

The Influence of Small-Scale Turbulence and Upwelling
on the Ecology of Larval Fishes

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Abstract

Environmental control of interactions between larval fish and their prey, and the potential influence of this relationship on fish feeding and recruitment, were assessed using empirical models developed using data drawn from the literature and developed in field studies. Ingestion rates of larval fish in laboratory and natural environments were found to differ in relation to food density. In laboratory studies, larvae show a strong functional response to prey density. Larvae situated in situ consume food at much higher rates than would be predicted from laboratory studies and these rates are independent of prey density at known in situ densities. This discrepancy between laboratory and field feeding rate - food density relationships can be partly explained by the in situ contribution of small-scale turbulence to predator-prey encounter rates. Field studies of the influence of wind on nearshore hydrography showed that wind-induced upwelling generated favorable combinations of nutrients, light, and small-scale turbulence for production by phyto- and zooplankton. The distribution of microplankton ($< 80 \mu\text{m}$) that resulted from these upwelling episodes was quantitatively described by the cumulative longshore wind velocity during the summer months. Microplankton abundance was greatest within 4 km of a major spawning site for capelin, Mallotus villosus, an economically and ecologically important forage species in the north Atlantic Ocean. Interannual variability in the intensity and frequency of upwelling-favorable winds was positively and significantly correlated with recruitment levels in the NAFO 2J3K capelin population. A new recruitment forecasting model, using an upwelling-related wind index as an input,

explained more of the variance in capelin recruitment than did a previously published model. These results suggest that larval capelin are more likely to be food-limited in years when wind conditions are unfavorable for upwelling, and that recruitment in this fish population may be determined during the larval phase.

Résumé

Le contrôle environnemental des interactions entre les larves de poissons et leurs proies, ainsi que l'influence potentiel de cette relation sur la nutrition et le recrutement, ont été étudiés dans le milieu marin ainsi qu'à l'aide d'un modèle empirique basé sur des données publiées. On a pu mettre en évidence une différence dans la relation entre le taux d'ingestion des larves de poissons et la densité de nourriture pour des valeurs en laboratoire et celles calculées in situ. Dans les études de laboratoire, on a démontré l'existence chez les larves d'une relation fonctionnelle entre la capture et la densité des proies. Les larves in situ consommaient la nourriture à un rythme beaucoup plus élevé que celui prédit par ces études de laboratoire. Ces taux d'ingestion étaient également indépendants de la densité des proies à des densités semblables à celles observées in situ. Ces différences dans la relation entre les taux d'ingestion et la densité des proies calculées en laboratoire et in situ peuvent être partiellement attribuable à la contribution in situ des turbulences à petites échelles qui influencent le taux de rencontre entre prédateurs et proies. Des études sur le terrain de l'influence du vent sur l'hydrographie côtière ont démontrées qu'une remontée d'eau génère des combinaisons de nutriments, de lumière, et de turbulence à petite échelle favorables à la production de phytoplancton et de zooplancton. La distribution du microplancton (plus petit que 80 microns) résultant de ces remontées d'eau épisodiques a été décrite quantitativement en fonction de la vitesse cumulative du vent soufflant le long de la côte durant les mois d'été. L'abondance du microplancton atteignait son maximum à moins de 4 km d'un site de ponton majeur du

capelan, Mallotus villosus, une espèce d'importance économique et écologique dans le nord de l'Océan Atlantique. La variation interannuelle de l'intensité et la fréquence des vents favorisant des remontées d'eau était corrélée de façon significative avec le recrutement chez la population de capelan des divisions 2J et 3K de l'OPANO. Un nouveau modèle de prédiction du recrutement utilisant comme variable de départ, parvenait à expliquer une plus grande proportion de la variance totale du recrutement chez le capelan que les modèles préalablement publiés. Ces résultats suggèrent que les larves de capelan sont probablement limitées par l'abondance de nourriture durant les années où les conditions de vents sont défavorables à l'apparition de remontées d'eau. Ils suggèrent également que le recrutement chez cette espèce de poissons est déterminé durant la phase larvaire.

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CONTRIBUTIONS TO ORIGINAL KNOWLEDGE

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

1. This thesis demonstrates that general ingestion rate - food density relationships for wild and enclosure-reared populations of larval fish differ fundamentally from those derived from laboratory experiments. This difference is based on the fact that, in nature, many populations of larval fish consume food at high rates, and independently of food density, even though natural prey densities are in the range that causes severe food limitation of ingestion rates by larvae in laboratory experiments.

2. Physical characteristics of the environment can partly explain why larval fish ingest food at unexpectedly high rates in nature. At small spatial and temporal scales (centimetres; seconds - minutes), the motion associated with wind- and tidally-induced turbulence substantially increases encounter rates of larval fish with individual prey. This effect is particularly important when prey densities are low, and for the weakest swimming larvae, which tend to be small in size. Small-scale turbulence is an important environmental characteristic, in addition to light and nutrient conditions, that is responsible for the high rates of plankton production in upwelling zones, tidally-mixed seas, and other dynamic environments.

At larger spatial and temporal scales (100's of metres; days - weeks), physical processes alter the absolute amount of prey for larvae

by stimulating rates of plankton production. If these rates are stimulated in the same area, and at the same time of year, over long periods of time (100's - 1000's of years), they can be an important factor that influences spawning decisions in fish populations.

The thesis also makes several additional contributions, which are narrower in scope but which were essential to the development of the general findings outlined above. These contributions are listed below:

1. The thesis develops, for the first time, empirical models which describe food consumption rates for larval fishes in laboratory and natural environments, and relates these rates to larval size, water temperature and food density. In laboratory experiments, the influences of container volume, density of fish larvae, and prey type on ingestion rates were relatively small, compared to the effects of larval size, water temperature and food density. The laboratory models show that there is a two-fold range in the average food ingestion rates of 12 species, after statistically removing the effects of body size, water temperature, and food density.

2. An empirical model was developed to estimate levels of small-scale turbulence in the mixed layer of aquatic environments. The principal input to this model is wind speed, which explains nearly 33 % of the variance in mixed layer small-scale turbulence estimates. This is the first multi-site statistical comparison of turbulent dissipation rates, and the first

quantitative assessment of factors associated with variation in these rates.

3. Simple measures of wind energy input can be used to estimate the abundance of chlorophyll a and microzooplankton in a coastal region dominated by intermittent upwelling and downwelling events. These events can transform a relatively unproductive environment into one which is more productive, and they can produce spatial gradients in the abundance of prey for larval fishes.

4. The findings described in #3 were used to develop a new recruitment forecasting model for a commercially exploited marine fish population, Mallotus villosus. The new model employs a wind term which represents the potential for wind-induced upwelling events to stimulate plankton production in the nearshore region adjacent to capelin spawning sites. This model explains more of the variance in recruitment than an existing empirical model. These results suggest that recruitment in this species may be determined by food conditions during the larval phase.

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GENERAL INTRODUCTION

Estimating the size of adult fish populations from the abundance of younger life stages, or from any other combination of variables, is one of the most important and perplexing problems in fisheries research (Sissenwine 1984; Leggett 1986; Beyer 1989; Taggart and Frank 1989). Much of this research is focussed on the egg and larval phases because only a very small fraction (e. g. 0.01%; Sale 1990) of the eggs produced by a fish population survive to become juveniles, and because most of the reduction in numbers in any given cohort occurs during the egg and larval phase.

Population loss during this period has historically been attributed to starvation of larvae (Hjort 1914; Cushing 1990), predation on eggs and larvae, or the interaction between these two processes (Sissenwine 1984; Leggett 1986). The hypothesis that food conditions during the larval phase are responsible for a major source of larval mortality was (Hjort 1914), and remains (Cushing 1990), an attractive explanation for the decrease in cohort size between the egg and juvenile stages. This is due to the fact that larvae cannot grow at high rates or survive for long periods without an abundance of suitable prey (e. g. Frank and Leggett 1986)

These observations have led to a large research worldwide effort designed to estimate relationships between mortality rates of larval fish (or indices of larval nutritional status) and measures of food abundance (Cushing 1990). Unfortunately, identifying this relationship within or among fish populations has proven difficult (Leggett 1986; Taggart and Frank 1989).

The failure to link larval mortality rates to larval prey densities suggests either that the relationship does not exist, or that currently employed methods to measure mortality rates and food densities misrepresent those actually experienced by fish in nature. The first possibility, that larval mortality rates are independent of food density, might be expected in situations where predation is the dominant source of mortality. This may, in some years, be the case for some species (Bailey and Houde 1989; Purcell and Grover 1990).

The second possibility relates to sampling methods used to study for larvae and their prey. Taggart and Frank (1989), McGurk (1989) and Kim and Bang (1990) have shown that mortality rate estimates, if they are to be reliable, must accommodate the variable nature of larval immigration and emigration from the target population during the sampling period. Mortality rate estimates are also known to be influenced by the duration of the time interval between sample collections (Taggart and Frank 1989). Estimates of mortality derived from studies having different sampling protocols cannot, therefore, be reliably compared. These sampling artifacts make it difficult to detect relationships between larval mortality rate and measures of food abundance.

Additional factors known to reduce the probability of detecting this relationship are a biased description of the larval food resource (e. g. Owen 1989) and the way in which larvae interact with their prey (Rothschild and Osborn 1988; Rothschild 1991). Assuming reliable estimates of larval mortality rate can be obtained, measurement error associated with the nature of the larval fish - prey interaction will continue to make the detection of the mortality rate - food density relationships

difficult. Lastly, attempts to relate estimates of either larval mortality rate or food abundance to *recruitment* are likely to fail, if measurement errors (e. g. Owen 1989; Taggart and Frank 1989; Bradford and Peterman 1990; Rothschild 1991) associated with any of these three variables are large.

These sampling-related biases prevent definitive acceptance or rejection of long-standing hypotheses concerning the influence of food abundance on either larval survival or recruitment in marine fish populations (Sissenwine 1984; Leggett 1986; Taggart and Frank 1989). If progress is to be made in the acceptance or rejection of food-related hypotheses of fish recruitment, estimates of larval mortality rate and the ways in which larvae locate and remain associated with their prey must be improved.

In this thesis, I address issues principally related to the association between larval fishes and their planktonic prey. Particular emphasis is placed on environmental control of this interaction. The thesis focuses primarily on wind-related phenomena (e. g. wind-induced turbulence in the upper layer of the water column, storms, and upwelling events), but will also consider the feeding ecology of larval fish, and more generally of zooplankton, in tidally influenced seas.

General effects of turbulence and upwelling on aquatic ecosystems

The influence of turbulence on aquatic ecosystems is perceived most dramatically by a human observer when strong winds create large waves. Wave-breaking is one of the most common mechanisms for generating turbulence in the water column (Lazier and Mann 1991), and is responsible for mixing heat and nutrients between the surface and deeper water masses.

However, even at lower wind speeds, mixing will continue to occur, even though it will be confined to shallower depths.

Turbulence, and the mixing that it causes, plays an important role in several aspects of plankton ecology. It is an important regulator of trophic structure in plankton communities (Cushing 1989; Legendre 1990) because it influences phytoplankton cell size (Margalef 1978), which, in turn, affects rates of ingestion and production by secondary producers (Kjørboe et al. 1990; Dam and Peterson 1991).

Theoretical models indicate that the turbulent motion of small eddies (scales of cm's) increases the velocity of a planktonic predator, relative to that of its prey (Rothschild and Osborn 1988). This, in turn, is believed to increase the rate of encounter between planktonic predators, including larval fish (Sundby and Fossum 1990), and their prey (Rothschild and Osborn 1988). This can result in shorter development times for some food-limited herbivorous zooplankton (Saiz and Alcaraz 1991).

At larger scales (eddy size: m's to 10's of m), storm-related mixing is known to supply nutrients to the photic zone where they can be used by nutrient-limited phytoplankton. This role will be most important during times of the year when, or at places where, surface nutrient levels are typically limiting. Wind-induced mixing events can, therefore, increase rates of phytoplankton production in otherwise unproductive ecosystems (e. g. Kjørboe and Nielsen 1990).

Mixing also disperses patches of plankton particles (Haury et al. 1990), which may be essential to the feeding success of larval fishes (Lasker 1975; Buckley 1984). Interannual differences in the frequency and intensity of mixing events could, therefore, have detrimental effects on

larval feeding and mortality rates (e. g. anchovy, Engraulis mordax; Peterman and Bradford 1987).

In some areas, winds produce important currents which transport plankton to new areas, and which bring nutrient-rich water higher into the photic zone. The upwelling of nutrient-rich water is an important phenomenon regulating plankton production in the coastal ecosystems near Peru, California and southwest Africa (Cushing 1975). Upwelling zones are the most productive regions of the world in terms of annual fish yield per unit area (Ryther 1969), and therefore, are economically important areas of the global ocean. In these systems, upwelling is relatively persistent at time scales of weeks to months and occupies spatial scales extending 10's of kms from shore along 100's of km of shoreline (Richards 1980; Lazier and Mann 1991).

In many other areas, upwelling may extend only 1 - 10 km from the coastline, and may be much less persistent in time (e. g. Atlantic coast of Nova Scotia; Platt et al. 1972; Izu Peninsula, Japan; Atkinson et al. 1987). This limited, episodic influence occurs primarily because wind patterns are less consistent in direction, frequency, and intensity. In these areas, therefore, the influence of upwelling, and its beneficial effects on nutrient supply to the photic zone, and on levels of turbulence within the water column, may be large in some years, but insignificant in other years. In addition, intermittent upwelling events will displace the nutricline closer to the surface. Phytoplankton associated with the nutricline (e. g. Parsons et al. 1977) could experience increases in light intensity and, potentially, higher rates of photosynthesis, as a consequence of vertical displacement (e. g. Lande and Lewis 1989) during

upwelling. Consequently fish larvae, which hatch at relatively precise times and places (Sinclair 1988; Cushing 1990), could enter an environment which is relatively food-rich and turbulent in some years because of high rates of upwelling, but in another year, when upwelling is less frequent, become associated with a food-poor and low turbulence environment.

In summary, the general influences of turbulence and upwelling on plankton ecology suggest that several characteristics of the larval food resource will vary across time and space depending on environmental conditions. These characteristics include the rate of production of larval prey, its vertical and horizontal distributions, and the rate of encounter of larvae with their prey.

The general objectives of this thesis were to describe quantitatively how environmental conditions influence interactions between larval fishes and their prey, and to use this information to identify those circumstances under which recruitment in capelin, Mallotus villosus, is likely to be determined by food-limitation during the larval phase. My specific objectives were:

- 1) to develop and compare empirical models that estimate rates of food consumption by larval fish in laboratory and natural environments.

- 2) to compare laboratory-based predictions of food ingestion rate with prey densities observed in nature.

- 3) to develop empirical models for estimating levels of small-scale turbulence in the wind-mixed layer of the water column for different wind speeds.

- 4) to use the results of objective #3, and previously-published models of tidally-induced turbulence, to assess whether turbulence induced

by wind or tide could account for any differences in feeding rates observed between laboratory and field populations of larval fish.

5) to quantify the cumulative effect of transient upwelling and downwelling events on distributions of larval fish prey adjacent to a major fish spawning site for capelin (Mallotus villosus).

6) to evaluate the significance of transient upwelling and downwelling events on recruitment capelin, as a test of the hypothesis developed in # 4 and # 5 above

The results of the thesis are presented in six chapters, each of which has been, or will be submitted to peer-reviewed scholarly journals for publication. The Faculty of Graduate Studies and Research, McGill University requires that the following text be included in all theses:

"The candidate has the option, subject to the approval of the Department, of including as part of the thesis the text, or duplicated published text, of an original paper or papers. Manuscript-style theses must still conform to all other requirements explained in the Guidelines Concerning Thesis Preparation. Additional material (procedural and design data as well as descriptions of equipment) must be provided in sufficient detail (e. g. in appendices) to allow clear and precise judgement to be made of the importance and originality of the research reported. The thesis should be more than a mere collection of manuscripts published or to be published. It must include a general abstract, a full introduction and literature review and a final overall conclusion. Connecting texts which provide logical bridges between different manuscripts are usually desirable in the interest of cohesion. It is acceptable for theses to include, as chapters, authentic copies of papers already published,

provided these are duplicated clearly and bound as an integral part of the thesis. In such instances, connecting texts are mandatory and supplementary explanatory material is always necessary. Photographs or other materials which do not duplicate well must be included in their original form. While the inclusion of manuscripts co-authored by the candidate and others is acceptable, the candidate is required to make an explicit statement in the thesis of who contributed to such work and to what extent, and supervisors must attest to the accuracy of the claims at the Ph. D. Oral Defense. Since the task of the Examiners is made more difficult in these cases, it is in the candidate's interest to make the responsibilities of authors perfectly clear.

The complete text of the above must be cited in full in the introductory sections of any theses to which it applies."

In response to these requirements, I offer the following. Chapters 1 (MacKenzie, Leggett, and Peters; Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the wild?) and 3 (MacKenzie and Leggett; Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide) have been published in Marine Ecology Progress Series (Volume 67: 209-225 [1990] and Volume 73: 149-160 [1991], respectively). Chapter 2 (MacKenzie and Leggett; Wind-based models for estimating turbulent energy dissipation rates in aquatic environments, and their potential for examining the influence of wind on plankton ecology) has been submitted to this same journal for publication. Chapters 4 (MacKenzie and Leggett; The effect of wind in determining water column attributes, and its potential influence on the nature and fate of

plankton production) and 6 (MacKenzie and Leggett; The influence of wind on capelin [Mallotus villosus] recruitment) will be submitted to Canadian Journal of Fisheries and Aquatic Sciences. Chapter 5 (MacKenzie and Leggett; Wind-mediated control of temporal and spatial patterns in prey availability for larval fishes) will be submitted to Marine Biology. Literature citations appear at the end of each chapter, and have been prepared according to journal guidelines.

The study was developed and executed by the author of the thesis. My supervisor, Dr. W. C. Leggett, assisted in an advisory and editorial capacity, participated in the collection of some of the field data, and provided funds and logistic support essential for the execution of the work. Chapter 1 resulted in part from assignments prepared by the author as requirements for a graduate course (Predictive Ecology; Biology 177-533) taught by Dr. Peters. Dr. Peters, who assisted in the conceptualization of this chapter and in the approaches to analysis, appears, therefore, as third author on the publication which resulted from this work.

Portions of the thesis have been presented in annual seminars in the Department of Biology, McGill University, and at several national and international scientific meetings. These external presentations are listed below:

Estimating the role of tidal and wind energy on encounter rates between planktonic predators and prey using the Simpson-Hunter index and empirical wind-based models. American Society of Limnology and Oceanography, 1991 Annual Meeting, Halifax, Nova Scotia; June 10-14, 1991.

Inter-relationships between tides, wind, and the rates of contact between larval fish and their prey. Canadian Conference for Fisheries Research, Guelph, Ontario; January 3-4, 1991.

The influence of episodic wind-induced upwelling on nearshore phytoplankton and zooplankton abundance. American Society of Limnology and Oceanography, 1990 Annual Meeting, Williamsburg, Virginia; June 10-15, 1990.

Predicting larval fish ingestion rates: are marine fish larvae food-limited in nature? Canadian Conference for Fisheries Research, Ottawa, Ontario; January 3-4, 1990.

Predicting larval fish ingestion rates: key variables and experimental bias. 13th Annual American Fisheries Society Larval Fish Conference, Mérida, Yucatan, Mexico; May 21-27, 1989.

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Chapter 1

Estimating Larval Fish Ingestion Rates:
Can Laboratory Derived Values be Reliably
Extrapolated to the Wild?

Introduction

Laboratory ingestion rate studies involving individual species of larval fish have established that larvae have a sharp functional response at low food densities and that ingestion rates become satiated at much higher densities (Theilacker and Dorsey 1980; Klumpp and von Westernhagen 1986; also Holling 1959; Ivlev 1961). These laboratory-derived functional responses are often used to evaluate the extent to which naturally occurring food levels may influence larval survival and year-class strength in marine fish populations (e. g. Houde 1978; Wroblewski and Richmann 1987; Anderson 1988).

However, extrapolation from laboratory estimates of food ingestion rates in this way could bias interpretations of larval feeding ecology (Anderson 1988; Jenkins 1988) because they assume that laboratory derived functional responses are similar in form and magnitude to the functional responses of larvae in nature. This assumption may not be valid because experimental conditions themselves can influence laboratory ingestion and growth rates of larval fish (Houde 1977; Theilacker and Dorsey 1980; Hunter 1981) and other zooplankton (Peters and Downing 1984; Delafontaine and Leggett 1987). The relative importance of these experimentally induced biases in laboratory ingestion rates has not yet been quantified relative to the influences of larval size, water temperature and food density.

Moreover, no quantitative comparison of in situ larval feeding rates in response to local food densities has been attempted for wild larval populations. Hence the validity of the assumption that laboratory and natural functional responses are similar remains in doubt, as does the utility of the application of experimentally derived ingestion rates to

wild populations (Rothschild and Osborn 1988).

In this study I sought to identify the variables that influence the magnitude and form of ingestion rate responses to varying prey densities both in the laboratory and in the wild. I also used empirical models developed in the course of this analysis to evaluate whether ingestion rates of wild marine fish larvae are likely to be food-limited.

Methods

Laboratory ingestion rates

Data collection and conventions: The data used in developing empirically based ingestion rate models were extracted from the literature relating to marine and estuarine species of fish larvae. I sought data on ingestion rate (I ; expressed as μg dry weight of food ingested per individual per day), larval dry weight (W ; $\mu\text{g}/\text{individual}$), prey dry weight (PW ; $\mu\text{g}/\text{individual}$) and prey density (Food ; L^{-1}). Body size and food densities were expressed in units of mass because these are known to represent energy flow better than units of length or numeric concentrations respectively (Houde 1978; Theilacker and Dorsey 1980).

Sixty percent of all larvae contained in the data set were preserved in formalin before dry weight determinations were performed. Losses in dry weight are known to occur in larval fishes as a consequence of preservation but the magnitude of this loss has not been thoroughly evaluated (Delafontaine and Leggett 1989; Giguère et al. 1989). Available estimates of preservation-induced dry weight loss range from 9 - 30 % (Theilacker and Dorsey 1980; Bailey 1982; Hay 1984). If reported dry weights had not been corrected for this preservation effect, I assumed a

20 % dry weight loss, which is the midpoint of the published ranges (Theilacker and Dorsey 1980; Bailey 1982; Hay 1984), before adjusting dry weight values accordingly.

In seven of the eleven laboratory based studies incorporated into my data set, prey dry weights were not reported. In these cases, prey dry weights were estimated from weight equivalents reported elsewhere in the literature (Table 1). This allowed numerical densities of prey components to be converted into equivalent dry weights in one of three ways: (1) in cases where the proportions of different prey items in the diet were reported ($N = 3$; Houde and Schekter 1981; Theilacker 1987; Chesney 1989), I calculated the total dry weight of all food offered in each experimental treatment as follows:

$$\text{Food} = \sum_{i=1}^N (P_i * PW_i * D)$$

where Food = food density ($\mu\text{g/L}$), P_i = numerical proportion (range 0.0 - 1.0) of component i in the total prey population, PW_i = dry weight equivalent of one prey item of component i , D = total prey population density (number/L), and N = number of prey components in the prey population; (2) in cases where the relative proportions of individual prey components were not reported ($N = 1$: Monteleone and Peterson 1986), the dry weight biomass of food was estimated with equation 1 by assuming that the diet was comprised of equal proportions of all prey; (3) in cases where only one size of prey was offered per experimental treatment ($N = 7$), the numerical density of prey was multiplied by the dry weight equivalent of an individual prey comprising the diet.

All eleven studies used in my analysis reported ingestion rate estimates for larvae of several sizes. To minimize potential bias caused

Table 1. Conventions, extracted from the literature, that were used to estimate the influence of food density on larval fish ingestion rates. Data sources are listed alphabetically below table.

Convention	Reference
preserved larval fish dry weight = 0.8 * unpreserved larval fish dry weight	5, 7, 8, 16
preserved zooplankton dry weight = 0.6 * unpreserved zooplankton dry weight	7, 18
carbon mass = 0.4 * dry mass (zooplankton)	15
carbon mass = 0.55 * dry mass (<u>Artemia</u> nauplii)	14
dry mass = 0.2 * wet mass (fish larvae)	12
specific gravity of zooplankton = 1 g/cm³	11

Table 1 (continued)

Convention	Reference
% ash = .11 * dry weight	1
<u>Acartia tonsa</u> nauplius = 0.26 μ g	6
<u>Artemia</u> nauplius = 1.85 μ g	2
<u>Brachionus</u> (mixed sizes) = 0.16 μ g	17
<u>Calanus finmarchicus</u> (nauplius) = 1.5 μ g	4
<u>Eurytemora affinis</u> (nauplius) = 0.28 μ g	3, 10
<u>E. affinis</u> (copepodite) = 2.2 μ g	3
<u>E. affinis</u> (adult) = 10.4 μ g (April-May in Chesapeake estuary)	9
<u>Pseudocalanus</u> (nauplius) = 0.26 μ g	13

Table 1 (continued)

Key - 1. Båmstedt 1986; 2. Benijts et al. 1975; 3. Burkhill & Kendall 1982 (see also Chesney 1989); 4. Davis 1984; 5. Delafontaine & Leggett 1989; 6. Durbin & Durbin 1981; 7. Giguère et al. 1989; 8. Hay 1984; 9. Heinle & Fremer 1975 (see also Chesney 1989); 10. Houde & Schekter 1981 (see also Chesney 1989); 11. MacCauley 1984; 12. McGurk 1986; 13. Monteleone & Peterson 1986; 14. Oppenheimer & Moreira 1980; 15. Peters 1983; 16. Theilacker & Dorsey 1980; 17. Theilacker & McMaster 1971; 18. Vidal & Smith 1986.

by over-representation of one or two species whose ingestion rates were measured several times in one study and at a narrow range of experimental conditions, I restricted my data to the lower and upper limits, and midpoint, of the reported size range of larvae used in each combination of experimental conditions.

All ingestion rate estimates (see Appendix 1) were standardized to a 12 h feeding period. I adopted this convention because larval fish are visual feeders (Hunter 1981; Blaxter 1988).

To evaluate the potential effects of methodological factors on laboratory estimates of ingestion rate, I included in the data set water temperature, experimental container volume, larval density (numbers per litre), and prey type (Brachionus and/or Artemia, or wild zooplankton). The results of earlier studies of ingestion rates of larval fish and other zooplankton (e.g. Rosenthal and Hempel 1970; Houde 1977; Barahona-Fernandes and Conan 1981; Peters and Downing 1984; de Lafontaine and Leggett 1987) suggested that these variables can be important contributors to observed variation in measured ingestion rates. Several other variables that are also believed to influence ingestion rates (e.g. turbulence, light intensity, turbidity; Chesney 1989) were not evaluated because they were reported too infrequently to be incorporated in the analyses.

Statistical techniques: All data were expressed in standard units as detailed above. Ingestion rates, larval and prey sizes, larval and food densities were logarithmically-transformed (base 10) prior to regression analysis to linearize allometric relationships and stabilize the variance in my data set (Peters and Downing 1984). In these analyses, interaction and higher order terms were intentionally excluded to retain simplicity

and to reduce the likelihood of fitting the model to outliers (Peters and Downing 1984), even though this exclusion may reduce the amount of variance explained.

Analysis of covariance (Zar 1974) was used to distinguish the possible effect of different prey types (e.g. Rosenthal and Hempel 1970; Vu 1983) on ingestion rates. I coded Artemia nauplii or Brachionus as 0 and wild zooplankton native to the larval habitat, whether collected from the sea or cultured in the laboratory, as 1.

Model construction:

Body size strongly influences ingestion rates in a wide variety of animals (Peters 1983) and influences many other life-history traits among larval fish (Miller et al. 1988). The effect of larval size on ingestion rates was first evaluated before considering other variables. I then used stepwise regression and scatterplots to evaluate the influence of the remaining variables on residual variation about the allometric model, and all subsequent models. The criterion for variable selection and retention was set at $P < 0.05$. All computations were performed with SAS 6.0 (PC version; SAS 1985a, b) and Systat 4.0 (Wilkinson 1988).

Larval feeding ecology in nature

Natural microzooplankton densities: The laboratory based functional response models developed here were used to investigate the likelihood that natural food densities permit wild larvae to feed at maximal rates. For this analysis, estimates of microzooplankton abundance for a variety of marine environments were compiled from the literature (Table 2).

In developing this data set I used only microzooplankton abundance estimates derived in studies that employed mesh sizes $< 200 \mu\text{m}$. This was

Table 2. Microzooplankton densities at 46 marine and estuarine sites worldwide. Densities in the table are listed as means; maxima.

Site	Size or Taxa	Prey Density ($\mu\text{g/L}$)	Reference
<u>SHELVES AND BAYS</u>			
Baltic Sea	> 90 μm	148; 240 377; 692	Kahru et al. 1984, Table 1; Aug. 1982. (fresh and salty sides of front, respectively).
Bering Sea (south- east region	Nauplii of <u>Pseudo-</u> <u>calanus</u>	5; 12	Dagg et al. 1984, Figure 5; May 1981
Biscayne Bay, Florida	> 20 μm	70; 88	Leak & Houde 1987, Table 7; assume 1 plankter = .33 μg (Houde & Schekter 1981)
Block Island Sound, R.I.	> 153 μm	33; 67	Deevey 1952, Figure 4; May -Sept. 1949
Bryants Cove, Newfoundland	90-130 μm	18; 201	Taggart & Leggett 1987, Table 1; June-Aug. 1981- 1983

Table 2 (continued)

Site	Size or Taxa	Prey Density ($\mu\text{g/L}$)	Reference
Buchan front, Scotland	30-200 μm	9; 15	Kjørboe & Johansen 1986, Figure 5; Sept. 1984
Buchan front, Scotland	30-200 μm copepods	10; 15	Kjørboe et al. 1988 1988, Figure 5; Sept.-Oct. 1985
California: San Diego to Isla Guadeloupe	35-202 μm	2.4; 2.6	Beers & Stewart 1969, Table 5; Feb. 1967. Oceanic stations.
California current transect	35-200 μm	1.3; 3.5	Beers & Stewart 1967, Table 4; Dec. 9-16, 1965. Oceanic stations.
Chesapeake Bay Patuxent R.	<u>A. tonsa</u> > 80 μm	177; 349	Heinle 1966, Table 5; Jul-Aug. 1964
Chesapeake Bay, North Inlet, South Carolina	> 153 μm	16; 233	Lonsdale & Coull 1977, Figure 2 ; Jan. 1974-Aug. 1975.

Table 2 (continued)

Site	Size or Taxa	Prey Density ($\mu\text{g/L}$)	Reference
English Chan.	80-200 μm	31; 37	Holligan et al 1984, Table 4; July 29, 1981
Georges Bank:			
well-mixed	> 64 μm	17; 25	Buckley & Lough 1987,
stratified		59; 117	Table 2; May 1983
stratified		90; 278	
Kiel Bight	20-200 μm	10; 21	Smetacek 1981, Figure 6; May Aug. 1973
Lancaster Sound, eastern Canadian	35-200 μm	20; 122	Paranjape 1988, Figure 5; Aug. 1980. Upper 40 m. Arctic (74 N)
Lind�spollene, Norway	> 75 μm	26; 45	�ksnes & Magnusen 1988, Figures 8 & 9A; June 1981
Lofoten Islands, Norway	> 90 μm	14; 36	Ellertsen et al. 1984, Figure 6; May 1980 - 1982 copepod nauplii (mainly <u>Calanus finmarchicus</u>).

Table 2 (continued)

Site	Size or Taxa	Prey Density ($\mu\text{g/L}$)	Reference
Long Island So., New York	> 64 μm	11; 14	Peterson & Ausubel 1984, Figure 5; May 19 - June 6, 1982. Nauplii of <u>Acartia</u> <u>tonsa</u> and <u>Pseudocalanus</u> sp.
Long Island So.,	> 64 μm	14; 23	Monteleone & Peterson 1986, table 5;
		100; 200	March (copepod nauplii) and April (copepodites) 1983.
Masfjorden, Norway	> 180 μm	27; 49	Åksnes et al. 1989, Figure 2; June and Oct. 1985
Narragansett Bay, Rhode Island	60-150 μm	90; 220	Durbin & Durbin 1981, Figure 6; May-Aug. 1976.
Newport River Estuary	> 160 μm	40; 72	Thayer et al. 1974, Figure 2; Feb.-April 1970- 1972.

Table 2 (continued)

Site	Size or Taxa	Prey Density ($\mu\text{g/L}$)	Reference
Northumberland coast, North Sea	> 44 μm	37; 62	Evans 1977; Fransz et al. 1984; May, July and September 1971-1972
Northwest Africa (beyond upwelling zone)	102-505 μm	11; 25	Blackburn & Nellen 1976, Figures 2-4; March-May 1974.
Nova Scotian Shelf (transect southeast from Halifax)	< 200 μm	8; 18	Paranjape et al. 1985, Table 1; Mar. 1980
Onslow Bay, No. Carolina	> 110 μm	57; 103	Paffenhofer 1980, Table 5; July-Aug. 1976. Surface, nonupwelled water mass.
Oyster Grounds (south-central North Sea)	> 50 μm	43; 56	Fransz et al. 1984; May, June and September.

Table 2 (continued)

Site	Size or Taxa	Prey Density ($\mu\text{g/L}$)	Reference
Peru (beyond upwelling zone)	> 102 μm	9	Smith et al. 1981, Figure 4, April 1976
St. Georges Bay, Nova Scotia Canada	25-250 μm	50; 70	Hargrave et al. 1985, Figure 6; May-Sept. 1977.
Southern Bight, North Sea	> 50 μm	97; 197 56; 67	Fransz et al. 1984, Table 5; 1973-1975. Coastal and offshore stations respectively.
Southwest Nova Scotia	80-153 μm	33 8	Frank 1988, Figure 4; May 1985 and 1986 respectively. Samples collected beyond upwelling zone described by Garrett & Loucks (1976).
Tampa Bay, Fla.	> 74 μm	41; 54	Hopkins 1977, Table 3; May- Aug. 1970.

Table 2 (continued)

Site	Size or Taxa	Prey Density ($\mu\text{g/L}$)	Reference
Tasman Bay, New Zealand	> 60 μm	233; 333	MacKenzie & Gillespie 1986, Oct.-Mar. 1982-1984.
Tikehau atoll, Tuamotu archipelago	35-200 μm	14; 40	Leborgne et al. 1989; April 1986; Table 1 and Figure 6
Wadden Sea (Sylt channel)	> 76 μm	99; 149	Martens 1980; May, June and September. See Fransz et al. 1984.

UPWELLING ZONES

Benguela Current, St. Helena Bay	< 500 μm	357; 724	James & Findlay 1989, table 4; April - May, 1985
California: San Diego to Isla Guadeloupe	35-200 μm	3.5; 4.5	Beers & Stewart 1969, Table 5; Feb. 1967. Slope stations.

Table 2 (continued)

Site	Size or Taxa	Prey Density ($\mu\text{g/L}$)	Reference
2California Current transect	35-200 μm	3.3; 4.6	Beers & Stewart 1967, Table 4; Dec. 9-16, 1965. Inshore stations.
South Taranaki Bight, New Zealand	> 100 μm	12; 25	Foster & Battaerd 1985, Figure 3; Feb. 1981 (16 - 82 km from coast).
Cape Kahurangi, New Zealand	> 100 μm	25; > 40	James & Wilkinson 1988, Figure 2; Mar.-April 1983
Northwest Africa	102-505 μm	132; 268	Blackburn & Nellen 1976, Figures 2-4; March-May 1974
Onslow Bay, No. Carolina	> 110 μm	97; 181	Paffenhofer 1980, Table 5; July-Aug 1976 (intrusion, upwelled water mass)
Oregon	> 120 μm	125, 200	Peterson et al. 1979, July - Sept. 1973; Aug. 1974

Table 2 (continued)

Site	Size or Taxa	Prey Density ($\mu\text{g/L}$)	Reference
Peru; 15 S	> 102 μm	17; 26	Smith et al. 1981, Figure 4; April 1976
Peru; 10 S	102-505 μm	31; 62	Whitledge 1981; Table 5; April 1977
Peru; 15 S	102-505 μm	17; 24	Whitledge 1981; Table 5; April 1977
South Taranaki Bight, New Zealand	> 100 μm	25; > 50	James & Wilkinson 1988, Mar-April 1983; Figure 3
Southwest Nova Scotia, Canada	80-153 μm	167 58	Frank 1988, Figure 4; May 1985 and 1986 respective ly. Samples collected within upwelling zone described by Garrett & Loucks (1976).

done because early stage larvae generally consume prey smaller than this size (Theilacker and Dorsey 1980; Frank 1988). In some studies zooplankton samples were size-fractionated prior to weighing. In these cases I used only those data which related to size classes which closely corresponded to the $< 200 \mu\text{m}$ component. This reduced, but did not eliminate, the possible effect of contamination by larger zooplankton on estimates of larval prey abundance.

I recorded the average and maximum (Owen 1989) prey density in each study. Many data were extracted directly from figures and tables. In some cases, authors reported prey densities as ranges or averages. In these cases range midpoints or averages were used as representative densities for the areas in question. In cases where distinct habitats were sampled (e. g. within and beyond an upwelling region), data were grouped accordingly in order to accurately reflect these different hydrographic regimes. In cases where the seasonal occurrence of fish larvae was known for a given area or habitat, zooplankton densities were used corresponding to that interval.

Ingestion rates of wild larvae: To examine how ingestion rates of wild larvae were related to food density, literature ingestion rates for wild and enclosure-reared larvae were gathered from the literature and compared as a group with those predicted by the laboratory-based model. Ingestion rates of wild larvae were estimated using either gut content analyses of field-collected specimens combined with a corresponding species-specific laboratory estimate of digestion rate ($N = 5$, Dagg et al 1984; Ellertsen et al. 1984), or were calculated from growth rate and in situ temperatures ($N = 31$; see Checkley 1984). In compiling this data base, I only included

data from field studies in which larvae and their prey were sampled simultaneously during a particular research survey. These estimated rates of ingestion (Appendix 2) and accompanying food densities are considered to represent average growth rates and food levels for larvae in the given geographic region during the time interval when plankton samples were being collected (Table 3).

Results and Discussion

Laboratory ingestion rate models

The best single predictor of laboratory ingestion rates was body size (Model 1; Table 4). Size was a powerful cross-species indicator of ingestion rates despite large differences in temperature, food density and other laboratory procedures (Table 5). Clearly, larval size effectively integrates a wide range of ecological and life-history traits in fish larvae (see also Miller et al. 1988; Peters 1983).

Physiological rates in larval, juvenile and adult fishes are either allometrically (Winberg 1956; Rombough 1988) or isometrically (Rombough 1988; Giguère et al. 1988) related to body size. The regression coefficients for body size in my laboratory models varied from 0.843 to 0.990 but the variance about these coefficients (Table 4) prevented me from distinguishing whether ingestion rates are allometrically or isometrically related to body size.

Temperature was the major contributor to explained variance in ingestion rates once the effect of body size was removed (Model 2). The

Table 3. Data sources used to estimate natural ingestion rates from gut content analysis or larval growth rates.

Reference	Species	Data and comments
Buckley & Lough 1987	<u>Gadus morhua</u>	Growth rate and T (9 °C) available in Table 7. W = 2950 µg (Table 5) and Food = 17 µg/L (Figure 4).
Buckley & Lough 1987	<u>Melanogrammus</u> <u>aeglefinus</u>	T = 6 and 9 °C (Table 7); W = 790-860 µg (Table 4). Food = 15 - 133 µg/L (Figure 4).
Dagg et al. 1984	<u>Theragra</u> <u>chalcogramma</u>	Food density was 15 <u>Pseudocalanus</u> nauplii/L (average density at 20 m; Figure 5). Larval lengths (5.2 mm) were converted to dry weight using length - dry weight relation (Bailey & Stehr 1986). T = 4.5 °C.
Ellertsen et al. 1984	<u>Gadus morhua</u>	T = 4.5 °C (Figures 3 & 8). Dominant prey of diet was <u>Calanus finmarchicus</u> nauplii; densities at 4 sites were 21, 6, 6 & 4 individuals/L (Figure 6). Gut clearance time for larval cod

Table 3 (continued)

Reference	Species	Data and comments
		at 5 °C is estimated to be 1.5 hours (Tilseth & Ellertsen 1984).
Frank & Leggett 1982a	<u>Mallotus villosus</u>	<u>In situ</u> enclosure experiments. Growth rates and food densities available in Figure 8. Assumed average size at hatch was 4.8 mm SL (Fortier & Leggett 1982; Table 3). Lengths converted to DW using length-weight relationship (Møksness 1982). Specific growth rates (dry weight basis) were used to estimate ingestion rates at midpoint of experiment (3.5 days). T = 6.5 °C.
Gamble & Houde 1984	<u>Gadus morhua</u>	<u>In situ</u> enclosure experiment. Average T and photoperiod were 8 °C and 17 hours. Average densities of copepod nauplii were 21.5 (range = 6-40) and 23/L; 80 % of all nauplii was <u>Pseudocalanus elongatus</u> , which dominated diets.

Table 3 (continued)

Reference	Species	Data and comments
Leak & Houde 1987	<u>Anchoa mitchilli</u>	Larval sizes at age 10 days were calculated from growth rate equations (Table 5). Mean T and microzooplankton densities available in Tables 1 & 5. Average weight of an individual particle comprising mixed Florida microzooplankton was 0.33 μg (Houde & Schekter 1981).
Monteleone & Peterson 1986	<u>Ammodytes</u> <u>americanus</u>	Average Food = 60.8 $\mu\text{g/L}$ for March April 1983 (Tables 2 & 5). Average T and photoperiod were 4 5 $^{\circ}\text{C}$ and 11 hours respectively. Specific growth rate = 4.0 % per day in nature. Average W in March = 992 μg (Table 3A).
Munk et al. 1986	<u>Clupea harengus</u>	Lengths converted to dry weights using "fall 1978" relationship given by Gamble et al. (1985; Table 8). T = 12 $^{\circ}\text{C}$ (Richardson et al. 1986; Figure 5A). Food = 6.2

Table 3 (continued)

Reference	Species	Data and comments
		$\mu\text{g/L}$ (Kiørboe & Johansen 1986; p. 50).
Peterson & Ausubel 1984	<u>Scomber scombrus</u>	W and growth rates presented in Table 3. Larvae were collected mostly in upper 10 m of water column. Authors considered <u>A. tonsa</u> and <u>Pseudocalanus</u> nauplii as larval prey. Densities of these prey are presented in Table 2 and Figure 5. Assume mean T where larvae were most abundant = 14° C; photoperiod = 15 h.

Table 4. Models that describe ingestion rates for laboratory (Models 1 - 4; n = 109 with 11 species) and wild (Model 5; n = 36 with 8 species) populations of larval fish. For Model 3, "Res" refers to residual ingestion rates which have been calculated as the difference between observed ingestion rates and those predicted using larval size and experimental temperature as inputs to Model 2. For Models 3 and 4, "Crit" refers to the critical food density beyond which ingestion rates are independent of food density. Thus Model 3 simplifies to $\text{Res} = 0.250$ when food densities exceed $173 \mu\text{g/L}$, and Model 4 simplifies to $\text{LogI} = 0.843 \cdot \log W + 0.038 \cdot T - 0.622$ when food densities exceed $185 \mu\text{g/L}$. s.e. = standard error of parameter estimate and x_i = independent variable. Data sources are listed alphabetically below table.

Model	s.e.	Range of x_i	R^2	Data Sources
1 $\log I = .881 \cdot \log W$	.077	.929 - 3.466	.56	2, 7, 8, 9, 10, 11,
- .270	.170			13, 16, 17, 18, 19
2 $\log I = .990 \cdot \log W$	.070	.929 - 3.466	.65	2, 7, 8, 9, 10, 11,
+ .036 $\cdot T$	.007	2 - 29		13, 16, 17, 18, 19
- 1.170	.224			

Table 4 (continued)

Model	s.e.	Range of x_i	R^2	Data Sources
3 Res = .869*logFood	.107	.860-4.944	.55	2,7,8,9,10,11,
- 1.696	.181			13,16,17,18,19
Crit = log(173)				
= 2.239	.105			
4 logI = .843*logW	.047	.929-3.466	.85	2,7,8,9,10,11,
+ .038*T	.004	2 - 29		13,16,17,18,19
+ .918*logFood	.077	.860-4.944		
- 2.704	.192			
Crit = log(185)				
= 2.268	.034			
5 logI = 1.162*logW	.077	1.373-3.470	.89	1,3,4,5,6,12
+ .029*T	.007	4 - 31		14,15
- 1.343				

Table 4 (continued)

Data sources: 1. Buckley & Lough 1987; 2. Chesney Jr. 1989, 3. Dagg et al. 1984; 4. Ellertsen et al. 1984; 5. Frank & Leggett 1982a; 6. Gamble & Houde 1984; 7. Govoni et al. 1982; 8. Houde & Schekter 1981; 9. Hunter & Kimbrell 1980; 10. Klumpp & vonWesternhagen 1986; 11. Kuronuma & Fukusho 1984; 12. Leak & Houde 1987; 13. Monteleone & Peterson 1986; 14. Munk et al. 1986; 15. Peterson & Ausubel 1984; 16. Stepien 1976; 17. Theilacker 1987; 18. Tucker 1989; 19. Werner & Blaxter 1981.

Table 5. Means and ranges of variables which were assessed for their influence on larval fish ingestion rates determined in the laboratory. Abbreviations: W = larval dry weight, Food = food density, D = fish density, T = temperature, V = tank volume, PW = prey dry weight, FT = type of prey offered in ingestion rate experiments.

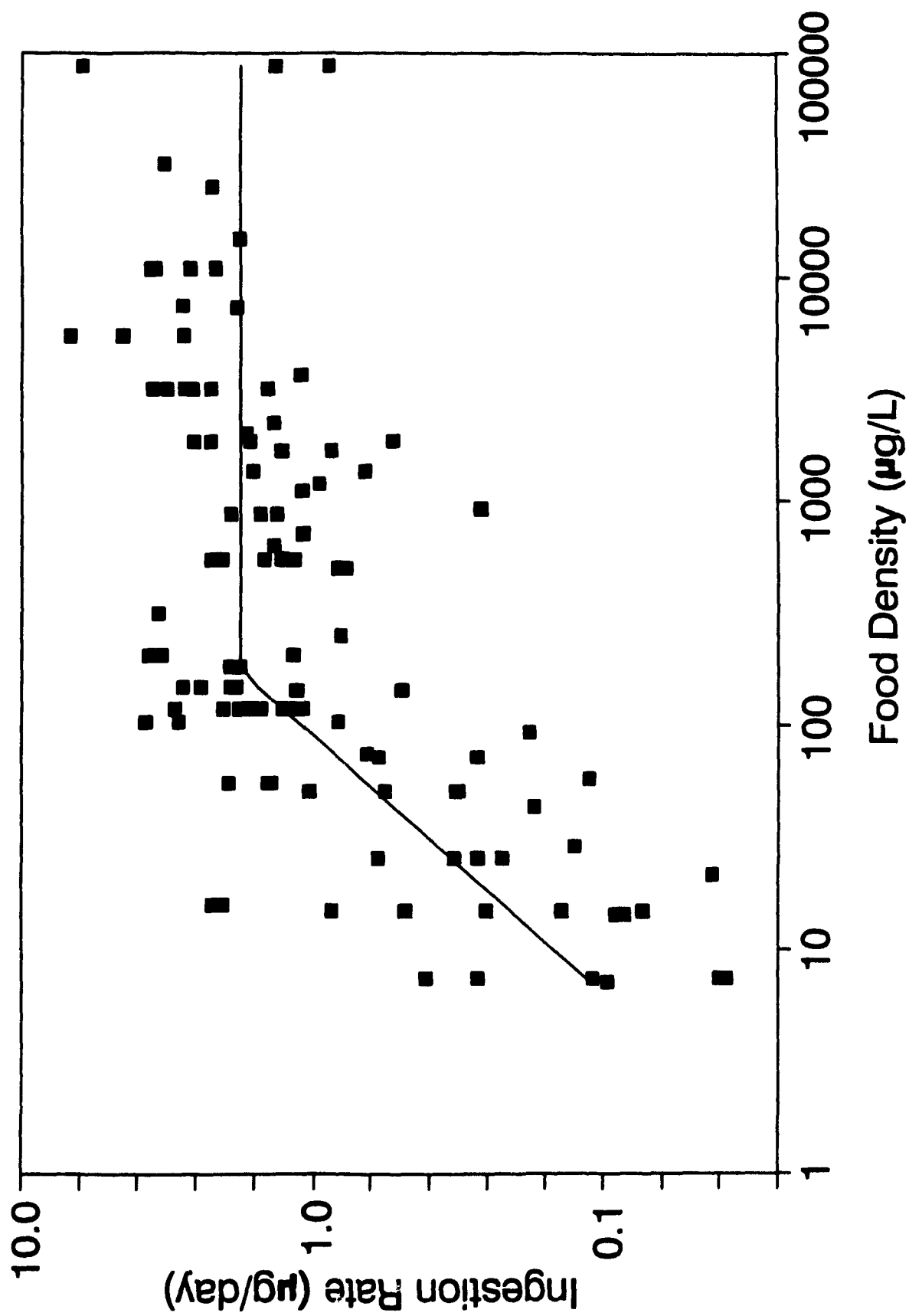
Variable	Mean	Range	N
log W (μg)	2.122	0.929 - 3.466	109
log Food ($\mu\text{g/L}$)	2.496	0.860 - 4.944	109
log D (N/L)	0.513	-1.000 - 1.824	70
T ($^{\circ}\text{C}$)	18.7	2 - 29	109
V (l)	20.3	0.6 - 75	88
log PW (μg)	-0.417	-0.921 - 0.322	109
PT	-	0 if <u>Artemia</u> or <u>Brachionus</u> (N = 56) 1 if wild zooplankton (N = 53)	109

regression coefficient for the temperature term in Model 2 equates to a Q_{10} value of 2.3 (95 % confidence limits = 1.6 and 3.2). The similarity of Q_{10} estimated from my data to that obtained in other general physiology studies (2 - 3; Prosser 1973) suggests that laboratory ingestion rates of larval fish respond to temperature in a manner similar to physiological rates in a wide variety of other organisms. Consequently larvae that hatch in low latitude areas can be expected to have higher ingestion rates and higher growth rates (see also Houde 1989), than those which hatch in boreal regions. Because Q_{10} values vary with temperature (McLaren 1963), my estimate is most appropriate for those temperatures near the mean in my data set (18.7° C).

A scatterplot of ingestion rates detrended for the effects of larval size and temperature using Model 2 qualitatively indicates that ingestion rates plateau at a food density of approximately 150 - 200 $\mu\text{g/L}$ (Fig. 1). Rectilinear regression (NONLIN program; Wilkinson 1988) was used to quantify more precisely the food density beyond which larvae were satiated (hereafter referred to as the critical food density), and to quantify the laboratory functional response at food densities below this level. This program iterates until it converges to parameter estimates that equalize the residual sum of squares for the inclining and plateau portions of the functional response relationship. Consequently, final parameter estimates are based on the entire range of food densities used in my data set.

This analysis (Model 3, Table 4) of residual variation from Model 2 revealed that the critical food density at which satiation occurred was 173 $\mu\text{g/L}$ (95 % confidence limits = 107 - 280 $\mu\text{g/L}$). At food levels below the critical food density of 173 $\mu\text{g/L}$, ingestion rates increased with food

Figure 1. Scatterplot of larval ingestion rates determined in laboratory experiments and expressed as a function of food density. The effects of larval size and experimental temperature were removed using Model 2 (Table 4) to isolate the influence of food density on ingestion rates. The fitted curve reflects a rectilinear model (Model 3; Table 4) which explicitly defines the critical food density at which satiation occurs.



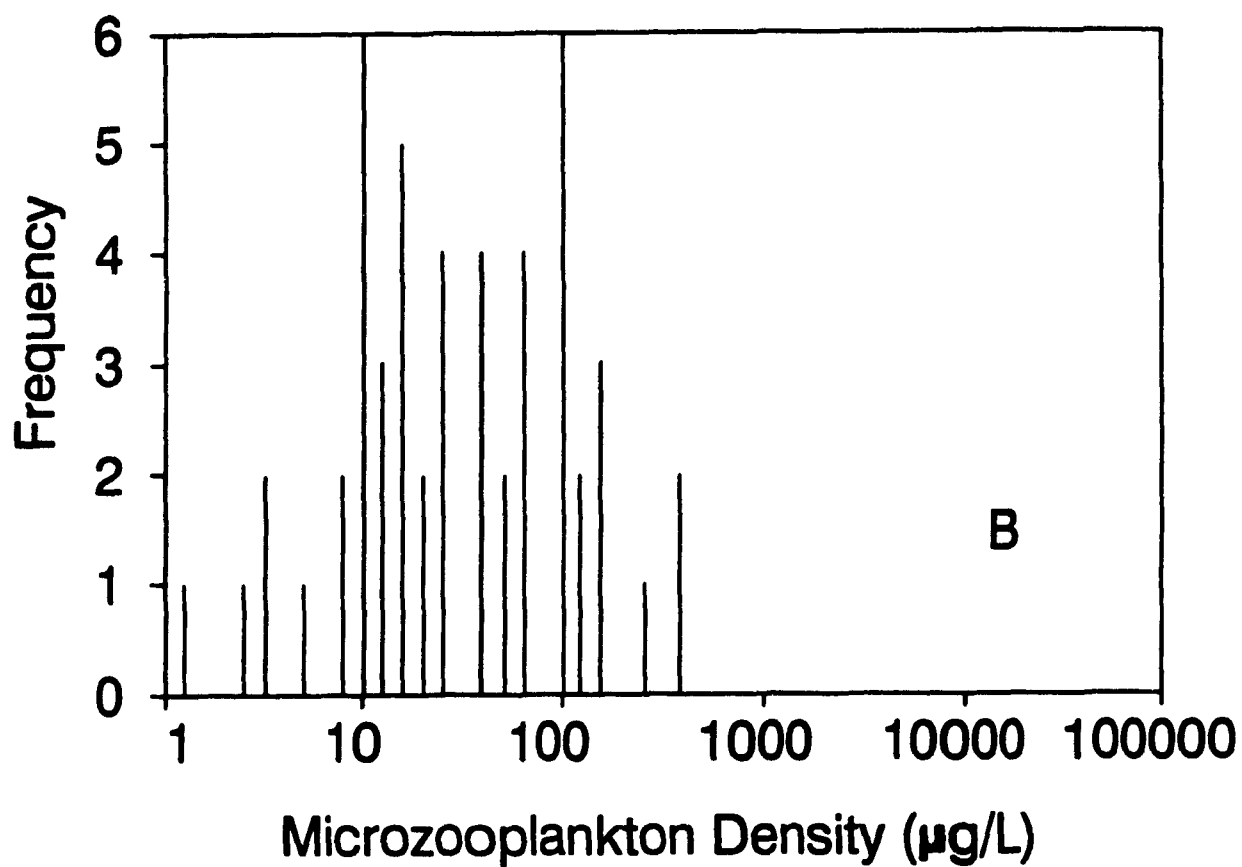
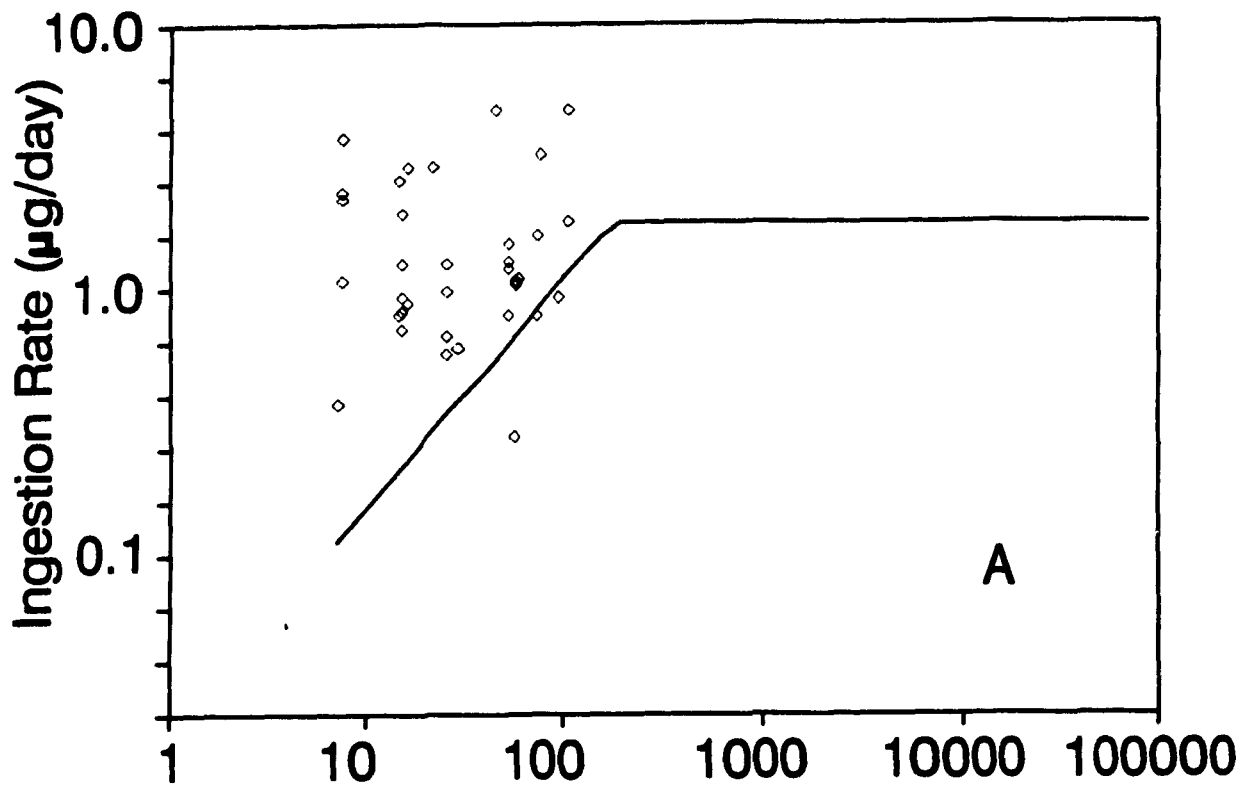
density in an approximately linear fashion (regression coefficient = 0.869; 95 % confidence limits = 0.657 - 1.080). Because nonlinear parameter estimates are approximations (Wilkinson 1988), and because of the variance in my data set, I did not attempt to distinguish between the three types of functional response curves reported by Holling (1959).

Many functional response relationships have been effectively modelled using a negative exponential equation, $Res = Res_{max} \cdot (1 - e^{-(a \cdot \log Food)})$ (e. g. Ivlev 1961, Houde and Schekter 1980; SAS Institute 1985b). I, therefore, fitted the negative exponential model to the data in Figure 1 to compare its explanatory power with the rectilinear model. The negative exponential model ($\log Res = 0.391 - 3.529 \cdot e^{(-1.077 \cdot \log Food)}$) explained slightly less variance ($R^2 = .54$) than the rectilinear model (Figure 1, $R^2 = .55$).

Given this finding, the rectilinear regression model is preferred because it (1) explicitly identifies the food density (and its confidence limits) at which ingestion rates become satiated, (2) has fewer parameters than other models (Holling 1959; Ivlev 1961) across the range of food densities that larvae are likely to encounter in nature (Figure 2B), (3) has power equal to more complex models in explaining the variance in ingestion rates detrended for the effects of larval size and experimental temperature; and (4) easily accommodates additional significant variables if required (e. g. laboratory artifacts).

I next developed a multivariate model (Model 4; Table 4) employing larval size, temperature and food density as inputs; food density was again treated rectilinearly (Wilkinson 1988). The resulting model (Model 4) is statistically equivalent to combining Model 2 and Model 3.

Figure 2. A. Scatterplot of ingestion rate estimates for wild larvae, and for larvae reared in mesocosms after the effects of larval size and experimental temperature have been removed using Model 2. The fitted line is that described by Model 3. B Frequency distribution of average microzooplankton densities sampled at 46 marine sites around the world. The median and 90th percentile of these data occur at 31 and 148 $\mu\text{g/L}$, respectively. All samplers used in these studies were capable of retaining particles $< 200 \mu\text{m}$. The geographical locations, their corresponding food densities and data sources are listed in Table 2.



Model 4 indicated that the average-sized larva ($132.4 \mu\text{g}$; Table 5) in this data set became satiated at a food density of $185 \mu\text{g/L}$ (95 % confidence limits = $158 - 217 \mu\text{g/L}$; average temperature = 18.7°C). This critical food density does not differ significantly from the output of Model 3. The predicted maximum ingestion rate for a $132.4 \mu\text{g}$ larva at 18.7°C at food densities equalling or exceeding the critical food density was $75.8 \mu\text{g/day}$ (57.0 % of dry body weight/day; Table 4)

Laboratory induced biases in ingestion rate estimates

The only experimental variables significantly correlated with residual variation from Model 4 were prey type and prey size (respectively, $R = -.22$; $P = .02$; $R = .22$, $P = .02$; $N = 109$). Larvae fed wild zooplankton consumed less food than those fed Artemia or Brachionus, and larvae offered larger prey ingested more food than those fed smaller prey.

Artemia nauplii were among the heaviest food organisms offered in these studies (Table 1). These nauplii are also slow, inefficient swimmers compared to copepod nauplii (Gauld 1959). The influence of prey density on larval ingestion rates in these analyses are therefore consistent with the hypothesis that fish larvae are most effective at capturing large, slow-swimming prey. However, prey preferences are known to vary widely among different species of larval fish and to depend on the behaviour of both larvae and prey, and on prey size and color (Checkley 1982; Peterson and Ausubel 1984). Generalizations are therefore difficult and dangerous. The strongest result of this analysis was the fact that the effects of prey type and prey size were very small relative to the effects of size, temperature and food density.

Fish density and container volume did not systematically bias the estimates of ingestion rate ($P = .86$; $N = 70$ and $P = .23$; $N = 88$ respectively). This observation is inconsistent with the results of enclosure and mesocosm experiments which have typically yielded growth rates that were higher than those reported from laboratory tanks (Blaxter 1988). The modest number and range of experimental conditions (Table 5) in my data set and the potential for confounding variables precluded the identification of such artifacts. For example, the positive correlation between larval and food densities ($R^2 = 0.53$; $P < 0.0001$; $N = 70$) in the experiments I surveyed may have reduced the likelihood that unnaturally high laboratory fish densities would suppress individual feeding rates.

Species-specific ingestion rates

The cumulative influence of size, temperature and food density on feeding rates in this data set is large (Table 4), and the influence of experimental factors on standardized feeding rates in this data set was relatively small. This suggests that the residual variation about Model 4 could be related to interspecific differences. This variation can be partitioned on a species-specific basis as follows:

$$I_s = 100 \cdot \text{antilog} \left[\frac{\sum_{i=1}^N (\log I_{i0} - \log I_{ip})}{N} \right]$$

where I_s = average relative ingestion rate for species s ;

I_{i0} = observed ingestion rate for each individual of species s ; I_{ip} = predicted ingestion rate (Model 4) within species s for each combination of larval size, water temperature and food density; N = number of larvae whose ingestion rates were estimated for species s .

This partitioning allows a relative comparison of species-specific standardized ingestion rates. The resulting ranking suggests that the average ingestion rate for each of the 11 species represented in my data set lies within a factor of approximately 2 of rates predicted by Model 4 (Table 6). This comparison must be considered approximate because methodological factors may covary with the species used in my analyses.

The validity of general regression models should always be checked against independent evidence because they incorporate a number of assumptions and approximations. To achieve this independent test, the ingestion rates predicted by Model 4 were evaluated by comparison with other fish bioenergetic models. The fraction of ingested energy used for routine metabolism can be estimated by combining Model 4 with a general model of fish respiration at 20° C (Winberg 1956; Peters 1983). Larvae were assumed to be feeding at their maximum rates. After allowing for the influence of temperature on larval ingestion rates and converting to common units (ingestion rate: watts; larval size: μg dry weight), the proportion of ingested energy used for routine metabolism by a 132.4 μg larval fish was found to be 31 %. This value is not significantly different from the average of those that have been experimentally determined (mean $\pm$ standard error = 28 ± 4.1 %; Table 7).

An estimate of gross growth efficiency (G/I) can be similarly derived if one assumes that

$$\underline{a} * I = R + G$$

where $\underline{a}$ = the physiologically useful fraction of ingested food ($\underline{a}$ = 0.8. see Winberg 1956; Paloheimo and Dickie 1966; $\underline{a}$ = 0.7: Ware 1975; Boehlert and Yoklavich 1984), I = ingested energy, R = energy respired for all

Table 6. Relative species-specific ingestion rates after removing the effects of larval size, experimental temperature and food density using Model 4 (Table 4). Data sources for each species are listed alphabetically below table.

Species	Relative Ingestion Rate	Reference
<u>Ammodytes americanus</u>	0.45	7
<u>Pagrus major</u>	0.70	6
<u>Blennius pavo</u>	0.72	5
<u>Achirus lineatus</u>	0.83	3
<u>Clupea harengus</u> (Baltic)	0.85	5
<u>Anchoa mitchilli</u>	0.87	3, 10
<u>Archosargus rhomboidalis</u>	0.95	3, 8
<u>Leiostomus xanthurus</u>	1.22	2
<u>Scomber japonicus</u>	1.27	4
<u>Centropristis striata striata</u>	1.34	10
<u>Engraulis mordax</u>	1.60	9
<u>Clupea harengus</u> (Clyde)	1.74	11
<u>Morone saxatilis</u>	2.02	1

Data sources: 1. Chesney 1989; 2. Govoni et al. 1982; 3. Houde & Schekter 1981; 4. Hunter & Kimbrell 1980; 5. Klumpp & von Westernhagen 1986; 6. Kuronuma & Fukusho 1984; 7. Monteleone & Peterson 1984; 8. Stepien 1976; 9. Theilacker 1987; 10. Tucker 1989; 11. Werner & Blaxter 1981.

Table 7. Laboratory estimates of the percentages of ingested energy which are used for metabolism (R/I) and growth (G/I) in larval marine fish. In all cases, ingestion rates were not food-limited. Data sources are listed alphabetically below table.

Species	R/I	G/I	Reference
<u>Anchoa lineatus</u>	18	20	3
<u>Anchoa mitchilli</u>	23	10	8
<u>Anchoa mitchilli</u>	9	14	3
<u>Archosargus rhomboidalis</u>	22	38	3
<u>Archosargus rhomboidalis</u>	--	27	6
<u>Blennius pavo</u>	38	60	5
<u>Centropristus striata striata</u>	30	15	8
<u>Clupea harengus</u> (Baltic)	55	23	5
<u>Clupea harengus</u> (Clyde)	--	40	2
<u>Clupea harengus</u> (mixed)	--	62	4
<u>Engraulis mordax</u>	17	30	7
<u>Merluccius productus</u>	28	42	1
<u>Pleuronectes platessa</u>	37	54	5
Mean	28	33	
Standard error	4.1	4.8	

Data sources: 1. Bailey 1982; 2. Checkley 1984; 3. Houde & Schekter 1981, 1983; 4. Kiørboe et al. 1987; 5. Klumpp & von Westernhagen 1986; 6. Stepien 1976; 7. Theilacker 1987; 8. Tucker 1989.

metabolic demands (i. e. $R = 0.31 \cdot I$), and G = energy retained as body tissue (i. e. growth rate). Using this model, the average-sized larva in this data set was estimated to have a gross growth efficiency of 39 - 49 %. This estimate seems reasonable when compared with those measured experimentally among larvae which were not food-limited (mean $\pm$ standard error = 33 ± 4.8 %; Table 7).

