Exxon Valdez Oil Spill
Restoration Project Annual Report

Biophysical Modeling and Validation Through Remote Sensing

Restoration Project 96320-R
Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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Study History: This project is the result of an internal reorganization within the Sound Ecosystem Assessment (SEA) program.. Some of the work performed under SEA core projects 95320-G and 95320-J in FY-94 and FY-95 is to be done under this project in FY-96 and beyond. We are continuing the trophodynamic modeling of phytoplankton and zooplankton begun in FY-95 and adding modeling of ichthyoplankton, herring larvae in particular. We are evaluating and verifying the model against field data collected using a variety of remote sensing and *in situ* sampling platforms.

Abstract: Coupled physical and biological modeling of phytoplankton and zooplankton dynamics in Prince William Sound and the Gulf of Alaska have shown there to be two general scenarios of springtime dynamics. Warm, quiescent springs lead to brief intense phytoplankton blooms, whereas, colder, stormy springs lead to longer phytoplankton blooms. These two types of phytoplankton blooms produce substantially different zooplankton blooms. The brief intense blooms occur too quickly for much biomass to be transferred into the upper trophic levels. Therefore, the following zooplankton bloom is substantially lower. In contrast, the longer duration phytoplankton blooms allow time for the zooplankton to "catch up" and produce high zooplankton concentrations. In FY-96, we completed and validated a one-dimensional model that accurately simulated these dynamics. This model is being expanded into the full three-dimensional domain during FY-97 and FY-98.

Key Words: biophysical modeling, biological oceanography, physical oceanography, phytoplankton, Prince William Sound, spring bloom, zooplankton

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Table of Contents:

List of Tables, Figures, and Appendices:

Executive Summary:

Numerical modeling of phytoplankton and zooplankton, in combination with field data collected as part of 320-G and 320-H, shows that phytoplankton and zooplankton populations in Prince William Sound and the northern Gulf of Alaska are determined by the winds and air temperatures which occur over a relatively short, critical time period in early spring. Although this critical time period may be as short as two weeks, the meteorological conditions occurring during that time will play a dominant role in the dynamics of the phytoplankton and zooplankton populations for the rest of the summer. Changes in the amount of convective mixing, caused by cold air, and of wind mixing, caused by high winds, during the early part of the phytoplankton bloom change the timing and duration of the bloom, the total primary production occurring during the bloom, and the partitioning of that primary production between the upper water column food chain, and the benthic food chain.

The spring phytoplankton bloom occurs when mixing of the surface waters stops and there is sufficient light for phytoplankton growth to occur. In Prince William Sound and the Gulf of Alaska, this typically occurs in sometime in April. Blooms can be roughly categorized into two types, brief, intense blooms and longer, less intense blooms. The weather conditions during the initial part of the bloom determine what type of phytoplankton bloom will occur. If it is a relatively calm, warm spring, the water column stratifies and forms a shallow surface mixed layer. Phytoplankton and nutrients within this mixed layer are isolated from those deeper in the water column. With abundant light in the surface layer, phytoplankton quickly reproduce and build up their standing stocks to fairly high levels. As a consequence of this growth, nutrients are soon depleted and phytoplankton sink out of the surface layer. Because zooplankton reproduce at much slower rates than phytoplankton, the zooplankton populations cannot consume much of the phytoplankton production. The non-grazed phytoplankton slowly sinks out of the surface layer to deeper waters where it may be consumed by deeper pelagic organisms, or by the benthic fauna. Therefore, a relatively warm, quiescent spring produces a relatively short phytoplankton bloom, with high phytoplankton biomass, however, much of the phytoplankton biomass does not get passed on to the zooplankton populations. Zooplankton biomass therefore remains at fairly low levels for the rest of the summer.

In contrast to this, a cooler, stormier spring leads to higher zooplankton biomass. Although the cold stormy weather may delay the stratification of the water column somewhat, the major effect observed in field data and model simulations is due to the progression of the phytoplankton bloom, not the time at which it began. Storms typically pass through the PWS area at a frequency of about once a week during late winter. If they continue on into early spring, they become important to the biological dynamics. In a cold stormy spring, stratification typically occurs between storms, and when it does occur, the surface mixed layer may be somewhat deeper than in warm calm springs. The phytoplankton bloom begins in this surface layer, but is interrupted by a cold windy storm. This deepens the mixed layer, which reduces phytoplankton concentrations and increases nutrient concentrations. The bloom then takes off again. Subsequent storms may repeat the process, but at some point the stabilization of the upper water

column, which has been increasing due to surface heating, becomes too strong and the seasonal mixed layer stabilizes. The phytoplankton bloom continues in this layer until nutrients are depleted. The net result of this type of spring weather is a deeper mixed layer, which took longer to become established. As a consequence of this, the phytoplankton bloom occurs over a longer period of time, and more nitrate is available for new primary production. In addition, the mixing of the surface layer has lengthened the total phytoplankton bloom period. During this longer period of high phytoplankton biomass, zooplankton increase in numbers and biomass and are thereby able to consume a higher proportion of the net production. Therefore, there is a transfer of more of the phytoplankton new production into the zooplankton population and zooplankton numbers and biomass remain high for the summer.

Both types of blooms have been observed in our four years of SEA field data. From the modeling work done as part of this project, we are able to determine the causes and interactions between the mixing regimes, phytoplankton, and zooplankton. This has allowed us to accurately simulate these processes. The zooplankton populations which have been modeled are of direct importance in the diet of juvenile pink salmon and larval and juvenile Pacific herring. Our understanding of the physical mechanisms that control the variable amounts of zooplankton (fish food, if you will) allows the SEA project to evaluate the effects of variability in the physical environment as it is propagated up through the phytoplankton and zooplankton, to the injured resources of Prince William Sound.

Introduction:

Pacific herring and pink salmon have been identified as non-recovering resources injured by the *Exxon Valdez* oil spill. An ecosystem approach has been recognized by the EVOS Trustee Council as being necessary to reaching an understanding of the underlying processes and variables which may be constraining recovery of these injured resources. The currently proposed work is critical to the ecosystem study being undertaken by the SEA program. The role of the physical environment in controlling phytoplankton, zooplankton, and ichthyoplankton populations, and the role of these populations in the life history of Pacific herring and pink salmon, must be understood for the intelligent, informed planning of successful restoration efforts.

This project directly addresses the SEA pink salmon and Pacific herring restoration objectives. The phytoplankton and zooplankton serve directly as food for both herring and pink salmon at various life stages. Two large calanoid copepod species, *Neocalanus cristatus* and *N. plumchrus*, in particular, are thought to be potentially important as both a dietary item and a refuge from predation for pink salmon. Larval and juvenile herring feed on different stages of calanoid copepods, which reproduce throughout the spring and summer. The reproductive effort of these copepods is dependent on the timing, magnitude, and duration of the phytoplankton primary production in the spring bloom period and throughout the summer. The interactions between the various types of phytoplankton (*e.g.*, diatoms, flagellates) and zooplankton (*e.g.*, oceanic copepods, neritic copepods) varies both between and within years. The timing of the major increase in biomass of phytoplankton or zooplankton, sometimes called the spring phytoplankton or zooplankton bloom, respectively, may be important to the first feeding and subsequent survival of the larval herring and juvenile herring and salmon, *e.g.* Cushing's match-mismatch hypothesis. This project examines these issues through the use of numerical models, remote sensing, and field observations.

Results through FY-96 indicate that physical forcing dominates the dynamics at the lower trophic levels. The physical signal propagates up through the food chain and has relevant consequences months after the physical interaction actually occurred. These effects are highly nonlinear, but can be accurately simulated using the present model.

Objectives:

The major objectives to be achieved over the life of this project as detailed in the FY-96 DPD were:

1. To construct a three-dimensional model of the physical/biological processes affecting phytoplankton, zooplankton, and ichthyoplankton dynamics in Prince William Sound.
2. To determine the relative roles of these processes in determining Pacific herring and pink salmon population levels.
3. To determine the spatial and temporal variability, both of the physical environment and of phytoplankton concentrations, using a combination of remote sensing techniques and field observations.

Additional minor objectives were:

4. To make laboratory measurements of the photosynthesis-irradiance parameters required to accurately model different phytoplankton populations.
5. To deploy and maintain an upgraded version of the CLAB buoy, which will provide high temporal resolution time series of wind velocity, air temperature, surface water temperature, and subsurface temperatures at 10 depths. This will be the primary data source for the development of the physical/biological dynamics portion of the model.

These objectives will enable us to test the following hypotheses:

1. That coupling between the physical environment and phytoplankton dynamics can be modeled reliably.
2. That phytoplankton dynamics drive zooplankton dynamics in a predictable manner, which can also be modeled.
3. That the survival of larval herring can be estimated by a combination of modeling and field work on eggs and 0-class juveniles.
4. That interactions between the physical environment, the zooplankton field, and juvenile pink salmon populations can be predicted using a coupled biological/physical 3-D model.
5. That the spatial variability of the SST and chlorophyll concentrations in Prince William Sound, observed in satellite remote sensing images, can be simulated by a 3-D model of physical and biological dynamics.

