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POPULATION DYNAMICS AND MANAGEMENT IMPLICATIONS OF LARVAL DISPERSAL

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Strong advective fields in coastal shelf ecosystems, particularly in eastern boundary currents, lead to significant longshore dispersal of the larval phase of meroplanktonic benthic invertebrates. Field observations of larvae and settlement in the California Current by recent workers are an example of the increasing research on the biological/physical mechanisms underlying larval transport. In particular, these studies identify physical/biological interactions that control the spatial distribution of larvae settling successfully. The current study demonstrates how the results of such studies contribute to (1) better understanding of population dynamics, and (2) better population management, using the cyclic covariability in the Dungeness crab *Cancer magister* population as an example of the former and management of the red sea urchin *Strongylocentrotus franciscanus* population as an example of the latter. Earlier modelling studies have shown that dispersal influences the stability and synchrony of variability in metapopulations such as the Dungeness crab, and that the spatial scale of covariability is roughly the scale of dispersal. The mechanism identified by recent research implies that the spatial scale of dispersal should be the distance between promontories in the California Current, roughly 100–200 km. Analysis of covariability between time-series of recruitment at different locations along the coast confirm that this is the spatial scale of longshore variability in the Dungeness crab. The spatial pattern in red sea urchin settlement caused by the identified mechanism provides: (1) the basis for spatially explicit management, and (2) an explanation for the observed spatial variability in the degree of overfishing. Research on larval dispersal is also providing the information necessary to design spatially explicit management strategies involving either permanent or temporary fishery closures. Both population dynamics and management require further research to describe the origins of larvae and the early larval phase, in addition to the transport just before settlement.

Whereas studies of the influence of physical oceanographic conditions on the larval stage of meroplanktonic species commonly focus on the effects of advection and hydrographic conditions on recruitment, physical conditions also affect an equally important aspect of population dynamics, larval dispersal. For the most part, interpretation of the advective effects has been in terms of advective losses, or conversely, recruitment success (Hjort 1914, Parrish *et al*. 1981, Simpson 1987, Hutchings 1992). This may be adequate for populations concentrated at a single location, or a well-mixed population, but for populations explicitly distributed over space, advection and hydrographic conditions also influence dispersal distance. Recent modelling studies have shown that larval dispersal patterns can have a critical effect on population dynamics and management (Botsford *et al*. 1994, 1998, Quinn *et al*. 1993). They influence the stability and variability of populations, synchrony over space and the effectiveness of spatially explicit management policies.

Larval dispersal patterns are particularly important to the dynamics and management of benthic invertebrates, an important component of shelf ecosystems. Because benthic invertebrates have relatively sedentary juvenile and adult stages, larval dispersal essentially represents all of their lifetime migration. Benthic invertebrates are a significant component of shelf ecosystems, economically, in terms of biodiversity, and as the subject of ecological study (Castilla and Camus 1992, Eekhout *et al*. 1992, Emanuel *et al*. 1992). They are also heavily impacted by both humans and ocean conditions in ways that frequently cannot be distinguished confidently (e.g. Castilla and Camus 1992).

It is demonstrated here how recent research on dispersal has benefitted both (1) the understanding of population dynamics and (2) the ability to manage populations, using two examples from field studies of larval transport in the California Current: the Dungeness crab *Cancer magister* and the red sea urchin *Strongylocentrotus franciscanus*. These field studies (Wing *et al*. 1995a, b, 1998a) are not just addressing the question of how much recruitment there will be under certain conditions; they also seek to determine the transport paths of meroplanktonic larvae. How this knowledge of dispersal patterns aids in the understanding of the causes of cycles in the Dungeness crab and management of the red sea urchin is addressed. Recent observations are combined with results from

