

## Algal interactions on shallow subtidal reefs in northern New Zealand: a review

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**Abstract** In north-eastern New Zealand, nearshore subtidal reefs are dominated by large brown algae of the orders Fucales and Laminariales. Species of the genera *Carpophyllum*, *Sargassum*, and *Landsburgia* are the most conspicuous fucaleans, whereas *Ecklonia radiata* is the only common laminarian. Three categories of events affect the composition of stands of these algae: first, the competitive effects of adult canopies on recruitment to the substratum below; second, the seasonality of spore release and availability of free space; and third, the demographic characteristics of species and their influence on recruitment. Adult canopies suppress recruitment of all species. Both reproduction and recruitment are seasonal in occurrence and most recruits appear within a few metres of adults of their own species. A comparison of representative Fucales and Laminariales shows important differences in how these taxa colonise substrata. Propagules of fucaleans are larger at settlement and fewer in number than those of laminarians. Compared to laminarians, however, higher numbers of fucalan adults are generally required to form a closed canopy. The number of recruits and the survival of each life history stage are affected by the population structure of algal stands. The importance of the demographic characteristics of individual species in assessing these processes is highlighted.

**Keywords** Laminariales; Fucales; kelp forest; competition; demography; northern New Zealand; life history

## INTRODUCTION

Kelp communities are characterised by mosaics of species. Algae of various sizes form distinct patches and canopy layers. Patches of many sizes may persist for several years, apparently suppressing invasion by other species. The mechanisms responsible for kelp community structure have been examined in several contexts and fall into four categories: (1) competitive interactions among algal species; (2) interactions within species which can affect the size structure and reproductive characteristics of algal populations; (3) herbivory, particularly by sea urchins, which may remove plants from the substratum and create patches of free space suitable for new recruitment; and (4) physical characteristics of the environment, especially light, nutrient levels, temperature, and water motion which can differentially affect species and also the various life history stages within a species. Recent reviews have discussed these topics in considerable detail (Dayton 1985; Foster & Schiel 1985; Schiel & Foster 1986).

Many of the studies carried out in the shallow marine environment in north-eastern New Zealand have centred on algae-dominated communities and have shown that the community structure of large brown algae can be influenced by a suite of common grazers, particularly sea urchins and herbivorous gastropods (Andrew 1988). At the same time, the presence of kelp may affect the abundance and distribution of other species in a community. For example, the structure of habitats and the occurrence of algal stands have been shown to have a major influence on the recruitment of sea urchins (Andrew & Choat 1985), and on the distribution and abundance of reef fish (Ebeling & Laur 1985; Jones 1988; Choat & Ayling 1987). For these reasons, an understanding of the establishment and maintenance of algal populations is essential to an assessment of community dynamics.

The aim of this paper is to review the work done in north-eastern New Zealand on the interactions among algal species. Because algal stands may persist for long periods without being affected by sea urchins, it is of interest to assess the effects of other

processes which influence the establishment and maintenance of algal populations. This paper describes algal distributions at several spatial scales and then discusses interactions between algal species and the life history events that affect these interactions, with reference to the published literature on these topics. The emphasis is on patterns within shallow reef sites (0–8 m depth) where many species of algae are abundant. Much of the work reviewed here was done in the Cape Rodney–Okakari Point Marine Reserve (36°16'S, 174°48'E), for which the habitats have been extensively described (Ayling 1978, 1981; Leum & Choat 1980; Kingett & Choat 1981; Andrew & Choat 1982; Choat & Schiel 1982; Jones 1984a, 1984b; Schiel 1985a).

