CASCADING EFFECTS OF FISHING CAN ALTER CARBON FLOW THROUGH A TEMPERATE COASTAL ECOSYSTEM

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Abstract. Mounting evidence suggests that fishing can trigger trophic cascades and alter food web dynamics, yet its effects on ecosystem function remain largely unknown. We used the large-scale experimental framework of four marine reserves, spanning an oceanographic gradient in northeastern New Zealand, to test the extent to which the exploitation of reef predators can alter kelp carbon flux and secondary production. We provide evidence that the reduction of predatory snapper (*Pagrus auratus*) and lobster (*Jasus edwardsii*) can lead to an increase in sea urchins (*Evechinus chloroticus*) and indirect declines in kelp biomass in some locations but not others. Stable carbon isotope ratios (δ^{13}C) of oysters (*Crassostrea gigas*) and mussels (*Perna canaliculus*) transplanted in reserve and fished sites within four locations revealed that fishing indirectly reduced the proportion of kelp-derived organic carbon assimilated by filter feeders in two locations where densities of actively grazing sea urchins were 23.7 and 8.3 times higher and kelp biomass was an order of magnitude lower than in non-fished reserve sites. In contrast, in the two locations where fishing had no effect on urchin density or kelp biomass, we detected no effect of fishing on the carbon signature of filter feeders. We show that the effects of fishing on nearshore trophic structure and carbon flux are context-dependent and hinge on large-scale, regional oceanographic factors. Where cascading effects of fishing on kelp biomass were documented, enhanced assimilation of kelp carbon did not result in the magnification of secondary production. Instead, a strong regional gradient in filter feeder growth emerged, best predicted by chlorophyll *a*. Estimates of kelp contribution to the diet of transplanted consumers averaged 56.9% ± 6.2% (mean ± SE) for mussels and 33.8% ± 7.3% for oysters, suggesting that organic carbon fixed by kelp is an important food source fueling northeastern New Zealand's nearshore food webs. The importance of predators in mediating benthic primary production and organic carbon flux suggests that overfishing can have profound consequences on ecosystem functioning particularly where pelagic primary production is limiting. Our results underscore the broader ecosystem repercussions of overfishing and its context-dependent effects.

Key words: carbon flow; context-dependence; detritus; fishing; food web; indirect effects; kelp forest; marine reserve; sea urchin; stable isotopes; temperate reef; trophic cascade.

INTRODUCTION

Growing evidence suggests that fishing can alter marine food webs and community dynamics via a cascade of indirect trophic interactions (Pinnegar et al. 2000, Frank et al. 2005, Daskalov et al. 2007, Myers et al. 2007). However, the ecosystem-level consequences of exploiting marine predators remain less well known. Moreover, the context-dependent effects of fishery-induced trophic cascades have not been thoroughly assessed, despite the pressing need to develop predictive ecosystem models (e.g., Walters 2000, Salomon et al. 2002) that can forecast the trophic effects of fishing across a range of conditions. Yet, some of the most

critical issues facing both fundamental community ecology and applied resource management require an understanding of the variation in the strength of species interactions and the feedbacks between community and ecosystem dynamics (Agrawal et al. 2007). Here, we used naturally occurring stable isotopes to trace the ecosystem response to large-scale experimental manipulations of fishing effort via no-take marine reserves in northeastern New Zealand. This work provides a novel assessment of how and under what conditions fishing can indirectly alter an important ecosystem function; the trophic transfer of carbon.

A rich history of theoretical models and empirical research has shown that the depletion of predators from food webs can cause a cascade of indirect effects on lower trophic levels (Hairston et al. 1960, Paine 1980, Carpenter et al. 1985). The magnitude of these cascading effects can vary as a function of biotic and abiotic factors such as system productivity and consumer

efficiency (Hunter and Price 1992, Power 1992, Pace et al. 1999). In marine systems, the cascading effects of exploiting top predators have been revealed in a variety of temperate nearshore ecosystems (Pinnegar et al. 2000) and recent evidence suggests that overfishing can have profound ramifications throughout pelagic food webs (Frank et al. 2005, Daskalov et al. 2007, Myers et al. 2007). Despite remarkable spatial variation in marine productivity and the many processes known to alter species interaction strength (Berlow et al. 2004), only recently have variations in the strength of trophic cascades triggered by fishing been addressed (Micheli et al. 2005, Frank et al. 2006, Shears et al. 2008). Our ability to forecast when, where and under what conditions fishery-induced trophic cascades are likely to occur hinges on our understanding of these context-dependent effects.

Much of the evidence on the cascading effects of fishing has come from changes in fisheries management policies in time or space. Marine reserves, for example, constitute large-scale, whole-system, fishing-exclusion experiments and provide controls by which to test the direct and indirect consequences of fishing at ecologically relevant scales. Some of the strongest evidence on the cascading effects of fishing comes from northeastern New Zealand's two oldest marine reserves, the Leigh Marine Reserve and Tawharanui Marine Park, where previously fished reef predators, snapper (*Pagrus auratus*) and rock lobster (*Jasus edwardsii*), are 14 and 3.7 times more abundant, respectively, compared to adjacent fished waters (Babcock et al. 1999, Kelly et al. 2000, Willis et al. 2003). Within the reserves, elevated predation rates on the sea urchin *Evechinus chloroticus* has released kelp (*Ecklonia radiata*) from grazing pressure allowing it to significantly increase (Babcock et al. 1999, Shears and Babcock 2002, 2003). The deforestation of kelp forests by sea urchins has been attributed to the depletion of urchin predators from temperate reefs worldwide (Estes and Duggins 1995, Sala et al. 1998, Lafferty 2004, Steneck et al. 2004). This implies that fishing, by indirectly reducing kelp biomass and thus benthic primary production, could have broad ecosystem-level consequences on nearshore organic carbon flux.

Because kelp forest productivity can exceed that of phytoplankton, kelp has long been thought of as a significant source of organic carbon fueling temperate coastal ecosystems (Mann 1973, 1988). In addition to direct consumption by grazers, kelp-derived organic carbon can enter food webs indirectly via detrital pathways as particulate and dissolved organic matter (POM and DOM) as kelps grow and senesce. Empirical evidence based on naturally occurring stable isotopes has confirmed that organic carbon originating from kelp photosynthesis is assimilated by a diverse assemblage of nearshore consumers (Dunton and Schell 1987, Bustamante and Branch 1996), flows upwards through food webs to higher trophic level predators (Kaehler et al.

2000, Fredriksen 2003) and can even magnify secondary production (Duggins et al. 1989). In the Aleutian Islands, where sea otters had recovered from overexploitation and suppressed their herbivorous sea urchin prey, productive kelp beds dominated and transplanted filter feeders (barnacles and mussels) grew two to five times faster compared to islands devoid of kelp where sea otter predators were scarce and urchin densities high. Stable isotope analyses revealed that kelp detritus was responsible for the magnification of secondary production. Ratios of heavy to light carbon isotopes (^{13}C to ^{12}C) can be used to trace the flow of kelp carbon through marine food webs because the isotopic signature of a consumer reflects those of its key food sources and kelps tend to be enriched in ^{13}C relative to phytoplankton (Fry and Sherr 1984).

Recent work has revealed that overfishing can modify the flow of carbon and nutrient cycling in tropical freshwater systems (Taylor et al. 2006, McIntyre et al. 2007), however, little is known about the effects of fishing on carbon flux in the ocean. Given the cascading effects of fishing on kelp biomass reported in northeastern New Zealand, we hypothesized that fishing may indirectly reduce the trophic transfer of kelp-derived organic carbon to other components of the nearshore food web. We predicted that (1) in the absence of fishing, enhanced kelp biomass could result in enriched consumer carbon signatures, (2) the ecosystem effects of fishing on kelp carbon flow would be greatest where the magnitude of indirect fishing effects on kelp were greatest, and (3) kelp carbon enrichment would lead to a magnification of secondary production where phytoplankton was limiting. To test these hypotheses we compared the isotopic signatures and growth rates of filter feeders transplanted to four no-take marine reserves and adjacent fished waters in four locations in northeastern New Zealand. First, we quantified the magnitude by which the reduction in snapper and lobster due to fishing affected the density and behavior of sea urchins and kelp biomass. We then determined if filter feeders, transplanted to fished and non-fished sites, varied significantly in their isotopic signature and if this translated into a variation in secondary production (i.e., growth rates). Finally, we examined the extent to which the ecosystem consequences of fishing were mediated by regional oceanographic patterns in predominant currents and upwelling regimes, chlorophyll *a* concentrations, and wave exposure.

