Ecosystem Effects on Harvested Populations:

Lower Trophic Level Dynamics in the Northeast Pacific and Its Implications on Sockeye Salmon (*Oncorhynchus nerka*) Survival

by

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Abstract

Almost all epipelagic fish species in the Northeast Pacific show an increase in population size between the late 1950s and the 1980s. The complexity of pelagic ecosystems makes speculations on the causes of these increases easy to justify, and thus various conjectures on the chain of events leading to increased fish survival have been put forward.

In this thesis I try to explain the variability in cohort survival, abundance and distribution of sockeye salmon (*Oncorhynchus nerka*) - the fish species that has experienced the largest increase in abundance and biomass of all epipelagic fish species in the Northeast Pacific between the late 1950s and the 1980s - by ecosystem effects. I assumed that sockeye salmon total survival rate is largely determined in early marine life due to exposure to predators, which is set by the time at risk of predation, itself a function of sockeye prey, i.e. mesozooplankton, abundance. I then developed two simple food chain models with three and four trophic levels, respectively, which include lower trophic level dynamics but not fish itself. Both population models were calibrated and tested for two locations in the Northeast Pacific through mean field simulations driven by abiotic environmental forcings. Using a 4-hour time step from 1950 to 1990, both calibrated population models were then run as spatially-explicit simulations with a resolution of one degree latitude and longitude for the whole area of the Northeast Pacific, a total of 1240 open ocean fields. To assess the relative importance of biological processes versus physical advection both population models were simulated with and without surface currents.

I have tried to design the best models within reason utilizing the best information on environmental forcings and biological processes available at the time. Simulation results do not suggest a clear linkage between prey density in the oceanic environment and sockeye salmon cohort survival. However, there are two fundamental lessons to be learned from this modeling

exercise: First, categorization of ecosystem components into trophic levels with no regard of the many life history strategies is one of the worst aggregation errors in ecology, one that implicitly includes errors of hierarchical organization as well as of spatio-temporal stability. And second, the complexity of ecosystems will always make results from trophodynamic simulations interpretable, even if these results bear no relationship to the natural system.

Table of Contents

List of Tables

List of Figures

Acknowledgments

"All right. I think it's amazing that you've done as well as you have. You've got hardly any theory of social organization, astonishingly backward economic systems, no grasp of the machinery of historical prediction, and very little knowledge about yourselves. Considering how fast your world is changing, it's amazing you haven't blown yourselves to bits by now. That's why we don't want to write you off just yet. You humans have a certain talent for adaptability - at least in the short term."
In C. Sagan (1985) *Contact*, pp. 360-361

I apologize to my wife Nani and my children Phoebe and Maia that I have chosen a profession which I thought would bear some cultural as well as socio-economic relevance in the future of humankind. I was wrong.

I thank André Steinhausen whom I have not seen for more than 18 years and who inspired my interest and fascination for "the order, the harmony, the uniformity and the universality of the laws of nature" (Chandrasekhar 1990). He was wrong, too.

I thank Paul LeBlond for accepting me as a graduate student at a time when nobody else would, and for providing the academic freedom to explore scientific space.

This work was funded in part by a grant to M.C. Healey, P.H. LeBlond, and C.J. Walters; and by a grant to P.H. LeBlond.

Input data used in the simulations (raw and spatially interpolated), simulation source code, simulation results, as well as the NE-Pacific MapViewer can be obtained from me upon request.

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1. INTRODUCTION

"*Cause-and-effect assertions ... are forever dubious because of the logical flaw of* post hoc ergo propter hoc *reasoning.*"
G. Hardin (1985)

1.1. In Which I Provide the Context

It is trite to say that an organism is ultimately dependent on its environment and that the components of this environment are biotic, i.e. food, competitors, predators, as well as abiotic, such as nutrients and climatic factors. However, traditionally different biological organization levels and associated processes and patterns have been studied in different sub-disciplines of ecology (Odum 1971). For example, energy circuits and biogeochemical cycles in Systems Ecology (Odum 1983), food webs and spatio-temporal diversity in Community Ecology, and abundance and distribution of individuals in Population Ecology. Thus, too little consideration has been given to the effects of populations, communities, and ecosystems onto each other (Yodzis 1989).

Additionally, there is no consensus on the answer to the most fundamental question in the environmental sciences: How to deal with the complexity of ecosystems (e.g. Krebs 1995; Oksanen 1991; Peters 1977)? Different scientists have adopted different approaches: Some use statistical analyses (e.g. Beamish & Bouillon 1993; Cyr & Pace 1993; Francis & Hare 1994; Moen & Oksanen 1991; Xie & Hsieh 1989), others suggest non-linear processes between an abiotic and a biotic variable (e.g. Adkison *et al.* 1996; Gargett 1997; Hinch *et al.* 1995; Hsieh *et al.* 1991; Welch *et al.* 1995), and again others study the dynamics (e.g. Lawton & Pimm 1978; May 1972b; May 1976b; Pimm 1982; Pimm & Lawton 1977; Pimm *et al.* 1991; Saunders 1978)

and energy transfers in fairly detailed food web models (e.g. Christensen & Pauly 1995; Frost 1993; Kremer & Nixon 1978; Odum 1983; Pauly *et al.* 1996; Walsh 1981). But although most authors acknowledge that their analyses cannot reveal all aspects of nature, only few demonstrate strategies on how to deal with its full complexity (e.g. Leirs *et al.* 1997).

In this thesis I try to explain variability at the population level by the variability in the ecosystems as a whole, i.e. biotic and abiotic variables, more specifically, the variability in cohort survival, abundance and distribution of sockeye salmon (*Oncorhynchus nerka*) by biological and physical processes occurring in the Northeast Pacific Ocean. It is an attempt "to pry open the black box of recruitment" (Steele 1996) in order to understand long-term trends and to identify what to look for in cases where specific predictions should be made. My study thus follows the recommendation that one needs "to look deeper ... to more fundamental studies of the basic biology involved" (Sugihara 1996) in order to resolve the long-standing debate between the 'biotic' and the 'climate' school in ecology (with the first declaring internal biotic mechanisms and the later external environmental forcings as ultimate causes for population limitation (Steele & Henderson 1994; Sugihara 1995) - a controversy known in fisheries as the Thompson-Burkenroad debate (Hilborn & Walters 1992).

The choice of sockeye salmon populations has several reasons (apart from the very practical one that I was partially funded by a strategic grant which focused on this species (see Acknowledgements):

(1) Sockeye salmon is a harvested anadromous species whose management requires annual stock-specific (British Columbia, Canada) or river-specific (Alaska, USA) abundance estimates for adults returning to their parental streams or lake systems. Its economic importance makes sockeye salmon a well studied species with a wealth of available information.

(2) Sockeye salmon is semelparous with a constant life cycle and clearly defined life history stages in different habitats (Burgner 1991), which make it easier to study than species with mixed life-history stages in a single habitat.

(3) Of all Pacific salmon species sockeye salmon shows the lowest proportion of variability in total mortality that is accounted for by the freshwater stage (43%; Bradford 1995).

(4) Between the periods 1955-1958 and 1980-1989 sockeye salmon experienced a 3.0-fold increase in abundance, the largest of all epipelagic fish species in the Northeast Pacific (Brodeur & Ware 1995).

And (5), available composite distribution data for sockeye salmon, i.e. summer months data of several years, show that the main increase in abundance between the periods 1955-1958 and 1980-1989 occurred south of the Alaska Peninsula with a decline in abundance off the British Columbia coast (Brodeur & Ware 1995). The physical distance between these locations represents a spatial scale that makes it possible to distinguish regional abiotic and biotic environmental conditions derived from available oceanographic data (Ingraham & Miyahara 1989; Woodruff *et al.* 1987) and a spatially-explicit ecosystem model.

The Northeast Pacific also provides some advantages to study ecosystem effects on populations:

(1) Large spatially-explicit observational as well as model data-sets are available for many physical (Ingraham & Miyahara 1989; Woodruff *et al.* 1987) and biological variables (Brodeur 1988; Brodeur & Ware 1992; Brodeur & Ware 1995; Falkowski & Wilson 1992; Parsons 1972; Parsons *et al.* 1966; Pearcy *et al.* 1988; Sugimoto & Tadokoro 1997; Xie & Hsieh 1995), in addition to the long-term point measurements at Ocean Weather Station *P* at 50°N 145°W (e.g. Miller 1993b; Miller *et al.* 1991b; Parsons 1972; Parsons & Lalli 1988; Wong *et al.* 1995).

(2) During their marine phase North American salmon reside almost entirely within the Northeast Pacific. Thus, the Northeast Pacific represents a large enough spatial scale (Steele 1991) to investigate the important ecological mechanisms for anadromous as well as marine fish population regulation, stock or river specific variation in survival rates, and spatio-temporal distribution.

And (3), two international multimillion dollar projects (PICES (Hargreaves & Sugimoto 1993), GLOBEC (deYoung *et al.* 1994)) have been launched in recent years to investigate the relationship between climate and biological production. Progress in these projects can be incorporated in my ecosystem models and, representing the information flux counterflow, results from my work potentially could be used to modify the observational programs of these projects with respect to biological organization level, area and/or time of interest. After all, as Oleg Gritsenko remarked, "the north Pacific Ocean may be the best laboratory in the world to study ... how carrying capacity [a population variable] relates to fluctuations in climate [the ultimate forcing function in an ecosystem]." (MacCall 1996, annotations in brackets by yours truly)

1.2. Interannual Variability: Facts and Speculations

Sockeye Salmon

Interannual variability in sockeye salmon survival for 12 Fraser River stocks and 8 Bristol Bay river systems (Table 1.1) can be seen in the survival time series plotted in Fig. 1.1 and Fig. 1.2, respectively. (Please note that although the basic biological unit of management and thus data availability is different for the Fraser River (stock) and Bristol Bay (river system), for reasons of clarity I will refer to sockeye populations as 'stocks' in the following discussion. Nevertheless, I acknowledge that the unit stock, i.e. a collection of individuals that is dominated by birth and death rather than migration processes, is not easy to identify in practice (Walters 1986)). Fraser River stocks show no clear temporal "regimes" (Steele 1996) of unusually low or high survival except that all cohorts of the brood years 1957 to 1962 seem to have had a period of low survival. On the other hand, stocks from Bristol Bay river systems consistently show an interval of low survival between 1967 and 1972 followed by five years of high survival when, in 1977, most stocks returned very suddenly to a low survival phase with a trend towards improved survival thereafter.

The more consistent temporal variation in the survival index among stocks in the Bristol Bay river systems is also reflected in the cross-correlations between different stocks within the same river system where only 36% of the Fraser River (Fig. 1.3a) but 71% of the Bristol Bay stocks (Fig. 1.3b) are significantly positively correlated. Although stock survival index correlations among river systems (Fig. 1.3c) show a range from significantly negative to significantly positive with the majority being uncorrelated, it should be noted that the two largest stocks from each river system, i.e. the Adams stock of the Fraser River and the Kvichak stocks of the Bristol Bay

Table 1.1: Descriptive statistics of the return size for different stocks of the Fraser River system and different river systems of Bristol Bay. n is number of years in the time series.

	Median (in 1000s)	Mean (in 1000s)	S. D. (in 1000s)	n
Fraser River System (Stocks)				
Adams	81.6	2051.2	3322.2	41
Chilko River and North End Lake	1046.8	1283.3	1029.2	41
Horsefly River	6.7	823.1	2169.4	41
Stellako River	356.3	463.9	352.3	41
Late Stuart	57.8	423.4	721.0	41
Birkenhead River	261.3	377.2	323.2	41
Early Stuart	173.6	317.7	383.3	41
Weaver Creek	152.4	238.6	307.3	41
Seymour River	68.8	152.7	190.8	41
Cultus Lake	54.8	75.8	87.2	41
Upper Pitt River	61.1	72.0	51.5	41
Bowron River	28.1	50.0	50.6	41
Bristol Bay River Systems				
Kvichak	5160	11801.4	14970.6	35
Egegik	2857.5	4882.3	5055.6	36
Naknek	2501	3322.3	2518.1	35
Wood	1909	2313.6	1276.8	35
Ugashik	1110.5	2249.9	2423.6	36
Igushik	536	858.5	829.5	35
Branch	358	475.1	417.7	35
Togiak	377	474.3	304.2	35

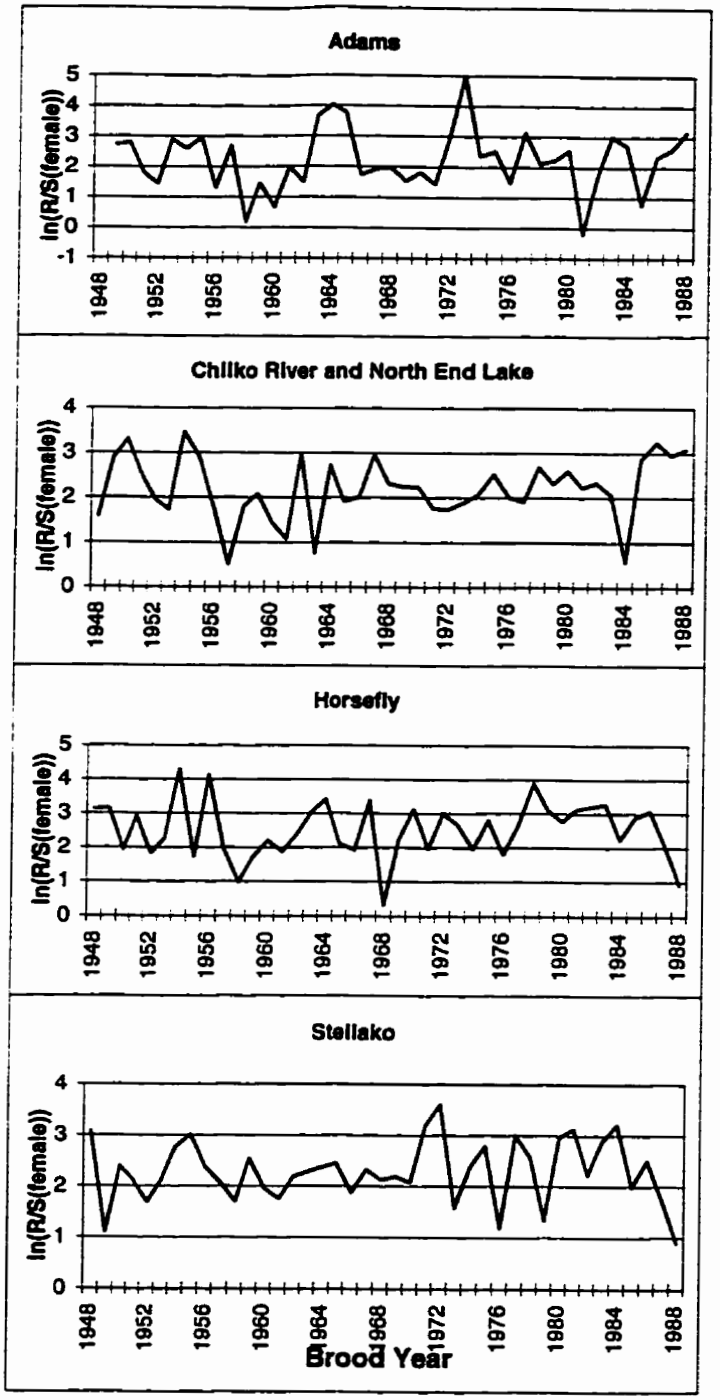
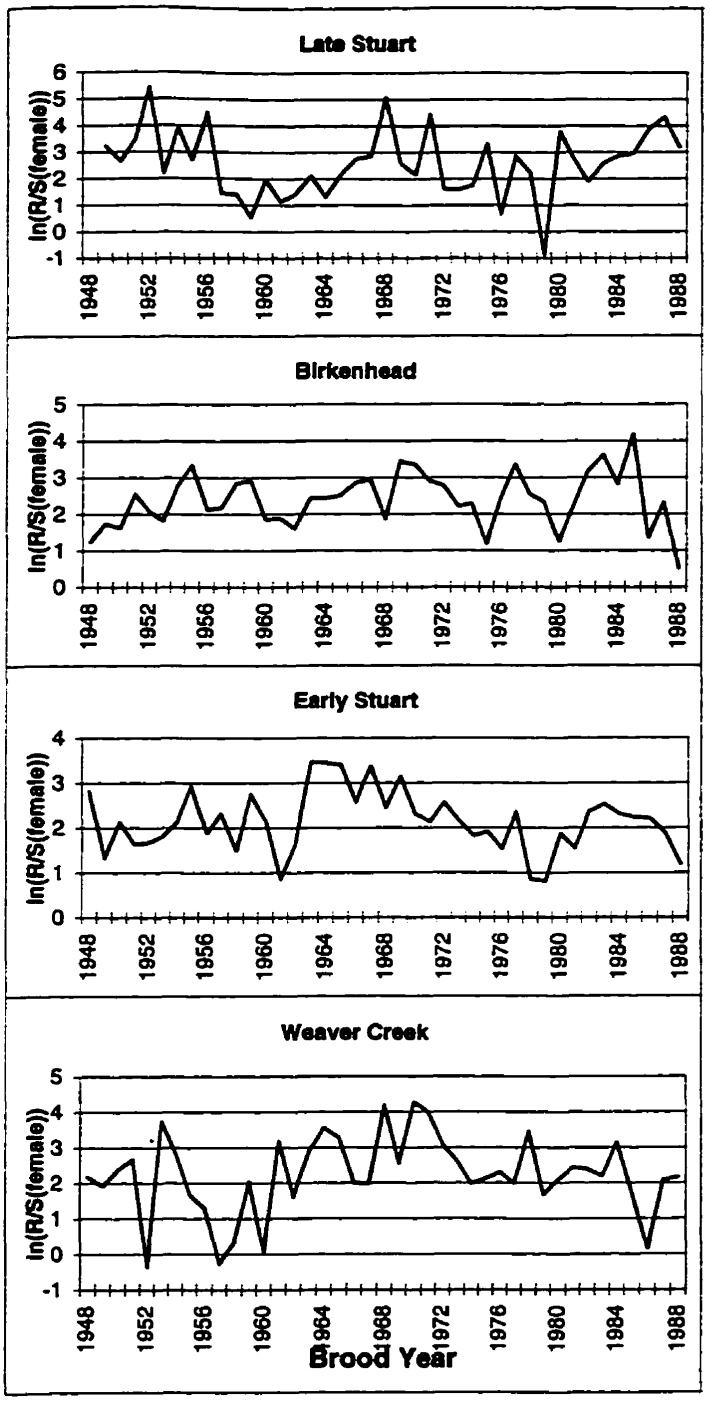


Fig. 1.1: Survival for 12 sockeye salmon stocks of the Fraser River system (British Columbia, Canada) for the brood years 1948-1988 with:

$$(\text{Survival Index})_{i,j} = \ln\left(\frac{\text{Total Recruitment of Brood Year Class i}}{\text{Female Escapement in Year i}}\right)_j .$$

i and j denote brood year and stock, respectively. For geographical location and coordinates of lakes or rivers see Groot and Margolis (1991): Geographical Index, p.523.



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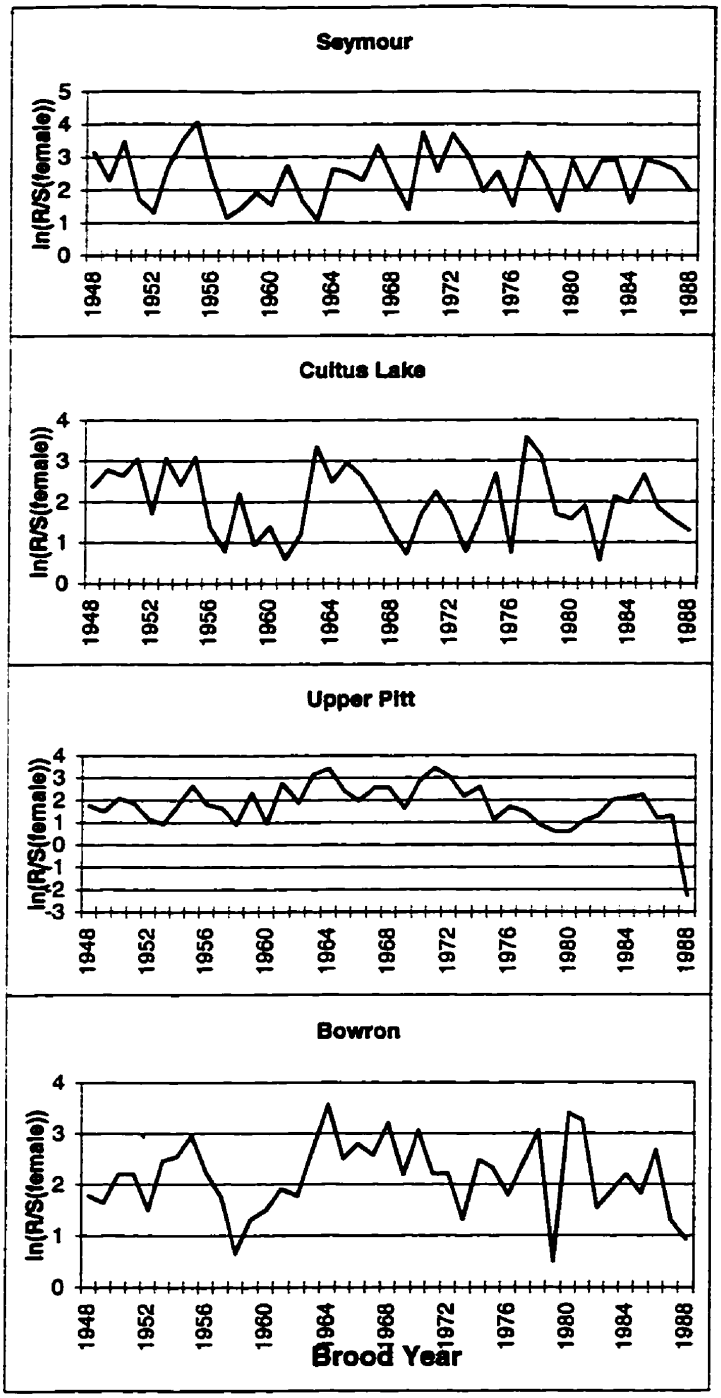

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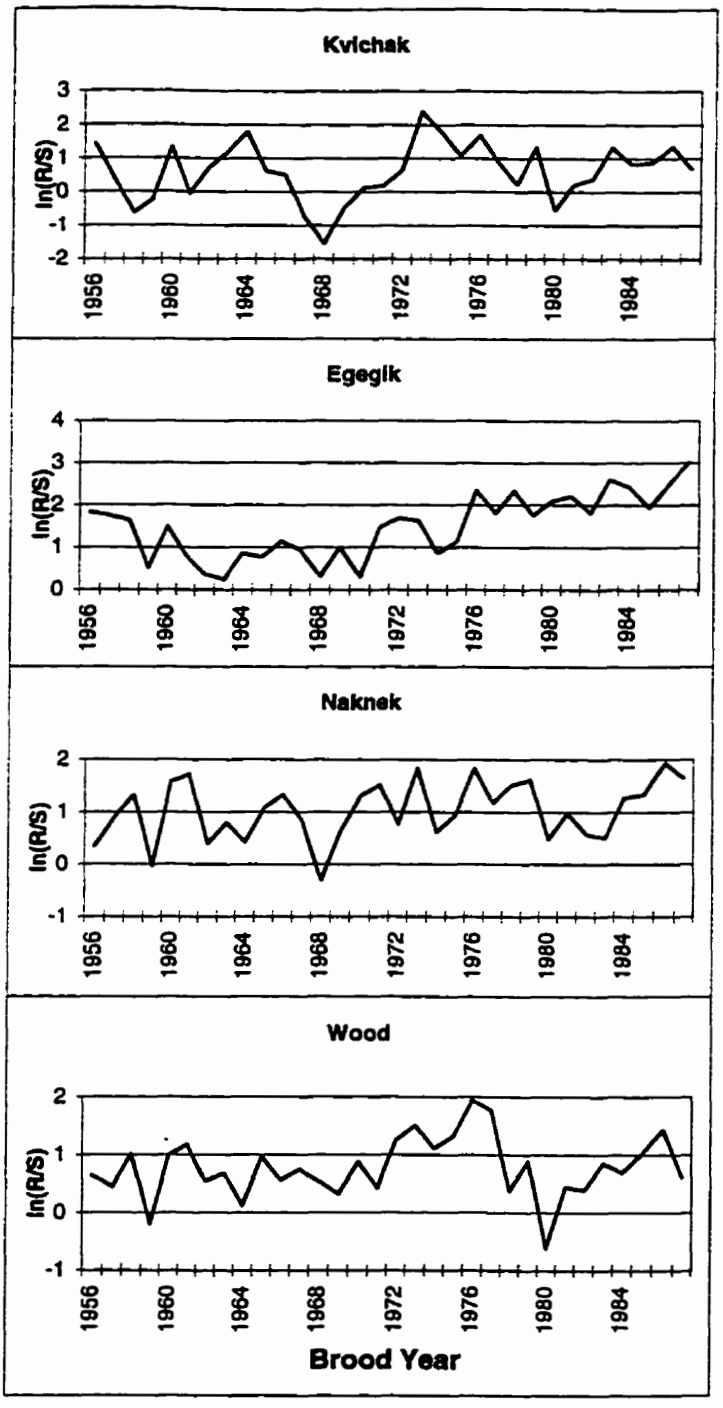
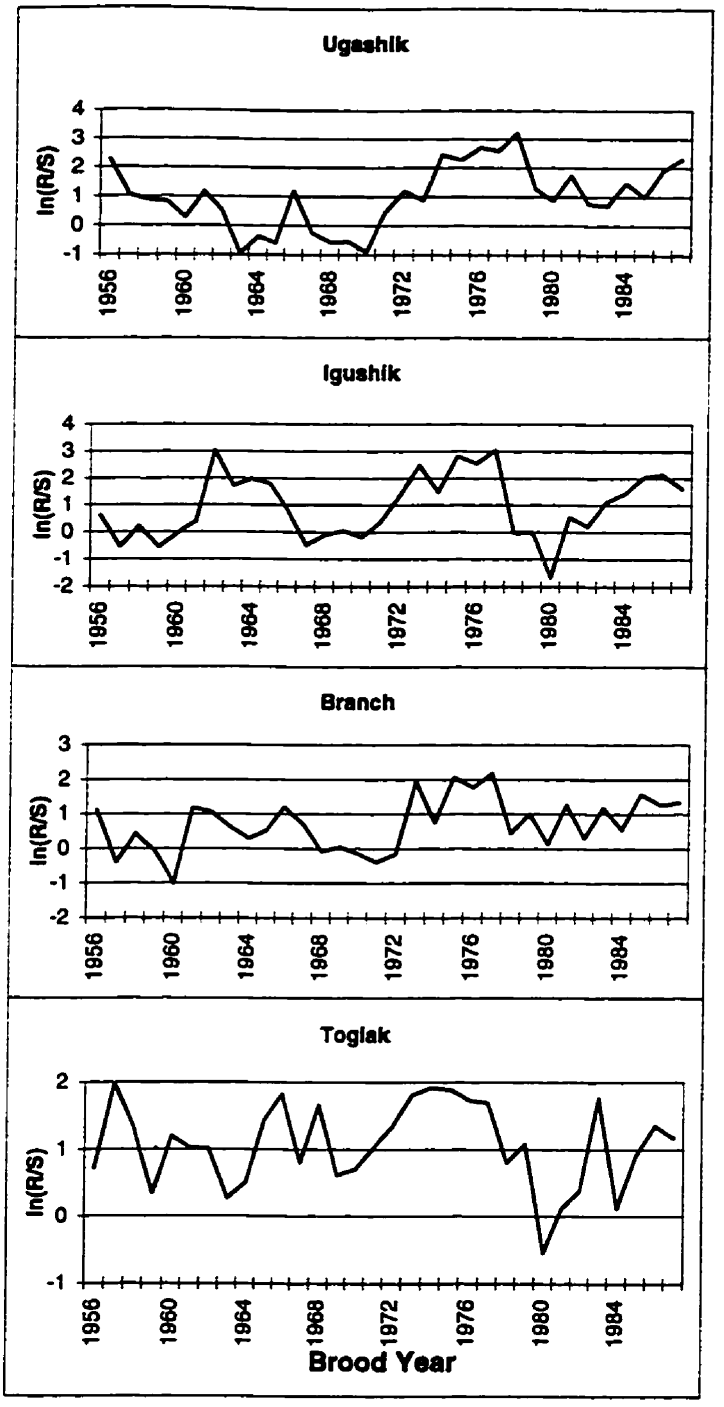


Fig. 1.2: Survival for 8 sockeye salmon river systems of the Bristol Bay area (Alaska, USA) for the brood years 1956-1987 with:

$$(\text{Survival Index})_{ij} = \ln\left(\frac{\text{Total Recruitment of Brood Year Class i}}{\text{Escapement in Year i}}\right)_j .$$

i and j denote brood year and river system, respectively. For geographical location and coordinates of lakes or rivers see Groot and Margolis (1991): Geographical Index, p.523.



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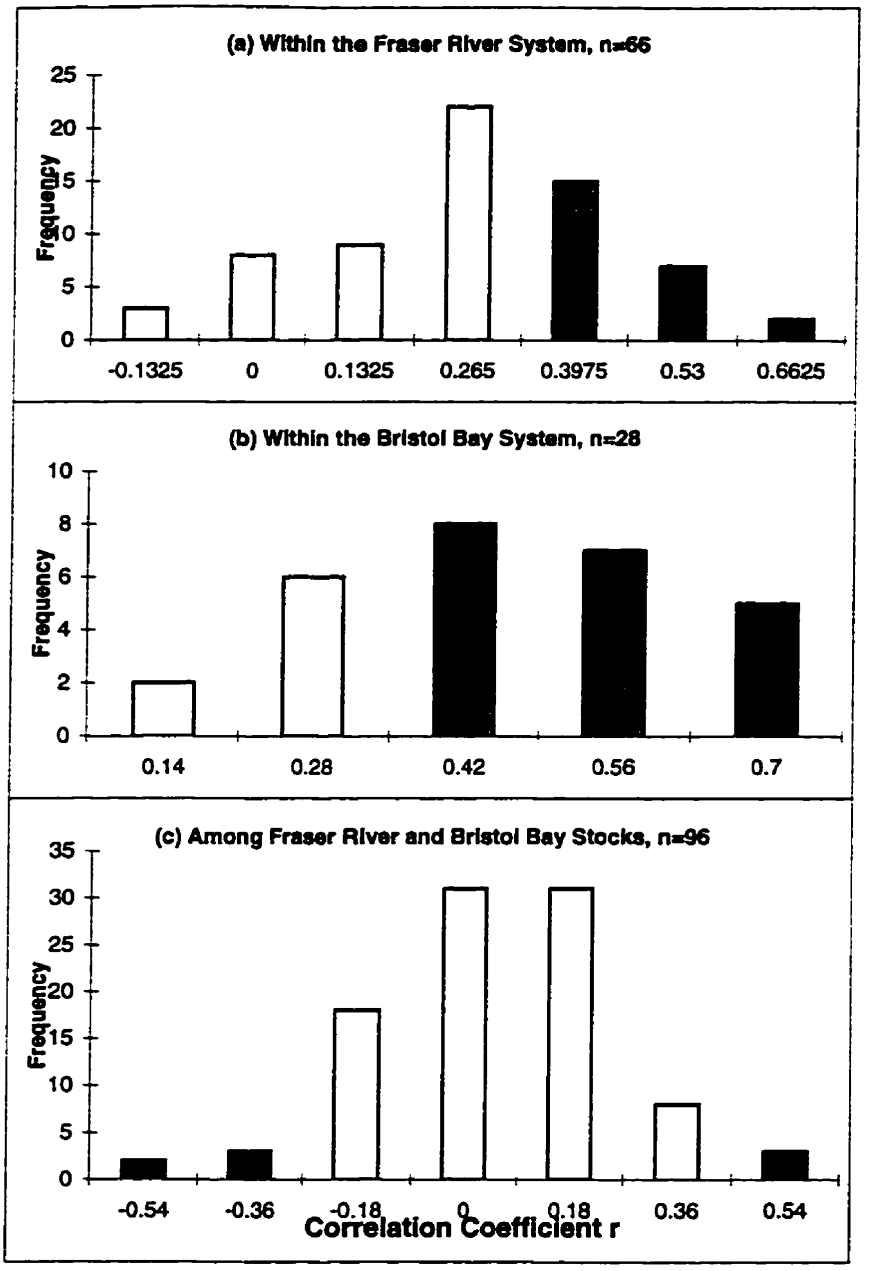


Fig. 1.3: Histograms of correlation coefficients from cross-correlations of survival indices for different sockeye salmon stocks. a) Stocks within the Fraser River system ($r_{0.05(1),38}$ = 0.264); brood years 1948-1988; b) Stocks within the Bristol Bay area ($r_{0.05(1),30}$ = 0.296), brood years 1956-1987; (c) Among stocks of the Fraser River system and Bristol Bay area ($r_{0.05(2),30}$ = 0.349), brood years 1956-1987. For definitions of survival indices see Fig.1.1 and Fig.1.2. Values in brackets are the critical values for the correlation coefficient r at the 0.05 significance level. Note that x-axis labels represent class maxima. Shaded bars are significant.

system, contributing 32.5% and 44.7% to the mean total return of the respective river system (Table 1.1), have a significant positive correlation coefficient of 0.42.

The cohort survival time series for combined Fraser River and combined Bristol Bay stocks (Fig. 1.4) show that the later have generally a greater variability. Combined Fraser River stocks had a phase of poor survival from 1956 to 1963 and that interannual variabillity seems to have increased from 1975 to 1988 compared to pre-1975. Bristol Bay stocks had a low survival phase from 1966 to 1971 and a five year high phase from 1972 to 1977. Most importantly, there is no indication of exceptional high survival in sockeye after a hypothetical change in carrying capacity 1976/77 (Brodeur & Ware 1995; Ebbesmeyer *et al.* 1991; Ishida *et al.* 1993; Kerr 1992; MacCall 1996; Venrick *et al.* 1987) as has been conjectured for many fish populations in the Northeast Pacific (Beamish 1993; Beamish & Bouillon 1993; Brodeur & Ware 1995) and which has been attributed to a shift in the ocean-atmosphere system in general and in the strength, extent and location of the Aleutian Low Pressure System in particular (Beamish 1995). Note that the lower survival rate of Bristol Bay sockeye in Fig. 1.4 is a consequence of different escapement indices used in the calculation of cohort survival rate, i.e. female spawners for Fraser River and total escapement for Bristol Bay stocks.

Inconsistencies

In spite of the acceptance by many scientists of (1) a climate shift event in the Northeast Pacific in the mid-1970s and (2) a link between climate and fish recruitment variability, there are several serious problems (Baumann 1998) associated with some of the data and conclusions that have been drawn from them, as well as conceptual flaws in the interpretation how ecosystems work, which I will discuss in the following paragraphs.

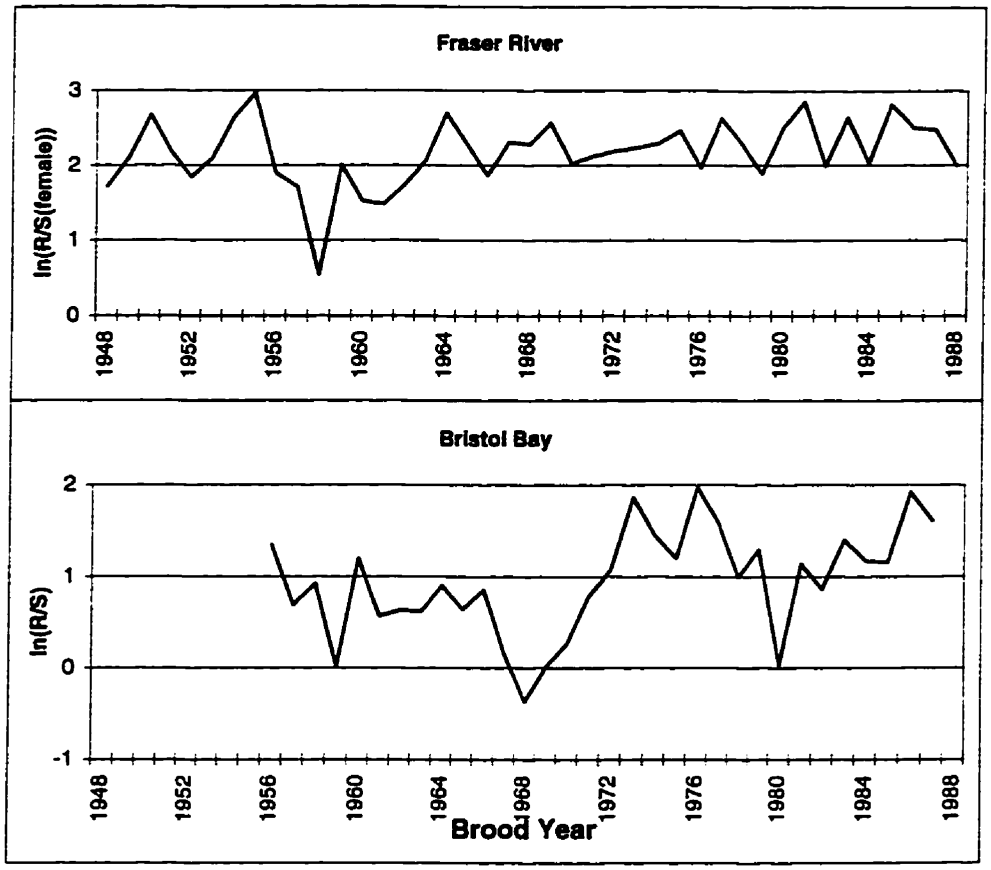


Fig. 1.4: Cohort survival for combined stocks of the Fraser River system (brood years: 1948-1988) and combined river systems of the Bristol Bay area (brood years: 1956-1987) with:

$$(\text{Survival Index})_i = \ln \frac{\sum_j (\text{Total Recruitment of Brood Year Class i})_j}{\sum_j (\text{Escapement in Year i})_j}.$$

i and j denote brood year and stock, respectively. Escapement is total female spawners for the Fraser River system and total escapement for the Bristol Bay area stocks.

Beamish & Bouillon (1993) state that "there was no significant correlation observed when we used linear regression analysis to compare the annual Aleutian Low Pressure Index, and the annual North Pacific Ocean Salmon Production ..." Surprising about this result is that in spite of using doubtful proxies (i.e. "index-of-measurement error" (Baumann & LeBlond 1996): ambiguous units, location and/or time of measurement) for salmon production (catch) and the Aleutian Low (sum of winter and spring means of the area of the North Pacific Ocean covered by the Aleutian Low pressure system with less than 100.5 hPa) plus various smoothing techniques, Beamish and Bouillon couldn't come up with a significant correlation. These authors also failed to report how many differently treated datasets they had scanned in search for a correlation, one of the quality control criteria suggested by Walters & Collie (1988). To make myself clear: There may well be a link between climate and fish production in the Northeast Pacific, but because of the many non-linear functional relationships in the causal chain of events it is unlikely to be detected by linear regression analysis - a problem which has already been addressed by others (e.g. Francis & Hare 1994).

Brodeur & Ware (1995) report that sockeye salmon experienced a 3.0-fold increase in abundance between the periods 1955-1958 and 1980-1989 (Fig. 1.5), the largest population growth of all epipelagic nekton in the Northeast Pacific. It could be argued that the increase in abundance after the hypothetical 1976/77 climate event should be the largest for sockeye salmon of all salmon species because it enters the ocean at a larger size that makes it possible to exploit spatially and temporally independent production patches the best. Or increased freshwater survival rates due to a temperature rise in lakes in Alaska could have affected the increase in total survival in some sockeye salmon stocks through higher body growth rates and thus larger

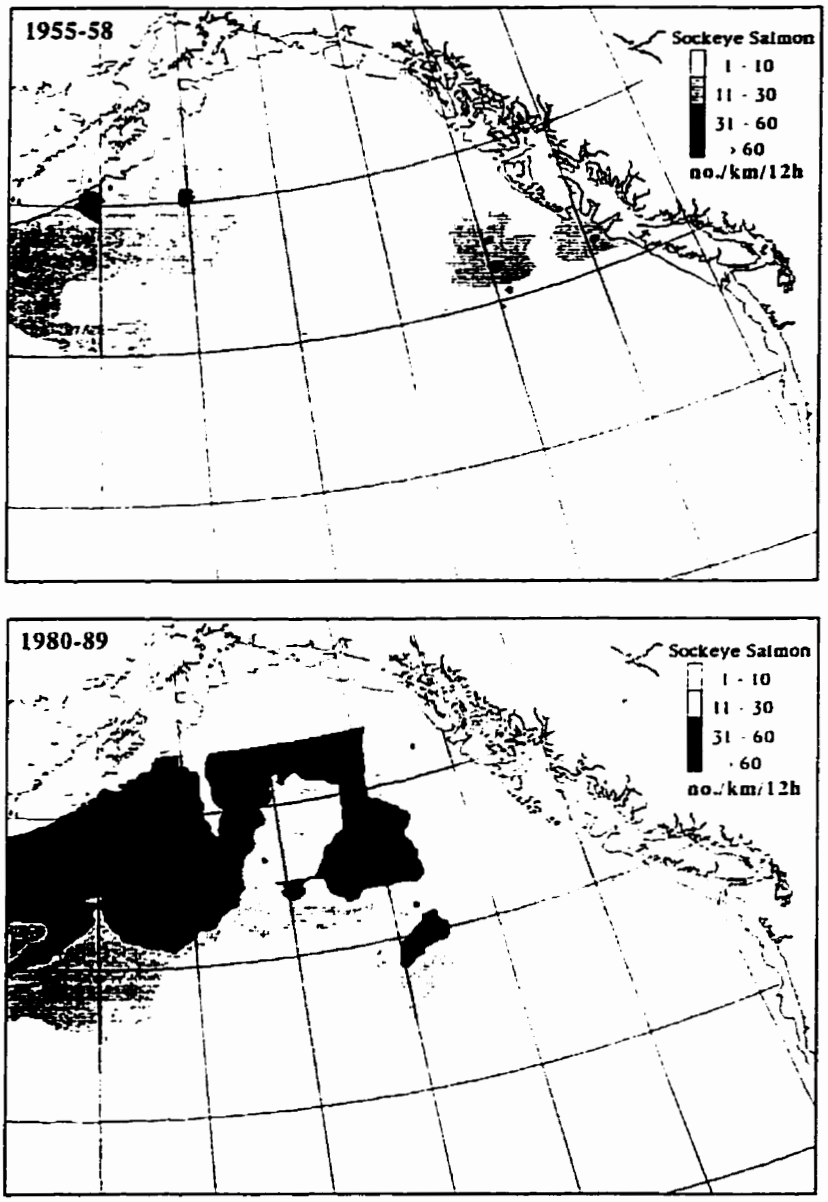


Fig. 1.5: Distribution and abundance of combined late juvenile and adult stages of sockeye salmon for the periods 1955-1958 and 1980-1989. Abundance is estimated as the number of fish caught per kilometer of surface gill net per 12 hours. Data were collected from May to August in both periods. Adapted from Brodeur and Ware (1995).

body size when entering the marine environment making it easier for this species to exploit prey patches better and escape predators. However, a look at escapement (Fig. 1.6) and cohort survival data (Fig. 1.4) for combined Fraser River and combined Bristol Bay stocks reveals, first, that total sockeye abundance in the Northeast Pacific is largely determined by Alaskan stocks, and second, that increased abundance in the 1980s may well be the result of an extremely large escapement in 1980, although cohort survival was rather low for that brood year.

I must admit that my objections do not resolve the increased abundance of other epipelagic nekton (Brodeur & Ware 1995), of which many are exclusively marine, nor the doubling in summer zooplankton (size: >350 μm) standing stock in the Northeast Pacific between the periods 1956-1962 and 1980-1989 (Fig. 1.7; Brodeur & Ware 1992). However, there have also been no explanations why higher trophic levels do not consume the increased zooplankton standing stock nor why it does not have any, depending on the structure of the food chain , positive or negative consequences on phytoplankton concentrations (Fig. 1.8) .

Physics → ... → Fish

Changes at various spatial and longer-than-seasonal temporal scales have been reported for several systems, or its components, of the North Pacific. These reports comprise interannual and interdecadal shifts in radiation flux (Sugimoto & Tadokoro 1997), sea surface temperature and wind speed (Royer 1989; Sugimoto & Tadokoro 1997; Ware 1995); in strength, location, spatial extent, and duration of the Aleutian Low Pressure System with the associated modification in strength and direction of ocean currents (Trenberth 1990), mixed layer depth and mixing events (Polovina *et al.* 1994), and spatio-temporal changes in upwelling (Xie & Hsieh 1995); in

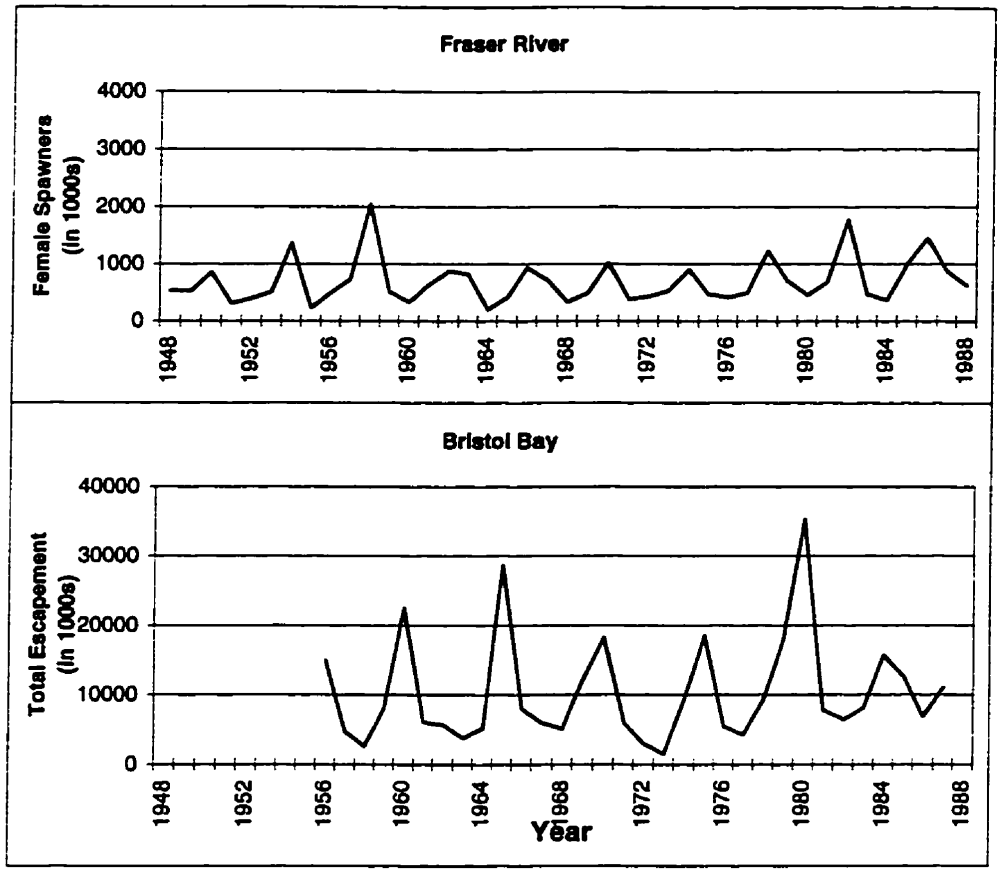


Fig. 1.6: Escapement index for combined stocks of Fraser River system (female spawners) and Bristol Bay area (total escapement). Note the different scales on the vertical axes and the large escapement for Bristol Bay sockeye in 1980.

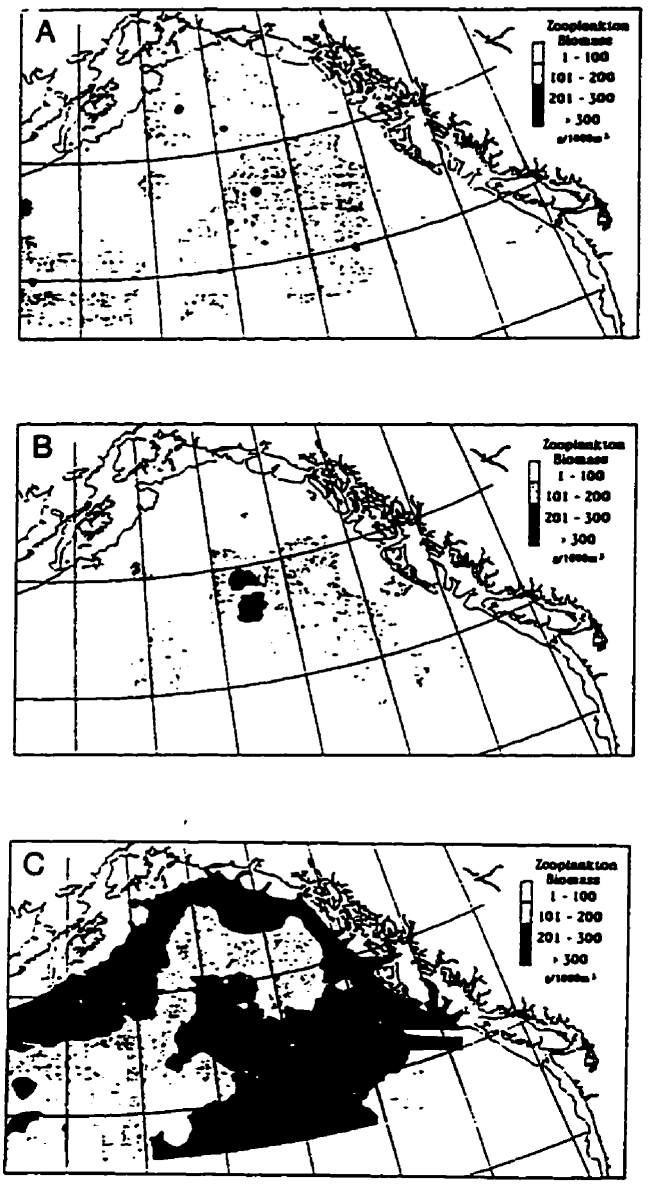


Fig. 1.7: Summer (15 June - 31 July) zooplankton (size: >350 μm) biomass concentrations (in g wet weight / 1000 m^{-3}) from composite data for (A) 1956-1959, (B) 1960-1962, and (C) 1980-1989 (without 1986). Adapted from Brodeur and Ware (1992).

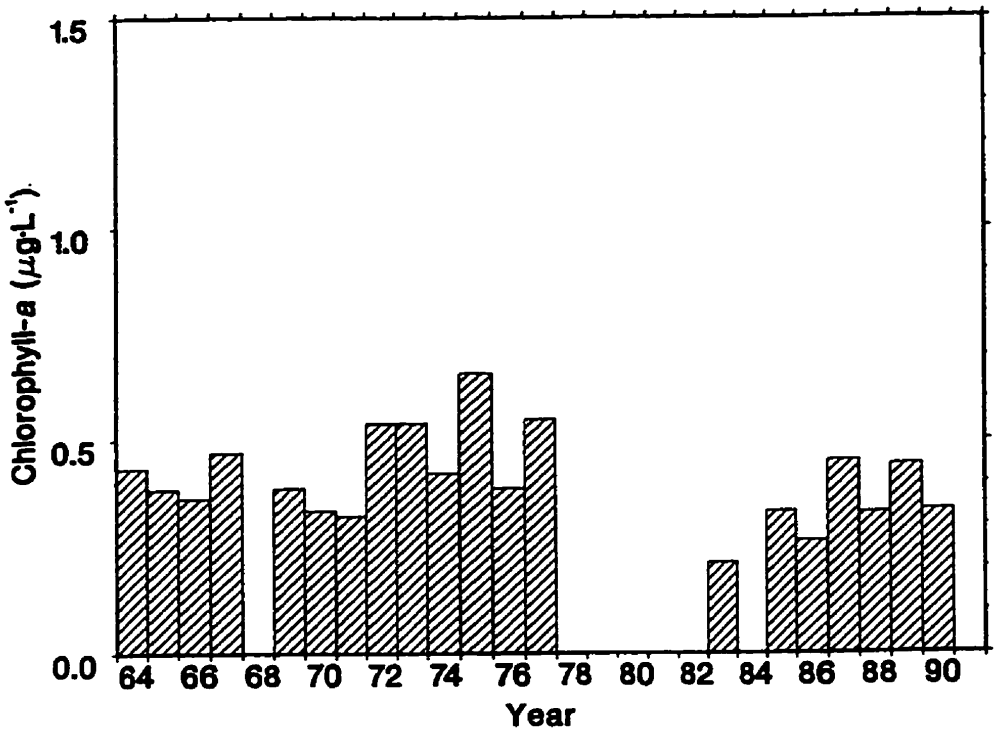


Fig. 1.8: Annual mean chlorophyll-a concentrations at Ocean Weather Station *P* (50°N 145°W) from 1964 to 1991. Note that variability around the mean is not reported, thus no conclusions about seasonal and or spatial variability (patchiness) in the samples can be inferred. Adapted from Wong et al. (1995).

chlorphyll-a concentration (Sugimoto & Tadokoro 1997; Venrick *et al.* 1987; but see also Falkowski & Wilson 1992; Falkowski & Wilson 1993; Welch 1993; Wong *et al.* 1995); PHOEBE in phytoplankton standing stock (McAllister 1972); in zooplankton concentration (Brodeur & Ware 1992; Longhurst *et al.* 1972; McAllister 1972; Sugimoto & Tadokoro 1997); in fish production (Beamish 1993; Beamish 1995; Beamish & Bouillon 1993; Brodeur & Ware 1995; Francis & Sibley 1991; Hollowed & Wooster 1992); and in many other environmental indicators (Ebbesmeyer *et al.* 1991; Polovina *et al.* 1994). Large-scale, long-term configurations in abiotic and biotic variables have been termed "regimes", with the relatively rapid (with respect to the mean persistence of a regime) potentially reversible transformations being called 'climate events' (Polovina *et al.* 1994), 'climate or regime shifts' (Francis & Hare 1994; Kerr 1992; Steele 1996), or 'changes in carrying capacity' (Brodeur & Ware 1995; Ishida *et al.* 1993; MacCall 1996; Venrick *et al.* 1987), depending on the system studied. Ware (1995) has identified abiotic environmental oscillations at various time scales with periods of 2-3 years, 5-7 years, 20-25 years and 50-75 years. He found that regime shifts (like that in 1976/77) occur when the two lower frequency oscillations are in phase, a general conclusion that may be questioned considering that only 100 years of data were available.

Reports on regime shifts usually include speculations on either their ultimate causes or the mechanistic chain of events leading from one phenomenon to another supposedly dependent phenomenon. Simple (as opposed to complex, i.e. including factor interaction, feedback loops, time lags, thresholds, limits and breakpoints (Baumann & LeBlond 1996)), although sometimes complicated (many components), linear explanations invoke external mechanisms that drive a change. Examples are changes in the total or spectral output of the sun (Kelly & Wigley 1992; Lacis & Carlson 1992; Maddox 1995; Schlesinger & Ramankutty 1992), or proxies thereof such

as the sunspot cycle (Friis-Christensen & Lassen 1991; Kerr 1987; Kerr 1991) or the atmospheric semi-diurnal tide (Cooper 1993), or variation in the earth's angular momentum (Beamish 1996 pers. comm.). More complex externally forced causes for regime shifts involve atmospheric teleconnections, such as El Niño - Southern Oscillation events (Kerr 1992; Mann & Lazier 1991; Parsons & Lalli 1988; Trenberth 1990; Ware 1995; Wooster & Fluharty 1985), climatic cycles (Latif & Barnett 1994; Ware 1995) and food chain considerations (Ware & Thomson 1991).

Further, speculations on the causal chain of events are easy to imagine given the many components and processes in an ecosystem (Walters & Collie 1988). Examples for the physical and biological interactions that have been investigated in order to understand the relationship between climate and fish production are: atmospheric pressure and fish production (Beamish & Bouillon 1993), wind and water column stability (Polovina *et al.* 1994), wind and nutrients (Blackett 1993), wind and chlorophyll concentration (Sugimoto & Tadokoro 1997), wind and primary production (Ware & Thomson 1991), wind and zooplankton standing stock (Brodeur & Ware 1992), wind and fish survival (Blackett 1993), water column stability and primary production (Parsons *et al.* 1966), water column stability and fish production (Gargett 1997), chlorophyll concentration and zooplankton standing stock (Sugimoto & Tadokoro 1997), phytoplankton standing stock and fish production (Ware & Thomson 1991), phytoplankton production and fish production (Iverson 1990), and fish abundance and zooplankton standing stock (Sugimoto & Tadokoro 1997). What these studies have in common is the often explicit but sometimes only implicit reference to primary production as the ultimate cause for changes in fish survival or growth. For example, increased water column stability in the northern Northeast Pacific will provide phytoplankton with more light (Gargett 1997), resulting in higher primary production which then will be transferred up the food chain to fish. However, the statement that

"fish production is ultimately dependent on primary production" (Francis & Sibley 1991) is only true if taken to its extreme: If there is no primary production in the ocean there will be no fish production. Assertions about merely qualitative effects of increased primary production on fish survival and growth should generally be distrusted. (Note that primary production has been successfully used to summarize fish production in mass-balance models (Baumann 1995; Christensen & Pauly 1995; Pauly & Christensen 1995a; Pauly & Christensen 1995b; Pauly *et al.* 1996), but the following two criticisms still apply.)

Although many interactions are supported by regression and/or more process oriented analysis, most authors do not take into account two important factors regarding fish. First, the biology of organisms on evolutionary and ecological time scales: Organisms are adapted to their environment and fish survival and production is not exclusively determined by bottom-up effects For example, phytoplankton species in low light high nutrients environments are usually larger than species in high light low nutrients environments (cf. Parsons *et al.* 1984, Fig.121). Size differences in primary producers in turn result in different communities (compare the extremes of the short food chain of the Peru Current upwelling system (Ware 1992) with the long food chain of the Subarctic Pacific (Parsons & Lalli 1988); see also references for ecosystem changes given in Sharp 1995) which determine the transfer of primary production up the food chain, i.e. the parameters in the simple energy transfer equation:

$$P_L = E^{L-1} P_{prim} \qquad \text{(Eq. 1.1)}$$

where P is production of trophic level L and primary producers (*prim*), and E represents the mean transfer efficiency (for a criticism of the trophodynamic concept see Cousins 1987; Peters 1977, as well as Chapter 5: Conclusions). Transfer efficiency between organisms of two adjacent trophic levels is the product of growth efficiency of the higher trophic level, determined by the

energy allocation within a predator organism (metabolism, body growth, reproduction), and predation efficiency, i.e. the proportion of prey production taken by the predator. Both of the later efficiencies are consequences of life history strategies that have developed in evolutionary time and the trade-off an organism has to make between predation risk and the benefits of other activities in ecological time, e.g. foraging (Lima & Dill 1990). Also, the more evolved an organism is, the less susceptible it is to the direct effects of the physical environment, which is why many aquatic predators are migratory and can thus exploit spatially and temporally independent production patches (Sharp 1995; Steele 1980).

And second, the spatial and temporal scales of mechanisms and supporting data: In many analyses there is a risk of committing an "index-of-measurement error", i.e. ambiguous units, location and/or time of measurement (Baumann & LeBlond 1996). Assuming that there exists a critical phase for cohort survival in Pacific salmon (Walters & Juanes 1993) and that this phase is the early marine life history stage, the space and time scales of possible mechanisms, the chain of events, and supporting data are crucial for an understanding of the ecological processes (Levin 1992). By analogy, why care about a low annual mean temperature in Europe as long as the weather is fine when you are in Rome on vacation.

In summary, one ultimate cause has been identified for increased fish production in the Northeast Pacific between the late 1950s and 1980s, i.e. the strengthening of the Aleutian Low pressure system prevalent during the winter months (e.g. Beamish & Bouillon 1993; Gargett 1997). Although "coupling of [higher trophic level] stocks to the production base is an almost untouched research area" (Miller 1993a) mechanisms connecting meteorological events with production processes, i.e. survival and growth, at higher trophic levels (e.g. fish) have been frequently suggested. I contend that without taking into account the biology of organisms at

ecological spatial scales, and evolutionary and ecological time scales, and without the development of rigorous coupled process models for higher trophic levels, i.e. environmentally-driven spatially-explicit trophodynamic simulations, such suggestions are mere opinions.

1.3. Seasonal Variability: A Summary of the Current Paradigm and Some of Its Flaws

Sockeye Salmon

This section is a summary of the current interpretation of the principal ecological mechanisms in the Northeast Pacific on the seasonal time scale. Literature is reviewed with respect to relevancy to sockeye salmon marine survival and distribution in the Northeast Pacific Ocean. Arguments are presented qualitatively and some perceived inconsistencies are discussed. More detailed and quantitative reviews on sockeye salmon marine feeding ecology, ecosystems and physical oceanography of the Northeast Pacific can be found in Chapter 2: Sockeye Salmon and the Marine Environment.

Usually after one or two years of residence in a lake (Burgner 1991; Pearcy 1992) North American juvenile sockeye salmon enter the Northeast Pacific Ocean from early to late summer (Fraser River stocks through Johnstone Strait in June - July; Bristol Bay stocks through passages in the Aleutian island chain in July - August; Burgner 1991), where they stay near the coast (D. Welch 1998 pers. comm.). At this life history stage and with a body length of about 10 cm (French *et al.* 1976) sockeye salmon feed mainly on mesozooplankton (size: 0.2-20 mm). At sea, juvenile sockeye salmon basically drift with the Alaska Current around the Alaskan Gyre. Sometime after the first winter at sea and with a body length around 20 cm (French *et al.* 1976) sockeye salmon change their prey size preference and switch to a diet of mainly macrozooplankton (2-20 cm). For a given size class, geographic (LeBrasseur 1966; Pearcy *et al.* 1988) and temporal differences (Favorite 1970; Healey 1991; Manzer 1968) in diet composition reflect changes in prey availability rather than food preferences. As a consequence, lists of stomach contents items represent the availability and hence the relative abundance of prey in the environment (Healey 1991). In summary, juvenile, immature, and maturing ocean sockeye

salmon are opportunistic (within a size class) polyphagous planktivores (Healey 1991; LeBrasseur 1966; Pearcy *et al.* 1988), with maturing sockeye additionally feeding on squid and fish (Favorite 1970; LeBrasseur 1966; Manzer 1968; see also review by Brodeur 1990).

Prey, Competitors and Predators

Food availability for North American sockeye salmon is dominated by production and advection processes in the Central Subarctic Domain (Brodeur & Hollowed 1993; Ware & McFarlane 1989; Wickett 1967), the largest of the four domains of the Northeast Pacific (Ware & McFarlane 1989). Here, while little information is available on macrozooplankton (2-20 cm), partly because of the problems associated with sampling of highly motile groups within the zooplankton community, mesozooplankton (0.2-20 mm) has been studied extensively (Mackas & Frost 1993; Parsons & Lalli 1988). Mesozooplankton is dominated by copepod species with an annual life cycle during which the organisms complete ontogenetic vertical migrations (Mackas *et al.* 1993; Miller *et al.* 1984) with early life history stages arriving at the surface in spring, and copepods reaching their greatest biomass density in May to June (Parsons & Lalli 1988), shortly before they start to migrate to depth (Miller *et al.* 1984). Mesozooplankton mainly feed on microzooplankton (20-200 μm) and are believed to control microzooplankton as well as microphytoplankton (20-200 μm) standing stocks (Booth *et al.* 1993; Dagg 1993; Gifford 1993; Landry *et al.* 1993a; Landry *et al.* 1993b; Mackas *et al.* 1993; Miller *et al.* 1991b).

Nauplii of large copepods may, at least in principle, be capable of feeding upon nanophytoplankton (2-20 μm) and thus assist microzooplankton control nanophytoplankton standing stock in spring, while the later life history stages of copepods also feed upon earlier life history stages of organisms of the same adult size class. Microzooplankton standing stock

consists of small heterotrophic flagellates and ciliates (Booth *et al.* 1993; Frost 1987) and attains its largest density in winter (LeBrasseur & Kennedy 1972) because of the absence of its mesozooplankton predators (Dagg 1993; Gifford 1993; Mackas *et al.* 1993). In winters with low primary productivity, i.e. larger depth of mixing, microzooplankton may be able to maintain high densities by shifting to a diet of particulate organic matter (POM) + associated bacteria (Morel *et al.* 1991). Microzooplankton are believed to control nanophytoplankton standing stock (Booth *et al.* 1993; Dagg 1993; Miller *et al.* 1991b; Strom *et al.* 1993; Welschmeyer *et al.* 1993).

Phytoplankton standing stock in the Northeast Pacific Ocean is supposedly constant throughout the year (Parsons & Lalli 1988; Wong *et al.* 1995) with an approximate doubling in primary productivity from winter to summer (Wong *et al.* 1995), a result of increased insolation and the stratification of the water column. Primary production per unit biomass does not seem to be bottom-up limited to any extent (Welschmeyer *et al.* 1993), which is reflected in the never depleted nitrate pool (Parslow 1981), thus grazing and sinking determine the standing stock. The dominant size class of primary producers in the Northeast Pacific is nanophytoplankton (size 2-20 μm; Booth *et al.* 1993; Parsons 1972) which outcompetes larger phytoplankton species, due to iron limitation of the latter (Martin & Fitzwater 1988; Martin *et al.* 1994). Nanophytoplankton standing stock is grazer-controlled by microzooplankton (Booth *et al.* 1993; Dagg 1993; Miller *et al.* 1991b; Strom *et al.* 1993; Welschmeyer *et al.* 1993), which has higher growth rates than their food source (Miller *et al.* 1991b). Because their feeding apparatus is too coarse, later life history stages of meso- and macrozooplankton are not able to consume nanophytoplankton (Miller *et al.* 1991a). However, episodic atmospheric deposition of iron, i.e. iron input events, can result in a dominance of microphytoplankton species over nanophytoplankton (Donaghay *et al.* 1991; Duce & Tindale 1991). Microphytoplankton will the be either nitrate limited or grazer-limited by

mesozooplankton. Microzooplankton is the same size class as microphytoplankton and is thus too small to control the larger primary producers (Miller *et al.* 1991b).

Only little quantitative information is available on competitors and predators of sockeye salmon. Main competitors in the Northeast Pacific are other salmon species (Groot & Margolis 1991), especially pink salmon (Burgner 1991). Other competitors in the marine environment are the saury, a small pelagic fish, and the larger pomfret, both of which are summer visitors to the Northeast Pacific (Brodeur 1988; Pearcy 1993) and have about the same diet as sockeye salmon (Pauly *et al.* 1996). Important predators on immature and maturing sockeye salmon are the daggertooth (Pauly *et al.* 1996), the salmon shark, and the blue shark, a summer visitor (Brodeur 1988). Little is known about predators on juvenile sockeye salmon, except for stocks on the west coast of Vancouver Island which in warm years suffer high mortality from northward expanding mackerel stocks from California.

Inconsistencies

There are some inconsistencies in the current theoretical framework of the ecosystems of the Northeast Pacific, and the question of what controls what, where and when has not been answered satisfactorily yet, although syntheses have been attempted (Frost 1987; Frost 1991; Frost 1993; Miller 1993a; Miller *et al.* 1991a; Miller *et al.* 1991b). Ignoring the ontogenetic vertial migrations of mesozooplankton for a moment and following a simple food chain argument (Hairston *et al.* 1960), if mesozooplankton biomass increases in summer this means that copepod density is bottom-up controlled rather than top-down. Microzooplankton biomass, which forms the main food source of mesozooplankton in the Central Subarctic Domain, is thus top-down controlled and should be reduced to a level where it is unable to control phytoplankton

density, hence phytoplankton biomass should increase until it is bottom-up limited. An increase in mesozooplankton standing stock has been observed in summer (Parsons & Lalli 1988) and so has the decline in microzooplankton density (LeBrasseur & Kennedy 1972). However, primary production per unit biomass is not bottom-up limited in summer (Welschmeyer *et al.* 1993) and phytoplankton standing stock has been reported constant throughout the year (Wong *et al.* 1995). It has also been speculated that the life-history-induced September minimum in copepod density might cause the observed slight increase in phytoplankton standing stock (Miller *et al.* 1984; Parsons & Lalli 1988). Yet, the life-history induced September minimum in copepod density should decrease rather than increase the phytoplankton standing stock in October.

One explanation for the inconsistency in the conceptual framework is that the constant phytoplankton standing stock is based on chlorophyll-a and not phytoplankton carbon concentrations. In a seemingly forgotten publication, McAllister (1969) reported changes in the carbon-to-chlorophyll-a ratio that, together with new data on chlorophyll-a concentrations (Wong *et al.* 1995), indicate a possible fivefold increase in phytoplankton standing stock in summer, which is supported by carbon-based summer estimates of phytoplankton concentrations (Booth *et al.* 1993). Another explanation may be found in the lack of resolution of the data with respect to spatio-temporal variability in population control processes. Because of the coarse spatio-temporal scale of the data used in my study, I will not be able to address this second explanation, but for a promising approach see Steele & Henderson (1992a).

Another interesting aspect related to trophic cascading (Carpenter *et al.* 1985), i.e. the direct and indirect effects of interactions within a food chain (Pimm 1992), is that although Brodeur and Ware report a doubling in summer mesozooplankton biomass (Brodeur & Ware 1992) and a similar increase in many fish populations (Brodeur & Ware 1995) in the Northeast Pacific

between the late 1950s and the 1980s, Wong et al. (Wong *et al.* 1995) could not detect any long-term signal in chlorphyll-a at Ocean Weather Station *P* from 1964 -1991. Data can possibly be reconciled with current understanding by looking at the spatio-temporal scales of observations (for example compare Brodeur & Ware (1992) with Longhurst *et al.* (1972)).

1.4. Approach, Assumptions and Anticipation

My attempt in this thesis is to go beyond the speculations of the effects of physical forcings on fish survival and distribution (e.g. Adkison *et al.* 1996; Beamish 1993; Beamish 1995; Beamish & Bouillon 1993; Beamish *et al.* 1994; Blackett 1993; Brodeur & Ware 1995; Welch *et al.* 1995; Xie & Hsieh 1989) even if these are sometimes ecologically more involved (Francis & Sibley 1991). I will try to put some of the presumed causes of variability in fish survival to a test using ecological coupled process models that are driven by abiotic environmental datasets (Woodruff *et al.* 1987) and a surface current model (Ingraham & Miyahara 1989). The complexities in these simulations arise when considering the interaction between species before the background of a fluctuating environment and advection.

Listed below are 4 general assumptions that I make, each followed by explicit explanations on its validity, from which the complex working hypothesis of this thesis has been synthesized:

Conjecture: Ecosystem processes in the Northeast Pacific largely determine the variability in sockeye salmon cohort survival. These ecosystem processes consist of biotic processes such as foraging, competition and predation, and the associated behavioral responses at ecological and evolutionary time scales, as well as abiotic environmental forcings such as water column stability and currents.

Assumption #1: Survival rates at different life history stages of sockeye salmon (e.g. lake, early marine, sub-adult) exhibit interannual variability, with the largest interannual variability occurring in early marine life, which thus will determine relative year class survivorship.

The number of individuals from a cohort surviving to life history stage t, i.e. the recruits to t, is given by the simple equation:

$$N_t = s_0 s_1 s_2 \ldots s_t N_0 \qquad \text{(Eq. 1.2)}$$

where N and s represent population size and survival rate, respectively, and subscripts indicate life history stages (or age classes). The product of all survival rates is called survivorship and represents the probability that an individual survives to various stages. The survival rate for any particular life history stage is usually a consequence of both density independent and density dependent effects (Beverton & Holt 1957; Peterman 1978). The life history stage that shows the greatest variability in survival rate for different cohorts will dominate variability in survivorship, which multiplied with the respective initial cohort size will determine year-class strength. Note however that the life history stage with the largest variability in survival may well vary from cohort to cohort for a given population, as well as from population to population for a given year class.

While the contributions of freshwater and marine phase to the variation in total cohort survival of sockeye salmon are still unresolved (Bradford 1995), "the annual variations in conditions encountered in individual environments at [the] early sea life stage are generally believed to be largely responsible for the variation seen in overall marine survival of cohort populations." (Burgner 1991) or even in total cohort survival (see also Francis & Hare 1994; Healey 1991; Pearcy 1992; Walters & Juanes 1993 and references therein, and Walters *et al.* 1978 for a discussion). Note also, that although only 43% of the variability in total mortality is

accounted for by the freshwater stage of sockeye salmon, the proportion of total mortality from freshwater is higher (58%) than that from the marine environment due the residence of sockeye salmon in a lake during its first year(s) (Bradford 1995). However, for the calculation of the components of recruitment, Bradford (1995) assumes that instantaneous mortality rates vary independent of density and of habitat, i.e. freshwater and marine environment, which might not be valid.

Assumption #2: Exposure to predators in the early marine life of sockeye salmon determines cohort survival rate, i.e. no fish starves to death. The amount of prey per sockeye salmon determines the time at risk and thus the exposure to predators.

