

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Population viability, ecological processes and biodiversity: Valuing sites for reserve selection

Anne K. Salomon^{a,*}, Jennifer L. Ruesink^a, Robert E. DeWreede^b

^aDepartment of Biology, University of Washington, Box 351800, Seattle, WA, 98195-1800, United States

^bCenter for Biodiversity Research, Department of Botany, University of British Columbia, Vancouver, BC, Canada V6T 1Z4

ARTICLE INFO

Article history:

Received 16 May 2004

Received in revised form

10 March 2005

Accepted 20 September 2005

Available online 27 October 2005

Keywords:

Reserve selection and design

Marine reserve

Species richness

Keystone species

Population viability

ABSTRACT

No-take reserves constitute one tool to improve conservation of marine ecosystems, yet criteria for their placement, size, and arrangement remain uncertain. Representation of biodiversity is necessary in reserve planning, but will ultimately fail for conservation unless factors affecting species' persistence are also incorporated. This study presents an empirical example of the divergent relationships among multiple metrics used to quantify a site's conservation value, including those that address representation (habitat type, species richness, species diversity), and others that address ecological processes and viability (density and reproductive capacity of a keystone species, in this case, the black chiton, *Katharina tunicata*). We characterized 10 rocky intertidal sites across two habitats in Barkley Sound, British Columbia, Canada, according to these site metrics. High-richness and high-production sites for *K. tunicata* were present in both habitat types, but high richness and high-production sites did not overlap. Across sites, species richness ranged from 29 to 46, and adult *K. tunicata* varied from 6 to 22 individuals m⁻². Adult density was negatively correlated with species richness, a pattern that likely occurs due to post-recruitment growth and survival because no correlation was evident with non-reproductive juveniles. Sites with high adult density also contributed disproportionately greater potential reproductive output (PRO), defined by total gonad mass. PRO varied by a factor of five across sites and was also negatively correlated with species richness. Compromise or relative weighting would be necessary to select valuable sites for conservation because of inherent contradictions among some reserve selection criteria. We suspect that this inconsistency among site metrics will occur more generally in other ecosystems and emphasize the importance of population viability of strongly interacting species.

© 2005 Elsevier Ltd. All rights reserved.

1. Introduction

There is little doubt that reserves are an important tool for conservation, both on land (Soulé, 1991; Margules and Pressey, 2000) and in the sea (Allison et al., 1998; National Research Council, 2001; Pauly et al., 2002). Ultimately, their purpose is to ensure the persistence of biodiversity and the

ecological processes that maintain it. Consequently, reserves implicitly reflect an ecosystem approach to conservation. Yet, the degree to which reserves are able to achieve this larger objective depends on how well they meet two goals: (1) representation, their ability to capture the full extent of biodiversity, and (2) persistence, the extent to which they support the long-term survival of species (Margules and Pressey,

* Corresponding author. Tel.: +1 206 685 6893; fax: +1 206 616 2011.

E-mail address: salomon@u.washington.edu (A.K. Salomon).

0006-3207/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2005.09.018

2000). Achieving these conservation goals is a three-step process. First, explicit objectives must be established and candidate reserve sites must be characterized according to their conservation value. Then, some method is used to select among sites given their value in reaching a predetermined set of conservation targets (Possingham et al., 2000). Design issues such as size, connectivity, and replication are also considered during this step. Finally, enforcement and monitoring are necessary to operationalize plans and test their effectiveness. Throughout, a typical set of limitations plague the reserve planning process: scarce funds, restricted knowledge, urgency for action, plus a plethora of conservation targets (Prendergast et al., 1999). In this paper we explore the first step in this process and the relationship among multiple metrics used to characterize the conservation value of candidate reserve sites, namely species richness, species diversity, habitat type and the viability of a keystone species. With an empirical example, we show that a site's conservation value differs according to which metric is considered. This is particularly problematic for reserve design because metrics relevant to population viability, particularly of strongly interacting species responsible for driving ecological processes and maintaining diversity (Paine, 1969; Power et al., 1996), tend to be difficult to collect and are often neglected in most reserve planning efforts.

The goal of representation has traditionally been given primacy in conservation plans (Pressey et al., 1993; Araújo and Williams, 2000), primarily because the metrics used to value a candidate site's contribution to this static goal are more easily obtained than those that describe a site's contribution to the dynamics of regional persistence (Williams, 1998; Cabeza and Moilanen, 2001). Species richness, a snapshot of species presence or absence, is the typical site metric considered by selection algorithms designed to optimize conservation targets related to representation (Prendergast et al., 1999), although biological or physical surrogates, such as habitat heterogeneity, are used when species data are unavailable or incomplete (Wessels et al., 1999). However, selecting sites that contain the greatest number of species is not the most efficient way to maximally represent biodiversity (Pimm and Lawton, 1998; Reid, 1998). Rather, conservation efficiency is achieved by maximizing complementarity, the smallest set of sites with the greatest combined coverage of species presence (Kirkpatrick, 1983; Pressey et al., 1993; Williams et al., 1996; Csuti et al., 1997; Kati et al., 2004). This is because the distributions of rare species are not always strongly nested within the distribution of more widespread species (Prendergast et al., 1993; Curnutt et al., 1994; Williams et al., 1996) and species richness of a particular taxon is seldom closely correlated with richness of all taxa (Lombard et al., 1995; Dobson et al., 1997; Howard et al., 1998; Andelman and Fagan, 2000; Tognelli, 2005), although these relationships are highly scale dependent (Prendergast et al., 1993; Curnutt et al., 1994; Vanderklift et al., 1998; Warman et al., 2004). Thus, the value of species-rich sites hinges on nestedness, that is, the extent to which species-poor sites contain subsets of species found in species-rich sites. Other metrics used to value potential reserve sites within the context of achieving representation include species diversity, rarity, endemism, habitat type and irreplaceability; the likelihood that a site will need to be protected to ensure

a regional conservation target is met (Pressey et al., 1993; Pressey, 1994; Ferrier et al., 2000; Tsuji and Tsubaki, 2004). However, it has become increasingly apparent that focusing on the representation of biodiversity does not guarantee the persistence of viable populations or the protection of ecological processes that maintain biodiversity (Smith et al., 1993; Araújo and Williams, 2000; Williams and Araújo, 2000; Cabeza and Moilanen, 2001; Araújo et al., 2002; Kareiva and Marvier, 2003).

Although the literature on conservation planning has long recognized the importance of viability (Margules et al., 1994; Williams et al., 1996; Margules and Pressey, 2000; Possingham et al., 2000), up until recently it had rarely been addressed in the site valuation process or applied site selection methods (Cabeza and Moilanen, 2001; Araújo et al., 2002). Fortunately, new ways of valuing sites are now being developed to account for population persistence. For instance, reserve planners have implicitly acknowledged the role of population dynamics in the placement of reserves by considering the proximity of a site relative to other potential reserve sites, with the intention of reducing reserve edge effects (Nicholls and Margules, 1993; Lombard et al., 1997; Leslie et al., 2003). Probabilities of species occurrences have been used to determine site quality (Cabeza et al., 2004) and, in other cases, have been transformed into estimates of persistence using information on expected threats and species vulnerability (Araújo and Williams, 2000; Williams and Araújo, 2000; Araújo et al., 2002). Areas of high population density, deemed more likely to contribute to a species' regional persistence than areas of low density, have also been used to reflect high quality habitat (Winston and Angermeier, 1995; Rodrigues et al., 2000). However, the theory of source–sink dynamics implies that population density is not necessarily a good indicator of site quality, since populations at high density may nevertheless be sink populations that would inevitably decline without migrants from source populations elsewhere (Pulliam, 1988).

Within a reserve, the persistence of populations is highly influenced by the dispersal ability of: (1) adult organisms the reserve is intended to protect (Zeller and Russ, 1998; Kramer and Chapman, 1999; Walters, 2000; Salomon et al., 2002; Parsons et al., 2003), (2) their offspring (Carr and Reed, 1993), and (3) their predators (including human harvesters) both inside and outside of the reserve (Walters, 2000; Salomon et al., 2002). In marine systems, larval production, retention and connectivity will all affect the population-level consequences of a reserve network (Carr and Reed, 1993; Dugan and Davis, 1993; Quinn et al., 1993; Roberts, 1997; Palumbi, 1999). Of course, population viability also depends on the protection of vulnerable life history stages (Johannes, 1998; Roberts, 1998; Warner and Swearer, 2000), the degree of human and natural threat (Pressey et al., 2004) and the maintenance of essential linkages to other ecosystems (i.e. trophic subsidies) (Bustamante et al., 1995; Roberts et al., 2003a). These various aspects of population persistence should be considered in both marine and terrestrial reserve design.

Marine and terrestrial reserve site selection and design theory has developed along markedly different paths, largely due to the unique ecological traits of these systems (i.e. open vs. closed populations) (Steele, 1985; Carr et al., 2003), the major conservation threats facing each system (Wilcove et al., 1998; Palumbi, 2002), and divergent conservation objectives

and expectations (Carr and Reed, 1993; Carr et al., 2003). Terrestrial reserve design has traditionally focused on the representation of biodiversity (through complementary sites) to address habitat loss, the major cause of endangerment in terrestrial systems (Wilcove et al., 1998). In contrast, because marine reserves (a.k.a. harvest refugia) are often designed as fisheries management tools, design theory has focused on protecting the persistence of spawning stock biomass within a reserve network while increasing production in adjacent fished areas via spillover (of both adults and larvae) that can then be fished (Auster and Malatesta, 1995; Bohnsack, 1996; Allison et al., 1998). Consequently, marine reserve network design has primarily addressed the population dynamics of individual species (for review see Gerber et al., 2003), although some multi-species, ecosystem-based models do exist (Walters, 2000; Salomon et al., 2002; Micheli et al., 2004). Thus, in antithesis to terrestrial reserve theory, population viability, indicative of high quality habitat, has been used more widely as a site metric for selecting marine reserve sites. If populations in a reserve cannot sustain themselves, the reserve will serve neither fishery nor conservation objectives. What remains unclear is how well metrics of persistence overlap with more widely used, easily measured site characteristics of representation, such as species richness.

