

# Report

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## Recruitment tolerance to increased temperature present across multiple kelp clades

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**Abstract.** Kelp systems dominate nearshore marine environments in upwelling zones characterized by cold temperatures and high nutrients. Worldwide, kelp population persistence and recruitment success generally decreases with rising water temperatures coupled with low nutrients, making kelp populations vulnerable to impending warming of the oceans. This response to climate change at a global scale, however, may vary due to regional differences in temperature variability, acclimation, and differential responses of kelp species to changing conditions. Culture experiments were conducted on 12 eastern Pacific kelp taxa across geographic regions (British Columbia, central California, and southern California) under three nitrate levels (1, 5, and 10  $\mu\text{mol/L}$ ) and two temperatures (12°C and 18°C) to determine sporophyte production (i.e., recruitment success). For all taxa from all locations, sporophytes were always present in the 12°C treatment and when recruitment failure was observed, it always occurred at 18°C, regardless of nitrate level, indicating that temperature is the driving factor limiting recruitment, not nitrate. Rising ocean temperatures will undoubtedly cause recruitment failure for many kelp species; however, the ability of species to acclimatize or adapt to increased temperatures at the warmer edge of their species range may promote a resiliency of kelp systems to climate change at a global scale.

**Key words:** distribution; kelp; nitrate; recruitment; temperature; tolerance.

### INTRODUCTION

Many natural systems are characterized by foundation species that disproportionately regulate local productivity and diversity. This is particularly true for marine species that simultaneously provide critical habitat and energy around which their associated communities are assembled (Dayton 1972, North 1994, Bruno et al. 2003, Graham 2004). Variability in the abundance, persistence, and population dynamics of such foundation species can result in wide-ranging consequences for the overall structure of the community and functioning of the ecosystem (Dayton et al. 1984, 1992, Steneck et al. 2002, Graham 2004). Accordingly, community- and

ecosystem-level responses to global change might be predicted by the vulnerability of foundation species to environmental factors (Sunday et al. 2017), especially when such factors affect specific life stages critical to the propagation of the species (Harley et al. 2012).

The identification of marine species as foundational can be challenging, as the experiments necessary to demonstrate their role in provisioning habitat and energy can be difficult to accomplish at ecologically relevant spatial and temporal scales (see Graham et al. 2016 for discussion regarding marine macrophytes). Consequently, researchers often refer to entire clades as having foundational roles in the system (e.g., kelps, seagrasses, hermatypic corals), even though direct evidence of disproportionate roles in habitat and energy provision is generally tested for few (often just one) species within the clade. However, even if most or all species within that clade provide a similar ecological function, it is unlikely that all species within a clade will respond equally to global change, nor will all populations within the species

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geographic range respond similarly. For example, the effect of ocean warming on poleward shifts in marine species distributions (reviewed in Harley et al. 2006) may be species-specific, and equatorward populations may be more adapted or acclimatized to thermal stress than poleward populations. Additionally, phylogenetic relatedness may constrain among-species variability in the response to environmental factors resulting in some taxonomic groups being more susceptible to global change than others (Willis et al. 2008). Understanding the importance of geographic distribution in mediating the responses of species to climate change is, therefore, critical to understanding how potential foundation species will respond to climate change at a global scale.

