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CONSUMPTION OF COPEPODS AND EUPHAUSIDS IN THE EASTERN BERING SEA AS REVEALED BY A NUMERICAL ECOSYSTEM MODEL

by

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ABSTRACT

The Division of Resource Ecology and Fisheries Management is formulating a Dynamic Numerical Marine Ecosystem (DYNUMES) Model for use in evaluating interactions of environmental and biological components. Initially, the model will be used in reference to the economically important eastern Bering Sea area, and a preliminary submodel which permits evaluation of the interactions of only 8 representative biological components in the area has been tuned to assess rough biomass balances. As a first step we have modelled general zooplankton consumption and compared this with zooplankton abundance. Results indicate that the monthly consumption is roughly equivalent to the monthly standing stock, an impossible situation. The usefulness of existing plankton data, which are obviously more qualitative than quantitative, in biological or ecosystem models is challenged, and cooperative integrated plankton and fisheries field studies are recommended to resolve the apparent dilemma.

INTRODUCTION

It was nearly a century and a half ago that the plankton net revolutionized marine biology studies and, although the cataloging of these microscopic forms has been reasonably complete for a number of years, there have been numerous controversies concerning the quantification of plankton data. The variety of sampling devices, net mesh sizes, and towing procedures are ample evidence of the difficulties in acquiring accurate samples. The variability in samples obtained by paired nets and replicate tows (in many instances as much as an order of magnitude or more) bear strong testimony as to the small-scale patchiness of organism distributions--not to mention the inherent large scale patchiness due to areas of convergence and divergence of various temporal and spatial dimensions. Fisheries groups have largely been willing to let biological oceanographers wrestle with this problem and have concentrated their efforts on ichthyoplankton assessments. However, the realization that only limited knowledge of fish species would stem from single species studies and that multi-species studies are required, has raised the issue that perhaps only through total ecosystem studies will adequate information on any one species be forthcoming.

During our attempts to formulate a conceptual ecosystem model of the eastern Bering Sea in order to evaluate the difficulties and complexities of such an undertaking, we were confronted with conflicting and confusing zooplankton data even though numerous studies have been made. In spite of the gross assumptions made with respect to the various coefficients used, there is a serious deficiency in the amount of zooplankton reported in the literature and an obvious requirement for forage by fish stocks calculated to be present. This, of course, poses a challenge to those ecosystem models that begin with primary and secondary production estimates. We believe that it is important to point out these discrepancies because extensive and costly plankton surveys are being made in the eastern Bering Sea as a result of requirements for environmental impact statements prior to awarding offshore oil leases, and routine, standard sampling of the plankton biomass especially to an arbitrary depth level (e.g., 80, 100, 150 m, etc.) may result in a totally unrealistic assessment of these populations.

The eastern Bering Sea is unique in that it has not only one of the widest continental shelves (>500 km) of the world's oceans, but this area is relatively isolated by the land masses of the Alaskan Peninsula and eastern Siberia from the usual alongshore flows that sweep along the lengths of most continents--although Bering Strait provides a narrow, shallow passage into the Arctic Ocean. In addition, the shelf area is largely covered with ice each winter, resulting in homogeneous water temperatures less than $-1^{\circ}C$; but, in summer, surface temperatures in excess of $15^{\circ}C$ occur, particularly in inshore areas. The varying conditions result in onshelf and offshelf movements of various biological components. It is an oceanic area that can reasonably be considered and treated as a fundamental ecosystem.

