

Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests

Christopher C Wilmers^{1*}, James A Estes², Matthew Edwards³, Kristin L Laidre⁴, and Brenda Konar⁵

We combine data collected from the past 40 years to estimate the indirect effects of sea otters (*Enhydra lutris*) on ecosystem carbon (C) production and storage across their North American range, from Vancouver Island to the western edge of Alaska's Aleutian Islands. We find that sea otters, by suppressing sea urchin (*Strongylocentrotus* spp) populations, allow kelp (Order Laminariales) ecosystems to develop with a net primary productivity (NPP) of 313–900 grams C per square meter per year ($\text{g C m}^{-2} \text{ yr}^{-1}$) and biomass density of 101–180 grams C per square meter (g C m^{-2}). In the absence of sea otters, these areas would have an NPP of 25–70 $\text{g C m}^{-2} \text{ yr}^{-1}$ and biomass density of 8–14 g C m^{-2} . Over an ecosystem area of approximately $5.1 \times 10^{10} \text{ m}^2$, the effect of sea otter predation on living kelp biomass alone represents a 4.4- to 8.7-teragram increase in C storage. At 2012 prices (US\$47 per ton of C), this stored C would be valued at US\$205 million–\$408 million on the European Carbon Exchange. Although questions remain concerning the pathways and compartments of kelp C flux and storage, sea otters undoubtedly have a strong influence on these elements of the C cycle. Predator-induced trophic cascades likely influence the rates of C flux and storage in many other species and ecosystems.

Front Ecol Environ 2012; 10(8): 409–415, doi:10.1890/110176 (published online 7 Sep 2012)

Atmospheric carbon dioxide (CO_2) concentrations have increased by approximately 40% since the start of the Industrial Revolution, causing or contributing to measurable global heat retention and elevated atmospheric temperatures, partial melting of the polar ice caps, ocean acidification, and a host of other impacts on Earth's environments (Pachauri and Reisinger 2007). Collectively, these impacts are viewed by most scientists and policy makers as a serious threat to human welfare. Although the mitigation of increasing atmospheric CO_2 (via source reduction or carbon [C] sequestration) is a pressing issue in global environmental conservation (Pachauri and Reisinger 2007), many of the proposed or imagined means for accomplishing this goal face major obstacles because of high societal costs and uncertain or detrimental associated environmental impacts. The management of plant assemblages might help sequester some of this atmospheric C while reducing these costs and impacts. Yet, apart from reforestation and agricultural strategies that maintain carbon stocks in plant biomass and/or soils (Richards and Stokes 2004), there has been relatively little analysis of how the manipulation of species interactions that link with autotrophs could be used as part of an

effective and environmentally friendly sequestration strategy.

Four facts point to the potential utility of using altered food web dynamics to reduce atmospheric CO_2 concentration. First, C is the elemental backbone of the living biosphere, comprising >50% by mass of all organic matter globally (Paul and Clark 1996). Second, the abundance and distribution of autotrophs, which hold much of the world's non-fossilized organic C in their tissues and transform inorganic C to organic C through photosynthesis, are strongly influenced by species interactions, especially herbivory (Herms and Mattson 1992). Third, food web dynamics worldwide have been extensively altered, especially through the loss of large vertebrate consumers (Ray *et al.* 2005; Terborgh and Estes 2010). And fourth, despite extensive global habitat destruction and fragmentation, large tracts of land and water remain in which food web structure and dynamics could be restored or altered with appropriate conservation and management. More than 50 years have now passed since the publication of the influential “green world hypothesis” (Hairston *et al.* 1960), which posited that predators increase autotrophs by limiting herbivores. Here, we explore a related idea – that predators acting through this same process might substantially influence the C cycle.

As a group, large apex predators are declining worldwide at rates exceeding those of other groups of species (Ray *et al.* 2005). The loss of apex predators from ecosystems often results in a decline in plant biomass as the abundance of herbivores and the intensity of herbivory consequently increase. This effect, termed the *trophic*

¹Environmental Studies Department, University of California, Santa Cruz, CA *(cwilmers@ucsc.edu); ²Ecology and Evolutionary Biology Department, University of California, Santa Cruz, CA; ³Department of Biology, San Diego State University, San Diego, CA; ⁴Polar Science Center, Applied Physics Laboratory, University of Washington, Seattle, WA; ⁵School of Fisheries and Ocean Sciences, University of Alaska, Fairbanks, AK

