Winter 1997

Modeling Plankton Community Structure Under Environmental Forcing on the Southeastern United States Continental Shelf

Andrew Glenn Edward Haskell
*Old Dominion University*

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MODELING PLANKTON COMMUNITY STRUCTURE
UNDER ENVIRONMENTAL FORCING ON THE
SOUTHEASTERN U.S. CONTINENTAL SHELF

by

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Bachelor of Science August 1994,
Long Island University. New York, USA

A Thesis submitted to the Faculty of
Old Dominion University in Partial Fulfillment of the
Requirement for the Degree of

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OLD DOMINION UNIVERSITY
December 1997

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ABSTRACT

MODELING PLANKTON COMMUNITY STRUCTURE UNDER ENVIRONMENTAL FORCING ON THE SOUTHEASTERN U.S. CONTINENTAL SHELF.

Andrew Glenn Edward Haskell
Old Dominion University, 1997
Director: Dr. Eileen E. Hofmann

A system of coupled ordinary differential equations was developed to investigate the time-dependent behavior of phytoplankton, copepod, and doliolid populations associated with upwelling features on the outer southeastern U.S. continental shelf. Model equations describe the interactions of nitrate, ammonium, two phytoplankton size fractions, five copepod developmental stages, doliolids, and a detrital pool. Model dynamics are based primarily upon data obtained from field and laboratory experiments made for southeastern U.S. continental shelf plankton populations. Numerous simulations were performed to investigate the effects of environmental variability on the temporal distribution of the structure of resident plankton populations. Variations on a reference simulation, which represents average upwelling conditions without doliolids, were done to determine the effect of inclusion of doliolids, different feeding strategies, temperature and nutrient variations, and variations in ambient food concentrations on the basic plankton community structure. These simulations provide a measure of the role of environmental versus biological interactions in structuring the planktonic food web on the southeastern U.S. continental shelf. Simulations show that, when present, doliolids reach maximum concentrations 5-7 days after the onset of the phytoplankton bloom resulting from an
upwelling event, which is consistent with observations from bottom intrusion upwelling events. The presence of doliolids results in a rapid decrease in copepod concentrations, with the doliolids eventually displacing the copepods. Additional simulations show that ambient temperature conditions modify the rate of increase of the doliolids and copepod populations and hence the relative abundance of these populations.
To my wife, with love

Heather Jean Haskell
ACKNOWLEDGMENTS

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inexhaustible ability to rapidly crunch numbers; without her this project would not have been possible. Finally, to my wife, Heather, I cannot express in words the heartfelt gratitude I have for all the love, support, help and comfort she has given me during the hard times as well as for creating the good times.

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1. INTRODUCTION

Stefánsson et al. (1971) first suggested that primary productivity on the outer SouthEastern U.S. continental Shelf (SEUSS) is affected by pulses of upwelled nutrients from the waters of the Gulf Stream. Since that time, many studies have examined the physical (e.g., Yoder et al., 1981; McClain and Atkinson, 1985; Lee et al., 1991) and biological (e.g., Deibel, 1982a,b; Paffenhofer et al., 1984; Verity et al., 1993) components of this region.

It is well known that Gulf Stream-induced upwelling provides a regular if not continuous source of nitrate and other nutrients to the outer SEUSS (e.g., Atkinson et al., 1978; Yoder et al., 1983; Paffenhofer et al., 1987a). These nutrients can be introduced to the outer continental shelf waters by cold-core Gulf Stream frontal eddies or by bottom intrusions of Gulf Stream water (e.g., Atkinson et al., 1987; Lee et al., 1991; Verity et al., 1993). Studies have shown that the biology and chemistry of the outer SEUSS are greatly affected by these frequent upwelling events of nutrient-rich Gulf Stream water (Atkinson et al., 1978; Yoder et al., 1983). The two types of upwelling processes differ in their spatial and temporal scales. The frontal eddies occur with a frequency of 2 to 14 days (Lee and Atkinson, 1983) and normally exist for a only few days (Lee et al., 1991), while the bottom intrusions occur every 14 to 40 days and may persist for up to 6 weeks (Atkinson et al., 1984, 1987).

Off Charleston, South Carolina (Figure 1) the residence time of the upwelled water is relatively long due to the presence of a semi-permanent Gulf Stream meander

The journal model for this thesis is the Journal of Plankton Research.
caused by a bathymetric rise near 32°N. Water there stays longer on the shelf than at similar isobaths located either north or south, which should allow for the development of populations of higher trophic levels (Paffenhofer et al., 1995). The upwelling resulting from the frontal eddies produces only transitory phytoplankton blooms on the outer SEUSS, while the longer residence time of the bottom intrusions on the shelf can be long enough for the phytoplankton to convert nearly all of the newly upwelled nitrate into plant biomass (Yoder et al., 1983, 1985) resulting in large subsurface phytoplankton blooms. Yoder et al. (1983) estimated that approximately 75% of this growth is new production resulting from the upwelled nitrate. The phytoplankton associated with the bottom intrusions show a succession from small to large cells with the phytoplankton in older intrusions being predominately large diatoms such as *Rhizosolenia* (Yoder et al., 1983, 1985; Paffenhofer et al., 1984; Paffenhofer and Lee, 1987). The input of large amounts of nitrogen results in rapid phytoplankton growth that trigger zooplankton increases soon after the inception of the phytoplankton bloom. The concentration of the zooplankton in the bottom intrusions can reach 10,000 animals m⁻³ (Paffenhofer et al., 1984; Paffenhofer, 1985). Among the dominant plankton components on the outer SEUSS are phytoplankton, calanoid copepods (*Paracalanus*), and doliolid tunicates (*Doliolletta*). Past studies (Deibel 1982a; Paffenhofer and Lee, 1987) suggest that high doliolid concentrations result in a great reduction of the other plankton components that normally dominate the ecosystem.
While the doliolids can respond quickly to increases in phytoplankton with generation times as rapid as 2 to 3 days (e.g., Heron, 1972), calanoid copepods on the southeastern shelf require 2 to 3.5 weeks to reach the next generation (Paffenhofer, 1993). The copepod abundances are not greatly affected by the frontal eddy upwelling, but pelagic tunicates, especially doliolids, are frequently observed in the upwelling events (Deibel, 1985).

Thaliacea are gelatinous zooplankton that can filter particles over a wide range of sizes, limited at the upper end only by the size of their body cavity opening (Deibel, 1982b). They exhibit rapid growth rates, short generation times, and near constant clearance rates regardless of food concentration. While calanoid copepods are suspension feeders that can spawn eggs continuously, the life cycle of the doliolids is more complex. Doliolids experience metagenesis, the alternation between sexual and asexual reproductive phases. The asexual reproductive stages allow the doliolids to rapidly produce large numbers of progeny, often much faster than sexual reproduction by copepods (Deibel, 1982a,b; Paffenhöfer et al., 1995), thereby allowing them to reach high population densities in short periods of time (Alldredge and Madin, 1982). If the doliolids reach appreciable densities, a significant decrease of the coexisting copepod populations could occur (Deibel, 1985). The doliolids themselves are consumed by a large number of fish species and their contribution to higher trophic levels is possibly important (Deibel, 1985; Heron et al., 1988; Paffenhöfer et al., 1995).

The barrel shaped doliolids use ciliary action to pump water through a large
pharyngeal cavity and can efficiently filter almost all particles that pass through their bodies (Alldredge and Madin, 1982). The ability of a large (1 to 8 mm) zooplankter to feed directly on food as small as 2 \( \mu \text{m} \) represents a short trophic link in the classic food chain and could be an efficient pathway by which energy is moved from lower to higher trophic levels (Crocker et al., 1991). Past studies have suggested that the exclusion of these zooplankton from ecosystem models will inadequately represent energy and material flow through planktonic food webs (Hamner et al., 1975; Deibel, 1982a).

To examine the dynamics of the lower trophic levels associated with Gulf Stream frontal eddy and bottom intrusions onto the outer SEUSS a time-dependent numerical model was used to analyze the biological interactions of the local plankton and the changes in the community structure resulting from varying environmental influences. The model describes the time-dependent interactions between nitrate, ammonium, two size classes of phytoplankton, five life stages of copepods, doliolids, and the detrital pool. The temperature and nitrogen content of the simulated ecosystem were varied to simulate the occurrence of Gulf Stream water upwelling onto the outer shelf as bottom intrusions or frontal eddies. More specifically, the rates and quantities of doliolid grazing on phytoplankton and the calanoid copepod, were examined by varying the initial abundance and metabolic rates of the various plankton components.

To enhance the previously published observations of primary production of the SEUSS waters, the role of upwelling events on the production of phytoplankton
blooms along the outer SEUSS will be re-examined, in the context of a time-dependent model, to enhance our knowledge regarding this subject. By comparing the model results to field results, rates of ingestion, growth and reproduction, can be quantified with greater precision than by either method alone.

By modeling planktonic community structure under environmental factors not yet observed in situ, the simulation results will provide an estimate of how plankton interactions affect the structure and function of the community. The general significance of this study is to further our understanding of how these fractions (phytoplankton, calanoid copepods, doliolids) of the outer shelf water community interact under environmental influences. To be able to adequately model an ecosystem, one must first understand it.

This study was designed to investigate the following research questions:

1. What are the effects of temperature changes on the relative abundance of the doliolids and the copepods?
2. What time scale is required, following an upwelling event, for the doliolid populations to reach concentrations that produce significant effects on the copepod abundances?
3. What are the concentrations needed, of all plankton fractions, for the doliolids to produce significant effects on the copepod abundances?
4. Do the doliolids affect the copepods directly (by direct predation) or indirectly (by consuming a large portion of the food sources available for the copepods)?
5. How do the relative abundances of small and large phytoplankton affect the doliolid/copepod population structure?

The following section presents background information on the physical circulation and chemical and biological processes associated with the SEUSS. Section 3 provides details about the model that was used to produce the results presented in Section 4. Included in Section 5 are comparisons of the model output to observed values and discussions of the simulation results. Finally Section 6 presents the conclusions from this study.
2. BACKGROUND

The following sections give a review of the research relevant to this study. The first portion gives an overview of the physical oceanography of the SEUSS. This is followed by a description of the biological characteristics of the region.

2.1 LOCATION AND PHYSICAL OCEANOGRAPHY

The ocean margins, consisting of the continental shelf and the adjacent slope, represent 10-20% of the surface area of the world's oceans but contribute 25-50% of the total marine primary production (Walsh 1988). This production results from increased nutrient inputs from many sources including: upwelling of oceanic waters, input of fluvial nutrients, and resuspension of sedimentary nutrients.

The waters that reside over the outer continental shelf of the southeastern United States are primarily influenced by the nearby Gulf Stream. If the following conditions occur simultaneously, water from greater depths of the Gulf Stream can be upwelled onto the continental shelf: a) an onshore position of the Gulf Stream, b) prolonged northward winds, and c) the passage of a Gulf Stream frontal eddy (Atkinson et al., 1987; Paffenhöfer et al., 1987a). In addition, for the eddy-induced upwelled water to reach the middle shelf, either the onshore position of the Gulf Stream or the northward winds must be sustained for at least four to eight days (Paffenhöfer, et al., 1987a).

The mean circulation of the SEUSS water is northward throughout most of the year. The intruding waters can sometimes enter the shelf in the region of St. Augustine, Florida and be transported north as a distinct water mass. This subsurface
cold water mass can become separated from the Gulf Stream by a ridge of warmer water along the shelf break (Atkinson et al., 1987). During periods of summer heating and cold water upwelling, the vertical temperature gradients in the shelf waters can be as high as 10°C, greatly increasing the stability of the water column. The main processes acting against this stratification are wind mixing at the surface and the interaction of the current with the bottom (Atkinson et al., 1987).

If wind mixing is absent, the temperature of the intrusions will not change significantly over the duration of the event. If wind mixing does occur while the intruded waters are over the shallow shelf, then summer warming of the intrusion can occur as the surface water mixes with the subsurface intrusion.

The southeastern U.S. continental shelf is broad, almost 200 km wide, but shallow, the depth of the shelf break is only 50 m, in contrast to that near the Florida Keys (10-20 m) and the Georges Bank area (150 m, Atkinson and Menzel, 1985). As the shelf floor still receives approximately 1% of the surface irradiation, the entire outer shelf is within the euphotic zone (Yoder, 1985). Winds over the shelf blow northeastward from April to August with an average speed of 2-4 m s\(^{-1}\). During the late fall and winter the winds are lighter and more variable (Blanton et al., 1985).

It is well known that upwelling from the Gulf Stream provides a regular source of nitrate to the outer SEUSS (e.g., Yoder et al., 1985; Paffenhöfer et al., 1987a). These nutrients can be introduced to the outer continental shelf waters by either cold-core Gulf Stream frontal eddies or by bottom intrusions of the Gulf Stream water. Several studies have shown that the biology and chemistry of the outer SEUSS are
greatly affected by these upwelling events of nutrient-rich Gulf Stream water (e.g., Atkinson et al., 1978; Yoder et al., 1983). The two types of upwelling processes differ in their temporal and spatial scales. The frontal eddies normally exist only for a few days (Lee et al., 1991), while the bottom intrusions may persist for up to several weeks (Atkinson et al., 1984, 1987).

2.2 FRONTAL EDDIES

Some of the various meanders and other disturbances of Gulf Stream that occur along the shoreward boundary, are known as frontal eddies. Frontal eddies are different from larger cold-core Gulf Stream rings that detach from the stream north of Cape Hatteras. Cold-core Gulf Stream rings are the product of entrainment of the resident shelf waters, while the cold core of a frontal eddy is the result of upwelling of North Atlantic Central Water, also known as Western North Atlantic Water (Bishop et al., 1980; Yoder et al., 1983). Frontal eddies are quite common on the outer SEUSS and occur year-round, independent of the wind field, with an average periodicity of about two weeks (Vukovich et al., 1979; Yoder et al., 1981). The dimensions of the frontal eddies vary with the location along the shelf, but are typically 100 km by 20 km for the along- and across-shelf dimensions, respectively (Lee et al., 1981). Frontal eddies have average northward propagation speed of approximately 35 km day⁻¹ (Lee and Atkinson, 1983).

The presence of a doming of the isotherms is often used as an indicator of a frontal eddy. These domes, however, may be caused by shelf break upwelling or from the cascading of cooled shelf water over the shelf break (Stefánsson et al., 1971).
Because the dome structures can be produced for a number of reasons it is difficult to identify the passage of Gulf Stream frontal eddies in hydrographic data (Atkinson et al., 1989).

Because the residence time of a frontal eddy is one week or less, there is insufficient time for a complete succession of the planktonic organisms. Although the act of bringing excess nitrate into the euphotic zone produces a short but productive phytoplankton bloom, the zooplankton are relatively unaffected by frontal eddies (Deibel, 1985).

2.3 BOTTOM INTRUSIONS

While the frontal eddies normally occur over a period of a few days, once the upwelled water of the bottom intrusion is transported onto the shelf, it can remain there for a month or more (Atkinson et al., 1984). This additional time, in comparison with the frontal eddies, allows for not only a phytoplankton bloom, but also the ensuing growth of the zooplankton. Bottom intrusions occur primarily during summer months when the shelf waters are stratified and the upwelling favorable winds prevail (Stefánsson et al., 1971; Atkinson et al., 1984; Atkinson et al., 1987). Bottom intrusions occur with an average periodicity of 14 to 40 days (Atkinson et al., 1984). Despite the duration and frequency of production of the various upwelling events, field observations do not indicate occurrences of one intrusion overtaking another or of two events mixing. Bottom intrusions, with observed areas of up to 10,000 km², can occupy areas almost five times as large as the frontal eddies (Paffenhöfer et al., 1987a).
2.4 CHARLESTON GYRE

This study is particularly concerned with the bottom intrusions in a specific portion of the South Atlantic Bight (SAB). As the Gulf Stream flows northward past the South Carolina coast a bathymetric rise near 32°N, known as the Charleston Bump (Figure 1), produces the Charleston Gyre, a cyclonic semi-permanent offshore meander that resides over the slope (Brooks and Bane, 1978).