Because mortality risk in early marine life of sockeye salmon, i.e. the time between smolt ocean entry in summer and the end of the first winter at sea, is very high everywhere, it has been argued that the best strategy for juvenile sockeye salmon is to grow as quickly as possible to outgrow its predators (M. Healey 1995 pers. comm.). Nevertheless, while mortality risk is probably homogeneous over a larger scale, say 100 m to 10 km, mortality risk at the small scale of fish schools might well be varying in such a way that fish near the center of a school have a spatio-temporal refuge from predation and active foraging at the school boundaries exposes the individual to predation risk (Walters & Juanes 1993; M. Healey 1995 pers. comm.). This view is also supported by results from Healey (1991) who found that estimated daily rations of juvenile pink, chum and sockeye salmon in Hecate Strait (British Columbia, Canada) were small enough to limit growth rates, this in spite of the fact that, "unless only a small fraction of total zooplankton production is available to the salmon" (Walters *et al.* 1978), ocean limitation of salmon is unlikely. So it is important to note that "during any given day, an animal may fail to

obtain a meal and go hungry, ..., but in the long term, the day's shortcomings may have minimal influence on lifetime fitness. Few failures, however, are as unforgiving as the failure to avoid a predator: being killed greatly decreases future fitness." (Lima & Dill 1990).

In summary, survival is determined by the amount of time an individual exposes itself to risk of predation, a complex interaction of (1) availability of prey (bottom-up and middle-out effects), (2) requirements and allocation of energy within the foraging organism, (3) abundance of predators (and parasites, top-down effects). It should be emphasized that the estimation of an organism's predation risk is not a trivial problem, neither for the organism (Abrams 1994) nor for the scientist who has to deal with several different spatial and temporal scales. Behavioral response to predation risk can lead to some interesting population effects, expected (Carpenter *et al.* 1987; Werner *et al.* 1983) and unexpected (Walters & Juanes 1993). Because little or no information is available on predator abundance and distribution, their behavior, and behavioral responses of juvenile salmon as a result of predation risk, and although deemed insufficient by some (Walters & Juanes 1993), I will focus on the availability of sockeye salmon prey in my study. I hope that by this approach I at least will be able to identify extremely poor and good survival years for sockeye cohorts and shed some light on ecosystem function in the Northeast Pacific.

Assumption #3: Prey for juvenile sockeye salmon is represented by the size class mesozooplankton (0.2-20 mm). For the pelagic ecosystems of the Northeast Pacific size classes of plankton organisms do represent trophic levels.

Traditionally the approach to large ecosystems in modeling and field studies has been to study only a few parts at a time by either taking a subset of high taxonomic resolution from a

community, or studying a whole community and lumping species into higher systematic categories (Yodzis 1989), e.g. invertebrates, vertebrates. Other approaches have used guilds, i.e. functional divisions such as trophic levels (Field *et al.* 1989; Hairston *et al.* 1960), or ataxonomic aggregations (Ulanowicz & Platt 1985), e.g. body-size classes (Boudreau & Dickie 1992; Boudreau *et al.* 1991; Thiebaux & Dickie 1993). For this study, I will assume that for plankton organisms different size classes actually represent different trophic levels, and flows of energy are only used as they relate to primary production, while for herbivores and higher trophic levels I have included behavioral responses to their environment. A conceptual model of the trophic pathways in the ecosystems of the Northeast Pacific is shown in Fig. 1.9.

The classification of plankton organisms into different size classes representing trophic levels seems to be a valid concept for pelagic ecosystems (Oksanen 1991; Sheldon *et al.* 1977; Walters *et al.* 1987): First, it represents well 'Pimm's principle' (Pimm 1982) which says that a combination of predation and competition by the same species should lead to the extinction of the victim and thus to a structural simplification of the food web (Oksanen 1988). And second, it takes into account life history by addressing changes in the prey composition as viewed from the perspective of the developing organisms (Caswell 1989), and the fact that what an individual animal eats depends on the capabilities at its particular life history stage as well as those of its prey organisms (Rice 1995). Compare this trophodynamic viewpoint which states that ecological efficiencies are the product of trophic structure, not vice versa (Hairston-Jr. & Hairston-Sr. 1993, supplemented with evolutionary theory (Gould & Lewontin 1979), to the systems-ecological approach (Odum 1971): For example, Parsons & Lalli (1988) have argued that an individual capable of feeding upon its competitors should include them in its diet when the transfer efficiency through the new longer food chain becomes larger than through the short food chain.

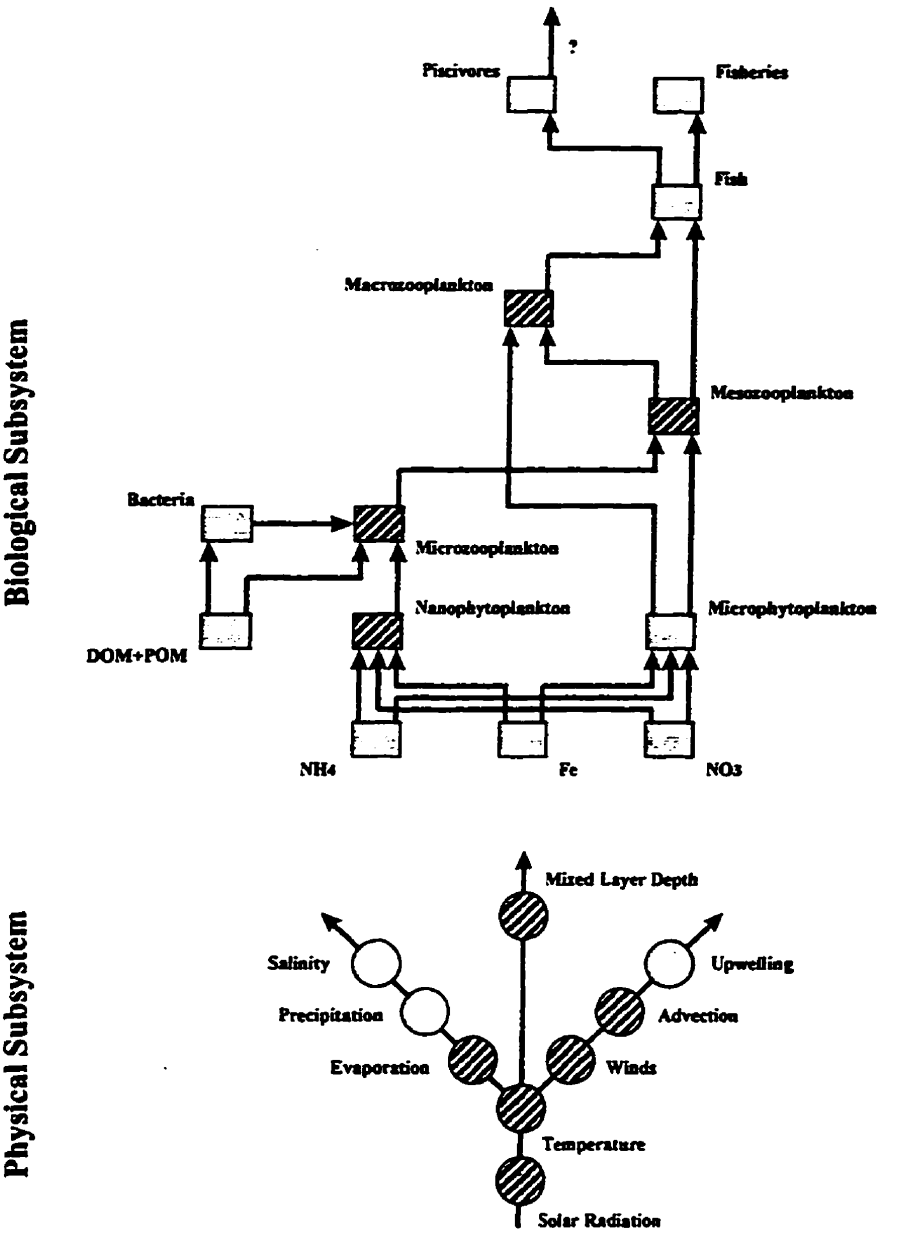


Fig. 1.9: Flow diagram of possible energy transfers in ecosystems of the Northeast Pacific. Environmental forcings (circles; Physical Subsystem) determine which of the possible food chains (boxes; Biological Subsystem) is realized. Note that for plankton organisms I assume that size class represents trophic level. Also note the respective spatial and temporal scales of processes at the different guild levels. Hatched boxes and circles represent state variables and environmental forcings included in the simulations. Not shown to simplify the diagram: import and export through sinking, advection, immigration and emigration; autocatalytic processes and heat sinks; sources for and regeneration of nutrients, and dissolved (DOM) and particulate organic matter (POM);"mesophytoplankton", e.g. chain-forming microphytoplankton, which can be consumed by fish directly.

(Transfer efficiency is defined here as biomass production of the predator per unit biomass production of its prey organism.)

Assumption #4: Spatio-temporal scope and detail used in my spatially-explicit single-layer simulations are sufficient to capture the effects of ecosystem processes in the mixed upper layer of the Northeast Pacific on sockeye salmon survival.

Ecosystem processes in the mixed upper layer of the Northeast Pacific are simulated on a georeferenced 1° x 1° (longitude, latitude) grid of unequal-sized areas encompassing the Pacific Ocean between 180 to 125°W and 35 to 62°N. Because the Northeast Pacific is not a distinct basin of the Pacific Ocean, but is rather delimited by the variable extent of ocean currents, it has been defined here by the approximate range in ocean distribution of North American Pacific salmon species (Groot & Margolis 1991; Welch *et al.* 1995). The spatial resolution of the simulations is a compromise between the spatial resolution of the input data (abiotic forcings (Woodruff *et al.* 1987) and the surface current model (Ingraham & Miyahara 1989)), the relevant scales of biological processes, and computation time. There are two shortcomings in spatial scope and resolution, especially when considering that sockeye salmon cohort survival is probably determined in or near the coastal domains (see Assumptions #1 and #2): First, the Bering Sea is only partially covered, and second, input data lack a high resolution coastal circulation model.

The choice of the 'right' spatial scales in ecological studies is not a trivial problem (Levin 1992) and because the spatial and temporal variability of different ecosystem properties is a function of spatial scale as well as the ecosystem property itself, it may be argued that there is "no right way to do it" (C. Walters 1994 pers. comm.). So the spatial resolution and scope of my

simulations should be viewed as one attempt to answer the question: What are the relevant spatial and temporal scales of ecological processes important for sockeye salmon survival? In my simulations I have tried to incorporate processes at smaller spatial scales than grid size by treating them spatially-implicitly (e.g. Type III functional response of predator consumption to prey density implicitly represents the effect of a partial refuge for the prey (Begon *et al.* 1990); see also Section 3.3: Population Models). Similar arguments apply for temporal scales and nested model design was used when appropriate.

I do not pretend that my models and simulations will capture most of the biological and physical intricacies that may occur in the ecosystems of the Northeast Pacific at the many different spatial and temporal scales, neither do I have the knowledge to do so nor do I think that this is this the purpose of modeling (e.g. Caswell 1988; Starfield & Bleloch 1991; Walters 1986, but see Casti 1997). Everyone studying complex, adaptive systems is faced with critical choices in the development of models, and the questions as well as the desired accuracy of the answers will determine the resolution, i.e. scope and detail (Starfield & Bleloch 1991), of the models and simulations. For example, in cases where accurate prediction was deemed necessary (as a result of a lot of money being involved) some have tried to simulate nature by accounting for every detail that might occur in a given system (Casti 1997). In other cases modelers have pondered the resolution of the input data (e.g. Kirkilionis 1995), and have even suggested to directly link ecosystem models to satellite remote sensing to make better predictions (predictions whose purpose was not clear to me).

In most ecosystem studies emphasis has been on understanding, not prediction, and conceptual flow diagrams (like that in Fig. 1.9) have frequently been developed and even in much greater detail (e.g. Brodeur 1988; Brodeur & Pearcy 1992; Kremer & Nixon 1978; Odum

1983; Platt *et al.* 1981). Usually the complexity of these models and the intrinsic problems of nonlinear equations (e.g. Cohen 1995; Crutchfield *et al.* 1986; Gleick 1987; May 1976b; Stone 1993) have restricted the scientific procedure to descriptive functional analysis (Briand 1983; Yodzis 1989) or linear network analysis of mass-balance models (e.g. Christensen & Pauly 1995; Laevastu & Larkins 1981; Odum 1971; Pauly *et al.* 1996; Wulff *et al.* 1989; for an interesting approach see Klepper 1995). On the other hand, some whole ecosystem simulations have been developed with varying acceptance in the scientific community (Platt *et al.* 1981). As an example consider the 'General Ecosystem Model of the Bristol Channel and Severn Estuary' (as described in Platt *et al.* 1981) with 225 parameters and more than $2.25 \cdot 10^{107}$ possible parameter combinations in a 'brute-force' sensitivity analysis where each parameter can only assume one of three values.

As a consequence, the guiding principle in the development of my simulations has been to simplify the natural system while still trying to capture the essence of non-linear real-world processes. Modeling of complex ecosystems is a long and tedious process on the narrow path between mathematical games and intractable pattern imitation (Baumann 1998). Exclusion and aggregation of interacting components should occur at the detailed levels and not at higher classes of components (Starfield & Bleloch 1991, but see Rice 1995), while - as usual - acknowledging that the real world is more complicated. I have tried to incorporate the most important ecosystem processes and pathways with respect to food availability to juvenile sockeye salmon by simplifying (1) the spatial-temporal variation in mesozooplankton production in the Northeast Pacific within a food chain context, (2) the transport of biological production within the Northeast Pacific, and (3) behavior of zooplankton and the effects on availability to juvenile salmon migrating along the Alaskan Gyre. Because of the complications stated in *Assumption #2*

(Walters & Juanes 1993, M. Healey 1995 pers. comm.) I have not explicitly included salmon in my model.

In summary, here is the attempt: Program the simplest plausible spatially-explicit single-layer ecosystem simulation to explain, at least in part, the interannual variability in sockeye salmon survival by the spatio-temporal variability in prey availability. A dynamic model like this must incorporate animal life history and individual daily behavior, seasonal biological production processes in the ocean, food chain dynamics, advection of biological production, as well as other physical forcings. It thus not only has to integrate various organization levels (ecosystems, communities, guilds, populations, individuals), but also the different spatial and temporal scales on which regulatory processes occur. This is not an easy task (Levin 1992; Levin *et al.* 1997) and the attempt is thus vulnerable to critique from each of the different sub-disciplines that I have tried to integrate. Criticism is anticipated. However, the goal of my work is an increased understanding of what does and what does not control salmon survival, rather than prediction, and I hope the reader will agree that this exercise leads to a deeper understanding.

2. SOCKEYE SALMON AND THE MARINE ENVIRONMENT

"If no use is made of the labors of the past,
the world must remain always in the infancy of knowledge."
Cicero (106 - 43 BC)

"Just as we suffer from excess in all things,
so we suffer from excess in literature."
Seneca (4 BC - AD 65)

In the following three sections I will review data together with current "understanding" of the ocean feeding ecology of sockeye salmon, and the biological and physical characteristics of the ecosystems of the NE-Pacific. This fairly detailed information was summarized with respect to its relevancy for ecosystem effects on sockeye salmon marine life in Chapter 1.

2.1. Ocean Feeding Ecology of Sockeye Salmon (*Oncorhynchus nerka*)

Understanding the trophic position of sockeye salmon requires knowledge of the food items eaten at different life history stages. I define these stages somewhat arbitrarily as juvenile (1.0 - 1.1 fish; for age classification systems in salmon see Groot & Margolis 1991) and, due to the similarity in their diet (Brodeur 1990), immature and maturing fish combined (1.1 salmon and older). Although body length and weight in sockeye salmon change continuously (Burgner 1991; French *et al.* 1976), the clustering of the ratio of predator to prey size for various pelagic organisms around a constant (ratio of equivalent spherical diameter of predator to that of prey ≈ 15 (Sheldon *et al.* 1977)) and the biomass (Boudreau & Dickie 1992; Boudreau *et al.* 1991; Thiebaux & Dickie 1993) as well as particle size spectra (Parsons & LeBrasseur 1970; Parsons *et al.* 1984; Sheldon & Parsons 1967) in the aquatic environment suggest that the size of sockeye

salmon prey organisms changes abruptly sometime after the first winter at sea, when sockeye length growth rate starts to fall off (French *et al.* 1976).

However, the establishment of a certain biomass spectrum (body mass distribution vs. biomass size) is a consequence of the interaction between various trophic levels and the development and evolution of its constituent species, all under the forcing conditions of the physical environment. Biomass spectra are thus emergent properties whose explicit theoretical treatment has only recently been initiated (Thiebaux & Dickie 1993).

Juvenile sockeye salmon (age class: 1.0)

After entering the ocean, juvenile sockeye salmon prey upon a very broad spectrum of organisms in the coastal environment (Pearcy 1992). These include (Brodeur 1990; percentages are stomach contents volume proportions):

euphausiids (Class: Malacostraca)

amphipods (54%; Malacostraca)

copepods

pteropods (Class: Gastropoda)

larval and juvenile fishes (11%)

squid larvae

decapod larvae (15%; Malacostraca,)

Diet composition is quite variable in different geographic locations, e.g.

larvaceans (Class: Appendicularia)

chaetognaths

insects (11%)

cladocerans (Class: Phyllopoda)

have been identified in various locations in the Strait of Georgia, British Columbia (Healey 1978). Healey (1991) reports large interannual variability in diet organisms, e.g. copepods with percentage volume contributions of 3% and 36% for 1986 and 1987, respectively, even though the frequency of occurrence of copepods in stomachs of juvenile sockeye was lower in 1987.

Generally sockeye juveniles showed a positive selection for neuston (i.e. organisms living only within centimeters below to the surface layer (Ott 1988)) compared to other pelagic guilds (Brodeur 1990). Although the density of neuston organisms may be very high, their total biomass over the whole water column is low because of the thinness of the layer they inhabit (Parsons *et al.* 1984). However, as visual predators (Burgner 1991) sockeye salmon successfully exploit this community in the sunlit surface layer.

Overall, spatial and temporal variability in diet composition can simply be attributed to differences in the availability of species within the preferred size class rather than food preferences (Brodeur 1990; Healey 1991). Using the size classification scheme in Parsons *et al.* (1984) the above prey organisms can be classified as mesozooplankton (0.2 - 20 mm).

Immature and maturing sockeye salmon (age class: 1.1 and older)

Favorite (1970) reports explicit stomach contents volume proportions (percentages given in brackets below) for immature and maturing sockeye salmon from samples taken in the Alaskan Stream area and Bristol Bay for May to August 1960:

euphausiids (12%)	copepods (7%),
amphipods (43%),	pteropods (2%),
fish (18%),	crustacean larvae
squid (16%),	pelagic polychaetes

However, samples taken in winter 1964 (January to February) across the Alakan Gyre show an overwhelming dominance of fish (71%) and squid (27%) in the diet of sockeye ranging in size from 26.5 to 59 cm (Manzer 1968).

Even more uncertainty is added by LeBrasseur's (1966) report on differences in stomach contents for different oceanic regimes from samples taken between May and June 1958. While sockeye caught in the Subarctic Pacific fed mainly upon squid (75 and 89% by weight for immature and maturing sockeye, respectively), in the coastal region they depended on euphausiids (48 and 60%), squid (31 and 9%), and fish (12 and 16%). Within the Alaskan Stream area sockeye preyed on euphausiids (50 and 21%) and amphipods (50% for immature) or fish (60% for maturing). Maturing sockeye migrating through the transition zone consumed mainly euphausiids (71%) and amphipods (27%).

These conflicting reports were somewhat reconciled by a major study by Pearcy *et al.* (1988) who collected data on salmon stomach contents (sockeye, pink (*O. gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), and steelhead (*O. mykiss*)) on six July cruises along 145°W (1980, 1981), 155°W (1984, 1985), and 55°N (1982, 1983). They concluded that salmon species forage opportunistically with large overlap between species (except chum). Prey choice was not random but selective for a certain size class.

In summary, spatial and temporal variability in the diet composition of immature and maturing sockeye salmon can be attributed to differences in the availability of species within the preferred size class (Brodeur 1990; LeBrasseur 1966; Pearcy *et al.* 1988). (Because of lack of independent support and its somewhat counterintuitive conclusions, I disregard here a study by Beacham (1986 as cited in Brodeur (1990) which suggests that with increasing sockeye size, the mean size of invertebrate prey decreases while that of fish prey increases.) Prey organisms for immature and maturing sockeye represent the larger size fraction of mesozooplankton (e.g. the copepod *Neocalanus cristatus* with a maximum adult length of 10 mm (Parsons & Lalli 1988)), macrozooplankton, and "macro"nekton (by definition: 2 - 20 cm (Parsons *et al.* 1984)).

Diet composition for sockeye salmon has also been reported in terms of trophic levels of prey items (Table 2.1; LeBrasseur 1972; Sanger 1972). An interesting change in the trophic position occurs when maturing sockeye migrate from the Central Subarctic Domain into the Coastal Domain. Using data given in LeBrasseur (1972), I calculated the fractional trophic levels of sockeye salmon in the two regions as 4.6 and 4.1, respectively (where the trophic level of primary producers = 1). The latter value is consistent with a fractional trophic level of 3.9 calculated from data given in Sanger (1972), assuming these data have been collected in the coastal zone. This is an effect of the shorter food chain of the Coastal Domain.

However, the analysis of fish stomach contents is very tedious and while prey species (or higher taxa) can be identified by persistent efforts of taxonomists, their size can hardly ever be reconstructed from the partially digested organisms found in the stomachs, let alone their (fractional) trophic levels. Also salmon tend to regurgitate food when caught in gill nets (Favorite 1970) which poses additional problems to the interpretation of certain results (e.g. Favorite 1970; LeBrasseur 1966; Pearcy *et al.* 1988). Furthrmore, it was previously believed that copepods in the NE-Pacific were mostly herbivorous (LeBrasseur 1972), while more recent studies have shown that they prey mostly on microzooplankton (see Section 2.2; Booth *et al.* 1993; Dagg 1993; Gifford 1993; Landry *et al.* 1993a; Landry *et al.* 1993b; Mackas *et al.* 1993; Miller *et al.* 1991b) which increases the trophic level of sockeye salmon accordingly.

Table 2.1: Diet composition of maturing sockeye salmon in terms of trophic levels of prey items (% composition of stomach contents by weight).

Life History Stage (Location)	Herbivores	Primary Carnivores	Secondary Carnivores	Reference
not available	15	80	5	Sanger (1972)
maturing (oceanic)	3	30	67	LeBrasseur (1972)
maturing (coastal)	6	82	12	LeBrasseur (1972)

Diet composition and foraging analysis for fish faces inherent methodological problems (Brodeur 1990). Usually fish caught in some fisheries are randomly sampled for stomach contents analysis, where the volume or weight contribution of a specific food item to total stomach contents and the frequency of occurrence of a specific food item in different stomachs are determined. The overall objective of most studies is to determine the degree of food preference. Food preference means that the proportion of a food item in the diet is greater than the proportion of the same item available to the foraging animal (Begon *et al.* 1990; Healey 1991). Unfortunately many studies rely on stomach analyses solely, or on food availability studies conducted somewhere or sometime else. Without proper reference to actual availability of food items, studies on preference and optimal foraging are not possible in principle. All that can be inferred is whether or not fish of different regions or caught at different times have similar stomach contents. Still, even in studies where the availability of food items is measured simultaneously and independently (Pearcy *et al.* 1988) one cannot be sure that the sample represents what is actually available to the foraging animal, i.e. the selectivity of the sampling gear may affect what may seem "available".

2.2. Ecosystems of the Northeast Pacific

Here, I define the Northeast Pacific as the range in ocean distribution of North American Pacific salmon species (*Oncorhynchus* spp.), i.e. approximately 40-66°N and 175°E -125°W (Groot & Margolis 1991; Welch *et al.* 1995). Ware & McFarlane (1989) have classified this region into four ecological upper-zone domains (Fig. 2.1): The borders of the Coastal Downwelling (Alaska and North British Columbia), Transitional (Central and South British Columbia, and Washington) and Coastal Upwelling Domains (Washington, Oregon, California) are spatially transient and determined by the bifurcation of the eastward Subarctic Current offshore of the North American continent into the northward Alaska Current and the southward California Current. The fourth domain, the Central Subarctic, represents the oceanic province of the NE-Pacific and is the main feeding ground for maturing North American Pacific salmon (Brodeur 1990; Burgner 1991).

These biogeographical provinces are characterized by different physical properties and as a consequence productivity patterns (flow of energy and nutrients) and ecological communities (species composition, size classes; LeBrasseur 1966; Ware & McFarlane 1989). I assert (in the form of a complex working hypothesis) that marine survival and possibly overall cohort-survival of Pacific salmon is largely determined by the end of their first winter at sea. Survival is controlled by physical-biological processes (e.g. food production, predation risk) in the Coastal Downwelling, Transitional and Central Subarctic Domains, as well as by the transport (advection, migration) of organisms and nutrients among those domains (Brodeur & Hollowed 1993; Ware & McFarlane 1989; Wickett 1967). Because only few salmon stocks enter the Coastal Upwelling Domain during their migration, I have excluded this area from the following discussion.

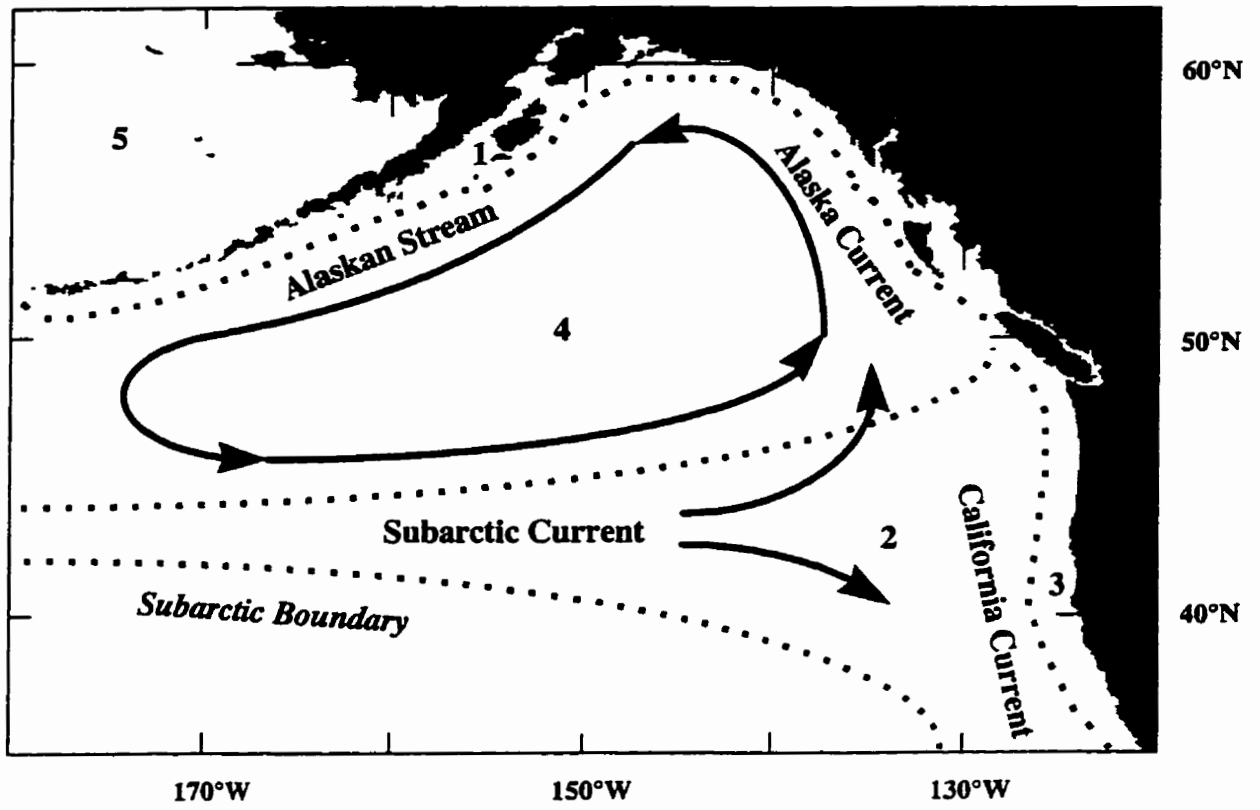


Fig. 2.1: Ecological upper zone domains and prevailing currents in the Northeast Pacific Ocean. 1 - Coastal Downwelling Domain, 2 - Transitional Domain, 3 - Coastal Upwelling Domain, 4 - Central Subarctic Pacific, 5 - Bering Sea. Dotted lines represent variable boundaries between domains. The Subarctic Boundary is a frontal region which separates the Subarctic Pacific to the north from the Subtropic Pacific to the south (Thomson, 1981). After Dodimead et al. (1963), LeBrasseur (1966), Sanger (1972a), Thomson (1981), and Ware and McFarlane (1989).

2.2.1. The Central Subarctic Domain

Phytoplankton

Phytoplankton standing stocks in the Central Subarctic Domain as estimated by chlorophyll-a concentrations at Ocean Weather Station *P* (50°N 145°W, henceforward called Station *P*) show little seasonal variability (Fig. 2.2). Mean Chl-a concentrations at Station *P* between 1958-1991 were around 0.4 mg Chl-a m^{-3} throughout the year (Parslow 1981; Parsons & LeBrasseur 1968; Wong *et al.* 1995), although June and October values appear somewhat above the respective adjacent months, with the October chlorophyll-a "maximum" possibly caused by the life-history induced September minimum in copepod biomass (Miller *et al.* 1984; Parsons & Lalli 1988).

Wong *et al.* (1995) do not report the variability around the monthly means, thus short-term increase in Chl-a concentrations cannot be completely excluded and no conclusions can be drawn about short-term and/or spatial variability (patchiness) in the samples (see also Parsons & LeBrasseur 1968 their Fig. 3(A)). However, cumulative composite data for Station *P* from 1959-1970 reveal that there are no phytoplankton blooms (here defined as concentrations >2 mg Chl-a m^{-3} and not as increased primary productivity) in the Central Subarctic Domain and that 1 mg Chl-a m^{-3} is only exceeded occasionally (Miller *et al.* 1984; Miller *et al.* 1991a; Miller *et al.* 1991b). On the other hand, an independent 1964-1976 time series (Parslow 1981) shows intermittent events of very high Chl-a concentrations with maxima of 3-5 mg Chl-a m^{-3} occurring abruptly without any indication in the data taken only days before the events.

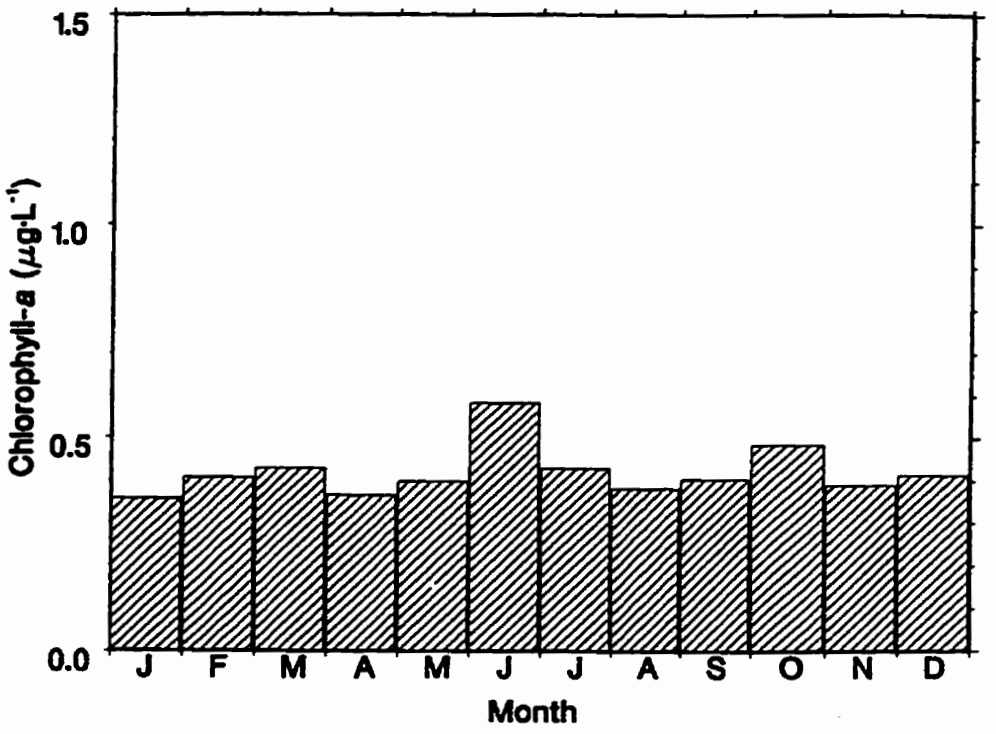


Fig. 2.2: Chlorophyll-a concentration at Ocean Weather Station *P* (50°N 145°W), as monthly averages 1964-1991. Note that variability around the mean is not reported, thus no conclusions about temporal and/or spatial variability (patchiness) in the samples can be inferred. Adapted from Wong et al. (1995).

Although it is somewhat unusual that two published data-sets of the same region (although Station *P* is nominally a point, due to advection processes measurements taken there represent regional data) with overlapping time periods present seemingly different results, I think these measurements might be reconciled by the patchiness apparent in plankton communities and the inherent delay of zooplankton-control of phytoplankton standing stock.

A somewhat different picture emerges when phytoplankton standing stock is estimated by carbon concentrations. Because phytoplankton concentrations are difficult to measure in units of carbon (P. Harrison 1997 pers. comm.) chlorophyll-a data must be multiplied by the carbon / chlorophyll-a ratio. Because the C/Chl-a ratio varies with light intensity (McAllister 1969) phytoplankton standing stocks at Station *P* could vary from 5.25 mg C m^{-3} (January C/Chl-a = 15) to >27.5 mg C m^{-3} (June C/Chl-a = 50), using Wong *et al.*'s (1995) Chl-a and McAllister's (1969) C/Chl-a data, i.e. a fivefold increase (see also the variability of the carbon-to-chlorophyll-a ratio estimates obtained during the summer SUPER-cruises in Frost (1993), his Table 3).

The methods used to estimate seasonal variability in C/Chl-a ratios are somewhat arbitrary (McAllister 1969) and could be misleading, thus questioning the numerical validity of the ratios as well as the overall conclusion of the possible fivefold increase in phytoplankton standing stock. In general, scientific knowledge about the carbon-to-chlorophyll ratio is surrounded by great uncertainty (Banse 1977), the reason for which seems to be that data from different dynamic processes are often used in one correlation analysis (Platt *et al.* 1981). T. Parsons (1997 pers. comm.) has pointed out that the increase in the C/Chl-a ratio could well be attributed to an increased standing stock of detritus, i.e. non-living particulate organic matter (POM) + associated bacteria (Parsons *et al.* 1984), during the summer months. Also, because the phytoplankton cellular C/Chl-a ratio is to some extent controlled by seawater nitrate concentrations which show

a decrease but no depletion in the Central Subarctic Domain in summer, phytoplankton standing stocks should remain more or less constant throughout the year. On the other hand, the relationship between nitrate concentrations and the C/Chl-a ratio is based on diatoms (see Parsons *et al.* 1984 their Table 10) which represent <10% of the primary producer biomass in the Central Subarctic Domain (Miller *et al.* 1991a). Also, high variability in phytoplankton measured in units of carbon has also been observed during the SUPER-cruises (SUbarctic Pacific Ecosystem Research; May and August 1984, 1988, June and September 1987 (Miller *et al.* 1991b)) with a mean standing stock of 20 mg C m^{-3} and a maximum of 74 (Booth *et al.* 1993).

Indirect evidence for an increased phytoplankton standing stock in summer comes from dilution experiments conducted during two SUPER-cruises in the Gulf of Alaska (Landry *et al.* 1993b; Miller *et al.* 1991b). While the specific rates for phytoplankton community growth and microzooplankton grazing were approximately the same (0.35 d^{-1}) in June 1987 and May 1988, phytoplankton (0.49 d^{-1}) by far exceeded microzooplankton (0.26 d^{-1}) in August 1988. Interestingly, this result has been interpreted as micrograzers controlling phytoplankton "in a dynamic and variable fashion" (Miller *et al.* 1991b), rather than a consequence of more complex food web interactions where life-history-induced changes in the abundance of mesozooplankton seasonally intensify and alleviate grazing pressure upon smaller zooplankton, which in turn are unable or apt to control phytoplankton standing stock.

Whatever the case, the possibility of a 5-fold increase in summer phytoplankton standing stock when measured in carbon has important implications for the realized food chain structure (see later chapters). After all, consumer metabolism depends on reduced carbon compounds and not on chlorophyll-a.

Considerable seasonal variability in primary productivity at Station *P* (from ≈20 in December to ≈350 mg C m^{-2} d^{-1} in July (McAllister 1969)) has recently been disputed. Using the Centre for Ocean Climate Chemistry composite dataset for 1984-1990 (Fig. 2.3) Wong *et al.* (1995) report a mean of 283 for winter (December-February) and 466 mg C m^{-2} d^{-1} for summer (June-August), although the winter value must be viewed with caution since it is based on only 2 samples taken on subsequent days in late February 1989. Furthermore, SUPER-scientists obtained a mean primary productivity of 661 mg C m^{-2} d^{-1} during their summer cruises (1984, 1987 and 1988; Miller *et al.* 1991b), with values up to 1 000 mg C m^{-2} d^{-1} or approximately one doubling per day (Booth *et al.* 1993; Welschmeyer *et al.* 1993).

Recent estimates for an annual primary production in the Central Subarctic Domain are 140 g C m^{-2} y^{-1} (Wong *et al.* 1995) and 170 g C m^{-2} y^{-1} (Welschmeyer *et al.* 1993), with the second probably biased due to sampling in summer only. Both these estimates lie within one standard deviation of an independently derived, though strongly debated (Falkowski & Wilson 1993; Welch 1993), estimate (Falkowski & Wilson 1992), and are two- to threefold higher than the previously reported values of 45-72 g C m^{-2} y^{-1} (McAllister 1972; see also Sanger 1972 his Figs. 1 to 4). The causes for these discrepancies are unknown and may be attributed to the cleaner sampling techniques with which the more recent data have been collected. However, all of the above measurements were taken from Station *P* only and therefore may reflect spatio-temporal variability in oceanographic conditions rather than basin-wide changes in primary production.

The seasonal onset of increased phytoplankton productivity can be attributed to the seasonal increase in insolation and the formation of the seasonal thermocline, and an increased critical depth and a shallower depth of mixing (Parsons 1988). The spatial distribution of this event in the NE-Pacific is such that water column stabilization in coastal areas occurs in about March

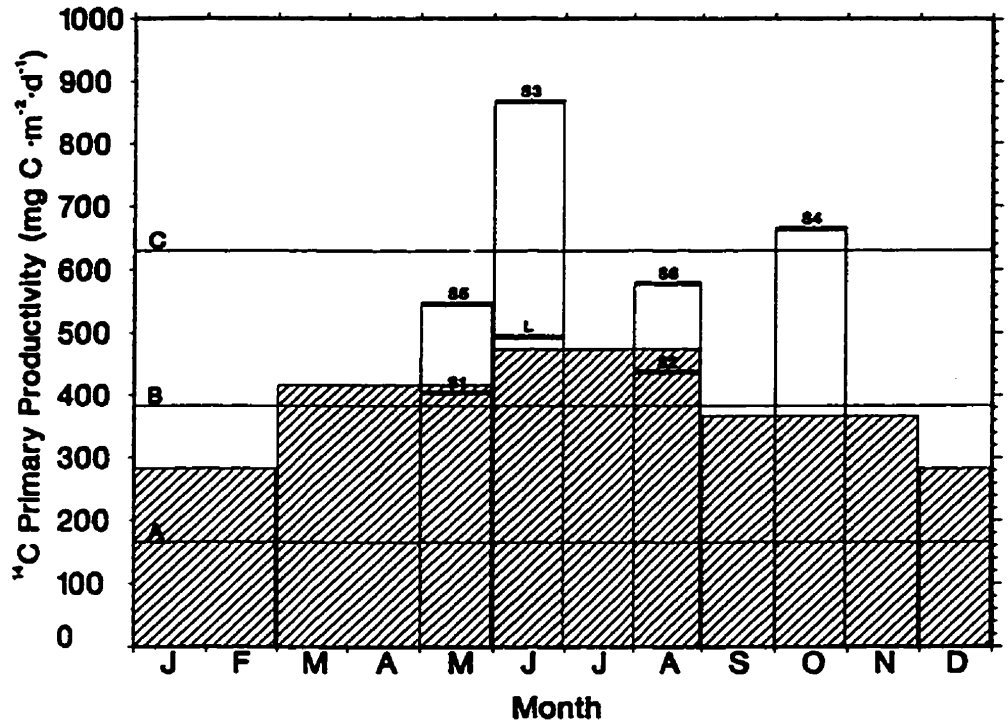


Fig. 2.3: Seasonal ^{14}C primary productivity at Station *P* from composite data 1984-90. A,B, and C levels represent historical annual primary production estimates of 60 g C m^{-2} y^{-1} (McAllister, 1972), 140 g C m^{-2} y^{-1} (Wong et al., 1995), and 230 g C m^{-2} y^{-1} (Welschmeyer et al., 1991*), respectively. The third value is based on SUPER-data from summer cruises only (S1-S6) and thus is likely to be biased. L are data from Booth et al. 1988*. Note again that variability around the seasonal means is not reported, thus no conclusions about temporal and/or spatial variability (patchiness) in the samples can be inferred. References with asterisk are given in Wong et al. (1995). Adapted from Wong et al. (1995).

(possibly influenced by haline stratification due to meltwater run-off from the American continent) progressing offshore so that the center of the Alaskan Gyre is reached in May (Fig. 2.4; Parsons *et al.* 1966; Parsons & LeBrasseur 1968). However, mixed layer depth and day-length during spring and summer cruises could only partly (25%) explain the variability in phytoplankton doubling rates (Booth *et al.* 1993). Primary production per unit biomass of nanophytoplankton, the dominant size class, does not seem to be bottom-up limited to any extent, thus grazing (Banse 1994) and sinking determine the standing stock (Welschmeyer *et al.* 1993), the production base.

The species composition of phytoplankton in the Central Subarctic Domain is highly variable on all time scales with a few species being present independent of the season (for a detailed listing see Parsons and Lalli (1988)). The dominant size class (>90% of biomass (Miller *et al.* 1991a)) of primary producers in the Central Subarctic is nanophytoplankton (size 2-20 μm (Booth *et al.* 1993; Parsons 1972)), using the classification scheme in Parsons *et al.* (1984, their Fig. 3), which occurs at densities of up to 10^6 cells l^{-1} and are dominated by the coccolithophorid species *Emiliana huxleyi* (Parsons & Lalli 1988). Concentrations of very small diatoms go up to 10^4 cells l^{-1} and that of the large (microphytoplankton: 20-200 μm) diatom species *Corethron criophilum* showed 6000 cells l^{-1} in July (Parsons & Lalli 1988).

Because nanophytoplankton species have a lower Michaelis-Menten constant for ammonium uptake (A. Milligan 1997 pers. comm.) as well as for nitrate (Parsons & Takahashi 1973) they outcompete the larger microphytoplankton for nitrogen. Microphytoplankton could convert nitrate, which is never depleted in the Central Subarctic Domain, into ammonium using the enzyme nitrate reductase, which requires the micronutrient iron (Fe) in minute quantities (Martin 1991; Martin *et al.* 1994; Martin & Fitzwater 1988; Morel *et al.* 1991). Iron is provided to the

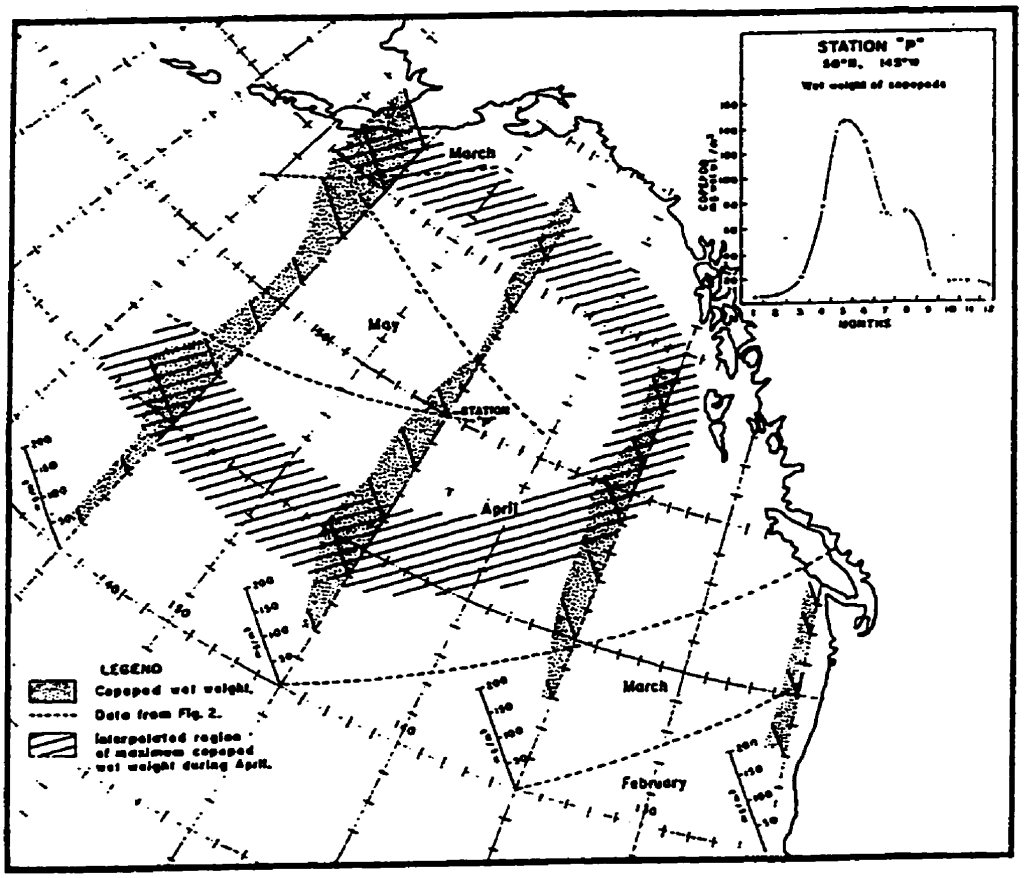


Fig. 2.4: Spatial distribution of the onset of increased primary productivity in the NE-Pacific. Broken line marks approximate temporal progression of the formation of the seasonal thermocline (derived from the least favorable conditions in order to show the greatest difference within the area of the NE-Pacific (Parsons and Lalli, 1988). Dotted areas represent copepod wet weights for April. The hatched horseshoe-shaped area represents the interpolated region of maximum copepod wet weight in April. Adapted from Parsons et al. (1966).

euphotic zone of the ocean mainly by atmospheric deposition and only in small quantities (Donaghay *et al.* 1991; Duce & Tindale 1991) which makes microphytoplankton production bottom-up iron limited.

Nanophytoplankton standing stock is controlled through grazing by microzooplankton (20-200 µm), i.e. small heterotrophic flagellates and ciliates (Booth *et al.* 1993; Frost 1987; Landry *et al.* 1993b; Strom *et al.* 1993). Microzooplankton can maintain growth rates of up to more than 5 doublings d^{-1} (Miller *et al.* 1991b) which are higher than the growth rates of their food source (Banse 1994) due to two reasons: First, microzooplankton is capable of cell division 24 hours per day (Miller *et al.* 1991a, and references cited therein), and second, it is spared the energetic costs of synthesizing basic biological molecules, such as sugars, proteins and fats which it finds in its food (Miller *et al.* 1991b).

The low growth rates of microphytoplankton, caused by the combination of iron limitation and resource (ammonium) use competition with nanophytoplankton, has the effect that mesozooplankton (200-2000 µm) can effectively control microphytoplankton standing stock, while microzooplankton due to its small size and a feeding apparatus restricted to ingestion of organisms ≤10 µm in diameter (Miller *et al.* 1991b) cannot exert any control on the microphytoplankton standing stock. Nevertheless, sediment trap data from Station *P* reveal largest biomass of diatom frustules from May to August (Parsons & Lalli 1988), the time of highest mesozooplankton density in the euphotic zone. In order to be consistent with mesozooplankton control on microphytoplankton standing stocks, these frustules must come from organisms that have not been completely ingested or digested, or belong to the smaller size class of nanophytoplankton.

It has been speculated that the life-history-induced September minimum in copepod density might cause the slight increase in phytoplankton standing stock (see first paragraph of this subsection; Miller *et al.* 1984; Parsons & Lalli 1988). Yet, if phytoplankton consists mainly of nanophytoplankton which is believed to be controlled by microzooplankton (Miller *et al.* 1991a), which in turn is controlled by mesozooplankton (mainly large copepods; Dagg 1993; Gifford 1993; Parsons & Lalli 1988; Ware & McFarlane 1989), and following a simple food chain argument (Hairston *et al.* 1960), the life-history induced September minimum in copepod density should rather decrease than increase the phytoplankton standing stock in October.

Nutrients

Phytoplankton-nutrient interactions in the Central Subarctic Domain can be characterized by 3 nutrients: the macronutrients nitrate (NO_3^-) and ammonium (NH_4^+) and the micronutrient iron (Fe). In general nitrate and iron concentrations are governed by external processes (i.e. upwelling, and atmospheric deposition in the case of iron) while recycling processes regulate ammonium (Miller 1993a; Miller *et al.* 1991a).

Year-around data 1966-1976 from Station *P* show a mean nitrate-maximum of about 15 μM in the surface layer in early March at the end of the winter mixing season (Parslow 1981). Between March and September the seasonal thermocline reduces the already meager (due to a permanent halocline at around 100 m) supply of nitrate to the mixed layer by creating a further barrier, above the halocline, to upward advective-diffusive fluxes. It is estimated that >70% of the total transport of sub-halocline concentrations of 30 to 45 μM into the euphotic zone is due to advective flux, i.e. upwelling (advective flux: 1.6 mmol nitrate m^{-2} d^{-1}; diffusive flux: 0.6 mmol nitrate m^{-2} d^{-1} (Miller *et al.* 1991b)). During the same time some nitrate is taken up by

phytoplankton which thus results in a steady decline of nitrate concentration and a mean NO_3- minimum of ≈7 μM by September (Miller *et al.* 1991b; Parslow 1981; Wheeler 1993). While there is variability at all time scales at Station *P*, nitrate is never completely used up, i.e. no mean below 5 μM and no single measurement below 1.5 μM has been recorded in the period 1966-1976 (see Parslow 1981 his Figs. 28 and 29).

Miller *et al.* (1991b) and Wheeler (1993) report ammonium concentrations at OSW *P* from the May 1988 SUPER cruise with values from almost 0 to 3.9 μM. Ammonium concentrations are wildly fluctuating (see Miller *et al.* 1991b their Fig.12) but little is known about the exact nature of the seasonal, interannual, and spatial variability. However, it is speculated that tight coupling (trophodynamic phasing) between primary producers and their consumers leads to rapid nutrient cycling involving particulate nitrogen and the microbial loop, and providing ammonium back to phytoplankton (Miller *et al.* 1991b; Wheeler 1993). Phytoplankton prefers ammonium (NH_4^+) over nitrate (NO_3^-) because it is already in an reduced state thus saving energy expenses for some biochemical redox-reactions which would be required for nitrate reduction.

Iron concentrations in the Central Subarctic Domain are very low (<0.1 nM (Morel *et al.* 1991, P. Harrison 1993 pers. comm.)). It is supplied to the euphotic zone of the ocean through rock weathering and subsequent transport in rivers (T. Pedersen 1995 pers. comm.), input from the deep ocean through upwelling, and deposition from the atmosphere after wind transport from land (Donaghay *et al.* 1991; Duce & Tindale 1991). Because iron is effectively removed from the water column during estuarine mixing (Boyle *et al.* 1977; Fletcher *et al.* 1983) it is estimated that approximately 75% of all Fe-input to the euphotic zone of the oceans comes from the atmosphere (Duce & Tindale 1991) and only in small quantities. See also arguments in Boyd *et al.* (1998).

The availability of iron limits the synthesis of the enzyme nitrate reductase in phytoplankton, an enzyme needed to reduce nitrate to ammonium. A key strategy for phytoplankton to ensure growth in low (micro-)nutrient areas is small cell size (Morel *et al.* 1991), and thus in the Central Subarctic Domain nanophytoplankton outcompete the larger microphytoplankton for all the nutrients. Nanophytoplankton is controlled by microzooplankton (Booth *et al.* 1993; Landry *et al.* 1993b; Strom *et al.* 1993) and the resulting tight trophodynamic phasing provides ammonium to nanophytoplankton. The untouched high nitrate concentration cannot be utilized by microphytoplankton after all, simply because iron is not available.

In summary, the combination of: 1) nanophytoplankton outcompeting the larger microphytoplankton for nitrogen and iron, because of lower macronutrient Michael-Menten constants as well as lower iron requirements of nanophytoplankton (P. Harrison 1998 pers. comm.); 2) ammonium availability suppressing nitrate uptake in all phytoplankton (Miller *et al.* 1991b; Wheeler & Kokkinakis 1990, A. Milligan 1997 pers. comm., but see also Price *et al.* 1991); and, 3) phytoplankton being bottom-up iron limited in the production of the enzyme nitrate-reductase, which is essential for the utilization of nitrate, makes the Central Subarctic Domain one of the three known high-nutrient-low-chlorophyll (HNLC) regions in the World Ocean (Longhurst 1996; Miller 1993a; The others are the eastern Equatorial Pacific and the Southern Ocean). However, a low chlorophyll concentration does not necessarily mean a low phytoplankton standing stock as the C/Chl-a ratio varies seasonally (see *Phytoplankton*). While the availability of certain micronutrients could set the realized size-class or other guilds of primary producers (Armstrong 1994) there is strong indication that the standing stock of nanophytoplankton in the Northeast Pacific (as measured in Chl-a concentration) may not at all be nutrient-, but rather light- and grazer-limited (Banse 1994; Booth *et al.* 1993).

Zooplankton

Zooplankton standing stocks at Station *P* show strong seasonal variability (Fig. 2.5). Copepods dominate zooplankton biomass in the Central Subarctic Domain (Mackas *et al.* 1993; Parsons & Lalli 1988; Ware & McFarlane 1989), and demonstrate January annual lows at around 0.44 mg C m^{-3} and May-June annual highs of 3 mg C m^{-3} (but values up to 20 mg C m^{-3} have been reported (Mackas & Frost 1993)). Carbon values were calculated from 1971-1974 composite mean wet weight concentrations in Parsons & Lalli (1988) and the conversion factors: (dry weight) / (wet weight) = 0.1 (Parsons & Lalli 1988); (Carbon weight) / (dry weight) = 0.4; (Parsons *et al.* 1984 their Table 11). The variability within the monthly samples is considerable with ranges 0.12-0.84 in January and 0.44-15.12 mg C m^{-3} in May. Both might be attributed to the spatially patchy distribution of copepods. May data are similar to the values published by McAllister (1969), Sanger (1972), Pearcy *et al.* (1988), and by Brodeur & Ware (1992), with the later having analyzed large spatial datasets for the NE-Pacific for the periods 1956-1962 and 1980-1989 for samples taken between 15 June and 30 July of each year. Estimates for zooplankton production have been 11-13 g C m^{-2} y^{-1} (McAllister 1969; McAllister 1972).

The dominant group of zooplanktonic biomass in the euphotic zone of the whole Central Subarctic Domain are copepods, in the size class mesozooplankton (0.2-20 mm). 80-95% of the total biomass (Mackas *et al.* 1993; Parsons & Lalli 1988; Ware & McFarlane 1989) consist of the large copepod species *Neocalanus plumchrus* (5.5 mm), *N. flemingeri* (Miller *et al.* 1991a, M. Wen 1995 pers. comm.), *N. cristatus* (10 mm; Mackas & Frost 1993; Mackas *et al.* 1993; Parsons & Lalli 1988; Ware & McFarlane 1989), and *Eucalanus bungii* (Mackas & Frost 1993; Mackas *et al.* 1993) which all undergo ontogenetic vertical migrations.

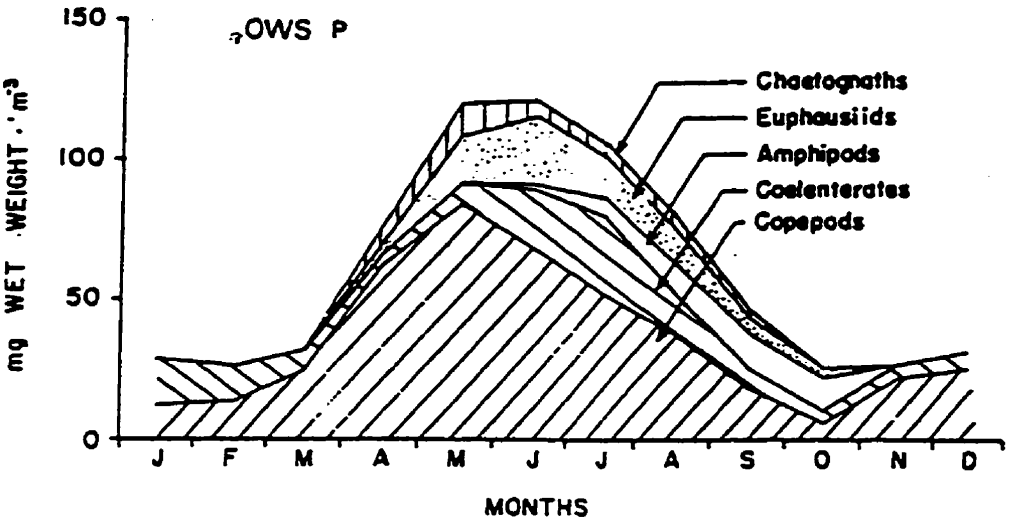


Fig. 2.5: Seasonal change in total biomass of net zooplankton (mesh size 350 μm, salps excluded) from composite data at Station *P* 1971-1974. Conversion used in text: (mg C m^{-3}) = 0.04 (mg wet weight m^{-3}). Note the relatively high zooplankton standing stock in winter. Decline in copepods from May to October maybe caused by emigration to depth or consumption by predatory mesozooplankton. Adapted from Parsons and Lalli (1988).

After the females of *Neocalanus* spp. spawn yolky eggs at around 400 m sometime between September and January, they die (Miller *et al.* 1984, M. Wen 1995 pers. comm.). Early larval stages migrate towards the surface where they arrive between November and March (Fig. 2.6). In surface waters larval development proceeds from Copepodite I to V in the first half of the year. Later larval stages carry out their migration to depth in the month May to July for *N. plumchrus* and July to September for *N. cristatus*, with the adult forms having reduced mouth parts (R. Goldblatt 1995 pers. comm.) and therefore not being able to feed but rather using accumulated oil reserves (Miller *et al.* 1991a; Miller *et al.* 1991b; Parsons & Lalli 1988). This annual, semelparous life cycle is contrasted by the biennial, iteroparous life cycle of *Eucalanus bungii*, another copepod, which reproduces in the mixed layer in early May and early July and overwinters in diapause (Copepodite stages III-VI) at depth of 250-500 m (Miller *et al.* 1984).

In late summer and fall the smaller copepod *Calanus pacificus* (3 mm) dominates mesozooplankton biomass and seems most abundant in waters with >13°C. However, sea surface temperature could induce *Neocalanus spp.* vertical migrations, to avoid high metabolic loss due to high temperature or due to any of the 13 possibilities that have been suggested (see Mangel and Clark (1988) p.149-151), thus rendering the temperature effect on *C. pacificus* indirect. Smaller copepod species, which may have more than one generation per year, are most abundant in late fall and winter and generally have a higher density of individuals than larger species which dominate the biomass and which may at times feed upon those smaller species (Parsons & Lalli 1988).

It has been shown in lab experiments that mesozooplankton is omnivorous and that it prefers microzoo- and microphytoplankton over nanophytoplankton (Dagg 1993; Gifford 1993).

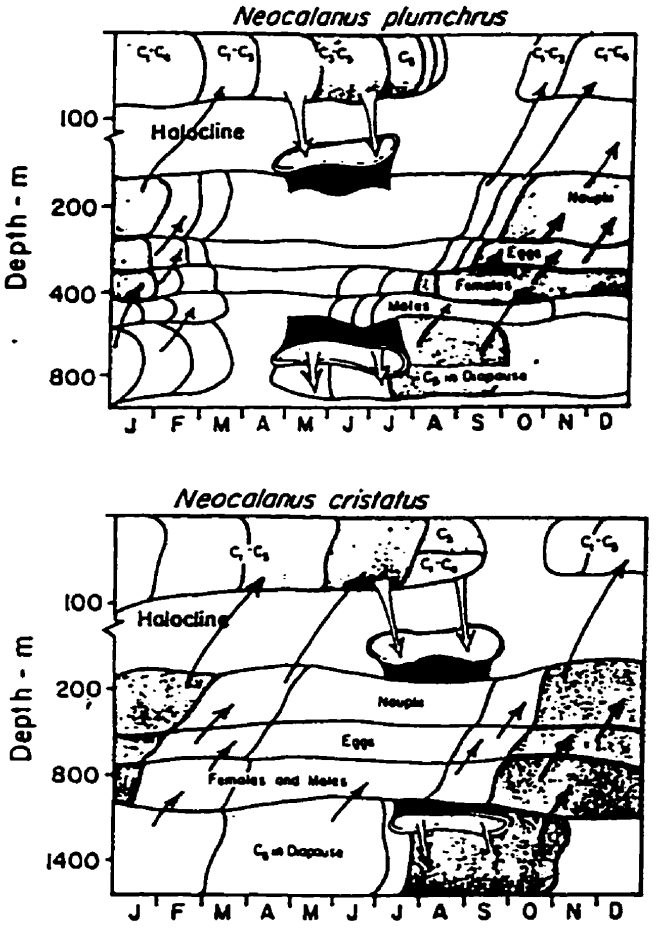


Fig. 2.6: Annual life cycles of *Neocalanus plumchrus* and *N. cristatus* with respect to depth distribution (dark shading indicates higher abundance). Note different depth scales. For explanations see text. Adapted from Miller et al. (1984).

However, because microphytoplankton represents only a small proportion of the phytoplankton standing stock in the Central Subarctic Domain, and because nanophytoplankton had to be presented in the lab experiments at much higher concentrations than found at Station *P* in order for mesozooplankton to thrive, mesozooplankton must be primarily carnivorous in the Central Subarctic Domain (Dagg 1993; Gifford 1993; Miller *et al.* 1991a; Parsons & Lalli 1988). Additionally it was found that the grazing capacity of copepods at Station *P* was never large enough to match phytoplankton growth rates and that the amount of ingested phytoplankton (as measured by the amount of phytoplankton pigments in copepod guts) was not large enough to support mesozooplankton respiration rates (Dagg 1993; Gifford 1993; Miller *et al.* 1991b). Using data in Miller *et al.* (1991b) calculation of the ratio of chlorophyll removal trough microzooplankton grazing to removal through macrograzers shows an increase from 2.3 to 13.3 from May to August (but note that data come from 4 cruises made between June 1987 and August 1988). This increase can be attributed to several factors including mesozooplankton switching preferred prey-size from small to larger prey during their ontogenetic development, greater availability of larger phytoplankton species in late spring and early summer, or ontogenetic migration to depth of large copepods in summer and fall. However, phytoplankton seems to be controlled by microzooplankton which in turn is consumed by mesozooplankton (Booth *et al.* 1993; Dagg 1993; Gifford 1993; Landry *et al.* 1993a; Landry *et al.* 1993b; Mackas *et al.* 1993; Miller *et al.* 1991b)

This view has been called the "mixing and micrograzer hypothesis" (Miller *et al.* 1991b), i.e. a shallow mixed layer in winter supports steady primary production and thus the micrograzer community which, due to its high growth rates of up to more than 5 doublings per day (Miller *et al.* 1991b), can control nanophytoplankton standing stock before environmental conditions (i.e.

seasonal mixed layer, increased illumination, high nutrient levels) could cause a bloom (Landry *et al.* 1993b). The "mixing and micrograzer hypothesis" has replaced the classical explanation that *Neocalanus* spp. life history causes mesozooplankton to arrive at the surface just in time to control phytoplankton standing stock (for a discussion see Parsons & Lalli 1988). The increase in mesozooplankton biomass immediately after the increase in primary productivity in spring (Wong *et al.* 1995) is probably caused by a combination of the arrival of seasonally, vertically migrating copepods as well as highly coupled grazing at the second transfer level.

It has also been suggested that mesozooplankton could feed on small phytoplankton cells that are attached to particles (Dagg 1993a, P. Boyd 1995 pers. comm.) or large POM *per se* (Mackas *et al.* 1993). Because cohort-survival of many species is determined early in life (Begon *et al.* 1990), the abundance of *Neocalanus* spp. is probably controlled by processes at great depth which might involve POM, but which are yet unknown.

Microzooplankton (i.e. heterotrophic flagellates and ciliates) plays an important role in the transfer of energy up the food chain and apparently in the control of nanophytoplankton standing stock (Booth *et al.* 1993; Landry *et al.* 1993b; Miller *et al.* 1991b; Strom *et al.* 1993). From published data (Strom *et al.* 1993) I have estimated microzooplankton spring and summer standing stock around 6.5 mg C m^{-3} (or $13 \cdot 10^6$ cells m^{-3}) for May/June and 4.8 mg C m^{-3} (or $10.3 \cdot 10^6$ cells m^{-3}) for August/September, with respective coefficients of variation of 65% (78%) and 25% (22%). However, my estimates are lower than the mean near-surface concentrations of 15 mg C m^{-3} reported by Booth *et al.* (1993). Note that Pauly *et al.* (1996) in their mass-balance model of the Alaska Gyre use a microzooplankton density that is too low by a factor of 3, an error attributable to taking into account the ciliate component of microzooplankton only, which is usually <40% (Booth *et al.* 1993). Highest abundance of microzooplankton occurs between

November and March/April (Fig. 2.7 (LeBrasseur & Kennedy 1972), which is consistent with decreased predation through copepods in fall and winter (Dagg 1993; Gifford 1993; Mackas *et al.* 1993). Also, in case nanophytoplankton is not readily available (e.g. in winters and/or locations with (depth of mixing) > (critical depth)) microzooplankton is able to maintain a high density by shifting to a diet of POM and associated bacteria (a mode of ecological interaction called "Microbial Loop" (Azam *et al.* 1983; Morel *et al.* 1991)). Note that the data given in LeBrasseur & Kennedy (1972) are 3-4 orders of magnitude smaller than those in Strom *et al.* (1993) which may be attributed to the coarse mesh size of 44 µm used in the former study and the modern analyzing equipment and thus higher resolution for small size classes in the later. Assuming there is no bias in LeBrasseur & Kennedy's (1972) errors,Fig. 2.7 shows seasonal changes in protozoa numbers rather than absolute concentrations.

Although the notion of a constant standing stock of phytoplankton throughout the year has already acquired the status of indisputable truth (Miller *et al.* 1991b; Parslow 1981; Parsons & Lalli 1988; Parsons & LeBrasseur 1968; Wong *et al.* 1995) and although this has been attributed to grazing limitation by microzooplankton (Booth *et al.* 1993; Dagg 1993; Miller *et al.* 1991b; Strom *et al.* 1993; Welschmeyer *et al.* 1993) doubts remain whether microzooplankton is capable of controlling the nanophytoplankton standing stock (see section *Phytoplankton* and experiments by Landry *et al.* 1993b).

Little is known about other zooplankton groups and size classes in the Central Subarctic Domain: Non-crustacean herbivorous suspension-feeding mesozooplankton (e.g. pteropods, salps, larvaceans) which deploy mucous nets to capture food particles (plankton and POM);

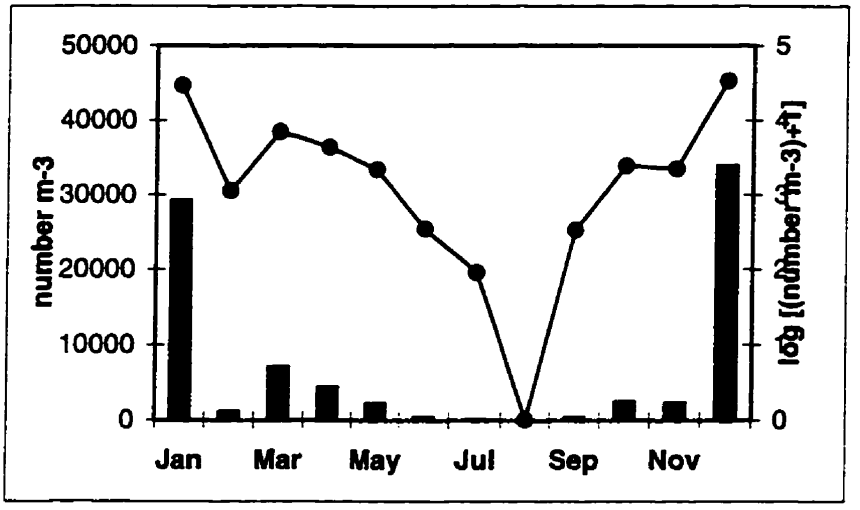


Fig. 2.7: Seasonal change in protozoa density at Station *P* (1966-1968). Note the high standing stock of microzooplankton in winter. For a discussion about the quality of the data as well as more recent estimates see text. Data from LeBrasseur and Kennedy (1972).

chaetognaths which feed on other mesozooplankton and especially on their smaller developmental stages; euphausiids which are usually omnivorous but due to low concentrations of microphytoplankton in the Central Subarctic Domain are mainly carnivorous, feeding on micro- and mesozooplankton; and gelatinous zooplankton which in certain zones at certain times dominate zooplankton biomass (Pearcy *et al.* 1988). For a detailed listing of zooplankton species in the Central Subarctic Domain see Parsons & Lalli (1988) or Pearcy *et al.* (1988). While juvenile salmon mostly feed on mesozooplankton, immature and maturing Pacific salmon rely also on little studied squid and macrozooplankton as their food source (Brodeur 1990); see also: Section 2.1. Feeding Ecology of Sockeye Salmon). Lack of information on squid and macrozooplankton is due to the problems associated with the sampling of highly motile and of gelatinous groups within the zooplankton community.

Fish and Higher Trophic Levels

Many of the estimates for fish and higher trophic levels in the Central Subarctic Domain come from Pauly *et al.* (1996). Unfortunately, I have identified many numerical errors in this workshop report especially for variables for which alternative sources are readily available. Thus, most values referenced under "Pauly *et al.* 1996" are not beyond doubt. Trites & Heise's (1996) section in Pauly *et al.* (1996) is a careful review of marine mammals in the NE-Pacific which I thus reference separately.

The total standing stock of fish in the epipelagic zone of the Central Subarctic Domain has been estimated to be around 3 g wet weight m^{-2} (plus around 4.5 g wet weight m^{-2} of diurnally migrating mesopelagics; Pauly *et al.* 1996), or 0.4 g C m^{-2} (plus 0.6 g C m^{-2} mesopelagics), using Iverson's (1990) fish carbon to wet weight ratio of 0.13. Total annual fish production has been

estimated at ≈3.9 g wet weight m^{-2} y^{-1} (plus 3.2 g wet weight m^{-2} y^{-1} from mesopelagics; Pauly *et al.* 1996), or around 0.5 g C m^{-2} y^{-1} (plus 0.4 mesopelagics). These recent estimates of fish production in the Gulf of Alaska open ocean ecosystem are >10 times previous estimates (Parsons 1986). This discrepancy can partially be attributed to the revised primary productivity estimates (Wong *et al.* 1995) and transfer up the food chain, and new information on the group of small pelagics which make up ≈80% of the total fish production (Pauly *et al.* 1996).

With a standing stock of <0.05 g C m^{-2} and an annual production of 0.06 g C m^{-2} y^{-1} (Pauly *et al.* 1996) anadromous North American Pacific salmon represent ≈10% of both the total fish standing stock as well as total fish production, excluding mesopelagics in both cases. While salmon species are rather insignificant in fish biomass and production for the Central Subarctic Domain their trophic niche certainly is important. The commercially important species pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and sockeye salmon undertake extensive migrations in this region (Groot & Margolis 1991) and during their early marine life history stages biological production processes in the Central Subarctic Domain may determine year-class strength and thus catch in the fishery when adults return to their spawning grounds a few years later (Brodeur & Hollowed 1993; Burgner 1991; the complex working hypothesis of my thesis). Coho and chinook salmon also migrate into the ocean but inhabit the Coastal and Transitional domains, rather than the Central Subarctic Domain, during their oceanic phase. Table 2.2 summarizes Pacific salmon life history characteristics.

The dominant small pelagic fish of the NE-Pacific is saury (*Cololabis saira*), which visits the NE-Pacific in the summer (Brodeur 1988; Pearcy 1993). Because of its small size (L_∞ = 35 cm

Table 2.2: Life history characteristics of North American Pacific salmon species (*Oncorhynchus spp.*). Adapted from Pearcy (1992).

