. I tested for deviations from a hypothetical distribution having equal proportions at each depth with a chi-square test (Sokal and Rohlf 1981).

RESULTS

The physical and biological properties of the waters in Bryant's Cove are temporally dynamic on a short time (2-6 days) scale (Taggart 1986). During offshore winds deep, cold, high saline water upwells in the cove. This water mass is characterized by relatively low abundance of particles in the <150 µm size classes. During onshore winds warm surface waters are advected onshore. These waters are characterized by high concentrations of particles <150 µm (Frank and Leggett 1982a). On average, the chlorophyll and particle concentrations in the Cove under either wind condition were much lower than those reported for estuarine (Chanut and Poulet 1982) or other coastal waters (Sheldon and Parsons 1967b; Maysaud et al. 1984), but more similar to oligotrophic oceanic waters (Flos 1984; Sheldon 1984). Evidence of these rapid temporal changes in the physical and biological characteristics of the waters outside the enclosures is given in Figure 2.

Temperature, Salinity, and Oxygen

The waters contained in both enclosure designs responded almost immediately to outside fluctuations in temperature, salinity and dissolved oxygen (Figure 2a,b,c). Correlation analysis for the hourly portion of the record (hour 1-24) revealed highly significant ($p<0.001$) coefficients between outside and inside conditions. When lags of 3 and 6 h were introduced, coefficients became nonsignificant ($p>0.1$), indicating a time response of less than 3 h. The effects of time, enclosure and sample depth on the overall variability of each parameter were tested by a three-way analysis of variance (Table 2). The time

Figure 2. Temporal variation in physical and biological properties at middepth (2m) inside and outside the experimental enclosures.

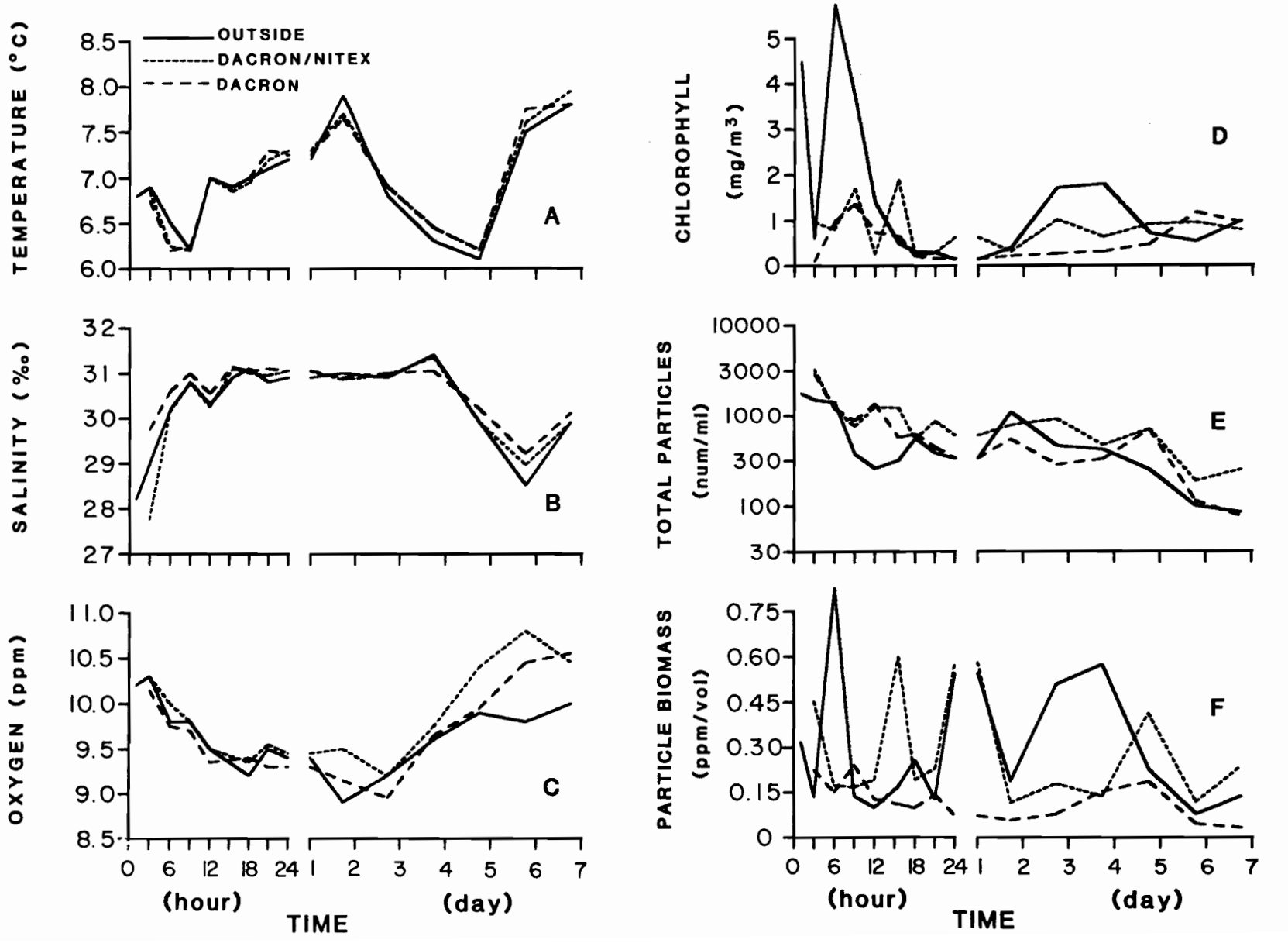

OUTSIDE
DACRON/NITEX
DACRON
TEMPERATURE (°C)
8.5
8.0
7.5
7.0
6.5
6.0
A
SALINITY (‰)
32
31
30
29
28
27
B
OXYGEN (ppm)
11.0
10.5
10.0
9.5
9.0
8.5
C
0 6 12 18 24
(hour)
1 2 3 4 5 6 7
(day)
TIME
CHLOROPHYLL (mg/m³)
5
4
3
2
1
0
D
TOTAL PARTICLES (num/ml)
10000
3000
1000
300
100
30
E
PARTICLE BIOMASS (ppm/vol)
0.75
0.60
0.45
0.30
0.15
0
F
0 6 12 18 24
(hour)
1 2 3 4 5 6 7
(day)
TIME

Table 2. Percentages of the sum of squares for the effect of time, enclosure and depth from a 3-way ANOVA of physical and biological properties. Chlorophyll and particle data were normalized by logarithmic transformation (log X+1) prior to the analysis.
Symbols are: Temp. - temperature; Sal. - salinity; D.O. - dissolved oxygen; R.F. - Relative fluorescence; Chl. - chlorophyll a. Significant variances (F-test): underlined = $p<0.0001$, ** = $p<0.01$, * = $p<0.05$.

Factor	Temp.	Sal.	D.O.	R.F.	Chl.	Particle Number	Particle Biomass
Time	70.34	78.24	56.92	38.34	24.77	47.02	7.90**
Enclosure	0.44	3.83	1.72	15.90	5.39	3.76	6.95
Time X Enclosure	0.50	8.06	4.17	11.28**	12.39*	6.05	10.67**
Depth	20.66	4.11	23.23	0.30	0.17	2.69	2.59**
Time X Depth	6.10	2.09	3.98	7.17	16.64**	7.58	5.49
Enclosure X Depth	0.34	0.58	1.88	0.20	1.76	2.00**	1.66
Time X Enclosure X Depth						5.98	8.07

effect explained 57-78% of the overall variance; less than 5% was explained by enclosure effects.

The internal and external vertical profiles of each physical variable, based on time averaged data, were similar (Figure 3a,b,c). The differences between enclosures at depths of 0, 2 and 5 m were tested by an analysis of variance followed by a GT2 multiple comparison test (Sokal and Rohlf 1981) (Table 3). In order to filter the temporal component of variability in the data, the analysis was performed on the residual values between the observed values of an enclosure and the mean value of all enclosures for each sampling time. On average, temperature differences were observed mainly at the bottom. The waters enclosed by the full Dacron enclosures were consistently, but only slightly more saline (0.3 0/00) than the surrounding waters at all depths, and dissolved oxygen levels were slightly higher (0.15-0.5 ppm) inside the Dacron/Nitex type. A Spearman rank correlation used to test whether the temporal events at 2 m shown in Figure 2 were also observed at other depths inside the enclosures reveals very strong correlation ($p<0.001$) between depths for all physical variables.

Chlorophyll and Particulate matter

Chlorophyll a concentrations, particle number and biomass (Figure 2d,e,f) were all more variable outside than inside the enclosures. The variance explained by the time effect was lower (8-47%) than was the case for the physical variates and the enclosure effect (either alone or its interactions) was more pronounced (Table 2). There were no significant ($p>0.1$) correlations between values of the biological variables measured outside and inside the enclosures. Time lags of up

Figure 3. Vertical profiles of physical and biological properties averaged over time inside and outside the enclosures. Curves are as defined in Figure 2.

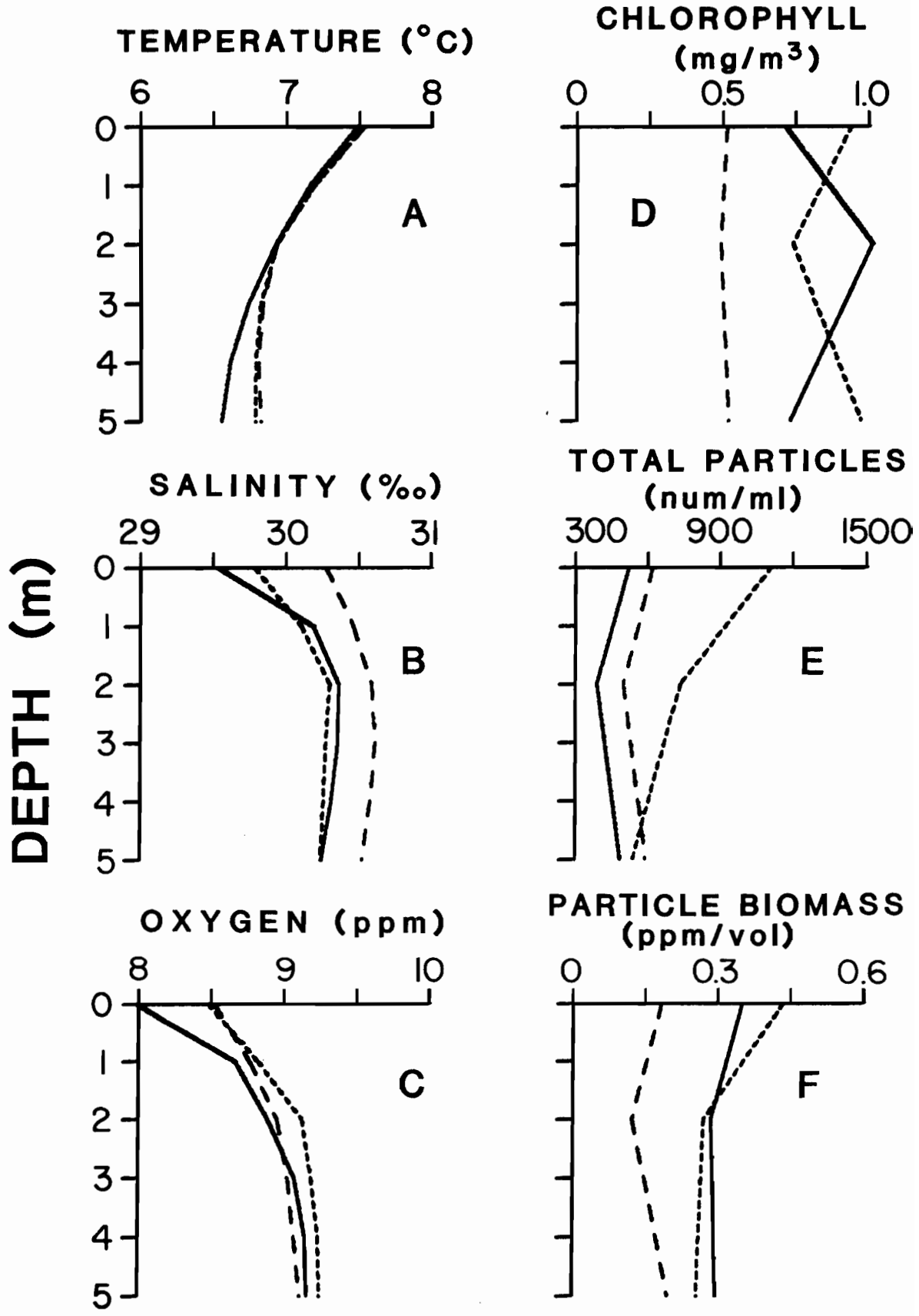

TEMPERATURE (°C)
6
7
8
0
1
2
3
4
5
A
CHLOROPHYLL
(mg/m³)
0
0.5
1.0
D
SALINITY (‰)
29
30
31
B
TOTAL PARTICLES
(num/ml)
300
900
1500
E
DEPTH (m)
OXYGEN (ppm)
8
9
10
C
PARTICLE BIOMASS
(ppm/vol)
0
0.3
0.6
F

Table 3. Comparison of physical and biological variables between enclosure types and outside based on GT2 multiple comparison test. O - outside; D - Dacron; N - Dacron with 53 μm Nitex. Underlined types are not significantly different ($p>0.05$). Enclosure types are ordered from low to high values (from left to right) for each variable.

	Sampling depth (m)		
Variable	0	2	5
Temperature	O D N	O D N	O N D
Salinity	O N D	N O D	N O D
Oxygen	O N D	O D N	D O N
Relative Fluorescence	D N O	D N O	D N O
Chlorophyll	D O N	D N O	D O N
Particle Number	O D N	O D N	O N D
Particle Biomass	D O N	D N O	D N O

to 9h did not significantly improve the coefficients ($p>0.1$). This suggests that the biological characteristics of the enclosures were not directly related to earlier external events. Particle and chlorophyll *a* concentrations were generally homogeneous with depth, but were lower inside the full Dacron enclosures than in the Dacron/Nitex types (Figure 3d,e,f; Table 3) as was expected given their lower porosity. Spearman rank correlations indicated significant ($p<0.001$) temporal correspondence between depths for chlorophyll *a* and particle concentrations but not for particle biomass ($p>0.1$).

Total particle number declined sharply with time, but particle biomass remained relatively constant (Figure 2e,f). This suggests that the size spectrum of particles varied over time. The size distribution of particles was dominated by a maximum in abundance at 40-100 μm (Figure 4) which probably corresponds to large diatoms (Harris *et al.* 1982; Takahashi *et al.* 1982). One possibility is that the general decline in particle numbers with time observed in the enclosures was due to sinking. The sinking rate necessary to produce this decline was estimated independently for particles smaller and larger than 10 μm. These rates were derived for each stratum sampled using equation 1 (Reynolds and Wiseman 1982):

$$S = Zm * (1 - (1/e^{-Ks * 24})) \quad (1)$$

where S is the sinking rate in m/day, Zm is the sampling depth interval (1m) and Ks is the decline rate in numbers calculated as follows:

$$Ks = (\log (N_{t+1} / N_t)) / t \quad (2)$$

where N_{t+1} is the number of particles at time t+1, N_t is the number of particles at time t, and t is the time interval (h) between samples. The average sinking rates of particles <10 µm from the upper (0 and 2 m) layers of the full Dacron and the Dacron/Nitex enclosures were 0.297 and 0.235 m/day respectively (Table 4). Average sinking rates of particles >10 µm in the Dacron and the Dacron/Nitex enclosures were 0.089 and 0.098 m/day respectively. These estimates did not differ significantly from 0 (Table 4).

To evaluate the effect of the porosity of the enclosure walls on the plankton size structure within the enclosures, the 210 particle size spectra obtained from the Coulter data were reduced to 6 similar size spectra by cluster analysis (Figure 4). Evaluation of the significance of these 6 spectra, and their distribution in the 2 enclosures types and in-situ (Table 5), was achieved by discriminant analysis as suggested by Green (1979). The 6 size spectra differed primarily in the abundance of particles >5 µm (Figure 4). Full Dacron enclosures, which had the lowest porosity, were dominated by groups 1 and 2 which had lower abundances of particles at all size classes. Size spectra 3-6 which were characterized by a greater abundance of particles at all size classes, were virtually absent inside the Dacron type although they were observed both outside and inside the Dacron/Nitex enclosures. It should be emphasized that the size classes provided by the Coulter counter are equivalent spherical diameters, which are derived from volume estimates. By this measure long slender particles, spherical diameter particles or even small spheres with long spines can have equal e.s.d. values. This explains the observed presence of particles larger than 53 µm e.s.d. in the Dacron/Nitex enclosures. Large particles (Groups 3-6) were not

Figure 4. Averaged particle size distributions of the six size spectra identified by cluster analysis.

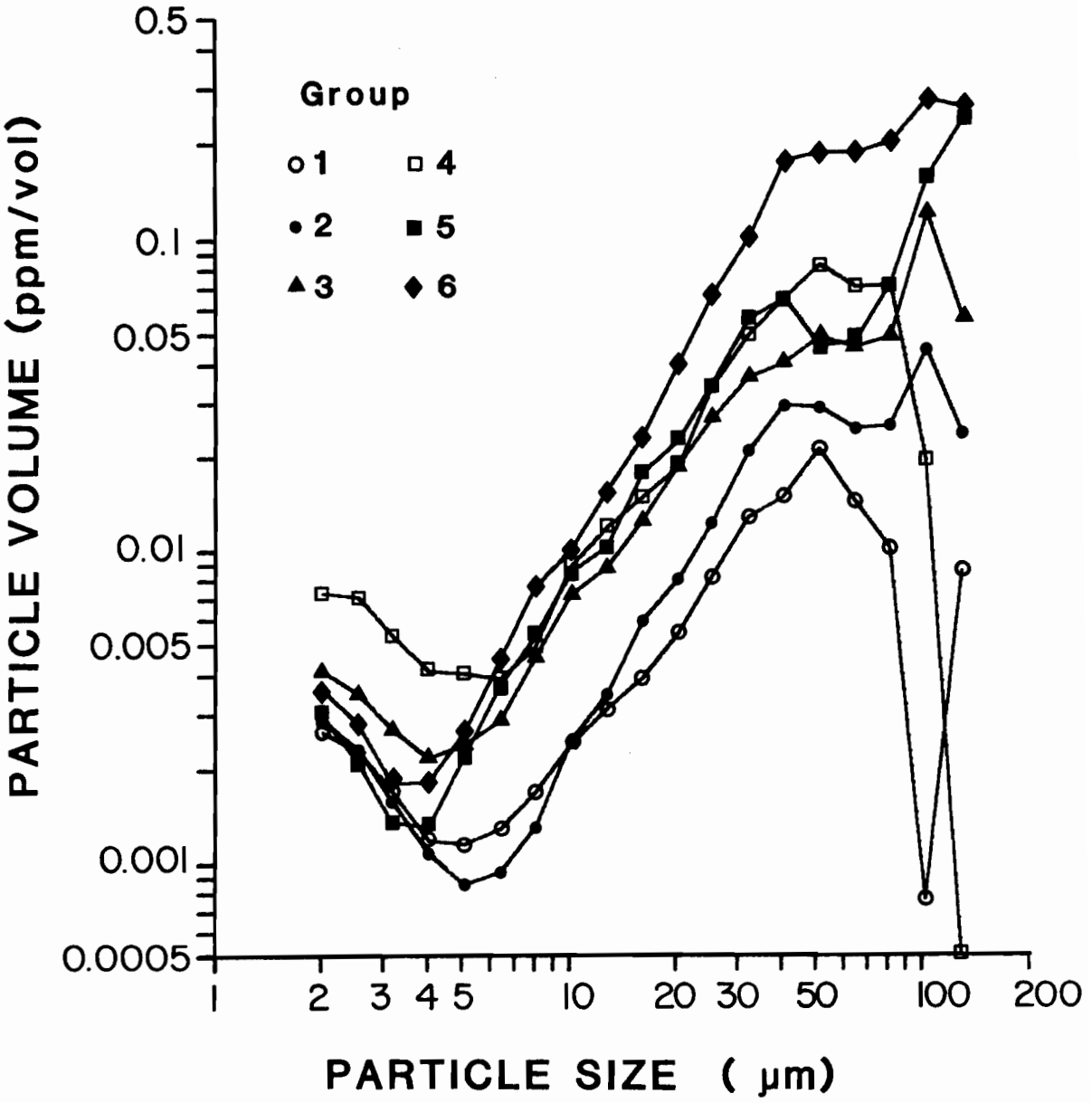

Group
1
2
3
4
5
6
0.5
0.1
0.05
0.01
0.005
0.001
0.0005
PARTICLE VOLUME (ppm/vol)
1
2
3
4
5
10
20
30
50
100
200
PARTICLE SIZE (µm)

Table 4. Sinking rate estimates for total particles lesser and greater than 10 μm (esd) in both replicates of each enclosure type. Decline rate (Ks) and sinking rate (S) were calculated for each depth. Regression coefficients (r^2) and probability level of significance (p) of equation 2 to calculate Ks are also tabulated.

Enclosure		Less than 10 μm				Greater than 10 μm			
Type	Depth (m)	r^2	p	Ks (h-1)	S (m/d)	r^2	p	Ks (h-1)	S (m/d)
Dacron	0	.70	.0002	-.0129	0.266	.15	.174	-.0037	0.086
	2	.63	.0006	-.0166	0.329	.25	.072	-.0045	0.102
	5	.15	.17	-.0067	0.148	.17	.133	+.004	---
	0	.68	.0003	-.0173	0.340	.22	.09	-.0056	0.126
	2	.44	.0095	-.0119	0.248	.08	.32	-.0019	0.045
	5	.48	.0056	-.0124	0.257	.11	.23	-.0037	0.085
Dacron /Nitex	0	.60	.0011	-.0142	0.289	.20	.107	-.005	0.113
	2	.34	.027	-.0095	0.204	.02	.667	-.0015	0.036
	5	.19	.11	-.0044	0.010	.04	.524	-.0033	0.075
	0	.32	.035	-.0097	0.208	.09	.30	-.0034	0.079
	2	.75	.0001	-.0111	0.234	.31	.037	-.0076	0.167
	5	.42	.013	-.0123	0.256	.05	.44	-.0022	0.053

Table 5. Partitioning (%) of particle size spectra within each enclosure type and outside. Group numbers correspond to size spectra in Figure 4.

Enclosure Type	Depth (m)	Groups of particles size spectra					
		1	2	3	4	5	6
Dacron	0	17.8	11.9	1.2	2.4	0	0
(n=84)	2	21.4	9.5	1.2	1.2	0	0
	5	10.7	40.5	4.8	4.8	0	0
	All	50.0	40.5	4.8	4.8	0	0
Dacron/ Nitex	0	11.9	10.7	3.6	0	0	2.4
(n=84)	2	15.5	8.3	7.1	0	1.2	1.2
	5	7.1	19.0	3.6	0	0	1.2
	All	34.5	38.1	14.3	0	1.2	4.8
Outside	0	9.5	7.1	7.1	4.8	2.4	2.4
(n=42)	2	16.7	7.1	2.4	2.4	4.8	0
	5	9.5	19.0	0	0	2.4	2.4
	All	35.7	33.3	9.5	7.1	9.5	4.8

restricted to the Nitex bottom region where they entered, but were quickly entrained within the full water column. No group separation due to sampling depth was evident in the discriminant analysis. Moreover, specific particle size groups did not persist over time in the Dacron/Nitex enclosures. Rather, they were repeatedly flushed and replaced by groups characteristic of the water mass surrounding the enclosures.

Larval distribution

Yolk-sac capelin larvae exhibited diel vertical migration within the enclosures. The number of larvae caught relative to the number present in the enclosure at the time of sampling averaged 5.7% (s.e. 0.3%) and was independent of sampling time. Due to the different number of larvae initially stocked in the enclosures and due to removal of larvae by sampling, the number of larvae sampled at each time varied between 32 and 224 (average 88 and s.e. 4.6). Larvae were proportionally more abundant near the surface and near the bottom of the enclosures (Figure 5); few larvae were sampled at mid-depths. Despite the differences in temperature, mean daily solar radiation and numbers initially stocked (Table 6), the proportion of larvae found at depth did not differ between years (Table 7 - YEAR effect, $p>0.1$). The pattern of larval distribution in the full Dacron enclosures (1982) and Dacron/Nitex enclosures (1983,1984) was thus similar. The pattern of diel migration did, however, vary between years (Table 7 - Interaction of YEAR and TIME, $p<0.001$) and appears to have been related to the corresponding presence or absence of zooplankton in the enclosures. In 1982 and 1983, when no zooplankton was stocked, the proportion of larvae

Figure 5. Vertical distribution of capelin larvae in the enclosures. Histogram width represents the percentage of larvae collected in a given stratum during each sampling session. Deviations from a uniform distribution (chi-square test) are presented (open histogram - $p<0.0001$; hatched histogram - $0.0001<p<0.05$; solid histogram - $p>0.05$).

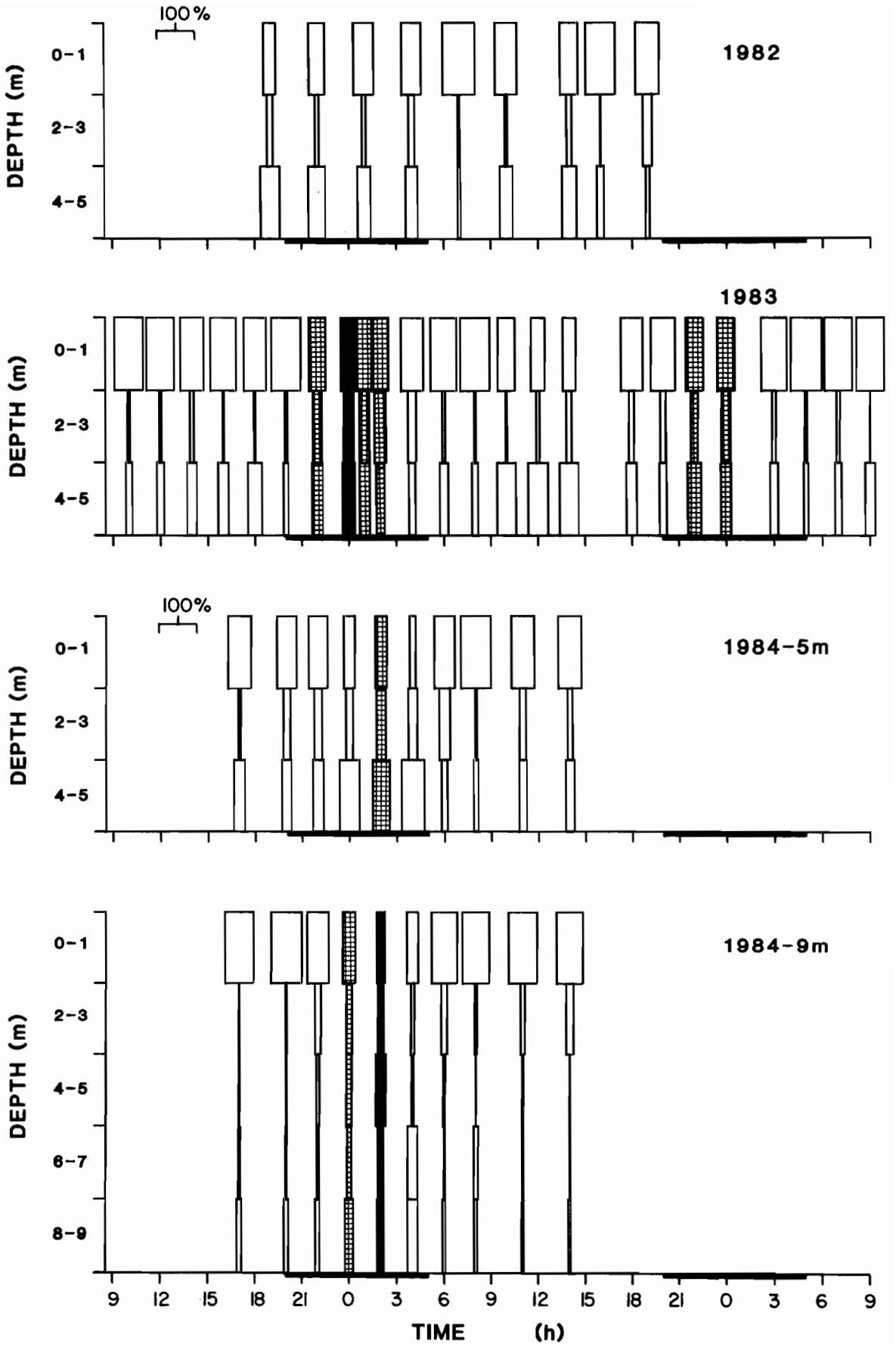

100%
1982
DEPTH (m)
0-1
2-3
4-5
1983
100%
1984-5m
1984-9m
6-7
8-9
9 12 15 18 21 0 3 6 9 12 15 18 21 0 3 6 9
TIME (h)

Table 6. Summary of conditions during vertical distribution experiments.

	Experiment			
	1982	1983	1984-5m	1984-9m
Enclosure type	Dacron	Dacron /Nitex	Dacron /Nitex	Dacron /Nitex
Enclosure Dimension (m) & Volume (m^3)	1 x 5 3.2	1 x 5 3.2	1 x 5 3.2	1 x 9 6.4
Replicates	4	4	1	1
Initial number of larvae	1500	2500	1500	1500
Duration (h)	22	48	21	21
Larvae removed by sampling (%)	43.7	56.1	34.9	32.1
Initial length (mm) of larvae. Mean	4.71	4.85	4.77	4.77
(s.d.)	(0.30)	(0.31)	(0.31)	(0.25)
Water Temperature (^{o}C) Mean	5.5	11.0	11.4	11.4
(s.d.)	(.57)	(.59)	(1.27)	(1.27)
Total Daily Radiation (MJ/m^2)	15.98	20.45	23.71	23.71

Table 7. Analysis of variance of proportion of larvae at each depth inside the enclosures.

Source of Variation	df	Sampling Depth (m) 0 F-value	p	2 F-value	p	5 F-value	p
Year	2	1.71	0.187	2.18	0.119	1.47	0.241
Time (day/night)	1	17.86	0.0001	40.53	0.0001	3.25	0.092
Enclosure (within year)	6	1.13	0.352	1.81	0.108	1.60	0.153
Year X Time	2	7.11	0.001	6.13	0.001	9.39	0.0002
Time X Enclosure	5	0.25	0.941	1.54	0.185	0.21	0.957

sampled near the surface exhibited two daily maxima centered on dawn and dusk, and two minima near mid-night and mid-day (Figure 5). The proportion of larvae at the 5m sampling depth showed a reciprocal pattern being greatest at mid-night and noon. In 1984, when both zooplankton and larvae were stocked, larvae aggregated near the surface during daylight hours with no sign of mid-day minimum. The proportion of larvae in the 5m zone was greatest at night.

The effect of bag dimension on the vertical distribution of larvae was examined in 1984 by launching an enclosure which was modified to have a depth of 9m and a volume of 6.4 cubic meters. Wild zooplankton was added to the enclosures with the larvae. Larvae were proportionally more abundant at surface during daylight hours and the proportion near the bottom was maximal at night (Figure 5). The pattern of diel migration in the 9m enclosure was thus similar to that observed in the 5m enclosure also deployed in 1984.

