

Optimal Wind Conditions for the Survival of Larval Northern Anchovy, *Engraulis mordax*: A Modeling Investigation

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ABSTRACT: How the frequency of storm events can influence the survival of larval northern anchovy, *Engraulis mordax*, was investigated by computer modeling. The hypothesis was as follows. While wind events dissipate layers of planktonic food, a total absence of wind mixing would reduce upward nutrient flux and retard plankton production. Therefore, there must be optimal conditions of wind speed, duration, and frequency of wind events for maximum survival of northern anchovy larvae. From numerical experimentation, all wind events were detrimental to post-yolk-sac larvae present in the water column at the time of the storm. However, if initial prey concentrations are insufficient for optimal growth of larvae, then a wind event which increases primary and secondary production may be beneficial to larvae emerging from the yolk-sac stage after the storm. The conclusion was that optimal conditions for larvae survival occur when a wind event strong enough to deepen the mixed layer into the nutricline is followed by a period of calm. This period between storms must be long enough for larvae to develop into a stage where short-term starvation can be endured.

In 1975, Lasker hypothesized that larval anchovy survival was dependent on the stability of the water column. Laboratory work (see Blaxter and Hunter 1982; and references therein) showed that first-feeding anchovy require very high concentrations of plankton food. These high concentrations are found in the upper water column, but only during periods of low winds and reduced turbulence (Lasker 1975; Owen 1989). Recently Peterman and Bradford (1987) performed a statistical analysis of wind and larva

mortality data from the field that confirms Lasker's hypothesis. There is a statistically significant relation between larva mortality rate and the frequency of calm, low wind speed periods which permit the maintenance of concentrated patches of food.

However, completely calm wind conditions cannot be ideal, because a stratified water column reduces the vertical flux of nutrients into the euphotic zone, reducing production of plankton (Lewis et al. 1986). Eppley and Renger (1988) recently measured the slight increase in nitrate in the surface layer owing to a moderate wind event in California coastal waters, and found the data consistent with the wind driven, nutrient flux dynamics of Klein and Coste (1984).

Consider the fact that northern anchovy, *Engraulis mordax*, populations off central and southern California spawn mostly during the winter and spring months (Smith 1972; Smith and Richardson 1977), not during the summer when winds are most calm and the water column most stratified by solar heating (Husby and Nelson 1982). The timing of the spawning of these populations may be an adaptation to maximize the survival of larvae.

This is the third in a series of modeling efforts (Wroblewski 1984; Wroblewski and Richman 1987) to simulate the environmental conditions which influence the survival of northern anchovy. Each successive model builds on the previous model by increasing complexity (and realism) in the biological and physical dynamics. Here we investigate by numerical experimentation the manner in which the frequency of storms during the spawning season of northern anchovy could influence survival of larvae. We find there is indeed a theoretical optimum condition of wind speed, duration of event, and frequency of events for maximum survival.

METHODS

Our model investigates the mortality of north-

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ern anchovy larvae for 15 days from first feeding. From histological indications of tissue condition, O'Connell (1980) showed that anchovy larvae less than 10 mm SL are vulnerable to starvation. For northern anchovy, yolk-sac absorption and first feeding occurs 3 to 4 days (depending on temperature) after egg hatching. Larvae obtain a standard length of 10 mm about 19 days after hatching (Blaxter and Hunter 1982). Thus the larvae are subject to starvation for 15 days after first feeding. The larvae metamorphose at 34 to 40 mm SL, about 56 to 60 days after hatching.

O'Connell (1980) suggested that larvae above 10 mm SL may be less vulnerable to starvation because of increasing nutriment (protein, carbohydrate, and lipid) reserves with growth. Early post-yolk-sac larvae have negligible reserves and will survive only two or three days without any food (Lasker et al. 1970; O'Connell and Raymond 1970). Larger (35 mm SL) larvae can survive two weeks of starvation as their lipid content declines (Hunter 1977).

Because of their small mouth size, first-feeding northern anchovy larvae are restricted to feeding on small prey (Hunter 1977). First-feeding northern anchovy are initially able to subsist on a diet of the unarmored dinoflagellate *Gymnodinium splendens* (Lasker et al. 1970). However, after a few days, their growth rate will be greatly depressed unless their diet includes more typical foods of young clupeoid larvae such as tintinnids, ciliates, copepod eggs, naupliar, and copepodite stages (Arthur 1976; Blaxter and Hunter 1982; Theilacker 1987). Therefore, in our model, we consider the prey of young anchovy larvae to be microzooplankton. We do discuss later the availability of *G. splendens* to first-feeding larvae under the turbulent mixing conditions predicted by the model.

Larval Fish Dynamics

Our formulation of growth and mortality of larval northern anchovy (see Wroblewski 1984) is based on the laboratory experiments of O'Connell and Raymond (1970), who determined the effect of various zooplankton prey concentrations on the survival of larvae over the first 12 days of life. The prey in the O'Connell and Raymond (1970) experiments were wild crustacean nauplii with some tintinnids and phytoplankton also present.

