SCALE-DEPENDENT CHANGES IN THE IMPORTANCE OF LARVAL SUPPLY AND HABITAT TO ABUNDANCE OF A REEF FISH

J. Wilson White[1,3] and Jennifer E. Caselle[2]

[1]*Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106 USA*
[2]*Marine Science Institute, University of California, Santa Barbara, California 93106 USA*

Abstract. While there is great interest in the degree to which local interactions "scale-up" to predict regional patterns of abundance, few studies in marine systems have simultaneously examined patterns of abundance at both the large scale (tens of kilometers) typical of larval movement and the small scale (meters) typical of post-settlement interactions. We addressed this gap by monitoring larval supply, adult survivorship, and giant kelp (*Macrocystis pyrifera*, a primary habitat-forming species) abundance for 13 populations of kelp bass (*Paralabrax clathratus*) spread over ~200 km in the Santa Barbara Channel, California, USA. At the small, within-site scale, both recruitment and adult survivorship of kelp bass were density-dependent and positively related to kelp abundance. At the larger, among-site scale, the spatial pattern of adult kelp bass abundance was predicted well by the pattern of kelp bass larval supply, but there was a consistent negative spatial relationship between kelp abundance and kelp bass larval supply despite the positive effects of kelp on kelp bass at the smaller spatial scale. This large-scale negative relationship was likely a product of a channel-wide spatial mismatch between oceanographic conditions that favor kelp survival and those that concentrate and distribute fish larvae. These results generally support the recruit–adult hypothesis: kelp bass populations are limited by recruitment at low recruit densities but by density-dependent competition for food resources and/or predator refuges at high recruit densities. At the same time, spatial variation in kelp abundance produced substantial spatiotemporal heterogeneity in kelp bass demographics, which argues for a multispecies, metacommunity approach to predicting kelp bass dynamics.

Key words: density dependence; giant kelp; kelp bass; larval supply; Macrocystis pyrifera; Paralabrax clathratus; *population dynamics; recruitment; Santa Barbara Channel, California, USA; spatial scale; survivorship; temperate reef fish.*

INTRODUCTION

A major goal of ecology is to characterize processes that generate large-scale patterns of species abundance. However, precise observations are often most tractable at relatively small spatial scales, so there is great interest in the degree to which results from such efforts "scale up" (Chesson et al. 2005). In general, extrapolation to larger spatial scales is less successful when large-scale environmental heterogeneity alters or reverses patterns generated by smaller-scale processes (Levin 1992, Downes and Keough 1998). For example, the population dynamics of many demersal marine species may be sensitive to processes occurring both at the smaller, within-population scale typical of interactions among benthic juveniles and adults, such as competition and predation (reviewed by Menge 2000, Hixon and Jones 2005), and at the larger, among-population scale of oceanographically driven pelagic larval movement (Kinlan and Gaines 2003).

While it is commonly asserted that a sensible description of marine population dynamics must incorporate both large- and small-scale processes (Kritzer and Sale 2004), few studies have actually done so. Widespread observations that large- and meso-scale oceanographic processes often produce consistent spatiotemporal patterns of recruitment (e.g., Cowen 1985, Hamilton et al. 2006) have inspired efforts to use oceanographic simulation models to describe and predict metapopulation dynamics (e.g., James et al. 2002). For simplicity, such models often assume that within-population processes are spatially invariant, so spatial differences in population size arise from dispersal-scale processes only. However, post-settlement mortality and growth may alter spatial patterns of abundance and size established at settlement (Jones 1991) and a growing number of studies document between-population variation in rates of mortality, growth, and fecundity (Gust 2004, Johnson 2006, White 2007). Metapopulation models incorporating such variation in post-settlement processes can therefore yield unexpected results (Kritzer and Davies 2005).

An alternative approach to describing marine population dynamics focuses on the importance of small-scale processes such as predation and competition (e.g.,

Menge 2000). This approach is often inspired by the observation that the dynamic stability of a marine metapopulation hinges on the density-dependent regulation of some demographic rate in at least one local population (Armsworth 2002). In many species, such regulation takes the form of density-dependent mortality arising from competition for specialized habitats or predator refuges (Roughgarden et al. 1985, Holbrook and Schmitt 2002). For several reef fish species, habitat preferences and competitive interactions initially detected at the scale of a few square meters can scale up to predict patterns of abundance at kilometer scales or greater (Munday 2002, Steele and Forrester 2005), although other species fail to show this pattern (Caselle and Warner 1996, Munday 2002, White and Warner 2007). These scaling efforts generally fail when small- and large-scale processes act in opposition (Levin 1992), such as when few larvae are delivered to areas where favorable habitat is abundant (e.g., Caselle and Warner 1996).

Efforts to predict spatial patterns of abundance of kelp bass (*Paralabrax clathratus*), a temperate eastern Pacific reef fish, suggest just such a conflict between small- and large-scale processes. Early, small-scale studies (Carr 1991, 1994) indicated that kelp bass abundance was predicted well by the density of giant kelp, *Macrocystis pyrifera*, and its preferred settlement habitat and that cannibalism by older kelp bass produced density-dependent mortality among recruits. Steele et al. (2002) discovered that these processes may not scale up: they monitored kelp bass larval supply and recruitment at a spatial scale larger than that used by Carr (1994) and found that recruitment was temporally consistent within sites but not related to either kelp abundance or conspecific density. However, with only four sites spread over 35 km of coastline, Steele et al. (2002) were unable to elucidate any larger-scale patterns. Kelp bass play an important predatory role in kelp forest communities (Horn and Ferry-Graham 2006) and support a recreational fishery (Love 2006); as such kelp bass are a key target of marine conservation efforts (Airamé et al. 2000, 2003), and a better understanding of their population dynamics is needed.