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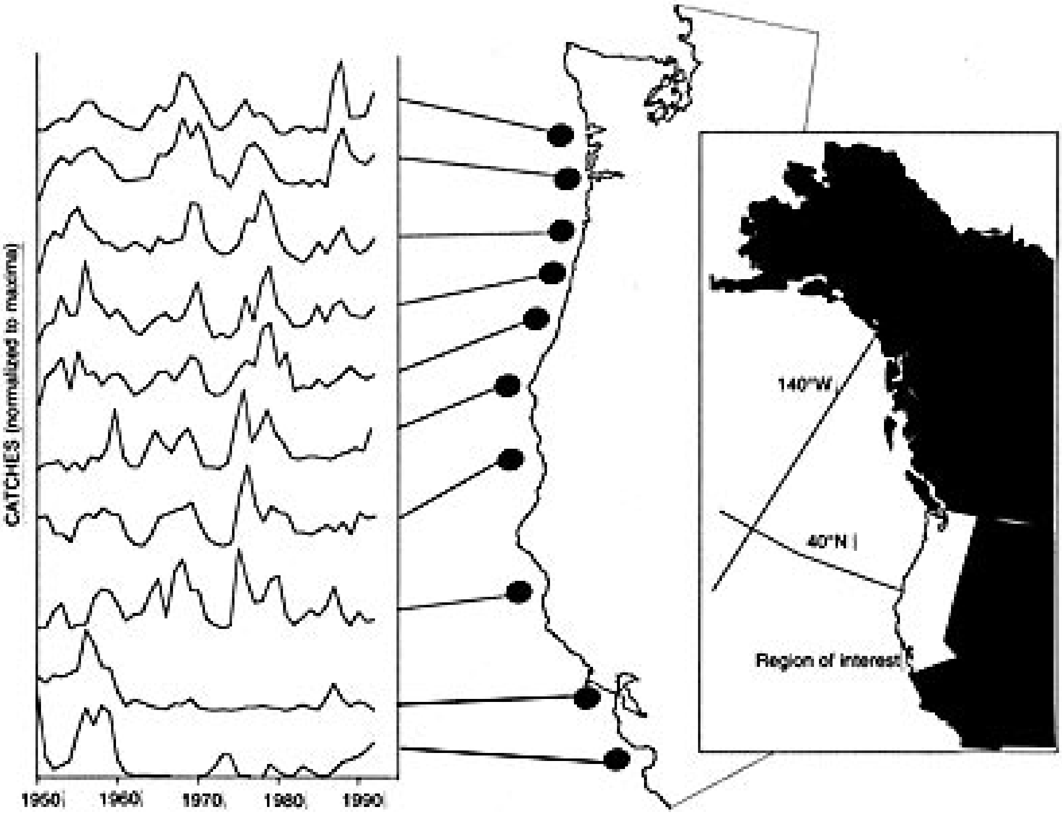

Fig. 1: Time-series of annual harvest of the Dungeness crab *Cancer magister* along the west coast of the United States, normalized to show the temporal cycles from Fort Bragg in the north, and the spatial covariability

population modelling studies to demonstrate the importance of knowing larval dispersal in various situations.

The observations of settlement and late stage larvae described in Wing *et al.* (1998a) identify an area of larval retention in an upwelling shadow (Graham *et al.* 1992, Graham and Largier 1997) in the lee of Point Reyes during active upwelling. Also, other retention zones near other promontories in northern California are proposed. During upwelling relaxation, these larvae are advected polewards in a coastally trapped current and settle north of the point. Recent settlement of red sea urchin indicates a similar phenomenon at the next point to the north, Point Arena. The interpretation of these results pursued here is that the retention zones and relaxation flows: (1) constrain the majority of successful larvae to settle within their embayment of origin, and (2) lead to a specific spatial pattern of recruitment. Because only settlement and the late larval phase were sampled, the former cannot be known with certainty on the basis of observations so far, but it is likely that investigation of its consequences is worthwhile. The implied scale of dispersal is the scale of an embayment or the distance between major promontories, roughly 100–200 km.

Dungeness crab are harvested along the west coast of North America from San Francisco to Alaska, but this study focuses on the populations in the contiguous U.S.A. (see reviews in Botsford *et al.* 1989, Botsford and Hobbs 1995). The fishery is regulated using a common approach to the management of crustacean fisheries, control of size, season and sex (Methot 1989). Only males with carapace width >159 mm can be landed, and only during the fishing season, which begins near 1 December each year. Considerable research has focused on the question of the cause of the apparent 10-year cycle in recruitment

