

# Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores

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**ABSTRACT:** The dependence of positive species interactions on the traits of individuals has rarely been explored, particularly in marine communities. Therefore, we have little idea about their generality, scales of variability, or reliance on local conditions. Transplant experiments and surveys conducted at 14 sites spanning across ~900 km of the central Chilean coast demonstrate that alongshore variation in upwelling, occurring over 10s to 100s of kilometers, explains among-site differences in growth rates of the turf-forming alga *Gelidium chilense*, which drives predictable landscape patterns in turf height. At upwelling centers, turf algae grew faster and attained taller heights than at warmer downstream locations, where the algal turf remained short because it grew slower and was pruned-back in winter. Replicated, reciprocal transplants of tall and short algal turf, combined with manipulations that controlled predator access to turf, revealed that recruitment of the mussel *Perumytilus purpuratus* was differentially enhanced by the turf; benefits were strong when the turf was short, but disappeared when the turf was tall. By determining mussel prey supply to higher trophic levels, upwelling-controlled facilitation has important consequences for community regulation. This is the first study to identify upwelling as a physical mechanism generating environmental conditions that (1) control trait-dependent habitat modification and (2) regulate the relative importance of facilitation in marine rocky intertidal communities.

**KEY WORDS:** Positive interactions · Habitat modification · Community regulation · Rocky intertidal · Upwelling · Macroalgae · Mussels · Chile

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## INTRODUCTION

Direct positive interactions that result from biotic habitat modification have recently received renewed attention (Stachowicz 2001, Bruno et al. 2003). These revitalized efforts have revealed facilitation to be a critical force structuring many communities, increasing diversity, population size, growth rate, distributional range, or individual fitness. The physical presence of facilitators assists other species in a wide variety of ways (see Bruno & Bertness 2001, Stachowicz 2001 for review). However, complex combinations of positive and negative interactions often operate between species, and their net outcome (positive, neu-

tral or negative) can vary over space and time (Callaway & Walker 1997, Holmgren et al. 1997, Jones et al. 1997). Factors that shift the balance from positive to negative are poorly understood, but it is expected that they will ultimately be intertwined with environmental conditions (Bronstein 1994).

Population or individual traits of a facilitator can also affect whether (or how much) it modifies the environment, determining the degree to which other species benefit. For example, increased density and architectural complexity of plants often increase abundance and diversity of associated organisms in the sea (Gee & Warwick 1994, Levin & Hay 1996, but see Kelaher 2003a for negative relationships), in freshwater sys-

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tems (Jeffries 1993) and on land (Callaway & Walker 1997). Therefore, factors controlling such traits can ultimately determine the relative balance of costs and benefits of interactions between species. Yet, in most systems, we still know little about the spatial and temporal scales of variability in such traits, and even less about the processes causing such variation. Despite this scarcity of information, Bruno & Bertness (2001) have speculated that trait-dependent facilitation may be driving a number of landscape patterns in marine communities.

A common positive interaction on rocky shores is facilitation generated by the physical habitat created by turf-forming algae. Algal turfs are important components of intertidal and subtidal communities worldwide, sometimes dominating extensive areas of the shore (Stephenson & Stephenson 1972, Santelices 1989, 1991). Turf-forming species show considerable morphological plasticity, and the physical structure of these biogenic habitats can alter turbulence and flow velocity (Eckman 1983), sediment and particle trapping (Kelaheer 2003b, Prathep et al. 2003), and moisture retention (Hay 1981, Taylor & Hay 1984). Therefore, morphological traits can change the environment and have a major influence on associated assemblages by providing substrate for settlement and recruitment of invertebrates (Eckman 1983), refuge from predators (Moreno 1995), shelter from desiccation (Hay 1981) and protection from wave forces (Whorff et al. 1995).

Along the rocky, wave-exposed shores of central Chile, algal turfs, composed largely of *Gelidium chilense* (hereafter *Gelidium*), form distinct and often extensive bands in the low intertidal zone (Santelices 1989). Previous studies in central Chile revealed that *Gelidium* turf facilitates recruitment of mussels, including the competitively dominant mussel *Perumytilus purpuratus* (E. Wieters, S. Navarrete & B. Broitman unpubl. data). Because mussels cannot settle on smooth rock surfaces (Navarrete & Castilla 1990a), the presence of a complex substrate that facilitates recruitment is critical for their successful colonization (Navarrete & Castilla 2003). Moreover, since mussels are the competitive dominants of the mid and low intertidal zones (Castilla & Duran 1985, Navarrete & Castilla 2003), such facilitation can have important consequences for community regulation. However, the height and morphology of turf vary greatly among sites along the coast (Santelices 1989, author's pers. obs.), which could influence the magnitude or nature of turf–mussel interactions.

Although diverse processes can affect macroalgal morphology, temperature and nutrient-induced changes in size and biomass have been highlighted in experimental and correlational studies in several coastal systems (Bosman et al. 1986, Bustamante &

Branch 1996, Nielsen 2001, Blanchette et al. 2002). Temperature and nutrient supply in marine systems is driven by nearshore oceanographic conditions, and along the coast of central and northern Chile the main process is seasonally variable, wind-driven upwelling that forces cold, nutrient-rich waters to the surface (Strub et al. 1998, Poulin et al. 2002a,b, Narváez et al. 2004). However, considerable alongshore variation in surface temperature and nutrient availability over scales of a few to 10s of kilometers is characteristic of such coastal systems (Shannon 1985, Strub et al. 1998), with upwelling intensity varying according to topography and coastline orientation (Jury 1985, Kelly 1985, Figueroa & Moffat 2000). In central Chile, Broitman et al. (2001) have shown that this meso-scale spatial variation in upwelling can influence patterns of abundance (cover) of some algal functional groups. Nielsen & Navarrete (2004) showed that growth rates of the red alga *Mazzaella laminarioides* are faster at upwelling centers than elsewhere.

In this study, I explored (1) whether turf-forming algae vary in size (height) over a geographic region of ~900 km in central Chile, (2) whether the growth rate and height of these turfs can be related to local differences in environmental conditions linked to upwelling focal points, and (3) whether the height of the algae influences their effects on mussel recruitment. To my knowledge, this is the first set of data that documents the physical factors generating environmental conditions that control trait-dependent habitat modification and facilitation over geographic scales in benthic marine communities.