Kelps (brown algae of the order Laminariales) dominate most temperate nearshore marine systems where rocky substrate is available, and several kelp species have the potential to act as foundation species across geographically extensive spatial scales (e.g., the giant kelp *Macrocystis pyrifera*; Graham 2004, Graham et al. 2007). Kelps are large habitat formers and the photosynthetic engines for some of the most productive ecosystems on the planet (Leigh et al. 1987, Steneck et al. 2002, Graham et al. 2016), with local kelp forests supporting hundreds of associated species (Graham 2004, Graham et al. 2007). More than 100 species of kelp have been described (Druehl 1970), ranging from polar/temperate regions to deep tropical reefs, and inhabiting all continents except Antarctica. Although there is ample evidence that kelp populations are vulnerable to environmental variables linked to global change (Dayton et al. 1999), including wave action (Byrnes et al. 2011), temperature (Novaczek 1984), and nutrient concentrations (Zimmerman and Robertson 1985, Deysher and Dean 1986b), kelp systems are considered more resilient than other foundation species to climate change and human impacts (Halpern et al. 2007). Whereas coral reefs (Pandolfi et al. 2003), seagrasses (Waycott et al. 2009), and mussel beds (Harley 2011) are showing decreases in distribution and function at local to global scales, recent data indicate that impacts on kelps are more equivocal with some populations decreasing, some increasing, and others remaining unchanged (Krumhansl et al. 2016). Such among-population variability in response to fluctuating environmental conditions hampers our ability to make useful predictions of the response of kelp systems to climate change at local to global scales.

The kelp life cycle is bi-phasic, with large macroscopic diploid sporophytes alternating with microscopic haploid gametophytes. Numerous studies have identified microscopic *M. pyrifera* life history stages as more vulnerable to environmental factors than the macroscopic sporophytes (Deysher and Dean 1986a, reviewed in Graham et al. 2007 and Harley et al. 2012) and studies of variable kelp population dynamics as a function of changing climate generally focus on the recruitment of macroscopic sporophytes from microscopic stages as

a critical ecological bottleneck (reviewed by Graham et al. 2007). Here, we orthogonally manipulated temperature and nitrate concentrations in the laboratory to study their effects on the recruitment of a suite of eastern Pacific kelp species over a broad geographic range. We specifically focused on kelp zoospore settlement, germination, gametogenesis, and sporophyte production. Ocean temperature and nitrate concentrations in the eastern Pacific are tightly (and negatively) coupled, and only a few studies have attempted to isolate the main effects and interactions between these two factors on kelp recruitment (Matson and Edwards 2007, Shukla and Edwards 2017). It is generally assumed that nitrate concentrations are the most important in regulating variability in kelp recruitment (Zimmerman and Kremer 1984, Deysher and Dean 1986b); however, the potential role for temperature and its role in modulating the influence of nitrate remains poorly explored on a broad scale. Species-specific studies have highlighted the importance of temperature on gametogenesis and sporophyte production, shown for other regions of the world where variability in nutrient concentrations is not driven by upwelling (Bartsch et al. 2013, Varela et al. 2018). For our study, we hypothesized that favorable levels of one factor may ameliorate the negative effects of stressful levels of the other factor (e.g., high nitrate concentrations would ameliorate high temperature stress). Additionally, we predicted that within a kelp species, populations from more equatorward (warmer, lower nutrient) locations would tolerate higher temperatures and lower nutrient concentrations than more poleward populations, due to adaptation and/or acclimatization to the environmental stressors. Finally, by testing these hypotheses across species from different kelp families we aimed to identify patterns of higher-level taxon responses to determine whether phylogenetic constraints are important in predicting climate change impacts on future kelp distributions and population persistence.

## MATERIALS AND METHODS

We focused our experiments on 12 eastern Pacific kelp species that were abundant in both our poleward “northern” (British Columbia/Washington State) and “central” (central California) regions of interest; 4 of these 12 species were also abundant in our most equatorward “southern” (southern California) region. This species pool included representatives from four of the six main kelp families (Jackson et al. 2017). All species from all regions were able to complete their life cycle and successfully recruit at 12°C, therefore, we considered 12°C to be a suitable temperature for all 12 species. To test the separate effects of temperature and nitrate on sporophyte production, kelp species were cultured in three nitrate treatments (1, 5, and 10  $\mu\text{mol/L}$ ) within two temperature treatments (12°C and 18°C). The two temperatures and three nitrate concentrations were chosen to represent

conditions that were more or less optimal yet within the realistic bounds of variation in the northeast Pacific, either now or in the near future. Species were targeted based on phylogenetic position and relatedness; we cultured species from four of the six families within the order Laminariales. The evolutionary history and distributional patterns of these families vary, potentially resulting in co-occurring kelp species differing in their tolerance to environmental variables (see Appendix S1 for culture and methodology details).

