AN ABSTRACT FOR THE DISSERTATION OF

Heather M. Leslie for the degree of Doctor of Philosophy in Zoology presented on May 13, 2004.

Title: Advancing Marine Reserve Science: From Field Experiments to Marine Conservation Planning Tools

Abstract approved: ______________________
Jane Lubchenco

Abstract approved: Bruce Menge
Bruce A. Menge

This dissertation focuses on science relevant to the design and implementation of marine reserves. The chapters explore a range of topics related to among-site variation in population, community, and ecosystem dynamics. My results demonstrate the value and feasibility of integrating this knowledge into more comprehensive conservation and management approaches. While the threats facing the oceans are serious, we in the scientific community have considerable information and tools to contribute to the development and implementation of solutions.

In Chapter 2, I report on the effects of conspecific density on multiple traits of the intertidal barnacle *Balanus glandula*. The primary effects of increased density were enhanced survival and higher reproductive rates. My results provide a strategy

for evaluating the relative importance of positive vs. negative intraspecific interactions when implementing reserves.

In Chapter 3, my co-authors and I investigated how variation in nearshore primary productivity influenced survival, growth, and reproduction in *B. glandula.* We found strong evidence for bottom-up (i.e. productivity) forcing of barnacle population dynamics. One site produced substantially more larvae than the others, demonstrating the importance of among-site variability. Our findings advance understanding of bottom-up influences on marine populations, and demonstrate the value of embedding reserves within a network.

In Chapter 4, my co-authors and I used benthic habitat data from the Florida Keys to show how a computer-based siting tool could be used to help design reserve networks. We found that many different combinations of sites produced satisfactory networks, and highlighted areas as potential conservation priorities. Our work was the first marine application of this tool and provided a starting point for applications in California and Australia.

In Chapter 5, I report on a synthesis of marine conservation planning cases globally. I found that the majority occurred in North and Central America, were based on biogeographic boundaries, and that biodiversity conservation was the primary objective. One of the most striking findings was the paucity of well-documented cases. My results suggested that planners consider knowledge of marine populations, communities, and ecosystems important when identifying priorities, but that they do not have clear guidelines for how to integrate this information appropriately.

Advancing Marine Reserve Science:
From Field Experiments to Marine Conservation Planning Tools

By

Heather M. Leslie

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APPROVED:

Jane Lubchenco

Co-Major Professor, representing Zoology

Bruce Menge

Co-Major Professor, representing Zoology

Chair of the Department of Zoology

Sally Francis

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Heather Leslie

Heather M. Leslie, Author

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CONTRIBUTION OF AUTHORS

Erin Breck collected data on larval production per barnacle for her Senior Honors Thesis (Chap. 3). Bruce Menge and Jane Lubchenco provided essential input on experimental design and analysis, as well as barnacle recruitment data (Chap. 3). Hugh Possingham, Sandy Adelman, Mary Ruckelshaus, and Ian Ball contributed to all phases of the siting tool application. In particular, Ian Ball developed the tool as part of his dissertation work at University of Adelaide, South Australia (Chap. 4).

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For my parents,

Kathleen and Sanford Leslie

Advancing Marine Reserve Science:
From Field Experiments to Marine Conservation Planning Tools

Chapter 1: Introduction to the Dissertation

Elucidating how marine ecosystems work is an urgent task, given the large-scale and increasingly severe anthropogenic perturbations to coastal and marine ecosystems globally. Ninety percent of large predatory marine fish biomass has been removed from the world's ocean by several decades of fishing (Myers and Worm 2003). In the US, >13% of coastal watersheds are developed (Beach 2002), and more than two-thirds of US estuaries and bays outside of Alaska are affected by land-based nutrient pollution (Boesch et al. 2000). Closer to home, in California, rocky intertidal ecologists have observed shifts in invertebrate species ranges that suggest species have begun to respond to climatic change (Barry et al. 1995). A number of changes in the distribution of non-indigenous species marine flora and fauna due to human introductions have been detected, as well. In Coos Bay, Oregon, for example, at least 57 species have been introduced (Ruiz et al. 2000).

While the oceans are in serious trouble, there are many reasons for hope. In the US, for example, we receive a wide range of goods and services from the 4.5 million square miles of US ocean waters, and 31% of the US Gross National Product is produced in coastal counties (US Environmental Protection Agency 2001). In addition to generating revenue via trade, tourism, and food and energy production, coastal marine ecosystems provide critical ecological services (e.g. water quality, storm mitigation, and nursery areas for fisheries) as well as opportunities for research, education, recreation, and preservation of natural and cultural heritage values (Peterson and Lubchenco 1997, Heinz Center 2002).

Increasingly, too, the public and policymakers seem to recognize the ocean's importance to human well-being. At the national level, two commissions composed of leaders from science, industry, and public policy (The Pew Commission and the US Commission on Ocean Policy) recently offered their visions for the future of US ocean stewardship. At the state level, Oregonians are near unanimous (94%) in saying that a healthy ocean is important to them personally, as well as important to Oregon's economic future (93%) and to the state's environmental future (94%) (Edge Research 2002).

This dissertation focuses on science relevant to the design and implementation of marine reserves. My ultimate objective in this work was to further understanding of how marine ecosystems work, so that we as a society can do a more effective job of managing and conserving these systems.

Marine reserves are areas of the ocean completely protected from all extractive or destructive activities except as necessary for monitoring or research to evaluate reserve effectiveness (National Research Council 2001, Lubchenco et al. 2003). Reserves are one type of marine protected area (MPA), which is a broader term that includes reserves and other area-based management strategies designated to enhance conservation of marine resources (National Research Council 2001, Lubchenco et al. 2003). The actual level of protection of living marine resources within MPAs varies considerably. In US National Marine Sanctuaries, for example, most areas are open to fishing and other types of resource extraction.

Marine reserves are one tool for coastal and ocean management. They are not meant to replace other management tools, but may provide a complementary and potentially more comprehensive approach to managing marine ecosystems and the people who use them. As a framework for communicating my dissertation research, I pose several key ecological questions related to reserve design and implementation:

1. How do marine populations, communities and ecosystems respond to reserve establishment?
2. Why do we need reserve networks, rather than single reserves?
3. If we think in terms of networks, where should individual reserves be located?
4. How has natural science been integrated into reserve design and other marine conservation planning efforts?

To answer these questions, I employed a variety of approaches, ranging from field experiments in Oregon's rocky intertidal areas (Chapters 2 and 3) to computer-based modeling for reserve design (Chapter 4) and synthesis of interviews and information from the peer-reviewed and gray literature (Chapter 5).

In Chapter 2 and 3, I used the marine intertidal barnacle *Balanus glandula* to investigate possible answers to the first two questions, in the context of Oregon's rocky intertidal ecosystems. Barnacles have a long and illustrious history as ecological models because of their abundance, their role as a major prey species in rocky intertidal communities (Connell 1961, Paine 1966, Connell 1970, Menge 1976), and the similarity of their life history to other species of ecological and commercial interest, including sea urchins, crabs, and seastars (Pechenik 2000). Also, they can be observed and experimented upon in the field quite easily, due to their sessile adult stage, small size, and relatively rapid time to maturity.

In Chapter 2, I addressed the first question (population responses to reserve establishment). When areas are protected from fishing and other extractive activities, in many cases, populations increase in abundance (Halpern 2003). Nonetheless, there are relatively few investigations of how increased population densities alter ecological interactions and the subsequent effects on life history traits of species of interest. Using barnacles as a model (in a non-reserve setting), I report on a series of experimental and observational investigations of the effects of conspecific density on key traits (survival, growth, reproduction) of *B. glandula*. Density was manipulated in mid intertidal barnacle populations living on both natural and artificial substrata, and monitored in natural populations.

In Chapter 3, my co-authors and I report on a series of investigations that tested whether bottom-up factors, specifically alongshore variation in nearshore primary productivity on the Oregon coast, influenced survival, growth, and reproduction in *B. glandula*. Ecologists now recognize that top-down (i.e. consumer driven) and bottom-up (i.e. variation in nutrients, productivity) forces act in concert to regulate ecological systems. Nonetheless, empirical examples of bottom-up effects on marine populations and communities are relatively rare. Based on previous work, we predicted that barnacle populations in the higher productivity region (Cape Perpetua) would experience increased survival, faster growth, and greater reproductive output when compared to those at lower productivity region (Cape Foulweather).

Chapter 3 addressed the second question (why reserve networks). While we found strong evidence of bottom-up forcing of barnacle population dynamics on the scale of the capes, one site within the higher productivity region produced substantially more larvae than the others. Our findings demonstrate that larval production "hotspots" exist in rocky intertidal ecosystems, and that areas along the shore are not necessarily ecologically equivalent. Networks of marine reserves provide one useful strategy for dealing with the inevitable uncertainty about the location of demographic sources and sinks of target species and other place-specific details of marine population and ecosystem dynamics.

In Chapter 4, my co-authors and I addressed the question of how to select marine reserves in a network context. Using benthic habitat data from the Florida Keys (USA), we demonstrated how siting algorithms could be used to help identify potential networks of marine reserves that comprehensively represent target habitat types. We applied a flexible optimization tool—simulated annealing—to represent a fixed proportion of different marine habitat types within a geographic area. We investigated the relative influence of spatial information, planning unit size, detail of habitat classification, and magnitude of the overall conservation goal on the resulting network scenarios. Our work was the first marine application of a siting tool of this kind, and it provided a starting point for several real-world applications in California's Channel Islands (USA), Australia and elsewhere.

In Chapter 5, I report on a synthesis and evaluation of marine conservation planning approaches from around the world. I focused particularly on how natural science has been integrated into marine reserve design and other marine conservation planning efforts. By 'marine conservation planning,' I am referring to spatially explicit, systematically planned coastal and ocean conservation and management activities. Governments and non-governmental organizations have engaged in conservation planning for decades, yet there are few comparative analyses of the approaches taken on land or in the sea. Data on the political and geographic scope of each case, the objectives and context, stakeholder involvement, and the criteria and tools used to make decisions were collected from the peer-reviewed and gray literature, the internet, and interviews with conservation scientists.

Answers to each of the questions posed above (i.e. the implications of my results for marine conservation and management) are presented in Chapter 6.

Chapter 2:

The Influence of Conspecific Density on Key Life History Traits of the Intertidal Barnacle *Balanus glandula*

Heather Leslie

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ABSTRACT

While high-density aggregations of conspecifics have long been presumed to have negative effects on individual fitness, this has not been adequately tested on multiple life history traits in the field. Here I report a series of investigations that comprehensively evaluate the influence of conspecific density on key traits (survival, growth, and reproduction) in the intertidal barnacle *Balanus glandula*. Density was manipulated in mid intertidal barnacle populations living on both natural and artificial substrata. Survival was positively related to density: populations at the lowest density level were 19 times more likely to experience 95+ % mortality than those at the highest level. In contrast, growth and individual reproductive output were negatively related to density: Animals at lower experimental densities (16-50 adult barnacles per 100 cm^2) grew to 1.5x the size of individuals living at higher densities (330 adults per 100 cm^2), and larger barnacles produced larger brood masses than smaller individuals. Surprisingly, density did not influence the frequency of brooding barnacles in experimental or natural populations. Estimation of the basic reproductive rate for the experimental animals indicates that the primary effect of increased conspecific density was enhanced survival and consequently, a larger mean number of larvae produced per original recruit. Thus, in this case, the positive intraspecific effects of high-density aggregations outweighed the negative effects. My results demonstrate key life history traits may not respond similarly to changes in density, and provide a strategy for evaluating the relative importance of positive vs. negative interactions. These findings also have important implications for the marine reserve design. Reserve establishment can result in increased abundance of organisms within reserves (particularly of

exploited species). Consequently, it is vital to anticipate and, when possible, to evaluate the full range of positive and negative interactions among conspecifics when designing and implementing reserves and other area-based management strategies.

INTRODUCTION

The role of density-dependent processes in population and community dynamics has long been an important area of investigation (Hixon et al. 2002). Until recently, ecologists have emphasized the roles of negative interactions, e.g. competition, predation, and the effects of abiotic stress, in structuring biological populations and communities (Bruno et al. 2003). Nevertheless, facilitation, such as when one organism ameliorates stressful abiotic or biotic conditions for another, also can play an important role (Connell and Slayter 1977, Menge and Farrell 1989, Bertness and Callaway 1994, Bertness et al. 1999b).

The focus on negative interactions has been particularly pervasive in the presumed negative relationship between conspecific density and individual fitness (Bruno et al. 2003). Increasingly, however, ecologists have documented the roles of positive intraspecific interactions in population and community dynamics, e.g. where conspecifics living at high densities survive, grow, or reproduce better than their more isolated counterparts (Lynch 1978, Bertness and Hacker 1994, Bertness and Leonard 1997, Callaway and Walker 1997, Bertness et al. 1999a, Bruno et al. 2003).

Here I focus on rocky intertidal marine communities. This community type, along with terrestrial and salt marsh plant communities, has served as a particularly rich testing ground for these concepts. In rocky intertidal ecosystems, considerable knowledge of population and community dynamics exists and organisms can be manipulated in field experiments with relative ease. Space is one of the primary limiting resources in these systems, particularly for sessile species (Connell 1961, Lubchenco and Menge 1978, Paine and Levin 1981).

For barnacles, for example, intraspecific competition for space can result in reduced growth rates and even death (Barnes and Powell 1950, Connell 1961, Dayton 1971, Menge 1976, Bertness 1989). Yet possible positive effects of high-density barnacle aggregations include increased settlement and recruitment (Knight-Jones 1953, Wethey 1984, Raimondi 1988, Bertness et al. 1999b), increased survival (Bertness 1989), improved feeding efficiency (Bertness et al. 1998), and greater reproductive output (Wu 1980, Wethey 1984). To date, individual investigations of the effects of conspecific density on barnacles have focused primarily on a single response, particularly recruitment. Earlier life history phases (e.g. larval production, planktonic larval stages) have been less studied, in part because of the logistical difficulties in tracking organisms with complex life histories.

Here I report on a series of studies that develop a more comprehensive approach. I evaluated the influence of conspecific density on multiple life history traits in the intertidal barnacle *Balanus glandula* by measuring responses across multiple life stages, from recruitment through larval production. Density was manipulated in barnacle populations living on both natural and artificial substrata, and tracked in natural populations.

METHODS

Study sites

The studies were conducted in the mid intertidal zone at Bob Creek (BC) and Fogarty Creek (FC), two exposed rocky intertidal sites in Oregon, USA (FC: 44.84 °N, 124.06 °W; BC: 44.24 °N, 124.11 °W). The acorn barnacle *Balanus glandula* occupies both primary and secondary space in this zone, which spans +1.5 to 2 m above mean lower low water (MLLW) at these sites (H. Leslie, *unpublished data*).

Air and water temperatures at each site were recorded with Onset StowAway TidbiT© loggers deployed at + 2 m (MLLW). The TidbiTs© logged temperature every 30 minutes, and the program SiteParser (Strickland et al. submitted) was used to extract daily high air temperatures from the temperature records.

Settlement plate experiment

Barnacles of a known age were maintained at standardized densities on plastic settlement plates, after Sanford and Menge (2001). The plates were made of an opaque gray 6.35 mm (¼") thick PVC, which was cut into 100 cm^2 squares and attached to the substrata with 6.35 cm (2½") stainless steel lag screws. Each plate had one of four arrays of shallow pits (1 mm in diameter, 0.3 mm deep) spaced at regular intervals (see Table A1 in Appendix A for specifications).

In late June 2002, I deployed 160 plates at Strawberry Hill, <1 km north of BC. To facilitate concurrent settlement, the plates were distributed within a 16-m^2 area in the low intertidal zone (+ 1 m MLLW). In early July 2002, settlement was observed. In mid August 2002, once the juvenile barnacles were ~2mm in basal diameter, the plates were sorted in the laboratory to cull out plates with low numbers of recruits. The remaining 100 plates were sorted randomly into 25 blocks of four plates (one of each density level), and out-planted to the BC mid intertidal zone (+ 2 m MLLW) over a 50 m stretch of exposed shoreline. Plates were photographed monthly, weather permitting, to track survival and growth of the original recruits. I removed new recruits monthly as needed to maintain the density levels. Whelks (primarily *Nucella emarginata*) were removed from the 400 cm^2 around each plate to minimize predation effects, although the snails were rarely observed in the vicinity of the experiment.

In April 2003, when the original *B. glandula* recruits were nine months old, the plates were collected and photographed in the laboratory. Based on photographs, original recruits were identified. Density per 100 cm^2 (i.e. per plate) was quantified in the laboratory. The density of potentially reproductively mature animals at the experiment's end included both survivors – those barnacles from the original cohort – and younger animals with basal diameters of 4+ mm who recruited subsequently. These younger individuals were large enough to potentially compete and mate with the original survivors (H. Leslie, *personal observation*).

The original recruits were dissected to quantify growth, morphology and reproductive condition, after storage at -20° C for several months. I measured the dimensions (height, basal diameter, and opercular diameter) of each barnacle. Basal diameter, rather than shell volume, was used as a measure of barnacle size as a barnacle growing under crowded conditions often does not occupy its entire carapace (H. Leslie, *personal observation*). As all barnacles were of similar age at the beginning of the experiment, basal diameter also provided a measure of growth.

Changes in morphology were quantified as the ratio of barnacle height to basal diameter, as less crowded animals have truncated cone-shaped shells and low ratios and more crowded individuals have more columnar forms and higher ratios (see Fig. A1 in Appendix A). I noted whether each animal had a brood (conspicuous yellow or dark brown egg lamellae), unfertilized ovarian material (viscous yolky yellow material), or no evident female reproductive tissue within the mantle cavity (Barnes and Barnes 1956, Walker 1992). A brood and unfertilized ovarian material co-occurred within the same animal in some instances; in these cases, individuals were scored as 'brooding.'

I then dissected each individual, separating the shell, body, and female gonadal (brood and ovarian) tissues. Dry weights of each material per individual (shell, body, and female gonad) were quantified, after drying them at 50-55 °C for 48+ hours (weights stabilized after 48 hours: H. Leslie, *unpublished data*). The number of larvae per brooding barnacle was estimated using the equation: $\ln(\#\text{larvae}) = 4.59 + 0.304(\text{basal diameter}) + 0.505(\text{ht: basal diameter})$. This relationship is based on information presented elsewhere (Chap. 3: *Results*).

Natural substrata experiment

Before deploying the plate experiment, I conducted a similar manipulation on natural rock surfaces. In May 2001, I cleared three sets (i.e. blocks) of 400-cm^2 plots in the mid intertidal zone (+ 2 m MLLW) at BC and FC. The sites were chosen to bracket a known gradient in nearshore primary productivity, as the area adjacent to BC has consistently higher phytoplankton concentrations (measured as Chlorophyll-*a*, a proxy for primary production) relative to FC (Menge et al. 1997a, Menge et al. 1997b).

Following *B. glandula* recruitment in early July 2001, one plot of each block was randomly selected as the 'thinned' treatment while the other was classified as 'natural.' For the next seven months, I maintained the 'thinned' treatment by manually removing barnacles in order to create plot densities considerably less than those in the 'natural' plots (Fig. A2). Plots were photographed monthly, weather permitting, to track barnacle densities, survival and growth. Individuals as small as 2 mm in basal diameter may brood larvae (H. Leslie, *personal observation*), so density per 100 cm^2 was estimated based on counts of all *B. glandula* 2+ mm in basal diameter in replicate sub-samples of the plots.

In February 2002, I collected a haphazard sub-sample of the seven month-old original recruits from each plot to quantify growth, morphology, biomass allocation and brooding frequency. *B. glandula* reproduces throughout the year in Oregon's mid intertidal zone (see Chap. 3), so the results of the two experiments are comparable. Animals were frozen on dry ice in the field, and stored at -20° C until laboratory processing. I then dissected them to quantify growth, morphology and reproductive condition, as described above.

Field surveys of B. glandula *populations*

To evaluate the relevance of the density manipulations to natural populations, I collected individuals from natural *B. glandula* mid intertidal populations at BC and FC in April 2003. I ran a 50 m transect through the center of the zone, and collected all barnacles within 12 randomly selected 100-cm^2 quadrats. Animals were frozen in the field on dry ice, and stored at -20° C until laboratory processing. Barnacles with 2+ mm basal diameters were counted to estimate density per 100 cm^2. Up to 50 animals per quadrat were measured and scored for reproductive condition, as described previously.

Statistical analyses

Analysis of variance models (ANOVAs) were constructed to evaluate the effects of density, site, and block on several response variables. Block was considered a random factor and variance components were estimated using the restricted maximum likelihood estimation (REML) method. REML is considered more reliable than the traditional Expected Mean Squares approach (Quinn and Keough 2002). Linear regression was used to examine relationships between continuous variables. Treatment groups were compared via Tukey-Kramer HSD tests based on least square means estimated from the relevant main effect or interaction term ($p<0.05$).

In the plate experiment, there were many cases of 100% mortality. Consequently, I analyzed the per capita mortality data as a contingency table; comparing those plates that experienced 95+ % mortality vs. those with lower mortality rates [after Ramsey and Schafer (1997) and Quinn and Keough (2002)]. Also, I eliminated those plates with <3 survivors for the growth and reproduction analyses. This resulted in three remaining blocks, with three replicate plates for each of the three higher density levels. All but two individuals died at the lowest density level, precluding growth and reproduction analyses.

Given the small sample sizes available to test most hypotheses, I report marginal effects ($p<0.1$). Upon inspection of residuals, the data were transformed ($\ln(y)$ for datasets with values >1 and $\ln(1+y)$ for datasets with values <1) to meet ANOVA assumptions. If transformations did not improve the spread of the data, untransformed values were used. ANOVA is generally robust to violations of most assumptions (Underwood 1997, Quinn and Keough 2002).

All analyses were conducted with JMP IN 4.0 (SAS 2001). Statistical tables are presented in Appendix A, as are supplementary figures.

RESULTS

Settlement plate experiment

The mean number of recruits per 100 cm^2 differed significantly among the four density levels in August 2002, as did the number of adult barnacles at the end of the experiment (Table 2.1, A2, *a-b*). As expected from the random allocation of plates to each block, the block effect on recruit density was insignificant (Table A2, *a*).

The number of survivors was strongly affected by density (Fig. 2.1C; Table 2.1, A2, *c*). Animals living at the lowest density level were 19 times more likely to experience 95+ % mortality than those living at the highest density level (χ^2 test: $\chi^2 = 26.745$, $p < 0.0001$; Table A3).

Animals living at the second lowest density (81 pits per plate) grew to 1.5x the size of barnacles living at the highest density (1360 pits per plate) [Fig. 2.2A; Table A2, *d*: $F=191.788$, $P<0.001$, $df=2, 4$]. As conspecific density increased, shell morphology changed as well (Fig. 2.2B; Table A2, *e*: $F=5.840$, $P=0.039$, $df=2, 6$).

Table 2.1. Barnacle densities in the three studies. Maximum densities were greater in the higher levels of the experiments than in the natural populations, but encompassed a comparable range. Means ± SE per 100 cm^2 are shown. A: Plate experiment densities of recruits in Aug. 2002, and reproductively mature adults and survivors, Apr. 2003 (n=24-25 plates per density level). B: Natural rock surface experiment densities, Feb. 2002 (n=3 plots per treatment). C: Natural population densities, Apr. 2003 (n=12 quadrats per site).

Density	Recruits	Adults[a]	Survivors
A. Plate experiment			
16 pits/100 cm^2	8 ± 1	3 ± 1	0 ± 0
81 pits/100 cm^2	49 ± 4	16 ± 4	2 ± 2
340 pits/100 cm^2	169 ± 14	129 ± 24	18 ± 7
1360 pits/100 cm^2	770 ± 84	329 ± 32	99 ± 20
B. Natural substrata experiment			
BC Thinned		50 ± 7	
FC Thinned		53 ± 6	
BC Natural		203 ± 94	
FC Natural		461 ± 44	
C. Natural population surveys			
BC		113 ± 36	
FC		65 ± 28	

[a] *In Study A, the count of adults included all barnacles 4+ mm in basal diameter. In Studies B and C, the count included all barnacles 2+ mm in basal diameter.*

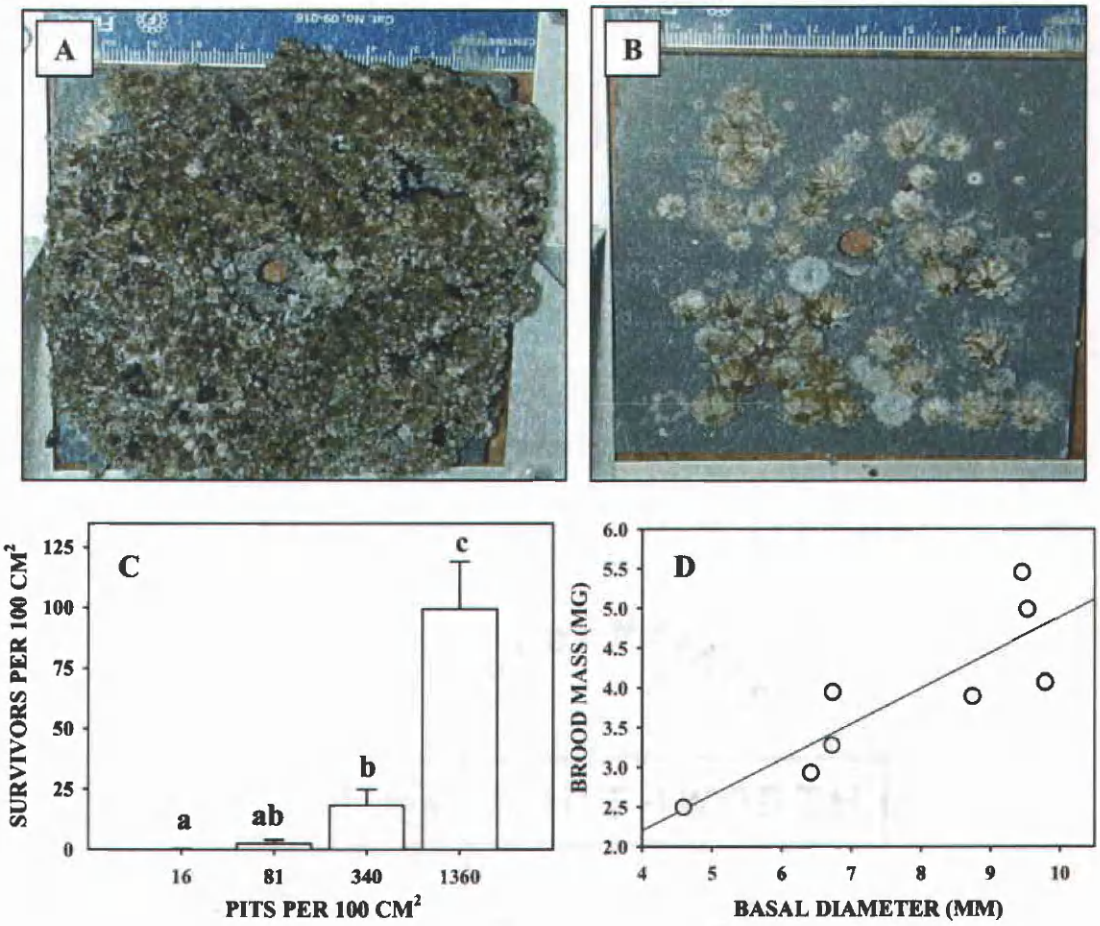


Fig. 2.1. Variation in conspecific density influenced barnacle morphology, survival, and larval production per individual. Representative plates with (A) 1360 pits vs. (B) 81 pits per 100 cm^2 demonstrate how altering density changed individual morphology and size. (C) The number of survivors per 100 cm^2 increased with density in the plate experiment. Means with dissimilar letters are different (Tukey-Kramer test on ln-transformed values, $p<0.05$). Means + SE are shown (n=24-25 plates per level). For the lowest level, the values (0.118 + 0.081) were too small to be visible. (D) Barnacle brood mass was positively related to barnacle size in the plate experiment (linear regression on ln-transformed values: $R^2=0.78$, $F=21.827$, $p=0.003$, df=1, 6). The regression equation was $\ln(y)= -0.426 + 0.868(\ln(x))$. Untransformed plate-level means are shown (n=8 with 3-8 barnacles sampled per plate).

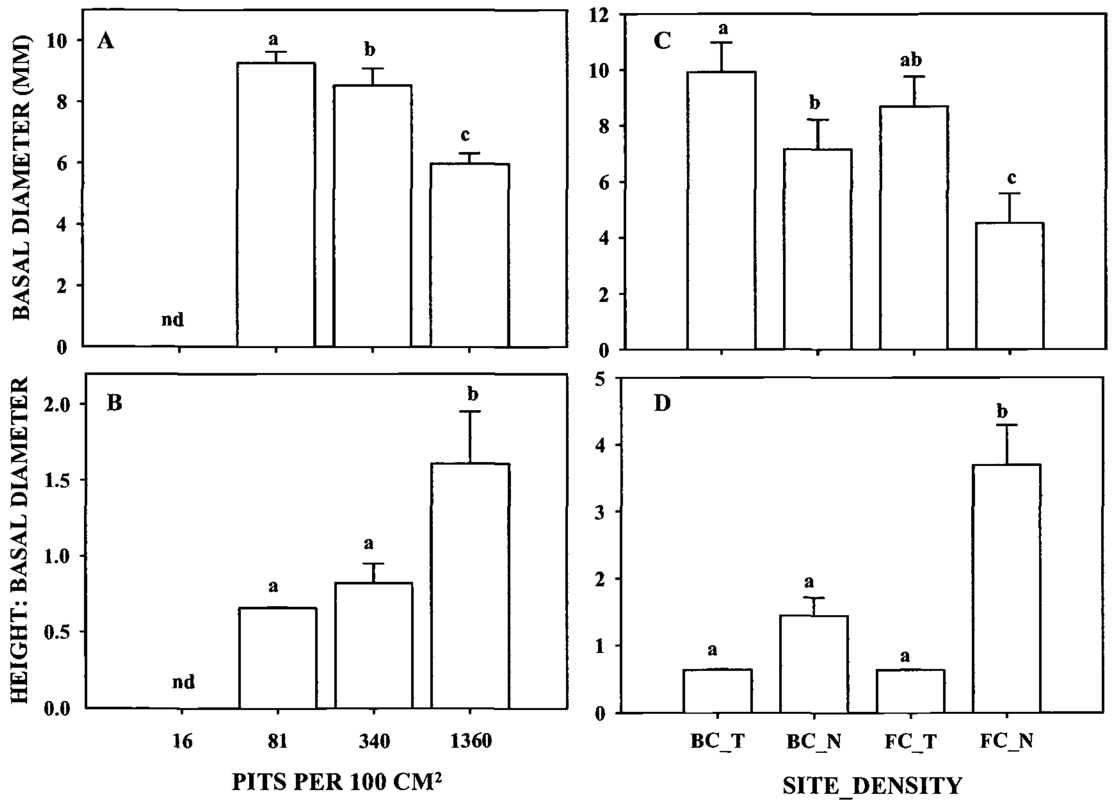


Fig. 2.2. Influence of density on barnacle growth and morphology in the two experiments. Barnacles living at lower densities grew to a larger size in the plate experiment (A) and the natural rock experiment (C). Barnacle morphology also changed with density, as more crowded animals had higher ratios of height to basal diameter in the plate experiment (B) and the natural rock experiment (D). 'T' and 'N' refer to the thinned and natural treatments of the natural rock experiment. Means with dissimilar letters are different (Tukey-Kramer tests, $p<0.05$). Means + SE are shown ($n=3$ plates, with 9-10 barnacles sub-sampled per plate and $n=3$ plots per site with 28-42 barnacles sub-sampled per plot). nd = no data.

Surprisingly, individual allocation to shell and somatic and reproductive tissues was not affected by conspecific density (Table A4). Consequently, I report the overall mean dry weights, averaged across density levels (Table 2.2).

Size-specific reproduction increased with basal diameter. As the median basal diameter per plate doubled from 5 mm to 10 mm, there was a 1.83 mg (95% Confidence Interval: 1.33-2.50) increase in median brood mass dry weight (Fig. 2.1D). In other words, larger barnacles (living at lower densities) had larger brood masses. The estimated number of larvae brooded per barnacle was strongly related to brood mass size (Fig. 2.3A), but not to adult density (Table A5, *a*). No barnacles were brooding at lowest conspecific density, where mortality was so high (Table A5, *b*). At the three higher densities, there was no relationship between brooding rates and conspecific density. Overall, brooding frequencies averaged 51 ± 14% (mean ± SE) among the three higher density levels (Table A5, *c*).

Natural substrata experiment

At the termination of the density manipulation on natural rock surfaces, barnacle populations in natural (unthinned) plots were 4x to 9x more abundant than those in the thinned plots (Table 2.1, A6, *a*: F=68.498, *P*=0.0001, df=1, 6). Barnacle densities were 2x higher in the FC natural than in the BC natural plots, perhaps due to differences in initial recruitment and survival (H. Leslie, *personal observation*).

Barnacles in the thinned treatments grew to 1.5x the size (as measured by mean basal diameter per plot) and exhibited a less crowded morphology (i.e. with lower ratios of height: basal diameter) than those in the natural treatments (Fig. 2.2C,

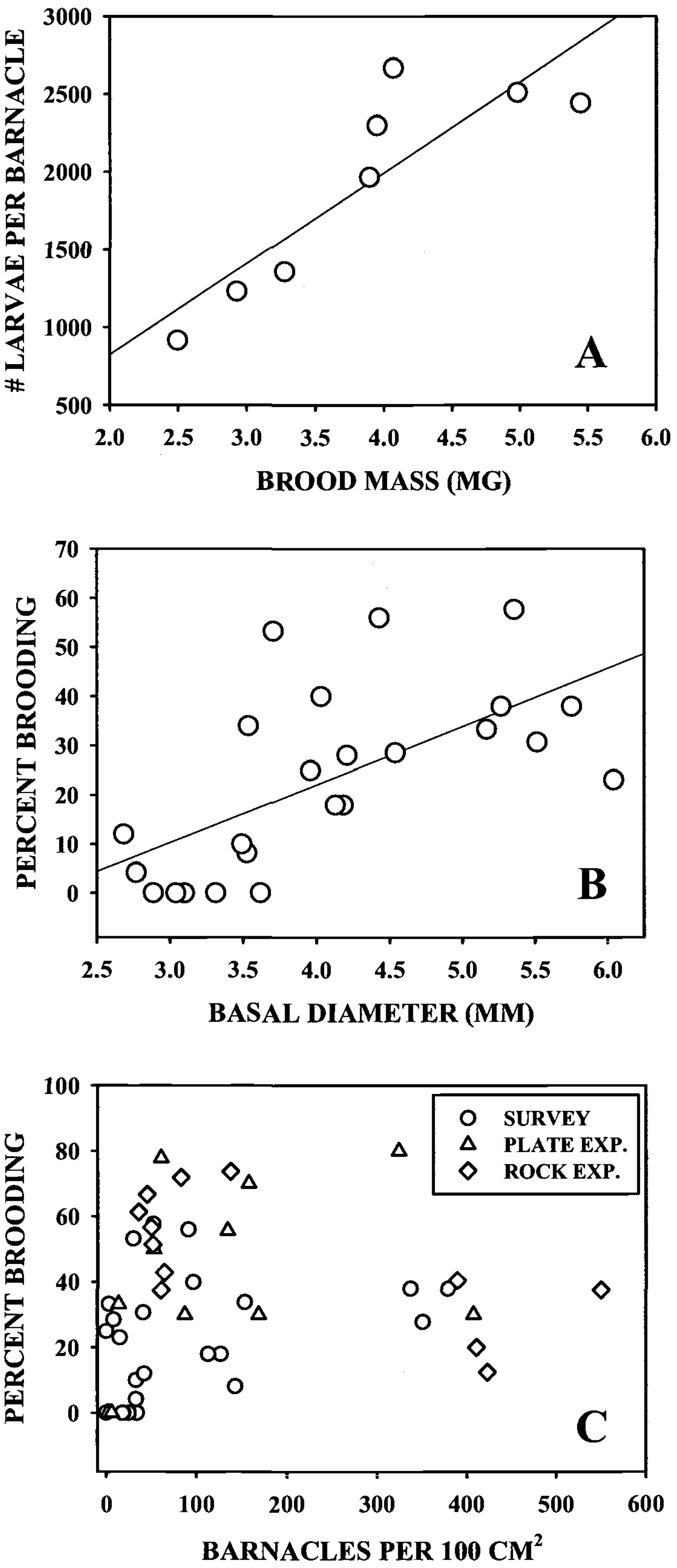
Table 2.2. Estimated biomass allocation per barnacle for the two experiments. Values were averaged across density levels, as there was no effect of density in either study. Means ± SE shown. A: Plate experiment values were averaged across the three higher density levels (n=8-9 replicate plates, with 3-10 barnacles sub-sampled per plate). B: Natural rock experiment values were averaged across the two density levels at each site (n=6 replicate plots per site, with 28-42 barnacles sub-sampled per plot). Percentages were estimated from the sum of somatic, female gonad and shell organic biomass.

