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From Martin Wahl, Stress Ecology in Fucus: Abiotic, Biotic and Genetic Interactions. In: Michael Lesser, editors: *Advances in Marine Biology*, Vol 59, Oxford: Academic Press; 2011, p. 37-106.

ISBN:978-0-12-385536-7

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STRESS ECOLOGY IN *Fucus*: ABIOTIC, BIOTIC AND GENETIC INTERACTIONS

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Abstract

Stress regimes defined as the synchronous or sequential action of abiotic and biotic stresses determine the performance and distribution of species. The natural patterns of stress to which species are more or less well adapted have recently started to shift and alter under the influence of global change. This was the motivation to review our knowledge on the stress ecology of a benthic key player, the macroalgal genus *Fucus*. We first provide a comprehensive review of the genus as an ecological model including what is currently known about the major lineages of *Fucus* species with respect to hybridization, ecotypic differentiation and speciation; as well as life history, population structure and geographic distribution. We then review our current understanding of both extrinsic (abiotic/biotic) and intrinsic (genetic) stress(es) on *Fucus* species and how they interact with each other.

It is concluded that (i) interactive stress effects appear to be equally distributed over additive, antagonistic and synergistic categories at the level of single experiments, but are predominantly additive when averaged over all studies in a meta-analysis of 41 experiments; (ii) juvenile and adult responses to stress frequently differ and (iii) several species or particular populations of *Fucus* may be relatively unaffected by climate change as a consequence of pre-adapted ecotypes that collectively express wide physiological tolerances.

Future research on *Fucus* should (i) include additional species, (ii) include marginal populations as models for responses to environmental stress; (iii) assess a wider range of stress combinations, including their temporal fluctuations; (iv) better differentiate between stress sensitivity of

juvenile versus adult stages; (v) include a functional genomic component in order to better integrate *Fucus*' ecological and evolutionary responses to stress regimes and (vi) utilize a multivariate modelling approach in order to develop and understand interaction networks.

1. INTRODUCTION

The shifting of environmental variables in the course of ongoing global climate change is expected to impact the performance, and ultimately the distribution, of numerous species in marine coastal systems (reviewed in Harley *et al.*, 2006; Parmesan, 2006; IPCC Climate Change, 2007). Many shallow coastal habitats, however, are defined by a physically demanding environment with steep abiotic gradients and drastic environmental fluctuations at small spatial and temporal scales. Marine organisms living in these intertidal or shallow subtidal habitats are regularly exposed to strong water motion and subjected to extreme fluctuations in temperature, pH, irradiance, salinity or nutrient availability, and the amplitude of these fluctuations far exceeds climate changes predicted for the coming decades (e.g. Thomsen and Melzner, 2010). Although organisms in these habitats cope with ambient abiotic stresses at least to the point of transient tolerance, they must also contend with stressful biotic interactions including competition, epibiosis, parasitism and herbivory, all of which have the potential to modulate the abiotic stresses (e.g. Wahl, 2008b). Understanding how organisms in harsh and fluctuating habitats cope with single and multiple stresses is essential to clarifying and evaluating the risks of global change.

Foundation species in the intertidal/shallow subtidal regions of northern hemisphere temperate coasts frequently include members of the algal genus *Fucus*, which typically consists of three to four zoned species across the intertidal-shallow subtidal gradient (Fig. 2.1). Their ecology, physiology and genetics have been the subjects of intense research during the past four decades, although some species have been studied since the mid-1800s. Thus, results of these many studies provide insights into stress ecology and may form the basis for understanding how global climate change will affect northern intertidal/subtidal habitats.

1.1. The concept of stress

Stress is defined here as the impact of any set of abiotic and/or biotic factors that adversely affects individual 'performance' and ultimately impairs population growth rate through reduced individual survival, growth and/or reproduction (Grime, 1989; Vinebrooke *et al.*, 2004).

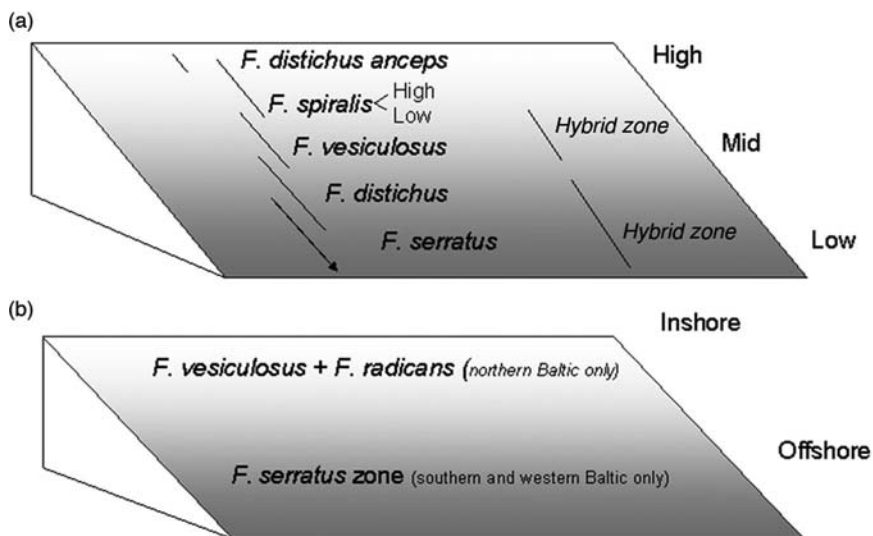


Figure 2.1 Zonation patterns characteristic of *Fucus* species along (a) intertidal and (b) atidal shores of the Baltic Sea.

In this sense, stress is ubiquitous and widespread, particularly at the margins of species' distributions (outside of which population growth remains negative) and at isolated locations within a distributional range.

Stress remains a contentious concept despite its widely recognized importance. Whether or not a factor is considered stressful depends on the target organism; the intensity, duration and recurrence of the stress; and on the various interactions among stresses. As stresses typically co-occur, it is crucial to determine whether a set of stresses is likely to act additively, antagonistically or synergistically, which in turn, will determine whether the combined impact will be minor or detrimental. Understanding interactions and feedbacks is one of the fundamental challenges for understanding ecological dynamics at a variety of scales (Green and Sadedin, 2005; Christensen *et al.*, 2006; Gamfeldt and Kallstrom, 2007) and is a necessary prerequisite for any prediction of responses to changing stress regimes. Nevertheless, most studies of stress have focused on the physiological responses of organisms to an unfavourable variable or set of variables (Crain *et al.*, 2008; Darling and Cote, 2008; Schiel, 2009) without linking those responses to the biotic interactions among the species being stressed or to the underlying phenotypes (Davis *et al.*, 2005; Hughes *et al.*, 2008).

Stresses act as selective agents for stress tolerance. Adaptability of a population therefore is determined by the interaction between the *extrinsic* components of stress—abiotic and biotic factors—and the *intrinsic*

component of stress (Bijlsma and Loeschcke, 2005) estimated as the standing genetic variation. If this evolutionary potential is compromised (i.e. in small, isolated populations or at range margins), then an extrinsic stress will be further magnified. It is now recognized that the temporal differential between ecological and genetic changes can be small or negligible (Spielman *et al.*, 2004). Thus, stress regimes can have a significant and nearly simultaneous impact in both ecological and evolutionary time scales. Understanding this coupling is the major challenge of ecological and evolutionary genomics (EEG) in natural communities (Tautz *et al.*, 2010).

1.2. Background studies and the constraints of monodisciplinary research

General reviews of intertidal/shallow subtidal ecology include Benedetti-Cecchi (2000), Connell (1972), Gruner *et al.* (2008), Menge (1995); for intertidal physiological ecology, see Helmuth *et al.* (2002); for intertidal community genetics, see Schmidt *et al.* (2008) and for environmental change impact on marine ecosystems, see Harley (2006), Helmuth *et al.* (2006), Hillebrand *et al.* (2010), Korpinen *et al.* (2007a), Parmesan (2006), Schiel *et al.* (2004) and Thompson *et al.* (2002). Although fucoids and other macrophytic algae are sometimes included in these reviews, most reviews are overwhelmingly focused on sessile invertebrates (but see Davison and Pearson, 1996).

Research on the genus *Fucus* has produced >1500 publications (excluding purely taxonomic contributions) over the past decades. Although the genus provides a unique system for examining individual, population, species and community level processes, these hierarchical levels have fostered persistent splits in research approaches (see review by Tomanek and Helmuth, 2002). For example, physiological ecologists are interested in testing thermal limits, photosynthetic capacity, desiccation tolerance and osmoregulation of species as the basis for upper-intertidal zonation or geographical range limits. Reviews of physiological stress and photobiology in algae *sensu lato* include Bischof *et al.* (2002), Chapman (1995), Davison and Pearson (1996), Dethier and Williams (2009), Dethier *et al.* (2005), Schiel and Foster (2006), Wiencke *et al.* (1992, 2006). Community ecologists, however, focus on biotic interactions related to competition, epibiosis, predation and defence strategies against the former, as well as on phenology, reproduction, recruitment and life-history traits as the key factors shaping populations and their inter-specific interactions in a community. Specific reviews have been published on the ecology of brown seaweeds in general (Schiel and Foster, 2006), on Laminariales and Fucales (Bartsch *et al.*, 2008), and on the Fucales (Chapman, 1995). Last but not least, molecular ecologists

(who entered the field in the 1990s) focus on the role of genetic variation, fitness, gene flow and selection as the determinant processes leading to adaptation. Consequently, a large body of research has accumulated on the roles of various types of stress on *Fucus* spp. but relatively little integration or synthesis has emerged.

Over the past 15 years physiological and community ecology studies have greatly expanded and become more rigorous, and when combined with advancing molecular approaches, have the potential to elucidate the complex pathways and networks of stress effects. Chapman (1995) focused his review of the genus *Fucus* on the years 1970–1993; our review focuses on subsequent studies.

We begin our review with an overview of *Fucus* and its ecological importance. We then turn to a review of studies on abiotic stresses, both single and multiple, and their reported impacts at different ontogenetic stages of *Fucus* life history. Next we introduce biotic interactions, how they can be shifted by abiotic stresses, and how these shifts may increase or buffer stress effects. Woven throughout this part of the review we also provide the results of a meta-analysis of stress combination studies. We then turn to the genetic level and review what is known about genetic stress and the potential for adaptation in the new perspective of ecological and evolutionary genomics. In the final section, we discuss our conclusions and prospects, aiming to inspire the research agenda for the coming years.

2. METHODS

In addition to a review of individual stress studies, a meta-analysis of multi-stress experiments was performed in an attempt to elucidate general effects of stress combinations on *Fucus*.

2.1. Data search

We searched for articles in Science Citation Index Expanded (ISI Web of Science) that conducted factorial experiments with at least two stresses using the following search parameters: (1) ts = (stress* or salinity or temperature or UV or irradiation or irradiance or desiccation or emersion or pollution or eutrophication or 'nutrient enrichment' or disturbance or osmoregulation or 'wave exposure' or 'wave energy' or 'water motion' or 'wave action' or 'ice scour' or competition or herbivor* or grazing or epibiot* or epiphyt* or fouling or pathogen* or parasit*), (2) ts = (interact* or antagonis* or synerg* or additiv* or non-additiv* or multiple or combined or factorial or experiment*), (3) ts = *Fucus* or fucoid* or fucales or fucaceae. The search yielded a total of 488 papers, but only 41 experiments with fully crossed factorial experiments, adequate replication

and response to stress (measured as a quantitative performance variable) were chosen for our analysis (Table 2.1).

2.2. Data acquisition

Figures were scanned from the original articles and the data (means and standard deviations for the different stress treatments) extracted using GRABIT v. 1.7.2 XP add-in for Microsoft Excel (Datatrend Software, USA). Some papers included multiple experiments from which data could be extracted yielding a final meta-analysis data set with 41 entries. The full data set is available in spreadsheet format in Appendix S1.

Note that for biological stresses (which often use an exclusion treatment to examine the effects of herbivory and competition), the exclusion treatment without the biological stress becomes the stress-free control in our meta-analysis.

2.3. Groupings

All groupings represent trade-offs, especially with respect to the number of studies available. Given the relatively small number of studies meeting our criteria and the large number of stresses tested, we opted for broad categories (Table 2.2).

Data were divided into subsets that included two-way interactions between treatments (i.e. abiotic \times abiotic, biotic \times biotic, abiotic \times biotic, abiotic \times nutrient enrichment and biotic \times nutrient enrichment). Three-way (or higher) interaction experiments were divided into separate two-way treatment combinations. In some cases, a single experiment could be divided and used in several analyses, thus the number of experiments used is larger than the number of articles listed in Table 2.1 and the number of comparisons used in any one grouping differed among tests depending on the combinations. For example, abiotic stress \times nutrient enrichment and abiotic stress \times biotic stress involve 15 and 12 comparisons, respectively. The interaction between nutrient enrichment 1 \times nutrient enrichment 2 was not analysed because only two experiments were found.