Larvae were more homogeneously distributed during darkness relative to the daylight period. Except for two occasions (0h in 1983 and 2h in 1984-9m), the vertical distribution of capelin larvae in the enclosures differed significantly from a uniform distribution ($\chi^2 > 5.99$, $p<0.05$ for 5m enclosures and $\chi^2 > 9.45$, $p<0.05$ for 9m). The probability level of the χ^2 values was, however, higher ($p<0.001$) during the day as opposed to the night ($0.001<p<0.05$) (Figure 5). Heterogeneity (variance/mean ratio) was significantly greater in the 9m enclosure relative to the 5m enclosure during daytime only ($F=41.4$, $p<0.0001$).

Zooplankton distribution

The vertical distribution of three size groups (group 1: 80-150μm,

group 2: 150-300 μm and group 3: >300μm) of zooplankton stocked into the enclosures in 1984 revealed diel movement which resulted in proportionally higher densities near the surface at night (Figure 6). The greatest migration amplitude was exhibited by the largest (>300μm) size groups. This group also showed a night surface peak that was both narrower and earlier than that of the two other groups. Day-night changes in proportion were significant at surface and at the bottom for both the 5m and 9m enclosures (Table 8). Chi-square analysis indicated that the zooplankton was more uniformly distributed at night than during daytime in both enclosures sizes. This effect was, however, more pronounced for small and medium sized organisms. Heterogeneity (variance/mean ratio) was independent of bag dimension for all size groups (F-test, $p>0.50$).

Figure 6. Vertical distribution of three size groups of zooplankton inside 5m and 9m long Dacron/Nitex enclosures. Histogram width represents the percentage of zooplankton collected in a given stratum during each sampling session. Deviations from a uniform distribution (chi-square test) are presented (open histogram - $p<0.0001$); hatched histogram - $0.0001<p<0.05$; solid histogram - $p>0.05$).

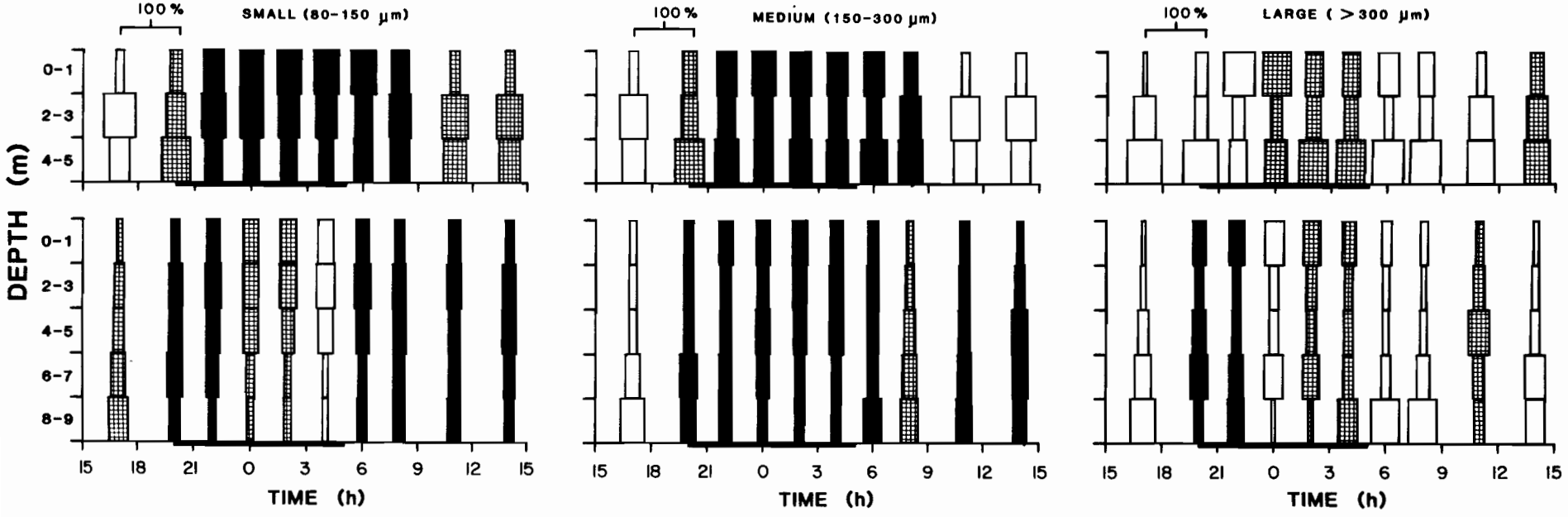

100 %
SMALL (80–150 µm)
100 %
MEDIUM (150–300 µm)
100 %
LARGE (>300 µm)
DEPTH (m)
0–1
2–3
4–5
6–7
8–9
15 18 21 0 3 6 9 12 15
TIME (h)

Table 8. Analysis of variance of the three size groups of zooplankton inside the enclosures in 1984. F-values for the effect of time (day/night) for each sampling depth. (* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$).

Group Size	Enclosure Size	Sampling depth (m) 0	2	5	7	9
Small (80-150 μm)	5m	7.12*	0.49	13.60**		
	9m	12.91**	5.54*	2.49	5.84*	13.48**
Medium (150-300 μm)	5m	11.87**	2.30	2.53		
	9m	36.57***	6.31*	2.53	5.08	16.46**
Large (>300 μm)	5m	7.07*	1.71	4.98		
	9m	15.94**	1.55	0.41	0.05	2.54

DISCUSSION

Physical and Chemical Properties

My data indicate that the physical and chemical conditions inside both enclosure designs closely mirror those in-situ. The time response to changes in in-situ conditions was almost instantaneous. This contrasts sharply with the performance of plastic bags which act as "lowpass" filters of in-situ temperature having a lagged time response of between 12 and 24 h (McAllister et al. 1961; Steele et al. 1977; Sonntag and Parsons 1979). Both enclosure types also had vertical temperature and salinity profiles similar to those occurring outside. This differs dramatically from the pronounced and stable stratified conditions which typically occur in plastic bags (Takahashi and Whitney 1977; Sonntag and Parsons 1979). The similarity in O_2 levels inside and outside the enclosures also differs markedly from the supersaturation (McAllister et al. 1961; Takahashi and Whitney 1977) or undersaturation (Gieskes and Kraay 1982) conditions typical of non porous bags.

Reduced vertical mixing is considered to be the most important problem of plastic bag enclosures. Boyce (1974) cautioned that the similarity of vertical temperature profiles inside such enclosures with in-situ profiles can result from lateral heat transfer and cannot be interpreted as evidence of vertical mixing. Steele et al. (1977) showed that vertical eddy diffusivity decreases with increasing bag size. They suggested that vertical mixing in plastic bags enclosures is probably due to wall movement and thermal forcing both of which are inversely related to bag dimension. von Brockel (1982) hypothesized that enclosures constructed of porous material would alter the energy profile

of enclosed systems much less than is the case for unpermeable enclosures. My data support this hypothesis. In my enclosures, both chlorophyll and particle profiles were virtually homogeneous vertically in both the full Dacron and the Dacron/Nitex types. Moreover, the profiles were similar to those observed in-situ (Figure 3, Table 5). In plastic enclosures, the sinking rate of particles, which has been often used as an index of turbulent mixing, is rapid during the first two weeks after filling and is positively related to particle size and bag dimension (von Brockel 1982; Bienfang 1982). The sinking rates calculated for both of my enclosure types (0.089 - 0.297 m/day) were much lower than those previously reported for plastic bags (0.32 to 5.0 m/day: von Brockel 1982; Bienfang 1982). The above lines of evidence suggest that the wall permeability and the smaller size of my enclosures enhanced internal turbulence, thereby creating conditions more typical of those found in-situ.

Biological Properties

Chlorophyll levels inside my enclosures remained low over the one-week duration of my experiments and never reached the peaks observed in-situ (Figure 2d). Previous work with plastic bags has also shown chlorophyll to remain relatively close to the initial concentration for approximately 1 week after filling, although significant increases commonly occur after that time (McAllister et al. 1961; Takahashi et al. 1975; Brockmann et al. 1977; Kuiper 1977; Kuiper et al. 1983). The differences in chlorophyll and particle concentrations I observed between the Dacron and the Dacron/Nitex enclosures are consistent with the porosity of the material used. The full Dacron enclosures appear to

create an effective biological barrier while the Dacron/Nitex design allows limited exchange of small biological material with the outside environment.

Larval Behavior

In nature, newly hatched capelin larvae are typically restricted to the upper (0-20m) layer of the ocean. Yolk-sac capelin larvae migrate on a diel basis by moving toward the surface at twilight, and being most abundant there at night (Fridgeirsson 1984; Taggart 1986). The diel migration exhibited by capelin larvae in the enclosures indicates that the migratory behavior they typically exhibit in-situ was not disturbed. However, the pattern of vertical migration I observed in my enclosures was inverse to that reported in-situ. In the enclosures, the larvae were distributed more homogeneously at night, and were proportionally more concentrated in the surface layer during the day (Figure 5). Gamble and Houde (1984) also found that recently hatched cod larvae were mainly concentrated in the top layer of an enclosure while in nature they are typically found in deeper strata (10-30 m) (Fridgeirsson 1984; Solemdal and Ellertsen 1984; Ellertsen et al. 1984; Lough 1984). Although the vertical movements exhibited by capelin larvae in enclosures are consistent with laboratory results for herring and red sea bream larvae whose activity was random in total darkness but vertically surface oriented in daytime (Woodhead and Woodhead 1955; Tsuda and Sakamoto 1983), there is no obvious explanation for the observed difference between enclosure and in-situ larval distribution. The diel vertical distribution of larvae (Figure 5) was unrelated to the diel distribution of the small (80-150 μm) zooplankton (Figure 6) which represent

potential food items for newly-hatched larvae (Courtois and Dodson 1986). Fortier and Leggett (1984) have also shown the vertical distribution of capelin larvae and their principal prey to be unrelated in-situ. At night the distribution of larvae was inversely related to that of medium (150-300 μm) and large (>300 μm) size zooplankters.

The vertical migration of zooplankton to the surface at night observed in my enclosures is consistent with previous observations by Kuiper et al. (1982) in a 3 m deep enclosure. The greater migration amplitude of larger zooplankton has also been reported for zooplankton in CEPEX bags by Harris et al. (1982). My results indicated that patchiness increases with animal size as previously reported by Grice et al. (1977). However, I also found it to vary on a diel basis becoming most pronounced during the day.

The migratory behavior of both fish larvae and zooplankton was unchanged in the 9m enclosure. Zooplankton patchiness did not differ between the 5m and the 9m enclosures, but the distribution of fish larvae was significantly more heterogeneous in the 9m enclosure during daylight periods. This reinforces the evidence that larval distribution was not directly associated with their potential food items.

The fact that the distribution of capelin larvae was, on average, more patchy than that of zooplankton and that the larvae did not directly follow their potential food items (small zooplankton) is puzzling given the several hypotheses on the importance of feeding and food patches for larval survival (Lasker 1975; Theilacker and Dorsey 1980; Fortier and Leggett 1984; Houde and Lovdal 1985). Much needed tests of these hypotheses could easily be conducted by manipulating the size spectrum of zooplankton available to larvae. I suggest that

enclosures may be useful tools for such experiments.

Conclusion

I conclude that the two enclosure types evaluated in this study have significant potential for studies of the early life history dynamics of marine fish. In addition to the accurate reproducibility of the physico-chemical conditions that larvae normally encountered at sea, the enclosures acted as effective biological barriers as required for manipulation purposes. Replicability of both the physical and biological properties and the natural behavior of enclosed organisms between enclosures and between years was also excellent. In comparison with laboratory experiments, enclosures confer the advantages of larger scale where the natural ratios of predator and prey can be achieved.

The choice of an enclosure design is primarily determined by the aims of the experiment and no "ideal" enclosure exists *per se*. The choice of design is analogous to the choice of a sampling gear which depends on the type of organisms to be studied (Green 1979). Recent research on larval fish contained in enclosures (Table 1) has been realized primarily in large enclosures and in concrete basins principally because the objectives were long-term. As I have previously noted these designs virtually preclude replication of experimental treatments and make difficult the design of short-term experiments.

The relatively low cost, ease of handling and the reproducibility provided by my enclosures make them particularly appropriate for short term, replicated experimental studies of the interactions between larval

fishes, their predators and prey. Enclosures of the design I describe have also been successfully used for short-term experiments on larval mortality induced by macrozooplankton predators (Frank and Leggett 1982a). The extent to which the properties of my enclosures will persist over longer time periods remains unknown. However, Kuiper et al. (1983) found no difference in the temporal development of phytoplankton in plastic bags of different sizes (1.5 to 30 m^3) over a four-week period and studies on fish larval growth and survival in relation to feeding regimes (Schnack 1981; Leggett 1986) have been successfully conducted in enclosures similar to the ones described in the present study. This suggests that these enclosures also have potential for longer-term experiments.

CHAPTER 2

Effect of container size on estimates of mortality and predation rates in experiments involving macrozooplankton and larval fish.

INTRODUCTION

Although predation is potentially a major source of natural mortality for larval fishes, its quantitative contribution to total larval mortality, and subsequent recruitment, remains unclear (Hunter 1984). The difficulty of assessing, in-situ, the natural mortality of fish larvae and estimating the proportion of this mortality attributable to predation has led many scientists to study predation in the laboratory. This laboratory work has sought an understanding of the functional relationship between predators and prey with the object of linking this relationship to their numerical in-situ abundance. The ultimate objective has been to describe and explain the dynamics of this predator-prey system.

Large pelagic invertebrates are important potential predators of larval fish (Hunter 1984; Möller 1984; Purcell 1985). The predation rate as a function of prey density, i.e. the predator's functional response (Holling 1966), has been experimentally determined for several pelagic invertebrates fed larval fish (Table 1). These studies show that macroinvertebrate predators can induce high mortality rates on the early larval stages of fish species under experimental situations. With the exception of the work of Frank and Leggett (1982a) who used $3m^3$ in-situ enclosures, most experimenters have worked with relatively small laboratory containers (< 5 l) which may not adequately represent the scale of field conditions. The use of small containers has also frequently demanded the use of larval densities that were much higher than those reported in-situ. In many cases the experimental

predator-prey ratio has also differed from that expected in nature. Moreover, the relatively short and the variable duration of many of these experiments may have biased the extrapolation of predation rates to a daily basis as required for larval population dynamics. The relevance of these laboratory studies to field situations must thus be judged with caution. Ideally, laboratory-style experiments should be executed (or pursued) at a scale approaching the field situation (Solemdal 1981; Hunter 1984).

The scale of the experimental container has been found to influence predation rates in other predator-prey systems. Luckingbill (1974) showed that the coexistence of a simple predator-prey system was prolonged by increasing the experimental container size. He suggested that, in the absence of refuges or physical heterogeneity, larger container sizes depressed predation rate by lowering the encounter rate between predator and prey. Kaiser (1983), in contrast, reported that the predation rate by mites was higher in larger arenas, primarily because of an "edge effect" which influenced both predator and prey distribution and increased the probability of encounter in larger arenas.

The predation rate of many planktonic organisms is typically expressed as filtration or clearance rate (volume of water cleared of food per animal per unit of time (Gauld 1951; Frost 1972)). Since the volume of the experimental container is incorporated in this parameter, the clearance rate is equivalent to the searching rate of a filter-feeding predator. In theory, then, clearance rate should not vary with container size, provided the prey is evenly distributed (Gauld 1951). Several studies have shown, however, that the clearance rates of

numerous plankters increase with container size (Marshall and Orr 1955; Ankaru 1964; Ikeda 1977; Fulton 1982; Cooper and Goldman 1982; Murtaugh 1983; Peters and Downing 1984). Landry (1978) and Andersen (1985), in contrast, found no effect of container size. In all of these experiments the prey density (No./l) was held constant between container sizes but the prey distribution may well have been influenced by the different experimental volumes (Kaiser 1983).

Clearly the relationship between predation rate and the experimental container is not a simple one. In fact the data available indicate that the common assumption, based on theory, that the functional response should depend only on the density of prey, irrespective of size, form and structure of the experimental container is frequently not met. It is thus important to evaluate such bias if reliable estimates of predator response and predation rates, and accurate extrapolations of laboratory results to field conditions are to be achieved.

The above lines of evidence suggest that container size may also directly influence estimates of larval mortality due to predation. This effect has not been measured previously. I investigated the effect of container size on the predation rate of a macroinvertebrate predator (Aurelia aurita) on yolk-sac capelin (Mallotus villosus) larvae. The null nypothesis was that predation rate was independent of the enclosure size.

Table 1. Summary of conditions employed in experiments of macrozooplankton predation on larval fish.

Predator Species	Container Volume (liter)	Duration (h)	Number of Predators	Number of Larvae	Maximum Predation Rate(prey/d)	Mortality Rate (%/d)	Reference
Copepods							
Euchaeta elongata	2	24	1	5-50	2- 5[a]	6-50[b]	Bailey & Yen 1983
Euchaeta norvegica	5	24	2	15	0.5-2.2[a]	6-29[a]	Bailey 1984
Labidocera jollae (female)	3.5	20	1	5-40	7-15[a]	30-100[b]	Lillelund &
(female)	3.5	21	2-30	30	12	60-100	Lasker 1971
(male)	3.5	24	5	30	2	33.3	"
Labidocera trispinosa (female)	3.5	20	2-3	5-45	1- 4[a]	20-60[b]	"
(male)	3.5	24	5	30	2	16-83[a]	"
Pontellopsis occidentalis (female)	3.5	24	1-6	30	11	36.7	"
(stage V)	3.5	24	1-6	30	3	10	"
Anomalocera ornata	1	20	3	10-50	5-10[a]	20-35[b]	Turner et al. 1985
Centropages typicus	1	20	5	10-50	1	0-5[b]	"
Cyclops sp.	0.2-40	120	10-150	20-30	<1	80-100	Fabian 1960
Euphausiids							
Euphausia pacifica (larval)	3.5	22	1	20	2	5-25	Theilacker &
(juvenile)	3.5	22	1	1-80	15	10-100[b]	Lasker 1974
(juvenile)	3.5	22	1	20	7	5-95	"
(adult)	3.5	22	1	50-80	17	10-50[b]	"
Thysanoessa raschii	5	24	2	15	0.5-4[a]	3-27[a]	Bailey 1984

Table 1. (suite)

Predator Species	Container Volume (liter)	Duration (h)	Number of Predators	Number of Larvae	Maximum Predation Rate(prey/d)	Mortality Rate (%/d)	Reference
Amphipods							
Hyperoche medusarum	0.5	2-10	1	1-50	11	19-60[b]	vonWesternhagen & Rosenthal 1976, 1979
	0.5	2-10	2-16	1-50	4	8-60[b]	
	0.5	5	8	50	4-20[a]	10-72[a]	
Parathemisto japonica	1	12	1	10-40	2-50[a]	40-59[b]	Yamashita et al.
	1	12	1	40	13-37[a]	32-92[b]	
Chaetognath							
Sagitta sp.	1	10	1	7-150	0.2-3[a]	0-22[b]	Kuhlmann 1977
Ctenophores							
Pleurobrachia sp.	3200	72	20	80-4280	15	2-17[b]	Frank & Leggett 1982a
Coelenterates							
Aurelia aurita	5	1	1	1-50	20-280[c]	8-50[b]	Bailey & Batty 1983
Aurelia aurita	5	24	1	15	1-15[a]	6-100[b]	Bailey 1984

a - variation due to larval size
b - variation due to larval density (Type II functional response)
c - variation due to predator size

MATERIALS and METHODS

My experimental containers were cylindrical Dacron *in-situ* enclosures with a Nitex (53 µm mesh) conical bottom section. The enclosures were moored in the nearshore waters of Bryants Cove, Newfoundland and were allowed to fill by diffusion of water through the walls. A complete description of these *in-situ* enclosures, of the mooring and hauling procedures employed, and of the physical and chemical properties of the water in the enclosures, relative to *in-situ* waters, is provided in Chapter 1. All enclosures were 1m in diameter. Their total depth was varied from 1 to 9 m yielding volumes ranging from 0.26 to 6.35 m^3. Each experiment involved nine enclosures and permitted three replicates of three different enclosure sizes. Experiments were conducted at three different times and a total of 5 different enclosure sizes were tested.

Simultaneous with the *in-situ* enclosures experiments, similar experiments were conducted in small land-based tanks each of which had a volume of 0.27 m^3 (91 cm long X 57 cm wide X 52 cm deep). Each tank was continuously supplied with running seawater pumped from the nearshore zone of Bryants Cove. The pump intake was located 50 m from the shoreline at a depth of 3 m. Inflowing seawater was filtered through a series of Nitex screen filters, the smallest of which had a mesh size of 53 µm. Water discharged from the tank through a 53 µm filter fixed on the overflow pipe.

The physical and chemical characteristics of water in the enclosures was similar to those *in-situ* with <3h lag (Chapter 1). I therefore used continous seawater temperature and salinity records

obtained from a Aanderaa currentmeter moored at a depth of 4.5 m and a distance of 30 m from the enclosures to monitor the experimental conditions. Water temperatures in the land-based tanks were continuously recorded with a telethermometer (YSI model 47) coupled to a strip chart recorder. Total daily radiation recorded at the St.Johns International Airport (approximately 25 km from my study site) was obtained from Atmospheric Environment Service, Canada.

Yolk-sac capelin larvae were used as prey. These were collected from the capelin spawning beach at Bryants Cove immediately prior to stocking. Beach gravel containing larvae was placed in a plastic bucket and mixed with seawater. Actively swimming larvae were removed with a wide bore pipette and enumerated. These larvae were placed in 500 ml glass jars filled with filtered seawater. The jars were suspended in the enclosures and tanks for about one hour to allow temperature acclimation prior to their release. For each experiment, an initial sample of forty larvae was preserved in 10% buffered formalin-seawater to assess the average initial total length and yolk volume of the animals used. Yolk volume was approximated by the following spheroid equation (Laurence 1973):

$$\text{Yolk volume} = 3.1416 * (\text{yolk length}) * (\text{yolk depth}^2) / 6$$

Predators (Aurelia aurita) were individually collected in glass jars by Scuba divers in the cove adjacent to the enclosures. They were transferred directly into the enclosures and tanks. Predator size was estimated at the end of the experiment following preservation in 10% buffered formalin-seawater solution. Correction for shrinkage due to preservation in formalin was applied by dividing preserved umbrella diameter by 0.79 (Möller 1980; Appendix 1).

Table 2. Summary of experimental conditions during three experiments conducted in this study.

	EXPERIMENT		
	I	II	III
Date	1983, July 15-17	1984, July 19-21	1984, July 17-19
Larval Number			
Tank	100 (4)	25, 50, 100	250, 500, 1000
Enclosures			
$0.26m^3$	75, 125, 250		
$0.89m^3$		100, 200, 400	250, 500, 1000
$1.67m^3$	150, 250, 500		
$3.21m^3$	250, 500, 1000	340, 680, 1360	250, 500, 1000
$6.35m^3$		650, 1300, 2600	250, 500, 1000
Predator Number			
Tank	2	2	2
Enclosure	2	3	3
Range of predator diameter (cm)			
Tank	3.53-5.02	5.03-6.77	4.36-7.37
Enclosure	4.51-8.38	3.74-7.68	3.59-8.84
Larval Size (n=40)			
Length (mm) Mean	5.17	4.91	4.56
(s.d.)	(0.24)	(0.20)	(0.31)
Yolk volume (mm^3)			
(n=40) Mean	0.0027	0.0088	0.0326
(s.d.)	(0.0046)	(0.0067)	(0.0130)
Water temp. (°C)			
Mean (s.d.) (n=40)			
Tank	11.78 (1.26)	16.22 (2.88)	13.11 (1.19)
Enclosure	11.59 (0.70)	8.67 (0.69)	7.67 (1.02)
Salinity (0/00)			
(n=40) Mean	31.10	30.41	30.49
(s.d.)	(0.056)	(0.090)	(0.115)
Radiation ($MJ/m^2/d$)	22.98	32.42	32.56

Details of the experimental designs are given in Table 2. In experiments I and II, the initial larval density (No./l) was approximately equal while in experiment III the initial larval number was kept constant. Hence in experiment III the larval density varied inversely with container volume. Larval density was varied between enclosures of a single container size to evaluate the relative importance of larval density and container size on realized predation rates. This was done because preliminary results of experiments conducted in 3.2 m^3 enclosures indicated that larval mortality rate was independent of the initial larval density. The predator/prey densities used were within the ranges commonly observed near the spawning beach in Bryant's Cove (Frank and Leggett 1982a). Control experiments involving enclosures stocked with capelin larvae, but lacking predators, were conducted to assess non predation mortality of larvae. The duration of all experiments varied between 36.4 and 45.1 h (mean 40.4 h).

At the end of each experiment, the enclosures and tanks were emptied and their contents was preserved in 10% buffered formalin seawater. The instantaneous daily mortality rate of larvae (Z : $predator^{-1}.day^{-1}$) was calculated as follows:

$$Z = \log (Ni/Nf) \ / \ P * T \qquad (1)$$

where Ni and Nf are respectively the initial and final number of larvae in the container, P is the number of predators used and T is the duration of the experiment in days. This equation takes exploitation rate into account as is required when prey are not replaced once eaten (Royama 1971; Rogers 1972). The equation involves the assumption that predators search at random and at a constant rate, and that searching

efficiency is independent of prey density (Hassell and May 1973). It provides a conservative estimate of mortality rate because larvae killed but not ingested are not accounted for. Predation rate, expressed as the number of larvae taken per predator per day, is obtained by Ni * (1 - exp(-Z)). The clearance rate (Frost 1972), was also calculated by multiplying the Z values by the volume (in liters) of the container used.

All statistical tests were run on the Z values. F-max tests (Sokal and Rohlf 1981) indicated homogeneity of variances for clearance rate ($p<0.05$) but not for mortality rate (Z) which exhibited a significant positive correlation between variance and mean ($r=0.998$, $p<0.0001$). Logarithmic transformation of the Z values removed this trend ($r=-0.261$, $p=0.62$) and yielded homogeneity of variances and a normal distribution of values (Kolmogorov - Smirnov test).

RESULTS

Larval mortality rates in the absence of predators

The proportion of capelin larvae recovered from control enclosures lacking predators were 96.7% (s.e. 2.3%) and 96.1% (s.e. 1.7%) for in-situ enclosures and land-based tanks respectively. These values did not differ significantly (T-test: 0.24, df= 11, $p>0.5$). Larval length slightly increased during the duration of my experiments, and yolk sac volumes declined significantly in all trials indicating that the larvae were active and used some of their yolk reserve (Chapter 3). In a completely different series of experiments (Chapter 3), I found that larval mortality due to handling (pipetting, counting, etc.) was negligible (<5%) during the first 4 days after collection.

Effect of container size

Mortality rate was inversely related to container volume (Figure 1), and clearance rate varied positively with container volume (Table 3). While the effect of enclosure volume was clear, mortality rate also varied within a given container volume. A two-way ANOVA (Sokal and Rohlf 1981) showed significant variation among experiments ($F=24.98$, $df=2,24$, $p=0.01$) and between container sizes ($F=50.21$, $df=5,24$, $p<0.001$) on instantaneous mortality rate (Z) but no significant interaction between the two ($F=2.74$, $df=4,24$, $p>0.05$). An a-posteriori Duncan test showed mortality rates in the three experiments to be different (I>II>III).

The between experiment differences in mortality rates may have resulted from differences in other variables (predator size,

Figure 1. Instantaneous larval mortality rate (Z) as a function of container size.

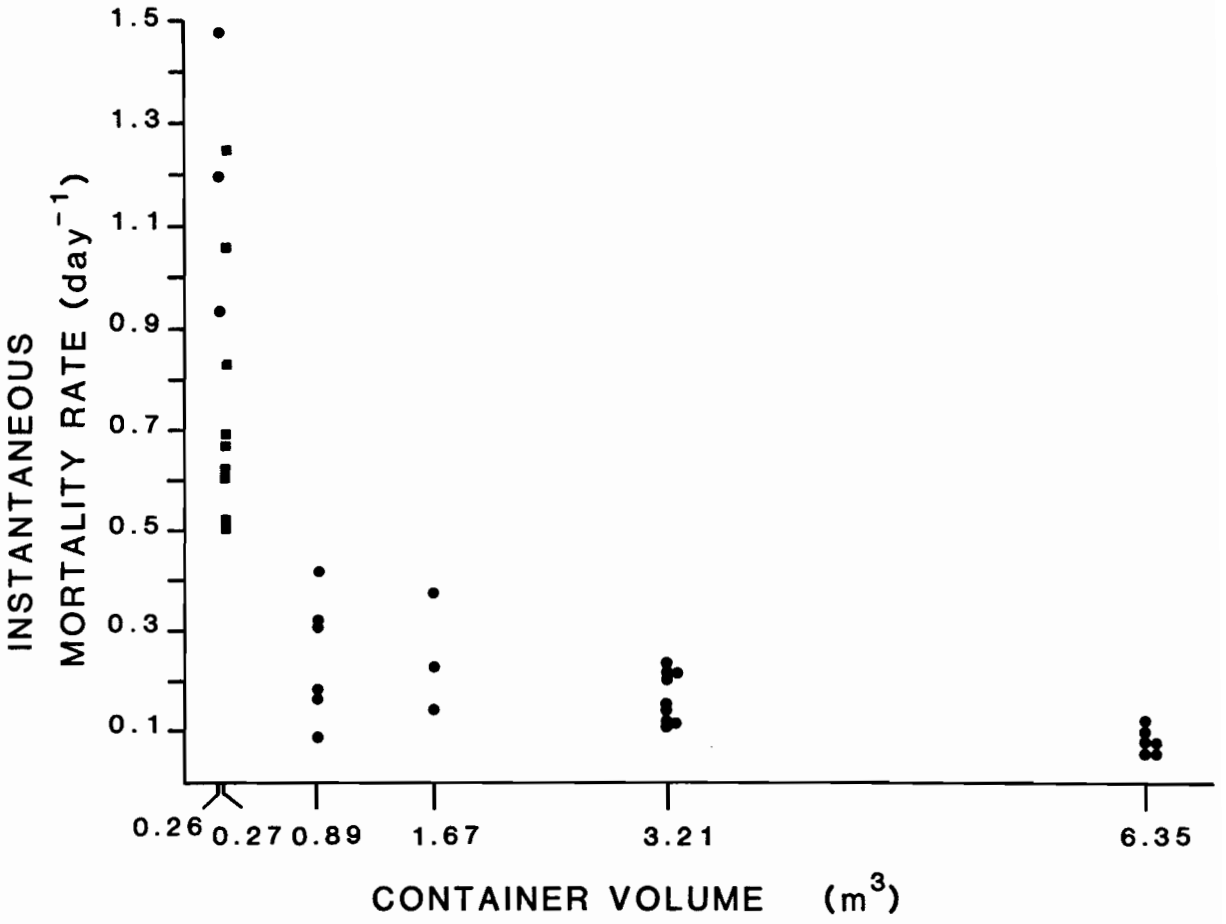

INSTANTANEOUS
MORTALITY RATE (day^{-1})
1.5
1.3
1.1
0.9
0.7
0.5
0.3
0.1
0.26
0.27
0.89
1.67
3.21
6.35
CONTAINER VOLUME (m^3)

Table 3. Average mortality rate (Z) and average mortality rate corrected for predator size (Za) and corresponding clearance rates (F and Fa) in enclosures of different size. Values in parantheses are standard deviations.