## MATERIALS AND METHODS

**The system and sites.** Studies were conducted along the open, high-energy coast of central Chile, which is characterized by large meso-scale variation (at the scale of 10s to 100s of kilometers) in sea surface temperature, particularly during spring and summer (Strub et al. 1998, Wieters et al. 2003, Narváez et al. 2004). The localized nature of upwelling along central Chile is easily observed in thermal imagery (AVHRR) and onshore temperature measurements (Broitman et al. 2001, Poulin et al. 2002b, Wieters et al. 2003, Narváez et al. 2004, Nielsen & Navarrete 2004). Areas of cold water nearshore correspond to localized upwelling centers, where clear, nutrient-rich waters are forced to the surface and rapidly advected away from the shore. In contrast, areas downstream from such cells are characterized by warmer water that has been near the surface for a few days. Here, aged surface water is more depleted in nutrients due to photosynthetic activity, but supports higher chlorophyll a con-

centrations (Wieters et al. 2003). The main upwelling centers within the region of this study include Punta Roncura-Toro (Pichilemu, Bucalemu), Punta Curaumilla (Curaumilla, Quintay), and Punta Lengua de Vaca (Talca), which have all been previously identified and described in the literature (Johnson et al. 1980, Fonseca & Farías 1987, Paolini & Barría 1999, Bello 2001). Warmer downstream areas corresponded to Las Cruces (ECIM), Tunquen, Montemar, Guanaqueros, and Temblador (Broitman et al. 2001, Poulin et al. 2002a,b, Wieters et al. 2003, Narváez et al. 2004, Nielsen & Navarrete 2004). Quisco, Molles, Buchupureo, and Oscuro are known to be areas of intermediate upwelling intensity, as upwelling only occurs there during persistent, strong southerly winds (e.g. Poulin et al. 2002a, Narváez et al. 2004).

Studies were conducted in the low intertidal zone of rocky outcrops with approximately similar slope (20 to 30°) and high wave exposure. In general, extensive areas (65 to 80 %) of the low intertidal zone at all sites were covered by a patchy mosaic of *Gelidium* turf and fleshy crustose algae (largely *Hildenbrandia* sp.), particularly where not directly exposed to strong wave action. Only Pichilemu and Bucalemu supported a more diverse macroalgal assemblage in the low zone (author's unpubl. data), but large monocultures of *Gelidium chilense* were still predominant there (~30 % cover).

**Sea surface temperature and nutrient concentrations.** To characterize the physical environment and to shed light on potential mechanisms driving variation in growth and/or morphology of *Gelidium* turf, I recorded onshore sea surface temperature (SST) at 8 sites along the coast (noted with asterisks in Fig. 1) that were expected to vary in upwelling intensity. Throughout the study, surface water temperature was recorded at 20 min intervals with Optic Stowaway (Onset Computer; ±0.1°C precision) submersible temperature loggers placed at approximately 1 m depth below the lowest low tide at each site. There are no data for Pichilemu for certain periods due to logger loss or failure.

SST is often used as a proxy for nutrient (nitrate) concentrations. To validate the relationship between SST and nitrate concentrations in onshore waters within the region, shore-based water samples were simultaneously collected at 5 sites (noted with † in Fig. 1) on 4 dates. On each sampling date, 3 water samples were taken from each of 3 benches (separated by 10s of meters) at each site, and this sampling scheme was repeated 2 times on each sampling date. Water samples were taken from a depth of 20 to 40 cm using 3 × 250 ml acid-washed plastic (high density polyethylene) dark bottles. Immediately after collection, 100 ml from each sample was filtered through a combusted GF/F Whatman glass fiber filter using a syringe and inline filter holder, and the filtrate was packed in ice and

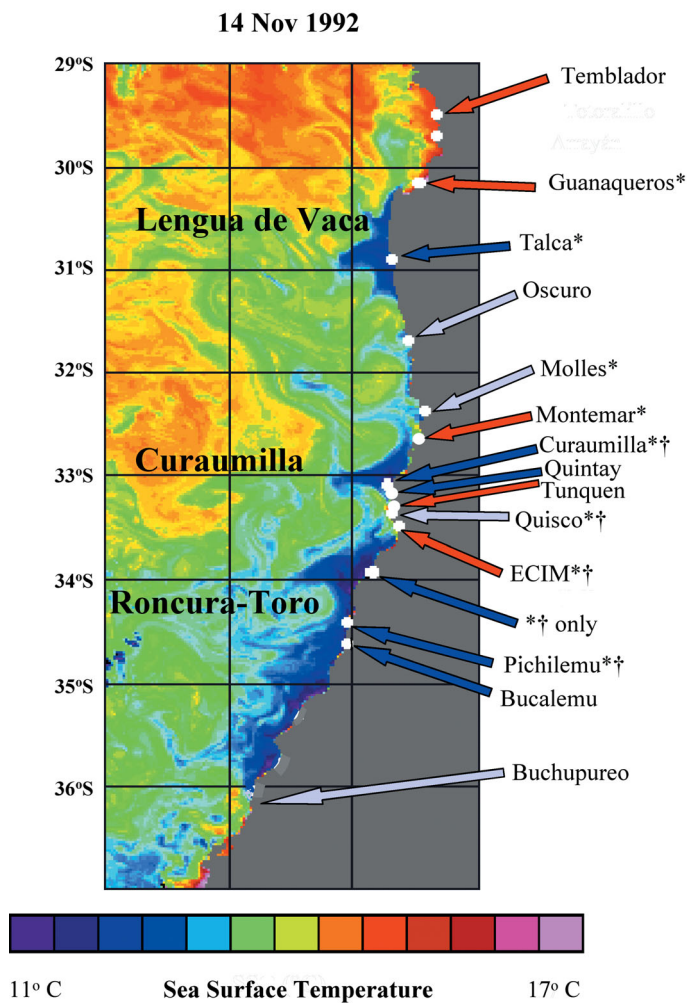


Fig. 1. AVHRR (Advanced Very High Resolution Radiometer) satellite image of sea surface temperature, also showing locations of field sites. Alongshore variation in temperature reflects the existence of cold upwelling centers with warm downstream areas in between. \*: sites with *in situ* temperature loggers; †: sites where nutrient samples collected; dark blue arrows: upwelling centers; light blue arrows: intermediate upwelling; red arrows: downstream sites

transported to the laboratory, where it was frozen until later analysis of nitrate and nitrite using a Traacs auto-analyzer (Bran+Luebbe).

