

Potential Importance of the Timing of Spring Plankton Blooms to Benthic-Pelagic Coupling and Recruitment of Juvenile Demersal Fishes

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Abstract Numerous studies have documented that during a relatively brief period the spring plankton bloom in temperate and high-latitude regions can deliver as much as half of the total annual input of organic carbon to the benthos. Further, it is known that the exact timing of the onset of phytoplankton blooms in relatively shallow inshore waters can be controlled by the amount of solar radiation received and hence is subject to variations in weather patterns, leading to interannual variations in the timing of the blooms. Earlier blooms may occur in colder water, which would reduce consumption by pelagic heterotrophs and result in the input of a greater proportion of planktonic production to the bottom sediments than in years when the bloom is later and occurs in warmer water. In addition, if nutrients are not limiting, an early bloom might continue for a longer time and result in greater overall production before being curtailed by zooplankton grazing, since development time and metabolic rates of those zooplankton species which propagate in response to the bloom should be slowed by the colder temperatures. The result would be enhanced benthic production in years of earlier blooms. Since the timing of the spring bloom may have a significant effect on benthic productivity in temperate and high-latitude, near-shore areas, this could lead in turn to interannual variability in the carrying capacity of the environment for the newly-metamorphosed juvenile demersal fishes that appear there in the following spring and summer.

Keywords phytoplankton, plankton bloom, benthic-pelagic coupling, timing, recruitment, demersal fishes gulf of Maine.

Introduction

The production and metabolism of benthic organisms below the euphotic zone are supported ultimately by organic matter produced in the surface waters that reaches the sediments. In high-latitude and temperate regions much of this material can be deposited on the bottom in a relatively short period of time associated with the spring plankton bloom; this brief pulse of organic matter input can amount to one-third of the annual phytoplankton production and may represent over one-half of the total annual input to the benthos in shallow waters (Parsons et al., 1977; Smetacek et al., 1978; Smetacek, 1980; Peinert et al., 1982; Forsskål et al.,

1982). Because the exact timing of the spring phytoplankton bloom in such near-shore areas is dependent on the amount of solar insolation received (e.g., Townsend and Spinrad, 1986), and hence is subject to variation in weather patterns, the timing of the bloom may be significantly advanced or retarded between years. One effect of this variation is that water temperature will vary accordingly, and because the metabolic rates of pelagic consumers are more sensitive to lower temperatures than photosynthesis by phytoplankton (Corkett and McLaren, 1970, 1978; Christian and Weibe, 1974; Ikeda, 1985; Pomeroy and Deibel, 1986; Walsh and McRoy, 1986; Kuparinen, 1987), the distribution of organic production between the pelagic and benthic systems should also be affected; that is, an early bloom in cold water could deliver a greater proportion of fresh phytoplankton to the benthos than could a later bloom. Because of the influence of temperature on the development time of the zooplankton grazers, a second effect of the variation in timing is that an early bloom that is not nutrient limited may have a longer overall duration and thus result in a greater amount of both planktonic and benthic production. We suggest, therefore, that the timing of the spring bloom may have a significant effect on benthic production in temperate and high-latitude, near-shore areas, leading in turn to variations in the carrying capacity of the environment for the newly-metamorphosed juvenile demersal fishes that appear later in the spring and summer.

Recruitment Variability

One of the earliest explanations for the variable recruitment of fishes was proffered by Hjort (1914) who proposed what has come to be known as the critical period concept; briefly stated, this concept maintains that there can be catastrophic mortalities of larval fishes upon completion of the resorption of their yolk sac energy reserves and the transition to exogenous feeding. This phenomenon had long been known to aquarists; Hjort speculated that in nature the same would occur if there were insufficient densities of food particles available to the larvae at this transitional life history phase. The idea gained favor when Cushing (1973) proposed that strong year classes could result from a match between the timing of fish reproduction and the seasonal plankton production cycle. This "match-mismatch hypothesis" was extremely attractive since it was known that most temperate and higher latitude species spawn at a time which results in their larvae being in the water column at a fairly predictable time of year, usually at the time of the spring phytoplankton bloom. Moreover, it was also known that the exact timing of the spring phytoplankton bloom could vary by a number of weeks between years.