Experimental container				Mortality Rate		Clearance Rate	
Volume (m^3)	Area/ Volume	Depth (m)	N	(Z) (day-1)	(Za) (cm-2.day-1)	(F) (1/d)	(Fa) ($1/cm^2/d$)
0.272	7.6	0.5	9	0.7511 A (0.2532)	0.03612 A (0.01059)	204.39 A (68.91)	9.83 A (2.88)
0.262	6.0	1.0	3	1.2365 B (0.3242)	0.04872 A (0.01402)	323.72 AB (84.87)	12.75 A (3.67)
0.890	4.6	1.8	6	0.2472 C (0.1221)	0.01220 B (0.00497)	220.01 A (108.7)	10.86 A (4.42)
1.675	4.3	2.8	3	0.2508 C (0.1182)	0.00801 BC (0.00043)	420.29 BC (198.03)	13.43 A (0.72)
3.207	4.2	4.8	6	0.1711 C (0.0482)	0.00642 C (0.00142)	548.72 C (154.72)	20.57 B (4.56)
6.346	4.1	8.8	6	0.0828 D (0.0273)	0.00399 D (0.00122)	525.64 C (173.63)	23.94 B (7.75)

A,B,C,D - indicates groups significantly different (Duncan test, $p<0.05$)

temperature, salinity, radiation, average larval size) which could not be controlled. A stepwise regression incorporated those variables, initial larval density, and container volume showed that container volume contributed 79.9% of the variability in Z while predator diameter (log transformed) and larval length significantly explained 8.3% and 2.3% of the total variance respectively (Table 4). No other variable was found to be significant.

The coefficient for the log-diameter of predator in this regression was 2.0. This suggests that larval mortality rate was directly related to the umbrella cross-sectional area of Aurelia aurita rather than its wet weight which varies as the cube of umbrella diameter (Möller 1980). All mortality rates were thus standardized by the predator cross-sectional area. The relationship between the standardized rates (Za = Z/umbrella area in cm^2) and container volume is presented in Figure 2. When subjected to a stepwise regression, only container volume (88.4%) and larval length (2.5%) contributed significantly to the variance in Za (Table 4). The positive coefficient for larval length in the regression analyses for both Z and Za suggests that larger larvae suffered higher mortality in these experiments.

Because of the potential covariation between variables, the effect of any particular variable might be confounded with that of an other. A simple correlation matrix (Table 5) indicated that temperature was highly correlated with both Z and container volume. These strong correlations may have precluded the selection of temperature in the stepwise precedure and may also have biased (overweighted) the influence of volume on mortality rates. The interaction between mortality rate and container volume was statistically evaluated by partial correlation

Figure 3. Relationship between larval mortality rate standardized for predator size (Za) and volume of experimental container. Mean and and standard deviation are presented for each container volume.

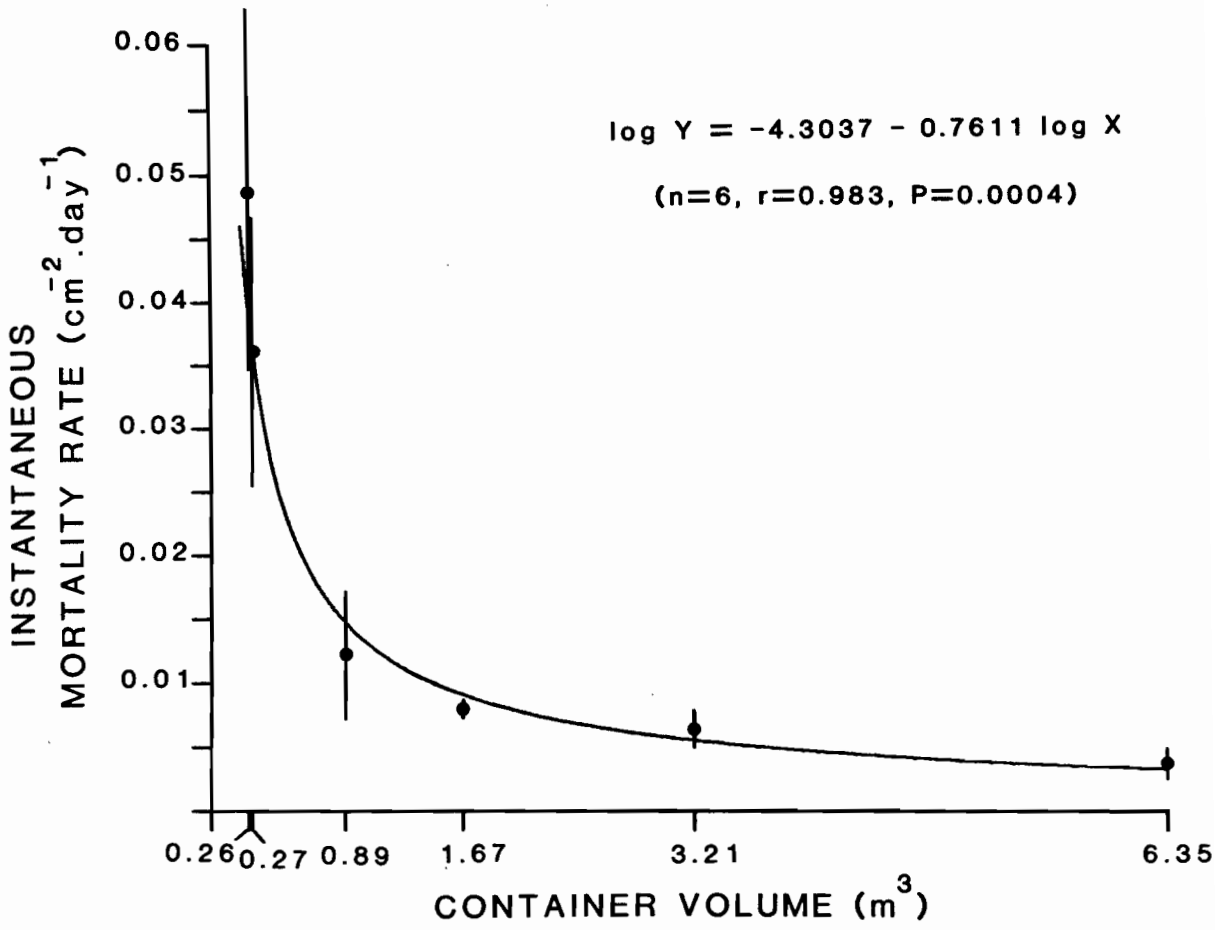

log Y = -4.3037 - 0.7611 log X
(n=6, r=0.983, P=0.0004)
INSTANTANEOUS MORTALITY RATE ($cm^{-2}.day^{-1}$)
0.06
0.05
0.04
0.03
0.02
0.01
0.26
0.27
0.89
1.67
3.21
6.35
CONTAINER VOLUME (m^3)

Table 4. Stepwise regression models for instantaneous mortality rate (Z) and standardized mortality rate (Za).

Step	Variate	Coefficient (s.e.)	F	p	r^2	% Variance explained
		Mortality rate (Z)				
1	Log volume	-0.6898 (0.0432)	131.04	0.0001	0.799	79.9
2	Log diameter	2.0102 (0.3850)	22.53	0.0001	0.882	8.3
3	Larval length	0.5462 (0.1992)	7.52	0.0100	0.905	2.3
	Intercept	-7.2341				
		Standardized mortality rate (Za)				
1	Log volume	-0.6918 (0.0417)	252.23	0.0001	0.884	88.4
2	Larval length	0.5822 (0.1978)	8.66	0.0060	0.909	2.5
	Intercept	-7.1701				

Table 5. Matrix of simple correlation coefficients for measured variables: Z = log-mortality rate, Vol. = log-volume of container, Diam. = log-diameter of predator, Length = larval length, Temp. = water temperature, Light = radiation.

	Vol.	Diam.	Length	Temp.	Light
Z	-0.895[c]	0.068	0.374[a]	0.752[c]	-0.310
Vol.		0.237	-0.245	-0.686[c]	0.197
Diam.			-0.055	0.126	-0.152
Length				0.467	-0.790[c]
Temp.					-0.399[a]

a = 0.05<p<0.01
b = 0.01<p<0.001
c = 0.001<p<0.0001

holding the effect of predator size and temperature constant. The correlation coefficient dropped from -0.895 to -0.859 as expected. This very slight decline clearly indicates, however, that container volume had the major influence on larval mortality rate, and that neither predator size nor temperature had sufficient effect, independent of container volume, to produce the variability observed.

Edge effect

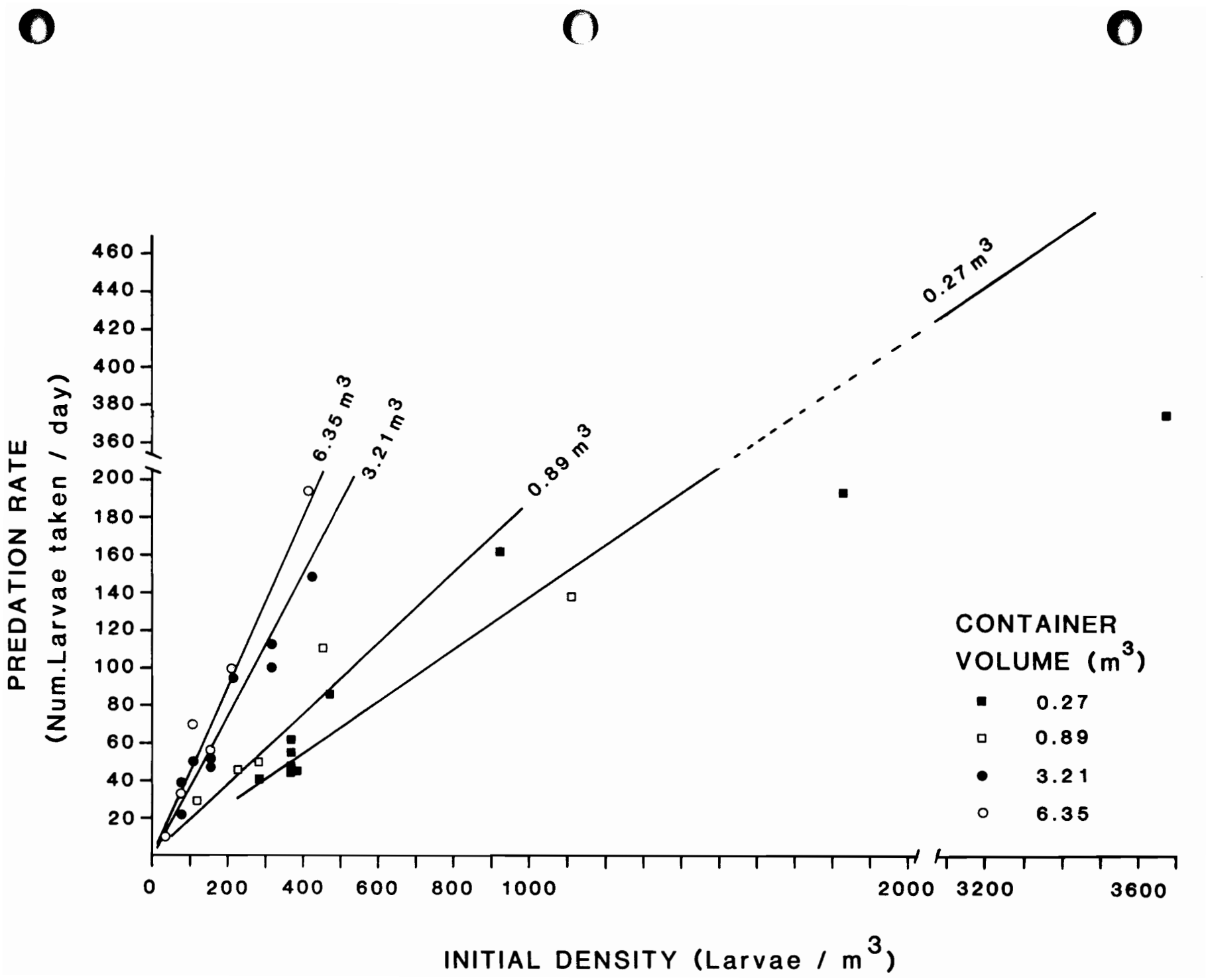
As previously indicated, the changes in enclosure volumes were achieved by varying container depth only. The containers therefore differed in their wall surface area/volume ratios (Table 3). Consequently, the mortality rates observed were also significantly correlated with container depth ($n=6$, $r^2=0.82$, $p=0.013$ for Z; $r^2=0.88$, $p=0.006$ for Za) and with the wall area/volume ratio ($r^2=0.72$, $p=0.03$ for Z; $r^2=0.80$, $p=0.016$ for Za). The goodness of fit of these regressions was however somewhat lower than that of the volume relationship ($r^2=0.92$, $p=0.0025$ for Z; $r^2=0.96$, $p=0.0004$ for Za). The slightly poorer fit of these regressions was primarily due to the non-significant difference ($p>0.05$) in the standardized mortality rates (Za) obtained in the land-based tanks and the smallest in-situ enclosures. These had approximately equal volumes but very different area/volume ratios and depths (Table 3). Correspondingly, while the wall area/volume ratios varied relatively little in the larger volume in-situ enclosures, mortality rates differed significantly (Table 3). This suggests that the "edge-effect" was less important than enclosure volume and/or water depth in determining the predation rate of jellyfish predators in these confined conditions (Table 3).

Effect of initial larval density

Neither initial larval density nor initial larval number contributed significantly to variation in larval mortality rate. This lack of relationship between mortality rate and initial prey density indicates that the predation rate (number of prey taken per predator per day) of Aurelia aurita on larval capelin is linearly related to the initial larval density. To further evaluate this hypothesis, I tested the effect of initial larval density on mortality rate standardized for predator size (Za) separately for each container size using regression analysis. No significant relation ($p = 0.17$ to 0.74) existed. I conclude that the predation rate was linearly related to the initial density of larvae offerred (Figure 3).

Handling time estimates, calculated from the functional response equation with exploitation rate (Rogers 1972) fitted for each container size, varied between -3.8 to 4.5 min. None of these values differed significantly ($p>0.05$) from 0. This supports my conclusion that predation rate was linearly related to the density of prey. The results also show that the predation rates varied with container size and that the container size differences in predation rates were constant over the range of larval densities used.

Figure 3. Predation rate (number of larvae taken per predator per day) as a function of initial larval densities in four container sizes. Predation rates have been standardized for a 5cm diameter predator, the average predator size used in this study. Regression lines calculated for each container size are shown.


PREDATION RATE
(Num.Larvae taken / day)
460
440
420
400
380
360
200
180
160
140
120
100
80
60
40
20
0
200
400
600
800
1000
2000
3200
3600
INITIAL DENSITY (Larvae / m3)
6.35 m3
3.21 m3
0.89 m3
0.27 m3
CONTAINER
VOLUME (m3)
0.27
0.89
3.21
6.35

DISCUSSION

Container Size and Mortality Rates

My results clearly demonstrate that the mortality rates of yolk sac larval capelin imposed by jellyfish predators varied inversely and non-linearly with container volume. Mortality decreased logarithmically from 71% per day (Z=1.236) to 7.9% per day (Z=0.0828), a decline of approximately one order of magnitude over the range of container sizes tested (Table 3, Figure 1). This inverse relationship indicates that experiments involving small small-scale containers typical of those used in laboratory based predation studies (Table 1) may seriously overestimate in-situ larval mortality rates due to predation. The extrapolation of the results of such laboratory studies to field situations should therefore be avoided. Absolute mortality rates were higher and more variable in small enclosures than in large ones, but the coefficients of variation (100 * s.d./mean) for Z varied between 26% and 49% (average 36%) irrespective of the container size. The mean coefficient of variation for Za was 26%.

Bailey (1984) and Bailey and Batty (1983,1984) investigated the predation rate of Aurelia aurita on larval fish in experiments using 5 l laboratory containers. In these experiments, predation rates were found to be dependent on several factors (larval density, larval size and species, predator size). The experiments also differed markedly in duration (1h and 24h). Calculated daily mortality therefore varied between 8 and 100%. At a non-saturation concentration of 5 mm larvae, predation rates, adjusted for cross-sectional area of Aurelia, ranged between 8 and 16 larvae per day (Table 3 & Figure 2 in Bailey 1984).

This corresponds to a daily mortality rate of 53% to 100%. By extrapolation of the relationship between mortality rate and container volume derived from my experiments (Table 4) to a 5 l container, I estimated a standardized instantaneous mortality rate (Za) of 0.5521, or 43% per day. Although this comparison is speculative, due to the differences in predator size and larval species used, my predicted value is only slightly lower than the minimum observed by Bailey. This correspondence gives strength to my finding that mortality rates developed from experiments using small experimental containers are seriously biased.

The logarithmic decline in mortality rates with increasing container volume (Figures 1 & 2) suggests that enclosures having a volume of $3m^3$ or greater should yield predation rates that may compare favorably with those occurring in-situ. A limited number of studies have been conducted in much larger experimental containers. While they did not specifically address the problem of larval mortality induced by jellyfish predators, reported instantaneous mortality rates in these enclosures (310 m^3) and basins (4000 m^3), where jellyfish were abundant, ranged from 0.015 to 0.12 (Gamble and Houde 1984; Oiestad, 1985). These values bracket those I observed (0.078) in my largest enclosures (Table 3).

The significant increase in mortality rate with predator size evident in my results is consistent with previous reports of a linear relationship between predation rates and the cross-sectional area Aurelia aurita <2 cm in diameter (Bailey and Batty 1983; Bailey 1984). A positive relationship between predation rate and predator diameter has been also reported for other gelatinous predators (Reeve et al. 1978;

Fulton and Wear 1985). The fact that predator diameter is more important than weight supports the hypothesis that the encounter rate of these predators is primarily related to their searching radius (Gerritsen and Strickler, 1977). A much wider range of predator sizes is needed to fully evaluate the validity of this relationship for Aurelia aurita.

The effect of larval size and larval density

Despite the small range of larval lengths used in my experiments (Table 2), a positive relationship between mortality rate and larval size was observed. Because larval length and yolk sac volume are negatively related (Table 2), it appears that larger capelin larvae with smaller yolk sac are more vulnerable to predation. This result could be explained by the dome-shaped relationship between larval size and predation mortality previously reported for different species of larvae (von Westernhagen et al. 1979; Bailey and Yen 1983; Bailey 1984). These relationships all indicated that predation induced mortality was most intense near the end of the yolk sac period. This variation in the vulnerability to predation during the early developmental stages may be related to the relative speeds of both prey and predator (Greene 1983) or to the reaction behavior of the larvae after encountering a particular predator (Webb 1981; Bailey and Batty 1984). Such behaviors have not been documented for capelin larvae. My own observations of the behavior of capelin larvae exposed to Aurelia aurita in a 10 l aquarium revealed that actively swimming capelin larvae bumped into the predator with no noticeable escape reaction.

Neither prey density nor temperature had a significant effect on

larval mortality rate. As a result I found a linear relationship between the predation rate of Aurelia aurita and initial larval density in each container size used (Figure 3). The feeding rates of other gelatinous predators have also been shown to be linearly related to prey density (Reeve et al. 1978; Purcell 1982; Fulton and Wear 1985) and independent of temperature (Fulton and Wear 1985).

Theory and Reality: Relationship between mortality rate and container size

The decrease in mortality rate with increasing container size was not unexpected. Most predation models assume that predators search randomly, and that the numbers of prey attacked is function of prey density but not of prey distribution (Rogers 1972; Hassell and May 1973; Hassell et al. 1976). Assuming a constant searching rate, the amount of space that can be searched by a given predator per unit of time is finite. The proportion of space surveyed by a predator during a fixed time period should thus vary inversely with an increase in the space available. These models also typically assume that, when confronted with an uneven prey distribution, the predator will forage for an equal time in each sub-unit of the total volume and will take a constant proportion of the prey in each sub-unit. Under this assumption, the number of prey consumed relative to the total number of prey present, when prey density is kept constant, should then be less in larger containers. The resulting mortality rate should then be inversely related to the container size. If these assumptions are valid in the three dimensional space within which plankton organisms interact, the mortality rate of prey should be inversely related to the container volume when prey

density is constant, and the slope of this relationship on a log-log basis should be equal to -1. This assumption underlies the calculation and the use of clearance rate to describe and standardize the predation rate by many planktonic organisms.

The most important result of my experiments was not the confirmation of a container size effect on mortality rate, but rather the finding that the slope of the relationship between mortality rate (both Z and Za) and container volume (Table 4) differed significantly from the expected value of -1. My results clearly indicate that both the predation rate and the clearance rate vary positively with enclosure size when prey density is held constant (Figure 3). This is not consistent with theory.

An alternative hypothesis to account for the positive relationship between predation rate and container size would be that the searching behavior of jellyfish predators may have been impaired in the smaller containers, perhaps due to more frequent contacts with the container walls (Reeve 1980; Purcell and Kremer 1983). However, the observed relationship between predation rates and the surface to volume ratios of the containers does not support this hypothesis. A specific test of this hypothesis, consisting of experiments conducted in enclosures having equal volume but very different surface/volume ratios (enclosures and tanks), showed no significant difference in mortality rates when these rates were corrected for differences in predator size (Table 3). I therefore conclude that the wall effect was not the sole or even a major factor contributing to the observed pattern.

Another possible reason for the failure to achieve the -1 slope in the relationship between log-mortality rate and log-container volume, as

predicted from theory, is an effect of enclosure size or shape on prey distribution. The vertical distribution of capelin larvae confined in in-situ enclosures of the types I employed is heterogeneous. The highest concentrations typically occur near the surface and the bottom while relatively few larvae occupy the intermediate depths (Chapter 1). This pattern was found to be independent of larval density. It also varied on a diel basis, with the larvae becoming more homogeneously distributed at night. The proportions of larvae found near the surface were similar in both 5m and 9m deep enclosures. Daytime vertical patchiness was thus greater in the 9m enclosure due to the increasing depth of the water column (Chapter 1). I believe the variation in mortality rates with enclosure size observed in the series of experiments reported here to be related to differences in the vertical spatial scale of prey patches between the various enclosures. Small distances between prey patches induced by reduced enclosure depth may produce higher encounter rates between predator and prey thus increasing larval mortality rates.

The calculated slope (-0.915, s.e. 0.168) of the log-log regression between standardized mortality rates (Za) and the total depth of containers did not differ significantly from -1. This suggests that the mortality rates are inversely proportional to water depth and supports my hypothesis that distance between the prey patches and the predator is more important than volume in determining the differences in predation rates between enclosures.

The variation of predation rates with container size implies that the pooling of data from experiments conducted in containers of different sizes could confound the interpretation of results. For example, the container size specific Type I functional response (Holling

1966) exhibited by Aurelia aurita in my experiments, can, if pooled, yield an erroneous curvilinear Type II functional response. I pooled my results from the 5m deep enclosures (volume 3.21 m^3) and the tanks (volume 0.27 m^3) and fitted them to the random predator equation (Rogers 1972). The fitted model was significant (r^2=0.61, p=0.013) and the two parameters of the functional response curve, i.e. the attack rate and the handling time value, were significantly different from zero. The pooled results could thus be incorrectly interpretated as a Type II curvilinear response.

Peters and Downing (1984), in an empirical comparison of clearance rates for marine copepods, found no significant effect of food concentration on clearance rate. They did, however, find a significant effect of the container volume. This finding also demonstrates that mixing different container sizes and prey densities yields erroneous results and makes difficult the comparison of predation rates obtained in different experimental conditions.

Although the effect of container size on the feeding rates of copepods has been recognized for 30 years (Marshall and Orr 1955), the strategy of combining results of experiments conducted in different container sizes in an effort to cover a wide range of prey densities is commonly applied (Fulton 1982; Yen 1983,1985; Paffenhoffer 1984a). This practice should be discarded.

The effect of prey distribution on mortality and predation rates

Prey distribution and prey patchiness are key elements in general theories of predator-prey dynamics and optimal foraging (Murdoch and Oaten 1975; Pyke 1984). Moreover, the concept of random search appears

unrealistic for many predators that alter their searching rate after encountering a prey (Murdie and Hassell 1973; Hassell et al. 1976; McClintock and Lawrence 1985). Theoretical models incorporating a non-random search have lead to various interpretations on the role of prey patchiness on predation rate (Oaten 1977; Hassell et al. 1976; Stephens and Charnov 1982; Taylor 1984; Cain 1985).

However, these models have typically investigated different prey distributions within experimental containers of similar size. This situation is not comparable to the conditions prevailing in my experiments where prey patchiness was altered by varying the container size. Kaiser (1983) observed that when the prey density was constant, the predation rate was higher in larger containers due to a more heterogeneous distribution of prey. My observations (Figure 3) are consistent with Kaiser's findings that the functional response depends not only on the density of prey but also on the relative distribution of predators and prey. In small containers, the predator may perceive the prey population as a relatively homogeneous unit. In larger containers the distinction of prey patches becomes more probable. This could explain the non-significant difference of mortality rates and filtration rates in small enclosures despite differences in shape and depth. These findings are consistent with the argument that prey distribution and the concept of patch itself should be defined according to the relevant spatial scale for foraging and prey detection by the predator (macropatch vs micropatch: Tinbergen 1981; Haccou and Hemerik 1985).

The evaluation of these concepts requires investigations on the behavior of the interacting individuals. Laboratory observations indicate that the swimming behavior of jellyfish (Arkett 1984), and

particularly of Aurelia aurita (Bailey and Batty 1983), is enhanced after encounters with prey. This suggests a non-random search component. Similar information would be difficult to obtain at the scale of my in-situ enclosures. However, I did evaluate the influence of vertical prey patchiness and predator movement on predation rates by means of simple models.

Simulation models were developed to generate and compare mortality rates of larvae in 1m, 5m and 9m deep enclosures. Real data on the vertical distribution of larvae in 5m and 9m enclosures (Chapter 1) were used. A homogeneous distribution of larvae was assumed for the 1m enclosure. To approximate my experimental conditions, models were initiated at 18:00 h and were run for 40h. The predator was assumed to search at a constant rate of 10 liters/h, which is close to the average clearance rate of a 5cm Aurelia aurita as measured in my 1m enclosures (Table 3). The number of larvae taken per hour was calculated as the product of the searching rate and the density of larvae within the layer surveyed. In the first series of simulations, the capture rate of the predator was not limited. A subsequent series of simulations were run in which maximum capture rate was set at 25 larvae per hour, which would not be unrealistic for a 5cm Aurelia aurita (Bailey and Batty 1983). The initial numbers of larvae were set at 100, 1000 and 2000 in the 1m, 5m and the 9m enclosures respectively. This approximated equal densities between containers. The number of larvae in each enclosure was iteratively calculated hourly after the initiation of the simulation. The instantaneous mortality rate (Z) was computed from the number of larvae remaining in the enclosures after 40h.

In model I, the predator remained at the same depth during the 40 h

period and three depths (surface, mid-depth and bottom) were simulated. In model II, the predator was moved up and down through the full water column and surveyed a 1m deep layer each hour. Predator behavior in model III simulated a diel vertical migration pattern in which the predator reached the surface layer only at night. Many jellyfish, including Aurelia aurita, are known to exhibit such light related migration (Hamner et al. 1982; Arkett 1984). In model IV, the predator remained in a given prey patch (depth layer) until feeding rates in that patch dropped below 15 larvae/h (60% of the maximum capture rate possible). At that time it moved to an adjacent depth layer. Model IV is equivalent to a non-random search in the presence of prey patches and follows one prediction of the optimal foraging theory (Pyke 1984). In model V, the criteria of models III and IV were combined to simulate a non-random search but with environmental constraint on the vertical movement of the predator imposed by the simulated diel light response. In all models except model I, the predator was initially positioned at mid-depth. Movement to an adjacent depth layer was generated via a uniform (0,1) random number function. Models II to V were run 100 times each to generate means and standard errors of the mortality rates for each enclosure. The 1m enclosure simulation was run only once because no predator movement was involved.

The simulation produced by models II and IV most closely approximated the mortality rates observed in my experiments (Table 6). Predictions from model I, in which predator was stationary, were either much higher or much lower than the observed, depending on predator location relative to the prey distribution. This suggests that predator

Table 6. Results of simulation models of instantaneous larval mortality in relation to predator movement and prey distribution in 1m, 5m and 9m deep enclosures. Values in parantheses are standard deviations from 100 iterations for models II to V.

Model		Mortality rates			Ratios		
		1m	5m	9m	1/5	1/9	5/9
		0.955					
I	surface		0.1948	0.2013	4.90	4.74	0.97
	mid-depth		0.0712	0.0244	13.41	39.14	2.92
	bottom		0.1415	0.0519	6.75	18.40	2.73
II			0.1106 (0.0082)	0.0611 (0.0119)	8.63	15.63	1.81
III			0.0864 (0.0060)	0.0411 (0.0059)	11.05	23.23	2.10
IV			0.1208 (0.0091)	0.1016 (0.0389)	7.90	9.40	1.19
V			0.1009 (0.0055)	0.0415 (0.0087)	9.46	23.01	2.43
Observed		0.974	0.1284	0.0800	7.58	12.17	1.58

movement is an important component of the observed predation rates. Model III and V, for which predator had limited vertical movement, predicted lower mortality rates and higher ratios of these mortality predictions relative to the observed. Identical results were obtained when models were run with a maximum capture rate. This is due to the low searching rate of Aurelia relative to the prey density in the containers. Given such a searching rate, a larval density of 2500 $1/m^3$ would be required for the predator to eventually catch 25 larvae. Bailey and Batty (1983) found that saturation of Aurelia aurita began at larval densities greater than 5000 $/m^3$ which is well above the densities used in my study and those typically reported for larval fish in-situ.

These simulation models neither prove nor disprove the existence of non-random search patterns by a jellyfish predator. They do however serve to indicate that the differences in mortality rates observed between the various containers may result from the differences in the relative distribution and movement of prey and their consequent effects on the predator-prey relationship.

The distribution of marine plankton in nature is both temporally and spatially heterogeneous and vertical patchiness is generally much more pronounced than horizontal patchiness on the scale of few meters (Steele 1976). The largest (5 & 9m) enclosures used in this study appeared to allow the reproduction of such small scale vertical pattern and thereby yield mortality rate estimates that are less biased.

The results of my study lead me to conclude that the relative vertical distribution of predator and prey may be the most important, but yet the least considered, factor controlling the predator-prey relationship between macrozooplankton and larval fish in-situ.

Fine-scaled field studies of the vertical distribution of both predator and prey and of the feeding activities of the potential predators of larval fish are still limited in number. Such studies are needed to adequately quantify the impact of predation on larval mortality.

Conclusion

I conclude that the large differences in predation rates I observed in enclosures of different sizes, irrespective of the initial density of larvae used, demand rejection of the null hypothesis that predation rate is independent of enclosure size. This implies that the parameters of the functional response, when derived from experiments using small containers typical of those used in laboratory studies to date, cannot be used to estimate the in-situ predation rate of macrozooplankton predators on larval fish, and cannot be reliably incorporated into larval population models. I concur with Kaiser's (1983) conclusion that small scale spatial heterogeneity influences the functional response curve. My results also indicate that larger scale enclosures which allow spatial heterogeneity in predator-prey distributions to develop, can yield reliable and reproducible data on predator-prey interactions that are more relevant to the field situations.

CHAPTER 3

Mortality rates imposed on larval fish by jellyfish predators: an experimental evaluation employing in-situ enclosures.

INTRODUCTION

Starvation and predation are believed to be the major causes of the very high mortality rates that characterize the early life stages of marine fishes (May 1974; Dahlberg 1979). Field evidence supporting the starvation and predation hypotheses is, however, both limited and circumstantial (Leggett 1986).

The dramatic decline typically seen in the numbers of pelagic fish eggs (Harding et al. 1978; de Ciechomski and Sanchez 1984) and the results of a limited number of predator exclusion experiments which indicated high larval survival (65-96% after 20 days) (Laurence et al. 1979; Oiestad and Mockness 1981; Mockness 1982; Mills 1982) are currently the main lines of evidence for the predation hypothesis. These observations, plus the paucity of solid evidence in support of the starvation hypothesis, in spite of over 60 years of study (Leggett 1986), has led to the repeated suggestion that predation may be the major source of death for fish eggs and larvae (Murphy 1961; Cushing and Harris 1973; Cushing 1974,1983; Ware 1975,1980; Johannes 1978; Hunter 1981,1984; Sissenwine 1984). Hewitt et al.'s (1985) recent study of the condition of sea-caught jack mackerel larvae and Taggart's (1986) demonstration that mortality of 40 cohorts of larval capelin during three consecutive years was consistently positively correlated with the abundance of chaetognaths and jellyfish predators, provide additional support for this position. Taggart (1986) also demonstrated that larval mortality was uncorrelated to larval food abundance and exhibited no evidence of density dependence.

