

***Ecological Archives A/E/M000-000-A#* {ESA Publications Office will assign this number}**

S. A. Navarrete, B. L. Broitman, and B. A. Menge. Year. Interhemispheric comparison of recruitment to rocky intertidal communities: pattern persistence and scales of variation. *Ecology* VOL: pp-pp.

Appendix A. A description of species ecology and field and statistical methods, a table showing temporal decorrelation scales and spatial scales of synchrony in recruitment rates, a table showing results of nested ANOVA on the maximum autocorrelation coefficient between lags 6–12 for each species and site, and a list of references.

Species Ecology

Along the Oregon-Northern California (OR-NCA) mussels *Mytilus* spp are conspicuous sessile species in the mid and mid-low intertidal zones from Alaska to Baja California (Dethier and Duggins 1988). The California mussel *M. californianus* is the dominant competitor for space and can exclude all other mussel, barnacle and algal species from the rock surface in the mid and low shores, whenever other controlling processes (e.g. predation) are removed (Paine 1974). The mussel *M. trossulus* (= *M. edulis* in earlier literature), is a native species that occupies the lower shore as well as patches within the beds of *M. californianus* from northern California to Alaska (Suchanek 1981, Rawson et al. 1999, Anderson et al. 2002). The species can attain high abundance, forming extensive temporary monocultures in the low shore of some sites in the Oregon and Washington coasts (Menge et al. 1994, Navarrete and Menge 1996). Along the central Chile coast (CC), the mussel *Perumytilus purpuratus* is the dominant competitor for space in the mid and low intertidal shore, while *Semimytilus algosus* can be locally abundant at some, but not most sites of the central coast (Broitman et al. 2001, Navarrete and Castilla 2003, Navarrete et al. 2005). The mussel *Brachidontes granulata* occurs at most sites in central and northern Chile, but it is usually found in crevices in the mid and low shore as well as in shallow subtidal habitats, but it never forms extensive beds. Recruitment of all these mussel species is captured by Tuffy pad collectors (see below) and are considered in this study.

Along the mid and high intertidal zones along the northeastern Pacific, the acorn barnacle *Balanus glandula* can dominate quickly colonize and completely cover the rock surface whenever bare space becomes available (Connell 1970, Gaines et al. 1985, Farrell 1989). The smaller acorn barnacle, *Chthamalus dalli* is also common in the low, mid and upper shore, but it is generally competitively displaced by *Balanus glandula* and other species (Farrell 1991, Navarrete 1996). Along the coast of central Chile, two chthamalid barnacle species, *Jehlius cirratus* and *Notochthamalus scabrosus*, occupy the upper intertidal zone, usually into the splash zone, way above the high tide mark, with the former species expanding slightly higher into the intertidal zone (Castilla 1981, Broitman et al. 2001).

All these sessile species produce free-swimming larvae. According to laboratory studies, all species examined have larval development times between 9 (*M. californianus*) and 35 days (*M. trossulus*), which were pooled together in analyses (see below). All the other species had pelagic larval durations between 15–22 days, depending on rearing temperature (Campos and Ramorino 1979, Ramorino and Campos 1979, 1983, Strathmann 1987, Venegas et al. 2000, Grantham et al. 2003).

Field Methods

The artificial collectors used to quantify larval recruitment of mussels and barnacles have been described in detail before, including discussions of their advantages and limitations (Menge et al. 1994, Menge et al. 1997, Martínez and Navarrete 2002, Navarrete et al. 2002). Briefly, plastic mesh pads (Tuffys,™ The Clorox Company, Oakland, CA) were used to quantify mussel recruitment while 10 x 10 cm plexiglass or PVC plates covered with SafetyWalk™ (3M Company, Saint Paul, MN) were used to quantify barnacle recruitment along the coasts of Chile and California-Oregon.

Five to eight replicate collectors were fastened to the rock with a stainless-steel screw in the mid intertidal zone (mussels and barnacles in Oregon, mussels in Chile) and the upper zone (barnacles in Chile) of each site, and replaced approximately every month. Mid zone collectors in Oregon were at about +1.5 to + 1.8 m above MLLW, with a total tidal range of about 4 m. Mid zone collectors in Chile were at about 0.9 m above the LLW and high zone collectors at about 1.45 m above LLW, with a total tidal range of about 1.8 m. The high intertidal zone was preferred for barnacles in Chile because chthamalid species recruit heavily at this elevation and it is where the bulk of the adult populations are found (Navarrete and Castilla 1990, Lagos et al. 2005, S.Navarrete and R. Venegas, *unpublished data*). Vertical differences in position of barnacle collectors between hemispheres should not influence conclusions because (1) we do not combine data between hemispheres to perform analyses, and (2) vertical differences in barnacle recruitment along central Chile are consistent across sites (Lagos et al. 2005).