The equation for growth rate of larval anchovy expresses the difference between metabolic

gains and losses,

$$\text{growth} = \text{ingestion} - \text{egestion and excretion.}$$

Ingestion of prey by larval anchovy is calculated, using the Ivlev (1955) formulation for the feeding of fishes. Egestion of fecal matter by anchovy larvae is taken to be a constant fraction of the ingested ration. Metabolic excretion is assumed to occur at a basal rate plus an additional excretion associated with feeding activity.

Larval anchovy mortality is expressed in the model as a function of weight at age, or in other words, the feeding history of the larvae,

$$\text{mortality} = \text{baseline growth rate/actual growth rate.}$$

Mathematical formulations for larval anchovy growth and mortality used here are the same as equations (5) and (6) in Wroblewski and Richman (1987).

Prey Dynamics

The equation for the concentration and vertical distribution of the prey of larval anchovy (microzooplankton) is one of a set of coupled partial differential equations describing the plankton ecosystem. These equations for phytoplankton, zooplankton, and dissolved nutrient (nitrate) in a one-dimensional water column are given as equations (1) to (4) in Wroblewski and Richman (1987). Analytical solutions to these plankton equations have been derived and sensitivity analyses have been performed so that one can fully understand how the concentration of prey responds to changes in the biological parameter values (see Franks et al. 1986; Wroblewski and Richman 1987).

The biological parameter values used here are the same as in table I of Wroblewski and Richman (1987), with the exception that the growth rate of the phytoplankton is reduced. In the previous study, it was assumed that the average growth rate in the euphotic zone (waters with greater than 1% surface light intensity) was 2 doublings day⁻¹, if nutrients were not limiting. Here we assume that the maximal growth rate of the phytoplankton at the surface is 2 d⁻¹. Below the surface, the growth rate of the plants is given by $V = V_m \exp(-kz)$, where V_m is 2 d⁻¹ and the light extinction coefficient k is 0.1 m⁻¹. The effect of this change in plant growth rate is to reduce the concentration

of phytoplankton in the water column, so that the simulated profile of phytoplankton (Fig. 1a) more closely resembles the observations off Southern California reported in Cullen et al. (1983) and Mullin et al. (1985).

The modeling studies by Wroblewski (1984) and Wroblewski and Richman (1987) examined how the concentration of prey responds to perturbations in the physical oceanographic environment caused by wind forcing. Wroblewski (1984) used scale analysis to deduce the thickness of the layer of prey which could be maintained during wind-induced turbulent mixing. He found that the effectiveness of turbulence in dispersing food for northern anchovy larvae is lowered by any ability of the prey to aggregate into patches. The conclusion was that first-feeding larvae could find sufficient concentrations of motile *G. splendens* in the pycnocline during moderate wind conditions.

Wroblewski and Richman (1987) coupled the plankton equations to a simplified model of mixed layer dynamics (Niiler 1975) to calculate wind-driven deepening of the mixed layer and

the turbulent diffusivity within the mixed layer during and after a wind event. Wroblewski and Richman found that wind events are always detrimental to larval northern anchovy, because wind mixing dissipates vertical structure in prey concentration as Lasker (1975) proposed. However, they discovered that interacting biological and physical processes determine the time interval before high concentrations of prey are re-established, i.e., the starvation period endured by the anchovy larvae. Reproduction by prey and their aggregation by swimming govern the rate of reestablishment of vertical structure in prey distributions, once wind conditions allow turbulence in the upper water column to dissipate. They noted as significant that first-feeding larval anchovy forage directly on *G. splendens* and microzooplankton which have the reproductive capacity and migration ability to reestablish high concentrations shortly after a storm.

Wroblewski and Richman (1987) were able to quantify the influence of wind event magnitude and duration on larval northern anchovy survival. However, as Niiler's (1975) mixed layer model does not permit restratification of the upper water column by solar heating between wind events, more complex physics was required to explore the influence of interstorm duration on larval anchovy survival.

Mixed Layer Dynamics

Here we use the mixed layer dynamics of Mellor and Yamada (1974; 1982) which predict both wind-driven deepening of the mixed layer and shallowing of the mixed layer by solar heating. Heat is absorbed at the sea surface and short-wave radiation penetrates the surface, attenuating exponentially in the manner formulated by Simpson and Dickey (1981).

Klein and Coste (1984) used the turbulence closure scheme of Mellor and Yamada (1974) to study the influence of wind forcing on nutrient transport into the mixed layer, but treated nitrate as a conservative quantity. Chen et al. (1988) used Mellor and Yamada (1974) dynamics with both wind and tidal forcing to simulate vertical nutrient mixing in Long Island Sound, but also considered biological consumption and production of nitrate. We refer the reader to Klein and Coste (1984) and Chen et al. (1988) for details on the implementation of Mellor and Yamada's (1974) level 2.5 dynamics in this type of physical-biological modeling study.