METHODS

Study area and regional oceanographic context

This research was conducted in northeastern New Zealand at 15 fished and 17 reserve sites nested within four geographic locations (Fig. 1). The Offshore Islands PKI/MKI location encompasses the Poor Knights Islands Marine Reserve (18.9 km^2, established 1998) and the fished Mokohinau Islands. This location lies in the middle of the northeastern continental shelf and is
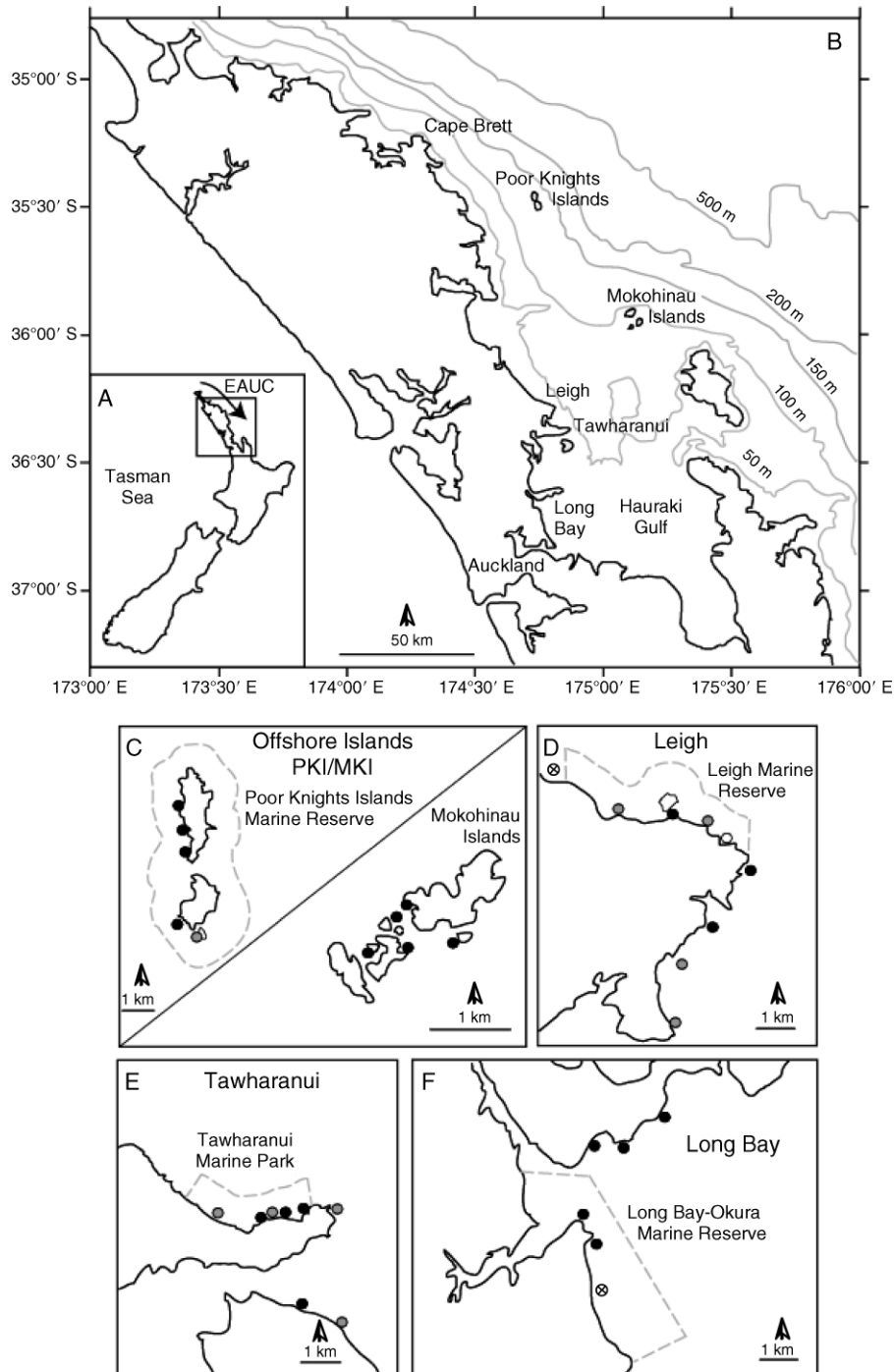
Fig. 1. (A, B) Location of research in northeastern New Zealand and the approximate position of the East Auckland Current (EAUC). Filter feeders were transplanted in fished and reserve sites nested within four geographic locations. (C) Offshore Islands PKI/MKI, (D) Leigh, (E) Tawharanui, and (F) Long Bay. Solid gray lines represent isobaths, while dashed gray lines indicate marine reserve boundaries. Mussels and oysters were retrieved from most sites (black circles), while some experimental transplants were lost entirely (⊗ symbols) or partially, such that only mussels (gray circles) or oysters (open circles) were retrieved.

bathed by the subtropical East Auckland Current (EAUC), a warm (16–22°C), saline (>35.4 psu), southeastward-flowing current low in phytoplankton (Chang et al. 2003, Zeldis et al. 2004). The Leigh and

Tawharanui locations contain New Zealand's two oldest marine reserves; the Leigh Marine Reserve (5.2 km², established 1975) and the Tawharanui Marine Park (5.0 km², established 1981). These two locations are subject

to wind-driven upwelling and relaxation events in the early spring and summer resulting in "boom and bust" phytoplankton dynamics (Chang et al. 2003, Zeldis et al. 2004). The Long Bay location, encompassing the Long Bay-Okura Marine Reserve (9.8 km^2, established 1995), lies within the Hauraki Gulf, a large shallow bay that is haline and thermally stratified. Nutrient-rich upwelled water is entrained in the Gulf from spring to summer, supporting persistently high phytoplankton concentrations (Chang et al. 2003). Long Bay is subject to high anthropogenic nutrient loading and sedimentation given its location close to Auckland, extensive agricultural districts and high river runoff.

Sea urchin density and macroalgal biomass

To compare sea urchin densities and macroalgal biomass between reserve and fished sites, we measured the test diameter of *Evechinus* and the maximum length of *Ecklonia*, *Carpophyllum flexuosum*, and *Carpophyllum maschalocarpum* found within five 1-m^2 quadrats haphazardly placed at 6–10 m depth in April 2003, except in Long Bay where the maximum reef depth is ~5 m. We noted whether urchins were openly grazing (exposed) or located in crevices (cryptic). At each site, biomass of the dominant macroalgal species (*Ecklonia*, *Carpophyllum* spp.) was quantified based on previously determined length to dry mass regressions (Shears and Babcock 2003).

Filter-feeder transplants

To detect whether local macroalgal biomass influenced the carbon source assimilated by filter feeders and their growth rates, we transplanted juvenile oysters (*Crassostrea gigas*) and green-lipped mussels (*Perna canaliculus*) to replicate sites nested within and adjacent to each marine reserve. Both species were chosen as indicators of kelp carbon flux due to their fast growth and were obtained as single, pre-reproductive juveniles from an aquaculture facility. While *Perna canaliculus* is native to northeastern New Zealand shallow rocky reefs, *Crassostrea gigas* is not, although it is common throughout the region. Fifty mussels (15–30 mm) were individually tagged and placed in cylindrical mesh cages large enough to avoid density dependent effects on growth rates. Ten single juvenile oysters (10–15 mm) were glued on 15 × 15 cm PVC plates and spaced to minimize competitive effects on growth rates. Stacks of five plates were spaced with rubber tubing forming an array housing 50 oysters. At each site, one mussel cage and one oyster array were anchored to the reef at 6–10 m depth and kept afloat 1.5 m above the reef with a float (Appendix A). Filter feeders were submerged for 50 days (±5 days) during mid March to mid May 2003 and maximum valve lengths (±0.01 mm) and wet mass (±1 mg) were recorded pre and post submersion. Similar filter-feeder size distributions were transplanted among sites. Mussel and oyster growth and biomass accrual rates were expressed as percentage increase per day to account for differences in initial length and body mass of individuals.