**Geographic variation in turf height.** To characterize meso-scale spatial variation in algal height, I surveyed 14 sites separated by 10s to 100s of kilometers and stretching across 7 degrees of latitude (see Fig. 1). Sites were chosen according to their proximity to major upwelling centers; 5 sites were at known upwelling centers (Bucalemu, Pichilemu, Quintay, Curaumilla, Talca), 5 at 'downstream' locations not directly affected by upwelling (ECIM, Tunquen, Montemar, Guanaqueros, Temblador), and 4 lay in intermediate conditions (Buchupureo, Quisco, Molles, Oscuro).

'Divet' samples were taken from the natural turf at each site during spring/summer of 2002–2003. Within the low intertidal zone, 8 to 10 samples of approximately 16 to 25 cm<sup>2</sup> of turf were haphazardly collected across 2 rock benches at each site. Divets were taken from areas with 100% *Gelidium* cover and all turf was removed, including holdfasts. In the laboratory, 10 intact fronds (with holdfasts) were randomly chosen from each sample and their maximum lengths were measured to the nearest 0.1 mm. Mean frond length was calculated for each divet and analyzed using ANOVA. Upwelling condition was considered a fixed factor, whereas site was considered a random factor (replicates) nested within upwelling condition. Visual inspection of the residuals plotted against predicted values revealed that variances were homogeneous, and normality was tested using a Shapiro-Wilks test.

**Turf growth rates.** To determine differences in growth rates between sites with different turf height, I conducted transplant experiments on 4 different occasions, covering the 4 seasons in 2002, at 2 sites, Pichilemu (an upwelling center) and ECIM (a downstream site). To then assess whether turf growth rates varied predictably along the coast, depending on proximity to upwelling centers, I conducted 2 further transplant experiments in the austral winter and spring of 2003 that included 9 sites stretched across a broad geographic region (Fig. 1); 4 sites at known upwelling centers (Bucalemu, Pichilemu, Curaumilla, Talca), 3 sites at 'downstream' locations not directly affected by upwelling (ECIM, Montemar, Guanaqueros), and 2 sites of intermediate upwelling (Quisco, Molles).

By transplanting turf originating from a single location, I was able to avoid potential confounding effects of spatial and temporal differences in turf morphology, physiology (e.g. nutrient reserves) and reproductive status. From a site lying between ECIM and Quisco, I collected large (7 to 10 cm) keyhole limpets, genus *Fissurella*, whose shells were naturally covered (80 to 100%) with short (5 to 10 mm), non-reproductive *Gelidium chilense*. Flesh was removed from the shells and the inner cavity of each shell was filled with marine epoxy to reduce breakage. Shells were then numbered and transplanted into the low intertidal zone, fixing them to the rock surface with a stainless steel screw that fit through the 'keyhole' of the shell. To reduce possible effects of herbivory, shells were placed atop a 1.5 cm diameter tube 3 cm tall. Ten shells were randomly placed in natural patches of turf at each site.

Growth of plants belonging to the *Gelidium* genus results from activity of apical cells. However, individual plants are difficult to identify, and growth often occurs via regeneration of erect fronds from creeping axes. Differences in growth might, therefore, be expressed as changes in frond length, frond density, or

spatial extension. Therefore, I measured frond elongation rates, as well as changes in biomass. Before transplant, and again at the end of each growth trial, each shell was photographed and 2 small (1 to 3 cm<sup>2</sup>) samples of turf were removed from (1) the center and (2) the edges of each limpet shell. The 2 areas of the shell were sampled to determine whether there was any spatial variation in turf growth at a scale of centimeters. In each case, the area sampled was measured and the turf was blotted dry and weighed. Ten intact fronds (with holdfasts) were randomly chosen from each sample and measured to the nearest 0.1 mm. There are no data available for Quisco during spring 2003, as all transplanted turf were lost, presumably due to human interference.

**Data analysis:** Since new shells were transplanted to new positions at each site in each trial, the different trials were independent and considered as a fixed factor ('season') in ANOVA. In all trials, there were no significant differences in growth rates between samples from the center and the edge of shells ( $p > 0.62$  on all occasions), so these 2 areas were then averaged and considered as subsamples within each shell. The results of the turf transplant experiments at Pichilemu and ECIM during 2002–2003 were analyzed using 2-way ANOVA, with site and season considered as fixed effects. The results for transplants across the larger geographic region were analyzed considering trial ('season') and upwelling condition as fixed factors, and site as the replicates (random factor) nested within upwelling condition. In all cases, results for changes in frond length and biomass were equivalent; therefore, for simplicity, I present only frond elongation rates.

**Effect of turf height on mussel recruitment.** To test whether between-site differences in turf height (tall vs short) modifies its facilitative role of augmenting mussel recruitment, I conducted a replicated, reciprocal transplant experiment between ECIM and Pichilemu during the austral summer (January to March) of 2003. Rock pieces (~150 to 200 cm<sup>2</sup>) covered with 80 to 100% *Gelidium chilense* were collected from sites that had either tall (~4 cm, Pichilemu) or short turf (<1 cm, ECIM). Rocks were then transplanted into the low intertidal zone by gluing them to the surface using a non-toxic submarine epoxy (Super As<sup>®</sup>). Turf transplants were placed within naturally existing turf beds, where I carefully scraped and chipped the surface in order to embed each transplant flush with the natural rock surface. Treatments included turf from (1) Pichilemu or (2) ECIM re-planted in their original sites to control for disturbance effects, (3) turf from Pichilemu transplanted to ECIM and (4) vice versa. Field observations suggested that small mussel recruits dominate the diet of the predatory seastar *Heliaster helianthus* in the low zone, which may influence mussel colonization. There-

fore, to determine potential interactive effects of turf height and predators on mussel recruitment, I combined transplants of tall/short algal turf with manipulations that controlled predator access to the plots. Predators were either (1) allowed free access to otherwise undisturbed transplants or (2) excluded by installing a 30 × 30 cm domed, plastic mesh cage. Potential effects of the cage itself were evaluated by installing a 2-sided mesh dome that provided similar shading and flow alteration as cages, while still allowing access to predators. Five replicates of all treatments were assigned in a completely randomized design. Percentage cover of all sessile species within the transplant was monitored each month, but the duration of the experiment was limited to 3 mo because turf height responded quickly to local environments, nullifying the intended treatments after this time. Translocating turfs to multiple sites simultaneously proved to be logistically impossible, largely due to the rapid morphological changes of the turf to their new environment and the amount of time required to extract, transport, and install turf transplants. Likewise, attempts to shorten existing tall plants dramatically changed turf morphology, making it distinct from that of natural short turf, and resulted in replacement by other species.

