ECOSYSTEM ECOLOGY

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Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in the northeast Pacific

Abstract Recent discussions on scaling issues in ecology have emphasized that processes acting at a wide range of spatial and temporal scales influence ecosystems and thus there is no appropriate single scale at which ecological processes should be studied. This may be particularly true for environmental disturbances (e.g. El Niño) that occur over large geographic areas and encompass a wide range of scales relevant to ecosystem function. However, it may be possible to identify the scale(s) at which ecosystems are most strongly impacted by disturbances, and thus provide a measure by which their impacts can be most clearly described, by assessing scale-dependent changes in the patterns of variability in species abundance and distribution. This, in turn, may yield significant insight into the relative importance of the various forcing factors responsible for generating these impacts. The 1997–98 El Niño was one of the strongest El Niños ever recorded. I examined how this event impacted giant kelp populations in the northeast Pacific Ocean at 90 sites ranging from central Baja California, Mexico to central California, USA. These sites spanned the geographic range of giant kelp in the Northeast Pacific and were surveyed just before, immediately following, several months after, more than 1 year after, and nearly 2 years after the El Niño. I used a hierarchical sample design to compare these impacts at five spatial scales spanning six orders of magnitude, from a few meters to more than 1,000 km. Variance Components Analyses revealed that the El Niño shifted control over giant kelp abundance from factors acting at the scale of a few meters (local control) to factors operating over hundreds to thousands of kilometers (regional control). Moreover, El Niño resulted in the near-complete loss of all giant kelp throughout one-half of the species' range in the northeast Pacific Ocean. Giant kelp recovery following El Niño was far more complex and variable at multiple spatial scales, presumably driven by numerous factors acting at those scales. Recovery returned local control of giant kelp populations within 6 months in southern California, and within 2 years in Baja California.

Keywords Disturbance · El Niño · Giant kelp · Kelp forest · Recovery

Introduction

Ecosystem-level patterns in species diversity are generated by processes acting at a broad range of spatial and temporal scales (Menge and Olson 1990; Chapman et al. 1995; Connell et al. 1997; Tilman and Kareiva 1997; Karlson and Cornell 1998). Even a cursory review of the literature on the issue clearly dictates that there is no single scale at which ecological processes should be studied (Dayton and Tegner 1984a; Weins 1989; Levin 1992, 2000). However, recent studies suggest that that is possible to determine the scales at which ecosystems are most strongly regulated, and thus identify their most important governing factors, by discerning scale-dependent patterns of variability in species abundance and then linking these to the appropriate forcing factors operating at those scales (e.g. Connell et al. 1997; Tilman and Kareiva 1997; Karlson and Cornell 1998; Hughes et al. 1999). One way of doing this is to design experimental and sampling protocols in a hierarchical (fully nested) manner and then use analytical procedures to either examine species' relationships (e.g. Hewitt et al. 2002) or estimate the amount of variability in species abundance (e.g. Hughes et al. 1999) at the different levels in the hierarchy. Such an approach may be particularly useful for studying the impacts of environmental perturbations that occur over large areas and encompass a wide range of scales (Carpenter 1998; Turner and Dale 1998). Yet, because of the difficulties associated with sampling and/or experimenting over large geographic areas and at multiple scales, most ecological studies focus on few, relatively small,

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scales and therefore may lack the ability to fully assess the scales at which these impacts most strongly occur (Levin 1992, 2000; Tilman and Kareiva 1997; Dayton and Tegner 1984a; Foster 1990; Carpenter 1998). Therefore, it is unclear whether a single comprehensive study done at many sites and spanning multiple scales will yield novel insights into the nature and magnitude of disturbance impacts relative to several small-scale studies done at numerous sites. Two important questions thus arise: (1) Can we identify the spatial scales at which ecosystems are impacted by and recover from environmental catastrophes? (2) Does this yield new information on the nature or magnitude of their impacts relative to that gained from smaller-scale studies done at one or numerous sites?

One of the most important large-scale perturbations to impact coastal ecosystems is the El Niño-Southern Oscillation (hereafter El Niño). Although generally thought of as low latitude events, El Niños can transfer energy to mid and high latitudes and thereby alter oceanographic and atmospheric conditions globally (Chelton et al. 1982; Glynn 1988; Neibauer 1985; Royer 1985; Wallace 1985; Chavez 1996). Historically, the northward extension of El Niño-related conditions into the northern Pacific Ocean has resulted in range extensions, habitat redistributions and massive mortalities in many seaweed, invertebrate, finfish, marine mammal and seabird populations (Chelton et al. 1982; Dayton and Tegner 1984b, 1990; Graybill and Hodder 1985; Pearcy 1985). Recovery of these populations following El Niño, in turn, can be facilitated by the transition to cool nutrient-rich (La Niña) conditions that follows some but not all El Niños (Hayward et al. 1999). Unlike other most large-scale disturbances, El Niños may take a year or more to develop at mid and high latitudes, thus making it possible to predict their arrival in the Northern Pacific months ahead of time (Fielder 1984; McPhaden 1999). This, along with their punctuated nature, make them ideal for studying both their impacts and how ecosystems recover following them.

Kelps (Order Laminariales, Phaeophyta) are the most conspicuous subtidal algae in the coastal zones of temperate to Polar regions. Driven by cold, nutrient-rich waters that are upwelled by the southward flowing California Current, eastern North Pacific kelp forests are among the most productive of global ecosystems. They form dense forests along rocky shores from the intertidal to >30 m that create habitat and food for numerous species, promote increased diversity, and enhance overall organism abundance (Dayton 1985; Foster and Schiel 1985). The giant kelp, *Macrocystis pyrifera*, dominants this ecosystem from central California, USA (37°06′N, 122°20′W) to central Baja California Sur, Mexico (27°11′N, 114°23′W). This span represents the primary geographic range of giant kelp in the northeast Pacific, although scattered pockets have been reported in southeast Alaska (Gabrielson 2000). As a consequence, loss of the giant kelp canopy (e.g. Anderson 1994) or changes to its population size structure (e.g. Carr 1994) can strongly impact the abundance and distribution of numerous species that rely on it for habitat and food.

Throughout its geographic range, a wide variety of factors such as hydrodynamic forces, grazing, substrate stability, light, ocean temperature and nutrient availability play important roles in influencing giant kelp distribution and abundance (reviewed in Dayton 1985; Foster and Schiel 1985). In addition, the periodic occurrences of anomalously warm nutrient-poor ocean water and unusually large storm-driven waves, and reduced coastal upwelling associated with El Niños can be especially important to giant kelp survival and reproduction. For example, the 1982–83 El Niño resulted in widespread losses of giant kelp along the California, USA and Baja California, Mexico coasts (Dayton and Tegner 1984b, 1990; Foster and Schiel 1985; Zimmerman and Robertson 1985) and a ~70 km northward relocation of giant kelp's southern range limit in Baja California Sur, from Punta San Hipólito to Bahía Asunción (Hernández-Carmona et al. 2000). Although these impacts were generally widespread, they were highly variable among even closely separated populations and among depths, with greater impacts typically observed in shallower depths (Foster and Schiel 1985; Dayton et al. 1992). Recovery following the El Niño was also variable, largely failing in some locations or at shallow depths due to the presence of even warmer more nutrient-poor waters (e.g. Dayton et al. 1992). What remain unclear are the spatial scales at which these impacts and recovery most strongly occurred. Understanding these may yield new insights into their nature and magnitude, and further discern the relative importance of the various forcing factors responsible for driving variability in these impacts and recovery from them. In this paper, I chronicle how the 1997–98 El Niño impacted giant kelp populations throughout the species' geographic range in the northeast Pacific and how these populations recovered following it. I describe these patterns at five spatial scales spanning six orders of magnitude (from meters to thousands of kilometers) and show that while they were strongly scale-dependant, the nature of this dependency differed between the disturbance itself and recovery from it.