Methods:

We are using a combination of coupled biological and physical models and satellite remote sensing data sets to achieve the above objectives. We are continuing the development of a coupled biological-physical model of lower trophic level, i.e. phytoplankton and zooplankton, dynamics for the near-surface layers of Prince William Sound (PWS). We are expanding the one-dimensional, depth-time model developed in FY-95 to include herring larvae. The 1-D model will describes the biological and vertical processes that occur through time at a single location. The biological processes contained in the 1-D model are being integrated into a larger three-dimensional model with appropriate vertical resolution. This 3-D model will use the vector fields produced by the circulation model being constructed by V. Patrick and C. Mooers as part of 320-J. A detailed description of the methodology used in the one-dimensional bio-physical model is given in the Methods section of Appendix A.

Our remote sensing work entails reception and processing of National Oceanic and Atmospheric Administration (NOAA) Nimbus series satellite data in Fairbanks, AK. Data from the Nimbus Advanced Very High Resolution Radiometer (AVHRR) sensors are processed to produce sea surface temperature (SST) images of both the northern Gulf of Alaska (Figure 1) and a more detailed image of Prince William Sound (Figure 2). These images are archived and made available to the SEA project for comparison with model and field data. An additional type of satellite data should soon be available from the Japanese Ocean Color and Temperature Sensor (OCTS) which is being flown aboard the Japanese Advanced Earth Observation Satellite (ADEOS). D. Eslinger is and ADEOS/OCTS investigator and is pursuing the necessary international agreements to get access to the OCTS data and processing software. In addition, the SeaWiFS satellite is scheduled for launch in mid-1997. Within about 3 months after launch, we should have access to that data stream as well.

Results:

Detailed results from the one-dimensional modeling work are given in the Results section of Appendix A. Briefly, the 1-D model accurately simulates the timing and magnitude of the phytoplankton and zooplankton blooms in 3 out of the four years for which we have field data (Figures 3 and 4). The consistent differences in the timing which are observed in the 1994 simulation highlight the need for a spatial component in this model. The expansion of the 1-D model into 3-D space is the major goal of our FY-97 effort presently underway.

We have been processing and archiving AVHRR SST since 1994, and presently have an archive of over 17,000 SST images available to the SEA project. These images are stored on 8 mm tape, CD-ROM, and hard disk. In early FY-97, we delivered a subset of these images to the Prince William Sound Science Center (PWSSC) in CD-ROM format, for use by the PWSSC SEA investigators.

The measurable tasks which we proposed to perform in FY-96 and which were accomplished are listed below.

- Model phytoplankton and zooplankton using 1995 field data. Begin herring model literature search.
- Recover CLAB buoy deployed under 95320-G.
- Deploy CLAB buoy for 1996 field season.
- Begin herring model.
- Collect, process, and analyze AVHRR images for 1996 field season.
- Complete FY-96 field collection efforts.
- 1-D phytoplankton, zooplankton model complete.
- Complete analysis of AVHRR data from 1994-mid 1996.
- Annual report on FY-96 work.

The following tasks were not completed in FY-96. The reasons are given below.

- Collect remote-sensing reflectance as part of cruises. Incomplete: no funding available for the bio-optical instrumentation.
- Begin to collect, process and analyze ocean color from SeaWiFS and/or OCTS. Incomplete: satellites not launched during field season. SeaWiFS still not launched.
- Initial herring model complete. Incomplete: Although we have a preliminary ichthyoplankton model working, it is not complete. This was a typographical error. A meaningful model can not be constructed in the six months of time as stated. The correct time for the completion of the initial ichthyoplankton/larval herring model is September of FY-97.

Discussion:

A full discussion of the model results is presented in Appendix A.

Conclusions:

The coupled bio-physical model being developed as part of this project is able to simulate the phytoplankton and zooplankton dynamics in the upper waters of Prince William Sound. In most years, this model requires measurements of only air temperatures and winds to accurately model the timing and magnitude of the phytoplankton and zooplankton blooms. The year in which the model is significantly less accurate highlights the need for the continued work on developing the fully three-dimensional biological-physical model. The development of this model will enable us to simulate concentrations of zooplankton, the primary food source for pink salmon fry and larval and juvenile Pacific herring, based on relatively easily measured meteorological variables.

Appendix A

DRAFT

Modeling Phytoplankton and Zooplankton Variability in Prince William Sound, Alaska

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Introduction

Prince William Sound is a deep, sub-arctic, semi-enclosed water body bordering the Gulf of Alaska, Figure 1. The Prince William Sound (PWS) region is the base for a large commercial fishing fleet. Phytoplankton and zooplankton in PWS are the main food sources for early life stages of several commercially important fishes, particularly Pacific herring and pink salmon. During the spring, phytoplankton and zooplankton biomass exhibit pronounced increases, often called spring blooms, within the Sound. These blooms vary in magnitude, timing, and duration both spatially and interannually. A well established theory for variations in the timing of the phytoplankton spring bloom was put forward by Sverdrup (1953), in which the relationship between the depth of water column mixing and the available light controlled the timing of the onset of the bloom. Eslinger and Iverson (*in press*) constructed a coupled biological-physical model for the spring phytoplankton bloom in the southeastern Bering Sea. That model replicated the initial spring diatom bloom over the Bering Sea shelf quite well. The accuracy of that model was due to the high vertical resolution, 2 meters, used. This high resolution enabled features such as self-shading and nutrient limitation to realistically interact with rapidly varying mixed layer depths. We have built upon the basic Eslinger and Iverson model (hereafter, the EI model) and constructed a model suitable for examining annual phytoplankton and zooplankton dynamics with a high temporal and vertical resolution.

In the following sections of this paper we will describe the physical and biological dynamics included in the model, compare model results to field data for four years and two locations, and discuss the conclusions that can be drawn from the model and field results.

Methods

Field Data

Model results were compared with field data collected as part of the Sound Ecosystem Assessment (SEA) project. Phytoplankton and zooplankton samples were collected during a series of cruises in 1994, 1995, and 1996, and daily at a field camp during 1995 and 1996. Chlorophyll concentrations were measured using standard fluorometric techniques (Strickland and Parsons, 1976) with extractions done in 90 percent acetone. Zooplankton settled volumes and biomass data were collected as part of 9x320-H. Techniques used are described in the annual report for that project. Data presented here are from tows made from depths less than 100 meters, generally 50 meters, to the surface.

Description of the Model

The coupled biophysical model used in this study is a major expansion of a spring diatom bloom model of Eslinger and Iverson (*in press*). The significant features of the EI model retained in our model are the high vertical resolution, 2 meters, and the realistic mixed-layer dynamics. We modified the EI model to apply to annual time periods by increasing the number and complexity of the chemical and biological processes included in the model. We have added ammonium and silicon dynamics; a flagellate component; three types of zooplankton: large *Neocalanus*-type copepods, smaller *Pseudocalanus*-type copepods, and euphausiids; and an unspecified carnivorous nekton component which preys upon the zooplankton. Details of the model are given below.

Physical Model and Forcing Variables:

The physical domain is the upper 100 meters of a significantly deeper water column. Therefore, there are no bottom boundary layer or tidally mixed layer effects. The physical model was a 50-layer, one-dimensional mixed-layer model based on the model of Pollard, *et al.* (1973) as modified by Thompson (1976). Meteorological forcing (due to wind mixing, solar heating, ocean-atmosphere heat fluxes) is applied at the surface and the water column mixes downward until there is a balance between the kinetic energy available for additional mixing and the potential energy cost of overcoming the existing stratification. This balance is determined by examining the Fruode number of the mixed layer. A full description of the 1-D physical model can be found in Eslinger (1990). Vertical grid resolution is 2 meters (a 50 layer model), and the time step is two hours. The model was run to examine interannual and spatial variability. When run in an interannual mode, the model was run beginning in late February or early March, depending on the availability of forcing data, and was run through approximately the middle of November for 1993, 1994, 1995, and 1996. Although the model was run for the greater part of the year, we will limit the remainder of this discussion to the spring and summer periods, when the planktonic dynamics are greatest. Meteorological forcing data were obtained from the Continuous-Linked Automated Buoy (C-LAB) moored buoy system initiated by Dr. Ted Cooney as part of the Cooperative Fisheries and Oceanographic Studies program. In 1995, buoy data were unavailable for the early portion of the year, so meteorological data from a National Weather Service (NWS) unmanned station on Middleton Island, Alaska, were used. The 1995 spatial variability analysis was performed using forcing data from two NWS stations: the Middleton Island, AK NWS station, and a NWS station located at Whittier, AK. For 1996, spatially varying winds were taken form two NOAA buoys in Prince William Sound. Locations at which all forcing data were collected are shown in Figure 1. Insolation data required by the model was calculated using the radiation model of Frouin *et al.* (1989).

Biological Dynamics:

Both diatoms and flagellates are included in the model. Maximum possible daily growth rates of both species were determined by temperature (Eppley, 1972), and were reduced by light or nutrient limitation. Nitrate, ammonium, and silicon are considered as potentially biologically limiting nutrients, and nutrient uptake rate is assumed to follow a Michaelis-Menten relationship (Dugdale, 1967). Ammonium inhibition of nitrate uptake is included (Wroblewski, 1977). Both phytoplankton species compete for the nitrogen nutrients; silicon is utilized only by the diatoms. Photosynthesis is calculated as a function of light intensity, with potential photoinhibition (Platt *et al.,* 1980). Maximum growth rate for each species was calculated by multiplying the temperature dependent growth rate by a non-dimensional value that was the minimum of the relative amount of limitation by nutrients or light. At very low nutrient concentrations, the uptake rate for the phytoplankton species with the slowest uptake rate was calculated based on the amount of nutrient available after uptake by the phytoplankton species with the fastest uptake rate.