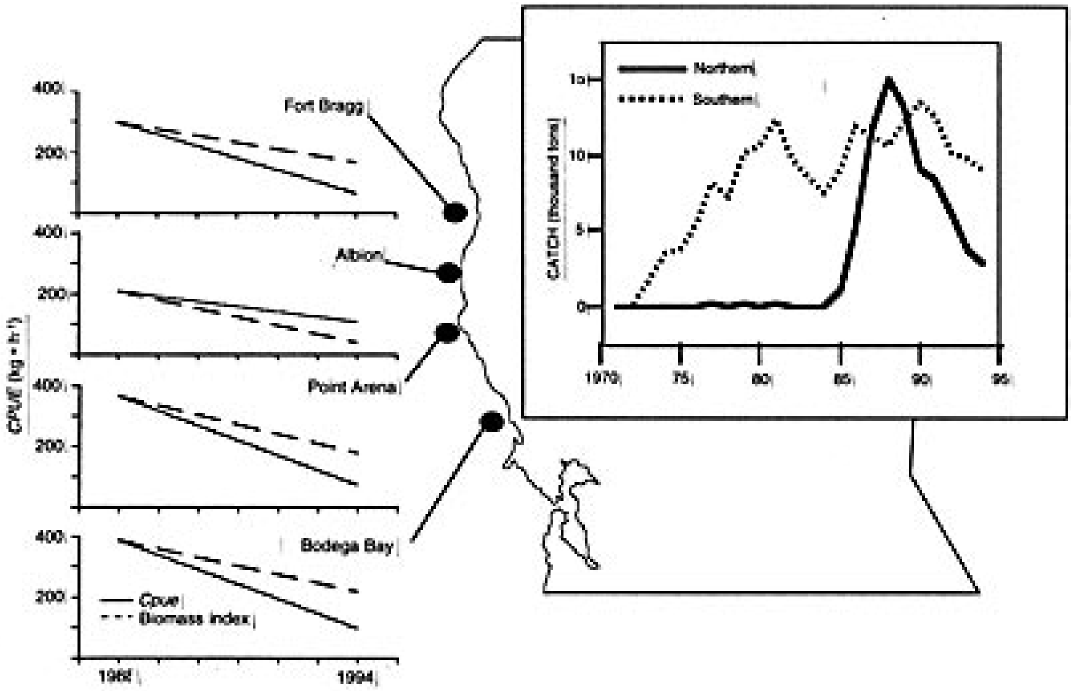

Fig. 2: Total catch of the red sea urchin *Strongylocentrotus franciscanus* in northern and southern California on the west coast of the U.S.A. Also shown is the decline in abundance (indexed by *cpue*) at the four major ports in northern California, following the dramatic increase in effort in 1988. The decline in abundance is compared to the decline expected from the "fishing up" effect of removing older larger individuals from the population (see Botsford *et al.* in prep. for further details)

reflected in the catch record (Fig. 1), with several proposed explanations involving influences of the environment on the larval stage. These include the effects of temperature (Wild 1980), wind stress (Johnson *et al.* 1986), cross-shelf transport (Hobbs *et al.* 1992) and longshore transport (McConnaughey *et al.* 1992, 1994). Larvae are released from females nearshore in December during a period of poleward, onshore flow, but they settle in May or June after the "spring transition" to strong upwelling winds and consequent equatorward, offshore flow (Hickey 1989, Largier *et al.* 1993). The five early stages last a total of roughly three months and are weakly swimming, non-vertical migratory zoea, whereas the last stage, a megalopa, lasts one month and is associated with strong swimming with a pronounced diel migration (Hobbs and Botsford 1992).

The red sea urchin fishery in California developed first in the south to a roughly constant value, then later in the north, the area of current research (Fig. 2). In northern California, the fishery increased rapidly, fueled by increased demand as a result of the depreciation of the U.S. dollar relative to the Japanese yen. Since 1988, however, catches have declined dramatically. Both catch per unit effort (*cpue*) and fishery independent surveys indicate this reflects a real decline in abundance. Recent proposals by managers to increase protection of the stock through more restrictive harvest regulations have been met with claims that the stock is not overfished, and that the decline in catch is an expected approach to an equilibrium condition. In northern California, most red sea urchin larvae are probably released in early spring, following the spring transition, and spend roughly three months in the plankton. The red sea urchin is somewhat unique among harvested species in that there are known changes in population dynamics at low densities. Two Allee effects are known for this species: a dependence of fertilization success of this broadcast spawner on adult density (Levitan *et al.* 1992) and protection of small juveniles under the spine canopy of adults (Tegner and Dayton 1977).

Investigation of dispersal involves the explicit acknowledgement that marine populations are distributed over space. Models of marine populations for fishery management and other purposes have evolved from simple biomass-based models (Graham 1935, Schaefer 1954) to models including age structure (e.g. Beverton and Holt 1957, Deriso *et al*. 1985, Megrey 1989), and to models and analyses involving size structure (Macdonald and Pitcher 1979, Fournier *et al*. 1990). Some recent questions regarding marine populations have involved spatial structure of populations, but there is neither a well-developed approach nor a wide appreciation of problems brought on by the fact that populations are distributed over space. Some analysts have pursued the correlations of subpopulations over space as a key to recruitment mechnanisms (Campbell and Mohn 1983, Koslow 1984, Koslow *et al*. 1987, Cohen *et al*. 1991, Elner and Campbell 1991). Others have investigated the dynamic behaviour of spatially distributed marine populations (Roughgarden and Iwasa 1986, Possingham and Roughgarden 1990, Botsford *et al*. 1994, 1998, Botsford 1995). Spatial distributions of populations are beginning to be accounted for in management analyses (Walters *et al*. 1993), and in the case of the American lobster *Homarus americanus*, a lesser harvested subpopulation has been proposed as the explanation for continued persistence of an overfished population (Fogarty 1998). The present study explicitly include the age and spatial structure of populations, and will assume a one-dimensional form (i.e. along a coastline) for the latter.