Site	Somatic tissue		Female gonad [1]		Shell organics [2]		Brood
	Biomass, mg	*%*	*Biomass, mg*	*%*	*Biomass, mg*	*%*	*Biomass, mg*
A. Plate Experiment							
BC	2.74 ± 0.26	37	3.19 ± 0.38	43	1.56 ± 0.14	21	3.88 ± 0.35
B. Natural rock surface experiment							
FC	1.82 ± 0.22	47	1.23 ± 0.09	32	0.81 ± 0.13	21	1.72 ± 0.28
BC	3.42 ± 0.34	49	2.23 ± 0.29	32	1.35 ± 0.12	19	2.90 ± 0.27

[1] *Includes both brooding and non-brooding individuals*

[2] *Shell organic matter biomass calculation assumed 1% of shell dry weight was organic (after Wethey 1984).*

Fig. 2.3. Reproductive output on the individual and population level in experimental and natural populations. (A) The estimated number of larvae per barnacle was positively associated with brood mass in the plate experiment (linear regression on the ln-transformed values: $R^2 = 0.84$, F=30.729, p=0.002, df=1, 6). The regression equation was $\ln(y) = 5.642 + 1.400(\ln(x))$. Untransformed plate-level means are shown (n=8, with 3-8 barnacles sub-sampled per plate). (B) Brooding frequency (a population level measure) was positively associated with barnacle size in the mid intertidal *B. glandula* natural populations surveyed at FC and BC in April 2003 (linear regression on untransformed values: $R^2 = 0.40$, F=14.381, p=0.001, df =1, 22). The regression equation was $y = -25.13 + 11.80x$. Quadrat-level means are shown (n=24). (C) Brooding frequency was not associated with density, when data from all three studies were pooled. A linear regression was not significant, while a quadratic fit was marginally significant (see text for details). Quadrat, plate and plot-level means are shown (n=44).


LARVAE PER BARNACLE
3000
2500
2000
1500
1000
500
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
BROOD MASS (MG)
A
PERCENT BROODING
70
60
50
40
30
20
10
0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
BASAL DIAMETER (MM)
B
PERCENT BROODING
100
80
60
40
20
0
0
100
200
300
400
500
600
BARNACLES PER 100 CM^2
○ SURVEY
△ PLATE EXP.
◇ ROCK EXP.
C

2.2D; Table A6, *b & c*). Barnacles in the FC natural plots were smaller and more crowded than those in the other treatments. Although there was no effect of density on mean individual biomass allocation per plot, these responses were greater at BC than FC (Table A7). Consequently, I present the estimated individual allocation by site (Table 2.2).

Neither density nor site had any effect on the estimated number of larvae produced per barnacle (results not shown). There was no relationship between brood mass and barnacle size (i.e. basal diameter) in this experiment, perhaps because barnacle densities and thus morphology were less controlled than in the plate experiment.

Brooding frequency did not vary consistently with site or density (Table A6, *d*: F=24.270, *P*=0.003, df=1, 6). The mean brooding frequency in the FC natural plots was 23 ± 7 %, whereas in the other three treatments, it was 56 ± 3% (mean ± SE). In the FC natural plots, *B. glandula* lived at much higher densities, developed a more crowded morphology, and brooded at lower frequencies than animals in the other treatments. Notably, the FC natural plot densities exceeded those in the highest level of the plate study (Table 2.1).

Field surveys of B. glandula populations

Surveys of mid intertidal natural populations of *B. glandula* at BC and FC indicated that densities at BC were marginally higher than those at FC (Table 2.1; one-way ANOVA on ln-transformed data: F=3.526, *P*=0.07, df=1, 22). As density increased in the natural populations, shell morphology changed as in the experiments, with higher mean ratios (of barnacle height to basal diameter) at higher densities (Fig. A3). There was no relationship between mean barnacle size and density, which makes sense given that the sampled animals were a mix of multiple size and age classes.

Brooding frequency was not influenced by density or site. The overall mean brooding frequency was 23 ± 4 %, and individual rates ranged from 0 to 58% (mean ± SE; results not shown). There was a strong association between brooding frequency and mean barnacle size, however (Fig. 2.3B). In quadrats where mean barnacle size was >4 mm in basal diameter, the frequency of brooding barnacles increased markedly, suggesting that this was a reasonable lower limit for quantifying reproductively mature barnacles.

DISCUSSION

Influence of density on multiple life history traits of B. glandula

In sum, conspecific density had strong effects on multiple life history traits of *B. glandula*. First, increased conspecific density resulted in increased survival; suggesting that at higher densities, facilitation played a stronger role than intraspecific competition in this case. This is intriguing given that the emphasis regarding intraspecific interactions in gregarious species has largely been on the negative effects.

Positive intraspecific interactions have been observed primarily under conditions deemed to be at the higher end of a given environmental stress gradient (e.g. Bertness 1989, Bertness et al. 1999b). In Bertness' (1989) barnacle study, for example, high intertidal temperatures on large rocks (most comparable to the broad intertidal benches at BC) reached 38°C during daytime low tides. During the first two months of my plate experiment (Aug.-Oct. 2002), when most of the mortality occurred, the daily high air temperature at BC ranged between 16.8 and 18.5 °C (95% Confidence Interval), although isolated daily highs of 30.6°C (Aug. 13) and 25.3°C (Sept. 15) were recorded. These data suggest that the abiotic conditions during the plate experiment in Oregon were not as severe as those observed in New England. Yet positive interactions were observed in both cases, suggesting that facilitation may occur over broader environmental gradients than previously thought.

Density also negatively influenced barnacle growth rates and morphology in both the plate experiment and natural substrata experiment. Barnacles at lower experimental densities grew to a mean size (as measured by basal diameter) 1.5x greater than those animals at higher experimental densities. At higher densities, barnacle morphology changed considerably, as well: from a volcano shape to a more elongated, cylindrical shape. This relationship between density and morphology also was observed in the surveys of natural populations. Previous investigators have documented similar changes in barnacle shell morphology (Knight-Jones 1953, Bertness 1989, Lopez and Gonzalez 2003).

The magnitude of reproduction per individual was strongly related to barnacle size. Larger barnacles (living at lower densities) produced larger brood masses. Based on information presented elsewhere (Chap. 3), I estimated that these heavier broods were composed of a greater number of larvae than lighter broods. Wethey (1984) observed that in natural populations of *B. glandula,* barnacles living at low densities had larger brood masses than those at higher densities. In experiments with *Semibalanus balanoides*, Hills and Thomason (2003) found that increased densities led to decreased larval production per individual. In an observational study with *Jehlius cirratus*, a chthamaloid barnacle in Chile, Lopez and Gonzalez (2003) also concluded that solitary animals produced more larvae per individual. Given these results, with larger sample sizes, I predict that density would alter individual biomass allocation. That is, I would expect that brood mass and ovarian tissue mass per individual would be greater in animals living at lower densities than in animals living at higher densities (provided that the animals were within fertilization distance of one another).

Brooding frequencies observed in the three studies varied widely, from zero to 80%. The individual studies indicated little relationship between brooding rates and conspecific density. But inspection of all the data suggests a marginal unimodal relationship between conspecific density and brooding (Fig 2.3C; quadratic fit of density: $R^2=0.16$, $F=4.020$, $P=0.025$). Barnacles living at very low densities (as in the lowest level of the plate experiment) and at very high densities (as in the FC natural plots) had low brooding frequencies. At moderate densities (<100 to 400 barnacles per 100 cm^2), per capita brooding rates were variable but often >30%. Given the weak relationship, it would be useful to sample more populations at the higher end of the density range, to investigate whether the unimodal function is supported.

These findings illustrate the importance of considering multiple life history traits when assessing the influence of intraspecific interactions (both negative and positive) on individual fitness, as well as on population and community dynamics. To evaluate the relative importance of the observed positive and negative effects of conspecific density on fitness of *B. glandula*, I adapted a standard life table approach to fit the available data.

Both individual fitness and persistence of populations are linked to the basic reproductive rate, R_0. The basic reproductive rate can be calculated as the sum of the mean number of larvae produced per original recruit during each life stage (i.e. $R_0 = \Sigma l_x m_x$). While age or size-specific reproductive output data are not available in this case (precluding calculation of a full life table), the plate experiment data on survival and the estimated number of larvae produced per individual barnacle can be used to estimate the mean number of larvae produced per original recruit ($l_x m_x$) for one stage, the 'reproductively mature adult stage' (Table 2.3). $l_x m_x$ provides a means of assessing the net effect of conspecific density on the survival, growth, and reproduction in *B. glandula* in the context of plate experiment. The mean number of larvae produced per original recruit increased with increasing conspecific density, suggesting that the positive effects of increased density outweighed the negative intraspecific effects in this case (Table 2.3, last column).

In these studies, I assumed that the influence of genetic variation was negligible, because the two experiments were based on cohorts of animals that recruited in close spatial and temporal proximity. Modeling could be a productive means of exploring the potential influence of genetic variation on individual and population-level responses to changes in density. For example, an individual-based model where barnacles grow, reproduce and die could be populated with a number of genotypes (with phenotypically distinct responses to conspecific density and other potential selective forces, such as variation in food availability). By varying the initial

Table 2.3. Comparison of the reproductive rates of barnacles living at different conspecific densities in the plate experiment. Reproductive rate ($l_x m_x$) is equivalent to the number of larvae produced per original recruit. Means are shown (n=25 for l_x and n=3 for m_x).

Density (Pits per 100 cm^2)	Proportion of original recruits surviving to the adult stage (l_x)	Larvae produced per surviving individual in the adult stage (m_x)	Larvae produced per original recruit in the adult stage ($l_x m_x$)
16	0.020	0	0.000
18	0.038	2538	96.090
340	0.079	1922	151.541
1360	0.149	1480	221.018

conditions (e.g. recruitment density, food availability), potential genotype-environment interactions could be explored.

Implications for population dynamics and marine management and conservation

These results also have implications for the design and management of marine reserves and other area-based management strategies. When areas are protected from fishing and other extractive activities, in many cases, populations (particularly of exploited species) increase in abundance (Halpern 2003). Nonetheless, there are relatively few investigations of how increased population densities alter ecological interactions and the subsequent effects on life history traits of species of interest. The considerable literature on density-dependent effects on survival, recruitment, and reproduction is certainly relevant to these questions, but reserve-based investigations are also crucial.

My results suggest caution in interpreting how increased population densities will impact the population dynamics of particular species, given that key life history traits may respond differentially to changes in density. Consequently, it is vital to anticipate and, when possible, to evaluate the full range of positive and negative interactions among conspecifics when designing and implementing reserves or other area-based management strategies.

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Chapter 3:

Bottom-up Control of Barnacle Growth and Reproduction in a Coastal Upwelling System

Heather Leslie, Erin Breck, Bruce Menge, and Jane Lubchenco

Journal to be determined

ABSTRACT

Ecologists now recognize that top-down (i.e. consumer driven) and bottom-up (i.e. variation in nutrients, productivity) forces act in concert to regulate ecological systems. While a number of empirical examples of bottom-up effects on marine populations and communities exist, the influence on reproduction in higher trophic levels has not been well investigated. Here we report how bottom-up factors, specifically alongshore variation in nearshore primary productivity in Oregon (USA), influenced reproduction, as well as survival and growth, in populations of the intertidal barnacle *Balanus glandula.* We found strong evidence for bottom-up forcing of barnacle growth and reproduction. Mean cumulative larval production per 100 cm^2 in natural populations in the region of higher primary productivity was 5x that in the less productive region. Barnacles living in experimental mid-intertidal populations in the more productive region grew to almost 2x the mean size and had heavier shells than barnacles living in the less productive region. Mean estimated larval production per individual in experimental populations in the more productive region was >2x that at the sites in the less productive region. Mean larval production per 100 cm^2 in the experimental populations in the more productive region was 28x greater than in the populations in the less productive region. One site within the higher productivity region produced substantially more larvae than the others, however, demonstrating that larval production "hotspots" exist in rocky intertidal ecosystems and that not all sites are ecologically equivalent. We also found that mid intertidal populations produced larvae through most of the year, whereas high intertidal animals brooded almost exclusively in the late winter-early spring. Thus,

mid zone animals likely contribute substantially to summer and fall larval production, which coincides with major recruitment pulses in this region. Our findings advance understanding of the role of bottom-up influences on population and community dynamics, and contribute data for the next generation of conceptual and quantitative models of marine community dynamics. They also demonstrate the importance of taking a network approach when designing marine reserves and other area-based marine management strategies, given among-site variability in marine population and ecosystem dynamics, such as we found. Particularly in coastal marine ecosystems, where the linkages between the benthic and pelagic environments are predicted to change with climatic change, embedding marine conservation and management strategies within a network context is essential.

INTRODUCTION

Elucidating how marine ecosystems work in order to inform effective management and conservation is an urgent task, given the increasingly severe and large-scale anthropogenic perturbations to coastal marine ecosystems (National Research Council 2001, Heinz Center 2002, Pew Oceans Commission 2003, U.S. Commission on Ocean Policy 2004). Marine ecosystems are influenced by biogeophysical processes on multiple spatial scales, ranging from organismal responses to environmental stress and species interactions (μm-m) to hydrographic influences on local (100s of m), regional (10s to 100s of km) and basin-wide scales (1000s of km). Understanding the degree of coupling among these different scales presents a tremendous challenge (Levin 1992, Menge et al. 2003).

After decades of focusing on top-down (i.e. consumer-driven) effects on population and community dynamics, ecologists have recognized that top-down and bottom-up (i.e. variation in nutrients, productivity) forces act in concert to regulate ecological systems (Hunter and Price 1992, Menge 1992, Power 1992, Menge et al. 2003). Nonetheless, empirical examples of bottom-up effects on marine populations and communities are relatively rare, in part because of the difficulty of manipulating potential factors on the appropriate spatial and temporal scales (Bertness et al. 1991, Menge 1992).

Comparative-experimental investigations across a series of local sites nested within areas varying in the factors of interest (Lubchenco and Real 1991) have been a main tool for insights into the relative importance of top-down and bottom-up factors in coastal marine ecosystems (Menge 2000). Food availability in particular can have strong bottom-up influences on primary consumer populations, leading to increased recruitment, growth, biomass accumulation, and reproduction (Duggins et al. 1989, Bertness et al. 1991, Bustamante et al. 1995, Sanford and Menge 2001, Bracken et al. in prep). These effects also can have significant community-level consequences (Branch et al. 1987, Menge 1992, Menge et al. 1994, Menge et al. 1997a, Menge et al. 1997b, Leonard et al. 1998, Menge et al. 1999, Menge et al. 2003, Freidenburg and Menge in prep).

The influence of local or regional scale variation in primary productivity (i.e. food for filter feeders) on reproduction has been less studied than other factors (Morgan 2001), in part due to the relatively open nature of marine populations. While considerable progress has been made in understanding the influence of recruitment of new individuals on marine population and community dynamics in the last two decades (Underwood and Denley 1984, Gaines and Roughgarden 1985, 1987, Roughgarden et al. 1988, Grosberg and Levitan 1992), the life history events that precede recruitment are still fairly opaque (Morgan 2001). Yet knowledge of reproduction and processes that contribute to it – individual allocation, fertilization success, larval production, survival, and dispersal – are critical in understanding how populations persist.

B. glandula and other intertidal barnacles have served as valuable models to investigate many of these issues because of their abundance, role as a major prey and early successional species, and similarity to other marine species of interest. Considerable information is available about the reproductive ecology of this species, as well, making it a useful model for exploring the influence of bottom-up effects on reproduction in higher trophic levels.

B. glandula, like many acorn barnacles, is a hermaphrodite, although it cannot self-fertilize (Walker 1992). Larvae are brooded within the adult for two to four weeks (Hines 1978), before being released into the water column. The larval period of *B. glandula* is estimated to last two to four weeks (Strathmann et al. 1981), during which the larvae develops through a series of six naupliar stages and a cyprid stage before metamorphosing into the sessile juvenile form.

Barnacle reproduction appears highly seasonal, based on studies from throughout the species' range: On Vancouver Island, brooding was observed in December and January, followed by a major release of larvae in January-March, and up to six secondary broods through the summer (Barnes and Barnes 1956). In

Washington State, *B. glandula* brooding frequency peaked in December-March, with secondary broods through the spring (C. Harley, *personal communication*). Similar patterns have been reported for central and southern California (Barnes and Barnes 1956, Hines 1978).

Here we report on a series of investigations designed to test whether bottom-up factors, specifically alongshore variation in nearshore primary productivity on the scale of 10s of kms, influenced survival, growth, and reproduction in the acorn barnacle *Balanus glandula*. Previous investigations in Oregon (USA) indicated that those rocky intertidal ecosystems adjacent to nearshore areas with higher levels of phytoplankton (measured as chlorophyll *a*, a proxy for primary productivity) had higher invertebrate biomass, faster barnacle growth rates, and higher mussel recruitment than those sites with consistently lower phytoplankton levels (Menge et al. 1994, Menge et al. 1997a, Menge et al. 1997b, Sanford and Menge 2001). These community-level differences were attributed to the wider continental shelf and more complex bottom topography at Cape Perpetua (the higher productivity region) relative to Cape Foulweather (the lower productivity region), 80 kms to the north (Fig. 3.1). The physical differences were hypothesized to facilitate retention of particulate food and recruits in the Cape Perpetua region (Menge et al. 1997a, Menge et al. 1997b). Subsequent work has documented the presence of a persistent eddy in the vicinity of Heceta Bank, offshore of Cape Perpetua. Based on these findings, we predicted that Cape Perpetua barnacle populations would show increased survival, greater growth, and greater reproductive output when compared to those at Cape Foulweather.

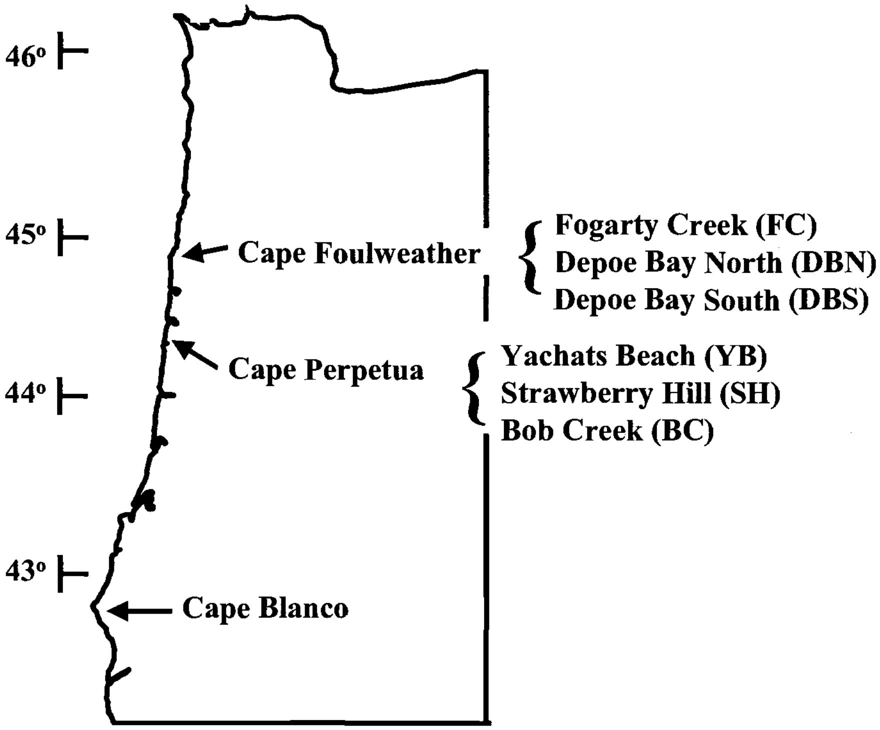


Fig. 3.1. Study site locations nested within Cape Foulweather and Cape Perpetua in Oregon, USA. Cape Blanco is shown for reference. See Table B1 for site coordinates.

METHODS

Study sites

Two to three sites within each cape were utilized for the surveys and experiment reported below. The three Cape Foulweather sites were Fogarty Creek (FC), Depoe Bay North (DBN) and Depoe Bay South (DBS). The Cape Perpetua sites were Yachats Beach (YB), Strawberry Hill (SH), and Bob Creek (BC) (Fig. 3.1).

The acorn barnacle *Balanus glandula* occurs in both the mid and high intertidal zones in this region, from ~ +1.5 m to + 3.5 m above mean lower low water (MLLW) (H. Leslie, *unpublished data*). It occupies both primary space (i.e. bare substrata) and secondary space (e.g. shells of the mussel *Mytilus californianus*) in the mid zone, and primary space in the high zone. Other mid zone sessile species include the mussels *Mytilus californianus* and *M. trossulus,* the barnacles *Chthamalus dalli*, *Semibalanus cariosus*, and *Pollicipes polymerus,* and the red algae *Mastocarpus papillatus*, *Endocladia muricata, and Mazzaella parksii* (Ricketts et al. 1985, Kozloff 1996). Mid-intertidal mobile invertebrates include the seastars *Pisaster ochraceus* and *Leptasterias hexactis*, the whelks *Nucella ostrina* and *N. canaliculata*, the crab *Hemigrapsus nudus*, the nemerteans *Amphiporus imparispinosus* and *Emplectonema gracile*, and the limpets *Lottia pelta*, *L. digitalis*, and *L. strigatella*. In the high zone, the barnacles *B. glandula* and *C. dalli* share space primarily with the algae *Fucus distichus* and *Pelvetiopsis limitata* and snails of the genus *Littorina*. Dipteran fly larvae of the genus *Oedoparena* (a potential predator of barnacles) occur in both the mid and high intertidal zones (H. Leslie, *personal observation*).

Haphazard field surveys of B. glandula populations

To track the reproductive potential of natural barnacle populations, we conducted surveys using two different sampling protocols, termed "haphazard" and "random." Haphazard field surveys were designed to sample reproductively mature *B. glandula* (4+ mm in diameter) that occupied primary space in the mid intertidal zone. Surveys were conducted monthly at two sites in the Cape Foulweather region (FC, DBN) and two sites in the Cape Perpetua region (SH, BC), July 2001 – June 2003. At each site, 25 barnacles were collected from each of five haphazardly selected gaps in the mussel bed. Animals were frozen in the field on dry ice, and stored at -20° C until laboratory processing.

In the laboratory, we measured the dimensions (height, basal diameter, and opercular diameter) of each barnacle and scored its reproductive condition (see protocol, Appendix B1). We noted whether the animal had a brood (a conspicuous yellow or dark brown lamellar mass), unfertilized ovarian material (viscous yolky yellow material), or no evident female reproductive tissue within the mantle cavity (Barnes and Barnes 1956, Walker 1992). A subset of the barnacles also was scored for male reproductive activity, based on the visibility and size of seminal vesicles within the soma (Walker 1992). A brood and unfertilized ovarian material co-occurred within the same animal in some instances; in these cases, individuals were scored as 'brooding.'

This sampling method took less time than the random surveys (below), but its haphazard nature limited inferences about population size structure and among-site variation in reproductive effort. These data provide a multi-year perspective on the timing of reproduction in *B. glandula* in this region, and resemble protocols of other investigators (Hines 1978; P. Raimondi, *personal communication*; C. Harley, *personal communication*).

Random field surveys

To more thoroughly quantify barnacle abundance, size structure, and reproductive effort in natural barnacle populations, we collected *B. glandula* individuals using random surveys at two sites in the Cape Foulweather region (FC, DBN) and two sites in the Cape Perpetua region (SH, BC) during six sampling periods: June 2002, August 2002, November 2002, February 2003, April 2003, and June 2003. Through the center of each zone, we ran a 50 m transect (tidal heights listed in Table B1). All barnacles within 12 randomly selected 100-cm^2 quadrats were collected. For the mid intertidal transect, we noted whether barnacles in each quadrat were occupying primarily primary or secondary space. Animals were frozen in the field on dry ice, and stored at -20° C until laboratory processing.

In the laboratory, barnacles with 2+ mm basal diameters were counted to estimate density per 100 cm^2. The size limit was based on observations of brooding individuals ~2 mm in basal diameters (H. Leslie, *personal observation*). Up to 50 animals per quadrat were measured and scored for reproductive condition, as described above. Basal diameter was used as a measure of barnacle size. Morphology was quantified as the ratio of barnacle height to basal diameter: more crowded barnacles have taller, thinner shells and higher ratios than their less crowded counterparts. The number of embryos per brood was enumerated, along with embryo size, for a subset of the randomly sampled barnacles.

Larval production per barnacle was estimated as a function of barnacle size and shape (for details, see *Results*). Larval production per 100 cm^2 was calculated as the product of the mean number of larvae produced per barnacle in a given quadrat and the estimated number of brooding barnacles per 100 cm^2. The number of brooding barnacles per 100 cm^2 was calculated as the product of the density and per capita brooding frequency for each quadrat. For sampling periods where density was not estimated (June and August 2002), the annual mean density for a given zone and site combination was substituted.

Outplant experiment

To evaluate whether survival, growth and reproductive effort in *B. glandula* differed between Cape Perpetua (YB, SH, BC) and Cape Foulweather (FC, DBN, DBS) populations, we conducted an outplant experiment with barnacles from a common source. Pitted plastic settlement plates were used to generate a common cohort of similar-aged recruits living at a standardized, relatively low density. The plates were made of opaque gray 6.35 mm (¼") thick PVC, which was cut into 100-cm^2 squares and attached to the substrata with 6.35 cm (2½") stainless steel lag screws. The plates had a regular array of shallow pits (1 mm in diameter, 0.3 mm deep) spaced at 1 cm intervals (n=81 pits per plate). Barnacles prefer to settle in these pits (Connell 1985, Blower and Roughgarden 1989, Sanford and Menge 2001), enabling us to control recruit densities.

To facilitate concurrent settlement, 205 plates were distributed within a 16-m^2 area in the SH low intertidal zone (+ 1 m MLLW) in mid August 2002. In late August 2002, settlement was observed. In early October 2002, once the juvenile barnacles were ~2-3 mm in basal diameter, the plates were sorted in the laboratory to cull out plates with low numbers of recruits. The remaining 158 plates were randomized into groups of 26-27 plates, and out-planted to the mid intertidal zone (+ 2 m MLLW) over a 50 m stretch of exposed shoreline at each site.

Plates were photographed monthly to track survival and growth of the original recruits. As new recruits settled on the plates, they were removed as needed to prevent crowding of the original recruits. Predatory whelks (primarily *N. ostrina*) were removed from the immediate vicinity of each plate (~400 cm^2 area) to minimize the effects of predation. In April 2003, when the original *B. glandula* recruits were ~eight months old, the plates were collected, photographed, stored at -20° C for several months, and then processed as described below.

In the laboratory, the original recruits (i.e. survivors) were identified based on the photographs, and then measured and scored for reproductive condition, as described above. Additional data were collected on survival, growth, and individual biomass allocation. Growth rate was approximated by basal diameter, since all barnacles were of similar age. To estimate individual biomass allocation, we dissected each survivor, separating the shell, body, and female gonadal (brood and ovarian) tissues. Dry weights of each material per individual were quantified, after drying at 50-55 °C for 48+ hours (weights stabilized after 48 hours: H. Leslie, *unpublished data*).

Based on the model of larval production developed from the random field survey data, we estimated larval production per original recruit. For the among-site comparison of larval production per individual, only estimates from brooding animals were used. Larval production per 100 cm^2 (i.e. per plate) was calculated as the sum of the estimated larval production per barnacle for all brooding original recruits per plate.

Statistical analyses

Analysis of variance (ANOVA), analysis of covariance (ANCOVA), linear regression, and multiple linear regression (MLR) models were used. Due to missing values, these models were restricted to balanced subsets of the haphazard and random field survey data (after Quinn and Keough 2002). Statistical tables are presented in Appendix B, Tables B2-B7. All analyses were conducted with JMP IN 4.0 (SAS 2001).

When possible, nested ANOVAs with cape and site nested within cape [i.e. site(cape)] were used. Cape was a fixed factor and site was a random factor. When missing data led to biased estimates of the cape effect in nested models (Quinn and Keough 2002), linear contrasts were used instead to test for a cape effect. Tukey-Kramer HSD tests also were used to test for treatment differences ($p<0.05$).

Site was treated as a random factor in all analyses, as the sites were selected as representative of the population of sites within each cape. In analyses with site as a random effect, the numerator mean square was tested over the mean square of the next lower source of variation containing that source. Variance components were estimated using the restricted maximum likelihood estimation (REML) method, unless negative variance components resulted, in which case the traditional Expected Mean Squares (EMS) approach was used. REML is considered more reliable than EMS (Quinn and Keough 2002).

For all analyses, data were transformed as needed to meet ANOVA assumptions, following inspection of residual and normality plots (ln(y) for datasets with values >1, ln(1+ y) for datasets with values <1, square root for counts, and arcsine-square root for proportions). If transformations did not improve the spread of the data, untransformed values were used. ANOVA is generally robust to violations of most assumptions (Underwood 1997, Quinn and Keough 2002).

To evaluate the effects of site and intertidal zone on larval production per barnacle, data collected in April 2003 from three sites (BC, SH, FC) were used. To evaluate the effect of sampling period, data from August 2002, April 2003, and June 2003 from two sites (SH, BC) were used. Other sites were not included due to missing data.

The random field survey data analysis was stratified by intertidal zone, because of the differential timing of reproduction and missing data. Mean barnacle basal diameter per quadrat may be positively correlated with brooding rates (see Chap. 2) and thus was incorporated as a covariate in the model of brooding frequency. For the mid zone model, three sites (FC, SH, BC) and six sampling periods were included in the multiple linear regressions. For the high zone model, four sites (FC, DBN, SH, BC) and five sampling periods were included.

For the outplant experiment, the experimental unit was the pitted plate and barnacles were sub-samples within each plate. To assess the influence of cape and site nested within cape on survival, growth, and reproduction, we used nested ANOVA models. We used nested ANCOVA models, with mean basal diameter per plate as the covariate, to evaluate the factors' effects on biomass allocation per individual. To test the influence of sampling period, cape, and site nested within cape on barnacle recruitment, we also used a nested ANOVA model.

RESULTS

Haphazard field surveys

For the two years in which reproductively mature size classes of barnacles were sampled, brooding in *B. glandula* on the Oregon coast peaked in late winter to early spring (Fig. 3.2, Table B2, *a*: F=7.793, *P*=0.001, df=6, 112). There was a significant interaction between sampling period and site nested within cape, indicating that the rank order of sites nested within Cape Foulweather (FC, DBN) and Cape Perpetua (SH, BC) varied through time (Table B2, *a*: F=14.768, *P*<0.0001, df=12, 112). Male and female reproductive activity tended to be synchronous through time, as indicated by the correlation between the frequencies of reproductively active males and females in the sampled populations (Correlation coefficient = 0.65, p=0.016, n=13).

Random field surveys

Cape Perpetua high intertidal populations were 2.5 to 6.5x more abundant (Fig. 3.3A, Table B2, *b*: F=5.303, P=0.024, df=1, 89) and 1.5x more crowded (Fig. 3.3B, Table B2, *c*: F=20.180, *P*<0.0001, df=1, 80) than other sampled populations, based on

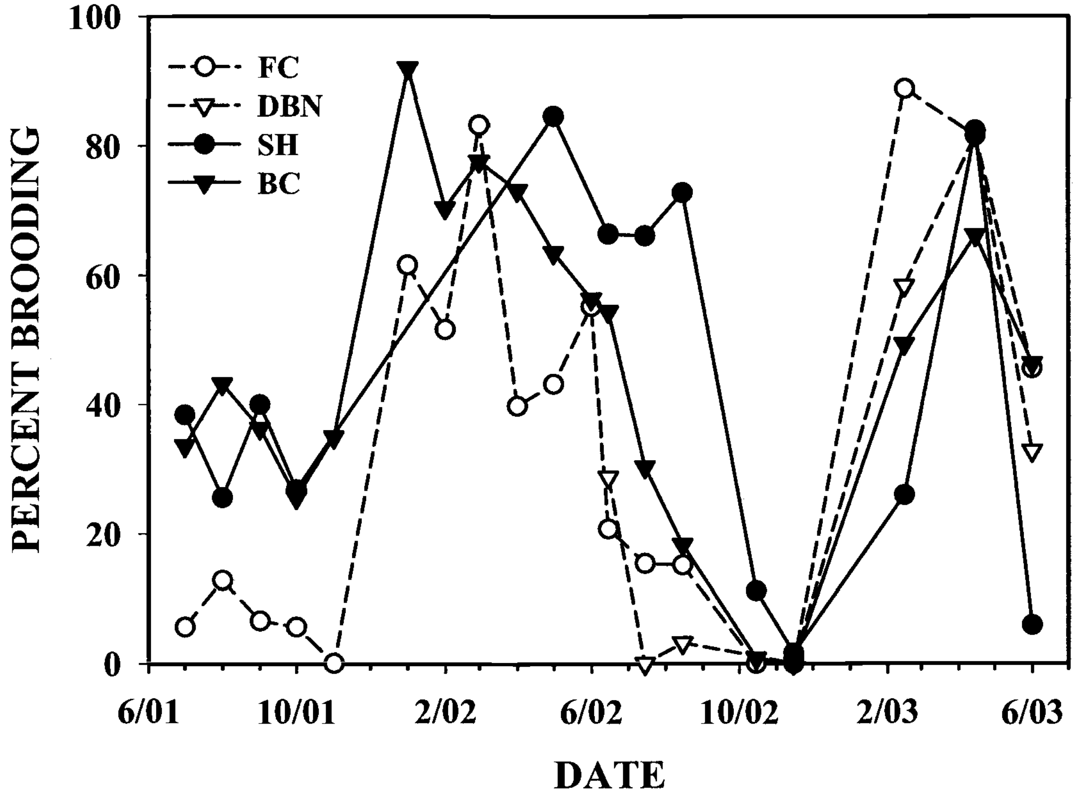
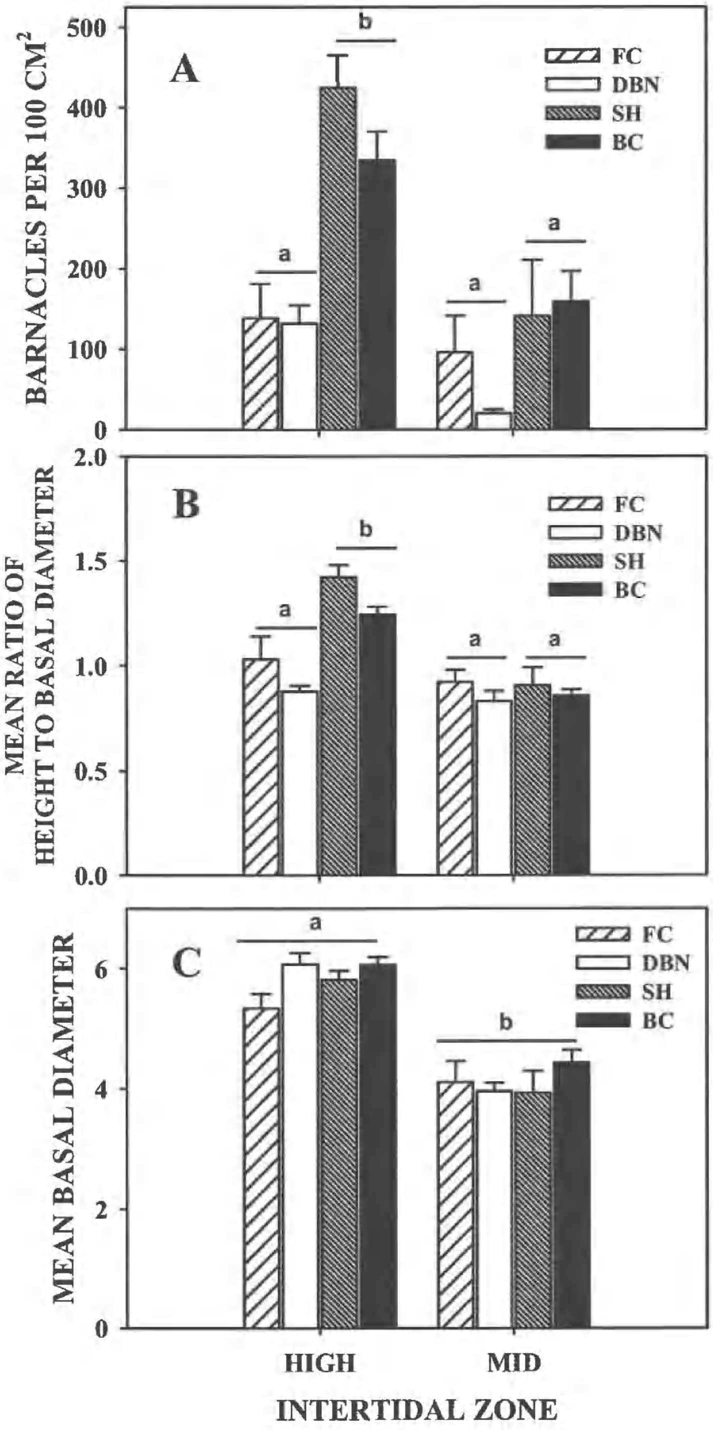


Fig. 3.2. Haphazard field surveys of reproductively mature size classes of the barnacle *B. glandula*. Brooding frequencies were highest in the late winter-early spring in Oregon (USA) (Tukey-Kramer test of LS Means by time, $p<0.05$). There was a significant interaction between sampling period and site nested within cape, indicating that the rank order of sites nested within Cape Foulweather (FC, DBN) and Cape Perpetua (SH, BC) varied through time. Error bars are not shown for clarity, but the common SE was 4.56. Untransformed means are shown (n=5 quadrats, with 25 sub-sampled animals per quadrat.

