Development, survival and timing of metamorphosis of planktonic larvae in a variable environment: the Dungeness crab as an example

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ABSTRACT: We use models to show how a variable environment can affect development, survival and timing of metamorphosis of meroplanktonic larvae. For a general case, we use an analytical model to explore the effect of temperature-dependent development and mortality rates on temporal patterns of metamorphosis. The distribution of metamorphosis over time is a lagged version of the pattern of larval release, distorted by changes in development and mortality rates. If temperature causes development rate to increase (decrease) linearly with time through the larval period, the timing of metamorphosis has a short (long) temporal range, a large (small) amplitude, and is shifted to the left (right). This implies that at locations with a decreasing trend in development rate (e.g. due to decreasing temperature), the timing of metamorphosis is more sensitive to larval release time than at locations with an increasing trend. Mortality of larvae can be influenced directly by the environment through sub-optimal conditions, or indirectly by environmentally induced changes in development rate, which change the duration of the larval period. If mortality rate is constant, the longer the larval period the greater the mortality. However, this result is not true if mortality rates change with the environment in the same way that development rates change. The common assumption of constant mortality rates needs to be critically reassessed. To apply these results to a specific example, we develop a model of the temperature- and salinity-dependence of Dungeness crab *Cancer magister* Dana larval development, using available laboratory data. We then use historical records of daily sea surface temperatures and salinities to examine the impact of these 2 variables on larval development and survival at coastal sites along the U.S. west coast. Based on calculations from 7 locations over a total of 233 yr, Dungeness crab larvae can take between 74 and 182 d to metamorphose, depending on location, year and time of release. Larvae in the northernmost part of the study region (Washington) have the longest mean annual development times (133 to 163 d), those in central and northern California have intermediate development times (81 to 134 d), and those in southern California have the shortest development times (74 to 84 d). Greatest relative intra- and interannual variability in mean development times and survival occurred in upwelling areas off central California. Observed latitudinal differences in timing of metamorphosis from zoeal to megalopal stages were consistent with differences predicted by the model. We conclude that variability in temperature and salinity can cause Dungeness crab larval periods to vary by a factor of 2. For meroplanktonic populations in general, complicated patterns of metamorphosis can result from variable temperatures during the larval period, even if hatching of larvae occurs at a constant rate.

KEY WORDS: Model · Meroplankton · Larvae · Environment · Development · Survival

INTRODUCTION

Physical oceanographic conditions have a strong influence on the dynamics of some marine populations.

In particular, variability in environmental conditions during the planktonic larval phase of species that have a benthic or pelagic adult phase (i.e. meroplankton) may have a significant influence on recruitment to adult populations (Rice et al. 1987, Roughgarden et al. 1988, Olson & Olson 1989, Underwood & Fairweather 1989, Rumrill 1990). Larval development and survival are affected by a large number of physical and biolog-

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ical factors, including physical transport (Methot 1983, Ainley et al. 1991, Gaines & Bertness 1992), temperatures and salinities encountered (Rothlisberg & Jackson 1987, Harding & Trites 1988, Hofmann et al. 1992a, Dekshenieks et al. 1993), food quantity, quality and availability (Scheltema & Williams 1982, Paulay et al. 1985, Olson & Olson 1989), and predation (Rumrill et al. 1985, Pennington et al. 1986, André et al. 1993). In this study we investigate the role of variability in some physical factors in determining development and survival of meroplanktonic larvae, and the timing of metamorphosis.

Environmental factors can affect larval survival to metamorphosis directly and indirectly. Direct effects include death as a result of extremes in environmental variables such as temperature and salinity. Indirect effects occur through the influence of the environment on growth or development rates, which may affect susceptibility of the larvae to predation or starvation. For example, cool temperatures can slow growth such that larvae spend extended periods in the plankton, and are exposed to the high mortality rates experienced at small sizes for extended periods (Rice et al. 1987). In addition, an increased larval period will increase the probability of transport away from suitable settlement (Roughgarden et al. 1988) or nursery (Hjort 1914, Hare & Cowen 1993) areas.

The timing of metamorphosis is affected by time-varying development rates. Different patterns of developmental or growth rates through a growing season can lead to variability in settlement times (e.g. in benthic crustaceans) or in the onset of first feeding (e.g. in larval fish). The timing of these events is important for survival, which usually depends critically on certain resources being available at the time of metamorphosis. For benthic invertebrate larvae, a critical resource at the time of settlement is suitable habitat (e.g. Cameron & Rumrill 1982), whereas for fish the resource typically is available food at the time of first feeding (Hjort 1914, Cushing 1975). If transport and food availability change seasonally, the timing of metamorphosis is vital to ensure that the animals encounter favourable conditions.

We demonstrate effects of varying environmental conditions on meroplanktonic larvae, using models and data for the Dungeness crab *Cancer magister* Dana from the California Current system. The Dungeness crab is a commercially important species found subtidally along the west coast of North America from Magdalena Bay, Mexico, in the south (MacKay 1942) to the Pribilof Islands, southeastern Bering Sea, in the north (Fig. 1; Jensen & Armstrong 1987). Historically, the exploited part of this population has undergone considerable fluctuations, as is documented in the catch records (Botsford et al. 1989, Pacific States

Marine Fisheries Commission 1993). These fluctuations occur with a period of approximately 10 yr, and with amplitudes that vary by as much as a factor of 10 between the minimum and maximum catch levels. No single factor has been found to account for the fluctuations (Botsford 1986), and it is reasonable to consider combinations of factors (possibly nonlinear). A useful first step is to determine what the effects of each factor are. Here we examine variability in settlement following the larval stage (Botsford et al. 1989, Armstrong & Gunderson 1991). We consider the effects of temperature and salinity on 2 aspects of larval biology that will affect dispersal and successful settlement: development times and survival. Laboratory studies have investigated the effects of temperature and salinity on survival and development of Dungeness crab larvae (Poole 1966, Reed 1969, Sulkin & McKeen 1989).

Fig. 1 Distribution of Dungeness crabs *Cancer magister* (shaded area) along the west coast of North America, and the coastal stations for which environmental data were obtained for executing the simulation model

Results of these studies are limited, because they were carried out under constant laboratory conditions, but they reflect relative rates at different temperatures and salinities. Field observations of Dungeness crab larvae also are limited because one cannot follow cohort development in the field (Lough 1976, Ebert et al. 1983, Hobbs et al. 1992). We use models, combining information from both field and laboratory studies, to simulate Dungeness crab larval development and survival.

The life history of Dungeness crab is known fairly well from laboratory studies and field observations (Poole 1966). Female Dungeness crabs spawn between late September and December (Wild 1980). The eggs remain attached to the abdomen of the female until they hatch between December and March (Waldron 1958, Wild 1980, Jamieson & Phillips 1990). The larvae are planktonic, spending between 3 and 6 mo in 5 zoeal stages and 1 megalopal stage (Poole 1966). They are released near shore (depth < 50 m), and must either remain near shore or return to the near-shore area for successful settlement on suitable sandy substrata (Carrasco et al. 1985, Jamieson et al. 1989, McConnaughey et al. 1992).