2.4. Effect sizes

Calculation of effect sizes followed Hedges *et al.* (1999). For each subset of the data we calculated the log response (effect) ratio (LRR), defined as the dimensionless ratio of the treatment over the control response value (effect = $\ln(\text{stress treatment}/\text{control})$). Thus, a LRR of 0.69 corresponds to a 100% increase in performance of the response variable, and a LRR of -0.69 corresponds to a 50% decrease. Each treatment and combination

Table 2.1 Summary of studies exploring interactions including those articles used for the meta-analysis

Interaction	Focal species	Performance trait	Quality of the interaction ^a	Method ^b	Reference	Used for meta-analysis
Abiotic–abiotic						
Nutrient enrichment × wave action	<i>F. serratus</i> , <i>F. vesiculosus</i>	Growth	X: no interaction of nutrient enrichment and wave action	M	Kraufvelin (2006)	Y
UVR × salinity	<i>F. vesiculosus</i>	Photosynthesis	An: low-salinity stress decreased the sensitivity of <i>F. vesiculosus</i> towards UV	M	Nygard and Ekelund (2006)	Y
UVR × temperature	<i>F. gardneri</i>	Germination rate, germling cell number	An: negative effects of UVR on germination are reduced under high temperatures. Ad: negative effects of UVR and low temperature on cell division	L	Hoffman <i>et al.</i> (2003)	N
Light × temperature	<i>F. vesiculosus</i>	Microbial fouling	An: low light counteracts the microfouling–enhancing impact of warming	L	Wahl <i>et al.</i> (2010)	N

Light × desiccation	<i>F. serratus</i>	Photoinhibition	An: desiccation reduces the photoinhibiting effects of high irradiation	F	Huppertz <i>et al.</i> (1990)	N
Salinity × temperature	<i>F. vesiculosus</i>	Germination	S: hyposalinity impact was enhanced by increasing temperature	L	Maczasek and Wahl (in prep.)	N
Salinity × nutrients	<i>F. vesiculosus</i>	Growth	Ad: low nutrients enhanced the effect of low salinity	L	Nygard and Dring (2008)	N
Desiccation × wave action	<i>F. distichus</i>	Survival adults	S ^c : desiccated thalli experienced a higher wave- induced mortality	L, F	Haring <i>et al.</i> (2002)	N
Nitrate enrichment × phosphate enrichment	<i>F. vesiculosus</i>	Germination	S: negative effect of phosphates enhanced by nitrate addition	L	Bergström <i>et al.</i> (2003)	Y
	<i>F. vesiculosus</i>	Biomass production	Ad: shading decreases biomass	F	Eriksson <i>et al.</i> (2006)	Y

(continued)

Table 2.1 (continued)

Interaction	Focal species	Performance trait	Quality of the interaction ^a	Method ^b	Reference	Used for meta-analysis
Nutrient enrichment × shade			production, nutrients have no consistent effects but tend to vary among habitats of different complexity			
Parental temperature × embryonic temperature	<i>F. vesiculosus</i>	Survival, growth	S: parental exposure to increased temperature enhanced heat-shock resistance of embryos	L	Li and Brawley (2004)	Y
Salinity × temperature	<i>F. vesiculosus</i> , <i>F. distichus</i> , <i>F. virusoides</i>	Growth of germlings	Ad-An ^d : hypo salinities and unfavourable temperature (high and low) affect germlings negatively and the combined effect is	L	Munda and Kremer (1977)	Y

Salinity × temperature	<i>F. vesiculosus</i> , <i>F. spiralis</i>	Survival of embryos	typically less than the sum of single stressor effects An: hypersalinity minimized negative heat- shock effects on survival	L	Li and Brawley (2004)	Y
Biotic–biotic Competition × grazing	<i>F. evanescens</i>	Growth rate	Ad: competition by red algal canopy and grazing impair growth rate	F	Worm and Chapman (1998)	Y
Competition × grazing	<i>F. vesiculosus</i>	Colonization success	Ad to (S) depending on grazer community. Negative effect of competition tends to be accentuated by gastropod grazing	F	Korpinen and Jormalainen (2008a)	Y

(continued)

Table 2.1 (continued)

Interaction	Focal species	Performance trait	Quality of the interaction ^a	Method ^b	Reference	Used for meta-analysis
Epibiotism × grazing	<i>F. vesiculosus</i>	Growth rate	Ad: epibiotism and grazing reduce growth	M	Jormalainen <i>et al.</i> (2008b)	Y
Consumption × parasitism	<i>F. distichus</i>	Endophytism	An: grazing by littorinids and gamarids reduces endophyte infection	F	Parker and Chapman (1994)	N
Grazing × grazing	<i>F. vesiculosus</i>	Defence induction	An: grazing by one consumer species reduces the impact of a second consumer species	L	Yun <i>et al.</i> (2010), Long <i>et al.</i> (2007)	N
Competition × grazing	<i>F. vesiculosus</i> , <i>F. serratus</i>	Cover	Ad: in <i>F. serratus</i> , competition by other canopy-forming algae decreased cover, limpet grazing had no effect. (S): in <i>F. vesiculosus</i> , grazing tended to amplify the negative effect of competition	F	Jenkins <i>et al.</i> (1999)	Y

Competition × grazing	<i>F. serratus</i> , <i>F. vesiculosus</i>	Cover, recruitment	Ad: competition by canopy algae and grazing reduce recruitment, sometimes to a degree that the interactive effect becomes An because there is no room for additive decrease as cover hits zero	F	Cervin <i>et al.</i> (2005)	N
Abiotic–biotic Warming × competition	<i>F. vesiculosus</i>	Cover	(Ad): heat-shock decreases cover development, no effect of inter-specific competition	F	Allison (2004)	Y
Emersion × epibiotism	<i>F. vesiculosus</i>	Fouling resistance	An ^c : emersion reduces fouling (by enhancing anti-fouling	L	Brock <i>et al.</i> (2007)	N

(continued)

Table 2.1 (continued)

Interaction	Focal species	Performance trait	Quality of the interaction ^a	Method ^b	Reference	Used for meta-analysis
Warming × grazing	<i>F. vesiculosus</i>	Growth	metabolite concentration) An ^c : warming reduces grazing by driving a shift from a voracious to the less voracious consumer	F	Moore <i>et al.</i> (2007)	N
Wave exposure × grazing	<i>F. vesiculosus</i>	Cover	S ^d : exposure promotes negative effect of grazing	F	Jonsson <i>et al.</i> (2006)	Y
Wave exposure × grazing	<i>F. vesiculosus</i>	Vulnerability to grazing	An: exposure reduces isopod grazing by toughening of thallus	F	Nietsch (2009)	N
Increasing depth × competition	<i>F. serratus</i>	Abundance	An ^c : competition with <i>F. vesiculosus</i> relaxes in deeper depth	C	Malm and Kautsky (2003)	N
Irradiance × grazing	<i>F. vesiculosus</i>	Palatability	An: light limitation decreases mannitol content and thus attractiveness of	L	Weinberger <i>et al.</i> (2011)	N

			<i>Fucus</i> to isopod grazers			
Increasing depth ^c × grazing	<i>F. vesiculosus</i>	Growth rate	S: negative effect of grazing increases with deeper depth	F	Jormalainen and Ramsay (2009)	N
Increasing depth ^c × epibiotism	<i>F. vesiculosus</i>	Growth rate	Ad: epibiotism and increasing depth reduce growth rate	F	Rohde <i>et al.</i> (2008)	Y
Irradiance × grazing	<i>F. vesiculosus</i>	Anti-grazer defence	Ad: light limitation decreases anti-grazer defences	L	Rohde <i>et al.</i> (2004)	Y
Desiccation × grazing	<i>F. distichus</i>	Growth, reproduction, survival	Ad: desiccation and grazing impair growth and reproduction	F, M	Dethier <i>et al.</i> (2005)	Y
Emersion × grazing	<i>F. distichus</i>	Growth, reproduction	An ^c : emersion reduces grazing pressure (but this was dependent on season)	C	Dethier and Williams (2009)	N
Wave exposure × grazing × competition	<i>F. vesiculosus</i>	Grazing loss	S: grazing pressure shifts from <i>F. serratus</i> to <i>F. vesiculosus</i> under increased exposure	M	Engkvist <i>et al.</i> (2004)	N

(continued)

Table 2.1 (continued)

Interaction	Focal species	Performance trait	Quality of the interaction ^a	Method ^b	Reference	Used for meta-analysis
Wave exposure × grazing	<i>F. vesiculosus</i> , <i>F. serratus</i>	Grazing loss	(Ad): negative effect of grazing but no effect of exposure on overall grazing loss	M	Engkvist <i>et al.</i> (2004)	N
Nutrient enrichment × grazing	<i>F. vesiculosus</i>	Colonization success	(S to An): depending on the grazer community	F	Korpinen and Jormalainen (2008a)	N
Nutrient enrichment × grazing	<i>F. vesiculosus</i>	Colonization success	An ^d : grazers counteract negative (indirect) effects of nutrient enrichment	F	Worm <i>et al.</i> (2001)	N
Nutrient enrichment × epibiotism	<i>F. vesiculosus</i>	Growth rate	S: nutrient enrichment enhances negative effect of epibiotism	M	Jormalainen <i>et al.</i> (2003)	Y
Nutrient enrichment × grazing	<i>F. vesiculosus</i>	Growth rate	An: gastropod grazing counteracts the negative effect (due to increased epibiotism) of	M	Råberg and Kautsky (2008)	Y

Nutrient enrichment × inter-specific competition	<i>F. vesiculosus</i>	Colonization success	nutrient enrichment S: nutrient enrichment enhanced the negative effect of competition	F	Korpinen and Jormalainen (2008a)	Y
Nutrient enrichment × temperature × inter-specific competition	<i>F. serratus</i> , <i>F. evanescens</i>	Germeling growth, germeling survival	S: warming and nutrient enrichment enhance competition effects	L	Steen (2004)	N
Nutrient enrichment × temperature × intra-specific competition	<i>F. serratus</i> , <i>F. evanescens</i>	Germeling growth, germeling survival	Ad: temperature increased competition and reduced growth. S: in <i>F. serratus</i> , negative effect of competition on survival increased with warming and	L	Steen and Scrosati (2004)	Y

(continued)

Table 2.1 (continued)

Interaction	Focal species	Performance trait	Quality of the interaction ^a	Method ^b	Reference	Used for meta-analysis
Season × eutrophication × competition	<i>F. vesiculosus</i>	Germination	nutrient concentration S: eutrophication favours competing annual algae more in spring than in autumn	F	Berger <i>et al.</i> (2004)	N
Nutrient enrichment × grazing	<i>F. vesiculosus</i>	Colonization success	An: negative grazing effect is dampened by negative effect of nutrient enrichment	F	Korpinen <i>et al.</i> (2007b)	Y
Nutrient enrichment × grazing × shade	<i>F. vesiculosus</i>	Number of recruits	Ad: low light, nutrient enrichment and grazing reduce recruitment	F	Eriksson <i>et al.</i> (2007)	Y
Nutrient enrichment × grazing	<i>F. vesiculosus</i>	Palatability	S ^c : nutrient enrichment enhances grazing	L	Hemmi and Jormalainen (2002)	N

Nutrient enrichment × grazing	<i>F. vesiculosus</i>	Growth (apical tip divisions)	(S): nutrient enrichment tended to increase grazing losses	M	Hemmi <i>et al.</i> (2005)	Y
Nutrient enrichment × grazing	<i>F. serratus</i>	Palatability	S ^c : nutrient enrichment enhances grazing	M	Kraufvelin <i>et al.</i> (2006)	N
Nutrient enrichment × competition × grazing	<i>F. vesiculosus</i>	Biomass	An: nutrients enhance competition (when grazers are present)	F	Worm <i>et al.</i> (2001)	Y

^a Ad, additive (sum = A + B), no significant interaction; S, synergetic (sum > A + B), positive interaction; An, antagonistic (sum < A + B), negative interaction; (), indicate a non-significant tendency (0.05 < P < 0.1) and X, no interaction.

^b L, lab experiment; M, flow-through outdoor mesocosm experiment; F, field experiment and C, correlative field data.

^c Interactive effect on algal performance interpreted from non-factorial designs where algal performance was not directly measured.

^d Interaction suggested, but statistical test lacking.

^e Light availability was the main abiotic factor (decreasing with increasing depth).

Table 2.2 Stress groupings used in the meta-analysis

Abiotic stress	Depth
	Desiccation
	Irradiance
	Salinity
	Shading
	Temperature
	Wave action
Biotic stress	Competition
	Herbivory
Nutrient enrichment	Nitrogen and phosphorous enrichment

was compared separately against a ‘stress free’ control (Elser *et al.*, 2007). For each separate experiment we calculated the natural LRRs using the following equations:

$$\text{LRR}_{\text{main effect stress A}} = (\ln \text{Mean}_{\text{A1B0}}) - (\ln \text{Mean}_{\text{A0B0}}) \quad (1)$$

$$\text{LRR}_{\text{main effect stress B}} = (\ln \text{Mean}_{\text{A0B1}}) - (\ln \text{Mean}_{\text{A0B0}}) \quad (2)$$

$$\text{LRR}_{\text{combined effect of stress A and B}} = (\ln \text{Mean}_{\text{A1B1}}) - (\ln \text{Mean}_{\text{A0B0}}), \quad (3)$$

where A and B refer to the different stresses in the two-way interaction. A1 and B1 refer to the treatments with the stresses added, and A0 and B0 refer to the unstressed controls. In order to account for differences in replication and precision associated with individual studies, we calculated average effects of experimental treatments as weighted averages of the natural log response ratios (LRRs) obtained in Equations (1)–(3) (LRR*; Hedges *et al.*, 1999). Statistical significance was tested by calculating the confidence interval around the weighted average (Hedges *et al.*, 1999). An effect was considered significant if the confidence interval *did not* cross the zero line.

Given two stresses, an additive interaction is the sum of the two stresses. While the basic analysis provides an indication as to whether there is a synergistic or antagonistic trend, as compared to a simple additive combined effect, it does not explicitly test for an interaction. Therefore, we conducted a second analysis using the equations developed in Gruner *et al.* (2008). Note that in this analysis we used unweighted effect sizes. In this approach, an interaction effect is additive if the interaction LRR does not differ from zero (i.e. the confidence interval *does* cross the zero line) and thereby generates a true statistical test of whether

the interaction effect differs from additivity. Given two stresses, synergistic interactions are indicated by a negative value and antagonistic interactions by positive interaction LRRs.

3. THE GENUS *FUCUS*

We describe stress ecology using *Fucus* because (1) the genus includes a set of ecologically important foundation species with a wide longitudinal and latitudinal distribution, (2) most *Fucus* species occur in stressful habitats of the intertidal or shallow subtidal and (3) some species (notably *Fucus vesiculosus*) are already experiencing losses and gains in their geographic distributions.

3.1. Global distribution and diversification

Fucus spp. commonly occur along protected and exposed rocky intertidal and shallow subtidal shores (Fig. 2.1), as well as in tidal marshes, over a wide latitudinal gradient within the North Pacific Ocean, North Atlantic Ocean and Baltic Sea (Lüning, 1990). The genus is rare in the Mediterranean, where a single species is found only in the northern Adriatic Sea. Only one species, the cold-adapted *Fucus distichus* (see Coyer *et al.*, 2006a for taxonomic notation used in this review) is found in both the Pacific and Atlantic oceans, ranging from Japan and Alaska in the North Pacific to Svalbard, northern Norway, the White Sea, Iceland and northern Scotland in the North Atlantic (with recent introductions to the North and Kattegat Sea and Bergen Harbor (Wikström *et al.*, 2006; Sjøtun, personal communication). Other species are found only in the North Atlantic (the Pacific occurrence of *Fucus spiralis* likely is an introduction; Coyer *et al.*, 2011a and references therein), where they range from northern Canada and northern Norway/White Sea to the Iberian peninsula, which is the southern limit for many but not all species. For example, while the distributions of *Fucus serratus*/high shore *F. spiralis* and *F. vesiculosus* end in northern and southern Portugal, respectively, the southern form of *F. spiralis* occurs in southern Portugal, the Canary Islands, the Azores and northern Morocco (Coyer *et al.*, 2003; Billard *et al.*, 2010; Zardi *et al.*, unpubl.).

In the North Atlantic, most *Fucus* species are characterized by hotspots of genetic and species diversity in southwestern Ireland and the Brittany peninsula of France or NW Iberia, all putative glacial refugia during the Last Glacial Maximum (Coyer *et al.*, 2003; Hoarau *et al.*, 2007; Coyer *et al.*, 2011c; Neiva *et al.*, 2010). On the other hand, genetic diversity is markedly reduced in populations of *F. vesiculosus* along the North American Atlantic coast a likely signature of postglacial recolonization

from Europe (Muhlin and Brawley, 2009) and in *F. serratus* at the edges of its southern distribution on the Iberian Peninsula (Coyer *et al.*, 2003).