Copepods dominate the spring and early summer zooplankton biomass in Prince William Sound and euphausiids are a significant fraction of the remaining biomass. The copepods can generally be broken down into two types. There is a group of larger species composed of *Neocalanus flemingeri, N. plumchrus, N. cristatus, Calanus marshallae, Eucalanus bungii,* and *Metridia ochotensis.* We will hereafter refer to these as the neocalanus-type copepods, or as just neocalanus. In contrast, there is a group of generally smaller species composed primarily of *Pseudocalanus spp., Acartia spp., Oithona spp.,* and *Metridia spp.* aside from *M. ochotensis.* We will hereafter refer to these as the pseudocalanus-type copepods, or as just pseudocalanus. These two groups make up approximately 90% of the springtime zooplankton biomass. In addition to size, these two types of calanoid copepods have dramatically different reproductive strategies. The neocalanus-type copepods undergo a dramatic ontogenetic migration, descending in late summer as stage copepidite V (hereafter, CV's) to a depth of 200-400 meters, where they overwinter. The following spring they mature, reproduce and die. Their eggs hatch at depth and the nauplii begin to ascend towards the surface, which they reach at about the time they mature to the CI stage. This is generally prior to the spring phytoplankton bloom. They feed and grow in the surface waters for approximately 65-75 days, after which they begin to descend again, as CV's (Fulton, 1973). In contrast, the pseudocalanus-type copepods spend the majority of their life cycle in the upper water column, and overwinter as adult, fertilized females. These females must feed on the spring phytoplankton bloom to begin reproducing, and can reproduce up to 10 times at approximately 5 day intervals (Corkett and McLaren, 1978). The life history descriptions given are representative and are a simplification for the purposes of creating this model. Several species of euphausiids occur in Prince William Sound. The most abundant genera are *Euphausia* and *Thysanoessa.* Euphausiid life history was also simplified in the model. Total euphausiid biomass was modeled and reproduction was included in the increases in population biomass.

Three types of zooplankton are included in the model: neocalanus-, and pseudocalanus-type copepods, and euphausiids. In the model, Neocalanus arrive in the surface (enter the model domain), as three groups of CI's, spaced over a 30 day time period, with the middle group containing one-half of the total biomass the other two groups containing one-quarter total biomass each. Both pseudocalanus and euphausiids were present in the model at the start of the run. Life history dynamics of both populations were simplified in the model by simulating total biomass for each population, with no attempt made at keeping track of life stages. This simplification introduced some errors, *e.g.*, individual weight-specific parameters, such as grazing rate, were constant for all life stages; and that egg biomass is included in total biomass when calculating population biomass-specific effects, *e.g.* zooplankton grazing. As will be seen, these assumptions did not prevent the model from accurately simulated the zooplankton populations. The model dynamics for all zooplankton include modified Ivlev-type grazing (Ivlev, 1945; Magley, 1990) on both diatoms and flagellates; fecal pellet production, excretion of ammonium, and natural mortality (6%/day). Actual rates of the various parameters differed between the three zooplankton types.

Results

The model results showed that small differences in the meteorological forcing over a short critical time early in the spring phytoplankton bloom could create order of magnitude variations in the standing stock of zooplankton later in the summer. These small changes had similar effects when they occurred at a single location due to interannual variation in meteorological conditions, and when they occurred at different locations in the same year due to fairly small horizontal gradients in meteorological conditions.

Interannual Variability

The model was run for 1993, 1994, 1995, and 1996. The simulations began with identical initial temperature and nutrient fields and initial concentrations of phytoplankton and zooplankton. The only differences were in the meteorological forcing data sets. Figure 2 shows winds speeds, air temperatures and simulated chlorophyll concentrations for the four years. In all years, the model phytoplankton blooms began during the first period of calm winds after the last cold storm event. Model chlorophyll concentrations are compared with C-LAB buoy fluorescence in Figure 3. In 1993, the model simulated the timing, magnitude, and duration of the spring phytoplankton bloom extremely well. The bloom was fairly short in duration, approximately 20 days, and maximum chlorophyll concentrations were reached approximately 5 days after the onset of the bloom (Figure 3 a). In 1994, the model bloom began approximately 10 days earlier than the bloom observed in the fluorescence data. The magnitude of the true bloom was correctly estimated in the modeled bloom, but the timing of the peak was off. In both the model results and field data, the chlorophyll initially increased rapidly in 1994, however, a number of strong cooling events occurred in the middle of the bloom and led to a more protracted phytoplankton bloom (Figures 2 b, 3 b). In the 1995 simulation, the initial chlorophyll increase began near day 90, but occurred over a much longer time than in previous years, due to periodic strong wind mixing events during the initial phase of the bloom (Figures 2 c, 3 c). In 1996, the bloom onset again was well modeled, with a very rapid small increase in chlorophyll, which decreased due to wind and convective mixing and a subsequent rapid increase to peak chlorophyll concentrations (Figure 2 d, 3 d). The model bloom was approximately ten days shorter than the bloom observed in the field.

Total modeled copepod biomass is compared with settled volumes in Figure 4. Euphausiids are not included because the field data are from the upper 20 m where there are no euphausiids. It is immediately apparent that in 1993 and 1996, zooplankton populations were much lower than in 1994 and 1995, in both the model and the field data. In addition, the model did a very good job of simulating the timing and duration of increases in the zooplankton populations. Figure 5 shows the simulated zooplankton by species. The most dramatic interannual differences occur in the pseudocalanus, which were able to fully utilize the longer phytoplankton blooms of 1994 and 1995. Maximum pseudocalanus biomass in 1994 and 1995 was about twice as high as that in 1993 and 1996. This large biomass persisted throughout the model run, with final pseudocalanus biomass 3 to 4 times higher in years with lengthy blooms than in years with very short blooms. Neocalanus and euphausiid populations also show differences, but not as large as those of the pseudocalanus. Recall that neocalanus are only within the upper water column for part of the year and begin to descend on day 135, completely leaving the upper 100 meters by approximately day 175. Therefore the biomass differences do not persist in the upper layer. Euphausiids also show persisting differences in biomass, but they are not as great as in the pseudocalanus because euphausiids are distributed throughout the water column, whereas pseudocalanus were only distributed within the upper 40 meters. This difference means that euphausiids have access to sinking phytoplankton, which provided them with additional food resources in 1993 and 1996 to which pseudocalanus did not have access. Therefore, the relative interannual differences between euphausiid biomass are not as great as for pseudocalanus.

Spatial Variability

For the analysis of spatial variability, simulations were run in 1995 using meteorological forcing data from Whittier, AK, located in northwestern Prince William Sound, and from Middleton Island, AK, located at the edge of the continental shelf, south of Prince William Sound (PWS). The Middleton Island data is assumed to be representative of the conditions over the Gulf of Alaska (GOA) shelf, which may impact the Sound. For the 1996 runs, meteorological data was available from two NOAA buoys, 46060 and 46061 located in Prince William Sound, and just outside of the Sound. See Figure 1 for locations. The model simulations presented below all began with identical initial concentrations of phytoplankton and zooplankton, temperature and nutrient fields. Figure 6 shows the wind and air temperature data sets used. Winds in the Gulf were generally slightly higher, and air temperatures slightly lower, than in the Sound. These small spatial differences produced pronounced differences in the phytoplankton and zooplankton. Figures 7 and 8 show the results of the spatial-variability model runs for phytoplankton and zooplankton respectively. Notice the dramatic differences in the phytoplankton and zooplankton populations caused by the small gradients in actual measured wind fields and air temperatures. Although field data at all locations are not presently available to compare to these results, as part of the SEA hypotheses, it was thought that Gulf of Alaska waters entering Prince William Sound determine phytoplankton and zooplankton concentrations at the AFK hatchery. Figure 9 shows field data from AFK compared to the Gulf model simulations. The model fit is extremely good, indicating that the SEA hypothesis is likely correct, and that the model is accurate.

Discussion

In both interannual and spatial simulations, meteorological factors were responsible for controlling both the timing of the initiation of the spring phytoplankton bloom, and the **character or nature** of the bloom. By character, we mean whether the bloom was a brief, intense event, or whether it was a more protracted event with a slower increase to, and duration of, maximal chlorophyll values. In cases when the bloom was brief and intense, *i.e.*, 1993, 1996 and the PWS spatial simulations, winds calmed, and remained relatively calm, for approximately 10 days (Figures 2, 6). This allowed a strong thermocline to develop, and the phytoplankton community responded with a rapid increase in biomass. This increase soon stripped the near surface, stratified layer of nutrients. and the phytoplankton spring bloom ceased (Figures 3, 7). Continued production in the near-surface layer was driven by recycling through the zooplankton. Zooplankton, whose grazing is a function of biomass, could not take full advantage of these brief intense blooms. Therefore, zooplankton biomass, and pseudocalanus biomass in particular, remained relatively low (Figures 6, 8).

