

EDDIES AND SPECIATION IN THE CALIFORNIA CURRENT

ROGER HEWITT

National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, CA 92038

ABSTRACT

Northern anchovy, Pacific sardine, and Pacific hake have population discontinuities in the vicinity of Punta Eugenia, Baja California. The same latitude has been described as a provincial boundary for several taxa, including coastal fishes, brachyurans, bryozoans, and molluscs. The distribution of wind stress over the surface waters of the California Current region has a persistent feature in the same area: the coastal impingement of a zone of surface water convergence, which elsewhere is parallel to the coast of the Californias and several hundred kilometers offshore. Semipermanent cyclonic eddies are evident north and south of Punta Eugenia, and it has been suggested that they play a role in the recruitment of pelagic larvae to the adult populations in these areas.

Limited communication between the eddies suggests a speciation mechanism that would be most effective on populations that time their spawning to coincide with strong eddy formation. One may also expect geminate species north and south of Punta Eugenia and few short-range endemics with long dispersal strategies along the coast of northern Baja California between the eddies.

RESUMEN

Existen discontinuidades en las poblaciones de anchoveta del norte, sardina y merluza en la zona de Punta Eugenia, Baja California. Esta latitud ha sido descrita como una frontera provincial de varios grupos taxonómicos, incluyendo peces costeros, braquiuros, briozoarios y moluscos. La distribución de esfuerzo del viento por las aguas de superficie de la región de la Corriente de California tiene una característica persistente en esta misma área, que es el encuentro con la costa de una zona de convergencia de aguas de superficie, que en otras partes ocurre paralela a la costa y a unos cientos de kilómetros afuera. Remolinos ciclónicos semipermanentes son evidentes al norte y al sur de Punta Eugenia, y se ha sugerido que éstos juegan un papel en el reclutamiento de larvas pelágicas a las poblaciones adultas en estas zonas.

La comunicación limitada entre los remolinos sugiere un mecanismo de especiación que sería más efectivo para poblaciones que fijan su época de desove

durante los períodos en que se forman fuertes remolinos. Puede esperarse encontrar especies geminadas al norte y al sur de Punta Eugenia y algunas especies endémicas de rango corto con estrategias de larga dispersión en la costa del norte de Baja California, entre los remolinos.

INTRODUCTION

Several coastal pelagic fish species display a population break in the vicinity of Punta Eugenia, Baja California. Distinct discontinuities in morphometric measurements, meristic counts, and proportion of selected protein polymorphs suggested restricted gene flow between populations north and south of approximately 28° N for *Engraulis mordax*, the northern anchovy (Hubbs 1925; McHugh 1951; Vrooman et al. in press), for *Sardinops caerulea*, the Pacific sardine (Clark 1947; McHugh 1950; Marr 1957, 1960; Sprague and Vrooman 1962; Vrooman 1964), and for *Merluccius productus*, the Pacific hake (Vrooman and Paloma 1977). Vrooman and Paloma (1977) referred to the southern population of *M. productus* as "dwarf hake" and suggested that it differs from *M. productus* and the more southern *M. angustimanus* at the species level. The southern populations of all three fishes (*Engraulis mordax*, *Sardinops caerulea*, and *Merluccius productus*) show similarities in some of the ways they differ from the northern population: growth is reduced after the first year resulting in a reduced maximum adult size, maturity occurs at an earlier age, and the life span is shorter; the southern forms have proportionally longer heads, longer snouts, and larger eyes.

The latitude of Punta Eugenia has been described as a provincial boundary for a wide variety of taxa including coastal fishes (Hubbs 1960), brachyurans (Garth 1960), bryozoans (Soule 1960), and molluscs (Hall 1964; Valentine 1966). These authors refer to a variously named warm-temperature fauna between Point Conception and Punta Eugenia and a distinct fauna of uncertain origin from Punta Eugenia south to Cabo San Lucas. Hubbs (1960) tentatively placed this region in the Panamic province but noted the "reduced tropical fauna," high endemism, and "insular characteristics" of the biota.