Fig. 3.3. Barnacle abundance and morphology in natural populations of *B. glandula*. Untransformed means + SE from Nov. 2002 are shown (n=12 quadrats). Means with dissimilar letters were different (Tukey-Kramer test on the LS means calculated from the cape*zone interaction term, $p<0.05$). (A) Cape Perpetua (SH, BC) high intertidal barnacle populations were most abundant among the sampled populations. (B) Cape Perpetua (SH, BC) high intertidal barnacles were more crowded than those in other populations. (C) High intertidal barnacles were larger than those in the mid intertidal zone.


A
BARNACLES PER 100 CM²
500
400
300
200
100
0
b
a
a
a
FC
DBN
SH
BC
B
MEAN RATIO OF
HEIGHT TO BASAL DIAMETER
2.0
1.5
1.0
0.5
0.0
b
a
a
a
FC
DBN
SH
BC
C
MEAN BASAL DIAMETER
6
4
2
0
a
b
FC
DBN
SH
BC
HIGH
MID
INTERTIDAL ZONE

surveys conducted in November 2002. Barnacles living in the high intertidal zone were 1.4x larger than those in the mid intertidal, but there was no effect of site or cape on barnacle size (Fig. 3.3C, Table B2, *d:* F=111.223, *P*<0.0001, df=1, 80).

Both the mean size of brooding barnacles and mean larval production per barnacle in April 2003 were greater in the high zone than the mid zone (Table 3.1). Site and zone had strong, context-dependent effects on larval production per barnacle (Table B3, *a*: F=6.311, *P*=0.002, df=2, 130), as did barnacle size (Table B3, *a*: F=56.376, *P*<0.0001, df=1, 130) and shape (Table B3, *a*: F=15.546, *P*=0.0001, df=1, 130). There was no effect of cape on larval production per barnacle (Table B3, *b*: F=1.374, *P*=0.243, df=1, 130). Separate regressions of larval production per barnacle and barnacle size (i.e. basal diameter) for each site and zone combination sampled in April 2003 are presented in Figure B1 (see Table B4 for statistics).

Larval production per barnacle also varied through time: barnacles sampled in the summer produced 57% more larvae per individual than those sampled in the spring (1492 vs. 951 larvae per barnacle) [Table B3, *c*: F=7.434, *P*=0.0009, df=2, 119]. The mean size of larvae produced per barnacle did not vary markedly with sampling period, site, or zone (Multiple linear regression results not shown: all *P*>0.05): on average, embryos produced by barnacles at these sites were 0.78 ± 0.005 mm in length (mean ± SE, n=238).

Although there was a significant interaction between site and zone in the model of larval production per barnacle (Table B3, *a*), the predicted number of larvae generated by the full model and a reduced model that included only barnacle size and

Table 3.1. Individual morphology and larval production in natural populations of the barnacle *B. glandula* in Oregon (USA), April 2003. Data are based on brooding individuals only. Arithmetic means (and SEs) are shown, except for the last column.

	n	Size[1]		Shape[1]		Larval production per barnacle			
		Mean	(SE)	Mean	(SE)	Mean	(SE)	LS Median[2]	(SE)
Mid zone:									
FC	24	4.924	(0.244)	0.986	(0.077)	694.852	(91.631)	1074.070	(1.169)
DBN	0	?[3]	?	?	?	?	?	?	?
SH	23	6.915	(0.389)	0.892	(0.049)	1824.683	(400.955)	1200.959	(1.151)
BC	25	5.940	(0.261)	0.925	(0.037)	1385.272	(208.189)	1604.416	(1.150)
High zone:									
FC	25	7.009	(0.259)	1.095	(0.072)	2597.980	(324.285)	1945.187	(1.141)
DBN	17	6.881	(0.312)	0.825	(0.030)	712.739	(123.733)	?	?
SH	25	8.500	(0.364)	1.331	(0.120)	2985.927	(565.222)	1183.691	(1.171)
BC	16	7.111	(0.296)	1.599	(0.124)	2423.964	(581.352)	1038.003	(1.200)

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[1] *Size = Basal Diameter (in mm); Shape = Ratio of barnacle height to basal diameter*

[2] *LS median values were generated by back-transforming LS mean values (as described in Ramsey and Schaffer 1999), which were based on the Site*Zone term from the multiple regression model (Table B3, a).*

[3] *Missing data denoted by '?.'*

shape (Table B3, *d*) were not significantly different (Paired t-test: t<0.0001, *P*=0.50, df=137). Consequently, site and zone were omitted from the predictive model of larval production (Table B3, *d*). We used this model [ln (#larvae per barnacle)= 4.59+ 0.304 (basal diameter) + 0.505 (ht: basal diameter)] to estimate larval production per barnacle for other random survey sampling periods and for the outplant experiment. As we found that larval production per barnacle was greater in the summer months than in April 2003 (see above), this predictive formula, which was based only on data from April 2003, is a conservative estimate of larval production per barnacle.

Temporal and spatial trends in brooding frequency and larval production differed markedly between intertidal zones. In the mid intertidal zone, both brooding frequencies and larval production per 100 cm^2 were fairly steady through time, declining only in November (Fig. 3.4A, 3.5A; Table 3.2, B5). Cape did not influence mid zone brooding rates (Table B5, *b*: F=2.499, *P*=0.116, df=1, 178) or larval production per 100 cm^2 (Table B5, *d*: F=2.766, *P*=0.098, df=1, 184). There was a marginally significant interaction between sampling period and site on mid zone brooding frequency (Table B5, *a*: F=1.912, *P*=0.046, df=10, 178), indicating that the rank order of the sites varied through time.

In the high intertidal zone, brooding frequencies and larval production peaked in February and April and were low in November. However, SH animals continued to brood in the summer, unlike barnacles at the other three sites (Fig. 3.4B, 3.5B; Table 3.2, B5). Consequently, in the summer, larval production per 100 cm^2 was markedly higher at SH than at the other three sites (Fig. 3.5B, Table 3.2). Also, DBN high intertidal larval production was unusually low relative to the other sites. Cape did not

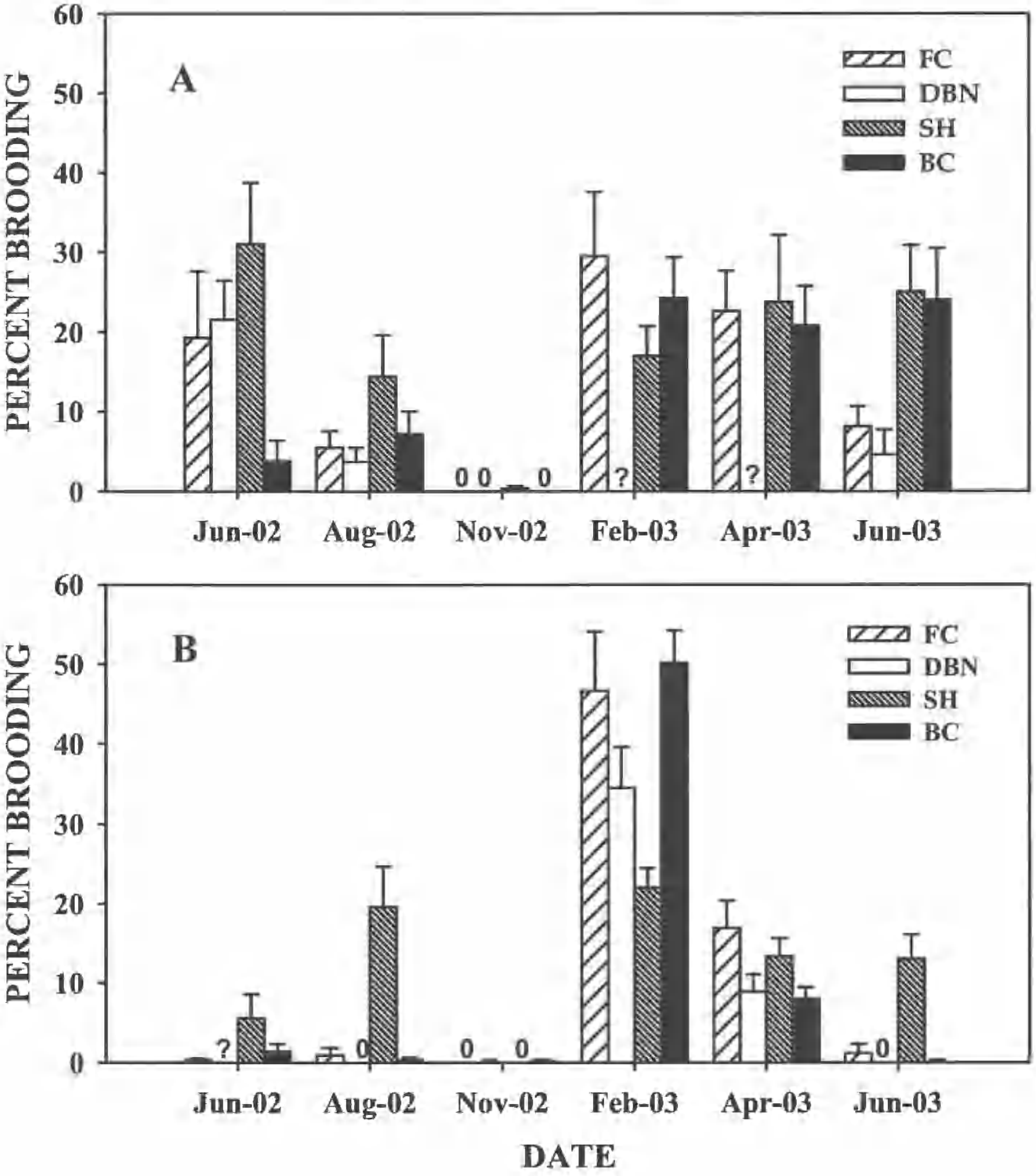

Fig. 3.4. Brooding frequencies in natural populations of *B. glandula*. Untransformed means + SE are shown. (A) Mid intertidal brooding frequencies were steady through time, with the exception of an overall low point in Nov. 2002 (Tukey-Kramer test on LS means by time, $p<0.05$). N=12 quadrats; DBN was omitted from statistical analysis due to missing data ('?'). (B) High intertidal brooding frequencies peaked in Feb. 2003, and SH brooding rates were higher than at the other sites in Aug. 2002 (Tukey-Kramer tests on LS means by time, $p<0.05$). N=12 quadrats, except for June 2002, where SH (n=5) and Aug. 2002, where FC (n=9). June 2002 was omitted from statistical analysis due to missing data ('?').

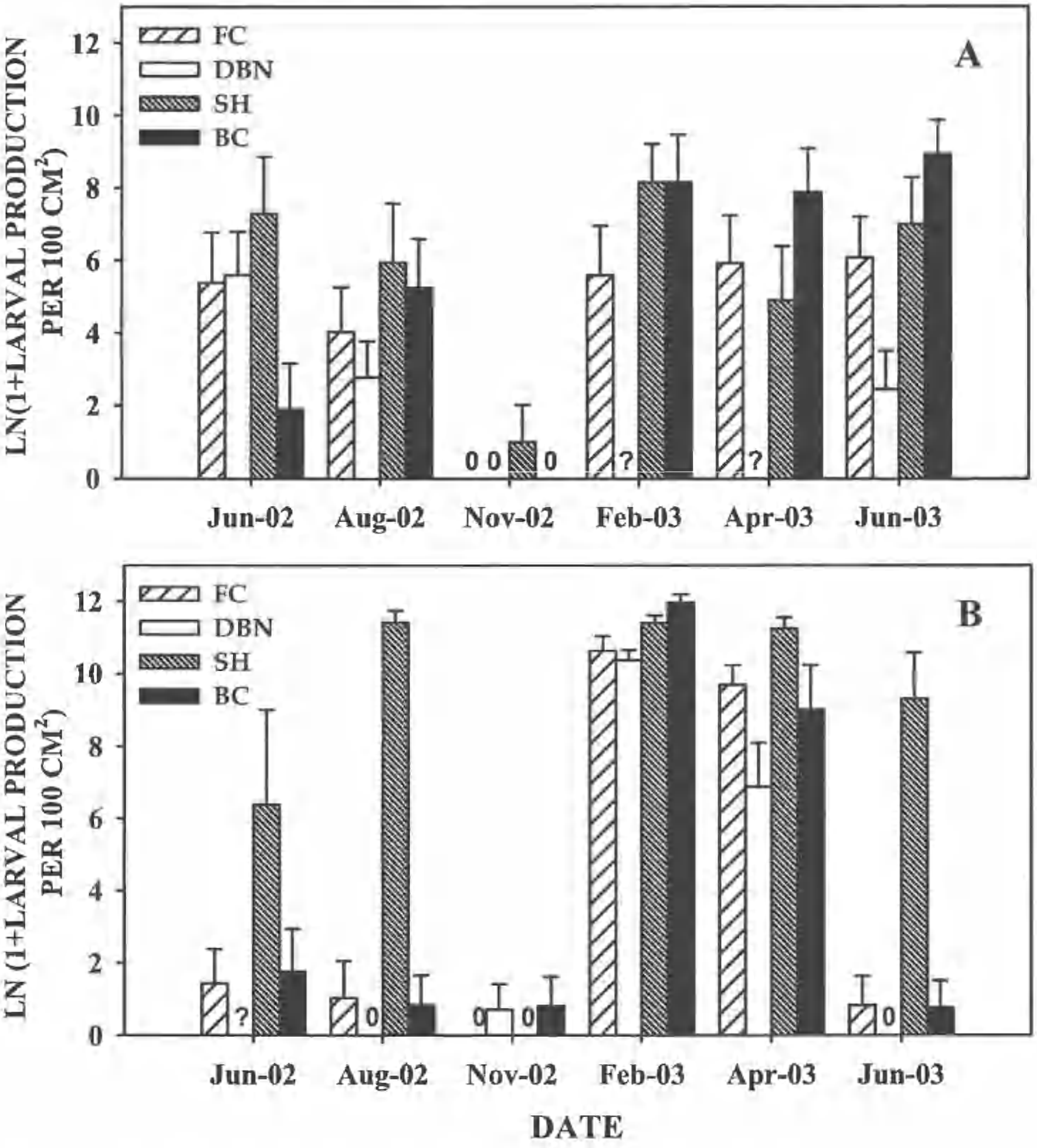

Fig. 3.5. Larval production in natural populations of *B. glandula*. Ln-transformed means + SE are shown. (A) Mid intertidal larval production per 100 cm^2 was steady through time, with the exception of an overall low point in Nov. 2002 (Tukey-Kramer test on LS Means by time, $p<0.05$). N=12 quadrats; DBN was omitted from statistical analysis due to missing data ('?'). (B) High intertidal larval production per 100 cm^2 peaked in Feb. and April 2003 and otherwise was low (except at SH). SH produced many more larvae than the other sites in the summer (Tukey-Kramer test on LS means calculated from the time*site(cape) term, $p<0.05$). N=12 quadrats, except for June 2002, where SH (n=5) and Aug. 2002, where FC (n=9)]. June 2002 was omitted from statistical analysis due to missing data ('?').

Table 3.2. Larval production per 100 cm^2 in natural populations of the barnacle *B. glandula* in Oregon (USA), 2002-2003. Arithmetic means (SE) are shown. For analyses, see Table B5.

	n	FC		DBN		SH		BC	
Mid zone:									
Jun-02	*a*	9183	(4018)	3108	(790)	49464	(17868)	6107	(4197)
Aug-02	12	2055	(826)	450	(228)	16698	(8026)	7046	(3061)
Nov-02	12	0	(0)	0	(0)	983	(983)	0	(0)
Feb-03	12	7307	(3033)	?	?	21600	(9468)	50699	(21025)
Apr-03	12	12395	(6327)	?	?	23503	(15239)	55080	(29722)
Jun-03	12	8238	(5375)	1052	(809)	23870	(12583)	38186	(11511)
Mid zone total		39,177		4,610		136,118		157,118	
High zone:									
Jun-02	*b*	482	(338)	?	?	30194	(16747)	6723	(4935)
Aug-02	*c*	1122	(1122)	0	(0)	147741	(42148)	1746	(1746)
Nov-02	12	0	(0)	380	(380)	0	(0)	634	(634)
Feb-03	12	79328	(22067)	45020	(10651)	112669	(23907)	193711	(34247)
Apr-03	12	42616	(13388)	10390	(3362)	116512	(30690)	49619	(10566)
Jun-03	12	1520	(1520)	0	(0)	80449	(23077)	684	(684)
High zone total		125,068		55,790		487,565		253,117	
Cumulative prod.[d]		164,245		60,400		623,683		410,235	

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[a] *Samples sizes varied: FC, DBN, and SH (n=12), BC (n=11)*

[b] *Samples sizes varied: FC and BC (n=12), SH (n=5), DBN (n=0)*

[c] *Samples sizes varied: DBN, SH and BC (n=12), FC (n=9)*

[d] *Cumulative production=sum of all available means. Missing data are denoted by '?.'*

influence high zone brooding (Table B5, *e*: F=0.001, *P*=0.983, df=1, 206) or larval production (Table B5, *f*: F=1.683, *P*=0.324, df=1, 210). However, there was a strong interaction between sampling period and site nested within cape on high zone brooding frequency (Table B5, *e*: F=16.413, *P*<0.0001, df=8, 206) and high zone larval production per 100 cm^2 (Table B5, *f*: F=14.619, *P*<0.0001, df=8, 210).

Brooding frequencies also varied with barnacle size, which was measured as basal diameter (Table B5, *a* & *e*). In the mid intertidal zone, barnacles living in plots characterized by larger mean basal diameters brooded at higher frequencies in April, June, and August (Fig. B2, Table B5, *a*: F=6.896, *P*<0.0001, df=5, 178). In the high intertidal, animals in plots with larger mean basal diameters brooded at higher rates only in April (Fig. B2, Table B5, *e*: F=6.823, *P*<0.0001, df=4, 206).

Mean cumulative production at the Cape Perpetua sites was 5x that at the Cape Foulweather sites (Table 3.2). Cumulative larval production varied markedly among sites: SH cumulative larval production per 100 cm^2 was 1.5 to 10x that at the other sites (Table 3.2). High zone production accounted for an average of 77% of the cumulative larval production (Table 3.2). Again, site differences were evident: SH's high intertidal cumulative larval production per 100 cm^2 was 2 to 10x that of the other high zone populations (Table 3.2).

In summary, we found strong seasonal patterns in brooding frequency and larval production in the random surveys of natural *B. glandula* populations. In terms of spatial variation, cape-level differences were evident in terms of the mean cumulative larval production per 100 cm^2, which integrated random survey data collected during the six sampling periods in 2002-2003. The most striking difference was at SH, where high zone barnacles continued to brood in June and August, and consequently produced many more larvae.

Outplant experiment

The mean number of recruits per plate (32.62 ± 0.02) was similar among the sites (Table B6, *a*: F=0.884, *P*=0.475, df=4, 143), enabling us to explicitly examine the effects of cape and site nested within cape on the experimental populations. Mortality was high across all sites (Fig. B3), with an overall mean of 87% (± 3.7) per plate, and was not influenced by cape (Table B6, *b*: F=0.330, *P*=0.597, df=1, 143).

Cape Perpetua barnacles attained a larger mean basal diameter per plate than those at Cape Foulweather (Fig. 3.6A, Table B7, *a:* F=64.625, *P*=0.001, df=1, 76). DBN and DBS barnacles were smaller than those at FC (Fig. 3.6A, Table B7). Individual allocation to shell mass tended to be greater at the Cape Perpetua sites, after accounting for variation in mean barnacle size per plate (Table B7, *b*: F=6.919, *P*=0.058, df=1, 70). Shell and gonad (both ovarian and brood) tissue biomass allocation varied idiosyncratically among the sites (Table 3.3, B7, *b & d*). Otherwise, individual biomass allocation was not influenced by cape or site, but only by mean barnacle size per plate (Table 3.3, B7). The strong associations between mean barnacle size and individual biomass allocation could provide a useful predictive tool (Fig. B4, Table B8).

Cape Perpetua experimental populations had marginally higher brooding rates than those at Cape Foulweather (Fig. 3.6B, Table B6, *c*: F=5.348 *P*=0.082, df=1, 143). There also were strong differences among the sites (Table B6, *c*: F=5.104, *P*=0.0007,

Fig. 3.6. Barnacle growth and reproduction in the outplant experiment. LS means + SE are shown (n=20-26 plates). Means with dissimilar letters were different (Tukey-Kramer test on LS means, $p<0.05$). (A) Mean barnacle basal diameter per plate, a measure of barnacle size and relative growth rate, varied among the capes and sites. (B) Brooding frequency per plate varied among sites: SH populations brooded at higher rates than those at the other sites. (C) Larval production per plate varied between the capes and among the sites. No brooding animals were found at DBN or DBS, so the estimated values were very small.

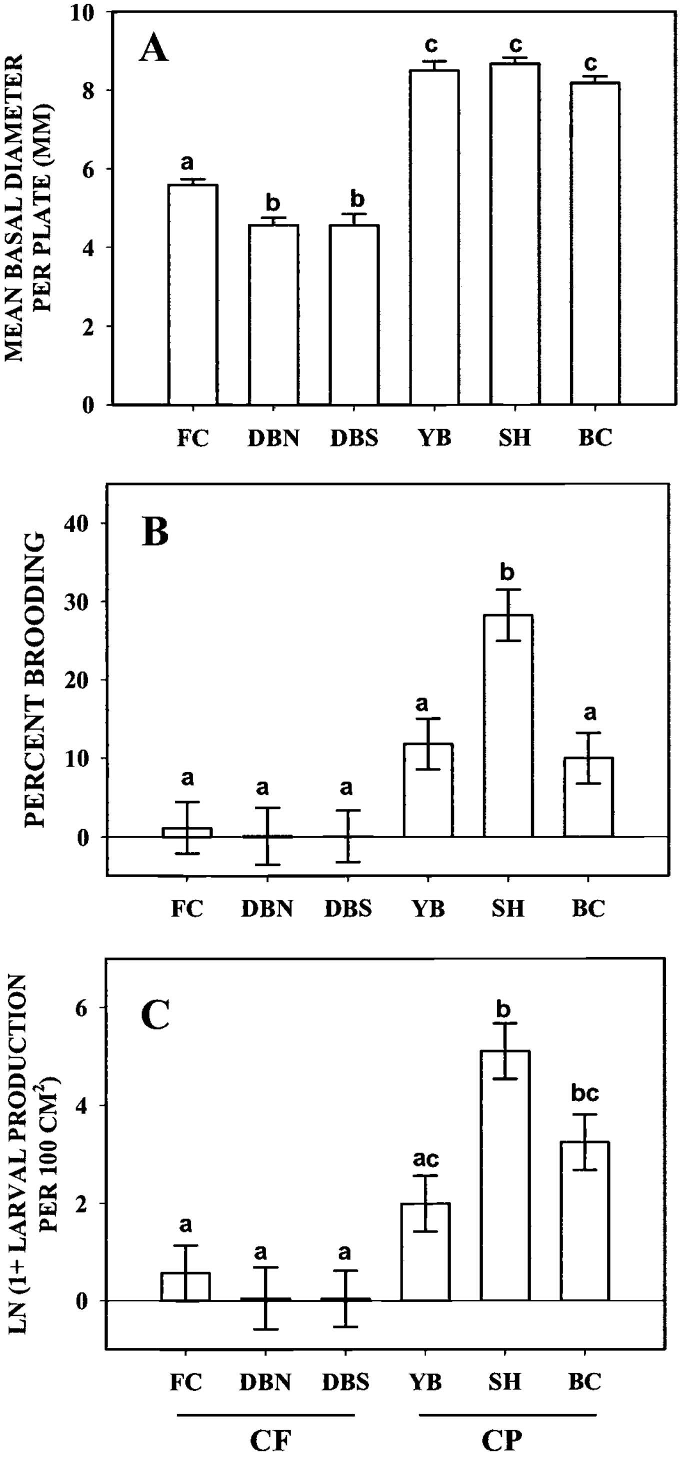
A
MEAN BASAL DIAMETER PER PLATE (MM)
0
2
4
6
8
10
a
b
b
c
c
c
FC
DBN
DBS
YB
SH
BC
B
PERCENT BROODING
0
10
20
30
40
a
a
a
a
b
a
FC
DBN
DBS
YB
SH
BC
C
LN (1+ LARVAL PRODUCTION PER 100 CM^2)
0
2
4
6
a
a
a
ac
b
bc
FC
DBN
DBS
YB
SH
BC
CF
CP

Table 3.3. Individual biomass allocation in experimental populations of *B. glandula* from Oregon (USA), April 2003. Arithmetic means (and SEs) of dry weights (in mg) are shown. See Fig. B4 for plots of associations with mean basal diameter per plate.

		Shell		Somatic tissue		Female gonad[1]		Brood	
	n	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Cape Foulweather:									
FC	26	31.320	(1.991)	0.851	(0.065)	0.278	(0.061)	1.028	(0.328)
DBN	20	16.071	(1.404)	0.444	(0.044)	0.005	(0.005)	--	--
DBS	25	14.190	(1.723)	0.284	(0.053)	0.000	(0.000)	--	--
Cape Perpetua:									
YB	26	111.577	(9.817)	2.184	(0.202)	2.767	(0.411)	3.452	(0.499)
SH	26	115.250	(8.442)	2.610	(0.267)	3.341	(0.419)	4.630	(0.456)
BC	26	92.857	(7.030)	1.886	(0.149)	1.838	(0.276)	4.096	(0.453)

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[1] Includes both ovarian and brood tissue

Table 3.4. Larval production in experimental mid intertidal populations of the barnacle *B. glandula* in Oregon (USA), April 2003. Arithmetic means (and SEs) are shown, except for the last column.

	n	Production/barnacle		Production/plate		Adj. Production[1]	
FC	26	859.922	(20.976)	363.006	(252.103)	0.768	(0.763)
DBN	20	--	--	0.000	(0.00)	0.053	(0.886)
DBS	25	--	--	0.000	(0.00)	0.044	(0.781)
YB	26	2120.321	(195.786)	1149.143	(511.974)	6.323	(0.763)
SH	26	2111.875	(123.984)	6637.057	(1756.030)	163.876	(0.763)
BC	26	2018.534	(167.504)	2493.098	(1167.812)	24.576	(0.763)

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[1] Adjusted larval production per 100 cm^2 was calculated as: exp (LS mean) - 1. LS means were calculated using a nested ANOVA based on ln-transformed values (see Fig. 3.6C; Table B6, f).

df=4, 143): at SH, barnacles brooded at much higher rates than at the other five sites (Fig. 3.6B). Based on the four sites where brooding barnacles were present, the mean estimated larval production per barnacle was greater in Cape Perpetua populations than in those at Cape Foulweather (Table 3.4, B6, *e*: F=21.561, *P*<0.0001, df=1, 29).

On a population level, larval production per plate was marginally higher at the Cape Perpetua sites than at the Cape Foulweather sites (Fig. 3.6C; Table 3.4, B6, *f*: F=7.907, *P*=0.048, df=1, 143). Comparison of the arithmetic means (Table 3.4) indicated that larval production per plate was 28x greater at the Cape Perpetua sites than at the Cape Foulweather sites. There were also considerable differences among sites: No larvae were produced at DBS and DBN, while SH produced 2.5 to 20x more larvae per plate than the other three sites (Table 3.4: comparison of arithmetic means). The same trend in larval production per plate was observed when the back-transformed least square means were compared (Table 3.4, last column: SH produced 1.6 to 9x more larvae per plate than the other three sites with brooding animals).

In summary, the mid zone experiment yielded qualitatively similar results to the surveys: barnacle populations in the Cape Perpetua region grew to a larger mean size and produced a greater number of larvae per unit area than their counterparts in the Cape Foulweather region. Again, clear among-site differences were evident, with the SH populations producing many more larvae per plate than those at the other sites and the DBN and DBS populations producing no larvae at all.

DISCUSSION

Evidence of bottom-up control of barnacle population dynamics

Our findings indicate that variation in bottom-up factors, specifically primary productivity, can have considerable influence on population dynamics. *B. glandula* populations exhibited strong differences between the higher primary productivity region, Cape Perpetua, and the lower productivity region, Cape Foulweather. Cape Perpetua high zone barnacle populations were 2.5 to 6.5x more abundant and 1.5x more crowded than those in other areas. The mean cumulative larval production per 100 cm^2 at the Cape Perpetua sites was 5x that at the Cape Foulweather sites, based on the random survey data collected in 2002-2003. Barnacles in experimental populations at Cape Perpetua grew to almost 2x the size and had heavier shells than barnacles at Cape Foulweather. Mean estimated larval production per individual in experimental mid-intertidal populations at the Cape Perpetua sites was >2x that at the Cape Foulweather sites, and mean larval production per plate at the Cape Perpetua sites was 28x greater than at the Cape Foulweather sites.

Because barnacles interact as competitors, prey, and habitat modifiers with other members of the rocky intertidal community, it is likely that the bottom-up effects we documented extend to the community level as well. Barnacles have occupied a central role in some quantitative models of benthic community dynamics (Connolly and Roughgarden 1998, 1999). The data reported here could be used to improve these models, particularly by incorporating more realistic estimates of larval production through space and time. Also our results could be used to translate barnacle abundance and size-frequency distribution data into estimates of individual biomass allocation. This would be useful both for estimating barnacle larval production as well as for estimating the barnacle biomass available to the keystone predator *Pisaster ochraceus*.

We also found striking among-site differences in barnacle growth and larval production within each region. In particular, SH natural and experimental populations produced many more larvae than those at the other sites. SH cumulative larval production per 100 cm^2, according to random surveys of natural populations, was 1.5 to 10x that at the other sites. SH experimental populations produced 2.5 to 20x more larvae than BC, YB, and FC (while the other two sites produced no offspring). The concurrence of the ranges of these estimates suggests they are robust. While SH's striking production is consistent with the bottom-up hypothesis, clearly much remains to be explained regarding the mechanisms underlying variation in benthic-pelagic coupling of marine communities within capes or headlands (1-10s of km) (see also Menge et al. accepted, Freidenburg and Menge in prep).

While these comparative studies were designed to test the role of the natural gradient in primary productivity between the two capes, variation in other factors could have contributed to our results. For example, abiotic conditions (e.g. wave exposure, emersion time, and heat and desiccation stress) are known to effect organismal functioning and thus population and community dynamics (Menge 1976, Menge and Sutherland 1976, Wethey 1983, Menge and Sutherland 1987, Bertness 1989, Sanford et al. 1994, Helmuth 1998, Menge et al. 2002). But wave exposure and tidal height were accounted for in these investigations, by limiting the studies to areas of high exposure and similar tidal height. Also, the existing data suggest that if anything, the Cape Perpetua sites are hotter than those to the north (Dahlhoff et al. 2001).

Alternatively, SH experimental populations may have outperformed those at the other sites because the animals were locally adapted to that site. However, previous work by Sanford and Menge (2001) showed that *B. glandula* transplanted from a common Cape Foulweather source (Boiler Bay) showed a similar response to that observed here, with transplanted animals at SH growing faster than those at BB. Also, Bertness and colleagues (1991) found similar trends in barnacle growth and reproduction when they compared individuals transplanted to Narragansett Bay vs. the open coast: animals living in the phytoplankton-rich bay grew to a larger size and had 10x the reproductive output compared to those living on the open coast. Our findings support the initial hypothesis that growth and reproduction are phenotypically plastic traits in barnacles that can be strongly influenced by variation in primary productivity. Certainly, further testing of the roles of bottom-up effects and how they scale up to spatial and temporal scales relevant for management and conservation is desirable.

Mid intertidal barnacles as an unexpected larval source

To our knowledge, the dramatic difference in the timing and magnitude of reproductive effort between mid and high zone barnacle populations has not been previously documented (see Bertness et al. 1991 for related work). High intertidal production accounted for an average of 77% of the cumulative larval production at each site. However, the timing of high intertidal production relative to recruitment suggests that many of the high zone offspring may be 'wasted.' Seventy percent of high zone larvae were produced during the early spring (Table 3.2). Recruitment of *B. glandula* on the Oregon coast occurred throughout the year in 2002-03 (Fig. 3.7), although for the past 15 years at least, the major recruitment pulses of *B. glandula* have tended to occur during summer and fall (B. Menge, *unpublished data*). Thus it is likely that mid intertidal animals contributed substantially to the observed recruitment pulses in summer 2002, when high zone production was so low. Also it is unlikely these summer recruits resulted from the high zone adults because barnacle larvae are thought to spend 2-4 weeks in the plankton (Strathmann et al. 1981), rather than the 3-4 months that would be required for high zone offspring to account for the usual heavy settlement in late summer.

The apparent large contribution of mid zone animals to future generations is potentially important for several reasons: On average, mid zone animals are smaller than those in the high zone and thus produce fewer larvae per individual. They are less abundant and therefore produce fewer larvae per 100 cm^2 in a given time period. Finally, they likely are younger and subject to much higher predation pressure (Connell 1970, Menge 1976, 1978). In many ways they are marginal populations. Perhaps the continuous reproduction effort of mid intertidal animals is a partial function of immersion time: they spend a much greater proportion of their lives underwater than high zone animals, and thus have more time to feed and have less exposure to heat and desiccation stress. Regardless, the dramatic difference between mid and high zone reproductive strategies warrants attention.

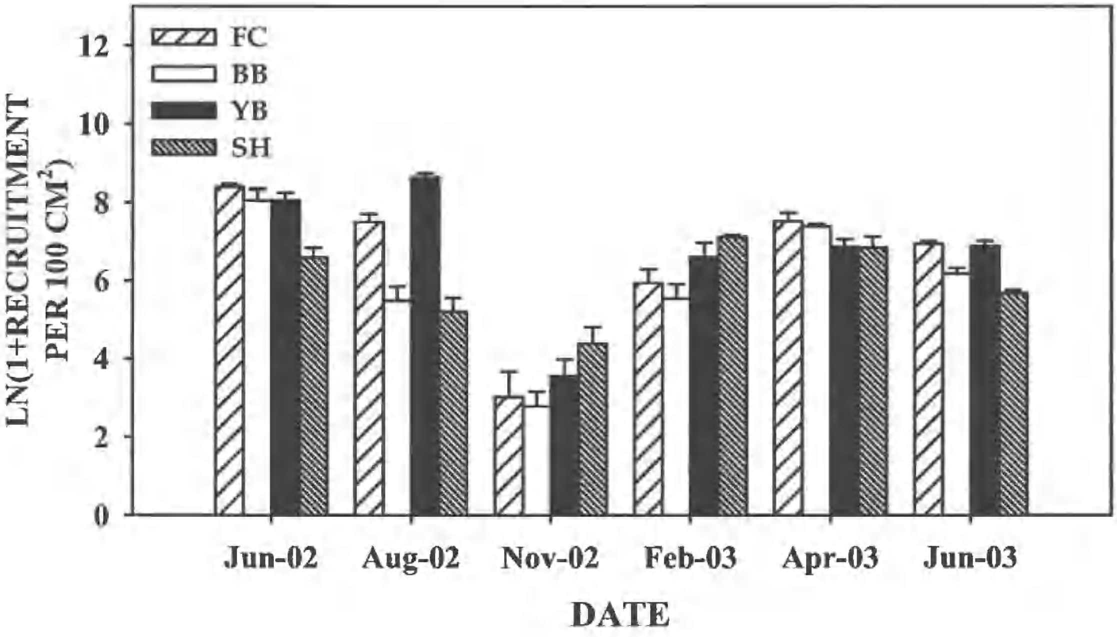

Fig. 3.7. Monthly mid intertidal recruitment of *B. glandula*. Recruitment varied through time, with a low point in November 2002. There was no effect of cape and the rank order of sites changed through time (Tukey-Kramer test on LS means calculated from the time*site(cape) term, $p<0.05$). Recruitment was monitored on standardized settlement plates covered in Safetywalk© adhesive tape, which were replaced monthly at each site ($n=5$). Ln-transformed means + SE are shown. The Cape Foulweather sites were Fogarty Creek (FC) and Boiler Bay (BB, 1 km south of FC) and the Cape Perpetua sites were Yachats Beach (YB) and Strawberry Hill (SH). See Table B5, *g* for statistical analysis.