The residence time of the upwelled water on the outer shelf off South Carolina is relatively long due to the presence of this Gyre (McClain and Atkinson, 1985). The gyre persists long enough for plankton populations, including those of higher trophic levels, to develop (Paffenhofer et al., 1995). A warm filament of the Gulf Stream often wraps around the Gyre, further isolating the Gyre from the ambient shelf waters and adding stability to the water column.

2.5 NUTRIENT INPUTS

All of these upwelling events bring nutrient-rich Gulf Stream water into the euphotic zone of the shelf. Bishop et al. (1984) estimated that intrusions can transport $2.2 \times 10^5$ metric tons of nitrogen annually onto the shelf which could result in 90,000 to 180,000 tons of carbon production per 40 day upwelling event. Although the SEUSS receives nutrient from sources other than bottom intrusions, e.g., estuarine inputs, the upwelling-induced nutrient input supplies the vast majority of the nutrients to the outer shelf. Estuaries and salt marshes along the Georgia and South Carolina coasts may export 0.1 and $1.2 \times 10^5$ metric tons of nitrogen annually, respectively (Bishop et al., 1984). However, most of this nitrogen is in the form of particulate
organic nitrogen or dissolved organic nitrogen (DON). Bishop et al. (1984) found that the phytoplankton directly use little of the DON for growth. Additionally, coastal fronts on the inner shelf inhibit the cross-shelf transport of nutrients to the outer shelf (Yoder 1985).

Although bottom intrusions of nutrient rich Gulf Stream water are advected onto the shelf at regular intervals during upwelling-favorable winds of the spring and summer (Verity et al. 1993), the magnitude of the intrusions varies with time and thus the quantity of upwelled nutrients varies between upwelling events. The frontal eddy upwelling is the single largest source of nitrate for the southeastern shelf (Yoder et al., 1981). Normally, however, these nutrients have a short residence time on the shelf as the outer shelf is flushed with each new passing eddy.

The outer SEUSS does not experience seasonal plankton blooms like those that occur on the continental shelf north of Cape Hatteras, North Carolina. Blooms in the South Atlantic Bight shelf waters are associated with the episodic upwelling and intrusions of Gulf Stream water onto the shelf (Atkinson et al., 1978; Yoder et al., 1981).

As the primary source of nitrogen on the outer SEUSS is the upwelled subsurface waters of the Gulf Stream, the regions of high phytoplankton biomass on the outer SEUSS are typically found within nutrient-enriched subsurface layers underlying a surface layer characterized by low chlorophyll (<0.5 μg liter⁻¹) and nutrients (Atkinson et al., 1978).
Under conditions devoid of upwelled nutrients, the ambient nitrate concentrations in the outer SEUSS waters are usually less than 0.5 μM (e.g., Bishop et al., 1980; Lee and Atkinson, 1983; Atkinson et al., 1987). In contrast, an upwelling event can increase the nitrate concentrations to a maximum of 10 to 15 μM within a period of only two or three days (Yoder et al., 1983, 1985). Ammonium concentrations in SEUSS waters, however, normally remain below 0.1 μM (Yoder et al., 1983, 1985).

2.6 BIOLOGICAL RESPONSE TO AN UPWELLING EVENT

The transport of nutrients into the euphotic zone of the shelf provides a food source for the development of the planktonic community (Lee et al., 1991). Yoder et al. (1983) determined that 75% of the upwelling-enhanced phytoplankton bloom is new production. The residence time of bottom intrusions on the shelf persists long enough for the light-limited phytoplankton to convert nearly all the upwelled nitrate into plankton biomass (Yoder et al., 1983). During the summer months, when the shelf is stratified, the subsurface intrusions of the nutrient-rich Gulf Stream water are able to penetrate across the shelf, while in the winter months the shelf waters are more evenly mixed and thus the phytoplankton blooms are restricted to the outer shelf (Yoder, 1985).

Since the upwelled water is on the shelf as a separate water mass, it is probable that the phytoplankton develop uniformly within this water. This can lead to the formation of a phytoplankton patch in the nutrient-rich intrusion (Yoder et al., 1981). Conditions of weak mixing in the vertical and horizontal directions and rapid
phytoplankton growth should result in a patch with sharp boundaries (Figure 2). In one observation of a frontal eddy (Yoder et al. 1981), the surface chlorophyll concentration was only 2% of the peak concentration in the eddy and surface concentrations on the shelf side were 10% of the maximum value in the patch. If mixing with adjacent water masses is limited, zooplankton, which develop in a phytoplankton patch, could themselves form a patch with similar dimensions (Paffenhofer et al., 1987a).

As intruded waters ‘age’ the composition of the plankton population undergoes species succession. Within the first few days following the initial upwelling event, the small phytoplankton (<10 μm) first show a rapid increase. After approximately a week, the larger phytoplankton (>10 μm) become dominant. This is followed closely by a bloom of zooplankton. The dominant copepods of the Gyre are the calanoid Paracalanus sp. and the cyclopoid Oithona sp. and the vast majority of doliolid tunicates are Dolioeletta gegenbauri (Paffenhofer et al., 1995).

Paracalanus and Dolioeletta both readily graze upon small and large phytoplankton, however, both genera have an upper limit as to the size of their prey. In the SEUSS waters, old intrusions are dominated by larger phytoplankton species of Rhizosolenia (>40 μm Equivalent Spherical Diameter), which cannot be grazed by most of the stages of Paracalanus (Paffenhofer and Knowles, 1978; Paffenhofer, 1984a,b).

Because of the Gulf Stream events, the composition of abundant copepods and chlorophyll a levels in the outer shelf waters can vary widely over intervals of several
Cross shelf intrusion of cold, nutrient rich Gulf Stream water

Stranding of an intrusion:
Concentrations of Nitrate and Chlorophyll-\(a\) across the intrusion

Stranding of an intrusion:
Abundance of Zooplankton

Fig. 2. Schematic of onshore-offshore distributions of: A) position, B) nitrate and chlorophyll \(a\), and C) zooplankton in an intrusion (from Paffenholzer et al., 1984).
days. Often, however, the surface waters are characterized, akin to the open ocean, by very low chlorophyll levels (Paffenhofer, 1991).

The main offshore current direction is northward and since many of the abundant calanoids and thaliaceans have also been observed year-round in the Florida Current, it has been postulated that the southeastern U.S. shelf receives a supply of seed populations of several zooplankton species which originate from the Gulf of Mexico and are advected, during the intrusion events, out of the Gulf Stream and onto the shelf (Paffenhofer, 1991).

Thaliacean (doliolid) occurrences are mostly episodic in nature. They do not occur continuously on the southeastern U.S. shelf throughout the year, and thus are most likely imported via the Florida Current (Lee et al., 1991; Paffenhofer et al., 1995). Thaliacea have, however, been observed regularly on the southeastern U.S. shelf during the summer (Paffenhofer et al., 1984).

2.7 DOLIOLIDS

Tunicates on the SEUSS are represented by appendicularians, salps, and doliolids. They all exhibit higher growth and reproduction rates and the ability to ingest a wider size range of food than most other planktonic metazoan herbivores. These abilities enable them to achieve high population densities in short periods of time, when predation is limited, and to adapt to the varying environmental conditions regularly encountered by marine plankton (Alldredge and Madin, 1982). Doliolids are mostly neritic and have been found throughout the world's oceans in temperatures ranging from 3 to 28°C (Paffenhofer and Lee, 1987; Hopkins and Torres, 1989).
Following the upwelling-induced phytoplankton bloom, both the copepod and
doliolid fractions, if present, experience a period of rapid growth. The doliolids,
however, have faster growth and reproduction rates than do the copepods and thus,
under appropriate conditions, the doliolids can quickly dominate the planktonic
ecosystem. Field studies by Deibel (1982b) indicate that normal, low, concentrations
of *D. gegenbauri* in SEUSS waters clear their resident volume of water in about four
months, but that the highly concentrated populations can clear their resident water
volume in less than one day.

If a seed population of doliolids is present during a bottom intrusion event, all
life stages of the doliolids could be found in high concentrations in the Charleston
Gyre. Under non-upwelling conditions the abundance of doliolids can be low or even
non-existent. Although copepod populations do not seem to be greatly affected by the
Gulf Stream frontal eddy upwelling, tunicates have been found in high numbers in
these upwelling features (Atkinson et al., 1978; Paffenholzer et al., 1984; Deibel 1985).
In the waters of a SEUSS bottom intrusion doliolids have been observed in quantities
as high as 4000 m$^3$ (Paffenholzer and Lee, 1987). In video microscopy of
microaggregations of plankton, gelatinous forms such as the tunicate *Doliolum* were
found in dense patches along the shelf transect that indicates that these species may be
the dominant grazers of phytoplankton (Davis et al., 1992).

Unlike the relatively common reproductive cycle of calanoid copepods,
doliolids possess a much more complex life cycle. Doliolids experience obligatory
metagenesis, the alternation of sexual and asexual reproduction. Gonozoooids release
eggs from which larvae hatch that develop into oozoids. Each oozoid asexually buds a colony of feeding trophozoooids and a colony of phorozoooids for dispersal; an oozoid later becomes a nurse which provides locomotion for its attached colonies. The phorozoooids asexually reproduce gonozoooids that reproduce sexually (Paffenhöfer et al., 1995). The two asexual stages of Dolioletta allow rapid production of large numbers of genetically identical progeny and may have a powerful transitory effect on algal biomass (Deibel, 1982a,b). Asexual reproduction by thaliacea is often much faster than sexual reproduction by copepods (Paffenhöfer et al., 1995) The extremely high fecundity of the doliolids means that only a few old oozoids are needed to start a bloom (Deibel, 1985).

Tunicates are periodically encountered in extremely high densities. Swarms of thaliaceans may extend hundreds of kilometers and may reach densities of 7000 animals m\(^{-3}\) (Deevey, 1952). Deibel (1980) observed doliolid colonies 1 meter in length that should have contained thousands of zooids. He measured nurse zooid densities between 1 and 31 m\(^{-3}\), which would graze between 0.6 and 19% of their resident volume per day, assuming colonies of 100 zooids and a constant grazing rate of 2.5 ml zooid\(^{-1}\). They are able to filter much larger volumes of water than copepods, they can ingest particles over a wide range of sizes and kinds, their life histories permit rapid, exponential population increases to take immediate advantage of increased food supplies and to exist without reproducing during periods of low food supply (Alldredge and Madin, 1982). In the Bay of Bengal, it has been suggested that Thaliacea contributes to the eutrophication of the system through the death and
disintegration of the phytoplankton blooms (Madhupratap et al., 1980). The barrel shaped doliolids pump water through a large pharyngeal cavity by the motion of cilia. They can remain stationary while filtering, but can also use a set of body muscles to pump short pulses for swimming (Alldredge and Madin, 1982; Bone and Trueman, 1984).

2.8 ADDITIONAL ASPECTS

Following the input of nitrogen via an upwelling event, Paffenhofer et al. (1987a) observed that nitrate concentrations decreased from about 15 to 1 μM in about two weeks. Then not only had the doliolid population greatly increased but the free living bacteria had reached concentrations of more than \(10^6\) ml\(^{-1}\) at all depths, exceeding normal concentrations by an order of magnitude. Grazing control of the medium sized particles in the intrusion was attributed to small calanoid copepods. An inverse correlation between the abundance of bacteria and doliolids suggested that these mucous-net feeders, when abundant, exerted some grazing control on bacteria. Tebeau and Madin (1994) tested the retention efficiency of doliolids on small particles and found that the grazing rate of 1 μm spheres was 30-56% of 2.5 μm spheres.

For many years people assumed that gelatinous zooplankton were a carbon sink as they had few predators. However, Kashkina (1986) found that over 100 species of fish consume salps on a regular basis. Doliolids, in contrast to salps, do not have to move to feed, and only occasionally move quickly and therefore might be far less conspicuous to predators than salps. The current paradigm is that doliolids are consumed by a large number of fish (Paffenhofer et al., 1995) and their value as food...
for higher trophic levels is much greater than previously assumed (Heron et al., 1988).

The ability of a 1 to 10 mm long metazoan to feed on bacterial-sized food represents a short link in the traditional food chain and indicates a potentially significant role for these gelatinous grazers in efficiently moving energy from lower to higher trophic levels (Crocker et al., 1991).

The results of this study should increase our knowledge of the interactions among the phytoplankton, copepods, and doliolids of the outer southeastern U.S. continental shelf water community.
3. METHODS

3.1 ORIGINAL MODEL EQUATIONS

The time-dependent model created in this study is a modification of the one developed by Hofmann and Ambler (1988) for the SEUSS waters. The model originally consisted of ten ordinary differential equations representing two size classes of phytoplankton, nitrogen, ammonium, five size classes of zooplankton (the copepod *Paracalanus* sp.), and a detrital term used for closure. All model components are expressed in terms of $\mu$gN l$^{-1}$. Modification of the ecosystem dynamics included in this model, to allow for the addition of the doliolids, are enclosed by braces, i.e., {}, in the following equations and are explained in greater detail in the following section. A schematic of the interactions of the time-dependent model is shown in Figure 3.

The phytoplankton are grouped into one of two size classes: larger than or smaller than 10 µm. By doing this the effects of each size class on primary production, nutrient uptake and trophic level transfer can be examined. Two of the primary classes of phytoplankton that are found on the SEUSS are small flagellates (Equivalent Spherical Diameter (ESD) 2-5 µm), and diatoms (ESD ~ 10-15 µm). *Rhizosolenia*, a larger diatom, can also be found in intrusions that have existed for several weeks but are not explicitly represented in the model and are part of the larger than 10 µm size fraction (Ambler, 1986). Model terms for the phytoplankton include growth, cell death, and zooplankton grazing.
Fig. 3. Schematic of the biological components and interactions included in the model.
These are expressed as follows:

for phytoplankton larger than 10 μm, $LP$,

$$
\frac{dLP}{dt} = \frac{P_{mi} I}{I_k + I} \frac{Chl}{C} \left[ \frac{NO_3}{k_a + NO_3} - \frac{NH_4}{k_a + NH_4} \right] LP - \delta LP
$$

$$
- \sum_{i=3}^{5} \frac{W_{i,LP}}{EPN_i} I_{mi} \left( 1 - e^{-\gamma_{EPN_i}} \right) ZN_i \left\{ - \frac{DOL}{DOLWT} LP \cdot F_{dol} \cdot K(LP, TH_{LP}) \right\}
$$

(1)

for phytoplankton smaller than 10 μm, $SP$,

$$
\frac{dSP}{dt} = \frac{P_{mi} I}{I_k + I} \frac{Chl}{C} \left[ \frac{NO_3}{k_a + NO_3} - \frac{NH_4}{k_a + NH_4} \right] SP - \delta SP
$$

$$
- \sum_{i=2}^{5} \frac{W_{i,SP}}{EPN_i} I_{mi} \left( 1 - e^{-\gamma_{EPN_i}} \right) ZN_i \left\{ - \frac{DOL}{DOLWT} SP \cdot F_{dol} \cdot J(SP, TH_{SP}) \right\}
$$

(2)

The first term in equations 1 and 2 represents phytoplankton growth, the second represents cell death, and the third term is copepod grazing, where, $ZN_i$ is the specific copepod feeding stage, $i$. The copepod preference for a given phytoplankton size fraction is given by the effective food concentration, $EPN$, as:

$$
EPN_i = W_{i,SP} SP + W_{i,LP} LP \cdot H(LP, TH_{COP,i})
$$

(3)

where $W_{i,SP(LP)}$, the selectivity coefficient, determines the preference for a particular phytoplankton size fraction. A feeding threshold imposed on the copepods, $TH_{COP,i}$, is approximately equal to the concentration of one copepod per liter, and is defined as:

$$
H(LP, TH_{COP}) = 0 \text{ for } LP < TH
$$

$$
H(LP, TH_{COP}) = 1 \text{ for } LP \geq TH
$$

(4)

The last term represents phytoplankton losses due to doliolid grazing where $DOL$ is the concentration of the doliolids, $DOLWT$ is the weight of an average doliolid, and $F_{dol}$ is the filtration rate of the doliolids. To prevent the phytoplankton from being
completely depleted, minimum grazing thresholds $TH_{SP}, TH_{LP}$, approximately equal to 15 doliolids per m$^3$, the lower range of doliolid concentrations found on the outer SEUSS, are also imposed on the doliolid ingestion of the small and large phytoplankton fractions with the corresponding threshold functions:

\[
J(SP, TH_{SP}) = \begin{cases} 0 & \text{for } SP < TH_{SP} \\ 1 & \text{for } SP \geq TH_{SP} \end{cases}
\]

(5)  

\[
K(LP, TH_{LP}) = \begin{cases} 0 & \text{for } LP < TH_{LP} \\ 1 & \text{for } LP \geq TH_{LP} \end{cases}
\]

(6)  

The large phytoplankton are grazed only by the three oldest classes of the copepods and the doliolids while the small phytoplankton are grazed by all the zooplankton classes except the first non-feeding egg through the nauplius 2 stage (EggN2). Definitions and values of all the parameters used in equations 1 and 2, except for those formulated for the doliolids, are given in Table I.