NUMERICAL ECOSYSTEM MODEL

The relatively complex conceptual numerical ecosystem model (DYNUMES), under development at the Northwest and Alaska Fisheries Center, has been described elsewhere (Laevastu, Favorite, and McAlister, 1976), and only those brief notes which are necessary to explain the findings presented in this paper are given below. The present 8-component model, a submodel of the DYNUMES model, permits deriving plausible standing stocks of pollock and herring using available data from the literature and an iterative method; other biological components such as mammals and birds are prescribed as monthly fields. The populations are distributed as available knowledge on migrations and occurrence dictates. Growth, fishing mortalities, and consumption by other species are computed in monthly time steps. Available data from literature on stomach content and food coefficients are used for computation of consumption rates, but in the present formulation, these factors do not have temporal and spatial variability. The food coefficient is computed as 1:2 for growth and 1% of body weight for maintenance, so an average food coefficient of ca 1:5 was used. The consumption of various "food items" (i.e., species or groups of species) is used, among others, to compute changes in population size of the consumed species and is stored on discs for various outputs, including summation over the entire computational area. Here we focus attention on the consumption of copepods and euphausids as computed by the model and discuss the consequences of the findings to fisheries problems.

Zooplankton Composition

There are considerable data on zooplankton in the Bering Sea reported by various U.S., Japanese and Soviet scientists. Although the mean standing stock reported varies between 100 and 300 mg/m^3, 700 to 800 mg/m^3 have been reported in the upper 20 meters of the water column during late summer in some areas, and maximum values of 2.5 g/m^3 have occurred. The species composition as well as the frequency of occurrence of major species is well agreed upon, however, reproduction cycles are not well known. Although there are about four dominant species of copepods (Eucalanus bungii, Calanus plumchrus, C. cristatus, and Metridia pacifica) present in summer, eurythermic plankters (Oithona similus, Sagitta elegans, Calanus glacialis, Parathemisto libellula) are predominant in winter. Acartia longiremis and Pseudocalanus spp. are dominant forms in inshore waters. Generally, copepods produce only one generation annually (Metridia pacifica may produce up to four) and these occur at different times: C. cristatus in early winter; C. glacialis in late spring, followed by Eucalanus bungii; and Metridia pacifica from late spring to late fall. About 70 to 80% of the plankton biomass is considered to consist of copepods. The four dominant forms of euphausids are Thysanoessa raschii, T. inermis, T. longipes, and T. spinifera, the first being primarily an inshore form, and it may require 2 years for these forms to reach maturity.

The data on zooplankton production are even less reliable than on standing stock, due to various indirect methods used for its estimation. The most frequently reported values of production are around 110 to 140 g/m^2 per year, variably referred to as copepod production and total zooplankton production. This value is in disagreement with some earlier estimates of zooplankton production in the Atlantic (3 to 8% of standing stock daily).

The zooplankton standing stock in the present submodel is created on the basis of available quantitative knowledge. It is made a function of time (month), latitude, and specific location (e.g., such as the continental shelf, etc.). Due to difficulty in obtaining reasonable values of zooplankton standing stock in time and space, it is more advantageous in the construction of an ecosystem model to compute the plausible consumption of zooplankton and to use only the relative zooplankton abundance for estimate of density dependent feeding. An example of areal distribution of zooplankton standing stock (in mg/m^3) as generated in our submodel for month of July, is shown in Figure 1. The monthly consumption of copepods and euphausids was computed in other subroutines, in connection with food requirements (in the DYNUMES model, the zooplankton standing stock size at any given location and time will be used for computation of food avilability; in this paper, we use it merely for comparison to consumption).

Zooplankton Consumption

The major consumers of zooplankton in our submodel are herring (and ecologically related species) and juvenile (pre-fishery) pollock. The total monthly amounts consumed are relatively constant through the year. fluctuating only little with the fluctuating biomass of consumers (Table 1), because the present submodel does not account for food density dependent feeding, nor variation of food coefficient with temperature. The monthly values of total zooplankton consumption in the Bering Sea imply that (a) there is little variation of total amounts consumed from month to month (the food composition and rate of consumption is constant year around in the present model, the zooplankton consumption by migratory birds is

