

SPATIAL AND TEMPORAL GENETIC PATCHINESS IN MARINE POPULATIONS AND THEIR IMPLICATIONS FOR FISHERIES MANAGEMENT

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ABSTRACT

A degree of genetic patchiness has been demonstrated in a variety of marine populations. When this “chaotic genetic patchiness” exists, populations a few kilometers apart may differ genetically by as much as those hundreds of km apart. Such genetic patchiness could be caused by any of several factors, including natural selection acting on a local level before or after settlement, and genetic drift before settlement. Hedgecock’s “sweepstakes-chance matching hypothesis” addresses the latter explanation, and is based in part on the observation of reduced genetic variability in young-of-the-year, relative to adult populations. This reduced genetic variability among recruits suggests that surviving young-of-the-year are the products of spawning by only a small fraction of the adult population, which, according to Hedgecock’s hypothesis, happened to produce their offspring at a place and time that was suitable for survival. The succession of such cohorts would then lead to the shifting genetic mosaic that is characteristic of marine populations displaying chaotic genetic patchiness. If generally true, this phenomenon has implications for all forms of fisheries management, including marine harvest refugia. To the extent that spawning success is spatially unpredictable, fisheries management should practice a degree of “spatial bet-hedging.” That is, within a biogeographical region of potentially panmictic larval transport, spawning biomass should be conserved broadly, in an attempt to ensure that propagules are available when and where favorable conditions for survival happen to occur.

CHAOTIC GENETIC PATCHINESS AND ITS CAUSES

Hedgecock (1994a, b) has recently reviewed the phenomenon of “chaotic genetic patchiness” in marine populations, a term used by Johnson and Black (1982) to describe small-scale, unpatterned, genetic heterogeneity among local populations. In many cases, populations separated by less than 10–100 km can be as genetically different as populations separated by 100–1,000 km. In addition, genetic composition may vary as much over time at one place as it does over large distances. Instances

of chaotic genetic patchiness have been described in populations from a variety of geographical areas and taxonomic groups, although most described cases are invertebrate animals (table 1). Additional cases that are consistent with Johnson and Black’s description, but were not recognized as such, may exist (e.g., Lacson and Morizot 1991). Furthermore, David et al. (1997) noted that detection of such fine-scale genetic patchiness may require large sample sizes.

While other geographic patterns of genetic structure have been described—including genetic differentiation among retention areas (e.g., Bernatchez and Martin 1995), widespread uniformity with little obvious underlying structure (e.g., Shulman and Bermingham 1995), and limited genetic variation at any spatial scale (e.g., Richardson and Gold 1997)—chaotic genetic patchiness may have important implications for fisheries management. In this paper, we attempt to bring attention to the topic of chaotic genetic patchiness in the context of fisheries management. We provide an overview of the potential causes for this phenomenon, emphasizing Hedgecock’s (1994a, b) “sweepstakes-chance matching” hypothesis, and we initiate discussion of the implications of Hedgecock’s hypothesis for fisheries management and marine no-take areas.

Chaotic genetic patchiness has been attributed to natural selection or to chance acting before settlement, or to natural selection acting after settlement (Johnson and Black 1982, 1984; Watts et al. 1990; Hedgecock 1994a, b). Natural selection acting after settlement has been observed in populations of invertebrates (e.g., Johannesson et al. 1995), producing genetic heterogeneity on very small scales. In these situations, genetic composition often shows clines that parallel environmental gradients, and in the absence of disturbance the genetic composition at one site is likely to remain constant, reflecting the consistent, site-specific effects of selection. However, several studies have shown that the genetic composition of a local population can vary over time (indicating a lack of consistent selection), and that the genetic composition of recruits can vary over time, both indicating that these cases of chaotic genetic patchiness are caused by factors acting prior to settlement (Johnson and Black 1982, 1984; Watts et al. 1990; Hedgecock 1994a, b).

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TABLE 1
 Some Examples of Chaotic
 Genetic Patchiness in Marine Populations

Organism and location	Reference
Limpet, <i>Western Australia</i>	Johnson and Black 1982, 1984
Crown-of-thorns starfish, <i>Great Barrier Reef</i>	Nash et al. 1988
Sea urchin, <i>Western Australia</i>	Watts et al. 1990
Bicolor damselfish, <i>Florida Keys</i>	Lacson and Morizot 1991
Queen conch, <i>Caribbean Sea</i>	Campton et al. 1992
Snail, <i>Western Australia</i>	Johnson et al. 1993
<i>Balanus</i> barnacles, <i>California</i>	Hedgecock 1994b
Northern anchovy, <i>California</i>	Hedgecock et al. 1994
Snail, <i>Sweden</i>	Johannesson et al. 1995
Purple sea urchin, <i>California</i>	Edmands et al. 1996
Clam, <i>France</i>	David et al. 1997