Rapid ecotypic diversification is reflected in patterns of zonation along the shore, as well as morphological variability, hybridization and polyploidy. The ecotypic attributes have resulted in >150 described species, subspecies and forms (www.AlgaeBase.org, Guiry and Guiry, 2010), although recent molecular phylogenetic studies suggest the number of taxa to be <10 (Serrão *et al.*, 1999a; Coyer *et al.*, 2006a; F. Canovas, C. Mota, E. Serrao and G. Pearson, unpubl. data).

The discovery of sibling and/or cryptic species by molecular methods is relevant to both ecological and evolutionary questions regarding stress, because smaller bounds need to be established on the distributions of some species. For example, recent work has demonstrated conclusively that *Fucus radicans* is not an ecotypic variant of *F. vesiculosus* (Bergström *et al.*, 2005), but is a separate species exclusively confined to the northeastern and northwestern Baltic and has evolved in the past 400–2000 years (Pereyra *et al.*, 2009). Other recent studies have revealed that the high- and low-shore form of *F. spiralis* are reproductively isolated (Billard *et al.*, 2010) and allopatric *F. spiralis* found in southern Portugal and North Africa constitutes a new species (Coyer *et al.*, 2011a; Zardi *et al.*, unpubl.).

Hybridization and introgression, which further complicate our understanding of the species' distribution, are well documented between *F. vesiculosus* and *F. spiralis* (Wallace *et al.*, 2004; Billard *et al.*, 2005a,b, 2010; Engel *et al.*, 2005; Coyer *et al.*, 2011a), as well as between *Fucus ceranoides* and *F. vesiculosus* (Neiva *et al.*, 2010), and *F. serratus* and *F. distichus* (Coyer *et al.*, 2002a,b, 2007). Some hybrids (*F. vesiculosus* × *F. spiralis*) or polyploidy variants (*F. vesiculosus*, Wallace *et al.*, 2004; Coyer *et al.*, 2006b) commonly occur, while other hybrids are less fit (*F. serratus* × *F. distichus*) (Coyer *et al.*, 2007).

In conclusion, a confusing taxonomy combined with complex processes of hybridization and rapid ecotypic differentiation make it advisable to genetically identify *Fucus* entities at the outset of any proposed study. With few exceptions (e.g. *F. serratus*, high shore *F. spiralis*, *F. vesiculosus* with vesicles), traditional (visual) taxonomy is unreliable.

3.2. Life history and demography

Fucoid life histories are monophasic with a diploid adult (van den Hoek *et al.*, 1995). Haploid sperm and eggs are produced in numerous conceptacles within each of several large receptacles on apical tips of thallus branches. Reproduction is iteroparous, with both dioecious and hermaphroditic species. Eggs are fertilized close to (or on) the female and the diploid zygotes typically settle and mature within meters of the female

parent (Serrão *et al.*, 1997; Pearson and Serrão, 2006; Schiel and Foster, 2006, and references therein). Limited dispersal of gametes, together with synchronous production of eggs and sperm, increases the probability of selfing and inbreeding in hermaphroditic species (Coleman and Brawley, 2005; Perrin *et al.*, 2007) and possibly breeding among closely related parents in dioecious species.

Fertilization is dependent on both water motion and temperature. Release of gametes typically occurs in *F. vesiculosus* at low turbulence and during daylight (Pearson and Serrão, 2006). Calm conditions are required to ensure fertilization success and facilitate recruitment of the non-dispersive zygotes within the adult habitat. Active photosynthesis is needed to detect turbulence (Serrão *et al.*, 1996b); in the absence of turbulence, photosynthesis depletes dissolved inorganic carbon in the boundary layer covering the thallus and this depletion, in addition to a general semilunar periodicity, is used as one cue for synchronous gamete release (Pearson and Brawley, 1998; Pearson *et al.*, 1998). Fertilization success typically approaches 100% (Berndt *et al.*, 2002). Temporal patterns of reproduction may vary even at the local scale. For example, the reproductive period varies between 4 and 12 months among *F. vesiculosus* populations separated by 100 km or less along the German Baltic coast (K. Maczasek, personal communication). Along the Swedish South and East coast summer- and autumn-reproducing forms of *F. vesiculosus* are heterogeneously distributed with a tendency for a dominance of autumn breeders on the central mainland coast and a dominance of summer breeders along the coasts of islands (Oland and Gotland) (Berger *et al.*, 2001). Autumn recruits are expected to suffer less from sedimentation and competing ephemeral green algae than spring recruits (Berger *et al.*, 2004). Although such differentiation of reproductive phenology may be expected to create temporal isolation and promote genetic differentiation, no genetic differentiation (using five microsatellites) was observed between the summer and autumn reproducing forms (Tatarenkov *et al.*, 2007).

Mortality in fucoids is typically very high during the microscopic stages (Schiel and Foster, 2006). Estimates of survival from an egg to a benthic settler vary from 1.5 to 10%, and from a settler to a visible germling from 5 to 12% (Chapman, 1995). As thalli grow, mortality decreases but remains temporally variable (Wright *et al.*, 2004). Egg production in the well-studied *F. distichus* is about $1 \times 10^5 - 2 \times 10^6$ eggs $\text{m}^{-2} \text{mo}^{-1}$ (Ang, 1991). Of these, only a few hundred per m^{-2} (i.e. less than 0.015%) succeed in the transition to a visible juvenile (Fig. 2.2). *Fucus* spp. typically reach an age of 5–10 years (Chapman, 1995). Due to high mortality of early life-history stages, there is often a paucity of juveniles in the mature stands, rendering populations vulnerable to catastrophic mortality (Dudgeon and Petraitis, 2005).

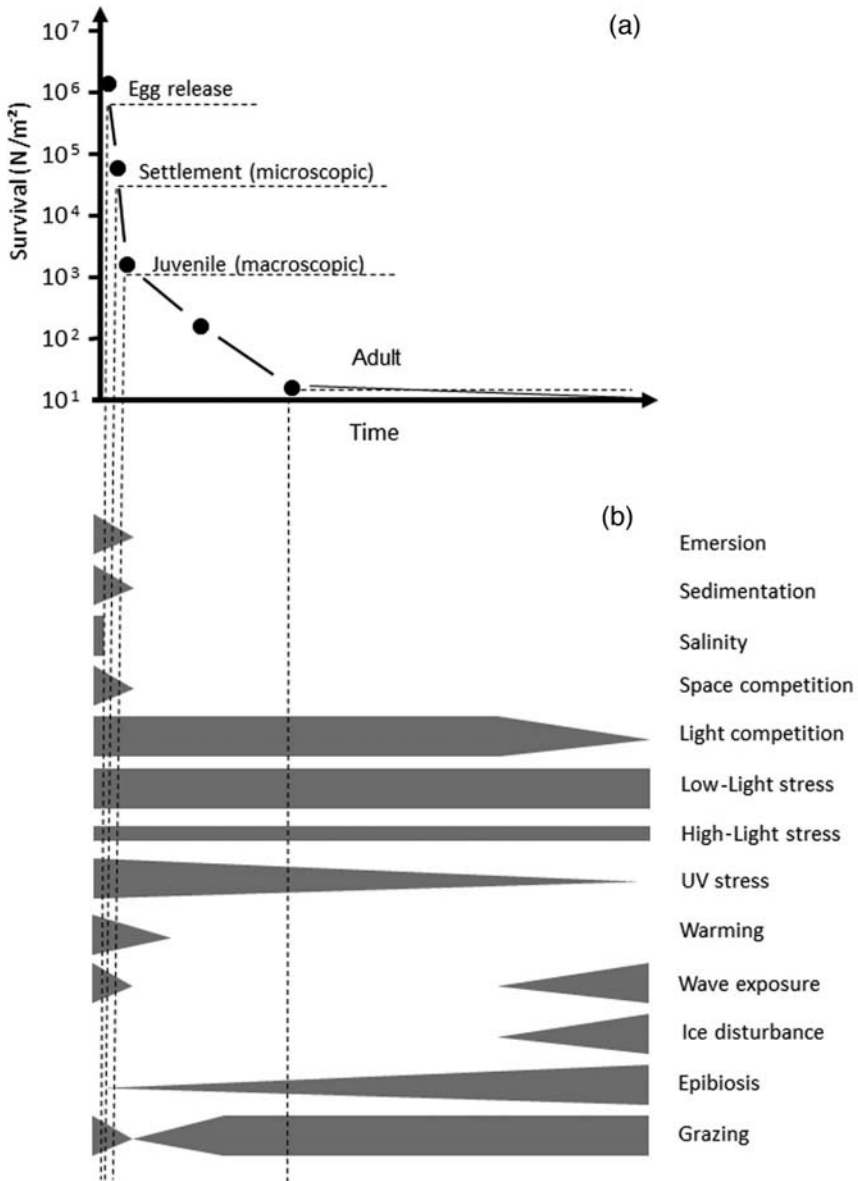


Figure 2.2 (a) Typical survivorship curve of *Fucus* species (expressed as surviving individuals $N\ m^{-2}$) through sequential developmental stages and (b) an indication of the relative sensitivities of the various stages to various stresses. The survivorship curve is an approximation based on data from *F. distichus* (Ang, 1991).

However, two recruitment strategies help counter the high early mortality and contribute to population replenishment. First, the microscopic stages may exhibit delayed growth of several months, which creates a propagule bank under the canopy (Schiel and Foster, 2006). A second strategy involves fragmentation (Tatarenkov *et al.*, 2005) and regeneration (Schiel and Foster, 2006), which allows population re-growth after catastrophic mortality. Asexual reproduction by reattachment of fragments has been documented at high frequency only in *F. radicans* (Tatarenkov *et al.*, 2005). Regeneration of fronds from attached adult holdfasts is common in *F. vesiculosus* (Kiirikki and Ruuskanen, 1996) and allows population recovery after mechanical damage, that is, by ice scour.

Dispersal is highly variable. As distinct rocky intertidal habitats are often separated by soft bottom areas unsuitable for *Fucus* attachment, reproduction takes place mostly among the local individuals (Coyer *et al.*, 2003). Direct estimates of average dispersal distances of furoid zygotes are only a few meters, rarely exceeding 10 m (Dudgeon and Petratis, 2001). Indirect estimates based on spatial auto-correlation and pairwise F_{ST} (θ) analysis suggested a panmictic unit (area of random reproduction) of 0.5–2 km (see Section 5) (Coyer *et al.*, 2003). Long-distance dispersal and gene flow are possible by rafting of intact individuals or detached pieces of receptacle-bearing thalli (Viejo and Arrontes, 1992; Thiel and Gutow, 2005).

3.3. Latitudinal and zonal shifts

Fucus spp. have high photosynthetic rates, surpassing phytoplankton species on a per-unit, bottom-area basis, and provide settlement substratum, food and shelter for a large number of microbial, algal and animal species (e.g. Kautsky *et al.*, 1992; Middelboe *et al.*, 2006; Rohde *et al.*, 2008). Consequently, population, as well as community dynamics of *Fucus* spp. will affect the well-being of numerous community members (Altieri *et al.*, 2007).

In the atidal Baltic Sea, *F. vesiculosus* has declined substantially in large areas over the past 50 years (e.g. Berger *et al.*, 2004; e.g. Vogt and Schramm, 1991, and references therein). The frequently observed upward shift of the lower depth limit has been attributed to direct and indirect effects of eutrophication such as decreased light availability and increased competition and sedimentation (Kautsky *et al.*, 1986; Eriksson *et al.*, 1998; Berger *et al.*, 2004; Korpinen *et al.*, 2007b). However, changes in top-down regulation through a cascading effect of fish abundance on mesograzers abundance may contribute to local shifts by impacting competing filamentous algae (Eriksson *et al.*, 1998) or the recruitment success of *Fucus* spp. (Korpinen *et al.*, 2007a). Ongoing eutrophication in the Baltic changes the composition of *F. vesiculosus* associated invertebrate

community (Korpinen *et al.*, 2010) and the decline of *F. vesiculosus* populations is expected to entail even more substantial changes (Wikström and Kautsky, 2007). Salinity sets the distributional edge for *F. vesiculosus* in the northern Baltic Sea, which is expected to shift southwards with the climate change associated increase in precipitation in the northern catchment area (The BACC Author Team, 2008).

A more complex situation exists along the rocky intertidal shores of the North Atlantic, as at least 2–3 species of *Fucus* commonly co-exist along with the large furoid *Ascophyllum nodosum* and small, high intertidal *Pelvetiaca canaliculata*. Latitudinal range shifts in seaweeds associated with sea surface temperature increases have been documented along the Portuguese coast (Lima *et al.*, 2007). There is also evidence that the southernmost populations of *F. serratus* are maladapted and more vulnerable to stresses than more northerly core populations (Pearson *et al.*, 2009). Although declines in overall abundance of furoids (mostly *A. nodosum*) have been reported from a number of European areas (Davies *et al.*, 2007), the specific changes in coverage of *Fucus* spp. have not been quantified. Reasons for furoid decline have ranged from increased limpet grazing to increased numbers/intensity of storms. Similarly, the relative abundances of *F. vesiculosus*, *F. distichus* and *F. spiralis* are changing in the Canadian Maritimes, where *F. vesiculosus* is gradually increasing its cover within *A. nodosum* beds independent of harvesting regimes (Ugarte *et al.*, 2010). The effect of climate change on range shifts in *Fucus* spp. specifically and along the rocky intertidal more generally is unknown (Thompson *et al.*, 2002). Nevertheless, growing evidence suggests that the distributional ranges of *Fucus* spp. are in a process of reorganization as a consequence of species introductions and stresses associated with climate change, eutrophication and, more indirectly, overfishing (e.g. Ugarte *et al.*, 2010).

3.4. Genomic introductions and invasions

Species introductions are also a major factor in shaping geographical distributions and community dynamics, including competitive displacement. For example, *F. serratus* was introduced to both Nova Scotia and Iceland from Europe within the last 100–200 years and in each area has expanded at a rate of 0.2–0.6 km yr⁻¹ (Coyer *et al.*, 2006c; Brawley *et al.*, 2009). In another example, *Fucus evanescens* (= *F. distichus*) was introduced to the Oslo fjord in the mid-1890s then expanded south into western Sweden (by 1933) and the southwestern Baltic (by 1992), where it experienced less herbivore pressure both compared to native *Fucus* species and to populations in the native range (Wikström *et al.*, 2006; Forslund *et al.*, 2010). While the genus *Fucus* is considered a powerful invader itself (Williams and Smith, 2007), it may be impacted by invaders into its home

range. Thus, the introduced red alga *Gracilaria vermiculophylla* impacts the native *Fucus vesiculosus* doubly, by direct competition and by favouring *Fucus* grazers (*Idotea baltica*) to which *Gracilaria* itself is relatively insensitive (Weinberger *et al.*, 2008).

