TROPHIC PHASING OF JUVENILE CHUM SALMON [*ONCORHYNCHUS KETA* WALBAUM] AND HARPACTICOID COPEPODS IN THE FRASER RIVER ESTUARY, BRITISH COLUMBIA

by

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Abstract

Within the environmental approach for the study of fluctuations in fish population abundance, factors that may regulate the overlap in time and space (phasing) of fishes, food supply, and predators, are sought. This trophic phasing analysis is based on the recognition that production of food is a process at least partially independent of the production of consumers. Trophic phasing analysis was applied in investigating production of chum salmon in the Fraser River estuary. Juvenile chum salmon were captured near a tidal flat; the abundance of salmon near the flat was highest in late May in 1985 and in early June in 1986. These salmon relied heavily on harpacticoid copepods as a food source. Individual taxa as well as the assemblage of main prey harpacticoids also had periods of highest abundance in the water column. The blooming period of the prey harpacticoid assemblage coincided with the appearance in the sediment of warming episodes. These warming episodes result from interactions between the daily heat cycle and specific tide patterns. Variations in the degree of overlap of the periods of highest abundance of salmon and harpacticoids could affect the survival of the fishes. The degree of overlap of those periods was hindcasted using indices for the temporal patterns of abundance of salmon and harpacticoids on the flat. The median date of downstream migration at a counting station upstream was used for the salmon; the timing of the second annual occurrence of tide conditions giving rise to a warming event in the sediment was used for harpacticoids. Difference in time between the two events was taken as a phasing index accounting for two degrees of freedom in the process of fish production. There is suggestion of a non-monotonic relationship between the index of survival of even broodyear chum salmon and the hindcasted phasing index.

Contents

List of Figures

List of Tables

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Chapter 1

General Introduction

A seemingly inherent characteristic of fishery resources is their variability on a wide range of temporal and spatial scales (Csirke & Sharp 1984; Steele 1984). To investigate this variability, two "radically different approaches" (Legendre & Demers 1984) have been developed. The difference between the two approaches can be appreciated by comparing the frameworks through which each addresses the issue of fish population variability. One approach proposes to investigate variability in fish abundance as the result of natural environmental fluctuations; the other proposes to investigate fish population variations as the result of anthropogenic activity, namely fishing. In 1914, Hjort proposed that the magnitude of a fish year-class was set by the success of the fishes in colonizing their environment during early life stages. This success was assumed to vary in accordance with some environmental factor(s) in such a manner that the size of the parental fish population would be of little importance, if any, in the determination of the filial year-class strength. A well known study along Hjort's proposition is that of Burkenroad (1948) on the Pacific halibut. Burkenroad submitted that major fluctuations in abundance of the halibut could be attributed to natural causes and that the relevance of the then current fish population regulation theories remained to be demonstrated. How-

ever, Burkenroad's thesis was perhaps simply balancing that of Thompson (1937) who, after studying the same fish. had concluded that fishing was responsible for the fluctuations in abundance of the Pacific halibut. In 1954, Ricker proposed a model, better known as "stock-recruitment model", by which the effect of fishing on subsequent fish stock sizes could be formally investigated. This model was based on the principle of population homeostasis through density-dependence, which states that the rate of increase of an animal population decreases as its size increases. The apparent soundness of the foundations of this model and its timeliness in a period when the reported world fish catch was sharply increasing, lead to substantial efforts in the investigation and modeling of the effects of fishing on the dynamics of fish populations. At the same time, investigation and modeling of the effects of environmental fluctuations on the dynamics of fish populations were disregarded (Larkin 1978). However, it later became obvious that even when many years' data were available, stock-recruitment models accounted for only a fraction, sometimes small, of the observed variability in typical fish abundance data (Hunter 1976; Sissenwine 1984). The interest in Hjort's thesis was reactivated since much of the blurring in stock-recruitment data was considered to be the result of environmental variability (Anonymous 1980) and since advances in biological oceanography were providing a much better understanding of the complex mechanisms hitherto lumped by fisheries biology into the single word "environment" (Larkin 1978). However, as pointed out by various sources (*e.g.* Ricker 1975; Gulland 1983; Sissenwine 1984; Larkin 1973,1984) recruitment models relating fish population fluctuations and environmental factors generally fail to predict post-publication events probably because of the often misleading significance of the supportive correlations.

Applications of either of the two radically different approaches for the investiga-

tion of fluctuations in fish abundance lead to inconclusive results when the nature and function of fish population regulation mechanisms are investigated. Sophistication of statistical and computational techniques aside, the situation today is not much different than it was 40 or 50 years ago: whether the size of a fish population is determined by that of the parental stock size or by some environmental factor(s) remains conjectural. The recent literature on fish population regulation is still characterized by a dichotomy of approaches between fisheries biology, honoring the parental stock hypothesis, and fisheries oceanography, finding in Hjort's thesis an attractive rationale for its concern for the environment of the fishes. This schism has resulted in an "apparent immiscibility of fisheries biology and oceanography" (Wooster 1983). The difficulty in reconciling the two approaches is apparent in the following semantic conflict. When the different regions of a curve relating parental and filial abundance of a fish population are qualified in fisheries biology and fisheries oceanography, totally opposite attributes are used for the same regions (Fig. 1.1). One who undertakes a study on fish population regulation can only be in a quandary when trying to select an appropriate approach. Clearly then, the development of a conceptual framework upon which to organize the research effort should be the initial step in a study aimed at gaining an understanding on the nature and function of the mechanisms regulating fish population abundance (Anonymous 1980; Csirke & Sharp 1984).

In this thesis, a study on the variability in abundance of the chum salmon (*Oncorhynchus keta* Walbaum) of the Fraser River is presented. For reasons mentioned above, chapter 2 consists of a review of the two current paradigms on the nature and function of the mechanisms regulating fish abundance. In this review, a framework is proposed that is termed "trophic phasing analysis". This framework

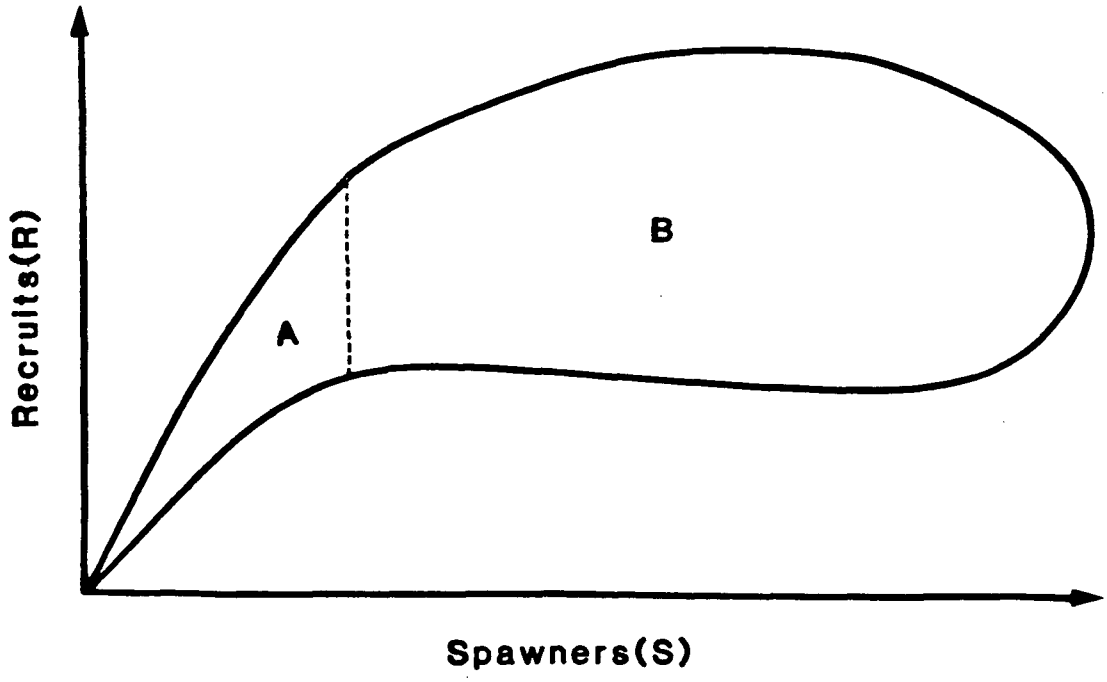

Figure 1.1: Density related attributes of a general stock recruitment relationship. Region "A" can be considered density-independent since $dR/dS \approx$ constant and region B can be considered density-dependent since $dR/dS \neq$ constant (parental filial thesis); alternatively, region "A" can be considered density-dependent since R appears to be of first-order with respect to S, and region "B" can be considered density-independent since R appears to be of 0-order w.r.t. S. (environment thesis).

requires the description of the spatial and temporal distributions of the fishes and knowledge of their trophodynamics. It is then possible to identify environmental factors that modulate the realized overlap of the fishes, their predators, and their food items, and which may regulate survival and abundance of the fishes. In subsequent chapters, forming the core of the experimental and analytical effort of this thesis, this proposed "trophic phasing analysis" is applied in a case study on the chum salmon. In chapter 3, the life-cycle of the chum salmon is reviewed with emphasis on the initial near-shore stage; the diet of the fish at that stage is described relative to food samples collected using an innovative technique and the main dietary items are identified. The spatial and temporal distributions of an assemblage of species of harpacticoid copepods are described in chapter 4. The assemblage is made up of those species preferentially preyed upon by the chum salmon. Effort is made to resolve some difficulties in locating harpacticoid copepods effectively consumed by the fish. The temporal variability of the same assemblage of harpacticoids is linked with specific patterns in the thermal regime in their environment. In chapter 5, potential limitation of chum salmon production in the Fraser River estuary is discussed in light of the information exposed in the two previous chapters. Available data on chum salmon survival from outmigrant juveniles to returning adults is related to a hindcasted index of phasing of the fish and harpacticoid copepods. In chapter 6, the results of this research effort are discussed at two different, but nested, levels. Applicability of the results in the management of the chum salmon are discussed; then, the use of trophic phasing analysis in the study of fish population regulation is appraised.

The orientation of this research project is based on the view that production of food organisms is a process at least partially independent of the feeding of predators

(Parsons *et al.* 1984 a). This thesis was undertaken with the aims of providing a contribution to the on-going debate on the nature and action of the mechanisms regulating fish abundance, and to contribute to our understanding of the ecology of harpacticoid copepods, which might help clarify their role in the diet of juvenile chum salmon.

Temperature data collected during the course of this study were deposited at the Data Library of the University of British Columbia in a machine-readable format (see D'Amours 1986).

Chapter 2

Fish Population Regulation

2.1 Introduction

After reviewing the population dynamics of the Pacific sardine, Clark & Marr (1956) concluded that for any particular fish species, the year-class strength could be determined by three possible scenarios:

1. year-class strength is a function of the parental stock size (parent-stock thesis)
2. year-class strength is determined by environmental factor(s) (environmental thesis)
3. year-class strength is determined by a mixture of 1. and 2. (dual thesis).

More than 30 years later, it seems that Clark & Marr's third scenario has gained wide acceptance. The strength of a year-class of fishes is generally considered as the result of density-dependent homeostatic balance operating on stages set by environmental factors (Cushing 1984; Wooster 1983; Larkin 1978; Beddington & May 1977). Considering scenario 1. or 2. independently of each other would be an "unfortunate dichotomy" (Gulland 1977). However, there is reason to believe that the wide acceptance of the "dual thesis" could be detrimental to progress in

understanding fish recruitment mechanisms. In this chapter, the foundations of the stock-recruitment theory (parent-stock hypothesis) are reviewed; the use of a stock-recruitment model in fisheries management is briefly discussed. A distinction is established between the operational usefulness of stock-recruitment models and the need for empirical evidence supporting either the parental-stock or the environmental thesis.

2.2 The stock-recruitment connection

A most fundamental observation in population biology is that animal populations do not increase without limits (Krebs 1978). In fisheries biology, which is but a special case of population biology, the equivalent statement is made when it is considered basic that fish populations are limited in size even when not fished (Ricker 1954; Beverton & Holt 1957). As a result of this observation, it must be concluded that some relation must exist between the abundance of the reproductive stock and the number of recruits produced (Ricker 1985). In fisheries biology, the relationship between the parental stock size and the number of recruits produced can be derived as follows. Let it be first mentioned that a stock-recruitment relationship can be established between any two points in the life cycle of a fish. Assume an initial number of fish eggs N_o that decline in time following

$$\frac{dN(t)}{dt} = F(N(t)). \tag{2.1}$$

The functionality between $dN(t)/dt$ and $N(t)$ could be established in various ways. For a population to stop increasing when a certain size is reached, either

- mortality increases
- fecundity decreases

- mortality increases *and* fecundity decreases.

The change of intensity in mortality and/or fecundity as the population increases is what sets a limit to the size a population can reach and is known as density-dependent population regulation, a concept developed by Nicholson (1933) (see Fig. 2.1).

In fisheries biology, it has generally been assumed correct and probably not misleading to incorporate the density related effects on the growth rate, in mortality (Z) (Gulland 1983). Eq. 2.1 can then be re-written as

$$\frac{dN(t)}{dt} = -Z(t)N(t). \tag{2.2}$$

With the simple case of linear density-dependent effect in Z, that is when

$$Z(t) = (M_1 + M_2 N_o),$$

(where M_1 and M_2 are mortality coefficient components)

eq. 2.2 can re-written as

$$\frac{dN(t)}{dt} = -(M_1 + M_2 N_o)N(t). \tag{2.3}$$

Integrating 2.3,

$$\log_e N(t) = -M_1 t - M_2 N_o t + const. .$$

At $t = 0$,

$$\log_e N_o = const. ,$$

then,

$$N(t) = N_o e^{-M_1 t} e^{-M_2 N_o t}.$$

Let $N_o = Sf$, and $N(t_r) = R$, where S=number of spawners, and f= number of eggs per spawner, t_r=time to recruitment, and R=number of recruits,

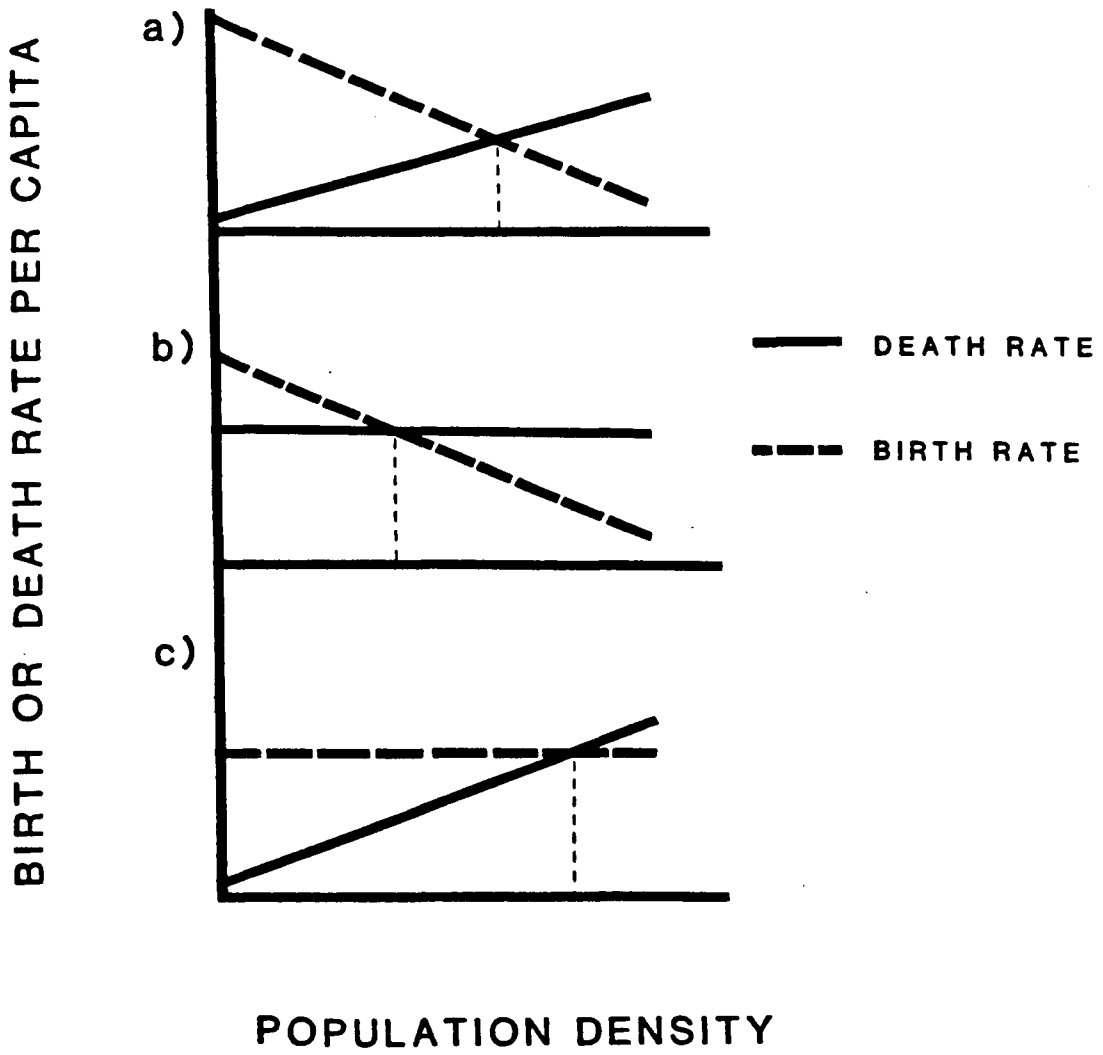

Figure 2.1: Density-dependent population regulation. As the size (density) of a population increases, either fecundity decreases and mortality increases (a), or fecundity decreases (b), or mortality increases (c) (redrawn from Krebs 1978).

then,

$$R = Sfe^{-M_1 t_r} e^{-M_2 S f t_r}. \tag{2.4}$$

With

$$\alpha = fe^{-M_1 t_r} = const.$$

and

$$\beta = M_2 f t_r = const.\ ,$$

eq. 2.4 reduces to

$$R = \alpha S e^{-\beta S}. \tag{2.5}$$

Eq. 2.5 is currently known as the Ricker type stock recruitment curve. In fisheries management, this relationship can be used to forecast the number of recruits, and determine what fraction of the recruits should be made available to fisheries. First, the relationship is parametrized with historical data of spawners and recruits abundance. A plot of this parametrized relationship is more or less dome-shaped, and the fraction of the stock available for harvest is that which lies above the replacement line (Fig. 2.2). To locate the maximum recruitment, R is differentiated with respect to S, *i.e.*

$$\begin{aligned} \frac{dR}{dS} &= \alpha e^{-\beta S} - \alpha S \beta e^{-\beta S} \\ &= \alpha e^{-\beta S}(1 - \beta S)\,. \end{aligned}$$

The maximum recruitment is obtained when

$$\frac{dR}{dS} = 0$$

that is, when

$$S = \frac{1}{\beta}\ ,$$

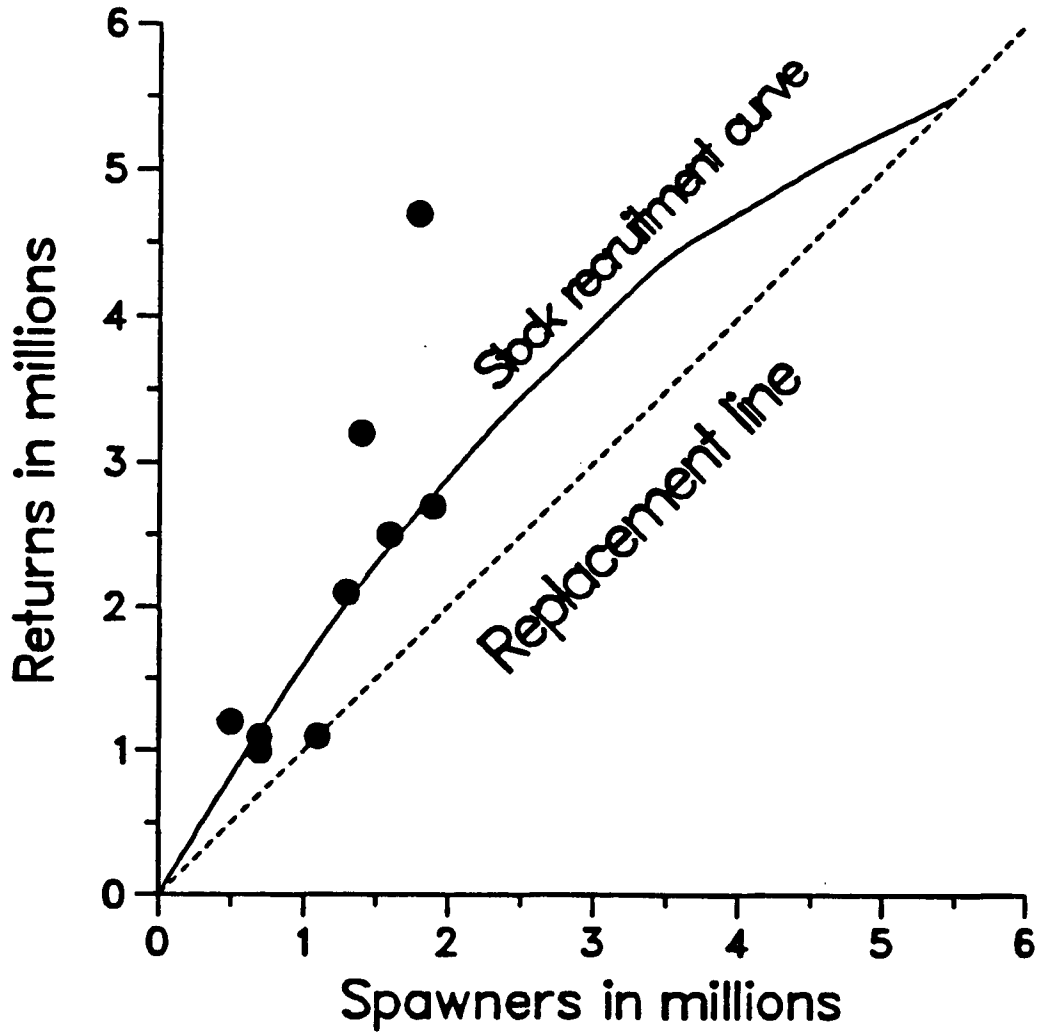

Figure 2.2: Ricker type stock-recruitment curve for even broodyears 1956-1976 of Fraser River chum salmon (from Beacham 1984). The fraction of the the stock above the replacement line (surplus recruitment) is available for harvest.

and will be equal to

$$\frac{\alpha}{\beta e} = \frac{0.3679\alpha}{\beta} .$$

The maximum surplus recruitment (MSR) will be obtained when

$$\frac{dR}{dS} = 1 ,$$

that is, when the production curve is at greatest distance from the replacement line (Hilborn & Peterman 1977). The solution for $dR/dS = 1$ is to be found by iteration, or can be approximated directly from the values of α and β (Hilborn 1985). For a fish like the salmon that is fished just before its once in a lifetime spawning, the MSR is practically equal to the maximum sustainable yield (MSY) (Ricker 1985). The MSY is that level of exploitation that can yield the highest return on a continuous basis.

Since the only variable of the whole fishing process under the control of fisheries managers is escapement (Hilborn 1983), establishment of quotas is a basic tool in fisheries management. Expanded as stock-recruitment models, the parent-stock hypothesis is one effective way to meet the requirements of fisheries managers of establishing quotas with consistency and objectivity. In that sense, the parent-stock hypothesis is no longer one among other hypotheses on the nature of fish population regulation mechanisms; it is a tool of proven operational usefulness for the determination of quotas by which escapement can be controlled.

As pointed out earlier, the fit of typical stock-recruitment data on the model is often very poor. Larkin (1978) summarized the situation as follows

> It is common gossip that if you didn't have the certain knowledge that zero adults produce zero offspring, we could fit à Ricker model, or a Beverton-Holt model, or a straight line, or a circle, with equal satisfaction.

Why, then, despite their poor empirical verification, are stock-recruitment models widely used, and more importantly in the present discussion, why must any hypothesis on the nature of fish population regulation (e.g. environmental thesis) be merged with the parent-stock hypothesis to avoid an "unfortunate dichotomy"? The possible answer to these two questions is the same: because of the operational usefulness of the formal extensions of the parent-stock hypothesis. While operational usefulness appears a reasonable criterion to adopt the parent-stock hypothesis for the business of management, operational usefulness does not prove the relevance of Nicholsonian stock-recruitment models as the best model for fish population regulation mechanisms. It is quite probable, then, that Clark & Marr's third scenario (dual thesis) owes its popularity to the difficulty of divorcing the idea of operational usefulness within the actual scheme of fisheries management.

Merging the parent-stock hypothesis and the environment thesis in the study of fish population regulation mechanisms could be premature. From an intuitive point of view, it may appear necessary that any animal population would become limited from increasing by its very own size. However, the nature and ways of operation of the mechanisms responsible for this self-regulation are still conjectural (as discussed by Krebs (1978)). As pointed out by this author, the conceptual frameworks for the study of animal population regulation must be validated against *real* populations. The parent-stock hypothesis seems easily applied to real populations. While all must agree that zero spawners produce zero offspring, there is no agreement on the validity of assuming that the observed maximal stock size is in any way related to the theoretical maximal size. This means that the parameters computed for the stock-recruitment relationship could be nothing but fitting parameters with only faint nominal statistical support (see Parsons *et al.* 1984 a).

Since the 1950's, most ecologists have chosen to abandon the tiresome arguments about density-dependence by choosing an empirical approach to the study of animal population; dogmatic theories of animal population regulation are replaced by more "fruitful arguments about empirical relationships" (Krebs 1978). Perhaps this evolution in the approach of ecologists studying population regulation would have been difficult had the notion of operational usefulness been kept in the forefront of research. Once the issues of operational usefulness and empirical verification are disentangled, it appears that the study of fish population regulation aiming at understanding recruitment mechanisms has at its disposition two theses, the parent-stock thesis and the environment thesis, both in want of empirical verification. In the case of general population biology, debates on whether the Nicholsonian principle of population regulation through density dependence is operative, have been replaced by a search for empirical arguments on real populations. Oceanography is providing an increasingly detailed knowledge of the environment of marine organisms; it appears reasonable to consider the study of fish population regulation through the environment thesis as a practical concern of oceanography (see Parsons *et al.* 1984 a).

2.3 The Environmental Thesis

Once it has been chosen to replace debates on density-dependence by "arguments about empirical relationships", environments of fishes become overwhelmingly rich aggregates of factors which might be considered as determinants of fish population abundance. The term environment is a broad one indeed, with the result that one is in a quandary when having to choose one particular environmental factor against which to analyse fluctuations in fish abundance. Nonetheless, a careful

selection is possible if knowledge is available on the mechanisms regulating growth and mortality of fishes. Such analysis based on environmental factors selected for sound biological reasons is considered to be less likely to result in spurious relationships (Ricker 1975). To make a sensible choice of environmental factor(s), some sort of conceptual framework with which to theorize and organize the research effort is required. By reviewing selected studies that yield new insights in fish recruitment mechanisms, recurring themes appear that could form the core of such a conceptual framework.

2.3.1 A Review of Selected Studies

Hjort (1914) was the first to suggest that hydrological and biological conditions could determine the "subsequent wealth or poverty of a [fish] year class". Today, this proposition is referred to as Hjort's hypothesis. Legendre & Demers (1984) have given the following interpretation of Hjort's hypothesis: recruitment depends on the success or failure of the annual colonization of their environment by the fish larvae, irrespective of the initial number of eggs produced. This interpretation emphasizes the role of the environment in determining fish year-class strength in early-life stages. A well articulated hypothesis in that sense was provided by Cushing (1975). Cushing submitted that fish abundance variability could result from differential matching of the fish larvae and their food resource. Larvae were assumed to be transported by currents to feeding grounds after fixed spawning periods. The onset of the production cycle on the feeding grounds was reported to be determined by the vertical stability of the water column. The timing of this onset could vary from year to year depending on fluctuations in meteorological conditions regulating the vertical stability of the water column. Any variation in

the relative timing of the arrival of the larvae on the feeding grounds and the onset of the production cycle could alter the food quantity available per fish. Fluctuations in food supply could then cause variability in survival by starvation. The whole hypothesis was named the match/mismatch hypothesis. However, as pointed out by Sinclair & Tremblay (1984), the match/mismatch hypothesis may owe some of its popularity to the attractiveness of its formulation rather than to its empirical support. Sinclair & Tremblay studied the distribution of the Atlantic herring and found no evidence in support of the coupling of the timing of spawning and the spring bloom onset central in Hjort's hypothesis. Instead, Sinclair & Tremblay proposed that the variability in the timing of spawning of herring is an adaptation to specific oceanographic retention characteristics. Herring retained in a region where a spring bloom allows a fast growth can be spawned in spring and still hatch before the next winter. Herring retained in a region with a depressed primary production would grow more slowly as a result of a lower food supply and would need to be spawned the previous fall to metamorphose in the same time envelope as those spawned in spring.

The concept of larval retention was put forward by Iles & Sinclair (1982). These authors proposed that hydrodynamics (tidal mixing) and fish larvae behaviour could interact so as to maintain an aggregated population of Atlantic herring larvae for many months. The hitherto unexplained variability of size *between* stocks could then be related to the extent of the respective retention areas: the larger the retention area, the larger the stock. Although the theory falls short of detailing the retentive mechanisms, it proposes an original stock concept. As for the *within* stock interannual variability in size, Iles & Sinclair submitted that it need not be associated in whole or in part with fluctuations in mean food supply since observed

interannual stock size fluctuations are far higher than those in mean food supply. Rather, interannual size fluctuations within a stock could result from variations in retentive characteristics. (It should be mentioned that this argumentation assumes that *mean* food supply is an appropriate factor to be related to fish abundance variability, which is surely arguable). If variations in retentive characteristics are to cause variations in survival of fish larvae, the next logical step is to ask what causes the "non-retained" larvae to be lost from recruitment?

A possible cause of death for non-retained fishes, if food supply is not regarded, could be sudden exposure to predators in "ecologically dangerous" sites (Frank & Leggett 1985). Frank & Leggett have reviewed evidence challenging the view that reciprocal oscillations of predators and prey should indicate trophic interactions. Rather, reciprocal oscillations observed at one point in the ocean could be the result of the passing of different water masses in which predators and prey are segregated for adaptive reasons. This would suppose that the concerned organisms could maintain their positions, actively or passively, in various water masses. For the prey, the adaptive value of being retained in an "ecologically safe site" where predators are absent seems obvious; it is not so clear that there would be any adaptive reason for the predators to stay away from their potential prey. Any relaxation of the retention of the prey in their "safe sites" could make them exposed to predators in "dangerous sites". This interruption of segregation could produce sudden predator-prey interaction more of the all-or-none type rather than of the continuous Ivlev type. Another possible, albeit very speculative, reason for the non-retained fishes to be lost from recruitment is that young fishes could need a minimum time of retention in order to be able to come back as spawners to the spawning site (parental stream hypothesis). The application of the concept

of the parental stream hypothesis to open ocean fishes could be an extension of the already noted analogy between the life-cycles of the salmon and the herring (Cushing 1973).

Another well developed hypothesis as to how environmental factors may affect fish survival is Lasker's (1975) stability hypothesis. Lasker showed that storms could dissipate food aggregates in the upper layers of the waters where anchovy (*Engraulis mordax*) feed. This dissipation would result in a reduced ration for the fishes; the following depressed growth and weakened condition of the fishes could increase physiological and predation mortality. Peterman & Bradford (1987) provided some evidence that indeed wind-driven turbulent mixing affects variability in survival of larval anchovy. These authors found the daily mortality rate of larval anchovy to be significantly correlated to an index of wind speed: the higher the wind index, the lower the survival. However, Peterman & Bradford's findings do not necessarily indicate that variability in larval mortality due to wind-driven turbulent mixing sets the level of recruitment: variability in post-larval stages unaccounted for by their model could obliterate any relationship between larval survival and final recruitment. Nonetheless, Peterman & Bradford's results support Lasker's proposed mechanism of variability in larval mortality of the anchovy. Vertical stability of the water column is the distal environmental factor regulating fish mortality via its effect on the food supply.

Common to those reviewed studies that yield new insights in fish recruitment mechanisms are the following two points:

- the spatial and temporal distribution of juvenile fishes is described
- the realized trophodynamics of the fishes is assumed to be determined by their degree of overlap with their food supply and/or their predators.

It has been suggested by Legendre & Demers (1984) that food supply be considered as the proxi through which the distal effects of environmental factors may be conducted up the food web to the fishes. Since predation could also be modulated by environmental factors (*e.g.* "safe sites" and "dangerous sites"), Legendre & Demers' proposition could be expanded as follows: trophodynamics is the proxi through which distal environmental variability may be conducted up or *down* the food web to the fishes.

The co-occurence of fishes, their food supply and their predators appears to be determined by various environmental factors. Variability of those factors can affect the realized overlap (i.e. phasing) of the components of the food web; such shifts in phase can greatly affect the time course of the system. Factors causing phase shifts between trophically related components of an ecosystem have been termed "phasing functions" (Parsons & Kessler 1986). In brief, there is a distinct research avenue within the environmental thesis that seeks to identify phasing functions by detailing the temporal and spatial distributions of organisms mutually involved in trophic relationships; for these reasons, this avenue could be termed "trophic phasing analysis".

2.3.2 Trophic Phasing Analysis

In order to represent formally the concept of trophic phasing analysis, the basic equation to describe the distribution of a non-conservative variable in the ocean may be used (see Wroblewski 1983). In a Lagrangian reference frame, the variation of a biological variable (P) can be written as :

$$\frac{\partial P}{\partial t} + u\frac{\partial P}{\partial x} + v\frac{\partial P}{\partial y} + w\frac{\partial P}{\partial z} = K_H\left[\frac{\partial^2 P}{\partial x^2} + \frac{\partial^2 P}{\partial y^2}\right] + K_V\frac{\partial^2 P}{\partial z^2} + B \qquad (2.6)$$

where u, v, and w are velocity components; K_H and K_V are vertical (V) and horizontal (H) diffusion coefficients; and B is the sum of sources and sinks.

From time t to time $t + i$ within one fish generation, there can be many sinks. In the reviewed studies, predation and starvation have come out to be the most often mentioned probable causes of mortality of fishes. However, there are no sources properly speaking. Only food-supply can be considered source-like in that fluctuations in food supply will cause fluctuations in mortality.

Equation 2.6 can be written for the fishes, their food items, and their predators. The time course of the phasing of the fishes and either or both of their food supply and their predators can then be investigated along combinations of spatial dimensions. Lasker's stability hypothesis is a 1-dimensional model (z;t), while the Match-Mismatch hypothesis is a 2-dimensional model (x,y;t). This allows clear identification of the functional space in which trophic interactions occur separate from the interactions themselves. In other words, the geometry of a trophic system is recognized as a distinct component that could separate species, or assemblages of species.

As it is, equation 2.6 provides a grid to assess systematically the adequacy of the knowledge on the life history of the fish species under study. This grid favours a structured approach towards the identification of phasing functions that may largely contribute to the determination of fish abundance by modulating the overlap of the fishes, their food supply (sink) and their predators (sink). In practice, this grid requires a thorough documentation on the trophodynamics of the fishes as well as a detailed description of the temporal and spatial distributions of the various components involved in it. Trophic phasing analysis may then be defined as the search for environmental factors that regulate the spatio-temporal overlap

of the components of a trophic structure.

2.4 Chapter Summary

Two theses prevail for addressing the issue of fish population variability. The parental-filial thesis postulates that regulative mechanisms can leap generations; this is an attractive thesis when the securing of a constant benefit from an exploited fish population is sought. The environment thesis postulates that real fish population abundance is determined by environmental factor(s), irrespective of the parental stock size. Environmental variability is assumed to be conducted to fish populations through the vector of food uptake in early life stages.

Chapter 3

Early Sea Life of Chum Salmon

3.1 Introduction

In the previous chapter, the need to describe the spatial and temporal distributions of fishes relative to their food supply and predators was emphasized. This description could eventually allow the identification of where and when in the life cycle the effects of environmental fluctuations may be transmitted to the fish through the vector of food uptake. To deal with the complexity of the life cycle of a fish, it is useful to identify distinct stages within this cycle, and investigate those stages the most likely to comprise determinants of year-class strength. The life history of the Pacific salmon can be realistically and conveniently divided into a series of stages, each characterized by risks of particular kinds of mortality (Larkin 1977). For the chum salmon *Oncorhynchus keta*, a more thorough understanding of the biological and physical processes that affect individual growth and production has been recognized as a central goal of fisheries research (Neave 1953; Wickett 1958; Volk *et al.* 1984). In this chapter, the life cycle of the chum salmon is briefly reviewed. The early near-shore life of the fish is identified as a distinct ecological stage and its diet at that stage is described.

3.2 Near-Shore Life of Juvenile Chum Salmon

The chum salmon is one of the five species of Pacific salmon (*Oncorhynchus* spp.) that occur naturally in the North American side of the Pacific ocean (as reviewed by Larkin 1977). All five species are anadromous and die after spawning. The spawning period is a convenient point to start and end a description of the life cycle of the Pacific salmon. In the fall of the year, females deposit their eggs in redds in rivers; the eggs are simultaneously fertilized by the male. After two to three months of incubation, eggs hatch and alevins remain in the gravel for a few more weeks, while gradually migrating to the overlaying waters. In spring, rising temperature or other environmental factors, in conjunction with their increased ability to swim, will cause the juvenile fishes to leave the gravel beds for a free-swimming life. At this time, chum salmon immediately start swimming and drifting to sea (Hoar 1951). In small rivers, the sea can be reached within days; in larger rivers, the sea may be reached only after weeks of fresh water life. Many chum salmon will remain in coastal waters until mid- or late summer before dispersing to offshore regions. By the end of their second season at sea, chum salmon originating from British Columbia are found over a wide area of the Gulf of Alaska. After two to three summers at sea, most chum salmon return to their parental streams to spawn. Chum salmon will then pass through estuaries twice during their life: once as juvenile outmigrants, and once as redd-bound mature adults. As juvenile outmigrants, chum salmon may reside in estuarine near-shore areas for variable periods. In estuarine near-shore areas of many rivers, juvenile chum salmon exhibit clear stenophagic feeding patterns (Kaczynski *et al.* 1973; Feller & Kaczynski 1975; Healey 1979; Sibert 1979). Despite a broad variety of available food, chum salmon rely heavily on harpacticoid copepods as a food source. In the Fraser River

estuary, intertidal habitats, vegetated and non-vegetated, are considered as having a substantial capacity for fish rearing; juvenile chum salmon are also known to occur seasonally in close proximity to these intertidal habitats (Gordon & Levings 1984; see also the review by Levings *et al.* 1983).