Guided by these early ideas, previous research on recruitment mechanisms focused on starvation as the major cause of larval mortality (Hunter, 1976). But field tests of this hypothesis met with little success and research efforts are now more sharply focused on the hypothesis that: ". . . recruitment variability is largely determined in the juvenile life stage and that prerecruit mortality is likely controlled by predation rather than starvation" (Anonymous, 1984). Sissenwine (1984) has discussed the rationale behind this shift in research emphasis and lists the following lines of evidence which led to the juvenile predation hypothesis: 1) With the exception of extremely low population levels, there is no clear rela-

tionship between the size of an adult spawning stock and recruitment of a species in the Northwest Atlantic; 2) There is no correlation between the abundance or production of larvae and year class strength; 3) Field measurements of potential planktonic prey concentrations appear to be adequate for survival of larvae; 4) There is no evidence from field collections that larvae starve; 5) Enclosure studies have demonstrated high survival rates of larvae when predators are excluded; 6) Many species of fishes and invertebrates have been identified as predators on each of the early life history stages of fishes.

These are compelling arguments and one must readily admit that new avenues of research into the mechanisms causing recruitment variability are certainly needed. But the possible importance of food limitation, even in the juvenile stage, must not be ruled out, and we maintain that the assumption of predation-limited survival of juveniles may be an oversimplification for two reasons. First, the transition from the yolk sac stage to exogenous feeding is not the only developmental transition which teleostean fishes undergo; the metamorphosis from the larval to the juvenile stage may represent another "critical period" in their early life histories. For many species of groundfish, this metamorphosis includes a transition from a planktonic to a demersal habitat. Second, the timing of the spring plankton bloom is not only important in controlling the abundances of planktonic food for first-feeding larvae, but it can also control the amount of organic material which reaches the benthos, and thus control the abundances of benthic invertebrates available as food to the newly metamorphosed juvenile fishes that utilize that habitat later in the year (e.g., Mahon and Neilson, 1987). We suggest, then, that the abundances of juvenile demersal fishes may be set by the carrying capacity of the benthic habitat in question, and, as we will argue in the following paragraphs, that this carrying capacity in turn may be determined by the timing and intensity of the early spring phytoplankton blooms each year, and the subsequent flux of this organic material to the benthos.

Benthic-Pelagic Coupling

As pointed out in the Introduction, benthic organisms below the euphotic zone are largely dependent on organic matter produced in the surface waters. At higher latitudes much of this material reaches the bottom soon after the spring plankton bloom, accounting for as much as one-half of the total annual input to the benthos in shallow waters; the pulse of organic matter can even be seen in some deep-sea sediments at 4000 m (Billet et al., 1983). Although there is a general relationship among primary production, water depth, and the abundance of benthos (Rowe, 1971; Rowe et al., 1974), the presence of a strongly pulsed seasonal input may be even more important than the magnitude of the total annual input of organic material to the bottom in determining benthic community structure and function (Hargrave and Peer, 1973; Rowe et al., 1975; Smetacek et al., 1978; Walsh, 1981; Davies and Payne, 1984; Pace et al., 1984).

The deposition of bloom material to the bottom should be important to the benthos not only because it can represent such a substantial proportion of the total annual input, but also because this material may arrive at the sediment surface more rapidly and in a less decomposed state than is typical for sedimented material during the rest of the year (Smetacek et al., 1978; Hargrave, 1980; Sme-

tacek, 1980; Wassman, 1983; Davies and Payne, 1984; Pace et al., 1984; Christensen and Kannevorff, 1985). Whole-ecosystem energy budgets which have been attempted for continental shelf ecosystems, specifically the North Sea (Steele, 1974) and the Scotian Shelf (Mills and Fournier, 1979; Mills, 1980), have underscored the problem of getting enough energy to the benthos to satisfy metabolic requirements. These studies have assumed, however, that most of the material flux to the benthos was in the form of fecal pellets and detritus, forms largely unavailable to benthic fauna without first being transformed by microbes; such a transformation would result in a net loss of perhaps half the available energy. The alternative scenario, that a large fraction of the material reaches the bottom in the form of living or relatively intact phytoplankton (as might occur during an early bloom in cold water), would mean that this material would presumably be much more readily available to meiofauna and macrofauna, thus increasing the efficiency of the transfer of energy to higher trophic levels.