We bridged the gap between large- and small-scale approaches by monitoring the dynamics of 13 kelp bass populations spread over ~200 km in the Santa Barbara Channel off the coast of southern California, USA. By tracking patterns of larval supply, population size structure, and giant kelp abundance across multiple sites, we sought to determine how small-scale (within-site) and large-scale (among-site) processes interact to determine the abundance of kelp bass. We first quantified the small-scale effects of kelp and conspecific density on kelp bass recruitment and survival, and then we determined whether large-scale patterns of kelp bass abundance were predicted best by a small-scale factor (kelp abundance, a proxy for habitat availability), a large-scale factor (larval supply), or their combination.

MATERIALS AND METHODS

Study species and sites

The kelp bass is a warm-temperate serranid found predominantly from Point Conception to Punta Abreojos along the west coast of North America (Young 1963). Kelp bass spawn in the early summer (Oda et al. 1993) and recruit to shallow rocky reef and kelp forest habitat in the late summer and early fall (Findlay and Allen 2002) after spending three to four weeks in the plankton (Shima and Findlay 2002). Kelp bass are 8–10 mm standard length (SL) at settlement and grow rapidly, so annual cohorts are distinguishable in visual surveys (Steele et al. 2002). Young kelp bass feed on invertebrates, but become piscivores (and cannibals) after three to four years (Coyer 1979); they may live 30 years and grow to 70 cm (Love et al. 1996). Tagging studies suggest that most kelp bass maintain home ranges on a single reef for multiple years (Lowe et al. 2003), although long-distance movements have been observed (Young 1963).

We monitored kelp bass populations at 13 sites throughout the Santa Barbara Channel and Channel Islands during 1999–2005 (Fig. 1A; also see Appendix A). Individual sites were sampled for two to seven years during that period (median, five years). All sites are rocky, subtidal reefs, 5–20 m depth, and are suitable habitat for both giant kelp and kelp bass. Circulation in this region is dominated by the cold California Current, flowing equatorward past Point Conception and the western Channel Islands, and the warm Davidson Current, flowing poleward along the coast and bathing the easternmost Channel Islands. During the summer and fall, the channel experiences persistent, cyclonic, eddy-like circulation and a sea surface temperature front (Harms and Winant 1998).

Estimation of kelp bass larval supply

Larval supply was estimated by counting the number of recently settled kelp bass juveniles on standardized artificial collectors known as SMURFs (standard monitoring units for recruitment of fishes; Steele et al. 2002, Ammann 2004). These artificial collectors provide a better estimate of larval supply than visual surveys of post-settlement fish on the reef because they minimize the effects of variation in natural habitat and consistently collect the smallest, youngest settlers without substantial post-settlement mortality (Ammann 2004). Because settlement to SMURFs is independent of the availability or quality of nearby settlement habitat, SMURFs estimate the relative abundance of competent larvae available for settlement at a site, not the number of larvae that actually choose to settle (Steele et al. 2002, Ammann 2004; J. E. Caselle, *unpublished data*).

