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COASTAL RETENTION AND LONGSHORE DISPLACEMENT OF MEROPLANKTON NEAR CAPES IN EASTERN BOUNDARY CURRENTS: EXAMPLES FROM THE CALIFORNIA CURRENT

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Nearshore larval retention mechanisms influence the dispersal and recruitment patterns for a wide variety of meroplanktonic species in eastern boundary regions. Areas of coastal larval retention associated with capes in eastern boundary currents provide important spatial structure to coastal populations of fish and invertebrates through their influence on longshore settlement variability. Some patterns observed in the northern California Current for three meroplanktonic species groups (crabs, sea urchins and rockfish) relative to two such apparent retention features are synthesized. It is found that spatial variability in settlement of crabs is predictable at the scale of headlands. Apparent timing of upwelling intermittency and variability on weekly time-scales, as indicated by temperature change, is critical to interannual settlement variability. The average magnitude of upwelling, measured by an upwelling index, is by comparison a poor predictor of interannual settlement variability. Distribution of planktonic larvae relative to a nearshore retention feature is dependent on taxon. These nearshore retention features may act as reservoirs for some taxa or as conduits to the coast for others, likely depending on larval behaviour, timing and cross-shelf location of release relative to upwelling features. The longshore variability in recruitment created by the above patterns can result in differences in subpopulation productivity. For example, strength of a cohort of sea urchins varies longshore in accordance with proximity to retention features.

One of the largest obstacles to understanding the population dynamics of organisms with dispersing larvae is a lack of knowledge of the mechanisms by which larvae disperse and the resultant spatial variability in settlement and eventual recruitment into adult populations. This shortcoming hampers the ability to predict a population's response to harvest and other stresses, and remains one of the fundamental problems in studies of marine populations. Simply stated, the problem is that most exploited invertebrates and some fish are made up of fairly discrete sedentary adult subpopulations spread along a coastline, together forming a network of populations connected by larval dispersal. However, the mechanisms for transition from production of eggs through the larval phase to settlement, particularly the physical processes acting on the larval phase, are not well known. For example, there are few known relationships between stock size and recruitment for invertebrates, and environmental variability is often a better predictor of reproductive success (e.g. Caputi 1993).

The spatial variability in success of reproduction could be high in coastal populations. That is, in a given year, a very small fraction of the population could contribute to most of the reproduction of the system as a whole, described as a "sweepstakes-chance matching of reproductive activity with oceanographic conditions conducive to spawning, fertilization, larval development and recruitment" (e.g. Hedgecock 1994). This could occur as an even contribution from subpopulations longshore. For example, if early spawning individuals produced successful larvae in a given year, they may make up similar proportions of the spawning biomass between subpopulations. Another possibility is that successful larvae are produced from a particular location, as with a strong source population (e.g. Pulliam 1988). These possibilities, particularly the latter, present risk to those concerned with managing coastal populations for harvest or predicting their response to other types of perturbation and underlie the critical need to understand the spatial scale of larval sources. This concern is particularly relevant to coastal marine populations whose subpopulations are vulnerable to serial depletion from harvest (e.g. Quinn *et al*. 1993). Managers and population biologists are starting to recognize that the spatial dynamics of larval dispersal in these systems is a vital parameter, as important as growth and death (e.g. Botsford *et al*. 1994).

This question is particularly irksome in the California Current system, where many commercially important coastal species such as Dungeness crab *Cancer magister*, red sea urchin *Strongylocentrotus franciscanus* and rockfish *Sebastes* spp. have motile

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larval forms in the plankton during the spring transition to the upwelling season and have peaks of settlement into onshore adult populations during the upwelling season (Wyllie Echeverria 1987, Wing *et al*. 1995a). Therefore, the motile larval phase is subject to strong offshore and equatorward advective fields within the current system. Investigators have for some time been interested in how these species, and others with similar timing of reproduction, maintain themselves at latitude, and are transported onshore into their juvenile habitat. For example, Parrish *et al*. (1981) proposed that meroplanktonic species would not reproduce during the upwelling season in order to conserve larvae by avoiding offshore advection. This immediately raises the question: why do certain species reproduce during upwelling, and how do they pass through the flow field and successfully recruit into adult populations?

Investigations have focused on the two-dimensional, cross-shelf influences of upwelling on larval distributions and transport onshore. For example, Roughgarden *et al*. (1988) and Farrell *et al*. (1991) proposed that settlement of barnacles into the intertidal zone was controlled by periods when an upwelling front that had collected high concentrations of cyprids collided with the shore during wind relaxation. In Oregon, maintenance of plankton distributions across the shelf have been explained by similar two-dimensional views of upwelling (Peterson *et al*. 1979, Wroblewski 1980). However, such two-dimensional models do not provide a comprehensive view of the complex flow patterns that influence the transport and distribution of meroplanktonic larvae longshore.