Because current and wind patterns in the California Current system vary intra-annually, development rates during the larval period, as well as the timing of larval release, can have a large effect on transport to suitable habitat. Dungeness crab larvae are found in the plankton of the California Current from December to July (Lough 1976, Reilly 1983). Three seasons have been identified in the coastal ocean in this region (Largier et al. 1993): storm, upwelling and relaxation. The storm season (December to March) is characterized by wind forcing associated with the passage of weather fronts, uniformly cold water, and fluctuating currents which are weakly equatorward over the outer shelf and weakly poleward over the inner shelf. Dungeness crab larvae hatch and disperse during the storm season. The upwelling season (April to July) has strong equatorward wind forcing, strong equatorward currents and upwelling of cold, salty water at the coast. Strong vertical and lateral shear is observed in the alongshore flow, and the intensity of offshore flow, associated with coastal upwelling, varies with position relative to capes. Dungeness crab larvae metamorphose primarily during the upwelling season, and must return to the nearshore area to settle, a direction of transport that often is opposite to that of the surface currents. The relaxation season (August to November) is characterized by weakening of the equatorward wind forcing, currents that are mostly poleward and increased water temperatures. Most larvae already have settled at the onset of the relaxation season, although those in the northern part of the range can be found in the plankton through August (Jamieson & Phillips 1990).

In addition to the intra-annual variability described above, interannual variability in physical conditions may cause variability in developmental and survival rates of Dungeness crab larvae. Interannual, large-scale changes in the ocean and atmosphere express themselves locally as variations in intra-annual patterns (Largier et al. 1993). These may be relatively rapid, large variations such as are caused by El Niño-Southern Oscillation (ENSO) events, or slow, small changes such as those projected from climate change. Changes are observed in the mean and variability of winds, currents and temperature, as well as in the timing and duration of the 3 oceanographic seasons (Largier et al. 1993). In particular, the timing of the transition from storm to upwelling seasons (the 'spring transition', Strub et al. 1987) may be important in influencing rates of successful settlement among years, because the spring transition generally occurs when most larvae are still in the plankton.

The general aim of this study is to investigate the effects of environmental variability on development, survival and the timing of metamorphosis of meroplanktonic larvae. This is carried out with due acknowledgement of the limitations imposed by uncertainties in the interactions between environmental variables and biological rates, especially when extrapolating from laboratory conditions to the field. We present an analytical model which indicates the general way in which factors such as time-varying temperatures shape patterns of metamorphosis. As a particular example, we investigate the possible effect of variations in temperature and salinity on Dungeness crab larvae. Laboratory-based information is used to develop an empirical model of the temperature- and salinity-dependence of development times and survival rates of zoeal and megalopal stages of Dungeness crab. We use these parameters to show general results from the analytical model, where seemingly straightforward trends in temperature can result in complicated patterns of metamorphosis for a population over a larval season. We then use historical temperature and salinity records in a simulation model to evaluate development and survival under real environmental conditions, for Dungeness crab larvae released at different times and at different locations along the U.S. west coast. Ultimately, we aim to use the simulation model to simulate larval development in a 3-dimensional physical circulation model of the region.

GENERAL ANALYTICAL MODEL

To demonstrate the influence of time-varying growth or development rate on the timing of metamorphosis,

we use the size-structured von Foerster equation (Sinko & Streifer 1967, Metz & Diekmann 1986) with a variable representing stage of development, m , instead of size. The stage of development is the fraction of time to settlement at a constant temperature. It is assumed to increase from 0 to 1 as an individual develops from hatch to metamorphosis, at which time a limiting resource can affect recruitment to the adult population. Metamorphosis can represent settlement of the benthic stage in the case of meroplanktonic benthic crustaceans, or the first-feeding stage in the case of larval fish. The density of individuals n at development stage m at time t is described by

$$\frac{\partial n(m,t)}{\partial t} = -\frac{\partial}{\partial m}[n(m,t)g(m,t)] - n(m,t)D(m,t) \quad (1)$$

where $g(m,t)$ is the development rate and $D(m,t)$ is the mortality rate. By the method of characteristics (Garabedian 1986), Eq. (1) can be transformed into a set of ordinary differential equations

$$\frac{dm}{ds} = g(m,t) \quad (2a)$$

$$\frac{dn}{ds} = -(g_m + D)n \quad (2b)$$

$$\frac{dt}{ds} = 1 \quad (2c)$$

where s represents time from release, and $g_m = \partial g / \partial m$. The solution to these equations for the number of individuals at the final stage of development ($m = 1$) in terms of the number of individuals at the initial stage of development ($m = 0$) is

$$n(1,t) = n(0,t-a(t)) e^{-\int_0^1 \frac{D(m,t)}{g(m,t)} dm} \quad (3)$$

where $a(t)$ is the age of an individual that reaches the final stage of development at time t , and we have assumed that development would be linear with time in a constant environment (i.e. $g_m = 0$). Because we have defined developmental stage as a fraction of the time to settlement, this assumption is unrelated to whether developmental rate is constant in terms of larval size or moult number. If the rate of larval release into the population is $R(t)$ and the rate of metamorphosis (settlement or first feeding) is $S(t)$, the boundary conditions are

$$R(t) = n(0,t) g(0,t) \quad (4a)$$

$$\text{and} \quad S(t) = n(1,t) g(1,t) \quad (4b)$$

at the initial and final stages of development, $m = 0$ and $m = 1$, respectively. Using these and Eq. (3) leads to

$$S(t) = R(t-a(t)) \frac{g(1,t)}{g(0,t-a(t))} e^{-\int_0^1 \frac{D(m,t)}{g(m,t)} dm} \quad (5)$$

where $a(t)$ is the age of an individual that reaches metamorphosis at time t (i.e. the solution to Eq. 2a).

Eq. (5) explicitly demonstrates how various factors affect the pattern of metamorphosis, and the different ways in which time-varying hydrographic conditions can influence this pattern through larval development and mortality rates. In essence, 3 factors determine the distribution of metamorphosis over time $S(t)$. The first factor is the pattern of release of larvae, $R(t)$. Release can occur in a variety of ways, ranging from continuous, constant release to a series of pulsed releases. The second factor affecting the pattern of metamorphosis is an indirect effect of development rate, and is reflected in the ratio of development rate at settlement $g(1,t)$ to development rate at release $g(0,t-a(t))$. Development rates will change with environmental variables such as temperature, and the way in which the ratio changes with time depends on the manner in which temperature changes with time. The third factor affecting $S(t)$ depends on the development and mortality rates, and how they change with time (temperature). There is a direct effect of mortality, reflected in the value of $D(m,t)$; an increase in $D(m,t)$ leads trivially to a decrease in survival. An indirect effect of development rate on mortality is reflected by $g(m,t)$ in the denominator of the integrand in the mortality term. For constant mortality rates, as development rate increases with time (e.g. due to increasing temperature), mortality effectively decreases. This is a commonly assumed result, but note that it depends critically on the assumption of constant mortality. For time-varying mortality, the relative ways in which the development and mortality rates respond to changes in temperature become important in determining overall survival, and the shape of the metamorphosis distribution. For example, if the temperature-dependence of mortality rate is identical to that of development rate, varying temperature will not change the third term in Eq. (5), and the length of the larval period will not affect overall mortality.