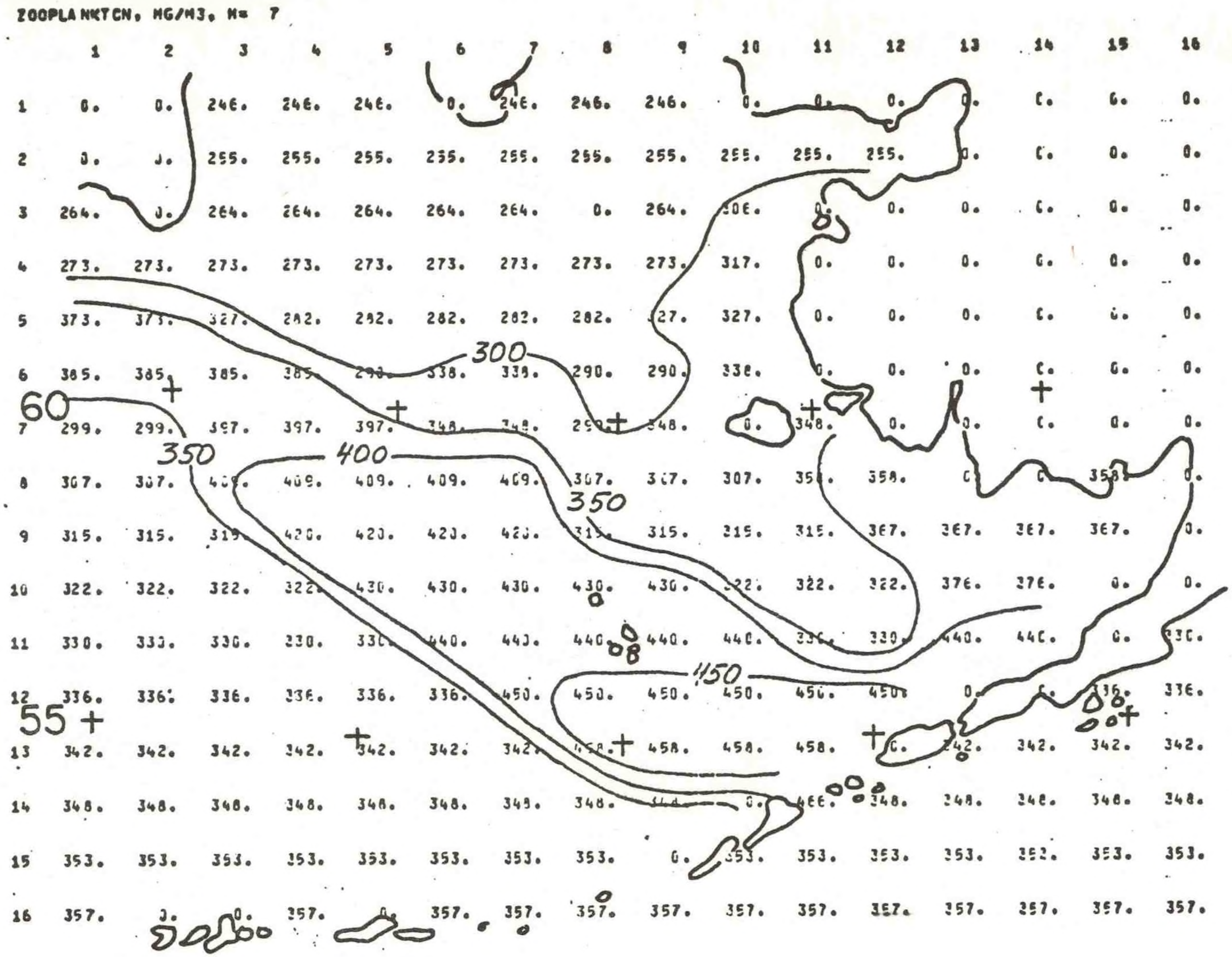

Figure 1.--Simulated standing stock of zooplankton (mg/m^3) in the eastern Bering Sea in July.

Table 1.--Examples of midseason monthly values of total consumption of copepods, euphausids, herring and pollock, in the Bering Sea, as computed with 8-component ecosystem submodel (in thousand tons).