In contrast, when the initial stratification of the water column was periodically interrupted during the bloom period, either by convective cooling, as in the 1994 and GOA 1996 simulations, or by intermittent strong wind mixing, as in 1995 and GOA 1995 simulations (*c.f.* Figures 2, 6), the phytoplankton bloom occurred over a longer period of time due to deeper mixing of the upper water column. This deeper mixing increased the total amount of nutrients available to phytoplankton in the euphotic zone, causing a longer phytoplankton bloom with more new primary production. The increased new production could support a higher zooplankton biomass, and the slower, more gradual phytoplankton bloom gave zooplankton time to increase their biomass at a rate more similar to that of the phytoplankton. This, in turn, lead to zooplankton biomass as much as five times greater than those found when the phytoplankton bloom was brief and shallow.

These differences in bloom dynamics lead to difference in the timing of, and mechanisms of, export of fixed organic carbon to the aphotic zone and/or benthos which are summarized in Table 1. In general, approximately 75 percent of the new production was exported out of the near-surface waters. When the phytoplankton spring bloom was short and intense, *e.g.*, in the 1993 and 1995 PWS spatial simulations, the new primary production during the bloom was low, and, due to the poor coupling between the phytoplankton and zooplankton populations, over 80 percent of the carbon flux was due to sinking of senescent phytoplankton cells, rather than due to zooplankton fecal material. In contrast, in the 1994 and 1995 simulations, when the phytoplankton bloom was protracted due to continued mixing, new production was high and the fecal flux contributed over 30 percent. Different springtime mixing regimes control both the total amount of new production which occurs and the partitioning of that production throughout the ecosystem. Differences in the timing of, and type of carbon sinking out of the surface waters has implications for the relative success or failure of benthic and mesopelagic species.

Table 1. Primary production and particle flux from surface waters

Simulation	New Production (g C/m^2)	Phyto flux (g C/m^2)	Phyto flux (%)	Fecal flux (g C/m^2)	Fecal flux (%)	Total Flux (g C/m^2)	Total Flux (percent)
1993	49.	29.	60	6.	12	35	72
1994	63.	31.	49	14.	22	45	72
1995	60	32.	53	12.	21	44	74
1996	48.	25.	53	6.	13	32	65
PWS, 1995	39.	26.	66	4.	10	30	76
GOA, 1995	60.	32.	53	12.	21	44	74
PWS, 1996	51.	27.	53	8.	16	35	68
GOA, 1996	62.	34.	55	9.	14	42	69

Conclusions

Numerical modeling of phytoplankton and zooplankton, in combination with field data collected as part of 320-G and 320-H, shows that phytoplankton and zooplankton populations in Prince William Sound and the northern Gulf of Alaska are determined by the winds and air temperatures which occur over a relatively short, critical time period in early spring. Although this critical time period may be as short as two weeks, the meteorological conditions occurring during that time will play a dominant role in the dynamics of the phytoplankton and zooplankton populations for the rest of the summer. Changes in the amount of convective mixing, caused by cold air, and of wind mixing, caused by high winds, during the early part of the phytoplankton bloom change the timing and duration of the bloom, the total primary production occurring during the bloom, and the partitioning of that primary production between the upper water column food chain, and the benthic food chain.

The spring phytoplankton bloom occurs when mixing of the surface waters ceases and there is sufficient light for phytoplankton growth to occur. In Prince William Sound and the Gulf of Alaska, this typically occurs in sometime in April. Blooms can be roughly categorized into two types, brief, intense blooms and longer, less intense blooms. The weather conditions during the initial part of the bloom determine what type of phytoplankton bloom will occur. If it is a relatively calm, warm spring, the water column stratifies and forms a shallow surface mixed layer. Phytoplankton and nutrients within this mixed layer are isolated from those deeper in the water column. With abundant light in the surface layer, phytoplankton quickly reproduce and build up their standing stocks to fairly high levels. As a consequence of this growth, nutrients are soon depleted and phytoplankton sink out of the surface layer. Because zooplankton reproduce at much slower rates than phytoplankton, the zooplankton populations cannot consume much of the phytoplankton production. The non-grazed phytoplankton slowly sinks out of the surface layer to deeper waters where it may be consumed by deeper pelagic organisms, or by the benthic fauna. Therefore, a relatively warm, quiescent spring produces a relatively short phytoplankton bloom, with high phytoplankton biomass, however, much of the phytoplankton biomass does not get passed on to the zooplankton populations. Zooplankton biomass therefore remains at fairly low levels for the rest of the summer.

In contrast to this, a cooler, stormier spring leads to higher zooplankton biomass. Although the cold stormy weather may delay the stratification of the water column somewhat, the major effect observed in field data and model simulations is due to the progression of the phytoplankton bloom, not the time at which it began. Storms typically pass through the PWS area at a frequency of about once a week during late winter. If they continue on into early spring, they become important to the biological dynamics. In a cold stormy spring, stratification typically occurs between storms, and when it does occur, the surface mixed layer may be somewhat deeper than in warm calm springs. The phytoplankton bloom begins in this surface layer, but is interrupted by a cold windy storm. This deepens the mixed layer, which reduces phytoplankton concentrations and increases nutrient concentrations. The bloom then takes off again. Subsequent storms may repeat the process, but at some point the stabilization of the upper water column, which has been increasing due to surface heating, becomes too strong and the seasonal mixed layer stabilizes. The phytoplankton bloom continues in this layer until nutrients are depleted. The net result of this type of spring weather is a deeper mixed layer, which took longer to become established. As a consequence of this, the phytoplankton bloom occurs over a longer period of time, and more nitrate is available for new primary production. In addition, the mixing of the surface layer has lengthened the total phytoplankton bloom period. During this longer period of high phytoplankton biomass, zooplankton increase in numbers and biomass and are thereby able to consume a higher proportion of the net production. Therefore, there is a transfer of more of the phytoplankton new production into the zooplankton population and zooplankton numbers and biomass remain high for the summer.

Both types of blooms have been observed in our four years of SEA field data. From the modeling work done as part of this project, we are able to determine the causes and interactions between the mixing regimes, phytoplankton, and zooplankton. This has allowed us to accurately simulate these processes. The zooplankton populations which have been modeled are of direct importance in the diet of juvenile pink salmon and larval and juvenile Pacific herring. Our understanding of the physical mechanisms that control the variable amounts of zooplankton (fish food, if you will) allows the SEA project to evaluate the effects of variability in the physical environment as it is propagated up through the phytoplankton and zooplankton, to the injured resources of Prince William Sound.

References

Corkett, C. J. and I. A. McLaren, 1978, The biology of *Pseudocalanus*. *Adv. Mar. Biol.*, 15:1-23.

Dugdale, R. C., 1967, Nutrient limitation in the sea: dynamics, identification, and significance, *Limnology and Oceanography*, 12:685-695.

Eslinger, D.L., 1990, *The Effects of Convective and Wind-driven Mixing on Springtime Phytoplankton Dynamics as Simulated by a Mixed-layer Model.* Ph.D. Dissertation, Florida State University, Tallahassee, FL.

Eslinger, D.L. and R. L. Iverson, 1996, The effects of convective and wind mixing on springtime phytoplankton dynamics in the southeastern Bering Sea shelf. *Accepted, Continental Shelf Research.*

Fulton, J., 1973, Some aspects of the life history of *Calanus plumchrus* in the Strait of Georgia, *J. Fish. Res. Bd. Canada*, 30:811-815.

Frouin, R., D. W. Lingner, C. Gautier, K. S. Baker, and R. C. Smith, 1989, A simple analytical formula to compute clear sky total and photosynthetically available solar irradiance at the ocean surface, *Journal of Geophysical Research*, 94:9731-9742.

Ivlev, V. S., 1945, The biological productivity of waters, *Usp. Sovrem. Biol.*, 19:98-120.

Magley, W.C., 1990, *A Phytoplankton-Zooplankton Model of the Middle and Outer Shelf Domains of the Southeast Bering Sea Shelf During Spring Bloom Conditions*, Ph.D. Dissertation, Florida State University, 1990.

Platt, T., C.L. Gallegos, and W.G. Harrison, 1980, Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton, *Journal of Marine Research*, 38:687-701.

Pollard, R.T., P.B. Rhines, and R. O. R. Y. Thompson, 1973, The deepening of the wind-mixed layer. *Geophysical Fluid Dynamics*, 4:381-404.

Strickland and Parsons, 1976 A Practical Handbook of Seawater Analysis.

Thompson, R. O. R. Y., 1976, Climatological numerical models of the surface mixed layer of the ocean, *Journal of Physical Oceanography*, 6:496-503.

Wroblewski, J. S., 1977, A model of phytoplankton plume formation during variable Oregon upwelling, *J. Marine Res.*, 35:357-394.