Mussel and barnacle recruitment rates were standardized to the number of individuals per collector (Tuffy ~100 cm³, plate = 100 cm²), per day by dividing recruit numbers by the days the collectors were in the field. While most sites were visited monthly, sometimes they were visited bimonthly due to their remote location and rough ocean conditions. Dividing by the number of days in the field helped adjust for these differences. Our estimates of recruitment were likely to be underestimates due to post-settlement mortality of recruits that occurred after deployment and before we replaced the collectors. Quantification of post-settlement mortality across these large spatial scales represents a major challenge, especially considering that the environmental factors causing mortality of early stages can be highly variable over time (Gosselin and Quian 1997, Berger et al. 2006) Although mortality is likely to vary through time, with a combination of steady background mortality and occasional pulses of mortality due to bouts of unusually stressful conditions, we reasoned this mortality is unlikely to introduce consistent biases among sites that were selected to have as nearly similar environmental conditions as possible in the first place (see below). Moreover, as reasoned by (Hughes et al. 1999), the large magnitude of variation in recruitment across sites (CV ~ 200%) is unlikely to be produced by mortality after settlement alone as the plates were

exposed for less than two months. Finally, since the total mortality of individuals should be some increasing function of time after settlement, and since over the 8 years of the study collectors have been in the field varying numbers of days, one should expect a negative correlation between days of collector exposure in the field and recruitment rate. This does not occur.

Although some have reported success in identifying recruits of the North American mussels *M. californianus* and *M. trossulus* (Martel et al. 1999), we found that using morphology to identify these species was unreliable. The relative proportions of each species undoubtedly varied among sites in NCA-OR, but the temporal patterns were generally very consistent, with a single autumnal peak of recruitment (B. Menge, *unpublished data*). Furthermore, no bimodality in location of larvae in the water column has been detected (G. Rilov et al. *unpublished data*), suggesting that both mussels vary similarly. We thus analyzed NCA-OR mussels as a single taxon.

The number and location of study sites was determined in part by accessibility and other logistical constraints, but sites were selected to be as similar as possible in terms of geomorphology, wave exposure, and habitat type. Details of sites and general descriptions of communities are provided elsewhere (Broitman et al. 2001, Menge et al. 2004). We used linear interpolation between sampling dates to standardize monthly recruitment rates to fall between the first day and the last day of each month across the sampling period. Not all sites were started at the same time and some sites (in Oregon) were terminated before 2004. The maximum number of months a site was monitored was 108 and the minimum was 40.

Statistical Methods

To determine whether there were coherent patterns of seasonality in recruitment within sites and across the region, we calculated the monthly “climatologies” in mussel recruitment as the mean recruitment for each calendar month of the year (note that usually climatologies are expressed as deviations from the long-term mean). Standard deviations (expressed as percentage of the mean, CV) were then obtained for the same calendar month, either across the different years (measure of temporal change in seasonality), or across different sites (measure of spatial change in seasonality). To determine whether there were repeatable cycles in recruitment time series of each species, such as seasonal or intra-seasonal cycles, and to quantify the temporal scale at which monthly recruitment becomes temporally decorrelated (decorrelation scale), we calculated the rank-based temporal autocorrelation of each time series at each site, considering each site as a replicate time series. We then averaged the resulting rank-correlations at each temporal lag to provide an average “regional autocorrelation” for each species. It must be noted that standard error and Confidence Intervals calculated across sites will excessively inflate Type II error rates because emphasis is placed on specific time-lags. Instead, seasonality is expected to vary somewhat across sites, showing up as strong autocorrelations between lags 6 and 12. Therefore, for each species and site we selected only the maximum autocorrelation between lags 6–12 months as a unique and independent estimate of the intensity of seasonality. These values were then compared using a nested ANOVA with Regions (OR-NCA, CC), Species nested within regions and sites as replicates nested within

species.

Estimates of variance components at the two spatial scales used in the sampling design were obtained through the maximum-likelihood method implemented in SAS computing software, which uses the W-transformation developed by Hemmerle and Hartley 1973. Before fitting the model, months in which there was no recruitment across sites were eliminated from the database. No transformations were applied to the resultant non-zero recruitment matrix. Monthly estimates of variance were then averaged to provide average variance components of each species at scales of meters and sites for the entire 8 years of the study and expressed as proportion of the total variance for the species. Note that we do not test hypotheses about the significance of these variance components.