These comparisons lead to the conclusion that Model 4 can be used to develop a priori estimates of laboratory feeding rates for larvae of fish species which cannot be (or have not been) raised in captivity. The model also facilitates post-hoc comparisons of feeding rates estimated with other methods. For example, Bailey (1982) used respirometry and growth experiments to estimate that first-feeding Pacific hake (Merluccius productus) larvae require 26 μg of prey per day to meet metabolic and growth demands ($T = 12^\circ \text{C}$; mean size of first-feeding larvae = 75.1 μg ; Table 5, Bailey 1982). This estimate is identical to that predicted by Model 4 for larvae whose feeding rates are not food-limited. Average ingestion rates by other species, however, could deviate by approximately two-fold from predictions made by Model 4 (Table 6).

Comparison of laboratory derived functional response with natural microzooplankton densities

The frequency distribution of natural zooplankton densities (Fig. 2B) suggests that larvae equivalent in size to the average in my data set (132.4 μg) will be unable to feed at maximal rates in nature (Fig. 2). This assumes, of course, that my derived ingestion rates can be extrapolated to the wild. This comparison also suggests that larval ingestion rates are most sensitive to changes in food abundance across

the range of food densities that are most likely to occur in nature (Fig. 2A, B). Consequently physical processes (eg Lasker 1975) and/or behaviours (Hunter and Thomas 1974, Fortier and Leggett 1982; Munk and Kjørboe 1985) which affect local distributions of larvae and their prey can be expected to have a dramatic effect on larval feeding rates in nature.

Natural ingestion rate model

The data set representing estimates of ingestion rates for wild larvae contained estimates for eight species. The ranges of temperature and food density reported in these studies were 4.5 - 30.7° C and 3.9 - 210 µg/L respectively. An empirical model of food ingestion rate based on larval size, in situ temperature and in situ food densities revealed that only size and temperature were significant predictors (Model 5). Natural rates were independent of food density ($P = 0.22$)

To facilitate direct comparison between wild and laboratory ingestion rates, ingestion rates of wild larvae were standardized for different larval sizes and water temperatures using Model 2 which was derived from laboratory data (Table 4). Thus standardized, feeding rates estimated for wild larvae typically exceeded those estimated from laboratory data at equivalent food densities (Figure 2A).

Synthesis

As anticipated, larval size, temperature and food density were the dominant sources of variance in laboratory based estimates of ingestion rate. In the data set I developed, ingestion rates detrended for the effects of larval size and experimental temperature reached a maximum at food densities exceeding 185 µg/L (95 % confidence limits = 158 - 217

$\mu\text{g/L}$) Although methodological effects were relatively small for this data set, two caveats are necessary. First, container size effects are known to occur if the range of container size is expanded. For example, mesocosm studies, while few in number to date, typically yield higher growth rates than those found using container sizes commonly used in laboratory studies (Øiestad 1985; Blaxter 1988). Second, in the experimental studies I evaluated, investigators exhibited a tendency to compensate for higher larval densities by providing higher prey densities. This may have otherwise obscured an obvious effect of methodology. These potential biases require further study

The laboratory based ingestion rate estimates I evaluated showed a sharp functional response in which satiation occurred only at prey densities near or above the maximum densities typically found at sea. If these results are realistic representations of feeding rates in the sea, larval ingestion rates in the wild are likely to be significantly below the maximum levels possible in most areas where larvae are found in nature.

However the independence of ingestion rates estimated for wild larvae and estimates of food density in the sea, coupled with the fact that these rates are uniformly near the maximum levels observed in laboratory studies, strongly suggests that laboratory functional response models seriously misrepresent natural feeding rates. However, before accepting this conclusion several alternative explanations should be explored.

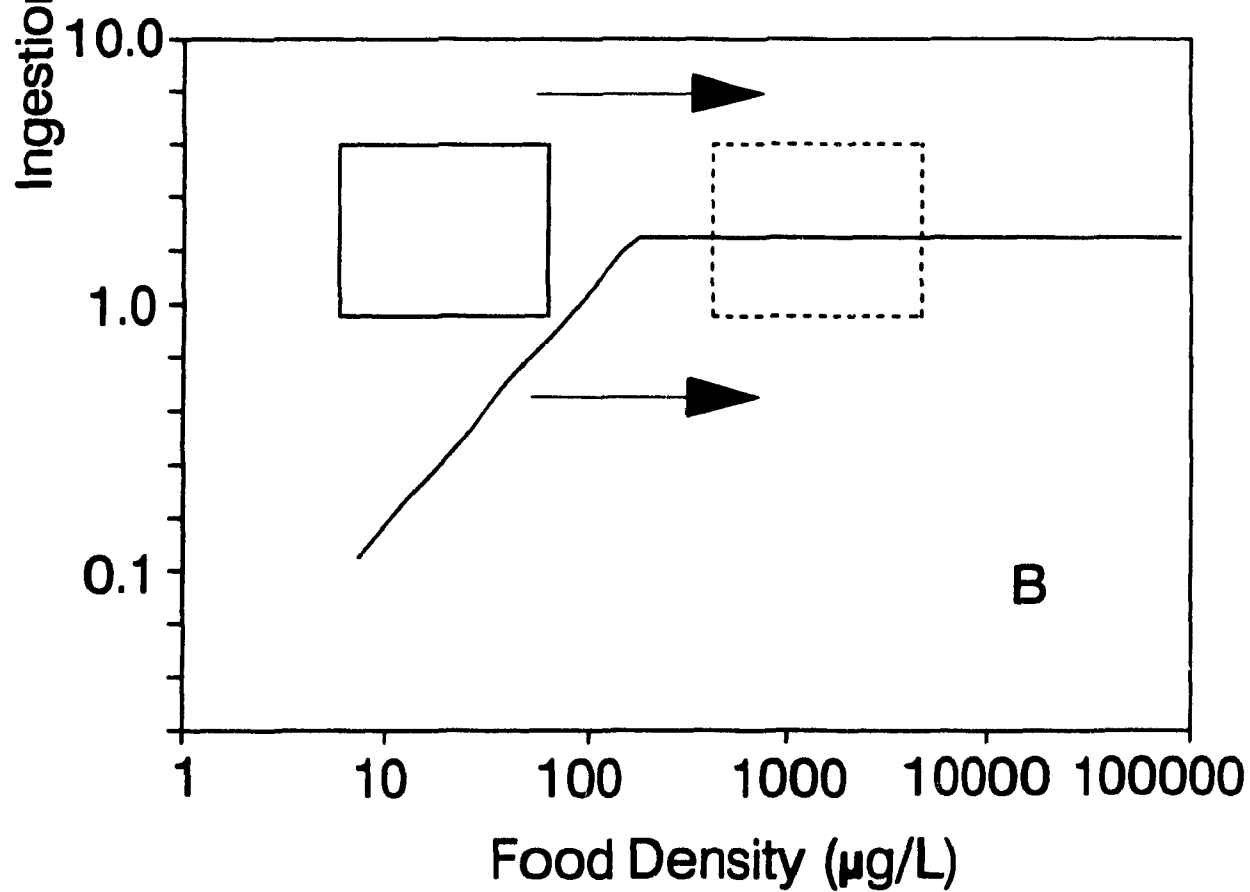
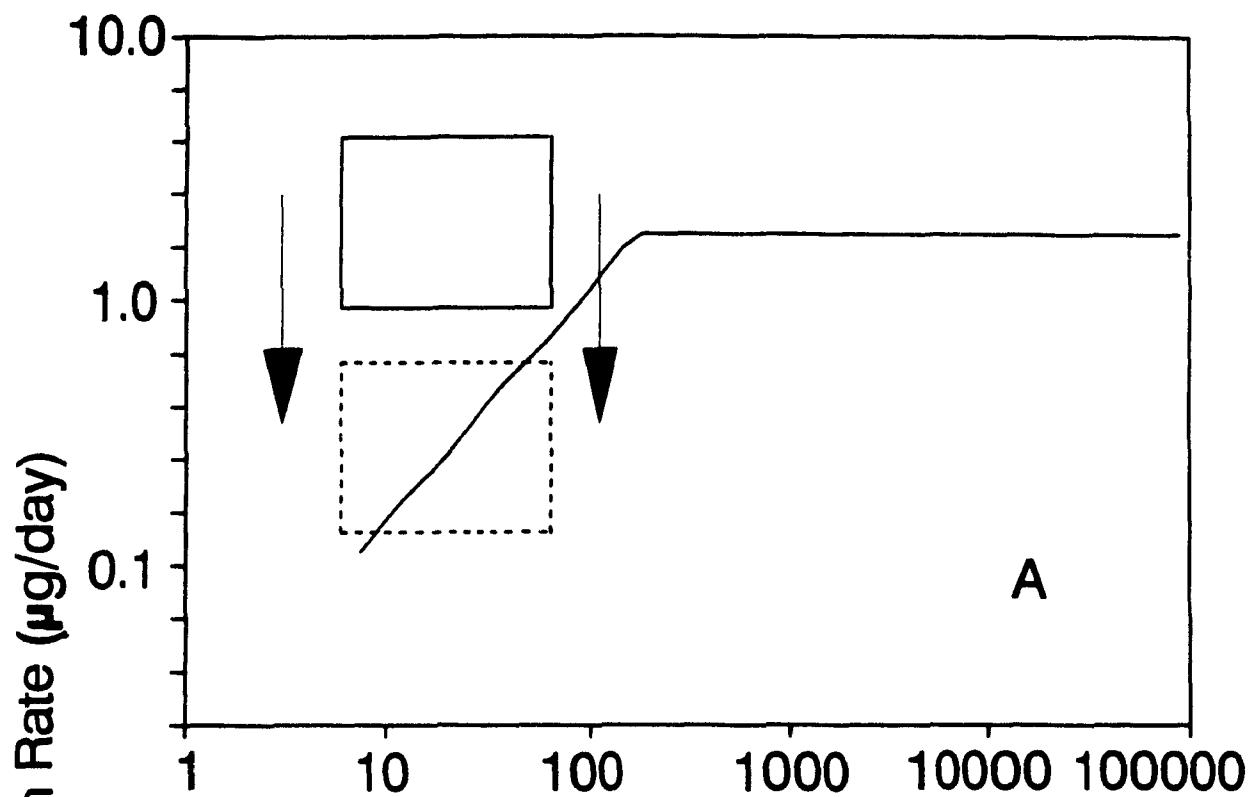
The low correspondence between ingestion rate estimates for wild larvae and local food densities could result either from overestimation

of ingestion rates for wild larvae, or, alternatively, from underestimating the larval food resource. The impact of these separate biases on the relationship between laboratory and field based estimates of ingestion rates is illustrated schematically in Figure 3.

It is important to recognize that the estimates of wild ingestion rate in Figure 2A represent rates for larvae that have been captured by plankton samplers, and that these rates could misrepresent the average ingestion rate for a given cohort. For example, if the larvae captured are the most effective individual foragers within a cohort, their ingestion rates, and levels of activity (Laurence 1972; Frank and Leggett 1982b; Yin and Blaxter 1987), would probably be higher than the average rate for the entire cohort. Average ingestion rates could be considerably lower than the maximum individual rate because of differences in capture success, attack success and swimming ability between individuals of equal size (Vladimirov 1975; Houde and Schekter 1980, p. 331). It is possible, therefore, that if the least active larvae had been removed from the water column by predators (Bailey and Batty 1984) prior to sampling, the resulting estimates of field ingestion rates could overestimate the population average.

Secondly, in my analyses I estimated 31 of 36 wild ingestion rates from reported in situ larval growth rates using a previously published growth model derived entirely from laboratory populations of larval fish (Checkley 1984). The extrapolation of this model to wild larvae by ourselves and others (e. g. Walline 1987) explicitly assumes that gross growth efficiencies of wild larvae are equivalent to those of laboratory populations. If gross growth efficiencies are higher in wild larvae, the

Figure 3. Schematic diagram offering two possible explanations for the observed high ingestion rates (larval size and temperature effects removed using Model 2) reported for wild larvae, relative to those determined from laboratory studies at equivalent prey densities. A. Feeding rates overestimated for a given food density B Larvae encounter prey at higher rates than census measures of food density would indicate In the latter case, observed ingestion rates would reflect the frequency of encounters between larvae and prey, but not the numerical densities of prey.



ingestion rates I estimated from field growth rates using the Checkley model (1984) would be overestimated.

However, these two potential sources of positive bias could be partially offset by others which could lead to underestimates of wild ingestion rates. For example, prey activity stimulates feeding responses in many predators of larval fish (e.g. chaetognaths and some species of copepods, amphipods and euphausiids; Bailey and Houde 1989). Because poorly-fed larvae are less active than well-fed larvae (Laurence 1972; Blaxter and Ehrlich 1974; Frank and Leggett 1982b), poorly-fed larvae will stimulate relatively fewer of those predators who rely on prey movement to elicit feeding stimuli. Lower activity levels in poorly nourished larvae could also reduce their encounter rate with slow-moving and ambush predators (p. 12. Bailey and Houde 1989). Consequently, under some circumstances, these interactions could allow weakened larvae to remain in the water column longer than more active larvae. If this bias was common in the studies I surveyed, it could result in an underestimation of field ingestion and/or growth rates.

Moreover, daytime plankton collections could overestimate the relative abundance of poorly-fed larvae because such larvae are probably less able to detect and avoid capture by plankton samplers (see Blaxter and Ehrlich 1974).

Capture by plankton gear causes some species of larvae to regurgitate or defecate the contents of their guts (e.g. Hay 1981). However this effect, and other potential sources of bias in determining ingestion rates from gut contents and clearance data (e.g. different digestibilities of various prey types; Rosenthal and Hempel 1970), is

likely to be small in this study because only 5 of the 36 field ingestion rates I report and used were based on the analysis of gut contents.

The cumulative magnitude and direction of these potential sources of bias is difficult to assess without a better knowledge of how different predators encounter and capture larvae that are feeding and growing at different rates in situ. Until such information becomes available, it is possible that the wild ingestion rates in my data set are biased by these and possibly other considerations.

However, there is sufficient information available regarding in situ zooplankton abundance estimates to question whether these estimates adequately reflect larval prey availability. For example, estimates of prey standing stock are known to neglect zooplankton production rates which typically range from 0.5 - 2.0 $\mu\text{g/L/day}$ in continental shelf ecosystems (Middlebrook and Roff 1986; McLaren et al. 1989). Moreover, episodic production events can greatly increase rates of plankton production. These phenomena are common both in nearshore regions (Tont 1981; Arcos and Wilson 1984; Atkinson et al. 1984; Takahashi et al. 1986; Lohrenz et al. 1988; Thresher et al. 1989) and in offshore areas of continental shelves (Checkley et al. 1988, Frank and Carscadden 1989). In addition, this new production is typically in the size range (e.g. Mullin et al. 1985; Checkley et al. 1988) required by early stages of larvae (Hunter 1981; Frank and Leggett 1986). Despite the probable importance of transient production events to larval feeding success, their influence is difficult to quantify and forecast with conventional methods (Côté and Platt 1983; Thresher et al. 1989).

Zooplankton is also known to be patchily distributed in the sea on

the spatial scale of larval feeding activity (metres to 100's of metres; see Jenkins 1988, Owen 1989). For example, the median prey density within a patch has been reported to be twice the density that would be obtained with integrative sampling gear (Owen 1989). However, patch intensity (number of prey per patch) can range up to ten fold higher than an integrated density estimate, particularly if wind speeds are favorable (Owen 1989). As a consequence, estimates of prey density based on integrative sampling techniques are likely to be much lower than those actually experienced by fish larvae (review by Leggett 1986; Jenkins 1988; Owen 1989).

Census estimates of prey density also fail to incorporate the positive effects of small-scale turbulence on plankton contact rates (Rothschild and Osborn 1988). Larvae of other aquatic taxa are known to exploit micro-scale differences in the physical environment to improve feeding success (e.g. black flies Simulium vittatum; Morin and Peters 1988; Ciborowski and Craig 1989). It seems plausible, therefore, that larval fish may also be capable of exploiting physical variability in their habitat for similar purposes.

Finally, larval fish are known to swim faster in nature than when confined in laboratory tanks (von Westernhagen and Rosenthal 1979). Greater routine swimming speeds by wild larvae relative to those reared in the laboratory would cause wild larvae to search larger volumes, thereby increasing the potential for contacts between larvae and prey.

For all of these reasons, underestimation of the frequency of contacts between larvae and prey in nature is likely to be a major factor influencing the discrepancy between laboratory and in situ ingestion rates

(Fig. 2). Similarly my comparisons suggest that failure to design laboratory experiments that account for processes that benefit high rates of contact between larvae and their prey (e. g. larval behaviours, patchiness, turbulence) are certain to result in low feeding rates, unless researchers provide unnaturally high prey densities in an attempt to compensate for artificial rearing conditions. Consequently those studies which are most effective at replicating the natural environment can be expected to produce growth rates approaching those observed in nature (e. g. Kjørboe and Munk 1986).

My observation that fish larvae in the sea can feed at rates near satiation, and that these rates appear to be largely independent of food density, is consistent with the results of several recent studies. High resolution sampling has shown that mortality rates can be independent of the food resource, in spite of large-scale variations in food abundance (Taggart and Leggett 1987), and confirms that prey densities in some nursery areas, where such sampling techniques have been employed, are unlikely to limit feeding rates (Jenkins 1987, 1988, Fortier and Harris 1989).

It must be acknowledged, however, that the absence of a relationship between natural ingestion or growth rates and food density is not universal (e. g. Frank and Leggett 1982a, 1986; Buckley and Lough 1987; Kjørboe et al. 1988). However typical in situ prey densities, when coupled with appropriate interactions between prey distributions, the physical environment (e.g. small-scale turbulence; Rothschild and Osborn 1988), and larval feeding and diel migratory behaviours (Hunter and Thomas 1974; Heath et al. 1988; Munk et al. 1989) appear to be sufficient to allow many

larval populations to feed at near-maximal rates in nature. In the absence of these (and possibly other) interactions, feeding rates at food densities less than $\approx 185 \mu\text{g/L}$ will probably be sub-maximal and could approach those predicted by my laboratory based functional response model (Model 4).

In particular, much of the potential variability in larval feeding rates that might be expected to occur in the sea because of natural variation in food densities has probably already been dampened by spawning behaviour: the spawning activity of temperate and boreal species of fish is known to be highly restricted in time and space (Sinclair 1988). It is likely that the historical average for the larval food resource at these times/places may be more suitable for larval feeding than at other times or places (see also Kiørboe and Johansen 1986). Interannual variations in hydrodynamic regimes, which are largely beyond the control of larvae and which influence recruitment (Cury and Roy 1989) and larval survival (Peterman and Bradford 1987) may, therefore, exert their influence through their effects on feeding success. These effects could simultaneously increase (or decrease) both the density of prey and the frequency of contacts between larval fish and their prey.

I conclude that increased attention to factors that influence the small-scale temporal and spatial dynamics of interactions between larval fish and their prey would contribute meaningfully to the resolution of the oldest question in recruitment dynamics "Does food abundance and its availability to larvae regulate yearclass strength in fishes?".

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Chapter 2

Wind-based Models for Estimating
Turbulent Energy Dissipation Rates
in Aquatic Environments, and Their Potential
for Examining the Influence of Wind on Plankton Ecology

Introduction

The rate of dissipation of turbulent kinetic energy in aquatic environments has recently been shown to have important effects on several aspects of plankton ecology. Turbulence can enhance encounter rates between individuals within plankton communities (Rothschild and Osborn 1988; Sundby and Fossum 1990; Marrasé et al. 1990), increase development rates of some stages of herbivorous consumers (Saiz and Alcaraz 1991), and disperse zooplankton and phytoplankton populations (Haury et al. 1990). Turbulent dispersal of phytoplankton populations reduces the vertical differences in photoadaptive properties (e. g. maximum photosynthetic rate) of these populations (Lewis et al. 1984) and is partly responsible for variability in phytoplankton cell size (Holligan and Harbour 1977; Margalef 1978) and growth rates (Lande et al. 1989).

The turbulent contribution to these aspects of plankton ecology are derived from measures of ϵ , the rate of dissipation of turbulent kinetic energy from large to small scales (Rothschild and Osborn 1988; Granata and Dickey 1990). This parameter has been measured in a variety of aquatic environments (Rothschild and Osborn 1990), and it is known to fluctuate with the rate at which kinetic energy is supplied by winds (Oakey and Elliott 1982), tides (Veth 1990), or other phenomena (e. g. convection, Shay and Gregg 1986; fish swimming behaviour, Farmer et al. 1987).

Within the surface layer of the ocean, several investigators have shown that dissipation rates increase when wind speeds are higher and that they decrease exponentially with increasing depth (Gargett 1989). When considered together, these two patterns indicate that the upper layer of the sea, and of lakes, is an environment characterized by frequent changes

in the levels of small-scale turbulence associated with variable wind stress.

This same environment is habitat for a large fraction of the plankton biomass of the global ocean (Riley 1970, Margalef 1978), and is associated with some of the highest rates of primary (Riley 1970; Delafontaine and Peters 1986) and secondary (Riley 1970) plankton production in the sea. Inputs of wind energy to the water column will, therefore, generate variability in rates of encounter (Rothschild and Osborn 1988) and growth (Lande et al. 1989; Saiz and Alcaraz 1991) among planktonic taxa living in the surface layers of the sea, and of lakes. This variability will occur temporally and in the horizontal and vertical dimensions of the spatial domain, independently of predator/prey population densities (Rothschild and Osborn 1988).

The rate of dissipation of turbulent kinetic energy is an important input variable in equations describing the dynamics of water column mixing (Lueck and Reid 1984; Dewey and Moum 1990). Theoretical models are available which describe how the rate of dissipation of kinetic energy varies with wind stress (e. g. Lumley and Panofsky 1964; Simpson and Bowers 1981). One of these models has been transferred from atmospheric boundary layer theory (Lumley and Panofsky 1964; Dillon et al. 1981) in order to describe patterns in dissipation rates in aquatic systems (Dillon et al. 1981; Oakey 1985).

However, to date, no statistical comparison of dissipation rates estimated by this model has been made with a large sample of in situ dissipation rate measurements obtained under diverse hydrographic conditions. Hence the reliability, the potential biases and the

statistical confidence of predictions made by the atmospheric boundary layer model remain unknown. Moreover, it is unclear how much of the variation in mixed layer dissipation rates can be explained by wind speed or by vertical position within the water column, independently of other processes known to generate turbulence in the water column (e.g. convection, upwelling), nor is it clear how much additional turbulence these other processes could superimpose on the turbulence induced by wind stress.

Given that the dissipation rate of turbulent kinetic energy is important to plankton ecology and to water column mixing, these models, if reliable in predicting in situ dissipation rates with depth from wind data, could help biological oceanographers, and limnologists, interpret plankton trophodynamics, distributions, and feeding adaptations when direct measures of dissipation rates are not available (e. g. Sundby and Fossum 1990; GLOBEC 1991). Such models, and the confidence limits associated with their predictions, would also be useful for assessing how these aspects of plankton ecology might vary with spatial and temporal fluctuations in mixed layer dissipation rates (e. g. Kjørboe et al. 1990a; Shimeta and Jumars 1991), including fluctuations caused by global climate change (Bakun 1990; see also GLOBEC 1991).

My objectives in this paper relate to these needs and were: (1) to quantify empirically how dissipation rates within the surface layer of the sea vary with wind speed and depth; (2) to quantify the fraction of the total variability in in situ dissipation rate measurements that can be explained by wind speed and sampling depth, and to compare levels of turbulence induced by wind and other processes; and (3) to assess how well

the available theoretical models describe observed patterns in the turbulent dissipation of wind-induced kinetic energy.

Methods

1. Data collection

(i) Dissipation rates of turbulent kinetic energy, ϵ

The analyses described below are designed to quantify general patterns in the variability of mixed layer turbulent dissipation rate (ϵ) that can be explained by easily measurable variables, such as wind speed and sample depth. To meet this objective, I developed a data set from literature values of ϵ that were obtained under a wide range of oceanographic and meteorological conditions.

In 9 studies surveyed (615 dissipation rate estimates), investigators provided the mixed layer depth in the text or tables of their report. In 3 other cases, mixed layer depths were estimated from temperature or density profiles obtained concurrently with the reported vertical turbulence profiles (280 dissipation rate estimates). I excluded all studies for which the mixed layer depth was not reported or could not be reconstructed for a turbulence profile. Dissipation rates measured within and below the pycnocline were also excluded from the data set. These steps were taken because stratification inhibits the rate of dissipation of kinetic energy (Denman and Gargett 1983, p 804; see also Fig. 1 in Yamazaki 1990), and because dissipation rates within the mixed layer are more likely to follow a lognormal distribution than are those from within the thermocline (Yamazaki and Lueck 1990). Observations of dissipation rate within the mixed layer are therefore more reliably

analysed with respect to wind energy inputs because these dissipation rates are less likely to be confounded by these, and possibly other, factors.

In cases where the mixed layer depth exceeded 150 m, data collection was restricted to depths shallower than 150 m. This range includes the photic zone in most areas of the sea (Jerlov 1968) and is, therefore, the depth range within which most primary and secondary plankton production occurs and within which plankton biomass is most concentrated (Riley 1970; Margalef 1978; de Lafontaine and Peters 1986). Where estimates of dissipation rate and sample depth were reported in figures, I used an image analyser to digitize the data. Dissipation rates obtained in this manner are accurate, on average, to within 3.8 % of those reported in the original papers; the maximum measurement error, which was associated with 12 % of all the observations in my data set was 9.3 %. The average error introduced into my analyses by digitizing turbulence data reported in figures was < 10 % of the errors associated with the original instruments used to measure dissipation rates (see Osborn 1978; Oakey and Elliott 1982; Lange 1981). The average and maximum errors created by digitizing sample depths were 1.1 m and 2.4 m respectively. All dissipation rates and sample depths obtained from figures, or from tables, were converted to units of $\text{Watts}\cdot\text{m}^{-3}$ and m respectively.

(ii) Wind speeds

I used the reported average wind speed during the 24 hours prior to in situ measurement of turbulence as a surrogate measure of the kinetic energy transferred into, and dissipated within, the water column. In one study (N = 6) where wind speed was reported only as a range (5 - 8 $\text{m}\cdot\text{s}^{-1}$

¹) for the entire sampling period (3 days; Lueck et al 1983), I chose the range midpoint as an estimate of the wind speed which prevailed when dissipation rates were being measured. All measures of wind speed, including those based on the Beaufort wind scale ($N = 176$; Osborn 1978), were converted to $m \cdot s^{-1}$ (Beer 1983). In cases where wind speeds were digitized from figures, measurement error was $\approx 2\%$ of the reported value.

The measures of wind energy inputs to the water column used in the following analyses assume steady state wind fields over 24 hour intervals and are, therefore, consistent with other simple descriptions of the influence of wind on mixed layer dissipation rates (Yamazaki and Kamykowski 1991). Nevertheless, employing this assumption excludes important aspects of the wind field (e. g. duration of wind speed in a particular direction, rate of change of wind speed or direction) which are very likely to have important influences on dissipation rates. Wind conditions can be variable at periods up to and exceeding 24 hours (Lumley and Panofsky 1964; Dewey and Moum 1990), and dissipation rates can respond to these high-frequency changes in wind speed (< 3 h: Dillon and Caldwell 1980; Dewey and Moum 1990; Haury et al. 1990). Some of the dissipation rate estimates in this data set do not, therefore, adequately reflect high-frequency fluctuations in wind conditions that may have occurred shortly before turbulence profiles were obtained. Any resulting mismatch of the time scales of the surrogate measure of wind energy input, and the response of the water column to these inputs, will cause the variance explained by the wind speed term in these analyses to be reduced. As a direct consequence, the results reported in this chapter should be viewed as *minimum* estimates of the variance in mixed layer dissipation rates that

can be explained by local wind conditions.

2 Comparing sources of variability in dissipation rates:

Linear regression analyses (SAS 1985) were used to quantify the fraction of the variability in vertical profiles of dissipation rate that could be explained individually by wind speed and depth. Three data transformations were conducted prior to these analyses. First, I cubed wind speed measurements because the kinetic energy input of the wind to the water column is proportional to the cube of the wind speed (Gargett 1989). Second, dissipation rates and (wind speed)³ were logarithmically transformed (base 10) because evidence from site-specific studies indicates that turbulence in the mixed layer increases exponentially with the cube of the wind speed (Oakey and Elliott 1982; Oakey 1985, Lueck 1988). Third, sampling depths were logarithmically transformed (base 10) because dissipation rates vary exponentially with depth (Gargett 1989).

Regression models were first developed which used either wind speed or sampling depth as inputs. I used the R^2 criterion as an approximate index of the relative importance of these predictors in explaining variability in the rate of dissipation of kinetic energy in nature. After quantifying the variance explained by each of these variables, I developed a multiple regression model employing both sampling depth and wind speed as estimators of turbulent dissipation rates.

Dissipation rates in coastal regions may be larger than those in oceanic regions because of the contributions of tides (Simpson and Bowers 1981; Lueck and Reid 1984), vertical current shear (Oakey and Elliott 1982; Haury et al. 1990), fronts (Lueck 1988), bottom topography (Wolanski and Hamner 1988) and coastal upwelling (Csanady 1989) to turbulent mixing.

In the studies that I surveyed, the importance of these effects could not be quantified individually because the relevant data were not routinely reported. As a first step towards a quantitative comparison of how large the aggregate influence of these factors might be relative to the influence of wind speed and depth, I used analysis of covariance (Draper and Smith 1966). Sampling sites on continental shelves and in lakes, which, on average, are likely to exhibit higher dissipation rates after the influence of wind is removed, were therefore coded 1 and those located elsewhere were coded 0. The effect of sampling site was found to be highly significant with coastal and continental shelf sites having, as expected, higher overall dissipation rates. I therefore included this variable in a subsequent regression model (Model 3) having wind speed, sampling depth and sampling environment as inputs. In the balance of this paper when discussing this model, I equate $ENV = 0$ with environments in which sources of turbulence beyond that associated with wind are small. In contrast, $ENV = 1$ is equated to environments having multiple important sources of turbulence.

To develop a more quantitative measure of the influence of some of these processes on turbulent dissipation rates, regression models were used to address how much additional turbulence convection and an upwelling meander could produce, beyond the level of dissipation induced by wind. For analyses involving convection, I used convectively-driven turbulence data gathered by Shay and Gregg (1986) in warm core ring 82-I in the northwest Atlantic during January 1983. As stated by these authors (p. 1783), sampling was conducted under conditions of large air-sea temperature contrast which would "maximize the chance of observing

convectively driven turbulence". Hence the data obtained by Shay and Gregg (1986, Fig. 12 and 16) should provide an estimate of the maximum effect that convection at temperate latitudes will have on oceanic mixed layer dissipation rates, independently of wind conditions.

I compared, therefore, the convectively driven turbulence measurements with those expected to occur as a consequence of prevailing wind conditions by plotting the observed dissipation rates relative to those predicted by my empirical dissipation rate models which used only wind speed and sample depth as inputs. The mean deviation between observed and predicted dissipation rates from such a scatterplot represents a measure of the increase in turbulence that can be attributed to convection.

To assess the influence of an upwelling meander, and its frontal region, on mixed layer dissipation rates, I used data gathered by Dewey and Moum (1990, Fig. 7). These authors measured dissipation rates at five stations along a transect which passed through a meander of upwelled water adjacent to the northern coast of California. I compared dissipation rates measured at the frontal and core stations of this transect (i. e. regions ii, iii, and iv in Fig. 7 of Dewey and Moum 1990) with those predicted by empirical dissipation rate models. This was done to assess how much additional turbulence was associated with the currents and frontal mixing in this meander. The amount by which the meander dissipation rates exceeded those predicted by wind and depth was quantified in a manner similar to that described above for the convectively-driven dissipation rates measured by Shay and Gregg (1986).

Neither the convectively driven dissipation rates (Shay and Gregg

1986), nor the upwelling meander dissipation rates (Dewey and Moum 1990, Fig. 7, regions ii, iii, iv), were used in the development of any of the empirical dissipation rate models presented here. Hence these two data sets are independent of those used in model development, and they were excluded from comparisons with theoretical dissipation rate models (see below, section 3).

3. Other dissipation rate models:

(i) Theory

Empirical analyses of the importance of wind and depth on the variability of ϵ involve numerous assumptions and simplifications which could contribute to substantial residual errors in, and misinterpretations of, the influence of these variables on dissipation rates. I, therefore, assessed whether previously published theoretically-based dissipation rate models were more effective in explaining the variance in reported in situ values of ϵ .

Dillon et al. (1981) and Oakey (1985) have demonstrated that the rate of dissipation of turbulent kinetic energy in an unstratified flow is inversely proportional to the distance from the surface:

$$\begin{aligned}\epsilon \text{ (watts}\cdot\text{m}^{-3}\text{)} &= (\rho_a/\rho_w)*C_D^{3/2} * W^3/0.4*h \\ &= 5.82*10^{-6}*W^3/h\end{aligned}\quad \text{(equation 1)}$$

where W is wind speed ($\text{m}\cdot\text{s}^{-1}$)

h is sample depth (m)

ρ_a is density of air ($1.2 \text{ kg}\cdot\text{m}^{-3}$; Loder and Greenberg 1986)

ρ_w is density of sea water ($1025 \text{ kg}\cdot\text{m}^{-3}$; Lueck 1988)

C_D is coefficient of drag between the water surface and the wind (0.0015; Loder and Greenberg 1986), and

0.4 is von Karmann's constant (Lumley and Panofsky 1964).

Eq 1 has been used to estimate turbulent dissipation within the atmospheric boundary layer (Lumley and Panofsky 1964, p. 120) and in the upper mixed layer of the sea (von Karmann's constant excluded; see Kullenberg 1977, p. 335). The dissipation rates predicted from this model can, therefore, be compared with those measured directly in the mixed layer.

A second description of the rate of dissipation of wind energy in the surface mixed layer can be derived from the Simpson and Bowers (1981) energy balance model of water column structure. This model assumes that an amount of heat, Q , is introduced into a water column of total depth h with uniform initial density ρ_b (Simpson and Hunter 1974). When Q is constant (as would be expected for geographic areas of limited extent, for short periods of time, and in the absence of convection) and when buoyancy sources from salinity gradients are negligible, the overall potential energy balance in a water column relative to the well-mixed condition can be quantified:

$$dV/dt = -\alpha g Q h / 2c + \beta k_b \rho_b u^3 + \delta k_s \rho_s W^3 \quad (\text{equation 2})$$

where $dV/dt = 0$ is the net change in energy content over time, α is the thermal expansion coefficient for sea water, g is gravitational acceleration, c is the specific heat content of sea water, β and δ are

mixing efficiencies associated with tidal velocity (u) and wind speed (W), k_b and k_s are drag coefficients, and ρ_b and ρ_s are the densities of sea water and air (Bowers and Simpson 1987).

In areas where inputs of tidally-generated turbulent kinetic energy ($\beta k_b \rho_b u^3$) are small, the tidal energy term in equation 2 will be negligible compared to the wind energy term. Eq 2 then becomes

$$\alpha g Q h / 2c = \delta k_s \rho_s W^3 \quad (\text{equation 3})$$

Eq 3 represents the energy balance between stratifying (L.H.S.) and mixing (R.H.S.) processes within a water column. If the amount of turbulent kinetic energy supplied by the wind exceeds $\alpha g Q h / 2c$, then the water column will be completely mixed, and turbulent kinetic energy will be dissipated at a rate $\geq \delta k_s \rho_s W^3 / h$ (assuming that the production and dissipation of turbulent kinetic energy are in equilibrium at local scales; Tennekes and Lumley 1972; Denman and Gargett 1983).

However, on other occasions or in other areas, the kinetic energy input from the wind may be insufficient to overcome the stratification induced by Q . In these cases, a steady state wind energy input will create a surface mixed layer which will only extend to a depth h_m , where $h_m < h$, and the dissipation rate will be $\delta k_s \rho_s W^3 / h_m$.

If $\delta = 0.023$ (Bowers and Simpson 1987), $k_s = 6.4 \times 10^{-5}$ (Bowers and Simpson 1987) and $\rho_s = 1.2 \text{ kg} \cdot \text{m}^{-3}$ (Loder and Greenberg 1986), then I can compare dissipation rates estimated from

$$\begin{aligned} \epsilon \text{ (watts} \cdot \text{m}^{-3}\text{)} &= \alpha g Q / 2c = \delta k_s \rho_s W^3 / h_m \\ &= 1.77 \times 10^{-6} W^3 / h_m \quad (\text{equation 4}) \end{aligned}$$

with those directly measured at different depths within the mixed layer ($1000 \text{ Watts} \cdot \text{m}^{-3} = 1 \text{ m}^2 \cdot \text{s}^{-3}$).

The atmospheric boundary layer model (Eq 1) and the energy balance model (Eq 4) are both capable of estimating ϵ within the mixed layer from measures of wind speed and water depth. After substituting typical values for the constants, their predictions will differ by a factor of $5.82/1.77 \approx 3.3$, with the atmospheric boundary layer model (Eq 1) yielding the higher estimates.

(ii) Using atmospheric and energy balance models to estimate field measurements of ϵ

The effectiveness with which Eq 1 and Eq 4 describe patterns in ϵ was estimated by regressing the reported in situ dissipation rate measurements against predictions of ϵ derived from these equations. The proportion of variance in the observed turbulence measurements explained by each model, R^2 , was used as one criterion of model accuracy.

In addition, I assessed the slope and intercept of these regression lines as further measures of the potential biases associated with estimates of small-scale turbulence, ϵ , derived from each model. By these measures, the model is considered to produce unbiased estimates of turbulence if the slope and intercept do not differ significantly from 1 and 0 respectively.

Results

The data set I assembled from the literature (Appendix 3) is summarized in Tables 1 and 2. These data were reported in 12 papers and were gathered at 11 sampling sites, ten of which were marine ($N = 889$ dissipation rate estimates), and one ($N = 6$ dissipation rate estimates) was a freshwater reservoir. Seven sampling sites ($N = 715$ estimates) were located beyond the limits of a continental shelf ($ENV = 0$), and 4 ($N = 180$) were from sites located in coastal regions or in a reservoir ($ENV = 1$). Most (75 %) of the observations used in analyses were recorded within the upper 57 m of the water column, and the remainder were recorded at depths between 57 and 150 m.

Quantifying sources of variance in observed dissipation rates:

Wind speed and sampling depth explained nearly equal portions of the variation in these dissipation rates. A linear regression model having wind speed as an input (Table 3) explained 31 % of the variance in turbulent dissipation rate (Model 1; $P < 0.0001$). Inclusion of sample depth in a multiple regression model increased the proportion of explained variance to 54 % (Model 2; $P < 0.0001$). In both Model 1 and Model 2, dissipation rates increased proportionally to the cube of the wind speed; regression coefficients for the wind input terms in both models were not significantly different from 1.0 ($P > 0.05$). In Model 2, dissipation rates decreased exponentially with depth (regression coefficient < -1 ; $P < 0.05$).

As expected, sampling sites located over continental shelves and in a reservoir showed higher dissipation rates, as a group, than sites

Table 1. Data sources, geographic location of sampling sites, number of observations extracted from each paper, and the oceanographic region in which turbulent dissipation rates were measured. For multiple regression analyses, those regions listed as oceanic were coded ENV = 0 (environments in which wind was assumed to be the principal source of turbulence) and those listed as coastal were coded ENV = 1 (environments were assumed to have multiple sources of turbulence). See Methods for further details.

<u>Reference</u>	<u>Region</u>	<u>N</u>	<u>Environment</u>
Dewey & Moum 1990	central coast of California (outside upwelling meander)	55	oceanic
Dillon & Caldwell 1980	Station P (50° N; 145° W)	49	oceanic
Dillon et al. 1981	Green Peter Reservoir	6	coastal
Haury et al. 1991	Monterey Bay, USA	103	coastal
Lange 1981	Station P (50° N; 145° W)	112	oceanic
Lueck 1988	≈ 30° N; 154° W	266	oceanic

Table 1 (continued)

<u>Reference</u>	<u>Region</u>	<u>N</u>	<u>Environment</u>
Lueck et al. 1983	$\approx 49^{\circ}$ N; 127° W	6	oceanic
Moum & Caldwell 1985	$\approx 0^{\circ}$ N; 140° W	24	oceanic
Oakey 1985	$\approx 59^{\circ}$ N; 12° W	27	oceanic
Oakey & Elliott 1982	Emerald Basin, Scotian Shelf	30	coastal
Osborn 1978	5 - 80 km west of Santa Maria, Azores	176	oceanic
Veth 1983	$54^{\circ} 30'$ N; $4^{\circ} 30'$ E	41	coastal

Table 2. Summary statistics of the variables used in developing and comparing models for estimating the dissipation rate of turbulent kinetic energy (ϵ) in aquatic environments. ϵ = dissipation rate of kinetic energy ($\text{watts} \cdot \text{m}^{-3}$), W = wind speed ($\text{m} \cdot \text{s}^{-1}$), and Z = depth at which dissipation rates were measured (m). $N = 895$.

Variable	Mean	Minimum	Maximum	Median	Standard Deviation
Log ϵ	-4.782	-7.543	-1.930	-4.486	1.093
W	7.3	1.6	15.5	6.0	3.37
Z	39.0	0.4	150.0	24.1	32.6

Table 3. Regression models and parameter estimates ($\pm$ standard error) for estimating dissipation rates of turbulent kinetic energy in the mixed layer of aquatic environments from measures of wind speed (W ; $m \cdot s^{-1}$), sampling depth (Z ; m) and sample site (ENV; low turbulence = 0 and high turbulence = 1). R^2 is the proportion of the total variance in dissipation rates explained by a given model; $P \leq 0.0001$ for all models. RMSE is the residual mean square error of observed values from estimated dissipation rates and $\bar{y}_1$ is the mean of all predicted values N is 895 for all models except for Model 4 where $N = 1095$. Model 5 is derived from the atmospheric boundary layer model (Lumley & Panofsky 1964, also Kullenberg 1977) and Model 6 is derived from the energy balance model (Simpson & Bowers 1981).

Model	R^2	RMSE	$\bar{y}_1$
1 $\log \epsilon = (1.013 \pm 0.051) \cdot \log W^3$ - (7.270 ± 0.128)	0.31	0.910	-4.784
2 $\log \epsilon = (0.963 \pm 0.041) \cdot \log W^3$ - $(1.429 \pm 0.067) \cdot \log Z$ - (5.092 ± 0.146)	0.54	0.740	-4.783
3 $\log \epsilon = (0.776 \pm 0.041) \cdot \log W^3$ - $(1.067 \pm 0.068) \cdot \log Z$ + $(0.842 \pm 0.067) \cdot \text{ENV}$ - (5.323 ± 0.136)	0.61	0.683	-4.783

Table 3 (continued)

	Model	R^2	RMSE	$\bar{y}_1$
4	$\log \epsilon = (0.762 \pm 0.034) \cdot \log W^3$ $- (1.039 \pm 0.056) \cdot \log Z$ $+ (1.040 \pm 0.045) \cdot \text{ENV}$ $- (5.331 \pm 0.115)$	0.65	0.660	-4.596
5	$\log \epsilon = \log(5.82 \cdot 10^{-6} \cdot W^3 / Z)$	0.52	0.753	-4.218
6	$\log \epsilon = \log(1.77 \cdot 10^{-6} \cdot W^3 / Z)$	0.52	0.753	-4.734

located beyond a continental shelf, after the effects of wind and depth were statistically removed (ANCOVA; $P < 0.0001$). A modified regression model explained 61 % of the variance in dissipation rates (Model 3, Table 3). This model included an indicator variable to distinguish environments likely to have multiple sources of turbulence ($ENV = 1$) from environments where wind is the principal source of turbulence ($ENV = 0$). In Model 3, the regression coefficient for wind speed was less than 1.0 ($P < 0.05$) and the regression coefficient for sample depth did not differ from 1.0 ($P > 0.05$). When this model is expressed in arithmetic units ($\epsilon_{ENV=0} = 4.75 \times 10^{-6} \cdot W^{2.328} / Z^{1.067}$; $\epsilon_{ENV=1} = 3.30 \times 10^{-5} \cdot W^{2.328} / Z^{1.067}$), its coefficients approximate those expected from theoretical considerations (Eq 1 and 4 in Methods).

As expected, all of the dissipation rates ($N = 133$) extracted from the study conducted in a warm core ring by Shay & Gregg (1986) exceeded those derived using wind speed and depth alone (range 3-24 fold for $ENV = 1$ and 0 respectively; Figure 1, 2). However, 81 (61 %) of these convectively-driven dissipation rates lie within the 95 % confidence limits for predictions made by Model 3 with $ENV = 0$ (in which wind is major source of turbulence). If the environment variable in Model 3 is coded as 1 (multiple sources of turbulence), 126 (95 %) of the convectively-driven turbulence measurements are found to lie within the 95 % confidence limits (Figure 2B).

These comparisons suggest that Model 3, which contains an appropriate code based on an a priori knowledge of processes that generate turbulence in nature, is capable of explaining a significant portion of the variance in the rates of dissipation of turbulent kinetic energy, even in environments characterized by strong convective mixing.

Fig. 1. Comparison between dissipation rates induced by convective mixing and local wind energy input. Symbols represent observed dissipation rates measured in the centre of warm-core ring 82-I during January 1983 (convectively-driven turbulence: Shay and Gregg 1986). For comparison purposes, solid lines show predicted dissipation rates obtained from Model 3 ($\log \epsilon = 0.776 \cdot \log(\text{WIND SPEED}^3) - 1.067 \cdot \log(\text{DEPTH}) + 0.842 \cdot \text{ENV} - 5.323$; input data are 895 mixed layer dissipation rates extracted from the literature). Dashed lines show approximate upper and lower 95 % confidence limits for predictions made by Model 3 for the 895 literature-derived dissipation rates. In panel A, observed rates are plotted against rates predicted using Model 3 with $\text{ENV} = 0$ (assumes an environment in which wind is the principal source of turbulence). In panel B, observed rates are plotted against rates predicted from Model 3 with $\text{ENV} = 1$ (assumes an environment in which there are multiple sources of turbulence). In both panels, wind and depth data are as reported by Shay & Gregg (1986).

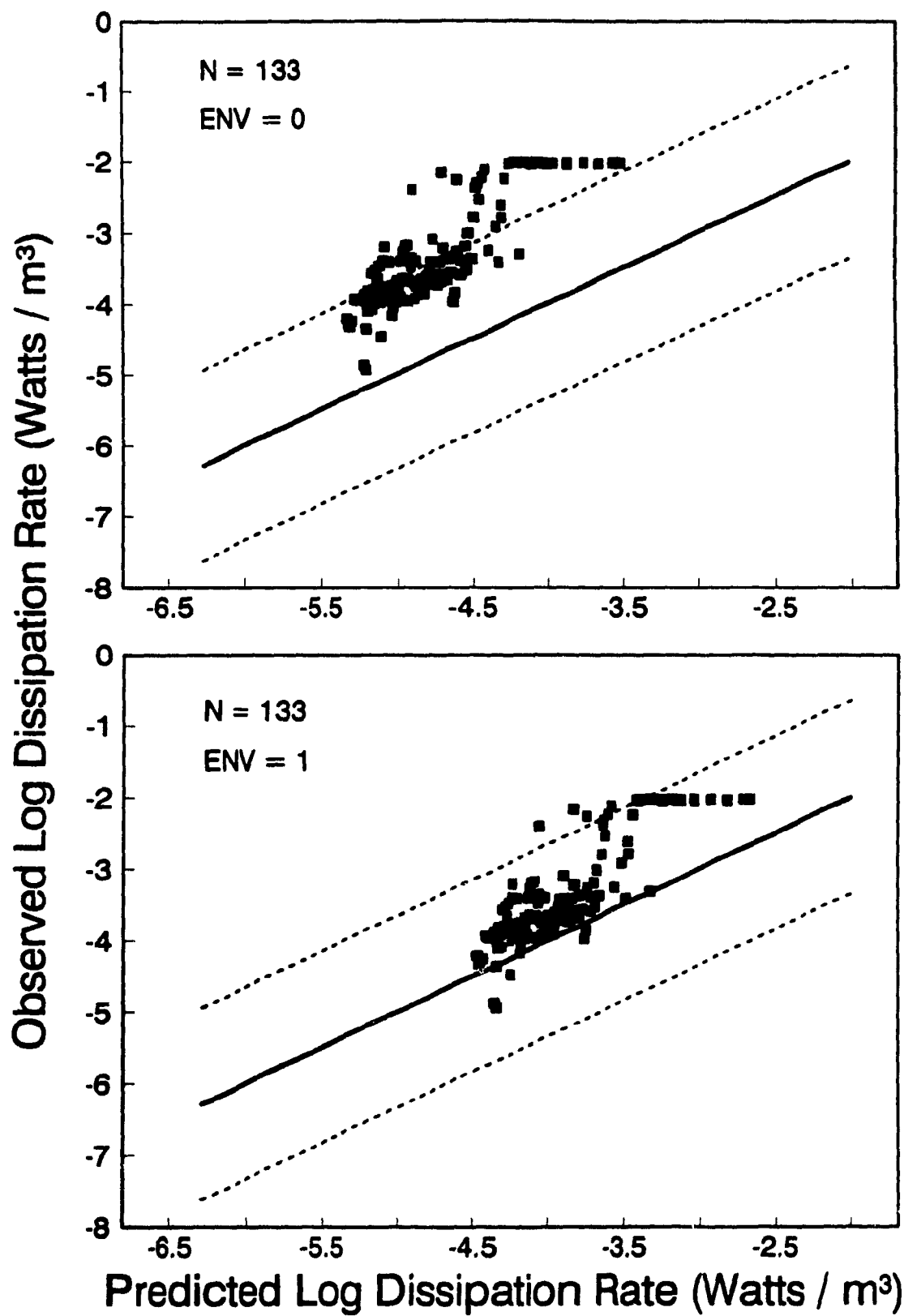
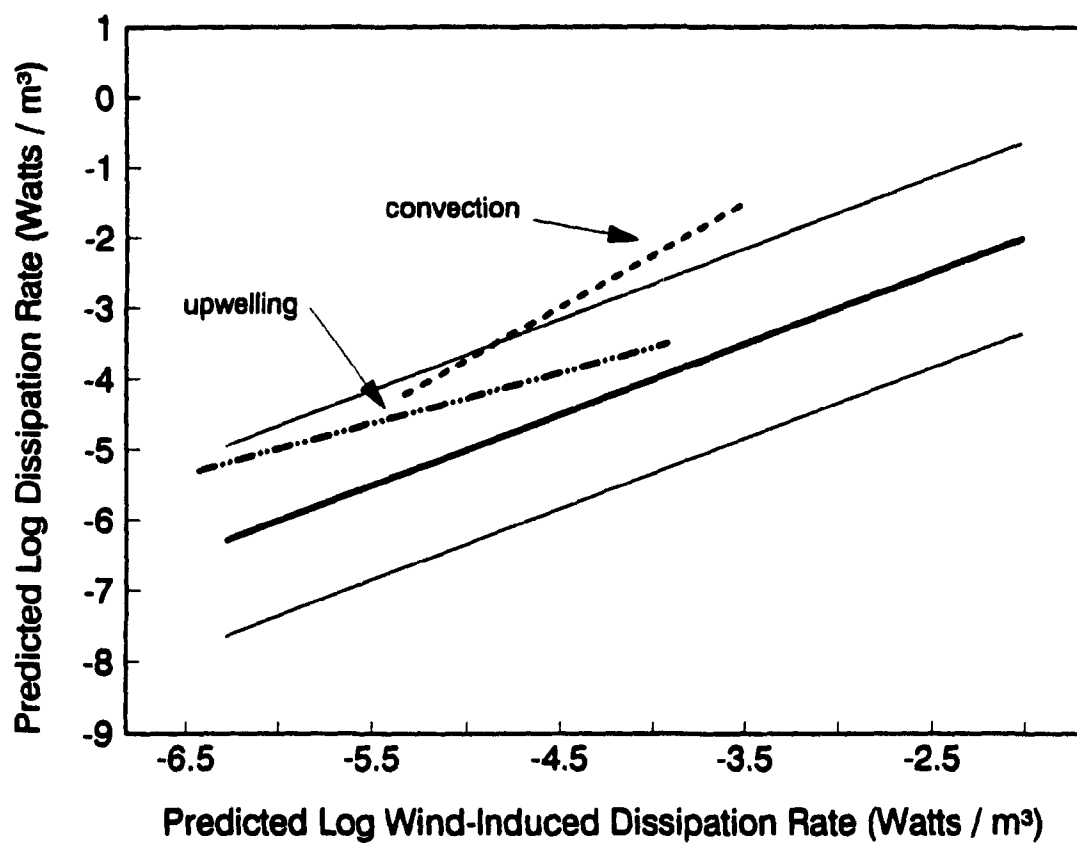


Figure 2. Comparison of dissipation rates associated with three different turbulence-generating phenomena. Solid, heavy line represents mixed layer wind-induced dissipation rates predicted from Model 3 ($\log \epsilon = 0.776 \cdot \log(\text{WIND SPEED}^3) - 1.067 \cdot \log(\text{DEPTH}) + 0.842 \cdot \text{ENV} - 5.323$). Solid, thin lines represent approximate upper and lower 95 % confidence limits for predictions from Model 3. Input data for these lines are derived from 895 literature-based dissipation rates. The dashed line represents the regression line (observed = $1.487 \cdot \text{predicted} + 3.713$; $R^2 = 0.72$) relating observed dissipation rates measured in January 1983 in warm core ring 82-I to values predicted using Model 3 with ENV = 0 (assumes an environment in which wind is the principal source of turbulence). Wind and depth data are as reported in Shay and Gregg (1986). The chained line represents the regression line (observed = $0.716 \cdot \text{predicted} - 0.686$; $R^2 = 0.65$) relating observed dissipation rates in the central and frontal regions of an upwelling meander off the central coast of California to dissipation rates predicted using Model 3 with ENV = 0 (assumes an environment in which wind is the principal source of turbulence). Wind and depth data are as reported in Dewey & Moum (1990).

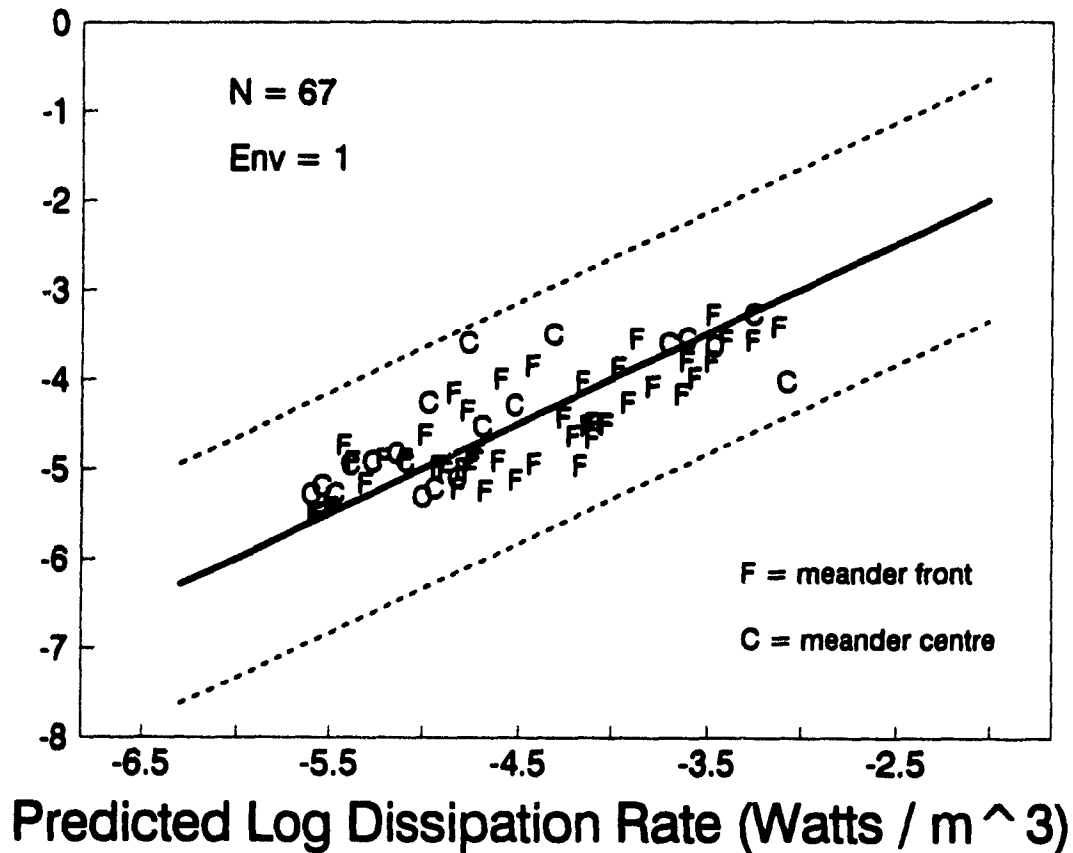
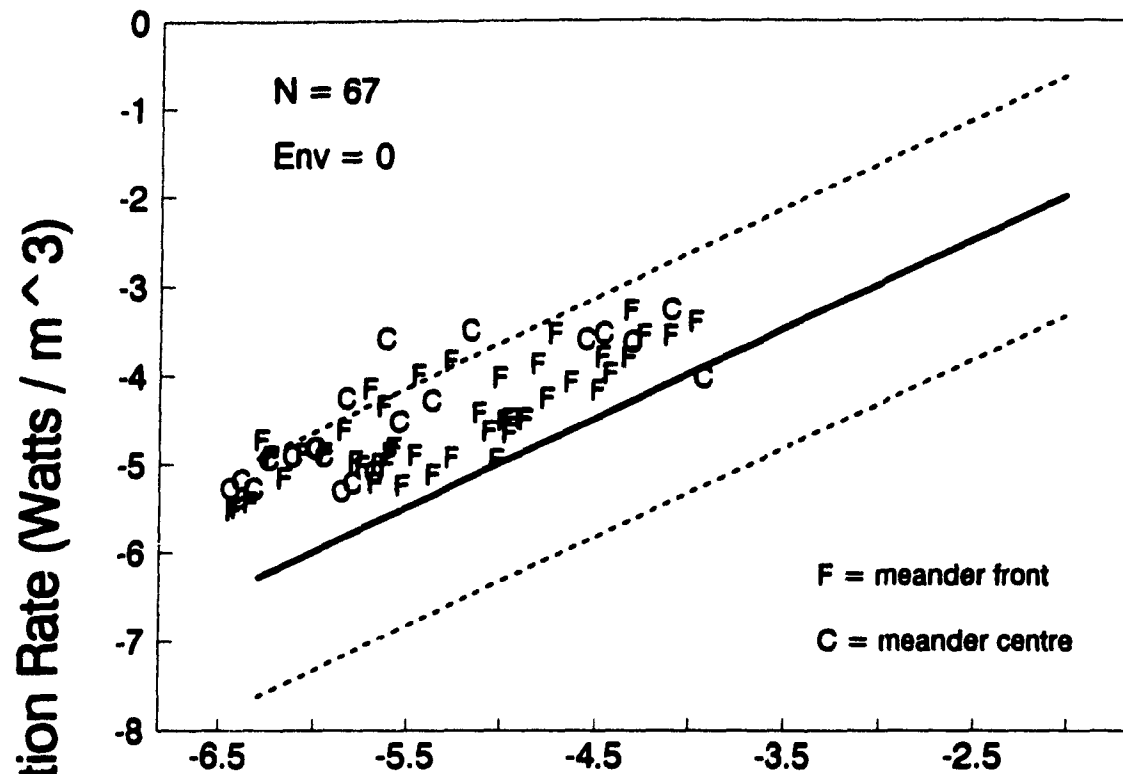


In fact, Model 3 explained 72 % ($P < 0.0001$) of the variance in rates reported by Shay and Gregg (1986). However, the slope and intercept of the observed vs. predicted scatterplot (based on Model 3 output) exceeded 1 and 0 respectively ($P < 0.05$; Figure 1). This indicates, as noted above, that Model 3 will underestimate dissipation rates that are generated by multiple causes, including convection.

As expected, nearly all (66 of 67) of the dissipation rates measured by Dewey and Moum (1990) in the central and frontal region of an upwelling meander also exceeded predictions made by Model 3 (Figure 2, 3A) which used wind and sample depth as inputs, and which assumed an environment in which wind was the only source of turbulence ($ENV = 0$). The mean difference between observed and predicted dissipation rate was 6.8-fold. A large majority (84 %) of the observed values were distributed within the 95 % confidence limits associated with predictions based on Model 3. When the environment was assumed to have multiple sources of turbulence ($ENV = 1$), all of the observed dissipation rates were observed to lie within the 95 % confidence limits of the predictions of Model 3 (Figure 3B). The factor by which observed rates differed from predicted rates under the assumption that multiple sources of turbulence were present (i. e. $ENV = 1$) was 0.97 (i. e. essentially unity). There was no systematic difference between dissipation rates measured in the core of the meander and at the frontal region of the meander (Figure 3).

Model 3 explained 65 % of the variance ($N = 67$; $P < 0.0001$) in dissipation rates measured within the upwelling meander. However the slope and intercept of the relationship between observed and predicted values differed from 1 ($P < 0.05$) and 0 ($P = 0.0529$) respectively (Figure 2).

Figure 3. Comparison of dissipation rates in an upwelling meander with those induced by local wind speed. Symbols represent observed dissipation rates measured in the centre (denoted as "C") and frontal (denoted as "F") regions of an upwelling meander off the central coast of California (Dewey and Moum 1990). For comparison purposes, solid lines show predicted dissipation rates obtained from Model 3 ($\log \epsilon = 0.776 \cdot \log(\text{WIND SPEED}^3) - 1.067 \cdot \log(\text{DEPTH}) + 0.842 \cdot \text{ENV} - 5.323$; input data are 895 mixed layer dissipation rates extracted from the literature). Dashed lines show approximate upper and lower 95 % confidence limits for predictions from Model 3 for the 895 literature-derived dissipation rates. Panel A: observed rates vs. rates predicted using Model 3 with $\text{ENV} = 0$ (assumes an environment in which wind is the principal source of turbulence). Panel B: observed rates vs. rates predicted using Model 3 with $\text{ENV} = 1$ (assumes an environment in which there are multiple sources of turbulence). All wind and depth data are as reported by Dewey & Moum (1990).



This indicates that, within the upwelling meander studied by Dewey & Moun (1990), as wind speed increased and/or as sampling depths became shallower, upwelling-related circulation became progressively less important in causing deviations from predictions of Model 3. However, at low wind speeds and/or in deeper water, upwelling circulation processes are likely to make a relatively greater contribution to observed mixed layer dissipation rates, thereby resulting in positive deviations from the predictions of Model 3

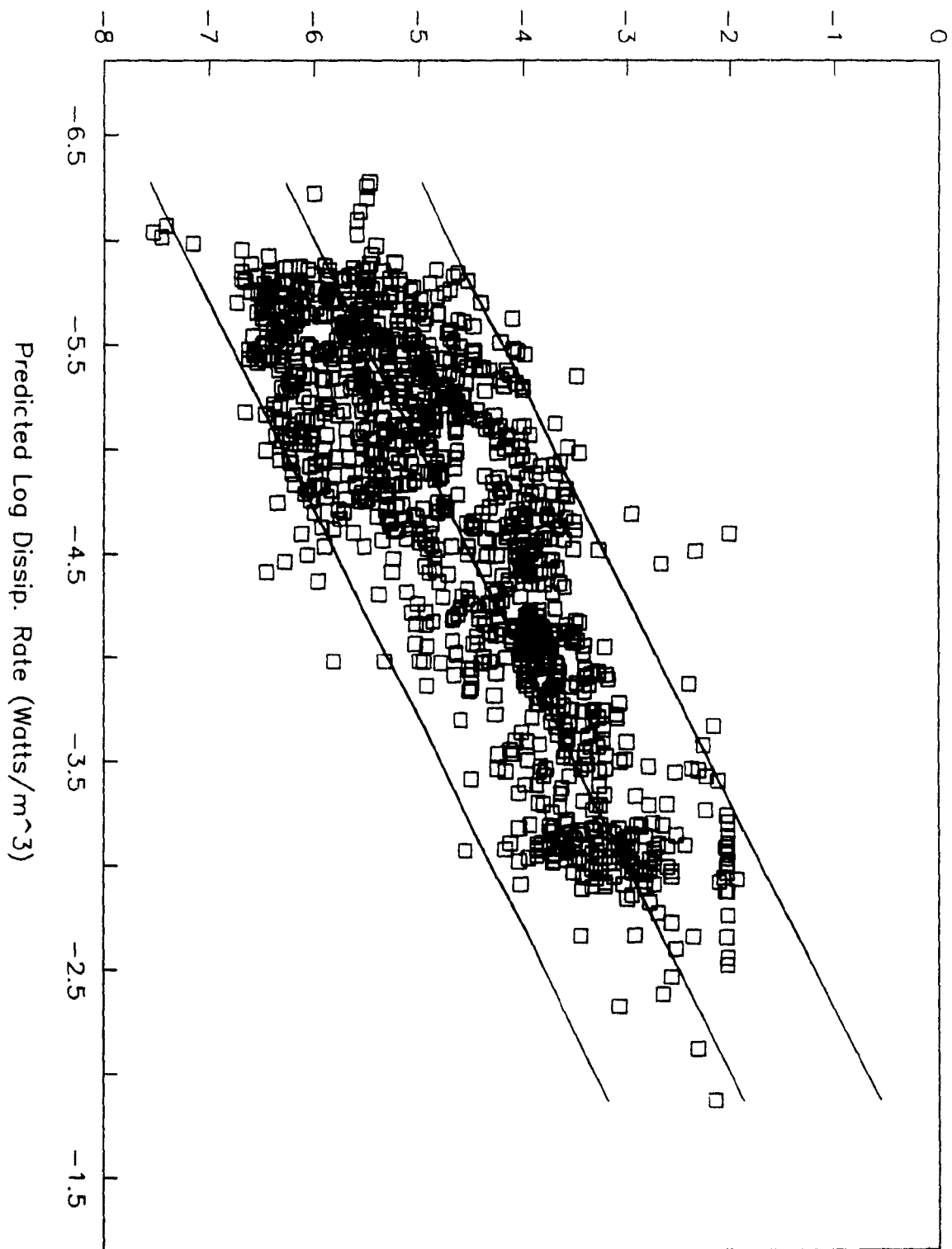
These results clearly show that the inclusion of an indicator variable, which distinguishes environments according to a priori expectations of their turbulence characteristics, may serve as a useful first-order approximation of spatial or temporal variability in turbulence associated with non-wind processes. A more general model which employs all of the mixed layer dissipation rate data, including convection and meander data, might, therefore, be useful in some circumstances. Such a model (Model 4; Table 3, Figure 4) which was based on a data set that included the convection and upwelling meander sites explained 65 % of the variance in these dissipation rates ($N = 1095$). However, the regression coefficients for this model were not significantly different from those associated with Model 3 from which convectively- and upwelling-driven turbulence was excluded (Table 3).

Evaluation of theoretical dissipation rate models:

The atmospheric boundary layer model (Eq 1; Model 5, Table 3) and the energy balance model (Eq 4; Model 6, Table 3) each explained 52 % of the variance in the in situ dissipation rates I assembled ($N = 895$; convection and upwelling meander data excluded from both comparisons). The

Figure 4. Scatterplot of observed rates of dissipation of turbulent kinetic energy vs. those predicted by Model 4 ($\log \epsilon = 0.762 \cdot \log(\text{WIND SPEED}^3) - 1.039 \cdot \log(\text{DEPTH}) + 1.040 \cdot \text{ENV} - 5.331$; $N = 1095$). The lines represent predicted values (slope = 1 and intercept = 0) and their estimated upper and lower 95 % confidence limits. The average of all predicted $\log \epsilon$ values is -4.596.