The copepods are grouped into five classes based on development stage which are: egg through the nauplius 2 stage (EggN2), nauplius 3 to nauplius 4 (N3N4), nauplius 5 to copepodite 3 (N5C3), copepodite 4 to copepodite 5 (C4C5), and adult (Adlt). The governing equations for the different copepod stages include assimilation, excretion, egg production, molting, and predation processes. These are expressed as follows:

for the nonfeeding category, $i=1$, EggN2 ($ZN_1$),

\[
\frac{dZN_1}{dt} = \phi E_{m} \left(1 - e^{-\lambda(t_{i}-E_{n})}\right)ZN_3 - D_{m_{2}} ZN_1 - \left(\frac{M_{p} ZN_1}{k_{1} + ZN_{1}}\right)ZN_1 \left\{- \frac{DOL}{DOLWT} ZN_1 \cdot F_{dol}\right\}
\]

(7)
Table I. Units, definitions, values, and sources for the parameters used in the phytoplankton and nutrient equations for bottom intrusions and frontal eddies (frontal eddy values, where different, are given in parenthesis).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Definition</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$LP$</td>
<td>$\mu gN \ l^{-1}$</td>
<td>Concentration of Large Phytoplankton size class</td>
<td>variable</td>
<td>calculated</td>
</tr>
<tr>
<td>$SP$</td>
<td>$\mu gN \ l^{-1}$</td>
<td>Concentration of Small Phytoplankton size class</td>
<td>variable</td>
<td>calculated</td>
</tr>
<tr>
<td>$P_m$</td>
<td>$mg C \ mg Chl a \ h^{-1}$</td>
<td>Maximum Assimilation Number</td>
<td>variable</td>
<td>Eppley, 1972</td>
</tr>
<tr>
<td>$I$</td>
<td>eins $m^{-2} h^{-1}$</td>
<td>Light intensity</td>
<td>variable</td>
<td>calculated</td>
</tr>
<tr>
<td>$I_0$</td>
<td>eins $m^{-2} h^{-1}$</td>
<td>Maximum light intensity</td>
<td>4.0</td>
<td>Yoder et al., 1983, 1985</td>
</tr>
<tr>
<td>$I_k$</td>
<td>eins $m^{-2} h^{-1}$</td>
<td>Light intensity $\frac{1}{2}$ saturation constant</td>
<td>1.11 (1.98)</td>
<td>Yoder et al., 1983</td>
</tr>
<tr>
<td>Chl C$^{-1}$</td>
<td>$mg Chl a \ mg C^{-1}$</td>
<td>Chlorophyll a : Carbon ratio</td>
<td>0.025</td>
<td>Yoder et al., 1983</td>
</tr>
<tr>
<td>$NO_3$</td>
<td>$\mu gN \ l^{-1}$</td>
<td>Nitrate Concentration</td>
<td>variable</td>
<td>calculated</td>
</tr>
<tr>
<td>$NH_4$</td>
<td>$\mu gN \ l^{-1}$</td>
<td>Ammonium Concentration</td>
<td>variable</td>
<td>calculated</td>
</tr>
<tr>
<td>$V_n$</td>
<td>$\mu M$</td>
<td>Maximum $NO_3$ uptake rate</td>
<td>0.187 (0.03)</td>
<td>Hofmann and Ambler, 1988</td>
</tr>
<tr>
<td>$k_n$</td>
<td>$\mu M$</td>
<td>$NO_3$ concentration at $\frac{1}{2} V_n$</td>
<td>1.55 (0.0)</td>
<td>Hofmann and Ambler, 1988</td>
</tr>
<tr>
<td>$V_a$</td>
<td>$\mu M$</td>
<td>Maximum $NH_4$ uptake rate</td>
<td>0.176 (0.03)</td>
<td>Hofmann and Ambler, 1988</td>
</tr>
<tr>
<td>$k_a$</td>
<td>$\mu M$</td>
<td>$NO_3$ concentration at $\frac{1}{2} V_a$</td>
<td>0.047 (0.0)</td>
<td>Hofmann and Ambler, 1988</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>none</td>
<td>$NH_4$ inhibition of $NO_3$ uptake</td>
<td>variable</td>
<td>calculated</td>
</tr>
<tr>
<td>$\delta SP$</td>
<td>day$^{-1}$</td>
<td>Natural death rate of the small phytoplankton size fraction</td>
<td>0.138</td>
<td>Estimated this study</td>
</tr>
<tr>
<td>$\delta LP$</td>
<td>day$^{-1}$</td>
<td>Natural death rate of the large phytoplankton size fraction</td>
<td>0.068</td>
<td>Estimated this study</td>
</tr>
<tr>
<td>$TH_{COP}$</td>
<td>$\mu gN \ l^{-1}$</td>
<td>Copepod feeding threshold on the Lg. Phytoplankton fraction</td>
<td>See Table III</td>
<td>Frost, 1975</td>
</tr>
<tr>
<td>$TH_{LP}$</td>
<td>$\mu gN \ l^{-1}$</td>
<td>Doliolid feeding threshold on both Phytoplankton fractions</td>
<td>0.12</td>
<td>Estimated this study</td>
</tr>
</tbody>
</table>
for the juvenile categories, $i=2,3,4$; N3N4, N5C3, and C4C5 ($ZN_2$, $ZN_3$, $ZN_4$),

\[
\frac{dZN_i}{dt} = \psi_i I_m \left( 1 - e^{-\gamma_i^{EPN_i}} \right) ZN_i - (\eta_i + \upsilon_i^{EPN_i}) ZN_i \\
+ D_{m_i} \left( 1 - e^{-\Lambda_i^{EPN_i}} \right) ZN_i - D_{m_i} \left( 1 - e^{-\Lambda_i^{EPN_i}} \right) ZN_i - \left( \frac{M_p ZN_i}{k_i + ZN_i} \right) ZN_i
\]

(8)

for the adults, $i=5$; Adlt ($ZN_5$),

\[
\frac{dZN_5}{dt} = \psi_5 I_m \left( 1 - e^{-\gamma_5^{EPN_5}} \right) ZN_5 - (\eta_5 + \upsilon_5^{EPN_5}) ZN_5 - \phi E_m \left( 1 - e^{-\lambda_i(1-\tau_i)} \right) ZN_5 \\
+ D_{m_5} \left( 1 - e^{-\Lambda_5^{EPN_5}} \right) ZN_5 - \left( \frac{M_p ZN_5}{k_5 + ZN_5} \right) ZN_5
\]

(9)

The first two terms in equations 8 and 9 are assimilated ingestion and excretion, respectively, which apply only to the feeding stages. The third and fourth terms of equation 8 are transfers from (to) previous (next) life stages. The first term in equation 7 and the third term in equation 9 is egg production and only applies to the egg stage, as a gain, and to the adults, as a loss. Definitions and values of all the parameters used in equations 7, 8 and 9 are given in Tables II and III.

The primary source of nitrogen for the model ecosystem is nitrate. The nitrate equation consists of a loss to phytoplankton via nitrogen uptake and an input term from upwelling events. The governing equation for these processes is:

\[
\frac{dNO_3}{dt} = \sum_{j=1}^{2} \left[ \frac{P_m I_{k_j} Chl}{I_{k_j} + I} \frac{NO_3}{k_s + NO_3} - \sigma \right] N_j + \left\{ \begin{array}{ll} S_0 / L, & \text{during upwelling events} \\
0, & \text{during all other times} \end{array} \right.
\]

(10)

The first term represents nitrogen uptake by each of the two phytoplankton size fractions, $P_j$, modified by ammonium inhibition, $\sigma$. The second term simulates the input of nitrate during upwelling events. The total nitrate input during a single upwelling event, $S_0$, is divided into $L$ equal time intervals based on the duration of
Table II. Units, definitions, values, and sources for the parameters used in the copepod equations.

<table>
<thead>
<tr>
<th>Parameter</th>
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<tbody>
<tr>
<td>$Z_{ti}$</td>
<td>µgN l$^{-1}$</td>
<td>Concentration of size fraction</td>
<td>variable</td>
<td>calculated</td>
</tr>
<tr>
<td>$\phi$</td>
<td>none</td>
<td>Sex ratio (fraction of females)</td>
<td>0.85</td>
<td>Checkley, 1980a</td>
</tr>
<tr>
<td>$E_m$</td>
<td>day$^{-1}$</td>
<td>Maximum egg production</td>
<td>0.5</td>
<td>Landry, 1983</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>day$^{-1}$</td>
<td>Egg production rate constant</td>
<td>1.848</td>
<td>Landry, 1983</td>
</tr>
<tr>
<td>$W_i$</td>
<td>none</td>
<td>Selectivity coefficient</td>
<td>See Table III</td>
<td>Ambler, 1986</td>
</tr>
<tr>
<td>$D_{m,ij}$</td>
<td>day$^{-1}$</td>
<td>Maximum development rate</td>
<td>See Table III</td>
<td>Paffenhöfer, Unpublished</td>
</tr>
<tr>
<td>$DR$</td>
<td>none</td>
<td>Ratio of minimum development time : egg development time @ 20°C</td>
<td>See Table III</td>
<td>Checkley, 1980b</td>
</tr>
<tr>
<td>$\Lambda$</td>
<td>l µgN$^{-1}$</td>
<td>Development rate constant</td>
<td>See Table III</td>
<td>Paffenhöfer, Unpublished</td>
</tr>
<tr>
<td>$\psi$</td>
<td>none</td>
<td>Assimilation efficiency</td>
<td>variable</td>
<td>calculated</td>
</tr>
<tr>
<td>$I_{mi}$</td>
<td>day$^{-1}$</td>
<td>Maximum Ingestion Rate</td>
<td>See Table III</td>
<td>Vanderploeg et al. 1984</td>
</tr>
<tr>
<td>$\eta$</td>
<td>day$^{-1}$</td>
<td>Excretion rate constant</td>
<td>See Table III</td>
<td>Paffenhöfer and Gardner, 1984</td>
</tr>
<tr>
<td>$\nu$</td>
<td>µgN$^{-1}$</td>
<td>Excretion rate constant</td>
<td>See Table III</td>
<td>Paffenhöfer and Gardner, 1984</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>l µgN$^{-1}$</td>
<td>Ingestion rate curve constant</td>
<td>See Table III</td>
<td>Vanderploeg et al. 1984</td>
</tr>
<tr>
<td>$M_p$</td>
<td>µgN l$^{-1}$</td>
<td>Maximum predation rate</td>
<td>variable</td>
<td>Hofmann and Ambler, 1988</td>
</tr>
<tr>
<td>$\Gamma$</td>
<td>day$^{-1}$</td>
<td>Fecal pellet remineralization rate</td>
<td>See Table III</td>
<td>Hofmann and Ambler, 1988</td>
</tr>
<tr>
<td>$k_i$</td>
<td>µgN l$^{-1}$</td>
<td>½ Max. Predation Rate</td>
<td>0.005</td>
<td>Hofmann and Ambler, 1988</td>
</tr>
<tr>
<td>$BW$</td>
<td>µgN</td>
<td>Body Weight</td>
<td>See Table III</td>
<td>Paffenhöfer, 1984b</td>
</tr>
<tr>
<td>$\rho_i$</td>
<td>day$^{-1}$</td>
<td>Fecal pellet sinking rate</td>
<td>See Table III</td>
<td>Hofmann and Ambler, 1988</td>
</tr>
</tbody>
</table>
Table III. Values for the Parameters Used in the Copepod Equations Where Different Values Are Needed for Different Copepod Size Fractions. Units and Sources are listed in either Table I or II.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$ZN_2$</th>
<th>$ZN_3$</th>
<th>$ZN_4$</th>
<th>$ZN_5$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$W_{SP}$</td>
<td>1.0</td>
<td>0.33</td>
<td>0.103</td>
<td>0.085</td>
</tr>
<tr>
<td>$W_{LP}$</td>
<td>0.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>$D_m$</td>
<td>0.321</td>
<td>0.193</td>
<td>0.365</td>
<td>-</td>
</tr>
<tr>
<td>DR</td>
<td>8.32</td>
<td>13.85</td>
<td>7.35</td>
<td></td>
</tr>
<tr>
<td>$\Lambda$</td>
<td>1.119</td>
<td>1.102</td>
<td>1.118</td>
<td>-</td>
</tr>
<tr>
<td>$I_m$</td>
<td>1.096</td>
<td>1.326</td>
<td>1.702</td>
<td>1.872</td>
</tr>
<tr>
<td>$\eta$</td>
<td>0.3942</td>
<td>0.2613</td>
<td>0.1134</td>
<td>0.1339</td>
</tr>
<tr>
<td>$v$</td>
<td>0.0062</td>
<td>0.0034</td>
<td>0.0010</td>
<td>0.0005</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>0.236</td>
<td>0.160</td>
<td>0.096</td>
<td>0.080</td>
</tr>
<tr>
<td>$\Gamma$</td>
<td>0.5</td>
<td>0.4</td>
<td>0.2</td>
<td>0.1</td>
</tr>
<tr>
<td>$TH_{COP}$</td>
<td>-</td>
<td>0.051</td>
<td>0.404</td>
<td>0.880</td>
</tr>
<tr>
<td>BW</td>
<td>0.0104</td>
<td>0.0509</td>
<td>0.403</td>
<td>0.880</td>
</tr>
<tr>
<td>$\rho$</td>
<td>0.003</td>
<td>0.03</td>
<td>0.10</td>
<td>0.10</td>
</tr>
</tbody>
</table>
each event. The total amount of nitrate upwelled during a single event, was specified using a linear nitrate-temperature relationship of the form suggested by Atkinson et al. (1984):

\[ \text{NO}_3 (\mu g \cdot l^{-1}) = 14.01(38.21 - 1.677T). \]  

(11)

The concentration of ammonium for the model ecosystem is expressed by

\[
\frac{dNH_4}{dt} = - \sum_{j=1}^{2} \left[ \frac{Pm \cdot Chl \cdot NH_4}{I_k + I \cdot C \cdot k_s + NH_4} \right] \gamma_j + \sum_{i=2}^{5} \left( \eta_i + \nu_i \cdot EPN_i \right) \gamma Z_i \\
+ \sum_{i=2}^{5} \eta_i \left( 1 - \psi_i \right) \left( 1 - \rho_i \right) \Gamma \left( 1 - e^{-\tau \cdot EPN} \right) \gamma Z_i \\
\left\{ + \frac{DOL}{DOLWT} \left[ DOLDW \cdot a(DOLDW) \cdot RQ \cdot 14 \right] + \Gamma_d \left( 1 - AE \right) \left( 1 - \rho_d \right) DOL \right\}.
\]

(12)

Uptake by the phytoplankton is given by the first term, and copepod excretion of ammonium represents the second term. The third is the fraction of copepod fecal pellets that are remineralized, as determined by \( \Gamma_t \), or that stay in suspension, denoted by \( \rho \). The final terms represent doliolid excretion and the remineralization and suspension of the doliolid fecal pellets.