There is now a considerable body of evidence showing that intertidal and shallow-water deposit-feeding macrofauna cannot obtain enough bacteria to satisfy their nutritional requirements and thus must be mainly utilizing some fraction of the living microalgae and the nonliving sediment organic matter (Lopez and Levinton, 1987; Lopez and Taghon, in press). Detailed carbon budgets have shown this to be true for several different species of deposit-feeders (Wetzel, 1977; Jensen and Seigismund, 1980; Cammen, 1980a; Kemp, 1986); in fact, it has never been demonstrated that a deposit-feeder in nature can subsist on bacteria alone. Based on an empirically determined relation between ingestion rate and body size for aquatic deposit-feeders and detritivores (Cammen, 1980b) and the typical levels of bacteria in marine sediments, it is unlikely that any non-selective, macrofaunal deposit-feeder can survive by ingesting bacteria alone (Cammen, in press). There are two caveats to this statement, however: first, it is possible (although it has never been demonstrated) that a highly selective deposit-feeder might be able to take in enough bacteria; and second, it is likely that even though bacteria do not appear to be important in terms of overall carbon or energy budgets, they may serve a vital role as sources of nitrogen or micronutrients. Unless macrofauna living below the euphotic zone are radically different in their physiology from shallow-water species, it is unlikely that they can survive solely on bacteria either, since bacterial abundance in deeper sediments appears to be either similar to or less than the abundance in shallow water once particle size and organic content are taken into account (Cammen, unpublished data from the Gulf of Maine and the Scotian Shelf). This means that any mechanism encouraging a rapid transport of fresh material to the benthos, such as an early bloom, could be extremely important in the nutrition of these animals and might be a critical factor determining the amount of benthic fauna an ecosystem can support.

If spring deposition events are as important as we and others (references above) suspect, then we would expect to see a strong signal in various benthic metabolic parameters in phase with the spring bloom, and, we suspect, in response to early and late blooms. A comprehensive study of a shallow-water region of the Kiel Bight (18–21 m) showed a series of benthic responses to the spring phytoplankton bloom (Graf et al., 1982, 1983; Meyer-Reil, 1983). There was a relatively rapid increase in heat production and ETS (electron transport system) activity in the upper few centimeters of the sediment even though bottom water temperatures remained between 1 and 4°C. Benthic ATP-biomass (excluding macrofauna) and

meiofaunal numbers increased a few weeks later. Although macrofaunal abundances did not increase, glycogen and lipid content increased markedly in the surface feeding clam *Macoma baltica*. Based primarily on heat production measurements, it was concluded that the benthos utilized more than the deposited amount of organic material within one month, the difference apparently reflecting additional organic inputs due to near-bottom advection from shallower areas. Both Ansell (1974a,b,c) and Christensen and Kanneworff (1985) found a marked response in growth and development of reproductive tissue by some shallow-water macrofauna to the input of bloom material to the bottom; there was even evidence of a succession in response pattern with filter feeders showing the initial response, followed by surface deposit feeders and then subsurface deposit feeders (Christensen and Kanneworff, 1985). Although shelf areas are the site of some of our most important demersal fisheries (Walsh, 1981), there is relatively little information about the transfer of organic material to the benthos and even less information about its fate once it reaches the sediment. In the single deep-water study that has addressed the question of how the benthos responds to the spring bloom, Smith and Baldwin (1984) found an increase in oxygen uptake in summer for both stations they studied. Since there was no temperature fluctuation at those depths (5900 and 3815 m), the change probably was in response to the spring bloom; this fits with the observation of Billett et al. (1983) that fresh organic material from blooms can reach the bottom even from 4000 m.