Observed Log Dissip. Rate (Watts/m³)



variance in ϵ explained by these models was, therefore, slightly less than that explained by Model 2, which employed wind and depth as inputs, and which can be expressed in arithmetic units in the form $\epsilon = 8.09 \times 10^{-6} W^{2.889} / Z^{1.429}$.

The intercept of the regression line for the observed vs. predicted scatterplot for predictions made by the atmospheric boundary layer model did not differ from 0 (Table 4), although the slope was slightly larger than 1.0 ($P < 0.05$). This indicates that the atmospheric boundary layer model underestimated mixed layer dissipation rates, but only by a small amount. However, predictions derived from the energy balance model underestimated dissipation rates by a larger amount because the intercept of the observed vs. predicted scatterplot was significantly greater than 0 ($P < 0.05$; Table 4), and the slope was slightly less than 1.0 ($P < 0.05$; Table 4). It must be emphasized, however, that the magnitude of underestimation by either of these models is very small relative to the substantial residual error associated with both the theoretical and the empirical models which I have considered here.

Discussion

Developing new models, and critically evaluating the power and reliability of existing models (e. g. Rice and Cochran 1984; Hall 1988) are important initial steps in estimating how natural phenomena or populations might vary at other times or places (Rice and Cochran 1984; Peters and Downing 1984; Hall 1988; GLOBEC 1991). These analyses represent the first statistical evaluations of factors associated with variability in estimates of the dissipation rate of turbulent kinetic energy in the

Table 4. Parameter estimates ($\pm$ standard error) of regression lines relating observed dissipation rates to those estimated by Models 5 and 6 in Table 3. P denotes the probability of a fitted value differing significantly from zero. The slopes and intercepts for Models 1 - 4 (Table 3) did not differ from 1 or 0 respectively ($P > 0.05$).

Model	Slope	P	Intercept	P
5	1.097 (0.035)	< 0.0001	-0.153 (0.149)	0.3047
6	1.097 (0.035)	< 0.0001	0.414 (0.167)	0.0135

mixed layer. They also provide the first direct quantitative comparison of the effectiveness of the two most frequently referenced theoretical models for representing the depth-dependent rate of dissipation of wind generated turbulent kinetic energy in aquatic systems.

The principle findings of these analyses are that wind speed and sample depth are nearly equally effective at explaining variability in the dissipation rates in this data set, and that, when combined with a knowledge of additional processes known to generate turbulence (e. g. convection; upwelling and other interactions between current flow and bathymetry), simple empirical or theoretical models based on existing data can explain up to 65 % of the variance in these rates.

The observation that up to 65 % of the variability in dissipation rates can be explained by wind speed, sample depth and an environmental coding variable may be surprising, given that replicate measures of dissipation rate under identical wind conditions can differ by at least an order of magnitude (e. g. Osborn 1978; Oakey 1985). Atmospheric forcing is generally believed to be the dominant source of variation in the dissipation of turbulent kinetic energy within the mixed layer (e. g. Kullenberg 1976; Oakey and Elliott 1982; Lueck and Reid 1984). Dissipation rates should, therefore, be expected to vary strongly and quantitatively with wind speed (Table 3; Gargett 1989).

The fact that Models 5 and 6 (Table 3), which are derived from theoretical considerations, explained identical fractions of the observed variance in in situ dissipation rates suggests that Model 6, the energy balance model (Simpson and Bowers 1981), can be used to estimate turbulent dissipation rates within the mixed layer at least as reliably as Model 5,

the atmospheric boundary layer model (Lumley and Panofsky 1964). This is due partly to the fact that turbulent dissipation rates, in general, are proportional to a cubed velocity measure divided by a length scale corresponding to the size of the largest eddy within the flow (Kullenberg 1977; Csanady 1986).

Potential errors in assessing the quantity of wind energy transferred to the water column prior to the sampling of dissipation rates, and the appropriate time lags in these respective measures (see Methods), are likely to contribute significantly to the residual variance associated with empirical and theoretical models of turbulent dissipation. These measurement inaccuracies also inflate the standard error of the regression coefficient for the wind term in empirical models. Because dissipation rates are known to respond quickly to high-frequency changes in wind stress (Dillon and Caldwell 1980; Dewey and Moum 1990), the relationship of dissipation rates in my data set to local wind conditions would be obscured by the integrated wind speeds I employed.

Simple wind-based models (Table 3) can, however, be much improved if and when the time response of water column mixing to changes in wind speed is defined more precisely. For example, cross-correlational and coherence analyses of time series records of wind speed and depth-specific dissipation rates would identify frequency-dependent lag times between these two variables. The incorporation of these time lags into empirical and theoretical models of mixed layer dissipation rates would be straightforward and could significantly improve existing models (Table 3) for estimating mixed layer dissipation rates from wind speeds.

In addition, much of the residual variability associated with these

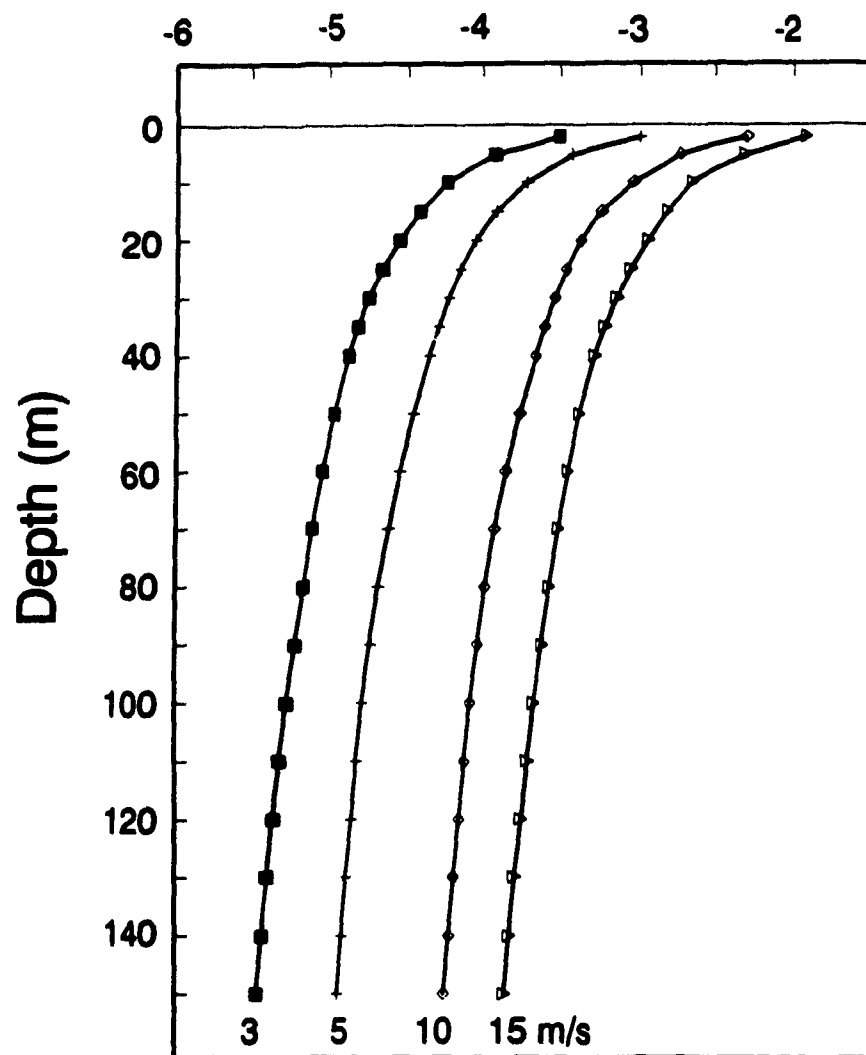
models can probably be reduced by collecting replicate dissipation rate profiles under identical conditions. If these individual profiles are subsequently averaged, the mean profile will be more closely related to wind conditions than the individual profiles (e. g. Dillon and Caldwell 1980, p. 1915; Oakey 1985, p. 1671; Shay and Gregg 1986, p. 1789; see also Gibson 1990).

Many published reports of marine turbulence failed to provide any measure of wind speeds during or adjacent to the times when dissipation rates were being measured. Consequently, these rates were excluded from the data set. Wind speed and direction are now routinely measured and recorded during oceanographic cruises. The fact that no other single variable has yet been shown to explain an equivalent amount of variance ($R^2 = 0.31$) in in situ dissipation rates within the mixed layer across sites and depths, indicates that future studies of turbulent dissipation should routinely include measurements of wind speed prior to and during the sampling interval. This minor improvement in data reporting protocol would facilitate further, and more detailed, comparisons of turbulence measurements obtained in different areas and under different wind conditions (e. g. Figure 2 and Model 3).

As expected, dissipation rates were inversely related to sample depth (Table 3; Figure 5). This occurs principally because water at shallower depths is closer to the source of turbulence (wind energy) than water at greater depths. Descriptions of mixed layer dissipation rate which provide a depth-averaged measure of ϵ (e. g. Oakey and Elliott 1982) will, therefore, underestimate dissipation rates close to the surface and overestimate dissipation rates near the bottom of the mixed layer.

Figure 5. Dissipation rates of turbulent kinetic energy at different combinations of depth and wind speed, as estimated with Model 4. In this simulation, the environment variable was assigned a value of 1 (assumes an environment in which there are multiple sources of turbulence).

Log Dissipation Rate (Watts / m³)



It is possible that the influence of depth on the dissipation rates in this data set could be associated with weak stratification within, or strong stratification near the bottom of, the surface mixed layer (Dewey and Moum 1990; Yamazaki 1990). If this occurred, some of the kinetic energy of turbulent motion would not be dissipated, but would instead be retained as potential energy by the new uniform density of the mixed layer (Dewey and Moum 1990).

However, the effect of stratification on dissipation rates within the mixed layer was probably small because analyses were intentionally confined to the mixed layer where vertical density gradients are known to be weak. This conclusion is supported by the correspondance between the empirical models and expectations based on theory. Theory (Kullenberg 1977; Denman and Gargett 1983; p. 804) suggests that the exponent for the depth term in models of turbulent dissipation within unstratified fluids subject to a surface stress should equal -1. The regression coefficient for depth as defined in Models 3 and 4, did not differ from -1.0. The results based on dissipation rates measured in diverse environments are, therefore, consistent with the theoretical nature of turbulent dissipation in unstratified fluids.

It is widely recognized that variance in turbulent dissipation rates can originate from many sources other than wind stress. These would include convection (Shay and Gregg 1986), upwelling meanders and jets (Csanady 1989; Dewey and Moum 1990), bottom topography (Wolanski and Hamner 1989), current shear (Haury et al. 1990), or the passage of schools of fish near the turbulence profiler during data collection (Farmer et al. 1987).

Identifying and quantifying these sources of variance will be a difficult task because of the high natural variability in dissipation rates in nature (Table 1, Fig. 1 - 4; see also Osborn 1978; Gibson 1990), and because multiple causes of turbulence can co-occur (convection and wind stress, Fig. 1 - 3; Gargett 1989). The chances of distinguishing such effects can probably be increased by (1) collecting replicate profiles under identical conditions, (2) removing the variability in averaged profiles that can be attributed to known sources (e. g. wind) and (3) subsequently comparing patterns in the residual dissipation rates with other phenomena suspected of being responsible for turbulent dissipation.

Applying this approach with a data base derived principally from unreplicated turbulence profiles (which often misrepresent both the magnitude and form of an averaged turbulence profile; Gibson 1990), two important patterns in dissipation rates associated with non-wind processes can be observed. First, the maximum increase in turbulent dissipation rates induced by free convection at temperate latitudes is likely to be, on average, 24-fold higher than that induced by wind speed (Figure 1, 2). Second, the amount of turbulence associated with one particular upwelling meander off the central coast of California was nearly 7-fold higher than the turbulence induced by local wind speed (Figure 2, 3).

These, and other, non-wind sources of turbulence were highly significant contributors to the overall variance explained by Models 3 and 4. An important shortcoming of this approach is that a new empirical model employing dissipation rates measured in other hydrographic situations (e. g. during periods of variable upwelling intensity; adjacent to the high velocity region of a warm core ring [Yentsch and Phinney

1985]; in areas of strong tidal currents [Bowers and Simpson 1987]) is likely to cause a change in the magnitude (but perhaps not the sign) of the coefficient for this variable. It would be preferable, therefore, to use continuous, rather than discontinuous, input variables in future models which attempt to quantify these influences. However, in the studies which provided data for these analyses such information was lacking

Biological implications

Variability in the dissipation rate of turbulent energy within aquatic ecosystems is an important component of the environmental heterogeneity experienced by planktonic organisms. Consequently, turbulent dissipation is likely to have a pervasive influence on several aspects of plankton ecology (Margalef 1978; Lewis et al. 1984; Rothschild and Osborn 1988; Lande et al. 1989; Hauray et al. 1990; Sundby and Fossum 1990; Shimeta and Jumars 1991). From an evolutionary perspective, the upper layer of stratified seas, and of lakes, represents a habitat that has predictably high rates of dissipation of kinetic energy relative to deeper layers (Table 3; Figure 5), and the magnitude of these rates can vary in predictable ways. For example, mixed layer dissipation rates can vary daily (Moum and Caldwell 1985), seasonally and annually (Rothschild and Osborn 1988) because of frequency-dependent variability in wind speed (Colin and Garzoli 1988; Harris et al. 1991) or heat input/loss (Moum and Caldwell 1985). Planktonic taxa, and benthic and nektonic taxa with planktonic life stages, have had ample time to adapt their behavioural and lifehistory characteristics to these predictable characteristics of mixed layer dissipation (Margalef 1978; also GLOBEC 1991).

The presence of a vertical gradient in dissipation rates within the

mixed layer suggests that distributions of those plankton species for which reproductive rates or swimming behaviours are insufficient to overcome the dispersive effects of turbulence are likely to be more homogeneous in the upper turbulent layers than in deeper, less turbulent layers (Owen 1989; Sundby 1990, Haury et al. 1990; Davis et al. 1991). Patch size and the number of organisms per patch (Owen 1989) is likely in some species to be greater in deeper water than closer to the surface. Consequently, even under constant wind conditions, planktonic predators (e. g. larval fish), whose rates of encounter with prey may depend on small-scale turbulence (Rothschild and Osborn 1988), can potentially experience very different feeding conditions, depending on their vertical position within the water column (Chapter 3). For example, near the surface, turbulence and light levels will be higher which would favor high encounter rates with prey, but these prey may be more dispersed than in calm water (e. g. Davis et al. 1991). Conversely, in deeper water, turbulence and light levels are lower but these factors could be offset by a more favorable distribution of prey (i. e. more patches and higher densities of prey within patches)

Turbulence also has an important role in determining the size of phytoplankton cells in different hydrodynamic environments (Holligan and Harbour 1977; Margalef 1978), and the rate at which these cells coalesce and settle from the water column (Kjørboe et al. 1990a). Pelagic food web structure (Kjørboe et al. 1990b), rates of secondary production by copepods (Dam and Peterson 1991), and the proportion of primary production which is consumed by higher trophic levels (including fish populations; Legendre 1990; Kjørboe et al. 1990b), may all depend on phytoplankton cell

size, which, in turn, is believed to be hydrodynamically controlled (Holligan and Harbour 1977, Margalef 1978; Cushing 1989, Legendre 1990). These findings suggest that interannual variability in pelagic food web structure ("classical" vs "microbial"; Kiorboe et al. 1990b) and in the rates of production at higher trophic levels in stratified seas, and lakes, may be partly determined by levels of turbulence induced by wind energy inputs, which can be estimated using simple models (Table 3)

In this connection, Models 3 and 4 (Table 3), and their 95 % confidence limits, can provide realistic bounds for in situ ranges of dissipation rate, and for parameters derived from these dissipation rates (e. g. encounter rates: Chapter 3), for varying combinations of wind and depth. Moreover, the confidence limits about some of these derived parameters may be substantially less than those associated with $\hat{\epsilon}$ itself, if $\hat{\epsilon}$ is subsequently used in nonlinear models whose terms have exponents smaller than 1.0.

Processes other than wind can generate large, positive deviations from predictions made by empirical and theoretical wind-based models. For example, the 7 - 24-fold increase in dissipation associated with an upwelling meander and a convection event are very likely to have had important consequences on predator-prey interactions and phytoplankton growth rates in such environments. These aspects of the physical environment would probably contribute to the higher rates of plankton production reported in upwelling regions (Cushing 1975), and subsequent to convection events in warm core rings (Tranter et al. 1980; Yentsch and Phinney 1985).

In conclusion, the dissipation rate models considered here (wind

energy), and elsewhere (tidal energy: Bowers and Simpson 1987), can be particularly useful in considering the potential influences of turbulence on biological processes when instrumentation for direct estimation of ϵ is unavailable. It is likely that improved models will soon be developed, given the increasing recognition of the importance of small-scale turbulence to plankton ecology (e. g. Lewis et al. 1984; Lande et al. 1989; Costello et al. 1990; Haury et al. 1990; Kjørboe et al. 1990a; Marrasé et al. 1990; Sundby 1990; Sundby and Fossum 1990; GLOBEC 1991; Granata and Dickey 1991; Chapter 3; Saiz and Alcaraz 1991; Shimeta and Jumars 1991). Given the assumptions required in these analyses, the potential for such improvement, with only minimal modification to existing sampling and reporting protocols, appears to be great. Towards this end, investigators should measure and report ϵ , and other relevant environmental variables (e. g. wind speed, stratification, etc.), more routinely and effectively in the future.

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Chapter 3

Quantifying the Contribution of Small-Scale Turbulence
to the Encounter Rates Between Larval Fish
and Their Zooplankton Prey: The Effects of Wind and Tide

Introduction

The dissipation of turbulent kinetic energy from large to small size scales is an inherent characteristic of the aquatic environment (e.g. Simpson et al. 1978; Lueck and Reid 1984; Thorpe 1985). Planktonic organisms respond both actively and passively to fluctuations in turbulent kinetic energy in their habitat (Yamazaki and Osborn 1988). For example, vertical differences in photoadaptive properties (e.g. maximum photosynthetic rate) of phytoplankton populations are reduced by high turbulence levels (Lewis et al. 1984) and plankton populations are more dispersed in turbulent than in calmer water masses (Lasker 1975; Haury et al. 1990).

Small-scale turbulence is suggested to be an important component of plankton trophodynamics (Rothschild and Osborn 1988), including larval fish (Murphy 1961; Hunter 1972; Sundby and Fossum 1990). Rothschild and Osborn (1988) showed analytically that zooplankton feeding rates may be underestimated by failure to consider turbulent motion when assessing the potential frequency of encounters between predators and prey. Sundby and Fossum (1990) found that the feeding rates of cod larvae increased twofold when winds were 6 m/s, compared to periods when winds were only 2 m/s.

These studies strongly suggest that contact rates, and hence feeding rates of zooplankton and larval fish, may be seriously biased by excluding the contribution of small-scale turbulence to these rates. This is consistent with observations (e.g. Chapter 1) that wild populations of larval fish collected during plankton surveys feed at higher rates than would be predicted from laboratory studies (in which turbulence is absent or reduced) when exposed to equivalent food and temperature conditions.

The nature and magnitude of this bias is likely to be related to differences in winds, tides, and water depths, all of which are known to influence the presence and character of small-scale turbulence in aquatic systems (e. g. Lueck and Reid 1984; Nixon 1988). The precise influence of these factors on plankton encounter rates has not yet been systematically investigated, although they can be evaluated through simulations.

The range of possible contact rates between larvae and prey in nature is vast, given the natural variability in dissipation rates (Osborn 1978; Oakey and Elliott 1982; Shay and Gregg 1986), prey densities (Owen 1989; Chapter 1) and swimming speeds of larvae (Miller et al. 1988) and prey (Checkley 1982). Individual larvae may be exposed to only a small portion of this variability because adult spawning and larval swimming behaviours may be adapted to place/maintain larvae in geographic areas (Sinclair 1988) and/or at depths (Munk et al. 1989) where feeding success is likely to be high (Kjørboe and Johansen 1986). Such locations might include sites of prey aggregations (e. g. thermoclines and fronts; LeFèvre 1986) or places where historic wind and tidal conditions increase turbulence, and hence the encounter rates between larvae and their prey.

In this paper I explore, through simulation, some of the meteorological and oceanographic circumstances under which small-scale turbulence created by wind and tide energy might significantly increase contact rates between larval fish and their prey. I also estimate the potential bias produced by failing to recognize the contribution of turbulent motion to the feeding ecology of larval fish in nature. Such knowledge is useful both as a first order guide to correcting larval fish and zooplankton feeding rates in the sea, and as a guide to improving the

designs of laboratory experiments in which predator/prey dynamics are explored (Chapter 1).

Methods

Estimating the dissipation rate of wind generated turbulent kinetic energy, ϵ

Oakey and Elliott (1982) identified an empirical relationship between wind speed and the depth-averaged rate of dissipation of turbulent kinetic energy, ϵ , in the mixed layer ($0 - \approx 20$ m) at a site on the Scotian Shelf, Canada. Sundby and Fossum (1990) used this model to estimate the influence of small-scale turbulence on the encounter rate between cod larvae and their prey near Lofoten, northern Norway. However, wind-induced turbulence in the upper layer is known to decrease inversely with depth (Dillon et al. 1981; Oakey 1985; Yamazaki and Kamykowski 1991). Many species of fish larvae (Heath et al. 1988; Frank and Carscadden 1989) and zooplankton (McLaren 1963; Williams et al. 1987) have complex vertical distributions. Larval fish and their prey will, therefore, be exposed to variations in turbulence caused by fluctuations of both wind speed and their distance from the water surface. It is, therefore, necessary to estimate small-scale turbulence at different depths within the water column. To assess this question, published reports of ϵ , the dissipation rate of wind-generated turbulent kinetic energy, were used to develop a multiple regression model incorporating wind speed, water depth and habitat (open ocean, coastal zone) as inputs.

Density gradients within the water column (stratification) may also be important in influencing the rate of dissipation of turbulent kinetic

energy (Yamazaki 1990; Rothschild and Osborn 1990). However these data were reported too infrequently to be included in my analyses. I attempted to minimize the influence of stratification on estimates of small-scale turbulence by using dissipation rates measured exclusively within the wind-mixed layer where density gradients are small relative to those within the pycnocline.

The model I developed is given by

$$\log \epsilon = -5.104 * Z^{0.79} + 0.748 * \log(W^3) + 0.945 * ENV \quad R^2 = 0.60 \quad (1)$$

where ϵ is dissipation rate of turbulent kinetic energy (watts/m³),

Z is water depth (m),

W is wind speed (m/s), and

ENV is environment (ENV = 0 if turbulence was measured at a site beyond a continental shelf; ENV = 1 if turbulence was measured on a continental shelf or in a lake).

This model is an earlier version of those presented in Chapter 2, and is based on 1138 measurements of the dissipation rate of turbulent kinetic energy at 12 different aquatic sites, of which 11 were marine (N = 1132) and 1 was freshwater (N = 6). Additional details regarding the development of wind-based models for estimating turbulent dissipation rates, and the data used in their derivation, can be found in Chapter 2.

I used turbulence values derived from Eq (1) to calculate the turbulent velocity contribution to the swimming velocity of a predator relative to its prey (Rothschild and Osborn 1988). In this formulation,

when the separation distance, r (metres), between predator and prey exceeds the Kolmogorov length scale, $\eta = 2\pi(\nu^3/\epsilon)^{0.25}$ (ν = kinematic viscosity $\approx 10^{-6} \text{ m}^2 \text{ s}^{-1}$), the turbulent velocity is given by

$$w^2 = 3.615*(\epsilon*r)^{2/3} \quad (2)$$

which is equation 4 in Rothschild and Osborn (1988). I assume that the separation distance r , is approximated by $N^{-3/3}$, where N = the number of prey per m^3 ($1 \text{ m}^3 = 10^3 = 10^6 \text{ cm}^3$).

The velocity of a larval fish relative to that of its prey, denoted as A (cm/s), can then be calculated from:

$$A = (s^2 + 3*t^2 + 4*w^2) / 3*(t^2 + w^2)^{1/2} \quad (3)$$

where s = swimming velocity of the prey (cm/s),

t = swimming velocity of the larva (cm/s), and

w = turbulent velocity (cm/s).

Prey contact rate, C , is then calculated as

$$C = A*D \quad (4)$$

where D is $\pi*R^2*N$, and R (cm) is the encounter radius of the predator (Rothschild and Osborn 1988).

In employing this derivation of contact rate, I assume, as did Sundby and Fossum (1990), that the encounter radius, R (also known as the reactive distance, RD ; Wanzenbock and Schiemer 1989), of larval fish is constant in all directions. This may not be strictly true (Rosenthal and Hempel 1970; Blaxter and Staines 1971; Wanzenbock and Schiemer 1989) but for the present purposes is a reasonable approximation.

In addition, encounter radii for a given predator, even when assumed constant in all directions, vary with factors such as light intensity,

size and swimming velocity of the predator, and prey size and conspicuousness (Gerritsen and Strickler 1977, Lazzaro 1987; Miller et al. 1988; Wanzenböck and Schiemer 1989). I have excluded exact values of πR^2 from the calculation of contact rate (Eq 4) to isolate the effects of turbulent velocity, w^2 , and relative velocity, A , on larval contact rates. In my simulations, therefore, D is taken to be proportional to prey density N . Consequently, contact rate, C , is expressed in units of prey/s/cm². Where the prey encounter radius, R , is known, these rates can be converted to prey/s by multiplying C by the appropriate value of πR^2 .

Wind effects on contact rates

I used the empirical turbulence model (Eq 1) to estimate the contact rates between larvae and prey at several combinations of wind speed and water depth, and at two larval swimming velocities. The wind speeds evaluated (0 - 15 m/s) spanned the range that occurs over many larval nursery areas (e. g. Bowers and Simpson 1987; Frank and Carscadden 1989). The depth range evaluated (0 - 60 m) encompasses the vertical range in distribution of many species of marine fish larvae (e. g. Buckley and Lough 1987; Heath et al. 1988; Munk et al. 1989; Frank and Carscadden 1989). All simulations assumed larvae were located in a continental shelf habitat where there were likely to be additional non-wind sources of turbulence (ENV = 1; Eq 1. See also Chapter 2).

Larval swimming speeds evaluated were 0.2 cm/s and 0.5 cm/s. The slower speed is close to the average cruising speed of first-feeding cod larvae (standard length = 4.5 mm; Sundby and Fossum 1990). Given the relationship between larval size and swimming speed across species, as reported by Miller et al. (1988), the 0.5 cm/s speed approximates that

for larvae of total length 5.7 mm. The two swimming speeds were used to evaluate the influence of identical turbulence levels on larvae having different swimming abilities (commonly associated with size; Miller et al. 1988).

The prey modelled were copepod nauplii which constitute the dominant prey of larvae of many commercially exploited marine fish species (Theragra chalcogramma, Dagget al. 1984; Gadus morhua, Ellertsen et al. 1984; Scomber scombrus, Peterson and Ausubel 1984 and Buckley and Lough 1987; Clupea harengus, Heath et al. 1989; Melanogrammus aeglefinus, Buckley and Lough 1987). These prey were assumed to swim at a velocity of 0.02 cm/s for the simulations involving larval swimming speeds of 0.2 cm/s. This prey velocity is considered to approximate that for Calanus finmarchicus nauplii (Sundby and Fossum 1990).

I assume that the difference in swimming speeds in the larvae in my simulations is due principally to differences in their sizes and thus, that the faster swimming larvae (0.5 cm/s) prefer larger prey (Hunter 1981). Prey swimming speeds in these simulations were increased to 0.05 cm/s. This tenfold difference in swimming speeds between prey and fish larvae is consistent with Gerritsen and Strickler's (1977) observation that vertebrate predators swim much faster than their prey.

I used two prey densities (5 and 35 nauplii/L) to compare how different levels of turbulence affect contact rates when food supplies differ. These prey densities approximate those found in many larval nursery areas (e. g. Cape Hatteras, North Carolina, Checkley et al. 1988; Lofoten, Norway: Ellertsen et al. 1984; Bering Sea: Dagget al. 1984), but

are lower than the median density found in 46 marine environments if one assumes that one copepod nauplius weighs $\approx 0.2 - 0.5 \mu\text{g}$ dry (Chapter 1).

The spatial distribution of zooplankton, an important characteristic of larval food resources (Owen 1989), is also likely to influence the encounter rate between larvae and their prey. The number, size, and intensity of prey patches is influenced by biotic (e.g. zooplankton migratory behaviours, growth and mortality rates; McLaren 1963, Williams et al. 1987; Owen 1989) and abiotic (wind conditions, water column turbulence; Owen 1989, Haury et al. 1990) factors. However, conventional plankton sampling methods are unreliable in identifying and quantifying the scale and density of these patches (Owen 1989). We, therefore, used my models to quantify (1) the bias in estimates of contact rates that may result when integrative sampling methods are employed and the contribution of turbulence to contact rates is ignored, and (2) how larval contact rates can change with storm-related redistribution of prey (e.g. Lasker 1975).

I compared turbulence-enhanced contact rates between slow-swimming larvae and prey under two scenarios: (1) prey were patchily distributed on a vertical spatial scale of 5 - 10 metres; and (2) prey were distributed homogeneously throughout the 60 m water column. The first scenario is analogous to a prey distribution which might occur prior to a wind mixing event (Lasker 1975; Frank and Carscadden 1989) or in areas of weak tidal currents (Bowers and Simpson 1987). This situation, therefore, considers prey patchiness within a mixed layer (e.g. Peterson and Ausubel 1984; Fortier and Harris 1989; Checkley et al. 1988), but not

patchiness associated with pycnoclines where Eq (1) may give unreliable estimates of turbulence.

The scenario involving homogeneously distributed prey corresponds to conditions which might prevail after passage of a storm (Lasker 1975; Owen 1989), or in tidally-mixed water columns (Bowers and Simpson 1987; Heath et al. 1989). The range of wind speeds used in these simulations was restricted to 0 - 10 m/s because it is unlikely that prey would remain heterogeneously distributed at higher wind speeds (Owen 1989).

In the pre- and post-storm scenarios, the depth-averaged prey density for the entire water column (0 - 60 m) was 20 nauplii per litre ($= 20,000/\text{m}^3$).

Tidally induced turbulence

To estimate the rate of dissipation of tidally-generated turbulent kinetic energy, the viscous dissipation of energy was derived from the large-scale dynamics (p. 19-20, 68; Tennekes and Lumley 1972) of tidal flow. In this formulation, the rate of energy supply from large-scale eddies to small-scale eddies is proportional to $\underline{u}'^3/\ell$, where ℓ is the largest eddy size associated with the flow or the width of the flow (Tennekes and Lumley 1972; Veth 1990).

Bowers and Simpson (1987) have shown that the potential for tidal flow to completely mix a water column is expressed by a tidal stirring parameter, $\underline{u}^3/\underline{h}$, where $\underline{u}$ is the depth-averaged tidal velocity of the M_2 tidal constituent (period = 12.42 h) and $\underline{h}$ is the water column height. Most of the dissipated tidal energy represented by $\underline{u}^3/\underline{h}$ is lost as heat (Bowers and Simpson 1987), but a percentage of $\underline{u}^3/\underline{h}$ is available for creating turbulent motion and vertical mixing within the water column

(Bowers and Simpson 1987). If this percentage is denoted as ζ , then the absolute amount of dissipated turbulent kinetic energy which results in vertical mixing, ϵ , can be estimated as

$$\epsilon = \zeta * \underline{u}^3 / \underline{h} \quad (5)$$

In Eq (5), I assume that $\underline{u}'^3 = \zeta * \underline{u}^3$ and that the largest eddy size, ℓ , is proportional to the water column height, $\underline{h}$ (Tennekes and Lumley 1972, Veth 1990).

Eq (5) and values for $\underline{u}$ and $\underline{h}$ (Bowers and Simpson 1987, Table 1) were used to estimate the depth-averaged turbulent kinetic energy dissipation rate at tidally-energetic sites on the northwest European continental shelf during the summer. In this region, tidal fronts, which delimit the transition zone between mixed and stratified water columns, are delimited by contours of $\underline{u}^3 / \underline{h} = 0.004 \text{ m}^2 \text{ s}^{-3}$ (Bowers and Simpson 1987). Depth-averaged turbulent kinetic energy dissipation rates (ϵ) in frontal areas can, therefore, be estimated (Eq 5) as

$$\begin{aligned} \epsilon &= \zeta * [\underline{u}^3 / \underline{h}] \\ &= 0.006 * [0.004 \text{ m}^2 \text{ s}^{-3}] && \text{(Bowers and Simpson 1987)} \\ &= 2.4 * 10^{-5} \text{ m}^2 \text{ s}^{-3} \\ &= 2.4 * 10^{-2} \text{ Watts m}^{-3} \end{aligned}$$

where $\zeta = 0.006$, the fraction of the dissipated tidal energy which is used for vertical mixing (Bowers and Simpson 1987). Values of ϵ exceeding $2.4 * 10^{-2} \text{ Watts m}^{-3}$ (i. e. values of $\underline{u}^3 / \underline{h} > 0.004 \text{ m}^2 \text{ s}^{-3}$) are typical of

tidally-mixed areas (Figure 1: Rothschild and Osborn 1988; Bowers and Simpson 1987; Otto et al. 1990; Veth 1990).

Dissipation rates of turbulent kinetic energy obtained from Eq (5) were then used as inputs in Eq (2) to enable calculation of $\underline{w}^2$, and $\underline{A}$, and, therefore, approximations of the importance of the tidal contribution to contact rates. It is important to note that the tidal velocity term, $\underline{u}$, in the stirring parameter is a depth-averaged value and that tidally-generated turbulence is concentrated near the sea-bottom (Loder and Greenberg 1986). The depth-averaged contact rates derived here will, therefore, overestimate contact rates for larvae that feed near the surface. The amount of overestimation will be small for frontal and tidally-mixed areas because the source of turbulent energy is, by definition, relatively close to the water surface and because the maximum eddy size from the tidal flow is order $\underline{h}$. However, the magnitude of the overestimation will, however, be large for stratified regions where the source of tidal energy is farther from the surface and because the largest eddy size from the tidal flow is $<$ order $\underline{h}$. For these reasons, I do not quantify the influence of tidal energy on plankton encounter rates in stratified areas. In any case, the contribution of tidal energy to plankton contact rates in the surface layer of a stratified water column is likely to be small relative to the contribution of wind, and in comparison to tidally energetic areas.

In my analysis of the influence of tidally generated turbulence, I conducted two types of simulations using only slow swimming larvae and slow swimming prey. First I assessed how spatial variations in tidally-generated turbulence might affect contact rates when prey densities were

uniform across three types of hydrographic environments (no tidal energy, frontal, well-mixed). This simulation was conducted with 4 prey densities: 5, 20, 35 and 70 nauplii per litre. Next I assessed how the combined spatial variance in both turbulence and prey distributions influenced contact rates across hydrographic environments.

Both the wind and the tidal simulations which follow intentionally focus on the evaluation of contact rates under conditions when standing stock prey densities are such that larval feeding success as measured in laboratory studies are low (Chapter 1). Clearly, numerous other combinations of larval/prey swimming speeds, prey density, tidal velocity, wind speed and water depth are possible, but I restricted my analyses to a small number to facilitate interpretations and to assess the general importance of the influence of small-scale turbulence on contact rates. Nevertheless, larval swimming speeds increase as larvae grow (Miller et al. 1988) and larvae in nature can encounter mixtures of prey species/sizes (Govoni et al. 1986; Kellerman 1990) having different swimming speeds and behaviours (Checkley 1982). These aspects of larval feeding ecology deserve attention and should be considered in future studies.

Results

Wind induced turbulence

(i) Homogeneous prey distributions

I consider initially the scenario involving a homogeneously distributed prey population and larvae swimming at 0.2 cm/s (Figure 1A, B). Under these conditions, contact rates are highest near the surface

and diminish with depth at all wind speeds. Contact rates are higher at all depths when there is wind than when there is no wind. The decrease in encounter rate with depth under all wind conditions reflects the expected decrease in turbulent kinetic energy with depth (Eq 1; Chapter 2)

These contact rate-depth profiles suggest that larval fish could, therefore, benefit from storm mixing events even when prey are homogeneously distributed before a storm. For example, consider larvae that swim slowly (0.2 cm/s) located at a depth of 20 m in a prey field of 5 nauplii/L (Figure 1A) with winds at 7.5 m/s (an approximate value for United Kingdom meteorological stations in summer, Bowers and Simpson 1987). If the wind velocity increases to 15 m/s causing larvae to actively migrate or passively mix to a depth of 60 m, these analyses predict that the new contact rate at 60 m ($0.00355 \text{ prey/s/cm}^2$) would still exceed that prevailing in shallower water at the lower (7.5 m/s) wind speed ($0.00334 \text{ prey/s/cm}^2$). Further, this new rate is more than 3 X higher than the contact rate at any depth in the absence of winds ($0.00100 \text{ prey/s/cm}^2$).

Fast swimming larvae have higher encounter rates than do slow swimming larvae. However as turbulence levels increase, the difference in encounter rates between fast and slow swimming larvae decreases (Figure 1B). In my simulation, at wind speeds of 15 m/s, contact rates of fast and slow swimming larvae located in the upper 10 - 15 m of the water column become equivalent.

The increase in contact rates created by small-scale turbulence is also relatively greater at lower prey densities (Figure 2). For example, at winds of 5 m/s, the contact rate for a larva feeding at a depth of 20 m and at a prey density of 5/L is predicted to be 155 % higher than that

Figure 1. A. Simulated contact rates between fish larvae and zooplankton prey at different wind speeds (0 - 15 m/s) and water depths (2 - 60 m). Prey density = 5 nauplii/L, larval swimming speed = 0.20 cm/s and prey swimming speed = 0.02 cm/s. B. The influence of larval and prey swimming speeds on contact rates between larvae and prey at wind speeds of 3 and 15 m/s and at depths of 2 - 60 m. Dashed lines, larval swimming speed = 0.20 cm/s and prey swimming speed = 0.02 cm/s. Solid lines, larval swimming speed = 0.5 cm/s and prey swimming speed = 0.05 cm/s. Prey density = 5/L.

100 x Contact Rate (prey/ s / cm²)

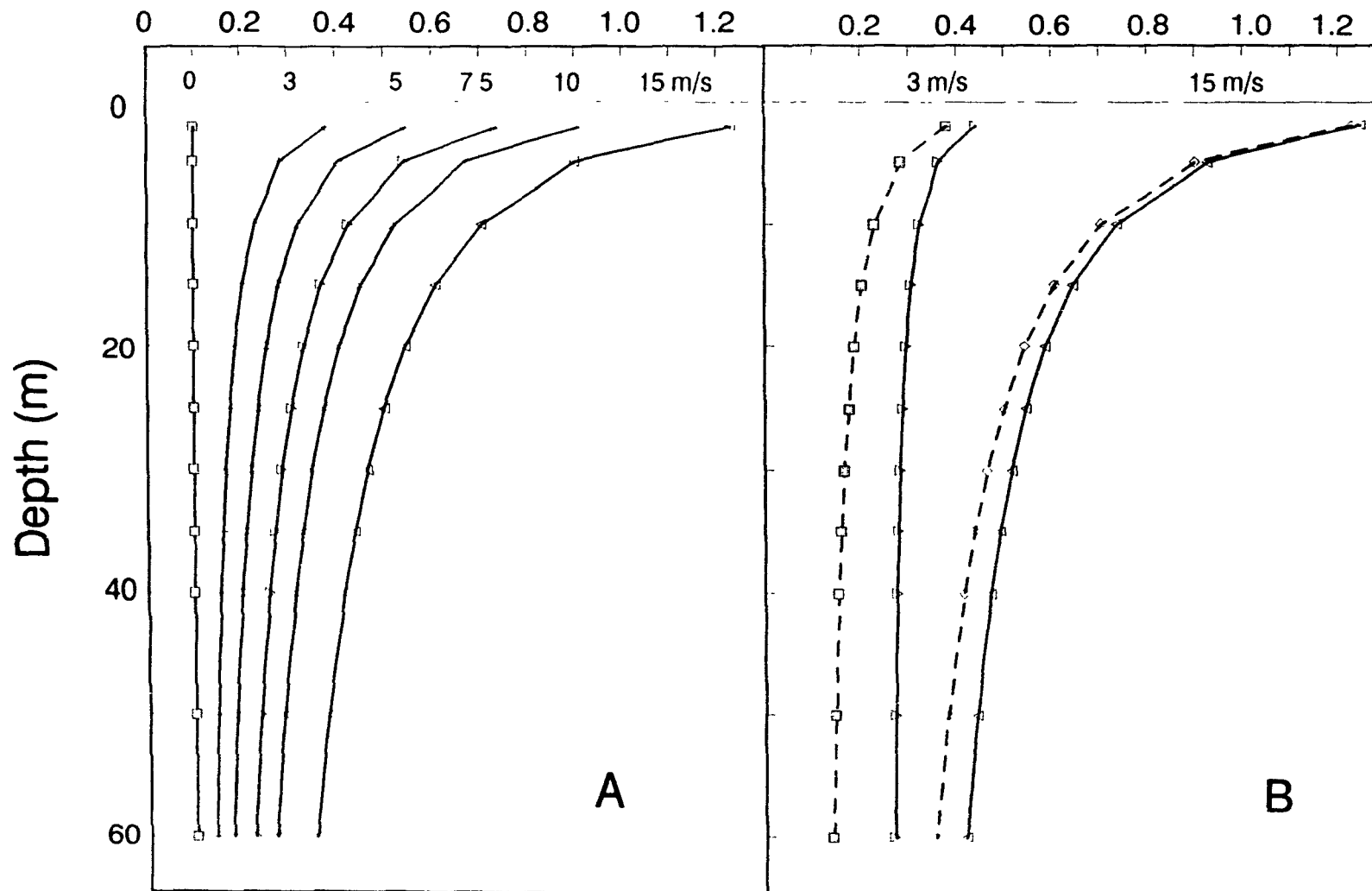
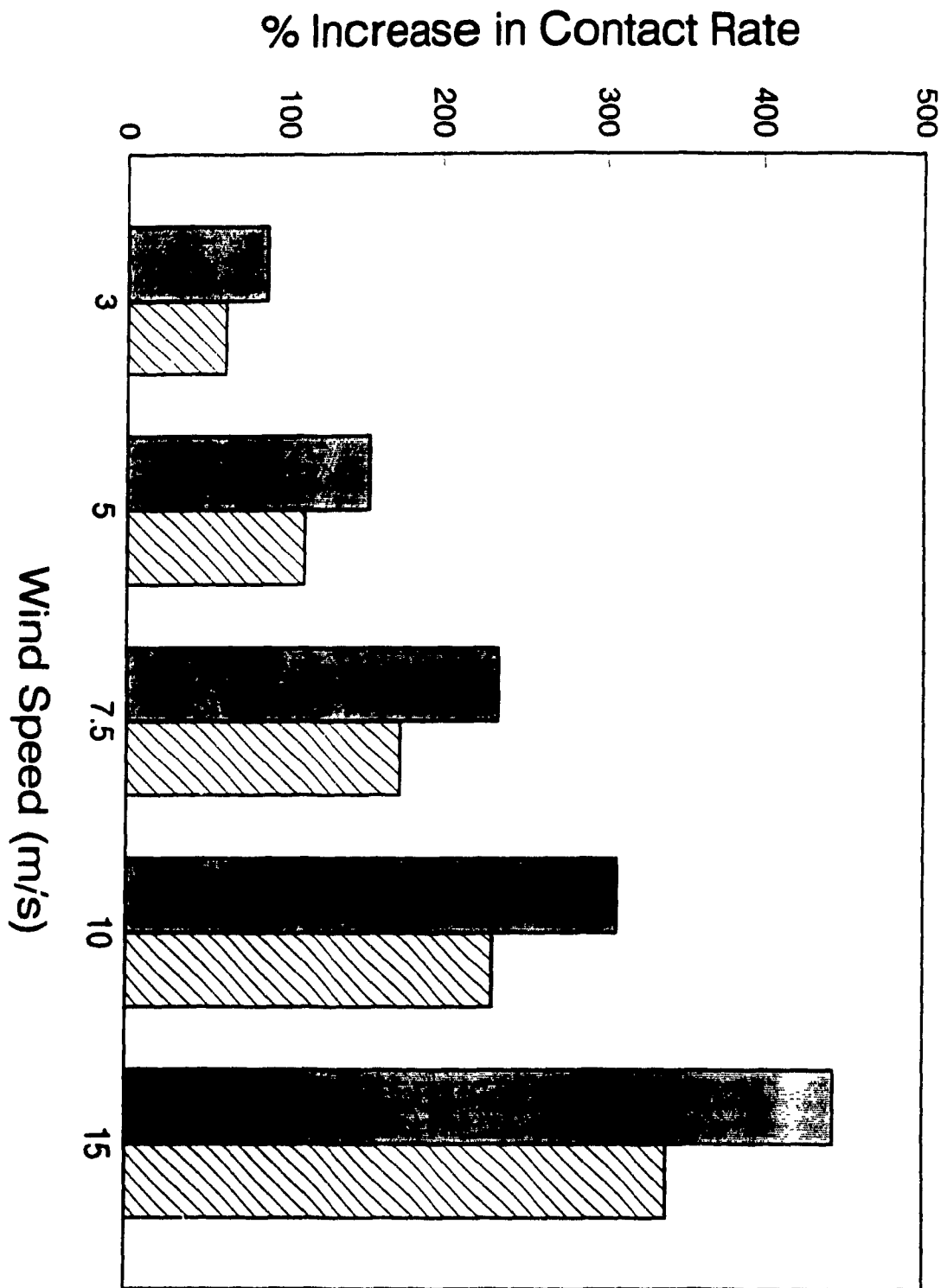


Figure 2. Percent increases in contact rate between fish larvae and zooplankton prey at two prey densities and at 5 wind speeds relative to the contact rates at equivalent prey densities but in the absence of wind-induced turbulence. Larval swimming speed = 0.20 cm/s and prey swimming speed = 0.02 cm/s. Solid bars: prey density = 5/L; striped bars prey density = 35/L. Percent increase = $[(\text{rate}_{\text{wind}} - \text{rate}_{\text{no wind}}) / \text{rate}_{\text{no wind}}] * 100 \%$.



for a larva in a nonturbulent environment. At prey densities of 35/L, the percent increase in contact rate due to turbulence is 112 %. The higher relative increase in contact rates at lower prey densities occurs because prey are separated by greater distances at 5/L than at 35/L (see Eq 2).

(ii) Heterogeneous prey distributions

I next consider the potential bias in estimated contact rates caused by failure to account for both prey patchiness and small-scale turbulence (Figure 3). If an investigator performs a depth-integrated plankton haul and ignores the contribution of wind-induced turbulence to larval contact rates, these rates would be assumed constant at all depths (Figure 3B, curve II).

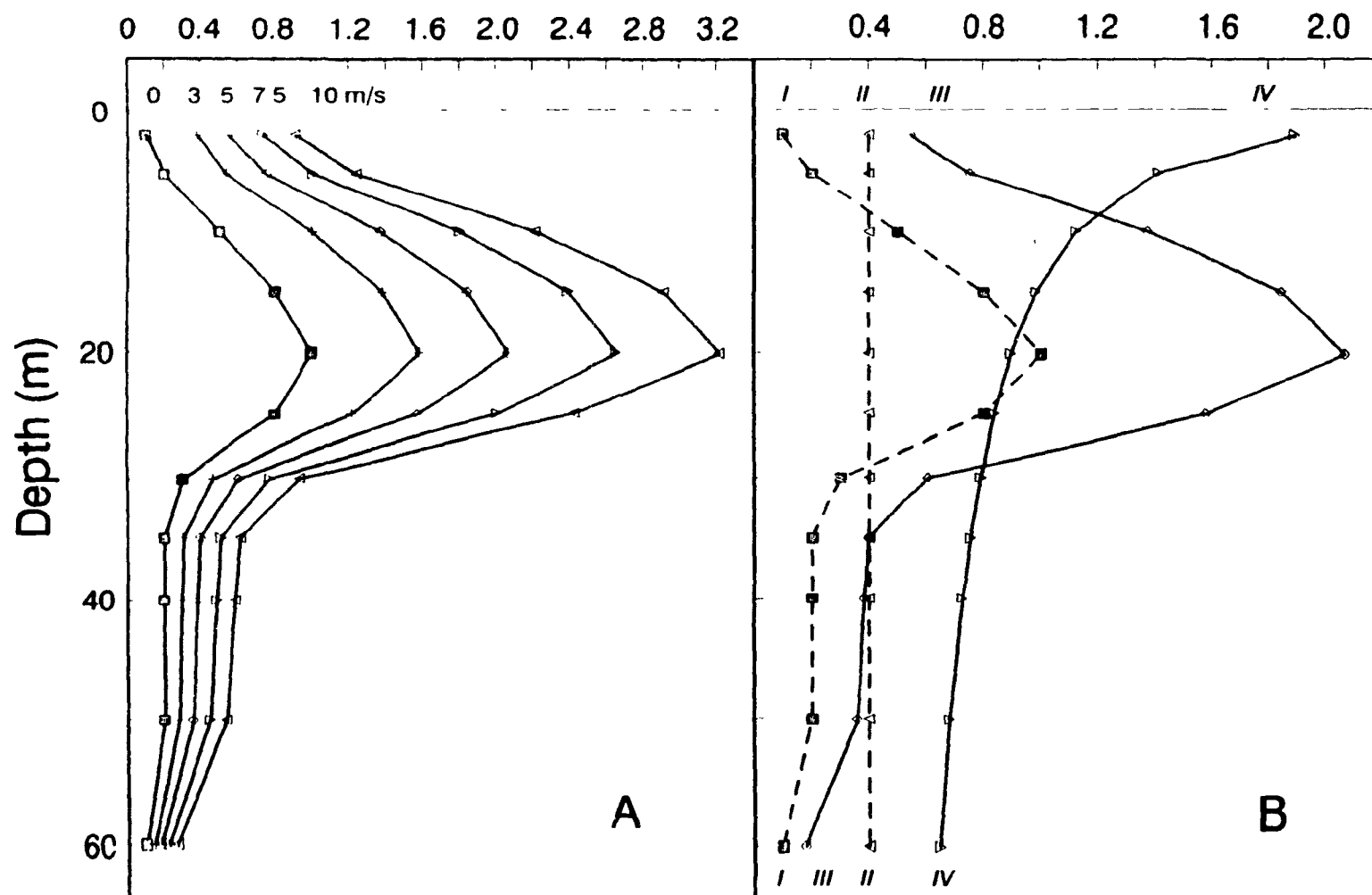
However, depth-stratified samples from the same environment, adjusted for the effect of wind-generated turbulence, reveal a $> 5 \times$ increase in contact rates for larvae located at a depth of 20 m (Figure 3B, curves I and III), but smaller increases at other depths. If the effect of turbulence is ignored when depth-stratified sampling is employed, contact rates of larvae located at 20 m depth would be underestimated by 100 % (Figure 3B, curves I and III).

The magnitude of the bias created by failure to recognize the important contribution of turbulence to contact rates increases with both wind speed and patchiness (Figure 3A and 3B). For example, at wind speeds of 7.5 m/s, a depth-integrated sample which failed to account for turbulence would underestimate contact rates of larvae located at 20 m by $> 6 \times$ (Figure 3A and 3B, curve II).

For some combinations of prey density and depth, contact rates estimated from vertically-integrated samples and without reference to the

Figure 3. The influence of prey distribution, wind-induced small-scale turbulence and zooplankton sampling protocols on simulated contact rates between fish larvae and zooplankton prey. Larval swimming speed = 0.20 cm/s and prey swimming speed = 0.02 cm/s. Note that the horizontal scale in A differs from that in B. A Simulated contact rates between larvae and prey at 5 wind speeds ranging from 0 - 10 m/s and at depths ranging from 2 - 60 m. Prey density = 5/L for depth = 2 and 60 m, 10/L for depth = 5, 35, 40, and 50 m, 15/L for depth = 30 m, 25/L for depth = 10 m, 40/L for depth = 15 and 25 m, and 50/L for depth = 20 m. The depth-averaged prey density is 20/L. B. Curve I depicts the contact rate between larvae and prey in the absence of wind. Prey are heterogeneously distributed as described in the legend for Figure 3A. Curve III describes contact rates under the same vertical prey distribution but in the presence of wind = 5 m/s. Curve II depicts contact rates when prey are homogeneously distributed in the absence of wind. Curve IV depicts contact rates when prey are homogeneously distributed but with wind = 5 m/s. In all four simulations the depth-integrated prey density = 20/L. Larval and prey swimming speeds were 0.20 and 0.02 cm/s respectively.

100 x Contact Rate (prey/ s / cm²)



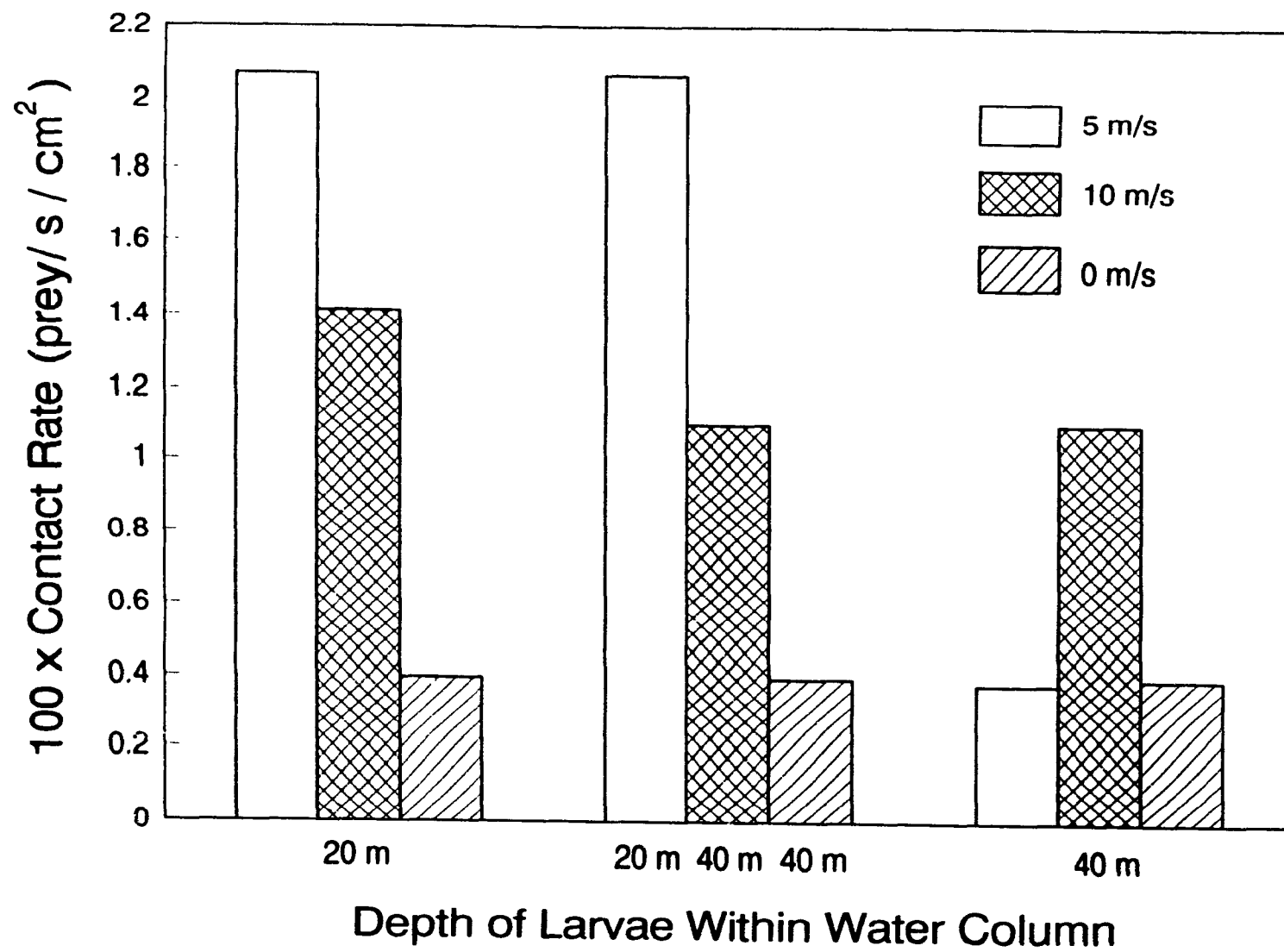
contribution of turbulent kinetic energy (Figure 3B, curve II) may actually overestimate contact rates (e g. 60 m; Figure 3B, Curves II and III).

(iii) Storm effects

The increases in small-scale turbulence and changes in prey distribution associated with storms can have either detrimental or beneficial effects on larval contact rates. For example, if larvae are located at 20 m where prey density is 50/L and if the wind speed is 5 m/s, their contact rates will decrease by 32 % during a storm having 10 m/s winds (Figure 4), assuming that the storm homogenizes prey densities throughout the water column. The decrease in contact rates would have been even greater if not for the increase in turbulence generated by a doubling of wind speed. Moreover if this same larva was mixed downwards or actively swam to deeper water (e. g. 40 m), its post-storm contact rate would be reduced by 46 % (Figure 4). These interactions probably contribute to the negative influence of strong wind events on in situ survival of larval anchovy (Peterman and Bradford 1987)

It is important to note, however, under other circumstances fish larvae may also benefit from storm events. In my simulation, larvae located at 40 m before the storm passed would experience a 187 % increase in encounter rates during the storm. This occurs because prey densities increased in deep water due to redistribution of prey from shallower waters, and because of the storm-related increase in small-scale turbulence. At these depths contact rates can be expected to diminish slowly as winds slacken and turbulence dissipates during the post-storm period. They will, however, continue to equal or exceed pre-storm levels

Figure 4. Simulated influence of a storm on contact rates between larval fish and their zooplankton prey. Pre-storm prey densities vary with depth as follows: 5/L for depth = 2 and 60 m, 10/L for depth = 5, 35, 40, and 50 m, 15/L for depth = 30 m, 25/L for depth = 10 m, 40/L for depth = 15 and 25 m, and 50/L for depth = 20 m. The depth-averaged prey density before the storm is 20/L. Prey densities during and after the storm are homogeneous with depth at 20/L. Wind speeds before, during and after the storm are 5, 10 and 0 m/s, respectively. Larval swimming speed is 0.20 cm/s and prey swimming speed is 0.02 cm/s.



because prey densities are now double the pre-storm levels.

Tidally induced turbulence

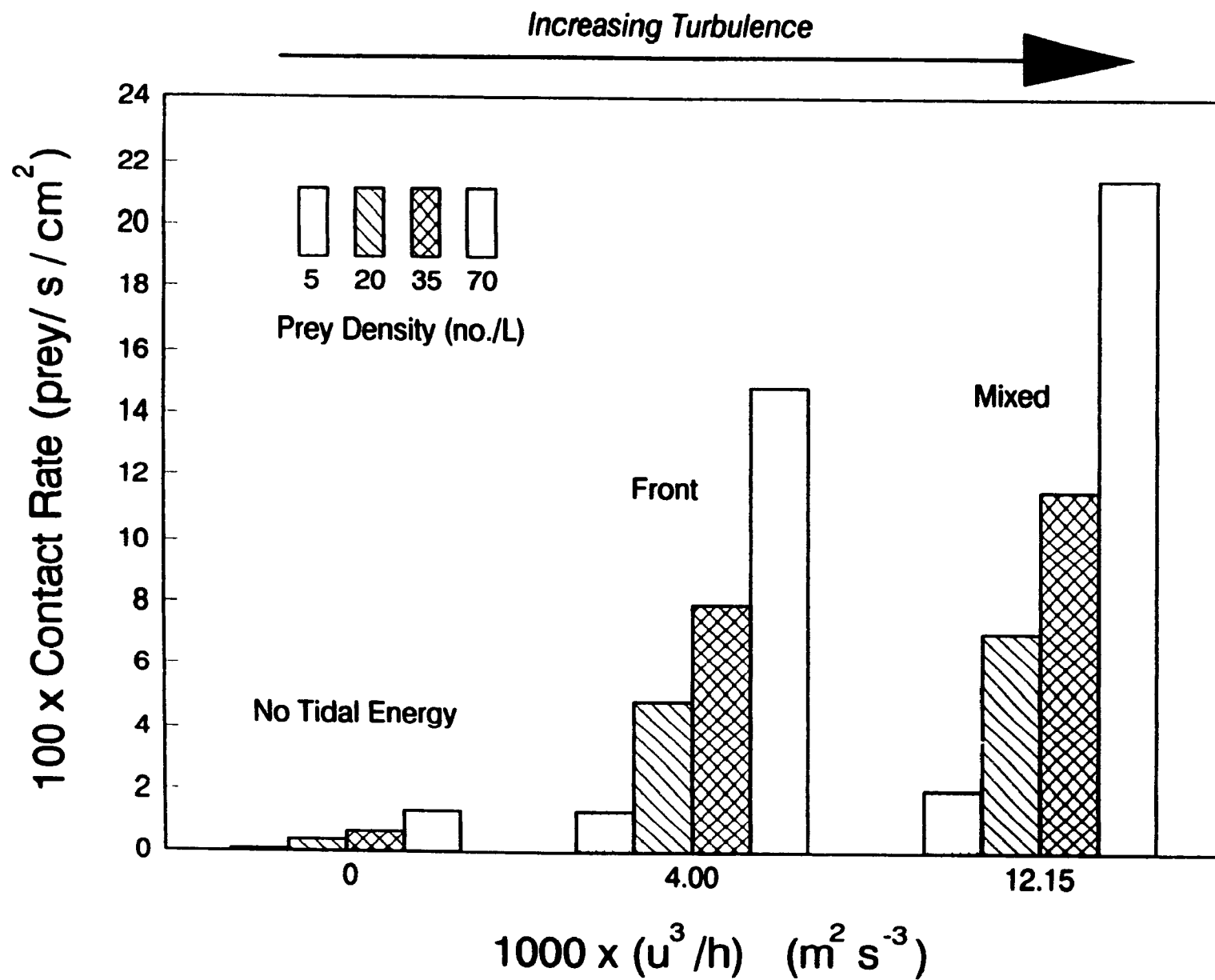
In simulations in which prey densities were uniform across three hydrographic regimes representing different levels of tidally-generated turbulence, contact rates increased with increased tidal mixing (Figure 5). For example, at prey densities of 35/L, an 11-fold increase in contact rate might be expected as a consequence of the tidal energy input that occurs in a frontal region ($\overline{u^3}/h = 0.004 \text{ m}^2 \text{ s}^{-3}$; Bowers and Simpson 1987).

When prey densities differ across hydrographic regions, the contribution of tidal energy to plankton contact rates can be even greater. For example, prey densities in a water column having no turbulence would have to be 14 X higher (70/L; Figure 5) to produce contact rates equivalent to those at a frontal zone where prey density is only 5/L.

Discussion

Estimating the realized food abundance and assessing its influence on feeding and growth rates of natural populations of larval fish is a major challenge in fisheries oceanography. Most conventional sampling programs can not estimate the quantity of prey available to larval fish at the appropriate spatial scales (Owen 1989). Further they fail to identify larval behavioural responses to prey patchiness at these scales (centimetres - metres, Hunter and Thomas 1974; Munk and Kjørboe 1985), and link mortality rates to coincident measures of food density (e. g. Taggart and Leggett 1987). In addition predators of larval fish have the potential to remove larvae selectively from the water column (Bailey and

Figure 5. The contribution of tidal energy to contact rates between fish larvae and their zooplankton prey at 4 prey densities. Larval swimming speed = 0.20 cm/s and prey swimming speed = 0.02 cm/s. The horizontal axis displays the Simpson-Hunter (1974) stratification index, from which ϵ , the dissipation rate of turbulent kinetic energy, can be estimated (see text, Eq 5). A value of $1000 \times (\underline{u}^3 / \underline{h}) = 4 \text{ m}^2 \text{ s}^{-3}$ occurs at tidally generated fronts (Bowers & Simpson 1987, p.37). Values of $1000 \times (\underline{u}^3 / \underline{h}) > 4 \text{ m}^2 \text{ s}^{-3}$ are characteristic of tidally-mixed water columns. In these simulations, tidal velocities, $\underline{u}$, were 0, 0.620 and 0.900 $\text{m} \cdot \text{s}^{-1}$, and $\underline{h} = 60 \text{ m}$.



Houde 1989). Larval populations which are captured in plankton collections may, therefore, be growing at rates different from the average for their cohort and independently of the potentially biased estimates of the larval food resource (Chapter 1).

The simulations which I developed from my estimates of wind and tidally induced turbulent energy demonstrate the important effect of small-scale turbulence on contact rates between fish larvae and their prey. Failure to recognize the influence of turbulence has undoubtedly biased earlier estimates of the contact rates between larvae and prey (Rothschild and Osborn 1988, and hence of in situ ingestion rates (Sundby and Fossum 1990; Chapter 1). Under the conditions used in one of my simulations, in which prey density was 5/L, these biases resulted in an underestimate of contact rates by 155 % at a wind speed of 5 m/s. my simulations also suggest that contact rates could be underestimated by as much as 11-fold for larvae located at frontal regions such as those on the northwest European continental shelf (prey density = 35/L; Figure 5). The magnitude of this bias will covary with wind speed and tidal energy, and with temporal and spatial variation in prey density, which is itself subject to other biases (Owen 1989).

My simulations involving heterogeneously distributed prey considered patchiness on the vertical dimension at scales of 5 - 10 m. Patchiness can exist in all three dimensions and at smaller spatial scales (Jenkins 1988; Owen 1989) than those which I have considered. I expect that the same general principles that I observe would operate at smaller scales (cm's - m's) closer to those of larval feeding activity. Moreover, patchiness on the scale of centimetres persists at wind speeds up to at

least 10 m/s (Jenkins 1988; Owen 1989), although the number of patches, and the density of individuals in the patch decrease as wind speeds increase (Owen 1989). Consequently, if larvae encounter such a patch, their contact rates with prey will be higher than if prey were homogeneously distributed.

Small-scale turbulence in the mixed layer is ubiquitous. This indicates that, in general, the surface layer must be considered a turbulent environment (Lueck and Reid 1984) when judged from the perspective of a larval fish and its prey. This is precisely the habitat occupied by first-feeding larvae of many species of marine fishes (Heath et al. 1988; Fortier and Harris 1989; Dauvin and Dodson 1990; Nielson and Perry 1990). This suggests that larval fish, and more generally zooplankton (e. g. Costello et al. 1990; Marrasé et al. 1990), should possess behaviours that enable them to capture and ingest prey under conditions of moderate turbulence.

As residents of this environment, larval fish are known to be periodically dispersed downwards, or to actively avoid the surface, during strong winds (Heath et al. 1988). Interactions between illumination, wind-induced turbulence (Heath et al. 1988), and prey density (Munk et al. 1989) are largely responsible for the vertical distributions of larval herring, and possibly for other species. For example, very high turbulence levels could allow prey to pass through the larva's visual field without being successfully captured because larval reaction times may be too slow to respond to fast-moving prey (e. g. see Checkley [1982] and Govoni et al. [1986] for factors affecting prey selection by larval fishes). In extremely turbulent environments larval feeding success may, therefore,

be lower than in less turbulent environments. It is likely, therefore, that larvae use combinations of light, turbulence and prey density to maximize in situ feeding success in the sea during both calm and storm periods.

In particular, larval vision (Hunter 1981; Wanzenböck and Schiemer 1989), and its dependence on illumination (Blaxter 1988), will influence the encounter radius, R . For example, the gut contents of many species of larvae that have been collected at regular intervals throughout the day and night reveal a diel cycle (Arthur 1976; Kellerman 1990; Young and Davis 1990), even though turbulence continues, and, in some areas even increases, at night (Moum and Caldwell 1985; Shay and Gregg 1986).