Prince William Sound, Alaska

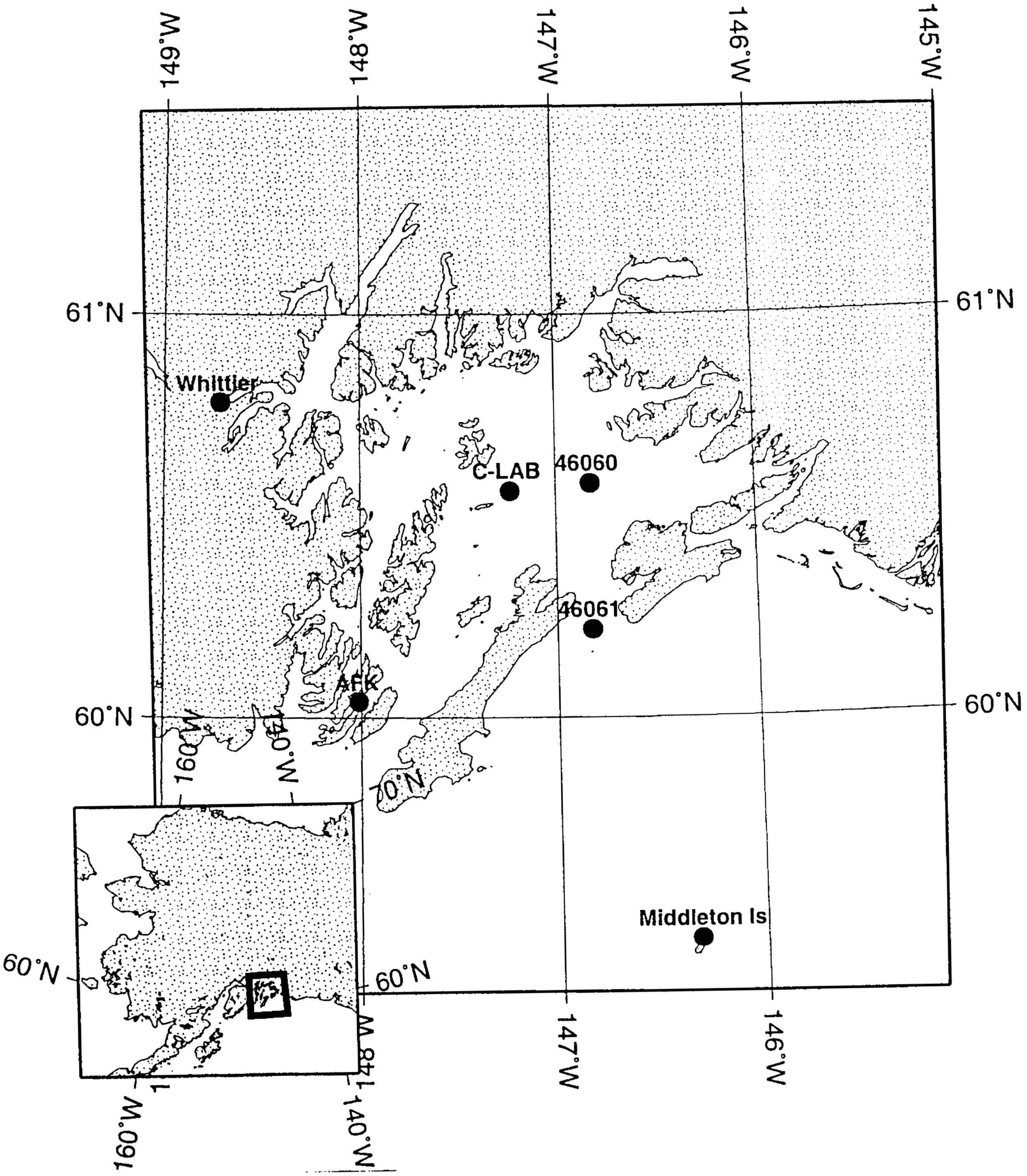

Figure 1. Prince William Sound, Alaska. Locations at which forcing data sets and field data were collected are shown by the dots. Meteorological data from Whittier and Middleton Island came from the National Weather Service. 46060 and 46061 are NDBC weather mooring. C-LAB is a mooring maintained by this project. AFK stand is a Prince William Sound Aquaculture Corporation hatchery at which phytoplankton and zooplankton data were collected.

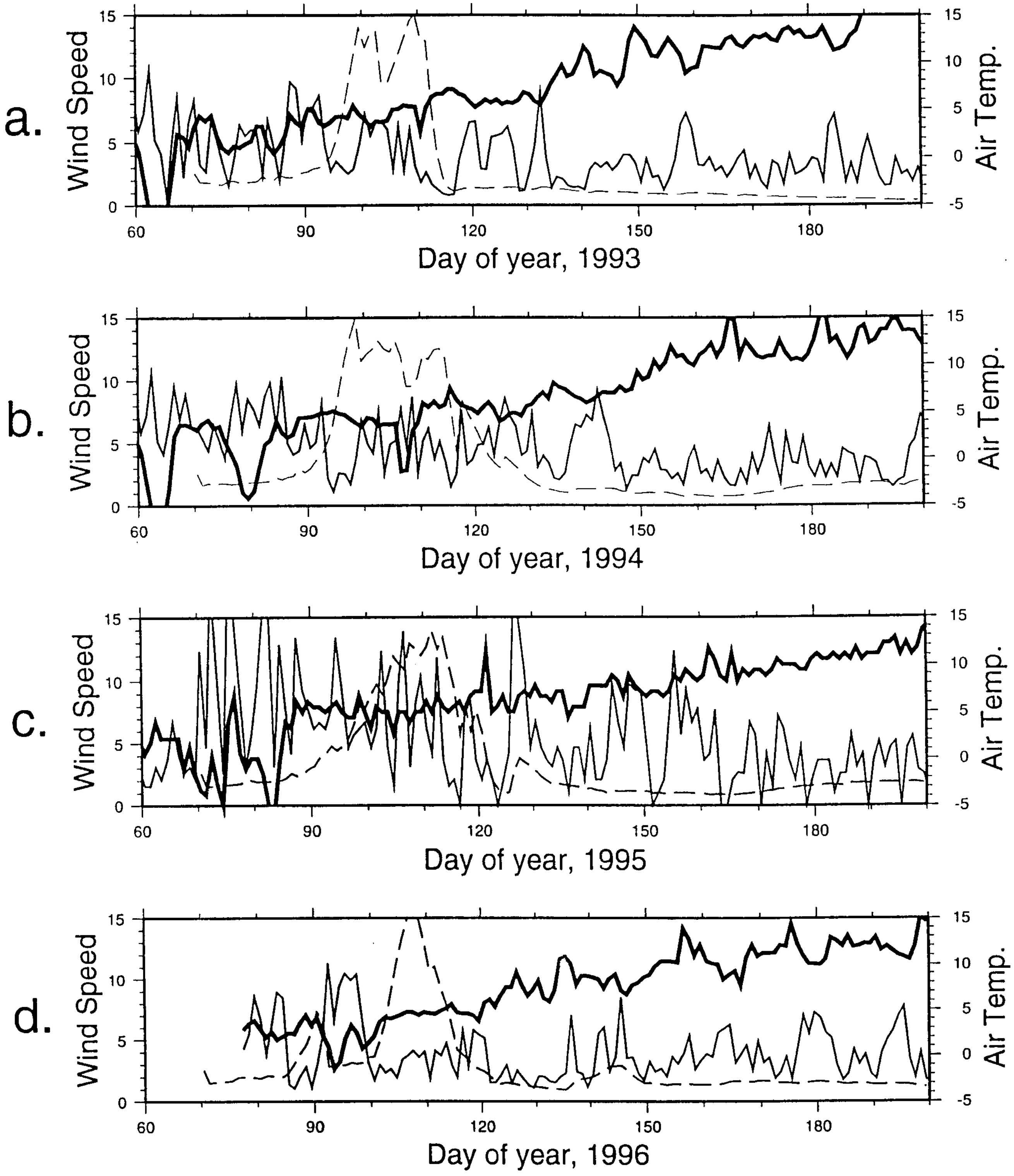

Figure 2. Wind speed (m s^{-1}; thin solid line), air temperature (°C; thick solid line), and modeled chlorophyll (mg Chl m^{-3}; thin dashed line) for a) 1993, b) 1994, c) 1995, and d) 1996.