The response of benthos to organic input has been shown to be strongly temperature dependent, and for this reason, some studies have not been able to demonstrate a clear benthic response to the spring bloom. For instance, there is often a strong relationship between benthic metabolism and seasonal bottom water temperatures, with rates of benthic metabolism generally highest in the warm summer months (Carey, 1976; Hargrave, 1969; Smith, 1971; Hale, 1975; Nixon et al., 1976, 1980). In effect, the colder temperatures in early spring may delay utilization of the newly deposited organic matter in the benthos, and a similar effect may be occurring in the water column, as zooplankton metabolism also shows a strong temperature dependence (Ikeda, 1985). A second cause for delay in some areas could be the relatively long development time for the macrofauna (Kemp and Boynton, 1981). In their study of shallow waters (3–6 m) in Chesapeake Bay, Kemp and Boynton found not only that temperature had the major influence on benthic respiration, but that the second most important factor, macrobenthic biomass, also peaked in the summer. A third reason why some investigators have not seen a marked response to the spring bloom is that in some areas the bloom may not contribute significantly to the total annual supply of organic matter to the benthos; despite the high rate of production, the extent of the bloom may be more important than the peak magnitude of the spring pulse. For example, Hargrave (1980) noted that although a spring deposition event of chlorophyll-rich material occurred in Bedford Basin, sediment respiration during the winter to midsummer period responded more strongly to steady increases in organic nitrogen sedimentation than to the pulsed bloom input, suggesting that the more important factor was a continuous deposition of fresh organic material to the bottom. In the study of Kiel Bight where a marked response of the benthos to the spring bloom was observed, potentially confounding effects were minimal: 1) Variation in bottom temperature during the bloom was slight (Graf et al., 1982); 2) Macrofauna were relatively unimportant in that system, accounting for less than 5% of

sediment heat production (Graf et al., 1982); and 3) The portion of the annual input to the benthos accounted for by the spring bloom was relatively high, about one-third (Smetacek et al., 1978).

Importance of Timing of the Spring Bloom

The onset of spring phytoplankton blooms in temperate and high latitudes is determined by a combination of events which result in a compromise between the amount of solar radiation received by a phytoplankton cell and the availability of essential inorganic nutrients (Sverdrup, 1953). In shallow inshore areas of the Gulf of Maine, for example, late winter-early spring phytoplankton blooms can occur beginning in early February (Bigelow et al., 1940; Townsend, 1984; Townsend and Spinrad, 1986) and go on into the early summer months in the deeper waters of the central Gulf. The principal factor triggering the onset of these earliest blooms in the nearshore waters of the Gulf of Maine is light (Townsend and Spinrad, 1986), since in inshore areas the upper mixed layer extends to the bottom and nutrients are in plentiful supply, having been replenished by winter convective overturn and not having been taken up by phytoplankton because of the low winter light levels. Townsend and Spinrad (1986) have suggested that the blooms in these waters will begin when the depth averaged, vertically integrated solar irradiance within the mixed layer exceeds 40 ly d^{-1} —a value also documented for a variety of bodies of water by Riley (1957, 1967), Barlow (1958), Gieskes and Kraay (1975), Pingree et al. (1976), Hitchcock and Smayda (1977), and Horn and Paul (1984). The depth of the mixed layer along much of the coast of the Gulf of Maine in late winter, when the waters are vertically isothermal, usually extends to the bottom; thus, since nutrients are not in short supply, one need only know the transparency of the water column and measure the incoming solar irradiation in order to predict the onset of the bloom for waters of a particular depth (Townsend and Spinrad, 1986).

Depending on the weather (i.e., cloud cover) in late winter and early spring, the onset of these early blooms may be advanced or delayed due to variations in the amount of available light. We believe that there are at least two ways the timing of such blooms may be important in determining the relative proportion of planktonic primary production which is consumed and respired in the water column versus that which reaches the benthos.

First, because water temperatures would tend to be quite cold during or soon after an early bloom, the metabolism of the pelagic heterotrophs that respire the bloom could be significantly slowed relative to rates of phytoplankton production (Corkett and McLaren, 1970, 1978; Ikeda, 1985; Pomeroy and Deibel, 1986; Walsh and McRoy, 1986). For example, in the Gulf of Finland, bacterial respiration did not become significant until after the spring diatom bloom when the water temperature warmed from 1.25 to 5°C (Kuparinen, 1987), and in the Southern Ocean, bacterial respiration was 4.4 times greater at 4° than at 1°C (Christian and Weibe, 1974). Thus, it appears that although cold waters may support high production rates of diatoms, and presumably dissolved organic matter, both bacterial production and the production of the 3- to 10- μm microheterotrophs which graze the bacteria (Azam et al., 1983) would be inhibited. While adult copepods and larger copepodites might do well grazing on diatoms, copepod nauplii that require

smaller cells, such as heterotrophic microflagellates, would face a reduced supply of potential food. In turn, larval fishes, which in general prefer copepod nauplii as food items, would not fare as well under this scenario during early blooms as during later blooms in warmer waters. The implication for benthic-pelagic coupling is that if the colder temperatures associated with early blooms result in less grazing and respiration in the water column, then a relatively greater fraction of the organic production should be available to reach the bottom, thus enhancing benthic production.