Quantification of the temporal persistence of the spatial pattern of recruitment was based on correlations among sites ranked from highest to lowest recruitment within each continent from one month to the next. This is comparable to an autocorrelation, but for the spatial structure of recruitment. In this manner, a correlation near 1 at a lag of one month means that the ranking of all sites remains nearly unchanged from one month to the next. Correlations closer to zero mean that the sites fluctuate over time. Rank correlations were preferred over parametric Pearson correlations because we wanted to focus on among-site variation and avoid the influences of regional-scale discontinuities or sites with unusually high recruitment that could drive the patterns. Only lags shorter than 36 mo were interpreted. Similar analyses were performed to examine pattern persistence at the scale of a collector. In this case, we examined the change in Spearman rank correlation of collectors meters apart within each site over the different time lags. Unfortunately, these analyses could only be performed for OR-NCA sites (16 for mussels, 14 for barnacles, respectively), where for a period of ~4 years the spatial location of each larval collector was recorded. In Chile there was no tracking of the position of collectors.

The characteristic spatial scale (Bjørnstad et al. 1999) in the monthly recruitment process was estimated through the spatial non-parametric covariance function (NCF). Using 1000 Monte Carlo bootstrap estimators of the covariance matrix of recruitment rates between sites varying distances apart, we calculated a spatial spline correlogram function from which we derived the regional correlation and estimated the spatial length scale of recruitment synchrony for each species (Bjørnstad et al. 1999). This method was preferred over the Mantel correlogram because it prevented the binning of spatial distance, allowing us to make more direct comparisons between continents.

All analyses were carried out using Matlab 7 R14.0.2 (The Mathworks, Natick, Massachusetts, USA), R 2.2.1 (R Foundation for Statistical Computing, Vienna, Austria) and SAS 9.0 for Windows (SAS Institute, Cary, North Carolina, USA).

TABLE A1. Temporal decorrelation scales and spatial scales of synchrony in recruitment rates for (A) Mussels and (B) Barnacles in the Oregon-northern California (OR-NCA) and central Chile (CC) regions. In the case of *Notochthamalus*, the temporal persistence of recruitment rates was nonsignificant at any time-lag, hence the length is 0 months. For *Brachidontes*, the spatial scale could not be resolved (n.s.). In

both cases, the lack of a characteristic scale suggests that the spatial and temporal frequency of the sampling scheme were inadequate to resolve characteristic scales of variation in recruitment rates of these species.

	Temporal (months)	Spatial (km)
Mussels		
Mytilus, OR-NCA	2	234
Perumytilus, CC	1	262
Semimytilus, CC	3	294
Brachidontes, CC	1	n.s.
Barnacles		
Balanus, OR-NCA	1	228
Chthamalus, OR-NCA	2	230
Notochthamalus, CC	0	235
Jehlius, CC	1	265

TABLE A2. Results of nested ANOVA on the maximum autocorrelation coefficient between lags 6–12 for each species and site. Species were considered nested within Region (OR-NCA, CC) and sites as replicates nested within species.

Source of Variation	df	SC	<i>F</i>	<i>P</i>
Region	1	1.14	15.22	0.0080
Species(Region)	6	0.45	2.45	0.0301
Error	96	2.94		

LITERATURE CITED

Anderson, A. S., A. L. Bilodeau, M. R. Gilg, and T. J. Hilbish. 2002. Routes of introduction of the Mediterranean mussel (*Mytilus galloprovincialis*) to Puget Sound and Hood Canal. *Journal of Shellfish*

Research 21:75–79.

Berger, M. S., A. J. Darrah, and R. B. Emlet. 2006. Spatial and temporal variability of early post-settlement survivorship and growth in the barnacle *Balanus glandula* along an estuarine gradient. *Journal of Experimental Marine Biology and Ecology* 336:74–87.

Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: analyzing pattern and processes of population synchrony. *Trends in Ecology and Evolution* 14:427–432.

Broitman, B. R., S. A. Navarrete, F. Smith, and S. D. Gaines. 2001. Geographic variation in southern Pacific intertidal communities. *Marine Ecology Progress Series* 224:21–34.

Campos, B., and L. Ramorino. 1979. Larval and early benthic stages of *Brachidontes granulata* (Bivalvia: Mytilidae). *Veliger* 22:277–283.

Castilla, J. C. 1981. Perspectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile central. II. Depredadores de alto nivel trófico. *Medio Ambiente* 5:190–215.

Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecological Monographs* 40:49–78.

Dethier, M. N., and D. O. Duggins. 1988. Variation in strong interactions in the intertidal zone along a geographical gradient: a Washington-Alaska comparison. *Marine Ecology Progress Series* 50:97–105.

Farrell, T. M. 1989. Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. *Journal of Experimental Marine Biology and Ecology* 128:57–73.

Farrell, T. M. 1991. Models and mechanisms of succession: an example from a rocky intertidal community. *Ecological Monographs* 61:95–113.