	Consumption of			
Month	Copepods	Euphausids	Herring	Pollock
February	2145	1704	114	176
May	2183	1706	122	192
August	2094	1564	103	216
November	2010	1509	99	178

relatively minor, and consumption by whales is not considered); and (b) the copepod consumption is approximately 60% whereas the euphausid consumption is 40%. An interesting observation from Table 1 is that the consumption of zooplankton and consumption of next lower link in food chain (e.g., herring) is about 1:10 to 1:20 (these numbers will change with additional tuning of model), supporting indirectly the general "one order magnitude less" relation between various food chain links in the ocean; this relation is a result of model computations rather than model input.

Examples of monthly consumption of zooplankton (the numbers represent mg/m^3, assuming a 50 m homogenous depth distribution) are shown in Figures 2 to 4. In April (Fig. 2), there were two areas of high consumption of zooplankton: (1) over the deep water off the shelf, where the bulk of pollock biomass is located, and (2) over the outer edge of continental shelf where the herring population has moved. By June (Fig. 3) the area of high consumption is over the central part of the continental shelf. In October (Fig. 4), the area of high zooplankton moves back toward the continental slope and, during winter, the area of zooplankton consumption is over deep water off the continental slope. Examination of these figures indicates that there are large areas where the zooplankton consumption is light and much of the production is consequently going primarily into a nutrient regeneration cycle and/or sinks to the bottom where it will be used by detritus feeding benthos. Furthermore, the seasonal shifts of areas of high consumption apparently allow subsequent recovery of standing stock and production in areas heavily grazed in periods before and, surely, some replenishment also occurs through transport of zooplankton by currents into these previously heavily grazed areas.