Second, because the rates of growth and development of those groups of zooplankton which propagate in response to the phytoplankton bloom would also be inhibited by cold water temperatures associated with an early bloom (e.g., Corkett and McLaren, 1978, 1978; Ikeda, 1985), there would be a slower increase in the grazing pressure which helps to curtail the bloom and thus the bloom might extend longer into the spring; a phytoplankton bloom of longer overall duration would result in more production and a greater input to the benthos. This effect may not necessarily be important in instances where blooms are self-limited due to nutrient depletion, but in coastal waters or fronts, for example, where nutrients are often available even when the bloom begins to decline, a delay in the onset of grazing pressure may be quite significant.

The timing of the bloom may also affect the ultimate fate of the phytoplankton production once the bloom material reaches the bottom. An early bloom would lengthen the time available for the benthic community to respond to and process the pulse of organic material prior to the settlement of the juvenile demersal fishes later in the year. The result should be enhanced production by higher trophic level benthic organisms of a size suitable as prey for the juvenile fish which in turn should tend to increase their growth and survival.

But how much interannual variation might be expected in the timing of the onset of the spring bloom? Evidence that the date of onset can indeed vary significantly among years is illustrated in Table 1 and Figure 1. These data represent hindcasts of the Julian day on which the spring phytoplankton bloom would be expected to have started in Sheepscot Bay for the years 1971–1980. Sheepscot Bay is located on the central coast of Maine, U.S.A. (43° 45' N), covers an area of about 50 km² and averages about 45 m depth; it was chosen for analysis because: a) it is known to be an important spawning area and juvenile nursery area for cod and other demersal fishes (Bigelow and Schroeder, 1953; Perkins, 1982), and b) because there exist multiyear data sets for water temperatures and solar radiation at nearby (<5 miles) laboratories in Wiscasset and Boothbay Harbor. We calculated the date for the onset of the phytoplankton bloom each year using data for solar irradiance received at Wiscasset. These daily values of total light data (covering the wavelengths 300 to 3000 nm) were used to compute the depth-averaged, vertically-integrated irradiance using the equation:

$$E^* = 1/z \int E_0 e^{-Kz} dz$$

where: $z = 45$ m, the average depth of Sheepscot Bay, $E_0 =$ solar irradiance reaching the surface, and $K =$ the diffuse attenuation coefficient, which is assumed to be 0.19, the typical value for these waters reported by Townsend and Spinrad (1986). This value is modified by solar elevation with the equation $K =$

Table 1

Estimates of the timing of the onset of the spring phytoplankton blooms in Sheepscot Bay on the coast of Maine, U.S.A., the estimated water temperature there at the time of the onset of the bloom and one month later, for the years 1971 to 1980. The water temperatures are those recorded at 1.6-m depth at the Boothbay Harbor dock, approximately two miles from Sheepscot Bay.

Year	Julian Day of Onset of Bloom	Temperature at Onset of Bloom (°C)	Temperature One Month Later (°C)
1971	35	1.8	1.0
1972	42	2.0	1.0
1973	49	0.9	2.8
1974	46	2.6	3.7
1975	47	1.9	3.0
1976	54	3.3	3.9
1977	39	2.1	1.3
1978	36	2.1	0.8
1979	41	2.1	1.6
1980	36	0.1	0.0

$K_0/\cos j$, where $K_0 = 0.19$ and j is the solar elevation (Aas, 1976). The Julian day upon which the running average of E^* for the previous five days exceeded 40 ly d^{-1} was assumed to represent a conservative, time-averaged estimate corresponding to the onset of the bloom for that year.

The results of this analysis showed that the timing of the onset of the phytoplankton bloom varied by as much as 20 days for the 10 years analyzed (Table 1). Interestingly, the water temperatures at the time of the onset of those blooms, given in Table 1 (surface water temperatures recorded at Boothbay Harbor), do not support the notion that the timing of the onset of earlier blooms necessarily corresponds with colder waters. Rather, the water temperatures during the month of February are quite variable among the years in question such that there is no significant correlation between the timing of the bloom and water temperature (Figure 2). In coastal Maine, then, an earlier than normal initiation of the spring phytoplankton bloom would not necessarily result in increased benthic productivity solely due to the effect of lower temperature on pelagic heterotrophic metabolism. Indeed, the overall duration of the bloom is probably more important since there is a strong correlation between the timing of the onset of the bloom and the temperature one month later. We assume that the later temperature would be that encountered by zooplankton populations propagating in response to the phytoplankton bloom, because it is about one month following the onset of the bloom that inshore zooplankton populations in these waters reach their peak abundances (Townsend, 1984); warmer water temperatures at that time would result in greater secondary production and hence greater pelagic consumption of phytoplankton.