EMPIRICAL MODELS OF DEVELOPMENT AND SURVIVAL RATES BASED ON LABORATORY DATA

Development of Dungeness crab larvae has been investigated in a number of experimental studies under a variety of temperature and salinity conditions. Mean durations of zoeal stages I to V were obtained from laboratory studies (Table 1). Only 2 reported instances were found of the complete development of a Dungeness crab larva from egg to the first juvenile instar under measured temperature and salinity conditions. A single individual reared by Poole (1966) at salinities of 26 to 30 ppt and 10.6°C moulted to juvenile

Table 1 *Cancer magister*. Ages (days) at the end of various life history stages of Dungeness crab at different temperature and salinity combinations. Z: each of 5 zoeal stages; M: megalopal stage. Values without parentheses are original data obtained from published information, values in parentheses are extrapolations, estimated from the proportions in Table 2 (see text for details)

Temp. (°C)	Salinity (ppt)	Z-I	Z-II	Z-III	Z-IV	Z-V	M	Source
6.1	30	42	-	-	-	(187)	(260)	Reed (1969)
10.0	20	29	-	-	-	108	(150)	Reed (1969)
10.0	25	20	-	-	-	90	(125)	Reed (1969)
10.0	29-30	13.2	24.5	37.2	50.9	69.4	(96)	Sulkin & McKeen (1989) ^a
10.0	30	23	-	-	-	90	(125)	Reed (1969)
10.6	26-30	18.2	29.4	43.0	57.6	80	111	Poole (1966)
12.0	33	9	19	30	42.5	57	(79)	Hartman (1977)
13.9	20	16	-	-	-	65	(90)	Reed (1969)
13.9	25	16	-	-	-	65	(90)	Reed (1969)
13.9	30	16	-	-	-	47	(65)	Reed (1969)
14.0	-	7.8	15.2	23.4	33.5	46.5	(65)	Ebert et al. (1983)
14.0	32	14	28	43.5	56	(77)	(107)	Hartman & Letterman (1978)
15.0	29-30	8.3	14.4	21.1	28.4	38.7	(54)	Sulkin & McKeen (1989) ^a
17.0	-	5	13	16	23	31	(43)	Ebert et al. (1983)
17.8	20	14	-	-	-	53	(74)	Reed (1969)
17.8	25	10	-	-	-	45	(63)	Reed (1969)
17.8	30	10	-	-	-	54	(75)	Reed (1969)
20.0	29-30	7.6	13.1	19	25.5	(35)	(49)	Sulkin & McKeen (1989) ^a
21.7	25	10	-	-	-	(45)	(62)	Reed (1969)
21.7	30	10	-	-	-	(45)	(62)	Reed (1969)
16	31-34					48	76	Reed (1969)

^aSulkin & McKeen (1989) investigated the influence of 3 different temperatures on zoeal development and survival in natural seawater (29 to 30 ppt; S. D. Sulkin pers. comm.). Their results from experiments on single individuals and on groups of individuals did not differ significantly (Sulkin & McKeen 1989), and average values are presented

instar I (Table 1), and Reed (1969) reported that a larva which moulted to megalopa after 48 d produced the first postlarval instar after 76 d at 16°C and 31 to 34 ppt. The available data (Table 1) were used to estimate the duration of each larval stage as a percentage of the total development time to megalopa (Table 2). The age at which the megalopae would settle was taken to be the age of metamorphosis to the megalopal stage multiplied by 1.49 (Table 2), an average factor obtained from the data of Poole (1966) and Reed (1969).

Development rate and mortality rate can vary with both temperature and salinity. The times taken for larvae to develop to megalopae under different temperature and salinity combinations were based on the data of Reed (1969). To simplify the development model, we assume that differences in development time resulting from salinity occur only at temperatures between 6 and 18°C, and that outside this temperature range salinity has little or no effect (Fig. 2). The effect of salinity and temperature on development times was computed by bilinear interpolation between data values (Press et al. 1986), giving a matrix of development times at temperatures from 6 to 22°C and salinities of 20 to 30 ppt (Fig. 2). To accommodate temperature and salinity

Fig. 2. *Cancer magister*. Development times (d) to megalopa of Dungeness crab larvae under different temperature and salinity conditions (after Reed 1969), based on the data of Table 1

Table 2. *Cancer magister*. Measured durations of each larval stage of Dungeness crab as a cumulative percentage of total development time to megalopa under different temperature and salinity combinations. Z: zoeal stage; M: megalopal stage; J: juvenile crab. Mean percentages are calculated for each stage up to megalopa

Temp. (°C)	Salinity (ppt)	Z-II	Z-III	Z-IV	Z-V	M	J	Source
10.0	20	26.9	–	–	–	100	–	Reed (1969)
10.0	25	22.2	–	–	–	100	–	Reed (1969)
10.0	29–30	19.0	35.3	53.6	73.3	100	–	Sulkin & McKeen (1989)
10.0	30	25.6	–	–	–	100	–	Reed (1969)
10.6	26–30	22.8	36.8	53.8	72.0	100	139	Poole (1966)
12.0	33	15.8	33.3	52.6	74.6	100	–	Hartman (1977)
13.9	20	24.6	–	–	–	100	–	Reed (1969)
13.9	25	24.6	–	–	–	100	–	Reed (1969)
13.9	30	34.0	–	–	–	100	–	Reed (1969)
14.0	–	16.8	32.7	50.3	72.0	100	–	Ebert et al. (1983)
15.0	29–30	21.4	37.2	54.5	73.4	100	–	Sulkin & McKeen (1989)
16.0	31–34	–	–	–	–	100	159	Reed (1969)
17.0	–	16.1	41.9	51.6	74.2	100	–	Ebert et al. (1983)
17.8	20	26.4	–	–	–	100	–	Reed (1969)
17.8	25	22.2	–	–	–	100	–	Reed (1969)
17.8	30	18.5	–	–	–	100	–	Reed (1969)
Mean		22.5	36.2	52.7	73.2	100	149	
SD		4.9	3.3	1.6	1.1	–	–	
n		15	6	6	6	–	2	

values outside these ranges, the matrix was extended to include all temperatures from 1 to 30°C and salinities from 10 to 40 ppt, by assuming that development times do not change at the boundaries of the matrix.

Probabilities of survival of Dungeness crab larvae to the megalopal stage were obtained from Reed (1969) for 25 temperature-salinity combinations. These data were used to calculate a response surface for zoeal survival

(Fig. 3), using bilinear interpolation between data points (Press et al. 1986). For salinities greater than the maximum of 30 ppt in Reed's (1969) experiments, we assume that survival changed only with temperature (Fig. 3).

SIMULATION MODEL

We use an individual-based simulation model of Dungeness crab larvae to evaluate the implications of the analytical model, and to explore further the effects of natural variation in environmental conditions in the California Current system. The simulation model is equivalent to a numerical solution of Eq. (1), with development and mortality rates dependent on temperature and salinity. Each model day, development rate (g) is computed from daily temperature and salinity values by bilinear interpolation (Press et al. 1986) from the matrix of development times at different temperatures and salinities (Fig. 2). Model larvae moult from one larval stage to the next when the value of the development variable m equals set values (see below). For Dungeness crab larvae, relative durations of each developmental stage do not appear to change significantly with temperature and salinity, i.e. the development is equiproportional.

