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# The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations

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**Abstract**—We synthesize the results of several modeling studies that address the influence of variability in larval transport and survival on the dynamics of marine metapopulations distributed along a coast. Two important benthic invertebrates in the California Current System (CCS), the Dungeness crab and the red sea urchin, are used as examples of the way in which physical oceanographic conditions can influence stability, synchrony and persistence of meroplanktonic metapopulations. We first explore population dynamics of subpopulations and metapopulations. Even without environmental forcing, isolated local subpopulations with density-dependence can vary on time scales roughly twice the generation time at high adult survival, shifting to annual time scales at low survivals. The high frequency behavior is not seen in models of the Dungeness crab, because of their high adult survival rates. Metapopulations with density-dependent recruitment and deterministic larval dispersal fluctuate in an asynchronous fashion. Along the coast, abundance varies on spatial scales which increase with dispersal distance. Coastwide, synchronous, random environmental variability tends to synchronize these metapopulations. Climate change could cause a long-term increase or decrease in mean larval survival, which in this model leads to greater synchrony or extinction respectively. Spatially managed metapopulations of red sea urchins go extinct when distances between harvest refugia become greater than the scale of larval dispersal. All assessments of population dynamics indicate that metapopulation behavior in general depends critically on the temporal and spatial nature of larval dispersal, which is largely determined by physical oceanographic conditions. We therefore explore physical influences on larval dispersal patterns. Observed trends in temperature and salinity applied to laboratory-determined responses indicate that natural variability in temperature and salinity can lead to variability in larval development period on interannual (50%), intra-annual (20%) and latitudinal (200%) scales. Variability in development period significantly influences larval survival and, thus, net transport. Larval drifters that undertake diel vertical migration in a primitive equation model of coastal circulation (SPEM) demonstrate the importance of vertical migration in determining horizontal transport. Empirically derived estimates of the effects of wind forcing on larval

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transport of vertically migrating larvae (wind drift when near the surface and Ekman transport below the surface) match cross-shelf distributions in 4 years of existing larval data. We use a one-dimensional advection–diffusion model, which includes intra-annual timing of cross-shelf flows in the CCS, to explore the combined effects on settlement of: (1) temperature- and salinity-dependent development and survival rates and (2) possible horizontal transport due to vertical migration of crab larvae. Natural variability in temperature, wind forcing, and the timing of the spring transition can cause the observed variability in recruitment. We conclude that understanding the dynamics of coastally distributed metapopulations in response to physically-induced variability in larval dispersal will be a critical step in assessing the effects of climate change on marine populations.

## INTRODUCTION

Significant physical changes in the coastal ocean are anticipated in response to changes in global climate. Clearly, to project the impact of climate change on biological productivity in these waters, we must understand how marine populations respond to changes in their physical environment. Many harvested populations are meroplanktonic metapopulations, i.e. they consist of a number of subpopulations of adults distributed along a coast, linked by dispersal of a planktonic larval stage. The subpopulations consists of juveniles and adults of various ages and sizes, which often are relatively sedentary compared to the larval stage. The physical environment affects metapopulation dynamics through its influence on the fraction of larvae that disperse and settle at various points along the coast.

Despite the potential impact of physical oceanographic conditions on meroplanktonic metapopulations, we have a poor understanding of their possible dynamic consequences. Such an understanding will require knowledge of both the physical environment and the biological populations, as well as the interactive combination of the two. For many systems we have a reasonable understanding of the coastal circulation that would underly transport and survival of meroplankton (e.g. as in the California Current), but models that can predict currents and hydrography only recently have become available (Haidvogel *et al.*, 1991a,b; Pares-Sierra and O'Brien, 1989; Tremblay *et al.*, 1994; Werner *et al.*, 1993).

Even if a complete description of coastal circulation and hydrography were available to compute larval transport and survival, it is not clear that we would be able to interpret the population dynamic consequences. Studies to date of the dynamics of populations distributed along coastlines do not comprehensively account for all important aspects of age, size, and spatial structure in conjunction with physical forcing. Most models and empirical analyses of the influence of the physical oceanographic environment on coastal populations treat the population as a single, local population, ignoring the spatial distribution of individuals along the coast and interactions over space due to dispersal. To our knowledge, no models or empirical studies have explicitly addressed a spatially distributed population with age or size structure and spatio-temporal environmental forcing. Trends toward a comprehensive, realistic description of physically forced, spatially distributed, age structured populations include a two-dimensional model of advection and diffusion of larvae from a population of identical individuals distributed along a coastline (Possingham and Roughgarden, 1990) and a model of an age-structured population distributed along a coastline with a common larval pool (Roughgarden and Iwasa, 1986). In conservation biology, models based on the concept of a metapopulation (Levins, 1970; Pulliam, 1988) have been used to study extinction and persistence of spatially distributed populations subject to environmental forcing (e.g. Quinn and Hastings, 1987; Harrison and Quinn, 1989).

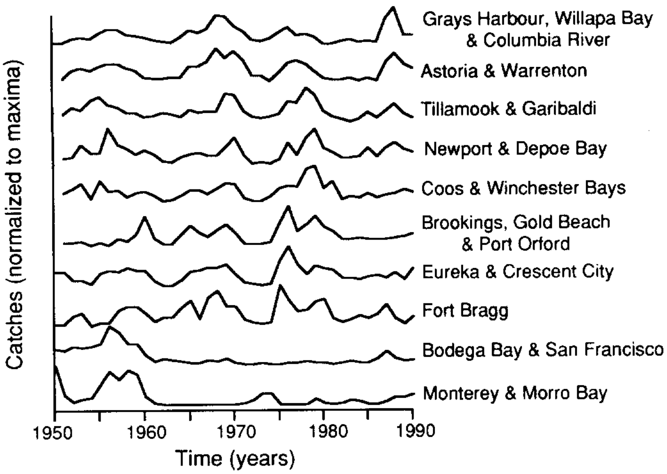

Fig. 1. Dungeness crab catch. Because of intense fishing pressure in this male only, size limited fishery, catch is a reasonable proxy for recruitment (METHOT and BOTSFORD, 1982). Note the cyclic variability from Eureka and Crescent City north, and the episodic shift to low levels near 1960 at lower latitudes.

Here we assess the dynamic implications of physically induced variability in the dispersing larval or juvenile stage of meroplanktonic metapopulations. We focus first on the dynamics of meroplanktonic metapopulations subject to general spatio-temperal variability in larval transport and survival, demonstrating the importance of knowing the underlying physical processes. We then describe the results of several different approaches to gaining an understanding of those processes.

As a first step in a larger suite of studies, we confine ourselves here to meroplanktonic metapopulations in which adults are relatively sedentary. There are a number of important benthic invertebrates to which our results would apply directly, including crustaceans, such as crabs, lobsters, shrimp, and barnacles; molluscs, such as abalone, oysters, clams, mussels, scallops, limpets and chitons; and echinoderms, such as sea cucumbers, sea stars and sea urchins [see CADDY (1989) for examples of harvested invertebrates]. Vertebrate examples to which results would apply directly include fish in which there is negligible adult migration, such as many reef fish. These results also can be considered a first step in better understanding of the dynamics of meroplanktonic fish populations in which older juveniles and adults migrate, in addition to larvae dispersing.

We demonstrate our general results using two California Current species as examples, the Dungeness crab (*Cancer magister*) and the red sea urchin (*Strongylocentrotus franciscanus*). Both species are distributed along the Pacific coast of North America and have meroplanktonic larvae. These two species span a range of attributes of benthic invertebrates. The Dungeness crab has large, active larvae that may disperse long distances, and adults that live on deep, sandy bottoms. Red sea urchins have small, relatively passive larvae, probably with more local dispersal, and adults that inhabit the shallow rocky subtidal.

Much past research has focused on the cause of cycles in Dungeness crab abundance that appear synchronous from northern California to the U.S.–Canada border (Fig. 1) (reviewed in BOTSFORD *et al.*, 1989). Physical influences on the 4-month larval stage, which

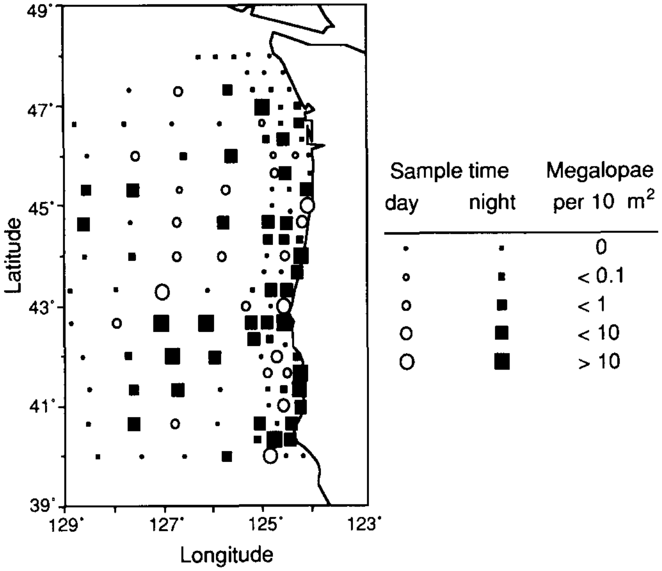

Fig. 2. The distribution of Dungeness crab megalopae during a cruise from 19 April to 10 May in 1985. These estimates are based on neuston and oblique Bongo tows from 5 to 360 km offshore, and are adjusted to account for the mortality which would have occurred during the cruise (see Hobbs *et al.*, 1992 for details).

occurs in the plankton from January through June, have been implicated as causes of the cycles through correlations between physical variables and catch. Analyses of population models have identified the characteristics of density-dependent recruitment mechanisms and life histories that are conducive to cycles and their consequent features, such as their temporal period. Both the correlation analyses and the modeling studies have treated the crab population as either a single unit or several independent units (usually divided along state or international borders). The dynamic consequences of the metapopulation structure have been neither accounted for nor explored.

Though they have not been considered in a metapopulation context, the nature of physical influences on the larval stage of Dungeness crab, and possible density-dependence in recruitment are both of current interest. For example, a topical issue of direct relevance to larval transport is whether the substantial numbers of larvae which are found several hundred km offshore (see Fig. 2 for an example) eventually return to settle in the nearshore environment or are simply larval wastage (Lough, 1976; Reilly, 1983; Hobbs *et al.*, 1992; McConnaughey *et al.*, 1992). Another issue, the cause of the observed cycles, has been evaluated by comparing the actual catch record with catch records generated by models with hypothetical density-dependent recruitment mechanisms, such as cannibalism, an egg predator worm, and density-dependent fecundity. For example, the period of cycles expected from each of these mechanisms has been compared to the observed period of 10 years (Botsford *et al.*, 1989). The studies of metapopulation dynamics described here shed further light on the effects of physical forcing on the Dungeness crab and provide guidance for future sampling.

The red sea urchin is harvested intensively from California to Washington. Urchins in general are notorious for dramatic shifts in population level (Estes *et al.*, 1989; Elner and

VADAS, 1990), and exhibit several Allee effects in recruitment (i.e. recruitment drops to zero before population abundance goes to zero) (LEVITAN *et al.*, 1992; TEGNER and DAYTON, 1977). Less is known of the larval phase of the red sea urchin than the Dungeness crab, but recruitment variability of a congener, the purple sea urchin, has been associated with differing oceanographic conditions near headlands (EBERT and RUSSEL, 1988). Also, patterns of wind-driven upwelling near headlands have been shown to influence red sea urchin settlement (WING *et al.*, submitted). In addition to an effect on recruitment, the varying physical environment is known to influence feeding, metabolism and reproduction in this species (DENNY and SHIBATA, 1989; LEVITAN *et al.*, 1992; PATTERSON, 1992; WING *et al.*, 1993; WING and PATTERSON, 1993). Because proposed management policies for red sea urchins involve either permanent refuges from harvest (QUINN *et al.*, 1993) or rotating spatial closures (BOTSFORD *et al.*, in press), spatial characteristics of larval dispersal along the coast are of direct practical value for management of this species.

The ultimate goal of the work herein is to describe the influence of climate change on populations in the California Current System. Projection of change in meroplanktonic populations due to future changes in climate is limited by the difficulty in predicting the physical effects of climate change on the coastal ocean. Because of poorly understood ocean-atmosphere coupling [reviewed by CHAHINE (1992)] and the coarse spatial scales of current global climate models (GCMs), it is not possible to predict detailed changes in a boundary current region such as the California Current. However, there is some empirical basis for expecting increased upwelling-favorable winds; an increasing trend has been noted, as might be expected from increased warming of coastal land masses (BAKUN, 1990; HSIEH and BOER, 1992). Also, indirect evidence from Cd/Ca ratios in foraminifera indicate that the cooling of North America over the past 4,000 years has been accompanied by decreasing upwelling (VAN GEEN *et al.*, 1992). There is also some empirical evidence of increasing ocean temperatures in the northeastern Pacific (COLE and MCLAIN, 1989; ROEMMICH, 1992). Preliminary studies with a dynamic ENSO prediction model indicate that a warmer ocean, as might result from global climate change, could increase the frequency and intensity of ENSO events (ZEBIAK and CANE, 1991). It is possible also that the increase in tropical sea surface temperature could generate more intense storms than at present (MEARNS *et al.*, 1990), although the predictions of generally increased temporal variation easily could be artefacts of missing feedbacks in existing GCMs (GOODESS and PALUTIKOF, 1992).

