

Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of bacterial degradation to food quality

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ABSTRACT: The nutritional value of kelp *Laminaria hyperborea* (Gunn.) Foslie and the importance of bacterial degradation in making kelp available to consumers were tested by no-choice feeding experiments. Fresh and dead kelp material degraded *in situ* was sampled. In the laboratory, fresh kelp was degraded for 3, 14 and 44 d by kelp associated bacterial communities under aerobic and anaerobic conditions. The fresh and degraded kelp products were fed to the kelp associated amphipods *Jassa falcata*, *Lembos websteri*, *Ampithoe rubricata* and *Gammarus locusta* and the gastropod *Rissoa parva*. None of the amphipods tested could survive or grow on fresh kelp, but bacterial degradation decreased the C:N ratio and the phlorotannin content and made kelp available as food. In contrast, the gastropod survived on both fresh and degraded kelp. ¹³C:¹²C and ¹⁵N:¹⁴N isotope analysis of fauna and possible food items sampled in the field suggested that kelp derived particulate organic matter (POM) is an important food source for kelp epifauna.

KEY WORDS: Kelp forest · Amphipods · Gastropods · Bacterial degradation · Feeding experiments · Food quality

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INTRODUCTION

Several papers in recent years have addressed the relationships between the fitness of macro-invertebrates associated with macroalgae and the quality of their food. The feeding habits of these animals include herbivory, detritivory and omnivory (Lawrence 1975, Nicotri 1977, Nair & Anger 1979b, Mann 1982b, Hagen 1983, Shillaker & Moore 1987, Hay et al. 1988, Duggins & Eckman 1997, Cruz-Rivera & Hay 2000b, 2001, Toth & Pavia 2002a,b). Laboratory experiments have shown how diets of different quality, consisting of red, green and brown algae, affect consumer fitness (Costa et al. 1996, Cruz-Rivera & Hay 2000a,b, Hemmi & Jormalainen 2002) and how consumer fitness may increase on mixed diets including additions of animal matter (Costa et al. 1996, Cruz-Rivera & Hay 2000a,b). Such experiments represent idealised situations in which growth can be maximised

by optimising diets and supplies, a situation that may not be a common situation in nature.

In NE Atlantic coastal waters, *Laminaria hyperborea* (Gunn.) Foslie forms extensive forests (Kain 1967). The kelp functions as a habitat that supports a diverse and numerous epifauna dominated by gastropods and amphipods (Moore 1972b, 1973, Schultze et al. 1990, Christie 1995). In addition, kelp primary production is a potentially important food source for these consumers. On the Norwegian coast the greatest standing stocks are 30 to 40 kg m⁻² wet weight, and the yearly primary production is large (Sjötun et al. 1995). Thus, any consumer able to exploit the kelp production will benefit from its ready availability.

Although grazing by sea urchins (Lawrence 1975, Mann 1982b, Hagen 1983) and a few gastropods (Fretter & Manly 1977, Toth & Pavia 2002a,b) are important exceptions, most of the standing stock in temperate kelp beds is not grazed, but released as

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particulate organic matter, POM (Mann 1982, Hay & Steinberg 1992). Several factors that prevent animals from eating various algae have been reported. These include rigidity (Steneck & Watling 1982, Padilla 1985, Taylor et al. 2002) and the production of deterrent secondary metabolites (Duggins & Eckman 1997, Poore & Steinberg 1999, Granado & Caballero 2001, Taylor et al. 2002). These characteristics are also found in *Laminaria hyperborea* (Toth & Pavia 2002a,b). In addition, kelp tissue C:N exceeds that of animal tissue. If the C:N of animal tissue is constant, then the N-limitation could limit C utilisation by the animal (Hessen 1992, Hessen & Sterner 1994), which must then compensate for the low food quality with an increased feeding rate (Cruz-Rivera & Hay 2000b). There may be a critical C:N ratio above which the algae can no longer support the growth of the consumer (cf. Hessen & Bjerkeng 1997). Russel-Hunter (1970) calculated that most animals require a C:N ratio below 17 in their diet. The kelp C:N ratio is higher than this for most of the year (Sjötun et al. 1996), and it may therefore be unsuitable as food for at least some parts of the year.

Bacterial degradation of eroded kelp fragments may make primary production available to consumers (Newell et al. 1982, Newell & Field 1983, Seiderer & Newell 1985, Duggins et al. 1989). Studies on *Laminaria digitata* (Huds.) Lamouroux have shown increased microbial activity on old parts of the laminae (Corre et al. 1989a,b). At least some of the eroded POM is transported onshore or into deeper waters (Thrush 1986, Vetter 1995, Bustamente & Branch 1996), but a lot of POM is expected to sediment within the kelp forest system. Dense bacterial communities on kelp surfaces (Armstrong et al. 2000) may degrade released POM and increase its nutritional value by reducing the C:N ratio and the content of phlorotannins. Such 'ageing' may make algae more suitable as invertebrate food (Duggins & Eckman 1997, Penning et al. 2000). The bacterial community itself may also represent an important contribution to the diet (Cummins 1974, Newell et al. 1982, Newell & Field 1983). Alternatively, primary production may be lost to the fauna through bacterial respiration. Kelp degradation is usually expected to be aerobic because kelp forests are found in exposed sites (Kain 1967). However, kelp accumulations on the sea floor may undergo anaerobic degradation (Thrush 1986).