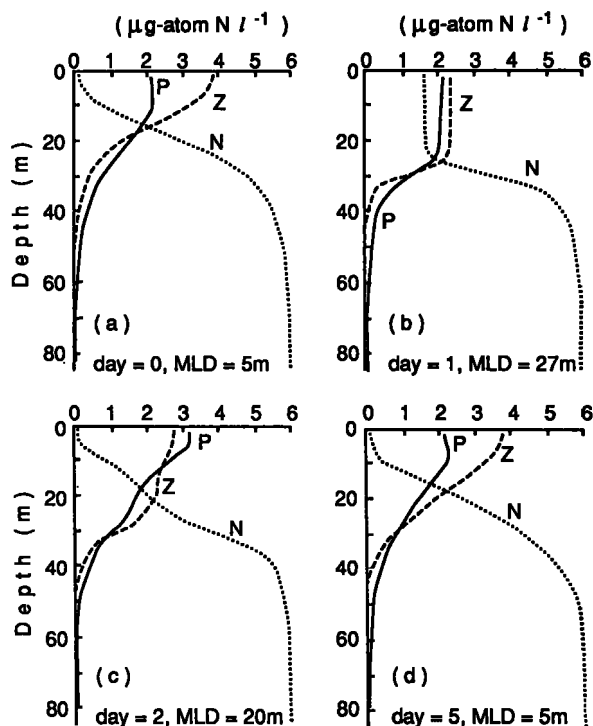


FIGURE 1.—Temporal evolution of the one-dimensional (vertical) plankton model in response to a single wind-mixing event. Initial conditions are the steady state profiles of phytoplankton (P), zooplankton (Z), and nitrate (N) shown in panel (a). The wind speed during the event is 16 m s^{-1} with 24 h duration. MLD refers to the mixed layer depth.

Initial Conditions

The initial conditions for a simulation are the steady state solutions of the plankton dynamics for a stratified water column (Fig. 1a). The initial temperature gradient is 4°C over the upper 100 m. The daily average surface heating is 50 W m⁻² which is divided equally between short- and long-wave radiation. A background eddy diffusivity of 10⁻⁴ m² s⁻¹ throughout the water column is assumed.

RESULTS

Multiple Wind Events

Figure 2 shows the wind speed, level of turbulent mixing at 3 m below the surface, and the mixed layer depth for the simulation where three wind events occur within a 15 d period. Fifteen days is the critical period after yolk-sac absorption when northern anchovy larvae are susceptible to starvation (O'Connell 1980). Each

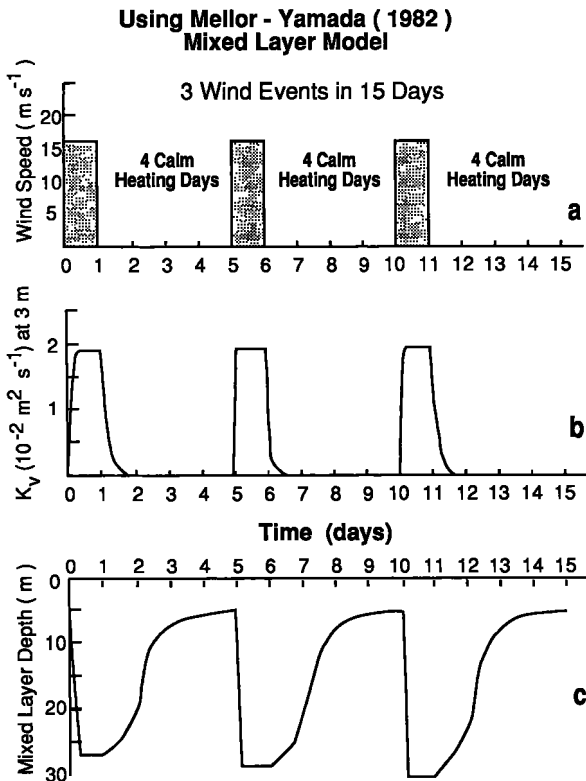


FIGURE 2.—The wind speed (a), vertical eddy diffusivity K_v at 3 m depth (b), and mixed layer depth (c) during a simulated 15 d period. The Mellor-Yamada (1982) model was used to calculate K_v and the mixed layer depth.

wind event has a wind speed of 16 m s⁻¹ and a duration of 24 hours. Between the events, the water column restratifies due to a solar heating of 25 W m⁻² at the surface and to a short-wave radiation flux of an additional 25 W m⁻² penetrating the upper 10 m of the water column.

In the Mellor-Yamada (1982) model, the turbulent diffusion coefficient K_v is predicted as a function of depth; it has a maximum within the mixed layer and decreases markedly below. Since we are primarily concerned with dissipation of plankton near the surface where the concentration of prey is greatest (due to high productivity of the phytoplankton), we plot in Figure 2b the value of K_v at 3 m depth over the 15 d period. The deepening of the mixed layer during each event and its shallowing after each wind event is shown in Figure 2c. Note that the mixed layer deepens slightly more with each subsequent event, as the water column does not completely restratify during the 4 d period between each wind event. The background diffusivity maintains a mixed layer 5 m deep.