The demonstration of the potential effect of small-scale turbulence on contact rates at tidal fronts (Figure 5) adds to the understanding of processes which enhance biological production in such areas. Previous explanations of the high production and/or standing stocks commonly observed at fronts have focused mainly on the positive effects of increased amounts of phytoplankton cells, light and nutrient conditions, and circulation processes which entrain organisms towards the front (see review by LeFèvre 1986). Much of the enhanced production may be attributable to increased encounter rates between secondary consumers and their prey as a result of small-scale turbulence characteristic of such regions. High turbulence levels in these areas reduce the size of the smallest eddies, whose mean length scale is related to the Kolmogorov scale (Lazier and Mann 1989; Granata and Dickey 1991). This suggests that a larger size range of organisms, and possibly more trophic levels within

the planktonic food web, will benefit from the high levels of turbulence found at tidal fronts.

Given the results of these simulations I would expect that in stratified regions of the sea and in lakes, that the relative contribution of wind energy (Lueck and Reid 1984), and the dependence of the biota on this energy source, will be more important than tidal energy in influencing trophodynamics among planktonic taxa. Moreover, wind energy inputs are less reliable ecological signals than tidal energy inputs. If larval fish and other zooplankton do require turbulence to offset the potentially negative effects of low food densities commonly reported for marine environments (Chapter 1; see also Huntley and Boyd 1984; Olson and Olson 1989), populations which inhabit nontidal regions may experience more variable encounter rates, and hence different selection processes, than populations inhabiting areas associated with more reliable inputs of turbulent kinetic energy (e. g. fronts).

My analyses, like those of Rothschild and Osborn (1988), indicate that the positive effects of turbulence are greatest on the slowest swimmers (Figure 1B), which tend to be the smallest larvae (Miller et al. 1988). First-feeding and young fish larvae are therefore most likely to benefit from small-scale turbulence. These larvae may, therefore, have lower foraging-related metabolic costs than in the absence of turbulence (Rothschild and Osborn 1990; also Wieser et al. 1988; Boisclair and Leggett 1989). As swimming ability develops, larvae are less dependant on extrinsic, abiotic energy sources (winds, tides) as a means to encounter prey (Rothschild and Osborn 1988). However, even for these larger larvae, should their physiological condition deteriorate to a point where swimming

ability is reduced (Blaxter and Ehrlich 1974; Frank and Leggett 1982), kinetic energy inputs, such as those that occur during direct wind-mixing, at fronts (Bowers and Simpson 1987), and during upwelling (Csanady 1989) can potentially increase contact rates of larvae with their prey.

This could reduce the likelihood that larvae would starve to death in the sea (e.g. Hovenkamp 1990) as well as the likelihood of finding starving larvae in the sea. However, if slow swimming larvae are indeed dependent on tidal or wind-generated turbulence for increasing their encounter rates with prey, then temporal and spatial changes in tidal circulation and wind speeds could result in intermittent periods of reduced feeding and growth rates (e. g. Buckley and Lough 1987; Hovenkamp 1990; see also Rothschild and Osborn 1988). Such changes could occur if (1) winds slacken, which would reduce turbulent motions that otherwise increase contact rates; (2) winds increase by so much that larvae are mixed, or actively swim towards, depths where light intensities reduce the ability of larvae to see their prey; or (3) larvae are physically displaced by whatever means from "geographically stable physical oceanographic systems" (Sinclair 1988, p. 37-38) and subsequently experience conditions where reduced turbulence results in lower prey encounter rates than those prevailing prior to displacement.

Reports of periods of intermittently poor larval growth linked to low prey numbers are relatively rare (e. g. Sinclair 1988, p. 137; Chapter 1). This may reflect difficulties in accurately estimating growth rates and larval prey abundance simultaneously. In any case, periods of reduced growth will protract the larval period (Houde and Schekter 1981; Chambers and Leggett 1987) and increase the time that larvae are exposed to

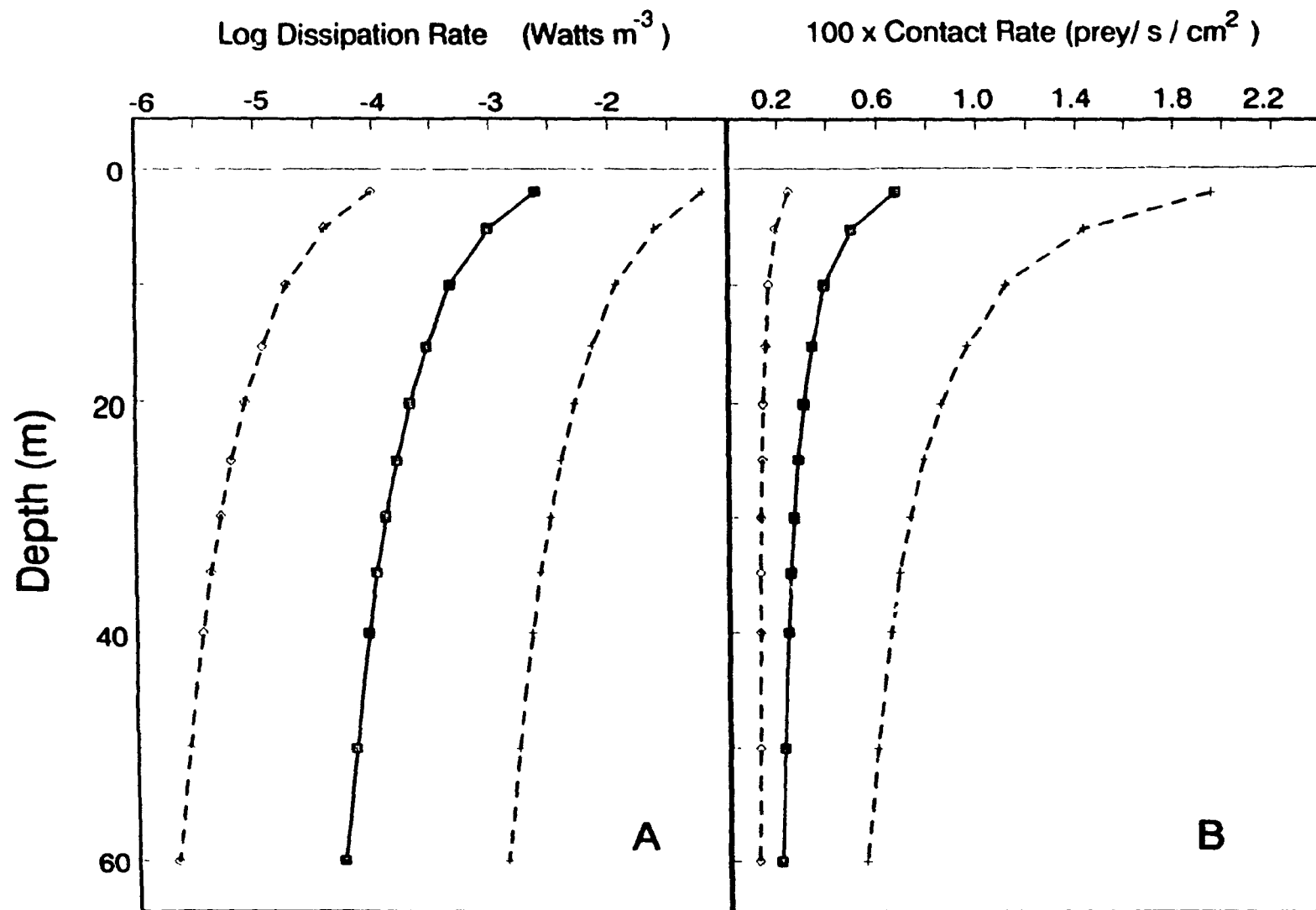
relatively high mortality (Folkword and Hunter 1986). In addition, the weakened condition of slow-growing larvae may make them more vulnerable to some predators (Bailey and Houde 1989).

A cautionary note

My interest in this chapter has been to explore quantitatively the potential influence of small-scale turbulence on encounter rates between fish larvae and their prey. The empirical wind-induced turbulence model developed for this purpose represents a first-order description of the variability in small-scale turbulence in nature. It should be remembered also that turbulence is itself patchily distributed and highly intermittent (Gezentsvey 1985; Lazier and Mann 1989; Yamazaki and Lueck 1990), and that all of the results reported here represent average values for contact rate. A sensitivity analysis of Eq (1) (Figure 6) showed that the 95 % confidence limits of a wind-induced turbulence estimate deviate by a factor of ≈ 10 from predicted values of ϵ . However, contact rates derived using these 95% confidence limits for $\hat{\epsilon}$ vary by only a factor of ≈ 3 (Figure 6B). This range approximates the range of biases in estimates of in situ larval food resources when determined by integrative sampling methods which fail to account for microscale plankton patchiness (Owen 1989).

Moreover, the contact rates I report are based on either wind- or tidally-generated turbulence. In frontal regions, these effects could interact in an additive way. In addition, coastal upwelling (Csanady 1989; Chapter 2), breaking internal waves, fish schools (Farmer et al. 1987) and other processes (Monin and Ozmidov 1985; Oakey 1985) can produce turbulence in nature which may, in local areas, also influence encounter

Figure 6. Sensitivity analysis of the influence of turbulence levels estimated from Eq. (1) on contact rates between larval fish and their zooplankton prey. The wind input used in this analysis is the mean value of $\log(W^3)$ (2.468; $W = 6.6 \text{ m}\cdot\text{s}^{-1}$) in our data set. The indicator variable for the sampling site was given a value of 1, which represents a coastal habitat. (A) Average dissipation rate of wind-induced turbulent kinetic energy as a function of depth. Dashed lines represent 95 % confidence limits calculated from Eq (8) in Peters and Downing (1984). (B) Contact rates for fish larvae and zooplankton prey for the turbulence levels shown in (A). Larval swimming speed is $0.20 \text{ cm}\cdot\text{s}^{-1}$ and prey swimming speed is $0.02 \text{ cm}\cdot\text{s}^{-1}$. Prey density is 5 l^{-1} . Note that the 95 % confidence limits for turbulent dissipation rate vary by a factor > 10 but that the confidence limits of contact rates derived using these confidence vary by a factor of ≈ 3 .



rates.

It is important, therefore, that more precise models be developed with which to predict the dissipation rate of turbulent kinetic energy, given the apparent importance of small-scale turbulence to plankton ecology. For example, coincident reporting of water column stratification and vertical turbulence profiles, together with wind field records over the sampling interval could significantly reduce the residual variance associated with Eq (1) (Lueck et al. 1983; Oakey 1985; Yamazaki 1990; Rothschild and Osborn 1990). It should be noted, too, that turbulence measurements in the upper mixed layer, including those used in developing Eq (1), sometimes depart from a lognormal distribution (Yamazaki and Lueck 1990; Yamazaki et al. 1990). This factor should be considered in the development of future models.

These simulations do, however, clearly illustrate the importance of turbulent energy to feeding rates in the plankton, and provide quantified estimates of the relative differences in contact rate that turbulent energy inputs can create in nature. They also provide insights into where in the vertical (wind) and horizontal (tidal) dimensions such increases are most likely to occur. Finally they clearly highlight some of the consequences of fluctuating turbulence levels on the rates of contact between fish larvae and their prey, and indeed, between zooplankton generally and their prey, and of the failure to incorporate knowledge of these effects into analyses of plankton dynamics. These results, and the models from which they are derived, can also aid in the interpretation of in situ larval growth and feeding rates when estimates of prey abundance

and turbulence, or at least measures of the wind or tidal velocity which generate this turbulence, are available.

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Chapter 4

The Effect of Wind in Determining Water Column
Attributes, and its Potential Influence
on the Nature and Fate of Plankton Production

Introduction

Stochastic inputs of external energy can be important regulators of physical characteristics of coastal marine (e. g. Harris et al. 1991) and lacustrine (e. g. Dunstall et al. 1990) environments. For example, variable wind conditions can cause rapid fluctuations in current flow, salinities, and water temperatures (Bohle-Carbonnel 1986; Taggart and Leggett 1987; Rose and Leggett 1988). In some cases these energy inputs to the water column can result in synchronous water mass exchanges in entire bays and inlets (Table 1) along 100's of km of coastline (Platt et al. 1972; Leggett et al. 1984; Rose and Leggett 1988). If these environmental perturbations occur after the spring bloom, they could change a stratified, nonturbulent water column into one that is well-mixed (Frank and Leggett 1982; Harris et al. 1991), more turbulent, and possibly more eutrophic (e. g. Platt et al. 1972; Dunstall et al. 1990a; Harris et al. 1991).

The response of coastal hydrography to wind energy inputs likely has important consequences on biological production processes. For example, the flux of nutrients (e. g. nitrate) into the photic zone, which is strongly controlled by physical processes (Levasseur et al. 1984; Lewis et al. 1986), is one of the principal factors limiting rates of primary production in the surface layer of the sea (Dugdale 1976; Levasseur et al. 1984; Lewis et al. 1986). Field evidence shows that replacement or conversion of a stratified, oligotrophic environment into one that is well-mixed and relatively nutrient-rich can stimulate growth rates of phytoplankton 1 - 3 days later at temperate and boreal latitudes (Iverson et al. 1974; Takahashi et al. 1986; Kiørboe and

Table 1. Geographic regions where episodes of wind-induced water mass exchange or upwelling have been observed. Sites are listed alphabetically by literature reference.

Region	Reference
Izu Peninsula, Japan	Atkinson et al. 1987
Lake Erie, Canada-U.S.	Dunstall et al. 1990
Bryants Cove, Newfoundland	Frank and Leggett 1982; Taggart and Leggett 1987
Adriatic Sea (northeast coast)	Ga íc et al. 1987
Sweden (east coast)	Gidhagen 1987
Western Greece	Lascaratos et al. 1989
Gullmar fjord, Sweden	Lindahl and Perissimotto 1987
Gulf of Lyons	Millot 1979
Sicily (south coast)	Piccioni et al. 1988
Nova Scotia (Atlantic coast)	Platt et al. 1972
Québec (lower north shore)	Rose and Leggett 1988
Gulf of Panama	Schaefer et al. 1958
Newfoundland (east coast)	Schneider and Methven 1988
Lake Ontario	Simons and Schertzer 1988
Trinity Bay, Newfoundland	Yao 1986
Favorite Channel, Alaska	Ziemann et al. 1991

Nielsen 1990). Moreover, the frequency of mixing and stratification events (e. g. storms, upwellings) determines phytoplankton succession (Levasseur et al. 1984), and the proportion of primary production which is either transferred to higher trophic levels or which enters the microbial food loop (LeFèvre and Frontier 1988; Kjørboe and Nielsen 1990).

In this chapter, I present physical oceanographic results from a field study designed to evaluate whether wind-induced coastal water mass exchange in Conception Bay, Newfoundland, Canada, occurs with sufficient frequency and magnitude to supply nutrients to the photic zone. I chose this particular site because interactions between wind and hydrography are common and variable both within and between years (Frank and Leggett 1982; Taggart and Leggett 1987), and, therefore, are likely to have important consequences on the distribution and abundance of plankton.

My objective in this study was, therefore, to investigate hydrographic characteristics of an embayment which is strongly influenced by inputs of wind energy, and to assess whether these inputs can convert a relatively nutrient-poor, nonturbulent environment into one that is nutrient-rich and more turbulent. I describe the frequency and magnitude of wind-induced upwelling during the summer months, the size of the spatial zone influenced by these events, and the relative nutrient status of surface and upwelled water masses. This information could help to explain temporal and spatial patterns in biological variables (e. g. rates of production and distribution of plankton) in Conception Bay, and in other regions (e. g. Table 1) where wind energy

inputs may be important regulators of nutrient supply to the photic zone, and of light conditions experienced by phytoplankton.

Methods

Study site

Conception Bay (≈ 65 by 25 km) is located on the northeast coast of insular Newfoundland. The major axis of the bay is oriented southwest - northeast. The residual circulation pattern in the bay has not been investigated thoroughly, but is presumed to be dominated by exchange with the Labrador Current (Butler 1971). This current flows south along the Labrador and Newfoundland coast (Hachey 1961; Butler 1971). The colder, slower moving ($8.3 \text{ km} \cdot \text{day}^{-1}$; Hachey 1961) inshore portion of the Labrador Current is believed to flow into Conception Bay along the western shore and out of the bay along the eastern shore (Butler 1971). The flow of water carried southward by the Labrador Current varies substantially between years (Hachey 1961), which likely contributes to differences in rates of exchange between shelf waters and those inside bays along the coast.

Conception Bay receives no major riverine inputs of nutrients; its surrounding watershed is sparsely populated ($\approx 75,000$; Statistics Canada 1988), and it supports little agriculture. Wind-generated upwelling and storms are likely to be particularly important processes governing nutrient supply to the surface layer after the spring bloom in Conception Bay, and in the numerous other similar bays along the northeastern coast of Newfoundland (Yao 1986; Schneider and Methven 1988) during the summer months.

Previous studies have shown that wind, as measured at St. John's,

Newfoundland airport (19 km from the centre of Conception Bay), is a significant factor in determining physical and biological characteristics (e. g. water temperatures, current speeds, microzooplankton abundance; coherence squared = 0.4 - 0.7) at a site (Bryants Cove) on the western shore of Conception Bay (Frank and Leggett 1982; Yao 1986; Taggart and Leggett 1987; Taggart and Frank 1988). Tidal energy inputs in this, and neighboring, regions are, in comparison, relatively small (Yao 1986; Taggart and Leggett 1987; Schneider and Methven 1988). Moreover, temperature fluctuations at this site are synchronous with nearshore temperatures at several other sites along at least 700 km of Newfoundland coastline (Leggett et al. 1984; also Schneider and Methven 1988). Consequently fluctuations in physical variables that are recorded in the vicinity of Bryants Cove are likely to broadly represent those along much of the northeast coast of Newfoundland.

Sampling plan

During the summers of 1987 and 1988, current flow and water temperatures were monitored at several locations seaward of Bryants Cove (Fig. 1; Table 2). A sampling frequency of 3 - 4 times per week is necessary to observe short-period fluctuations (2 - 6 days; Yao 1986; Taggart and Leggett 1987; Schneider and Methven 1988) in these physical oceanographic variables. This sampling frequency was accomplished by collecting vertical temperature and nutrient profiles several times per week during the periods July 14 - August 19, 1987 and June 8 - August 13, 1988, and by continuously recording water temperatures, current

speeds and current directions with moored instruments during the periods June 15 - August 15, 1987 and 1988.

Data collection:

(i) Vertical temperature and nutrient profiles.

I obtained vertical temperature profiles along a transect approximately perpendicular to the principal axis of Conception Bay and originating near Bryants Cove (Figure 1). Nearshore stations (< 3.9 km from the western shore of Conception Bay; 90 m bathymetric contour) were spaced at intervals < 2 km apart (Figure 1; Table 2) and those beyond 3.9 km were spaced at 2 km intervals. This distribution was designed to provide greater sampling resolution in the nearshore area where I anticipated the largest fluctuations in abiotic and biotic variables (see Taggart and Leggett 1987).

Temperature at depth was measured by recording the temperature of seawater pumped from fixed depths to the boat deck. Flow rates were ≈ 900 -1000 L/minute, and water transit time (13 - 15 seconds) was sufficiently fast to avoid significant temperature changes during the pumping. (Mean temperature difference [depth = 40 m] between that at the pump outfall, and that recorded simultaneously at depth 40 m by an Aanderaa current meter was < 0.4 C [N = 20, SD = 0.25 C]. All temperature pairs were recorded between June 17 and August 12, 1988.) The pumping system is described by Taggart and Leggett (1984), although I replaced the pressure transducer at the hose intake, which they used for depth determination, with a boat-mounted meter wheel. A 75 kg weight held the hose intake at depth.

Temperatures were recorded at 5 m depth intervals within the

Figure 1. Map of Conception Bay showing location of sampling transect, orientation of wind and current velocity vectors and latitude and longitude coordinates of sampling stations. The longshore positive vector is oriented parallel to the principal axis of the bay, and takes on positive values when winds are directed out of the bay. The cross-shore positive vector is oriented perpendicular to the principal axis of the bay, and is directed away from the western shore. Inset: Map of insular Newfoundland. Wind speeds and directions were measured at St. John's.

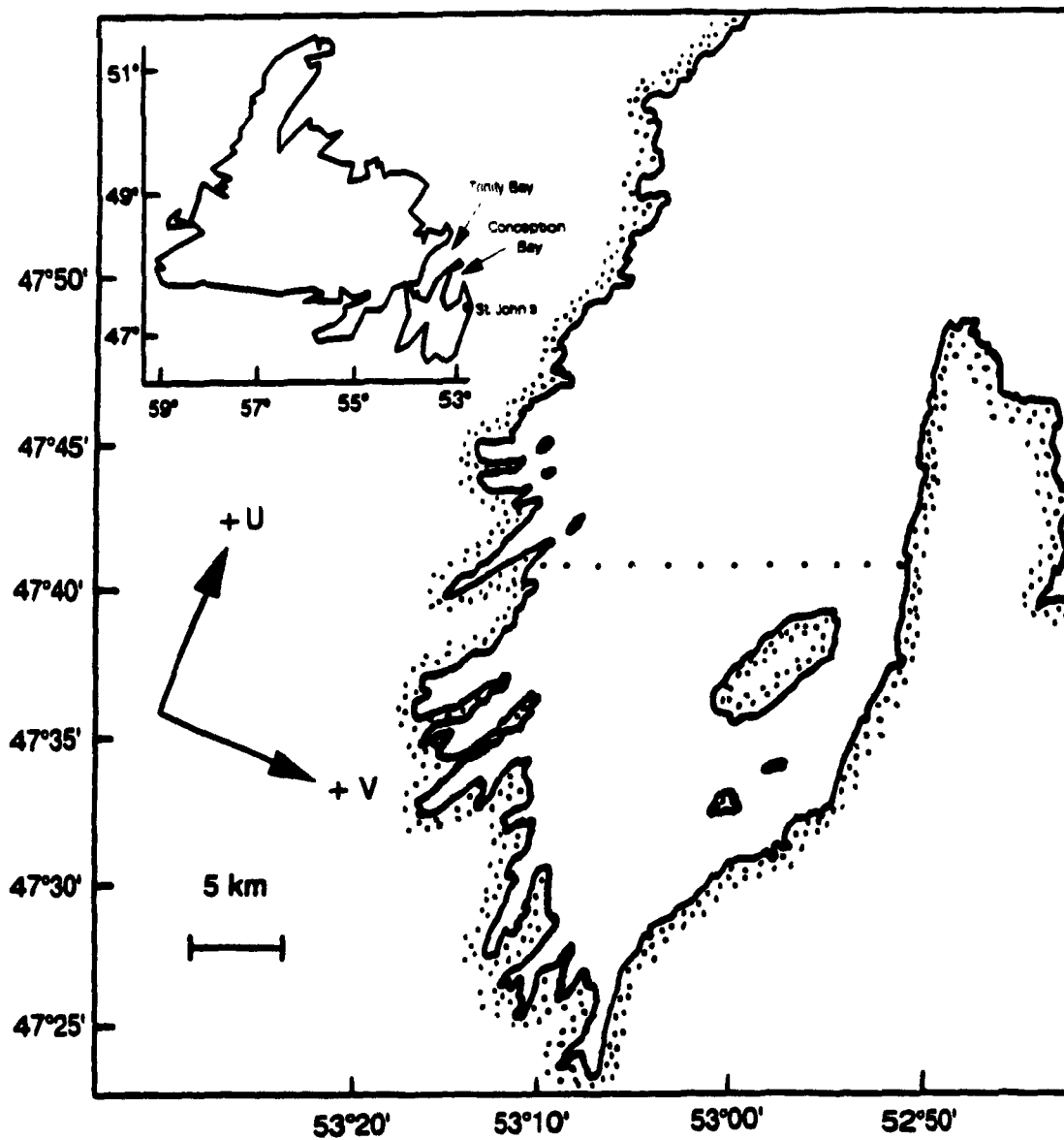


Table 2. Latitude and longitude coordinates of sampling stations employed during the summers of 1987 and 1988.

Station No.	Latitude	Longitude
1	47° 40' 88"	53° 10' 30"
2	47° 40' 78"	53° 9' 48"
3	47° 40' 68"	53° 8' 3"
4	47° 40' 65"	53° 6' 40"
5	47° 40' 62"	53° 4' 55"
6	47° 40' 59"	53° 2' 90"
7	47° 40' 57"	53° 1' 20"
8	47° 40' 56"	52° 59' 35"
9	47° 40' 54"	52° 57' 55"
10	47° 40' 53"	52° 56' 60"
11	47° 40' 52"	53° 54' 00"
12	47° 40' 51"	52° 52' 28"

surface mixed layer and the thermocline. The sampling interval was increased to 10 m below the thermocline to a maximum depth of 50 m. On all but five occasions, transects were restricted to the western 10 km of Conception Bay. I extended the transect to include the entire cross-bay distance (≈ 22 km) on three occasions in 1987 and two occasions in 1988.

Pumped water samples were retained to determine nitrate concentrations in surface and subsurface water. Vertical nitrate profiles were obtained in 1988 at approximately 3-week intervals. On each date, all nitrate samples were taken at a single station at which the vertical temperature profile indicated a strongly stratified water mass. Nutrient samples were drawn from depths identical to those from which water temperatures were recorded. This facilitated estimation of surface, thermocline and subthermocline nitrate concentrations.

Water samples used for nitrate determinations were placed in darkened containers and held in closed refrigerated coolers until the research vessel returned to shore (maximum holding period ≈ 7 h). Samples were then immediately filtered through Whatman GF/C filters and frozen at -20°C . Frozen samples were held for no more than 4 weeks before being assayed. Analytical procedures followed those described by Strickland and Parsons (1968).

(ii) Sea-surface temperature measurements.

On each sampling day, sea-surface temperature (SST) was recorded continuously as the boat travelled between sampling stations. Temperatures were recorded at 10 and 3 s intervals in 1987 and 1988,

respectively, using a digital temperature logger. During the transect survey, researchers noted station locations and the times at which the research vessel passed them. The time scale of the temperature observations was converted to a distance scale by noting and interpolating the cruise time between stations which were located by Loran C and radar fixes. These data were used to quantify in real-time the spatial extent of upwelling in the offshore direction, and how the size of the upwelling zone varied with wind conditions.

(iii) Depth of photic zone.

On each sampling date, and at each station, water column transparency was measured with a 40 cm Secchi disk. These measures were used to estimate the water column extinction coefficient, k ($k = 1.7/\text{Secchi depth}$; Parsons et al. 1977), and the depth of the photic zone ($Z_{eu} = 4.605/k$; Parsons et al. 1977). All estimates of photic zone depth were derived from transparency determinations made between 07:00 and 19:00 h. Light intensity (400 - 700 nm spectral response; $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was recorded on the boat deck with a Biospherical Instruments QSR-240 solar reference hemispherical light sensor. These measurements were used with estimates of the extinction coefficient, k , to calculate light levels at depth.

(iv) Wind Time Series.

Hourly records of wind speed and direction were obtained from the Atmospheric Environment Service for the meteorological station located at St. John's Airport, St. John's, Newfoundland. The raw wind records

were resolved into longshore and cross-shore components of wind velocity according to:

$$W_{Long} = -W \cdot \cos(A - 20); \text{ and}$$

$$W_{Cross} = -W \cdot \sin(A - 20)$$

where W is the unresolved wind speed and A is the angle of the wind direction relative to true north (Schneider and Methven 1988). The principle axis of Conception Bay was set at 20° . The longshore component was oriented approximately parallel to the major axis of Conception Bay; this component was designated to have positive values (> 0) for winds originating approximately from the southwest. The cross-shore component was oriented perpendicular to the major axis of the bay; this component was designated to have positive values (> 0) when winds originate from a northwesterly direction (Figure 1). In Conception Bay, Trinity Bay and along the east coast of Newfoundland south of St. John's, the longshore wind component is more influential than the cross-shore component in determining nearshore water temperatures (Taggart and Leggett 1987; Schneider and Methven 1988), current speed (Yao 1986; Taggart and Leggett 1987), and fluctuations in zooplankton size and community structure (Frank and Leggett 1982, 1986; Taggart and Leggett 1987; Taggart and Frank 1988). Therefore, in most analyses I use the longshore wind component as a measure of wind energy input.

Hourly wind velocity components were smoothed with an equally-weighted 4-point moving average. Wind velocities extracted from this series at 4-hour intervals were used in time series analyses to assess relationships between wind conditions and hydrographic fluctuations (see

Oceanographic Time Series below).

(v) Oceanographic Time Series.

An array of Aanderaa current meters (depth 6, 25, 40, 56 m) and Ryan temperature recorders (depth 15 and 32 m) was deployed at the second station (2.2 km from shore; water column depth = 60 m) seaward of Bryants Cove on our transect (Fig. 1). A similar array was deployed at the same site in 1987 except that current meters were moored at depths 7 and 56 m, and temperature recorders were moored at two intermediate depths (25 and 40 m). The Aanderaa instruments recorded water temperature, salinity, and current speed and direction. Instruments were deployed at a site and at depths where the results of previous studies (Frank and Leggett 1985; Taggart and Leggett 1987) had indicated that I could expect surface, thermocline, and subthermocline variations in the recorded variables.

Current meters recorded data at 20 and 15 min intervals in 1987 and 1988, respectively. Temperature recorders collected data at 20 minute intervals in both years. Values extracted at 4-hour intervals from these series were used in subsequent data analyses.

Current directions were rotated 180° to be consistent with the orientation of wind vectors (see above). They were then decomposed into U (longshore; positive northeast) and V (cross-shore; positive northwest) components resolved around the major axis of Conception Bay (20° ; Figure 1).

I conducted exploratory analyses of the time series data to identify major anomalies in the records. This involved, for example,

scrutiny of the raw time series plots of temperature or current velocities recorded at various depths. These preliminary analyses enabled a visual identification of the occurrence and duration of probable upwelling events. These exploratory analyses also helped in locating vertical displacements of the nutricline, and to identify occasions when countercurrent flow between water masses occurred.

Time series of physical oceanographic variables commonly show lagged responses to other oceanographic and meteorological variables measured at adjacent depths or sites (Taggart and Leggett 1987; Rose and Leggett 1988). I used cross-correlation analyses (Chatfield 1989) to quantify the time required for water temperatures and longshore and cross-shore current components at different depths to respond to changes in wind condition.

I also analysed time series records spectrally (Chatfield 1989; SAS Proc Spectra, SAS 1985) to identify those frequencies which contributed maximally to the total variance in the data series (Chatfield 1989). Raw spectral estimates from periodograms were smoothed using a triangular-shaped smoothing window (18 degrees of freedom; $n = 9$, Thompson 1979). Power spectra are presented in the variance-conserving convention, in which the area under the curve is proportional to the total variance in the time series (Platt and Denman 1975).

All time series were seasonally detrended using linear regression prior to cross-correlational or spectral analyses (Chatfield 1989).

Results

(i) Winds

The frequency distributions of longshore wind velocities differed significantly between 1987 and 1988 (Kolmogorov-Smirnov test; $P < 0.001$). Longshore wind velocities and the frequency of longshore positive winds were generally higher in 1988 than in 1987 (Fig. 2).

Visual inspection and spectral analyses of the time series of the longshore wind components for 1987 and 1988 revealed that the 1987 series was more variable. Variance in longshore wind velocities was also concentrated at longer periods in 1987 (peaks at periods of 4 and 10 days) than in 1988 (peaks at periods of 1.6 and 2 - 4 days; Fig. 2).

(ii) Temperatures and nitrate concentration

Variability in wind stress within and between years was associated with large and rapid fluctuations in hydrographic conditions along the sampling transect (Fig. 3-5). The surface temperature evidence of spatial temperature variability was diverse. Some SST - distance plots were approximately linear (Fig. 3: July 17/87; Fig. 4: June 23/88, July 12/88), while others exhibited a stepped relationship between temperature and distance (Fig. 3: August 6/87, Fig. 4: June 4/88, July 18/88). Most of the surface temperature variability was confined to within 4 km of shore (Fig. 5), where temperatures tended to be lower (Fig. 3-5), and temperature - distance gradients steepest (Fig. 3-4). When the sampling transect was extended to include the entire width of Conception Bay, surface temperatures were consistently lower and more variable on the western half of the Bay (Fig. 6).

Horizontal variations in sea surface temperature were accompanied by large variations in the vertical position of thermocline and sub-

Figure 2. Time series of longshore wind velocities during the summers of 1987 and 1988. Frequency distributions of longshore wind velocities and variance-conserving power spectra are shown in lower panels.

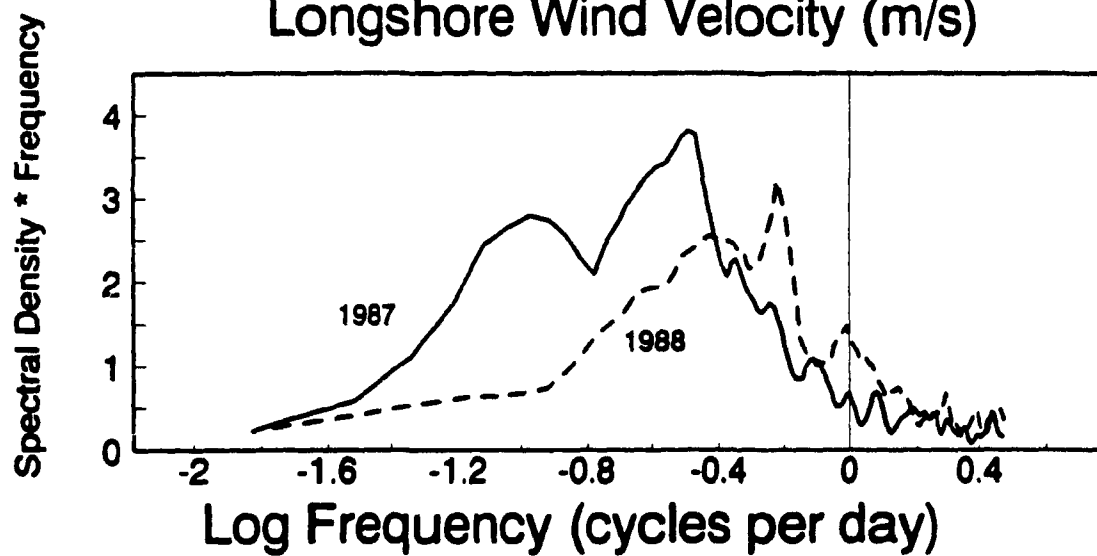
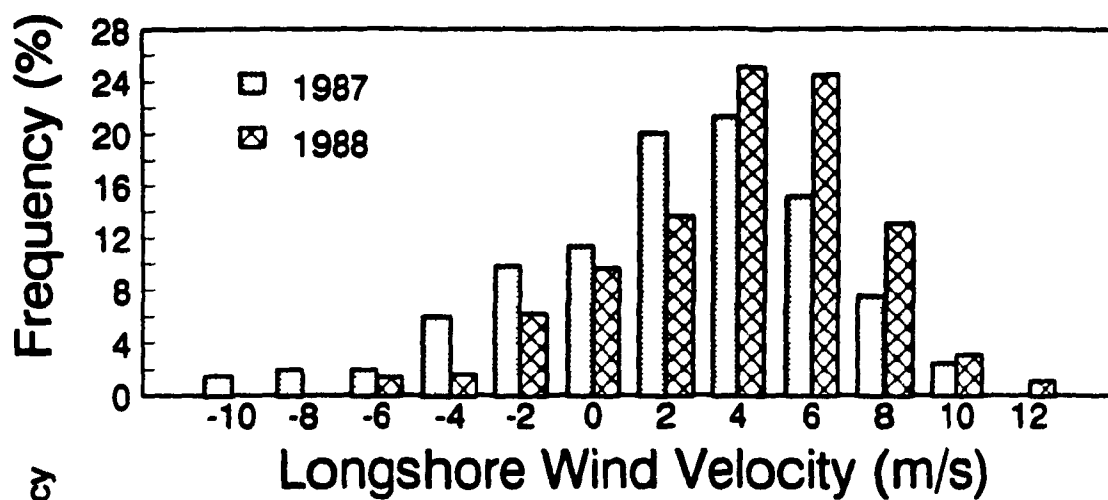
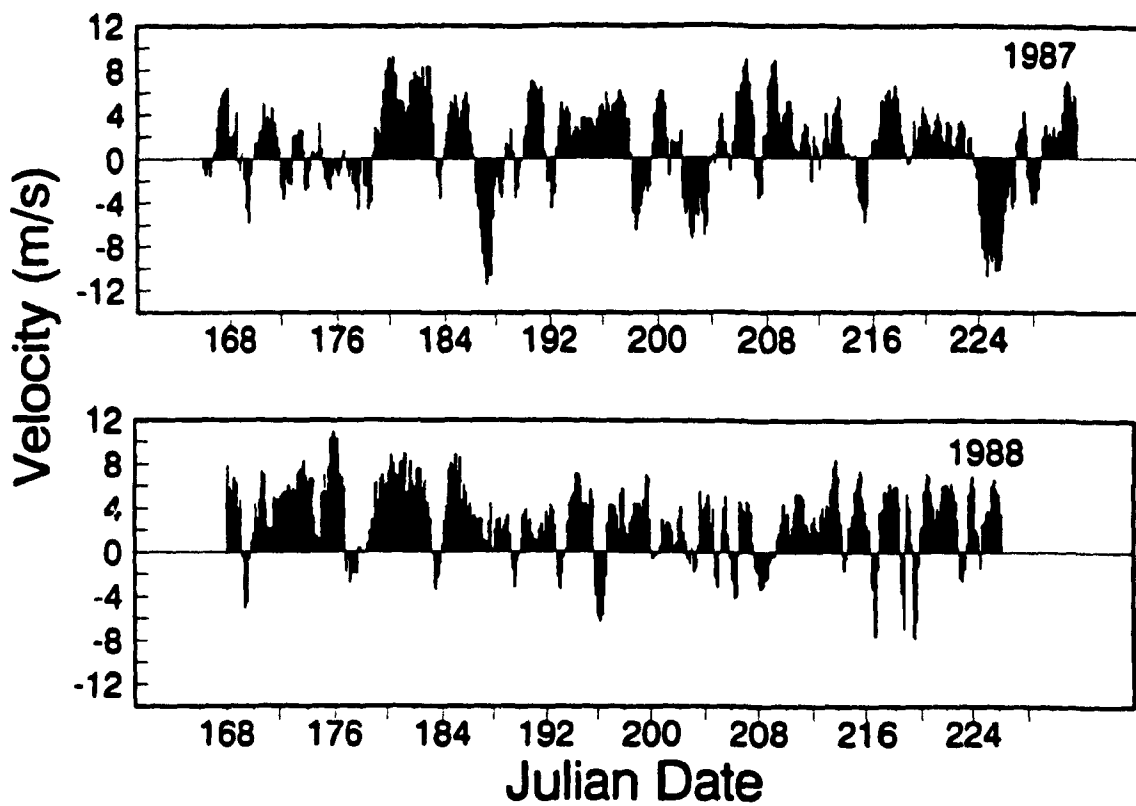


Figure 3. Sea-surface temperatures measured in 1987 at 10 second intervals along the transect shown in Figure 1. Note that temperatures were recorded at only 8 sites on July 23.

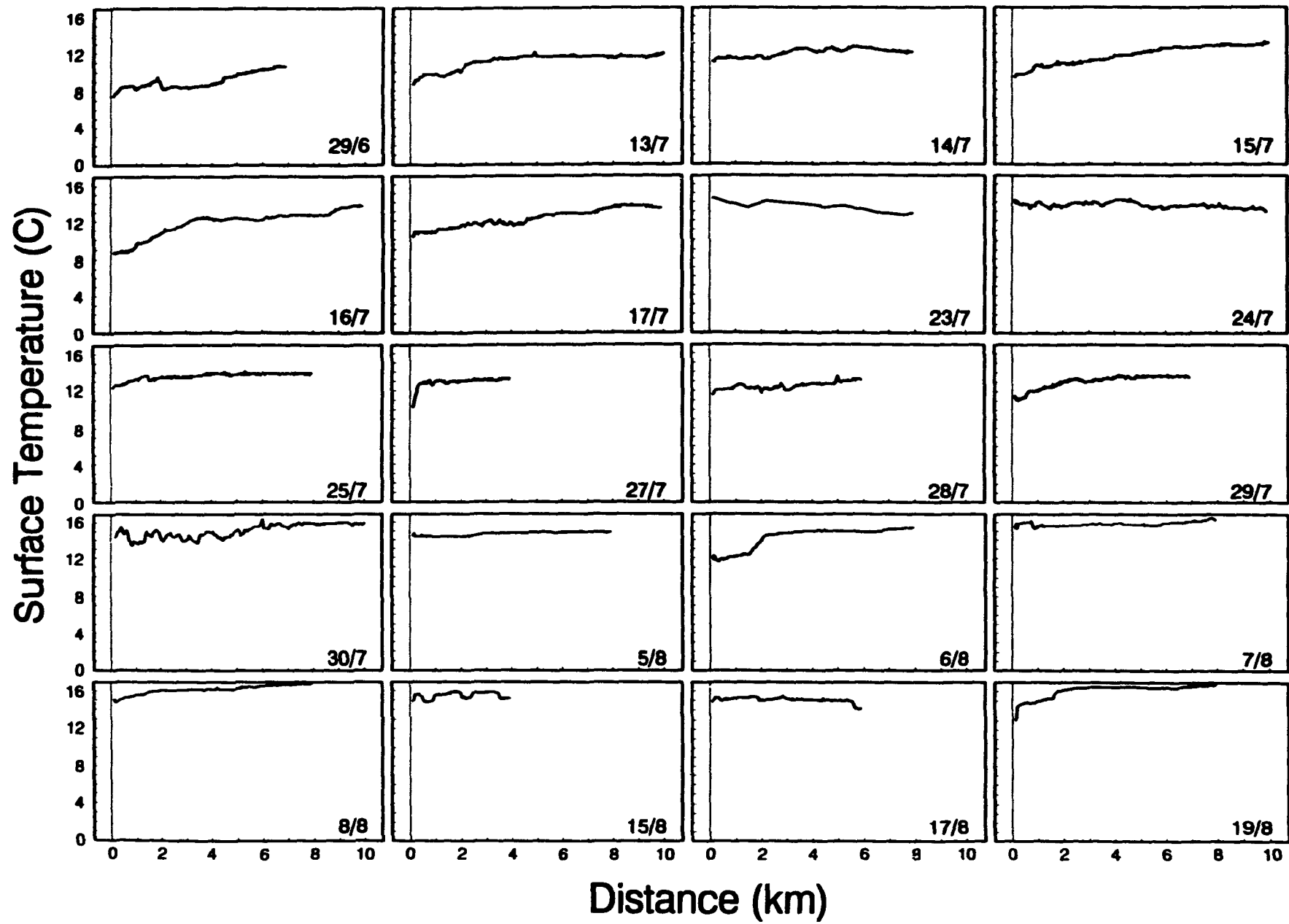
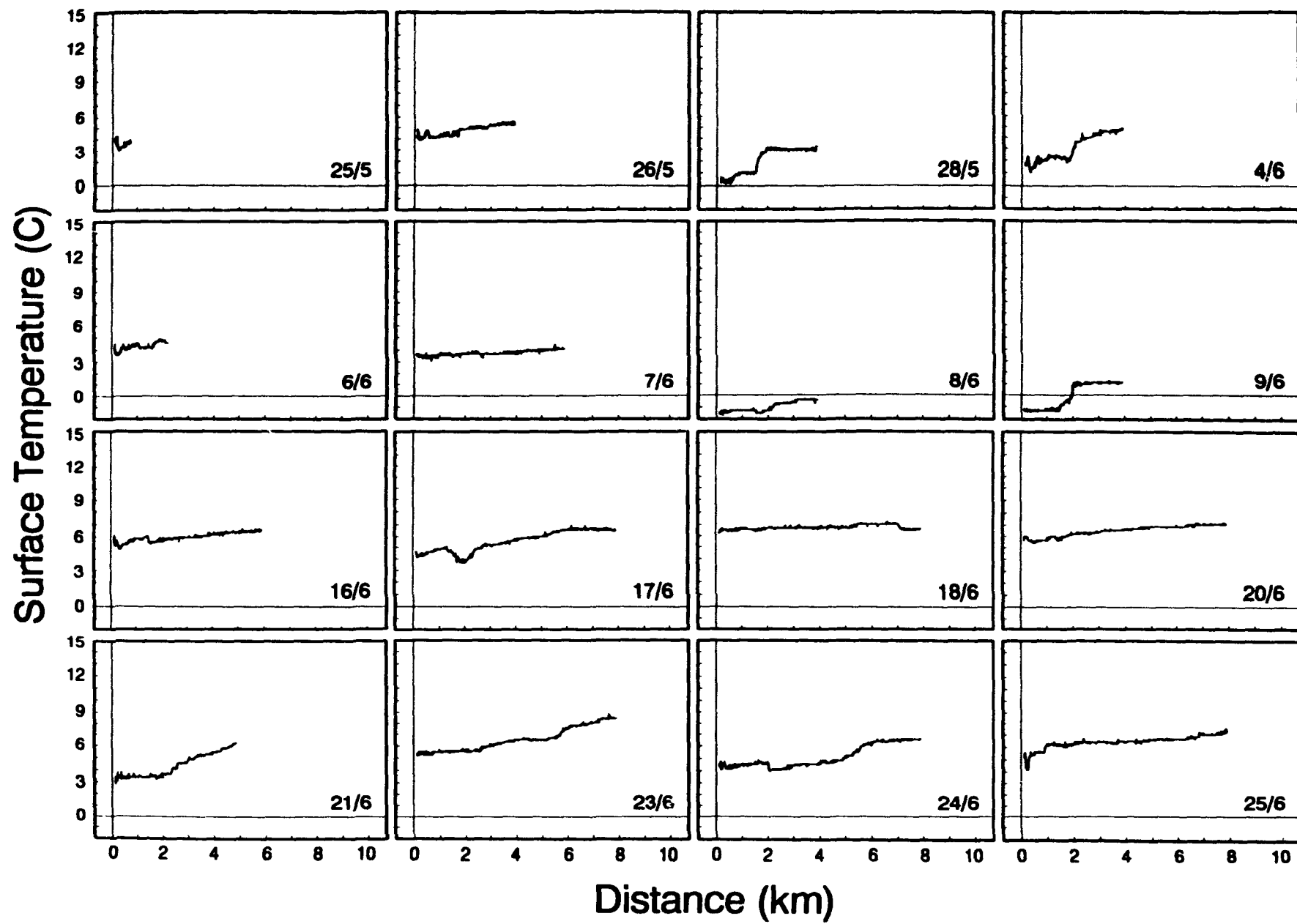
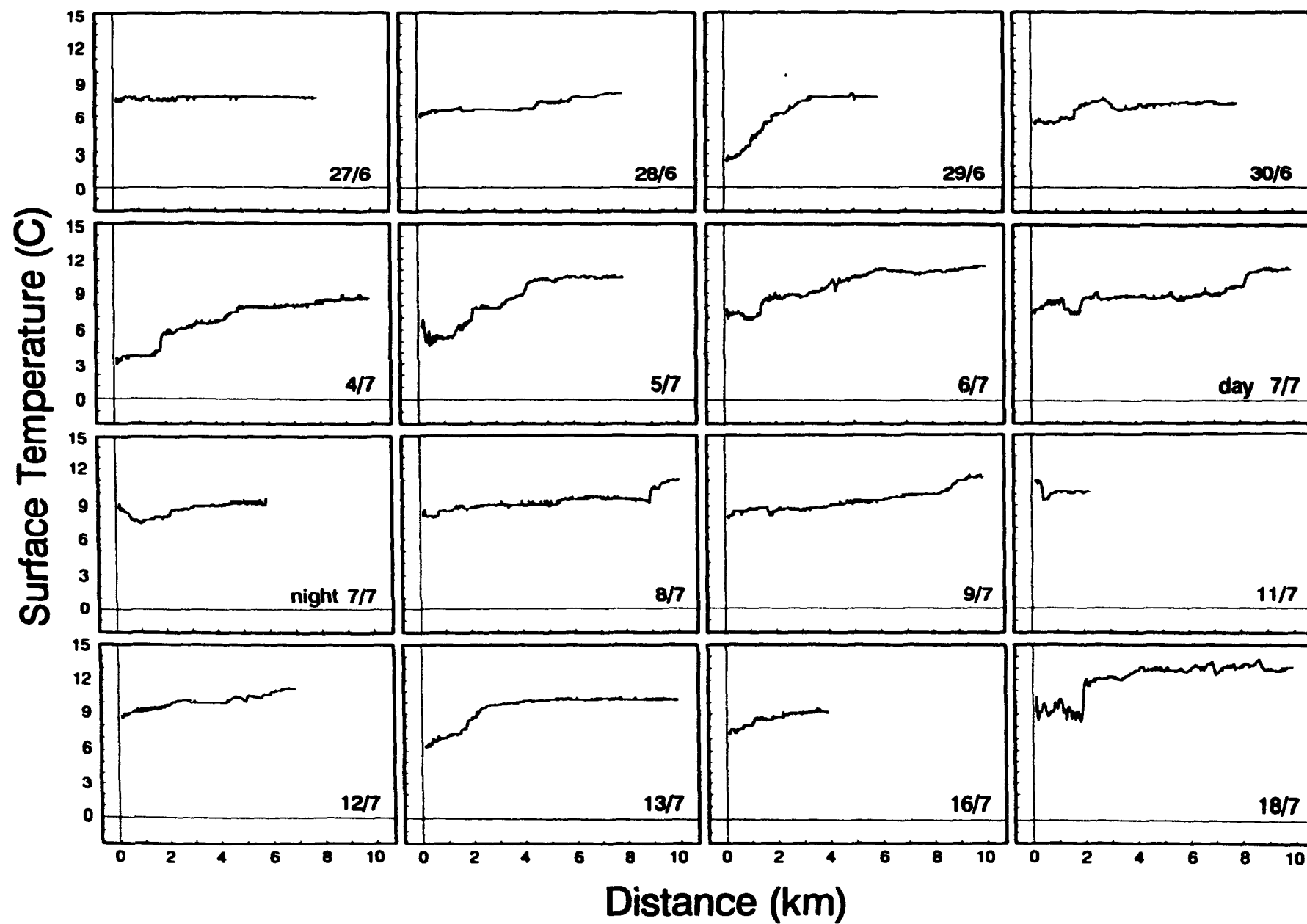


Figure 4. Sea-surface temperatures measured in 1988 at 3 second intervals along the transect shown in Figure 1. Note that the range in temperature (17° C) is identical to that for 1987, but is shifted to lower values in 1988.





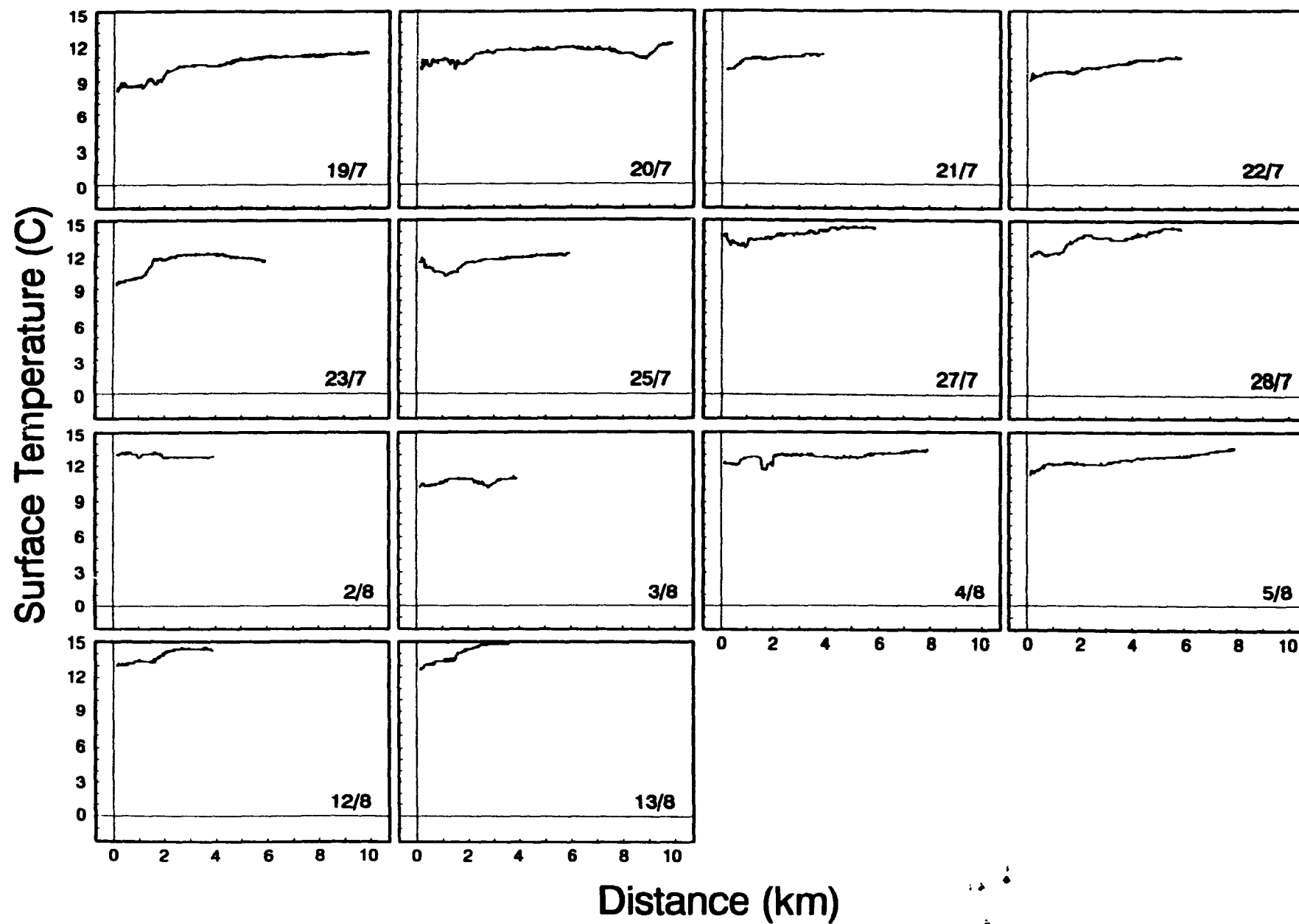


Figure 5. A. Seasonal variation in sea -surface temperatures measured at transect stations during 1988. The equation for the regression line is $SST = 0.0182 \cdot GDD + 0.580$ ($R^2 = 0.77$; $N = 339$) where GDD is the cumulative number of growing degree days $> 5^\circ C$ starting on May 1, 1988.

B. Sea-surface temperature variation relative to distance from shore. Sea surface temperatures shown here are the residuals from the regression relationship presented in Fig. 5A.

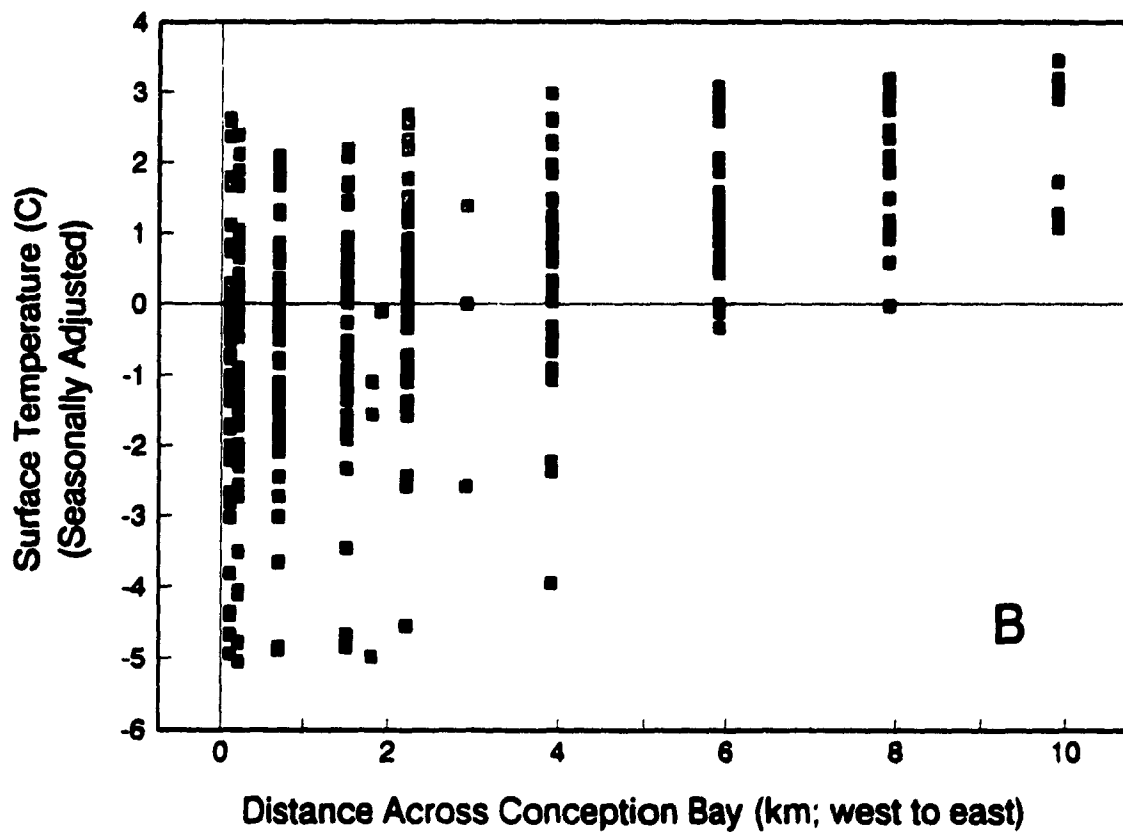
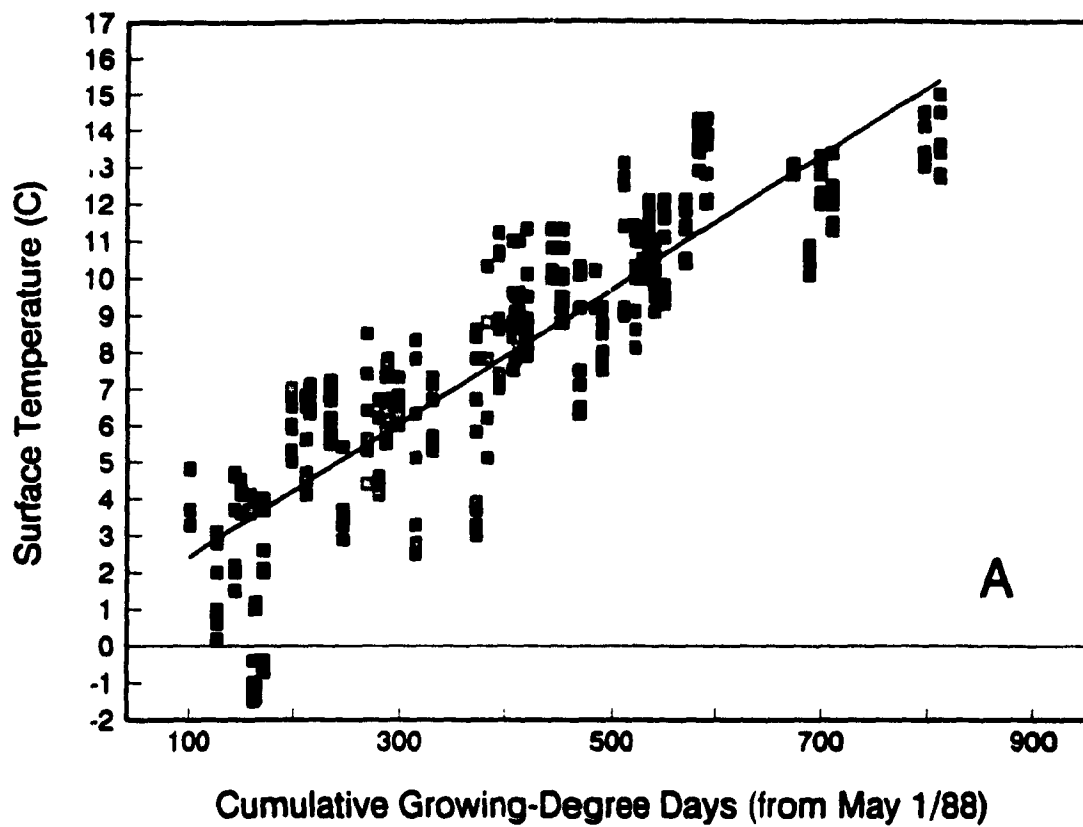
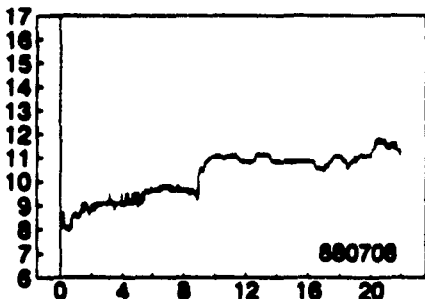
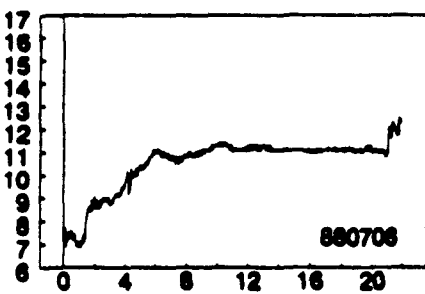
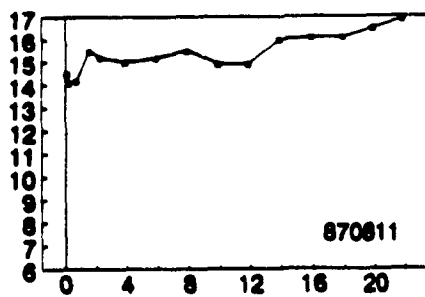
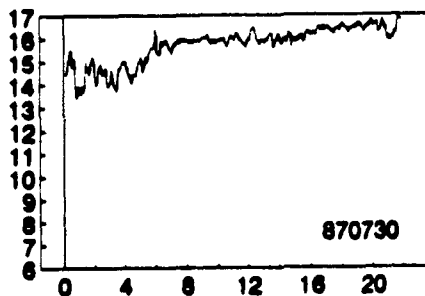
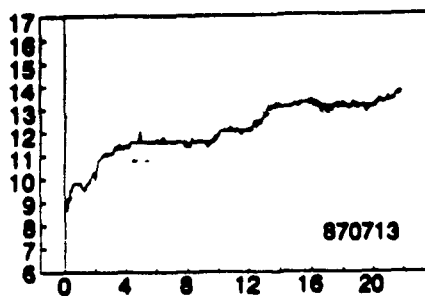
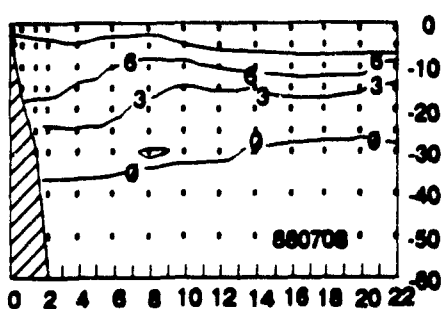
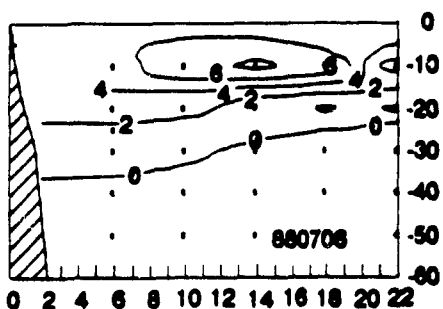
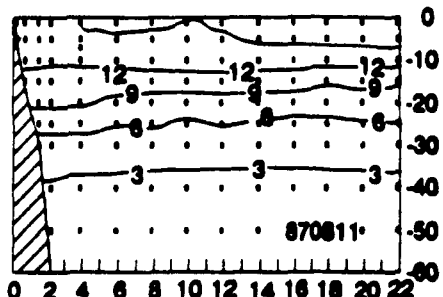
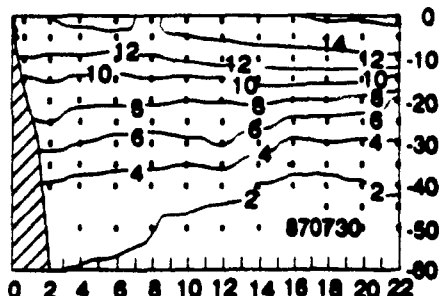
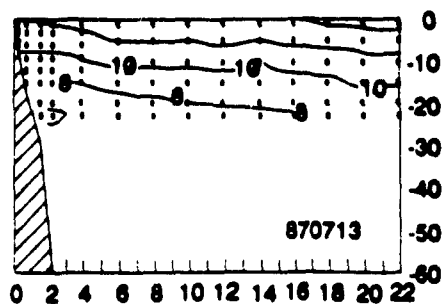


Figure 6. Left column: Sea surface temperatures recorded continuously on five occasions across the entire width of Conception Bay. (Temperatures on August 11, 1987 were measured at spot locations corresponding to hydrographic stations listed in Table 2). Right column: Isotherms across Conception Bay. Note warmer water at surface on eastern side of the bay and sloping isotherms in 1987. Isotherms are spread farther apart on the western side of the bay in 1988.

Surface Temperature (C)



Distance (km)



Distance (km)

Depth (m)

thermocline water masses (Fig. 7). Under stratified conditions, the thermocline, at a station located 22 km offshore, occurred at a depth of 20 - 30 m (Fig. 8, 9). This depth also coincided with the nutricline (Fig. 8), and was typically above the mean depth (35 m; $N = 149$; $SD = 8.2$) of the 1% light level, where light intensity was $\approx 7 \mu E \cdot m^{-2} \cdot s^{-1}$ (median of all measurements of incident light intensity = $737.4 \mu E \cdot m^{-2} \cdot s^{-1}$; $N = 148$). Under stratified conditions, the light intensity at the nutricline (25 m) averaged $\approx 3\%$ of the incoming light intensity, or $21 \mu E \cdot m^{-2} \cdot s^{-1}$ (calculation employed the mean extinction coefficient of $0.139 m^{-1}$).

When coastal waters were cold and well mixed, indicating upwelling (e. g. Fig. 9: June 7 - 8/88; June 18 - June 23/88; June 27 - July 4/88), the thermocline and nutricline were displaced upwards by as much as 25 m, although most thermocline displacements were 10 - 15 m. These thermocline and nutricline movements elevated dissolved nitrate levels by 2 - 3 fold (from 1 - 2 μM to 4 - 5 μM) at a depth of 12.5 m (Fig. 8, 9), where light intensities were $\approx 18\%$ of incoming values ($\approx 130 \mu E \cdot m^{-2} \cdot s^{-1}$). Phytoplankton cells normally resident in nutricline water would therefore be exposed to an increase in light intensity of approximately 6-fold under upwelling conditions. In addition, phytoplankton normally resident in the surface mixed layer would become exposed to increased levels of nitrate and other nutrients because of mixing between water masses during upwelling/downwelling.

Time series of water temperatures recorded continuously by surface-moored Aanderaa current meters (Fig. 10), revealed 7 occasions in 1987 and 9 in 1988 when water temperatures declined by more than 2.5°

Figure 7. Temperature sections in the western portion of Conception Bay measured on sampling dates in 1988.