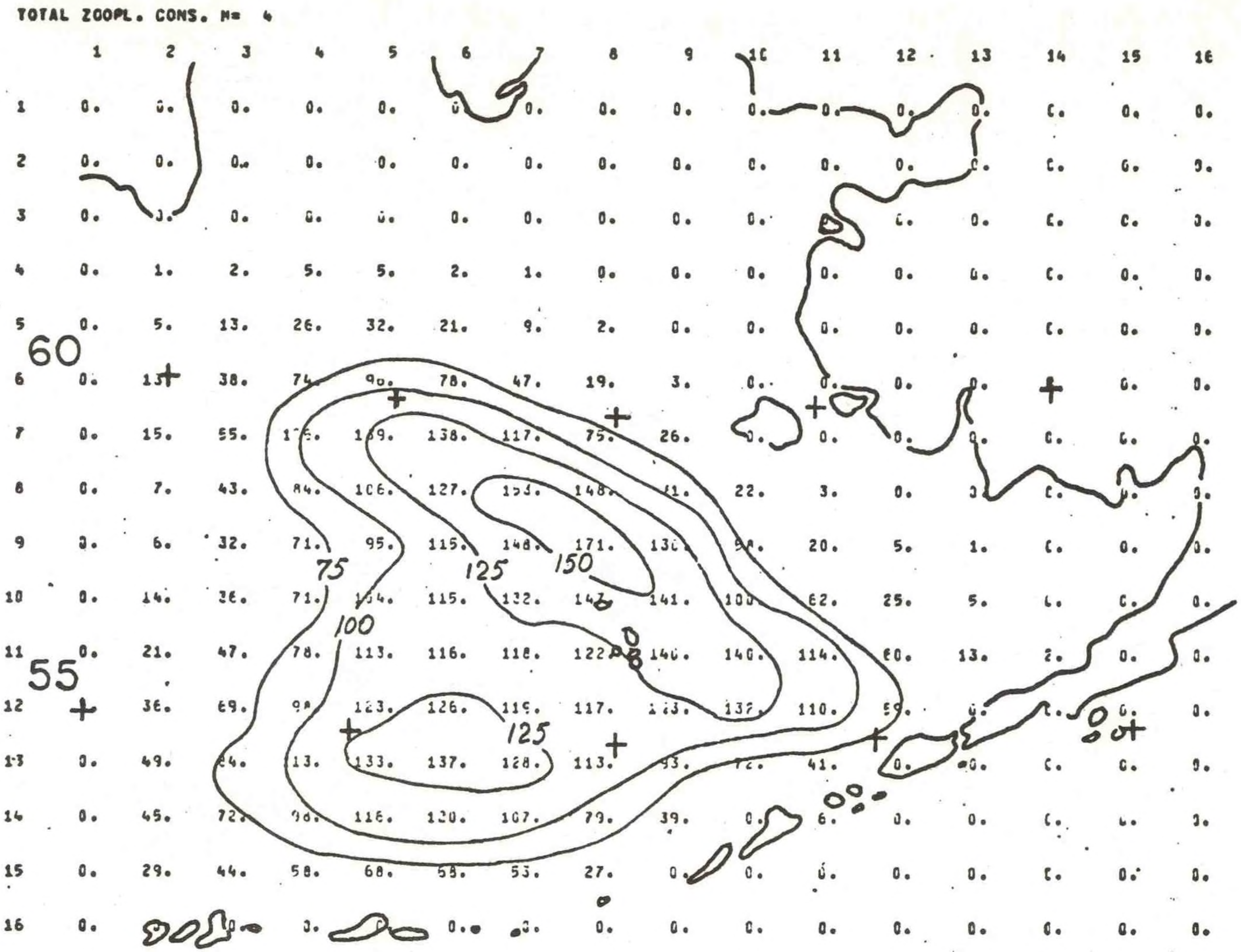

Figure 2.--Computed consumption of zooplankton (mg/m^3) in the eastern Bering Sea in April.