A remaining challenge is to design reserves (and manage unprotected matrix habitats) in ways that protect the ecosystem processes that maintain diversity. It is now widely understood that the decline of strongly interactive species can have ramifying changes on ecosystem dynamics and biodiversity in both marine (Dayton et al., 1995; Botsford et al., 1997; Fogarty and Murawski, 1998; Jackson et al., 2001; Walters and Kitchell, 2001; Dayton et al., 2002) and terrestrial systems (Terborgh et al., 1999; Oksanen and Oksanen, 2000; Schmitz et al., 2000). Indeed, the argument has been made that human impacts are best addressed through the conservation of ecological interactions, rather than species per se. The former emphasizes the persistence of strongly interacting species that drive system dynamics (Soulé et al., 2003, 2005). While an emphasis on interactions accords with ecosystem-based management (Pikitch et al., 2004), it starkly contrasts with valuing sites purely on species presence or absence which may not include strongly interacting species at functional densities and implies that species' identity is immaterial. Such an omission is worrisome given that the loss of species interactions and their ecological functions may be more dire than the loss of species themselves (Levin and Levin, 2002; Soulé et al., 2003).

The objective of this research was to examine the degree of overlap among metrics used to quantify a site's conservation value in meeting the regional goals of biodiversity representation and persistence. We characterized 10 sites by species richness, nestedness, species diversity, habitat type and the viability of a strongly interacting species, the black chiton, *Katharina tunicata*. This keystone grazer is known to regulate intertidal ecosystem dynamics in the Pacific Northwest and is directly exploited by humans in some coastal areas. We focused on three population-level attributes that contribute to population viability: density, size structure, and potential reproductive output (PRO). Therefore, we were able to address a subpopulation's potential contribution to

K. tunicata's regional larval pool. We hypothesized that site valuation would be complicated by the addition of a metric that reflects site dynamics, namely the production of a strongly interacting species, to more common site metrics of species richness and habitat type. However, population viability, particularly of species known to be primary drivers of ecosystem dynamics, must be considered as an important metric for valuing a site's contribution to the persistence of regional biodiversity.

2. Methods

2.1. Study area and species

This research was conducted at 10 rocky intertidal sites within the Deer Group archipelago located in Barkley Sound, British Columbia, Canada (Fig. 1(a)–(c)). Each site consisted of one side of a small island experiencing similar environmental conditions. In Barkley Sound, predominant wind and ocean swell originate from the northwest, creating a gradient of wave exposure from west to east within the archipelago. Site aspect plus adjacent seafloor topography dampened or magnified the degree of wave exposure at each site. We expected differences in wave exposure to influence intertidal species richness and the performance of particular species (Dayton, 1971; Bustamante and Branch, 1996), in this empirical case, the black chiton, *K. tunicata*.

K. tunicata is a dominant herbivore known to greatly influence intertidal community structure in the Pacific Northwest of Canada and the United States (Dethier and Duggins, 1984; Dethier and Duggins, 1988; Paine, 1992; Markel and DeWreede, 1998; Paine, 2002). It is exploited as a subsistence fishery by Native tribes in Alaska (Stanek, 1985; Fall and Utermohle, 1999; Chugachmiut, 2000) and represents an important component of some coastal native diets and cultures along the west coast, although less so now in Barkley Sound. *K. tunicata* consumes bladed macroalgae, articulated coralline algae, epiphytic diatoms and small sessile benthic invertebrates in the mid-low rocky intertidal zone (Dethier and Duggins, 1984). In Washington, *K. tunicata* reportedly has the highest per capita interaction strength among all intertidal molluscan grazers (Paine, 1992). Perhaps most importantly, this keystone grazer has been shown to fundamentally alter algal species composition, decrease algal species diversity, and reduce algal productivity by an order of magnitude (Paine, 2002).

Like many marine species, *K. tunicata* is a broadcast spawner subject to metapopulation dynamics. Its larvae are pelagic for approximately 6 days (Strathmann, 1987), therefore, we presume that larvae recruiting to the Deer Group Archipelago come from within Barkley Sound and/or the west coast of Vancouver Island depending on the degree of retention and the strength and direction of prevailing ocean currents. *K. tunicata* is an ideal species to use to explore the relationship between local species richness, species diversity, habitat, and the potential reproductive output of a strongly interacting species because of its important functional role in intertidal ecosystems and its propensity to become locally depleted in areas where it is fished (Salomon et al., 2004).

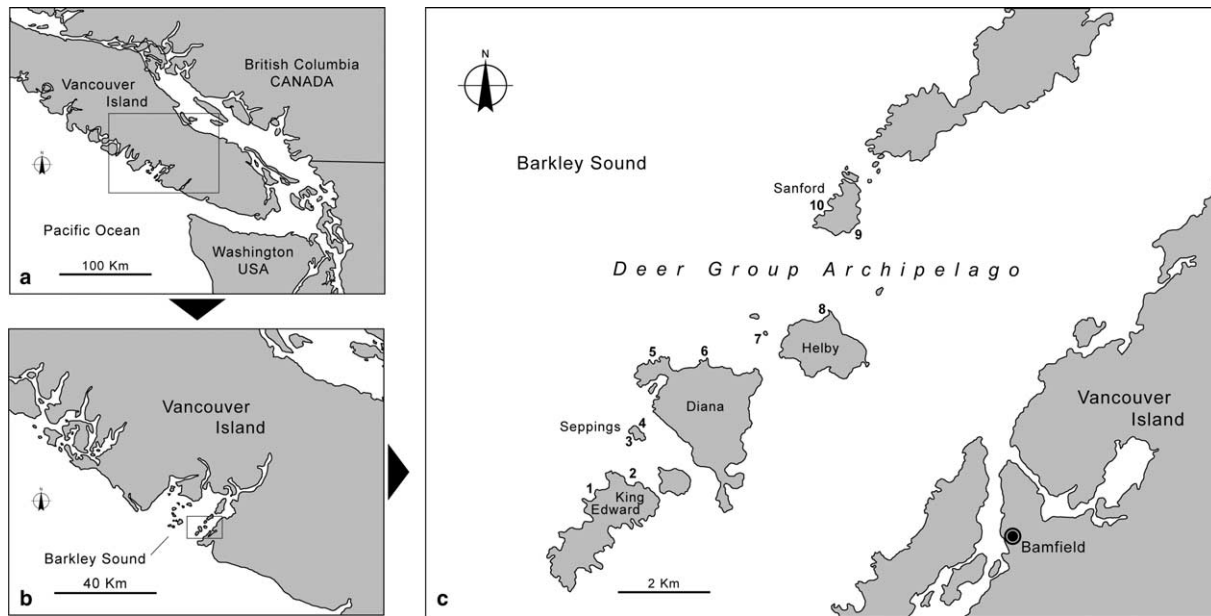


Fig. 1 – The Deer Group archipelago is located (a) on the west coast of Vancouver Island, British Columbia, Canada, (b) within Barkley Sound. (c) Outer islands located to the southwest are more exposed than inner islands located to the northeast. 1 = Edward King Exposed, 2 = Edward King Sheltered, 3 = Seppings Exposed, 4 = Seppings Sheltered, 5 = Diana Sheltered, 6 = Diana Exposed, 7 = Helby Sheltered, 8 = Helby Exposed, 9 = Sanford Exposed, 10 = Sanford Sheltered.

2.2. Site metrics addressing the representation of biodiversity

2.2.1. Habitat type based on wave exposure

Habitat type was classified based on wave exposure, which was quantified at each site using a maximum wave force recorder (Bell and Denny, 1994) that was deployed and revisited up to three times per low tide series in August, September and October 1999. On each visit, spring extensions were measured to the nearest 0.5 mm and were reset. Spring extension data collected in the field were then converted into maximum wave force (Newtons) with calibration curves established earlier in the lab. These data were used to confirm our classification of sites into two habitats, wave-exposed and semi-protected. All 10 rocky intertidal sites included *Hedophyllum sessile*, a brown alga indicative of suitable *K. tunicata* habitat (Kozloff, 1973; O'Clair and O'Clair, 1998).

2.2.2. Species richness and diversity

To quantify intertidal species diversity, a 40 m long transect line was placed horizontally to the shore in the middle of the *Hedophyllum sessile* zone. The percent cover of all macroscopic invertebrates and algae was quantified within ten 0.0625 m² quadrats randomly stratified along the transect line. Each quadrat had 50 points randomly positioned on a grid and organisms appearing under each point were recorded. To account for extensive species overlap and the three-dimensional nature of the community, 3 distinct layers were surveyed per quadrat: the canopy, understory and substrate. The percent cover for each species was expressed as a percentage of the number of points occupied over the total number of points. With 50 points per layer, each random

point occupied was equivalent to 2% cover. In 3 layers, the total number of points was 150; consequently, the total percent cover possible in one quadrat was 300%. To account for species rarity, any organism within the quadrat that was not found directly below a random point was accounted for as <1%. Species accumulation curves reached a plateau after approximately eight quadrats across all 10 sites. Therefore, a sample size of 10 quadrats adequately captured the species diversity at each site. Site-specific species diversity was calculated with the Shannon–Wiener diversity index (H').