Kelp-associated animals may have dietary requirements reflecting different activity levels and habitat adaptations. They are mainly associated with epiphytic algae on the kelp stipes and in the holdfasts (hapteron), and it is possible to discriminate between epiphyte- and holdfast-associated fauna according to their habitat preferences (Norderhaug et al. 2002). A

more vigorous environment on the epiphytes than in the holdfasts may require more mobile species on the epiphytes, but a different distribution of food generalists and specialists between epiphytes and holdfasts may also be expected. The holdfasts function as sediment traps (Moore 1972a, Conradi et al. 1997), and are therefore expected to accumulate smaller and more degraded detritus particles than the epiphytes. The fauna living on epiphytes are more mobile than the holdfast fauna (Norderhaug et al. 2002). This may reflect their need to find food rapidly when it is in short supply and a need to exploit any available food sources, even those of low quality. Fauna on epiphytes may have mixed diets, while the holdfast fauna may be more discriminating. On the other hand, the more mobile epiphyte-associated fauna may require a higher food quality than the more sedentary holdfast species (cf. Cruz-Rivera & Hay 2000a, 2001).

This study tested the hypotheses that POM from kelp can serve as food for kelp associated macrofauna and that bacterial degradation is important in increasing the quality of POM. To test the hypotheses, selected macrofaunal species were fed fresh and degraded kelp in no-choice feeding experiments in the laboratory. Survival and growth were monitored. Isotope data ($^{15}\text{N}:$ ^{14}N and $^{13}\text{C}:$ ^{12}C) were obtained for the same animal species and potential food items were sampled in the field to determine food (carbon) sources and the trophic position of the animals *in situ* (Rau et al. 1983, 1989, Dunton 2001).

MATERIALS AND METHODS

Field sampling. *Laminaria hyperborea* lamina tissue and macro-invertebrates for laboratory experiments were sampled in the archipelago of Møre og Romsdal county (Finnøy, 62° 50' N) in Norway. Here, the standing stock of *L. hyperborea* is 16.3 (\pm 3.6) kg m⁻² (wet weight, own data) and the associated faunal communities are well developed (Norderhaug et al. 2002). Kelp laminae were sampled by SCUBA at 5 m depth. Also, dead and decomposed kelp was sampled nearby in a back eddy where kelp accumulates at 10 m depth (hereafter called *in situ* degraded kelp). Discs of lamina tissue of fresh and decomposed kelp were cut off with a knife and dried at 60°C for 72 h for later feeding experiments. Samples were taken in August (2000) when kelp C:N is high (Sjötun et al. 1996). The bacterial community of lamina surfaces was isolated, cultivated in the laboratory, and stored at 5°C for later decomposition of kelp in the laboratory.

We carefully sampled 4 common amphipod and 1 gastropod species alive, and transported them to the

laboratory, where they were kept at 12 to 14°C in a closed-circuit 1500 l aquarium system. They were chosen to represent common kelp forest invertebrate families (Rissoidae, Ischyroceridae, Aoridae, Amphithoidae and Gammaridae). One of the dominant gastropods in kelp forests is the small thick-shelled *Rissoa parva* (da Costa) (Schultze et al. 1990, Christie 1995); it feeds on algae surfaces (Mann 1982a, Warén 1996). *Jassa falcata* (Montagu) is numerically the dominant kelp forest amphipod, and is associated with kelp epiphytes (Norderhaug et al. 2002), whereas *Lembos websteri* (Bate), a typical holdfast-associated species, is rather sedentary. Both are reported to be omnivorous (Nair & Anger 1979b, Shillaker & Moore 1987). *Ampithoe rubricata* (Montagu) is a large epiphyte-associated amphipod; no data are available on its feeding biology, but related species are herbivorous or omnivorous (Nicotri 1977, Cruz-Rivera & Hay 2000a,b, 2001). Although most numerous in the tidal zone, *Gammarus locusta* (Linnaeus) is also common in the kelp forest. It is omnivorous, with a diverse diet including algae, deposit-feeding, and other animals (Costa & Costa 1999) and it is even cannibalistic (Authors' pers. obs.).

For ^{13}C : ^{12}C , and ^{15}N : ^{14}N isotope analysis, we sampled 106 to 110 individuals each of the macro-invertebrate species listed above, kelp laminae, the common epiphytic red algae *Palmaria palmata* (Linnaeus) Kuntze, *Rhodomela confervoides* (Hudson) Silva, *Callophyllis laciniata* (Hudson) Kützing, *Delesseria sanguinea* (Hudson) Lamouroux, *Ptilota gunneri* Silva, *Membranoptera alata* (Hudson) Stackhouse and *Phycodryas rubens* (Linnaeus) Batters, phytoplankton and POM. POM was sampled in sediment traps placed in a dense kelp forest (height 25 cm, diameter 5 cm) at 5 m depth from August to October (2000) at 2 sites. Phytoplankton was sampled by towing a plankton net (mesh size 20 μm) through the surface waters offshore. Samples were filtered through pre-combusted GF/C filters and frozen. Entire filters were ground to a powder prior to analysis. The macro-invertebrates were frozen.