In order to discuss the potential effects of the feeding patterns of the chum salmon on its growth and production in the Fraser River estuary, its diet in this particular area had to be described and compared with the results of other similar studies. The particular site selected for the study was chosen because juvenile salmon have been reported in its immediate vicinity (Gordon & Levings 1984) and it was vegetated with eelgrass (*Zostera marina* L.). Although no detailed description of the meiofauna on the study site was available, eelgrass beds are known to harbour populations of harpacticoid copepods (as reviewed by Hicks & Coull 1983); Levings *et al.* (1983) further report the presence of harpacticoid copepods on a vegetated section of Roberts Bank, of which the selected site is part.

3.3 Study Site and Methods

The sampling station for chum salmon was located near the Westshore Terminal Causeway on Roberts Bank, British Columbia (Fig. 3.1). A detailed biosedimentological description of the area is provided by Swinbanks & Luternauer (1987). Swinbanks & Luternauer's description is based on aerial photographs taken in 1977, prior to expansion of the causeway. Harrison (1987) documents changes in the eelgrass cover on the same section of Roberts Bank from 1969 to 1984. The eelgrass cover expanded from *ca* 250 ha in 1969, the date of the construction of the causeway, to *ca* 430 ha in 1984 (from sources cited in Harrison 1987). In this region of the Strait of Georgia, the character of the tide is mixed, mainly semi-diurnal

(as reviewed by LeBlond 1983). The range of the tide at the port of reference (Point Atkinson) is 3.3 m for mean tide and 4.9 m for large tide. The eelgrass cover at sampling station H was up to 100 shoots/m^2 in mid-spring (D. Webb, U.B.C. Oceanography, unpublished data), which is similar to the values reported by Harrison (1987). Chum salmon were caught with a beach seine (length: 15 m; height: 1.85 m; bunt: 3 m) with 1 cm mesh (stretched) in the wings and 3 mm mesh (stretched) in the bunt. At low tide (*ca* 5 hours after the onset of the ebb at the port of reference, Point Atkinson), the beach seine was dragged from the beach with a motorized boat to *ca.* 10 m from the shoreline; the seine was then stretched parallel to the beach and retrieved with lines from the shore. This operation was repeated 3 times at each sampling. The number of chum salmon in each of the hauls was recorded; a random sample of fishes was kept for gut-content analysis after fixation in 4% formaldehyde-sea water solution. Chum salmon were identified according to McConnel & Snyder (1972) and Phillips (1977). On May 13, 1986, 30 chum salmon were measured immediately after capture and prior to fixation in formaldehyde; the same fishes were re-measured subsequently to assess the effect of fixation on length measurements. Fish lengths reported are in all cases fork lengths (FL) (from the tip of the snout to the inside of the tail notch). The sum of the chum salmon in the 3 hauls was reported as the catch per unit effort (C.P.U.E.). Beach seining was repeated fortnightly during the sampling season. The sampling season extended from March 22 to July 5 in 1985, and from March 5 to July 10 in 1986. In the laboratory, fish were measured to the nearest mm (FL); fish length measurements were made at least a few weeks after fixation in formaldehyde. The mid-guts of the fishes were extracted and their contents identified and counted. At each sampling date, the gut contents of at least 10 fishes were determined. Zoo-

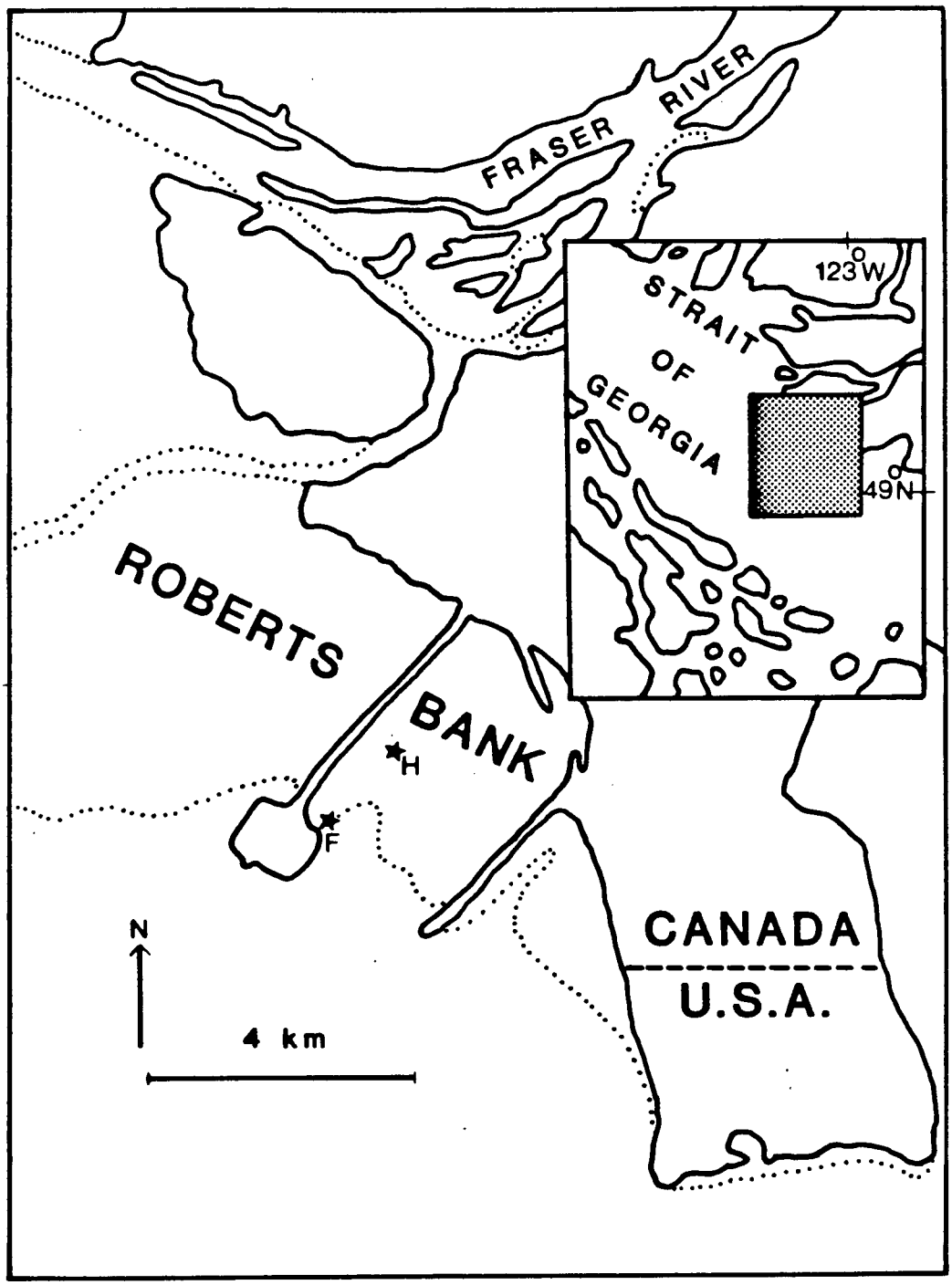

Figure 3.1: Map of study area. Chum salmon were fished at station F; harpacticoid copepods were collected at station H (the dotted line indicates the limit of the tidal flat).

plankton samples against which to compare the fish gut contents were collected amidst an extensive eelgrass bed on Roberts Bank, close to the salmon fishing station (Fig. 3.1). Zooplankton samples were collected bi-weekly from March 1 to July 5 in 1985, and from February 7 to July 10 in 1986. Samples were collected with a stratified sled-sampler (Fig. 3.2) operated by a SCUBA diver. The sled-sampler consisted of 5 butyrate cylinders (internal diameter: 83 mm; length: 150 mm) serially mounted on a stake fixed on a skid-pad. The butts of the cylinders were closed with 64 μm Nitex© gauze, thus forming filtering baskets. The centered height of each of the 5 cylindrical baskets above the sediment was 56, 156, 256, 356, and 456 mm respectively. At low tide, transect line(s) (1 in 1985; 3 in 1986) were spread on the sediment surface at station H. In 1985, the single transect was always oriented towards the east; in 1986, the 3 transects had a common origin and were respectively oriented towards the south, east, and north, which was also the order of their execution. For both years, sampling of the zooplankton with the sled-sampler was initiated *ca.* 1 hour after slack high tide (2.5 to 3 m of water above the station). The sled-sampler was opened at the surface prior to descending on the transect(s). This allowed wetting of the 64 μm mesh of the filtering baskets that otherwise seemed to resist flow by surface tension. The sled-sampler was then capped and the diver descended to the transect(s). After properly orienting the sled-sampler, the diver uncapped the sled-sampler and pushed it along a transect line always keeping the skid-pad in contact with the sediment; this assured a constant height above sediment for the filtering baskets. At the end of the transect, the sled-sampler was capped and brought back to the tending boat. Baskets were removed from the sled by the tender, rinsed, and their contents stored in 4% filtered (40 μm) sea water-formaldehyde. The baskets were re-installed on the sled-sampler

Figure 3.2: Photograph of diver-operated sled-sampler (scale bar=15 cm) (see text for description).

and the operation repeated for the subsequent transects. When 3 transects were done (1986), the sampling operation was completed in less than 1 hour, and accordingly less when only 1 transect was done (1985). In the laboratory, zooplankton samples were treated according to the procedures recommended by Uhlig *et al.* (1973) for meiofauna. Certain taxa of harpacticoid copepods were identified to the species according to the procedures recommended by Coull (1977). Other taxa were identified to major groups. In all cases, the total number of animals in each basket of each transect was counted. Principal keys consulted for the identification of harpacticoid copepods were those of Lang (1948 ; 1965) and of Wells (1976).

The gut contents of the salmon were compared to the zooplankton samples using Ivlev's (1961) electivity index. This electivity index ($E.I.$) is defined as:

$$E.I. = \frac{r_i - p_i}{r_i + p_i} ,$$

where r_i is the numerical proportion of a prey in the ration, and p_i is the numerical proportion of the same animal in the reference food sample.

This electivity index varies between -1 and +1; a negative value indicates avoidance, while a positive value indicates preference. The unidentified copepods in the sled samples were not included in the computation of the electivity index; their number in the water column was such that the electivity index for the prey zooplankters would have been highly distorted. Those unidentified copepods (reported as UCOP in Appendix B) were mostly early copepodites, and were very rarely, if ever, observed in gut contents. The unidentified copepods in the gut contents were included, since they represented adult individuals of various species (reported as UNCO in Appendix A).

3.4 Results and Discussion

During both sampling years, a pulse of juvenile chum salmon was observed on Roberts Bank (Fig. 3.3). In 1985, chum salmon were first observed on March 29 (day 88); in 1986, chum salmon were first observed on April 1 (day 91). Subsequent temporal patterns in the abundance of salmon are similar for both years. First, a low peak was observed (on April 10 (day 100) in 1985 and on April 15 (day 105) in 1986). There followed a second and more important peak which rapidly declined until no more juvenile salmon were observed. The significance of the peaks can not be assessed for a lack of variance estimation. Because of limited logistic support, only a very limited number of beach seine hauls were done. However, the similarity in the temporal patterns of abundance of fish on the flat between years suggests that the two peaks may reasonably be assumed to represent meaningful features of abundance. The first peak of salmon may represent a pulse of fish from stocks from nearer spawning areas, or earlier outmigrants, or hatchery reared fishes. As to the last possibility, no fish with clipped adipose fin, which identifies some of the hatchery reared fishes, was ever observed despite close observation. The second and highest peak of abundance occurred on May 27 (day 147) in 1986, and on June 6 (day 157) in 1985. The proportion of the Fraser chum stock represented by those peaks is unknown. It can only be assumed, as in Valiela and Kistritz (1980) who discussed the abundance of chum salmon in Fraser river marsh ecosystems, that at least a proportion of the whole stock utilizes tidal flats for a period of time during their outmigration. The size of the juvenile chum salmon captured in 1985 ranged from 47.5 to 62.1 mm (FL), and from 31.3 to 54.2 mm (FL) in 1986 (Table 3.1). Why the upper limit of the size range was lower in 1986 than in 1985 is unclear. In 1986, several chum salmon were observed with yolk-sac

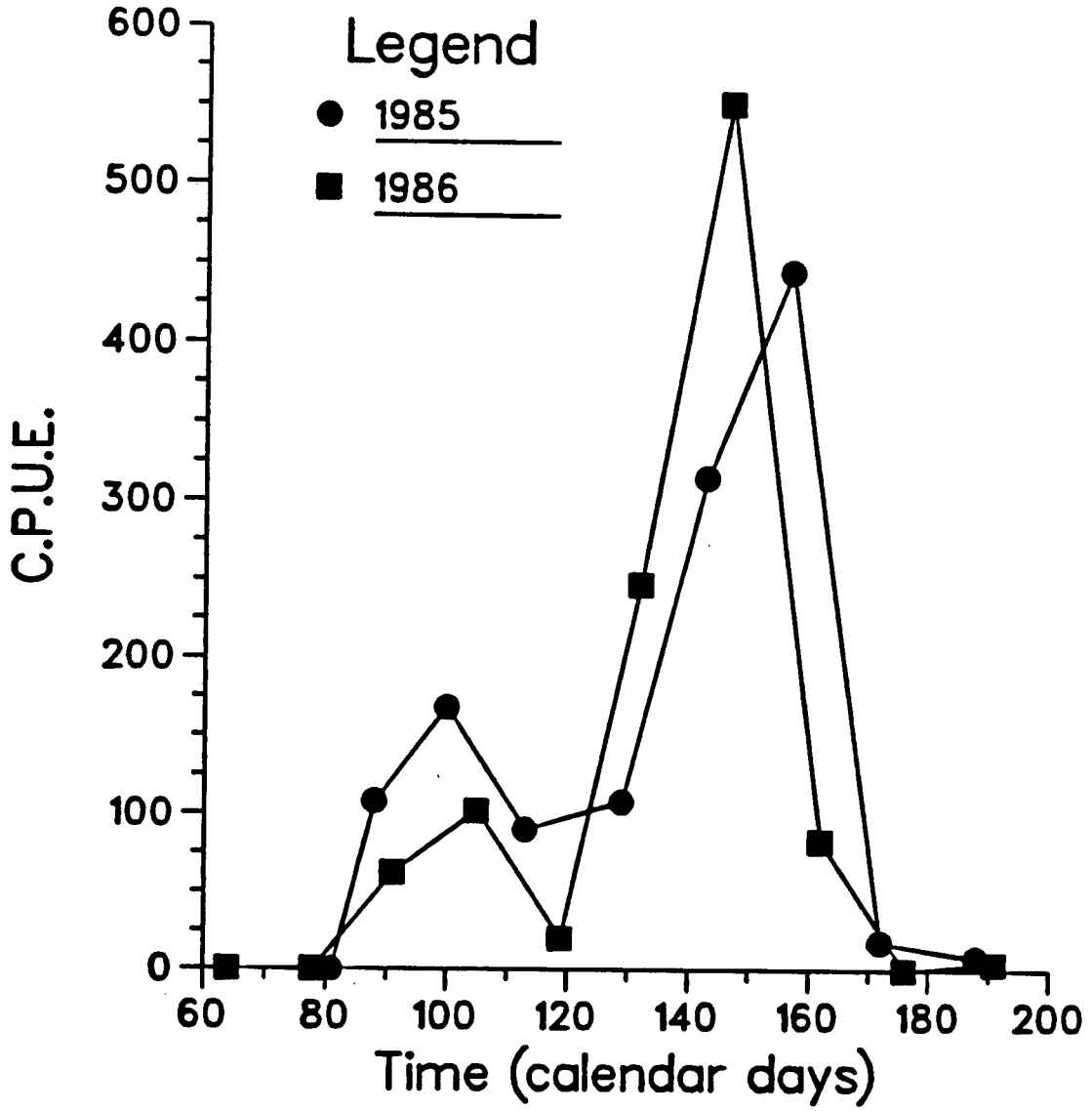

Figure 3.3: Catches of juvenile chum salmon on Roberts Bank in 1985 and 1986 (C.P.U.E.=catch per unit effort; 1 unit effort=3 beach seine hauls).

CHUM SALMON FORK LENGTH			
1985		1986	
Date (day)	Length (mm) mean+/- 1 S.E.	Date (day)	Length (mm) mean +/- 1 S.E.
March 29 (88)	47.5 +/- 1.0	March 19 (78)	31.3 +/- 1.8
April 10 (100)	53.6 +/- 0.9	April 1 (91)	44.3 +/- 1.2
April 23 (113)	49.2 +/- 2.5	April 15 (105)	48.8 +/- 2.5
May 9 (129)	53.8 +/- 2.1	April 29 (119)	37.0 +/- 0.5
May 23 (143)	55.8 +/- 3.2	May 13 (132)	44.7 +/- 1.1
June 7 (157)	55.0 +/- 1.1	May 27 (147)	47.6 +/- 1.3
June 21 (172)	62.1 +/- 2.8	June 11 (162)	54.2 +/- 1.4
July 5 (188)	53.0 +/- 1.9		

Table 3.1: Length (fork) of juvenile chum salmon on Roberts Bank in 1985 and 1986 (length measured on fishes preserved in formaldehyde).

FIXATION SHRINKAGE					
Fish #	Length (mm)		Fish #	Length (mm)	
	May 13	May 20		May 13	May 20
1	46	43	16	43	40
2	45	42	17	40	38
3	40	38	18	42	40
4	39	35	19	42	40
5	40	38	20	55	52
6	37	34	21	43	40
7	39	37	22	49	46
8	34	31	23	47	44
9	42	38	24	33	33
10	38	36	25	35	33
11	35	33	26	40	37
12	45	44	27	40	38
13	40	36	28	40	40
14	36	34	29	39	38
15	44	41	30	35	34

Table 3.2: Comparison of chum salmon fork length before and after fixation (1 week in 10% sea water-formaldehyde solution).

scar still present, which were not present in 1985. The fixation in formaldehyde had an effect on the measurements of fish fork length. The mean size of recently caught fresh fishes was 40.8 +/- 0.9 (S.E.) mm; after a week of fixation, the mean length of the same group of fishes had dropped to 38.4 +/- 0.8 (S.E.) mm, which is significant (one-tailed *t*-test; $p<0.05$) (Table 3.2). Globally, fish shrank by 5.9 % because of the fixative within 1 week. Subsequent measurements indicated no further appreciable shrinking. Chum salmon size corrected for fixative shrinking ranged from 50.5 to 66.0 mm in 1985, and from 33.2 to 57.6 mm in 1986.

Gut contents analysis showed that for both sampling years, juvenile chum salmon relied heavily on harpacticoid copepods as a food source (Fig. 3.4). In

1985, the digestive tracts of 92 fishes (10–15 fishes per fishing effort) were analyzed; in 1986, the digestive tracts of 66 fishes (at least 10 per fishing effort) were analyzed; gut contents analysis results are summarized in Appendix A. In 1985 and 1986, 77.2% and 71.8% (numerical abundance) of the prey of the juvenile salmon were either *Harpacticus uniremis* Kroyer 1842, *Zaus aurelii* Poppe 1884, or *Tisbe* spp. (this taxa assemblage is subsequently referred to as the H+Z+T+ assemblage). Other unidentified adult harpacticoids (UNCO in Fig. 3.4) accounted for 8.0% and 2.5% of the fish's diet in 1985 and 1986 respectively. For both years, calanoids accounted for *ca* 8% of the food items. Other food items (amphipods, cypris, fish larvae, isopods, ostracods, cumaceans) each accounted for less than 5% of the diet, except in 1986 when cumaceans accounted for 11.7% of the diet. Other food items were observed (euphausids, insect larvae, isopods) that each accounted for less than 0.1% of the diet in both or single years (not visible on Fig. 3.4).

Within the H+Z+T assemblage, *Harpacticus uniremis* was the dominant taxon (64.2% in 1985 and 46.3% in 1986); respectively for 1985 and 1986, *Zaus aurelii* accounted for 26.7% and 35.8% of the assemblage while *Tisbe* spp. accounted for 9.1% and 17.9% of the assemblage (Fig. 3.5).

In 1985, the zooplankton taxonomic composition of the combined 5 sampling levels of the sled-sampler were analyzed; in 1986, the sum (3 transects) of the combined 5 sampling levels of the sampler were analyzed; the results of these taxonomic descriptions are detailed in Appendix B. The composition of the samples collected with the sled-samplers differed from that observed in juvenile salmon gut contents for both years (Fig. 3.6). The H+Z+T assemblage accounted for 58.7% and 76.5% of the total numerical abundance of the animals in 1985 and 1986 respectively; the proportion of calanoids was *ca* 4 times higher in 1985 compared

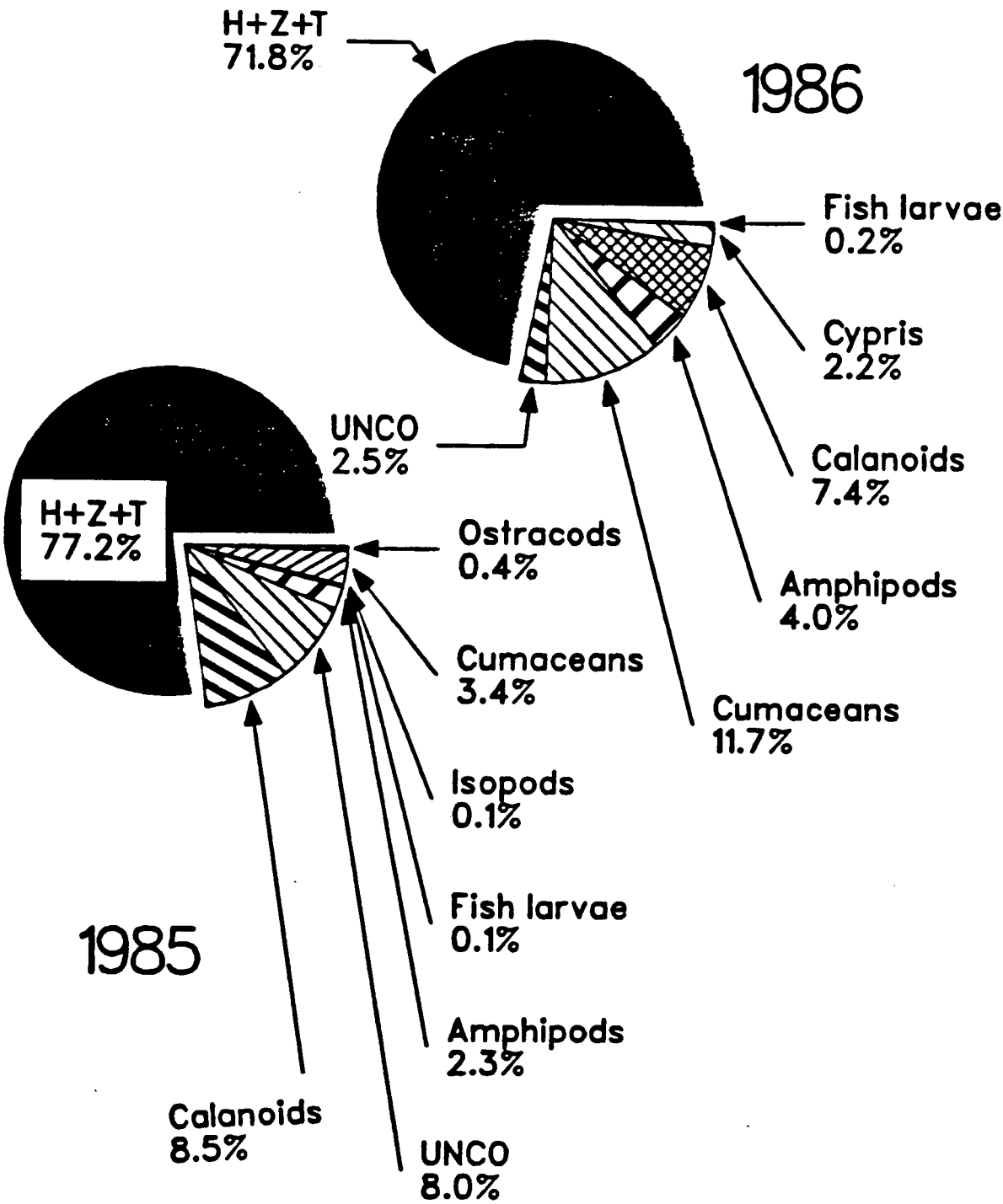

Figure 3.4: Chum salmon gut contents in 1985 and 1986.

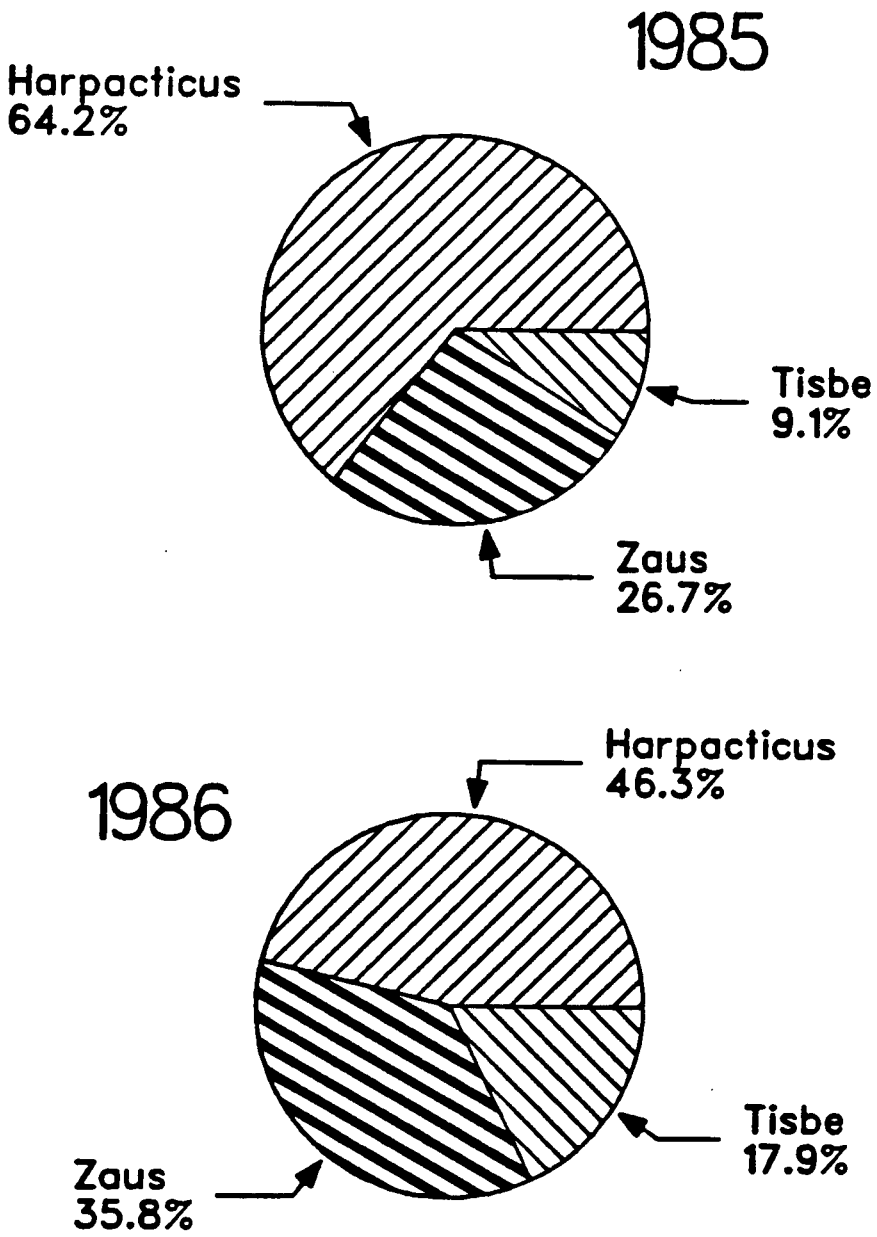

Figure 3.5: Relative proportions of *Harpacticus uniremis*, *Zaus aurelii* and *Tisbe* spp. in H+Z+T assemblage in 1985 and 1986 (gut contents).

to 1986 (32.7% *vs* 7.8%). In 1986, adult harpacticoids (UNC0) other than those of the H+Z+T+ assemblage were observed in appreciable amount (3.2%); *Mesochra* sp. accounted for 9.6% of the total amount in the sled-samples. Within the H+Z+T assemblage in the sled-samples, *Tisbe* spp. was by far the dominant taxon (98.9% in 1985 and 80.7 in 1986); for 1985 and 1986 respectively, the proportion of *Zaus aurelii* was 0.6% and 14.9%, and that of *Harpacticus uniremis*, 0.6% and 4.5%. (Fig. 3.7).

Between years, the proportion of the H+Z+T assemblage in the water column appeared to fluctuate principally because of changes in the abundance of calanoids. The dominance of the H+Z+T assemblage in the gut contents was similar for both years. Globally, then, the H+Z+T assemblage was the dominant taxonomic feature in the sled-samples as well as in the gut contents. However, there is a striking difference in the relative proportion of *Tisbe* spp., *Zaus aurelii*, and *Harpacticus uniremis* in the H+Z+T assemblage when sled samples and gut contents are compared (Figs. 3.7 & 3.8). The dominant species (*H. uniremis*) of the assemblage in the gut contents was the least abundant in the sled-samples for both years (64.2% & 46.3% *vs* 0.6% & 4.5%), and *vice versa.* Similarly for *Z. aurelii*, the proportion in the gut contents (26.7% & 35.8%) was higher than that in the water column (0.6% & 14.9%). This is interpreted as an indication of the high preference of juvenile chum salmon for *H. uniremis* and *Z. aurelii.*

This evidence for highly selective feeding of juvenile chum salmon must however be considered with caution. Some of the difference in specific proportion in the H+Z+T assemblage between gut contents and sled-samples could be caused by the fishes feeding on areas with faunal composition different from that on the sled sampling station. Horizontal heterogeneity (zonation or patchiness) is a well

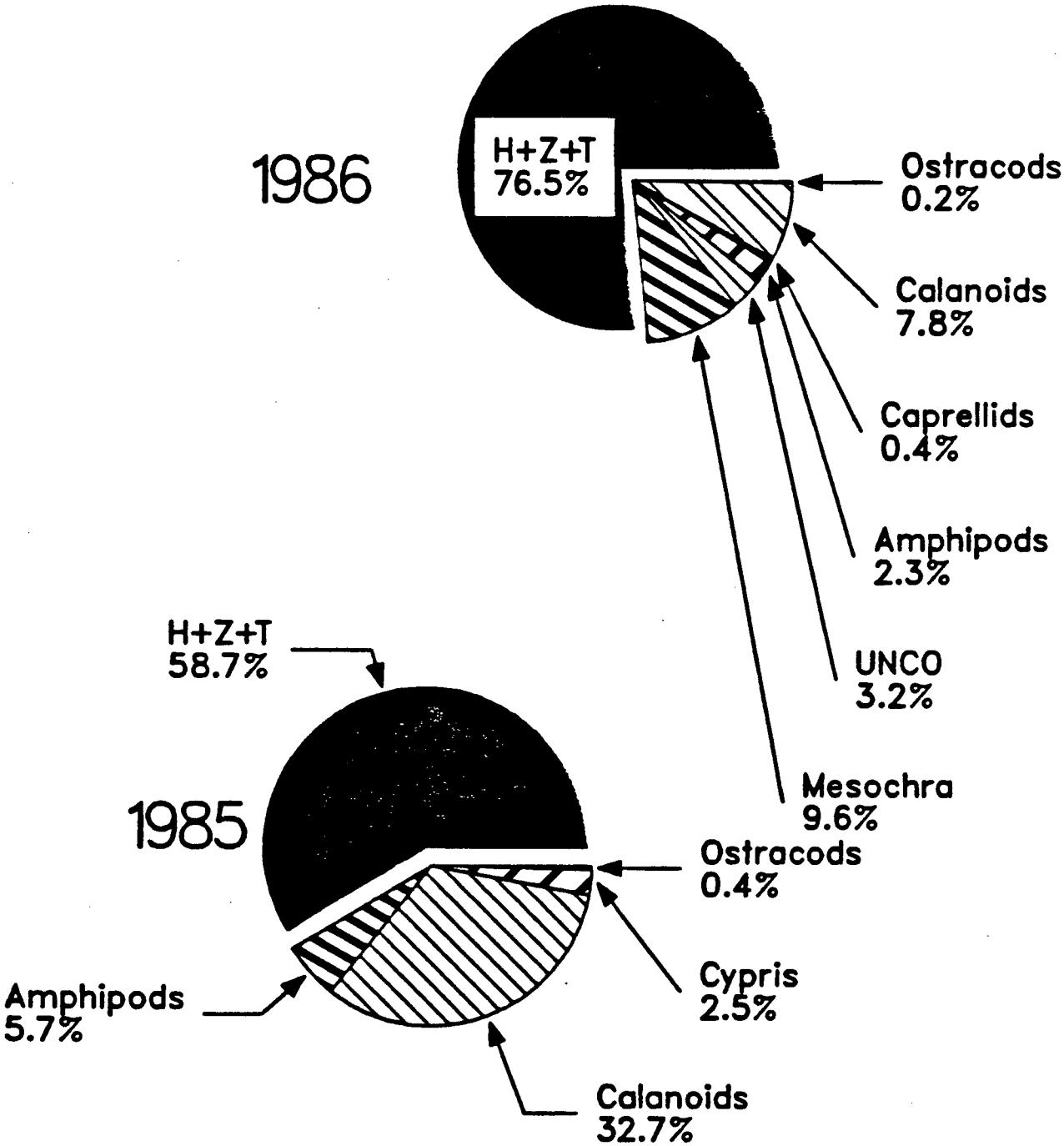

Figure 3.6: Zooplankton composition in the water column in 1985 and 1986 (unidentified copepodites are not included).

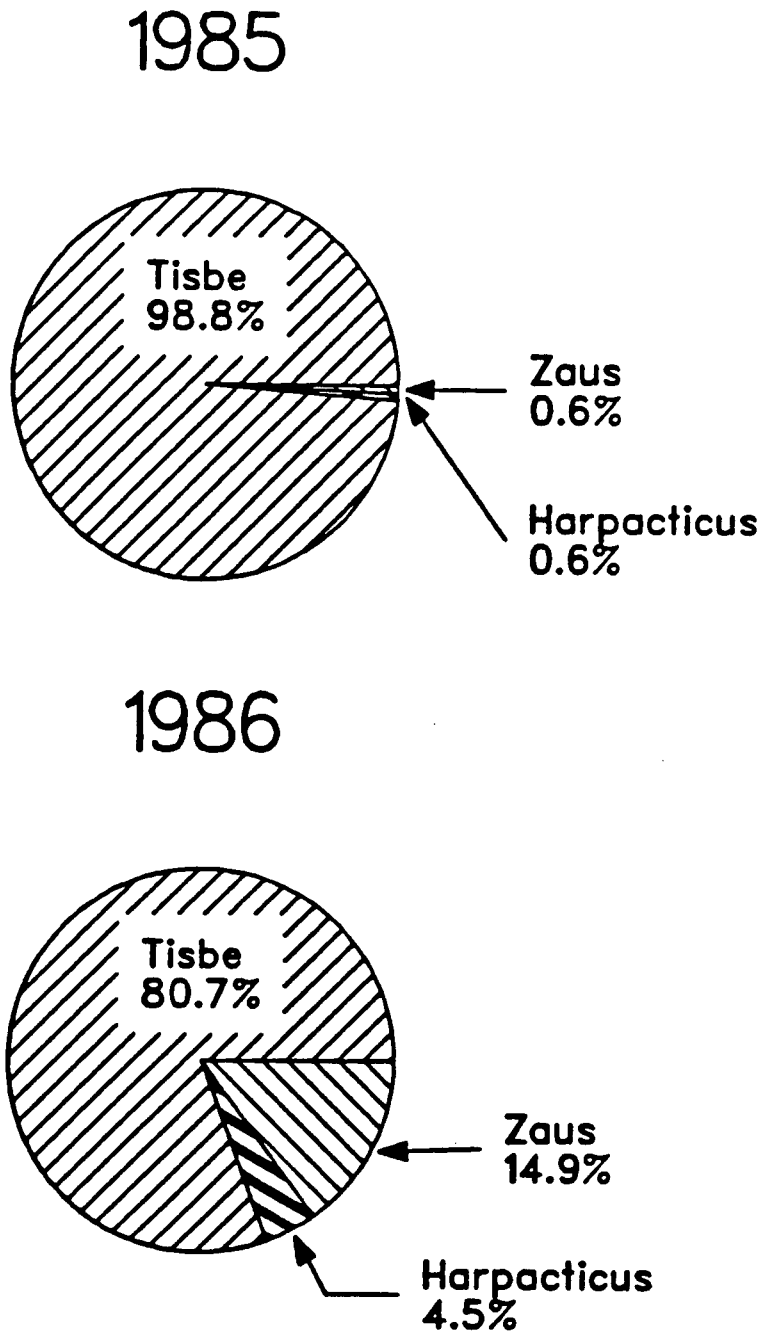

Figure 3.7: Relative proportion of *Tisbe* spp., *Zaus aurelii*, and *Harpacticus uniremis* in the H+Z+T assemblage in 1985 and 1986 (water column).

recognized characteristic of harpacticoid copepods on tidal flats (as reviewed by Hicks & Coull 1983). Also, it could be that harpacticoid species preferentially preyed upon by juvenile chum salmon could be more easily caught by the fish than by the sled-sampler. As it is, *H. uniremis* and *Z. aurelii* are members of the Harpacticidae family, which is characterized by the presence of strongly prehensile legs for clinging on substrate, especially on plant surfaces. Contrary to *Tisbe* spp., *H. uniremis* and *Z. aurelii* were often observed on the surface of eelgrass blades.