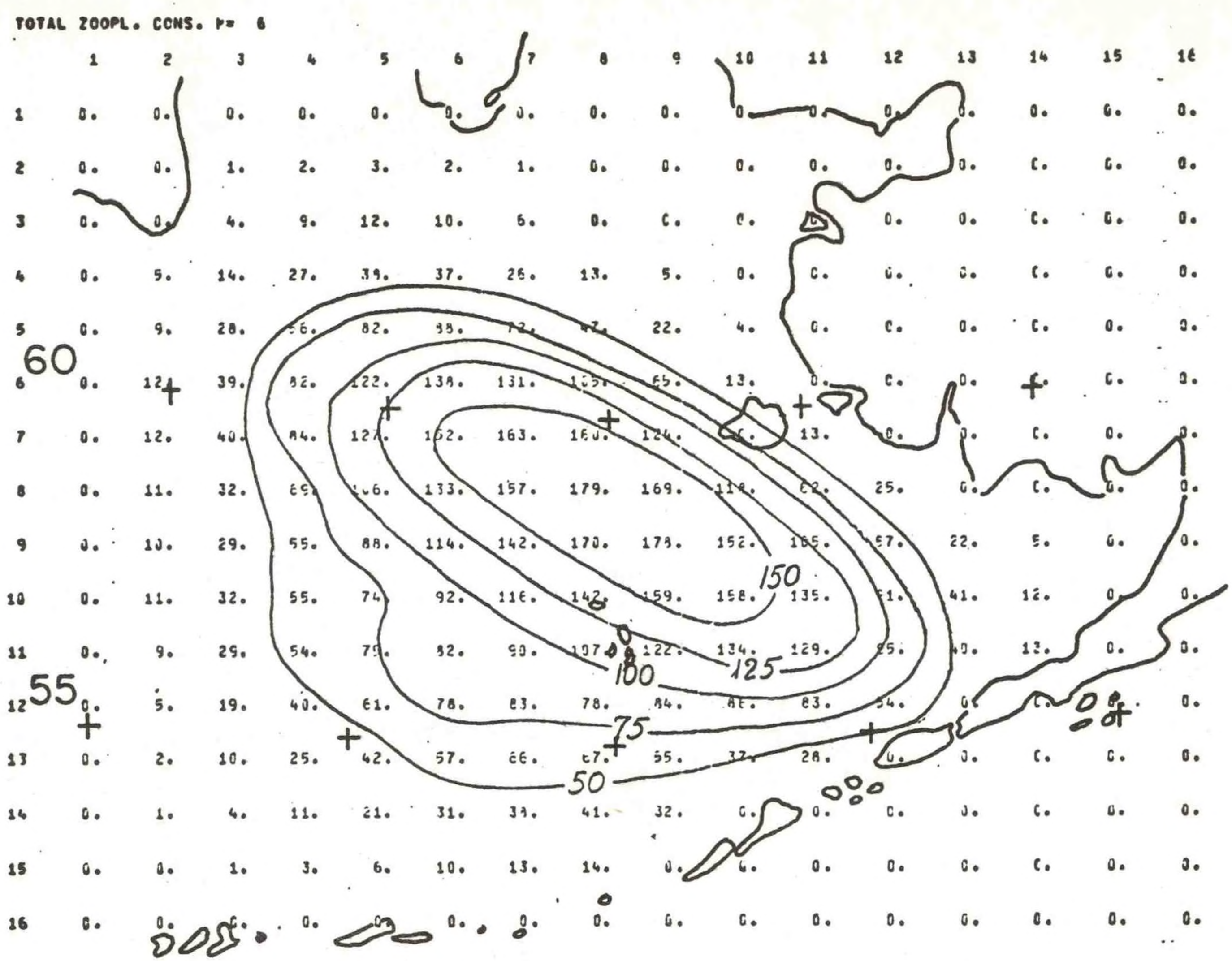

Figure 3.--Computed consumption of zooplankton (mg/m^3) in the eastern Bering Sea in June.