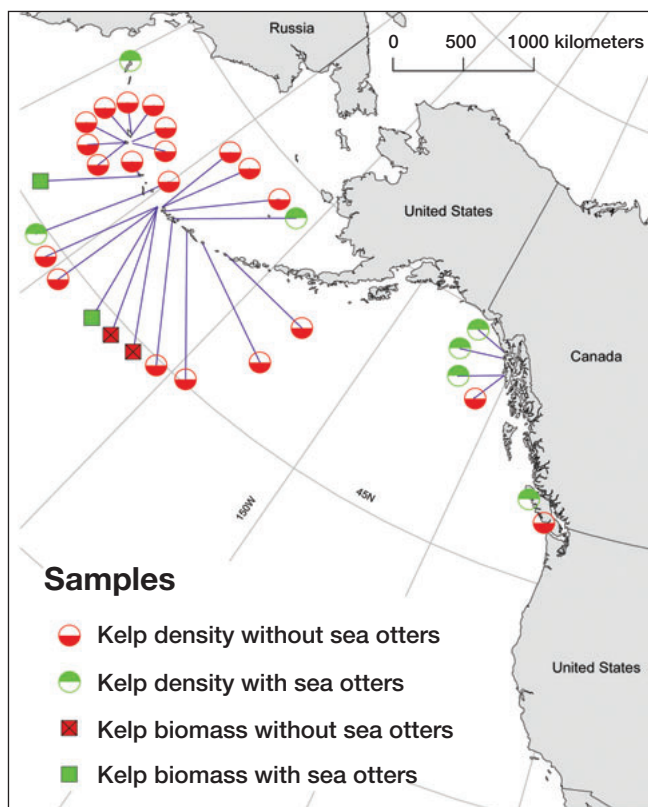


Figure 1. Equidistant conical projection of the North American range of sea otters from the California–Mexico border to the tip of the Aleutian Islands. Sampling locations of kelp density and biomass are shown. At some locations, kelp measurements were made over multiple years, with sea otters present in some years and not in others. We restrict our calculations of sea otter effects on carbon storage and flux to the area between southern Vancouver Island and the western tip of the Aleutian archipelago.

cascade (Paine 1980), has been identified in diverse terrestrial and aquatic ecosystems (Pace *et al.* 1999), thus raising the possibility that the restoration of apex predators could convert some amount of atmospheric CO₂ to organic C in the tissues of autotrophs and their consumers.

Here, we use sea otters (*Enhydra lutris*) and kelp forests (eg *Laminaria*, *Eularia*, *Nereocystis*, *Macrocystis*, and *Pterygophora* spp) in the North Pacific to explore the dynamics and potential consequences of this process. Sea otters have a positive indirect effect on kelp biomass by preying on sea urchins (*Strongylocentrotus* spp), a kelp grazer (Estes and Palmisano 1974). When sea otters are present, urchins seek refuge in rock crevices and subsist on kelp detritus. In the absence of sea otters, urchins often adopt a mobile feeding strategy of grazing on living kelp (Harrold and Reed 1985; Konar and Estes 2003), thus reducing kelp density and kelp bed distribution (Estes and Duggins 1995). This results in a strong positive relationship between the abundance of sea otters and the abundance of kelp (Estes *et al.* 2010). Since growing kelp has previously been proposed as a strategy for

sequestering C (Packer 2009) because of its high rate of uptake of atmospheric CO₂, it stands to reason that sea otters might well increase the rate of C sequestration through their positive indirect effect on kelp.

Here we ask, how do sea otters impact C standing stocks and flux through their indirect effects on kelp populations? We provide an initial answer to this question by combining data collected over the past 40 years on differences in kelp abundance between systems with and without sea otters, the chemical composition of kelp, the net primary productivity (NPP) of kelp forests, and the areal extent of habitat suitable for kelp forest development across 5400 km of the sea otter's range in the North Pacific Ocean. We then discuss the implications of these results for atmospheric C sequestration.

Methods

We investigated the role of sea otters in influencing the productivity of kelp beds and their resulting influence on the C cycle in two ways: (1) by measuring the carbon density C_d (g C m⁻²) in living kelp from coastal ecosystems with and without the influence of sea otter predation, and (2) on a flux, or NPP basis, by estimating the g C m⁻² yr⁻¹ cycling through kelp forests with and without sea otters. The flux of C through this ecosystem can be thought of as a balance between the C taken up by kelp during photosynthesis and the C ultimately released through respiration, decomposition, and deep-sea sinkage.

We estimated kelp biomass density (B) between rocky reef habitats with (B_w) and without (B_{wo}) sea otters at ecologically effective densities (Estes *et al.* 2010) by measuring kelp biomass on two reefs characteristic of those with sea otters (one each at Kiska and Ogliuga islands in the Aleutian archipelago) and two reefs typical of areas that have been deforested by sea urchin grazing (at Skagula and Ogliuga islands) following the recent collapse of sea otter populations in southwest Alaska (Estes *et al.* 1998; Doroff *et al.* 2003). We did this by clipping and weighing all of the kelp plants from 10 randomly selected 0.25 m² quadrats at each of the four areas.