With those cautions in mind, the electivity index was computed for each taxon of the H+Z+T assemblage (Fig. 3.8). In 1985, the electivity index for *H. uniremis* and *Z. aurelii* was always positive, and constantly very near 1. This suggests a very strong preference of the fish for those species. At the opposite, the electivity index for *Tisbe* spp. in 1985 was always negative, and strongly so most of the time. In 1986, the electivity indices were somewhat different. The electivity index of *H. uniremis* was still always positive, although not as strongly as in the previous year. The electivity index of *Tisbe* spp. was also negative throughout, albeit less strongly than in 1985. The sharpest difference in electivity index between 1985 and 1986 was observed with *Z. aurelii*: in 1986, the electivity index was negative (very close to -1) in early season and then shifted to positive (as throughout 1985) in later season. Globally, the electivity index for the 3 taxa over the 2 sampling periods indicated

- a strong preference for *H. uniremis*;
- a strong avoidance of *Tisbe* spp.;
- a least a period of strong preference for *Z. aurelii* in both years with a period of avoidance in 1986.

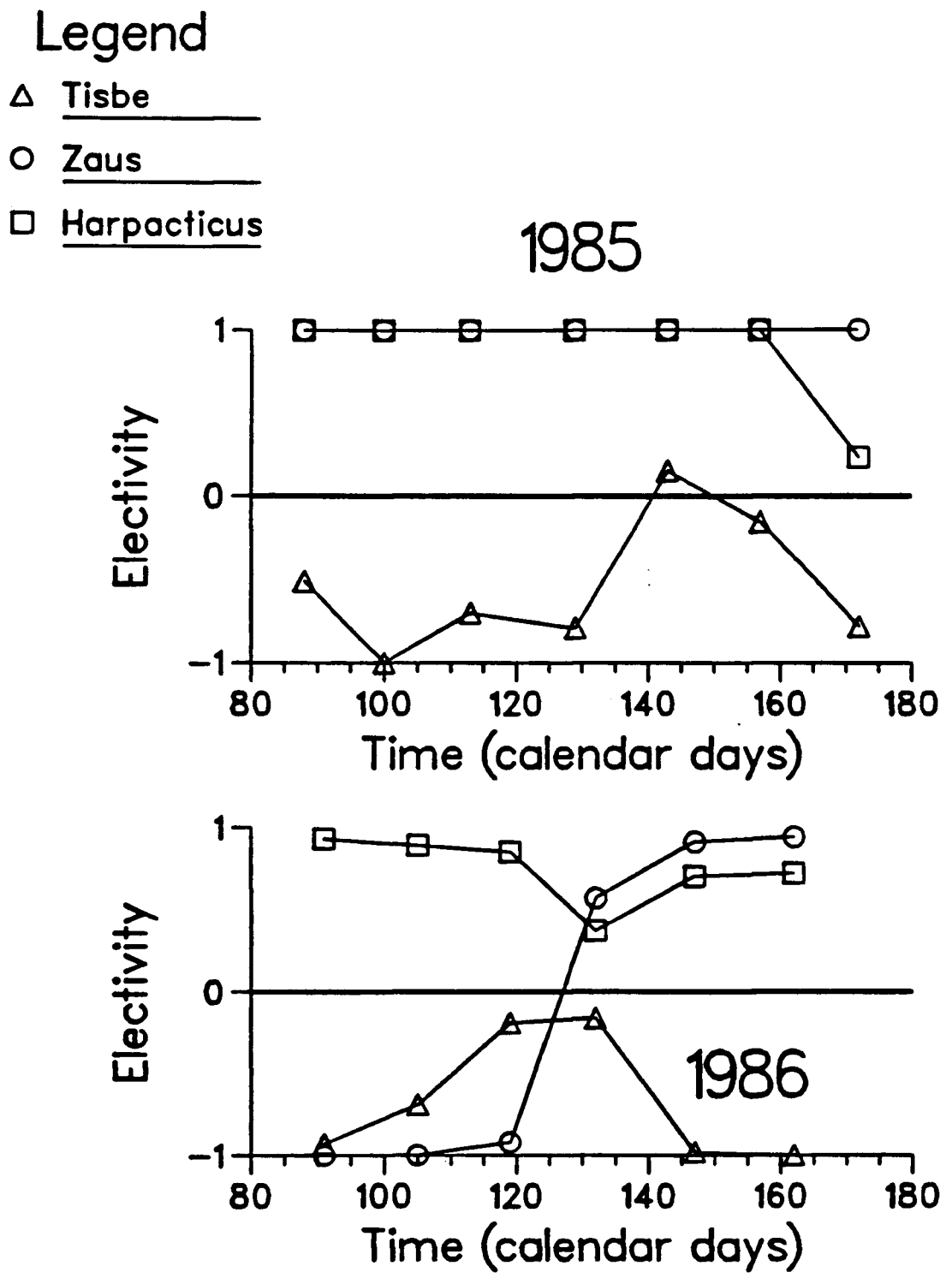

Figure 3.8: Electivity index for *Tisbe* spp., *Harpacticus uniremis*, and *Zaus aurelii* in 1985 and 1986.

Harpacticoid copepods can the be considered as the main food items as well as the most important food items of juvenile chum salmon (*sensu* Berg 1979). The shift from avoidance to preference for *Z. aurelii* in 1986 and its absence in 1985 could be interpreted as follows. In 1985, the abundance of *H. uniremis* was always very low (data in Appendix B) and the electivity index for *Z. aurelii* was always high. In 1986, the period for the negative electivity index of *Z. aurelii* is coincident with an abundance of *H. uniremis* much higher than the previous year. It might be that when *H. uniremis* is available in quantity, anything else is disregarded by the juvenile chum salmon. The reasons for such a possibly high preference for *H. uniremis* over any other food item might be its dark coloration (green to dark green), its large size (up to 1.5 mm), or any other yet to be identified behavioral idiosyncrasies (e.g. Marcotte 1984).

3.5 Chapter Summary

Juvenile chum salmon were most abundant in the vicinity of Roberts Bank in late May or early June. Juvenile chum salmon captured ranged in size from 33 to 60 mm (means of a sample of fish from each fishing effort). The chief food items of the juvenile chum salmon were harpacticoids, mostly *H. uniremis*, *Z. aurelii*, and to a lesser extent, *Tisbe* spp.; the electivity index for the first species was always positive and high; that for the second species varied from low negative to high positive perhaps as a result of fluctuations in absolute abundance of *H. uniremis*; the electivity index for *Tisbe* spp. was always negative, and generally strongly so. Horizontal heterogeneity and/or particular harpacticoid behavior need further investigation to state more clearly why such patterns of electivity were observed.

Chapter 4

Spatio-Temporal Distribution of Natant Harpacticoid Copepods

4.1 Introduction

In chapter 2, the description of the spatio-temporal distribution of each component of a trophic structure was recognized as a prerequisite for the identification of environment-coupled mechanisms that may regulate fish population abundance. In chapter 3, the spatio-temporal distribution of juvenile chum salmon was discussed and the preferred food items of the fish were identified as being harpacticoid copepods. In this chapter, the spatial (vertical) and temporal (seasonal) distributions of harpacticoid copepods on which juvenile chum salmon heavily rely as a food source, are described. The following summary of the ecology of harpacticoid copepods is extracted from the comprehensive review provided by Hicks & Coull (1983).

Harpacticoida is one of seven Orders of the subclass Copepoda; it contains small copepods ranging in size from 200 to 2500 μm. Harpacticoid copepods occur in almost all aquatic habitats and are a major component of the meiobenthos, *i.e.* those benthic organisms passing through a 2000 μm mesh, but retained on a mesh of 40-100 μm. Harpacticoida is primarily a benthic free-living Order. Those

harpacticoids closely associated with the sea bed can be separated into three groups:

- interstitial
- burrowing
- epibenthic.

Interstitial forms are usually vermiform, while burrowers are either broadened anteriorly to push sediment particles or equipped with flattened appendages to dig in muddier sediment. Epibenthic forms often have the ability to swim, and have various body shapes. Other species of harpacticoid copepods are common on aquatic macroalgae and angiosperms, and are equipped with strongly prehensile appendages; these epiphytic species are often adapted also for free-swimming. Globally, harpacticoid copepods comprise from 4 to 95% of the total sediment meiobenthos, and from 11 to 60% of the phytal meiobenthos. Collectively, benthic harpacticoid copepods feed on epipelic or epiphytic diatoms, phytoflagellates, bacteria, either as aggregated cells or detritus associates, fungi and yeasts, blue green algae, mucoid substances, and ciliates. There is growing evidence that harpacticoids may well be the most important fraction of the meiofauna as a food source for larval and juvenile fishes. Whether the reproductive activities of harpacticoid copepods are continuous or protracted as a general rule is not clearly established. Some studies have shown clear periodicity in reproduction, while others suggest a rather continuous reproductive activity. However, for particular species, or species assemblages in given environmental conditions, temporal patterns in reproductive periodicity have been identified. The female benthic harpacticoid carries its eggs in an external egg sac (ovisac) which is paired in some species. Harpacticoids possess naupliar larvae which hatch from the ovisac directly in the habitat of the adult af-

ter an incubation period of generally 1 to 8 days. The post-embryonic development includes six naupliar stages and six copepodite stages; the sixth copepodite stage corresponds is the adult. Development rates are known to be greatly influenced by temperature and food supply. In the laboratory, egg to adult time is known to vary from 20 to 70 days, in inverse proportion to temperature. The life-span of a harpacticoid copepod appears to range from 4 to 13 months in nature. Many field studies have shown one to three annual generations to be the usual occurrence.

4.2 Vertical Distribution of Selected Species of Natant Harpacticoid Copepods

Harpacticoid copepods are known to occur in the water column on vegetated tidal flats (Sibert 1981). An early attempt at quantifying the abundance of water-borne (natant) harpacticoids on a vegetated tidal flat has shown their density varies from 9 to 94 individuals l^{-1} within 10 cm of the sediment surface (Sibert *et al.* 1977). Further, there is evidence that the vertical distribution of natant harpacticoids exhibits persistent patterns. Sibert (1981) sampled the water column in a vegetated tidal channel in the Nanaimo estuary, British Columbia. Water samples were pumped from within 5 and 30 cm of the sediment surface, and the density of animals nearer to the bottom always exceeded that at the higher level by a factor of 2 to 20. Clearly then, and as recommended by Bell *et al.* (1984) for tidal seagrass systems, sampling programs aimed at quantifying the abundance of harpacticoids on vegetated tidal flats should be designed with consideration of the three possible sub-habitats of the animal:

- plant surface
- sediment

- water column.

In order to correctly estimate the abundance of harpacticoids in the water column, a detailed description of the animals' distribution therein is required. This section reports the results of a study on the vertical distribution of an assemblage of species of natant harpacticoids on a vegetated tidal flat. The taxa in the assemblage are *Tisbe* spp., *Zaus aurelii*, and *Harpacticus uniremis*. Those species were previously reported as the dominant food items in the diet of the juvenile chum salmon caught near Roberts Bank (chapter 3).

4.2.1 Methods

The location of the study site and the methods of collecting natant harpacticoids have previously been described (chapter 3). The salient points to recall are that natant harpacticoids were collected with a stratified sled-sampler and that the centered height above the sediment at each sampling level was 56, 156, 256, 356, and 456 mm respectively. In 1986, 3 transects were done on each sampling trip, while in 1985, only 1 transect was done on each sampling trip. All sampling was done at station H (see Fig. 3.1). The total number of adults, or near-adults (copepodites 4 and 5) of each of the 3 selected species was determined at each sampling level of each transect for every sampling efforts. The detailed taxonomic composition of the water-borne zooplankton samples is reported in Appendix B. All unidentified harpacticoid copepods (sub-adults or early copepodites) are reported as unidentified copepodites. Only the adult or near-adult copepodites were enumerated to species since juvenile chum salmon have been shown to feed almost strictly on adult or near-adult stages.

4.2.2 Results and Discussion

Specific and persistent patterns were observed in the vertical distribution of the harpacticoid taxa under study (Figs. 4.1, 4.2, and 4.3). The maximum abundance of *Zaus aurelii* was observed at the intermediate sampling level (156-256 mm) (Fig. 4.1). On either side of this maximum, abundance decreased in more or less linear fashion. The distribution curve of *Zaus aurelii* in the water column was roughly pyramidal in shape throughout most of the season. The maximum abundance of *Harpacticus uniremis* was observed at the lowest sampling level (56 mm) for half of the sampling period (days 91, 105, and 119) and at the intermediate level (156 mm) for the remainder of the time (Fig. 4.2). The abundance of *Harpacticus uniremis* was not consistently decreasing with height above sediment after the level of maximum abundance had been reached (days 78, 91, and 147). The maximum abundance of *Tisbe* spp. was observed at the lowest sampling level (56 mm) except for the last sampling efforts of the season when their absolute abundance was low (days 132 and on) (Fig. 4.3). When the abundance of *Tisbe* spp. was maximal at the lowest sampling level (days 55 to 119), the abundance of animals at each successive level was always lower than that at the previous. The decline in abundance from one sampling level to the next was faster at lower levels. Throughout most of the sampling period, the distribution curve of *Tisbe* spp. in the water column appeared to have the characteristics of a negative exponential function.

The number of adults of the 3 selected harpacticoid taxa per transect (sum of animals in the 5 sampling baskets) varied little from one transect to another at any sampling date (Fig. 4.4). This low variance in the number of harpacticoids per transect for the assemblage as a whole is assumed to be representative of the variability in number between corresponding levels of transect. The specific com-

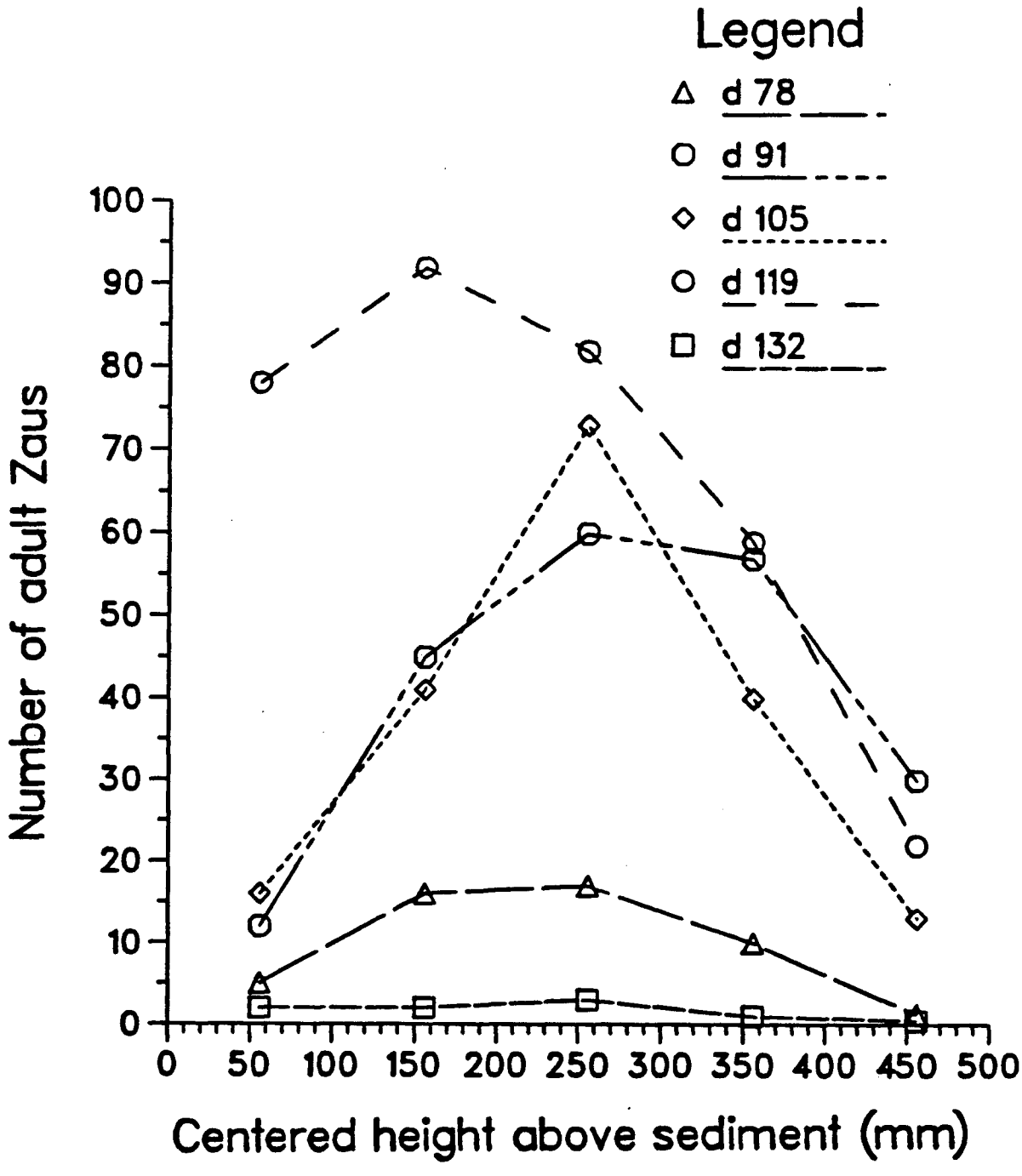

Figure 4.1: Vertical Distribution of *Zaus aurelii* at station H in 1986.

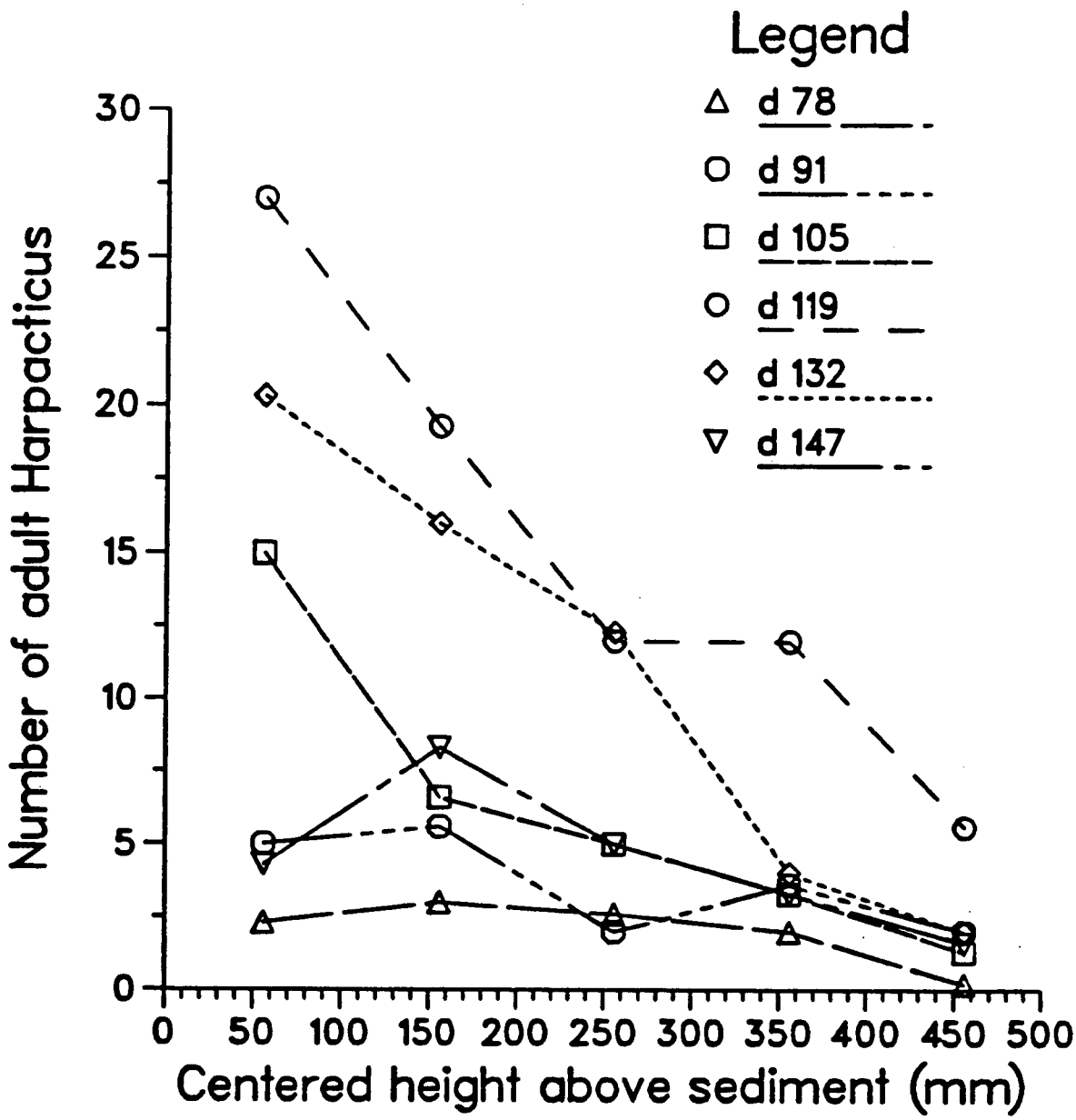

Figure 4.2: Vertical distribution of *Harpacticus uniremis* at station H in 1986.

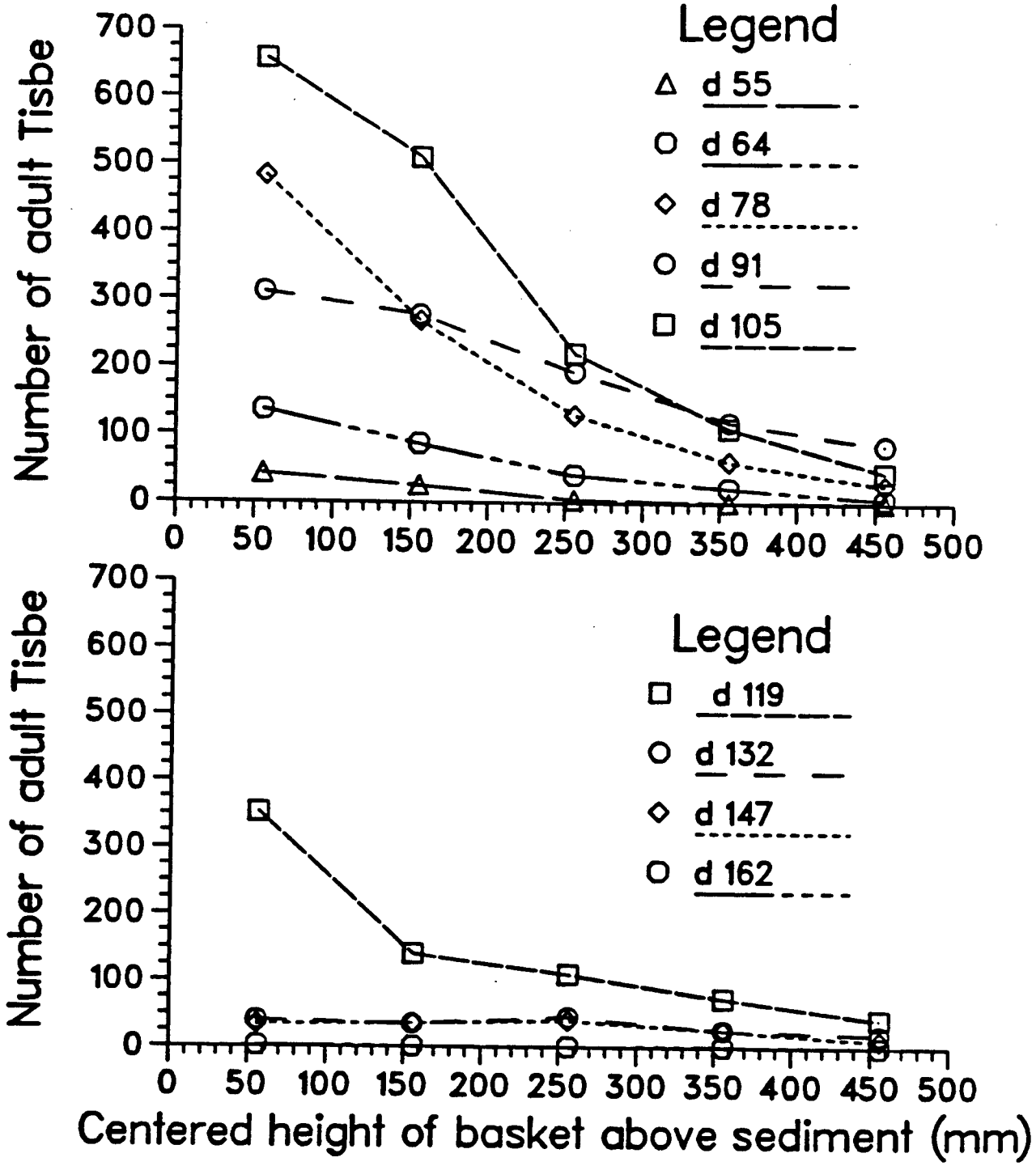

Figure 4.3: Vertical distribution of *Tisbe* spp. at station H in 1986.

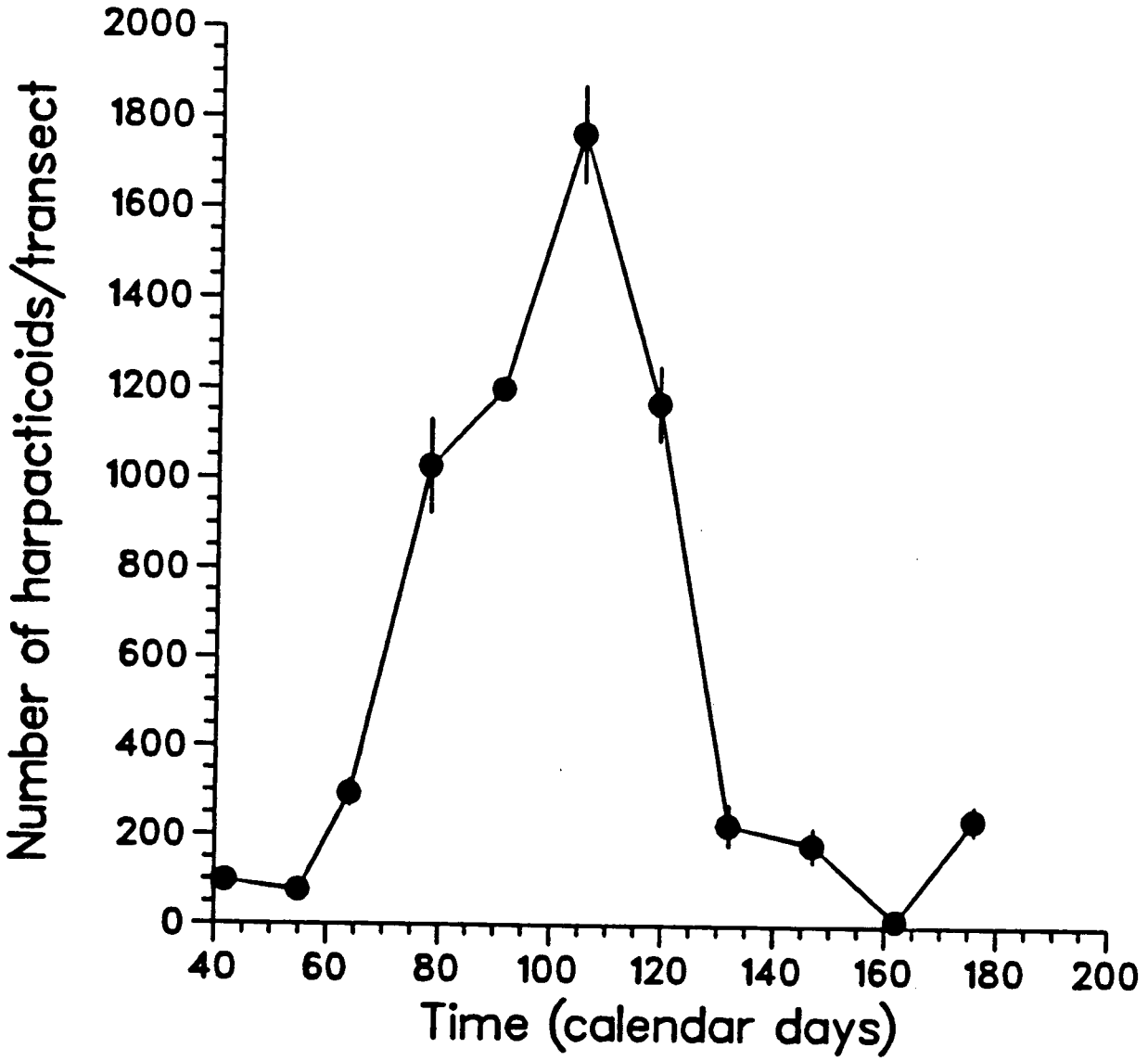

Figure 4.4: Mean number of the harpacticoid species assemblage H+Z+T per transect at station H in 1986 (mean of 3). Error bars are +/- 1 S.E. of mean; n=3.

position of the harpacticoid assemblage also varied very little between transects at any sampling date (Fig. 4.5). For the 3 harpacticoid taxa considered, a maximum of abundance in the water column was bracketed with the sled-sampler. This suggests that the sled-sampler extended sufficiently in the water column. The patterns observed in the vertical distribution of the selected taxa of harpacticoids are then reasonably assumed to be representative of the bulk of the population.

Once their vertical distribution in the water column is described, it is possible to estimate the total abundance of natant harpacticoids by computing the area under their vertical distribution curves. The distribution curves of *Zaus aurelii* and *Harpacticus uniremis* (Figs. 4.1 & 4.2) were closed by extending straight lines fitted through the first two and last two observed data points respectively. Intercepts (on the vertical or horizontal axis, depending) were derived from those fitted lines to add closing intervals on each distribution curve (Tables 4.1 & 4.2). The abundance of *Zaus aurelli* and *Harpacticus uniremis* in the water column was computed by numerically integrating the closed distribution curves as follows:

$$\sum_{i=1}^{6} \overline{N}_i L_i \tag{4.1}$$

where i = interval number, $\overline{N}_i$ = mean number of animals in interval i, and L_i = length of interval (mm).

For *Tisbe* spp., the rate of change of the animal abundance in the water column was assumed to be described by

$$\frac{dN(z)}{dz} = -kN(z) \tag{4.2}$$

where N =number of animals, k =decay coefficient, and z =height above sediment.

Equation 4.2 proved to be a reasonable assumption. The abundance of *Tisbe* spp.

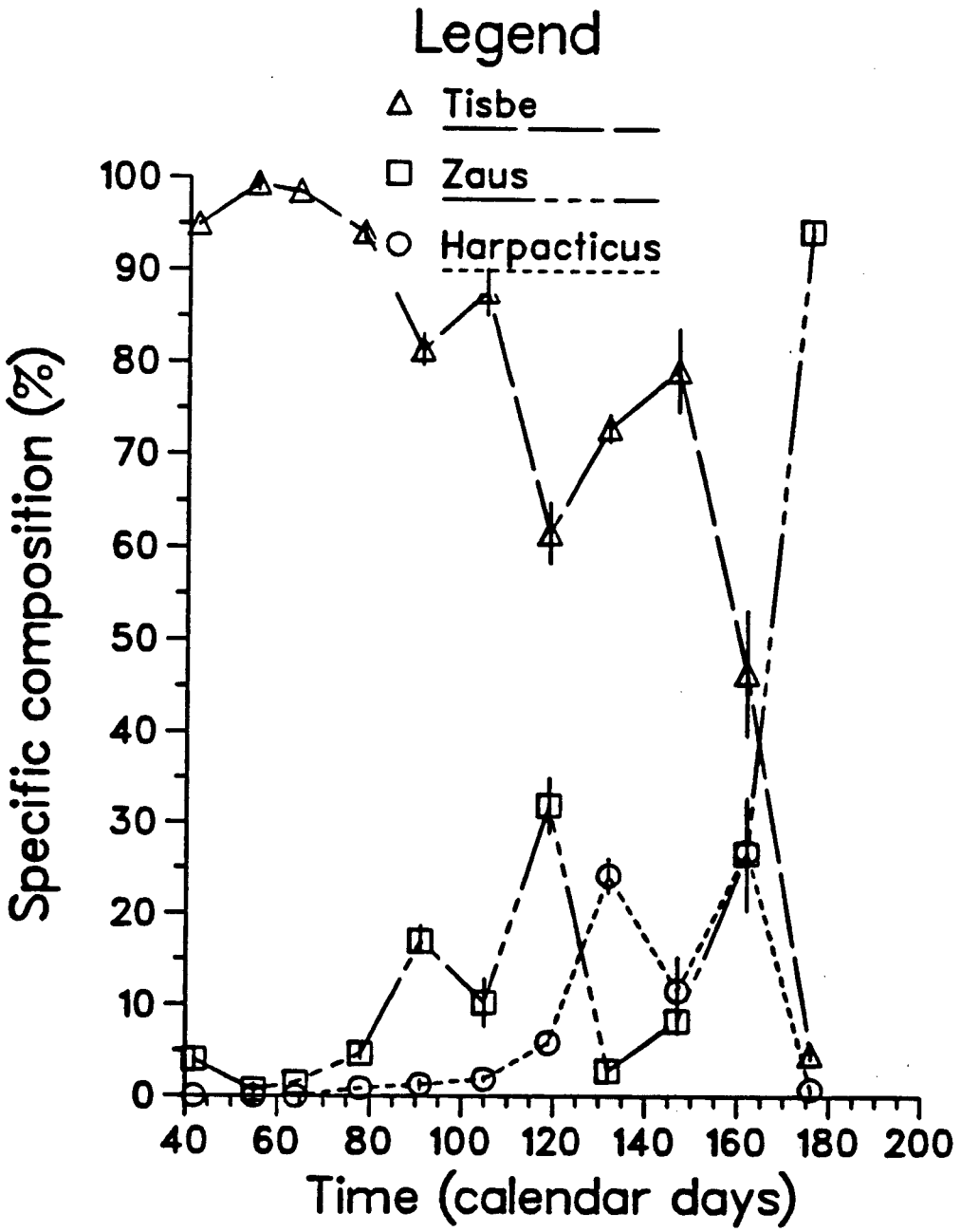

Figure 4.5: Specific composition of natant harpacticoids in the H+Z+T assemblage at station H on Roberts Bank during sampling period in 1986. Error bars are +/- 1 S.E. of the mean; n=3.

Date	Sampling level height (number of *Zaus aurelii*)						
78	10.5(0)	56(5)	156(16)	256(17)	356(10)	456(1.3)	471(0)
91	19.6(0)	56(12)	156(45)	256(17)	356(10)	456(1.3)	567(0)
105	0(2)	56(16)	156(41)	256(73)	356(40)	456(13)	504(0)
119	0(70)	56(78)	156(41)	256(82)	356(59)	456(22)	515(0)
132	0(2)	56(2)	156(2)	256(2)	356(1)	456(1)	556(0)

Table 4.1: Sampling level heights and corresponding abundance of *Zaus aurelii* (in brackets) for various sampling efforts (date in calendar days).

Date	Sampling level height (number of *Harpacticus uniremis*)						
78	1.9(0)	56(2.3)	156(3)	256(2.6)	356(2)	456(0.2)	467(0)
91	0(4.7)	56(5)	156(5.6)	256(2)	356(3.6)	456(2)	581(0)
105	0(19.7)	56(15)	156(19.3)	256(12)	356(12)	456(5.6)	543(0)
132	0(22.7)	56(20.3)	156(16)	256(12.3)	356(4)	456(2)	556(0)
147	0(0.21)	56(4.3)	156(8.3)	256(5)	356(3.3)	456(1.6)	550(0)

Table 4.2: Sampling level heights and corresponding abundance of *Harpacticus uniremis* (in brackets) for various sampling efforts in 1986 (date in calendar days).

at each sampling level was regressed versus the corresponding centered height of the basket (Z) for various sampling efforts according to

$$\log_e N(Z) = \log_e N - kZ$$

which provided a good fit for most of the sampling efforts (Table 4.3). According to this model, the total abundance of *Tisbe spp.* in the water column is equal to:

$$\frac{N_o}{k} \tag{4.3}$$

However, due to the finite size of the opening of the sampling baskets on the sled-sampler, the intercept N_o in eq. 4.3 is somewhat biased. This bias introduced in the computation by relating the number of harpacticoids in a basket to the corresponding centered height must be evaluated to assess the accuracy of the estimates of abundance of the animals. The volume intersected by a cylinder (centered at height Z and with radius a) through a density surface described by $dN(z)/dz = -kN$ with true intercept N_0^*, is equal to (Fig. 4.6):

$$\int_{Z-a}^{Z+a} \int_{-\sqrt{a^2-(z-Z)^2}}^{+\sqrt{a^2-(z-Z)^2}} N(z)dydz$$

$$= 2N_o^* \int_{Z-a}^{Z+a} e^{-kZ}\sqrt{a^2-(z-Z)^2}\,dz$$

$$= 2N_o^* e^{-kZ} \int_{-a}^{+a} e^{-ku}\sqrt{a^2-u^2}\,du$$

$$= 2N(Z) \int_{-a}^{+a} e^{-ku}\sqrt{a^2-u^2}\,du$$

$$= 2a^2N(Z) \int_{-1}^{+1} e^{-kav}\sqrt{1-v^2}\,dv$$

$$= 2a^2N(Z) \sum_{j=0}^{\infty} \frac{(-ka)^j}{j!} \int_{-1}^{+1} v^j\sqrt{1-v^2}\,dv$$

$$= 4a^2N(Z) \sum_{j=0}^{\infty} \frac{(ka)^{2j}}{2j!} \int_{0}^{1} v^{2j}\sqrt{1-v^2}\,dv$$

$$= N(Z)\pi a^2\{1 + \frac{(ka)^2}{8} + \cdots\}$$

which finally reduces to

$$= N_o^* e^{-kZ}\{1 + \frac{(ka)^2}{8} + \cdots\} \quad , for\ area\ \pi a^2 .$$

With consideration of the two leading terms in the above expansion, the relationship between the biased intercept N_o (eq. 4.5) and the true intercept N_o^* can be written as

$$\frac{N_o^*}{N_o} = \frac{1}{1 + \frac{(ka)^2}{8}} .$$

The corrected expression for the computation of the abundance of animals in the water column is then written as

$$\int_0^\infty N_o^* e^{-kz} dz = \frac{N_o^*}{k} = \frac{N_o}{k} \frac{1}{1 + \frac{(ka)^2}{8}} .$$

The absolute number of harpacticoid copepods in the water column was reported in individuals/m^2 by dividing the computed amount by the bottom area shaded by the sled-sampler (= length of transect (1960 cm) $\times$ diameter of baskets (8.3 cm) =16848 cm^2) (Table 4.4). The mean number of each harpacticoid taxon per transect was determined for each sampling effort, which provided an index of abundance by which to determine the temporal patterns of abundance of the animals. The temporal patterns observed with the index of abundance series were then compared to those observed with the absolute abundance series determined by integration of the distribution curves; for *Tisbe* spp., the biased and corrected estimates of absolute abundance were also compared (Figs. 4.7, 4.8, and 4.9).