Understanding the timing and longshore variability of physical influences on larval dispersal is important to understanding of population dynamics of coastal populations, and their response to harvest (e.g. Possingham and Roughgarden 1990, Botsford *et al*. 1994, 1998). Motivated by these considerations, a field study was initiated in 1992 to try to understand how coastal oceanographic processes influence the transport of crab and sea urchin larvae to coastal populations around Bodega Head (38.2°N) in the northern California Current. The focus has been on answering what controls the longshore and temporal variability of settlement in these species groups.

MATERIAL AND METHODS

A synthesis is provided here of several field studies that investigate the influence of variability in the physical environment on the shelf off northern California on the timing and longshore distribution of larval abundance, settlement and cohort strength in meroplanktonic species during upwelling. These studies focus on mesoscale variability in settlement rates brought about through interaction of larvae with physical oceanographic features that act on the scale of capes and headlands (hundreds of km). The focus is on timing of interactions that occur on weekly and seasonal scales, and interannual variability is inferred from processes on the scale of the intermittency of upwelling (6–10 days, Send *et al*. 1987). Data are presented on three species groups: crabs, sea urchins and rockfish, which share the characteristics of having relatively sedentary adults confined to coastal habitat and motile larvae that are found over the continental shelf, and primarily settle during upwelling season (Wyllie Echeverria 1987, Wing *et al*. 1995a).

Oceanographic data

Previous studies of the longshore, three-dimensional dynamics of transport during intermittent upwelling provided a model for the physical influences on larval distribution for the present studies. These came primarily from investigations during the Coastal Ocean Dynamics Experiment (CODE) off northern California, which described some of the longshore (three-dimensional) transport dynamics on the shelf during bouts of upwelling-favourable winds followed by more quiescent periods (Kosro 1987, Send *et al*. 1987). Along this coast, and probably in other upwelling systems around the world, transport could be primarily longshore rather than cross-shelf during upwelling and relaxation.

Physical oceanographic data used in this study were collected from a variety of sources. Satellite, advanced very high resolution radiometer (AVHRR), images of the region and daily upwelling indices were obtained from the U.S. National Oceanic and Atmospheric Administration (NOAA), time-series of temperature, and salinity from the Bodega Marine Laboratory (BML) at Bodega Head, and temperature and wind from NOAA buoys NDBC 46013 (38°14′N, 123°20′W), and NDBC 46026, (37°45′N, 122°42′W).

Settlement collectors

During spring and summer (30 April–13 August) of 1992–1996, the settlement rates of crabs and sea urchins were monitored on a weekly time-scale at a number of sites along the northern California coast from the Gulf of the Farallones (37.5°N) to Albion

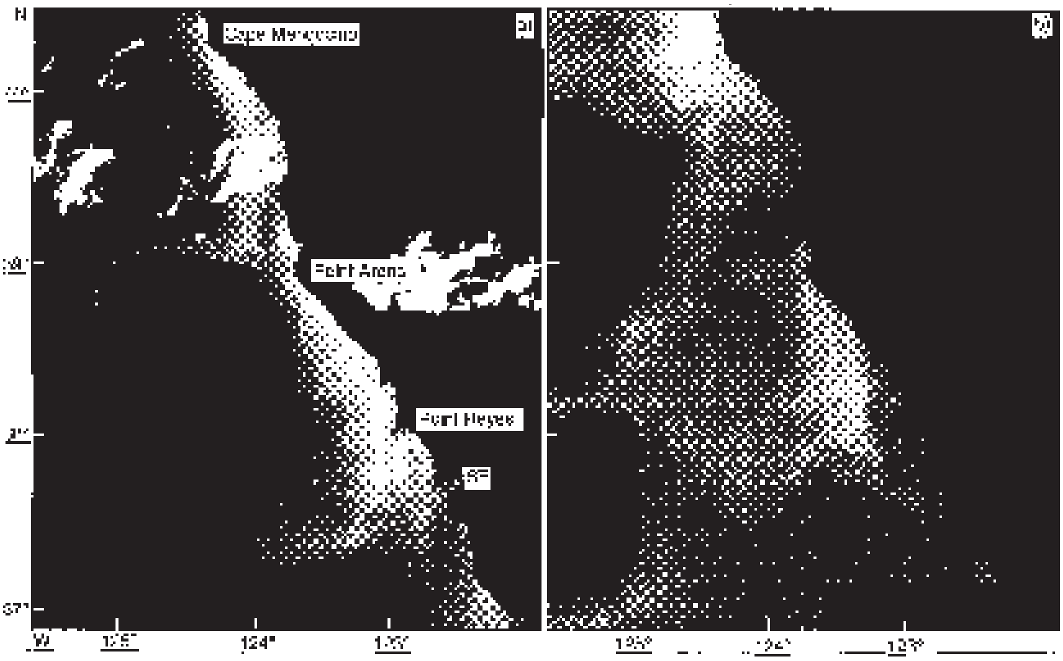

Fig. 1: AVHRR images of surface temperature on (a) Day 163, during upwelling (12 June 1993, 23:00 GMT) and (b) Day 212, during relaxation from upwelling (31 July 1993, 15:00 GMT). The temperature scale ranges from 9°C (light grey) to 16°C (darkest gray)

(39.2°N). At each site, six collectors were deployed over 100 m of the 10–12 m isobath. These arrays of collectors were exposed to the dominant ocean swell and set on a rocky substratum. They were retrieved every 5–8-days.