Given their numerical abundance and their wide distribution, macrozooplankters are frequently considered the most important "potential" predators of the early larval stages of fishes (Harding and Talbot 1973; Möller 1980,1984; Purcell 1985). Three main lines of evidence support this hypothesis: 1) negative correlations of predators and larval fish densities in-situ; 2) evidence of in-situ feeding by macrozooplankton predators on larval fish; and 3) laboratory studies of predator-prey interactions. Negative correlations between the relative abundance of macroinvertebrate predators and fish larvae have frequently been interpreted as evidence of predation mortality (Möller 1984). Frank and Leggett (1985) have challenged this interpretation arguing, on the basis of original research and reanalysis of previously published studies, that the negative correlations result from aliasing caused by selective occupation of different water masses by larvae and potential predators. Their research (Frank and Leggett 1982a,1983) has demonstrated that larvae of several fish species selectively occupy water masses rich in potential food for larvae and depauperate of predators. They classified these water masses as "safe sites".

In-situ feeding studies involving gut content analyses of potential predators have indicated relatively high rates of predation on larval fish (16% by copepods - Hartig et al. 1982; 0.1 - 45% by amphipods - Yamashita et al. 1985; 2 - 60% by various jellyfish species - Möller 1980; Purcell 1981,1984,1985). However, these estimates have been based on assumed constant feeding rates and were strongly dependent on assumed digestion rates. Moreover, they do not account for temporal and spatial variability in the distribution and size of both predators and prey. Where predators were collected during plankton surveys, caution is also

required in interpretating the mortality estimates because of possible "cod-end" feeding (Nicol 1984, Brewer et al. 1984). The impact of this "apparent" predation on larval mortality rates ultimately requires a more direct quantitative determination of predation rates (Brewer et al. 1984).

Numerous laboratory studies of predation have helped to identify the potential predators of larval fish (Hunter 1981,1984; Purcell 1985). To date, quantitative laboratory studies on several species of macrozooplankton including copepods, euphausiids, amphipods, chaetognaths, ctenophores and jellyfish, have typically produced asymptotic relationships between predation rate and larval density. Studies involving jellyfish as predators have yielded the highest predation rates (up to 300 larvae per day - Bailey and Batty 1983,1984; Bailey 1984; Purcell 1985). However, extrapolation of these laboratory results to field conditions must be approached with caution. Larval mortality rates imposed by jellyfish predation are strongly dependent on the size of the experimental container employed (Chapter 2). The small container size typically employed in laboratory studies (from 0.2 to 5 liters) have yielded mortality rate estimates that are seriously biased (Chapter 2).

Predator-prey dynamics as they apply to larval fish in-situ also remains poorly understood. Several authors have argued that the low densities of fish eggs and larvae that typically occur in-situ (as a result of rapid dispersal during pelagic drift) should elicit little or no aggregative (numerical) response in predator populations (Murphy 1961; Hempel 1965; Harding and Talbot 1973; Cushing 1983). If this hypothesis is correct, predation mortality during the early life stages

of fish should be proportionnal to predator numbers (Hempel 1963; Jones 1973; Ware 1975; Cushing 1983). Laboratory studies of predators feeding on larval fish provided evidence of a Type II functional response (Holling 1966). However, all these studies employed larval densities (frequently up to 10000 larvae per m^3) much higher than those generally reported in-situ. There is thus reason to question the existence of a Type II functional response in nature.

Frank and Leggett (1982a,1983,1985) have hypothesized that the synchronous mass releases observed in some larval fish species are an adaptation to saturate the predators present during release events. If predator satiation does occur in nature, selective occupation of "safe-sites" by larvae may represent an evolutionary adaptation to minimize larval mortality due to predation by means of both a numerical response (to spatially avoid their potential predators) and a functional response (by saturation of the feeding rates of those predators that are encountered) (Leggett 1985). Johannes (1978) hypothesized that breeding synchrony may serve a similar predator avoidance function in coastal tropical fishes. "Safe-site" hypotheses linking reproductive synchrony and predator avoidance have also been proposed for plant-herbivore interactions (Janzen 1978; O'Dowd and Gill 1984), insects (Sweeney and Vannote 1982), other zooplankton (Forward et al. 1986) and some mammals (Estes 1976). Quantitative description of the functional relationship between predation rate and prey density is prerequisite to evaluation of the "safe-site" hypothesis. It also represents the basic requirement for quantitative assessment of larval fish mortality due to predation.

Several other variables (the presence of alternate prey, predator density, size of predators and prey) are also known to be important

determinants of the rate and form of the predator/prey relationship (Murdoch and Oaten 1975; Hassell 1978; Taylor 1984; Houck and Strauss 1985). Murdoch et al. (1984) have recently shown that information on the factors affecting the functional response can lead to effective decriptions of predator/prey relationship in aquatic systems. The impact of these factors on larval fish mortality due to predation is also poorly described. The addition of alternate prey was shown to decrease the predation rates on larval prey for some predators (copepods - Lillelund and Lasker 1971; Bailey and Yen 1983; chaetognaths - Kuhlmann 1977; amphipods - von Westernahgen and Rosenthal 1976) but not for others (euphausiids - Theilacker and Lasker 1974). The effect of alternate food on the predation rates of jellyfish predators remains unquantified. Predation rates have generally been found to increase with predator size (Theilacker and Lasker 1974; von Westernhagen et al. 1979; Bailey and Batty 1983,1984; Yamashita et al. 1984). However, the effect of larval size is less predictable and varies with the types of predators and larvae investigated. An inverse relationship between predation rates and larval size has frequently been reported (Lillelund and Lasker 1971; Theilacker and Lasker 1974; Webb 1981; Yamashita et al. 1984; Bailey 1984), but a dome-shaped relationship has also been observed (von Westernhagen et al. 1979; Bailey and Yen 1983). The relative importance of these factors in determining the relationship between predation rate and larval density remains problematic. This has precluded development of a general understanding of predator/prey relationships as they apply to larval fishes.

In this study, I examined the effect of predator and prey density on larval fish mortality rates imposed by jellyfish predators. The

effect of alternate prey on these rates was also evaluated. Specifically I evaluated the following hypotheses: 1) larval mortality due to predation should be directly proportional to the abundance of jellyfish predators; 2) larval fish mortality due to predation should be inversely related to the initial larval density; and 3) larval mortality due to predation should be significantly reduced in the presence of alternate food available for predators.

MATERIALS and METHODS

Enclosure studies

Predation experiments were conducted in Bryant's Cove, Newfoundland during the summers of 1982, 1983 and 1984. I used 3,2 cubic meters in-situ enclosures (Chapter 1) which were moored 250m from the shoreline in 8m of water. Dacron enclosures with a conical bottom composed of 53 µm Nitex were employed in all but two series of experiments conducted in 1982. In these two experiments full Dacron enclosures were used. All enclosures were allowed to fill by diffusion of water through the porous walls. This eliminated particles larger than 100 µm (equivalent spherical diameter) (Chapter 1). Procedures for deployment and retrieval the enclosures are described in Chapter 1.

Experiments were initiated shortly before dusk (90% between 17:00 and 21:00). Some experiments lasted up to 96 h, but the majority (89%) had a duration of 36 to 46 h (average 44 h, mode 39 h). At the end of each experiment, all enclosures were lifted, and their contents (fish larvae, predators, alternate food) were preserved in 10% buffered seawater formalin. Because temperature, salinity and oxygen levels inside the enclosures were similar to levels in-situ (Chapter 1), temperature and salinity recorded at a depth of 4.5 m with a Aanderaa currentmeter moored 30 m from the enclosures were used to monitor the conditions in the enclosures.

Yolk-sac larvae of capelin (Mallotus villosus) were used as prey. All larvae were collected from the spawning beach at Bryant's Cove immediately prior to stocking. To collect larvae, beach gravel containing recently hatched larvae was mixed with seawater in a bucket

to release the larvae. Actively swimming larvae were captured with a wide bore pipette, counted and placed in 500 ml glass jars filled with filtered seawater. The closed jars were suspended in the enclosures for approximately one hour to allow temperature acclimatation prior to the release of larvae. In 1983 and 1984, a sample of 100 larvae from each stocking was preserved in 10% buffered formalin-seawater immediately after capture. These were used to determine the physical condition of the larvae initially stocked.

To assess the levels of larval mortality caused by capture and handling, 150-200 capelin larvae were placed in each of 15-20 sealed jars filled with 1 liter filtered seawater. The jars were then immersed in a land-based tank supplied with continously running seawater pumped from the nearshore zone of Bryants Cove. Water temperature continuously monitored in the tank varied with changes in Cove temperature (+ 2 C). Two or three times each day for a period of one week, one jar was randomly selected and all dead larvae in the jar were isolated. Dead and live larvae were then separately preserved in 10% buffered formalin-seawater. Later, total length, body depth and yolk sac volume were measured for a maximum of 40 dead larvae and 40 live larvae from each jar. This experiment was repeated three times (16-24 July 1983, 14-22 July 1984 and 21-29 July 1984).

Jellyfish predators used in the experiments were individually collected adjacent to the enclosures by scuba. Individual predators were trapped in glass jars and transferred immediately to the enclosures. The number of predators added to each enclosure was constant within each experiment, but varied between experiments (2-5 per enclosure), depending upon their availability. The resulting predator densities

(0.6-1.5 per m^3) approximated the average in-situ densities of predators in this area (range = 0.1 - 10 per m^3; Frank and Leggett 1982a).

To assess the effect of alternate prey for the predators on larval mortality due to predation, I performed 10 experiments in which wild zooplankton was added to the enclosures. This zooplankton was collected with a large-volume plankton pump (Taggart and Leggett 1984) operated at a monitored flowrate of 250-300 l/min. The depth of the pump intake was constantly varied between 0 and 5 m during collection. To avoid adding predators during pumping, the pump discharge was passed through a 1000 µm screen suspended inside the enclosures. Three samples of volumes equivalent to those added to the enclosures were taken during each food addition to each enclosure. These were used to determine the initial abundance and size distribution of the zooplankton added. The number of capelin larvae accidentally added to the enclosures during pumping was also estimated from these samples. Larval densities were subsequently corrected for this bias. These additions proved to be minimal.

The effect of larval density on predation mortality was determined for four jellyfish species: Catablema vesicarium (Hydrozoa, Anthomedusae), Staurophora mertensi (Hydrozoa, Leptomedusae) Cyanea capillata (Scyphozoa), and Aurelia aurita (Scyphozoa). These species have previously been shown to kill and ingest fish larvae (Fraser 1969; Purcell 1985).

In 1982, replicated larval density experiments were conducted to assess the effect of larval density on predation mortality. In these experiments, three enclosures each containing predators and one control enclosure containing larvae but lacking predators were simultaneously deployed. Because the number of enclosures available was limited,

experiments involving different larval densities were conducted on different dates. In these experiments only Catablema vesicarium and Staurophora mertensi were used as predators. In 1983 I modified the experimental design to simultaneously test a wider range of unreplicated larval densities. These experiments were replicated in time. The design employed a maximum of 10 enclosures. During each trial, one enclosure, stocked at a pre-selected larval density, but lacking predators served as control. While this design was statistically less precise because of the lack of replicates at each prey density (Houck and Strauss 1985), it eliminated the co-variability of both time and larval density.

The initial density of capelin larvae in all experiments was varied between 12 and 780 larvae per m^3. This spans the natural range of densities of newly emergent capelin larvae reported for Bryant's Cove (Frank and Leggett 1981,1982a; Taggart 1986) and for the estuary and Gulf of St.Lawrence (Jacquaz et al. 1977; de Lafontaine et al. 1984; Fortier and Leggett 1985).

The effect of predator density on larval mortality was evaluated in one experiment conducted in 1984. A fixed number of larvae (300) were stocked into 9 enclosures containing 1, 4, 7 or 10 Aurelia aurita. In this experiment, three replicates were used for enclosures containing 1 and 4 predators. Two replicates were employed for enclosures containing 10 predators and only one enclosure was used for the density involving 7 predators.

The effect of alternate food on the larval mortality imposed by jellyfish predators was investigated in 1983 and 1984. I first conducted experiments to evaluate the effect of a wide range of larval densities on mortality rates in the presence of relatively constant

alternate food densities. In each experiment, two control enclosures containing larvae and alternate food but lacking predators were employed to evaluate possible interaction effects between zooplankton and larvae. Three series of such experiments employing Staurophora mertensi and Aurelia aurita as predators were originally performed. However, the results of the third experiment involving Aurelia aurita conducted on August 8, 1983, were discarded because of the unsatisfactory condition of predators at retrieval. In these experiments the quantity of zooplankton added to each enclosure was regulated by pumping equal volumes of water into each enclosure. However, because of small scale patchiness, some between enclosures variation (C.V. 1-23%) in initial zooplankton density occurred. The density of zooplankton added also varied between series of experiments because of seasonal variation in in-situ zooplankton abundance. To evaluate the effect of this variation in alternate food density on predation rates, I conducted a second series of experiments in which the number of capelin larvae (250) was fixed and the quantity of zooplankton added was varied by altering the volumes pumped by a ratio of 1:15. Because it was impossible to determine a-priori the densities of zooplankton achieved, no replication was attempted within trials. Five series of such experiments were completed, two using Aurelia aurita as predators and three using Staurophora mertensi.

In all experiments, treatments were randomly assigned to the enclosures.

Laboratory analyses

The number of larvae recovered from each enclosure at the termination of the experiments was determined. Total length, body height behind the pectoral fins and yolk-sac volume were measured for a maximum of 40 larvae selected at random. Yolk sac volume was estimated using the spheroid equation (Laurence 1973):

$$\text{Yolk volume} = (3.14159 * \text{Yolk length} * (\text{Yolk depth}^2)) / 6.$$

I computed the ratio of total length to body height as an index of larval fish condition (Ware et al. 1981). Predator size (umbrella diameter) was measured and was corrected for shrinkage due to formalin preservation (Möller 1980; Appendix 1). Jellyfish fresh weight was estimated from umbrella diameter/fresh weight relationships because the loss in wet weight during formalin preservation continues beyond 5 months in preservative (Appendix 1). Initial and final counts of zooplankton were made with a Coulter model TA-II particle counter using a 2000 µm aperture tube. This provided estimates of the size distribution of alternate prey in the 80 to 520 µm equivalent spherical diameter (e.s.d) size range. Total abundance (No/Liter) and total biomass (mg/Liter - derived from volume estimates assuming a density of 1.0) were estimated for each zooplankton sample. The ratio of total particle biomass to total particle abundance was computed to estimate the average size (µm) of alternate food added to the enclosures in each experiment. Mean and standard deviations of water temperature during each experiment were computed from currentmeter data. Standard deviation in water temperature was used as an index of variability of water conditions in the enclosures during experiments.

Statistical treatment

The instantaneous daily larval mortality rate due to predation (Z: predator^{-1}.day^{-1}) was calculated as:

$$Z = (\log(Ni/Nf) - \log(Ni/Nc)) / T * P \qquad (1)$$

where Ni is the initial number of larvae stocked, Nc and Nf are the final number of larvae in the control enclosures and in the enclosures with predators respectively, T is the duration of the experiment in days and P is the number of predators added to the enclosures. This equation corrects for prey depletion during experiments in which ingested prey are not replaced (Royama 1971; Rogers 1972; Arditi 1982). Daily predation rates (No. larvae/predator/day) were calculated using the equation:

$$I = Ni * (1-\exp(-Z)). \qquad (2)$$

All statistical tests were done on the Z values because I sought to identify the factors that affect predation mortality on larvae rather than to define the exact parameters of the functional response. I choose this approach because: 1) the exact parameterization of the functional response is statistically difficult and can yield biased interpretations in comparative studies (Arditi 1982; Livdahl and Stiven 1983; Houck and Strauss 1985; Williams and Juliano 1985); 2) the variation of the two parameters of the functional response (attack rate and handling time) relative to different factors (predator size, prey size, abundance of alternate food, environmental conditions) is difficult to resolve given the mathematical form of the curve.

The relationship between Z and initial larval density was

investigated using an analysis of variance blocked by time, and by a regression analysis. Correlation analyses were also performed to investigate the interrelations between Z, larval density and predator size within each experiment. The coefficients of correlation between Z, larval density, predator size, water temperature, larval size, larval yolk sac volume, and abundance of zooplankton added as alternate food were also calculated between experiments. The relationships between the calculated daily predation rates (I) and the initial larval densities were investigated by regression analysis.

The statistical significance of the effect of alternate food on larval mortality rates was evaluated by comparing results from experiments conducted in which alternate food was present and absent. The data from different experiments were pooled and standard regression residuals were computed. These residuals were analysed by F-test (ANOVA) and also by non-parametric Mann-Withney U-test. While the non-parametric test is less powerful than the F-test derived from the general linear model, it is not subject to the assumptions of normality, independence and equality of variance for the error term. It is thus recommended for comparative analysis of predation rates (Houck and Strauss 1985).

RESULTS

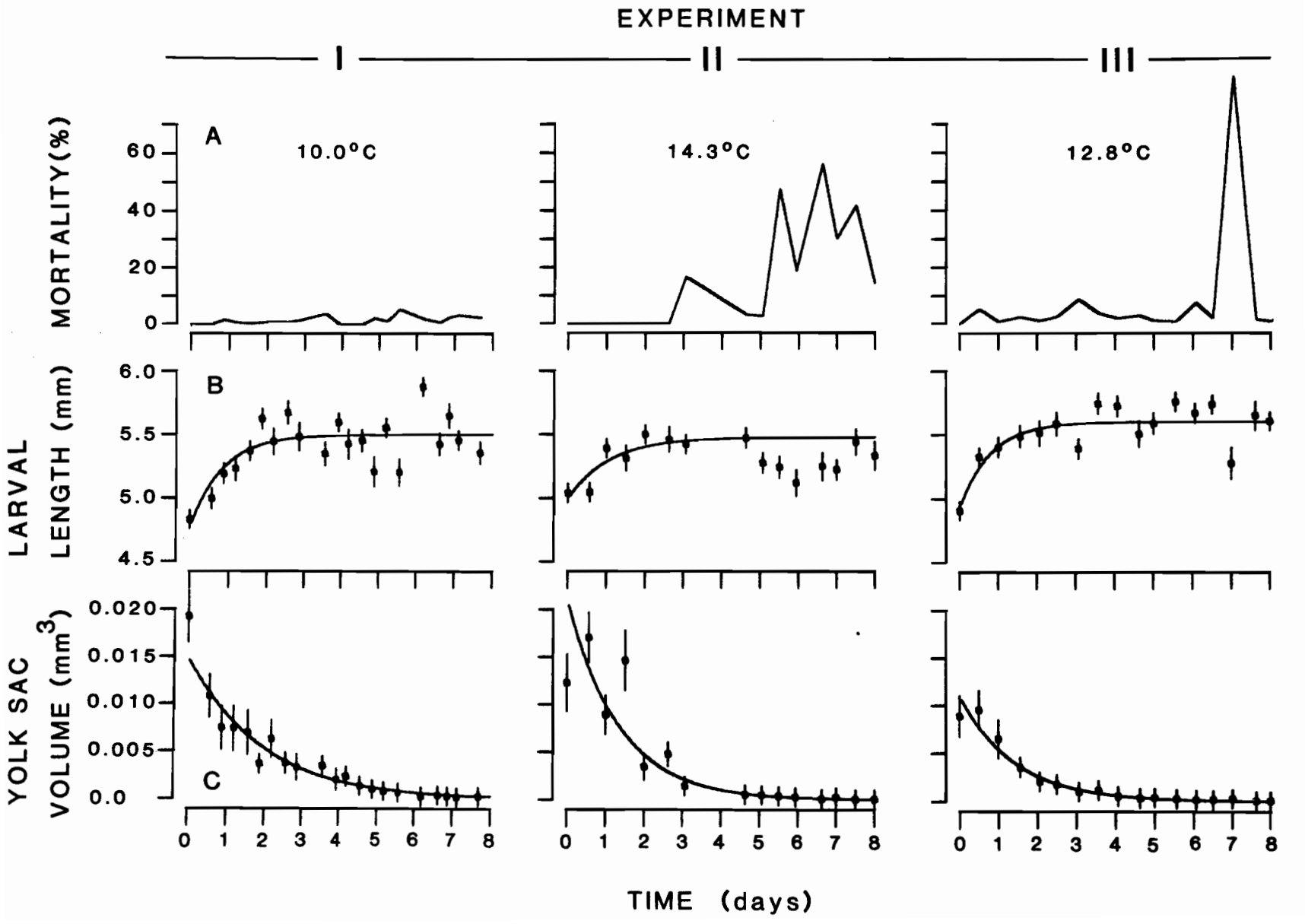
Larval mortality due to capture and handling

Cumulative larval mortality due to capture and handling (% dead) was consistently <5% during the first 96 hours (Figure 1a). The high mortality observed after 5 days in experiment II is believed to have resulted from starvation. I conclude that larval mortality induced by capture and handling was negligible during my predation experiments which averaged 39 hours in duration and had a maximum duration of 96 hours.

The total length of live capelin larvae held in jars without food increased initially and reached a maximum size after 3 d (Figure 1b). This initial growth was mainly at the expense of yolk sac reserves which were virtually exhausted by day 4 (Figure 1c). Larval growth rate was determined by fitting the modified Brody-Von Bertalanffy equation (Ricker 1975) to the length data. The rate of yolk sac utilization was estimated from a negative exponential function relating yolk sac volumes to time. The coefficients of the two equations for each experiment are given in Figure 1.

Larval size at yolk sac resorption and the time to complete exhaustion of the yolk sac in my experiments were very similar to those reported for capelin larvae developing in the beach sediments (Frank and Leggett 1982b). However, the curvilinear growth I observed differed from the linear growth pattern reported by Frank and Leggett (1982b). The higher growth rate observed in my experiments may be due to higher water temperatures which influence both growth rates and yolk utilisation rates of larval capelin (Frank and Leggett 1982b).

Figure 1. Percent mortality, total length (mm) and yolk sac volume (mm^3) of capelin larvae held for one week in glass jars without food during 3 different experiments. Relationships of larval length (TL) over time (t) are: Exp. 1, $TL = 5.5 - 0.725 * \exp(-0.051\ t)$, $r^2=0.83$; Exp. 2, $TL = 5.45 - 0.461 * \exp(-0.044\ t)$, $r^2=0.80$; Exp. 3, $TL = 5.6 - 0.671 * \exp(-0.052\ t)$, $r^2=0.82$. Relationships between yolk sac volumes (YV) and time (t) are: Exp. 1, $YV = 0.0133 \exp(-0.021\ t)$, $r^2=0.95$; Exp. 2, $YV = 0.0117 \exp(-0.028\ t)$, $r^2=0.95$; Exp. 3, $YV = 0.0084 \exp(-0.024\ t)$, $r^2=0.96$. Time is in hours. All regressions are significant ($p<0.001$). Vertical bars represent standard errors of the mean.


EXPERIMENT
I
II
III
A
10.0°C
14.3°C
12.8°C
MORTALITY(%)
60
40
20
0
B
LARVAL LENGTH (mm)
6.0
5.5
5.0
4.5
C
YOLK SAC VOLUME (mm3)
0.020
0.015
0.010
0.005
0.0
0 1 2 3 4 5 6 7 8
TIME (days)

The mean total length of dead larvae (3.68, s.e.= 0.066, n= 155) was significantly (32%) less than of live larvae (mean = 5.42, s.e. 0.009, n=1252; F-test, $p<0.0001$). Hay (1981) reported a rapid reduction (17%) in total length of herring larvae within 1 hr after natural death. This change in length was independent of subsequent shrinkage due to formalin fixation and delayed fixation increased the total shrinkage observed (natural plus fixation). This, plus natural differences in condition which may exist between dying and healthy larvae produced differences in the computed index of larval condition (total length/ body height) (Live: 32.36, s.e. 3.13; Dead: 20.09, s.e. 6.07). A two-way ANOVA showed that these measures differed significantly between the dead and live larvae ($F=1240.2$, $p<0.0001$), but did not vary between experiments ($F=1.04$, $p=0.31$). This result justified my use of the index as an indicator of the proportion of dead and live larvae at the termination of each enclosure experiment.

Larval mortality in the absence of predators

The rate of recovery (%) of larvae from control enclosures lacking predators was much higher than recovery rates from enclosures containing predators (Figure 2). Because the possibility exists that not all larvae recovered at the end of a trial were alive, I evaluated larval survival by determining larval condition (total length/body height) for 10 experiments conducted in 1983 and 1984. The frequency distributions of the condition of larvae at the time of stocking were compared to those of larvae recovered from control enclosures and from enclosures containing jellyfish (Figure 3). The condition of larvae from both control and experimental enclosures were significantly higher than those

Figure 2. Frequency distribution of percent of larvae recovered from enclosures under various experimental conditions.

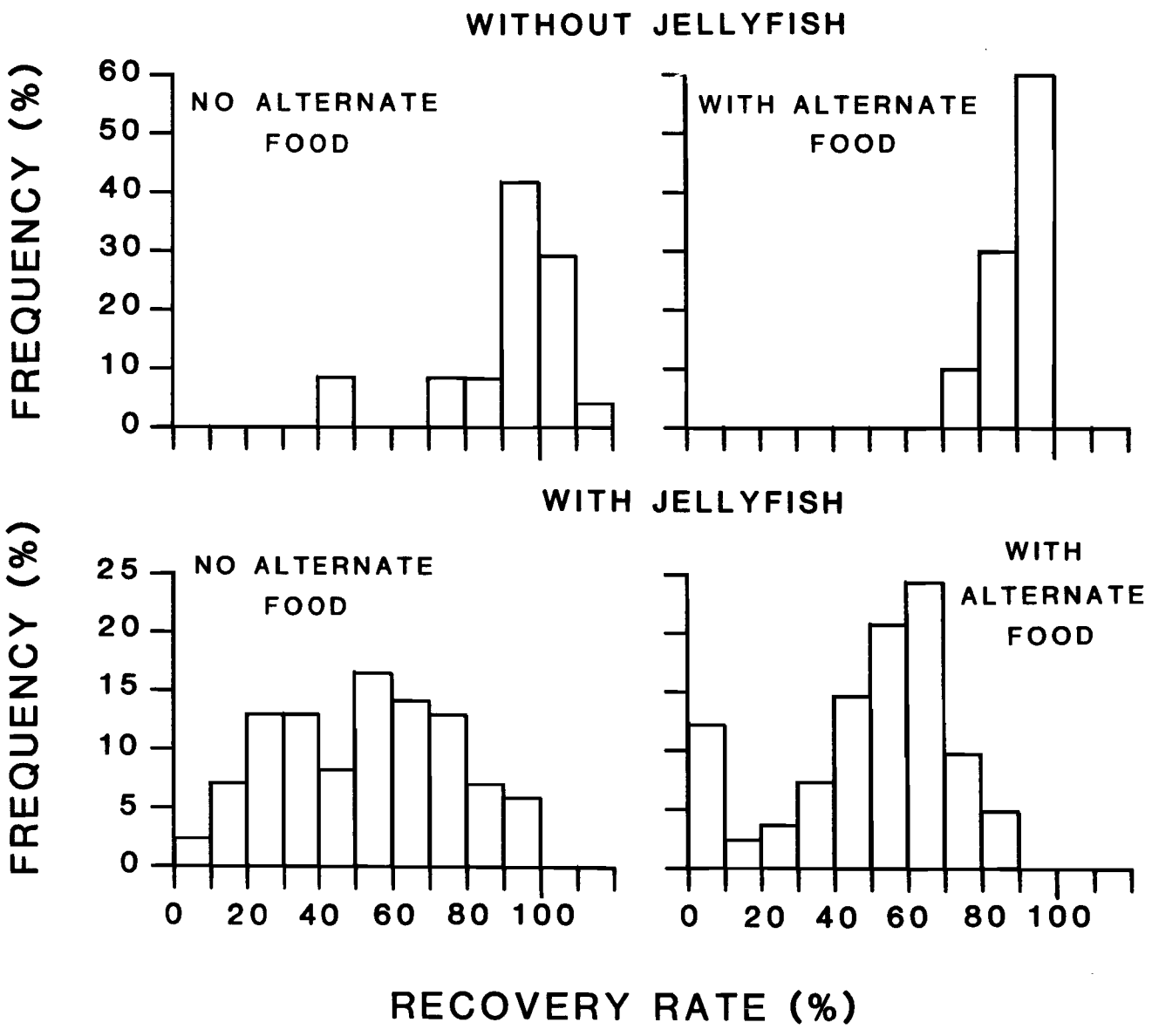
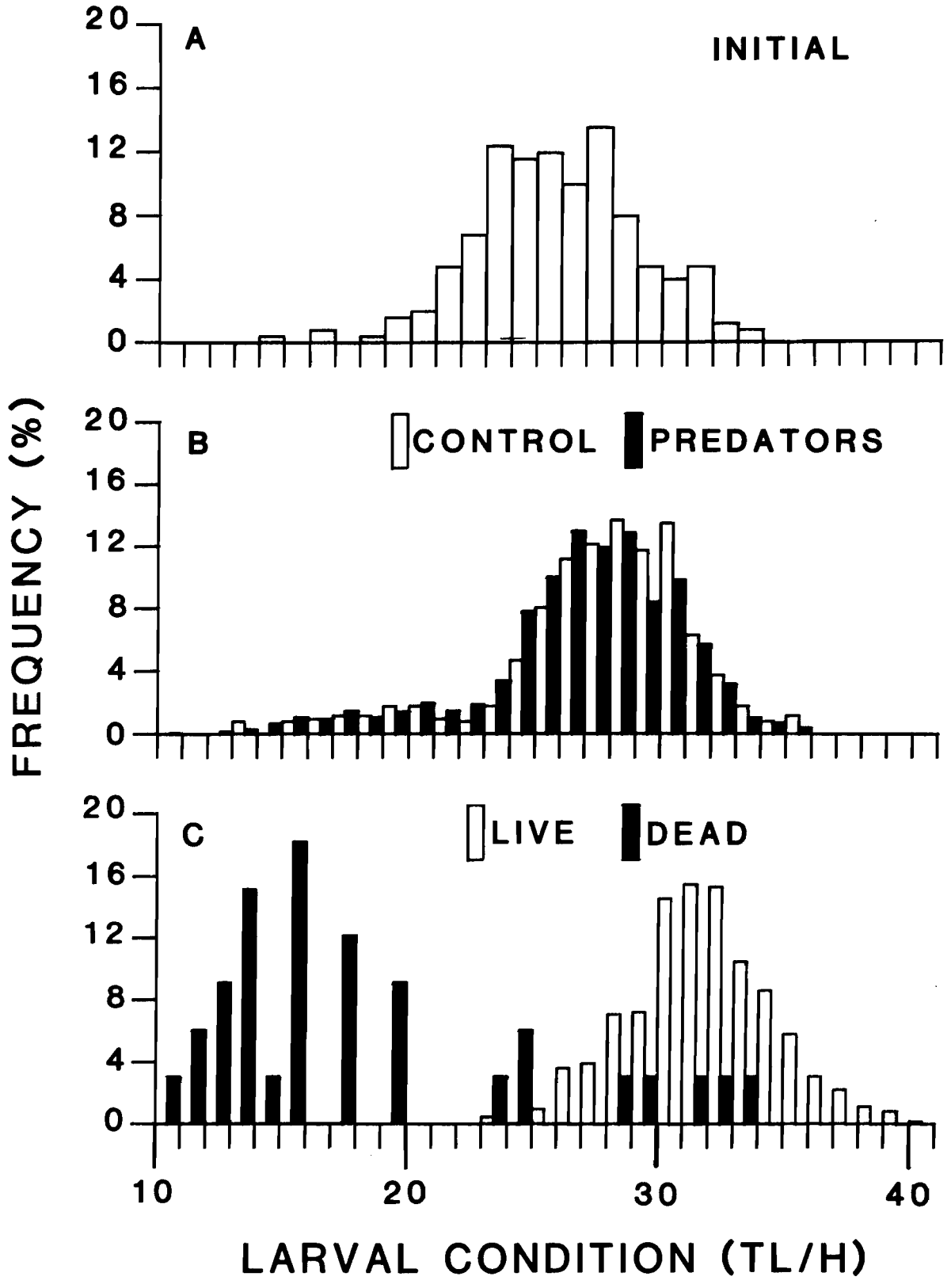

WITHOUT JELLYFISH
NO ALTERNATE FOOD
WITH ALTERNATE FOOD
FREQUENCY (%)
60
50
40
30
20
10
0
WITH JELLYFISH
NO ALTERNATE FOOD
WITH ALTERNATE FOOD
FREQUENCY (%)
25
20
15
10
5
0
0 20 40 60 80 100
0 20 40 60 80 100
RECOVERY RATE (%)

Figure 3. Frequency distribution of larval condition index (total length/body height for larvae initially stocked to the enclosures (top); for larvae recovered from control enclosures and from enclosures with jellyfish predators (middle); and condition of dead and live larvae recovered from the jar experiments (bottom).