Another important aspect of species introductions is the notion of genomic invasions (e.g. Mallet, 2005), which can be inter-specific (i.e. congeneric contact between sibling species of *Fucus*) and/or intra-specific (i.e. conspecific contact among different biogeographic populations of a single species). In a natural example of genomic invasion, a process of 'genetic surfing' involving asymmetric introgression and exclusive northward spread of alien (*F. vesiculosus*) organellar genomes following postglacial range expansion in *F. ceranoides* was recently discovered (Neiva *et al.*, 2010). In this case, the background nuclear genome of *F. ceranoides* was observed to retain remarkable integrity despite organellar introgression. Congeneric introductions of *Fucus* species create hybrid zones (as described in Section 3.1), thus complicating species identification and potentially resulting in long-term competitive displacement of parentals through evolution of new lineages via multiple generations of reproductive F1 hybrids, as well as by exchange of genes between parental species (introgression) via backcrossing with hybrids. In extreme cases, extensive backcrossing and interbreeding among hybrids could lead to complete homogenization of parental genomes or a hybrid swarm (extinction through hybridization) (see Coyer *et al.*, 2007).

Perhaps even more worrisome are conspecific introductions that go unnoticed. A new species of *Fucus* might be easily recognized as not part of the local marine flora but a foreign population of a resident *Fucus* species would not be. This is almost certainly the case in Nova Scotia (Brawley *et al.*, 2009) where *F. serratus* was conclusively identified as an introduction from Europe and was of interest because it was not part of the Canadian Maritime flora. However, it is highly probable that European *F. vesiculosus* is also a part of the Canadian *F. vesiculosus* flora although this has not been confirmed. The significance of this from the stress perspective lies in the fact that conspecific hybridization potentially leads to outbreeding depression and lower fitness of an individual or population, as has been shown in intertidal copepods (Edmands *et al.*, 2005). Thus, increased extrinsic stresses might have even greater effects on such populations. Alternatively, it is also possible that intra-population hybridization might simultaneously release beneficial variation and faster development (Edmands, 2008). Doubtlessly, human-mediated transport will increasingly bring hitherto separated species and populations into contact, as will climate change. For example, as the Arctic Ocean opens on a more permanent basis, contact between Pacific and Atlantic biotas will accelerate (Vermeij and Roopnarine, 2008).

4. THE STRESSFUL ENVIRONMENT

While marginal habitats may be dominated by single stresses (e.g. low salinity in the eastern Baltic, low light with increasing depth), environmental change typically involves the simultaneous shift of many stresses (Harley *et al.*, 2006; IPCC Climate Change, 2007; Darling and Cote, 2008; Przeslawski *et al.*, 2008). It is therefore important to understand the nature and influence of single stresses as well as their many combinations.

4.1. Abiotic stress

4.1.1. Single stresses

Single stresses along environmental gradients can influence the performance and distribution of *Fucus* spp. although acclimation and adaptation to marginal and stressful habitats is possible to some degree (Kawecki, 2008). At the largest scale, latitudinal gradients (thousands of kilometres) are governed primarily by sea surface temperatures and light regimes (Lüning, 1990). At regional scales (tens of kilometres) there are transitions between fully marine and low salinity conditions in fjords and estuaries, as well as eutrophication gradients. Finally, the local scale (several metres) includes (1) the intertidal, where desiccation, high light and excessively high and low temperatures (air and water) create sharp and fluctuating gradients over a distance of a few metres and (2) the subtidal, where light and turbulence can be rapidly attenuated by depth, the former being further modulated by plankton blooms, turbidity or epibiosis. Below we provide an overview of the major abiotic stresses and how their effects may vary with *Fucus* life-history stage.

4.1.1.1. Irradiance Light is likely the most variable abiotic component of inter- and subtidal shores (Schubert *et al.*, 2001) and is an obvious essential resource for all photo-autotrophic organisms. Nevertheless, both, an excess and deficit of light are significant stresses. Low-light stress occurs when irradiance is below the light compensation point of a photosynthetic species and compromises carbon accumulation (Lehvo *et al.*, 2001; Middelboe *et al.*, 2006). In the northern Baltic Sea, for instance, the lower distribution limits of *F. vesiculosus* correlate strongly with light penetration through the water; and in exposed areas (low sedimentation) *F. vesiculosus* individuals can survive down to 9–10 m depth (Kautsky *et al.*, 1986; Eriksson and Bergström, 2005). When *F. vesiculosus* of the western Baltic, where the lower distributional limit is about 3 m, is transplanted to greater depths, some acclimation to the resulting low-light stress occurred (Rohde *et al.*, 2008). However, the observed increase in chlorophyll-*a* concentration (by a factor 1.4 following transplantation from 1 to 6 m depth) does not compensate for

the simultaneous decrease in irradiance (by a factor 7.3). With respect to seasonal irradiance regimes, *F. vesiculosus* is able to acclimate by shifting its compensation point between $35 \mu\text{mol m}^{-2} \text{s}^{-1}$ (summer) and $8 \mu\text{mol m}^{-2} \text{s}^{-1}$ (winter) (Middelboe *et al.*, 2006). Similarly, in the northeastern Pacific intertidal *F. distichus* becomes saturated at $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ in summer and $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ in winter (Dethier and Williams, 2009). In the western Baltic the daily dose of irradiation (24 h average) falls below the compensation point of *F. vesiculosus* between October and March at 1 m depth and between August and April at 3 m depth (Wahl, unpublished) but—following the law of reciprocity—a few hours of high light per day may suffice for an equilibrated energy budget. *Fucus* species, like many brown algae, are able to store surplus solar energy in the form of mannitol (Lehvo *et al.*, 2001), which sustains individuals through extended periods of sub-compensation. However, the observation that *F. vesiculosus* can survive the dark winter period in the western Baltic at 1 m depth but rarely occurs at 3 m depth or deeper (Rohde *et al.*, 2008) may indicate limitations in the energy storage. Though it is likely that low-light stress affects all developmental stages equally, smaller individuals are often subject to additional shading by larger neighbours as a result of their understory position. In the western Baltic Sea, the development of juvenile *F. vesiculosus* over a growing season was limited by shade from the adult canopy in a field experiment manipulating both light and canopy cover (Eriksson *et al.*, 2006).

Light exceeding the saturation level for photosynthesis may produce reversible photoinhibition as a protection mechanism or, at more extreme intensities, irreversible photodamage (Huppertz *et al.*, 1990). Photodamage only occurs when the cellular mechanisms of photo-protection are exceeded. Particularly severe stress may be caused by high-energy short wavelengths (UVA and B), which have negligible photo-morphogenic effects, but potentially large photo-destructive effects (Hanelt *et al.*, 1997). *Fucus* species are often exposed to high levels of UV radiation, especially for intertidal populations during emersion. Repair mechanisms or shield compounds can accumulate in tissue to reduce UV stress, but may bear some metabolic cost and, thus, reduce physiological performance. While intertidal populations of *Fucus* exhibit regular photoinhibition, mostly in response to afternoon intensities, photodamage and reduction in physiological performance seem rare (Huppertz *et al.*, 1990; Hanelt *et al.*, 1997; Michler *et al.*, 2002).

The high mitotic activities during germination may be particularly susceptible to UV radiation (Wiencke *et al.*, 2000), although some adaptation to increased UV in particular habitats (e.g. UV absorbing compounds) can be expected. For example, embryos and juveniles of *F. distichus* in the upper intertidal on Spitsbergen, and *F. serratus* in the mid-intertidal on Helgoland, exhibited high sensitivity to UVA and

particularly UVB radiation at natural levels, while upper-intertidal *F. spiralis* from Helgoland were insensitive (Schoenwaelder *et al.*, 2003). UV sensitivity in *F. serratus* was highest at the zygote stage and decreased non-linearly with age (Altamirano *et al.*, 2003). Phenolic phloroglucinol (a naturally occurring monomer of brown algal phlorotannins) tends to be more concentrated in younger tissue and was found to provide UV protection for developing embryos (Schoenwaelder *et al.*, 2003). Early life stages of *F. spiralis* are less sensitive to ultra-violet radiation (UVR) than those of *F. serratus* presumably due to the higher density of phlorotannin-containing physodes in the former (Schoenwaelder *et al.*, 2003).

4.1.1.2. Temperature Temperature stress is typically caused by the long-wavelength range of solar radiation (720 nm–300 μ m), which is photosynthetically inactive, but thermally effective. The severity of stress caused by warming depends not only on the absolute temperature but also on the duration of exposure to it in air (emersion) and water (submersion), and the developmental stage considered. In intertidal areas, both high- and low-temperature stresses are generally more extreme during emersion. While germination success of *F. vesiculosus* is reduced by 90% at 25 °C compared to 15 °C in Kiel Bight (Germany), adults during emersion can survive transitory heating of up to 45 °C (Maczassek and Wahl, unpublished). Moderately warm temperatures, as in many other poikilotherm species, actually increased growth in *A. nodosum* (Keser *et al.*, 2005). Severe high-temperature stress begins when the rate of protein denaturation cannot be neutralized by mechanisms such as increased production of chaperons (heat-shock proteins) or acceleration of protein biosynthesis (Csikasz-Nagy and Soyer, 2008). However, stress can also occur at sub-denaturing temperatures because impaired biochemical pathways may accumulate harmful intermediates (Davison and Pearson, 1996) and/or because repair mechanisms may be costly (Weidner and Ziemens, 1975). Elevated temperatures also negatively influence membrane properties that are crucial for gas exchange and nutrient uptake (Maheswari *et al.*, 1999).

Low-temperature stress reduces metabolic rates, but can be partially compensated by an increase in the concentration of key enzymes (reviewed in Middelboe *et al.*, 2006). Nonetheless, growth may be severely reduced in winter (but see Lehvo *et al.*, 2001; Dethier and Williams, 2009) and biomass losses to grazing, ice scouring or wave action cannot be regained before spring growth. As fucoid tissue can recover from extended freezing (Davison *et al.*, 1989; Pearson and Davison, 1993; Pearson *et al.*, 2000), the primary detriment of ice scouring is physical detachment of the holdfast. In some species, holdfasts remain intact following ice scour and may sprout new fronds in the subsequent growth season (see Section). In the northern Baltic Sea, subtidal *F. vesiculosus*

have two distinct strategies to avoid ice damage (Kiirikki and Ruuskanen, 1996). In exposed areas, pack ice can reach several meters depth and an effective regeneration from holdfasts enables fast recovery of the vegetation in the shallow zone. In sheltered areas, ice forms on the surface and here the large growing individuals decrease their buoyancy during winter, which causes them to lie flat on the bottom and thereby prevent them from freezing into the ice cover.

4.1.1.3. Desiccation Extended exposure to air, especially in summer, can lead to variable degrees of desiccation for intertidal species of *Fucus*. Severe desiccation and the associated osmotic stress, especially when combined with high temperatures and light, can increase mortality (Pearson *et al.*, 2009). For example, increasing duration of daily air-exposure for *Fucus gardneri* (*F. distichus* complex) had a negative effect on the growth rate of the adult thalli, as well as a cumulative negative effect on survival of all life-history stages (Wright *et al.*, 2004).

Juveniles are most susceptible to emersion and associated stresses (Schoenwaelder *et al.*, 2003; Henry and Van Alstyne, 2004). For example, fucoid germlings lose their photosynthetic ability within a few hours of air exposure, although they can recover quickly after re-immersion (Lamote *et al.*, 2007). High mortality may result from desiccation, high light and high temperatures (Dudgeon and Petraitis, 2001; Wright *et al.*, 2004). The smaller life stages, however, may gain a refuge from emersion stress under a canopy of adults (Lamote *et al.*, 2007). For example, germling survival under an intertidal canopy approaches 100%, whereas survival is near zero on adjacent bare rock or on exposed habitats (Brawley and Johnson, 1991).

4.1.1.4. Pollution Pollution is defined as the accumulation of toxic compounds and/or abnormally high levels of nutrients in a local environment and/or tissue. Toxic compounds are an important marine stress because of bioaccumulation (Volterra and Conti, 2000). *Fucus* spp. readily adsorb and accumulate heavy metals (e.g. Mata *et al.*, 2008) with concomitant negative effects on germination and growth (Andersson and Kautsky, 1996; Brooks *et al.*, 2008; Nygard and Dring, 2008). In addition, a biotic toxin (nodularin) produced by cyanobacteria is biosorbed by *F. vesiculosus* and induces oxidative stress (Pflugmacher *et al.*, 2007). Increased nutrient loads mostly affect macroalgae indirectly through increased shading (pre-empting light) (e.g. Vogt and Schramm, 1991) and organic sedimentation (pre-empting space for recruitment; Eriksson and Johansson, 2003). Nutrient enrichment may enhance surface-fouling ranging from biofilms (Wahl *et al.*, 2010) to ephemeral macroalgae (Korpinen *et al.*, 2007b) and epifauna with diverse effects on the host (see Section 4.2). Nutrient enrichment also alters the selective environment favouring fast growing species (Berger *et al.*, 2004) or by

changing the palatability of the thallus to grazers (Hemmi and Jormalainen, 2002). Direct effects arise through high concentrations of nitrate, which delayed attachment and decreased germination success in *F. vesiculosus* zygotes (Bergström *et al.*, 2003).

4.1.1.5. Osmotic stress Salinity stress mostly affects populations in the middle and uppermost intertidal. Rainfall increases the water potential (Ψ) of the environment, whereas evaporation and desiccation obviously decreases the potential. Sensitivity to low-salinity stress varies enormously among *Fucus* species, populations and (presumably) life-history stages (e.g. Pearson *et al.*, 2000). For example, *F. vesiculosus* and *F. radicans* have adapted to the low salinity of the Baltic Sea (Serrão *et al.*, 1996a), but fertilization success in *F. serratus* decreases substantially with strongly reduced salinity: a fertilization success of 87% at 9 psu declines to 5% at 6 psu (Malm *et al.*, 2001). In a western Baltic population of *F. vesiculosus*, however, fertilization success was not affected by salinity between 7 and 17 psu (Maczasek and Wahl, unpublished). Low salinity decreases swimming performance and fertilization ability of fucoid sperm (Serrão *et al.*, 1996a) and increases the rate of polyspermy (Serrão *et al.*, 1999b). The present range of *F. vesiculosus* in the Baltic Sea corresponds to the osmotic tolerance of its gametes (Serrão *et al.*, 1996a), illustrating that environmental factors affecting performance of a particular life-history stage may be important determinants of distributional ranges and colonizing abilities.