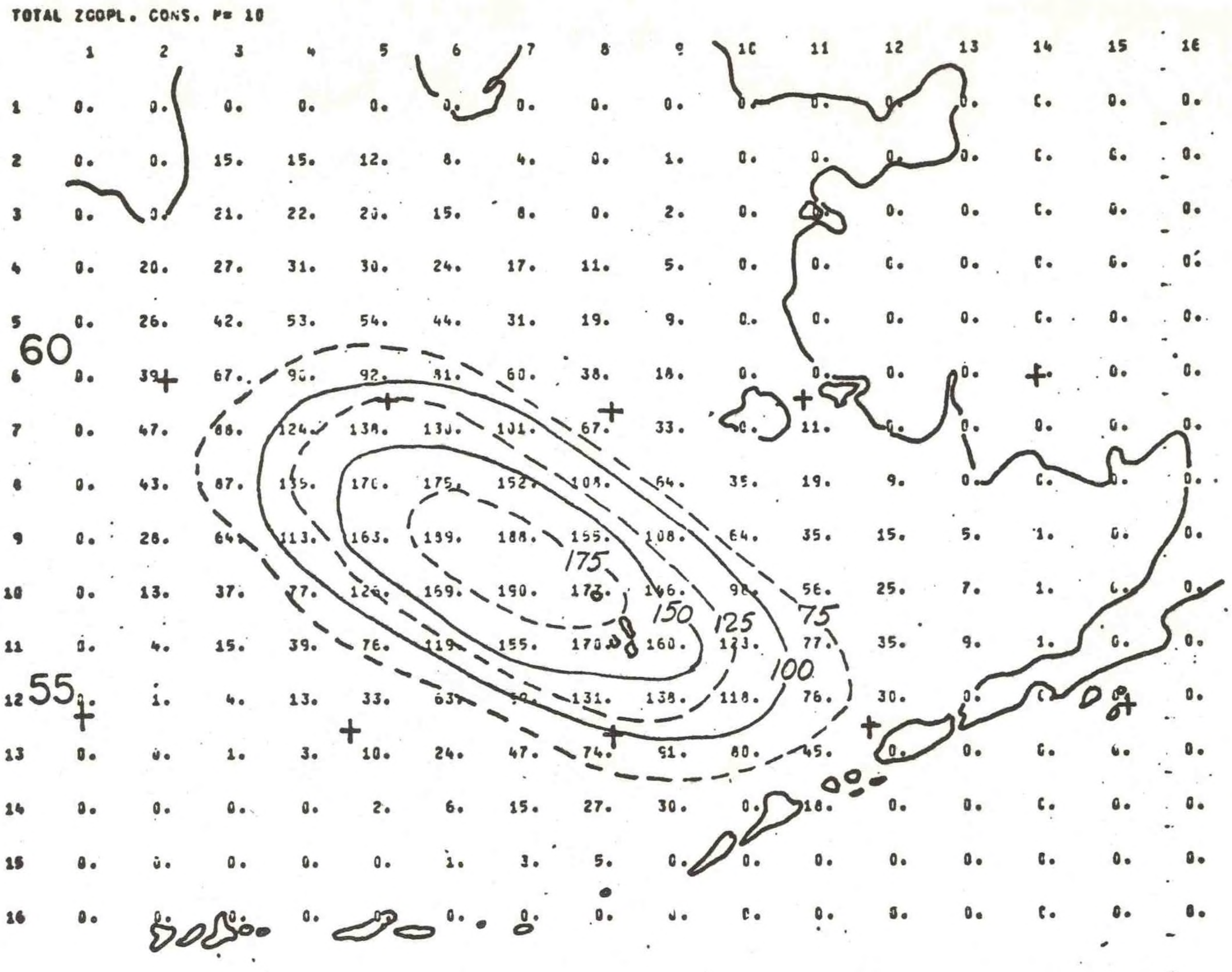

Figure 4.--Computed consumption of zooplankton (mg/m^3) in the eastern Bering Sea in October.

STARVATION OR INADEQUATE PLANKTON SAMPLING?

In comparing, quantitatively, the reported standing stock of zooplankton (Fig. 1) with the computed consumption (Figs. 2 to 4), one finds that in relatively large areas the monthly zooplankton consumption nearly equals or is only slightly lower than the standing stock. In reality, this is not possible. Thus, the cause of the discrepancy (too low standing stock or too high consumption) must be sought either in the model results or in the zooplankton data.

Excessive consumption values can be obtained by the model only if (a) the actual food coefficient is much lower than about 1:5; (b) the proportion of plankton in the diet of grazers is lower than that prescribed; (c) the standing stock of grazers (fish and birds) is lower than assumed in the model; (d) there is widespread starvation, which implies that availability of food is the limiting factor for abundance and growth for most species in the marine ecosystem; or (e) our quantitative knowledge of zooplankton standing stocks is inadequate. Condition (a), above, seems very unlikely, considering the pertinent data available in the literature. Condition (b) also seems unlikely, as the lowest possible values were selected for this particular model run. Likewise, condition (c) seems unlikely, as relatively low estimates of the consumers of plankton were used and not all fish species which consume plankton were included in the present model (also whale consumption is excluded); pollock and herring standing stocks were iteratively determined in other subroutines as the smallest biomass which is sustainable with the lowest possible ecosystem internal consumption and maximum fishery, even assuming highest possible growth rate and considering natural mortality (i.e., the mortality from "old age"), nearly nil. This leads us to accept conditions (d) or (e) as a proper conclusion. That there may be widespread starvation in other biological components is supported by the results from other subroutines in the model. It also suggests that our quantitative knowledge of zooplankton standing stocks is inadequate, (which is probably true with respect to larger, more mobile organisms, such as euphausids, which are relatively scarce in quantitative zooplankton reports, but which occur in stomach content analyses).

The requirement for high zooplankton abundance also raises an important question about the grazing on ichthyoplankton (fish eggs and larvae) and its consequences. If the zooplankton is grazed down to a low level, the ichthyoplankton would be grazed to the same degree, or possibly to a higher degree, if selective feeding occurs. If areas of high consumption coincide with areas of high concentrations of pelagic fish eggs and larvae, the spawning success, and consequent year class strength, may be determined largely by pelagic, post-spawning grazing, rather than by number of spawners.

FUTURE RESEARCH

As the large and more mobile zooplankters, such as euphausids, constitute a large proportion of the forage for fish <u>and</u>, as selective feeding is expected on such larger organisms <u>and</u>, as our quantitative knowledge on these organisms is scarce indeed, it seems to be desirable to emphasize quantitative studies on this group of organisms with fine-meshed midwater trawls and especially, near the bottom, with similar fine-meshed beam (or slide) trawls.