A
INITIAL
B
CONTROL
PREDATORS
C
LIVE
DEAD
FREQUENCY (%)
20
16
12
8
4
0
10
20
30
40
LARVAL CONDITION (TL/H)

of larvae initially stocked (Kolmogorov-Smirnov test, $p<0.001$). This suggests that larvae grew during the 36-48 h duration of my experiments.

A comparison of the condition factor of larvae recovered from the enclosures and that of dead larvae from the jar experiments demonstrated that the majority of larvae recovered from the enclosures were alive when enclosures experiments were terminated (Figure 3). The condition of larvae recovered from the enclosures was slightly lower than that of live larvae from the jars. This difference is believed to have resulted from shrinkage of larvae following death during enclosure hauling. Larval shrinkage following death due to plankton net sampling has been previously reported (Blaxter 1971; Theilacker 1980). The frequency distributions of condition of larvae recovered from enclosures were slightly skewed to the left (Figure 3). This skewing could represent larvae that were dead at time of recovery. If a value of 20 is arbitrarily designated as the threshold between dead and live larvae (Figure 3c), approximately 6-7% of the larvae would be classified as dead. This result does not differ meaningfully from the estimate of mortality due to capture and handling larvae prior to stocking (5%).

The condition of larvae recovered from control enclosures did not differ significantly from that of larvae recovered from enclosures containing jellyfish (Kolmogorov-Smirnov test, $p>0.5$). When each experiment was analysed separately, significant difference was observed in only one case. These results suggest that larval size selection by predators did not occur within each experiment.

Controls with alternate food

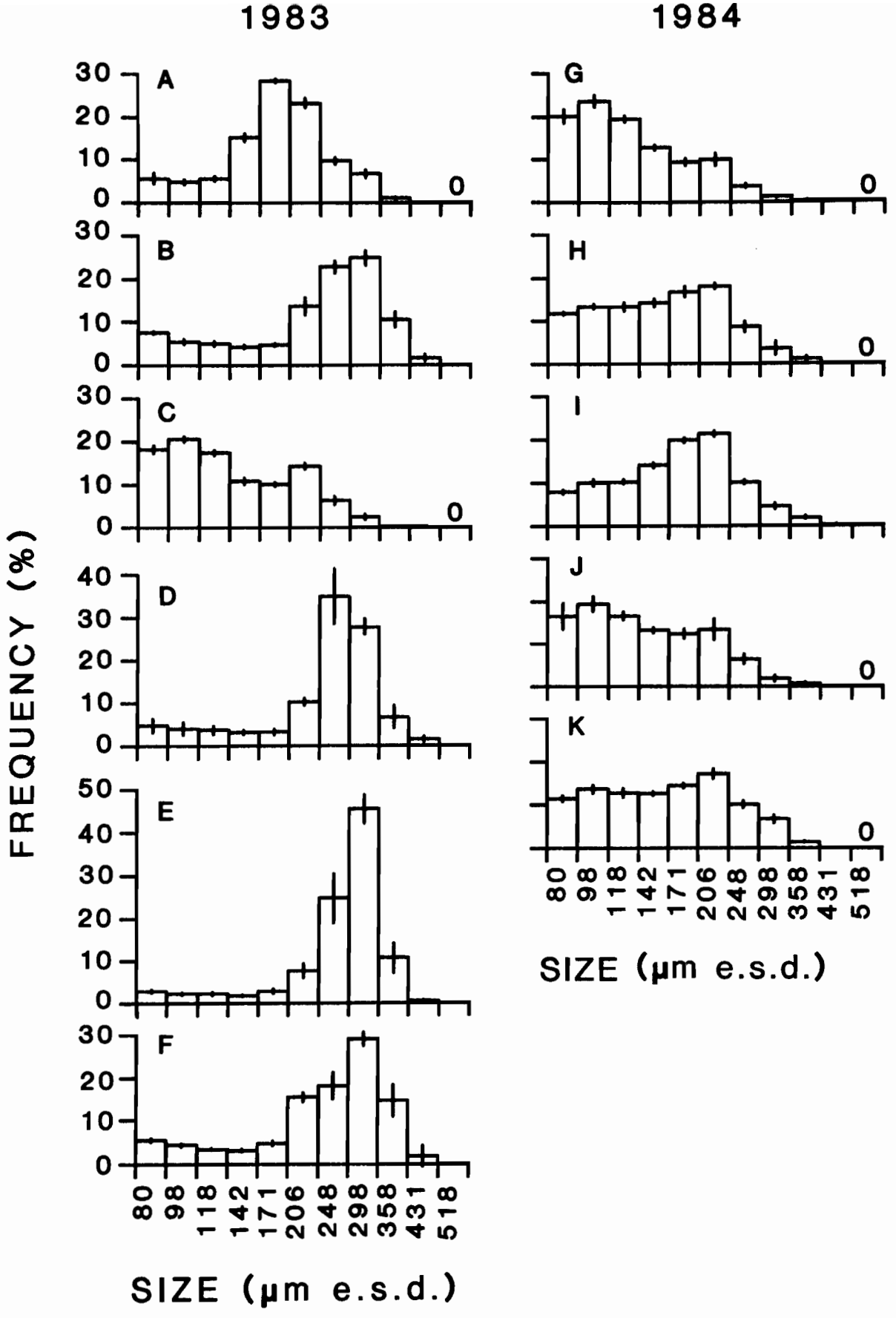
Control enclosures without alternate food yielded better survival (96.3%, s.e. 2.0) than did control enclosures with alternate food (91%, s.e. 1.4, $F=1,30=9.0$, $p=0.0005$). In addition to errors in counting both initially stocked and recovered larvae (<5%), the duration of the experiment and the number of days between the initiation of an experiment and the median date of spawning contributed significantly ($r^2=0.26$, $p=0.012$) to the total variance. The number of days from the median date of spawning was used as an index of the initial condition of larvae. This was done because no estimates of the initial larval condition were made in 1982. When this effect became apparent, I instituted the analyses for 1983 and 1984. Those data revealed a significant decline in yolk sac size with time since spawning. Two experiments having a long duration (>3 days) and which were conducted 25 and 30 days after the median spawning date in 1982 yielded recovery rates <50%. The larvae recovered from both control and predator enclosures in these experiments were severely damaged (most consisted of heads and body parts). These two experiments were not included in the analyses. The recovery rates of larvae from all other control enclosures which lacked alternate food were not correlated with initial larval density stocked ($r=0.05$, $p=0.82$) or with water temperature during the experiments ($r=0.10$, $p=0.63$).

The results indicated that the presence of alternate food in the enclosures increased mortality rates. The overall abundance (Table 1) and the size frequency distribution (Figure 4) of zooplankton added varied between experiments. A canonical discriminant analysis indicated that the eleven size spectra of the alternate food differed primarily in

Table 1. Abundance, biomass and average size of zooplankton used as alternate prey in predation experiments. Size spectrum letters correspond to those in Figure 4.

		Abundance		Biomass		Average Size		
Date	N	No./L	(C.V.)	mg/L	(C.V.)	volume (10^6 μm^3)	esd μm	Size Spectrum
1983								
July 17	3	19.614	(22.5)	0.1055	(20.6)	5.4099	217.8	A
July 19	3	24.387	(17.6)	0.3072	(27.4)	12.4347	287.4	B
July 28	3	133.541	(17.5)	0.4057	(26.7)	3.0024	179.0	C
August 2	3	13.464	(19.3)	0.1695	(18.5)	12.5957	288.7	D
August 6	2	30.753	(0.8)	0.4681	(8.5)	15.2270	307.5	E
August 8	3	6.988	(8.9)	0.0999	(18.1)	14.2249	300.6	F
1984								
July 13	3	275.740	(20.2)	0.6243	(10.8)	2.2949	163.6	G
July 23	3	176.342	(25.3)	0.7119	(8.5)	4.1544	199.5	H
July 25	2	121.307	(51.0)	0.6152	(51.0)	5.0715	213.2	I
July 27	4	201.148	(57.5)	0.6550	(69.8)	3.1008	180.9	J
July 31	4	147.329	(11.9)	0.7089	(9.3)	4.8367	209.8	K

Figure 4. Frequency distribution of the size spectra of zooplankton abundance added as alternate food in different experiments. The 0 value indicates no particles in the corresponding size class. Letters refer to size spectra in Table 1.

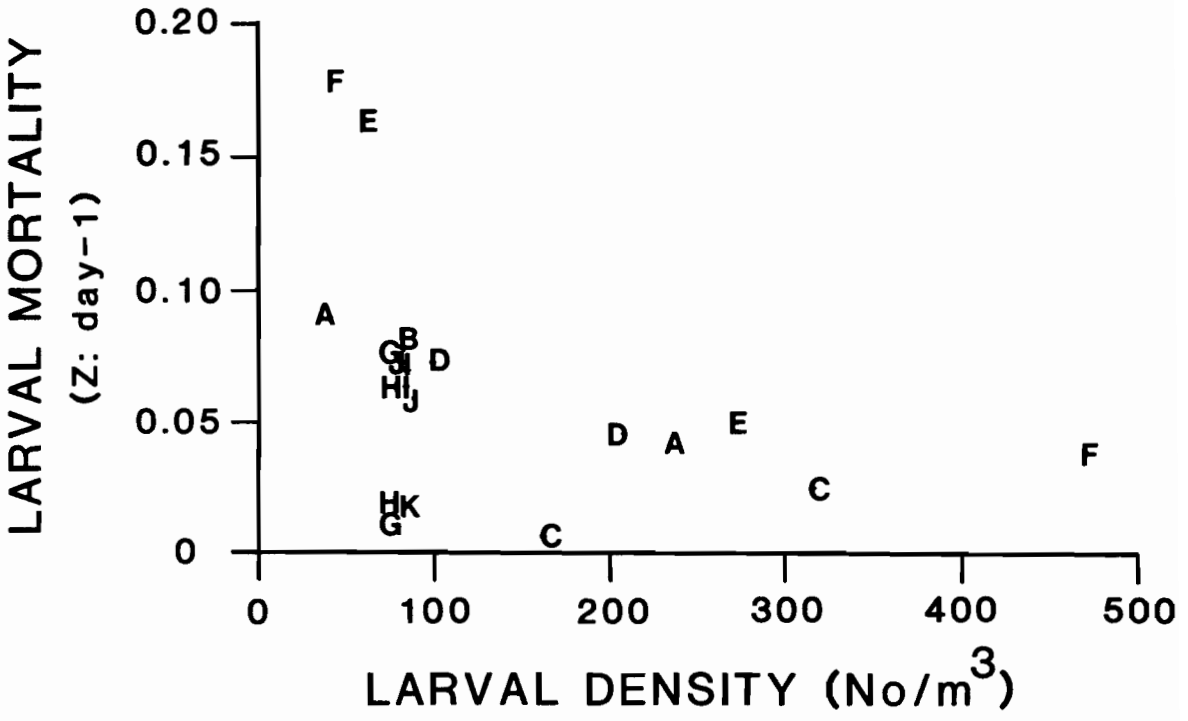

1983
1984
A
B
C
D
E
F
G
H
I
J
K
FREQUENCY (%)
SIZE (µm e.s.d.)
SIZE (µm e.s.d.)
80
98
118
142
171
206
248
298
358
431
518

the abundance of particles < 250 µm (axis 1- 62.6%) versus those > 300 µm (axis 2- 31.1%). Experiments B,D,E & F formed a distinct group of spectra (Figure 4).

Instantaneous larval mortality rates (Z) in control enclosures with alternate food were negatively correlated with the abundance of particles in each size class <250 µm e.s.d. (r=-0.47 to -0.51, p=0.02 to 0.035), but positively correlated with the abundance of particles >518 µm e.s.d. (r= 0.50, p=0.026) and with the average size of zooplankton (r= 0.53, p=0.016). A stepwise regression analysis was used to investigate the effect of initial density of larvae, average size of alternate food, abundance of particles (total and for each size class), temperature and initial condition of larvae (from yolk sac measurements and also from the time since median spawning) on observed mortality rates of larvae in enclosures. The average size of zooplankton (X1) and the initial density of larvae (X2) were the only variables selected. They explained 40.3% and 29.4%, respectively, of the overall variability in mortality rates ($Z = 0.2753 + 5.814\ X1 - 0.044\ \log(X2)$, $r^2 = 0.70$, $p<0.0001$).

The inverse relationship between mortality rates in the control enclosures and initial larval density is indicative of a Type II functional response (Figure 5). Larval mortality rates were highest when the alternate food were dominated by large-sized particles (Expts. B,D,E,F Figure 5) and can be attributed to predation by the large size classes of zooplankton. The negative correlation between Z and the abundance of particles <250 µm is explained by the negative correlations between small and large zooplankton in the enclosures. This inverse relationship typifies the condition in-situ in Bryants Cove (Frank and

Figure 5. Instantaneous mortality rate (Z) of larval capelin as a function of initial larval density in enclosures stocked with alternate food but lacking jellyfish predators. Letters correspond to experiments with size spectra shown in Figure 4.

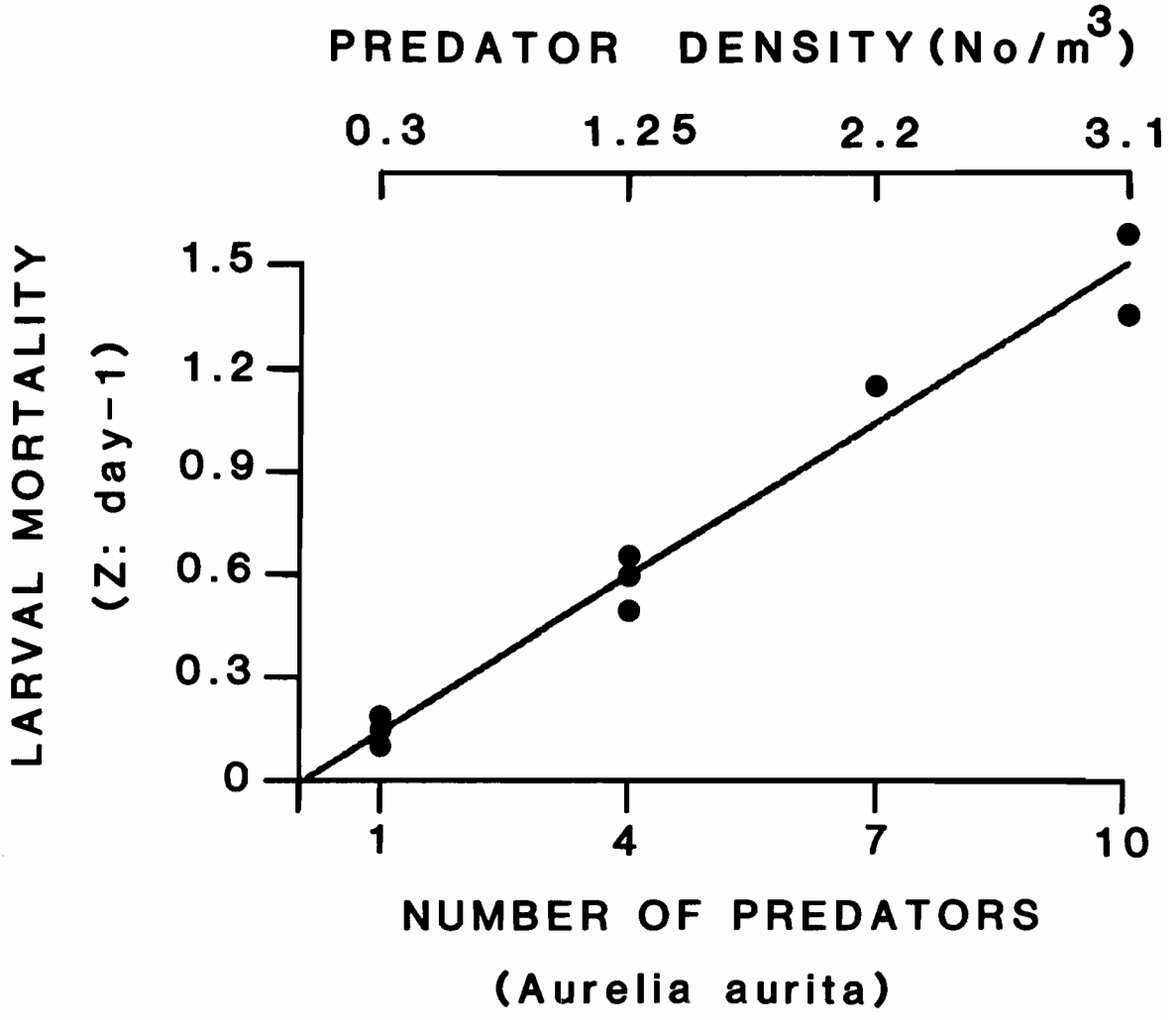

LARVAL MORTALITY
(Z: day-1)
0.20
0.15
0.10
0.05
0
F
E
A
B
G
I
H
J
D
D
A
E
F
C
H
K
G
C
0
100
200
300
400
500
LARVAL DENSITY (No/m3)

Leggett 1982a). The species composition of the >518 µm size class was not determined in this study. However, samples collected at Bryants Cove during the course of my experiments in 1983 showed this size class of zooplankton to be composed primarily of large copepods, small euphausiids and small chaetognaths (C.T. Taggart, Bedford Institute of Oceanography, Halifax, N.S., pers. comm.). Both laboratory and field studies have identified these plankters as predators of larval fish (Bailey 1984; Bailey and Yen 1983; Hartig et al. 1982; Hartig and Jude 1984; Kuhlmann 1977; Lillelund and Lasker 1971; Theilacker and Lasker 1974; Turner et al. 1985).

Effect of predator density

Instantaneous larval mortality, uncorrected for the number of predators in the enclosures (Z: day^{-1}), was linearly related to the numbers of predators present in the enclosures (Figure 6). The instantaneous larval mortality rate imposed per predator (Z: $predator^{-1}.day^{-1}$) was independent of the predator number (ANOVA: $F_{3,5} = 0.19$, $p=0.90$). The coefficients of variation (100*s.d./mean) in mortality rate per predator were low ranging from 11% to 24 % (average 15%). Covariance analysis revealed no significant effect of predator size ($p=0.98$) on the residual variability observed. These results indicate that the predation rate (I) of individual jellyfish predators was not influenced by the presence of other predators in the enclosures. This justifies my decision to correct Z for the number of predators present (equation 1).

Figure 6. Relationship between instantaneous larval mortality (Z: day^{-1}) and the number of jellyfish (Aurelia aurita) in the enclosures.


PREDATOR DENSITY (No/m3)
0.3
1.25
2.2
3.1
LARVAL MORTALITY
(Z: day-1)
1.5
1.2
0.9
0.6
0.3
0
1
4
7
10
NUMBER OF PREDATORS
(Aurelia aurita)

Effect of larval density

Product-moment correlations between instantaneous mortality rates, initial larval density and predator size (Table 2), calculated for all experiments analysed separately, revealed no significant correlation between instantaneous larval mortality (Z) and initial larval density. The one exception was the 1982 experiment involving Staurophora mertensi. Correlation coefficients of the relationship between Z and predator size were often greater and sometimes more significant than those between Z and larval density. Because the average size of predators in the environment increased with time, between experiment variation in predator size was greater than within experiment variation (Table 3). Within and between experiment variations in temperature were similar. A more detailed treatment of these results, by predator species, is presented below.

In the first two series of experiments involving Catablema vesicarium (Figure 7) and Staurophora mertensi (Figure 8), larval densities were replicated simultaneously. Both experiments exhibited a negative relationship between Z and initial larval density (Table 4). However, the relationship was significant only for Staurophora mertensi (ANOVA $F_{4,7}= 7.46$, $p=0.01$) (Catablema vesicarium $F_{5,10}= 1.47$, $p=0.28$). In the case of Staurophora, the curvilinear relationship suggests a Type II functional response between the predation rate and the initial density of larvae. However, for both species, each level of replicated larval densities corresponded to experiments conducted at different dates. The initial density of larvae thus covaried with predator size in both species (Figures 7 & 8) and with water temperature ($r=-0.86$, $p<0.001$) in the series of experiments using Staurophora mertensi.

Table 2. Product-moment correlation coefficients between larval mortality (Z), initial larval density (L) and predator umbrella diameter (D) for predation experiments. Logarithmic transformation (lnX) was applied to some variables to evaluate potential curvilinearity.

Predator Species	Figure	n	Z/L	lnZ/L	Z/lnL	lnZ/lnL	Z/D	lnZ/lnD	L/D
No alternate food									
C. vesicarium	7	16	-0.31	-0.19	-0.39	-0.23	0.42	0.42	-0.34
				*	*	**	*	**	**
S. mertensi	8	12	-0.56	-0.69	-0.68	-0.80	0.67	0.78	-0.76
S. mertensi	9b	9	-0.16	-0.06	0.01	0.13	-0.59	-0.57	-0.15
							*	*	**
C. capillata	9a	7	0.68	0.64	0.61	0.60	0.76	0.75	0.88
A. aurita	10a	7	-0.60	-0.67	-0.60	-0.60	0.30	0.22	0.08
	10b	7	-0.53	-0.50	-0.59	-0.55	0.18	0.20	-0.01
	10c	8	-0.20	-0.16	-0.06	-0.01	0.54	0.58	0.49
	10d	7	-0.21	-0.15	-0.08	-0.07	-0.24	-0.06	-0.27
With alternate food									
S. mertensi	11a	8	0.36	0.33	0.36	0.29	-0.03	-0.10	-0.19
	11b	5	0.27	0.28	0.40	0.41	-0.20	-0.17	-0.42
	11c	7	-0.07	0.03	-0.05	0.04	0.30	0.37	0.36
A. aurita	11d	7	0.42	0.44	0.46	0.46	0.68	0.71	0.66
	11e	7	0.09	0.18	-0.05	0.06	-0.50	-0.46	0.26

* = $0.01<p<0.05$
** = $0.001<p<0.01$

Table 3. Means and coefficients of variation (CV 100 sd/mean) of instantaneous larval mortality (Z predator^{-1}.day^{-1}) due to predation by four jellyfish species. Date, predator size (mean, CV, range of umbrella diameter) and water temperature (mean,CV,range) are listed for each experiment.

Experiment & Predator Species	Date	Larval mortality			Predator diameter				Water temperature			
		n	mean	cv(%)	n	mean	cv(%)	range	n	mean	cv(%)	range
Predator density												
A. aurita	29 July 1984	9	0.122	14.9	42	6.85	19.9	4.00-10.57	41	9.3	9.8	8.0-11.3
Larval density												
C. vesicarium	1982[a]	16	0.055	63.2	80	1.70	21.7	0.70- 2.52				2.8- 8.8[b]
S. mertensi	1982[a]	12	0.140	66.6	51	6.13	46.4	2.38-12.32				6.0-10.5[b]
"	4 Aug. 1983	9	0.131	38.7	36	12.99	15.3	8.55-17.16	40	10.1	14.8	7.1-11.9
A. aurita	2 July 1983	7	0.034	40.9	21	2.60	19.4	1.91- 3.60	41	8.2	15.3	5.8- 9.8
"	4 July 1983	7	0.059	18.4	28	3.17	19.2	2.17- 4.80	40	7.4	18.1	5.8- 9.6
"	7 July 1983	8	0.081	16.9	32	3.75	15.8	2.20- 4.68	43	8.7	10.5	7.3-10.4
"	24 July 1983	7	0.039	80.4	14	7.06	17.9	5.38- 8.76	38	8.5	24.2	5.2-10.6

a- Experiments conducted on different dates
b- Range of mean temperature in different experiments

Table 3. (suite)

Experiment & Predator Species	Date	Larval mortality			Predator diameter				Water temperature			
		n	mean	cv(%)	n	mean	cv(%)	range	n	mean	cv(%)	range
Larval density with alternate prey												
A. aurita	17 July 1983	7	0.052	16.4	14	6.82	21.0	4.48- 9.58	39	1.2	179.6	-0.9- 4.8
"	19 July 1983	7	0.147	41.2	14	6.32	26.9	3.76-10.74	39	5.5	48.8	0.4- 9.3
S. mertensi	28 July 1983	8	0.053	60.1	32	9.38	21.5	5.33-14.27	37	7.0	22.4	3.8- 9.3
"	2 Aug. 1983	7	0.300	60.8	28	12.55	18.9	7.60-16.95	40	10.0	14.8	7.1-11.9
"	6 Aug. 1983	7	0.127	28.8	28	14.11	15.1	8.67-18.06	39	8.5	12.0	5.9- 9.9
Alternate prey density with fixed larval density												
A. aurita	13 July 1984	8	0.095	26.5	24	4.07	17.6	2.86- 5.85	38	6.8	24.4	4.6- 9.0
"	25 July 1984	8	0.085	25.0	24	6.48	15.6	4.15- 8.13	38	5.4	15.8	3.8- 6.8
S. mertensi	23 July 1984	7	0.163	38.2	21	6.44	17.1	4.56- 8.85	40	6.0	15.1	4,5- 7.9
"	27 July 1984	8	0.147	54.1	24	6.09	21.3	3.87- 9.26	40	8.5	23.1	6.4-12.9
"	31 July 1984	8	0.151	27.5	16	10.90	15.0	8.40-13.54	41	6.6	14.3	4.8- 8.3

Figure 7. Predation experiment with the jellyfish Catablema vesicarium. Larval mortality as a function of initial larval density (A); average predator size (umbrella diameter) at corresponding tested larval densities (B); and standardized larval mortality as a function of initial larval density (C).

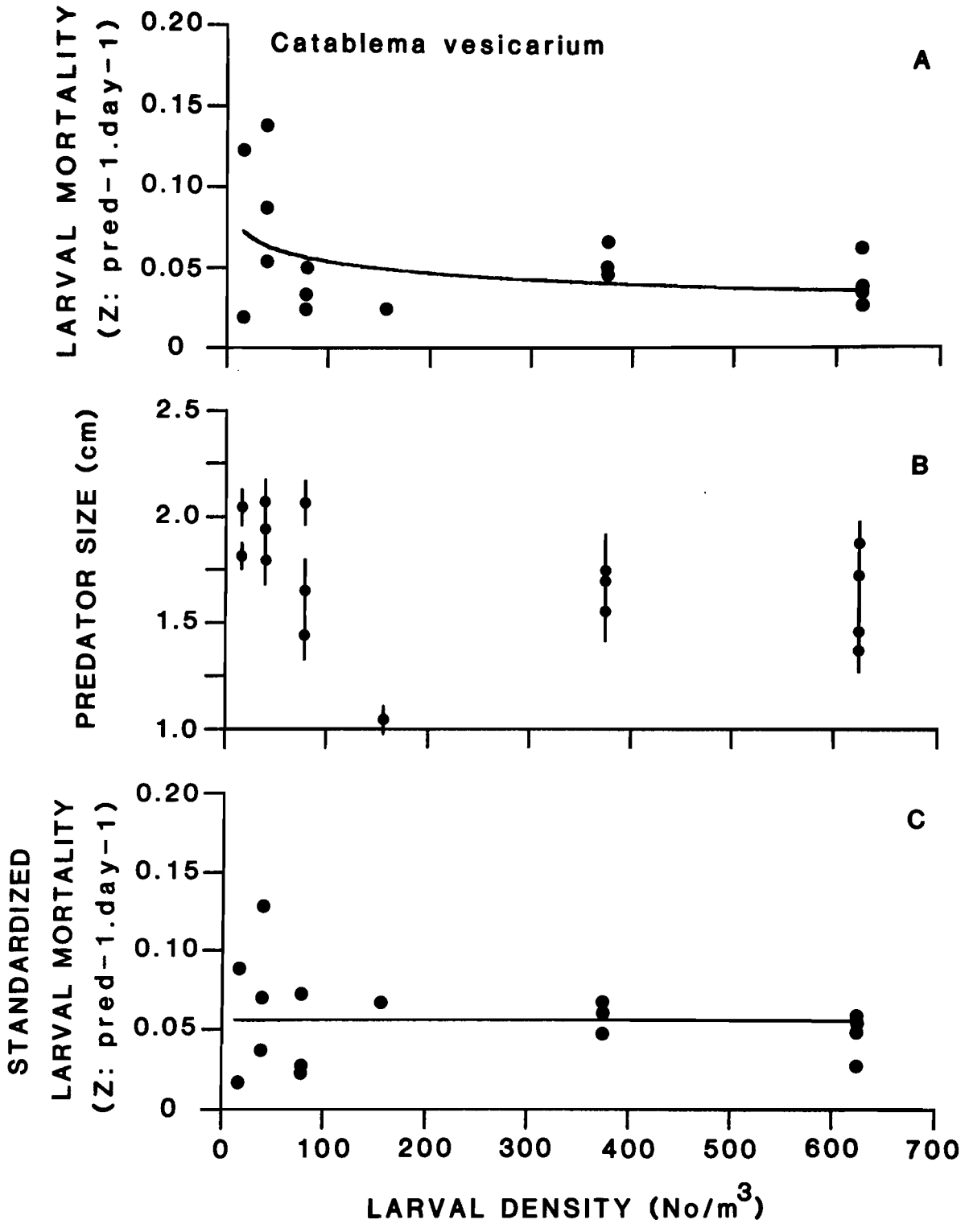

Catablema vesicarium
A
B
C
LARVAL MORTALITY
(Z: pred-1.day-1)
PREDATOR SIZE (cm)
STANDARDIZED
LARVAL MORTALITY
(Z: pred-1.day-1)
0.20
0.15
0.10
0.05
0
2.5
2.0
1.5
1.0
0
100
200
300
400
500
600
700
LARVAL DENSITY (No/m3)

Figure 8. Predation experiment with the jellyfish Staurophora mertensi. Larval mortality as a function of initial larval density (A); average predator size (umbrella diameter) at corresponding tested larval densities (B); and standardized larval mortality as a function of initial larval density (C).