The highest abundance of *Zaus aurelii* in the water column (1.96 individuals /cm^2) was observed on on April 29 (day 119) (Fig. 4.7). The early and late season

Date	N_o	k	R^2
42	112	-0.0099	0.96
55	73	-0.0098	0.87
64	249	-0.0075	0.97
78	782	-0.0072	0.96
91	426	-0.0035	0.96
105	1196	-0.0069	0.97
119	390	-0.0049	0.96
132	49	-0.0017	0.64

Table 4.3: Intercept (N_o), decay coefficient (k), and coefficient of determination (R^2; $n = 5$) of the exponential distribution curves of *Tisbe* spp. in the water column (date in calendar days).

	Tisbe spp.		*Z. aurelii*		*H. uniremis*	
Date	N_o/k	$\#/cm^2$	$\sum_1^6$	$\#/cm^2$	$\sum_1^6$	$\#/cm^2$
42	1145	0.7				
55	7521	0.5				
64	33240	2.0				
78	107850	6.6	4731	0.28	949	0.05
91	120807	7.4	20183	1.2	1867	0.11
105	174186	10.7	17666	1.05	3289	0.19
119	79312	4.9	33053	1.96	7839	0.46
132	28383	1.7	912	0.05	5539	0.33
147					2453	0.14

Table 4.4: Total abundance of *Tisbe* spp., *Zaus aurelii*, and *Harpacticus uniremis* in the water column at station H during the sampling period in 1986.

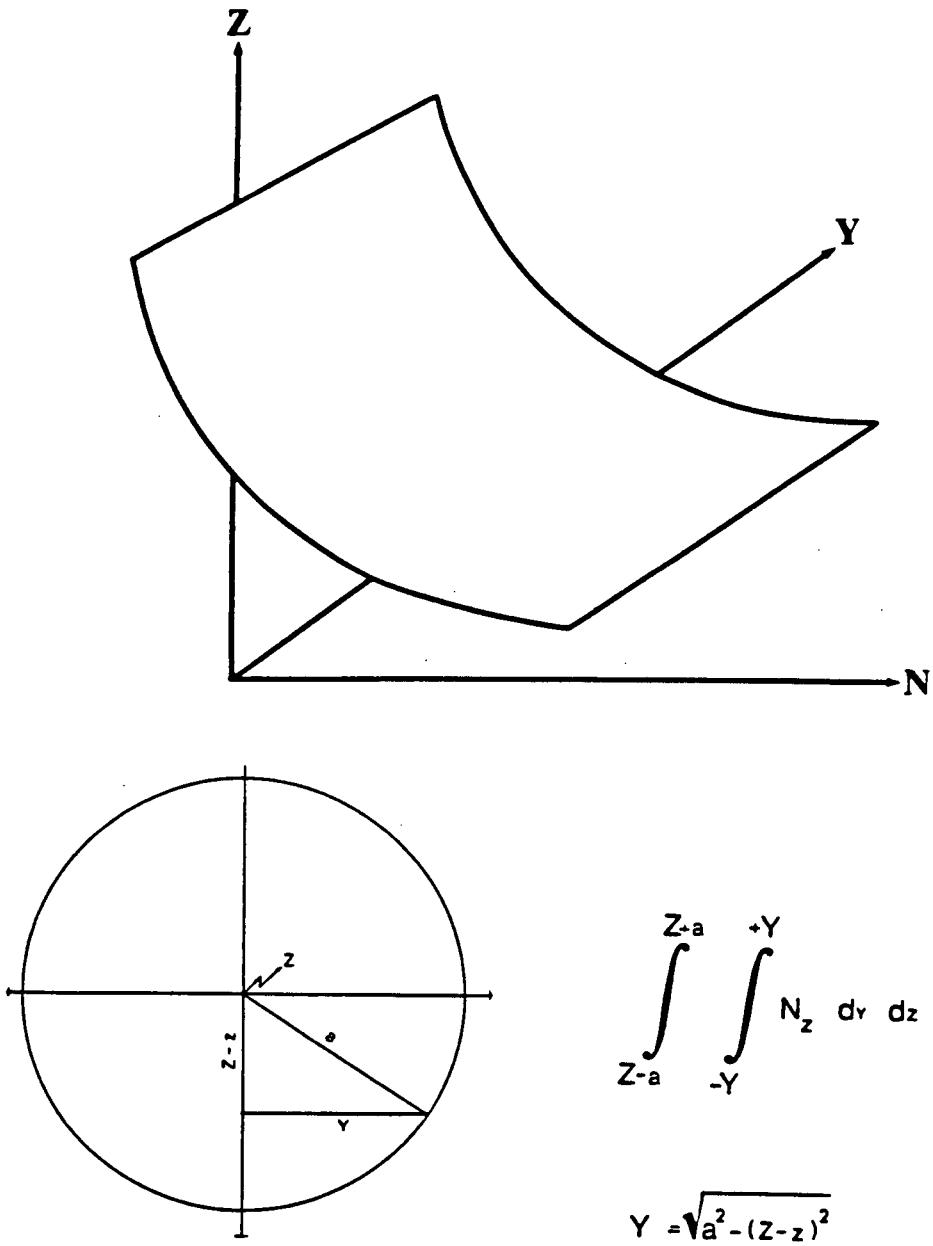

Figure 4.6: Volume intersected by a cylinder of radius a through a density surface described by $dN(z)/dz = -kN(z)$. Note that the horizontal axis has the dimension of N, not of length.

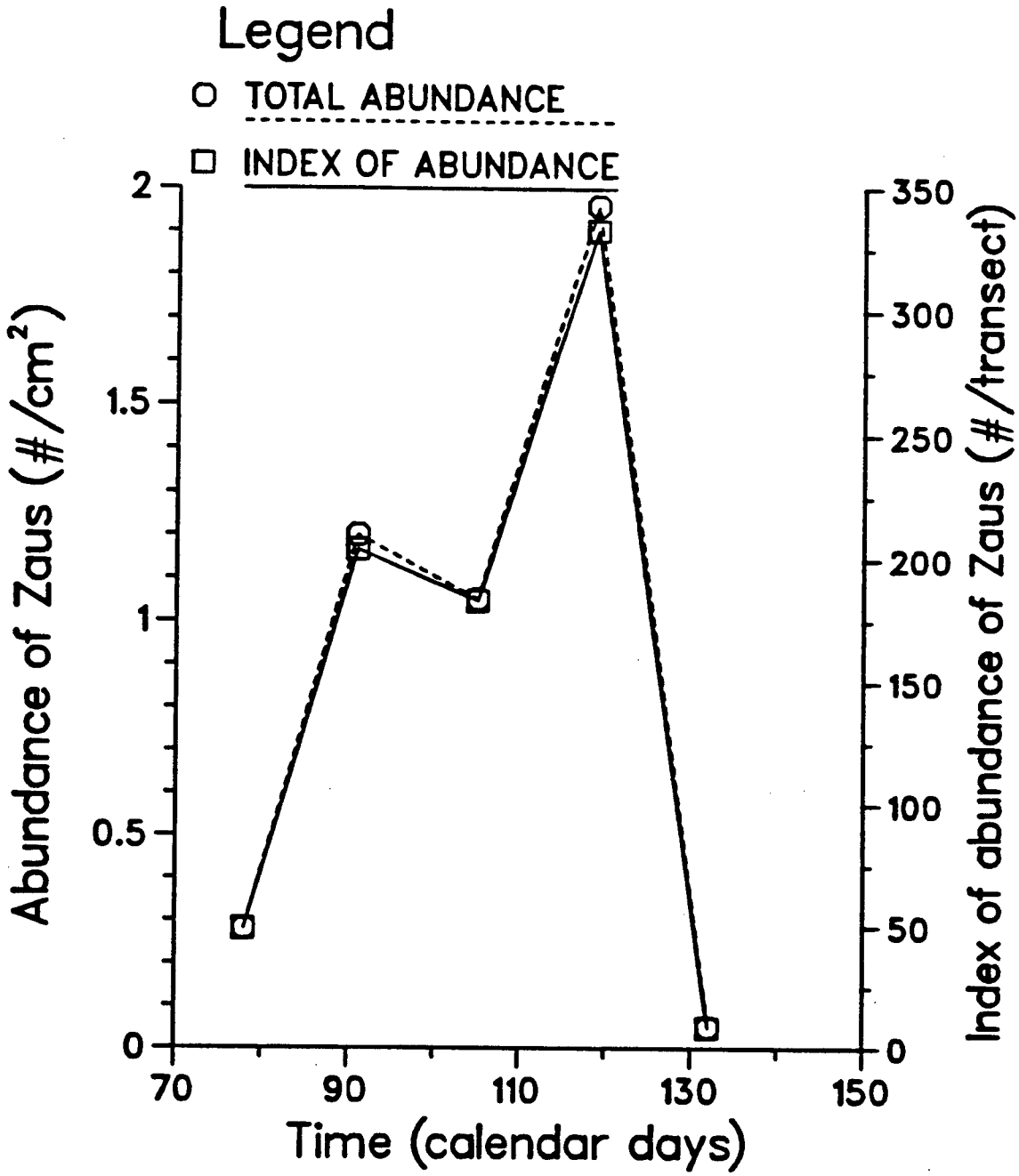

Figure 4.7: Absolute abundance and index of abundance of *Zaus aurelii* in the water column during the sampling period in 1986 at station H.

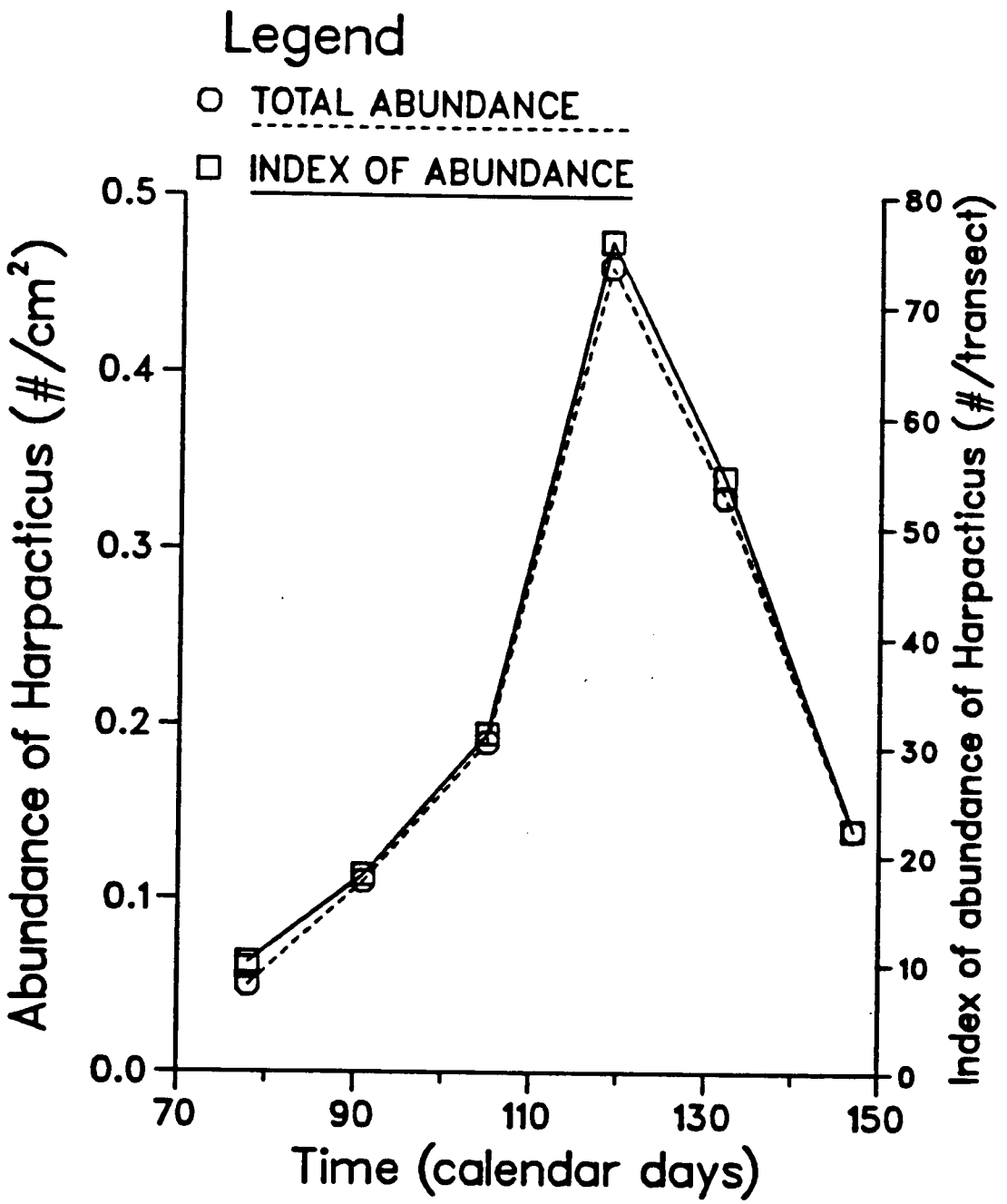

Figure 4.8: Absolute abundance and index of abundance of *Harpacticus uniremis* in the water column during the sampling period in 1986 at station H.

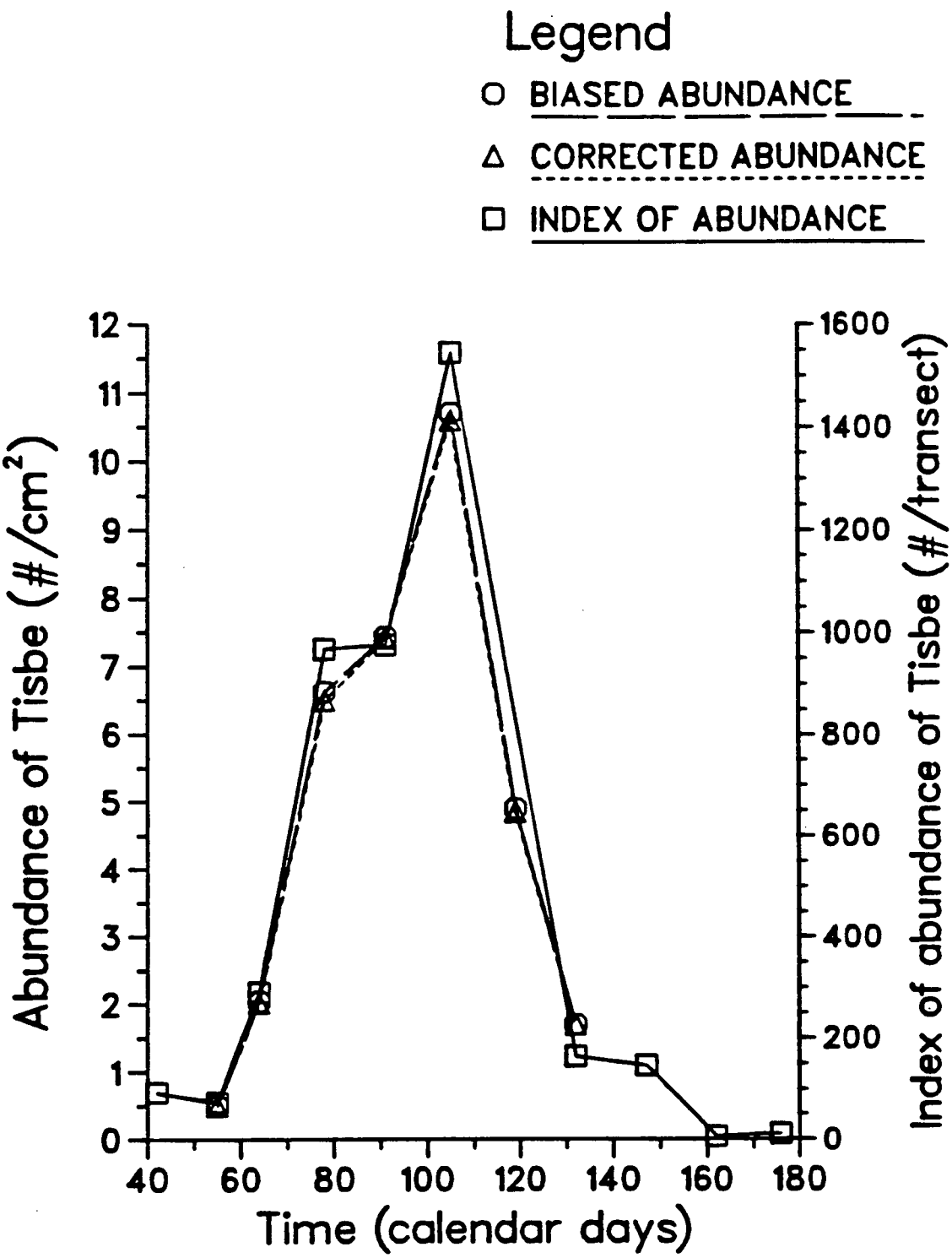

Figure 4.9: Absolute abundance (biased and corrected) and index of abundance of *Tisbe* spp. in the water column during the sampling period in 1986 at station H.

minima of abundance were 0.28 individuals/cm^2 on March 19 (day 78) and 0.05 individuals/cm^2 on May 13 (day 134). The temporal patterns in the abundance of animals in the water column observed in the computed absolute abundance series closely paralleled those observed in the index of abundance series. The maximal abundance of *Harpacticus uniremis* (0.46 individuals/cm^2) was also observed on April 29 (day 119) (Fig. 4.8). The early and late season minima were 0.05 individuals/cm^2 on March 19 (day 78) and 0.14 individuals/cm^2 on May 27 (day 147). Again, there was a close match between the temporal patterns in the total abundance series and in the index of abundance series. The maximal corrected abundance of *Tisbe* spp. (10.6 individuals/cm^2) was observed on April 15 (day 105) (Fig. 4.9). The early and late season minima were 0.5 individuals/cm^2 on February 24 (day 55) and 1.7 individuals/cm^2 on May 13 (day 132). The biased absolute abundance was only slightly different (less than 1%) from the corrected absolute abundance (biased maximum abundance: 10.7 individuals/cm^2; corrected maximum abundance: 10.6 individuals/cm^2). This indicates that the size of the filtering baskets on the sled-sampler (8.3 cm internal diameter) was appropriate for the decay coefficients of harpacticoids in the water column ($k = -0.006$ to -0.011) (Table 4.3). By relating the number of animals in a basket to the corresponding centered height above sediment to parametrize the exponential decay curve, it was implicitly assumed that within the opening of the basket, the decay curve was linear. This assumption was required to obtain an analytical expression of the decay curve. The small size of the truncation error introduced in the computations suggest that this assumption is reasonable. Similar patterns in the temporal abundance of *Tisbe* spp. in the water column were observed in the computed absolute abundance series and in the index of abundance series. For the 3 harpacticoid taxa

under study, a simple index of abundance (number of animals/transect) appears to be sufficient to track the temporal patterns in the abundance of the animals. However, as illustrated in the case of *Tisbe* spp., small differences between the index of abundance and the absolute abundance series can lead to substantially different speculations. Between March 19 (day 78) and April 1 (day 91) (Fig. 4.9) the index of abundance of *Tisbe* spp. remains the same, suggesting a plateau. One might propose that this plateau could result from a sudden predation pulse on the harpacticoid population. However, the observed temporal patterns of abundance leading to this proposition are less obvious when considering the computed absolute abundance data: during the same period extending from days 78 to 91, the computed absolute abundance does not indicate such a flat plateau as the index of abundance does. As it is, the salient feature in the absolute abundance during this period is a decrease in the decay coefficient k (from -0.0072 to -0.0035) (Table 4.3).

4.2.3 Discussion

In various estuaries, harpacticoid copepods have been recognized as a dominant food item for juveniles of commercially important fishes (Feller & Kaczynski 1975; Sibert 1979). However, some difficulties arise when interpreting the relationships between predators and prey due in part to a lack of knowledge of the local prey distribution (Sibert 1981). Patterns in the distribution of natant harpacticoids such as those demonstrated here could help in the investigation of the trophic relationships between predatory juvenile fishes and harpacticoid copepods. Further, the impact on the global dynamics of estuaries of such trophic relationships should only be assessed with due consideration of the total abundance of natant

harpacticoids. Healey (1979) submitted that the salmonid-harpacticoid trophic relationships had little effect on the dynamics of the Nanaimo estuary as a whole; this conclusion was reached with considering only the abundance of harpacticoids in the sediment, and many of the harpacticoid prey species were those that have shown to be substantially abundant in the water column in this study.

The sampling technique used to collect harpacticoids in this study appears to be appropriate. The simplicity of use of the sled-sampler makes it a convenient field tool; importantly, information obtained on the localized distribution of natant harpacticoids can provide estimations of absolute abundance. Studies reporting absolute abundances of animals rather than index of abundance could be easier to compare, and provide a more detailed basis for the understanding of the trophodynamics of estuaries. One technical point remains to be clarified with respect to the sled-sampler. As pointed out earlier, the flow of water in each sampling basket seemed to be less than ideal probably because of the high aspect-ratio of the sieve and the elementary design of the basket. For this reason, the estimations of absolute abundance of natant harpacticoids are probably biased towards lower values. Probably balancing this underestimation of abundance is the contamination of the natant harpacticoid samples by epiphytic animals scraped off eelgrass blades by the sled-sampler. This contamination problem remains to be investigated with a micro-scale sampling approach. Despite these difficulties, evidence for the existence of specific localized patterns in the distribution of natant harpacticoids is presented. A theoretical basis for the assessment of the derived computations of total abundance is developed. This also provides an objective basis for choosing an appropriate sampling basket opening. Indeed, as pointed out earlier, studies on harpacticoid copepods on vegetated tidal flats should take into account the 3

potential sub-habitats of the animals; further, such studies should as well take into account the specificity of the distribution patterns of each species or assemblages of species of harpacticoid copepods in the water column.

4.3 Thermal Regime and Seasonal Abundance of Selected Species of Natant Harpacticoids

The reproductive cycle of most temperate and boreal invertebrates is decisively affected by temperature (Kinne 1970). A relationship between the seasonal abundance of marine invertebrates and the annual temperature cycle is then expected. Evidence for the existence of such a link between temperature and invertebrate abundance has been reported for meiofauna on various tidal flats, especially for some groups of harpacticoid copepods (Muus 1967; Ito 1971; Harris 1972; Jewett & Feder 1977; Coull 1985). In a most general sense, these studies report that the density of certain species or assemblages of species of harpacticoid copepods tend to fluctuate in relation to temperature. Whether the link between animal abundance and temperature has a physiological or trophic basis is yet to be established. For harpacticoids, the mechanism responsible for the apparent coupling between thermal regime and seasonal abundance is thought to be the effect of temperature variations on development time (Heip & Smol 1976). However, a concomitant increase in food supply has been suggested as a possible alternative or complementary mechanism (Hicks 1979; Coull 1985). Irrespective of the nature of the mechanism(s) involved, the observed relationship between temperature and abundance of some harpacticoid copepods is described in the broadest of terms. Possible reasons for this broadness are the spottiness of the temperature data against which the seasonal abundance of the animal is compared, and the variation

in observational methodologies. Any identification of the fine temporal patterns in the thermal regime is difficult–only the broad patterns are obvious, from which an equally broad definition of the link between animal abundance and thermal regime is derived.

Variability of temperature on a wide range of temporal scales is a well described environmental characteristic of temperate tidal flats (Vugts & Zimmerman 1975,1985; Harrison 1984,1985; Harrison & Phizacklea 1987). These detailed studies of temperature on tidal flats indicate that the thermal regime of such areas is characterized by periodic and aperiodic fluctuations as a result of interactions between radiative heating and cooling, and sensible and latent heat exchange with overlaying air and water. It is suggested in the same studies that temperature could be a prime environmental factor in the ecology of the fauna associated with the tidal flats.

Ecological studies detailing the seasonal abundance of harpacticoid copepods in relation to temperature on tidal flats could benefit from standardized thermometric techniques providing a more detailed description of the thermal regime. Conversely, detailed studies of the thermal regime on tidal flats merely suggest the potential relevance of such knowledge for an understanding of the ecology of those areas. In this section, the results are reported of a study of the seasonal abundance of an assemblage of harpacticoid copepod species in relation to the thermal regime on a tidal flat. The target assemblage of harpacticoids is composed of 3 taxa (*Tisbe* spp., *Zaus aurelii*, *Harpacticus uniremis*) that have been recognized as dominant food items in the diet of juvenile chum salmon. The abundance of harpacticoid copepods was monitored on a time-scale recognized as appropriate in such studies seeking to identify seasonal patterns of abundance (Montagna *et al.* 1983). The

thermal regime in the sediment was monitored on a high resolution time-scale.

4.3.1 Material and Methods

The study site and the technique for collecting natant harpacticoids have previously been described in chapter 2. A time-series of the abundance of the selected species of harpacticoids in the water column was obtained by taking the mean number of adult harpacticoids per transect (n=3 in 1986). As discussed in the previous section, the index of abundance (number of animals/transect) appears appropriate to identify seasonal patterns of abundance: the temporal patterns are the same as those identified in the absolute abundance series. The reason for choosing the index of abundance to be analyzed in relation to temperature instead of the computed absolute abundance is that the computation of a standard error is straightforward with the index of abundance.

Temperature in the sediment was recorded with Peabody-Ryan© thermographs[1] from February 15 to July 8 in 1985, and from February 19 to July 9 in 1986. Each thermograph was encased in a protective PVC© tube; the tube was cribbled with holes to allow water percolation. The upper extremity of the protective casing did not extend beyond the tip of the thermograph sensor; a 1 kg lead weight was attached to the lower end of the casing. At low tide, the thermographs were buried in the sediment, sensor up. The thickness of the sediment above the tip of the probe was recorded after leveling the replaced sediment with the surrounding surface. Further checks during the season proved that the thickness of sediment above the probe remained constant. In 1985, 1 thermograph was successfully moored at station H; the tip of the probe was covered by 5 cm of sediment. In 1986, two

[1]Peabody-Ryan 402-6 6th Street South P.O. Box 599 Kirkland, WA 98033, U.S.A.

thermographs were successively moored at station H; the probe of one was covered by 1 cm of sediment, and that of the other, by 5. Upon retrieval of the thermographs, temperature data were visually extracted from the recording chart paper. Data were read at the nearer 0.5 °C at every 4 hours of recording. Temperature time-series were then subjected to a first-difference filter:

$$\Delta_t = T_{t+1} - T_t$$

with

$$\Delta_t = \begin{cases} \Delta_t & \text{if } \Delta_t \geq 1 \\ 0 & \text{otherwise,} \end{cases}$$

where T =temperature and t=time.

This filter removes the lower frequency components from the signal, emphasizing the higher frequency components (Jenkins & Watts 1968). Due to reading uncertainty in each temperature datum, and to emphasize the *warming* of the sediment, only temperature differences (Δ_t) greater than or equal to 0 were retained.

Sediment pigment concentrations were measured as recommended by Parsons *et al.* (1984 b). Sediment samples were collected at station H at high tide by a SCUBA diver: 9 cores were taken at random in a 100-cell 0.25 m^2 quadrat. Cores were collected with syringes (5.31 cm^2 opening). Loaded coring devices were brought to the tending boat, and sediment was extruded so as to retain only the top cm; the retained sediment fraction was transferred to a plastic bag and kept on ice in the dark. In the laboratory, samples were frozen for at most 10 days before processing. Frozen samples were transferred to a mortar and ground for 5 minutes in 30 ml 90% (v/v) acetone with a few drops of a suspension of $MgCO_3$. The sediment-acetone slurry was transferred to a graduated plastic centrifuge tube and the total volume made up to 50 ml with additional 90% acetone. The samples were left for two

hours in the dark at 5 °C. After this period, the samples were centrifuged @ 800 g for 10 minutes. The volume of the sediment plug was recorded after centrifugation. A fraction of the extract was transferred to a 1 cm path cuvette. Extinction was measured against a 90% acetone blank with a spectrophotometer (Bausch & Lomb Spectronic© 2000) at wavelengths of 6650 and 7500 Å. For the determination of phaeophytin *a* concentrations, the samples were acidified by adding a few drops of 10% HCl; the cuvette was stopped with a tin foil and lightly shaken for 30 s, and the extinction remeasured at 6650 and 7500 Å. The concentrations of chlorophyll *a* and phaeophytin *a* were calculated by the equations of Parsons *et al.* (1984):

$$Chlorophyll\ \underline{a}(mg/m^3) = \frac{26.7(6650_o - 6650_a) \times v}{V \times l}$$

$$Phaeophytin\ \underline{a}(mg/m^3) = \frac{26.7(1.7[6650_a] - 6650_o) \times v}{V \times l}$$

where 6650_o and 6650_a are the extinctions at 6650 $\mathring{A}$ before and after acidification (corrected for extinction at 7500 $\mathring{A}$), v is the volume of acetone extract (ml), V is the volume of the sediment plug (l), and l is the path length of the cuvette (cm).

The pigment concentrations were reported in g/m^2 following:

$$Pigment(g/m^2) = mg/m^3(1883 \times V)\ ,$$

where 1883 is the ratio between 1 m^2 and the surface opening of a coring device (5.31 cm^2).

The number of ovisacs in the bottom level (centered height above sediment: 56 mm) of the sled-sampler was determined for each transect of each sampling effort in 1986. The lowest sampling level was assumed to be representative of the population as a whole since the study on vertical distribution had revealed that

the bulk of the animals were concentrated near the bottom. It was recognized that some species are not concentrated near the bottom (*e.g. Zaus aurelii*), but the dominant taxon was bottom-concentrated (*Tisbe* spp.), and the egg masses were not identified to the species. The amount of water covering sampling station H relative to the predicted tide height at the port of reference (Point Atkinson) was measured during flowing tide on May 24, 1986. The water level was measured by observing a graduated stake installed at station H, from the shoreline.

4.3.2 Results and Discussion

Natant Harpacticoid Abundance

The abundance of natant harpacticoid copepods showed a pronounced seasonality (Fig. 4.10). In 1985, the abundance of natant harpacticoids (number/transect) ranged from a winter low of 254 to a spring high of 1131. Shortly after the spring high, the assemblage nearly disappeared; secondary small peaks were then observed. In 1986, the natant harpacticoid abundance ranged from a winter low of 77 to a spring high of 1765; secondary small peaks were also observed. The relative abundance of the 3 harpacticoid taxa in the assemblage under study was determined for both sampling years (Table 4.5). In 1985, *Tisbe* spp. was the dominant taxon for most of the sampling period; *Zaus aurelii* and *Harpacticus uniremis* only made up to a few percent of the assemblage. In late spring, *Tisbe* spp. declined and the proportion of *Zaus aurelii* increased, but the total abundance was low (Fig. 4.10). The relative abundance of each taxon was different in 1986 (Table 4.5): *Tisbe* spp. dominated by far in early spring; *Zaus aurelii* became the dominant species later in the season as its absolute abundance increased when that of *Tisbe* spp. declined. In mid-season, *Harpacticus uniremis* became relatively abun-

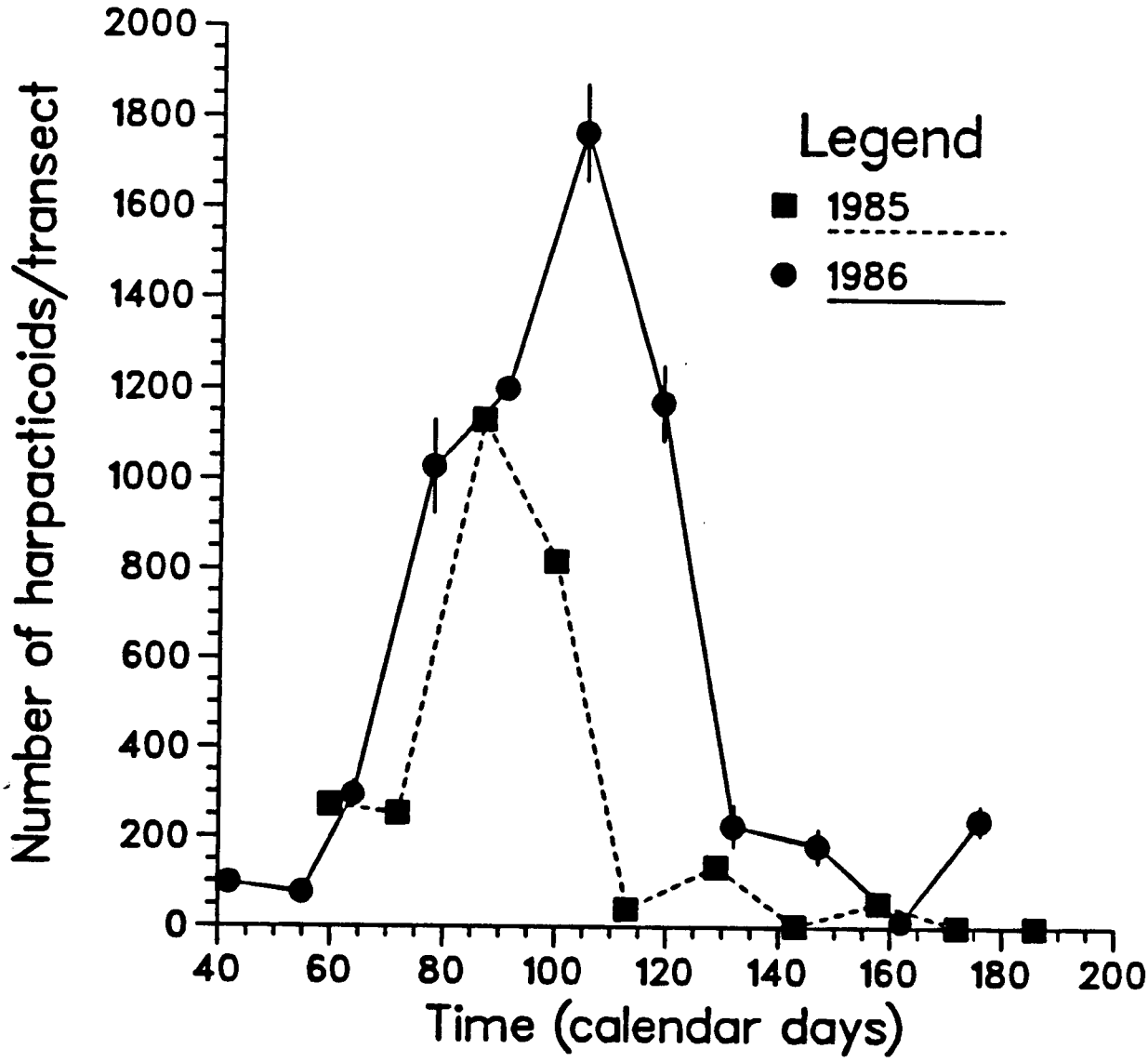

Figure 4.10: Seasonal abundance (individuals/transect) of natant harpacticoids at station H in 1985 and 1986 (for 1986: mean +/- 1 S.E., n=3).

Time	1985			1986		
	T	Z	H	T	Z	H
42	96	4	0			
55	99	1	0			
60				99	1	p
64	98	2	p			
72				98	1	1
78	94	5	1			
88				99	p	p
91	81	18	1			
100				98	1	1
105	88	10	2			
113				99	0	1
119	62	32	6			
129				98	1	1
132	73	3	24			
143				99	0	p
147	79	9	12			
158				94	6	p
162	46	27	27			
172				65	10	25
176	5	94	1			
186				p	66	33

Table 4.5: Relative abundance (%) of *Tisbe* spp. (T), *Zaus aurelii* (Z), and *Harpacticus uniremis* (H) in the natant harpacticoid assemblage in 1985 and 1986 at station H (for 1986: mean of 3 transects). Time in calendar days; p=present, but less than 1 %.

dant. The variance in the number of natant harpacticoids among the 3 transects for each sampling effort was very low in 1986 (Fig. 4.10). It was assumed that this variance was similarily low in 1985, for which the data of only one transect for each sampling were available. The natant harpacticoid time-series of abundance for both sampling years are both characterized by a period of most rapid increase in March (calendar days 60 to 90). In 1985, the steepest increasing section of the natant harpacticoid abundance curve is located between March 13 and 29 (days 72–88) and between March 5 and 19 (days 64–78) in 1985.