The model prediction of the increase in larval anchovy mortality for the three wind event case is shown as curve b in Figure 3. For comparison the mortality rate for larvae which experienced only a single event of the same wind speed and duration is shown as curve a in Figure 3. Curves a and b are the same until day 5 when the second wind event begins. The mortality rate for larvae experiencing a second and then third wind event continues to increase with time, while the mortality rate for larvae enduring only one event declines as turbulence in the water column dissipates and food concentrations are reestablished (see Figure 1, panels c and d).

The mortality rate after 15 days for larvae having endured a single wind event is about 6% d⁻¹. If no wind event had occurred, their mortality rate would be about 4% d⁻¹ (curve e in Figure 3). Thus a single event does not have a great cumulative effect. However, for larvae having endured 3 wind events over their 15 d development period, the mortality rate increases to 13% d⁻¹ (curve b in Figure 3).

The mortality rate increases dramatically with the frequency of wind events. Curve c in Figure 3 shows the influence of 5 wind events each of wind speed 16 m s⁻¹ and 24 hours duration on a cohort of larvae reaching the first feeding stage at time zero. The mortality rate at the end of 15 days is 21% d⁻¹.

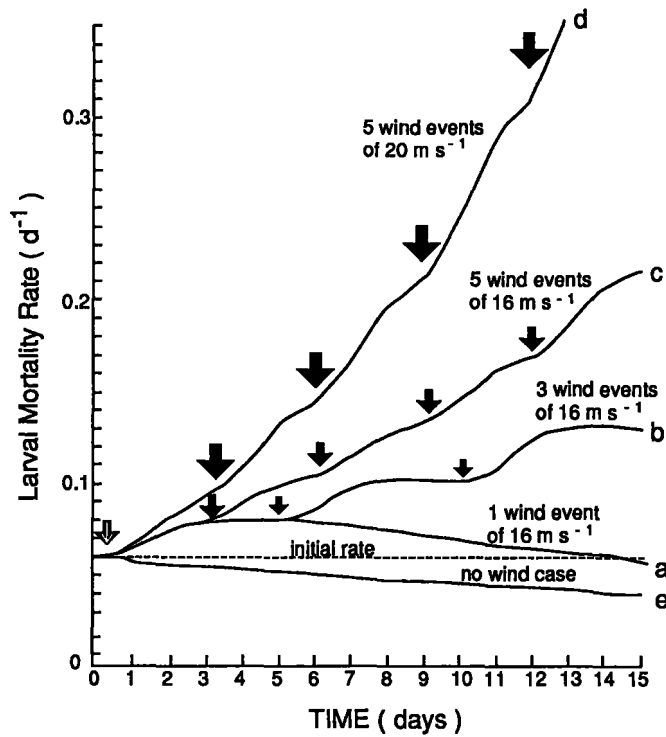


FIGURE 3.—Mortality rate predicted for larval northern anchovy positioned at 3 m depth in the water column (the depth of maximum growth and survival in the model water column). Curve a shows the predicted mortality rate for an event where the wind blows at 16 m s⁻¹ for 24 hours. Curves b, c, and d show the mortality rate for larvae experiencing multiple wind events. Curve e gives the mortality rate where winds are calm during the simulated 15 d period. Day zero is the day of first feeding of a cohort of larvae. Arrows indicate the beginning of wind events.

The mortality rate also increases with the strength of the storms. For larvae enduring 5 wind events of 20 m s⁻¹ wind speed, each lasting 24 hours, the mortality rate at day 13 is 35% d⁻¹ and 45% at day 15 (curve d in Figure 3). Five storms of this magnitude occurring within a 2 wk period are not likely. However, our predicted mortality rates of between 10 and 20% d⁻¹ for more common wind conditions (Fig. 4) are in the same range as rates calculated from field data (see figure 1 of Peterman and Bradford 1987).

Food Limiting Conditions

The next model experimentation was conducted to determine the circumstances under which wind events might prove beneficial. Up to this point we have assumed that initial prey concentrations near the surface are sufficient to support optimal growth of northern anchovy larvae before any wind mixing disperses these concen-

trations. As we have seen above, under these circumstances, all wind events are detrimental to developing larvae. However, we shall now demonstrate that if initial food levels are not sufficient for rapid growth of larvae, a storm may actually enhance the survival of larvae emerging from the yolk-sac stage after the storm.