Materials and methods

Spatial design and sampling methods

I used a hierarchical sampling design to identify scale-dependent patterns of spatial variability in giant kelp abundance and population size structure (Figs. 1, 2). I divided giant kelp's range into three geographic regions as determined by large-scale differences in oceanic climate (Kerr 1998). These regions were identified as: (1) central California (Santa Cruz to Point Conception, Calif., USA), (2) southern California (Point Conception to Punta Banda, BC, Mexico), and (3) Baja California (Punta Banda to Bahía Asunción, BCS, Mexico (Fig. 1A). Within each region, I selected four to five locations separated by tens to hundreds of kilometers (Fig. 1B, C, Table 1). Within each location, I identified three 8–12 m deep areas separated by 1–5 km (Fig. 1D), and within each area, I established two sites separated by 100–300 m. Within each site, I established three randomly directed 20 m ×2 m radial transects, along which giant kelp density (hereafter abundance) was estimated. This fully nested design allowed for the total amount of spatial variability in

kelp abundance to be partitioned among these five spatial scales using Variance Components Analyses (Searle 1992; Underwood 1997; Graham and Edwards 2001). It should be recognized however, that (1) while these scales represent logical a priori units of measure for giant kelp, they are arbitrary measures of spatial separation, and (2) while this method works well for partitioning the total variability among the spatial scales, the power for detecting statistical differences among replicate units within each scale varies among levels in the hierarchy according to their degrees of freedom (Tilman and Kareiva 1997).

I identified the spatial scale at which the 1997–98 El Niño most strongly impacted giant kelp by assessing how spatial variability in giant kelp density changed at each scale during the El Niño. I used El Niño's early prediction to survey giant kelp populations at 90 sites spanning their latitudinal range limits just before (August 1997) and immediately after (June 1998) the El Niño impacted the west coast of North America. I identified the spatial scales at which giant kelp recovered following the El Niño by resurveying the sites in October 1998, June 1999, September 1999 and June 2000. On each survey date, I estimated giant kelp abundance by counting all individuals >1 m tall within each transect using SCUBA. Exceptions to this occurred at Bahía Tortugas, Baja California in June 1999, and Big Creek, central California in October 1998, October 19999 and June 2000 when large ocean waves and/or logistical difficulties prevented access to my study sites. Once the scales of disturbance impacts and recovery were identified, I estimated how giant kelp abundance, population size structure, and frond density (a better estimate of population carrying capacity and habitat availability than plant density, Dayton et al. 1992) were impacted by and recovered following the El Niño. I estimated giant kelp population size
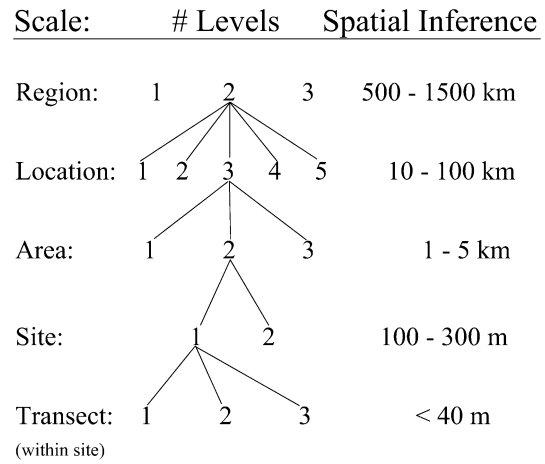

Fig. 2 Hierarchical sampling design used to measure variability in giant kelp density at five spatial scales. Each scale is nested within the scale above it. The left column (*Scale*) refers to scale names as denoted by italics in the text; the middle column (*# Levels*) refers to the number of replicates of each scale that are nested within the scale above them; the right column (*Spatial Inference*) indicates the distance by which replicate levels are separated

structure and frond density by counting the number of fronds on all plants at one meter above the bottom and by characterizing each plant at the time of sampling as either canopy forming (one or more

Fig. 1A–D Maps showing the hierarchical association among spatial scales and the relative location of survey locations. **A** The west coast of California, USA and Baja California, Mexico showing all survey locations (denoted by letters, see Table 1) and the geographic boundaries of the three survey regions used in this study. Specific geographic locations referred to in the text are also shown. **B** Central California at the scale of "region" showing the Monterey Bay and Peninsula; **C** the Monterey Bay and Peninsula at the scale of "location"; **D** Otter Point, Lovers Point and the Monterey Bay Aquarium (*OP*, *LP* and *MBA* respectively) showing the three survey "areas" along the Monterey Peninsula and the two survey "sites" within each of these areas (*shaded circles*). A similar hierarchical spatial allocation of survey areas and sites was used for all other survey locations shown in **A**
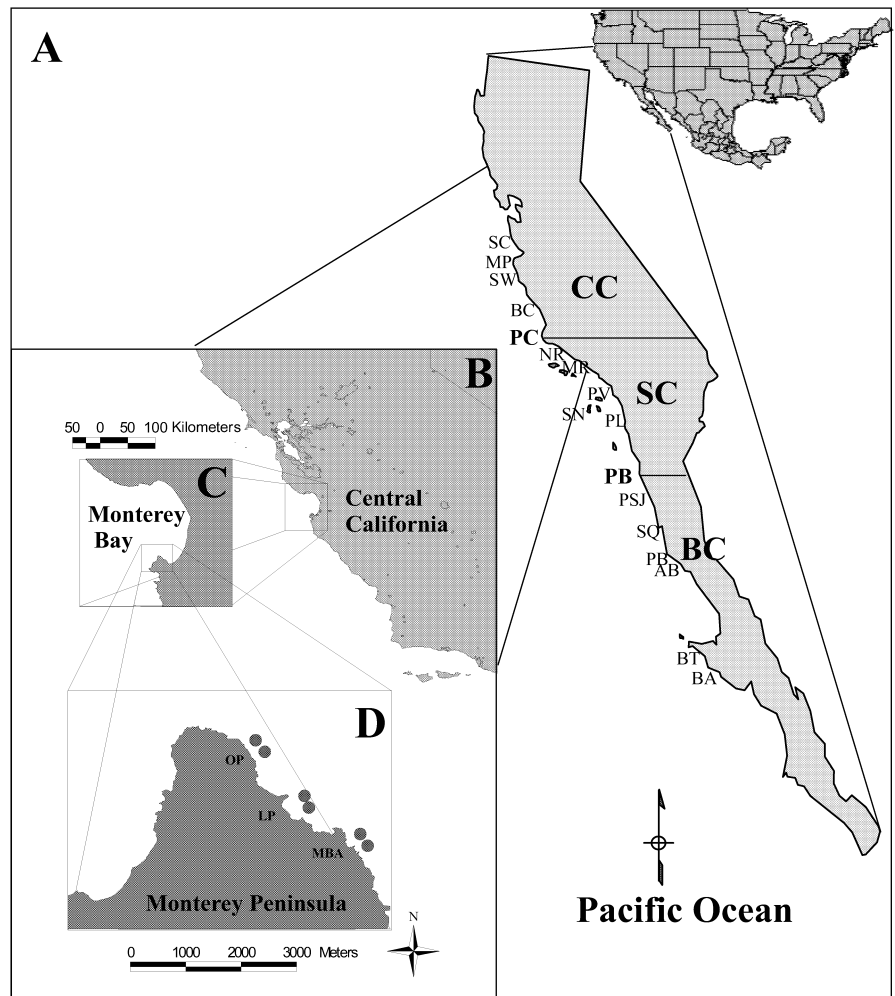
Table 1 List of locations where kelp surveys were done, the region each location occurs in, and their latitude and longitude in decimal degrees. The two-letter code refers to their placement in Fig. 1, and bold face identified breaks between geographic regions

