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# Land-to-sea connectivity: linking human-derived terrestrial subsidies to subtidal habitat change on open rocky coasts

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**Abstract.** Spatial subsidies are considered strong where differences in resource availability between donor and recipient systems are greatest. We tested whether human activities on land can increase subsidies of terrigenous nitrogen to open rocky coasts and whether these differences can predict apparent deforestation of kelp forests. We first identified landscape-scale variation in the human-mediated transfer of dissolved inorganic nitrogen (DIN) from natural, agricultural, and urban catchments to temperate coasts after episodes of rainfall. Compared to natural catchments, subsidies of DIN were on average 8–407 times greater in urban catchments, and 1–63 times greater in agricultural catchments. Urban derived nitrogen was attributed to the release of sewage effluent, as delineated by  $\delta^{15}\text{N}$  isotopic values of transplanted algae. Having made this link, we then assessed whether this catchment-scale variation may account for variation in structure of subtidal habitats, particularly as related to theory of nutrient-driven shifts of habitat from perennial (i.e., canopy-forming algae) to opportunistic species (i.e., turf-forming algae). We not only detected patterns consistent with this theory, but also established that the size and total proportion of patches of turf-forming algae were greater where the ratio of donor:recipient nitrogen loads was greater (i.e., size of subsidy). An important realization was that deforestation may be more strongly related to variation in the size of subsidy rather than size of human populations, particularly among urban catchments. These data directly link the type of human activity within catchments to the modification of land-to-sea subsidies and indirectly support theory that predicts terrestrial inputs to have greater ecological effects where the disparity in resource availability between donor and recipient is exacerbated. Our evidence has been used by coastal managers to reconsider their management of coastal systems and has subsequently contributed to new water-recycling policy and initiatives.

**Key words:** canopy-forming algae; coastal development; habitat loss; kelp; nutrients; regime shift; South Australia; spatial subsidy; terrestrial runoff; turf-forming algae; *Ulva australis*.

## INTRODUCTION

Recognition that disparate habitats are often energetically and dynamically linked by spatial subsidies has been an important contribution to ecological theory that seeks to integrate phenomena across scales and systems (Turner 1989, Oelschaeger 1991). Natural subsidies (i.e., fluxes of energy, materials, or organisms from productive to less productive habitats) are ubiquitous among ecological landscapes and exert strong influences on the community dynamics of receiving systems (Polis et al. 1997). While natural subsidies are considered fundamental to the maintenance of ecological systems (Polis and Hurd 1996, Connolly et al. 2005), there has been comparatively less recognition of the central influence that human modification of landscapes has on rates of subsidy between spatially linked systems, many of which

are under increasing pressure from human development. Human activities liberate large amounts of materials that are otherwise limiting within natural systems (e.g., nutrients and sediments), which are invariably exported to adjacent “recipient” systems.

Aquatic systems are susceptible to increased subsidies of nutrients, and links from land to rivers, lakes and estuaries have been well established (McClelland et al. 1997, Carpenter et al. 2001, Gillanders and Kingsford 2002, Vander Zanden and Sanzone 2004). There has, however, been substantially less recognition of such landscape-scale effects in open coastal habitats, possibly because the effects of nutrients are insidious compared to more conspicuous drivers of habitat change (e.g., fishing, population outbreaks, and invasive species). While there is increasing concern that human export of nutrients (particularly nitrogen; Seitzinger et al. 2005) can alter the magnitude of cross-habitat subsidies to drive change in recipient systems, such links are seldom made in coastal environments where nitrogen limitation (Howarth and Marino 2006) means that such inputs could rival climate change in their environmental effects

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(Vitousek et al. 1997a). A more comprehensive understanding of the land-to-sea connection is relevant to managing ecological sustainability of increasingly human-dominated coasts (Kay and Alder 1999).

Human activities such as urbanization and industrial and agricultural production have altered the natural nutrient cycle, increasing concentrations of nitrogen within the biosphere (Tilman et al. 2001, Rabalais 2002). The degree to which these enhanced resources affect natural systems is contingent on both their ambient and historical concentrations and the capacity of the system to assimilate these additional nutrients. Subsidies have strong effects where the ratio of the subsidized resource between donor and recipient system is large (Marczak et al. 2007). In this context, there is emerging concern that systems of naturally low resources are disproportionately vulnerable to human enhancement of these same resources (e.g., input of nutrients to nutrient poor coasts; Connell and Irving 2008). The transfer of nitrogen across ecosystem boundaries is considered one of the more important forms of natural subsidy, owing to its strong influence on both biological and abiotic characteristics of recipient systems (Polis et al. 1997). In this way, the addition of nitrogen from human activities along increasingly developed coastlines has the potential to drive serious and perhaps irreversible change to subtidal habitats (Connell et al. 2008; see Plate 1).

Undesirable habitat change is often characterized by shifts from perennial species with structurally complex communities to opportunistic species with simple and less diverse elements (Tilman et al. 2001, Hughes et al. 2005). On temperate coasts, the subtidal equivalent centers on the replacement of canopy-forming algae (e.g., kelps) by turf-forming algae (e.g., Australia [Connell et al. 2008]; Baltic Sea [Worm et al. 1999]; North Sea [Eriksson et al. 2002]; and Mediterranean Sea [Rodriguez-Prieto and Polo 1996]). The driver of such shifts appears to be the ability of turfs, which are generally ephemeral and opportunistic, to persist under conditions of elevated nutrients (Worm et al. 2000; S. D. Connell, B. D. Russell, D. Gorman, and A. Airoidi, *unpublished manuscript*) and subsequently inhibit the recruitment of canopies (Airoidi 2003). In this regard, we propose that regime-shifts (i.e., from canopies to turfs) are more likely on coasts with greater disparity in nitrogen concentration between human inputs (i.e., nitrogen enriched donor) and recipient waters (i.e., nitrogen poor recipient). If this theory is valid, then variation in subsidy ratios (donor:recipient) should correlate to variation in the frequency and extent of substratum occupied by turf-forming algae.

The use of catchment-scale observations to assess land-to-sea linkages provides a framework to assess human driven changes at scales relevant to practical management and ecological application. This landscape-scale perspective focuses on the collective abiotic environment rather than individual sources of pollution

and their small scale dynamics (e.g., the diversity of pollutants and their hourly, weekly, and monthly variation). It also brings into focus longer-term issues such as the effects of historical land use (Lotze et al. 2006) and the degree of habitat degradation across one of the most intensely and historically developed zones of human habitation; the coastal zone. South Australia represents an exceptional opportunity to investigate land-to-sea subsidies as a product of past, current and future human activity because major coastal use has been very recent and well documented. Coastal occupation (1.2 million people) has occurred since European colonization (1836), with accelerated coastal development since early 1980s. Regime shifts (canopy-to-turf) are quantitatively understood (i.e., past environments recognized; Connell et al. 2008), spatially restricted (i.e., spatial “controls” are possible) and can be studied with reference to replicate catchments of natural vegetation (i.e., “controls” for urban runoff); a possibility that is not available on the vast majority of the globe's coastlines (Airoidi and Beck 2007).