Each settlement collector consisted of 4 × 7-inch, wood-backed scrub brushes, with polypropylene bristles attached to a polypropylene line with net floats for buoyancy, anchored to the bottom with a 25 kg cement anchor so that when deployed they floated 0.5–1 m above the bottom. Upon retrieval, the collectors were washed in freshwater and the resulting material sorted for newly settled crabs and sea urchins, which were fixed in ethanol for later identification.

Species identifications of crabs was accomplished using guidelines given by Lough (1974). In all, nine species of juvenile crabs were identified: *Cancer antennarius*, *C. productus*, *C. magister*, *C. gracilis, Petrolisthes cinctipes*, *Loxorhynchus crispatus*, *Pugettia producta*, *Pagarus* spp. and *Hemigrapsus nudus*. For analysis of settlement variability, only total crabs have been considered here, including all crab species.

Larval survey

During 1994, planktonic larval distributions and the hydrography both south and north of Point Reyes were sampled during upwelling to test whether high concentrations of crab larvae and rockfish larvae were retained in the upwelling shadow in the lee of the point. Data for this study were collected from 18 to 22 June 1994 aboard the NOAA R.V. *David Starr Jordan*. Shipboard sampling followed 3 × 60-mile longshore transects at distances of 3–5 (coastal), 25 (shelf) and 50 (oceanic) miles offshore. Each station of the transects was sampled with a 0.236 m^2 Bongo net (505 and 333μm nets), cast to 70 m, and a CTD cast during the day, and with a 0.133 m^2 neuston net during the night. Current profiles were collected with an RDI Acoustic Doppler Current Profiler (ADCP) continuously during the sampling, and surface temperature and salinity were collected continuously with a Seabird thermosalinograph. During the cruise, AVHRR images (Channel 4) of the region were supplied to the ship from NOAA Coast Watch and used to direct sampling. The volume of water filtered by each net was recorded with calibrated General

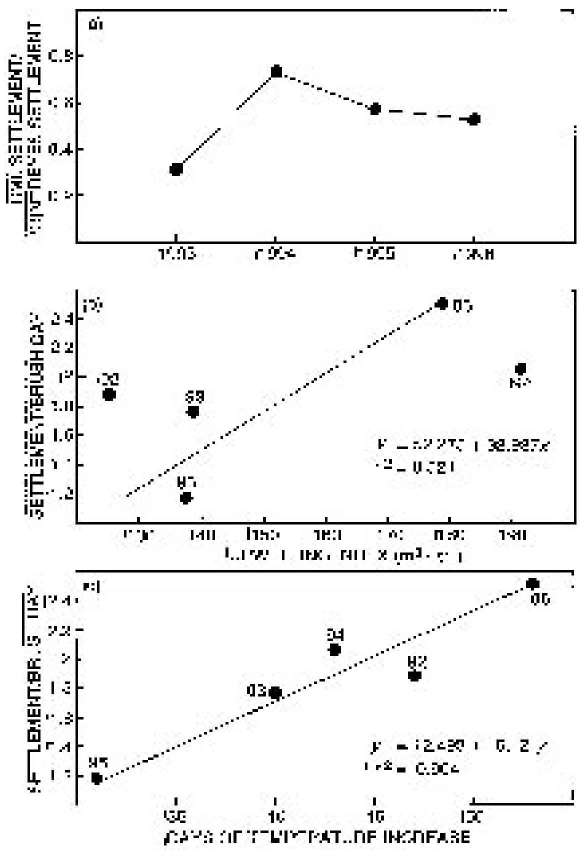

Fig. 2: (a) Ratio of seasonal settlement rates (30 April–13 August) of total crabs from Bodega Head and Point Reyes, 1993–1996; (b) relationship between seasonal settlement rates for total crabs at Bodega Head and average seasonal upwelling index (30 April–13 August) at 39°N, 122°W; (c) relationship between seasonal settlement rates for total crabs at Bodega Head and number of days of rapid sea surface warming between 30 April and 13 August for each year from 1992 to 1996

Oceanic flowmeters, and depth and temperature profiles were double-checked with a temperature/depth recording devise (TDR). All plankton samples were preserved in Etoh, which was replenished after 12 h.