Sediment Temperature

The thermal regime in the sediment at the study site exhibited temporal patterns on various time scales (Figs. 4.11, 4.12, and 4.13). In 1985, the temperature in the sediment ranged from 4 °C in winter to 15 °C in early summer (Fig. 4.11); in 1986, the temperature in the sediment ranged from 3 °C in winter to 15 °C in early summer (Figs. 4.12 & 4.13).The range in temperature for both years closely matches the reported annual temperature range of the surface waters in the Strait of Georgia (5-18 °C) (Harrison *et al.* 1983). Superimposed on this seasonal increasing trend in mean temperature are sharp daily fluctuations apparent for both years. The amplitude of those daily fluctuations increased throughout the season. When comparing the two temperature time-series obtained in 1986 (Fig. 4.12, recording depth: 1 cm; Fig. 4.13, recording depth: 5 cm), a dampening of features is apparent. The temperature data collected deeper in the sediment showed consistently lower amplitudes in daily fluctuations: around March 1 (day 60), temperature fluctuations were up to 3 °C at recording depth of 1 cm, but no more than 1 °C at recording depth of 5 cm. When comparing time-series for

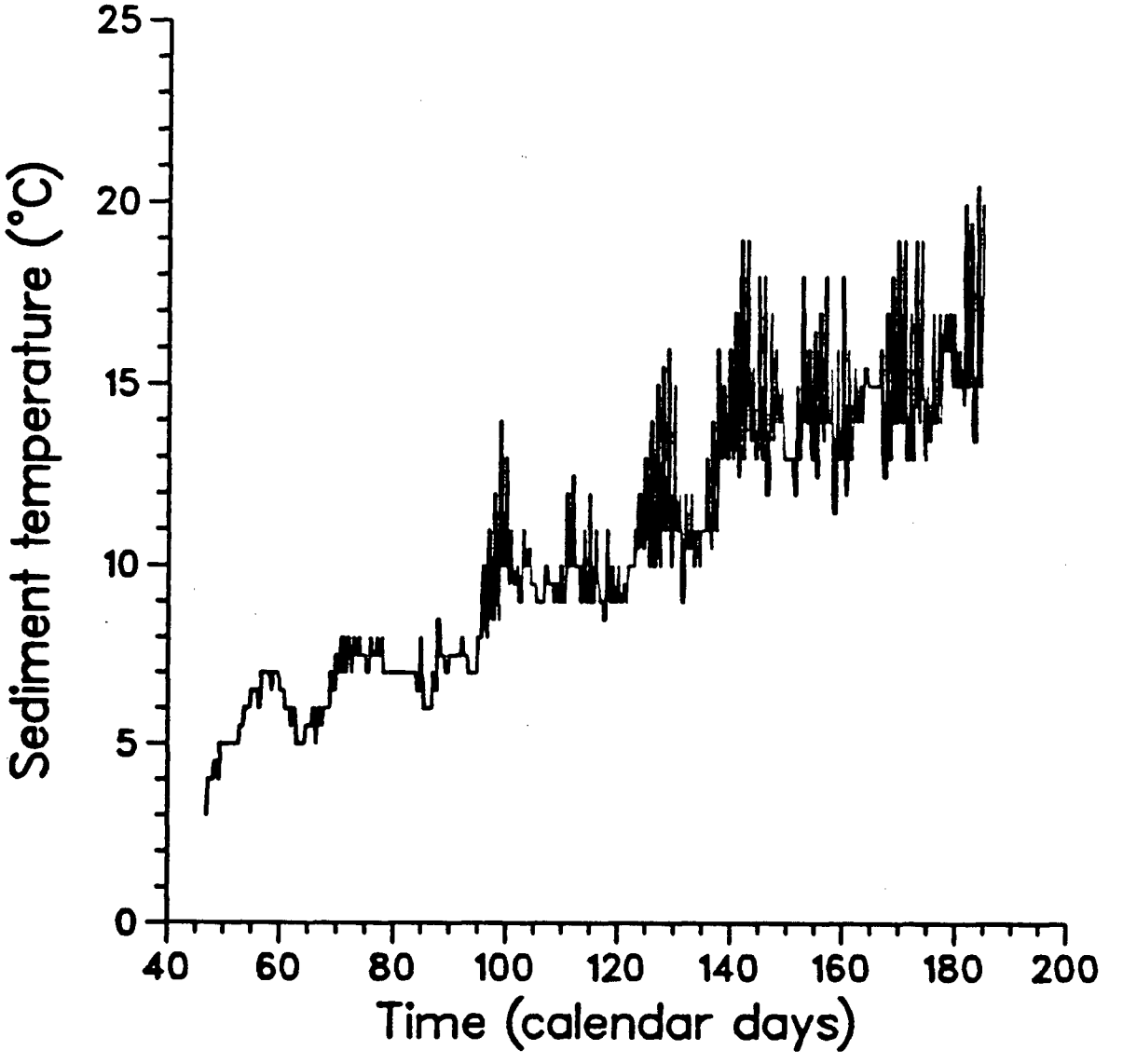

Figure 4.11: Temperature in the sediment at station H during sampling period in 1985. Depth of recording: 5 cm.

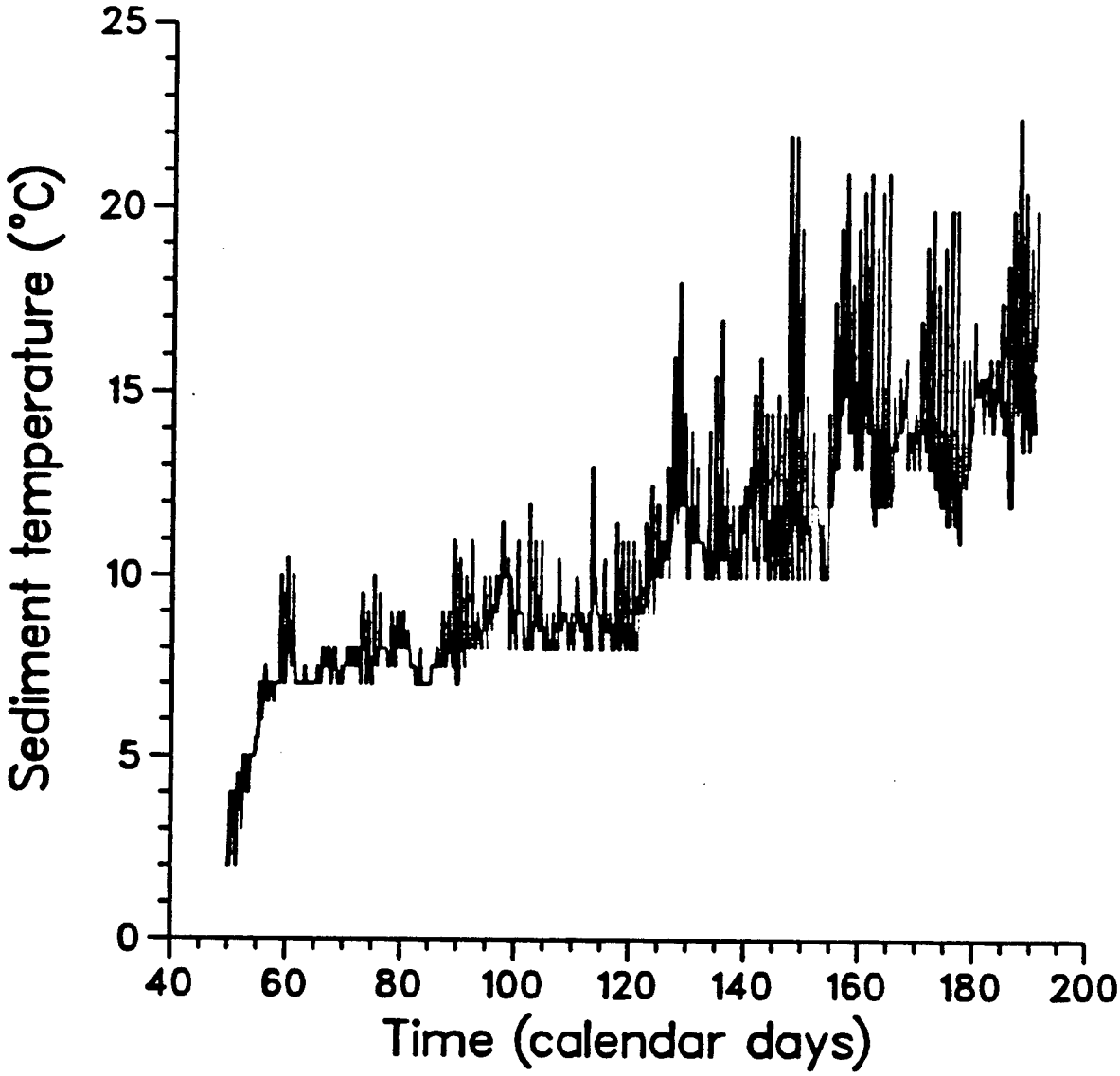

Figure 4.12: Temperature in the sediment at station H during sampling period in 1986. Depth of recording: 1 cm.

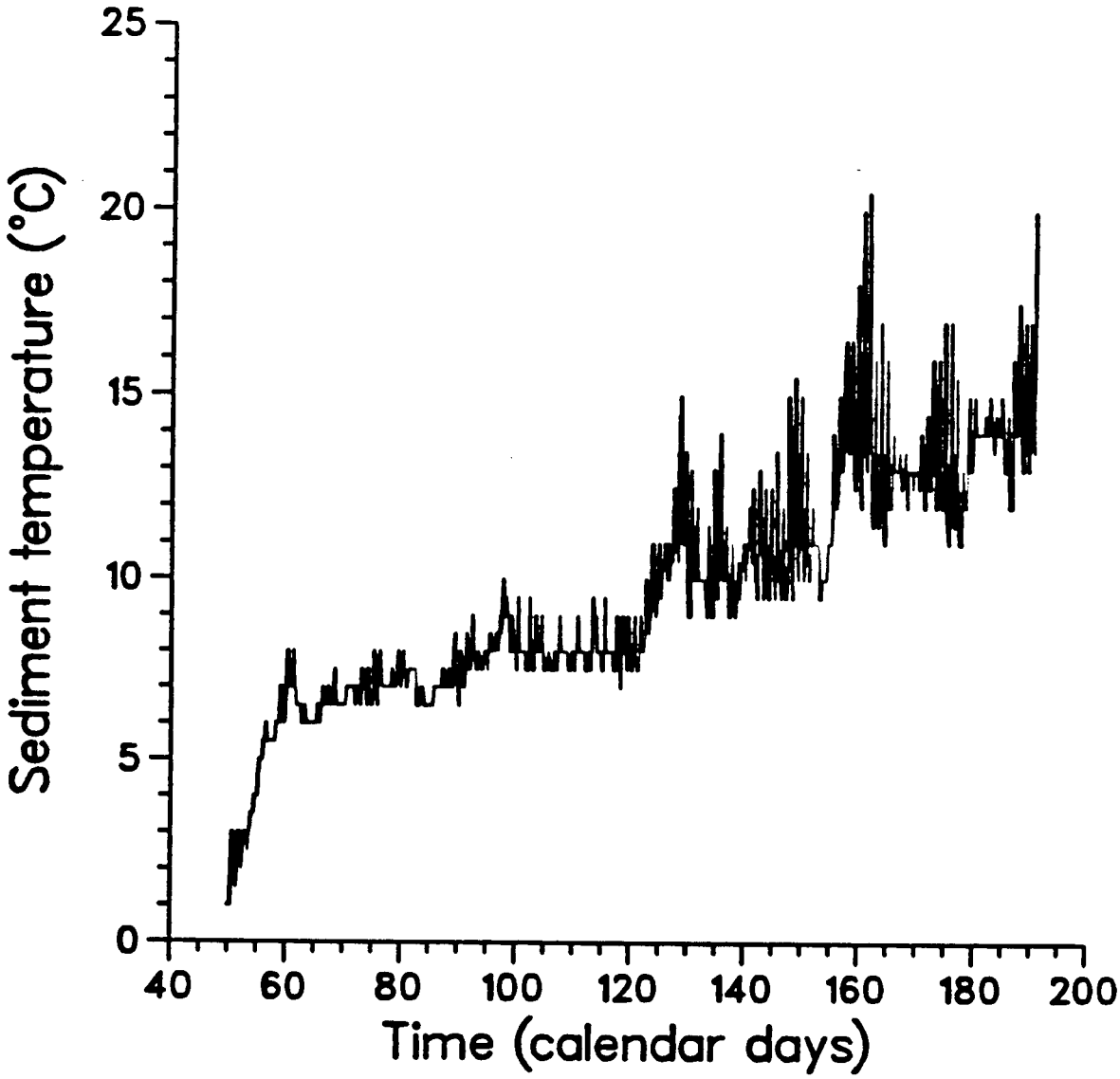

Figure 4.13: Temperature in the sediment at station H during sampling period in 1986. Depth of recording: 5 cm.

different years, but for similar recording depth (Figs. 4.11 & 4.13: recording depth: 1 cm) daily temperature fluctuations are of similar amplitude (*ca* 1 °C for the first two weeks of recording). The depression in the mean temperature appearing between March 2 (day 60) and March 12 (day 70) in 1985 (Fig. 4.11) is coincident with a colder period: during those days, minimum daily air temperature was 2 to 5 °C lower than for the same days in 1986 (Environment Canada Weather Records).

Pigments and Ovisacs

The chlorophyll *a* concentration (mg/m^2) in the sediment in 1985 went from a winter low of 27 (March 2 (day 60)) to a spring high of 57 (April 11 (day 100)); it then reached a low of 29.9 (May 10 (day 129))and leveled off around *ca* 45 for the remainder of the sampling period. The phaeophytin *a* concentration (mg/m^2) went from a winter low of 54 (March 15 (day 73)) to a spring high of 112.4 (May 28 (day 157)) and remained in this range for the remainder of the sampling season (Fig. 4.14).

The number of ovisacs at level A of the sled-sampler (centered height above sediment: 56 mm) ranged from a winter low of 15 (March 20 (day 78)) to a spring high of 282 (May 3 (day 132)) (Fig. 4.15). The distribution of ovisacs was bi-modal, with a first peak of 217 on April 15 (day 105) and a second one of 282 on May 12 (day 132), with an in-between low of 133 on April 29 (day 119).

Tide level

At the date of recording (May 24, 1986), the level of water on the station started to rise at 1445 H (PST) (Fig. 4.16). For this time, the predicted tide level at the port of reference was calculated to be 1.6 m.

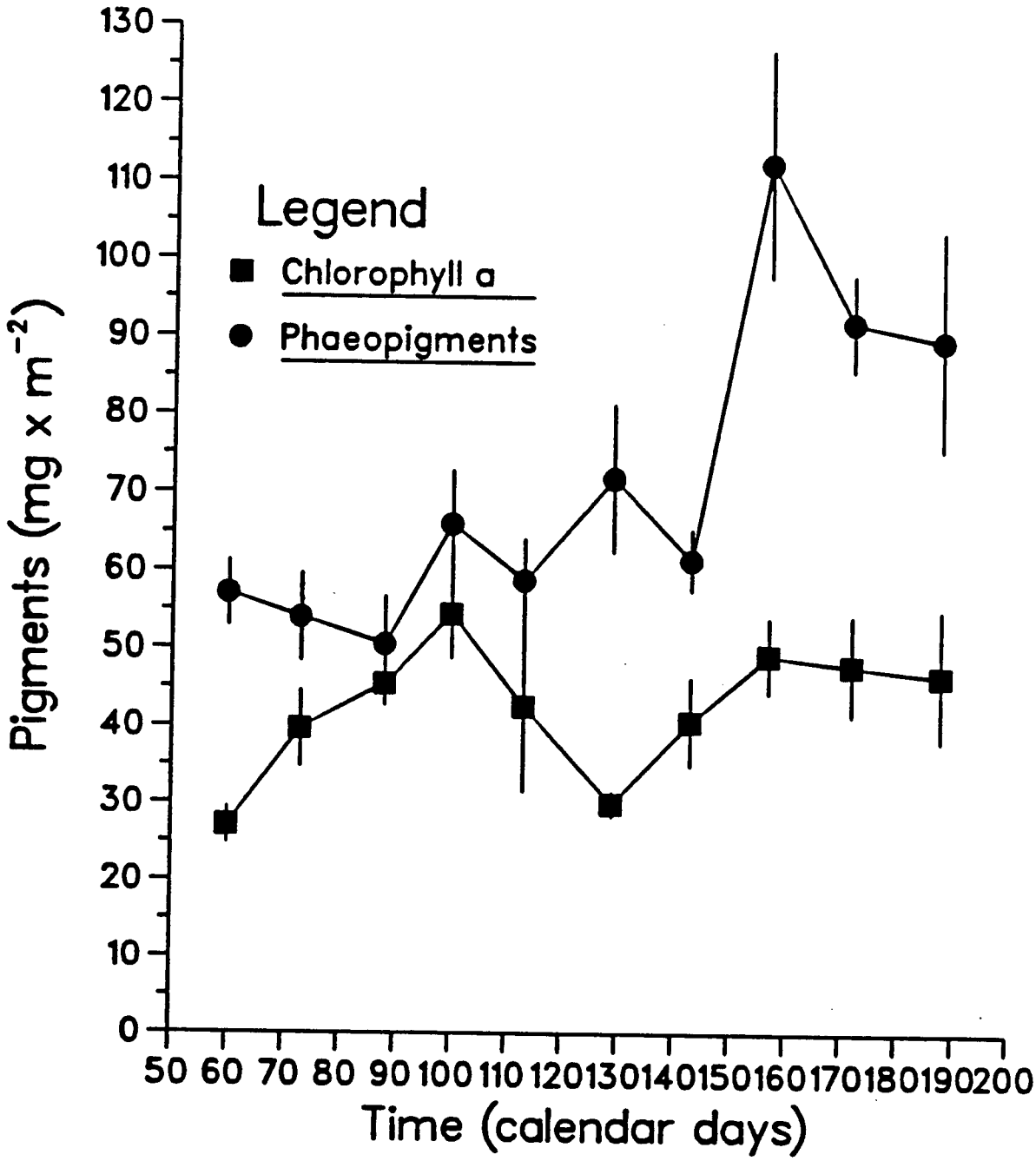

Figure 4.14: Chlorophyll *a* and phaeophytin *a* concentrations in the sediment at station H in 1985 (mean +/- 1 S.E., n=3).

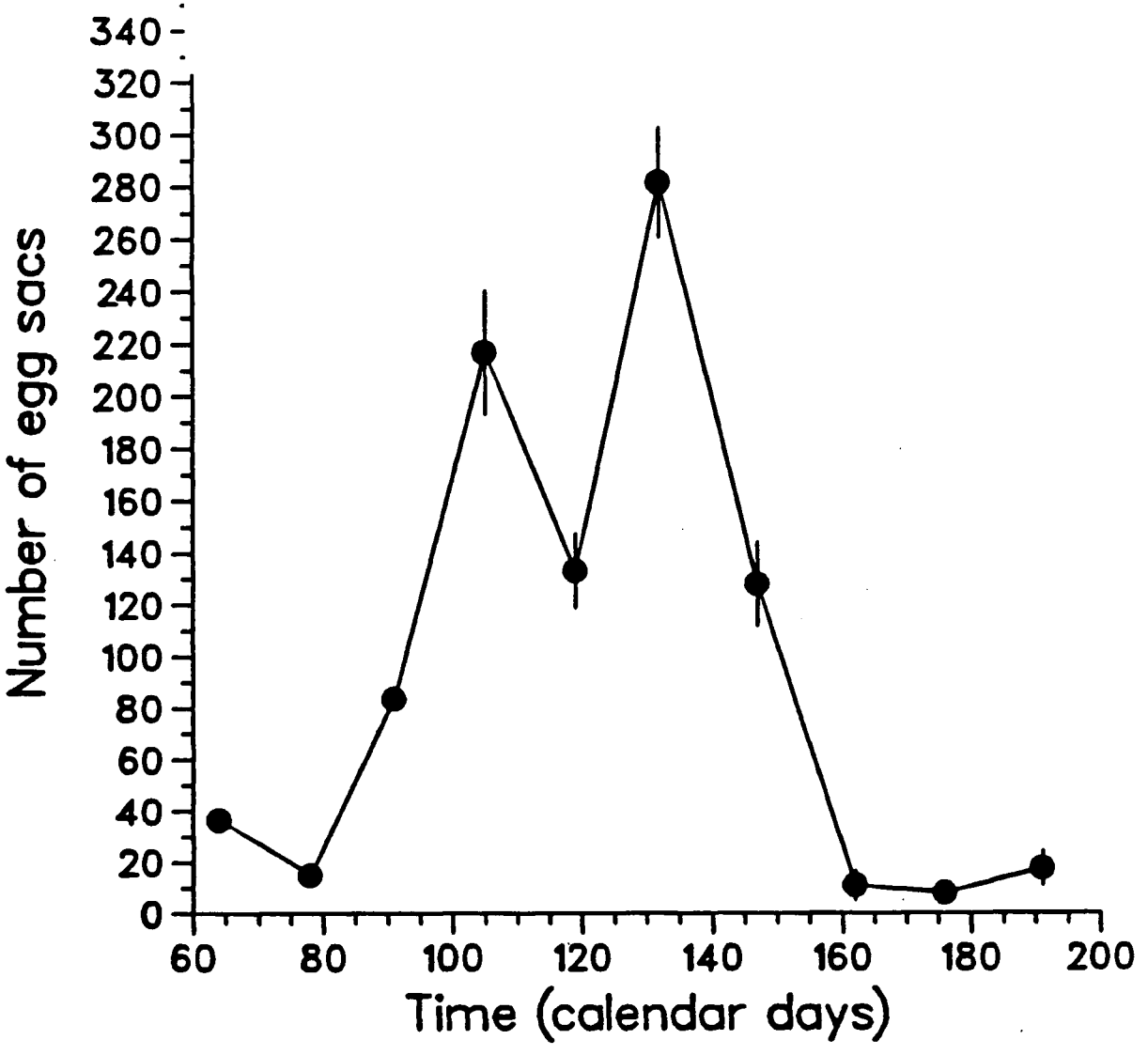

Figure 4.15: Number of harpacticoid ovisacs at level A of the sled-sampler in 1986 (mean +/- 1 S.E. n=3) (n.b. in some cases the error bars are contained within the size of the symbol).

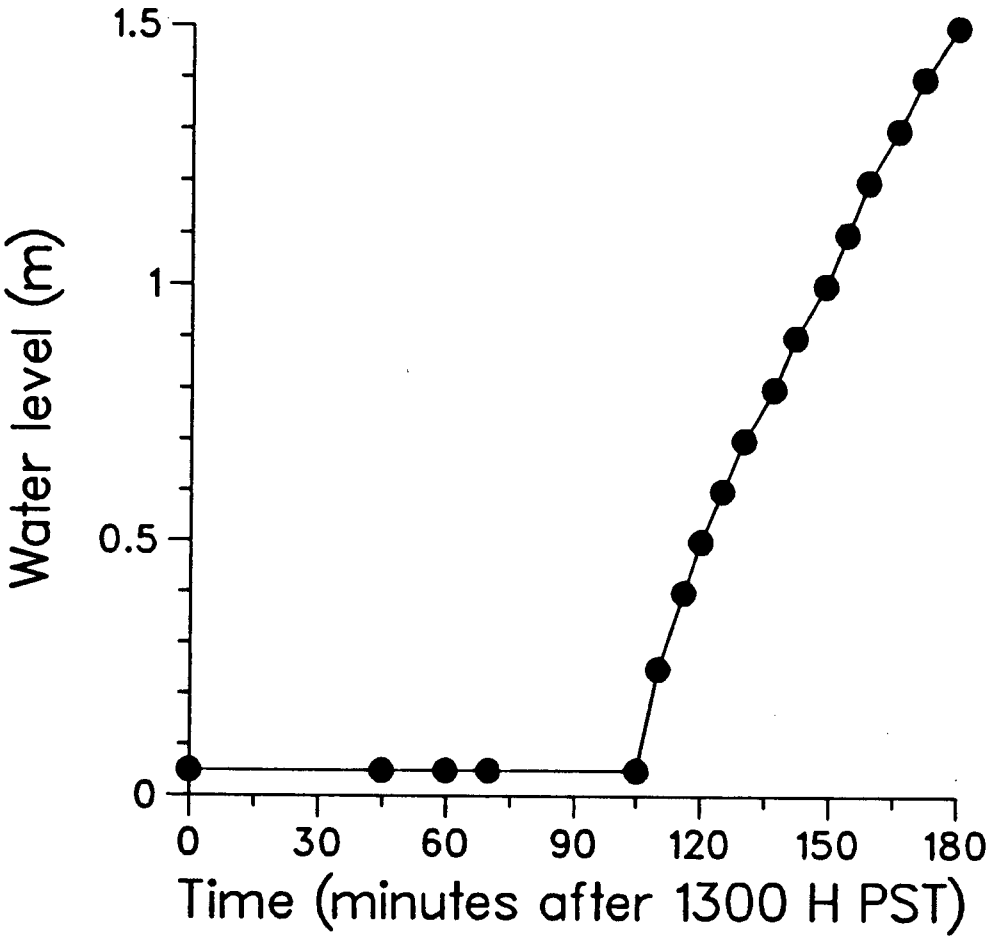

Figure 4.16: Water level over station H during flowing tide on May 24, 1986.

Discussion

The aim of this section is to describe the seasonal abundance of natant harpacticoid copepods in relation to the thermal regime in the sediment. By comparing the data of animal abundance and of the thermal regime on the tidal flat (Figs. 4.10, 4.11, 4.12, and 4.13), the broad conclusion can be made that the animal abundance and the temperature within the sediment tend to fluctuate similarly, at least for the period of increase in animal abundance. However, such a description of the link between animal abundance and thermal regime is of limited use for further advancement due to the broadness of its formulation. While this description suggests a potential physiological or trophic basis for this link, it would be difficult to verify its validity in the field. The reason for this is the asymmetry in the time-scales of the two events related: the spring increase in abundance of the harpacticoid assemblage occurs over a brief period while the seasonal increase in temperature in the sediment is a long, progressive event. If the harpacticoid blooming period happens anywhere between late-winter and mid-summer, it will always be coincidental with an increase in mean temperature in the sediment. Defining the harpacticoid increase in relation to the increase in mean temperature is then potentially heuristic on physiological or trophic grounds, but of little use in term of prediction. In this study, the thermal regime in the sediment was monitored on a fine temporal scale (1 measurement every 4 hours). A description of the natant harpacticoid seasonal abundance in relation to fine-scale temporal patterns in the thermal regime in the sediment is then possible.

Daily temperature fluctuations are apparent throughout the sampling period for both years (Figs. 4.11, 4.12, and 4.13). Only for their amplitudes, all 3 temperature time-series appear to have the same variability structure. The following detailed

description of high frequency variations of temperature in the sediment is derived from the data recorded nearer to the surface in 1986 (Fig. 4.12), which for reasons to be discussed, show the highest amplitude of variation.

From February 19 to 24 (days 50 to 55), daily downwards peaks were observed, while from March 1 and on, daily upwards peaks were observed. From February 19 to 24, lower daily tide occurred during night time; thermograph records indicate that the lower temperature values in the downwards peaks were reached when the flat was exposed during the winter night. From March 1 and on, low tides had started to occur during day time and the higher temperature values in the daily upwards peaks were reached at maximal exposure of the flat during daylight hours. This is in agreement with the results of previous studies on the thermal regime of tidal flats by Johnson (1965) and Harrison (1984). Both authors showed that when the tide falls below the level at which the flat becomes exposed during daytime, there is a heat gain in the sediment from solar radiation; when this exposure happens during night, the magnitude and direction of temperature changes in the sediment is dependent upon the atmospheric conditions (air temperature and wind) (Fig. 4.17). Another characteristic of the temperature records at station H is that the amplitude of the daily fluctuations itself has a periodicity. This is best illustrated by comparing the series of temperature peaks around March 1 (day 60), March 16 (day 75), and March 31 (day 90) (Fig. 4.12): a maximum in amplitude of the daily temperature variations is reached *ca* every 15 days. This fortnightly cycle has been described in detail by Vugts & Zimmerman (1975,1985) and Harrison (1985). These authors showed theoretically and experimentally that on M_2-dominated temperate tidal flats, the precession of the timing of the tide relative to the solar day gives rise to a beat in both the mean and amplitude of

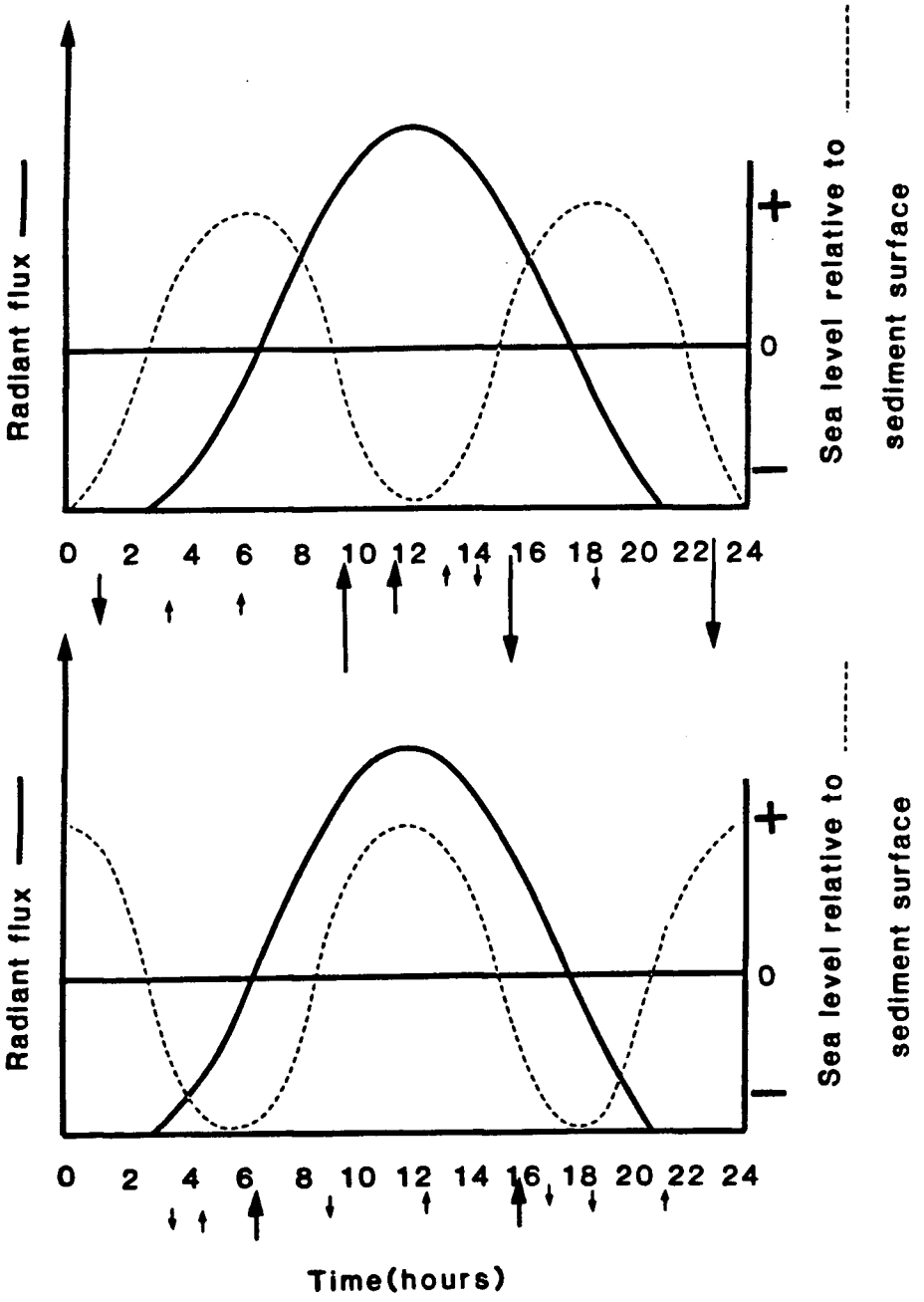

Figure 4.17: Potential effect of time of high water on the magnitude and direction of change in sediment surface temperature. The arrows indicate the direction and magnitude of temperature changes in the sediment (redrawn from Harrison (1984)).

temperature fluctuations in the water and in the sediment: this beat has a period of 14.72 d. One crucial observation in the temperature data from station H is that this fortnightly beat in mean and amplitude of temperature fluctuations only starts to become visible as sharp daily peaks at a specific time during spring. As the season progresses, the beat becomes more and more obvious, although later in the season, aperiodic fluctuations probably related to local atmospheric conditions tend to blur the signal. This increase in the daily temperature peaks can be related to the gradual increase in coincidence of the lower low waters and the daily solar zenith. In other words, the precession of the timing of the tide relative to the solar day, which is continuous, appears as an apparent fortnightly temperature beat only when lower low waters start to occur during day time. This beat in temperature, then, is a seasonal phenomenon and has a specific timing of onset. The shift of timing of lower low tides from night in winter to day in spring was recognized in the Strait of Georgia by Waldichuk (1957). This author also pointed out that the actual pattern of the shift itself is a transitory feature in the Strait: this shift varies with its own period of slightly more than 900 y.

The above description of temperature variability is directly applicable to the temperature records from 1985 (Fig. 4.11) and 1986 (deeper recording level)(Fig. 4.13) that only differ by degrees of intensity. The amplitude of temperature variations recorded deeper in the sediment (Figs. 4.11 & 4.13) is smaller than that of temperature variations recorded nearer to the surface (Fig. 4.12). This dissipation of features in temperature records with increasing depth of recording in the sediment was recognized in land soil temperature analysis (Carson 1961) as well as in previous tidal sediment temperature analysis (Johnson 1965; de Wilde & Berghuis 1979). Differences in absolute values in temperature records between the two years,

for same recording level, are attributed to differences in meteorological conditions. All temperature time-series recorded in the sediment at station H, despite differences in magnitude of amplitude caused by varying depth of recording or between year meteorological fluctuations, exhibit seasonal, daily, and intermediate-scale cycles; all temperature data sets also indicate the seasonality and the specificity of onset time of recurrent strong warming episodes in the sediment related to the interaction of the tide cycle and the daily heat cycle.

Temperature time-series were filtered according to the previously described procedures (see Methods) to emphasize the higher frequency components of variability (Figs. 4.18, 4.19, and 4.20). In 1985, 3 small individual peaks appear between February 17 (day 48) and February 26 (day 57) (Fig. 4.18). Thermograph records indicate that these peaks, although positive, do not correspond to warming episodes of the sediment. Rather, these peaks seem to be caused by the flooding of the flat with water warmer than the cooled sediment surface. A similar series of peaks is seen in 1986 filtered temperature data from February 19 (day 50) to February 24 (day 24) (Figs. 4.19 & 4.20). In both cases, the flat had been exposed during night time and accordingly cooled off; the return of relatively warmer water later in the night or early in the morning is recorded as temperature increases in the sediment. Those temperature increases not related to warming of the sediment by the sun, but instead to a return to overlaying water temperature after cooling, correspond to the daily inverted peaks already mentioned in the description of the non-filtered temperature data. When these temperature increases are over-looked, the specific timing of appearance and gradual amplification of warming events in the sediment become more obvious. In 1985 (Fig. 4.18) the first of the warming episodes in the sediment is seen as a series of pulses from March 10 (day 69) to

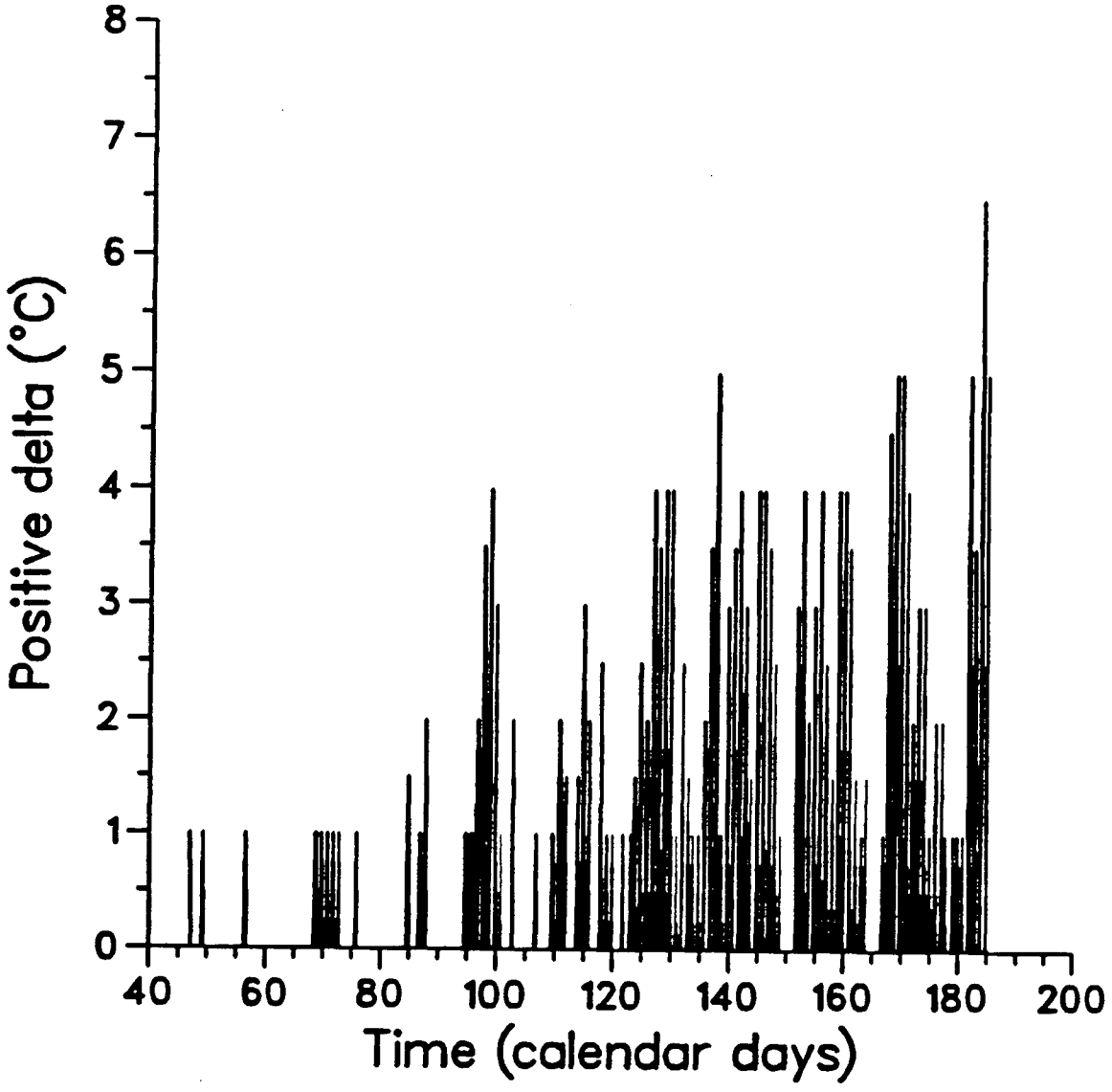

Figure 4.18: High frequency temperature fluctuations in the sediment at station H in 1985 (depth of recording: 5 cm).