## RESULTS

The laboratory culture experiments showed that increasing temperature from 12°C to 18°C decreased recruitment success for all kelp taxa throughout most of their geographic range, and resulted in complete recruitment failure for most of the species limited in distribution to our northern and central regions (Fig. 1). Nitrate concentrations did not significantly affect final sporophyte

densities in 11 of the 26 comparisons and temperature nitrate interactions were significant in 4 of the 11 comparisons (Appendices S2, S3). Surprisingly, decreased nitrate concentrations never resulted in complete recruitment failure for any species in any region (Appendices S2, S3), sporophytes were produced in all nitrate levels (1, 5, and 10  $\mu\text{mol/L NO}_3$ ) within the 12°C temperature treatment, regardless of species and geographic distribution (Appendix S2). The overarching pattern across the 12 kelp taxa was that recruitment success (sporophyte production) was limited by temperature due to the impairment of sporophyte production in the elevated (18°C) temperature treatment for most species. Species responded to the elevated temperature treatment at different stages within the kelp life cycle and stage-specific responses were associated with geographic distribution (Fig. 1). Six of the eight species found only in the northern and central sampling regions (*Lessoniopsis littoralis*, *Alaria marginata*, *Dictyoneurum reticulatum*, *Nereocystis luetkeana*, *Postelsia palmaeformis*, and *Laminaria ephemera*) were unable to

Present in the northern and central regions only			Settlement	Germination	Gametophyte	Sporophyte	
Alariaceae	<i>Lessoniopsis littoralis</i>	North Center	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	
	<i>Alaria marginata</i>	North Center	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	
Agaraceae	<i>Dictyoneurum reticulatum</i>	North Center	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	
	<i>Costaria costata</i>	North Center	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	
Laminariaceae	<i>Laminaria ephemera</i>	North Center	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	
	<i>Laminaria setchellii</i>	North Center	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	
Arthrothamnaceae	<i>Nereocystis luetkeana</i>	North Center	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	
	<i>Postelsia palmaeformis</i>	North Center	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	<div><div></div><div></div></div>	
Present throughout all regions			Settlement	Germination	Gametophyte	Sporophyte	
Alariaceae	<i>Pterygophora californica</i>	North Center South	<div><div></div><div></div><div></div></div>	<div><div></div><div></div><div></div></div>	<div><div></div><div></div><div></div></div>	<div><div></div><div></div><div></div></div>	
Arthrothamnaceae	<i>Macrocystis pyrifera</i>	North Center South	<div><div></div><div></div><div></div></div>	<div><div></div><div></div><div></div></div>	<div><div></div><div></div><div></div></div>	<div><div></div><div></div><div></div></div>	
		<i>Ecklonia arborea</i>	North Center South	<div><div></div><div></div><div></div></div>	<div><div></div><div></div><div></div></div>	<div><div></div><div></div><div></div></div>	<div><div></div><div></div><div></div></div>
			<i>Egregia menziesii</i>	North Center South	<div><div></div><div></div><div></div></div>	<div><div></div><div></div><div></div></div>	<div><div></div><div></div><div></div></div>

FIG. 1. Response to elevated temperature (18°C) by life history stage, settlement, germination, gametogenesis (gametophyte), and fertilization (sporophyte). Solid (green) circles indicate successful development to the stage indicated, open (red) circles indicate unsuccessful development, and filled in circles indicate that the species was not available in a particular region. Species constrained to the central and northern regions of the study tended to be affected at earlier life history stages. Note that all species completed their life cycles at 12°C regardless of the region of origin.