Both the Dungeness crab and the red sea urchin are good candidates to demonstrate the potential influences of climate change on species in the coastal ocean. The strength and pattern of upwelling winds have been implicated in the recruitment of each (HOBBS *et al.*, 1992; WING *et al.*, submitted), and larval transport of at least the Dungeness crab may be influenced by changes in alongshore flows accompanying ENSO events (*cf.* MCCONNAUGHEY *et al.*, 1992). ENSO events are also known to have a dramatic effect on kelp biomass in California kelp beds and therefore on the sea urchin populations associated with them (DAYTON and TEGNER, 1990; TEGNER and DAYTON, 1991). Episodic shifts in population abundance on decadal or century time scales (e.g. in clupeids, SOUTAR and ISAACS, 1974) are possible indicators of past changes in climate. The central California populations of Dungeness crabs provides an example of these episodic shifts in equilibrium, having collapsed to low levels in the late 1950s, and only recently shown some signs of recovery.

In this paper, we synthesize the results of a number of related modeling studies aimed at improving our understanding of the dynamic behavior of spatially distributed metapopulations with age structure and a dispersive larval stage in a variable physical environment. We first describe the physical environment we are using as an example, the California Current System, emphasizing the features that may be important to dispersal and survival of meroplanktonic larvae. We then present a general model which uses the physically modulated larval dispersal to link age-structured subpopulations of a metapopulation distributed along a coastline. The general problem separates naturally into two subproblems on different temporal and spatial scales. Dynamic behavior of this coupled physical/biological system reflects the influences of physical conditions on individual organisms on daily (or less) time scales and 1 m (or less) spatial scales, while these individuals are members of populations (or metapopulations) that extend over thousands of km with important temporal fluctuations on a scale of decades or more. We present the metapopulation results first. Analyses of the dynamic behavior of many age-structured populations linked via temporally and spatially varying dispersal of a larval stage reveal the dependence of metapopulation dynamics on the nature of the dispersal. These results lead naturally into a description of our investigations of larval–physical interactions. We examine how larval characteristics, such as metabolic demands and vertical migration, in the presence of realistic flow fields and hydrographic conditions lead to transport, survival and successful recruitment. The complexity of this problem requires an approach in which we analyze component parts of it and understand their dynamics before we are in a position to assemble these to attempt to understand the system as a whole.

## PHYSICAL SETTING

The California Current System (CCS) refers to the system of currents found at mid-latitude in the eastern North Pacific. As an eastern boundary current similar to systems in the eastern South Pacific (Humboldt Current), Southeast Atlantic (Benguela Current) and Northeast Atlantic (Canary Current), it is an eastern, equatorward-flowing arm of a basin-scale anticyclonic gyre. The CCS spans over 20° latitude stretching from the poleward-flowing Alaskan Current in the north to the poleward-flowing Costa Rica Current in the south. The California Current itself is the general equatorward flow which exhibits a typical velocity of the order of 0.1 m $s^{-1}$ and extends several hundred km west of the North American coast (Hickey, 1989). It is strongest in summer, and in winter it moves offshore, being replaced by the poleward Davidson Current in the east, particularly in the northern parts of the CCS (Hickey, 1979). A poleward undercurrent exists throughout the year but varies seasonally, and apparently is strongest in summer. In addition to seasonal variations, the CCS has been shown to exhibit significant interannual fluctuations associated with ENSO events.

In early spring, the North Pacific high pressure system moves north to mid-latitudes, and the mean wind forcing in the CCS shifts from northward to southward, an event referred to as the spring transition (Strub *et al.*, 1987). This southward wind results in offshore Ekman transport near-surface, upwelling of cold water at the coast and a strong southward flow over the shelf. The winds and resultant currents are strongest and most persistent off central California (Nelson, 1977; Hickey, 1979; Largier *et al.*, 1993; Dorman and Winant, submitted). Coldest water, highest nutrient concentrations and largest productivity are found nearshore, decreasing offshore.

After the spring transition, a large number of mesoscale structures ($L \sim 100$ km, $T \sim$ weeks–months) is superimposed on this large-scale structure ($L \sim 1000$ km,

$T \sim$ seasons–years). These jets, eddies and meanders which appear to develop as instabilities in the large-scale flows (STRUB *et al.*, 1991), exhibit velocities which are much larger than that of the general southward flow. KOSRO *et al.* (1991) and SWENSON *et al.* (1992) have observed velocities in excess of 1.0 m $s^{-1}$ in summer. Specific recurrent features are related to coastal promontories, such as the jet–filament off Point Arena. In addition to the more obvious offshore transport of coastal waters, highlighted by cold water in AVHRR imagery, this system of jets and eddies should also lead to substantial onshore transport of offshore waters at some points.

Nested within the large-scale CCS is a shelf circulation system which is primarily forced by wind and, in places, by freshwater outflow. These forced circulation features are comparable in size to the offshore mesoscale structures. Freshwater outflow, particularly from the Columbia River, results in buoyant plumes which tend to flow north in winter, under the influence of the earth's rotation, and south in summer, being driven by southward winds. Elsewhere in the CCS, the circulation over the shelf and upper slope is dominated by wind forcing, both local and remote (i.e. due to propagating coastal, trapped waves). In winter, the strongest winds are associated with propagating storm systems. Although wind speeds are large during these winter storms, the winds are variable and only a weak mean velocity is observed—northward off Washington and southward off California (NELSON, 1977; DORMAN and WINANT, submitted). The resultant mean currents are similar, although over the inner shelf off California a northward flow is observed in the fall, presumably due to a northward pressure gradient (HICKEY and POLA, 1983; LARGIER *et al.*, 1993).

In the presence of capes, upwelling varies substantially alongshore (LARGIER *et al.*, 1993; ROSENFELD *et al.*, in press). In particular, one can expect enhanced upwelling and strong southward flow at capes and suppressed upwelling and weak southward flow upstream and downstream of capes (e.g. Cape Mendocino). Further, if there is a substantial area of weak winds downstream of a cape (i.e. in the lee of the cape), an "upwelling shadow" can be found, as in northern Monterey Bay (GRAHAM *et al.*, 1992). Associated with these patterns of upwelling, due to inhomogeneous wind forcing or current–topography interactions, are local onshore and offshore flows that are in addition to those associated with the field of mesoscale features found farther offshore in the larger-scale California Current (e.g. MAGNELL *et al.*, 1990; Rosenfeld *et al.*, in press). This coastal (i.e. shelf) circulation exhibits greatest variability in the seasonal and synoptic meteorological frequency bands, but interannual fluctuations also are expected (e.g. WING *et al.*, submitted). When upwelling winds relax, shelf waters tend to move northward; in addition to polward barotropic forcing, baroclinic forcing may occur, as observed most strikingly in the northward propagation of warm buoyant water that had collected in an upwelling shadow south of Point Reyes (SEND *et al.*, 1987; LARGIER *et al.*, 1993; WING *et al.*, submitted).

Close inshore there is a third boundary system, the nearshore system that is characterized by a combination of forcing by waves, tides and patchy winds as well as an absence of stratification and associated vertical circulation. Extending about a kilometer offshore, this small-scale system is strongly affected by topography and includes many recirculating cells in which residence times may be large. This nearshore region is probably only important to those larvae that are spawned or that settle in this region (e.g. barnacles, kelp bed organisms such as the red sea urchin).

In summary, the CCS contains three nested systems that may be important to the dispersal of meroplanktonic larvae. At the largest scale (oceanic) is the CCS itself, within the CCS is the wind-driven shelf circulation and within the shelf circulation is the nearshore circulation. The relevance of each scale of circulation to larvae of a particular species will depend on the locations of spawning and settlement as well as on the timing and duration of the planktonic period. Little is known of what controls the exchange between the different scales of circulation. How could larvae dispersed offshore in the CCS return to the coastal and nearshore systems? Can some larvae traverse frontal structures? What is the relative importance of eddy diffusion processes, localized cross-shore flows (jets, filaments, squirts, rips, etc.) and episodic, shoreward shifts in the positions of fronts (e.g. see FARRELL *et al.*, 1991; ROUGHGARDEN *et al.*, 1991). To what extent is alongshore transport important in producing the observed patterns of larval distribution and settlement (*cf.* JOHNSON *et al.*, 1986; MCCONNAUGHEY *et al.*, 1992, WING *et al.*, submitted)? The answers to these questions and their effect on the population dynamics of merplanktonic species along the coast are the larger scope of questions addressed here.

## GENERAL MODEL

A comprehensive model of the effects of physical forcing on a meroplanktonic population would require both a realistic description of the influence of the physical environment (e.g. winds, currents, temperature) on the larval phase, and a description of the consequences of that variability on the adult metapopulation. However, to avoid a prohibitive level of complexity, the description of the physical–biological interactions during the larval stage can be decoupled from the description of juvenile and adult population dynamics. This decoupling is possible because many temperate zone meroplanktonic species reproduce only once each year with a larval phase lasting less than a year. Physically and biologically realistic models of planktonic larval life are appropriately formulated on short time scales (e.g. days or months), whereas annual to decadal or longer time scales are appropriate for analysis of age structured models of adult populations. The results of the larval analyses can be phenomenologically summarized at each point, for each year, as a distribution of net dispersal distances along the coast. The population level analyses explore population dynamics of spatially distributed populations with this distribution of survival and dispersal varying in time and space.

In general, the larval population over the period of the year during which larvae are in the plankton can be described in terms of a density of larvae at each position $(x,y,z)$ and size $s$ at each time $t, l(x, y, z, s, t)$. This distribution ideally would be obtained by solving a continuity equation formulation for biological aspects such as mortality and growth rates, coupled to a hydrodynamic model which provided the spatially and temporally varying environment that influenced growth, mortality and position. We could write this as

$$\frac{\partial}{\partial t} l(x, y, z, s, t) = F[x, y, z, s, t] \tag{1}$$

where $F[x, y, z, s, t]$ is a function describing flow in the $x$, $y$ and $z$ spatial dimensions on a physical basis (currents) and a biological basis (e.g. larval behavior such as vertical migration), as well as larval growth and mortality, which also involve physical influences. As a practical matter, the numerical solution to such a model probably would be obtained by embedding models of the growth and survival of individual larvae as active (i.e.

swimming or vertically migrating) particles in a coastal circulation model. For each year a solution would be obtained for a coastal boundary condition which generated larvae during the first part of the larval season, and absorbed larvae at the end of the larval season.

Solutions to such a model for each year can be expressed as the fraction of individuals reproduced at location $y'$ that survives and disperses to location $y$ in year $t$. We refer to this summary of biological–physical interactions over the larval period of each year as the *dispersal kernel*, $p(y, y', t)$. A number of such summaries for each of a number of years then becomes the annually varying spatial forcing function for the general metapopulation model. The metapopulation model consists of discrete-time (1-year time interval) local models of juvenile and adult subpopulations that are linked by a dispersal function which describes movement between them. Recruitment per unit coastline at each point $y$ along the coast, $R(y,t)$, is the sum (integral) of all larvae dispersing to that point from other locations ($y'$) along the coast. All larvae are produced by local adult egg production and are subject to density-dependent recruitment, both before and after dispersal,

$$R(y,t) = f[C(y,t); y]\int_{y_l}^{y_u} p(y,y',t)\, g[W(y',t)y']\, B(y',t)\, \mathrm{d}y'. \tag{2a}$$

Taking each term in ontogenetic order (which reads from right to left) the spatial density (i.e. per unit space) of total egg production at location $y'$, $B(y',t)$, is the standard weighted sum over all age classes.

$$B(y',t) = \sum_{l}^{a_u} b(a)\, n(y',a,t) \tag{2b}$$

where, $a_u$ is the maximum age, $b(a)$ is individual fecundity, and $n(y', a, t)$ is the density per unit space of individuals of age $a$ at time $t$. The fraction of these that survive to be dispersed from location $y'$ is the density-dependent survival, $g[W(y',t);\ y']$, which depends on location $y'$ and a weighted sum of the adult population density,

$$W(y',t) = \sum_{l}^{a_u} w(a)\, n(y',a,t). \tag{2c}$$

$W(y',t)$ is the effective density of the adult population as it effects pre-dispersal survival, and w(a) is the contribution of an individual of age a to the pre-dispersal density-dependence. For example, if pre-disposal density-dependence were due to reduced prey leading to reduced fecundity, $w(a)$ might be metabolic demand for food at age $a$.