This research examined land-to-sea linkages by relating variation in donor–recipient subsidies to variation in subtidal habitat. The first step identified variation in donor:recipient ratios of dissolved inorganic nitrogen (DIN) among catchment types. While nutrient assays provide useful information of short term DIN concentrations, they tend to fluctuate widely across short timescales and hence do not provide a time integrated assessment of available nitrogen. In contrast, nitrogen isotope values of rapidly growing algal indicator species (e.g., *Ulva australis*) provide an assessment of the available nitrogen pool over weeks (Aguilar et al. 2003, Teichberg et al. 2007) and can be used to identify its source (i.e., wastewater, agricultural products or atmospheric deposition; Cole et al. 2004). This technique has been successfully applied to identify linkages between terrestrial catchments and estuarine habitats (e.g., McClelland and Valiela 1998, Valiela et al. 2000, Bowen et al. 2007) but not on open rocky coasts. The second step, therefore, assessed links between elevated subsidies derived from human sources of nitrogen (i.e., sewage effluent, fertilizer) using stable isotope values of an algal indicator (Peterson and Fry 1987, Costanzo et al. 2001). The third step assessed whether there was a relationship between the donor:recipient ratios and the relative covers of habitats, particularly as predicted from knowledge of nutrient driven regime-shifts (i.e., replacement of canopy-forming with turf-forming algae). If we reveal these parameters to be related, such information can be used to improve interpretations of past habitat change and predictions of the consequences of future coastal development.

## METHODS

### *Catchment types*

This study was done in South Australia, a region that comprises multiple catchments of urban activity (i.e.,

residential and industrial) interspersed among catchments of agricultural activity (i.e., livestock grazing) and nature conservation (i.e., natural forests with no development). Within developed catchments (urban and agricultural), sources of land-derived nutrients include fertilizers, animal wastes, sewage effluent, and discharges from factories and refineries. In urban catchments, the delivery of human-derived nutrients to coastal systems tends to be continuous and pervasive, contrasting with agricultural and natural catchments which are pulse driven by winter precipitation patterns (June–September; annual average  $\sim 447$  mm). The population sizes in urban catchments were estimated at 4000, 12 000, 26 000, and 150 000 people, and ranged from six to 60 people in agricultural catchments and 0 people in natural catchments. We selected a subset of four replicate catchments of each catchment type (i.e., urban, agricultural and natural) based on accessibility and population density (Australian Bureau of Statistics, Population Census 2006). Estimates of variation among the three catchment types, therefore, were based on a hierarchical design in which the four replicate catchments (termed “sites”;  $n = 4$  sites per catchment type) were nested within catchment type.

#### *Links between catchment use and coastal nitrogen*

Catchment-related variation in dissolved inorganic nitrogen concentration was estimated in coastal seas during rainfall events when rainfall was heavy (90.8 mm monthly total) and light (59.2 mm monthly total) during the Austral winter of 2005. On the first rainfall event (90.8 mm), we assessed whether differences in nutrient concentration could be detected among catchments when rainfall was heavy (sampling  $\sim 50$  m from the input of surface runoff). On the second rainfall event (59.2 mm), we tested whether catchment related patterns observed under heavy rainfall could also be detected under light rainfall, again sampling  $\sim 50$  m from terrestrial input. On this second occasion, additional sampling was done 500 m away from input to assess the extent of influence under light rainfall (i.e., 50 vs. 500 m), and repeated 1000 m offshore to estimate background variation where the effects of terrestrial discharge are considered substantially less or even undetectable (Gaston et al. 2006). Samples were obtained at 1–2 m depth using sterile 25-mL syringes before being filtered through 0.45- $\mu\text{m}$  glass fiber filters. Filtered samples were frozen in situ and transported to the laboratory where they were analyzed for dissolved inorganic nitrogen (DIN; nitrite + nitrate + ammonium) using a Lachat QuickChem 8500 Flow Injection Analyzer (Hach, Loveland, Colorado, USA). Nutrient concentrations (reported as mg/L) were validated against natural seawater certified reference material.

#### *Links between catchment use and benthic use of nitrogen*

Catchment related variation in nitrogen sources was assessed using changes in nitrogen stable isotope values

of benthic algae (i.e., transplants), which provide a sensitive and time-integrated assessment of the source of in situ nitrogen (Gartner et al. 2002). Within each catchment type, we transplanted *Ulva australis* (Areschoug) with typical marine isotopic values (i.e., mean  $\pm$  SE;  $\delta^{13}\text{C}$ ,  $-20.7\text{‰} \pm 0.3\text{‰}$  and  $\delta^{15}\text{N}$ ,  $5.9\text{‰} \pm 0.5\text{‰}$ ) from an offshore island characterized by nutrient-poor waters (West Island; Russell and Connell 2005). This transplantation from a standard source allows for clearer interpretation of any change in isotopic values caused by uptake of human-derived sources of nutrients without the confounding influence of natural spatial variation (Costanzo et al. 2001). Transplants comprising of replicate algal fronds ( $n = 3$ ) were placed within transparent chambers ( $n = 3$  chambers per replicate site; noting that storm-related loss of chambers reduced replication from  $n = 5$  at each site), that were anchored to rocky substratum at depths of 5–10 m ( $>100$  m apart) within each replicate catchments ( $n = 4$  per catchment type). Transplant sites were located  $<500$  m from land (i.e., within the land–sea interface) and were chosen based on similarities in reef topography, wave exposure and preexisting algal community structure. Transplant chambers were constructed from perforated transparent plastic tubes with mesh sealing the ends to facilitate sufficient water flow. Transplants were collected after  $\sim 60$  days (recognizing that the catchment related differences may reflect values of ambient sources over shorter timescales), stored on ice for transport to the laboratory, rinsed in deionized water, cleaned of visible epiphytes and dried at  $60^\circ\text{C}$  (for 24 h) before being ground to a powder. Samples were then acid washed using 3 mol/L HCl to remove carbonates, re-dried to a constant mass ( $60^\circ\text{C}$  for 48 h), placed in tin capsules and analyzed on an Isoprime isotope-ratio mass spectrometer (Isoprime, Manchester, UK). The ratios of  $^{15}\text{N}/^{14}\text{N}$  and  $^{13}\text{C}/^{12}\text{C}$  for all samples were calculated as the relative per mille (‰) difference between the sample and the recognized international standard (air for nitrogen; Pee Dee Belemnite limestone carbonate for carbon). Precision of the mass spectrometer, using the values from duplicate samples, was 0.3‰ for  $^{15}\text{N}$  and 0.1‰ for  $^{13}\text{C}$ . In addition, we report the concentrations of nitrogen and carbon in algal tissue via spectroscopic analysis.