Variation in the genetic composition in recruits, which may produce genetic heterogeneity on a local level, can be produced by at least three processes. First, drift of larvae from different source populations, which themselves differ in genetic composition, may lead to variation in the genetic composition of recruits. Purcell et al. (1996) postulated that this might be responsible for temporal differences in the genetic composition of haddock on Georges Bank. Roberts (1997) also suggested that this process could have led to small-scale differences in the genetic composition of bicolor damselfish in the Florida Keys, as observed by Lacson and Morizot (1991). Shulman and Bermingham (1995) suggested that on a large scale, variation in currents can introduce novel genotypes into new areas, although they did not investigate particular episodes of larval transport leading to gene flow. Where there are large-scale differences in genetic composition, large-scale transport is always a means for generating temporal variation in genetic composition in local populations. However, in some presumed examples of this process—such as the Purcell et al. (1996) or Lacson and Morizot (1991) studies—other factors, as discussed below, could also have been important.

Another factor that could lead to genetic differences among recruits is natural selection acting on larvae prior to settlement. Johnson and Black (1984) suggested that this mechanism was responsible for temporal variation in recruits of a limpet off western Australia, citing in particular the genetic uniformity of the “cloud” of recruits arriving at their study areas at any one time, and correlations between weather conditions and the frequencies of particular alleles. Hedgecock et al. (1994) also thought that selection (among other factors) could have produced genetic heterogeneity in northern anchovy. David et al. (1997) discuss the difficulties of demonstrating selection during the larval phase, and Hedgecock (1994b) noted that selection explains clinal variation better than chaotic patterns.

Hedgecock (1994a, b) developed a third hypothesis for spatial and temporal genetic variation among recruits;

this mechanism was also mentioned by David et al. (1997). Hedgecock proposed that genetic variation among recruits might be due to large variance in reproductive success among adults, so that a resulting year class is the result of spawning by only a small portion of the adult population. This “instantaneous (genetic) drift effect” (David et al. 1997, p. 1,321) would then lead to reduced genetic variation among recruits, to differences between the genetic composition of recruits and the adult population as a whole, and, to the extent that different portions of the adult population contribute successful progeny in different years, to differences in the genetic composition of recruits over time. This variation in recruits then produces the “genetic mosaic fluctuating in time” (David et al. 1997, p. 1,321) which is characteristic of populations that demonstrate chaotic genetic patchiness. Hedgecock (1994a, b) postulated that spatiotemporal variation in oceanographic conditions, producing limited windows for larval survival, is responsible for the variation in reproductive success among adults. This “sweepstakes-chance matching” of place and time of spawning, he proposed, leads to random variation in the portion of the adult population that produces surviving offspring, and therefore to the variation in genetic composition of recruits observed in chaotic genetic patchiness.

Hedgecock (1994a, b) described two testable predictions of this hypothesis. One prediction is that genetic drift in the population as a whole should be measurable over time, demonstrating that effective population size is much smaller than actual population size. His study of oyster populations in Dabob Bay, Washington, suggested that effective population sizes were about 400 individuals in actual populations that were several orders of magnitude larger (Hedgecock 1994a). The second prediction was that recruits should show a smaller degree of genetic variation than the adult population, as a result of the “instantaneous drift” experienced between spawning and the establishment of the year class. Li and Hedgecock (1998) found that the genetic composition of young oyster larvae in Dabob Bay varied over time, in a manner consistent with Hedgecock’s hypothesis. Julian (1996) found reduced genetic variability in late pelagic juveniles of shortbelly rockfish relative to both adults and larvae off central California, also supporting Hedgecock’s prediction. In addition, the lowest genetic variability among pelagic juveniles in Julian’s study occurred in the most abundant patch of individuals, suggesting that selection, which would act to reduce numbers, was not the likely factor acting on the genetic composition of that population.

Therefore, in addition to evidence of microscale genetic heterogeneity and variation in the genetic composition of recruits, some genetic evidence exists to

support Hedgecock's hypothesis as well. Clearly, as noted by Hedgecock (1994b), much more work would be required to establish the generality of "sweepstakes-chance matching." Some recent reviews of marine population genetics barely (if at all) address chaotic genetic patchiness, focusing instead on how larval drift affects population subdivision (e.g., Shulman 1998), or on how postsettlement selection affects small- and large-scale population structure (e.g., Hilbish 1996). Other studies that do address chaotic genetic patchiness may not even mention Hedgecock's hypothesis as a potential explanation for the pattern (e.g., Edmands et al. 1996), or dismiss the hypothesis (e.g., Purcell et al. 1996).