Because our measures of B in kelp forests versus sea urchin barrens were based on relatively few samples from a limited region, we recalibrated these using our large and geographically extensive dataset on kelp numerical densities (N) in areas with (3215 randomly placed 0.25 m² quadrats from 153 randomly selected locations at six islands or regions; $N_w = 12.39$ plants × 0.25 m⁻² [standard error {SE} = 6.36]) and without (5665 plots from 271 locations at 20 islands or regions; $N_{wo} = 1.02$ plants × 0.25 m⁻² [SE = 1.41]) sea otters ($t_{8878} = 33.99$, $P < 0.001$) (Figure 1). We chose a recalibration procedure designed to minimize the difference in scenarios with and without sea otters so that our inferences about sea otter impacts on kelp abundance would be conservative. Specifically,

we scaled our estimates of B by the ratio of N with and without sea otters

$$\frac{N_w}{N_{wo}} = 12.15$$

to calculate estimated lower

$$\hat{B}_w = 12.15 \cdot B_{wo}$$

and upper

$$\hat{B}_{wo} = \frac{B_w}{12.15}$$

values in the range of kelp densities in areas with and without sea otters, respectively. We base our results and subsequent analysis on this range of B with (\hat{B}_w to B_w) and without (B_{wo} to \hat{B}_{wo}) sea otters. Areas with sea otters have not only more kelp individuals per unit area but also more biomass per individual kelp. As such, scaling by just the ratio of numerical densities is likely to underestimate the sea otter effect.

Carbon density calculations

Carbon content in living kelp was determined in the following manner. The samples were first dehydrated in a drying oven at 60°C to a constant mass ($\bar{x}_{\% \text{ water}} = 82.7$, standard deviation [SD] = 1.92). Samples were further desiccated on silica gel for no less than 2 weeks, then removed from the silica gel, brushed to remove any remaining silica, and ground in a Wiley Mill plant grinder. We analyzed ground samples for C content, recorded as a percentage per dry weight of each sample ($\bar{x}_{\% \text{ carbon}} = 26.6$, SD = 2.80), using an NCS 2500 elemental analyzer (Carlo Erba Instruments).

We calculated the mass of C in kelp forests within the North American range of sea otters from the various estimates of B described above; percent kelp dry mass (P_d); percent kelp carbon (P_c); and the total area of sea otter–kelp forest habitat (mean lower low water to 20-m depth contour) from southern Vancouver Island to the western end of the Aleutian archipelago (A_o). Kelp individuals within this area are limited largely to rocky reefs. Thus, we also calculated the total area of rocky reef habitat (A_r) within A_o . Estimates of A_o were obtained through the Shuttle Radar Topography Mission 30-arc second resolution bathymetric GRID from US Geological Survey Earth Resources Observation and Science (available at http://topex.ucsd.edu/WWW_html/srtm30_plus.html). Rocky reef area (A_r) was estimated for British Columbia (Gregr *et al.* 2008) and Alaska (Yodzis 1976). Carbon density was related to these variables by

$$C_d = \frac{B \cdot P_c \cdot P_d \cdot A_r}{A_o}$$

The positive indirect effects of sea otters on kelp forests discussed above have been well doc-

umented from the western Aleutian Islands to southern Vancouver Island (Estes and Duggins 1995; Watson and Estes in press). While similar positive indirect effects of sea otters on kelp occur along the outer coast of Washington State (Kvitek *et al.* 1998), the spatial extent of this effect has not been rigorously measured, and we have not yet evaluated the impact of sea otters on kelp forests in more southern areas. We therefore restrict our analysis to areas north of southern Vancouver Island. Further study will be required to extend our analysis to the sea otter range south of Vancouver Island.

Carbon flux calculations

The range of C flux (NPP) through kelp forests with and without sea otters was estimated from the published range of kelp production to biomass ratios (3.1–5.0 yr⁻¹; Reed and Brzizewski 2009). We multiplied these values by our range of standing kelp C biomass to estimate ranges of annual NPP in scenarios with and without sea otters. Miller *et al.* (2011) concluded that phytoplankton is not compensatory when kelp canopies are removed; nevertheless, because some nutrients would be exported with kelp, there is likely some compensation between macroalgae and phytoplankton. However, evaluating the importance of this possible compensation mechanism is outside the scope of the present work. We also do not consider the storage and flux of C in higher trophic levels because (1) data are not yet available to make these determinations and (2) the effects are likely to be small relative to those of autotrophs.