Code	Location	Region	Latitude	Longitude
SC	Santa Cruz	central	36.97 N	122.03 W
MP	Monterey Peninsula	central	36.62 N	121.90 W
SW	Stillwater Cove	central	36.56 N	121.94 W
BC	Big Creek	central	36.04 N	121.36 W
PC	**Point Conception**	**break**	**34.58 N**	**120.65 W**
NR	Naples Reef	southern	34.42 N	119.95 W
MR	Mohawk Reef	southern	34.39 N	119.71 W
PV	Palos Verdes	southern	33.42 N	118.18 W
SN	San Nicolas Island	southern	33.25 N	119.51 W
PL	Point Loma	southern	32.69 N	117.26 W
PB	**Punta Banda**	**break**	**31.70 N**	**116.67 W**
PS	Punta San José	Baja	31.47 N	116.61 W
SQ	San Quintín	Baja	30.47 N	116.10 W
PJ	Punta Baja	Baja	29.91 N	115.72 W
AB	Agua Blanca	Baja	29.95 N	115.81 W
BT	Bahía Tortugas	Baja	27.37 N	114.50 W
BA	Bahía Asunción	Baja	27.16 N	114.42 W

fronds reached the surface) or subsurface (no fronds reached the surface). Exceptions to this occurred in August 1997 when all locations in Baja California except Isla San Martín were surveyed for plant density only. Because the precise relocation of exact site centers could not be guaranteed on all survey dates, sites and transects were randomly reselected on each survey date. As a consequence, while changes between successive surveys at the three largest spatial scales (regions, locations and areas) reflect temporal changes in kelp abundance, changes at the two smallest scales (sits and transects) also include spatial variability due to the random placement of sample units, which may important given giant kelp's dynamic nature in shallow water (Dayton et al. 1999). However, given the nature of the disturbance impacts (see Results) these problems did not appear to confound interpretations made at larger scales.

Statistical analyses

On each survey date, I assessed differences in giant kelp abundance among replicate units of each spatial scale using five-factor nested ANOVAs. Following each ANOVA, I partitioned the total amount of spatial variability in giant kelp abundance among the five spatial scales using Variance Components Analysis (Searle 1992; Underwood 1997). I estimated the variance measured at each spatial scale by determining their variance components, and estimated relative amount of variability (percent of the total variability) associated with each scale by determining their magnitudes of effect (Graham and Edwards 2001). I corrected for negative variance estimates, a problem often observed in hierarchical models by "pooling the minimum violators" and then recalculating the variance components (Thompson 1962; Thompson and Moore 1963; Graham and Edwards 2001). Within each region, I assessed differences in the abundance of canopy-forming giant kelp, and the average plant size and mean frond density of all giant kelp >1 m between sequential sample dates using single factor ANOVAs followed by post hoc Bonferoni-adjusted planned comparisons, except for tests of abundance immediately before and after the June 1998 survey (mean abundance and variance were zero) and tests of plant size and frond density between the August 1997 and June 1998 surveys in Baja California (only mean values were available due to the reduced sampling effort during the first year). I compared these metrics with their corresponding expected values using one-sample t-tests (abundance: H_o: $\mu=0$), (plant size: H_o:$\mu=20$) and (frond density: H_o:$\mu=5.2$). For cases where multiple tests were used to test similar hypotheses, I report Bonferoni-adjusted probabilities to prevent Type I error inflation. Prior to testing, data for frond number were log transformed to correct for heteroscedacity and then rechecked to ensure the problems were corrected.

Results

The scale of El Niño impacts

The 1997–98 El Niño was one of the strongest ever recorded (Wolter and Timlin 1998), with storm-driven waves exceeding 8 m along parts of central California and ocean temperatures reaching 28°C along parts of Baja California (Edwards 2001; Hernández-Carmona et al. 2001). Individually or combined, these factors resulted in the near-to-complete loss of all giant kelp throughout the southern one-half of the species' geographic range in the northeast Pacific (Edwards and Estes, unpublished data), and ultimately increased large-scale variability in giant kelp abundance while decreasing small-scale variability. Specifically, prior to the onset of El Niño conditions (August 1997), most of the total range-wide variability in abundance (86%) was accounted for at the smallest spatial scale examined (among transects within sites), while very little (<3%) was accounted for at the largest scale examined (among regions; Fig. 3A). Then, immediately following the El Niño (June 1998), there was an overall decrease in the total amount of spatial variability in giant kelp abundance, with the remaining variability being redistributed among the five spatial scales (Fig. 3B). Thus, when compared with the pre-El Niño conditions, differences among regions accounted for considerably more of the total variability (37% vs 3%), as did differences among areas within locations (19% vs 5%), while differences among transects within sites (44% vs 86%) and differences among locations within regions (0% vs 6%) explained less of the total variability. Differences among sites within areas remained unchanged (0%). Perhaps most important is that the variance measured (hereafter the variance component) among regions increased during this period (regions became more dissimilar), while the variance components observed at all other spatial scales either decreased or did not change (Fig. 4A). This disparity supports Underwood's (1997) claim that restricting our analyses to examining only changes in relative variability may be misleading in cases where the total amount of variability also changes. However, when both relative variability and variance components were considered, it became clear that the El Niño resulted in the three regions becoming more dissimilar while replicate units of all other spatial scales either became more similar or did not change, thus identifying region as the scale at which giant kelp populations were most strongly impacted during the El Niño.

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Fig. 3 Components of variation (%) for canopy-forming giant kelp density during **A** August 1997, **B** June 1998, **C** October 1998, **D** June 1999, **E** October 1999, and **F** June 2000. The total spatial variability is partitioned among the five spatial scales and expressed as a percentage of the total (relative variability). Negative variance estimates were accounted for by "pooling-the-minimum-violator" (see Methods). *Bars with asterisks* denote spatial scales where giant kelp density was significantly different among the levels of that scale (* *P* <0.05; ** *P* <0.01) as determined by nested ANOVA
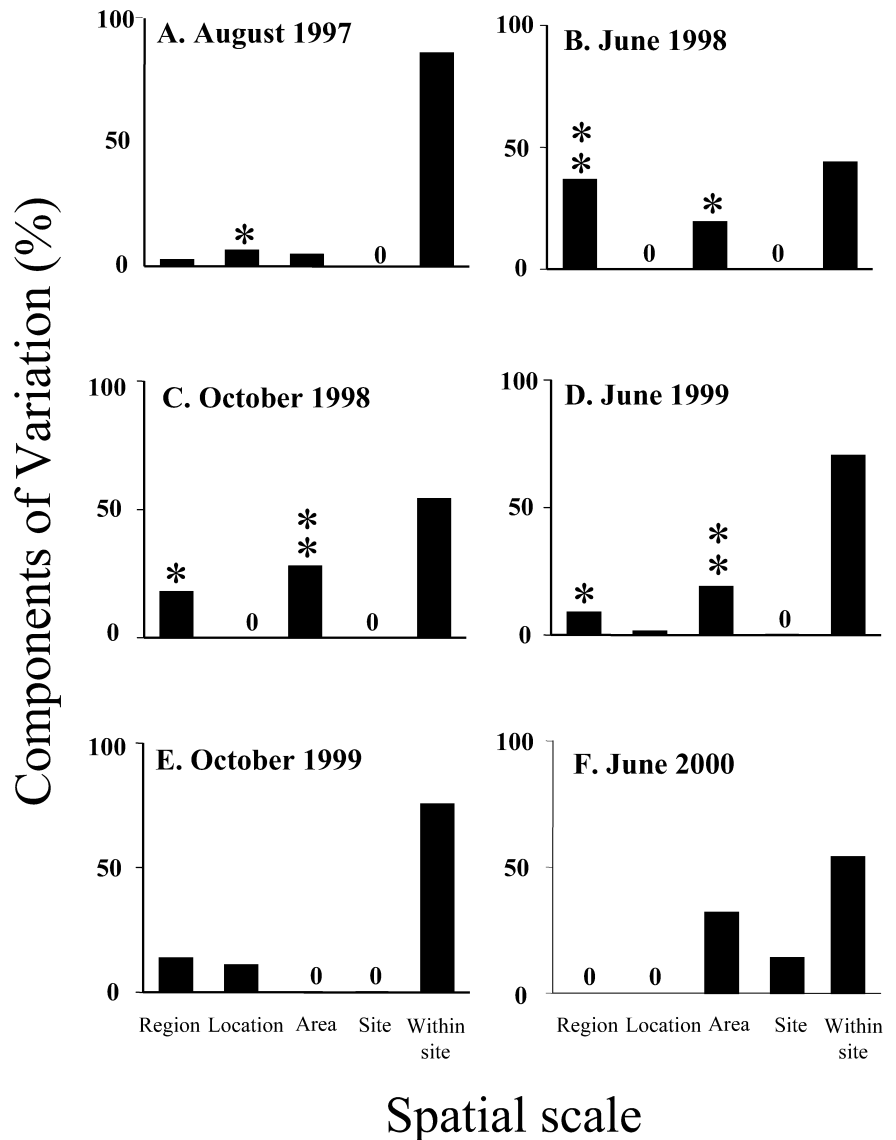
Understanding that giant kelp populations were most strongly impacted by the El Niño at the regional scale provided a metric by which the nature and magnitude of these impacts can most clearly be assessed. Prior to the onset of El Niño conditions, the abundance of canopy-forming giant kelp was not significantly different among the three regions (ANOVA: *P* =0.217), whereas differences were highly significant immediately following the El Niño (ANOVA: *P* <0.001, Fig. 3A, B). These differences resulted from a near-to-complete mortality of all canopy-forming giant kelp in Baja California, a large mortality in southern California, but only a small mortality in central California (Edwards and Estes, unpublished data, Fig. 5). The heavy losses of all large individuals (>20 fronds plant^{-1}) combined with the strong recruitment of small individuals (<4 fronds plant^{-1}), resulted in a significant reduction in mean plant size in southern (Bonferoni: *P* =0.05) and Baja (*t*-test: *t* =39.35, *df* =4, *P* <0.01) California (Fig. 6). In contrast, although a large number of smaller individuals recruited in central Cali-