## DESCRIPTION OF ALGAL COMMUNITIES

An understanding of the processes affecting the production and maintenance of algal communities must be based on a knowledge of the spatial organisation of the important organisms in these communities. Several spatial scales of distribution and abundance of species have been examined around northern New Zealand. Choat & Schiel (1982) described abundance patterns of large brown algae and herbivores along depth gradients at several localities, separated by hundreds of kilometres, and found broad similarities among them (Fig. 1). Along a depth gradient, both the highest numbers and largest biomass of algae occur inshore, in waters shallower than 8 m. The commonest canopy-forming species are *Carpophyllum maschalocarpum*, *C. angustifolium*, *Sargassum sinclairii*, and *Landsburgia quercifolia* (Order Fucales) and *Ecklonia radiata* (Order Laminariales). Sea urchins, *Evechinus chloroticus*, occur mostly in the interstices between boulders inshore but are occasionally found on boulder tops at this depth. At an intermediate depth (8–10 m), larger macroalgae are scarce and *Evechinus* is abundant. High densities of sea urchins and herbivorous gastropods, of  $>5 \text{ m}^{-2}$  and  $>20 \text{ m}^{-2}$  respectively, may persist for many years on extensive areas commonly referred to as "rock flats" (Ayling 1981; Andrew & Choat 1982, 1985). Along deeper areas of reef (11–20 m), *Ecklonia* is virtually the only large algal species encountered. Some fuclean algae may occur in this deeper zone, but they generally do not attain a large size (Schiel 1981).

Despite these broad similarities, there is considerable variation in species composition and abundances between widely spread geographic localities (Choat & Schiel 1982), and also between sites within a single locality. The latter was demonstrated by a survey of the Poor Knights Islands (off north-eastern New Zealand) where there was significant variability in the composition of algal stands between sites only a few hundred metres apart (Schiel 1984).

At shallow depths (about 3–8 m) within sites, species tend to be arrayed in patches, often coincident with the distribution of boulders. For one large reef examined in the Cape Rodney–Okakari Point Marine Reserve, for example, over 70% of boulders had a predominant canopy of a single species, with adjacent boulders often being occupied by different species (Schiel unpubl. data). For experimental purposes, therefore, the importance of within-site variability offers some justification for examining interactions within a localised reef area.

On a smaller spatial scale, several canopy layers are usually present within a stand of kelp. Primary substratum is almost invariably covered by encrusting and articulated coralline algae and various other understorey species of filamentous and foliose red algae. Above this, fuclean and laminarian algae form another canopy. Unlike areas where large, surface-canopy forming kelps occur (Schiel & Foster 1986), the species found in northern New Zealand have a generally similar canopy height of 1–2 m.

## EXPERIMENTS ON COMPETITION

Competition is considered to be one of the main structuring forces in most communities (Connell 1983; Schoener 1983; references in Strong et al. 1984). The patterns of species associations are often highly suggestive that competition is occurring, or has occurred in the past (Connell 1980; Wise 1984; Underwood 1986). Direct evidence for competition, however, requires experimental manipulations and has proved to be much more difficult to gather (Connell 1975; Wiens 1984; Underwood & Denley 1984). Potentially limiting resources are often difficult to measure or manipulate in controlled experiments in nature. In many studies, especially those on marine algal communities, indirect evidence for competition has been gathered by removing a species or altering its

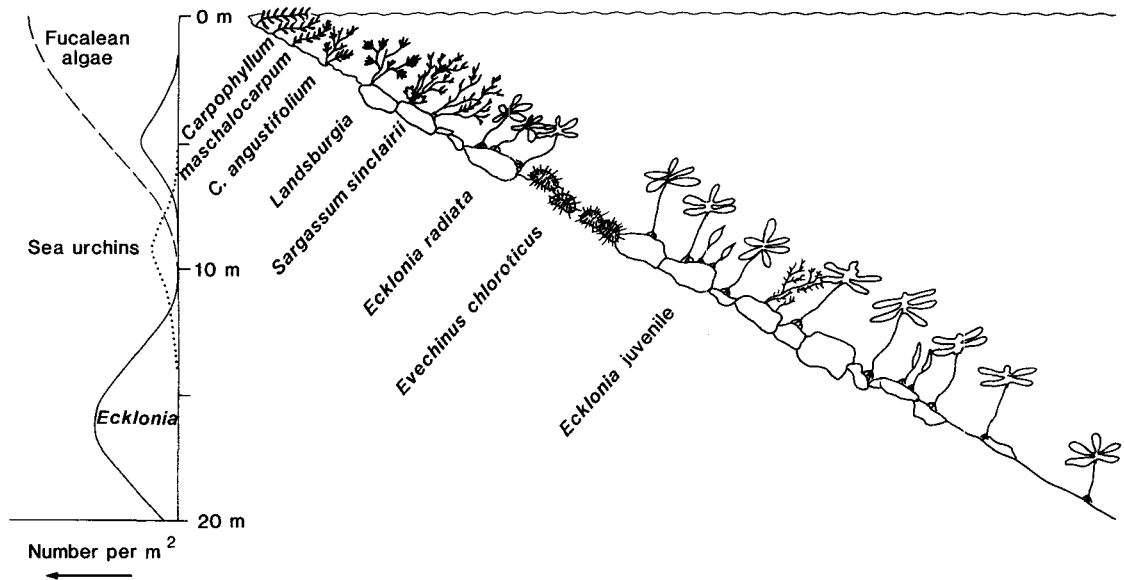


Fig. 1 Schematic representation of the depth distribution of prominent species on shallow reefs.