produce gametophytes at 18°C whether they were close to their southern range limit or not, suggesting that temperature restricts these species to cooler regions by limiting the survivorship and maturation of microscopic gametophytes. *Costaria costata* and *Laminaria setchelli* were the only species with a northern/central distribution that were able to complete their life cycle and successfully recruit at 18°C, though only in the southern part of their range; for northern populations held at 18°C, *C. costata* zoospores never produced gametophytes, and *L. setchelli* gametophytes never matured. Of the four species that were present in all three sampling regions (northern, central, and southern), only *Pterygophora californica* was unable to recruit at 18°C; *P. californica* was able to produce fertile gametophytes at all temperatures in all regions, but sporophytes were never observed at 18°C, suggesting that *P. californica* in the southern region of its range requires periods of cold temperatures for successful fertilization (Matson and Edwards 2007). *Macrocystis pyrifera*, *Ecklonia arborea*, and *Egregia menziesii* produced sporophytes at 18°C in all regions, except the northern population of *E. menziesii*, which produced mature gametophytes, but sporophytes were never observed. These three species are abundant and successful recruiters throughout their geographic range.

#### DISCUSSION

Kelp systems of the eastern Pacific occur in nearshore environments where ocean nitrate concentrations and temperature are tightly correlated. Here, we disentangled the combined effects of nitrate and temperature on the recruitment success of kelp microscopic stages, and, across all species and all treatment combinations, increased temperature was the ubiquitous determinant of recruitment failure and decreased nitrate concentrations alone never resulted in sporophyte production failure. Variable nitrate concentrations are likely important to the success of kelp recruitment during periods of cool temperatures (Appendix S2), as various nutrients are critical to kelp gametogenesis and sporophyte production (Matson and Edwards 2007, Carney and Edwards 2010). Our results, however, suggest that kelp recruitment failure, commonly observed during periods of warm nutrient-poor oceanographic conditions, is most likely driven by the negative effects of high temperature, not low nitrate. This result is useful for the prediction of long-term broad-scale effects of global change on kelp recruitment, as spatial and temporal variability in temperature is more easily and commonly monitored across local to global scales, especially through remote sensing. It is important to state that the abiotic factors tested here affect adult populations of sporophytes as well and may affect them differently. Nutrients and nitrate likely become more important during growth periods when large amounts of biomass are produced.

Despite the nearly universal negative effects of increased temperature on kelp recruitment, sporophyte

production response of individual kelp populations to temperature stress was not uniform. Recruitment failure often correlated with position of the species within the kelp phylogenetic tree (Fig. 2) and the location of each population within its geographic range (e.g., proximity of the population to warmer southern waters). Although among-species variability in the recruitment response to elevated temperature was high, a distinct phylogenetic pattern emerged (Fig. 2). Species from the family Alariaceae were never able to cope with the elevated temperature treatment. Interestingly, *P. californica*, which forms populations as far south as Baja California, Mexico, never produced sporophytes at 18°C. This was true even when sporogenous tissue was collected from reproductive adults in the warmer southern region (this study, Matson and Edwards 2007). Previous studies have suggested that Alariaceae is (1) the oldest kelp family, diverging from the rest of the kelp early in their evolutionary history (Jackson et al. 2017), and (2) a clade that evolved primarily in high-latitude colder regions of the Northern Hemisphere (Lane et al. 2007). As such, the restriction of Alariaceae recruitment success to colder waters makes sense. It remains to be seen whether the sole warm water representative of this family (*Undaria pinnatifida*, which was not tested here) fits this pattern, although its recent introduction to numerous warm temperature systems and dormant life history stages at high temperature (Saito 1975) suggest that it may possess greater tolerance to warm water than the rest of the Alariaceae. The uniform intolerance of the cold-water Alariaceae tested here to 18°C contrasts with the variable levels of tolerance observed in the other three families (Agaraceae, Laminariaceae, and Arthrothamnaceae). The Agaraceae, Laminariaceae, and Arthrothamnaceae each had at least one representative species that was able to tolerate warmer temperature at the southern end of its range, and recruit at 18°C, yet none of these families were uniformly tolerant of warmer water (i.e., some species within a clade tolerated warmer waters, whereas others did not). This phylogenetic pattern suggests that warm water tolerance of kelp recruitment may have evolved multiple times in multiple clades (Fig. 2), or evolved at the base of the Agaraceae, Arthrothamnaceae, and Laminariaceae, and has been lost multiple times. With our current sampling we cannot definitively determine which scenario is most likely, as they are all equally parsimonious. Either way, predictions of species responses to global change (other than the uniformly negative response of the Alariaceae) cannot be made at the family level, as individual species within the Agaraceae, Laminariaceae, and Arthrothamnaceae will respond differently. For example, in the Arthrothamnaceae, *Nereocystis* and *Postelsia* never recruited at warmer temperature, *Egregia* recruited at warmer temperatures in both the central and southern regions, and *M. pyrifera* and *E. arborea* tolerated the warmer water throughout their range. However, to fully test the effects of phylogeny, more data are needed, here we can only describe patterns. Recognizing that