#### *Links between catchment use and habitat structure*

If humans modify coastal conditions to cause loss of canopy-forming algae in favor of turf-forming algae (i.e., models of Benedetti-Cecchi et al. 2001, Eriksson et al. 2002, Connell et al. 2008) we predict that patches of turf-forming algae would be larger and occupy proportionally more space (and patches of canopy-forming algae smaller and occupy less space) adjacent to catchments of increasing human domination. To test this prediction, we sampled the percentage cover of all canopy-forming algae (i.e., *Ecklonia radiata*, *Cystophora* spp., *Sargassum* spp.) and thin filamentous, turf-forming

algae (commonly *Feldmannia* spp.) in early summer of 2005. This sampling was done adjacent to each catchment type (i.e., within 500 m from the entrance of terrestrial sources of input, and thereby covering a 1 km area in which elevated nutrient concentrations were identified, Table 1). These canopy-forming species act as foundation species to entire subtidal communities on these southern coasts (see review in Connell 2007a) and their extent and patch sizes within and among catchments are described (*Results*; Figs. 3 and 4).

The relative sizes (diameter) of patches of canopy and turf-forming algae were quantified among catchments using replicate  $1 \times 100$  m transects ( $n = 4$  per site) separated by 50–100 m. At a  $1\text{-m}^2$  scale, habitat was conservatively identified as canopy-forming algae where at least one individual canopy-forming alga was present (i.e., 25% cover of  $1\text{ m}^2$ ). We classified habitat at this scale (i.e.,  $1\text{ m}^2$ ) because the presence of canopy-forming algae is negatively related to turf-forming algae this scale (Irving and Connell 2006). Transects were oriented normal to the shoreline and started as close to mean low water as the prevailing conditions would allow. The distance along each transect at which the type of habitat changed was recorded, providing information on the relative size of each patch of habitat and the proportion of rock occupied under each transect (see similar methodology; Dayton et al. 1992, Goodsell et al. 2004). The seaward extent of rocky substratum at most sites varied between ~80 and 150 m, and sampling either stopped at the seaward edge of rock or at 100 m where rock extended past this point. For each habitat quantified, the percentage of the total recorded habitat was calculated (minus any sandy substratum).

#### *Strength of subsidy–habitat associations*

We assessed the capacity for differences in the magnitude of subsidy (i.e., donor:recipient ratio) and population size (number of people per catchment) to predict apparent change in subtidal habitat. For each catchment, the magnitude of subsidy (i.e., donor:recipient ratio) was estimated by calculating the ratio between DIN in donor waters (i.e., samples taken <50 m away from nutrient input in heavy rainfall) and recipient waters. Recipient waters were estimated for two temporal periods (i.e., pre-European or “historical” and “contemporary”). It is not possible to obtain historical records, so we used natural catchments to represent the historical state of uncleared terrestrial forests (i.e., the average of all samples taken in natural catchments <50 m away from nutrient input in heavy rainfall). This use of “space” as a surrogate for “time” was also applied to estimates of “contemporary” (i.e., background) concentrations among catchment types. To acquire background estimates that were less affected by pulses of nutrient discharge, we sampled seawater from the adjacent catchment at 1000 m seaward of discharge during light rainfall. These two types of sampling

TABLE 1. Dissolved inorganic nitrogen (DIN) concentrations of terrestrial runoff (i.e., donor DIN) and their proportional relationship to recipient waters (i.e., donor:recipient ratio; where recipient is scaled to 1).

Catchment	DIN concentration (mg/L)	Donor:1
a) Urban		
Heavy rainfall (<50 m)	$0.814 \pm 0.148$	$42.8 \pm 7.8$
Light rainfall (<50 m)	$0.303 \pm 0.037$	$16.0 \pm 2.0$
Light rainfall (>500 m)	$0.091 \pm 0.021$	$4.8 \pm 1.1$
b) Agricultural		
Heavy rainfall (<50 m)	$0.126 \pm 0.019$	$6.7 \pm 1.0$
Light rainfall (<50 m)	$0.051 \pm 0.004$	$2.7 \pm 0.2$
Light rainfall (>500 m)	$0.021 \pm 0.003$	$1.1 \pm 0.2$
c) Natural		
Heavy rainfall (<50 m)	$0.002 \pm 0.001$	$0.1 \pm 0.0$
Light rainfall (<50 m)	$0.039 \pm 0.001$	$2.1 \pm 0.1$
Light rainfall (>500 m)	$0.023 \pm 0.003$	$1.2 \pm 0.1$

*Notes:* Data are presented for each catchment type (i.e., urban, agricultural, and natural catchments) at different rainfall intensities and distances from terrestrial runoff. Values are means  $\pm$  SE.

enabled us to test which estimates best correlated with habitat change in this system.

Our estimate of habitat change is based on the model of nutrient-driven expansion of covers of turf-forming algae at the expense of the cover of canopy-forming algae (described in Connell et al. 2008). Habitat change is estimated, therefore, by calculating the proportional difference between percentage cover of canopies in natural catchments (i.e., as mean cover among all natural catchments) and percentage cover of canopies in each transect ( $n = 4$  transects per catchment) in each catchment of agricultural and urban use ( $n = 4$  catchments per catchment type).

#### *Analysis of data*

Analysis of variance was used to test for differences in measured variables (i.e., DIN,  $\delta^{15}\text{N}$ , percentage cover of habitat) among catchment types and was based on a hierarchical design in which the four replicate catchments (sites;  $n = 4$  sites per catchment type) were nested within catchment type (treated as fixed factor). Kolmogorov-Smirnov tests were used to test for differences in the size frequency distributions of turf-forming and canopy-forming algae between catchment types. Pearson's product-moment correlation was used to assess the most strongly correlated variables with habitat structure.

## RESULTS

### *Links between catchment use and coastal nitrogen*

Dissolved inorganic nitrogen (DIN) concentrations of recipient coastal waters followed a predictable pattern related to intensity of catchment use (Table 1). DIN concentrations of waters adjacent to urban catchments (<50 m from input of surface runoff) were greater than agricultural and natural catchments regardless of



TABLE 2. Results of three-factor ANOVA testing for catchment-related differences in dissolved inorganic nitrogen concentrations (DIN) of coastal waters (a) close to point sources of terrestrial runoff (<50 m) during heavy and light rainfall and (b) close to (<50 m) and far from point sources of terrestrial runoff (>500 m) during light rainfall.