At each site, three replicate SMURFs were placed on separate mooring lines ~500 m from one another and 200–500 m offshore of kelp beds at sites where kelp were present or 200–500 m from shore at sites where no kelp
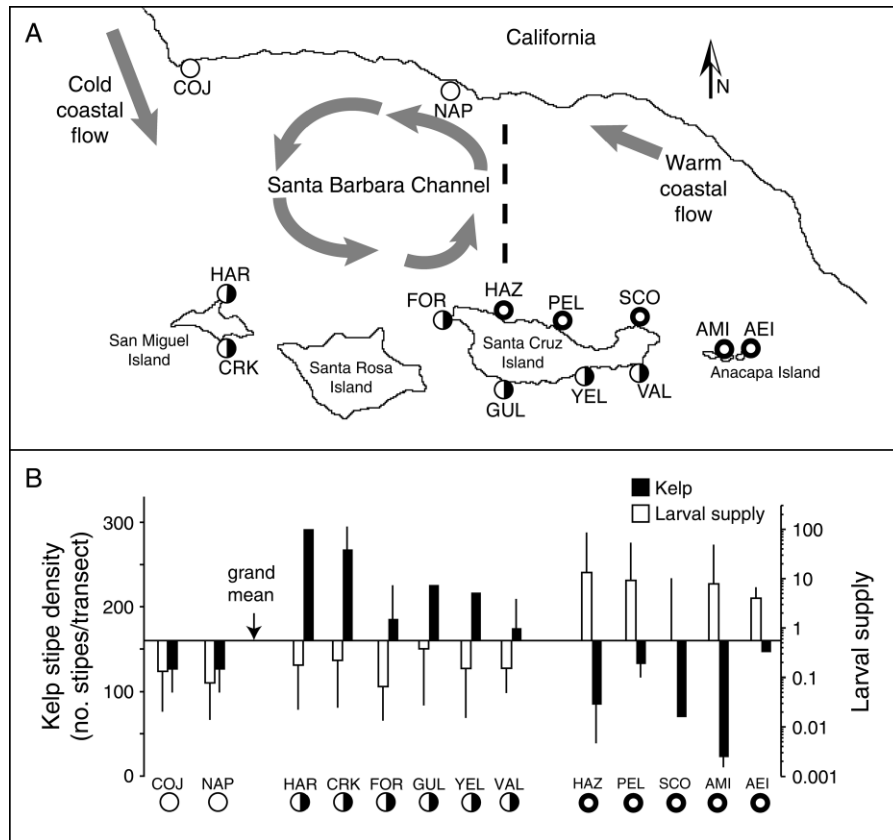
FIG. 1. (A) Map of study area, showing study sites and general pattern of surface currents (gray arrows) and sea surface temperature front (dotted line) in summer and autumn (after Harms and Winant 1998, Nishimoto and Washburn 2002). (B) Density of giant kelp (*Macrocystis pyrifera*) stipes and kelp bass (*Paralabrax clathratus*) larval supply across all years for each study site (mean ± SE). Larval supply data (originally measured as number of settlers in standard monitoring units for recruitment of fishes [SMURFs]) were log-transformed prior to analyses. Horizontal axis indicates grand mean for each variable; bars indicate deviation from grand mean. Site abbreviations: COJ, Cojo; NAP, Naples; HAR, Harris Point Reserve; CRK, Crook Point; FOR, Forney; GUL, Gull Island; YEL, Yellowbanks; VAL, Valley; HAZ, Hazards; PEL, Pelican; SCO, Scorpion; AMI, Anacapa Middle Island; AEI, Anacapa East Island. Open circles denote mainland sites, vertically divided circles denote western and southern island sites, and heavily outlined circles denote northern and eastern island sites.

were present (the presence and proximity of kelp forests do not strongly affect the settlement of kelp bass to SMURFS; J. E. Caselle, *unpublished data*). All moorings were located in ~15 m of water depth, and SMURFs were placed ~3 m below the surface buoy, a depth at which kelp bass larval collection tends to be highest (Steele et al. 2002). We collected kelp bass settlers from each SMURF biweekly (on first quarter and third quarter moons) from April through November. Earlier studies with daily sampling regimes indicated that biweekly sampling is sufficiently frequent to estimate larval supply accurately without substantial post-settlement mortality (Steele et al. 2002, Ammann 2004).

Estimation of giant kelp and kelp bass abundance

Diver surveys of fishes and giant kelp were conducted annually at all sites as part of a larger survey of community structure on central and southern California rocky reefs. The number of giant kelp stipes were counted on 12 30 × 2 m transects at each site during the summer months (June to August). As part of the same program, we also counted all fish and recorded total length (TL) of each individual on 24 30 × 2 m transects at each of the same locations in autumn (August to October). Both types of transects were systematically stratified in both the alongshore and offshore directions at each site. The stratified design was used to ensure that the kelp forest and underlying rocky reef habitats were sampled consistently across all sites. For each site–year combination, the density of giant kelp stipes (hereafter, "kelp density") and fish density were estimated as the grand mean taken across all transects in the annual survey.

Because they recruit in an annual pulse, kelp bass are easily separated into year classes according to length. We placed kelp bass into three age classes: fish ≤8 cm TL = young-of-the-year (YOY) age class; fish >8 cm TL and ≤15 cm TL = 1-year-old age class; and fish >15 cm TL = 2+-year-old age class (Carr 1994, Steele et al. 2002). The 1- and 2+-year-old age classes include both

juvenile and mature fish (Love et al. 1996), and hereafter we collectively term 1+-year-old individuals "older" fish.

Data analysis

This study was observational, not experimental, so we adopted a model selection approach to data analysis, which allowed us to find the most parsimonious explanatory model. We compared alternative explanatory models using Akaike's Information Criterion with sample-size correction (AIC$_c$) for regression analyses (Burnham and Anderson 1998) and the conceptually similar deviance information criterion (DIC) for Bayesian analyses (Spiegelhalter et al. 2002); we also report traditional parametric statistics when possible.

We first examined the within-site processes affecting kelp bass recruitment and survival. We explored the relationship between larval supply and kelp bass abundance by comparing the density of YOY kelp bass (i.e., recent recruits) observed in each annual survey to the total number of kelp bass settlers (i.e., larval supply) collected on SMURFs at that site prior to the annual survey that year. Kelp bass recruitment could be affected by the abundance of both kelp habitat and larger, cannibalistic conspecifics (Carr 1994, Steele et al. 2002), so we used multiple regression to examine the effects of kelp density and 2+-year-old kelp bass density on the relationship between larval supply and the density of YOY kelp bass. We considered 13 candidate regression models (see Appendix B) including every combination of the predictor variables (kelp density, 2+-year-old kelp bass density, and larval supply) and their pairwise interactions. This analysis was limited to the 28 site–year combinations in which both SMURF and annual survey data were collected (see Appendix A).