fornia (Fig. 6), the generally high survival of larger individuals resulted in only small (insignificant) changes in mean plant size throughout the region (Bonferoni: *P* >0.9). As a result, mean frond density (i.e. carrying capacity) did not change significantly in central California (Bonferoni: *P* >0.9) but was significantly reduced throughout southern (Bonferoni: *P* =0.04) and Baja (*t*-test: *t* =134.21, *df* =4, *P* <0.001) California (Fig. 7).

Scales of recovery following El Niño

Following the El Niño, the west coast of North America was subjected to a period of anomalously cold nutrient-rich ocean conditions during the strong 1998–99 La Niña (Hayward et al. 1999). These conditions facilitated giant kelp recovery between June and October 1998 and redistributed the patterns of variability in its abundance among the five spatial scales. In general, recovery decreased the relative amount of large-scale variability

Fig. 4 Changes in the measured variance ($\Delta\sigma^2$) following pooling of the minimum violators (and isolated from all other scales) between survey periods: **A** between August 1997 and June 1998, **B** between June 1998 and October 1998, **C** between October 1998 and June 1999, **D** between June 1999 and October 1999, and **E** between October 1999 and June 2000. *NC* spatial scales where changes in absolute variance were not observed
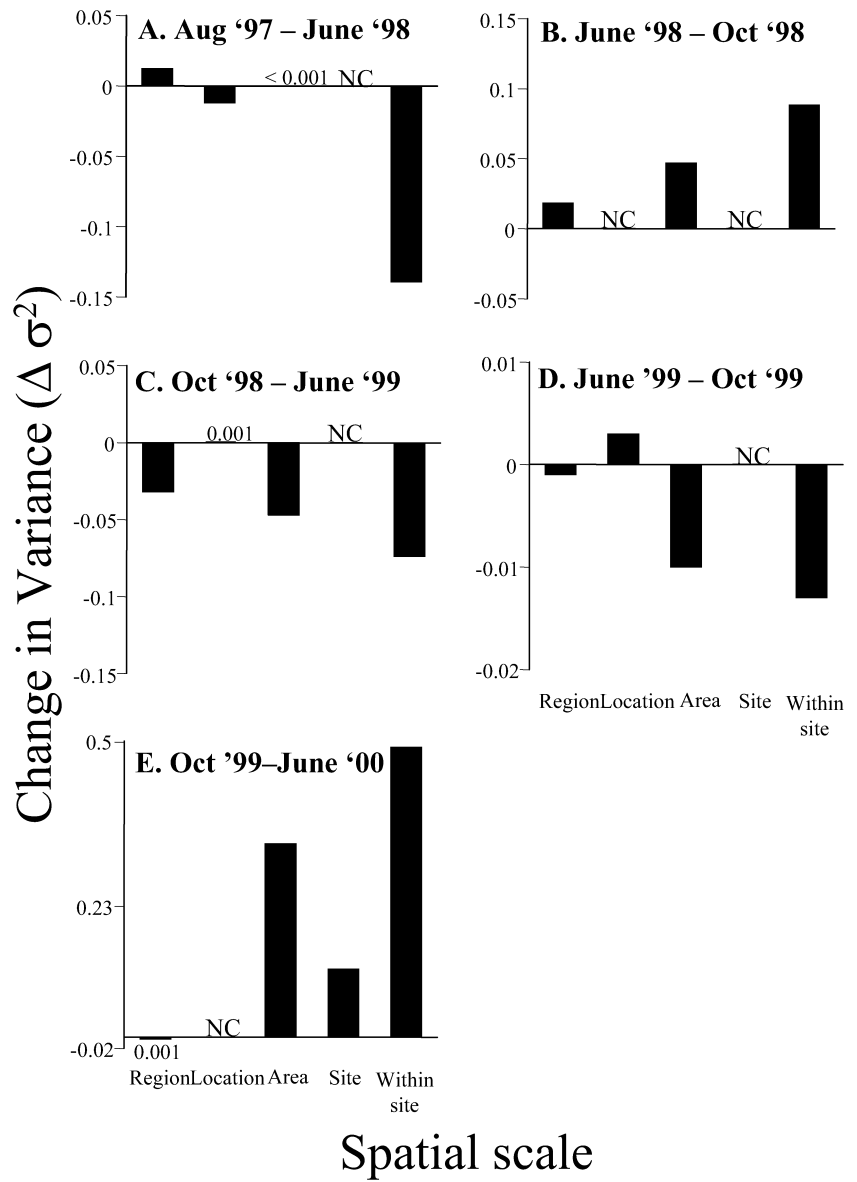
and increased the relative amount of small-scale variability. Specifically, the amount of variability accounted for at the largest scale examined (among regions) decreased from 37% to 18% of the total while the amount of variability accounted for at the smallest scale (among transects within sites) increased from 44% to 54% of the total (Fig. 3C, B). This was opposite to the changes observed during the El Niño. Furthermore, recovery increased the variance components measured at three of the five spatial scales, including regions (Fig. 4B). Thus, changes in both the relative variability and variance components together suggested that recovery following the El Niño was complex, variable at multiple scales, and likely influenced by a number of factors operating at those scales. However, given the large regional differences in El Niño impacts, I assessed recovery during the next 2 years (1998–2000) within each region separately.