Experimental degradation of kelp. Fresh-collected, dried kelp was crushed in liquid nitrogen to a powder consisting of particles covering a broad size range to meet species-specific differences in food particle-size preferences (Shillaker & Moore 1987). We incubated 15 g of kelp powder in 200 ml C-free but N- and P-rich Nivens medium, with 4 ml (5×10^5 cells ml^{-1}) kelp bacteria culture at 12°C, in darkness, and under aerobic conditions (aerated) for 3, 14, or 44 d. For the same number of days, 6 g of kelp powder were incubated in 50 ml medium and 0.8 ml kelp bacteria culture in closed, unaerated bottles and degraded anaerobically. The degraded kelp samples were dried (60°C for 72 h) for later feeding experiments.

Feeding experiments. Juvenile *Ampithoe rubricata* and *Gammarus locusta* were used in short-period growth experiments terminated after 15 d. In *Jassa falcata* (females only since male survival was lower) and *Lembos websteri* (both sexes, with no differences between females and males detected) adult survival only was monitored because there were too few juveniles. All animals were starved 24 h in advance and placed individually in 20 ml wells on culture plates with food in excess. They were fed fresh kelp, *in situ* degraded kelp, and kelp experimentally degraded in aerobic and anaerobic conditions for 3, 14 and 44 d. We used 2 control treatments. One provided no food and the other provided Tetra minTM, (a highly nutritional commercial fish food consisting of crustaceans, fishes and algae) with added spinach. Each treatment used 60 *J. falcata*, 50 *L. websteri* and 30 specimens each of juvenile *A. rubricata* and *G. locusta*. The survival experiments were terminated when all control individuals in the no-food control treatment were dead. To avoid possible effects of drying, kelp that was frozen only and then degraded as described above were fed to juvenile *G. locusta*: 10 individuals in each treatment were given fresh frozen kelp and frozen kelp that had been degraded for 3 and 44 d. No difference was detected between the to preservation methods by a 2-way ANOVA test with preservation method (df = 1, MS = 1.0, $F = 1.1$ and $p = 0.36$) and degradation as factors.

In the case of *Rissoa parva*, 10 individuals were placed in each of 10 small bowls with discs of fresh kelp in excess. Individuals given no food served as controls. Gastropods feed by rasping algal surfaces (Hickman et al. 1993, Warén 1996), and *R. parva* was therefore only given food that could be served as discs (approximately 1 × 1 cm in size), i.e. fresh kelp and *in situ* degraded kelp, but not experimentally degraded kelp (particles). In all experiments, water and food were changed and survival was monitored daily or every other day.

In the amphipod growth experiments, each individual was anaesthetized on the first and every fifth day (by low concentrations of ethyl carbamate, $\text{C}_3\text{H}_7\text{NO}_2$ in seawater) and photographed before being quickly returned to its culture plate. Individual length (rostrum to telson) was monitored using Scion Image (www.scioncorp.com), and individual growth was calculated. When photographed, some amphipods lay in a more curved manner than others. This influenced the overlap of the body segments and thus the measured length. To compensate for this error, straight lines rather than a curved line were drawn from the rostrum to the telson. In this way the length were corrected for the most strongly curved individuals whose length would otherwise have been overestimated.

At the end of the experiments, all animals were dried (72 h, 60°C) and crushed with a piston prior to C:N

analysis to determine to what extent the different species were able to regulate their tissue C:N content according to their food. Gastropod shells were removed prior to analysis using 1 M HCl.

Phlorotannin assays and C:N analysis. The phlorotannin content of kelp was analysed according to the method of Van Alstyne (1995) with some modifications (Dr. M. Abdullah pers. comm.). Phlorotannins were extracted in 9 ml water with 1 ml of 1 M pyrophosphate from finely crushed algal material. The slurry was repeatedly stirred and allowed to react for 72 h at room temperature. Folin-Ciocalteu assays were performed to quantify the phlorotannin content in the extracts, using phloroglucinol (Sigma P 3502) as a standard (Van Alstyne 1995). The absorbance of the solutions was measured at 765 nm.

The C:N content of 3 replicate 0.5 to 1.5 mg samples of each kelp and animal sample was analysed using a Carlo Erba Elemental analyser (Model 1106).

^{13}C : ^{12}C and ^{15}N : ^{14}N isotope analysis. Prepared samples (3 to 10 replicates of 1 to 2 mg each) of kelp, red algae, phytoplankton, invertebrates and POM from sediment traps were combusted in sealed tin capsules in an elemental analyser (Carlo Erba NA 1500). The combustion products CO_2 , N_2 and H_2O , were separated in cryogenic traps, leaving pure CO_2 and N_2 to be analysed on-line in a mass spectrometer. The results are expressed in standard δ -notation (^{13}C : ^{12}C or ^{15}N : ^{14}N) relative to PDB and atmospheric air respectively:

$$\delta X = \left\{ \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right\} \times 1000$$

where X is C or N and R is the ratio of the heavy to the light isotope.