Superimposed on the distributions of coastal animals are the distributions of invertebrate species as-

sociated with oceanic water masses. The distribution of oceanic euphausiids and copepods, indicators of subarctic, equatorial, and central waters, have a common terminus at Punta Eugenia (Brinton 1962, 1967, 1973; Fleminger 1964, 1967). The junction of these distributions appears to move northward or southward in concert with temperature anomalies as described in CalCOFI Atlas Number 1 (Anonymous 1963) and by Wyllie and Lynn (1971), although shallow-water forms show a much clearer response than do deeper forms (Brinton 1960).

HYDROGRAPHY

The general hydrography off the coast of the Californias is determined by the California Current and is related to the anticyclonic circulation of the central North Pacific; however, significant features can be associated with local wind patterns and topography (Sverdrup et al. 1942; Smith 1968). Long-term monthly mean distributions of wind stress show alongshore flow throughout the year, weakest in the winter and strongest in the summer (Nelson 1977). Resolved on a 1° grid, however, net Ekman transport, proportional to and at right angles to the wind stress, shows considerable spatial variability. In general, an area of divergence parallels the coast, bounded by a zone of convergence 200-300 km from the coastline. The position of change from offshore divergence of surface water to convergence corresponds with the position of maximum wind stress, which intensifies, winter to summer, as the gradient between the semipermanent high pressure cell over the eastern Pacific Ocean and the low pressure cell over the southwest United States increases. The zone of convergence impinges the coasts at Punta Eugenia; this feature persists throughout the year and may preclude any poleward movement of water near the coast (Nelson 1977).

Surface current patterns, which describe cyclonic eddies in the Los Angeles Bight and southwest of Punta Eugenia, confirm Nelson's prediction (Bakun and Nelson 1977). Surface flow of the California Current appears to be diverted offshore at Point Conception and again at Punta Eugenia, while semipermanent eddies are apparent south of these headlands (Reid et al. 1958). Owen's (1980) description of baroclinic eddies and their persistence is in accord with this description.

DISCUSSION

The above-mentioned taxa have planktonic larval stages. The coastal eddies may play a role in recruitment to coastal adult populations by entraining a fraction of the larvae, thus offsetting to some extent

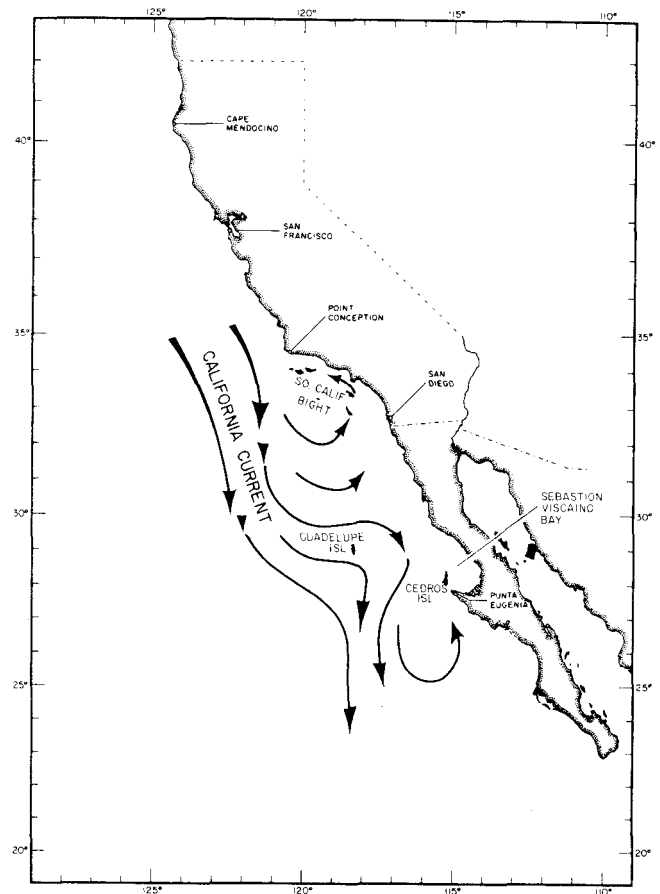


Figure 1. Large, persistent coastal eddies, south of Point Conception and Punta Eugenia, may entrain pelagic larvae and thus contribute to the recruitment to resident adult populations. Isolation of the eddies may constitute a speciation mechanism.