At the same time we need "synoptic" studies of the fish and other grazers, especially their stomach content, to establish the "selectivity coefficient" of various species in relation to the species spectrum present. Such "synoptic" plankton-fish studies might enlighten other open questions, such as 1) is there a lower threshold value of plankton concentrations which causes plankton feeding fish to disperse and leave the low standing stock area for search of more adequate food, 2) or does starvation and its consequences, such as slower or no growth, higher mortality and non-maturation of gonads, prevail for longer periods in given areas and conditions.

It would be worthwhile to investigate where and when areas of high zooplankton consumption might coincide with areas of known abundance of pelagic egg and larvae of given species. The possible effect of excessive consumption of ichthyoplankton during periods of low standing stock of zooplankton raises interesting questions concerning fish behavior that would be difficult to answer in an oceanic regime but might be addressed in an isolated regime such as the eastern Bering Sea. Certainly the marked external and internal environmental factors provide an easily recognized time-frame. Although fish spawning occurs as a cyclic event, dictated by instinct and environmental and other factors, it is possible that predation on eggs and larvae is a result of learned behavior rather than by instinct or chance encounter. If so, one might ask that if in an area where the shallow depths could permit spatial orientation do the predators use time-space guideposts in the search for ichthyoplankton (much like the fisherman who returns to a particular fishing location) or do they seek, in addition, the environmental conditions that trigger the various spawning events? If unable to associate the latter, then large year classes could result from the spawners adjusting to anomalous geographical displacements of optimum spawning conditions, where the eggs and larvae would not be subjected to normal predation. Further studies on zooplankton abundance, distribution (including depth distribution under the ice) and related fish behavior, particularly data on feeding behavior under the ice are also definitely needed.

The exciting aspect of the model is that fish population dynamics is considered in the context of variability in its environment, thereby providing insights into those factors which affect their distribution, abundance and productivity, and ultimately lead to quantification of these relationships and prediction models. However, the ability to compute accurate assessments of these interactions will require extensive and orderly acquisition of vast amounts of new information related to the entire ecosystem.

SUMMARY

A numerical, gridded ecosystem model with 8 components was used to compute the consumption of copepods and euphausids in the eastern Bering Sea. The principal zooplankton consumers in this model were pollock, herring, and marine birds.

Zooplankton consumption was, in some areas and months, nearly equal to zooplankton standing stock as ascertained from available literature, even though the model does not include all zooplankton consumers, and relatively low coefficients of consumption were used. After evaluating other possible causes for this discrepancy, it was concluded that either our existing knowledge on standing stock, production, and turnover rates

of zooplankton is deficient, or starvation in the sea is rather common. Either there is a lack of quantitative data on the larger, more mobile zooplankton organisms such as euphausids (which occur in relatively large proportions in stomachs of pollock, herring, and ecologically related species, but whose numbers are not caught sufficiently in routine plankton survey work), or the data on the number of generations and production rates of zooplankton need considerable revision.

The model indicates that areas of high consumption of copepods and euphausids change monthly, primarily due to the migrations of grazers, and that, on the other hand, there are large areas where zooplankton consumption is very low and production goes into a regeneration cycle or is consumed by benthos. The transport of copepods and euphausids by currents seems to be an important factor both for providing food for grazers and providing brood stock to areas of high consumption. If the areas of high utilization of zooplankton coincide with the areas of abundance of ichthyoplankton, survival of fish larvae and, subsequently, year class strength of a given species in these areas may be determined almost entirely by grazing.

As the process of feeding on plankton, including selective feeding, is a prey density-dependent process, it is important in fisheries research to know how food availability affects the behavior of fish, such as migrations, dispersals, etc. Thus, it is necessary to couple zooplankton research intimately with other fisheries research operations. Other information on planktivoros fish (e.g., abundance by sonar surveys and experimental fishing, stomach analyses, etc.) must be collected concurrently with plankton sampling. Knowledge of abundance, survival and behavior of zooplankton and fish during periods of ice cover is also required.

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