The detrital component increases as the zooplankton produce fecal pellets and decreases as the doliolids ingest the floating fecal pellets. The detrital component is initialized before each simulated upwelling event. This is expressed mathematically as:

\[
\frac{dDET}{dt} = \sum_{i=2}^{5} \left( 1 - \Gamma_i \right) \left( 1 - \psi_i \right) \rho \left( 1 - e^{-\tau \cdot EPN} \right) \gamma Z_i \\
\left\{ + \left( 1 - \Gamma_d \right) \rho_d \left( 1 - AE \right) I - DET \cdot N(t,m,inv) \right\}.
\]

(13)

where the first component represents the fecal pellets produced by the copepods that
remain in the water column, the second represents the doliolid fecal pellets and the last term determines the time scale of the re-initialization of the detrital component. The modular function, \( \text{REM} \), determines this time scale.

To ensure mass conservation, a state variable, \( \text{LOST} \), was used to account for the nitrogen that would be lost via advective and other biological processes, as:

\[
\frac{d\text{LOST}}{dt} = \sum_{j=1}^{2} \delta_j P_j + \sum_{m=1}^{5} \left( \frac{M}{k_m + ZN_m} \right) ZN_m + \frac{\text{DOL}}{\text{DOLWT}} \cdot \text{NAT}_{\text{max}} + \text{DOL} \cdot \text{PRED}_{\text{max}} \left( 1 - e^{-\gamma_{\text{DOL-THPRED}}} \right) \cdot M \left( \text{DOL}, \text{TH}_{\text{PRED}} \right) + \sum_{i=2}^{5} (1 - \Gamma_i) (1 - \psi_i) (1 - \rho_i) (1 - e^{-\gamma_{\text{EPN_i}}}) ZN_i + (1 - \Gamma_d) (1 - \psi_d) (1 - \rho_d) I + \text{DET} \cdot N(tm, inv)
\]

where the first term represents dead phytoplankton, the second term is the fraction of the copepod life stages that are consumed through predatory processes. The third and fourth terms symbolize doliolid losses through natural causes and through predatory processes, respectively. The final two terms account for the fraction of fecal pellets, from the copepods and doliolids, that sink to the shelf benthos.

Light intensity, \( P(I) \), is modeled as a function of time and is used to produce the light dependency for phytoplankton growth. Light is modeled as:

\[
P(I) = \frac{P_m I}{I_k + I}
\]

where \( P_m \) is the maximum assimilation number, \( I_k \) is the half-saturation light intensity, and \( I \) is the light intensity (Table I). The light intensity used in the time-dependent model represents a value that had been averaged over a depth of 20 to 40 meters, the approximate depth range covered by a frontal eddy or a bottom intrusion. The time
dependency of light was modeled with a sine function to give equal twelve hour periods of light and dark. This function is shown as:

\[
I(t) = I_0 \begin{cases} 
\sin \left( \frac{t-6}{24} \pi \right), & \text{for } 6 < t < 18 \\
0, & \text{for } t < 6 \text{ or } t > 18
\end{cases}
\] (16)

where \( I_0 \) is the maximum daily light intensity and \( t \) is the time of day, in hours. The maximum assimilation number is calculated from an empirical function modified from Eppley (1972) that relates carbon assimilation and temperature dependent specific growth rates as

\[
P_m = \left(2^\mu - 1\right) \frac{C}{Chl}
\] (17)

where \( \mu=1.850(1.048)T \) and \( T \) is the temperature (°C).

The uptake of nitrate and ammonium follows Michaelis-Menten uptake kinetics of the form:

\[
V = \frac{V_m N}{k_m + N}
\] (18)

where \( V \) is the uptake rate of nutrient \( N \), \( V_m \) is the maximum uptake rate, and \( k_m \) is the concentration at which \( V \) is one-half of the maximum rate. Values for \( V_m \) and \( k_m \) were calculated from rates measured for natural phytoplankton populations associated with bottom intrusions (Table I) (See Hofmann and Ambler, 1988).

Ammonium inhibition of nitrate uptake was modeled as:

\[
\sigma = e^{-\beta NH_4}
\] (19)

where \( \beta \) is the rate of decrease of uptake with increasing ammonium concentration.
(See Table I).

Plankton predation, development, ingestion, and egg production were given a temperature dependence based on available $Q_{10}$ values (Kremer and Nixon, 1978; Huntley and Boyd, 1984). The rates were formulated for 20°C and then modified to allow for temperature dependence. For this study, a $Q_{10}$ of 3 was used for ingestion and predation. The terms in the rate equations for these processes were multiplied by the factor, $0.1108 e^{0.1107 T}$ which is 1 at 20°C and increases or decreases exponentially above and below 20°C. Development and egg production rates of the copepods, $D(T)$, can be related to temperature (Checkley, 1980b) and were derived using a modified Bělehrádek function of the form

$$D_i(T) = 1/[(432DR_i(T + 2.97)^{2.25}]$$

for $i = 2, 3, 4$. (20)

The value for $DR$ for the nonfeeding EggN2 category was 3.64 d$^{-1}$ (Checkley, 1980b), the values for the juvenile copepod categories are given in Table III.

### 3.2 MODEL MODIFICATIONS

The intent of the study was to include explicit doliolid dynamics in the existing southeastern U.S. continental shelf ecosystem model. Previous studies have shown that the *Doliioletta* gonozooids and phorozooids feed at similar rates and can therefore, for the purpose of this model, be treated as a single class (Deibel, 1982b, Crocker et al., 1991).
The abundance of the doliolids, \( \text{DOL} \), over time \( (t) \) is determined by:

\[
\frac{d\text{DOL}}{dt} = AE \left( \frac{\text{DOL}}{\text{DOLWT}} \right) \frac{p_i}{F_{\text{dol}}} - \frac{\text{DOL}}{\text{DOLWT}} \frac{DOLDW \cdot a(DOLDW)^b RQ \cdot 14}{22.4 \cdot CN} \\
\text{DOL} \cdot \text{PRED}_{\text{max}} \left( 1 - e^{-l(DOL \cdot TH_{\text{res}})} \right) \cdot M(DOL, TH_{\text{PRED}}) - \frac{\text{DOL}}{\text{DOLWT}} \text{NAT}_{\text{max}}
\]

The formulations of each of the above terms in the right hand side of equation 21 are described in detail below.

### 3.3 DOLIOLID INGESTION

The doliolid, being a nonselective filter feeder, ingests particles at a rate \( I \) depending on the concentration of the particle and the filtration rate of the doliolid, which is expressed in the model by the following equations:

\[
I = I_{\text{SP}} \cdot J(SP, TH_{\text{SP}}) + I_{\text{LP}} \cdot K(LP, TH_{\text{LP}}) + I_{\text{Egg}N2} + I_{\text{det}}
\]

where \( I_{\text{SP}} \) is the ingestion rate of the small phytoplankton size fraction given by:

\[
I_{\text{SP}} = \left( \frac{\text{DOL}}{\text{DOLWT}} \right) SP \cdot F_{\text{dol}}.
\]

Ingestion of the large phytoplankton size fraction, \( I_{\text{LP}} \), the copepod egg through nauplius 2 stage, \( I_{\text{Egg}N2} \), and detritus, \( I_{\text{det}} \) all have formulations similar to the expression in equation 23. The concentration of the doliolids is given by \( \text{DOL} \), \( \text{DOLWT} \) is the weight of an average doliolid, and \( F_{\text{dol}} \) is the filtration rate of the doliolids expressed as:

\[
F_{\text{dol}} = F_{\text{dol}}^{\text{max}} e^{-0.01 LP}
\]

where \( F_{\text{dol}}^{\text{max}} \) is the maximum flow of water through the doliolid body cavity. The exponential term represents a decrease in flow due to clogging of the animal's filtering
apparatus by the large phytoplankton class (Deibel, 1982b). The filtration rate was formulated for 20°C and then modified to allow for temperature dependence. Because there are currently no good estimates of the \( Q_{10} \) for the doliolids, a \( Q_{10} \) of just under 3, assuming a 'standard' poikilothermic organism, was used for this study. The equation term for this process was multiplied by the factor, \( 0.1189e^{0.107T} \) which is 1 at 20°C and increases and decreases exponentially above and below 20°C. Values and references for the parameters used in the doliolid equations are listed in Table IV.

The efficiency with which *Doliioletta* assimilates food was assumed to vary with ingestion rate (Moisan and Hofmann, 1996). The assimilation efficiency \( AE \) can be expressed in terms of a maximum, \( AE_{\text{max}} \), and minimum value, \( AE_{\text{min}} \) as:

\[
AE = AE_{\text{min}} + \left( (AE_{\text{max}} - AE_{\text{min}}) e^{-\tau} \right)
\]

where the e-folding scale given by \( \tau \) is modified by the ingestion rate \( I \) (Landry et al., 1984). As higher food concentrations produce a higher ingestion rate, the assimilation efficiency decreases toward the minimum value. Assimilated ingestion, \( DI \), can be calculated from the ingestion rate and the assimilation efficiency by:

\[
DI = AE \cdot I
\]

### 3.4 DOLIOLID EXCRETION

The excretion rate, \( EX \), for *Doliioletta* was obtained using a relationship suggested by Omori and Ikeda (1984) and modified by Moisan and Hofmann (1996) that relates body weight and temperature as:

\[
EX = \frac{\text{DOL}}{\text{DOLWT}} \frac{\text{DOLDW}a(\text{DOLDW})^b RQ \cdot 14}{22.4CN}.
\]
Table IV. Units, Definitions, Values, and Sources for the Parameters Used in the Doliolid Equations.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Definition</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$I$</td>
<td>$\mu gN \ l^{-1}$ s$^{-1}$</td>
<td>Ingestion rate variable calculated</td>
<td>variable</td>
<td>calculated</td>
</tr>
<tr>
<td>$DOL$</td>
<td>$\mu gN \ l^{-1}$</td>
<td>Dolioletta concentration variable calculated</td>
<td>variable</td>
<td>calculated</td>
</tr>
<tr>
<td>$DOLWT$</td>
<td>$\mu gN (dol^{-1})$</td>
<td>Weight of average doliolid</td>
<td>8.33</td>
<td>Mackas et al., 1991</td>
</tr>
<tr>
<td>$DOLDW$</td>
<td>$\mu g (dol^{-1})$</td>
<td>Total dry weight of an average doliolid</td>
<td>83.3</td>
<td>Moisan, 1993</td>
</tr>
<tr>
<td>$F_{dol}^{max}$</td>
<td>l s$^{-1}$</td>
<td>Maximum filtration rate</td>
<td>$1.678 \times 10^{-6}$</td>
<td>Deibel, 1982a,b</td>
</tr>
<tr>
<td>$AE_{max}$</td>
<td>none</td>
<td>Maximum assimilation efficiency</td>
<td>0.95</td>
<td>Omori and Ikeda, 1984</td>
</tr>
<tr>
<td>$AE_{min}$</td>
<td>none</td>
<td>Minimum assimilation efficiency</td>
<td>0.70</td>
<td>Omori and Ikeda, 1984</td>
</tr>
<tr>
<td>$\tau$</td>
<td>$\mu gN^{-1} l^{-1}$</td>
<td>Assimilation efficiency curve constant</td>
<td>$1.466 \times 10^{4}$</td>
<td>Estimated this study</td>
</tr>
<tr>
<td>$\Gamma$</td>
<td>day$^{-1}$</td>
<td>Fecal pellet remineralization rate</td>
<td>0.10</td>
<td>Moisan, 1993</td>
</tr>
<tr>
<td>$\rho_d$</td>
<td>day$^{-1}$</td>
<td>Fecal pellet sinking rate</td>
<td>0.60</td>
<td>calculated</td>
</tr>
<tr>
<td>$RQ$</td>
<td>none</td>
<td>Respiratory quotient</td>
<td>0.97</td>
<td>Omori and Ikeda, 1984</td>
</tr>
<tr>
<td>$CN$</td>
<td>$\mu gC \ \mu gN^{-1}$</td>
<td>Carbon to Nitrogen ratio</td>
<td>4.20</td>
<td>Omori and Ikeda, 1984</td>
</tr>
<tr>
<td>$PRED_{max}$</td>
<td>s$^{-1}$</td>
<td>Maximum predation rate</td>
<td>$1.736 \times 10^{-7}$</td>
<td>Estimated this study</td>
</tr>
<tr>
<td>$\varepsilon$</td>
<td>$\mu gN^{-1} l$</td>
<td>Predation rate curve constant</td>
<td>0.06935</td>
<td>Estimated this study</td>
</tr>
<tr>
<td>$TH_{PRED}$</td>
<td>$\mu gN \ l^{-1}$</td>
<td>Minimum doliolid concentration for predation to occur</td>
<td>1.0</td>
<td>Moisan, 1993</td>
</tr>
<tr>
<td>$NAT_{max}$</td>
<td>s$^{-1}$</td>
<td>Maximum natural death rate</td>
<td>$1.736 \times 10^{-7}$</td>
<td>Moisan, 1993</td>
</tr>
</tbody>
</table>
where the effect of temperature, \( T \), is included in the coefficients that modify the doliolid dry weight and are expressed as:

\[
\begin{align*}
a &= 10^{0.02438 - 0.1838 T} \\
b &= -0.010907 - 0.1082 T.
\end{align*}
\]

(28)  

(29)  

The values for these weight-modifying coefficients for *Doliioletta* were obtained using a relationship suggested by Omori and Ikeda (1984) and modified by Moisan and Hofmann (1996). The ingestion, assimilation, and excretion of the doliolids are dependent on the effective food concentration (Figure 4).

### 3.5 DOLIOLID PREDATION AND NATURAL MORTALITY

Predation mortality, \( PRED \), of *Doliioletta* ranges from zero below some threshold concentration, \( TH_{PRED} \), of the *Doliioletta* to a maximal predation rate, \( PRED_{\text{max}} \), given by:

\[
PRED = DOL \cdot PRED_{\text{max}} \left( 1 - e^{-\epsilon(DOL - TH_{PRED})} \right) \cdot M(DOL, TH_{PRED}),
\]

(30)  

where the threshold function is expressed as follows:

\[
M(DOL, TH_{PRED}) = \begin{cases} 
0 & \text{for } DOL < TH_{PRED} \\
1 & \text{for } DOL \geq TH_{PRED}.
\end{cases}
\]

(31)  

Natural mortality, \( NAT \), of *Doliioletta* is a linear function of the doliolid concentration expressed as:

\[
NAT = \frac{DOL}{DOLWT} \cdot NAT_{\text{max}}.
\]

(32)  

The maximum natural mortality rate, \( NAT_{\text{max}} \), is chosen such that the turnover time, excluding predation pressures, is within the average *Doliioletta* lifespan of 29-41 days.
Fig. 4. Relationships between the doliolid processes and effective food concentration (EPN) at 20°C: Ingestion, assimilation efficiency, assimilation, and excretion.
3.6 DATA SETS

The data sets needed for this modeling study consist of growth and ingestion rates of *Paracalanus* and *Dolioletta*, growth and uptake data for the resident shelf phytoplankton, and nutrient and temperature data for the SEUSS ecosystem. Data for the doliolid components were taken from unpublished studies performed by Dr. G.-A. Paffenhofer, from the Skidaway Institute of Oceanography, Savannah GA., on the genus *Dolioletta*, and from data from Deibel (1982a,b), Moisan (1993), and Paffenhofer et al. (1995). Copepod growth and ingestion rates were taken from Hofmann and Ambler (1988), Paffenhofer et al. (1995) and from unpublished data from Dr. Paffenhofer. Growth and uptake rates of the phytoplankton come from Eppley et al. (1969), and Yoder et al. (1981,1983,1985). Nutrient and hydrographic data are available from many sources e.g., Stefánsson et al. (1971), Atkinson et al. (1984), and Hofmann and Ambler (1988).