To establish the generality of sweepstakes-chance matching, it will be important to demonstrate spatial and temporal variation in the genetic composition of recruits, to demonstrate the reduction of genetic variation in recruits relative to the adult population, and to compare the genetic composition of recruits to the genetic composition of adults from different portions of the geographical range (to rule out the effect of drift of larvae from genetically different portions of the population). It will also be important to determine whether features of population structure such as the distribution of adults and the dispersal of larvae influence the likelihood of sweepstakes-chance matching. However, the apparent occurrence of this phenomenon both in Dabob Bay oysters with a localized population and a larval phase lasting weeks, and in shortbelly rockfish with a coastwide population and a pelagic stage lasting months suggests that the sweepstakes-chance matching could occur in a variety of species. Finally, it will be important, but difficult, to distinguish between the effect of chance events and selection as factors influencing the genetic composition of recruits prior to settlement.

MANAGEMENT IMPLICATIONS OF THE SWEEPSTAKES-CHANCE MATCHING HYPOTHESIS

Chaotic genetic patchiness in itself may not have major implications for fisheries management. Any effects of localized selection after settlement may be difficult to detect in the mobile animals that make up most fisheries, and mobile animals may be less subject to localized selection after settlement than are sessile animals, because of their greater ability to choose conditions for living. If selection after settlement did exist, it is difficult to see how this would have a major effect on fisheries management, unless a fishery were to concentrate in one habitat or location and as a result exert a disproportionate mortality on a certain portion of the gene pool. The factors affecting genetic composition of recruits prior to settlement may have greater consequences, depending on the mechanism that is responsible. The effects of

natural selection on larvae are difficult to gauge, but might simply be considered a part of variability in recruitment. The effect of large-scale structure in populations and drift of larvae from different sources is an important consideration in fisheries management (Ryman and Utter 1987). This factor is also widely addressed in the context of marine harvest refugia (e.g., Carr and Reed 1993; Carr and Raimondi 1998; Morgan and Botsford 1998). In this paper, however, we wish to speculate primarily upon the effects of sweepstakes-chance matching on fisheries management and the establishment of harvest refugia.

The processes envisioned to produce sweepstakes-chance matching are not new ideas. Temporal variation in the survival of larvae within a season may be quite common, as indicated by the existence of temporal pulses of survivors (e.g., Methot 1983; Woodbury and Ralston 1991; Larson et al. 1994; Lenarz et al. 1995). Spatial variation in the survival of larvae is more difficult to demonstrate, but has been observed (e.g., Lasker 1978; Kjørboe and Johansen 1986; Frank 1988). Julian (1996) showed both a temporal and spatial component in the genetic composition and, presumably, survival of pelagic-stage shortbelly rockfish in 1994. As in many years with poor year-class strength in shortbelly rockfish (Lenarz et al. 1995), survival of larvae was greatest late in the 1994 season. In addition, the bulk of the surviving pelagic juveniles were strongly aggregated in two frontal areas, and one of these patches (the only one analyzed) was less diverse genetically than adults and newborn larvae, and its genetic composition differed significantly from the apparent spawning population (Julian 1996).

What is surprising in these results and in Hedgecock's general thesis is not that there is spatial and temporal variation in the survival of larvae, but that the pool of adults from which the survivors were drawn was so small as to affect the genetic diversity of the survivors. We think that the significance of this phenomenon for fisheries management lies primarily in the potential for stochastically varying, spatially restricted survival of larvae. Temporal variation in larval survival should not have a great effect on strategies for fisheries management unless different stocks spawn at different times or unless the fishery is for spawners. If the fishery is for spawners, and if periods of good larval survival cannot be predicted, then efforts might be taken to ensure that reasonable levels of escapement are allowed throughout the spawning season.

Stochastic spatial variation in the sources of successful larvae implies that, within a region that is panmictic and mainly self-replenishing in the long term, the particular sources of surviving recruits vary unpredictably over time. To the extent that this is true, we think that fisheries management should act to conserve the distri-

bution as well as the total spawning potential of an exploited population. For example, management of most commercially exploited species of rockfish seeks to preserve a minimal "spawning biomass per recruit" (Pacific Fisheries Management Council 1996). But if much of the spawning potential for a population has become restricted to a small area, leaving the remainder of the range with less potential for spawning, the probability that good conditions for larval survival will coincide with areas of larval production may be reduced. This may reduce the chance for good year classes. This thesis may be most applicable to species with a wide spawning distribution, and less applicable to species that migrate to restricted spawning grounds.

At face value, the spatial stochasticity of successful spawning would also argue for a spatial dispersion of harvest refugia, if these harvest refugia were to be the basis for managing the exploitation of a population. However, as pointed out by Steve Ralston (NMFS, Tiburon Laboratory, pers. comm.), if a certain percentage of the range were set aside as reserves and the locations of successful spawning in any given year were random and pointlike, it would not matter whether the reserve areas were distributed as one large area or an equal area of smaller reserves. But if the locations of successful spawning, though still random, were larger and had some chance of intersecting smaller reserves, it might be better if the reserves were dispersed rather than congregated. Again, this dispersion of reserves would increase the chance that some spawners would release larvae into conditions favorable for survival.