Cohort strength

During 1995 and 1996, size frequencies of red sea urchin *S. franciscanus* populations were determined from 11 different sites extending from Bodega Head (38.2°N) to Casper Cove (39.4°N) in northern California. Using SCUBA, collections were made of more than 300 individuals from each of two depth strata (5–10 and 10–20 m) at each site. Test diameter was measured to the nearest millimetre. At Bodega Marine Life Refuge, Salt Point Marine Reserve and Casper Cove Closure Area, additional sites outside those protected areas were sampled and combined for the analysis.

RESULTS

Oceanographic data

Daily temperature, salinity and wind stress data indicated fluctuations in upwelling and provided evidence for the longshore northward flow of warm water of low salinity during upwelling-relaxation, which typically lasted several days. Wind relaxation typically result in rapid sea surface warming at Bodega Head, combined with lowering in salinity as water from the Gulf of the Farallones is advected longshore (Wing *et al.* 1995a). These patterns in sea surface temperature can be seen in satellite images of the region. For example, Figure 1a shows a typical temperature pattern during upwelling, with a well developed coastal jet, cold filaments at the capes, with evidence for retention of warm waters in Drakes Bay, in the lee of Point Reyes, and in the offshore eddy near Point Arena. Typically, sea surface temperature patterns during relaxation from upwelling indicate the movement of warm water from the lee of Point Reyes polewards along the coast, and warm water from the offshore eddy at Point Arena onshore north of that cape and poleward along the coast to Cape Mendocino (Fig. 1b).

Settlement collectors

Spatial variability in settlement of crabs is predictable at the scale of headlands. For example, the ratio of seasonal settlement rates for total crabs for the years 1993–1996 at Point Reyes (Point Reyes was not sampled in 1992) and at Bodega Head indicates that settlement is consistently greater at the Point Reyes site, which lies inside the retention area (Fig. 2a). Intra-annual timing of upwelling intermittency and variability on weekly time-scales is critical to interannual settlement variability (Wing *et al.* 1995a, b). The number of days in a settlement season (30 April–13 August) associated with relaxation conditions is a good predictor of seasonal settlement rates for total crabs at Bodega Head (Fig. 2c). Relaxation conditions are defined