2.2.3. Analysis of species nestedness

The degree of species nestedness among sites was quantified to determine if low-richness sites contained subsets of species found at high-richness sites. We used the 'Nestedness Calculator' software package (Atmar and Patterson, 1993) <http://www.bvis.uic.edu/museum/science/science.html>) and the metric T to calculate the extent of nestedness in our species by site data. T provides a standardized measure of matrix disorder by assessing the deviation of an observed presence–absence matrix from one of the same rank and fill that is perfectly nested. T equals the ratio of this sum of squared deviations to its maximum value (estimated by simulation), multiplied by 100. T ranges from 0°, a perfectly nested matrix, to 100°, one that is completely disordered and not nested. A Monte Carlo simulation, run with 500 iterations, was used to estimate the statistical significance of the observed matrix's T value (i.e. the probability that a nested distribution was randomly produced). The species presence–absence matrix from which T was estimated represented the full complement of species ($n = 86$), across all the sites surveyed ($n = 10$).

2.2.4. Analysis of community structure

Differences in the community structure among sites were explored with non-metric multidimensional scaling (NMDS), an iterative optimization ordination method. The Sorensen (Bray-Curtis) distance measure was used with PC-ORD ordination software (McCune and Grace, 2002). Only species existing in more than 1 site among the 10 surveyed were considered in this analysis, thereby reducing the total number of species in this analysis from 86 to 62. Species data was arcsine-square root transformed and multiplied by $2/\pi$ to rescale the data from 0 to 1. In a preliminary analysis, we used a Monte Carlo randomization test to determine the dimensionality of the data. This test was conducted with random starting points, 100 runs with real data and 50 runs with randomized data. The final solution was run with 500 iterations and a starting configuration determined by the preliminary analysis. Final stability was examined by plotting stress versus iteration number. The proportion of variance represented by each axis was based on the coefficient of determination (r^2) between Euclidean distances in ordination space and Sorensen (Bray-Curtis) distances in original space.

A multi-response permutation procedure (MRPP), using the Sorensen (Bray-Curtis) distance measure, was used to test for differences in species assemblages between habitat types. The chance-corrected within-group agreement statistic, A , described within group homogeneity, compared to the random expectation. Essentially, A is a measure of effect size, independent of sample size. When all items are identical within groups, the observed $A = 1$, the highest possible value for A . If heterogeneity within groups equals expectations by chance, $A = 0$ (McCune and Grace, 2002).

2.3. Site metric addressing the persistence of biodiversity

2.3.1. Population density and size structure

At each site, *K. tunicata*'s density and population size structure were estimated using five 0.5 m wide bands that ran perpendicular to the shoreline. Bands were randomly stratified along a 40 m transect and spanned the entire *Hedophyllum sessile* zone, where *K. tunicata* is found. Because each site had a slightly different slope, the *H. sessile* zone width varied across the 10 sites surveyed (low angle slopes have a larger expanse of *H. sessile* habitat relative to high angle slopes). As a consequence, the vertical band transects were not a set length across all sites. The transects were terminated when densities fell below 2 individuals per 0.25 m² at the bottom of the *H. sessile* zone; continued sampling never discovered higher-density aggregations further down in the *Laminaria* zone. Bands were divided into adjacent 0.25 m² quadrats, within which we measured maximum body length for all individuals (nearest 0.5 cm). This vertical band sampling procedure was used to account for variations in size-frequency distributions of *K. tunicata* with respect to intertidal elevation (i.e., larger individuals are found at lower intertidal elevations relative to smaller individuals).

We compared size-frequency distributions of *K. tunicata* among sites using Kolmogorov–Smirnov tests with sequential Bonferroni adjustment for 45 pairwise comparisons among the 10 sites (Sokal and Rohlf, 1969). To do this, all bands were combined at a site. Bands were used as replicates to calculate site-specific density and potential reproductive output.

2.3.2. Potential reproductive output

We examined site- and size-specific differences in *K. tunicata* reproduction by measuring gonad mass of 69 individuals. *K. tunicata* were randomly collected from five sites of varying exposure (Seppings Exposed, Seppings Sheltered, Helby Exposed, Helby Sheltered, and Diana Exposed) in May 1999, just prior to spawning season. The maximum body length of each individual was measured (nearest 0.5 cm). After noting the sex, we excised the gonads of each individual and weighed them (nearest 0.01 g) after drying at 20 °C for 24 h. *K. tunicata* smaller than 3.5 cm were not collected because individuals below this length are not yet reproductive (Strathmann, 1987).

Gonad biomass was regressed against body length after cube-root transforming gonad biomass to account for expected allometry of volume and length. Variations in the length–fecundity relationship between sexes and among sites were examined with ANCOVA, with length as the covariate. Potential reproductive output (PRO) for each band was calculated by summing the expected gonad mass of all reproductive individuals, both male and female, and dividing by the total area of the band. We tested for differences in PRO among sites using a Kruskal–Wallis test, the non-parametric analogue of ANOVA, because variances were heterogeneous.

2.4. Comparisons of sites metrics

Finally, the association between species richness, species diversity, *K. tunicata* density and potential reproductive output across all 10 sites was investigated in a correlation analysis (Sokal and Rohlf, 1969). We also tested if species richness, diversity, chiton density and productivity varied between exposed and semi-protected habitats using two tailed t-tests assuming equal variances. These data were tested for normality (Shapiro–Wilks) and homogeneity of variance (Bartlett test) and all data met both criteria.

3. Results

3.1. Site metrics addressing the representation of biodiversity

3.1.1. Habitat type based on wave exposure

In September, maximum wave force varied by more than an order of magnitude from 2.3 Newtons (N) at Sanford Sheltered to 31.2 N at Edward King Exposed. In October, measured wave forces reached 104 N and must have been substantially higher at two sites (Edward King Exposed, Sanford Exposed) that were impossible to visit due to extreme ocean conditions. In all months, wave force data confirmed our selection of exposed and semi-sheltered sites because wave forces were consistently higher at exposed sites, although the rank order of sites within each category was variable from time to time.

3.1.2. Species richness, diversity and nestedness among sites

A total of 86 algal and invertebrate species were documented across the 10 sites surveyed. Species richness ranged from 29 to 46 species across sites (Table 1). Average species richness was similar at wave-exposed (36.60 ± 2.62 SE, $n = 5$) and semi-sheltered sites (41.80 ± 2.11 SE, $n = 5$, $t = -1.55$, $p = 0.16$).

Table 1 – Species richness per phyla across the 10 sites studied within the Deer Group Archipelago

Species group (phylum, class)	EK E	EK S	Sep E	Sep S	Di E	D I S	Hel E	Hel S	San E	San S
Sponges (Porifera, Demospongiae)	2	1	3	3	1	2	2	2	2	2
Ascidians (Urochordata, Ascidiacea)	3	2	3	3	0	2	0	0	0	1
Tube worms (Annelida, Polychaeta)	1	2	2	2	2	2	2	2	2	2
Bryozoans (Bryozoa)	2	1	2	1	1	2	0	0	0	2
Hydroids (Cnidaria, Hydrozoa)	1	0	1	0	0	1	0	0	0	0
Sea anemones (Cnidaria, Anthozoa)	2	1	1	1	1	2	1	1	2	1
Sea stars (Echinodermata, Asteroidea)	2	3	2	2	1	3	2	1	1	1
Sea cucumbers (Echinodermata, Holothuroidea)	0	0	0	1	0	0	0	0	0	0
Sea urchin (Echinodermata, Echinoidea)	1	0	1	1	0	1	0	0	1	0
Chitons (Mollusca, Polyplacophora)	4	5	4	5	4	4	4	3	3	3
Limpets (Mollusca, Gastropoda)	2	1	2	2	2	2	2	3	2	2
Snails (Mollusca, Gastropoda)	2	0	1	0	1	2	0	0	0	1
Sea slugs (Mollusca, Gastropoda)	0	0	1	0	0	1	0	0	0	1
Mussels (Mollusca, Bivalvia)	1	0	0	0	0	1	1	0	0	0
Barnacles (Crustacea, Cirripedia)	4	3	3	4	4	2	2	3	5	3
Brown algae (Phaeophyta)	4	5	2	2	4	2	3	3	5	5
Green algae (Chlorophyta)	2	3	1	3	1	1	1	3	1	3
Red algae (Rhodophyta)	11	15	11	12	11	15	9	12	13	18
Sea grass (Anthophyta, Zosteraceae)	0	0	0	0	0	0	0	1	0	1
Total	44	42	40	42	33	45	29	34	37	46

Sites with highest species richness included the most protected (Sanford Sheltered, Diana Sheltered, Seppings Sheltered) and the most exposed sites (Edward King Exposed, Sanford Exposed). Species diversity (H') did not vary across habitats (Exposed $H' = 2.46 \pm 0.92$ SE; Semi-sheltered $H' = 2.68 \pm 0.13$ SE) ($n = 5$, $df = 8$, $t = -1.44$, $p = 0.19$).

The 10 intertidal sites surveyed within the Deer Group Archipelago in Barkley Sound are significantly nested ($T = 42.86$, $p = 7.39 \times 10^{-5}$) suggesting that species poor sites are subsets of species-rich sites (Fig. 2).

3.1.3. Analysis of community structure

After 50 randomized runs, the Monte Carlo test recommended a two-dimensional solution to the community data (Axis 1 $p = 0.04$, Axis 2 $p = 0.04$; where $p =$ probability that a similar final stress could have been obtained by chance). A scree plot of final stress versus the number of dimensions confirmed the Monte Carlo assessment of dimensionality. The final solutions suggested that two major gradients captured the variance in algal and invertebrate communities among sites. The first two dimensions contained 69.3% and 23.4% of the variance respectively (cumulative = 92.7%) (Fig. 3). Higher dimensions improved the model very little.

Stress dropped quickly and stabilized smoothly after 10 iterations, indicating a stable final solution.

The multi-response permutation procedure (MRPP) suggested that there was no significant difference in the algal and invertebrate communities between the 5 wave-exposed and 5 semi-exposed sites ($A = 0.02$, $p = 0.20$).