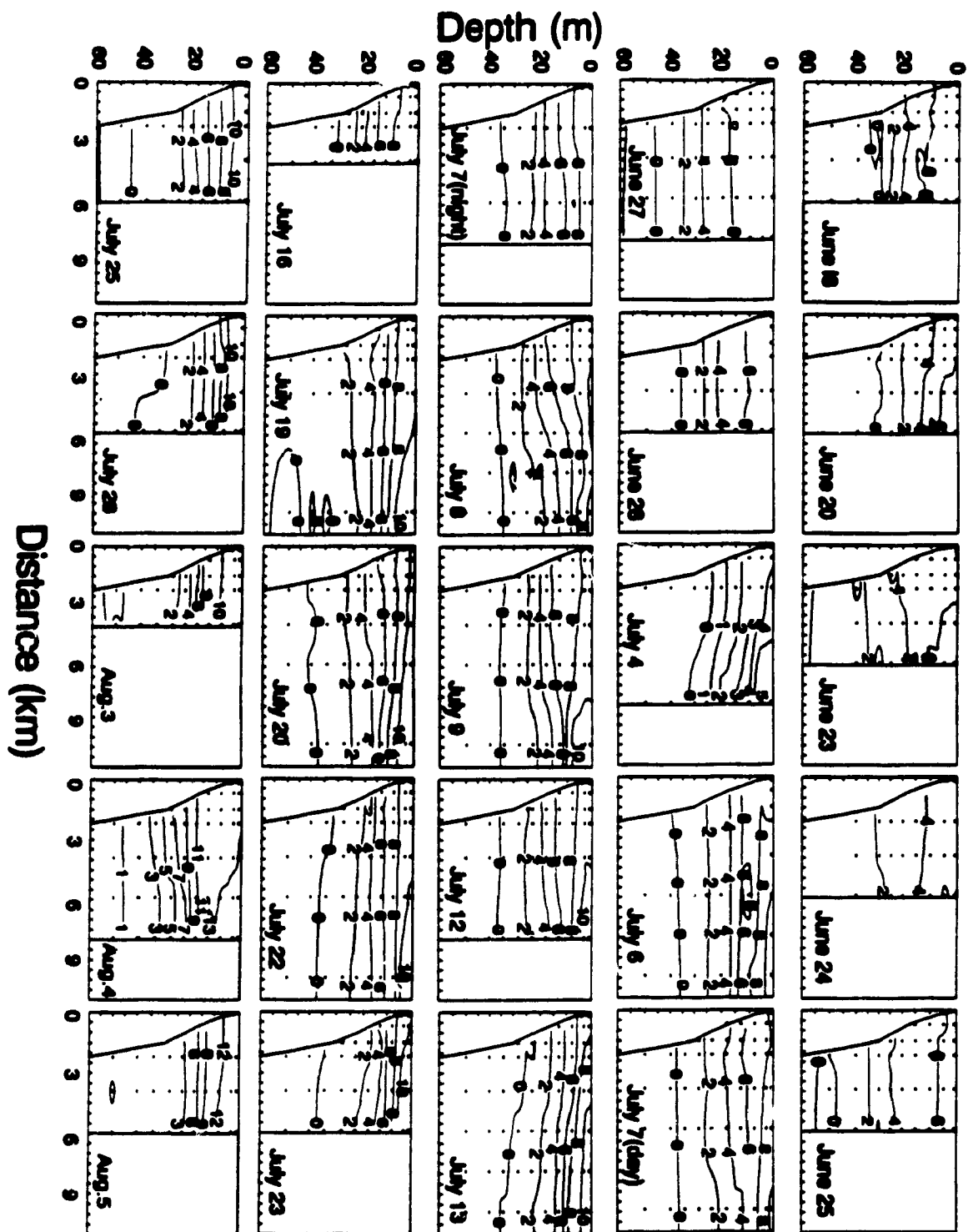


Figure 8. Vertical profiles of temperature (solid line) and nitrate concentration (dashed line) during 1988. Note that the vertical scales for June 7 and July 4 differ from those for the remaining dates. Nitrate levels in the nutricline (20 - 30 m) are $\approx 50\%$ of those in deep (150 m) water. All profiles were obtained in stratified water 2 - 4 km from shore.

Temperature (C)

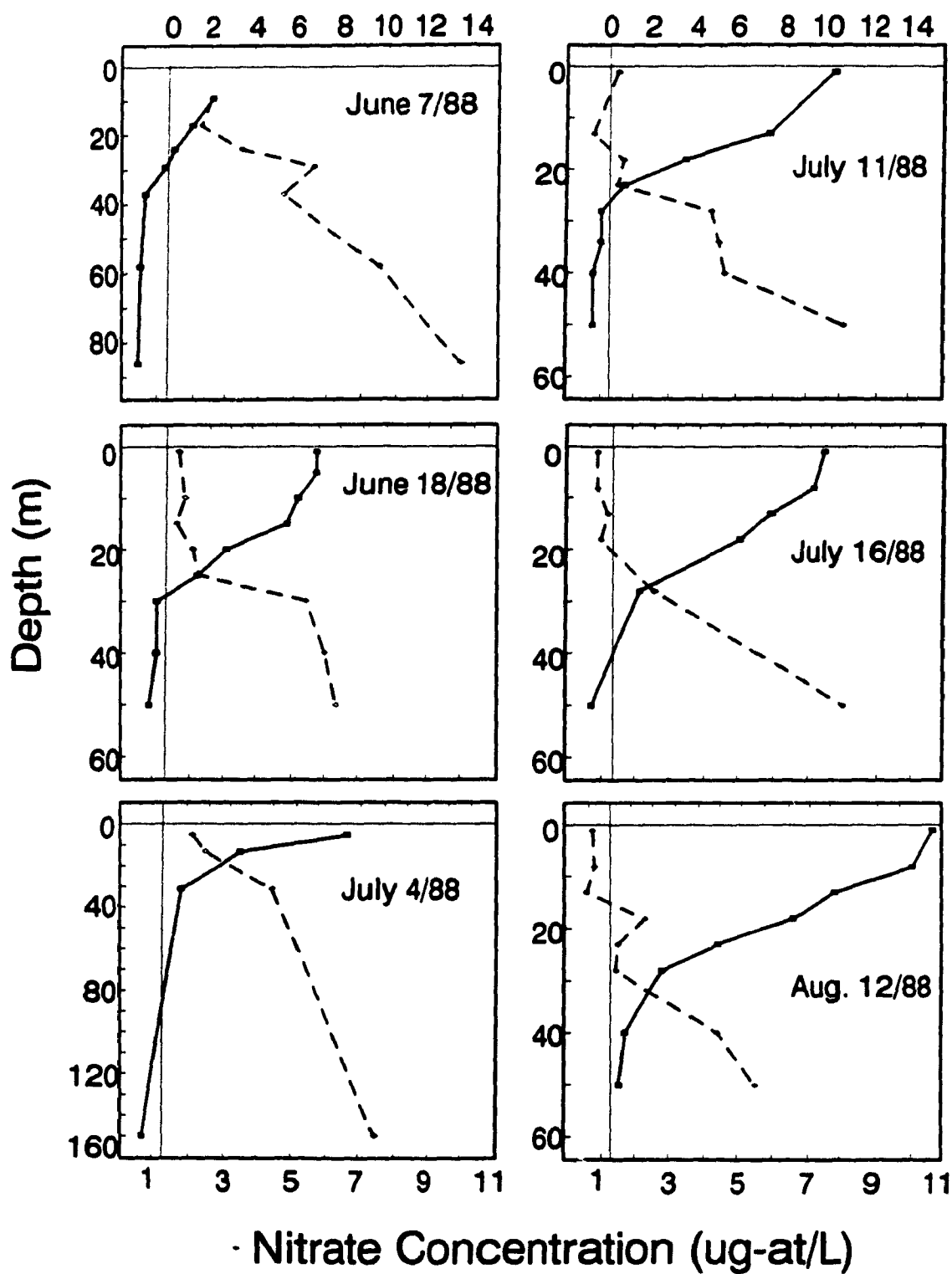


Figure 9. Temperature profiles collected at a Station 2 (2.2 km from shore; Fig. 1) during the summer of 1988. Arrows indicate vertical movements of the thermocline and nutricline. See Figure 8 for nutricline depths.

Temperature (C)

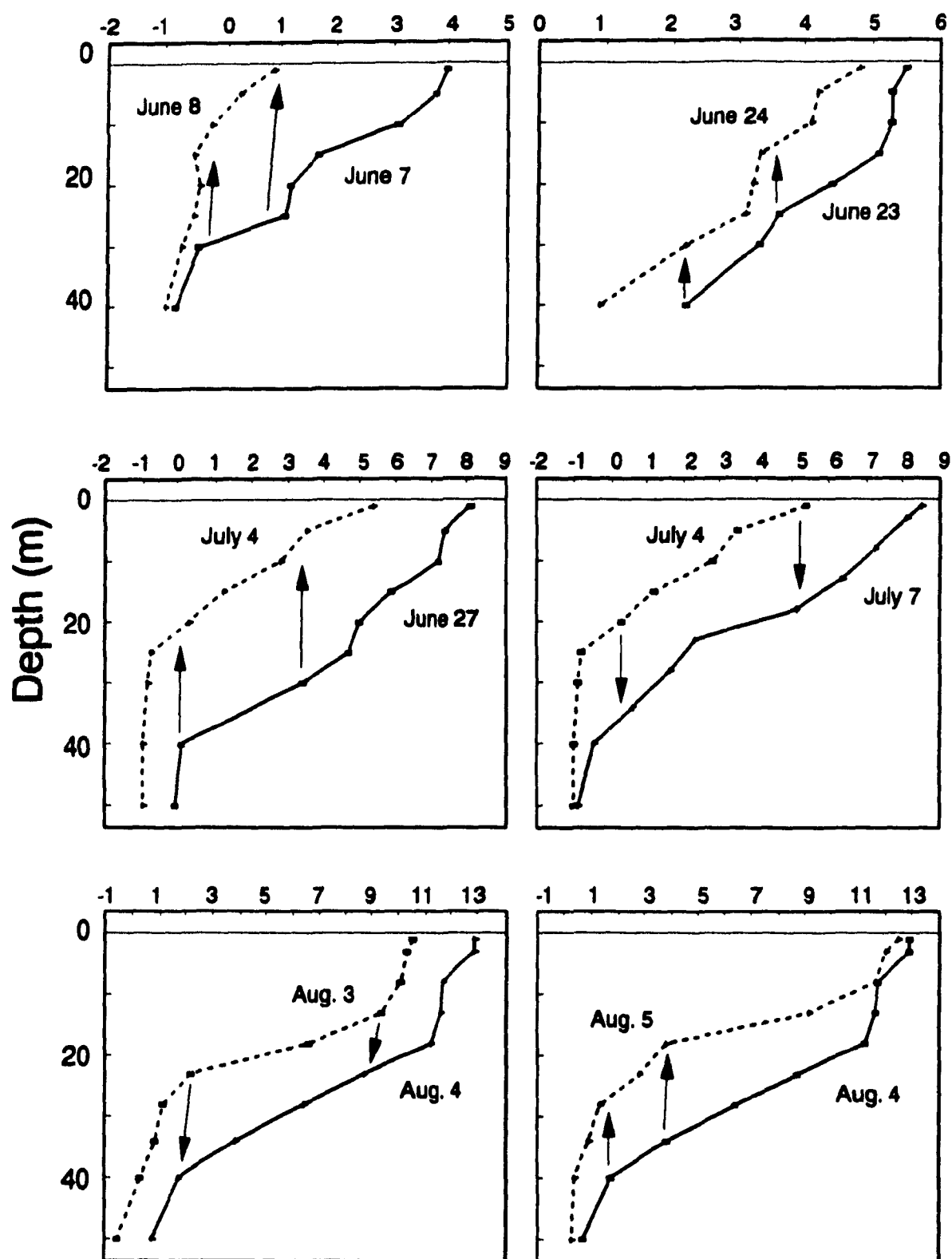
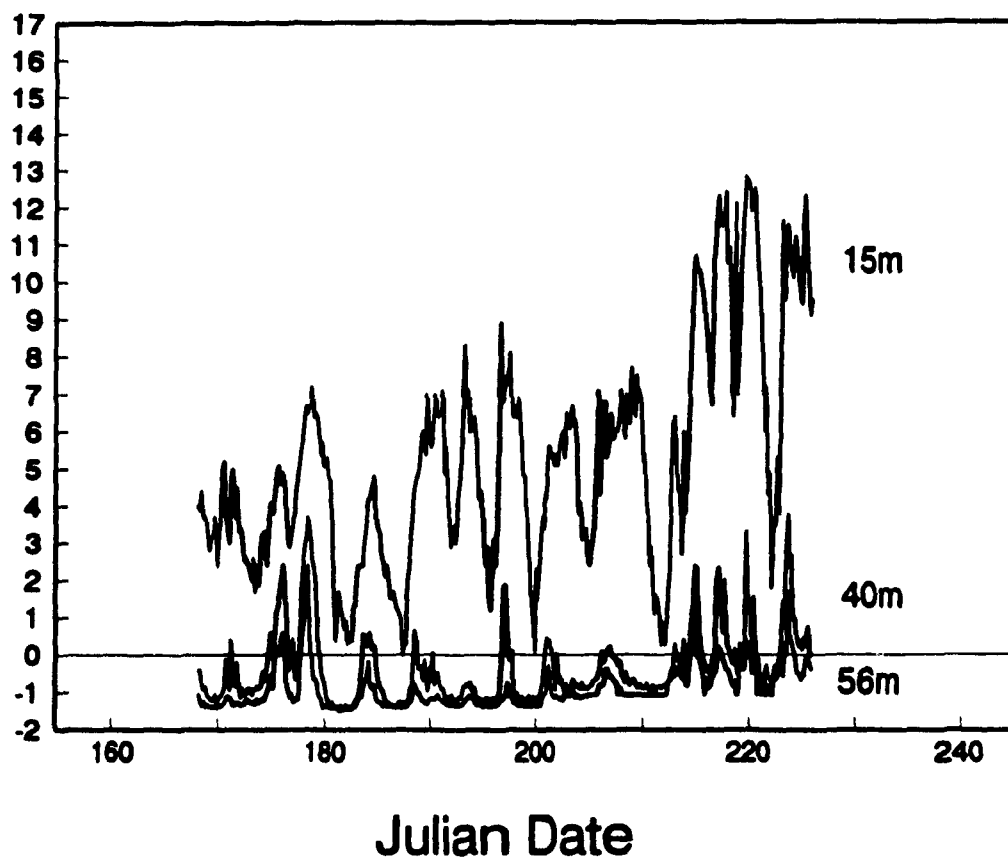
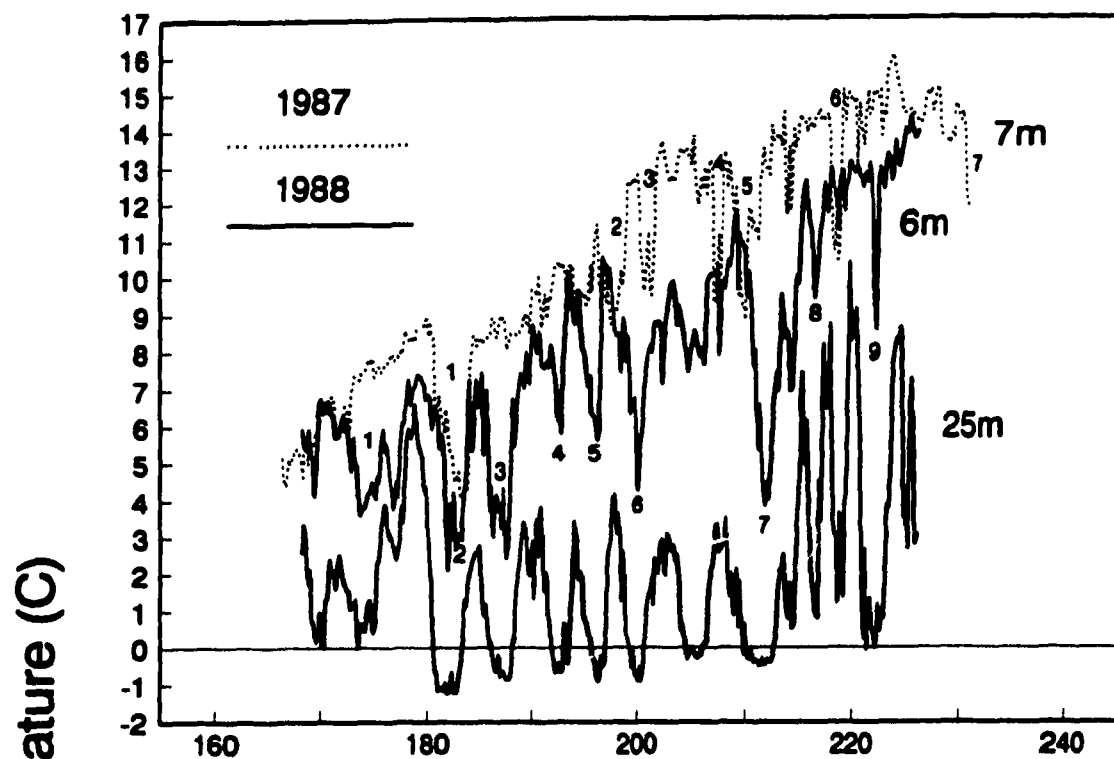


Figure 10 Time series of water temperatures recorded at depth 6, 15, 25, 40 and 56 m in 1988 at Station 2 (2.2 km from shore; Fig. 1). Also shown is the time series of water temperatures recorded at depth 7 m at the same site in 1987 (dashed line top panel).



C within 24 hours. This corresponds to an upwelling frequency of 1 moderately-sized event per 7.5 days. Upwelled, nutrient-rich water remained higher in the photic zone for 2 - 3 days during some upwelling events (e. g. June 29 - July 2; July 4 - 6; Fig. 10). On other occasions, upwelling events persisted for more than 24 hours (e. g. August 3, 4 and 5; Fig. 10). Consequently, the magnitude of temperature decline and the duration of individual cold-water episodes varied within years. Moreover, such episodes were more common in 1988 than in 1987

An approximate measure of the amount of time that cold water appeared near the surface in each year can be obtained by summing the durations of each cold water event, and then expressing this summation as a percentage of the entire sampling period (1987: 66 days; 1988: 59 days). According to this measure, cold water appeared at the surface 23 % and 55 % of the time in 1987 and 1988, respectively. However these values should only be considered approximate because in many cases, temperatures remained low at the surface for only 1 day, but continued to be low for longer durations in deeper water. For example, event no 9 in 1988 lasted only 1 day at 6 m but lasted $\approx$ 3.5 days at 25 m. Similar differences in duration of temperature decline between depths are also obvious for events 4 and 5 in 1988 (Fig. 10).

Overall, the frequency of upwelling episodes, as estimated visually from the temperature time series, was broadly consistent with the results of spectral analyses of these two series (Fig. 11). Temperatures recorded at 6 m in 1988 had spectral peaks at periods of 2.4 and 6.3 days; variance was also high at longer periods (6.3 - 10 days). The spectrum for temperatures recorded at a similar depth (7 m)

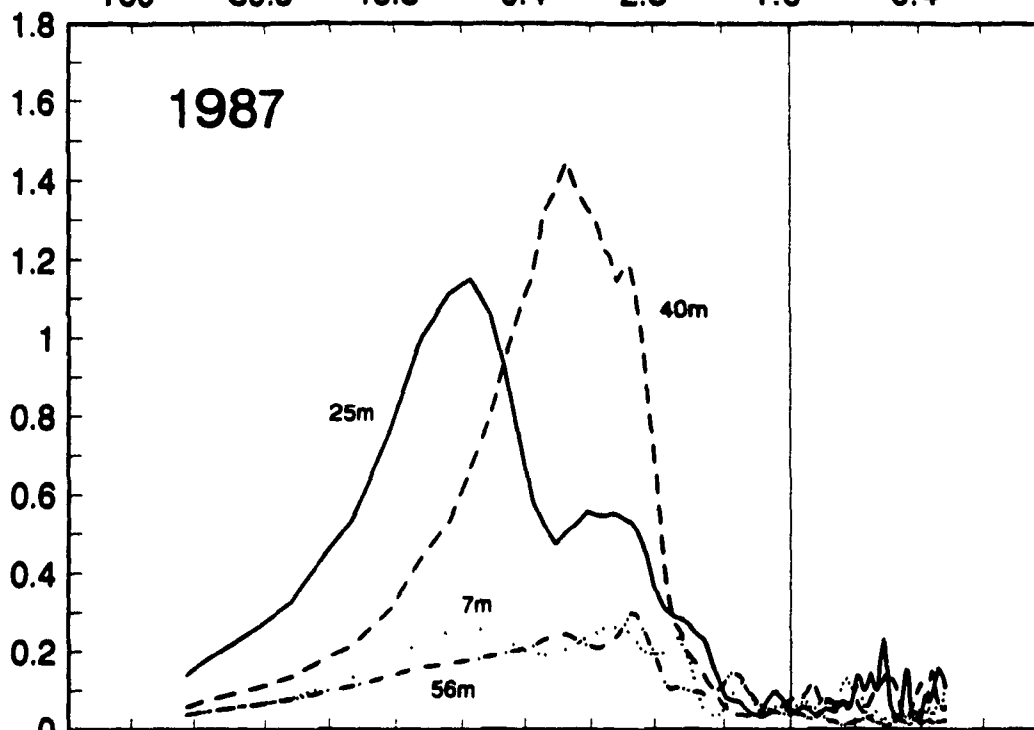
Figure 11. Power spectra for temperatures recorded at Station 2 (2.2 km from shore; Fig. 1) in 1987 and 1988.

Period (days)

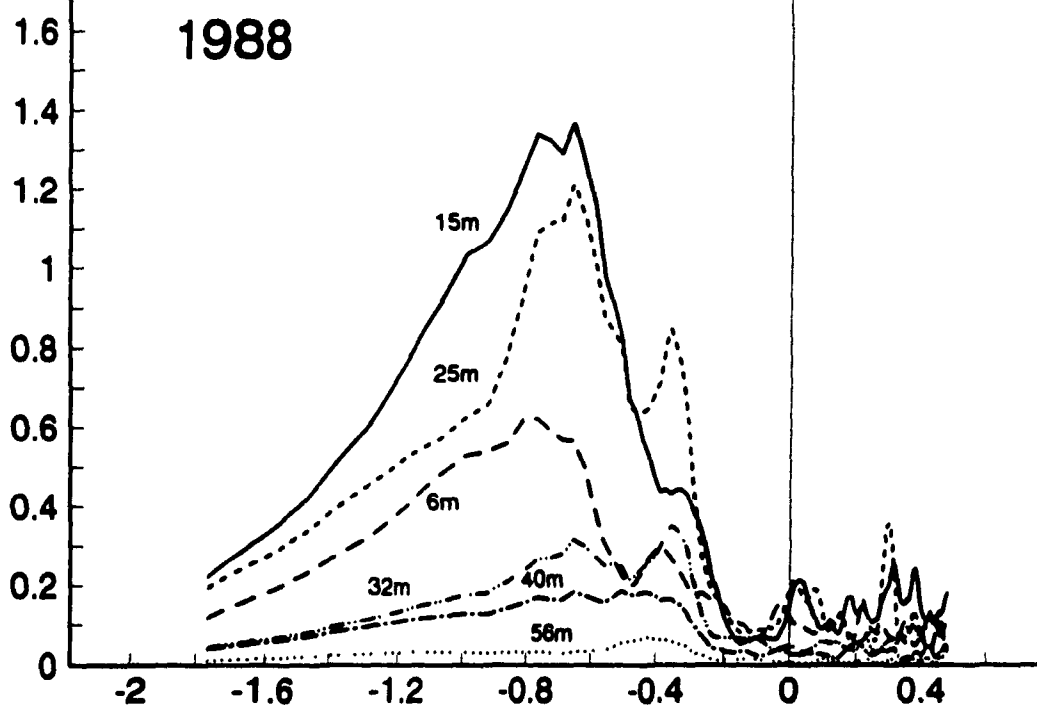
100 39.8 15.8 6.4 2.5 1.0 0.4

Spectral Density * Frequency

1987



1988



Log Frequency (cycles per day)

in 1987 did not have obvious peaks, but was instead lower than that for temperatures at 6 m in 1988, and was broadly distributed across periods 2.2 - 10 days.

Spectral analyses of temperatures recorded at greater depths (15, 25, and 40 m) during 1987 and 1988 showed even greater temperature fluctuations than those at the surface (Fig. 11). In particular, temperatures at 25 and 40 m were more variable than those at 7 m in 1987, and temperatures at 15 and 25 m were more variable than those at 6 m in 1988. Temperatures recorded at 56 m were least variable in both years.

High variability in mid-depth temperature is probably a direct consequence of vertical displacements of the thermocline about the instruments moored at depths of 15 and 25 m (Fig. 9; 10). In contrast, temperature fluctuations at 6 and 7 m, were probably associated with the advection of cold upwelled (or warm downwelled) water seaward (or landward) past the instruments.

(iii) Current speeds and directions

The compass direction of current flow was generally bimodal with peaks separated by 180 - 200° (Fig. 12). When direction and speeds were resolved into vector components, surface (6 m) flow was generally oriented along an axis of 20° - 220°, corresponding broadly to the dominant axis of the local wind field. Deeper currents were shifted progressively towards an axis of $\approx 70^\circ$ - 260°.

The frequency distributions of the longshore component of surface current flow differed between 1987 and 1988 (Kolmogorov-Smirnov test: $P = 0.002$; Fig. 13 - 15). In 1987, longshore flow (parallel to the coast)

Figure 12. Percent frequency distributions for current directions measured during the summers of 1987 and 1988 (2.2 km from shore; Fig. 1). Directions shown are in the oceanographic convention, and therefore represent the direction to which the current is flowing.

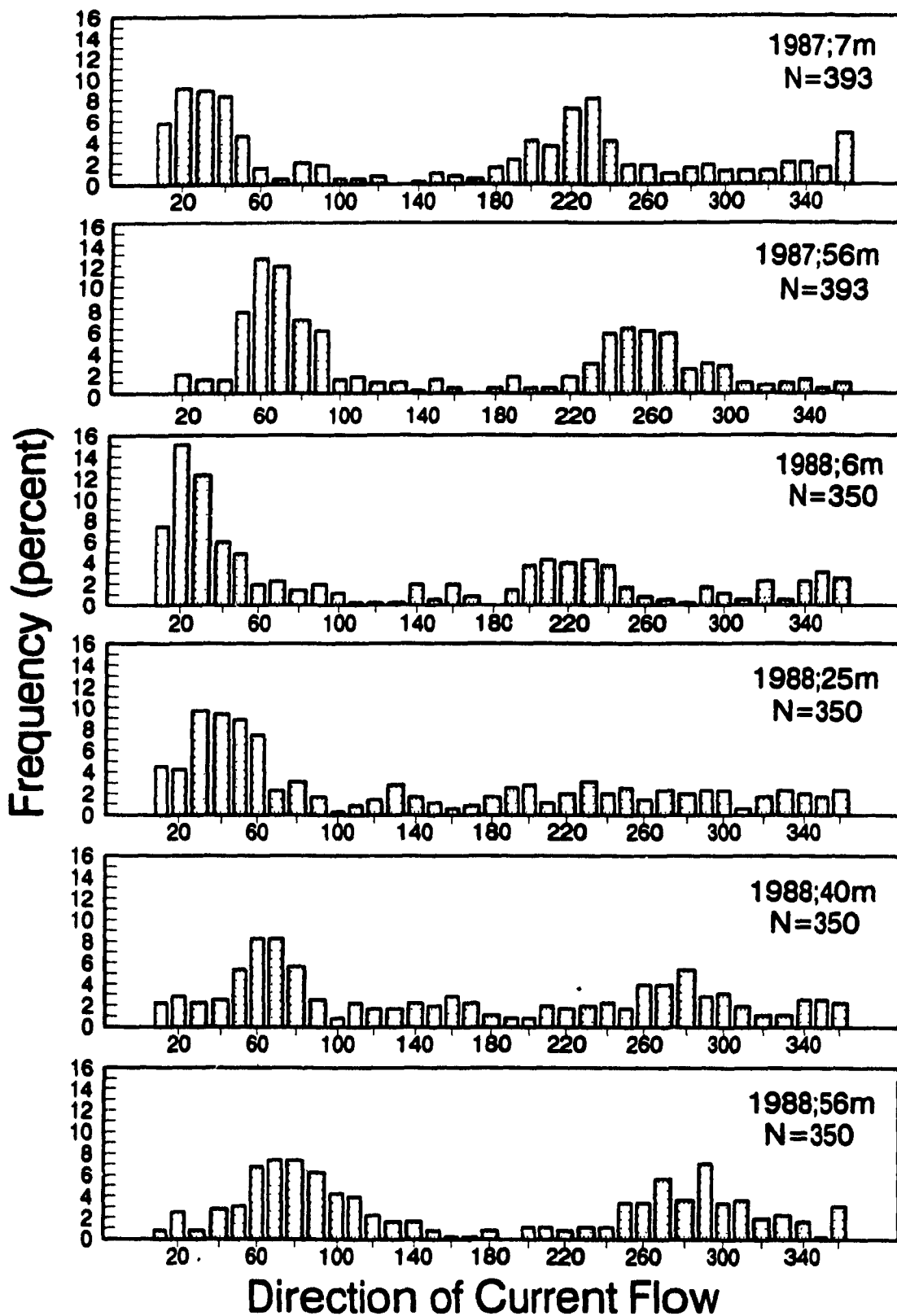
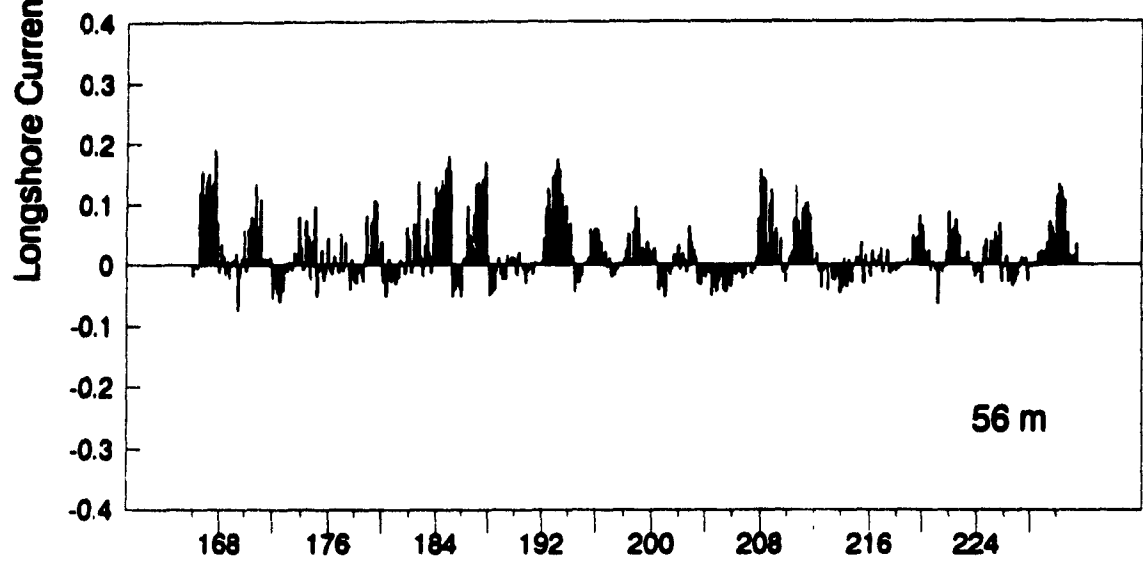
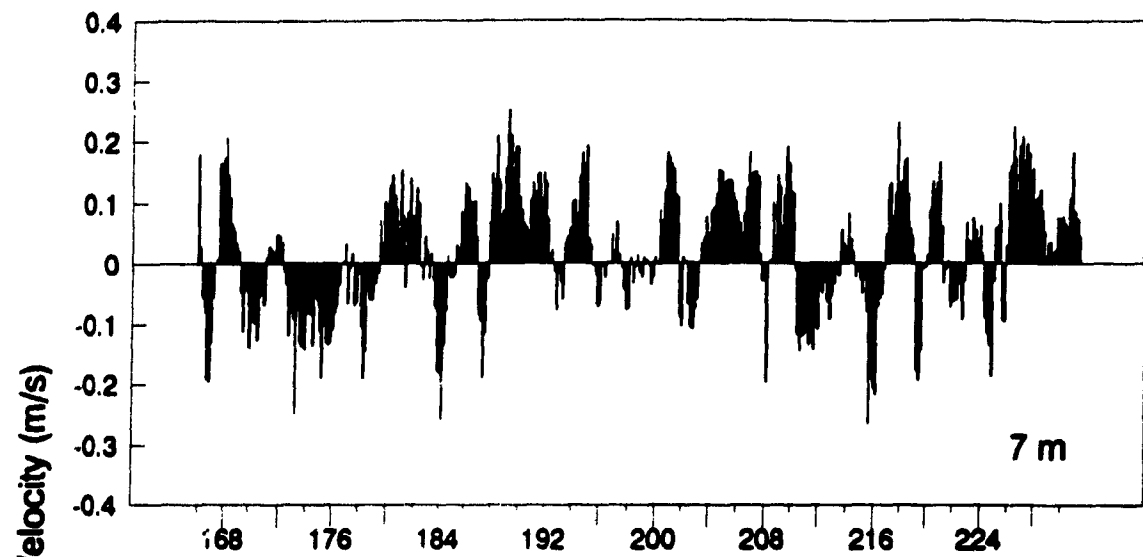


Figure 13. Time series of longshore current velocity recorded in 1987 at Station 2 (2.2 km from shore; Fig. 1) at depths 7 and 56 m.



Julian Date (1987)

Figure 14. Time series of longshore current velocity recorded in 1988 at Station 2 (2.2 km from shore; Fig. 1) at depths 6, 25, 40 and 56 m.

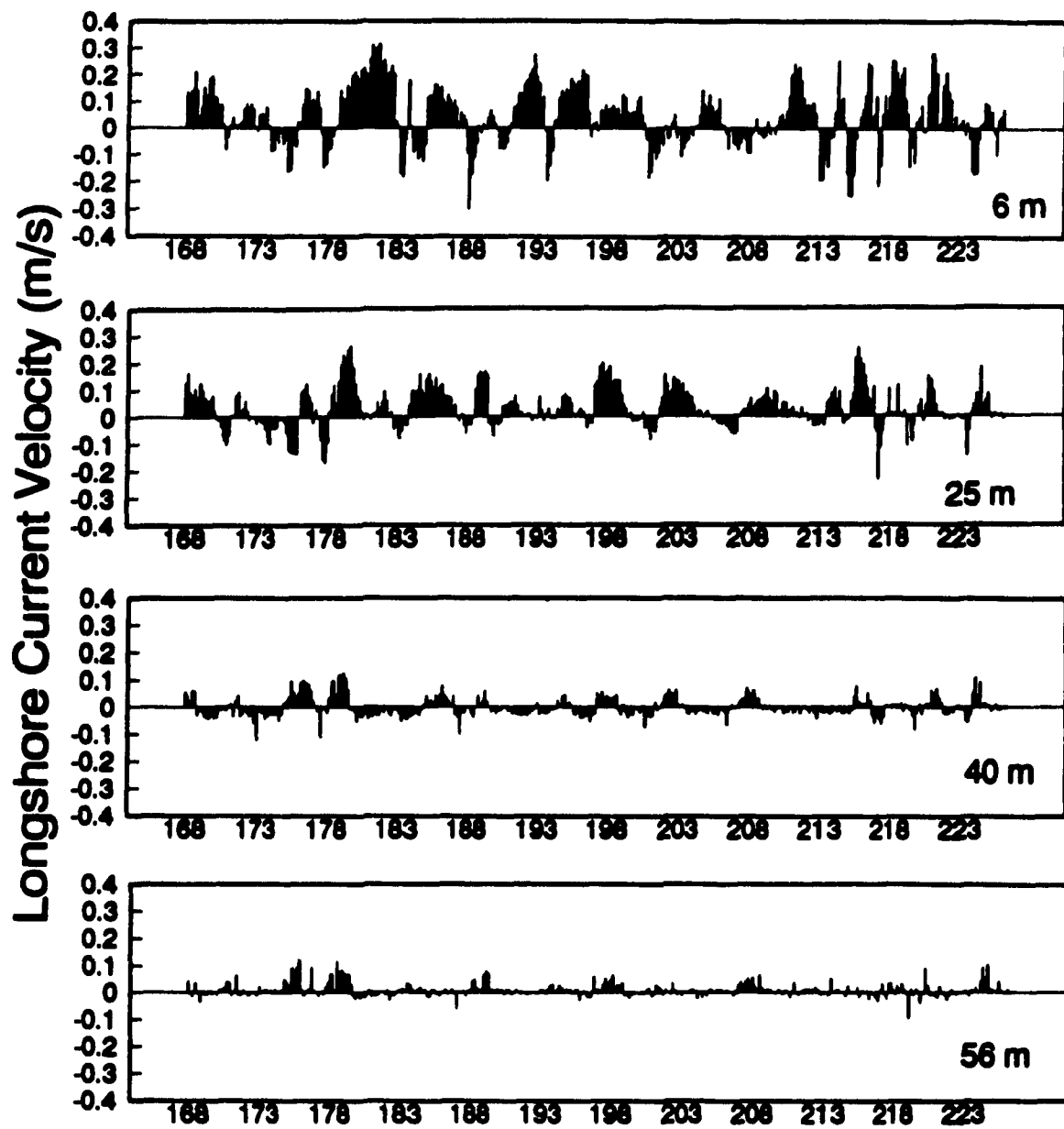
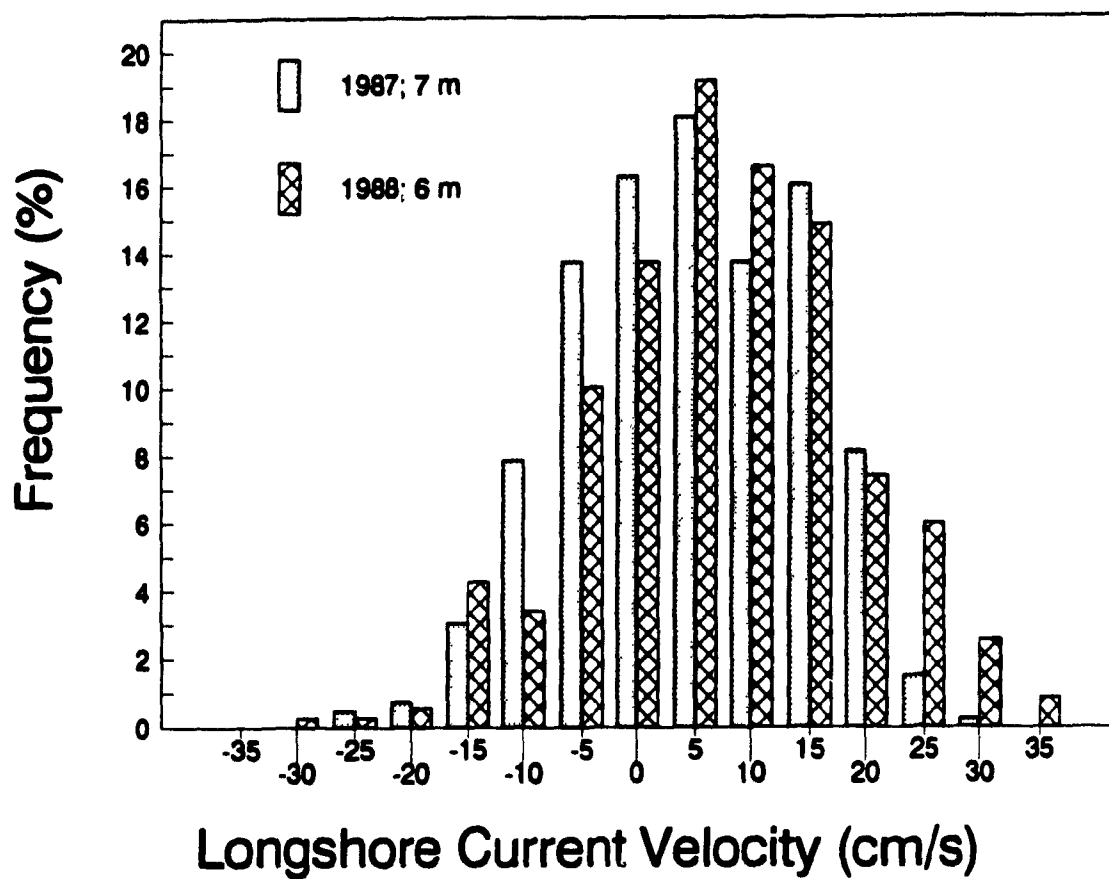


Figure 15. Percent frequency distribution of longshore current velocity measured at depth 7 and 6 m in 1987 and 1988, respectively.



was directed more frequently into the bay (negative velocities), than in 1988. In addition, when currents were flowing into the bay, the magnitude of their velocities was higher in 1987 than in 1988 (Fig. 15). Conversely, positive longshore velocities (parallel to coast and out of the bay) were more frequent in 1988 than in 1987, and these velocities were higher than the 1987 positive longshore velocities.

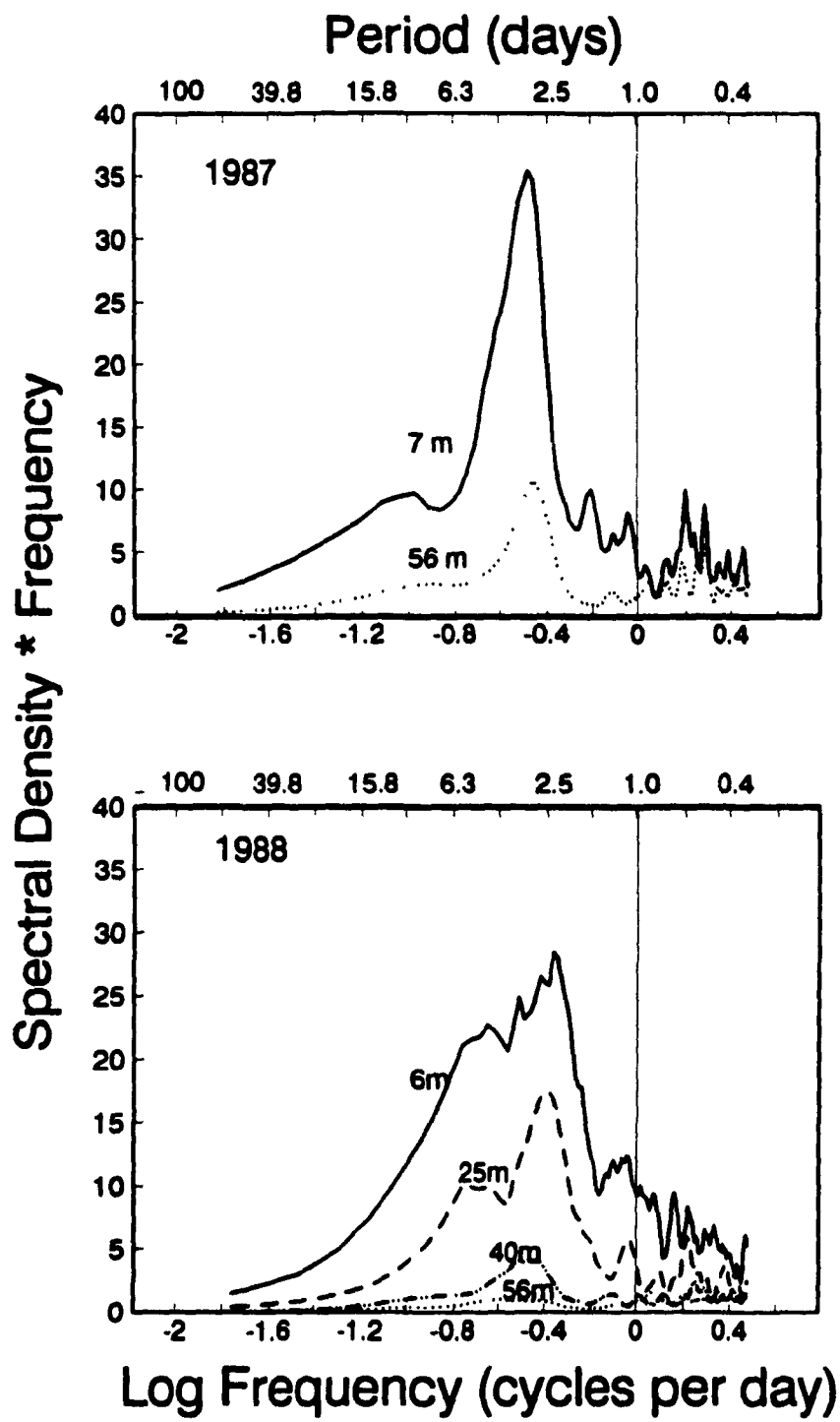
The variance in longshore current velocity peaked at periods of ≈ 2.9 days in 1987 (Fig. 16), but was distributed across a broad range of periods in 1988 (1.6 - 6.3 days; Fig. 16). In both years, longshore current velocities measured in the surface layer were more variable than those at depth (Fig. 16). Complete reversals of flow were common (e. g. Fig. 15: June 30 - July 2 [Julian days 180-182]; July 31 - Aug. 5 [Julian days 213-218]), as were counterflowing currents at different depths (e. g. Fig. 15. 25 and 40 m on June 27 - 30 [Julian days 179-182]).

The variance in longshore current velocities at tidal periods ($\approx 2 \cdot \text{day}^{-1}$) was small when compared with that at longer periods. Current velocities and temperatures were, therefore, dominated by non-tidal external energy inputs.

(iv) Dynamics of inter-relationships among meteorological and oceanographic variables

Our expectation for the response of the water column to wind energy inputs was broadly based on the Ekman model for coastal upwelling (Pond and Pickard 1983). Yao (1986), Taggart and Leggett (1987), and Schneider and Methven (1983) have shown that the wind velocity component (positive direction) parallel to the principal axis of the coast was

Figure 16. Variance-conserving power spectra for longshore current velocities measured at Station 2 (2.2 km from shore; Fig. 1) in 1987 and 1988.



associated with dramatic and rapid fluctuations in water temperature and current velocities in Newfoundland. Consequently, it was anticipated that deep water flow would be in the onshore direction shortly after, or simultaneous with, increases in surface longshore velocity in the positive direction (see Fig. 1 for orientation of vector components). It is also anticipated that the deep onshore flow would lead to, and be coherent with, reduced surface temperatures due to coastal, bathymetrically induced upwelling.

The field observations were fully consistent with these predictions. Variations in longshore wind and longshore current velocities at 6 m were positively correlated with longshore wind velocities ($P < 0.05$) at lags of 0 - 36 hours (wind leads current; Fig. 17). Surface flow was, therefore, in the direction of the wind at these time lags. At depths > 6 m, however, we observed significant inverse correlations between wind and current velocities. These first occurred at lags of 12 - 36 hours (wind leads current).

Surface (6 m) and deep (25 m) longshore current velocities were, therefore, inversely correlated (Fig. 18). However, this correlation was highest when 25 m currents were lagged, relative to those at 6 m, by 12 - 24 h. Positive longshore currents at 6 m (out of the bay) at time t will, therefore, be followed 12 - 24 hours later by a negative current at 25 m (into the bay). Winds which persist for periods longer than 24 h are, therefore, likely to create current shear and turbulent mixing at the interface between these two currents. Similar patterns were evident for other depth combinations (Fig. 18).

Cross-correlation analyses also showed that deep water (56 m)

Figure 17. Cross-correlations between longshore (LS) wind velocity and longshore current velocity measured in 1988 at 4 depths at station 2 (2.2 km from shore; Fig. 1). Correlations for negative lags relate values for longshore wind to values of current velocity that number of periods earlier. Correlations at positive lags relate longshore wind velocity to subsequent values of longshore current velocity. Dashed lines represent minimum significant correlation coefficient ($P < 0.05$).

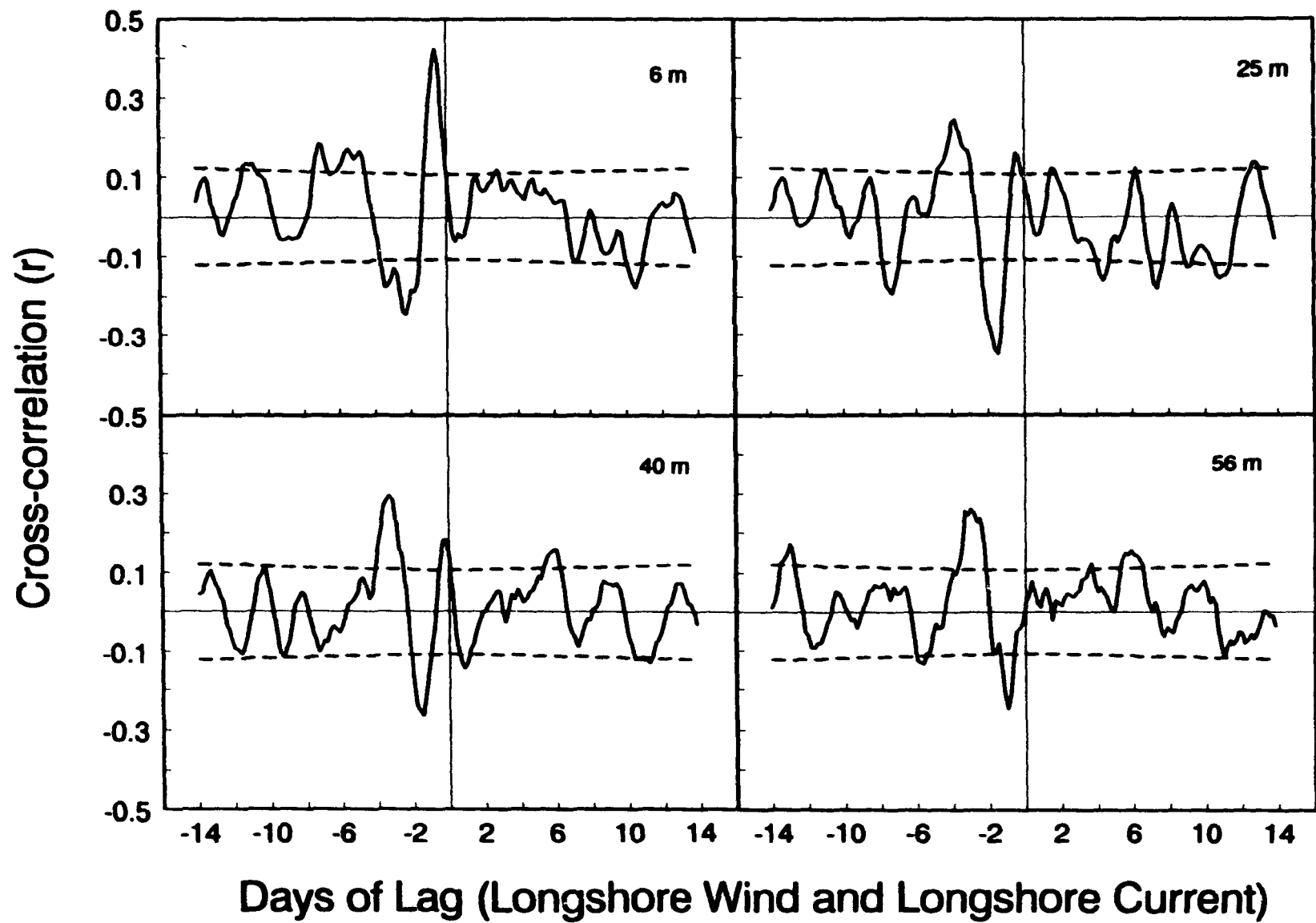
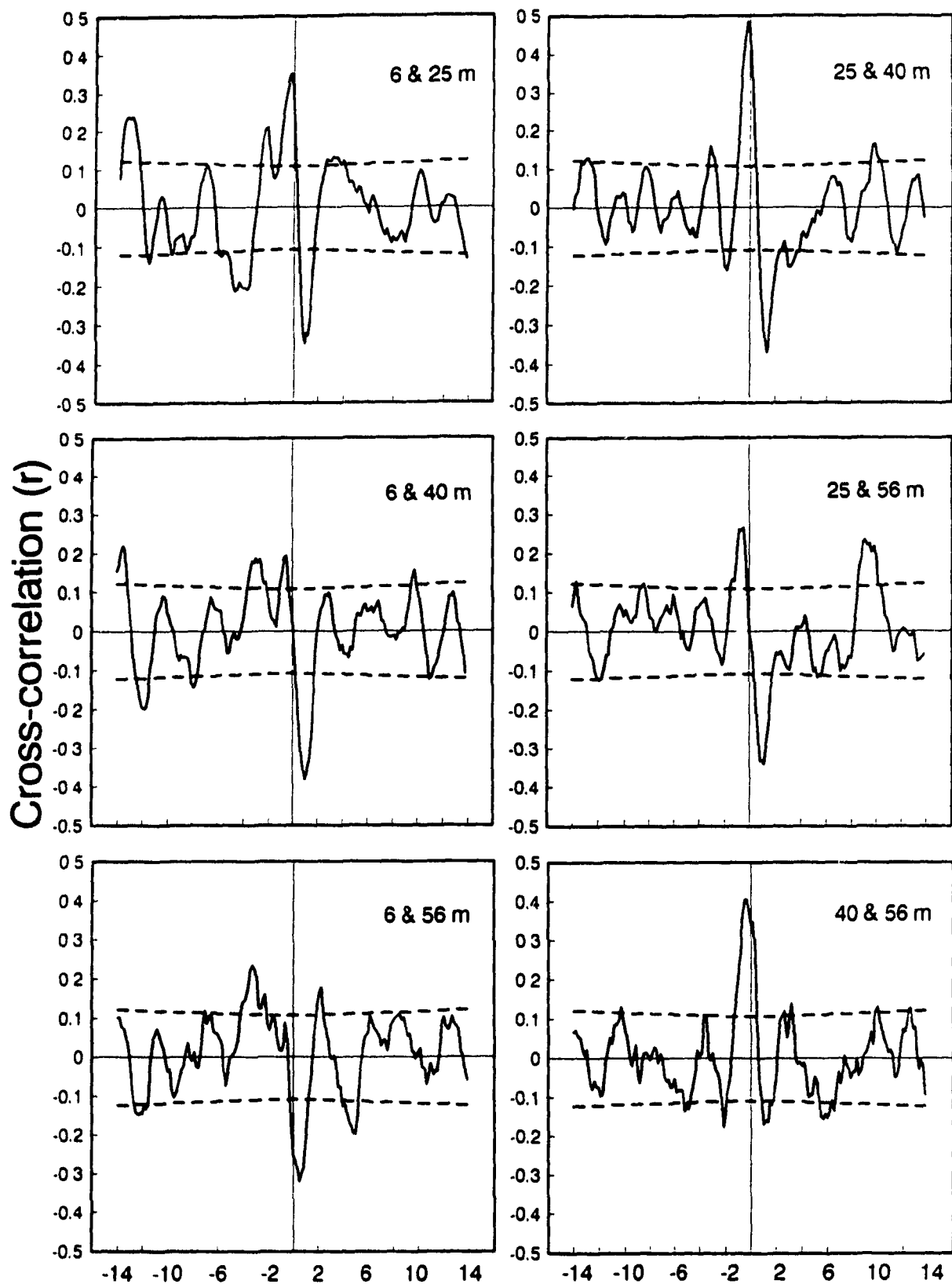


Figure 18. Cross-correlations between longshore (LS) current velocities measured at two different depths in 1988 at Station 2. Correlations for negative lags relate values of surface velocity to values of deep velocity that number of periods earlier. Correlations at positive lags relate values of surface velocity to subsequent values of deep velocity. Dashed lines represent minimum significant correlation coefficient ($P < 0.05$).



Days of Lag Between Longshore Current Velocities

flowed towards the coast when surface flow was out of the bay (Fig. 19C). This correlation was strongest at zero lag, indicating nearly instantaneous (i. e. < 4 h) response of deep water velocities to changes in surface current velocities. Significant negative cross-correlations were also evident between the velocity of the surface (6 m) longshore current and the velocity of the 25 m and 40 m cross-shore current (Fig. 19A, B). However, these correlations were maximal at positive lags of 24 - 36 h (surface current leads deep current).

Offshore flow (positive cross-shore current velocity) in deep water led to higher surface temperatures, and onshore flow (negative cross-shore velocity) in deep water led to lower temperatures (Fig. 20). This indicates that the appearance of cold water at the surface (Fig. 3-5) was associated with the flow of deep water towards the coast. These correlations (Fig. 20) occurred at short ($\approx 12 - 16$ h) or zero lags (current leads temperature). The strength of these relationships, as measured by R^2 , increased as the vertical distance between instruments measuring temperature and cross-shore current velocity (56 m) decreased (i. e. $r_{40m \text{ temp} / 56m \text{ XS current}} > r_{25m \text{ temp} / 56m \text{ XS current}} > r_{6m \text{ temp} / 56m \text{ XS current}}$; LS and XS denote longshore and cross-shore respectively). Hence negative cross-shore currents (onshore flow) at 56 m were followed less than 4 h later by reduced temperatures at 40 m, compared with a 12 - 16 h lag at depth 6 m.

Discussion

Intermittent periods of wind-induced upwelling introduced relatively nutrient-rich, deep cold water higher into the photic zone of western Conception Bay at intervals of 2.5 - 6 days during the summer of

Figure 19. Cross-correlations between longshore (LS) current velocity at 6 m and cross-shore (XS) current velocity at depths 25, 40, and 56 m (panels A, B, C respectively). All data were collected in 1988, except for chained line in panel C, which represents data collected in 1987. Dashed lines represent minimum significant correlation coefficient ($P < 0.05$).

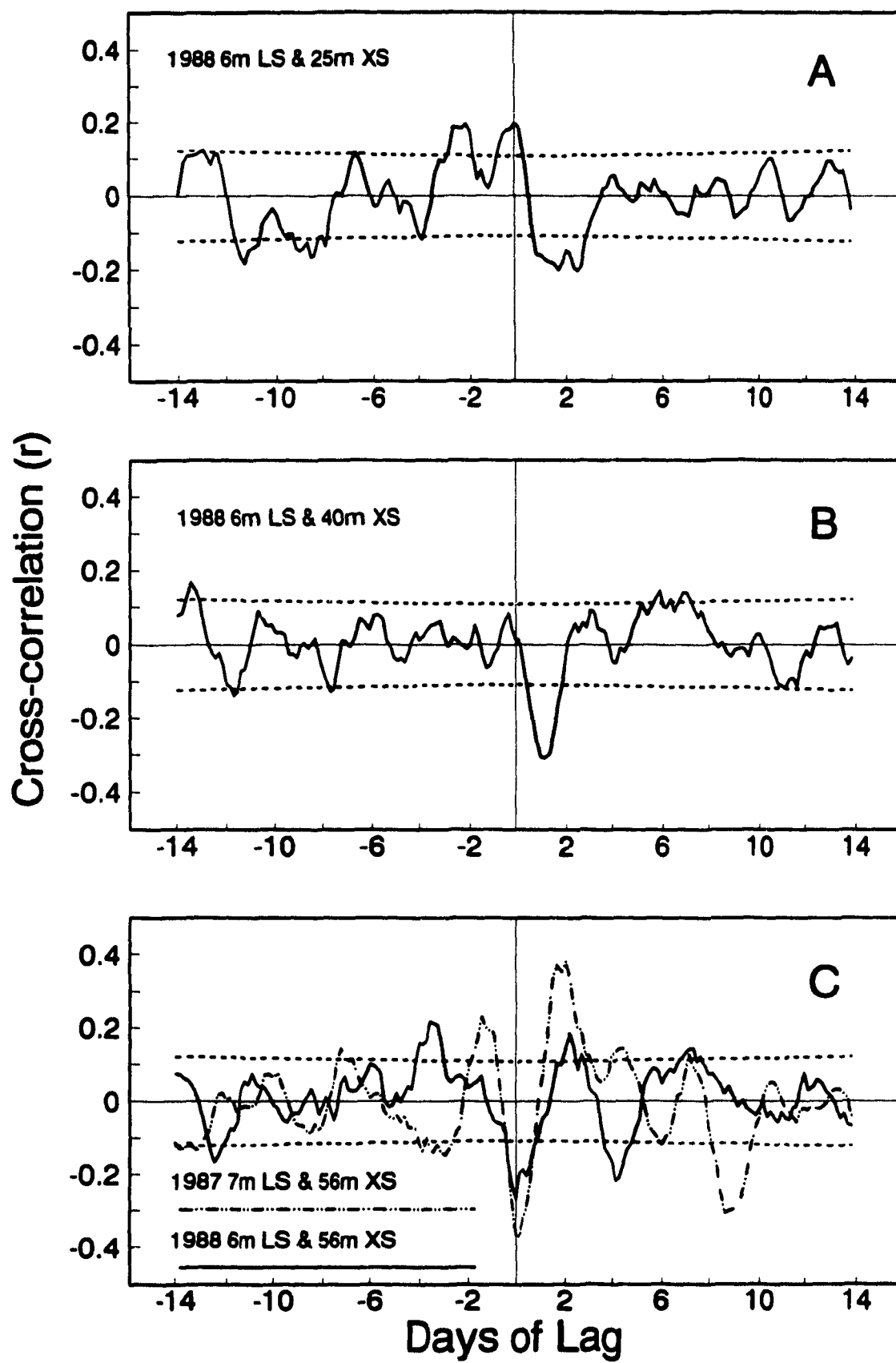
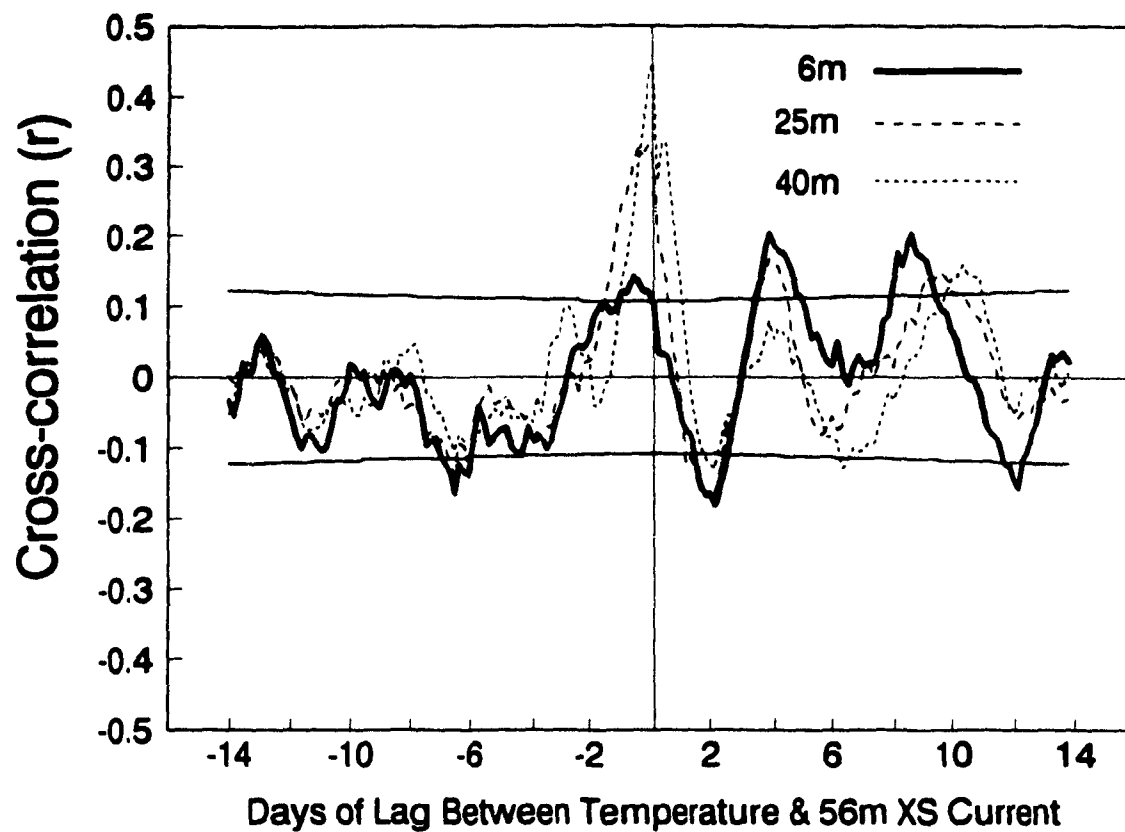


Figure 20. Cross-correlations between water temperature (6, 25 and 40 m) and cross-shore (XS) current velocity at 56 m measured in 1987 and 1988. Correlations for negative lags relate temperature values to current velocity that number of periods earlier. Correlations at positive lags relate values for temperature to subsequent values of current velocity. Thin solid lines represent minimum significant correlation coefficient ($P < 0.05$).



1988 and at less frequent intervals during the summer of 1987.

Temperature and current velocities responded predictably and rapidly to longshore wind velocities. The residence time of this upwelled water at shallower depths can be as long as 2 - 3 days, or as brief as 18 h.

The spatial extent of upwelling in 1988 was 4 - 6 km. However, in other years, the upwelling zone could be expanded or contracted, depending on prevailing wind conditions. For example, in 1987, when winds were unfavorable for upwelling, the upwelling zone was narrow or nonexistent (Fig. 3). These observations suggest that an upwelling index for this region could be derived from either a cumulative measure of the spatial zone occupied by cold water on successive days, or alternatively, and with greater ease, from the longshore wind velocity that is associated with this upwelling.

Horizontal variations in temperature are accompanied by dramatic and rapid temperature fluctuations in the vertical dimension (Fig. 10). These variations and their associations with wind conditions, are similar to those observed in the intertidal and nearshore zone of Bryants Cove (Frank and Leggett 1982; Taggart and Leggett 1987).

The upwelling episodes observed in 1987 and 1988 were primarily the result of classical wind-driven Ekman flows in which the net transport is to the right of the wind direction in the northern hemisphere and to the left of the wind direction in the southern direction (Pond and Pickard 1983). When current directions were resolved into vector components, the directions and velocities of surface and deep currents were consistent with the expectation of a deep shoreward flow replacing water advected away from the coast. Surface temperatures

also responded to longshore and cross-shore current velocities in a manner (time lags, direction of change) that was consistent with Ekman upwelling.

Upwelling events such as those observed in western Conception Bay and elsewhere (Table 1) are likely to benefit the local phytoplankton population in at least two ways. First those phytoplankton initially resident in the upwelled, nutrient-rich water mass were exposed to a 6-fold increase in light intensity, which would bring them closer to optimal light levels for photosynthesis (Eppley 1977; Prezelin 1987). Second, phytoplankton initially resident in the surface mixed layer are likely to benefit from elevated nutrient levels caused by upwelling and surface mixing resulting from flow reversals and countercurrent flow during upwelling/downwelling. The nearshore zone in 1988 was, therefore, probably more productive than in 1987 because of more frequent events of wind-induced nutrient supply to the photic zone, and because light-limited phytoplankton residing in deep, nutrient-rich water would periodically experience large increases in light intensity. These increases in light levels persisted for sufficiently long periods (18-72 hours) that some phytoplankton species were likely able to adapt physiologically to the new light conditions (Auclair et al. 1982; Lewis et al. 1984) experienced during an upwelling episode.

In addition, small-scale turbulence which increases plankton contact rates (Rothschild and Osborn 1988; Chapter 3) would also be greater in the nearshore zone in 1988 than in 1987. This is because higher longshore wind velocities in 1988 (Fig. 2) would produce more turbulence within the mixed layer (Chapter 2) than in 1987, and because

upwelling-related mixing (Csanady 1989) can substantially increase turbulence levels beyond those predicted by empirical and theoretical wind-based models of turbulent energy dissipation rates (e. g. 7-fold increase for one upwelling meander off California; Chapter 2). On the basis of field (Sundby and Fossum 1990), experimental (Saiz and Alcaraz 1991), and theoretical (Granata and Dickey 1991; Davis et. al. 1991) results of the influence of small-scale turbulence on encounter rates between planktonic predators and their prey, and on plankton growth rates, it is likely that rates of secondary production were higher in 1988 than in 1987, assuming all other factors (e. g. temperature, food density) are considered equal.