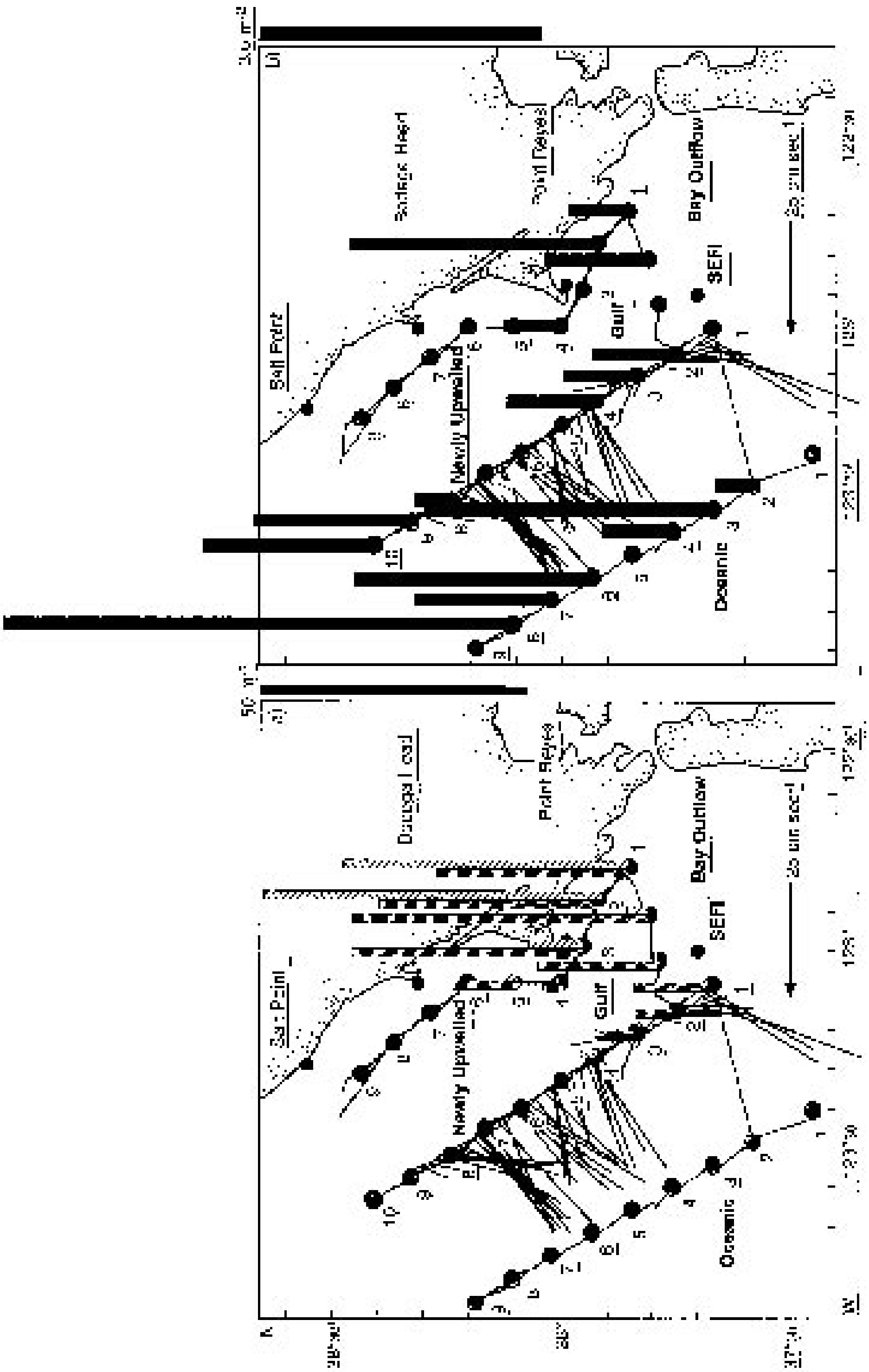

Fig. 3: Horizontal distribution of (a) total crab, megalopae and zoeae and (b) total rockfish larvae during R.V. *David Starr Jordan* Cruise 9406 (18–22 June 1994). Vertical bars indicate number of crab larvae in a 1 m^2 column of water 70 m deep. Flow vectors are from the upper 16 m of the water column

here as periods of >2 days, when the temperature increases at a rate that indicates advective warming (see Send *et al*. 1987) and salinity decreases indicating the arrival of "Gulf" waters. In contrast, the average seasonal upwelling index is a poor predictor of seasonal settlement rates at Bodega Head (Fig. 2b). Further, it is shown that relaxation from upwelling conditions is necessary but not sufficient to ensure successful settlement at this site: timing of the relaxation events is perhaps just as important as magnitude. For example, early season events can dominate the magnitude of seasonal settlement for crabs (Wing *et al*. 1995b).

Larval surveys

The upwelling jet seawards of Point Reyes and the upwelling shadow in its lee were evident from the velocity structure in the surface layer and the temperature and salinity signature of the surface waters during the larval survey (Figs 1, 3). Distinct frontal regions marked the boundaries between four water masses: newly upwelled (<10.5°C, >33.7 × 10^{-3}); oceanic (>11.5°C, <33.7 × 10^{-3}); San Francisco Bay outflow (11–12°C, <33.0 × 10^{-3}); and a mixture of these water type origins as "Gulf" water (>10.5°C, >33.7 × 10^{-3} – Fig. 3). These fronts and water masses were characterized by different species compositions of meroplankton. In general, crabs of several species were found in all stages of larval development within, but not outside of, the retention feature in the lee of Point Reyes (Fig. 3a). In contrast, rockfish were found at the boundary between newly upwelled and Gulf water in the retention region, and in high concentration offshore in oceanic waters (Fig. 3b).

Cohort strength

The unusually large cohort of newly settled juvenile sea urchins observed on settlement collectors in 1992 (Wing *et al*. 1995a) shows up as a distinct transient mode in the adult size distributions collected in 1995 (Fig. 4). It was found that the sites with the largest transient mode in the smaller size-classes are those where warm water currents, observed in AVHRR images of the region, most often impinge on the coast during relaxation from upwelling (Fig. 4). This observation lends support to the argument that settlement variability is controlled by longshore relaxation flows that are found on a weekly time-scale in this region. In this case, longshore variability of recruitment on the mesoscale is coherent with two separate oceanographic features that impact the coast during upwelling relaxation.

DISCUSSION

Marine populations with complex life cycles may persist only if closure of the life cycle is achieved at a specific location. Following the member/vagrant hypothesis, patterns of abundance are defined by the geographic pattern over which closure takes place (Sinclair 1988). Absolute abundance is proportionate to the total area of closure, and variability in abundance is controlled by intergenerational losses of individuals (Sinclair 1988). Further, such losses are often dominated by physical forcing in populations with a motile larval stage (Sinclair 1988). This aspect of variability in marine populations is perhaps the most elusive and most important structuring feature in these systems, recognized early in Hjort's (1914) second hypothesis for the maintenance of fish populations. This notion that dynamics of populations can be controlled by supply has been reiterated by Roughgarden *et al*. (1988). The examples cited here, and others, demonstrate that larval supply is variable longshore, dependent on mesoscale physical forcing on the motile larval phase that acts on a weekly time-scale (e.g. Wing *et al*. 1995b). The implications for population dynamics of predictable larval transport and longshore settlement variability driven by the hydrology around capes in eastern boundary currents are many.