Species	Freshwater Residence Time	Month of Ocean Entry	Size at Ocean Entry	Estuarine Residence Time	Ocean Residence Time
Pink (*O. gorbuscha*)	days-weeks	May-Jun	30-40 mm	<1 week	1.6 years
Chum (*O. keta*)	days-weeks	Mar-Jun	30-40 mm	1-2 weeks	2-4 years
Sockeye (*O. nerka*)	0-2 years	May-Jun	60-100 mm	<1 week	1-5 years
Coho* (*O. kisutch*)	0-4 years	May-Jun	60-120 mm	<1 week	0.5-1.5 years
Chinook* (*O. tshawytscha*)	0-2 years	May-Oct	40-110 mm	<1 week-months	0.5-6 years

* Species does not inhabit Central Subarctic Domain during oceanic phase.

total length) and the use of gill nets in surveys, abundance estimates are difficult to obtain for this species. Saury mostly feeds on copepods (50% of stomach contents by weight), euphausiids, amphipods, and smaller fish (Pauly *et al.* 1996).

An ecologically important fish species is the pomfret (*Brama japonica*) which again is a summer visitor (Brodeur 1988; Pearcy 1993) and has the highest abundance (catch rates of up to >400 fish (km^{-1} gillnet) $(12\ h)^{-1}$ (Brodeur & Ware 1995)) of all vertebrate species in the epipelagic zone of the open ocean. Pomfret have an asymptotic total length (L_∞) of 61 cm and an asymptotic weight (W_∞) of 3860 g and are longlived (9 years (Pauly *et al.* 1996)). Pomfret prey consists mainly of cephalopods and fish (>50% by weight), and euphausiids, amphipods and decapods (11-49% by weight (Pauly *et al.* 1996)).

An important fish predator might be the daggertooth (*Anotopterus pharao*), a large (85 cm total length) bathypelagic fish that preys on adult, immature and possibly juvenile salmon. Daggertooth slash marks have been found on 12% of adult sockeye salmon returning to British Columbia (Welch et al. 1991 as cited in Pauly *et al.* (1996). Little is known about abundance, life history, diet and population dynamics of the daggertooth (Pauly *et al.* 1996).

Larger fish predators in the Central Subarctic Domain are the salmon shark (*Lamna ditropis*), which can be found all year round, and the blue shark (*Prionace glauca*), a summer visitor from warmer waters (Brodeur 1988; Pauly *et al.* 1996; Pearcy 1993). The densities of sharks in the Gulf of Alaska are unknown; however, bycatch data provide lower bound estimates of 0.05 metric tons km^{-2} for both sharks combined. Salmon sharks prey upon immature and mature salmon (coho (*O. kisutch*), sockeye, pink, and chum), other pelagic, and mesopelagic fish. Blue sharks feed mainly on squid, mesopelagics, saury and pomfret (Brodeur 1988).

Seabird populations for the total Central Subarctic Domain (here Sanger's definition, with an area of 3.79 10^6 km^2 (Sanger 1972a)) have been estimated at 0.57 birds km^{-2} in winter and 4.40 birds km^{-2} in summer, or 0.33 and 2.41 kg live weight km^{-2}, respectively (Sanger 1972a). A more recent estimate for the summer seabird population is 9.49 birds km^{-2} and 6 kg live weight km^{-2} (Pauly *et al.* 1996). Available data do not allow the estimation of a production / biomass ratio but indicate a very high food consumption / biomass ratio of 101 (Pauly *et al.* 1996), which can be attributed to the high metabolic requirements of these small endotherms. Diet composition shows that small pelagic fish (48%) and cephalopods (45%) make up the bulk of the total food consumption for all birds combined (Pauly *et al.* 1996). Marine birds prey upon juvenile salmon while salmon migrate through the Coastal Downwelling Domain during their seaward migration, however, at what stage in the marine environment juvenile salmon attain a large enough body size and thus escape speed to reduce avian predation remains unknown.

Thirteen species of marine mammal species are at least temporary residents of the Central Subarctic Domain (Trites & Heise 1996). Because marine mammal standing stock and production, as well as diet composition and ingestion quantity data are very sparse only two species may directly impact salmon and are thus summarized here. A more explicit discussion on marine mammals can be found in Trites & Heise (1996).

The Northern Fur Seal (*Callorhinus ursinus*) is present in the Alaskan Gyre from April to September with population sizes estimated at 130 000 individuals during their migrations between April and September and a mere 5 000 (if any at all considering the harsh winter-conditions in that region) in the rest of the year. The production / biomass ratio of these pinnipeds is estimated at 6% per year (with a maximum of 0.12 y^{-1}). Summer diet for these

pinnipeds is dominated by squid (78%) and only a few salmon are consumed (11% (Trites & Heise 1996); stomach contents percentage is not defined as weight or volume).

Little is known about a third and newly discovered subspecies of killer whales (*Orcinus orca*), the oceanic killer whale, which apart from having been observed migrating towards the open ocean has some morphological traits related to its dorsal fin (J. Ford 1994 pers. comm.). From their intense hunting communication, similar to resident killer whales and unlike the rather quietly hunting mammal-eating transients, it has been inferred that oceanics must be fish eating. Future research will hopefully shed some light on the ecology of this subspecies.

Because the topic of interest in this study is the interannual variability in sockeye salmon (marine) survival and because higher trophic levels in the Central Subarctic Domain feed mostly on later life history stages of salmon, higher trophic levels in the Central Subarctic Domain probably have a minor impact on salmon cohort-survival, which I conjecture to be set early in marine life.

2.2.2. The Coastal Downwelling and the Transitional Domain

The Coastal Downwelling Domain reaches from Cape Scott at the north tip of Vancouver Island to the Andreanof Islands in the Aleutian chain (Fig. 2.1). Its width from the coastline follows the continental shelf and ranges from a few kilometers (off the Queen Charlotte Islands, British Columbia) to more than 200 km northeast of Kodiak Island (Alaska). This domain can be characterized as a non-tropical shelf ecosystem with an annual primary production of 200-300 mg C m^{-2} (Pauly & Christensen 1995b; Ware & McFarlane 1989) and microphytoplankton at the base of a three- to four-level food chain (Ware & McFarlane 1989). Annual zooplankton production is in the order of 10-50 g C m^{-2} y^{-1} (Ware & McFarlane 1989). Because of onshore

advection from the Central Subarctic Domain (Brodeur & Hollowed 1993; Ware & McFarlane 1989; Wickett 1967) the zooplankton community in the Coastal Downwelling Domain is dominated by the same species as the oceanic environment, except for the summer when smaller neritic copepods become more abundant (Ware & McFarlane 1989, and references cited therein).

Dominant fish species in this region are Walleye pollock, Pacific cod, Sablefish, and Pacific halibut (Ware & McFarlane 1989). Their bentho-pelagic life suggests that trophodynamic phasing (Parsons 1988; Parsons & Kessler 1987; Parsons & Lalli 1988; Parsons *et al.* 1984) in the euphotic zone may not be as tight here as in the Central Subarctic Domain, i.e. organic matter is exported from the surface and drives a benthic food chain at depth. Pacific herring and of course juvenile salmon on their migration into the Central Subarctic Domain form the pelagic fish group (Ware & McFarlane 1989).

Unfortunately, little information is available on this ecosystem (Ware & McFarlane 1989). Nevertheless, the importance of regional zooplankton production and advection from the Central Subarctic Domain into this region as well as of resident predator populations for survival of juvenile salmon and hence its year-class strength should be emphasized (Burgner 1991; Healey 1991; Parsons *et al.* 1984; Pearcy 1992; Peterman 1978; Walters *et al.* 1978).

Seabird populations for the total Coastal Domain (using Sanger's definition, with an area of $1.36\ 10^6$ km^2 (Sanger 1972a)) have been estimated at 1.6 birds km^{-2} in winter and 7.8 birds km^{-2} in summer, or 0.63 and 4.79 kg live weight km^{-2}, respectively (Sanger 1972a). Diet data from the Central Subarctic Domain indicate that marine birds mostly feed upon small pelagic fish (Pauly *et al.* 1996) and show that the Sooty shearwater population may consume ≈150 kg of small fish km^{-2} over the summer half year, which is the equivalent of 10 000 juvenile fish km^{-2}, assuming a

rather high body weight of 15 g per juvenile fish, which is equivalent to the highest mean body weight a sockeye smolt may attain (Burgner 1991).

Resident killer whales (*Orcinus orca*) live close to the coast and population size is estimated at 240 individuals (Trites & Heise 1996). The production / biomass ratio of toothed whales is estimated to be ≈3% per year (with a maximum of 0.04 y^{-1}). Stomach contents data are not available for the Gulf of Alaska but inferring from different sources Trites & Heise (1996) estimate that 80% of the summer and 60% of the winter diet consists of salmon. Back of the envelope calculations show that resident killer whales consume ≈5 million salmon per year, hardly a number that could dominate salmon cohort-survival considering that these could be produced by only 2000 female spawners.

The Transitional Domain is a somewhat arbitrary construction of a zone characterized by high seasonal and interannual variability in oceanographic conditions, caused by the bifurcation of the eastward Subarctic Current into the northward Alaska Current and the southward California Current. Nutrient and phytoplankton samples taken along Line *P* (from the south tip of Vancouver Island out to Station *P* (50°N 145°W) show the following sequence (P. Harrison 1995 pers. comm.): Iron limitation of microphytoplankton west of 140°W. No nitrate limitation in an approximately 50 km wide band from the coast with diatoms as the dominating microphytoplankton group. In-between, a zone where nitrate is limiting and diatoms as well as dinoflagellates can be found. These results demonstrate that the Transitional Domain has its own ecological characteristics, whose influences on salmon (marine) survival is unknown.

2.3. Physical Oceanography of the Northeast Pacific

The Northeast Pacific is not a distinct basin of the Pacific Ocean but is rather defined by the variable extent of ocean currents, especially the Subarctic Current. However, for the purpose of this study the Northeast Pacific is defined as the ocean area between 40 and 66°N, and 175°E and 125°W, i.e. the approximate range in ocean distribution of North American Pacific salmon species (Groot & Margolis 1991; Welch *et al.* 1995). For classification of the Northeast Pacific into four upper zone domains see Section 2.2. and Fig. 2.1.

Two aspects of the physical oceanography of the Northeast Pacific play an important role for sockeye salmon: First, the seasonal change in the vertical and horizontal temperature and salinity structure which is crucial to water column stratification, and thus primary production (Parsons & Lalli 1988), and ocean distribution of salmon (Brett *et al.* 1969; Welch *et al.* 1995). And second, the major circulation patterns which transport biological production (Brodeur & Hollowed 1993; Ware & McFarlane 1989; Wickett 1967) and influence migration routes of nekton (Scandol *et al.* 1996).

Additionally two restrictions apply: First, due to the lack of a coastal circulation model, in connection with salmon survival especially needed for the Coastal Downwelling Domain and Bering Sea, I have not included the coastal physical oceanography of the Northeast Pacific in this discussion; lack of biological data justifies a similar argument (Ware & McFarlane 1989). Second, because sockeye salmon are visual predators (Burgner 1991) I have only discussed processes within the mixed upper layer, i.e. the euphotic zone, although it has been suggested that salmon occasionally forage in waters below 150 m (Pearcy *et al.* 1988).

Temperature and salinity distribution

In winter the open Northeast Pacific is characterized by an isothermal, isohaline upper layer with temperatures around 5°C and low salinities around 32.7 parts per thousand which extends down to a depth of 100 - 200 m (Dodimead *et al.* 1963; Thomson 1981). Below the mixed upper layer lies a narrow (few meters) but steep thermocline with a total temperature decrease of 1°C which tops the cold-water sphere, the vast zone of slow but continuous temperature decrease with depth. The thermocline is on top of a thicker (around 50 m) permanent halocline with a total salinity increase of 1 part per thousand. Just like the change in temperature, though with opposite sign, below the halocline salinity increases slowly but continuously to a depth of up to 4000 m (Thomson 1981).

A different picture emerges in summer when a shallow (10 - 20 m) isothermal layer with temperatures of 12 - 15°C overlies a thicker (around 50 m) very steep thermocline with a total temperature difference up to 10°C below which temperature again decreases slowly and steadily, i.e. temperature rate of increase is faster than mixing. Within the mixed layer salinity increases stepwise from about 32.5 to 33.0 parts per thousand at the top of the halocline at 100 - 200 m, and further to 33.7 parts per thousand in the approximately 50 m wide halocline. Thus there is little seasonal variability in the halocline, hence the term "permanent" halocline.

Notwithstanding that there is spatial and temporal variation in the annual cycle of stratification (Parsons *et al.* 1966; Parsons & LeBrasseur 1968), an average location within the open Northeast Pacific in an average year could be characterized as follows: At the end of the winter mixing season around March increased solar radiation heats up the surface layer and wind and wave action transport heat to depth. Reduced mixing due to a weakening in winds during the summer month results in a shallow isothermal stratum to a depth of 10 - 20 m that overlies a

number of layers of rapid temperature decrease, the remains of the seasonal thermoclines (Fig. 2.8). After August cooler air temperatures lead to a net heat transfer from the ocean into the atmosphere and the cooler and thus heavier surface water parcels give rise to convective mixing of the upper layer, which allows colder water to penetrate deeper than wind mixing alone would. However, the simultaneous action of convective, wind and wave mixing during fall and winter results in an isothermal surface layer by January that extends to the top of the halocline, i.e. the layer of salt-controlled stability of the water column (Thomson 1981). Although the permanent halocline may not seem to be a spectacular feature I want to emphasize that it is the result of non-trivial dynamic hydrological processes such as freshwater input (rainfall, continental run-off), evaporation, and wind, wave and convective mixing, and that its presence has large implications for the biology of the Central Subarctic Domain (see Section 2.2. Ecosystems of the Northeast Pacific; Parsons & Lalli 1988).

Spatial patterns in the Northeast Pacific in winter are almost zonal for temperature from approximately 12°C at 40°N to 4°C at 55°N with isothermals bending northward near the coast. Salinity is spatially more structured with maxima occurring within the Alaskan Stream (Fig. 2.1) in winter and the center of the Alaskan Gyre in summer. Coast-near low salinities are due to continental freshwater run-off. Summer temperature distribution is latitudinal up to 45°N (15°C) and then describes concentric circles centered around 10°C in the Alaskan Stream. Low temperatures and high salinities in the Coastal Upwelling Domain (Fig. 2.1) are caused by upwelling of cold deep water.

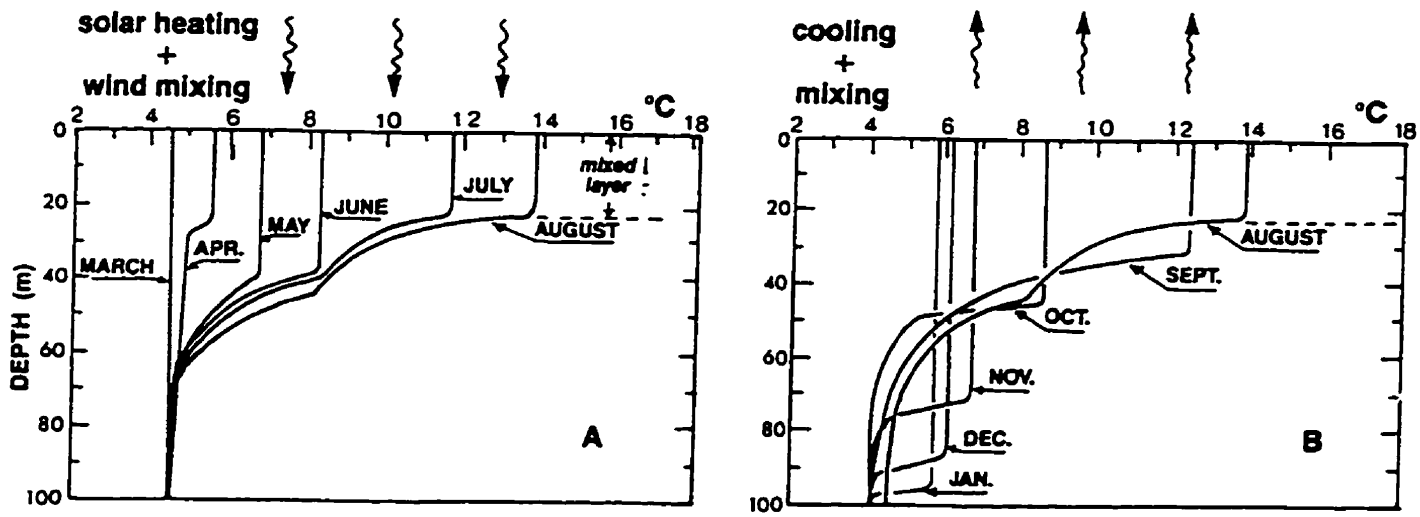


Fig. 2.8: Development (A) and deterioration (B) of seasonal thermoclines in the open Northeast Pacific. This qualitative model has been derived by Thomson (1981) from single day data collected in August 1977 and February 1978 at Station *P*, and from arguments in Dodimead et al. (1963). Adapted from Thomson (1981).

Currents

Main current patterns in the Northeast Pacific are shown in Fig. 2.1. The Subarctic Current originates in the Kuroshio-Oyashio system off Japan and travels eastward at only 5 - 10 cm s^{-1}. Approaching the North American continent and in a zone which, due to its large variability in currents on all space and time scales, is called Transitional Domain (Fig. 2.1), the Subarctic Current then bifurcates into the southeastward California Current (mean speed ≈20 cm s^{-1}) and the northwestward Alaska Current. The Alaska Current continues along the coasts of British Columbia and Alaska at mean speeds of 25-35 cm s^{-1} in summer and winter, respectively, but southeast winds in winter may accelerate it up to 75 cm s^{-1}. South of the Aleutian island chain the Alaska Current becomes a narrow and fast (≥ 1m s^{-1}) westward boundary current, then called the Alaskan Stream, which feeds water masses into the Bering Sea and also southward. Subarctic Current, Alaska Current and Alaskan Stream form the cyclonic Alaskan Gyre, which represents the main part of the Central Subarctic Domain (Fig. 2.1), with Ekman pumping at its center.

With the exception of a few coastal currents, which are density-driven, major currents in the Northeast Pacific are wind-driven. Wind direction and speed are mainly controlled by the intensity, i.e. spatial extent and strength, location and duration of two pressure systems, the Aleutian Low and the North Pacific High. The Aleutian Low develops around the Aleutian Island from August to January, when it reaches its peak, and then shifts to the west and simultaneously gets weaker until it is finally undetectable in July. Then the cycle starts again. Winter winds in the Gulf of Alaska and on parts of the North American W-coast (Alaska, British Columbia, Washington, Oregon) are from southwest to southeast. In contrast, the North Pacific High is located at about 35°N and remains present year round, although with variable spatial extent. It reaches a maximum, in terms of strength as well as horizontal dimensions, in July and August

(Favorite *et al.* 1976). Main wind direction in the Northeast Pacific under the influence of the North Pacific High is southeastward.

A look at smaller scales reveals mesoscale and smaller eddies (Thomson *et al.* 1990) all with their characteristic shorter time scales and ecological effects. However, because of the 1° longitude x 1° latitude resolution of the spatially-explicit simulations (Chapter 4), small scale ocean features have been ignored in this study. I have also omitted teleconnections with respect to ENSO-events (El Niño - Southern Oscillation) which can have large physical (Dodimead 1985; Hamilton & Emery 1985; Huyer & Smith 1985; Kerr 1992; Tabata 1985; Trenberth 1990), biogeographical and biological effects (Brodeur & Pearcy 1992; Fulton & LeBrasseur 1985). A good general discussion on the sequence of events of ENSO can be found in (ann & Lazier (1991), and on its specific effects in the Northeast Pacific in Wooster & Fluharty (1985).

3. POPULATION MODELS, ENVIRONMENTAL FORCINGS, AND MEAN FIELD SIMULATIONS

"There is no unique way to find out the characteristic properties of a system. The most important source remains intuition."
R.E. Ulanowicz and G. Radach (1981)

In this Chapter I will introduce two population models each of which will then be used for a mean field ecosystem simulation using abiotic environmental forcings at two sites (Station *P* (50°N 145°W) and a near-coast location at 50°N 130°W) from 1981 to 1984. The objective of the mean field simulations is to explore and to "tune" (Platt *et al.* 1981) population models for the spatially-explicit simulations to follow in Chapter 4 in which both population models will be coupled to spatial physical environmental datasets (Woodruff *et al.* 1987) and a surface current model (Ingraham & Miyahara 1989). In order to explore the sensitivity of the ecosystem-simulations to model structure, initial conditions, biological parameters, and functional relationships of component interactions, components and processes of the ecosystems of the Northeast Pacific have been radically simplified to the bare essentials deemed necessary to explain variability in sockeye salmon cohort survival.

3.1. Essential State Variables

While in predictive studies one usually justifies the inclusion of system components into a dynamic model (e.g. resource management (Holling 1978; Walters 1986)), I find that in hindcast studies of systems for which abundant information is already available it is more useful to start out with a synthesis of the current mechanistic understanding in the form of a complicated flow

diagram, and then to justify the exclusion of various state variables and subprocesses considered not necessary for the complex process under investigation (see also Chapter 1 in Starfield & Bleloch 1991). Although the remaining 'minimum model' still represents a subjective choice of all available information, this choice seems less arbitrary because ecosystem components and processes have been rationally excluded rather than simply left out.

The Biological Subsystem in Fig. 1.9 (Chapter 1) shows a conceptual flow diagram of the different energy pathways in the ecosystems of the Northeast Pacific. The complex working hypothesis of this thesis, i.e. the variability in sockeye salmon survival can be explained by the variability in mesozooplankton availability for juvenile sockeye, a function of ecosystem processes in the open Northeast Pacific (see Section 1.4: Conjecture), allows the following exclusions, which represent a set of assumptions for the population models described below (compare Figs. 3.1 and 1.9):

The dominant size class of primary producers in the Central Subarctic Domain is nanophytoplankton (size 2-20 μm (Booth *et al.* 1993; Parsons 1972)) which typically represents >90% of the biomass (Miller *et al.* 1991a). This dominance is the result of the complex nutrient dynamics in the Central Subarctic as well as the capability of copepods to immediately graze down any small-scale short-term increase in microphytoplankton. Thus microphytoplankton has been completely excluded from the models.

The objective of this thesis is to explain the variability in sockeye salmon survival, as derived from stock-recruitment data, by the variability in mesozooplankton availability to the juveniles. However, because of the complications in modeling processes at higher trophic levels in an ecosystem context (see Section 1.4) I have not explicitly included fish species in my models. As a consequence, neither piscivores nor fisheries can be modeled in any meaningful way and thus

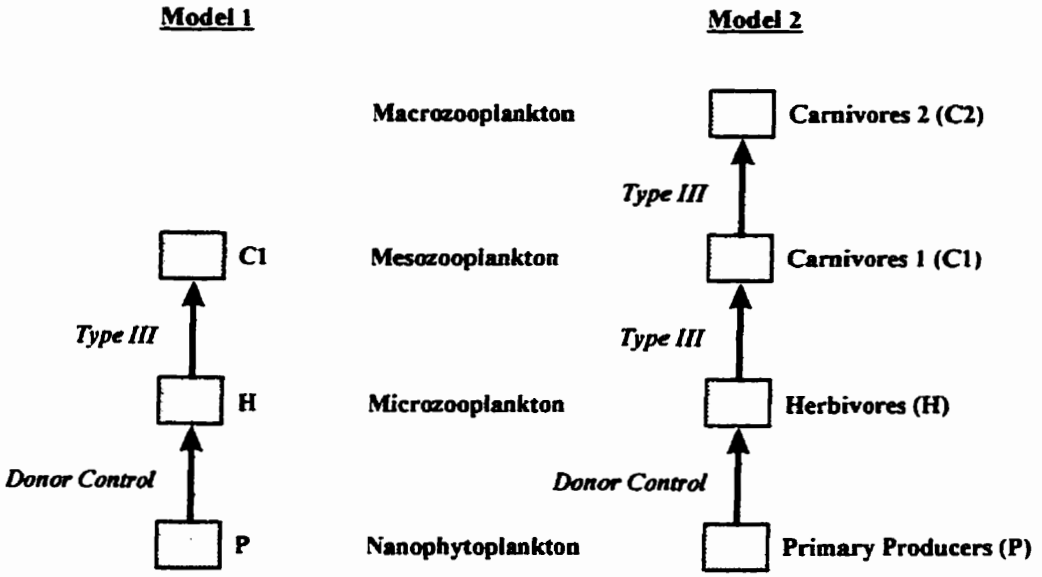


Fig. 3.1: Flow diagrams for two population models. Model 1 includes three, Model 2 four trophic levels. Biomass transfers between trophic levels are labeled according to the functional form of predation rate to prey density (for explanations see Section 3.3).

have been left out.

Nutrient dynamics in the Northeast Pacific are the result of complex biogeochemical (Donaghay *et al.* 1991) and eco-physiological processes (Morel *et al.* 1991; Wheeler & Kokkinakis 1990) and thus have received a lot of attention (e.g. Miller 1993b; Parsons 1988; for details see Section 2.2.). However, while the availability of certain micronutrients could set the realized size-class of primary producers (Armstrong 1994) there is strong indication from observations (Booth *et al.* 1993; Landry *et al.* 1993b) as well as from modeling studies (Frost 1991; Frost 1993) that phytoplankton standing stock in the NE-Pacific may not be nutrient-, but is rather light- and grazer-limited (Banse 1994). In fact, primary production per unit biomass does not seem to be bottom-up limited to any extent during the spring and summer months (Welschmeyer *et al.* 1993), the period of time in which at least nutrient limitation is most likely to occur. Consequently, standing stock and dynamics of nutrients have been excluded from the population models below. Furthermore, since nutrient recycling seems to occur at a faster rate than would be limiting for primary production, i.e. phytoplankton standing stock never reaches a level where nutrient uptake is greater than nutrient supply, components of the microbial recycling process (dissolved (DOM) and particulate organic matter (POM), and bacteria) have been excluded from the models as well.

The exclusion of nutrients from a plankton model might seem unusual and thus deserves further justification: In general, different aquatic ecosystems have been modeled by variations of nutrient-phytoplankton-zooplankton (N-P-Z) models (Steele & Henderson 1992) to gain insight into biogeochemical processes (e.g. Kishi & Kawamiya 1995), population dynamics (e.g. Walters *et al.* 1987), or both of these aspects (e.g. Frost 1993), as well as community structure (e.g. Armstrong 1994). Historically the first plankton models were developed in the early 1940s

(Banse 1994) for regions where observational data were readily available, i.e. the continental shelves and the North Atlantic. Incidentally these regions exhibit regular seasonal phytoplankton blooms associated with a decrease in nutrient concentrations (Banse 1994; Parsons *et al.* 1984), and consequently, models of these ocean regions have included nutrients as a state variable. Knowledge obtained from these coastal ecosystems, in combination with Liebig's Law of the Minimum (Odum 1971) and the Redfield ratio (Parsons *et al.* 1984), was then extrapolated to the open ocean situation and nutrient limitation was also presupposed there.

Today, there is ample evidence that open ocean phytoplankton community structure is conditioned by trace element or micronutrient availability and its standing stock is grazer- rather than nutrient-limited (Armstrong 1994; Banse 1994). Consequently, recent realistic ecosystem models for the Northeast Pacific do not contain dependence on nutrient concentration in the phytoplankton rate equation (Frost 1993), while older (Frost 1987) or more conventional ones do (Kishi & Kawamiya 1995; Matear 1995). For most open ocean systems phytoplankton concentrations (as measured in Chl-a) change seasonally only by a factor of two (Banse 1994); the exception is the greater than one order of magnitude seasonal change in Chl-a for the North Atlantic (Parsons & Lalli 1988), the "oddball" (Banse 1994) among temperate oceans. Furthermore, low seasonal variability in open ocean systems seems to be independent of macronutrient concentrations in the respective regions (Banse 1994), indicating grazing limitation with rapid nutrient cycling that provides ammonium back to phytoplankton (Frost 1993; Miller *et al.* 1991b; Wheeler & Kokkinakis 1990; see also Section 2.2.; Note that the arguments on the carbon-to-chlorophyll-a ratio presented in Subsection 2.2.1. and in Frost (1987, 1993) and McAllister (1969) apply to open ocean systems in general.)

It is important to distinguish between the effects of nutrients on phytoplankton community structure, e.g. nanophytoplankton species outcompeting the larger microphytoplankton for ammonium, and their effects on phytoplankton specific growth rates. A more precise usage of the term 'nutrient limitation' in scientific publications would be helpful. Further, biomass production at any trophic level can be said to be bottom-up or top-down controlled. (I ignore here what has been called "middle-out control" because competition effects are by definition not addressed by the aggregation of species into trophic levels.) Bottom-up control describes the effects that physical forcings or lower trophic levels have on the specific growth rate of a particular population, while top-down control refers to the predation effects of higher trophic levels on the standing stock of that population. (Phytoplankton standing stock could in principle be controlled by pathogens. However, because viruses are species specific and the phytoplankton community is very diverse, viruses probably do not remove more than 3% of the daily primary production (C. Suttle 1998 pers. comm.).) Biomass production of a population or any other biological aggregation is given by

$$\frac{dN}{dt} = r(A,B,...)N \qquad \text{(Eq. 3.1)}$$

where N represents biomass, and $r(A,B,...)$ is the specific growth rate that is regulated by factors $A,B,....$ There is no inherent reason why production could not be regulated by both terms on the right hand side of Eq. 3.1 at the same time or in a dynamically alternating fashion, i.e. abiotic factors or lower trophic levels affecting r, predation limiting the population N.

The inclusion of a particular state variable in a model is not only bound by the natural processes being modeled (and the objectives of the model) but also by their spatial and temporal scales. As a consequence, non-repeatable and/or non-stationary phenomena (Walters 1986) at

various spatial and temporal scales either have to be addressed explicitely or excluded altogether. Consequently I assume that spatio-temporal structural changes in the natural ecosystems of the Northeast Pacific within the simulation period 1950-1990 are negligible (a not completely unreasonable assumption (Steele & Henderson 1984; but see Pauly *et al.* 1998)).

3.2. Environmental Forcings

Physical environmental variables that have been explicitly included in the mean field simulations for Station *P* (Section 3.4) are: solar radiation, sea surface temperature, clouds (evaporation), winds, and mixed layer depth (Fig. 1.9 in Chapter 1). In addition to these, the spatially-explicit simulations of Chapter 4 contain advection fields (currents). Only sea surface temperature, winds, and cloudiness are observed variables, all other abiotic forcings used in my simulations are derived from them, with the exception of sea surface currents which come from simulation results by Ingraham & Miyahara (1989).

In all my simulations, monthly data where assigned to the 15^{th} of each month (with the simplification of 30 days for each month, thus only 360 days per year) with linear temporal interpolation between months.

3.2.1 Observed Variables

Monthly arithmetic means for sea surface temperature, scalar wind speed and total cloudiness data from 1950-1990 were taken from the Comprehensive Ocean-Atmosphere Data Set (COADS). COADS is a statistical summary of global marine observations with a spatial resolution of 2° longitude x 2° latitude (even-numbered) for each month of each year from 1854 up to the present (for details on data collection, archiving, statistics, and quality control see Slutz *et al.* 1985 and Woodruff *et al.* 1987). Because the spatial resolution of my spatially-explicit simulations (Chapter 4) is 1° longitude x 1° latitude and because data were not available for every 2° x 2° box, I have spatially interpolated data from COADS using bilinear interpolation (Press *et al.* 1992).

Fig. 3.2 shows the seasonal and interannual variability in mixed layer temperature (sea surface temperature) at Station *P* (50°N 145°W) and for a near-coast location at 50°N 130°W for four successive years (1981-1984).

3.2.2. Derived Variables

Incident Solar Radiation (Insolation)

The total daily insolation on a horizontal surface at depth z, I_z, is given by:

$$I_z = I_0 e^{kz} \qquad \text{(Eq. 3.2a)}$$

where I_0 is the daily sea surface insolation and z is given in negative values, i.e. as a depth coordinate. k represents the extinction coefficient, which is a function of the concentrations of particulate and dissolved matter, and water itself (Parsons *et al.* 1984). Because the effects of chlorophyll-a concentration onto the extinction coefficient are very small (see Eq. (2) in Frost 1987) and because detritus, which can have a substantial effect on the extinction coefficient, was not included into the models, the extinction coefficient for each month was calculated as the mean value (Fig. 3.3) of the observed monthly minimum and maximum for the period 1960 to 1964, as summarized in Parsons *et al.* (1966).

Further, as suggested by Frost (1993) 70% of the total solar radiation was considered as photosynthetically active radiation $I_{PAR,z}$, up from the 50% used earlier (Frost 1987; Parsons *et al.* 1984):

$$I_{PAR,z} = 0.7 I_z \qquad \text{(Eq. 3.2b)}$$

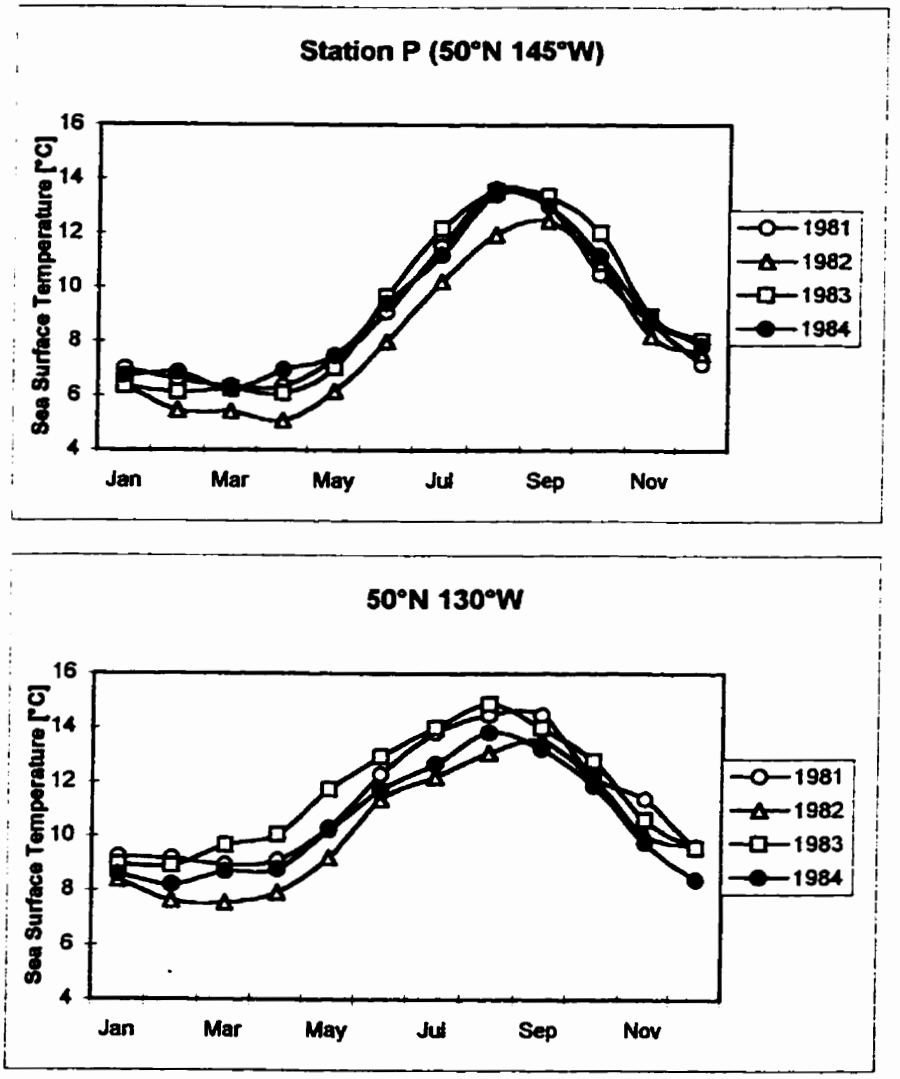


Fig. 3.2: Seasonal and interannual variability in sea surface (mixed layer) temperature at Station *P* (50°N 145°W) and at 50°N 130°W for 1981 to 1984.

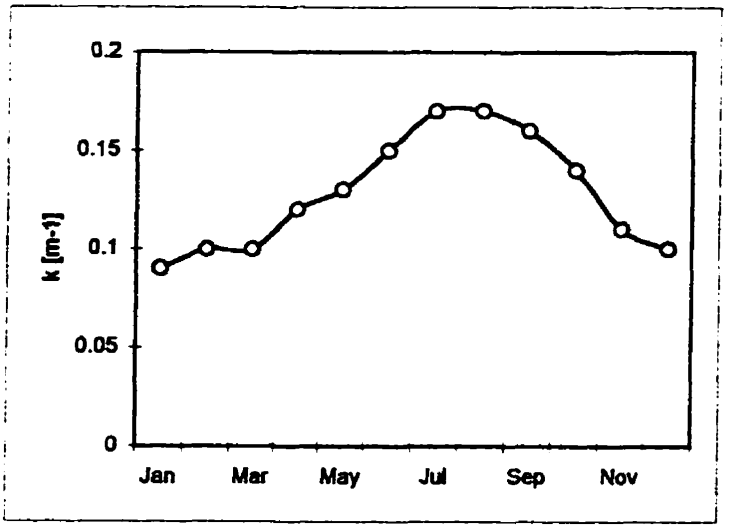


Fig. 3.3: Seasonal variability in the extinction coefficient k in the Northeast Pacific. The extinction coefficient for each month was calculated as the mean value of the observed monthly minimum and maximum for the period 1960 to 1964. Data from Parsons et al. (1966).

Daily sea surface insolation (I_0 in Eq. 3.2a) was calculated as a function of daily insolation at the top of the clouds (I_s) and cloudiness (C) by:

$$I_0 = I_s(1 - 0.08875C) \qquad \text{(Eq. 3.2c)}$$

This is a variation of the Sverdrup Equation (Sverdrup *et al.* 1947) with cloudiness C in units of eights (or 12.5%) of sky covered by clouds, as given by COADS. Note however that cloudiness is a very crude estimator for light reflection and absorption due to clouds (Kremer & Nixon 1978).

Daily insolation at the top of the troposphere (I_s) was derived from first principles (for the complete derivation see Peixoto & Oort (1992) their Chapter 6) with an assumed atmospheric transmissivity above the troposphere of τ_s=0.75 (Ott 1988; Schneider 1989):

$$I_s = \tau_s S \cdot 2\left(\eta \sin\varphi \sin\delta + \cos\varphi \cos\delta \sin\eta\right) \cdot \frac{43200}{\pi} \qquad \text{(Eq. 3.2d)}$$

where S is the solar constant (1360 W m^{-2} (Peixoto & Oort 1992)), η represents the hour angle from the local meridian at sunrise and sunset (a function of the time of the year), φ is latitude, and δ is declination. Eq. 3.2d integrates instant irradiance over one day. Further,

$$\eta = \arccos\left(-\tan\varphi \tan\delta\right) \qquad \text{(Eq. 3.2e)}$$

$$\delta = \arcsin(\sin\nu \sin d) \qquad \text{(Eq. 3.2f)}$$

where 2η is daylength in radians, ν represents the obliquity of the ecliptic (i.e. 23.45°) and d is number of days after vernal equinox.

Fig. 3.4 shows the seasonal and interannual variability in daily sea surface insolation as calculated from Eqs. 3.2c-f at Station *P* and at a near-coast location for 1981-1984. Station *P* model results resemble closely the data shown in Frost (1993 his Fig.1).

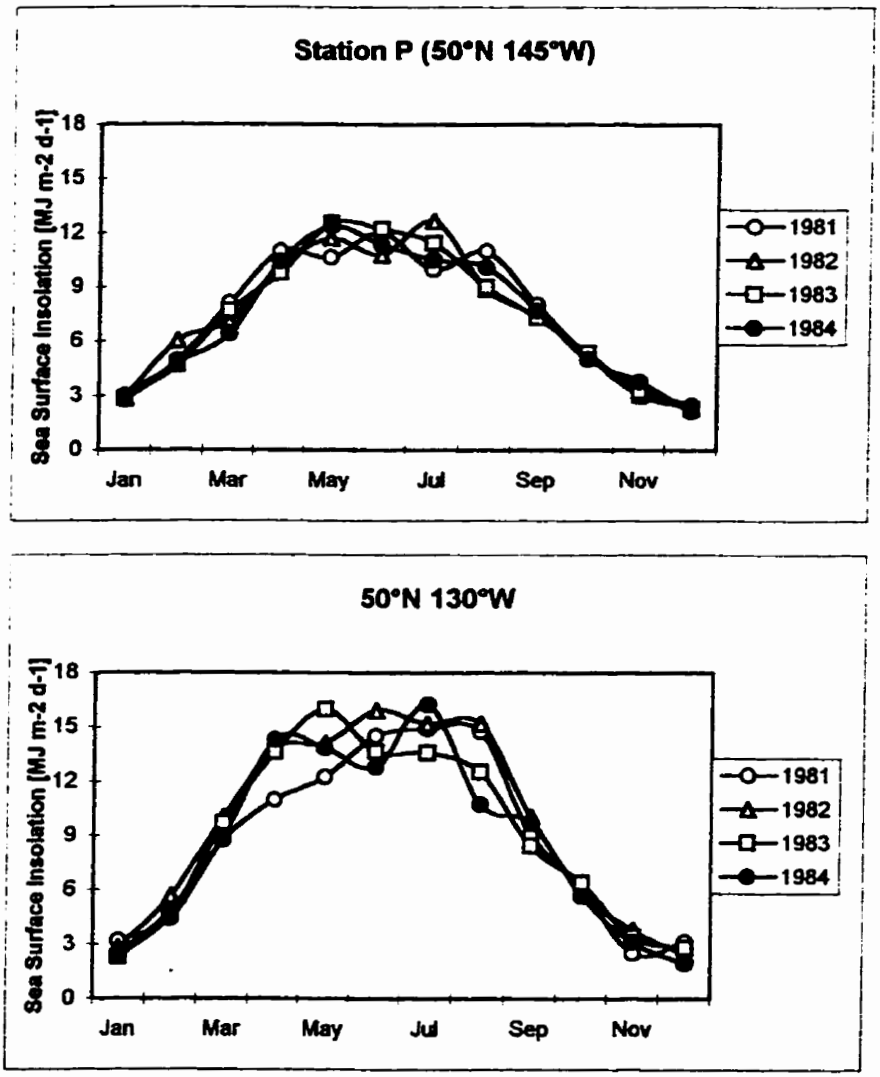


Fig. 3.4: Seasonal and interannual variability in sea surface insolation at Station *P* (50°N 145°W) and at 50°N 130°W for 1981 to 1984. Sea surface insolation was calculated from first principles and COADS cloudiness data.

Mixed Layer Depth

Lacking a long-term and spatially-explicit data set of the mixed layer depth (z_{ML}, negative values as mixed layer depth was regarded as a depth coordinate) in the Northeast Pacific I took the monthly statistical summaries of mixed layer depth at Station *P* (50°N 145°W) for the years 1947-1963 published in Parsons & LeBrasseur (1968). From the Comprehensive Ocean-Atmosphere Data Set (COADS; see Subsection 3.2.1.) I calculated the monthly mean sea surface temperature (T) and scalar wind speed (w) for the same period. Next I performed a linear regression analysis for mixed layer depth as a function of sea surface temperature (Eq. 3.3a) and scalar wind speed (Eq. 3.3b), respectively (coefficient of determination in brackets):

$$z_{ML} = 11.99T - 178.59 \ (r^2 = 0.83) \qquad \text{(Eq. 3.3a)}$$

$$z_{ML} = -10.46w + 23.53 \ (r^2 = 0.26) \qquad \text{(Eq. 3.3b)}$$

Furthermore, I fitted a two variable (sea surface temperature and scalar wind speed) linear-normal model (Brown & Rothery 1993) to the data using the least squares method:

$$z_{ML} = 11.10T - 3.33w - 139.80 \ (r^2 = 0.85) \qquad \text{(Eq. 3.3c)}$$

For comparison, I took an empirical model originally obtained by Tabata *et al.* (1965) for the summer isothermal surface layer and extrapolated it over the whole year:

$$z_{ML} = -2.06w + 2.3 \ (r^2 = 0.26) \qquad \text{(Eq. 3.3d)}$$

Fig. 3.5 shows the data from Parsons & LeBrasseur (1968) and results obtained from the different models. Although the sea surface temperature model (Eq. 3.3a) explains 83% of the variability in the data the two variable linear-normal model (Eq. 3.3c) was used for the mean field simulations for Station *P* (Section 3.4) as well as the spatially-explicit simulations

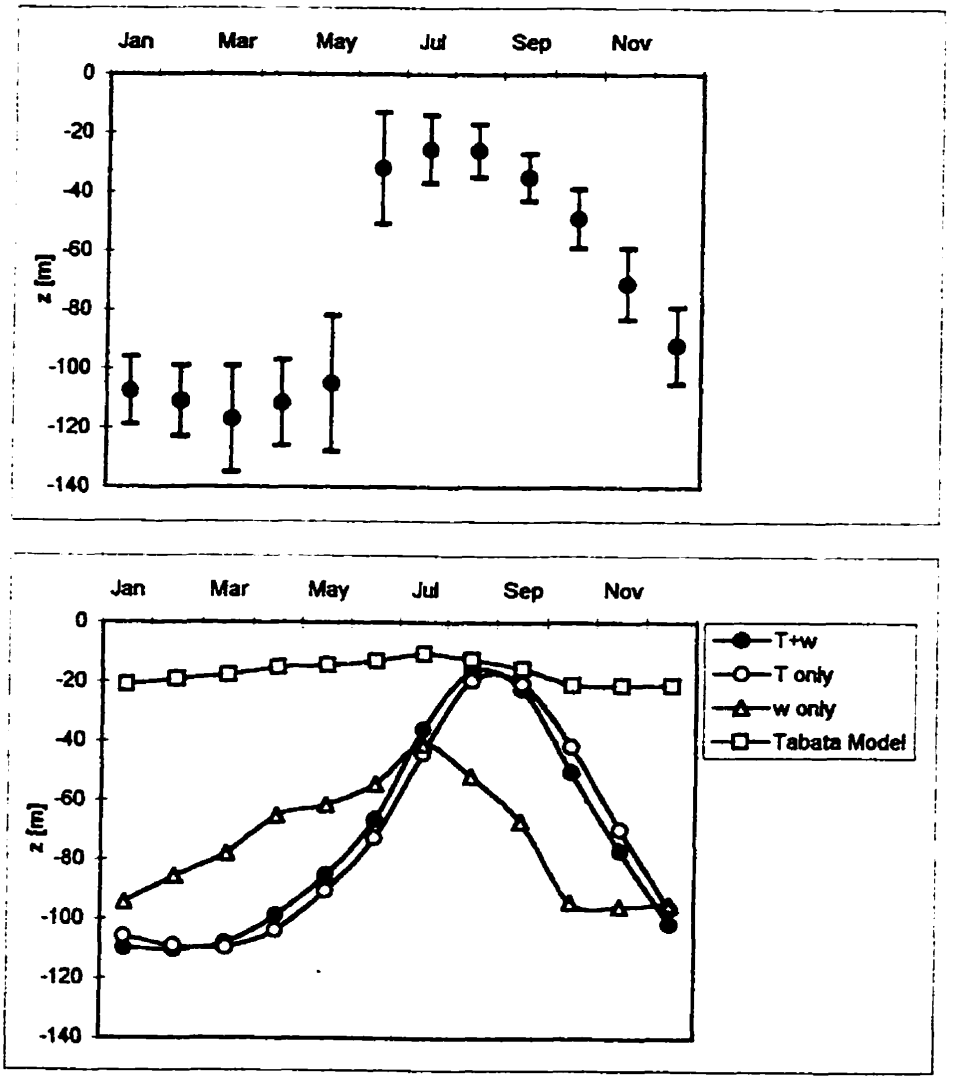


Fig. 3.5: Upper panel: Observed monthly mean mixed layer depth plus/minus one standard deviation at Station *P* (50°N 145°W) for the period 1947-1963. Data from Parsons et al. (1968). Lower panel: Various models for mixed layer depth using sea surface temperature (T), scalar wind speed (w), or both. The Tabata Model (Tabata et al. 1965) gives the relationship between summer isothermal surface layer and wind speed and performs poorly when extrapolated beyond its valid statistical universe of inference in summer (for details see text).

(Chapter 4) for the following reasons: First, only pre-analyzed, i.e. monthly statistical summaries, mixed layer depth data for only one station were available for the regression analyses which thus gives a very narrow picture of the whole Northeast Pacific. Consequently, the model that fits the data even only marginally better seems justified. Second, testing for the differences between monthly variance for the years 1947 to 1963 in the mixed layer depth data and mixed layer depth from model calculations revealed that the two variable linear-normal model had only four (Apr, Sep-Nov) statistically significant differences at the 5% level, and two (Oct, Nov) at the 1% level (2-tailed variance ratio test (Zar 1996)), while all other models had a larger number of statistically significant differences (note that here a statistically significant difference means that the monthly variances in the data and the model do not the come from the same population). And third, in general the mechanisms of stratification involve both temperature and wind mixing (see Section 2.3.).

Note that in case of calm wind conditions any sea surface temperature >12.60 °C in Eq. 3.3c will result in a positive mixed layer depth coordinate. Because temperatures greater than that can occur at least locally anywhere in the Northeast Pacific in the summer and do in general occur south of 40°N in winter (Thomson 1981), an upper maximum for the mixed layer depth coordinate of -15 m has been assumed in the simulations.

Fig. 3.6 shows the seasonal and interannual variability in mixed layer depth at Station *P* and at a near-coast location for 1981-1984. Station *P* model results again resemble closely the data shown in Frost (1993 his Fig.1).

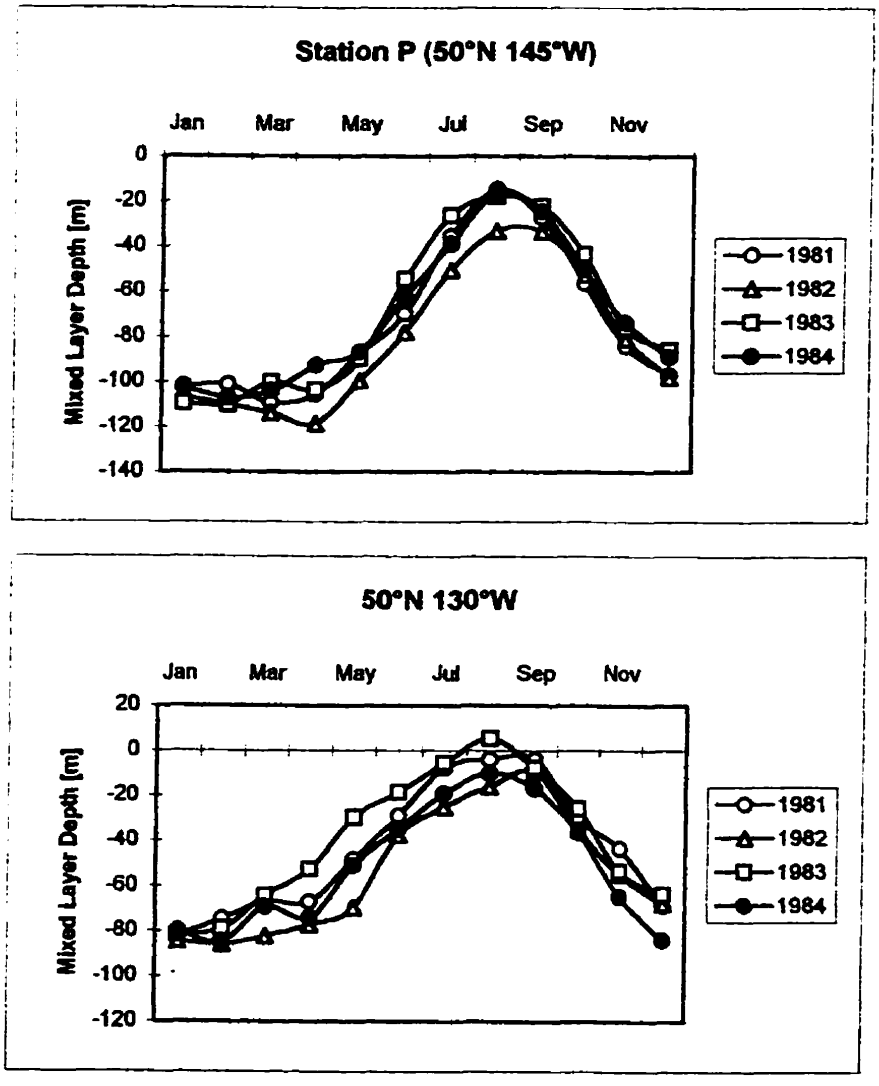


Fig. 3.6: Seasonal and interannual variability in mixed layer depth at Station *P* (50°N 145°W) and at 50°N 130°W for 1981 to 1984. Mixed layer depth coordinate (negative values) was calculated as a function of sea surface temperature and scalar wind speed (both from COADS) using a two variable linear-normal (Eq. 3.3c). Note that mixed layer depths are plotted before truncation (for details see text), resulting in a positive mixed layer depth at 50°N 130°W in 1983. Because the variability in mixed layer depth is largely explained ($r^2 = 0.83$) by mixed layer temperature their seasonal and interannual patterns are similar (compare Fig. 3.2).

Advection, Divergence and Sinking

Surface current data for the Northeast Pacific from 1950 to 1990, used in the spatially-explicit simulations described in Chapter 4, come from the Ocean Surface Current Simulation (OSCURS). OSCURS is a hydrodynamic simulation that combines COADS vector wind data with mean geostrophic currents and returns daily values for currents in the mixed upper layer (Ingraham & Miyahara 1989). To save computer space currents were averaged for each month and then linearly interpolated in time for daily values (Scandol *et al.* 1996). OSCURS has a spatial resolution of 1° longitude x 1° latitude and thus does not simulate small scale oceanic (e.g. mesoscale eddies) or coastal processes (e.g. tides, estuarine circulation).

From the monthly means of OSCURS current vectors (u, v) I calculated the divergence (D) for each 1° longitude x 1° latitude for the period 1981 to 1984, with x, y and z as axes in a right-handed coordinate system:

$$D = -\frac{\Delta w}{\Delta z} = \frac{\Delta u}{\Delta x} + \frac{\Delta v}{\Delta y} \qquad \text{(Eq. 3.4)}$$

Mean divergence ($\overline{D} = 0.72 \cdot 10^{-3}$ d^{-1}, standard deviation: $s = 2.28 \cdot 10^{-7}$ d^{-1}, sample size: n=59520) for the whole area of the Northeast Pacific (120-180°W, 35-62°N) for 1981-1984 shows excess export of water, which is replaced by Ekman pumping from depth. Because in my simulations I assume that there is no life below the surface mixed layer (see Section 3.4.) and because nutrient dynamics have been excluded from the simulations (see Section 3.1.), upwelling processes and the associated decrease in concentrations of biological products is essentially accounted for by surface export due to advection. Downwelling, on the other hand, can in principle remove organisms from the mixed layer but because the mean value of negative divergence was very low ($\overline{D}_{neg} = -7.42 \cdot 10^{-3}$ d^{-1}, sample size: $n = 27844$, i.e. on average less than

1% of the mixed layer concentration gets exported every day), and because oceanic species of phytoplankton and zooplankton have been selected for an array of morphological, physiological, or behavioral adaptations to prevent them from sinking out of the mixed surface layer, vertical export of living plankton from the mixed layer to depth has been assumed negligible in my simulations compared to changes due to biological production and physical advection processes.

Fig. 3.7 shows the seasonal and interannual variability in Ekman pumping at Station *P* and at a near-coast location for 1981-1984 as calculated from the product of divergence (D) and mixed layer depth (z_{ML}). Mean Ekman pumping for the summer months (Apr-Sep) is 0.04 m d^{-1} (standard deviation: $s = 0.13$ m d^{-1}, sample size: $n = 24$, 1981-1984) which is within the range of 0.01-0.1 m d^{-1} reported by Miller *et al.* (1991b).

Carbon-to-Chlorophyll-a Ratio

Despite the constant chlorophyll-a concentration in the Northeast Pacific (e.g. Parsons & Lalli 1988; Wong *et al.* 1995) there is presumably seasonal variation in phytoplankton standing stock when measured in carbon concentration (McAllister 1969, P. Harrison 1997 pers. comm.). This is due to the variability in the intracellular carbon-to-chlorophyll-a ratio in phytoplankton, which increases with increasing insolation, i.e. under a high light regime fewer and/or smaller chloroplasts are able to maintain the same photosynthetic rate as more and/or larger chloroplasts under low light conditions. Because chloroplasts are complex cytomorphological structures and chlorophyll-a is a complex macromolecule (Denffer *et al.* 1983), potentially higher growth rates of phytoplankton cells with more chlorophyll-a are probably offset by the high metabolic costs of its synthesis and maintenance.

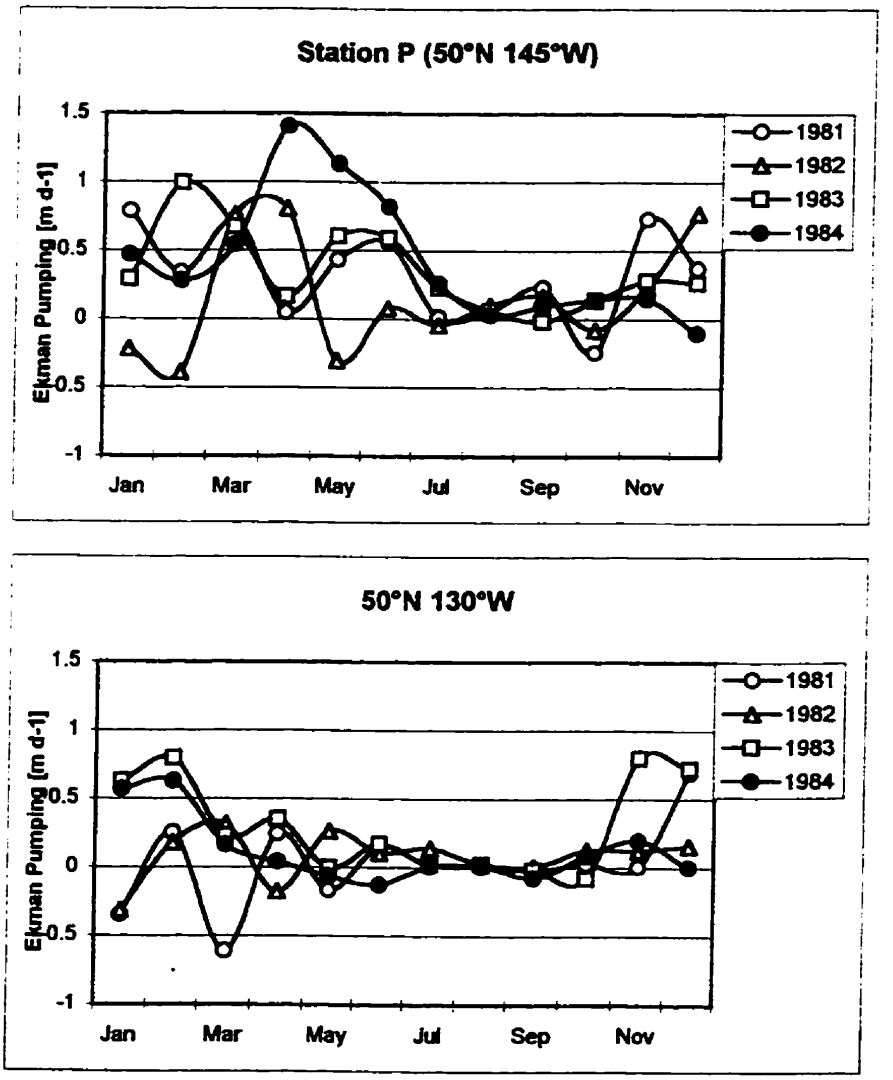


Fig. 3.7: Seasonal and interannual variability in Ekman pumping at Station *P* (50°N 145°W) and at 50°N 130°W for 1981 to 1984. Positive Ekman pumping indicates upwelling, negative Ekman pumping downwelling. Variability in Ekman pumping reflects the variability in local advection processes. Compare the large interannual variability in Ekman transport to those in other environmental variables (Figs. 3.2, 3.4, and 3.6).

To account for the latitudinal variability in the carbon-to-chlorophyll-a ratio caused by the variability in insolation, I performed a linear regression analysis using the carbon-to-chlorophyll-a ratio (χ) "data" for Station *P* in McAllister (1969) and monthly sea surface insolation (I_0, in units MJ m^{-2} d^{-1}) at Station *P* for 1981-1984 as calculated from the model described above (coefficient of determination in brackets):

$$\chi = 3.44 I_0 + 5.68 \ (r^2 = 0.68) \qquad \text{(Eq. 3.5a)}$$

Considering a time-lag between changes in sea-surface insolation and changes in mixed layer depth (McAllister 1969; compare Figs. 3.4 and 3.6) as well as a physiological adaptation period, I also tried a delayed regression (Fig. 3.8):

$$\chi_{month} = 4.07 I_{0,month-1} + 1.00 \ (r^2 = 0.95) \qquad \text{(Eq. 3.5b)}$$

Because Eq. 3.5b yields an annual minimum carbon-to-chlorophyll-a ratio of $\chi = 2$ at 62 N° in January (with $I_{0,Dec} = 0.26$ MJ m^{-2} d^{-1} under full overcast conditions) and an annual maximum of $\chi = 133$ at 43 N° in July (with $I_{0,Jun} = 32.33$ MJ m^{-2} d^{-1} under clear sky) the carbon-to-chlorophyll-a ratio was limited to the range $9 \leq \chi \leq 90$ (P. Harrison 1993 pers. comm.). Unfortunately though, McAllister's (1969) estimates of the carbon-to-chlorophyll-a ratio are based upon only two observations (the winter minimum and the summer maximum) obtained from, presumably shipboard, phytoplankton cultures with interpolations in-between, which makes Eq. 3.5b a weak functional statement.

Fig. 3.9 shows the seasonal and interannual variability in the carbon-to-chlorophyll-a ratio at Station *P* and at a near-coast location for 1981-1984 as calculated from Eq. 3.5b.

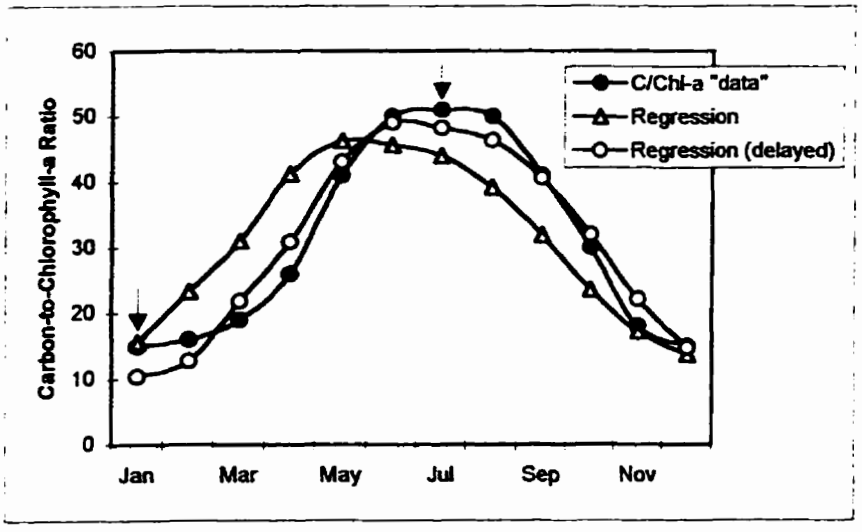


Fig. 3.8: Seasonal variability in the carbon-to-chlorophyll-a ratio (data points from McAllister 1969) and two regression models (carbon-to-chlorophyll-a ratio as a function of sea surface insolation) for Station *P* (for details see text). Arrows indicate the only two observations made by McAllister (1969).

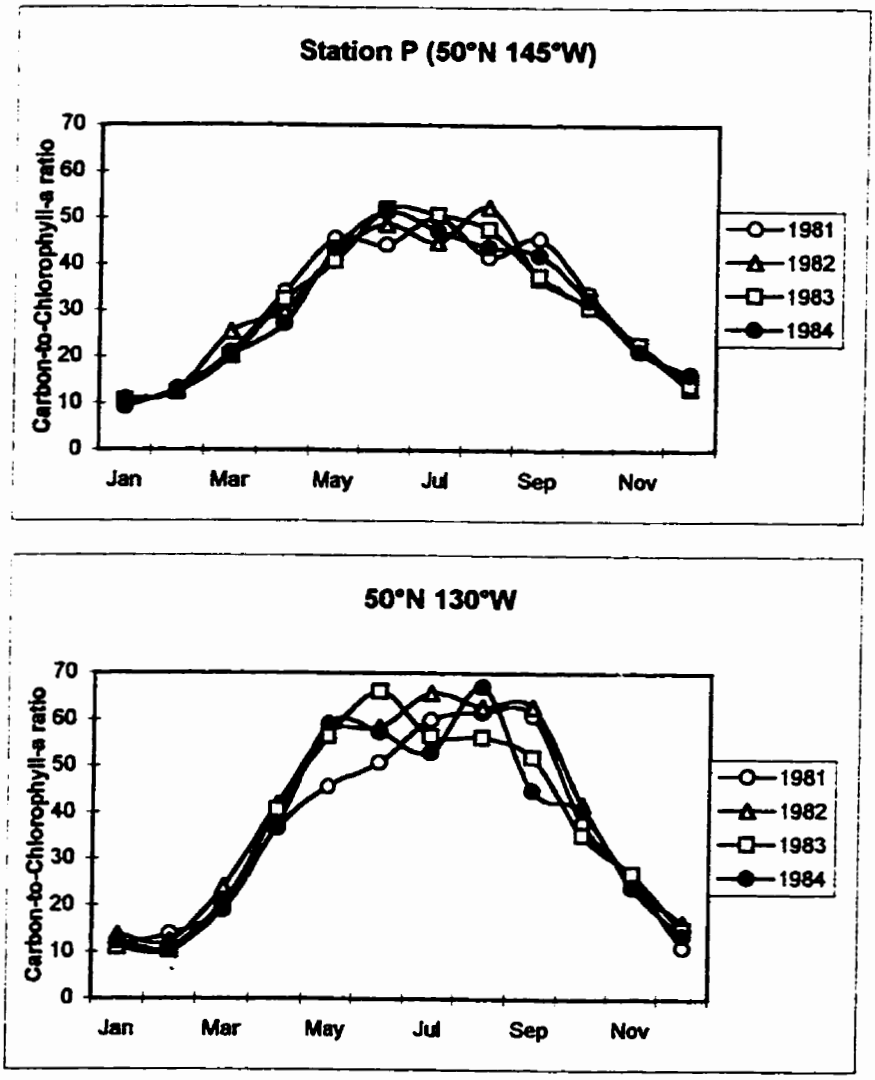


Fig. 3.9: Seasonal and interannual variability in the carbon-to-chlorophyll-a ratio at Station *P* (50°N 145°W) and at 50°N 130°W for 1981 to 1984. Note that because the carbon-to-chlorophyll ratio is calculated as a function of sea surface insolation their seasonal and interannual patterns are similar (see Fig.3.4).

3.3. Population Models

Fig. 3.1 (Section 3.1.) shows the conceptual flow diagrams for two different population models that I have developed for the lower trophic levels of the Northeast Pacific. State variables explicitly included in the population models can be seen in an ecosystem context in Fig. 1.9 (hatched boxes there).

To test for effects of linear community structure on community dynamics, i.e. the sensitivity to model structure, I have developed two different population models: Model 1 contains three state variables, i.e. primary producers, herbivores, and primary carnivores, and Model 2 contains four state variables, i.e. a secondary carnivore trophic level is added . Because upper (predatory) closure has been found to have marked effects on model behavior (Steele & Henderson 1992) using models with odd and even numbers of trophic levels should maximize the contrast in model behavior (Pimm 1992).

For each state variable the following equation with its components applies:

$$\frac{d(\text{Biomass})}{dt} = \text{Gain} - \text{Loss} + \text{Import} - \text{Export} \qquad \text{(Eq. 3.6)}$$

$$\begin{aligned} \text{Gain} &= \text{Ingestion} + \text{Recruitment} \\ \text{Loss} &= \text{Egestion} + \text{Respiration} + \text{Deaths} + \text{Retirement} \\ \text{Import} &= \text{Immigration}_{x,y,z} + (\text{Passive Import})_{x,y,z} \\ \text{Export} &= \text{Emigration}_{x,y,z} + (\text{Passive Export})_{x,y,z} \end{aligned}$$

Note that because Eq. 3.6 is the rate equation for biomass, births are not considered in the "gain" term, i.e. there is no biomass change associated with the birth process. On the other hand the change in biomass due to deaths has to be included. Recruitment and Retirement designate terms used in age-structured population models (e.g. Rice 1995) and have only been added for completeness but have not been included in the population models below. The terms for import

from and export to x- and y-dimensions, but not from and to depths, will be applied in Chapter 4: Spatially Explicit Simulations. Eq. 3.6 says of course nothing about the details of the biotic and abiotic interactions but represents a useful general framework for developing models because it identifies all the possible flows.

The rate equations for the state variables below follow the same structure, with first a term for gross energy consumption, followed by a term which denotes the loss due to respiration, and at last a term for predation. The following rate equations apply (Table 3.1; see Table 3.2 for symbols):

Table 3.1: Rate Equations for State Variables

Primary Producers (P_0)	$P_0 = \chi P_{Chl}$	(Eq. 3.7)
Herbivores (H)	$\frac{dH}{dt} = b_P P_0 - m_H H - \frac{a_{HC_1} H^2}{K_{HC_1}^2 + H^2} C_1$	(Eq. 3.8)
Carnivores 1 (C_1)	$\frac{dC_1}{dt} = \frac{a_{HC_1} H^2}{K_{HC_1}^2 + H^2} C_1 - m_{C_1} C_1 - \frac{a_{C_1C_2} C_1^2}{K_{C_1C_2}^2 + C_1^2} C_2$	(Eq. 3.9)
Carnivores 2 (C_2)	$\frac{dC_2}{dt} = \frac{a_{C_1C_2} C_1^2}{K_{C_1C_2}^2 + C_1^2} C_2 - m_{C_2} C_2$	(Eq. 3.10)

Table 3.2: Important symbols used in models and simulations.

State Variables and Parameter Subscripts

C_1	smaller carnivorous zooplankton (mesozooplankton) carbon concentration [mg C m^{-3}]
C_2	larger carnivorous zooplankton (macrozooplankton) carbon concentration [mg C m^{-3}]
H	herbivorous zooplankton (microzooplankton) carbon concentration [mg C m^{-3}]
P_0	phytoplankton carbon concentration [mg C m^{-3}]
P_{Chl}	phytoplankton chlorophyll-a concentration [mg Chl-a m^{-3}]

Physical Forcings

I_0	daily sea surface insolation on a horizontal plane at sea surface [MJ m^{-2} d^{-1}]
T	mixed layer temperature [°C]
z_{ML}	mixed layer depth [m]
H_d	daylength [h]
k	extinction coefficient [m^{-1}]

Parameters

α	photosynthetic efficiency [mg C (mg Chl-a)$^{-1}$ d^{-1}]
χ	carbon-to-chlorophyll-a ratio
a_{XY}	maximum specific predation rate of predator Y on prey X [mg C (mg C)$^{-1}$ d^{-1}]
b_P	specific growth rate for phytoplankton [mg C (mg C)$^{-1}$ d^{-1}]
K_{XY}	half-saturation constant for predation of predator Y on prey X [mg C m^{-3}]
m_X	specific respiration or non-predatory death rate of population X [mg C (mg C)$^{-1}$ d^{-1}]
p_P	photosynthetic rate [mg C (mg Chl-a)$^{-1}$ d^{-1}]

Equation 3.7

Phytoplankton density is assumed to be simply a function of the seasonally varying carbon-to-chlorophyll-a ratio χ (see Subsection 3.2.2.) multiplied by the constant chlorophyll-a concentration P_{Chl} of 0.4 mg Chl-a m^{-3} for the Northeast Pacific (Wong *et al.* 1995). Further, because seasonally the phytoplankton carbon concentration increases as a maximum from 3.6 to 36 mg C m^{-3} (see Section 3.2.2: *Carbon-to-Chlorophyll-a Ratio*), and because the observed photosynthetic rate is generally high (e.g. 60 mg C (mg Chl-a)$^{-1}$ d^{-1} for Station *P* in summer (Welschmeyer *et al.* 1993)), the necessary increase in phytoplankton carbon concentration from the carbon-to-chlorophyll-a ratio is negligible with respect to total primary production. Hence, I assume that all primary production is immediately assimilated by herbivores.