Post-hoc examination of the larval supply data revealed that in all but four site–years, the bulk of kelp bass settlers arrived after annual surveys had already been performed at a particular site. Such mismatches in survey timing would produce underestimates of the total number of YOYs recruiting to the site in that year, complicating any analysis of the survival of that cohort. As such, we focused on factors affecting the survival of older (1- and 2+-year-old) fish instead. We assumed that survivorship for these older fish was constant with age and modeled the survivorship from one annual survey to the next as an exponential process:

$$N_{2+,t+1} = (N_{1,t} + N_{2+,t})e^{\lambda \mathbf{X}\tau} + \varepsilon \qquad (1)$$

where $N_{a,t}$ is the abundance of age class a in year t, λ is a row vector of fitted parameters, $\mathbf{X}$ is a column vector of covariates (each element of λ corresponds to a column of $\mathbf{X}$), τ is the time between surveys, and ε is a lognormally distributed error term. The covariates ($\mathbf{X}$) we considered were kelp density, kelp bass density (all older fish), and their interaction. All models also included a term describing density-independent mortality (see Appendix C). We estimated parameter values with a Bayesian approach using a one-at-a-time

Metropolis-Hastings algorithm (Gilks et al. 1996) implemented in MATLAB 7.0 (MathWorks, Natick, Massachusetts, USA); we estimated the posterior distribution of each parameter using the final 10 000 post-convergence Markov chain steps after a 10 000-step burn-in and ran three parallel chains for each model to ensure convergence and adequate mixing. We assumed that the survivorship associated with each site–year combination was statistically independent, yielding a sample size of 37 for this analysis. Empirical estimates of survivorship in excess of unity were constrained to one. The exact locations of the study sites at Cojo and Anacapa Middle Island were adjusted slightly each year from 1999 to 2002, preventing accurate estimation of annual survivorship, so these sites were excluded from this analysis.

To evaluate the relative ability of large-scale and small-scale processes to predict large-scale patterns of kelp bass abundance, we compared the effects of larval supply (a factor driven by large-scale, among-site processes) and kelp density (a factor describing small-scale, within-site habitat availability) on the density of older fish in the annual survey following the last year of SMURF sampling at each site. For sites where SMURFing ended in 2001 or 2002 (Appendix A, Table A1), the predictor variables were the mean larval supply and kelp stipe density in all years that SMURFs were sampled and the response variable was the density of older fish in the year following the final SMURF sampling year (2002 or 2003, respectively). For sites where SMURFing ended in 2005 (Appendix A, Table A1), the predictor variables were the mean larval supply and kelp density in all years except 2005 and the response variable was the density of older fish in 2005. We performed multiple regressions using all combinations of integrated larval supply, integrated kelp density, and their interaction to identify the best predictive model.

Sample variances increased with effect size in the larval supply, recruit, and older fish density data; to remedy this we applied a log($x + 0.01$) transformation. All regressions were performed in JMP 6.0 (SAS Institute, Cary, North Carolina, USA). To visualize multivariate relationships, we used coplots (Cleveland 1993), which illustrate the conditional relationship between the response variable and each of two predictor variables. Coplots consist of a series of panels, each showing the bivariate relationship between the response and primary predictor for a narrow range of values of the secondary predictor. To represent the continuous nature of the multivariate relationship, these ranges overlap such that a few points with intermediate values of the secondary predictor are duplicated in each of two adjacent panels (in all cases presented here, two points overlap between adjacent panels). The number of panels and ranges of the secondary predictor are chosen using the equal-count algorithm for clarity of presentation
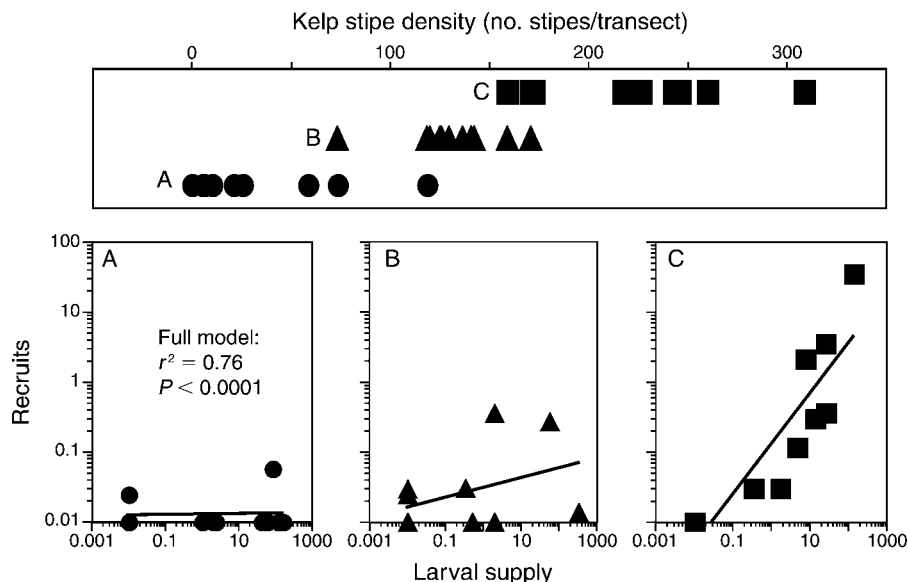
FIG. 2. Coplot showing effect of kelp bass (*Paralabrax clathratus*) larval supply on kelp bass recruitment, conditional on density of giant kelp (*Macrocystis pyrifera*) stipes. (A–C) Kelp bass recruit density (originally measured as numbers of young-of-year per transect) as a function of kelp bass larval supply (originally measured as numbers of settlers in standard monitoring units for recruitment of fishes [SMURFs]) for the values of giant kelp stipe density indicated in the top panel. Each point in (A–C) represents data from one of the 28 site–year combinations; to illustrate the continuous nature of the multivariate relationship, points with intermediate values of kelp density are duplicated in each of two adjacent panels. Curves and statistics are derived from the most parsimonious multiple linear regression model for the entire data set; each curve was generated from the parameters in Appendix B (Table B2) using the mean kelp density for that panel. Range intervals were calculated using the equal-count formula (Cleveland 1993). Recruit density and larval supply were $\log(x + 0.01)$-transformed prior to analysis.