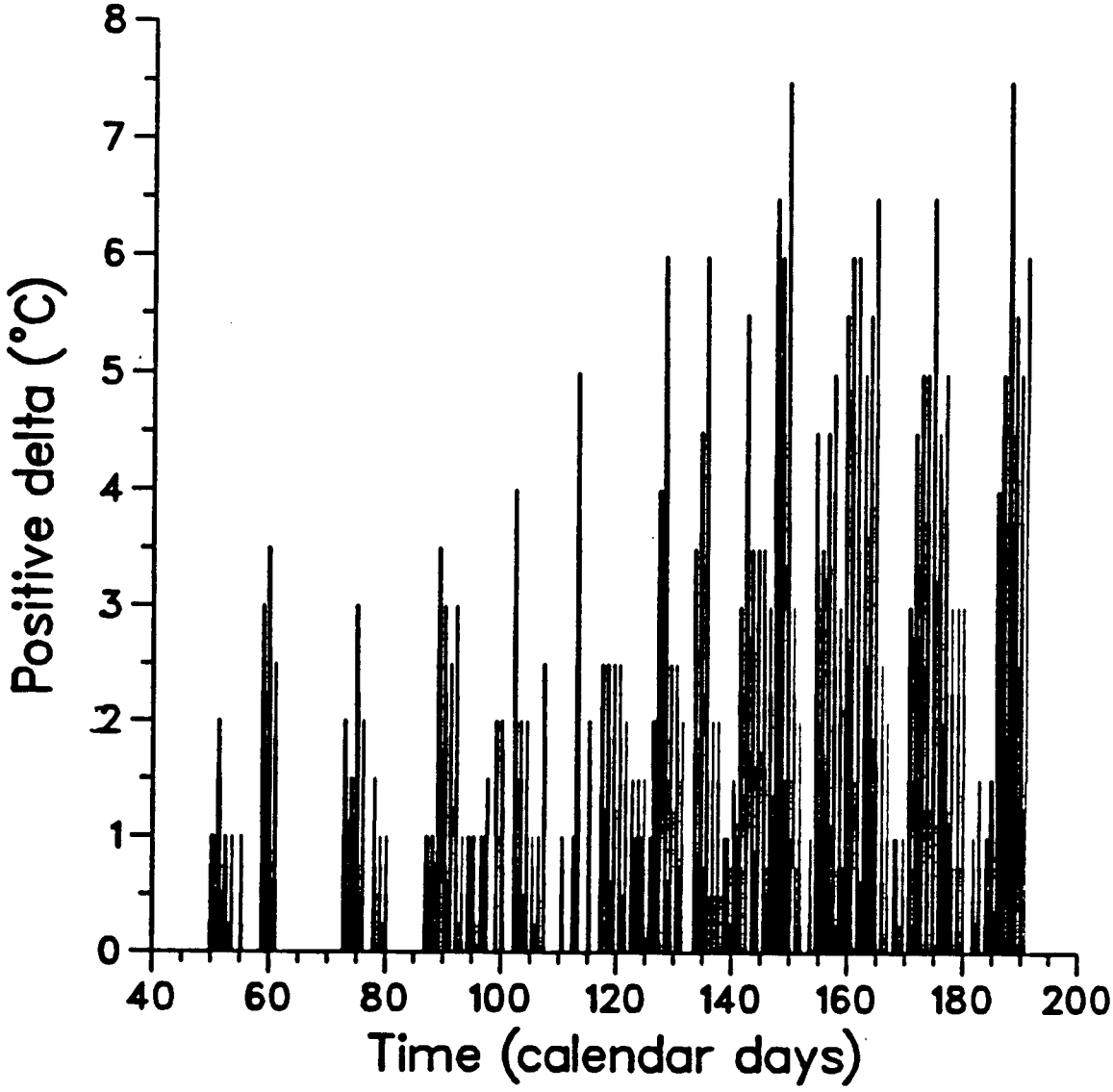

Figure 4.19: High frequency temperature fluctuations in the sediment at station H in 1986 (depth of recording: 1 cm).

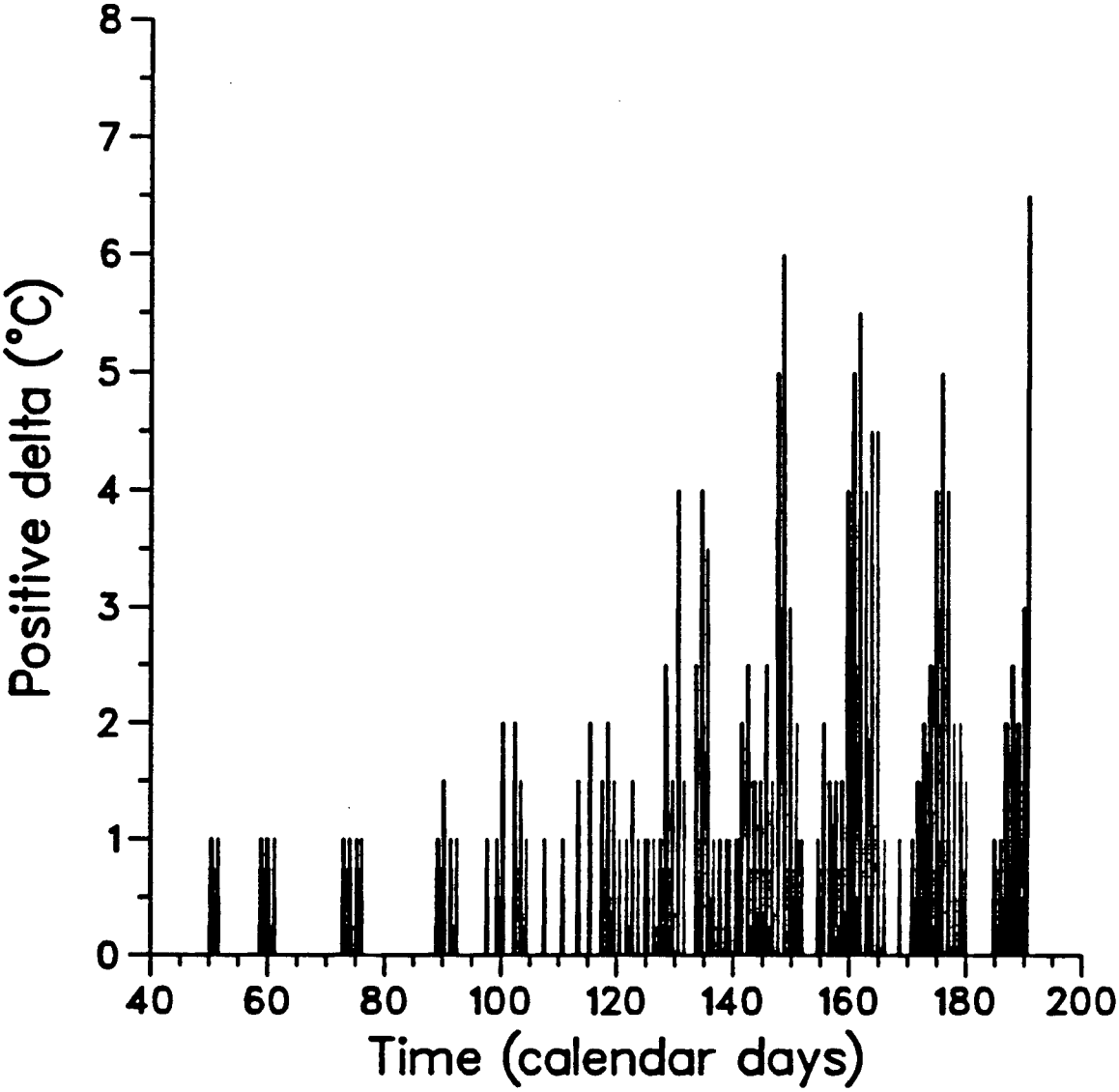

Figure 4.20: High frequency temperature fluctuations in the sediment at station H in 1986 (depth of recording: 5 cm).

16 (day 75); the second warming episode, of higher amplitude, follows from March 25 (day 84) to 29 (day 88); the third warming episode, of even higher amplitude, appears from April 4 (day 94) to 12 (day 102). In 1986 (Figs. 4.19 & 4.20) similar patterns are observed: the first warming episode occurs between February 28 (day 59) and March 2 (day 61); the second one from March 13 (day 72) to 21 (day 80); and the third one from March 27 (day 86) to April 4 (day 94). After the third warming episodes of both years, apparently aperiodic pulses tend to mask the signal, although a periodicity is still apparent. The attenuation of temperature variability with depth of recording is more apparent in the filtered data time-series: temperature pulses recorded at 5 cm in 1986 (Fig. 4.20) are clearly smaller than those recorded at 1 cm during the same year (Fig. 4.19). The filter has emphasized the higher frequency components of temperature variability and those components are the most dampened with increasing depth of record as a result of the thermal inertia of the sediment.

Sediment warming episodes and harpacticoid bloom

The natant harpacticoid assemblage under study went through its period of maximal increase from March 13 (day 72) to 29 (day 88) in 1985, and from March 5 (day 64) to 19 (78) in 1986. For both years, these blooming periods coincide with the appearance of warming episodes in the sediment (Fig. 4.21). The warming episodes have variable durations within and between years. Tide tables indicate that the observed daily temperature pulses, that make up warming episodes, only started to appear and kept appearing as long as the tide level at the port of reference (Point Atkinson) fell below 1.6 m during daytime (from 0800 H PST to 1630 H PST). This critical level is precisely the elevation of sampling station H above chart datum as

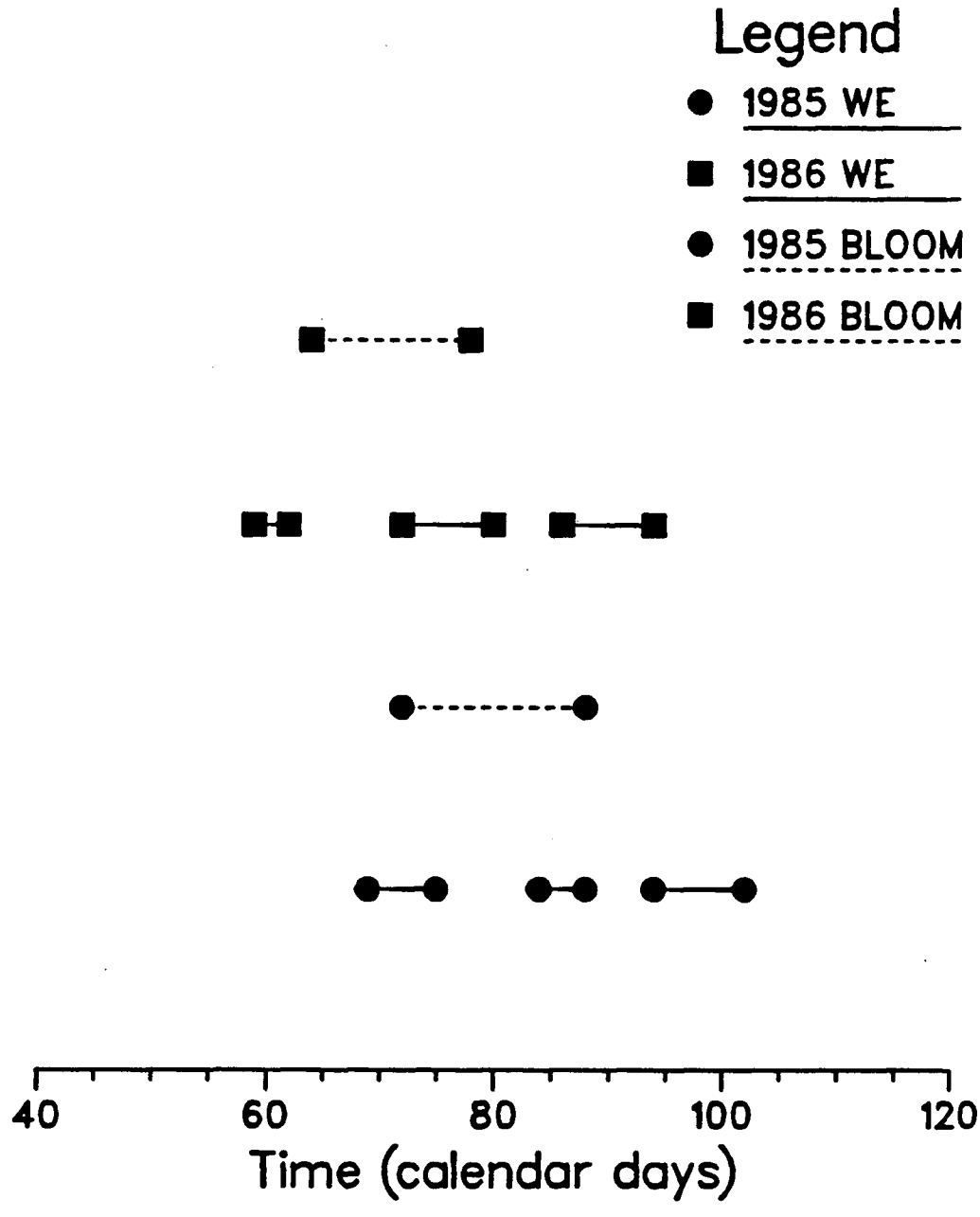

Figure 4.21: Timing and duration of initial warming episodes (WE) in the sediment and of natant harpacticoid blooming periods (BLOOM) at station H in 1985 and 1986.

determined earlier (Fig. 4.16). This suggests that a constraint must be added in addition to the shift in the pattern of exposure of the flat (lower low tide during night in winter; lower low tides during daytime in summer) in order to define the appearance and recurrence of warming episodes in the sediment: the lower low waters must fall during daytime *and* below 1.6 m at the port of reference. This critical level is equal to the elevation of the station; this suggests that indeed the thermal inertia of water is great and that the station has to be minimally covered to record warming episodes in the sediment. However, contrary to what the above data might suggest, station H was never observed to be totally dry, even during the lowest tides of the years; a residual slick of *ca.* 5 cm was always remaining before the onset of the following flood. This slick was apparently retained by the eelgrass mat. In 1985 and 1986, the warming episodes, once initiated, seemed to recur on a fortnightly basis. For both years, the first low waters below 1.6 m (port of reference) during daytime were followed by similar low waters every 2 weeks for at least the next 4 weeks. This would explain the consistent coincidence of the fortnightly lower low waters and the warming episodes. However, the warming episodes in the sediment need not be fortnightly themselves. Inspection of tide tables for years other than 1986 and 1985 indicate that the first lower low waters to fall below 1.6 m (port of reference) during daytime (0800 H - 1630 H PST) are not always followed by similar lower low waters two weeks later. Early warming episodes in the sediment could then be separated by more than 2 weeks in early spring in some years.

Warming episodes in the sediment started to occur 10 days earlier in 1986 than in 1985 (Fig. 4.21). The onset of the natant harpacticoid blooming periods also appear to be phased by a similar period of time between the two years. The

temperature data were collected every 4 hours; those for the natant harpacticoid assemblage, every two weeks. A phasing of 10 days between corresponding features in the temperature time-series can reasonably be considered as significant; a similar phasing between the harpacticoid bloom onsets can not be considered significant. Nonetheless, it may suggest that the natant harpacticoid bloom could be linked with a specific (the second) warming episode of the early spring ones.

The above results suggest that the link between natant harpacticoid abundance and the thermal regime in the sediment be defined in terms of the coincidence of the animal spring bloom and the onset of recurrent, although not necessarily periodic, warming episodes in the sediment. In 1986, the blooming period extended from day 64 to 78, while the first and second warming events were respectively observed from day 59 to 61, and from day 72 to 80. In 1985, the blooming period extended from day 72 to 88, while the first and second warming events were respectively observed from day 69 to 75, and from day 84 to 88. Because of the overlap of the blooming periods during both years with the second warming event, it may be suggested, albeit quite tentatively, that the harpacticoid bloom could coincide with the second of the early warming episodes. This definition of the link between harpacticoid abundance and temperature is based on variability components of the thermal regime with periods much shorter than the seasonal mean temperature trend. The similarity of the time scales of the initial warming episodes and of the harpacticoid blooming period makes the above definition more robust than one linking harpacticoid abundance with the seasonal trend in mean temperature: its applicability to other harpacticoid species or assemblages of species, other tidal flats, other times, is readily verifiable. Future research effort in this direction should aim at improving this proposed definition of the link between harpacticoid

abundance and thermal regime by increasing the correspondence of the sampling time scale for the harpacticoids with that for the reference signature in the thermal regime. To achieve this, the abundance of the natant harpacticoid assemblage would need to be monitored on a time-scale allowing the identification of small between year differences in blooming period onset; the co-variance between the harpacticoid blooming period and any specific warming episodes could then be more rigorously evaluated.

The pattern of abundance of the natant harpacticoid assemblage after the spring bloom is not addressed in this study. As seen above (Fig. 4.10), the spring maximum of abundance is followed by a period of most rapid decline. The factors responsible for this decline are probably varied, of both biological and environmental origin, and coupled in intricate fashions. The identification and study of these factors is likely to be eased if some of the variability in the seasonal abundance of natant harpacticoids can be accounted for by specific environmental signals such as warming episodes in the sediment as suggested in this study.

As pointed out earlier, the reason(s) for the existence of a link between harpacticoid abundance and temperature in the sediment remains rather speculative. Results of the study of chlorophyll *a* in the sediment show that the pigment concentration (in mg/m^2) ranged from 27 to 54. Those values are intermediate between those reported by Harrison (1981) on Sturgeon Bank (32 to 186 mg/m^2, calculated with 5 cm deep cores) and those reported by Bawden *et al.* (1973) on Roberts Bank (62.7 to 423.7 mg/m^2, calculated with 1 to 2 cm deep cores). In 1985, the harpacticoid bloom occurred between March 13 (day 72) and 29 (day 88) (Fig. 4.10). In the same year, the chlorophyll *a* concentration in the sediment doubled between March 1 (day 60) and April 10 (day 100) (Fig. 4.14). This overlap could

be taken as suggesting a trophic basis for the link between temperature and animal abundance. However, the lack of a clear lag between pigment increase and animal increase requires a careful consideration of this overlap. A possible reason for the lack of a distinct relationship between pigment and animal abundance is that biomass of pigment could be an inappropriate measurement of the availability of food for harpacticoids: instead, rates of production could have indicated a sharp increase in productivity without being necessarily accompanied by an equivalent increase of concentration of pigments. Also, harpacticoids may feed on various food sources, and a monitoring of chlorophyll *a* does not account for the variability in time of other potential food sources. As summarized by Fenchel (1978), temporal patterns of abundance of meiofauna are probably largely controlled by the increase in photosynthetic production in the spring, reproductive potential of the different groups, and by predation. Obtaining more than an elementary description of the covariability of those factors and the temporal variability of harpacticoid copepod abundance would require an independent and very involved research program. As for the phaeopigments, a gradual increase in concentration was observed during the sampling period in 1985. Harrison (1981) observed a similar increase in phaeopigments and suggested that it might be associated with the decay of filamentous diatoms accumulating on the sediment surface. Similar accumulation of filamentous diatoms was observed on the sediment at station H during the course of this study, and it is proposed this might account for the increase in phaeopigments. However, settling of chlorophyllous material from the water column could also account for some of this accumulation of phaeopigments.

In 1986, the number of ovisacs in level A of the sled-sampler increased from 15 on March 19 (day 78) to 217 on April 15 (day 105) (Fig. 4.15). In the same

year, the harpacticoid blooming period occurred between March 5 (day 64) and March 19 (day 78) (Fig. 4.10). This increase in the abundance of ovisacs follows the bloom and must be interpreted as the offsprings of the year-class, and not as its origin. However, the animals appearing during the blooming period must come from ovisacs. As it is, ovisacs were observed before the blooming period, albeit is small quantity. It may then be suggested that the low abundance of eggs in winter is at the origin of the spring bloom animals, and that later increase in egg number is the year-class production. Obviously then, a year-round tracking of the abundance of ovisacs would be required to state more clearly on the potential effect of temperature fluctuations on the harpacticoid development schedule.

One aspect of the sampling must be discussed at this point, namely the sampling of harpacticoids in the water column and the measurement of temperature in the sediment. The initial reason for doing this was technical: it was obvious that a thermograph left at the surface of the sediment would collect drifting plants and become heavily fouled, which could cause serious measurements errors. Inserting the thermographs in the sediment seemed the ideal simple solution to alleviate this problem. The second reason for considering as relevant the measurement of temperature in the sediment is that the bulk of the natant harpacticoid population is very near the bottom and definitely close to the sediment surface at low tide. Although natant, the harpactocoid taxa considered may also spend some time on the sediment (as reviewed by Hicks & Coull 1983), which only makes the temperature in the sediment more relevent to them. Lastly, the sediment may actually be acting as a filter which removes aperiodic rapid temperature fluctuations; these fluctuations could otherwise blur the periodic components and make difficult the identification of a specific signature to be related to the animal blooming period.

4.4 Chapter Summary

In this chapter, the temporal and the spatial variability of an assemblage of species of harpacticoid copepods was investigated. By sampling the animals on a fine vertical scale, persistent and specific patterns of distribution were observed in the water column. Importantly, knowledge of the shape of these distributions allowed a quantitative estimation of the natant harpacticoid abundance. Comparing absolute abundances and indices of abundance justified the use of an index of abundance to track the temporal patterns in the abundance of harpacticoids. Once it was realized that natant harpacticoid copepods were abundant in the water column, and that their abundance could be quantitatively expressed, it became possible to identify the vernal blooming period; the vernal harpacticoid bloom was defined as that period of most rapid increase of abundance (as identified with the sampling time-scale used). This blooming period was related with the appearance of warming episodes in the sediment. The occurrence of those warming episodes in the sediment is seasonal; the beginning of the period during which those warming episodes will be observed is not constant between years. The timing of onset of warming episodes of the sediment varied by 10 days between the two sampling years. There is indication that the onset of the blooming periods of harpacticoids may have varied by a similar amount of time between the two years. The association of the harpacticoid bloom with the appearance of warming episodes seems very plausible; it also provides a more robust basis for the definition of the link between harpacticoid abundance and thermal regime. The association of the harpacticoid bloom with any specific warming episode (the second?) is much more tentative owing to the difference in time-scales used to describe both. However, the harpacticoid bloom coinciding with the second warming episode could be possible.

Chapter 5

Early Near-Shore Life and Survival of Chum Salmon

In the previous chapters, the spatial and temporal distributions of chum salmon and harpacticoid copepods were described. Those descriptions were considered prerequisites for the identification of environment-coupled mechanisms potentially regulating the abundance of the fish. In this chapter, the results of selected studies on some aspects of the ecology of juvenile chum salmon are briefly reviewed. Adding information on the spatio-temporal distribution of natant harpacticoid copepods from the present study to those previous results, provides a basis for discussing regulation of salmon abundance in estuaries in an original manner.

5.1 Introduction

Stocks of chum salmon in British Columbia are known to fluctuate considerably in abundance (Hoar 1951; Wickett 1958). Between 1965 and 1969, the estimated number of Fraser River chum salmon caught in Johnstone Strait ranged from 0 to 228 000, while 10 000 to 196 000 chum salmon were caught in the Fraser River proper; these marked fluctuations in abundance have not been satisfactorily accounted for (Beacham & Starr 1982). To investigate environment coupled mech-

anisms that may regulate fish abundance, it is convenient to divide the fish's life cycle in stages, and identify the particular risks of mortality at each stage. Early life stage in nearshore regions is regarded by many as a critical time in the life of the chum salmon when the strength of the year-class may substantially be altered. For these reasons, a more thorough understanding of the biological and physical processes that affect individual growth and production of chum salmon in estuaries and near-shore nursery grounds is a central goal in fisheries research (Neave 1953; Wickett 1958; Volk *et al.* 1984).

Central in any discussion on the ecology of chum salmon is the fact that mortality tends to be high in early life (reviewed by Ricker 1976), and that this mortality appears to be caused by predation and is size-selective (Parker 1966, 1971; Hargreaves & LeBrasseur 1986). The latter authors showed that yearling coho salmon *O. kisutch* (112–130 mm FL) consumed the smaller fishes within an available array of prey ranging in size from 43 to 63 mm (FL). Parker (1966, 1971) had already suggested that predatory mortality of chum salmon was size-dependent, and that outgrowing their predators would reduce chum salmon mortality. The ponderal growth of a juvenile fish can be represented by

$$\frac{dW(t)}{dt} = GW(t) \ , \tag{5.1}$$

where W=ponderal size, t=time, G=growth coefficient.

From eq. 5.1, the time (T) to grow through a given size interval $W_1 - W_2$ can be derived:

$$T = \frac{lnW_2/W_1}{G} \ .$$

For a fixed size interval, T will vary with G (Fig. 5.1) that is, the faster the growth of the fish, the briefer the time it spends in this size range where size-selective

predation is acting. This is commonly referred to as predation field escapement (e.g. Cushing 1973). Since G can be written as (Parsons *et al.* 1984 a)

$$G = aR - C\,,$$

(where a=assimilation efficiency; R=ration; C=sum of metabolic costs)

it can be concluded that the time to grow through a given size interval will be minimal when aR is maximal and C is minimal. The mortality rate of fish can be represented as

$$\frac{dN(t)}{dt} = -ZN(t)\,, \tag{5.2}$$

where N=number of fishes; t=time; Z=mortality coefficient.

Integrating eq. 5.2,

$$N_t = N_o e^{-Zt}\,, \tag{5.3}$$

where N_o=initial number of fishes.

If mortality of fishes is only, or mainly, effective over a certain size range, and if the fishes are within the limits of this range for variable time, survival will be variable. Variations of the growth coefficient resulting from variations in ration, assimilation efficiency, or metabolic costs, can then cause variations in fish survival as they result in variable time of exposure to size-selective predation within a certain size range.

There is evidence that harpacticoid copepods provide chum salmon with a high growth coefficient. Volk *et al.* (1984) fed the harpacticoid copepod *Tigriopus californicus* to juvenile chum salmon and food conversion efficiency K ($K = G/R \times 100, G \,\&\, R$ both in % body weight/day (b.w./d)) was much higher than for other food taxa. When fed the amphipod *Paramorea mohri* and the calanoid copepod

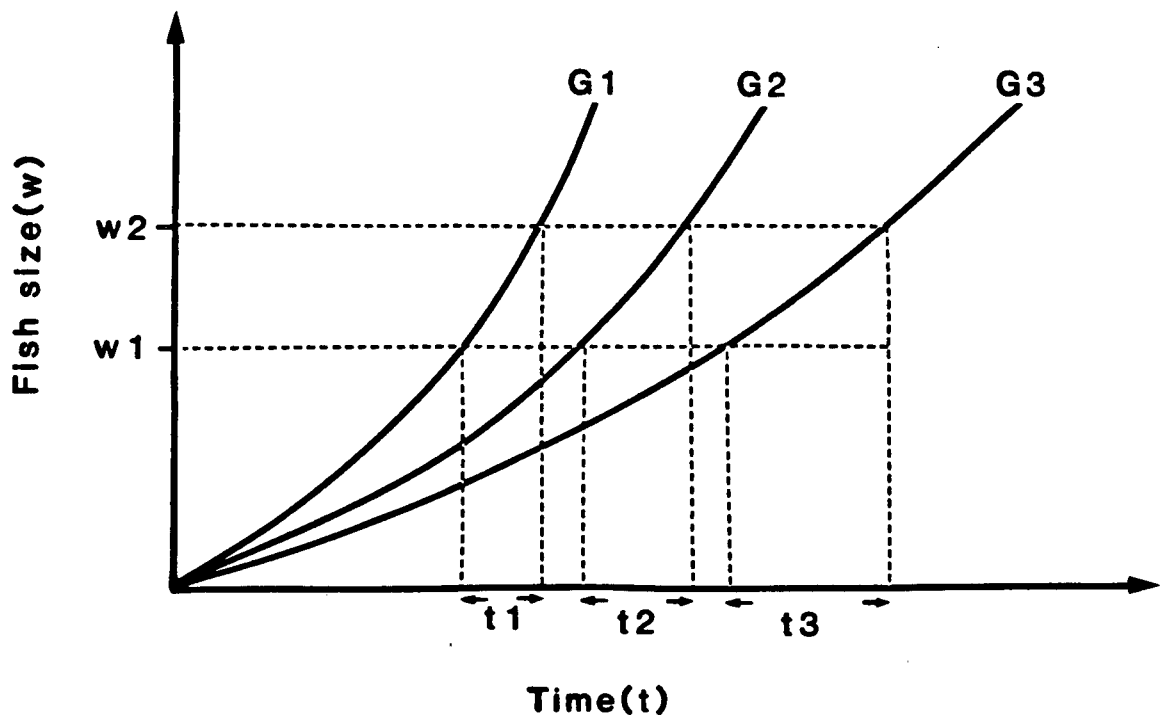

Figure 5.1: Variation of time to grow through a given size interval $W_1 - W_2$ for various growth coefficients (G).

Pseudocalanus minutus, the salmons' maximum food conversion efficiencies were 16.3 and 20% for rations of 9.8 and 9.5% b.w./d respectively. When the fish were fed the harpacticoid, the maximum food conversion efficiency was 40.1% for a ration of 5.7% b.w./d. The authors concluded that a high assimilation efficiency and a low cost of capture could explain the high food conversion efficiency of chum salmon feeding on harpacticoids. Similar high food conversion efficiencies for other species of harpacticoid copepods could justify why harpacticoid copepods have been considered a better nutritional source than many other meiobenthic organisms (Hicks & Coull 1983).

For the remainder of this chapter, the life cycle of the chum salmon can be simplified by making the following assumptions, based on the aforementioned evidence. First, most of the mortality of the fish will be assumed to occur in early near-shore life, be caused by predation (assumed constant), and be size-selective. It will also be assumed that a substantial fraction of the Fraser River chum salmon stock does feed on harpacticoid copepods in near-shore nursery grounds, and that each fish spends a substantial amount of time feeding on harpacticoid copepods (as discussed in chapter 3).

As discussed in chapter 4, the assemblage of natant harpacticoid copepods on which chum salmon preferentially feeds has a clear seasonality of abundance. The abundance of chum salmon on the tidal flats appeared to be equally seasonal. If the relative timing in the seasonal cycle of abundance of the fish and the harpacticoid copepods varies, the ratio of abundance of both will also vary. The overlap of harpacticoid and chum salmon populations on the flat is determined by extrinsic and intrinsic factors. The extrinsic factors are those that determine the timing of the downstream migration of the fishes and the onset of the harpacticoid bloom.

These extrinsic factors have nothing to do with fact that there exists a trophic relationship between salmon and harpacticoids. The intrinsic factors are the results of the trophic interactions that determine the growth and/or death rates of both populations. Extrinsic and intrinsic factors are intimately linked. If extrinsic factors are such that the bulk of the outmigrating chum salmon starts feeding on a poorly developed harpacticoid population, the prey population density may never be high as it is grazed faster than it can increase. The amount of food available per fish would be low. Similarly, if the extrinsic factors are such that the bulk of the salmon population can feed on the harpacticoid population only after it has sharply declined, the ration available per fish will be low. The maximum ration of harpacticoids available for the maximum number of fishes will then occur at some intermediate degree of overlapping of the 2 pulses. This variation in overlapping of predator and prey with resulting variation in ration available has been described by Cushing (1975) (Fig. 5.2). Although developed for herring, Cushing's description of the effect of varying degree of overlap of predator and prey on feeding success of predator, the concept of variation in the timing of phasing of predator and prey seems relevant for any species. As it is, the proposition that variation in overlap of predators and harpacticoid copepods could affect the time course of the prey population abundance was put forward by Muus (1967). Muus suggested that an early warming of the shallow waters allows the harpacticoid to take an early lead over the consumers. Variations in the degree of phasing of chum salmon and harpacticoid copepods could then result in variations of survival of the fish for reasons previously discussed. Since the abundance of both chum salmon and harpacticoid copepods on the flat have been shown to be transitory, an index of the degree of phasing of both could be obtained by measuring the time between well identified

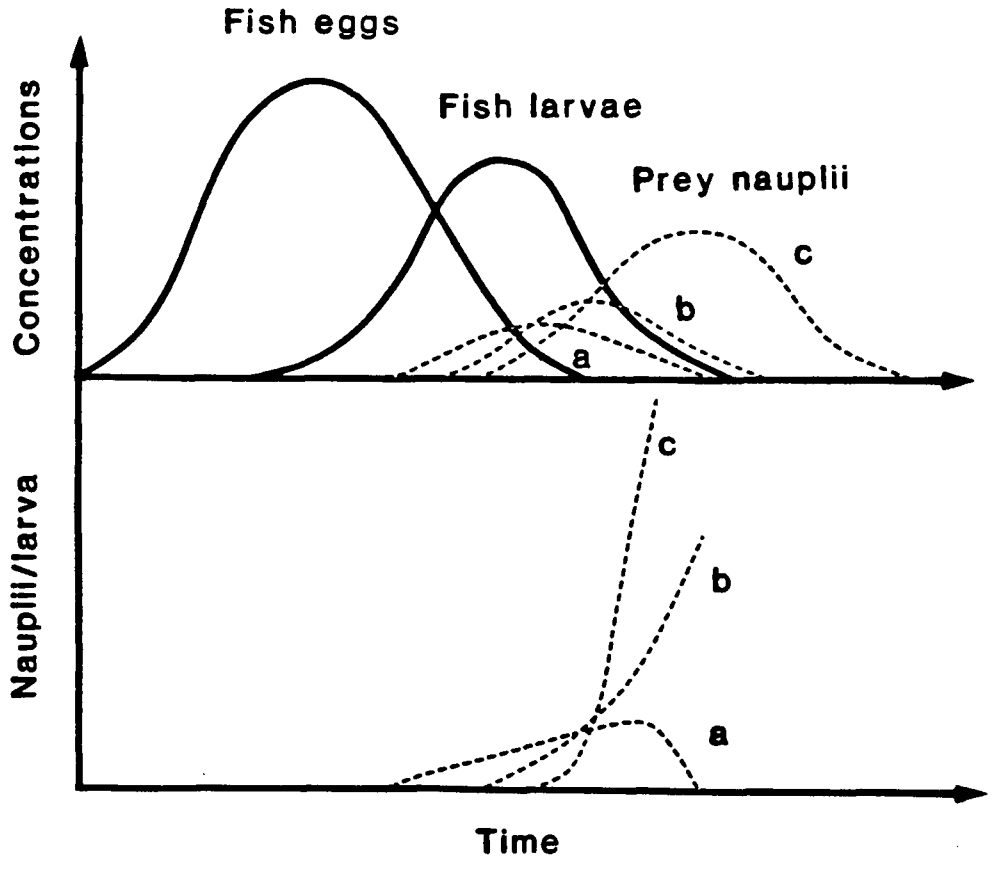

Figure 5.2: The match or mismatch of larval production to that of their larval food. The number of nauplii/larva represents the degree of feeding success. The three curves represent three conditions of copepod nauplii production and hence three conditions of feeding success, $a < b < c$ (from Cushing 1975).

and consistent signatures in respective abundance time-series. Ideally, this index of abundance would be available for many years with concurrent records of juvenile salmon survival. In the Fraser River, the abundance of outmigrating chum salmon has been monitored at Mission City, 80 km upstream from Roberts Bank. Daily sampling of the number of outmigrant chum salmon during the duration of the migration season provides an estimate of the fish's migration pattern (Fig. 5.3). From the daily patterns of outmigrant salmon migration, the median date of downstream migration at Mission City was obtained (Table 5.1). The median date of downstream migration at Mission was taken as an index of abundance of chum salmon on Roberts Bank. This assumes the existence of a consistent relationship between the temporal patterns of salmon abundance at Mission and on Roberts Bank. In chapter 3, evidence was provided that the abundance of chum salmon on Roberts Bank is characterized by a period of highest density. The salmon counts at Mission City indicate that the downstream migration also has a period of highest activity. Assuming that the periods of highest downstream migration activity at Mission City and of highest density on Roberts Bank could be related, albeit with a certain lag, is probably reasonable due to the already mentioned preference of chum salmon for salt water which translates into rapid downstream migration, and to the relative proximity of Mission City and Roberts Bank. However, no statistical verification of this assumption is possible with the extant data of abundance of chum salmon on Roberts Bank. If data on salmon abundance on Roberts Bank from various sources all indicate the transitory nature of the salmon temporal distribution on the flat (this study; Gordon & Levings 1984; Conlin *et al.* 1981), grouping them to obtain sufficient data for statistical analysis would not be reasonable because of the variations in sampling techniques and frequency between the different studies.

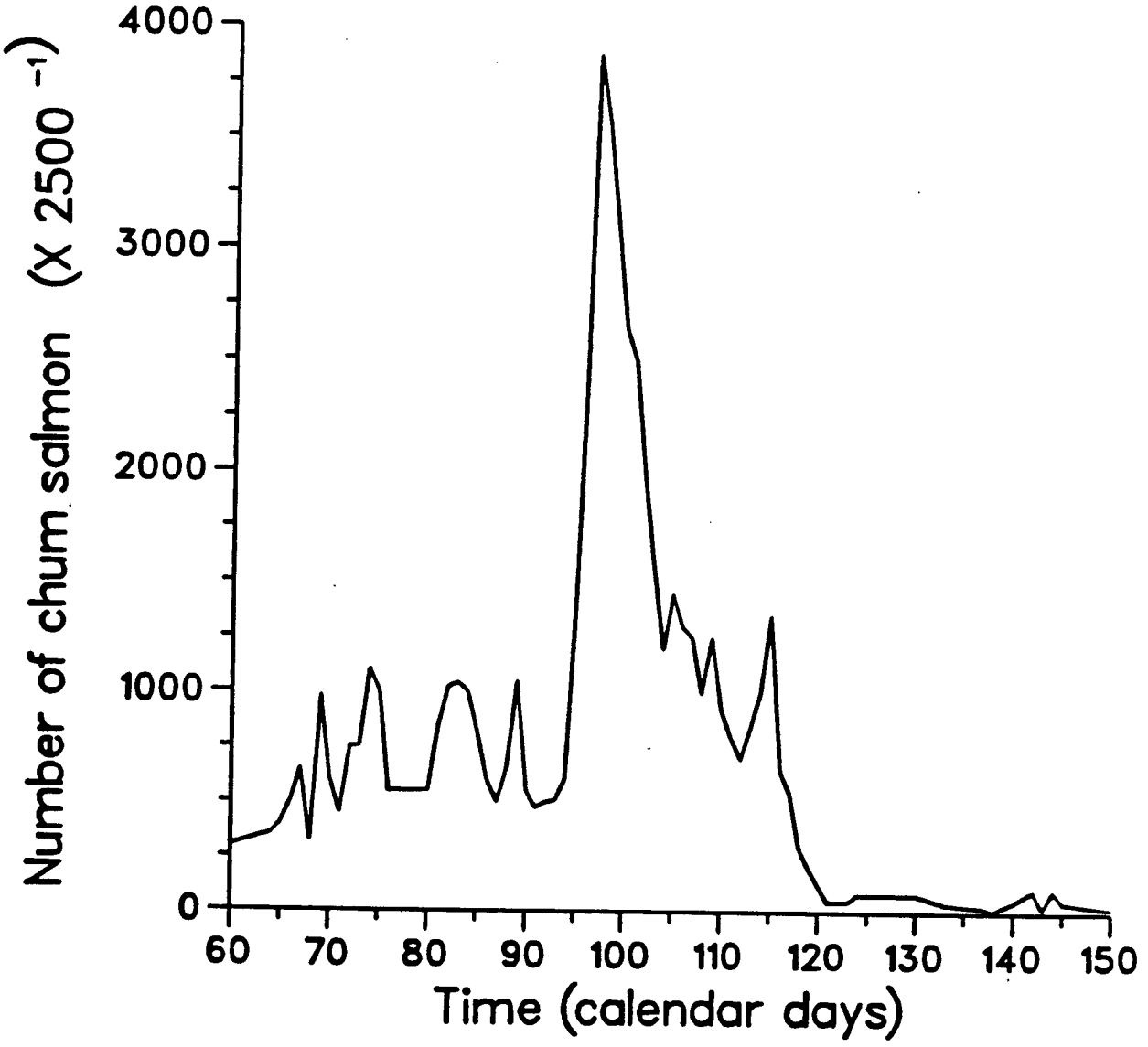

Figure 5.3: Daily abundance of outmigrant Fraser River chum salmon at Mission City in 1972 (provided by the Department of Fisheries & Oceans, Canada).