This premise is predicated on data showing both reduced genetic variation in recruits relative to the adult population and temporal variation in the genetic composition of recruits themselves. Consistent genetic composition of recruits over time in any area would indicate a consistent source of recruits or a consistent system of retention. How the sweepstakes-chance matching concept fits with concepts of larval drift and population structure such as larval retention and source/sink areas (Carr and Reed 1993; Roberts 1997; Carr and Raimondi 1998; Morgan and Botsford 1998; and others) must still be resolved. If genetic variation in recruits indicates stochastic variation in the times and places of larval survival, how can this be reconciled with systems of larval supply or retention that are treated as essentially deterministic?

At one extreme, recurrent patterns of larval distribution and settlement (e.g., Wing et al. 1995; Caselle and Warner 1996) may represent typical patterns of recruitment, but the larvae contributing to such patterns may have been derived from different sources within that recruitment-retention system. At another extreme, a recurrent pattern may exist, but may constitute only one

of several patterns of recruitment in an area. Another, more intermediate possibility is that the delivery of larvae to shore may follow a consistent pattern, but that the surviving larvae which enter such patterns may have come from a variety of areas, both within the geographical area of a local recruitment-retention system, and outside of that system. For example, the aggregations of pelagic juvenile shortbelly rockfish seen in 1994 are relatively common (associated with fronts related to upwelling), but the distinct genetic composition of fish in one such aggregation (Julian 1996) implies that there is no consistent source of shortbelly rockfish that come to exist in those aggregations. It would be very helpful to carry out fine-scale genetic analyses on some of the better-studied systems, because much of current thinking about the design of marine harvest refugia is based on defining regular patterns of larval sources, while the sweepstakes-chance matching hypothesis argues for greater stochasticity in larval sources.

The sweepstakes-chance matching hypothesis and its implications share some features with Cowen's (1985) study of recruitment off southern California and Baja California. He found that recruitment of the California sheephead was relatively consistent in the center of its range off central Baja California, and occurred to the north and south only during periods of unusual transport (what he termed "high-level" events). Pringle (1986) found a very similar pattern of larval distribution in spiny lobster. Cowen's findings contributed strongly to the notion of "sources and sinks" in marine populations (Ebeling and Hixon 1991), in that reproduction at the center of the range was seen as maintaining populations at the extremes of the range. However, another part of Cowen's thesis was that populations at the extremes of the range experience irregular recruitment because there are fewer sources of recruits than at the center of the range. The center of the range, in contrast, experiences more consistent recruitment in part because there are more places that could supply it with recruits, under a wider range of environmental conditions. In that respect, unless populations at the extremes of the range are sterile, they contribute to the consistency of recruitment at the center of the range and do not act entirely as sinks.

If larval survival varies stochastically in space as suggested by the sweepstakes-chance matching hypothesis, this aspect of Cowen's hypothesis may also act on a smaller spatial scale. That is, the consistency of recruitment at any point within a potentially panmictic region may depend on the number of different places within the region that can produce larvae, therefore increasing the chances that at least some larvae are produced in circumstances that permit their survival. This notion is similar to Cowen's idea that the effects of "low-level"

variation in transport are influenced by the proximity of larval sources.

We conclude that the potential for both “high-level” (El Niño-scale) and “low-level” variation in transport, and the potential for spatial variation in the conditions favorable for larval survival, mean that recruitment patterns and the relation between production of larvae and settlement of recruits can be variable. The potential for such variation may be as important as the presumed average conditions in the design of successful marine harvest refugia.

Comparison of the sweepstakes-chance matching hypothesis with Cowen’s (1985) discussion raises the issue of the spatial scale, in relation to the potential for dispersal, of various processes affecting the sources of larvae in a local population. The spatial component of variation in larval survival is the aspect of sweepstakes-chance matching that we consider to be most applicable to fisheries management, yet it is the aspect that is the least well documented, both genetically and ecologically. In addition, the spatial scale of processes involved in sweepstakes-chance matching are not well resolved at all. On large scales, variations in larval drift may influence both the demography (e.g., Cowen 1985; Pringle 1986) and the genetic composition (e.g., Shulman and Bermingham 1995) of local populations. The small-scale genetic variation seen in cases of chaotic genetic patchiness would suggest that factors may also act on a smaller scale. Therefore, if sweepstakes-chance matching is a process leading to chaotic genetic patchiness, we would suggest that it acts on a smaller scale. What that scale is, and how that scale is influenced by factors such as larval duration, remains to be determined. Once these features of spatial scale can be resolved, perhaps modeling studies can more critically evaluate the consequences of both small- and large-scale variation in recruitment on fisheries management and the design of marine no-take areas.

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