The initial condition profiles of phytoplankton, zooplankton, and nutrients for the case of insufficient, prestorm prey concentrations are shown in Figure 5a. Notice that the concentration of zooplankton near the surface is only 2.7 μg atom N ℓ⁻¹ where the initial concentration of zooplankton in the previous simulations was 3.7 μg atom N ℓ⁻¹. As before, it is assumed that only 25% of this total zooplankton biomass is suitable as food for larval anchovy (estimated from data of Mullin et al. 1985). With this food limiting condition, the growth rate of northern anchovy larvae feeding near the surface is only 15% d⁻¹. The mortality rate of the larvae

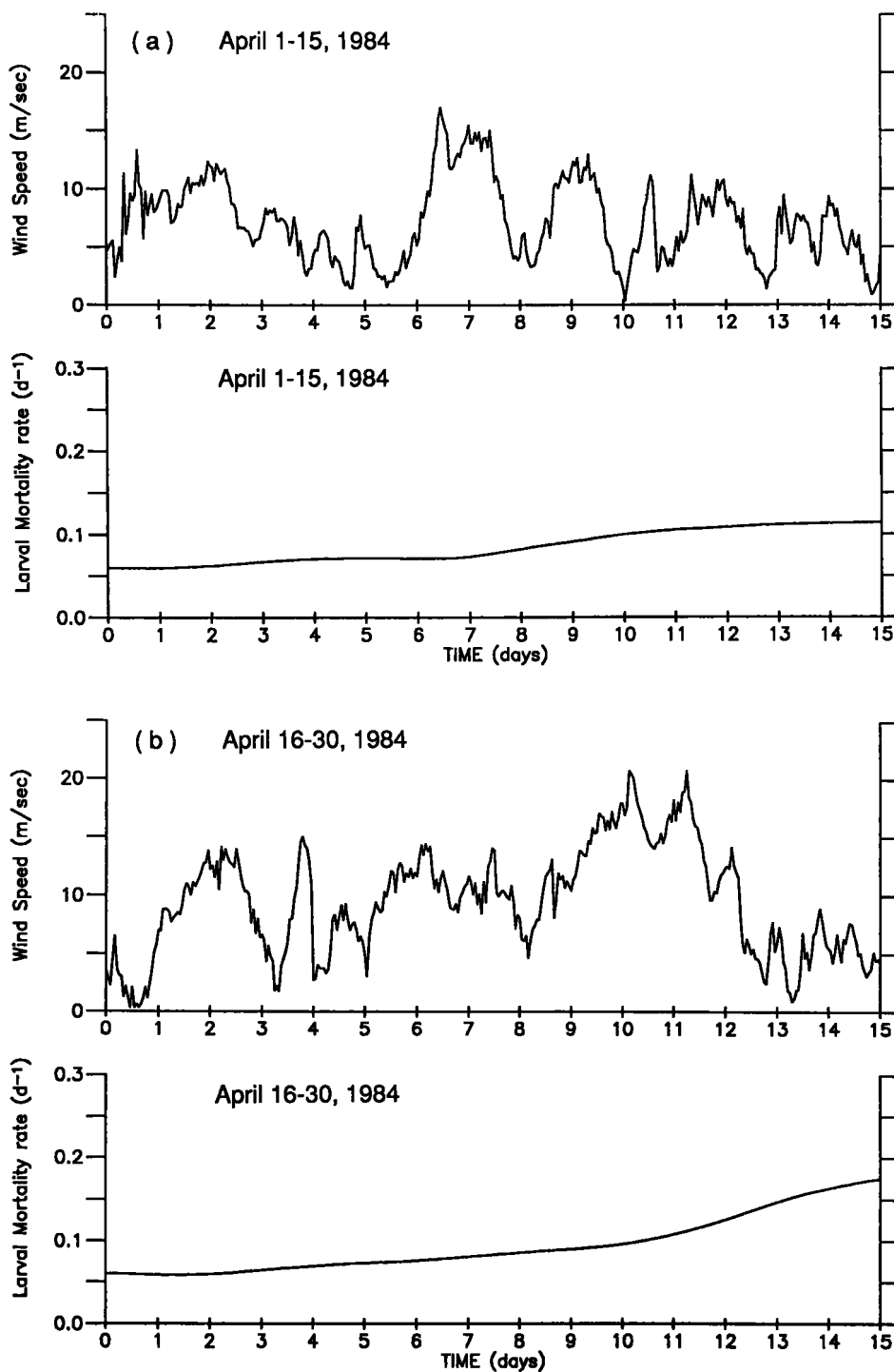


FIGURE 4.—Larva mortality rate of the northern anchovy predicted by the model using wind data from April 1984 recorded by NDBO (National Data Buoy Office, NOAA) mooring 46012 located at lat. 37.4°N, long. 122.7°W. The wind record is typical for the southern California coast in spring. (a) The wind speed and larva mortality rate for the period 1–15 April. Day zero is the day of first feeding for larvae emerging from the yolk-sac stage on 1 April. (b) Same as (a) but for the period 16–30 April, with first feeding beginning on 16 April.