3.2. Site metrics which address the persistence of biodiversity

3.2.1. Population density and size structure

Densities of adult *K. tunicata* (≥ 3.5 cm long) varied significantly among sites ($n = 10$, $MS = 169.21$, $F_{9,40} = 8.82$, $p = 3.71 \times 10^{-7}$) and ranged from 6 to 22 individuals m^{-2} (Fig. 4). Total density, including new recruits, also varied significantly among sites ($n = 10$, $MS = 306.84$, $F_{9,40} = 7.06$, $p = 4.94 \times 10^{-6}$) and ranged from 9 to 32 total individuals m^{-2} . However, the density of adult *K. tunicata* was not significantly correlated to the density of juvenile individuals ($n = 10$, $df = 8$, Pearson's Product $r = 0.54$, $p = 0.10$) and there was no significant difference in adult density ($n = 5$, $df = 8$, $t = 1.10$, $p = 0.31$) between wave-exposed and semi-sheltered sites.

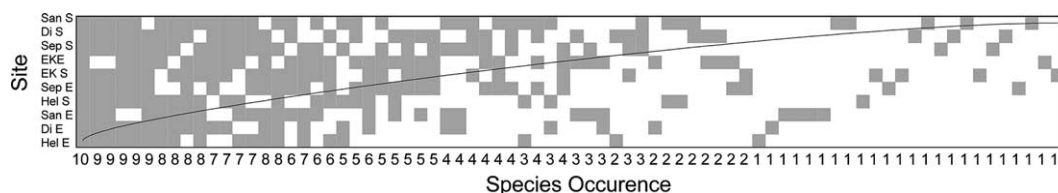


Fig. 2 – This maximally packed species richness by site occurrence matrix, sorted as to minimize Atmar and Patterson's (1993) index of nestedness (T), indicates that the 10 intertidal sites surveyed within the Deer Group Archipelago in Barkley Sound are significantly nested ($T = 42.86$, $p = 7.39 \times 10^{-5}$). This suggests that species poor sites are subsets of species-rich sites. The smooth line represents the line of perfect order. Note: Although all 10 sites and all 86 species were used in this analysis, 10 duplicate, fully filled columns were removed from the left hand side of the matrix.

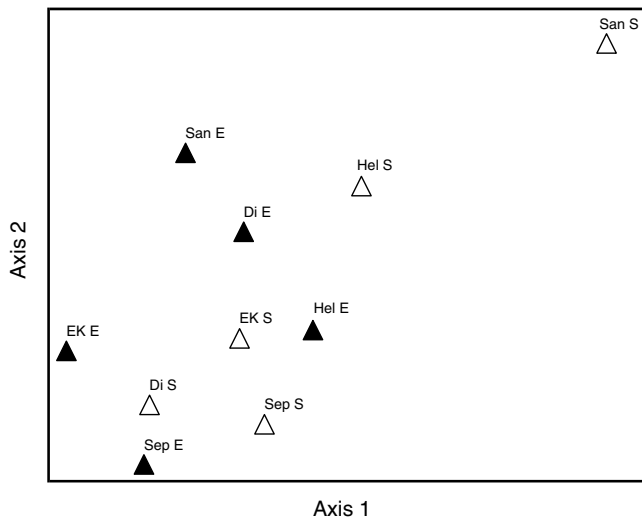


Fig. 3 – According to a non-metric multidimensional scaling analysis, two major gradients captured the variance in community structure among wave exposed (▲) and semi-protected (△) sites. The first two dimensions contained 69.3% and 23.4% of the variance, respectively. However, a multi-response permutation procedure (MRPP) suggests that wave exposed and semi-protected sites did not differ in their overall community structure.

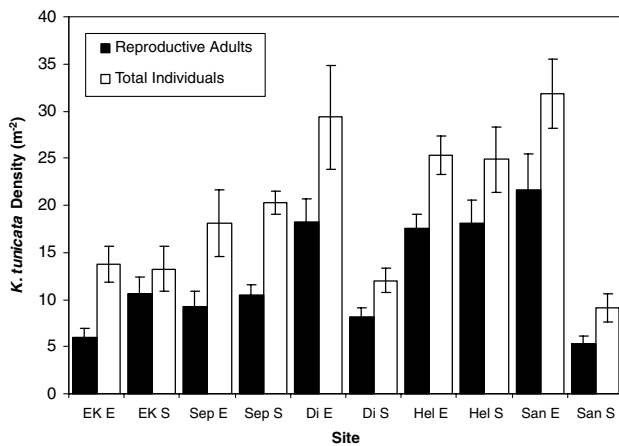


Fig. 4 – Densities of adult *Katharina tunicata* (≤ 3.5 cm \pm SE) ($n = 10$, $MS = 169.2$, $F_{9,40} = 8.8$, $p = 3.71 \times 10^{-7}$) and total density including new recruits ($n = 10$, $MS = 306.8$, $F_{9,40} = 7.1$, $p = 4.94 \times 10^{-6}$).

Size-frequency distributions of *K. tunicata* varied among sites (Fig. 5). Generally, *K. tunicata* were smaller at wave-exposed compared to semi-sheltered sites. However, after sequential Bonferroni adjustment of paired Kolmogorov–Smirnov tests only 10 out of the possible 45 pairwise comparisons encompassed subpopulations that were significantly different in size-frequency from each other. The size-frequency of Edward King Sheltered was significantly different from all of the other sites except for Sanford Sheltered and the size-frequency distribution of Helby Sheltered was significantly different from that of both Seppings Exposed and

Sanford Exposed. Individuals greater than 8.5 cm were found only at Edward King Sheltered.

3.2.2. Potential reproductive output

Gonad dry weight increased significantly with *K. tunicata* body length, according to the following length–fecundity relationship:

$$\sqrt[3]{\text{Gonad dry weight}} = 0.101 \times (\text{Length}) - 0.096,$$

($n = 69$, $R^2 = 0.53$, $p = 1.07 \times 10^{-12}$; Fig. 6). This relationship did not vary among sites or between sexes (Table 2). Although the potential reproductive output (PRO) of *K. tunicata* populations varied by a factor of 4 among sites ($n = 10$, $df = 9$, $KS = 26.22$, $p = 0.002$), PRO did not vary significantly among wave-exposed and semi-sheltered sites ($n = 5$, $df = 8$, $t = -0.08$, $p = 0.94$). The data required to calculate PRO, including both size structure and gonad mass, were substantially more detailed than that required to calculate density. However, this additional effort provided new insight into chiton performance across sites, because total density was not a sufficient indicator of PRO.

3.3. Relationships among site metrics

Species richness and density of adult *K. tunicata* were significantly negatively correlated across sites ($n = 10$, $df = 8$, Pearson’s Product $r = -0.85$, $p = 0.002$) (Fig. 7(a)). Similarly, species richness and the potential reproductive output (PRO) of *K. tunicata* were significantly negatively correlated across sites ($n = 10$, $df = 8$, Pearson’s Product $r = -0.65$, $p = 0.04$) (Fig. 7(b)). An inverse relationship also existed between species diversity (H') and PRO but was not significant ($n = 10$, $df = 8$, Pearson’s Product $r = -0.33$, $p = 0.36$), as enhanced richness was due to the presence of additional rare species. At the most species poor site, *K. tunicata*’s estimated gonad mass per area was greater by a factor of 3.5 relative to the most speciose site that encompassed 50% more species. However, species richness and density of non-reproductive juvenile individuals, including new recruits, were not correlated ($n = 10$, $df = 8$, Pearson’s Product $r = -0.53$, $p = 0.12$) (Fig. 7(c)). When regressed against species richness, the density of reproductive *K. tunicata* accounted for 73% of the variance ($n = 10$, $R^2 = 0.73$, $p = 0.002$).

4. Discussion

4.1. Multiple criteria to characterize candidate reserve sites

Across the rocky intertidal sites surveyed, species richness, diversity and community structure were consistent between wave-exposed and semi-protected habitat types (Fig. 3), suggesting that the annual magnitude of difference in wave exposure between these two habitat types was relatively slight. However, species-rich sites experiencing higher wave exposure contained additional invertebrate species, whereas semi-protected sites contained additional algal species (Table 1). Species at low-richness sites were a nested subset of those at higher richness sites (Fig. 2), in contrast to other studies done at larger spatial scales in which distinct species appear