Statistical analysis. Differences in amphipod survival of each species on the different treatments were tested by log-rank tests. In the *Rissoa parva* survival experiment, each bowl of 10 individuals was treated as 1 replicate and an ANOVA test on slopes (survival) was performed, followed by a multiple comparison according to the Tukey method.

In the growth experiments, amphipods were monitored individually, and each individual was treated as a replicate. To avoid violating the assumption of independent measurements resulting from repeated measures of the same individual, the slopes of the growth curve were calculated for each individual and used in ANOVA tests.

In ANOVA tests of growth (slopes), species (*Gammarus locusta* and *Ampithoe rubricata*) and treatment (animals fed kelp degraded *in situ* and experimentally [aerobically and anaerobically] for 3, 14 and 44 d, and Tetra minTM + spinach) were used as factors. The tests were probably slightly conservative because the experiment-induced mortality was expected to affect the weakest, slowest growing individuals most severely

and kill more slow-growing individuals in the low-quality food treatments than in the high-quality treatments. All tests were performed with the S-PLUS (6.0) computer package.

RESULTS

Significant differences in the survival of the gastropod *Rissoa parva* between treatments were found (ANOVA, 2 df, MS = 0.02, $F = 26.1$, $p = 4.9 \times 10^{-7}$). The gastropod survived better on fresh kelp than on no food (Tukey's test, estimate = -0.07 , lower bound = -0.10 , upper bound = -0.04 , Fig. 1) and there was no significant difference in survival between gastropods fed on fresh or *in situ* degraded kelp (estimate = 0.001, lower bound = 0.011, upper bound = -0.026). The gastropod also survived longer without food than any amphipod.

There were significant differences in the survival of all amphipods between treatments (diets) (Fig. 2), but in contrast to the gastropod, fresh kelp had no positive effect on survival of the amphipods used in the experiments. According to log-rank tests, survival was even lower for *Jassa falcata* ($\chi^2 = 24.2$, 1 df, $p = 8.8 \times 10^{-7}$) and *Gammarus locusta* ($\chi^2 = 12.5$, 1 df, $p = 4.2 \times 10^{-4}$) fed fresh kelp than for control individuals given no food, but for *Lembos websteri* ($\chi^2 = 2.6$, 1 df, $p = 0.10$) and *Ampithoe rubricata* ($\chi^2 = 0.5$, 1 df, $p = 0.49$) there was no difference in survival between the 2 treatments. More amphipods survived on aerobically degraded kelp than on fresh kelp (Fig. 2), and log-rank tests confirmed that survival increased with increasing aerobic degradation for *J. falcata*: ($\chi^2 = 26.1$, df = 2, $p = 2.2 \times 10^{-7}$) and *G. locusta* ($\chi^2 = 12.5$, df = 2, $p = 4.2 \times 10^{-4}$). There was, however, only weak evidence for such a relationship for *A. rubricata* ($\chi^2 = 2.8$, df = 1, $p = 0.09$) and *L. websteri* ($\chi^2 = 5.4$, df = 2, $p = 0.07$). They both survived well on kelp degraded for the short period (3 d) and kelp degraded for

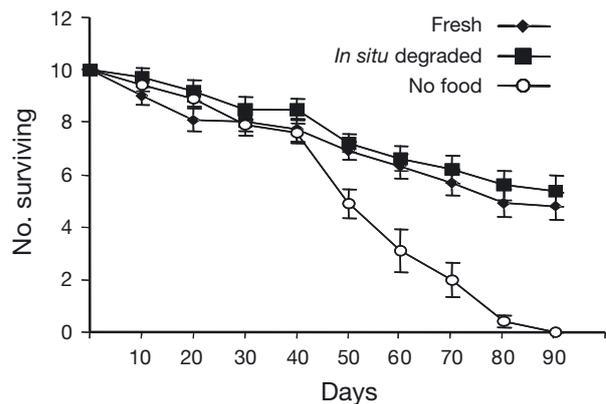


Fig. 1. *Rissoa parva*. Average (\pm SE) survival (10 replicates each of 10 individuals) fed fresh and *in situ* degraded kelp. No food: controls