Isotopic signatures

To quantify variation in carbon sources and consumer isotopic signatures, we collected blades from the dominant canopy-forming kelp *Ecklonia* (n = 1–3 blades) and excised oyster gill (n = 4 oysters) and mussel pedal foot (n = 4 mussels) from the filter feeders transplanted at each site. Kelp and animal tissue was acid-rinsed in 10% HCl followed by deionized water, dried at 65°C for 24 h, individually ground, weighed, and packaged in 8 × 5 mm tin capsules for stable isotope analysis. Phytoplankton isotope signatures were acquired from the National Institute of Water and Atmospheric Research (S. Bury, *unpublished data*) from sampling stations within each location (Appendix B). Aliquots of 500 mL of seawater, collected between 1–19 m depth, was filtered through 0.7-μm pre-combusted GF/F filters, immediately frozen, then thawed and dried in the lab. All samples were analyzed for isotopes of carbon (^{13}C, ^{12}C) and nitrogen (^{15}N, ^{14}N). Carbon isotopes were used to determine the relative contribution of kelp vs. phytoplankton-derived carbon assimilated by transplanted consumers, while nitrogen isotopes were analyzed to detect changes in terrestrially derived nitrogen and consumer trophic level. Stable isotope ratios are expressed in the standard delta (δ) notation, defined as parts per mil (‰) deviation from a standard; δ^{13}C or δ^{15}N $= ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

Isotopic-mixing model

We used a simple two-source mixing model to estimate the contribution of kelp carbon assimilated by transplanted filter feeders:

$$\%\text{C}_{\text{kelp derived}} = \frac{(\delta^{13}\text{C}_{\text{filter feeder}} - \delta^{13}\text{C}_{\text{phytoplankton}} - \Delta\delta^{13}\text{C})}{(\delta^{13}\text{C}_{\text{kelp}} - \delta^{13}\text{C}_{\text{phytoplankon}})} \times 100$$

where $\delta^{13}\text{C}_{\text{filter feeder}}$, $\delta^{13}\text{C}_{\text{kelp}}$, and $\delta^{13}\text{C}_{\text{phytoplankton}}$ represent the C isotopic signatures of filter feeders, kelp, and phytoplankton, respectively, and $\Delta\delta^{13}\text{C}$ is the average post-photosynthetic fractionation of δ ^{13}C per trophic level. We used a conservative fractionation value for marine invertebrate herbivores ($\Delta\delta^{13}$C = 1‰;(Vander Zanden and Rasmussen [2001]), so that our model would yield conservative estimates of kelp contribution to secondary production.

Estimates based on these methods, like those reported in the published literature, have their limitations. Obtaining a pure phytoplankton signature is difficult because filtered seawater contains a variable mix of living and dead phytoplankton, bacteria, and possibly kelp detritus (Fry and Sherr 1984), yet incubated phytoplankton cultures inoculated from ambient sea water (e.g., Duggins et al. 1989) may not reflect the

natural assemblage ingested by primary consumers and are sensitive to the dissolved inorganic carbon in which the cultures are grown. Furthermore, simple linear mixing models do not account for uncertainties in source signatures nor variability among consumers. Determining the relative contribution of kelp to POM and developing mixing models that account for uncertainty and variability will vastly improve our ability to quantify the importance of kelp to coastal food webs.

Local oceanographic variables

Mean chlorophyll *a* concentration (mg/m^3) over the transplant period was quantified for each site based on daily satellite-derived estimates from MODIS sensors (1.1-km resolution). Daily site-specific chl *a* values were calculated by averaging data from the 10 nearest pixels. To validate satellite-derived chl *a* estimates, we compared these data to in situ empirical measurements of chl *a* from surface water samples collected throughout northeastern New Zealand during the same time period. Agreement between empirical and satellite-derived data was high ($R^2 = 0.81$, $n = 16$ water samples taken from seven sites on different days, $P < 0.00001$; Appendix C) suggesting that remotely sensed chl *a* provided reasonable estimates of chl *a* in the nearshore. Wave exposure was estimated at each site by summing fetch for each 10-degree sector of the compass rose.

Data analyses

To detect differences in urchin density, kelp biomass, filter feeder growth rates, consumer isotopic signatures, and kelp contribution to secondary production between reserve and fished sites among locations, we constructed generalized linear mixed models in SAS (2004) and fit them with residual (restricted) maximum likelihood (REML). Site was treated as a random effect and protection Status and Location were considered fixed. Status and Location were specifically chosen as treatments to be tested, the former to detect a fishing effect, the later to detect an effect of oceanographic context. We tested the fixed effect of protection status within each location using planned post hoc contrast comparisons. Differences in urchin densities were analyzed with a Poisson error distribution and log link function. Differences in macroalgal biomass, filter feeder growth rates, and isotopic signatures (log[$x + 1$]-transformed) and percent kelp contribution (arcsine-square-root transformed) were analyzed with normal error distributions and identity link functions.

To determine the main factors responsible for regional variation in filter feeder growth, we compared alternative models of growth as a function of chl *a*, kelp biomass, and wave exposure, with small-sample bias-corrected Akaike's Information Criterion (AIC$_c$) standardized to the best fit model to produce ΔAIC$_c$ values (Burnham and Anderson 1998). The level of empirical support for a model is substantial when ΔAIC$_c$ is ≤2. Nonlinear models representing saturating growth rates

with wave exposure and local kelp biomass as covariates, were fit with maximum likelihood assuming normally distributed errors. We normalized the model likelihoods to a set of positive Akaike weights (w_i) representing the strength of evidence in favor of a given model. Variable weights (w_v), representing their importance, were calculated by summing the Akaike weights of each model in which that variable was found. The direction of variable effect was based on the sign of its coefficient.

Along with the unique benefits derived from this large-scale, whole-ecosystem policy experiment come several important limitations. First, we treat marine reserves as non-fished controls and adjacent fished sites as experimental treatments of fishing yet fished sites likely experience variable intensities of fishing effort and may be exposed to intensified fishing pressure if the displacement and concentration of fishing effort post reserve establishment occurs. Second, our fished sites were not equally distributed around each reserve in the Leigh and Tawharanui locations due to limitations in available rocky reef habitat and the loss of several transplant sites due to storm events. While this introduces a potential for bias, all fished and reserve sites in these locations are subject to similar environmental factors and are directly comparable (Shears et al. 2008). Finally, we could not statistically separate the effect of reserve age from the effect of regional oceanography because the four reserves vary in age and two of the four are located in unique oceanographic settings. Nonetheless, comparisons of fished and non-fished sites within a location remain valid on a pairwise basis and any effect of age on the results are likely to be minimal for ecological reasons discussed below and described in detail in Shears et al. (2008).

RESULTS

Urchin density and macroalgal biomass

We detected a significant positive effect of fishing on exposed urchin densities, but the magnitude of this effect varied among locations (Fig. 2A, Table 1). At fished sites within Leigh and Tawharanui, densities of exposed urchins were 23.7 and 8.3 times more abundant than adjacent reserve sites (post hoc contrasts at Leigh, $F_{1,23} = 11.81$, $P = 0.002$; Taw, $F_{1,23} = 7.47$, $P = 0.012$). Fishing had no effect on exposed urchin densities within Long Bay ($F_{1,23} = 0.00$, $P = 1.00$) or the Offshore Islands PKI/MKI ($F_{1,23} = 0.02$, $P = 0.898$). The density of cryptic urchins did not vary significantly with protection status or between locations (Table 1).