(Cleveland 1993) and are unrelated to the mechanics of the underlying multivariate analysis.

RESULTS

Within-site patterns of kelp bass recruitment

We considered 13 candidate models describing the relationship between larval supply and recruitment (see Appendix B, Table B1). The most parsimonious model had an AIC_c score 3.5 units lower than the next-best model and an Akaike weight near one ($w = 0.82$), strong evidence that it was superior to the other candidate models. This model describes a joint effect of larval supply and kelp on recruitment: at low kelp densities, recruitment is close to zero even when larval supply is quite high. At higher kelp densities, the relationship between recruitment and larval supply becomes increasingly positive (Fig. 2; also see Appendix B, Table B2). At the highest kelp densities, the slope of the log–log relationship is still less than unity (for the mean kelp density represented by the points in Fig. 2C, the 95% confidence interval on the slope of the larval supply–recruit relationship is 0.08–0.31), suggesting a decelerating curve in the untransformed data.

Within-site patterns of older kelp bass survivorship

We considered eight candidate models describing the survival of older kelp bass between annual censuses. The

most parsimonious of these was the full model with terms for density-independent mortality, older kelp bass density, kelp density, and their interaction. This model had a DIC score 9.0 units lower than the next best model and $w = 0.97$, strong evidence for its superiority (Appendix C, Table C2). In this model, the effect of conspecific density on survivorship is strongly dependent upon local kelp density: at low kelp densities, survivorship declines with kelp bass density; as kelp density increases, survivorship becomes density independent and then increases with density (Fig. 3; also see Appendix C, Table C2).

Among-site patterns of kelp and kelp bass abundance

Mean kelp bass larval supply (taken over the duration of the study period) varied considerably in space and was highest at sites along the north shore of Santa Cruz Island and Middle Anacapa Island (Fig. 1B), although these differences were not significant (ANOVA, $F_{12,37} = 1.66$, $P = 0.11$), likely because all sites experienced near-zero recruitment in 2003. When this year was excluded from analysis, there was a significant difference among sites (ANOVA, $F_{12,27} = 2.67$, $P = 0.017$). Mean kelp density did differ significantly among sites (ANOVA, $F_{12,44} = 5.40$, $P < 0.001$), but had a spatial pattern nearly opposite that of larval supply: high densities at San Miguel Island and the southern shore of Santa Cruz Island and lower densities elsewhere (Fig. 1B; Pearson
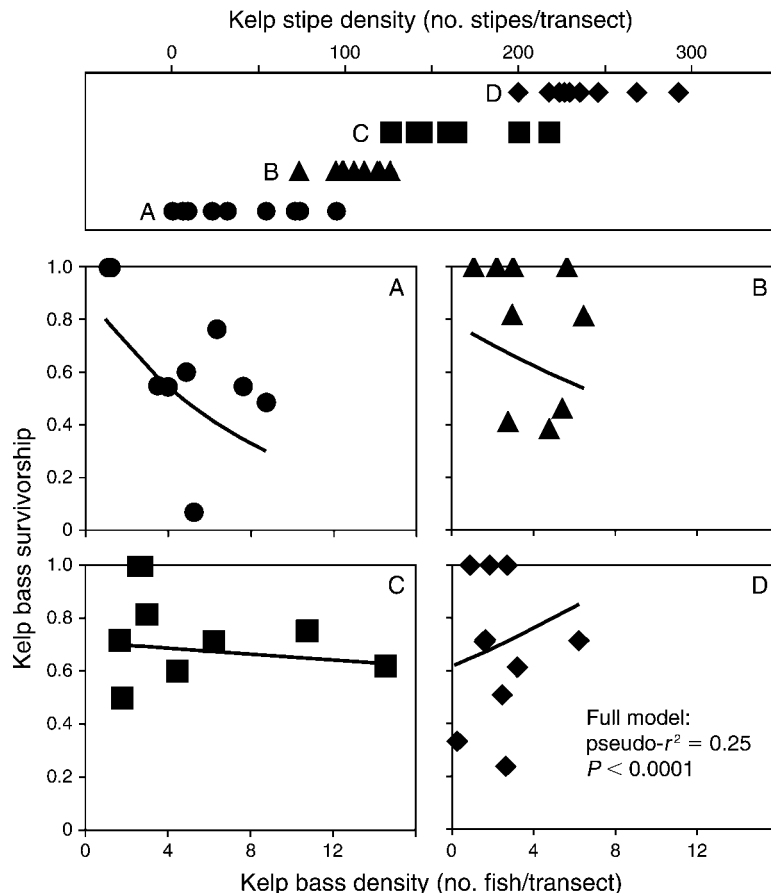
Fig. 3. Coplot showing effect of older (1- and 2+-year-old) kelp bass (*Paralabrax clathratus*) density on older kelp bass annual survivorship, conditional on density of giant kelp (*Macrocystis pyrifera*) stipes. (A–D) Older kelp bass survivorship as a function of older kelp bass density for the values of giant kelp stipe density indicated in the top panel. Each point represents data from one of the 37 site–year combinations; to illustrate the continuous nature of the multivariate relationship, points with intermediate values of kelp density are duplicated in each of two adjacent panels. Curves and statistics are derived from the most parsimonious Bayesian-estimated model for the entire data set; each curve was generated from the parameters in Appendix C (Table C2) using the mean kelp density for that panel. Range intervals were calculated using the equal-count formula (Cleveland 1993). Pseudo-r^2 and likelihood-ratio test P values were calculated relative to the model with a single density-independent term.