Results

We calculated the ranges of C_d in living kelp at 101–180 g C m⁻² and 8–14 g C m⁻² for ecosystems with and without sea otters, respectively (Table 1; Figure 2). Thus, the difference in kelp C_d between systems with and without sea otters – the “predator effect” – is 87–172 g C m⁻². The total habitat area (A_o) is 51 551 km², within which A_r is

Table 1. Comparison of kelp carbon dynamics between scenarios with and without sea otters at ecologically effective densities

	Sea otters absent	Sea otters present
Kelp biomass (wet weight)	75–133 g m ⁻²	911–1618 g m ⁻²
Kelp carbon	8–14 g C m ⁻²	101–180 g C m ⁻²
Net primary productivity	25–70 g C m ⁻² yr ⁻¹	313–900 g C m ⁻² yr ⁻¹
<i>Difference in scenarios with and without otters throughout their North American range</i>		
Kelp carbon	+4.4 to 8.7 Tg C	
Atmospheric carbon pool	–5.6 to 11%	
Atmospheric carbon pool since pre-industrial times	–21 to 42%	
Value of kelp carbon standing stock	+US\$205 million to \$408 million	

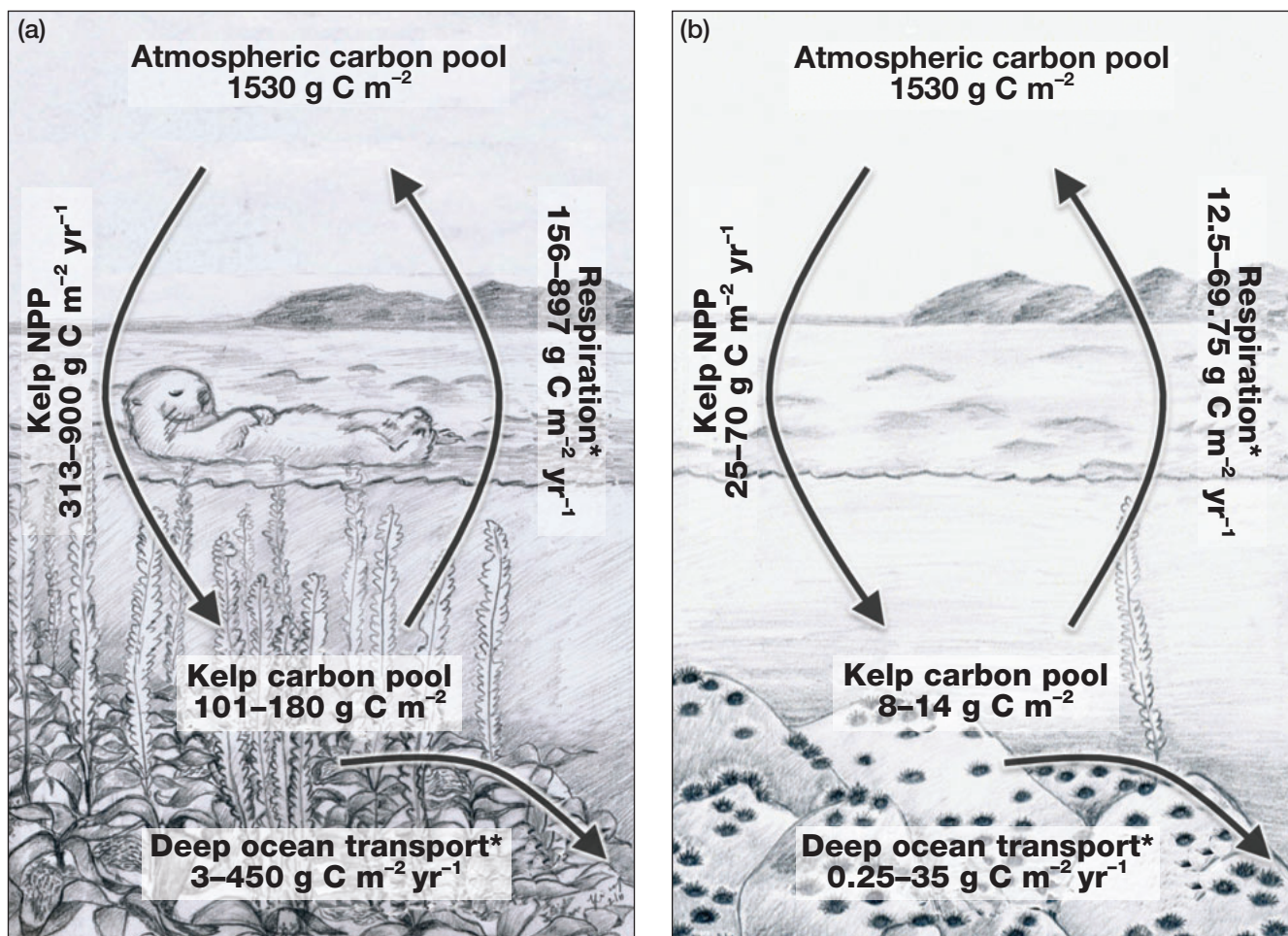


Figure 2. (a) When occurring at ecologically effective densities, sea otters reduce sea urchins, resulting in large kelp standing stocks and high net primary productivity (NPP). (b) When sea otters are absent, urchins decimate kelp stands, resulting in small kelp standing stocks and low NPP. *The percentage of annual kelp NPP that is transported to the deep oceans can be high, but its magnitude throughout the North American sea otter range is currently unknown. Transport numbers displayed here are based on scenarios where 1–50% of annual kelp NPP is transported to the deep ocean.

$12\,231 \text{ km}^2$. Applying these measurements and estimates to the North American range of sea otters within our study area results in a 4.4- to 8.7-teragram (Tg) increase in C due to the indirect effects of sea otters on kelp.

Net primary productivity in ecosystems with sea otters was $313\text{--}900 \text{ g C m}^{-2} \text{ yr}^{-1}$, as compared with $25\text{--}70 \text{ g C m}^{-2} \text{ yr}^{-1}$ in ecosystems without sea otters (Table 1; Figure 2). Thus, the increased flux of C through kelp ecosystems due to the addition of sea otters (the predator effect) is roughly $243\text{--}875 \text{ g C m}^{-2} \text{ yr}^{-1}$.

Discussion

Developing habitat use strategies that more effectively sequester C is a pressing global issue. Our results suggest that sea otters, and perhaps other predators, can substantially alter ecosystem C budgets through their indirect effects on plants. The one-time 4.4–8.7-Tg C increase in living kelp biomass due to sea otters represents 5.6–11% of the total C in a volume of atmosphere, the horizontal dimension of which is delineated by the sea otter's North