Treatment	df	MS	F	P
a) DIN concentrations (<50 m) sampled during heavy and light rainfall				
Catchment type	2	242.202	29.32	***
Site (catchment type)	9	8.261	30.59	***
Rainfall	1	21.860	5.13	*
Catchment type $\times$ rainfall	2	79.939	18.76	***
Rainfall $\times$ site(catchment type)	9	4.262	15.78	***
Residual	216	0.270		
b) DIN concentrations at <50 and >500 m sampled during light rainfall				
Catchment type	2	0.468	8.28	**
Site(catchment type)	9	0.057	15.81	***
Distance	1	0.303	6.96	*
Catchment $\times$ distance	2	0.143	3.29	NS
Distance $\times$ site (catchment type)	9	0.044	12.19	***
Residual	216	0.004		

Notes: Consistency of pattern among catchments is assessed between (a) rainfall events (i.e., temporal consistency) and (b) across distances (i.e., spatial consistency). Data were  $\ln(x + 1)$ -transformed to meet the assumptions of heterogeneity of variance. SNK (Student-Newman-Keuls) tests on significant catchment  $\times$  rainfall term in panel (a) showed, for heavy rain, urban > agriculture > natural catchments; and for light rain, urban > agriculture = natural catchments. SNK tests on significant main effects terms in panel (b) showed, for catchment type, urban > agriculture = natural catchments; for distance, close > far.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; NS, not significant.

rainfall event (Table 2a). During heavy rainfall, DIN concentrations of waters adjacent to agricultural catchments were greater than natural catchments, but they did not differ during light rainfall (Table 2a, significant catchment  $\times$  rainfall interaction term, Student-Newman-Keuls (SNK) tests). Depending on intensity of rainfall, the ratio of donor-to-recipient DIN was between 40:1 and 192:1 in urban catchments, between 5:1 and 12:1 in agricultural catchments, and between 1:1 and 3:1 in natural catchments.

Elevated DIN concentrations extended to at least 500 m away from point of input (i.e., along the sampled coastal strip of >1 km), but showed a general decrease in concentration by 3.6 times in urban and 2.5 times in agricultural catchments compared to 50 m samples. The significant "catchment type" term (Table 2b) detected DIN concentrations to be greater within urban than agricultural and natural catchments (SNK test: urban > agricultural = natural) across both short and long distances (i.e., 50 and 500 m, respectively). DIN decreased with distance from input among all catchment types (Table 2b, SNK tests).

#### Links between catchment use and benthic use of nitrogen

Enrichment of nitrogen isotope values ( $\delta^{15}\text{N}$ ) of transplanted *Ulva australis* (i.e., increase relative to original value) was greater within urban catchments than agricultural and natural catchments (Fig. 1a; ANOVA:  $F_{2,9} = 5.87$ ,  $P < 0.05$ ; SNK test; urban > agricultural = natural). The isotopic values of algae transplanted to urban catchments (Fig. 1b) were indicative of assimilation of a large proportion of sewage-derived nitrogen (e.g., Gartner et al. 2002). As the  $\delta^{15}\text{N}$  values provide an integrated measure of sources of available nitrogen over weeks (Cole et al.

2004), the values obtained for transplants in urban catchments show that sewage derived nitrogen was assimilated by algae during extended periods following translocation. There was a slight, but nonsignificant shift in  $\delta^{13}\text{C}$  values between natural catchment and the two developed catchment types (Fig. 1b; ANOVA:  $F_{3,37} = 0.33$ ,  $P > 0.05$ ).

Tissue %N values of transplanted algae had a positive correlation to both  $\delta^{15}\text{N}$  stable isotope values (Pearson's correlation:  $r = 0.661$ ,  $P < 0.05$ ) and DIN concentrations of recipient waters ( $r = 0.658$ ,  $P < 0.05$ ) across all sites ( $n = 12$  sites; i.e., three catchment types, four replicate transplants per site). Across all catchment types the ratio of donor to recipient (contemporary) concentrations of DIN was positively correlated with both tissue %N values (Fig. 2a) and  $\delta^{15}\text{N}$  (Fig. 2b) of transplanted algae ( $P < 0.05$  and  $P < 0.001$ , respectively). Urban catchments were associated with the greatest subsidy, tissue %N and  $\delta^{15}\text{N}$ .

#### Links between catchment use and habitat structure

Patches of canopy-forming algae were up to 40 m in diameter within agricultural and natural catchments, but typically less than 10 m in diameter within urban catchments (Fig. 3). The size-frequency distribution of patches of canopy-forming algae in urban catchments differed from both agricultural (Kolmogorov-Smirnov  $K_{d93,110} = 0.359$ ,  $P < 0.05$ ) and natural catchments ( $K_{d93,117} = 0.209$ ,  $P < 0.05$ ), but the distributions between agricultural and natural catchments did not differ ( $K_{d110,117} = 0.181$ ,  $P > 0.05$ ). Turf-forming algae, the major occupiers of space in the absence of canopies (93.3%  $\pm$  6.0% of canopy gaps across all observations:  $n = 44$  transects), were typically small (<5 m diameter) within agricultural and natural catchments, but reached

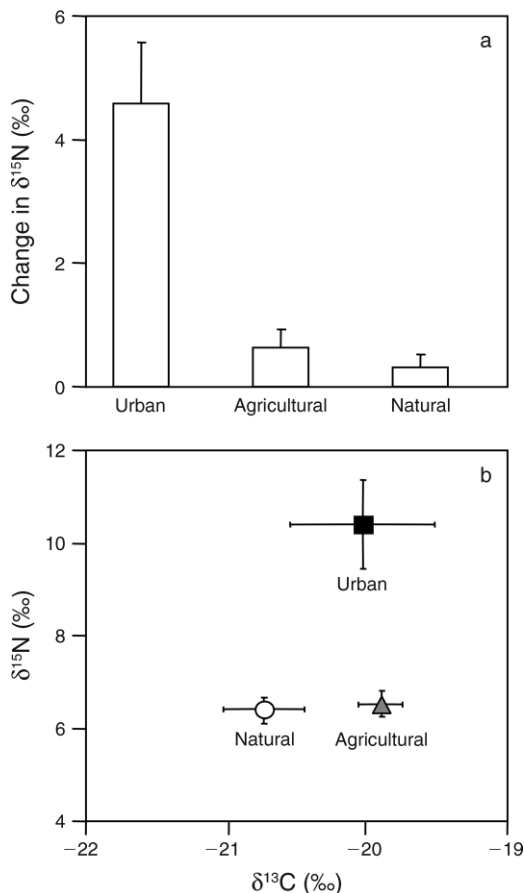


FIG. 1. (a) Change in mean tissue  $\delta^{15}\text{N}$  for *Ulva australis* transplanted ( $\sim 60$  days) among catchment types ( $n = 3$  transplants per catchment, nested within four replicate catchments per catchment type) and (b) dual isotope plot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for algal transplants. Values shown are means, and error bars indicate SE.