**Data analysis:** In some treatment combinations with long turf, the effects were so strong that there were no mussels in any replicate at the end of the experiment (see 'Results'), which precluded statistical analyses of the complete experiment. Therefore, I restricted statistical analysis to short turf treatments. Mussel covers after 3 mo were analyzed with a 2-way ANOVA, with site and predator access considered fixed factors. Data were transformed ( $\ln [x + 1]$ ) to meet model assumptions, which were checked by visual inspection of the residuals plotted against predicted values and tested using a Shapiro-Wilks test for normality.

## RESULTS

### Sea surface temperature and nutrient concentrations

Onshore nitrate concentrations were strongly, inversely related to SST in the study area (Fig. 2 and see Fig. 1b in Nielsen & Navarrete 2004). Strikingly, 81% of the variation in onshore nitrate concentrations along the central Chilean coast was explained by a simple measure of SST.

Consistent among-sites differences in onshore daily mean SST were repeated alongshore, following spatial patterns of upwelling intensity along the coast (Fig. 3). ECIM had consistently warmer temperatures than the colder conditions at Pichilemu (Fig. 3a), Montemar was consistently warmer than Curaumilla (Fig. 3b), and

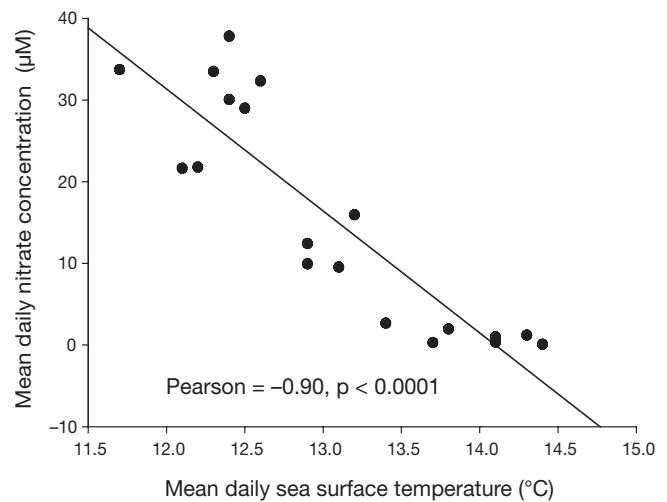


Fig. 2. Relationship between onshore mean daily *in situ* water temperature and nitrate concentration. The Pearson correlation coefficient was statistically significant at  $p = 0.05$ . Data were generously provided by S. A. Navarrete

Guañaqueros was consistently warmer than Talca (Fig. 3c). Temperatures at Quisco and Molles (squares in Fig. 3) were intermediate to their proximate upwelling centers and downstream sites. During 2002, the differences in SST between ECIM and Pichilemu persisted (Fig. 4a) and were similar to differences observed among other sites along the coast. Differences among sites were most pronounced during spring, when downstream sites (ECIM, Montemar, Guañaqueros) showed marked seasonal warming in contrast to the overall colder temperatures that resulted from more frequent and prolonged temperature drops at upwelling centers (Pichilemu, Curaumilla, and Talca; Figs. 3 & 4a). Likewise, cooling events at Montemar and Guañaqueros were smaller in magnitude, brief, and lagged behind those at Curaumilla and Talca, respectively. These patterns of alongshore variability in upwelling frequency and intensity were also apparent in AVHRR satellite images, as has been described previously (e.g. see Fig. 1).

### Geographic variation in turf height

The geographic pattern of mean frond length remarkably matched the alongshore pattern in relative intensity of upwelling (Fig. 5, upwelling effect:  $F_{2,11} = 6.73$ ,  $MS = 4707.21$ ,  $p = 0.011$ ). The longest turfs were present at upwelling centers (mean frond length  $\pm$  SE =  $34.7 \pm 1.9$  mm), while turfs at downstream sites were shortest ( $9.0 \pm 1.1$  mm). Sites of intermediate intensity and frequency of upwelling had intermediate turf heights ( $14.6 \pm 3.1$  mm). However, turf size also varied