American range. Put slightly differently, this is 21–42% of the increase in atmospheric C in that same volume of atmosphere since the beginning of the Industrial Revolution. Because atmospheric CO_2 equilibrates rapidly and the sea otter range covers a mere one ten-thousandth of the Earth's surface, actual atmospheric CO_2 levels are unlikely to change substantially even if sea otters are restored throughout their historical range. The magnitude of this effect on a proportional basis, however, demonstrates the potential importance of indirect effects of trophic cascades on atmospheric C budgets, especially if similar species interactions occur on a global scale.

The effect of sea otters on C sequestration through time (ie on C flux) is more difficult to quantify. In terrestrial ecosystems, conversion of land use from agriculture to perennial grasslands or forests results in a one-time gain in C biomass sequestered in living tissues as well as annual changes in soil C accumulation. Rates of soil accumulation vary widely but average approximately $33 \text{ g C m}^{-2} \text{ yr}^{-1}$ for both forest and grassland establishment (Post and Kwon 2000). The restoration of sea otters

yields a large change in kelp NPP, but the fate of this increase in NPP with respect to atmospheric C levels remains unclear. A portion of the photosynthetically fixed C probably returns rapidly to the atmosphere through decomposition and gas exchange, but some of it undoubtedly remains as organic C for longer periods, especially if it is transported to the deep ocean where the time scale of mixing with the atmosphere is roughly many hundreds of years (Elderfield 2006). Deep ocean storage thus provides a potential oceanic analog to annual terrestrial soil C sequestration.

Little information exists on the percentage of annual kelp NPP that is transported to the deep oceans; one study (Harrold *et al.* 1998) revealed that levels of transport can be large (45.2 mg C m⁻² per day for one species of kelp) but variable depending on the proximity of the kelp bed to the deep ocean. However, the overall magnitude of this effect is unknown. If only 1% of the annual increase in NPP due to sea otters sank into the deep ocean, this would represent an annual sequestration of 2.4–8.8 g C m⁻² yr⁻¹ or 1.3–4.5 × 10⁵ metric tons (t) C yr⁻¹ range-wide. If 50% of the annual increase in NPP were transported to the deep ocean, 121–437 g C m⁻² or 0.6–2.3 × 10⁷ t C yr⁻¹ range-wide would be sequestered (Table 2). These values are roughly equivalent to the annual C emission of 100 000 automobiles (at the 1% kelp sequestration level) and about 5 million automobiles (at the 50% kelp sequestration level). For comparison, British Columbia and Alaska collectively had approximately 2.5 million registered passenger vehicles in 2011. Substantial amounts of kelp C may also be retained in beach wrack and in drifting plants, which continue to photosynthesize for extended periods.