Larval survival is affected directly by temperature and salinity, reflecting the environmental range to which the larvae are adapted. Such responses typically are measured in laboratory studies under constant con-

Fig. 3. *Cancer magister*. Proportions surviving to megalopa for Dungeness crab larvae under different temperature and salinity conditions in the laboratory (after Reed 1969)

ditions. We use these laboratory results (Fig. 3) to estimate daily zoeal mortality d_1 (proportion dying per day) due to stress under varying environmental conditions as

$$d_1 = 1 - p(\text{temperature, salinity})^{\frac{1}{\alpha(\text{temperature, salinity})}} \quad (6)$$

where $p(\text{temperature, salinity})$ is the laboratory-derived probability of surviving to the megalopal stage at the ambient temperature and salinity conditions, and $\alpha(\text{temperature, salinity})$ is the theoretical age (days) at which the megalopal stage is reached, based on ambient temperature and salinity conditions. In the absence of any information on temperature- and salinity-dependent survival of the megalopal stage, we assume d_1 for megalopae is 0.

Other sources of mortality for larvae include natural ecological factors such as starvation and predation, which would be present in the field but are not seen in laboratory culture. These sources are represented by a mortality rate d_2 , such that daily survival is the combination of mortalities d_1 and d_2 :

$$\text{Daily survival} = (1 - d_1)(1 - d_2) \quad (7)$$

We calculate d_2 by using an average instantaneous mortality rate of 0.066 d^{-1} estimated from field data in the California Current system (Hobbs et al. 1992):

$$(1 - d_2) = e^{-0.066} \quad (8)$$

The simulation model was executed using a database of historical records of daily sea surface temperatures and salinities (Table 3) (e.g. Scripps 1988), obtained from the Pacific Fisheries Environmental Group (NMFS, NOAA) at Monterey, California (Franklin Schwing pers. comm.). Data were used for 7 locations along the west coast of the USA (Fig. 1): Neah Bay, Crescent City, Trinidad Bay, Farallon Islands, Granite Canyon, Balboa and La Jolla. This data set has

numerous gaps. In cases where up to 6 d of continuous missing data occurred, the gaps were filled by linear interpolation. In a few instances where a large portion of data was missing from an otherwise complete data set, the gap was filled by using the mean daily values for that period, calculated from all years for which there were data available. At 2 locations (Neah Bay and Crescent City) there were no daily salinity data available, and monthly mean values (Cayan et al. 1991) were applied to each day of the calendar month in the simulations. In using these historical, point-source data to execute the simulation model, we have to assume that larvae would remain at 1 locality throughout their development period.

To assess intra-annual variability in development time due to variability in release time in the simulation model, larvae were released every day from 1 December until 1 March (Reed 1969, Lough 1976, Wild 1980, Ebert et al. 1983, Reilly 1983). Simulations continued until all larvae in the model had developed to the stage where they were competent to settle. In total, 233 yr of data were used in the simulations: 133 yr from southern California, 72 yr from central and northern California, and 28 yr from northern Washington (Fig. 1).

RESULTS

Analytical results for a general case

We use the analytical model to explore how each factor in Eq. (5) influences the pattern of metamorphosis. With a constant release rate $R(t)$, zero mortality and variable temperatures, the time course of metamorphosis is affected by the ratio of development rates in Eq. (5). If development rate increases with time (due to temperature increasing), the ratio of development rate at metamorphosis $g(1, t)$ to development rate at release

Table 3. Summary of the historical sea surface temperature and salinity data used as input to the model. The number of years in the data file for which there are sufficient data to include in the crab model is indicated by n. For any 2 adjacent years in a time series, the data run from 1 December of the first year until 26 August of the second year, i.e. 270 d for each annual period

Locality	n	Years
Neah Bay ^a	28	1955/56–62; 1963/64–66; 1968/69–80; 1981/82; 1983/84–86; 1987/88–89
Crescent City ^a	7	1961/62; 1976/77–78; 1984/85–89
Trinidad Bay	3	1977/78; 1981/82; 1985/86
Farallon Islands	44	1925/26–40; 1941/42; 1957/58; 1959/60–64; 1965/66–69; 1971/72–89
Granite Canyon ^b	18	1971/72–89
Balboa	60	1929/30–89
La Jolla	73	1916/17–89

^aMean monthly salinity data were used (Cayan et al. 1991)

^bSalinity data were available only for 1986 to 1989. Mean daily values from these 4 years were applied to the years 1971/72–85

Fig. 4. *Cancer magister*. Results of the analytical model, showing the continuous release, $R(t)$, and settlement, $S(t)$, of Dungeness crab larvae under hypothetical temperature conditions, and with different assumptions about larval mortality rates. (a) Hypothetical temperature trend; (b) hypothetical pattern of release of larvae, $R(t)$; (c) settlement with no mortality; (d) settlement with constant mortality; (e) settlement with temperature-dependent mortality, where mortality rate increases with temperature. Capital letters (A to E) identify groups of larvae at release and settlement, and subscripts (1 and 2) refer to sub-groups. The widths of the time segments in (c), (d) and (e) change from those in (b) because of temperature changes during development

$g(0, t - a(t))$ is greater than 1. However, at the same time that development rate increases, the lag between the final and initial development rates $a(t)$ decreases, tending to decrease values of successive ratios of final to initial development rates. To clarify the relative influence of these and other effects, we apply a hypothetical temperature profile to the model (Fig. 4a), using parameters for Dungeness crab larvae and with larval release rate $R(t)$ constant (Fig. 4b). We assume that the development rate $g(m, t)$ (in increments of m per day) depends only on time-varying temperature, not on stage m . We use data from Sulkin & McKeen (1989) to obtain the temperature-dependence of g :

$$g(m, t) = 0.010 \log_e[\text{temperature}(t)] - 0.015 \quad (9)$$

In the example, temperature starts at a constant minimum value, then increases linearly to a maximum where it remains for a period, before decreasing again to the minimum value where it again remains constant (Fig. 4a). The periods (designated A, B, C, D, E) were chosen to group larvae that were released under similar conditions. The temporal pattern of metamorphosis $S(t)$ (Fig. 4c) which results from this temperature sequence can be understood from the expression for the rate of change of S [with $D(m, t) = 0$]:

$$\frac{dS}{dt} = \frac{g(0, t - a(t)) g'(1, t) - g(1, t) g'(0, t - a) a'}{g^2(0, t - a(t))} \quad (10)$$

where g' and a' indicate rates of change with time. The rate of metamorphosis will increase (i.e. $dS/dt > 0$) only when

$$\frac{g'(1, t)}{g(1, t)} > \frac{g'(0, t - a)}{g(0, t - a)} \frac{da}{dt} \quad (11)$$

In the example, at first $S(t) = R(t)$ (Fig. 4c: A₁), because there is no change in development rate at the time of metamorphosis or at the time of release: $g'(1, t) = g'(0, t - a(t)) = 0$. When larvae are released during times of constant temperature (Fig. 4b: A₂) but metamorphose during times of increasing temperature (Fig. 4c: A₂), $g'(1, t) > 0$, but $g'(0, t - a(t)) = 0$, so $S(t)$ will increase, regardless of the value of a' . During period B₁, both release (Fig. 4b: B₁) and metamorphosis (Fig. 4c: B₁) occur in an environment with constantly increasing temperature. During this period $g'(1, t) = g'(0, t - a(t)) > 0$, and $S(t)$ will increase only if

$$\frac{da}{dt} < \frac{g(0, t - a(t))}{g(1, t)} \quad (12)$$

which is not the case here, i.e. $S(t)$ decreases with time (Fig. 4c: B₁). Larvae which are released during the period of increasing temperature (Fig. 4b: B₂) and metamorphose at a time of constant temperature (Fig. 4c: B₂), have a constant final development rate [$g'(1, t) = 0$], but initial development rate increases with time [$g'(0, t - a(t)) > 0$], hence $S(t)$ must decline. From Day 570.5, larvae are both being released (Fig. 4b: C₁) and metamorphosing (Fig. 4c: C₁) with a fast, constant development rate, and $S(t)$ has the same constant value as before the increase in temperature (Fig. 4c: A₁). These same conditions can be applied similarly to the ramp decline in temperature in Fig. 4.