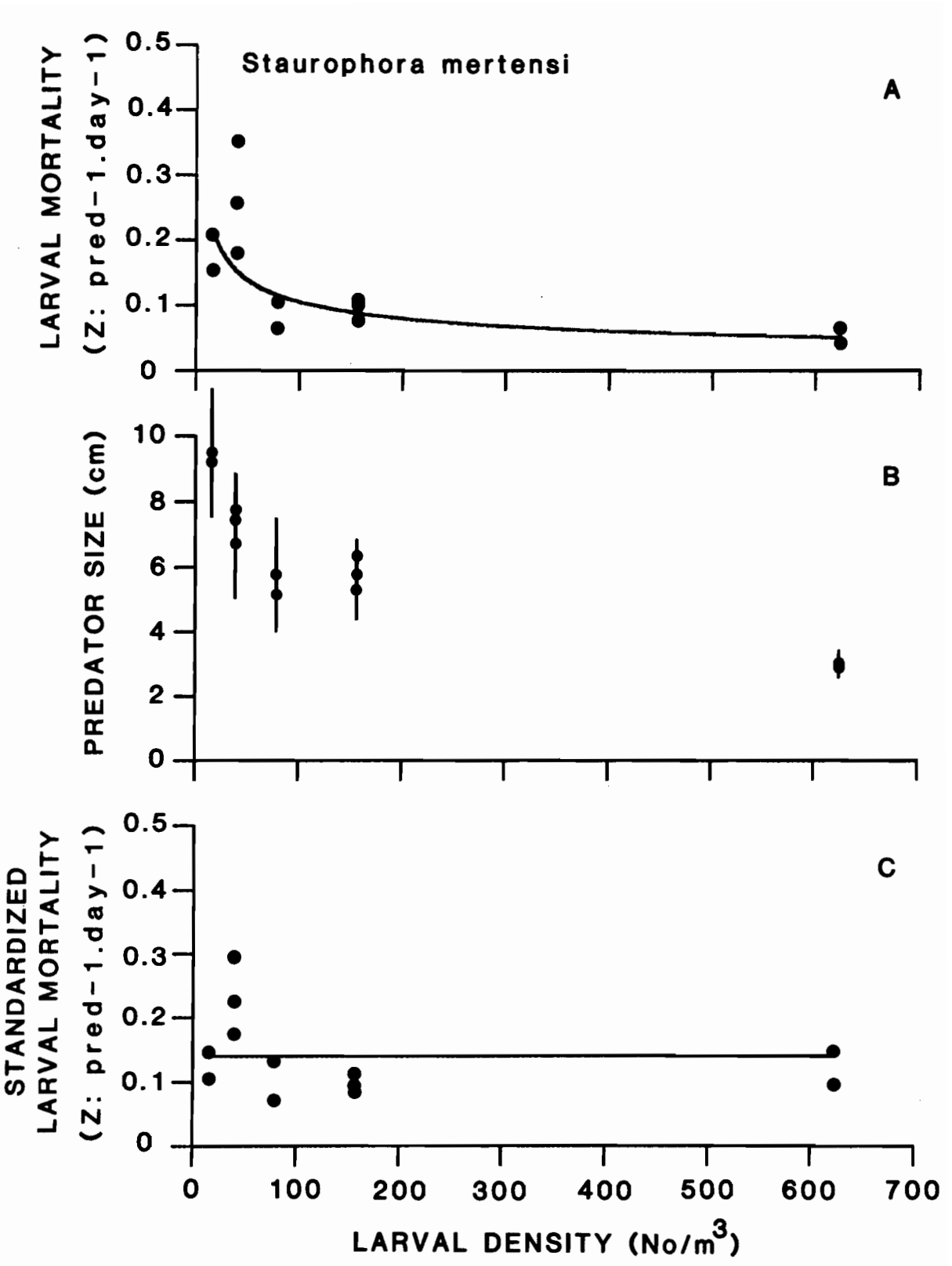

Staurophora mertensi
A
B
C
LARVAL MORTALITY
(Z: pred-1.day-1)
PREDATOR SIZE (cm)
STANDARDIZED
LARVAL MORTALITY
(Z: pred-1.day-1)
0.5
0.4
0.3
0.2
0.1
0
10
8
6
4
2
0
0
100
200
300
400
500
600
700
LARVAL DENSITY (No/m3)

Table 4. Regression analysis between instantaneous larval mortality (Z) and larval density (L) for all predation experiments. Analysis for instantaneous larval mortality standardized for predator size (Zs) is also presented. Corresponding figure is indicated for each experiment.

Predator Species	Figure	Larval mortality Z	r^2	p	Standardized larval mortality Zs	r^2	p
C. vesicarium	7	Z: 0.102 - 0.0103 log(L)	0.32	.24	Zs: 0.059 - 0.000027 L	0.13	.48
S. mertensi	8	Z: 0.369 - 0.0515 log(L)	0.46	.01	Zs: 0.152 - 0.000076 L	0.07	.42
"	9b	Z: 0.140 - 0.000033 L	0.03	.69	Zs: 0.138 - 0.000033 L	0.03	.63
C. capillata	9a	Z: 0.528 + 0.00212 L	0.46	.09	Zs: 0.952 + 0.000069 L	0.01	.95
A. aurita	10a	log(Z): -3.073 - 0.0030 L	0.44	.10	log(Zs): -3.047 - 0.0031 L	0.49	.08
	10b	Z: 0.068 - 0.000071 L	0.29	.21	Zs: 0.069 - 0.000073 L	0.30	.20
	10c	Z: 0.084 - 0.000025 L	0.04	.63	Zs: 0.087 - 0.000054 L	0.24	.22
	10d	Z: 0.048 - 0.000027 L	0.04	.65	Zs: 0.048 - 0.000028 L	0.05	.64
S. mertensi	11a	Z: 0.040 + 0.000054 L	0.13	.38	Zs: 0.040 + 0.000056 L	0.15	.35
	11b	Z: 0.391 - 0.000095 L	0.07	.65	Zs: 0.392 - 0.000027 L	0.01	.92
	11c	Z: 0.131 - 0.000012 L	0.01	.88	Zs: 0.133 - 0.000025 L	0.02	.75
A. aurita	11d	Z: 0.048 + 0.000042 L	0.18	.34	Zs: 0.050 - 0.000018 L	0.05	.62
	11e	Z: 0.141 + 0.000055 L	0.01	.84	Zs: 0.119 + 0.000020 L	0.02	.73

Consequently, the relationships between Z and initial larval density may have been subjected to the confounding effect of these variables. This possibility is supported by the fact that in both experiments, larval mortality rates were more strongly correlated to predator size than to initial larval density (Table 2).

The slope of the relationship between the log of larval mortality and the log of predator diameter (Table 5) did not differ significantly from 1.0 for either species (T-test, $p>0.25$). This confirmed that the variables were linearly related. Larval mortality rates were therefore standardized for predator size using the following equation:

$$Zs_i = \frac{Z_i * \sum_{i=1}^{n} (D_i/n)}{D_i} \qquad (3)$$

where Zs and Z are the standardized and the non standardized mortality rates, D is umbrella diameter and n is the number of observations (enclosures) in each series of experiments. There was no significant relationship between initial larval density and standardized mortality rate for either predator (Catablema: ANOVA $F_{5,10}$: 0.96, $p=0.48$, Figure 7c; Staurophora: ANOVA $F_{4,7}$: 1.5, $p=0.25$, Figure 8c). This suggests a linear (Type I) functional response for these jellyfish species.

These two experiments provided estimates of the level of variation in mortality to be expected in experiments in which the initial larval density and other external variables are constant. In these experiments the coefficients of variation (100*s.d./mean) of replicated mortality rates ranged from 18 to 101% (mean 46%) for Catablema vesicarium and from 14 to 42% (mean 26%) for Staurophora mertensi. These estimates are slightly larger than those observed for the predator

Table 5. Relationships between larval mortality (Z) and predator umbrella diameter (D) for each predation experiment.

Predator Species	Figure	log (Z) = a + b log(D) a	(s.e.)	b	(s.e.)	r^2	p
C. vesicarium	7	-3.767	(0.428)	1.347	(0.781)	0.18	0.11
C. capillata	9a	-2.578	(1.006)	1.067	(0.429)	0.55	0.05
S. mertensi	8	-4.501	(0.596)	1.328	(0.330)	0.62	0.002
	9b	-4.199	(3.385)	-2.459	(1.321)	0.33	0.10
	11a	-2.137	(3.737)	-0.416	(1.672)	0.01	0.81
	11b	-0.088	(2.617)	-0.322	(1.024)	0.03	0.77
	11c	-6.276	(4.692)	1.581	(1.774)	0.14	0.41
	12a	-6.806	(1.169)	2.664	(0.631)	0.78	0.008
	12b	-6.624	(1.363)	2.551	(0.756)	0.66	0.015
	12c	-5.528	(1.905)	1.514	(0.798)	0.37	0.11
A. aurita	10a	-4.244	(1.552)	0.811	(1.633)	0.05	0.64
	10b	-3.914	(2.396)	0.927	(2.076)	0.04	0.67
	10c	-4.210	(0.961)	1.277	(0.728)	0.34	0.13
	10d	-1.563	(15.51)	-0.991	(7.936)	0.01	0.90
	11d	-6.558	(1.587)	1.877	(0.827)	0.51	0.07
	11e	-0.399	(1.377)	-0.875	(0.750)	0.21	0.29
	12d	-3.582	(1.313)	0.857	(0.936)	0.12	0.39
	12e	-3.214	(1.553)	0.390	(0.832)	0.03	0.66

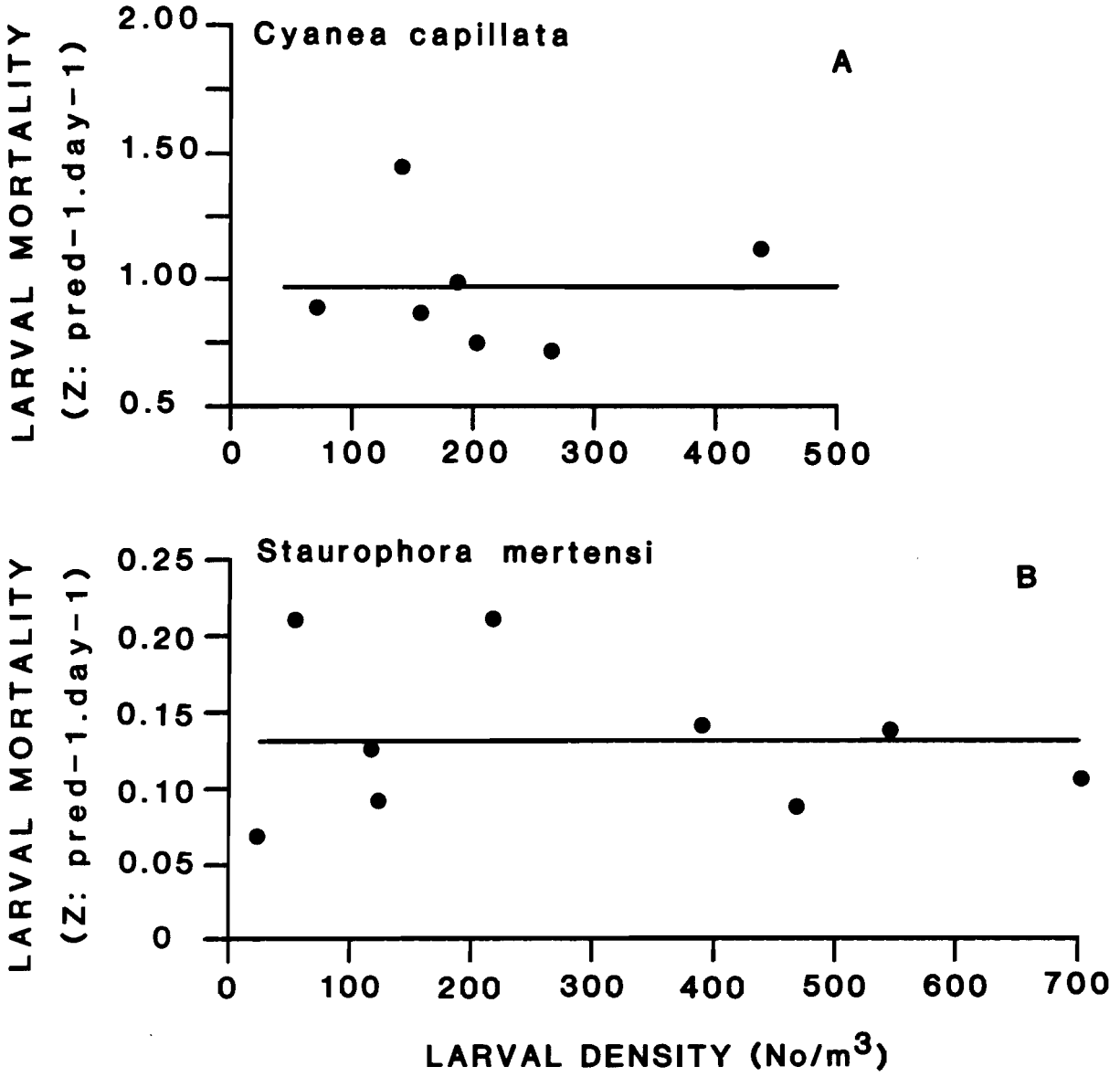
density experiment (11-25%) and are very close to estimates (26-49%, mean 36%) obtained when the jellyfish Aurelia aurita was used as predator (Chapter 2).

These two series of experiments also demonstrated that the temporal variability in uncontrolled variables may bias the effect of larval density on mortality due to predation. The temporal variability in Z appeared to be related to the unexpected large variation in predator size between experiments. To minimize the temporal variation in predator size and other variables (water temperature, initial larval condition), I modified the experimental design to achieve a wide range of larval densities within a single experiment.

An experiment with Staurophora mertensi using this alternative design again showed larval mortality to be independent (r^2=0.03, p=0.69) of the initial density of larvae (Figure 9b). Predator size was not significantly correlated with larval mortality (r=-0.59, p=0.10) or with initial larval density (r=-0.15, p=0.69) (Table 2). Very low natural abundances of Catablema vesicarium in subsequent years prevented repetition of the experiments with this species.

Larval mortality due to predation by the jellyfish Cyanea capillata was positively, but not significantly, correlated with the initial larval density. Mortality was, however, significantly ($p<0.05$) correlated with predator size (Tables 2 & 5). The slope of the log-log relationship between Z and predator diameter did not differ significantly from 1.0 (Table 5, T= 0.157, p=0.80). Standardized larval mortality (Zs - using equation 3) was not significantly correlated with initial larval density (Figure 9a, r^2:0.001, p=0.94). The overall coefficient of variation was 26%.

Figure 9. Effect of initial larval density on larval mortality due to predation by (a) Cyanea capillata and (b) Staurophora mertensi.


Cyanea capillata
A
LARVAL MORTALITY
(Z: pred-1.day-1)
2.00
1.50
1.00
0.5
0
100
200
300
400
500
Staurophora mertensi
B
LARVAL MORTALITY
(Z: pred-1.day-1)
0.25
0.20
0.15
0.10
0.05
0
0
100
200
300
400
500
600
700
LARVAL DENSITY (No/m3)

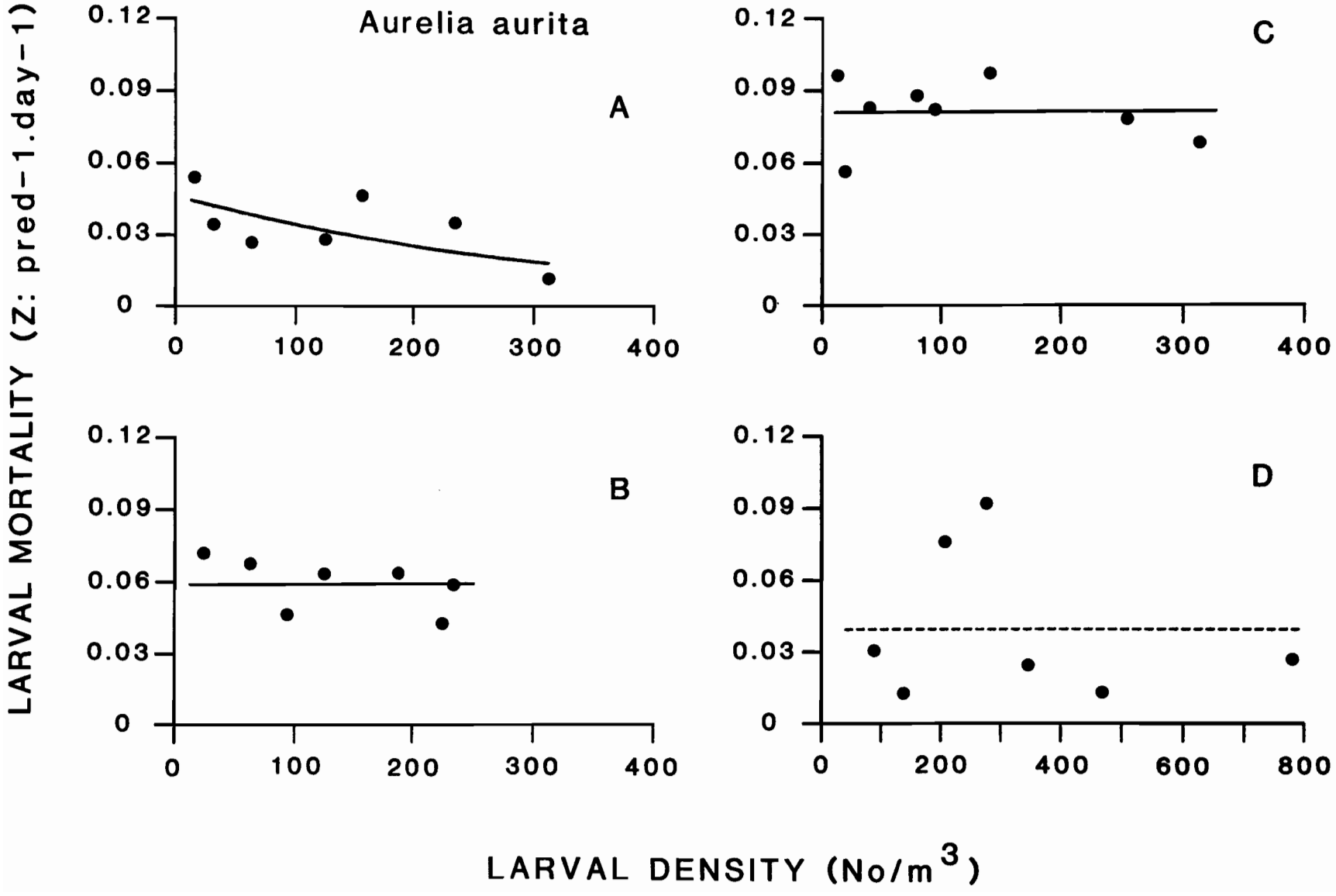
Four experiments were conducted to evaluate the effect of larval density on mortality rates imposed by Aurelia aurita (Figure 10). Larval mortality rates were consistently negatively correlated with initial larval density, but none was significant (Tables 2 & 4). The coefficients of variation in mortality rates in the first three trials were low (17-41%) and within the range of those observed in the replicated larval density experiments. A high CV (81%) occurred in the fourth experiment. This was due principally to two high Z values at intermediate larval densities (Figure 10d). Mortality rates and predator size were positively, but not significantly ($p>0.05$; Tables 2 & 5) correlated in the first three experiments and negatively correlated in the last. These relationships were not improved by standardizing Z for predator size (equation 3; Table 4). Because mortality rates in the fourth experiment were inversely related to predator size (slope = -1.0; Table 5), mortality rates were standardized using the following equation:

$$Zs_i = \frac{Z_i * D_i}{\sum_{i=1}^{n} (D_i/n)} \qquad (4)$$

The high variability observed in this experiment was not reduced by this procedure.

The variances of mortality rates were homogeneous (Fmax test: 8.5, $p>0.05$). An ANOVA performed on larval mortality rates due to Aurelia aurita revealed a significant difference between experiments ($F_{3,25}= 10.15$, $p<0.0001$). An a-posteriori multiple mean test (Duncan test, SAS 1982) indicated that significant differences in mortality rates occurred

Figure 10. Effect of initial larval density on larval mortality due to predation by jellyfish Aurelia aurita in four different experiments. Letters indicate temporal sequence in experiments.


Aurelia aurita
A
B
C
D
LARVAL MORTALITY (Z: pred-1.day-1)
LARVAL DENSITY (No/m3)
0.12
0.09
0.06
0.03
0
0
100
200
300
400
600
800

among the first three experiments, but that no difference existed between the first and the last experiments. Temporal variability was thus more important than the effect of larval density on measured mortality rates due to predation. The increase in mortality rates during the first three experiments paralleled the increment in mean predator size (Table 3).

Effect of alternate food

No significant relationship was observed between larval mortality and initial larval density in five experiments in which alternate food was offerred (Figure 11). Two very low mortality rates were observed at very high larval densities (>500/m^3) during the second experiment with Staurophora mertensi. These low mortality may have been caused by the death of predators during the course of the experiment. Larval mortality rates were not significantly related to predator size (Table 5), and standardizing the mortality rates did not modify the relationships between Z and initial larval density (Table 4). These results clearly indicate that the Type I functional response previously identified for these jellyfish species was not altered by the addition of alternate food.

The mean larval mortality rates in experiments involving alternate food varied significantly between experiments (time effect) for both Staurophora ($F_{2,17}=141.3$, $p<0.001$) and Aurelia ($F_{1,12}= 38.25$, $p<0.001$). A portion of this variance might be due to temporal differences in the abundance and size distribution of the alternate prey added to the enclosures (Table 1).

Experiments in which larval density was constant (80/m^3) and

Figure 11. Effect of initial larval density on larval mortality due to predation by two jellyfish species in the presence of a fixed abundance of alternate prey consisting of wild zooplankton. Temporal sequence in experiments within each species is represented by alphabetical order.

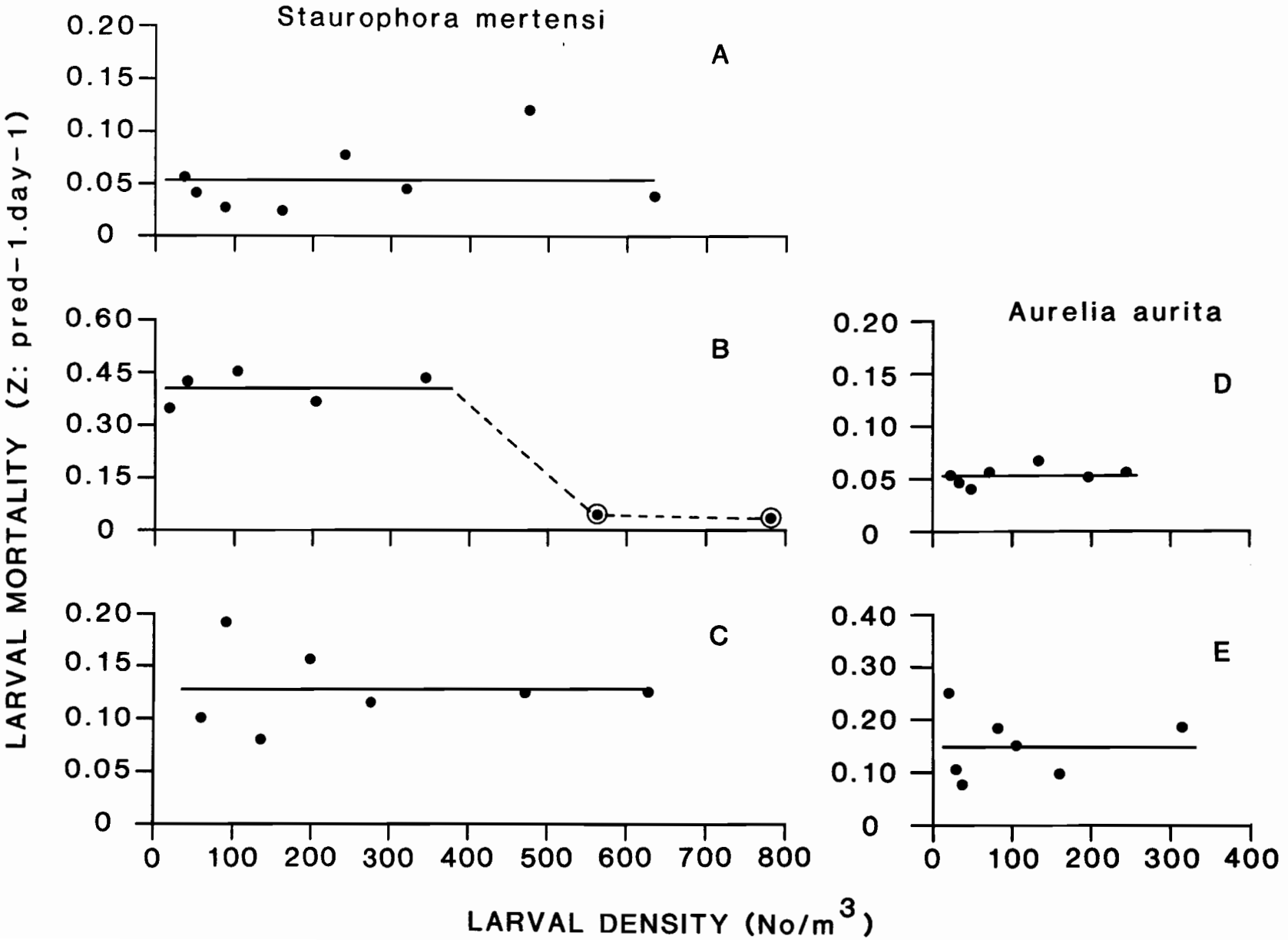

Staurophora mertensi
A
B
C
Aurelia aurita
D
E
LARVAL MORTALITY (Z: pred-1.day-1)
LARVAL DENSITY (No/m3)
0.20
0.15
0.10
0.05
0
0.60
0.45
0.30
0.40
100
200
300
400
500
600
700
800

Figure 12. Effect of abundance of alternate prey consisting of wild zooplankton on larval mortality due to predation by two jellyfish species at a fixed initial larval desnity. Letters indicate sequence in experiments for each predator species.

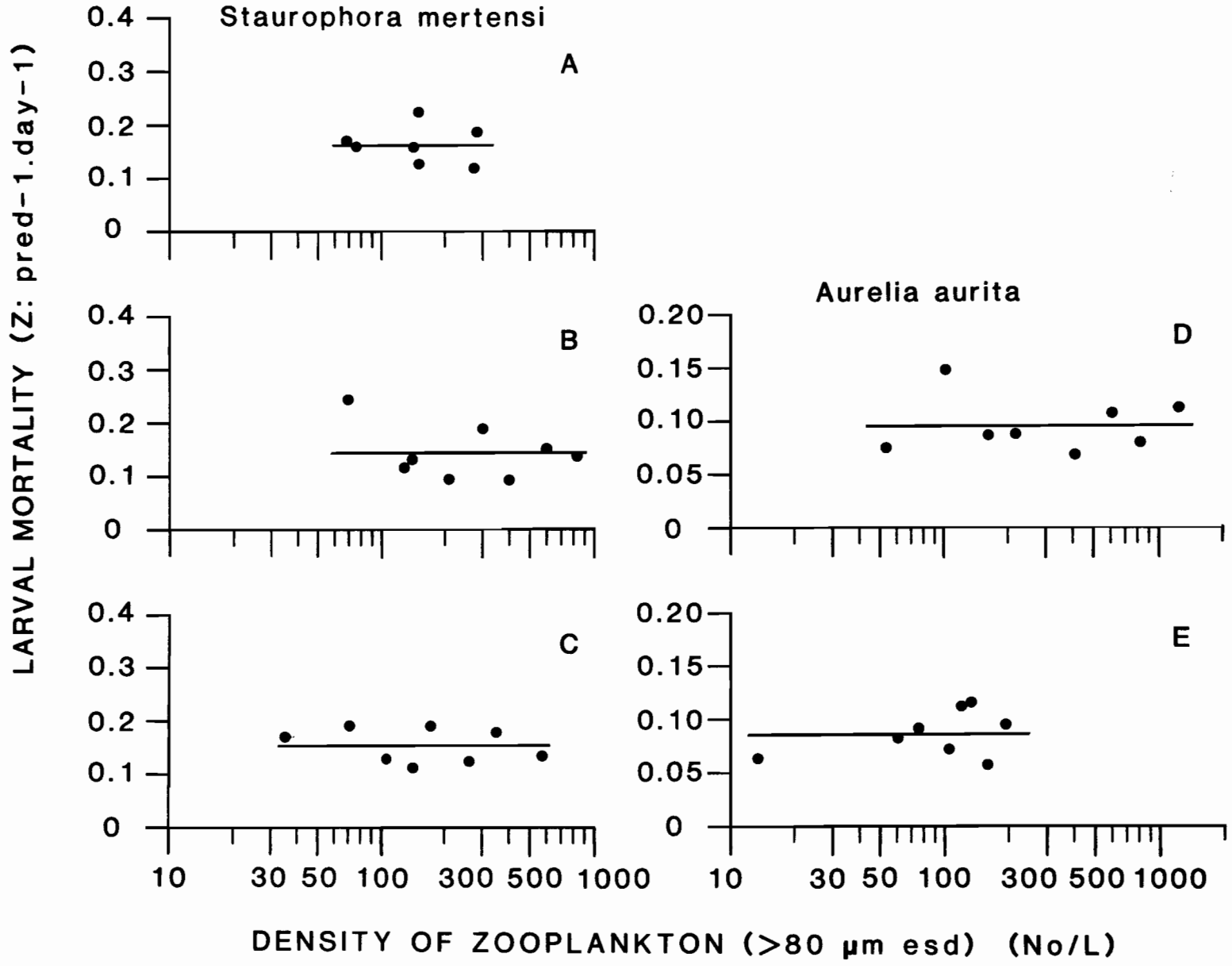

Staurophora mertensi
A
B
C
Aurelia aurita
D
E
0.4
0.3
0.2
0.1
0
0.20
0.15
0.10
0.05
10
30 50 100 300 500 1000
LARVAL MORTALITY (Z: pred-1.day-1)
DENSITY OF ZOOPLANKTON (>80 µm esd) (No/L)

Table 6. Regression analyses between instantaneous larval mortality rate (Z: unstandardized and Zs: standardized) for predator size) and abundance of alternate food (AF) in experiments involving Staurophora mertensi and Aurelia aurita. Experiments are as indicated in Figure 12.

	Z = a + b AF				Zs = a + b AF			
Experiment	a	b	r^2	p	a	b	r^2	p
			Staurophora mertensi					
12a	0.150	0.000079	0.01	.82	0.159	0.0000013	0.01	.97
12b	0.166	-0.000057	0.04	.65	0.156	0.0000072	0.03	.65
12c	0.129	0.000102	0.18	.29	0.144	0.0000028	0.03	.68
			Aurelia aurita					
12d	0.093	0.000036	0.01	.89	0.101	-0.0000035	0.05	.58
12e	0.073	0.000113	0.09	.45	0.072	0.0000202	0.09	.46

alternate prey density was deliberately varied revealed no significant relationship between larval mortality and the initial abundance of alternate prey when employing Staurophora mertensi and Aurelia aurita as predators (Figure 12). Larval mortality rates were unrelated to predator size (Table 5) in these experiments, and standardized mortality rates did not alter the relationships between Z and zooplankton density (Table 6). Between experiment differences in larval mortality were nonsignificant for both Staurophora ($F_{2,20}$= 0.13, p=0.88) and Aurelia ($F_{1,14}$=0.65, p=0.43).

