Geographic variation in demography of a temperate reef snail: importance of multiple life-history traits

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ABSTRACT: Individual- and population-level performance may reflect trade-offs between energy allocation to different key demographic processes, such as growth and reproduction, which can, in turn, be influenced by local biotic and abiotic conditions. We explored geographic variation in demographic rates of an exploited benthic species, the wavy-turban snail *Megastraea undosa*, along the Pacific coast of Baja California, Mexico. We compared key life-history traits (i.e. fecundity, size at maturity, growth, and survivorship) of populations existing between 20 and 170 km apart under different conditions of ocean temperature and food availability. Trade-offs between growth and reproduction were evident across this environmental gradient, with higher growth rates in warmer locations leading to lower size-specific investment in gonad production. Because later onset of reproduction in populations from warmer areas was compensated by greater fecundity at larger sizes, geographic variation in life-history strategies resulted in similar age-specific reproductive output among different populations. However, we observed that, while there is substantial variation in demographic rates of the study species, harvest management is applied uniformly, and this results in southern populations achieving lower reproductive output before they reach a legally harvestable size. Our results highlight the importance of considering geographic variation in multiple life-history traits when managing across a mosaic of land- and seascapes characterized by varying environmental conditions.

KEY WORDS: Demographic rates · Geographic variation · *Megastraea undosa* · Fisheries management · Temperature · Resource availability · Life history

INTRODUCTION

A major goal of marine conservation and management efforts is to identify and protect 'source' habitats and populations that contribute disproportionately to local populations and regional metapopulation dynamics (Pulliam 1988, Gaines et al. 2010). Demographic rates of individuals and populations, such as reproduction, growth, and survival, influence these dynamics and may vary across the seascape in response to variable environmental conditions and species interactions (Leslie et al. 2005, Lester et al. 2007, Costello et al. 2010). Documenting this variation is critical to predicting species responses to climate change and the effectiveness of resource management and conservation strategies (Costello et al. 2010, Doak & Morris 2010, Gaines et al. 2010). For example, mismatches between the scales at which populations vary and the scales of fisheries regulations have been implicated in causing the declines of many targeted species (Hilborn et al. 2005, Wilson 2006, Costello et al. 2010).

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Ecological niche theory and life-history theory provide contrasting views on how variable environmental conditions across landscapes and seascapes can lead to geographic variation in demographic rates and resulting population dynamics. Ecological niche theory predicts that optimal individual performance is found in areas where environmental conditions are physiologically optimal (Hutchinson 1957). Local environmental conditions and stochasticity, availability of food and habitat, and species interactions can affect how individuals allocate resources to reproduction, growth, maintenance, and survival, which ultimately determines population performance (Stearns 1992). Although ecological niche theory can be useful for predicting spatial patterns of individual and population performance, it is generally applied in a hierarchical manner, where performance shows an ordered response to environmental conditions. Under this conceptual framework, the worst conditions lead to mortality, better conditions permit survival and growth, and the best conditions allow survival, growth, and reproduction (Townsend et al. 2000).

In contrast, life-history theory suggests that increased performance in a single life-history trait may be accompanied by compensatory resource allocation and decreased performance in another trait (Stearns 1992, Vindenes et al. 2008). For example, under poor-quality or uncertain food supply, individuals may invest energy in reproduction at the expense of growth or maintenance (Siems & Sikes 1998, Stoeckmann & Garton 2001). Recognizing that these different demographic rates are linked and affect each other challenges the hierarchical view of niche theory, making it difficult to predict how population performance will vary in relation to environmental conditions when looking at single demographic parameters (Siems & Sikes 1998, Doak & Morris 2010). Several species show phenotypic plasticity in response to environmental factors by allocating resources in a non-hierarchical manner to somatic growth, reproduction, and maintenance (e.g. Siems & Sikes 1998, Stoeckmann & Garton 2001, Petes et al. 2008), suggesting that trade-offs among life-history traits exist and can lead to unexpected predictions of population performance.

Consideration of multiple life-history traits and the trade-offs among them may lead to alternative interpretations of individual and population performance in a geographic context under niche theory versus life-history theory. Under ecological niche theory, individuals with faster growth rates are assumed to have higher fitness because of the positive effects of growth on age-specific fecundity and survival (de

Roos et al. 2003). However, in some environments, trade-offs among traits may occur; for example, rapid growth may reduce fitness through structured intrinsic physiological trade-offs (Petes et al. 2008) or environment-dependent mortality risks (Trussell et al. 2003). As such, environments that result in increased growth rates but decreased reproductive investment may lead to lower relative benefits of reproducing at a larger size (Schaffer 1974). Alternatively, conditions leading to increased reproductive investment may be accompanied by reduced growth or survival, resulting in smaller individuals with lower lifetime reproductive output and lower relative fitness. Environmentally mediated spatial variation in energy allocation among life-history traits may be common (Frederiksen et al. 2005), yet most studies focus on single life-history parameters (e.g. Leslie et al. 2005, Phillips 2005, Lester et al. 2007, Menge et al. 2008), which may result in erroneous interpretations of population dynamics and ultimately misdirect management and conservation efforts.

Despite the potential for geographic variation in key demographic rates to profoundly impact population dynamics (Boyce et al. 2006, Vindenes et al. 2008), few studies examine variation in multiple demographic rates and resulting impacts of management. Under ecological niche theory, areas that show elevated performance in one trait may be presumed to indicate increased performance overall. This might lead scientists and managers to presume that these areas are worthier of protection (e.g. Leslie et al. 2005) or lead to higher productivity than other areas (e.g. Menge et al. 2008). However, if, as according to life-history theory, trade-offs among traits exist, then areas with increased performance in one trait may be accompanied by reduced performance in another, leading to incorrect assumptions about overall productivity in those areas. Management targets should adjust to variation in performance (Hilborn et al. 2005), but, to do so, managers must be able to predict how performance will change across the management area. Thus, managers and scientists should consider multiple traits when assessing population performance across the seascape.

A suite of physical variables (e.g. temperature, ocean currents) and biological processes and interactions (e.g. productivity, predation, competition) that affect the allocation of energy among life-history traits vary at multiple spatial scales across the seascape. Coastal upwelling, which influences both temperature and primary productivity, is a prominent feature that varies across nearshore marine ecosystems and may drive spatial variation in demographic rates at re-

gional scales (i.e. tens to hundreds km) (Broitman & Kinlan 2006, Broitman et al. 2008). Temperature can influence growth rates by affecting metabolic demands and consumption rates for many organisms (Somero 2002, Yee & Murray 2004). But temperature is often negatively correlated with food availability and quality in nearshore marine ecosystems (Mann & Lazier 1991), which also affect both growth rates and reproductive output (Foster et al. 1999, Ponce-Diaz et al. 2004, Menge et al. 2008). Furthermore, high variability can exist in demographic rates at local scales due to local effects of wave action, predation, competition, facilitation, or habitat characteristics. For example, local-scale (1 to tens km) variation in wave-exposure leads to local-scale variation in the allocation of energy to reproduction, growth, and stress-resistance in intertidal mussels (Petes et al. 2008). The manner in which spatial variability in environmental conditions at multiple scales translates into life-history trade-offs remains poorly understood, particularly for temperate subtidal rocky reef species.