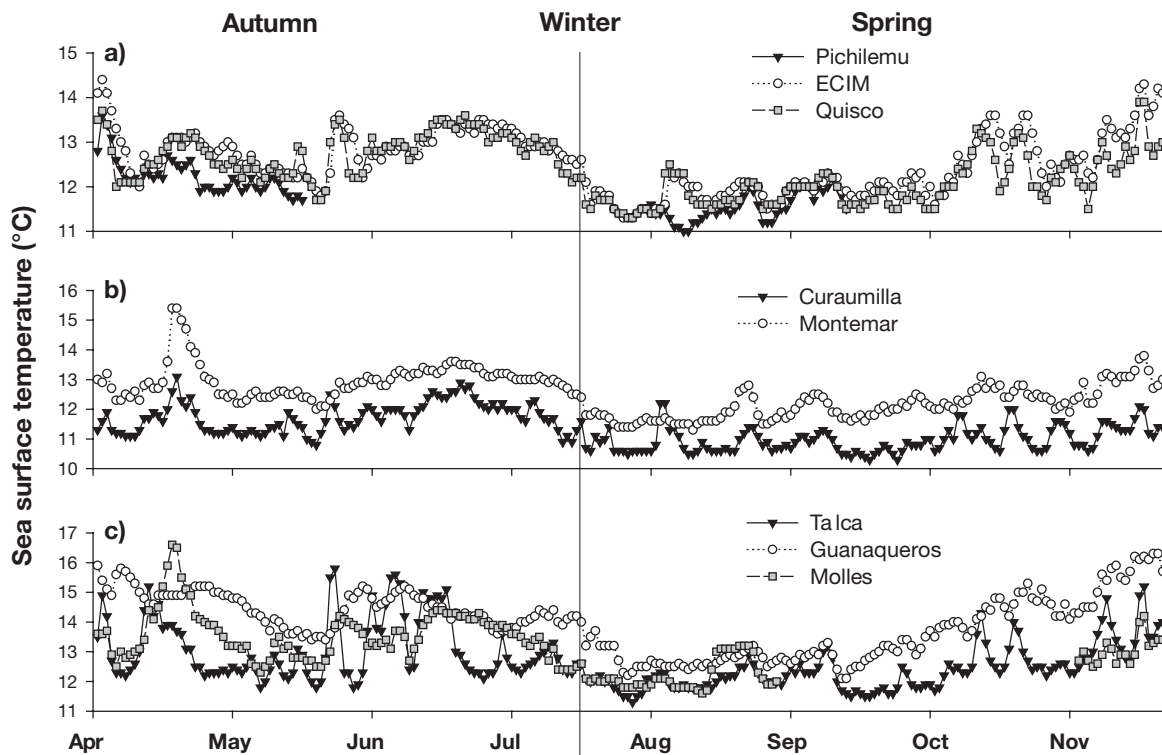


Fig. 3. Mean daily *in situ* sea surface temperatures in 2003 from onshore loggers at all growth trials sites except Bucalemu. The vertical line indicates the end of winter trials and the start of spring growth trials. ▼: upwelling centers; ◐: intermediate upwelling; ○: downstream sites. There were no data for Pichilemu for certain periods

significantly among sites within upwelling categories (site [upwelling] effect:  $F_{11,122} = 29.02$ ,  $MS = 965.34$ ,  $p < 0.0001$ ), and a general trend of decreasing turf height to the north was observed for upwelling centers (black bars in Fig. 5).

#### Turf growth rates

Distinct and persistent differences in algal turf growth rates were evident between sites during 2002 (Fig. 4b, site effect:  $F_{1,43} = 135.1$ ,  $MS = 0.043$ ,  $p < 0.0001$ ). *Gelidium* at Pichilemu grew 3 to 6 times faster than turf at ECIM. Moreover, Pichilemu exhibited positive growth rates throughout the year and even the slowest growth rates there (winter and spring) were still faster than any ever observed at ECIM. In contrast, growth at ECIM was persistently slow, and in winter, plants had negative growth rates, suggesting that energy expenditure and tissue loss due to necrosis of frond tips exceeded photosynthetic rate. Therefore, the magnitude of seasonal (between trials) differences between sites changed (trial  $\times$  site effect:  $F_{3,43} = 6.44$ ,  $MS = 0.002$ ,  $p = 0.001$ ). Negative growth rates at ECIM were again observed during the following winter (see Fig. 6), which suggests that negative growth and

pruning of turf is a regular occurrence at this site during winter months.

There were striking, persistent alongshore differences in growth rates of transplanted turf, which varied predictably according to upwelling intensity (Fig. 6; upwelling effect:  $F_{2,10} = 8.15$ ,  $MS = 0.0117$ ,  $p = 0.007$ ). The fastest growth rates were observed at upwelling centers (mean growth rate  $\pm$  SE =  $0.034 \pm 0.005$  mm d<sup>-1</sup>), while downstream sites exhibited the slowest algal growth rates ( $-0.001 \pm 0.006$  mm d<sup>-1</sup>). As expected, sites of intermediate upwelling had intermediate rates of growth ( $0.012 \pm 0.01$  mm d<sup>-1</sup>). These differences were similar between seasons (trial  $\times$  upwelling effect:  $F_{2,10} = 1.13$ ,  $MS = 0.0016$ ,  $p = 0.366$ ), but were most pronounced during autumn-winter, when all downstream sites exhibited negative growth (Fig. 6). During spring, growth rates at downstream sites increased, achieving positive, albeit low, values similar to those at sites with intermediate upwelling. Turf growth rates also varied significantly among sites within upwelling categories (site [upwelling, trial] effect:  $F_{10,84} = 2.78$ ,  $MS = 0.0014$ ,  $p = 0.0051$ ), and a general trend of decreasing growth rates to the north was observed for upwelling centers (black bars in Fig. 6).

Most of the variation in natural turf height along the central coast of Chile was explained by turf growth