Effect of predator size

Two series of experiments in which larval densities were replicated (Figures 7 & 8) both showed larval mortality to be significantly influenced by predator size. Despite the effort made to minimize the effect of predator size in subsequent experiments, the relationship between Z and predator size was occasionally more significant than the controlled effect of either larval density (Table 4) or alternate food density (Table 6). Moreover, the relationship between Z and predator size for both Staurophora mertensi and Aurelia aurita was variable (Table 5), being generally positive for small predators and negative for large predators.

I evaluated the effect of predator size on larval mortality in the absence of alternate food by pooling all data available for Staurophora mertensi and Aurelia aurita. The data set for Aurelia aurita also included mortality rates obtained in the predator density experiment (Figure 6) and from the 3.2 m^3 enclosures in the container size experiment (Chapter 2). For both species, the relationship between Z

and predator diameter was non linear and dome-shaped (Figure 13 a,b).

The relationships were first explored by stepwise regression analysis. The following independent variables were included: predator umbrella diameter, umbrella surface area, estimated wet weight, water temperature (both mean and standard deviation) and initial larval length for Aurelia only, larval length data not taken for 1982 experiments involving Staurophora.

Both regression models were highly significant ($p<0.0001$) and explained 49% and 72% of the observed variability for Staurophora mertensi and and Aurelia aurita respectively (Table 7). For Staurophora mertensi, only predator size was found significant. For Aurelia aurita, variability in water temperature (SDT: standard deviation in temperature) accounted for 50% of the overall variability in Z. Predator size explained 22% of the total variability (44% of the residual variance when the effect of temperature was removed).

Because of potential covariability between mean temperature, temperature variability and predator size in experiments involving both species, a second analysis was performed by fitting a curvilinear model relating Z and predator size. A non linear regression technique (NLIN procedure, SAS 1982) was employed to fit the following equation:

$$Z = a * Size * \exp^{-Size} \qquad (5)$$

Residuals from the non linear model were examined for their relationship with temperature variables and initial larval length. This procedure differs from the stepwise analysis by forcing a specific relationship between larval mortality and predator size.

Non-linear models based on predator size alone explained 45% and

Figure 13. Relationship between larval mortality (Z) and predator size for Staurophora mertensi and Aurelia aurita. Relationships are shown for experiments without alternate food (A,B) and for experiments in absence (o) and in presence (●) of alternate food (C,D). Curves depict the best fitted relationship (from Table 7) in absence of alternate food.

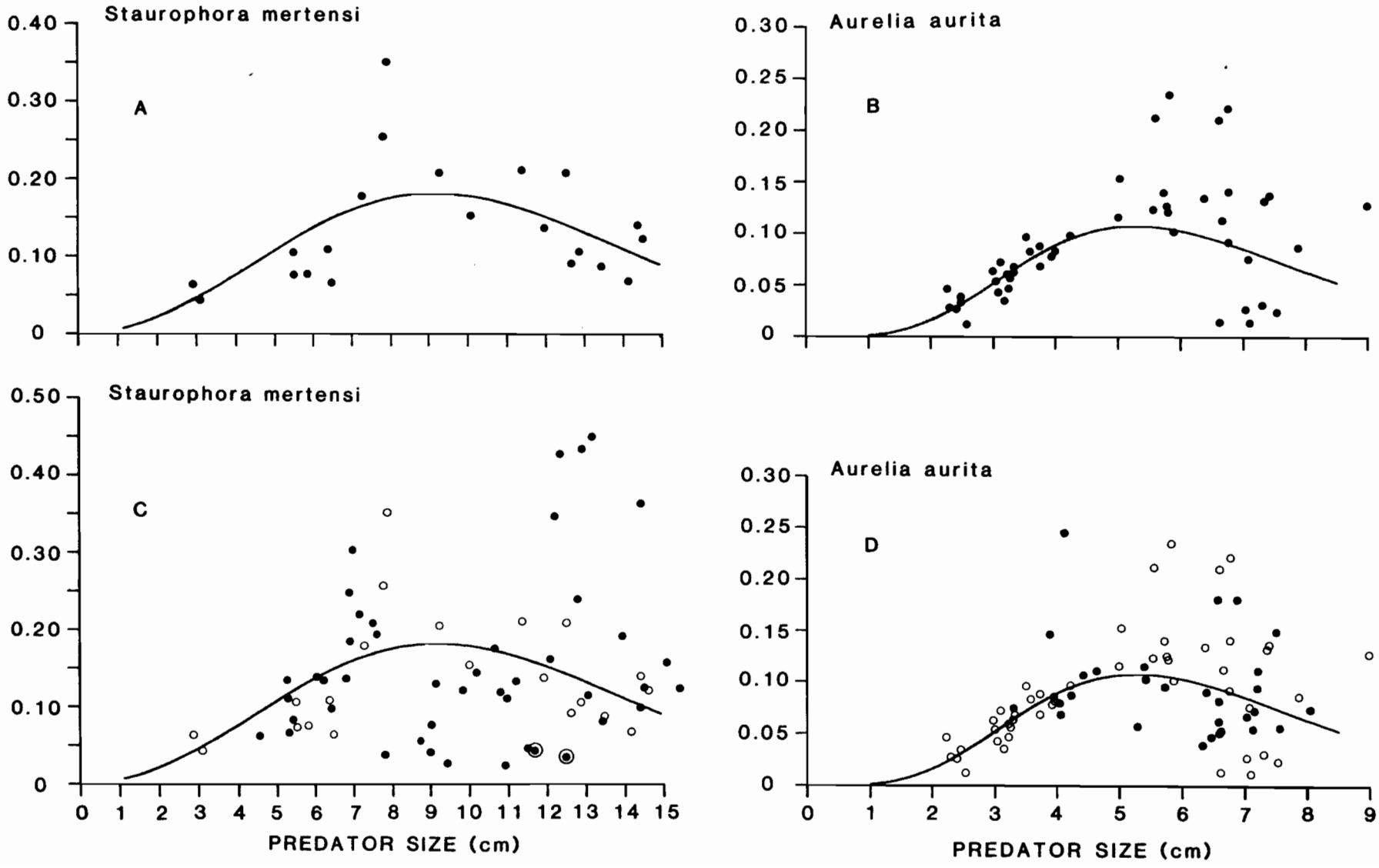

Staurophora mertensi
A
0.40
0.30
0.20
0.10
0
Aurelia aurita
B
0.30
0.25
0.20
0.15
0.10
0.05
0
Staurophora mertensi
C
0.50
0.40
0.30
0.20
0.10
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
PREDATOR SIZE (cm)
Aurelia aurita
D
0.30
0.25
0.20
0.15
0.10
0.05
0
0 1 2 3 4 5 6 7 8 9
PREDATOR SIZE (cm)

Table 7. Stepwise multiple regression models of larval mortality (Z) due to predation by Staurophora mertensi and Aurelia aurita. Results are presented for experiments in absence of alternate food only, and for all expriments including those with alternate food. Mortality were log-tranformed prior to the analysis. Best predictive relationships between Z and predator size (all other variables kept constant) are given.

Jellyfish	Variate	Coefficient	(s.e.)	r^2	F-value	p
		WITHOUT ALTERNATE FOOD				
S. mertensi	log Diameter	2.046	0.514	0.34	15.88	0.0009
	Umbrella area	-0.016	0.005	0.49	11.14	0.0037
(n=21)	Intercept	-5.219				
	log Z = -5.219 + 2.046 log Diameter - 0.016 Area					
A. aurita	SDT	-1.206	0.152	0.50	68.10	0.0001
	log Diameter	2.815	1.056	0.69	7.10	0.0037
(n=47)	Diameter	-0.435	0.227	0.72	5.12	0.0287
	Intercept	-3.143				
	log Z = -4.789 + 2.815 log Diameter - 0.435 Diameter					
		ALL EXPERIMENTS				
S. mertensi	Larval length	1.324	0.319	0.30	17.24	0.0001
	SDT	-1.116	0.251	0.44	19.74	0.0001
(n=52)	Temperature	0.321	0.081	0.52	15.58	0.0003
	Area	-0.018	0.005	0.56	10.98	0.0018
	log Diameter	2.097	0.790	0.62	7.04	0.0109
	Intercept	-13.071				
	log Z = -4.816 + 2.097 log Diameter - 0.0185 Area					
A. aurita	SDT	-0.928	0.145	0.32	40.90	0.0001
	log Diameter	3.915	1.047	0.42	13.98	0.0004
(n=77)	Diameter	-0.705	0.221	0.54	10.17	0.0023
	Total Zoop.	0.0008	0.0003	0.56	5.65	0.0209
	Size Zoop.	-0.063	0.036	0.58	3.07	0.0850
	Intercept	-4.001				
	log Z = -5.034 + 3.915 log Diameter - 0.705 Diameter					

39% of the variability in Z for Staurophora mertensi and Aurelia aurita respectively ($p<0.0001$). For Staurophora, there was no relationship between mortality residuals and any other variable tested. For Aurelia, temperature variability (SDT) was the only variable contributing significantly ($r^2=0.42$, $p<0.0001$) to the variance in the mortality residuals. These results are consistent with the results of the stepwise regression analyses.

I next added larval mortality estimates obtained from experiments in which alternate food was present to these data sets and repeated the analyses including abundance (both in numbers and biomass) and mean size of alternate prey as independent variables. The absence of data on initial larval size for experiments conducted in 1982 resulted in the exclusion of 12 data points from the stepwise analysis for Staurophora mertensi. The presence of alternate prey did not alter larval mortality due to predation by jellyfish (Figure 13c,d). Despite the scatter induced by temporal effects, the dome-shape relationship between Z and predator size remained evident.

Stepwise regression analysis performed separately for each predator again indicated that larval mortality was principally related to predator size and environmental conditions (Table 7). The models were significant ($p<0.0001$) and explained 62% and 58% of the observed variability in larval mortality imposed by Staurophora mertensi and Aurelia aurita respectively. In experiments involving Staurophora mertensi as predator, larval mortality was positively correlated with larval length. This was the first variable selected by the regression and it explained 30% of the overall variance. Variability in water temperature (SDT) during experiments, and mean temperature (which varied

between experiments), contributed 25% and 8% respectively. Predator size contributed 9.7% to the overall variance (20% of the variability when larval length and water temperature were stabilized). Despite the fact that the 1982 data were not included, the coefficient for the log-diameter variable was again very close to 2.0. This suggests that mortality rate was primarily a function of the umbrella surface area of Staurophora mertensi.

Larval mortality due to predation by Aurelia aurita was primarily related to variability in water temperature (SDT) and predator size which contributed 32% and 19% to the variability respectively. The density of zooplankton added to the enclosures and its size composition explained only 5% of the overall variance in Z. Contrary to expectation, Z was positively related to the density of alternate prey ($p=0.02$). The negative effect of average size composition was not significant ($p=0.08$).

Product-moment correlations calculated to evaluate the effect of covariability among variables showed the size of both Staurophora mertensi and Aurelia aurita to be significantly correlated with the average size of alternate food (Table 8). Predator size was also positively correlated with temperature in the case of Staurophora mertensi and with larval size for Aurelia aurita. These positive correlations reflect the seasonal trend in these variables (Tables 1 & 3, Figure 4).

Non-linear models relating Z to predator size (equation 5) were significant for Aurelia aurita ($r^2=0.25$, $p=0.001$), but not for Staurophora mertensi ($r^2=0.09$, $p=0.23$). The residuals from these models were negatively related to variability in water temperature (SDT) in

Table 8. Product-moment correlation coefficients between measured variables in all experiments involving Staurophora mertensi and Aurelia aurita. Variables are: larval density(Larvae), predator size (Diam.), water temperature (Temp.), variability in water temperature (SDT), larval length (Length) yolk sac volume (Yolk), abundance of alternate food (Total), average size of alternate food (Size) and larval mortality (Z and logZ).

Staurophora mertensi (n : 64)

	Larvae	Diam.	Temp.	SDT	Length	Yolk	Total	Size	Z	logZ
Larvae	-	0.15	0.07	0.05	-0.33*	-0.02	-0.21	0.03	-0.22	-0.25
Diam.	0.13	-	0.43***	-0.12	-0.18	-0.56***	-0.25	0.53***	0.25	0.25
Temp.	0.19	-0.22	-	0.32**	0.01	-0.35*	-0.30*	-0.04	0.22	0.26
SDT	0.08	0.21	-0.54***	-	-0.19	0.47***	0.36**	-0.32**	-0.31*	-0.30*
Length	-0.13	0.36**	0.46***	-0.54***	-	-0.63***	0.27	0.24	0.32*	0.55***
Yolk	-0.16	-0.41***	-0.07	-0.07	-0.49***	-	0.22	-0.36**	-0.26	-0.48***
Total	-0.14	-0.09	-0.11	0.08	-0.14	-0.17	-	-0.05	-0.09	-0.04
Size	-0.19	0.32**	-0.63***	0.67***	-0.01	-0.33	0.06	-	0.34**	0.30*
Z	-0.13	0.25*	0.23*	-0.15	0.34**	-0.17	0.02	0.21	-	-
logZ	-0.26*	0.22	0.14	-0.21	0.37**	-0.15	0.09	0.23*	-	-

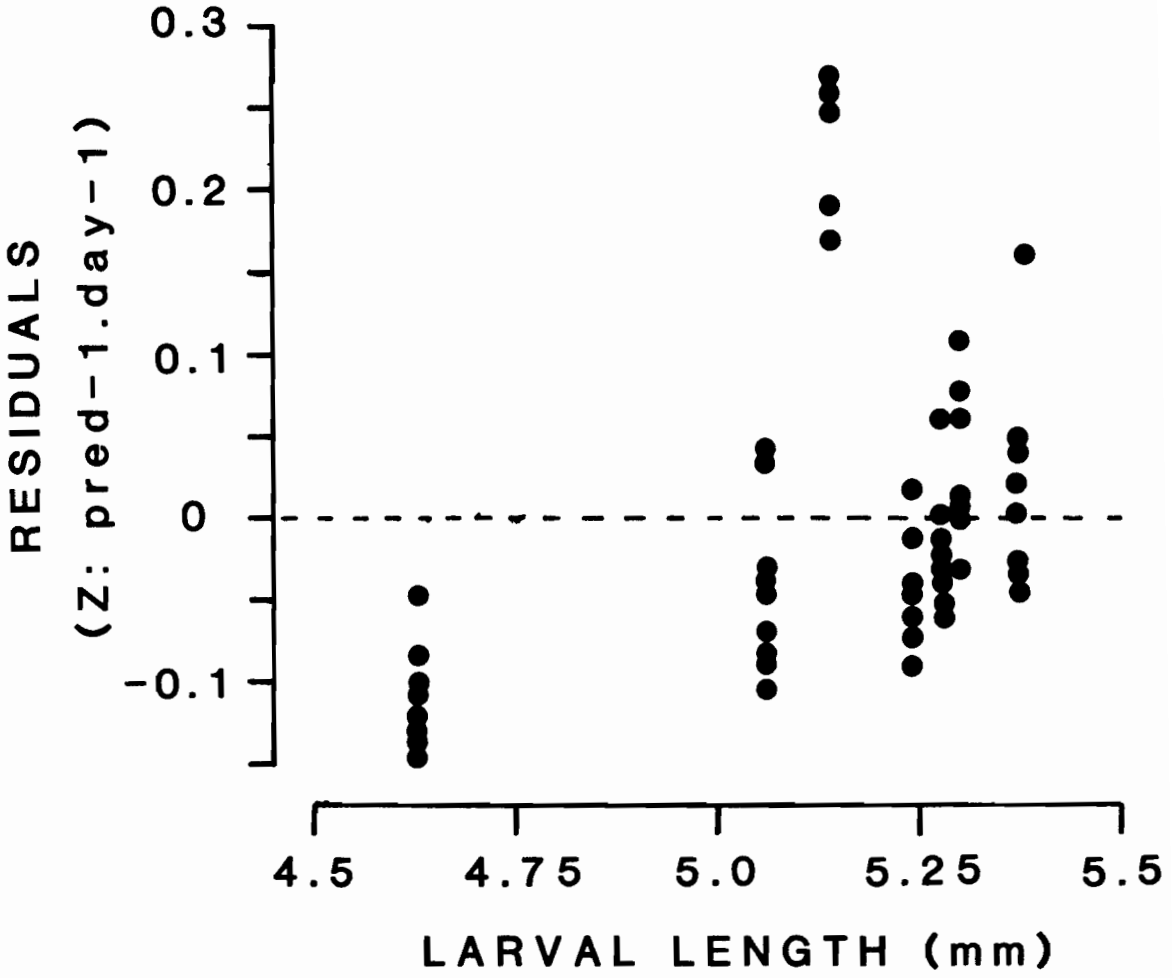
Aurelia aurita (n : 77)

* p<0.05; ** p<0.01; *** p<0.001.

both cases. For Staurophora mertensi, the residuals were also significantly correlated with larval size (Figure 14). These results paralleled those obtained by stepwise regression.

The residuals from the non-linear models were also evaluated to further test the hypothesis that alternate food would reduce larval mortality. One-way ANOVA indicated no significant differences between mortality rates observed when alternate food was present or absent (Staurophora p=0.92; Aurelia p=0.27). A non-parametric test (Mann-Withney U-test) showed no relationship between mortality residuals and alternate food levels in experiments involving Staurophora mertensi (p=0.72). For Aurelia aurita, a weak (p=0.05) positive effect of zooplankton additions on Z was revealed. These results were consistent with those derived from the exploratory stepwise regression analyses.

Figure 14. Relationship between larval mortality (residuals from non linear regression) and larval length for experiments involving Staurophora mertensi.


RESIDUALS
(Z: pred-1.day-1)
0.3
0.2
0.1
0
-0.1
4.5
4.75
5.0
5.25
5.5
LARVAL LENGTH (mm)

DISCUSSION

This study represents the first intensive effort to experimentally evaluate larval fish mortality resulting from jellyfish predation at scales relevant to natural systems. My findings and those from the preliminary work of Frank and Leggett (1982a) clearly indicate that studies of the dynamics of interactions between larval fish and their invertebrate predators can be successfully and reliably achieved with in-situ enclosures of the type employed. Larger in-situ enclosures (310 m^3) and large artificial basins (4000 m^3) have been previously employed to investigate larval mortality in-situ (reviewed in Chapter 1). However, the cost and the logistic difficulties associated with these large scale systems precluded the realisation of controlled experiments. In several cases, the larval mortality imposed by macrozooplankton predators that accidentally occurred in these large enclosures and basins was more inferred than quantitatively measured (Oiestad and Mockness 1981; Mockness 1982; Oiestad 1985). The size of these systems also precluded the realisation of short-time scale experiments as are often required in quantitative studies of predator-prey interactions.

In this study, the coefficients of variation (CV) of larval mortality in replicated experiments varied between 11 and 101%, with the majority (72%) of the values being < 50%. Coefficients of variation in Z ranging from 11 to 50% correspond to CV in predation rates (I) varying from 10 to 40%. Previously published laboratory studies have not explicitly reported the degree of variability in predation rates of different predators fed on larval fish. I therefore used published results to calculate the CV in predation rates measured in small

laboratory containers. Replicated predation rates were highly variable for copepods (CV= 22-53% - Lillelund and Lasker 1971; CV= 23-78% - Bailey and Yen 1983; CV= 33-150% - Bailey 1984; CV= 7-43% - Turner et al. 1985), euphausiids (CV= 45-64% - Theilacker and Lasker 1974; CV= 20-200% - Bailey 1984), amphipods (CV= 1-18% - von Westernhagen et al. 1979; CV= 52-58% - Yamashita et al. 1984), and small jellyfish (CV= 2.5-53% - Bailey and Batty 1983; Bailey 1984). These values, obtained in small (0.2 to 5 liter) containers, are equivalent to those measured in my in-situ enclosures. I conclude that the small laboratory containers, whose use has been justified on the basis of the greater control that can be achieved under laboratory conditions, do not yield meaningfully better precision in estimates of predator feeding rates. This observation, and the finding that container size has a strong influence on realised predation rates (Chapter 2), indicate that in-situ enclosures of the type I employed provide equally reproducable and more realistic estimates of the larval mortality imposed by macrozooplankton predators.

Effect of predator density.

The effect of jellyfish density on larval mortality has not previously been described. Larval fish mortality due to predation was linearly related to the density of jellyfish predators in enclosures (Figure 6). This indicates that the feeding rate of individual jellyfish was neither impaired (interference effect, Hassell et al. 1976), nor facilitated, by the presence of conspecifics. Studies of copepods (Fabian 1960; Lillelund and Lasker 1971) and amphipods (von Westernhagen and Rosenthal 1976) feeding on fish larvae have shown that

the larval mortality imposed by an individual predator decreased as the number of predators increased. von Westernhagen and Rosenthal (1976) argued that the decline in mortality rate per individual amphipod predator could be an artifact caused by more than one predator attacking the same prey. A similar observation was reported for copepod feeding in-situ (Hartig et al. 1982). This situation is unlikely to occur with jellyfish predators which are larger than their larval prey and do not actively pursue their prey. Although different types of predators were investigated in these separate studies, the differences in the sizes of the experimental containers used might also explain the differences in these results and mine. The copepod and amphipod studies reported above were conducted in small containers (500 ml and 3.5 l). In addition to the potential effect that confining large numbers of predators (up to 10 and 16) in such small volumes might have on their individual searching and feeding behavior, the use of small containers also caused rapid depletion of prey (85 and 100%) during some of these experiments (Fabian 1960; Lillelund and Lasker 1971). Mortality of this magnitude creates a serious problem in predation experiments in which ingested prey are not replaced (Murdoch and Oaten 1975; Arditi 1982; Houck and Strauss 1985) and may bias the effect of predator density. It is thus imperative, in these situations, to account for prey depletion in calculating the individual predation rate.

The densities of jellyfish predators employed in my experiment varied between 0.3 and 3.0 per m^3. Such densities are not unusual for adult jellyfish which often appear in dense swarms (frequently >10 per m^3, Yasuda 1969; Möller 1980; van der Veer and Oorthuysen 1985). The relationship between larval mortality and jellyfish density revealed in

this study indicates that these "blooms" can have a major impact on co-occurring larval fish populations. The selective occupation by fish larvae of water masses having lowered abundances of predators (Johannes 1978; Frank and Leggett 1982a,1983,1985) is an effective strategy for significantly lowering mortality due to planktonic predators.

Effect of larval density

The magnitude of larval fish mortality imposed by jellyfish was independent of initial larval densities (Figures 7-11). This finding strongly suggest that jellyfish exhibit a Type I functional response when feeding on larval fish. The relationships between daily predation rates (I), calculated from equation 2, and larval density are given in Appendix 2. The slopes of the log-log relationship between these two variables did not differ significantly from 1.0. This additional test confirmed that the feeding rate (I) of jellyfish was linearly related to the initial larval density. These results support my preliminary observation that the predation rate of jellyfish was linearly related to the initial larval density in containers of different size (Chapter 2). The feeding rates of these predators were never limited even when the larval densities offered exceeded those reported in nature (>400 m^3).

I found no evidence of the Type II functional response that has been frequently reported for several other macrozooplankton predators (copepods: Lillelund and Lasker 1971; Bailey and Yen 1983; Turner et al. 1985; euphausiids: Theilacker and Lasker 1974; amphipods: von Westernhagen and Rosenthal 1976,1979; Yamashita et al. 1984; chaetognaths: Kulhmann 1977; ctenophores: Frank and Leggett 1982a; jellyfish: Bailey and Batty 1982). One reason for this difference could

be the size of containers employed. Most previous studies used small containers in which the number of larval fish offered corresponded to densities greatly in excess of that observed in nature (Solemdal 1981). Bailey and Batty (1983), who used densities equating to 7000 - 10000 larvae per m^3, have argued that these high larval densities might correspond to situations in which a predator forages within a "patch" of fish larvae. However, no in-situ densities approaching these levels have ever been reported. I have previously shown that small containers can cause larval mortality due to predation to be overestimated by at least one order of magnitude (Chapter 2). This large variability was attributed to differences in the relative distribution of both predators and prey in containers of different sizes. While it is theoretically possible that the feeding rate of a predator will eventually reach a maximum as prey density increases, my results suggest that at scales approaching those occurring in nature prey density, and hence the probability of encounter between predators and prey, are sufficiently reduced that they yield a linear relationship between predation rate and larval density.

Frank and Leggett (1982a), using enclosures similar to mine, found that mortality rates in larval capelin exposed to predation by ctenophores (Pleurobrachia sp.) were inversely related to the initial larval density. However, this relationship was derived by combining the results of several experiments conducted on different dates (K. Frank, Bedford Institute of Oceanography, Halifax, Canada, pers. comm). My results clearly indicate that even relatively small between experiment variations in predator size, larval size and environmental conditions can seriously bias the interpretation of the observed relationship

between larval mortality and larval density (Figures 7 & 8). Since these potential sources of variability were not considered by Frank and Leggett (1982a), the evidence for satiation in the case of ctenophore predators remains questionnable. Reeve et al. (1978) reported that the feeding rate of the ctenophore Pleurobrachia pileus preying on copepods was linearly related to copepod abundance but the slope of the relationship varied as a function of predator size.

Prey depletion can also influence the functional response and lead to erroneous interpretations of the effect of prey density on predator feeding rate. Arditi (1982) mathematically demonstrated that the "averaging effect" of long-term experiments would result in a linearization of the functional response when predation rate is calculated as the number of prey taken per unit of time. This bias can be removed by calculating mortality rates from equations that account for prey depletion (Arditi 1982). My calculation of mortality rate accounted for prey depletion, as recommended by Arditi (1982). The Type I (linear) functional response observed in my experiments cannot, therefore, be attributed to an artifact caused by "averaging effect" of conducting 40 h experiments.

The difference in functional response observed in my experiments relative to previous studies may also have been an effect of predator size. The small container size typically used in experiments to date has demanded that small predators be used. These small predators may have limited capacity for ingesting larval fish because of limited gut capacity, slow digestion processes, long handling times, and/or low energy demands. Bailey and Batty (1983) reported that the predation rate imposed on herring larvae by jellyfish Aurelia aurita, averaging 1.3 cm

in diameter, reached a maximum at larval densities ranging from 35 to 50 larvae / 5 liter (equivalent to 7000 to 10000 larvae per m^3). These predators were about 50% the size of the smallest Aurelia aurita used in my experiments. The possibility that small jellyfish become satiated at naturally occurring prey densities remains to be verified. The possibility that smaller macrozooplankton predators may have a limited feeding rate on larval fish is supported by the inverse relationship observed between larval mortality and initial larval density in control enclosures containing wild zooplankton as alternate food (Figure 5). Larval mortality was significantly and positively correlated with the abundance of large (>518 µm esd) plankters and with the average size of the zooplankton added to these enclosures.

The linear functional response exhibited by the four jellyfish species I employed is consistent with previous reports of the feeding rates of other gelatinous zooplankton (Reeve and Walter 1978; Reeve et al. 1978; Purcell 1982; Fulton and Wear 1985) preying on copepods. The linear (Type I) functional response is considered to be characteristic in filter feeding organisms (Holling 1965; Murdoch and Oaten 1975). Poulet (1974,1978) and Conover (1978) have both reported that the ingestion rates of several copepod species feeding on natural particles exhibited no evidence of saturation. These authors argued that the asymptotic ingestion curve observed in several copepods feeding studies may have been an artifact which resulted from sudden exposure to increasing food sources. When exposed to ambient food concentrations, copepods were found to exhibit a linear functional response typical of filter-feeding organisms. Jellyfish do not actively pursue their prey and, while they are not strictly filter feeders, their feeding rate is

essentially dependent on the probability of encounter between predators and prey. These characteristics satisfy the assumptions of Gerritsen and Strickler's (1977) predation model for non-visual invertebrate predators in aquatic environments. This model predicts that the feeding rate of such predators should be linearly related to their prey density, and that prey encounter rate (and mortality rate) should be a positive function of predator size and the relative speeds of both predator and prey. Bailey and Batty (1983) reported that this model underestimated the feeding rate of Aurelia aurita on herring larvae in small containers, and that it failed to account for the predator satiation observed in their experiments. However, my results indicate that mortality is more strongly related to predator and larval size and is independent of larval density. My observations, which were made at scales which more closely approximate those occurring in-situ, are consistent with the predictions of the Gerritsen and Strickler (1977) model.

Effect of Alternate Food

The presence of alternate prey did not alter the shape of the functional response exhibited by jellyfish (Figure 11), and did not significantly reduce the instantaneous larval mortality rates imposed by Staurophora mertensi and Aurelia aurita (Figure 13). This finding differs from theoretical expectations and from empirical observations of other predator/prey systems. A shift in the functional response (from Type II to Type III) in the presence of alternate prey is common (reviewed in Murdoch and Oaten 1975; Hassell 1978; Arditi 1982). There is, however, evidence that the linear functional response of

filter-feeding copepods is unaltered by the presence of alternate food (Landry 1978; Roman 1984, Paffenhoffer 1984a,b; Paffenhoffer and van Sant 1985). My results for jellyfish are consistent with that finding.

Studies with copepods have also shown that they tend to feed on the most abundant food items (Poulet and Chanut 1975) and that ingestion rates of individual food items decrease when offered in a mixture of prey (Landry 1981; Paffenhoffer 1984a,1984b; Paffenhoffer and van Sant 1985). These findings have led to the suggestion that filter-feeders are opportunistic (Conover 1978). The stability of jellyfish feeding rates on larval fish even when alternate food exceeded natural densities by 5 times (Figure 12) does not support the hypothesis of opportunism. While I did not specifically evaluate prey selectivity, my data suggest that jellyfish feed indiscriminately on larval fish (Glasser 1982).

Factors influencing larval mortality rates

My results indicate that neither prey density nor the presence of alternate food have a strong impact on larval mortality rates resulting from predation by jellyfish predators. Larval mortality was, however, strongly dependent on predator size, larval size and environmental conditions during the experiments. The dome-shape relationship between larval mortality and predator size observed for Staurophora mertensi and Aurelia aurita is atypical of other published studies in which a positive curve was generally observed (Theilacker and Lasker 1974; von Westernhagen et al. 1979). Bailey and Batty (1983 and Bailey (1984) reported that the predation rates of Aurelia aurita was linearly related to the surface area of the umbrella. However, their conclusions were based upon the results of experiments in which a restricted size range

(1.0-2.5 cm in diameter) of predators was employed. My results are consistent with these findings when small jellyfish are considered. The decline in mortality rates as predator size increased has not previously been reported. The strong correlations between various measures of size (body diameter, surface area and body weight) make it difficult to establish which of these variables is the principal determinant of the dome-shape relationship observed.

The one-year life cycle of Staurophora mertensi and Aurelia aurita is characterized by rapid growth during the medusan stage culmulating in reproduction and death near the end of the summer (Möller 1980; Hernroth and Gröndahl 1983,1985; Yasuda 1969; van der Veer and Oorthuysen 1985). While the maximum size achieved prior to reproduction varies between locations and between years within an area (10-20cm average), the release of gametes is known to induce pronounced physiological and morphological changes including tentacle reduction, diameter reduction, and slower movement (Möller 1980). These factors may contribute to the reduced feeding rates I observed in large jellyfish. An alternative hypothesis would be that fish larvae can visually detect and avoid larger predators more effectively.

The significant positive relationship between larval mortality and larval size observed in my experiments involving Staurophora mertensi (Figure 14) suggest that larger larvae are more vulnerable to predation by jellyfish predators. It is unlikely that this increase in larval vulnerability with size resulted from active selection by jellyfish, because size selective mortality was not observed in individual experiments (Figure 3). It is more likely that this difference in vulnerability resulted from size related differences in behavior. von

Westernhagen et al. (1979), Bailey and Yen (1983) and Bailey (1984) have reported that larval vulnerability to predation increased during resorption of the yolk sac and the early feeding stages. Increased vulnerability to predation during intermediate developmental stages has also been frequently observed in other planktonic organisms (Lynch 1980; Greene 1983; Greene and Landry 1985; Landry 1978; Landry et al. 1985). Larval susceptibility to predation by jellyfish may decline at even larger sizes. Bailey and Batty (1984) and Bailey (1984) reported that the vulnerability of five species of post yolk sac larvae declined as larval size increased.