Giant kelp recruitment immediately following the El Niño (June to October 1998) was generally strong in both central and southern California, although it was much stronger in southern California where survival of canopy-forming individuals was lower (Figs. 5, 6). As a result, whereas little-to-no change was observed in the number of larger individuals, average plant size, or mean frond density in central California during the El Niño, and the populations thus resembled their pre-El Niño condition for these parameters, the resulting populations in southern California were made up primarily of smaller (≤4 stipes plant^{-1}) individuals that had recently recruited and the average plant size and mean frond density remained lower than they were prior to the El Niño (Figs. 5, 6, 7). In contrast, recruitment in Baja California immediately following the El Niño was generally poor and only observed at a small number of locations (e.g. Bahía Tortugas and Isla San Martín; Edwards and Estes, unpublished data; Fig. 6). As a result, the number of larger individuals, average plant size, and mean frond
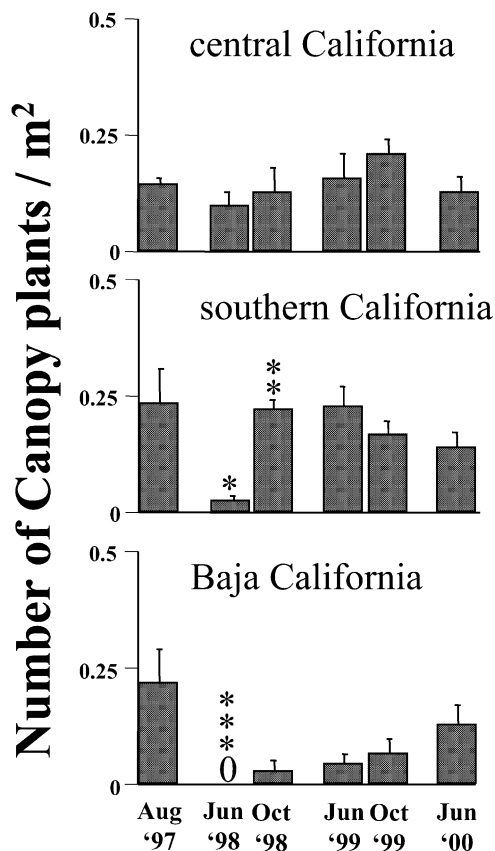
Fig. 5 Mean density of adult (canopy-forming) giant kelp (+1 SE) at the scale of regions in August 1997, June 1998, October 1998, June 1999, October 1999 and June 2000. Giant kelp density was estimated by counting all individuals ≥1 m tall along randomly directed 20 m ×2 m transects. Each individual was considered as an adult in they had at least 4 stipes / plant and were at least 1 m tall, while individuals ≤4 stipes / plant are not included to avoid confounding mortality estimates with individuals that recruited after the El Niño conditions subsided. *Asterisks* indicate significant changes in adult density relative to the survey period immediately prior (* P <0.05; ** P <0.01; *** P <0.001) as determined by one-way ANOVAs followed by post hoc Bonferoni-adjusted planned comparisons, and one-sample t-tests

density remained substantially lower than in southern and central California.

The giant kelp that recruited immediately following the El Niño grew during the next 8 months (October 1998 to June 1999) thus increasing the number of larger individuals in all three regions (Fig. 6). However, recruitment was weak and growth slow in Baja California, resulting in only slight increases in the abundance of canopy-forming individuals, average plant size, and mean frond density (Figs. 5, 6, 7). In contrast, growth was strong in southern and central California, resulting in larger (although not significant) increases in mean frond density (Fig. 7) but no changes in the abundance of canopy-forming individuals as these abundances already resembled their pre-El Niño condition (Fig. 5). Southern and central California differed with regard to recruitment of smaller individuals and its effect on average plant size; recruitment was strong in central California thus offsetting the effects of growth and resulting in little-to-no changes

in average plant size, while recruitment was poor in southern California thus resulting in growth over the previous 8 months increasing average plant size (Figs. 6, 7). Altogether, the differences in recruitment and growth among the three regions during the year following the El Niño revealed high among-region differences in recovery; giant kelp had returned to its pre-El Niño condition for the abundance of canopy-forming individuals, average plant size, population size distribution, and mean frond density in southern and central California but not in Baja California where recovery remained poor and geographically variable (Figs. 5, 6, 7). In general, though, there appeared to be a return to the pre-El Niño condition for variance structure where most of the total variability (71%) was again accounted for at the smallest scale (among transects within sites) and little (9%) was accounted for at the largest scale (among regions, Fig. 3D).

Giant kelp continued to recover in Baja California over the next 4 months (June–October 1999), becoming similar to southern and central California with respect to population size structure, average plant size, and mean frond density by October 1999 (Figs. 6, 7). This again redistributed the variability in giant kelp abundance among the five spatial scales such that most of the variability (76%) was accounted for at the smallest spatial scale examined while little of the variability (13%) was accounted for at the largest scale (Fig. 3A, E). In addition, a continued low recruitment to some locations in Baja California (e.g. Bahía Asuncion and Punta Baja) resulted in increases in both the variance measured among locations within regions (Fig. 4D) and in the relative amount of variability accounted for by differences among locations within regions from 2% to 11% of the total (Fig. 3E, D), and suggested that recovery in Baja California was not yet complete (Fig. 5).

By June 2000, the abundance of canopy-forming individuals, population size distribution for the larger size classes, average plant size, and mean frond density were similar among the three regions (Figs. 5, 6, 7). This, along with similarities in these parameters to their pre-El Niño condition in both southern and central California, and the return to a situation where most of the total range-wide variability in abundance was accounted for at the smallest spatial scales examined while very little of the variability was accounted for at the largest scale examined (Fig. 3F), suggested a near-complete recovery of giant kelp in the Northeast Pacific almost two years after the El Niño ended. Further, these analyses identified increases in both the variance components (Fig. 4E) and the amount of relative variability (Fig. 3E, F) observed at the scales of sites within areas, and areas within locations. This was the first time during the study that variability among sites within areas accounted for a substantial portion of the total variability and coincided with large outbreaks of purple (*Strongylocentrotus purpuratus*) and red (*S. franciscanus*) urchin populations that formed barren grounds at some sites and areas in southern California (e.g. Naples Reef and San Nicolas Island; unpublished data) and the California Channel Islands (D. Kushner, personal com-

Fig. 6 Size frequency distributions for giant kelp at the scale of region. Stipes were counted at 1 m above the bottom on all giant kelp measured during surveys and mean number of stipes per plant (±SE) are given for each region on each sample date. Data for individual plants are not available for Baja California in August 1997. Graphs are oriented in three columns corresponding to the three regions and in six rows corresponding to the six survey periods in sequential order

central California · **southern California** · **Baja California**

Count (# per size class)