Estimations of larval production based on barnacle cover may overestimate the contribution of high intertidal animals to future recruitment. Given that nearshore primary productivity tends to be greatest during the summer months (Menge et al. 1997*b*, Menge et al., *unpublished data*), the timing of high vs. mid zone reproduction also raise questions about the condition and survival of the larvae and recruits produced by high vs. mid zone animals.

The similar magnitude and timing of mid zone larval production and barnacle recruitment in 2002-2003 is also quite intriguing (Fig. B5: Correlation of ln-transformed larval production and recruitment values for SH and FC in 2002-2003: correlation coefficient=0.66, p=0.02, n=12). Whether this is evidence of fairly low mortality, subsidies from a more spatially extensive larval pool, larval retention, or some combination of these and other factors remains to be tested.

Strong seasonality in reproduction

The observational studies reported above revealed striking seasonal fluctuations in brooding frequency and larval production in *B. glandula*. Both responses peaked in the early spring (February-April) in Oregon, largely due to the pulse of activity from high zone animals. These observations parallel those reported by other investigators (Barnes and Barnes 1956, Hines 1978, C. Harley, *personal communication*). The temporal coherence in larval production in this species suggests that coast-wide production is fairly predictable on a seasonal basis, and that some of the proximate cues to barnacle mating, brooding, and larval release extend over the scale of 1000s of km. Relating these trends to decadal scale shifts in oceanic conditions (e.g. the Pacific Decadal oscillation) and forecasting how production in this and other benthic marine species may shift with climatic change is an intriguing area of future research.

Implications for management and conservation

These results demonstrate that larval production "hotspots" exist in rocky intertidal ecosystems, and that not all sites are equivalent in terms of their population and community dynamics. While animals at YB and BC grew to a similar size as those at SH, they did not contribute commensurately to larval production. This differential production of offspring across 10s of kms is important to consider in the context of protecting barnacle populations or (more appropriately) rocky intertidal communities. While barnacles grew more quickly throughout the Cape Perpetua region, they produced many more offspring at only one of the three sites, SH.

These findings also demonstrate the importance of incorporating seemingly marginal populations into conservation and management strategies. Although barnacles were more abundant and achieved a larger mean size in the high zone, mid intertidal populations were more consistent contributors to the regional larval pool. Populations like the mid intertidal barnacles may be more central to local or regional persistence than they appear.

Rarely, however, is the level of demographic information presented here available for target species, let alone entire marine communities. Consequently, bet hedging should be an important aspect of marine conservation planning. Networks of marine reserves or other types of marine protected areas provide one useful strategy for dealing with the inevitable uncertainty about the productivity of particular populations and other mechanistic details of marine populations and ecosystems (National Research Council 2001, Roberts et al. 2001, Lubchenco et al. 2003). For a network to work, the sites must be linked by larval dispersal, migration of juveniles and adults, and/or movement of nutrients and particulate food. Particularly in coastal marine ecosystems, where these linkages are predicted to change with climatic change, embedding marine conservation and management strategies within a network context is essential.

Conclusions

We found strong evidence of bottom-up control of barnacle growth and reproduction, as well as significant within and among-site variability in larval production. Larval production was highly seasonally overall. Mean cumulative larval production per 100 cm^2 in natural populations in the Cape Perpetua region was 5x that in the Cape Foulweather region. Barnacles living in experimental mid-intertidal populations in the Cape Perpetua region grew to almost 2x the mean size of barnacles living in the Cape Foulweather region. Mean estimated larval production per individual in experimental populations in the Cape Perpetua region was >2x that at the sites in the Cape Foulweather region. Mean larval production per 100 cm^2 in the experimental populations in the Cape Perpetua region was 28x greater than that in the Cape Foulweather region. One site within the higher productivity region, SH, produced substantially more larvae than the others, however, indicating the importance of among-site variability. Our findings advance understanding of the role of bottom-up influences in population and community dynamics, and contribute data for the next generation of conceptual and quantitative models of marine community dynamics. Our results also demonstrate the importance of taking a network approach when designing marine reserves and other area-based marine management strategies.

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Chapter 4:

Using Siting Algorithms in the Design of Marine Reserve Networks

Heather Leslie, Mary Ruckelshaus, Ian R. Ball,
Sandy Andelman, and Hugh P. Possingham

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ABSTRACT

Using benthic habitat data from the Florida Keys (USA), we demonstrate how siting algorithms can help identify potential networks of marine reserves that comprehensively represent target habitat types. We applied a flexible optimization tool—simulated annealing—to represent a fixed proportion of different marine habitat types within a geographic area. We investigated the relative influence of spatial information, planning unit size, detail of habitat classification, and magnitude of the overall conservation goal on the resulting network scenarios. With this method, we were able to identify many adequate reserve systems that met the conservation goals, e.g., representing at least 20% of each conservation target (i.e., habitat type) while fulfilling the overall aim of minimizing the system area and perimeter. One of the most useful types of information provided by this siting algorithm comes from an ''irreplaceability analysis,'' which is a count of the number of times unique planning units were included in reserve system scenarios. This analysis indicated that many different combinations of sites produced networks that met the conservation goals. While individual 1-km^2 areas were fairly interchangeable, the irreplaceability analysis highlighted larger areas within the planning region that were chosen consistently to meet the goals incorporated into the algorithm. Additionally, we found that reserve systems designed with a high degree of spatial clustering tended to have considerably less perimeter and larger overall areas in reserve—a configuration that may be preferable particularly for sociopolitical reasons. This exercise illustrates the value of using the simulated annealing algorithm to help site marine reserves: the approach makes efficient use of available resources, can be used interactively by conservation

decision makers, and offers biologically suitable alternative networks from which an effective system of marine reserves can be crafted.

INTRODUCTION

There is a great deal of international interest in marine reserves and their potential for biodiversity conservation. Many countries throughout the world have initiated strategies that include the development of representative marine reserve networks as part of integrated coastal-zone management programs (Kelleher et al. 1995, ANZECC Task Force on Marine Protected Areas 1998, Department of Fisheries and Oceans Canada 2000, Federal Register (USA) 2000). Such efforts have arisen as recognition has grown of the pressures on marine resources, which include coastal land development, aquaculture and fisheries. At present, we have a unique opportunity to create the kind of marine reserve systems we would have established in terrestrial ecosystems before some habitats were almost entirely modified for alternative uses. Once we acknowledge the urgency of developing a system of marine reserves, the question is how best to design and implement marine reserves to efficiently conserve biodiversity and achieve other possible reserve objectives most effectively.

The purpose of this paper is to describe how reserve-siting algorithms can be used to help identify marine reserve systems that comprehensively represent all habitat types in a sensible spatial arrangement. Reserve-siting algorithms have rarely been used in marine contexts (see Ward et al. (1999) for a notable exception), although several applications (e.g., Channel Islands National Marine Sanctuary, Great Barrier Reef Marine Park) have been initiated since we began this work. As in terrestrial systems, the designation of marine reserves has primarily been ad hoc in the past, and driven by opportunity rather than strategic objectives and systematic approaches. We believe that systematic, strategic reserve selection is always preferable to an ad hoc approach, as it maximizes the chances of creating a representative system of reserves, ensures a transparent and defensible process, and makes the most efficient use of available resources (Pressey et al. 1993, Margules and Pressey 2000). Furthermore, once alternative scenarios for comprehensive and efficient marine reserve networks have been identified, they can be used as benchmarks against which to evaluate the advisability of pursuing site-specific conservation opportunities that may arise.

Here we focus on the problem of representing a group of conservation targets, specifically benthic marine habitats, within a geographic area. This basic approach has been applied in terrestrial systems in the past (Margules et al. 1988, Groves et al. 2002) and more recently in marine systems (Ward et al. 1999, Beck and Odaya 2001). In marine environments, community- and ecosystem-level characteristics may be better captured by schemes based on habitat types, as opposed to species richness or endemism (Schwartz 1999, Ward et al. 1999). We illustrate this approach to reserve design by applying simulated annealing, a relatively new and flexible optimization tool (Kirkpatrick et al. 1983, Ball 2000), to a data set from the Florida Keys. Using this method, we were able to identify potential systems that met the conservation goals (i.e., specified level of habitat representation). In other words, we generated multiple network scenarios that included ≥10, ≥20, or ≥30% of all habitat types within the study region while minimizing a combination of reserve system area and reserve system perimeter.

Algorithms: one reserve-selection tool

In order to explain our choice of the simulated annealing algorithm, we review the underlying rationale of using computer-based siting algorithms to help solve reserve selection problems. Consider, for example, a group of conservation decision makers whose efforts are focused on three species, or conservation targets, which they want to represent in at least two sites. If there are ten sites from which to create a network, it is feasible that the reserves could be selected ''by inspection,'' i.e., by searching through the options and arriving at one or more combinations that meet the conservation goals. Alternatively, if the decision makers have tens or even hundreds of conservation targets and thousands of potential sites, as is often the case in regional conservation planning situations (Davis et al. 1999), the selection problem quickly becomes intractable. If there are 1500 possible sites (or planning units, as they are often called), then there would be 2^n or 21,500 possible reserve systems! Computer-based siting algorithms can be used to reduce this enormous set of possibilities to a reasonable suite of network scenarios that meet the conservation goals.

At the core of reserve selection problems, whether marine or terrestrial, is the overall objective of minimizing the area encompassed with the network of reserves (Pressey et al. 1993). This objective is derived from the idea that, while from a biodiversity-conservation perspective one might want to maximize the area within reserves, social and economic constraints demand an efficient and limited area within reserves (Possingham et al. 2000). Given this aim, the representation of defined conservation targets, such as species or habitat types, enters into the model as a constraint. Such constraints are often referred to in the conservation planning literature as ''conservation goals,'' whereas ''conservation targets'' refer to the specific species, habitats, or biological communities of conservation interest [e.g., Groves et al. (2002)]. We follow that convention here.

The various algorithms available to solve the ''minimum representation problem,'' as it was first defined by Kirkpatrick et al. (1983), may be broadly divided into several types: iterative, optimizing, and simulated annealing. Iterative algorithms order each planning unit according to a set of criteria, and then choose the highest-ranking site. Some of the most popular iterative or heuristic algorithms are focused on maximizing species richness (the ''greedy'' algorithm) or representing rare species within the network (the ''rarity'' algorithm). While iterative algorithms run quickly and operate in a fairly intuitive manner (Margules et al. 1988, Rebelo and Siegfried 1992, Nicholls and Margules 1993, Pressey et al. 1997), they generate only one solution and it is very unlikely to be the optimal one (Possingham et al. 1993, Underhill 1994, Pressey et al. 1997).

Alternatively, the reserve-selection problem can be formulated as an Integer Linear Program (ILP) and standard mathematical programming methods then can be used to find the optimal solution (Cocks and Baird 1989, Church et al. 1996). Pressey and colleagues (1997) compared heuristic algorithms with the solution found using an ILP, and found that heuristics generated solutions within 5–20% of the optimal one. Unfortunately, the optimization method fails when the number of potential planning units is large (more than a few hundred), because of the tremendous computing time needed to solve such a large problem in a reasonable time (Possingham et al. 2000). Additionally, ILPs produce only one optimal solution; whereas multiple solutions are often desirable in a conservation planning situation. Finally, if we are interested in reserve systems that are spatially clustered, then the Integer Linear Programming problem becomes a Non-linear Integer Linear Programming problem. In these cases it is even harder to guarantee optimal solutions.

Because of the findings reviewed above, we chose to use the third type of algorithm, simulated annealing, in this illustrative exercise. Simulated annealing minimizes objective functions based on the process of annealing metals or glass (Kirkpatrick et al. 1983). The algorithm starts with a completely random reserve system, and trial solutions are iteratively explored through sequential random changes to the set of planning units in the system. At each step, the new set of units is compared with the previous set, and the best one is accepted (Possingham et al. 2000). The strength of this approach is its avoidance of local optima. Yet by allowing the selected set of planning units, or sites, to move through sub-optimal space, the algorithm creates more opportunities to reach the global minimum. As the process continues, the algorithm becomes choosier about what changes lead to the ''best'' system of sites.

The simulated annealing algorithm consistently has outperformed simpler iterative or heuristic algorithms, such as the greedy and rarity-based selection algorithms, in that it delivered solutions composed of the same or a smaller number of sites (Ball 2000, Possingham et al. 2000). Also, the use of simulated annealing enables us to explicitly and efficiently incorporate spatial information into the reserve selection process. In the past, most reserve-siting algorithms have ignored space, and selected a system of sites from those available without explicitly considering the spatial relationship among sites (Possingham et al. 2000). Where space has been incorporated in iterative site-selection methods, it has typically been accomplished by merely selecting sites that are in close physical proximity to one another (Nicholls and Margules 1993). This approach, termed an adjacency constraint, is unlikely to deliver efficient systems because there will be a tendency to build on initially selected sites without exploring completely new alternatives.

Here we explore scenarios for reserve networks that represent conservation targets—in this case, marine habitats—efficiently with respect to both the total area and perimeter of the system. By designing systems with low perimeter values, or boundary lengths, we generate options that are well connected, a quality that may be preferable for both biological and sociopolitical reasons (Roberts et al. 2001, Roberts et al. 2003a). For example, currents and other oceanographic phenomena can greatly influence the transport and dispersal of many marine organisms, especially the early planktonic larval stages (Roberts 1997). Connectivity among reserve sites can provide for transfer of larvae and material among biological populations and ecosystems, and a spatially condensed network may reduce enforcement and management costs (see Roberts et al. 2001, Roberts et al. 2003b).

METHODS

Our goal in this exercise was to investigate how siting algorithms can be used to help evaluate the merits of possible marine reserve networks using objective criteria. The data we used and the conservation goals of representing 10, 20, and 30% of all habitat types within the region were chosen for illustrative purposes only. The choice of a particular habitat classification scheme can significantly influence the scenarios identified by this and other decision support tools. To move beyond this heuristic exercise and actually apply this approach to a specific planning situation would require (1) articulation by stakeholders of clear conservation objectives (e.g., preserve the habitat diversity within the Florida Keys National Marine Sanctuary [FKNMS]), (2) identification of conservation targets including habitats, species, or surrogates (e.g., focus conservation on the 26 habitat types defined and mapped for the FKNMS), (3) delineation of appropriately scaled sites or planning units based on the targets chosen (e.g., use a 1-km^2 planning unit for accounting of habitat representation in the reserve systems), and (4) specification of conservation goals, or desired levels of representation of the targets (e.g., include 20% of the total area of each habitat type in the final reserve system), as well as a clear statement about the underlying rationale for those choices. Our intent is to show how siting algorithms can contribute to the network design effort once those requirements have been met.

The reserve selection problem

The implicit objective of this reserve design exercise was to minimize the total ``cost'' of the system, in terms of area and boundary length, while ensuring that the conservation goal for each habitat type was achieved. These goals were expressed as a proportion of the overall distribution of each habitat type within the region covered by the data set (Table 4.1). The magnitude of the conservation goals may be based on biological (e.g., the results of a population viability analysis of a target species), or policy information (e.g., a national mandate to protect 20% of the coral reefs in U.S.

Table 4.1. Twenty-percent conservation goals for each of the 23 target habitat types.

Habitat types	Conservation goal (ha)
Bare substrate	
Carbonate mud	29.8
Carbonate sand	11.5
Organic mud	3,300.8
Patch reef	
Aggregated	549.5
Coral or rock patches	1275.9
Halo	19.8
Individual	168.0
Aggregated with halo	104.6
Platform reef margin	
Remnant	2,781.2
Drowned spur and groove	2,051.3
Shallow spur and groove	71.8
Reef rubble	231.4
Back reef	8.8
Hard bottom	
Soft corals, sponges, algae	244.0
<50% seagrass	20,111.5
Continuous seagrass	
Moderate to dense	38,200.0
Dense patches in matrix of small patches (<50%)	671.6
Continuous seagrass (sparse)	422.4
Patchy seagrass	
Moderate to dense with blowouts	22,287.0
Dense patches with hard bottom	3,323.4
Sand/mud with small seagrass patches	4,524.0
Scattered seagrass patches	135.8
Unknown bottom	17,832.8
Unclassified ocean water	0
Inland water	0
Land	0

Note: Goals are based on the total expanse (in hectares) within the study region.

waters), or even on social considerations (e.g., the inclusion of reserve areas for recreation or educational values). The reserve system cost may be the actual cost of the area, or more likely in a marine context, the opportunity cost or management cost incurred when marine reserves are implemented. Additional reserve network objectives beyond the selection of the most efficient, least costly set of sites can be incorporated as mathematical equations in the algorithm.

For example, given the cost-minimization objective and the constraints imposed by the user (in this case, protect 20% of every habitat type), the situation can be formulated as a standard mathematical programming problem (Possingham et al. 2000) as follows.

Minimize the objective function

$$\sum_{i=1}^{M} c_i x_i + \text{BLM}\left[\sum_{i=1}^{M} x_i l_i - \sum_{i=1}^{M} \sum_{k=1}^{M} x_i x_k b_{ik}\right]$$

subject to the following constraints:

$$\sum_{i=1}^{M} a_{ij} x_i > t_j \sum_{i=1}^{M} a_{ij} \qquad \text{for all } j = 1, \ldots., N$$

$$x_i \in \{0, 1\} \qquad \text{for all } i = 1, \ldots, M$$

where x_i are the control variables such that if $x_i = 1$ then site i is selected for the reserve system and if $x_i = 0$ then site i is not in the reserve system; c_i is the ''cost'' of site i, in this paper simply the area of site i; l_i is the perimeter or boundary length of site i; b_{ik} is the common boundary length of sites i and k; and BLM is a Boundary Length

Modifier that converts the reserve system area and its boundary length into a common currency. The constraints ensure an adequate fraction of each habitat type is conserved where a_{ij} is the area of habitat type j in site i, and t_j sets the target fraction for each habitat type (in this paper we assume $t_j = 10$, 20, or 30% for all j, depending on the scenario in question). There are N different habitats spread across M different sites.

Interpreting the mathematical programming problem we note that a feasible solution is one that selects a set of sites (using the control variables x_i) such that all the constraints are satisfied (which means the conservation goals, such as 20% of each habitat type are met by the network scenarios generated). These constraints, one for each habitat type, can be thought of collectively as a biodiversity-conservation constraint or overall conservation goal and can be modified to suit different cases. For example, we may wish to set the level of representation >20% for certain habitat types.

Our objective was to find feasible solutions that minimized the objective function. In this case the objective function was a nonlinear combination of the total area of the reserve system and the boundary length of the reserve system. The boundary length modifier, BLM, determines the relative importance placed on minimizing the boundary length relative to minimizing area. When the BLM is very small then the solution algorithm will concentrate on minimizing area, whereas when the BLM is relatively large then the solution method will put highest priority on minimizing the boundary length of the feasible reserve system.

There are many methods for solving nonlinear integer programming problems such as the one above. However, for large data sets with hundreds or thousands of possible sites and tens of habitat types there are no methods that guarantee finding the optimal solution in a reasonable time. Consequently we chose to use simulated annealing to solve the problem because it can quickly find a variety of good solutions. Previous studies indicate that simulated annealing solutions are almost always superior to those found by heuristic algorithms (Ball 2000).

Reserve selection algorithm

We used the reserve design package SPEXAN (version 3.1; Ball and Possingham, Adelaide University, Adelaide, Australia) to identify potential adequate reserve systems for the Florida Keys problem (Ball and Possingham 1999). By adequate, we mean systems that meet the articulated conservation goals. SPEXAN is an acronym for SPatially EXplicit ANnealing, and the program applies a combination of algorithms for selecting reserves centered around simulated annealing (Kirkpatrick et al. 1983, Csuti et al. 1997), but also allowing heuristic and iterative improvement (Ball and Possingham 1999). The program has been interfaced with a geographical information system (ArcView 3.2, Environmental Systems Research Institute, Redlands, California, USA) project, enabling the user to map the network scenarios generated using different conservation targets.

The information needed to run the software includes a unique identification number for each site, a unique number (and name) for each of the habitat types, and the area of each habitat type j within each site i, a_{ij}. The user then specifies conservation goals, or the total fraction of each habitat in the data set that must be represented in the final set of reserve sites chosen (the t_i in the reserve design problem). A cost function can be used to vary the relative value of sites included in a reserve system, depending on their attributes (e.g., habitat or species type). In this case the cost of each site was simply the area of each site and hence the same for each site (c_i=1 or 100 km^2). In this exercise, our objective was to minimize the total cost of the system in terms of area and total perimeter, while ensuring that at least 10, 20, or 30% of every one of the 23 target habitat types was represented across the entire system. Inland water, land, and unspecified ''water'' habitat types were also delineated in this database, but these types had conservation goals of zero. Thus they were included in the reserve scenarios only due to their proximity to the other habitat types with nonzero goals. Although we sought to represent all conservation target equally in this case (i.e., we tried to include as much soft, muddy bottom as seagrass bed), tools like SPEXAN enable the user to incorporate other, differential conservation goals very easily.

The simulated annealing algorithm generates multiple reserve systems, one during each run. By changing the boundary length modifier (BLM), we varied the relative importance of reserve system perimeter to reserve system area to explore how reserve systems changed with varying degrees of aggregation among the individual planning units (Fig. 4.1). In SPEXAN 3.1, if BLM is set at one, reserve scenarios are heavily weighted towards a high degree of aggregation, as more emphasis is placed on the minimization of the total perimeter rather than the total area of the reserve system. More highly aggregated marine reserve networks are often preferable, particularly for effective management, enforcement, and monitoring of the reserve system (Roberts et al. 2001).

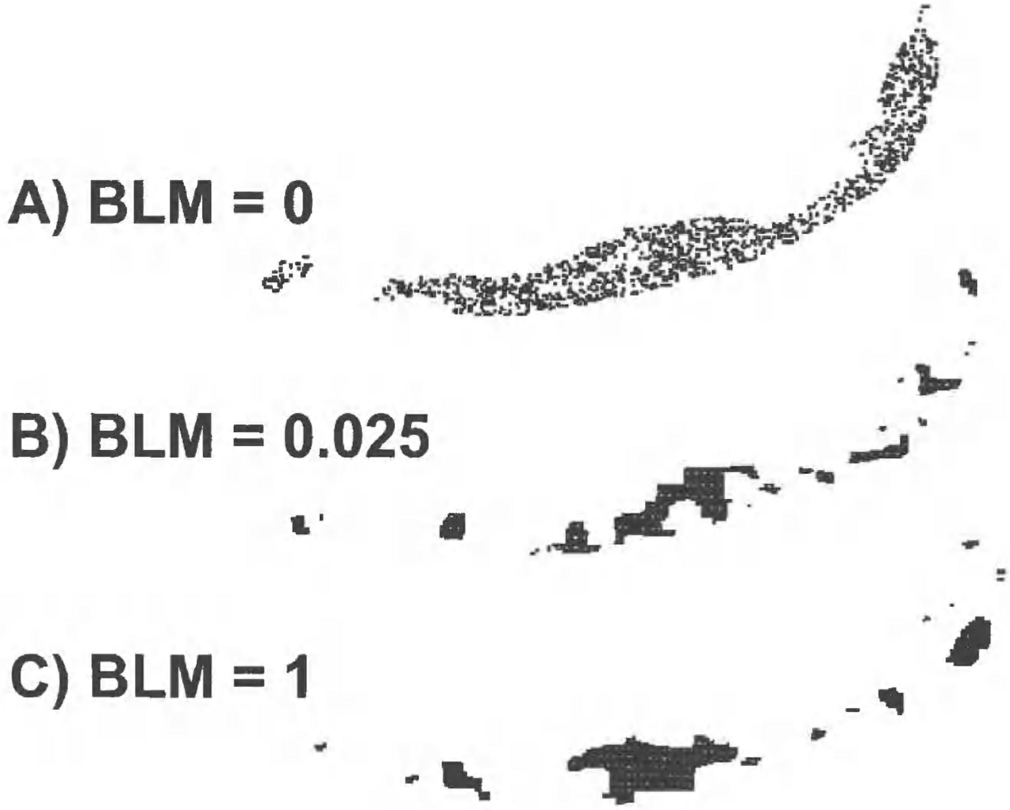


Fig. 4.1. The best reserve network scenarios generated with SPEXAN 3.1 using the 20% conservation goal, 1-km^2 planning units, and 26 habitats. As the boundary length modifier (BLM) increases, placing more weight on minimizing the overall system perimeter rather than the system area, the selected units form more spatially clustered reserves. The scenario where BLM=0.0001 is not shown, as it looks nearly identical to the BLM=0 scenario.

The data set

The 9,500 km^2 of the Florida Keys National Marine Sanctuary (FKNMS) includes the archipelago of the Florida Keys, as well as areas of Florida Bay, the Gulf of Mexico, and the Atlantic Ocean (Fig. 4.2). Based on aerial photographs taken between December 1991 and April 1992, the National Ocean Service (NOS) and the Florida Department of Environmental Protection's (DEP) Florida Marine Research Institute mapped the habitats within the sanctuary, classifying them in four major categories: reefs, seagrasses, hardbottom, and bare substrata (National Ocean Service and the Florida Department of Environmental Protection (NOS/FLDEP) 1999). Twenty-three more specific habitat types also were identified within these groups (e.g., halo patch reefs, dense continuous seagrass), in addition to inland water, land, and unspecified ''water,'' so we included a total of N=26 habitats in the reserve selection problem. The total area of each habitat type within the planning region was used to calculate the conservation goals of 10, 20, and 30% for the first 23 habitats (Table 4.1). The minimum mapping unit was 0.5 ha (0.005 km^2) for all habitat types (NOS/FLDEP 1999). The data are available on CD-ROM in digital format (ArcInfo and shapefile) with full documentation (NOS/FLDEP 1999).

We imposed a selection grid over the mapped habitat data to delineate the spatial location of potential sites to be included in the reserve system (the M sites in the reserve selection problem). The grid consisted of either (1) 10 x 10 km squares or (2) 1 x 1 km squares; we chose these two sizes in order to compare the influence of spatial resolution on the solutions. These 1- or 100- km^2 sites included one or more (up to 26) benthic habitat types. The amount of each habitat, j, in each site, i, was the

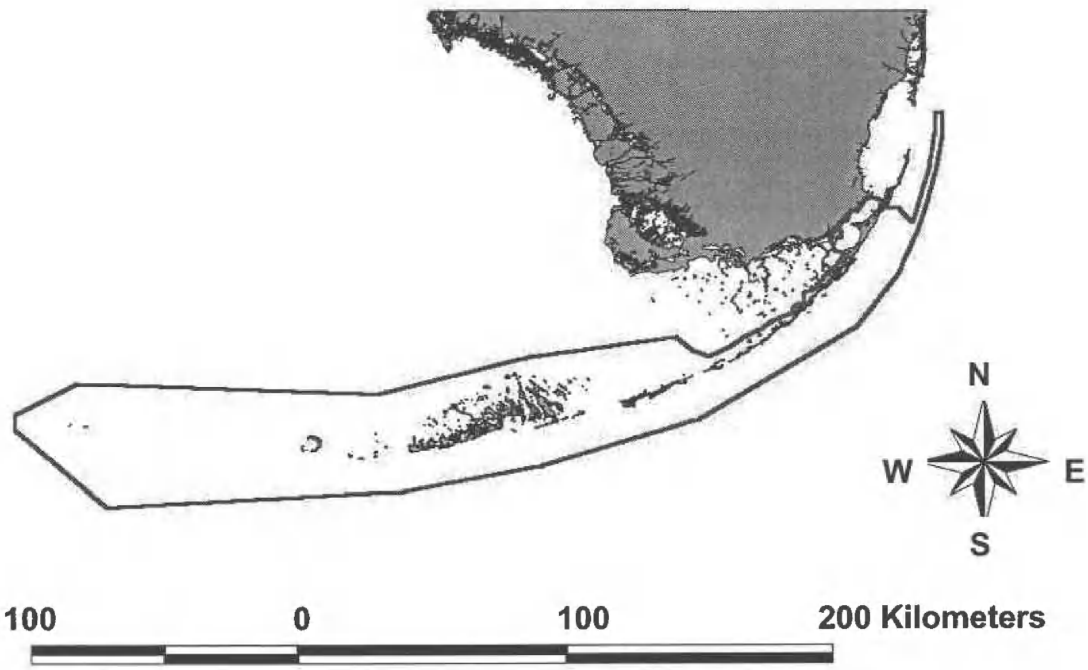


Fig. 4.2. The Florida Keys National Marine Sanctuary (FKNMS) encompasses 9,500 km^2 of coastal and marine habitats in South Florida, USA.

basic data matrix, a_{ij}, input to the reserve selection problem.

Scenarios explored

Clustering of sites included in a system of reserves may be desirable for sociopolitical reasons, such as facilitating enforcement, as well as for biological reasons, depending on the scale of dispersal and disturbance in the system of interest. However there is a trade-off between clustering sites and the total area of the reserve system. We can change the emphasis placed on clustering by modifying the boundary length modifier (BLM) parameter in the objective function of the reserve design problem (and hence the algorithm SPEXAN). We ran 100 iterations of the simulated annealing algorithm using four different values of BLM=0, 0.0001, 0.025, and 1, for the grids of 1- and 100-km^2 planning units. By increasing the BLM to 1, we gave preference to the inclusion of sites that minimized the overall perimeter, thereby clustering the sites in the reserve system. We compared the ''best'' of the 100 runs for each of the boundary length modifiers. The ''best'' scenario had the lowest value of the objective function (a weighted sum of area and boundary length) in the reserve design problem.

We also explored how the fineness of the habitat classification data influenced the reserve scenarios generated. By collapsing the 26 habitat types into six coarser types (seagrass, reef, hard bottom, bare space, unknown habitat, and non-target [i.e., inland water, land, and unspecified ''water'']) we were able to investigate how the detail of habitat classification influenced the reserve systems generated.

We investigated how efficiently SPEXAN represented each habitat type to learn which habitats tended to be significantly over-represented in the 1-km^2 unit, 26-habitat case. We could not evaluate which habitats may be more vulnerable to exclusion from a reserve network with this analysis because the overall aim of SPEXAN is to represent each habitat as efficiently as possible and to still minimize the cost of the overall network scenario. But we can comment on which habitats are likely to be over-represented, given the conservation goals and overall objective of minimizing the network cost. In addition to reporting whether the conservation goal was fulfilled, SPEXAN reports the ''target proportion met'' (p), that is, how closely the reserve network scenario meets the conservation goal for each habitat type. These values theoretically can range between zero and infinity, though ours fell between 1.0 and 6.4. A target proportion value of 1.0 means the habitat type is represented in the reserve system at exactly the desired area, whereas a value of 6.4 means that the habitat type is over-represented in the system by an area 640% larger than the stated goal. We define ''over-representation'' to be a value ≥30% greater than the goal ($p \geq 1.3$). ''Efficiency of representation'' was defined as the number of those habitat types with proportion values close to 1.0 among each of the best runs, for the BLM= 0 or 1, for the three levels of the conservation goals.

We used a subset of the data to compare the performance of the simulated annealing algorithm with the iterative ''greedy'' algorithm, both of which are available in the SPEXAN 3.1 software package (Ball and Possingham 1999). For a subset of the 1-km^2 site problem we carried out an ad hoc irreplaceability analysis (Pressey et al. 1996) where we defined irreplaceability as the number of times a site was included in the reserve system out of 100 SPEXAN runs. This concept is inspired by, but different from, Pressey and colleagues' (1994) notion of irreplaceability (Pressey et al. 1994). We used this analysis to evaluate how different the network scenarios generated by the simulated annealing were from one another, and to investigate which habitats dominated the ''irreplaceable'' sites. This analysis was intended to identify those areas of the planning region that would be hardest to replace in a comprehensive reserve system and consequently those areas of highest priority for inclusion in a system of marine reserves. Planning units with a high irreplaceability value are the first sites that should be targeted for protection.

RESULTS

We varied several parameters of interest—the boundary length modifier (four levels), the planning unit size (1 km^2 or 100 km^2), the number of conservation targets (26 or 6 habitats), and the overall conservation goal— to explore how they influenced the generated reserve network scenarios. Twenty-six habitat types were included and the conservation goal was fixed at 20%, unless otherwise stated.

Influence of spatial clustering and planning-unit size

We used two combinations of parameters to examine the influence of spatial clustering and planning-unit size: (1) 26 habitats and 1-km^2 planning units and (2) 26 habitats and 100-km^2 planning units (Table 4.2, Fig. 4.1). The boundary length modifier (BLM) was set at 0, 0.0001, 0.025, or 1 for each set of 100 SPEXAN runs. For the grid of 1-km^2 planning units with no accounting for the spatial arrangement of

Table 4.2. Reserve system solutions generated by the greedy and simulated annealing (SA) algorithms for 1-km^2 selection units.

Algorithm BLM*	Best area (km^2)	Minimum area (km^2)	Maximum area (km^2)	Best perimeter (km)	Minimum perimeter (km)	Maximum perimeter (km)
Simulated annealing						
0.0000	1228	1228	1249	3953	3899	4110
0.0001	1227	1223	1248	3489	3489	3718
0.0250	1473	1265	1690	720	720	1040
1.0000	1574	1288	2066	526	526	831
Greedy	1182	1182	1184	3428	3376	3506

* *BLM, Boundary length modifer.*

Table 4.3. Reserve system solutions generated by the simulated annealing algorithm for 100-km^2 selection units.

Algorithm BLM*	Best area (km^2)	Minimum area (km^2)	Maximum area (km^2)	Best perimeter (km)	Minimum perimeter (km)	Maximum perimeter (km)
0.0000	1600	1600	2000	592	504	696
0.0001	1800	1700	2300	349	309	481
0.0250	2800	2100	3500	298	298	395
1.0000	2800	2300	3400	298	298	376

* *BLM, Boundary length modifer.*

Notes: The minimum area corresponds to the network scenario with the smallest area, and the maximum area corresponds to the scenario with the largest area, both out of 100 runs. Notation is similar for the perimeter values, also out of 100 runs. Evaluation of the best scenarios (both area and perimeter) was based on the minimization of the reserve network cost, which is a combination of the total area and perimeter. SPEXAN 3.1 was used to generate the solutions. Assumptions were a 20% conservation goal, n=100 runs, and 26 habitat types. The greedy algorithm did not take into account a BLM value, and therefore it is not listed.

the units (BLM=0) the lowest scoring or best reserve system had an area of 1228 km^2. A change in the boundary length modifier from zero to 0.0001 resulted in a 12% drop in the total perimeter (i.e., boundary length) of the best reserve system scenario and a loss of one 1-km^2 planning unit from the area of the reserve system. Further increasing the boundary length modifier, to 0.025 and then to 1, resulted in further decreases of 79% and then 27% in the perimeter and additions of 246 km^2 and 101 km^2 of area to the network scenarios, respectively (Table 4.2, Fig. 4.3). The most highly connected (BLM=1) best scenarios composed of 1-km^2 units had 87% less total perimeter than those scenarios generated without regard to spatial clustering (BLM=0). As inspection of the best reserve scenarios indicates, the increase in the boundary length modifier resulted in a more clustered set of reserves (Fig. 4.1).

For the grid of 100-km^2 planning units and taking no account of reserve perimeter (BLM=0) the lowest scoring or best reserve system had an area of 1600 km^2. Changing the boundary length modifier from zero to 0.0001 resulted in a 41% decrease in the total perimeter and two additional sites. Further increases in the boundary length modifier to 0.025 and then to 1, resulted in a further 14% decrease in the total perimeter of the best reserve systems. When the overall perimeter of the reserve scenario generated with a boundary length modifier of zero was compared to that generated with a boundary length modifier of 1, a 50% perimeter reduction was observed. As with the smaller planning units, an increase in the BLM resulted in a more highly connected network scenario (Table 4.3).