Then, the median date of downstream migration at Mission City is considered only as an index of abundance of chum salmon on Roberts Bank, and the particular relationship between this index and actual maximum of abundance of salmon on the flat remains to be further investigated along the following lines. The variability in this lag is likely to increase as the lag itself increases. However, a low variability in this lag must be assumed for the relationship between specific patterns in the abundance of salmon at Mission City and on Roberts Bank to be meaningful in the model. With a lag variability assumed small, it is likely that the feature in the temporal abundance of fish on the flat to be linked with the median date of downstream migration at Mission, should be the first peak of abundance instead of the second (Fig. 3.3). In 1985 and 1986, the first salmon peaks on Roberts Bank were respectively observed on days 100 and 105, while the second peaks occured more than 40 days later. Since the median date of downstream migration at Mission ranged from days 96 to 119 (Table 5.1) in the years for which data are available, the shortest lag is obtained with the first peak.

An historical index of abundance of natant harpacticoid copepods on Roberts Bank was then required to match the historical index of abundance of chum salmon on Roberts Bank provided by the historical records of downstream migration at Mission. As discussed in chapter 4, a pattern in the seasonal abundance of natant harpacticoid which seemed to represent a consistent signature was the timing of blooming period onset. This blooming period onset has been related to the appearance of warming episodes in the sediment, and there was indication that it may have been linked with the second of the warming events. Warming events in the sediment on Robert Bank have been proved to occur when the tide level on the flat would fall below 1.6 m at the port of reference between 0800H PST and

1630H PST. The date at which the tide level at the port of reference (Point Atkinson) fell to or below 1.6 m for the second time of the year between 0800H PST and 1630H PST was determined by inspection of the Canadian Hydrographic Tide Tables. This date was then taken to represent the onset of the natant harpacticoid blooming period. One assumption must be made here, namely that the various taxa in the natant harpacticoid assemblage appear in a consistent temporal succession. Only then can the timing of the pulse of the natant harpacticoid assemblage (mostly composed of *Tisbe* spp.) be considered as an indication of the timing of appearance of *H. uniremis* and *Z. aurelii*. The difference in days between the median date of downstream migration of chum salmon at Mission and the date of the hindcasted natant harpacticoid blooming period onset was defined as a phasing index ($\Delta\Theta$) which gives a measure of the overlap of salmons and harpacticoids on Roberts Bank (Table 5.1). The median date of downstream migration varied little over the years (range: 23 days; coefficient of variation: 5.2) when compared to the hindcasted bloom onset date (range: 36 days; coefficient of variation: 17.4). The extremes of median date of downstream migration of chum salmon at Mission did not correspond to the extremes of phasing index. The earliest date of median downstream migration (April 6, 1976)) and the latest date of downstream migration (April 28, 1971) have corresponding phasing indices of 29 days and 55 days respectively; the smallest phasing index is for 1980 (17 days), and the highest, for 1974 (65 days). The earliest hindcasted bloom onset occurred in 1970 (February 16), and the latest, in 1980 (March 24). The year with the latest hindcasted bloom onset is also the year with the smallest phasing index (1980). During the year with the highest phasing index (1974), the hindcasted bloom occured only one day after the earliest hindcasted bloom of all (1970) (day 48 in 1974; day 47 in 1970).

Broodyear	Mission_{50}		Bloom		$\Delta\Theta$	% Survival (DFO)
	Date	Day #	Date	Day #		
1965	April 17	107	February 24	55	52	31.0
66	April 24	114	March 14	73	41	31.4
67	April 20	111	March 3	62	49	14.3
68	April 17	107	February 21	52	55	52.0
69	April 18	108	February 26	57	51	33.0
1970	April 17	107	February 16	47	60	32.4
71	April 28	119	March 4	64	55	27.0
72	April 21	111	February 21	52	59	24.5
73	April 16	106	February 26	57	49	22.5
74	April 23	113	February 17	48	65	34.8
75	April 11	102	March 5	65	37	36.8
76	April 6	96	March 8	67	29	12.8
77	April 13	103	March 12	71	32	28.2
78	April 22	112	March 17	76	36	35.4
79	April 13	104	March 18	78	26	29.7
1980	April 10	100	March 24	83	17	15.1
81	April 16	106	March 16	75	31	19.4

Table 5.1: Median date of chum salmon downstream migration at Mission City (Mission_{50}), date of hindcasted natant harpacticoid bloom onset at station H on Roberts Bank (Bloom), phasing index ($\Delta\Theta$), and juvenile-to-adult chum salmon survival (% Survival (DFO)).

This indicates that the variations in the phasing index are more closely associated with the variations in the hindcasted dates of harpacticoid bloom onset than with variations in median dates of downstream migration of salmon. This was expected, since the coefficient of variation of hindcasted blooming dates proved to be larger than that of median date of downstream migration. Also, Table 5.1 indicates that the actual value of the phasing index for each year is a bivariate parameter, in that it results from the difference in timing of two events with independent degrees of variability.

Data on juvenile-to-adult survival of Fraser River chum salmon were obtained to be related to the hindcasted phasing index of chum salmon and natant harpacticoid copepods on Roberts Bank (Table 5.1). These data on survival represent the ratio of returning adults to the actual count of outmigrant juvenile salmons during a fixed counting effort, and as such are an index of survival. The index of survival was plotted *versus* the hindcasted phasing index for years 1965 to 1981 (Figs. 5.4, 5.5, and 5.6). When the odd and even broodyears are grouped (Fig. 5.4), no particular structure is evident in the plot, except perhaps for the suggestion of a monotonic increase in survival index with an increase of phasing index. However, this is not what would be expected if the survival were to optimize at some intermediate value of index of phasing. One reason why no optimization of survival is observed at intermediate value of phasing index could be that the available data set does not bracket all possible values of phasing index and consequently, the possible decline in survival with increasing phasing could simply be absent from the data. Another possible reason is that grouping data for odd and even broodyears could blur possible relationships between phasing and survival indices because of the presence of pink salmon (*O. gorbuscha*) every other year. In

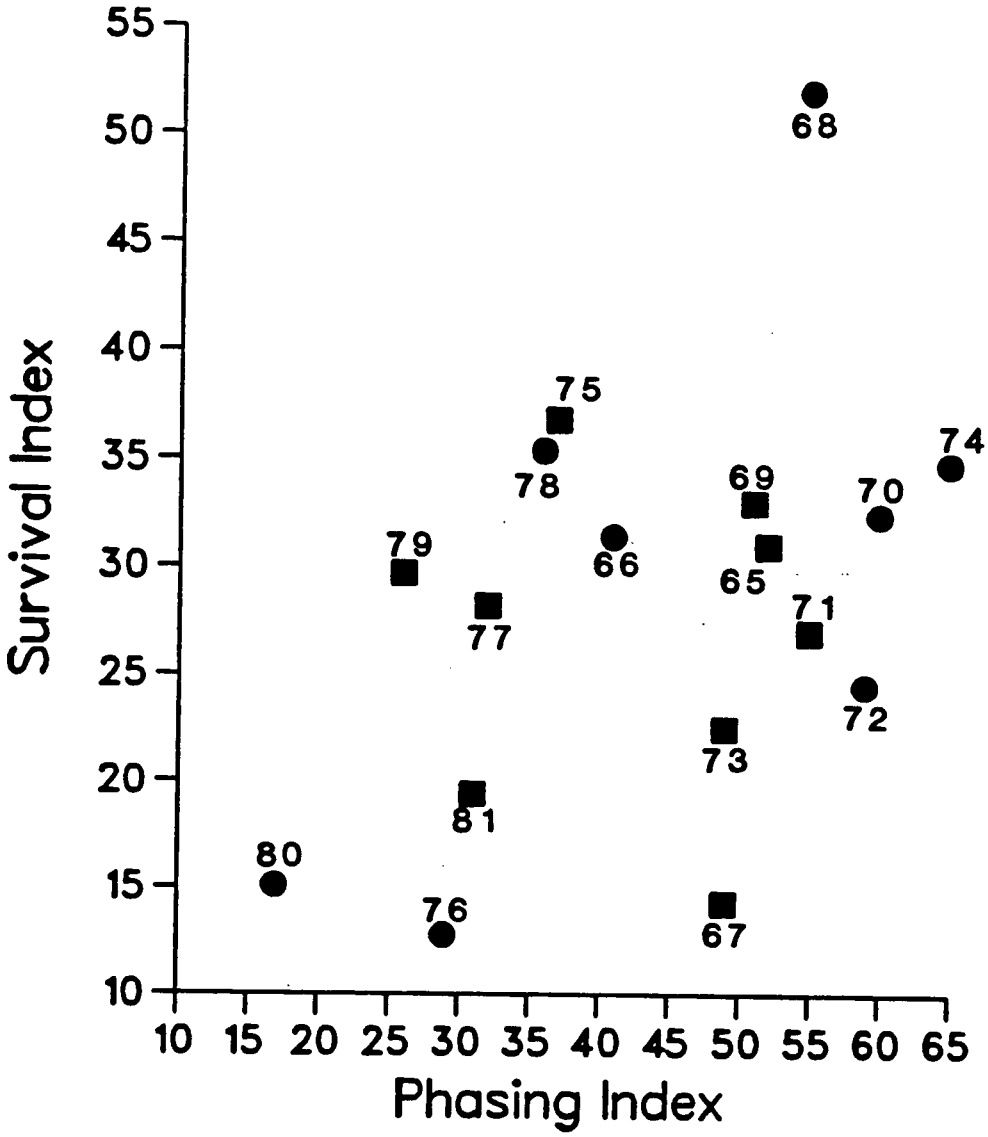

Figure 5.4: Index of survival *versus* phasing index for Fraser River chum salmon from 1965 to 1981 (odd & even broodyears).

the Fraser River, outmigrant pink salmons only occur in even years. This means that even-year outmigrant juvenile chum salmon (that were spawned the previous spring, and thus are part of an odd broodyear) will share their migration route with pinks. Pink salmon are known to feed on harpacticoid copepods (e.g. Levy *et al.* 1979); gut-contents of pink salmon caught on Roberts Bank in this study did not seem to differ in composition from those of chum salmon (D. Webb, Depart. of Oceanography, U.B.C., pers. comm.). It may well be, then, that pink and chum salmon feed equally on harpacticoids. In the Fraser River, the average number of juvenile outmigrants of pinks is about twice that of chum (DFO). Although there is indication that pink salmon residence in estuaries and near-shore environment is shorter than that of the chum, juvenile outmigrants of chum and pink may then be trophically equivalent to a certain point. If this is the case, a phasing index computed with the median date of downstream migration of chum salmon could be invalid when applied to years when pinks are present. If pink and chum are trophically equivalent with respect to harpacticoids, this phasing index would have to be based on the median date of downstream migration of the combined total of pink and chum. For these reasons, the odd- and even broodyear data were plotted separately (Figs. 5.5 & 5.6). For odd broodyears (Fig. 5.5), the plot of index of survival *versus* phasing index suggests no pattern. As discussed above, a reason for this might be that the median date of downsteam migration for chum salmon only is inappropriate for those broodyears that will share the migration route with pink salmons. For even broodyears (Fig. 5.6), there is indication that indeed, survival could optimize at some intermediate value of phasing index. Broodyears 1980 and 1976 had survival indices of 15.1 and 12.8 with phasing indices of 17 and 29. Broodyears 1970, -72, &-74 had survival indices of between 24.5 and 34.8 with

phasing indices of between 55 and 65. Broodyears 1966, -68, & -78 had survival indices of between 31.4 to 52.0 with phasing indices of between 36 and 55.

For an approximation of the location of the apex ($\Delta\Theta_{opt}$) on the plot of survival index (S.I.) *versus* phasing index for even broodyears, two straight lines were respectively fitted in the ascending and decreasing sections of the data points (Fig. 5.6):

$$S.I. = -7.69 + 1.04\Delta\Theta \ (R^2 = 0.83, \ n = 5) \tag{5.4}$$

for the ascending section, and

$$S.I. = 123.72 - 1.47\Delta\Theta \ (R^2 = 0.27, \ n = 4) \tag{5.5}$$

for the descending section. The slope of Eq. 5.4 was significantly different from zero (p=0.03; F=15.2) while that of Eq. 5.5 not. For these reasons, the increase in survival with an increase of phasing is considered significant up to a phasing index value of 55 days; after this value of phasing, the apparent decline in survival can only be considered as a suggestion of a reversal of the trend in the relationship between survival and phasing indices. Keeping those qualifications in mind, the apex is found by equating Eq. 5.4 and Eq. 5.5:

$$-7.69 + 1.04\Delta\Theta_{opt} = 123.72 - 1.47\Delta\Theta_{opt} \ ,$$

which indicates a survival index (S.I.) of 46.76 for $\Delta\Theta_{opt}$=52.36 days.

The survival *vs.* phasing relationship can then be described by:

$$S.I. = \begin{cases} -7.69 + 1.04\Delta\Theta & \text{if } \Delta\Theta \leq 52.36 \\ 123.72 - 1.47\Delta\Theta & \text{otherwise.} \end{cases} \tag{5.6}$$

It must also be pointed out that the indication of optimization of survival at intermediate values of phasing index is heavily dependent on broodyear 1968, and that

further data are needed to assess the significance of the seemingly highest survival of chum salmon at intermediate values of the phasing index. The data point for broodyear 1976 also may contribute unduly to the appearance of a hump in the survival curve of even broodyear chum salmon versus hindcasted phasing index. In 1977, the year during which the bloom onset must be hindcasted for the 1976 fish broodyear, the first hindcasted warming episode in the sediment was not followed by a similar warming episode 15 days later. The first occurrence of a low tide falling below 1.6 m during daytime (as previously defined in chapter 4) was on February 9; *ca* 15 days later, when another similar tide is expected, the tide level did not fall lower than 1.7 m during daytime. Only 4 weeks after the first warming episode (on March 8) did the tide fall below 1.6 m during daytime. This requires the second warming episode, to which the harpacticoid bloom was tentatively associated, to be hindcasted 4 weeks after the first one, contrary to 2 weeks if the tide conditions required for the occurrence of a warming episode in the sediment had been defined with a lower critical tide height. This causes the phasing index for 1976 to be small (29 d) instead of 43 d if the second warming episode had been hindcasted 15 days after the first one. If the survival datum for broodyear 1976 was moved to a corresponding $\Delta\Theta$=43 d (Fig. 5.4), suggestion of the presence of a hump in the survival *vs.* phasing indices plot would be somewhat diminished. However, if one chooses to consider the quasi-warming episode happening 15 days after the first one in 1976 as the one to which the harpacticoid bloom should be related, the definition of the tide conditions required for the occurrence of a warming episode in the sediment has to be modified. Attempts at modifying this definition only resulted in further ambiguous situations. Since the definition for the occurrence of warming events in the sediment had been *a priori* defined with 1.6 m as the critical

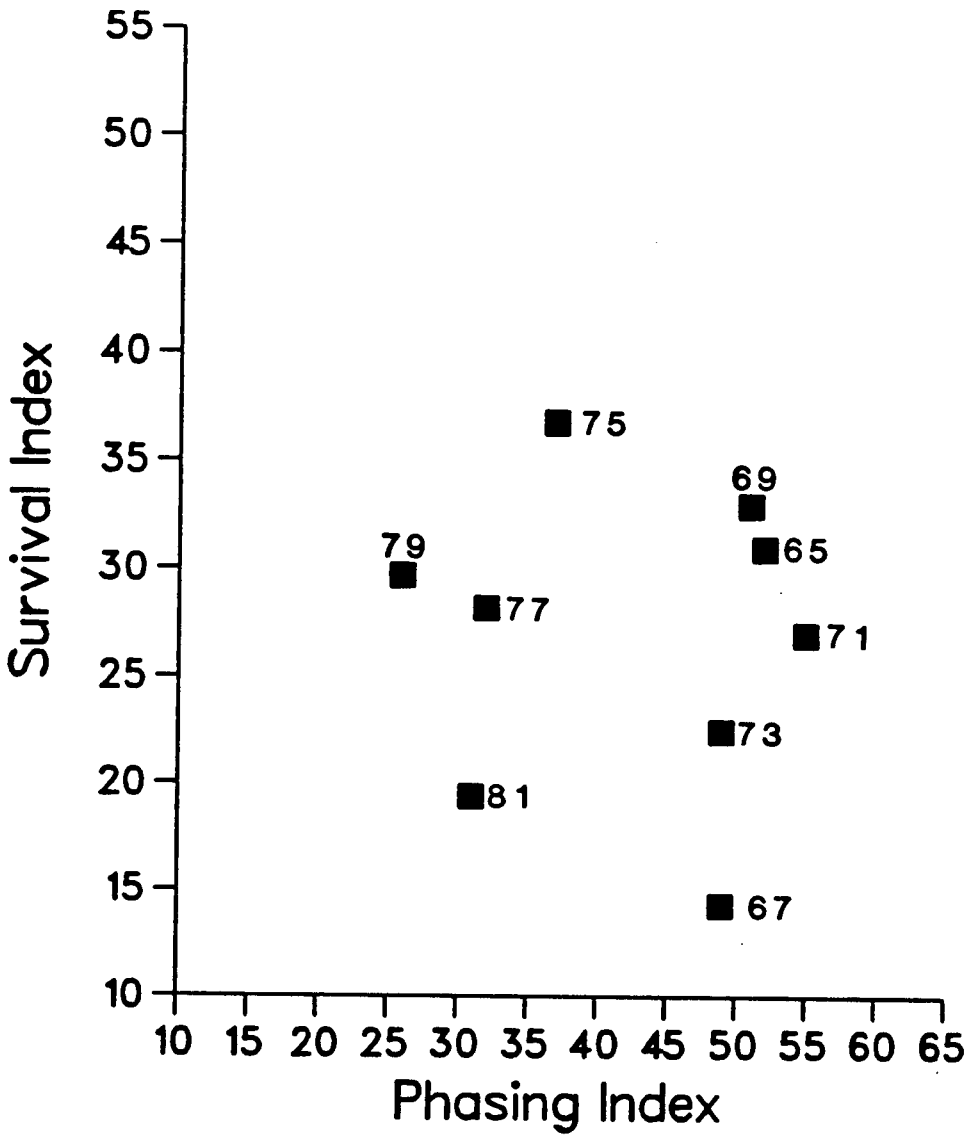

Figure 5.5: Index of survival *versus* phasing index for Fraser River chum salmon from 1965 to 1981 (odd broodyears).

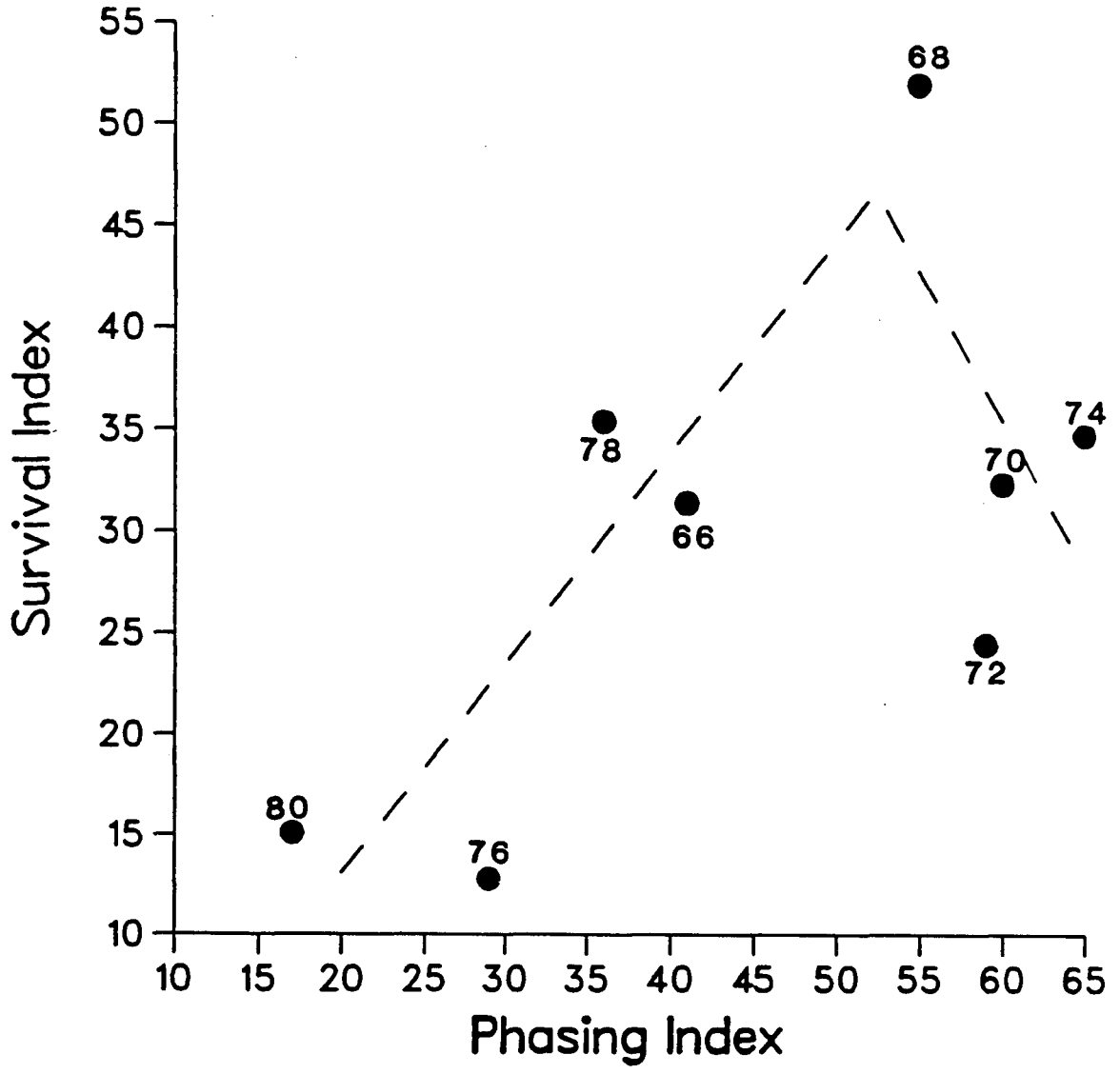

Figure 5.6: Index of survival *versus* phasing index for Fraser River chum salmon from 1965 to 1981 (even broodyears). The increasing dashed line was fitted with the data points from 1966, 1968, 1976, 1978 & 1980; the decreasing dashed line was fitted with the data points from 1968, 1970, 1972 & 1974.

Point Atkinson (1980)		
%	ΔT	ΔH
48.8	<5 min	
78.7	<10 min	
92.2	<15 min	
31.2		<5 cm
56.4		<10 cm
73.2		<15 cm

Table 5.2: Comparison of predicted and observed tides at Point Atkinson (1980). Percent (%) of the time when observed timing of tide deviated from predicted (timing deviation (+ or -)= ΔT), and percent of the time when observed tide height deviated from predicted (height deviation (+ or -)=ΔH) (data provided by the Canadian Hydrographic Service, IOS).

tide level following empirical evidence, and to be as consistent as possible, it was chosen to consider as the second warming episode the later date in 1977 (March 8), keeping in mind all the potential implications of this choice.

To assess the validity of the hindcasted date of harpacticoid bloom onset based on the hindcasted second warming event, the accuracy of predicted tide levels must be evaluated. The observed level of tide usually differed little from the predicted level (Table 5.2). In 1980, which is used as a paradigm, the observed and predicted timings of tide (high or low) never differed for more than 15 min for 92 % of the time at Point Atkinson (port of reference). The predicted and observed tide levels never differed by more than 15 cm for 73 % of the time. It can be concluded that predicted tide height and timing are accurate, and that the definition of tide conditions (level and timing) to generate a warming event should be reliable in fore- or hindcasting.

Beacham & Starr (1982) analysed various environmental factors that could reg-

ulate the abundance of chum salmon in early life stages. The median date of downstream migration of the fish (also at Mission) was one of the factors investigated (Fig. 5.7). What must be emphasized here is that in that study, the median date of downstream migration was used directly in the analysis as a univariate parameter. Beacham & Starr (1982) suggested that there seemed to be a decrease of survival of the fish with later median dates of downstream migration. The conclusions of Beacham & Starr on the survival of chum salmon in relation to median date of downstream migration can not be compared to those of the present study. The reason for this is that they used migration and survival data based on estimates of total abundance of downmigrant frys. Today, the techniques to estimate total abundance of frys are no longer used, and migration dates and survival rates are computed directly from the actual count of frys (T. Beacham, Pacific Biological Station, pers. comm.). However, it is possible to see if conclusions derived from analysing survival index *versus* phasing index (bivariate) will differ from those derived from analysing survival index *versus* median date of downstream migration *per se* (univariate). Data on chum salmon juvenile-to-adult index of survival were plotted *versus* median dates of downstream migration for even & odd years, odd years, and even years (Figs. 5.8, 5.9, and 5.10). The general suggested trends in the dispersion patterns of the chum salmon survival index data in relation to median date of downstream migration (Figs. 5.8, 5.9, & 5.10) differ from those of the same data in relation to the hindcasted phasing index of the fish and natant harpacticoids (Figs. 5.4, 5.5, & 5.6). For all broodyears (Fig. 5.8), the data are very dispersed and no trend is suggested. For odd broodyears alone (Fig. 5.9), the index of survival generally decreases with later median dates of downstream migration. For even broodyears alone (Fig. 5.10), the index of survival of chum

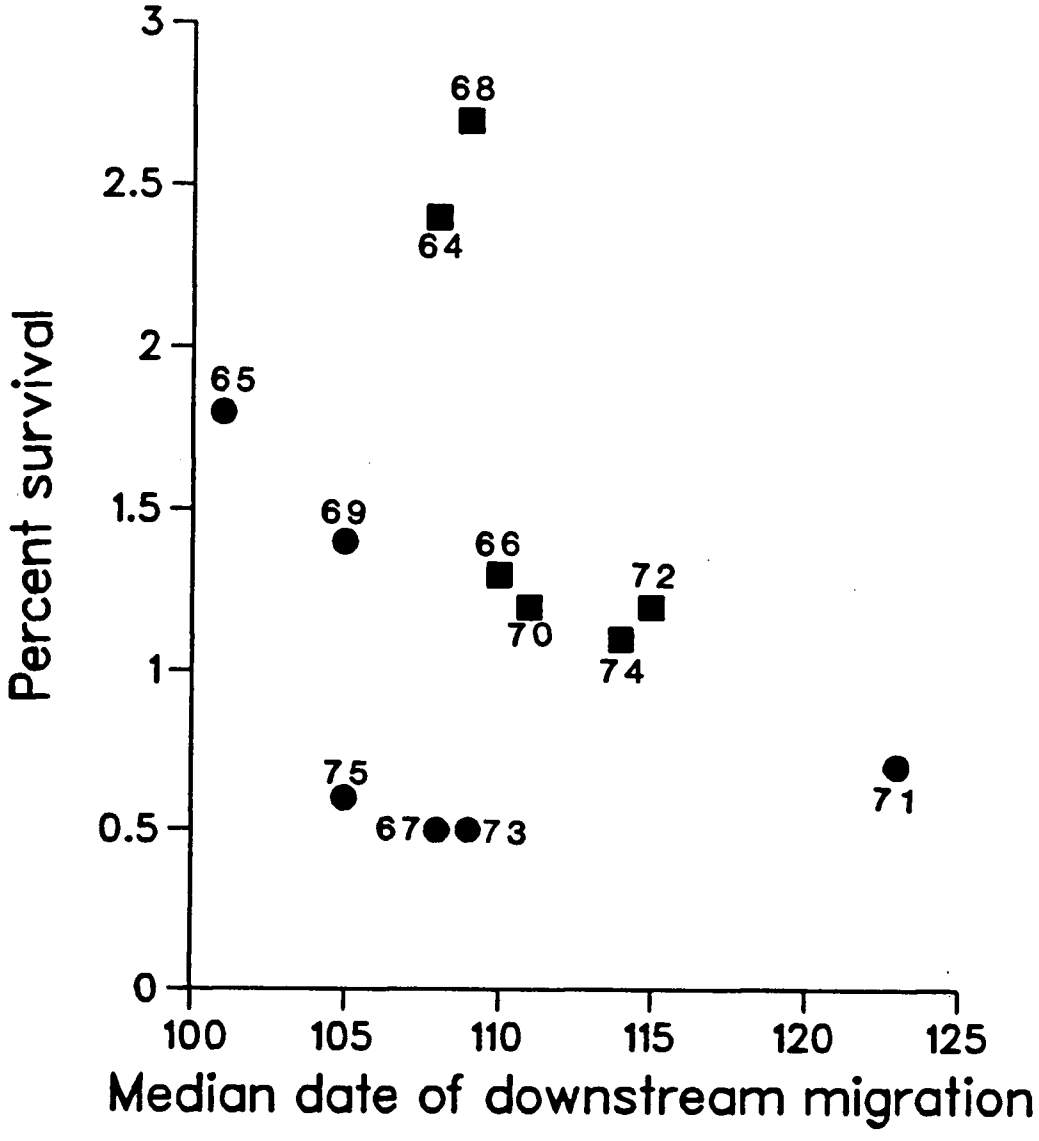

Figure 5.7: Juvenile-to-adult survival of chum salmon *versus* median date of downstream migration at Mission (redrawn from Beacham & Starr (1982)).

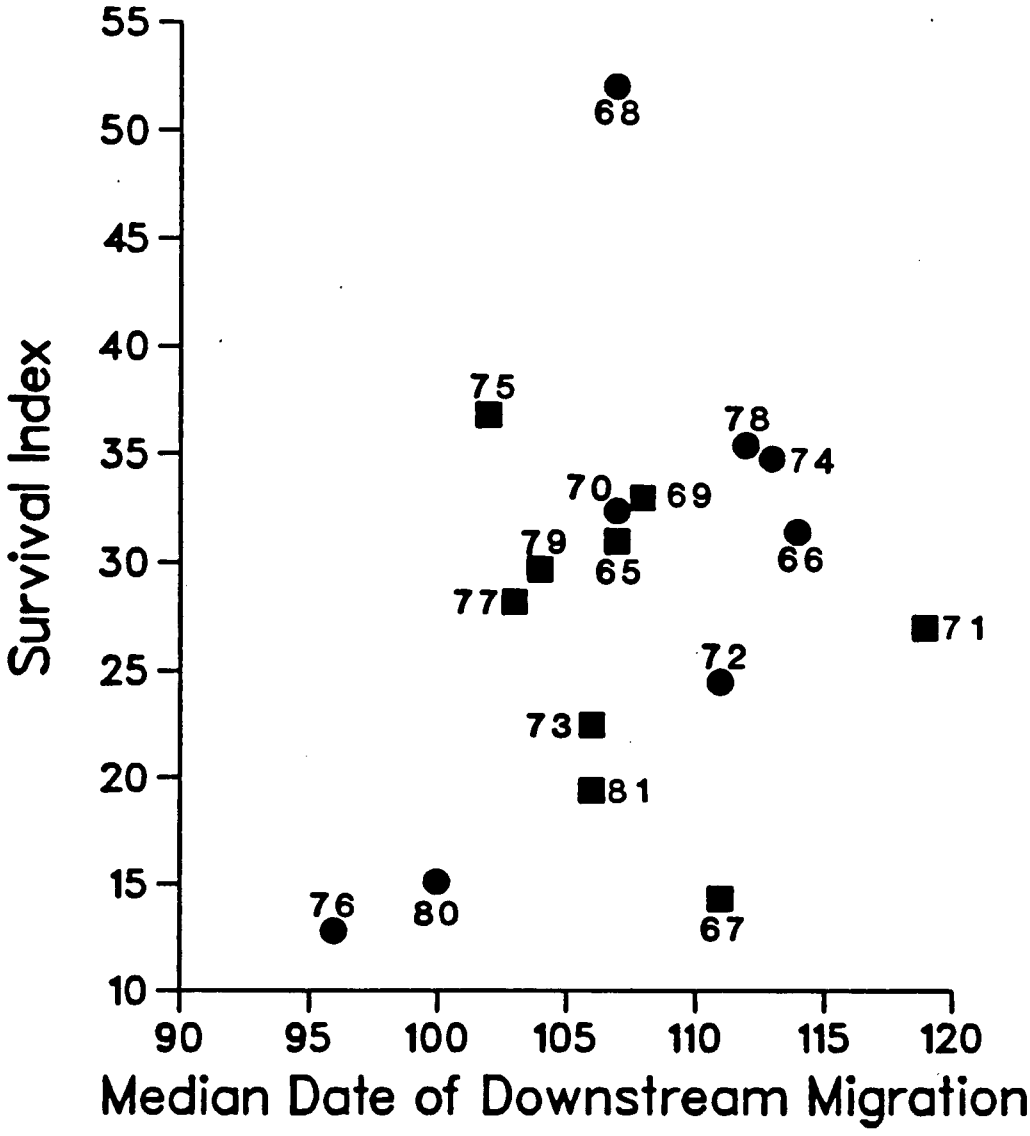

Figure 5.8: Juvenile-to-adult index of survival of chum salmon *versus* median date of downstream migration at Mission (even + odd broodyears).

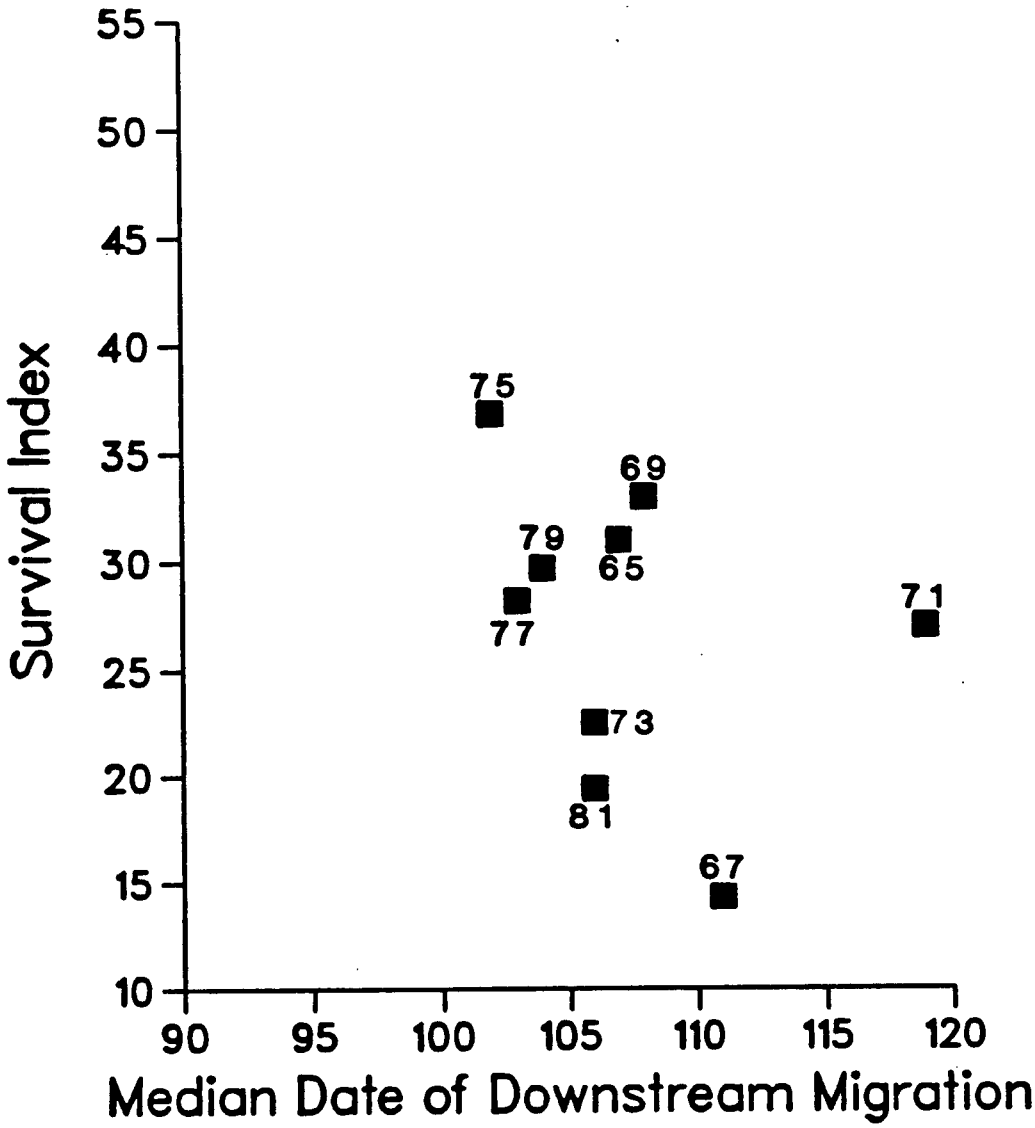

Figure 5.9: Juvenile-to-adult index of survival of chum salmon *versus* median date of downstream migration at Mission (odd broodyears).