Thus, phytoplankton standing stock is completely controlled by herbivorous zooplankton in that any increase in phytoplankton carbon concentration above the grazing threshold χP_{Chl} is immediately grazed by microzooplankton. Microzooplankton growth rates of up to more than 5 doublings d^{-1} (Miller *et al.* 1991b) make control of phytoplankton, with growth rates of 1 doubling d^{-1} (Welschmeyer *et al.* 1993), plausible even for low microzooplankton densities.

The assumption of a χP_{Chl} grazing threshold for herbivores is more difficult to justify. The grazing threshold could arise from patterns and processes at the microscale: For example, microzooplankton detection of phytoplankton could be temperature dependent in that higher phytoplankton carbon concentrations, i.e. χP_{Chl}, in summer associated with higher molecular diffusivity due to increased temperature smear gradients of organic compounds and thus make it more difficult to locate an individual phytoplankton cell. Or, phases of high and low feeding activity by herbivorous microzooplankton in response to microscale predation by mesozooplankton, could - via cascading effects of predation pressure - provide temporal refuges

for phytoplankton (C. Walters 1998 pers. comm.; see also Walters *et al.* 1997; Walters & Juanes 1993). However, these arguments are mere speculations because observations on spatial and temporal microscales in the ocean environment are logistically extremely difficult or simply impossible (in the sense of Heisenberg's uncertainty principle), and lab experiments may not mimic natural conditions (J. Mitchell 1997 pers. comm., R. Luchsinger 1998 pers. comm.). Nevertheless, the firm empirical evidence for a year-round constant chlorophyll-a concentration in the Northeast Pacific (e.g. Parsons & Lalli 1988; Wong *et al.* 1995) implies a phenomenological grazing threshold of χP_{Chl}, whether its a spatio-temporal predation effect, or arises from system dynamical or other biological causes.

From a heuristic point of view, it is important to note that in environmentally-driven, large-scale spatially-explicit, non-equilibrium simulations, parameter and state variable combinations may occur that will eradicate the primary energy source, and which may not be obvious at all nor easily detectable (for the unpredictable dynamics of much simpler systems see May 1976b). The use of a donor-controlled biomass flow at the transfer from phytoplankton to microzooplankton will prevent the primary energy source from becoming locally extinct and thus represents a methodological save-fail design (Holling 1976).

Equation 3.8

In the first term on the right hand side of Eq. 3.8 I assume that throughout the year all primary production is immediately assimilated by herbivores. I hereby follow summer observations by Booth *et al.* (1993), who concluded that the grazing capacity of heterotrophic flagellates averaged 100% of the total primary production. Because microzooplankton has higher growth rates than their food source (Miller *et al.* 1991b) the effects of microzooplankton biomass on food

consumption can be neglected, i.e. donor-controlled prey consumption. Thus when P and H are in equilbrium Eq. 3.8 follows from the simple fast variable analysis:

$$\frac{dP}{dt} = b_P P_0 - a_{PH}(P - P_0)H \qquad \text{(Eq. 3.11a)}$$

$$\frac{dH}{dt} = a_{PH}(P - P_0)H - m_H H \qquad \text{(Eq. 3.11b)}$$

where P and H are phytoplankton and zooplankton standing stocks, respectively, and P_0 represents the phytoplankton threshold that cannot be grazed by herbivorous microzooplankton (parameters see Table 3.2). At equilibrium:

$$P_e = \frac{m_H}{a_{PH}} + P_0 \qquad \text{(Eq. 3.11c)}$$

$$H_e = \frac{b_P P_0}{m_H} \qquad \text{(Eq. 3.11d)}$$

Returned into rate equation 3.11b:

$$\frac{dH}{dt} = a_{PH}(\frac{m_H}{a_{PH}} + P_0 - P_0)\frac{b_P P_0}{m_H} - m_H H \qquad \text{(Eq. 3.11e)}$$

$$\frac{dH}{dt} = b_P P_0 - m_H H \qquad \text{q.e.d. (Eq. 3.11f)}$$

The second term on the right side of Eq. 3.8 accounts for respiration and non-predatory losses where m_H is a temperature dependent variable (see Section 3.4.). The third term stands for losses due to predation by mesozooplankton with a Type III functional response for the functional relationship between prey consumption per predator per time, i.e. the specific predation rate, and prey density (Fig. 3.10).

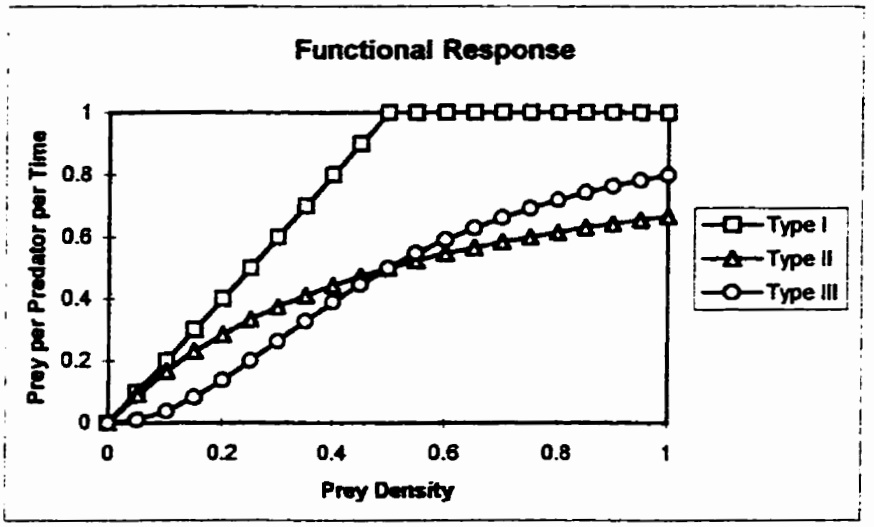


Fig. 3.10: Possible functional responses of a predator to prey density (see text). Type I: Prey consumption per predator per time rises linearly up to a maximum, where further increase in prey density has no effect on the specific predation rate. Type II: Functional response follows the equation:

$$f(P) = \frac{aP}{K + P}$$

with *f(P)* prey consumption per predator per time, i.e. specific predation rate, a maximum specific predation rate, P prey density, and K the half-saturation constant, i.e. the prey density at which the specific predation rate equals $a/2$. Type III: Functional response follows the equation:

$$f(P) = \frac{aP^2}{K^2 + P^2}$$

with variables as for Type II. Values used to generate particular graphs: $a = 1$, $K = 0.5$.

Originally, the Type III functional response was derived from behavioral responses of the predator to variation in prey density (Holling 1965), i.e. an increase in the rate of effective search (C. Walters 1994 pers. comm.) or a decrease in handling time (Begon *et al.* 1990) as a consequence of increased availability of prey organisms. Phenomenologically a Type III functional response provides a partial refuge for prey organisms, i.e. a low specific predation rate at low prey density. Further, partial refuges also occur whenever prey density is patchily distributed in space (Begon *et al.* 1990) and plankton is usually patchily distributed at scales greater than 1 m (e.g. Levin 1992; Steele 1980). As a result the mathematical form of a Type III functional response is sufficient to account for the patchy distribution of plankton (Steele 1985).

On the other hand, the Type II functional response was derived from time-budget considerations (Holling 1959) and does not show a low specific predation rate at low prey density (see Fig. 3.10). In general, a Type II functional response has a destabilizing while a Type III functional response has a stabilizing effect on population dynamics. However, these effects "depend on the extent to which consumption rate accelerates or decelerates over the range of densities normally experienced by the prey population." (Begon *et al.* 1990)

Equation 3.9

The first term on the right hand side of Eq. 3.9 stands for the assumed complete assimilation of microzooplankton H, i.e. no energetic losses due to egestion. Again the second term represents respiration and non-predatory losses, where m_{CI} is a function of temperature and size. The size dependence for the specific respiration rate m_{CI} is different for Models 1 and 2 (see Section 3.4.). The third term in equation 3.9 denotes losses due to predation by macrozooplankton. For Model

1 (Fig. 3.1) macrozooplankton density C_2 is zero by definition which makes mesozooplankton loss due to predation zero.

Equation 3.10

The first term on the right hand side of Eq. 3.10 stands for the assumed complete assimilation of ingested mesozooplankton, where the specific predation rate again follows a Type III functional response. The second term denotes respiration and non-predatory losses with m_{C2} as a function of temperature and size. For Model 1 (Fig. 3.1) macrozooplankton density C_2 is zero by definition which makes Eq. 3.10 equal to zero.

Note that for the system of differential equations in Table 3.1 upper model closure is density independent. Density-dependence states that the specific birth, growth, death, and migration rates are related to population density, which in many cases are not (Krebs 1995). Although the frequently applied density dependent closure is a convenient mathematical form to regulate modeled population densities and thus prevent numerical explosion of state variables, mechanisms limiting zooplankton populations (e.g. food shortage, predation, allelopathy) are not well studied (see also arguments in *Equation 3.7* above). The assumption for the system of differential equations in Table 3.1 is the following: In the natural world there exist predators that feed on the highest modeled trophic level. These predators themselves can become prey for even higher predators (Rice 1995) and thus avoid exposure to predation risk (e.g. Lima & Dill 1990; Walters & Juanes 1993, see also Section 1.4. and Carpenter *et al.* 1985). Consequently they are unable to regulate population density of the highest modeled trophic level (see Models 1 and 2 in Fig. 3.1) which is then limited by density-independent factors.

3.3.1. Point Equilibria and Stability Analysis

Point equilibria (subscript *e*) for the system of differential equations in Table 3.1 can be found by setting:

$$\frac{dH}{dt} = \frac{dC_1}{dt} = \frac{dC_2}{dt} = 0 \qquad \text{(Eq. 3.12a)}$$

Case 1: H>0, $C_1 = C_2 = 0$

$$H_e = \frac{b_P P_0}{m_H} \qquad \text{(Eq. 3.12b)}$$

***Case 2: H>0, C_1>0, $C_2 = 0$* (Model 1)**

$$H_e = \sqrt{\frac{m_{C_1} K_{HC_1}^2}{a_{HC_1} - m_{C_1}}} \qquad \text{(Eq. 3.12c)}$$

$$C_{1,e} = \frac{1}{m_{C_1}}\left(b_P P_0 - m_H H_e\right) \qquad \text{(Eq. 3.12d)}$$

***Case 3: H>0, C_1>0, C_2>0* (Model 2)**

$$C_{1,e} = \sqrt{\frac{m_{C_2} K_{C_1C_2}^2}{a_{C_1C_2} - m_{C_2}}} \qquad \text{(Eq. 3.12e)}$$

H_e is the solution of the cubic equation:

$$H^3 - \frac{1}{m_H}\left(b_P P_0 - a_{HC_1} C_{1,e}\right)H^2 + K_{HC_1}^2 H - \frac{b_P P_0 K_{HC_1}^2}{m_H} = 0 \qquad \text{(Eq. 3.12f)}$$

$$C_{2,e} = \frac{C_{1,e}}{m_{C2}}\left(\frac{a_{HC_1} H_e^2}{K_{HC_1}^2 + H_e^2} - m_{C_1}\right) \qquad \text{(Eq. 3.12g)}$$

For simple systems of simultaneous homogeneous 1^{st}-order nonlinear ordinary differential equations (e.g. Lotka 1925; Volterra 1926) local stability analysis of equilibrium values can usually be done analytically (Murray 1993; Renshaw 1991; Yodzis 1989). The mathematical methods involve finding the equilibrium values of the system of nonlinear differential equations, linearizing the system, and solving the linearized system by calculating the eigenvalues of the community matrix at equilibrium values (Brown & Rothery 1993). The sign of the largest eigenvalue then determines the dynamics of a system in equilibrium that is locally perturbed (Pimm 1982), i.e. if one eigenvalue is positive the equilibrium is unstable.

Further, local stability does not imply global stability, where a globally stable system is defined as one that returns to equilibrium values from any initial conditions not just close to equilibrium values (Pimm 1982), nor does local instability imply global instability (May 1972a), e.g. stable limit cycles may occur. Analytical techniques to determine whether a system of differential equations is globally stable are scarce and involve finding the Lyapunov function, which is so difficult to determine and interpret for multispecies models that this approach is only of limited use (Pimm 1982; Renshaw 1991). Thus, while there is a whole array of graphical (Rosenzweig & MacArthur 1963) and analytical mathematical procedures available for the analysis of simple models involving one predator and one prey (e.g. Brown & Rothery 1993; Caswell 1989; Murray 1993; Pimm 1982; Renshaw 1991; Yodzis 1989) mathematically exact methods for complex models remain scarce and one has to rely on simulations instead (Levin *et al.* 1997). Fig. 3.11 and 3.12 show the numerical stability analyses for population Models 1 and 2 (Fig. 3.1, Table 3.1).

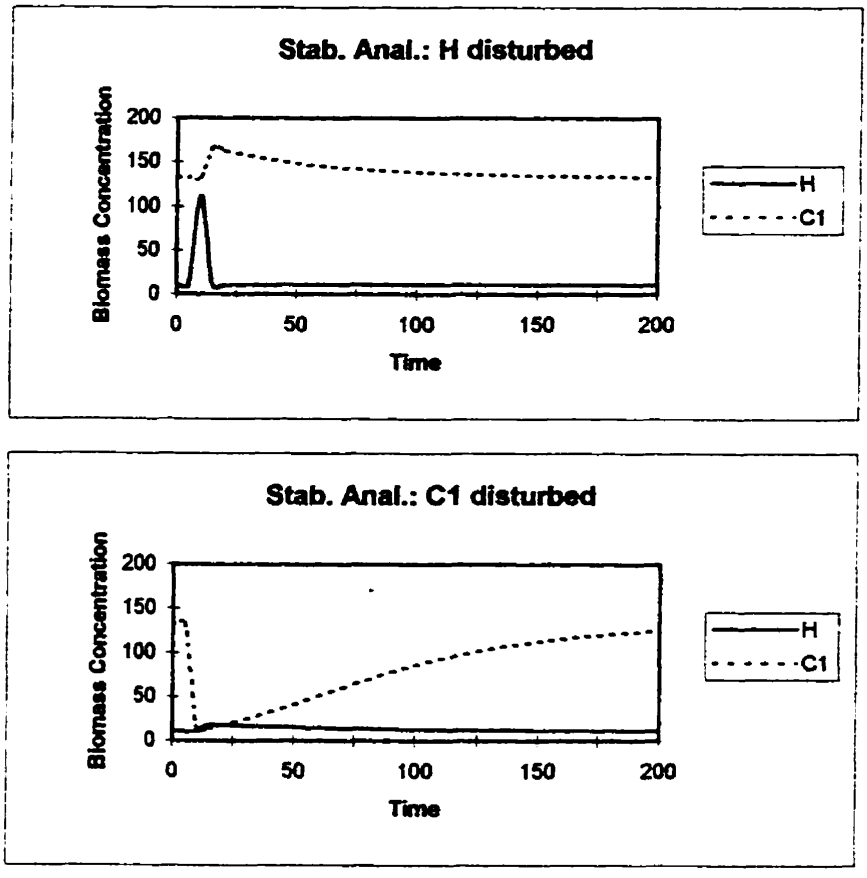


Fig. 3.11: Stability analysis of the 3-Trophic-Levels Model. Simulation runs with equilibrium state variables up to Time = 10 when perturbation of the respective state variable occurs. Magnitude of perturbation: Upper panel: 10-fold increase in microzooplankton (H). Lower panel: 90% decrease of mesozooplankton. Simulations run with standard run parameter values (Table 3.3), and biotic and abiotic environmental conditions at Station P in June (see Fig. 3.2 and 3.14), with $b_P P = 10$ mg C m^{-3} d^{-1} and $m_H = 0.5$. Note different scales on the ordinates.

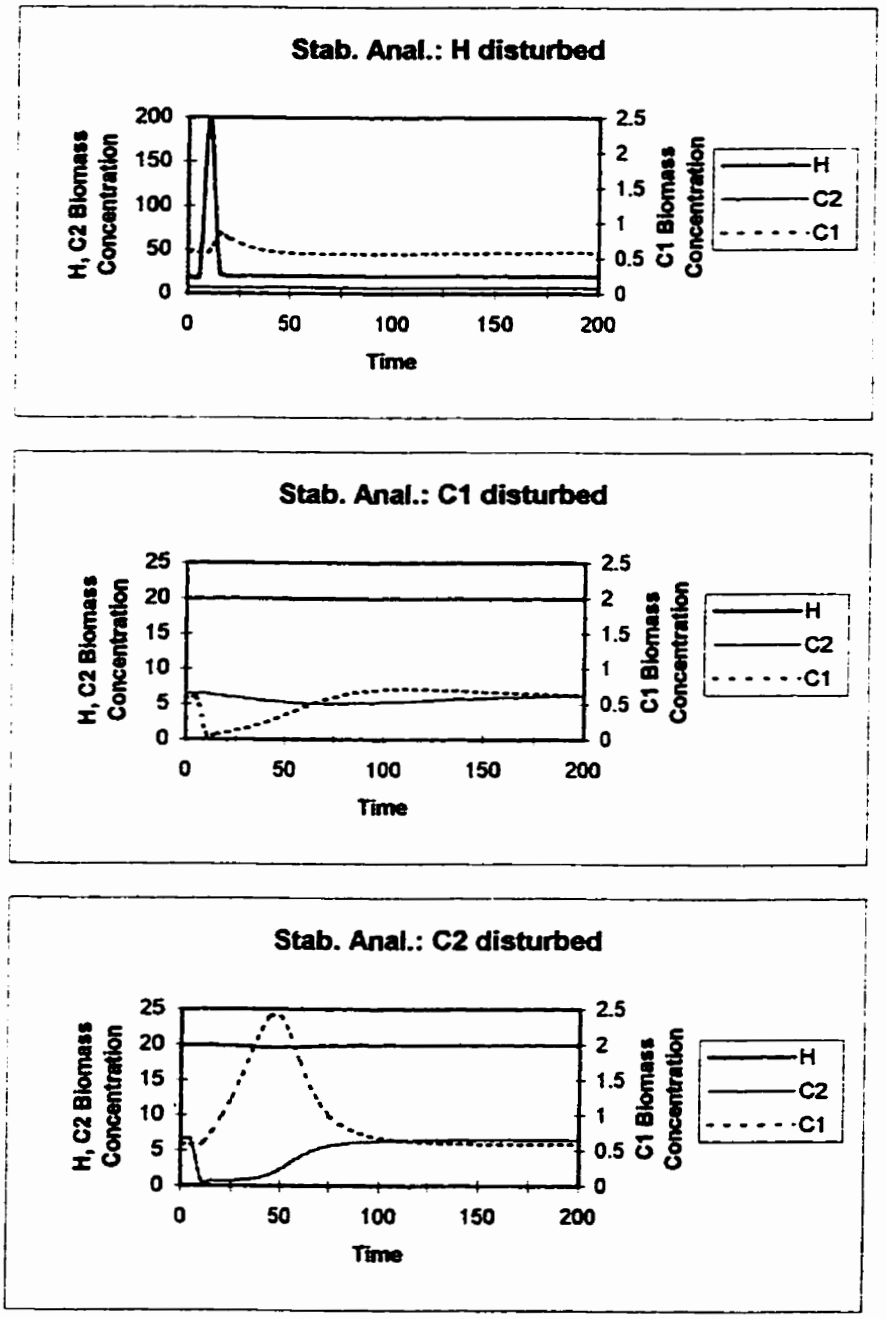


Fig. 3.12: Stability analysis of the 4-Trophic-Levels Model. Simulation runs with equilibrium state variables up to Time = 10 when perturbation of the respective state variable occurs. Magnitude of perturbation: Upper panel: 10-fold increase in microzooplankton (H). Middle and lower panel: 90% decrease in mesozooplankton or macrozooplankton respectively. Simulations run with standard run parameter values (Table 3.3), and biotic and abiotic environmental conditions at Station P in June (see Fig. 3.2 and 3.14), with $b_P P = 10$ mg C m^{-3} d^{-1} and $m_H = 0.5$. Note different scales on the ordinates.

For standard run parameter values (Table 3.3) the *Case 1* equilibrium point is globally stable because the microzooplankton rate equation (Eq. 3.8) has a negative slope for all positive microzooplankton concentrations H. Using mathematical software (*Maple V*), analytical results show that for positive biomass concentrations, *Case 2* has one solution with two negative real eigenvalues and is thus stable.

For *Case 3* analytical results confirm the linear stability of the equilibrium points: H, C_1, and C_2 have one real and two complex roots (from the solution of the cubic equation Eq. 3.12f), and three negative real eigenvalues. In fact, H_e will have one real root and two complex roots for any combination of parameters as long as they satisfy the condition (B. Bergersen 1998 pers. comm.):

$$d = r^2 + q^3 > 0 \qquad \text{(Eq. 3.12h)}$$

where,

$$r = \frac{2a^3 - 9ab + 27c}{54} \qquad \text{(Eq. 3.12i)}$$

$$q = \frac{a^2 - 3b}{9} \qquad \text{(Eq. 3.12j)}$$

and a, b, and c are the coefficients in the cubic equation Eq. 3.12f.

I should mention, that the stability concept emerged from an equilibrium view of systems (Shubik 1996) and that while some biological components of an ecosystem might have evolved regulation mechanisms that are stabilizing to populations and communities, other parts could have adopted different strategies which are at the mercy of environmental forcings and in fact require non-equilibrium conditions to subsist (see Steele 1974; Steele 1980; Steele 1991; Steele & Henderson 1994).

As can be calculated from standard run parameter values (Table 3.3), and from 1981 to 1984 environmental forcings at Station *P* (50°N 145°W) and at 50°N 130°W (see Section 3.2. and 3.4), and presumably at many other locations in the Northeast Pacific, equilibrium values for C_1 (Eq. 3.12d) in the 3-Trophic Levels Model (Fig. 3.1, Table 3.1) can assume negative sign between October and April. Consequently, equilibrium model simulation through environmentally-driven parameters, as demonstrated by Walters *et al.* (1987) for a lake ecosystem, cannot by applied for the Northeast Pacific. Negative equilibrium values for C_1 and C_2 do not occur for the 4-Trophic-Levels Model. However, for advective systems an equilibrium approach will be justified only if the local equilibration processes are more rapid than the changes caused by advection. This is not the case in simulations that include currents (Chapter 4).

3.4. Mean Field Simulations

The key assumptions of the mean field approach is that one point in space, i.e. the mean field, is representative of patterns and processes over a much larger area. Of course, this is not to say that all locations in the Northeast Pacific experience the same timing of events; rather in order to tune the population models I ignore the spatial variability in abiotic environmental forcings in the Northeast Pacific. Because of a longterm and still ongoing sampling program at Station *P* (50°N 145°W) I have chosen this location as the reference point for my mean field simulations. Additionally, for the purpose of spatial comparison I ran mean field simulations for the location at 50°N 130°W, i.e. a position at the same latitude as Station *P* but approximately 1000 km closer to the Canadian coast.

The biological variables in the mean field simulations are driven by abiotic environmental data (see Section 3.2.) for both stations for the period 1981 to 1984, with a timestep of one day. Input data are: daily sea surface insolation, mixed layer depth, mixed layer temperature, the extinction coefficient, daylength, and the carbon-to-chlorophyll-a ratio. In general, observed as well as derived input data have a temporal resolution of one month (values assigned to mid-month) with linear interpolation between month for the one day timestep. Units of biomass concentrations are [mg C m^{-3}].

Physical structure

The model ecosystem for the Northeast Pacific consists of a mixed upper layer and a deep layer. Biological processes are assumed to occur only in the mixed upper layer whose depth varies seasonally. The underlying deep water layer is assumed to be void of life. Horizontal and vertical advection and diffusion are ignored (see Subsection 3.2.2). Further, I assume that the

mixed layer is homogeneously mixed and that mixing takes place at very short time scales so that biological production at any depth is immediately homogenized.

The above assumptions evidently represent gross simplifications: In the natural system phytoplankton persists and reproduces below the thermocline (Frost 1987) and many fish and zooplankton species undertake diel and/or seasonal and/or ontogenetic migrations to depth (Mangel & Clark 1988); some spend their entire life in deep water (see Section 2.2). Also, the seasonal thermocline (the boundary between the mixed upper layer and the deep water layer) is not a step function but rather a smooth transition zone (Fig. 2.8). Dilution effects on phytoplankton and zooplankton concentrations due to deepening of mixed layer are assumed negligible because changes due to biological processes are much larger in magnitude. However, losses of total biomass in the water column due to a shallowing of the mixed layer have been accounted for in the simulations.

Phytoplankton

The biological process primarily affected by abiotic environmental forcings in the Northeast Pacific Ocean is primary production, i.e. phytoplankton growth rate ($b_P P_0$ in Eq. 3.8, [mg C d^{-1}]). The photosynthetic rate of phytoplankton (p_P, [mg C (mg Chl-a)$^{-1}$ d^{-1}] is a function of photosynthetically active radiation at depth z ($I_{PAR,z}$ [J m^{-2} d^{-1}]):

$$p_P = p_{P,\max} \tanh\left(\frac{\alpha I_{PAR,z}}{p_{P,\max}}\right) \qquad \text{(Eq. 3.13a)}$$

where $p_{P,max}$ is the maximum photosynthetic rate (the value of p_P at light saturation), and photosynthetic efficiency α ([mg C (mg Chl-a)$^{-1}$ d^{-1} (J m^{-2})$^{-1}$]) represents the initial slope of the photosynthesis vs. irradiance curve (Jassby & Platt 1976). Eq. 3.13a is the equation for a

hyperbolic tangent and was found to be the best fit to experimental photosynthesis vs. irradiance data of eight different equations tested by Jassby & Platt (1976), and thus was preferred in my simulations over other formulations (e.g. Michaelis-Menten equation (Platt *et al.* 1981), Smith function (Smith 1936)). Note that Eq. 3.13a does not account for photo-inhibition at high irradiance levels. However, because primary production was summed over depth at 1 m intervals starting at z = -1 m, and because no primary production below the thermocline was assumed, the effects of photo-inhibition on primary production are likely to be compensated for in the model. In general, equations describing photo-inhibition effects (e.g. Platt *et al.* 1981; Steele 1962) are only rarely used in ecosystem models (e.g. Kawamiya *et al.* 1995) simply because photo-inhibition requires the estimation of at least one more independent parameter (Platt *et al.* 1981).

The maximum photosynthetic rate ($p_{P,max}$ [mg C (mg Chl-a)$^{-1}$ d^{-1}]) is related to the maximum specific growth rate for phytoplankton ($b_{P,max}$, [mg C (mg C)$^{-1}$ d^{-1}] by the carbon-to-chlorophyll-a ratio (χ [mg C (mg Chl-a)$^{-1}$]):

$$p_{P,\max} = \chi b_{P,\max} \qquad \text{(Eq. 3.13b)}$$

Further, $b_{P,max}$ is a function of the daily doubling rate ($b_{P,doubl}$ [doublings d^{-1}] of phytoplankton (Eq. 3.13c), which itself is a function of temperature (T; Eq. 3.13d (Eppley 1972)):

$$b_{P,\max} = \left(2^{b_{P,doubl}} - 1\right)\frac{H_d}{24} \qquad \text{(Eq. 3.13c)}$$

$$b_{P,doubl} = 0.851 \cdot 10^{0.0275T} \qquad \text{(Eq. 3.13d)}$$

As Eq. 3.13d was calculated for laboratory cultures under 24-hour illumination (Eppley 1972), Eq. 3.13c takes into account photo-respiration and its last term corrects for daylength (H_d [h]). Equation 3.13d has a Q_{10} value of 1.88 (very close to the default value $Q_{10} = 2$ suggested by van't Hoff's temperature rule for enzyme reactions (Denffer *et al.* 1983)).

Because of different insolation at different depths and the assumed fast mixing, the phytoplankton concentration change due to primary production for the mixed layer is then:

$$b_P P_0 = -\frac{1}{z_{ML}} \int_{z_{ML}}^{0} p_P P_{Chl}\, dz \qquad \text{(Eq. 3.13e)}$$

where phytoplankton concentration in units of carbon (P_0 [mg C m^{-3}]) relates to chlorophyll-a concentration (P_{Chl} [mg Chl-a m^{-3}]) by:

$$P_0 = \chi\, P_{Chl} \qquad \text{(Eq. 3.13f)}$$

The full equation for the growth rate of primary producers per volume ($b_P P$ in Eq. 3.8) in the mixed upper layer is:

$$b_P P_0 = -\frac{1}{z_{ML}} \int_{z_{ML}}^{0} \left(\left(2^{0.851 \cdot 10^{0.0275T}} - 1\right) \frac{H_d}{24} \tanh\left(\frac{\alpha\, I_{PAR,z}}{\chi \left(2^{0.851 \cdot 10^{0.0275T}} - 1\right) \frac{H_d}{24}} \right) P_0 \right) dz \qquad \text{(Eq. 3.13g)}$$

Zooplankton

For the zooplankton rate equations (Eqs. 3.8-3.10) parameters under environmental control are the specific respiration or non-predatory death rates m_X (X stands for the population). Herbivore respiration rate m_H [d^{-1}] was defined as a function of temperature (T):

$$m_H = m_{H.0} 2^{0.1T} \qquad \text{(Eq. 3.14a)}$$

where $m_{H.0}$ represents the specific respiration or non-predatory death rate at 0°C. To produce microzooplankton growth efficiencies (defined as production per unit ingested food or energy) similar to those found in nature (Parsons & Lalli 1988) $m_{H.0}$ was set at 0.25 for the standard run, i.e. a growth efficiency of microzooplankton of 50% at 10°C. The exponent in Eq. 3.14a reveals the assumption that $Q_{10} = 2$.

The respiration rate for mesozooplankton (m_{C1}) and macrozooplankton (m_{C2}) was defined as a function of body-mass in relation to herbivore respiration rate m_H. Using the mean length of the zooplankton size classes (Parsons *et al.* 1984; microzooplankton: 110 µm, mesozooplankton: 10.1 mm, macrozooplankton: 110 mm) and assuming half-sphere shaped organisms, respiration per unit body mass was calculated from Eckert & Randall (1983):

$$m_X = aX^{-0.25} \qquad \text{(Eq. 3.14b)}$$

where a is a species-specific conversion factor, here assumed to be the same for all zooplankton, and X is body mass. Eq. 3.14b yields the ratios: $\frac{m_{C_1}}{m_H} = \frac{1}{30}$ and $\frac{m_{C_2}}{m_{C_1}} = \frac{1}{6}$. However, because in dynamic food chain models the natural trophic levels beyond the scope of the model are factually assumed collapsed into the highest model trophic level, to account for implicit additional losses I doubled the mass-specific losses of the highest model trophic level in each model. Thus for the model with three trophic levels $\frac{m_{C_1}}{m_H} = \frac{1}{15}$, and with four trophic levels $\frac{m_{C_2}}{m_{C_1}} = \frac{1}{3}$.

It may be argued that zooplankton biology and life history have been simplified too much in Models 1 and 2 (Eqs. 3.8-3.10). For example, 80-95% of the total biomass of mesozooplankton consists of species that perform ontogenetic vertical migrations and have rather complicated life histories (Mackas *et al.* 1993; Parsons & Lalli 1988; Ware & McFarlane 1989; see also Section 2.2.), yet, in the simulations mesozooplankton is represented as a homogeneous group inhabiting the mixed upper layer. These simplifications were necessary because there are essentially no answers (R. Goldblatt 1998 pers. comm.) to the following two questions:

(1) What determines the time of ascent and descent in the ontogenetic migration of *Neocalanus* species?

It has been shown that the peak biomass in *Neocalanus plumchrus* in the Northeast Pacific in the 1990s is about 60 days earlier than in the 1950s (D. Mackas 1997 pers. comm.). Further, it is assumed that the environment at depth hardly changes over decades, and thus, that the biomass pattern is rather a consequence of the time of descent than ascent. For *Neocalanus* spp. the time of descent is given by the developmental stage of the organism (stage 4 or 5 copepodites, depending on the species, migrate to depth (Miller *et al.* 1984)) which itself is determined by the development rate, a complex function of processes occurring in surface waters (R. Goldblatt 1998 pers. comm.). Whether and how food supply (R. Goldblatt 1998 pers. comm.), total temperature exposure (D. Mackas 1997 pers. comm.), stage-specific mortality rates (D. Mackas 1997 pers. comm.), or other factors (e.g. predation pressure) determine development rate is unknown.

(2) What determines the survival of *Neocalanus* species at depth?

Even less is known to answer this question. Intuition (under the density dependent paradigm) suggests that it is likely that the number of nauplii that ascend in winter and spring is correlated with the number of stage 5 copepodites (C_5) that descended the previous year, but that the number of larvae that survive to C_5 varies significantly from year to year. "Or maybe not. No-one knows." (R. Goldblatt 1998 pers. comm.)

Lack of information also applies to the whole group of macrozooplankton (see Section 2.2.).

Although vertical migration can easily be implemented in simulations by brute-force, especially in the absence of data, this approach is likely to make my simulations shimmy almost any way I want, a rather poor modeling practice. Further, because I try explain the variability in sockeye salmon survival by the variability in mesozooplankton availability to the juveniles,

which implies a critical period during the winter month (see Chapter 4) vertically migrating mesozooplankton species are not available for juvenile sockeye salmon in the Northeast Pacific (Fig. 2.6) and may thus not even be relevant for the objective of this thesis (see Chapter 1).

3.4.1. Simulation Results: 3-Trophic-Levels Model

The 'standard run' simulation (Table 3.3) shows a seasonally varying phytoplankton standing stock (in units of carbon) corresponding to the seasonally varying carbon-to-chlorophyll-a ratio (Fig. 3.13, Fig. 3.9). Phytoplankton concentration peaks in June to July, and it is assumed that throughout the year 100% of the daily primary production is consumed by the herbivorous microzooplankton while the reproducing phytoplankton standing stock is not grazed (donor-controlled flow; Section 3.3.). For both locations the simulated summer phytoplankton standing stock is close to the observed phytoplankton carbon concentrations during the SUPER-cruises (SUbarctic Pacific Ecosystem Research; May and August 1984, 1988, June and September 1987 (Miller *et al.* 1991b)) with a mean standing stock of 20 mg C m^{-3} and a maximum of 74 (Booth *et al.* 1993).

The annual herbivore peak is a result of primary productivity and grazing pressure from mesozooplankton and trails behind the phytoplankton peak at Station *P* but precedes it at 50°N 130°W. Summer concentrations microzooplankton for both locations are close to observed mean of 15 mg C m^{-3} at Station *P* (Booth *et al.* 1993). Microzooplankton concentrations >30 mg C m^{-3} have only been rarely observed (Booth *et al.* 1993) and the high microzooplankton concentrations in 1981 (Fig. 3.13) are an artifact of the initial conditions of the simulations (see Subsection 3.5.1.).

Table 3.3: 'Standard Run' initial conditions and parameter values for the mean field simulations of the 3- and 4-Trophic Levels Models.

Initial Values [mg C m^{-3}]	**3-Trophic Levels Model**	**4-Trophic Levels Model**
P_0*	$f(I_0)$	$f(I_0)$
H	1	1
C_1	0.5	0.5
C_2	-	0.1
Parameter [Units]	**3-Trophic Levels Model**	**4-Trophic Levels Model**
α [mg C (mg Chl-a)$^{-1}$ d^{-1}]	96	96
$m_{H.0}$ [d^{-1}]	0.25	0.25
m_{C1}/m_H	1/15	1/30
m_{C2}/m_{C1}	-	1/3
a_{HC1} [mg C (mg C)$^{-1}$ d^{-1}]	0.2	0.2
K_{HC1} [mg C m^{-3}]	25	25
a_{C1C2} [mg C (mg C)$^{-1}$ d^{-1}]	-	0.4
K_{C1C2} [mg C m^{-3}]	-	5

* Phytoplankton standing stock is calculated as 0.4 mg Chl-a m^{-3} times the carbon-to-chlorophyll-a ratio, a function of sea surface insolation in the previous month (see Subsection 3.2.2.).

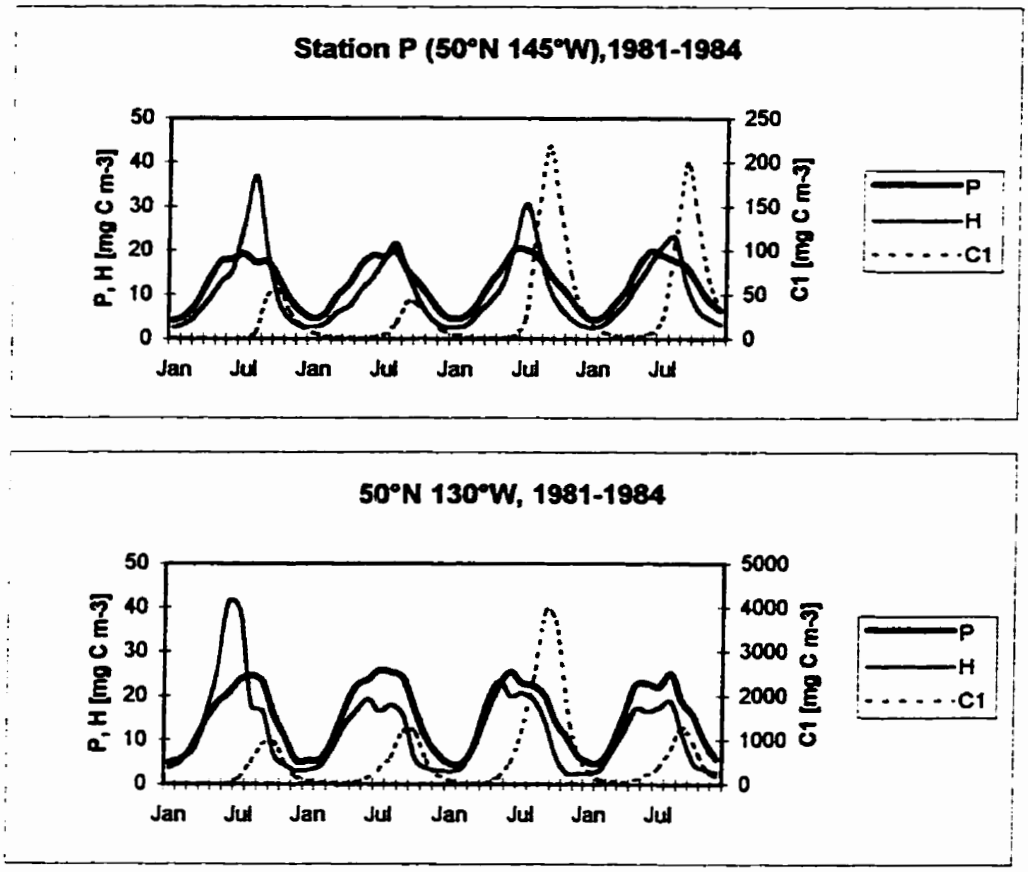


Fig. 3.13: Simulated carbon concentrations for phytoplankton (P), microzooplankton (H), and mesozooplankton (C_1) at Station *P* (50°N 145°W) and at 50°N 130°W for 1981 to 1984. Note different scales on the ordinates.

At Station *P* as well as at 50°N 130°W simulated mesozooplankton reaches its peak by late September, considerably later than the observed mean peak of 3 mg C m^{-3} (maximum 20 mg C m^{-3}) in May-June (Mackas & Frost 1993). Maximum simulated standing stocks exceed maximum observed mesozooplankton concentrations by about one order of magnitude at Station *P* and even more for the near-coast location at 50°N 130°W. This discrepancy can be caused by the following:

(1) Because in trophodynamic models the natural trophic levels beyond the scope of the model are aggregated into the highest model trophic level, and because total energy must be conserved, the biomass density of the highest model trophic level is actually expected to exceed observed values. Compare simulated mesozooplankton densities of the 3-Trophic-Levels Model (Fig. 3.13) and of the 4-Trophic-Levels Model (Fig. 3.17).

(2) The lack of information on mesozooplankton species that perform ontogenetic vertical migrations has forced me to exclude this group completely (see Section 3.4., *Zooplankton*). It is clear that these species consume large quantities of microzooplankton during their stay in or near the mixed upper layer during the first half of the year, zooplankton biomass that then migrates to depth. In fact, simulation results (Fig. 3.13) suggest that the first six month should be the time when interspecific resource-use competition is at its minimum, and are thus consistent with the life-history strategy of ontogenetically migrating mesozooplankton which could have adapted to exploit the microzooplankton surplus, which then is not available for the mixed upper layer community.

(3) Observed densities of larger zooplankton are usually reported in grams wet weight m^{-3}. Because the units used in simulations are mg C m^{-3} a conversion of 1 g wet weight = 0.04 g C (see Subsection 2.2.1.) was used for comparison of observations and simulation results. 0.04 is a

rather conservative estimate of the wet weight to carbon conversion factor, and for the North Pacific a mean of 0.10 and a maximum of 0.24 have been reported for crustacean plankton (see Parsons *et al.* (1984) their Table 11). These higher estimates of the conversion factor reduce the discrepancy between simulation results and observations by a factor of 2.5 and 6, respectively.

Simulated daily primary productivity (Figs. 3.14) is consistent with observations (compare Figs. 3.15 and Fig. 2.3). Note that simulated winter primary productivity for Station *P* is lower than that reported by Wong *et al.* (1995). However, their winter estimates are based on only two observations on two consecutive days in late February 1989 (almost two month after the winter solstice) and are thus likely to be biased towards higher values. Primary productivity for the near-coast location is higher because of higher sea summer temperature there (Fig. 3.2) and thus shallower mixed layer depth (Fig. 3.6). 1981 to 1984 simulated mean annual primary production was 114 g C m^{-2} at Station *P* (all four years lie within ± 5% of the mean), a little lower than the observed 1984 to 1991 mean of 140 g C m^{-2} (Wong *et al.* 1995). Nevertheless, because the fall and winter season has only been sampled 5 times during the seven year period, the reliability of Wong *et al.*'s (1995) estimate is uncertain. 1981 to 1984 simulated mean annual primary production at 50°N 130°W was 151 g C m^{-2}. Here too, all four years lie within ± 5% of the mean.

Simulated microzooplankton net production, i.e. ingestion minus respiration and non-predatory loss, for both locations is positive throughout the year (Fig. 3.14). This means that the decline in microzooplankton biomass in fall is caused by mesozooplankton predation rather than excessive microzooplankton respiration due to high sea surface temperatures. Simulated mesozooplankton net production for both locations is positive in spring and summer (Fig. 3.14)

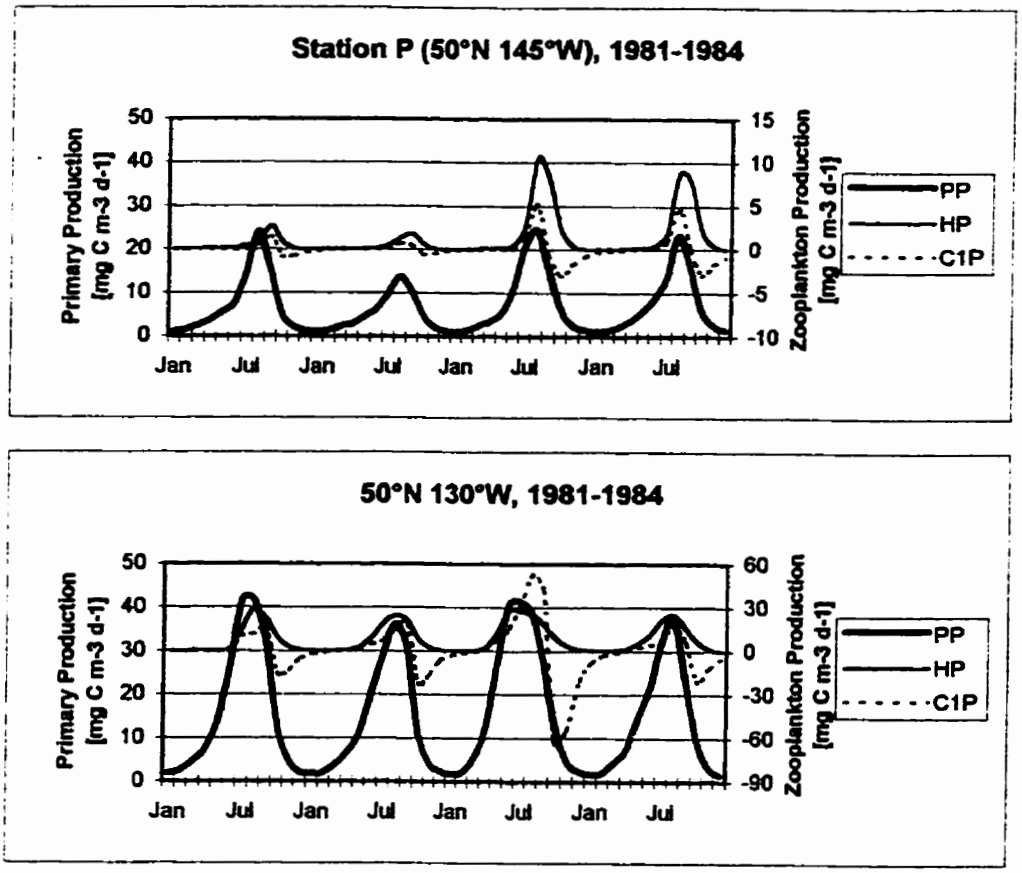


Fig. 3.14: Simulated production per cubic meter and day for phytoplankton (P), microzooplankton (H), and mesozooplankton (C_1) at Station *P* (50°N 145°W) and at 50°N 130°W for 1981 to 1984. Note different scales on the ordinates.

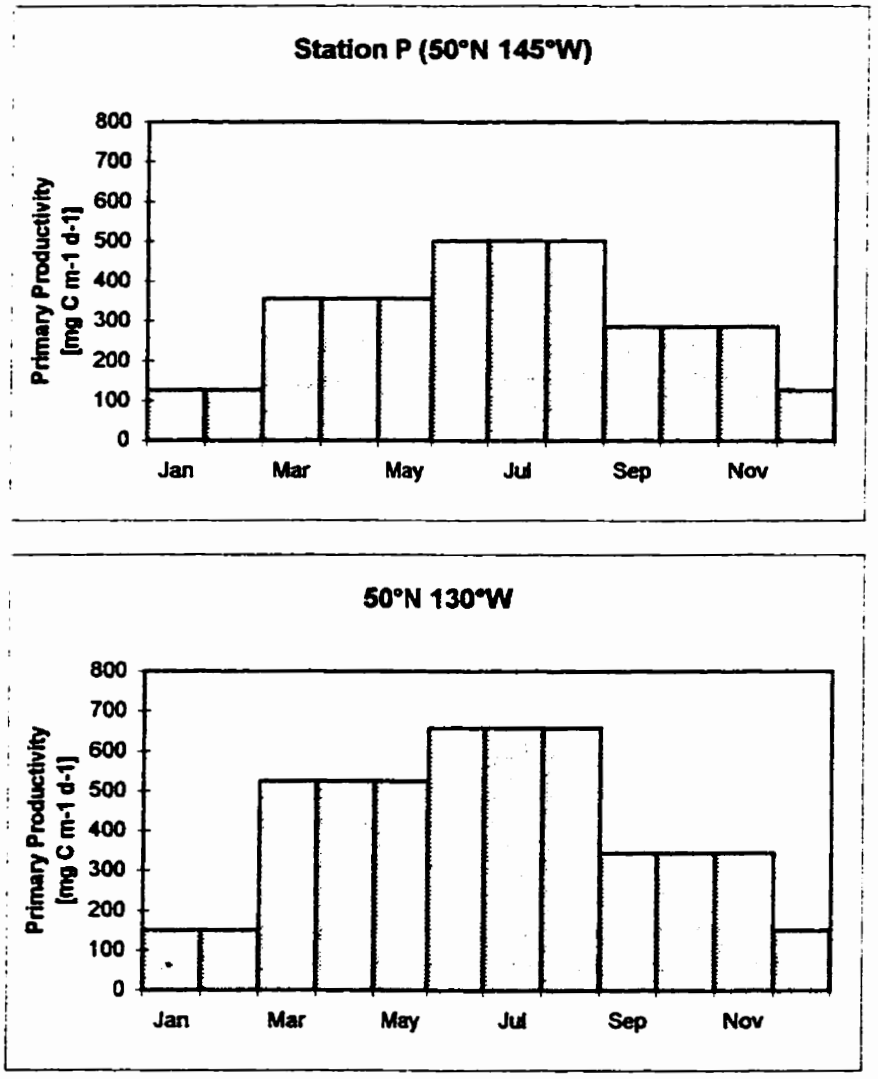


Fig. 3.15: Seasonal primary productivity at Station *P* (50°N 145°W) and at 50°N 130°W from 1981-84 simulation results. For the purposes of comparison the same format was used as in Fig. 2.3.

and becomes negative in the fall as a consequence of the lower primary production that is transferred through microzooplankton to mesozooplankton, and through the effects of high sea surface temperatures (Fig. 3.2) on the mass-specific respiration or non-predatory death rates of both zooplankton size classes (Eq. 3.14).

1983 and 1984 microzooplankton transfer efficiencies calculated from mean field simulations for Station *P* are 27 and 26% respectively, close to the 22% estimated for the open Northeast Pacific (Parsons & Lalli 1988). I define transfer efficiency of a trophic level here as the biomass production at that trophic level divided by the biomass production of its prey organisms (Baumann 1995; see also Chapter 1). However, 1981 and 1982 microzooplankton transfer efficiencies of 7 and 8%, respectively, appear too low for Station *P*. For the near coast location at 50°N 130°W, the 1981 to 1984 mean microzooplankton transfer efficiency of 55% appears too high. As expected for a mature ecosystem, net community production, i.e. net primary production minus total heterotrophic respiration (Odum 1971), is close to zero for both locations.

In order for model mesozooplankton to have some resemblance to its real-world counterpart it is important that mesozooplankton mass-specific clearance or filtration rate F_{CI} be close to the observed range of 0.4 to 3.6 liters (mg C)$^{-1}$ d^{-1} (Frost 1987). F_{CI} can be calculated from the daily grazing rate G_{CI} [mg C m^{-3} d^{-1}] as follows (for symbols Table 3.2; see also rate equations in Table 3.1):

$$G_{C_1} = \frac{a_{HC_1} H^2}{K_{HC_1}^2 + H^2} C_1 \qquad \text{(Eq. 3.15a)}$$

$$F_{C_1} = \frac{G_{C_1}}{HC_1} 1000 \qquad \text{(Eq. 3.15b)}$$

F_{Cl} is independent of C_l and has a maximum $F_{C_1,max} = \frac{a_{HC_1}}{2K_{HC_1}} 1000$ at $H=K_{HCl}$. For the standard run parameter choice (Table 3.3) $F_{Cl,max}$ is 4 liters (mg C)$^{-1}$ d^{-1}. Fig. 3.16 shows the simulated mesozooplankton filtration rate at Station *P* and at 50°N 130°W for 1981-1984.

3.4.2. Simulation Results: 4-Trophic Levels Model

Simulated phytoplankton concentration and productivity for the 4-Trophic Levels Model standard run (Table 3.3) is the same as in the simulation of 3-Trophic Levels Model (Compare Fig. 3.17 and 3.13, Fig. 3.18 and 3.14; Fig. 3.15). This is a consequence of the assumption of a χP_{Chl} grazing threshold and the donor-controlled biomass transfer between phytoplankton and microzooplankton (Section 3.3.).

Summer concentrations of simulated microzooplankton are approximately twice as high for Station *P* and almost four times as high for the near-coast location, as the observed mean of 15 mg C m^{-3} at Station *P* (Booth *et al.* 1993). Compared to the 3-Trophic Levels Model (Subsection 3.4.1.) this higher standing stock is a consequence of the top-down control of macrozooplankton which releases microzooplankton from predation pressure by mesozooplankton (see Fig. 3.1). At Station *P* mesozooplankton reaches its annual peak in late summer, a little earlier than in the 3-Trophic Levels Model but still much later than the observed peak in May-June (Mackas & Frost 1993). At the near-coast location the timing of the mesozooplankton peak from the simulations coincides with that observed at Station *P*. Simulated maximum mesozooplankton concentrations for both locations are a little lower (except 1981, which is an initial conditions effect) than the

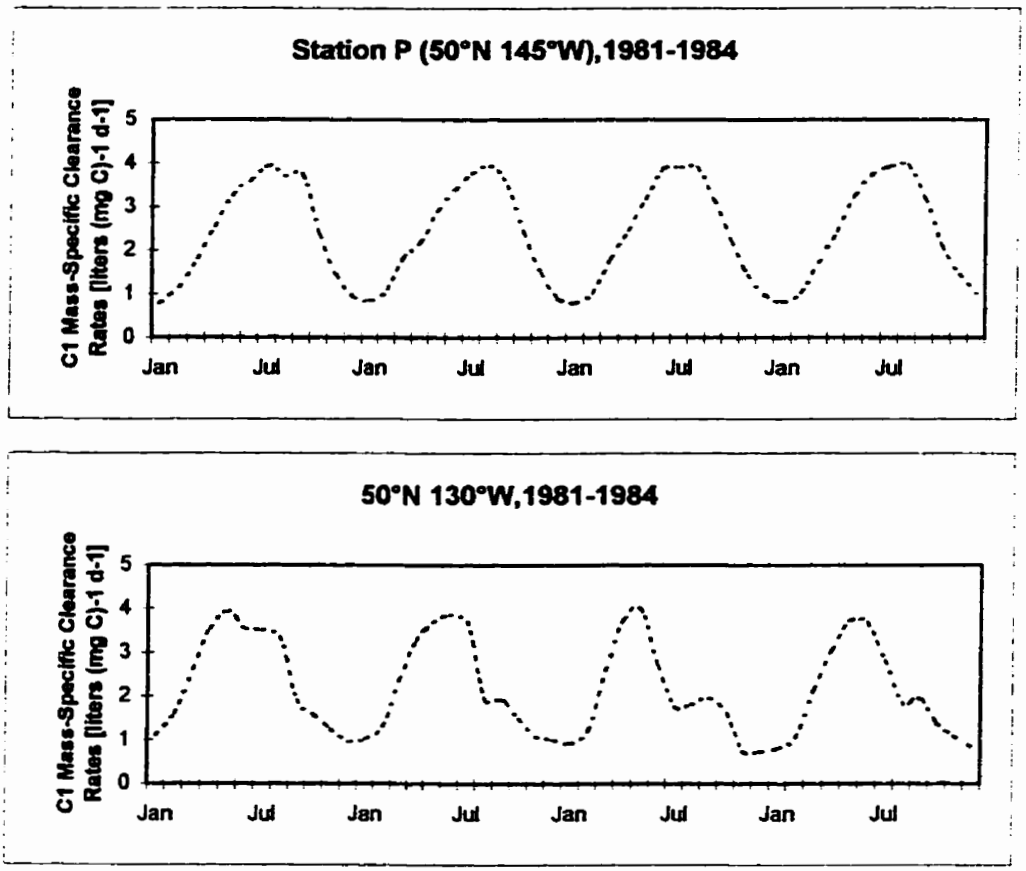


Fig. 3.16: Simulated mass-specific clearance or filtration rates [liters (mg C)$^{-1}$ d^{-1}] for mesozooplankton (C_1) at Station *P* (50°N 145°W) and at 50°N 130°W for 1981 to 1984.

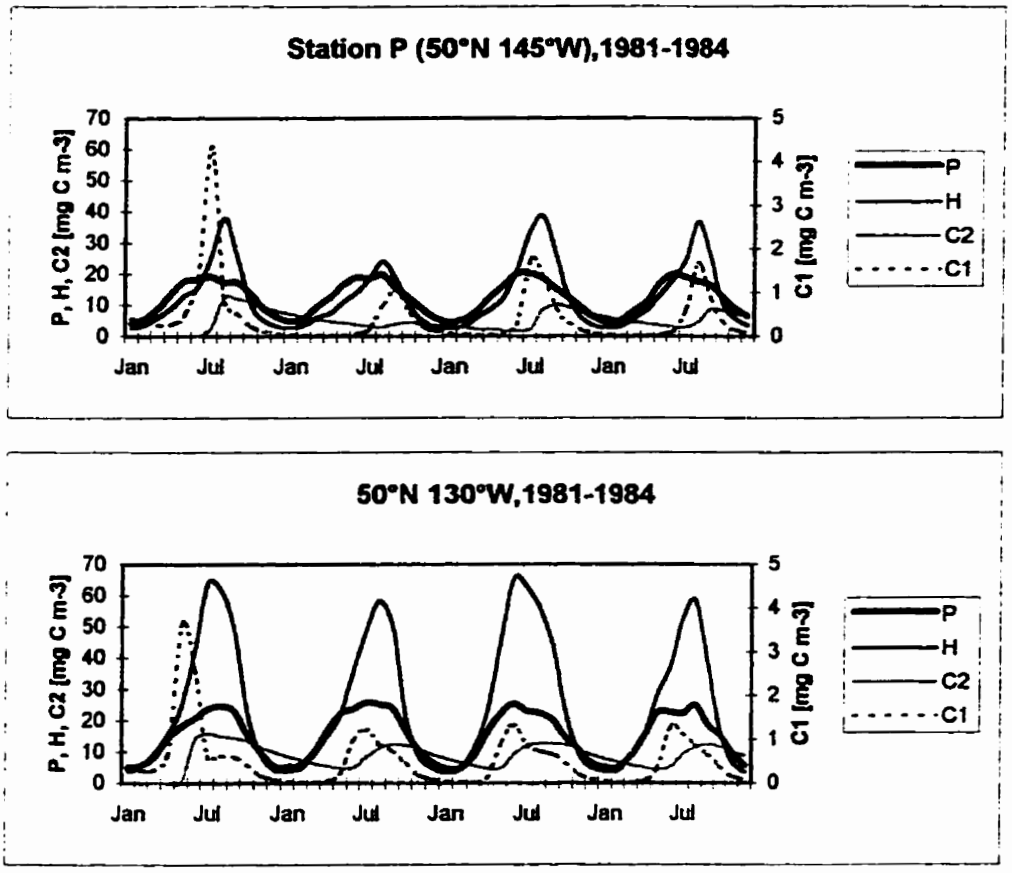


Fig. 3.17: Simulated carbon concentrations for phytoplankton (P), microzooplankton (H), mesozooplankton (C_1), and macrozooplankton (C_2) at Station *P* (50°N 145°W) and at 50°N 130°W for 1981 to 1984. Note different scales on the ordinates.

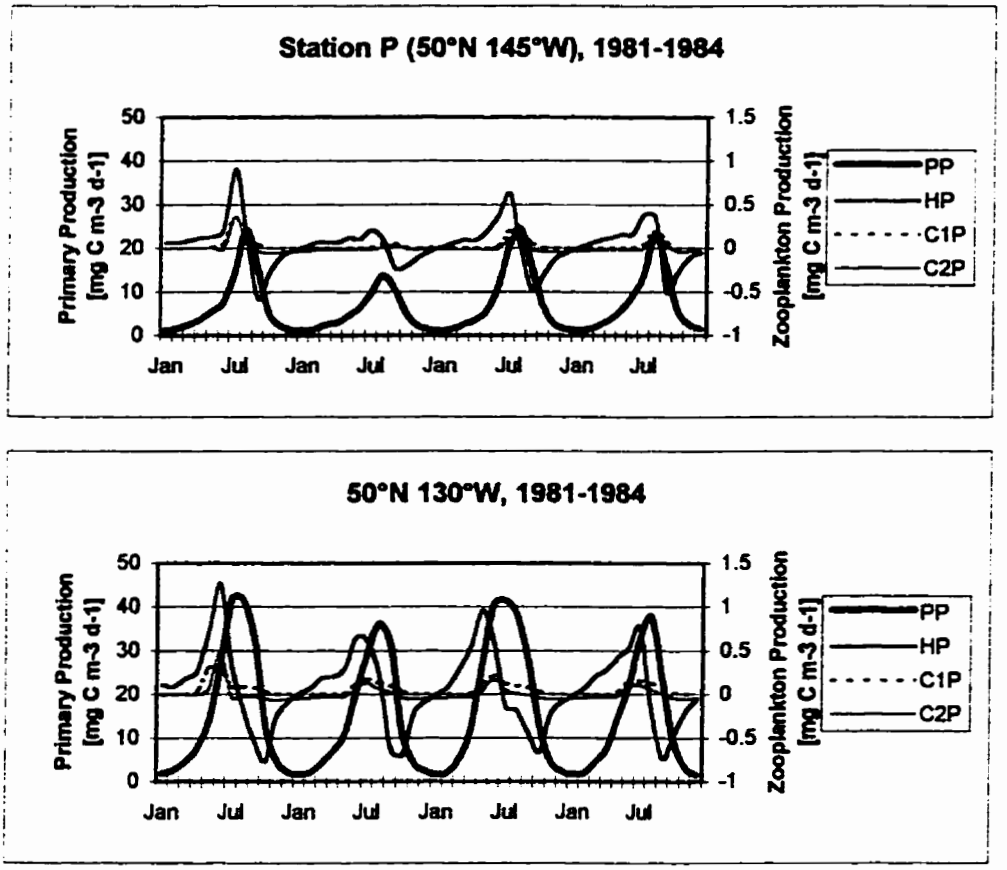


Fig. 3.18: Simulated production per cubic meter and day for phytoplankton (P), microzooplankton (H), mesozooplankton (C_1), and macrozooplankton (C_2) at Station *P* (50°N 145°W) and at 50°N 130°W for 1981 to 1984. Note different scales on the ordinates.

observed May-June mean peak of 3 mg C m^{-3} at Station *P* (Mackas & Frost 1993). Simulated macrozooplankton concentrations behave at least qualitatively as expected. Lack of data (see Section 2.3.), however, do not permit any comparison to the natural world.

Because in the 4-trophic levels model microzooplankton is released from mesozooplankton grazing pressure, microzooplankton net production becomes negative (microzooplankton respiration exceeds primary productivity) in late summer for both locations when sea surface temperatures are high. As a consequence, microzooplankton transfer efficiency is only around 0.5%, much lower than the 22% estimated for the open Northeast Pacific (Parsons & Lalli 1988), or the "tried-and-true" 10% (Slobodkin 1961; but see Baumann 1995; Pauly & Christensen 1995a; Pauly & Christensen 1995b; Slobodkin 1980). Because mesozooplankton is top-down controlled by macrozooplankton much of its production is consumed rather than used up by respiration and non-predatory losses. Thus, mesozooplankton has a transfer efficiency of around 80%. Although these values intuitively appear wrong little is known about the exact bioenergetic relationships in the open ocean ecosystem. Again as expected net community production, i.e. net primary production minus total heterotrophic respiration (Odum 1971), for the 4-trophic levels model is close to zero for both locations.

Fig. 3.19 shows the simulated mass-specific filtration rates for mesozooplankton and macrozooplankton at Station *P* and at 50°N 130°W for 1981-1984. Maximum mass-specific clearance or filtration rates, as calculated from Eq. 3.15 and using parameters of the standard run (Table 3.3), are 4 liters $(mg\ C)^{-1}\ d^{-1}$ for mesozooplankton and 40 liters $(mg\ C)^{-1}\ d^{-1}$ for macrozooplankton. Note that while mesozooplankton mass-specific filtration rates go up to its maximum value of 4 liters $(mg\ C)^{-1}\ d^{-1}$, macrozooplankton never reaches its mass-specific filtration potential.

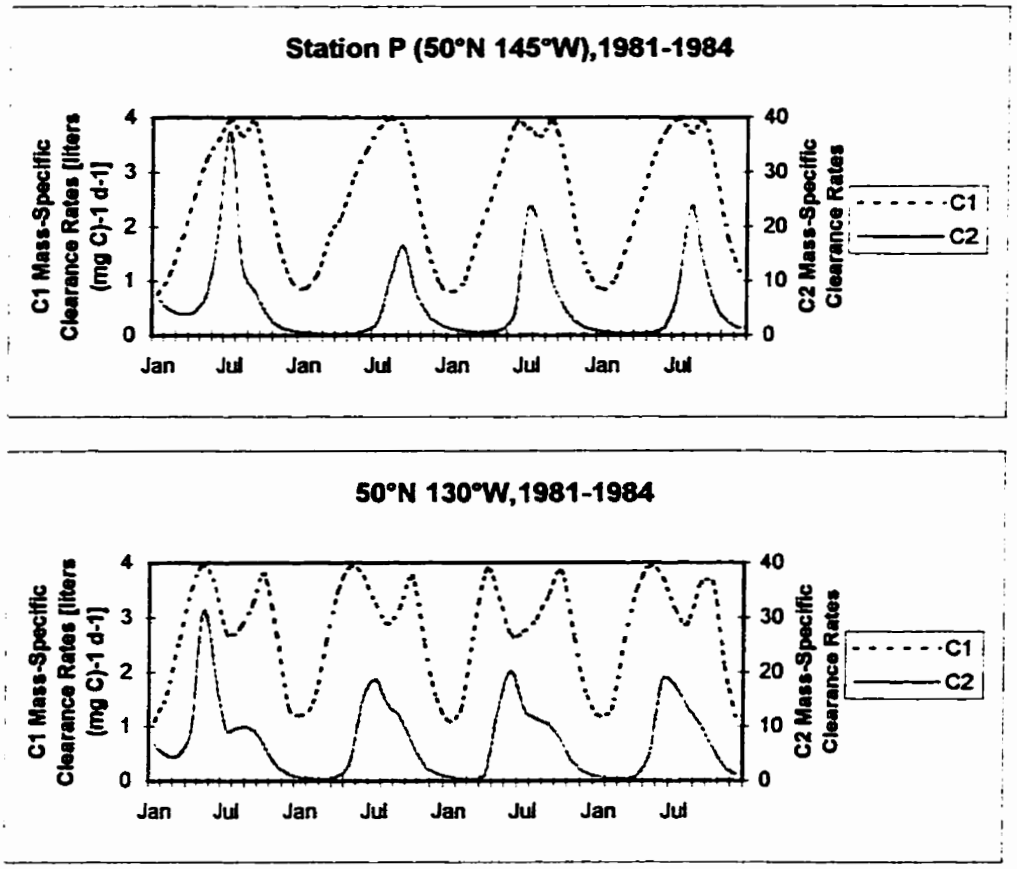


Fig. 3.19: Simulated mass-specific clearance rates or filtration rates [liters $(mg\ C)^{-1}\ d^{-1}$] for mesozooplankton (C_1) and macrozooplankton (C_2) at Station *P* (50°N 145°W) and at 50°N 130°W for 1981 to 1984. Note different scales on the ordinates.

3.5. Sensitivity Analyses

3.5.1. Sensitivity Analyses: 3-Trophic-Levels Model

Sensitivity analyses for the 3-trophic-levels model were conducted with respect to initial conditions, the biological parameters α (Eq. 3.13a), $m_{H,0}$ (Eq. 3.14a), m_{Cl} (Eq. 3.14b), a_{HCl} and K_{HCl} (Eqs. 3.18 and 3.19), and the functional response (Eq. 3.8, Fig. 3.10). Results are plotted as deviations from the standard run, i.e. modified run results minus standard run results, in percent of standard run. Standard run initial conditions and parameter values can be found in Table 3.3.

Sensitivity to Initial Conditions

Sensitivity to initial conditions was tested by doubling the initial values of one state variable at a time and running the simulation for Station *P* from 1981 to 1984. Simulated biomass densities were then compared to those of the standard run at Station *P* for the same period of time (Fig. 3.13). Results in Fig. 3.20 show that a doubling in microzooplankton initial density (H) has almost no effect on both microzooplankton and mesozooplankton densities (C_l), while a doubling in mesozooplankton initial density has larger effects that persist for more than 2 years. Consequently, for the sensitivity analyses to follow, only the years 1983 and 1984 have been considered. To avoid initial condition effects, spatially-explicit simulations in Chapter 4 were given a two year pre-run time without advection before simulation results were recorded.

Sensitivity to Parameters

Parameters that were tested in the sensitivity analyses where increased by 10% compared to their standard run values (Table 3.3).

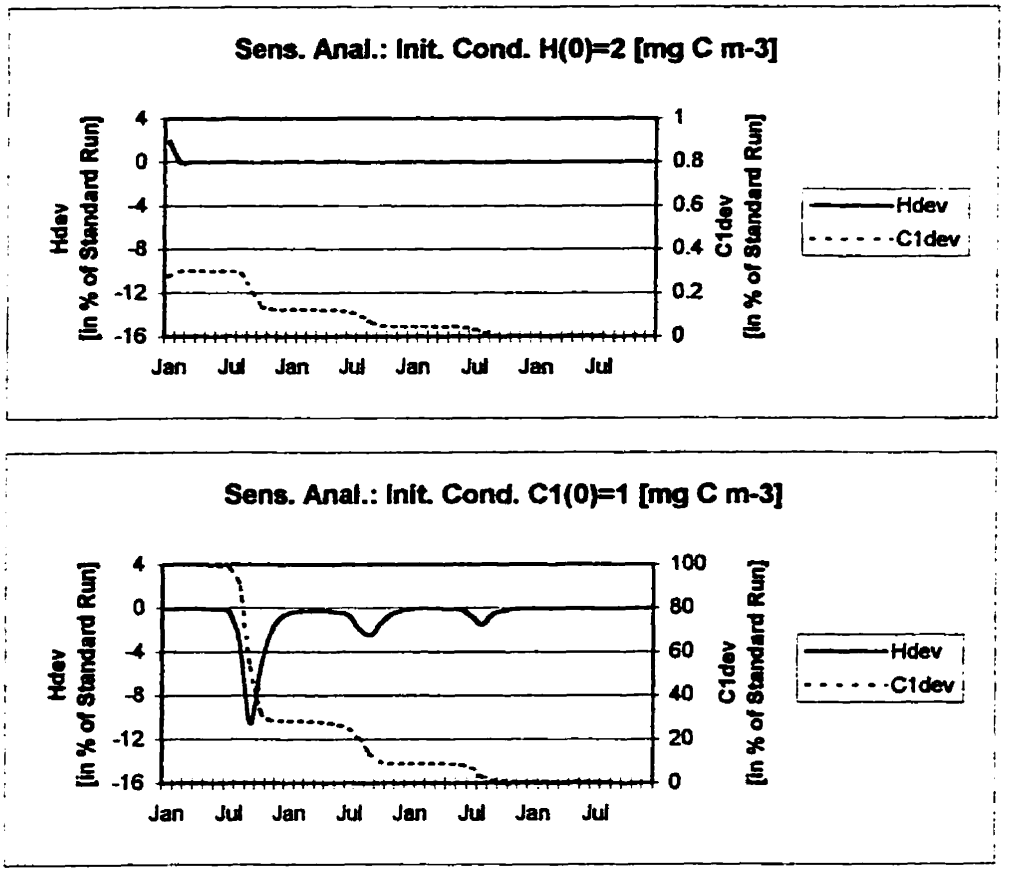


Fig. 3.20: Sensitivity to initial conditions in the 3-Trophic-Levels Model: Deviation of microzooplankton (Hdev) and mesozooplankton (C_1dev) concentrations from the respective concentrations of the standard run after a doubling of the initial density in microzooplankton (upper panel) and mesozooplankton (lower panel). Simulation period: 1981-1984. Note different scales on the ordinates.

An increase in the photosynthetic efficiency α leads to a higher density of the top-predator, i.e. primary production is transferred through microzooplankton to mesozooplankton (Fig. 3.21). Increase of mesozooplankton (C_1) is largest in early summer, when light limitation is at a minimum (Figs. 3.4 and 3.6), which leads to a suppression in microzooplankton density (H) in late summer.

Changes in the specific respiration or non-predatory death rates $m_{H,0}$ and m_{C1} have large effects on population densities. A 10% increase in the microzooplankton specific respiration rate at 0°C $m_{H,0}$, which triggers a parameter change in m_{C1} (see Eqs. 3.14), almost completely eradicates the mesozooplankton standing stock (Fig. 3.22, upper panel). Although microzooplankton densities in winter and spring are in general a little lower than in the standard run as a consequence of the larger losses due to respiration, in summer decreased predation pressure from mesozooplankton results in an increased microzooplankton stock. Increased mesozooplankton respiration rate m_{C1} represents the case when m_H remains unchanged from the standard run simulation and thus effects have less amplitude (Fig. 3.22, lower panel).