Along the west coast of North America, when upwelling-favourable winds (longshore equatorward) are strong, centres of upwelling typically form in areas where the coastal topography produces local maxima in the wind field, such as on the downwind side of some capes (e.g. Dorman and Winant 1995). Examples can be demonstrated clearly in the California Current from sea surface temperatures at Cape Mendocino, Point Arena, Davenport, Point Sur and Point Conception. Upwelling and equatorward wind-forcing produces a pronounced coastal jet of cold, high salinity water that typically separates from the coast to form cold filaments at headlands (e.g. Cape Mendocino, Point Arena, Kosro and Huyer 1986). On the equatorward side of these filaments, warm-core eddies form (e.g. Washburn *et al*. 1993). In the lee of some capes (e.g. northern Monterey Bay, Santa Barbara Channel, Drakes Bay), warm coastal water is retained close to shore during upwelling-favourable conditions and forms persistently stratified warm cyclones (e.g. Wing *et al*. 1995b, Graham and Largier 1997). Sea surface temperature patterns suggest that similar features are found at other eastern boundary current locations (e.g. St Helena Bay, Table Bay, Gulf of Farallones, Monterey Bay, Bahia Conception, Ria de Arosa, Cap Vert). When upwelling-favourable winds relax, warm buoyant water from areas of

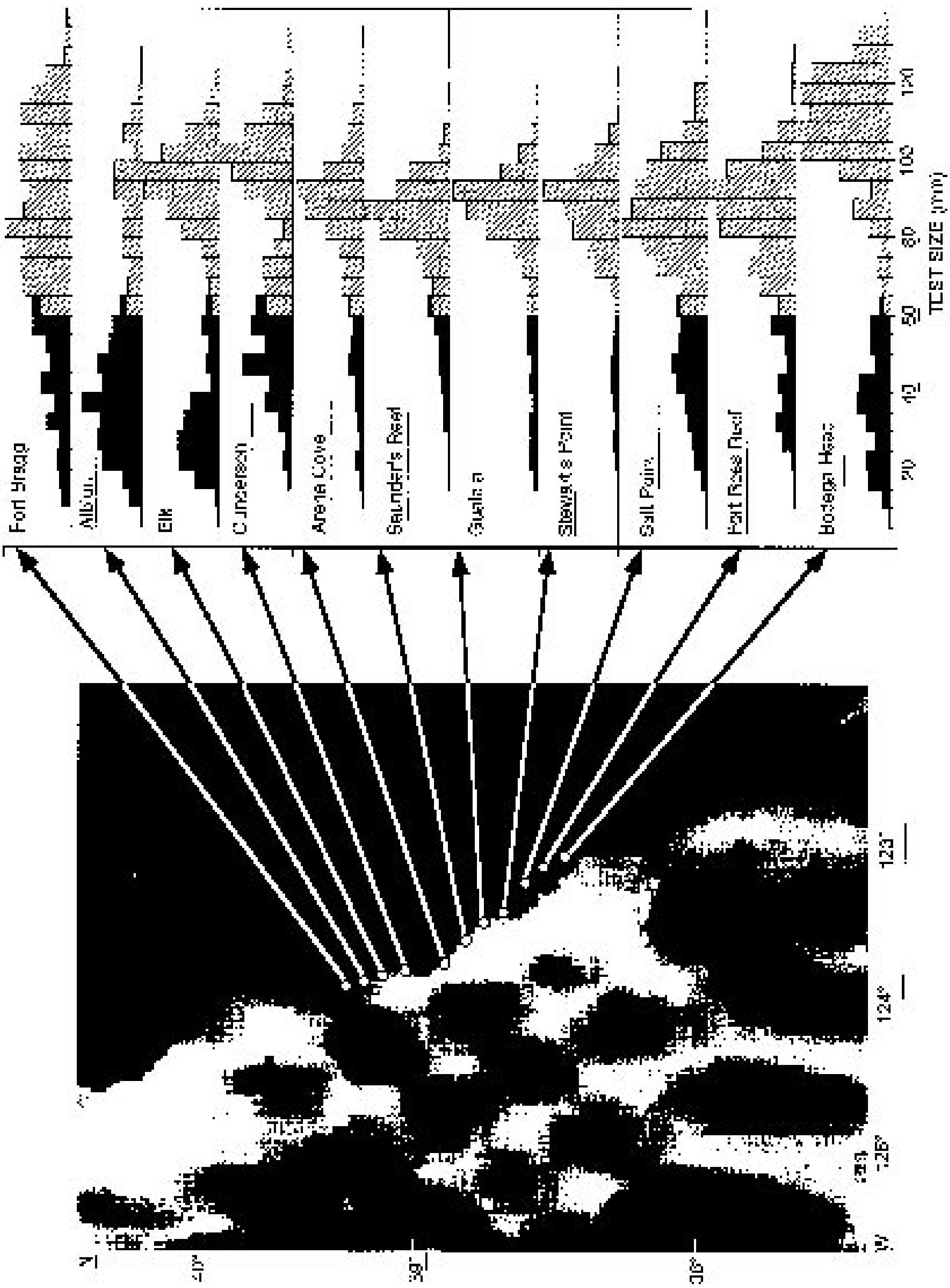

Fig. 4: Map of size distributions of Red Sea urchins *S. franciscanus* relative to two relaxation features in northern California. Size distributions show frequency of different test sizes in each of 11 subpopulations (each n >600). Dark bars indicate individuals <60 mm. AVHRR image shows sea surface temperature during typical relaxation conditions, ranging from 9°C (lightest grey) to 16°C (darkest grey)

coastal retention propagates polewards as coastally trapped, buoyancy-forced currents, providing significant longshore transport (Send *et al.* 1987). Similarly, offshore warm features may expand across the shelf towards shore and become coastally trapped as poleward-moving features.