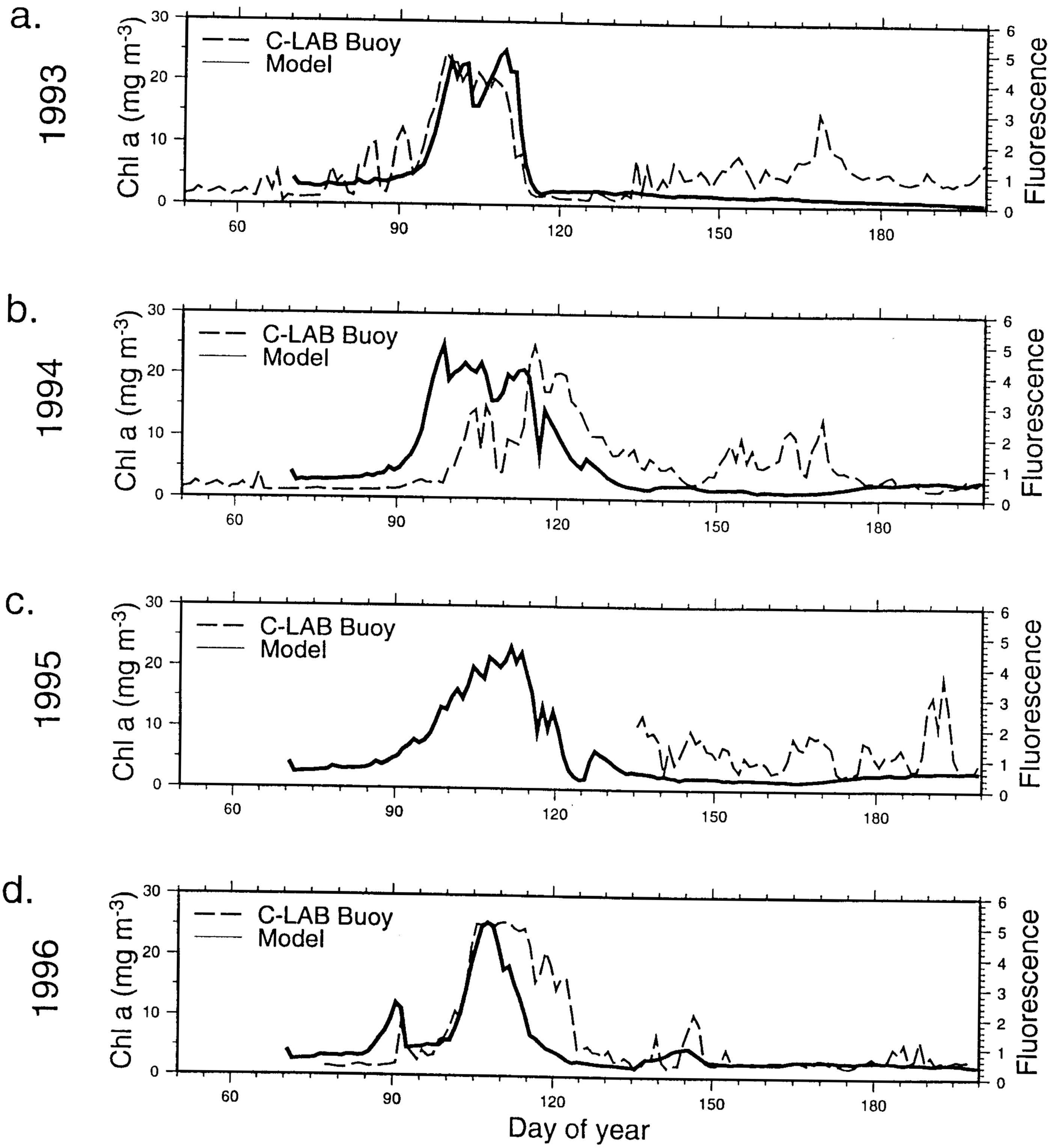

Figure 3. Model chlorophyll concentration (mg Chl m^{-3}) and C-LAB measured fluorescence (Volts) ,both measured at 10 m, for a) 1993, b) 1994, c) 1995, and d) 1996.

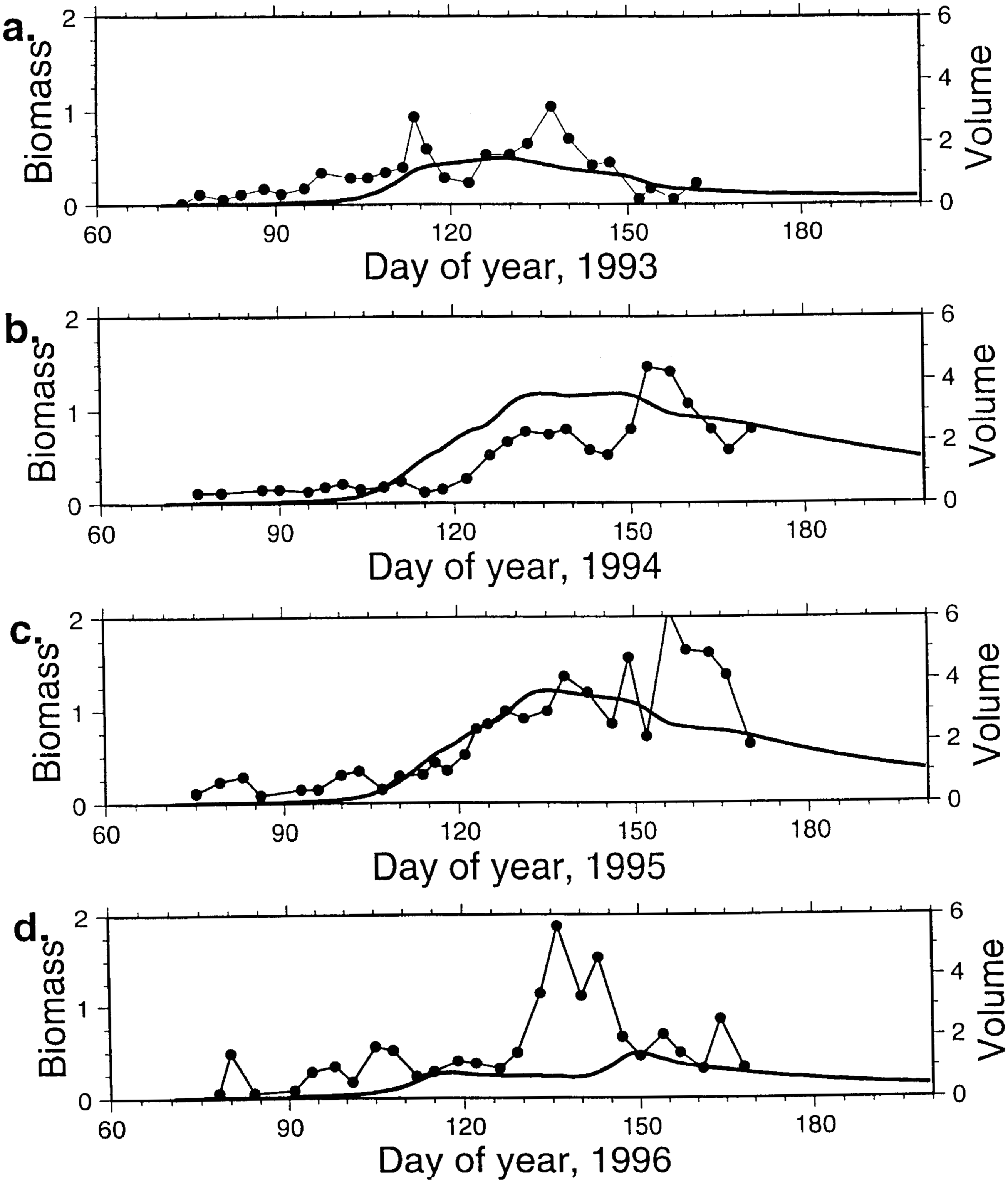

Figure 4. Model copepod biomass (g wet weight m^{-2}; thick solid line) and settled volume (; thin line with symbols) from the AFK hatchery for a) 1993, b) 1994, c) 1995, and d) 1996.