In the present study, we investigated geographic variation in demographic traits of an ecologically and commercially important marine gastropod, *Megastraea undosa*, and resulting implications for conservation and management of marine populations. We asked the following questions: (1) Are there detectable geographic differences in reproductive output, growth, or mortality rates among natural populations of *M. undosa* in regions differing markedly in physical oceanographic conditions? (2) If *M. undosa* shows variation in demographic rates between regions, do the rates among different demographic processes change in a hierarchical manner or do these differences reflect trade-offs in energy allocation, according to life-history theory? Specifically, does *M. undosa* exhibit decreased reproductive output followed by decreased growth rates, followed by decreased survival, or rather are higher growth rates associated with reduced size-specific reproductive effort? Our results indicate that divergent strategies exist in different environments, and emphasize the importance of considering spatial variation in multiple key demographic rates when managing coastal populations.

MATERIALS AND METHODS

Study system

This research was conducted in 2 regions separated by 170 km along the Vizcaino Peninsula in cen-tral Baja California, Mexico (Fig. 1). The western shelf of Baja California is situated at the southern terminus of the California Current Large Marine Ecosystem and is characterized by regions of intense and persistent coastal upwelling separated by regions of weak and infrequent upwelling (Zaytsev et al. 2003). The northern study region (Bahia Tortugas) encompassed a region of persistent upwelling with cool ocean temperatures (11 to 23°C), high nutrient availability, and high macroalgal biomass (Hernandez-Carmona et al. 2001, Zaytsev et al. 2003, Espinosa-Carreon et al. 2004). The southern study region (Punta Abreojos) encompassed a region of weak upwelling that experiences warm ocean temperatures (14 to 28°C), low nutrient availability, and has low macroalgal biomass (Hernandez-Carmona et al. 2001).

The wavy turban snail *Megastraea undosa* is a large (shell up to 150 mm basal diameter) herbivorous subtidal marine gastropod found along the west coast of North America from Pt. Conception, California, south to Bahía Magdalena, Baja California Sur (BCS), Mexico (Morris et al. 1980). The primary food source of *M. undosa* is the giant kelp *Macrocystis pyrifera* (hereafter '*Macrocystis*') (Cox & Murray 2006); however, as generalist herbivores they consume a variety of fleshy and calcareous macroalgae (Aguilar Rosas et al. 1990, Halliday 1991). *Macrocystis* forms extensive kelp forests in the upwelling region, but is absent where upwelling is weak and variable. In regions of weak upwelling and warm ocean temperatures, *Eisenia arborea* (hereafter '*Eisenia*') is the dominant subtidal kelp.

Megastraea undosa is targeted by dive fisheries throughout its range, with the greatest fisheries production occurring along the Vizcaino Peninsula. Our study regions spanned the jurisdiction of 3 of the 10 fishery cooperatives that participate in la Federación Regional de Sociedades Cooperatives de la Industria Pesquera 'Baja California' (FEDECOOP) (Fig. 1). Fishing cooperatives that participate in FEDECOOP are granted exclusive fishing rights to several benthic invertebrate species, including *M. undosa*. All cooperatives enforce identical management measures for *M. undosa*, including fishing quotas at the scale of local reefs (1 to 10 km), a seasonal closure (from November 1 to February 28), and a minimum legal size of 90 mm in basal diameter, and the proportional fished biomass of the species is similar in both regions.

We employed a regional-comparative approach by nesting 3 sampling sites within each region (Fig. 1). Regional-comparative approaches are necessary for
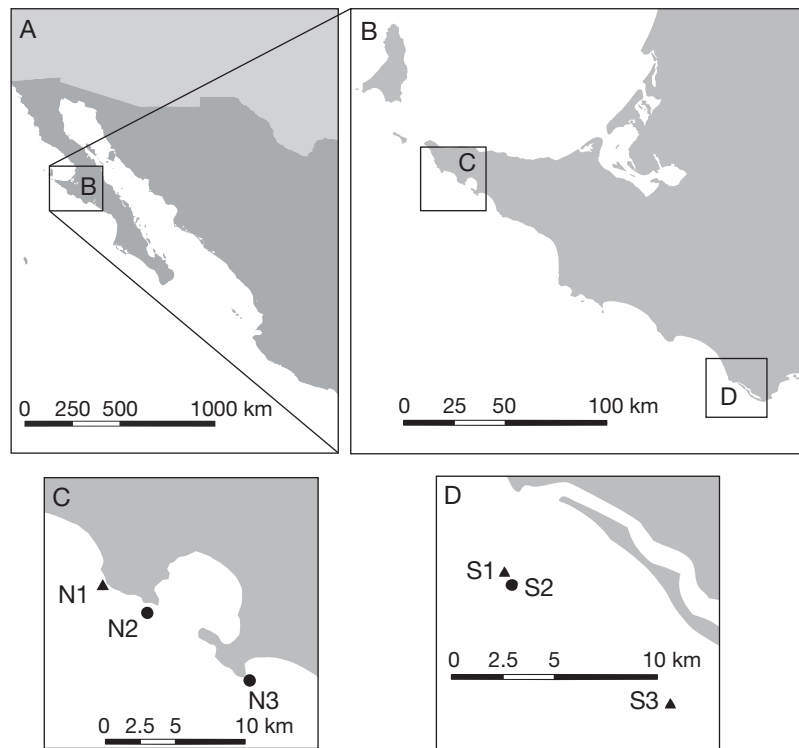
Fig. 1. (A) Geographic region of *Megastraea undosa*, from Point Conception, California, USA, to Bahia Magdalena, Baja California, Mexico. (B, inset) Vizcaino Peninsula, Baja California, Mexico. (C) Northern region and (D) southern region, with sampling sites within each region indicated (north: N1 to N3; south: S1 to S3). ●: sites where all vital rates were measured (growth, survival, reproductive investment); ▲: additional sites where only reproductive investment was measured

studying ecological processes at large spatial scales, but cannot be used to statistically infer cause-and-effect relationships as a result of spatial pseudoreplication (Hurlbert 1984, Hargrove & Pickering 1992). In the present study, because we did not have spatially replicated upwelling regimes, the factor 'region' was spatially confounded. To address this, we tested for an effect of 'upwelling region type' (intense vs. weak) by treating 'upwelling' as a random factor nested within site. All sites were located 0.5 to 5.0 km from shore and encompassed rocky reef habitats ranging in depth between 10 and 12 m below mean lower low water. Northern sites (N1, N2, N3) were dominated by *Macrocystis*, whereas southern sites (S1, S2, S3) were dominated by *Eisenia*.