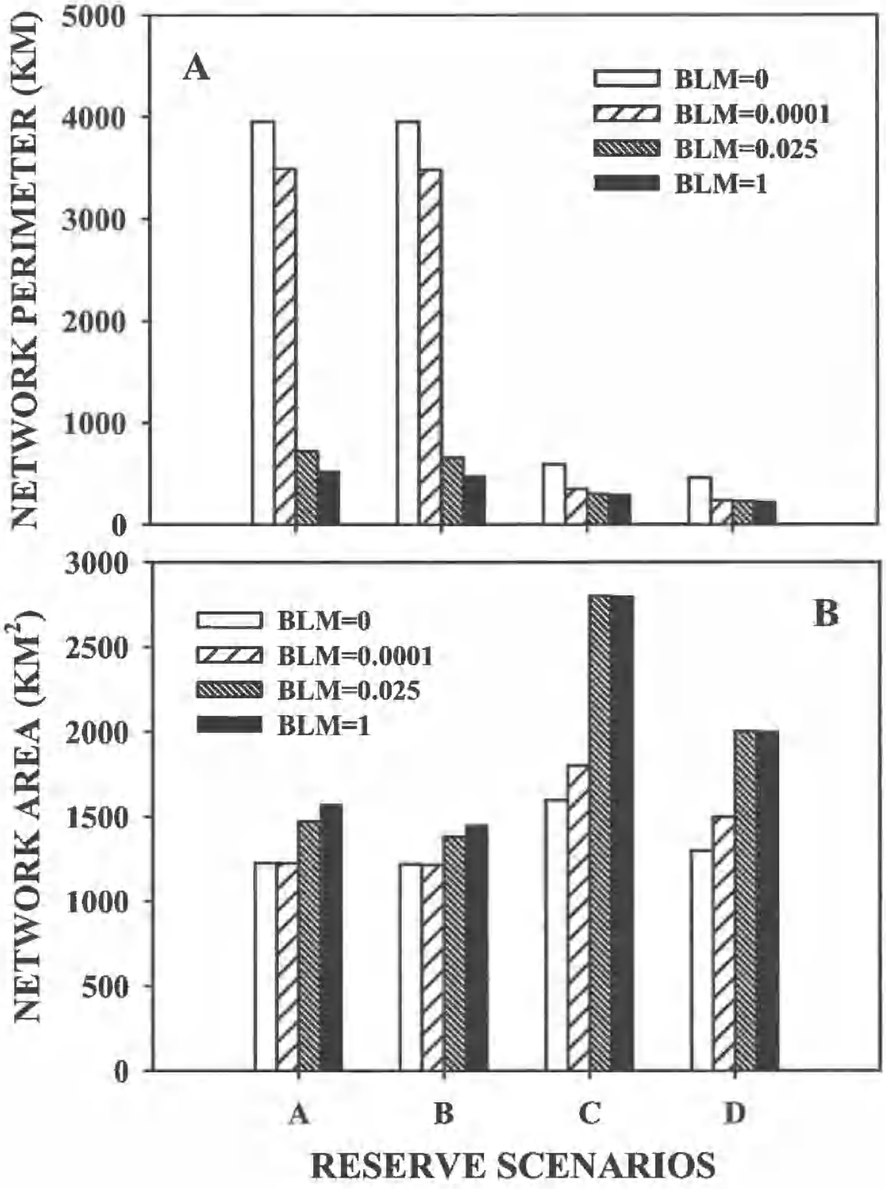


Fig. 4.3. Influence of the fineness of the planning-unit size (1- vs. 100-km^2 planning units) and the degree of habitat classification (26 vs. 6 habitat types) on the (A) total perimeter and (B) total area of the best reserve network scenarios (SPEXAN 3.1, n=100). Key to reserve scenarios: A, 26 habitats and 1-km^2 units; B, 6 habitats and 1-km^2 units; C, 26 habitats and 100-km^2 units; D, 6 habitats and 100-km^2 units. ''Best'' is defined as the lowest cost network, which is a function of the area and perimeter of the system. The conservation goal was fixed at 20%. BLM stands for boundary length modifier.

Influence of the habitat-classification scheme

We used four combinations of parameters to simultaneously examine the influence of the detail of the habitat classification and planning unit size: (A) 26 habitats and 1-km^2 planning units; (B) six habitats and 1- km^2 planning units; (C) 26 habitats and 100-km^2 planning units; and (D) six habitats and 100-km^2 planning units (Fig. 4.3). The BLM was set at 0, 0.0001, 0.025, or 1.

With the 1-km^2 planning units, using six rather than 26 habitat types did not change the total area of the network scenarios generated considerably (Fig. 4.3B). In contrast, with the 100-km^2 units, the two levels of habitat classification did not match up as well; the best scenario run with 26 habitats required 800 km^2 more area than the best scenario generated with six habitats (Fig. 4.3B). This suggests that the scale of the habitat patches themselves were more closely aligned with the scale of the smaller planning unit. We also observed that the total perimeter of the best reserve scenarios depended primarily on the use of 1- vs. 100-km^2 planning units and less on the number of habitat types (Fig. 4.3A). Overall, networks with smaller planning units had larger perimeters, while scenarios with larger units encompassed more area for a given boundary length modifier, BLM. Notably, the best aggregated network scenario (BLM = 1) generated using 100-km^2 planning units and 26 habitats required considerably more area than any other parameter combination to meet the 20% conservation goal.

Influence of conservation goal

Based on the results above, we chosen to focus on the scenarios generated using 26 habitat types and the 1-km^2 planning units. A change in the conservation goal from 20% to 10% or 30% of each habitat type within the reserve network affected the total area and perimeter of the network (Figs. 4.4, 4.5). With an increase in the BLM, and thus much greater aggregation of planning units, the total perimeter of the best scenarios was reduced dramatically in all three cases (Fig. 4.4A). Concurrently, the total network area grew with the increase in the BLM and the overall conservation goal (Figs. 4.4B, 4.5). Although this result is not surprising, the maps of lowest cost scenarios for the three conservation goals provide an instant visual guide as to how much area will be required to meet the different goals (Fig. 4.5). This feature of the tool has proven quite useful in interactive marine conservation planning settings (Airamé et al. 2003).

Efficiency of habitat representation

The conservation goals were met in all simulated annealing runs, for all parameter combinations. We investigated how efficiently SPEXAN represented each habitat type to learn which habitats tended to be significantly over-represented in the 1-km^2 unit, 26-habitat case. ''Efficiency of representation'' was defined as the number of those habitat types with proportion values close to 1.0, among each of the best runs, for BLM=0 or 1, for the three conservation goals. The efficiency of representation did not change dramatically among the three conservation goals (Fig. 4.6). The number of over-represented habitats (where $p \geq 1.3$) decreased as the conservation goal increased:

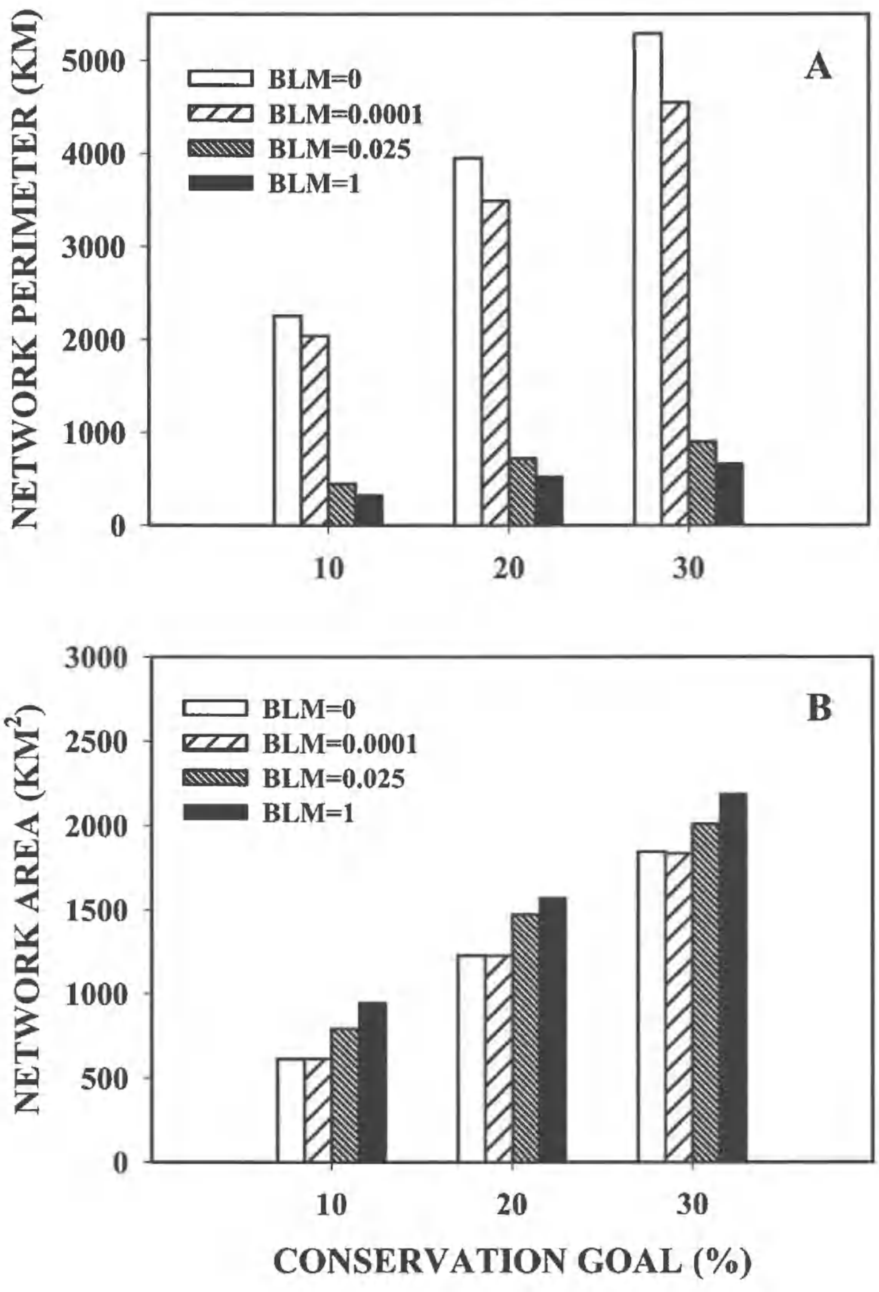


Fig. 4.4. Influence of the conservation goal (10%, 20%, or 30%) on (A) total perimeter and (B) total area of the best reserve network scenarios. ''Best'' is defined as the lowest-cost network, which is a function of the area and perimeter of the system (SPEXAN 3.1, n=100, 26 habitat types, 1-km^2 planning units, boundary length modifier [BLM] = 1).

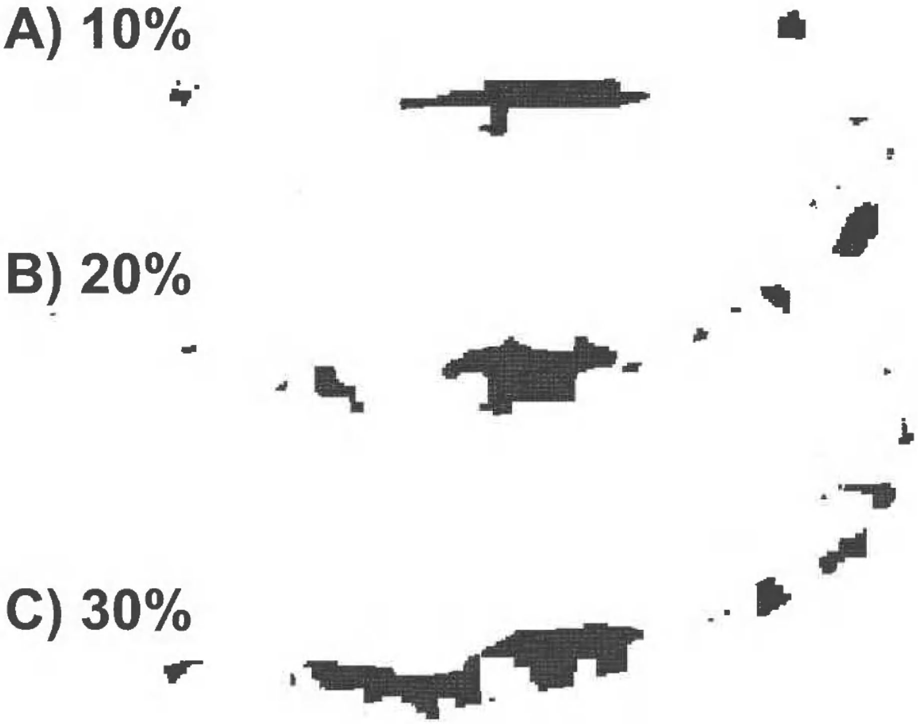
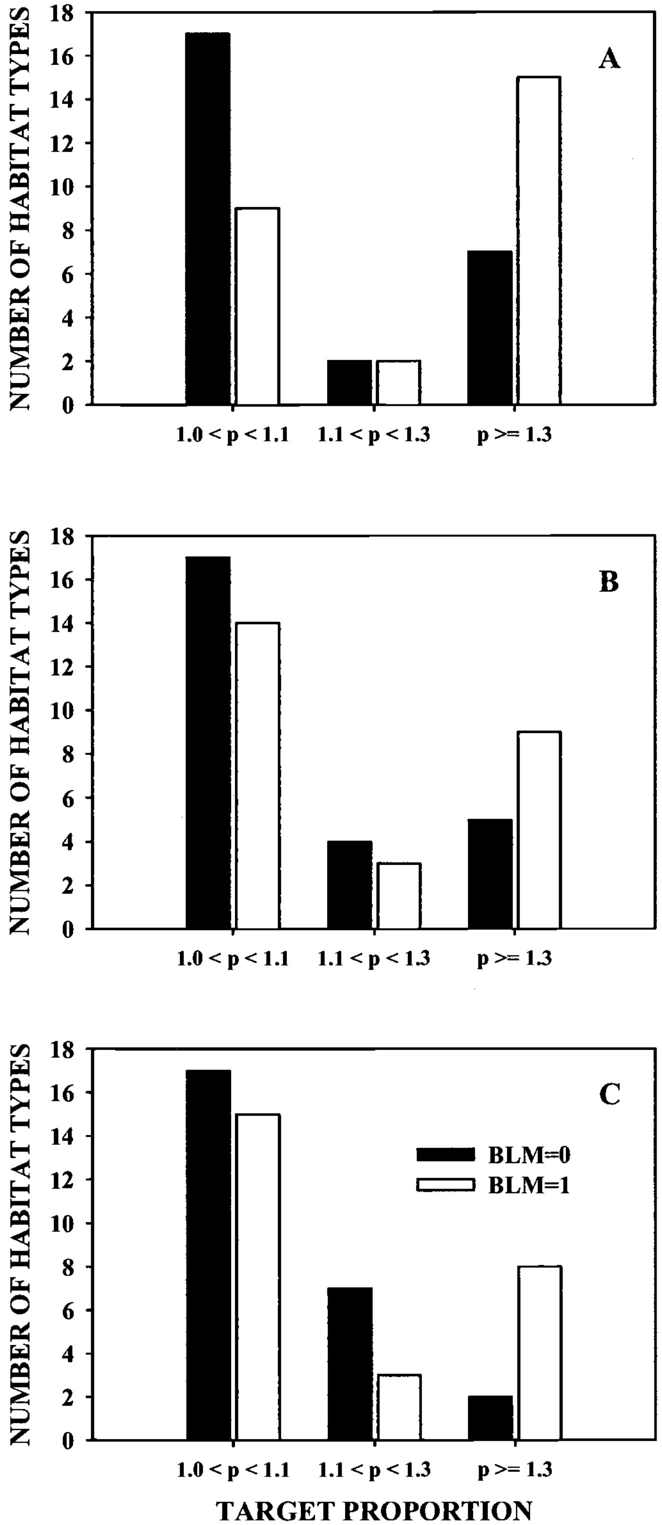


Fig. 4.5. The best reserve network scenarios generated to meet the 10%, 20%, and 30% conservation goals (SPEXAN 3.1, n=100, 26 habitat types, 1-km^2 planning units, boundary length modifer=1).

Fig. 4.6. The efficiency of representation of the conservation targets (i.e., habitats) for the conservation goals of (A) 10%, (B) 20%, and (C) 30% (SPEXAN 3.1, n=100, 26 habitat types, 1-km^2 planning units, BLM=0 or 1). Efficiency of representation was defined as the number of those habitat types with proportion values (*p*) close or equal to 1.0, indicating that the network scenario meets the conservation goal for the habitat. Over-representation was defined as a value ≥30% greater than the goal ($p \geq 1.3$). BLM stands for boundary length modifier.


NUMBER OF HABITAT TYPES
0
2
4
6
8
10
12
14
16
18
A
1.0 < p < 1.1
1.1 < p < 1.3
p >= 1.3
NUMBER OF HABITAT TYPES
0
2
4
6
8
10
12
14
16
18
B
1.0 < p < 1.1
1.1 < p < 1.3
p >= 1.3
NUMBER OF HABITAT TYPES
0
2
4
6
8
10
12
14
16
18
C
BLM=0
BLM=1
1.0 < p < 1.1
1.1 < p < 1.3
p >= 1.3
TARGET PROPORTION

this may have been an artifact of the data or a real trend worthy of further inquiry. There were fewer over-represented habitats present in the best scenarios created using a BLM of zero, compared those generated with a BLM of one. In the most extreme case, for the 10% goal, the best reserve system scenario encompassed 15 over-represented habitats, including various types of seagrass beds, coral reef, hard bottom and bare substrata, as well as the ''unknown'' type.

Performance of the greedy vs. simulated annealing algorithm

When the reserve scenarios generated by the simulated annealing algorithm (BLM=1) were compared to those from an iterative ''greedy'' algorithm (also included in the SPEXAN program), interesting results emerged. Based on the data set with 26 habitat types and 1-km^2 planning units, with the conservation goal of 20% in reserve, the iterative algorithm produced a lower cost solution than the simulated annealing, with 392 km^2 less area (Table 4.2). But the total perimeter of the reserve system generated by the greedy algorithm was 3,428 km, while the simulated annealing's system perimeter was 85% shorter, at 526 km. This difference is reflected in the maps of the best ''greedy'' and simulated annealing solutions (Fig. 4.7), where one can see how the planning units generated through the iterative process are much more dispersed. Notably, not all conservation goals were met in all runs of the greedy algorithm. For four of the 100 runs, one conservation target (i.e., habitat type) was not adequately represented. The simulating annealing took approximately four hours to process the 11,000 line data set (n=100 runs), while a single run of the greedy algorithm required two hours.

Fig. 4.7. The greedy iterative algorithm (A) creates a best (lowest cost) reserve scenario with less area but more total perimeter than that created by the simulated annealing algorithm (B). Data mapped in ArcView 3.2 using output from SPEXAN 3.1 (20% conservation goal, n=100, 26 habitat types, 1-km^2 planning units, boundary length modifier=1).

Irreplaceability analysis

We ran an ad hoc irreplaceability analysis on the network scenarios generated by simulated annealing using 26 habitat types and a BLM of one. We examined the results from both the 1- and 100-km^2 planning-unit grids, recording how many times each site was chosen during the 100 runs. For the 1-km^2 planning-unit case, which included 11,893 sites with habitat information, very few planning units were chosen >50% of the time to meet the 10, 20, or 30% conservation goals (Fig. 4.8). For the 20% goal specifically, 22 units were chosen ≥50% of the time, although no one site was chosen >59% of the time. This result indicates that no planning unit is absolutely irreplaceable in this case. Nonetheless, a small number of sites were consistently represented in the reserve network scenarios, indicating sites for priority protection. More than 2,000 planning units were never chosen during the 100 runs either because the target habitats were not represented or the data were not available. In the planning units chosen ≥50% of the time, the following habitats represented ≥30% of at least one planning unit: dense continuous seagrass beds, bare substrate (carbonate sand), patchy or sparse seagrass beds, and land.

For the 100-km^2 planning-unit case when the conservation goal was 20%, we had 164 sites with habitat data. Twenty-four planning units were chosen during the majority of the runs, and of these, five were chosen during every one of the 100 runs (Fig. 4.9). This result makes sense given that because there are so few planning units in the 100-km^2 case, there is less flexibility in selecting particular units. Even as the magnitude of the conservation goals and the scale of the planning units change

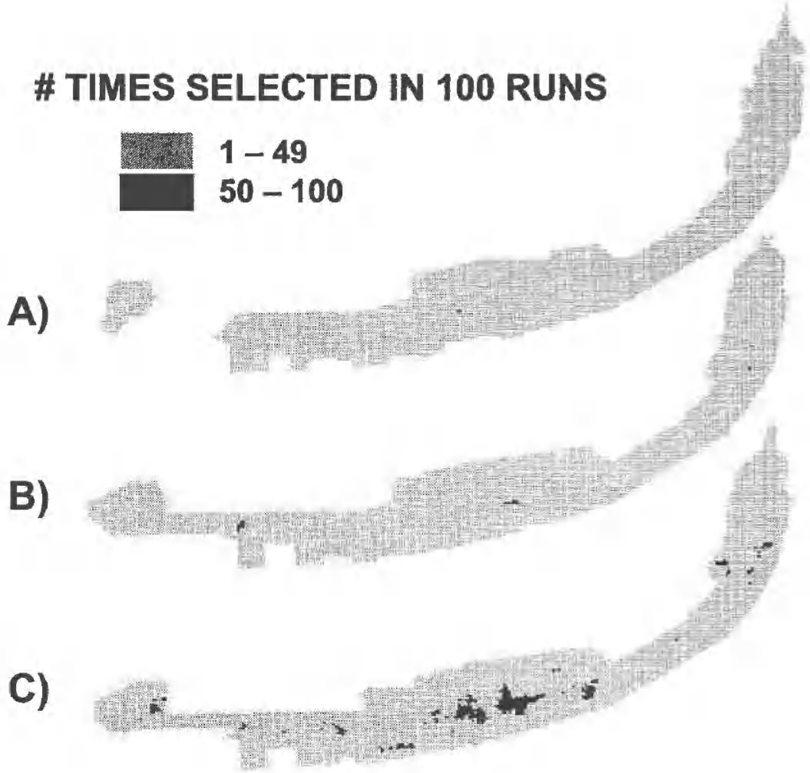


Fig. 4.8. Irreplaceability analyses of the (A) 10%, (B) 20%, and (C) 30% conservation goal. The number of 1-km^2 planning units displayed in the majority of runs increased with the level of the conservation goal. The figure was mapped in ArcView 3.2 using output from SPEXAN 3.1 (n=100, 26 habitat types, 1-km^2 planning units, boundary length modifer=1).

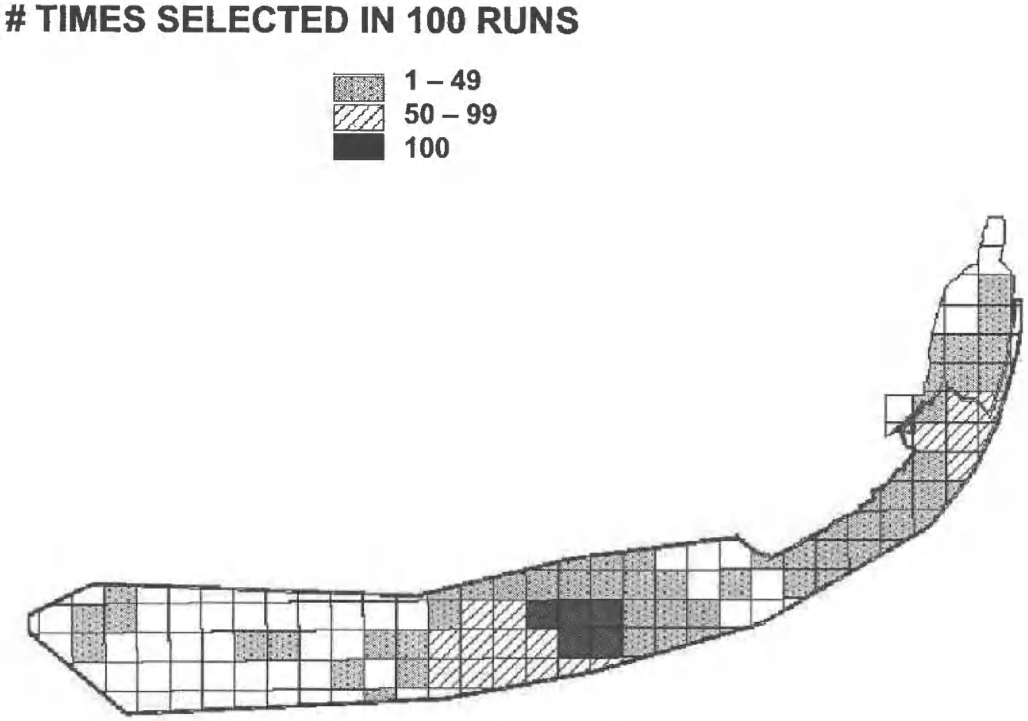


Fig. 4.9. Irreplaceability analysis of the reserve-network scenarios based on the 100-km^2 planning units with a 20% conservation goal. The figure was mapped in ArcView 3.2 using output from SPEXAN 3.1 (n 5 100, 26 habitat types, boundary length modifier=1).

(Figs. 4.8, 4.9), the same central area within the study region is consistently selected. This suggests a focal area for conservation and management activities.

We did a similar analysis on the results of the ‘‘greedy’’ algorithm for the scenarios generated using 26 habitat types, 1-km^2 planning units, and a conservation goal of 20%. Of the 11,893 possible sites within the region, 1,045 planning units were chosen ≥50% of the time, including 651 that were chosen during every one of the runs. The vast majority, 9,000 sites, was never chosen during the 100 runs. We found that the ‘‘greedy’’ algorithm produced many fewer different solutions in comparison to the simulated annealing scenarios, indicating that the iterative method did not effectively identify irreplaceable sites.

DISCUSSION

This paper reports on one of the first and few applications of reserve siting algorithms to marine systems to date (see also Beck and Odaya 2001, Sala et al. 2002, Airamé et al. 2003). Using simulated annealing we were able to incorporate spatial information into the reserve network selection process, and explore how several key parameters—planning unit size, the detail of habitat classification, and the overall conservation goals—can influence the network scenarios generated. We found that simulated annealing produces many adequate reserve systems that meet the conservation goals and fulfill the overall objective of minimizing the system area and perimeter.

Comprehensive habitat representation can be achieved with systems that have varying degrees of spatial clustering. Network scenarios of scattered, largely disconnected reserves adequately represent the habitats (Fig. 4.1), but they require considerably more perimeter than more connected networks. More compact reserve systems tend to have considerably less perimeter and larger overall areas in reserve. More compact reserve systems may be preferable for both ecological and sociopolitical reasons, as they can facilitate movement of organisms and biological materials, as well as enforcement and management of reserves (see Roberts et al. 2001, Roberts et al. 2003b).

Identifying ''irreplaceable'' sites within the study area is a very useful output of siting algorithms such as this, no matter what the objectives of the planning exercise. Such an analysis offers an effective way to glean valuable information about priority areas, while acknowledging the uncertainty inherent in the delineation of targets, model assumptions, and other parameters. In this case, very few 1-km^2 planning units were found to be absolutely irreplaceable (Fig. 4.8). That is, many different combinations of sites produced networks that met the conservation goals. The apparent lack of ''irreplaceability'' of any one site is encouraging in that it suggests there are many ways to create a reserve network that will meet the incorporated goals. Nonetheless, the analysis also highlighted those sites that were consistently included in the network scenarios: 22 sites of the 11,893 possible planning units in the region were included in the reserve scenarios during the majority of the runs. An analysis like this can be used to prioritize marine conservation planning and implementation activities across a broad region, indicating which areas within the region consistently contribute to meeting the conservation goals.

These results illustrate the value of considering multiple iterations of the conservation goals in the initial stages of planning a network of marine reserves, so that stakeholders gain a visual sense of how different goals affect potential network designs and implementation strategies. In this case, we examined the reserve networks that were generated using 10, 20, and 30% conservation goals. Both the total area and perimeter in reserve scaled linearly with the increases in the goal (i.e., the magnitude of habitat area to be protected). In contrast, efficiency of habitat representation did not. The 10% goal was the least efficient (Fig. 4.6). The networks that included 30% of each target habitat were more efficient than the 10% or 20% scenarios, as they encompassed the areas truly needed to fulfill the conservation goals. These findings make a strong case for designing aggregated networks of marine reserves since these networks meet conservation goals more efficiently and require less enforceable perimeter. The data also suggest that higher conservation goals may yield greater returns.

The results reported here suggest several general recommendations for interactive reserve design with siting algorithms like SPEXAN. First, build in time during the reserve design process for data compilation. Data compilation and management are among the most time-consuming and resource-intensive steps of designing a marine reserve network. If the decision is made to pursue a systematic approach to siting a network of marine reserves, reserve planners and stakeholders should expect to invest considerable time and money into gathering and analyzing the data needed to make informed decisions.

Second, make articulation and refinement of reserve network objectives an explicit part of the design process. While data are compiled, the design team can refine the network objectives as well as consider alternative combinations of them, including protecting species of concern, preserving habitat linkages, maximizing public access, or enhancing fisheries. These network objectives can then be translated into appropriate conservation targets (species, habitats, etc.) and goals (or levels of protection or representation within the network)—which then can be incorporated into the algorithm. Mapping out the selection process and how scientific and socioeconomic data, expert opinions, and public input will be brought together is a step that can create a sense of common purpose among the stakeholders, regardless of their specific aims for the reserve network.

Third, use SPEXAN's multiple solutions as a starting point for network design. The strength of the simulated annealing algorithm is that it offers a variety of scenarios that meet the incorporated goals. With more options, stakeholders have a greater chance of creating an ecologically and socially sustainable system of marine reserves. Simulated annealing offers users a fast, interactive approach to summarizing information contained in large data sets. Its mapping capabilities enable stakeholders to gain a tangible sense of how the conservation goals translate into specific recommendations for marine reserve networks and how changing the goals can influence the possible network scenarios. Additionally, siting algorithms force clear articulation of the network objectives, which may further the siting process just as much as the generation of alternative network scenarios.

Finally, it is important to remember that simulated annealing is one of many tools that can be used in the design of marine reserve networks. In most cases, the reserve network design process will be an iterative one (e.g., Airame′ et al. 2003). A team will generate reserve scenarios that meet the initially articulated goals, the results will be presented to a larger group of stakeholders for comment, and then the team will use the algorithm and other siting tools, like expert opinion workshops, again to refine the goals and generate further network scenarios. In this case we focused on habitat representation in formulating our goals, but many other types of goals can be incorporated into the algorithm, such as representation of a certain number of occurrences of a species of concern, or inclusion of particular sites already in protected status. Data on species of special concern, recreational and fishing pressure, and land-based activities also could be incorporated into the algorithm. Some types of information are less easily incorporated into the algorithm, though they may be quite relevant. For example, anecdotal or non-quantitative data about fish spawning areas or the trajectory of development in abutting coastal counties may well inform placement of reserves, but may not be as easily incorporated into the algorithmic stage of the selection process. This information can be used after scenarios have been created to refine and create a reserve network that meets the overall network objectives. Regardless of what types of constraints (or goals) are incorporated in the siting process, SPEXAN and other siting algorithms are most effective when used in tandem with other types of decision support tools, including expert workshops, geographic information systems and other mapping tools.

In terms of further avenues for research, these results suggest that the simulated annealing algorithm is a promising and powerful tool for marine reserve network design. Its ability to generate multiple biologically suitable scenarios is an exciting result that should be tested in other ecological systems and with other types of conservation targets. We are particularly interested in exploring how currents and other oceanographic features that connect marine populations and ecosystems can be incorporated into systematic siting tools, and in exploring how the spatial and temporal variability in these phenomena affect the network scenarios generated. Such information could be included by formulating an additional constraint within the algorithm, such as a score related to coastal upwelling intensity or the presence of retention zones. As the biological information on connectivity among marine populations and habitats evolves (Swearer et al. 1999, Cowen et al. 2000), our ability to design connected marine reserve networks will improve.

In addition, this tool offers a powerful means of integrating the natural (e.g., biological and oceanographic) and social (e.g., economic, sociological, and anthropological) science information needed to implement effective marine reserve networks, as well as to other types of marine conservation planning efforts. As this paper went to press, several efforts in North America are moving in that direction (information on algorithm applications is available at the MARXAN website (http://www.ecology.uq.edu.au/marxan.htm). One potential obstacle is the availability of data. Biological data are often difficult to obtain for marine ecosystems, particularly those far from shore. Gathering economic data presents other challenges; in many cases the relevant information are confidential or proprietary. Efforts to facilitate data exchange and compilation will be critical to systematic conservation planning, whether algorithms or other types of tools are employed.

Marine protected areas like the Florida Keys National Marine Sanctuary (FKNMS) offer a unique opportunity to test reserve design theory and implementation ideas. Fully protected marine reserves were a key part of South Florida's coastal zone management program long before the Sanctuary's establishment in 1990. In 1997, 23 fully protected marine reserves were established within the FKNMS with the primary objectives of biodiversity protection and sustainable marine resource management (http://www.fknms.nos.noaa.gov/). In 2001, the 517 km^2 Tortugas Ecological Reserve was established in the westernmost part of the FKNMS, increasing the fully protected area Sanctuary-wide tenfold. The Tortugas 2000 process, as it was known, was led by a working group of stakeholders who analyzed the relevant economic, ecological and social information over a two-year period. To our knowledge, siting algorithms were not employed. Interestingly, however, the results of the analysis presented here resonated strongly with several Florida fisheries biologists and marine managers with whom we shared our work.

ACKNOWLEDGEMENTS

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Chapter 5:

A Synthesis of Marine Conservation Planning Approaches

Heather Leslie

Conservation Biology (in review)

Society for Conservation Biology, Arlington, VA

ABSTRACT

Knowledge of biogeophysical, social and institutional differences between terrestrial and marine systems suggest an explicit evaluation of marine conservation planning approaches is needed. Here I report on the prototype of a database that synthesizes marine conservation planning approaches from around the world. Data were collected on the political and geographic scope of each case, the objectives and context, stakeholder involvement, and the criteria and tools used to make decisions. The majority of the 27 documented cases occurred in North and Central America, were regional in nature, and were based primarily on biogeographic boundaries. Biodiversity conservation was the primary objective. Outcomes included priority-setting plans and implementation of marine reserves and other marine protected areas. The data suggested governments and local non-governmental organizations led more participatory processes than national and international non-governmental organizations. Twenty-five cases included both fine scale (species) and coarse scale targets (ecosystems, habitats). Eleven cases considered biogeophysical criteria first, whereas 16 relied on integrated criteria (biogeophysical plus socioeconomic data and other pragmatic considerations) to select priority areas for conservation and management action. Key tools for data integration and synthesis included expert workshops, maps, and siting algorithms. My results suggest that planners consider knowledge of marine population and ecosystem dynamics to be important when identifying priority areas, but do not necessarily have clear guidelines for how to integrate this information effectively. One of the most striking findings was the paucity of well-documented cases. Our ability to develop effective models for marine

conservation planning and to assess the success of various approaches would be significantly strengthened by documentation of more cases that are: 1) Outside of North and Central America, 2) Led by local organizations, or 3) Motivated by objectives other than biodiversity conservation.

INTRODUCTION

Governments and non-governmental organizations have engaged in systematic conservation planning for decades, yet there are few comparative analyses of the approaches taken on land or in the sea (Johnson 1995, Sloan 2002, Beck 2003, Redford et al. 2003). According to Margules and Pressey (2000), systematic approaches are more effective than opportunistic or ad hoc approaches because of the former's efficient use of limited resources, flexibility in response to competing resource uses, and accountability. Systematic conservation planning is based on clear objectives, with specific conservation targets (e.g. species, ecosystems) and an explicit and transparent decision-making framework (Margules and Pressey 2000). While the primary objective under consideration is often biodiversity conservation (Noss 1996, Groves 2003, Redford et al. 2003), other objectives include sustaining ecosystem goods and service, preserving cultural and spiritual values, and providing places for research and education (Daily et al. 2000, National Research Council 2001).

Redford and colleagues (2003) described some of the major approaches that people have used to advance biodiversity conservation in terrestrial environments. They include the 'hotspot' analyses of Myers and his colleagues (Myers et al. 2000), based on the distribution of vertebrate and vascular plant species richness throughout the world, and World Wildlife Fund's prioritization of the 200 most vulnerable ecoregions across the globe (Olson and Dinerstein 2002). Based on their review of 21 approaches implemented by 13 institutions (primarily conservation non-governmental organizations and federal governments), Redford and colleagues concluded that further collaboration among conservation practioners is urgently needed, in order to build consensus on what conservation targets, actions, and measurable results will further global conservation. Jennings (2000) issued a similar call for increased sharing of information and organizational resources among institutions, based on his survey of the US National Gap Analysis Program. Yet few comprehensive sources of information exist to facilitate such partnerships.