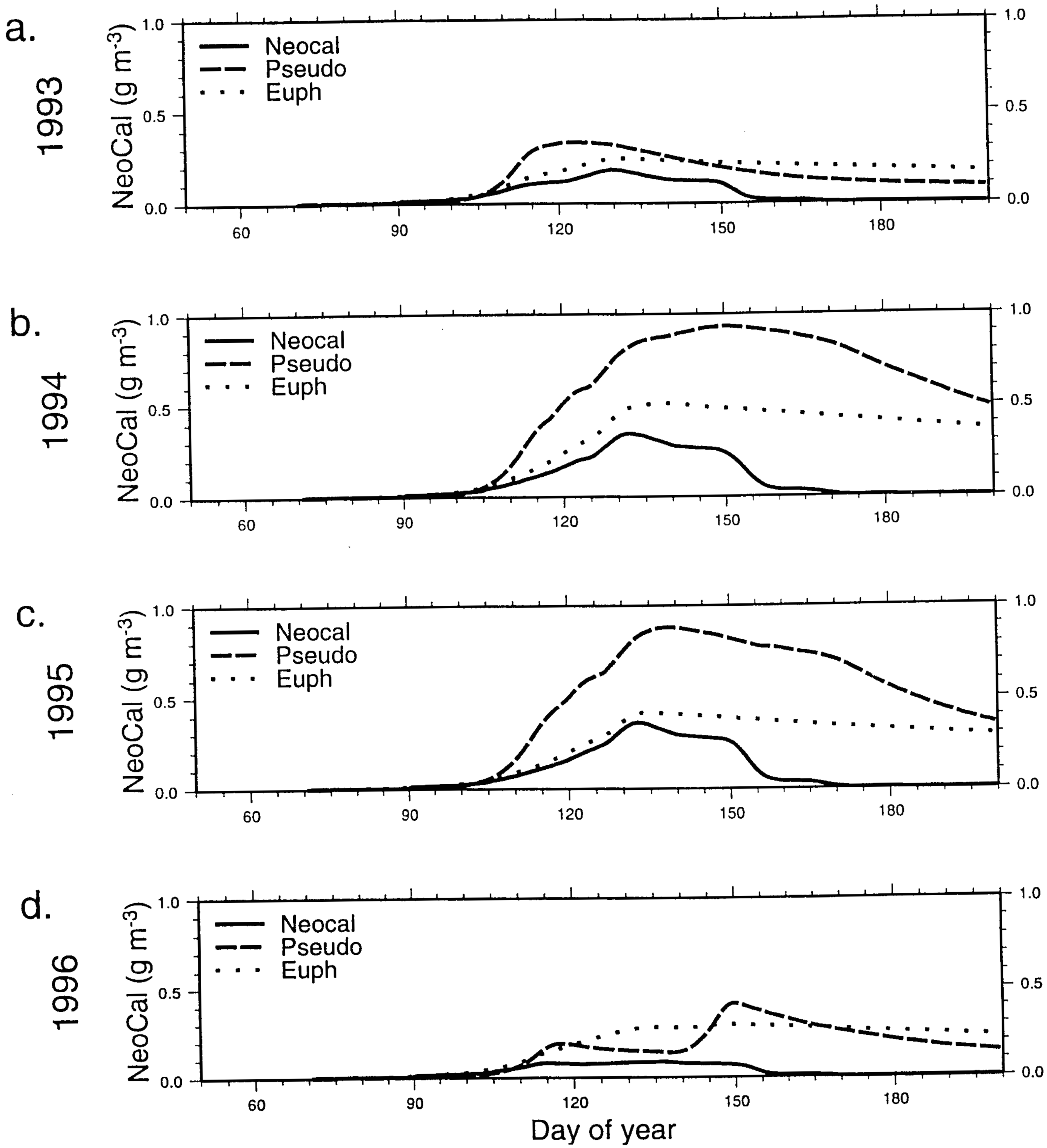

Figure 5. Model zooplankton biomass (g wet weight m^{-2}) by group for a) 1993, b) 1994, c) 1995, and d) 1996.

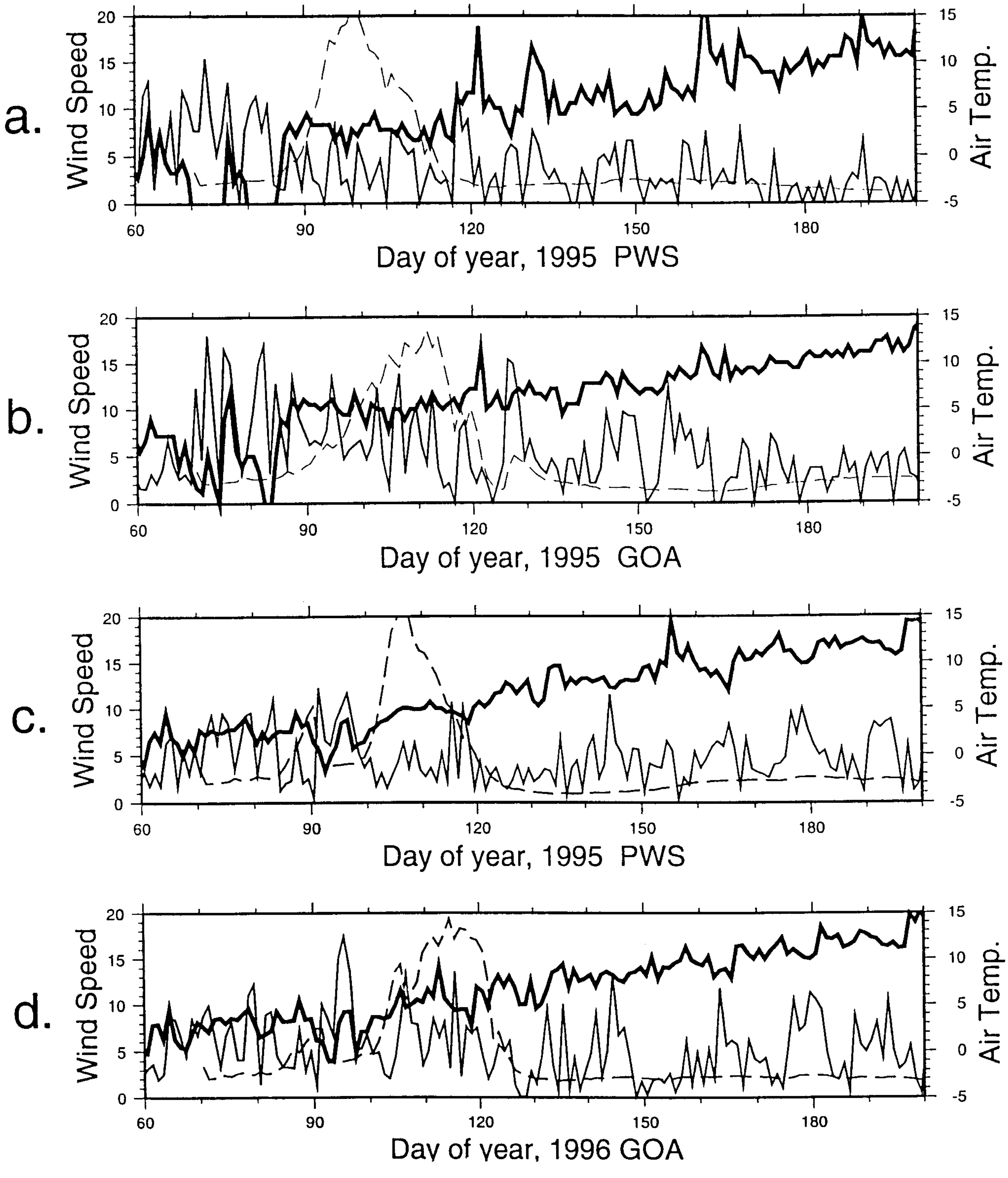

Figure 6. Wind speed (m s^{-1}; thin solid line), air temperature (°C; thick solid line), and modeled chlorophyll (mg Chl m^{-3}; thin dashed line) for a) Prince William Sound, 1995; b) Gulf of Alaska, 1995; c) Prince William Sound, 1996; and d) Gulf of Alaska, 1996.

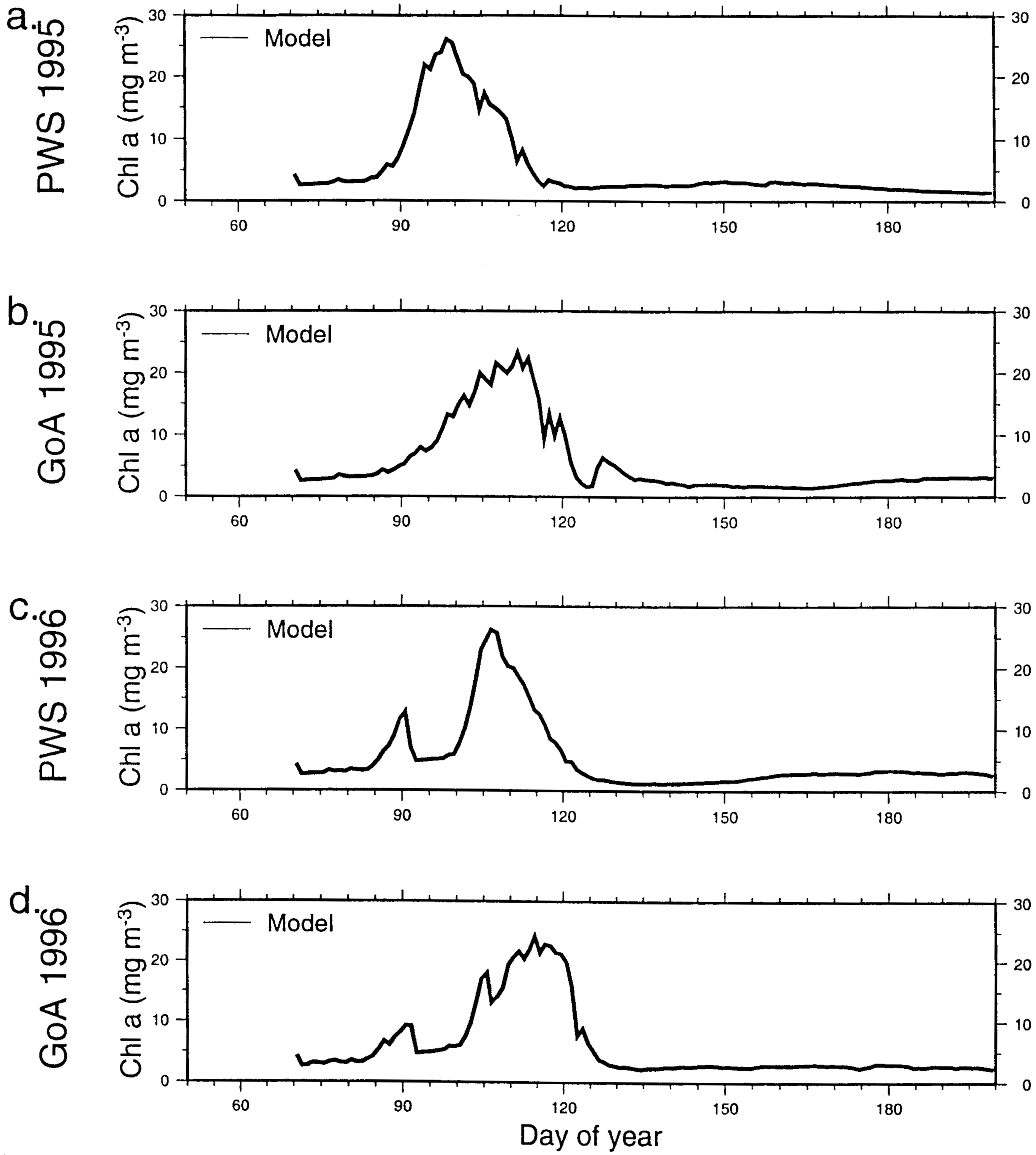

Figure 7. Model chlorophyll concentration (mg Chl m^{-3}) measured at 10 m, for a) Prince Willaim Sound, 1995; b) Gulf of Alaska, 1995; c) Prince William Sound, 1996; and d) Gulf of Alaska, 1996.