Fishing had a significant negative effect on kelp biomass, however, this effect varied among locations (Fig. 2B, Table 1). In the absence of fishing, kelp biomass was over an order of magnitude greater within the Leigh and Tawharanui reserves compared to adjacent fished sites (post hoc contrasts at Leigh, $F_{1,23} = 60.66$, $P < 0.0001$; Taw, $F_{1,23} = 69.95$, $P < 0.0001$). We detected no effect of fishing on kelp biomass at Long
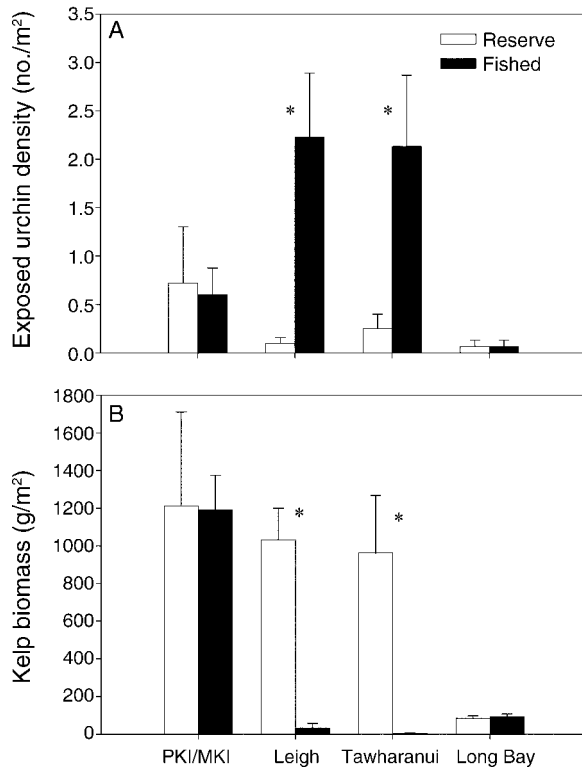
FIG. 2. Densities (mean + SE) of (A) exposed sea urchins (*Evechinus chloroticus*) and (B) kelp (*Ecklonia radiata*) biomass within reserve and adjacent fished sites at four locations in northeastern New Zealand.

* $P < 0.05$.

Bay nor the Offshore Islands (Long Bay, $F_{1,23} = 0.69$, $P = 0.415$; PKI/MKI, $F_{1,23} = 0.14$, $P = 0.715$). We observed similar patterns in total macroalgal biomass between reserve and fished sites among locations, however total

macroalgal biomass at Long Bay was considerably higher due to high densities of *Carpophyllum* spp. (Leigh, $F_{1,23} = 43.57$, $P < 0.0001$; Taw, $F_{1,23} = 56.74$, $P < 0.0001$; Long Bay, $F_{1,23} = 0.05$, $P = 0.819$; PKI/MKI, $F_{1,23} = 0.13$, $P = 0.721$; Appendix D).

Spatial variation in producer and consumer isotopic signatures

We detected a significant effect of fishing on the carbon isotope signatures ($\delta^{13}C$) of oysters, but this effect varied among locations (Fig. 3A, Table 1). Within the Leigh and Tawharanui reserves where kelp biomass was an order of magnitude greater than fished sites, oysters were significantly enriched in ^{13}C compared to oysters transplanted in adjacent fished sites yielding significantly more positive values of $\delta^{13}C$ (Leigh, $F_{1,14} = 5.41$, $P = 0.036$; Taw, $F_{1,14} = 5.61$, $P = 0.033$). We found no effect of fishing on the carbon signature of oysters at Long Bay ($F_{1,14} = 1.31$, $P = 0.271$) nor the Offshore Islands PKI/MKI ($F_{1,14} = 0.98$, $P = 0.338$) where the effect of fishing had no effect on kelp biomass. Transplanted mussels showed similar but nonsignificant patterns (Fig. 3B, Table 1). Within the Leigh and Tawharanui reserves, mussels tended to have more enriched carbon signatures compared to those transplanted outside of the reserves (Leigh, $F_{1,21} = 3.64$, $P = 0.070$; Taw, $F_{1,21} = 1.90$, $P = 0.183$). We found no effect of fishing on mussel carbon signatures in Long Bay ($F_{1,21} = 0.00$, $P = 0.978$) nor Offshore Islands PKI/MKI ($F_{1,21} = 0.38$, $P = 0.545$) where kelp biomass was equivalent at fished and unfished sites. We found no effect of fishing on the nitrogen isotopic signatures of either filter feeder (Fig. 3, Table 1), however, both mussels and oysters became increasingly enriched in ^{15}N (higher $\delta^{15}N$ values) inshore and south toward the Hauraki Gulf, as did *Ecklonia* (Appendix E).

TABLE 1. The effect of fishing (Status) and oceanographic context (Location) on exposed and cryptic sea urchin (*Evechinus chloroticus*) densities, kelp (*Ecklonia radiata*), total benthic macroalgal biomass (*Ecklonia radiata* and *Carpophyllum* spp.), and transplanted filter feeder isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) in northeastern New Zealand.

| | Fixed effect | | | | | | | | | Random effect | |
| | Location | | | Status | | | Location × Status | | | Site(Location, Status) | |
Response variable	F	df	P	F	df	P	F	df	P	Z	P
Sea urchin density											
Exposed	3.22	3,23	0.042	7.64	1, 23	0.011	2.77	3, 23	0.065	1.57	0.059
Cryptic†	0.50	2,19	0.615	1.12	1, 19	0.302	0.79	2, 19	0.469	2.07	0.019
Macroalgal biomass											
Kelp	23.96	3,23	<0.0001	65.64	1, 23	<0.0001	22.20	3, 23	<0.0001	2.57	0.005
Total	16.86	3,23	<0.0001	49.60	1,23	<0.0001	19.83	3, 23	<0.0001	2.68	0.004
Oyster isotopic signature											
$\delta^{13}C$	14.34	3,14	0.0001	8.16	1, 14	0.013	3.32	3, 14	0.051	2.58	0.005
$\delta^{15}N$	174.53	3,14	<0.0001	2.58	1, 14	0.131	2.12	3, 14	0.143	2.23	0.013
Mussel isotopic signature											
$\delta^{13}C$	2.58	3,21	0.081	1.89	1, 21	0.184	1.40	3, 21	0.270	2.25	0.012
$\delta^{15}N$	169.28	3,21	<0.0001	0.72	1, 21	0.407	2.71	3, 21	0.071	2.41	0.008

† Sites in Long Bay were excluded from the cryptic urchin analysis because if they were included residual (restricted) maximum likelihood (REML) could not converge, due to a 100% lack of cryptic urchins at these sites.
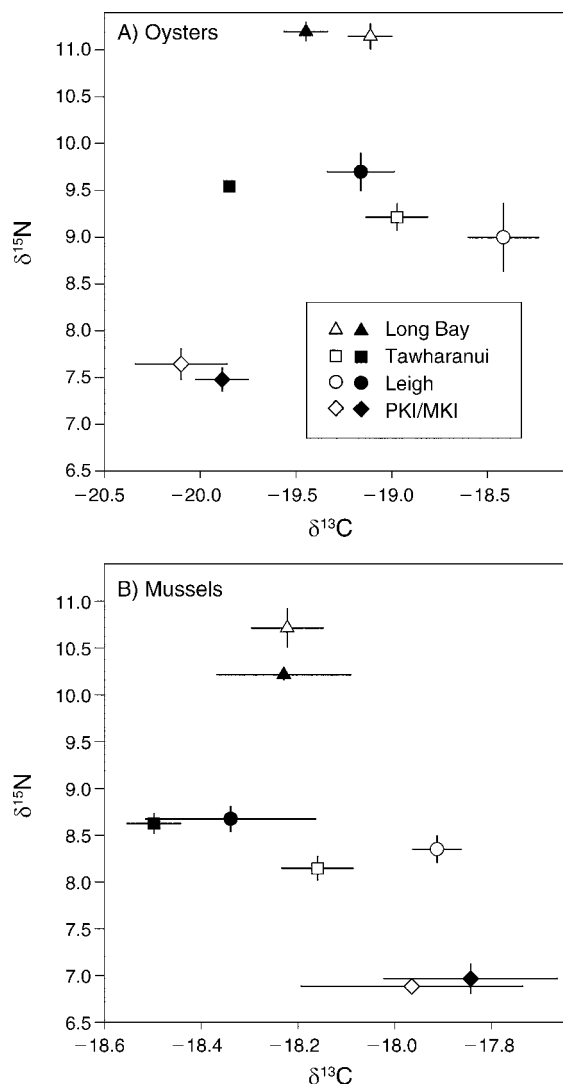
FIG. 3. Carbon and nitrogen isotopic signatures (mean ± SE) of (A) oysters and (B) mussels in reserve sites (open symbols) and fished sites (solid symbols) at four locations in northeastern New Zealand.