The fraction of individuals which have been reproduced and have survived pre-dispersal density-dependent survival at location $y'$, that then survive and are transported to location $y$ is reflected in the dispersal kernal $p(y, y', t)$. The density of potential recruits in the interval $(y, y + \mathrm{d}y)$ at time $t + 1$ is then an integral of the dispersed individuals over all possible origins (at time $t$), in which $y_l$ and $y_u$ are the lower and upper limits of the single spatial dimension over which the population is distributed. The argument $t$ represents the fact that this dispersal relationship varies interannually.

The fraction of dispersed individuals that arrive at point $y$ from all points $y'$ which is actually recruited is determined by the post-dispersal density-dependent survival function,

$f[C(y,t);\ y]$. The weighted sum, $C(y,t)$ is the total effective population size for the post-settlement survival function,

$$C(y,t) = \sum_{l}^{a_u} c(a)n(y,a,t), \tag{2d}$$

where $c(a)$ is the contribution of an individual of age $a$ to the post-dispersal density-dependent mechanism. For example, if post-dispersal density-dependence were due to cannibalism on newly settled individuals, $c(a)$ would be the relative numbers cannibalized by an individual at age $a$.

The rest of this model is a standard discrete-time, age-structured model with time-independent survival to age $a$, $\sigma(a)$, at each location,

$$\begin{aligned} n(y, a+1, t+1) &= n(y,a,t)\sigma(a) \quad && a > 1 \\ n(y, 1, r+1) &= R(y,t) && a = 1. \end{aligned} \tag{3}$$

These expressions merely move individuals from one age to the next each year, with no effects of environment or density on juvenile and adult survival.

With the general problem posed and the model presented, it is useful to briefly note the meagerness of our understanding of the dynamics of this system. Population biologists have a moderately good understanding of the behavior of local populations with density-dependent recruitment and age structure, but our knowledge of the explicitly nonlinear behavior is weak. There is little understanding of population behavior when a number of these populations is linked via larval dispersal, even if the dispersal is deterministic. On the larval–physical side, we know that meroplanktonic larvae and their food and predators are transported and otherwise influenced by currents and hydrographic conditions in the coastal ocean, yet we have only a vague understanding of broadscale characteristics of the physical features, especially as they affect larvae. Consequently, we cannot currently predict the fate of larvae released into a system such as the California Current.

With this meager understanding as a starting point, we next proceed on the metapopulation side to attempt to determine the important population dynamic consequences of various aspects of net larval dispersal [equation (2)], and on the larval–physical side to attempt to determine the ways in which oceanographic conditions in the California Current might affect meroplanktonic larvae [equation (1)]. We first describe the behavior of a spatially distributed population with age structure and density-dependent recruitment subject to temporal variability in dispersal of young (i.e. time-varying dispersal kernels). We then describe progress in determining the spatial and temporal variability in dispersal that would result from varying physical oceanographic conditions in the California Current (i.e. processes leading to the dispersal kernels).

## POPULATION DYNAMICS

The aspects of coastal, meroplanktonic metapopulation dynamics in which we are primarily interested are the amplitude of fluctuations in abundance that can be expected, their associated time scales, whether they are synchronous along the coast, and the conditions under which populations will persist. Uncertainty regarding the degree to which the environment affects these populations, implies we need to understand the dynamics of unforced, deterministic models. Further, behavior of environmentally forced models often is best understood in the context of deterministic behavior. To interpret and understand the behavior of metapopulation models such as equation (2) with randomly varying dispersal kernels, it is first necessary to know the behavior to be expected from a local subpopulation by itself.

### *Local subpopulations*

A local subpopulation can be described by ignoring the spatial dimension in equation (2)

$$R(t) = f[C(t)]\,B(t) \tag{4}$$

where we have combined pre-dispersal and post-dispersal density dependence into a single function $f$, assuming they both depend on age in the same way (*cf.* HOBBS and BOTSFORD, 1989). We are interested in the how time scales and amplitudes of fluctuations from this model population depend on life history characteristics such as growth rates, reproductive rates, survival rates, and the strength of density-dependence.

Some aspects of the dynamic behavior of the local subpopulation model are fairly well understood, based primarily on stability analyses of linearized versions, and simulation (BOTSFORD and WICKHAM, 1978; CUSHING, 1980; DIEKMANN *et al.*, 1986; LEVIN, 1981; LEVIN and GOODYEAR, 1980; MCKELVEY *et al.*, 1980; RICKER, 1954; RORRES, 1976; ROUGHGARDEN *et al.*, 1986; TULJAPURKHAR, 1987). This model can be locally unstable producing quasi-periodic limit cycles with period roughly twice the generation time. Whether this happens depends on the age structure as it affects recruitment, and the normalized slope of the recruitment survival function $f$ at equilibrium. The age structure is determined by the weighting functions $b(a)$ and $c(a)$ and survival to each age, combined to reflect the positive effect of reproduction ($b(a)$) and the negative effect of density-dependence ($c(a)$). A broad, flat age structure at low ages typically is more stable than a narrow, peaked age distribution at high ages. The normalized slope of $f$ reflects the strength of density-dependence, the sensitivity of survival to density. A steep normalized slope of recruitment survival is less stable than a shallow slope.

Nonlinear behavior of the local subpopulation model is especially important when the slope of the recruitment survival function is very steep or the strength of environmental forcing is great, but it is currently poorly understood (GUCKENHEIMER *et al.*, 1977; LEVIN and GOODYEAR, 1980; LEVIN, 1981). Some aspects of nonlinear behavior have been studied using the delayed recruitment model, which is the simplest general approximation to age structured models with density-dependent recruitment (CLARK, 1976; BOTSFORD, 1991).

$$N_{t+l} = h[N_{t-T}] + sN_t \tag{5}$$

where $N$ is total number of reproducing adults, $T$ is the age of maturation, $s$ is annual survival, and $h[N]$ is *a* the number of recruits that result from an adult stock $N$ (i.e. a stock-recruitment function). Stability of a linearized version of this model decreases as the slope of the function $h[.]$ becomes steeper, the age of first maturity increases, or survival decreases (CLARK, 1976; BOTSFORD, 1991). These characteristics would be expected from the general description of stability above (e.g. increasing the age of maturity and decreasing adult survival would make the age structure more narrow and peaked at higher ages). Non-linear behavior of this model without age structure (i.e. with adult survival $s$ = 0) involves cycles of period 2, followed by period doubling, then chaotic behavior as the slope of the recruitment survival function is increased (*cf.* MAY and OSTER, 1976). However, at values of maturation delay and survival which are more typical of harvested populations (i.e. $T = 3$ and $s = 0.6$), the model is much more stable, and the expected limit cycles of period twice the generation time are more common (BOTSFORD, 1991).

To be able to interpret fluctuations in abundance of subpopulations, we need to know when they are going to produce cyclic fluctuations of period twice the mean generation time and whether this behavior will break down leading to cycles on longer time scales (i.e. period doubling) which appear erratic, and possibly are chaotic. We also need to know the amplitude of fluctuations to be expected for various values of life history parameters. Because many coastal populations are harvested, which involves an age-selective change in mortality rate, it is critical to know how changes in adult age structure affect population dynamics.

To understand the deterministic behavior of age-structured populations with density-dependent recruitment, we examined the behavior of the delayed recruitment model [equation (7)] over a range of typical parameter values (HIGGINS *et al.*, in prep.). We used the Ricker stock-recruitment function to represent the function $h$.

$$h[N] = \exp\,[r(1 - N_t/K)] \qquad (6)$$

where $r$ and $K$ are constants. For any age of maturation $T$, when adult survival $s$ is zero, as the slope parameter $r$ is varied from zero to higher values, this model displays the well-known period doubling route to chaos with initial period $T$. However, for adult survivals in the range from 0.4 to 0.8 the population typically exhibits the cycles of period roughly twice the mean age which would be expected from the linearized analysis. Our research has focused on how model populations switch between these two kinds of behavior as values of population parameters are varied.

The way in which the amplitude of fluctuations and their associated time scales depend on adult survival can be portrayed graphically in a plot of the values of population abundance which occur for each value of survival (i.e. a bifurcation diagram), a plot of the largest Lyapunov exponent, and time series of abundance for specific values of survival (Fig. 3). For a maturation age of 3, $r = 3.25$ and $K = 1$, abundance is periodic or quasi-periodic with period near twice the mean age when survival is greater than about 0.36 [Fig. 3(a)]. For lower values of survival, chaotic behavior is indicated bythe largest Lyapunov exponent being positive [e.g. Fig. 3(b),(d), and (e)]. However, even the time series exhibiting chaotic behavior appear regular, on time scales near twice the mean generation time [Fig. 3(d) and (e)] (see HASTINGS *et al.*, 1993) for an accessible explanation of chaos in a population context). Variability on shorter time scales appears for survivals less than 0.15. For other ages of maturation, model behavior involves similar patterns; cycles of period roughly twice the mean age occur at high values of annual survival and less predictable, high frequency behavior occurs at low values of survival (see HIGGINS *et al.*, in prep. for further details).

These general results raise the question of whether the Dungeness crab population could exhibit similar high frequency behavior. To test this, we evaluated the nonlinear behavior of an age-structured Dungeness crab model (BOTSFORD *et al.*, in prep.). Several different hypothetical density-dependent recruitment mechanisms were used to determine whether behavior was of the observed period and magnitude. With high and low equilibrium values as well as with male only and two-sex harvest, either periodic or quasiperiodic cycles were produced with period roughly that predicted by the results from

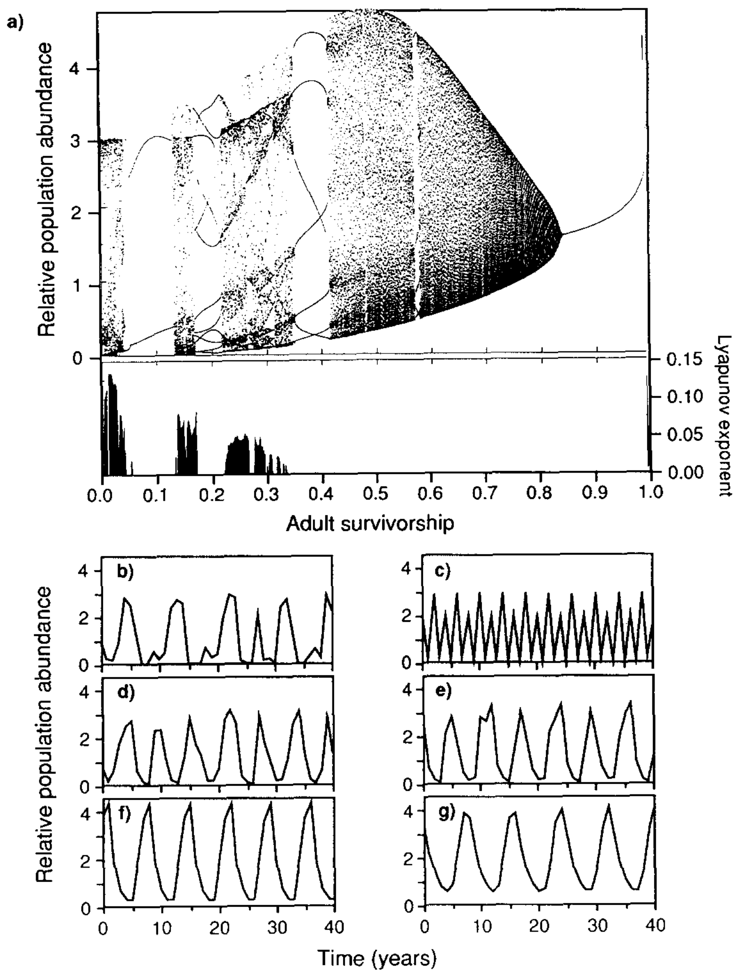

Fig. 3. (a) A bifurcation diagram for a delayed recruitment model with a Ricker stock-recruitment function with $r = 3.25$, $K = 1.0$, and $T = 3$, as adult survivorship ($S$) is varied from 0.0 to 1.0. The lower plot is the value of the largest Lyapunov exponent, which indicates chaotic behavior when greater than zero. (b)–(g). Time series that result from the model in (a) for specific values of adult survival: (b) $S = 0.0$; (c) $S = 0.05$; (d) $S = 0.15$; (e) $S = 0.23$; (f) $S = 0.39$; (g) $S = 0.6$.

the linearized model. However, the amplitude varied widely; high:low abundance ratios ranged from 0.5 to 0.05 (the ratio reflected in the crab catch data is roughly 0.1, an order of magnitude). The age structure corresponding to values of $c(a)$ based on crab cannibalism data had the broadest range of amplitudes [Fig. 4(a)]. Lower equilibrium values of $f$[.] also lead to higher amplitude ranges (see Botsford *et al.*, in prep. for further details). Figs 4(a) and (b) demonstrate how the amplitude of the fluctuations can vary with the normalized slope of the recruitment survival function, but that the behavior of this model is long period cycles over a wide range of slopes.