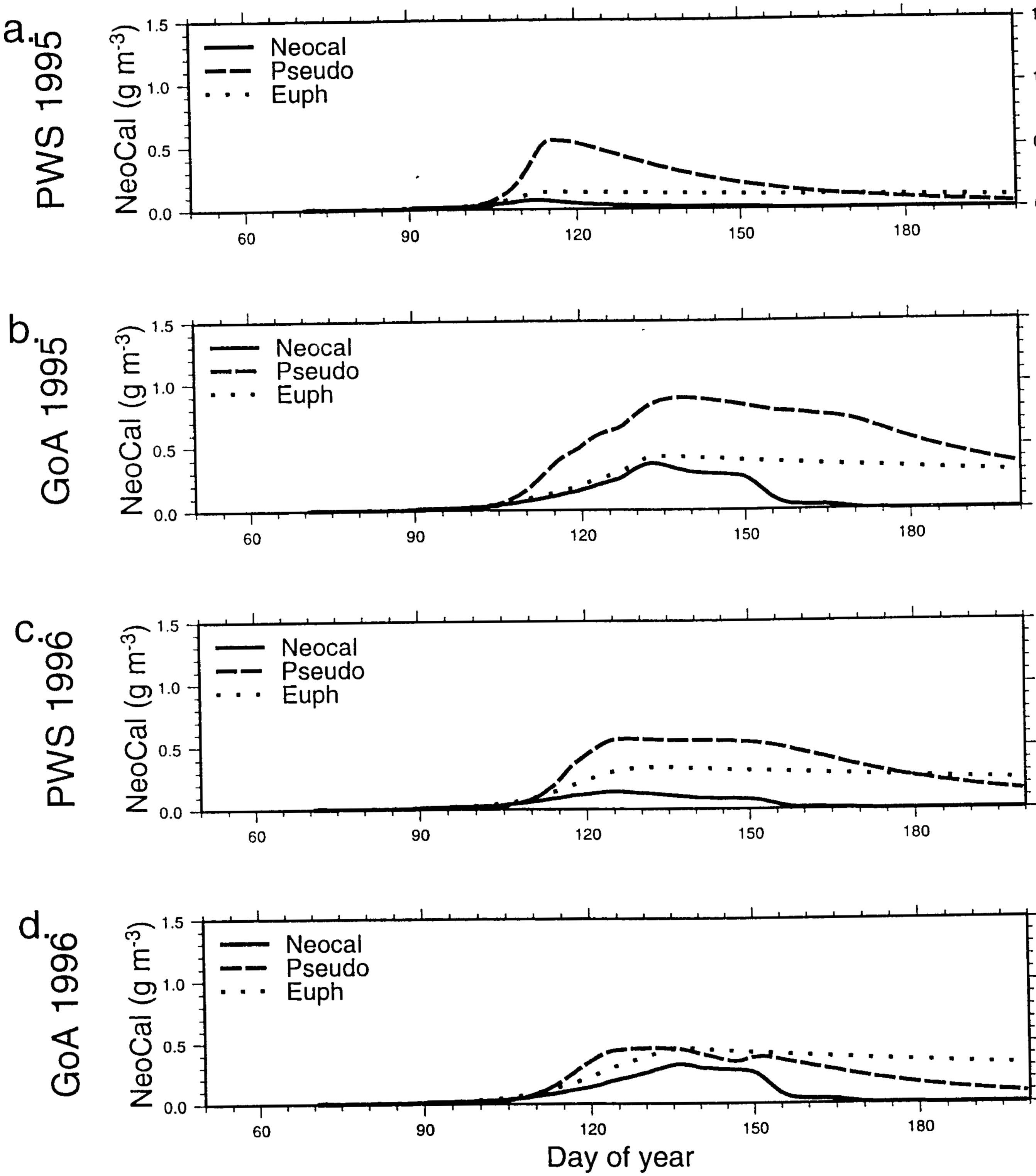

Figure 8. Model zooplankton biomass (g wet weight m^{-2}) by group for a) Prince William Sound, 1995; b) Gulf of Alaska, 1995; c) Prince William Sound, 1996; and d) Gulf of Alaska, 1996.

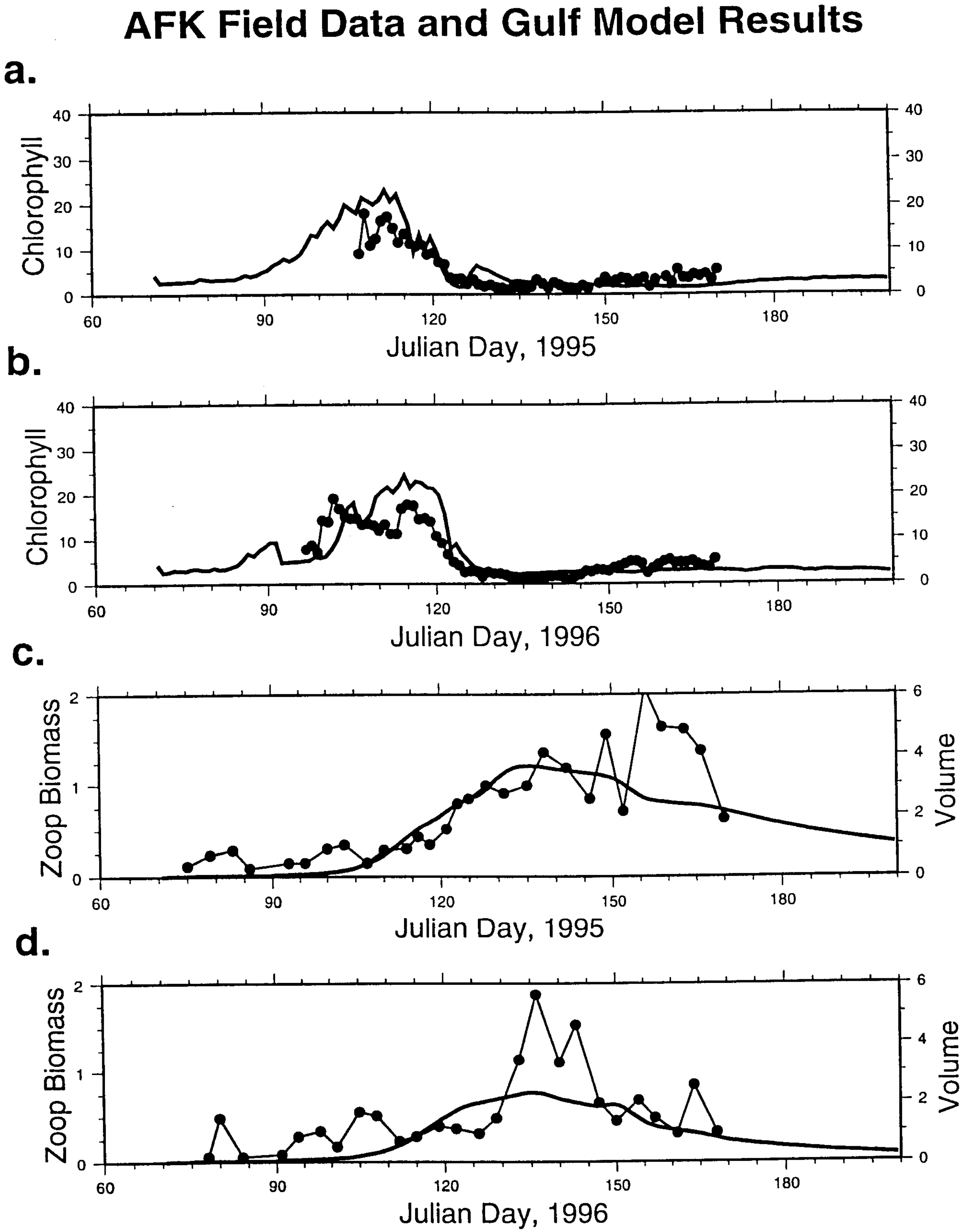

Figure 9. AFK field data and results from Gulf of Alaska simulations. In all cases the thick solid line shows the model result and the thin line with symbols shows the field data: a) chlorophyll (mg Chl m^{-3}) at 10 m for 1995, b) chlorophyll (mg Chl m^{-3}) at 10 m for 1996, c) model zooplankton biomass (g wet weight m^{-2}) and settled volume () in 1995, and d) model zooplankton biomass (g wet weight m^{-2}) and settled volume () in 1996.