DISPERSAL AND POPULATION DYNAMICS

An understanding of the effects of dispersal on metapopulation dynamics requires an understanding of the behaviour of the subpopulations linked by larval dispersal. Variability in harvested marine populations has been investigated by examining stability of population models, i.e. the propensity of a population to seek a constant level of abundance or biomass. Because the early, biomass-based logistic models were always stable, investigation of stability of marine populations began when age structure was introduced into population models with density-dependent recruitment. Ricker (1954) showed that populations with density-dependent recruitment became more stable and exhibited longer period cycles as age structure was added. The deterministic dynamics of this type of population with compensatory density-dependence are now relatively well understood (reviewed in Botsford 1997). Early results, based on simulations and analyses of linearized models indicated that age-structured populations with density-dependent recruitment were more likely to produce cycles when recruitment survival declined more sharply with increasing density, and the age structure was narrower and at older ages (Ricker 1954, Botsford and Wickham 1978, McKelvey *et al*. 1980, Levin 1981). The period of the cycles was typically twice the generation time (Botsford and Wickham 1978, Levin 1981, Bergh and Getz 1988). Botsford and Wickham (1978) showed that size-selective fishing could be destabilizing (cf. Ricker 1954), so the effects of size structure (Botsford 1984), variable fishing presssure (Botsford *et al.* 1983) and an egg-predator worm (Hobbs and Botsford 1989) were incorporated to study the causes of cycles in the Dungeness crab fishery along the west coast of the U.S.A. (cf. McKelvey *et al.* 1980). A similar modelling approach was taken by Roughgarden *et al*. (1985) in their study of space-limited recruitment in an open population of barnacles. Gaines and Roughgarden (1985) showed through field studies of several populations that one of the potentially destabilizing factors, a high supply of propagules, did indeed cause more cyclic fluctuations (but see Possingham *et al.* 1994).

Some nonlinear aspects of behaviour of age-structured populations with density-dependent recruitment (Guckenheimer *et al.* 1977, Levin 1981, Botsford 1991, Tuljapurkar *et al.* 1994) are probably important in real marine populations, but there has been little analysis of their effects. A recent explicit analysis of nonlinear behaviour showed that the results described above, based on linearized models, break down as adult survival decreases. Behaviour is no longer periodic or quasi-periodic with a period near twice the generation time, but rather it is of higher frequency and sometimes chaotic (Higgins *et al.* 1997). However, over a large range of parameters, the results for age-structured models consistent with several proposed mechanisms of density-dependent recruitment for Dungeness crab indicate cycles of roughly twice the generation time (Botsford *et al.* 1994, Botsford and Hobbs 1995).

Some of the effects of a random environment on populations with density-dependent recruitment and age structure have been identified from stochastic versions of these models. The effects of small amounts of random variability in recruitment survival are greater for populations that are inherently less stable (Horwood and Shepherd 1981, Horwood 1983, 1984, Reed 1983). Also, stable populations are most sensitive to variability on time-scales near the period of the cycles that would be produced if the population were unstable (Botsford 1986). As in the deterministic models above, these analyses do not cover the range of possible nonlinear responses to

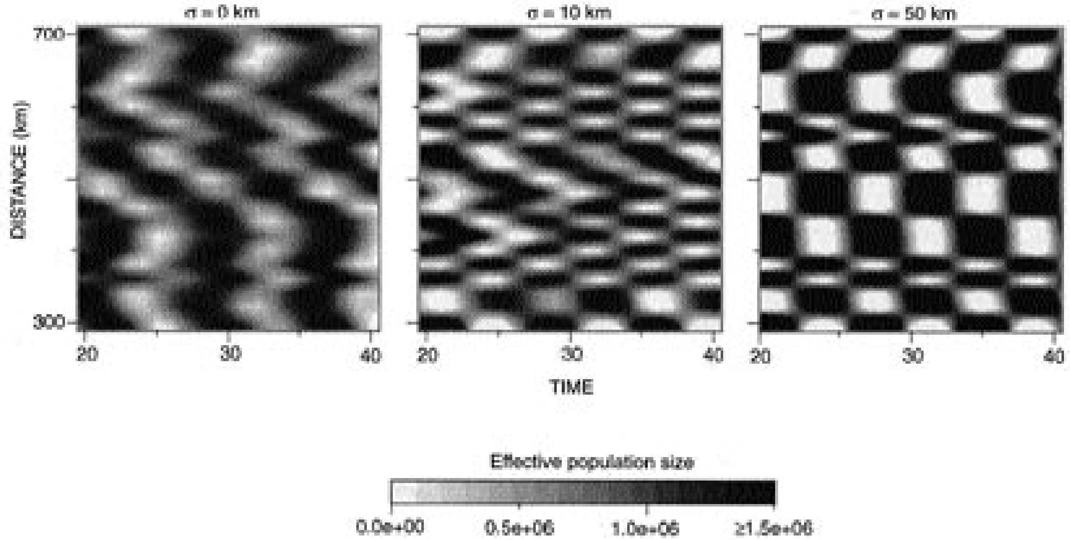

Fig. 3: The effect of dispersal distance on synchrony of temporal cycles in abundance along the coast from a metapopulation model described by Equation 1. With no dispersal (i.e. σ = 0), cycles are not synchronized. As the dispersal width s increases from 0 to 50 km, the asynchronous cycles form into longshore spatial patterns whose spatial scale increases with dispersal distance (after Botsford *et al.* 1998)