Size class (# stipes / plant)
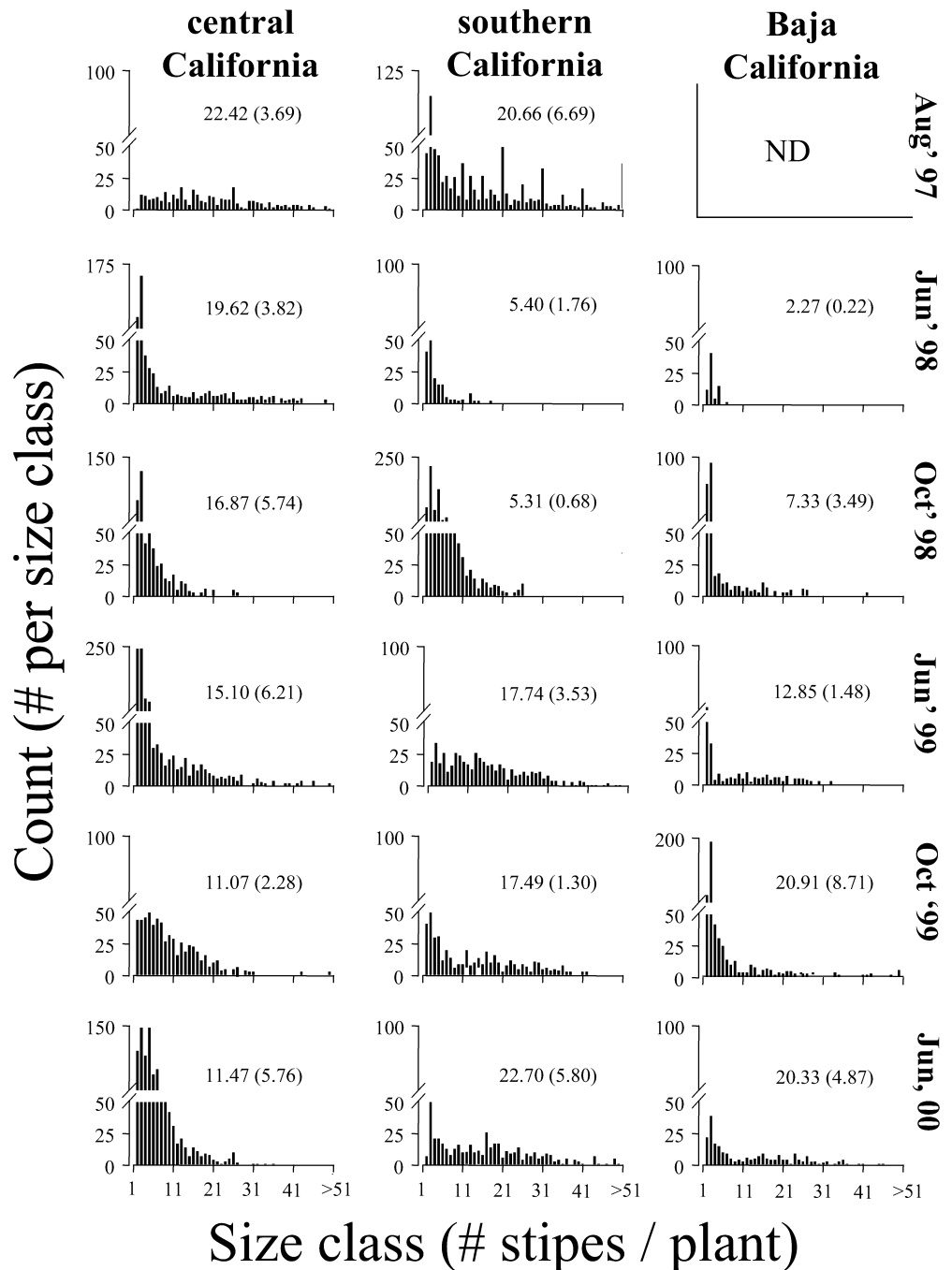
municipation). This further demonstrated a return to pre-El Niño conditions where the kelp communities are most strongly regulated by biological processes acting at small spatial scales (Dayton et al. 1992, 1999).

Discussion

Recent discussions have emphasized the importance of addressing the issue of scale in the design of ecological studies (Dayton and Tegner 1984a; Levin 1992, 2000; Tilman and Kareiva 1997). As a result, it has become clear that while some populations may be most strongly

influenced by processes acting at a particular scale at a given time, they may be more strongly influenced by processes operating at very different scales at other times (Connell et al. 1997; Karlson and Cornell 1997; Hughes et al. 1999; this study). Understanding the spatial and temporal nature of this scale-dependency, then, may provide a clearer assessment of the relative importance of these processes to overall ecosystems dynamics. Studies that treat space as a continuous variable can collect data on species abundance at uniformly spaced intervals, determine the amount of spatial separation between sample units, and then estimate their degree of autocorrelation (Legendre 1993). Other studies use spatially explicit
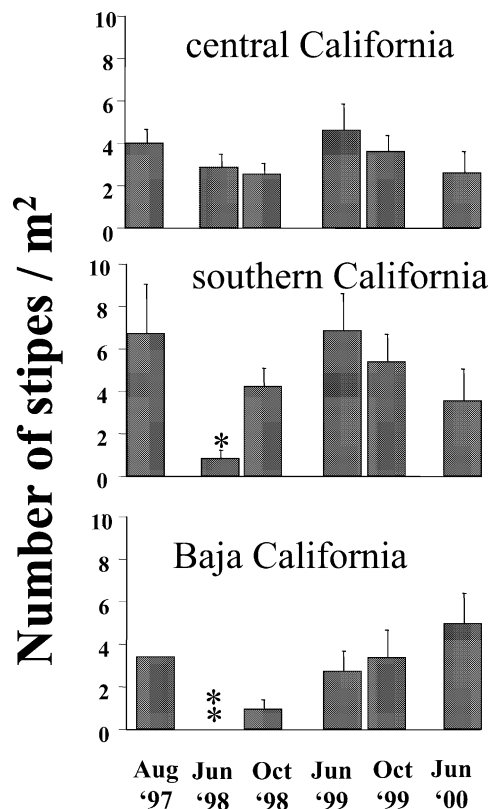
Fig. 7 Mean density of giant kelp stipes (+1 SE) at the scale of region in August 1997, June 1998, October 1998, June 1999, October 1999 and June 2000. Data for Baja California in August 1997 were obtained from a reduced sampling effort. Stipe density was estimated by counting all stipes on all giant kelp ≥1 m tall along each of the randomly directed 20 m ×2 m transects. *Asterisks* indicate significant changes in adult density relative to the survey period immediately prior (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$) as determined by one-way ANOVAs followed by post hoc Bonferoni-adjusted planned comparisons

computer models to estimate scales of organization for a number of species (Deutschman et al. 1997). Studies that treat space as a discrete variable based on a priori hypotheses or logistical constraints may rely on hierarchical sampling designs and Variance Components Analyses to estimate scales of variability (Underwood 1997; Hughes et al. 1999). This approach may be particularly valuable to studying the impacts of a large-scale disturbance on species over large geographic areas.

The 1997–98 El Nino was one of the strongest events ever recorded (Wolter and Timlin 1998), resulting in anomalously warm nutrient-poor water and unusually large ocean waves impacting the west coast of North America during the winter and spring 1997 and 1998. These conditions caused widespread mortality of giant kelp in the Northeast Pacific and a shift in the spatial scales at which the remaining populations were organized. This reflected a change from "local control", where giant kelp abundance and distribution were influenced most strongly by biological and physical factors acting at the scale of a few meters (e.g. Dayton et al. 1992) to "regional control", where giant kelp abundance and distribution

were most strongly influenced by oceanographic factors acting at the scale of hundreds to thousands of kilometers (e.g. Tegner et al. 1997). Immediately following the El Niño, the west coast of North America experienced a period of anomalously cold, nutrient-rich ocean conditions during the strong 1998–99 La Niña. These conditions facilitated the recovery of giant kelp and a return to local control, although the rate of recovery varied greatly among Baja, southern and central California, and among locations within each region. Furthermore, the return to local control was characterized by numerous changes in the scales at which giant kelp populations were organized, revealing shifts in the relative importance of the various factors influencing its recruitment, growth and survival. This agrees with evidence from other studies that suggests these processes are driven by a complex interaction of multiple biological and physical factors (e.g. ocean temperature, proximity to areas of coastal upwelling, propagule availability, grazing, and competition with understory algae and other kelp species; Reed and Foster 1984; Deysher and Dean 1986; Dayton et al. 1992, 1999; Graham et al. 1997; Tegner et al. 1997; Ladah et al. 1999; Hernández-Carmona et al. 2001).