Changes in predation parameters, i.e. the maximum specific predation rate of mesozooplankton on microzooplankton (a_{HC1}) and the half-saturation constant of the predator specific predation rate (K_{HC1}), have large effects on biomass densities. Increased a_{HC1} allows mesozooplankton to increase its standing stock substantially compared to the standard run, while microzooplankton remains largely unaffected and is suppressed only in late summer (Fig. 3.23, upper panel), quite similar in pattern to the increase in photosynthetic efficiency (Fig. 3.21). This means that for most of the year mesozooplankton consumes microzooplankton biomass that would otherwise be lost to microzooplankton respiration. On the other hand, an increase in K_{HC1} makes microzooplankton less available to mesozooplankton an thus reduces mesozooplankton

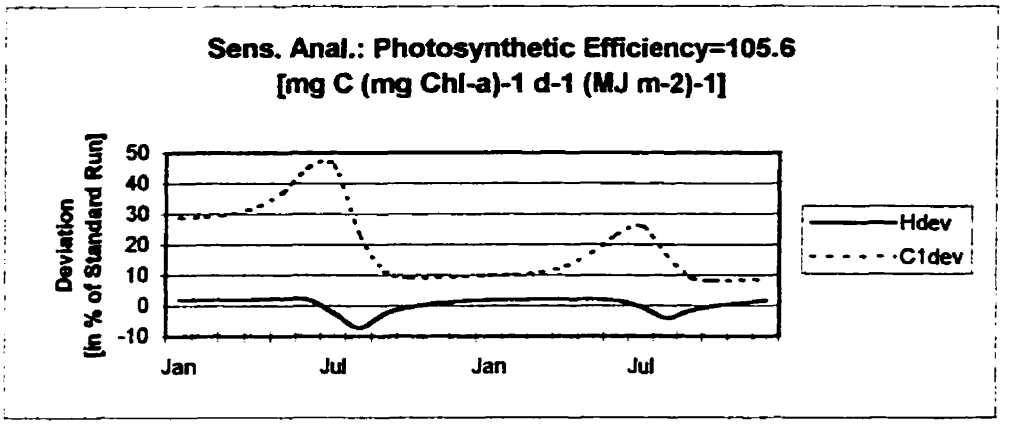


Fig. 3.21: Sensitivity to photosynthetic efficiency α in the 3-Trophic-Levels Model: Deviation of microzooplankton (Hdev) and mesozooplankton (C_1dev) concentrations from the respective concentrations of the standard run after a 10% increase in photosynthetic efficiency. Simulation period: 1983-1984 (see *Sensitivity to Initial Conditions*).

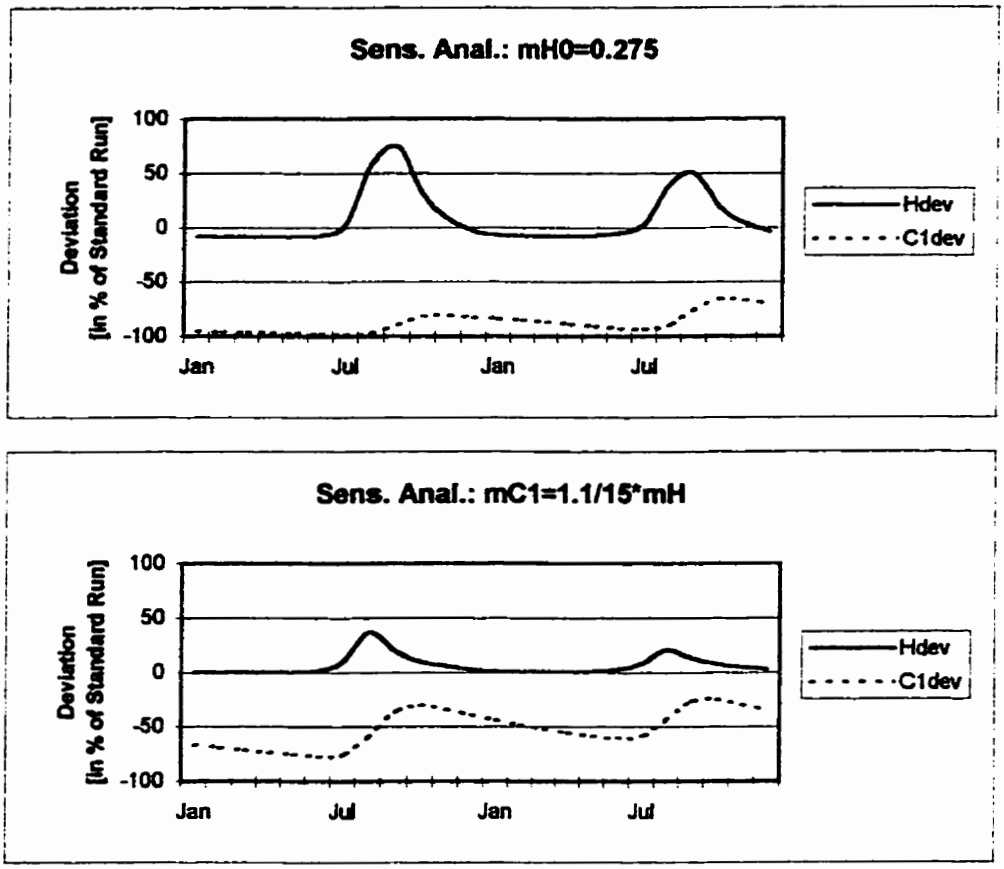


Fig. 3.22: Sensitivity to specific respiration or non-predatory death rates in the 3-Trophic-Levels Model: Deviation of microzooplankton (Hdev) and mesozooplankton (C_1dev) concentrations from the respective concentrations of the standard run after a 10% increase in: Upper panel: herbivore specific respiration rate at 0°C ($m_{H,0}$). Lower panel: the ratio of mesozooplankton (m_{C1}) to microzooplankton (m_H) specific respiration rate. Simulation period: 1983-1984 (see *Sensitivity to Initial Conditions*).

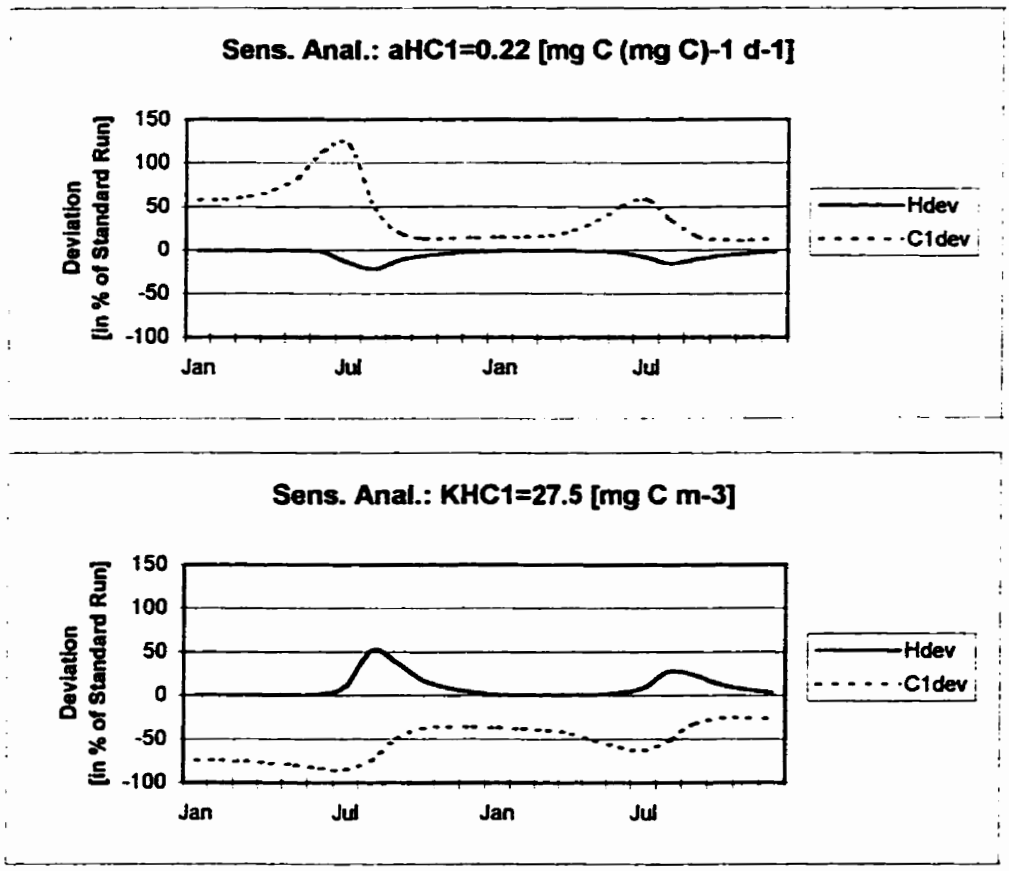


Fig. 3.23: Sensitivity to predation parameters in the 3-Trophic-Levels Model: Deviation of microzooplankton (Hdev) and mesozooplankton (C_1dev) concentrations from the respective concentrations of the standard run after a 10% increase in: Upper panel: the maximum specific predation rate of mesozooplankton on microzooplankton (a_{HC1}). Lower panel: the half-saturation constant of the predator specific predation rate (K_{HC1}). Simulation period: 1983-1984 (see *Sensitivity to Initial Conditions*).

biomass too very low levels (Fig. 3.23, lower panel), a pattern very similar to that obtained from increased non-predatory death rates (Fig. 3.22). High non-predatory losses in microzooplankton keep its density the same as in the standard run simulations, except for late the summer months.

Sensitivity to Functional Response

Here I tested for the effects of a Type II functional response of the specific predation rate to prey density (see discussion in Section 3.3). A Type II functional response for predation of mesozooplankton (C_1) on microzooplankton (H) makes the whole system rather unstable (Fig. 3.24). Microzooplankton is generally suppressed and wildly fluctuates compared to the standard run. Mesozooplankton shows peaks 43 times larger than the already high concentrations in the standard run.

3.5.2. Sensitivity Analyses: 4-Trophic-Levels Model

Sensitivity analyses for the 4-trophic-levels model were conducted with respect to initial conditions, the biological parameters α (Eq. 3.13a), $m_{H.0}$ (Eq. 3.14a), m_{C1} and m_{C2} (Eq. 3.14b), a_{HC1} and K_{HC1} (Eqs. 3.8 and 3.9), a_{C1C2} and K_{C1C2} (Eqs. 3.9 and 3.10), and functional response combinations (Eqs. 3.8 and 3.9, Fig. 3.10). Again, results are plotted as deviations from the standard run, i.e. modified run results minus standard run results, in percent of standard run. Standard run initial conditions and parameter values can be found in Table 3.3.

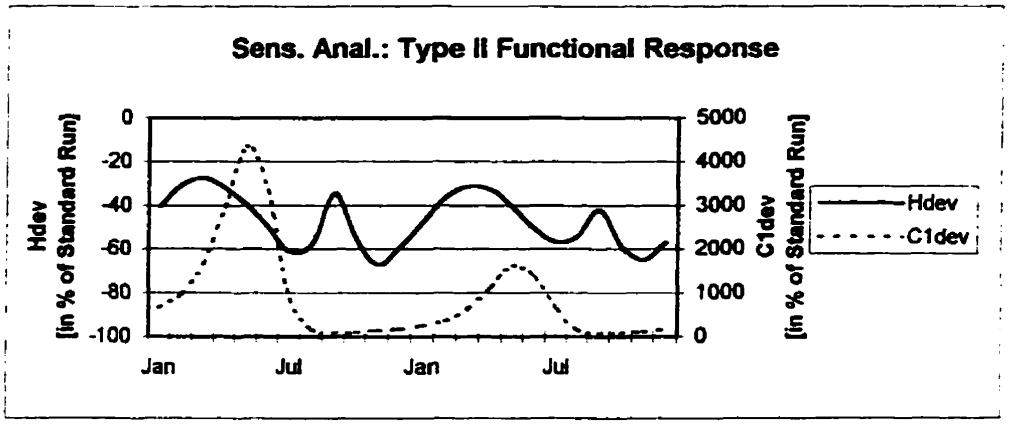


Fig. 3.24: Sensitivity to the functional response in the 3-Trophic-Levels Model: Deviation of microzooplankton (Hdev) and mesozooplankton (C_1dev) concentrations from the respective concentrations of the standard run with a Type II functional response of the mesozooplankton specific predation rate to microzooplankton density. Simulation period: 1983-1984 (see *Sensitivity to Initial Conditions*). Note different scales on the ordinates.

Sensitivity to Initial Conditions

Sensitivity to initial conditions was tested by doubling the initial values of one state variable at a time and running the simulation for Station *P* from 1981 to 1984. Simulated biomass densities were then compared to those of the standard run at Station *P* for the same period of time (Fig. 3.17). Results in Fig. 3.25 show that the effects of a doubling of the initial density of any state variable will have effectively vanished after two years. Again, for the sensitivity analyses to follow, only the years 1983 and 1984 have thus been considered. To account for initial condition effects in the 4-trophic-levels model, spatially-explicit simulations in Chapter 4 were given a two year pre-run time without advection before simulation results were recorded.

Sensitivity to Parameters

Parameters that were tested in the sensitivity analyses where increased by 10% compared to their standard run values (Table 3.3).

Compared to the standard run simulation, increased photosynthetic efficiency α leads to a stable higher density of microzooplankton (H), a trophodynamically fluctuating mesozooplankton density (C_1), and a generally higher macrozooplankton density (Fig. 3.26). Note that, somewhat contrary to the simple version of the trophic cascade argument (Pimm 1992) and as a consequence of the Type III functional response (Section 3.3.), all three trophic levels show increased standing stocks from fall 1983 to summer 1984 as a result of increased photosynthetic efficiency. Increase in macrozooplankton is much smaller than in mesozooplankton in the 3-trophic-levels model, just as expected from the bioenergetic losses that occur during trophic transfers.

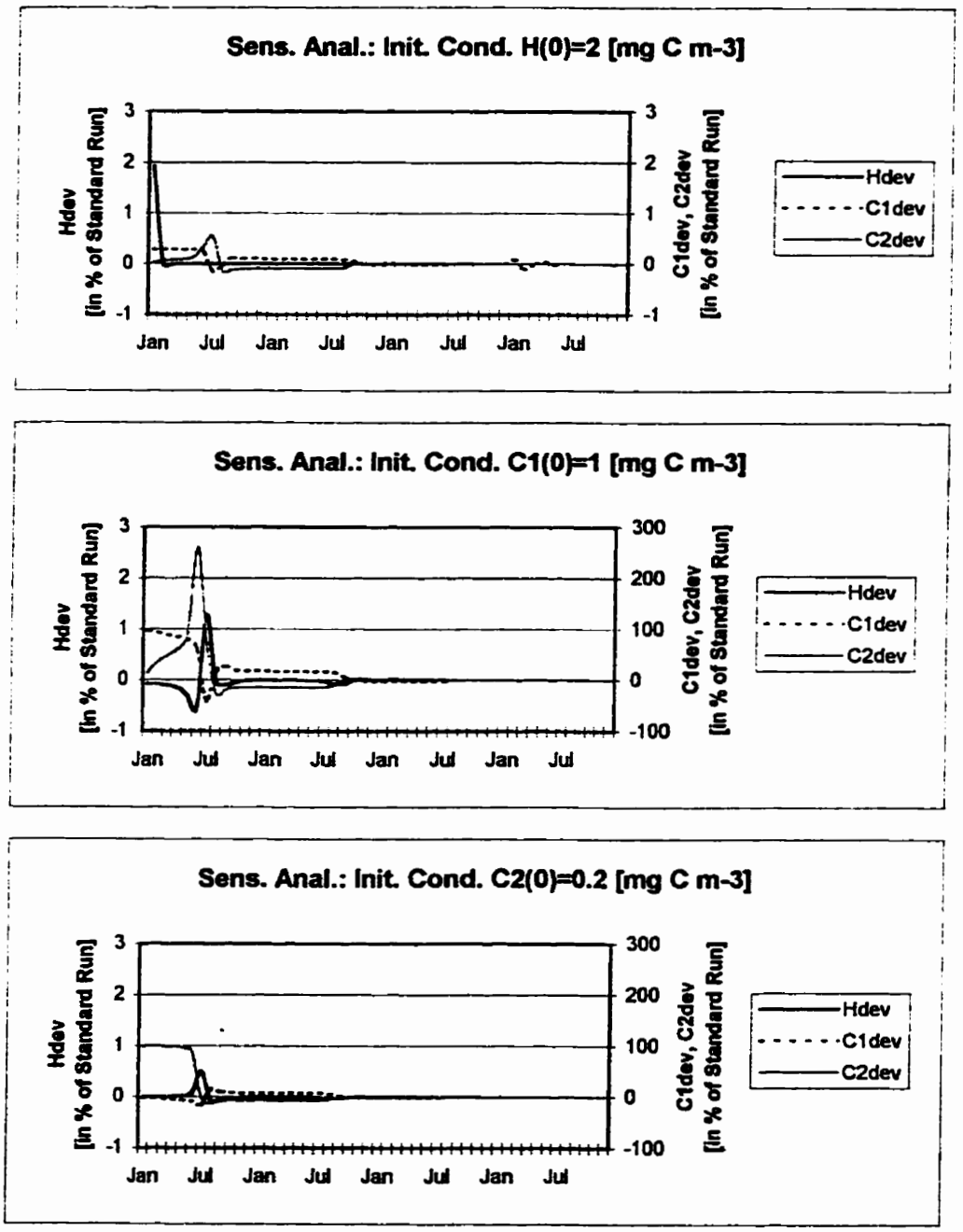


Fig. 3.25: Sensitivity to initial conditions in the 4-Trophic-Levels Model: Deviation of microzooplankton (Hdev), mesozooplankton (C_1dev), and macrozooplankton (C_1dev) concentrations from the respective concentrations of the standard run after a doubling of the initial density in microzooplankton (upper panel), mesozooplankton (middle panel), and macrozooplankton (lower panel). Simulation period: 1981-1984. Note different scales on the ordinates.

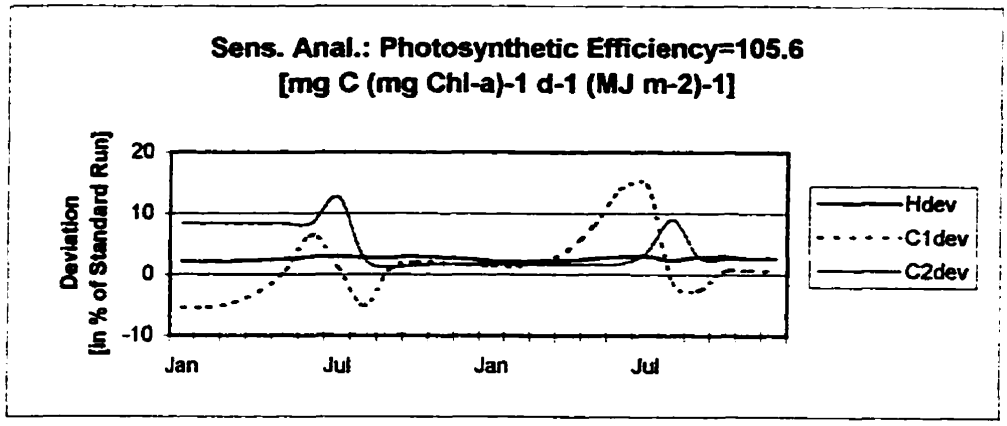


Fig. 3.26: Sensitivity to photosynthetic efficiency α in the 4-Trophic-Levels Model: Deviation of microzooplankton (Hdev), mesozooplankton (C_1dev), and macrozooplankton (C_2dev) concentrations from the respective concentrations of the standard run after a 10% increase in photosynthetic efficiency. Simulation period: 1983-1984 (see *Sensitivity to Initial Conditions*).

In general, changes in the specific respiration or non-predatory death rates $m_{H,0}$, m_{C1}, m_{C2} have smaller effects on population densities in the 4- than in the 3-trophic-levels model (Figs. 3.27 and 3.22). Again the largest effect comes with a 10% increase in the microzooplankton specific respiration rate at 0°C $m_{H,0}$, which triggers a parameter change in m_{C1} and m_{C2} (see Eq. 3.14). Here, microzooplankton densities are generally suppressed by less then 10% compared to the standard run simulation (Fig. 3.27, upper panel), but otherwise follow the same seasonal pattern as the standard run (Fig. 3.17). Increased mesozooplankton respiration rate m_{C1} represents the case when m_H remains unchanged and m_{C2} is changed as well (Eq. 3.14) from the standard run simulation (Fig. 3.27, middle panel). Increased macrozooplankton respiration rate m_{C2} represents the case when both m_H and m_{C1} remain unchanged from the standard run simulation (Fig. 3.27, lower panel). Again deviations from standard run simulations have less amplitude the less effects a particular parameter change has on other parameters.

Changes in predation parameters, i.e. maximum specific predation rates of carnivores (a_{HC1}, a_{C1C2}) and the half-saturation constants of predator specific predation rates (K_{HC1}, K_{C1C2}), have very different effects on the biomass densities depending on the trophic level where the changes occur. Increase in a_{HC1} will result in the same pattern than an increase in primary productivity (compare Figs. 3.28 and Fig. 3.26), and the effect, at least in pattern, of increased K_{HC1} is similar to increased non-predatory death rates (compare Fig. 3.28. and Fig. 3.27). On the other hand, increase in the predation parameter values for macrozooplankton (a_{C1C2}, K_{C1C2}) have interestingly the same effects on predator (macrozooplankton) and prey (mesozooplankton), while having almost no effect on herbivorous microzooplankton (Fig. 3.29), again contrary to the argument of simple trophic cascading (Pimm 1992).

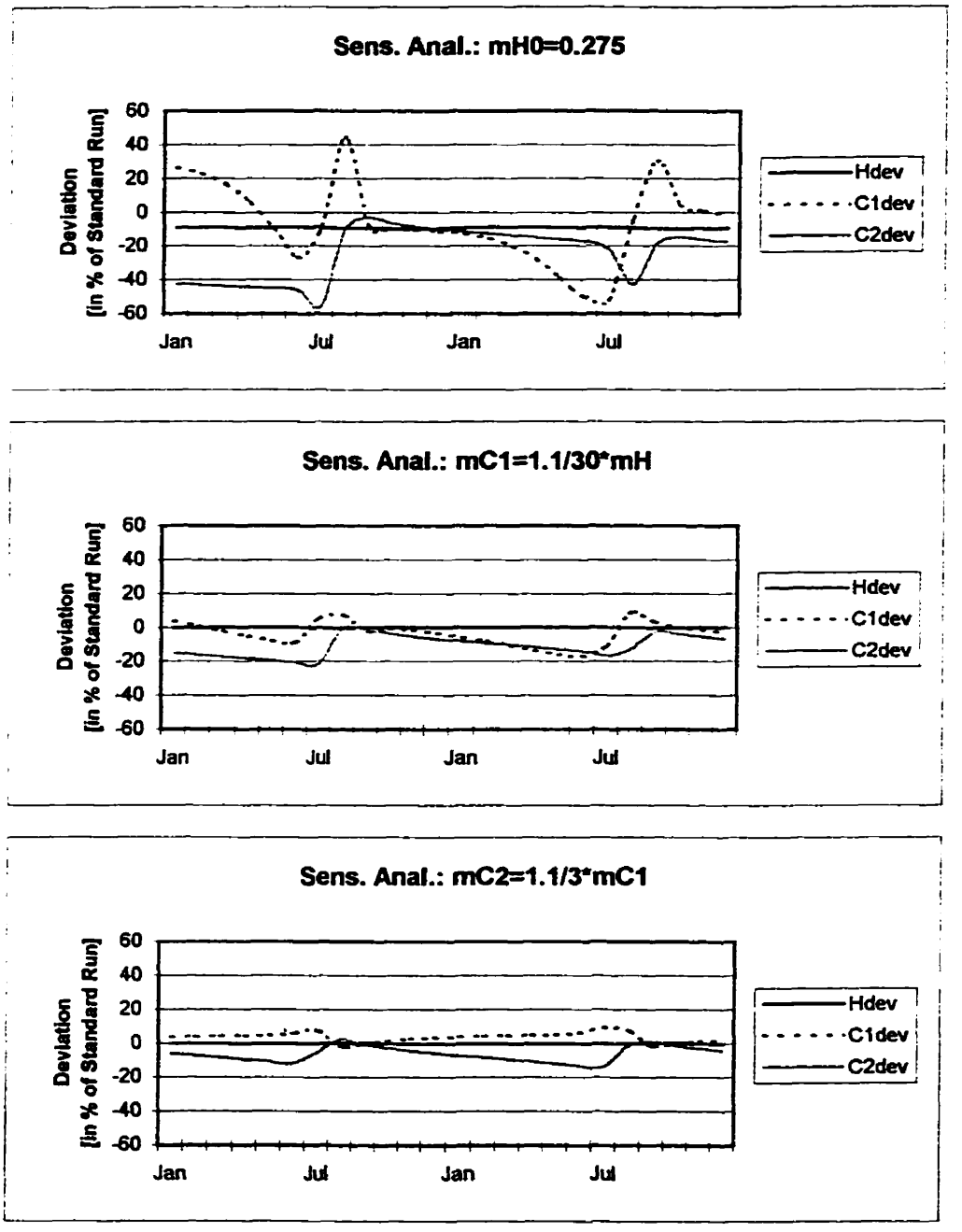


Fig. 3.27: Sensitivity to specific respiration or non-predatory death rates in the 4-Trophic-Levels Model: Deviation of microzooplankton (Hdev), mesozooplankton (C_1dev), and macrozooplankton (C_2dev) concentrations from the respective concentrations of the standard run after a 10% increase in: Upper panel: herbivore specific respiration rate at 0°C ($m_{H,0}$). Middle panel: the ratio of mesozooplankton (m_{C1}) to microzooplankton (m_H) specific respiration rate. Lower panel: the ratio of macrozooplankton (m_{C2}) to mesozooplankton (m_{C1}) specific respiration rate. Simulation period: 1983-1984 (see *Sensitivity to Initial Conditions*).

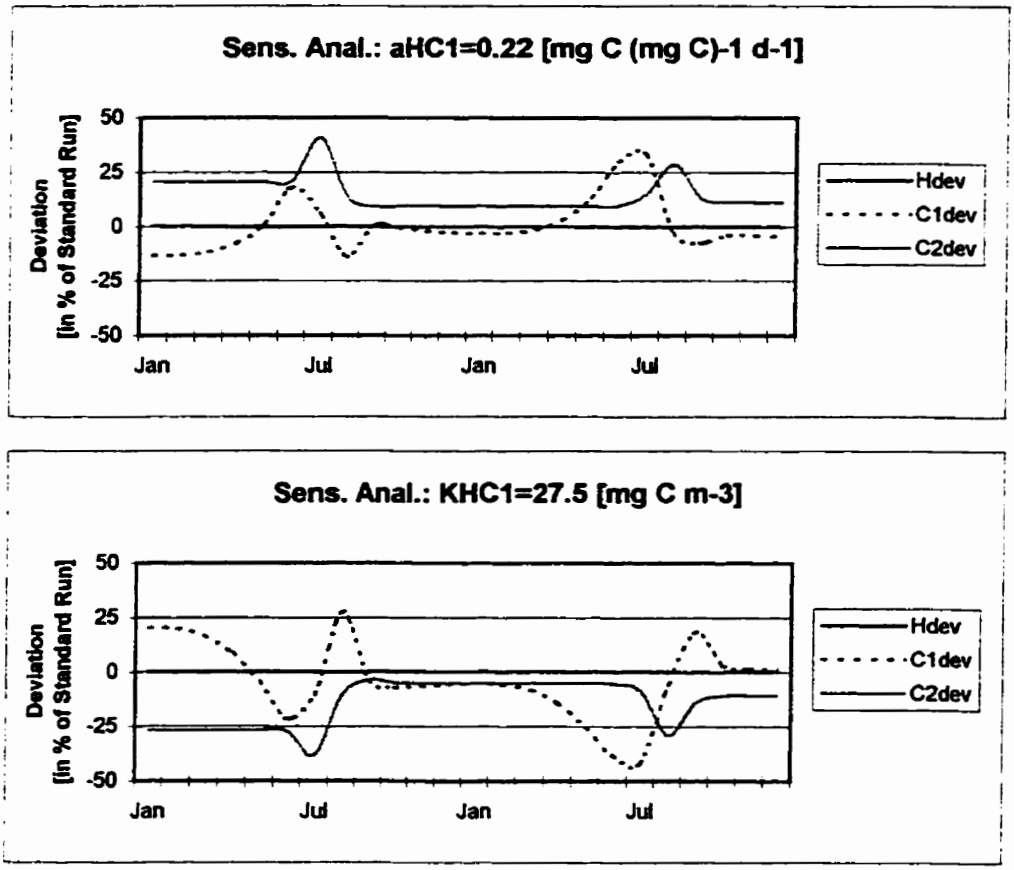


Fig. 3.28: Sensitivity to predation parameters in the 4-Trophic-Levels Model: Deviation of microzooplankton (Hdev), mesozooplankton (C_1dev), and macrozooplankton (C_2dev) concentrations from the respective concentrations of the standard run after a 10% increase in: Upper panel: the maximum specific predation rate of mesozooplankton on microzooplankton (a_{HC1}). Lower panel: the half-saturation constant of the predator specific predation rate (K_{HC1}). Simulation period: 1983-1984 (see *Sensitivity to Initial Conditions*).

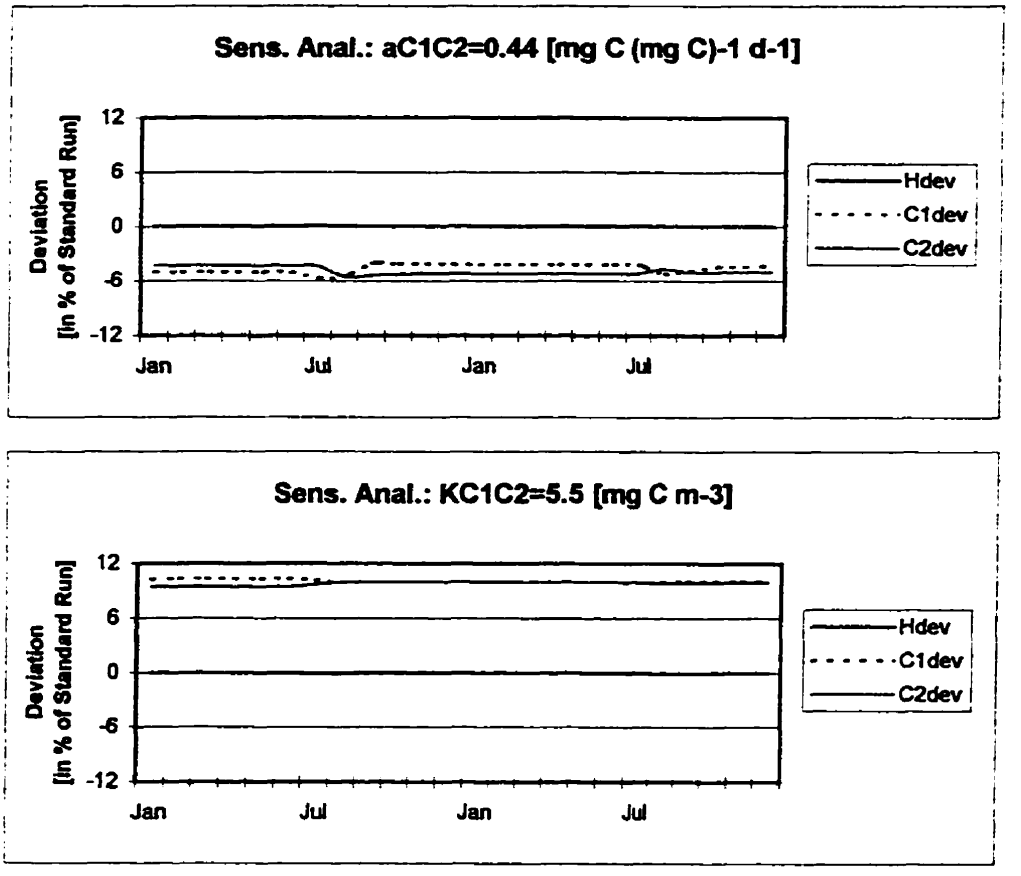


Fig. 3.29: Sensitivity to predation parameters in the 4-Trophic-Levels Model: Deviation of microzooplankton (Hdev), mesozooplankton (C_1dev), and macrozooplankton (C_2dev) concentrations from the respective concentrations of the standard run after a 10% increase in: Upper panel: the maximum specific predation rate of macrozooplankton on mesozooplankton (a_{C1C2}). Lower panel: the half-saturation constant of the predator specific predation rate (K_{C1C2}). Simulation period: 1983-1984 (see *Sensitivity to Initial Conditions*).

Sensitivity to Functional Response

I tested for the effects of various functional response combinations between the three explicitly modeled trophic levels (Eqs. 3.8-3.10). A Type II functional response at the transfer between mesozooplankton C_1 and macrozooplankton C_2 (Fig. 3.1) will eradicate both, first mesozooplankton and consequently its predator (Fig. 3.30, upper and lower panel). A Type II / Type III combination for the microzooplankton (H) to mesozooplankton, and mesozooplankton to macrozooplankton transfer, respectively, leaves microzooplankton a little suppressed and wildly fluctuating compared to the standard run. Mesozooplankton shows peaks 13 times larger standard run, a somewhat damped version of the pattern in the 3-trophic-levels model (Fig. 3.24). Macrozooplankton shows on average a slight increase compared to the standard run.

In summary, the small sensitivity to initial conditions of the 3- and the 4-trophic-levels model (Fig. 3.1, Table 3.1) can be compensated by a 2-year pre-run time in longterm simulations. Both models are mostly sensitive to predation parameters at the biomass or energy transfer between microzooplankton and mesozooplankton, whose effects are similar in pattern but larger in magnitude to changes in primary productivity and specific respiration rates. Regarding stability, Type III functional responses appear to be a valid assumption. Nevertheless, it should be said that density-independent migration, such as caused by advection, can exert a stabilizing effect on populations dynamics (McCallum 1992; Stone 1993, but see Steele 1974).

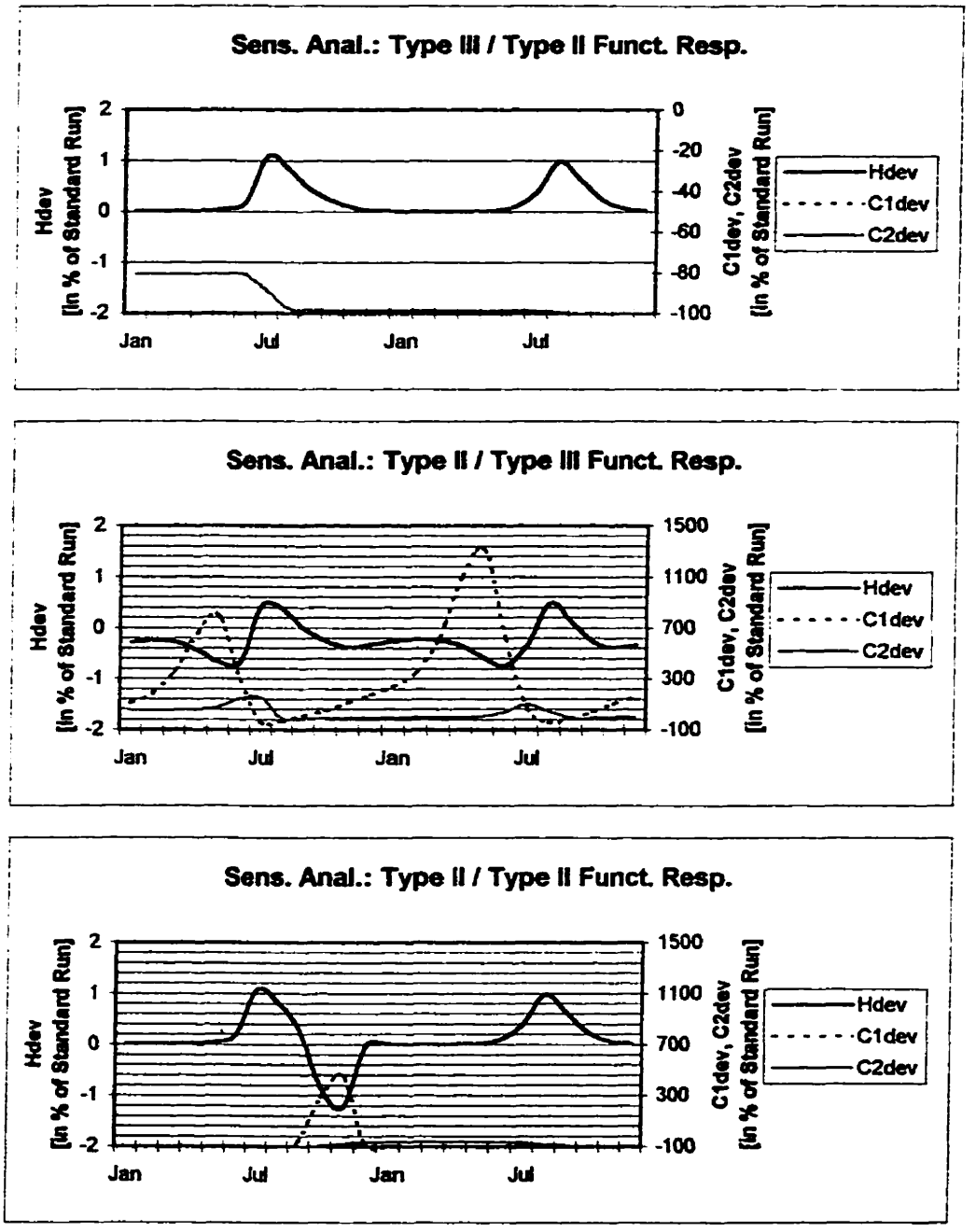


Fig. 3.30: Sensitivity to the functional response in the 4-Trophic-Levels Model: Deviation of microzooplankton (Hdev), mesozooplankton (C_1dev), and macrozooplankton (C_2dev) concentrations from the respective concentrations of the standard run. Upper panel: Type III functional response of mesozooplankton specific predation rate to microzooplankton density. Type II functional response of macrozooplankton specific predation rate to mesozooplankton density. Middle panel: Type II / Type III. Lower panel: Type II / Type II. Simulation period: 1983-1984 (see *Sensitivity to Initial Conditions*). Note different scales on the ordinates.

4. SPATIALLY-EXPLICIT SIMULATIONS

Ockham's Razor: A plurality of reasons should not be posited without necessity.
William of Ockham (1285-1349)

"No aphorism is more frequently repeated ... than that we must ask Nature few questions, or ideally, one question at a time. [I am] convinced that this view is wholly mistaken. ... Indeed if we ask [Nature] a single question, she will often refuse to answer until some other topic has been discussed."
R.A. Fisher (1890-1962)

4.1. Spatio-Temporal Resolution and Advection

Spatio-Temporal Resolution

Spatially-explicit simulations of ecosystem processes in the mixed upper layer of the Northeast Pacific were run on a georeferenced 1° longitude x 1° latitude grid covering the ocean surface between 180 to 125°W and 35 to 62°N. (For primary production processes only, the vertical spatial resolution was one meter from the surface down to the base of the mixed layer.) The spatio-temporal resolution of the simulations is a compromise between the resolution of the input data (see 3.2. Environmental Forcings), the assumed relevant scales of biological processes, and computation time. There are two shortcomings in spatial scope and resolution, especially when considering that sockeye salmon cohort survival is probably determined in or near the coastal domains (see Section 1.4.): First, the Bering Sea is only partially covered, and second, input data lack a high resolution coastal circulation model.

Every 1° x 1° field in the spatially-explicit simulations was identified by the longitude and latitude of its southwest corner. A field was classified as open ocean habitat if and only if each of the field's four corners was represented in the Ocean Surface Current Simulation (OSCURS; Subsection 3.2.2) and thus had two current vectors (one in x- and one in y-direction) assigned to

its geographic coordinates. Only fields classified as open ocean habitat were considered in the spatially-explicit ecosystem simulations, in sum 1240 fields. In order to compare local biological to spatial advection effects simulations were run without and with advection for both, the 3- and 4-trophic levels model (Chapter 3). Simulations without advection were run from 1949 to 1990 with a time step of one day. Because initial condition effects persisted for approximately two years in the mean field simulations (see 3.5. Sensitivity Analyses) model output was considered reliable from 1951 onwards. Simulations that included advection were run from 1951 to 1990, and initial conditions for biological state variables were obtained from the spatially-explicit simulations without advection. As in the mean field simulations the time step for biological processes was one day. However, tests on the OSCURS input data showed that some fields in the spatially explicit simulations would export almost twice the biomass concentration they contain when run on a 1° x 1° grid with a daily time step, a computational problem that would effectively generate biomass by simply moving it on a grid. As a result, I decreased the time step for advection to 4 hours (alternatively, one could increase the spatial grid size) which eliminated the computational problem. In order to minimize computational errors in the simulations that included advection, advection and ecological processes were run in subsequent order rather than simultaneously, i.e. each day biomass was first advected by surface currents then biological processes occurred. When calculated on a 486-66 microprocessor, computation of the spatially-explicit simulation of the 4-trophic levels model including advection takes approximately two weeks.

Advection

Moving concentrations in space is not a trivial problem especially if the physical sizes of the spatial dimensions of the different fields in a spatially-explicit simulation differ from one another. For example, the latitude of each 1° x 1° field determines the area it spans, and neighboring fields have different mixed layer depths as calculated from sea surface temperature and scalar wind speed (Subsection 3.2.2.). Advection of concentrations was computed by defining import as positive from the west and south, and export as positive to the east and north for each field. Daily import and export vectors were taken as the mean values of the respective daily u- and v-vectors that were calculated for each longitude and latitude from monthly mean vectors of the Ocean Surface Current Simulation (OSCURS; for spatio-temporal data interpolation see Subsection 3.2.1.).

When some field 1 with a biomass concentration C_1 and a mixed layer depth z_{ML1} exports water masses into an adjacent (eastern) field 2 with a deeper mixed layer (i.e. $z_{ML1} > z_{ML2}$; z_{ML} in negative values as mixed layer depth was regarded as a depth coordinate) total exported biomass ΔB_1 per time step Δt is given by:

$$\frac{\Delta B_1}{\Delta t} = -u_{12} \Delta y \, z_{ML_1} C_1 \qquad \text{(Eq. 4.1a)}$$

where u_{12} is the (eastward) current vector from field 1 to field 2, and Δy (= $\Delta y_1 = \Delta y_2$) represents the field's length in y-dimension. Biomass concentration in field 1 changes by:

$$\frac{\Delta C_1}{\Delta t} = -\frac{u_{12}}{\Delta x} C_1 \qquad \text{(Eq. 4.1b)}$$

where Δx (= $\Delta x_1 = \Delta x_2$) represents the field's length in x-dimension, which is a function of latitude. Due to the deeper mixed layer depth biomass concentration in field 2 changes by:

$$\frac{\Delta C_2}{\Delta t} = +\frac{u_{12}}{\Delta x}\frac{z_{ML.1}}{z_{ML.2}}C_1 \qquad \text{(Eq. 4.1c)}$$

When now field 2 with a biomass concentration C_2 and a mixed layer depth z_{ML2} exports water masses into an adjacent (eastern) field 3 with a shallower mixed layer (i.e. $z_{ML2} < z_{ML3}$; z_{ML} in negative values as mixed layer depth was regarded as a depth coordinate) total exported biomass ΔB_2 per time step Δt is given by:

$$\frac{\Delta B_2}{\Delta t} = -u_{23}\Delta y\, z_{ML_3} C_2 \qquad \text{(Eq. 4.2a)}$$

where u_{23} is the (eastward) current vector from field 2 to field 3. Note that here water masses were moved between fields considering the shallower mixed layer z_{ML3}. The rationale for this is the following: The transition at depth between two adjacent fields with different mixed layer depths is a step function. (Ideally one should apply a gradual transition. However, that would require a higher spatial resolution, which in turn affords a shorter time step, and whose combined effect is a nonlinear increase in computation time.) A biomass flow from field 2 into 3 could be written as:

$$\frac{\Delta B_2}{\Delta t} = -u_{23}\Delta y\, z_{ML_2} C_2 \qquad \text{(Eq. 4.2b)}$$

Note that in Eq. 4.2b water masses are moved considering the deeper mixed layer depth. However, this would mean that parts of the water column of field 2 end up below the mixed layer depth of field 3, i.e. a net biomass loss due to transport. It has been pointed out that in biological simulations one has to be careful not to create (e.g. due to a too large timestep) or destroy organisms when moving them on a grid (Walters 1986) thus Eq. 4.2b seemed unrealistic.

To avoid the problem of destroying biomass when moving it one could increase the total biomass in field 3 by the amount calculated in Eq. 4.2b. This, however, would represent a

concentration process whereby the total exported biomass form the field with the deeper mixed layer is compressed into a volume with a shallower mixed layer. This scenario as well seemed unrealistic.

Eq. 4.2a thus represents the most realistic representation of advection of concentrations especially when considering that OSCURS current vectors where calculated from COADS vector wind data (see Section 3.2.) and wind-induced currents in nature produce highest current velocities at the surface, and which are decreasing towards depth within the mixed layer. Following from Eq. 4.2a then:

$$\frac{\Delta C_2}{\Delta t} = -\frac{u_{23}}{\Delta x}\frac{z_{ML.3}}{z_{ML.2}}C_2 \qquad \text{(Eq. 4.2c)}$$

$$\frac{\Delta C_3}{\Delta t} = \frac{u_{23}}{\Delta x}C_2 \qquad \text{(Eq. 4.2d)}$$

The same rules apply to transport in north-south direction.

Spatial Closure

Spatially-explicit ecosystem simulations were restricted to the open Northeast Pacific, excluding processes in the open Pacific west of 180°W and south of 35°N, and the coastal regions. However, because the Northeast Pacific cannot be considered a closed system when advection is included, assumptions have to be made about the boundary conditions. Three different boundary conditions for biomass concentrations were tested in simulations were biomass concentrations (initial biomass concentration for all open ocean fields: 1 mg C m^{-3}) were subjected to advection but <u>not</u> to biological processes, i.e. growth and death. (Note that for the mixed layer depth zero-gradient boundary conditions had to be adopted, otherwise gross export from the Northeast Pacific would be zero (see Eq. 4.2c).):

(1) Zero Boundary Conditions: All boundary fields towards the open Pacific and towards the coast have a biomass concentration of zero.

(2) Zero-Gradient Boundary Conditions: A boundary field towards the open Pacific or towards the coast has the same biomass concentration as the adjacent (in x- or y-direction) open ocean field that is included in the simulation.

(3) Combined Zero / Zero-Gradient Boundary Conditions: All boundary fields towards the coast have biomass concentrations of zero. A boundary field towards the open Pacific has the same biomass concentration as the adjacent (in x- or y-direction) open ocean field that is included in the simulation.

As expected from general circulation patterns (Fig. 2.1) simulations with zero boundary conditions, i.e. no gross import of biomass, accumulate biomass on the eastern side of the Northeast Pacific in the course of one year (Fig. 4.1). There is also a slight accumulation of biomass south of the Aleutian Islands, the region where Bristol Bay sockeye salmon enter the open ocean realm (Burgner 1991). While the high biomass density south of the Aleutian Islands must be a consequence of reduced export from that region in simulations with zero boundary conditions, the even higher concentrations in that area in simulations with zero gradient boundary conditions (Fig. 4.2) are a consequence of the boundary conditions themselves. In order to minimize the accumulation effects of zero-gradient boundary conditions in the coastal regions on the biomass concentration south of the Aleutian Islands and still have the realistic open boundary conditions with respect to gross import and export, combined zero /

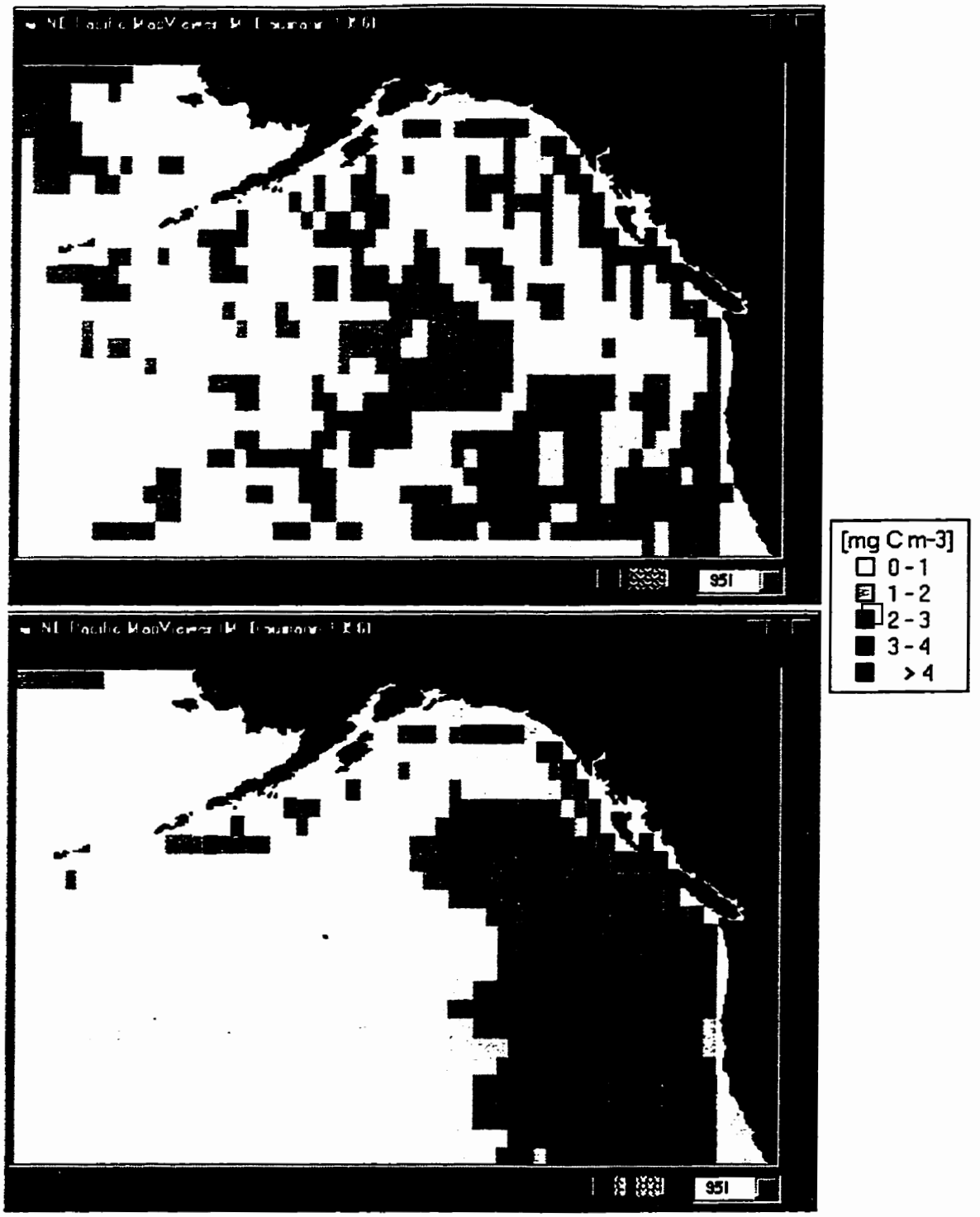


Fig. 4.1: Simulated biomass concentration [mg C m^{-3}] for zero boundary conditions for January, April, July and October 1951. Simulation included advection but no biological processes. Initial (30 Dec 1950) biomass concentration for all open ocean fields was 1 mg C m^{-3}. All maps are depicted as displayed by the Northeast Pacific Map Viewer, a mapping program that I wrote in 1996. Displayed on the bottom of each panel (from left to right): longitude and latitude of the cursor position, month and year. Poor text quality is a consequence of bitmap size reductions.

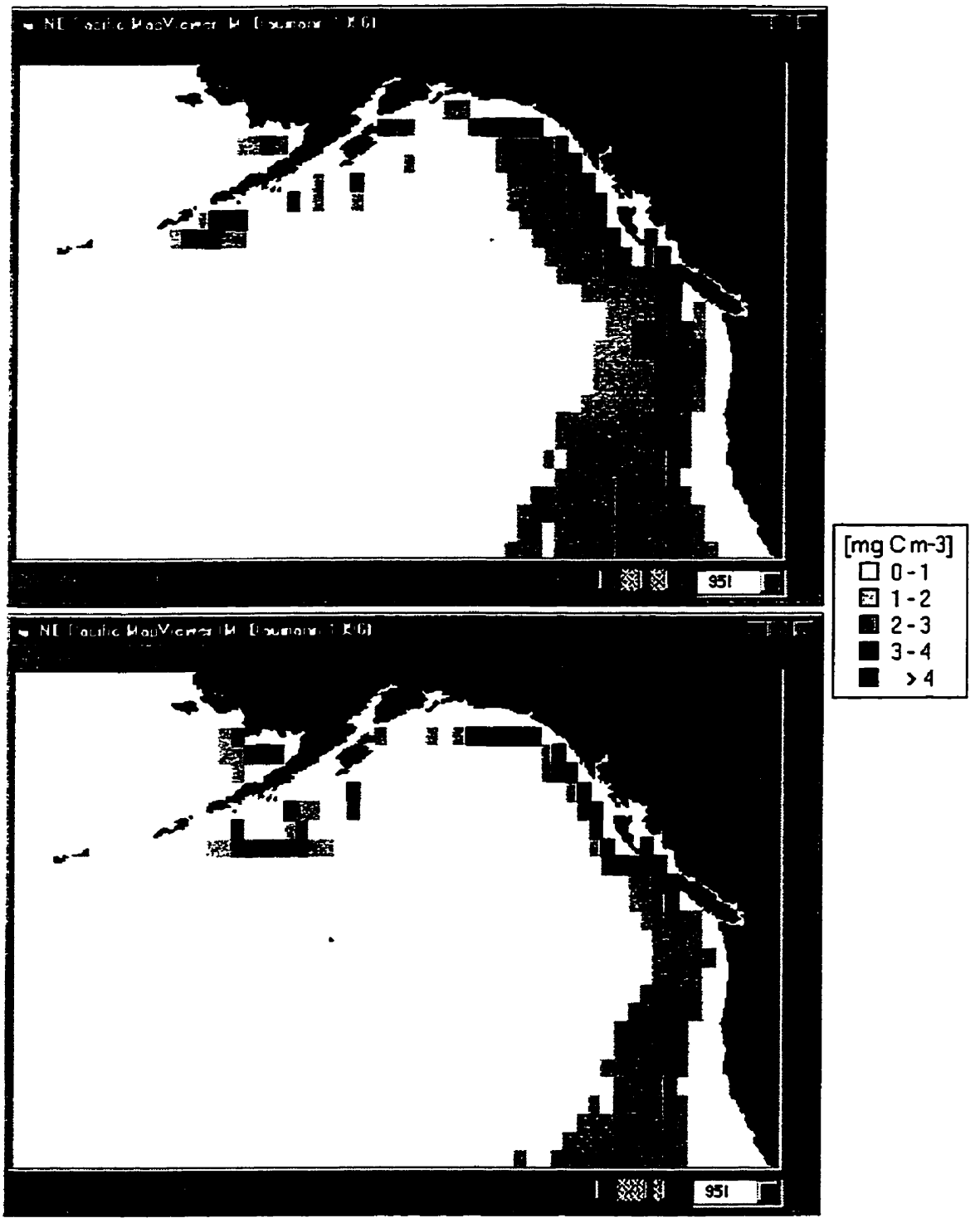


Fig. 4.1: Continued

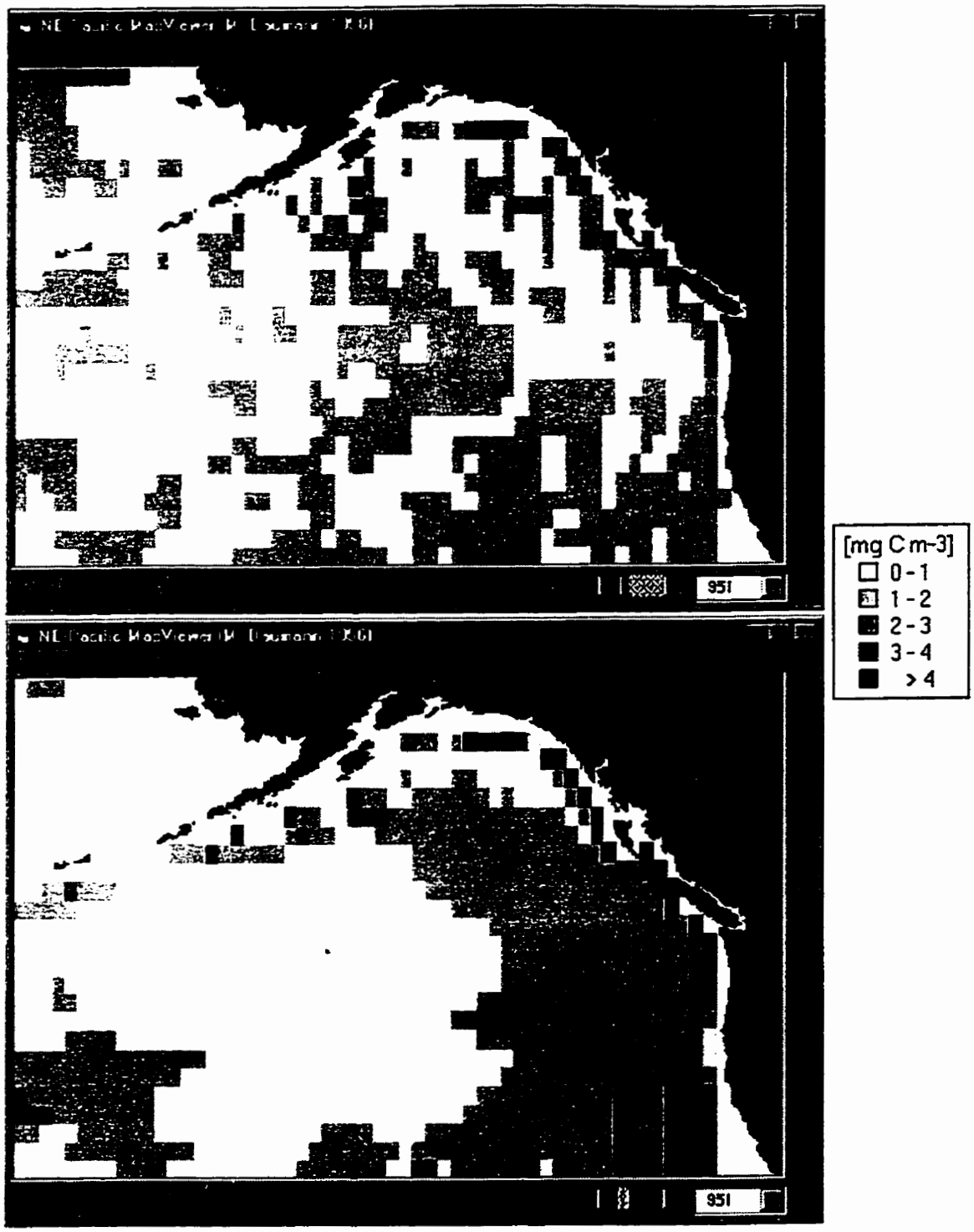


Fig. 4.2: Simulated biomass concentration [mg C m^{-3}] for zero-gradient boundary conditions for January, April, July and October 1951. Simulation included advection but no biological processes. Initial (30 Dec 1950) biomass concentration for all open ocean fields was 1 mg C m^{-3}.

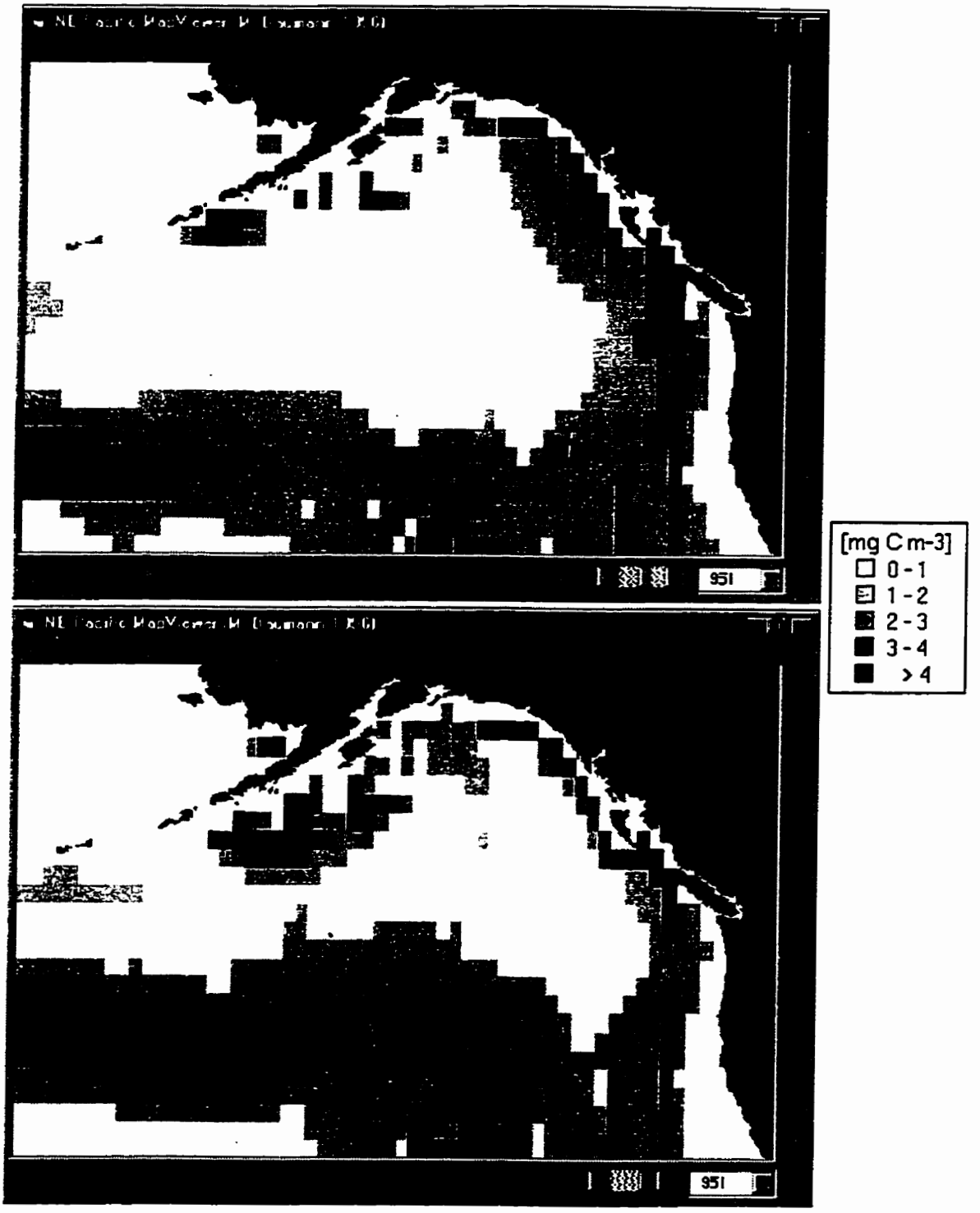


Fig. 4.2: Continued

zero-gradient boundary conditions (Fig. 4.3) were applied for the whole-ecosystem simulation. The severity of accumulation effects due to zero-gradient boundary conditions becomes obvious when looking at longer time scales: Fig. 4.4 compares the biomass concentrations in Gulf of Alaska with zero-gradient boundary conditions and combined zero / zero-gradient boundary conditions after a period of 10 years.

I also tested for the effects of initial conditions on the biomass distribution by running the biomass advection simulation (again without biology) from 1951 to 1960. Each field was given a uniformly-distributed random initial biomass concentration between 0 and 1. For repeated runs biomass concentration patterns looked very similar within less than a year (Fig. 4.5). This is not surprising as circulation patterns are similar over large areas and random initial conditions should average out over large areas.

In summary, tests using advection results from the Ocean Surface Current Simulation (OSCURS) show that for a spatial resolution of 1° longitude x 1° latitude, the maximum tolerable time step in order not to generate biomass by simply moving it on the grid is 12 hours. To allow for smoother biomass advection, this maximum time step in the advection sub-component of the whole ecosystem simulations was reduced to 4 hours. Furthermore, combined zero boundary conditions (towards the coast) / zero-gradient boundary conditions (towards the open ocean) were applied in order to avoid excessive biomass accumulations in the Gulf of Alaska.

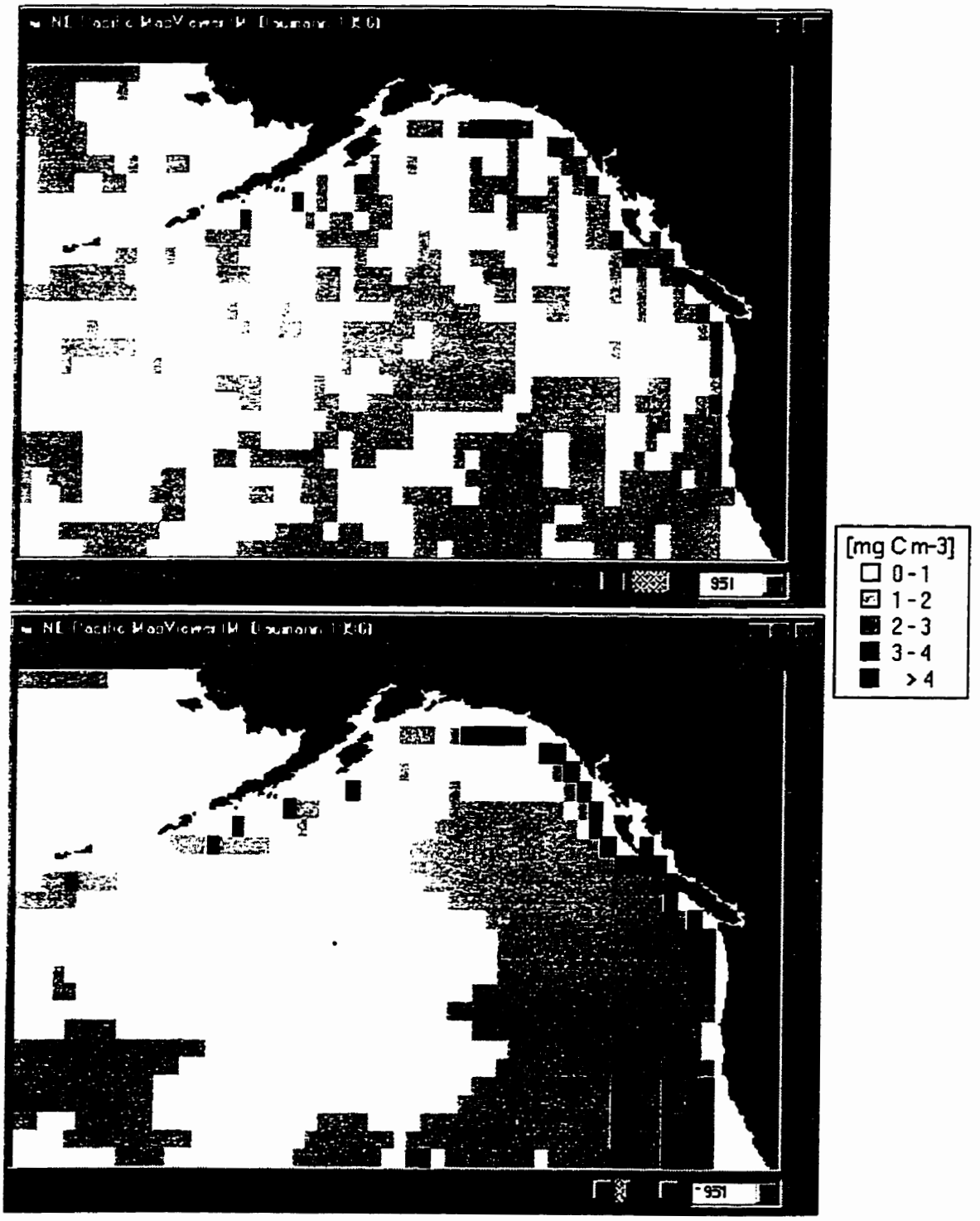


Fig. 4.3: Simulated biomass concentration [mg C m^{-3}] for combined zero / zero-gradient boundary conditions (see text) for January, April, July and October 1951. Simulation included advection but no biological processes. Initial (30 Dec 1950) biomass concentration for all open ocean fields was 1 mg C m^{-3}.

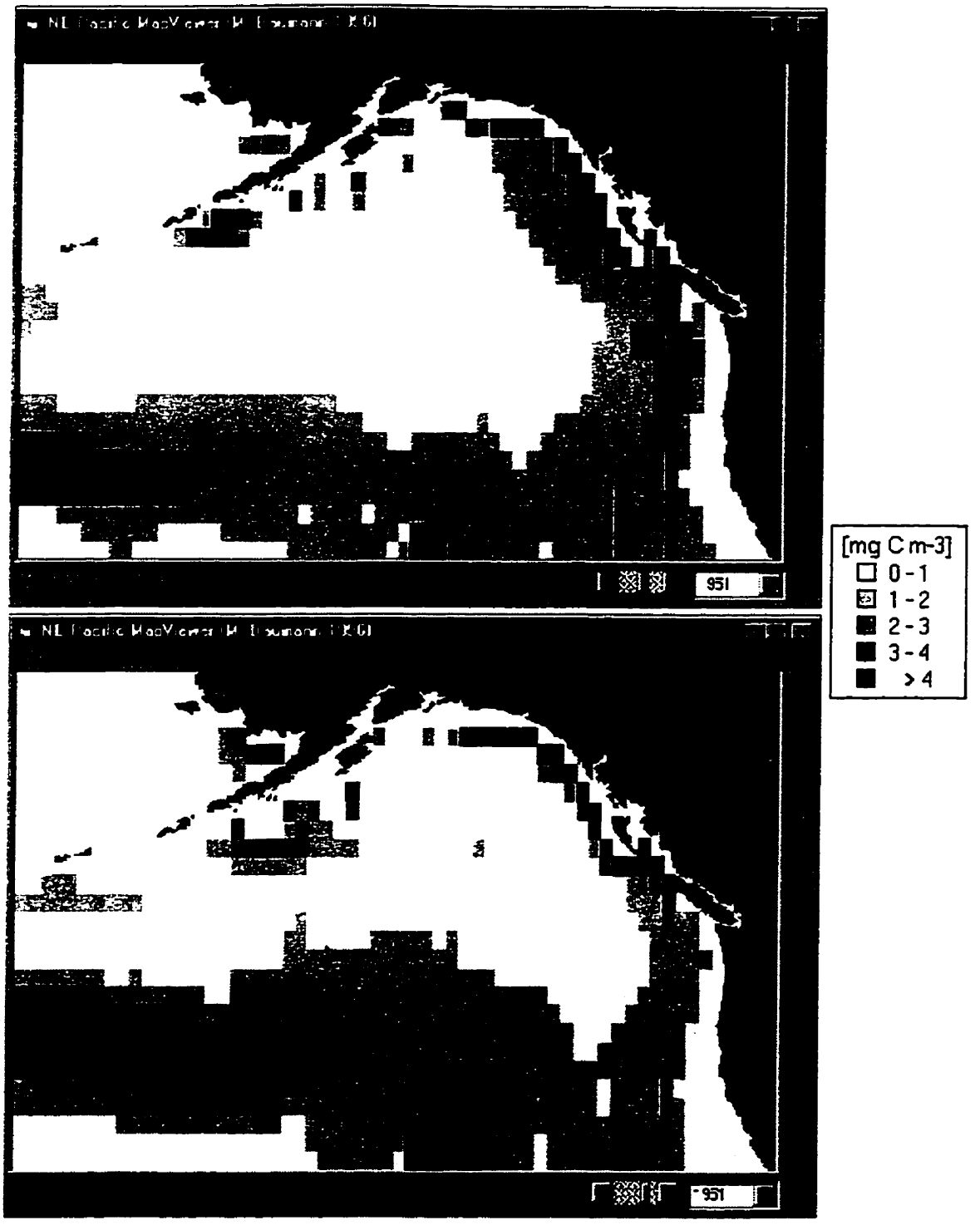


Fig. 4.3: Continued

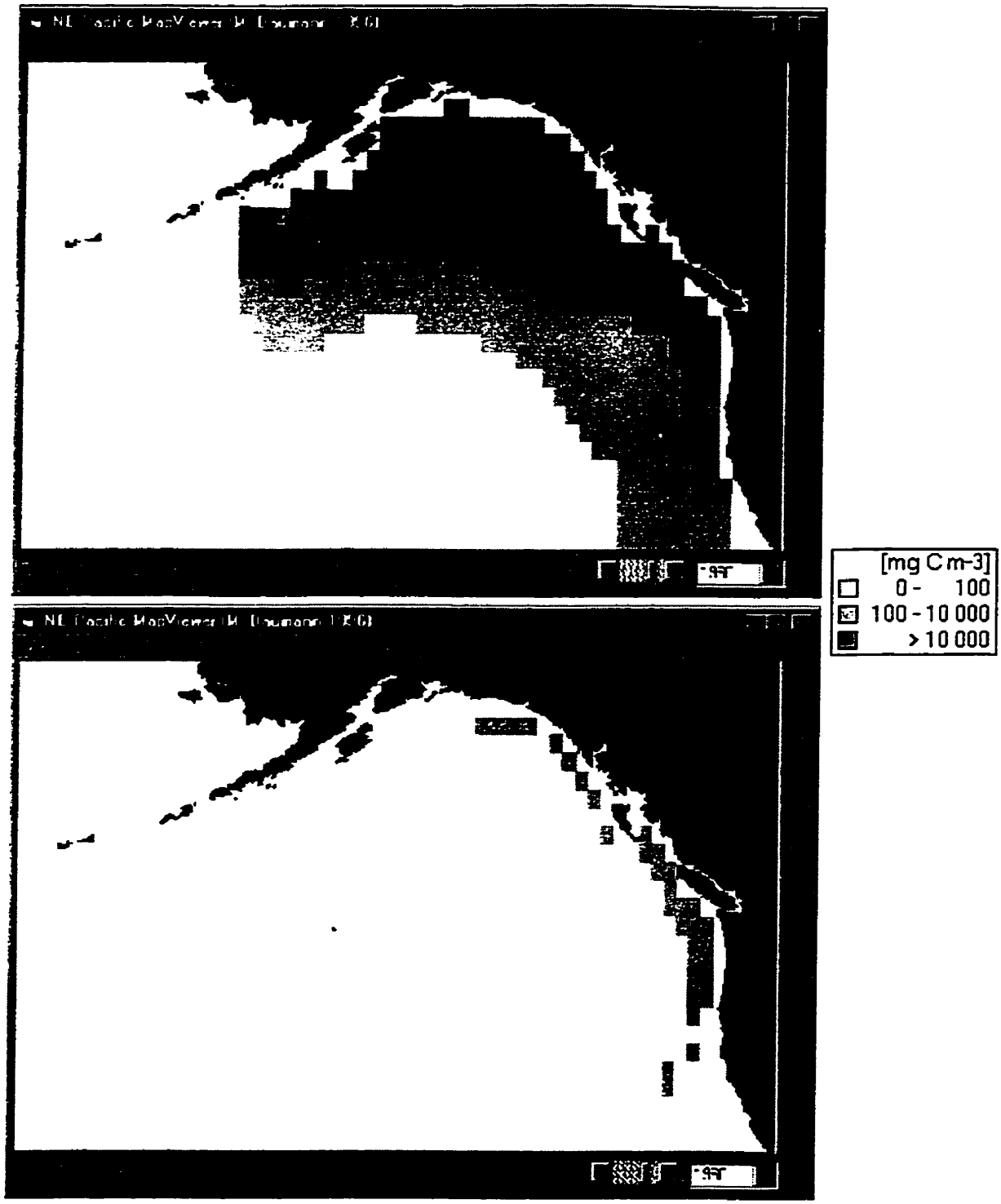


Fig. 4.4: Simulated biomass concentration [mg C m^{-3}] for October 1960 (after 10 years of simulation). Upper panel: Zero-gradient boundary conditions. Lower panel: Combined zero / zero-gradient boundary conditions. Simulation included advection but no biological processes. Initial (30 Dec 1950) biomass concentration for all open ocean fields was 1 mg C m^{-3}.