the random environment. Important examples include episodic transient disturbances, such as those observed in the California Current in response to *El Niño* – Southern Oscillation (ENSO) periodicities, and coastwide good recruitment years (e.g. Hollowed *et al.* 1987). The nonlinear effect of an exceptionally good year of recruitment can be to depress recruitment for several years, essentially making the temporal scale of variability to which populations will respond amplitude-dependent (Botsford *et al.* 1994).

Whereas the behaviour of a single population at one location is well understood, there is less understanding of how several of these populations linked by larval dispersal will behave. The most parsimonius, initial guess at the effect on population behaviour of linking several populations together through dispersal is that it will not change stability conditions, but rather serve merely to synchronize populations along the coast. However, one recent result indicates that this may not always be the case. Botsford *et al.* (1994, 1998) used a model of a meroplanktonic metapopulation distributed along a coastline to investigate this issue. Recruitment at location *x* along the coast was represented as

$$R_t(x) = f\,[C_t(x), x] \int_{x_1}^{x_u} P_t(x\ y)g[W_t(y), y]B_t(y)dy \ . \quad (1)$$

In this model, individuals are generated at location *y* by reproduction $B_t(y)$, which is the weighted sum of the number of individuals at each age at location *y*, with fecundity-at-age as the weighting factor. They then experience pre-dispersal density-dependence, denoted by *g*, and are dispersed from location *y* to location *x,* as reflected in *p*(*x,y*), before experiencing postdispersal density-dependence, denoted by *f*, i.e. interactions between settling individuals and resident juveniles and adults after dispersal. Both *f* and *g* depend on local effective population size (C_t and W_t), which are weighted sums over the number at each age, similar to B_t, except that the weightings reflect the age-dependence of the influence on density-dependence rather than fecundity. For Dungeness crab, for example, pre-dispersal density-dependence could be a density-dependent influence on fecundity (cf. McKelvey *et al.* 1980), and post-dispersal density-dependence could be cannibalism (cf. Gotshall 1977, Botsford and Hobbs 1995). Dispersal is represented by *p*(*x,y*), which is the fraction of larvae originating at location *y* that settle at location *x*. This part of the model would be determined from the type of research on the influence of physical conditions on larval survival and transport described in Wing *et al.* (1998b). The question of interest here is how the shape of *p*(*x,y*) influences the stability and variability of this population.

To gain an initial understanding of possible qualitative types of behaviour, and the effect of dispersal scale, Botsford *et al.* (1994, 1998) analysed this model with the simplest type of dispersal, i.e. Gaussian-shaped dispersal from each point to varying distances longshore. They showed that, for cases in which the density-dependence in recruitment occurred before dispersal, the effect of increased dispersal was in fact as would initially be predicted, i.e. synchrony of cyclic behaviour. However, when the density-dependence occurred after dispersal, the effect of increased dispersal was to introduce a spatial pattern into the fluctuations along the coast (Fig. 3). The spatial scale of the alternating spatial pattern depended on the width of the dispersal pattern.

Because a form of post-dispersal, density-dependent cannibalism is significant in this population (Gotshall 1977, Botsford and Hobbs 1995), spatial structure is expected in the cyclic fluctuations, on the scale of dispersal distances. The mechanism described in Wing *et al.* (1998b) provides an initial estimate of the scale of dispersal of 100–200 km. This is consistent with independent information from another source; an initial analysis of the data from the population level (i.e. the data in Fig. 1) shows spatial covariability in recruitment (using catch as a proxy) over distances of several hundred kilometres (Botsford *et al.* 1998). The implied greater similarity between adjacent populations can be seen in Figure 1. Therefore, research on dispersal provides a spatial scale of dispersal that, together with model results, predicts the scale of spatial variability actually seen in the recruitment data.