Little is known of the response of age structured models with density-dependent recruitment to random environments. For small environmental fluctuations, a linearized

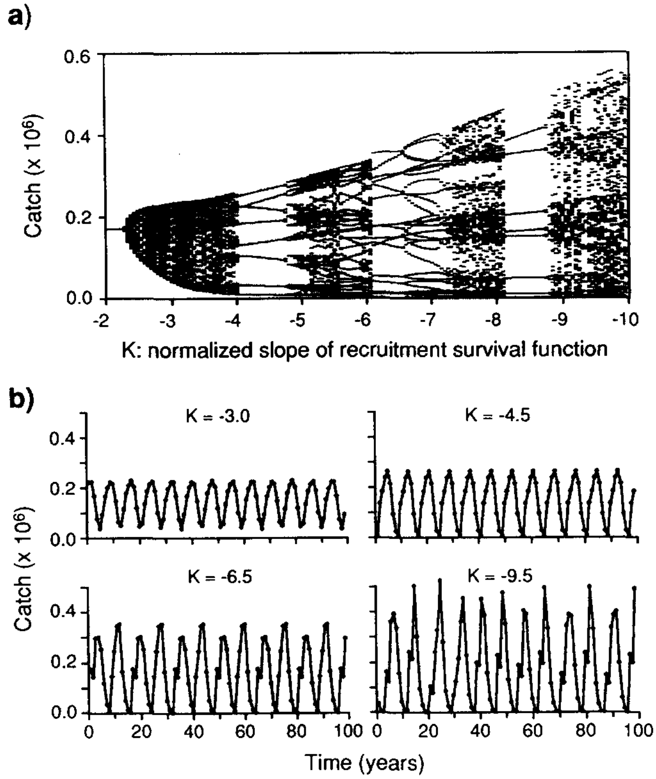

Fig. 4. (a) A bifurcation diagram indicating the magnitude and period of cyclic catch as the normalized slope of the recruitment survival function $K$ is varied for a model with equilibrium recruitment survival of 0.1. (b) Time series from the model in (a) for various values of the normalized slope of the recruitment survival function.

model does reasonably well at predicting the effect of multiplying recruitment by symmetrically distributed random noise. In models that are not quite unstable, as the model approaches instability it responds selectively to frequencies in the environmental noise which are close to the period of cycles in the unstable model, in a resonance phenomenon (BOTSFORD, 1986; *cf.* HORWOOD and SHEPHERD, 1981; REED, 1983).

The true nature of environmental forcing on populations in the California Current may not be reflected in these small amplitude approximations, but rather may involve occasional very good or bad years. For example, the year 1963 was a good year for recruitment of several groundfish along the west coast of the U.S. We therefore examined the response of a Dungeness crab model to exceptionally good and bad years (BOTSFORD *et al.*, in prep.). Years of exceptionally good recruitment survival (i.e. multiplied by 10) could depress recruitment for extended periods of time (10–20 years) (Fig. 5), whereas years of reduced survival (multiplied by 0.1) had little long-lasting effect. The impact of years of good survival depended on effective lifetime fecundity [see BOTSFORD *et al.* (in prep.) for details].

These results have implications for the response to physical forcing. Fluctuations in the physical environment, and their effects on marine populations often are referred to as

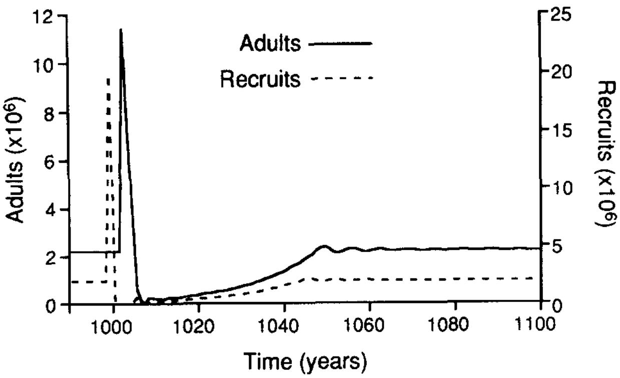

Fig. 5. The response of recruitment and adult population size to a single year of exceptionally good recruitment survival (i.e. 10 times better than normal).

occurring at a certain frequency [e.g. cycles in ENSO events (Quinn *et al.*, 1978 and others, *cf.* Ware, 1991)]. These may not be strictly periodic (i.e. repeating themselves every *T* years), but rather may occur at a certain average rate (i.e. a Poisson process). Simulations of both periodic and Poisson distributed forcing indicate that models which are susceptible to long-term suppression of recruitment do not respond substantially to environmental forcing on time scales that are shorter than the period of suppression of recruitment. For example, if recruitment is suppressed for a period of 10 years by an exceptionally good year, the population will not be as affected by forcing in which good years appear more frequently than 10 years as it will be forcing on time scales greater than 10 years [see Botsford *et al.* (in prep.) for further details].

### *Metapopulation behavior*

We can now analyze the behavior of a number of age-structured subpopulations distributed along a coastline and linked by temporally and spatially varying larval dispersal [equation (1)]. The analysis of this metapopulation also must proceed from the simplest deterministic models to more complex nonlinear, stochastic models. Because these models incorporate aspects of SPace, AGE structure and TIme, we refer to them as SPAGETI models. We assess whether the single population results still hold when a number of populations are linked along a coastline, and explore ways to relate them to metapopulation behavior.

One of the first steps taken to characterize dynamic behavior of SPAGETI models was analysis of a linearized version of equation (1) with a Gaussian shaped deterministic dispersal kernel and no spatial variation in habitat (Hobbs and Botsford, submitted). Although the results of linearized analyses are limited in that they apply over only a limited part of the parameter space, in this case they were informative. They enabled us to build on what we knew about the influence of life history characteristics on stability of subpopulations, and to incorporate characteristics of the dispersal kernel to see how both sets of characteristics determined stability. In addition to stability, we also were able to describe an additional aspect of population behavior: synchrony along the coastline.

By making some mild assumptions, we were able to construct a useful graphical

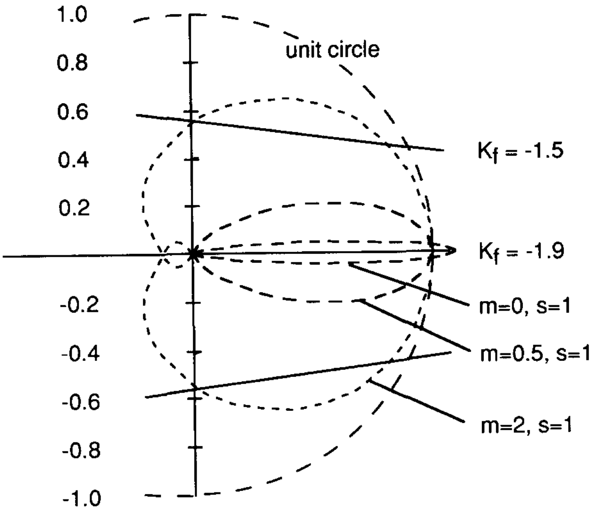

Fig. 6. For a metapopulation with a deterministic Gaussian dispersal kernel along an infinite coastline, plots of the values of spatial eigenvalues that would make the population unstable for two different values of recruitment survival slope (i.e. $K_f = -1.5$ and $-1.9$). Also plotted are the locus of spatial eigenvalues associated with dispersal kernels with three different values of net alongshore advection: means of 0, 0.5 and 2.0 times the standard deviation. The metapopulation is unstable for combinations for which the latter type of line is anywhere farther from the origin than the former.

indication of how life history parameters and dispersal characteristics influence stability and synchrony of a SPAGETI model (Fig. 6) (HOBBS and BOTSFORD, submitted). We assumed the solution was separable into spatial and temporal components, and that density-dependence did not vary along the coast. For each set of life history parameters and slopes of recruitment survival functions, we plotted lines such as the solid lines in Fig. 6 labeled $K_f = -1.5$ and $K_f = -1.9$. These lines represent the inherent stability of a subpopulation with a specific age structure and slope of the density-dependent recruitment survival function ($K_f$). When these lines are close to the origin (0,0), the metapopulation is inherently less stable. The lines in Fig. 6 correspond to Dungeness crab life histories, and normalized slopes of the post dispersal recruitment survival function $f[.]$ of $-1.5$ and $-1.9$. For each dispersal kernel we also constructed lines such as the dashed lines in Fig. 6 corresponding to varying degrees of alongshore advection [i.e. values of the mean ($m$) of the dispersal kernel]. These dashed lines represent the stabilizing or destabilizing effects of linking the subpopulations together in specific ways. When they are far from the origin, the metapopulation is stable.

Stability of the metapopulation is determined by the relationship between the two types of lines in Fig. 6. In cases where the solid line that reflects the dispersal characteristics is farther from the origin than the dashed line that reflects the life history characteristics at any point(s), the metapopulation is unstable and cyclic or some other nonconstant behavior will be observed. For example, if subpopulations with Dungeness crab life history characteristics and a slope of post-dispersal density-dependent recruitment of $-1.5$ are linked by Gaussian shaped dispersal, with no advection or advection along the coast, of 0.5 standard deviations, the metapopulation will be stable, whereas if the advection is 2 standard deviations, the metapopulation will not be stable.

Figure 6 illustrates a general characteristic of stability; adding spatial structure to a model will not be stabilizing. If a subpopulation is unstable, linking a number of subpopulations together will not produce stable populations. In Fig. 6, as $K_f$ becomes more negative indicating less stable subpopulations, the life history line moves toward the abscissa, eventually lying on the abscissa for the value of $K_f$ at which the subpopulation becomes unstable. Obviously, no dispersal lines can lie inside that set of life history lines. This general result has been obtained in several other similar models of spatially distributed population dynamics (LEVIN, 1974; HASTINGS, 1992).

In addition to stability, we can also determine whether variability in an unstable population will be synchronous along the coast. When the point (1, 0), which is always on the dispersal line, is outside the life history lines, the populations will be synchronous along the coast. If not, the solutions will involve non-zero spatial frequencies, and populations will not be synchronous along the coast. For example, in Fig. 6, the metapopulation will be unstable if the pre-dispersal recruitment survival functions in the subpopulations ($K_f$) have a slope of $-1.5$ and the mean dispersal along the coast ($m$) is 2 standard deviations (of the dispersal kernel), and these unstable solutions will not be synchronous.

The results obtained from this linearized analysis have been verified by simulation, but as was the case for local subpopulations in the previous section, there is no guarantee that hey tell us much about highly non-linear behavior (i.e., when values of $K_f$ are extremely negative).

To understand the non-linear behavior of equation (1), we began with a simple form: semelparous (i.e. species which reproduce only once in their lifetime) populations with Ricker stock-recruitment relationships, linked by a Gaussian shaped dispersal kernel of various widths. A particularly surprising general aspect of the behavior is the very long time it takes such a spatially structured system to approach its long-term behavior if nonlinear effects are important. HASTINGS and HIGGINS (1994) found that typically, not only does it take a very long time to reach the final dynamics (more than 10,000 years!), but the nature of the transient dynamics can be very different from the final dynamics. The transients can be essentially chaotic with the final dynamics simply periodic or vice versa. One implication of this result is that analyses of long-term dynamics can be misleading, and that sudden changes in the form of dynamics may be inherent properties of the system, not necessarily due to changes caused by human activities or climate.

We also have investigated numerically the nonlinear behavior of a number of age-structured Dungeness crab population models linked by Gaussian-shaped dispersal kernels along a finite coastline. These SPAGETI simulations have revealed an unexpected and potentially important consequence of the combination of density-dependent recruitment, age structure and larval dispersal. Simulations involving a number of populations (51) distributed along a coastline of a certain length (here 1000 km) when dispersal is not important (i.e. when the populations are independent), is as expected. Each subpopulation behaves as it would alone, and there is no tendency to become synchronous [Fig. 7(a)]. However, when dispersal is added, as the dispersal distance increases in the presence of moderate to strong density-dependent recruitment (i.e. normalized slope of the recruitment survival function, $K_f = -2$ or $-3$), the subpopulations along the coast become synchronized in such a way that several subpopulations in a row are in phase, but are of the opposite phase from the next several subpopulations [Fig. 7(b)–(d)]. Note that as the width of the dispersal kernel increases, so does the scale of the alongshore spatial variability. The lack of spatial synchrony would be expected from the graphical analysis of

Fig. 6, as discussed above, in cases where instability is indicated at non-zero spatial frequencies.

Because we are ultimately interested in environmentally forced populations, we briefly explore the consequences of random variability for this kind of behavior. We added a moderate amount of synchronous coastwide variability by multiplying recruitment survival of all subpopulations by a uniformly distributed random number between 0.5 and 1.5 each year (Fig. 8). This random environment does not appear to alter substantially the spatio-temporal pattern of abundance, except in the case in which there is no dispersal [Fig. 8(a)]. Coastwide synchronous environmental forcing appears to have the greatest synchronizing effect on populations with little or no dispersal. A necessary caveat on this conclusion is that our interpretation thus far is based solely on these two-dimensional plots which indicate only discrete amplitudes.