When a constant, non-zero mortality rate is included in these computations (Fig. 4d), the effects of the first 2 factors in Eq. (5) remain, but the magnitude of metamorphosis is dominated by the mortality term. As development rate changes, the third term in Eq. (5) can vary over several orders of magnitude. When develop-

ment rate is slow in cold temperatures, a is large and survival is low (Fig. 4d: A). As temperature increases, a decreases and survival increases. This effect is an example of the well-known sensitivity of estimates of larval survival to development time, resulting from the fact that mortality rates of invertebrate larvae are high (e.g. Underwood & Fairweather 1989).

The final case we consider (Fig. 4e) is one in which mortality and development rates change in a similar fashion with temperature. This case is biologically reasonable; if mortality primarily is due to predation by other poikilotherms, it is likely that a change in temperature will change mortality rate similarly to its effect on development rate. As can be seen from the third factor in Eq. (5), if the effects on development and mortality rates are similar, these 2 terms cancel in the integrand, and one is left with the effects of the first 2 terms. We show an example in which mortality and development rates change in a similar, but not identical, fashion with temperature (Fig. 4e). The greatest numbers of larvae metamorphosing are those that were released and settle during a time of increasing temperature (Fig. 4e: B), which contrasts with the period of greatest metamorphosis in Fig. 4d, which occurs for larvae released and metamorphosing when temperatures are warmest (Fig. 4d: C). Note that although we did most of our computations using mortality rates that did not vary with development stage (or size), the dependence of larval survival on development rate in the model holds regardless of the size- or stage-dependence of mortality rate.

Simulation results depicting intra-annual variability

The seasonal trends in surface temperature for the 7 locations display 2 distinct patterns (Fig. 5). At the northernmost (Neah Bay and Crescent City) and southernmost (Balboa and La Jolla) locations, temperature is minimum in the winter and maximum in the summer, whereas at the central California locations (Farallon Islands and Granite Canyon) temperature is minimum in the spring, reflecting the influence of spring and summer upwelling which reduces surface

Fig. 5. Intra-annual trends in mean ($\pm$ SD) daily sea surface temperature and salinity at 7 coastal locations (a) to (g) along the west coast of the USA. The daily data were used in executing the simulation model

temperatures. Although the northernmost and the southernmost locations show similar patterns of variability, they differ in means; temperatures at Neah Bay are much colder than at any other station, whereas the 2 southern California stations have much warmer temperatures than other locations. Salinity on the other hand shows the same trend at all locations (Fig. 5), being low and variable through winter, and high and much less variable in late spring and summer. The lowest and most variable salinity values occur in the north; this clearly reflects riverine inputs associated with winter rainfall and spring snow-melt in the region.

The implied development times for each location, plotted against hatching dates from the model, reflect these temperature trends (Fig. 6). In the north, larval development times progressively become shorter for later-hatched larvae (Fig. 6a, b), as one would expect with increasing temperatures. In contrast, in central

Fig. 6. *Cancer magister*. Results of the simulation model showing intra-annual trends in mean ($\pm$ SD) development times (d) of Dungeness crab larvae hatched from December through February at 7 coastal locations (a) to (g) and for a number of years (n)

California development times are longer for late- than early-hatched larvae (Fig. 6d, e). At the 2 southern California locations, development times increase slightly for larvae that are hatched through December, and then decrease by a small amount for larvae hatched in January and February (Fig. 6f, g). However, the ranges of development times in these cases are reduced compared with other locations (note different vertical scales of the graphs). When development times are averaged over release dates and years (Fig. 7), they are longest at Neah Bay (147 d), have intermediate durations in northern and central California (112 d), and are shortest in southern California (79 d) (SNK test, $p < 0.05$; Zar 1984). For megalopae, there are no differences in mean development times among 4 of the 5 northern locations (37 d, $p > 0.05$). Crescent City has

an intermediate megalopal period (33 d), and southern California has a significantly shorter megalopal period (25 d) (SNK test, $p < 0.05$; Zar 1984).

Intra-annual variability in development times is indicated by both the maximum differences in development times and the coefficients of variation (CV), over the range of release times from December 1 to March 1 for each year (Table 4). The greatest difference within 1 year in total larval development time was 58 d at Granite Canyon, and in megalopal development was 44 d at the Farallon Islands. These 2 locations also have the greatest within-year CV estimates, indicating that regions with strong upwelling may be variable also in terms of larval biology and survival.

The mean numbers of model larvae settling during each month are shown in Fig. 8. To show how various release times contribute to settlement patterns, we compute settlement for a constant release rate from December 1 to March 1. The direct effects of temperature and salinity on survival (d_1) are represented on the left side, whereas the right side includes also the effects of other sources of natural mortality (d_2), using a constant rate of mortality. For the same hatch date, larvae metamorphose earlier in the south (February to April) than in the north (May to July). A uniform distribution of releases would also lead to metamorphosis occurring over a wider spread of dates in central California (approximately 5 mo) than in Washington or northern and southern California (3 to 3.5 mo), as would be expected from the temperature trends at those locations. This implies that settlement time is more sensitive to release time in central California than at other locations. When a constant natural mor-

Fig. 7. *Cancer magister*. Results of the simulation model showing the mean ($\pm$ SD) development times to metamorphosis, and the mean ($\pm$ SD) megalopal period, of Dungeness crab larvae at the 7 coastal locations. The results were averaged over all release dates and all years. Means with the same symbol combinations do not differ significantly

Table 4. *Cancer magister*. Results of the simulation model showing the minimum and maximum differences in development times within any 1 year for the megalopal and total larval periods of Dungeness crab, and the minimum and maximum coefficients of variation (CV = SD/mean) for mean development times within any 1 year. The number of years for which the model was executed at each site is given by n

Location	n	Intra-annual difference (d)				Intra-annual CV (%)	
		Megalopal period		Total larval period		Total larval period	
		Min. diff.	Max. diff.	Min. diff.	Max. diff.	Min.	Max.
Neah Bay	28	1 (1957, 1969)	21 (1964)	2 (1957)	44 (1986)	0.8 (1957)	9.0 (1986)
Crescent City	7	4 (1962)	19 (1985)	13 (1978)	34 (1989)	3.6 (1978)	5.5 (1962)
Trinidad Bay	3	7 (1982)	17 (1978)	8 (1986)	12 (1978)	1.8 (1986)	3.1 (1978)
Farallon Islands	44	3 (1979)	44 (1966)	2 (1979)	45 (1977)	0.6 (1979)	13.7 (1978)
Granite Canyon	18	6 (1982)	22 (1977)	5 (1972)	58 (1977)	1.2 (1982)	18.2 (1977)
Balboa	60	0 (•)	9 (1939, 1949)	0 (••)	16 (1972)	0 (••)	6.4 (1972)
La Jolla	73	0 (+)	10 (1939)	0 (++)	18 (1917)	0 (++)	7.1 (1917)

•: 1931, 1940, 1941, 1958, 1959, 1978
 ••: 1931, 1940, 1941, 1958, 1959, 1978, 1983, 1984
 +: 1940, 1941, 1958, 1959, 1978, 1983, 1986
 ++: 1927, 1930, 1940, 1941, 1958, 1959, 1961, 1978, 1981, 1983, 1984, 1986, 1987

tality rate is included in the calculations, fewer larvae are available for settlement in the northern locations than in the south (Fig. 8, right side), because long development times result in reduced numbers of survivors. In regions such as Granite Canyon, which has a wide spread of potential settlement dates (Fig. 8e), greater settlement occurs for larvae released early rather than late in the spring. Increased mortality of slow-developing late-released larvae results in reduced settlement later in the year.