Ocean temperature and food availability

We compared ocean temperatures between regions by deploying temperature loggers (Onset Hobo Temp Pro) at 2 sites in each region between January 2006 and November 2007. We compared food availability for *Megastraea undosa* between regions by comparing kelp biomass. We measured size and density of *Macrocystis* (number of stipes) and *Eisenia* (number of sporophytes >50 cm) in 4 belt transects (10 × 2 m) at each site in July 2006.

We estimated biomass of the dominant kelps separately, due to the differences in their morphology (i.e. individual *Eisenia* have 1 stipe, while *Macrocystis* individuals can have multiple stipes). We estimated the biomass of *Eisenia* at each site using an individual weight (mean ± SE = 323.1 ± 101.6 g, n = 28) applied to adult (i.e. >50 cm, the size at which mature sporophytes provide canopy cover; Clare & Herbst 1938) densities within each transect. We estimated mean *Macrocystis* biomass at each site using the relationship between the depth of the holdfast and the number of stipes and fronds (Mahoney & Wiley 2007).

To evaluate regional differences in kelp nutritional quality we measured C:N ratios of *Macrocystis* and *Eisenia*. Low C:N ratios indicate high food quality for herbivores (Cruz-Rivera & Hay 2000, Ponce-Diaz et al. 2004). We collected a 10 cm section of frond tissues from 5 *Macrocystis* and 5 *Eisenia* sporophytes at each site (n = 15 region^{-1} species^{-1}). Clean algal material was oven dried at 80°C and ground to a fine powder using mortar and pestle. The percent tissue C and N were determined using a continuous flow organic elemental analyzer (flash combustion method), and C:N ratios were determined on an atomic weight basis.

We compared C:N ratios between regions (*Eisenia* only) and species (northern region only) using linear mixed effects models (R package 'lme'). We tested for effects of 'species' (fixed) and 'site' (random) comparing *Macrocystis* and *Eisenia* C:N ratios from sites in the northern, upwelling-intense region. We tested for an effect of 'upwelling region type' (intense vs. weak) comparing *Eisenia* C:N ratios from the northern and southern regions by treating 'upwelling' as a random factor.

Life-history traits

Reproductive output

To determine whether energetic investment in re-production differed between regions, we compared individual size-at-maturity, size-specific reproductive investment (i.e. gonad weight and gonad index), and size-specific egg production. We collected 30 to 60 snails ranging from 25 to 131 mm basal diameter at each site using SCUBA (Fig. 1). For each individual, we measured basal diameter (size) to the nearest 0.01 mm. We defined gonad index as the ratio of the hepatogonadal complex (g) to the weight (g) of the whole organism (body + viscera + hepatogonadal complex), thus capturing the proportion of biomass allocated to gonads. Individuals were sexed by visual examination of the gonad, classified as males or females and later confirmed histologically, and were analyzed separately.

Samples of each gonad were taken for histological preparation from the mid-section (Belmar-Perez et al. 1991). All gonad samples were fixed in 10% formalin for at least 72 h and then transferred to 70% ethanol. Tissues were then processed for paraffin histology. De-paraffinized 5 to 8 µm sections were mounted on slides and stained with hematoxylin and eosin (Luna 1968) for examination using light microscopy. Histological sections were used to classify individuals into different reproductive stages: immature juveniles (Stage I), early gametogenic individuals (Stage II), and mature adults (Stage III) (Belmar-Perez et al. 1991). Individual sizes were binned into 10 mm size classes, and we calculated the size at which 50% of females reached maturity — a metric commonly used to set size limits for fisheries management.

To estimate the relationship between individual fecundity and size, we estimated the number of eggs produced per volume of gonad. The medial section of the hepatogonadal appendage (Belmar-Perez et al. 1991) was cut radially, and the ratio of gonad to hepatopancreas tissue area in the section was measured. We assumed that the ratio of gonadal tissue to hepatopancreas tissue is constant throughout the entire hepatogonadal appendage (Belmar-Perez et al. 1991) and estimated the total gonad volume by multiplying the proportion of gonad tissue in the section to the volume of the entire appendage, which was obtained by measuring the displacement of the hepatogonadal appendage in water (Rogers-Bennett et al. 2004).

We analyzed a subset of mature females from 3 sites (N2: n = 15, N3: n = 19, S1: n = 19) for oocyte size and fecundity. Digital photographs were taken of 2 to 3 slides per individual, and 3 to 5 sections were analyzed per slide using Image J™ software. The 3 largest oocytes were haphazardly chosen in each section to estimate the maximum area of each oocyte, as the largest were most likely to capture the radius of the oocyte and could be used to calculate maximum oocyte area. Maximum oocyte area was not significantly different between sites (ANOVA between sites: $F_{2,50}$ = 0.8293; p = 0.44). We assumed that each oocyte approximates a sphere and calculated the radius of an average oocyte (r = 86 µm), and, applying this radius, we calculated the volume of a single oocyte. The number of eggs produced by a given individual was then calculated as the volume of the gonad divided by the volume of a single oocyte.

We tested for differences in reproductive investment (gonad weight and gonad index) between regions using linear mixed effects models with basal diameter as a fixed factor, site included as a random effect, and 'upwelling region type' as a random factor nested within site. Due to limited numbers of females sampled from each site for fecundity estimates, we pooled across sites to test for regional differences in fecundity using AN-COVA, with region as a 2-level random factor and basal diameter as a covariate. Data were log-transformed when appropriate.

Growth and survival

We employed mark-release-recapture studies to compare *Megastraea undosa* growth and survival rates between regions. We collected snails from 3 sites (N2, N3, S1; Fig. 1) in January and July 2006, and March 2007.

Individuals were brought to the laboratory, initial size measured, and epibionts removed. We tagged shells with 0.8 × 1.4 cm numbered yellow plastic tags (Floy Tag & Mfg) externally attached with 2-part epoxy (Z-spar). Tagged snails were selected to represent a range of sizes (basal diameter = 25 to 131 mm, mean ± SE = 89.4 ± 0.4 mm, n = 1243). Snails tagged in January 2006 were recaptured in July 2006 to assess growth over the cool spring–early summer period. Snails tagged in July were recaptured in March 2007 to assess growth over the warm period. Individuals tagged in January 2006 were also recaptured in March 2007 to assess annual growth over the entire 14 mo study period. We measured change in basal diameter of recaptured snails to determine

individual growth (mm d^{-1}). We used ANCOVA to test for differences in growth rates between sites and between seasons within each site using initial size as the covariate. Scheffe tests were used for unplanned post hoc comparisons (Sokal & Rohlf 1981, Ruxton & Beauchamp 2008).

To determine if survival rates differed among sites, we used the computer program MARK (White & Burnham 1999) to compute maximum-likelihood estimates of Φ, the apparent survival probability, and *p*, the recapture probability, using capture-mark-recapture data for each individual *Megastraea undosa* (total number of capture events = 1337). We used a Cormack-Jolly-Seber (CJS) model to test for differences in recapture rates and survivorship between sites and to test whether there was an effect of size on survivorship probability (Lebreton et al. 1992). Our global starting model incorporated different survival and recapture rates among populations at the 3 different sites where animals were marked, and all further models applied to the data were special cases of this model.