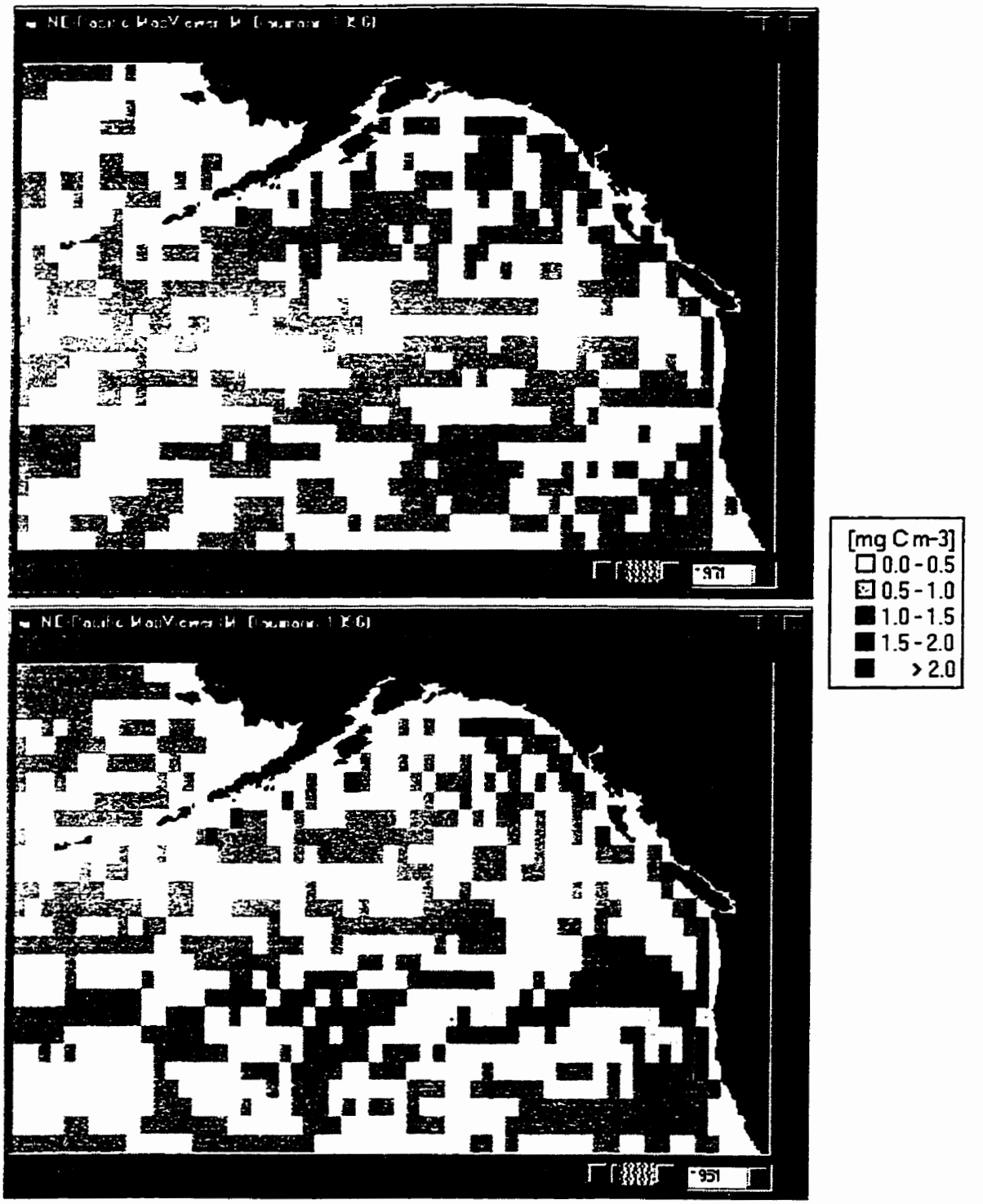


Fig. 4.5: Simulated biomass concentration [mg C m^{-3}] from two runs with random initial conditions. Simulations included advection (but no biological processes) with combined zero / zero-gradient boundary conditions (see text). First two panels show January, second two panels October biomass concentrations.

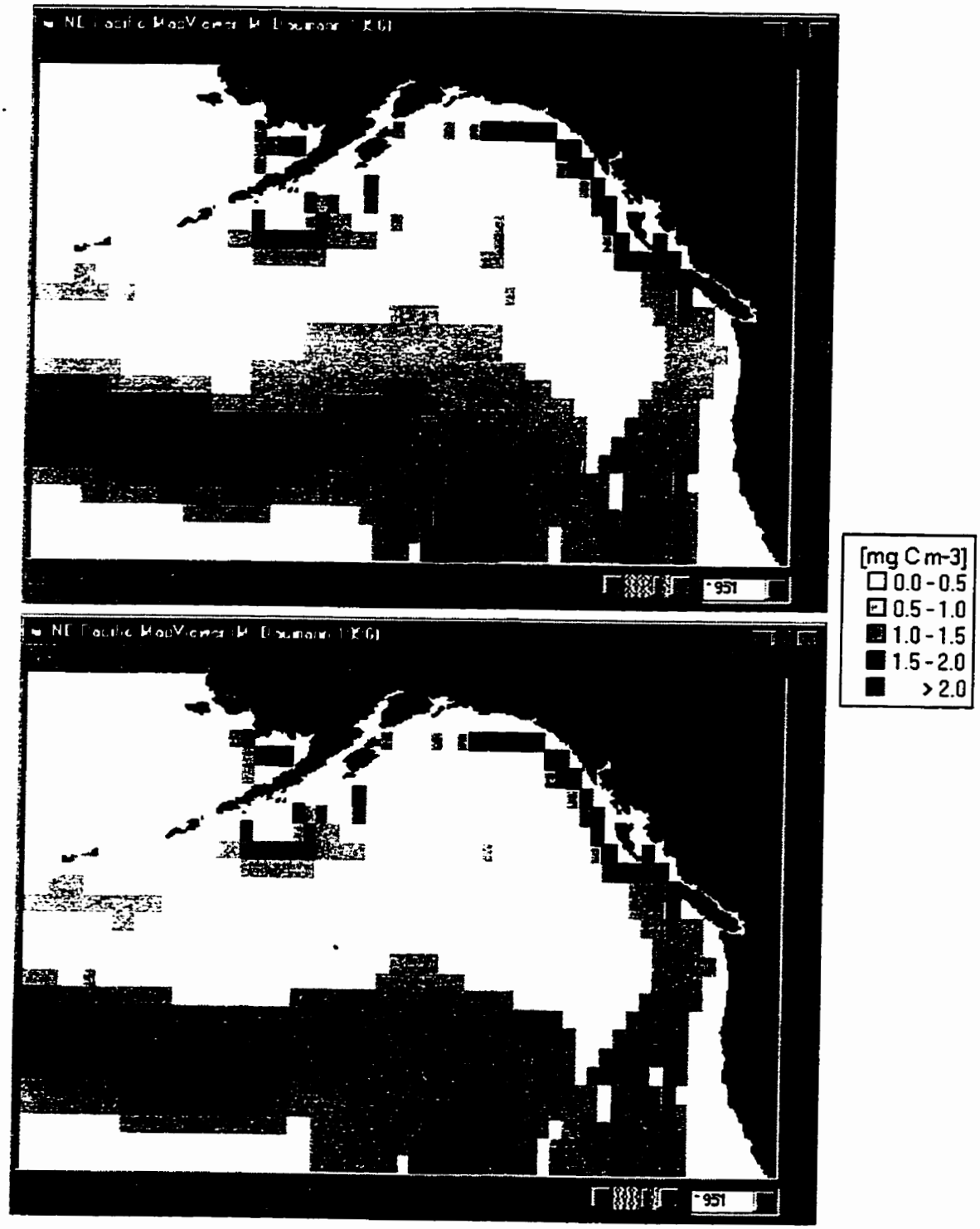


Fig. 4.5: Continued

4.2. Simulation Results and Analysis

While my models and simulations have the potential to address many specific questions about the ecosystem of the Northeast Pacific, the evaluation of outputs has various interpretive pitfalls starting at the level of quality, and spatial and temporal resolution of the input data to the mechanics represented in the models. I set the following minimum requirements for model validation:

(1) Empirical Validation: Models must be consistent with *relevant* observational data, thus incorporating *justifiable* mechanisms at the correct spatial and temporal scales (a basic requirement lacking in some of the 1-dimensional ecosystem models of the Northeast Pacific Ocean funded by GLOBEC).

(2) Operational Validation: The simulations must be able to provide answers to the question for which I have designed the models.

4.2.1. Empirical Validation

Only a few spatially-explicit datasets are available for empirical validation of model results. In cases where no observational data were available I analyzed the model starting with the *intuitively* most realistic model representation of natural processes in the ecosystem of the Northeast Pacific, i.e. the simulation of the 4-trophic levels model including advection, and working my way backwards via the 3-trophic levels model including advection, and the 4-trophic levels and 3-trophic levels models without advection. The effort was directed towards plausible(!) explanations of discrepancies between simulation results and current knowledge in

the light of the simplification process that necessarily must occur with model design (see Chapter 7 in Holling 1978).

Nonetheless, let me emphasize that ecological processes occur at various organizational, spatial and temporal scales, which generate characteristic patterns in the natural environment (e.g. food webs, biogeographical distribution). Unfortunately, similar processes do not always result in similar patterns, and similar patterns can often be explained by a variety of processes. Consequently, causation in ecosystems is a relatively simple task and one must be cautious (as an analyst as well as a reader) when identifying the 'true' mechanism.

Seasonal and Interannual Variability: Primary Productivity

The spatial evolution of simulated daily primary productivity (Fig. 4.6) follows qualitatively that which has been inferred from estimations of the critical depth and the mixed layer depth, as well as from zooplankton data (Fig. 2.4; Parsons *et al.* 1966; Parsons & LeBrasseur 1968). However, the development of the horseshoe-shaped pattern of increased daily primary productivity in spring occurs about three months later in simulations than in Parsons et al.'s results. This time lag has two potential explanations:

(1) Simulation results (Fig. 4.6) and observations (Fig. 2.4) do not cover the same years. This is true, as Parsons *et al.* (1966) used composite data from various sources for the years 1947 to 1963 while I present 1982 and 1983 simulation results. However, their result is a conceptual model of the average spatio-temporal onset of the "spring bloom", i.e. when critical depth becomes shallower than mixed layer depth, rather than actual data. Also, the reason why I have mapped the spatio-temporal evolution of daily primary production for 1982 and 1983 is that these two years represent two very different oceanographic conditions in the Northeast Pacific

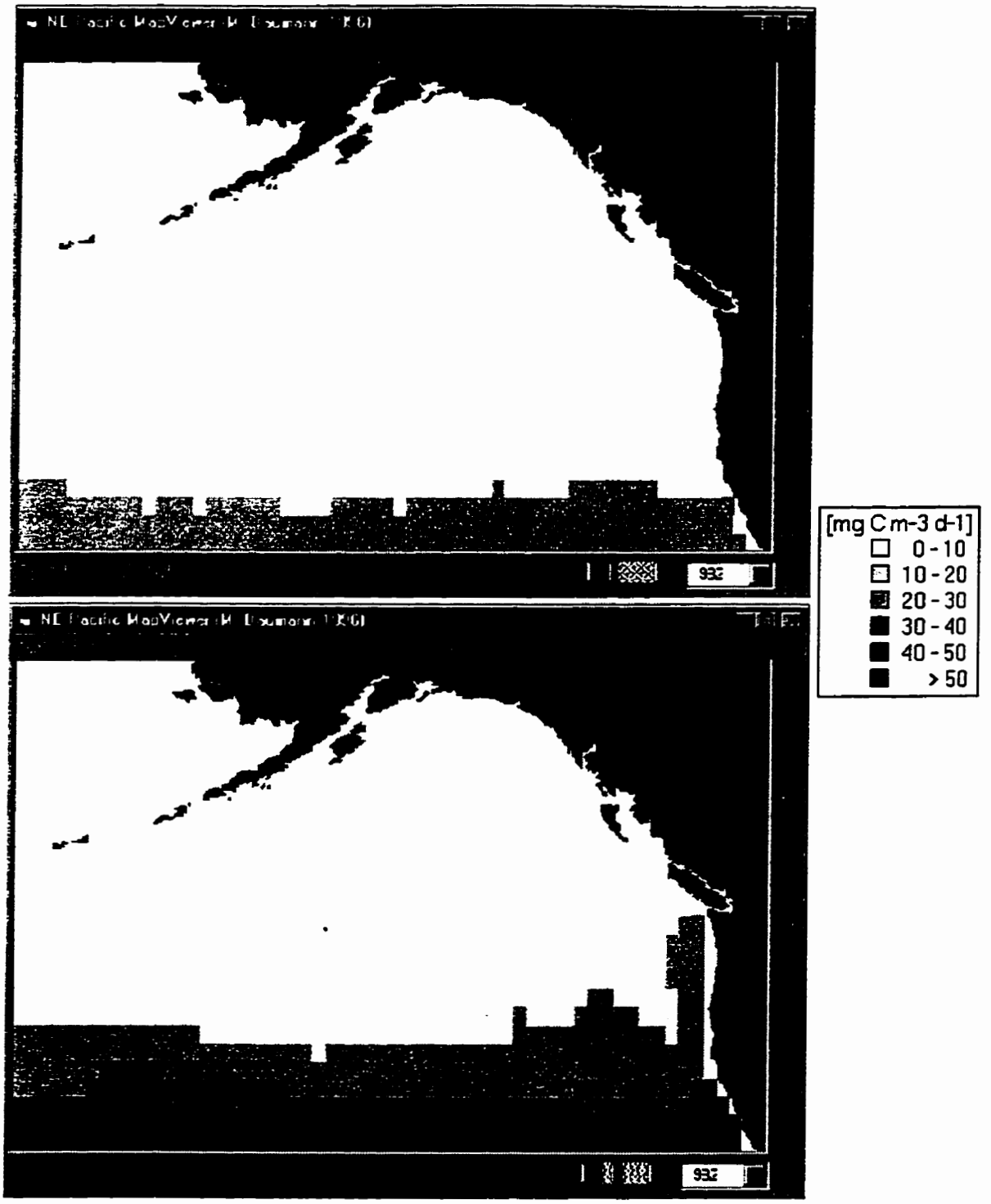


Fig. 4.6: Simulated daily primary productivity [mg C m^{-3} d^{-1}] for January, April, July and October of 1982 and 1983.

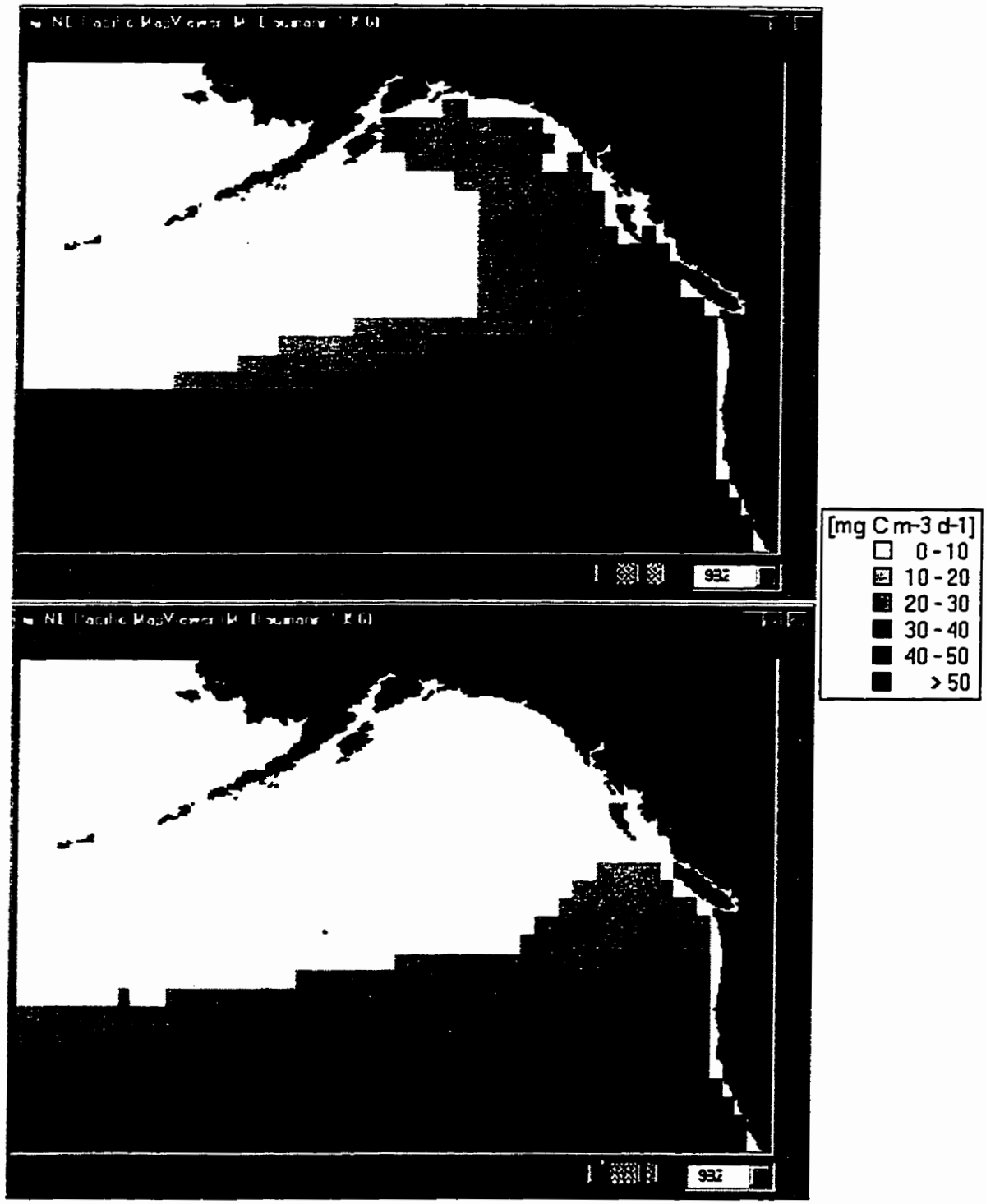
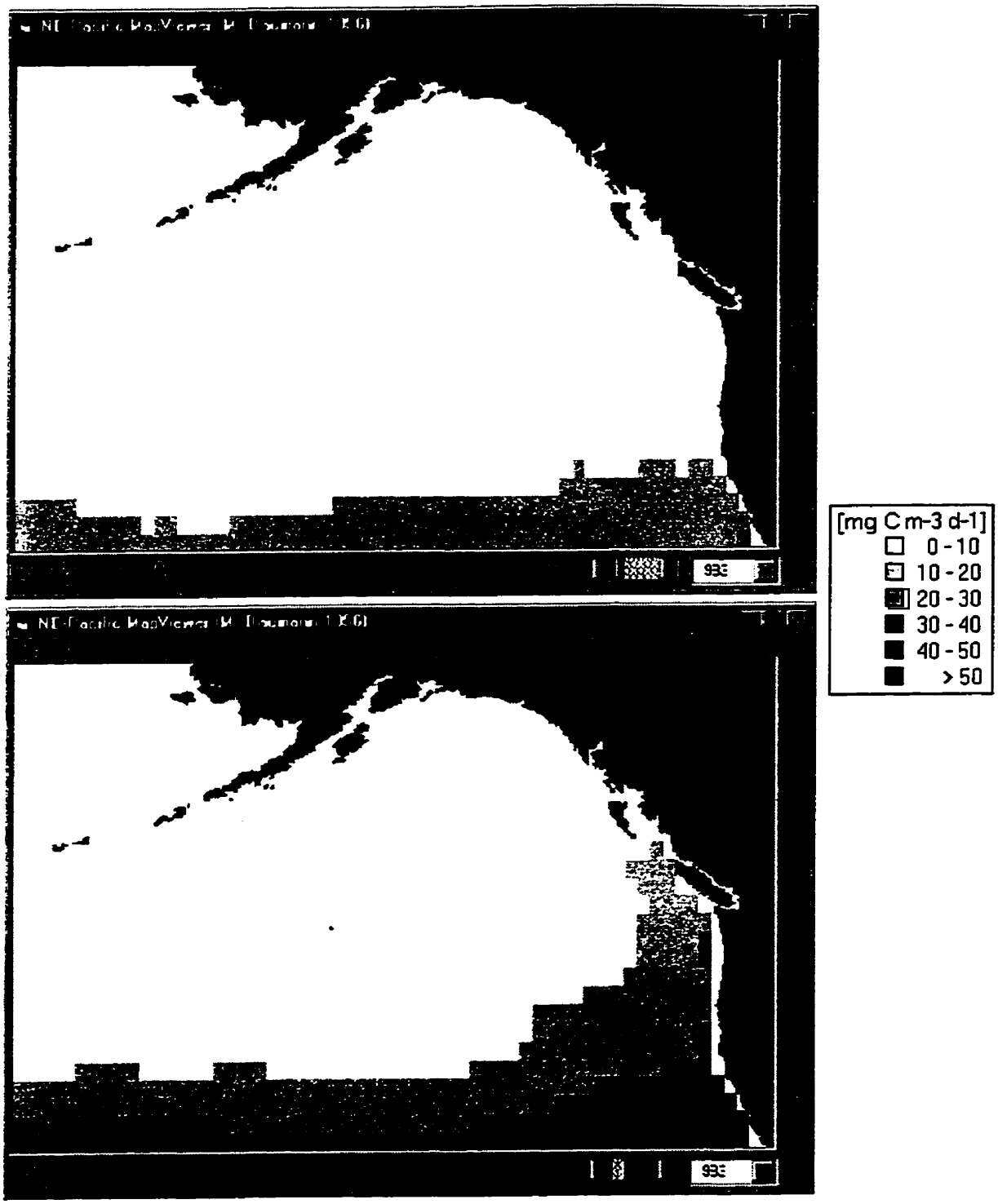


Fig. 4.6: Continued



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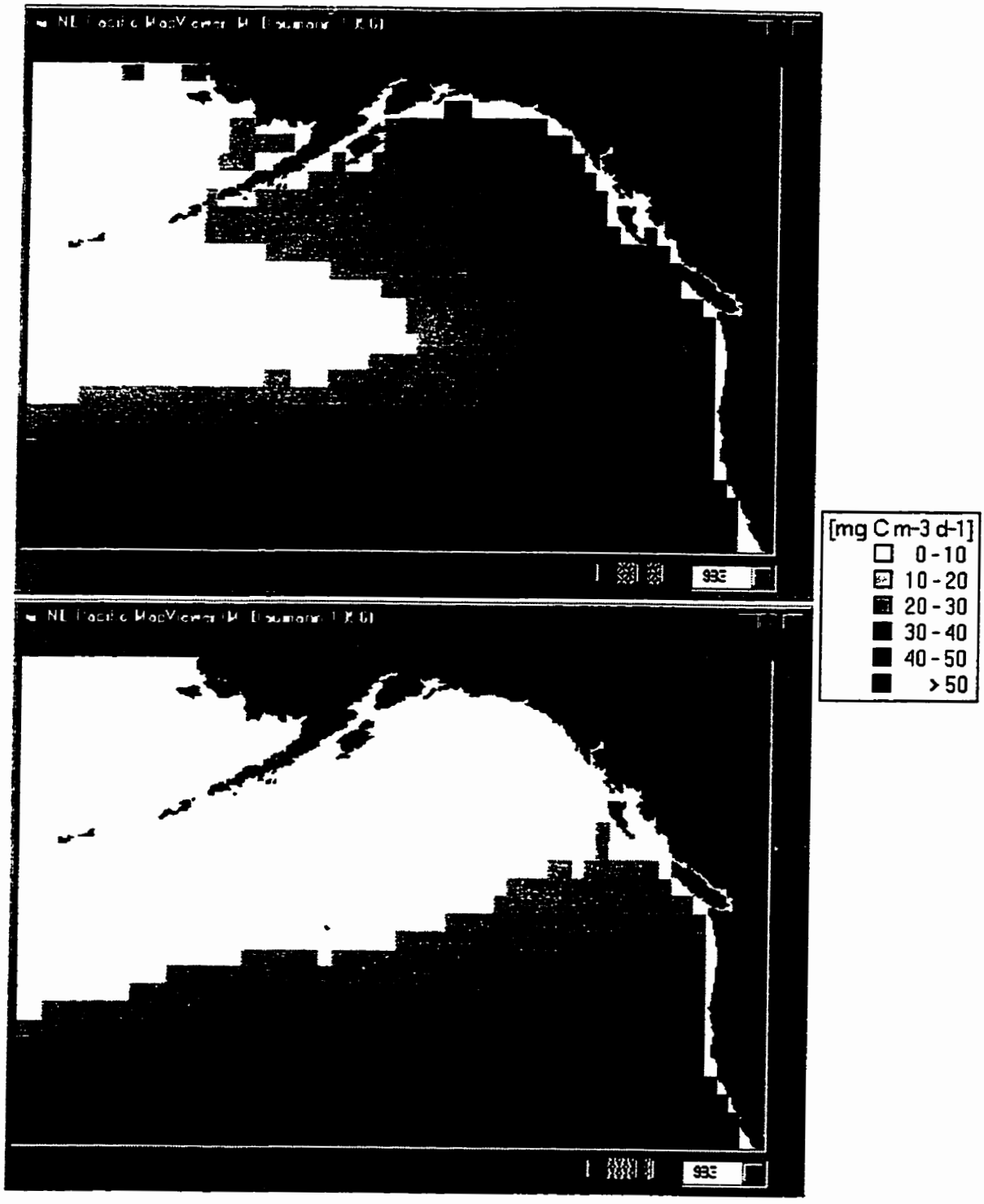


Fig. 4.6: Continued

(Brodeur & Pearcy 1992): rather low temperatures in 1982; and very warm conditions in 1983, caused by the 1982/83 El Niño-Southern Oscillation (ENSO) event, the strongest on record before 1997.

(2) The time lag between simulated and observed primary productivity increase is caused by the way primary productivity is modeled (see Eq. 3.13g). Primary productivity is a nonlinear function of various environmental variables (i.e. mixed layer depth, sea surface temperature, daily photosynthetically active radiation, and the carbon-to-chlorophyll-a ratio) as well as the chlorophyll-a concentration, which has been defined constant throughout the year, and the photosynthetic efficiency, which represents the initial slope of the photosynthesis vs. irradiance curve. Except for sea-surface temperature, which is an observed variable (Subsection 3.2.1), each of the environmental variables is itself a nonlinear function of one or more other environmental variables (e.g. mixed layer depth is a function of sea surface temperature and scalar wind speed (Subsection 3.2.2)). Consequently, any of the functional relationships relating these variables or parameters to primary production has the potential to cause this time lag.

As for interannual variability, simulation results show that while January conditions in 1982 and 1983 are very similar (Fig. 4.6), the increase in primary productivity progresses northward faster in spring 1983 although with less of a latitudinal gradient. In July and August of both years the front of increased primary production reaches its northernmost point with a horseshoe-shaped coastal maximum. In 1983 the primary production front reaches further northward and has higher coastal maxima than in 1982. By fall 1983 the effects of the 1982/83 ENSO-event have almost completely disappeared with respect to primary productivity.

Seasonal and Interannual Variability: Herbivores (Microzooplankton)

No observational data on the seasonal, annual or decadal spatio-temporal distribution of microzooplankton in the Northeast Pacific are available.

Results from the 4-trophic level simulation with advection show that microzooplankton biomass concentrations (Fig. 4.7) exhibit spatio-temporal patterns that are similar to those of primary productivity (Fig. 4.6). This is not surprising because:

(1) daily herbivore assimilation was defined to be equal to daily primary production (Eq. 3.8), and

(2) mesozooplankton density is strongly reduced in the winter month (Fig. 4.8), due to a combination of lack of primary production and high predation pressure from a large macrozooplankton standing stock (Fig. 4.9).

Thus microzooplankton is effectively uncontrolled in early spring and accumulates quickly, even preceding the front of increased primary productivity (compare Figs. 4.7 and 4.6). On the other hand results obtained from the 3-trophic level simulation with advection show much less similarity in patterns between microzooplankton biomass concentrations (Fig. 4.10) and daily primary productivity (Fig. 4.7). This is because, in this case, mesozooplankton concentrations are not being regulated by a higher trophic level, mesozooplankton can build up biomass quickly in spring and thus control microzooplankton standing stock effectively.

Further, as can be seen from the 4-trophic levels simulations the consequences of the 1982/83 El Niño do not manifest themselves in the microzooplankton standing stock and primary production in the Northeast Pacific until late spring 1983, and have disappeared by fall (Fig.4.7). A comparison of simulation results with and without advection shows that advection had only minor effects on microzooplankton spatio-temporal distribution patterns in the 4-trophic levels

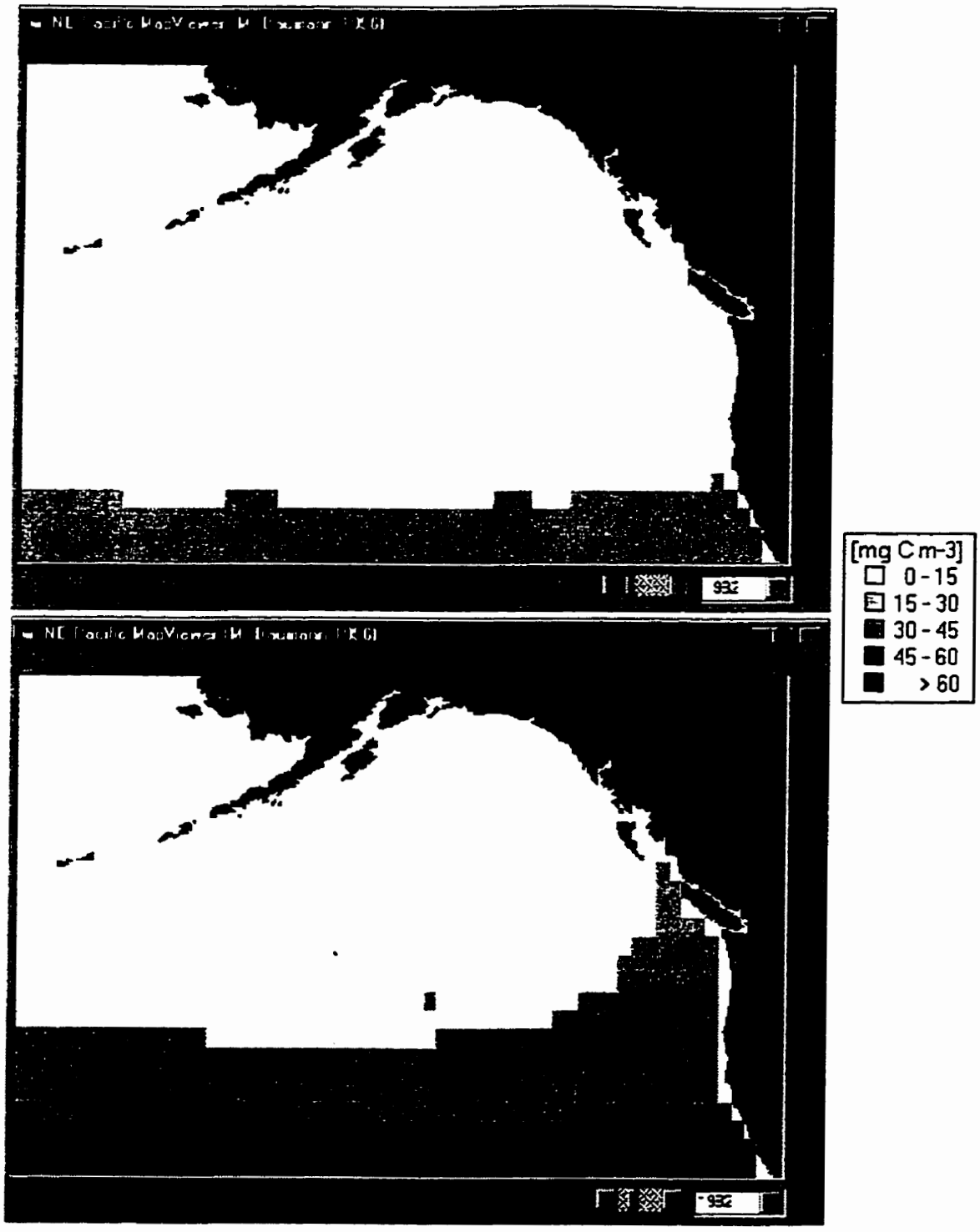


Fig. 4.7: Simulated microzooplankton concentration [mg C m^{-3}] for January, April, July and October of 1982 and 1983. Simulation: 4-trophic levels models with advection. Simulation period: 1951-1990.

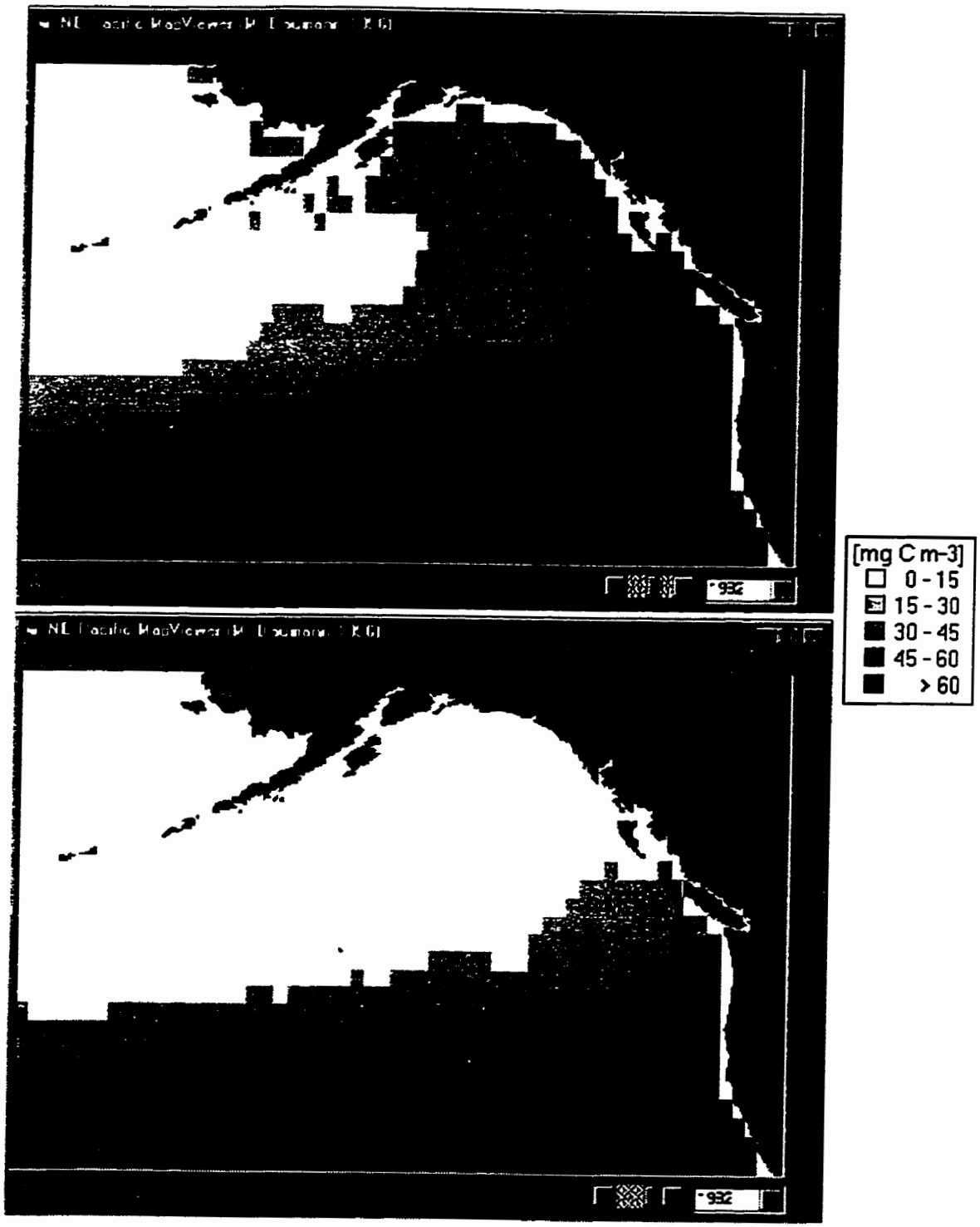
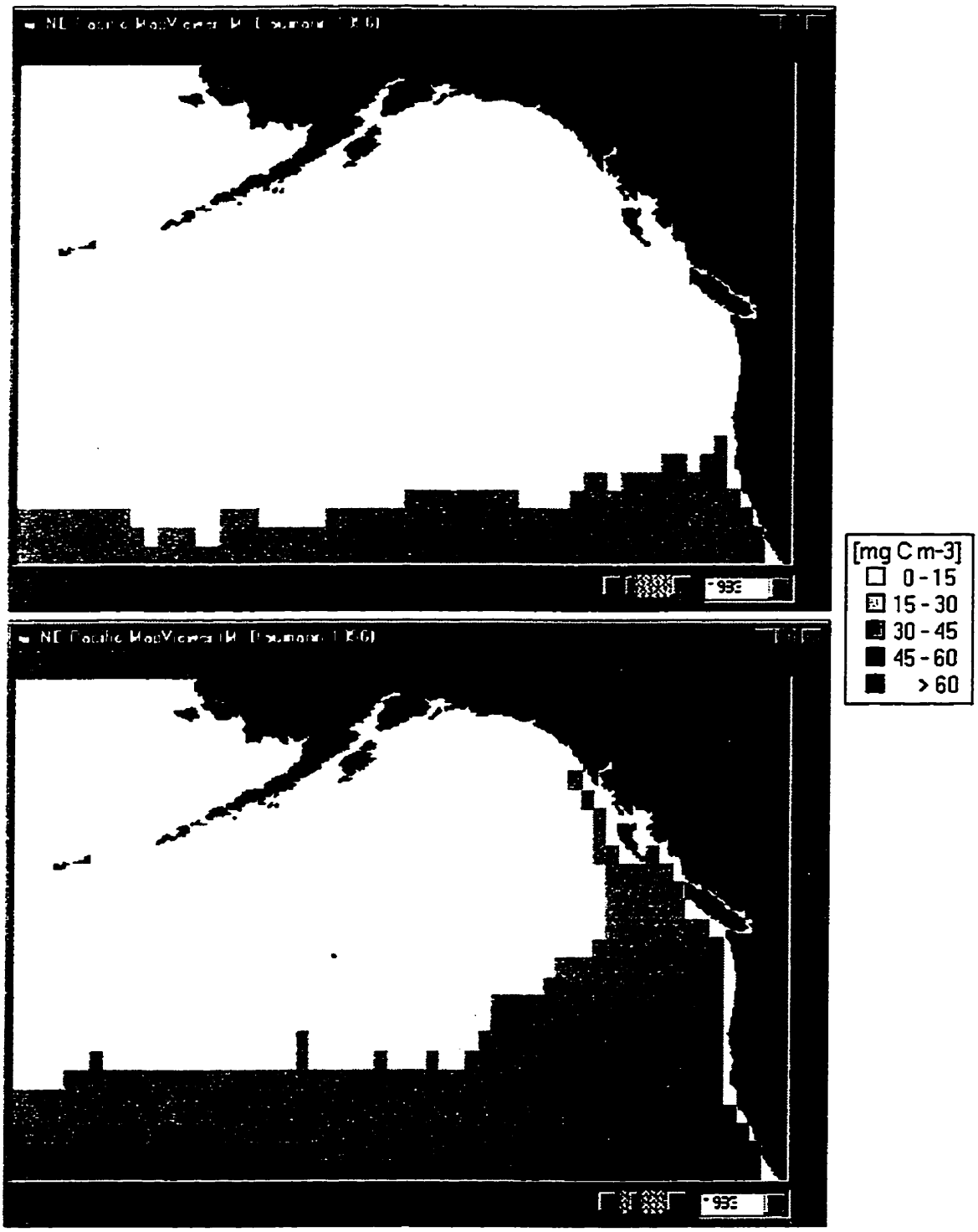


Fig. 4.7: Continued



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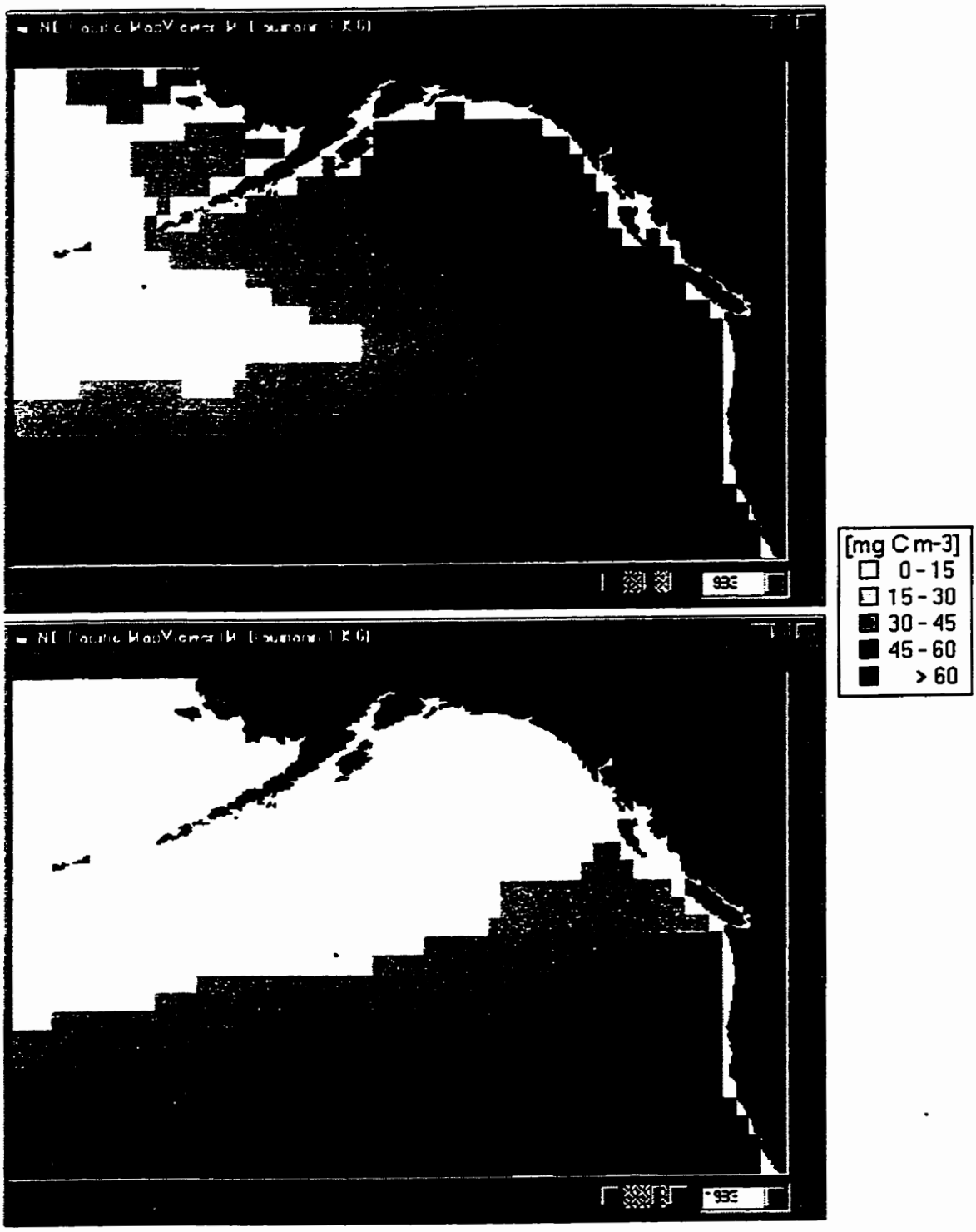


Fig. 4.7: Continued

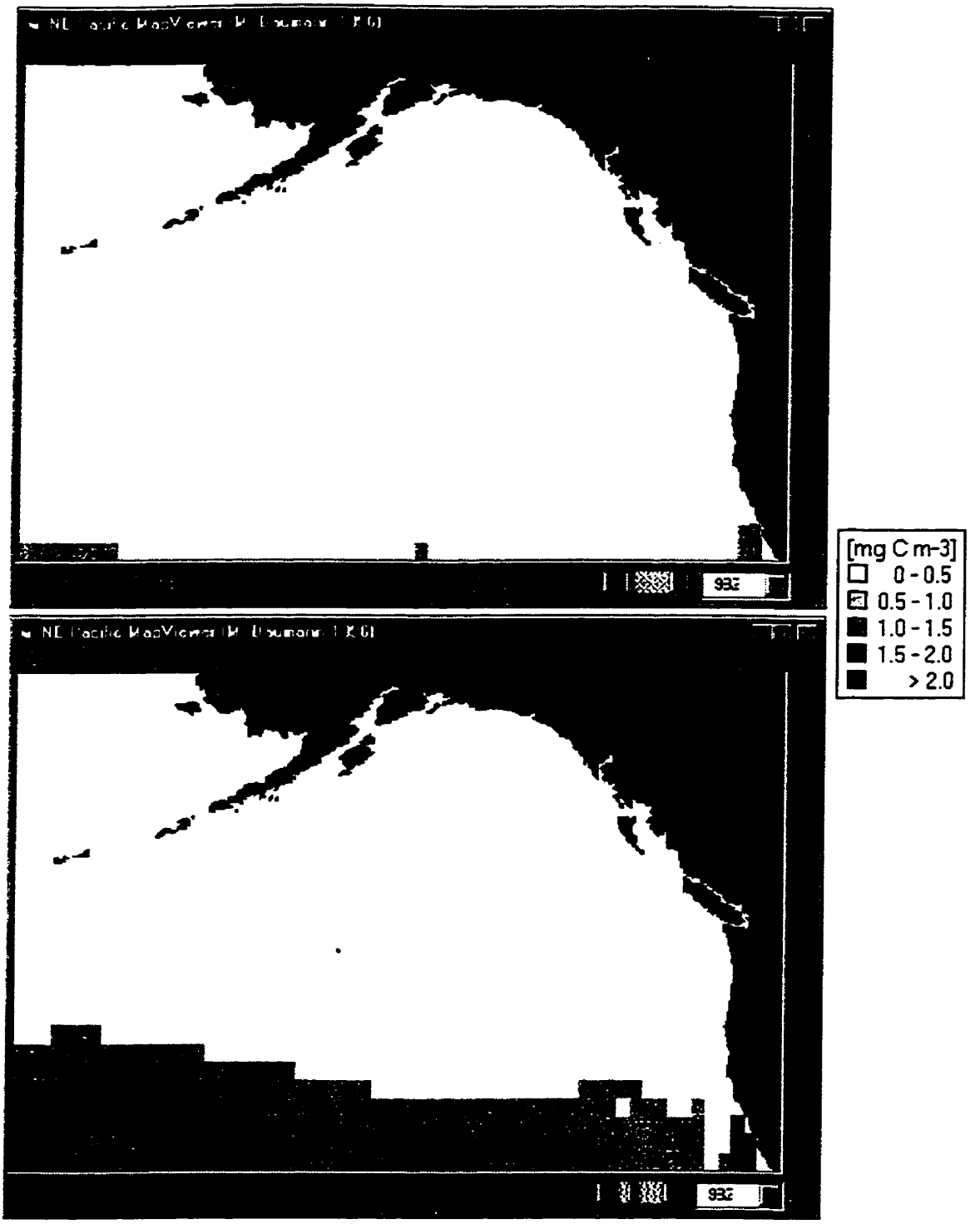


Fig. 4.8: Simulated mesozooplankton concentration [mg C m^{-3}] for January, April, July and October of 1982 and 1983. Simulation: 4-trophic levels models with advection. Simulation period: 1951-1990.

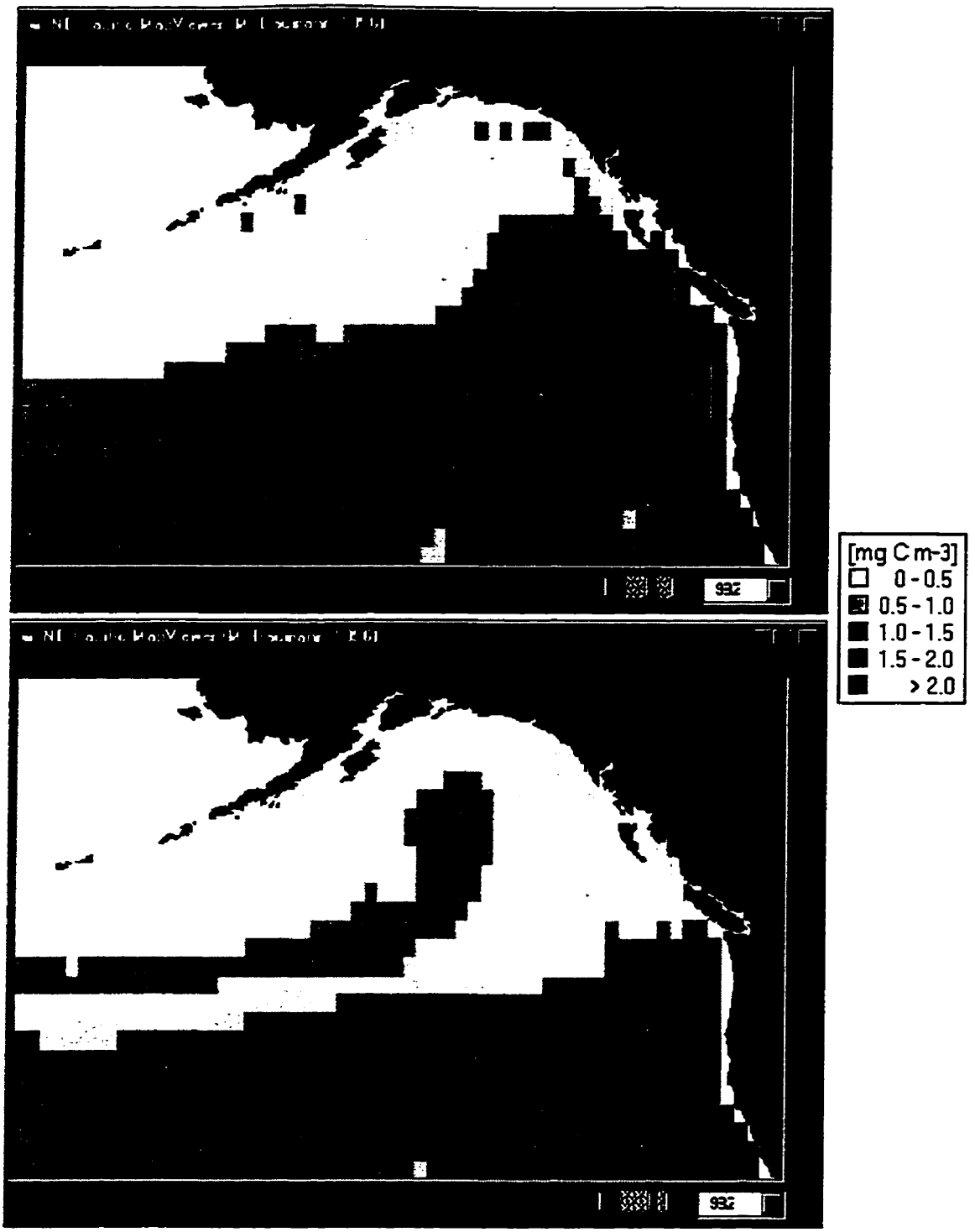
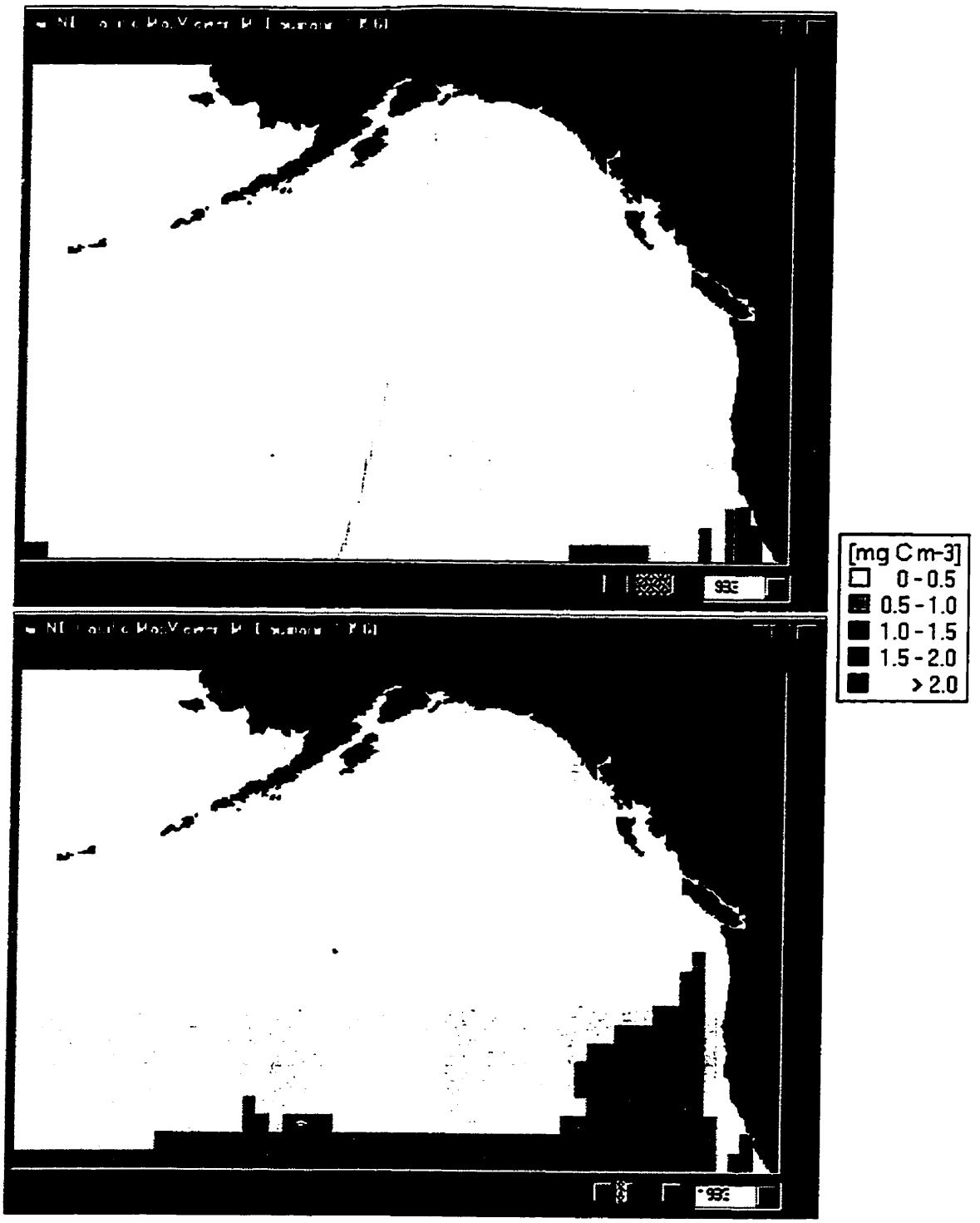


Fig. 4.8: Continued



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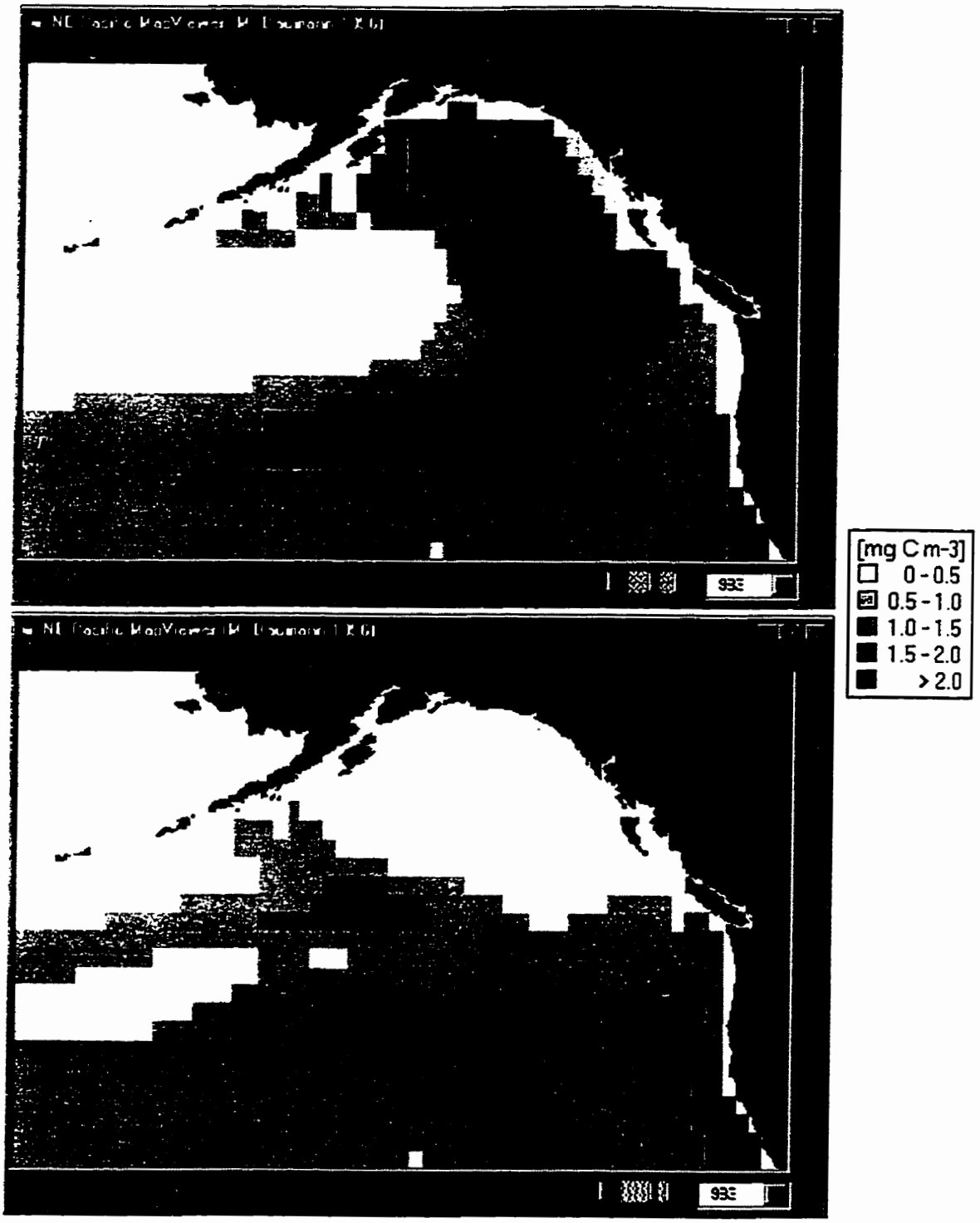

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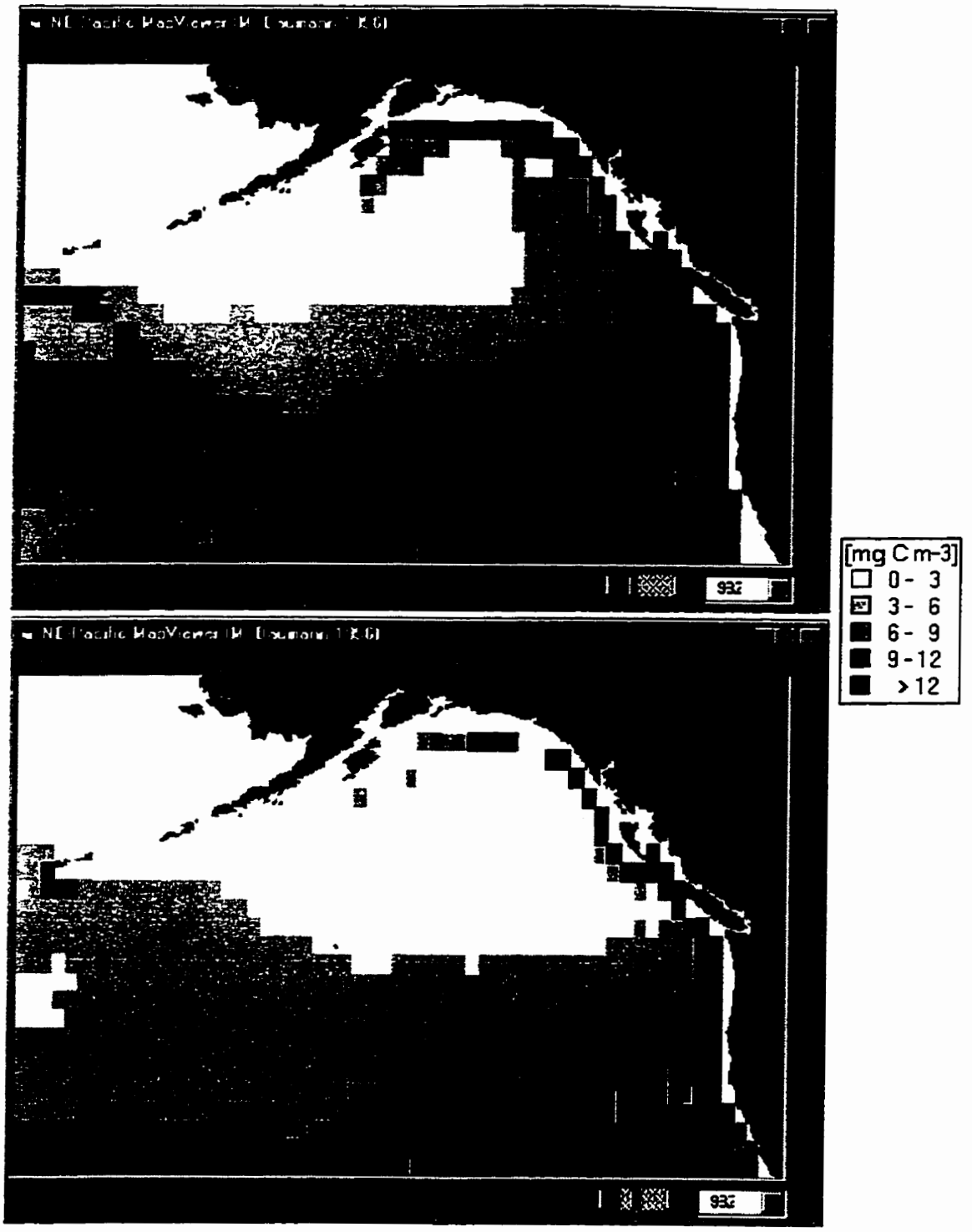


Fig. 4.9: Simulated macrozooplankton concentration [mg C m^{-3}] for January, April, July and October of 1982 and 1983. Simulation: 4-trophic levels models with advection. Simulation period: 1951-1990.

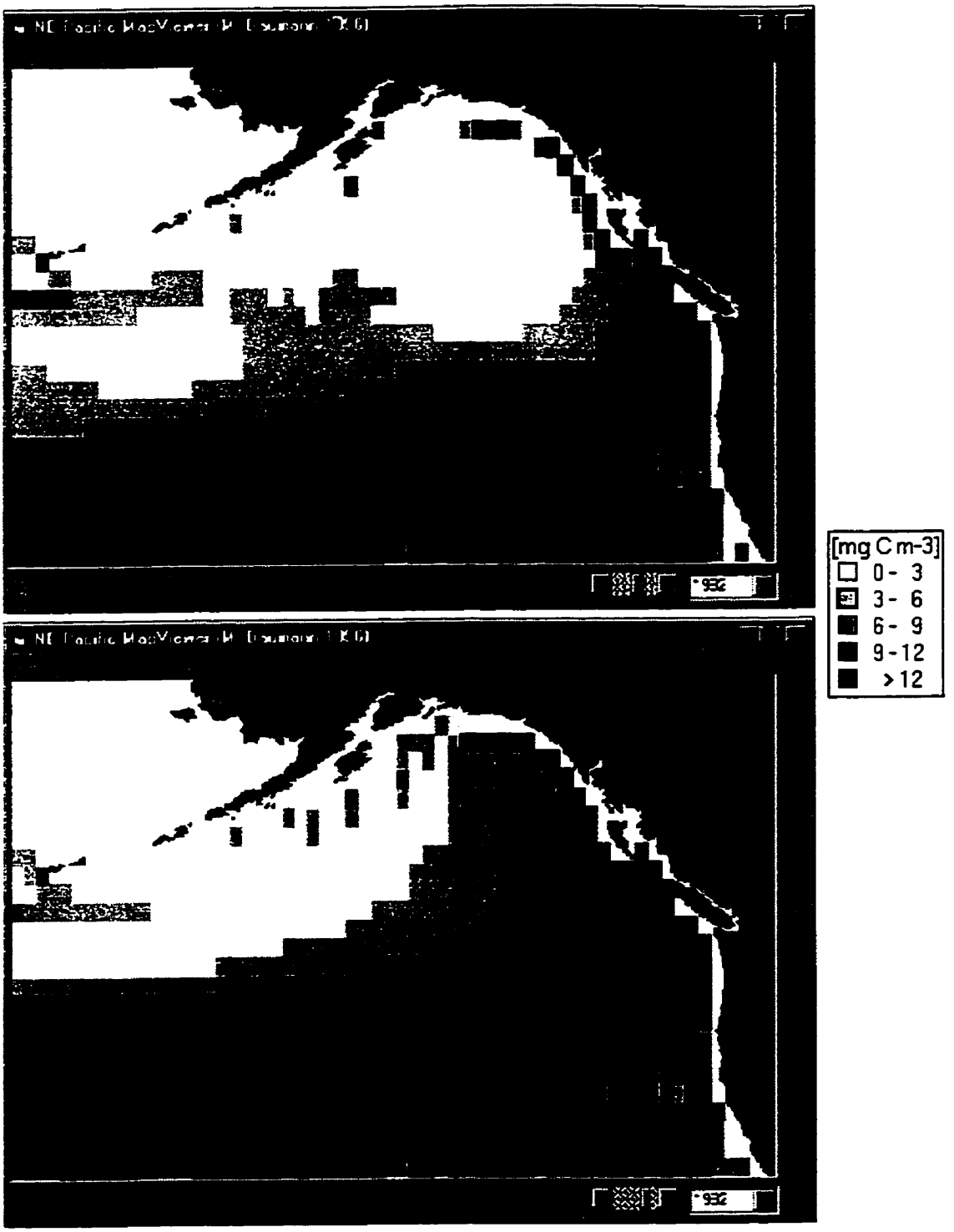
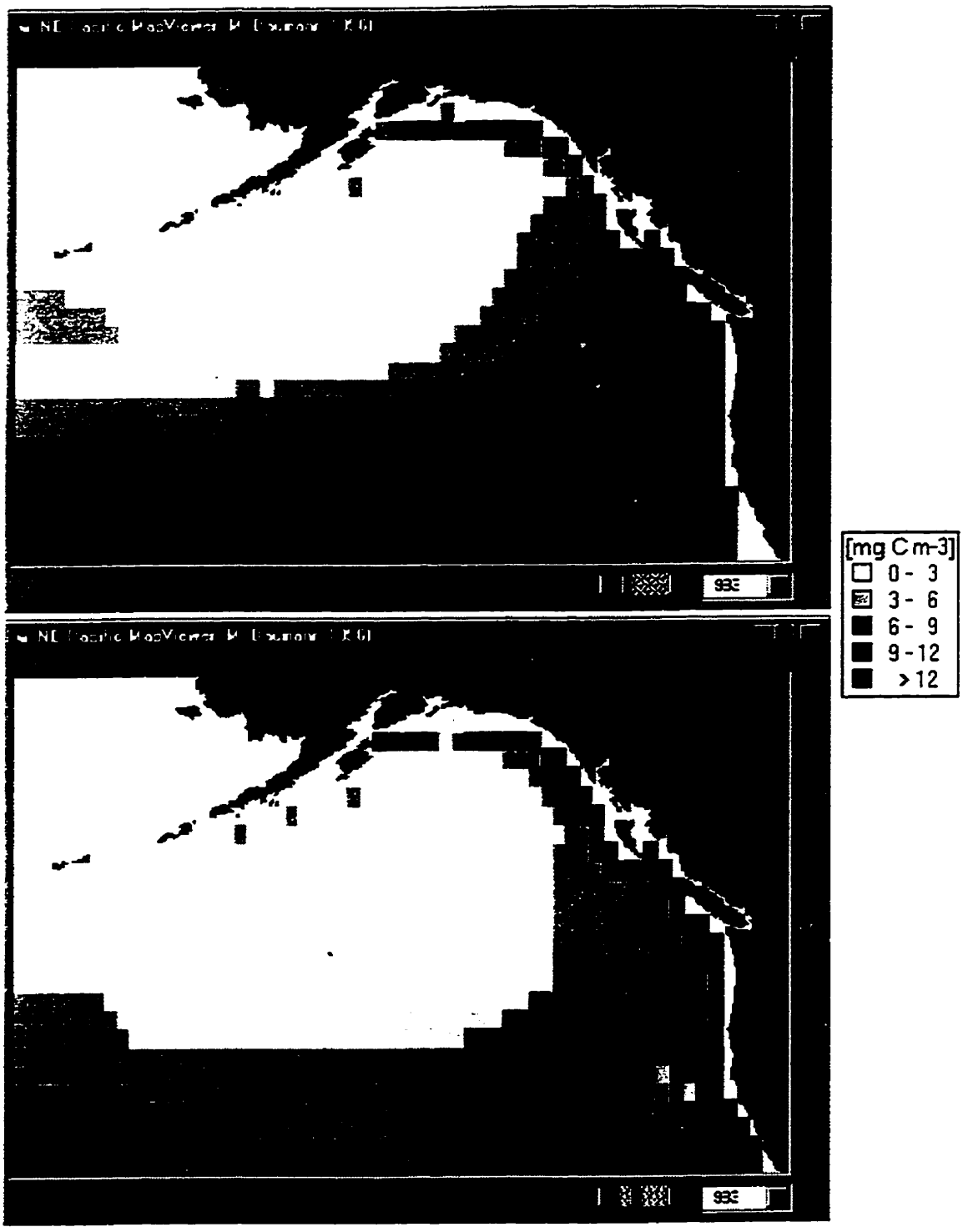


Fig. 4.9: Continued



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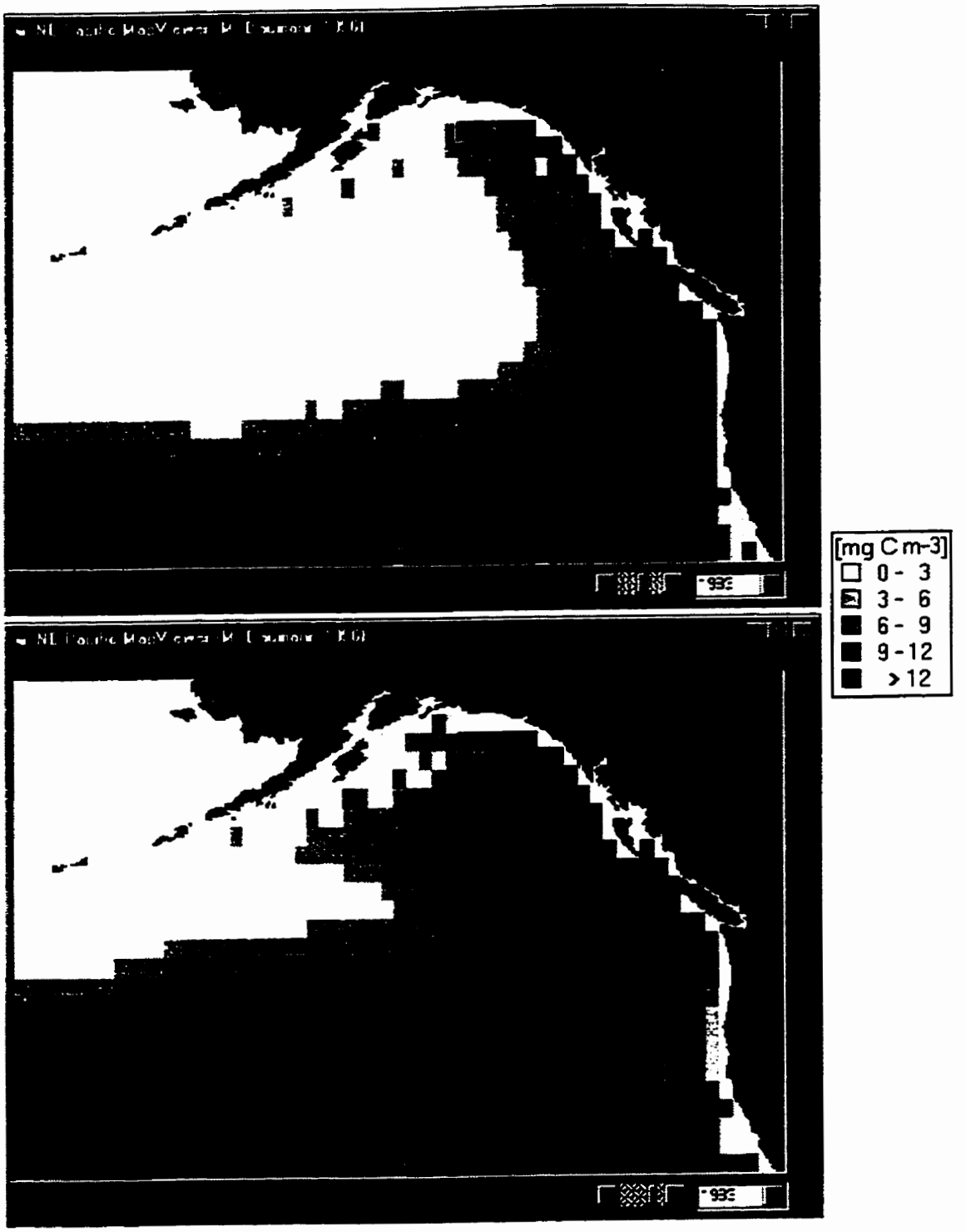


Fig. 4.9: Continued

model in both years (compare Figs. 4.7 and 4.11), while in the 3-trophic levels simulations advection had a much larger effect on the spatio-temporal distribution of microzooplankton in 1982 than in the 1983-El Niño year (compare Figs. 4.10 and 4.12).