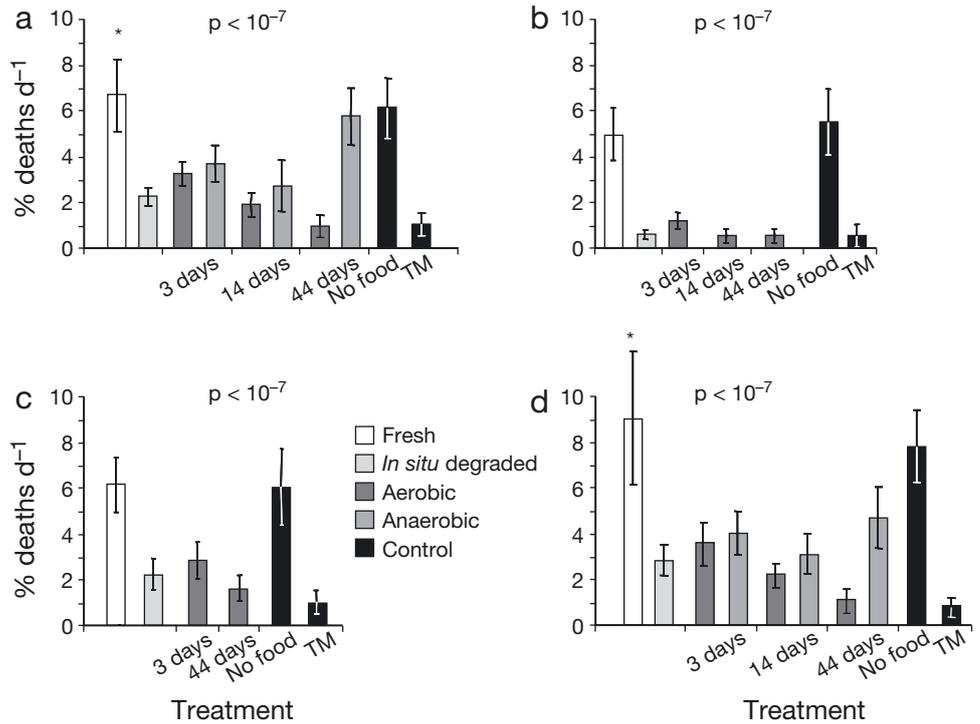


Fig. 2. (a) *Jassa falcata*, (b) *Lembos websteri*, (c) *Ampithoe rubricata* and (d) *Gammarus locusta*. Average (\pm SE) death rates. Also shown are p values of log-rank tests on differences in survival: (a) $\chi^2 = 391,9$ df; (b) $\chi^2 = 358,6$ df; (c) $\chi^2 = 88,5$ df; (d) $\chi^2 = 218,9$ df. Amphipods were fed fresh, dried and degraded kelp; controls were either not fed, or were fed a commercial fish food, Tetra minTM. *No individuals survived to last day of experiment

the longest period (44 d). In the treatments using kelp that had been aerobically degraded for the longest period (44 d), survival was almost the same as in the treatments using the highly nutritional Tetra minTM + spinach treatment. Survival was generally lower on anaerobically degraded than on aerobically degraded kelp.

There was significant differences in growth between treatments (diets) for both *Gammarus locusta* and *Ampithoe rubricata* (Table 1). No significant differences were found between the 2 species. Growth paralleled survival and was higher for individuals given aerobically degraded kelp and *in situ* degraded kelp than for those given fresh kelp (Fig. 3). Growth

Table 1. *Gammarus locusta* and *Ampithoe rubricata*. Two-way ANOVA testing differences between growth of 2 amphipod species fed kelp degraded *in situ* or aerobically degraded experimentally for 3, 14 or 44 d, or fed with Tetra minTM + spinach. Only individuals surviving to the last day of the experiment were included in the analysis (individuals given no food or fed on fresh kelp were therefore not included). Residuals = df 177; MS = 0.62

	df	MS	F	p
Species (S)	1	0.13	0.21	0.64
Treatment (T)	4	14.7	23.7	$< 10^{-8}$
S \times T	3	0.14	0.24	0.86

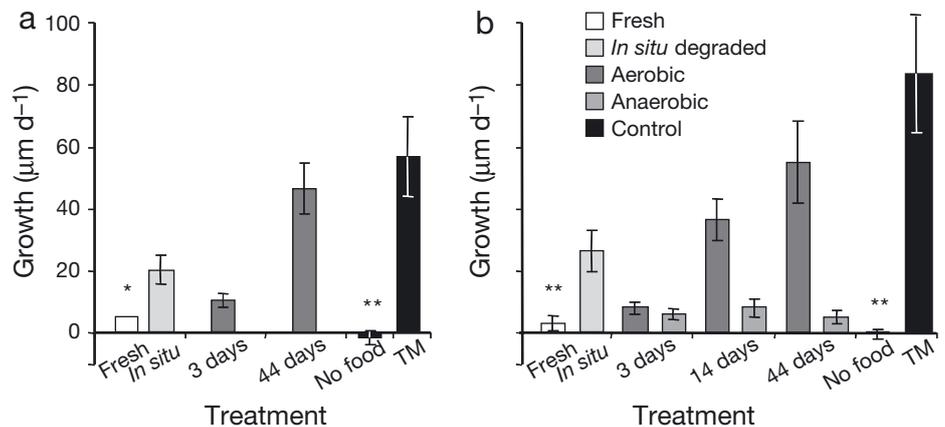


Fig. 3. (a) *Ampithoe rubricata*; (b) *Gammarus locusta*. Average (\pm SE) growth of juveniles fed fresh and degraded kelp. Anaerobically degraded kelp was fed to *G. locusta* only. *Only 1 *A. rubricata* survived on fresh kelp for 15 d; **no individual survived for 15 d, data therefore show growth until death