We compared different candidate models and estimated apparent survival and recapture probabilities (Lebreton et al. 1992) using Akaike's information criterion (AIC) (Burnham & Anderson 2002). We used the corrected index (AIC$_c$) because it provides more accurate results when sample sizes are small (Morris & Doak 2003). From AIC$_c$, normalized Akaike weights (range = 0 to 1) and ΔAIC$_c$ were calculated as the difference in AIC$_c$ between the current model and the model with the lowest AIC$_c$. When selecting models, the model component for recapture rate (*p*) was selected first, by running models differing only in this component. The component for survival rate (Φ) was not altered and thus included variation among all sites (i.e. the global model for survival). After selecting the best model for recapture rate, the same process was performed on the component for survival rate, where we kept the selected model for recapture rate fixed and tested different models for survival rate (Appendix 1).

Age-specific growth and reproduction

To determine age-specific size and fecundity we estimated size-at-age from the mark-recapture data because it was not possible to directly determine ages of individuals in the field. To estimate size-at-age and growth trajectories, we used the Fabens (1965) estimation of the 2-parameter Brody von Bertalanffy growth function (VBGF) (Von Bertalanffy 1938) that describes the maximum basal diameter (BD) at age *t* (BD$_t$):

$$BD_{recapture} = BD_{tag} + (BD_\infty - BD_{tag}) \times (1 - e^{(-kT)}) \quad (1)$$

where BD$_\infty$ is the maximum size (i.e. basal diameter) reached after an infinite period of growth, *k* is the exponential rate at which growth slows as individuals approach maximum size, BD$_{tag}$ and BD$_{recapture}$ are sizes at mark and recapture, respectively, and *T* is time between mark and recapture. These deterministic models were fit using non-linear mixed effects models in R. To calculate error estimates of the growth model parameters, we randomly sampled the variance–covariance matrix from the modeled growth data for each region, calculated the resulting parameters, BD$_\infty$ and *k*, and then determined size-at-age from 1 to 12 yr, as 12 yr is likely the maximum age of *Megastraea undosa* (Gluyas-Millan et al. 1999). We assumed that the distribution of the fitted parameters followed a multivariate normal distribution centered at the maximum-likelihood estimate of the variance–covariance matrix. We ran this model iteratively 1000 times and calculated the 95% CI around the average growth model (Efron & Tibshirani 1998).

To estimate age-specific fecundity, we first determined the relationship between fecundity and size from log-linear regressions between the number of eggs per gonad volume and basal diameter for each region (see above). We calculated error around the parameter estimates from the log-linear regression by bootstrapping from the variance–covariance matrix. We assumed that the distribution of the fitted parameters follows a multivariate normal distribution centered at the maximum-likelihood estimate of the variance–covariance matrix. We obtained 1000 parameter estimates for the fecundity-size relationship. Given that measures of fecundity and growth are independent, we then combined these 1000 parameter estimates with the 1000 bootstrapped parameter estimates obtained from the von Bertalanffy growth model to estimate the relationship between fecundity and age.

To test whether there were significant differences in size-at-age and fecundity-at-age, we used non-parametric randomization tests (Gotelli & Ellison 2004). We compared the differences of the mean size-at-age and the mean fecundity-at-age for each age-class between the north and south. All analyses were performed using R (2011).

RESULTS

Variation in environmental conditions

Daily bottom temperatures were lower in the northern, upwelling-intense region than in the southern, upwelling-variable region, with temperature differences between the regions as high as 8.5°C (Fig. 2). During the summer (July to September) and fall (October to November) temperatures were, on average, 3.4 and 2.4°C lower, respectively, in the north (mean ± SE; summer: 16.9 ± 0.3°C; fall: 21.4 ± 0.2°C) compared to the south (summer: 20.3 ± 0.4°C; fall: 23.8 ± 0.2°C). However, during winter (December to February) and spring (March to June), temperatures were, on average, only 1.0 and 0.5°C lower, respectively, in the north (winter: 18.3 ± 0.20°C; spring: 12.4 ± 0.07°C) compared to the south (winter: 19.3 ± 0.19°C; spring: 12.9 ± 0.06°C).

Kelp standing stock biomass was significantly higher in the north compared to the south ($F_{1,4}$ = 16.8, p = 0.01) due to the presence of the giant kelp *Macrocystis* in the north but not in the south, where the only kelp species is the understory *Eisenia* (Fig. 3). Food quality was also higher in the north compared to the south, as *Macrocystis* has significantly lower C:N ratios than *Eisenia* (17.0 ± 0.9 and 20.9 ± 0.8, respectively) ($F_{1,26}$ = 21.7, p ≤ 0.0001) (Fig. 4). C:N ratios of *Eisenia* tissues were not significantly different between the north and south ($F_{1,4}$ = 0.68, p = 0.45). Thus, the northern region is characterized by both greater availability and nutritional quality of the preferred macroalgae consumed by *Megastraea undosa*.

Variation in life-history parameters

Reproduction

Females of *Megastraea undosa* reached maturity (Stage III) at smaller sizes in the north (50 to 60 mm BD) than in the south (60 to 70 mm BD). At both the northern and southern sites, 50% of females reached reproductive maturity by 80 to 90 mm. However, a greater percentage of individuals <80 mm BD were mature in the north (N2: 33.3%; N3: 41.2%) compared to the south (S1: 21.3%).
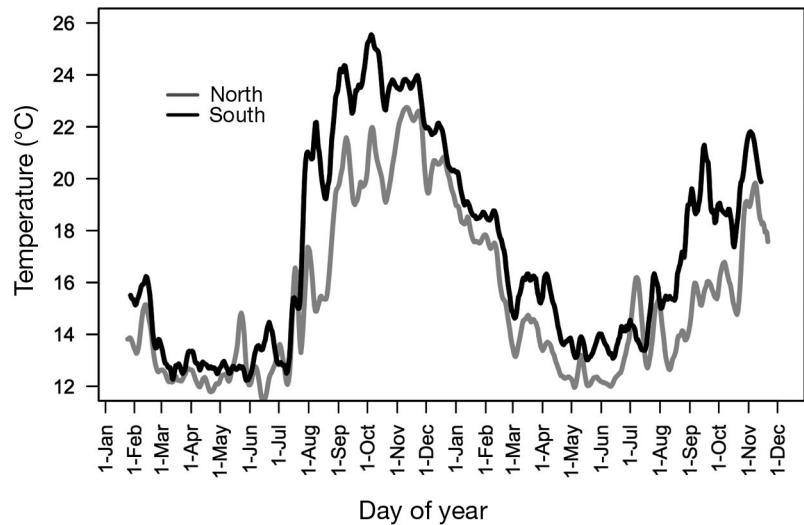

Fig. 2. Mean daily bottom temperature in the north (gray line) and south (black line) from January 2006 to November 2007

Gonad weight and gonad index increased with size (Fig. 5, Table 1), with a trend for larger individuals having a larger proportion of their weight allocated to gonads than smaller individuals, although gonad index did not increase with size significantly in the south. Females and males showed significantly higher gonad weight and gonad indices in the north compared to the south (Fig. 5, Table 1).