population density and by measuring the response in terms of growth, survival, reproductive output, or recruitment of another species (Dayton 1975; Dayton et al. 1984; Wise 1984; Underwood 1986).

Observational studies of marine algal communities indicate that competitive interactions may occur among species. Predominantly monospecific patches of kelps may persist for long periods of time, perhaps over a few generations, without significant changes in their borders with other species (Dayton et al. 1984). Many studies have shown or suggested that the canopy of one species may suppress recruitment of all species on the substratum below, thereby preventing the invasion of stands by other species (Black 1974; Kain 1979; Kirkman 1982; Reed & Foster 1984; Santelices & Ojeda 1984; Schiel & Foster 1986). These data offer a relatively simple explanation of how patches of species may be able to persist. Species abundances, however, clearly do change with time (Chapman 1981; Dayton & Tegner 1984; Foster & Schiel 1985). Seasonal or episodic events of mortality due to storms (Cowen et al. 1982; Dayton et al. 1984; Foster & Schiel 1985), grazing (Breen & Mann 1976; Mann 1977; Duggins 1980; Dean et al. 1984), disease and senescence (Andrews 1977; Goff & Glasgow 1980) alter these mosaics and provide the opportunity for new patches to form through recruitment and successional events.

At least two of the potentially limiting resources are increased when adult kelp plants are removed from the substratum. Dense canopies may remove over 98% of light available at the sea surface (Reed & Foster 1984), reducing it to levels below which gametogenesis will not occur (Luning 1981; Deysher & Dean 1984). Not only is adequate light available when canopies are removed, but free primary substratum often becomes available when holdfasts are torn loose (Dayton et al. 1984). Because much of the substratum may be covered by holdfasts and understory species, the availability of free space can affect recruitment of kelp species (Chapman 1984; Reed & Foster 1984; Schiel 1985b). Nutrient levels may also be locally increased by canopy removals, but not much is known about small-scale abundances of nutrients. Large species such as the giant kelp *Macrocystis pyrifera* may deplete nutrients from surrounding waters (Jackson 1977; Gerard 1982), but the effects of smaller kelps on nutrient levels may not be large.

Once canopies have been removed and resources are locally increased, spore availability, settlement success, demographic events, and successional processes interact to determine how available space will be re-occupied.

#### Effects of canopy removals

Several experiments by Schiel (1981) examined the effects of adult canopies on recruitment (i.e.,

appearance of plants visible in the field). The design consisted of three treatments, two involving canopy removals and one a control (Table 1). Removals were initiated in two seasons using predominantly monospecific stands, with replicates randomised among different boulders. These experiments tested: (1) effects of canopy removal of several species; (2) effects of pre-emption of space by new recruits of the cleared species; (3) effects of different intact canopies; and (4) seasonal effects.

Results were similar in many respects for *Ecklonia* and fucal species. After adult *Ecklonia* canopies were removed during spring there was a large recruitment of *Ecklonia* within three months. Where *Ecklonia* recruits were continuously removed, a sparse (i.e., not closed) canopy of *Sargassum* eventually developed in most replicates. Canopy removals during summer allowed *Sargassum* and *Carpophyllum* species to recruit first. These provided only a sparse recruitment, however, and large numbers of *Ecklonia* appeared six to nine months later. During both clearance periods, there was little recruitment of any species beneath intact canopies.