Ecologically, the impacts of the 1997–98 El Niño on giant kelp populations in the northeast Pacific were catastrophic, resulting in their near-to-complete loss along Baja and southern California. In fact, with the exception of a small population that survived at Punta San José in northern Baja California (Ladah et al. 1999), this reflected a near-total mortality of all giant kelp throughout the southern ~500 km (one-third to one-half) of their geographic range and a temporary northward relocation of the species' southern range limit in Baja California (Edwards and Estes, unpublished data). Although such widespread mortality of a species is certainly rare (but see examples for the California sea otter, *Enhydra lutris*, in the north Pacific—Estes and Palmisano 1974; the black urchin, *Diadema antillarium*, in the Caribbean sea—Carpenter 1985; and the green urchin *Strogylocentrotus droebachiensis* in the northwest Atlantic—Scheibling 1984), similar patterns for giant kelp have likely occurred during past El Niños (Dayton and Tegner 1984b, 1990; Gerard 1984; Dayton 1985; Foster and Schiel 1985; Zimmerman and Robertson 1985; Tegner and Dayton 1987; Hernández-Carmona et al. 2000). However, past studies have observed substantial variability in El Niño impacts at smaller scales (among locations and among areas within locations), suggesting processes acting at those scales were also important (Dayton et al. 1992; Foster and Schiel 1992). In contrast, the near-lack of small-scale variability and the large amount of among-region variability in these impacts observed here likely resulted from corresponding large-scale differences in the synergistic effects of elevated ocean temperature, reduced nutrient availability, and increased wave intensity, with these factors masking smaller-scale processes (see also Tegner et al. 1997; Karlson and Cornell 1998; Edwards and Estes, unpublished data). While data for comparing the impacts of different El Niños come primarily from a

few locations in each region (primarily southern California), a full comparison of these impacts of across giant kelp's entire range may require an estimate of these impacts over this range and a better metric by which these impacts can most clearly be quantified. Consequently, comparing the impacts of future El Niños with one another should start by assessing whether their impacts exhibit the same scale-dependency.

Given the large regional differences in El Niño impacts, giant kelp recovery following the El Niño was assessed in each region separately. Recovery was generally poor and geographically variable in Baja California immediately following the El Niño, occurring at some locations (e.g. Bahía Tortugas) within 6 months after the El Niño ended, but requiring up to 2 years to occur at other locations (e.g. Bahía Asunción, Edwards and Estes, unpublished data). These initial differences were likely due to variability in the presence (i.e. survival) of microscopic life stages (Ladah et al. 1999; Hernández-Carmona et al. 2001). Following the return to cool nutrient-rich conditions and adequate propagule availability (June 1998–June 2000), locational differences in giant kelp recovery in Baja California appeared to result from variability in factors such as competition with sessile invertebrates, understory algae and other kelp species, and the availability of appropriate substrates (Ladah et al. 1999; Hernández-Carmona et al 2001; Edwards and Estes, unpublished data; Edwards and Hernández-Carmona, unpublished data). In contrast, recovery occurred within ~6 months at all locations in southern and central California, presumably facilitated by the strong La Niña (Hayward et al. 1999) and the presence of microscopic life stages (e.g. Dayton 1985; Edwards 2000). Then, nearly 2 years after the El Niño ended (June 2000), outbreaks of purple and red urchins (*Strongylocentrotus* purpuratus and *S. fransiscanus*) denuded the kelp at some sites within certain areas in southern California (e.g. at San Nicolas Island, Naples Reef, Channel Islands) but not at others, ultimately resulting in the slight region-wide decreases in total kelp abundance observed within southern California and increases in the variability observed at these scales. Following these outbreaks, giant kelp populations again appeared largely under local control.

That giant kelp populations are normally under local control is not surprising given discussions by Menge and Olson (1990), Karlson and Cornell (1998), Hughes et al. (1999) who suggest that many biological communities, including kelp forests (e.g. Dayton et al. 1992, 1999), are primarily regulated by processes acting at small spatial scales. Also not novel is the idea that large-scale processes can periodically mask the importance of local factors (e.g. Tegner et al. 1997; Karlson and Cornell 1998). However, while similar conclusions about the impacts of El Niños on giant kelp can be drawn from a review of the numerous studies on the subject (e.g. Dayton and Tegner 1984b, 1990; Zimmerman and Robertson 1985; Foster and Schiel 1992; Ladah et al. 1999; Hernández-Carmona et al. 2000, 2001), this study is unique in that it (1) was a single comprehensive investigation of these impacts across giant kelp's geographic range, (2) identified the scale at which these impacts were strongest, and thus provided a metric by which their nature and magnitude could most clearly be described, and (3) showed that while the scales of disturbance impacts were clear, the scales of recovery were spatially more complex, presumably driven by different forcing factors. It should be realized, however, that while all study sites were established in 8–12 m depth, previous studies have found depth to play a major role in influencing reproduction and survival in giant kelp, especially during El Niños (Dayton et al. 1992). However, while the patterns of recovery may have differed among depths, again demonstrating their greater complexity, a total lack of surface canopy at most locations in southern and Baja California immediately following the El Niño, along with qualitative observations made during dozens of "bounce" dives to depths below 20 m at numerous locations in all three regions (personal observation), suggested that the disturbance impacts were consistent across all depths. Further investigation of depth-specific hypotheses should be tested. The main point of this study then, is not to present new information on how giant kelp populations are organized during non-El Niño years or even how these populations are impacted by El Niños, but rather to demonstrate how a single comprehensive study done at multiple scales can provide substantial insight into the scale-dependent nature of ecosystem regulation, with particular attention to how an ecosystem's competitive dominant and primary habitat-forming species can be impacted by and recover from a large-scale environmental disturbance. Whether such an approach can be generalized to other ecosystems is unclear, but it is clear that many disturbances occur over large geographic areas (Zholdasova 1997; Carpenter 1998; Romme et al. 1998; Turner and Dale 1998) and that ecological research on their impacts will benefit by incorporating scale-dependent analyses (Dayton and Tegner 1984a; Levin 1992, 2000). Linking processes at various scales to their corresponding forcing factors (e.g. Hewitt et al. 2002) or to process operating at other scales (e.g. Thrush et al. 2000) will undoubtedly enhance our ability to resolve difficult issues concerning generality in the field of ecology.

References

Anderson TW (1994) Role of macroalgal structure in the distribution and abundance of a temperate reef fish. Mar Ecol Prog Ser 113:279–290

Carpenter RC (1985) Sea urchin mass-mortality: effects on reef algal abundance, species composition, and metabolism and other coral reef herbivores. Proceedings of the Fifth International Coral Reef Congress 4:53–60

Carpenter SR (1998) The need for large-scale experiments to assess and predict the response of ecosystems to perturbation. In: Pace ML, Groffman PM (eds) Successes, limitations, and frontiers in ecosystem science. Springer, Berlin Heidelberg New York, pp 287–312

Carr MH (1994) Effects of macroalgal dynamics on recruitment of a temperate reef fish. Ecology 75:1320–1333

Chapman MG, Underwood AJ, Skilleter GA (1995) Variability at different spatial scales between a subtidal assemblage exposed to the discharge of sewage and two control assemblages. J Mar Biol Ecol 189:103–122

Chavez FP (1996) Forcing and biological impact of onset of the 1982–83 El Niño in central California. Geophys Res Lett 23:265–268

Chelton DB, Bernal PA & McGowan JA (1982) Large-scale interannual physical and biological interaction in the California Current. J Mar Res 40:1095–1125

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol Monogr 67:461–488

Dayton PK (1985) Ecology of kelp communities. Annu Rev Ecol Syst 16:215–245

Dayton PK, Tegner MJ (1984a) The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In: Price PW, Slobodchikoff CN, Gaud WS (eds) A new ecology: novel approaches to interactive systems. Wiley, New York

Dayton PK, Tegner MJ (1984b) Catastrophic storms, El Niño, and patch stability in a southern California kelp community. Science 224:283–285

Dayton PK, Tegner MJ (1990) Bottoms beneath troubled waters: benthic impacts of the 1982–1984 El Niño in the temperate zone. In: Glynn PW (ed) Global ecological consequences of the 1982–83 El Niño-Southern Oscillation. Elsevier, Miami