$>10$  m diameter within urban catchments (Fig. 3). Comparison of size frequency distribution of patches of turf-forming algae indicated that urban catchments differ from natural catchments ( $K_{d24,85} = 0.28$ ,  $P < 0.05$ ), but not agricultural catchments ( $K_{d40,85} = 0.257$ ,  $P > 0.05$ ).

As a percentage of substratum per transect, canopy-forming algae was least extensive adjacent to urban catchments than agricultural and natural catchments (Fig. 4a, Table 3a). This pattern was contrasted by the percentage covers of turf-forming algae, which were more extensive in urban catchments than agricultural and natural catchments (Fig. 4b, Table 3b).

#### Strength of subsidy-habitat associations

The correlation between the size of subsidy (i.e., donor:recipient ratio) and our estimate of habitat change was strong (Fig. 5;  $r = 0.786$ ,  $P < 0.001$ ). These data not only indicate that urban catchments (larger subsidies) have a greater influence on habitat structure than agricultural catchments (smaller subsidies), but they also reveal this relationship to hold well within each

catchment type. An important realization was that these relationships are stronger when the size of subsidy (i.e., donor-recipient ratio) is based on historical estimates (Fig. 6a;  $r = 0.891$ ,  $P < 0.005$ ;  $n = 8$  catchments) rather than contemporary estimates of the DIN concentration of recipient waters (Fig. 6b;  $r = 0.849$ ,  $P < 0.01$ ;  $n = 8$  catchments). These results provide important insights into the usefulness of these ratios when it is realized that they are a better predictor of our proxy of habitat change than DIN concentration alone (Fig. 6c;  $r = 0.798$ ,  $P < 0.05$ ;  $n = 8$  catchments), which is currently the principal means of assessing coastal eutrophication. Population size correlated well with habitat change across all catchments (Fig. 6d;  $r = 0.883$ ,  $P < 0.005$ ;  $n = 8$  catchments), but it is noteworthy that this association becomes less strong with increasing population size (i.e., the urban catchments).

In many instances, ecologists will need to contrast environmental affects among urban catchments, and our small sample size ( $n = 4$  urban catchments) reveals that very small urban populations (i.e.,  $\sim 4000$  people) may

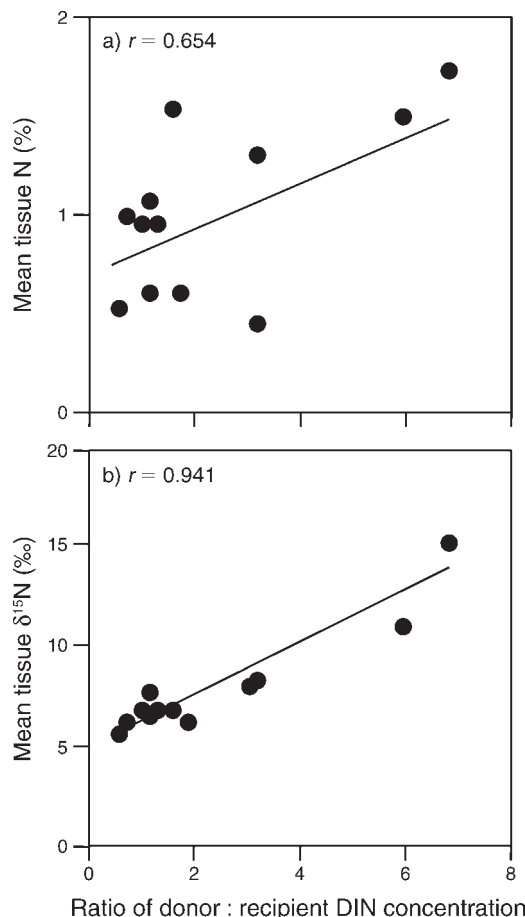


FIG. 2. The relationship between subsidy (i.e., ratio of donor:recipient dissolved inorganic nitrogen [DIN] concentrations, measured as mg/L) and (a) tissue N concentrations and (b)  $\delta^{15}\text{N}$  values of *Ulva australis* transplanted to alternate catchment types.

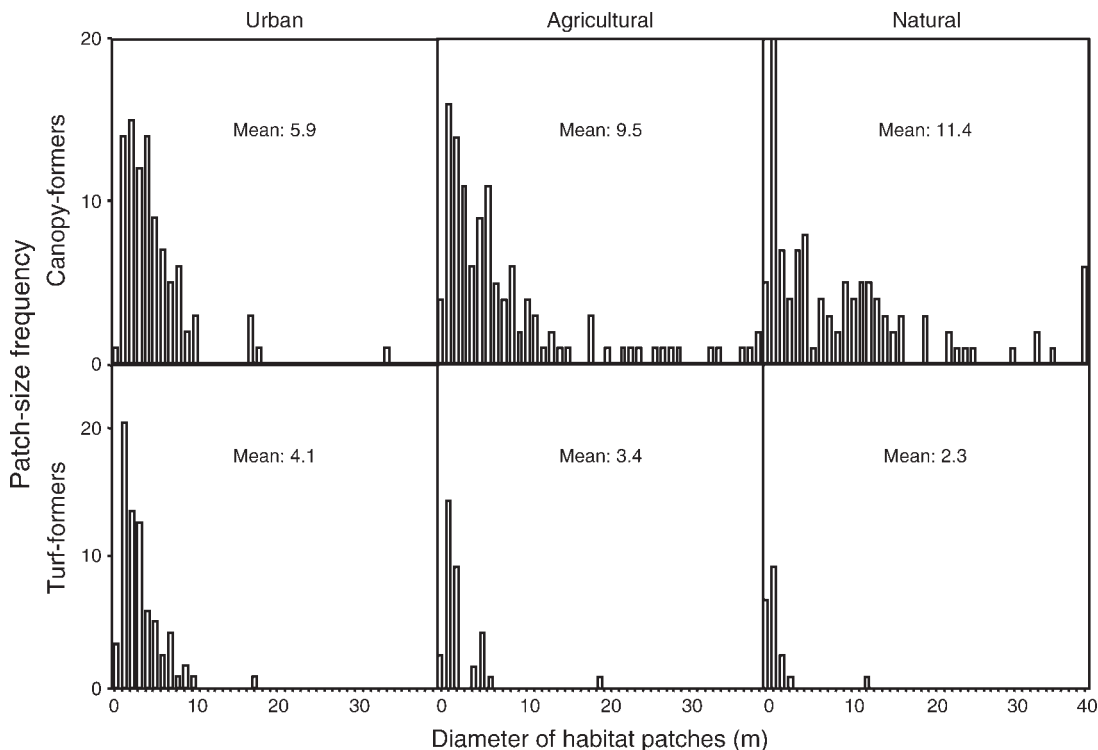


FIG. 3. Size (patch diameter) frequency distribution of patches of habitat-forming algae among catchment types ( $n = 4$  transects per catchment, subsamples of four replicate catchments nested within three catchment types).

create subsidies and impacts that are similar to populations many times their size (i.e.,  $\sim 26,000$  people). Such comparisons among urban catchments appear to be better related to estimates of the magnitude of subsidy (donor–recipient subsidies) (Figs. 5 and 6).