3.7 MODEL SIMULATIONS

Numerous simulations (Table V) were run to address the research questions given in the Introduction. The simulations were compared to a reference simulation, consisting of a constant temperature of 20°C, an initial copepod concentration equivalent to 500 copepods m$^{-3}$, initial equal phytoplankton size fractions totaling 1 mg Chl $a$ m$^{-3}$, and no doliolids. These reason for these values are as follows: newly upwelled Gulf Stream water in bottom intrusions ranges in temperature from 18 to 20°C (Yoder et al., 1983; Atkinson et al., 1987). A concentration of 500 copepods m$^{-3}$
Table V. Initial Conditions for the Model Simulations.  See Text for Explanation.

<table>
<thead>
<tr>
<th>Simulation</th>
<th>Temp. (°C)</th>
<th>Doliolids (µg N l⁻¹)</th>
<th>Copepods (µg N l⁻¹)</th>
<th>LP (µg N l⁻¹)</th>
<th>SP (µg N l⁻¹)</th>
<th>LP Loss (day⁻¹)</th>
<th>SP Loss (day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>20</td>
<td>0.00</td>
<td>0.50</td>
<td>3.0</td>
<td>3.0</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>2</td>
<td>20</td>
<td>0.42</td>
<td>0.50</td>
<td>3.0</td>
<td>3.0</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>3</td>
<td>20</td>
<td>0.42</td>
<td>0.50</td>
<td>3.0</td>
<td>3.0</td>
<td>0.07</td>
<td>0.11</td>
</tr>
<tr>
<td>4</td>
<td>20</td>
<td>0.42</td>
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<td>3.0</td>
<td>3.0</td>
<td>0.11</td>
<td>0.17</td>
</tr>
<tr>
<td>5</td>
<td>20</td>
<td>0.00</td>
<td>0.50</td>
<td>3.0</td>
<td>3.0</td>
<td>0.07</td>
<td>0.11</td>
</tr>
<tr>
<td>6</td>
<td>20</td>
<td>0.42</td>
<td>0.50</td>
<td>0.3</td>
<td>3.0</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>7</td>
<td>20</td>
<td>0.42</td>
<td>0.50</td>
<td>9.0</td>
<td>9.0</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>8</td>
<td>20</td>
<td>0.42</td>
<td>0.50</td>
<td>3.0</td>
<td>3.0</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>9</td>
<td>20</td>
<td>0.42</td>
<td>5.00</td>
<td>3.0</td>
<td>3.0</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>10</td>
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<td>0.12</td>
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<td>0.07</td>
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<tr>
<td>11</td>
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<td>3.0</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>12</td>
<td>18</td>
<td>0.42</td>
<td>0.50</td>
<td>3.0</td>
<td>3.0</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>13</td>
<td>25</td>
<td>0.42</td>
<td>0.50</td>
<td>3.0</td>
<td>3.0</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>14</td>
<td>18-25</td>
<td>0.42</td>
<td>0.50</td>
<td>3.0</td>
<td>3.0</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>15</td>
<td>18-25*</td>
<td>0.42</td>
<td>0.50</td>
<td>3.0</td>
<td>3.0</td>
<td>0.07</td>
<td>0.14</td>
</tr>
</tbody>
</table>

All simulations were run with a nitrate input of 5 µM except for (*) which had a nitrate input of 8 µM.
corresponds to approximately 0.5 \( \mu g \) N l\(^{-1}\) which is at the low end of concentrations observed in SEUSS waters (Atkinson et al., 1978; Paffenhofer et al., 1987b). A chlorophyll concentration of about 1 mg Chl a m\(^{-3}\) is representative of the concentrations found on the outer shelf during non-upwelling conditions (Yoder et al., 1983, 1985).

During almost all of the following simulations, the temperature either remained at a constant 20°C, representing an average temperature for the outer SEUSS, or increased linearly from 18°C to 25°C, representing the intrusion of cold subsurface Gulf Stream water mixing with the warmer shelf water. The relative concentrations of the two phytoplankton size fractions were adjusted by varying the loss rate, which is a compensation factor used to account for transfers of phytoplankton to components not explicitly included in this model.

### 3.8 PARAMETER DETERMINATION

The biological model that has just been described includes more than one hundred coefficients. Thus, before the specific numerical experiments can be run, it was necessary to determine a set of parameters that would produce results similar to the observed biological processes associated with bottom intrusions on the outer SEUSS.

#### 3.8.1 Phytoplankton Uptake and Growth Rates

The uptake of nitrate and ammonium is assumed to follow Michaelis-Menten kinetics (Equation 18). Nitrate and ammonium uptake rates in upwelled waters associated with bottom intrusions have been calculated from experimental data.
obtained from a bottom intrusion study in the summer of 1981 (Figures 5a and 5b, respectively, Hofmann and Ambler, 1988). These rates show a response to an increasing concentration that can be described by equation 18. The derived values for the maximum uptake rates, $V_n$ and $V_a$, and half saturation constants, $k_n$ and $k_a$, are given in Table I. Uptake rates observed during frontal eddies in the spring of 1979 and 1980 (data from Dr. J. A. Yoder, not shown) show little variation with increasing nitrate concentration and are mostly less than 0.03 hr$^{-1}$. The half saturation values for both nutrients were assumed to be zero and that ammonium and nitrate uptake in frontal eddies both proceed at a constant maximal rate (Hofmann and Ambler, 1988). Also from the summer 1981 data, ammonium inhibition of nitrate was modeled using the formulation of equation 19 where $\beta$ (Table I) is the decrease of the uptake of nitrate as ammonium concentration increases (Figure 5c).

The maximum growth rate of the phytoplankton was determined by $P_m$ (equation 17). This maximum rate was modified as a function of light intensity and nutrient concentration. At high nutrient levels, growth is primarily light limited, however as the light intensity decreases, the growth becomes light limited even at high nutrient concentrations.

The half saturation light intensity, $I_k$, varies between bottom intrusions and frontal eddies. Yoder et al. (1983,1985) gives ranges of $I_k$ that were measured for phytoplankton populations associated with both types of upwelling from which two representative values were chosen (Table I).
Fig. 5. Uptake rates and ammonium inhibition of nitrate for natural phytoplankton populations associated with bottom intrusions. Solid line indicates the curve fit to the data and the equation describing the curve is shown. A) Nitrate uptake rate versus nitrate concentration. B) Ammonium uptake rate versus ammonium concentration. C) Nitrate uptake rate as a function of ammonium concentration. The data were provided by Dr. J. A. Yoder.
3.8.2 Phytoplankton Loss Rates

Phytoplankton loss is modeled by a linear term where $\delta$, in equations 1, 2, and 14, represents the fraction of the phytoplankton that are removed from the system each day. This term represents all phytoplankton losses other than through copepod and doliolid grazing e.g., cell autolysis. Previous models (Wroblewski, 1977; Hofmann and Ambler, 1988) with phytoplankton components have assumed a time scale for cell loss that reduces a nutrient- or light-limited phytoplankton population to a factor of approximately $e^{-1}$ in ten days. Starting with an initial assumption of 0.1 d$^{-1}$ for both phytoplankton size fractions, the actual value was adjusted to produce concentrations similar to those observed on the SEUSS. After examining the effects of varying the two loss rates, values of 0.07 and 0.14 d$^{-1}$ were chosen for the large and small phytoplankton size classes respectively.

3.8.3 Copepod Growth Rates

The copepod ingestion rates are a modified Ivlev formulation given by:

$$I_i = I_{mi} \left(1 - e^{-\gamma_i EPN_i} \right),$$  \hspace{1cm} (33)

where $I_{mi}$ is the maximum ingestion rate (Ambler 1986), $\gamma_i$ is a constant affecting the slope of the curve (Ambler 1986), and $EPN_i$ is the effective food concentration (Vanderploeg et al., 1984) as defined in equation 3. The maximum ingestion rate and $\gamma_i$ are both functions of copepod body weight (Ambler 1986). The effective food concentration is also a function of copepod body weight as well as the phytoplankton size fraction (Ambler 1986). The ingestion formulas are based upon data obtained from feeding experiments of Paracalanus from SEUSS waters (Paffenhöfer, 1984b).
In a study by Landry et al. (1984) the portion of ingested food that is assimilated by the copepods showed an exponential decrease as food concentrations increased. Correspondingly, for this model, the assimilation efficiency was set at 90% at low food concentrations and decreased asymptotically to 70% at high food concentrations. The ingestion, assimilation and excretion of the different feeding stages of the copepods are dependent on the effective food concentration of the water (Figure 6).

3.8.4 Detrital Components

The question of how to properly treat the detrital component of biological models still lacks a definite answer. Many studies have looked at the size, sinking rate and production rate of pellets produced by different zooplankton species (e.g., Pomeroy and Deibel, 1980; Bruland and Silver, 1981; Uye and Kaname, 1994). Zooplankton fecal pellets are known to play an important role in the downward transport of organic material in the ocean and shelf waters. Grazing organisms may ingest many small, slowly sinking, phytoplankton cells and particles and defecate the unassimilated remains in relatively large packages. As the rate of fecal production is closely related to the rate of ingestion (Dagg & Walser, 1986), the size composition of the grazer community can affect the transport rate of material out of the euphotic zone.

The fate of smaller pellets has been addressed in detail by only a few studies (e.g., Paffenhöfer and Knowles, 1979; Hofmann et al., 1981). Hofmann et al. (1981) modeled the fate of fecal pellets produced by *Paracalanus* on the SEUSS and found that the percentage of fecal pellets reaching the benthos was directly related to the size...
Fig. 6. Relationships between the copepod processes and effective food concentration (EPN) at 20°C for the four feeding life stages: Ingestion, assimilation efficiency, assimilation, and excretion.
of the fecal pellet. *Paracalanus* nauplii produced pellets with a volume of $1 \times 10^4 \, \mu m^3$ (Paffenhofer and Knowles, 1979). These pellets are buoyant enough that, according to the results of Hofmann et al. (1981), only 0.3% of the nauplii produced pellets reached the sea floor. For the copepodid and adult stages, the values are 3 and 10% respectively (Hofmann et al., 1981). These numbers are the values that are used for $\rho_1$ in the model.

The literature does not contain any estimates of percentage of doliolid fecal material reaching the benthos of the southeastern shelf. To estimate this quantity, a clearance rate of 4.4 ml zooid$^{-1}$ hr$^{-1}$ (Deibel, 1982b; Crocker et al., 1991; Tebeau and Madin, 1994) and a high doliolid concentration of 2000 doliolids m$^{-3}$ was assumed. Using these values, the resident doliolid population will clear the entire water column in 4.74 days. Deibel (1990) found that while most of the pellets produced by laboratory specimens of doliolids fed only naturally occurring particles do not sink, those fed a concentration of particles adjusted to approximate the phytoplankton bloom associated with upwelling conditions sank at rates of 60-400 m day$^{-1}$. Deibel (1990) estimated that doliolid fecal pellets on the SEUSS would have a residence time of two days or less under upwelling conditions. Thus, if the fecal pellets reach the benthos in two days, the doliolids should only be able to ingest approximately 40% of the fecal pellets in the water column. This value of 40% was used in the model as the percentage of doliolid fecal pellets that remain available for ingestion.

Along with the removal of fecal pellets via transport to the benthos, degradation of the pellets by physical and biological processes also needed to be
quantified. Recycled ammonium could possibly be a significant source of nitrogen in the late stages of a bottom intrusion. The rates at which ammonium is regenerated by bacterial decomposition of fecal pellets in the outer SEUSS waters, and their possible importance to the ecosystem, are currently not well known. The modeling study by Hofmann et al. (1981) indicated that the younger copepod stages produced the most fecal pellets but that these pellets were not transported to the sea floor and were recycled in the water column. Adult copepod fecal pellet production was lower but accounted for most of the vertical transport. As decomposition rates of sediment trap carbon ranged from 1% to 50% per day (Iseki et al., 1980), values representing this range were chosen (Γ, in Table III). The fecal pellet remineralization rate for the doliolids was estimated to be similar to that used for the adult copepods because, although the doliolid fecal pellets are larger than the copepod pellets, they are less tightly compacted (Deibel, 1990; Uye and Kaname, 1994) and are more easily subjected to degradation.

3.9 MODEL IMPLEMENTATION

3.9.1 Numerical Integration

The solutions for the previously described system of coupled ordinary differential equations were determined using a fourth order Runge-Kutta numerical model with a time step of five minutes. The model was integrated forward in time until repeatable cycles were observed. As will be shown in greater detail in a subsequent section, this eliminated the effects of the initial conditions on the model
solutions. The total nitrogen in the model (including all losses not recycled) was calculated at each time step to verify mass conservation.

The model was run forward in time with the temperature and nitrate variations repeating every 40 days, until steady cycles in the plankton structure are produced. A cycle of 40 days is used for two reasons; because it provides a sufficient period for the biological interactions to come to equilibrium and because 40 days roughly approximates the time interval between bottom intrusion events (Atkinson et al., 1984, 1987).

### 3.9.2 Initial Conditions

Before running the model and obtaining solutions to the equations and parameters described earlier this chapter, it is necessary to specify the initial conditions for each of the biological variables. The purpose of the time-dependent biological model is to investigate the effects of Gulf Stream intrusions on the biological populations of the SEUSS. Therefore, the initial values were chosen to represent actual shelf water conditions prior to these upwelling events.

Under conditions devoid of upwelled nutrients, the ambient nitrate concentrations in the outer SEUSS waters are usually less than 0.5 μM (e.g., Bishop et al., 1980; Lee and Atkinson, 1983; Atkinson et al., 1987). An upwelling event can increase the nitrate concentrations to a maximum of 10 to 15 μM within a period of two or three days (Yoder et al., 1983, 1985). To simulate this nitrate input, the total amount of nitrate to be supplied to the model ecosystem was calculated using the relationship discussed previously that exists between temperature and nitrate for
subsurface Gulf Stream waters along the SEUSS (Equation 11). The upwelling simulations described in the following chapter were done using an initial temperature of 18 or 20°C and the corresponding initial nitrate concentration of approximately 8 or 5 μM, respectively, was input over a total of two days. Ammonium concentrations in SEUSS waters are normally below 0.1 μM (Yoder et al., 1983, 1985). Thus, the initial concentration for all simulations was assumed to be zero.

Both of the phytoplankton size fractions were initially set to 3 μg N l⁻¹, which, assuming a N:Chl a ratio of 6, corresponds to a chlorophyll concentration of 1.0 μg Chl a l⁻¹. As will be shown in the following section, however, the final solution is independent of all the initial plankton concentrations.

The initial concentration for the four non-adult copepod stages were set to zero and the adults were either set to zero or set to 0.5 μg N l⁻¹, which corresponds to nearly 500 animals m⁻³. This is at the low end of observed copepod concentrations for the SEUSS (Paffenhofer et al., 1987a, 1995).