We can take this explorative analysis one step further by simulating a hypothetical influence of climate change. We introduced a shift to high or low recruitment survival rates, such as might be caused by a change in physical mechanisms that either retain larvae near the coast or promote return to nearshore settlement areas. For metapopulations with no dispersal, when mean recruitment survival is increased, populations appear less synchronized [Fig. 9(a)]. When mean recruitment survival is decreased, mean abundance is reduced, but the degree of synchrony and the general spatio-temporal pattern do not appear to change [Fig. 9(b)]. For metapopulations with dispersal over long distances, increasing mean recruitment survival appears to reduce synchrony slightly [Fig. 9(c)]. A decrease in mean recruitment survival causes the metapopulation to go extinct in this example [Fig. 9(d)]. Extinction occurs in a metapopulation with large dispersal distances, but not in a population with small dispersal distances because more larvae are lost at the boundaries of the population distribution.

In addition to stability and synchrony, we also have investigated persistence of coastal metapopulations (QUINN *et al.*, 1993). There is a growing interest in managing coastal metapopulations by setting aside certain areas as refuges from harvest to provide sources of larvae to seed other areas. In the context of the red sea urchin, which has strong Allee effects in recruitment, we demonstrated that spatial management of meroplanktonic species can have significant biological benefits over traditional methods by preventing population crashes in exploited populations, and ensuring sustainable catches in the face of harvesting intensities that are high or difficult to control. A model of a sea urchin metapopulation with harvest and unharvested refuges along the coast showed that refugia substantially slowed the decline of overfished populations and prevented ultimate extinction, even under intense fishing pressure. The performance of this scheme, in particular the allowable spacing between refugia depended critically on average larval dispersal distance (QUINN *et al.*, 1993).

## PHYSICAL INFLUENCES—LARVAL TRANSPORT AND SURVIVAL

Although the results regarding metapopulation behavior have identified some important unexpected aspects, they are nonetheless limited, focussing initially on deterministic dispersal kernels, with only explorative evaluation of possible environmental variability. However, they clearly show that metapopulation behavior depends strongly on the nature of larval dispersal patterns. The graphical analysis of the combined influences of life history characteristics and dispersal characteristics showed a dependence on net advection

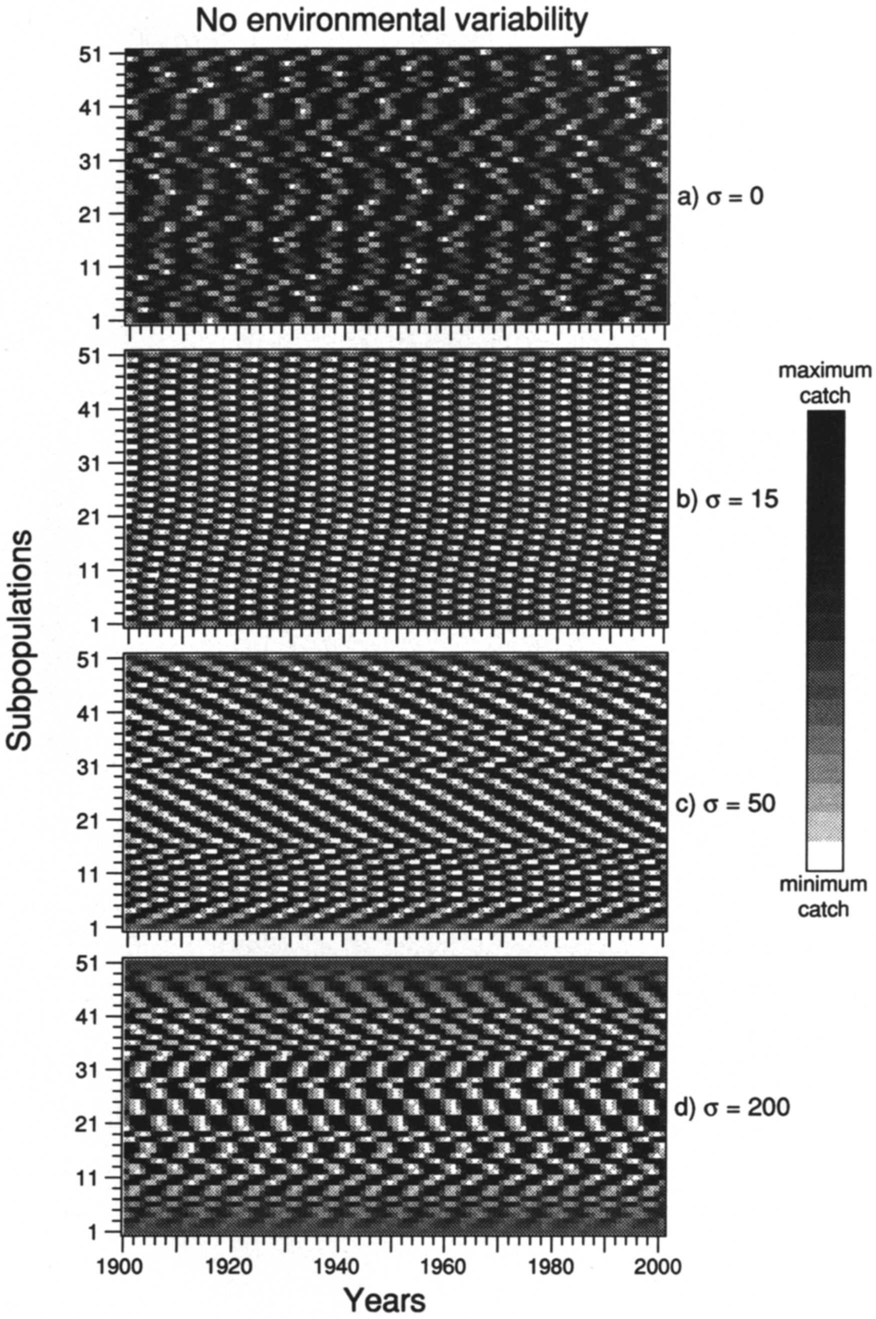

Fig. 7. Normalized catches from 51 age-structured Dungeness crab subpopulations with slope of density-dependent post-dispersal recruitment survival $K_f = -3$, linked along a 1000 km coastline by deterministic, Gaussian-shaped dispersal (mean = 0, standard deviation = $\sigma$). (a) Starting from a random spatial pattern with no dispersal (i.e. $\sigma = 0$), populations remain asynchronous. (b) With the same random start, but a small amount of dispersal ($\sigma = 15$ km), the populations begin to lock into a spatial pattern which becomes more pronounced at increased dispersal of $\sigma = 50$ km (c), but changes at high dispersal of $\sigma = 200$ km (d).

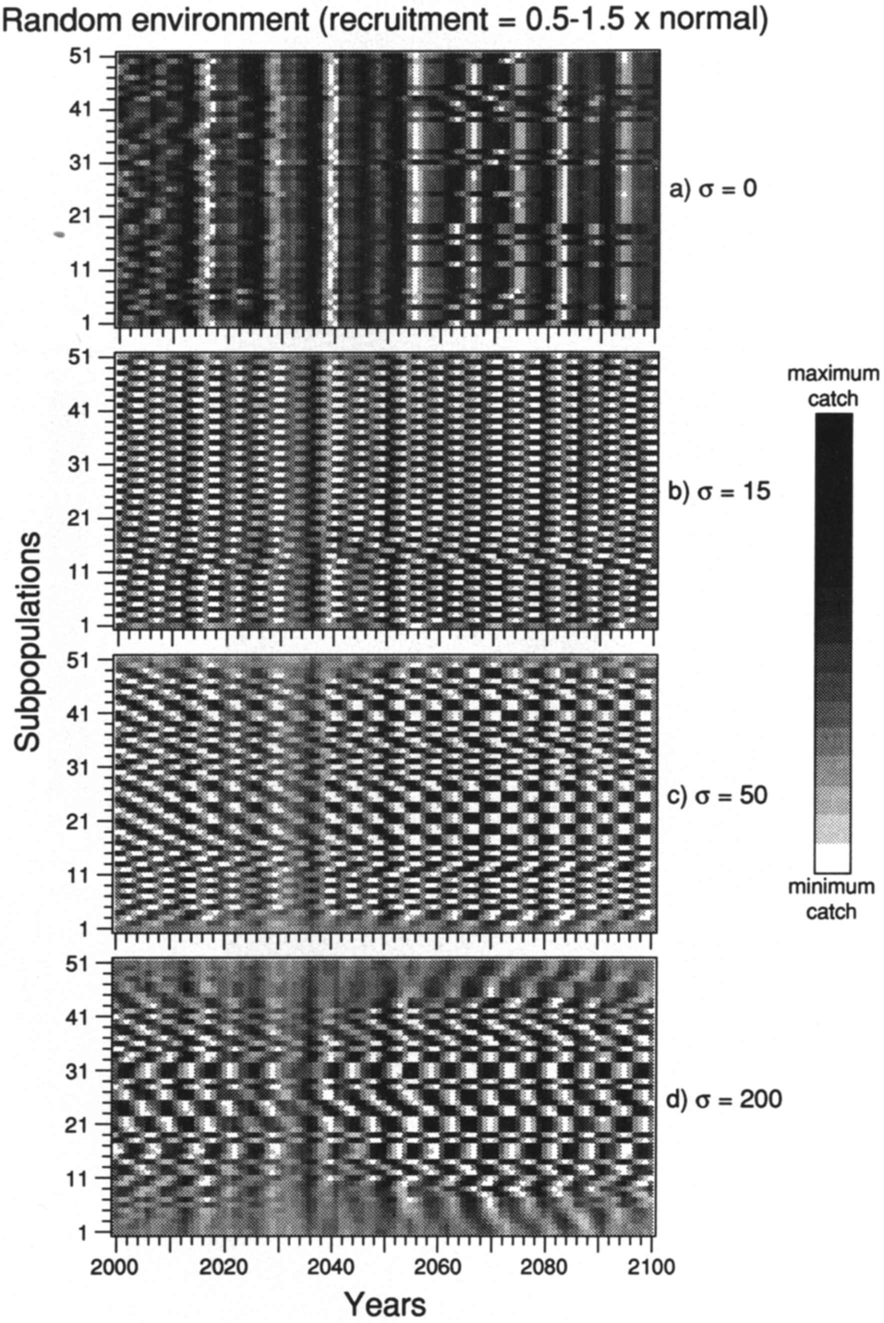

Fig. 8. Normalized catches from 51 age-structured Dungeness crab subpopulations with slope of density-dependent post-dispersal recruitment survival $K_f = -3$, linked along a 1000 km coastline by deterministic, Gaussian-shaped dispersal (mean = 0, standard deviation = $\sigma$), with a random environment which multiplies recruitment along the coast by a uniform random variable (between 0.5 and 1.5) each year. (a) No dispersal, $\sigma = 0$; (b) $\sigma = 15$ km; (c) $\sigma = 50$ km; (d) $\sigma = 200$ km.