This analysis suggests that the timing of the bloom in coastal waters may indeed have a significant effect on the amount of organic material reaching the bottom and its subsequent utilization by the benthos. Such interannual fluctuations have

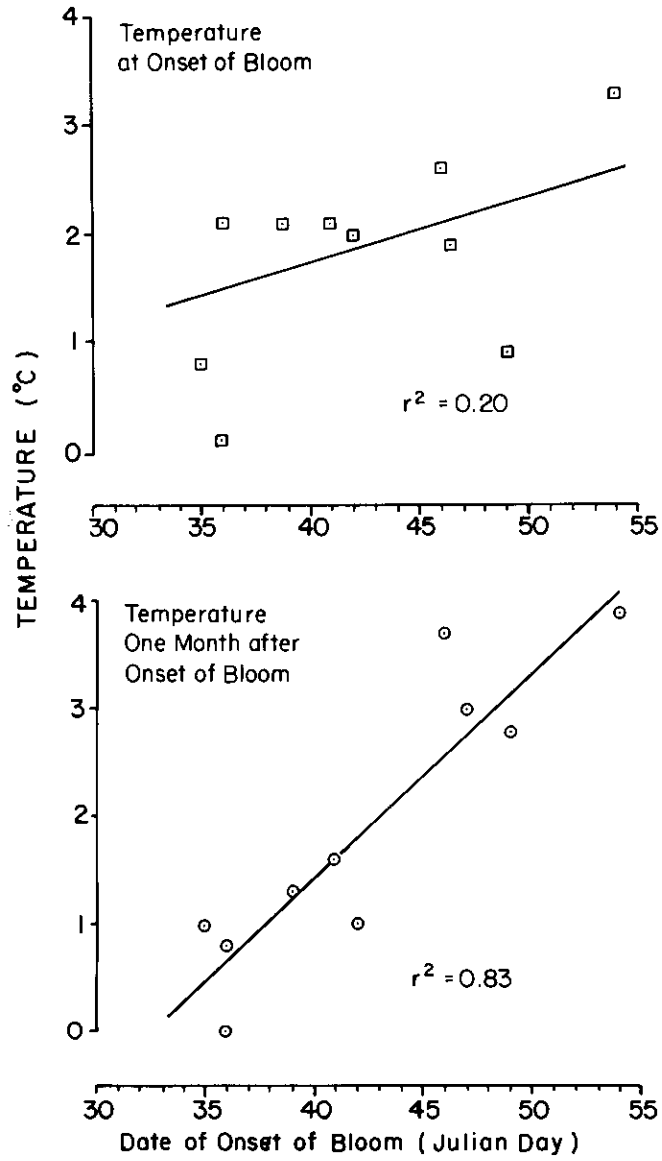


Figure 1. Relation of water temperature to the date of the onset of the spring phytoplankton bloom. Surface (1.6 m) water temperature recorded in Boothbay Harbor is given for the Julian day predicted for the onset of the bloom (upper panel) and for one month later (lower panel).