Mean survival of model larvae differs among localities. When only the direct effect (d_1) of temperature and salinity is considered (Fig. 9a), survival is relatively high, except at Neah Bay where very cold temperatures in December and January result in large mortality in the model. The inclusion of other sources of mortality (d_2) reduces survival at all locations by approximately 2 orders of magnitude (Fig. 9b). Locations in southern California that have the shortest development times display the greatest survival. At Neah Bay survival is reduced by a factor of 10^{-4} . However, as discussed below, this result may be unrealistic, because it is based on the assumption of constant mortality rates.

Simulation results depicting interannual variability

Interannual variability in mean larval development times is relatively large at all locations; variability indices (VI = range/midpoint) for the mean development times among years range from 19 to 48% (Table 5). The greatest relative variability among years occurs at the 2 central California locations: Farallon

Islands (VI = 48%) and Granite Canyon (VI = 48%). Overall, the model results indicate that mean annual larval development times can range between 74 and 163 d, and mean annual megalopal development times between 24 and 47 d (Table 5). These large differences potentially may have a large influence on larval dispersal and survival.

DISCUSSION

Dungeness crab development times

There is a large amount of natural variability in the model calculations of larval development times, caused by daily variability in recorded temperature and salinity. The total range of development times from the simulation model was 74 to 182 d (Table 5). These results should be viewed in the context of the simplifying assumptions underlying the model. The 4 most important assumptions will be discussed briefly.

First, we have assumed that it is valid to apply experimental results from controlled, laboratory conditions to conditions in the natural environment. The development times measured in the laboratory may not be accurate for field conditions, but the effects of temperature and salinity on development rate probably apply.

Second, we do not allow for food-limitation in the simulation model. In general, it is believed that crustacean larvae probably are food-limited at certain times, because they rely on small zooplankton as well as phytoplankton for growth (Olson & Olson 1989). Food-dependent development rates under natural conditions should be slower than those under the food-

Fig. 8. *Cancer magister*. Results of the simulation model showing the distribution of metamorphosis dates for Dungeness crab larvae, based on a single larva released each day from December through February at each of the 7 coastal locations (a) to (g). Daily results are grouped into weeks, and averaged over the number of years for which the model was executed. Mean ($\pm$ SD) numbers of larvae settling are shown. The shaded area represents the approximate timing of the spring transition (Strub et al. 1987). The left panel shows abundances with zero natural mortality, except for that resulting from suboptimal temperatures and salinities, and the right panel shows abundances for a constant mortality rate of 0.066 d^{-1} .

replete conditions that occur in laboratory studies. A model of the effects of food on oyster *Crassostrea virginica* larval development on the southeast coast of the U.S. and the Gulf of Mexico (Dekshenieks et al. 1993) showed a 10 d decrease in the minimum larval period under good food conditions. To date, only a limited amount of information is available on diets and feeding of Dungeness crab larvae, most of this resulting from culture studies using unnatural diets (Poole 1966, Lough 1976, Hartman 1977, Hartman & Letterman 1978). Dungeness crab larvae probably are omnivorous (Lough 1976); they feed on both plants and

animals in culture situations (Hartman & Letterman 1978). Unfed larvae of Dungeness crab will starve within 10 d, most of the mortality occurring within 5 to 6 d (Hartman & Letterman 1978). It is not known what effect sub-optimal food concentrations have on Dungeness crab larvae, although size differences that have been noted among different 'cohorts' of larvae have been attributed partly to differences in diets (Dinnel et al. 1993). In the case of king crab *Paralithodes camtschatica* (Tilesius), Paul et al. (1989) showed that first-feeding larvae could starve if the right food were not available in sufficient concentrations, but that reduced food apparently did not affect development times of the larvae that survived. This latter result can be contrasted with the increased development times that were found during food-limited growth of 5 invertebrate species from coastal waters of the San Juan Islands, Washington, USA (Paulay et al. 1985), and for larvae of the barnacle *Balanus eburneus* (Scheltema & Williams 1982).

Our third assumption in the simulation model is that settlement would occur as soon as the larvae are ready to metamorphose. However, in many species larval settlement can be delayed until the larvae encounter a suitable substratum. For example, competent larvae of the sea hare *Bursatella leachii* can stay in the plankton for up to 5 mo in search of a suitable settlement area (Paige 1988). These above 3 assumptions all should result in the model underestimating the total larval period.

Finally, we have assumed that the sea surface temperatures and salinities measured at coastal locations would be similar to those experienced by larvae at sea. We know very little about the distribution of Dungeness crab larvae in the plankton (e.g. Hobbs et al. 1992), and even less about the paths followed by individual larvae or cohorts. Even if this information were available, we do not have any temperature and salinity measurements with the required spatial and temporal coverage. However, as our understanding of larval behaviour and small and mesoscale physical processes progresses, modelling studies can make a start at addressing some of these problems (e.g. Botsford et al. 1994).

Table 5. *Cancer magister*. Results of the simulation model showing interannual variability in projected development times of Dungeness crab larvae under varying natural temperature-salinity conditions at localities along the U.S. west coast. The ranges of mean, minimum and maximum development times among all years are shown. Variability indices (VI = range/midpoint) for the mean total development times are presented as percentages

Locality	Years	n	Megalopal development (d)			Total larval development (d)			
			Means	Minima	Maxima	Means	VI (%)	Minima	Maxima
Neah Bay	1956–1989	28	33–42	30–41	34–53	133–163	20	119–151	134–182
Crescent City	1962–1989	7	30–38	26–35	33–48	99–132	29	91–119	109–140
Trinidad Bay	1978–1986	3	35–41	30–36	43–47	105–127	19	101–120	113–131
Farallon Islands	1926–1989	44	27–45	24–41	31–68	82–134	48	80–129	89–137
Granite Canyon	1972–1989	18	28–47	24–42	36–51	81–134	48	76–126	96–138
Balboa	1930–1989	60	24–29	24–26	25–33	75–91	21	75–84	75–96
La Jolla	1917–1989	73	24–28	24–25	25–34	74–89	19	74–83	75–96

Given the assumptions above, we can assess the extent to which the simulation model provides 'realistic' estimates under naturally varying hydrographical conditions, by comparing model results with estimates based on field observations. For Oregon, USA, Poole (1966) estimated a larval development time of 128 to 158 d, based on the time from when females first release larvae to when juvenile crabs first are observed. This estimate is similar to the model results for Neah Bay (Fig. 7, Table 4). Lough (1976) estimated a larval period of 130 d (89 to 143 d) for central Oregon,

based on the times of first appearance of zoeae and last appearances of megalopae in the plankton. This estimate is intermediate between the model results for Neah Bay and those for central and northern California (Fig. 7, Table 4). Reilly (1983) calculated a larval period of 105 to 125 d for central and northern California, based also on the first and last occurrences of different stages of larvae in the plankton for samples from 1949 to 1980; this compares well with model results which predict a mean larval period of 112 d for this region. For the megalopal stage, a laboratory study in central California, using local larvae and seawater temperatures that cycled between 13 and 17.5 °C, indicated that durations should be approximately 22 to 30 d (Hatfield 1983). This is similar to the model results for southern California (Fig. 7), where mean temperatures more closely resemble the experimental temperatures (Fig. 5f, g) than do those of central California (Fig. 5d, e). The model therefore provides estimates of development times that are similar to those estimated from field observations. The advantage of the model estimates is that they not only indicate the relative magnitudes and variability we should expect in nature, but also some of the factors causing the variability.