#### DISCUSSION

##### *Land-to-sea linkages among alternate catchment types*

We provide evidence that link human activities to the magnitude of land-to-sea subsidies at a landscape scale, and then linked this variation to its predicted consequences in kelp forest ecology. This evidence was based on (1) greater dissolved inorganic nitrogen (DIN) loads of coastal waters adjacent to urban catchments when compared to less developed catchments, (2) the delineation of sewage-derived nitrogen as a relatively persistent component of the DIN pool utilized by subtidal algae, and (3) the strength of the relationship between magnitude of subsidy (and size of human population) and the relative proportion of perennial habitats (canopy-forming algae) compared to ephemeral habitats (turf-forming algae).

Terrestrial subsidies of nitrogen to subtidal systems in this study are likely to arrive in rainfall driven pulses (sensu Anderson et al. 2008), notwithstanding the more or less continuous subsidy from sewage effluent in urban catchments. In our system, heavy rainfall can deliver pulsed concentrations of DIN to urban coasts that are

up to 400 times greater than less-developed catchments. While we acknowledge that estimates based on DIN may slightly underestimate absolute loads of bio-available nitrogen (c.f. TDN which produces overestimates; Seitzinger et al. 2002), our results provide a robust test of the differences among alternative catchment types. Given the limiting nature of nitrogen within coastal ecosystems (Howarth and Marino 2006), and that the effect of spatial subsidies may be proportional to the ratio between donor and recipient systems (Marczak et al. 2007), it can be anticipated that habitat change would be greater within urban catchments.

Numerous studies have shown the importance of wastewater as a source of human-derived nitrogen entering estuarine systems based on  $\%N$  and  $\delta^{15}N$  values of submerged aquatic vegetation (e.g., McClelland and Valiela 1998, Costanzo et al. 2003) but this has not been demonstrated in open coastal systems. In this study, the magnitude of enrichment observed in algal transplants within urban catchments was large (enrichment by  $\sim 4.5\%$ , to approach mean values of  $10.4\%$ ), similar to changes reported for the same species exposed to secondary treated effluent in both field and laboratory experiments (Gartner et al. 2002). This level of enrichment in algal tissue provides a direct link to sewage-derived sources of DIN, as seen in estuarine systems (McClelland and Valiela 1998), and we suggest that it similarly represents a strong and continuous source of nitrogen from urban catchments to recipient



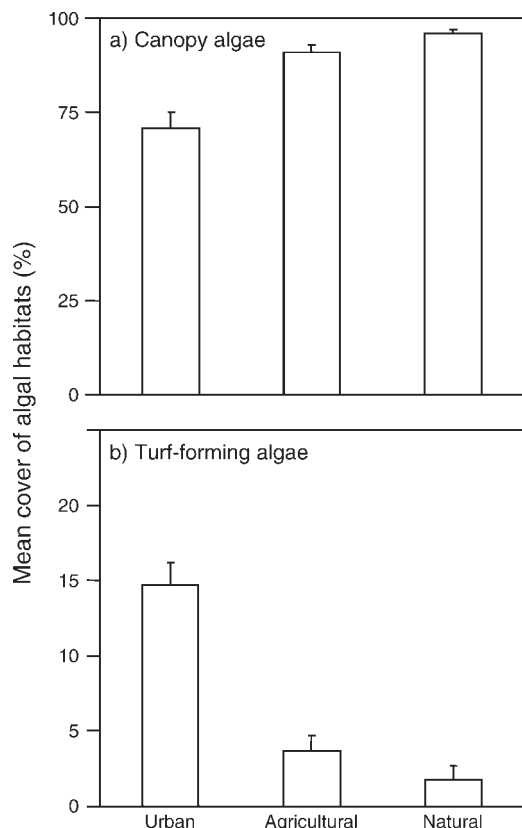


FIG. 4. Percent cover of (a) canopy-forming algae and (b) turf-forming algae among catchment types ( $n = 4$  transects per catchment, subsamples of four replicate catchments nested within three catchment types). Values are means + SE.

systems on open rocky coasts. It follows then that this release of material, which is often substantial, increases the magnitude of land-to-sea subsidy, particularly within coastal seas of naturally low nutrient status.

The magnitude of human-derived subsidy may be proportional to the population size of humans, but in some circumstances poor wastewater treatment (e.g., old and leaking septic systems) may provide contingent conditions. Septic systems are a major source of nitrogen in groundwater (Valiela et al. 1997), and are often used

in catchments with small population sizes because of the scales of economy involved with expensive tertiary treatment.  $\delta^{15}\text{N}$  values of marine plants increase in proportion to inputs of wastewater (Cole et al. 2005), which may explain our observation that the values associated with small urban catchments with aged and leaking septic systems ( $10.9\% \pm 0.8\%$ ; ~4000 people in Second Valley) approached values in catchments that export greater volumes of tertiary treated water ( $14.8\% \pm 0.6\%$ ; >150 000 people in Onkaparinga). As populations expand into undeveloped coast, there is an increasing need to understand how catchment management (e.g., retainment or rehabilitation of terrestrial vegetation) may counter increased N delivery of septic tanks. We suggest, therefore, that the effectiveness of wastewater treatment coupled with ambient and historical concentrations of nutrients within catchments (i.e., size of disparity between donor–recipient resources) may create substantial variance in associations between size of human population and size of subsidy from local through regional scales.

South Australia has highly seasonal rainfall and few permanent natural sources of terrestrial input to coastal systems (e.g., rivers) resulting in little export of terrestrial-derived nutrients to coastal systems outside rainfall events. It is no surprise, then, that we found donor:recipient subsidy (i.e., DIN concentration) during rainfall events to be a good predictor of the condition of subtidal habitats in our system. In regions of relatively constant natural (e.g., the large river systems of North America) or human inputs (e.g., wastewater of large populations), however, the load of nutrients within discreet rainfall events is likely to be minor compared to the annual terrestrial export to marine systems. In such cases, the total nutrient load being exported may be a better predictor of subsidy than concentration of nutrients.