Similarly, size-specific fecundity varied between the 2 regions, with higher mean log-transformed size-specific fecundity in the north compared to the
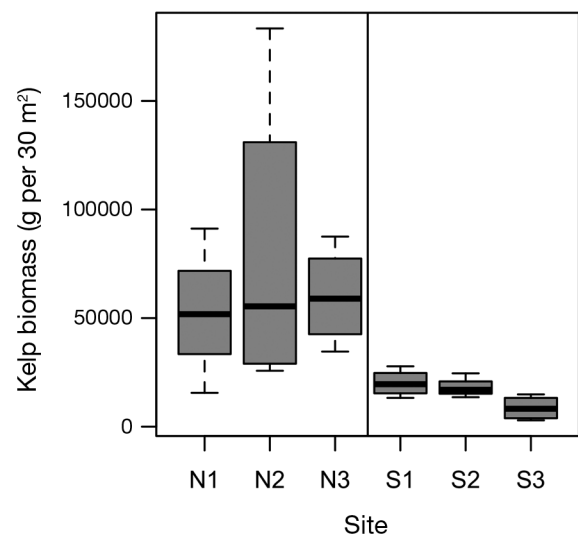

Fig. 3. *Macrocystis pyrifera*, *Eisenia arborea*. Boxplots (median, box: 25% and 75%, whiskers: minimum and maximum values) of total kelp biomass at 3 sites each in the north and south
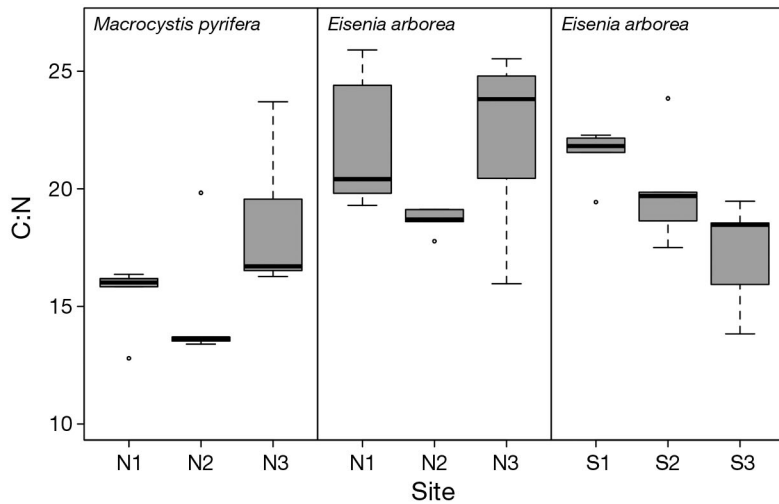
Fig. 4. *Macrocystis pyrifera*, *Eisenia arborea*. Boxplots (median, box: 25% and 75%, whiskers: minimum and maximum values) of C:N ratios of *M. pyrifera* and *E. arborea* from the 3 northern sites and *E. arborea* from the 3 southern sites

south (ANCOVA: BD: $F_{1,69} = 415.0$, p ≤ 0.0001; region: $F_{1,4} = 3.8$, p = 0.055; BD × Region: $F_{1,69} = 0.32$, p = 0.47) (Fig. 6).

Growth

Individual growth rates did not differ among sites over the initial 6 mo of the mark-release-recapture experiment (ANCOVA: $F_{2,88} = 2.2$, n = 92, p = 0.11) (Fig. 7A), but showed significant between-site variation over 8 and 14 mo (ANCOVA 8 mo: $F_{2,24} = 12.5$, n = 28, p < 0.001; 14 mo: $F_{2,48} = 7.3$, n = 52, p = 0.002), with the southern site having higher growth rates than the 2 northern sites (Scheffe tests, 8 mo: S1 > N2, p < 0.001, S1 > N3, p < 0.001; 14 mo: S1 > N2, p = 0.012, S1 > N3, p < 0.002), and no significant differences between the 2 northern sites (Scheffe tests, 8 mo: N2 = N3, p = 0.83; 14 mo: N2 = N3, p = 0.58) (Fig. 7B,C). The significant difference in growth rates between the north and south occurred during the summer and fall (June 2006 to March 2007), when temperatures were 2 to 3°C warmer in the southern region, on average, but not in winter and spring (January to June 2006), when bottom temperatures were similar in the 2 regions.

Survival

The estimated recapture rate was 0.22 (±0.04 SE), with no difference in recapture rates among sites

(Appendix 1). Using this recapture rate, the most parsimonious model for survival rate had survival varying between sites, with lower survival at N2 (Φ = 0.27 ± 0.06) than at N3 and S1 (Φ = 0.56 ± 0.08) (Appendix 1). This model had 3 times as much support in terms of AIC_c weight as the next most parsimonious model, which showed survival varying among all sites. These 2 most parsimonious models did not include size as an effect, suggesting that the effect of size on survival does not vary significantly among these populations.

Age-specific growth and reproduction

Brody-Bertalanffy growth curves were calculated separately for each region, pooling the 2 northern sites (Fig. 8A). k was estimated to be 0.26 (95% CI: 0.11 to 0.33) in the north and 0.23 (95% CI: 0.14 to 0.35) in the south. BD_∞ was estimated to be 113.7 mm (95% CI: 106.5 to 134.6 mm) in the north and 131.2 mm (95% CI: 117.8
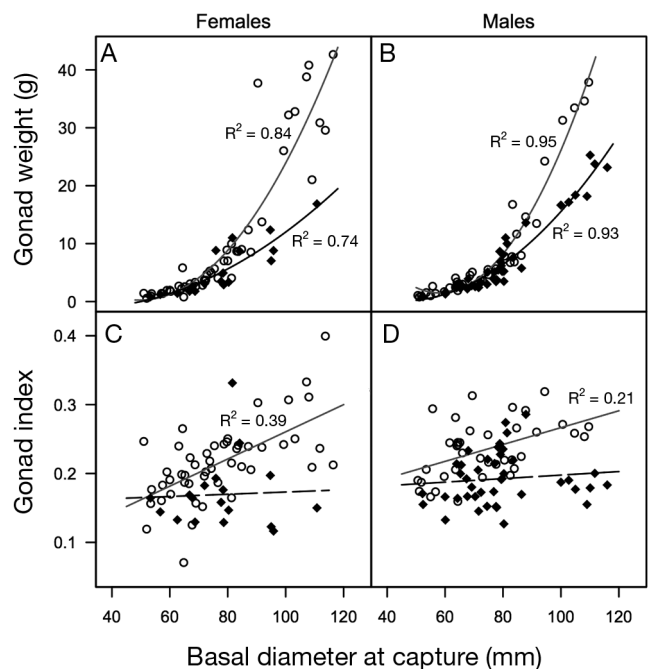