The storage and flux of C in heterotrophs, and how these vary between systems with and without sea otters, also remains to be determined. Systems without sea otters typically have higher biomass densities of benthic invertebrates (Riedman and Estes 1990), which store some unknown amount of C. On the other hand, systems with sea otters have substantially higher coastal fish biomass densities (Reisewitz *et al.* 2005; Markell 2011), which also store some unknown amount of C. These effects are probably small relative to those of the autotrophs.

The effects of trophic cascades on C flux and storage also have a potentially important economic dimension, given that the sale of C is a rapidly evolving enterprise and C markets have recently been created in Europe and the US for the trade and sale of C stocks. An alluring idea would thus be to sell the C indirectly sequestered by the sea otter–kelp forest trophic cascade, possibly as a way to pay for their re-introduction and management or to compensate losses to shellfisheries from sea otter predation. To date, the arguments surrounding sea otter–shellfisheries conflicts have in-

involved different currencies – money and economic livelihoods from the fisheries side versus aesthetics and ecological function from the sea otter conservation side. We did not evaluate the legal and regulatory feasibility of this option, but it is instructive nonetheless to consider how much the C that sea otters indirectly sequester might fetch on the open market. Based on the December 2012 futures from the European Carbon Exchange, the value of increased kelp C standing stock due to sea otters is US\$205–408 million. If this one-time payment were invested with an 8% yield (the approximate long-term average return of the Dow Jones Industrial Average), it would provide US\$16–33 million annually. Deep sea storage of kelp would fetch US\$6–21 million annually if 1% of increased NPP were to sink and US\$294–1060 million annually if 50% were to sink.

Other species and ecosystems?

While the potential impact of sea otters and kelp forests on atmospheric C levels is high in proportion to the surface area they cover, this impact on the global C cycle is, not surprisingly, very small, as is the case for almost all other particular species and ecosystems. However, our findings raise the question of whether the further loss or restoration of predator effects in other ecosystems would substantially influence atmospheric CO₂ concentration. The magnitude and direction of any such effects will depend on three factors: the overall influence of predators on autotrophs through trophic cascades across global ecosystems; food chain length and the resulting degree to which the trophic cascades have a positive or negative influence on associated plant populations; and the standing plant biomass and NPP for each particular ecosystem.

Trophic cascades occur broadly in nature (Pace *et al.* 1999; Terborgh and Estes 2010), although their strength varies across ecosystems (Shurin *et al.* 2002; Baum and Worm 2009). Food chain length also varies across ecosystems and thus the net effect of apex predators and trophic cascades on plant biomass remains uncertain. While the rapid and dramatic state change from abundant to sparse vegetation with the removal of sea otters might be unique to this aquatic system, the process by which predators have a positive indirect effect on plant biomass by suppressing herbivores is known in terrestrial communities

Table 2. Potential yearly value of sea otter impact on atmospheric carbon sequestration by kelp

Sequestration scenarios	Carbon sequestration (t C yr ⁻¹)	Yearly value*
1%	(1.3–4.5) × 10 ⁵	\$6 million to \$21 million
5%	(0.6–2.3) × 10 ⁶	\$29 million to \$106 million
10%	(1.3–4.5) × 10 ⁶	\$58 million to \$212 million
50%	(0.6–2.3) × 10 ⁷	\$294 million to \$1060 million

Notes: Scenarios represent the percentage of yearly kelp NPP that is transported to the deep ocean where it may persist for long periods of time. We present over an order of magnitude variation in scenarios because there is much uncertainty regarding total carbon transport to the deep ocean. *Yearly value is based on December 2012 futures on the European Carbon Exchange and converted to US dollars.

from the tropics to high latitudes. Among terrestrial and nearshore ecosystems, which store much of the C contained in living macrophyte biomass globally, kelp forests are near the low end of the range of standing biomass density ($\bar{x} = 369 \text{ g C m}^{-2}$, range = 120–2250 g C m^{-2}) but near the high end of the range of NPP ($\bar{x} = 1284 \text{ g C m}^{-2} \text{ yr}^{-1}$, range = 400–1750 $\text{g C m}^{-2} \text{ yr}^{-1}$) (Reed and Brzezinski 2009). The difference between systems with and without predators in terms of the rate at which atmospheric C is sequestered by autotrophs is therefore probably lower in most terrestrial ecosystems than it is for kelp forests, whereas the capacity to store C may be two orders of magnitude greater in terrestrial forest ecosystems than in kelp forests.