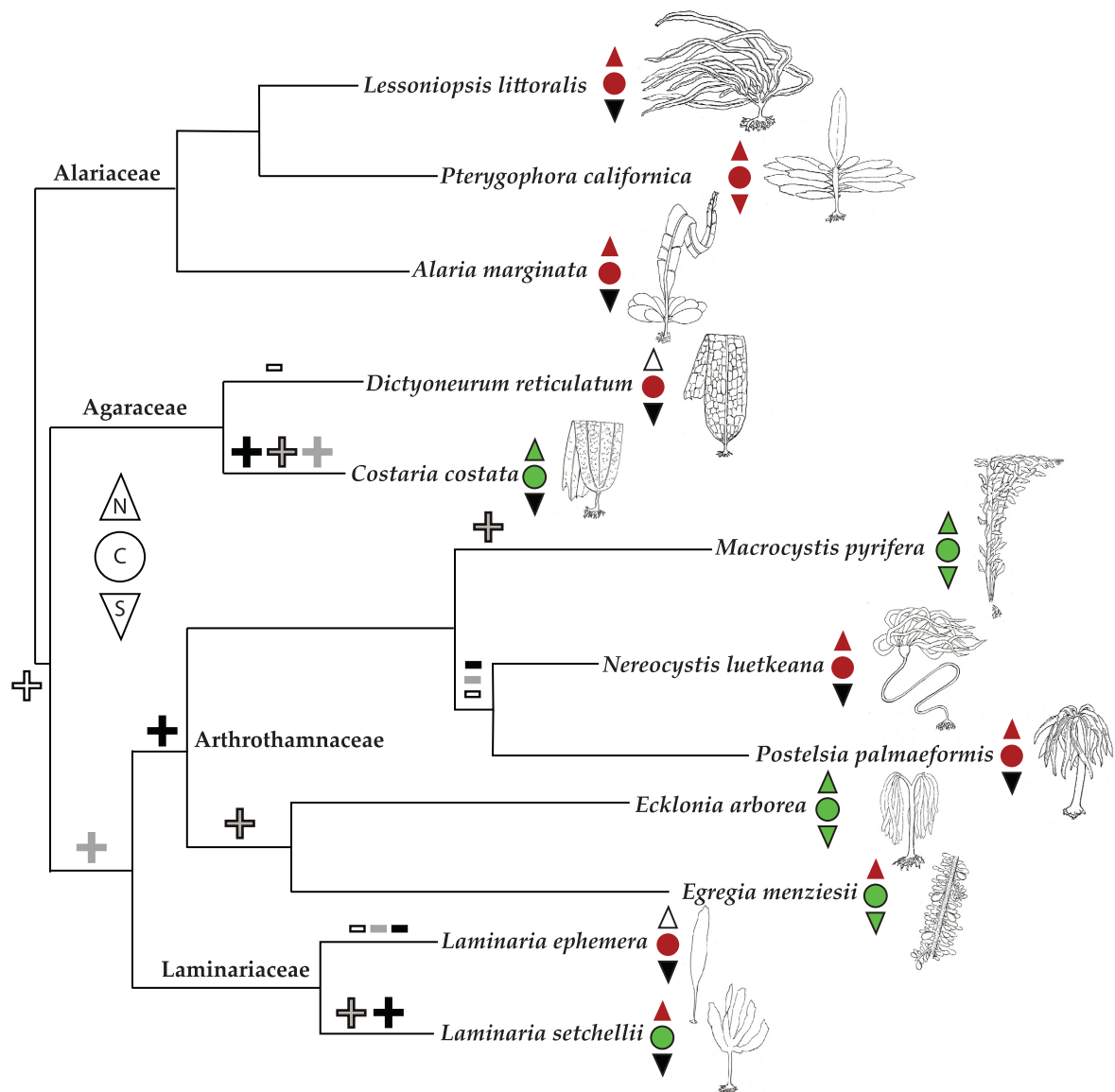


FIG. 2. Phylogenetic relatedness of the kelp species cultured and their response to increased temperature treatment (18°C). Upward pointing triangles correspond to northern regions (British Columbia and Washington), circles to central regions (central California), and downward pointing triangles (southern California) to southern regions. White, not cultured; open (red), could not produce sporophytes in 18°C; solid (green), could produce sporophytes in 18°C; black, outside of their distribution. Plus signs indicate a possible gain of warm water tolerance, with minus signs indicating a loss. Multiple scenarios are possible, represented by the different colors, including gain after the split from the Alariaceae (white), at the divergence from the Agaraceae (light gray), at the base of the Arthrothamnaceae (black) or multiple independent events (dark gray). Drawings by Emily Underwood.

temperature has a more definitive effect on kelp recruitment success than nitrate concentrations allows for more specific predictions to be made on future populations and their distributions as the oceans warm. IPCC sea surface temperatures estimate a 0.6–4°C increase by 2100. Based on results from this study, the Alariaceae would be most vulnerable to such temperature increases, likely shifting their distributions poleward due to decreased recruitment success at southern latitudes. Given that this clade is restricted to the Northern

Hemisphere (except for a few introduced populations of *Undaria* in Argentina, New Zealand, and Australia), and the most abundant Alariaceae populations are at mid to high latitudes (Lane et al. 2007), increasing temperatures may greatly restrict the worldwide abundance of these species. In contrast, although some conspicuous species in the Agaraceae, Laminariaceae, and Arthrothamnaceae will also likely retreat poleward (e.g., *P. palmaeformis* and *N. luetkeana*), some species may be able to tolerate the warming and continue to dominate at lower latitudes.