Fig. 5. *Megastraea undosa*. Gonad weight (A,B) and gonad index (C,D) by size of females (A,C) and males (B,D) in the north (n = 3 sites; ○) and south (n = 3 sites; ◆). Juveniles (<40 mm) not shown. Solid lines = significant relationships; dashed lines = insignificant relationships

Table 1. *Megastraea undosa*. Linear mixed effects models testing for regional variation in (a) gonad weight and (b) gonad index by size (BD, basal diameter), calculated for females and males, separately

Source	Females (n = 67)			Males (n = 80)		
	df	*F*	p	df	*F*	p
(a) ln(gonad weight)						
(Intercept)	1,59	1336.9	<0.0001	1,72	2979.2	<0.0001
ln(BD)	1,59	531.2	<0.0001	1,72	983.2	<0.0001
Region	1,4	13.6	0.02	1,4	28.6	0.006
ln(BD) × Region	1,59	1.6	0.21	1,72	1.4	0.24
(b) Gonad index						
(Intercept)	1,59	1297.0	<0.0001	1,72	1854.6	<0.0001
BD	1,59	22.7	<0.0001	1,72	5.6	0.020
Region	1,4	13.7	0.02	1,4	20.5	0.01
BD × Region	1,59	4.5	0.04	1,72	3.6	0.06

pensated for reduced size-specific fecundity, producing similar fecundity at a given age.

DISCUSSION

Spatial variation in demographic rates

Life-history traits of *Megastraea undosa* vary between regions along the Baja California coast that differ in upwelling regime, temperature, nutrient availability, and kelp biomass.

to 149.9 mm) in the south. Non-parametric randomization tests indicated that significant differences exist between the populations in the 2 regions starting at Age 4 (Table 2), with the southern population showing significantly faster growth rates (Fig. 8A, Table 2).

Despite differences in size-specific fecundity between the northern and southern populations (Fig. 6), age-specific fecundity was not significantly different between the 2 regions (Fig. 8B, Table 2). There were no significant differences between the populations at any age (Table 2), suggesting that faster growth rates in the southern population com-
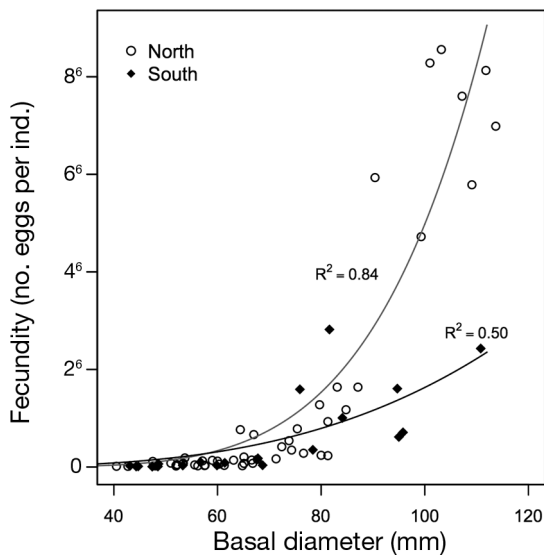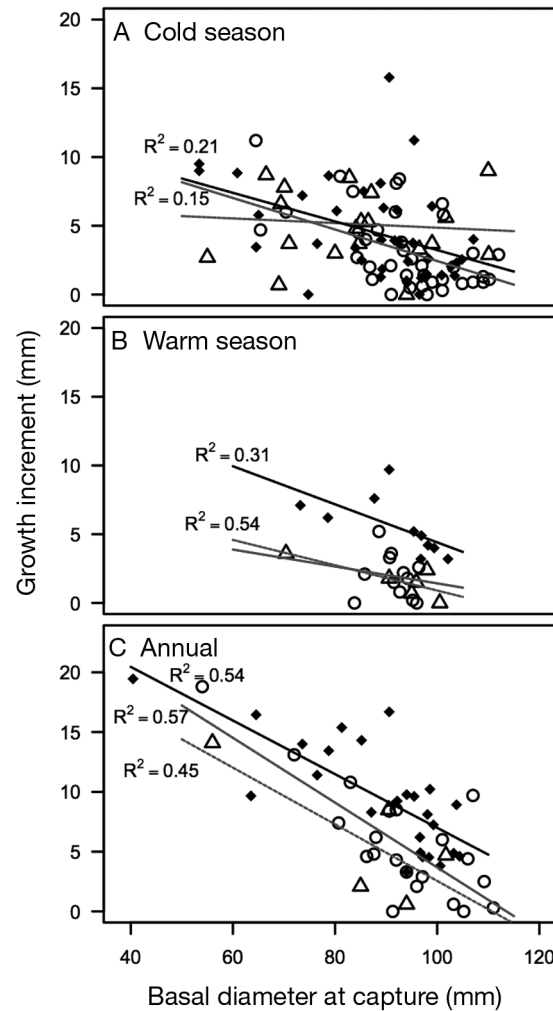

Fig. 6. *Megastraea undosa*. Relationship between fecundity (number of eggs produced per individual) and size (basal diameter) for females in the north (○) and south (◆)

Fig. 7. *Megastraea undosa*. Relationship between growth increment and size (basal diameter) of *M. undosa* individuals at 3 sites: N2 (△), N3 (○), and S1 (◆). Growth periods are (A) the 'cold season' (January to July 2006), (B) the 'warm season' (July 2006 to March 2007) and (C) 'annual' (January 2006 to March 2007)

Environments supporting higher growth rates (Figs. 7 & 8A) are accompanied by lower size-specific gonad investment (Figs. 5 & 6), but populations in areas with reduced size-specific gonad investment compensate with faster growth to produce similar average population-level age-specific fecundity. These results support t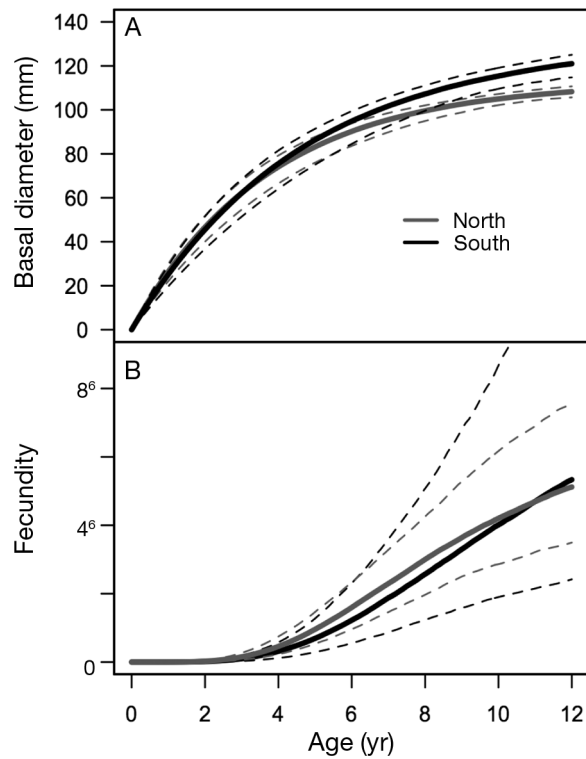he hypothesis corresponding to life-history theory, where variable environmental conditions among regions lead to trade-offs between demographic rates and similar population performance, rather than the premise of niche theory, which would predict populations with hierarchical allocation of energy to demographic rates and variable performance among regions.