In general, we would expect predators in food webs with odd and even numbers of trophic levels to have sequestering effects on atmospheric C pools and to enhance atmospheric C pools, respectively. This influence alone complicates the assessment of predator effects on C in aquatic systems because food chain length varies considerably among aquatic systems. Large predators in most terrestrial ecosystems occupy the third trophic level, thus implying a more consistent sequestering effect of predators on C for the terrestrial realm. However, terrestrial ecosystems are rife with other complexities – such as predator interference, omnivory, and defended plant tissue – that make it difficult to form general conclusions about the magnitude of such effects.

Earth's capacity for increased plant production and standing crops is yet another key variable in assessing how predators and trophic cascades might influence the global C cycle. Much of the world's terrestrial land mass currently supports substantially less vegetation biomass than it could, given its climate potential (ie the levels of plant biomass an ecosystem can support based on soil conditions and climate; Bond 2005); using Dynamic Global Vegetation Models (complex models analogous to global circulation models designed to explore global change impacts on vegetation), Bond *et al.* (2005) demonstrated that global forest vegetation cover is roughly half its climate potential (after discounting the effects of deforestation). This suggests strong control of terrestrial vegetation by consumers and/or fire. How much of this control is due to the effects of trophic cascades is currently unknown. However, these findings further suggest that the control of food chain length by managing predator populations could have a major impact on C sequestration.

Although the manipulation of food webs holds promise for promoting atmospheric C sequestration, attempts at carrying this out should carefully consider the complexity inherent in natural ecosystems. For instance, a killer whale (*Orcinus orca*) diet shift from large marine mammals to sea otters in southwest Alaska recently caused nearshore ecosystems there to revert from the kelp- to urchin-dominated phase state (Estes *et al.* 1998). Simply removing killer whales to bring back kelp forests would

ignore the ultimate causes of diet shifts, which are likely related to the legacy of whaling (Springer *et al.* 2003). Top-down forcing on ecosystems might also interact in ways that decrease C sequestration. The outbreak of rinderpest in the Serengeti caused a crash in the wildebeest (*Connochaetes taurinus*) population, which subsequently resulted in an increase in fire frequency (Holdo *et al.* 2009). This increase in fire events limited tree recruitment, which subsequently lowered soil and biomass C pools. Finally, non-native predators might also lead to increases in ecosystem C sequestration. Predation by invasive rats on seabird nesting islands has been shown to increase soil C sequestration by changing nutrient cycling pathways (Wardle *et al.* 2007), but invasive rats can also lead to local seabird extinctions.

In sum, our findings, obtained using a sea otter and kelp forest model, suggest that predators can strongly influence the C cycle in general and atmospheric CO₂ in particular through top-down forcing and trophic cascades. The extent to which these effects can be extrapolated across species and global ecosystems remains to be determined. However, we now know that predators exert strong indirect effects on autotrophs in many ecosystems (Terborgh and Estes 2010), and our findings indicate that these effects might therefore be manipulated in ways that could appreciably influence the concentration of atmospheric C. Although we are not yet at the point of incorporating these effects into management decisions, the potential utility of using food web dynamics to manage C is high and thus further work in this area is clearly warranted.

■ Acknowledgements

We thank Y Wang for the drawings in Figure 2, the Alaska Maritime National Wildlife Refuge for field support, and S Carpenter, C Darimont, R Paine, and D Reed for critiques of the manuscript. We thank KY Kim for assistance with partial pressure of CO₂ measurements. Financial support was provided by National Science Foundation (NSF) grant 0647663 to JAE; NSF grants 0963022, 0729707, and 0713994 to CCW; and a National Oceanic and Atmospheric Administration National Undersea Research Program grant to ME.

■ References

- Baum JK and Worm B. 2009. Cascading top-down effects of changing oceanic predator abundances. *J Anim Ecol* **78**: 699–714.
- Bond WJ. 2005. Large parts of the world are brown or black: a different view on the “green world” hypothesis. *J Veg Sci* **16**: 261–66.
- Bond WJ, Woodward FI, and Midgley GF. 2005. The global distribution of ecosystems in a world without fire. *New Phytol* **165**: 525–38.
- Doroff AM, Estes JA, Tinker MT, *et al.* 2003. Sea otter population declines in the Aleutian archipelago. *J Mammal* **84**: 55–64.
- Elderfield H (Ed). 2006. The oceans and marine geochemistry: treatise on geochemistry. Oxford, UK: Elsevier–Pergamon.
- Estes JA and Duggins DO. 1995. Sea otters and kelp forests in Alaska – generality and variation in a community ecological