The increased susceptibility to predation I observed in late yolk sac and early feeding larvae, and the similar results reported by von Westernhagen et al (1979) and Bailey and Yen (1983) may result from higher predator encounter rate due to improved swimming ability or from reduced avoidance behavior possibly due to poorer general condition. Irrespective of cause, these findings indicate that larvae are more susceptible to predation mortality at the time of transition from endogenous to exogenous feeding. An increase in larval mortality at the time of yolk sac resorption has frequently been sought as evidence for the starvation hypothesis (Marr 1956; May 1974; Dalhberg 1979). Such evidence has rarely been observed in-situ (but see Fortier and Leggett 1985). My findings indicate that even if repeated evidence of higher mortalities at this developmental stage is forthcoming it would be premature to ascribe these losses solely to starvation effects. My results also indicate that the hypothesis that larval mortality due to predation will be a inverse function of larval size (Cushing 1974; Ware 1975) is not general.

Temperature variability during experiments significantly influenced larval mortality rates. This effect is believed to be an artifact caused by conducting experiments at a fixed location subjected to short-term variations in the water mass characteristics. The coefficients of this variable were very similar for the series of experiments involving both Staurophora mertensi and Aurelia aurita. This suggests that this effect was similar in magnitude in all experiments.

The "safe-site" hypothesis

Frank and Leggett (1982a,1983,1985) proposed that the synchronous initiation of larval drift observed in several larval fish species represents an active response to reliable environmental signals. This behavior permits larvae to select specific water masses ("safe sites") that are rich in potential food and low in predator abundance. This "safe site" seeking behaviour was viewed as an evolutionnary adaptation that both avoids predation pressure by high density of macrozooplankton predators and satiates other predators whose distributions are more uniform in time and space and hence can not readily be avoided. My finding that even very high larval densities caused no reduction in predation rates by jellyfish, and that predation rate was directly proportional to predator numbers supports one component of this hypothesis. Even massive synchronous releases characteristic of capelin appear to be incapable of satiating jellyfish predators. Reduced mortality due to jellyfish predation is thus achievable only by timing emergence to occur during periods when jellyfish numbers are naturally reduced. The observation that smaller zooplankton predators whose numbers are both higher and more stable in time than those of jellyfish

(Frank and Legett, 1982a) appear to be satiated by high larval densities (alternate food experiments Figure 5) is also consistent with the "safe site" hypothesis.

A comparison of the average larval mortality imposed by the four predator species I investigated (Table 9) reveals a positive relationship between larval mortality and the average body weight of the different predator species. The mean diameter of Aurelia aurita, Staurophora mertensi and Cyanea capillata were very similar, but their average wet weights differed greatly. The greater mass of Cyanea capillata is mainly due to its larger tentacles and manubrium. The total biomass of alternate food added to the enclosures (mean = 1.52 g, range 0.32-2.24 g), induced larval mortality rates (mean Z= 0.062, s.e. 0.010) equal to those generated by experiments involving small Catablema vesicarium of equivalent total mass. While these data are insufficient to develop a general relationship, this finding is consistent with the empirical evidence, and the theory, which indicates that ingestion rates of both terrestrial and aquatic organisms are related to their total mass (Peters 1983; Peters and Downing 1984). This suggests that the magnitude of predation losses to larval fish populations resulting from a complex of predators would best be estimated by a measure of the total biomass of potential predators rather than by an estimate of their numerical abundance.

The "match/mismatch" concept revisited

Cushing (1972,1975) hypothesized that the interannual variability in larval fish mortality resulted from variability in the temporal co-occurrence of larval fish and their food (the "match/mismatch"

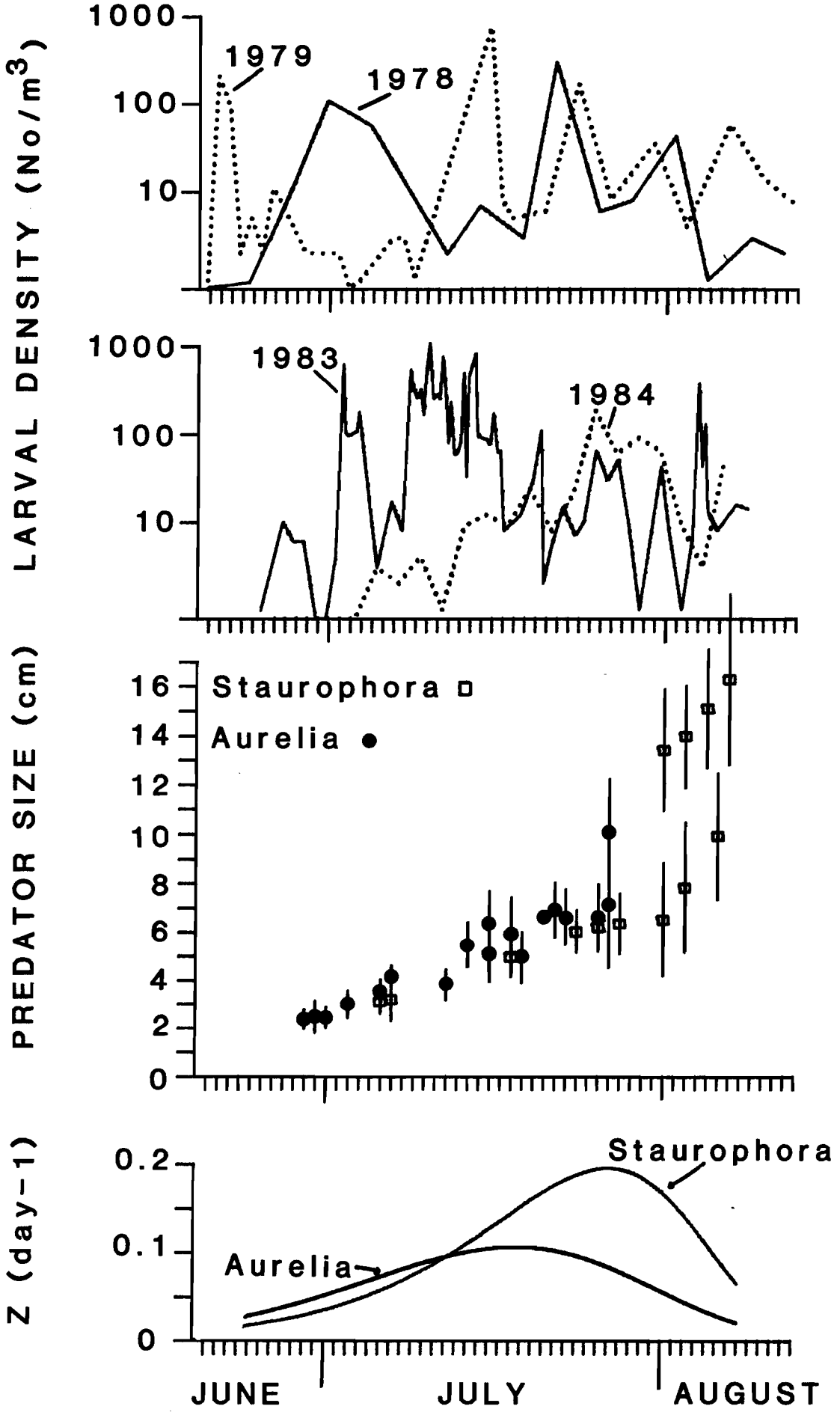
Table 9. Umbrella diameter (cm), estimated wet weight (g) and average instantaneous larval mortality rate (Z = predator-1.day-1) due to predation by four jellyfish species. Mean, standard deviation and range are given for each variable.

Jellyfish Species	N	Umbrella Diameter mean (s.d.)	Wet Weight mean (s.d.)	Mortality Rate (Z) mean (s.d.)
Catablema vesicarium	16	1.70 (0.28) 1.04-2.07	2.17 (0.82) 0.55-3.39	0.055 (0.035) 0.018-0.137
Aurelia aurita	77	5.34 (1.74) 2.24-9.00	9.59 (7.16) 0.67-32.85	0.092 (0.052) 0.012-0.245
Staurophora mertensi	64	9.54 (3.38) 2.87-15.25	38.35 (30.95) 1.07-107.9	0.152 (0.099) 0.023-0.451
Cyanea capillata	7	10.60 (2.74) 7.54-15.00	127.8 (78.4) 40.5-301.5	0.969 (0.366) 0.632-1.587

concept). This theory implicitly assumes that larval mortality is modulated by the availability of food principally, but not exclusively, when exogenous feeding is initiated. The theory is based on the reality that interannual variation in climate can and does modify the amplitude and the timing of the production cycle. Cushing (1975) argued that the resulting match or mismatch of larvae and food distributions in time or space was primarily responsible for recruitment variability.

My results lead me to propose an alternative hypothesis which is based on interannual variation in the temporal co-occurrence of larvae and their principal predators. An examination of the temporal pattern of abundance of capelin larvae in Bryants Cove waters in the years 1978, 1979, 1983 and 1984 revealed that larval densities were temporally variable due to periodic mass emergences induced by onshore winds events as had previously been demonstrated by Frank and Leggett (1981). Although in all years the emergence is concentrated during the early summer months, the stochastic nature of onshore wind events causes the timing of larval releases to be variable from year to year and to be spread over a period of about 30-40 days (Figure 15). Over the same time period, jellyfish Staurophora mertensi and Aurelia aurita typically grow rapidly from an average size of 1-2 cm to 15-17 cm in diameter (Figure 15). Using the relationship between larval mortality and predator size alone derived from my enclosures experiments (Table 7), I estimated the larval mortality rate imposed by these predator species as a function of time (Figure 15). The temporal variability of mortality rates indicates that larval mortality due to jellyfish predation could vary between 5 and 20 % per day due to the "match or mismatch" in the emergence timing of capelin larvae relative to the growth trajectory of

Figure 15. Temporal variation of capelin larval abundance (No/m^3) at Bryants Cove, Newfoundland, during four years; growth rate of Staurophora mertensi and Aurelia aurita (data pooled from 1982, 1983, 1984) and estimated larval mortality rate due to predation. Larval abundance data for 1978 and 1979 are redrawn from Frank and Leggett (1981). Larval abundance data for 1983 were kindly provided by Dr. C.T. Taggart and those for 1984 are from de Lafontaine (unpubl. data).


LARVAL DENSITY (No/m3)
1000
100
10
1979
1978
1983
1984
PREDATOR SIZE (cm)
16
14
12
10
8
6
4
2
0
Staurophora
Aurelia
Z (day-1)
0.2
0.1
0
Staurophora
Aurelia
JUNE
JULY
AUGUST

Staurophora mertensi and Aurelia aurita. Mortality due to predation is minimized when cohorts of larvae emerge while jellyfish are small (1979) and increases if the major releases are delayed in time (1984). It is clear that the interaction between larval emergence and predator growth can induce large variability in larval survival between years as well as within a year. Interannual covariability in predator abundance would further influence the mortality rates. Taggart (1986) provided evidence that mortality in larval capelin is highly variable both between years and between cohorts within a given year. The fact that this variability was unrelated to food availability, but was consistently correlated with predator abundance supports, but does not confirm, my hypothesis. A further analysis of the contribution of predator size to the reduction in unexplained variance in mortality is required.

The mortality estimates derived from my studies varied between 5% to 20% per day at an average predator density of 0.3 per m^3. Such densities are high for a single species. Single species densities more typically range from 0.005 to 0.5 per m^3 (Möller, 1980; Yasuda 1969,1970; van der Veer and Oorthuysen 1985; van der Veer 1985; Fancett 1986). However, the cumulative impact of two or more co-existing jellyfish species could easily induce larval mortalities equivalent to those I calculated (Figure 15). Taggart (1986) and Fortier and Leggett (1985) estimated that mortality rates of larval capelin during the first days following their release averaged 40% to 60% per day. My results, and Taggart's (1986) observation that predator density was the sole variable correlated with intra- and interannual variability in larval mortality, suggest that macroinvertebrate predation has the potential of being the primary regulator of larval survival as has previously been

proposed (see Introduction).

The fact that neither larval density nor alternate food were important regulators of the larval mortality rates imposed by macrozooplankton predators, suggests that future studies of the impact of jellyfish predation on larval fish, whether involving experiments or in-situ sampling, should emphasize the interactive effects of predator and prey size, and the chronology of their interaction.

THESIS CONCLUSION

The importance, and the dynamics, of predation on the survival of the early developmental stages of fish has been more frequently inferred than quantitatively evaluated during the past 60 years. In the general introduction of this thesis, I reviewed the existing literature on the subject and concluded that the evidence for predation as a major regulator of larval mortality was poor. Failure to evaluate predation at scales that are relevant to both predator and prey has seriously impaired the development of knowledge in this area and has contributed to the debate on the relative importance of predation and starvation on the mortality of larval fish in nature. I also concluded that a comprehensive evaluation of the interactions between larval fish and their potential predators is a prerequisite to further advancement and evaluation of the current hypotheses concerning the mortality of fish larvae.

The impact and the role of macrozooplankton predators on larval fish survival has often been emphasized, but has also been critically questionned due to the uncertainty of extrapolating laboratory results to natural situations and the misinterpretation of the negative relationships between the relative abundance of predators and prey in field studies.

In this study, I have shown that experimental quantification of mortality rate due to predation can be successfully and reliably achieved with the use of in-situ enclosures. These enclosures were shown to adequately reproduce the natural conditions of the waters in

which both larvae and predators occur (Chapter 1). The behavior exhibited by fish larvae in enclosures was also shown to be similar to that reported in nature (Chapter 1). These attributes of my enclosure designs make them appropriate for the manipulative study of predator-prey interactions at scales larger than any that had previously been used.

The relevance of this larger scale approach was clearly made evident in experiments that demonstrated that mortality rates previously obtained in experiments which used small laboratory containers were overestimated by at least one order of magnitude (Chapter 2). I have also produced data which indicate that this difference resulted primarily from differences in the encounter rate between predator and prey as determined by the relative distribution of interacting organisms in different container sizes. The hypothesis that predation rate is solely a function of prey density and is unrelated to prey distribution was rejected (Chapter 2).

Mortality rates imposed by four jellyfish species ranged from 3 to 35% per day and were independent of larval density within the range of densities reported for capelin larvae in-situ (Chapter 3). The linear (Type I) functional response of the predators and the absolute mortality rates imposed by predation were similar in the presence or absence of alternate food. My study showed for the first time that the main determinants of larval fish mortality imposed by jellyfish predators are predator abundance, predator and prey size (Chapter 3).

My findings support the general hypothesis that predation mortality during the early life stages of fish should be proportional to predator numbers (Murphy 1961; Hempel 1963; Ware 1975). My data also suggest

that larval mortality is more dependent upon the relative biomass of the predator populations than upon their numerical abundance. This conclusion is based on the finding that 1) larval mortality was more strongly related to predator size within as well as between predator species and, 2) predator growth is very rapid in-situ and leads to large temporal variability in larval mortality due to predation. My study indicates that the potential impact of predation by large invertebrate predators can be sufficiently large to explain the intra- and interannual variability in larval mortality measured in-situ.

Further evaluation of the impact of predation on larval survival should concentrate on a better description of the relative distribution of both predator and prey and on refinement of the effect of predator and prey size on larval mortality both from experimental and field studies. To date, field studies have mainly focused on the horizontal distribution of the predator-prey interactions between macrozooplankton and larval fish. The results of this thesis indicate that the relative distribution of both predator and prey in the vertical plane may have a pronounced effect on estimated mortality rates.

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APPENDIX 1

Changes in umbrella dimensions and weight of planktonic coelenterates during formalin preservation.

INTRODUCTION

Most marine plankton samples are preserved in formalin-seawater solution because it is seldom feasible to measure the size and weight of fresh specimens immediately after capture. The process of formalin preservation alters body measurements of organisms, principally through shrinkage (Steedman 1976; Omori and Ikeda 1984). These changes should be taken into account if accurate estimates of growth and biomass are required. The amount of shrinkage due to formalin preservation is a function of numerous factors: concentration of formalin (Hay 1982,1984; Tucker and Chester 1984; Leuven et al. 1985), buffer use (Omori 1978) salinity of seawater (Hay 1982,1984; Tucker and Chester 1984), initial size of organisms within a species (Fowler and Smith 1983; Hay 1984) and duration of preservation (Parker 1963; Ahlstrom and Trailkill 1963; Fowler and Smith 1983; Tucker and Chester 1984). More important, changes in body measurements vary among taxa and are related to the water content and body structure of organisms (Grandperrin and Caboche 1968).

Planktonic coelenterates have a water content approximating 95%, and are susceptible to large changes in size and weight during preservation. However, information on the effect of formalin preservation on gelatinous plankton remains poor. Ahlstrom and Trailkill (1963) reported shrinkage values of up to 70% in volume after 2 years in formalin, but these results were derived from whole plankton samples and not for individual organisms. Grandperrin and Caboche (1968) found wet weight losses ranging from 39 to 52% for different gelatinous species after 7 months in preservative, but change over time

in preservative was not investigated. Möller (1980) showed that the shrinkage in the umbrella diameter of Aurelia aurita varied between 15 and 30% increasing with the initial size of the organisms, and that shrinkage was stable after two months in formalin. However, no data were given for body weight changes.

The purpose of this study was to evaluate the degree of change in size and weight of the planktonic coelenterates Staurophora mertensi and Catablema vesicarium after preservation in 10% formalin-seawater solution. These species are important components of the plankton community in the coastal waters of eastern Canada and are important predators on larval fishes.

MATERIALS and METHODS

Staurophora mertensi (Order Leptomedusae) has a flattened umbrella with numerous (up to 3000) short marginal tentacles. Catablema vesicarium (Order Anthomedusae) has an elongated bell-shaped umbrella with few (up to 32) long marginal tentacles. Specimens were collected by Scuba divers on July 9, 1984, in the coastal waters of Bryants Cove, Conception Bay, Newfoundland and the specimens were kept alive in separate glass jars until preservation. Wet weight and size measurements of these fresh specimens were taken within 1 hr of capture. The medusae were fixed with a 10% formalin-seawater solution (1 part of 40% formaldehyde in 9 parts of seawater 31-32 0/00) buffered to saturation with sodium tetraborate. The preservative solution was prepared 2-3 weeks before the experiment and was filtered (GF/C filters) before use to remove any undissolved borate crystals which may be

detrimental to the preservation of gelatinous plankton (Omori and Ikeda 1984).

Umbrella diameter of both species, and umbrella height of Catablema vesicarium were measured to the nearest 0.01 mm with a dial caliper. Prior to weighing, each individual was placed on a piece of 250 um nylon material (Nitex) and blotted on absorbant paper. Weight was determined to the nearest 0.01 g on a Mettler electronic balance. Following preservation each medusa was measured and weighed at 1.5, 6, 14, 30, 60 and 154 days. Shrinkage in umbrella dimensions and loss in weight was expressed as a percentage of the initial fresh value. These data were normally distributed for each species and for each occasion that measurements were taken. Data transformation was therefore not required.

RESULTS

The average reduction in umbrella dimensions and weight for each species of medusae is presented in Figure 1. The shrinkage in umbrella diameter and loss in weight were significantly different for the two species (Table 2). The mean umbrella diameter and mean weight of both species decreased sharply during the first day following fixation and preservation in formalin. Mean diameter and mean weight after 1.5 day in preservative were respectively 90.4 and 71.3% of the initial values for Staurophora mertensi and 80.7 and 67.0% for Catablema vesicarium. The mean umbrella diameter declined at a much slower rate afterwards and tended to stabilize after 2 months. Rates of changes in weight were also slower after the first day, but no stable weight was achieved for

either species. At 154 days, mean umbrella diameter and weight were reduced to 84.9 and 37.9% of initial values respectively for Staurophora and to 67.8 and 30.5% respectively for Catablema.

A least squares Model I regression was used to calculate the change in average body measurements with time. An exponential model ($Y = a*\exp(-bT)$) and a polynomial model ($Y = a + b*T + c*T,$) were tested where Y is the shrinkage estimate (% of initial value) and T is the square root of the number of days following preservation ($T>0$). The square root transformation was applied to distribute more equally the measurement intervals of the time axis and thus minimize the influence of extreme values of T on the regression analysis. The correlation coefficient between predicted values from each model and the observed values was used as the criteria for selection of the "best" model.

On purely statistical grounds, the polynomial model provided a superior fit to the data in every case, although the difference between the two models is generally very small (Table 3). However, if extrapolated beyond the data, the polynomial model would eventually predict increases in mean umbrella diameter or mean weight with increasing preservation times. If extrapolation is required, and this should always be approached with caution, the exponential model should provide more reliable estimates. For purely predictive use within a time period of 5 months, the polynomial model would be more precise and is recommended for preservation corrections.

The incorporation of initial diameter or weight into the models did not significantly ($p>0.1$) improve the regression. This indicates that initial umbrella diameter or weight (within the range used here) has no effect on changes in size or weight due to preservation. However the

positive coefficients of these variables in the regression suggest that large organisms may shrink proportionnally more than smaller organisms of the same species.

Table 1. Initial size and wet weight of the medusan species. Mean, standard deviation and range of values are given.

Species		Weight (g)	Diameter (mm)	Height (mm)
Staurophora mertensi (n=26)	mean	2.61	36.53	
	s.d.	2.39	9.88	
	range	0.68-10.54	25.34-62.45	
Catablema vesicarium (n=9)	mean	1.36	15.61	25.71
	s.d.	0.95	3.54	4.01
	range	0.75-3.83	12.48-24.02	21.90-34.0

Figure 1. Shrinkage in umbrella dimensions and loss in weight (expressed as a percentage of initial value) as a function of time in preservative solution. Mean (± 2 s.e.) values are indicated as is the fitted line derived from the polynomial model.

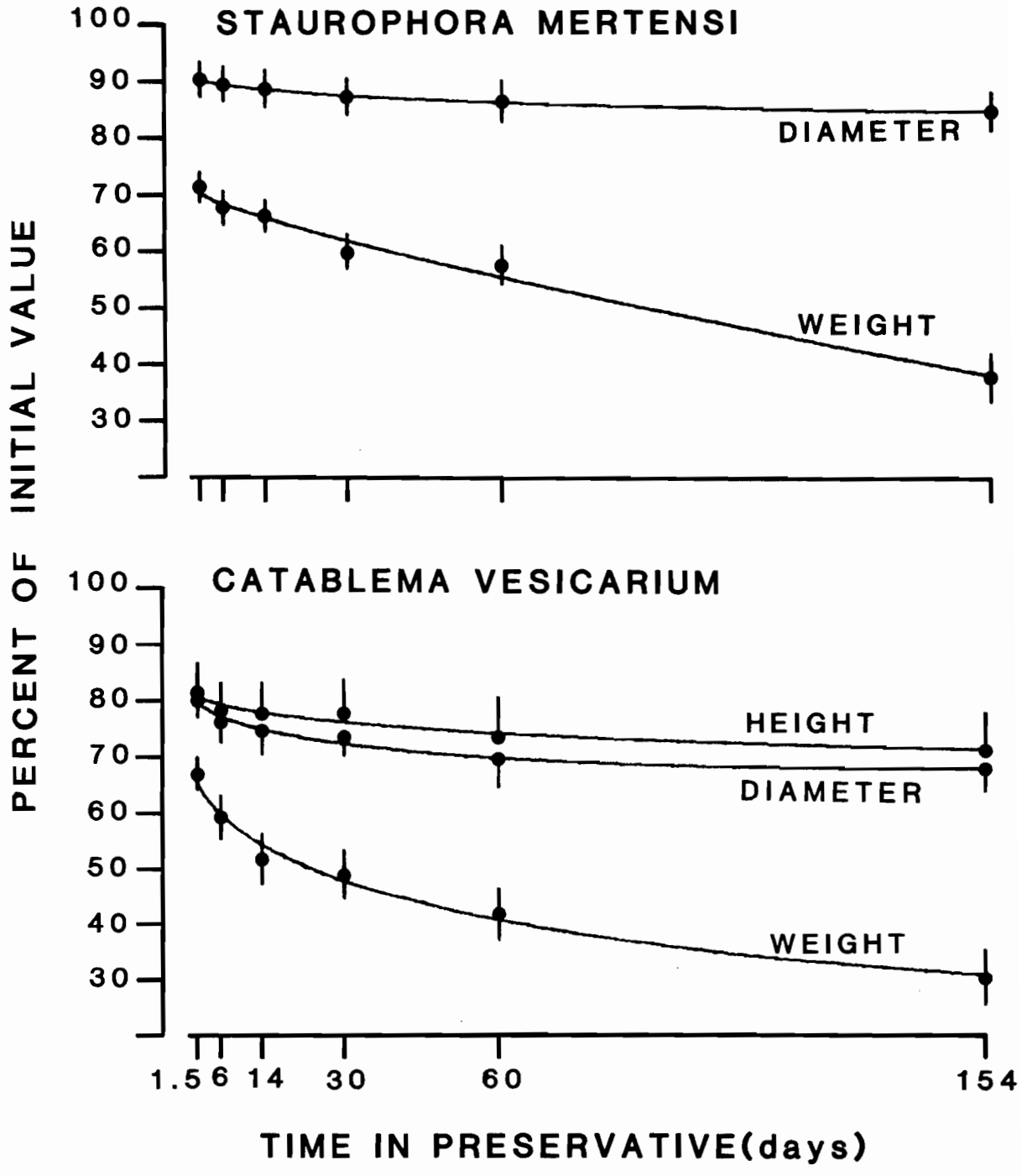
STAUROPHORA MERTENSI
100
90
80
70
60
50
40
30
DIAMETER
WEIGHT
CATABLEMA VESICARIUM
HEIGHT
DIAMETER
WEIGHT
PERCENT OF INITIAL VALUE
1.5 6 14 30 60 154
TIME IN PRESERVATIVE(days)

Table 2. Two-way ANOVA for testing the effects of Time and Species on shrinkage in size and weight due to preservation.

Source of variation	df	Diameter Sum of Squares	F	p	Weight Sum of Squares	F	p
Time	1	0.00853	21.5	0.0017	0.13951	73.11	0.0001
Species	1	0.06505	164.2	0.0001	0.03158	16.61	0.0036
Time X Species	1	0.00098	2.5	0.1551	0.00001	<0.01	0.9609
Error	8	0.00317			0.01521		

Table 3. Parameter values for exponential (E) and polynomial (P) models of shrinkage in weight and size with time for each species of medusae as a result of preservation. Regression coefficient (r^2) of predicted values versus observed values is given for each model.

Species	Model	a	b	c	r^2
Staurophora mertensi					
Weight	E	0.7963384	-0.054432	-3	0.929
	P	0.719904	-0.010902	1.3072.10	0.986
Diameter	E	0.9072312	-0.00557701	-4	0.979
	P	0.913249	-0.00767059	2.029718.10	0.995
Catablema vesicarium					
Weight	E	0.7031627	-0.067646	-3	0.985
	P	0.715942	-0.051268	1.488269.10	0.986
Diameter	E	0.7973672	-0.014560	-4	0.893
	P	0.827006	-0.024271	9.900639.10	0.966
Height	E	0.8155839	-0.011376	-4	0.916
	P	0.824910	-0.013260	3.372209.10	0.928

DISCUSSION

The initial sharp reduction in body measurements following fixation and preservation in formalin has been previously observed for other taxa (Lockwood and Daly 1975; Schnack and Rosenthal 1978; Tucker and Chester 1984). Size reduction of fish larvae has been shown to occur within the first hour following preservation (Hay 1981; Tucker and Chester 1984). The shrinkage of the planktonic Coelenterates presented here are much higher than those previously reported for any other zooplankton taxa (Steedman 1976; Hay 1982,1984; Fowler and Smith 1983; Williams and Robins 1982; Leuven et al. 1985) but are close to reported values for gelatinous zooplankton (see Introduction).

Our values for size reduction are smaller than those reported for Aurelia aurita at similar size (Møller 1980). Møller (1980) used a formalin-seawater solution of lower salinity (16 0/00 vs 31 0/00 in our study). Although the salinity of seawater used in the preservative solution is known to affect the degree of shrinkage of the organisms (Hay 1982,1984; Tucker and Chester 1984), the difference attributable to this effect is small relative to the difference between Møller's estimates and our own. This observation, plus the significant difference found between the two species we evaluated leads us to conclude that changes in size and weight due to formalin preservation is species or morphological type specific. Lockwood and Daly (1975) also reported difference in shrinkage between two species of flatfish larvae of similar size.

The large reduction in weight is within the range of values previously reported for Coelenterates (Ahlstrom and Trailkill 1963;

Grandperrin and Caboche 1968). This weight loss must be considered when estimates of the fresh weight biomass of gelatinous plankton are made from preserved samples. The continous decline in weight observed over the five months of this study makes the use of a constant correction factor for weight estimates incorrect when preservation duration is unknown. The different rates of shrinkage and weight losses between species also cause the coefficients of diameter-weight relationships to vary over time (Table 4). This precludes the use of such relationships for biomass estimates. We recommend that size-weight relationships be developed for a sample of fresh specimens of each species under investigation. Size (umbrella height and diameter of medusae) measurements of preserved specimens can then be accurately corrected for the effect of preservation. Estimates of fresh weight of preserved medusae can be calculated from the appropriate fresh weight-diameter relationships. A less reliable alternative is to apply correction factors directly to weight estimates, but care should be taken when extrapolating beyond the 154 days limit in the present study.

Table 4. Parameters of the allometric relationships ($W = a D^b$) between umbrella diameter (D) and weight (W) at different times in preservative solution. Model II functional regression (Ricker 1973) was used.

Time (days)	*Staurophora mertensi* a	b	r^2	*Catablema vesicarium* a	b	r^2
0	-9.194	2.762	0.817	-5.146	1.946	0.645
1.5	-9.842	2.937	0.960	-6.563	2.521	0.693
6	-9.339	2.784	0.930	-5.517	2.105	0.624
14	-9.162	2.731	0.940	-6.288	2.381	0.751
30	-8.884	2.632	0.934	-6.689	2.540	0.724
60	-8.753	2.588	0.944	-6.488	2.445	0.838
154	-9.566	2.711	0.844	-7.617	2.815	0.815

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APPENDIX 2

Relationships between predation rate (I) and initial number of larvae (L) stocked into the enclosures in different experiments. Slopes of log-log relationships between these two variables are also indicated.

Predator Species	Figure	I = a + b L: a	b	r^2	p	Log-log slope (s.e.)
C. vesicarium	7c	1.77	0.043	.96	0.0005	0.976 (0.100)
C. capillata	9a	-30.67	0.657	.94	0.0002	0.994 (0.111)
S. mertensi	8c	0.11	0.111	.99	0.0003	0.916 (0.124)
	9b	12.96	0.103	.88	0.0001	1.043 (0.116)
	11a	-2.92	0.063	.58	0.0286	1.148 (0.197)
	11b	-3.34	0.346	.99	0.0003	1.033 (0.042)
	11c	1.79	0.116	.97	0.0001	1.015 (0.139)
A. aurita	10a	4.30	0.017	.44	0.1056	0.733 (0.162)
	10b	2.10	0.049	.89	0.0012	0.874 (0.086)
	10c	2.62	0.069	.97	0.0001	0.999 (0.061)
	10d	16.03	0.019	.26	0.2465	0.926 (0.459)
	11d	-0.61	0.055	.98	0.0001	1.081 (0.070)
	11e	-7.06	0.160	.94	0.0003	1.026 (0.180)