These results highlight the importance of documenting geographic variation in several demographic processes simultaneously. Focusing on a single life-history parameter presents an incomplete and possibly erroneous picture of the spatial variation of population demography and, ultimately, population dynamics. For example, if we had documented only size-specific gonad weight as a measure of reproductive performance, we would conclude that northern populations have greater reproductive output than southern populations. In contrast, if we had focused solely on growth, we would conclude that southern populations exhibit enhanced performance and that fecundity and lifetime reproductive output may also be greater because individuals would be expected to reach maturity in a shorter time. However, when we consider both reproductive allocation and growth, 2 processes that are energetically linked, we note that these disparate life-history strategies lead to similar average age-specific fecundity (Fig. 8B). This trade-off between reproduction and growth results in 2 different life-history strategies, but this may result in similar average cumulative reproductive output across populations, especially if mortality rates are similar between populations.

Consistent patterns were seen across multiple sites within regions for the variables measuring reproductive investment (i.e. size-specific reproductive invest-

Fig. 8. *Megastraea undosa*. (A) size-at-age (von Bertalanffy growth model) and (B) age-specific fecundity for individuals in the south (black lines) and north (gray lines). Means and 95% CEs (dotted lines)

Table 2. *Megastraea undosa*. Mean size-at-age and fecundity-at-age for northern and southern populations, and absolute differences between regions; p in **bold**: significant differences between regions from non-parametric permutation tests

Age	Mean size-at-age				Mean fecundity-at-age			
	North	South	|Difference|	p	North	South	|Difference|	p
1	2.61×10^1	2.64×10^1	3.04×10^{-1}	0.12	6.00×10^2	6.01×10^2	6.48×10^{-1}	0.52
2	4.63×10^1	4.75×10^1	1.19×10^0	0.1	2.29×10^4	2.01×10^4	2.86×10^3	0.37
3	6.18×10^1	6.42×10^1	2.38×10^0	0.078	1.45×10^5	1.22×10^5	2.24×10^4	0.34
4	7.37×10^1	7.74×10^1	3.71×10^0	**0.048**	4.08×10^5	3.79×10^5	2.94×10^4	0.43
5	8.29×10^1	8.80×10^1	5.07×10^0	**0.022**	9.48×10^5	8.15×10^5	1.33×10^5	0.32
6	9.00×10^1	9.64×10^1	6.37×10^0	**0.006**	1.60×10^6	1.41×10^6	1.92×10^5	0.33
7	9.55×10^1	1.03×10^2	7.57×10^0	**0.002**	2.33×10^6	2.10×10^6	2.27×10^5	0.34
8	9.97×10^1	1.08×10^2	8.67×10^0	**<0.001**	3.07×10^6	2.84×10^6	2.26×10^5	0.36
9	1.03×10^2	1.13×10^2	9.64×10^0	**<0.001**	3.76×10^6	3.57×10^6	1.90×10^5	0.39
10	1.05×10^2	1.16×10^2	1.05×10^1	**<0.001**	4.38×10^6	4.26×10^6	1.24×10^5	0.46
11	1.07×10^2	1.19×10^2	1.12×10^1	**<0.001**	4.92×10^6	4.88×10^6	3.86×10^4	0.51
12	1.09×10^2	1.21×10^2	1.19×10^1	**<0.001**	5.37×10^6	5.43×10^6	5.83×10^4	0.50

ment, size-specific fecundity). For growth parameters, we lack replicate sites in the southern region due to the challenges of replicating labor-intensive mark-recapture experiments underwater. Although our study only examined 1 site in the south, significant differences in growth between the southern site and both northern sites support the hypothesis of between-region variation. Furthermore, in a separate study, we measured growth from opercular marks at multiple sites within each region, and found significant differences in growth between regions during 2006 (Martone 2009), supporting our conclusion of regional differences in growth from mark-recapture experiments.

Environmental factors influencing variation in demographic rates

Regional differences in energy allocation to growth and reproduction and resulting life-history strategies are likely governed by a combination of temperature-driven bioenergetic constraints and food availability and quality. Southern populations of *Megastraea undosa* living in warmer summer and fall temperatures had significantly faster growth rates and lower size-specific gonad weight and fecundity, despite lower food availability and quality, than northern populations, which live in year-round cooler temperatures with higher food availability and quality. Reduced resource availability and quality have been shown to decrease reproductive output (Foster et al. 1999, Leslie et al. 2005, Lester et al. 2007) and growth (Menge et al. 2008). However, if food quantity and quality alone limited individual performance of *M. undosa*, then both reproductive investment and growth rates would have been lower in the south. Instead, growth rates were higher in the south (Fig. 7), where fall and winter temperatures were up to 8.5°C warmer than in the north. Furthermore, significant differences in growth rates between regions were found during the season when temperature differences were higher (July to March), but not during the cooler upwelling season (January to July). For generalist herbivores, elevated temperatures may lead to increased growth rates, but reduced food availability and quality may limit the ability to meet metabolic demands and simultaneously maximize reproductive investment. Higher temperatures have been shown to increase growth rates of marine mollusks (Ponce-Diaz et al. 2004, Menge et al. 2008), as metabolic rates increase with temperature, up to some threshold, for many organisms (Somero 2002, Yee & Murray 2004), including *M. undosa* (Schwalm 1973). Thus, in coastal marine systems, where higher temperatures are often accompanied by lower food availability or quality (e.g. Menge et al. 2008) trade-offs in energetic allocation among key demographic rates may be common.

Other factors that vary across mesoscales can influence demographic rates. For example, differences in size-specific predation among populations can lead to differences in size at maturity and higher predation risk of small size-classes may select for organisms with faster growth rates and delayed maturity (Chase 1999). Conversely, predation risk in the absence of a size-refuge can lead to an early onset of reproduction, smaller size at maturity, and increased reproductive investment (Chase 1999). The presence of predators can also limit foraging time and thus result in lower overall available energy stores (Trussell et al. 2003). Although we did not measure predation rates directly, survivorship did not vary between regions. Furthermore, while a slight effect of size on survival may exist, this did not vary between regions. Thus, the regional-scale differences in energy allocation among life-history traits are likely not due to differences in predation pressure between the 2 regions.