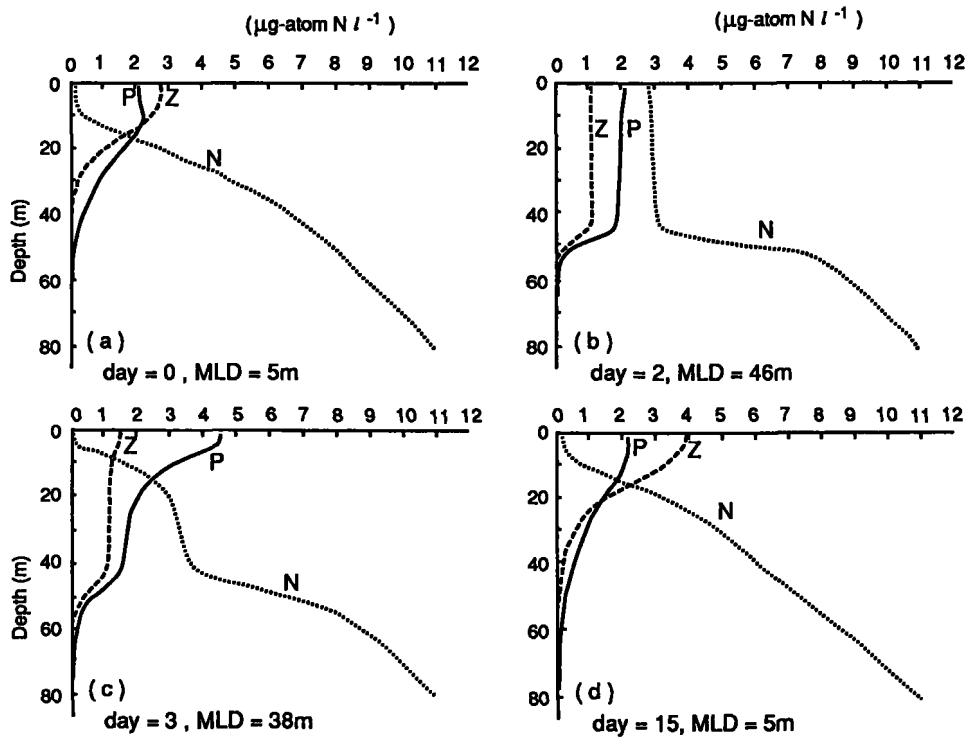


FIGURE 5.—Temporal evolution of the plankton model in response to a wind event of 20 m s^{-1} blowing for 48 hours. The initial conditions shown in (a) are different from those in Figure 1a, as the nitrate concentration continues to increase with depth. This allows more nutrients to be added to the euphotic zone by wind mixing. The initial zooplankton concentration is less than sufficient for optimal growth of northern anchovy larvae.

increases over time even in the absence of any wind event (Fig. 6, curve a).

With these initial conditions, we now determine the influence of a storm with a wind speed of 20 m s^{-1} blowing for 48 hours. The mixed layer deepens to 46 m, entraining nutrients into the euphotic zone while dissipating the existing vertical structure in the upper plankton and nutrient profiles (Fig. 5b). Curve b in Figure 6 shows the decrease in the zooplankton concentration at 3 m depth because of this mixing. However, after the winds cease and turbulence in the water column dissipates, the zooplankton concentration begins to increase. Zooplankton biomass increases as the grazers utilize increased phytoplankton biomass (Fig. 5d). By day 6 (four days after the storm) the zooplankton concentration has surpassed the initial concentration, and by day 8 it has reached concentrations high enough to support optimal growth of anchovy larvae.

However only larvae beginning to feed after the storm truly benefit from poststorm increases in zooplankton biomass. Larvae which existed before and during the storm are adversely af-

ected by the initial decrease in prey concentrations owing to wind mixing. Their growth rate slows and their mortality rate increases to 30% per day by model day 6 (Fig. 6, curve c). But larvae entering the first-feeding stage two days after the storm when zooplankton concentrations are increasing have only a slight initial increase in mortality rate, and then a decrease (Fig. 6, curve d). Larvae emerging from the yolk-sac stage four days after the storm has passed, experience a reduction in mortality even below the initial rate of 6% per day (Fig. 6, curve e) because there is sufficient prey concentrations to support optimal growth.

DISCUSSION

It would appear advantageous for adult northern anchovy to spawn after a storm, so that by the time the eggs hatch and the larvae emerge from the yolk-sac stage, the first-feeding larvae will have high concentrations of prey (induced by the storm) upon which to feed. There is recent evidence that Atlantic menhaden, *Brevoortia tyrannus*, are stimulated to spawn by the pas-