The depth from which water upwells following a given wind input, and the nutrient concentration of this upwelled water, could vary because of other non-wind factors. These factors would include seasonal heat and freshwater inputs, which cause the water column to stratify (Simpson and Bowers 1981). For example, the cumulative number of degree-days (an approximate measure of seasonal heating of the water column; Frank and Leggett 1982) during the period May 1 - August 31 in 1987 and 1988 was 855.3 and 993.4, respectively, and the cumulative precipitation during the same time periods was 239.4 and 319.3 mm (Monthly Meteorological Summaries, Environment Canada, Downsview, Ontario, Canada). Consequently, even though the potential for water column stratification was much greater in 1988 than in 1987 because of greater heat and freshwater inputs, these effects were largely overcome by the stronger winds in 1988. These winds were more effective in forming a deeper mixed layer, and in promoting more frequent upwelling in 1988

than in 1987. This finding emphasizes the important role that wind will have on the physical structure of aquatic habitats.

Given the variation in local weather (wind: Husby and Nelson 1982, Bakun and Parrish 1990; heat input. Bowers and Simpson 1990; freshwater runoff: Skreslet 1986), annual deviations from mean values and frequencies could favor higher (lower) rates of mixing or upwelling of new nutrients into the photic zone, and of turbulent energy dissipation. These water column attributes (rates and occurrence of turbulent mixing) strongly influence the size structure of phytoplankton communities (Cushing 1989; Legendre 1990, Kiørboe et al. 1990), and the degree to which primary production is utilized by the "traditional" food chain (Nielsen and Kiørboe 1991).

In summary, the significant air-sea interactions that occur in western Conception Bay suggest that interannual variability in the combination of energy inputs that mix or stratify the water column and alter the frequency and intensity of small-scale turbulence, will be important in the conversion of what would otherwise be an unproductive, stratified environment to an environment whose nutrient, light and turbulence characteristics are favourable for the support of high rates of primary and secondary production. Such interactions, which are now known to occur over large areas of the east coast of Newfoundland (Leggett et al. 1984; Yao 1986; Schneider and Methven 1988), along the north shore of the Gulf of St. Lawrence (Rose and Leggett 1988), and presumably in other areas (Table 1), may be fundamental to the high production of these cold water environments.

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Chapter 5

Wind-mediated Control of Temporal and Spatial Patterns in Prey Availability for Larval Fishes

Introduction

Transient periods of wind-induced upwelling and mixing cause rapid and dramatic changes of physical characteristics in coastal aquatic environments (see Table 1 in Chapter 4). For example, nutrient supply to the photic zone (Chapter 4; Kiørboe and Nielsen 1990; Harris et al. 1991), irradiance levels at the nutricline (Lande and Yentsch 1988), and rates of turbulent energy dissipation within the surface mixing layer (Chapter 2) can all increase during an upwelling episode or storm-related mixing.

These phenomena are likely to be important in determining the availability of phytoplankton and zooplankton prey for larval fishes, and more generally, the availability of nutrients, light, and prey for primary and secondary consumers. The importance of these events to primary plankton production is likely to be greatest at times (places) when (where) production rates are expected to be low (e. g. after the spring diatom bloom; Cushing 1975). Consequently, if upwelling and mixing events occur regularly during the post-bloom period, they have the potential, in some years, to transform a typically unproductive environment into one whose rates of phytoplankton production are higher than usual for a particular region.

Moreover, increases in turbulence associated with wind energy inputs which cause upwelling or mixing, together with the additional turbulence associated with upwelling circulation (Chapter 2; Csanady 1989), could increase rates of secondary production through their beneficial effect on rates of encounter among planktonic predators and prey (Rothschild and Osborn 1988; Costello et al. 1990; Marrasé et al. 1990; Chapter 3). Turbulence increases feeding, development, and metabolic rates of some

secondary consumers (Gadus morhua Sundby and Fossum 1990; Acartia grani Saiz and Alcaraz 1991; Daphnia pulex, Acartia sp. Alcaraz and Saiz 1991). In addition, ingestion rates of larval fish in nature, where turbulence is ubiquitous and variable, exceed ingestion rates predicted by empirical models derived from laboratory experiments, where turbulence is absent or reduced (Chapter 1). Spatial and temporal differences in turbulent dissipation rate may, therefore, partly determine feeding success by larval fishes (Sundby and Fossum 1990; Chapter 1, 3), and rates of plankton production at several trophic levels within plankton communities.

In this chapter, I evaluate how interactions between wind, nutrients, light and turbulence affect the availability of prey for larval fish, and more generally, the temporal and spatial distribution of phytoplankton and zooplankton in a coastal pelagic ecosystem. The site of these studies was western Conception Bay, Newfoundland, Canada where commercially exploited populations of capelin, Mallotus villosus, and several other species (Frank and Leggett 1983) spawn in the intertidal and subtidal zones during the summer months (Taggart and Nakashima 1987). Larvae of capelin dominate the local ichthyoplankton community (Frank and Leggett 1982, 1983). Their diets at first-feeding include diatoms (Courtois and Dodson 1986), tintinnids (Courtois and Dodson 1986) and copepod eggs and nauplii (Frank and Leggett 1986). These prey are members of the first and second trophic levels. Because of their small size and physiological adaptability, they can rapidly enter food chains following upwelling-related pulses in nutrients (Takahashi et al. 1986; Kjørboe and Nielsen 1990), light (Auclair et al. 1982; Lewis et al. 1984), or phytoplankton (Kjørboe et al. 1985, Verity 1986; Peterson and Bellantoni

1987).

My objectives were to assess the degree to which plankton distributions, and the availability of prey for larval fishes, are controlled by intermittent upwelling/downwelling events. Episodes of upwelling and downwelling occur at approximately weekly intervals in Conception Bay and individual upwelling events can persist for periods lasting 0.75 - $\approx$ 6 days (see also Yao 1986; Taggart and Leggett 1987, Schneider and Methven 1988). During an upwelling episode, the nutricline is displaced upwards by, on average, 10 - 15 m. This displacement temporarily increases nutrient levels in the lower portion of the photic zone by 2 - 3 fold, and increases the light intensity received by phytoplankton within the nutricline by, on average, 6-fold (Chapter 4). I hypothesized that upwelling-related gradients in nutrients, light and turbulence would be reflected in the temporal and spatial distributions of phytoplankton and zooplankton, and that these gradients may be important in the feeding success of larval fishes.

Methods

Study site

A complete description of the study site is given in Chapter 4. Briefly, Conception Bay is a fjord-like embayment ($\approx$ 65 by 25 km) located on the northeast coast of Newfoundland, Canada. It is typical of numerous such bays and inlets on the east coast of Canada. In summer, transient periods of wind-induced upwelling and downwelling occur in this, and neighboring regions (Yao 1986; Schneider and Methven 1988), at periods of 2 - 6 days (Chapter 4; Taggart and Leggett 1987). Tidal energy inputs are

relatively small (Taggart and Leggett 1987, Chapter 4). The high frequency of this environmental variability necessitates the collection of biological samples at a frequency of several times per week to resolve biological variation at similar time scales.

Sampling plan

I monitored hydrographic fluctuations continuously during the summers of 1987 and 1988. The collection of the physical oceanographic and meteorological data is described in Chapter 4. In general, hydrographic variability (water current speed and direction, water temperature, salinity) was monitored with 4 current meters and 2 temperature recorders deployed at 6 depths at a site ($47^{\circ}40'78''$ N, $53^{\circ}9'48''$ W) located 2.2 km from the western shore of Conception Bay. This station was situated on a sampling transect whose point of origin was Bryants Cove, and whose orientation was approximately perpendicular to the principal axis of Conception Bay (Fig 1, Chapter 4).

Sea surface temperatures were continuously recorded during travel between stations. This record provided real-time spatial description of the magnitude of upwelling occurring on each sampling day. Most sampling was conducted within 10 km of shore, except for 3 occasions in 1987 and 2 occasions in 1988 when biotic and abiotic data were collected across the entire cross-Bay distance (≈ 22 km).

I used plankton sampling methods that enabled simultaneous estimation of biotic and abiotic variables. A modified pump sampler (Taggart and Leggett 1984; see Chapter 4 for design changes) was used, to provide depth-specific samples of known volumes of seawater. These samples were used to estimate vertical temperature, chlorophyll and zooplankton

profiles

Sampling methods for vertical temperature profiles are fully described in Chapter 4

Water samples to be used for the determination of extracted chlorophyll a concentration (a commonly used index for approximating the abundance of phytoplankton, de Lafontaine and Peters 1986, Harrison 1990) were collected by pumping seawater from the water column at 5 m depth intervals within the surface mixed layer, the thermocline and the subthermocline waters to a maximum depth of 50 m. In all cases the pump intake was maintained at one depth during pumping. Water samples (1 L) were held in darkened, refrigerated containers until the research vessel returned to the laboratory (maximum holding period $\approx$ 7 h)

Immediately upon return to the laboratory, 250 ml of seawater from each sample was filtered through Whatman GF/C filters (pore size 1.2 μ m). All filters were then frozen before pigment extraction. Approximately 75 % of the filters were frozen at -20° C for a period of 2 - 3 weeks before extraction. The remaining 25 % were shipped by air cargo from St. John's, Newfoundland to Montreal, Quebec in packages containing dry ice; in Montréal, filters were held at -80° C for 6 - 8 weeks before processing. After frozen storage, all filters were transferred to darkened plastic tubes containing 12 ml 95 % acetone for chlorophyll extraction (Strickland and Parsons 1968) at room temperature; the extraction period was 24 hours. Fluorescence of the extracted pigment solution was measured before and after acidification using a Model 110 Turner fluorometer. These measurements enabled estimation of the concentration of chlorophyll a and pheopigments (Strickland and Parsons 1968). The fluorometer was calibrated

with standard solutions of chlorophyll a

Seawater from the pump outfall was also used for the collection of zooplankton samples. Zooplankton was retained by choking a 20 μ m mesh plankton net (diameter = 30 cm; length = 1.2 m) around the end of the effluent hose of the pump sampler. Particles retained by this net were immediately rinsed into jars containing 10 % buffered formalin. These samples were subsequently enumerated and sized in the laboratory.

Zooplankton was collected from several depth intervals at each station. During the period June 8 - July 4, 1988. Depth-integrated zooplankton samples were obtained by raising and lowering the pump intake during pumping. Samples were taken at 5 m depth intervals from the surface to 25 m; below 25 m, one sample was collected in the depth interval 25 - 40 m. After July 4, 1988, the pump intake was maintained at one depth during pumping; sample depths during this period were 3, 8, 13, 18, 23, 28 and 40 m. All depths were determined with a shipboard-mounted meter wheel.

The volume of seawater pumped from each depth was 2000 L, except for depth intervals spanning a depth range exceeding 5 m (e. g. 25 - 40 m). Here the sample volume was increased proportionally (e. g. 6000 L). Sample volumes were monitored in real time by a flow meter installed directly in the pump effluent (see Taggart and Leggett 1984). The vessel was stationary during each sample interval. These sample volumes (2000 - 6000 L), which are considerably smaller than those used in larger scale oceanographic surveys (10^4 - 10^5 L), significantly increases the probability of detecting microscale patches (< 1 m) of zooplankton prey (Jenkins 1988; Owen 1989).

Zooplankton samples were enumerated and sized with Coulter TA/II and Multisizer II electronic particle counters. In this chapter, analyses are focussed on two size classes (40 - 80 μm equivalent spherical diameter and 80 - 161 μm e. q. s.) of zooplankton known to be potential prey for first-feeding larval fish (Courtois and Dodson 1986; Frank and Leggett 1986), and which, because of their small size, are likely to respond quickly to temporal and/or spatial variability in their food supply.

The biovolume measures of prey abundance obtained from the particle counters were converted into estimates of dry weight biomass ($\mu\text{g}\cdot\text{l}^{-1}$) by assuming that zooplankton are neutrally buoyant ($1\text{ g}\cdot\text{cm}^{-3}$) and that 20 % of zooplankton body mass is dry material (Parsons et al. 1977). These assumptions enabled comparison of Conception Bay prey abundance estimates with those obtained for other sites around the world (Chapter 1).

Water column transparency at the time of plankton sampling was measured with a 40 cm Secchi disk. Incident light intensities (400 - 700 nm spectral response; $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were measured with a Biospherical Instruments QSR-240 solar reference hemispherical light sensor. These data were used to estimate light intensities within the water column and the depth of the photic zone (Parsons et al. 1977; see also Chapter 4).

Data analyses

Linear regression analyses were used to quantify seasonal patterns in depth-averaged plankton biomass. The depth range chosen for these analyses, 0 - 30 m, comprises larval fish habitat in Conception Bay, encompasses the photic zone and the surface mixed layer (Chapter 4), and is likely to be more turbulent than deeper layers during wind-forcing (Chapter 2). In addition, during transient upwelling events, the

nutricline is displaced vertically from its usual summer position (20 - 30 m) to depths shallower than 15 m (Chapter 4). These considerations suggest that wind energy inputs could be associated with seasonal increases in plankton biomass. These same wind inputs could also produce spatial gradients in plankton biomass because of the beneficial effect of wind-induced upwelling on plankton production.

These hypotheses were evaluated with a seasonal wind index which approximates the cumulative amount of upwelling during the each summer. This wind index was calculated as the daily average of the 24 hourly values of longshore wind component (see Chapter 4 for calculation) derived from daily wind records gathered at St. John's airport (19 km from the centre of Conception Bay; Environment Canada Monthly Meteorological Summaries). Daily measures of this wind index were summed starting from June 1 (approximately the end of the spring bloom; Pomeroy et al. 1991). Cumulative values of this index were used as inputs to linear regression models relating temporal variability in depth-averaged plankton biomass to wind conditions during the summers of 1987 and 1988.

Another important variable which influences rates of plankton production (Eppley 1972; Huntley and Boyd 1984), and which could be highly correlated to seasonal distributions of plankton biomass (Frank and Leggett 1982), is water temperature. Seasonal warming of the water column could, therefore, be a significant correlate of plankton biomass. This hypothesis was assessed by comparing estimates of depth-averaged plankton biomass with the depth averaged (0 - 30 m) water temperature recorded at the time of plankton sampling.

The residual variability from the seasonal plankton - wind and

plankton - temperature relationships was used to assess the hypothesis that plankton was more abundant in the nearshore zone where upwelling was most intense. For these analyses, multiple regression models were developed that employed cumulative wind speed and distance offshore as input variables.

Encounter rates of larval capelin with prey

Zooplankton densities measured in 1988, and an empirical estimate of turbulent dissipation rate, ϵ , were used to estimate encounter rates of capelin larvae with their prey for different combinations of wind speed and prey density. Prey were considered to be tintinnids, which are important components of larval capelin diets (Courtois and Dodson 1986). Jonsson (Table 1, 1989) measured vertical velocities of two tintinnid genera, Parafavella denticulata, and Tintinnopsis sp. which occur in Conception Bay (Davis 1982). Jonsson (p. 43, 1989) states that these vertical velocities are more than half the swimming speeds for these species. I, therefore, increased the vertical velocities reported by Jonsson (1989) by 2-fold, and subsequently used the average of these swimming velocities ($0.095 \text{ cm} \cdot \text{s}^{-1}$) in encounter rate simulations.

Larval capelin swimming velocity was estimated using an empirical swimming speed - body size relationship derived from 9 species (Miller et al. 1988). As input for this relationship, I assumed that first-feeding larval capelin were 4.8 mm in standard length (Fortier and Leggett 1982); swimming velocity as calculated from Miller et al. 1988) was $0.42 \text{ cm} \cdot \text{s}^{-1}$. Predator velocity was, therefore, $\approx$ 4-fold higher than prey velocity.

Newly-hatched larval capelin are principally distributed within the upper 20 of the water column (Fortier and Leggett 1982; Frank and

Carscadden 1989) I assumed that the centre of mass of capelin larvae in Conception Bay was located at a depth of 15 m for these simulations

The prey densities used in these simulations were the mean and 95 % confidence limits of the abundance of small-sized plankton (40 - 80 μm) observed at two stations situated 2.2 and 9.9 km from the western shore on the transect across Conception Bay. They represent environments exposed to different levels of upwelling intensity (Chapter 4) and, presumably, small-scale turbulence (Chapter 2). Prey biomass, $\mu\text{g dry weight}\cdot\text{l}^{-1}$, was converted to number of individuals $\cdot\text{l}^{-1}$ by assuming that the geometric mean diameter of particles in the 40 - 80 μm size class was 57 μm . Individual particle weight in this size class was, therefore, $0.019 \mu\text{g}\cdot\text{l}^{-1}$.

Turbulent dissipation rates, ϵ , were estimated from an empirical model that uses wind speed, depth from the water surface and an environmental code as inputs (Chapter 2). Three wind speeds, including 0 $\text{m}\cdot\text{s}^{-1}$ (no turbulence), and the median (4.2 $\text{m}\cdot\text{s}^{-1}$) and 75th percentiles (5.8 $\text{m}\cdot\text{s}^{-1}$) from the distribution of positive longshore wind velocities (i. e. those most likely to cause upwelling in Conception Bay; Chapter 4) were used in these simulations. The environmental code approximates the additional amount of turbulence that can be induced by phenomena other than wind (e. g. upwelling; Chapter 2). This variable was assigned a value of 1 for simulations involving the nearshore site, and values of 0 and 1 for separate simulations involving the offshore site.

Further details regarding the estimation of encounter rates from turbulent dissipation rates, prey-predator swimming speeds and prey densities are described in Chapter 3.

Results

Wind-driven upwelling of cold water was a common and intermittent phenomenon in 1988. Upwelling also occurred in 1987, but was less frequent and less intense (Fig. 1, also Chapter 4). This upwelling caused mixing between water masses and the vertical displacement of isotherms towards the surface (Fig. 2 - 4).

Chlorophyll *a* distributions: temporal patterns

During the summer of 1988, chlorophyll *a* concentrations within 10 km of the western shore of Conception Bay ranged from $< 0.05 - 3 \text{ l } \mu\text{g l}^{-1}$ during the summer of 1988 and were generally highest at mid-depth (e.g. June 27, July 7 - 13; Fig. 2 - 5). During upwelling, the subsurface chlorophyll layer was elevated with the nutricline (20 - 30 m; Chapter 4) into shallower water (e.g. July 4; Fig. 3, 5). On these occasions, phytoplankton residing in deep water became exposed to large increases in light intensity. Those phytoplankton associated with the $4.5 - 5^{\circ} \text{C}$ isotherms received ≈ 100 -fold higher light intensity during one upwelling event in 1988 (Fig. 6). This increase in light intensity occurred during a period when bright sunshine coincided with strong wind-induced upwelling (Fig. 2, 3), which brought the 5°C isotherm from a depth of 25 m to 2 m. Smaller displacements of the thermocline (10 - 15 m) caused light intensities associated with this isotherm to increase by amounts ranging from 5 - 25 fold (Fig. 6).

Depth-averaged chlorophyll *a* concentrations within 10 km of the western shore of Conception Bay increased by 10 - 15 fold during the summers of 1987 and 1988 (Fig. 7). These increases were highly correlated with the cumulative wind energy input to the water column in both 1987 and

Figure 1. Water temperatures recorded during the summers of 1987 and 1988 at 3 depths at a site ($47^{\circ} 40' 78''$, $53^{\circ} 9' 48''$) located 2.2 km from the western shore of Conception Bay. Total water column height is 60 m

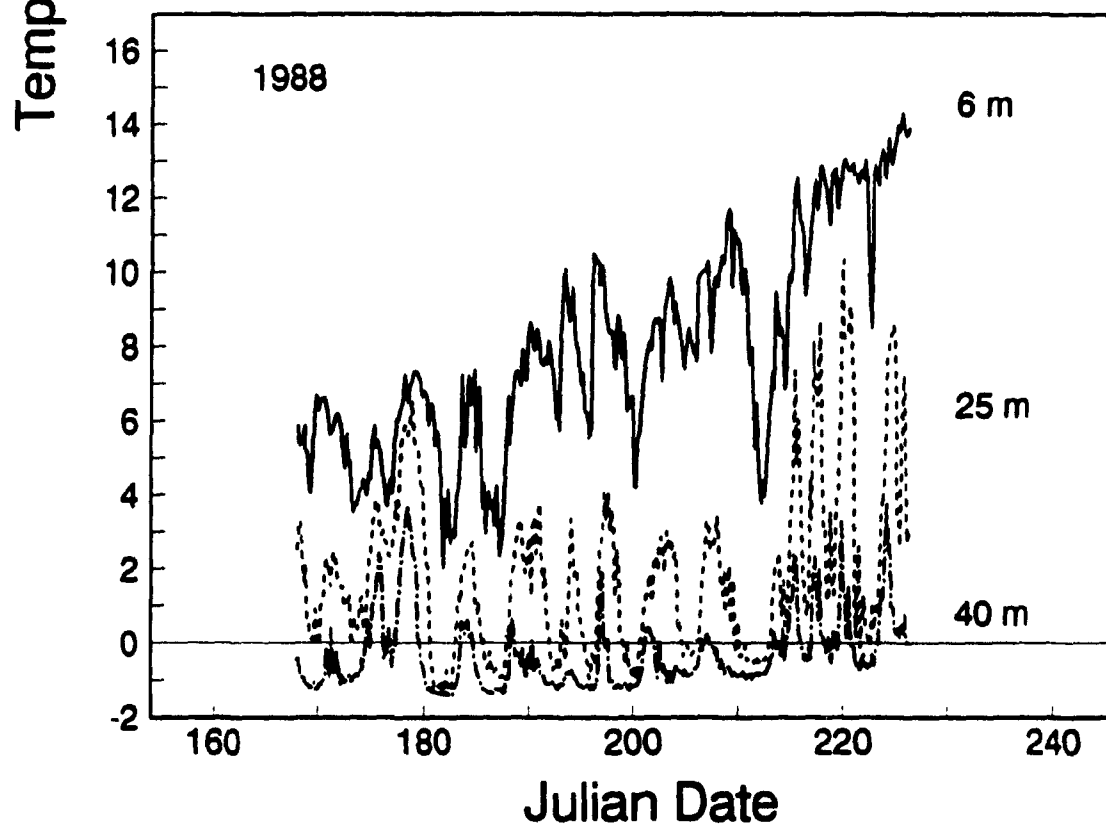
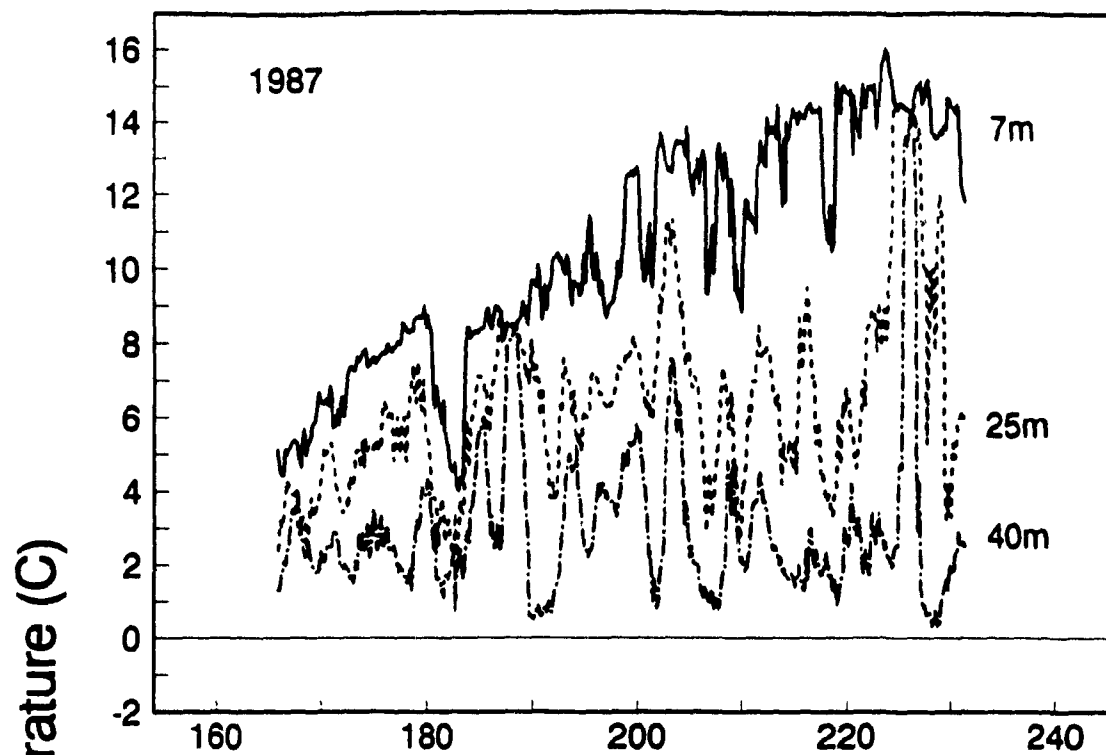


Figure 2 Vertical sections of water temperature (top row), chlorophyll a concentration ($\mu\text{g}\cdot\text{l}^{-1}$; middle row), and the biomass of microzooplankton ($\mu\text{g dry weight}\cdot\text{l}^{-1}$; size class 40 - 80 μm equivalent spherical diameter; bottom row) during June 18 - June 27, 1988 at coastal sites in western Conception Bay.

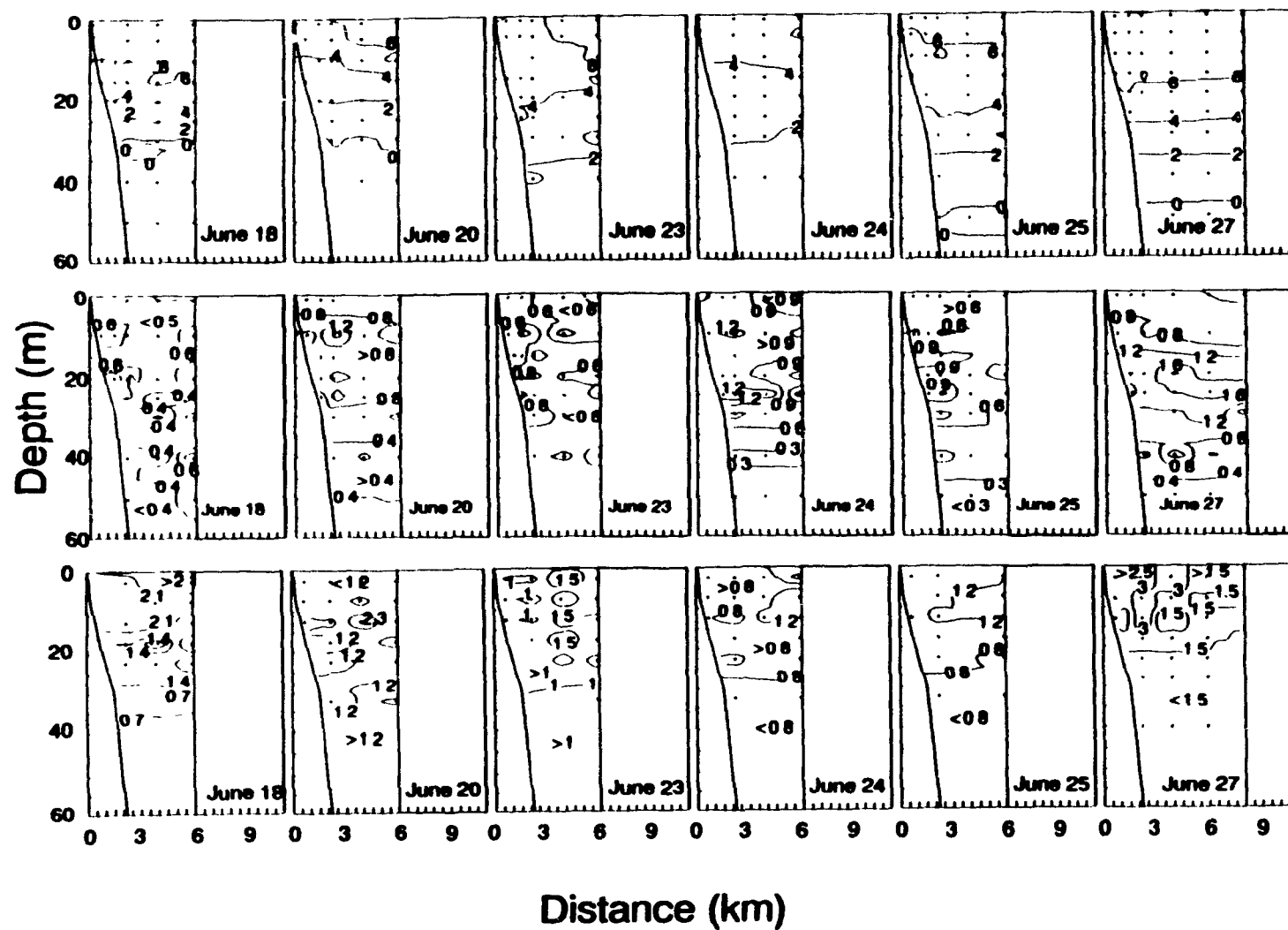


Figure 3 Vertical sections of water temperature (top row), chlorophyll a concentration ($\mu\text{g}\cdot\text{l}^{-1}$; middle row), and the biomass of microzooplankton ($\mu\text{g dry weight}\cdot\text{l}^{-1}$; size class 40 - 80 μm equivalent spherical diameter, bottom row) during June 27 - July 7, 1988 at sites at coastal western Conception Bay.

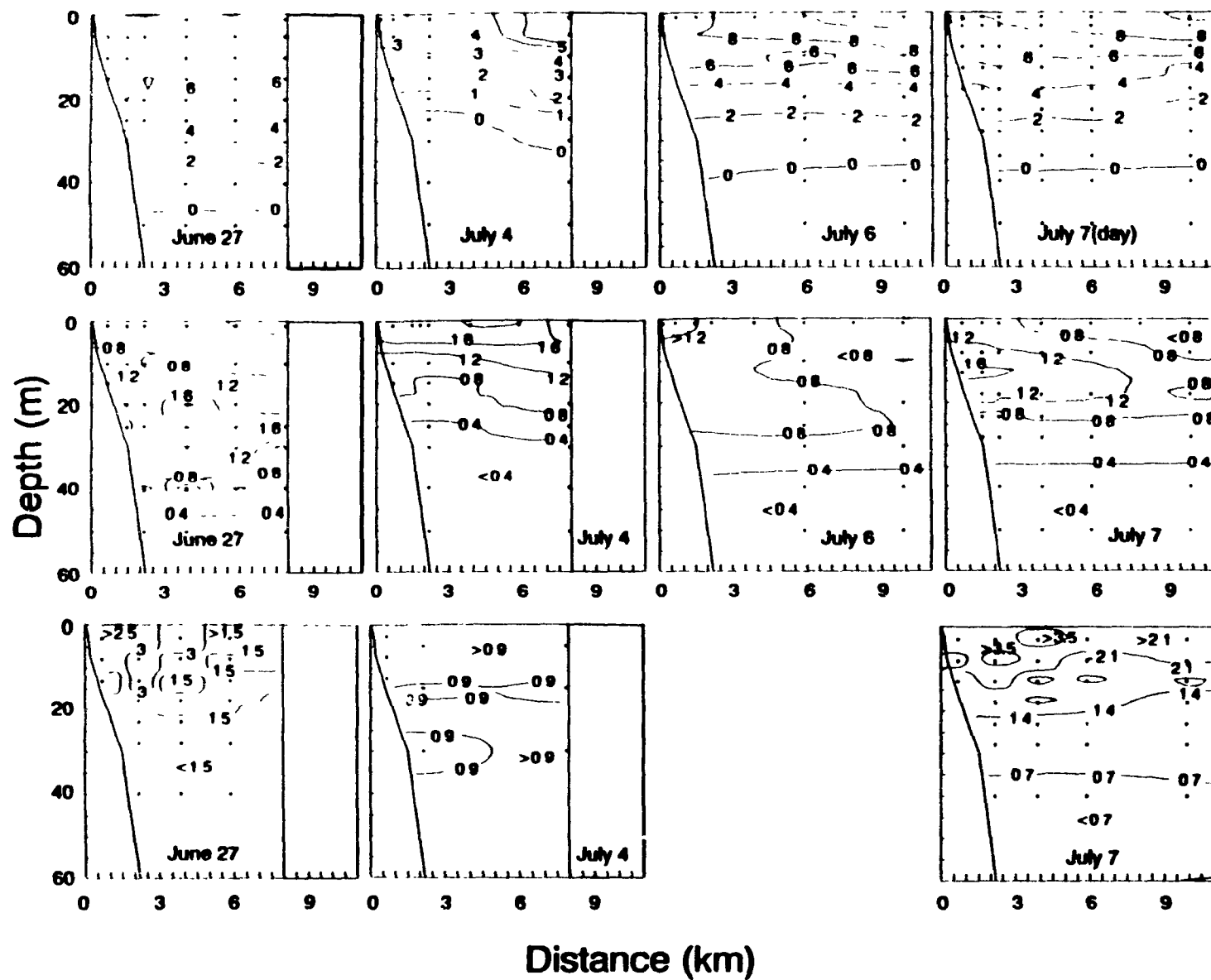


Figure 4 Vertical sections of water temperature (top row), chlorophyll a concentration ($\mu\text{g}\cdot\text{l}^{-1}$; middle row), and the biomass of microzooplankton ($\mu\text{g dry weight}\cdot\text{l}^{-1}$; size class 40 - 80 μm equivalent spherical diameter; bottom row) during July 9 - July 13, 1988 at coastal sites in western Conception Bay.

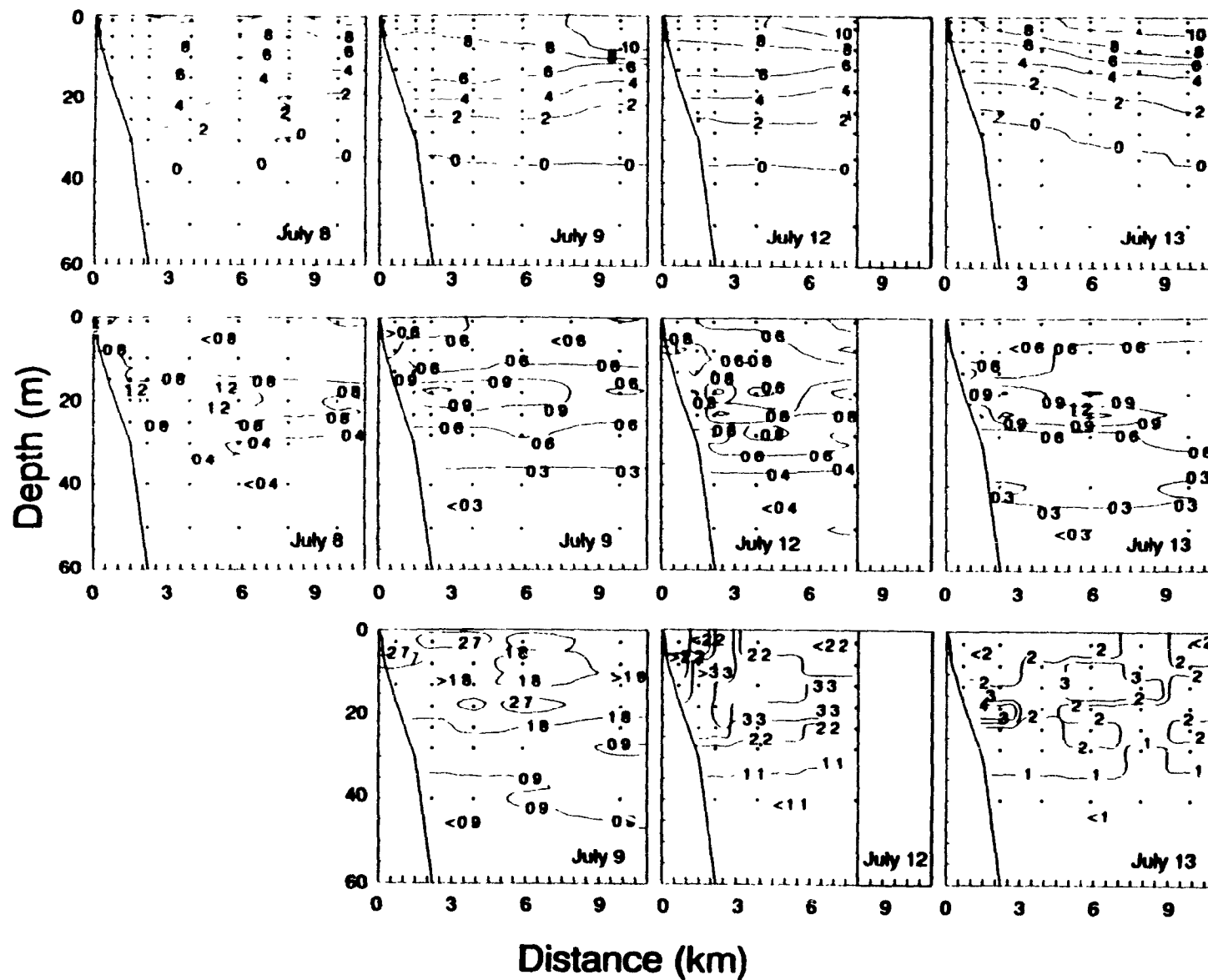


Figure 5 Vertical sections of chlorophyll a concentration ($\mu\text{g}\cdot\text{l}^{-1}$) in western Conception Bay during the summer of 1988.

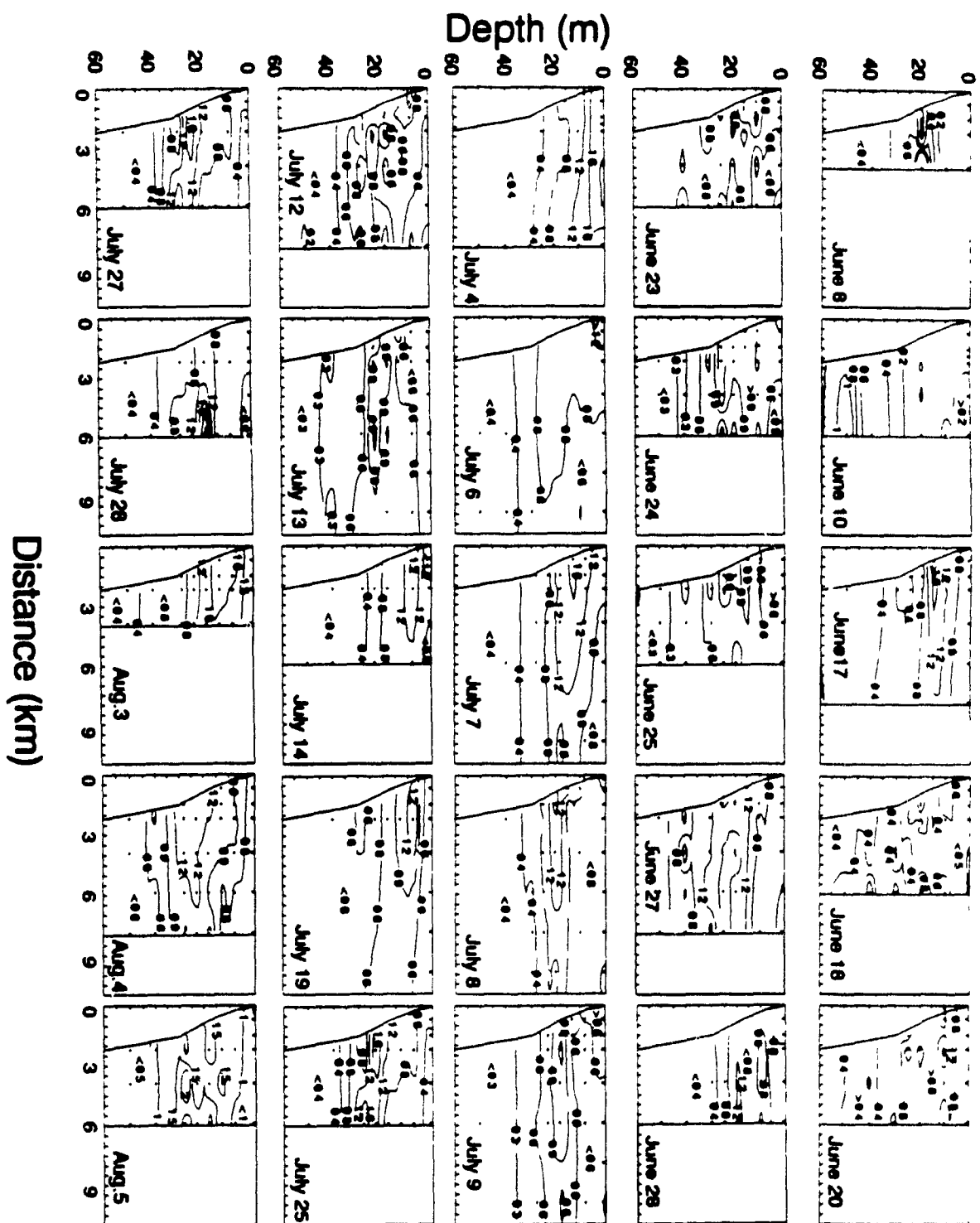


Figure 6. Light intensity at the depth of the 4.5 - 5° C isotherm during periods of upwelling and downwelling in 1988. Light intensities were estimated from extinction coefficients calculated from depths of secchi depth disappearance and from incident light intensities measured on the research vessel. The numbers shown on the line indicate the depths at which the isotherm was located on particular sampling days. Water temperature data are those associated with vertical profiles collected during plankton sampling.

Light Intensity Fluctuations During Upwelling & Downwelling

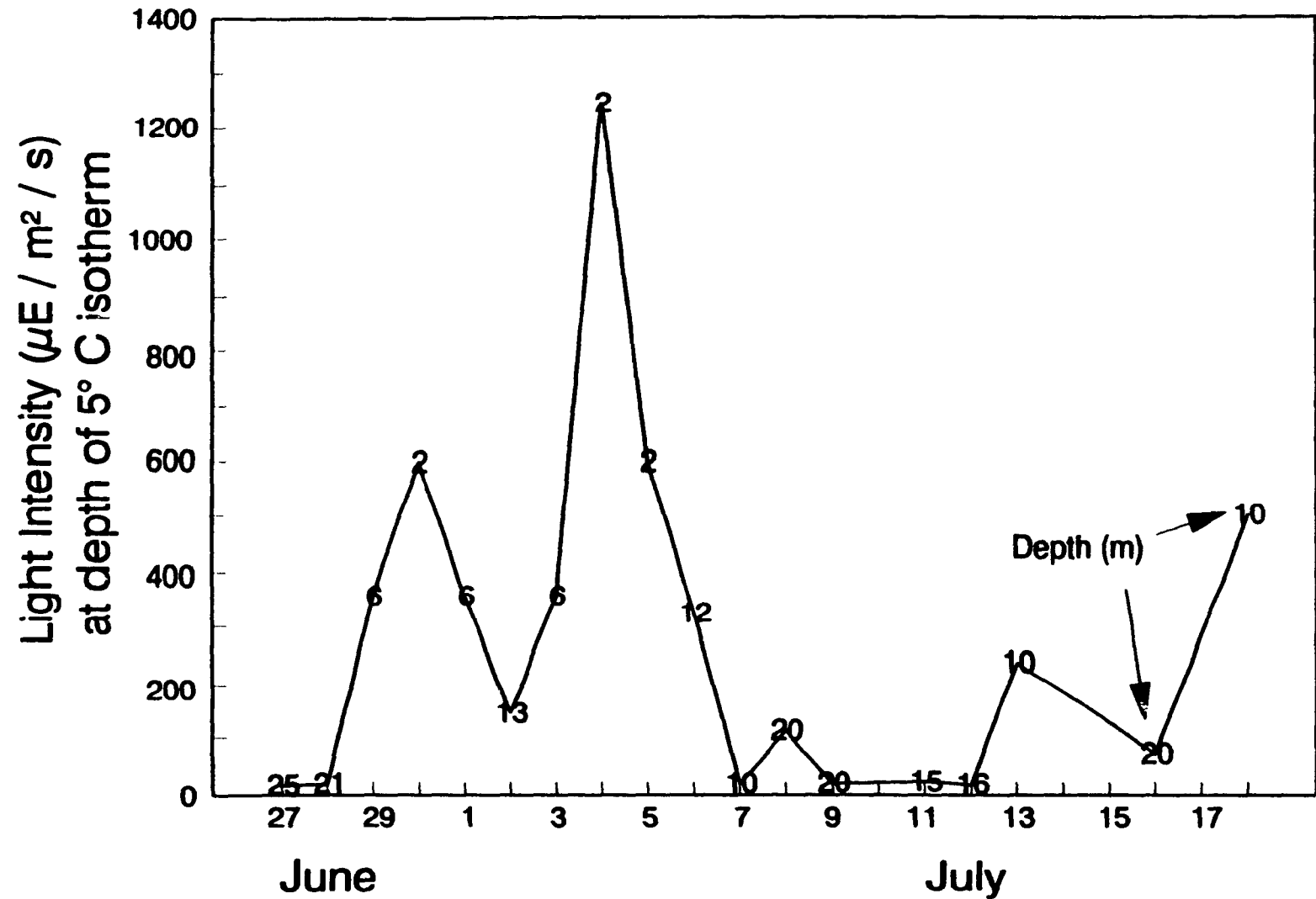
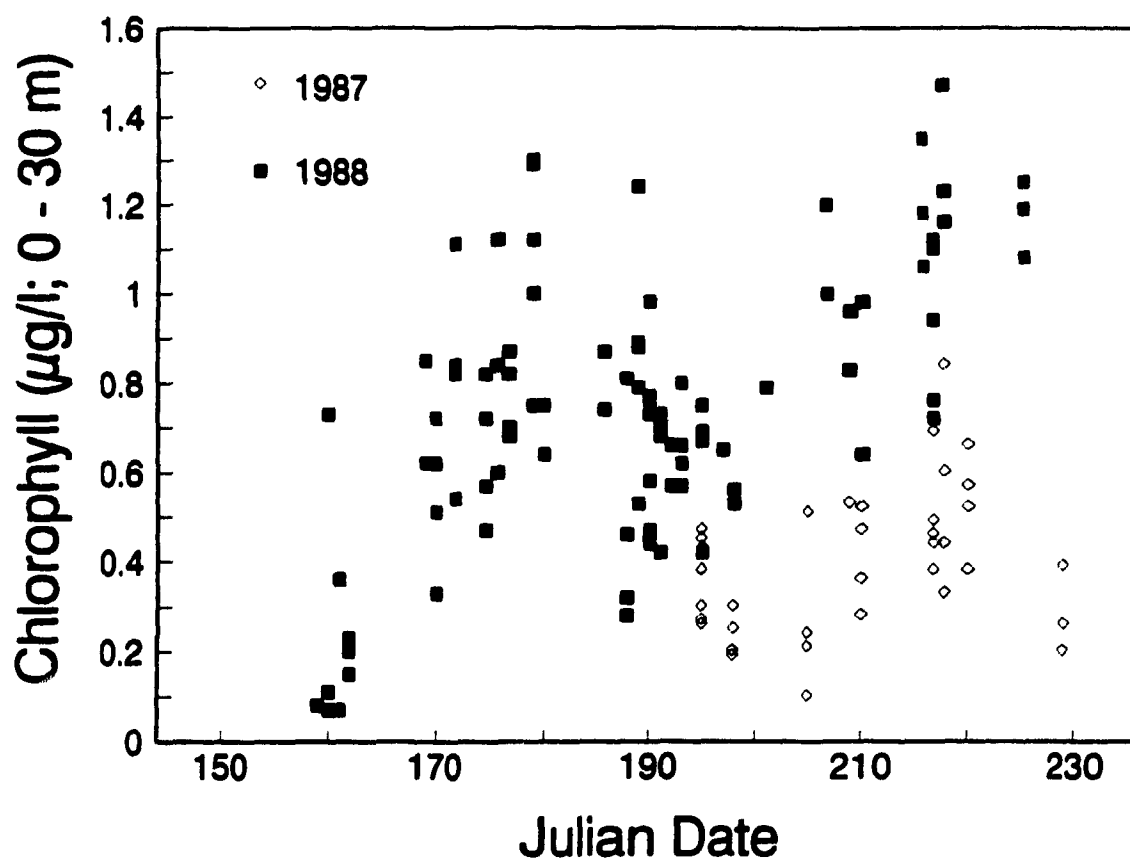


Figure 7 Seasonal changes in depth-averaged chlorophyll a concentration (0 - 30 m; $\mu\text{g}\cdot\text{l}^{-1}$) for 1987 (diamonds) and 1988 (squares). 1988 (Fig 8A, Model 1 and 2, Table 1).



1988 (Fig. 8). The slopes of the 1988 and 1987 linear regression models relating chlorophyll *a* to wind inputs (Models 1 and 2) did not differ significantly (*t*-test; $P > 0.50$). However, the intercept for the 1988 regression model was significantly larger than that for 1987 (ANCOVA: $P < 0.0001$), reflecting the higher overall chlorophyll *a* levels in 1988. A multiple regression model (Model 3, Table 1) employing, as inputs, the cumulative wind speed, and a dummy variable to account for interannual variability, explained 52 % of the variance in seasonal chlorophyll *a* concentration in 1987 and 1988 (Model 3, Table 1).

Depth-averaged water temperature explained an equivalent fraction of the variance in the 1988 chlorophyll *a* concentrations as cumulative wind speed (Fig. 9A; Model 4, Table 1). However when 1987 chlorophyll *a* concentrations were compared with predictions calculated from the 1988 chlorophyll - temperature relationship, the 1987 chlorophyll values differed dramatically and significantly from the 1988 pattern (Fig. 9B). In 1987, chlorophyll *a* concentrations decreased with increases in water temperature, and, more generally, were distributed towards lower values than those measured in 1988 (Kolmogorov-Smirnov test; $P < 0.001$; Fig. 7).

Chlorophyll *a* distributions: spatial patterns

The chlorophyll - wind speed regression models (Models 1 and 2, Table 1) were used to quantify the spatial distribution of chlorophyll *a* concentration. Residuals from the 1988 chlorophyll - wind speed regression model (Model 1) were significantly higher ($P < 0.05$; $R^2 = 0.08$) nearshore than offshore (Fig. 8C; Model 5, Table 1). In 1987, there was no significant pattern in the residuals from the 1987 chlorophyll - wind speed regression model (Fig. 8D; Model 2, Table 1).

Figure 8. Seasonal and spatial distributions of chlorophyll a concentration at stations along a transect across the western portion of Conception Bay, Newfoundland during 1987 and 1988. A. Relationship between depth-averaged chlorophyll a concentration (0 - 30 m) and cumulative longshore wind velocity starting from June 1, 1988. B. Comparison of 1987 seasonal chlorophyll a concentration and cumulative longshore wind velocity. The thin line represents predicted chlorophyll concentrations derived from the 1988 regression model (Model 1, Table 1). C, D. Spatial distribution of seasonally-detrended chlorophyll a concentrations measured in 1988 and 1987. Values in panels C and D are residuals from the best-fit regression models shown in panels A and B. Distances are specified as originating from the western shore of Conception Bay, Newfoundland at a site near Bryants Cove. In D, the fitted line is same as that shown in C.

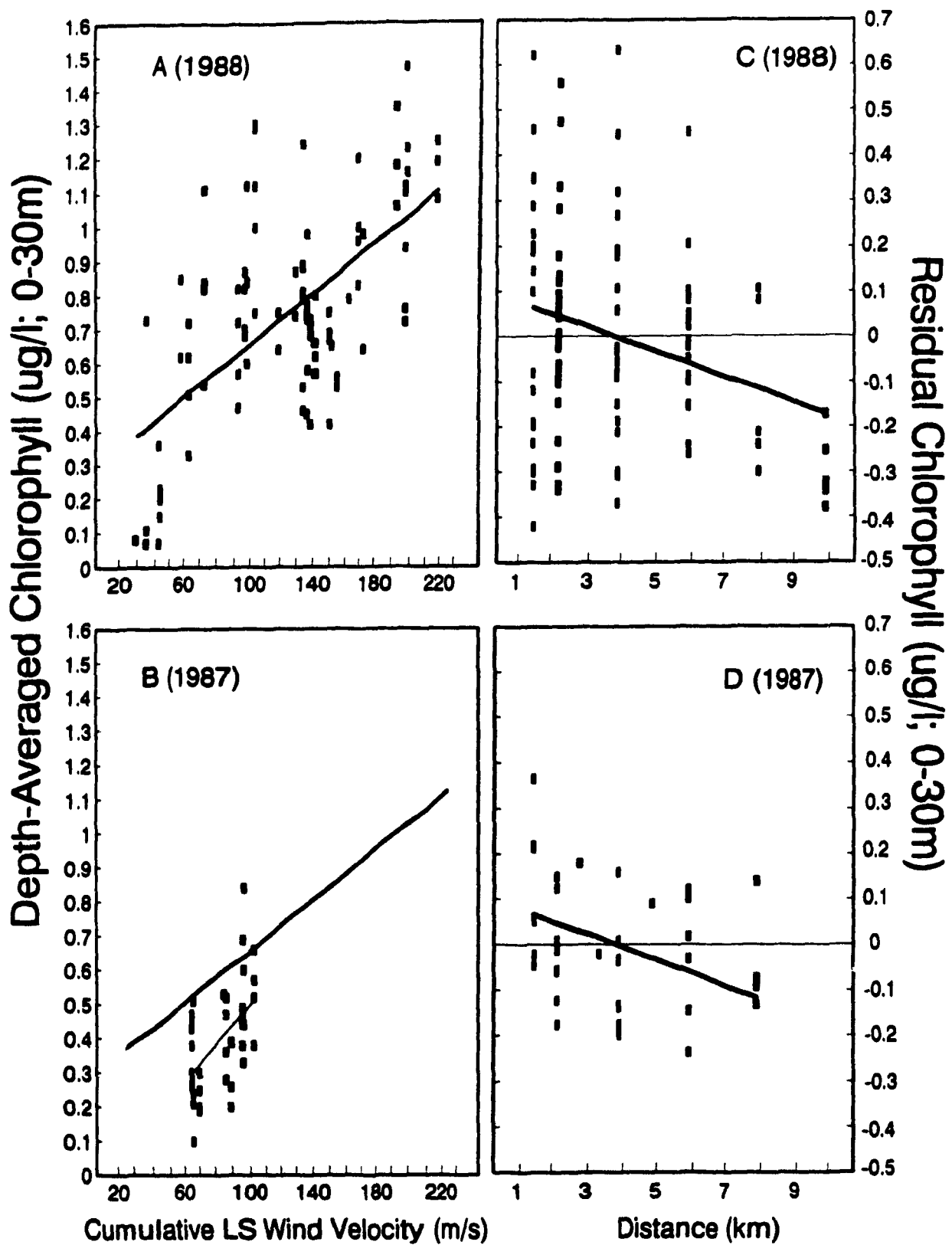


Table 1. Regression models and related statistics for describing temporal and spatial patterns in the distribution of chlorophyll *a* and microzooplankton biomass during the summers of 1987 and 1988. The fitted regression coefficient and its standard error are given for each model. R^2 is the proportion of total variance in the dependent variable that is explained by the independent variables. P denotes the significance level for fitted regression coefficients. RMSE is the residual mean square error of observed values from those predicted by the fitted model. N is sample size. CHLOR = depth-averaged chlorophyll *a* concentration ($\mu\text{g}\cdot\text{l}^{-1}$), SUM = cumulative longshore wind velocity ($\text{m}\cdot\text{s}^{-1}$), YEAR = dummy variable for sample year (if 1987, YEAR = 0; if 1988, YEAR = 1), TEMP = depth-averaged water temperature, DIST = distance (km) from western shore of Conception Bay, and ZOO = depth-averaged abundance of microzooplankton (40 - 80 μm size class; μg dry weight $\cdot\text{l}^{-1}$). RES8 and RES9 = residual zooplankton densities derived from Models 8 and 9 respectively. All depth-averages are calculated for the upper 30 m of the water column.

	Model	Year(s)	P	R^2	RMSE	N
1	CHLOR = $(0.00374 \pm 0.0005) \cdot \text{SUM}$ + (0.281 ± 0.069)	1988	< 0.0001 < 0.0001	0.37	0.244	93
2	CHLOR = $(0.00594 \pm 0.0016) \cdot \text{SUM}$ - (0.094 ± 0.135)	1987	0.0008 0.4917	0.28	0.137	37

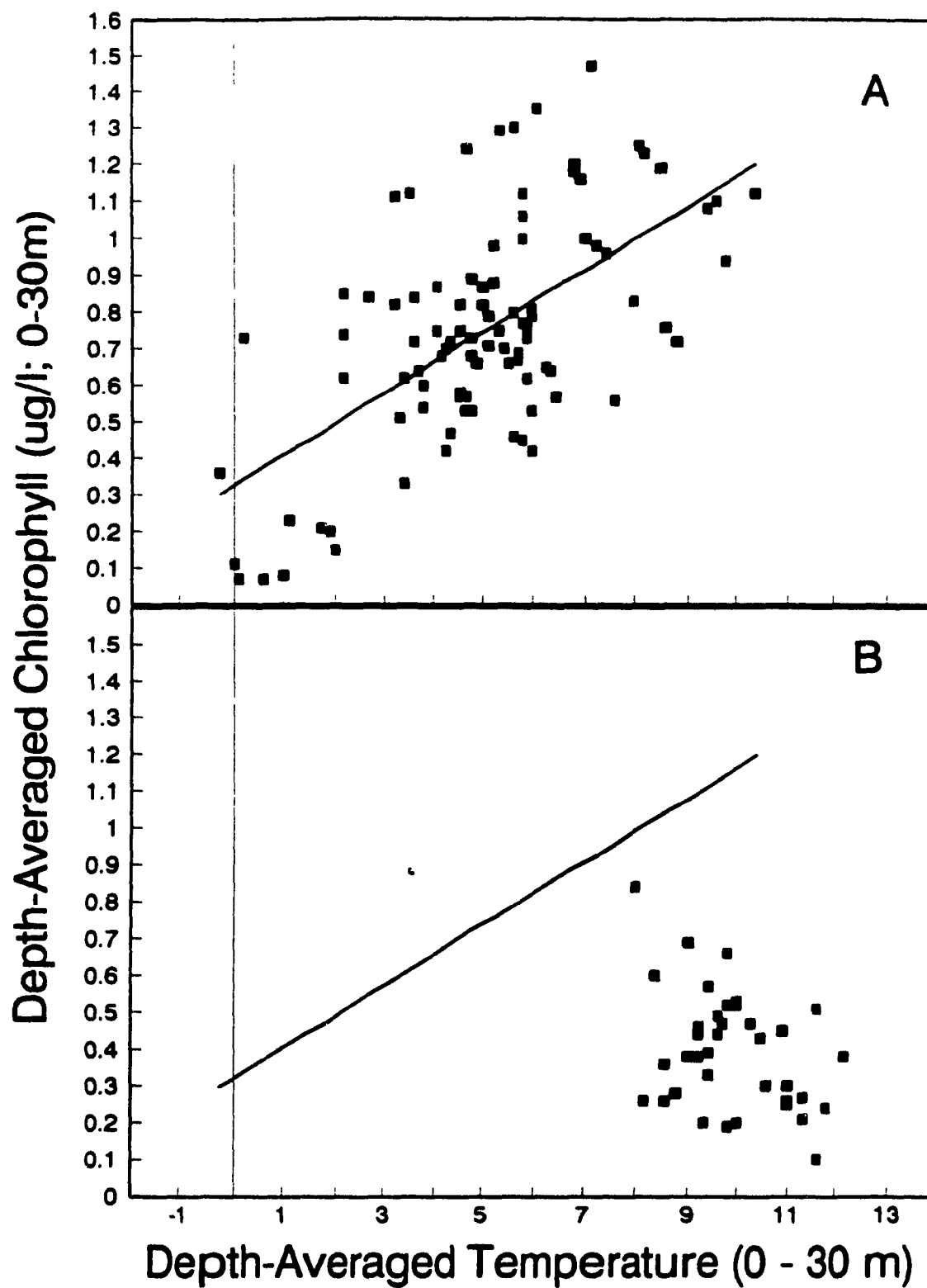
Table 1 (continued)

	Model	Year(s)	P	R ²	RMSE	N
3	CHLOR = (0.00380 ± 0.0045)•SUM + (0.190 ± 0.046)•YEAR + (0.082 ± 0.052)	87&88	< 0.0001 < 0.0001 0.1164	0.52	0.219	130
4	CHLOR = (0.084 ± 0.011)•TEMP + (0.326 ± 0.062)	87&88	< 0.0001 < 0.0001	0.37	0.242	93
5	CHLOR = (0.00385 ± 0.0005)•SUM - (0.0283 ± 0.010)•DIST + (0.376 ± 0.075)	87&88	< 0.0001 0.0076 < 0.0001	0.41	0.236	93
6	CHLOR = (0.00384 ± 0.0005)•SUM - (0.028 ± 0.0056)•DIST + (0.374 ± 0.068)	87&88	< 0.0001 < 0.0001 < 0.0001	0.46	0.230	99
7	CHLOR = (0.00389 ± 0.0004)•SUM - (0.027 ± 0.0005)•DIST + (0.183 ± 0.044)•YEAR + (0.182 ± 0.052)	87&88	< 0.0001 < 0.0001 < 0.0001 0.0006	0.56	0.208	136
8	ZOO = (0.122 ± 0.046)•TEMP + (1.202 ± 0.255)	1988	0.0107 < 0.0001	0.10	0.585	65

Table 1 (continued)

	Model	Year(s)	P	R ²	RMSE	N
9	$Z00 = (0.0050 \pm 0.019) \cdot \text{SUM}$ $+ (1.179 \pm 0.257)$	1988	0.0089 < 0.0001	0.10	0.584	65
10	$Z00_{\text{RES}} = - (0.062 \pm 0.027) \cdot \text{DIST}$ $+ (0.628 \pm 0.165)$	1988	0.0254 0.0018	0.14	0.462	36
11	$Z00_{\text{RES}} = - (0.048 \pm 0.030) \cdot \text{DIST}$ $+ (0.447 \pm 0.184)$	1988	0.1150 0.0204	0.07	0.515	36

Figure 9 A Scatterplot of depth-averaged chlorophyll a concentration (0 - 30 m) vs depth-averaged water temperature (0 - 30 m) at the time of sample collection during the summer of 1988. B. Same variables as shown in Fig. 10A, but for samples collected during the summer of 1987. The line represents predictions of 1987 chlorophyll a concentration derived from the 1988 chlorophyll - temperature regression model (Model 5) shown in A.



Vertical chlorophyll *a* profiles on two occasions in 1988 for the entire width of Conception Bay (Fig 10) were obtained. Chlorophyll *a* concentrations at sites on the western side of the sampling transect were 2 - 3 fold higher than those at sites on the eastern side of the transect. A new model (Model 6) including data from the two cross-Bay transects explained 46 % of the temporal and spatial variance of chlorophyll *a* concentration in 1988. The regression coefficients of this model were not significantly different from those associated with Model 5 (spatial scale = 0 - 10 km; 1988 data). Model 6 explained 30 % of the variance in the 1987 chlorophyll concentrations; the slope (1.03) of the regression model relating the observed 1987 chlorophyll *a* concentrations to chlorophyll *a* concentrations predicted by the 1988 model (Model 6) did not differ from 1 ($P > 0.05$), and the intercept (-0.21) had a standard error (± 0.30) which included 0. In total, 56 % of the seasonal, spatial, and interannual variability of depth-integrated chlorophyll *a* concentrations was associated with cumulative longshore wind speed, distance from the western shore, and a dummy variable for year (Model 7, Table 1).

Distributions of microzooplankton

As expected, the density of microzooplankton was greater in the upper 30 m of the water column than in deeper water (one-way ANOVA [$P < 0.0001$] and Student-Neumann-Keuls multiple comparison test [$P < 0.05$]; Fig. 11). Depth-related variation was greater for the larger size class; the abundance of plankton in the large and small size classes in the upper 30 m layer were > 3 -fold and ≈ 2 -fold higher, respectively, than densities in deeper water.

Within the upper 30 m, the overall mean densities of particles in

Figure 10 Horizontal and vertical distribution of chlorophyll *a* concentration on July 6 and 8, 1988 along a transect across Conception Bay, Newfoundland.