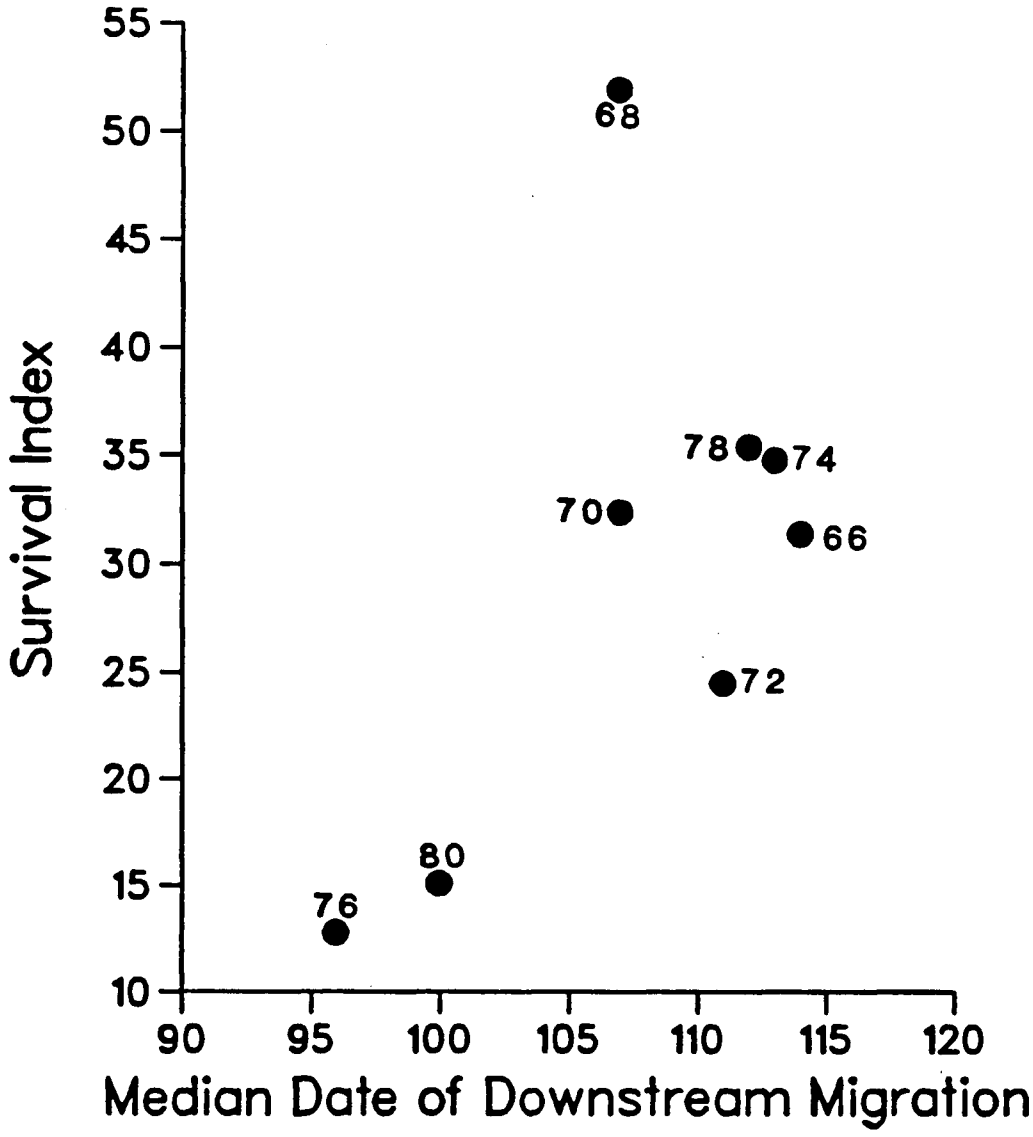

Figure 5.10: Juvenile-to-adult survival of chum salmon *versus* median date of downstream migration at Mission (even broodyears).

salmon generally increases with later median dates of downstream migration. None of those trends is statistically significant ($\alpha = 0.05$), and even if they are considered as indicative of some patterns, those patterns would be monotonic. However, as indicated by Parsons & Kessler (1987), survival of juvenile salmonids should vary non-monotonically with monotonic changes in forcing functions. Those authors modeled the survival of pink salmon (*O. keta*) under various conditions of environmental factors. Their main conclusion was that the salmon biomass increase was maximal at an optimum (intermediate) level of each environmental factor studied. This maximum was attained in each case largely through the phasing of zooplankton and phytoplankton production in such a way as to maximize the standing stock of the former, and hence, the growth rate of the salmon. In the same study, it was also concluded that the timing of salmon arrival after the initiation of the spring bloom was a relatively inconsequential event for the survival of the fish under the most favourable growing conditions for zooplankton. However, this does not disconnect the conclusions of their study from the present. In the present study, it is not solely the availability of food which is assumed to regulate salmon growth and survival, but the quality of harpacticoid copepods specific food items that provide the fish with the highest growth rates. It was shown earlier that this provision of specific food resource was an ephemeral event. If the bulk of the fish population overshoots this event, food is still available, but with less growth effectiveness. For the fishes, this would be equivalent to grazing on zooplankton growing under less than favourable conditions, which could reduce the amount of food available. In these conditions, Parsons & Kessler (1987) suggested that timing of salmon arrival could be consequential for the fish survival. Survival of chum salmon increased with increasing phasing index for low phasing values; at higher phasing values, there is

at least no evidence of further increasing of survival, and there is suggestion of decrease in survival, which appears to be consistent with the results of modeling investigations by Parsons & Kessler of the survival of juvenile salmonids.

For all the above reasons, it can be concluded that the phasing index ($\Delta\Theta$) appears as an appropriate covariate of chum salmon survival since a non-monotonical change in the survival of the fish is suggested with monotonic changes in their index of phasing with harpacticoid copepods.

5.2 Summary

Growth of chum salmon has been considered as a way for the fish to escape their size-selective predators by outgrowing them. The food quality of natant harpacticoid copepods could promote the fastest growth in chum salmon. However, the period of availability of natant harpacticoid copepods is brief. The overlap of the salmon pulse and the harpacticoid pulse can vary so as to affect individual growth of fish, and hence affect survival. The survival of the fish should optimize at some intermediate overlap (phasing). It appears that an index of phasing measuring the overlap of chum salmon and harpacticoid (using the median date of downstream migration as proxi for the fish and a predictable tide pattern signature for the copepods) is an appropriate covariate of the chum salmon survival index. It is concluded that using the median date of downstream migration within a bivariate phasing index as the co-variate of salmon survival is more appropriate than using it *per se* since the latter approach indicates a continuous trend in the survival *vs.* phasing relationship, while the former indicates a discontinuous trend.

Chapter 6

General Discussion and Conclusion

The initial aims of this research project were to contribute to the on-going debate on the nature and action of mechanisms regulating fish population abundance, and to elucidate some aspects of the ecology of harpacticoid copepods to increase our understanding of their role in the diet of juvenile chum salmon. To meet those aims, a conceptual framework (trophic phasing analysis) was proposed to address the issue of fish abundance variability, and was subsequently applied in a case study. In this chapter, a brief evaluation of accomplishments in the case study on chum salmon is presented. Potential usefulness of trophic phasing analysis in fisheries oceanography is then discussed in light of those accomplishments.

6.1 Chum Salmon Abundance and Early Near-Shore Life

Discussions on potential limitation of production of chum salmon during the fish's early near-shore life are generally very open-ended. After studying the feeding habits of juvenile chum salmon in the Nanaimo estuary, Healey (1979) concluded that "it is probably common in estuaries for continuous production of salmon to

depend upon the conservation of specific food resources and the habitat characteristics that make these resources available to the salmon". In their study of the feeding of juvenile chum salmon in the Puget Sound, Kaczynski *et al.* (1973) explicitly stated that the results of the "trophic analysis... was to be used in the predictive models of... [chum salmon]...return". The main conclusion reached by Kaczynski *et al.* in that study was that the onshore stages of development appeared to be a distinct ecological stage in the life cycle of chum salmon.

Despite such substantial gains of insight in the ecology of juvenile chum salmon in previous trophic analyses, the assessment of potential limitation of production of chum salmon in estuaries is yet to be completed. A possible reason for this is that hitherto, trophic analyses of chum salmon have focused on describing the diet of the fish without considering the production dynamics of the prey items. Harpacticoid copepods have been recognized as the chief food item of juvenile salmon; the period of reliance on harpacticoids by the fish has even been called, perhaps excessively so, as "obligate" (Chandler 1986). While it is generally recognized that changes in availability of harpacticoids could cause fluctuations in growth and survival, very little, if any, of the spatio-temporal variability of harpacticoids is taken into account in previous trophic analysis. As emphasized earlier, the production of food is a process at least partially independent of the effects of predators (Parsons *et al.* 1984 a). Attempting to assess limitation of salmon production in estuaries with trophic analysis and not including the dynamics of prey production is likely to be inconclusive since it disregards one of the degrees of freedom of the fish production process.

In this study, some aspects of the spatio-temporal variability of harpacticoid copepods were considered; an essential characteristic of the production dynamics

of some harpacticoid copepods, namely the association of the spring bloom with a distinct signature in the thermal regime, was investigated in detail. This allowed assessement of the potential limitation of salmon production in estuaries with consideration of two degrees of freedom of the fish's production process–the time course of salmon abundance on the flat, and the time course of harpacticoid abundance on the flat.

The results of this study could have some practical applications. It is one of the stated objectives of the Salmon Enhancement Program (SEP) to identify the most appropriate time to release hatchery produced chum salmon to maximize their chances of survival (SEP Annual Report 1983). The results of this research could provide the basis to establish this date and orient future research in this direction. As indicated in the previous chapter, the apex of the survival-phasing relationship appears to correspond to a phasing index of 52 days; although based on limited amount of data, this figure provides the first quantitative expression of the potential effect on salmon survival of the fish's migration schedule, based on a structural analysis. Also, the environmental characteristics that make harpacticoid copepods available to juvenile chum salmon could be defined precisely and monitored if need be. These environmental conditions could be defined in terms of the link between harpacticoid abundance and thermal regime on the tidal flats. Any modification in the thermal regime could be readily monitored (and at low cost). Factors potentially affecting the thermal regime on tidal flats are those affecting the water balance on the flat (slope, plant cover, porosity). The results of this study could provide some objective criteria to define and monitor some aspects of the environment quality on tidal flats. Another indirect practical aspect of this research is the effect it could have on the annual decision that has to be taken by

the Department of Fisheries & Oceans as to whether or not continue the monitoring of outmigrant juvenile salmon at Mission City (C.D. Levings, DFO, pers. comm.). The fact that historical data on juvenile chum salmon migration could indeed be useful in assessing potential limitation of fish production in estuaries could contribute to securing the practice of salmon outmigration monitoring.

A most desirable practical application of such research would be establishing a relationship from which returns of chum salmon could be confidently predicted. Although it is suggested that the results of this study are consistent with recent advances in modeling of survival of juvenile salmonids, it would be premature to attempt building predictive models with these results. The three principal reasons for this are the following:

1. no estimation of confidence limits around the index of survival of chum salmon are available;

2. evidence of optimization of chum survival at intermediate level of phasing is heavily reliant on a limited number of data points;

3. the proportion of the Fraser River stock of chum salmon actually using tidal flats as feeding grounds remains speculative.

Nonetheless, this study has clarified some aspects of the ecology of harpacticoids, which allowed discussion of their role in the diet of chum salmon in an original manner. This led the way to a discussion on the potential limitation of production of chum salmon in estuaries which is more robust, as much for the synthesis of extant information this research provides, as for the clearer identification of future research priorities it also provides.

The application of trophic phasing analysis to a case study yielded new information on the mechanisms that may regulate fish abundance, and this information could have practical applications. It may be suggested that trophic phasing analysis could be applied to several fish species for further insights in environment coupled fish recruitment mechanisms, which is the object of fisheries oceanography.

6.2 Trophic Phasing Analysis and Fisheries Oceanography

The study of animal population regulation is a central effort in ecology, irrespective of the particular species concerned. In ecology, it has been recognized that the dogma of density dependence should be replaced by more fruitful arguments about observations on real animal populations. In that sense, the goal of studies on fish populations should be the elucidation of the mechanisms regulating animal abundance; only then should concerns about exploitation be addressed. However, one fundamental characteristic of fish populations makes the issues of operational usefulness of population regulation models paramount in fisheries research. Collectively, fisheries resources represent a major source of animal protein (*ca* 75 10^6 t/y (landed)) and yet, of all the intensively exploited animal populations, fishes (*sensu largo*) are the animals on whose environment little, if any, control is possible. This, in conjunction with the Malthusian belief that an animal population should reach equilibrium through density-dependent regulation, has led the rationale to secure a lasting benefit from this resource to be developed around the parental-filial theme. Sustainable yield strategies depend on quantifying density dependence in stock recruitment relationships (Sissenwine 1984). The whole theory of fishing depends on the existence of compensation: an unexploited fish population is in near equilib-

rium with no surplus production (recruitment and growth are balanced by natural mortality); fishing reduces population size which responds (compensates) with a surplus production available for harvest (Sissenwine 1984). Parental-filial relationships have gained wide acceptance perhaps more for their usefulness in establishing quotas, for which at least consistency is required, than for their validation as models for the mechanisms of fish population regulation. If it is chosen to further investigate fish population regulation mechanisms, empirical verification of models must be separated from operational usefulness.

When the operational usefulness of stock recruitment models is set aside, the relevance of the parental-filial theory must be addressed at the level of its foundations. The most fundamental tenet in the parental-filial theory is that the abundance of an animal population (N) should vary in time (t) until an equilibrium level (K) is reached, that is (see Morey 1980)

$$\lim_{t \to \infty} N(t) = K.$$

Without such an assumption on the time course of the fish population abundance, the functionality between parental and filial generations would be impossible to be formulated, let alone quantified. There is indication that the assumption by fisheries management of a natural persistence at equilibrium level in fish stocks is questionable (Anonymous 1980; Steele 1984; Steele & Henderson 1984). The reason for the widespread belief in equilibrium of non-exploited fish stocks is perhaps the ease with which the undeniable fact that animal populations do not grow beyond certain limits can be equated with the assumption that these limits are the levels at which populations would settle if left to themselves. Equating the latter assumption with the former observation provides the only justification of stock recruitment theory as a model for fish abundance regulation. However, if

doubts can be raised on the existence of "equilibrium levels" of virgin populations, doubts can also be raised on the parental-filial theory for animal population regulation. If parental-filial theory is only one approach for the investigation of fish abundance variability, the environmental thesis can itself be considered as a distinct and complete approach, especially since advances in oceanography are making the hitherto overlooked environment of the fishes increasingly better understood. For its concern for the environment of fishes, fisheries oceanography appears as a comprehensive field of research on fish population regulation, and trophic phasing analysis appears an appropriate methodology.

Besides its use to describe the methodology of fisheries oceanography, the concept of trophic phasing analysis permits the avoidance of confusion in the terms previously criticized by Sinclair & Tremblay (1984). Those authors pointed out that the expression "Match-Mismatch" was often used to refer to various oceanographic or meteorological phenomena that may cause fish abundance variability through fluctuations in food supply for early life stages. As it is, the concept of "Match-Mismatch" was developed to describe the variability in overlap of the spring phytoplankton bloom due to seasonal stratification changes in the water column in the drifting environment of larval fishes, which is a very specific definition. It can be suggested that the "Match-Mismatch" is but one case of variable trophic phasing that may influence fish abundance, as are the "Stability Hypothesis" or the "Larval Retention Area Hypothesis". This would help recognize that the environment of fishes is perhaps much more reticulated than perceived, and that it is unlikely that a single environment coupled mechanism would account for the variability in abundance of every fish species.

The goal of fisheries oceanography is to identify those environmental conditions

that may cause drastic changes in the abundance of fish populations. However, it has been suggested that this goal was not achievable. Walters (1984) pointed out that some stock recruitment data are log-normally distributed about the fitted stock recruitment curve; this is what would be expected if variations in recruitment are caused by many independent small variations throughout the life of the fish. In that case, it is unlikely that a single environmental factor could be identified as the main source of variability in fish abundance. Walters submits that if many environmental factors are acting independently on the survival of fishes, the task of determining the contribution of each in the variations of fish abundance would be impossible. This argument could temper research efforts in fisheries oceanography if it was not using a stock recruitment curve to determine the type of distribution of the data points. In doing so, environmentally induced variability is perceived as noise on the *a priori* parental filial curve. However, Walters' (1984) argument that prediction of fish stock size is but an option for management must be stressed. This emphasizes that much of the the concerns of fisheries management is not physiocratic in nature, and that the argument of better predictability of fish stock abundance to justify research on fish population variability should be kept in that perspective. As reviewed by Alverson & Paulik (1973):

> If one had to classify the basis for regulation governing the uses of marine living resources... the status of the stock would be the rationale most frequently given for a management action. However, allocation of the resources and economic status of the user are obviously involved. Although the key word [in] international management is also "conservation", more frequently the contentious issue involves allocation of a resource among multiple user groups...

6.3 Conclusion

This study was undertaken with the view that noise in fish stock recruitment curves could be reduced by studying the environment of the animal. The main thesis as to how environment may influence animal abundance was derived from Hjort's (1914) seminal paper. Hjort submitted that fish abundance may be regulated by environmental factors during early life stages, irrespective of the parental population size. However, after trying to apply this view to a case study, it became apparent that research on fish population regulation had become dominated by the imperative of operational requirements for fisheries management. The environmental thesis and the parental-filial thesis should be compared at the level of their foundations, and substantiated by empirical verification. Rather, a common orientation in research is to argue strongly in favour of the role of the environment in the determination of fish abundance, and then to try to amalgamate this argument with parental-filial theory. This persistent return to parental-filial theory is probably the result of difficulties in divorcing the idea of operational usefulness of the parental-filial theory in the actual scheme of fisheries management.

My greatest gain in this research was the realization that research on fish abundance variability is but one special case of the study of animal population regulation. The theory of animal population regulation is yet to be completed, and the dogma of density dependence seems tenacious because of the counter-intuitiveness of proposing non-equilibrium ecological tenets. Perhaps the dogma of density dependence is as tenacious as our drive to see, and impose if need be, order in Nature. No one else but Hjort, in the same paper already referenced (1914) could have summarized the situation better. Wrote Hjort:

> In the interest of biological research, also, it must be of the greatest

importance to ascertain the nature of the laws which govern the renewal of the animal populations, especially when taking into consideration all that has been written from time to time about overpopulation and the struggle for existence in the animal world, all from the point of view of human conditions.

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Appendix A

KEY CODE FOR 1985 GUT CONTENTS

#=fish number l=fish fork length (mm) 1=*Harpacticus uniremis* 2=*Zaus aurelii* 3=*Tisbe* spp. 4=Calanoids 5=Amphipods 6=UNCO 7=*Scutellidium* spp. 8=Fish larvae 9=Cumaceans 10=Cypris 11=Ostracods

March 29, 1985 (day 88)												
#	l	1	2	3	4	5	6	7	8	9	10	11
1	48	18	9	4	13	7	1		1	17		
2	42	74	34	182	3		14			2		
3	85	62	8	4	3		8					
4	51	12	8	34	6	1	2		1			
5	111	27	60	2	36					7		
6	43	19	1	3	3				1	3		
7	44	11		53	10					4		1
8	54	15	54	56		12				1		1
9	43	4	1		5					12		
10	46	36	10		8	3				2		
11	57	13	27	30		26			1	3		
12	41	16	14	3					2			
13	49	26	2	1	5							
14	46	1		2	4	4			1	4		
15	45	13	1	1	1	1				1		
16	51		6	3	2				2	5		
17	40	24	8	6				1				
18	40	36	5	8	3					1		
19	49	41		11	22							
20	54	45	22	6		22				6		

April 10, 1985 (day 100)												
#	l	1	2	3	4	5	6	7	8	9	10	11
1	51	46	4		3					1		
2	57	102	157	1	1							1
3	45	72	170	2			2					
4	52	104	202	1	1		2			1		
5	52	122	88	2	8		5					
6	56	113	30		1							
7	53	122	65	1			2					
8	51	68	12		2		4			1		
9	57	74	7	1	3		3			7		
10	58	135	116	8			3			4	2	
11	55	143	92	3	1	2	1			1		
12	54	146	124			1	4				2	
13	55	46	55	1		2	4			10		
14	63	5	244	5	1	2	2			4		
15	57	101	50	10		3	10				1	
16	51	55	3		1							
17	58	64			2	2				3		
18	42	54	41		2					4		
19	51	53	60		4	5			1			
20	47	40	34		4							

April 23, 1986 (day 113)												
#	l	1	2	3	4	5	6	7	8	9	10	11
1	46				1	1			1			
2	36	19	3	13	1	6	4			2		
3	56	50		48	3	11	11			8		
4	48	24		2	1	1				1		
5	48	56					5			2		
6	43	29		1		5						
7	58	13	1	19	1	15	1			13		
8	67	11		1		3	5			7		
9	50	14		4		9			2	4		
10	45	137	2			4	14			20		
11	44	16		3	1	2						

May 9, 1985 (day 129)												
#	l	1	2	3	4	5	6	7	8	9	10	11
1	51	221		6	48	11						
2	50	155	1	23	160				1			1
3	57	328		78		43	12			9	2	
4	47	413				14	2				6	2
5	46	346		1	4	13						1
6	65	252		12	100	16				1	8	
7	64	339		27	3	24				3	34	
8	65	362			3	28				4	9	
9	44	285		7		13	1					
10	51	411	2			2	1				3	
11	59	711		1		34	4				10	
12	52	455	1		1	5	2				4	
13	52	455	1		1	5	2				4	

May 23, 1985 (day 143)												
#	l	1	2	3	4	5	6	7	8	9	10	11
1	78								3			
2	52		11	1	10	7	30				7	
3	47		34	5	22	2	9				2	
4	61			1		2	1			1		
5	62	12	72	14	1	28	10			7	27	
6	50	37	69	18		3	9			84	4	
7	48		23	2	2	22				1		
8	49		16	41	4	23						
9	48		6	1	53	6	25					
10	63				3				3			

June 7, 1985 (day 157)												
#	l	1	2	3	4	5	6	7	8	9	10	11
1	53		6	12	16		5			50	80	
2	57		2	6	66	3	7				2	
3	51		6	8	113	7	4			35	11	
4	56	1	3	3	150	117	4				18	
5	50	2	20	10	17	25	4				30	
6	61	1	6	6	25	11	6				39	
7	51		3	8	9		11			1	7	
8	57		12	9	120	12	20					
9	57	2	7	12	27	17	12				60	
10	57					2				136	1	

June 21, 1985 (day 172)												
#	l	1	2	3	4	5	6	7	8	9	10	11
1	66						3			39		
2	69	2				2			1			
3	50	3	260	6			6			6		
4	81	8	2							236		
5	62		6							288		
6	60	6	224			3	25		2	145		
7	62									325		
8	56	2	15	5	4	2	6			169		
9	51	12	444	3		2	12			40	1	
10	64				4				2			

July 5, 1985 (day 188)												
#	l	1	2	3	4	5	6	7	8	9	10	11
1	48	21				10	7			4		
2	50	33	10		4	12	3			1	1	
3	60	23			4	19				29	5	
4	58	1				3	2			39		
5	51	18	4	1	3	8	3			12		

KEY CODE FOR 1986 GUT CONTENTS

#=fish number l=fish fork length (mm) 1=*Harpacticus uniremis* 2=*Zaus aurelii* 3=*Tisbe* spp. 4=Calanoids 5=Amphipods 6=*Longipedia* sp. 7=*Orthopsyllus* sp. 8=UNCO 9=*Scutellidium* sp. 10=Isopods 11=Fish larvae 12=Diptera 13=*Dactylopodia* sp. 14=Cumaceans 15=Cypris 16=Ostracods 17=*Diarthrodes* sp.

April 1, 1986 (day 91)																		
#	l	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	43	53	4		96	7	56	1	6									
2	46	1									6							
3	45	16			90		1											
4	46	5			40		3		5									
5	45	31				3	5	2	10									
6	43	1										2	1					
7	41	15			8	1		11	7				1					
8	44	15				10	1							2				
9	41	80		11		8	15		16									
10	39	120		4	25		5	10										
11	54	70	1	3	23	3	3											

April 15, 1986 (day 132)																		
#	l	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	46	32		9					3						3			
2	43	1				1									1			
3	59	8		3					3						7			
4	64	4				2									12			
5	38	18		3					6						1			
6	50	3		3			3					1						
7	51	3		5					1						6			
8	37	17		3	1	1		3										
9	43	28		11			1		3									
10	59			2					2						14		2	
11	39	3		7			1		3									
12	38	4							3								1	
13	42	34					5		5						1			

April 29, 1986 (day 119)																		
#	l	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	36	100		5	1				4							14		
2	37	66	1	47					1						1			
3	36	3		6		1			9							2		
4	35	79	2	69					4									
5	38	100	2	13		7			7									
6	40	41	3	96		1			7									
7	35	110		7		2			9									
8	39	129	2	18					6						1	5		
9	38	31		76					9							1		
10	36	52	1	20					4	1								

May 13, 1986 (day 132)																		
#	l	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	47	24	3	22	15	5			10					4		2		
2	48	15	10	22					4			1				6		
3	47	1										1			3			
4	48	14		63	6	2							1					
5	45	65	1	3	9	1										8		
6	44	45	2	37	52				8							1		
7	43	43		30	37				3			1		2		2		
8	39	20	17	5	15				2					2				
9	47	22	7	11	1				5							2		
10	39	5	2	60	2	2				2			1					

May 27, 1986 (day 147)																		
#	l	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	45	15	35	2													6	1
2	50	20	60					1						5			3	1
3	42	1	10						2									
4	48	21	55											2				
5	49	60	150			1		2						10				
6	53	33	50			7								10	3			
7	48	25	92															
8	45	15	12			13			6									
9	54	8	80												2		8	
10	42	empty stomach																

June 11, 1986 (day 162)																		
#	l	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	52	8	120			2			4						12	8		
2	54	5	26			45			6						2		2	
3	64		6			2			1						14			
4	44		15						2							4		
5	54	8	22						5							17		
6	57	2	210			4			10							6		
7	54	56	65			1			7						2	17		
8	52	28	40						3						4	6		
9	58	6	42						8						4	37		
10	56	2	90						6							26		
11	54	4	110						9							7		
12	51	1	17	1		6			5						21			

Appendix B

KEY CODE FOR 1985 AND 1986 SLED SAMPLES CONTENTS

AMPH=amphipods CALA=calanoids CAPR=caprellids CUMA=cumaceans CYPR=cypris DACT=*Dactylopodia* sp. DIAR=*Diarthrodes* sp. DIOS=*Diosaccus* sp. FLAR=fish larvae GAST=gastropods ORTH=*Orthopsyllus* sp. HARP=*Harpacticus uniremis* ISOP=isopods MESO=*Mesochra* sp. OSTR=ostracods SCUT=*Scutellidium* sp. TISB=*Tisbe* spp. UCOP=unidentified copepodites ZAUS=*Zaus aurelii*

March 1, 1985 (day 60)					
Level	A	B	C	D	E
TISB	135	101	24	8	2
MESO	4	4	5		
DIAR		4			
ZAUS		2	1		
DACT	1	1	1		
AMPH	3				
CALA	2	48	44	64	82
OSTR	2				
UCOP	126	56	29	10	7

March 13, 1985 (day 72)					
Level	A	B	C	D	E
TISB	183	59	5	1	1
MESO	8	2			1
ZAUS	1				
DACT	7	4		1	
HARP	1				
SCUT	1				
AMPH	8	5			
CALA	6	19	18	9	12
FLAR			1		
UCOP	711	153	12	10	8

March 29, 1985 (day 88)					
Level	A	B	C	D	E
TISB	481	418	147	63	20
MESO	1	3	4	3	7
HARP					2
DACT	1		2	2	
AMPH	2				
CALA	2	2	2	5	3
UCOP	515	440	208	113	43

April 10, 1985 (day 100)					
Level	A	B	C	D	E
TISB	514	223	48	19	6
MESO	1		2	1	1
DIAR					1
ZAUS	2	2			
DACT	3	1		1	
HARP		1	1	2	
AMPH	5				
CALA	10	11	11	1	4
CAPR	1				
CYPR		9	21	25	24
UCOP	449	182	45	13	10

April 23, 1985 (day 113)					
Level	A	B	C	D	E
TISB	14	9	12	5	
DACT		1			
HARP			1		
AMPH	3	2	1	1	
CALA	1				
CYPR					2
CAPR	1				
UCOP	37	12	14	5	3

May 9,1985 (day 129)					
Level	A	B	C	D	E
TISB	47	43	27	6	9
ZAUS	1	1			
HARP	1				
AMPH	40	18	10	6	
CALA	147	78	61	14	7
CYPR		2	2	1	
UCOP	175	129	76	45	20

May 23, 1985 (day 143)					
Level	A	B	C	D	E
TISB	7		3		
DIAR			1		
AMPH	19	2	4	9	
CAPR	1				
CYPR		1	6	1	1
UCOP	173	183	176	117	80

June 7, 1985 (day 157)					
Level	A	B	C	D	E
TISB	6	9	14	11	12
MESO	3	6	3	1	2
DIAR		2		1	
ZAUS	1	1	1		
AMPH	8	2	1	1	1
CALA	107	112	105	84	77
UCOP	161	151	93	105	95

June 21, 1985(day 172)					
Level	A	B	C	D	E
TISB	9	2	2		
MESO	12	7	4		
DIAR	1	1		1	
HARP	3	2			
ZAUS	2				
DACT	4	1	2		
AMPH	18	10	2		
CALA	50	39	41	28	16
CAPR		8	6		
CYPR		1			
UCOP	282	276	85	55	31

July 5, 1985 (day 188)					
Level	A	B	C	D	E
TISB					1
MESO	2				
DIAR	2				
DACT			2		1
HARP	2				
AMPH	20	31			
CALA	20	6	14	19	13
CUMA		1			
UCOP	1172	361	216	106	67

February 11, 1986 (day 42)															
Transect	1					2					3				
Level	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
TISB	35	13	7	4	1	49	27	14	2	1	54	48	20	3	1
MESO	35	25	14	5	1	31	19	17	8	5	134	42	24	6	4
DACT	1	1					1	1		4	1	2	2	3	2
ZAUS	2	1				1	1	3			1		4	1	1
DIOS						1									
AMPH	2					1									
GAST	2		1			1	4				9	4	5		
OSTR	4	1				7	3	3	1		13	5	1	1	
CAPR						1	1				1				
CALA							2	3	2	5		3		1	8
UCOP			1		3		3	1	1	1	3	2	2	1	

February 24, 1986 (day 55)															
Transect	1					2					3				
Level	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
TISB	43	21	2	1	1	44	38	8	1	3	40	17	4	1	1
MESO	18	14	3	1		27	11	7	4		39	20	6	2	4
DACT			1			3	2	1		1	2	1	4	2	
ZAUS						1	1								
DIAR				1											
DIOS							2	1	2	2				2	
OSTR	3					3					3	3			
CALA	4	2		1	2	1	1	6	7	14		1			
AMPH		1				1	1	1				1			
GAST	1					1					5				
UCOP	5	3	2	1		4	9		1	3	4	2	1		

March 5, 1986 (day 64)															
Transect	1					2					3				
Level	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
TISB	136	60	22	12	7	138	91	42	27	1	130	108	60	27	11
HARP											1				1
MESO	63	34	26	7	1	50	25	26	10	6	62	29	13	8	10
DACT	10	3	2	2		7	7		3	1	6	5			1
ZAUS	2		2			2	1	1			3		1		1
DIOS	1	4	1			11	12	7	4	2	11	14	4		2
OSTR	11	1		1		7	2				8	8	1		2
AMPH	9	5	2	1		11	5	2			2	4	4	2	
CALA	3		1			2	5	1	3	4	3	3	1		5
GAST					1										
ISOP										5					
CYPR											3				
ORTH								1							
UCOP	23	11	3	3		9	4	6	3		22	10	2	3	

March 19, 1986 (day 78)															
Transect	1					2					3				
Level	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
TISB	486	321	150	90	28	490	279	160	76	44	474	205	74	17	10
MESO	83	43	34	51	33	23	81	25	19	18	54	35	20	12	2
DACT	3	1	1			2	1		1	2	2		2		
HARP	2	2	4	5	1	2	4	2	1	1	3	3	2		
ZAUS	3	6	21	11	2	8	25	21	18	1	4	17	8	2	1
DIOS	6	2	7	5	2		1	2	4	2	1	1			
SCUT		3				1					4	1			
DIAR	18	5	1	4	5	8	6	1	5	3	10	7	3	4	
AMPH	10	13	10	3	1	23	11	2	3		11	8	1		
CALA	3			3	1	6		2		2	3	1			
OSTR	3	8				8	9	1			6				
GAST		2				1	3	1							
UCOP	1453	647	276	201	101	2070	630	370	194	138	1435	719	224	79	31

April 1, 1986 (day 91)															
Transect	1					2					3				
Level	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
TISB	347	294	183	124	75	312	265	208	102	93	273	277	186	104	86
MESO	32	40	5	14	16	27	10	14	9	25	17	13	11	16	11
DIAR	3	2	1		1	3	1		1		5	4	1		
DACT		2	1		1	3	1		1		5	4	1		
HARP	6	6	4	1	3	7	8	2	6	4	2	3		4	2
ZAUS	8	47	58	36	15	20	42	44	76	50	7	45	79	60	25
SCUT	1					4	8	3	1		2	5	3	1	
AMPH	16	6	5	2		7	19	10	3		9	15	7	2	
CALA	5				5	1		1		1					4
CAPR	1	2		1		2	3					1			
UCOP	1454	1018	538	215	164	2269	1128	633	276	210	1996	1496	630	255	194

April 15, 1986 (day 105)															
Transect	1					2					3				
Level	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
TISB	690	514	165	88	32	668	561	244	119	63	613	459	253	123	42
MESO	58	37	10	9	6	43	9	2	6	5	35	13	11	8	3
DIAR	2	1													
HARP	18	13	3	5	2	10	4	7	2	3	17	6	6	3	2
ZAUS	20	28	28	16	13	14	48	72	32	5	14	48	118	72	21
DACT	9	5			1	4	1	1			7	2			
SCUT	3						3								
AMPH	7	5	2	1	3		5	3	1	2	2	4	1	1	
CALA	13	10	14	11	13		13	16	10	6	28	10	12	11	8
CAPR	2					1					3				
UCOP	1345	533	272	196	126	1070	552	403	206	152	1167	678	395	244	130

April 29, 1986 (day 119)															
Transect	1					2					3				
Level	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
TISB	416	136	103	82	28	256	134	105	66	54	387	150	121	74	43
MESO	82	70	69	55	18	54	41	35	60	39	102	34	47	38	20
DIAR						1					3				
DACT	23	26	5	9	1	22	14	11	19	11	37	11	18	8	3
HARP	22	19	11	13	4	16	20	7	20	12	43	19	18	2	1
ZAUS	81	93	62	45	8	62	78	117	73	34	90	105	194	58	24
SCUT							2		2			4	1		
AMPH	11	9	5	5	3	8	46	10	1	6	6	12	2	7	7
CALA	37	19	5	9	8	16	9	7	9	4	14	5	10	3	3
CAPR						2			1		3				
UCOP	2775	2173	1297	1551	643	1802	1239	1036	1364	849	2982	1170	941	1031	807

May 13, 1986 (day 132)															
Transect	1					2					3				
Level	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
TISB	95	30	37	27	13	20	26	29	15	10	4	49	69	37	35
MESO	25	10	8	5	2	9	5	3	4		9	11	7	3	2
DACT	11	3	3	7	1	3	1	2	1		2	5	4	1	1
HARP	30	10	11	4	6	12	12	2	4		19	26	24	5	3
ZAUS	2		2				2	4		1	1	2	1		1
DIOS				1						1					
AMPH	7	4	2	2	1	3	1		1		2	4	7	2	2
CALA	79	11	6	4	4	14	14	6	5		2	14	24	14	10
CAPR	2	1	2			1						3	2		
CUMA												1			
UCOP	933	317	364	319	154	197	234	369	173	183	138	629	653	481	373

May 27, 1986 (day 147)															
Transect	1					2					3				
Level	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
TISB	14	21	31	25	10	47	39	41	22	5	41	49	47	32	16
MESO	11	28	13	8	3	21	21	22	14	3	12	12	7	10	4
DACT	7	13	15	11	3	5	4	5	7	8	6	12	14	8	6
HARP	3	16	5	3		6	3	3	3	3	4	6	7	1	2
ZAUS	1	1	2	5	7	3	1	4	1	3	5	2	7	2	
DIAR		2	1				1				1				
SCUT												1	2		
AMPH	1	4	8	5	1	7	3	3	2	2	5	4	1	1	
CALA	20	30	25	48	22	43	27	26	17	7	55	64	59	62	33
CAPR	7	7	7			3	6				15	6			
CUMA			2				1					1			1
UCOP	46	93	96	164	88	130	130	156	115	59	162	197	159	138	73

June 11, 1986 (day 162)															
Transect	1					2					3				
Level	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
TISB	3			2	2	3	2	2	2				2	1	
MESO	2			1	2								3	1	
DIAR	3	3	1		1		1	1	1			2	1		
HARP	1	1	2		2	3					1		1		
SCUT	2		2				1								
DACT	2		1			5					3	2		2	
AMPH		5			2			1			1	2			
CAPR	6					4				1	2				
UCOP	49	22	19	12	9	24	16	25	23	22	43	29	36	18	15

June 25, 1986 (day 176)															
Transect	1					2					3				
Level	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
TISB	6	3				10	4	1			4	1	1	4	
MESO	3	9		2		6	2	2			10	5			
DACT	28	21		12		27	12	6	7		15	22	11	9	
DIAR	3	1		6	2	1	1	1	1	1	1	4	2	3	2
HARP	1								1				1	2	
ZAUS	10	16	66	73	72	36	32	64	83	61	15	15	49	63	28
SCUT	2	3			2	4	1	2	1		3	5		2	1
AMPH	8	2		2	1	1	5	1					2		
CALA	165	154	95	83	62	146	155	71	36	40	210	147	121	105	23
CAPR	1	1			1										
CUMA						1									
UCOP	76	83	81	47	39	48	45	41	30	16	81	71	55	60	21