Initial doliolid concentrations were also set to either zero, for simulations without doliolids, or to low observed concentrations for the SEUSS, 0.42 μg N l⁻¹ which is approximately equal to 50 zooids m⁻³. As stated above, the initial plankton concentration did not affect the final solution.

3.9.3 Determination of the Time Step

Before the addition of the doliolids to the model, a time step of 15 minutes was used in the model, however, the filtration and ingestion rates of the doliolids progress at a rate that the 15-minute time step could adequately resolve. Decreasing the time
step to 5 minutes, with the doliolids present in the simulations, produced significant differences, most noticeably in the concentration of the two phytoplankton size fractions. Further reducing the time step, e.g., 0.5 minutes, did not result in any appreciable changes (Table VI). All the simulations for this study were thus run with a time step of 5 minutes, regardless of whether doliolids were present.

3.9.4 Detrital Flushing

Initial model analyses showed that the use of the detrital box, DET, to account for the nitrogen that would be lost from the model ecosystem via death, predation, advection, etc., resulted in an overabundance of doliolids. To compensate for this, a state variable, LOST, was used to account for the nitrogen lost from the model domain. The detrital component was periodically flushed to prevent unrealistic concentrations from occurring in the model. The flushing of the entire detrital component occurred at the beginning of each new upwelling event. This is accomplished in the model with the switching function $N$:

$$
\begin{align*}
N(tm, inv) &= 0 \quad \text{for } MOD(tm, inv) \neq 0 \\
N(tm, inv) &= 1 \quad \text{for } MOD(tm, inv) = 0
\end{align*}
$$

(34)

where $tm$ is the current time step value, $inv$ is the number of time steps in each upwelling event and $MOD(tm, inv)$ is the remainder of $tm/inv$.

3.9.5 Verification Criteria

Verification for the simulation results was accomplished by comparing the model solutions to criteria obtained from field and laboratory observations of the individual biological components represented here.
Table VI. Values of maximum concentration of model components of simulation 2 (See Table V) run at different time steps.

<table>
<thead>
<tr>
<th>Time step (min)</th>
<th>LP (µg N l⁻¹)</th>
<th>SP (µg N l⁻¹)</th>
<th>Σ copepods (µg N l⁻¹)</th>
<th>DOL (µg N l⁻¹)</th>
<th>Σ phytoplankton* (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>24.7</td>
<td>17.8</td>
<td>6.7</td>
<td>15.8</td>
<td>7.7</td>
</tr>
<tr>
<td>10</td>
<td>22.4</td>
<td>19.5</td>
<td>6.3</td>
<td>15.3</td>
<td>8.6</td>
</tr>
<tr>
<td>5</td>
<td>20.9</td>
<td>21.2</td>
<td>6.3</td>
<td>14.7</td>
<td>8.6</td>
</tr>
<tr>
<td>1.5</td>
<td>20.9</td>
<td>21.4</td>
<td>6.4</td>
<td>14.5</td>
<td>8.6</td>
</tr>
<tr>
<td>0.5</td>
<td>20.8</td>
<td>21.5</td>
<td>6.4</td>
<td>14.5</td>
<td>8.6</td>
</tr>
</tbody>
</table>

* From the initiation of a nitrate upwelling event.
4. RESULTS

4.1 REFERENCE SIMULATION

4.1.1 General Characteristics

Once the parameters set was determined, the model was run to investigate the time evolution of the biological interactions in intrusions on the outer SEUSS. The basic scenario was assumed to represent only phytoplankton and copepod interactions at a constant temperature of 20°C (Figure 7). The model required about five cycles before repeated cycles were observed in the simulated distributions.

After the model had adjusted, the solution of the biological variables over time showed the succession that has been observed during outer SEUSS upwelling events. The phytoplankton maximum occurred approximately nine days after the nitrate maximum and the copepod biomass peaked nearly seven days following the phytoplankton bloom (Figure 7a). The values of ammonium were <0.1 μM throughout the simulation with the highest concentrations lagging 2-3 days behind the copepod maximum concentration.

Initially, the concentrations of the two phytoplankton size fractions remained approximately equal, (Figure 7b), however, after about eight days the concentration of the large phytoplankton size fraction, >10 μm, increased and remained dominant until the end of the phytoplankton bloom. Then the preferential feeding of the copepods for the large phytoplankton reduced the >10 μm size fraction to levels below that of the smaller phytoplankton.

The phytoplankton blooms resulting from individual upwelling events initiated
Fig. 7. Reference simulation (Simulation 1 in Table V). Simulated time-dependent daily averaged distributions of: A) nitrate, ammonium, total phytoplankton biomass and total copepod biomass and B) doliolid biomass, large phytoplankton size fraction (>10 μm), small phytoplankton size fraction (<10 μm) and total copepod biomass. The percentage of the total copepod biomass in each stage category is shown in panel C.
a cohort of copepods that develop over time (Figure 7c). During the time of peak biomass, the adults and older copepodites accounted for approximately 60% of the total copepod biomass. The generation time for the simulated copepods, as determined by the times of peak biomass, was about 14 days, and two cohorts were produced during the cycle.

The portion of new versus regenerated primary production for the two simulated phytoplankton size classes differ over the course of an upwelling cycle (Table VII). The percent new production was 88 and 73% for the large and small phytoplankton size fractions, respectively, which fall within the measured new production values of 50-90% (Yoder et al., 1985). Forty percent of the total primary production in the upwelling simulations occurred within the first week after the introduction of the nitrate.

The maximum calculated daily growth coefficient for the copepods in this simulation was 0.69 day⁻¹, which is slightly higher than the laboratory values of 0.4-0.6 observed by Paffenhofer (unpubl). However this high value occurred only briefly during the period of rapid growth and the majority of the growth period fell within the stated values.

The ammonium excreted by the zooplankton plus that produced by fecal pellet remineralization supported the regenerated primary production. The amount of production that resulted from recycled ammonium accounted for 19% of the total. By comparing the total ammonium excretion to the total regenerated production (Table VII), it can be seen that the copepod excretion was the primary nitrogen source for the
Table VII. Production values for the small and large phytoplankton size fractions and excretion values for the copepods calculated from the results of simulation I (See Table V). All values are from the 40-day fifth cycle.

<table>
<thead>
<tr>
<th>Phytoplankton</th>
<th>&lt;10 μm</th>
<th>&gt;10 μm</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cumulative new production (µg N l(^{-1}))</td>
<td>27.3</td>
<td>39.6</td>
<td>67.0</td>
</tr>
<tr>
<td>Cumulative regenerated production (µg N l(^{-1}))</td>
<td>10.2</td>
<td>5.4</td>
<td>15.6</td>
</tr>
<tr>
<td>% regenerated production of total production</td>
<td>12.4</td>
<td>6.5</td>
<td>18.9</td>
</tr>
<tr>
<td>% regenerated production supported by fecal pellet remineralization</td>
<td></td>
<td></td>
<td>14.5</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Copepods</th>
<th>EggN2</th>
<th>N3N4</th>
<th>N5C3</th>
<th>C4C5</th>
<th>Adult</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cumulative NH(_4) excretion (µg N l(^{-1}))</td>
<td>_</td>
<td>3.2</td>
<td>3.0</td>
<td>1.5</td>
<td>5.6</td>
<td>13.4</td>
</tr>
</tbody>
</table>
regenerated primary production. The remineralization of the fecal pellets accounted for only 14% of the total regenerated primary production.

The biological model was also used to investigate the interactions in frontal eddy upwelling events. The primary difference between the two upwelling types is the duration of time over which the events occur. Bottom intrusions can persist for up to six weeks (Atkinson et al., 1987), while frontal eddies exist for only five to seven days (Lee et al., 1991). The residence time of bottom intrusions on the shelf persists long enough for the light-limited phytoplankton to convert nearly all the upwelled nitrate into plankton biomass (Yoder et al., 1983).

The values of phytoplankton nitrate and ammonium uptake rates as well as the half saturation of the light intensity also vary between the bottom intrusions and frontal eddies (Yoder et al., 1983, 1985). The results of the frontal eddy simulation did not differ significantly from the first 10 days of the bottom intrusion (cf. Figure 7). In the five to seven days following the nitrate input, the simulated phytoplankton concentrations increased rapidly. However, the relative concentrations of the two size fractions remained approximately the same. Observations by Yoder et al. (1983) found that the phytoplankton in frontal eddies do not show a prevalence by any size fraction. They also found that the frontal eddies are characterized by evanescent but productive phytoplankton blooms.

The bottom intrusion simulation in Figure 7 shows that approximately thirty days were required for the observance of the complete cycle from nitrate input to the collapse of the copepod bloom. Bottom intrusion simulations occurring at intervals
greater than thirty days did not alter the final solutions shown in Figure 7. Intervals of
less than thirty days (Figure 8) produced results that are different from those shown in
the forty-day solution. Intervals of time scales that are less than the time required for
the depletion of the nitrate resulted in the depression of the large phytoplankton
maxima. The copepod population did not decrease to background levels before the
next event and began the new cycle at concentrations that are effective at hindering the
growth of the preferred large phytoplankton size class. This, however, is not a realistic
scenario as there are no reports of one intrusion overriding another or of two intrusions
mixing (Hofmann and Ambler, 1988).

4.1.2 Specific Properties

The ratio of new production to total production is commonly referred to as the
\( f \)-ratio (Eppley and Peterson, 1979). The maximum calculated \( f \)-ratio for the
simulation without doliolids (cf. Figure 7) was 0.92. The \( f \)-ratio values dropped to
zero within 7 to 10 days of the nitrate input as all the allochthonous nitrogen was
exhausted and all the primary production was fueled by ammonium. This is close to
the upper limit of Yoder et al. (1985) who estimated that new production in the
SEUSS waters ranges from 50 to 90%. The \( f \)-ratio of the simulation results also
dropped to zero when the concentrations of ammonium reached levels of 0.5 \( \mu \text{M} \) or
greater. Harrison et al. (1987) also found that, for coastal waters, nitrate uptake is
effectively stopped at ammonium concentrations approaching 1 \( \mu \text{M} \).
Fig. 8. Simulated time-evolution produced when nitrate is input at a 20-day interval. Figure details are the same as those given for Figure 7.
4.2 ADDITION OF DOLIOLIDS

4.2.1 General Characteristics

To examine the effects of tunicates on the resident phytoplankton and copepod populations, a simulation was done in which doliolids were added to the reference scenario (Figure 9). After model adjustment, the simulated distribution shows the succession of the various plankton components. Following the input of nitrate, the phytoplankton began their bloom, but in this case the rapidly increasing number of doliolids, to nearly 2000 m$^3$, ingesting the phytoplankton without any size preference, prevented the separate phytoplankton size distributions seen in the reference case (cf. Figure 7). The doliolids did not, however, reach concentrations quickly enough to significantly reduce the overall peak phytoplankton biomass of the bloom. The duration of the simulated phytoplankton bloom was shortened from approximately fifteen days, in the reference scenario to between eight or nine days (Figure 7 vs. Figure 9). The results show that the presence of the doliolids inhibited the copepod secondary production and the peak copepod biomass was reduced by 47% and the second copepod cohort was reduced in comparison to the second cohort in the reference scenario (Figure 7). The peak in doliolid biomass occurred a little more than 5 days later than the maximum phytoplankton concentration.

Simulated daily growth rates for the copepods, when doliolids were present, dropped slightly to 0.60 day$^{-1}$. The simulated daily growth rates for the doliolids were 0.32 day$^{-1}$, which falls within the 0.3 - 0.4 range observed under laboratory conditions by Dr. G.-A. Paffenhöfer (unpubl).
Fig. 9. Simulated time-dependent daily averaged distributions for simulation 2 of Table V. A) nitrate, ammonium, total phytoplankton biomass and total copepod biomass and B) doliolid biomass, large phytoplankton size fraction (>10 μm), small phytoplankton size fraction (<10 μm) and total copepod biomass. The percent of the total copepod biomass in each stage category is shown in panel C. The simulation was run with a constant temperature of 20°C.
4.2.2 SPECIFIC PROPERTIES

Model results indicate that the addition of doliolids increased the regenerated primary production, in comparison to the reference simulation, while the cumulative new production remained about the same (Table VIII). New production, at 54%, still dominated and remained in the range observed for bottom intrusions (Yoder et al. 1985). The cumulative ammonium excretion by the various life stages of the copepods in the model ecosystem had dropped in concordance with the decreased numbers of copepods in the water column (Table VIII). The doliolids produced a great deal more ammonium than did the copepods which accounts for the extra ammonium, when compared to the reference case, supplying the regenerated primary production.

By varying the phytoplankton loss rate in the model, the effects of the relative abundances of the large and small size fractions on the doliolids and copepods could be investigated. Simulations 1 and 2 (Table V) were run with the loss rates of the phytoplankton set such that the resulting distributions corresponded with observed distributions. For comparison purposes, simulations with high loss rates (0.11 and 0.17 day\(^{-1}\) for the large and small phytoplankton respectively) and low loss rates (0.04 and 0.11 day\(^{-1}\) for the large and small phytoplankton, respectively) were run (Figure 10). See Table V for details on specific simulations.

In the absence of grazing pressure, the simulated distributions show that high phytoplankton loss rates produced low abundances and vice versa. While altering the loss rates did not greatly change the overall abundance of the phytoplankton, the
Table VIII. Production values for the small and large phytoplankton size fractions and excretion values for the copepods calculated from the results of simulation 2 (See Table V). All values are from the 40-day fifth cycle.

<table>
<thead>
<tr>
<th>Phytoplankton</th>
<th>&lt;10 μm</th>
<th>&gt;10 μm</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cumulative new production (μg N l⁻¹)</td>
<td>35.9</td>
<td>31.0</td>
<td>66.9</td>
</tr>
<tr>
<td>Cumulative regenerated production (μg N l⁻¹)</td>
<td>40.7</td>
<td>16.8</td>
<td>57.5</td>
</tr>
<tr>
<td>% regenerated production of total production</td>
<td>32.7</td>
<td>13.5</td>
<td>46.2</td>
</tr>
<tr>
<td>% regenerated production supported by fecal pellet remineralization</td>
<td></td>
<td></td>
<td>20.6</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Copepods</th>
<th>EggN2</th>
<th>N3N4</th>
<th>N5C3</th>
<th>C4C5</th>
<th>Adult</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cumulative NH₄ excretion (μg N l⁻¹)</td>
<td></td>
<td>1.9</td>
<td>2.4</td>
<td>1.1</td>
<td>3.7</td>
<td>9.2</td>
</tr>
</tbody>
</table>

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Fig. 10. Steady state simulated distributions attained for: A-C) normal phytoplankton loss rates (Simulation 1); D-F) low loss rate for both phytoplankton size fractions (Simulation 3); and G-I) high loss rates for both phytoplankton size fractions (Simulation 4). See Figure 7 for figure details. See Table V for simulation conditions.
relative concentrations of the large and small phytoplankton size fractions varied significantly between simulations.

When the loss rates were low (Figure 10d-f), the concentration of the doliolids in the model domain responded positively and doliolid abundances reached 3000 zooids m\(^{-3}\), which is the upper limit of doliolid concentrations observed in the Charleston Gyre (Paffenhofer et al., 1995). The increased doliolids depressed the copepod growth rates and the life stage distribution of the copepods began to reach an equilibrium (Figure 10f). The amount of time required for the phytoplankton to reach peak biomass was reduced from 8.6 days (Simulation 1, Figure 10a-c) to 6.8 days.

In contrast, the simulation with high phytoplankton loss rates (Figure 10g-i), required 10.7 days to reach full bloom conditions. In these results, the doliolids never achieved concentrations greater than 600 m\(^{-3}\) but the copepods exhibited strong growth rates, approaching 0.70 day\(^{-1}\) and copepod abundances were 20% greater than when the phytoplankton loss rates were high.