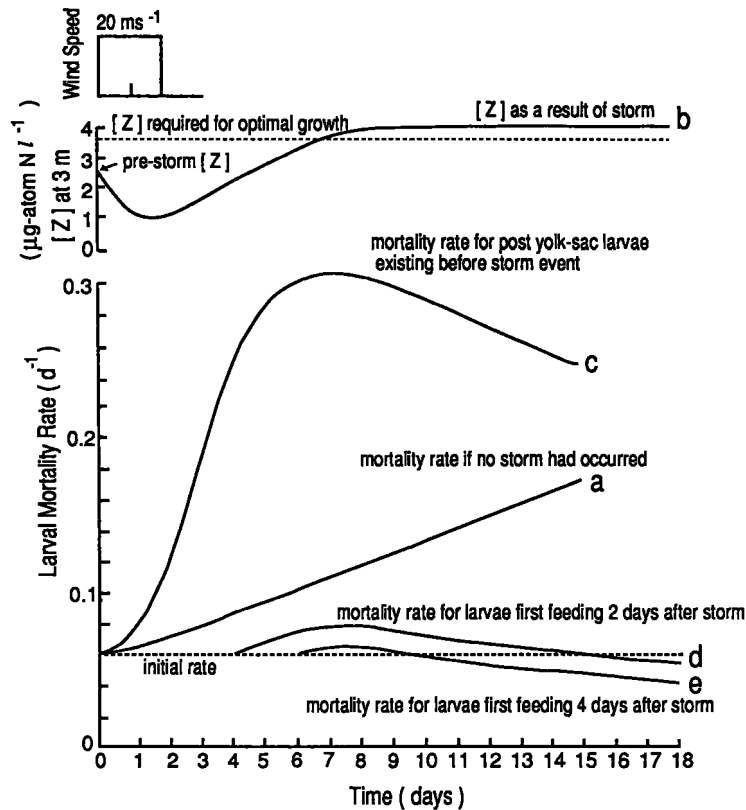


FIGURE 6.—Mortality rate predicted for larval northern anchovy positioned at 3 m depth in the simulation shown in Figure 5. Curve a shows the predicted mortality rate where winds are calm during the simulated 15 d period. Mortality rate increases because food is limiting larva growth. Curve b shows the increase in zooplankton biomass at 3 m depth owing to the wind event which entrains nutrients into the euphotic zone. Curve c shows the predicted mortality rate for larvae feeding in the water column during and after the storm. Day zero is the day of first feeding for the cohort of larvae described in curves a and c. Curves d and e show the enhanced survival of larvae first feeding 2 days and 4 days respectively, after passage of the storm.

sage of a storm (Checkley et al. 1988). The strategy of northern anchovy is to spawn continuously (Methot 1981) so that some larvae will be emerging from the yolk-sac stage at just the right time to feed upon high concentrations of microzooplankton induced by a storm.

Since any wind event which falls on the heels of the first beneficial storm will be detrimental, optimal conditions consist of a storm followed by a period of calm during which the larvae can grow into a less vulnerable stage. Any beneficial effect of the first storm will depend on the time required to concentrate new prey biomass. If the first storm is quickly followed by subsequent wind events, the prey will remain disbursed and the first-feeding larvae may not withstand the starvation period. But if the storm is followed by a period of calm winds, turbulence will dissipate,

the water column will restratify, and the enhanced secondary production will become concentrated. As the time to complete development from post-yolk-sac stage to this less vulnerable stage is about 15 days (O'Connell 1980), a 2 wk period of calm following a storm strong enough to deepen the mixed layer into the nutricline is theoretically ideal for the survival of the northern anchovy larvae.

These theoretical results may apply as well to other clupeoid species, such as the Atlantic menhaden. Checkley et al. (1988) inferred that the adaptive significance of spawning by *B. tyrannus* during storms derives, in part, from the enhancement of microzooplankton prey for young larvae owing to the storm-induced upwelling. One criterion for maximal survival of the larvae of any clupeoid species would be a close

match between the interstorm duration and the critical development period of the larvae, i.e., the development to a stage where starvation is no longer a major factor.

Survival of northern anchovy larvae in the sea depends on the right type (50–100 μ in size and high nutritional quality) of prey being present in abundance at first feeding (O'Connell and Raymond 1970). Lasker (1975) maintained that the dinoflagellate *Gymnodinium splendens* is small enough to be ingested, has sufficient nutritional qualities, and is abundant enough in subsurface layers to sustain first-feeding anchovy larvae. Lasker regarded microzooplankton as not abundant enough to contribute significantly to larval survival during the first week of life.

Let us assume for the moment that *G. splendens* is the preferred prey of first-feeding anchovy larvae. Let us also assume that this dinoflagellate species is present in the phytoplankton community after a wind event (e.g., as observed by Mullin et al. 1985). The concentration of this motile organism after a wind event depends on its ability to aggregate in the face of turbulent mixing in the water column.

Wroblewski (1984) showed that the vertical diffusivity which just balances the dinoflagellates' ability to aggregate is given by

$$K_v = H W_s$$

where H is the vertical scale of the dinoflagellate layer and W_s is the swimming speed of the dinoflagellate. Cullen and Horrigan (1981) found that if nitrate is available in the upper water column (as after a strong storm), *G. splendens* will migrate to the surface into a layer several meters thick. If the wind event is weak and nitrate is not available in the surface layer, the dinoflagellates will aggregate near the nitracline in a subsurface layer. Assuming H is 5 m and W_s is 1 m h⁻¹ (Kiefer and Lasker 1975; Cullen 1985), *G. splendens* should be able to aggregate against a diffusivity of 14×10^{-4} m² s⁻¹.