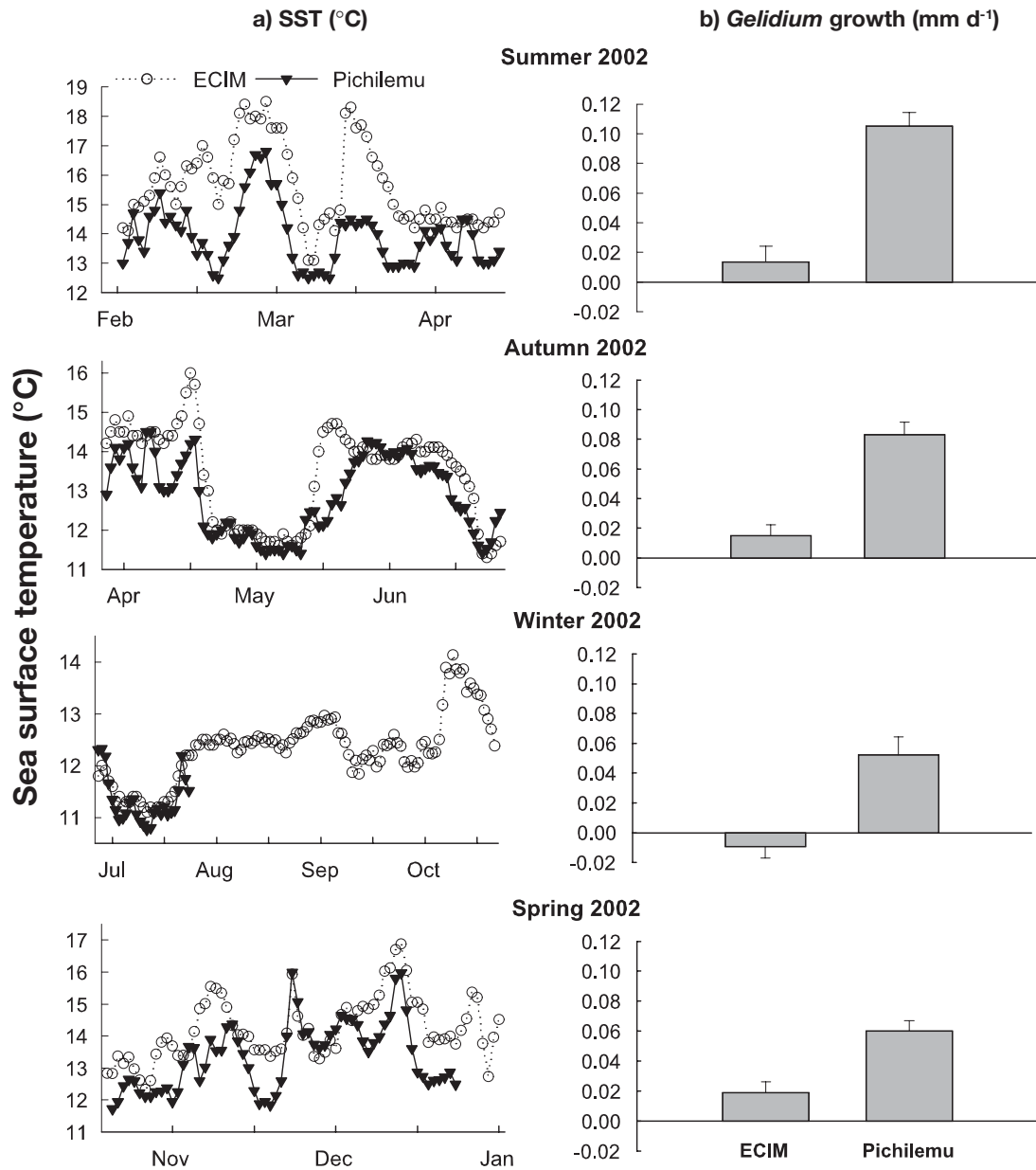


Fig. 4. (a) Mean daily *in situ* sea surface temperature during growth trials run during 2002 at ECIM and Pichilemu. ▼: Pichilemu; ○: ECIM. There were no data for Pichilemu between August and October. (b) Mean daily growth rate (+SE) of algal turf

rates, resulting in a striking positive correlation between growth rates and overall turf height (Pearson = 0.89,  $p = 0.0032$ ,  $n = 8$ ).

**Effect of turf height on mussel recruitment**

The height of the turf (tall vs. short) had a large effect on mussel colonization at both sites, regardless of the origin of the plants. Virtually no mussels colonized and grew enough in the long turf at either site to be able to

register a change in mussel cover, regardless of the presence or absence of predators (Fig. 7). Short turf strongly facilitated mussel colonization, and the effect of predator access to short turf was highly significant and consistent between sites (predator effect for short turf:  $F_{2,23} = 26.88$ ,  $MS = 29.43$ ,  $p < 0.0001$ ; site  $\times$  predator interaction for short turf:  $F_{2,23} = 1.95$ ,  $MS = 2.13$ ,  $p = 0.16$ ). Contrasts revealed that mussel covers were similarly low in controls and 2-sided domes ( $F_{1,23} = 0.51$ ,  $MS = 0.56$ ,  $p = 0.48$ ), making it unlikely that cage artifacts contributed to the predator effects. Both controls

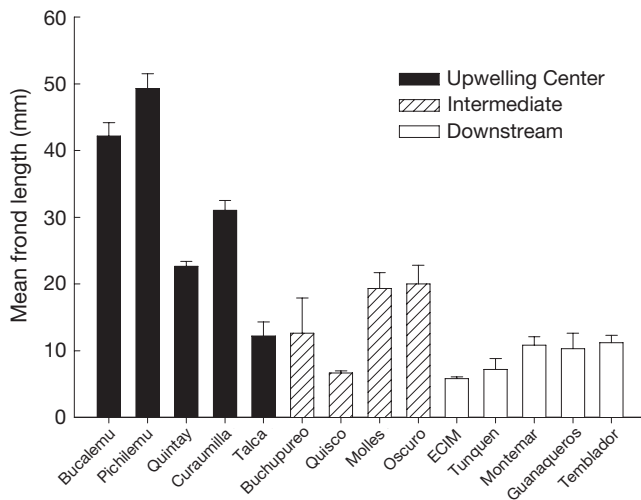


Fig. 5. Mean turf size (+SE) in the low intertidal zone at 14 sites along the coast (29 to 36°S). Within each upwelling condition, sites are ordered from south to north

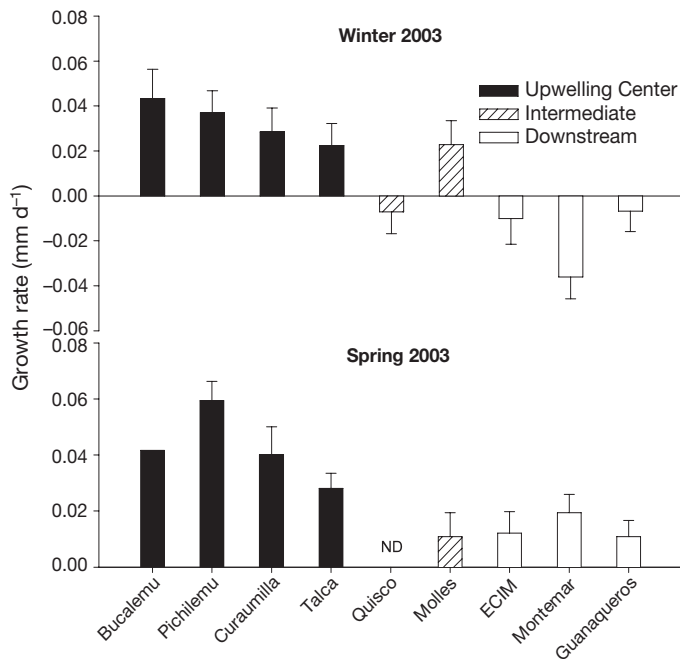


Fig. 6. Mean daily growth rate ( $\pm$ SE) of algal turf during winter and spring of 2003 at 9 sites along the coast (29 to 36°S). Within each upwelling condition, sites are ordered from south to north. ND: no data

and 2-sided domes differed from areas where predators had been excluded ( $F_{1,23} = 50.82$ ,  $MS = 55.65$ ,  $p = 2.92e^{-7}$ ). Where predators were excluded from the short turf, mussels quickly colonized (within ~2 mo) and began to overgrow the short turf. The magnitude of the positive effect of the short turf on mussel cover did not significantly differ between sites (site effect:  $F_{1,23} = 3.37$ ,  $MS = 3.69$ ,  $p = 0.08$ ).