4.1.1.6. Water motion Water motion is an important consideration for shallow water organisms; as with light, too much or too little is stressful to an individual. In the case of *Fucus* and other large macrophyte genera, increasing flow speeds and/or wave action increases mechanical stress through increased drag, which must be counterbalanced by structurally resistant thalli and holdfasts (Haring *et al.*, 2002). A negative correlation exists between increasing water motion and thallus size, as evidenced by extensive piles of beach wrack following high wave action. In *F. vesiculosus* and *F. spiralis*, a flow speed of $7\text{--}8\text{ m s}^{-1}$ completely dislodges individuals larger than $\sim 10\text{ cm}$ (Jonsson *et al.*, 2006). Consequently, exposed sites have smaller-sized individuals than sheltered sites, either due to high mortality (especially of the larger individuals) or size reduction by thallus tattering of the larger individuals (Blanchette, 1997). The risk of dislodgement is more pronounced in areas where *Fucus* attaches to pebbles or mussel shells in lieu of bedrock.

One strategy to deal with wave-induced forces is thallus toughening. In both the North Sea and the Baltic Sea, thalli from exposed *F. vesiculosus* were 30% more resistant to tear and breakage as compared with conspecifics from more sheltered sites (Nietsch, 2009). The formation of

bladders on *F. vesiculosus* seems to be a disadvantage under conditions of high turbulence and is negatively correlated with wave exposure (Burrows and Lodge, 1951).

Fucoids enhance fertilization success by releasing gametes only under hydrodynamic conditions that optimize sperm–egg encounters (Pearson and Brawley, 1996; Serrão *et al.*, 1996b; Pearson and Serrão, 2006). Water motion can interact with timing of gamete release during tidal cycles in species-specific ways, affecting gamete and zygote dispersal (Ladah *et al.*, 2008). Low wave exposure is also critical to successful attachment and survival of zygotes (Vadas *et al.*, 1990), and the rate of fucoid recruitment is negatively correlated with wind speed (Lamote and Johnson, 2008). Consequently, water motion strongly influences local distribution patterns of *Fucus* spp. (Ladah *et al.*, 2003, 2008).

Conversely, calm conditions leading to a thicker boundary layer result in a slower absorption of nutrients and CO₂, and a faster accumulation of O₂ and exudates at the thallus/water interface (Jørgensen and Revsbech, 1985). The effects of depletion/enrichment, however, may be compensated for by morphological adaptations, enhancing surface area and thallus rugosity that in turn reduces the boundary layer by enhanced microturbulence (Steen, 2003; Stewart and Embrey, 2003). Furthermore, calm conditions may facilitate sedimentation on algal thalli (Umar *et al.*, 1998), resulting in shading and oxygen deficiency (if the sediment is rich in organic particles) (Kautsky *et al.*, 1986; Duggins *et al.*, 1990). High sedimentation rates on rocky substrata also impede attachment of *Fucus* embryos and decrease the survival and growth of juveniles through scour and burial (Eriksson *et al.*, 1998; Chapman and Fletcher, 2002; Schiel *et al.*, 2006). In field and laboratory bio-assays, increasing amounts of deposited matter have been shown to decrease germling survival of *F. vesiculosus* by >60% (Berger *et al.*, 2003), while experimental removal of sediment in the field increased recruitment twofold (Eriksson and Johansson, 2003). Thus, sedimentation regimes partly define recruitment opportunities of fucoid propagules, and strongly influence distributional patterns at the regional and local scale (Eriksson *et al.*, 1998; Berger *et al.*, 2003; Eriksson and Johansson, 2005).

4.1.2. Simultaneous abiotic stresses

Stresses vary strongly in space and time. Spatial variation is usually linked to habitat properties such as depth, exposure or geographical position. Temporal variations may be rhythmic (diurnal, seasonal, decadal) or stochastic (rainfall, storms). Likewise stress sensitivity of an individual will vary with genotype, life-history stage or physiological phase (Fig. 2.2), which will determine the impact of a given stress at various scales (see Section 3.2). Temporal variations tend to decrease with increasing depth (e.g. Wahl *et al.*, 2010) and lower latitudes. When different stresses

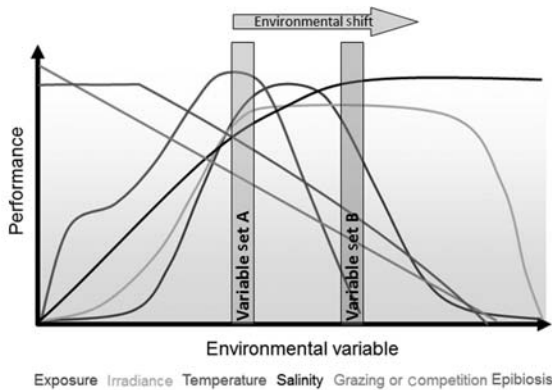


Figure 2.3 Hypothetical effects of single environmental factors on performance. Condition sets A and B exemplify conditions in different habitats or seasons where the combined effects of stressors determine a species' performance. Environmental shift typically realizes as changes in the levels of several stressors, that is, a change in stress regime. If single stressor effects alone are considered, the stressor level with a minimum performance within a set of conditions determines performance. With additive stressor effects, performance is determined by the sum of negative stressor effects. With interactive stressor effects, performance cannot be predicted without knowledge on the quality of the interaction.

fluctuate at different frequencies and/or amplitudes, the variability of their combined action may be complex (Fig. 2.3).

Responses to combined abiotic stresses included antagonistic (5), synergistic (4) and additive (5) effects (Table 2.1). These studies collectively highlight the role of local conditions and local adaptation to stresses, not only in determining tolerance of single stresses but also in modulating the combined stress effects. For example, low nutrients and low salinity together decreased the performance of *F. vesiculosus* in an additive manner (Nygard and Dring, 2008). Antagonistic interactions were found in stresses including temperature, salinity, desiccation and UV, but the type of interaction was sometimes equivocal. In one case, low-salinity stress decreased the sensitivity of *F. vesiculosus* to UV in a population originating from the Atlantic (Nygard and Ekelund, 2006), but in a population from the Baltic Sea, the effects of salinity and UVR were additive. In another example, the combined effect of UV and temperature was either antagonistic or additive depending on the response variable (Hoffman *et al.*, 2003). The microfouling-enhancing effect of warming in one study was buffered by light reduction (Wahl *et al.*, 2010). Similarly, emersion and consequent partial desiccation antagonistically reduced the damage inflicted by high irradiation (Huppertz *et al.*, 1990). Antagonistic interactions were also described for the combination of hyposalinity with unfavourably high or low temperature for various *Fucus* spp. (Munda

and Kremer, 1977), as well as of hypersalinity with stressful heat-shock for *F. spiralis* and *F. vesiculosus* (Li and Brawley, 2004).

As an example of a synergistic stress effect, Maczasek (unpublished) found that experimental reductions of temperature (15–5 °C) and salinity (17–10 psu) lowered germination rates by 15 and 46%, respectively, when acting in isolation; but when the two stresses were present simultaneously, the germination rate was lowered by 90% (the additive expectation being 61%). Other synergistic interactions were found between desiccation and wave action, between additions of different nutrients and between cold-temperature stress at parental stage and heat-shock at embryonic stage (Table 2.1). The last case provides an example of temporally separated synergistic stresses, where a stress in one ontogenetic stage (parent) amplified the stress response in another stage (embryo) (Li and Brawley, 2004).

4.1.3. Meta-analysis of abiotic stresses

Results of the meta-analysis indicated that a single abiotic stress decreased algal performance of *Fucus* spp. by 40–50%, on average, as compared with the control (Fig. 2.4a and b). However, depending on the type of experiment, the average stress effect was significant only in experiments conducted in recruit/germling stages (lab experiments only, Fig. 2.4a) or only with adults (mainly field experiments, Fig. 2.4b).

Averaged over all combinations, the effect of co-occurring abiotic stresses was highly variable but on average additive (Fig. 2.4a, Fig. S1a). The same was true with the combined effect of abiotic stress and nutrient enrichment (Fig. 2.4b, Fig. S1b). It is worth noting that nutrient enrichment alone had neither negative nor positive average effects (Fig. 2.4b). However, behind the average combined effects there was considerable variability of interactive effects within individual experiments (Fig. S1a and b) as noted earlier. This variability illustrates how a second abiotic stress may modulate the impact of a first abiotic stress and how much the outcome depends on the nature of stresses combined and the environmental setting.

4.2. Biotic stress

4.2.1. Single biotic stresses

The biotic stresses of grazing, fouling and competition vary enormously over space and time. For example, the number of grazer and epibiont species decreases from the fully marine North Atlantic Ocean into the brackish Baltic Sea (e.g. Kautsky *et al.*, 1986; Ojaveer *et al.*, 2010) as does genetic diversity (Johannesson and André, 2006). Although the various biotic stresses interact in myriad ways in nature, understanding the effect of single biotic stresses is a necessary first step to understanding the higher order interactions.

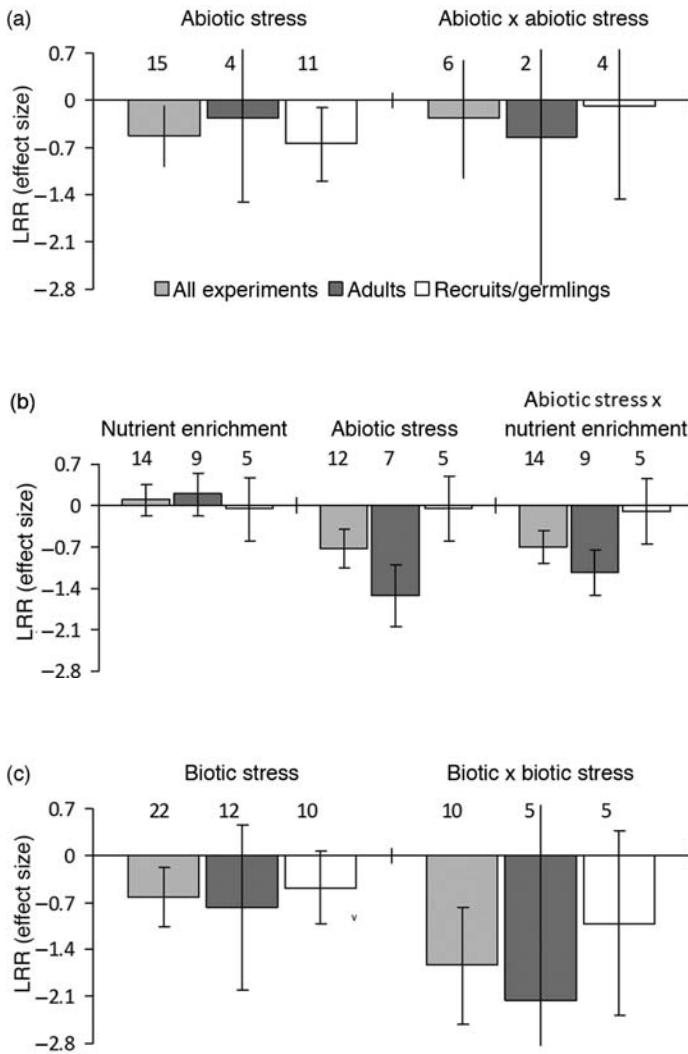


Figure 2.4 Effects of single and combined stresses based on a meta-analysis of 41 experiments extracted from articles in Table 2.1. Effect size (LRR) is plotted against a single stress or stress category (a–f) and their combined effects (see Table 2.2) following the method of Hedges *et al.* (1999). The number of experiments compared is given above each bar. The error bar depicts the 95% confidence interval of the mean effect ratio. When the confidence interval does not include zero, the stress is considered significant. Note that for different meta-analyses (a–f) different sets of experiments were used, which accounts for differences in the magnitude of a particular result. See Section 2 for details of the assumptions and calculations using the method of Hedges *et al.* (1999). See Figure S1 for results based on the method of Gruner *et al.* (2008).

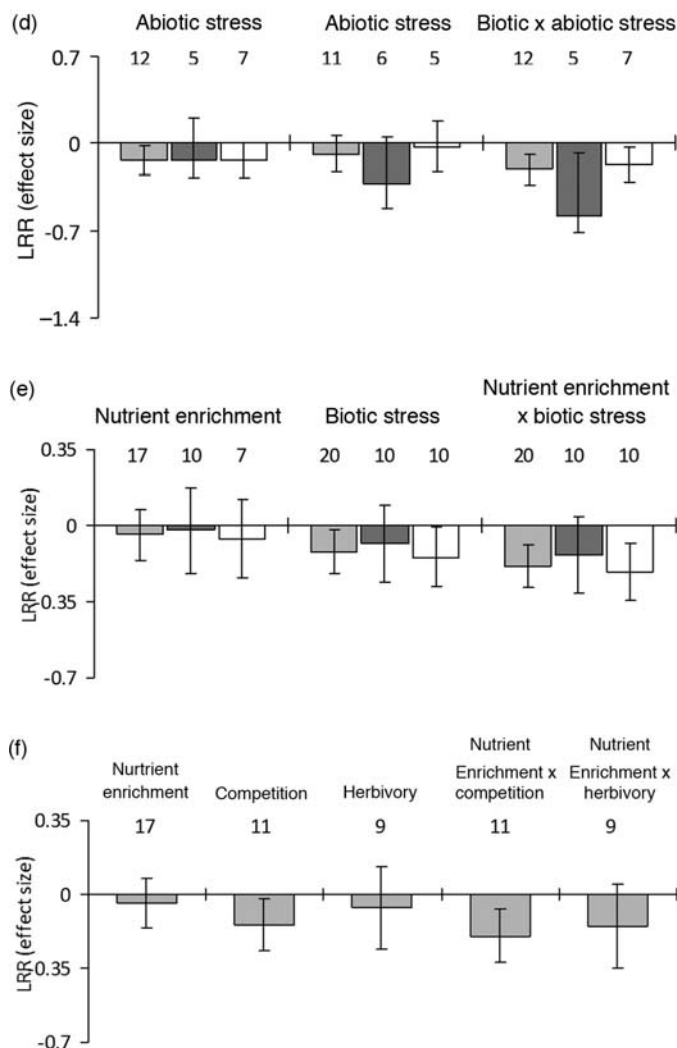


Figure 2.4 Continued

4.2.1.1. Competition and epibiotism The strong intertidal zonation patterns typically exhibited by *Fucus* species (Fig. 2.1), together with other macroalgae and sessile animals, clearly reveals the importance of competition and competitive displacement among these species (reviewed in Karez and Chapman, 1998; e.g. Schonbeck and Norton, 1978; Schonbeck and Norton, 1980). Ultimately, the ability of *Fucus* to persist and successfully compete intra- or inter-specifically is determined by its growth rates (Airolidi, 1998; Johnson *et al.*, 1998), canopy height (Dayton *et al.*, 1984), reproductive output (Malm and Kautsky, 2003),

production of allelopathic compounds (Gross, 2003) and tolerance towards biotic and abiotic stresses (e.g. Worm and Chapman, 1998; Pearson *et al.*, 2009; Schiel, 2009).