Summer removals of *Carpophyllum* canopies were followed by a large recruitment of fucal species within three months. Where stands were allowed to develop, *C. maschalocarpum* areas returned to dense canopies of that species, while *C. angustifolium* areas developed into mixed stands of *Carpophyllum* and *Sargassum*. The continuous removal of *Carpophyllum* recruits resulted in a sparse cover of *Ecklonia*. Winter removals of *Carpophyllum* canopies were followed by a small recruitment of *Ecklonia* during the following three months and a few recruits of fucal species during the following summer. These clearances did not recover their former abundances of algae. Beneath intact canopies, several species recruited but did not survive.

As in studies elsewhere (Kain 1979; Schiel & Foster 1986), these experiments clearly show that adult canopies suppress recruitment. Other important features are that the invasion of stands by other species depends on the timing of clearances and often requires the removal of recruits of the canopy species. These results are largely explained by the reproductive periodicity and dispersal capabilities of each species and by differences between the life histories of fucal and laminarian algae. These are discussed below.

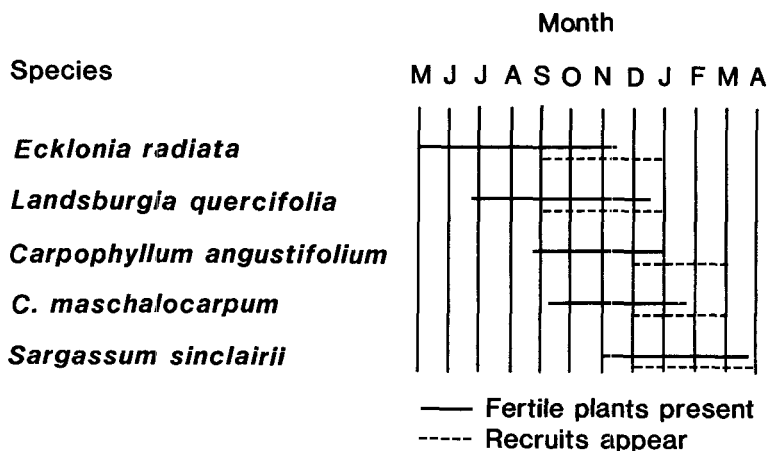
### Periodicity of reproduction and recruitment

The fertility of plants and the appearance of recruits are both distinctly seasonal (Fig. 2). *Ecklonia* is reproductive for the longest period of the year, with some members of shallow populations possessing fertile sori from May to late November (Novacek 1984b). Recruits (about 5 mm in length) appear from September to late December with peak numbers during October to November. *Landsburgia* plants are fertile from July to late December. Recruits appear from September to January, with a peak occurring in October. The fertile periods of *Carpophyllum angustifolium* and *C. maschalocarpum* are relatively similar, occurring from September to January. However, most plants have shed their reproductive structures by early December. Peak recruitment occurs in late December to early January, although recruits continue to appear until March. *Sargassum sinclairii* is the last of the species examined to become reproductive, with plants developing fertile conceptacles in late spring (November to December) and finishing in late summer (March). Peak recruitment occurs during the summer months of January to March. All of these species appear to have fairly consistent patterns of reproduction and recruitment between years (Schiel 1981; Novacek 1984a).

**Table 1** Summary of canopy clearance experiments from Schiel (1981). Clearances of 1 m<sup>2</sup> plots ( $N = 5$ ) of adult plants were done within and outside of the reproductive season (cf. Fig. 2) for *Ecklonia* and *Carpophyllum* stands. Treatments are: 1, canopy clearance and continuous removal of recruits of canopy species; 2, canopy clearance only; 3, canopy left intact as a control. The resulting dominant canopies from these treatments are indicated.

	Clearance of <i>Ecklonia</i>		Clearance of <i>Carpophyllum</i>	
	In Spring	In Summer	In Summer	In Winter
1. Continuous removal	Sparse <i>Sargassum</i>	Sparse mixed fucoids	Sparse <i>Ecklonia</i>	Sparse <i>Ecklonia</i>
2. One removal	<i>Ecklonia</i>	<i>Ecklonia</i> + fucoids	<i>Carpophyllum</i>	Sparse mixed fucoids
3. Canopy intact	<i>Ecklonia</i>	<i>Ecklonia</i>	<i>Carpophyllum</i>	<i>Carpophyllum</i>

**Fig. 2** Periods of the year when plants of the common large brown algae in shallow subtidal populations bear reproductive structures and also when visible recruits appear. Data from Schiel (1981) and Novaczek (1984a).