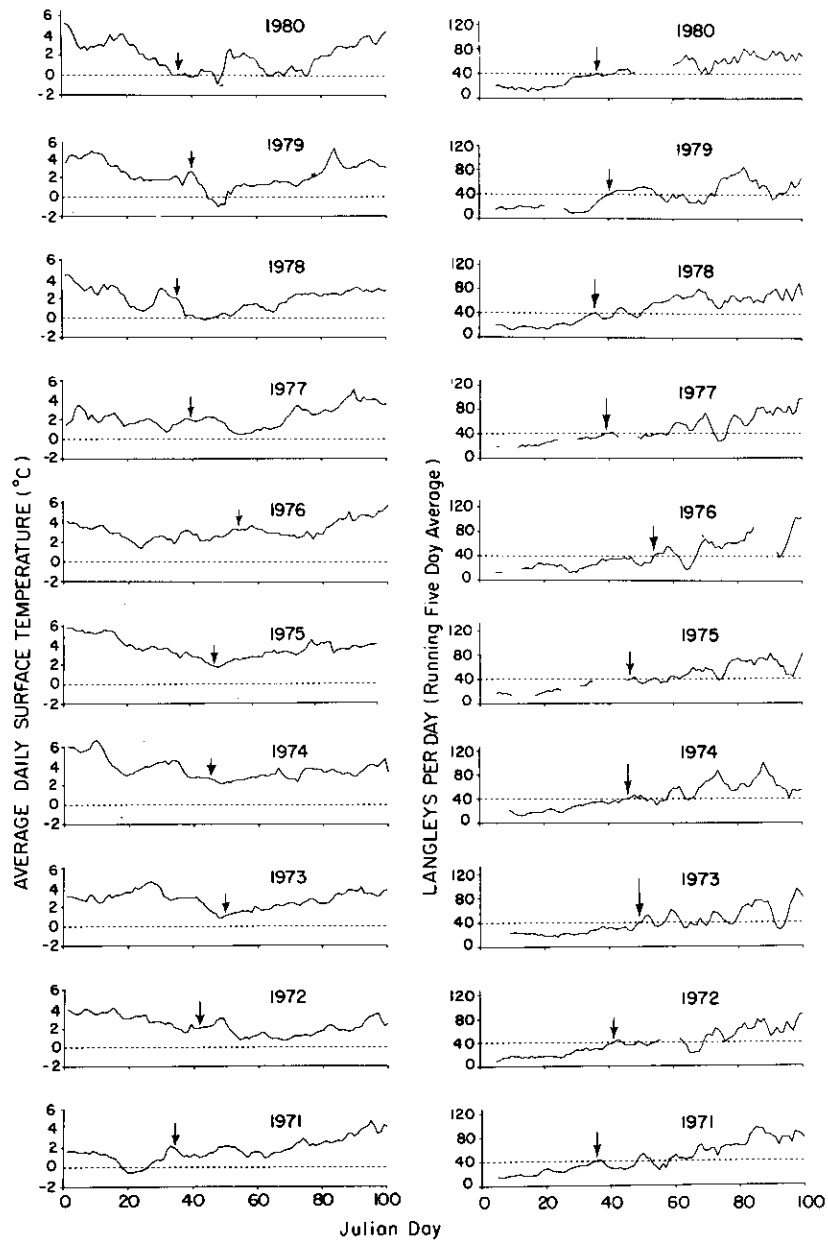


Figure 2. Depth-averaged, vertically-integrated light and surface (1.6 m) water temperature data for the first 100 days of 1971–1980 near Boothbay Harbor. Calculation of depth-averaged, vertically-integrated light (right panel) is detailed in the text; the dashed line indicates 40 ly d^{-1} , the irradiance level indicating the initiation of the bloom (see discussion in text). Water temperatures (left panel) are from Boothbay Harbor; the dotted line indicates 0°C . The predicted date of the onset of the spring bloom is indicated for each year with an arrow.

implications not only for attempts to model ecosystem energetics, but also for efforts to understand the factors determining recruitment success for some coastal fisheries. Early blooms with a greater delivery of material to the bottom could enhance the production of suitable benthic food items which would favor growth and survival of juvenile demersal fishes. On the other hand, late blooms in warmer waters might facilitate growth and survival of pelagic fish larvae through enhanced production of zooplankton, providing larvae are fortunate enough to be present at that time. The hypothesis that the timing of the spring plankton bloom, through its effect on benthic-pelagic coupling, can affect not only pelagic, but also demersal recruitment processes, is worthy of further testing; it is important to understand the effects of variation in the onset of spring blooms and the role of each of the possible modes of action discussed above. Assessing the relative merit of these possibilities as each affects recruitment represents a new approach to an old problem, but it requires at the outset a fundamental understanding of the dynamics of benthic-pelagic coupling in shelf waters—a subject which has not yet received attention proportional to its potential importance to coastal ecosystems.

Acknowledgements

The authors thank Laurice Churchill of the Maine Department of Marine Resources and the Environmental Studies Department of Maine Yankee Atomic Power Company for allowing the use of their light and temperature data. This project was partially supported by University of Maine Sea Grant and NSF Biological Oceanography (OCE-8511281, OCE-8614187). This is Bigelow Laboratory for Ocean Sciences Contribution No. 87016.

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