Gaines, S., S. Brown, and J. Roughgarden. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67:267–272.

Gosselin, L. A., and P. Y. Quian. 1997. Juvenile mortality in benthic marine invertebrates. *Marine Ecology Progress Series* 146:265–282.

Grantham, B. A., G. L. Eckert, and A. L. Shanks. 2003. Dispersal potential of marine invertebrates in diverse habitats. *Ecological Applications* 13:s108–s116.

Hemmerle, W. J., and H. O. Hartley. 1973. Computing maximum likelihood estimates for the mixed AOV model using the W-transformation. *Technometrics* 15:819–831.

- Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 1999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397:59–63.
- Lagos, N., S. A. Navarrete, F. Véliz, A. Masuero, and J. C. Castilla. 2005. Meso-scale spatial variation in settlement and recruitment of intertidal barnacles along central Chile. *Marine Ecology Progress Series* 290:165–178.
- Martel, A. L., C. Robles, K. Beckenbach, and M. J. Smith. 1999. Distinguishing early juveniles of eastern Pacific mussels (*Mytilus* spp.) using morphology and genomic DNA. *Invertebrate Biology* 118:149–164.
- Martínez, P., and S. A. Navarrete. 2002. Temporal and spatial variation in settlement of the gastropod *Concholepas concholepas* in natural and artificial substrata. *Journal Marine Biological Association, U.K.* 82:257–264.
- Menge, B. A., E. L. Berlow, C. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64:249–286.
- Menge, B. A., C. Blanchette, P. T. Raimondi, T. L. Freidenburg, S. Gaines, J. Lubchenco, D. P. Lohse, G. Hudson, M. M. Foley, and J. Pamplin. 2004. Species interaction strength: Testing model predictions along an upwelling gradient. *Ecological Monographs* 74:663–684.
- Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997. Benthic-pelagic links and rocky intertidal communities: bottom-up effects on top-down control? *Proceeding of the National Academy of Sciences USA* 94:14530–14535.
- Navarrete, S. A. 1996. Variable predation: Effects of whelks on a mid intertidal successional community. *Ecological Monographs* 66:301–322.
- Navarrete, S. A., B. Broitman, E. A. Wieters, G. R. Finke, R. M. Venegas, and A. Sotomayor. 2002. Recruitment of intertidal invertebrates in the southeast Pacific: inter-annual variability and the 1997-1998 El Niño. *Limnology and Oceanography* 47:791–802.
- Navarrete, S. A., and J. C. Castilla. 1990. Barnacle walls as mediators of intertidal mussel recruitment: effects of patch size on the utilization of space. *Marine Ecology Progress Series* 68:113–119.
- Navarrete, S. A., and J. C. Castilla. 2003. Experimental determination of predation intensity in an intertidal predator guild: dominant versus subordinate prey. *Oikos* 100:251–262.
- Navarrete, S. A., and B. A. Menge. 1996. Keystone predation: interactive effects of two predators on their main prey. *Ecological Monographs* 66:409–429.

Navarrete, S. A., E. Wieters, B. Broitman, and J. C. Castilla. 2005. Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top down control. *Proceedings of the National Academy of Sciences USA* 102:18046–18051.

Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15:93–120.

Ramorino, L., and B. Campos. 1979. Desarrollo larval y postlarval de *Perumytilus purpuratus* (Lamarck, 1819). Bivalvia: Mytilidae. *Anales Museo Historia Natural, Valparaíso, Chile* 12:207–218.

Ramorino, L., and B. Campos. 1983. Larvas y postlarvas de *Mytilidae* de Chile (Mollusca: Bivalvia). *Revista de Biología Marina, Valparaiso* 19:143–192.

Rawson, P. D., V. Agrawal, and T. J. Hilbish. 1999. Hybridization between the blue mussel *Mytilus galloprovincialis* and *M. trossulus* along the Pacific coast of North America: evidence for limited introgression. *Marine Biology* 134:201–211.

Strathmann, M. F. 1987. Reproduction and development of marine invertebrates of the northern Pacific coast. University of Washington Press, Seattle, Washington, USA.

Suchanek, T. H. 1981. The role of disturbance in the evolution of life history strategies in the intertidal mussels *Mytilus edulis* and *Mytilus californianus*. *Oecologia* 50:143–152.

Venegas, R. M., V. Ortiz, A. Olguín, and S. A. Navarrete. 2000. Larval development of the intertidal barnacles *Jehlius cirratus* and *Notochthamalus scabrosus* (Cirripedia: Chthamaloidea) under laboratory conditions. *Journal of Crustacean Biology* 20:495–504.

[\[Back to A/E/M000-000\]](#)