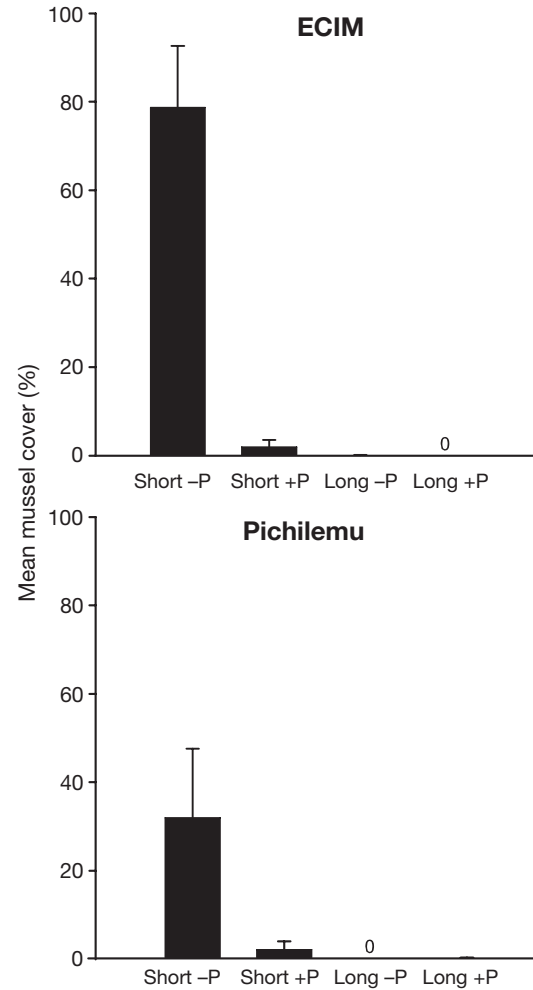


Fig. 7. Effects of algal turf height (short vs. tall) and predators (+P or -P) on mean mussel cover (+SE) at ECIM and Pichilemu

## DISCUSSION

The concept of facilitation is well established in the literature, and empirical and theoretical studies have shown the important consequences that positive interactions can have for population and community dynamics (Stachowicz 2001). The extent to which facilitation is dependent on the traits of the participating species has, however, seldom been investigated under natural conditions. Here, I describe a case of conditional facilitation of recruitment of a dominant mussel competitor by an algal turf, in which oceanographically determined changes in the traits of the facilitator, occurring over meso-scales of 10s to 100s of kilometers, ultimately determine the strength of the positive interaction and the effects on local community regulation.

As evidenced by satellite imagery and verified by *in situ* temperature data, there are persistent differences



in upwelling intensity along the coast of central Chile. Mimicking this pattern, field surveys showed that fronds of the turf-forming corticated alga *Gelidium chilense* were longer ('taller') in regions of intense and frequent upwelling than at sites downstream from such upwelling centers. Seaweeds exhibit a great range of morphology and size, as they quickly acclimate to local habitat conditions (Norton et al. 1982). The large differences in turf height that I observed among sites along the coast are indicative of the plastic nature of *Gelidium chilense* and the differences in the conditions experienced by the turf. Indeed, transplant experiments to sites with contrasting upwelling regimes demonstrated that morphological differences in height are not due to genetically determined variation among local populations, but rather to environmentally determined differences in growth rates. The negative growth rates observed during the winters of 2002 and 2003 at some sites are central to understanding why turfs remained short at these sites, since spring-summer gains can be overcome by losses during winter, preventing growth accumulation over time. Further studies spanning multiple years are necessary to determine the temporal generality of these seasonal trends.

The mechanism by which upwelling controls turf height and growth is likely to be tightly linked to nutrients. It has been shown that onshore nutrient concentrations along central Chile are higher at areas of more intense coastal upwelling and colder temperatures (Nielsen & Navarrete 2004), and my data also revealed high correlation between nutrient concentration and SST. Increased growth and changes in morphology appear to be a common response of *Gelidium* species to increased nutrient loadings, whether nutrient supplies are driven by upwelling, fertilization of commercialized crops, or domestic pollution (Santelices 1991). Working in the mid-intertidal zone at 4 sites within the same study region, Nielsen & Navarrete (2004) observed similar among-site differences in growth rates of a different corticated algal species, *Mazzaella laminarioides*. They also found that the highest growth rates of *Mazzaella* were associated with upwelling centers, which matched well with the meso-scale pattern of abundance of this alga across the region (Broitman et al. 2001). Thus, the positive correlation between upwelling intensity and growth rates could be a general characteristic of corticated algae in this eastern boundary ecosystem.

The growth of *Gelidium* is controlled by complex interactions between light, temperature, nutrients and water movement (Santelices 1991). Therefore, observed differences in net turf growth and final height might result from direct or indirect effects of nutrients. For example, short-term stresses associated with

extreme light, desiccation and/or heat during spring-summer low tide periods may interact with nutrients to differentially constrain growth and frond length. Bleaching of *Gelidium* turf, followed by necrosis, is common along the central coast after days of high solar radiation (Santelices 1991, author's pers. obs.), although these events appear to vary among years and sites. Laboratory studies with *Gelidium* and related genera suggest that sensitivity to such stressful events can be modulated by nutrients, especially nitrate (Santelices 1991). Therefore, higher nutrient concentrations at upwelling centers may not only act to increase production, but may also buffer the turf from abiotic stresses, such as solar radiation.

Besides the differences in nutrient inputs among sites, the differences in SST could directly affect growth of algae. Laboratory studies have shown that *Gelidium* growth increases with increasing temperature, at least up to about 15°C, after which growth remains unchanged with increasing temperature (Santelices 1991). However, I observed the opposite pattern in the field; highest growth rates occurred at the coldest sites and slowest growth rates at the warmest sites, strongly suggesting that temperature is not the primary controlling factor.

Likewise, water movement or turbulence could potentially co-vary with natural, meso-scale variation in upwelling and nutrient supply, since upwelling centers are fixed in place by coastal topography. However, local study benches were specifically chosen to be of similar slope, orientation, and wave exposure in attempt to standardize effects of water movement and immersion, and field observations suggest that these were not likely causative factors of variation in turf growth and morphology. Moreover, independent measurements of wave forces and flow rates at exactly these same study sites have shown that no significant differences occur among sites (S. Navarrete & G. Finke unpubl. data).