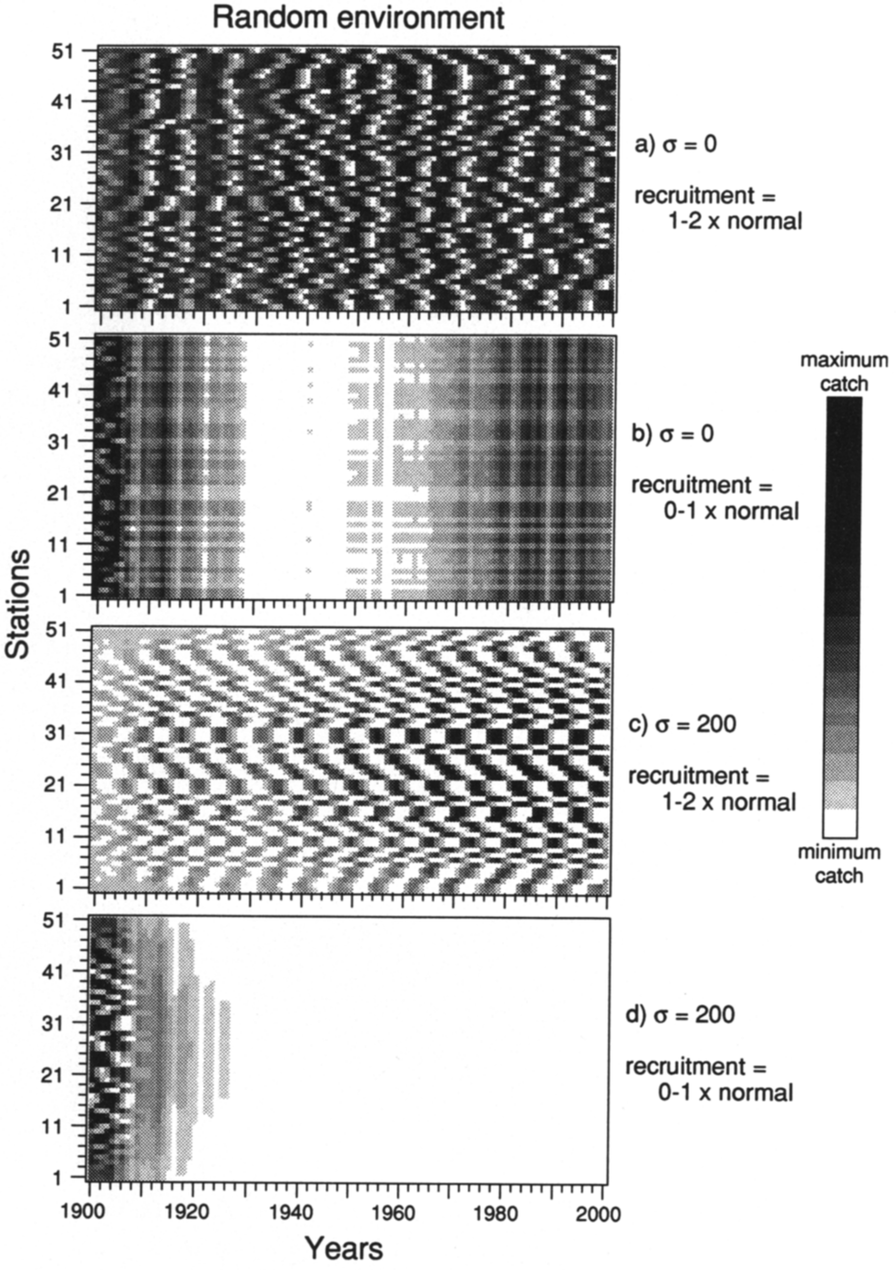

Fig. 9. Normalized catches from 51 age-structured subpopulations with slope of density-dependent post-dispersal recruitment survival $K_f = -3$, linked along a 1000 km coastline by deterministic, Gaussian-shaped dispersal (mean = 0, standard deviation = $\sigma$), with a random environment which multiplies recruitment along the coast by a uniform random variable each year. (a) No dispersal ($\sigma = 0$) and greater than average recruitment (random variable between 1 and 2), (b) no dispersal ($\sigma = 0$) and smaller than average recruitment (random variable between 0 and 1); (c) $\sigma = 200$ km and greater than average recruitment (between 1 and 2); (d) $\sigma = 200$ km and smaller than average recruitment (between 0 and 1).

in the dispersal kernel. The nature of spatial patterns in the deterministic simulations depended on the presence of dispersal as well as dispersal distances. Synchronicity in the simulations of environmentally forced systems depended on dispersal distances, and the response to increased or decreased recruitment survival due to climate change was different for metapopulations with and without dispersal. Persistence of harvested metapopulations managed using harvest refugia depended critically on larval dispersal distances.

It is clear that an important challenge in understanding the dynamics of metapopulations is to determine larval transport as a function of season and region. An ideal, complete model of larval transport and the resultant settlement distribution would be based on: (1) abiotic factors: a description of the three-dimensional current field and hydrographic variables, such as temperature, salinity and nutrients; and (2) biotic factors: a description of the growth, survival and behavioral responses of individual larvae to their abiotic and biotic environment (e.g. responses to variations in light, temperature, pressure and food availability). Unfortunately, there are no complete descriptions of the abiotic environment nor of the biotic response. We have therefore addressed various components of the larval dispersal problem for Dungeness crab, then combined them in an abstraction of transport and survival-related processes in the cross-shelf dimension of transport in the California Current System. We first determined the effects that temperature- and salinity-dependent development time and survival will have on successful larval settlement at various points along the coast. We then evaluated the importance of vertical migration of the megalopal stage using two approaches: (1) comparing horizontal transport with various assumed vertical migratory behavior in a slightly modified version of an existing primitive equation model; and (2) computing expected transport from local estimates of wind and currents. We then combined results from these studies and general knowledge of seasonal currents into the simplest possible framework, an advection–diffusion model.

### *Temperature and salinity*

While larvae are being transported by currents, their vital rates respond to hydrographic conditions in ways that affect their eventual dispersal. Development rate and survival of Dungeness crab larvae depend on temperature and salinity. This kind of dependence often is important for meroplanktonic species, and is particularly important for the Dungeness crab because vertical migratory behavior changes with ontogenetic stage and current fields in the California Current System change with season. We modeled the dependence of development rate of individual crab larvae on temperature and salinity using laboratory data from others (MOLONEY *et al.*, submitted). This model, in conjunction with examples of daily temperature profiles at several locations for several years, indicated that the larval period can vary between 74 and 182 days. This effect alone can lead to a variation of a factor of 400 in settlement, at the estimated larval mortality rate (0.066 day$^{-1}$; HOBBS *et al.*, 1992). Development periods varied with time of release, latitude and interannually. Varying release time from 1 December to 1 March led to variability in development time of as much as 20%. A general result in this regard is that at points along the coast where temperature (and thus development rate) increases during the larval season, settlement date is less sensitive to date of hatching or larval release. Mean development times were almost 50% greater off Washington than off California. Interannual variability in temperature at some locations caused variability in development time of 50%. The

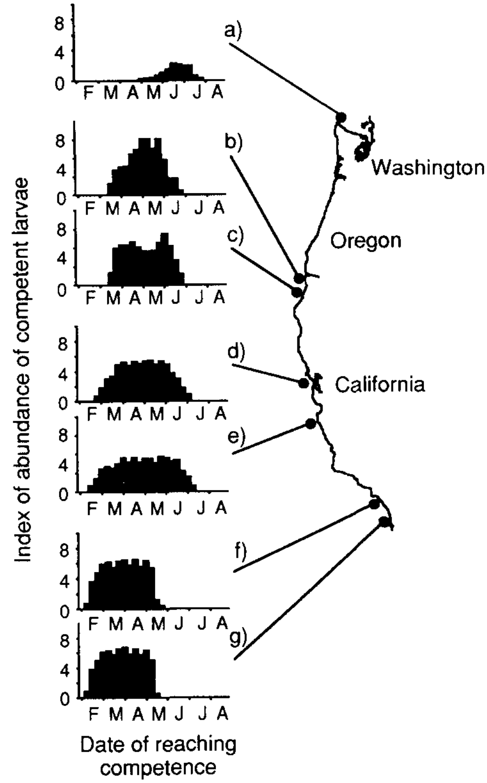

Fig. 10. The temporal distributions of settlement that would result from a uniform distribution of hatching from 1 December to 28 February at various points along the coast (Moloney *et al.*, submitted). Development times are based on the effects of locally observed temperatures and salinities. (a) Neah Bay; (b) Crescent City; (c) Trinidad Beach; (d) Farallon Islands; (e) Granite Canyon; (f) Balboa; (g) La Jolla.

influence of varying temperature on development rate also influences the shape of the distributions of competency and settlement dates. Assuming a constant uniform distribution of hatching times from 1 December to 1 March, the distribution of settling time varies substantially both along the coast (Fig. 10), and in the same location from year to year.

### *Vertical migration*

A behavioral characteristic of larvae, which is important in many meroplanktonic organisms, is vertical migration in the water column, usually on a diel basis. It has long been known that the varying vertical position of larvae in a water column with vertical velocity shear can have a substantial impact on transport (Hardy, 1935). We have evaluated the effect of vertical migration of Dungeness crab larvae in two different ways, one based on a primitive equation model and the other on local wind and current estimates.

Vertical migration is believed to be important only in the megalopal stage of Dungeness

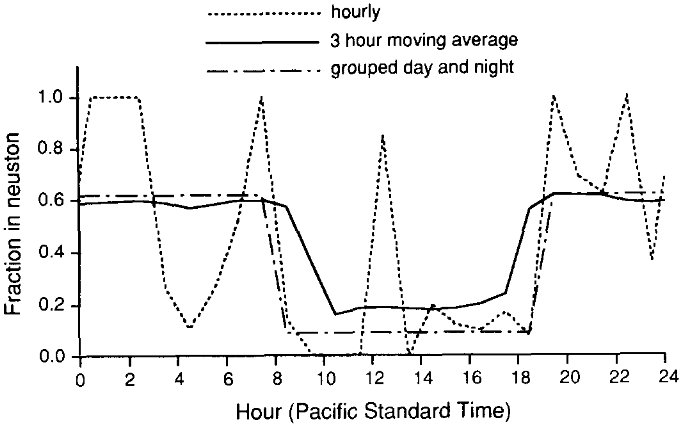

Fig. 11. The estimated fraction of megalopae in the neuston by time of day, based on month long cruises in 4 years in the early 1980s (Hobbs and Botsford, 1992). These estimates are from neuston and bongo tows, using three different ways of lumping samples to reduce variability.

crabs because the zoeal stages are found throughout the water column with no apparent diel pattern. Comparison of neuston samples and oblique bongo plankton tows indicated that 62% of the megalopae are in the neuston at night (19:00–08:00 PST) and 8% are in the neuston during the day (08:00–19:00 PST) (Hobbs and Botsford, 1992; Fig. 11).

The Semi-spectral Primitive Equation Model (SPEM), developed by Haidvogel *et al.*, (1991a) can reproduce the large-scale California Current flows while resolving mesoscale features like filaments, jets and eddies. The model is a diabatic primitive equation model that allows for thermal and wind forcing. It uses coordinate transformations to incorporate irregular geometry and large variations in coastal topography. The vertical dimension is represented by a bottom-following coordinate system. This model has been implemented previously for the CCS, where it was used to investigate the formation of an offshore filament (Haidvogel *et al.*, 1991b), and in Lagrangian particle-tracking experiments (Hofmann *et al.*, 1991).

We have used the SPEM to study the effects of vertical migratory behavior near mesoscale features such as those found near points and capes. A Lagrangian model is used in the SPEM to compute the transport of drifters which represent larvae, using a fourth-order Runge Kutta scheme to solve for the three-dimensional trajectories (Hofmann *et al.*, 1991). We have implemented additional routines that allow one to specify the time-dependent vertical positions of drifters. The simplest of these vertical migration schemes is presented here, and compared with results in which there is no vertical migration. We use the velocity field generated by Haidvogel *et al.* (1991b) for the California Current, running the model from day 140 to day 170. There is no wind forcing in this particular simulation. As a consequence, the characteristic nearshore surface transport features of upwelling environments, such as an Ekman layer, are lacking. To investigate the effects of wind on the verticallly migrating larvae, the model was run also with a constant surface stress in a southward direction.

Comparison of results from this model under various assumed forcing and larval behavior clearly indicate the importance of vertical migration (Fig. 12). As a baseline case, we show the transport of passive drifters at the surface in the absence of wind. The

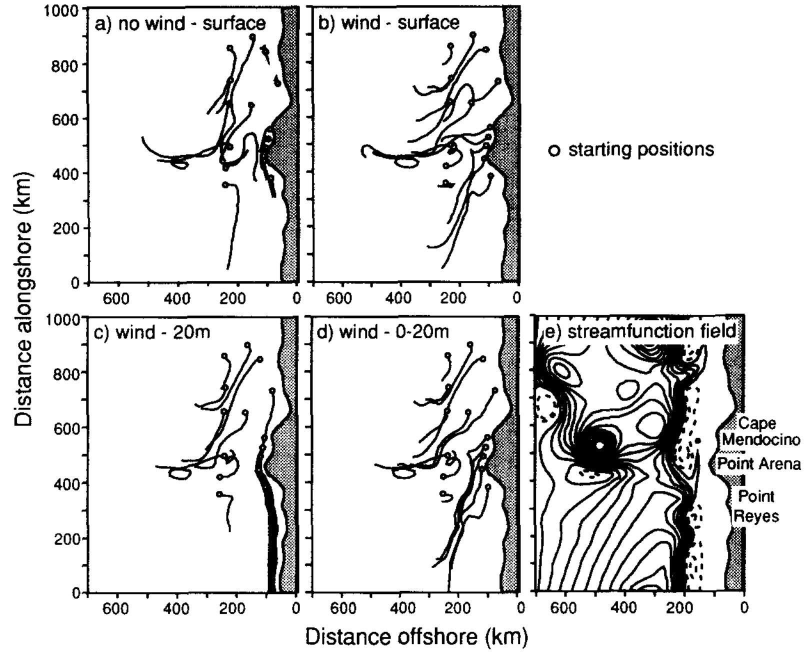

Fig. 12. Larval drift tracks from the semi-spectral primitive equation model (SPEM), executed for days 140–170 of the coastal transition zone simulation of Haidvogel *et al.* (1991b). (a) No wind forcing, larvae at the surface; (b) Wind forcing, larvae at the surface; (c) Wind forcing, larvae at 20 m depth; (d) Wind forcing, larvae migrate each day between the surface and 20 m; (e) contour plot of the stream function field at day 140.

movement of the drifters can be compared with the simulated streamfunction field [Fig. 12(e)], where the direction of flow is parallel to the streamlines. When we include wind in the simulation, the larval drift tracks change. When the larvae are at the surface at all times [Fig. 12(b)], their transport tends to be directed more offshore than in the absence of wind, especially for those larvae located close to the coast. If the larvae remain at 20 m-depth at all times [Fig. 12(c)], as might occur for some of the zoeal stages of Dungeness crab, their patterns of movement resembles that of the no-wind case more closely than that of Fig. 12(b). In Fig. 12(d) we have emulated “typical” Dungeness crab megalopal behavior by allowing the larvae to migrate between the surface at night and 20 m-depth during the day. In this instance, their drift tracks indicate less offshore transport than in Fig. 12(b), and a smaller alongshore component than in Fig. 12(c).