Marine conservation planning activites have received less attention than those in the terrestrial realm. By 'marine conservation planning,' I am referring to spatially explicit, systematically planned coastal and ocean conservation and management. These efforts have benefited greatly from the more developed science and practice of terrestrial conservation planning (Beck 2003). Nonetheless, knowledge of the biogeophysical differences among terrestrial and marine systems (Beck 2003, Carr et al. 2003) and of differences in tenure, resource management, and governance structures (Pew Oceans Commission 2003), suggest an explicit synthesis and evaluation of marine conservation planning approaches is needed.

Knowledge of how ecosystems and social systems work is essential to the design and implementation of effective resource management and conservation (Lubchenco et al. 1991, Scheffer et al. 2000). Numerous examples of the natural and social sciences' contributions to marine conservation and management exist, including design and implementation of marine protected areas (Kelleher 1999, National Research Council 2001), fisheries management (National Research Council 1999) , and water quality restoration (National Research Council 2000). Analysis of the natural and social sciences' contributions to marine conservation planning would contribute data about what types of information and conceptual frameworks could be most useful for implementation and evaluation. As an ecologist, I am most able to evaluate the roles of natural science, and so that is the focus here. Social sciences' contributions (e.g. analysis of organizational structures, drivers of collective action, tenure and governance arrangements, and valuation of ecosystem services) are no less crucial, and remain a vital area of research (Daily et al. 2000, Scheffer et al. 2000, Ascher 2001).

Here I report on the prototype of a database designed to facilitate the documentation and synthesis of marine conservation planning approaches from around the world, and describe preliminary trends that emerge from the cases within the database thus far. The guiding questions included: Where have marine conservation planning cases been well documented? What was the geographic extent of these cases, and who participated? What contributions did natural science make?

METHODS

I developed the structure of the marine conservation planning database, and then populated it with as many cases as I could find based on the following criteria:

1. The case described a conservation planning process with explicit spatial boundaries.
2. The case included, but was not necessarily restricted to, coastal and marine areas.
3. The case focused on specific targets of conservation action, e.g. vulnerable species or ecosystems.
4. The case involved more than one group of stakeholders, and was led by an identifiable institution.
5. The case was either completed or sufficiently developed that it was likely to result in specific, real-world marine conservation and management activities.
6. Information documenting the case, and particularly the planning process by which conservation decisions were made, was available (e.g. through peer-reviewed literature, published reports, or websites).

In each case, data were collected on the political and geographic scope, the objectives and context, stakeholder involvement, and the criteria and tools used to make decisions (Table 5.1). In terms of political scope, each process was scored as local, regional, national or global. Local processes were limited to one community (e.g. a fishing cooperative or local government). Regional processes transcended the political boundaries of states, provinces or nations. National processes were delineated by national political boundaries, and global processes encompassed all of the world's oceans. The primary objective of each case was noted, along with the lead institution, the types and number of stakeholder groups involved, and the length of the

Table 5.1. Primary data types in the marine conservation planning database

1) Location
2) Sources of information & contacts
3) Primary objective(s)
4) Primary outcome
5) Lead institution
6) Political scope (local, regional, national or international)
7) Geographic scope (size of the overall planning region, planning units, and priority areas)
8) Stakeholder groups involved
9) Criteria used to select priority areas
10) Primary conservation targets
11) Scientific tools used

planning process. When possible, information was collected on the spatial extent of the region of interest (i.e. planning region) and of the smaller areas within the region (i.e. planning units), including those where conservation activities were focused (i.e. priority areas).

The cases also were classified as focused on one of three primary outcomes: marine reserve implementation, implementation of other types of marine protected areas, or priority-setting plans. While these outcomes are not mutually exclusive, in each case a primary outcome was apparent. For the purposes of this analysis, marine reserves are areas of the ocean completely protected from all extractive or destructive activities, except as necessary for monitoring or research to evaluate reserve effectiveness (National Research Council 2001, Lubchenco et al. 2003). Marine protected areas (MPAs) include reserves and other area-based management schemes designated to enhance conservation of marine resources (National Research Council 2001, Lubchenco et al. 2003). The actual level of protection of living marine resources within MPAs varied considerably. Priority-setting plans were cases where the primary outcome was a portfolio of priority areas used to direct conservation and management activities, such as MPA implementation or environmental education. The term ‘priority-setting plan’ encompasses what Groves (2003) refers to as a ‘biodiversity conservation plan’ and Beck (2003) calls a ‘marine regional plan’. I use the former term because not all priority-setting plans in the marine environment are focused primarily on biodiversity conservation (see Appendix C [online] for examples: Bahamas and Fiordland cases).

Preliminary examination of the cases suggested three major roles for natural science:

1. To inform scientific knowledge and selection of conservation targets,
2. To provide guidance on the choice of biogeophysical criteria used to select priority areas, and
3. To develop and apply scientific tools for information synthesis and selection of priority areas, reserves, and other types of marine protected areas.

Data were collected on each of these roles. Conservation targets include species and ecosystems, physical features or a combination of biotic and abiotic elements (Groves et al. 2002). In many cases, marine habitats serve as biodiversity surrogates and are assumed to incorporate other targets, such as species (Beck 2003). Most conservation planning processes, particularly those focused on reserve or MPA implementation, use criteria to identify priority areas. Criteria may be biogeophysical, socioeconomic, or a combination of the two (Johnson 1995). To evaluate the roles of natural science, I scored the biological criteria used in each case based on criteria detailed by Roberts and colleagues (2003a). Criteria were scored as 'included' if they were mentioned in the documentation or interviews.

Scientists also may design and apply tools for data synthesis and priority area selection as part of conservation planning efforts. Such tools can help ensure a transparent and defensible process, and make the most efficient use of available resources (Margules and Pressey 2000). I noted the use of three main tools: expert workshops, maps, and computer-based siting tools. Expert (or Delphi) workshops bring together people knowledgeable about the biogeophysical, and sometimes socioeconomic, aspects of the identified study region (Groves 2003). Maps included analog, digital, and geographic information system (GIS) sources. Computer-based siting tools included the heuristic and simulated annealing (e.g. SPEXAN, Sites, and MARXAN) algorithms used to generate networks of protected or priority areas (see Chap. 4, Possingham et al. 2000).

Some caution is warranted in interpreting these data. In some cases the primary objective and other key variables had to be inferred, as they were not explicitly reported. The iterative nature of planning processes may complicate interpretation of the stakeholder groups involved and the criteria and tools used. Finally, the database is limited to cases that were well documented. To be included in the database, information for at least 60% of the cells in the database had to be available from written materials. As a starting point, information resources were restricted to English-language publications (see Table 5.3 for key references). In all cases, follow-up interviews with participating individuals were conducted to verify the data collected from the written documents and to fill in missing information.

To my knowledge, this is the first effort to synthesize information on marine conservation planning cases from around the world in this level of detail. I hope this database will serve as a prototype of what could be a very useful resource for future implementation and assessment. The full database (Appendix C) can be downloaded as a Microsoft Excel file at http://david.science.oregonstate.edu/~leslieh/Marine_Planning/. I encourage additions and changes.

RESULTS

Characteristics of the documented marine conservation planning cases

The majority of the 27 documented cases were in North and Central America (Fig. 5.1, Table 5.2). Thirteen were within the US Exclusive Economic Zone (0-200 nautical miles offshore). Eighteen cases had 'regional' planning regions, meaning they transcended political boundaries and were based primarily on biogeographic boundaries. Three cases were global in focus (Fig. 5.2A). The geographic scale of the planning regions ranged from 2,400 to 3.6 x 10^8 km^2, with an average region size of 3.1 x 10^7 km^2 and a median size of 1.4 x 10^6 km^2 (n=25 cases, Table 5.2).

Biodiversity conservation was the primary objective in 20 cases (Fig. 5.2A, Table 5.2). Creation of areas for scientific research was the lead objective in two cases, and sustainable fisheries in five cases (Fig. 5.2A). Two cases had dual primary aims of biodiversity conservation and sustainable fisheries: in the Channel Islands, USA (Airamé et al. 2003) and Fiordland, New Zealand (Teirney 2002).

Planners selected priority or protected areas in each case based either on a standardized set of planning units (e.g. 2.5 km^2 hexagons or 1 degree grid squares) or based on a set of differently sized units delineated by environmental or political factors (Appendix C). Of those cases for which planning unit size was available, two-thirds included units of variable sizes. The mean size of individual planning units ranged from 0.3 to 1.1 x 10^6 km^2, with an average of 67,000 km^2 and a median of 740 km^2 (n=22 cases). As planning regions increased in area, mean individual priority

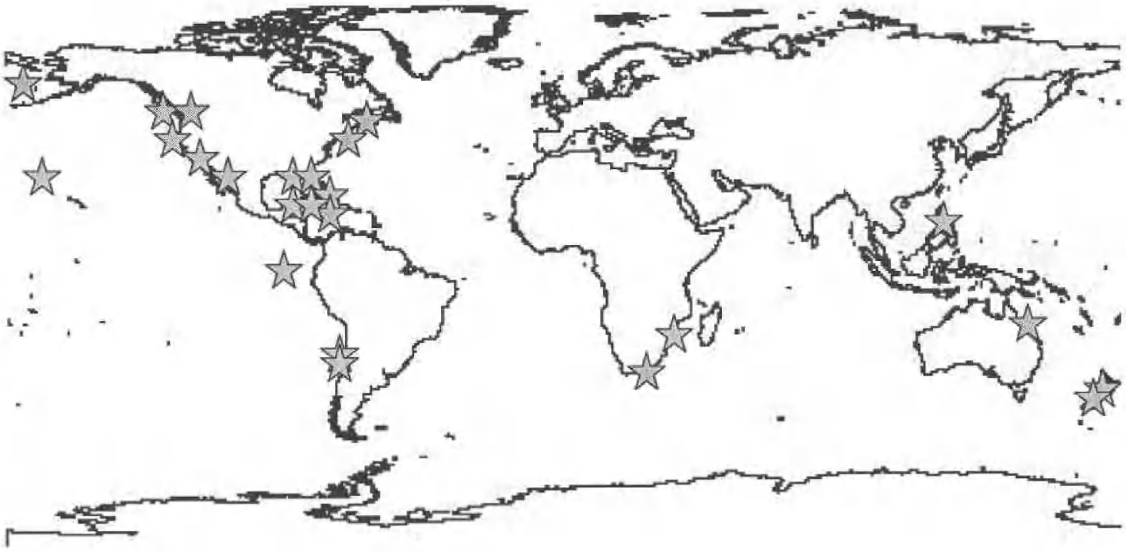

Fig. 5.1. Grey stars denote documented marine conservation planning cases included in the database. The map was created with the Internet Map Server of the Large Marine Ecosystems of the World program (http://www.edc.uri.edu/lme/ims-intro.htm).

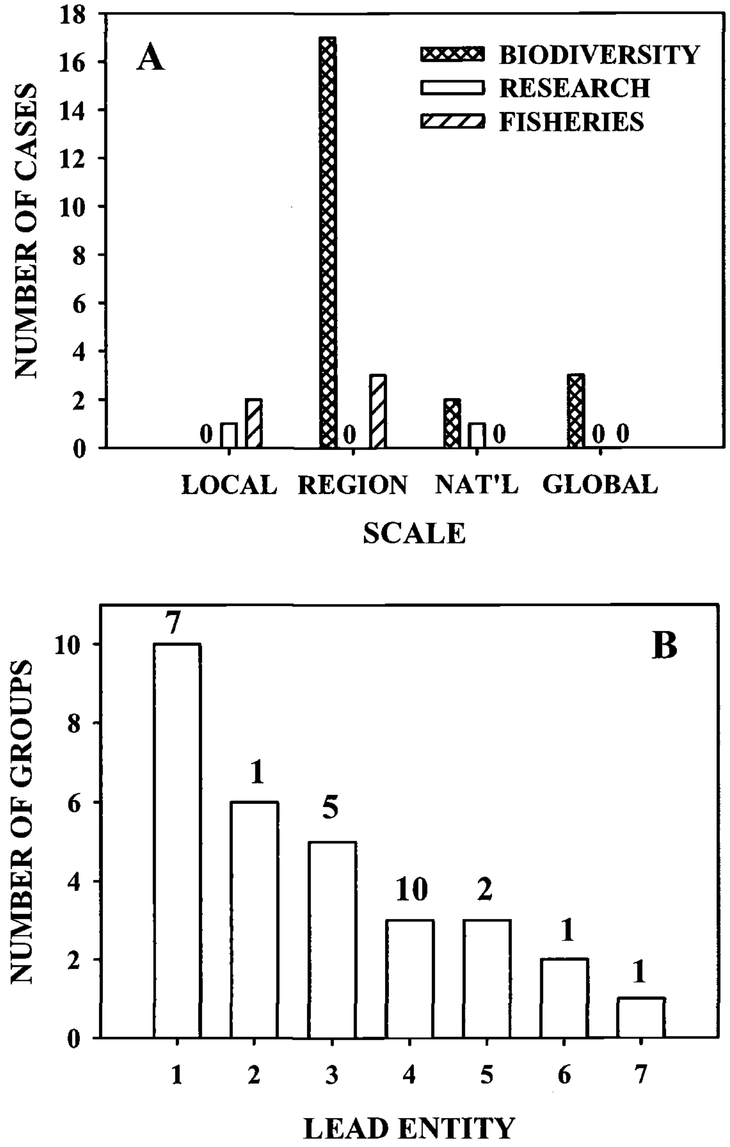

Fig. 5.2. Objectives and stakeholder involvement in the documented marine conservation planning cases. (A) Primary objectives included biodiversity conservation, areas for research, and sustainable fisheries management. Cases were classified as local, regional, national or global in spatial scale. (B) Governments and local non-governmental organizations (NGO) led more participatory processes than national and international NGOs based on the mean number of stakeholder groups involved in each process. The number of cases per institution type is listed above each bar. Institution types are coded as (1) Federal government, (2) County government, (3) Local NGO, (4) International NGO, (5) National NGO, (6) International development agency, and (7) University.

Table 5.2. Key characteristics of the documented marine conservation planning cases. Cases are listed by planning region size. See *Methods* for explanations of the headings.

Location	Primary objective[a]	Primary outcome	Lead entity and partners	Planning region size (km^2)	Primary conservation targets
Management and Exploitation Area managed by the Caleta El Quisco, Chile	1	MPA	Sindicato del Quisco (local fishermen's cooperative)	<< 1,000	Commercially valuable species
Punta El Lacho, Las Cruces, Chile	3	Marine Reserve	Estacion Costera de Investigaciones Marina (ECIM), Universidad Catolica de Chile	<< 1,000	n/a
San Juan County Bottomfish Recovery Zones, WA State, USA	1	MPA	San Juan County Marine Resources Committee, a committee of stakeholders	2,435	Historically productive bottomfish habitats
Fiordland, New Zealand	1, 2	Priority-setting plan	Guardians of Fiordlands's Fisheries & Marine Environment Inc	4,076	Marine habitats, communities, and biodiversity (including indicator and exploited species) that represent Fiordland's marine environment, or are hotspots of biodiversity.
Channel Islands National Marine Sanctuary, USA	1, 2	MPA Network	US National Marine Sanctuary Program	4,295	Primarily habitat types, but also species of special concern

[a] *Primary objectives are coded as (1) Sustainable fisheries, (2) Biodiversity conservation, and (3) Research.*

Table 5.2 (Continued). Key characteristics of the documented marine conservation planning cases.

Location	Primary objective[a]	Primary outcome	Lead entity and partners	Planning region size (km^2)	Primary conservation targets
Galapagos Islands, Ecuador	2	Reserve Network	Charles Darwin Research Station, Galpagos National Park Service, and World Wildlife Fund	6,177	Coastal and nearshore habitat types, along with species of special concern
Florida Keys National Marine Sanctuary's 18 Sanctuary Preservation Areas (18), USA	2	Reserve Network	US National Marine Sanctuary Program	9,500	Habitat types of interest, as well as degree of user conflict
Tortugas Ecological Reserve, Florida Keys National Marine Sanctuary, USA	2	Marine Reserve	US National Marine Sanctuary Program	9,500	Habitats, high biodiversity areas, as well as areas of importance to commercially and recreationally valuable species
Willamette Valley-Puget Trough-Georgia Basin Ecoregion, USA and Canada	2	Priority-setting plan	The Nature Conservancy, in partnership with the WA Dept. of Natural Resources and Fish and Widlife, and the US Fish and Wildlife Service	15,097	134 targets, includling 40 ecosystem types and 94 focal species

[a] *Primary objectives are coded as (1) Sustainable fisheries, (2) Biodiversity conservation, and (3) Research.*

Table 5.2 (Continued). Key characteristics of the documented marine conservation planning cases.

Location	Primary objective[a]	Primary outcome	Lead entity and partners	Planning region size (km^2)	Primary conservation targets
Bahamas	1	Priority-setting plan	Bahamas Reef Environment Educational Foundation, Bahamas Dept. of Fisheries	20,000	Reef and mangrove habitat; commercially valuable fisheries
British Columbia Central Coast, Canada	2	MPA Network	Living Oceans Society	22,303	Primarily habitat types, but also species of special concern
Northern Gulf of Mexico Ecoregion, USA	2	Priority-setting plan	The Nature Conservancy, in partnership with the US Environmental Protection Agency	33,600	Eight biological communities/habitat types and five primary species of interest
Gulf of California, Mexico	2	Reserve Network	Scripps Institution of Oceanography and World Wildlife Fund	120,000	Primarily habitat types, but reef species richness, spawning aggregation sites, and sites with lower fishing pressure
New Zealand	3	Reserve Network	New Zealand Department of Conservation	160,000	Habitat types of interest, particularly unique ones
Global (Coral Reef Hotspots)	2	Priority-setting plan	Conservation International, partnered with academia, non-governmental organizations, and the UN Environment Programme	284,300	Restricted-range coral reef species as indicators of reef biodiversity hotspots globally

[a] *Primary objectives are coded as (1) Sustainable fisheries, (2) Biodiversity conservation, and (3) Research.*

Table 5.2 (Continued). Key characteristics of the documented marine conservation planning cases.

Location	Primary objective[a]	Primary outcome	Lead entity and partners	Planning region size (km^2)	Primary conservation targets
Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve's Reserve Preservation Areas, USA	2	MPA Network	US National Oceanic and Atmospheric Administration (NOAA)	341,360	Protected species and ecosystems of interest
Great Barrier Reef Marine Park: Representative Areas Program, Australia	2	Reserve Network	Great Barrier Reef Marine Park Authority	345,400	Ecosystems primarily, along with unique species
Mid-Atlantic Priority Ocean Areas, USA	2	Priority-setting plan	Natural Resources Defense Council	367,000	Habitats of high biodiversity, organismal abundance, or of particular importance for threatened and endangered species
Mesoamerican Reef: Mexico, Belize, Guatemala, and Honduras	2	Priority-setting plan	World Wildlife Fund	464,263	Focal taxa and guilds, as well as habitats, which were used as surrogates for species occurrences

[a] *Primary objectives are coded as (1) Sustainable fisheries, (2) Biodiversity conservation, and (3) Research.*

Table 5.2 (Continued). Key characteristics of the documented marine conservation planning cases.

Location	Primary objective[a]	Primary outcome	Lead entity and partners	Planning region size (km^2)	Primary conservation targets
Eastern Africa Marine Ecoregion	2	Priority-setting plan	World Wildlife Fund	727,174	Six coastal habitats (including mangroves, reefs, seagrass beds, wetlands) and a number of species of special concern (including birds, mammals, turtles, sharks)
Northwest Atlantic (Gulf of Maine/Bay of Fundy/Scotian Shelf/Georges Bank), USA and Canada	2	Priority-setting plan	World Wildlife Fund in collaboration with the Conservation Law Foundation and other non-governmental organizations	800,000	Seascapes served as proxies for biological communities, habitats and species of interests, along with the distribution of focal species and ecological processes
South Africa	2	Priority-setting plan	Government of South Africa	1,050,000	Vulnerable habitats and species (particularly endemic, rare, and exploitable species)
Bering Sea, Russia and USA	2	Priority-setting plan	The Nature Conservancy and World Wildlife Fund	1,432,965	Unique species or habitat assemblages, areas of outstanding abundances, key to ecological phenomena, e.g. migration

[a] *Primary objectives are coded as (1) Sustainable fisheries, (2) Biodiversity conservation, and (3) Research.*

Table 5.2 (Continued). Key characteristics of the documented marine conservation planning cases.

Location	Primary objective[a]	Primary outcome	Lead entity and partners	Planning region size (km^2)	Primary conservation targets
Philippines	2	Priority-setting plan	Conservation International, Philippine government, and academia	2,200,000	Habitats (including mangroves, reefs, and seagrass beds) and species of special concern (including dugong, cetaceans, elasmobranches, turtles)
Central Carribean Ecoregion	2	Priority-setting plan	The Nature Conservancy, Biodiversity Support Program (BSP), and US Agency for International Development (USAID)	2,654,945	Natural communities, including coral reefs and coral-associated species
Global (Kelleher et al. 1995)	2	Priority-setting plan	The World Bank, along with the IUCN (The World Conservation Union) and the Great Barrier Reef Marine Park Authority	361,059,000	Ecosystems and species of special concern
Global (WWF)	2	Priority-setting plan	World Wildlife Fund	361,059,000	Ecoregions, i.e. relatively large areas delineated by biotic and environmental factors that regulate the structure and function of ecosystems within them, as well as focal taxa

[a] *Primary objectives are coded as (1) Sustainable fisheries, (2) Biodiversity conservation, and (3) Research.*

Table 5.3. Key and accessible references for the documented marine conservation planning cases (see *Appendix C* for complete list). Cases are listed by planning region size.

Location	Reference
Management and Exploitation Area managed by the Caleta El Quisco, Chile	Castilla and Fernandez 1998. Small-scale benthic fisheries in Chile: On co-management and sustainable use of benthic invertebrates. Ecological Applications 8: S124-S132.
Punta El Lacho, Las Cruces, Chile	Castilla, J.C. and L. R. Duran. 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on Concholepas concholepas (Gastropoda). Oikos 45:391-399.
San Juan County Bottomfish Recovery Zones, WA State, USA	Klinger, T. 2001. Marine protected areas: Examples from the San Juan Islands, Washington. Endangered Species UPDATE 18(2): 55-58.
Fiordland, New Zealand	Guardians of Fiordlands's Fisheries & Marine Environment Inc. 2002: Draft Integrated Management Strategy for Fiordland's Fisheries and Marine Environment.
Channel Islands National Marine Sanctuary, USA	Airame, S. J. E. Dugan, K. D. Lafferty, H. Leslie, D. A. McArdle, and R. R. Warner. 2003. Applying ecological criteria to marine reserve design: A case study from the California Channel Islands. Ecological Applications 13: S170-S184.
Galapagos Islands, Ecuador	R. Bensted-Smith (Editor). 2002. A biodiversity vision for the Galapagos Islands. Puerto Ayora, Galapagos: Charles Darwin Foundation and World Wildlife Fund.
Florida Keys National Marine Sanctuary's 18 Sanctuary Preservation Areas (18), USA	Bohnsack, J. A. 1997. Consensus development and the use of marine reserves in the Florida Keys, USA. Proceedings of the 8th International Coral Reef Symposium 2: 1927-1930.
Tortugas Ecological Reserve, Florida Keys National Marine Sanctuary, USA	http://www.fknms.nos.noaa.gov/tortugas/ welcome.html
Willamette Valley-Puget Trough-Georgia Basin Ecoregion, USA and Canada	Beck, M. W. 2003. The sea around: marine regional planning. pp. In Groves, C. R. Drafting a conservation blueprint: a practitioners' guide to planning for biodiversity. Island Press. Pp. 314-344.

Table 5.3 (Continued). Key references.

Location	Reference
Bahamas	Stoner, A.W., M.A. Hixon, and C.P. Dahlgren. 1999. Scientific review of the marine reserve network proposed for the Commonwealth of the Bahamas by the Bahamas Department of Fisheries.
British Columbia Central Coast, Canada	Ardron, J., J. Lash and D. Haggarty. 2002. Modelling a network of marine protected areas for the central coast of British Columbia. Ver. 3.1. Living Oceans Society. Sointula, British Columbia, Canada. http://www.livingoceans.org/library.htm
Northern Gulf of Mexico Ecoregion, USA	Beck, M.W. and M. Odaya 2001. Ecoregional planning in marine environments: identifying priority sites for conservation in the northern Gulf of Mexico. Aquatic Conservation: Marine and Freshwater Ecosystems 11:235-242.
Gulf of California, Mexico	Sala, E., O. Aburto-Oropeza, G. Paredes, I. Parra, J. C. Barrera, and P. K. Dayton. 2002. A general model for designing networks of marine reserves. Science 298: 1991-1993.
New Zealand	Walls, K. 1998. Leigh Marine Reserve, New Zealand. Parks 8(2):5-10.
Global (Coral Reef Hotspots)	Roberts et al. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295:1282-1285.
Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve's Reserve Preservation Areas, USA	http://hawaiireef.noaa.gov/
Great Barrier Reef Marine Park: Representative Areas Program, Australia	http://www.gbrmpa.gov.au/corp_site/key_issues/conservation/rep_areas/rep_area_overview.html
Mid-Atlantic Priority Ocean Areas, USA	Azimi, S. 2001. Priority Ocean Areas for Protection in the Mid-Atlantic: Findings of NRDC's Marine Habitat Workshop. New York, NY: Natural Resources Defense Council. http://www.nrdc.org/water/oceans/priority/poainx.asp

Table 5.3 (Continued). Key references.

Location	Reference
Mesoamerican Reef: Mexico, Belize, Guatemala, and Honduras	Kramer, P. A. and P. R. Kramer. (ed. M. McField). 2002. Ecoregional conservation planning for the Mesoamerican Caribbean Reef. Washington, DC. World Wildlife Fund.
Eastern Africa Marine Ecoregion	World Wildlife Fund. 2002. Proceedings of the Eastern African Marine Ecoregion Visioning Workshop: 21-24 April 2001. Prepared by C. Horrill, WWF Tanzania Programme Office, Dar es Sallaam, Tanzania.
Northwest Atlantic (Gulf of Maine/Bay of Fundy/Scotian Shelf/Georges Bank), USA and Canada	Day, J. C. and J. C. Roff. 2000. Planning for representative marine protected areas: A framework for Canada's Oceans. Report prepared for World Wildlife Fund Canada, Toronto. http://www.wwf.ca/MPA-planning/
South Africa	Hockey, P. A. R. and G. M. Branch. 1997. Criteria, objectives, and methodology for evaluating marine protected areas in South Africa. South African Journal of Marine Science 18:369-383.
Bering Sea, Russia and USA	Banks, D., M. Williams, J. Pearce, A. Springer, R. Hagenstein, and D. Olson. 1999. Ecoregion-based conservation in the Bering Sea: Identifying important areas for biodiversity conservation. WWF and TNC of Alaska.
Philippines	Ong, P.S., L. E. Afuang, and R. G. Rossell-Ambal (eds.). 2002. Philippine Biodiversity Conservation Priorities: A Second Iteration of the National Biodiversity Strategy and Action Plan. Dept. of Environment and Nat. Res. -Protected Areas and Wildlife Bureau, C.I. Philippines, Biodiversity Conservation Pgm.-U. of the Philippines Center for Integrative and Development Studies, and Foundation for the Philippine Environment, Quezon City, Philippines
Central Carribean Ecoregion	Sullivan Sealey, K. and G. Bustamante. 1999. Setting geographic priorities for marine conservation in Latin America and the Caribbean. The Nature Conservancy, Arlington, Virginia, USA.

Table 5.3 (Continued). Key references.

Location	Reference
Global (Kelleher et al. 1995)	Kelleher, G, C. Bleakley, and S. Wells. 1995. A global representative system of marine protected areas. Vol I of IV. Washington, DC: The World Bank.
Global (WWF)	Olson, D. M. and E. Dinerstein. 2002. The Global 200: Priority ecoregions for global conservation. Annals of the Missouri Botanical Gardens 89:199-224.

area and total protected or priority area increased (n=21 cases: analyses not shown).

Both governments and non-governmental organizations led planning processes (Table 5.2). Governments were more active in MPA and reserve implementation efforts than non-governmental organization, which dominated development of priority-setting plans. Universities and multilateral development institutions rarely played the lead role. Based on the average number of stakeholder groups involved in cases led by each institution type, government and local non-governmental organizations led more participatory processes than national and international NGOs (Fig. 5.2B). Completed or more fully developed processes seemed to include more stakeholder groups.

Outcomes of marine conservation planning

Of the 27 marine conservation planning cases evaluated, 15 were designed to set priorities for conservation efforts, and resulted in priority-setting plans. Four cases involved the implementation of marine reserves or reserve networks, and eight, MPAs. Priority-setting plans were particularly common at the regional and global political scales. At the local and regional scales, cases tended to focus on marine reserve or MPA implementation (Table 5.2).

An example of a priority-setting plan is the Mid-Atlantic case led by the Natural Resources Defense Council (NRDC). They convened scientists with expertise in Mid-Atlantic marine species and ecosystems to identify priority areas. Participants chose candidate areas based on seven major criteria and their knowledge of the region. They produced a composite map of all the candidate sites. Areas of great overlap were designated as 'priority areas' (Azimi 2001). As a first step, NRDC used the portfolio of priority areas to advocate for changes in fisheries management through the Mid-Atlantic Fishery Management Council process (L. Speer, *personal communication*).

An example of MPA network implementation occurred in the Channel Islands National Marine Sanctuary. The Sanctuary staffed a 'marine reserve working group', which was charged with designing a network of reserves and other types of MPAs to meet biodiversity conservation and fisheries management objectives (Airamé et al. 2003, Helvey 2004). The two-year process was highly participatory and public. State-of-the-art natural and social science information generated by scientists from government, non-governmental organizations (NGOs), and universities played a key role. In October 2002, the California Fish and Game Commission designated approximately 25 percent of state waters surrounding the Channel Islands as MPAs (primarily as marine reserves); complementary federal action is expected in 2005.

Role of science in marine conservation planning

Both fine scale (species) and coarse scale targets (ecosystems, habitats) were included in 25 of 27 cases (Table 5.2). While the majority emphasized ecosystem-based approaches, 25 cases included some species-level targets; often those deemed focal, keystone, or umbrella species.

Eleven of the 27 cases considered biogeophysical criteria first, whereas 16 relied on integrated criteria (biogeophysical plus socioeconomic data and other pragmatic considerations) in order to select priority areas for conservation and management action. None of the documented cases considered social and economic criteria first. Explicit biogeophysical criteria were considered in 26 cases. Nongovernmental organizations tended to give biogeophysical criteria priority, whereas government-led initiatives tended to integrate social and economic criteria into the decision-making processes earlier and more explicitly. Presence of species of special concern, representation of biogeographic regions and habitat types, and inclusion of vulnerable habitats and life stages were considered in at least 20 of the 27 cases (Fig. 5.3). The criterion considered least often was the provision of ecosystem services.

'Connectivity' was included as a criterion in 15 cases. Marine scientists have documented multiple mechanisms by which marine ecosystems are connected through the movement of nutrients, primary production or other particulate food resources (Duggins et al. 1989, Bustamante et al. 1995), larvae (Palumbi and Warner 2003), and/or adult organisms (Johnson et al. 1999). Such linkages are critical to the maintenance of functioning marine populations and ecosystems (Lubchenco et al. 2003, Roberts et al. 2003b). In addition, 17 cases mentioned the desirability of a 'network' approach in drafting priority areas for conservation (Appendix C). In marine reserve design literature, a network refers to a set of individual reserves within a biogeographic region, connected by larval dispersal and juvenile or adult migration (National Research Council 2001, Lubchenco et al. 2003). Interestingly, not all processes that alluded to networks necessarily considered connectivity explicitly, or vice versa.

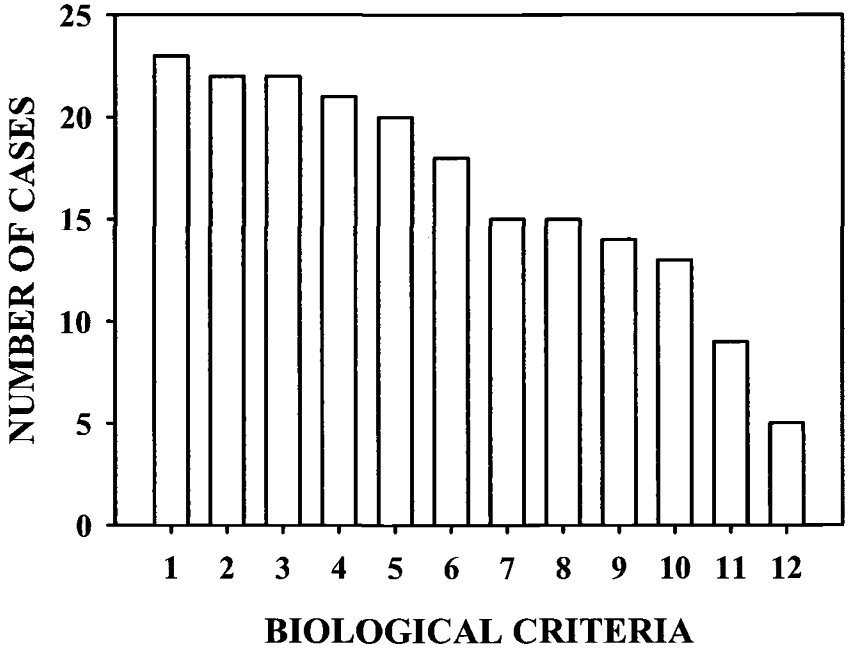

Fig. 5.3. The biological criteria used in each case were compared to those detailed by Roberts and colleagues (2003). Criteria are coded as (1) Species of special concern, (2) Biogeographic representation, (3) Habitat representation, (4) Vulnerable habitats, (5) Vulnerable life stages, (6) Exploitable species, (7) Connectivity, (8) Ecosystem functioning, (9) Anthropogenic catastrophes, (10) Size, (11) Natural catastrophes, and (12) Ecosystem services.

In terms of scientific tools, expert workshops were used in all 27 cases. 'Experts' were most often scientists and resource managers, but in some efforts included other stakeholder groups such as fishermen and local residents. In some cases, such as in Eastern African Marine Ecoregion (Horrill 2002) and in the Galapagos Islands (Bensted-Smith 2002), expert workshops were used to develop a common vision of conservation action for the area. In other cases, such as in the Bering Sea (Banks et al. 1999) and the Mid-Atlantic region (Azimi 2001), the assembled experts actually drew lines on maps, and produced a list of priority areas for conservation action.

Maps were used to help make decisions in at least 24 cases. Detailed distributions of habitats, species occurrences, and in some cases, human use patterns (e.g. fishing, recreation), were mapped in GIS (geographic information systems) in at least 17 cases. In the Northwest Hawaiian Islands, staff from the National Oceanic and Atmospheric Administration initially relied on nautical charts and sketched in information from scientists, managers, fishermen, and conservationists about fishing effort and vulnerable habitats to locate individual marine protected areas (R. Griffis, *personal communication*). On a global scale, Roberts and colleagues (2002) synthesized existing information on the distributions of restricted-range coral reef associated species and threats to coral reefs in a series of GIS maps. They then used these maps to identify priority areas for coral reef conservation worldwide.

Computer-based siting tools (i.e. algorithms such as SPEXAN, Sites, and MARXAN) were used in 8 cases. These siting tools generated potential networks of sites that met explicit objectives dictated by the users. Conservation goals (e.g.

representation of a certain proportion of marine populations or habitats) were formulated as constraints within a cost function (Possingham et al. 2000). In the northern Gulf of Mexico, for example, The Nature Conservancy used Sites to help prioritize coastal and marine activities in the region (Beck and Odaya 2001). In the Gulf of California, Sala and colleagues (2002) used MARXAN to help create potential reserve networks that met biodiversity objectives while minimizing the costs to small-boat fishermen in the region. In the Great Barrier Reef Park of Australia (S. Slegers, *personal communication*), as well as in the Channel Islands of southern California (Airamé et al. 2003), stakeholder groups worked through possible reserve network configurations using similar tools. The Gulf of California and Australia efforts were among the first to explicitly incorporate socioeconomic constraints, thereby enabling planners to examine the trade-offs among different conservation goals and network configurations. All eight of these cases are part of ongoing marine conservation planning efforts (Appendix C).

DISCUSSION

In the Gulf of California (Sala et al. 2002), the Channel Islands (Airamé et al. 2003), Puget Sound (Ferdana 2002, Beck 2003), and coral reefs worldwide (Roberts et al. 2002) processes, natural science played particularly central roles. Similarities among these cases included:

1. The overall objective was fairly well defined.

2. The planning region was delineated based on biogeographic rather than political boundaries.
3. The planning process – from setting objectives and conservation targets, integrating relevant information, identifying priority areas for conservation and management, and implementing appropriate strategies – engaged multiple institutions and stakeholder groups.
4. The planning process was science-based, with information from multiple sources integrated using multiple tools.