### Effects of dispersal distance

The removal experiments discussed above showed that recruitment is temporally limited and closely linked to reproductive periodicity for all species. This suggests that the microscopic stages of these algae do not remain viable for long. In addition to these temporal patterns, there is a spatial component to recruitment success. This is indicated by the fact that the species most likely to recruit into a cleared patch is the canopy species. The effective dispersal distances of these algae appear to be only a few metres from fertile adults. Schiel (1981) found that 75% of recruits occurred within 8 m distance from adults for *Ecklonia* and within 3–4 m for *C. maschalocarpum*, *C. angustifolium*, *L. quercifolia*, and *S. sinclairii*. Settlement (i.e., attachment of spores or germlings) may occur over greater distances but little is known about this in natural habitats. The recruitment distances for algae in northern New Zealand, however, are similar to those reported from studies elsewhere (Anderson & North 1966; Dayton 1973; Paine 1979; Deysher & Norton 1982; Dayton et al. 1984; Sousa 1984; Schiel 1985a, 1985b). Most species have no means for long-range dispersal, although the zoospores and sperm are motile over short distances. The exception in northern New Zealand is *S. sinclairii*. As for other species of *Sargassum*, recruits are found near fertile adults, but longer-range dispersal may also occur via drifting fertile plants (Deysher & Norton 1982). Members of this genus are notoriously invasive, and one species in particular, *S. muticum*, has spread over a wide area of Great Britain and the west coast of North America in a short time (Norton 1977, 1981; Farnham et al. 1981; Critchley 1983). In

north-eastern New Zealand, *S. sinclairii* is the major component of drifting algae found during the spring and summer months (Kingsford 1986).

### COMPARISONS OF FUCALEAN AND LAMINARIAN ALGAE

Morphological differences in fucalean and laminarian algae affect their ability to secure space and suppress recruitment. Because adult *Ecklonia* have large primary and secondary laminae, as few as 20 adult plants per m<sup>2</sup> may form a closed canopy. Depending on the species, fucalean algae require 4–10 times this number to have the same shading effects. The layered hapteral holdfasts of *Ecklonia* may be several centimetres wide and occupy more space than do most fucalean holdfasts. These morphological differences become important, however, only after plants have actually settled and begin growing. The life history events that produce these recruits in the first instance are considerably different between the orders of large brown algae. For laminarian algae, millions of zoospores may reach the substratum and some of these eventually develop into gametophytes. When these mature, the female gametophytes must be fertilised, and then microscopic sporophytes develop. These eventually produce visible recruits. This entire process may take several months, depending on the species and conditions (Dayton 1973; Deysher & Dean 1984, 1986a, 1986b; Novaczek 1984b).

Fucalean development is more direct. The *Carpophyllum* species and *S. sinclairii* extrude oogonia, the eggs of which are fertilised while still attached to the receptacles of parent plants. These

develop to a stage where a rhizoid tuft is present (about 200  $\mu\text{m}$  in length), detach from parent plants, and fall to the substratum where they immediately attach by the rhizoids (cf. Norton 1981; Norton & Fetter 1981). After 40–50 days, they are visible as recruits (Schiel 1981).

A comparison of abundances at various life stages shows the orders of magnitude difference between these processes for two representative species (Table 2). Chapman (1984) recorded the abundances of every stage in the life cycle of two species of laminarians. For one species, *Laminaria longicuris*, he found that  $9 \times 10^9$  spores (half of which eventually produce ova) from plants in one area gave rise to about nine million microscopic sporophytes per  $\text{m}^2$  per year. These eventually produced about 1 adult plant. The survival from microscopic recruitment (2N) to an adult stage was  $10^{-5}\%$ . Schiel (unpubl. data) dislodged *Sargassum sinclairii* germlings from parent plants, settled them onto cement plates, and placed the plates onto subtidal reefs. Germling survival was recorded through time. Natural recruits at similar sizes and densities were also followed through to maturity. From one set of treatments, microscopic recruits at an extrapolated density of  $3 \times 10^4 \text{ m}^{-2}$  gave rise to about 1500 visible recruits, and eventually 115 adults developed from these. In this case, survival from microscopic settlement was 0.4%.