- paradigm. *Ecol Monogr* **65**: 75–100.
- Estes JA and Palmisano JF. 1974. Sea otters: their role in structuring nearshore communities. *Science* **185**: 1058–60.
- Estes JA, Tinker MT, and Bodkin JL. 2010. Using ecological function to develop recovery criteria for depleted species: sea otters and kelp forests in the Aleutian archipelago. *Conserv Biol* **24**: 852–60.
- Estes JA, Tinker MT, Williams TM, and Doak DF. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**: 473–76.
- Gregg EJ, Nichol LM, Watson JC, *et al.* 2008. Estimating carrying capacity for sea otters in British Columbia. *J Wildlife Manag* **72**: 382–88.
- Hairston NG, Smith FE, and Slobodkin LB. 1960. Community structure, population control, and competition. *Am Nat* **94**: 421–25.
- Harrold C, Light KL, and Lisen S. 1998. Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forests. *Limnol Oceanogr* **43**: 669–78.
- Harrold C and Reed DC. 1985. Food availability, sea-urchin grazing, and kelp forest community structure. *Ecology* **66**: 1160–69.
- Hermis DA and Mattson WJ. 1992. The dilemma of plants – to grow or defend. *Q Rev Biol* **67**: 283–335.
- Holdo RM, Sinclair ARE, Dobson AP, *et al.* 2009. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLoS Biol* **7**: e1000210.
- Konar B and Estes JA. 2003. The stability of boundary regions between kelp beds and deforested areas. *Ecology* **84**: 174–85.
- Kvitek RG, Iampietro PJ, and Bowlby CE. 1998. Sea otters and benthic prey communities: a direct test of the sea otter as keystone predator in Washington State. *Mar Mammal Sci* **14**: 895–902.
- Markel RW. 2011. Rockfish recruitment and trophic dynamics on the west coast of Vancouver Island: fishing, ocean climate, and sea otters. (PhD dissertation). Vancouver, Canada: University of British Columbia.
- Miller RJ, Reed DC, and Brzezinski MA. 2011. Partitioning of primary production among giant kelp (*Macrocystis pyrifera*), understory macroalgae, and phytoplankton on a temperate reef. *Limnol Oceanogr* **56**: 119–32.
- Pace ML, Cole JJ, Carpenter SR, and Kitchell JF. 1999. Trophic cascades revealed in diverse ecosystems. *Trends Ecol Evol* **14**: 483–88.
- Pachauri RK and Reisinger A (Eds). 2007. Climate change 2007: synthesis report. Geneva, Switzerland: IPCC.
- Packer M. 2009. Algal capture of carbon dioxide; biomass generation as a tool for greenhouse gas mitigation with reference to New Zealand energy strategy and policy. *Energ Policy* **37**: 3428–37.
- Paine RT. 1980. Food webs: linkage, interaction strength and community infrastructure. *J Anim Ecol* **49**: 667–85.
- Paul EA and Clark FE. 1996. Soil microbiology and biochemistry. San Diego, CA: Academic Press.
- Post WM and Kwon KC. 2000. Soil carbon sequestration and land-use change: processes and potential. *Glob Change Biol* **6**: 317–28.
- Ray JC, Redford KH, Steneck RS, and Berger J (Eds). 2005. Large carnivores and the conservation of biodiversity. Washington, DC: Island Press.
- Reed DC and Brzezinski MA. 2009. Kelp forests. In: Laffoley D and Grimsditch G (Eds). The management of natural coastal carbon sinks. Gland, Switzerland: IUCN.
- Reiswitz SE, Estes JA, and Simenstad SA. 2005. Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian archipelago. *Oecologia* **146**: 623–31.
- Richards KR and Stokes C. 2004. A review of forest carbon sequestration cost studies: a dozen years of research. *Climatic Change* **63**: 1–48.
- Riedman ML and Estes JA. 1990. The sea otter (*Enhydra lutris*): behavior, ecology, and natural history. Washington, DC: US Fish and Wildlife Service.
- Shurin JB, Borer ET, Seabloom EW, *et al.* 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecol Lett* **5**: 785–91.
- Springer AM, Estes JA, van Vliet GB, *et al.* 2003. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *P Natl Acad Sci USA* **100**: 12223–28.
- Terborgh J and Estes JA. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Washington, DC: Island Press.
- Wardle DA, Bellingham PJ, Fukami T, and Mulder CPH. 2007. Promotion of ecosystem carbon sequestration by invasive predators. *Biol Lett* **3**: 479–82.
- Watson J and Estes JA. Stability, resilience, and phase shifts in kelp forest communities along the west coast of Vancouver Island, Canada. *Ecol Monogr*. In press.
- Yodzis P. 1976. Species richness and stability of space-limited communities. *Nature* **264**: 540–41.