Competition for light and space occurs among *Fucus* individuals (conspecifics and congeners), as well as with epibionts attached to their thalli surfaces (Creed *et al.*, 1996; Karez and Chapman, 1998; Karez, 2003a,b). In general, competition varies with ontogenetic stage. For example, periphyton and ephemeral algae may decrease germling survival (Lubchenco, 1983; Lotze *et al.*, 2000), whereas microalgae and sessile invertebrates decrease growth, interfere with nutrient absorption and increase drag on the thallus (Brock *et al.*, 2007; Jormalainen *et al.*, 2008b; Rohde *et al.*, 2008; reviewed in Wahl, 1996; see also Wahl and Mark, 1999; Wahl *et al.*, 2010).

Epibionts on *Fucus* thalli also include bacterial biofilms (microfoulers), a largely unknown interaction that may be important, particularly as a host-specific assemblage of microbes influences many interactions of the host with its environment (Dobretsov, 2008; Lachnit *et al.*, 2009). Furthermore, microfouling pressure is a conditioning phase in the fouling process and varies substantially with temperature, light and depth. For example, in the western Baltic fouling pressure (substratum occupation per unit time) by macroscopic species is 30 times lower in February as compared to July, and the number of simultaneously settling species is 10 times lower in winter than in summer (Thomsen and Melzner, 2010; Wahl *et al.*, 2010). By colonizing the functional interface between the host alga and the environment, dense epibiosis will clearly modulate most interactions of the host (Wahl, 2008a).

4.2.1.2. Herbivory and parasitism Herbivory on *Fucus*, primarily by isopods and, to a lesser extent, by amphipods and snails, ranges from mild to severe and may differentially impact *Fucus* from the germling stage through the adult stage (Pennings *et al.*, 2000; Long *et al.*, 2007; Dethier and Williams, 2009). High grazing rates by isopods (mainly the genus *Idotea*) can eliminate local *Fucus* stands (i.e. Engkvist *et al.*, 2000), while grazing by herbivorous fishes is less common in the distributional range of *Fucus* (Connell and Slatyer, 1977; Floeter *et al.*, 2005).

In the species-poor northern Baltic Sea, grazing pressure by isopods varies seasonally (e.g. Kotta *et al.*, 2006): low in winter (when isopods are inactive) and early summer (when isopod densities are low); high in late summer, which is characterized by high densities of juvenile isopods (Engkvist *et al.*, 2000; Korpinen *et al.*, 2010). Grazing pressure also varies spatio-temporally with exposure (wave action) (e.g. Jonsson *et al.*, 2006) and the patchy distribution of consumers (e.g. Korpinen and Jormalainen, 2008b). Isopod grazing pressure may also vary with fishing pressure on isopod predators (e.g. Bostrom and Mattila, 2005; Jormalainen and

Ramsay, 2009). Simultaneous grazing by several consumer species may interact. Thus, defences developed by *F. vesiculosus* against one herbivorous species may reduce grazing by another species (Long *et al.*, 2007; Yun *et al.*, 2010).

Very little is known about parasitism or infections in *Fucus*. Coles (1958) identified parasitic nematodes that caused galls on *F. vesiculosus* and *F. serratus* along the Cornwall coast and Zuccaro *et al.* (2008) recently detected a number of fungal species associated with *F. serratus*. Unlike *A. nodosum*, which harbours an obligate endophytic fungus (Xu *et al.*, 2008, and references therein), few, if any mycobionts are associated with species of *Fucus* (but see Parker and Chapman, 1994 for impact by endophytes). However, the potential for increased biotic interactions involving invasive parasites or pathogens is on the rise in many marine systems (e.g. Torchin *et al.*, 2002).

4.2.2. Simultaneous biotic stresses

Because *Fucus* exists within a multi-species community, it will simultaneously or sequentially interact with a multitude of micro- and macro-foulers, competitors (annual or perennial macroalgae, sessile animals) and consumers (crustaceans, molluscs), as well as an unknown number of pathogens and parasites. Consequently, the co-occurrence of different biotic stresses is expected to be as common as the co-occurrence of abiotic stresses. However, only few studies have investigated the interactive effects of two or more biotic stresses (Table 2.1).

Several studies illustrate the complexity of interactive biotic effects. The competitive impact of turf algae (Rhodophyta) on *F. vesiculosus* is alleviated by limpet grazing, but not the similarly negative effect of larger canopy algae (Jenkins *et al.*, 1999). Similarly, limpet grazing and competition with turf algae had an additive effect on *Fucus* recruitment, but at the same time limpet grazing inhibited recruitment of *A. nodosum* that has the potential to suppress *Fucus* by canopy effects (Cervin *et al.*, 2005). In another study, epibiotism and grazing had an additive effect on the growth of *F. vesiculosus*, but the effects were functionally interrelated in the sense that fouling attracted grazers (Jormalainen *et al.* 2008b). Finally, in *F. distichus*, grazing by littorinids and gammarids has been reported to reduce the rate of fatal endophyte infections (Parker and Chapman, 1994). Thus, if grazers feed on both the host and the epibiota, epibionts may attract grazers with consequent 'shared doom' for both, epibionts and host. On the other hand, if the epibionts are resistant to grazers, the host may gain associational resistance.

4.2.3. Results of the meta-analysis of biotic stresses

Experiments with two biotic stresses revealed additive (5), synergistic (1) and antagonistic (2) interactions (Table 2.1). The meta-analysis of single

biotic stresses (competition, herbivory and epibiotism) showed a mean 10–50% decrease in performance relative to controls (Fig. 2.4c and d) and no differences in biotic stress responses among life-history stages. With all life-history stages combined, both the single and combined effects of biotic stresses were statistically significant, which was not the case when the data were stratified by life-history stages (Fig. 2.4c). The meta-analysis indicated that the combined effect of two biotic stresses, in general, was additive (Fig. 2.4c, Fig. S1c). Still, the high variation in interaction effect sizes reflects the contingency of multi-stress responses in which interactive effects are more complex and depend on the host spectrum and feeding preferences of the grazers (Wahl and Hay, 1995; Karez *et al.*, 2000).

4.3. Protection against abiotic and biotic stresses

Fucus spp. have evolved several defence mechanisms for a variety of abiotic and biotic stresses. One example is development of an elastic, but tough thallus that resists mechanical damage (e.g. Nietsch, 2009), whereas wound healing and re-sprouting from holdfasts should favour fast population recovery when damage has occurred (e.g. Malm *et al.*, 2001; Tatarenkov *et al.*, 2005). High concentrations of phlorotannins may offer protection from UV radiation (Pavia *et al.*, 1997; Swanson and Druehl, 2002) or deter herbivory (e.g. Hay and Steinberg, 1992; Jormalainen and Honkanen, 2008). Metabolic repair mechanisms of UV damage exist, but may be jeopardized under multiple stresses (e.g. Hoffman *et al.*, 2003). Palatability of *Fucus* species to grazers is affected by a number of lipophilic and polar metabolites; in particular, it is augmented by high concentrations of mannitol and proteinic amino acids, as well as by high water content, and reduced by high concentrations of phlorotannins and high toughness of the thallus (Tuomi *et al.*, 1989; Hemmi and Jormalainen, 2004; Nietsch, 2009; Jormalainen *et al.*, 2011; Weinberger *et al.*, 2011). Although the reduction of nutritive value (e.g. fewer storage compounds such as mannitol) may save energy and discourage grazing (Viejo and Arrontes, 1992; Worm *et al.*, 1999; Engkvist *et al.*, 2004), it may also jeopardize the chances to survive seasons of low energy supply (Lehvo *et al.*, 2001).

Chemical defences are present in many terrestrial and marine species, but their production, storage and ultimate detoxification may well impose fitness costs on the producer (reviewed in Stamp, 2003; Pohnert, 2004). Costs of chemical defence traits have been documented in macroalgae (Dworjanyn *et al.*, 2006; Jormalainen and Ramsay, 2009), but because the relevance of costs varies with resource availability (Davison and Pearson, 1996; Dethier *et al.*, 2005), and may vary with respect to the measured fitness component, costs have not been detected in all studies of chemically defended algal species (Rohde and Wahl, 2008; Pansch *et al.*, 2009; Appelhans *et al.*, 2010). In addition, net defence costs are only expected to

arise under conditions in which natural enemies do not impose significant performance costs and thus when defences are superfluous.

Nevertheless, at least four *Fucus* species employ chemical defences against fouling and herbivory. For example, *F. vesiculosus* alters the composition of epibiotic fouling by producing a combination of pro- and anti-fouling compounds (e.g. Lachnit *et al.*, 2010), and macrofoulers such as barnacles are deterred by secondary metabolites of *F. vesiculosus* (Brock *et al.*, 2007; Jormalainen *et al.*, 2008b; Rohde and Wahl, 2008) and *F. evanescens* (= *F. distichus*, Wikström and Pavia, 2004). Seasonal fluctuations in anti-microfouling chemical activity have been reported in *F. vesiculosus* (Wahl *et al.*, 2010), but whether this is resource-driven (availability of energy) or demand-driven (fouling pressure) and whether similar rhythms exist in anti-macrofouling defences has not yet been investigated. Induced chemical defences against herbivores have been detected in *F. distichus* (van Alstyne, 1989), *F. vesiculosus* (Rohde *et al.*, 2004), *F. serratus* (Rohde and Wahl, 2008) and *F. evanescens* (Rohde and Wahl, 2008). While some chemical defences are produced or deployed at variable intervals after the onset of herbivory ('induced'), they may also be reduced before herbivory is terminated (Weinberger *et al.*, 2011).

4.4. Modulation of stresses

When two negatively interacting species exhibit unequal sensitivities towards a given abiotic stress, the least sensitive species may indirectly benefit, as the more sensitive species is more strongly inhibited. Furthermore, when abiotic stress jeopardizes the production of defence chemicals, the overall stress impact will be magnified. Thus, when the costs of defence and of stress compensation mechanisms must be paid from the same limited resource, defences may decline, subsequently increasing biotic stress between two species. Accordingly, acute abiotic stress should most impact inducible defences that are produced *de novo*, rather than as a by-product of some primary metabolic pathway.

The meta-analysis revealed that, on average, interactions between abiotic and biotic stresses were additive (Fig. 2.4d and e), although there was a wide scatter of variable effects among separate experiments, varying from synergistic to highly antagonistic ones (Fig. S1d and e). Below, we focus on studies examining how abiotic stress modulates various biotic interactions among *Fucus* species, their grazers, competitors and epibiota. Although several studies did not utilize a factorial design, they do provide indirect evidence about the possible type of stress interactions.

4.4.1. Irradiance effects on biotic interactions

Sensitivity to high and low light stress contributes to the patterns of intertidal zonation exhibited by *Fucus* species (Karez and Chapman,

1998). Although epibiont shading may help to protect *Fucus* thalli against excessive irradiation (as shown for other organisms by Przeslawski *et al.*, 2008), the effect is often transient, as epibiota rapidly increase and thus exacerbate light limitation for the host (Oswald *et al.*, 1984). Low light may weaken anti-microfouling defences in *F. vesiculosus* and uncontrolled bacterial fouling, in turn, can reduce available light by more than 90% within a few weeks (Wahl *et al.*, 2010). Low light and fouling had additive negative effects on growth (Rohde *et al.*, 2008) and both macro- and microepibionts may raise the light compensation depth by 2 m in the western Baltic (Rohde *et al.*, 2008). Susceptibility to light stress (and competitive interactions) also is influenced by emersion time. For example, *F. serratus* is more susceptible to high light stress during emersion than *F. vesiculosus* (Malm and Kautsky, 2003) and this can alter local distribution patterns of the species.

Low light stress also affects the susceptibility of *Fucus* spp. to herbivory, although there is no indication that irradiation affects the behaviour of herbivores directly (e.g. Eriksson *et al.*, 2006). For example, light limitation can reduce the production of chemical defences in *F. vesiculosus* thus enhancing consumption by the isopod *I. baltica* (Weinberger *et al.*, 2011). At the same time, reduced growth rates under light limitation (e.g. Rohde *et al.*, 2008) increases the effect of herbivory, as grazed tissue is more slowly replaced; an effect that may be countered by decreased mannitol production in low light, which subsequently renders the alga less attractive to isopod grazers (Weinberger *et al.*, 2011). A synergistic effect of grazing and low light stress has been demonstrated, as grazing losses in *F. vesiculosus* increase under low light, possibly by decreasing resistance to herbivory (fewer defence chemicals) (Jormalainen and Ramsay, 2009).

Deleterious effects of UVR on the defence capacity have been shown in some macroalgae (Cronin and Hay, 1996; Pavia *et al.*, 1997), but not in others (Macaya *et al.*, 2005). While enhanced UVR exposure in various *Fucus* spp. increases phlorotannin concentration (Pavia and Toth, 2000; Schoenwaelder *et al.*, 2003; Henry and Van Alstyne, 2004), it is unclear whether increased levels constitute an anti-herbivore defence or protection from UVR (reviewed in Amsler and Fairhead, 2006). Defence against epibionts is another consideration and in *F. vesiculosus*, is strongest at moderate irradiance (Wahl *et al.*, 2010) or levels typical of its normal depth distribution (1–2 m) in the western Baltic Sea.

4.4.2. Temperature effects on biotic interactions

Increasing temperatures (>15 °C) enhance biotic stress in Baltic Sea *Fucus* by (1) increasing micro- and macrofouling rates (Wahl *et al.*, 2010); (2) increasing grazing rates of *I. baltica* in summer (but not in the other seasons) (M. Zimmer, personal communication) and (3) decreasing levels of defence chemicals (under both high and fluctuating temperatures)

(Weinberger *et al.*, 2011). In contrast, anti-fouling defence chemicals in *F. vesiculosus* were unaffected by a 2-week exposure to temperatures between 8 and 23 °C (Wahl *et al.*, 2010). Thus, temperature and grazing stress can generate synergistic interactions, whereas temperature and fouling stress are additive.

Freezing temperatures can shift competitive interactions among *Fucus* spp. Laboratory experiments revealed that *F. vesiculosus* had a higher tolerance to freezing than its congener *F. serratus*: aerial exposure to −15 °C for 1 h killed *F. serratus*, while *F. vesiculosus* survived (Malm and Kautsky, 2003). Thus, for this species pair freezing and competitive stress is likely to be antagonistic for *F. vesiculosus* (direct physiological stress partially compensated for by reduced competition) and negatively synergistic for *F. serratus*.