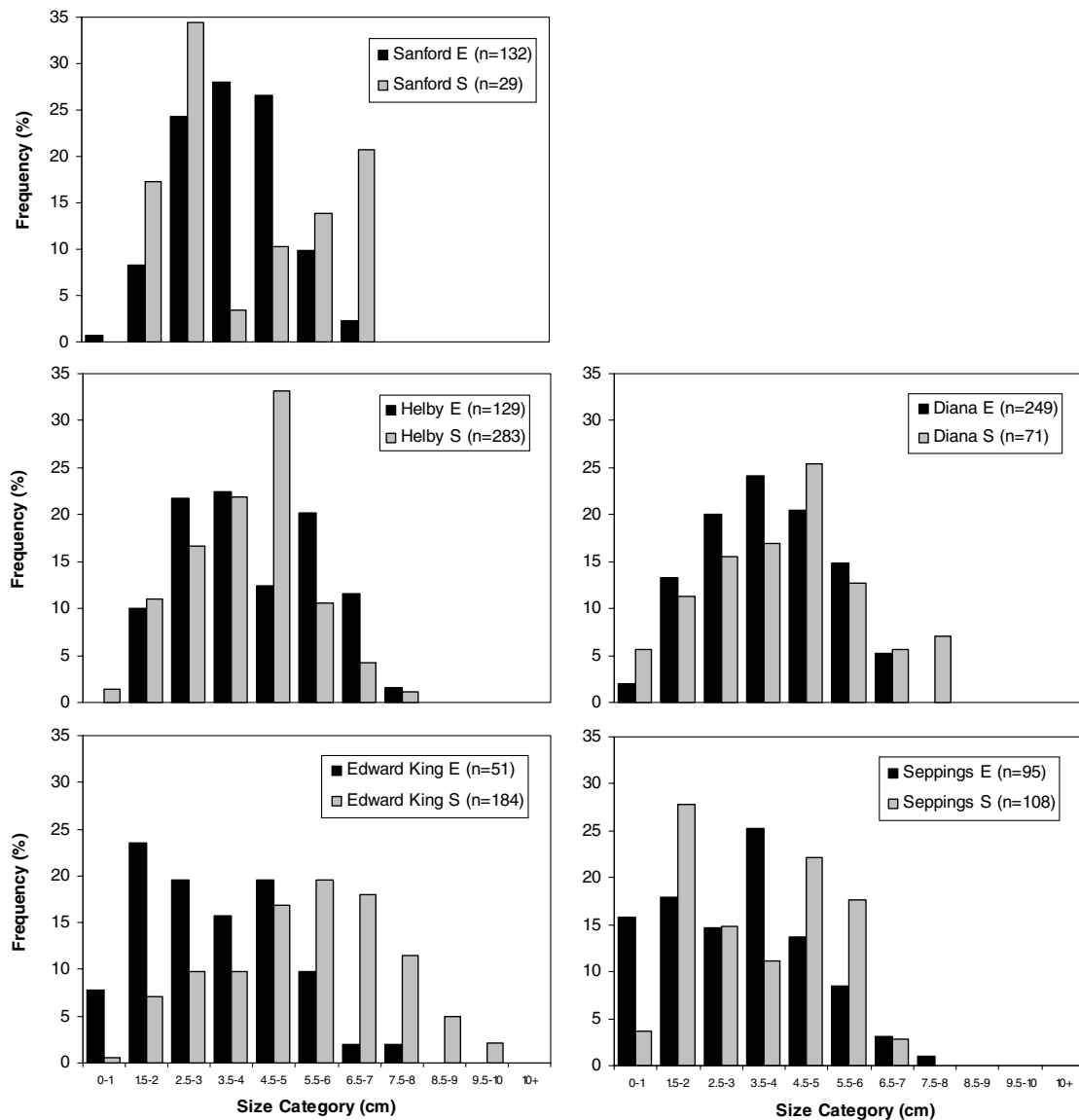


Fig. 5 – Population size structure of *Katharina tunicata* at each site. Bonferroni-adjusted Kolmogorov–Smirnov paired comparisons indicated those frequency distributions that are significantly different from one another (see text) (E = exposed, S = sheltered).

at low-richness sites (Prendergast et al., 1993; Curnutt et al., 1994; Williams et al., 1996). Consequently, at this scale, habitat type, species richness and species diversity, three widely used metrics of site quality, were coincident: valuable sites for protection encompassed high-richness and high-diversity sites in each habitat.

In contrast, site metrics addressing persistence were not consistent with metrics emphasizing representation. Instead, the density of reproductive *K. tunicata* and their estimated reproductive output were significantly negatively correlated with intertidal species richness (Fig. 7(a) and (b)). A reserve network developed for species-rich sites would consequently be expected to provide the worst protection for this strongly interacting species. In contrast to adult density, juvenile *K. tunicata* density did not vary systematically with species richness (Fig. 7(c)). Thus, spatial variation in adult density

and reproductive output does not appear to derive from initial differences in recruitment. Rather, those sites where *K. tunicata* grow and survive well generate populations of abundant adults (moderate densities of large individuals or high densities of medium individuals).

Two possible mechanisms generate the negative relationship between the abundance of this strongly interacting species and total species richness. Either *K. tunicata* may itself reduce species richness, or some external factor(s) may influence *K. tunicata* in a manner opposite to its effects on other species. *K. tunicata* is well-known to reduce algal density and diversity and shift species composition (Duggins and De-thier, 1985; Paine, 1992). Indeed, in our data, the density of reproductive *K. tunicata* explained 70% of variation in species richness among sites. However, grazing impacts on species richness remain to be studied explicitly in Barkley Sound.

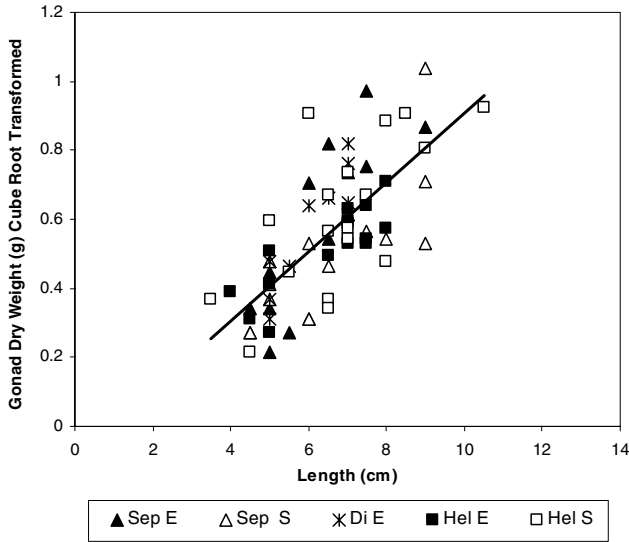


Fig. 6 – The relationship between *Katharina tunicata*'s length and gonad dry weight cube root transformed ($n = 69$, $df = 1$, $R^2 = 0.533$, $p = 1.07 \times 10^{-12}$) (E = exposed, S = sheltered).

Table 2 – Analysis of covariance of *Katharina tunicata*'s gonad mass cube root transformed at five sites of varying wave exposure and population density within the Deer Group Archipelago

Source	Sum-of-squares	df	F-ratio	P value
Site	0.154	4	2.415	0.059
Sex	0.012	1	0.767	0.385
Site \times Sex	0.151	4	2.363	0.064
Length	1.426	1	89.441	2.225×10^{-11}

We propose that a combination of grazing impacts and wave exposure may contribute to the negative correlation between adult *K. tunicata* and species richness in Barkley Sound. The gradient in species richness across semi-sheltered sites was driven primarily by changes in algal richness. At sheltered sites where *K. tunicata* densities were low, possibly existing at an ecological range edge (ex: Sanford Sheltered), higher algal species richness occurred, likely due to a release from *K. tunicata* grazing pressure. The removal of *K. tunicata* in the neighboring US state of Washington caused localized increases in macroalgal canopy cover (Dethier and Duggins, 1984), sporeling density (Paine, 1992), biomass, and species richness (Duggins and Dethier, 1985; Paine, 1992; Paine, 2002). Lower densities of *K. tunicata* at the sites would lead to lower site-specific PRO values.

At wave-exposed sites, high invertebrate species richness occurred where zonation was blurred and species were identified that were ordinarily found in higher or lower neighboring intertidal zones. Within the *Hedophyllum* sessile zone at Edward King Exposed and Seppings Exposed, we recorded species such as *Nucella canaliculata*, *Pollicipes polymerus*, *Chthamalus dalli*, *Balanus glandula* and *Mytilus californianus*, characteristic of higher zones, and *Balanus nubilus*, *Phidiana crassicornis*, and *Aplidium* spp., characteristic of lower zones.

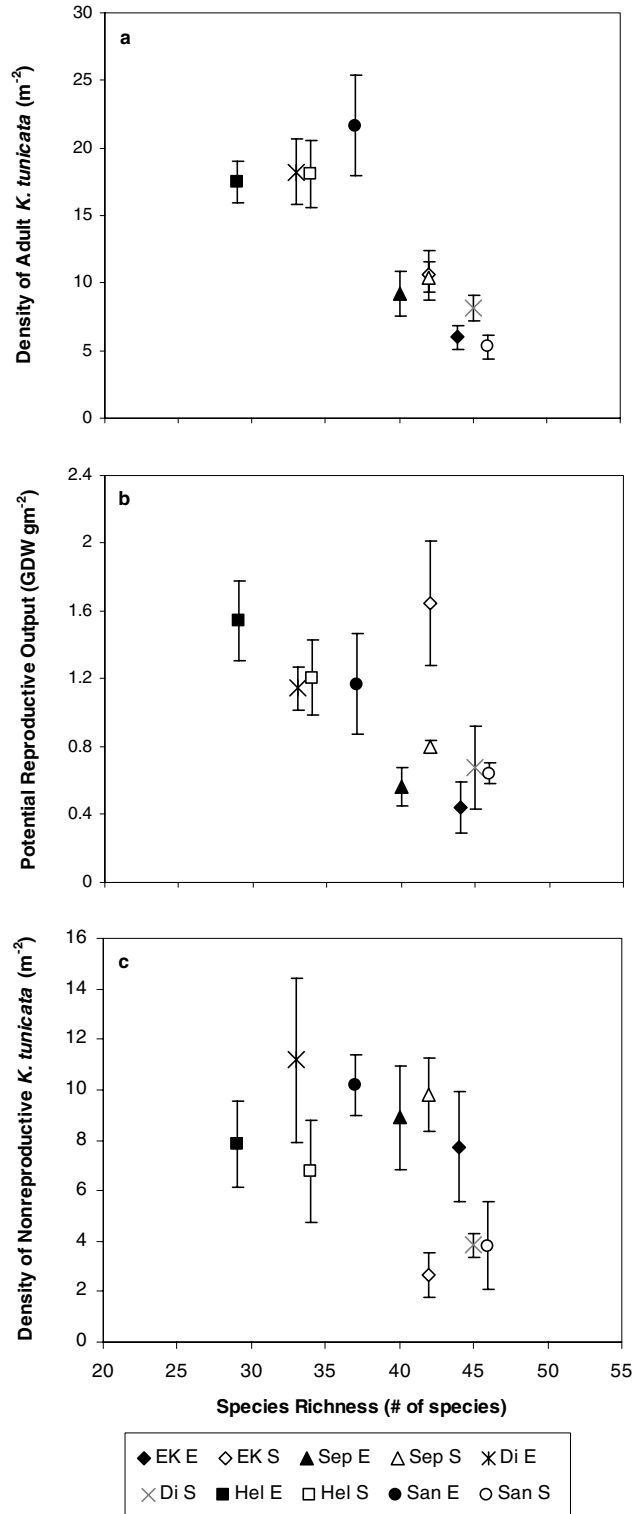


Fig. 7 – (a)–(c) Species richness was significantly negatively correlated with (a) the density of reproductive *K. tunicata* individuals ($n = 10$, $df = 8$, Pearson's Product $r = -0.8515$, $p = 0.0018$) and (b) potential reproductive output ($n = 10$, $df = 8$, Pearson's Product $r = -0.6499$, $p = 0.0419$). In contrast, (c) the density of non-reproductive juveniles, including new recruits, was not correlated with species richness ($n = 10$, $df = 8$, Pearson's Product $r = -0.5254$, $p = 0.1188$).