As the simulated concentration of the large phytoplankton size fraction increased, the abundance of the copepods increased accordingly (Figure 10e,h). The doliolids showed the opposite reaction, not only to the increased competition from the copepods but also to the decreased supply of the small phytoplankton size fraction.

The maximum calculated \(f\)-ratio for the simulation with doliolids (cf. Figure 9) was 0.92. The \(f\)-ratio values dropped to zero within 7 to 10 days of the nitrate input after all the externally input nitrogen was exhausted and the primary production began to be fueled by ammonium. As previously stated, this \(f\)-ratio is close to the upper limit...
of Yoder et al. (1985) who estimated that new production in the SEUSS waters ranged from 50 to 90%.

### 4.2.3 Direct vs. Indirect Affect of Doliolids on Copepods

Several simulations were run to determine if the reduction of the copepods in the presence of doliolids was caused primarily by food competition or by direct predation of the doliolids on the copepod eggs. In addition to the reference case without doliolids (cf. Figure 7) and the similar simulation including doliolids (cf. Figure 9), two additional simulations were performed. The first did not include doliolids but was run with reduced phytoplankton concentrations to show the effect of reduced food but without the grazing pressure of the doliolids (Simulation 5). The second includes doliolids, but with the phytoplankton concentrations again set lower than in the reference scenario (Simulation 6).

When comparing the reference simulation (Simulation 1) to Simulation 5, it can be seen that the maximum concentration of the copepods had dropped (Figure 11a-b vs. Figure 11c-d). However, the maximum percent biomass that is classified as being in the EggN2 stage was reduced by less than 1% (Table IX). The EggN2 stage was chosen because it is the only copepod life stage that is directly preyed upon by the doliolids and thus changes in this stage should be more indicative of direct and indirect doliolid effects than would the other copepod life stages. Lowering the simulated phytoplankton biomass reduced the copepod biomass but does not significantly affect the percentage of copepods in each life stage. The greatest change, 8%, appeared in the N5C3 stage. In contrast to this, the addition of doliolids (Figure 11e-f) not only
Fig. 11. Simulated time-dependent daily averaged steady state distributions for: A-B) Simulation 1; C-D) Simulation 5; and E-F) Simulation 2. See Table V for simulation details. See Figure 7 for figure details.
Table IX. Maximum percentage (%) of total copepod biomass during 40-day upwelling cycle for the simulation without doliolids and with normal phytoplankton (Simulation 1). This value and the magnitude of the percent change from simulation 1 (in parenthesis) is shown for simulations without doliolids and with low phytoplankton (Simulation 5) and with doliolids and normal phytoplankton (Simulation 2), respectively. Similar calculations are presented for the percentage of total copepod biomass at peak biomass.

Maximum percentage (%) of total copepod biomass during 40 day cycle

<table>
<thead>
<tr>
<th></th>
<th>Simulation 1</th>
<th>Simulation 5</th>
<th>Simulation 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>EggN2</td>
<td>13.0</td>
<td>12.9 (0.7)</td>
<td>11.9 (8.3)</td>
</tr>
<tr>
<td>N3N4</td>
<td>15.0</td>
<td>13.9 (7.6)</td>
<td>14.3 (5.0)</td>
</tr>
<tr>
<td>N5C3</td>
<td>20.4</td>
<td>18.7 (8.2)</td>
<td>21.7 (6.4)</td>
</tr>
<tr>
<td>C4C5</td>
<td>24.1</td>
<td>26.0 (7.9)</td>
<td>19.8 (17.8)</td>
</tr>
<tr>
<td>Adult</td>
<td>73.0</td>
<td>72.2 (1.1)</td>
<td>76.6 (4.9)</td>
</tr>
</tbody>
</table>

Percentage (%) of total copepod biomass at time of peak biomass

<table>
<thead>
<tr>
<th></th>
<th>Simulation 1</th>
<th>Simulation 5</th>
<th>Simulation 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>EggN2</td>
<td>11.5</td>
<td>11.7 (2.0)</td>
<td>9.6 (16.0)</td>
</tr>
<tr>
<td>N3N4</td>
<td>12.2</td>
<td>11.1 (9.1)</td>
<td>11.2 (8.0)</td>
</tr>
<tr>
<td>N5C3</td>
<td>11.3</td>
<td>10.9 (3.6)</td>
<td>13.5 (20.0)</td>
</tr>
<tr>
<td>C4C5</td>
<td>17.0</td>
<td>17.8 (4.8)</td>
<td>19.6 (15.3)</td>
</tr>
<tr>
<td>Adult</td>
<td>48.1</td>
<td>48.6 (1.0)</td>
<td>46.1 (4.3)</td>
</tr>
</tbody>
</table>

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reduced the simulated copepod population, but also reduced the percentage of copepods in the EggN2 stage by almost 10%. The addition of doliolids also produced a decrease in the maximum concentration of the late copepodites and adult copepods by as much as 17%. When comparing similar data taken from the time of peak copepod biomass, the same trend can be seen but the changes seen when doliolids are present are even more pronounced (Table IX).

4.3 INITIAL CONDITIONS

Running the model until repeated cycles are produced negates effects that initial conditions might cause. For verification, six simulations were run (Simulations 6-11 in Table V) with varying initial conditions and the values of some of the parameters of the steady state solution were examined (Table X). Altering the initial phytoplankton, adult copepod, or doliolid components produced only transitory effects that did not alter the final solutions.

4.4 PHYSICAL PARAMETERS

4.4.1 Temperature

Several simulations were done to examine the effects of temperature on the biological process in bottom intrusion waters. As 18°C upwelled water contains a higher concentration of nitrate than 20°C upwelled water (Atkinson et al., 1984), simulations were run at different temperatures without changing the quantity of the nitrate input to assess the solo effect of temperature on the plankton rates. The nitrate input was set to 5 μM which is the value calculated for 20°C subsurface Gulf Stream water (Atkinson et al., 1984). Steady state cycles for 18°C, 25°C, and a third scenario...
Table X. Steady state values of maximum concentration of simulated model components run with different initial condition. See Table V for initial conditions of each simulation.

<table>
<thead>
<tr>
<th>Simulation</th>
<th>LP (µg N l⁻¹)</th>
<th>SP (µg N l⁻¹)</th>
<th>Σ copepods (µg N l⁻¹)</th>
<th>DOL (µg N l⁻¹)</th>
<th>Time to maximum Σ phytoplankton* (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>21.1</td>
<td>21.1</td>
<td>6.0</td>
<td>15.0</td>
<td>8.6</td>
</tr>
<tr>
<td>7</td>
<td>21.1</td>
<td>20.9</td>
<td>6.2</td>
<td>15.0</td>
<td>8.6</td>
</tr>
<tr>
<td>8</td>
<td>21.1</td>
<td>21.0</td>
<td>6.0</td>
<td>15.0</td>
<td>8.6</td>
</tr>
<tr>
<td>9</td>
<td>21.3</td>
<td>20.7</td>
<td>6.4</td>
<td>14.8</td>
<td>8.6</td>
</tr>
<tr>
<td>10</td>
<td>21.2</td>
<td>20.9</td>
<td>6.2</td>
<td>14.9</td>
<td>8.6</td>
</tr>
<tr>
<td>11</td>
<td>21.0</td>
<td>20.8</td>
<td>6.2</td>
<td>15.2</td>
<td>8.6</td>
</tr>
</tbody>
</table>

* From the initiation of a nitrate upwelling event.
simulating an event that moves alongshore for ten days and then moves across the shelf during the next twenty days all the while mixing with the surrounding water, were determined (Figure 12).

In all three cases, the total cumulative production was approximately the same at 80-85 μg N l⁻¹, as expected when the total nitrate input remains the same. The key differences lie in the relative abundances of the small and large phytoplankton size fractions and in the time scales from upwelling to maximum biomass of either the phytoplankton or the zooplankton. In the 18°C simulation, the colder water depressed the metabolic rates of all the plankton and the phytoplankton maximum occurred several days later than in the 20°C scenario. Likewise, the copepod maximum was delayed by several days. Both the phytoplankton and copepod maximum concentrations are 5-10% lower than in the 20°C case.

The 25°C simulation was done to show the effect of the warmer water on the plankton assemblage even though nitrate values of 5 μM are not associated with 25°C waters. The simulated phytoplankton began their increase much sooner after the nitrate input and reached higher overall concentrations but the bloom duration was much shorter (Figure 12d). The metabolic rates of the copepods were greatly increased at this warm temperature and three cohorts can be seen in one upwelling cycle. The rapid excretion of the copepods resulted in a greater percentage of the total primary production being regenerated production, 29% at 25°C versus 19% at 20°C.

In a more realistic temperature scenario, increasing the temperature from 18 to 25°C over 40 days resulted in a closer relative abundance of the two phytoplankton
Fig. 12. Simulated time-dependent daily averaged 40 day steady state distributions for the temperature profiles shown in the top panels. A-C) constant temperature of 18°C (simulation 12). D-F) constant temperature of 25°C (simulation 13). G-I) water intrudes at 18°C, then slowly mixes with 25°C shelf water (simulation 14). All three simulations were run with a nitrate input of 5 μM over the first 2 days of each 40 day cycle. See Figure 7 for figure details. See Table V for simulation details.
size fractions but with the larger size fraction dominating during the majority of the bloom (Figure 12g-i). The lower temperature during the initial portion of the upwelling delayed the development of the copepods and thus decreased the grazing on both phytoplankton size classes. This allowed the smaller phytoplankton to increase. As the temperature increased, the copepods preferentially ingested the larger phytoplankton. The increased temperatures during the later portion of the cycle caused the second cohort of the copepods to be more productive than the first cohort.

4.4.2 Nitrate Input

Figure 13 shows the time distribution of the biological parameters, first with a constant temperature of 20°C (Figure 13a-c), then under the same temperature conditions of Figure 12g-i, however in this second scenario, the quantity of nitrate introduced at the beginning of each upwelling cycle has been calculated from the relationship determined by Atkinson et al. (1984). The doliolids achieved concentrations greater than 3500 animals m$^{-3}$ which, while greater than the number usually reported for the SEUSS, are still less than the maximum concentration observed by Paffenhöfer and Lee (1987). Paffenhöfer (1980) reported that copepods in the Georgia Bight can take three weeks to respond to upwelling events. The copepods reach peak biomass approximately seven days after the onset of the phytoplankton bloom (Figure 13d-f) but, based on the peaks in life stages, the generation times of the copepods are about three to four weeks, agreeing with the observations of Paffenhöfer (1980).
Fig. 13. Simulated steady state solution for: A-C) constant temperature of 20°C, nitrate input of 5 μM over the first 2 days of the cycle (simulation 1). D-F) temperature profile shown in the top panel, nitrate input of 8 μM (simulation 15). See Table V for simulation details. See Figure 7 for figure details.
4.5 FECAL PELLET REMINERALIZATION AND SINKING RATES

The remineralization rates in the reference simulation ranged from 50% day\(^{-1}\) for the small copepod nauplii fecal pellets to 10% day\(^{-1}\) for the adult copepod and doliolid pellets. To determine the effect of the remineralization rates on the simulated plankton community structure, simulation 2 was run with high and low remineralization rates. High and low rates were calculated by multiplying the initial remineralized rates (Tables III and IV) by 1.50 and 0.50, respectively. Modifying the remineralization rates of the fecal pellets did not appear to have a significant effect on the steady state simulated solutions (Figure 14a-c).

The same process was applied to the fecal pellet sinking rates. Simulation 2 was modified to include high and low sinking rates (Figure 14d-f). As before, high and low rates were calculated by multiplying the initial sinking rates (Tables III and IV) by 1.50 and 0.50, respectively. The higher sinking rates significantly lowered the doliolid concentrations while the lower sinking rates allowed the doliolid numbers to increase. The greater abundance of the doliolids, when the sinking rates were low, had a direct inverse effect on the copepod and phytoplankton populations.
Fig. 14. Simulated steady state time-dependent distributions of varying fecal pellet remineralization and sinking rates at 20°C for: A) normal remineralization rates (See Tables II-IV); B) high remineralization rates (1.5 normal); C) low remineralization rates (0.5 normal); D) normal sinking rates (See Tables II-IV); E) high sinking rates (1.5 normal); F) low sinking rates (0.5 normal). See text for details. See Figure 7 for figure details.
5. DISCUSSION

5.1 COMPARISON OF REFERENCE SCENARIO TO OBSERVATIONS

Gulf Stream intrusions onto the outer Southeastern U.S. continental shelf produce dramatic changes in the physical and biological characteristics of the SEUSS waters. Frontal eddies and bottom intrusions bring subsurface Gulf Stream water into the euphotic zone of the outer SEUSS (e.g., Ishizaka and Hofmann, 1988; Yoder et al., 1983, Lee et al., 1991). These Gulf Stream intrusions can bring $2.2 \times 10^5$ metric tons of nitrogen in the SEUSS waters annually (Bishop et al., 1987) which greatly affect the resident phytoplankton populations, and thus, indirectly affects the higher trophic levels as well. Studies of intrusions associated with Gulf Stream upwelling, have shown that the intrusions greatly influence the surface chlorophyll field (Yoder et al., 1983, 1985).

The time-dependent biological model presented in this study represents a classic food web where phytoplankton production is driven chiefly by nitrate uptake rather than regenerated production from zooplankton excretion or fecal pellet remineralization. Yoder et al. (1985) gives data, from a bottom intrusion on the SEUSS, that shows that during the first 7-10 days following a nitrate upwelling event, oxygen production is inversely related to nitrate uptake by diatoms. This suggests that, rather than zooplankton depleting the oxygen and producing ammonium, the phytoplankton are consuming nitrate and producing oxygen.

Yoder et al. (1985) reported new primary production values of 50 to 97% for bottom intrusion events in the SEUSS waters. However, during the advanced stages of
a simulated bottom intrusion event, new production dropped to near zero levels and there was a small increase in the <10 μm phytoplankton size fraction that was supported entirely by regenerated production (cf. Figure 7).

Gulf Stream frontal eddies are short lived but productive events (Yoder et al., 1983; 1985). Observations show that the frontal eddies are characterized by increased primary production and phytoplankton biomass. Copepod populations are, however, relatively unaffected by frontal eddy upwelling (Atkinson et al., 1978; Deibel, 1985). This is because the zooplankton are unable to respond with the required alacrity to take advantage of the ephemeral phytoplankton bloom (Paffenhofer et al., 1995).

The time-dependent biological model only included two size fractions of phytoplankton. Although doliolids are not selective in their feeding behaviors, the copepods exhibit a preference for the >10 μm size fraction. Because of this, it was necessary to increase the loss rate of the smaller phytoplankton size fraction, relative to the large size fraction, to reproduce observed relative abundances (cf. Figure 7). This increased rate represents a loss that is currently not included explicitly in the model. The addition of microzooplankton that can graze small cells could produce the relative abundances of the phytoplankton size fractions observed on the southeastern shelf.

In the SEUSS waters, as intrusions develop, they become dominated by large species of *Rhizosolenia* (>40 μm ESD), which cannot be grazed by most of the stages of *Paracalanus* (Paffenhofer and Knowles, 1978; Paffenhofer, 1984a,b). However, the model phytoplankton for the >10 μm size class is *Thalassiosira* (about 12 μm...
ESD). Ambler (1986), using data from Paffenhöfer (1984b), found that, while there is a general linear correlation between copepod size and the size of the phytoplankton that were preferentially grazed, the large diatoms, i.e. *Rhizosolenia*, are only grazed preferentially by adult females and then only at high food concentrations. Because of this, the model can not adequately represent both of these larger phytoplankton and, during the tail end of the intrusion, will misrepresent the large phytoplankton size fraction. The components included in the reference simulation (cf. Figure 7) do, however, adequately represent the major features of Gulf Stream upwelling onto the outer SEUSS.