A more empirical approach to evaluating vertical migration indicated that the vertical migration may be important in returning larvae to nearshore settlement areas or retaining them nearshore (Hobbs *et al.*, 1992). We used the U.S. Navy’s Fleet Numerical Oceanographic Center (FNOC) meteorological wind fields to compute progressive vector diagrams of the possible effects of vertical migration, winds and currents on transport of the megalopal stage (see Hobbs *et al.*, 1992 for methods). The FNOC winds are estimated geostrophic winds based on wind and pressure measurements, rotated and reduced in velocity to reflect boundary conditions. In evaluating vertical migration, we considered a range of transport scenarios: (1) Ekman transport (i.e. below the surface, no vertical

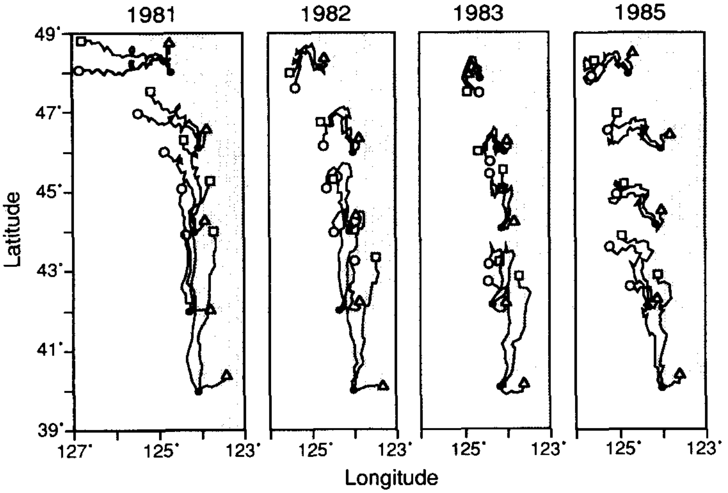

Fig. 13. Progressive vector diagrams of the influence of physical conditions on larval transport at several different points over 45 days prior to a sample date from late April to early June (Hobbs *et al.*, 1992), based on vertical migrating larvae and FNOC winds using three hypothetical mechanisms: Ekman transport (△), Ekman transport for 12 h and 3% of the wind velocity for the remaining 12 h (□), and Ekman transport for 12 h and 3% of the wind speed 15° to the right of the wind (○). The last vector value is connected to the sampling point (●).

migration); (2) Ekman transport during the day and at 3% of the windspeed in the direction of the wind at night (i.e. below the surface during the day migrating to near the surface at night); and (3) Ekman transport during the day and 3% of the windspeed, 15° to the right of the wind direction at night (same assumed migration, different assumed transport). Progressive vector diagrams of these calculations over a 45 day period prior to a sampling date showed that this component of transport varies with latitude and from year to year, especially for the cases with vertical migration (Fig. 13). Onshore transport was greater in the north, and varied from zero to 400 km over the 45 day period (about 0.1 m $s^{-1}$ onshore). For the case with vertical migration and wind transport 15° to the right of the wind, the relative amount of computed onshore transport over these four years matched the observed larval density within 50 km (Hobbs *et al.*, 1992).

### *Advection–diffusion model*

We have described the effects of temperature and salinity on larval development period and survival, and the effect of vertical migratory behavior on horizontal advection. To evaluate the combined effects of these processes, we used the derived rates and timing parameters in a one-dimensional (cross-shelf) advection–diffusion model (Largier *et al.*, in prep.). The complex nature of water circulation in the coastal ocean makes it difficult to predict the destination of larvae that are released into this system. Primitive equation models currently cannot incorporate all the accumulated empirical knowledge of the CCS. While models being developed make strides in these directions, we have chosen to approximate the circulation in a simple advection–diffusion model. Using this simple model, we can begin to evaluate the impact on dispersal of emerging information on development rates, survival rates, and possible advective rates within the context of seasonal currents in the CCS. At the very least, this simplest of dispersion models can be constructed as a null hypothesis, testing whether the dispersal of larvae is a simple diffusive process (as modeled here), or depends critically on active behavior and particular flow features.

Although our ultimate goal is a two-dimensional advection–diffusion model into which we can incorporate results from empirical or more detailed modeling studies, most of our effort so far has been in formulating a simple one-dimensional offshore–onshore model. By omitting alongshore terms at this stage we are not ignoring the importance of mesoscale features such as eddies and upwelling plumes. Rather, we are constructing a sub-region model that integrates over the mesoscale variability associated with capes and filaments. Support for this approach to crab dispersal is obtained from the large alongshore scales exhibited by variation in recruitment. Based on catch records (Fig. 1), recruitment appears coherent over distances of the order of hundreds of km alongshore.

The model expresses temporal changes in concentration in terms of advection, diffusion and mortality.

$$\frac{\partial l(x,t)}{\partial t} = -\frac{\partial}{\partial x}[A(x)\ l(x,t)] + \frac{\partial}{\partial x}\left[D(x)\frac{\partial l(x,t)}{\partial x}\right] - M\,l(x,t) \qquad (7)$$

where $l(x, t)$ is the density of larvae a distance $x$ from shore at time $t$, $A(x)$ is the rate of advection in the cross-shore direction, $D(x)$ is the rate of diffusion in the cross-shore direction, and $M$ is the mortality rate of larvae. Each parameter may contain a number of mechanisms—the nomenclature of advection, diffusion and mortality are not meant in a strict sense. Rather, these parameters express the net effect integrated over the various mechanisms, over depth and over some alongshore distance.

While analytical solutions can be found for constant coefficients (homogeneous diffusion) and simple boundary conditions (e.g. Jackson and Strathmann, 1981), the required assumptions seem unrealistically limiting. Rather we have developed numerical solutions to this equation, allowing for an investigation of a variety of functions of $A(x)$ and $D(x)$, as well as various boundary conditions. Biologically, numerical solutions allow us to incorporate substantial detail in spatial and temporal patterns of spawning, development and settlement of the larvae.

The realism of this model depends on the careful choice of simple but representative boundary and initial conditions and on the careful determination of empirically-derived coefficients of advection and diffusion. To obtain values of parameters for $A(x)$ and $D(x)$ other than those resulting from our studies of vertical migration, we reviewed three sources of information from the CCS: directly observed larval dispersion, observations of drifter tracks and current meter observations [see Largier *et al.* (in prep.) for details]. We assumed that A goes to zero at the coast, as required for flow continuity, and that D also goes to zero at the coast as the cross-shore spatial scale of eddy diffusive flows decrease to zero. Further, because the water depth limits the cross-sectional area over which these fluxes are active (e.g. inshore of the 50-m isobath), both $A$ and $D$ must decrease near the coast because the water depth does not appear separately in this simple model. At some distance offshore, we assumed that the values of $A$ and $D$ were constant with $x$, taking values representative of the large-scale California Current and mesoscale eddy field.

We began with a baseline case in which larvae with nominal life history timing were exposed to nominal diffusion and no advection (Largier *et al.*, in prep.). We adopted nominal stage lengths of a 90-day zoeal stage and a 30-day megalopal stage (Moloney *et* *al.*, submitted), followed by a 20-day competency period during which larvae settle at a certain rate if they are within 10 km of the coast. For the baseline, we assumed $D = 200$ m$^2$ s$^{-1}$ for both the zoeal stage and the megalopal stage (Largier *et al.*, in prep.) and the mortality rate $M = 0.066^{-1}$ (Hobbs *et al.*, 1992). We solved equation (7) numerically under the assumption that no larvae settle or are lost at the coast (i.e. a reflecting boundary condition) until 120 days, then assumed that all larvae within 10 km of the coast settle at a rate proportional to density (with rate constant 1.0 day$^{-1}$) for 20 days. For this case with diffusion only, our numerical results agreed with the analytical results of Jackson and Strathmann (1981), justifying our numerical approach in other cases for which we have no analytical solution.

We varied this baseline case by adding different rates of advection before and after the spring transition, the advective rates that would result from wind forcing and vertical migration as discussed above, and the variability in development time that would result from temperature-dependent development rate. Rates of advection both before and after the spring transition should vary with latitude (see above). For California, we let $A$ be zero before the spring transition, and $A = 0.05$ m s$^{-1}$, beginning at 10 km offshore and declining linearly to zero at the coast, after the spring transition. For conditions off Washington, we set $A = -0.02$ m s$^{-1}$ before the spring transition and $A = 0.02$ ms$^{-1}$ after the spring transition. We changed advective rates at various points in the larval life to evaluate the effects of relative timing of larval release and the spring transition. For example, changing advective rates at 60 days could correspond to larval release on 1 February and spring transition on 1 April or larval release on 1 January and spring transition on 1 March, etc. Based on the wind-driven advection of a vertically migrating larva computed above (Hobbs *et al.*, 1992; Fig. 13), we assumed a rate of 0.01 m s$^{-1}$ onshore for California, and 0.1 m s$^{-1}$ onshore for Washington. To reflect the temperature and salinity dependence of development rate, we varied the durations of the zoeal, megalopal, and competency stages by ±25%.

The results of these versions of the models were used to evaluate several issues: (1) whether enough larvae settle to sustain a population; (2) whether there is enough natural variability in a phenomenon to be the cause of observed cycles; (3) the degree of latitudinal variability in settlement; (4) how well spatial distributions in the model represented observed larval distributions; and (5) the sensitivity of all of the above issues to poorly known parameters. For the first issue, we compared the fraction settling to the fraction required to sustain a population, which was estimated to be 100 post-larvae settled per million larvae released based on fecundity and survival from settlement to reproduction [see Largier *et al.* (in prep.) for details]. For the second issue, we compared variability to the level of variability seen in the catch record, (a ratio of high to low abundance of approximately one order of magnitude). For the third issue, we compared advective rates which correspond to Washington and northern California, using observed currents and the results of the vertical migration calculations.

Examples of cases with various parameter values provide an indication of how different combinations of biological–physical processes will affect larval recruitment in the CCS (Table 1). We summarize the results here with regard to the specific issues raised above [see Largier *et al.* (in prep.) for details and additional results].

Cases without wind-forced onshore transport did not provide enough settlement to sustain the population. With diffusion only, settlement was comparable to the required number. Adding advection before and after the spring transition, reduced this number several orders of magnitude below the required level in both California and Washington (Table 1, cases I and II). Invoking the maximum onshore advective rates assumed for vertical migrating larvae led to sufficient numbers settling off Washington, but not off California, for nominal temperatures and timing of the spring transition (60 days after larval release) (Table 1, case III). However, when the differences in development rates due to differing nominal temperatures were accounted for, both locations had sufficient settlement [see Largier *et al.* (in press) for details].

Observed interannual variability in temperature (effect on development time in cases IV and V in Table 1), surface winds (effect on advection of the megalopal stage, compare case II to case III), and the timing of spring transition (a change of 1 month typically changed settlement by an order of magnitude) each appeared to produce order-of-magnitude variability in settlement. These physical variables would of course covary, and combinations of them produced even greater variability in settlement. Settlement consistently was greater off Washington than off northern California without accounting for temperature differences, but they were similar when differences in development time were accounted for. The cross-shelf distribution of larvae at the beginning of the competency period compared favorably with observed larval distributions (Fig. 14). At this age, model larval distributions for cases which had adequate settlement were typically within 100 km of the coast, as they also were in observations made in May and June [1981 and 1982, Fig. 14(b) and (c)]. Results were not particularly sensitive to the choice of parameter values and model structure, except that settlement was sensitive to advection and survival rates (see Largier *et al.*, in prep.).