dispersion to the southwest via the California Current. Johnson (1960) has suggested such a mechanism for maintaining populations of *Panulirus interruptus*, the spiny lobster, in the Southern California Bight and southwest of Punta Eugenia. Boehlert (1977) recognized the possible importance of the Southern California Eddy to the recruitment of *Sebastes* spp., rockfishes. Early ichthyoplankton studies off the coast of the Californias found relatively few sardine eggs and larvae off northern Baja California and characterized these waters as a "marine desert" bounded by "rich" waters to the north and south (Anonymous 1952).

If the eddies are important to the process of recruitment, then the limited communication between them suggests a restricted gene flow between populations in the Southern California Bight and those south of Punta Eugenia. This postulated mechanism for speciation lends itself to several predictions:

1. Genetic differentiation between populations, within a species, should be greatest for those forms that time their spawning to coincide with

strong eddy formation as opposed to those forms that may time their spawning in response to other cycles (e.g. primary productivity).

2. There should be evidence of geminate species north and south of Punta Eugenia; e.g. *Labidocera trispinosa* and *L. johnsoni* (Fleminger 1975).
3. On the coast of northern Baja California, between the eddies, there should be a low proportion of dispersal types among sessile populations. A pelagic larval phase would imply dependence on long-range dispersal from the north; instead there should be selection for short pelagic phases or none at all.
4. The latitude of the hydrographic barrier may vary and be obscured by the convergence of oceanic water masses in the same general area which appears to be most pronounced in the upper layers.

ACKNOWLEDGMENTS

I am indebted to E. Brinton, A. Fleminger, W. Newman, R. Rosenblatt, and P. Smith for their willingness to indulge me on this subject.