Kelp was enriched in ^{13}C ($-17.12‰ ± 1.74‰$ [mean ± SD], $n = 57$ kelp tissue samples) relative to phytoplankton ($-22.07‰ ± 1.35‰$, $n = 17$ phytoplankton samples) (Appendix E). The depleted carbon signature of phytoplankton approximates values reported from other temperate coastal locations (Fry and Sherr 1984, Duggins et al. 1989).

Kelp contribution to consumers

Fishing had a significant effect on the percentage of kelp-derived organic carbon assimilated by the transplanted filter feeders yet this effect varied in magnitude among locations (Fig. 4A B, Table 2). Overall, kelp contribution to secondary production ranged from 11.8% to 80.6%. Within the Leigh and Tawharanui reserves, kelp contribution to filter-feeder growth was significantly greater than adjacent fished sites for both oysters (Leigh, $F_{1,14} = 8.80$, $P = 0.010$; Taw, $F_{1,14} = 5.07$, $P = 0.041$) and mussels (Leigh, $F_{1,21} = 21.52$, $P = 0.0001$; Taw, $F_{1,21} = 6.88$, $P = 0.016$). In the absence of fishing in Leigh, kelp carbon contributed 68.8% ± 4.3% to oyster growth and 80.6% ± 1.2% to mussel growth compared to 44.8% ± 3.5% and 61.4% ± 3.6% for oysters and mussels transplanted in nearby fished sites. A similar pattern emerged in Tawharanui; kelp carbon contributed 49.5% ± 3.3% to oyster growth and 66.3% ± 1.5% to mussel growth at reserve sites compared to 28.7% and 54.0% ± 1.0% for oysters and mussels transplanted at fished sites outside the reserve. At Long Bay, where the effect of fishing has had no effect on urchin density or kelp biomass, we found no significant differences in kelp contribution to oysters ($F_{1,14} = 0.59$, $P = 0.455$) or mussels ($F_{1,21} = 0.63$, $P = 0.435$) transplanted at reserve and fished sites. At the Offshore Islands, kelp contribution to oyster growth was significantly greater at the Poor Knights Reserve (40.0% ± 3.1%) compared to the fished Mokohinau Islands (11.0% ± 3.5%; PKI/MKI, $F_{1,14} = 42.02$, $P < 0.0001$) but no difference was detected for mussels (PKI/MKI, $F_{1,21} = 1.10$, $P = 0.306$)

Secondary production in an oceanographic context

We did not observe an effect of fishing on filter-feeder growth rates (Fig. 4C, D, Table 2). However, significant variation in growth rates existed among locations such that a distinct regional gradient in filter-feeder growth emerged; oysters grew twice as fast and mussels 11 times as fast in Long Bay relative to the northern Offshore Islands, with intermediate growth occurring at Leigh and Tawharanui. This regional pattern in growth mirrored a regional pattern in chl a; filter feeders in Long Bay were exposed to 13.2 times more chl a (3.03 ± 0.15 mg/m^3) than those transplanted offshore (0.23 ± 0.02 mg/m^3) and 3.8 and 2.5 times more chl a than those transplanted in Leigh (0.79 ± 0.04 mg/m^3) and Tawharanui (1.21 ± 0.07 mg/m^3; Fig. 5A, B). Saturating growth models as a function of chl a were best supported by the data, explaining 72% and 78% of the variance in oyster and mussel growth respectively (Fig. 5C; Table 3). This provides strong evidence that chl a is the best overall predictor of both oyster and mussel growth. Yet, there is substantial empirical support that, in addition to chl a, oyster growth was moderately negatively affected by wave exposure ($\Delta AIC_c = 1.179$, $R^2 = 0.743$, $w_v = -0.300$) and moderately positively affected by local macroalgal biomass ($\Delta AIC_c = 1.193$, $R^2 = 0.742$, $w_v = 0.299$), while mussel growth was moderately negatively influenced by local maroalgal biomass ($\Delta AIC_c = 1.125$, $R^2 = 0.790$, $w_v = -0.356$).

DISCUSSION

This research provides empirical evidence that effects of fishing can cascade down food webs and alter the trophic transfer of carbon back up. Comparisons among large oceanographic areas, however, reveal that the
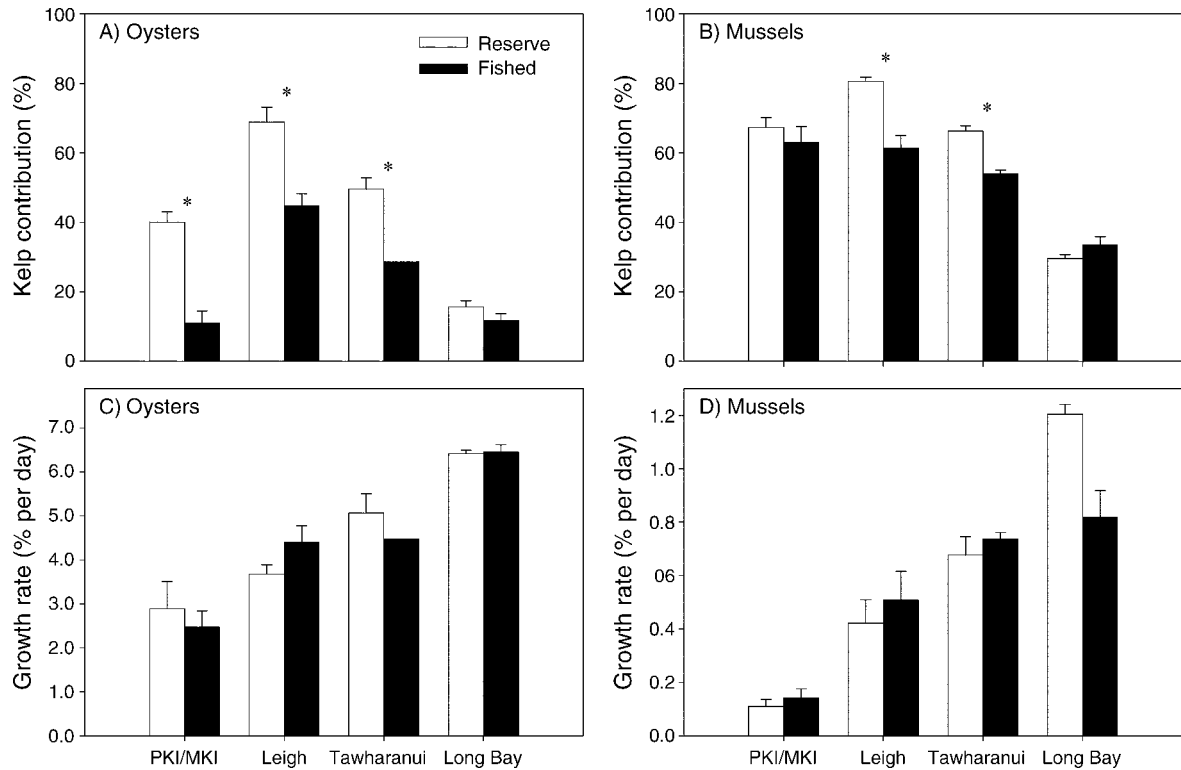
FIG. 4.   (A, B) Percentage of carbon photosynthesized by kelp (*Ecklonia radiata*) found in the tissue of transplanted (A) oysters and (B) mussels in reserve and fished sites within four locations in northeastern New Zealand, given a trophic fractionation of 1‰. (C, D) Growth rates for (C) oysters and (D) mussels in reserve and fished sites within four locations in northeastern New Zealand. *$P < 0.05$.

ecosystem consequences of reducing top predators differ as a function of regional oceanography. This highlights the complexity of forecasting where fishery-induced trophic cascades are likely to occur and the magnitude of their ecosystem-level ramifications.