The distribution of meroplanktonic larvae on the inner shelf is strongly influenced by these areas of coastal retention. Contrasted here are the patterns observed in the distribution of crab larvae, which are released shorewards of the coastal upwelling jet, with rockfish larvae that can be released seawards of the coastal upwelling jet. Observations of larval distributions and hydrography suggest that coastal retention features such as the upwelling shadow at Point Reyes act to retain crab larvae, during all stages of development, close to shore. Rockfish larvae, on the other hand, are found in high concentration offshore, but are also found nearshore associated with the retention feature. This feature provides a pathway along which distinct pools of both types of larvae are likely to be transported to suitable juvenile habitat within the Gulf and to the north.

The above-mentioned horizontal patterns in distribution of larvae are translated into patterns of longshore variability in settlement via poleward transport during upwelling relaxation. Evidence for this comes from several sources. For example, it is apparent that crab settlement north of Point Reyes is more dependent on relaxation conditions than crab settlement to the south, and that the warm poleward-moving relaxation features contain high concentrations of crab larvae (Wing *et al.* 1995b). This mechanism is responsible for predictable spatial pattern in settlement, demonstrated by the more continuous and more abundant settlement of crabs at Point Reyes, within the retention feature, than at Bodega Head, outside the retention feature (Fig. 2a, Wing *et al.* 1995b).

Intra- and interannual variability in settlement are relatively unpredictable and highly influenced by timing of oceanographic events that are intermittent and/or remotely forced. For example, Wing *et al.* (1995a) show that crab settlement variability at Bodega Head is influenced by relaxation events on a weekly time-scale. It is shown here that interannual variability in settlement is more a function of weekly variability in indicators of local oceanographic conditions (days that temperature is increasing) than seasonal averages of an upwelling index (e.g. Figs 2b, c).

Physically modulated gradients of settlement rate influence longshore patterns of productivity across adult population networks. For example, at the coast-wide scale, Ebert *et al.* (1994) show that settlement of sea urchins is more sporadic at a site in northern California, where upwelling is strong, than in southern California where physical oceanographic conditions are more quiescent. Further, Ebert and Russell (1988) suggest that settlement of purple sea urchins varies between headlands. This study shows that the longshore variability in strength of a single cohort of sea urchins *S. franciscanus* is similar to patterns of warming during upwelling relaxation in northern California. These differences in local cohort strength may drive longshore variability in adult productivity in this species. This suggests a direct effect of coastal circulation on the productivity of adult subpopulations via differences in larval supply.

Such patterns of productivity may produce heterogeneity in the impact of a fishery on coastal populations. In terms of Sinclair (1988), areas may be removed from the region of life-history closure, and represent a tear in the fabric of the metapopulation. Knowledge of the longshore variability of recruitment can be used to alleviate this consequence of harvest. This is shown in a simple model by Wing *et al.* (1998, and see Tuck and Possingham 1994), who demonstrate that knowledge of the longshore patterns of recruitment can be used to decrease risk of overfishing in a metapopulation.

Spatial and temporal variability of year-class strength in coastal populations is strongly influenced by physical variability in shelf environments, particularly in eastern boundary currents where upwelling produces strong advection acting on the larval phase of meroplanktonic species. Upwelling dynamics and its influence on larval dispersal and supply for some coastal populations varies on a weekly time-scale and on the mesoscale in the California Current system. Physical oceanographic variability on similar scales is important in other eastern boundary systems (e.g. Benguela, Humboldt and Canary currents). These scales of variability are likely important structuring agents in the formation and spatial structure of year-class strength within coastal population networks in many eastern boundary currents, including the Benguela.

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LITERATURE CITED

BOTSFORD, L. W., MOLONEY, C. L., HASTINGS, A., LARGIER, J. L., POWELL, T. M., HIGGINS, K. and J. F. QUINN 1994 — The influence of spatially and temporally varying oceanographic conditions on meroplanktonic populations. *Deep-Sea Res. II* **41**: 107–145.

BOTSFORD, L. W., WING, S. R. and J. L. LARGIER 1998 — Population dynamic implications of larval dispersal in meroplanktonic populations. In *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources*. Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington. *S. Afr. J. mar. Sci.* **19**: 131–142.