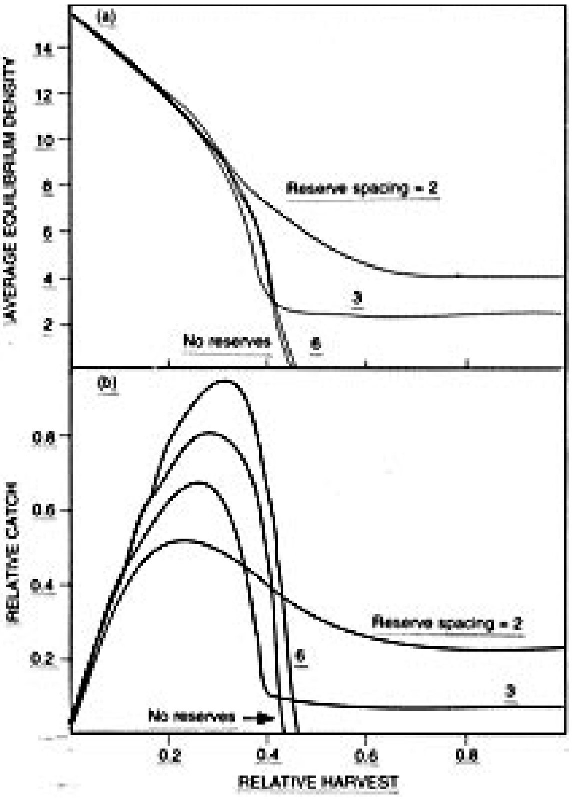

Fig. 4: Equilibrium values of (a) population density and (b) catch as harvest rate is increased for a metapopulation model in which dispersal occurs over the two adjacent subpopulations on each side, for various values of reserve spacing (after Quinn *et al.* 1993)

DISPERSAL AND POPULATION MANAGEMENT

The nature of dispersal is an important consideration in the design of spatially specific management strategies. One of those strategies is to increase harvest efficiency by tailoring harvest rates to observed variability in productivity. Other strategies involve spatial closures and are motivated by the difficulties and uncertainties involved in monitoring and controlling effort. These are of two basic types: (i) rotating spatial harvest, in which the total area of a fishery is divided into *N* groups and each area is harvested only every *N* years (Sluczanowski 1984, Botsford *et al.* 1993, Pfister and Bradbury 1996), and (ii) marine reserves, in which specified areas are closed permanently (e.g. Dugan and Davis 1993, Quinn *et al.* 1993).

There is general recognition that the effectiveness of management strategies involving spatial closures will depend on dispersal characteristics, and much of the current research on marine reserves is research on movement of target species (e.g. Attwood and Bennett 1994). However, because of the current paucity of knowledge of dispersal patterns, there has been little formal evaluation of the relationships between dispersal patterns, reserve size and spacing, and achievable harvest levels.

For the red sea urchin, Quinn *et al.* (1993) formulated a model in which 24 subpopulations were distributed along a coastline with dispersal between them. Each stage-structured subpopulation contained both of the Allee effects known for this species, declining fertilization efficiency with declining density and spine canopy protection of juveniles. Results from this model for an arbitrarily chosen dispersal pattern, dispersal from each area to the adjacent two areas on each side, showed what will probably be a common feature of marine reserves: higher yields are possible without reserves at low rates of harvest, but as harvest-