Interestingly, the two most warm-water-tolerant genera that we studied, *Macrocystis* and *Ecklonia*, have both crossed the equator to establish populations in the Northern and Southern Hemispheres and are abundant in both the warmer and colder regions of their geographic ranges. As such, the evolution of warm water tolerance in the Arthrothamnaceae has likely been critical to the founding of kelp populations (and their associated communities) in the Southern Hemisphere.

Cold-water affinity in kelp families is a basal trait and certain families (e.g., Alariaceae) are dominated by species that are limited to cold-water environments. However, even the Alariaceae contain the invasive kelp *U. pinnatifida*, and this species is tolerant to increased temperatures (Saito 1975). Results from this study reveal multiple warm water adaptation events in multiple families. Increasing ocean temperatures will likely cause the loss of some kelp species, but certain species are either adapted to tolerate high temperatures (e.g., *M. pyrifera*), or exhibit local adaptation and acclimatization (e.g., *C. costata*) that suggests that gene flow and physiological plasticity may prevent the collapse of certain cold-water populations. Each family within Laminariales has a representative species with the ability to tolerate warm temperatures and these species are found on the front lines of the environmental thresholds of kelp persistence and will be important for the longevity of the ecological function of kelp beds in a changing climate.

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## SUPPORTING INFORMATION

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