The simulation results indicate that there should be latitudinal differences in development times of Dungeness crab larvae, caused by much slower development in the cold northern regions than in the warm south (Fig. 7). In modelling studies similar to this one, latitudinal differences have been demonstrated in the patterns and amounts of spawning (Hofmann et al. 1992b) and larval development (Dekshenieks et al. 1993) of oyster *Crassostrea virginica* populations on the south-east coast of the USA and in the Gulf of Mexico. In these 2 studies, the latitudinal differences also were related primarily to changes in sea temperature, with the planktonic duration of oyster larvae decreasing from north to south (Dekshenieks et al. 1993). For Dungeness crab larvae, the larval period also should decrease from north to south.

Fig. 9. *Cancer magister*. Results of the simulation model showing the mean survival to metamorphosis of Dungeness crab larvae, based on a single larva released each day from December through February at each of the 7 coastal locations. (a) Simulations with zero natural mortality, except for that caused by suboptimal temperatures and salinities; (b) simulations with a constant mortality rate of 0.066 d⁻¹

Timing of metamorphosis

Environmental variables often display pronounced seasonal patterns on a time scale that encompasses the total larval period of many marine organisms. Temperature is known to be an important environmental factor affecting developmental duration of marine crustaceans (Scheltema 1986). In contrast, salinity has been found to have little effect on development (e.g. Fig. 2), although usually it affects survival (Harms 1992). Larvae released at different times through the season experience different environmental conditions, which affect their developmental and survival rates and hence the fraction surviving to metamorphose, as well as the date of metamorphosis.

The timing of metamorphosis is important to fish or invertebrate larval success because the resources available at metamorphosis (food or space) typically vary seasonally. Dungeness crab larvae at the center of the species' distribution (in California and Oregon) may be affected by the timing of the spring transition, which heralds the start of the upwelling season. During upwelling periods, there is net offshore transport of surface waters, which may reduce the ability of planktonic larvae to move to the coast to settle. The spring transition has a large alongshore scale, and occurs over a 3 to 10 d period each year (approximately late March to mid April), starting in the south and moving north (Strub et al. 1987). The range of dates for the spring transition between 1971 and 1983 is shown in Fig. 8 (hatched area). At stations in Washington and northern California (Fig. 8a, b, c), most larvae probably will not have metamorphosed at the time of the spring transition. Northern California is a region of intense upwelling (Largier et al. 1993), and this has important implications for larval settlement and recruitment in the area. Megalopae are strong swimmers (Jacoby 1982), and they may rely on a combination of vertical migration out of surface waters, and their own swimming abilities to return to shore (Jamieson et al. 1989, Hobbs et al. 1992). Aspects of larval transport are being addressed further in separate studies (e.g. Botsford et al. 1994).

The importance of the timing of metamorphosis is a component of the oldest as well as the most recent hypotheses of recruitment success in marine populations. Hjort's (1914) 'critical period' hypothesis states that recruitment success of fish depends on (1) whether suitable food is available at the end of the yolk-sac stage, and (2) whether larvae have been transported to areas of favourable biological and physical conditions. Cushing (1975) has elaborated on Hjort's first point with his 'match/mismatch' hypothesis, and Hjort's second point is related to Sinclair's (1988) 'member/vagrant' hypothesis. Here we have shown how the

timing of metamorphosis can be affected by changes in development rates, caused by temperature (and salinity) changes through the larval period. Some of these effects are non-trivial.

In general, the analytical model indicates that at least 3 factors should be considered when interpreting patterns observed in the timing of metamorphosis. Of the 3 factors, the one that most commonly is invoked is the pattern of release of eggs and/or larvae. For example, a bimodal pattern of recruitment of bluefish *Pomatomus saltatrix* on the east coast of the USA has been inferred to result from 2 distinct spawning events (Kendall & Walford 1979, Chiarella & Conover 1990, but cf. Hare & Cowen 1993). We urge caution in considering only a single causal factor, because changes in environmental variables (like temperature) also can affect patterns of metamorphosis. Our model indicates that these effects can occur through changes solely in development rates, and also through relative changes in both development and mortality rates. We have shown how simple, linear trends in temperature can result in final patterns of metamorphosis that differ substantially from the release pattern (Fig. 4). When realistic temperatures were used in the Dungeness crab simulation model, settlement patterns varied greatly, including skewed (Fig. 8a, left panel) and bimodal (Fig. 8c, left panel) distributions, even though the initial release pattern was constant over time.

The simulation results indicate that settlement of Dungeness crab megalopae should occur earlier in the south than in the north (Fig. 8). Megalopae in northern Washington should have peak abundances in the plankton during May and June, whereas those in California should be most abundant during April and May. These predictions are consistent with field evidence. Hobbs et al. (1992) present quasi-synoptic plots of megalopal distributions during 4 years. During 2 cruises in May (1981 and 1982) most of the megalopae occurred in the northern regions of the study (Oregon and Washington), whereas during a cruise in April–May (1985), most of the megalopae occurred in central and northern California. Competent larvae have been collected from Drakes Bay (central California) in May (Poole 1966), and in central Oregon larvae have been found in the plankton until late May (Lough 1976, Dinnel et al. 1993). In contrast, in the waters off British Columbia, Canada, megalopae are found from April to August, with a peak in May–June (Jamieson & Phillips 1990, Dinnel et al. 1993), and in the Puget Sound Basin (Washington) large megalopae originating from further south tend to settle in early spring, whereas small megalopae which originate in the basin settle during early summer (Orensanz & Gallucci 1988, Dinnel et al. 1993).

Fig. 10. *Cancer magister*. Results of the simulation model showing a change in mean ($\pm$ SD) overall survival of Dungeness crab larvae for the Neah Bay simulations when release dates are shifted by 1 mo. (a) Release of a single larva per day from 1 January to 31 March; (b) release of a single larva per day from 1 December to 28 February

Experimental studies have shown also that Dungeness crab spawning and hatching are delayed by cold temperatures (Wild 1980, Shirley et al. 1987). Temperature-based delays in hatching will enhance the differences between localities, shifting settlement dates to later in the year. For example, when the hatching period in the model was shifted by 1 mo for Neah Bay (Fig. 10), a shift in settlement dates occurred. Along the Washington coast hatching generally occurs in January and February (Cleaver 1949), and off the west coast of Vancouver Island and in Puget Sound most hatching occurs in January through March (Jamieson & Phillips 1990, Dinnel et al. 1993). Peak hatching of Dungeness crab larvae occurs in late January in Oregon (Lough 1976). Changing the hatching dates of larvae in the model may also change the overall survival. Larval survival was increased by a factor of 4 at Neah Bay under conditions of constant natural mortality (Fig. 10), because environmental conditions were more favourable for the larvae later than earlier in the year.