correlation between mean larval supply and kelp densities: $r = -0.57$, $P = 0.04$). The general spatial patterns did not vary greatly over time, although the absolute magnitude of larval supply did vary greatly from year to year (J. E. Caselle, *unpublished manuscript*).

The abundance of older kelp bass in the final survey year had a significant, positive relationship with mean larval supply in the preceding years (linear regression on log-transformed data, adjusted $r^2 = 0.50$, $n = 13$ sites, $P = 0.007$; Fig. 4A) but a significant, negative relationship with mean kelp density (linear regresson on log-transformed data, $r^2 = 0.31$, $n = 13$ sites, $P = 0.049$; Fig. 4B). The most parsimonious regression model included only larval supply as a predictor; this model had an AIC_c score 4.3 points lower than the next best model and $w = 0.81$. The slope of this log–log relationship was less than unity (Fig. 4A), indicating a decelerating curve in the untransformed data.

DISCUSSION

The dynamics of marine metapopulations are influenced by both large-scale processes affecting the movement of pelagic larvae and small-scale processes affecting post-settlement growth and survival (Roughgarden et al. 1988). However, debate remains as to which set of processes (pre- or post-settlement) is more important to the ecology of reef fishes (Doherty and Williams 1988, Caley et al. 1996). A more synthetic view posits that populations are limited by recruitment when and where larval supply is low, but limited by density-dependent resource competition (for food or space) when larval supply is greater (Gaines and Roughgarden 1985). This synthesis, sometimes termed the "recruit–adult hypothesis" (Menge 2000) has recently gained traction in reef fish ecology (Carr and Syms 2006) on the basis of small-scale field experiments (e.g., Schmitt et al. 1999) and reanalysis of older data sets (e.g., Hixon and
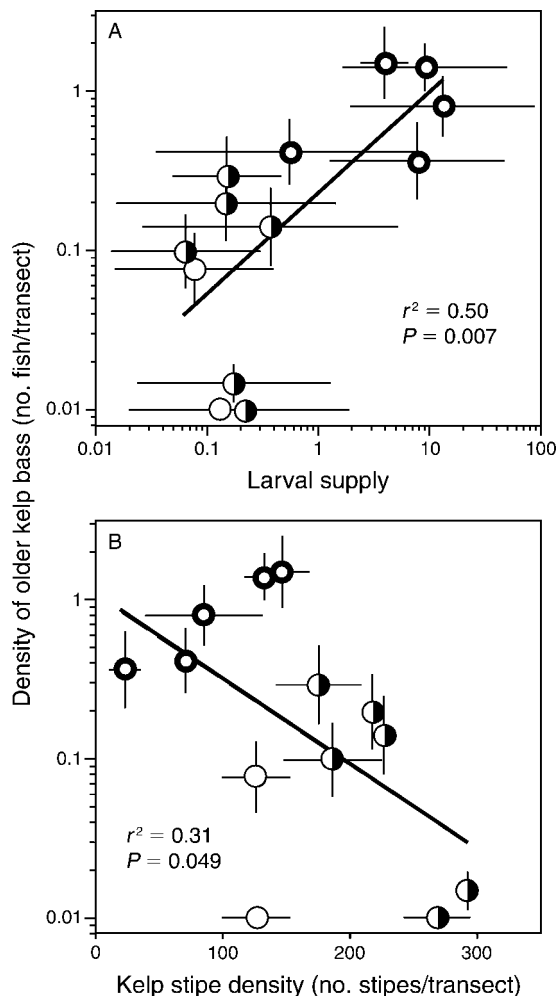
FIG. 4. Density of older (1- and 2+-year-old) kelp bass (*Paralabrax clathratus*) in the final survey year as a function of (A) mean kelp bass larval supply in the preceding years and (B) mean giant kelp (*Macrocystis pyrifera*) stipe density in the preceding years. Each point represents data from a single site; regions are coded using the same symbols as in Fig. 1. Density of older kelp bass (originally measured as number of fish per transect) and mean larval supply (originally measured as number of settlers in standard monitoring units for recruitment of fishes [SMURFs]) were log-transformed prior to analyses. Error bars are ±SE.