Cascading effects of fishing can alter carbon flux

At fished sites within Leigh and Tawharanui densities of actively grazing sea urchins were 23.7 and 8.3 times higher compared to reserve sites, while kelp biomass was over an order of magnitude lower (Fig. 2). These

patterns are consistent with previous studies that have demonstrated that the reduction of snapper and lobster by fishing has had cascading effects on kelp communities in these locations (Babcock et al. 1999, Shears and Babcock 2002). At Leigh and Tawharanui we also detected an effect of fishing on filter feeder isotopic signatures. Filter feeders transplanted at fished sites were depleted in ^{13}C (more negative δ^{13}C values) relative to those transplanted in adjacent reserve sites where kelp biomass was an order of magnitude more abundant (Fig. 3). We estimated that kelp-derived organic carbon

TABLE 2.   The effects of fishing (Status) and oceanographic context (Location) on the kelp contribution to secondary production and growth rates of transplanted filter feeders in northeastern New Zealand.

	Fixed effects									Random effect	
	Location			Status			Location × Status			Site(Location, Status)	
Model	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	*Z*	*P*
Oysters											
Kelp contribution	27.93	3, 14	<0.0001	31.50	1, 14	<0.0001	3.60	3, 14	0.041	2.42	0.008
Length	12.37	3, 14	0.0003	0.03	1, 14	0.875	0.28	3, 14	0.838	2.59	0.005
Biomass	10.12	3, 14	0.0008	0.14	1, 14	0.713	0.43	3, 14	0.736	2.62	0.004
Mussels											
Kelp contribution	55.77	3, 21	<0.0001	13.62	1, 21	0.001	5.26	3, 21	0.007	2.21	0.014
Length	53.88	3, 21	<0.0001	0.38	1, 21	0.544	2.57	3, 21	0.081	2.91	0.002
Biomass	42.54	3, 21	<0.0001	0.00	1, 21	0.995	2.48	3, 21	0.089	2.93	0.002

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TABLE 3. Alternative models explaining the variation in oyster and mussel growth rates across northeastern New Zealand based on three explanatory variables: chl a (X), wave exposure (W), and local macroalgal biomass (M).

Models (M_i)	N	k	ΔAIC_c	$L(M_i | Y)$	w_i	R^2
Oyster growth =						
($aX/[b + X]$)	22	3	0.000	1.000	0.451	0.720
($aX/[b + X]$) + dW	22	4	1.179	0.555	0.250	0.743
($aX/[b + X]$) + eM	22	4	1.193	0.551	0.248	0.742
($aX/[b + X]$) + dW + eM	22	5	4.385	0.112	0.050	0.745
Mussel growth =						
($aX/[b + X]$)	30	3	0.000	1.000	0.589	0.779
($aX/[b + X]$) + eM	30	4	1.125	0.570	0.335	0.790
($aX/[b + X]$) + dW	30	4	4.734	0.094	0.055	0.763
($aX/[b + X]$) + dW + eM	30	5	6.688	0.035	0.021	0.771

Notes: Models, with varying numbers of parameters (k), were compared with differences in small sample, bias-corrected Akaike Information Criterion (ΔAIC_c), the likelihood of the model given the data $L(M_i | Y)$, and normalized Akaike weights (w_i) indicating the weight of evidence in favor of model i (M_i).

assimilated by filter feeders transplanted in the absence of fishing was up to 1.7 times greater than those filter feeders transplanted in the presence of fishing (Fig. 4A, B).

Unlike Leigh and Tawharanui, fishery-induced trophic cascades were not evident at the Offshore Islands PKI/MKI or Long Bay, two geographic locations that differed markedly in their regional oceanography. At the Offshore Islands, we found no difference in exposed urchin densities between fished and unfished sites (Fig. 2A) despite a 7.4-fold increase in snapper density recorded within the Poor Knights Islands Marine Reserve (Denny et al. 2004). Exposed urchins at the Offshore Islands occurred at densities below 1 urchin/m^2, the threshold density shown to be necessary to maintain urchin barrens at mainland sites (Shears and Babcock 2003). We detected no difference between fished and reserve sites; rather, kelp biomass was high among all sites within this location (Fig. 2B). Similarly, we found no effect of fishing on urchin densities or kelp biomass at Long Bay. Unlike the Offshore Islands, however, both urchin and kelp biomass remained low at both fished and unfished sites at Long Bay (Fig. 2). We did not detect an effect of fishing on the isotopic signatures of transplanted filter feeders at either the offshore island PKI/MKI or Long Bay locations (Fig. 3), where kelp biomass was equivalent at fished and non-fished sites. However, kelp contribution to oysters at the Poor Knights Islands Marine Reserve was notably greater than that at the fished Mokohinau Islands (Fig. 4A). We believe that variation in the effects of fishing on urchins, kelp, and kelp carbon flux are mediated by regional oceanography.

Variation in regional oceanography modifies the strength of fishery-induced trophic cascades

Our results suggest that regional oceanographic context can alter the magnitude of fishery-induced trophic cascades across northeastern New Zealand, as can local-scale environmental variation (Shears et al. 2008). At Long Bay, we documented low densities of

urchins (<0.07 urchins/m^2) and kelp (<92 g/m^2) and no differences between reserve and fished sites (Fig. 2A, B). Located within the inner Hauraki Gulf, Long Bay experiences high freshwater runoff, elevated sedimentation, minimal wave exposure, low water clarity, persistently high phytoplankton biomass (Chang et al. 2003, Zeldis et al. 2004, Shears et al. 2008), and high chl a concentrations (Fig. 5A, B). These oceanographic factors can limit both urchin and kelp populations; high sedimentation reduces the survival and settlement success of urchin larvae and post settlement recruits (Phillips and Shima 2006, Walker 2007), while low light, low salinity, and competition for nutrients with phytoplankton can compromise kelp production. In contrast, Leigh and Tawharanui, located on the semi-exposed coast of the outer Hauraki Gulf, are subject to low levels of sedimentation, moderate wave exposure, and high urchin recruitment. In these locations, urchins reached densities greater than 2 urchins/m^2 at fished sites (Fig. 2A), far surpassing the threshold density of at least 1 urchin/m^2 required to maintain urchin barrens (Shears and Babcock 2003). Given the abiotic conditions of Long Bay that preclude urchins and kelp from thriving, the manifestation of a trophic cascade akin to that observed within the Leigh and Tawharanui reserves is unlikely in the inner Hauraki Gulf, regardless of an increase in reef predators within the Long Bay-Okura Marine Reserve.