Survival of larvae

Temperature measurements used in the simulation model only rarely were warm enough ($>20^{\circ}\text{C}$) or cold enough ($\leq 6^{\circ}\text{C}$) (Reed 1969, Sulkin & McKeen 1989) to kill all the larvae. Large-scale mortalities occurred in 8 of the 28 years modelled for Neah Bay, and at the Farallon Islands a single measured temperature of 5.1°C in February 1966 killed all larvae in the model that were hatched before that date. It is not known whether

such large-scale mortality occurs in the field. Salinities also were rarely at lethal values in the simulation model. Salinities less than 15 ppt are dangerous for Dungeness crab larvae (Reed 1969), and salinities of 20 ppt are tolerated only if temperatures are favourable (10 to 17°C ; Reed 1969, Sulkin & McKeen 1989). Larvae occurring in the northern regions probably are exposed to variable-salinity water, because of a large influx of fresh water from rivers during winter and early spring (Fig. 5). This water also tends to be very cold (Fig. 5a). It is possible that larvae would occur in such cold, low-salinity features only if they were released into them directly, in which case they may not be as severely stressed as larvae which are advected from warmer and/or more saline water. It also is possible that larvae hatched in northern regions (e.g. the Alaskan Dungeness crabs) are genetically more tolerant of the cold than those from further south. However, the observed occurrence of megalopae in waters off Washington, putatively derived from adults in more southerly regions (DeBrosse et al. 1990, Dinnel et al. 1993), indicates that some Dungeness crab larvae may encounter lethal temperatures during their dispersal. The extent to which the larvae may become acclimated to changing environmental temperatures and salinities needs to be assessed.

In contrast to the situation in the northern part of the study region where cold temperatures delay spawning, hatching and settlement (Shirley et al. 1987), the southernmost locality in the model (La Jolla) has mean temperatures in July that exceed 20°C . These warm temperatures should be lethal for Dungeness crab larvae (Fig. 3). Thus towards the extremes of the species' distribution there are windows of favourable temperature conditions during which complete larval development can occur.

In addition to these direct temperature and salinity effects on survival, temperature can affect larval survival indirectly by changing the duration of the larval period. The analytical model has shown that the length of the larval period is the primary factor determining survival and the pattern of metamorphosis (Fig. 4d), if we assume that the mortality rate is constant. The model is very sensitive to this assumption. When constant mortality is included in the model, and when temperature and salinity are within the tolerance ranges of the larvae (i.e. excluding episodes of 100 % mortality), the mean numbers of larvae surviving were reduced by a minimum factor of 110 at La Jolla (where larval periods were shortest) and a maximum factor of 4400 at Neah Bay (where larval periods were longest) (Fig. 9). From these results, it would be easy to conclude that overall survival of larvae should be greatest in warm waters. This is not necessarily the case. If mortality rate varies with the environment in a way similar

to that of development rate, a very different pattern emerges (Fig. 4e) than if mortality rates are constant (Fig. 4d). In this case, the settlement pattern is determined by the changing ratios of development rates at release and settlement times. It is probable that as development rates increase in water where the temperature is increasing, so too should the predation rates on the larvae increase. This modifies the commonly held belief that a small change in development rate, which leads to a change in stage duration, results in a large change in numbers surviving the larval stage (because of the high mortality rate) (e.g. Underwood & Fairweather 1989). We require better understanding of the relative change in developmental and mortality rates with changes in the environment, because this is an important factor determining total numbers of larvae that survive.

One of the reasons the model is so sensitive to the assumption of constant mortality rates is that invertebrate larvae in general experience high mortality during their larval stages. The instantaneous mortality rate of Dungeness crab larvae (0.066 d^{-1}) is of a similar order of magnitude to estimates for other invertebrate larvae. For king crabs in the Bering Sea, instantaneous mortality rates have been estimated as 0.095 d^{-1} for *Paralithodes camtschatica* and 0.075 d^{-1} for *P. platypus* (Wainwright et al. 1991), and estimates of instantaneous mortality rates for planktonic larvae of other benthic marine invertebrates (Rumrill 1990) range from 0.0754 d^{-1} for *Polydora ciliata* to 0.8018 d^{-1} for the bivalve *Mya arenaria*. Larvae of *Cancer pagurus* were estimated to have mortality rates of 0.006 d^{-1} , based on field sampling studies off the northeast coast of England (Nichols et al. 1982). This last study underestimated mortality rates by about an order of magnitude because of advection of larvae into the study area, which highlights the problems involved in trying to derive estimates of natural mortality in the field.

A related, simplifying assumption with regard to mortality rates is that these are constant with stage (size). In experimental studies with Dungeness crab larvae, the largest mortality occurred during the first and last zoeal stages (Poole 1966, Sulkin & McKeen 1989), and estimates of field predation rates on the larvae of the sand dollar *Dendraster excentricus* are larger for early than late stages (Pennington et al. 1986). Such stage-dependent effects may be particularly important in a variable environment, where a short period of unfavourable conditions early in larval development can have a large impact on overall survival to metamorphosis. The wide range of theoretical possibilities for estimating survival underscores the importance of careful measurements of larval responses, rather than premature assumptions (e.g. assuming constant mortality rate with time).

Interannual differences

Changes in global climate are believed to be causing measurable changes in physical conditions of coastal oceans. In the California Current system, such changes may be manifested as an intensification of coastal upwelling as a result of increased intensity of along-shore winds (Bakun 1990), and in a possible increased frequency of ENSO events, as indicated by an increase in mean temperatures in the northeast Pacific (Cole & McLain 1990, Roemmich 1992). To predict the potential impacts of such changes on local populations requires information on the manner in which the physical environment affects organisms, and the response of organisms to varying environmental conditions. Sea temperatures and salinities vary with latitude, with time of year, and interannually. Model results have highlighted latitudinal differences in intra-annual patterns, with long development times and delayed settlement in the north compared with the south. There also is much interannual variability in model results, with large differences in mean development times among years (Table 4). The Cancridae have the longest known larval development times of all families of brachyuran decapods (Hines 1986). The combination of long larval periods and the variable physical environment of the California Current system should result in dispersal of Dungeness crab larvae being controlled primarily through physical processes (Jackson 1986), although these physical influences may be modified through larval behaviour (Sulkin 1984, Shanks 1986, Hobbs et al. 1992).

The model results indicate that warmer than usual years, as occur during ENSO events, should result in fast development of larvae. Warm temperatures could decrease larval survival because warm temperatures can be lethal (Fig. 3), or because of increasing predation rates (Fig. 4e). Low chlorophyll concentrations (Strub et al. 1990) and reduced biomasses of zooplankton (Mullin & Conversi 1988) have been found in the California Current during ENSO years. At these times, food, not temperature, may be the most important variable determining survival of Dungeness crab larvae. These considerations emphasize that the growth, development and metamorphosis of meroplanktonic larvae, such as those of the Dungeness crab, need to be considered in relation to the 3-dimensional structure and dynamics of their physical and biological environment. The environment affects the larvae, their food organisms and their predators.

In this study we have tackled only 1 aspect of the biological-physical interactions that influence Dungeness crab larval development and survival. In other studies we will link the larval development model to a 3-dimensional physical oceanographic model, to ad-

dress aspects of transport and behaviour. However, to address questions about the important processes governing variability in larval recruitment satisfactorily, a better understanding of the larvae in their natural environment is required through field programs.

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