## CONCLUDING REMARKS

While confident predictions regarding the impact of climate change on coastal ecosystems remain beyond our grasp, we have identified a critical gap in our understanding of the

*Table* 1. *Fate of larvae as computed by the one-dimensional advection–diffusion model. Results show the numbers of larvae that settle, the numbers that survive but remain in the plankton, and the mean and mode of their distances* (km) *from shore at the start of the competent period. The spring transition occurs at* 60 *days of age and megalopal advection begins at* 90 *days of age*

| | | Numbers per million released | | Distance (km) | |
|---|---|---|---|---|---|
| Case | | Settled | In plankton | Mean | Mode |
| I | Baseline, $D = 200\ \mathrm{m^2\,s^{-1}}$ | 46 | 80 | 31 | 9.3 |
| II | With spring transition: | | | | |
| | California | $1.5 \times 10^{-7}$ | 97 | 358 | 357 |
| | Washington | 0.03 | 97 | 134 | 126 |
| III | With spring transition and megalopal advection: | | | | |
| | California | 0.36 | 97 | 102 | 93 |
| | Washington | 267 | $2.0 \times 10^{-7}$ | 0.16 | 0 |
| IV | Baseline, but different development rates: | | | | |
| | 25% faster | 403 | 789 | 25 | 8 |
| | 25% slower | 6 | 8 | 38 | 11 |
| V | With spring transition, megalopal advection and different development rates: | | | | |
| | 25% faster | 378 | 772 | 26 | 4 |
| | 25% slower | 0.001 | 10 | 186 | 185 |

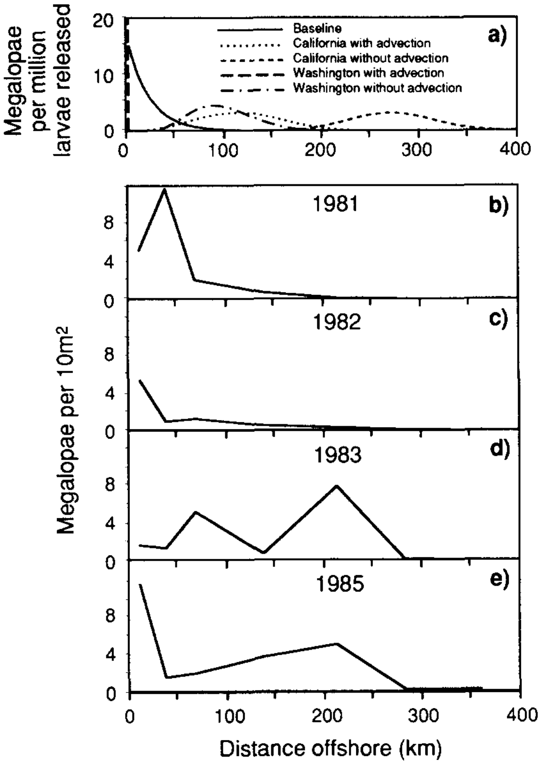

Fig. 14. (a) The spatial distribution of larvae from the advection–diffusion model at 120 days of age (the beginning of the component period) for the baseline case (diffusion only) and four cases from Washington and California, all with a spring transition but with and without megalopal advection due to wind forcing and vertical migration. (b)–(e) The cross-shelf distribution of megalopae in four different years. Sampling dates in 1981 and 1982 are about 3 weeks later than in 1983 and 1985.

processes which underly potential impacts on metapopulations with a meroplanktonic stage. We cannot simply add the effects of a variable physical environment to a metapopulation and predict results on the basis of intuition. Rather, the behavior of a group of connected subpopulations itself is a source of uncertainty, in addition to the uncertainty associated with projecting the effect of circulation and hydrography on larval dispersal. Population behavior depends in a fundamental way on the spatio-temporal nature of that dispersal. At this point, however, we have only scratched the surface, leaving unanswered questions regarding such additional realism as varying habitat along a coast and actual spatio-temporal variability in dispersal kernels.

Our demonstration of the critical effects of the spatio-temporal nature of dispersal on meroplanktonic metapopulations elevates the importance of transport in the consideration of causes of fluctuations in marine populations and expands the context within which it should be considered. For fish, the study of factors controlling population abundance has focused on recruitment, and essentially began with Hjort's (1914) proposal that recruitment depends on: (1) whether sufficient food is available at the end of the yolk-sac stage; and (2) whether larvae have been transported to areas of favorable biological and physical conditions. Most subsequent investigations of the effects of transport have focussed on whether larvae were transported to a favorable area. For examples in the CCS, Parrish *et al.* (1981) evaluated reproductive strategies in terms of how well they avoided larval loss due to offshore transport, and Simpson (1987) evaluated several different physical mechanisms in terms of whether they transported larvae to areas of high food or low predation. This view of transport is limited in that it is essentially a single population view. Our results indicate that transport has a much wider effect on population dynamics. It is not merely one of the factors determining recruitment to a population each year. Rather the (temporally varying) spatial pattern of transport within a population (i.e. the dispersal kernel), is an integral determinant of fundamental population dynamics. Transport is not merely a source of noise or environmental forcing, but rather a critical element of population structure. Steps in the direction of an expanded, comprehensive view of the importance of transport include Sinclair's (1988) member/vagrant hypothesis, which stresses the importance of spatial constraints to life cycle closure, and Frank's (1992) argument for accounting for age-specific dispersal between stocks in fish population models.

The effects of projected climate change on coastal marine populations are difficult to assess because we do not know much about the mechanisms by which physical conditions influence recruitment in coastal populations. For the CCS example, even if we were to accept simplified physical responses to climate change, such as increased upwelling and increased frequency or magnitude of ENSO events, we could not confidently project their consequences. We could estimate gross changes in productivity from empirical relationships with physical variables (e.g. Reid, 1962; Chelton *et al.*, 1982), but whereas starvation has been observed in some fish and physical impacts on food availability have been invoked as limiting mechanisms (reviewed in Botsford *et al.*, 1989), it would be difficult to tie shelf productivity concretely to recruitment in coastal meroplanktonic species. For populations in which recruitment is determined in part by transport of meroplanktonic larvae, we can expect changes in recruitment due to the changes in cross-shelf and alongshore flow associated with variation in upwelling or ENSO events. However, even these simple conclusions are problematic as changes in flow would lead to changes in water temperature, for example, and the effects of temperature on development times could change recruitment rates in subtle, complex ways. Here we have made only crude, explorative forays into the effects of climate change, by simulating the effects of increasing and decreasing coastwide recruitment success. This exercise merely illustrates the possibilities at this point.

Though in this paper we fall considerably short of confident projections regarding the effects of climate change, we have shown that the dynamic behavior of environmentally forced, age-structured, meroplanktonic metapopulations is not necessarily what we would expect intuitively. There has been an increasing research emphasis on early life history stages of marine fish and invertebrates, on the physical influences on transport and survival as well as smaller scale effects such as the influence of turbulence on feeding (Squires and Yamazaki, 1994; Keiyu *et al.*, 1994). However, little attention has been paid to their consequences at the metapopulation level, the level at which these influences will be integrated and be likely to have their most significant influence on ecosystem dynamics and human food production. Further research on this level will be essential in attempting to understand and project the impact of future climate change on coastal ecosystem function and productivity.

Perhaps the most surprising result of our work thus far is the spatial patterning which appears in metapopulation solutions for models with post-recruitment density-dependence and deterministic larval dispersal. We are continuing to investigate the characteristics of age structure and dispersal which induce this behavior. It appears to be an example of Turing-type diffusive instabilities arising from age-dependent diffusion, as discussed in HASTINGS (1992).

Another dynamic characteristic of general importance is the switch from variability on generational time scales to variability on annual time scales in subpopulations with strong density-dependence and low adult survival (HIGGINS *et al.*, in prep.; BOTSFORD, 1991). As the areas of suitable habitat are modified by climate change and adult survivals continue to be modified by harvest, these effects may be observed. The fact that similar models of semelparous populations, when linked along a coastline, can shift suddenly between different qualitative kinds of behavior introduces a possibility that must be considered in evaluating episodic shifts in marine populations (HASTINGS and HIGGINS, 1994).

Although we do not have a complete circulation model, we have been able to use a simple dispersion model to assess the degree of latitudinal, intra-annual and interannual variability possible from combinations of temperature-dependent development time and the transport that could arise from vertical migration, in the context of seasonal variability of cross shelf currents in the CCS. This result is not completely new—it is an extension of the long-appreciated sensitivity of recruitment to small changes in larval development rate due to high larval mortality rates (e.g. UNDERWOOD and FAIRWEATHER, 1989). The additional dynamic aspects introduced by seasonal and ontogenetic changes in advective rates have not been explored previously. They underscore the importance in relative timing of natural events in a way that is similar to CUSHING'S (1975) match–mismatch hypothesis. The bulk level advection–diffusion approach may be useful in other situations in which more mechanistic circulation models are not yet available. Advection–diffusion models easily can incorporate qualitative understanding of seasonal changes and they can be improved by incorporating special features and transport mechanisms.

The results obtained here have some implications for ongoing research on the two species we used as examples, the Dungeness crab and the red sea urchin. With regard to the crab, if the assumptions that larvae disperse and recruitment is density-dependent lead to behavior which appears to differ from observed behavior (Fig. 1), then one of these assumptions is incorrect; there may be no dispersal and/or no density-dependence. We are currently further quantifying the degree to which model behavior and observations differ (e.g. how synchronous are the catch records in Fig. 1?). Having no density-dependence presents the problem that cyclic behavior then requires cyclic forcing by the environment (*cf.* JOHNSON *et al.*, 1986). Having no dispersal also seems unlikely, but it is possible that there is wide spacing between patches of adults along the coast. It is also possible that the spatial patterns observed in the solutions with density-dependent recruitment and dispersal depend critically on some other special characteristic of the model (e.g. lack of interannual variability in alongshore dispersal, sharp habitat boundaries) and will disappear when those are accounted for in the model. We continue to evaluate the consequences for population behavior of increasing the realism of the metapopulation models. Issues such as alongshore variation in habitat, and random variability in alongshore dispersal are high priorities for future research.

The metapopulation studies of the red sea urchin under various forms of spatial harvest underscore a direct practical application of the understanding of the physical–biological interactions that underly larval dispersal (BOTSFORD *et al.*, in press; QUINN *et al.*, 1993). Harvest policies which include spaces set aside as refuges to produce the larval supply to other areas are being considered increasingly as means of maintaining this species and other meroplanktonic metapopulations, thereby increasing the importance of understanding dispersal processes. Ongoing field studies suggest that transport of both crabs and urchins may involve alongshore flow associated with intraseasonal variability in upwelling, on 10 km spatial scales, comparable to those considered for refuges (WING *et al.*, submitted). Our ongoing work on the red sea urchins also focusses on their sensitivity to population collapse due to declining efficiency of broadcast spawning with population density and in the presence of turbulent flow (LEVITAN *et al.*, 1992; DENNY and SHIBATA, 1989).

For both the red sea urchin and the crab, population dynamic results point clearly to the critical dependence of spatially distributed population dynamics on dispersal patterns. Additional modeling of the physical–biological interactions, as well as direct sampling, obviously are needed. Field programs using recently-developed techniques for tracking marine invertebrate larvae (LEVIN, 1990) should contribute much to our understanding of larval dispersal. Sampling of cross-shelf distributions of larvae are needed to determine which of the three nested systems of the CCS we should be considering when attempting to describe transport (*cf.* HOBBS *et al.*, 1992; MCCONNAUGHEY *et al.*, 1992). Field investigations of vertical position, the interaction between larvae and special features such as upwelling fronts, and the length of the competent larval stage would all improve our ability to project transport. Results could either be evaluated through particle tracking in a circulation model (*cf.* Fig. 12) or they could be approximated through an advection–diffusion approach. Sampling of variation in distribution on intra-seasonal scales would provide an empirical basis for testing proposed transport mechanisms. Further modeling and statistical analysis could possibly explain interannual variability on the basis of changes in intra-annual variability (*cf.* work on the Lasker hypothesis involving the role of intermittency of wind on food supply and recruitment, and later modeling and statistical studies; LASKER, 1978, 1981; PETERMAN and BRADFORD, 1987).

Specific local examples of invertebrate populations to which these considerations are relevant would include scallop *Placopecten magellanicus* on George's Bank, blue crab *Callinectes sapidus* in the southeastern U.S. and the American lobster *Homarus americanus* in the northeastern U.S. and the Canadian maritimes. Varying physical transport of scallop larvae between the three major adult subpopulations as described by TREMBLAY *et al.* (1994) are an example of spatial variability in habitat and a circular, rather than a linear coastal geometry. Blue crab metapopulations are subject to environmental influences on the larval stages of metapopulations within large embayments, such as Chesapeake Bay (GOODRICH *et al.*, 1989; JOHNSON and HESS, 1990), and there is potential for transport alongshore in the coastal jet invoked in descriptions of larval transport (e.g. in JOHNSON *et al.*, 1984). Relevant issues in lobster biology include larval exchange between coastal and offshore, bank populations, the ability of coastal populations to sustain high catches when egg production per recruit is less than 1% of unfished, and the recent dramatic, regional increase in abundance (HARDING *et al.*, 1983; CAMPBELL, 1989).

Some fish populations exhibit similar characteristics to these meroplanktonic populations, although juvenile and adult migration may also require further consideration and analyses. A number of studies have investigated the spatial synchrony of cod and haddock populations along the east coast of the U.S. to determine whether large scale environmental forcing is present (e.g. KOSLOW *et al.*, 1987; COHEN *et al.*, 1991), but they have not explicitly considered the dynamic consequences of larval-based interconnections such as might be implied by the bank circulation model of WERNER *et al.* (1993). There has, however, been some recent appreciation for the dynamic implications of juvenile migration among some of these stocks (FRANK, 1992).

In summary, it appears that the influence of physical conditions on meroplanktonic larvae and their consequences for metapopulation dynamics will be central to the issue of how climate change is going to affect food production in the coastal ocean. Although there is much to do to improve our understanding of these influences, progress will be limited until we understand the physical–biological linkages which underly the spatio-temporal variability in dispersal kernels, and their implications for metapopulation dynamics. There are substantial challenges at both the metapopulation level and the individual larval level in both ocean physics and biology.

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