While we acknowledge that agricultural development can constitute a significant source of land to sea nutrients (e.g., Costanzo et al. 2003), the lack of change in isotope values of transplants in these catchments (i.e., neither depletion, suggestive of the use of fertilizers, or enrichment, indicative of animal wastes; Heaton 1986)

TABLE 3. Two-factor ANOVA testing for differences in (a) canopy-forming and (b) turf-forming algal communities among sites and catchments.

Treatment	df	MS	F	P
a) Canopy-forming algae				
Catchment	2	4291.6374	25.27	***
Site(catchment)	9	169.8330	2.81	*
Residual	36	60.4037		
b) Turf-forming algae				
Catchment	2	1327.8783	17.27	***
Site(catchment)	9	76.8814	2.43	*
Residual	36	31.6424		

Notes: Data were arcsine-transformed percentages. SNK test on canopy-forming algae: urban < agriculture = natural. SNK test on turf-forming algae: urban > agriculture = natural. \*  $P < 0.05$ ; \*\*\*  $P < 0.001$ .

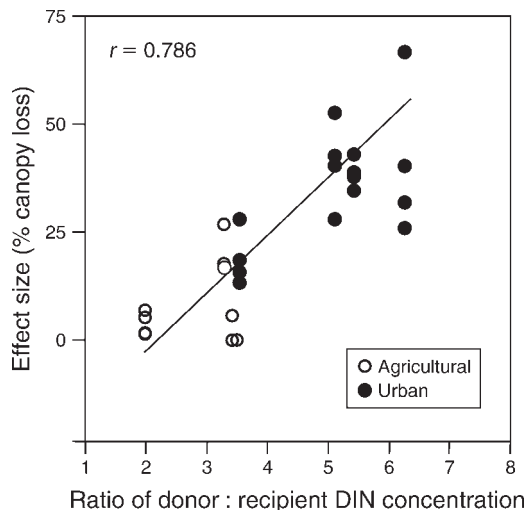


FIG. 5. The potential of catchment-related nitrogen subsidy to predict apparent habitat change (i.e., canopy loss; effect size) among replicate transects ( $n = 4$  per replicate catchment). The subsidy (i.e., ratio of donor–recipient DIN concentrations, measured as mg/L) is based on historical estimates of nutrients in recipient waters (see Fig. 6 for comparison).

suggest that these activities, at their current level of intensity (i.e., mostly sparse populations of livestock with some intensive viticulture), do not constitute an important source of nitrogen to this particular coastal system.

#### *Habitat alternation and variation in its susceptibility*

Increasing shoreline development has been associated with increasing availability of water column nitrogen which drives the replacement of longer-lived and slow-growing habitats (e.g., seagrass and large macroalgae) with opportunistic and fast-growing and smaller macroalgae (Duarte 1995). In rocky subtidal systems, nutrient-driven changes to habitat center on the replacement of canopy-forming algae (e.g., kelp) with filamentous turfs (see review in Connell 2007b). Turfs lack the capacity to store nutrients and are normally ephemeral, but are able to persist under the continual elevation of nitrogen (S. D. Connell, B. D. Russell, D. Gorman, A. Airoidi, unpublished manuscript). The persistence of dense covers of turf creates positive feedbacks, trapping sediment and preventing the recruitment of canopy-forming algae (Airoidi 2003). Persistent turfs may initially occur through local loss of kelp in small patches (e.g., storm-driven clearings of  $<3\text{--}6\text{ m}^2$ ; Kennelly 1987) which increase in size over time to coalesce into larger patches when adjacent to urban coast (Gorgula and Connell 2004). Over longer periods (e.g., several decades), it is possible to observe the wholesale loss of perennials in favor of opportunistic adjacent to developed coast (Eriksson et al. 2002, Connell et al. 2008). Such habitat alteration is considered to be quite general to developed coastlines (Worm et al. 1999, Airoidi 2003, Connell

2007b), observed as a shift from highly productive and structurally complex habitats to less productive and complex habitats, representing a fundamental shift in ecological function (e.g., habitat provision) and export of energy (Vitousek et al. 1997b).

We provide indirect evidence to support the idea that habitat alternation is more likely where there is a greater disparity between donor (amount of enhanced subsidy) and receiver resources (ambient and historical). Understanding such donor–recipient ratios (Marczak et al. 2007) would also assist efforts to integrate cross-scale (e.g., local–regional–biogeographic) variation in coastal responses to development (Connell and Irving 2008). This effort may identify localities of probable habitat shifts from the global set of coastlines with large human populations. For example, biogeographic variation in productivity (Rochford 1980, Russell et al. 2005) may explain regional anomalies where the role of wastewater outfalls are often deemphasised around Australia's largest city (e.g., Sydney, on a coast of higher productivity; Chapman et al. 1995), but their role is considered profound around a small coastal city at a similar latitude (e.g., Adelaide, on coast of lower productivity; Connell et al. 2008). By achieving this understanding across successively larger scales, ecologists may assist the appropriate scale-dependent perspectives needed by management. Such knowledge may not only provide practical advice to authorities that decide local environmental policy, but it may also allow for better regional and biogeographic policy under governance of state or national institutions. Until now, it has been hard to understand why managers of small coastal populations should have legitimate concerns for nutrient pollution when those of much larger population centers and their more intensely researched coastlines fail to share the same concerns. Donor:recipient ratios have the capacity to reconcile such differences by recognizing that while certain water-quality guidelines may be appropriate for some regions and their managers (e.g., eastern Australia with similarly high donor-to-recipient concentrations), they may be inappropriately liberal for other regions and managers (e.g., southern Australia with lower N delivery, but substantially lower recipient concentrations).