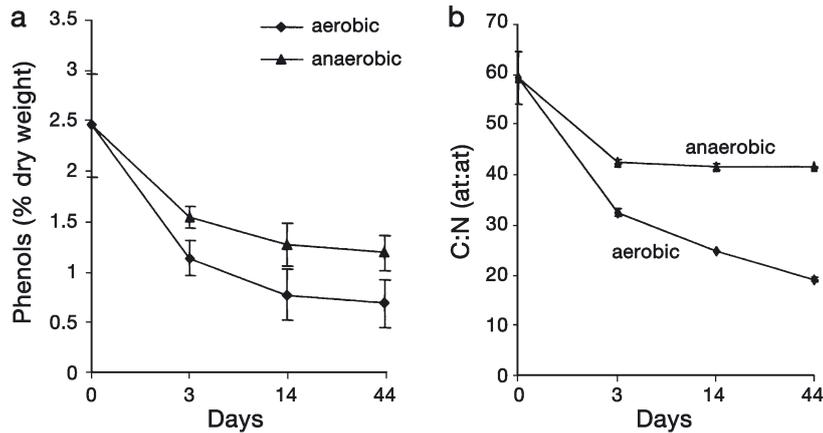


Fig. 4. *Laminaria hyperborea*. (a) Total phlorotannins content in fresh kelp (0 d), and kelp experimentally degraded (aerobically and anaerobically for 3, 14 and 44 d); (b) average (\pm SE) C:N at:at ratio of kelp degraded aerobically and anaerobically for 0 (fresh), 3, 14 and 44 d

was higher on kelp degraded aerobically for longer periods. Growth on anaerobically degraded treatments was low and differed little (Fig. 3, $df = 2$, $MS = 0.25$, $F = 0.37$, $p = 0.68$ in a global test on differences between any 3 anaerobic treatments for *G. locusta*) and was significantly lower than growth on the aerobic treatments ($df = 1$, $MS = 9.3$, $F = 13.4$, $p = 4.2 \times 10^{-4}$).

The content of phlorotannins in kelp decreased in parallel with increasing degradation in the laboratory, probably through leakage or bacterial degradation. It was almost 2.5% (dry weight) in fresh kelp and decreased to less than 1% in kelp experimentally degraded for 44 d (Fig. 4a). The decrease was larger and more rapid during aerobic degradation than during anaerobic degradation. The phlorotannin content of *in situ* degraded kelp was $0.89 (\pm 0.36)\%$.

Likewise, the C:N (at:at) ratio of the combined mass of kelp and bacteria decreased rapidly with increasing degradation (Fig. 4b). After only 3 d of aerobic degradation, the C:N ratio had dropped from almost 60 in fresh kelp to nearly 30. After this initial drop, C:N decreased more slowly, reaching <20 after 44 d. The ratio in the *in situ* degraded kelp was $24.2 (\pm 5.2)$.

The C:N of the anaerobically degraded kelp decreased similarly, but degradation was slower and the ratio did not drop further than approx. 40. Even after 44 d, no trace of sulphur was detected in any of the samples.

Amphipod tissue C:N was stable (approx. 5, Fig. 5), indicating that the experimental individuals could not regulate their tissue C:N according to food quality. However, the C:N ratio in tissue from the gastropod *Rissoa parva*

was higher than in amphipod tissue and differed according to treatment, indicating that it was more variable. It was lower in control individuals given no food than in those fed on kelp.

POM has approximately the same $^{13}\text{C}:^{12}\text{C}$ ratio as kelp (Fig. 6), suggesting that it is dominated by kelp derived material. The $^{13}\text{C}:^{12}\text{C}$ ratio of the invertebrates examined is closer to that of kelp and POM than to that of phytoplankton and most of the epiphytic red algae they use as a habitat, suggesting that kelp, in some form, is an important food source. The $^{13}\text{C}:^{12}\text{C}$ value of the red alga *Palmaria palmata* is however also close to those of both kelp and these species. The $^{15}\text{N}:^{14}\text{N}$ ratio was not very different in the invertebrates

investigated than in the primary producers, suggesting that many macro-invertebrates occupy a position low in the food web and include algal material in some form in their diet. The variance in their isotope values probably reflects the fact that most of them are omnivorous and include material other than that of algal origin in their diet.