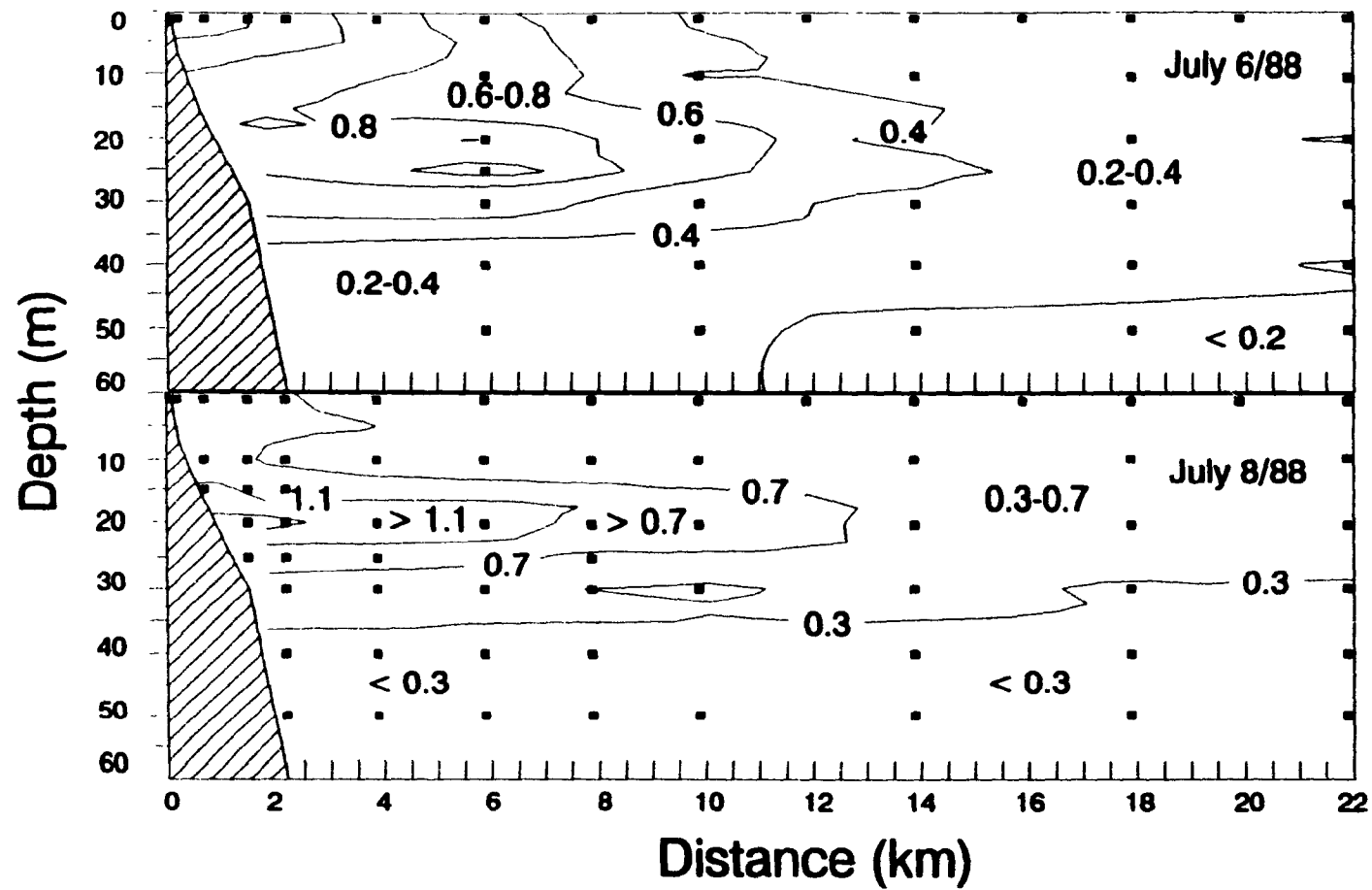
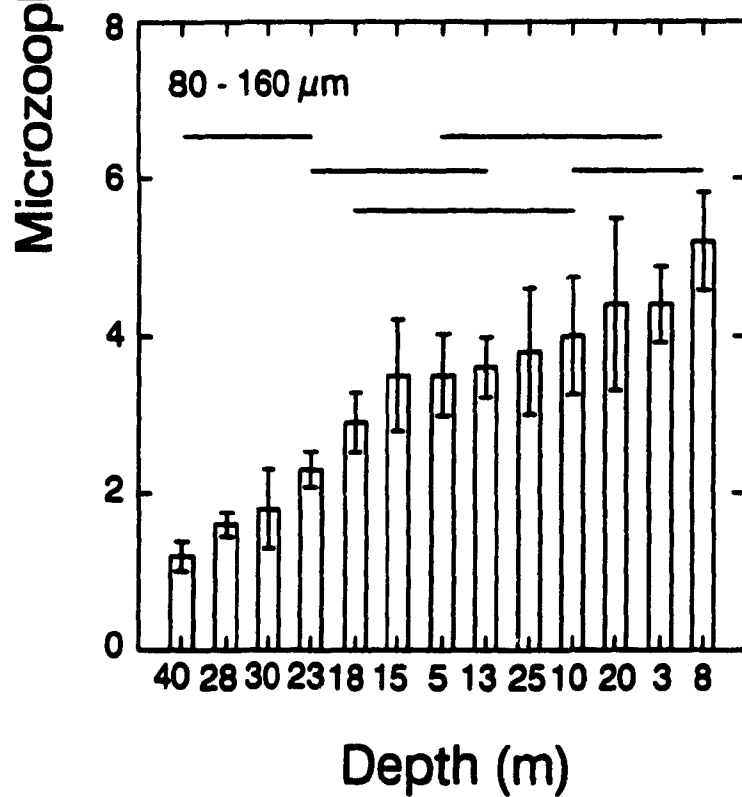
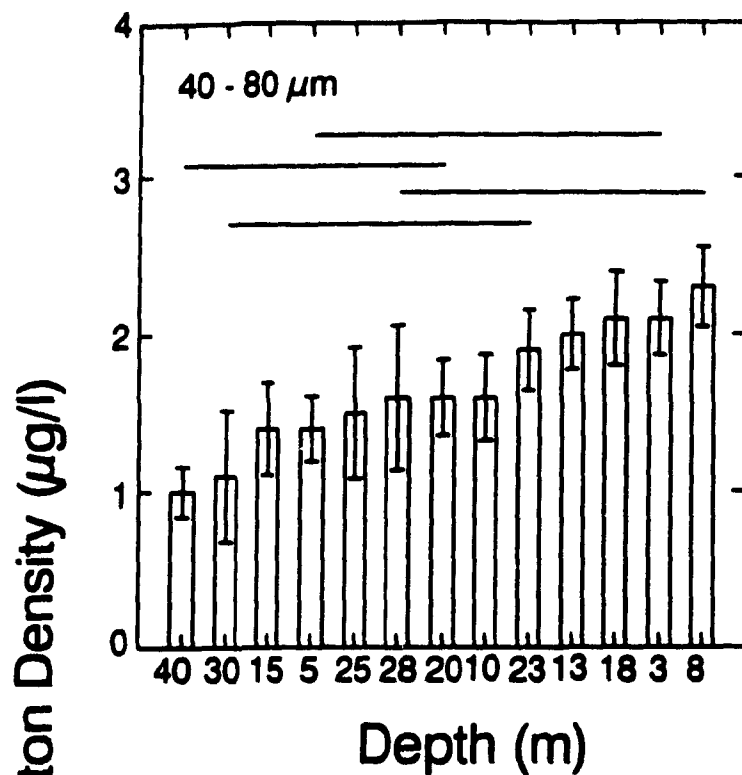


Figure 11. Depth-specific variation in the standing stock of two size classes of microzooplankton during 1988 (mean $\pm$ 2 standard errors) Note that depths are arranged in ascending order of the abundance of microzooplankton. Horizontal lines near the top of each panel join depths at which microzooplankton biomass did not differ significantly (Student-Neumann-Keuls test; $P < 0.05$).

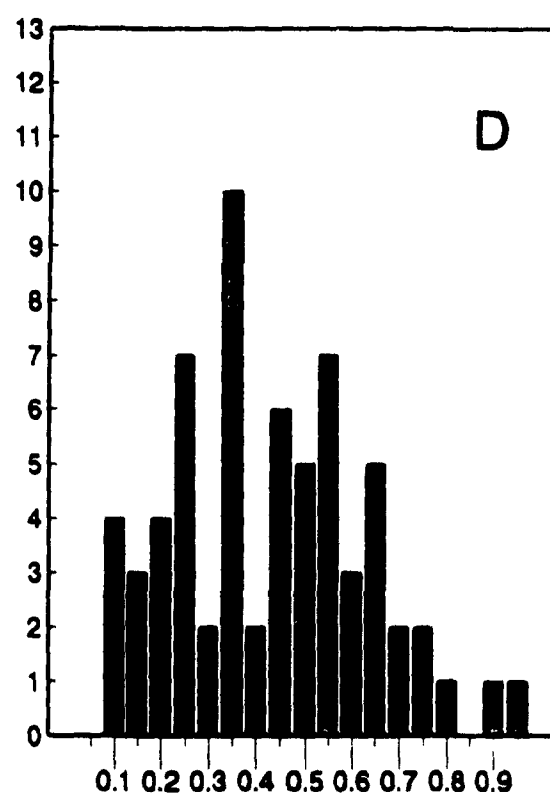
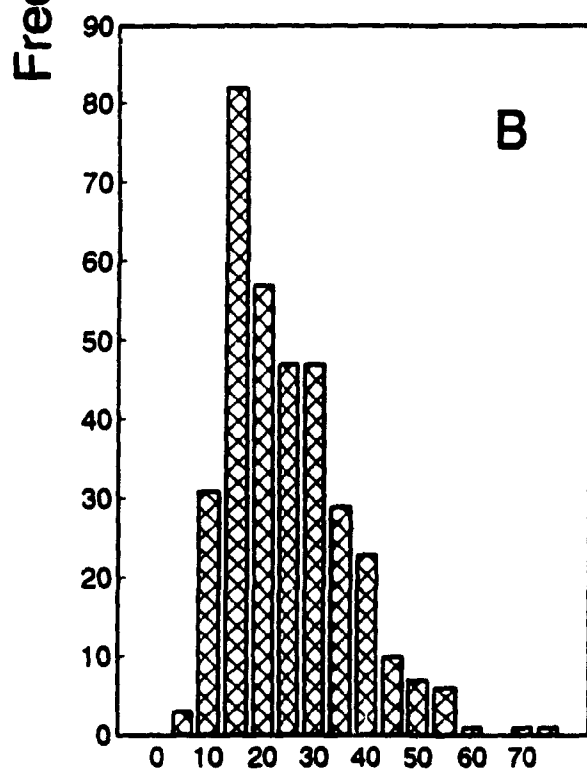
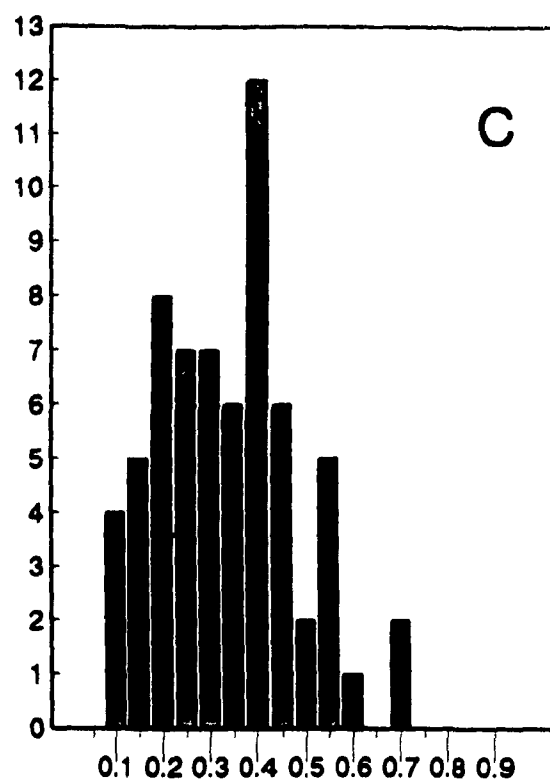
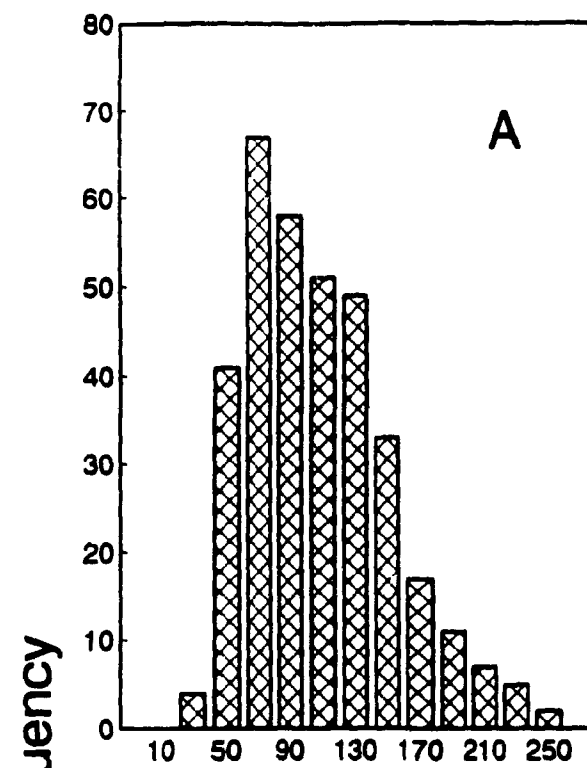


the 40 - 80 μm and 80 - 160 μm size classes were 98 ind. $\cdot\text{l}^{-1}$ (Fig. 12A; N = 345; SD = 43.9; CV = SD/mean = 0.45) and 22 ind. $\cdot\text{l}^{-1}$ (Fig. 12B; N = 345, SD = 11.5, CV = 0.52). The frequency distributions of the individual density estimates (Fig. 12A, B) for both size classes were skewed to the right, indicating that there were patches of high plankton density on some occasions during the summer. Densities within these patches exceeded overall median densities by 2 - 3 fold (Fig. 12A, B).

However, at any given station on any given sampling date, the variation in zooplankton density within the 30 m layer was relatively small. The mean (and median) values of the coefficients of variation associated with each depth-averaged zooplankton density estimate (Fig. 12C, D; N = 65) for each sampling date at each station were 0.31 and 0.41 for the 40 - 80 μm and 80 - 160 μm size classes, respectively (Fig. 12C, D). Hence, the primary zooplankton prey available to larval fish at these spatial scales appears to be distributed relatively homogeneously within the upper 30 m of the water column.

The depth-averaged zooplankton density within the upper 30 m of the water column increased significantly as depth-averaged water temperatures increased, and as longshore wind input increased during the summer ($R^2 = 0.10$; $P \leq 0.01$; Fig. 13A, B; also Models 8 and 9, Table 1). On sampling dates when both offshore (8 - 10 km from western shore of Conception Bay) and nearshore (< 8 km from shore) stations were sampled, residuals calculated from the zooplankton - temperature regression model (Model 8) were significantly higher closer to shore (Fig. 13C; $P = 0.0254$; N = 36. See also Model 10, Table 1). This pattern was also evident for residuals derived from the zooplankton - wind speed regression model (Model 9, Table

Figure 12. A, B. Frequency distributions of microzooplankton density at different depths within the upper 30 m of the water column. Panel A. distributions of the 40 - 80 μm size class; panel B: distributions of the 80 - 160 μm size class. C, D. Coefficients of variation (SD/mean) for depth-averaged microzooplankton densities within the upper 30 m of the water column. Panel C: distribution of the 40 - 80 μm size class. Panel D. distribution of the 80 - 160 μm size class.



Zooplankton Density (no./L)

Coefficient of Variation (SD/Mean)

1), although the level of statistical significance was lower ($P = 0.1150$; $N = 36$; Fig. 13D. See also Model 11, Table 1).

Seasonal changes in biomass of the larger zooplankton size class (80 - 160 μm) varied independently of both water temperature and cumulative longshore wind velocity ($P > 0.05$; $N = 65$).

Simulated encounter rates between larval capelin and microzooplankton

Prey densities used in these simulations were estimated from an empirical model relating zooplankton density to water temperature and distance from shore on those sampling dates when both nearshore (< 8 km) and offshore (> 8 km) stations were sampled ($ZOO = 0.343 \cdot TEMP - 0.097 \cdot DIST + 0.706$; $N = 36$; $R^2 = 0.36$; $P = 0.0002$). Simulated encounter rates for capelin larvae preying on microzooplankton prey at the nearshore site (2.2 km from shore; mean prey density = $170 \text{ particle} \cdot \text{l}^{-1}$; 95 % confidence limits = 123 - 217) were 19 % and 30 % higher for wind speeds of 4.2 and $5.8 \text{ m} \cdot \text{s}^{-1}$, compared to a nonturbulent environment (i. e. wind = $0 \text{ m} \cdot \text{s}^{-1}$; Fig. 14). At the offshore site (mean prey density = $130 \text{ particles} \cdot \text{l}^{-1}$; 95 % confidence limits = 85 - 175), where the influence of upwelling-generated turbulence is likely to be smaller, wind-induced small-scale turbulence increased simulated encounter rates by 4 - 7 % over those estimated for $0 \text{ m} \cdot \text{s}^{-1}$ wind speed.

Overall, larvae located at the nearshore station had higher encounter rates than those at the offshore station. For example, at a wind speed of $4.2 \text{ m} \cdot \text{s}^{-1}$, larvae located in the nearshore zone are estimated to encounter 50 % more prey than those at the offshore station. This is due to the combined effects of higher mean prey density at the nearshore station, compared to that at the offshore station, and to the additional

Figure 13. A, B. Relationships between the biomass of depth-averaged microzooplankton (40 - 80 μm), and depth-averaged water temperature (A) and cumulative longshore wind velocity (B) at stations on a sampling transect in the western portion of Conception Bay, Newfoundland C, D Spatial distribution of residuals from the best-fit regression model shown in panel A (see Table 1 for model parameters). Note that in panels C and D the sample size is smaller ($N = 36$) than in panels A and B ($N = 65$) because sampling dates when offshore stations (those beyond 8 km from shore) were not sampled have been excluded.

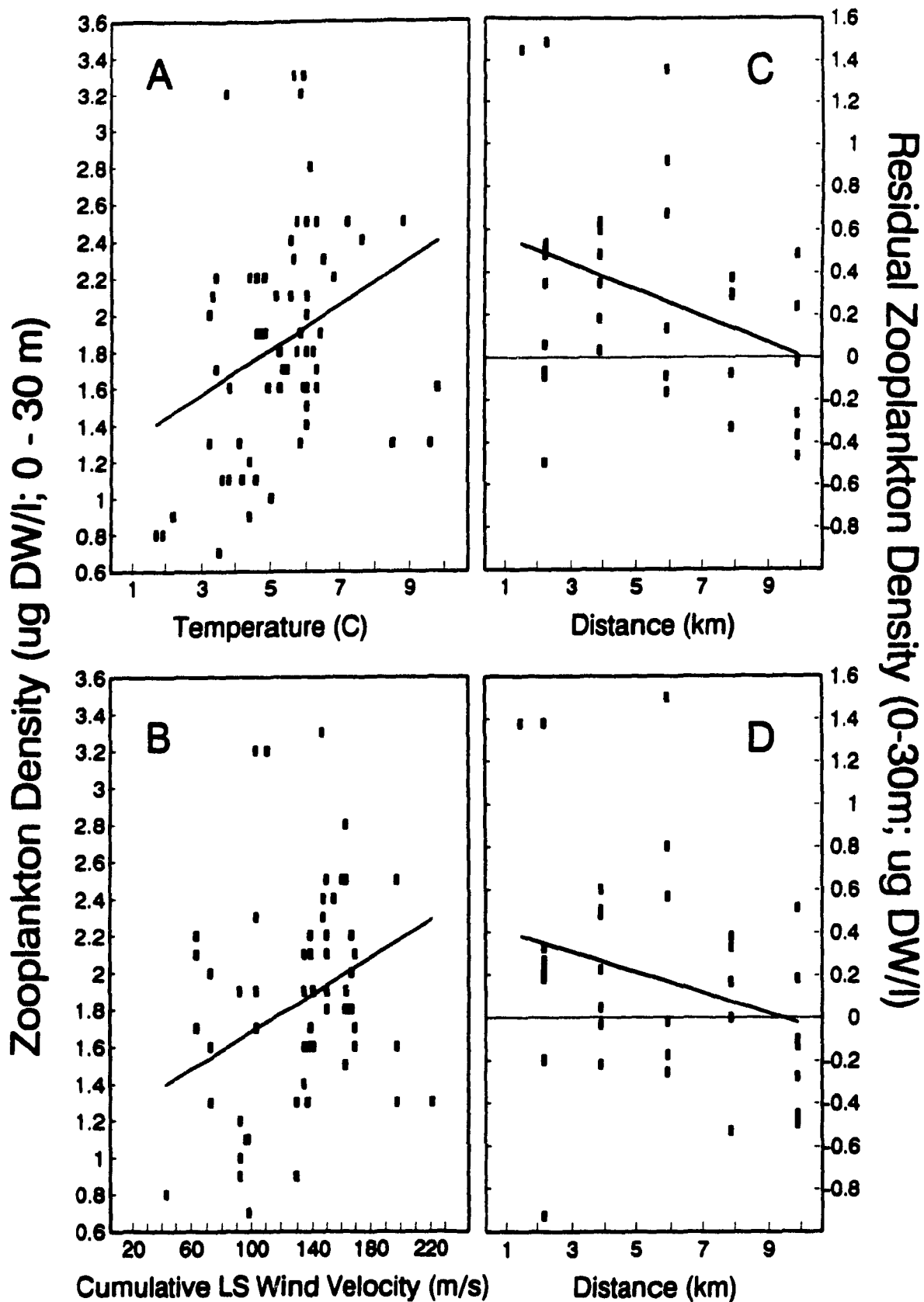
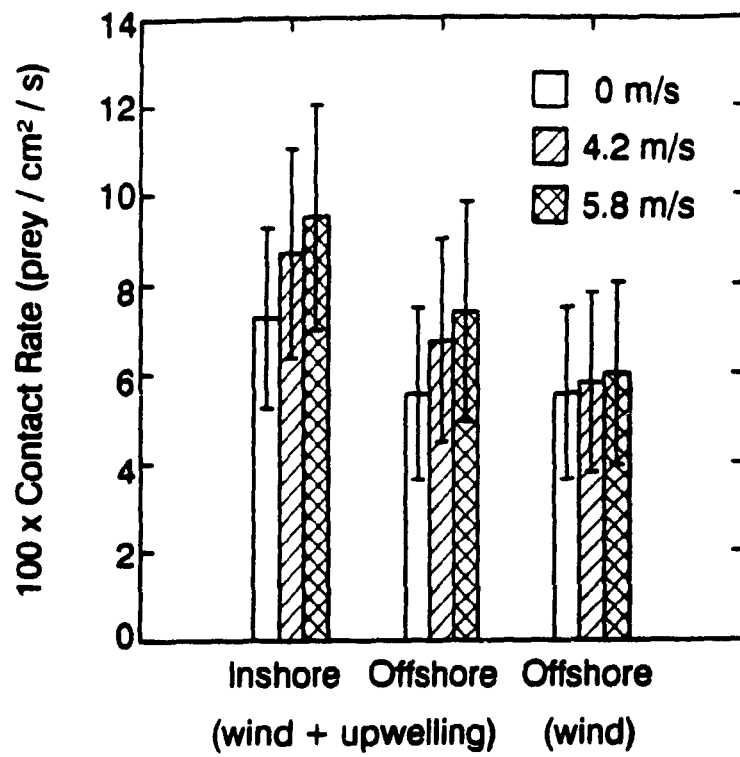


Figure 14. Simulated encounter rates between larval capelin, Mallotus villosus, and microzooplankton prey in the 40 - 80 μm size class for three wind speeds and at 2 sites exposed to different magnitudes of intermittent upwelling. The inshore site, located 2.2 km from land, is more likely to be exposed to intermittent upwelling/downwelling than is the offshore site (9.9 km from shore; see Chapter 4). Zooplankton densities (inshore mean = 170 $\text{prey} \cdot \text{l}^{-1}$; 95 % C. L. = 123 - 217, offshore mean = 130 $\text{prey} \cdot \text{l}^{-1}$, 95 % C. L. = 85 - 175) in these simulations were estimated from those sampling dates when stations located > 7 km from shore were sampled ($200 = 18.05 \cdot \text{TEMPERATURE} - 5.12 \cdot \text{DISTANCE} + 37.16$). Dissipation rates used as inputs for the estimation of contact rate were estimated from an empirical model (Chapter 2, Model 4). The inshore site was assumed to have turbulence generated by both wind and upwelling-related shear and mixing, while for the other two simulations, the offshore site was assumed to have turbulence generated by wind and upwelling circulation, and only by wind.



turbulence nearshore generated by upwelling circulation.

Discussion

General features of plankton distributions in Conception Bay

Seasonal patterns in the concentration of chlorophyll *a* varied more predictably with wind energy inputs than with water temperature during the summers of 1987 and 1988. This pattern is consistent with the concept of hydrodynamic regulation of primary production (Margalef 1978; Levasseur et al. 1984) and suggests that the influence of wind on phytoplankton abundance and production was similar during both summers. The most probable explanation for these patterns derives from the effects of wind on both nutrient supply to the photic zone, and on the light regime experienced by the phytoplankton community associated with the nutricline.

Wind-induced mixing during upwelling/downwelling events transported nutrients higher into the photic zone. These upwelling events can increase photic zone nutrient levels to within $\approx 50\%$ of pre-bloom levels (see Chapter 4). In other areas, similar relative increases in photic zone nutrient levels have been shown to cause secondary phytoplankton blooms (e. g. Ziemann et al. 1991). The sporadic supply of nutrients to the photic zone in western Conception Bay is, therefore, highly likely to be at least partly responsible for the increase in chlorophyll *a* concentration observed during the summers of 1987 and 1988 in this region.

Upwelling/downwelling events also alter the irradiance levels to which phytoplankton living in deep water are exposed. The increased irradiance at nutricline depth during upwelling is comparable to that which maximizes photosynthesis and doubling rates in both laboratory and

natural populations of diatoms and dinoflagellates ($100 - 250 \mu\text{Ein}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; Eppley 1977, Chan 1978, Platt et al. 1982; Lewis and Smith 1983). During most upwelling episodes in 1987 and 1988, vertical displacements of isotherms were approximately 10 - 15 m (Chapter 4). These displacements increased irradiance levels at the nutricline from ≈ 20 to $\approx 200 \mu\text{Ein}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 6) and typically persisted for at least 24 hours (Fig. 1), a time sufficient to enable phytoplankton to adapt to higher light intensities (Auclair et al. 1982; Lewis and Smith 1983; Gallegos et al. 1983). Phytoplankton populations periodically exposed to higher irradiance during upwelling episodes would, therefore, experience near-maximal rates of photosynthesis after a short period (< 6 h; Gallegos et al. 1983) of physiological adjustment. The influence of episodic upwelling on photosynthesis rates is, therefore, likely to be broadly consistent with theoretical analyses of the beneficial effect of other forms of vertical motion (e.g. internal waves and surface layer mixing) on rates of photosynthesis and photoadaptation (Lande and Yentsch 1988; Lande and Lewis 1989).

The magnitude of the chlorophyll *a* concentration, as expressed by the intercept derived from relationships linking seasonal chlorophyll *a* concentration to wind energy inputs (Model 1 and 2), differed between years. This may be a consequence of interannual variability in the size and taxonomic composition of the residual phytoplankton community remaining after the spring bloom. Phytoplankton that participate in the spring bloom often remain viable as they sink through the water column (Ziemann et al. 1991), and can continue to make important contributions (10 - 50 %) to primary production during their descent (10 - 50 %; Ziemann

et al. 1991). If one or more mixing or upwelling events were sufficiently strong to advect a portion of this phytoplankton community back into the photic zone, or if such events re-distributed nutrients and phytoplankton back into the surface layer, primary production rates, and possibly the standing stock of phytoplankton cells, would increase. These phenomena have been observed in lakes exposed to artificial mixing during the summer (Lund 1971). Moreover, the phytoplankton cells which become re-distributed during mixing or upwelling/downwelling will serve as the phytoplankton inoculum in the post-bloom water column.

The timing of wind events, relative to the sinking rate of the bloom community, is therefore likely to be an important factor in determining the initial abundance and physiological status of the post-bloom phytoplankton community. Subsequently, the frequency, magnitude and duration of mixing and upwelling/downwelling events will act to regulate the general level of phytoplankton abundance during the post-bloom period (Fig. 8). It follows that, given a particular inoculum phytoplankton community, an important factor determining the abundance, taxonomic composition, and rate of production of phytoplankton during the remainder of the summer will be hydrodynamic forcing caused by wind energy inputs (e. g. Margalef 1978; Levasseur et al. 1984; Harris 1986). These replenish the nutrient supply in the lower portion of the photic zone, and periodically free phytoplankton from light-limitation.

There were also important spatial patterns in the distribution of chlorophyll a. At those sampling stations most frequently and dramatically influenced by upwelling, depth-averaged chlorophyll a concentrations were highest (i. e. within $\approx$ 5 km of shore). This pattern was most obvious

after the cumulative influence of wind was removed statistically, and was more apparent during the summer of 1988 when upwelling was stronger and more frequent. The seasonal accumulation of chlorophyll *a* nearshore is also likely to be assisted by local patterns in current flow which include occasional periods of downwelling. These are likely to retain new production near its site of synthesis, and therefore, in the region where it can be consumed by secondary producers, including first-feeding larval fish.

The temporal and spatial patterns in zooplankton abundance were similar to those observed for chlorophyll *a* concentrations. Densities of particles in the smaller size class (40 - 80 μm) increased during the summer, but were more strongly associated with water temperature than wind energy input. This may be due to the fact that this group consists principally of protozoan and metazoan herbivores (e. g. tintinnids, copepod eggs and nauplii) which are less directly influenced by fluctuations in light and nutrients, and whose rates of feeding and production are more likely to be influenced by water temperature (e. g. Davis 1987), food supply (e. g. Dagg 1977; Beckman and Peterson 1986, Verity 1986), and levels of small-scale turbulence (Rothschild and Osborn 1988; Chapter 3).

As expected, therefore, the abundance of this size class was also significantly greater at nearshore stations than at offshore stations. Nearshore stations had more phytoplankton prey for consumption, and were more turbulent because of mixing associated with upwelling and downwelling (Chapter 2; Csanady 1989).

There were no significant patterns in the distribution of the larger

zooplankton size class (80 - 160 μm). Plankton in this size class (eggs, nauplii and copepodite stages of copepods; larger tintinnid species), or adults in larger size classes that produce offspring in this size range (e. g. Pseudocalanus minutus and Calanus finmarchicus; Dagg 1977), would require more time and larger quantities of food before reproducing (Kjørboe et al. 1985; Verity 1986; Peterson 1988). During this interval, populations would likely be re-distributed within the sampling domain through advection and mixing during upwelling and downwelling. They might also be completely exported from the sampling domain (Frank and Leggett 1982; Taggart and Leggett 1987).

The growth and/or reproductive response of larger zooplankton, and perhaps of other size classes to wind-induced upwelling could perhaps be more effectively modeled if wind inputs, seasonal temperature variability, or local in situ prey densities were compared to rate variables (e. g. copepod egg production rate; grazing rate), rather than to standing stock as was done in this study. For example, metazoan (e. g. copepod) reproductive rates are known to respond quickly (24 - 48 hours, Durbin et al. 1983; Kjørboe et al. 1985; Beckman and Peterson 1986) to temporal variability in food abundance. Even though I observed no spatial patterns in the distribution of zooplankton in the larger size class, the rate of production of small zooplankton, and their rates of development (Saiz and Alcaraz 1991) and metabolism (Alcaraz and Saiz 1991), may still have been higher nearshore because this region has more phytoplankton and is more turbulent.

Overall, zooplankton densities in western Conception Bay were low compared to those estimated for several other geographic areas (Chapter

1, Fig. 3) The difference between zooplankton densities observed in Conception Bay and elsewhere is, however, partly a consequence of comparing the abundance of zooplankton in different size classes. In this study, I intentionally restricted the size class of zooplankton studied to the 40 - 80 μm range in order to quantify the abundance of suitable prey for larval capelin. The zooplankton densities compiled in Chapter 1 encompass a much larger size range (e. g. 102 - 505 μm). This differences in size classes makes any comparison of plankton densities among sites, including Conception Bay, difficult.

To more accurately assess food availability for larval capelin, I compared zooplankton densities observed in 1988 with those used in laboratory and field experiments in which larval fish ingestion and growth rates were measured.

Plankton densities observed in 1988 would be expected to produce low ingestion rates based on predictions made by an empirical model derived from laboratory experiments (see Model 4, Chapter 1). Food densities observed in Conception Bay were below the range of food densities (7.2 - 88000 $\mu\text{g}\cdot\text{l}^{-1}$) used to derive this model. However, if the minimum food density in the laboratory food density range (7.2 $\mu\text{g}\cdot\text{l}^{-1}$) is used for estimating capelin ingestion rates, the predicted food consumption rate is 0.28 $\mu\text{g}\cdot\text{day}^{-1}$, or 1.3 % body weight $\cdot\text{day}^{-1}$. This estimate assumes that a newly hatched capelin larva is, on average, 4.8 mm long (Fortier and Leggett 1982) and weighs 21 μg when dry (dry weight - standard length relationship given by Moksness 1982).

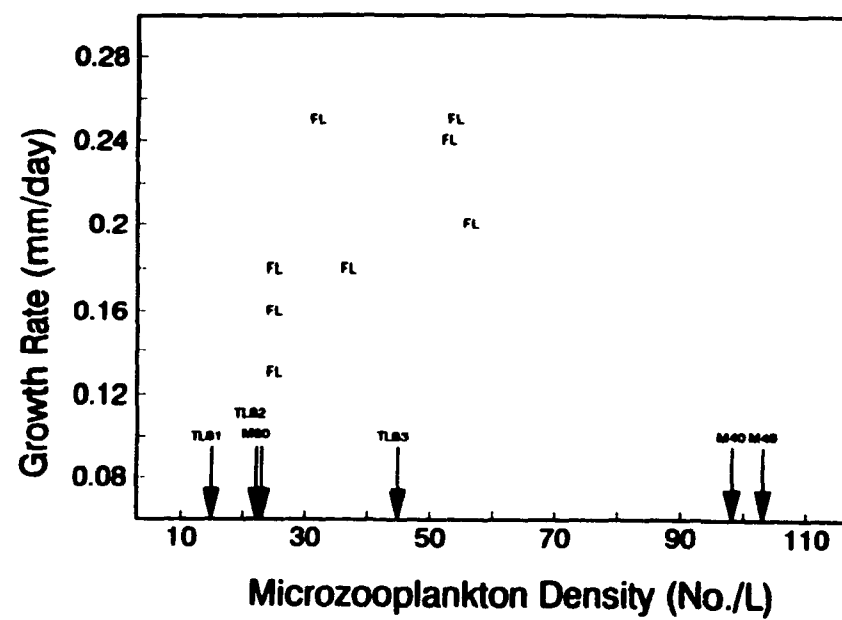
When larval capelin were reared in predator-free in-situ enclosures at food densities of 0.5 - 1.2 $\mu\text{g}\cdot\text{l}^{-1}$ (25 - 56.5 prey $\cdot\text{l}^{-1}$; size = 40 - 80

μm ; dry weight = $0.019 \mu\text{g}$ per prey), growth rates were $0.13 - 0.25 \text{ mm}\cdot\text{day}^{-1}$ (temperature = 6.5°C , Frank and Leggett 1986). These growth rates equate to specific growth rates of $6.7 - 12 \%$ body weight $\cdot\text{day}^{-1}$. Assuming a gross growth efficiency of 33% (mean for 9 species; see Table 7, Chapter 1) and 12 hours of light for feeding, the ingestion rates of larval capelin reared by Frank and Leggett (1986) were $16 - 29 \%$ body weight $\cdot\text{day}^{-1}$. By comparison, the predicted maximum ingestion rate (food density $\geq 185 \mu\text{g}\cdot\text{l}^{-1}$) for newly-hatched capelin larvae at 6.5°C is $5.5 \mu\text{g}\cdot\text{day}$ or 26% body weight $\cdot\text{day}^{-1}$ (see Model 4, Chapter 1). Consequently, even though prey densities in the enclosure experiments of Frank and Leggett (1986) were > 100 -fold lower than prey densities required to maximize feeding rates in the laboratory, estimated ingestion rates were near maximal (i.e. $16 - 29 \%$ vs. 26% predicted by the laboratory-based ingestion rate model).

These comparisons indicate that larval capelin, as with larvae of many other species (e.g. Economou 1987, Jenkins 1987) can grow at near maximal rates in nature, even though (1) food densities are very low (Fig. 15), and (2) laboratory experiments would predict low ingestion rates (Chapter 1). The comparisons also show that the range of prey densities (Fig. 12A, B) observed at Conception Bay sampling stations in 1988 probably supported near-maximal rates of growth and ingestion in larval capelin (Fig. 15), assuming that other components of the 1988 diet (e.g. prey visibility, escape behaviour, chemical composition, Checkley 1982; Govoni et al. 1986) were similar to those in the experiments of Frank and Leggett (1986).

Fish larvae feeding in the coastal area of Conception Bay in 1988 are unlikely to have benefitted from finescale prey patchiness (5 m

Figure 15. Growth rates for larval capelin relative to the densities of prey in the 40 - 80 μm size class, as estimated by Frank and Leggett (1986). These data are denoted as FL. Also shown for comparison are mean zooplankton densities measured in Conception Bay during the summers of 1981, 1982, 1983 (Taggart and Leggett 1987; size class = 90 - 130 μm ; denoted as TL81, TL82, TL83), 1988 (denoted as M40 for size class 40 - 80 μm and as M80 for 80 - 160 μm size class), and the median density (denoted as M46) for 46 other sites around the world (see Fig. 2B, Chapter 1), as estimated by assuming a particle dry weight of 0.20 μg per individual.



vertical scale). Patches in the vertical dimension contained prey densities only $\approx 30 - 40 \%$ higher than depth-averaged prey densities. Nevertheless, it is possible that microscale patches of prey occurred at scales of cm's to m's. Such patches would occupy water volumes less than 2 m^3 and would be averaged by pump sampling. Densities of zooplankton within such patches are typically 2 - 10 fold higher than the density obtained by averaging individual plankton densities (Jenkins 1988, Owen 1989).

Small-scale turbulence increased estimated encounter rates of larval capelin in Conception Bay during the summer of 1988 by 4 - 30 %. This increase is small relative to the potential increases observed elsewhere (Chapter 3). This occurred because prey densities (range = $85 - 217 \text{ ind.} \cdot \text{l}^{-1}$) and swimming speeds assumed to be representative of those for larvae ($0.42 \text{ cm} \cdot \text{s}^{-1}$) and their prey ($0.095 \text{ cm} \cdot \text{s}^{-1}$) are considerably larger than those used in earlier encounter rate simulations (Chapter 3; prey density = $5 - 35 \text{ ind.} \cdot \text{l}^{-1}$; prey velocity = $0.02 - 0.05 \text{ cm} \cdot \text{s}^{-1}$; larval velocity = $0.2 - 0.5 \text{ cm} \cdot \text{s}^{-1}$).

In addition, wind speeds in Newfoundland during summer (Chapter 4; Taggart and Leggett 1987) are relatively low compared to those measured at other areas or times of the year (e.g. United Kingdom meteorological stations [Bowers and Simpson 1987]; California [Husby and Nelson 1982]). tidally-generated turbulence is also relatively small in Conception Bay. Finally, a wind-based model of mixed layer turbulent dissipation rate may underestimate small-scale turbulence in western Conception Bay because additional turbulence generated by upwelling circulation and mixing may not have been adequately quantified. All of these factors reduce the

estimated contribution of turbulence to encounter rates between predators and prey when compared to its potential impact on larval encounter rates in other environments (Chapter 3).

Synthesis upwelling, plankton distributions and larval capelin emergence behaviour

As discussed by Frank and Leggett (1982; 1983), air-sea interactions which influence the nearshore hydrography of Conception Bay, and other sites distributed over 700 km of Newfoundland coastline, have exerted a strong influence on the spawning behaviour of the local ichthyofauna. Most capelin spawning occurs during late June - early July at sites having appropriately-size beach sediments (Carscadden et al. 1989) and where the local hydrography is dominated by frequent upwelling episodes (Frank and Leggett 1981; Leggett et al. 1984). As shown here, these create significant temporal and spatial patterns in the distribution of plankton in Conception Bay, and probably elsewhere along the east coast of Newfoundland and Labrador. These gradients are associated with increased nutrient flux to the photic zone and with increased irradiance received by the phytoplankton community near the nutricline during upwelling episodes.

The timing and location of spawning by capelin are lifehistory characteristics shared by several other fish species in Conception Bay (Frank and Leggett 1982; 1983). Larvae produced in shallow water by these species occupy the same water masses as do larval capelin (Frank and Leggett 1982; 1983). In regions where plankton biomass is low but is distributed in consistent spatial patterns across years, there is likely to be strong natural selection for spawning sites and behaviours that

place first-feeding larvae near such sites. In Conception Bay, these areas are located along the western shore where upwelling is most frequent (Chapter 3) and where high plankton densities occur. During downwelling events, larvae of these species can expect to enter a water column which is relatively turbulent, and whose prey densities are higher than those below the thermocline (e. g. 30 m; Fig. 5, 12), and higher than those in the central and eastern portions of the bay (Fig. 8, 10, 13)

These findings suggest additional mechanisms by which the timing, frequency and magnitude of interactions between wind-induced upwelling, plankton production, and larval emergence behaviour may determine interannual variability in larval feeding success, and possibly, in capelin recruitment rates. An existing capelin recruitment-forecasting model (Leggett et al. 1984) indicates that post-hatch beach residence time, which depends on the time interval between onshore winds, is inversely related to capelin yearclass strength. The patterns in plankton distribution observed in 1987 and 1988 indicate that interannual differences in the intensity of upwelling produces statistically significant temporal and spatial gradients in the biomass of plankton in the size range which can be ingested by larval capelin. Processes responsible for the development and intensification of these gradients may, therefore, be important for the successful first feeding of larvae produced by this species. Consequently, a seasonal upwelling index, which serves as a surrogate for the potential biomass of plankton near capelin spawning beaches, could be a significant additional correlate of capelin recruitment. This hypothesis will be evaluated in Chapter 6.

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Chapter 6

The Influence of Wind on
Capelin (Mallotus villosus) Recruitment

Introduction

Wind-induced upwellings and storms intermittently increase the abundance and production of primary and secondary producers (Takahashi et al. 1986; Checkley et al. 1988, Kiørboe et al. 1988; Thresher et al. 1989, Harris et al. 1991; Chapter 5). The size of plankton produced after the input of external energy to the water column is often in the size range that can be ingested by larval fishes (Checkley et al. 1988; Kiørboe and Nielsen 1990; Thresher et al. 1989). Timing and magnitude of transient production events may, therefore, be important for the feeding /success of some species of larval fishes. These species would include those whose distributions are restricted to environments that are relatively unproductive (e. g. the surface layer of a stratified water column in the summer months), as opposed to those whose larvae inhabit relatively productive areas (e. g. tidal fronts, estuaries).

These observations suggest that larvae of some fish species may be food-limited in some years because the frequency and intensity of wind-induced upwelling and mixing are less than usual. Alternatively, food-limitation might occur because of dispersion of prey patches by these same processes (Lasker 1975). Food-limitation caused by these, and other, processes is believed to contribute to high rates of mortality during the larval period (Peterman and Bradford 1987; Kiørboe et al. 1988; Cushing 1990), and may be important in determining recruitment rates in some fish species (e. g. haddock: Buckley and Lough 1987; see also Cushing 1990).

However, many larval fish populations do not appear to be food-limited (Leggett 1986; Taggart and Leggett 1987; Fortier and Harris 1989; Owen et al. 1990), whereas populations of larval fish in other areas or

at other times have been shown to be feeding or growing at food-limited rates (Frank and MacRuer 1989; Fortier and Gagné 1990; Jenkins et al. 1991). The probability of detecting food limitation in larval fishes is likely to increase as improved techniques for diagnosing larval nutritional status (e. g. Buckley 1984; Frank and MacRuer 1989; Fraser 1990; Pedersen et al. 1990; Hovenkamp 1990) are developed, and as they become more routinely employed in field sampling programs

Reports of food-limitation (and food-satiation) may also increase as sampling methods are improved. This may allow estimation of the realized abundance of prey that larvae, diagnosed as either healthy or unhealthy, actually experienced prior to capture (Owen 1989; Chapter 1; Chapter 3; Rothschild 1991) at the appropriate temporal and spatial scales (see Taggart and Frank 1989). However, the demonstration of a relationship between direct or indirect measures of food abundance (e. g. storm dispersion of prey patches) and larval condition or mortality rate, even if derived from several years of data, does not necessarily establish a predictive relationship between the abundance of eggs or larvae and recruitment (Peterman et al. 1988).

Attempts to use field data for identifying relationships between larval condition or mortality rate and food abundance will, therefore, still leave unanswered the nature of the relationship between either larval condition or mortality rate and recruitment. In this chapter, I chose, instead, to assess whether a general knowledge of biological and physical oceanographic processes known to influence rates of plankton and fish production (e. g. Iverson 1990) can be used to predict recruitment in fish populations.

The existing recruitment forecasting model (Leggett et al. 1984) for beach spawning populations of capelin, Mallotus villosus, in Eastern Newfoundland uses wind and water temperature indices as inputs. This model explained 49 % of the variance in 12 years of data (Model 1, Table 3). The input variables were specified after laboratory experiments and field sampling showed that meteorological and hydrographical factors influenced key features of capelin natural history.

The wind index in this model is a quantitative expression of the probability that larvae will emerge in robust condition into the water column from embryonic incubation sites located in inter- and subtidal zone beach sediments. Larval capelin are known to react to changes in water temperature changes associated with onshore winds by actively emerging from their beach incubation sites. The exact form of the wind index is the maximum number of days between onshore winds in the 10-day period following the annually estimated date of median hatching (Leggett et al. 1984).

The temperature term in this model was assumed to provide a relative measure of the interannual variability in food abundance for larval capelin (Leggett et al. 1984). Frank and Leggett (1982) observed that seasonal variation in the biomass of zooplankton (150 - 250 μm size range) near a capelin spawning beach was significantly correlated with the cumulative number of growing degree days measured at St. John's, Newfoundland commencing on April 1. Warmer temperatures generally stimulate plankton production (Eppley 1972; Davis 1987) and larval fish ingestion (Chapter 1; Houde 1989) and growth rates (Houde 1989). The temperature index was configured to be the sum of the mean monthly depth-

averaged (0 - 20 m) water temperatures recorded 3.7 km from St. John's, Newfoundland during the period July - December. These months span the duration of the first growing season for larval capelin.

Water temperature may not, however, be the most effective descriptor of prey abundance for larval fishes in Newfoundland coastal waters (Chapter 5). In particular, phytoplankton abundance (expressed as chlorophyll *a* concentration) at stations along a transect across Conception Bay during June - August 1987 and 1988 was more effectively described by longshore wind velocities than water temperatures (Chapter 5). These wind inputs were associated with upwelling episodes (Chapter 4, 5) which increase nutrients levels 2 - 3 fold in the lower portion of the photic zone, and which are very likely to free photosynthetic rates of the nutricline phytoplankton community from light limitation. These upwelling and downwelling events would also increase turbulent dissipation rates in the nearshore region where upwelling was most intense (Chapter 2). As a consequence of these interactions, gradients develop in the abundance of both phytoplankton and microzooplankton (Chapter 5). The biomass of these taxa are highest in the immediate nearshore (0 - 5 km) zone. It is this zone into which first feeding capelin larvae first emerge during dispersal from inter- and subtidal spawning sites.

Phytoplankton (diatoms) and tintinnids are major components of the diet of larval capelin (Courtois and Dodson 1986). Zooplankton in the size range 40 - 50 μm , which, in Conception Bay, includes tintinnids and copepod eggs and nauplii (Frank and Leggett 1986) promotes high growth and survival rates in enclosure-reared capelin larvae (Frank and Leggett 1986). Wind energy inputs which influence the production and distribution

of these prey (Chapter 5) could therefore be responsible for fluctuations in larval mortality and recruitment rates

I evaluated this hypothesis using the 12 years of data originally used to derive the Leggett et al. (1984) capelin recruitment model. The influence of wind conditions on the feeding and growth rates of larval capelin subsequent to emergence and the onset of larval drift, and the effect of this factor on recruitment, has not yet been explored. However, evidence from other species indicates that survival, or measures of feeding success (e. g. food abundance, larval gut contents, ingestion rates), may be reduced (Peterman and Bradford 1987), increased (Checkley et al. 1988; Thresher et al. 1989), or be unaffected (Butler 1991) by wind events.

Methods

Capelin recruitment data (number of two-year old fish; denoted as LNREC) for NAFO region 2J3K, estimated median larval hatch dates, and the wind (denoted as WIND) and water temperature (denoted as TEMPSUM) data associated with the original recruitment forecasting model were provided by Dr. K. T. Frank (Marine Fish Division, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada). A complete description of how these data were originally gathered and derived is available in Leggett et al. (1984).

A wind index representing the cumulative upwelling or mixing occurring during the summer months was developed. In Conception Bay, Newfoundland, the spring bloom depletes the surface layer of nutrients. This process is usually completed by the end of May (Pomeroy et al. 1991).

During June, July and August, therefore, the frequency, duration and magnitude of upwelling and mixing events is important in replenishing the photic zone with nutrients, and in stimulating rates of primary and secondary production (Chapter 5). It is during this period (Frank and Leggett 1982; Taggart and Leggett 1987) that capelin spawn (late June - early July), embryos develop (July) and larvae hatch and emerge into the water column (July - August).

In Newfoundland, upwelling is associated with winds originating from the southwest sector. Wind directions and speeds measured at St. John's airport were decomposed into longshore and cross-shore components (Schneider and Methven 1988; Chapter 4). The longshore wind component in the positive direction (i. e. winds blowing approximately from the southwest towards the northeast) has been shown to be highly correlated to hydrographic fluctuations in Conception Bay (Chapter 4; Taggart and Leggett 1987), and at other sites in Newfoundland (Yao 1986; Schneider and Methven 1988) and Atlantic Canada (Platt et al. 1972; Rose and Leggett 1988). These fluctuations in physical oceanography and wind velocities are most highly correlated after lags of 12 - 36 hours (Chapter 4), although upwelling can intensify if longshore winds persist for periods exceeding this duration (Chapter 4).

I therefore tallied the number of occasions on which the daily averaged longshore wind velocity equalled or exceeded $5 \text{ m}\cdot\text{s}^{-1}$ for each of three consecutive days. This tally, denoted as UP35, was calculated for the period June 1 - August 31 for each summer from 1966 to 1978. The wind data used to derive this index were measured at St. John's airport by Environment Canada, and are reported in Monthly Meteorological

Summaries.

The threshold wind speed of $5 \text{ m}\cdot\text{s}^{-1}$ was chosen because higher wind speeds disperse phytoplankton patches (Legendre and Demers 1984; Cury and Roy 1989). At wind speeds $< 5 \text{ m}\cdot\text{s}^{-1}$, phytoplankton patchiness is largely controlled by biotic factors (reproduction, grazing, swimming activity; Legendre and Demers 1984; Cury and Roy 1989). This value has also been used in conceptual models of physical oceanographic regulation of recruitment in some fish populations (Cury and Roy 1989). In addition, the median longshore wind speed at St. John's during summer is $4 - 6 \text{ m}\cdot\text{s}^{-1}$ (Chapter 4; Taggart and Leggett 1987). All of these observations suggest that $5 \text{ m}\cdot\text{s}^{-1}$ may be a useful first-order approximation of the role of wind events on biological oceanographic processes in Atlantic Canadian waters during the summer months. Similar indices based on threshold wind speeds of 4 and $6 \text{ m}\cdot\text{s}^{-1}$ (denoted as UP34 and UP36 respectively) were also developed and evaluated for their ability to explain variability in capelin recruitment.

The timing of larval hatching relative to the occurrence of wind-induced upwelling events could also influence capelin recruitment. For example if, in a given year, most wind events occurred before the majority of larvae hatched, it is possible that they might not benefit from wind effects on plankton production and encounter rates. To address this possibility, I used the estimated median hatching dates to identify how many 3-day $5 \text{ m}\cdot\text{s}^{-1}$ wind events occurred after most larvae had hatched. This wind index, UPHAT35, represents the amount of upwelling and mixing that most larvae would actually experience, and it was analysed in a fashion similar to the other wind indices (see below).

Data analysis

Recruitment data were log-transformed (Hennemuth et al. 1980) before analyses to stabilize the variance. All time series were then evaluated for stationarity (Chatfield 1989), autocorrelation, and multicollinearity. None of the time series used in these analyses were increasing or decreasing with time (Table 1), and none were significantly autocorrelated at lags 1, 2 or 3 (Table 2). It was not necessary therefore to reduce the number of independent observations in each series for autocorrelation between adjacent values (Drinkwater et al. 1991). Correlations between potential independent variables were generally insignificant ($P > 0.05$; Table 3).

Potential relationships between capelin recruitment and wind indices were then evaluated using multiple linear regression. I hypothesized that the introduction of a second, and new, wind input variable into the model (to account for the positive effect of the wind on production) would be more effective at explaining recruitment variation than was the temperature term in the existing model. A positive, significant wind term would support the hypothesis. A negative, but statistically significant wind term, on the other hand, would suggest that upwelling and mixing may disperse prey patches which are known to be important for successful feeding by larvae of other fish species (Lasker 1975; Peterman and Bradford 1987; Cury and Roy 1989). Finally, a non-significant term could indicate that (1) upwelling and mixing have no effect on prey availability for larval capelin; (2) the effects of upwelling and mixing are beneficial in some years, but detrimental in others; or (3) the anticipated effects

Table 1. Regression models for evaluating stationarity of time series variables. The models fitted were $Y = a \cdot \text{year} + b$, where the values for year were represented by sequential codes (i.e. 1966 = 1; 1967 = 2, etc.) so that the range in raw values was relatively large compared to the mean. R^2 = the amount of variation explained by the yearly codes and P denotes the significance level of the fitted model.

Variable	Mean	SD	R^2	P
LNREC	24.218	1.042	0.04	0.5233
WIND	5.1	2.3	0.00	0.9196
TEMPSUM	46.68	2.64	0.12	0.2758
UP34	12.9	7.5	0.00	0.8856
UP35	4.6	3.9	0.05	0.4854
UP36	1.4	2.0	0.01	0.7065

Table 2. Autocorrelation coefficients for time series used in developing capelin recruitment models. r is the autocorrelation coefficient and r_{MIN} is the minimum autocorrelation that is statistically significant ($P < 0.05$)

Variable	Lag	r	r_{MIN}
LNREC	1	0.380	± 0.554
	2	-0.148	± 0.632
	3	-0.337	± 0.642
WIND	1	-0.088	± 0.554
	2	0.208	± 0.560
	3	-0.078	± 0.582
TEMPSUM	1	-0.031	± 0.554
	2	0.072	± 0.556
	3	0.224	± 0.558
UP34	1	-0.028	± 0.554
	2	-0.119	± 0.556
	3	-0.425	± 0.562
UP35	1	-0.092	± 0.554
	2	-0.398	± 0.560
	3	-0.035	± 0.640
UP36	1	-0.321	± 0.554
	2	-0.043	± 0.610
	3	0.038	± 0.610

Table 3. Correlation matrix for variables used in developing capelin recruitment models. The top value is the correlation coefficient, r , and the bottom value is the probability level that r is statistically greater than 0. $N = 12$

	LNREC	WIND	TEMP	UP34	UP35	UP36	UPHAT35
LNREC	1.000	-0.615	0.659	0.338	0.593	0.508	0.390
	0.0	0.034	0.020	0.282	0.042	0.092	0.210
WIND		1.000	-0.398	0.157	-0.116	-0.123	0.049
		0.0	0.200	0.626	0.719	0.678	0.879
TEMP			1.000	0.597	0.471	0.496	0.411
			0.0	0.040	0.122	0.101	0.184
UP34				1.000	0.739	0.648	0.613
				0.0	0.006	0.023	0.034
UP35					1.000	0.829	0.861
					0.0	<0.001	<0.001
UP36						1.000	0.927
						0.0	<0.001
UPHAT35							1.000
							0.0

of upwelling or mixing are small compared to other processes that operate at different life stages and which influence recruitment (Peterman et al. 1988).

The criterion used for comparing the best-fit models was the proportion of total recruitment variance explained by independent variables such as WIND and UP35. The explained variance indices (R^2) used in this study have been adjusted for the loss in degrees of freedom associated with multiple input parameters. Fitted regression coefficients were assessed for statistical significance by the probability level, P , that they differ significantly from 0.

Results

A multiple regression model using the original wind index (representing capelin survival in beach sediments) but substituting a new upwelling-based wind index based on the frequency of 3 day intervals having winds > 5 m/sec for the original TEMPSUM term, explained 58 % of the variance in 12 years of capelin recruitment data (Model 2; Table 4). By comparison, the original capelin recruitment model (Model 1) explained 49 % of the variance in capelin recruitment (Table 4). In the new model, the significance levels for the two independent variables (WIND and UP35) are both $P = 0.02$. In the original model the significance levels for WIND and TEMPSUM were $P = 0.1084$ and 0.0652 , respectively.

Recruitment models using wind indices based on 4 and 6 $\text{m}\cdot\text{s}^{-1}$ threshold wind speeds explained less of the variance than did Model 2 (threshold wind speed = $5 \text{ m}\cdot\text{s}^{-1}$; Table 4). For Models 3 and 4, regression coefficients for the new wind indices (UP34 and UP36) were not significant

Table 4. Multiple regression models and related statistics for describing interannual variability in capelin recruitment (number of 2-year old fish) from abiotic variables. For each model, the fitted regression coefficient and its standard error are listed. P denotes the significance level for fitted regression coefficients. RMSE is the residual mean square error of observed values from those predicted by the fitted model. R^2 is the amount of variance explained by the fitted model. P_{TOTAL} is the overall significance level of the fitted model.

Model	P	R^2	RMSE	P_{TOTAL}
1 LNREC = $(-0.186 \pm 0.104) \cdot WIND$ + $(0.194 \pm 0.092) \cdot TEMPSUM$ + (16.093 ± 4.562)	0.1084 0.0652 0.0064	0.49	0.744	0.0197
2 LNREC = $(-0.246 \pm 0.088) \cdot WIND$ + $(0.142 \pm 0.053) \cdot UP35$ + (24.802 ± 0.570)	0.0207 0.0254 < 0.0001	0.58	0.678	0.0085
3 LNREC = $(-0.283 \pm 0.099) \cdot WIND$ + $(0.129 \pm 0.068) \cdot UP34$ + 25.220 ± 0.585	0.0190 0.0907 < 0.0001	0.46	0.768	0.0261
4 LNREC = $(-0.305 \pm 0.098) \cdot WIND$ + $(0.062 \pm 0.031) \cdot UP36$ + (24.962 ± 0.625)	0.0127 0.0743 < 0.0001	0.48	0.754	0.0127
5 LNREC = $(-0.283 \pm 0.099) \cdot WIND$ + $(0.129 \pm 0.068) \cdot UPHAT35$ + (25.220 ± 0.585)	0.0190 0.0907 < 0.0001	0.46	0.768	0.0261

at the 0.05 significance level. The regression coefficients for the original wind input variable, WIND, in the three new models were not significantly different ($P > 0.05$).

These analyses suggest that food availability during the first feeding stages may be important in regulating capelin recruitment. When the original TEMPSUM variable was included as an input to the three new models (Table 4), it was found to be statistically insignificant in each case ($P = 0.4107, 0.2541, 0.226$, respectively for models using WIND and either UP34, UP35, or UP36 as inputs).

Removing the variable describing the wind events prior to larval hatch from the model did not improve the ability to predict capelin recruitment (Model 5, Table 4). The regression coefficient for UPHAT35 was not significant ($P = 0.0907$; Table 4).

Discussion

The approach used here builds on an existing model and is an extension of ideas originally presented in Leggett et al. (1984). The new analyses incorporate recent information pertaining both to the specifics of the particular system under study (Chapters 4 and 5), and to marine ecosystems in general (Chapters 2 and 3; Iverson 1990). They have resulted in development of a more powerful model for describing fluctuations in capelin recruitment, and they quantify the manner in which biotic and abiotic processes interact to generate temporal variability in abundance of a marine fish population.

As with all empirical environmentally-based models, the correlations observed reflect patterns inherent in the available data. Model parameters

could change significantly when extrapolated to different environments, or if different methods are employed to collect the input data. A second drawback to empirical models, particularly those based on relatively short time series, is that recruitment may also be sensitive to changes in events which fluctuate at a longer time scale than that associated with the original data series (Walters and Collie 1988). Lastly, processes responsible for recruitment in one year, or even a series of years, may be insignificant in other years. In these cases, different factors would be important in influencing recruitment. Given the poor performances of updated environmentally-based recruitment models (Frank 1991, Drinkwater et al. 1991), it is possible that Model 2 would also perform poorly if its predictions of recruitment for the 2J3K stock were compared with new data.

Despite these shortcomings, the model does suggest a mechanism by which recruitment in the capelin populations of the 2J3K statistical area was mediated by environmental conditions over a 12-year period. The frequency and magnitude of upwelling events during the summer months, as represented by UP35, appear to be important to the feeding success of larval capelin, and, the statistical analyses suggest that larval feeding success may have been responsible for a significant portion of the recruitment variability in this species over the time interval considered. The positive sign of the regression coefficient for the upwelling-related wind index in Model 2 indicates that upwelling conditions favour enhanced recruitment. The improvement in R^2 in the new, two wind term, model relative to the original wind-temperature model (Leggett et al. 1984), coupled with the fact that the new wind term focuses the interval of importance on the first feeding stages of larvae, suggests that the

temperature term in the original model may not have been a surrogate for feeding conditions during larval drift as Leggett et al. hypothesized. As the analyses in Chapter 5 revealed, an upwelling-related wind term, such as that developed here, was a more effective predictor of phytoplankton and microzooplankton abundance and distribution than was temperature.

Winds, and the upwelling associated with them (Chapter 4), are also known to generate turbulence (Chapter 2), which influences phytoplankton cell size (Margalef 1978), and, in turn, determines the efficiency of copepod feeding (Dam and Peterson 1991) and rates of copepod egg production (Peterson and Bellantoni 1987; Kiørboe et al. 1990). Turbulence also increases encounter rates between planktonic predators and prey (Rothschild and Osborn 1988; Chapter 3, 5). All of these phenomena affect pelagic food web structure in plankton communities (Legendre 1990; Kiørboe et al. 1990) and the degree to which primary production is transferred to consumers at higher trophic levels (Kiørboe et al. 1990).

It is possible that strong longshore winds could regularly affect capelin recruitment through dispersion of prey patches (Lasker 1975; Lough 1984). However, microzooplankton prey were relatively evenly distributed within the upper 30 m of the water column during 1988 (Chapter 5). During that summer, 5 3-day periods of daily longshore wind velocity $\geq 5 \text{ m}\cdot\text{s}^{-1}$ occurred. This frequency matches the 12-year mean (4.6; Table 1). Despite the relatively homogeneous distribution of prey within the upper layer of the water column, prey densities were sufficiently high to maximize larval growth rates (Chapter 5). Given the relatively homogeneous vertical distribution of zooplankton observed (Chapter 5), if exceptionally strong winds do occur during the summer, it is unlikely that there will be a

significant effect on vertical prey distribution due to patch dispersion

In Newfoundland coastal waters, upwelling brings populations of invertebrate predators of larval capelin closer to the surface (Frank and Leggett 1982). This can potentially expose larvae to larger populations of predators (e. g. jellyfish; deLafontaine and Leggett 1988), especially as water masses, and their distinctive plankton communities (Frank and Leggett 1982; 1985), become mixed during flow reversals. However, the negative effects of increases in predation mortality caused by upwelling must have been small relative to the positive effects of upwelling on food availability/encounter because the overall effect of longshore wind events on recruitment was positive (Table 4).

It is important to note that model 2 is open to further development and that the new wind term (UP35) presents new opportunities for further research. For example, there is little in situ evidence for a multi-specific relationship between prey density and larval ingestion rates (Chapter 1). However, the significant influence of upwelling on capelin recruitment (Model 2, Table 4) suggests that, in some years, capelin larvae may be food-limited. The hypothesis of food-limitation in larval capelin could be evaluated by comparing a reliable measure of larval condition across summers, or within a summer at different sites exposed to different amounts of upwelling.

Such indices, acquired for a sufficient number of years, and over a sufficiently broad spatial scale, could be used to evaluate directly the hypothesis that larval condition and recruitment is linked. While this hypothesis is attractive and has occasionally been attempted, it has not yet been carried out for a sufficient number of years to establish whether

such linkages exist. This failure is partly due to the difficulty in predicting, on an annual basis, when and where hatching will occur, and what the larval distributions will be after hatch. Such information is essential to the design of a sampling grid that will be effective in increasing the probability of capturing for diagnosis of condition.

The restricted spawning sites and larval hatch dates, characteristic of capelin, coupled with the fact that hatch dates can be reliably estimated in advance (Leggett et al. 1984) and that the timing of the appearance of these larvae in the water column can be estimated from easily measurable variables (Leggett et al. 1984) makes the species an ideal candidate for such a study.

The modelling results presented here suggest that an index based on the accumulation of favorable events (upwelling episodes) may be more useful in estimating capelin recruitment than one derived from a process whose influence spans a continuous and extended interval (e. g. 6 months). The pattern observed in this data set is, therefore, consistent with several other recent studies which have demonstrated the direct influences of transient phenomena (e. g. storms, calm periods, changes in wind direction) on the ecology of larval fishes (Leggett et al. 1984; Peterman and Bradford 1987; Checkley et al. 1988; Thresher et al. 1989).

Because these events are typically associated with changes in food densities and/or water temperatures, they are likely to produce distinguishing features in the calcareous parts of surviving fish (e.g. otolith ring widths: Maillet and Checkley 1989; Sr:Ca ratios in otoliths; Radtke et al. 1990; number of vertebrae: Frank 1991). These data can be used to identify events in the past which removed individuals from the

initial population (Rice et al. 1987; Maillet and Checkley 1989). It may be possible, therefore, to couple data from derived growth trajectories with environmental data in order to identify those processes which are most likely to selectively remove some individuals from the population, and to identify the periods in larval ontogeny when such processes are likely to be most severe.

This information, if available, would potentially allow refinement, and possibly validation, of environmentally-based recruitment models, particularly if data were collected across years or habitats. This combined approach is the current focus of several major fisheries oceanography studies (e. g. Canadian Ocean Production Enhancement Network; United States South Atlantic Bight Recruitment Experiment).

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THESIS CONCLUSION

Thesis Conclusion

This thesis addressed several hypotheses relating to the environmental control of interactions between larval fish and their food resource. This required that I develop and apply models that estimate rates of food consumption by larval fishes in the laboratory and in situ, and the levels of small-scale turbulence induced by wind and tide. This research shows that at small spatial (cm) and temporal (seconds to minutes) scales, environmental control of larval fish-prey interactions are particularly sensitive to turbulent motion. This motion has the potential to increase encounter rates by several fold, and explains, in large part, the anomaly between feeding rates expected on the basis of laboratory studies and those realized in situ. More importantly, these results help to explain the consistent failure to demonstrate strong relationships between in situ food levels, larval mortality and recruitment in nature as predicted by Hjort (1914) and Cushing (1990).

These effects of turbulence are predicted to be most important for the smallest larvae, and in environments where prey densities are lowest. If higher rates of encounter result in higher feeding rates, as might be expected under conditions of food limitation, these observations suggest that the probability of finding malnourished larvae in turbulent environments will be less than that in non-turbulent environments, given equal prey densities. However, although storms can disperse patches of larval prey (Lasker 1975; Lough 1984), some larvae, depending on their pre- and post-storm vertical distributions relative to those of larval prey, might benefit from the re-distribution of these prey and the increased turbulence associated with storms (Figure 4, Chapter 3).

In addition to its direct effect on plankton contact rates, turbulence is the major determinant of the trophic structure of pelagic food webs in plankton communities (Cushing 1989; Legendre 1990, Kjørboe et al 1990). Interannual variability in the levels of wind-induced mixing and in the intensity of upwelling, will have important effects on all trophic levels within plankton communities located in areas where the water column would otherwise stratify during summer.

Field-based studies, detailed in chapters 4 and 5, have shown that, at larger spatial and temporal scales, intermittent upwelling events can improve feeding conditions for larval fishes. Research conducted in Conception Bay, Newfoundland showed that In Chapters 5 and 6, it has been shown that, in localized areas, these phenomena can be very important in determining the distribution and abundance of plankton in the size range that can be ingested by larval fish.

The potential for this coupling between wind inputs and biological/physical oceanographic responses, as demonstrated in both modelling (Chapters 1, 2, and 3) and field (Chapters 4 and 5) to influence recruitment in marine fish populations was evaluated by applying the insights gained in these studies to an existing wind and temperature based recruitment model for capelin. A new model, incorporating a wind-driven upwelling term, significantly increased the explained variance in interannual recruitment estimates for this species. This model suggests that larval fish may be more food-limited, and suffer higher rates of mortality, in years when upwelling-favorable winds were rare and/or weak.

This modified wind-based model has smaller confidence limits than those associated with the previous empirical recruitment model (Leggett

et al. 1984). It could, therefore, potentially contribute positively to the management of this important marine fish population which is not only commercially exploited, but is also the key forage species for large populations of fish, seabirds, seals and whales in the North Atlantic ocean (Bailey et al. 1977; Whitehead and Carscadden 1985). The model also produces several new and testable hypotheses concerning environmental control of larval fish-prey interactions, and their possible linkage with recruitment.

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Appendix 1

Ingestion Rates of Larval Fish in
Laboratory Environments

Appendix 1. Ingestion rates by larval fish in laboratory environments.

These data were used to derive Models 1-4, Table 4, Chapter 1. Age is days since hatch, size is larval dry weight uncorrected for preservation effects (see Methods, Chapter 1), pres. is a code indicating whether larvae were weighed dry fresh (pres = 0) or were weighed dry after being preserved (pres = 1), temp. is water temperature ($^{\circ}$ C), food is food density (μg dry weight of prey $\cdot\text{l}^{-1}$), prey is 0 if food was Brachionus or Artemia and is 1 if prey were natural zooplankton, fish is fish density during feeding experiments (no. of fish $\cdot\text{l}^{-1}$), vol. is container volume used in estimating feeding rates (litres), ingest is daily ingestion rate per fish (μg dry weight consumed $\cdot\text{fish}^{-1}\cdot\text{day}^{-1}$). Codes for species and author are listed at the bottom of the table. No data code = -1.