At these same sites, PRO values were low due to few large *K. tunicata* (Fig. 7(b)). Larger individuals may be more likely dislodged than smaller individuals at wave exposed sites simply due to hydrodynamic forces that set a mechanical limit to body size (Denny et al., 1985).

4.2. Species richness vs. population persistence

It is not clear if the challenge posed to conservation by *K. tunicata* is shared by other intertidal species, let alone species in different habitats. Ecological theory suggests that high diversity may occur where coexistence is promoted by intermediate levels of disturbance (Connell, 1978) or heterogeneity (e.g. ecotones). These mechanisms could lead to a more general inverse relationship between viability and richness. Consider a case in which areas of high species richness are generated by the coincidence of many marginal populations (Araújo and Williams, 2001) because richness rises where range edges overlap (Odum, 1971). Here, peripheral populations existing in inferior quality habitat at lower densities may be more prone to demographic stochasticity and less resilient to extrinsic perturbations than are core populations (Brown, 1984; Caughley et al., 1988; Lawton, 1995; Curnutt et al., 1996). Under these circumstances, species-rich sites may encompass populations whose likelihood of persistence is low. Our results at wave-exposed sites, where intertidal ranges appeared to expand, thereby increasing richness where *K. tunicata* performed least well, may be an example of this phenomenon.

Food web theory also provides a potential mechanism for why high richness and poor performance of particular species might be associated. If the particular species is a consumer, but site richness is largely based on its prey, then prey species may remain uneaten only where the consumer is rare. Herbivores have been shown to reduce plant diversity in a broad range of studies under unenriched conditions (Proulx and Mazumder, 1998), and *K. tunicata* at semi-protected sites also provides circumstantial evidence. Under this scenario, maximizing representation of species may be at odds with conserving ecologically important consumers. Ultimately, the relationship between species richness and population persistence likely depends on the mechanisms driving species richness and the scale at which they are operating.

4.3. Challenges of measuring population viability

Many conservation biologists now recognize the need to design reserve networks (in combination with other conservation tools) in which species have high probabilities of persisting (Margules and Pressey, 2000; Roberts et al., 2003b). Otherwise, reserves only briefly encompass desirable structures and functions of ecosystems. Indeed, reserve designs based simply on the representation of biodiversity have been shown to fail in their protection of species (Rodrigues et al., 2000), and designs that incorporate metrics of viability often differ substantially from those addressing only representation (Cabeza and Moilanen, 2001; Araújo et al., 2002; Cabeza and Moilanen, 2003; Cabeza et al., 2004). However, this dynamic perspective is difficult to

achieve in practice because spatially explicit demography requires more effort to measure than the spatial distribution of a species.

We used gonad mass per area as an index of potential reproductive output despite the fact that little is known about the relationship between gonad mass and larval production. Clearly, the proximity and behaviour of conspecifics and local fluid dynamics may significantly affect individual fertilization success (Allee, 1938; Denny and Shibata, 1989; Levitan, 1991). Furthermore, high larval output from a site does not guarantee that these larvae will recruit successfully and contribute to metapopulation persistence. Indeed, the connections among subpopulations in marine organisms with planktonic dispersal are just beginning to be explored (Gillanders and Kingsford, 1996; Jones et al., 1999; Swearer et al., 1999; Warner and Swearer, 2000; Gillanders, 2002; Swearer et al., 2002). Even if sites that contribute disproportionately to regional recruitment (population sources) could be identified, these may not remain consistent among years due to variable tides, winds, and currents.

The difficulty of linking PRO to population persistence is compounded because PRO is influenced by density, which integrates both recruitment and post-recruitment processes. Populations with high PRO might be able to persist in a lone reserve if recruitment occurs locally. However, consider the opposite extreme case: if recruitment derived wholly from outside the site, protecting only a site with high PRO would lead to inevitable declines because that site would not be self-sustaining (population sink) (Pulliam, 1988). For instance, high recruitment of *K. tunicata* in our data does not necessarily coincide with areas that are apparently good for growth and survival. Implicitly in this case, valuable sites for conservation of *K. tunicata* occur where those individuals that arrive are relatively likely to contribute to future generations. This conclusion has interesting parallels to rules of thumb to protect spawning aggregations where successful adults gather to breed (Johannes, 1998; Roberts, 1998).

An unsatisfactory alternative is to measure only density to designate sites according to their contribution to viability (although this has been done to good effect in some cases; (Winston and Angermeier, 1995; Rodrigues et al., 2000)). Due to source-sink dynamics, the abundance of a species may not be sufficiently informative about how each site contributes to population persistence (Van Horne, 1983; Paine, 1994) (Fig. 7(c)). Instead, demographic information for species across sites may be necessary to evaluate site quality (Van Horne, 1983; Rogers-Bennett et al., 2002). Our metric of PRO, based on size structure and density, is a first approximation of site-to-site variation in *K. tunicata* production.

4.4. Implications for marine reserve site selection

To achieve conservation goals through a network of reserves, the first step is to evaluate potential sites. Regardless of which site selection algorithm is later applied, the outcome clearly depends on which site characteristics are considered, and how the algorithm accounts for conflicting metrics (Rodrigues et al., 2000). Our empirical example from rocky intertidal sites demonstrates that sites appear to have

different qualities for conservation depending on which metrics are considered.

Although counterintuitive, selecting sites to encompass the most species may not always be the optimal way to conserve biodiversity. This is simply because the representation of species does not guarantee the persistence of all species a reserve is intended to protect, nor does it guarantee the protection of ecosystem processes responsible for maintaining species richness. If the primary objective of a marine reserve or network of marine reserves is to ensure the persistence of ecosystem dynamics and/or maintain productive populations of a harvestable species, the ecological mechanisms necessary to promote and preserve natural dynamics must be protected. A few recent examples show that it can be done (Araújo and Williams, 2000; Williams and Araújo, 2000; Araújo et al., 2002; Cabeza et al., 2004). Exceptional site evaluation frameworks address multiple ecological criteria: critical species interactions, links among ecosystems, vulnerable life stages, behavioral characteristics, and rates of propagule production, retention and connectivity (Roberts et al., 2003a; Roberts et al., 2003b).

The third step in reserve design, implementation and monitoring, is arguably the most important, as its absence cripples both good and bad planning processes. Because of the difficulty of gathering data on all relevant site characteristics, reserves may need to be established in an explicitly adaptive context, in which new knowledge on source–sink dynamics or species interactions emerges from management (Walters, 1986; Carpenter and Gunderson, 2001). Although here we focus on ecological criteria for siting reserves, it is our sense that the involvement of stakeholders in the reserve planning process from its inception is a critical element for the successful implementation of reserve networks (Salomon et al., 2001; Aíramé et al., 2003; Roberts et al., 2003a; Roberts et al., 2003b).

This case study indicates that a single strongly interacting species would be least well protected in reserves selected to maximize species richness. We do not know if this relationship is general, although others have found non-overlapping patterns of diversity and centers of density (Winston and Angermeier, 1995; Araújo and Williams, 2001). Of course, multiple objectives must be balanced simultaneously and effective conservation could not be achieved if only a single species' performance was considered. This research suggests that conservation biologists and protected area managers may find it challenging to maintain viable populations in reserves designed to represent biodiversity efficiently. In the end, our conservation success will be judged on the persistence of populations and ecosystem processes, rather than the short-term symbolic collection of species in a few small areas.

Acknowledgements

We thank D. Orihel, S. Strube, and S. Martell for their help and enthusiasm in the field and the staff of the Bamfield Marine Station for their dedicated logistical support. We are especially grateful to the Huu-ay-aht First Nations for allowing us to work on their traditional land. A. Sinclair, T. Tomascik,

D. Haggarty, and M. Healey provided insight into this project. Comments by S. Andelman, C. Harley, B. Paine, D. Schindler, M. Wonham, E. Wagner and two anonymous reviewers greatly improved this manuscript. L. McCoy kindly provided graphical assistance. This work was funded by Parks Canada, NSERC operation grant # 5-89872 to R.E.D, and an NSERC postgraduate scholarship to A.K.S.