CAPUTI, N. 1993 — Aspects of spawner-recruit relationships, with particular reference to crustacean stocks; a review. *Aust. J. mar. Freshwat. Res*. **44**: 589–607.

DORMAN, C. E. and C. D. WINANT 1995 — Buoy observations of the atmosphere along the west coast of the United States, 1981–1990. *J. geophys. Res*. **100**(C8): 16029–16044.

EBERT, T. A. and M. P. RUSSELL 1988 — Latitudinal variation in size structure of the west coast purple sea urchin: a correlation with headlands. *Limnol. Oceanogr*. **33**: 286–294.

EBERT, T. A., SCHROETER, S. C., DIXON, J. D. and P. KALVASS 1994 — Settlement patterns of red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in California, USA. *Mar. Ecol. Prog. Ser*. **111**: 41–52.

FARRELL, T. M., BRACHER, D. and J. ROUGHGARDEN 1991 — Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnol. Oceanogr*. **36**(2): 279–288.

GRAHAM, W. M. and J. L. LARGIER 1997 — Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. *Continent. Shelf Res*. **17**: 509–532.

HEDGECOCK, D. 1994 — Does variance in reproductive success limit effective population sizes of marine organisms? In *Genetics and Evolution of Aquatic Organisms*. Beaumont, A. R. (Ed.). London; Chapman & Hall: 122–134.

HJORT, J. 1914 — The fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P-v. Réun. Cons. perm. int. Explor. Mer* **20**: 228 pp.

KOSRO, P. M. 1987 — Structure of the coastal current field off northern California during the Coastal Ocean Dynamics Experiment. *J. geophys. Res*. **92**(C2): 1637–1654.

KOSRO, P. M. and A. HUYER 1986 — CTD and velocity surveys of seaward jets off northern California, July 1981 and 1982. *J. geophys. Res*. **91**(C6): 7680–7690.

LOUGH, R. G. 1974 — Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast, 1969–1971. Ph.D. thesis, Oregon State University: 299 pp.

PARRISH, R. H., NELSON, C. S. and A. BAKUN 1981 — Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr.* **1**(2): 175–203.

PETERSON, W. T., MILLER, C. B. and A. HUTCHINSON 1979 — Zonation and maintenance of copepod populations in the Oregon upwelling zone. *Deep-Sea Res*. **26**(5): 467–494.

POSSINGHAM, H. P. and J. ROUGHGARDEN 1990 — Spatial population dynamics of a marine organism with a complex life cycle. *Ecology* **71**: 973–985.

PULLIAM, H. R. 1988 — Sources, sinks and population regulation. *Am. Naturalist* **132**: 652–661.

QUINN, J. F., WING, S. R. and L. W. BOTSFORD 1993 — Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus. Am. Zool*. **33**: 537–550.

ROUGHGARDEN, J., GAINES, S. and H. POSSINGHAM 1988 — Recruitment dynamics in complex life cycles. *Science* **241**: 1460–1466.

SEND, U., BEARDSLEY, R. C. and C. D. WINANT 1987 — Relaxation from upwelling in the Coastal Ocean Dynamics Experiment. *J. geophys. Res*. **92**(C2): 1683–1698.

SINCLAIR, M. 1988 — *Marine Populations. An Essay on Population Regulation and Speciation*. Washington Sea Grant Program, Seattle; University of Washington Press: 252 pp.

TUCK, G. N. and H. P. POSSINGHAM 1994 — Optimal harvesting strategies for a metapopulation. *Bull. mathl Biol*. **56**: 107–127.

WASHBURN, L., SWENSON, M. S., LARGIER, J. L., KOSRO, P. M. and S. R. RAMP 1993 — Cross-shelf sediment transport by an anticyclonic eddy off northern California. *Science* **261**: 1560–1564.

WING, S. R., LARGIER, J. L., BOTSFORD, L. W. and J. F. QUINN 1995a — Settlement and transport of benthic invertebrates in an intermittent upwelling region. *Limnol. Oceanogr.* **40**: 316–329.

WING, S. R., BOTSFORD, L. W., LARGIER, J. L. and L. E. MORGAN 1995b — Spatial structure of relaxation events and crab settlement in the northern California upwelling system. *Mar. Ecol. Prog. Ser*. **128**: 199–211.

WING, S. R., BOTSFORD, L. W. and J. F. QUINN 1998 — The impact of coastal circulation on the spatial distribution of invertebrate recruitment, with implications for management. In *Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management*. Jamieson, G. S. and A. Campbell (Eds). *Spec. Publ. Can. J. Fish. aquat. Sci*. **125**: 285–294.

WROBLEWSKI, J. S. 1980 — A simulation of the distribution of Acartia clausi during Oregon upwelling, August 1973. *J. Plankt. Res*. **2**: 43–68.

WYLLIE ECHEVERRIA, T. 1987 — Thirty-four species of California rockfishes: maturity and seasonality of reproduction. *Fishery Bull.*, Wash. **85**: 229–250.