These figures will undoubtedly vary depending on many environmental factors. Nevertheless, they strongly suggest that the processes necessary to secure recruitment are different between these two taxa of algae. The potential for recruitment is much greater for laminarians, but this numerical advantage can be offset by the larger sizes, advanced development, and higher survival rates of fuclean germlings.

## CONCLUSION

Competitive processes can be important in structuring algal communities in northern New Zealand. Recruitment of most species is poor

beneath canopies, the removal of which usually results in a large recruitment. It is assumed that light is the primary resource affected by adult plants. Both quantity and quality of light can influence recruitment and development. Reed & Foster (1984) showed that light levels beneath dense laminarian canopies can fall below the levels required for gametogenesis. Blue light is essential for gametogenesis (Luning 1981) and this can be affected by adult canopies. Nutrient levels may also be affected by adult algae, although this has not been shown for stipitate laminarians. Dean & Jacobsen (1986) found that nutrient levels may be stratified only a few centimetres from the substratum. The resource of free space for attachment can also be important but the effects of understory species may be complicated. Possible interactions between understory species and settlers include: shading and pre-emption of space (Foster 1975), biological or chemical inhibition (Breitberg 1984; Johnson & Mann 1986), surface sloughing of cells (Chapman 1984; Breitberg 1984), effects of microscopic grazers (Kennelly 1983), and reduced light and abrasion due to sand and sedimentation in algal mats (Norton 1978; Deviny & Volse 1978).

How important overall are competitive interactions among algae in structuring stands? It appears that major effects are due to canopies, either suppressing recruitment altogether or inhibiting the growth of juveniles. These factors can only be important, however, once algal propagules arrive at an area, and demographic processes of individual species dictate this event. For a species to capture space through recruitment, there are several requirements: (1) the availability of space must occur in a season when plants are releasing spores; (2) the available space must be near fertile adults; (3) spores or germlings must arrive in sufficient quantities for successful recruitment to occur. The probability of successful recruitment therefore depends on the coincidence of these processes plus the availability of adequate nutrients and light.

**Table 2** Comparison of numbers at various life stages for a fuclean and a laminarian. *S. sinclairii* data are approximated from Schiel (1981; unpubl. data). *L. longicuris* data are from Chapman (1984). Numbers shown are in  $\text{m}^{-2} \text{ year}^{-1}$ .

	<i>Sargassum sinclairii</i>	<i>Laminaria longicuris</i>
Potential numbers of ova	$\sim 2 \times 10^6$	$4.5 \times 10^9$
Benthic recruits	$3 \times 10^4$	$9 \times 10^6$
Visible recruits	$10^3$	1–10
Adults	$\sim 10^2$	$\sim 1$

Observations suggest that these factors often do coincide. Stands of *Ecklonia*, *Carpophyllum*, and *Landsburgia* have persisted for 5–10 years despite perturbations (Schiel & Choat unpubl. data). The structure of algal stands changes, however, when these conditions do not co-occur. Throughout the winter and spring months, storms occur of sufficient magnitude to dislodge algae (Schiel 1985a). If *Carpophyllum* spp. are dislodged during winter, *Ecklonia* may capture the space. However, this probably occurs infrequently as *Carpophyllum* species are very long-lived and are relatively resistant to removal by storms and grazing (Schiel 1981, 1982). *Ecklonia* may be removed at any time of the year by episodic storms and occasional grazing by sea urchins, sometimes resulting in the development of patches of other species.

In addition to space availability and proximity to adults, there is considerable variability in the abundance of algal recruits from year to year. For example, in one area the relationship between the number of adults and the number of recruits for the annual alga *S. sinclairii* was different between years (Schiel 1981, 1985a). Self-replacement of a stand occurred for two consecutive years, but recruitment in the following year was not sufficient to maintain the stand.

Whereas studies in several areas of the world have shown that algal canopies can have a suppressive effect on recruitment (review in Schiel & Foster 1986), only a few have provided information on demographic aspects of algal species (Dayton et al 1984; Chapman 1986). Algal studies in northern New Zealand reinforce the argument that such studies of competition are only interpretable when the demographic history of species is known. Furthermore, there is still a need to examine directly in field studies the effects of the resources themselves and also associated factors such as micrograzers and sedimentation.

#### ACKNOWLEDGMENTS

I thank Drs M. S. Foster, R. Cole and an anonymous referee for comments on this manuscript.

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