REFERENCES

- Aíramé, S., Dugan, J.E., Lafferty, K.D., Leslie, H., McArdle, D.A., Warner, R.R., 2003. Applying ecological criteria to marine reserve design: A case study from the California Channel Islands. *Ecological Applications* 13, S170–S184.
- Allee, W.C., 1938. *The Social Life of Animals*. Norton, New York.
- Allison, G.W., Lubchenco, J., Carr, M.H., 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* 8, S79–S92.
- Andelman, S.J., Fagan, W.F., 2000. Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Science* 97, 5954–5959.
- Araújo, M.B., Williams, P.H., 2000. Selecting areas for species persistence using occurrence data. *Biological Conservation* 96, 331–345.
- Araújo, M.B., Williams, P.H., 2001. The bias of complementarity hotspots towards marginal populations. *Conservation Biology* 15, 1710–1720.
- Araújo, M.B., Williams, P.H., Fuller, R.J., 2002. Dynamics of extinction and the selection of nature reserves. *Proceedings of the Royal Society of London B. Biological Sciences* 269, 1971–1980.
- Atmar, W., Patterson, B.D., 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96, 373–382.
- Auster, P.J., Malatesta, R.J., 1995. Assessing the role of non-extractive reserves for enhancing harvested populations in temperate and boreal marine systems. In: Shackell, N.L., Willison, J.H. (Eds.), *Marine Protected Areas and Sustainable Fisheries*. Science and Management of Protected Areas Association, Wolfville, NS, pp. 82–89.
- Bell, E.C., Denny, M.W., 1994. Quantifying wave exposure: A simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology* 181, 9–29.
- Bohnsack, J.A., 1996. Marine reserves, zoning, and the future of fisheries management. *Fisheries* 21, 14–16.
- Botsford, L.W., Castilla, J.C., Peterson, C.H., 1997. The management of fisheries and marine ecosystems. *Science* 277, 509–515.
- Brown, J.H., 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124, 255–279.
- Bustamante, R.H., Branch, G.M., 1996. Large scale patterns and trophic structure of Southern African rocky shores: The roles of geographic variation and wave exposure. *Journal of Biogeography* 23, 339–351.
- Bustamante, R.H., Branch, G.M., Eekhout, S., 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: Subsidy by subtidal kelps. *Ecology* 76, 2314–2329.
- Cabeza, M., Moilanen, A., 2001. Design of reserve networks and the persistence of biodiversity. *Trends in Ecology and Evolution* 16, 242–248.
- Cabeza, M., Moilanen, A., 2003. Site-selection algorithms and habitat loss. *Conservation Biology* 17, 1402–1413.
- Cabeza, M., Araújo, M.B., Wilson, R.J., Thomas, C.D., Cowley, M.J.R., Moilanen, A., 2004. Combining probabilities of

- occurrence with spatial reserve design. *Journal of Applied Ecology* 41, 252–262.
- Carpenter, S.R., Gunderson, L.H., 2001. Coping with collapse: Ecological and social dynamics in ecosystem management. *BioScience* 51, 451–457.
- Carr, M.H., Reed, D.C., 1993. Conceptual issues relevant to marine harvest refuges: Examples from temperate reef fish. *Canadian Journal of Fish and Aquatic Science* 50, 2019–2028.
- Carr, M.H., Neigel, J.E., Estes, J.A., Andelman, S., Warner, R.R., Largier, J.L., 2003. Comparing marine and terrestrial ecosystems: Implications for the design of coastal marine reserves. *Ecological Applications* 13, S90–S107.
- Caughley, G., Grice, D., Barker, R., Brown, B., 1988. The edge of the range. *The Journal of Animal Ecology* 57, 771–785.
- Chugachmiut, 2000. *Sugpiat Lucit; The ways of the Sugpiaq*. Taylor Productions, Anchorage, AK.
- Connell, J.H., 1978. Diversity in tropical rainforests and coral reefs. *Science* 199, 1302–1310.
- Csuti, B., Polasky, S., Williams, P.H., Pressy, R.L., Camm, J.D., Kershaw, M., Kiester, A.R., Downs, B., Hamilton, R., Huso, M., Sahr, K., 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biological Conservation* 80, 83–97.
- Curnutt, J., Lockwood, J., Luh, H., Nott, P., Russell, G., 1994. Hotspots and species diversity. *Nature* 367, 326–327.
- Curnutt, J.C., Pimm, S.L., Maurer, B.A., 1996. Population variability of sparrows in space and time. *Oikos* 76, 131–144.
- Dayton, P.K., 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41, 351–389.
- Dayton, P.K., Thrush, S.F., Agardy, M.T., Hofman, R.J., 1995. Environmental effects of marine fishing. *Aquatic Conservation* 5, 205–232.
- Dayton, P.K., Thrush, S., Coleman, F.C., 2002. *Ecological Effects of Fishing in Marine Ecosystems of the United States*. Pew Oceans Commission, Arlington, VA. pp. 1–45.
- Denny, M.W., Shibata, M.F., 1989. Consequences of surf-zone turbulence for settlement and external fertilization. *American Naturalist*, 859–889.
- Denny, M.W., Daniel, T.L., Koehl, M.A.R., 1985. Mechanical limits to size in wave-swept organisms. *Ecological Monographs* 55, 69–102.
- Dethier, M.N., Duggins, D.O., 1984. An “indirect commensalism” between marine herbivores and the importance of competitive hierarchies. *The American Naturalist* 124, 205–219.
- Dethier, M.N., Duggins, D.O., 1988. Variation in strong interactions in the intertidal zone along a geographical gradient: A Washington-Alaska comparison. *Marine Ecological Progress Series* 50, 97–105.
- Dobson, A.P., Rodriguez, J.P., Roberts, W.M., Wilcove, D.S., 1997. Geographic distribution of endangered species in the United States. *Science* 275, 550–553.
- Dugan, J.E., Davis, G.E., 1993. Applications of marine refugia to coastal fisheries management. *Canadian Journal of Aquatic Science* 50, 2029–2042.
- Duggins, D.O., Dethier, M.N., 1985. Experimental studies of herbivory and algal competition in a low intertidal habitat. *Oecologia* 67, 183–191.
- Fall, J.A., Utermohle, C.J., 1999. Subsistence harvest in 8 communities ten years after the Exxon Valdez Oil Spill. Technical Report No. 252. Alaska Department of Fish and Game, Anchorage, Alaska, pp. 1–646.
- Ferrier, S., Pressey, R.L., Barrett, T.W., 2000. A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. *Biological Conservation* 93, 303–325.
- Fogarty, M.J., Murawski, S.A., 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Banks. *Ecological Applications* 8, S6–S22.
- Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R., Andelman, S., 2003. Population models for marine reserve design: a retrospective and prospective synthesis. *Ecological Applications* 13, S47–S64.
- Gillanders, B.M., 2002. Connectivity between juvenile and adult fish populations: Do adults remain near their recruitment estuaries?. *Marine Ecological Progress Series* 240, 215–223.
- Gillanders, B.M., Kingsford, M.J., 1996. Elements in otoliths may elucidate the contribution of estuarine recruitment to sustaining coastal reef populations of a temperate reef fish. *Marine Ecological Progress Series* 141, 13–20.
- Howard, P.C., Viskanic, P., Davenport, T.R.B., Kigenyi, F.W., Baltzer, M., Dickinson, C.J., Lwanga, J.S., Matthews, R.A., Balmford, A., 1998. Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* 394, 472–475.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–638.
- Johannes, R.E., 1998. The case for data-less marine resource management: Examples from tropical nearshore fin fisheries. *Trends in Ecology and Evolution* 13, 243–246.
- Jones, G.P., Milicich, M.J., Emslie, M.J., Lunow, C., 1999. Self-recruitment in a coral reef fish population. *Nature* 402, 802–804.
- Kareiva, P., Marvier, M., 2003. Conserving biodiversity coldspots. *American Scientist* 91, 344–351.
- Kati, V., Devillers, P., Dufrene, M., Legakis, A., Vokou, D., Lebrun, P., 2004. Hotspots, complementarity or representativeness? Designing optimal small-scale reserves for biodiversity conservation. *Biodiversity Conservation* 120, 471–480.
- Kirkpatrick, J.B., 1983. An iterative method for establishing priorities for selection of nature reserves: An example from Tasmania. *Biological Conservation* 25, 127–134.
- Kozloff, E.N., 1973. *Seashore Life of the Northern Pacific Coast; An Illustrated Guide to Northern California, Oregon, Washington, and British Columbia*. The University of Washington Press, Seattle.
- Kramer, D.L., Chapman, M.R., 1999. Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes* 55, 65–79.
- Lawton, J.H., 1995. Population dynamics principles. In: Lawton, J.H., May, R.M. (Eds.), *Extinction Rates*. Oxford University Press, Oxford.
- Leslie, H., Ruckelshaus, M., Ball, I.R., Andelman, S., Possingham, H.P., 2003. Using siting algorithms in the design of marine reserve networks. *Ecological Applications* 13, S185–S198.
- Levin, P.S., Levin, D.A., 2002. The real biodiversity crisis. *American Scientist* 90, 6–8.
- Leviton, D.R., 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biological Bulletin* 181, 261–268.
- Lombard, A.T., Nicholls, A.O., August, P.V., 1995. Where should nature reserves be located in South Africa? A snake’s perspective. *Conservation Biology* 9, 363–372.
- Lombard, A.T., Cowling, R.M., Pressey, R.L., Mustart, P.J., 1997. Reserve selection in a species-rich and fragmented landscape on the Agulhas plain, South Africa. *Conservation Biology* 11, 1101–1116.
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243–253.
- Margules, C.R., Nicholls, A.O., Usher, M.B., 1994. Apparent species turnover, probability of extinction and the selection of nature