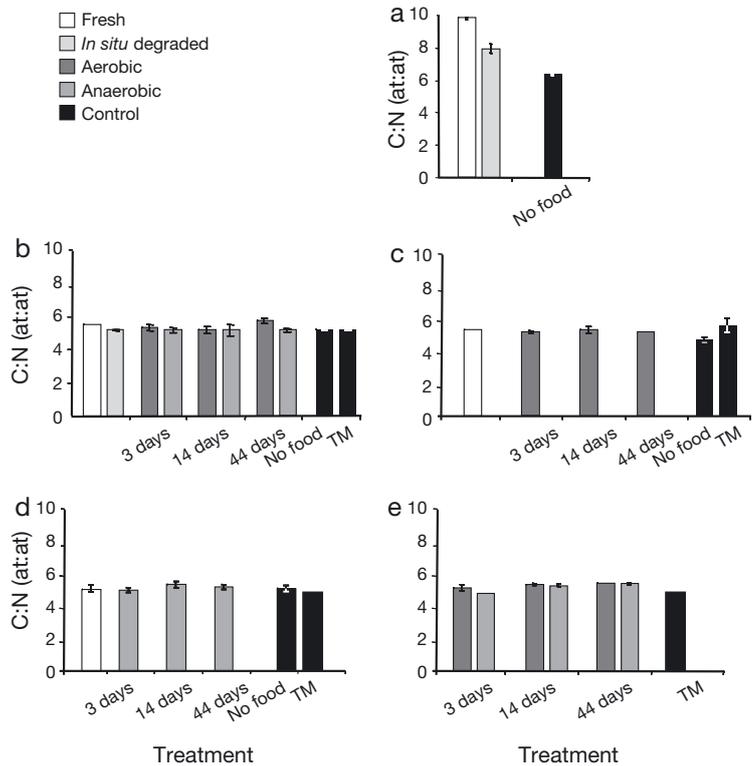


Fig. 5. (a) *Rissoa parva*; (b) *Jassa falcata*; (c) *Lembos websteri*; (d) *Ampithoe rubricata*; (e) *Gammarus locusta*. Average (\pm SE) C:N content after feeding experiments. Spaces indicate missing data

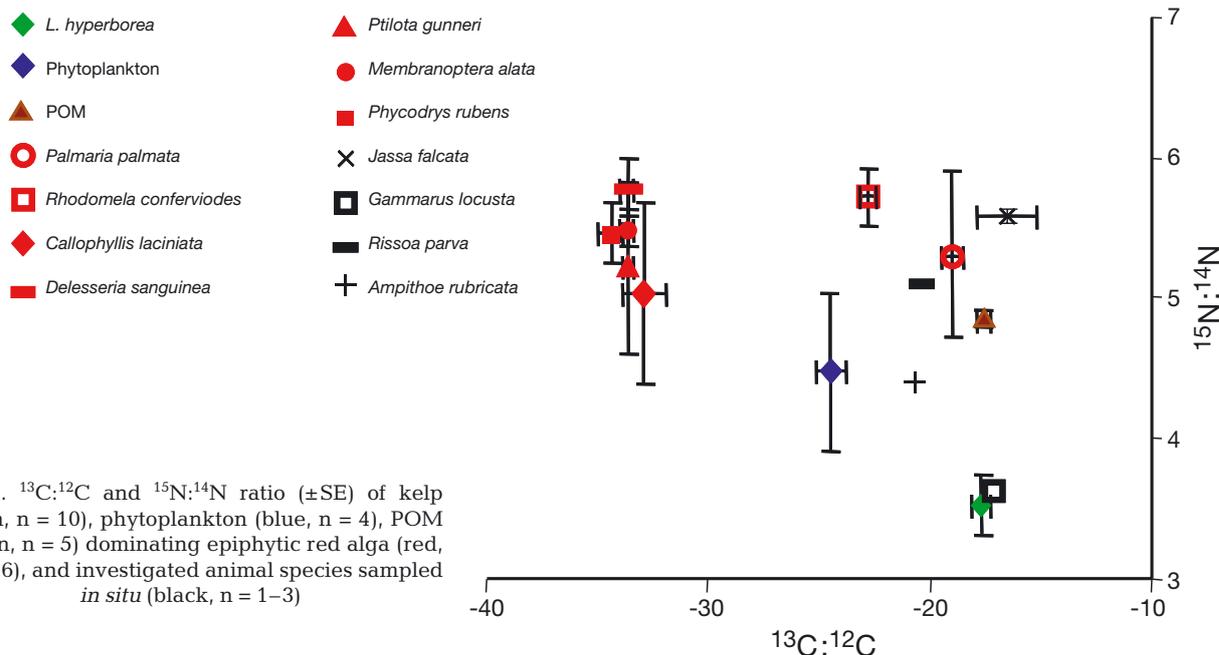


Fig. 6. $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$ ratio (\pm SE) of kelp (green, $n = 10$), phytoplankton (blue, $n = 4$), POM (brown, $n = 5$) dominating epiphytic red alga (red, $n = 3-6$), and investigated animal species sampled *in situ* (black, $n = 1-3$)

DISCUSSION

This study has demonstrated that the large primary production in *Laminaria hyperborea* forests is a potentially important food source for common kelp forest macrofaunal species. It has also demonstrated that this importance depends on bacterial degradation making kelp available as food for common amphipods. Bacterial communities on kelp surfaces thus seem to play a key role in transferring kelp forest primary production to higher levels in the food web. The gastropod *Rissoa parva*, but none of the investigated amphipod species, was able to live or grow on fresh kelp. The C:N ratio was high in *R. parva*, and more variable than the stable values found in amphipod tissue, suggesting that gastropods may be able to exploit food sources with a higher C:N than the crustaceans. This is also reflected in the high resistance to starvation of *R. parva* compared to amphipods. After some time, control *R. parva* given no food withdrew into their shells, probably to save energy. This behaviour kept them alive for a long time but reduced their body mass noticeably (authors' pers. obs.). Survival of 2 of the 4 amphipod species investigated was lower in individuals fed fresh kelp than in controls given no food. This may have been due to a combination of the negative effect of phlorotannins and the poor nutritional value of fresh kelp, as the C:N ratio was nearly 60. Food C:N ratios lower than 60 have been shown to reduce growth and survival in related species (Poore & Steinberg 1999, Cruz-Rivera & Hay 2000b).