### 5.2 DOLIOLID INFLUENCE ON COMMUNITY STRUCTURE

The seasonal occurrence of doliolid blooms, i.e., mainly in late winter and spring, may be due to the seasonal changes in the physical aspects of the SEUSS waters. Deibel (1985) suggests that a band of cold-core upwelled water may have to be stranded on the shelf between two fronts for a doliolid bloom to occur. Filaments of warm surface Gulf Stream water wrap around the cyclonic core of the Charleston Gyre increasing vertical stability in the absence of strong winds. During the summer months, frequent NE winds and storm events may break down, or even eliminate the stratification of the Charleston Gyre. These processes help to explain why doliolids are more abundant during mid-winter and spring than in summer and fall in the Charleston Gyre.

The presence of doliolids in the outer SEUSS waters significantly alters the plankton populations observed when doliolids do not exert a strong presence (cf.
Figure 9). The doliolids may be the only zooplankters, aside of protozoa, in the SEUSS waters that are capable of rapidly responding to the short-lived phytoplankton blooms associated with Gulf Stream frontal eddies (Deibel, 1985). The results of the simulations presented in this study suggest that these doliolid blooms impact the energy flow of the SEUSS ecosystem by sequestering phytoplankton biomass and converting it into tunicate biomass and fecal material.

5.3 PHYSICAL PROCESSES

The temperature of the upwelled water in bottom intrusion events generally ranges from 18 to 20°C (Atkinson et al., 1987). These events can be identified as masses of cold subsurface water as they move onshore and alongshore. In the absence of wind mixing, the temperature of the intrusions does not change significantly over the lifetime of the event. If wind mixing does occur while the intruded waters are over the shallow shelf, then warming of the intrusion can occur as the surface water mixes with the subsurface intrusion. Since the upwelled water is on the shelf as a separate water mass, it is probable that phytoplankton develops uniformly within this water. This can lead to the formation of a phytoplankton patch in the nutrient-rich intrusion (Yoder et al., 1981). Weak mixing in the vertical and horizontal directions and rapid phytoplankton growth should result in a patch with sharp boundaries. If mixing with adjacent water masses is limited, zooplankton, which develop in a phytoplankton patch, could themselves form a patch with similar dimensions (Paffenhöfer et al., 1987a).
Model simulations (cf. Figures 12 and 13) show that both the temperature and quantity of the introduced nutrients are important factors in determining the response of the zooplankton to the intrusions of the subsurface Gulf Stream water onto the outer SEUSS. While the cooler temperatures seen immediately following an upwelling event decreases the metabolic rates of the zooplankton, allowing the phytoplankton to fully utilized the newly input nutrients, increased grazing at the higher temperatures of the resident shelf waters directly affects the relative abundance of the two phytoplankton size fractions and thus alters the species composition of the zooplankton themselves.

The current formulation of the model requires a mixing temperature regime (cf. Figure 12g-i) to produce a copepod biomass peak that sufficiently lags the peak in phytoplankton biomass. This suggests that the effects of temperature on the metabolic rates of the zooplankton need to be better assessed.

5.4 DETRITAL FACTORS

The formulations for the detrital factors in the ecosystem model include fecal pellet remineralization rates and fecal pellet sinking rates. As only 15-20% of the regenerated production is supported by fecal pellet remineralization, and regenerated production is only 15-20% of the total production, fecal pellet remineralization accounts for only 2-4% of the total primary production.

In contrast to the fecal pellet remineralization rates (cf. Figure 14), the model ecosystem is much more sensitive to fecal pellet sinking rates (cf. Figure 15). This occurs because doliolids ingest detritus at the same rate as phytoplankton and copepod
eggs. Near the end of an upwelling cycle, fecal pellet mass, in the model system, can be greater than 10% of the total phytoplankton biomass and can be five times greater than the total copepod biomass. Although there is currently no experimental evidence to support this, detritus could play a significant portion of the diet of the doliolids, especially when food of high quality can only be found in low abundances.

The question of how to properly treat the detrital component of biological models still lacks a definite answer. Many studies have looked at the size, sinking rate and production rate of pellets produced by different zooplankton species (e.g., Pomeroy and Deibel, 1980; Bruland and Silver, 1981; Uye and Kaname, 1994). Zooplankton fecal pellets are known to play an important role in the downward transport of organic material in the ocean and shelf waters. Grazing organisms may ingest many small, slowly sinking, phytoplankton cells and particles and defecate the unassimilated remains in relatively large packages. As the rate of fecal production is closely related to the rate of ingestion (Dagg & Walser, 1986), the size composition of the grazer community can affect the transport rate of material out of the euphotic zone.

The grazing on phytoplankton and the subsequent production of fecal pellets are fundamental roles of many zooplankton in the marine ecosystem. Zooplankton fecal pellets have been considered to be the most important vehicle by which the flux of material out of the surface is achieved. Both theoretical and empirical studies indicate that large fecal pellets, e.g., those produced by doliolids, are a prime vehicle for this vertical flux, since larger pellets have high sinking rates (Uye and Kaname, 1994).
5.4.1 Fecal Pellet Remineralization

Along with the removal of fecal pellets via transport to the benthos, degradation of the pellets by physical and biological processes also need to be quantified. Recycled ammonium could possibly be a significant source of nitrogen in the late stages of a bottom intrusion. The rates at which ammonium is regenerated by bacterial decomposition of fecal pellets in the outer SEUSS waters, and their possible importance to the ecosystem, are currently not well known. The modeling study by Hofmann et al. (1981) indicated that the younger copepod stages produced the most fecal pellets but that these pellets were not transported to the sea floor and were recycled in the water column. The model simulations indicate that the fecal pellet remineralization rate does not have a large effect on the resulting plankton community structure (cf. Figure 14a-c).

5.4.2 Fecal Pellet Sinking Rates

The fate of smaller pellets has been addressed in detail by only a few studies (e.g., Paffenhöfer and Knowles, 1978; Hofmann et al., 1981). The literature does not contain any estimates of percentage of doliolid fecal material reaching the benthos of the southeastern shelf.

In contrast to fecal pellet remineralization rates, the sinking rates of the fecal pellets, and thus the rate of removal of a potential food source for the doliolids does produce significant differences in the model results (cf. Figure 14d-f). The model is most sensitive to the sinking rates of the doliolid, in comparison to the copepod, fecal matter, as the doliolids produce more than 50% of all the fecal material in the water...
column. As a suggestion for future work, possessing accurate production, remineralization and sinking rates of doliolid fecal pellets would increase the validity of models such as the one presented here. In order for the model to produce solutions that corresponded with observations, the doliolids were assumed to ingest 40% of the fecal material in the water column. The remaining 60% thus leaves the model ecosystem. There is the possibility that the excess fecal material could provide a significant food source to the benthic ecosystem of the outer SEUSS, however, since the outer shelf is flushed with an average periodicity of 14 days, the most likely situation is that most of the material is advected out into the Gulf Stream, leaving the outer shelf.

5.5 DIRECT EFFECTS OF DOLIOLIDS ON COPEPODS

Paffenhofer et al. (1995) found that when large doliolids were present in concentrations of 600 m$^{-3}$ or more, the doliolids were inversely correlated with copepod concentrations in the water column. Two possible reasons for this inverse abundance relationship between copepods and doliolids are a) the doliolid ingestion of copepod eggs and nauplii and b) the removal, by the doliolids, of the food source for the copepods. The results presented in this study suggest that the direct effect of doliolids on the copepod population is at least as significant as the indirect effect of reducing the food of the copepods.

During simulation 2 (cf. Figure 9) the chlorophyll $a$ concentrations do not fall below 0.5 $\mu$g l$^{-1}$ throughout the steady state upwelling event. At this level, Paracalanus should have been able to maintain its population and to reproduce at least
near half of their maximal rate (Checkley, 1980b). Thus, food abundance was most likely not severely limiting the copepod growth. Paffenhöfer et al. (1995) performed a gut content analyses on doliolids taken near the Charleston Gyre in January 1990 and found that almost 15% of the doliolid fecal pellets and 12% of the doliolids themselves contained one or more copepod eggs.

Model results show that the presence of doliolids produces a larger decrease in copepod eggs than does a decrease in the food supply to the copepods (cf. Figure 11). These results imply that, while the doliolids inhibit the growth of the copepods through food competition, the direct effect of ingesting the copepod eggs has an equal if not greater effect than by the reduction of the food source. Paffenhöfer et al. (1995) made this same hypothesis based on observations from the Charleston Gyre.

Because of the high asexual fecundity and growth rates of the doliolids, each mature oozoid, i.e. a nurse with a chain, can produce literally hundreds of gonozooids in a period of several days, much shorter than the 2-4 weeks of the generation times of the other SEUSS zooplankton. The frequent flushing of the shelf with subsurface Gulf Stream water during the winter and spring can potentially maintain a temporally new community that is often dominated by the rapidly responding doliolids (Deibel, 1985). During these periods, one would expect to regularly encounter high concentrations of all the life stages of the doliolids along with a decreased in the other net zooplankton.

5.6 IMPORTANCE OF DOLIOLIDS IN ECOSYSTEM MODELS

Modeling allows us to make predictions on the results of specific physical and biological phenomena that have not yet been observed. These predictions can help to
focus future studies to maximize the knowledge gained per research undertaking. Modeling itself is not possible without understanding of the processes being modeled.

While a limited number of models currently include gelatinous zooplankton (e.g., Andersen and Nival, 1988; Moisan and Hofmann, 1996), the exclusion of these organisms from models of ecosystems where gelatinous zooplankton represent a significant portion of the zooplankton biomass could misrepresent the flow of matter and energy through the planktonic food webs (Hamner et al., 1975; Deibel, 1982a).

The ability of a large (1 to 8 mm) zooplankter to feed directly on food as small as 2 μm represents a short trophic link in the classic food chain. If doliolids are then consumed by the outer shelf nekton, this could represent an efficient pathway by which energy is moved from lower to higher trophic levels (Crocker et al., 1991).

Gelatinous zooplankton are preyed upon, regularly or occasionally, by over 100 fish species thus they are not a trophic dead-end as was previously believed (Kashkina, 1986; Verity and Smetacek, 1996). Most of these observations, however, are based on salps and few observations have been reported on the function of doliolids as prey. As doliolids do not have to feed to move and only move quickly on occasion, in contrast to salps that swim continuously, doliolids may be far less conspicuous than salps and consumed proportionally less often. The abundance of doliolids during certain times of the year could possibly be a significant food source to fish or larvae of the area.
6. CONCLUSIONS

The simulation results shown in this study approximate the observed biological processes for the waters affected by the Charleston Gyre notwithstanding that the model currently represents only a part of the SEUSS food web. While, by definition, all models provide a truncated version of the real world, time scales can be decreased and additional components can be added to try to compensate for this inherent disability. For this particular model the addition of two more planktonic components has already been proposed.

Cyclopoid copepods will be added to contrast the different feeding and breeding habits of the two types of copepods. While calanoid copepods, such as *Paracalanus*, modeled here, are filter feeders that continuously spawn their eggs, cyclopoid copepods, e.g., *Oithona*, are raptorial feeders that periodically release a brood of nauplii. Cyclopoid copepods are omnivorous predators that feed in a selective fashion and are known to prey on calanoid copepods and copepod nauplii as well as phytoplankton (Wickham, 1995). The ability of the cyclopoid copepods to hold onto the eggs during the initial development could prevent the doliolids from ingesting the same proportion of calanoid eggs, which could result in greater abundances of the cyclopoids. Indeed, Oithonids are the most successful free-living cyclopoids in the marine pelagic ecosystem (Uye and Sano, 1995). They occur in a wide variety of eutrophic and oligotrophic marine habitats ranging from the poles to the tropics and from open oceanic to shallow coastal regimes (Paffenhöfer, 1993).

Microzooplankton, especially ciliates, are an integral part of the SEUSS water
column and are also a planned addition to the model. The exclusion of bacteria and protozoa from the model could explain why the small phytoplankton size class needed a higher death rate than the large phytoplankton class to produce the phytoplankton composition observed in SEUSS waters. Also, doliolids are able to graze on small particles and the lack of the microzooplankton could potentially have a noticeable effect in the doliolids populations as well. In a test of retention efficiency of doliolids on various sized small spheres, the grazing rate of 1 \( \mu m \) spheres was still 30-56% of the 2.5 \( \mu m \) spheres (Tebeau and Madin, 1994).

While doliolids have ingestion rates of approximately 1.6 \( \mu gC \) body \( C^{-1} \) day\(^{-1} \) (Paffenhöfer, unpubl), 30 \( \mu m \) ciliates can attain ingestion rates of approximately 2.5 \( \mu gC \) body \( C^{-1} \) day\(^{-1} \) (Verity, 1991). Verity (unpubl) found ciliates in concentrations of up to 15 \( \mu gC \) l\(^{-1} \) in the outer shelf waters. This concentration is equivalent, in carbon biomass, to a doliolid concentration of about 1800 m\(^3\). These values suggest that ingestion by ciliates could equal or exceed that of doliolids. However, there is the possibility that high concentrations of doliolids would consume a large percentage of the ciliates in the water column but the potential for competition is there.

The source of doliolids in the bottom intrusions remains unsettled. Paffenhöfer et al. (1995) and Deibel (1985) state that their unpublished observations indicated the frequent occurrence of doliolids on the southeastern shelf during winter and spring and possibly year round. The extremely high fecundity of the doliolids means that only a few old oozoids are needed to start a bloom (Deibel 1985). Deibel (1985) also stated that his observations did not support the theory that the doliolids are advected into the
shelf waters from the Gulf Stream, which is in contrast to the thinking of Paffenhöfer et al. (1995), who theorized that since Thaliacean (doliolid) occurrences are mostly episodic in nature, they do not occur continuously on the SEUSS throughout the year, and thus are most likely imported via the Florida current from the Gulf of Mexico. Adding advective inputs to the model could help to resolve this issue.

The outer SEUSS waters are inhabited by various species of planktivorous fish, e.g., menhaden, during various times throughout the year (Yoder et al., 1981). Primary production fueled by Gulf Stream frontal eddies or bottom intrusions could be an important factor in sustaining the transient fish populations. In addition, the high concentrations of doliolids that sometime occur in the Charleston Gyre and other intrusion areas could represent a significant source of food to the many species of fish that are known to ingest gelatinous zooplankton.

While this study discussed the biomass distribution during Gulf Stream frontal eddies and bottom intrusions on the outer SEUSS, the carbon flux budgets were not thoroughly investigated. Additional venues of experimentation could include the flux of carbon between the outer shelf and the Gulf Stream; the outer and inner shelves; and the outer shelf water column and outer shelf benthos. If we assume doliolids are advected onto the outer SEUSS from Gulf Stream waters, then we must also assume an input of phytoplankton and copepods. Although there is a considerable input of nitrogen supplied to the shelf waters from the coast of the SAB, most of the nutrients and plankton appear to be trapped on the inner shelf with little occurrence of a cross-shelf exchange. Although this model has ignored the possibility of nutrient input via
resuspension of the sediments, incorporating a flux of biomass or nutrients at a lower boundary of the model domain could be future addition.

One of the important issues of this study is that it can show how a western boundary current, such as the Gulf Stream, can dominate the biology and chemistry of adjacent shelf waters. It is dramatic in the SEUSS because the shelf waters are broad and shallow so that a small action by the Gulf Stream can cause large variability in the shelf waters. The results of this study should also increase our knowledge of the interactions among the phytoplankton, copepods, and doliolids of the outer southeastern U.S. continental shelf water community.
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