- reserves: A case study of the Ingleborough limestone pavements. *Conservation Biology* 8, 51–56.
- Markel, R.W., DeWreede, R.E., 1998. Mechanisms underlying the effect of the chiton *Katharina tunicata* on the kelp *Hedophyllum sessile*: Size escapes and indirect effects. *Marine Ecology Progress Series* 166, 151–161.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach.
- Micheli, F., Amarasekare, P., Bascompte, J., Gerber, L.R., 2004. Including species interactions in the design and evaluation of marine reserves: Some insights from predator-prey models. *Bulletin of Marine Science* 74, 653–669.
- National Research Council, 2001. *Marine Protected Areas; Tools for Sustaining Ocean Ecosystems*. National Academy Press, Washington, DC.
- Nicholls, A.O., Margules, C.R., 1993. An upgraded reserve selection algorithm. *Biological Conservation* 64, 165–169.
- O'Clair, R.M., O'Clair, C.E., 1998. *Southeast Alaska's Rocky Shores*. Plant Press, Auk Bay, Alaska.
- Odum, E.O., 1971. *Fundamentals in Ecology*. W.B. Saunders, Philadelphia.
- Oksanen, L., Oksanen, T., 2000. The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist* 118, 240–261.
- Paine, R.T., 1969. A note on trophic complexity and community stability. *The American Naturalist* 1103, 91–93.
- Paine, R.T., 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* 355, 73–75.
- Paine, R.T., 1994. *Marine Rocky Shores and Community Ecology: An Experimentalists Perspective*. Oldendorf, Germany.
- Paine, R.T., 2002. Trophic control of production in a rocky intertidal community. *Science* 296, 736–739.
- Palumbi, S.R., 1999. The prodigal fish. *Nature* 402, 733–735.
- Palumbi, S.R., 2002. *Pew Oceans Commission*. Arlington, Virginia.
- Parsons, D.M., Babcock, R.C., Hankin, R.K.S., Willis, T.J., Atken, J.P., O'Dor, R.K., Jackson, G.D., 2003. Snapper *Pagrus auratus* (sparidae) home range dynamics: Acoustic tagging studies in a marine reserve. *Marine Ecological Progress Series* 262, 253–265.
- Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. *Nature* 418, 689–695.
- Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P.K., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., Sainsbury, K.J., 2004. Ecosystem-based fishery management. *Science* 305, 346–347.
- Pimm, S.L., Lawton, J.H., 1998. Planning for biodiversity. *Science* 279, 2068–2069.
- Possingham, H., Ball, I., Andelman, S., 2000. Mathematical methods for identifying representative reserve networks. In: Ferson, S., Burgman, M. (Eds.), *Quantitative Methods for Conservation Biology*. Springer, New York, pp. 291–306.
- Power, M.E., Tilman, D., Estes, L.E., Menge, B.A., Bond, W.L., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones. *Bioscience* 46, 609–620.
- Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C., Gibbons, D.W., 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365, 335–337.
- Prendergast, J.R., Quinn, R.M., Lawton, J.H., 1999. The gaps between theory and practice in selecting nature reserves. *Conservation Biology* 13, 484–492.
- Pressey, R.L., 1994. Shades of irreplaceability: Towards a measure of the contribution of sites to a reservation goal. *Biodiversity Conservation* 3, 242–262.
- Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, R.I., Williams, P.H., 1993. Beyond opportunism: Key principles for systematic reserve selection. *Trends in Ecology and Evolution* 8, 124–128.
- Pressey, R.L., Watts, M.E., Barrett, T.W., 2004. Is maximizing protection the same as minimizing loss? Efficiency and retention as alternative measures of the effectiveness of proposed reserves. *Ecology Letters* 7, 1035–1046.
- Proulx, M., Mazumder, A., 1998. Reversal of grazing impacts on plant species richness in nutrient-poor vs. Nutrient-rich ecosystems. *Ecology* 79, 2581–2592.
- Pulliam, H.R., 1988. Sources, sinks, and population regulation. *The American Naturalist* 132, 652–661.
- Quinn, J.F., Wing, S.R., Botsford, L.W., 1993. Harvest refugia in marine invertebrate fisheries: Models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *American Zoologist* 33, 537–550.
- Reid, W.V., 1998. Biodiversity hotspots. *Trends in Ecology and Evolution* 13, 275–280.
- Roberts, C.M., 1997. Connectivity and management of Caribbean coral reefs. *Science* 278, 1454–1457.
- Roberts, C.M., 1998. Sources, sinks, and the design of marine reserve networks. *Fisheries* 23, 16–19.
- Roberts, C.M., Andelman, S., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpren, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D.A., Possingham, H.P., Ruckelshaus, M., Warner, R.R., 2003a. Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications* 13, S199–S214.
- Roberts, C.M., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpren, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D.A., Ruckelshaus, M., Warner, R.R., 2003b. Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecological Applications* 13, S215–S228.
- Rodrigues, A.S.L., Gregory, R.D., Gaston, K.J., 2000. Robustness of reserve selection procedures under temporal species turnover. *Proceedings of the Royal Society of London B. Biological Sciences* 267, 49–55.
- Rogers-Bennett, L., Haaker, P.L., Karpov, K.A., Kushner, D.J., 2002. Using spatially explicit data to evaluate marine protected areas for abalone in Southern California. *Conservation Biology* 16, 1308–1317.
- Salomon, A.K., Ruesink, J.L., Semmens, B.X., Paine, R.T., 2001. Incorporating human and ecological communities in marine conservation; an alternative to Zacharias and Roff. *Conservation Biology* 15, 1452–1455.
- Salomon, A.K., Waller, N., McIlhagga, C., Yung, R., Walters, C., 2002. Modeling the trophic effects of marine protected area zoning policies: A case study. *Aquatic Ecology* 36, 85–95.
- Salomon, A.K., Ruesink, J.L., Tanape, N., Glahn, D., McCollum, Huntington, H., 2004. Disentangling the Relative Roles of Subsistence Harvest and Natural Factors in Altering Coastal Marine Food Webs and Ecosystem Productivity in South Central Alaska. *World Fisheries Congress, Vancouver, BC, Canada*. pp. 108.
- Schmitz, O.J., Hamback, P.A., Beckerman, A.P., 2000. Trophic cascades in terrestrial systems: A review of the effects of carnivore removal on plants. *American Naturalist* 155, 141–153.
- Smith, T.B., Bruford, M.W., Wayne, R.K., 1993. The preservation of process: The missing element of conservation programs. *Biodiversity Letters* 1, 164–167.
- Sokal, R.R., Rohlf, F.J., 1969. *Biometry*. W.H. Freeman and Company, San Francisco.
- Soulé, M.E., 1991. Conservation: Tactics for a constant crisis. *Science* 253, 744–750.
- Soulé, M.E., Estes, J.A., Berger, J., Del Rio, C.M., 2003. Ecological effectiveness: Conservation goals for interactive species. *Conservation Biology* 17, 1238–1250.

- Soulé, M.E., Estes, J.A., Miller, B., Honnold, D.L., 2005. Strongly interacting species: Conservation policy, management, and ethics. *BioScience* 55, 168–176.
- Stanek, R.T. 1985. Patterns of wild resource use in English Bay and Port Graham, Alaska. Technical paper No. 104. Alaska Department of Fish and Game, Anchorage, Alaska, pp. 1–214.
- Steele, J.H., 1985. A comparison of terrestrial and marine ecological systems. *Nature* 313, 355–358.
- Strathmann, M.F., 1987. Reproduction and Development of Marine Invertebrates on the Northern Pacific Coast: Data and Methods for the Study of Eggs, Embryos, and Larvae. University of Washington Press, Seattle, WA.
- Swearer, S.E., Caselle, J.E., Lea, D.W., Warner, R.R., 1999. Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402, 799–802.
- Swearer, S.E., Shima, J.S., Hellberg, M.E., Thorrold, S.R., Jones, G.P., Robertson, D.R., Morgan, S.G., Selkoe, K.A., Ruiz, G.M., Warner, R.R., 2002. Evidence of self-recruitment in demersal marine populations. *Bulletin of Marine Science* 70, 251–271.
- Terborgh, J., Estes, J.A., Paquet, P.C., Ralls, K., Boyd-Heger, D., Miller, B., Noss, R., 1999. Role of top predators in regulating terrestrial ecosystems. In: Soulé, M.E., Terborgh, J. (Eds.), *Continental Conservation: Design and Management Principles for Long-term, Regional Conservation Networks*. Island Press, Washington, DC.
- Tognelli, M.F., 2005. Assessing the utility of indicator groups for the conservation of South American terrestrial mammals. *Biological Conservation* 121, 409–417.
- Tsuji, N., Tsubaki, Y., 2004. Three new algorithms to calculate the irreplaceability index for presence/absence data. *Biological Conservation* 119, 487–494.
- Van Horne, B., 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47, 893–901.
- Vanderklift, M.A., Ward, T.J., Phillips, J.C., 1998. Use of assemblages derived from different taxonomic levels to select areas for conserving marine biodiversity. *Biological Conservation* 86, 307–315.
- Walters, C., 1986. *Adaptive Management of Renewable Resources*. MacMillan Publishing Company, New York.
- Walters, C., 2000. Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: How large should protected areas be? *Bulletin of Marine Science* 66, 745–757.
- Walters, C., Kitchell, J.F., 2001. Cultivation/depensation effects on juvenile survival and recruitment: Implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Science* 58, 39–50.
- Warman, L.D., Sinclair, A.R.E., Scudder, G.G.E., Klinkenberg, B., Pressey, R.L., 2004. Sensitivity of systematic reserve selection to decisions about scale, biological data, and targets: Case study from southern British Columbia. *Conservation Biology* 18, 655–666.
- Warner, R.R., Swearer, S.E., 2000. Larval accumulation and retention: Implications for the design of marine reserves and essential fish habitat. *Bulletin of Marine Science* 66, 821–830.
- Wessels, K.J., Freitag, S., van Jaarsveld, A.S., 1999. The use of land facets as biodiversity surrogates during reserve selection at a local scale. *Biological Conservation* 89, 21–38.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48, 607–615.
- Williams, P.H., 1998. Key sites for conservation: area-selection methods for biodiversity. In: Mace, G., Blamford, A., Ginsberg, J.R. (Eds.), *Conservation in a Changing World: Integrating Process into Priorities for Action*. Cambridge University Press, Cambridge, UK, pp. 211–249.
- Williams, P.H., Araújo, M.B., 2000. Using probabilities of persistence to identify important areas for biodiversity conservation. *Proceedings of the Royal Society of London Biological Sciences* 267, 1959–1966.
- Williams, P., Gibbons, D., Margules, C., Rebelo, A., Humphries, C., Pressey, R., 1996. A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conservation Biology* 10, 155–174.
- Winston, M.R., Angermeier, P.L., 1995. Assessing conservation value using centers of population density. *Conservation Biology* 9, 1518–1527.
- Zeller, D.C., Russ, G.R., 1998. Marine reserves: Patterns of adult movement of the coral trout (*Plectropomus leopardus* (serranidae)). *Canadian Journal of Fisheries and Aquatic Science* 55, 917–924.