Webster 2002). To date, few studies have been conducted at a spatial and temporal scale large enough to directly evaluate this hypothesis (but see Hughes et al. 1999, 2000). Here, using data collected over seven years at sites spread over 200 km, we found strong effects of habitat availability (i.e., giant kelp abundance) and conspecific density on kelp bass recruitment and survivorship at the smaller, within-site scale. Nonetheless, the large-scale, among-site pattern of older kelp bass abundance was best explained by spatial variation in larval supply, although the positive relationship between larval supply and older kelp bass abundance was saturating (a slope < 1 in log–log space; Fig. 2C),

which indicates the presence of density-dependent regulation at high levels of larval supply. These results support the recruit–adult hypothesis and agree with theoretical predictions that populations experiencing stochastic fluctuations in larval supply will show a correlation between larval supply and population size, even in the presence of strong density dependence (Hixon 1998).

Unlike many prior studies of population regulation in reef fishes, which generally focused on a single life-history stage (reviewed by Hixon and Webster 2002), we were able to examine processes across the life span of kelp bass, from recent settlers to mature adults. This approach revealed that older kelp bass, like juveniles, are dependent upon the availability of kelp habitat. Older kelp bass survivorship decreased with population density at low kelp densities but not at high kelp densities, suggesting that kelp is a limiting resource for post-recruitment fish. Kelp bass may compete for kelp-associated prey or for refuges from their own predators in the high-complexity kelp forest habitat (cf. Hixon and Jones 2005). This finding is consistent with the strong preference for kelp habitat exhibited by older kelp bass (Lowe et al. 2003). Because our survivorship estimates are derived from annual censuses, not a mark–recapture study, we cannot rule out the possibility that density-dependent losses at low-kelp sites represent emigration, not mortality. However, tagging studies suggest that site fidelity is high and among-site movement is rare in older kelp bass (Young 1963, Lowe et al. 2003). Density-dependent survivorship of older kelp bass could be important to the regulation of kelp bass population dynamics (Hixon et al. 2002), although it is difficult to judge the relative importance of density dependence in older fish without additional information on mortality in the YOY age class, since reef fish mortality is often most intense and strongly density-dependent immediately after recruitment (Hixon and Webster 2002). Unfortunately, logistical constraints made it impossible to perform annual surveys after the kelp bass settlement pulse had ceased, precluding the accurate census of the entire YOY cohort that would be necessary to perform a rigorous analysis of YOY survivorship. Nonetheless, there is some evidence for density-dependent YOY survivorship: if initial YOY density is estimated from larval supply and kelp stipe density using the regression equation given in Appendix B, then compared to the density of 1-year-old fish at the same site in the next year, the resulting estimate of YOY survivorship is negatively density-dependent (see Appendix D).

We caution that in constructing our explanatory models for kelp bass recruitment and survivorship, we did not consider a variety of other potential influences on kelp bass population dynamics, including other reef fish predators (the identity and importance of which is not well known), severe storms (which can destroy kelp habitat), and climatic variation in currents and sea surface temperatures (which could affect larval survival

and transport in complex ways). In particular, the El Niño-Southern Oscillation (ENSO) can have strong effects on reef fish communities in the Southern California Bight (Cowen 1985), although our data set spanned only one relatively weak ENSO event (2002–2003). However, data collections continue at these sites, and future work may be able to address climatic influences on population dynamics in the Santa Barbara Channel.

We found strong spatial patterns of variation in kelp bass settlement throughout the Santa Barbara Channel region. Except for 2003, when there was a channel-wide kelp bass recruitment failure, sites on the north shore of the eastern islands received more settlement than either south shore sites or mainland sites. In particular, two sites on the western part of the north side of Santa Cruz Island (Pelican and Hazards) received 65% of all settlement in this study. Interestingly, this pattern of high settlement to the north shore sites was observed for the majority of species of fish that settle to SMURFs, including several species of rockfishes (*Sebastes* spp.; J. E. Caselle, *unpublished data*). The physical oceanography in the Santa Barbara Channel is complex and dynamic, but several persistent features may contribute to the spatial patterns of kelp bass larval supply. A major feature of summertime circulation is the formation of a topographically steered anticyclonic eddy situated roughly in the middle of the channel over a deep basin (Harms and Winant 1998). Nishimoto and Washburn (2002) found that this eddy aggregated larval and pre-settlement juveniles of fishes and other organisms, although they did not examine the potential link between larval aggregation and delivery to a reef (e.g., settlement) and their study took place too early in the year to detect kelp bass larvae. Another well-described physical feature in the channel is a strong sea surface temperature front that separates colder, California Current water in the west from warmer, Southern California Bight water in the eastern part of the channel (Broitman et al. 2005, Selkoe et al. 2006). Although not completely stable in its location, the front tends to be located midway (in the east-to-west direction) along the north shore of Santa Cruz Island. Fronts such as this have been shown to aggregate larvae and result in higher settlement in nearby areas (Sponaugle et al. 2002). Finally, Harms and Winant (1998) and our own unpublished oceanographic data (*available online*)[4] show slow current speeds in this region of the north shore relative to current velocities on the mainland and south shores of the islands. It appears that the area of high settlement is characterized by slow and often converging currents as well as the strong temperature front. We hypothesize that these features contribute to the observed spatial patterns of larval delivery and explain the consistency of settlement of multiple species to these