In our model, K_v quickly decays to a background diffusivity of 1×10^{-4} m² s⁻¹ after cessation of wind forcing (Fig. 2b). Solar heating adds buoyancy at the surface and the turbulent kinetic energy in the mixed layer dissipates through friction. Thus, first-feeding northern anchovy larvae should be able to subsist on layers of *G. splendens* within a day after a storm. The short period of starvation when *G. splendens* are dispersed during the storm should not result in a significant increase in larvae mor-

tality, unless the storm continues for several days. A few days after successful first feeding, the developing anchovy larvae must include microzooplankton in their diet. Our assumption that anchovy larvae feed on microzooplankton is appropriate when simulating larvae mortality over a 15 d period from first feeding.

The concentration of prey required for survival of anchovy larvae is controversial. The laboratory feeding experiment of O'Connell and Raymond (1970) indicated a prey concentration > 800 copepod nauplii ℓ^{-1} were required for maximal survival. More recent laboratory experiments (Houde and Schekter 1981; Munk and Kiorboe 1985) suggest the minimum concentration of prey may be as low as 200 copepod nauplii ℓ^{-1} , but of course the larvae would be expected to grow at a much slower rate (O'Connell and Raymond 1970).

Even concentrations of 200 nauplii ℓ^{-1} are high compared to estimates of average densities of microzooplankton in the sea (Beers and Steward 1967). However, as pointed out by Owen (1989), maximal concentration of prey rather than average concentration (estimated from integrating net hauls or pump samples) is the relevant quantity.

The highest zooplankton concentration in the model (at 3 m depth in Figure 1a) is about 4 μ g atom N ℓ^{-1} of which 25% or 1 μ g atom N ℓ^{-1} is larval anchovy food (e.g., copepod nauplii). This is equivalent to about 14 μ g N ℓ^{-1} of copepod nauplii. The nitrogen content of *Paracalanus* stage I nauplii is about 5 ng (Checkley 1980) and of *Calanus* is about 20 ng (Corner et al. 1965; Mullin and Brooks 1967). Thus, 14 μ g N ℓ^{-1} of copepod nauplii is equivalent to 2,800 *Paracalanus* stage I nauplii ℓ^{-1} or 700 *Calanus* stage I nauplii ℓ^{-1} . These concentrations correspond roughly to the prey densities used experimentally by O'Connell and Raymond (1970), but are two orders of magnitude higher than the median numbers m⁻³ observed in pump samples from the sea taken by Mullin et al. (1985) before and after a storm.

The overestimation of zooplankton biomass in the model is due to the omission of vertical loss processes such as sinking of phytoplankton and zooplankton fecal pellets which reduce the total nitrogen available to the plankton ecosystem in the upper water column (Walsh 1983; Checkley 1985). However, we would get the same response in the mortality of larval anchovy presented above, if we altered the model to simulate more realistic zooplankton concentrations, while

also reducing the concentration of prey required for the baseline growth rate of the anchovy larvae. The crux of the model is the lowering of prey concentration due to wind mixing, a corresponding decrease in ingestion and growth rate of anchovy larvae, and an increase over time of the larval mortality rate with suppressed growth.

Owen (1989) showed that microzooplankton do occur in concentrations greater than 100 organisms ℓ^{-1} on the microscale (centimeters) in patches of fine scale (meter) size. Owen found that concentrations of organisms within the patches were greater at low wind speeds. Motile organisms showed higher patch concentrations than would be expected solely from reproduction of the organisms. Rothschild and Osborne (1988) discovered mathematically that a beneficial effect of moderate turbulence is to increase the encounter rate of prey and predator on these microscales. These recent observations and theory emphasize the need to examine the feeding and survival of larval northern anchovy on microscale and fine scales. Our model with a 2.5 m vertical grid spacing does not resolve biological and physical processes on these scales. Future modeling research should compare the beneficial (e.g., productivity enhancement) and detrimental (e.g., prey dispersion) effects of storm-induced mixing on the microscale feeding environment of larval anchovy (see Vlymen 1977; Lasker and Zweifel 1978).

We conclude that wind conditions during the spawning period which are optimal for the survival of northern anchovy larvae encompass 1) wind speeds high enough ($>10 \text{ m s}^{-1}$, depending on the water column stratification) to deepen the mixed layer into the nutricline; 2) wind event durations long enough (greater than half an inertial period, or about 8 hours at lat. 35°N) to maximally deepen the mixed layer, but short enough to maximize calm periods between storms; and 3) wind event frequency low enough (one major storm every two weeks) to allow development of larvae to a stage where carbohydrate, protein, and lipid reserves can mitigate subsequent starvation periods (about 15 days of development, depending on water column temperature).

Our conclusions are supported by the observation that northern anchovy populations off central and southern California spawn during the winter and spring months, when wind conditions can be optimal by our theoretical calculations. They do not spawn during the summer when

winds are most calm and the water column is highly stratified, as one would expect considering Lasker's hypothesis alone.

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