At the Offshore Islands PKI/MKI, exposed urchin densities at reserve and fished sites were below the threshold density of 1 urchin/m^2, and overall kelp biomass was high (Fig. 2A, B). In fact, the highest kelp biomass recorded among all four locations was at the Poor Knights Islands Reserve (1212 g/m^2) and the fished Mokohinau Islands (1190 g/m^2). We suspect that higher productivity rates of *Ecklonia* at the Offshore Islands may overwhelm urchin grazing rates. Located at the edge of the continental shelf, these island groups are bathed by the East Auckland Current (EAUC; Fig. 1). Surface waters are extremely low in chl a (Fig. 5A, B), phytoplankton biomass (Chang et al. 2003), and
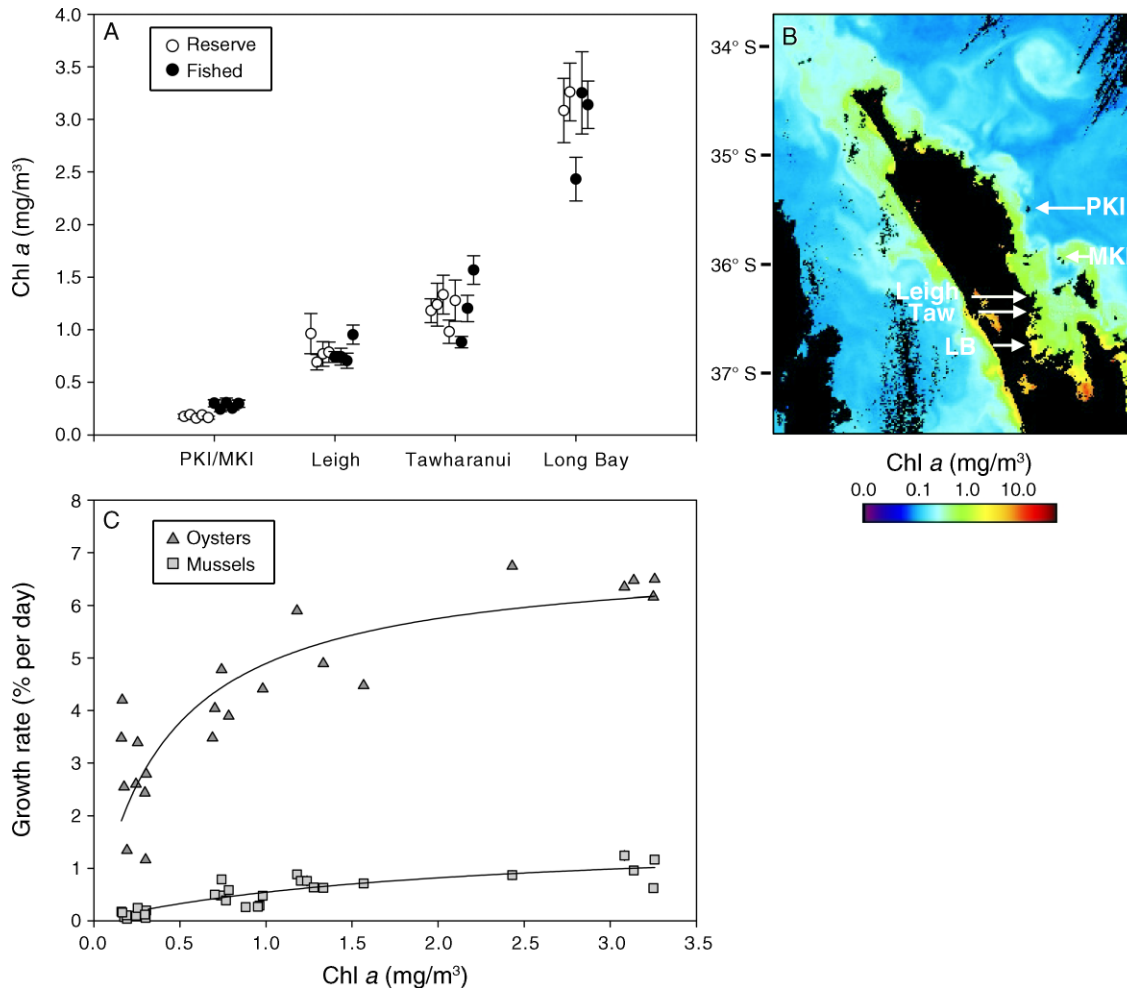
FIG. 5. (A) Satellite-derived chl *a* estimates (mean ± SE) at reserve and fished sites in four locations during the filter-feeder submersion period March–May 2003. (B) Satellite image of chl *a* concentrations (mg/m^3) across the northeastern continental shelf of New Zealand on 3 March 2003. Arrows indicate locations: Poor Knights Islands/Mokohinau Islands (PKI/MKI), Leigh, Tawharanui (Taw), and Long Bay (LB). Black represents missing data (i.e., cloud cover) and land mass. (C) Filter-feeder growth rates as a function of chl *a*.

suspended sediments resulting in higher water clarity and light levels than mainland sites (Shears et al. 2008). Under these oceanographic conditions, neither light nor nutrients appear limiting for *Ecklonia* resulting in an ideal environment for high kelp production. While we do not have any direct data on kelp productivity, other studies of *Ecklonia* show that productivity is positively related to light availability (Kirkman 1989). Under these oceanographic conditions, it is possible that the threshold density of urchins required to maintain urchin barrens offshore might be even higher than that required at Leigh and Tawharanui. A reduction in reef predators will only lead to urchin barrens where urchin grazing rates can offset macroalgal growth rates.

Our results at the Offshore Islands differ in some details from those of Shears et al. (2008) who found lower densities of exposed urchins and higher macroalgal biomass at the Poor Knights Islands Reserve compared to the fished Mokohinau Islands and on average higher densities of urchins in both places. Shears et al. (2008) sampled nine sites at both island groups and found that urchins were positively correlated with wave exposure at depths equivalent to those sampled here (7–9 m). All of the sites we sampled were located on the protected side of both island groups, which explains the low numbers of urchins (<1 urchin/m^2) and predominance of kelp we observed. The contrasting results between the two studies appear to be due to variation in the sites and depths sampled and highlight the importance of addressing local-scale environmental variation when comparing reserve and fished sites. Shears et al. (2008) suggested that the differences they observed between the Poor Knights and Mokohinau Islands are not a result of fishing and are more likely a function of oceanographic processes fuelling higher macroalgal productivity at the Poor Knights.

Another potential factor that may be limiting the cascading effects of fishing at PKI/MKI and Long Bay is time. The Poor Knights Islands and Long Bay-Okura Marine Reserves were five and eight years old, respectively, when this study was conducted and it took more than 15 years for kelp forests to recover in the Leigh Marine Reserve (Babcock et al. 1999). However, given that urchins were rare at fished sites within the Offshore Islands and Long Bay, any trophic effects associated with the recovery or removal of predators are likely to be more subtle than the community-level changes observed at Leigh and Tawharanui. Given that trophic cascades are by definition dynamic interactions, variation in their strength and duration is the norm and should be anticipated (Carpenter et al. 1985). Consequently, the indirect effects of fishing on carbon flow can also be expected to vary across both space and time as a function of oceanographic context.

Local kelp enrichment did not yield greater growth

We hypothesized that if phytoplankton is a limiting resource and if kelp-derived organic carbon is available, then secondary production, reflected by consumer growth rates, should be magnified where kelp detritus is abundant. At non-fished sites in Leigh and Tawharanui where kelp biomass was an order of magnitude greater than adjacent fished sites, enriched filter-feeder carbon signatures suggested an increase in kelp assimilation (Fig. 4A, B). Even so, this enrichment did not translate into elevated growth rates after 50 days of submersion (Fig. 4C, D) for various possible reasons. Leigh and Tawharanui are located downstream of northeastern New Zealand's primary upwelling area, known to drive some of the highest spring and summer phytoplankton concentrations on the entire continental shelf (Fig. 5B; Chang et al. 2003, Zeldis et al. 2004). Therefore, phytoplankton in these two locations was probably not limiting during the end of summer transplant period. The contribution of kelp to coastal food webs and secondary production may actually be greatest in winter, when phytoplankton production is lowest and kelp is either senescing or being physically degraded by storms (Duggins et al. 1989). Furthermore, we surmise that the benefits of kelp subsidies to filter-feeder growth may accumulate over time, particularly after an extended period of low pelagic productivity. Consequently, significant differences in growth may have been observed if the transplant duration was greater than 50 days. Lastly, consumers may also profit from kelp subsidies in ways other than increased growth, such as enhanced survival and/or fecundity.