Dayton PK, Tegner MJ, Parnell PE, Edwards PB (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecol Monogr 62:421–445

Dayton PK, Tegner MJ, Edwards PB, Riser KL (1999). Temporal and spatial scales of kelp demography: the role of oceanographic climate. Ecol Monogr 69:219–250

Deutschman DH, Levin SA, Devine C, Buttel LA (1997) Scaling from trees to forests: analysis of a complex simulation model. Science 277:1688

Deysher LE, Dean TA (1986) In situ recruitment of sporophytes of the giant kelp *Macrocystis pyrifera* (L.) C.A. Agardh: effects of physical factors. J Exp Mar Biol Ecol 103:41–63

Edwards MS (2000) The role of alternate life-history stages of a marine macroalga: a seed bank analogue? Ecology 81:2404–2415

Edwards MS (2001) Scale-dependent patterns of community regulation in giant kelp forests, Ph.D. thesis, UC Santa Cruz

Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. Science 185:1058–1690

Fielder PC (1984) Satellite observations of the 1982–1983 El Niño along the U.S. Pacific coast. Science 224:1251–1254

Foster MS (1990) Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. Hydrobiologia 192:21–33

Foster MS, Schiel DC (1985) The ecology of giant kelp forests in California: a community profile. Biological Report 85 (7.2). U. S. Fish & Wildlife Service, Washington, D.C.

Foster MS, Schiel DR (1992) Zonation, El Niño disturbance, and the dynamics of subtidal vegetation along a 30 m depth gradient in two giant kelp forests. Proceedings of the Second International Temperate Reef Symposium, pp 151–162

Gabrielson PW, Widdowson TB, Lindstrom SC, Hawkes MW, Scagel RF (2000) Keys to the benthic marine algae and seagrasses of British Columbia, Southeast Asia, Washington, and Oregon. University of British Columbia, Dept. Botany, Vancouver

Gerard VA (1984) Physiological effects of El Niño on giant kelp in Southern California. Mar Ecol Prog Ser 5:317–322

Glynn PW (1988) El Niño-Southern Oscillation 1982–1983: nearshore population, community, and ecosystem responses. Annu Rev Ecol Syst 19:309–345

Graham MH, Edwards MS (2001) Statistical significance versus fit: estimating the importance of individual factors in ecological analysis of variance. Oikos 93:503–513

Graham MH, Harrold C, Lisin S, Light K, Watanabe JM, Foster MS (1997) Population dynamics of giant kelp *Macrocystis pyrifera* along a wave exposure gradient. Mar Ecol Prog Ser 148:269–279

Graybill MR, Hodder J (1985) Effects of the 1982–83 El Niño on reproduction of six species of seabirds in Oregon. In: Wooster WS, Fluharty DL (eds) El Niño North. Washington Sea Grant Program, Seattle, pp 205–210

Hayward TL, Durazo R, Murphree T, Baumgartner TR, Gaxiola-Castro G, Schwing FB, Tegner M.J, Checkley DM, Hyrenbach KD, Mantyla AW, Mullin MM, Smith PE (1999) The state of the California Current in 1998–1999: transition to cool-water conditions. CalCOFI Rep 40:29–62

Hernández-Carmona G, García O, Robledo D, Foster MS (2000) Restoration techniques for *Macrocystis pyrifera* (Phaeophyceae) populations at the southern limit of their distribution in México. Bot Mar 43:273–284

Hernández-Carmona G, Robledo D, Serviere-Zaragoza E (2001) Effect of nutrient availability on *Macrocystis pyrifera* recruitment survival near its southern limit of Baja California. Bot Mar 43:273–284

Hewitt JE, Thrush SF, Legendre P, Cummings VJ, Norkko A (2002) Integrating heterogeneity across spatial scales: interactions between *Artina zelandica* and benthic macrofauna. Mar Ecol Prog Ser 239:115–128

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. Nature 397:59–63

Karlson RH, Cornell HV (1998) Scale-dependent variation in local vs. regional effects on coral species richness. Ecol Monogr 68:259–274

Kerr RA (1988) La Niña's big chill replaces El Niño. Science 241:240–241

Ladah LB, Zertuche-González JA, Hernández-Carmona G (1999) Giant kelp (*Macrocystis pyrifera*, Phaeophyceae) recruitment near its southern limit in Baja California after mass disappearance during ENSO 1997–1998. J Phycol 35:1106–1112

Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Levin SA (2000) Multiple scales and the maintenance of biodiversity. Ecosystems 3:498–506

McPhaden MJ (1999) Climate oscillations—genesis and evolution of the 1997–98 El Niño. Science 283:950–954

Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. Trends Ecol Evol 5:52–57

Neibauer HJ (1985) Southern Oscillation/El Niño effects in the eastern Bering Sea. In: Wooster WS, Fluharty DL (eds) El Niño North. Washington Sea Grant Program, Seattle, pp 116–120

Pearcy W, Fisher J, Brodeur D, Johnson S (1985) Southern Oscillation/El Niño effects in the eastern Bering Sea. In: Wooster WS, Fluharty DL (eds) El Niño North. Washington Sea Grant Program, Seattle, pp 188–204

Reed DC, Foster MS (1984) The effects of canopy shading on algal recruitment and growth in a giant kelp forest. Ecology 65:937–948

Romme WH, Everham EH, Frelich LE, Moritz MA, Sparks RE (1998) Are large, infrequent disturbances qualitatively different from small, frequent disturbances? Ecosystems 1:524–534

Royer TC (1985) Coastal temperature and salinity anomalies in the northern Gulf of Alaska. In: Southern Oscillation/El Niño effects in the eastern Bering Sea. In: Wooster WS, Fluharty DL (eds) El Niño North. Washington Sea Grant Program, Seattle, pp 107–115

Scheibling RE (1984) Echinoids, epizootics and ecological stability in the rocky subtidal off Nova Scotia, Canada. Helgol Meeresunters 37:233–242

Searle SR, Casella G, McCullouch CE (1992) Variance components. Wiley, New York

Tegner MJ, Dayton PK (1987) El Niño effects on Southern California kelp communities. Adv Ecol Res 17:243–279

Tegner MJ, Dayton PK, Edwards PB, Riser KL (1997) Large-scale, low-frequency oceanographic effects on kelp forest successions: a tale of two cohorts. Mar Ecol Prog Ser 146:117–134

Thompson WA Jr (1962) The problem of negative estimates of variance components. Ann Math Stat 33:273–289

Thompson WA Jr, Moore JR (1963) Non-negative estimates of variance components. Technometrics 5:441–449

Thrush SF, Hewitt JE, Cummings VJ, Green MO, Funnell GA, Wilkenson MR (2000) The generality of field experiments: interactions between local and broad-scale processes. Ecology 81:399–415

Tilman D, Kareiva P (1997) Spatial ecology—the role of space in population dynamics and interspecific interactions. Princeton University Press, New Jersey

Turner MG, Dale VH (1998) Comparing large, infrequent disturbances: what have we learned? Ecosystems 1:493–496

Underwood AJ (1997) Experiments in ecology. Cambridge University Press, Cambridge

Wallace JM (1985) Atmospheric response to equatorial sea-surface temperature anomalies. In: Wooster WS, Fluharty DL (eds) El Niño North. Washington Sea Grant Program, Seattle, pp 9–21

Weins JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397

Wolter K, Timlin MS (1998) Measuring the strength of ENSO events: How does the 1997/98 rank? Weather 53:315–324

Zholdasova I (1997) Sturgeons and the Aral Sea ecological catastrophe. Environ Biol Fish 48:373–380

Zimmerman RC, Robertson DL (1985) Effects of El Niño on local hydrography and growth of the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California. Limnology and Oceanography 30:1298–1302