#### *Managing connected land-to-seascapes*

Humans are embarking on the final phase of coastal development of the world's temperate coastlines. Whilst land-river and land-lake connections have long been recognized (Carpenter et al. 1998), the land-to-sea connections have received comparatively little attention along human-dominated coastlines (Cloern 2001). Land-to-sea connections have primarily focused on changes in estuaries and bays (see reviews in Rabalais 2002, Bowen et al. 2007), showing strong links between catchment related nitrogen and shifts in abundance of submerged aquatic vegetation from slow-growing seagrasses and large macroalgae to fast-growing macro-

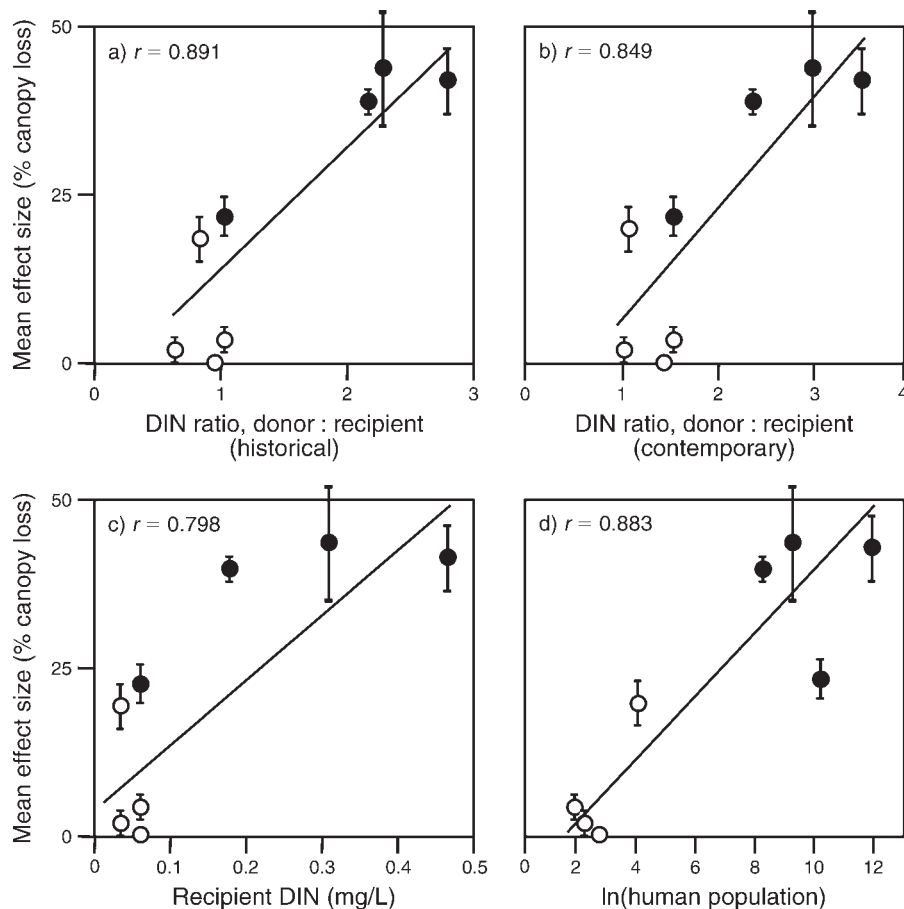


FIG. 6. The potential of catchment-related nitrogen and human population size to predict apparent habitat change (mean effect size). The magnitude of subsidy (ratio of donor: recipient DIN) is more strongly related to effect size when based on (a) historical estimates of nutrients in recipient waters than (b) contemporary estimates, or (c) concentrations of DIN. Population size (d) is well correlated across the range of population sizes, but this relationship appears weak among urban catchments. Key: Open circles, agricultural catchments; solid circles, urban catchments. All nitrogen data and population values are  $\ln(x + 1)$ -transformed, except for (c) absolute concentrations of DIN. Values are means  $\pm$  SE.

algae (e.g., Duarte 1995, Deegan et al. 2002). Our present work appears to be the only available assessment that specifically links variation in human-use of land with variation in such phase-shifts on open coastlines. In this regard, it also represents a departure from the traditional explanations of kelp deforestation that centre on top-down impacts on ecosystem drivers; i.e., trophic cascades that cause populations of sea urchins to increase via the decline in their predators (Steneck et al. 2002). In fact, the ecological study of open coasts has been largely preoccupied with understanding the ecological effects of what humans remove from the sea (e.g., effects of fishing on trophic cascades) rather than what humans add to the sea (e.g., effects of nutrients and sediments). The reality is that alteration of both producers (e.g., nutrient-driven change) and consumers (e.g., extraction of consumers) require attention to the synergies they may create (see review in Connell 2007b).

Some regions may be more susceptible to nutrient-driven habitat alteration where the consumers of greater

productivity (e.g., herbivores of ephemeral algae; Worm et al. 2000, Korpinen et al. 2007, Russell and Connell 2007) are reduced by the direct or indirect effects of harvesting (Bellwood et al. 2004). Where such synergies occur, knowledge of these interactions may contribute to the justification of Marine Protected Areas (MPA) because they have jurisdiction over the governance of sea-based extraction (i.e., fishing-driven declines of consumers that counter the effects of pollution), albeit not land-based addition of pollutants (i.e., catchment use). Marine Protected Areas appear to have less ecological justification on coasts which lack functional groups of herbivores which can counter the effects of nutrient enhancement (e.g., South Australia) and for which top-down effects are weak (Connell and Irving 2008). In these cases, MPAs alone will be insufficient to maintain habitats and more innovative management that recognizes solutions for both land-based and sea-based challenges is required (e.g., recycling land-based water).



PLATE 1. The replacement of canopy-forming algae (e.g., kelp-dominated landscapes pictured on the top) by structurally simple and less productive habitats comprising turf-forming algae (e.g., turf-dominated landscapes pictured on the bottom) have been linked to changes in land management. The relative vulnerability of systems to such switches may be understood by identifying changes in the ratio of donor (e.g., land) to recipient (e.g., sea) subsidies. Photo credits: (top) S. D. Connell; (bottom) D. Gorman.

The recent recognition of land-to-sea connectivity along climate affected coasts (i.e., drying and drought prone coasts) has caused implementation of solutions for the sea (policy on reducing discharge) that can also act as solutions for the land (policy on establishing new sources of water that do not rely entirely on rainfall). For example, new cross-government acceptance of nutrient driven habitat loss (i.e., Connell et al. 2008) has motivated policy initiatives that aim to recycle nearly 45% of Adelaide's wastewater and save supplies of drinking water. Wastewater treatment plants can be upgraded to produce recycled water (for residential and

industrial zones, recreational parks and agriculture) so that most of the nutrient rich discharge (nearly three billion liters per annum in Adelaide) can be used more effectively to manage the land (reduce reliance on rainfall) and sea (reduce nutrient pollution), and their connection.

In conclusion, our research demonstrates a landscape-scale approach that can provide information needed to integrate land-to-sea dynamics of ecological change at scales relevant to their governance and practical management. We provided direct evidence that human-mediated subsidies from land-to-sea can alter the



flow of energy to subtidal systems. Our indirect evidence (i.e., relationship between magnitude of subsidy and apparent habitat alteration) suggests that the human enhancement of subsidies across the terrestrial to marine boundary may bring greater ecological change to coastal populations that do not manage large increases of land (donor) to sea (recipient) subsidies of limiting resources. On many coasts this change may be prevented, or even reversed, where ecologists assist managers recognize the land-to-sea connection and thereby enable joint solutions to the challenges of land-based and sea-based sustainability.

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