These cases differed in the degree of stakeholder involvement, choice of conservation targets (species, ecosystems and/or ecological processes) and use of criteria and quantitative siting tools. Based on the cases analyzed here, these factors seem to be partially a function of the type of institution leading the process and the quality and quantity of information and technical expertise available.

The assembled database raises a couple of points relevant to future marine conservation planning efforts: First, both conservation targets and tools should be well matched to the overall objectives of the initiative. For example, if the aim is to preserve marine biodiversity (and all the genes, species, ecosystems 'biodiversity' encompasses), siting priority areas based primarily on the distribution of seabirds and marine mammals is not scientifically defensible. Including both species and ecosystem-based targets resonates with current scientific understanding (Groves 2003). Nonetheless, there have been few systematic tests of the value of using species vs. ecosystems as targets (Ward et al. 1999, Gladstone 2002). This is an important area for future research and practice.

Likewise, the use of ecological processes (e.g. the occurrence of spawning sites, upwelling areas, or migratory pathways) as conservation targets deserves further attention. Inclusion of such areas may benefit specific species, which may or may not correspond with the overall objectives of the planning process. It may be that such spatially and temporally dynamic processes are more appropriately considered as criteria, rather than as conservation targets in and of themselves. This matter is more than semantics as considering an ecological process as a 'target' vs. a 'criterion' will influence the way this information – which is indisputably important for preserving functioning ecosystems – is integrated in decision-making processes, particularly when siting algorithms are used.

Applications of computer-based siting tools to date have focused primarily on representing marine habitats and focal species to meet biodiversity conservation objectives (Table 5.2). They have not explicitly integrated ecological concepts like connectivity, reserve size, and the probability of catastrophes, even though these factors are widely recognized as important (Pressey 2001, Bensted-Smith 2002, Allison et al. 2003, Beck 2003, Groves 2003, Roberts et al. 2003a). Some planners have incorporated these factors through expert review, after using a siting tool to generate preliminary network configurations (Beck and Odaya 2001; Z. Ferdana, *personal communication*). Others have used features of the siting tools to implicitly incorporate connectivity and other considerations (Sala et al. 2002, Airamé et al. 2003). This is an important area of future research and practice, as well.

Second, many have asserted that marine conservation planning decisions should be grounded in knowledge of marine population and ecosystem dynamics (National Research Council 2001, Roberts et al. 2003a). Yet among these 27 cases, ecosystem services were rarely considered (Fig. 5.3), even though humanity receives benefits from a number of ecosystem services generated by coastal and marine ecosystems (Peterson and Lubchenco 1997). Also, not all cases that explicitly considered connectivity articulated the importance of networking individual sites. These findings suggest that planners consider knowledge of marine population and ecosystem dynamics to be important when identifying priority areas, but do not necessarily have clear guidelines for how to synthesize and apply this information effectively (for some ideas, see Daily et al. 2000, Warner and Cowen 2002).

In closing, the assembled marine conservation planning cases indicate the varied approaches people have taken and the types of information that would be useful to document in the future. One of the most striking findings was the paucity of well-documented cases. Lack of documentation of past and ongoing cases hampers both practical and scholarly progress in marine conservation planning. Our ability to develop effective models for marine conservation planning and to assess the success of various approaches would be significantly strengthened by a more diverse set of well-documented cases. In particular, it would valuable to document cases that are:

1. Outside of North and Central America,
2. Led by local organizations or coalitions of stakeholders and institutions, or
3. Motivated by objectives other than biodiversity conservation.

With such additions, I anticipate the structure as well as the content of the database will evolve. In particular, more case-specific social, economic, and monitoring information, as well as measures of success, would increase the database's utility. These data were not accessible for the vast majority of analyzed cases, indicating the need for more documentation and synthesis in these areas.

Given increasing interest in evaluating the effectiveness of conservation and management activities (Salafsky et al. 2002), a database such as this could further efforts to assess success of marine conservation planning approaches thus far and to develop standards for marine conservation planning (Pressey 2001, Noss 2003). I hope this template will encourage conservation practitioners and contributing scientists to document the processes by which marine conservation planning decisions are made and to share this information with the broader community, in order to advance conservation and management of the world's oceans.

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Chapter 6: Conclusions to the Dissertation

Given the title of this thesis, this chapter seems the appropriate place to reflect on how the findings summarized in the previous chapters advance science relevant to the design and implementation of marine reserves. The questions articulated in the Introduction provide a framework for this reflection.

How do marine populations and ecosystems respond to reserve establishment?

In Chapter 2, I reported on a series of investigations that evaluated the influence of conspecific density on key life history traits of the intertidal barnacle *Balanus glandula*. While survival was positively associated with increased density, growth and individual reproductive capacity were negatively affected. These findings demonstrate that key traits may exhibit conflicting responses to changes in density or other demographic parameters that alter intraspecific interactions. Overall, the reproductive rates of adult barnacles were greater at higher conspecific densities, indicating that the positive intraspecific effects outweighed the negative effects in this context.

The results also have implications for the design and management of marine reserves. When areas are protected from fishing and other extractive activities, in many cases, populations (particularly of exploited species) increase in abundance (Halpern 2003). Given that traits may respond differentially to changes in density, it is vital to anticipate, and when possible, to evaluate the full range of positive and negative interactions among conspecifics when designing and implementing reserves or other area-based management strategies.

Why do we need networks of reserves, rather than single reserves?

In Chapter 3, my coauthors and I reported how bottom-up factors, specifically alongshore variation in nearshore primary productivity, influenced survival, growth, and reproduction in the intertidal barnacle *Balanus glandula*. We found strong evidence for bottom-up forcing of barnacle population growth and reproduction. Mean cumulative larval production per 100 cm^2 in natural populations in the region of higher primary productivity was 5x that in the less productive region. Barnacles living in experimental mid-intertidal populations in the more productive region grew to almost 2x the mean size and had heavier shells than barnacles living in the less productive region. Mean estimated larval production per individual in experimental populations in the more productive region was >2x that at the sites in the less productive region. Mean larval production per 100 cm^2 in the experimental populations in the more productive region was 28x greater than at the sites in the less productive region. One site within the higher productivity region produced substantially more larvae than the others, however, demonstrating that larval production "hotspots" exist in rocky intertidal ecosystems and that not all sites are ecologically equivalent.

Our findings advance understanding of the role of bottom-up influences on population and community dynamics, and contribute data for the next generation of conceptual and quantitative models of marine community dynamics.

Our findings also demonstrate the importance of taking a network approach when designing marine reserves, because of among-site variability in population and community dynamics, such as what we documented. Networks of reserves or other types of marine protected areas provide one useful strategy for dealing with the inevitable uncertainty about the demography of target species and among-site variability in marine ecosystem dynamics (Roberts et al. 2001, Lubchenco et al. 2003). Particularly in coastal marine ecosystems, where the linkages between the benthic and pelagic environments are predicted to change with climatic change, embedding marine conservation and management strategies within a network context is essential.

If we think in terms of networks, where should individual reserves be located?

In Chapter 4, my co-authors and I described how detailed scientific findings like those above could be integrated into reserve network design using a computer-based siting tool. We applied a flexible optimization tool—simulated annealing—to develop scenarios of potential reserve networks for the Florida Keys National Marine Sanctuary. Our goal was to represent at least 20% of each benthic habitat type within the reserve network while minimizing its overall area and perimeter. Using the siting tool, we identified many adequate reserve network scenarios that met these goals. One of the most useful types of information provided by this siting tool came from an "irreplaceability analysis," or count of the number of times unique planning units were included in reserve network scenarios. This analysis indicated that many different combinations of sites produced satisfactory networks, and highlighted larger areas within the planning region as potential priorities for conservation action.

This exercise illustrated how the simulated annealing algorithm could be used to help site marine reserves. Perhaps most importantly, the result that there were multiple ecologically suitable ways to design a reserve network provides considerable latitude in the choice of specific sites. This flexibility has been very useful in real-world design and implementation efforts (e.g. Airamé et al. 2003). In the Channel Islands, multiple biologically adequate network scenarios also were found, suggesting that this may be a general result. The tool has since been used in the Channel Islands, Great Barrier Reef Marine Park, British Columbia, and elsewhere to facilitate marine conservation planning efforts and design networks of marine reserves.

How has natural science been integrated into reserve design and other marine conservation planning processes?

Finally, in Chapter 5, I reported on a synthesis of marine conservation planning approaches from around the world. The goal was to bring together disparate information sources, much available only in the gray literature or from conservation practitioners themselves, to evaluate how natural science has been integrated into marine conservation planning (including reserve design processes). I found that the majority of 27 documented cases occurred in North and Central America, were regional in nature, and were based on biogeographic boundaries. Biodiversity conservation was the primary objective. Outcomes included priority-setting plans and implementation of reserve networks and other marine protected areas. Nongovernmental organizations tended to give biogeophysical criteria priority, whereas government-led initiatives tended to integrate social and economic criteria into decision-making processes earlier and more explicitly. In terms of specific criteria, presence of species of special concern, representation of biogeographic regions and habitat types, and inclusion of vulnerable habitats and life stages were considered in at least 20 of the 27 cases. Key tools for data integration and synthesis included expert workshops, maps, and siting algorithms.

Analysis of the database raised three points relevant to future marine conservation planning efforts. First, conservation targets and tools should be well matched to the overall objectives of the initiative. Second, my findings suggest that planners consider knowledge of marine populations, communities, and ecosystems to be important when identifying priorities, but that they do not have clear guidelines for how to integrate this information appropriately. Finally, one of the most striking findings was the paucity of well-documented cases. Better documentation of planning processes would enable conservation practitioners and other scientists who contribute to such efforts to learn from what others have done, as well as to begin to develop standards for marine conservation planning.

Concluding Remarks

The above results can be summarized in three main messages relevant to marine reserve design and other conservation planning efforts:

1. Anticipate surprises

In investigating barnacle population dynamics on the Oregon coast, I found that key life history traits responded differentially to environmental variability, both in terms of nearshore primary productivity and conspecific density. If I had only measured growth of *B. glandula* (and not reproductive output) at sites within Cape Perpetua and Cape Foulweather, I would have concluded that bottom-up forcing on barnacle populations at these sites was much more uniform than the additional quantification of survival and reproduction indicated. Anticipating such surprises by using multiple approaches to investigate the dynamics of populations and ecological communities is essential to further understanding of how marine populations and ecosystems persist in space and time, and thus to effective ocean management and conservation.

2. Embrace uncertainty

The high barnacle larval production at Strawberry Hill illustrates the potential magnitude of among-site variability in coastal marine systems. While reasonable hypotheses have been offered to explain such variability (Menge et al. 1997a, Menge et al. 1997b, Freidenburg and Menge in prep), delineation of specific mechanisms is challenging at the spatial and temporal scales at which the relevant biogeophysical factors are operating. Furthermore, the detail of demographic information reported in Chapters 2 and 3 cannot possibly be replicated for all marine populations of interest. Consequently, marine reserves and other area-based marine management strategies should be envisioned in the context of ecologically connected networks, where sites are linked by larval dispersal, migration, and flows of limiting resources. By applying the considerable information we have about marine population, community and ecosystem dynamics, we can design reserve networks that account for the inevitable uncertainty regarding particular components. Such scientifically informed reserves will be more likely to meet the objectives for which they have been established.

3. Think creatively

Creative application of tools and approaches borrowed from other fields, as in the siting tool demonstration in Chapter 4, can help synthesize and apply existing knowledge of marine ecosystems. Siting algorithms like the one we used were initially developed by operations researchers, and later applied to reserve design by Australian forest managers. Also, many workable solutions to a given biological problem often exist, as we demonstrated in the Florida Keys case.

My results demonstrate the value and the feasibility of integrating knowledge of marine population, community, and ecosystem dynamics into more comprehensive approaches to conservation and management. While the threats facing the oceans off Oregon and globally are serious and require strong and concerted policy responses on multiple levels, we in the scientific community have considerable knowledge and tools to contribute to the development and implementation of solutions.

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Appendices

Appendix A. Supplementary Materials, Chapter 2

Table A1. 100-cm^2 pitted settlement plates were used to manipulate density of the barnacle *B. glandula.* Pits were ~1 mm in diameter and 0.3 mm deep, and were drilled in regular arrays using a computer-controlled drilling machine.

Density Level	No. pits per 100 cm^2	Spacing among the pits (cm)
Lowest	16	2
Low	81	1
High	340	0.5
Highest	1360	0.25

Table A2. Results of the one-factor analysis of variance models for the recruitment, survival, and growth responses in the plate experiment. Effects with p<0.05 are in bold.

Source of variation	df	ss	*F*	*P*	VC[a]	% of Total
a) ln (Recruits per 100 cm^2), August 2002						
Density level	3	268.339	367.785	< **0.001**	--	--
Block	24	2.005	0.344	0.998	0.021	7.909
Error	72	17.511	--	--	0.243	92.091
b) ln (Barnacle density per 100 cm^2), April 2003						
Density level	3	305.760	100.830	< **0.001**	--	--
Block	24	51.415	2.119	**0.008**	0.536	34.634
Error	72	72.779	--	--	1.011	65.366
c) ln (1+Survivors per 100 cm^2), April 2003						
Density level	3	152.375	24.487	< **0.001**	--	--
Block	24	35.977	0.723	0.812	0.377	15.392
Error	71	147.273	--	--	2.074	84.608
d) Mean barnacle basal diameter per 100 cm^2 [b]						
Density level	2	17.919	191.788	< **0.001**	--	--
Block	2	3.132	33.524	**0.003**	0.522	91.786
Error	4	0.187	--	--	0.047	8.214
e) Mean ratio of barnacle height to basal diameter per 100 cm^2 [b,c]						
Density level	2	1.558	5.840	**0.039**	--	--
Error	6	0.800	--	--	--	--

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[a] *VC=Variance components*

[b] *Analysis excluded the lowest density level, due to lack of data.*

[c] *Including block as a random factor in the analysis resulted in negative various components. Consequently, I report the results of a one-way ANOVA. Qualitatively the results were similar.*

Table A3. Per capita mortality was significantly influenced by density in the plate experiment.

A. Contingency table analysis

Density Level	Per capita mortality		
(pits/100cm^2)	*95+ %*	*< 95%*	Row totals
16	23	2	25
81	21	3	24
340	17	8	25
1360	8	17	25
Column totals	69	30	

ChiSquare likelihood ratio test: ChiSquare = 26.75

$p<0.0001$

B. Odds ratio calculation

What were the odds that 95+% per capita mortality affected a low density plate (16 pits/100cm^2) vs. a high density plate (1360 pits/100cm^2)?

Odds ratio	19.35
ln(odds ratio)	2.96
SE	0.85
95% CI of ln(odds ratio)	1.29-4.63
95% CI of odds ratio	3.63-102.51

Table A4. Results of the one-factor analysis of variance models for the individual biomass allocation responses in the plate experiment. All analyses excluded the lowest density level, due to lack of data.

Source of variation	df	ss	*F*	*P*	VC[a]	% of Total
a) Mean shell dry wt., mg [for all barnacles]						
Density level	2	940.684	0.603	0.590	--	--
Block	2	7733.352	4.957	0.083	1288.892	62.297
Error	4	3120.247	--	--	780.062	37.703
b) Mean body dry wt., mg [for all barnacles]						
Density level	2	0.459	0.519	0.630	--	--
Block	2	1.572	1.778	0.280	0.262	37.215
Error	4	1.768	--	--	0.442	62.785
c) Mean gonad dry wt., mg [for all barnacles]						
Density level	2	0.729	0.603	0.590	--	--
Block	2	5.921	4.900	0.084	0.987	62.025
Error	4	2.417	--	--	0.604	37.975
d) Mean brood dry wt., mg [brooding barnacles only]						
Density level	2	2.458	2.002	0.280	--	--
Block	2	0.949	0.773	0.536	0.202	24.787
Error	3	1.842	--	--	0.614	75.213

[a] *VC=Variance components*

Table A5. Results of one-factor analysis of variance models for individual and population-level reproductive output in the plate experiment. Effects with p<0.05 are in bold.

Source of variation	df	ss	*F*	*P*	VC[a]	% of Total
a) Estimated number of larvae/barnacle (lowest level omitted)						
Density level	2	0.283	4.629	0.121	--	--
Block	2	0.468	7.647	0.066	0.105	77.470
Error	3	0.092	--	--	0.031	22.530
b) Brooding frequency						
Density level	3	0.587	6.935	**0.022**	--	--
Block	2	0.124	2.192	0.193	0.015	35.398
Error	6	0.169	--	--	0.028	64.602
c) Brooding frequency (with lowest level omitted)						
Density level	2	0.008	0.146	0.868	--	--
Block	2	0.186	3.396	0.137	0.031	53.096
Error	4	0.109	--	--	0.027	46.904

[a] *VC=Variance components*

Table A6. Results of the two-way analysis of variance models for density, growth, morphology and brooding frequency in the natural substrata density experiment. Effects with $p<0.05$ are in bold.

Source of variation	df	ss	*F*	*P*	VC[a]	% of Total
a) ln (Barnacles per 100 cm^2)						
Site	1	0.921	7.330	**0.035**	--	--
Density	1	8.604	68.498	**0.0001**	--	--
Site * Density	1	0.664	5.283	0.061	--	--
Block	2	0.500	1.991	0.217	0.063	33.235
Error	6	0.754	--	--	0.126	66.765
b) ln (Mean barnacle basal diameter per 100 cm^2)						
Site	1	0.261	31.543	**0.001**	--	--
Density	1	0.721	87.192	< **0.0001**	--	--
Site * Density	1	0.080	9.682	**0.021**	--	--
Block	2	0.024	1.464	0.303	0.003	26.798
Error	6	0.050	--	--	0.008	73.202
c) ln [1+ (mean ht: basal diameter per 100 cm^2)] [b]						
Site	1	0.316	13.427	**0.006**	--	--
Density	1	1.505	63.942	< **0.0001**	--	--
Site * Density	1	0.322	13.657	**0.006**	--	--
Error	8	0.188	--	--	--	--
d) Brooding frequency						
Site	1	0.083	13.945	**0.010**	--	--
Density	1	0.030	5.077	0.065	--	--
Site * Density	1	0.145	24.270	**0.003**		
Block	2	0.112	9.354	**0.014**	0.014	70.048
Error	6	0.036	--	--	0.006	29.952

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[a] *VC=Variance components*

[b] *Including block as a random factor in the analysis resulted in negative various components. Consequently, I report the results of a two-way ANOVA. Qualitatively the analyses were similar.*

Table A7. Results from the two-way analysis of variance models for individual biomass allocation in the natural substrata density experiment. Effects with p<0.05 are in bold.

Source of variation	df	ss	*F*	*P*	VC[a]	% of Total
a) Mean shell dry wt., mg [for all barnacles]						
Site	1	8723.253	10.545	**0.018**	--	--
Density	1	1141.484	1.380	0.285	--	--
Site * Density	1	521.327	0.630	0.458		
Block	2	1255.158	0.759	0.508	156.895	15.942
Error	6	4963.657	--	--	827.276	84.058
b) Mean body dry wt, mg [for all barnacles]						
Site	1	7.739	49.513	**0.0004**	--	--
Density	1	0.199	1.272	0.303	--	--
Density * Site	1	1.016	6.500	**0.044**		
Block	2	2.415	7.726	**0.022**	0.302	65.889
Error	6	0.938	--	--	0.156	34.111
c) ln(1+gonad dry wt, mg) [for all barnacles]						
Site	1	0.369	16.637	**0.007**	--	--
Density	1	0.038	1.725	0.237	--	--
Density * Site	1	0.035	1.593	0.254		
Block	2	0.094	2.130	0.200	0.012	34.743
Error	6	0.133	--	--	0.022	65.257
d) brood dry wt, mg [brooding barnacles only]						
Site	1	4.212	9.308	**0.022**	--	--
Density	1	0.456	1.007	0.354	--	--
Site * Density	1	0.001	0.001	0.974		
Block	2	0.507	0.560	0.598	0.063	12.287
Error	6	2.715	--	--	0.452	87.713

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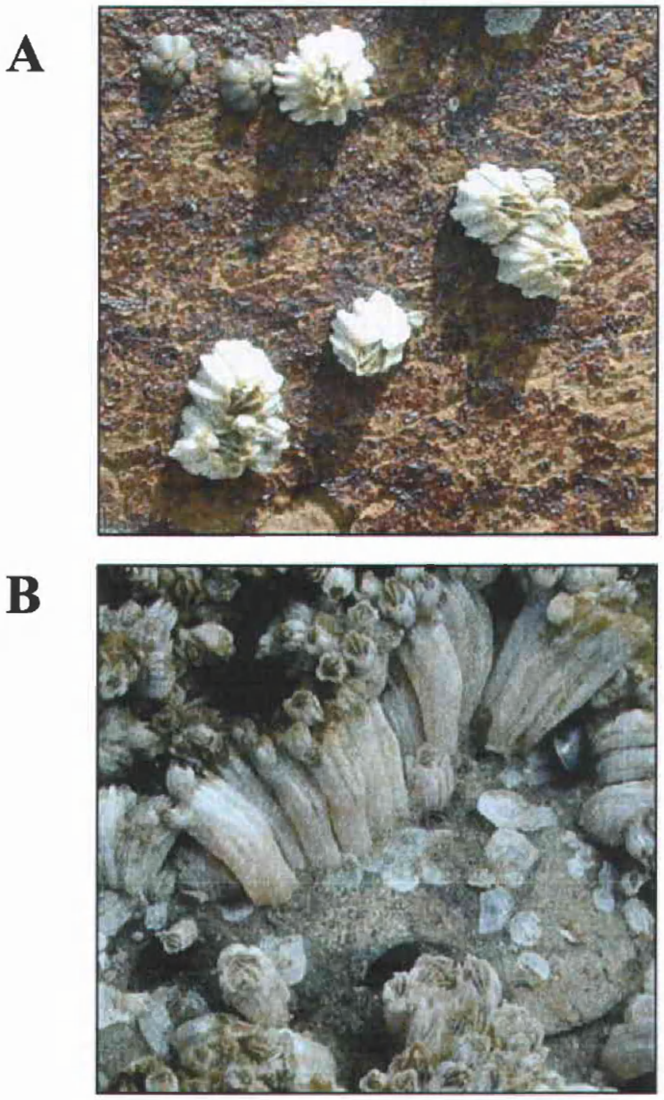
[a] *VC=Variance components*



Scale for both photos: 1 cm

Fig. A1. The influence of conspecific density on barnacle shell morphology. (A) Barnacles living at low density. (B) Barnacles living at high density.

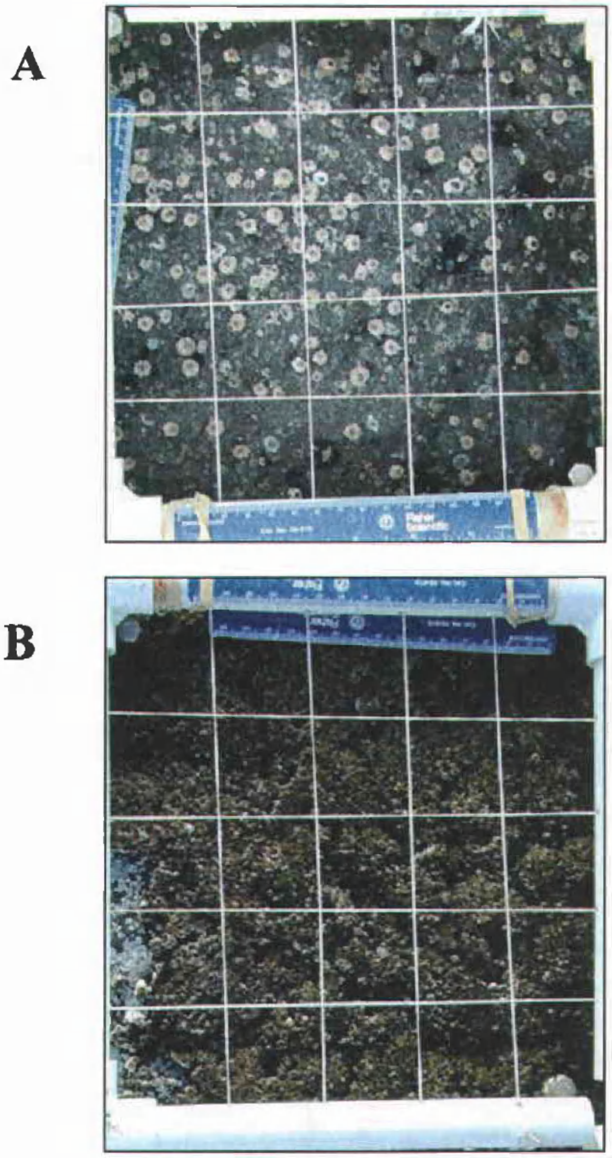


Fig. A2. The natural substrata density experiment. Density was manipulated on natural rock surfaces by clearing substrata and thinning natural barnacle populations following simultaneous recruitment by *B. glandula*. Representative 400-cm^2 plots are shown at the end of the experiment. (A) BC thinned treatment (mean=50 barnacles per 100 cm^2). (B) FC natural treatment (mean = 461 barnacles per 100 cm^2).

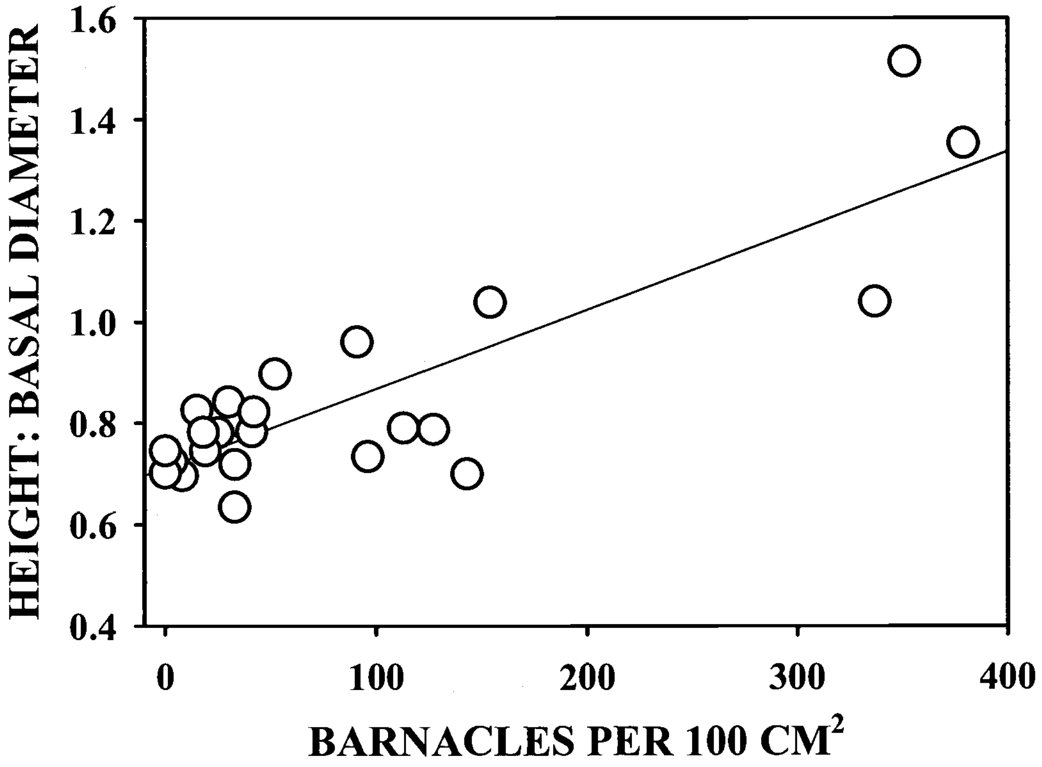


Fig. A3. Association between density and barnacle morphology in natural populations. Barnacle morphology was positively associated with barnacle density in the mid intertidal natural populations of *B. glandula* surveyed at FC and BC in April 2003 (linear regression on untransformed values: R^2=0.72, F=57.368, $p<0.0001$, df=1, 22). The regression equation was $y = 0.711 + 0.002x$. Quadrat-level means are shown (n=24).

Appendix B. Supplementary Materials, Chapter 3

Appendix B1. Protocols for random surveys of barnacle reproduction

This 5-page appendix describes the field and laboratory protocols used in the random surveys reported in Chapter 3. Supplemental figures and tables for Chapter 3 follow.

Field Equipment

1. Cooler(s) with ice for the samples
2. Labelled ziplock bags for the samples
3. 50 m quadrat for each team
4. 2 0.25 m^2 quadrats for each team
5. 2 paring knives for each team (bring extras)
6. 2 pair of straight forceps for each team (bring extras)
7. Knee pads or a gardening pad for each person
8. Gloves, for gardening or surfing, to avoid abrasions
9. Field notebooks and pencils for each team
10. Rulers for each team (to figure out what 2 mm is)

Field Protocol

1. Identify and if needed, stratify intertidal habitat of interest, e.g. mid vs. high zones.
2. Lay a 50 m transect through the biological center of each zone (or other sub-habitat). Based on random numbers, sample 12 quadrats along the 50 m transect.
3. Record the date, time started, and participants. Write the random numbers (bring 15, in case a couple are in tide pools) in your notebook, and record which you use and whether the center 100 cm^2 sampled is primarily (> 50%) mussel bed or 'gap' habitat. This information is useful to explore small-scale variation in barnacle density and reproduction, as well as the patchiness of gap vs. mussel bed habitat.
4. Within each 0.25 m^2 quadrat, locate the center 100 cm^2. Collect all barnacles (of the species *Balanus glandula*) greater than 2 mm in basal diameter within this center square. Collecting all the animals is important, in order to get a measure of barnacle density. In Oregon, *B. glandula* tend to be whiter and taller than *Chthamalus* spp., with distinct opercular plates. *Balanus* individuals have fewer ridges on their carapaces than *Semibalanus cariosus*. *Balanus* individuals have an opaque basal plate, whereas *Semibalanus* individuals do not.
5. Place collected barnacles in the labeled bag, and when done with the quadrat, put the sealed bag in the cooler.
6. Do again, till you are done with your assigned quadrats/transects!
7. Bring the barnacles back to the lab. If you aren't going to process them that day, collect them on dry ice and putting them in a –20 deg F freezer immediately. They keep better.

Note When I sampled mid and high zones at a specific intertidal site (with a 2.5-5 hr window of low water), I worked either alone or with one or two helpers. With one helper, we worked simultaneously on the same transect, as a 'team'. I laid out the quadrats for the other person to sample within, based on the random numbers and she collected the barnacles as directed. With a team of two people (a helper and myself), we usually finished the two zones' transects (24 quadrats total, but many fewer animals in the mid zone) in 2.5-3 hours.

Lab Equipment

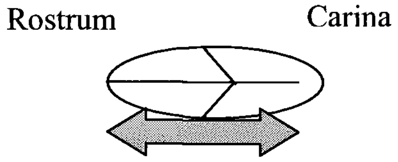
1. Dissecting kit (primarily a pointy tool, to examine the animal)
2. Calipers (ideally digital),
3. Light (to see the samples better)
4. Paper towels, and
5. Data sheet
6. Counter (to record densities)

Lab Protocol for Reproduction

(Adapted from a protocol written by H. Leslie and E. Breck)

1. Prepare data sheet and then remove a sample bag (for one quadrat) from the cooler or freezer.
2. Remove barnacles from the replicate bag, and lay on paper towel. If they are small barnacles, don't put them directly in the light – they'll dry out fast. Let larger animals defrost 5-10 minutes before recording reproductive status. But you can measure them while you're waiting.
3. Start processing: measure height and diameters.
4. Record reproductive status – see the notes below.
5. Process up to 50 animals per quadrat. If you have more than 50 individuals that are > 2 mm in basal diameter, count them and record the TOTAL number / quadrat as a measure of abundance/100 cm^2.
6. See comments below regarding barnacle morphology and reproduction.

Measurements taken for laboratory processing of barnacles.

Measurement	Description
Height	Measure the maximum height (in mm)
Basal diameter	Measure the maximum basal diameter (mm), where the shell is fairly complete all around.
Opercular diameter 	Measure the distance of the valves (mm) from the carina to the rostrum (the two end plates) of the barnacle. This is the only non-maximum measurement you take.

Measurements (continued).	
Gonadal score	b = brood yy = yellow yolky ovary py = pale yolk (also ovary), lacking yellow color s = abdomen visible, without yolky material The ‘brood’ is a distinct grainy mass, whereas ‘yy’ is a gooey and opaque yellow fluid. Check the material in a bit of ‘instant ocean’ underneath the scope if you aren’t sure: The brood mass of embryos will consist of distinct yellow ellipsoids. More mature embryos will have black or red eyes. Broods that are early in development are more bright yellow, late broods (close to hatching) are often more orange or chocolate in color.
Brood Stage	Brood stage = ‘early’ or ‘late’. This indicates the age of the embryos. a. Early: yellow embryos do not have eyes yet and are fairly early in development. If the brood mass is a shade of yellow, label it ‘early’ UNLESS > 1/2 of the embryos have red or dark eyes. In that case, score the brood as 'late', meaning close to hatching. b. Late: The chocolate or orange brood masses have embryos close to hatching, often with red or black eyes. Some of the late-stage broods will ‘hatch’ and students will be able to see the naupliar forms.
Shell weight	Classify the shell weight based on a pinch test: - Thin: crushes easily - Med: crushes - Thick: doesn’t crush without sig. effort
Seminal vesicle size	Score from 0 (not visible) to 3 (distended and highly visible) by examining the white vesicles within the soma.

Laboratory protocol for counting broods

(Courtesy of E. Breck, and adapted from a protocol from M. Berger)

To quantify the number of larvae per brood, we carefully dissected out broods from adult animals in the lab (following the activities described above), and counted replicate sub-samples of the embryos (or larvae, depending on their age) in solution to estimate the overall brood size.

In order to count the embryos, they must first be gently dissociated from the lamellar membrane – particularly if they are early stage embryos.

A. Membrane Destruction:

1. Remove protease (see recipe below) from freezer and defrost for 15 minutes.
2. Tap the lamellae to the bottom of the centrifuge tube.
3. Using a pipette, add protease in a volume of 20 uL, 50 uL, or 100 uL to lamellae of small, medium and large size respectively. Enough protease is added to just cover the lamellae.
4. Allow the lamellae to sit in protease for 45 minutes.
5. After 45 minutes, centrifuge the tube for 1 minute at 1,000 rpm.
6. Carefully pipette off the layer of protease.
7. Add 300 uL of 100 mM Na_2HPO_4 and NaOH buffer solution to tube in order to wash embryos – this stop stops the protease reaction.
8. Tap the tube gently, vortexing the embryos in the wash.
9. Centrifuge the tube for 1 minute at 1,000 rpm.
10. Carefully pipette off the top layer of wash, being careful not to entrain embryos.
11. Add 300 uL of the 100 mM Na_2HPO_4 and NaOH buffer solution to the tube.
12. Allow the embryos to sit in this solution until you are ready to count them. If they will sit longer than 1 hour, place vials back in 11° C fridge. ** Do not leave in this condition for more than 2 days.

B. Counting Embryos:

1. Remove vials from the fridge.
2. Centrifuge the tube for 1 minute at 1,000 rpm.
3. Pipette off the 100 mM Na_2HPO_4 and NaOH buffer solution.
4. To vial add 1 mL of sterile seawater (e.g. Instant Ocean).
5. Swirl the vial and pour the contents into a 50 mL centrifuge tube.
6. Repeat steps 4 and 5, four times in order to remove all embryos from vial.
7. Use a pipette to deliver 14 mL Instant Ocean to the 50 mL centrifuge tube.
8. If clumps of embryos remain in the solution use a syringe to break them apart. This is done by gently drawing the embryo clumps into the syringe and slowly pushing them out the tip. Repeat as necessary.
9. To remove the embryos that remain in the syringe, rinse the syringe with 1mL Instant Ocean and place the rinse water into the 50 mL centrifuge tube. To

those tubes that require no syringe action, use a pipette to add 1mL Instant Ocean. This ensures that the volume in all tubes remains the same.

10. If prepared to count, turn the vortex machine on at lowest setting and place centrifuge tube on it to vortex (if not prepared to count see step 13).
11. Carefully vortex the solution in the vile while removing a 1 mL sample using a pipette. Place the sample in a row of the counting tray. Under a microscope, count the number of embryos and record.
12. We suggest eight replicate counts be done to estimate brood size. So repeat step 11 seven times.
13. If not prepared to count, place the 50 mL centrifuge tube at 11° C until ready to proceed with counting. ** Leave in fridge no longer than 2 weeks.