Local-scale variability in grazer densities, intraspecific competition, primary productivity, and algal species composition may also influence local resource availability to individuals. Large observed variation in growth and reproduction among individuals at local scales suggests that individual performance and energy allocation may also be influenced by local factors, such as local predation rates or density of conspecifics. Snail densities varied by a factor of 3 among northern sites, ranging from 0.5 to 2 individuals m^{-2}, on average (Martone 2009). Additional studies quantifying predation rates, feeding rates, and intraspecific competition are needed to tease apart the effects of predation and resource availability at local scales, separately from regional-scale temperature and food effects.

Implications for natural resource management and conservation

Documenting spatial variation in multiple life-history traits and understanding the ecological and biogeophysical processes underlying this spatial variation are critical for natural resource management and conservation. For example, to fulfill biodi-

versity conservation and fisheries goals, marine reserves and other marine protected areas are often expected to act as 'sources' (Pulliam 1988, Gaines et al. 2010) providing offspring to other areas in the oceans. Identifying spatial variation in reproductive output is an important step towards understanding meta-population dynamics in the marine environment. Several previous investigations have identified reproductive hotspots as a function of reproductive traits, such as gonad index (Leslie et al. 2005, Lester et al. 2007), yet our data suggest that populations with lower fecundity may compensate by having faster average growth rates, thus leading to populations with similar average egg production across the seascape. Consequently, marine population models must consider multiple life-history traits when determining areas of protection in the oceans.

While geographic variation in demographic rates may lead to similar average age-specific fecundity, it may give rise to very different impacts from human intervention on natural populations. Worldwide declines in fisheries resources have been attributed, in part, to oversight of the spatial variability in the demography of target species (Hilborn et al. 2005, Wilson 2006). For example, here and in many other fisheries a single minimum size limit is applied across populations that vary in their demographic rates. In this case, by ignoring spatial variation in demography, fisheries management strategies, such as setting minimum size limits for the fisheries, may differentially impact the populations they target, which could lead to serial depletion of stocks. In the case of *Megastraea undosa*, because a single minimum size of 90 mm is applied across these regions, fishing may lead to lower lifetime reproductive output in the southern region, where individuals have lower size-specific reproductive investment and a delayed onset of maturity. On average, applying the 90 mm size limit, an individual captured in the fishery from the southern population would produce approximately one-third the amount of eggs prior to harvest compared to an individual captured from the north. More sophisticated fisheries models can be used to test whether incorporating locally or regionally derived estimates of biological parameters is important for evaluating the impacts of fisheries management strategies on reproductive output, yield, and, ultimately, on population persistence.

While our research highlights which factors may influence population dynamics and which scales are likely more appropriate for managing benthic species in coastal kelp forest ecosystems, other factors may preclude setting management measures at appropri-

ate scales. These include (1) a lack of political will or interest and (2) the inability to enforce regulations at fine spatial scales (Prince 2005, Wilson 2006). To fully understand the factors that influence sustainable management a coupled social-ecological approach is required, including both the acquisition of information about the ecology of the system, such as biophysical factors, population dynamics, species interactions, and ecosystem-level processes, as well as socio-economic factors, such as mechanisms for facilitating compliance with regulations and perceived incentives and social mechanisms for collective decision-making. In the case of Baja California, cooperative behavior and enforcement among fisheries is in part facilitated by perceived incentives and disincentives. Through a system of co-management and exclusive access rights to fisheries resources in the region, the federation of fishing cooperatives of the Vizcaino region—FEDECOOP—is able to implement local- and region-specific fisheries regulations. This is partially attributable to the ability to achieve high levels of compliance (McCay et al. in press), in part due to perceived benefits from membership in the cooperatives, such as access to resources, income, infrastructure, and participatory decision-making (McCay et al. in press). This highlights the importance of interdisciplinary approaches to understand and facilitate the capacity of communities to manage for sustainability in ecosystems.

CONCLUSIONS

Demographic variation across spatial environmental gradients may be common in natural populations (Frederiksen et al. 2005). Variation can arise from trade-offs between energetically costly activities such as growth and reproduction, particularly in marine ecosystems where environmental factors may be correlated in ways that reduce the amount of energy available to allocate among life-history traits. By elucidating the processes and scales at which life-history traits and population dynamics vary, the goals of sustainable fisheries and population persistence can be met, as long as institutional norms are in place to set appropriate management targets and achieve compliance with fisheries regulations. We conclude that regional-scale variation in temperature and food availability can lead to regional variation in life-history strategies of harvested species, and that spatial variation in biological parameters should be taken into account when managing across a mosaic of land- and seascapes.

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Appendix 1. Selection of the best model for recapture rate, p; and survival rate, Φ. Notation: (g) = rates different among all three sites (N2, N3, S1); $(\cdot)$ = rates constant among all 3 sites; BD = basal diameter. AIC_c = Akaike's information criterion

Model		AIC_c	ΔAIC_c	AIC_c weights	No. param.
Recapture rate					
$\Phi(g)$	$p(\cdot)$	1177.33	1.85	0.16	4
$\Phi(g)$	$p(g\!: \text{N3} = \text{S1} \neq \text{N2})$	1197.04	3.57	0.06	5
$\Phi(g)$	$p(g\!: \text{N2} = \text{N3} \neq \text{S1})$	1179.19	3.72	0.06	5
$\Phi(g)$	$p(g\!: \text{N2} = \text{S1} \neq \text{N3})$	1179.34	3.87	0.05	5
$\Phi(g)$	$p(g)$	1181.01	5.54	0.03	6
Survival rate					
$\Phi(g\!: \text{N3} = \text{S1} \neq \text{N2})$	$p(\cdot)$	1175.48	0.00	0.49	3
$\Phi(g)$	$p(\cdot)$	1177.33	1.85	0.16	4
$\Phi(g \times \text{BD})$	$p(\cdot)$	1178.04	2.57	0.07	10
$\Phi(g \times \text{BD})\!: \text{N3} = \text{S1} \neq \text{N2}$	$p(\cdot)$	1178.87	3.40	0.05	7
$\Phi(g \times \text{BD})\!: \text{N2} = \text{S1} \neq \text{N3}$	$p(\cdot)$	1197.51	18.03	0.00	7
$\Phi(g\!: \text{N2} = \text{S1} \neq \text{N3})$	$p(\cdot)$	1195.96	20.48	0.00	3
$\Phi(\text{BD})$	$p(\cdot)$	1198.55	23.07	0.00	4
$\Phi(g\!: \text{N2} = \text{N3} \neq \text{S1})$	$p(\cdot)$	1198.82	23.34	0.00	3
$\Phi(g \times \text{BD})\!: \text{N2} = \text{N3} \neq \text{S1}$	$p(\cdot)$	1199.93	24.46	0.00	7
$\Phi(\cdot)$	$p(\cdot)$	1201.28	25.81	0.00	2