sites over time. Kelp bass have a long pelagic larval duration (Shima and Findlay 2002), and genetic data suggest that larvae commonly disperse throughout the Santa Barbara Channel (Luzier and Wilson 2004, Selkoe et al. 2006), so it is quite likely that larvae spawned throughout the surrounding metapopulation could be aggregated and redistributed by these oceanographic features. Such consistent, oceanographically driven, large-scale patterns of larval supply and/or recruitment have been identified for many other taxa in a variety of study locations (Lipcius et al. 1997, Hamilton et al. 2006, Mace and Morgan 2006). Recent evidence suggests that reef fish populations on isolated oceanic islands might be characterized by high rates of self-replenishment (Cowen et al. 2000, Almany et al. 2007), but there is no evidence for strong self-recruitment of kelp bass to individual reefs or kelp beds in the Santa Barbara Channel (Luzier and Wilson 2004, Selkoe et al. 2006), so it is unlikely that the spatial settlement patterns we identified were driven by spatial differences in local larval production.

The importance of larval supply to kelp bass abundance was accentuated by relative paucity of kelp habitat at sites receiving the most kelp bass larvae (the northern shores of Anacapa and Santa Cruz Islands). This pattern produced a negative correlation between kelp and older kelp bass abundance at the largest spatial scale, despite the positive effects of kelp on kelp bass recruitment and survivorship at smaller scales. In fact, for that group of sites receiving high kelp bass larval supply, there appeared to be a weak, positive relationship between kelp and older kelp bass abundance (see symbols with thick outline in Fig. 4B). This pattern provides an additional example of reef fish habitat preferences failing to scale up because of a countervailing large-scale pattern of larval delivery (Caselle and Warner 1996, Munday 2002). This conflict between small- and large-scale processes may be mirrored in other systems with abiotically driven dispersal. Hydrodynamic flows strongly affect the structure of aquatic and intertidal communities by altering the strength of local competitive and predatory interactions (Swan and Palmer 2000, Menge et al. 2004), and both wind and riverine flows can shape the patterns of patch occupancy in aquatic metacommunities (Downes and Keough 1998, Krawchuk and Taylor 2003).

The large-scale negative relationship between kelp density and kelp bass larval supply was likely a by-product of oceanographic factors affecting kelp abundance. Kelp thrives in the cold, nutrient-rich upwelled water that usually bathes San Miguel and the south-western side of Santa Cruz Island (Harms and Winant 1998) and may not fare as well in the warmer waters common at sites with higher kelp bass larval supply. Conversely, kelp bass are members of a warm temperate and tropical family and thus have a strong affinity for warmer water. These warmer sites may also experience low levels of kelp larval supply. Unlike kelp bass larvae,

which may disperse across the breadth of the Santa Barbara Channel (Selkoe et al. 2006), kelp spores generally have dispersal distances on the order of only tens to thousands of meters (Kinlan and Gaines 2003, Reed et al. 2004), so they are unlikely to be entrained and redistributed by the same large-scale oceanographic features that appear to deliver multitudes of kelp bass larvae to northern Santa Cruz and Anacapa Islands.

Although benthic organisms are commonly used as model systems for experimental examination of the mechanisms of population regulation (Hixon et al. 2002) and despite the considerable interest in the population dynamics of exploited species such as kelp bass (Love 2006), few studies have monitored both larval supply and post-recruitment abundance over long periods or at large spatial scales. Here, our larval collectors revealed patterns of larval supply unaffected by the intense post-settlement mortality common in most benthic systems (Hixon and Webster 2002; cf. recruitment analyses in Doherty and Fowler 1994, Hughes et al. 1999). Furthermore, the spatial extent of our sampling was comparable to the scale at which management decisions are made in this system (Airamé et al. 2003), a necessity for marine systems in which within-patch interactions do not necessarily scale up (Hobbs 1998). Nonetheless, this was still a "short-term" study by most standards, forcing us to eschew traditional time series analysis in favor of a focus on annual, within-site processes and the predictability of final census densities.

While the large-scale pattern of kelp bass abundance was predicted well by mean larval supply, the spatial mismatch between kelp and kelp bass abundance at the large scale coupled with the strong effect of kelp on kelp bass recruitment and survival within sites produced considerable spatiotemporal heterogeneity in kelp bass demographic rates. Because metapopulation models that do not account for such demographic heterogeneity can produce inaccurate predictions (Kritzer and Davies 2005), any effort to predict kelp bass metapopulation dynamics will need to incorporate the dynamics of giant kelp as well. This interdependency argues for a metacommunity approach that considers the abiotic requirements and dispersal patterns of multiple interacting species (Guichard et al. 2004).

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APPENDIX A

A summary of the sampling regime (*Ecological Archives* E089-080-A1).

APPENDIX B

A summary of the multiple regression analysis of the relationship between kelp bass larval supply and kelp bass recruitment (*Ecological Archives* E089-080-A2).

APPENDIX C

A summary of the Bayesian analysis of older kelp bass survivorship (*Ecological Archives* E089-080-A3).

APPENDIX D

A description of the estimation of post-settlement mortality function for kelp bass (*Ecological Archives* E089-080-A4).