4.4.3. Salinity and emersion effects on biotic interactions

Emersion may decrease salinity by removing seawater and/or exposing intertidal organisms to rain and/or freshwater runoff or increase salinity by evaporation. The combination of diverse factors associated with emersion will determine the strength or even the sign of stress during emersion. In *F. vesiculosus*, for example, emerged individuals experienced a transient refuge from aquatic herbivory and epibiont settlement, as well as an accumulation of anti-fouling defence chemicals at the thallus surfaces, which produced a more effective defence after re-immersion (Brock *et al.*, 2007). Thus, emersion and fouling may act as antagonistic stresses.

4.4.4. Water motion effects on biotic interactions

Canopy sweeping or whiplash removes or tatters early post-settlement stages (Vadas *et al.*, 1992) and illustrates how wave action, which is not a strong stress for small individuals or recruits, may be lethally amplified by the presence of larger (con)specific individuals. Thus, whiplash represents a synergistic stress for juveniles and may shift competitive interactions between *F. serratus* and *F. vesiculosus* in favour of *F. serratus* because *F. serratus* juveniles are less sensitive to whiplash (Vadas *et al.*, 1992; Malm and Kautsky, 2003). However, because *F. vesiculosus* can regenerate from hold-fasts, the slight competitive advantage of *F. serratus* recruits ultimately may be negligible (Kiirikki and Ruuskanen, 1996; Malm and Kautsky, 2003; Malm and Isaeus, 2005).

Whiplash also reduces the abundance of competing filamentous epiphytic and understory macroalgae (Kiirikki, 1996), as well as the effect of swimming grazers (either intertidally or subtidally) (Davis *et al.*, 2003), thus creating an antagonistic interaction between wave action and both competition and herbivory. As isopods (*I. baltica*) experience more attachment difficulties on *F. serratus* than on *F. vesiculosus* due to differences in surface morphology, in high water motion grazing intensity is shifted to

F. vesiculosus (Engkvist *et al.*, 2004). Thus, the effects of water motion and grazing in a mixed stand of *F. serratus* and *F. vesiculosus* are antagonistic for *F. serratus* and synergistic for *F. vesiculosus*. Though not tested, it is conceivable that where the two species compete, *F. serratus* may benefit from a combined wave action and grazing stress, as long as *F. vesiculosus* density remains at or above some threshold level. In the more exposed mid- to high-intertidal zone, non-swimming grazers such as limpets (*Patella vulgata*) are dominant and their grazing preference for *F. vesiculosus* and *F. spiralis* over *F. serratus* further affects the competitive hierarchy by allowing *F. serratus* to move upshore (Jonsson *et al.*, 2006). An additional consideration is that while the risk of thallus dislodgement is higher at wave-exposed sites, water motion may indirectly lead to reduced grazing by inducing increased toughness of the thallus (Nietsch, 2009).

4.4.5. Eutrophication effects on biotic interactions

Nutrient enrichment has been the most frequently studied abiotic modifier of biotic interactions, with individual responses being additive (2), antagonistic (3) or synergistic (9) (Table 2.1).

With respect to nutrient enrichment–herbivory interaction, grazers counteract the negative effect of high nutrient availability on colonization success of *F. vesiculosus* by reducing competition for space (Lotze *et al.*, 2000). In later stages, gastropod grazing counteracts nutrient stress by removing epibiota (Jormalainen *et al.*, 2003; Råberg and Kautsky, 2008). Field experiments on *F. vesiculosus* in the Baltic Sea (where abundant gastropod grazers regularly graze early recruits and nutrient enrichment severely restricts recruitment success) showed that negative effects of grazing and nutrient enrichment on recruitment success remained additive, but varied depending on the community structure of other grazers (Korpinen and Jormalainen, 2008a) and the presence of canopy species (Eriksson *et al.*, 2007). On the other hand, synergistic effects of nutrient enrichment and herbivory may arise when nutrient enrichment improves the nutritional quality of *Fucus* thalli. Thus, high-quality *Fucus* tissue greatly benefits growth and reproduction of *I. baltica* (Hemmi and Jormalainen, 2002) and the amphipod, *Gammarus locusta* (Kraufvelin *et al.*, 2006), which concomitantly leads to higher grazing pressure. Palatability of *F. vesiculosus* to littorinid grazers also increases as a result of increased nutritive value (increased N: Yates and Peckol, 1993; increased mannitol: F. Weinberger, personal communication). Finally, negative effects of grazing on *F. vesiculosus* may be stronger under increased nutrient conditions (Hemmi *et al.*, 2005).

With respect to nutrient enrichment and competition, interactions were mainly synergistic (Table 2.1), suggesting that nutrient enrichment benefits competitors/epibiota of *Fucus* more than *Fucus* itself (Jormalainen *et al.*, 2003, 2008b). As expected, growing *F. vesiculosus* in

a nutrient enriched environment without epiphytes positively affected growth (Jormalainen *et al.*, 2003). Thus, two effects of epibiosis have a synergistic impact on their *Fucus* host by shading and inhibiting nutrient uptake (through insulation or a 'smothering' effect). Furthermore, nutrient enrichment may completely reorganize competitive hierarchies as eutrophication typically favours ephemeral, fast growing algae (Berger *et al.*, 2004) at the cost of slow growing perennials (Korpinen *et al.*, 2010).

The addition of an abiotic stress to two biotic stresses may render the biotic–biotic interactive effects more complex and non-additive. For example, under ambient levels of nutrients, grazers had a large positive and competitors a slightly negative effect on growth of *F. vesiculosus* recruits, with an additive or a minor synergistic interaction (Worm *et al.*, 2001). Under nutrient enrichment, however, the combined effect turned highly antagonistic as the increased competition cancelled out the positive grazing effect.

4.4.6. Biotic modulation of abiotic stress

Biotic interactions may, in turn, modulate the impact of abiotic stresses. Thus, as shown for non-*Fucus* spp., epibionts may protect their host from UVR radiation and desiccation stress (Penhale, 1977; Przeslawski *et al.*, 2008). However, they may also render the fouled host more vulnerable to drag (Witman and Suchanek, 1984; Wahl, 1997). Furthermore, canopy-forming algae, which might act as inter- or intra-specific competitors, may at the same time shelter small *Fucus* from abiotic stress during emersion (Brawley and Johnson, 1991; Lamote *et al.*, 2007).

Results of the meta-analysis showed that the average combined effect of herbivory or competition (or both) with nutrient enrichment did not differ from additivity (Fig. 2.4e and f). However, the nutrient enrichment–herbivory interaction was less consistent than the nutrient enrichment–competition interaction, which was also found in the individual studies.

5. GENETIC LEVELS OF STRESS RESPONSE

On a temporal scale, responses to stress range from fast acclimation by phenotypic plasticity to slower adaptation by stress-driven selection (i.e. adaptive evolution or ecotypic differentiation). The efficacy of both relates to an individual's or a population's genetic composition. Traditionally, physiologists and ecologists have been more interested in immediate responses, while population geneticists have been more interested in changes over multiple generations (Allendorf and Luikart, 2007). However, it is now realized that the temporal differential between ecological and genetic changes can be small or negligible and most species

are not driven to local extinction before genetic factors play a role (Spielman *et al.*, 2004). In short, dynamic selective regimes in the environment can have a significant and nearly simultaneous impact on both ecological and evolutionary processes, which subsequently shape genetic structure and performance of populations. The ability to distinguish these effects is an emerging challenge.

5.1. Sensitivity versus genetic diversity of a population: stress from the evolutionary perspective

The extrinsic component of stress (abiotic and biotic factors in the environment) shapes the phenotype through natural selection and leads to changes in allele frequencies and new gene complexes, collectively resulting in adaptation (i.e. the integration of the phenotype with the genotype). But it is crucial to also recognize the intrinsic component of stress tolerance (Bijlsma and Loeschcke, 2005), estimated as the standing genetic variation or diversity (evolutionary potential) of a population.

Genetic diversity stems from the relationship between the effective population size (roughly the number of individuals that successfully contribute to the next generation) and the processes of gene flow, selection, genetic drift and mutation. Effective population size (N_e) is a crucial parameter for assessing the adaptive potential of a population. Large sexually reproducing populations with high N_e have more genetic diversity and collectively experience fewer negative ramifications from the stochastic effects of genetic drift (random gain and loss of alleles through time). Moreover, at least some individuals within large populations are likely to have genotypes that are already able to cope (pre-adapted) with a new selective pressure such as a higher temperature. In contrast, populations with low N_e —often arising from habitat fragmentation or isolation—tend to have less genetic diversity, are highly subject to the negative effects of genetic drift, and are collectively more likely to be affected by stress due to their low adaptive potential (Harley *et al.*, 2006). As pre-adapted genotypes in these populations would be few or absent, it follows that they also are at higher risk of local extinction. Estimating N_e is extremely difficult. Direct estimates require extensive tagging studies over long time periods, whereas indirect estimates are based on temporal changes in allelic frequencies. Recent work on *F. serratus* using microsatellites suggested that despite large census population sizes N_e was very small with a concomitant loss of fitness (Coyer *et al.*, 2008). If loss of genetic variation is combined with a deteriorating environment, then a negatively synergistic effect is likely to arise in which a population's susceptibility and tolerance to extrinsic stress is magnified.

5.2. Indirect detection of adaptation to stress on relevant spatial scales

Neutral loci are not under selection and as they are affected only by gene flow and genetic drift, cannot be used to directly measure adaptation. Neutral loci do, however, provide necessary basic information for studies of adaptation by resolving genetic population structure, measuring gene flow and providing indirect evidence for adaptation when correlated with environmental parameters.

Genetic population structure can identify spatial scales over which selection (e.g. adaptation to stress at a population level) may act and has been assessed at one or more spatial scales for *F. serratus* (Coyer *et al.*, 2003; Hoarau *et al.*, 2007), *F. vesiculosus* (Engel *et al.*, 2005; Tatarenkov *et al.*, 2007), *F. distichus* (Coyer *et al.*, 2011c) and *F. spiralis* (Engel *et al.*, 2005; Coyer *et al.*, 2011a) using microsatellite (Coyer *et al.*, 2002a,b,c, 2009; Engel *et al.*, 2003, 2005) and mitochondrial loci (mt DNA) (Hoarau *et al.*, 2007; Engel *et al.*, 2008). Population structure may be homogenized by gene flow as high gene flow dampens local adaptation to a stress (Kawecki, 2008). However, estimates of gene flow for *F. serratus* based on population differentiation at the regional scale (1–100 s km) suggest that gene flow can be as little as 500 m to 2 km (Coyer *et al.*, 2003), between 10 m and <1 km in *F. vesiculosus* from the Baltic Sea (Tatarenkov *et al.*, 2007) and 150 m to 20 km in Brittany (estimated from Billard *et al.*, 2005a). In the Kattegat Sea, gene flow distances for *F. serratus* increased to 70 km (Coyer *et al.*, 2003). Taken together, the aforementioned results illustrate how oceanographic currents and local coastal topologies affect dispersal and variation (see below).

Changes in putatively neutral allele frequencies along various stress gradients in replicated geographic locations provide strong correlative evidence for adaptation. This, however, is not conclusive as long as the actual genes involved in the stress response remain unknown. Conversely, strong changes in phenotypic traits may be observed across a gradient that are not mirrored by neutral allele frequencies. In *Fucus* spp., both of these situations have been encountered. For example, no correlation was found in the neutral allele frequency of *F. vesiculosus* along a gradient in salinity from the North Sea (35 psu), to the Kattegat, and the SW Baltic Sea (12 psu) using neutral markers (Tatarenkov *et al.*, 2005; Johannesson and André, 2006), despite strong phenotypic differences in emersion stress tolerances (*F. vesiculosus* is submerged in the atidal Baltic Sea) (Pearson *et al.*, 2000) and fertilization success (Serrão *et al.*, 1996a,b). Deeper within the Baltic Sea (from Bornholm and then extending north into the Bothnian Gulf), however, a strong shift in allele frequencies is correlated with decreasing salinity and a transition to clonal reproduction of *F. radicans* (Tatarenkov *et al.*, 2005). The salinity shift is even considered a strong

enough selective force to contribute to the recent and rapid formation of the newly described endemic species *F. radicans* within the past 400–2000 years (Pereyra *et al.*, 2009). In *F. serratus*, there is no change in neutral allele frequencies over salinity gradients either within or between the Kattegat and Baltic Seas (Coyer *et al.*, 2003) or along steep salinity gradients in a Norwegian fjord (Coyer *et al.*, 2011b). However, using a genome scan approach these authors found evidence for selection in six candidate loci (three derived from expressed sequence tag (EST) libraries and three from anonymous libraries; see Section 5.3) of which at least one was related to osmotic stress (Coyer *et al.*, 2011b). Thus, a lack of correlation using neutral markers does not imply a lack of selection.

At the local scale of a single patch or stand, populations may display variation in quantitative genetic traits as has been shown in *F. vesiculosus* from the Baltic Sea regarding the resistance to both epiphytes and grazers (Jormalainen and Honkanen, 2008; Jormalainen *et al.*, 2008b; Koivikko *et al.*, 2008; Jormalainen and Ramsay, 2009), as well as to concentrations of phlorotannins (Jormalainen and Honkanen, 2004). Similarly, strength and/or inducibility of anti-herbivory and anti-fouling defences may vary enormously among conspecifics of *F. vesiculosus*, *F. serratus* and *F. evanescens* (Rohde *et al.*, 2004; Wahl *et al.*, 2010; F. Symanowski, unpublished). This variation indicates the potential for local adaptation to natural enemy regimes.

5.3. Direct detection of adaptation to abiotic and biotic stress

The interplay between environment and genes is the focus of the new field of EEG (Ouborg and Vriezen, 2007; Tautz *et al.*, 2010). Until full genome sequences are available for the various *Fucus* spp. (whose genomes range in size from 800 to 1000 Mb, Kapraun, 2005), a more rapid and economical approach is to develop EST libraries, which represent the expressed genes of the individual under a given stress condition (compared to a recovery condition). EST libraries provide a rich source for gene discovery and the development of gene-linked markers that can be tested for evidence of selection using genome scans (Storz, 2005). Comparative gene expression studies based on EST libraries provide a snapshot of organismal physiology and a fine-scale picture of plastic and constitutive changes in cellular metabolism associated with acclimation and genetic adaptation to the stress under investigation. Thus, EST-linked markers and genomic scans can distinguish phenotypic plasticity (acclimation capacity) from ecotypic differentiation directly rather than correlatively.

Salinity clines and heat-shock in *Fucus* spp. have recently been investigated in an EEG framework. Species distributions from the North, Kattegat and Baltic Seas are governed by both salinity and (emersion) temperature gradients. Replicated clinal variation along such parallel

environmental gradients provides good evidence for natural selection in the wild. For example, four populations of *F. serratus* along a 12-km long salinity gradient (2.6–33.0 psu) in a northern Norwegian fjord were investigated with a genome scan approach using both anonymously and EST-linked microsatellite loci (Coyer *et al.*, 2011b). Six genes revealed putative signatures of selection, of which one was annotated to a putative mannitol transporter (Coyer *et al.*, 2011b). As mannitol is regulated in highly saline environments to control cell turgor (Iwamoto and Shiraiwa, 2005, and references therein), significant selection has occurred for at least some part of the mannitol pathway over the 12-km scale. Disentangling the dual roles of mannitol in osmoregulation and energy storage will require manipulative mesocosm experiments, which have not yet been performed.