Seasonal and Interannual Variability Carnivores 1 (Mesozooplankton)

The spatio-temporal distribution of mesozooplankton is of greatest interest to this study as it is the size class that represents the most important food source for oceangoing juvenile sockeye salmon (see Conjecture in Section 1.4; see also Section 2.1. and Subsection 4.2.2).

A comparison of simulation results with data shows that the spatio-temporal increase in mesozooplankton concentration in the 4-trophic level simulation (Fig. 4.8) occurs about three months later than indicated in the data (Fig. 2.4; Parsons *et al.* 1966). This discrepancy can be explained by the following:

(1) Copepod species collected by Parsons *et al.* (1966) are not represented in the model. As pointed out in 3.4. Mean Field Simulations, there is no information available on what determines the time of ascent and descent in the ontogenetic migration of *Neocalanus* species (the dominant copepods in the Northeast Pacific; see Section 2.2.), nor what determines the survival of *Neocalanus* species at depth. Consequently, I had no other choice than excluding them from my simulations.

(2) It may well be that copepods that have been collected at near-coast locations were actually produced in coastal ecosystems and were then transported into the open ocean regions by surface currents (a possibility implicit in the modeling results described in 4.1. Spatio-Temporal Resolution And Advection: *Spatial Closure*). However, the coastal ecosystems have not been modeled at all (see Section 3.1.).

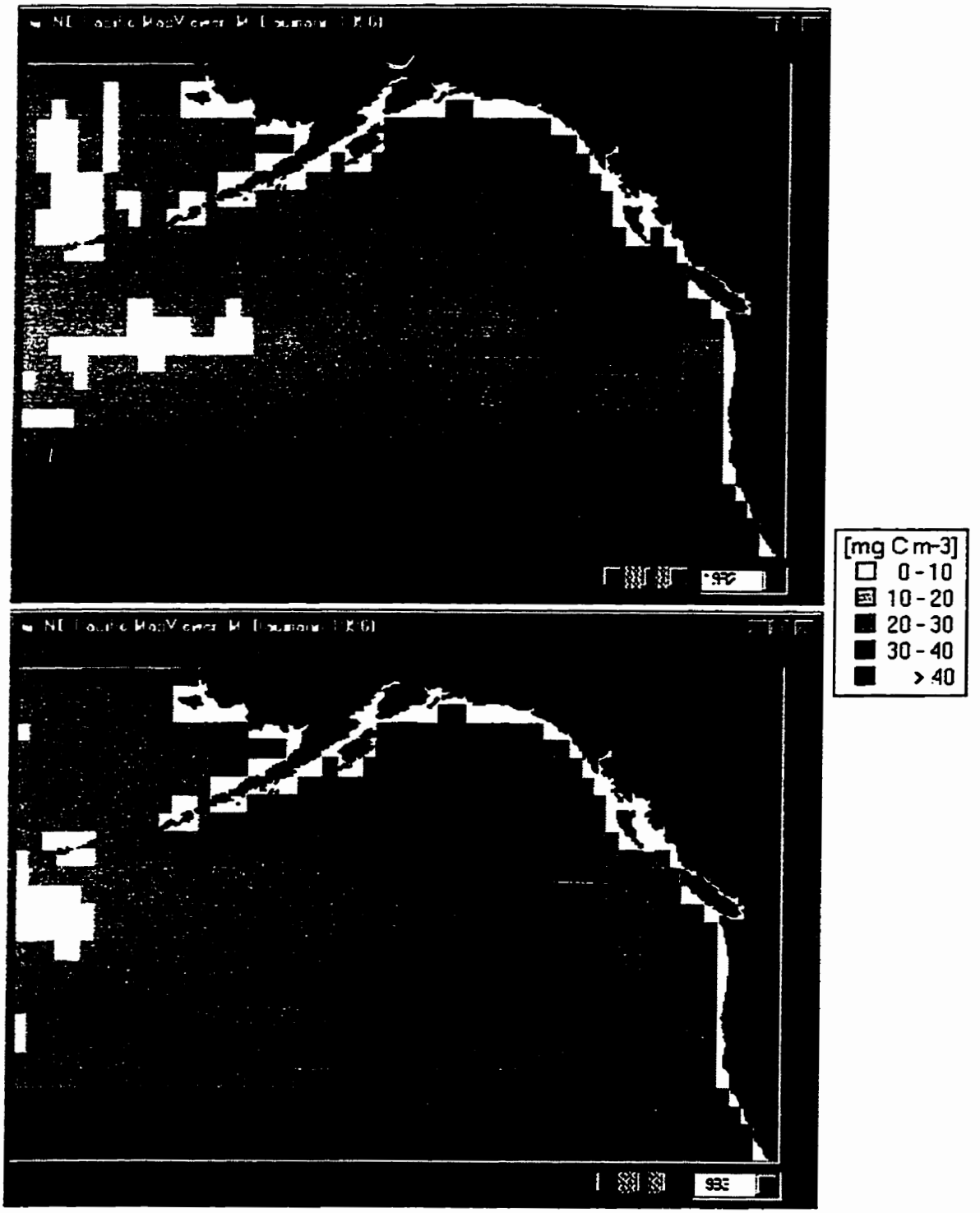


Fig. 4.10: Simulated microzooplankton concentration [mg C m^{-3}] for July of 1982 (upper panel) and 1983 (lower panel). Simulation: 3-trophic levels models with advection. Simulation period: 1951-1990. Note the different scaling of biomass concentrations compared to Fig. 4.6.

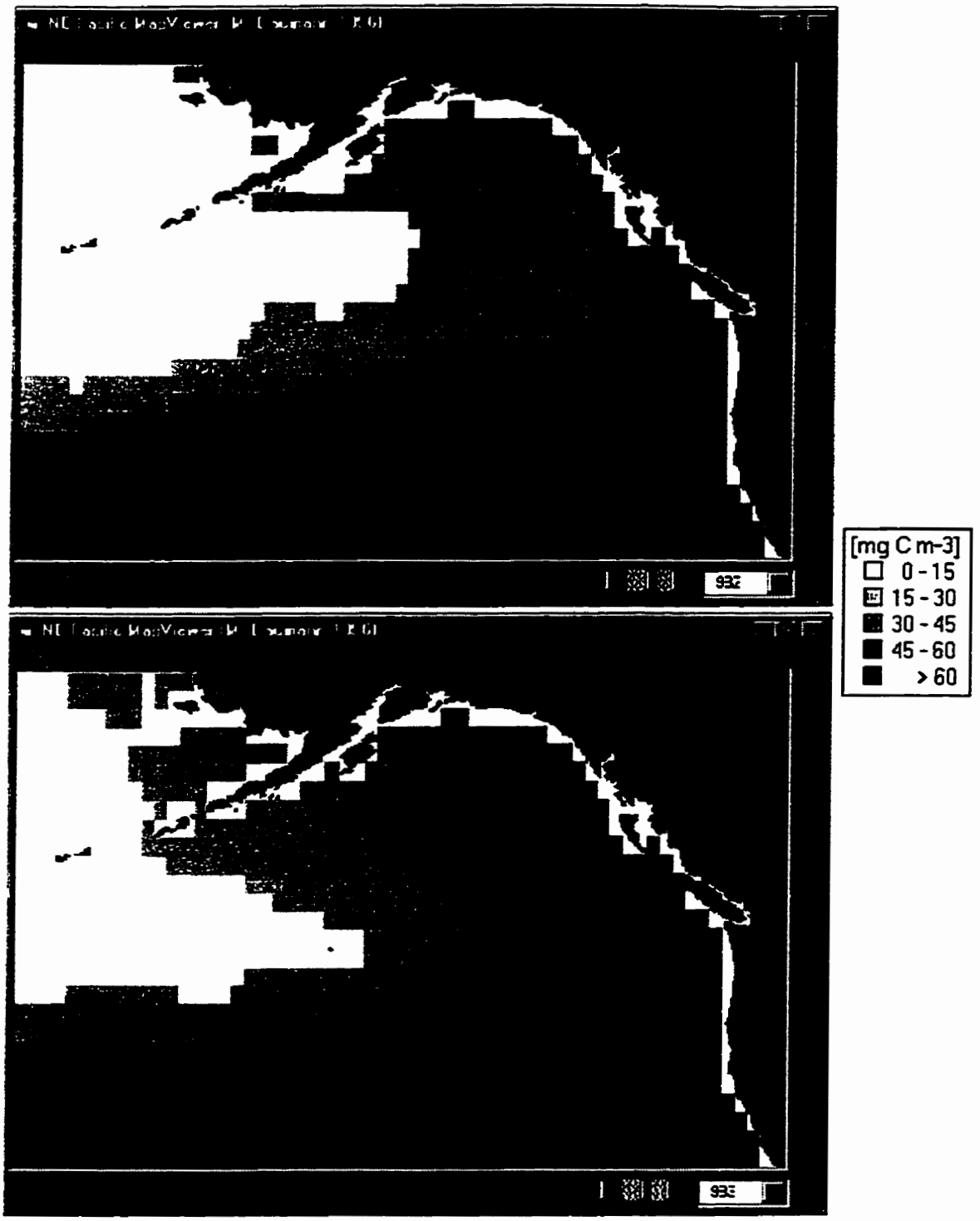


Fig. 4.11: Simulated microzooplankton concentration [mg C m^{-3}] for July of 1982 (upper panel) and 1983 (lower panel). Simulation: 4-trophic levels models <u>without</u> advection. Simulation period: 1951-1990.

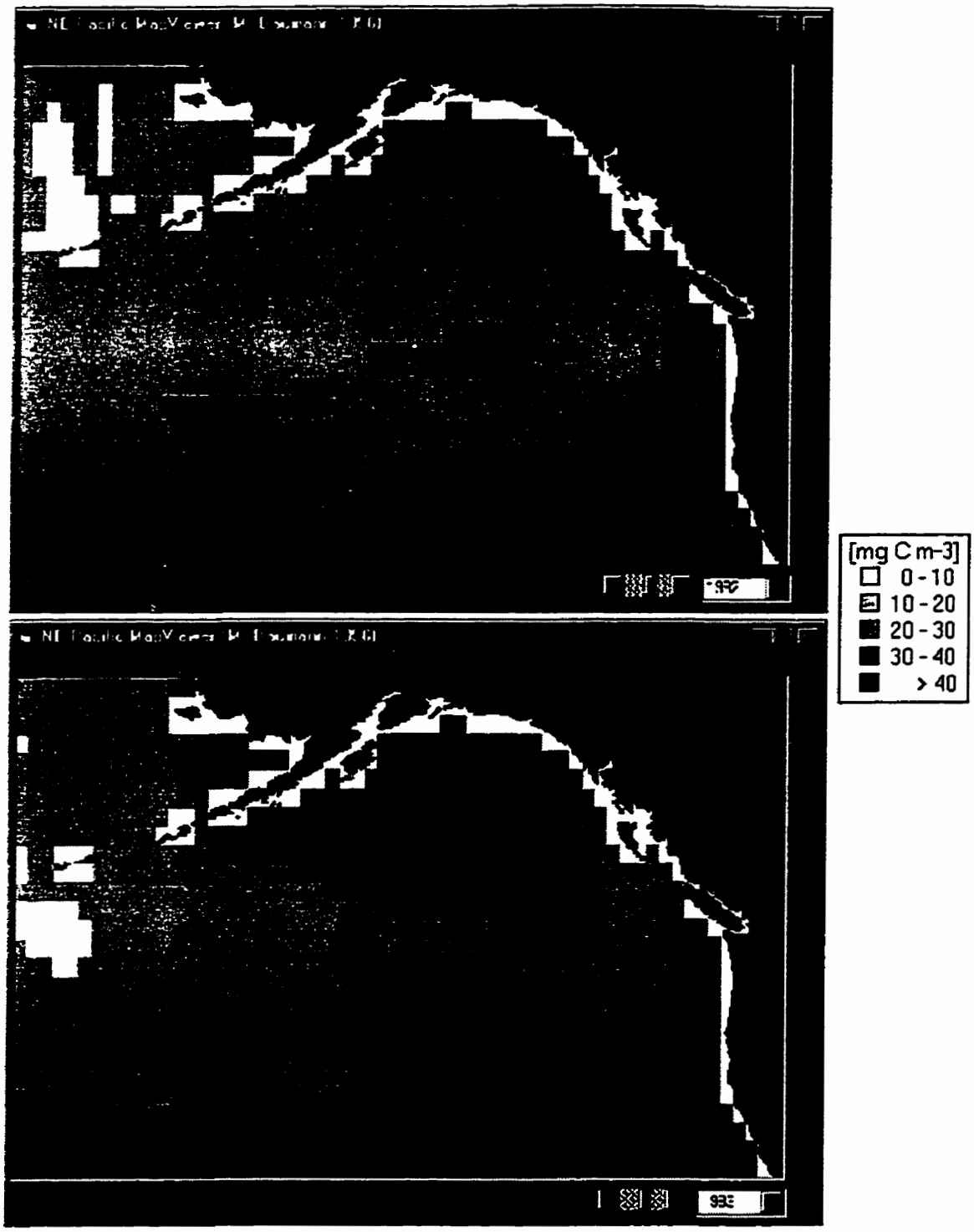


Fig. 4.12: Simulated microzooplankton concentration [mg C m^{-3}] for July of 1982 (upper panel) and 1983 (lower panel). Simulation: 3-trophic levels models without advection. Simulation period: 1951-1990.

Despite these two shortcomings the simulated mesozooplankton concentration attains the horseshoe-shaped structure in 1983 but not in 1982 (Fig. 4.8). Nevertheless, the horseshoe-shaped spatial distribution of mesozooplankton manifests itself in simulations of 1962 and 1963, the years where the data have been collected (Fig. 4.13).

While simulations using the 4-trophic levels model produce mesozooplankton concentrations that are within the observed range (for Station *P*: 0.5 - 3 mg C m^{-3}) simulated mesozooplankton densities from the 3-trophic levels are much too high (in certain areas by 2 orders of magnitude; see discussion in 3.4. Mean Field Simulations); however, the establishment of a horseshoe-shaped high-density belt for mesozooplankton around the edge of the Gulf of Alaska can still be observed in summer (Fig. 4.14). This pattern is clearer in 1983 than in 1982, just as in the 4-trophic levels simulation with advection.

Regarding the effects of surface currents, a comparison of the results of the 4-trophic levels simulation with (Fig. 4.8) and without advection (Fig. 4.15) shows that accumulation effects are again (as for microzooplankton) generally small but are larger in summer.

Seasonal and Interannual Variability: Carnivores 2 (Macrozooplankton)

No observational data on the seasonal, annual or decadal spatio-temporal distribution of macrozooplankton in the Northeast Pacific are available.

Simulated macrozooplankton concentrations (Fig. 4.9) appear to be more patchily distributed (on the large 1° longitude x 1° latitude scale) than concentrations of organisms from lower trophic levels (Figs. 4.7 and 4.8). A comparison of results from simulations with (Fig. 4.9) and without advection (Fig. 4.16) reveals that the patchiness is an effect of currents. Furthermore,

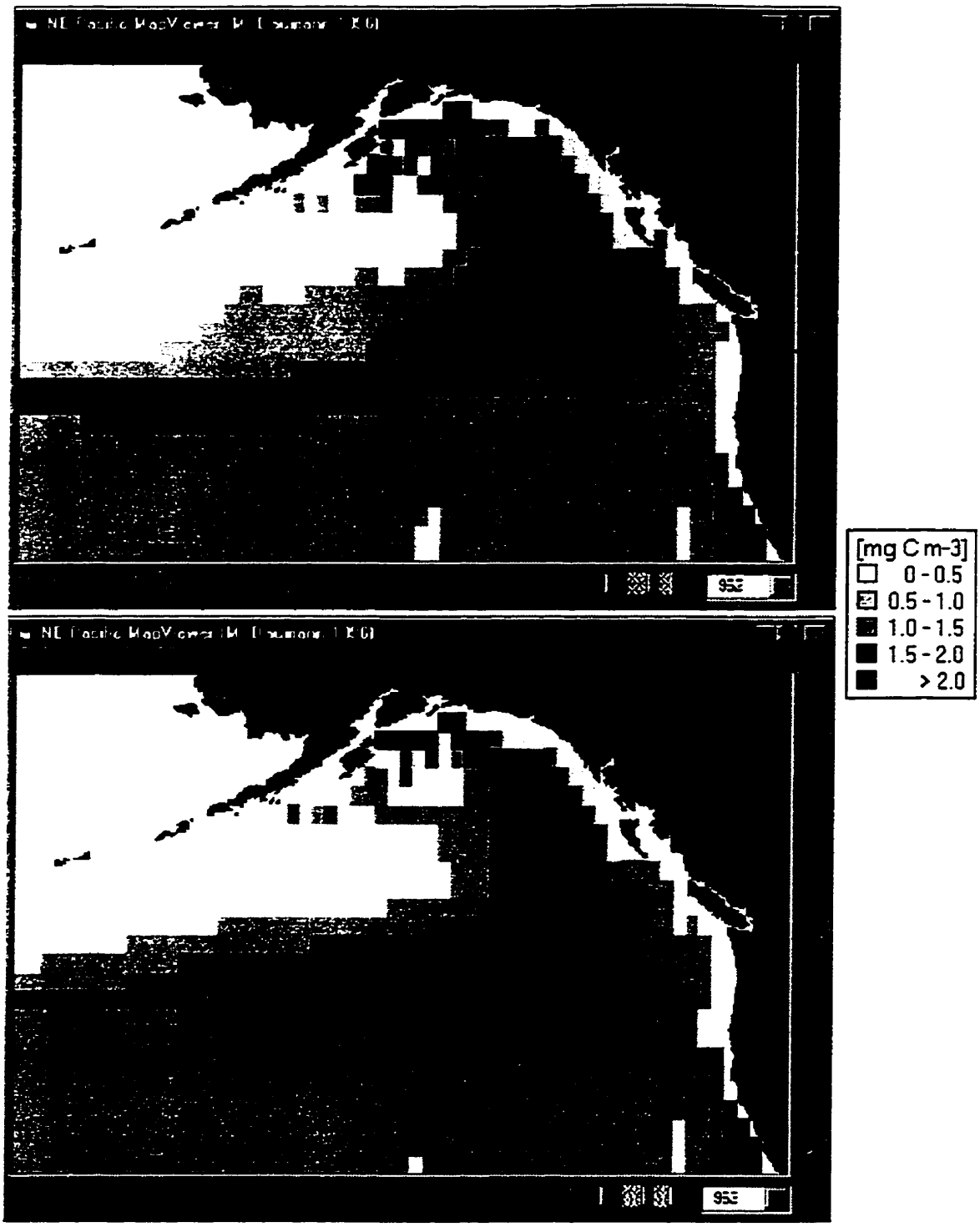


Fig. 4.13: Simulated mesozooplankton concentration [mg C m^{-3}] for July of 1962 (upper panel) and 1963 (lower panel). Simulation: 4-trophic levels models with advection. Simulation period: 1951-1990.

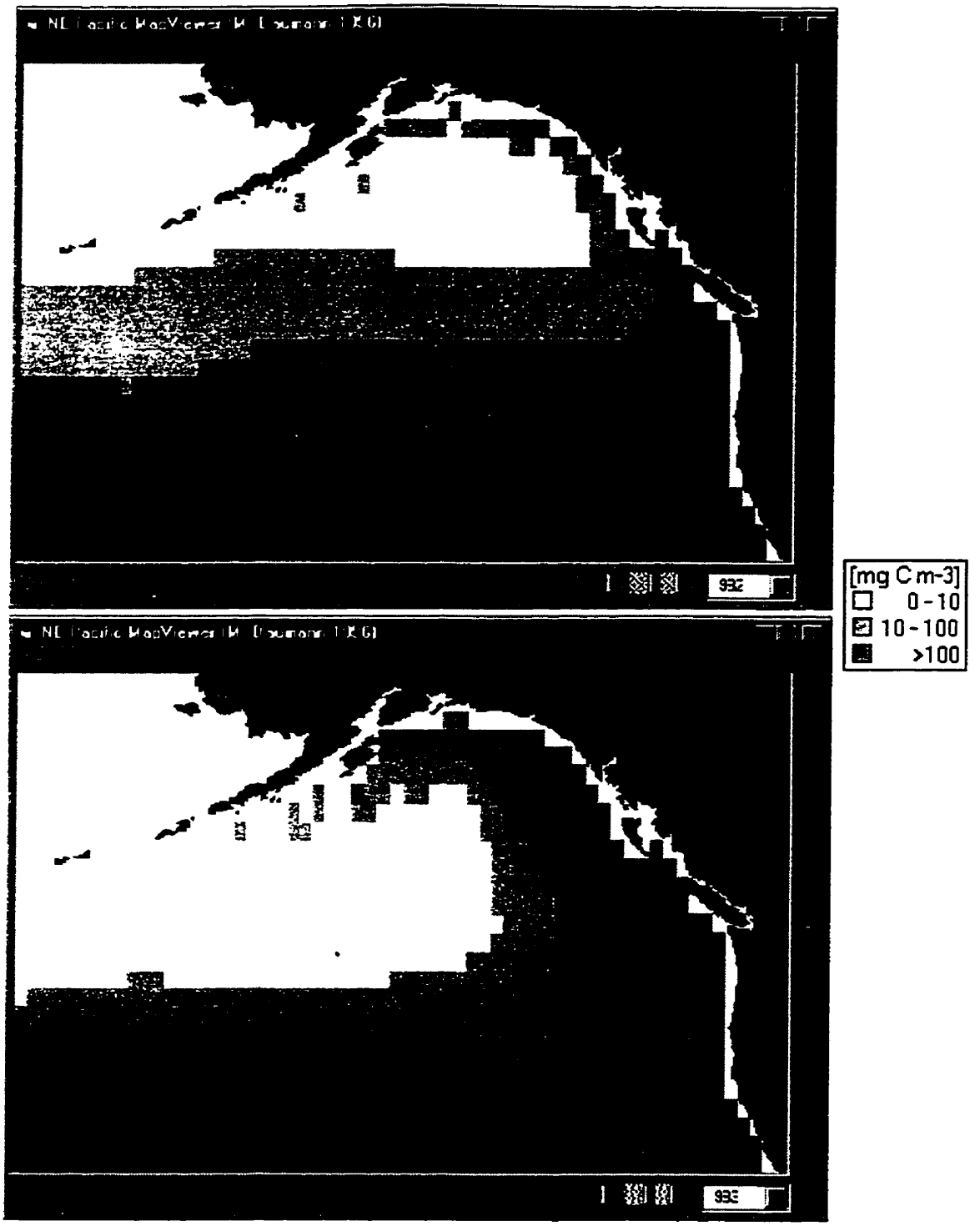


Fig. 4.14: Simulated mesozooplankton concentration [mg C m^{-3}] for July of 1982 (upper panel) and 1983 (lower panel). Simulation: 3-trophic levels models with advection. Simulation period: 1951-1990.

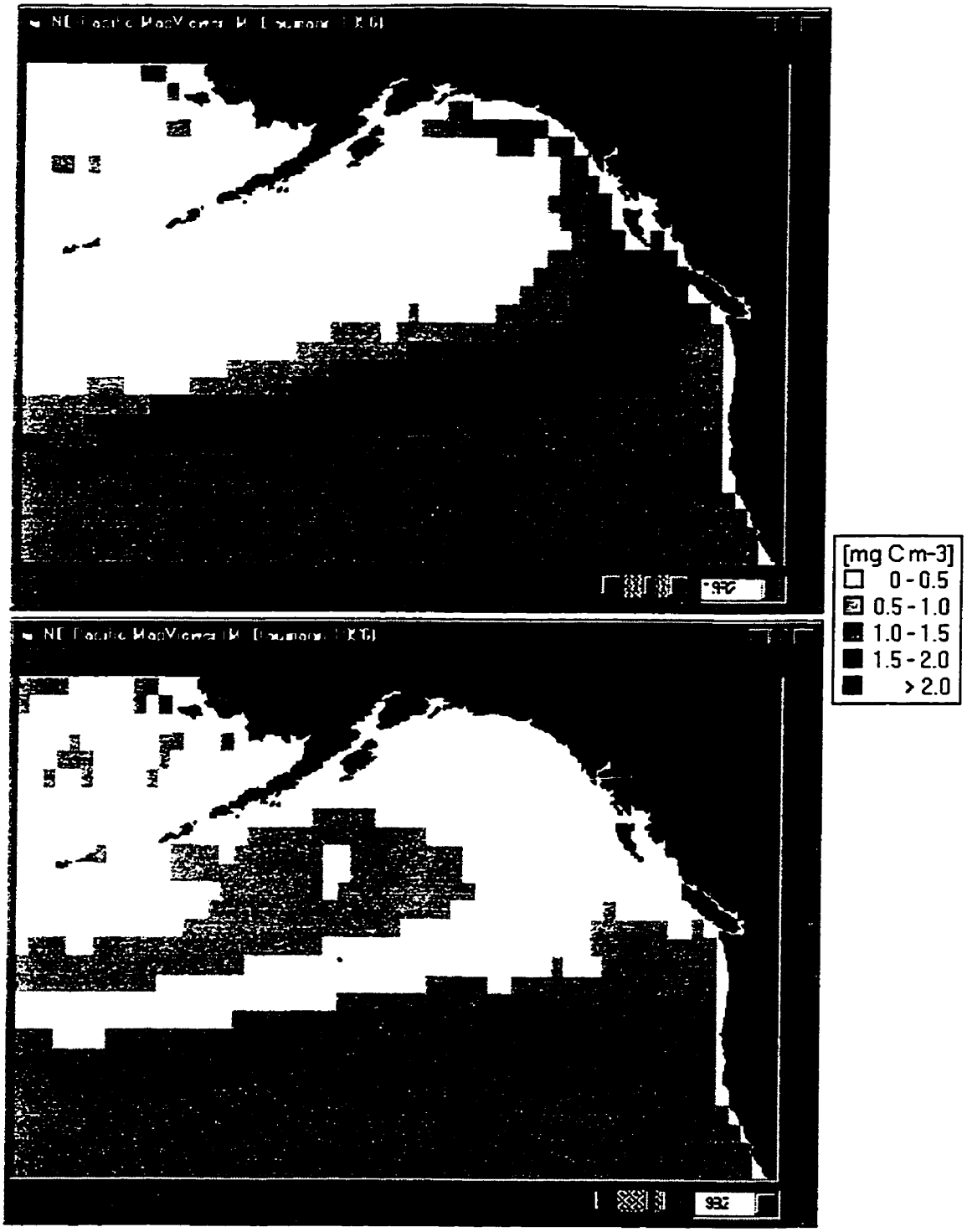
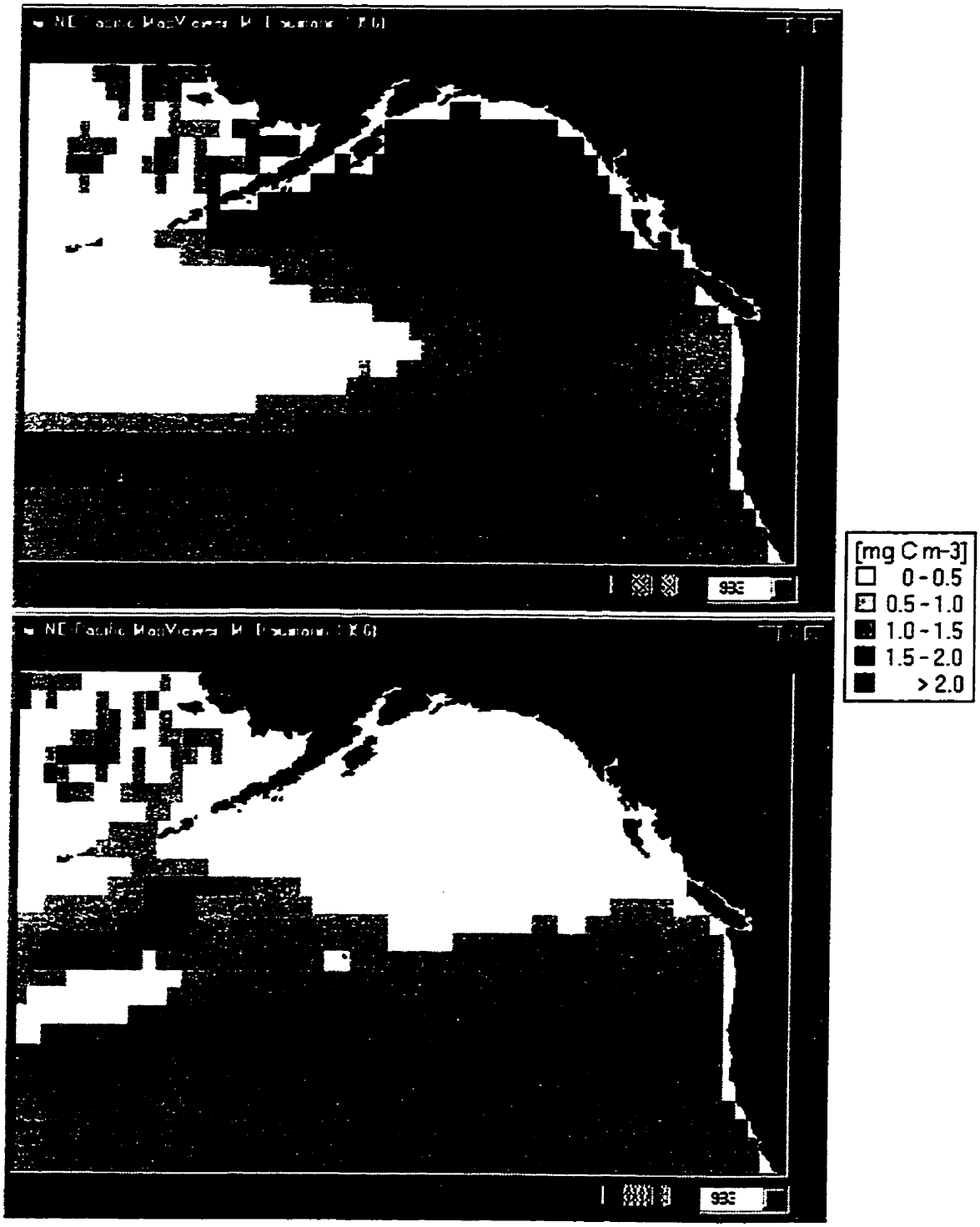


Fig. 4.15: Simulated mesozooplankton concentration [mg C m^{-3}] for July and October of 1982 (first two panels) and 1983 (second two panels). Simulation: 4-trophic levels models without advection. Simulation period: 1951-1990.



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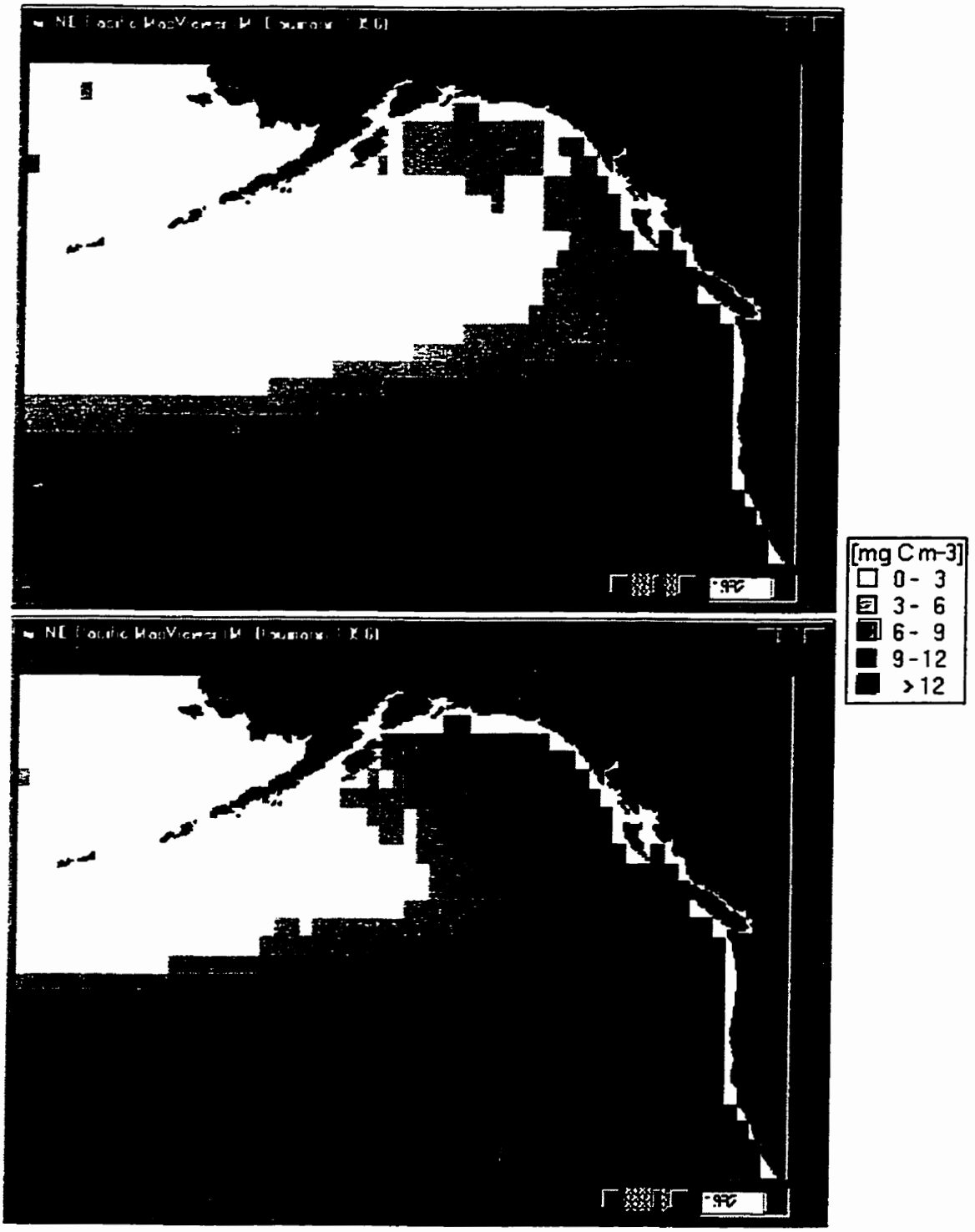


Fig. 4.16: Simulated macrozooplankton concentration [mg C m^{-3}] for July and October of 1982 (first two panels) and 1983 (second two panels). Simulation: 4-trophic levels models without advection. Simulation period: 1951-1990.

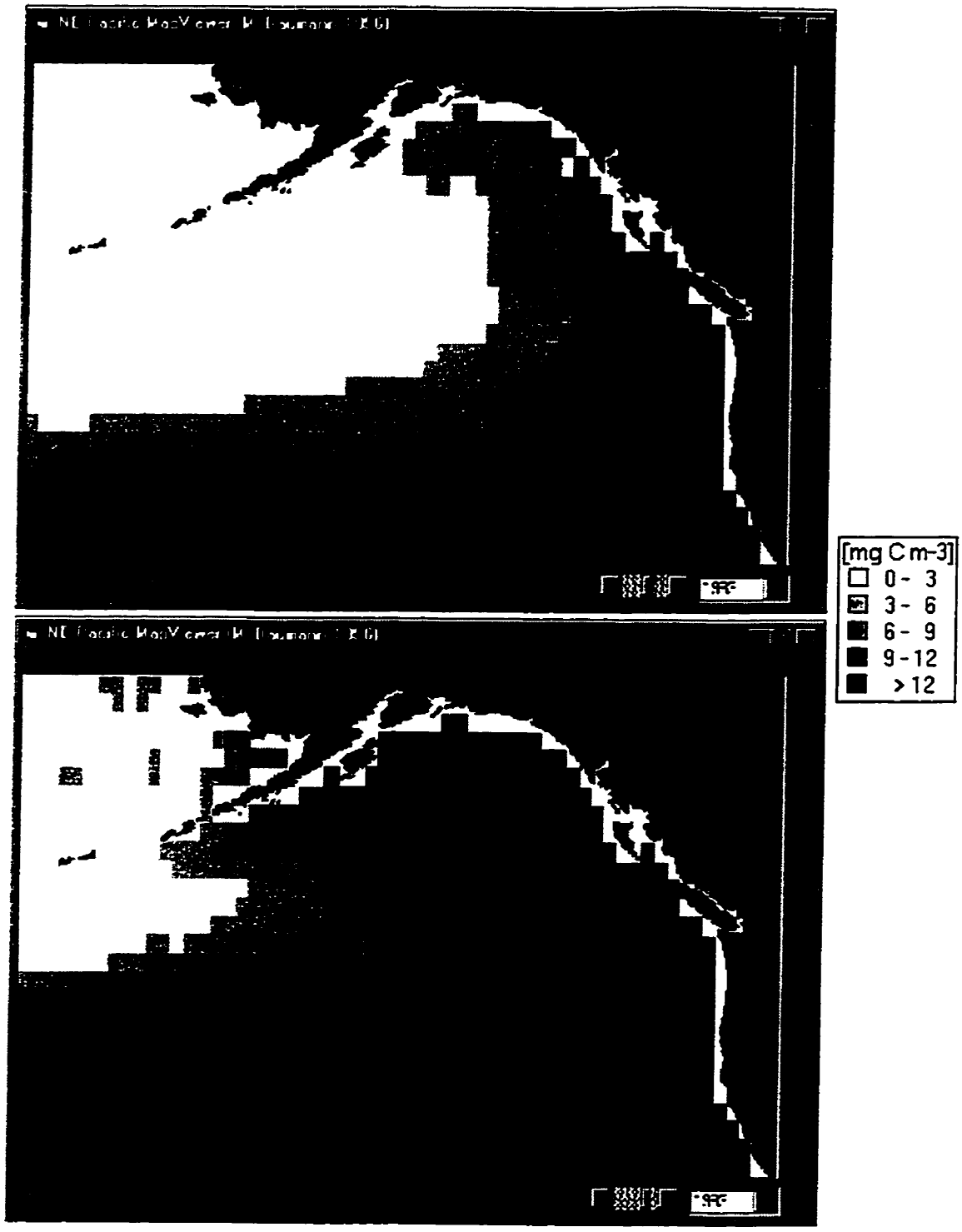


Fig. 4.16: Continued

these currents lead to the very high concentrations of simulated macrozooplankton along the coastal fringe of the Gulf of Alaska.

Simulation results from the 4-trophic levels model with advection show that spatio-temporal biomass concentrations of macrozooplankton (Fig. 4.9) and mesozooplankton (Fig. 4.8) appear to be inversely related (except for the northwestern part of the study area where both biomass concentrations are low in general). However, in summer the simulated macrozooplankton distribution seems to follow the distribution of microzooplankton (and thus primary productivity; Figs. 4.7 and 4.6), a result consistent with the concept of trophic cascading (Carpenter *et al.* 1985; Carpenter *et al.* 1987).

While it has been shown empirically that species assemblages and trophic relationships off the North American west coast change as a consequence of an ENSO event (Brodeur & Pearcy 1992), my simulation results show that the interannual variability in macrozooplankton biomass concentrations in the southern part of the study area are only small. However, it is in the southern regions where the many assumptions made during model and simulation design (see Chapter 3) might not hold.

Interdecadal Variability: Carnivores 1 (Mesozooplankton)

Mean simulated mesozooplankton concentrations for the month of July 1956 to 1959 and 1980 to 1989 (Fig. 4.17) almost completely contradict observations made in the same time periods (Fig. 1.7; Brodeur & Ware 1992 their Figure 1.). Not only do the simulated results suggest a decrease in overall mesozooplankton concentrations between the late 1950s and the 1980s but this decrease also occurs in locations where the strongest increase has been measured (on the northern fringe of the Gulf of Alaska) . This discrepancy can be explained by the fact that the modeled mesozooplankton species do not represent the sampled mesozooplankton species reported by Brodeur & Ware (1992); see also 3.4. Mean Field Simulations). It is important to note how one's perception of the interdecadal variability in zooplankton standing stock changes when you look at the simulation results for the month of August for both periods of time (Fig. 4.18).

In summary, model and simulation design (Chapter 3) followed the current mechanistic understanding of processes in the ecosystem Northeast Pacific (Chapter 2). Spatio-temporal scales and resolution of the simulations were a compromise between the resolution of the input data, the assumed relevant scales of biological processes, and computation time requirements. As for observations: While many biological variables have been collected at Station *P*, most of which are irrelevant for my simulations (e.g. nutrients, chlorophyll-a, ontogenetically migrating zooplankton species; see Chapter 3), spatially-explicit biological data are rare. Since all observational data were taken from the published literature and were therefore not designed to test any particular hypothesis of the models, empirical model validation is a difficult task (see Chapter 5). However, it must be emphasized that the simulations of the 4-trophic levels model

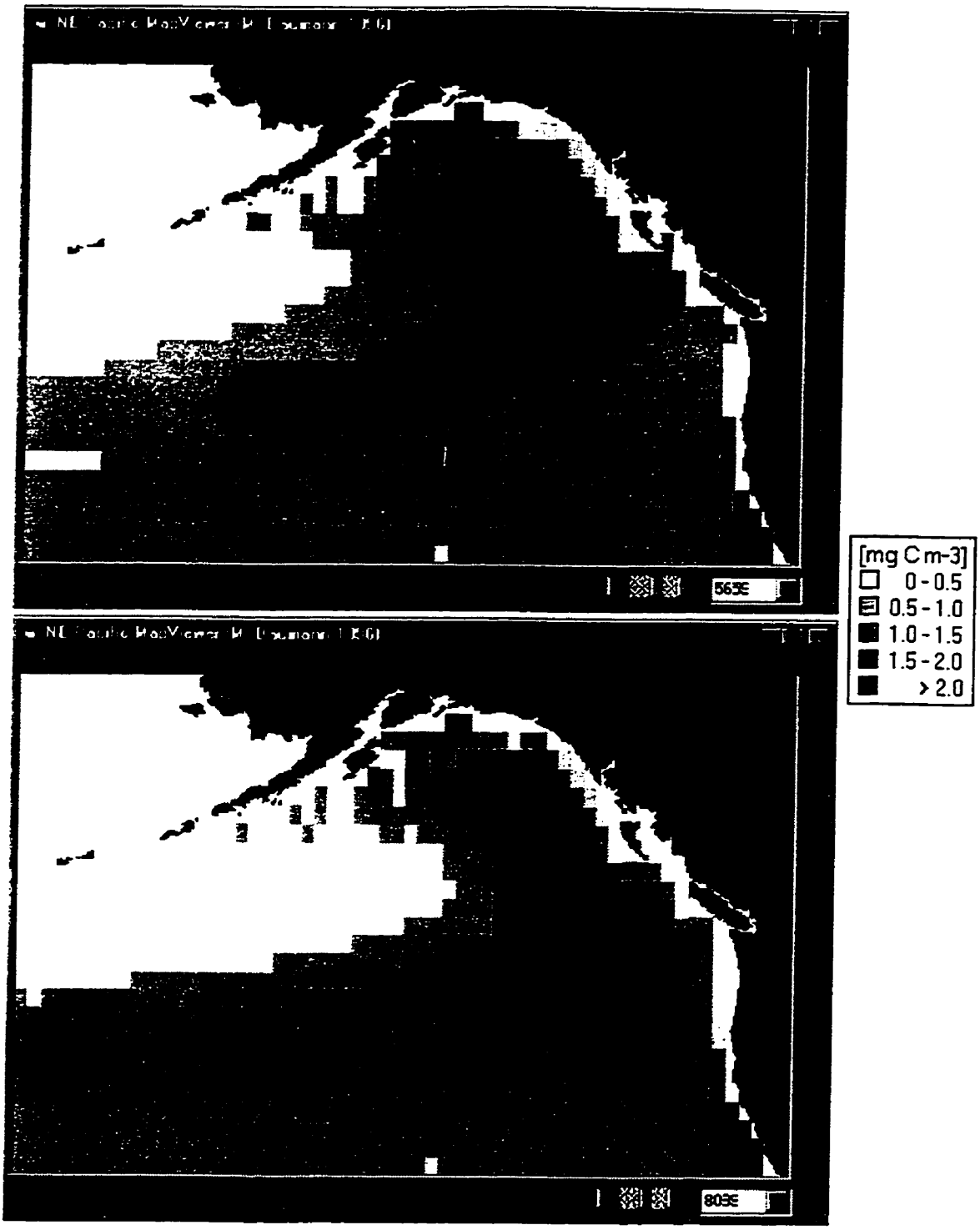


Fig. 4.17: Mean simulated mesozooplankton concentrations [mg C m^{-3}] for the month of July 1956 to 1959 (upper panel) and 1980 to 1989 (lower panel). Simulation: 4-trophic levels models with advection. Simulation period: 1951-1990.

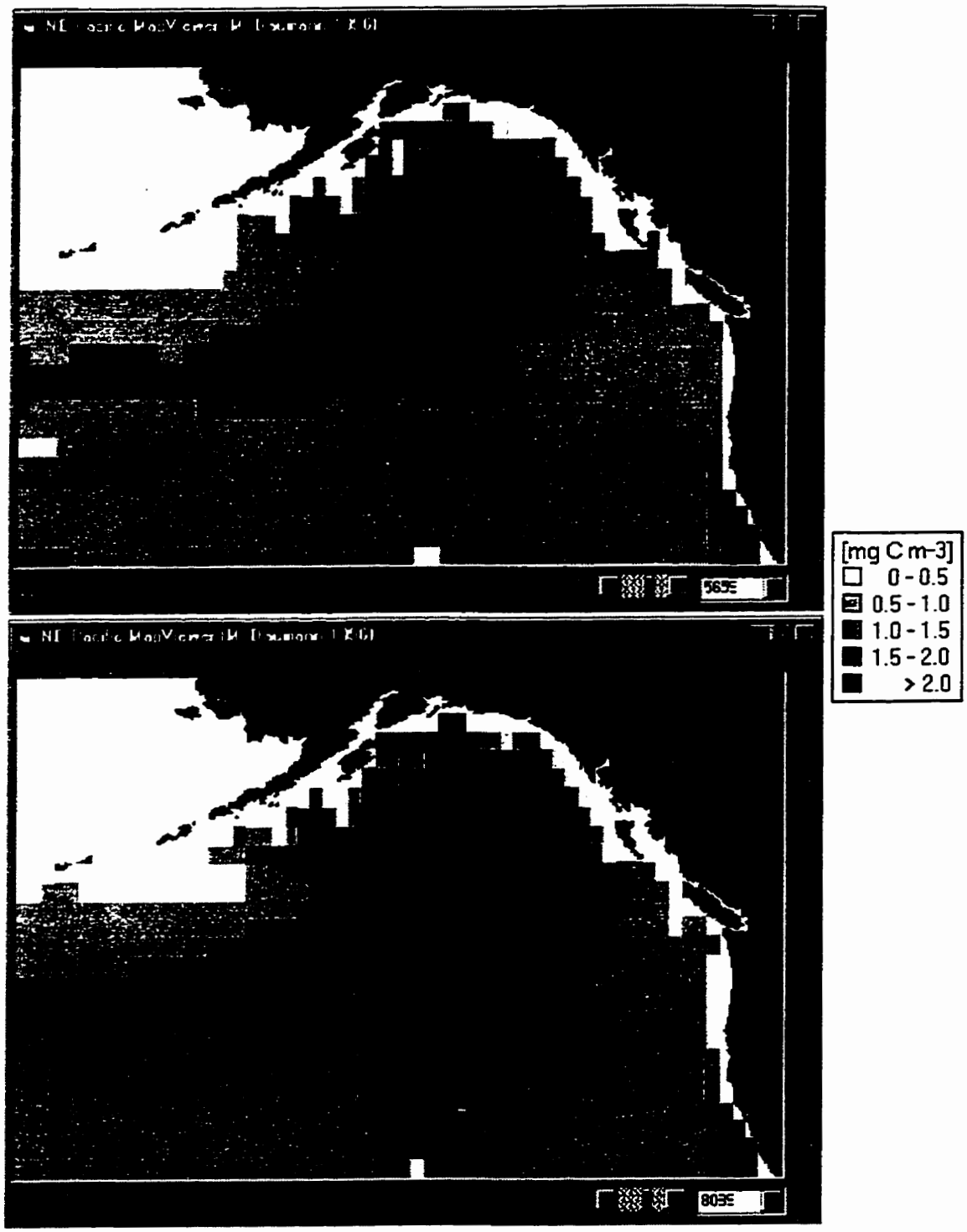


Fig. 4.18: Mean simulated mesozooplankton concentrations [mg C m^{-3}] for the month of August 1956 to 1959 (upper panel) and 1980 to 1989 (lower panel). Simulation: 4-trophic levels models with advection. Simulation period: 1951-1990.

including advection produced seasonal spatio-temporal biomass concentrations that are in general agreement with intuitive expectations (which, of course, is hardly a measure of validity).

4.2.2. Operational Validation

We must now see whether the simulations provide answers to the questions for which I have designed the models (see Conjecture in Section 1.4.): How, if at all, does the availability of prey organisms, whose density at a particular location and time is the result of biological production processes as well as advection, affect sockeye salmon cohort survival?

To answer this question I have looked at the spatial progression of simulated mesozooplankton density from July to the following February for years with the lowest and the highest cohort survival of combined Fraser River stocks and combined Bristol Bay river systems, respectively (see Fig. 1.4). All simulation results are from the 4-trophic levels model including advection.

Fraser River Stocks

After emergence from gravel Fraser River sockeye salmon spend one winter in freshwater and two winters in the ocean (Burgner 1991 his Table 2). I first scanned for cohorts with low and high survival rates, respectively, and then looked at the simulated spatio-temporal distribution of mesozooplankton in the year the respective year-class entered the ocean. Brood years with the respective lowest and highest survival rate of combined Fraser River stocks are 1958 and 1955 (see Fig. 1.4). However, in order to avoid spatial initial condition effects, 1955 is close to the simulation starting point in 1951, I considered the cohort with the second highest survival rate, i.e. the brood year class 1981. Thus monthly maps have been plotted for July 1960 to February

1961 (1960: ocean entry of low survival cohort; Fig. 4.19), and for July 1983 to February 1984 (1983: ocean entry of high survival cohort; Fig. 4.20).

A comparison of the respective months of the low (Fig. 4.19) and high survival years (Fig. 4.20) shows for July, i.e. the month when juvenile sockeye salmon leave the Strait of Georgia through Johnstone Strait and are confronted with the open ocean for the first time (Burgner 1991), simulated mesozooplankton maxima were both higher and larger in extent in the eastern part of the Gulf of Alaska in the high survival year. However, in August the situation reversed, and in the high-survival year the horseshoe-shaped high density ridge was far offshore. Simulated prey availability in September (without considering risk of predation on part of sockeye salmon) actually suggests that sockeye salmon should fare better in the low survival year. The spatio-temporal distribution of simulated mesozooplankton in October of the high survival year shows a high concentration about 700 km south of Kodiak Island, too far offshore for juvenile sockeye which at this time still live close to or even in coastal waters. The spatial distributions of simulated mesozooplankton densities from November to February look similar,and if anything suggest that the low survival year should have produced high cohort survival rates.

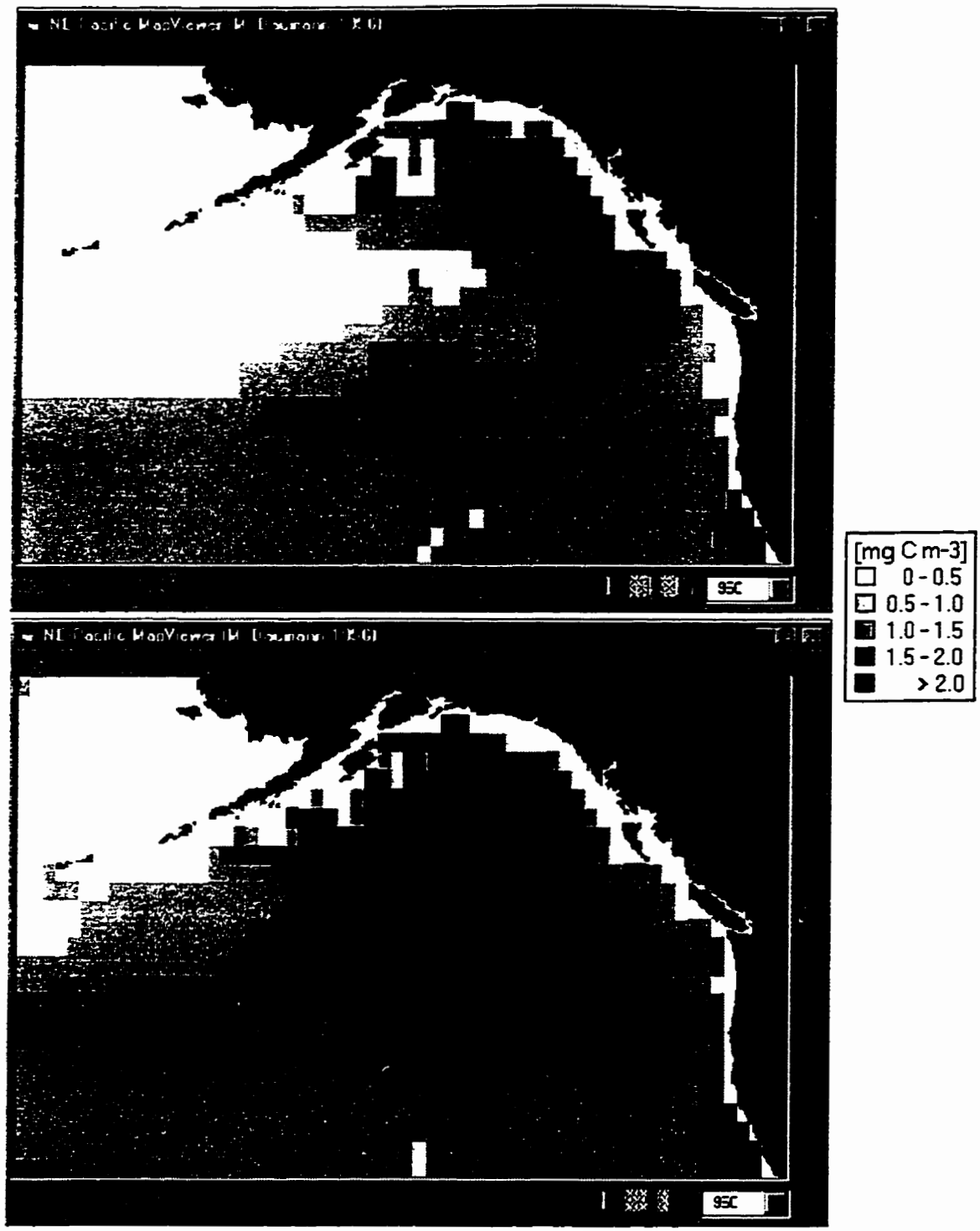


Fig. 4.19: Monthly simulated mesozooplankton concentrations [mg C m^{-3}] for July 1960 to February 1961 (low survival year for Fraser River sockeye salmon). Note the change in scale for November to February maps. Simulation: 4-trophic levels models with advection. Simulation period: 1951-1990.

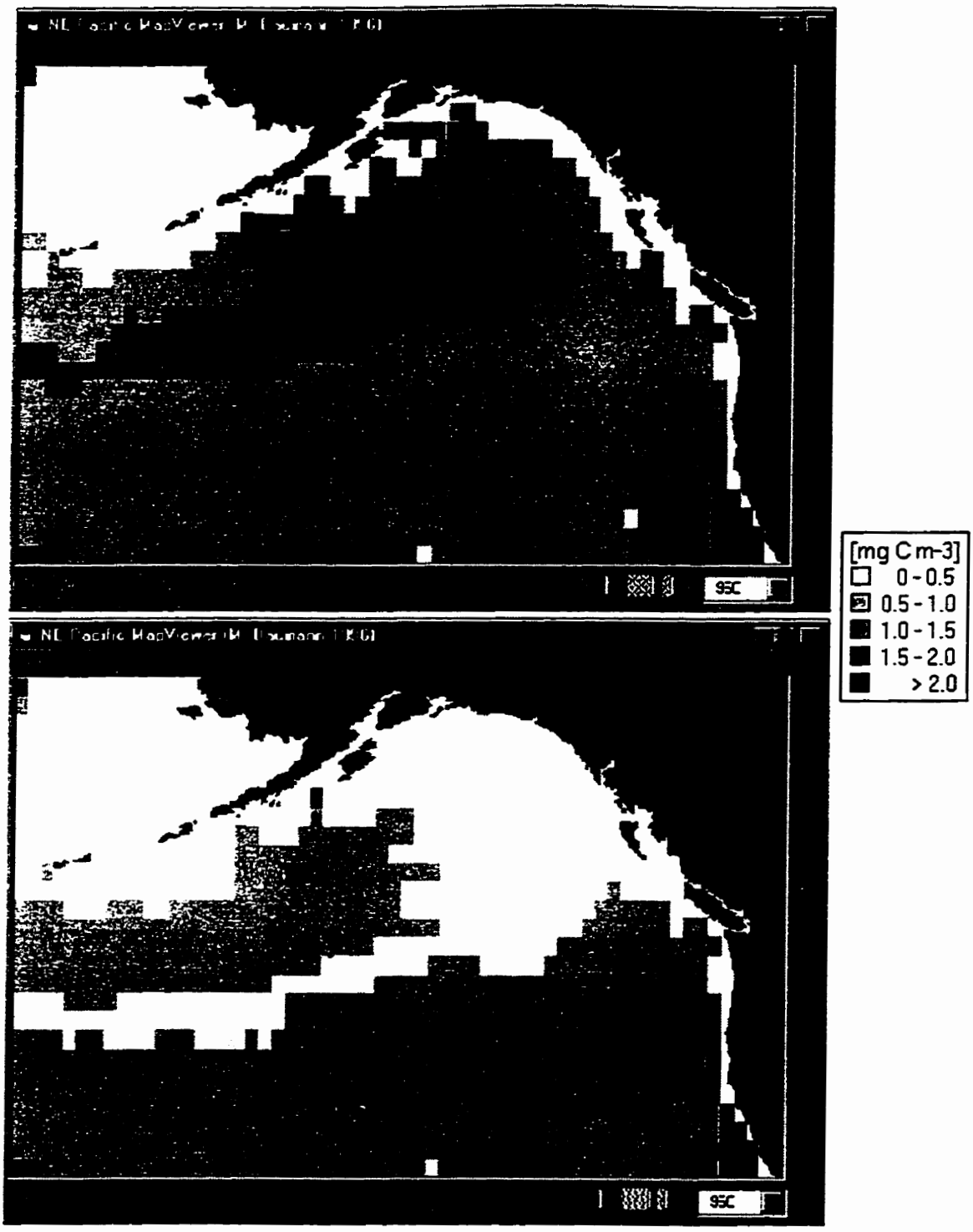


Fig. 4.19: Continued

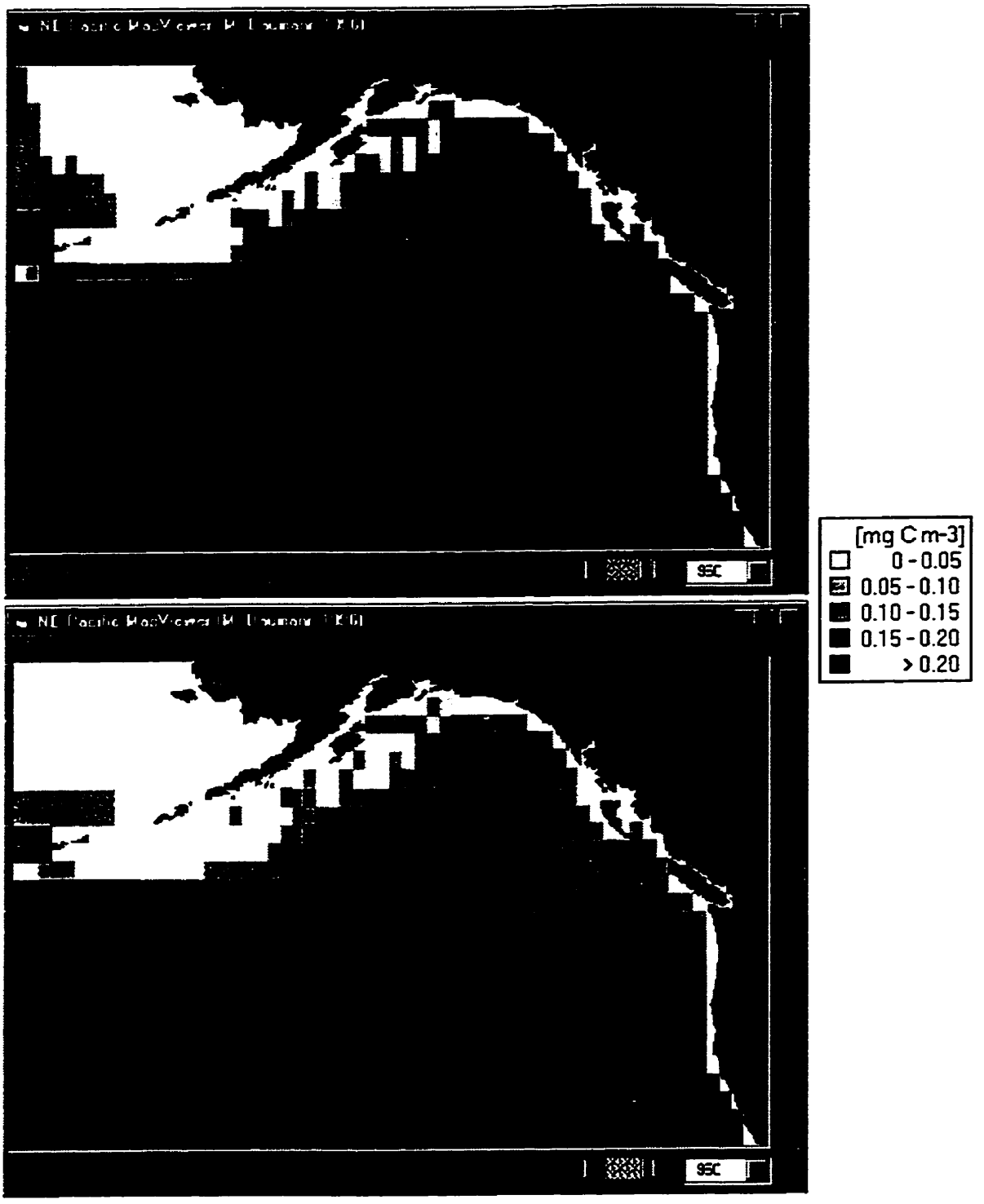
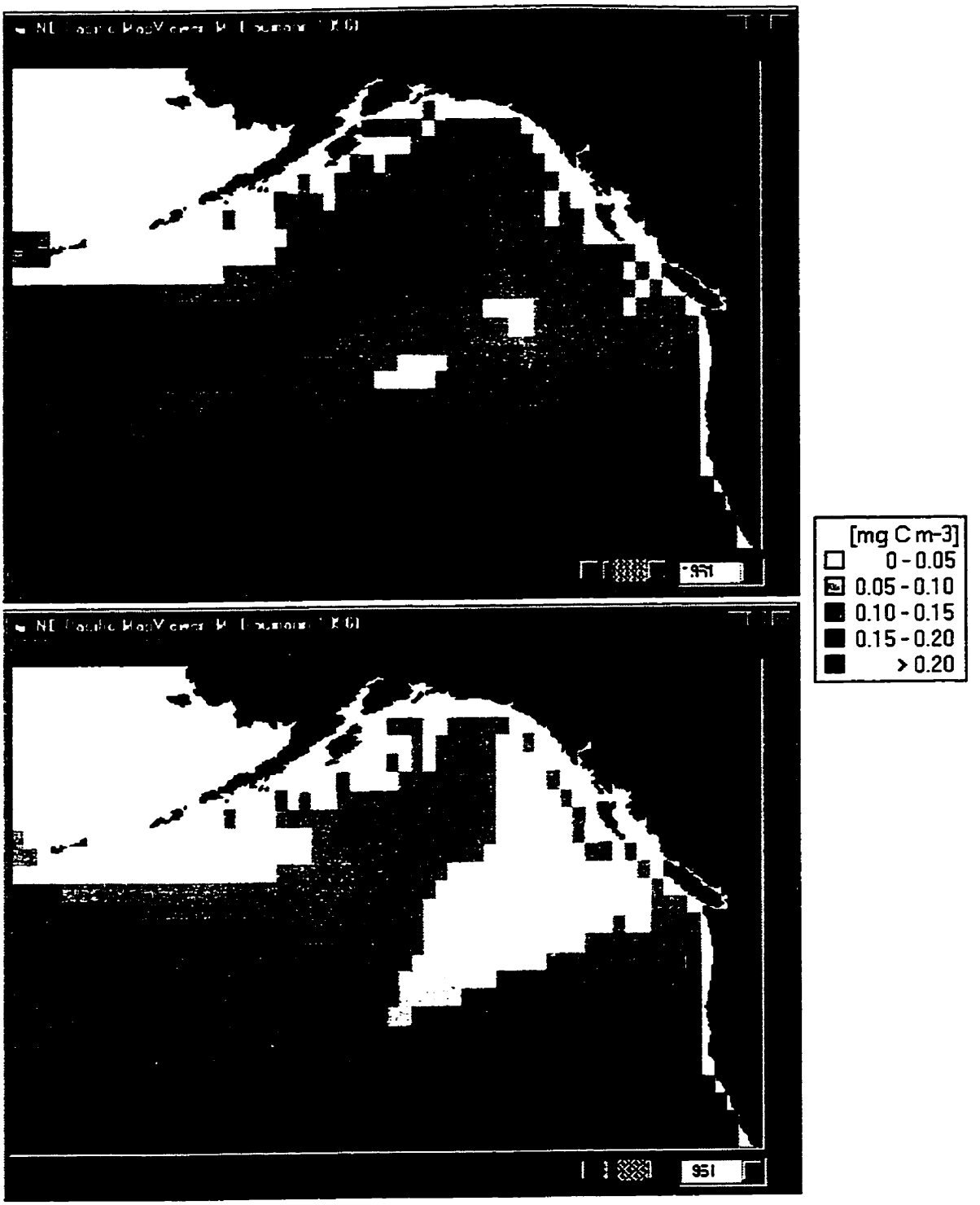


Fig. 4.19: Continued



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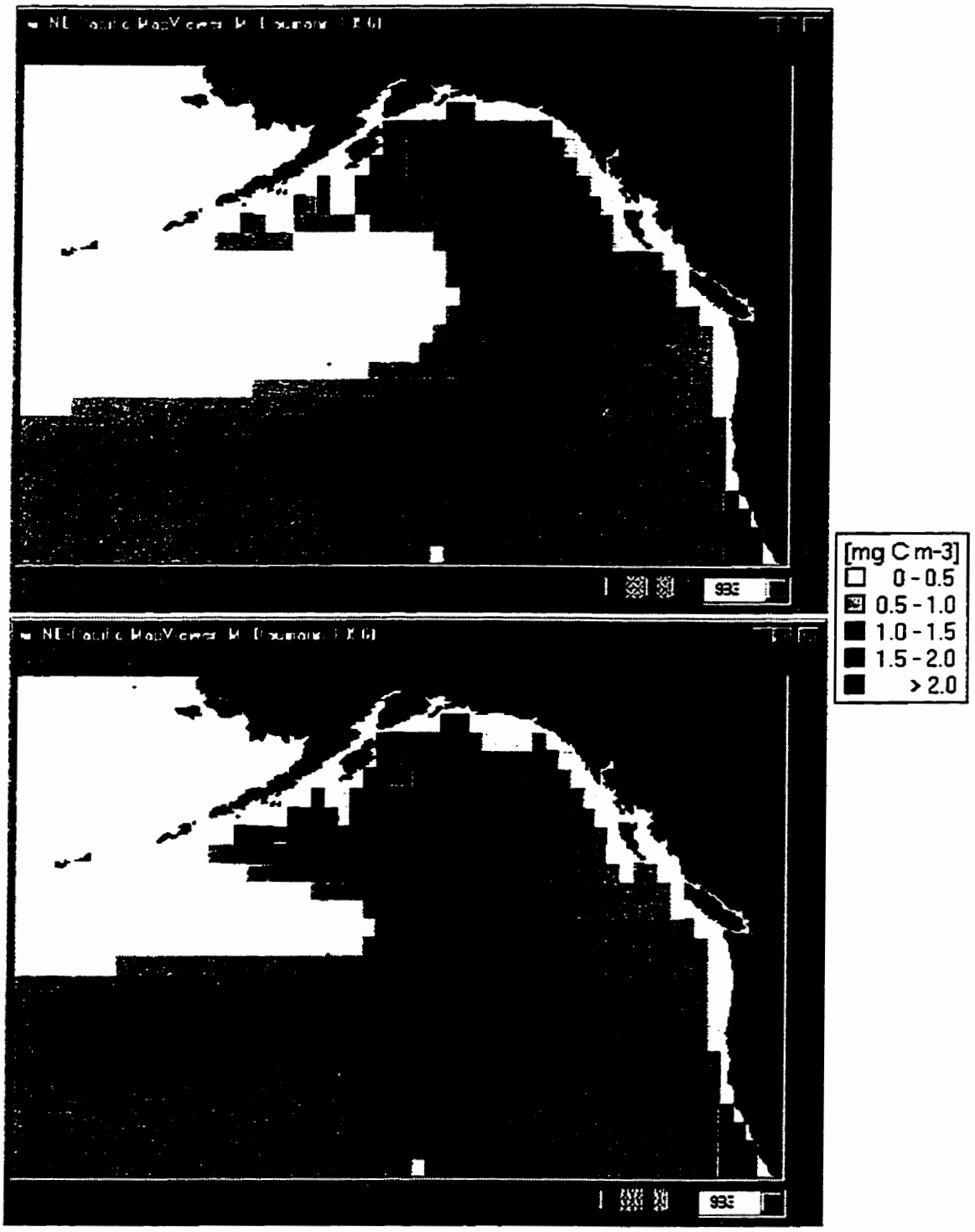


Fig. 4.20: Monthly simulated mesozooplankton concentrations [mg C m^{-3}] for July 1983 to February 1984 (high survival year for Fraser River salmon). Note the change in scale for November to February maps. Simulation: 4-trophic levels models with advection. Simulation period: 1951-1990.