Species	Age	Size	Pres.	Temp.	Food	Prey	Fish	Vol.	Ingest	Author
1	3	37.8	0	19	25120	0	-1	-1	26.5	1
1	4	43	0	19	7520	0	-1	-1	38.1	1
1	5	84.6	0	19	31680	0	-1	-1	86.2	1
2	2	7	1	26	7.5	1	2	10	0.2	2
2	11	50.1	1	26	25.5	1	1.2	10	21	2
2	21	594.9	1	26	25.5	1	0.4	10	111.1	2
2	2	7.7	1	26	15	1	2	10	1.4	2
2	11	73	1	26	51	1	1.2	10	53.3	2
2	21	820.7	1	26	51	1	0.4	10	177.2	2
2	2	8.7	1	26	150	1	2	10	11.4	2
2	9	97.2	1	26	150	1	1.2	10	189.7	2
2	15	767.1	1	26	510	1	0.4	10	404.9	2
3	2	12.9	1	26	7.5	1	2	10	1	2
3	9	37.4	1	26	7.5	1	1.2	10	10.8	2
3	15	133.8	1	26	25.5	1	0.4	10	21	2
3	2	11.5	1	26	15	1	2	10	0.6	2
3	9	45.6	1	26	15	1	1.2	10	27.9	2
3	15	211.1	1	26	51	1	0.4	10	82.2	2
3	2	13.1	1	26	75	1	2	10	6.1	2
3	9	138	1	26	255	1	1.2	10	77.3	2
4	3	9.5	1	28	7.5	1	2	10	0.3	2
4	9	22.1	1	28	7.5	1	1.2	10	5	2
4	17	98.8	1	28	25.5	1	0.4	10	26.6	2
4	3	10.2	1	28	15	1	2	10	1.2	2
4	9	33.2	1	28	15	1	1.2	10	13.3	2
4	17	182.1	1	28	51	1	0.4	10	48.1	2
4	3	9.7	1	28	150	1	2	10	15.7	2

Species	Age	Size	Pres.	Temp.	Food	Prey	Fish	Vol.	Ingest	Author
4	7	35.9	1	28	150	1	1.2	10	72.4	2
4	13	253.7	1	28	510	1	0.4	10	171.7	2
5	7	128	1	9.2	5550	0	-1	-1	99.4	3
5	21	223.7	1	9.2	5550	0	-1	-1	263.5	3
5	42	704	1	9.2	5550	0	-1	-1	332.6	3
5	7	128.6	1	9.2	1850	0	-1	-1	36.7	3
5	21	360	1	9.2	1850	0	-1	-1	138.2	3
5	42	665.4	1	9.2	1850	0	-1	-1	289.4	3
5	7	118.4	1	9.2	555	0	-1	-1	25.9	3
5	21	366.7	1	9.2	555	0	-1	-1	140.4	3
5	42	613.8	1	9.2	555	0	-1	-1	218.2	3
5	7	128.6	1	9.2	185	0	-1	-1	41	3
5	21	297.5	1	9.2	185	0	-1	-1	90.7	3
5	42	580	1	9.2	185	0	-1	-1	190	3
5	7	140	1	9.2	55.5	0	-1	-1	34.6	3
5	21	180.3	1	9.2	55.5	0	-1	-1	60.5	3
5	42	335	1	9.2	55.5	0	-1	-1	79.9	3
6	7	64	0	22.2	2240	0	66.7	30	35.8	4
6	7	64	0	22.2	1360	0	66.7	30	42.2	4
6	7	64	0	22.2	640	0	66.7	30	35.8	4
6	11	200	0	19.6	1680	0	50	30	84	4
6	11	200	0	19.6	1120	0	50	30	72	4
6	11	200	0	19.6	560	0	50	30	84	4
6	15	634	0	22.2	2000	0	50	30	431	4
6	15	634	0	22.2	720	0	50	30	279	4
6	15	634	0	22.2	1680	0	50	30	221.9	4
6	23	2740	0	22.8	1200	0	33.3	30	1096	4
6	23	2740	0	22.8	1360	0	33.3	30	753.5	4
7	7	22	0	20	88000	0	-1	-1	47	5
7	31	1376	0	20	88000	0	-1	-1	404.5	5
7	47	2301	0	20	88000	0	-1	-1	1021.5	5
3	3	15.5	0	23	120	1	4.7	75	10.5	6
3	6	30.1	0	23	120	1	2.3	75	16.9	6
3	8	46.1	0	23	120	1	2	75	23	6
3	2	9.8	0	26	120	1	4.7	75	11.4	6
3	6	29.2	0	26	120	1	2.3	75	27.5	6
3	8	50	0	26	120	1	2	75	42.7	6
3	2	11.6	0	29	120	1	4.7	75	25.4	6
3	5	30.5	0	29	120	1	2.3	75	39.8	6
3	8	79.1	0	29	120	1	2	75	62.5	6
8	8	83.8	0	9	555	0	-1	20	13.4	7
8	17	101.4	0	9	555	0	-1	20	28.4	7
8	33	247	0	9	555	0	-1	20	49.4	7
9	22	2925.4	0	24	925	0	-1	20	355.2	7
9	22	2925.4	0	24	1850	0	-1	20	710.4	7
9	22	2925.4	0	24	3700	0	-1	20	1487.4	7
9	22	2925.4	0	24	7400	0	-1	20	2442	7
9	22	2925.4	0	24	14800	0	-1	20	2397.6	7
10	5	17.4	0	15.5	320	0	-1	10	14.1	8
10	5	18.8	0	15.5	16	0	-1	10	9.9	8
10	6	21.1	0	15.5	11000	0	-1	10	18.1	8

Species	Age	Size	Pres.	Temp.	Food	Prey	Fish	Vol.	Ingest	Author
10	6	21.6	0	15.5	16	0	-1	10	10.5	8
10	7	25.5	0	15.5	11000	0	-1	10	21.1	8
10	7	24.9	0	15.5	880	0	-1	10	11.3	8
10	11	54.3	0	15.5	11000	0	-1	10	33.8	8
10	11	43.5	0	15.5	880	0	-1	10	15.6	8
10	14	96	0	15.5	11000	0	-1	10	48.7	8
10	14	66.2	0	15.5	880	0	-1	10	20.8	8
11	6	225	1	19	105	1	4	32	71.8	9
11	13	612.2	1	19	105	1	3.3	32	679.4	9
11	20	1665.8	1	19	105	1	2.8	32	2376.1	9
11	6	225	1	19	210	1	4	32	102.2	9
11	13	670.6	1	19	210	1	3.4	32	850.6	9
11	20	1998.4	1	19	210	1	2.7	32	2770	9
12	0	53	1	7	14.5	1	1.7	0.6	0.7	10
12	0	53	1	7	72.5	1	1.7	0.6	2.1	10
12	0	53	1	7	145	1	1.7	0.6	3.8	10
12	0	132	1	7	14.5	1	1.7	0.6	1.6	10
12	0	132	1	7	29	1	1.7	0.6	2.4	10
12	0	132	1	7	43.5	1	1.7	0.6	3.3	10
12	0	533	1	7	7.25	1	1.7	0.6	7.3	10
12	0	533	1	7	72.5	1	1.7	0.6	44.9	10
12	0	533	1	7	145	1	1.7	0.6	86.7	10
12	0	533	1	2	21.75	1	1.7	0.6	2.1	10
12	0	533	1	2	58	1	1.7	0.6	5.6	10
12	0	533	1	2	94.25	1	1.7	0.6	9	10
2	2.8	9.8	0	24	3200	0	15	10	6.8	11
2	5.8	13.6	0	24	3200	0	15	10	18.1	11
2	8.8	22	0	24	3200	0	15	10	23.7	11
13	6.5	24.5	0	20	3200	0	15	10	26.8	11
13	8.5	34.7	0	20	3200	0	15	10	30.9	11
13	10.5	49.2	0	20	3200	0	15	10	60	11

Species codes: 1, Scomber japonicus; 2, Anchoa mitchilli; 3, Archosargus rhomboidalis; 4, Achirus lineatus; 5, Clupea harengus (Clyde); 6, Pagrus major; 7, Leiostomus xanthurus; 8, Clupea harengus (Baltic); 9, Blennius pavo; 10, Engraulis mordax; 11, Morone saxatilis; 12, Ammodytes americanus; 13, Centropristis striata striata.

Author codes: 1, Hunter and Kimbrell 1980; 2, Houde and Schekter 1981; 3, Werner and Blaxter 1981; 4, Kuronuma and Fukusho 1984; 5, Govoni et al. 1982; 6, Stepien 1976; 7, Klumpp and von Westernhagen 1986; 8, Theilacker 1987; 9, Chesney, Jr. 1989; 10, Monteleone and Peterson 1984; 11, Tucker, Jr. 1989.

Appendix 2

Ingestion Rates of Wild and Enclosure-Reared Populations of Larval Fish

Appendix 2. Ingestion rates of wild and enclosure-reared populations of larval fish. These data were used to derive Model 5, Table 4, Chapter 1. Size is larval dry weight uncorrected for preservation effects (see Methods, Chapter 1), temp. is water temperature ($^{\circ}$ C), food is food density (μ g dry weight of prey $\cdot$ l $^{-1}$), ingest is daily ingestion rate per fish (μ g dry weight consumed $\cdot$ fish $^{-1}\cdot$ day $^{-1}$). Codes for species and author are listed at the bottom of the table.

Species	Size	Pres.	Temp.	Food	Ingest	Author
1	25.2	0	6.5	15	2.5	1
1	25.6	0	6.5	20	2.8	1
1	23.6	0	6.5	20	1.5	1
1	24.2	0	6.5	24	1.8	1
1	23.9	0	6.5	30	1.6	1
1	24.8	0	6.5	42	2.2	1
1	26.3	0	6.5	48	3.5	1
1	27.2	0	6.5	55	4.5	1
1	25.8	0	6.5	57	3	1
1	26.1	0	6.5	68	3.2	1
1	27.5	0	6.5	80	4.9	1
1	27.9	0	6.5	210	5.6	1
2	147	0	8	5	42.3	2
2	202	0	8	5	64.6	2
3	992	0	4.5	57	25.1	3
2	59	1	4.5	31.5	25.6	4
2	84	1	4.5	9	21.4	4
2	54	1	4.5	9	13.8	4
2	76.7	1	4.5	6	9.6	4
4	88.1	1	4.5	3.9	3.8	5
5	38	0	14	14	15.2	6
5	67	0	14	14	17.2	6
5	107	0	14	11.25	20.5	6
5	160	0	14	6.25	27	6
5	230	0	14	12	33.1	6
6	138.4	0	29	56.76	105.2	7
6	90.6	0	24.4	54.45	55.8	7
6	119.9	0	28.1	87.12	73.6	7
6	115.5	0	30.7	82.5	75.1	7
2	2950	0	9	17	1121	8
7	2010	0	9	17	330	8
7	860	0	6	37.5	423.1	8
7	790	0	6	15	237	8
7	860	0	9	133.3	543.5	8
7	790	0	9	83.3	338.1	8
8	166.2	0	12	6.2	23.1	9

Species codes: 1, Mallotus villosus; 2, Gadus morhua; 3, Ammodytes americanus; 4, Theragra chalcogramma; 5, Scomber scombrus; 6, Anchoa mitchilli; 7, Melanogrammus aeglefinus; 8, Clupea harengus (unknown stock).

Author codes: 1, Frank and Leggett 1982; 2, Gamble and Houde 1984; 3, Monteleone and Peterson 1984; 4, Ellertsen et al. 1984; 5, Dagg et al. 1984; 6, Peterson and Ausubel 1984; 7, Leak and Houde 1987; 8, Buckley and Lough 1987; 9, Klørboe and Johansen 1986.

Appendix 3

Dissipation Rates of Turbulent Kinetic Energy
in the Surface Mixed Layer of Aquatic Environments

Appendix 3 Dissipation rates of turbulent kinetic energy (ϵ ; Watts $\cdot$ m $^{-3}$) extracted from the literature (see Methods, Chapter 2) Also listed is wind speed (m $\cdot$ s $^{-1}$), sample depth, depth of the surface mixed layer, the environmental indicator variable (ENV), the number of the profile (or Figure number) in the original data source from which dissipation rates were extracted, and the author(s) of studies which provided data Author codes are listed alphabetically at end of table.

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
3.8	9.2	70	-4.04444	0	1	1
3.8	10.1	70	-4.16296	0	1	1
3.8	15.6	70	-4.84444	0	1	1
3.8	19.3	70	-4.99259	0	1	1
3.8	24.8	70	-5.05185	0	1	1
3.8	30.3	70	-5.37777	0	1	1
3.8	35.9	70	-5.55555	0	1	1
3.8	39.5	70	-5.55555	0	1	1
3.8	44.1	70	-5.43703	0	1	1
3.8	49.7	70	-5.43703	0	1	1
3.8	55.2	70	-5.52592	0	1	1
3.8	59.8	70	-5.34814	0	1	1
3.8	65.3	70	-5.22963	0	1	1
3.8	70.8	70	-5.43703	0	1	1
4.4	7.6	50	-3.57037	0	5	1
4.4	10.4	50	-3.83703	0	5	1
4.4	15.1	50	-4.25185	0	5	1
4.4	19.9	50	-4.63703	0	5	1
4.4	25.6	50	-4.93333	0	5	1
4.4	31.2	50	-4.93333	0	5	1
4.4	30.3	50	-4.96296	0	5	1
4.4	35	50	-5.34814	0	5	1
4.4	39.8	50	-5.34814	0	5	1
4.4	44.5	50	-5.2	0	5	1
4.4	50.2	50	-4.93333	0	5	1
2.5	10.4	60	-4.10526	0	6	1
2.5	15.1	60	-5.00751	0	6	1
2.5	20.8	60	-5.18797	0	6	1
2.5	25.6	60	-5.45864	0	6	1
2.5	31.2	60	-5.39849	0	6	1
2.5	35	60	-5.57894	0	6	1
2.5	40.7	60	-5.57894	0	6	1
2.5	44.5	60	-5.54887	0	6	1
2.5	51.1	60	-5.48872	0	6	1
2.5	54	60	-6	0	6	1
2.5	57.8	60	-5.48872	0	6	1

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
2.5	60.6	60	-5.45864	0	6	1
5.4	6.7	45	-3.2647	0	10	1
5.4	10.5	45	-3.88235	0	10	1
5.4	15.3	45	-4.05882	0	10	1
5.4	20.1	45	-4.11764	0	10	1
5.4	24.9	45	-4.23529	0	10	1
5.4	29.7	45	-4.58823	0	10	1
5.4	35.4	45	-4.7647	0	10	1
5.4	40.2	45	-4.88235	0	10	1
5.4	46	45	-5	0	10	1
12	7.6	50	-3.06666	0	15	1
12	10.4	50	-3.33333	0	15	1
12	15.1	50	-3.51111	0	15	1
12	20.8	50	-3.68888	0	15	1
12	24.6	50	-3.71851	0	15	1
12	31.2	50	-3.74814	0	15	1
12	35	50	-3.83703	0	15	1
12	40.7	50	-3.95555	0	15	1
12	45.4	50	-4.01481	0	15	1
4.2	11.4	60	-4.0303	1	2	1
4.2	14.3	60	-4.42424	1	2	1
4.2	20	60	-4.93939	1	2	1
4.2	24.8	60	-5.12121	1	2	1
4.2	30.5	60	-4.90909	1	2	1
4.2	35.2	60	-5.24242	1	2	1
4.2	41.9	60	-5	1	2	1
4.2	45.7	60	-5	1	2	1
4.2	50.5	60	-4.15151	1	2	1
4.2	55.2	60	-5.0303	1	2	1
4.2	60	60	-4.96969	1	2	1
2.8	6.6	40	-3.50375	1	3	1
2.8	10.4	40	-4.28571	1	3	1
2.8	15.1	40	-4.52631	1	3	1
2.8	19.9	40	-5.09774	1	3	1
2.8	25.6	40	-5.21804	1	3	1
2.8	29.3	40	-5.30827	1	3	1
2.8	36	40	-4.91729	1	3	1
2.8	39.8	40	-4.82706	1	3	1
3.1	6.6	25	-4.63636	1	4	1
3.1	10.4	25	-3.84848	1	4	1
3.1	15.1	25	-4	1	4	1
3.1	19.9	25	-4.81818	1	4	1
3.1	20.8	25	-4.87878	1	4	1
3.1	24.6	25	-5.21212	1	4	1
2.1	9.5	55	-4.34586	1	7	1
2.1	15.2	55	-4.61654	1	7	1
2.1	19	55	-4.88721	1	7	1
2.1	24.8	55	-4.88721	1	7	1
2.1	30.5	55	-5.15789	1	7	1

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
2.1	35.2	55	-4.91729	1	7	1
2.1	39	55	-4.73684	1	7	1
2.1	44.8	55	-5.42857	1	7	1
2.1	51.4	55	-5.48872	1	7	1
2.1	54.3	55	-5.51879	1	7	1
1.8	6.7	40	-3.59398	1	8	1
1.8	10.5	40	-4.25563	1	8	1
1.8	15.3	40	-4.82706	1	8	1
1.8	20.1	40	-4.91729	1	8	1
1.8	25.9	40	-4.94736	1	8	1
1.8	30.7	40	-5.27819	1	8	1
1.8	35.4	40	-5.18797	1	8	1
1.8	40.2	40	-5.27819	1	8	1
4.9	8.6	15	-3.54545	1	9	1
4.9	10.5	15	-3.87878	1	9	1
4.9	12.4	15	-4.48484	1	9	1
4.9	14.3	15	-4.48484	1	9	1
4.9	14.3	15	-4.48484	1	9	1
4.9	15.2	15	-4.51515	1	9	1
6.9	7.6	35	-3.28244	1	12	1
6.9	10.4	35	-3.80152	1	12	1
6.9	15.1	35	-4.07633	1	12	1
6.9	19.9	35	-4.25954	1	12	1
6.9	25.6	35	-4.50381	1	12	1
6.9	30.3	35	-4.65648	1	12	1
6.9	35	35	-4.96183	1	12	1
9.5	6.6	25	-4.0303	1	13	1
9.5	9.5	25	-3.27272	1	13	1
9.5	15.1	25	-3.63636	1	13	1
9.5	20.8	25	-3.54545	1	13	1
9.5	25.6	25	-3.60606	1	13	1
11.7	11.3	35	-3.41353	1	14	1
11.7	15.1	35	-3.56391	1	14	1
11.7	20.7	35	-3.56391	1	14	1
11.7	24.5	35	-3.80451	1	14	1
11.7	30.1	35	-3.98496	1	14	1
11.7	34.8	35	-4.16541	1	14	1
5.5	12	30	-5.69767	0	1	2
5.5	12.7	30	-6.09302	0	1	2
5.5	13.6	30	-5.95348	0	1	2
5.5	14.1	30	-6.18404	0	1	2
5.5	14.9	30	-5.39534	0	1	2
5.5	15.6	30	-5.67441	0	1	2
5.5	16.3	30	-5.46511	0	1	2
5.5	17	30	-6.04651	0	1	2
5.5	17.7	30	-5.18604	0	1	2
5.5	18.4	30	-5.53488	0	1	2
5.5	18.8	30	-5.79069	0	1	2
5.5	19.4	30	-5.44186	0	1	2

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
5.5	20.1	30	-5.4186	0	1	2
5.5	20.7	30	-5.53488	0	1	2
5.5	21.5	30	-5.16279	0	1	2
5.5	22	30	-5.23255	0	1	2
5.5	22.6	30	-5.44186	0	1	2
5.5	23.1	30	-6.23255	0	1	2
5.5	23.7	30	-5.88372	0	1	2
5.5	24.3	30	-5.30232	0	1	2
5.5	24.9	30	-4.86046	0	1	2
5.5	25.5	30	-5.48837	0	1	2
5.5	26.3	30	-5.13953	0	1	2
5.5	27	30	-4.90697	0	1	2
5.5	27.4	30	-4.8372	0	1	2
5.5	28.3	30	-4.65116	0	1	2
5.5	28.7	30	-4.53488	0	1	2
5.5	29.7	30	-4.53488	0	1	2
5.5	30	30	-5	0	1	2
15.5	16.1	30	-3.97727	0	2	2
15.5	16.8	30	-4	0	2	2
15.5	18.4	30	-4.25	0	2	2
15.5	19.2	30	-4.47727	0	2	2
15.5	19.9	30	-3.65909	0	2	2
15.5	20.4	30	-4.79545	0	2	2
15.5	21.9	30	-4.36363	0	2	2
15.5	22.4	30	-4.04545	0	2	2
15.5	23.2	30	-3.88636	0	2	2
15.5	23.8	30	-3.72727	0	2	2
15.5	24.5	30	-4.93181	0	2	2
15.5	25	30	-3.95454	0	2	2
15.5	25.9	30	-4.11363	0	2	2
15.5	26.3	30	-4	0	2	2
15.5	26.9	30	-3.81818	0	2	2
15.5	27.5	30	-3.86363	0	2	2
15.5	28	30	-3.68181	0	2	2
15.5	28.8	30	-3.72727	0	2	2
15.5	29.3	30	-4.20454	0	2	2
15.5	29.7	30	-4.06818	0	2	2
4.8	0.4	6	-3.0641	1	1	3
4.8	1.4	6	-3.42307	1	1	3
4.8	2.4	6	-3.5	1	1	3
4.8	3.5	6	-3.85897	1	1	3
4.8	4.5	6	-4.48718	1	1	3
4.8	5.5	6	-3.96153	1	1	3
12	1.1	22	-2.14084	1	1	4
12	1.9	22	-2.30985	1	1	4
12	3.4	22	-2.64788	1	1	4
12	4.1	22	-2.56338	1	1	4
12	5.5	22	-2.52112	1	1	4
12	6.3	22	-2.35211	1	1	4

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
12	7.3	22	-2.56338	1	1	4
12	8.1	22	-2.69014	1	1	4
12	9.1	22	-2.77464	1	1	4
12	9.8	22	-2.94366	1	1	4
12	11.3	22	-2.09859	1	1	4
12	11.6	22	-1.92957	1	1	4
12	11.8	22	-2.05633	1	1	4
12	10.8	22	-3.32394	1	1	4
12	10.8	22	-3.19718	1	1	4
12	10.7	22	-2.8169	1	1	4
12	11	22	-2.73239	1	1	4
12	11.4	22	-2.8169	1	1	4
12	11	22	-3.02816	1	1	4
12	11.3	22	-3.19718	1	1	4
12	11.8	22	-3.28169	1	1	4
12	12	22	-3.11267	1	1	4
12	12.3	22	-2.8169	1	1	4
12	12	22	-2.56338	1	1	4
12	12.7	22	-2.56338	1	1	4
12	13.3	22	-2.60563	1	1	4
12	13	22	-2.85915	1	1	4
12	12.7	22	-2.9014	1	1	4
12	12.6	22	-2.94366	1	1	4
12	12.6	22	-2.8169	1	1	4
12	12.7	22	-3.23943	1	1	4
12	13.1	22	-3.32394	1	1	4
12	13.5	22	-2.94366	1	1	4
12	13.1	22	-2.77464	1	1	4
12	13.8	22	-2.73239	1	1	4
12	13.8	22	-2.94366	1	1	4
12	13.9	22	-3.15493	1	1	4
12	14.3	22	-2.98591	1	1	4
12	14.3	22	-2.77464	1	1	4
12	14.7	22	-2.73239	1	1	4
12	15.4	22	-2.73239	1	1	4
12	14.8	22	-2.98591	1	1	4
12	14.8	22	-3.11267	1	1	4
12	14.8	22	-3.19718	1	1	4
12	14.8	22	-3.28169	1	1	4
12	14.7	22	-3.4507	1	1	4
12	14.4	22	-3.49295	1	1	4
12	14.4	22	-3.57746	1	1	4
12	14.2	22	-3.70422	1	1	4
12	14.2	22	-4.04225	1	1	4
12	14.7	22	-3.95774	1	1	4
12	15	22	-3.87324	1	1	4
12	15	22	-3.70422	1	1	4
12	15.6	22	-3.57746	1	1	4
12	15.5	22	-3.32394	1	1	4

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
12	15.3	22	-3.32394	1	1	4
12	15.3	22	-3.02816	1	1	4
12	15.8	22	-2.98591	1	1	4
12	15.8	22	-2.98591	1	1	4
12	16	22	-3.11267	1	1	4
12	16.3	22	-3.02816	1	1	4
12	16.5	22	-2.94366	1	1	4
12	16.1	22	-2.73239	1	1	4
12	16.5	22	-2.60563	1	1	4
12	16.7	22	-2.43662	1	1	4
12	16.9	22	-2.69014	1	1	4
12	16.9	22	-3.23943	1	1	4
12	16.7	22	-3.07042	1	1	4
12	16.4	22	-3.36619	1	1	4
12	16.3	22	-3.61971	1	1	4
12	16.3	22	-3.66197	1	1	4
12	16.3	22	-3.87324	1	1	4
12	16.1	22	-3.87324	1	1	4
12	15.9	22	-3.87324	1	1	4
12	16.1	22	-4.16901	1	1	4
12	15.9	22	-4.54929	1	1	4
12	17.1	22	-4.12676	1	1	4
12	16.9	22	-3.74647	1	1	4
12	16.9	22	-3.87324	1	1	4
12	17.3	22	-3.83098	1	1	4
12	17.3	22	-3.57746	1	1	4
12	17.5	22	-3.66197	1	1	4
12	18	22	-3.66197	1	1	4
12	18.1	22	-3.28169	1	1	4
12	17.7	22	-3.02816	1	1	4
12	18.1	22	-2.98591	1	1	4
12	18.4	22	-2.8169	1	1	4
12	18.6	22	-2.52112	1	1	4
12	18.8	22	-2.94366	1	1	4
12	19.3	22	-3.15493	1	1	4
12	19	22	-3.11267	1	1	4
12	19.2	22	-3.53521	1	1	4
12	19.5	22	-3.4507	1	1	4
12	20	22	-3.32394	1	1	4
12	19.9	22	-3.07042	1	1	4
12	20.4	22	-2.85915	1	1	4
12	20.6	22	-2.64788	1	1	4
12	20.7	22	-2.9014	1	1	4
12	20.7	22	-3.23943	1	1	4
12	21	22	-3.57746	1	1	4
12	20.5	22	-3.74647	1	1	4
12	20.1	22	-3.70422	1	1	4
12	20.1	22	-4.04225	1	1	4
8.6	6.1	30	-4.63953	0	12	5

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
8.6	7.1	30	-4.67441	0	12	5
8.6	8.9	30	-4.67441	0	12	5
8.6	10.5	30	-5.02325	0	12	5
8.6	11.7	30	-5.37209	0	12	5
8.6	13.4	30	-5.96511	0	12	5
8.6	14.8	30	-6.45348	0	12	5
8.6	16.5	30	-6.27907	0	12	5
8.6	17.7	30	-6.06976	0	12	5
8.6	19.4	30	-5.51162	0	12	5
8.6	20.7	30	-5.3372	0	12	5
8.6	22.4	30	-5.61627	0	12	5
8.6	23.8	30	-5.93023	0	12	5
8.6	25.6	30	-5.26744	0	12	5
8.6	27.1	30	-5.05813	0	12	5
8.6	28.6	30	-5.30232	0	12	5
5.6	6.3	30	-2.66666	0	14	5
5.6	7.2	30	-2.33333	0	14	5
5.6	8.7	30	-2	0	14	5
5.6	10.7	30	-2.95238	0	14	5
5.6	12	30	-3.95238	0	14	5
5.6	13.5	30	-4.19047	0	14	5
5.6	14.9	30	-4.28571	0	14	5
5.6	16.7	30	-4.85714	0	14	5
5.6	17.9	30	-5.42857	0	14	5
5.6	19.4	30	-5.66666	0	14	5
5.6	21	30	-5.90476	0	14	5
5.6	22.7	30	-6.09523	0	14	5
5.6	24.2	30	-6.23809	0	14	5
5.6	25.9	30	-5.5238	0	14	5
5.6	27.2	30	-5.23809	0	14	5
5.6	29	30	-5.33333	0	14	5
2.2	6.1	30	-4.8	0	16	5
2.2	7.4	30	-4.88571	0	16	5
2.2	8.9	30	-5.05714	0	16	5
2.2	10.5	30	-5.14285	0	16	5
2.2	12	30	-5.18571	0	16	5
2.2	13.4	30	-5.65714	0	16	5
2.2	14.9	30	-6.12857	0	16	5
2.2	16.5	30	-6.42857	0	16	5
2.2	17.9	30	-6.68571	0	16	5
2.2	19.4	30	-6.6	0	16	5
2.2	21	30	-6.42857	0	16	5
2.2	22.5	30	-6.68571	0	16	5
2.2	24.1	30	-7.15714	0	16	5
2.2	25.8	30	-7.45714	0	16	5
2.2	27.2	30	-7.54285	0	16	5
2.2	29.1	30	-7.41428	0	16	5
7.7	6.1	30	-4.30769	0	18	5
7.7	7.4	30	-4.61538	0	18	5

Wind	Depth	Z_{mixed}	Log ϵ	ENV	Profile	Author
7.7	8.9	30	-4.76923	0	18	5
7.7	10.4	30	-4.80769	0	18	5
7.7	11.9	30	-4.84615	0	18	5
7.7	13.5	30	-4.84615	0	18	5
7.7	14.9	30	-4.92307	0	18	5
7.7	16.5	30	-5.11538	0	18	5
7.7	17.9	30	-5.23076	0	18	5
7.7	19.4	30	-5.26923	0	18	5
7.7	20.9	30	-5.38461	0	18	5
7.7	22.5	30	-5.76923	0	18	5
7.7	24.2	30	-6.34615	0	18	5
7.7	25.8	30	-5.88461	0	18	5
7.7	27.1	30	-5.53846	0	18	5
7.7	28.8	30	-5.92307	0	18	5
8.6	6.1	30	-3.8761	0	21	5
8.6	7.4	30	-4.11504	0	21	5
8.6	9	30	-4.40708	0	21	5
8.6	10.4	30	-4.30088	0	21	5
8.6	11.9	30	-4.24778	0	21	5
8.6	13	30	-4.14159	0	21	5
8.6	14.7	30	-3.95575	0	21	5
8.6	16.6	30	-3.9823	0	21	5
8.6	17.7	30	-4.08849	0	21	5
8.6	19.5	30	-4.08849	0	21	5
8.6	20.8	30	-4.00885	0	21	5
8.6	22.3	30	-3.79646	0	21	5
8.6	23.5	30	-3.66371	0	21	5
8.6	25.5	30	-3.69026	0	21	5
8.6	26.9	30	-3.76991	0	21	5
8.6	29.1	30	-3.71681	0	21	5
4.3	6.1	30	-5.71428	0	24	5
4.3	7.2	30	-5.54285	0	24	5
4.3	8.8	30	-5.34285	0	24	5
4.3	10.3	30	-5.91428	0	24	5
4.3	11.7	30	-6.45714	0	24	5
4.3	13.3	30	-6.02857	0	24	5
4.3	14.6	30	-5.68571	0	24	5
4.3	16	30	-6.11428	0	24	5
4.3	17.6	30	-6.65714	0	24	5
4.3	19	30	-5.88571	0	24	5
4.3	20.7	30	-5.2	0	24	5
4.3	22.3	30	-5.17142	0	24	5
4.3	23.9	30	-5.2	0	24	5
4.3	25.6	30	-5.14285	0	24	5
4.3	27.1	30	-4.91428	0	24	5
4.3	29.5	30	-5.02857	0	24	5
3	6.1	30	-6.11392	0	25	5
3	7.3	30	-6.30379	0	25	5
3	8.7	30	-6.37974	0	25	5

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
3	10.1	30	-6.22784	0	25	5
3	11.7	30	-6.03797	0	25	5
3	13.1	30	-6.30379	0	25	5
3	14.7	30	-6.56962	0	25	5
3	16.2	30	-6.45569	0	25	5
3	17.7	30	-6.22784	0	25	5
3	19.3	30	-6.37974	0	25	5
3	20.6	30	-6.45569	0	25	5
3	22.3	30	-6.11392	0	25	5
3	23.6	30	-5.58227	0	25	5
3	25.3	30	-5.0886	0	25	5
3	27	30	-4.82278	0	25	5
3	28.9	30	-5.0886	0	25	5
8	4.8	100	-3.67289	0	10	6
8	7.9	100	-3.85981	0	10	6
8	11.1	100	-3.93457	0	10	6
8	15.9	100	-3.89719	0	10	6
8	17.5	100	-4.19626	0	10	6
8	20.6	100	-4.48286	0	10	6
8	22.2	100	-5.75389	0	10	6
8	23.8	100	-6.00311	0	10	6
8	27	100	-6.04049	0	10	6
8	30.2	100	-6.06542	0	10	6
8	31.7	100	-5.96573	0	10	6
8	36.5	100	-5.99065	0	10	6
8	39.7	100	-5.99065	0	10	6
8	41.3	100	-6.3271	0	10	6
8	42.9	100	-6.23987	0	10	6
8	49.2	100	-6.14018	0	10	6
8	50.8	100	-6.30218	0	10	6
8	54	100	-6.23987	0	10	6
8	57.1	100	-6.20249	0	10	6
8	60.3	100	-6.23987	0	10	6
8	61.9	100	-6.31464	0	10	6
8	66.7	100	-6.1651	0	10	6
8	71.4	100	-6.37694	0	10	6
8	76.2	100	-6.05295	0	10	6
8	81	100	-6.1028	0	10	6
8	84.1	100	-5.90342	0	10	6
8	88.9	100	-6.30218	0	10	6
8	92.1	100	-6.20249	0	10	6
8	96.8	100	-5.90342	0	10	6
8	100	100	-6.1028	0	10	6
4	3.1	35	-4.00628	0	18	6
4	4.7	35	-4.45911	0	18	6
4	9.4	35	-4.01886	0	18	6
4	12.5	35	-4.34591	0	18	6
4	14.1	35	-4.64779	0	18	6
4	18.8	35	-4.01886	0	18	6

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
4	21.9	35	-3.47798	0	18	6
4	23.4	35	-4.32075	0	18	6
4	28.1	35	-4.47169	0	18	6
4	31.3	35	-4.22012	0	18	6
4	33.5	35	-5.32704	0	18	6
8	16.1	150	-3.51063	0	23	6
8	19.7	150	-3.49645	0	23	6
8	21.5	150	-3.9929	0	23	6
8	25.1	150	-4.31914	0	23	6
8	28.7	150	-3.92198	0	23	6
8	30.5	150	-3.58156	0	23	6
8	34	150	-3.97872	0	23	6
8	39.4	150	-3.69503	0	23	6
8	41.2	150	-4.07801	0	23	6
8	44.8	150	-3.4539	0	23	6
8	46.6	150	-4.1773	0	23	6
8	50.2	150	-4.24822	0	23	6
8	55.5	150	-4.64539	0	23	6
8	57.3	150	-4.6312	0	23	6
8	59.1	150	-4.30496	0	23	6
8	62.7	150	-4.37588	0	23	6
8	66.3	150	-4.27659	0	23	6
8	69.9	150	-4.43262	0	23	6
8	73.5	150	-5.04255	0	23	6
8	77	150	-4.61702	0	23	6
8	80.6	150	-4.68794	0	23	6
8	82.4	150	-4.56028	0	23	6
8	86	150	-4.3617	0	23	6
8	89.6	150	-4.00709	0	23	6
8	93.2	150	-4.07801	0	23	6
8	96.7	150	-4.21985	0	23	6
8	98.5	150	-4.61702	0	23	6
8	102.1	150	-4.13475	0	23	6
8	107.5	150	-4.16312	0	23	6
8	109.3	150	-4.40425	0	23	6
8	112.9	150	-4.95744	0	23	6
8	116.4	150	-4.60283	0	23	6
8	120	150	-4.46099	0	23	6
8	123.6	150	-4.58865	0	23	6
8	127.2	150	-3.9929	0	23	6
8	130.8	150	-4.06383	0	23	6
8	132.6	150	-4.46099	0	23	6
8	137.9	150	-4.58865	0	23	6
8	139.7	150	-4.9007	0	23	6
8	145.1	150	-4.65957	0	23	6
8	148.7	150	-5.25531	0	23	6
8	148.7	150	-6.3617	0	23	6

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
8	150	150	-5.42553	0	23	6
14	3.6	125	-3.24548	0	27	6
14	7.3	125	-3.57761	0	27	6
14	9	125	-3.08664	0	27	6
14	12.7	125	-3.53429	0	27	6
14	14.5	125	-3.99639	0	27	6
14	16.3	125	-4.38628	0	27	6
14	19.9	125	-3.99639	0	27	6
14	21.7	125	-4.4296	0	27	6
14	25.3	125	-3.98195	0	27	6
14	27.1	125	-3.98195	0	27	6
14	29	125	-4.41516	0	27	6
14	30.8	125	-4.48736	0	27	6
14	32.6	125	-4.51624	0	27	6
14	36.2	125	-4.16967	0	27	6
14	38	125	-3.85198	0	27	6
14	41.6	125	-4.19855	0	27	6
14	45.2	125	-3.66426	0	27	6
14	48.9	125	-3.72202	0	27	6
14	50.7	125	-4.05415	0	27	6
14	52.5	125	-3.92418	0	27	6
14	56.1	125	-3.8953	0	27	6
14	59.7	125	-3.88086	0	27	6
14	62.6	125	-4.15523	0	27	6
14	65.2	125	-4.14079	0	27	6
14	68.8	125	-4.28519	0	27	6
14	70.6	125	-4.11191	0	27	6
14	72.4	125	-4.03971	0	27	6
14	76	125	-3.99639	0	27	6
14	79.6	125	-4.05415	0	27	6
14	81.4	125	-4.81949	0	27	6
14	86.9	125	-4.76173	0	27	6
14	88.7	125	-5.16606	0	27	6
14	90.5	125	-4.74729	0	27	6
14	94.1	125	-5.48375	0	27	6
14	99.5	125	-5.42599	0	27	6
14	102.3	125	-5.29602	0	27	6
14	105	125	-5.42599	0	27	6
14	108.6	125	-5.35379	0	27	6
14	110.4	125	-5.16606	0	27	6
14	114	125	-5.05054	0	27	6
14	115.8	125	-4.84837	0	27	6
14	117.6	125	-4.80505	0	27	6
14	121.3	125	-4.77017	0	27	6
14	124.9	125	-5.02166	0	27	6
5	8.1	115	-4.10791	0	29	6
5	10.8	115	-4.21582	0	29	6
5	12.2	115	-4.23741	0	29	6
5	13.5	115	-4.64748	0	29	6

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
5	14.9	115	-4.64748	0	29	6
5	17.6	115	-5.23021	0	29	6
5	18.9	115	-5.32733	0	29	6
5	20.3	115	-5.31654	0	29	6
5	23	115	-5.34892	0	29	6
5	24.2	115	-5.02518	0	29	6
5	25.7	115	-4.90647	0	29	6
5	28.4	115	-4.77697	0	29	6
5	31.1	115	-4.7446	0	29	6
5	32.4	115	-4.73381	0	29	6
5	36.5	115	-4.70143	0	29	6
5	39.2	115	-4.37769	0	29	6
5	41.9	115	-4.69064	0	29	6
5	43.2	115	-4.7446	0	29	6
5	44.6	115	-5.04676	0	29	6
5	45.9	115	-5.30575	0	29	6
5	48.6	115	-5.30575	0	29	6
5	51.4	115	-5.01438	0	29	6
5	54.1	115	-5.08992	0	29	6
5	55.4	115	-5.06834	0	29	6
5	56.8	115	-4.72302	0	29	6
5	58.1	115	-4.70143	0	29	6
5	60.8	115	-4.46402	0	29	6
5	63.5	115	-4.55036	0	29	6
5	64.9	115	-4.6151	0	29	6
5	66.2	115	-5.52158	0	29	6
5	68.9	115	-5.55395	0	29	6
5	71.6	115	-4.9928	0	29	6
5	73	115	-5.44604	0	29	6
5	74.3	115	-5.44604	0	29	6
5	77	115	-5.66187	0	29	6
5	81.1	115	-5.35971	0	29	6
5	83.8	115	-5.88848	0	29	6
5	86.5	115	-5.87769	0	29	6
5	87.8	115	-5.70503	0	29	6
5	89.2	115	-5.51079	0	29	6
5	91.9	115	-5.51079	0	29	6
5	94.6	115	-5.4892	0	29	6
5	95.9	115	-4.89568	0	29	6
5	98.6	115	-4.51798	0	29	6
5	102.7	115	-4.65827	0	29	6
5	106.8	115	-4.6151	0	29	6
5	110.8	115	-4.83093	0	29	6
5	113.5	115	-6.27697	0	29	6
5	114.9	115	-6.23381	0	29	6
6	7.1	120	-4.03468	0	40	6
6	9.5	120	-3.82659	0	40	6
6	12.5	120	-4.3815	0	40	6
6	14.3	120	-5.50867	0	40	6

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
6	16.7	120	-5.59537	0	40	6
6	23.8	120	-5.3526	0	40	6
6	26.2	120	-5.68208	0	40	6
6	28	120	-6.0289	0	40	6
6	35.7	120	-5.00578	0	40	6
6	38.1	120	-5.85549	0	40	6
6	42.9	120	-5.56069	0	40	6
6	47.6	120	-5.49133	0	40	6
6	50	120	-5.54335	0	40	6
6	52.4	120	-5.8208	0	40	6
6	57.1	120	-5.10982	0	40	6
6	61.9	120	-5.56069	0	40	6
6	63	120	-6.30635	0	40	6
6	65.3	120	-6.34104	0	40	6
6	66.7	120	-6.39306	0	40	6
6	69	120	-6.56647	0	40	6
6	73.8	120	-6.39306	0	40	6
6	75.6	120	-6.47976	0	40	6
6	78.6	120	-6.39306	0	40	6
6	83.3	120	-6.32369	0	40	6
6	85.7	120	-6.32369	0	40	6
6	90.5	120	-5.71676	0	40	6
6	92.9	120	-6.28901	0	40	6
6	97.6	120	-6.34104	0	40	6
6	102.4	120	-5.94219	0	40	6
6	104.8	120	-6.06358	0	40	6
6	106.7	120	-6.47976	0	40	6
6	109.5	120	-6.49711	0	40	6
6	114.3	120	-6.21965	0	40	6
6	119	120	-6.13294	0	40	6
5	2.4	110	-3.60115	0	41	6
5	4.8	110	-3.96531	0	41	6
5	9.6	110	-4	0	41	6
5	14.4	110	-3.63583	0	41	6
5	16.8	110	-3.56647	0	41	6
5	21.6	110	-3.68786	0	41	6
5	24	110	-4.84971	0	41	6
5	26.4	110	-5.50867	0	41	6
5	31.2	110	-5.33526	0	41	6
5	40.8	110	-5.94219	0	41	6
5	42.2	110	-6.16763	0	41	6
5	43.8	110	-6.42774	0	41	6
5	45.5	110	-5.95953	0	41	6
5	47.9	110	-5.85549	0	41	6
5	50.3	110	-6.06358	0	41	6
5	52.7	110	-5.78612	0	41	6
5	57.5	110	-5.69942	0	41	6
5	64.7	110	-5.50867	0	41	6
5	67.1	110	-6.1156	0	41	6

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
5	71.9	110	-6.49711	0	41	6
5	74.3	110	-5.97687	0	41	6
5	79.1	110	-5.28323	0	41	6
5	81.5	110	-5.8208	0	41	6
5	83.9	110	-6.30635	0	41	6
5	86.3	110	-6.53179	0	41	6
5	88.7	110	-6.60115	0	41	6
5	95.9	110	-6.28901	0	41	6
5	98.3	110	-6.65317	0	41	6
5	100.7	110	-6.68786	0	41	6
5	103.1	110	-6.54913	0	41	6
5	105.5	110	-6.4104	0	41	6
6	4.8	75	-4.32758	0	42	6
6	7.1	75	-4.94827	0	42	6
6	9.5	75	-4.94827	0	42	6
6	11.9	75	-5.2931	0	42	6
6	14.3	75	-5.55172	0	42	6
6	16.7	75	-6	0	42	6
6	19	75	-6.20689	0	42	6
6	21.4	75	-6.22413	0	42	6
6	28.6	75	-6.36206	0	42	6
6	33.3	75	-6.06896	0	42	6
6	35.7	75	-6.46551	0	42	6
6	37	75	-5.53448	0	42	6
6	40.5	75	-5.0862	0	42	6
6	42.9	75	-5.18965	0	42	6
6	47.6	75	-4.77586	0	42	6
6	50	75	-4.53448	0	42	6
6	52.4	75	-4.93103	0	42	6
6	54.8	75	-4.98275	0	42	6
6	59.5	75	-5.03448	0	42	6
6	61.9	75	-6.53448	0	42	6
6	64.3	75	-6.62069	0	42	6
6	69	75	-6.18965	0	42	6
6	71.4	75	-6.62069	0	42	6
6	73.8	75	-5.55172	0	42	6
6.5	5.2	15	-5.07508	0	6	7
6.5	10.5	15	-4.51194	0	6	7
6.5	10.5	15	-5.90443	0	6	7
6.5	6.7	15	-4.52127	0	12	7
6.5	12	15	-4.89361	0	12	7
6.5	12	15	-6.12766	0	12	7
6.7	20	40	-3.85864	0	1	8
6.7	40	40	-3.99997	0	1	8
5.1	20	40	-3.93782	0	2	8
5.1	40	40	-4.4089	0	2	8
7.9	20	40	-3.63679	0	3	8
7.9	40	40	-3.93782	0	3	8
10.6	20	40	-3.5954	0	4	8

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
10.6	40	40	-3.50113	0	4	8
10.4	20	40	-3.63679	0	5	8
10.4	40	40	-3.58243	0	5	8
9.9	20	40	-3.83516	0	6	8
9.9	40	40	-3.66675	0	6	8
8.4	20	40	-3.79169	0	7	8
8.4	40	40	-3.68255	0	7	8
7	20	40	-3.99997	0	8	8
7	40	40	-4.15967	0	8	8
7.2	20	40	-3.81288	0	9	8
7.2	40	40	-4.03367	0	9	8
8.4	20	40	-3.7337	0	10	8
8.4	40	40	-3.88346	0	10	8
9.3	20	40	-3.75218	0	11	8
9.3	40	40	-3.71597	0	11	8
9.3	20	40	-3.71597	0	12	8
9.3	40	40	-3.60876	0	12	8
2	12	40	-4.69135	0	99	9
2.1	12	40	-4.98765	0	99	9
2.6	12	40	-5.29629	0	99	9
2.3	12	40	-4.11111	0	99	9
3.3	12	40	-5.01234	0	99	9
3.6	12	40	-5.71604	0	99	9
4.9	12	40	-5.80246	0	99	9
4.1	12	40	-4.98765	0	99	9
4.3	12	40	-4.92592	0	99	9
5.1	12	40	-5.09876	0	99	9
4.5	12	40	-4.76543	0	99	9
5.6	12	40	-4.82716	0	99	9
7.9	12	40	-4.71605	0	99	9
4.4	12	40	-4.24691	0	99	9
5.1	12	40	-4.09876	0	99	9
6.1	12	40	-3.87654	0	99	9
6.9	12	40	-3.91358	0	99	9
7.7	12	40	-4.01234	0	99	9
7.6	12	40	-4.07407	0	99	9
2.3	12	40	-4.11111	0	99	9
8.3	12	40	-3.79012	0	99	9
10	12	40	-3.44444	0	99	9
9.9	12	40	-3.48148	0	99	9
10.1	12	40	-3.58024	0	99	9
11	12	40	-3.50617	0	99	9
15.3	12	40	-3.32098	0	99	9
15.3	12	40	-3.22222	0	99	9
1.6	20	20	-4.60812	1	1	10
2.8	20	20	-4.45851	1	2	10
3.2	20	20	-4.25379	1	3	10
3.2	20	20	-4.3404	1	4	10
3.5	20	20	-3.93882	1	5	10

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
3.6	20	20	-4.14355	1	6	10
3.9	20	20	-4.57662	1	7	10
3.9	20	20	-4.03331	1	8	10
4.3	20	20	-4.65536	1	9	10
4.3	20	20	-4.23804	1	10	10
4.7	20	20	-4.25379	1	11	10
4.7	20	20	-3.84434	1	12	10
4.7	20	20	-3.82071	1	13	10
5.1	20	20	-3.78922	1	14	10
5.9	20	20	-3.81284	1	15	10
6	20	20	-3.7026	1	16	10
6.3	20	20	-4.26953	1	17	10
6.8	20	20	-3.3089	1	18	10
7	20	20	-3.26166	1	19	10
7.8	20	20	-3.21442	1	20	10
8.1	20	20	-3.3404	1	21	10
7.9	20	20	-3.57662	1	22	10
7.9	20	20	-2.99394	1	23	10
8.5	20	20	-3.39552	1	24	10
9	20	20	-3.42701	1	25	10
9.1	20	20	-3.25379	1	26	10
9	20	20	-3.19079	1	27	10
8.7	20	20	-3.05694	1	28	10
10.2	20	20	-3.19867	1	29	10
11.7	20	20	-2.74985	1	30	10
9.5	19.1	100	-4.36513	0	3	11
9.5	24.2	100	-4.68092	0	3	11
9.5	30.6	100	-4.87829	0	3	11
9.5	35.7	100	-4.73026	0	3	11
9.5	42	100	-5.3125	0	3	11
9.5	47.1	100	-5.59868	0	3	11
9.5	52.2	100	-5.40131	0	3	11
9.5	57.3	100	-5.39144	0	3	11
9.5	63.7	100	-5.26315	0	3	11
9.5	68.8	100	-5.09539	0	3	11
9.5	73.9	100	-5.08552	0	3	11
9.5	79	100	-5.08552	0	3	11
9.5	85.4	100	-4.90789	0	3	11
9.5	91.7	100	-4.90789	0	3	11
9.5	99.4	100	-5.9046	0	3	11
4.2	8.9	80	-5.2388	0	5	11
4.2	14	80	-5.0398	0	5	11
4.2	19.1	80	-4.95024	0	5	11
4.2	24.2	80	-4.83084	0	5	11
4.2	30.6	80	-5.1592	0	5	11
4.2	35.7	80	-5.68656	0	5	11
4.2	44.6	80	-6.17412	0	5	11

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
4.2	48.4	80	-6.21393	0	5	11
4.2	54.8	80	-6.18408	0	5	11
4.2	57.3	80	-5.26865	0	5	11
4.2	62.4	80	-5.0597	0	5	11
4.2	68.8	80	-5.26865	0	5	11
4.2	75.2	80	-5.52736	0	5	11
4.2	7.9	55	-4.28205	0	6	11
4.2	11	55	-4.6282	0	6	11
4.2	17.3	55	-4.57692	0	6	11
4.2	22	55	-4.1923	0	6	11
4.2	26.8	55	-4.52564	0	6	11
4.2	31.5	55	-4.47435	0	6	11
4.2	36.2	55	-4.6923	0	6	11
4.2	44.1	55	-5.20512	0	6	11
4.2	47.2	55	-4.80769	0	6	11
4.2	53.5	55	-4.39743	0	6	11
4.2	13.1	75	-5	0	8	11
4.2	18	75	-5.50666	0	8	11
4.2	23	75	-5.61333	0	8	11
4.2	29.5	75	-5.84	0	8	11
4.2	31.1	75	-5.52	0	8	11
4.2	37.7	75	-5.49333	0	8	11
4.2	42.6	75	-4.96	0	8	11
4.2	47.5	75	-4.81333	0	8	11
4.2	54.1	75	-5.34666	0	8	11
4.2	59	75	-4.74666	0	8	11
4.2	67.2	75	-5.48	0	8	11
4.2	72.1	75	-6.01333	0	8	11
5.8	6.3	150	-3.97435	0	9	11
5.8	10.9	150	-5.14102	0	9	11
5.8	15.6	150	-5.25641	0	9	11
5.8	20.3	150	-5.93589	0	9	11
5.8	26.6	150	-6.26923	0	9	11
5.8	31.3	150	-5.97435	0	9	11
5.8	35.9	150	-6.32051	0	9	11
5.8	42.2	150	-6.26923	0	9	11
5.8	46.9	150	-6.24359	0	9	11
5.8	53.1	150	-6.33333	0	9	11
5.8	59.4	150	-6.47435	0	9	11
5.8	64.1	150	-6.52564	0	9	11
5.8	68.8	150	-6.48717	0	9	11
5.8	76.6	150	-6.57692	0	9	11
5.8	81.3	150	-5.66666	0	9	11
5.8	85.9	150	-5.73076	0	9	11
5.8	92.2	150	-6.48717	0	9	11
5.8	98.4	150	-6.53846	0	9	11
5.8	103.1	150	-6.44871	0	9	11
5.8	107.8	150	-6.26923	0	9	11
5.8	115.6	150	-6.43589	0	9	11

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
5.8	120.3	150	-6.28205	0	9	11
5.8	126.6	150	-5.97435	0	9	11
5.8	132.8	150	-6.21794	0	9	11
5.8	137.5	150	-5.71794	0	9	11
5.8	143.8	150	-5.87179	0	9	11
5.8	148.4	150	-6.42307	0	9	11
5.8	17.2	135	-4.36111	0	11	11
5.8	24.1	135	-6.04166	0	11	11
5.8	27.6	135	-6.125	0	11	11
5.8	32.8	135	-5.77777	0	11	11
5.8	39.7	135	-4.56944	0	11	11
5.8	43.1	135	-5.45833	0	11	11
5.8	53.4	135	-5.29166	0	11	11
5.8	56.9	135	-5.29166	0	11	11
5.8	63.8	135	-4.97222	0	11	11
5.8	67.2	135	-5.54166	0	11	11
5.8	74.1	135	-5.51388	0	11	11
5.8	81	135	-5.43055	0	11	11
5.8	86.2	135	-5.76388	0	11	11
5.8	89.7	135	-6.30555	0	11	11
5.8	96.6	135	-5.88888	0	11	11
5.8	101.7	135	-6.30555	0	11	11
5.8	108.6	135	-6.73611	0	11	11
5.8	115.5	135	-6.47222	0	11	11
5.8	119	135	-6.5	0	11	11
5.8	124.1	135	-6.43055	0	11	11
5.8	132.8	135	-6.47222	0	11	11
5.8	9.8	100	-5.81304	0	12	11
5.8	14.8	100	-5.83913	0	12	11
5.8	19.7	100	-5.0826	0	12	11
5.8	24.6	100	-4.91304	0	12	11
5.8	31.1	100	-4.86086	0	12	11
5.8	37.7	100	-5.2	0	12	11
5.8	42.6	100	-5.73478	0	12	11
5.8	45.9	100	-6.17826	0	12	11
5.8	52.5	100	-6.15217	0	12	11
5.8	57.4	100	-5.6826	0	12	11
5.8	62.3	100	-5.70869	0	12	11
5.8	67.2	100	-6.03478	0	12	11
5.8	75.4	100	-5.6826	0	12	11
5.8	80.3	100	-5.70869	0	12	11
5.8	85.2	100	-6.1913	0	12	11
5.8	91.8	100	-6.17826	0	12	11
5.8	95.1	100	-5.90434	0	12	11
5	4.5	120	-5.25806	0	13	11
5	9	120	-5.22177	0	13	11
5	13.5	120	-4.84677	0	13	11
5	21.1	120	-5.04032	0	13	11
5	25.6	120	-5.45161	0	13	11

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
5	31.6	120	-5.64516	0	13	11
5	34.6	120	-5.92338	0	13	11
5	40.6	120	-5.16129	0	13	11
5	46.6	120	-5.88709	0	13	11
5	52.6	120	-5.56048	0	13	11
5	57.1	120	-5.46371	0	13	11
5	63.2	120	-5.70564	0	13	11
5	69.2	120	-5.5	0	13	11
5	79.7	120	-6.44354	0	13	11
5	87.2	120	-6.45564	0	13	11
5	91.7	120	-6.12903	0	13	11
5	97.7	120	-6.26209	0	13	11
5	103.8	120	-5.65725	0	13	11
5	109.8	120	-5.34274	0	13	11
5	115.8	120	-5.89919	0	13	11
5	18.7	120	-5.575	0	14	11
5	22.7	120	-4.92142	0	14	11
5	28	120	-4.66428	0	14	11
5	34.7	120	-5.35	0	14	11
5	38.7	120	-5.68214	0	14	11
5	45.3	120	-5.59642	0	14	11
5	50.7	120	-6.27142	0	14	11
5	57.3	120	-6.28214	0	14	11
5	62.7	120	-6.27142	0	14	11
5	66.7	120	-5.62857	0	14	11
5	72	120	-5.07142	0	14	11
5	78.7	120	-5.81071	0	14	11
5	84	120	-6.19642	0	14	11
5	89.3	120	-5.86428	0	14	11
5	94.7	120	-6.15357	0	14	11
5	100	120	-5.18928	0	14	11
5	104	120	-5.875	0	14	11
5	110.7	120	-5.85357	0	14	11
5	113.3	120	-5.61785	0	14	11
5	120	120	-5.23214	0	14	11
5	8.7	120	-4.07586	0	15	11
5	12.2	120	-3.97931	0	15	11
5	20.9	120	-4.04827	0	15	11
5	22.6	120	-4.40689	0	15	11
5	29.6	120	-4.65517	0	15	11
5	33	120	-5.52413	0	15	11
5	40	120	-5.53793	0	15	11
5	45.2	120	-5.8	0	15	11
5	50.4	120	-5.09655	0	15	11
5	55.7	120	-5.74482	0	15	11
5	62.6	120	-5.3862	0	15	11
5	67.8	120	-5.53793	0	15	11
5	73	120	-5.08275	0	15	11
5	78.3	120	-5.08275	0	15	11

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
5	85.2	120	-5.27586	0	15	11
5	88.7	120	-6.07586	0	15	11
5	95.7	120	-6.25517	0	15	11
5	100.9	120	-5.70344	0	15	11
5	106.1	120	-5.60689	0	15	11
5	111.3	120	-6.06206	0	15	11
5	114.8	120	-6.14482	0	15	11
4.8	2.6	15	-3.30434	1	1	12
4.8	7.9	15	-2.1581	1	1	12
4.8	12.4	15	-2.39525	1	1	12
8.2	2	70	-2.0196	1	26	12
8.2	5.9	70	-2.0196	1	26	12
8.2	11.1	70	-2.78431	1	26	12
8.2	15.7	70	-2.52941	1	26	12
8.2	20.9	70	-2.2549	1	26	12
8.2	24.9	70	-3.21568	1	26	12
8.2	30.1	70	-3.41176	1	26	12
8.2	34.7	70	-3.64705	1	26	12
8.2	39.9	70	-3.35294	1	26	12
8.2	43.8	70	-3.37254	1	26	12
8.2	49.1	70	-3.96078	1	26	12
8.2	53.7	70	-3.7647	1	26	12
8.2	58.9	70	-3.82353	1	26	12
8.2	64.1	70	-3.47058	1	26	12
8.2	69.4	70	-3.94117	1	26	12
9.8	3.2	150	-2.01953	1	33	12
9.8	6.5	150	-2.03906	1	33	12
9.8	10.4	150	-2.03906	1	33	12
9.8	15.5	150	-2.23437	1	33	12
9.8	20.1	150	-3.25	1	33	12
9.8	25.3	150	-3.36718	1	33	12
9.8	29.1	150	-3.38671	1	33	12
9.8	34.3	150	-3.36718	1	33	12
9.8	38.9	150	-3.58203	1	33	12
9.8	44	150	-3.71875	1	33	12
9.8	49.2	150	-3.77734	1	33	12
9.8	52.5	150	-3.79687	1	33	12
9.8	57	150	-3.71875	1	33	12
9.8	62.8	150	-3.67968	1	33	12
9.8	68	150	-3.64062	1	33	12
9.8	73.8	150	-3.67968	1	33	12
9.8	79	150	-3.8164	1	33	12
9.8	84.2	150	-3.875	1	33	12
9.8	89.4	150	-3.8164	1	33	12
9.8	95.2	150	-3.89453	1	33	12
9.8	99.7	150	-3.89453	1	33	12
9.8	104.9	150	-4.07031	1	33	12
9.8	109.5	150	-3.8164	1	33	12
9.8	115.3	150	-3.95312	1	33	12

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
9.8	119.8	150	-3.93359	1	33	12
9.8	126.3	150	-3.95312	1	33	12
9.8	130.2	150	-3.93359	1	33	12
9.8	136	150	-4.24609	1	33	12
9.8	141.2	150	-4.32421	1	33	12
9.8	145.7	150	-4.20703	1	33	12
8.2	2.7	80	-2.03205	1	1283	12
8.2	3.4	80	-2.01602	1	1283	12
8.2	4.4	80	-2.01602	1	1283	12
8.2	5.4	80	-2.03205	1	1283	12
8.2	5.8	80	-2.03205	1	1283	12
8.2	6.5	80	-2.01602	1	1283	12
8.2	7.1	80	-2.01602	1	1283	12
8.2	7.8	80	-2.01602	1	1283	12
8.2	8.5	80	-2.01602	1	1283	12
8.2	9.2	80	-2.01602	1	1283	12
8.2	9.9	80	-2.03205	1	1283	12
8.2	11.2	80	-2.60897	1	1283	12
8.2	11.6	80	-3.41025	1	1283	12
8.2	12.2	80	-2.91346	1	1283	12
8.2	14.3	80	-2.11217	1	1283	12
8.2	15	80	-2.22435	1	1283	12
8.2	16	80	-2.30448	1	1283	12
8.2	16.3	80	-2.36859	1	1283	12
8.2	16.7	80	-2.78525	1	1283	12
8.2	18	80	-3.00961	1	1283	12
8.2	18.4	80	-3.52243	1	1283	12
8.2	18.7	80	-3.18589	1	1283	12
8.2	19.7	80	-3.58653	1	1283	12
8.2	20.7	80	-3.26602	1	1283	12
8.2	21.2	80	-3.84294	1	1283	12
8.2	21.8	80	-3.97115	1	1283	12
8.2	22.4	80	-3.55448	1	1283	12
8.2	23.5	80	-3.66666	1	1283	12
8.2	24.5	80	-3.58653	1	1283	12
8.2	25.5	80	-3.68269	1	1283	12
8.2	26	80	-3.41025	1	1283	12
8.2	26.9	80	-3.73076	1	1283	12
8.2	28.9	80	-3.08974	1	1283	12
8.2	29.3	80	-3.65064	1	1283	12
8.2	30.6	80	-3.52243	1	1283	12
8.2	32	80	-3.60256	1	1283	12
8.2	32.7	80	-3.85897	1	1283	12
8.2	34	80	-3.71474	1	1283	12
8.2	35	80	-3.84294	1	1283	12
8.2	37.1	80	-3.39423	1	1283	12
8.2	37.8	80	-3.74679	1	1283	12
8.2	38.1	80	-3.92307	1	1283	12
8.2	39.5	80	-3.68269	1	1283	12

Wind	Depth	Z _{mixed}	Log ϵ	ENV	Profile	Author
8.2	40.5	80	-3.47435	1	1283	12
8.2	42	80	-3.95512	1	1283	12
8.2	41.8	80	-3.65064	1	1283	12
8.2	42.5	80	-3.16987	1	1283	12
8.2	43.5	80	-3.39423	1	1283	12
8.2	44.6	80	-3.18589	1	1283	12
8.2	45.9	80	-3.26602	1	1283	12
8.2	47.3	80	-3.39423	1	1283	12
8.2	47.6	80	-3.90705	1	1283	12
8.2	49	80	-3.77884	1	1283	12
8.2	50	80	-3.89102	1	1283	12
8.2	50.7	80	-3.74679	1	1283	12
8.2	51.7	80	-3.875	1	1283	12
8.2	52.7	80	-4.03525	1	1283	12
8.2	53.4	80	-4.16346	1	1283	12
8.2	54.1	80	-3.74679	1	1283	12
8.2	54.8	80	-3.875	1	1283	12
8.2	55.8	80	-3.41025	1	1283	12
8.2	56.8	80	-3.95512	1	1283	12
8.2	58.2	80	-3.85897	1	1283	12
8.2	59.9	80	-3.20192	1	1283	12
8.2	60.2	80	-3.76282	1	1283	12
8.2	60.9	80	-3.39423	1	1283	12
8.2	61.6	80	-3.875	1	1283	12
8.2	62.2	80	-4.46794	1	1283	12
8.2	63.6	80	-3.98717	1	1283	12
8.2	63.9	80	-3.92307	1	1283	12
8.2	64.6	80	-3.875	1	1283	12
8.2	65.6	80	-3.65064	1	1283	12
8.2	66.7	80	-3.79487	1	1283	12
8.2	67.3	80	-3.52243	1	1283	12
8.2	68.7	80	-3.79487	1	1283	12
8.2	70.4	80	-3.57051	1	1283	12
8.2	71.8	80	-4.0032	1	1283	12
8.2	73.1	80	-3.875	1	1283	12
8.2	74.1	80	-3.90705	1	1283	12
8.2	74.8	80	-4.09935	1	1283	12
8.2	75.5	80	-4.0032	1	1283	12
8.2	76.2	80	-4.35576	1	1283	12
8.2	76.5	80	-4.93269	1	1283	12
8.2	77.9	80	-3.875	1	1283	12
8.2	78.6	80	-4.86859	1	1283	12
3.9	10	20	-5.81818	1	1	13
3.9	10	20	-5.32323	1	1	13
3.9	10	20	-5	1	1	13
3	10	20	-4.59596	1	1	13
3.9	10	20	-4.31313	1	1	13
3.9	10	20	-3.80808	1	1	13
5.5	10	20	-4.0202	1	1	13

Wind	Depth	Z_{mixed}	$\text{Log } \epsilon$	ENV	Profile	Author
6.1	10	20	-4.11111	1	1	13
6.1	10	20	-4.23232	1	1	13
7.1	10	20	-3.86868	1	1	13
8.6	10	20	-3.93939	1	1	13
8.1	10	20	-3.71717	1	1	13
8.9	10	20	-3.72727	1	1	13
9.9	10	20	-3.69697	1	1	13
10.3	10	20	-3.71717	1	1	13
7.2	10	20	-3.61616	1	1	13
8	10	20	-3.31313	1	1	13
9	10	20	-3.41414	1	1	13
10.3	10	20	-3.41414	1	1	13
14.7	10	20	-3.43434	1	1	13
12.3	10	20	-2.98989	1	1	13
14.7	10	20	-2.91919	1	1	13
3.9	15	20	-5.03355	1	1	13
2.4	15	20	-4.5302	1	1	13
4.4	15	20	-4.02684	1	1	13
7.2	15	20	-4.12751	1	1	13
8	15	20	-3.84563	1	1	13
7.9	15	20	-3.77516	1	1	13
8.9	15	20	-3.63422	1	1	13
11.1	15	20	-3.49328	1	1	13
13	15	20	-3.50335	1	1	13
4.9	20	20	-5.04362	1	1	13
6	20	20	-4.93288	1	1	13
7.1	20	20	-4.5906	1	1	13
9	20	20	-4.23825	1	1	13
10.1	20	20	-4.04698	1	1	13
7	20	20	-3.9161	1	1	13
8.9	20	20	-3.83557	1	1	13
7.1	20	20	-3.32214	1	1	13
13.2	20	20	-3.74496	1	1	13
13.2	20	20	-3.64429	1	1	13

Data sources: 1, Dewey and Moum 1990; 2, Dillon and Caldwell 1980; 3, Dillon et al. 1981; 4, Haury et al. 1990; 5, Lange 1981; 6, Lueck 1988; 7, Lueck et al. 1983; 8, Moum and Caldwell 1985; 9, Oakey 1985; 10, Oakey and Elliott 1982; 11, Osborn 1978; 12, Shay and Gregg 1986; 13, Veth 1983.