LITERATURE CITED

- Anonymous. 1952. California Cooperative Sardine Research Program: Progress Rep. 1 January 1951 to 30 June 1952, 51 p.
- . 1963. Atlas of 10-meter temperatures and salinities 1949 through 1959. Calif. Coop. Oceanic Fish. Invest. Atlas No. 1.
- Bakun, A., and G. Nelson. 1977. Climatology of upwelling related processes off Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 19:107-127.
- Boehlert, G. 1977. Physiological and morphological adaptations in the surface-to-benthic migration of *Sebastes diploproa* (Pisces, Scorpaenidae). 1960 Ph.D. Dissertation, Scripps Institution of Oceanography, Univ. Calif. San Diego.
- Brinton E. 1960. Changes in the distribution of euphausiid crustaceans in the region of the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 7:137-146.
- . 1962. The distribution of Pacific euphausiids. Scripps Inst. Oceanogr. Bull. 8(2):51-270.
- . 1967. Distributional atlas of Euphausiacea (Crustacea) in the California Current region. Part I. Calif. Coop. Oceanic Fish. Invest. Atlas No. 5.
- . 1973. Distributional atlas of Euphausiacea (Crustacea) in the California Current region. Part II. Calif. Coop. Oceanic Fish. Invest. Atlas No. 18.
- Clark, F. 1947. Analysis of the populations of the Pacific sardine on the basis of vertebral counts. Calif. Fish Game Bull. 65, 26 p.
- Fleminger, A. 1964. Distributional atlas of calanoid copepods in the California Current region. Part I. Calif. Coop. Oceanic Fish. Invest. Atlas No. 2.
- . 1967. Distributional atlas of calanoid copepods in the California Current region. Part II. Calif. Coop. Oceanic Fish. Invest. Atlas No. 7.
- . 1975. Geographical distribution and morphological divergence in American coastal-zone planktonic copepods of the genus *Labidocera*. Estuarine Res. 1:342-419.
- Garth, J. 1960. Distribution and affinities of the Brachyuran Crustacea. Symp: The Biogeography of Baja California and Adjacent Seas. Syst. Zool. 9 (3 and 4):105-123.
- Hall, C. 1964. Shallow water marine climates and molluscan provinces. Ecology 45(2):226-234.
- Hubbs, C. 1925. Racial and seasonal variation in the Pacific herring, California sardine and California anchovy. Calif. Fish Game, Fish Bull. 8:1023.
- . 1960. The marine vertebrates of the outer coast. Symp: The Biogeography of Baja California and Adjacent Seas. Syst. Zool. 9 (3 and 4):134-147.
- Johnson, M. 1960. Production and distribution of larvae of the spiny lobster, *Panulirus interruptus* (Randall) with records on *P. gracilis* Streets. Scripps Inst. Oceanogr. Bull. 7(6):413-462.
- Marr, J. 1957. The subpopulation problem in the Pacific sardine, *Sardinops caerulea*. U.S. Fish Wildl. Serv., Spec. Sci. Rep., Fish. No. 208:108-120.
- . 1960. The causes of the major variations in the catch of the Pacific sardine, *Sardinops caerulea* (Girard). Proc. World Scientific Meeting on Biol. Sardines and Related Species. FAO/UN Vol. III:667-791.
- McHugh, J. 1950. Variations and populations in the clupeoid fishes of the North Pacific. Ph.D. Dissertation, Univ. Calif. Los Angeles.
- . 1951. Meristic variations and populations of northern anchovy (*Engraulis mordax*). Scripps Inst. Oceanogr. Bull. 6(3):123-160.
- Nelson, G. 1977. Wind stress and wind stress curl over the California Current. NOAA Tech. Rep., NMFS, SSRF-714, 87 p.
- Owen, R.W. 1980. Eddies of the California Current system: physical and ecological characteristics. In: D. M. Power (ed.), The California Islands. Proc. Multidisciplinary Symp., Santa Barbara Mus. Nat. Hist., p. 237-263.
- Reid, J., G. Roden, and J. Wyllie. 1958. Studies of the California Current system. Calif. Coop. Oceanic Fish. Invest. Rep., 1 July 1956-1 January 1958:27-57.
- Smith, R. 1968. Upwelling. Ocean Mar. Biol. Ann. Rev. 6:11-46.
- Soule, J. 1960. The distribution and affinities of the littoral marine bryozoa (Ectoprocta). Symp: The Biogeography of Baja California and adjacent seas. Syst. Zool. 9 (3 and 4):100-104.
- Sprague, L., and A. Vrooman. 1962. A racial analysis of the Pacific sardine (*Sardinops caerulea*) based on studies of erythrocyte antigens. N. Y. Acad. Sci. 97:131-138.
- Sverdrup, H., M. Johnson, and R. Fleming. 1942. The Oceans. Prentice Hall, 1087 p.
- Valentine, J. 1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. Limnol. Oceanogr. 11:198-211.
- Vrooman, A. 1964. Serologically differentiated subpopulations of the Pacific sardine, *Sardinops caerulea*. J. Fish. Res. Board Can. 21(4):691-701.
- Vrooman, A., and P. Paloma. 1977. Dwarf hake off the coast of Baja California, Mexico. Calif. Coop. Oceanic Fish. Invest. Rep. 14:67-72.
- Vrooman, A., P. Paloma, and J. Zweifel. In press. Subpopulations of the northern anchovy, *Engraulis mordax*. Calif. Fish Game 67(1).
- Wyllie, J., and R. Lynn. 1971. Distribution of temperature and salinity at 10 meters, 1960-69 and mean temperature, salinity and oxygen at 150 meters, 1950-68 in the California Current. Calif. Coop. Oceanic Fish. Invest. Atlas No. 15.