Intertidal gradients present several physiological stresses and it is along these gradients that classical transplant experiments have been conducted with several species of *Fucus* (see Section 4.1 and Table 2.1). Using an EEG approach, Pearson *et al.* (2009) compared emersion stress at the distributional centre versus the distributional edges in two *Fucus* species. Southern edge populations of *F. serratus* (northern Portugal) were less resilient to desiccation and heat-shock than central (UK) populations and expression of heat-shock genes was higher at the same temperatures, suggesting greater cellular stress (Pearson *et al.*, 2009). In contrast, *F. vesiculosus* showed no such divergence in heat-shock response and little variation in gene expression. These results suggest that for *F. serratus*, edge populations are maladapted, less genetically diverse and display lower fitness. Thus, changing climate conditions may threaten small, fragmented and/or marginal populations because of inherently reduced fitness and lower adaptive capacity.

Using comparative gene expression studies of several heat-shock proteins in naturally occurring, sympatric populations of Baltic Sea *F. radicans* and closely related *F. vesiculosus*, Lago-Leston *et al.* (2010) were able to show that *F. radicans* was more sensitive to mild heat-shock than *F. vesiculosus*. Also from earlier experiments, the tolerance of *F. vesiculosus* did not vary substantially in contrast to its physiological variability in desiccation and freezing tolerance (Pearson *et al.*, 2000). At present, the interpretation of these results remains general, but suggests that changes in transcriptional regulation, combined with local ecological dynamics, may significantly impact functional traits in marginal habitats, coincident with genome-wide reductions in genetic diversity due to genetic drift (Pearson *et al.*, 2009).

At the level of biotic stress (i.e. community genomics), comparative transcriptomics is still in its infancy with the exception of host–parasite and plant–herbivore studies conducted mainly on model systems (e.g. Walley and Dehesh, 2010).

In order to explore the genetic basis of inducible chemical defence against herbivores in *F. vesiculosus*, a cDNA microarray has been developed from libraries based on grazed and non-grazed *F. vesiculosus* (Weinberger *et al.*, unpublished). *F. vesiculosus* is capable of inducing a chemical defence when exposed to grazers (Rohde *et al.*, 2004). Both chemical elicitors (oligoguluronate, methyl-jasmonate) and direct feeding by isopod grazers altered gene expression.

While *Fucus* has not yet entered the post-genome era, the rapidity of advances in next generation sequencing technologies (Metzker, 2010) is paving the way for the types of multi-level experiments essential to understanding complex ecological interactions involving stress (Gilad *et al.*, 2007). Importantly, the demands for multi-factorial experimental designs and sufficient replication are already accessible and the costs are coming within reach of individual investigator budgets.

6. CONCLUSIONS

The simultaneous effects of different stresses and the dynamics of positive and/or negative feed-backs form the selective environment on the genetic potential to determine whether a given species can (1) tolerate a transient stress regime (plasticity, acclimation); (2) adapt to a permanent regime (ecotypic differentiation via selection) or (3) become locally extinct (unable to maintain positive population growth). As the combination of stresses is variable over space and time, the challenge for an individual is to cope with the spectrum of stresses occurring during its lifetime; the challenge for the population is to adapt to shifting stress regimes within a few generations. Finally, in the context of climate change, abiotic stress-driven effects on biotic interactions are expected to shift stress impact from the population level to the community level by altering competitive hierarchies and feedbacks among trophic and other interactions.

At this point, we have a reasonable understanding of the effects of individual stresses on *Fucus* spp. at the population level, but our knowledge of their higher order interactions remains rudimentary. Consequently, our ability to predict interactions and their effects on community maintenance/assembly declines precipitously as the number of stresses increases. The model in Fig. 2.5 is a hypothesis of the network of single stressor effects and their interdependencies that may generate various interactive effects as they are currently understood. However, rigorous testing of this network of system-level hypotheses will require a different approach that takes into account non-linear and stochastic dynamics (Section 7).

Results from the meta-analysis (Fig. 2.4) show that although all combined effects were, on average, additive this was not necessarily the case for

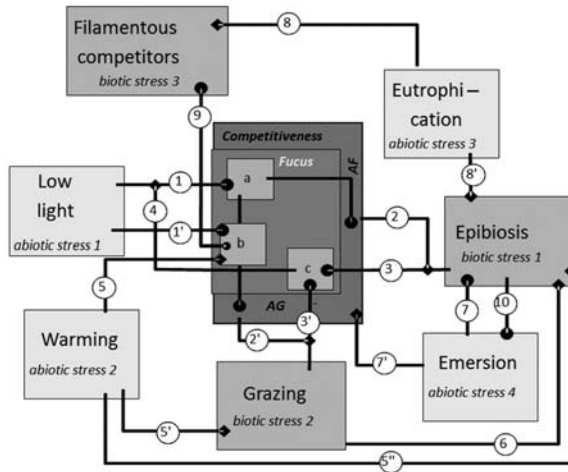


Figure 2.5 Example of an interaction network of abiotic and biotic stresses on *F. vesiculosus* (based on Wahl *et al.*, 2010; Weinberger *et al.*, 2011, Table 2.1). Black circles used as arrow heads indicate negative interactions, black diamonds indicate positive interactions. Dark grey shading indicates biotic variables and light grey shading indicates abiotic variables. Examples: shading weakens energy reserves (a) leading to weakened anti-fouling (AF) and anti-grazing (AG) defences, which enhances fouling (2) and grazing (2') pressure. Both reduce (3, 3') the photosynthetic area of the thallus (c), which amplifies (4) the energy shortage under low light conditions. Low light (1') and temperature-stress ('warming', 5) reduce growth (b), which jeopardizes the alga's ability to compensate for tissue lost to grazers, the activity of which is enhanced by temperature stress (5'). Emersion reduces fouling and strengthens anti-fouling defences (7'). Eutrophication, in contrast, enhances fouling (8') and competition (8) by favouring filamentous algae relative to *Fucus*. 1-2-3-4 is one of several examples for a positive feedback loop, which may be amplified or dampened by other abiotic and biotic stresses.

individual case studies. There, the interaction between two stresses was often synergistic or antagonistic contingent upon the environmental context. The statistical test of interaction effects (Fig. S1) suggested a similar result although a slight trend towards synergistic interactions was stronger and more evident given the range of variation in individual studies. We emphasize that the results from the meta-analysis must be interpreted with caution, as the number of published studies fulfilling all requirements (factorial design, adequate replication, controlled treatments) was small.

7. PROSPECTS

The many species of *Fucus* span 45° of latitude in the northern hemisphere with dominance in the North Atlantic. Collectively they

Table 2.3 Distribution of *Fucus* species (left) and regions with habitats (right) used in the meta-analysis

<i>F. distichus</i>	1	Baltic Sea (subtidal)	16
<i>F. evanescens</i>	2	Eastern Atlantic (intertidal)	15
<i>F. gardneri</i>	3	Eastern Pacific (intertidal)	1
<i>F. serratus</i>	9	Western Atlantic (intertidal)	1
<i>F. spiralis</i>	2		
<i>F. vesiculosus</i>	26		

inhabit a broad suite of habitats: exposed outer coast to sheltered bays/fjords; fully marine to nearly freshwater; rocky substrata to saltmarsh; high intertidal to shallow subtidal.

Despite this diversity, however, experimental work on stress is highly skewed with >60% of the experiments having been conducted on *F. vesiculosus* in the Baltic Sea or eastern North Atlantic (Table 2.3) and >95% of all studies having been conducted in the mid-range of the biogeographic distribution of the genus. Clearly, a fuller understanding of how members of the genus have colonized and continue to successfully exploit northern hemisphere shores, requires greater emphasis on the less studied species, as well as greater emphasis on their performance across clines and along distributional edges. Indeed, studies at distributional edges are likely to offer insights on how *Fucus* (and other species) will respond to global climate change (Pearson *et al.*, 2009).

7.1. Experiments and modelling

Our call for research on all species of *Fucus* and over their respective clinal and distributional ranges also acknowledges that our growing capacity to integrate physiology, genetics and experimental ecology provides numerous avenues to understanding the role of stress. In methodological terms, this will require (1) the design of manipulative experiments in a factorial manner to address multivariate interactions, (2) the up-scaling of experiments by including several interacting groups and by allowing enough time for effects to spread from the individual to the community level, (3) comparison of stress impact on marginal versus core populations, (4) attention to genotypic–phenotypic links and (5) the use of multivariate modelling techniques to explore and analyse the network system. Factorial ecological experiments with appropriate replication for >3 stress factors, however, are logistically difficult (if not impossible) in the field and are only slightly less daunting to establish and maintain in the laboratory (mesocosms). Thus, future studies should strategically acquire

data that are appropriate for complex analyses as it is precisely the multivariate effects that need to be understood.

Structural equation modelling (SEM) provides a framework for estimating causal effects through the study of path relations (reviewed in Grace, 2006; Grace *et al.*, 2010). Because the focus of SEMs is on understanding direct and indirect pathways, the approach is well suited for both building and testing hypotheses of multiple stress processes (e.g. Tonsor and Scheiner, 2007, *Arabidopsis*). In a marine setting, SEM has been used to model indirect facilitation of the benthic communities of kelp forests (Arkema *et al.*, 2009). Its application to the hypothetical interaction network proposed in Fig. 2.5 has not yet been attempted but would greatly contribute to our understanding of community stress.

7.2. Next generation molecular ecology

Ecologists as a group tend to shun molecular methods in their research programs (Johnson *et al.*, 2009). Nevertheless, the capacity to examine interactions among stress reactions—almost all of which are complex, multi-gene-regulated traits—will open fundamentally new avenues in community genetics–genomics. At this stage, we still know very little about the genetic basis of osmoregulation, thermal tolerance, chemical defence and the boundaries between plastic and selective responses for any of these traits.

As distinguishing phenotypic plasticity from ecotypic differentiation can be approached directly by examining gene expression/regulation via differential transcription and structural changes in the DNA sequences of key genes, it is increasingly possible to integrate our understanding of ecological stress with complex genetic responses (Tautz *et al.*, 2010). Thus, integrating the genetic perspective into field studies of stress ecology will enable us to (1) more finely identify plasticity in stress responses and expression of stress-related genes; (2) evaluate the adaptive potential of populations and (3) investigate how selection driven by one stress affects sensitivity towards other stresses. For example, differential mortality in response to one stress will lead to the survival of a non-random (selected) sub-sample of the original genotypic diversity, which in turn will harbour a sub-sample of traits ancillary to tolerance for the selective stress (e.g. tolerance to a subsequent stress, productivity, light harvesting, etc.). Traits of the genotypic sub-sample may be non-random if the traits are linked to the tolerance of the first stress, or random if they are not.

7.3. How will climate change affect fucus?

As a foundational taxon, the genus *Fucus* has a large influence on the associated community as a whole; likewise, the associated community

influences *Fucus*. This duality highlights the importance of gaining a more integrative understanding of stress responses in species of *Fucus* and the communities they support.

Species with wide ecological niches are more easily able to cope with change; likewise, the ongoing and rapid diversification of the genus creates multiple overlapping niches. This suggests that *Fucus* spp. from stressful and fluctuating habitats may be better equipped to tolerate (via pre-adaptation) the superimposition of increased fluctuations (e.g. Schneider, 2008) than species from habitats with more subtle fluctuations (e.g. the deep subtidal, or low latitude habitats). As the predicted changes in the North Atlantic region over the next one or two centuries (3–6 °C increase in temperature, a 0.5 units decline in pH, IPCC Climate Change, 2007) are small relative to the daily environmental fluctuations characterizing any temperate northern hemisphere intertidal habitat, the *direct* impact of rapid climate changes on *Fucus* may be small.

In contrast, the *indirect* impacts could be large if *Fucus* spp. were to be competitively displaced (as, e.g. by *de novo* interactions with introduced competitors, consumers and/or parasites and pathogens). However, the niche breadth of several sympatrically occurring *Fucus* spp. taken together, provides further insurance in terms of holding space and by ensuring its own 'invasive' potential (Peterson, 2003). As more than a third of *Fucus* spp. have been characterized as successful invaders (Williams and Smith, 2007), the genus has high expansion potential, be it by anthropogenic or natural means. Invasiveness, that is, the ability of a species to establish in new habitats, might be a proxy for its capacity to tolerate climate change. Reproductive success in a new environment is favoured by phenotypic plasticity and/or rapid ecotypic selection. Even if the effects of climate change are disproportionally strong on marginal habitats (Melzner *et al.*, 2010; Thomsen and Melzner, 2010), *Fucus* spp. certainly represent promising candidates to colonize areas abandoned by more sensitive macroalgae.

The scale and importance of *indirect* effects of stresses, however, are only beginning to be understood. As a complicated yet realistic hypothetical example, moderate warming may not affect *Fucus* directly, but could have a large indirect impact via a synergistic interaction involving (i) a slight increase in the metabolic rate of consumers (=increased grazing pressure); (ii) a slight decrease in the defence strength of *Fucus* leading to; (iii) slightly higher fouling pressure and, in turn leading to; (iv) a slight decrease in available solar energy, further reducing; (v) defence strength and (vi) overall fitness (Fig. 2.5). The key realization is that accumulation of small effects acting in a non-linear manner could suddenly move towards a tipping point and major regime shift (Scheffer and van Nes, 2004; Christensen *et al.*, 2006; Harley *et al.*, 2006).

7.4. Open questions

Stress ecology has gained a new dimension of relevance and urgency in our contemporary world. At the same time we are in a position to integrate disciplines and exploit new types of data and multivariate analyses to address the role of climate change at the species and community level. With these considerations in mind, the following questions are now tractable.

- Are there consistent combinations of stress interactions that may provide general predictions about community responses to climate change?
- What suites of genes are associated with particular stress interaction networks affecting, for example, salinity or temperature tolerance, chemical defence and susceptibility to predation?
- What is the potential of biotic interactions to modulate the effects of abiotic stress and community resources; and how does this feedback to the long-term resilience of *Fucus* communities?
- Will marginal and core populations differ in their response to global change?
- What specific insights about climate change effects can be gained from understanding the responses of *Fucus*-based communities as compared with other foundational species and their associated communities (e.g. seagrasses, mussels)?

APPENDIX A

SUPPLEMENTARY MATERIALS

Supplementary data associated with this chapter can be found, in the online version, at [doi:10.1016/B978-0-12-385536-7.00002-9](https://doi.org/10.1016/B978-0-12-385536-7.00002-9).

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