Differential grazing was also unlikely to have generated the observed patterns in turf growth and height. The most common grazers in the low zone are keyhole limpets and chitons, but their densities do not vary consistently with upwelling (author's unpubl. data and see Fig. 4 of Broitman et al. 2001) as has been reported for small patellid limpets that graze on ephemeral algae in the mid-zone at a subset of these sites (Nielsen & Navarrete 2004). Moreover, neither benthic herbivores nor scrape/bite marks were encountered on experimental turf during monthly observations of transplants. Grazers seem to have little direct effect on established turf, but can indirectly influence turf abundance by foraging on less resistant competitors (Ojeda & Santelices 1984, Santelices 1990, Ojeda & Muñoz 1999).

The microhabitat provided by short algal turf from ECIM strongly facilitated mussel recruitment, a phenomenon observed in many other mussel species (Bayne 1964, Suchanek 1978). Since the competitively dominant *Perumytilus purpuratus* cannot settle onto smooth surfaces (Navarrete & Castilla 1990a, 2003), the presence of recruitment mediators is critical for mussel colonization. In contrast, tall turf from Pichilemu simply did not augment mussel recruitment/colonization. Results from a separate set of experiments conducted across multiple sites and years advocate that these observed differences in mussel recruitment are best explained by turf morphology, rather than by site-specific effects or differences in algal genetic structure. Across the central coast, mussel colonization in the absence of predators was similarly dependent on the height of turf naturally inhabiting sites; mussels quickly colonized sites characterized by short turf, but did not colonize where the turf was tall (E. Wieters, B. Broitman & S. Navarrete unpubl. data). It is still unclear why mussels do not do well in tall turf, but it may inhibit mussels in a variety of ways. Tall turf likely modifies local flow velocity and turbulence differently from short turf, which may negatively influence larval contact with the substrate (Eckman 1983) and explain why relatively few mussel settlers are found in tall turf (mean  $\pm$  SE =  $77 \pm 12.7$  ind.  $100 \text{ cm}^{-2}$ ) as compared to densities in short turf ( $310 \pm 127$  ind.  $100 \text{ cm}^{-2}$ ) or in a matrix of conspecific mussels ( $421 \pm 81$  ind.  $100 \text{ cm}^{-2}$ ) (B. Kelaher & E. Wieters unpubl. data). Alternatively, increased 'whiplash' (Jenkins et al. 1999) and/or sediment deposition (Kelaher 2003b, author's pers. obs.) may be more associated with tall turf, leading to increased physical disturbance of mussel settlers. Tall turf may also diminish food supply for mussel recruits, limiting growth and/or survival. In addition, other aspects of the physical architecture of turf (e.g. surface area, frond density) often covary with height and may play a role in differentially attracting or inhibiting mussel recruits. Whatever the mechanisms, the results are consistent with the hypothesis that turf morphology dictates the relative importance of facilitation, and that the interaction may switch from facilitation to inhibition when long *Gelidium* turf overgrows other recruitment mediators.

Critical examination of the influence of bottom-up processes on the regulation of marine communities is a relatively new endeavor among benthic marine ecologists (Menge 2000b). On rocky shores, bottom-up factors are represented by (1) plankton and particulate matter which influence the growth of sessile filter feeders, which in turn are consumed by carnivores, or (2) nutrients that influence algal productivity. Nielsen & Navarrete (2004) recently described clear upwelling influences on plant–herbivore interactions in the mid-

intertidal zone of central Chile. Stronger upwelling led to increased growth rates of the common corticated alga *Mazzaella laminarioides* but this increased productivity did not propagate up to the herbivore trophic level because this alga is unpalatable to small grazing molluscs. My results reveal a new, previously unforeseen 'path' by which variation in nutrients driven by upwelling can penetrate the benthic food web through the algal turf, eventually determining the input of recruits of a dominant filter-feeding species, *Perumytilus purpuratus*, and potentially propagating up to higher trophic levels when these are consumed by carnivores. Recruitment is likely the most important determinant of sessile invertebrate prey production, as variation is often orders of magnitude greater than that of growth, and can drive the intensity of competition for space and the supply of food for predators (Underwood 1978, Sutherland & Ortega 1986, Navarrete & Castilla 1990b). Cage experiments showed that carnivores readily consume all the mussels that continuously settle into the short turf and, therefore, increased mussel colonization increases food supply and may lead to increased carnivore biomass and stronger top–down interactions. In any case, my results introduce a new mechanism by which upwelling can regulate rocky shore communities, through modifying the strength of a positive interaction between algae and mussels. Interestingly, since upwelling centers are generally locked into position by coastal topography, the locations and spatial extent over which facilitation is likely to be important are predictable and can lead to repetitive, alternating patterns in variation of mussel recruitment rates.

The consequences of trait-dependent facilitation for community structure ultimately depend upon its relative importance compared to other processes (Menge 2000a, Bruno & Bertness 2001). In this case, since carnivores are able to remove all mussels that colonize the short turf in the low intertidal zone, and since mussels do not colonize the long turf, there are no apparent differences in terms of abundance (cover) of mussel beds or algal turfs between upwelling centers and areas downstream from upwelling, leading to remarkably consistent patterns of low-intertidal community structure along central Chile (Broitman et al. 2001). However, this similarity in structure results from contrasting regulatory processes (cf. Robles 1997). In my case, tall turf inhibits establishment of mussels at upwelling centers, whereas predators prevent colonization of mussel recruits in short turf at downstream sites. Thus, facilitation interacts with trophic dynamics to modify the relative importance of predators. Predators are critical in maintaining the short turf by preventing it from becoming overgrown by mussels, but seem to play a non-significant role where the turf is tall.

## CONCLUSIONS

The role of upwelling in community regulation now appears more complex, and multi-faceted, than originally perceived (Menge 2000b). By regulating landscape patterns in facilitator traits (turf height) that determine differences in mussel recruitment over meso-scales (10s of kilometers), upwelling controls bottom-up propagation of prey supply to higher trophic levels in the low intertidal zone along central Chile. At upwelling centers, turf-forming algae grow faster, attain taller heights that repress facilitation of mussel recruitment, and predators play a minor role. At warmer downstream locations, algal turf remains short because it grows slower and is pruned-back in winter. This short turf enhances mussel recruitment, but predators prevent mussels from establishing and are critical in maintaining the turf. In contrast to direct trophic pathways, these results (1) describe a new 'path', via habitat modification and facilitation, by which the effects of upwelling penetrate the food web to link bottom-up and top-down processes and (2) highlight how local, ecological processes can be modulated by those acting over larger scales.

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