Solutions to Prepare Before Counting Broods

1% Protease Solution:

1. Weigh 25 mg protease (Type VIII Bacterial from Sigma-Aldrich, Stock # P5380) and place in Erlenmeyer flask
2. To this flask use a pipet to add 2,475 uL Instant Ocean. This gives a concentration of 1%
3. Place a lid on the flask and vortex it for five minutes in order to dissolve protease.
4. Using a repeating pipet place 100 uL portions of the solution into individual centrifuge tubes.
5. Label the tubes and place them in a storage box in freezer at -20 ° C.

Buffer Solution: 100 mM Na_2HPO_4 solution, titrated with NaOH to a pH of 11.0

1. Weigh 14.2 grams of Na_2HPO_4 in weigh boat.
2. In an Erlenmeyer flask add 300 mL deionized water; to this volume add the Na_2HPO_4 weighed out in step 1.
3. Rinse the weigh boat and sides of Erlenmeyer flask with deionized water to remove any remaining powder of Na_2HPO_4 (approximately 5mL for rinse).
4. Place the flask on a stir plate, put stir bar inside flask and stir until Na_2HPO_4 is completely dissolved.
5. Next fill the Erlenmeyer flask with deionized water to the 800 mL mark.
6. Place a calibrated pH probe into the flask and titrate the solution to a pH of 11.0 using 1M NaOH.
7. Transfer the solution to a 1L volumetric flask and fill this flask to a 1L volume.
8. Using a filter, transfer the solution to a bottle, label and store at 11° C.

Appendix B2. Supplementary Tables and Figures, Chapter 3

Table B1. Coordinates and estimated tidal heights for each site. Heights (meters above mean lower low water: m, MLLW) were determined using standardized survey methods during minus tides. Where random surveys were conducted, the approximate midpoint of each zone is listed.

Site	Latitude, Longitude	Tidal Height	
		Mid	High
Cape Foulweather			
Fogarty Creek (FC)	44.84 °N, 124.06 °W	+2	+3
Depoe Bay North (DBN)	44.81 °N, 124.06 °W	+3	+3.5
Depoe Bay South (DBS)	44.80 °N, 124.07 °W	--	--
Cape Perpetua			
Yachats Beach (YB)	44.32 °N, 124. 11 °W	--	--
Strawberry Hill (SH)	44.25 °N, 124.11 °W	+2	+2.5
Bob Creek (BC)	44.24 °N, 124.11 °W	+2	+2.5

Table B2. Analysis of variance results from the haphazard (a) and random (b-h) field surveys of the barnacle *B. glandula* in Oregon (USA), 2002-2003. Effects with p<0.05 are in bold.

Source of variation	df	ss	*F*	*P*	Vc[a]	% of Total
a. Brooding frequency (Haphazard survey: June 2002-2003)						
Time	6	71667.388	7.793	**0.001**	--	--
Cape	1	2328.452	1.843	0.307	--	--
Time * Cape	6	26409.812	2.872	0.057	--	--
Site (Cape)	2	2526.347	0.824	0.462	-7.703	-2.017
Site(Cape) * Time	12	18393.349	14.768	**<0.0001**	285.797	74.838
Error	112	11624.706	--	--	103.792	27.179
b. Barnacle abundance (i.e. square-root (Barnacles per 100 cm^2)) [b]						
Cape	1	905.857	111.376	**0.009**	--	--
Site(Cape)	2	16.260	0.232	0.794	-1.136	-3.345
Zone	1	1233.092	35.125	**<0.0001**	--	--
Cape * Zone	1	186.168	5.303	**0.024**	--	--
Error	89	3124.450	--	--	35.106	103.345
c. Mean ratio of barnacle height to basal diameter per quadrat [b]						
Cape	1	0.210	5.474	0.144	--	--
Site(Cape)	2	0.222	2.893	0.061	0.005	11.901
Zone	1	1.461	38.026	**<0.0001**	--	--
Cape * Zone	1	0.775	20.180	**<0.0001**	--	--
Error	80	3.074	--	--	0.038	88.099
d. Barnacle size (i.e. mean basal diameter per quadrat) [b]						
Cape	1	0.362	0.633	0.510	--	--
Site(Cape)	2	1.020	0.892	0.414	0.024	4.016
Zone	1	63.547	111.223	**<0.0001**	--	--
Cape * Zone	1	0.011	0.020	0.888	--	--
Error	80	45.708	--	--	0.571	95.984

---

[a] *VC=Variance components, which were calculated using the REML method, except when negative variance components occurred. In these cases, the traditional EMS approach was used. See Methods for details.*

[b] *Site(Cape)*Zone term was non-significant (P>0.05), and thus was eliminated from the model.*

Table B3. Multiple regression results for larval production per barnacle based on subsets of the random field survey data. Effects with p<0.05 are in bold.

Source of variation	R^2	df	ss	*F*	*P*	VC[a]	% of Total
a. ln (number of larvae produced per barnacle) [Apr03: FC, SH, BC]							
Basal diameter	0.50	1	24.359	56.376	**<0.0001**	--	--
Height:Bas. diam.		1	6.718	15.547	**0.0001**	--	--
Site		2	0.698	0.141	0.876	-0.055	-11.424
Zone		1	0.043	0.025	0.887	--	--
Site * Zone		2	5.454	6.311	**0.002**	0.106	21.952
Error		130	56.171	--	--	0.432	89.472
*b. Larval production per barnacle contrast based on the Site*Zone term*							
Cape effect[b]		1	0.594	1.374	0.243	--	--
Error		130	56.171	--	--	--	--
c. ln (number of larvae per barnacle) *[Aug02, Apr03, Jun03, mid zone SH and FC]*							
Basal diameter	0.60	1	44.513	112.617	**<0.0001**	--	--
Height:Bas. diam.		1	16.748	42.372	**<0.0001**	--	--
Time		2	5.877	7.434	**0.0009**	--	--
Error		119	47.036	--	--	--	--
d. ln (number of larvae per barnacle) [Apr03: FC, SH, BC]							
Basal diameter	0.44	1	43.155	92.318	**<0.0001**	--	--
Height:Bas. diam.		1	7.197	15.396	**0.0001**	--	--
Error		135	63.107	--	--	--	--

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[a] *VC=Variance components were calculated using the traditional EMS approach due to the presence of negative variance components.*

[b] *Cape effect linear contrast compared FC vs. SH, BC.*

Table B4. Regression results regarding barnacle size and larval production per barnacle for each site and intertidal zone combination sampled in April 2003.

Source of variation	R^2	df	ss	*F*	*P*
a. ln (larval production per barnacle) [FC mid zone]					
Mean basal diameter	0.0002	1	0.002	0.005	0.947
Error		22	8.906		
Equation:	ln(#larvae/barn) = 6.40 - 0.01(basal diameter)				
b. ln (larval production per barnacle) [FC high zone]					
Mean basal diameter	0.16	1	1.959	4.263	0.050
Error		23	10.569		
Equation:	ln(#larvae/barn) = 6.10 - 0.22(basal diameter)				
c. ln (larval production per barnacle) [SH mid zone]					
Mean basal diameter	0.55	1	13.564	25.732	< **0.0001**
Error		21	11.069		
Equation:	ln(#larvae/barn) = 4.10 - 0.42(basal diameter)				
d. ln (larval production per barnacle) [SH high zone]					
Mean basal diameter	0.30	1	3.207	9.702	**0.005**
Error		23	7.603		
Equation:	ln(#larvae/barn) = 6.04 - 0.20(basal diameter)				
e. ln (larval production per barnacle) [BC mid zone]					
Mean basal diameter	0.48	1	4.681	20.848	**0.0001**
Error		23	5.165		
Equation:	ln(#larvae/barn) = 5.03 - 0.34(basal diameter)				
f. ln (larval production per barnacle) [BC high zone]					
Mean basal diameter	0.05	1	0.819	0.787	0.390
Error		14	14.558		
Equation:	ln(#larvae/barn) = 5.95 - 0.20(basal diameter)				
g. ln (larval production per barnacle) [DBN high zone]					
Mean basal diameter	0.45	1	5.244	12.088	**0.003**
Error		15	6.508		
Equation:	ln(#larvae/barn) = 3.22 - 0.45(basal diameter)				

Table B5. Analysis of variance and covariance results for barnacle reproduction based on subsets of the random field survey data. Effects with $p<0.05$ are in bold.

Source of variation	df	ss	*F*	*P*	VC[a]	% of Total
a. Mid zone brooding frequency (DBN excluded, Jun02-Jun03)						
Time	5	12262.056	5.677	**0.008**	--	--
Site	2	611.624	0.683	0.527	-2.396	-0.940
Time * Site	10	4510.442	1.912	**0.046**	21.439	8.407
Basal diameter	1	12080.687	51.197	**<0.0001**	--	--
Time * Bas. diam.	5	8136.205	6.896	**<0.0001**	--	--
Error	178	42001.395	--	--	235.963	92.532
*b. Mid zone brooding frequency contrast based on the Site*Time term*						
Cape effect[b]	1	589.747	2.499	0.116	--	--
Error	178	42001.395	--	--	--	--
c. Mid zone ln (1+larval production/100 cm^{2}) [Jun02-Jun03, no DBN]						
Time	5	1023.143	6.828	**0.005**	--	--
Site	2	52.687	0.881	0.444	-0.053	-0.287
Time * Site	10	299.870	1.707	0.082	1.110	5.956
Error	184	3233.243	--	--	17.572	94.331
*d. Mid zone larval production contrast based on the Site*Time term*						
Cape effect[2]	1	48.610	2.766	0.098	--	--
Error	184	3233.243	--	--	--	--

[a] *VC=Variance components were calculated using the traditional EMS approach due to the presence of negative variance components.*

[b] *Cape effect linear contrast compared FC vs. SH, BC.*

Table B5 (Continued). Analysis of variance and covariance results regarding barnacle reproduction.

Source of variation	df	ss	*F*	*P*	VC^a	% of Total
e. High zone brooding frequency (All sites, Aug02-Jun03)						
Time	4	45416.150	9.667	**0.004**	--	--
Cape	1	0.353	0.001	0.983	--	--
Site(Cape)	2	1249.509	0.533	0.606	-10.043	-6.173
Time * Cape	4	3071.986	0.696	0.616	--	--
Time * Site(Cape)	8	9431.584	16.413	**<0.0001**	100.898	62.021
Basal diameter	1	774.935	10.789	**0.001**	--	--
Time * Bas. diam.	4	1960.277	6.823	**<0.0001**	--	--
Error	206	14796.576	--	--	71.828	44.152
f. High zone ln (1+larval production/100 cm^2) [All sites, Aug02-Jun03]						
Time	4	253.566	11.302	**0.002**	--	--
Cape	1	9.437	1.683	0.324	--	--
Site(Cape)	2	20.643	1.840	0.220	2.722	17.856
Time * Cape	4	16.875	0.752	0.584	--	--
Time * Site(Cape)	8	655.935	14.619	**<0.0001**	6.915	45.355
Error	210	1177.824	--	--	5.609	36.788
g. Mid zone ln(1+recruitment/100 cm^2) [Jun02-Jun03]						
Time	5	24.674	12.110	**0.001**	--	--
Cape	1	0.030	0.074	0.812	--	--
Site(Cape)	2	0.937	1.149	0.355	11.812	0.143
Time * Cape	5	2.018	0.990	0.470	--	--
Time * Site(Cape)	10	32.538	7.985	**<0.0001**	54.623	0.663
Error	92	37.491	--	--	33.565	0.408

---

[a] VC=Variance components, which were calculated using the REML method, except when negative variance components occurred. In these cases, the traditional EMS approach was used. See Methods for details.

Table B6. Analysis of variance results for the population-level responses in the plate experiment.

Source of variation	df	ss	*F*	*P*	VC[a]	% of Total
a. Number of recruits per 100 cm^2						
Cape	1	0.068	0.000	0.984	--	--
Site(Cape)	4	587.288	0.884	0.475	-0.780	-0.472
Error	143	23758.210	--	--	166.141	100.472
b. Per capita mortality						
Cape	1	0.008	0.330	0.597	--	--
Site(Cape)	4	0.854	9.202	**<0.0001**	0.008	26.506
Error	143	3.317	--	--	0.023	73.494
c. Brooding frequency						
Cape	1	1652.728	5.348	0.082	--	--
Site(Cape)	4	6310.240	5.104	**0.0007**	61.231	16.536
Error	143	44195.512	--	--	309.060	83.464
d. ln(larval production per barnacle) [FC, YB, SH, BC]						
Site	3	1.229	7.391	**0.0008**	0.152	73.265
Error	29	1.607	--	--	0.055	26.735
e. Linear contrast re larval production per barnacle						
FC vs. YB, SH, BC	1	1.195	21.561	**<0.0001**	--	--
Error	29	1.607	--	--	--	--
f. ln (1+larval production per 100 cm^2) [All sites]						
Cape	1	75.522	7.907	**0.048**	1.585	14.233
Site(Cape)	4	162.913	4.264	**0.003**	9.551	85.767
Error	143	1365.820	--	--	--	--

---

[a] *VC=Variance components, which were calculated using the REML method, except when negative variance components occurred. In these cases, the traditional EMS approach was used. See Methods for details.*

Table B7. Analysis of variance results for the individual-level responses in the plate experiment.

Source of variation	df	ss	*F*	*P*	VC[a]	% of Total
a. Barnacle size (i.e mean basal diameter per plate)						
Cape	1	33.091	64.625	**0.001**	--	--
Site(Cape)	4	14.014	6.842	**<0.0001**	0.246	32.444
Error	76	38.916	--	--	0.512	67.556
b. ln (1+ mean shell mass, mg)						
Cape	1	0.249	6.919	0.058	--	--
Site(Cape)	4	0.486	3.381	**0.014**	0.012	24.525
Mean bas. diam.	1	4.759	132.387	**<0.0001**	--	--
Error	70	2.516	--	--	0.036	75.475
c. ln (1+mean somatic tissue mass, mg)						
Cape	1	9.378×10^{-7}	3.636×10^{-5}	0.995	--	--
Site(Cape)	4	0.022	0.214	0.930	0.0005	1.854
Mean bas. diam.	1	2.019	78.301	**<0.0001**	--	--
Error	74	1.909	--	--	0.026	98.146
d. Mean gonad mass, mg [All barnacles]						
Cape	1	0.640	0.853	0.408	--	--
Site(Cape)	4	11.662	3.886	**0.006**	0.203	21.280
Mean bas. diam.	1	32.018	42.672	**<0.0001**	--	--
Error	74	55.523	--	--	0.750	78.720
e. Mean brood mass, mg [Brooding barnacles only]						
Site	3	0.133	0.583	0.631	0.008	9.215
Mean bas. diam.	1	2.087	27.521	**<0.0001**	--	--
Error	28	2.124	--	--	0.076	90.785

[a] *VC=Variance components were calculated using the REML method. See Methods for details.*

Table B8. Regression results regarding barnacle size and individual biomass allocation in the plate experiment.

Source of variation	R^2	df	ss	*F*	*P*
a. ln (1 + mean shell mass, mg)					
Mean basal diameter	0.94	1	51.854	1189.790	**<0.0001**
Error		75	3.269		
b. ln (1+mean somatic tissue, mg)					
Mean basal diameter	0.85	1	11.378	441.815	**<0.0001**
Error		79	2.035		
c. ln (1+mean gonadal tissue, mg)					
Mean basal diameter	0.78	1	24.400	275.735	**<0.0001**
Error		79	7.850		
d. ln (1+mean brood mass, mg)					
Mean basal diameter	0.49	1	2.395	29.895	**<0.0001**
Error		31	2.484		

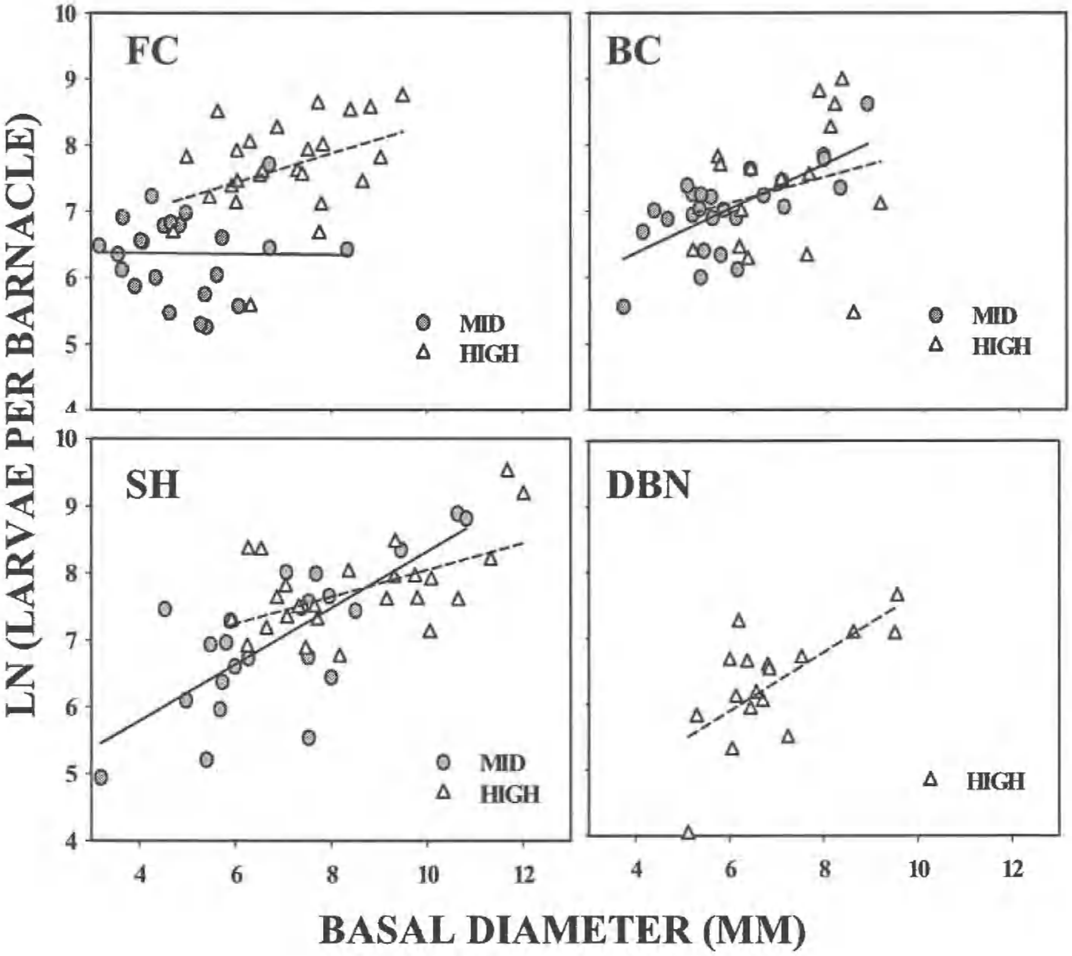

Fig. B1. Associations between barnacle size and larval production per barnacle in natural populations. Each site (FC, SH, BC, and DBN) and intertidal zone (mid vs. high) combination sampled in April 2003 is shown. Mid and high zone regression lines are coded as solid and dashed lines, respectively. DBN data are shown for comparative purposes only, as they were not included in the statistical analyses in Table B3.

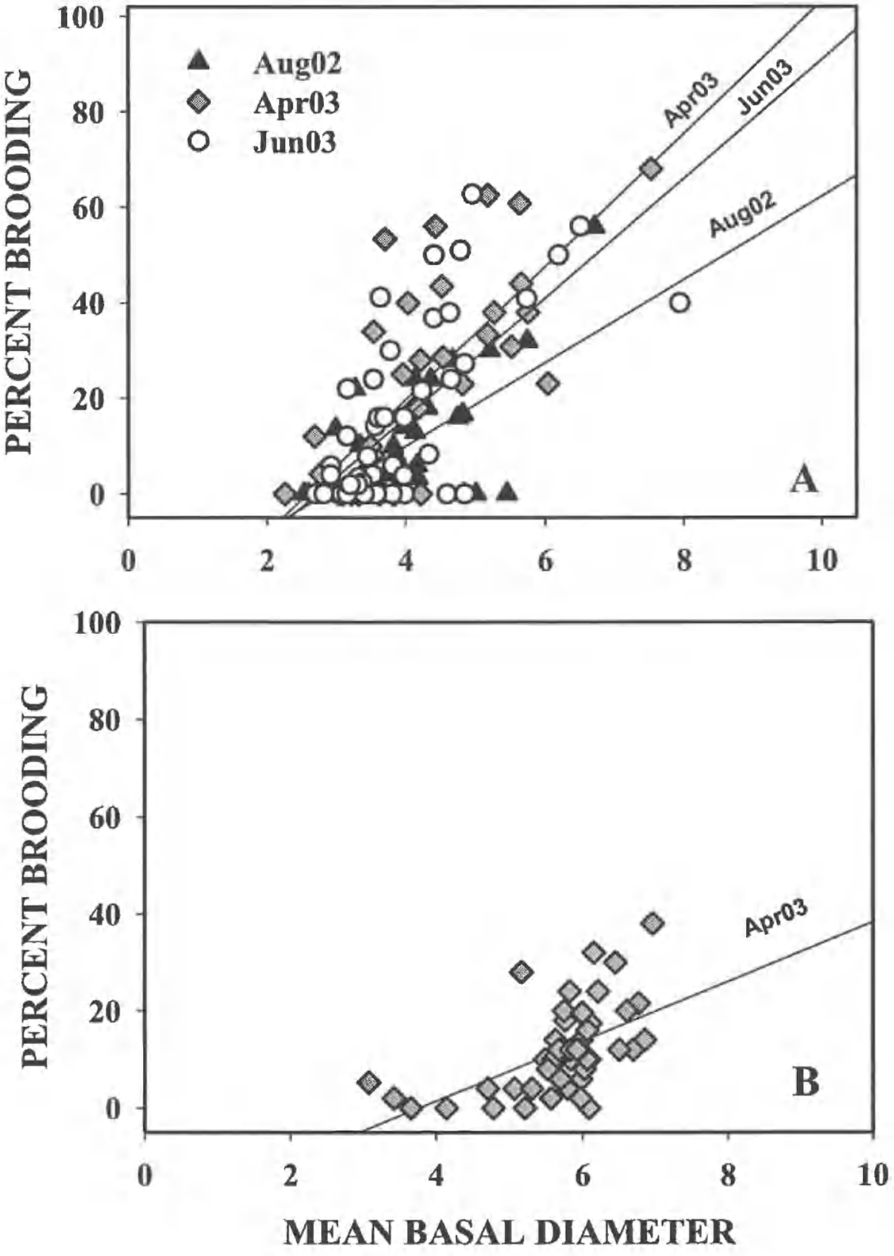

Fig. B2. Associations between barnacle size and brooding frequency in natural populations. (A) In the mid intertidal zone, significant associations occurred in Aug. 2002 (Linear regression (LR): $R^2=0.47$, $p<0.0001$, df=1,44), April 2003 (LR: $R^2=0.53$, $p<0.0001$, df=1,34), and June 2003 (LR: $R^2=0.47$, $p<0.0001$, df=1,46). (B) In the high intertidal zone, a significant association occurred only in April 2003 (Linear regression: $R^2=0.30$, $p<0.0001$, df=1,46).

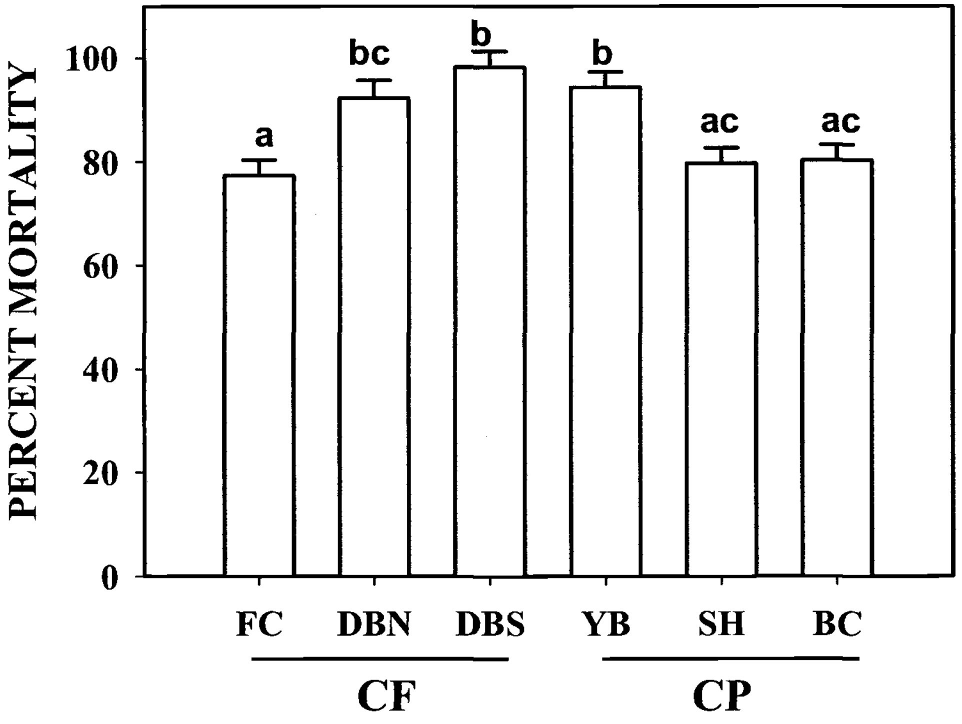

Fig. B3. Percent mortality in the outplant experiment. Cape Foulweather (CF) sites were FC, DBN and DBS. Cape Perpetua (CP) sites were YB, SH, and BC. See Fig. 1 for full site names. Means with dissimilar letters were different (Tukey-Kramer test on LS means, $p<0.05$). LS means + SE are shown (n=20-26 plates).

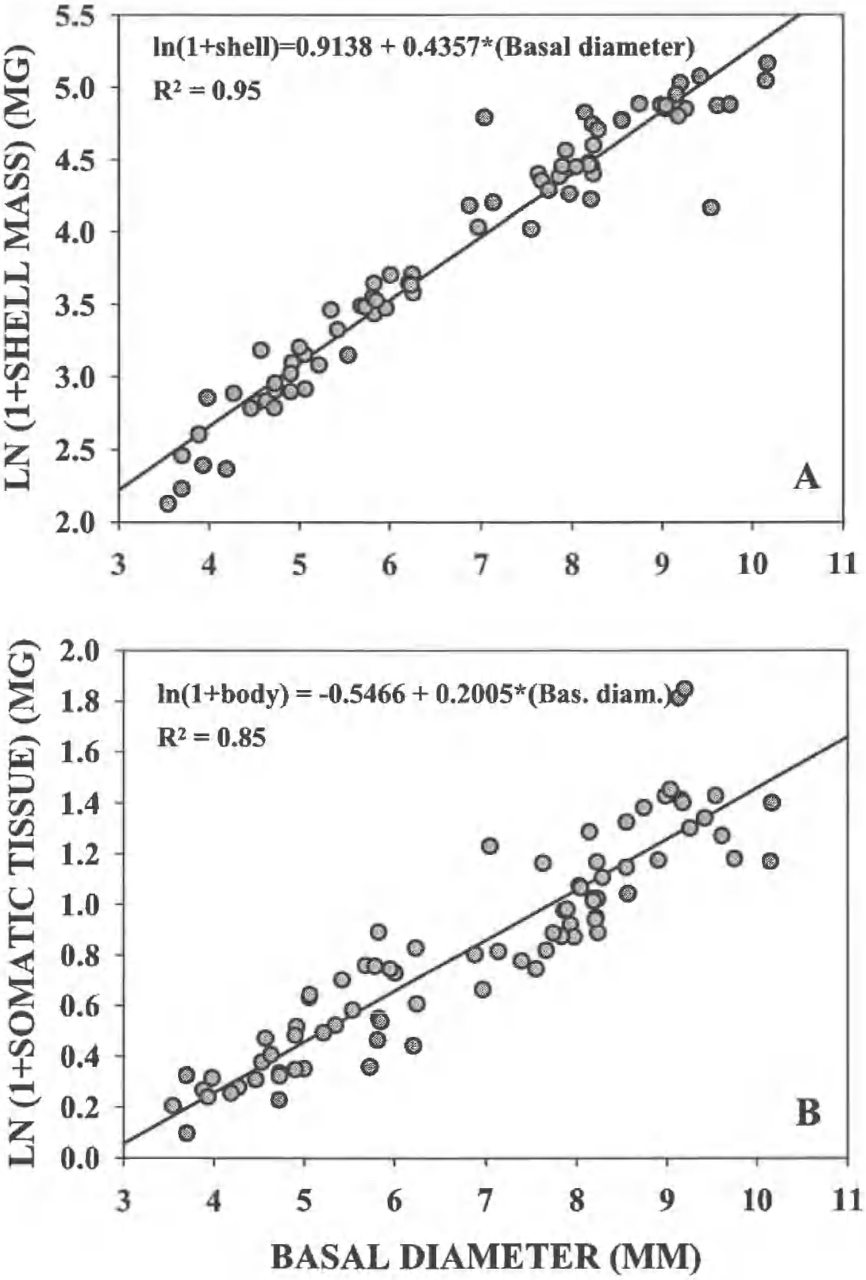

Fig. B4. Relationships between barnacle size and individual biomass allocation in the outplant experiment. The associations were quite strong, based on data from experimental barnacle populations at six sites in Oregon (USA), April 2003. Plate-level means are shown. Regression results are presented in Table B8. (A) Shell mass (mg) vs. basal diameter (mm) (n=77 plates). (B) Somatic tissue mass vs. basal diameter (n=81).

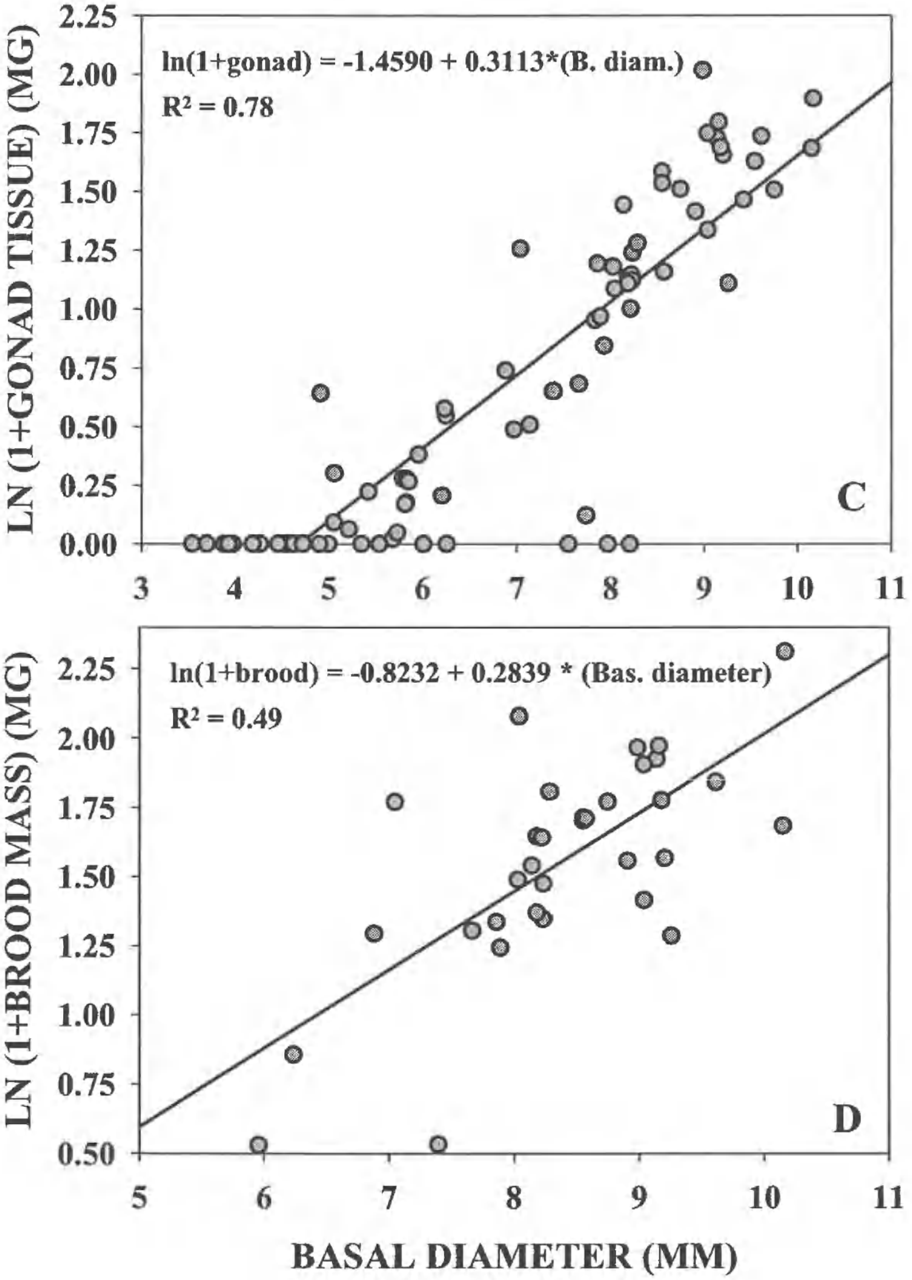

Fig. B4 (Continued). Relationships between barnacle size and individual biomass allocation in the outplant experiment. Plate-level means are shown. (C) Gonadal tissue mass (both broods and ovaries) vs. basal diameter (n=81). (D) Brood mass vs. basal diameter (n=33).

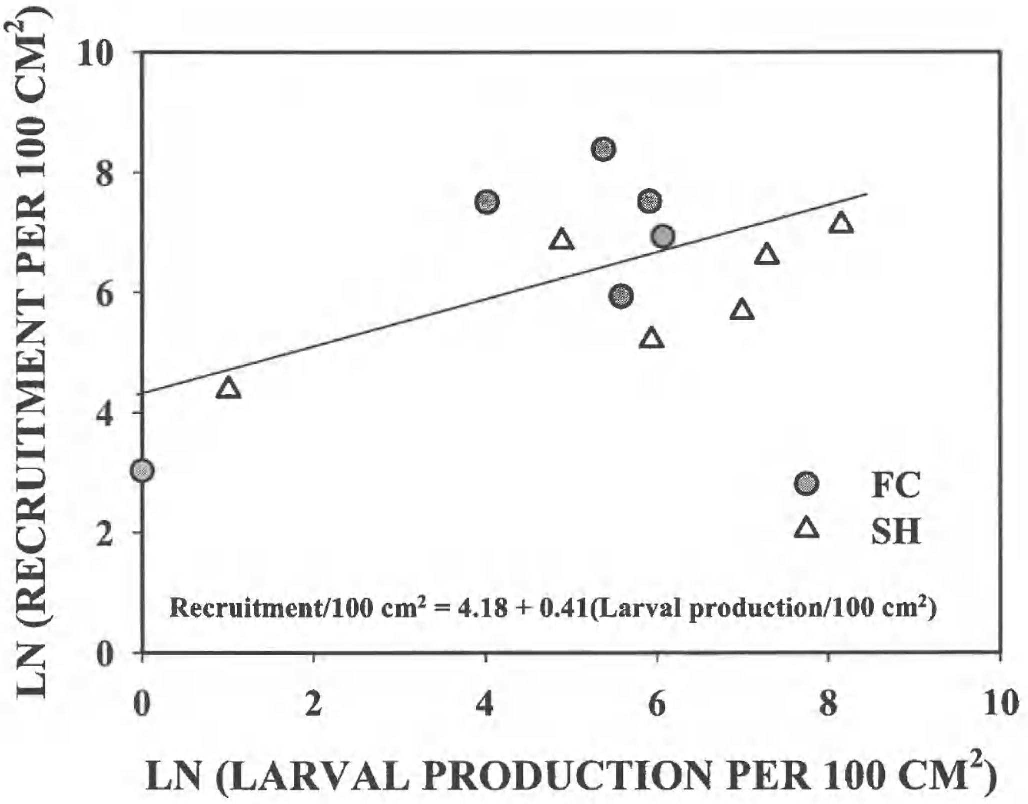

Fig. B5. Correlation between mid zone barnaclelarval production and recruitment in 2002-2003. Ln-transformed values for larval production and recruitment per 100 cm^2 are shown for Fogarty Creek (FC) and Strawberry Hill (SH). Each point is the mean of five replicate samples. The regression line denotes the significant association between larval production and recruitment when data from six sampling periods were pooled across the two sites (Linear regression results: R^2=0.43, F=7.514, *P*=0.021, df=1, 10).