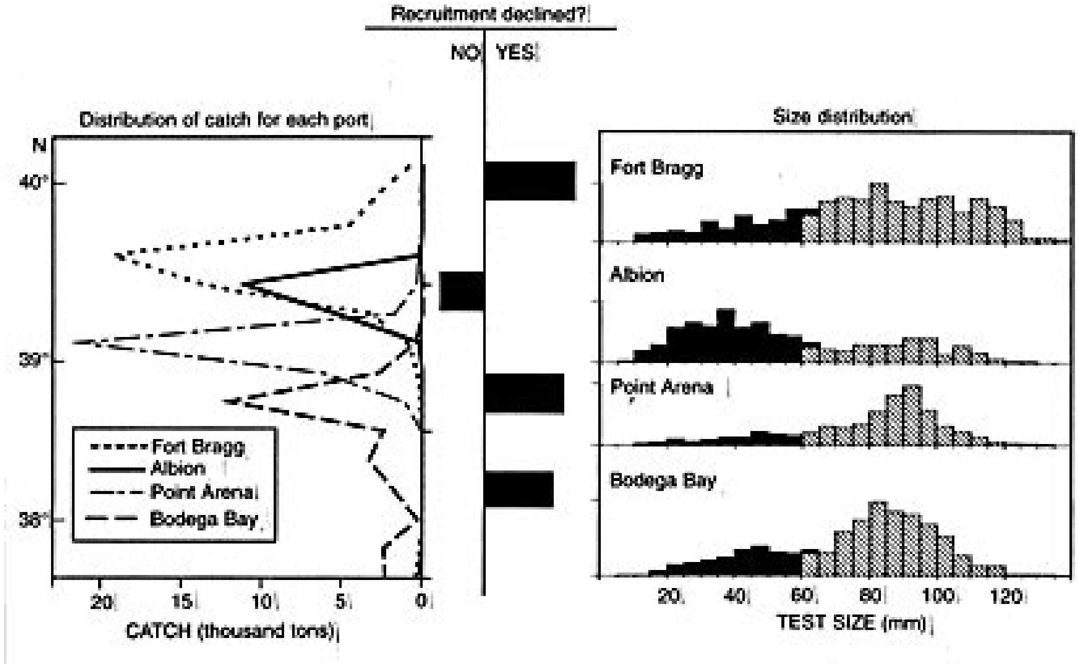

Fig. 5: A comparison of the decline in recruitment implied from Figure 1 at each of the four major ports of the fishery for red sea urchin to the level of recent recruitment indicated by size distributions in 1995 (after Fig. 4 of Wing *et al.* 1998b). The degree of decline in recruitment is taken to be the difference between the slopes of the lines indicating the decline in *cpue* and the decline in biomass expected on the basis of the changes in the size distribution, divided by the standard error (after Botsford *et al.* in prep.). The size distributions are taken from the location that contributes the most to each port (i.e. the peaks of the distribution curves in the plot on the left)

ing rates increase, only reserve spacings below a certain value produce sustainable populations (Fig. 4). Clearly, the nature of the trade-off between harvest and reserve spacing will depend on the dispersal pattern. Another interesting feature of these results was that, even in the unsustainable case, the population declined to zero much more slowly with reserves than without them (Quinn *et al.* 1993).

Knowledge of dispersal also provides valuable information for the purpose of spatially specific management that does not involve area closure. Motivated by the spatial differences in annual crab settlement to the north and south of Point Reyes, Wing *et al.* (1998a, b) formulated a simple model in which two subpopulations contributed to a larval pool in specified amounts and the larval pool redistributed larvae to the two subpopulations in specified fractions. Wing *et al.* (1998a) used their model to demonstrate an improvement in harvest made possible by knowing the redistribution pattern, i.e. the pattern learned through the research described in Wing *et al.* (1998b). The authors showed that there was a positive benefit to knowing the redistribution pattern, even if the relative contributions to the larval pool were unknown (as they are currently in the Point Reyes case), but that harvest could be further improved if they were determined.

Even before it is used in the actual formulation of spatially specific management strategies, knowledge of dispersal patterns can provide useful corroborative evidence or explanations for observed spatial patterns. California's fishery for red sea urchin provides examples on several scales. On a state-wide scale, monitoring in both northern and southern California has shown that settlement is much more sporadic in northern than in southern California (Ebert *et al.* 1994). This is consistent with the monitoring in northern California, in which substantial settlement was observed only twice in five years (Wing *et al.* 1998b). It is also consistent with oceanographic differences; southern California has much weaker upwelling (hence less offshore transport) than northern California. It is possible that the more frequently recruiting southern California populations can sustain a higher removal rate than can northern California.

On a scale of tens of kilometres, the pattern of recent recruitment to the fishery for red sea urchin shown in Wing *et al*. (1998b) provides a consistent explanation for results of an independent assessment of spatial variability in the impact of fishing. In response to the proposal that the declining northern California fishery was overfished, Botsford *et al*. (in prep.) compared the decline in abundance reflected by *cpue* to the decline in legal abundance to be expected from the "fishing up effect" on a virgin stock (i.e. the effect of removing the older individuals from the populations, Ricker 1975). Because harvesting rate varies over space in this type of fishery, Botsford *et al*. (in prep.) made this comparison for specific locations, each of the four major northern California ports, Fort Bragg, Albion, Point Arena and Bodega Bay (Fig. 2). The authors showed that, for one of the ports, Fort Bragg, abundance declined more rapidly than would be expected from fishing up at constant recruitment, so recruitment had declined. For Albion, the reverse was true. For the other two ports, a decline in recruitment was indicated, but the difference between the actual decline and the expected, constant recruitment decline were not significant.

These results regarding the degree to which recruitment appears from fishery data to have declined in each stock are consistent with the spatial pattern in recent settlement observed in the recent size distribution, which in turn is consistent with the upwelling/relaxation mechanism proposed in Wing *et al*. (1998b, Fig. 5). The port that showed the least decline in recruitment, Albion, is the port with the largest recent settlement, and presumably the largest settlement over long time periods.

DISCUSSION

Outlined herein is the way in which knowledge of the longshore pattern of dispersal can contribute to both a better understanding of population dynamics and better management. Contributions to population dynamics are best exemplified by the case of the Dungeness crab. The dynamics of metapopulations of linked subpopulations is much more complex than would be envisioned on the basis of the dynamics of individual subpopulations. The dispersal research provides an explanation for the observed scale of spatial variability that is consistent with modelling results and metapopulation level data. However, this picture is far from complete; there are additional elements of spatial and temporal variability. For example, mesocale variability in coastal circulation associated with embayments between promontories is not found along the straighter coastline north of central Oregon, so it is necessary to explore the effects of different dispersal patterns over part of the range.