One might expect the contribution of kelp detritus to secondary production to be more important offshore, where phytoplankton biomass was most limiting. Sure enough, kelp assimilation by oysters was greater at the Poor Knights Islands where, compared to the Mokohinau Islands, chl a was lowest and phytoplankton the most depleted. Amid a dessert of phytoplankton, these oysters appear to have taken advantage of available kelp detritus, yet this did not significantly enhance growth. Notably, the difference in estimated kelp contribution to oysters at fished and reserve sites offshore was almost certainly not an indirect effect of fishing (there was no difference in urchin density or kelp biomass between sites) but was likely due to very different phytoplankton $\delta^{13}C$ signatures (PKI, $-24.23‰ \pm 0.60‰$; MKI, $-21.32‰ \pm 0.35‰$) in addition to less overall phytoplankton biomass at PKI. This reinforces the importance of considering oceanographic differences among sites unrelated to fishing pressure when assessing the ecosystem consequences of exploiting reef predators.

Transplanted filter feeders and collected kelps became increasingly enriched in nitrogen from offshore to inshore and toward the inner Hauraki Gulf (Fig. 3A, B, Appendix E). This could reflect increased terrestrial runoff and anthropogenic nutrient loading from agriculture, sewage, and industrial activities near Auckland. Because $\delta^{15}N$ is typically increases by 3.4‰ $\pm$ 1‰ (mean $\pm$ SD) with every trophic transfer (Post 2002), ^{15}N enrichment among filter feeders also suggests that nitrogen may enter the food web indirectly through a trophic intermediate (e.g., microbes).

Regional variation in filter feeder growth

While there was no effect of fishing on filter feeder growth, we found a striking regional gradient in growth among locations. Oysters grew twice as fast and mussels 11 times as fast in Long Bay compared to the Offshore Islands, while growth at Leigh and Tawharanui was intermediate (Fig. 4A, B). Regional variation in filter-feeder growth was best explained by chl a; filter feeders in Long Bay were exposed to 13.2 times more chl a than those transplanted offshore and 3.8 and 2.5 times more chl a than those transplanted in Leigh and Tawharanui (Fig. 5A, B). Saturating growth models based on chl a values alone were best supported by the data, explaining 72% and 78% of the variance in oyster and mussel growth, respectively (Table 3; Fig. 5B).

This regional pattern in growth and chl a can be explained in part by regional patterns in oceanography. Throughout the spring, upwelling and relaxation events in northeastern New Zealand's inner shelf, encompassing Leigh and Tawharanui, cause high but variable phytoplankton concentrations in comparison to Long Bay, where nutrient-rich upwelled water is entrained. At Long Bay, where transplanted filter feeders grew the fastest, terrestrial influences combined with nutrient rich water and persistent stratified hydrodynamics support consistently high levels of phytoplankton from spring to early summer (Chang et al. 2003, Zeldis et al. 2004). High growth rates, low kelp biomass, depleted isotopic signatures, and low estimates of kelp contribution to secondary production in Long Bay suggest that transplanted consumers were largely assimilating phytoplankton and taking advantage of its constant supply.

In addition to differences in phytoplankton biomass and persistence, the inner shelf and Hauraki Gulf waters are composed of very different phytoplankton assemblages, with dinoflagellates consistently dominating in the Gulf (Chang et al. 2003). This has important implications for secondary production because dinoflagelates have three to five times greater nutritional value per unit volume than diatoms and thus provide a richer food source. Furthermore, in contrast to the Gulf, the inner shelf is subject to the onshore flow of oligotrophic surface water intrusions from the EAUC in the late summer (Zeldis et al. 2004), when this experiment took place. This may have contributed to lower chl *a* values we observed in Leigh and Tawharanui compared to Long Bay (Fig. 5A, B). The enriched isotopic signatures of filter feeders transplanted in the reserve sites of Leigh and Tawharanui, where they were exposed to 3.8 and 2.5 times less chl *a*, respectively, and up to 11 times more kelp biomass than Long Bay, suggest that detrital kelp comprised a significant proportion of the carbon they used in growth.

Although chl *a* concentrations are typically interpreted as measures of phytoplankton standing stock, strong evidence from microscopic and stable isotope analyses elsewhere suggests that chl *a* concentrations also reflect residual chlorophyll in fresh and decaying kelp fragments (Kaehler et al. 2006). Consequently, the regional relationship we found between filter-feeder growth and chl *a* (Fig. 5B) may reflect growth as a function of both phytoplankton and detrital kelp biomass.

The importance of kelp carbon to nearshore food webs in northeastern New Zealand

Across all four locations, among both fished and reserve sites, estimates of kelp assimilation by oysters and mussels suggest that kelp is an important source of carbon fueling secondary production within northeastern New Zealand's nearshore food webs (Fig. 4A, B). These estimates of kelp contribution to secondary production correspond to the range of estimates reported from temperate reefs elsewhere (Duggins et al. 1989, Bustamante and Branch 1996, Kaehler et al. 2000, Fredriksen 2003).

At the Offshore Islands, where phytoplankton was limiting and kelp abundant, slow-growing mussels relied heavily on kelp detritus (Fig. 4B) as did oysters transplanted at the Poor Knights (Fig. 4A). Even at sites with low abundances of kelp biomass (e.g., Long Bay), kelp detritus still played a role as a source of carbon assimilated by consumers likely via detrital kelp subsidies originating elsewhere. Kaehler et al. (2006) documented that kelp-derived particulate organic matter can be transported and assimilated by consumers tens of kilometers downstream of kelp beds. At our sites of low kelp biomass, kelp carbon could originate from kelps in shallower and deeper depth strata outside the depths where grazing urchins are most abundant (Shears et al. 2008) and from kelp forests "upstream." Certainly, local

topography, wave exposure, and hydrodynamic regimes likely play a role in the creation, transport, and retention of kelp detritus. Furthermore, vast amounts of dissolved organic matter originating from kelp mucilage can be produced and has been shown to be energetically significant (Newell et al. 1980). Given the likely transport of kelp carbon from kelp forest ecosystems (Kaehler et al. 2006), it is possible that some "spillover" of kelp carbon from the Leigh and Tawharanui reserves takes place, however the absence of data on spatial gradients in kelp-derived organic carbon in POM means that for the time being there is no evidence to support this hypothesis.

The indirect alteration of available kelp carbon by fishing will likely elicit different responses among consumers. Here, mussels tended to assimilate more kelp detritus than oysters (Fig. 4A, B). This could be because these filter feeders have evolved unique structures to select, capture, and assimilate different types and sizes of food particles or because the different tissues sampled (mussel pedal foot vs. oyster gill) turnover at different rates. Regardless, the isotopically enriched signatures of both oysters and mussels reveal a pervasive occurrence of organic carbon originally derived from kelp photosynthesis. Given that it takes organic carbon to feed fish and shellfish, and that kelps are an important and indeed preferred component of some detrital food webs (Mann 1973, 1988, Crawley et al. 2007), a reduction in kelp carbon could cause a reduction in future fishable production where pelagic primary production is limiting.

Because the primary production required to sustain global fisheries in upwelling and shelf ecosystems ranges from 24% to 35% (Pauly and Christensen 1995), it behooves us to understand the extent to which fishing activities themselves alter the production of organic carbon. In fact, organic carbon flux could be used as a common currency by which to assess ecosystem-based management strategies. Although our current understanding of how various marine ecosystem processes respond to the reduction of major predators remains rudimentary, our results offer two important insights. The cascading effects of fishing nearshore can alter kelp carbon flux, yet, the magnitude of these effects depends on regional oceanographic context. In sum, this research provides evidence that fishing can have ecosystem-level consequences far beyond the fishery itself and begins to offer a novel pathway to help guide and evaluate ecosystem approaches to conservation and management.

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APPENDIX A

Photographs of experimental subtidal filter feeder transplants (*Ecological Archives* A018-066-A1).

APPENDIX B

Map of phytoplankton sampling stations (*Ecological Archives* A018-066-A2).

APPENDIX C

Relationship between satellite-derived chl *a* and empirical measurements of chl *a* (*Ecological Archives* A018-066-A3).

APPENDIX D

Total macroalgal biomass at reserve and adjacent fished sites among locations (*Ecological Archives* A018-066-A4).

APPENDIX E

Carbon and nitrogen stable isotope signatures of kelp and phytoplankton sampled across northeastern New Zealand (*Ecological Archives* A018-066-A5).