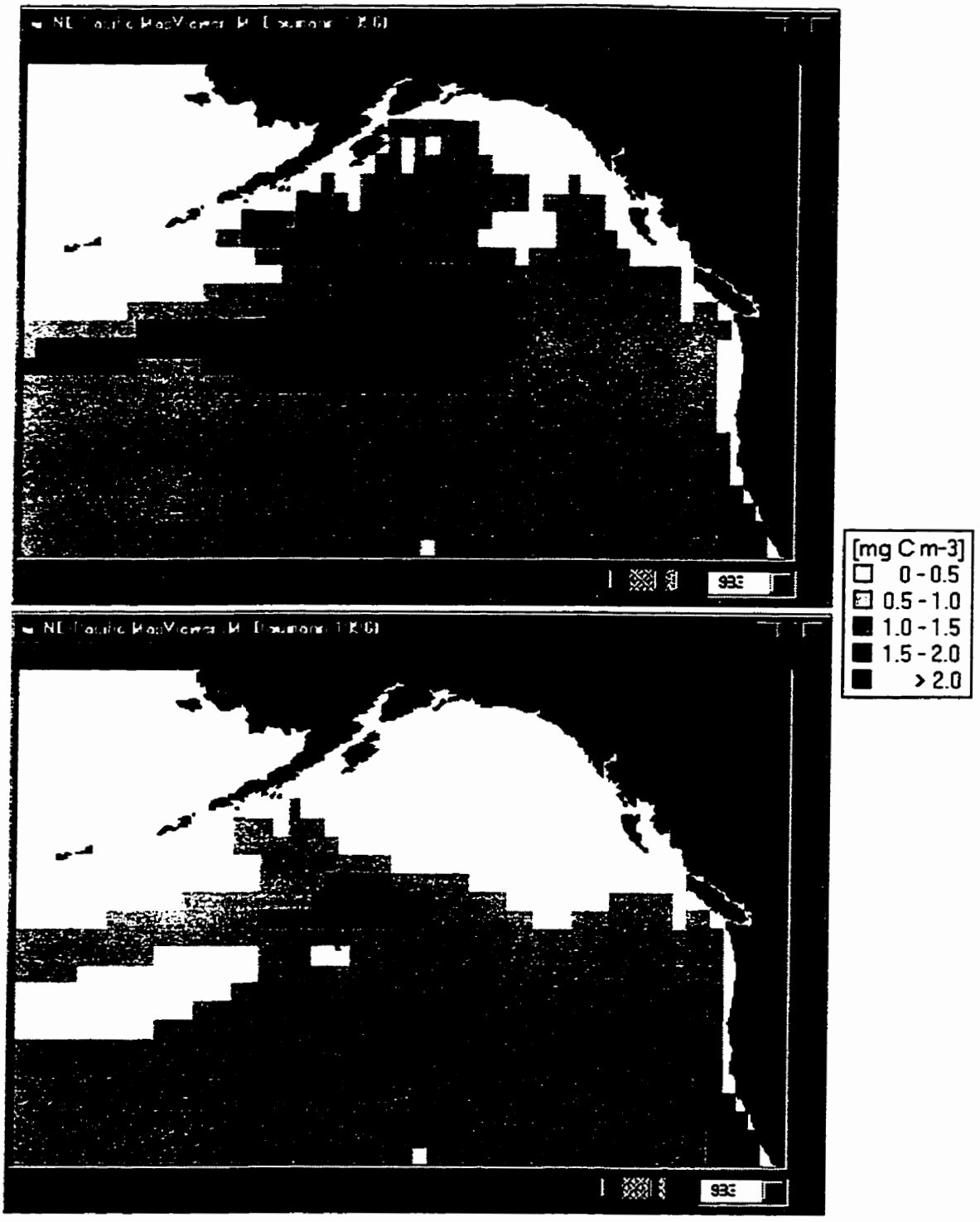
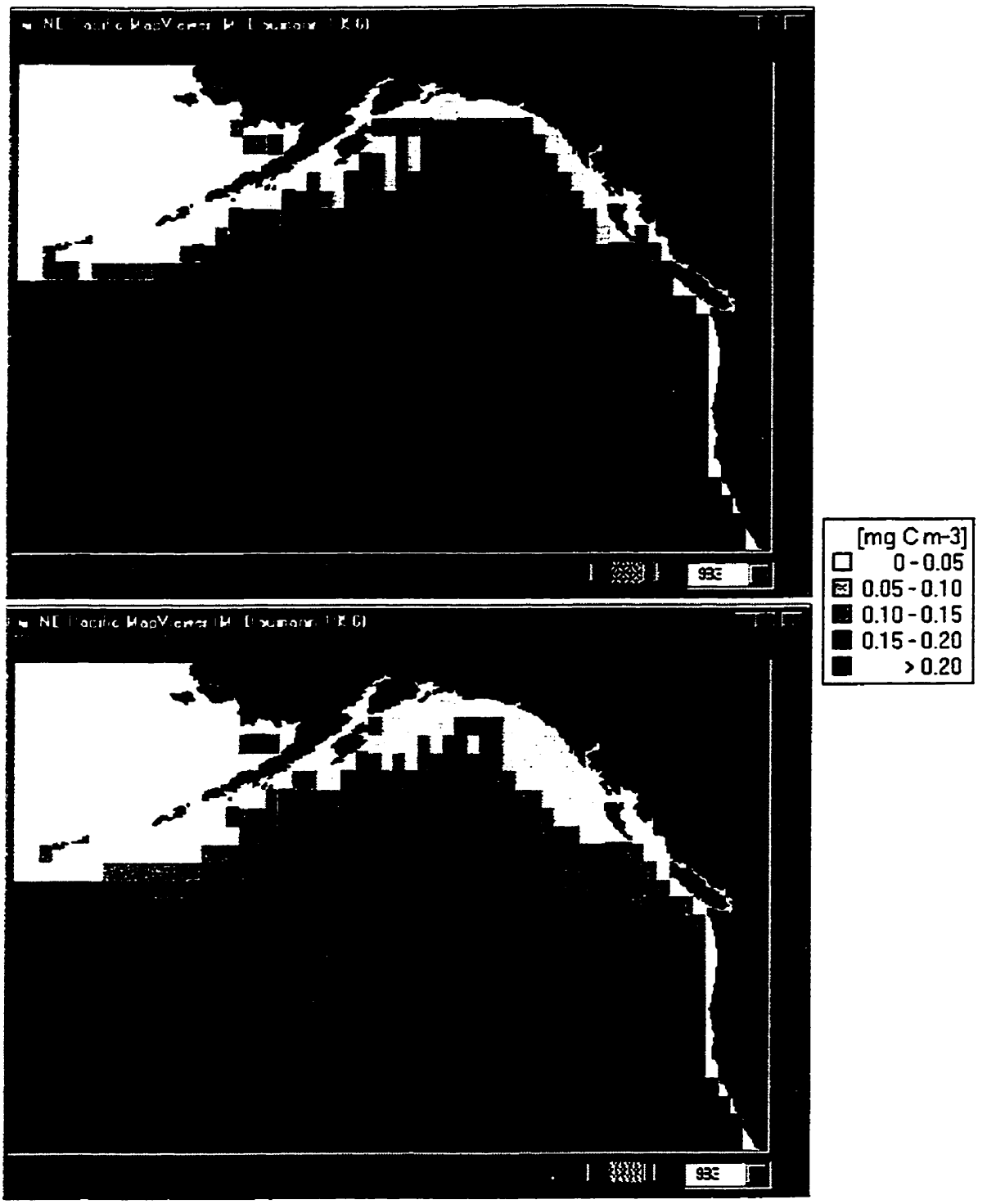


Fig. 4.20: Continued



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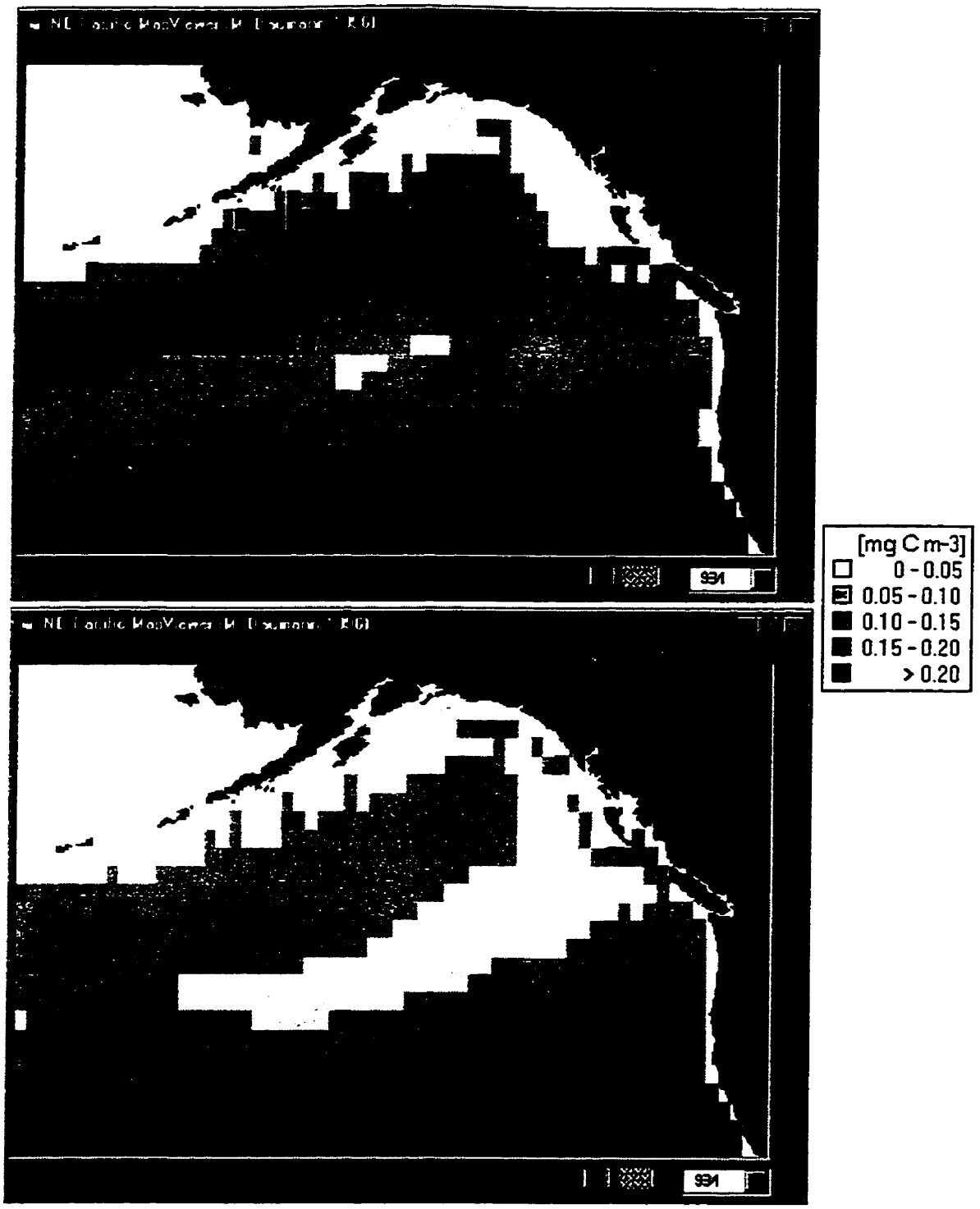


Fig. 4.20: Continued

Bristol Bay River Systems

Bristol Bay sockeye salmon spend one or two winters in freshwater and two or three winters in the ocean (Burgner 1991 Table 2). To account for the variability in seaward migration I first scanned the data for pairs of successive brood years with low and high survival rates, respectively, and then looked at the spatio-temporal distribution of mesozooplankton two years after that later year, i.e. the time when a 1.x fish that was spawned in that later year would migrate to sea. The pairs of brood years with low and high survival are 1968/1969 and 1976/77 (see Fig. 1.4). Monthly maps have been plotted for July 1971 to February 1972 (low survival year; Fig. 4.21), and for July 1979 to February 1980 (high survival year; Fig. 4.22).

Comparing Figs. 4.21 (low survival year) and 4.22 (high survival year) shows that the high density mesozooplankton front progresses westward much faster and reaches further west in the high survival year. By August, i.e. the time when juvenile Bristol Bay sockeye salmon migrate southward into the Gulf of Alaska, a region with high mesozooplankton density has established itself for the high survival year (Fig. 4.22), while for the low density year the westward movement of the front has stagnated (Fig. 4.21). The September map shows an aggregation of simulated mesozooplankton just south of the Alaska Peninsula in the high survival year, traces of which still can be found in October (Fig. 4.22). The spatial distribution of simulated mesozooplankton concentrations in November and December indicates a relatively high standing stock on the southeastern fringe of the Gulf of Alaska for the low survival year and an offshore western accumulation south of the Aleutian Islands for the high survival year. January and February maps for both years show the same spatial distributions than in the respective previous months only with now lower concentrations.

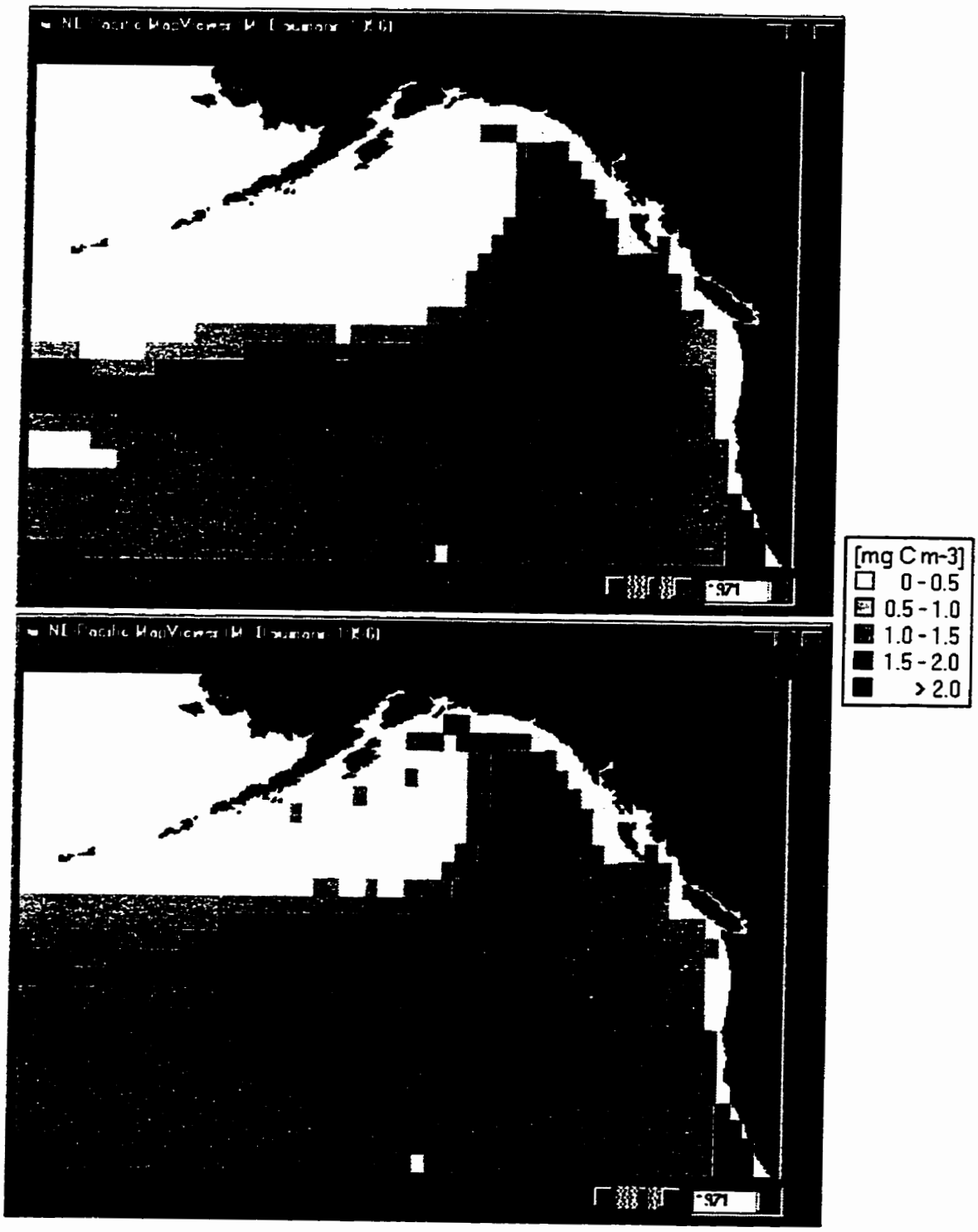


Fig. 4.21: Monthly simulated mesozooplankton concentrations [mg C m^{-3}] for July 1971 to February 1972 (low survival year for Bristol Bay sockeye salmon). Note the change in scale for November to February maps. Simulation: 4-trophic levels models with advection. Simulation period: 1951-1990.

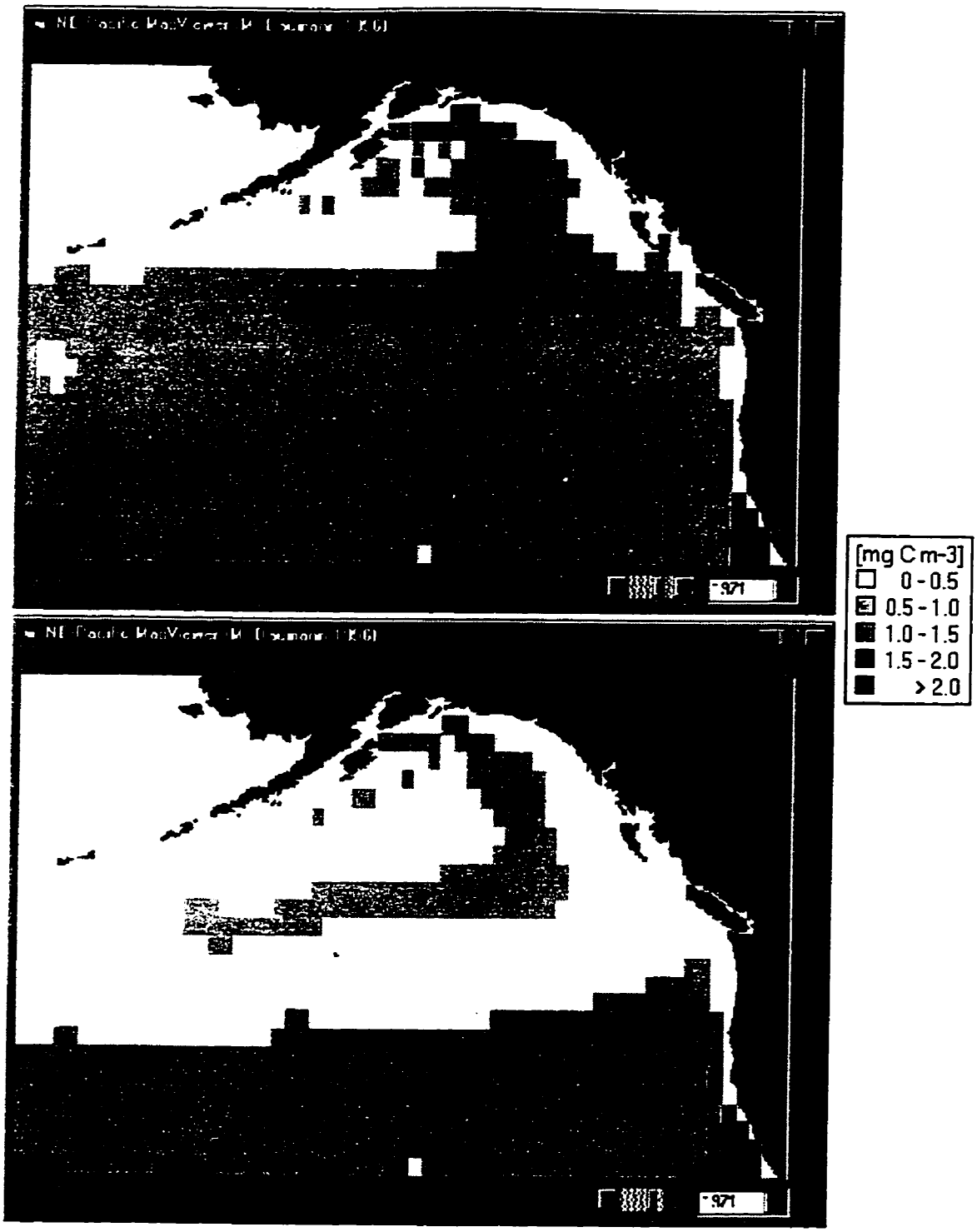


Fig. 4.21: Continued

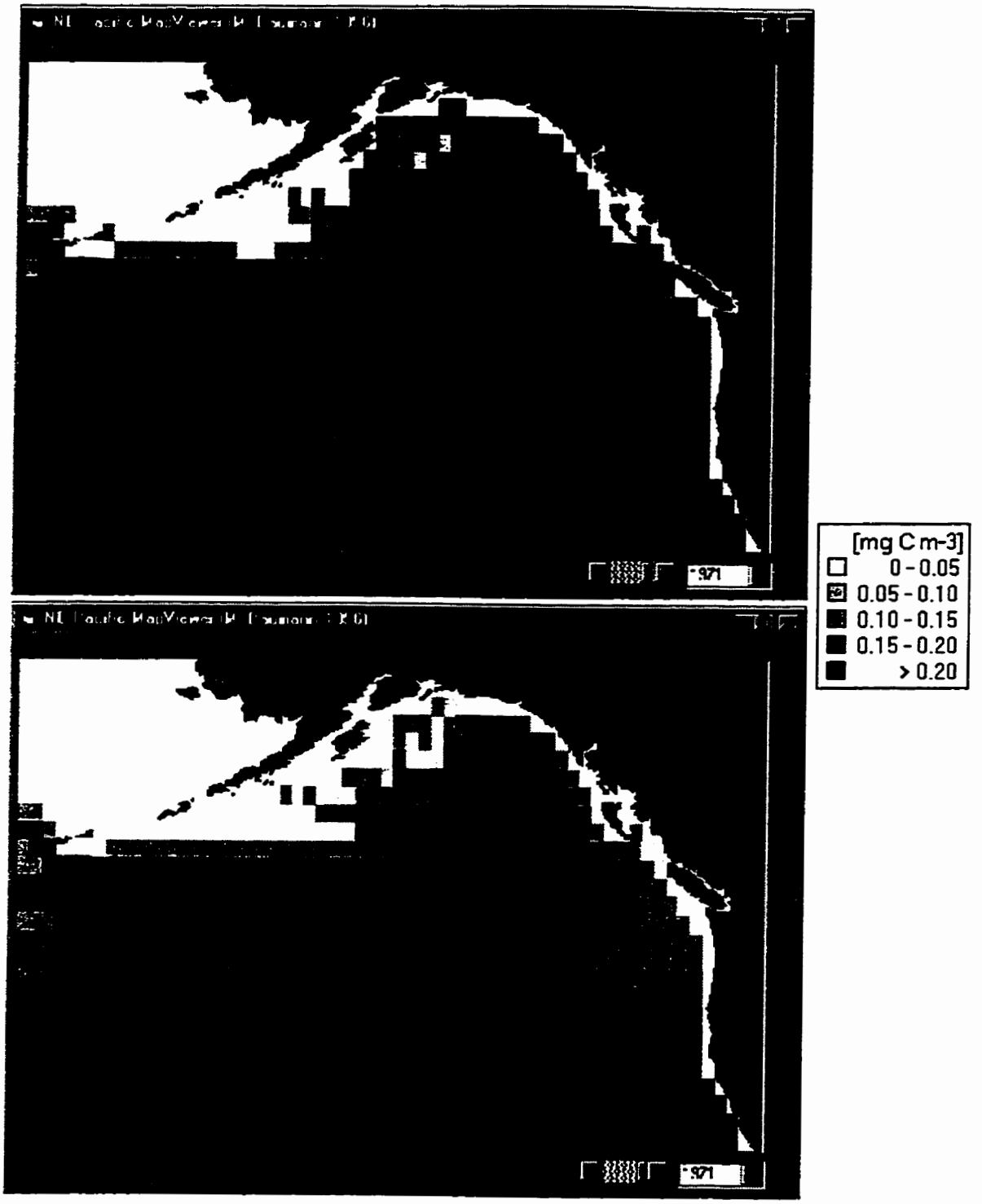
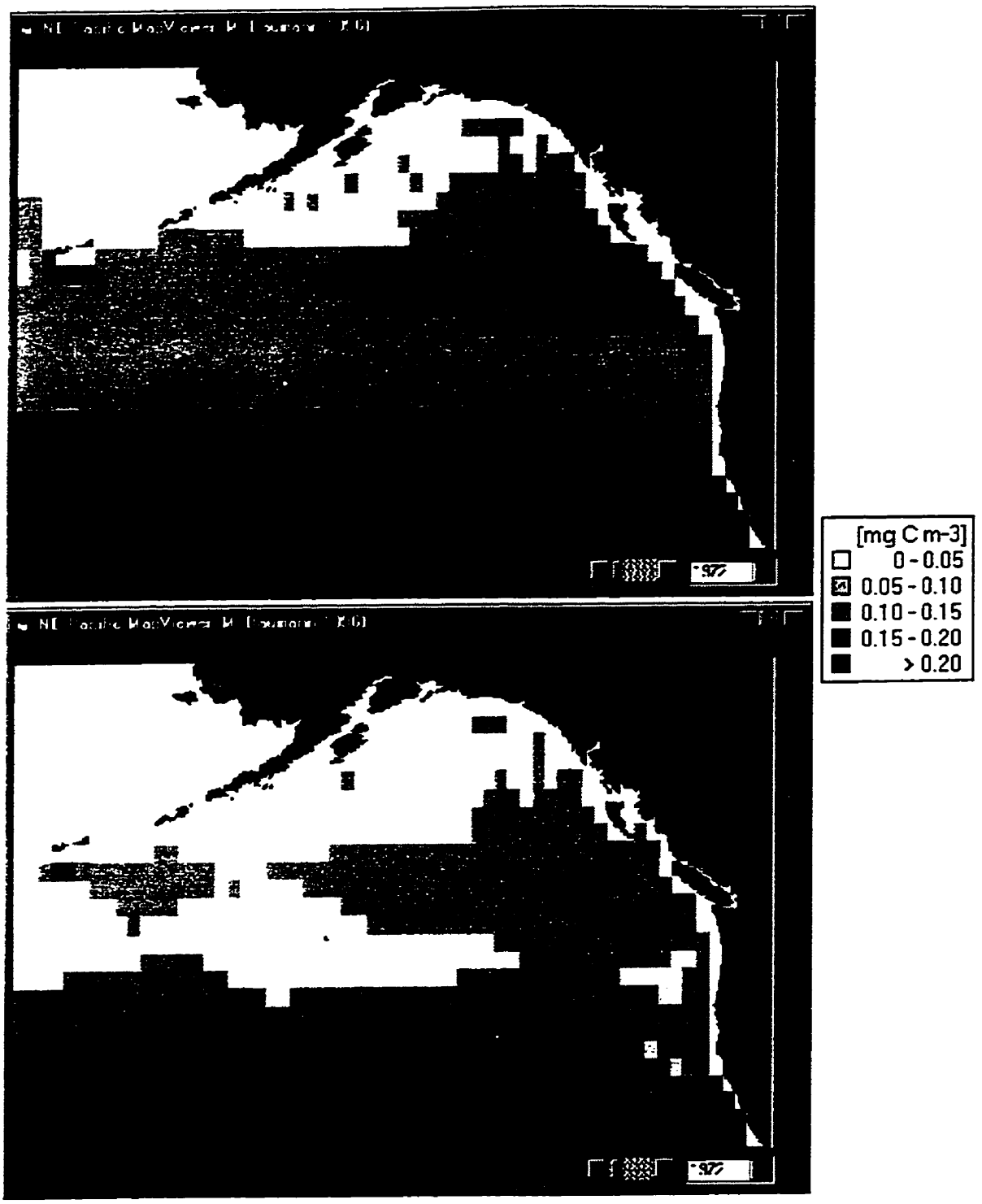


Fig. 4.21: Continued



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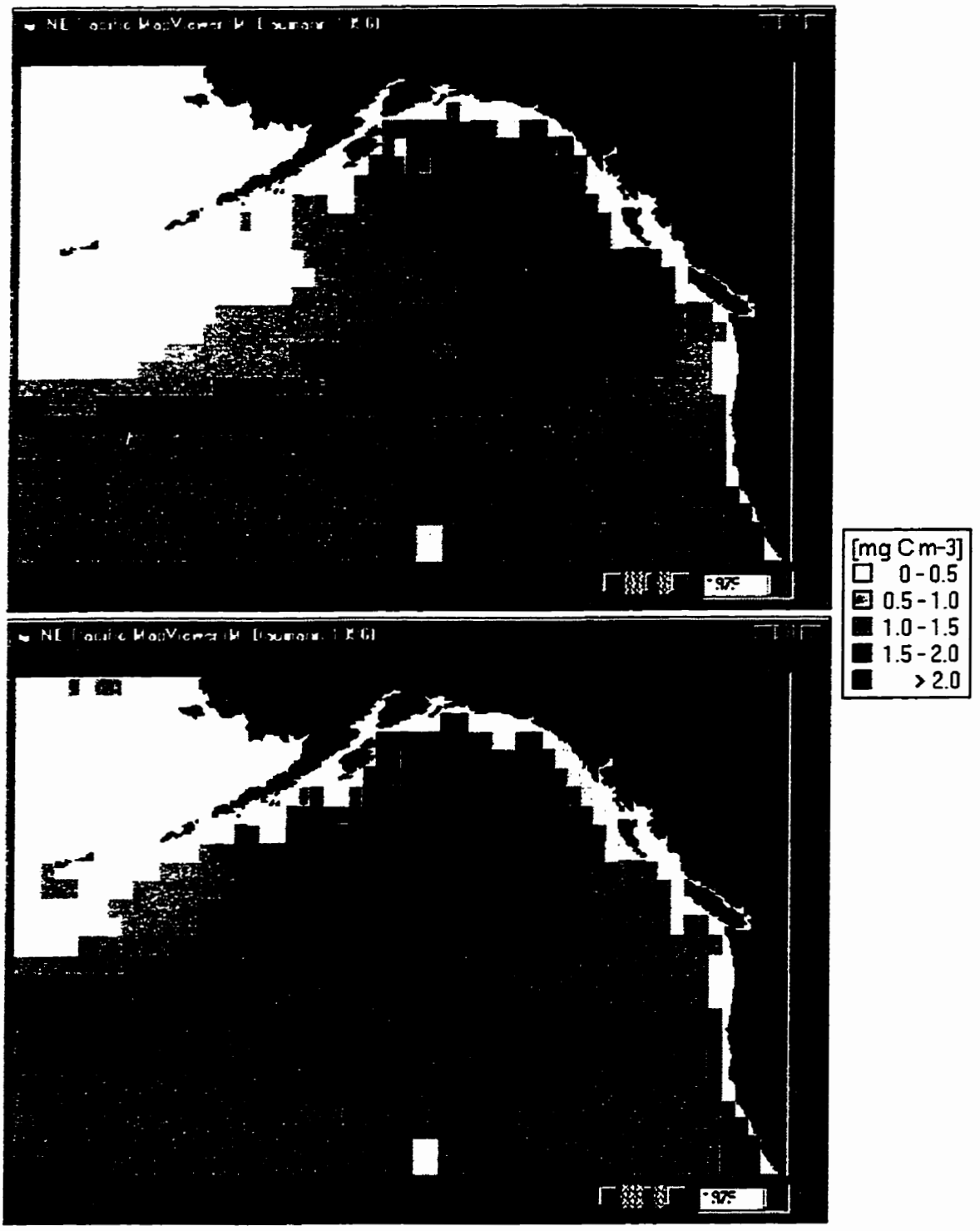


Fig. 4.22: Monthly simulated mesozooplankton concentrations [mg C m^{-3}] for July 1979 to February 1980 (high survival year for Bristol Bay sockeye salmon). Note the change in scale for November to February maps. Simulation: 4-trophic levels models with advection. Simulation period: 1951-1990.

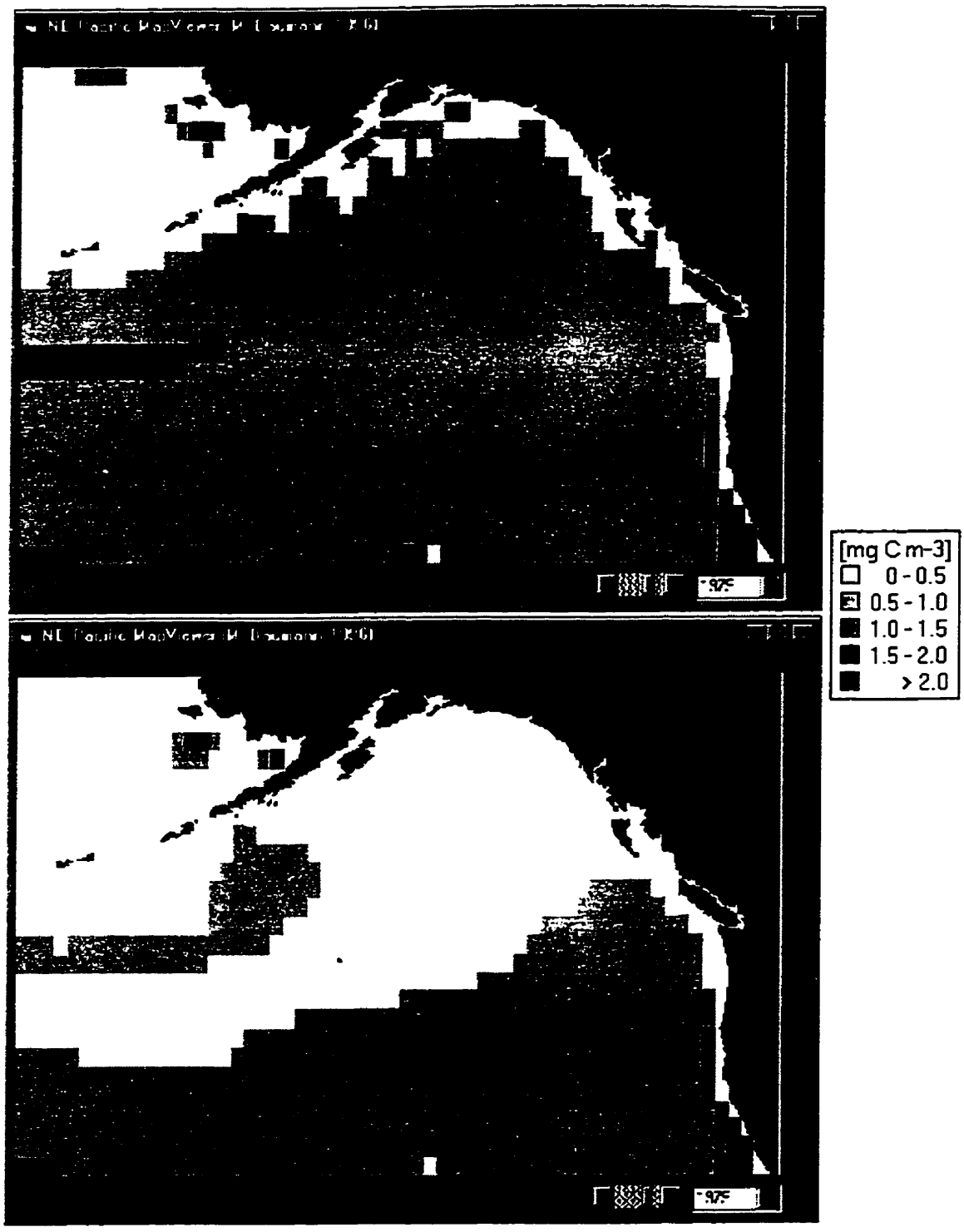
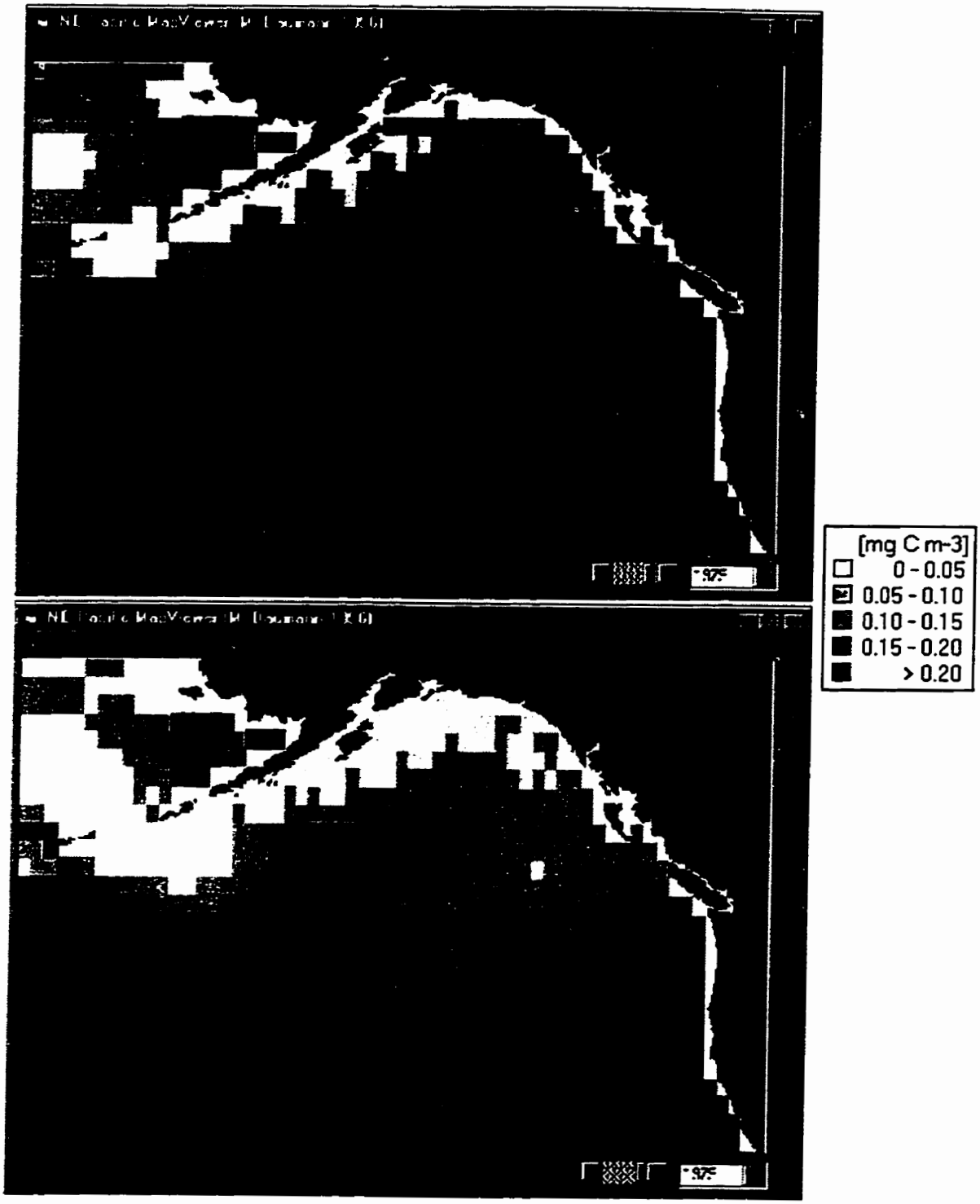


Fig. 4.22: Continued



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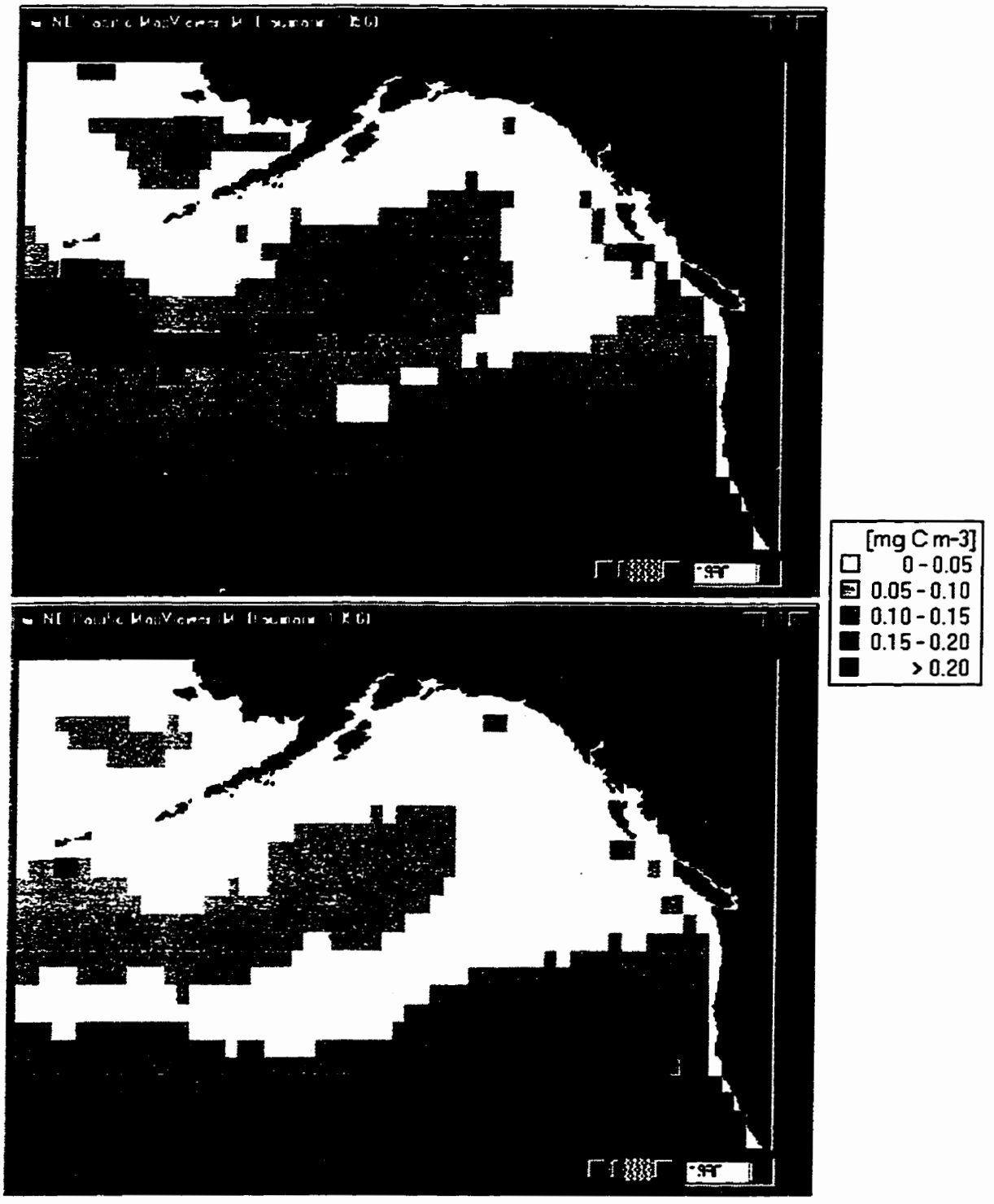

Fig. 4.22: Continued

In summary, effects of the spatio-temporal distribution of prey for juvenile sockeye salmon, i.e. mesozooplankton (see Section 2.1.), on the survival rates of combined stocks are more plausible for Bristol Bay sockeye salmon than for combined Fraser River stocks. This is consistent with the fact that survival rates of the Bristol Bay river systems are more frequently cross-correlated with each other than Fraser River stocks are with each other (see Fig. 1.3). However, knowing better than anybody else the shortcomings of the input data as well as all the assumptions that went into the population models and ecosystem simulations, my interpretation of the result is rather devastating: Simulation results of my spatially-explicit simulations do not suggest a clear linkage between prey density in the oceanic environment and sockeye salmon cohort survival (see also Chapter 5).

5. CONCLUSIONS

"The primary value of models is heuristic."
N. Oreskes et al. (1994)

"But many of our pictures are incarnations of concepts masquerading as neutral descriptions of nature. These are the most potent sources of conformity ..."
S.J. Gould (1989) Wonderful Life

The conclusions to my research are stated under the assumption that input data (Section 3.2.) as well as data used to validate simulation results (Section 4.2.) somehow reflect the natural world. This assumption is probably reasonable even though it has been questioned in principle; clearly, without it any interpretation is possible. Furthermore, I will abstain from suggesting lists of improved input data, and critical data (variables, locations, time) for model and simulation validation, as well as from suggestions for model improvements. Although such propositions are standard practice, they are either obvious (e.g. If crucial data of a specific kind at a particular location for a certain period of time have not yet been collected, they should be collected in the future.) or implicit in the model and simulation development (Chapter 3 and Section 4.1.) and simulation results (Sections 3.4. and 4.2.).

Conclusion: I have tried to design the best models within reason utilizing the best information on environmental forcings and biological processes available at the time. Nevertheless, my results do not suggest a clear linkage between prey density in the oceanic environment and sockeye salmon cohort survival.

Corollary #1: While life history strategies are a nuisance to trophodynamic modeling, they are the essence of life.

Sockeye Salmon

The environment that has been simulated represents at best a fraction of the space and time of sockeye salmon lifetime habitat (i.e. the integral of abiotic and biotic factors that affect sockeye salmon in certain locations at certain times): After emergence a juvenile sockeye salmon spends one or two winters in a lake, followed by a migration to the sea where its spends another one to three winters (Burgner 1991). In each of the encountered habitats (i.e. creek, river, lake, river, estuary, coastal ocean, open ocean, coastal ocean, estuary, river, creek) a sockeye salmon interacts with local populations by foraging upon prey, outwitting intraspecific and interspecific competitors, and avoiding predators, all before a background of abiotic environmental conditions (e.g. temperature and salinity), with the simple goal to survive and reproduce. As an individual enters each of these habitats it will have to make behavioral decisions (e.g. when to forage, hide, emigrate) depending on its body size (a function of previous habitats and thus historical contingent), predation risk and growth potential (both complex functions of biotic and abiotic components of the habitat it is in). What's more, an individual will adapt to the situation at hand within the larger context of the average behavior (i.e. life history strategy). Although the sockeye salmon life cycle is relatively simple (semelparous, constant life cycle with clearly defined life history stages in different habitats) the complexity of the specifics is clearly overwhelming.

While it is assumed that earlier life history stages have higher specific mortality rates as well as higher variability in specific mortality rates than later ones, it is not known whether one particular life history stage determines year class survivorship of sockeye salmon nor whether it

is the same for every cohort of every stock (see Assumption #1 in Section 1.4.). Yet, it might well be that for some stocks in some years cohort survival is determined early in marine life. However, even if early marine life determines year class survivorship, how likely is it that I will see similar temporal patterns in sockeye cohort survival and spatio-temporal distribution of prey density in the northeastern Gulf of Alaska? Not very, because of the following:

(1) Top-down argument: Juvenile fish don't usually starve to death but are rather preyed upon by predators. However, neither fish nor predators are included in my models (see Section 3.1.), and even if they were, current computational limitations do not allow implementation of behavioral responses at the correct spatio-temporal scales (see Assumptions #2 and #4 in Section 1.4.).

(2) Bottom-up argument: It has been shown that in the first months at sea (July to February) juvenile British Columbia sockeye salmon migrate with the main currents (see Fig. 2.1) along the coastal regions of the Gulf of Alaska (J. Scandol 1996 pers. comm. (simulations); D. Welch 1998 pers. comm. (data)). However, insufficient information on the ecosystem of the Coastal Downwelling Domain (Subsection 2.2.2.), the lack of a coastal advection model, and the spatio-temporal resolution of the input data (Section 3.2.) forced me exclude the coastal region from my simulations. Further, while in nature one sees a transition from open ocean to coastal ecosystems with a variable seasonal and interannual gradient (steepness, space, time) in species distributions (D. Mackas 1996 pers. comm.), all habitats were simulated as open ocean ecosystems, notably with no consideration for the seasonal variability in chlorophyll-a and macronutrient concentrations (Section 3.1.).

(3) Argument of spatio-temporal scales: Let's for a moment assume that the mesozooplankton densities determine year-class survival in sockeye salmon. How well do the

prey distributions depicted in the maps in Section 4.2. reflect the availability of prey to sockeye salmon in the natural environment (even in the absence of predators)? The maps show monthly mean concentrations with a spatial resolution of 1° longitude x 1° latitude (approximately 100 x 100 km). Consequently, natural patchiness below that resolution is not represented in the simulations. Thus, a school of juvenile sockeye salmon that enters the simulated ocean habitat in July will find a completely uniform 100 x 100 km patch which it will cross within four days or so. The school will then enter the next completely uniform 100 x 100 km patch, and so on. While the outmigration timing has been deemed important (culminating in the conceptual match-mismatch hypothesis) the spatio-temporal scales of the ecological processes involved are extremely difficult to assess. It is unlikely that a coarse 100 x 100 km grid does provide the correct spatial and temporal scales to account for population level ecological processes (see Assumption #4 in Section 1.4.).

Zooplankton

The obviously important question is: Does increased zooplankton abundance affect fish survival, and if so, what determines zooplankton abundance, how, when and where? One important aspect of the open ocean ecosystem of the Northeast Pacific are ontogenetically migrating copepod species. Unfortunately, until now only descriptive studies covering limited spatio-temporal domains (the period when certain developmental stages inhabit the surface) have been conducted (R. Goldblatt 1998 pers. comm.), mostly due to the logistic difficulties of exploring a mesopelagic ecosystem. Important questions on the life history of ontogenetically migrating zooplankton species are:

(1) What determines their time of ascent and descent in the ontogenetic migration?

(2) What determines their survival at depth?

(3) How do surface and deep-water currents affect their distribution?

While little is known about the agents in the life history of mesozooplankton (i.e. *Neocalanus* spp.) even less information is available on macrozooplankton. Not only are certain gelatinous and fast swimming groups of macrozooplankton undersampled by standard sampling devices (Parsons & Lalli 1988) but the lack of knowledge about the biology of the organisms of this size class also compelled me to model macrozooplankton mortality (in the 4-trophic levels model) as a density-independent function of adult body size and temperature (Section 3.4.). Although it is possible in principle, mortality is not likely to be density-independent at all life-history stages.

Since life-history strategies at all trophic levels have the potential of altering simulation results significantly future modeling and simulation excercises will ultimately have to address them.

Corollary #2: Trophodynamic simulations are inadequate to predict effects of ecosystems on the dynamics of a particular population.

Trophodynamic models and simulations are of the type developed in this thesis where various groups of organisms are aggregated into hypothetical trophic levels which through consumption and production process energy (in the from of reduced carbon compounds). During model design I assumed that for plankton organism different size classes do represent different trophic levels (see Assumption #3 in Chapter 1). However, there are several problems associated with this trophodynamic approach (see also Cousins 1987; Peters 1977, and for a synthesis Oksanen 1991):

(1) Particular species cannot be catalogued to a particular integer trophic level, i.e. most species have a mixed diet. Some authors (e.g. Pauly & Christensen 1995a; Pauly & Christensen 1995b; Wulff *et al.* 1989) have tried to go around this problem by allocating organisms to partial trophic levels (TL), or effective trophic positions (Field *et al.* 1989), following the simple formula:

$$TL = 1 + \sum_i \left[\frac{(\text{weight of food item i in stomach contents})}{(\text{total weight of stomach contents})} (\text{trophic level of food item i}) \right] \quad \text{(Eq. 5.1)}$$

where the sum represents the mean trophic level of the prey organisms. However, instead of weight (wet, dry, carbon?) one could use volume or energy content (Lindemann 1942), and instead of stomach contents, i.e. ingested food, one could use assimilated food. Determining trophic levels of all the food items in a food web is thus not only tedious but also ambiguous. See also the six different definitions for "trophic level" given in Yodzis (1989).

(2) While the aggregation of biospecies into trophic levels is generally a function of knowledge about the system (Rice 1995) and will thus result in unequal resolution of aggregation, aggregation by size class as done in my models seems less arbitrary than any other categorization in marine systems. However, if we look at sockeye salmon we find that some organisms are prey for sockeye salmon or food for its prey, and so on. Others are competitors (residing in the 'fish' box in Fig. 1.9) or predators of sockeye salmon, yet others prey upon sockeye competitors or predators thus improving survival of sockeye salmon, while sockeye salmon itself is predator, competitor, prey, or cause of indirect positive or negative effects on other populations. (Any indirect effects which non-adjacent trophic levels have onto each other are called trophic cascading (Carpenter *et al.* 1985; Carpenter *et al.* 1987).) So, for example it

might well be that mesozooplankton production and availability increases while sockeye salmon survival decreases.

Thus, more important than the concept of trophic level itself is the heterogeneity (diversity in species and life history strategies) that one will incorporate into whatever aggregation one is going to choose. As I have tried to demonstrate life history strategies are very complex concepts (Corollary #1), and consequently it is not guaranteed that the "average" simulated plankton organism representing a certain size class will respond to abiotic (e.g. temperature) and biotic (e.g. prey density) in the same way as the diversity of species in the natural system (see Brown & Rothery (1993) their Section 8.15).

(3) A particular species will not occupy the same trophic level at different locations, times and life history stages (see also Corollary #1). An obvious example is the change in diet that follows ontogenetic growth and development of an individual, i.e. metaphoetesis. As shown in Eq. 3.6 (Chapter 3) any increase in biomass of a particular size class is due to assimilation of food (i.e. ingestion - (egestion + respiration)), recruitment or import. However, lacking data on recruitment (e.g. births, and molding and body growth processes), biomass changes had to be restricted to feeding (Eqs. 3.8-3.10). This means that a unit of assimilated prey biomass immediately assumes the foraging specific abilities of an average predator organism of a particular size class. (A similar problem can be found in simulations where organisms are expressed in units of numbers of individuals and where a newly born individual immediately assumes the abilities of an adult organism. In fact, simulation in units of numbers and biomass should run simultaneously.)

(4) Detritus food chains and microbial loops do not fit the trophodynamic concept of unidirectional energy transfers. Consequently, the role of microzooplankton, which represents a

crucial part of the microbial loop (see Fig. 1.9), for the dynamics of higher trophic levels is not adequately addressed in my simulations.

Furthermore, it has been shown that simple experimental systems with more than one species per clearly definable trophic level exhibit fairly complex, and not at all intuitive, dynamics (Leibold & Wilbur 1992; Pimm 1992). Obviously, the linear and fairly tractable trophodynamic approach to ecosystem research is inadequate, or to quote Jake Rice (1995):

"Although we may wish for systems that are more tractable, it may be necessary to accept the limits of predictability of marine ecosystems. ... When we try to predict trophic consequences of the environmentally driven changes in abundances, science quickly becomes fiction."

In my opinion, the categorization of ecosystem components into trophic levels is one of the worst aggregation errors in ecology, one that implicitly includes errors of hierarchical organization as well as of spatio-temporal stability. Consequently, the development of a new trophodynamic theory will be necessary, one that reflects life history strategies of many very different interacting species more appropriately (see also Corollaries #5 and #1). However, this development will be closely linked to biodiversity research, a field that has become scientifically locked in for decades and which is not likely to make major advances in the near future (compare the classic dogma by Hutchinson (1961) with the little known publication by Ghilarov (1984)).

Corollary #3: 'What if' questions are irrelevant when important variables and processes are unresolved in models and simulations.

Again, simulation results do not suggest a clear linkage between prey density in the oceanic environment and sockeye salmon cohort survival.. So, I could proceed by modifying several aspects of my model(s) and simulations: e.g. include nutrient dynamics; add another size class of phytoplankton, or another trophic level, or a whole coastal ecosystem model; change the numerical values of biological parameters or the functional relationships between environmental forcings and dependent physical or biological variables; increase or decrease the spatial resolution; include a forced ontogenetic vertical migration of mesozooplankton, macrozooplankton, fish ... . At what point would I decide that further modifications of the model(s) or simulations are no longer necessary or justifiable? When the simulation results fit the observations? There are two problems with this: First, "what we call data are inference-laden signifiers of natural phenomena to which we have incomplete access." (Oreskes *et al.* 1994; see also Corollary #4). I realize that this is a rather destructive argument for the cause of science in general but obviously for any natural ecosystem (and for the Northeast Pacific in particular) there will never be enough data to exclude a variety of alternative explanations for any observed phenomenon (a characteristic of all open systems). And second, model and simulation results are non-unique, i.e. possibly many other models representing very different mechanisms will exhibit the same result.

The futility of simulation experiments becomes even more clear when considering the following: Suppose that one would like investigate the effects of a 10% temperature increase in the surface layer of the Northeast Pacific onto the mesozooplankton spatio-temporal distribution using a completely verified model (although I agree that verification is not possible in principle;

see Oreskes *et al.* 1994). Considering the many non-linearities in the natural world, we cannot know if the natural system would not undergo major fundamental changes (e.g. phase transitions in community structure, species life histories) under new environmental forcings, changes that could not have been anticipated at the time of original model design. Simulation experiments will thus always push a model beyond its domain of inference (but if they wouldn't, why conduct a simulation experiment in the first place?).

It has also been suggested that stochastic dynamic models (Brown & Rothery 1993; Levin *et al.* 1997; Steele 1985; Steele & Henderson 1994) might be a better representation of natural phenomena because "... deterministic ecosystem concepts and models are not so easily applicable." (Steele 1985) Assuming that this is true (see also Corollary #4), does it make ecosystem research less ambiguous? The first question that arises is: Where in the model should we add random components? To one (many, all?) environmental input variables, to one or more population parameters, to population processes (such as births and deaths)? And if so how large a random disturbance, where and at what time? Unfortunately, simulation results of even simple (single population and predator-prey) models are often contradictory and depend critically on the terms (variable, parameter) to which stochastic noise has been added (Pimm 1982).

Looking at Corollaries #2 and #3, one might suggest that trophodynamic models could at least be improved to the extent as to correctly predict (or hindcast) the behavior of the dominating ecosystem aggregations (e.g. fish in Fig. 1.9). While it can be argued that this proposition is false in principle (since we do not know the importance of the less apparent species to the functioning of the ecological community), empirical evidence suggests that we are still far away from such predictions even for systems with, for all practical purposes, unlimited

research funding and data: E.g. Try to predict (or hindcast) the behavior of the Dow-Jones Industrial Index (which summarizes the behavior of 30 (agreed upon!) representative industrial stocks); or, for the sake of disproving Corollary #2, the behavior of any particular stock from the behavior of Standard and Poor's 500 Stock Index.

Corollary #4: System complexity and human nature make it impossible to predict the behavior of ecosystem components by all practical standards. False predictions can always easily be explained by a variety of components and processes whose effects have not been considered in an ecosystem analysis and synthesis.

Corollary #4 is the consequence of a mistake I originally made when preparing the maps in Fig. 4.17: Instead of plotting the mean simulated mesozooplankton concentrations for the month of July 1956 to 1959, and 1980 to 1989 as a result of the 4-trophic levels simulation with advection (Fig. 4.17), I plotted the mean simulated mesozooplankton concentrations for the month of July 1956 to 1959 as a result of the 4-trophic levels simulation without advection (Fig. 5.1., upper panel), and for the same month for the years 1980 to 1989 as a result of the 4-trophic levels simulation with advection (Fig. 5.1, lower panel). Fig. 5.1 resembles very much observational data (see Fig. 1.7). So, naturally when I found the mistake for a second or so I wished I had not rechecked the maps, and less than two hours later I could come up with at least a dozen explanations why Figs. 4.17 and 1.7 don't resemble each other.

Ecosystem research confronts scientists very quickly with an overwhelming amount of detail and information (e.g. see Table 1 in Briand 1983, Table II in Parsons & Lalli 1988, Tables 3 and 4 in Healey 1991). In order to process the wealth of information about an ecological, or any other complex adaptive, system in a 'meaningful' way, simplifications have to be made. It is not

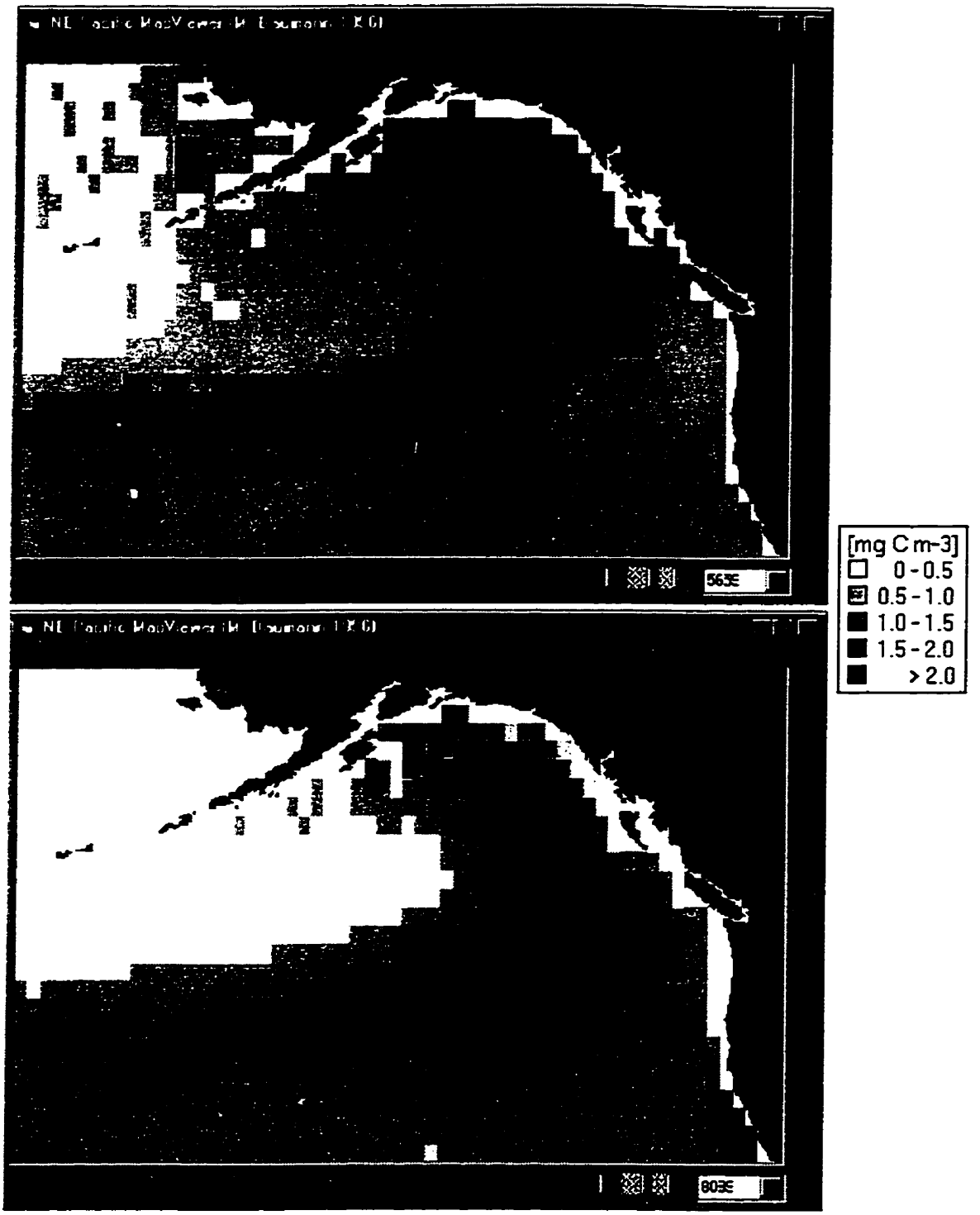

Fig. 5.1: Mean simulated mesozooplankton concentrations [mg C m^{-3}]. Upper panel: For the month of July 1956 to 1959 as a result of the 4-trophic levels simulation without advection. Lower panel: For the month of July 1980 to 1989 as a result of the 4-trophic levels simulation with advection.

unreasonable to assume that the simplification (or cognitive model building) process that occurs in our brain is the result of natural selection and thus reflects abilities that were relevant for our survival (but not necessarily relevant for science). Evolutionary epistemologists have studied this problem and have developed four theorems about human cognitive behavior (Riedl 1984, R. Riedl 1989 pers. comm.). The human analytical/logical-deductive apparatus behaves:

(1) as if the most likely explanation is true (Hypothesis of Apparent Truth).

(2) in order to magnify similarities and ignore differences (Hypothesis of the Comparable).

(3) as if similar consequences have similar causes (Hypothesis of the First Cause).

(4) as if similar causes have similar consequences (Hypothesis of the Purposeful).

(As many of you will note, the first theorem provides an explanation for the many schools of thought in the scientific community as 'most likely' is a consequence of the interpretation of incomplete data (see Corollary 3).) It thus follows from the complexity of the natural ecosystem and the architecture of the human mind that:

(1) a modeler's knowledge about the modeled system as well as about the simplifications that went into the model will (hopefully) always enable her or him to identify alternative explanations, and

(2) he or she will actually 'believe' in these explanations.

Corollary #5: The development of new analytical and synthetic methodologies is crucial for the study of complex systems.

What do my conclusions then mean in practical terms for ecosystem research? We have little predictive capacity about spatio-temporal changes in physical forcings. We have little understanding about biological organizational adaptation as well as spatio-temporal ecological

patterns and processes that occur in even constant environments. And we have even less knowledge about the effects of physical forcings on ecological processes (e.g. spatio-temporal distribution, competition, predator-prey relationships), not to mention changes in physical forcings (Davis *et al.* 1998). Worst of all because ecosystems are so complex and we have only limited access to data (which are likely to document only interesting events anyway; for a discussion see Durlauf 1997; May 1976a; Rice 1995) we will believe in any reasonable explanation set by the evolutionary constraints of our mind.

While we humans have certainly acquired cognitive capabilities during our phylogenetic development that allow us to make predictions necessary for survival and reproduction (Survive and reproduce are fairly simple rules!), the true nature of complex systems may well lie beyond the scope of our understanding, and our simplification apparatus may simply be not adapted to deal with complex systems such as ecosystems or stock markets. What solutions do I suggest?

(1) With respect to understanding the working of ecosystems, future ecological research should focus on the full complexity of ecosystems and try to implement into computers synthetic systems with a large number of components that are able to adapt (i.e. Artificial Life). As demonstrated in this thesis simple trophodynamic models are simply too vague and assumption-laden as to contribute to a deeper understanding of ecological systems.

(2) And with respect to prediction of complex systems behavior: While we humans do admit to the fact that algorithmic computing outperforms human arithmetic capabilities indefinitely for all practical purposes, the idea that intelligent computational platforms perform complex analytical tasks (assimilation of uncertain data and advanced logical operation) that lie beyond human comprehension, may well be unsettling for many (as it was for me when I started

developing ideas to that end). However, qualitatively new tasks will require qualitatively new methodology. We should consider the possibilities of our own limitations.

The purpose of simulations is to test hypotheses, and the complex hypothesis that I have tested in my simulations can be stated as: Is it enough to consider lower trophic level dynamics in the oceanic environment in order to explain the variability in sockeye salmon cohort survival? Since my results do not suggest a clear linkage between prey density in the oceanic environment and sockeye salmon survival, obviously other factors (e.g. sockeye salmon, its competitors and predators, in various habitats, and possibly with the whole spectrum of individual complex behaviors) have to be included in the conceptual (or otherwise) models in order to provide a satisfactory explanation for sockeye salmon cohort survival. Future sampling programs, experiments and computer simulations should take the next step and investigate ecosystems from the viewpoint their components' life history strategies rather than trophic relationships. Considering how little information is available on even well-studied organisms (e.g. Neocalanus sp., Subsection 2.2.1.), this is not an easy task. Simple (even abstract models) should enable us to at least assess how successful this approach might be and what kinds of data at what spatio-temporal resolution will be necessary. Only then we should make choices on future research topics.

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IMAGE EVALUATION
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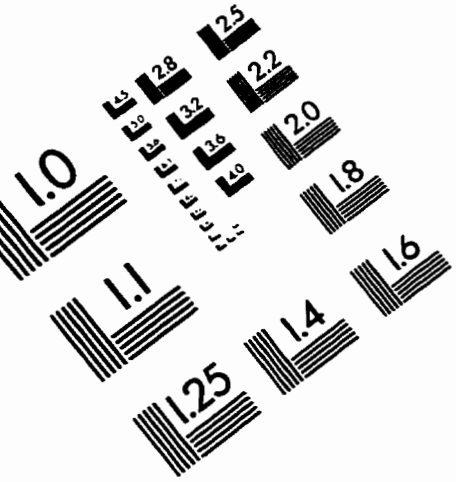

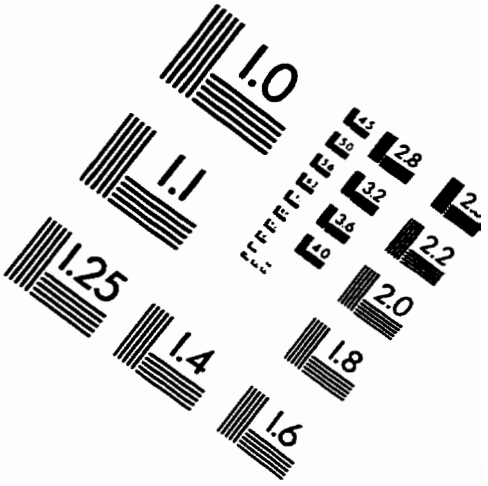

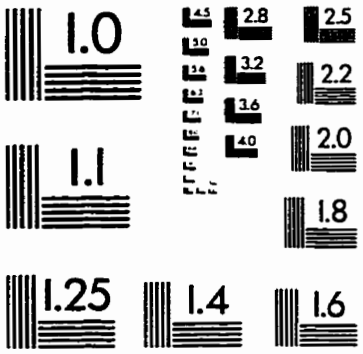

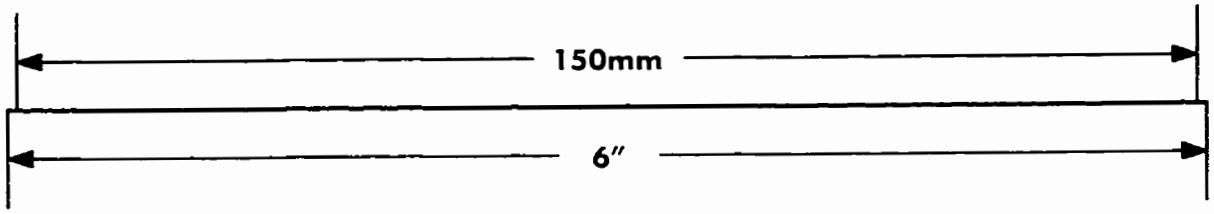

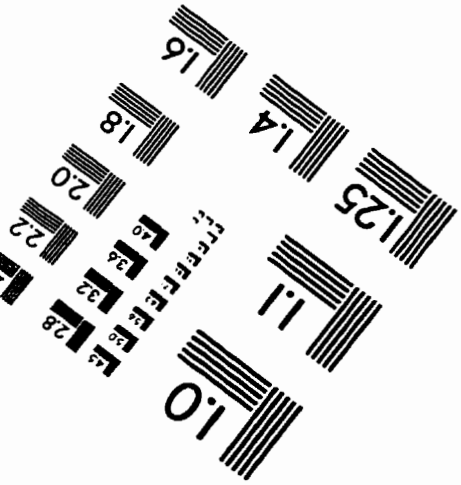

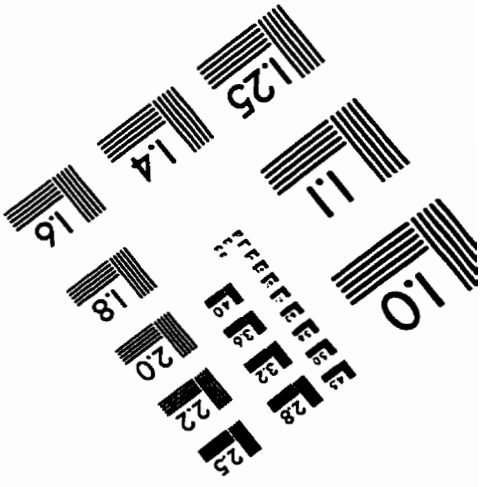

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