Contributions to better management are best illustrated by the case of the red sea urchin in northern California. In that example, research on the nature of dispersal provides the basis for better management through the assignment of different rates of harvesting along the coast. It also provides a consistent explanation of the spatial pattern of the effects of past harvest; the distribution of areas that may be showing the effects of overfishing (i.e. a local decline in recruitment). The size distributions reflecting recent recruitment at some locations also provide the basis for expecting increased harvests at those locations during the next several years. This will also serve as an additional test of the mechanism proposed in Wing *et al*. (1998b), testing whether the influence of coastal circulation on settlement actually carries through to the fishery.

Both of these metapopulations also underscore a common research need involving dispersal, the need for information on the ultimate origin of larvae to complete knowledge of the dispersal paths. For the sake of efficiency, in order to avoid studying larvae that would end up as wastage, the present study has focused initially on the last part of the larval stage. However, it is clear that for both a better understanding of population dynamics and for management, it is necessary to know the early part of the dispersal path. With regard to the population dynamics of Dungeness crab, the spatial scale of longshore variability depends on the scale of dispersal pattern, from the beginning of dispersal to the end. Hence, it is important to verify that all retained larvae originate in the embayment, in other words, to determine how leaky each embayment is. With regard to management of the red sea urchin, any strategy involving marine reserves or rotating spatial harvest depends critically on knowing how far larvae are dispersed from each point. Also, an assessment of overfishing at each port is also hampered by lack of knowledge of the complete dispersal paths in this metapopulation. On current knowledge, it can be said that there has been a decline in recruitment at one location at least, but the degree to which local harvesting is responsible is unknown.

This study has focused so far on stability and variability of subpopulations within metapopulations, with little discussion of their persistence. The persistence of single populations has been investigated in the context of endangered marine fish populations (e.g. Cisneros-Mata, *et al*. 1997) and overfishing (Sissenwine and Shepherd 1987, Rosenberg *et al*. 1994). There is not as complete a general understanding of the persistence of age-structured populations with density-dependent recruitment as there is of stability, but some examples have been analyzed (e.g. Shelton 1987, Emlen 1995). The problem of overfishing has so far been handled by maintaining the fraction of virgin egg production above a specified number that seems to be safe on an empirical basis. This approach could be improved by also considering age structure, spatial structure and other characteristics that contribute to persistence (Rosenberg *et al.* 1994). For populations at an abundance low enough that the compensatory effects of density on recruitment are no longer operative, some results for random populations from population viability analysis may be useful (Tuljapurkar and Orzack 1980, Tuljapurkar 1982, Lande and Orzack 1988, Cisneros-Mata *et al.* 1997). However, Cisneros-Mata *et al.* (1997) recently tested the accuracy of the resulting estimates of extinction rates of long-lived fish populations and found that they may not hold when there is large variability in recruitment, a common occurrence.

Whereas the linear analysis and a few simulations provide some basis for estimating the persistence of single marine populations, there has been little investigation of the effects of linking them by varying levels of dispersal. However, it is clear that linking populations together through larval dispersal has the effect of increasing persistence (see Quinn and Hastings 1987, Gilpin and Hanski 1991). The probability of two independent populations becoming extinct will be reduced by linking them so that one can repopulate the other following an extinction. Moreover, considering the benthic adult phase in addition to the larval dispersal, "source" populations (i.e. net exporters of larvae), are able to sustain "sink" populations (i.e. net importers of larvae) which would not exist without dispersal (see Pulliam 1988). It is clear that the degree to which persistence is improved will depend critically on the nature of the dispersal pattern.

Larval dispersal is likely to be significant in benthic invertebrates in eastern boundary currents because of the strong longshore flow, and the ensuing dispersal patterns are likely to be complex and variable in time and space because of the strong meteorological forcing on the inner shelf. Larval periods of several months as found, for example, in the red sea urchin and the Dungeness crab described here, and in the loco *Concholepas concholepas* off Chile (J. C. Castilla, Pontificia Universidad Catolica de Chile, pers. comm.) suggest that larvae could be in the plankton through a major flow reversal such as the spring transition in the California Current (Strub *et al.* 1987, Largier *et al.* 1993). However, the value of these resources to coastal communities, national economies and natural heritage imply that continued research on this dispersal will be worth the effort, in terms of benefit to the understanding of variability in coastal benthic populations and their management. This implies that physical and biological oceanographers investigating recruitment should pay attention to processes that transport larvae settling successfully longshore, not just to the processes that lead to advective loss.

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