Amphipod survival and growth increased with increasing aerobic degradation of the kelp diet. The im-

pact of bacterial degradation on kelp was great. The phlorotannin content and the C:N ratio decreased quickly when kelp was degraded by bacteria in densities not exceeding those recorded *in situ* (Armstrong et al. 2000). Survival and growth were lower on all kelp diets than on Tetra minTM + spinach (even though growth rates for closely related species investigated in other studies suggested that this diet is also poor [Cruz-Rivera & Hay 2000a, H. Christie unpubl. data]). The phlorotannins may have suppressed growth, since the phlorotannin concentration decreased with increasing kelp degradation. Secondary metabolite concentration has previously been reported to be more important than nutritional quality to food suitability (Poore & Steinberg 1999, Granado & Caballero 2001). However, the use of diets of lower C:N in the above-mentioned studies suggests that the effect of dietary C:N was more critical in our study. Low survival and growth probably also reflected a higher food C:N than the preferred 17 (Russel-Hunter 1970). We expected the amphipods to suffer from N limitation as a result of the high food C:N ratio in their food, and therefore to benefit from processes (or additions to the diet) which decreased this ratio. The stable tissue C:N ratio of the amphipods regardless of treatment supports this, implying that N limitation may have acted as a constraint on C utilisation, and that either they were not able to compensate successfully for lack of quality by increasing their food intake, or that a higher intake of food increased the deleterious effect of the phlorotannins. However, growth differences decreased in treatments as a function of decreasing C:N, indicating more successful compensatory feeding when at lower dietary C:N levels.

The results of the experiments with amphipods suggest that only kelp in an advanced stage of degradation can maintain these animals. The C:N ratio and phlorotannin content of the kelp changed little after an initial drop during the first 3 d of degradation. Nevertheless, survival and growth of *Jassa falcata* and *Gammarus locusta* were markedly higher on kelp aerobically degraded for periods longer than 3 d. Anaerobic degradation did not have the same positive effect on animal fitness, although C:N and phlorotannin content of the kelp decreased in a similar (but less marked) manner with increasing degradation. These discrepancies may have been related to other food characteristics that were not considered, such as protein (Mattson 1980, Bowen et al. 1995) and water (Pennings et al. 2000) content, which may be important factors. Secondary metabolites such as phlorotannins may render seaweeds unpalatable to consumers before their bioactive metabolites are degraded (Hay 1996). We measured only 'total phlorotannin content', but the molecule size (Boettcher & Targett 1993) and structural characteristics (Van Altena & Steinberg 1992) of phlorotannin may modify its effect on consumers, and consumer response to phlorotannins may differ between species (Stern et al. 1996, Ayres et al. 1997, Targett & Arnold 1998) and populations (Sotka & Hay 2002). Other processes that take place when kelp is 'aged' have not been considered, but should not be ruled out, as several different processes are expected to occur simultaneously. The reduction in the C:N ratio and degradation of phlorotannins are probably 2 important factors.

Although the general trends were the same for the amphipods, i.e. no amphipod could survive on fresh kelp but both survival and growth was better on aerobically degraded kelp, some interspecific differences were found. Adults of the holdfast species *Lembos websteri* survived better on low-quality food (high C:N and phenolic content), and displayed smaller differences in general between treatments than adults of the epiphyte-associated amphipod *Jassa falcata*. This could indicate that *L. websteri* is a better compensatory feeder than *J. falcata*, perhaps due to its more sedentary behaviour, i.e. the more mobile epiphyte fauna (Norderhaug et al. 2002) require food of higher quality (Cruz-Rivera & Hay 2000b). Shillaker & Moore (1987) also found *L. websteri* to have a wide feeding repertoire. The holdfasts function as sediment traps (Moore 1972a, Conradi et al. 1997) that probably accumulate smaller and more degraded particles. If holdfast-associated species are more efficient compensatory feeders, they would be expected to be able to exploit a larger part of the kelp production. Even when better quality detritus (lower C:N and phenolic content) is available, they can concurrently utilise food of lower

quality than the epiphyte-associated amphipods. The epiphyte-associated fauna are expected to be more dependent on a diet including other constituents, and this may be an important reason for their greater mobility. However, survival differed between the 2 epiphyte-associated amphipods *Jassa falcata* and *Ampithoe rubricata* (Fig. 2). The former was negatively affected by fresh kelp, but not the latter. Such differences demonstrate that more data is needed to establish the relationship between the food requirements of the kelp fauna and their ecology.

Laboratory experiments have shown that many crustaceans increase their fitness by high-quality diets or mixed diets (Costa et al. 1996, Cruz-Rivera & Hay 2000a,b). Such studies, along with multiple-choice feeding experiments (Pavia et al. 1999, Karez et al. 2000), reflect idealised situations. In nature, any individual will be restricted by the food sources available at any one time. Its intake of food items may also be related to factors such as habitat provision or predator refuge (Nicotri 1980, Wakefield & Murray 1998, Jormalainen et al. 2001). Our results indicate that kelp derived detritus is an important food source for the rich macrofauna of the kelp forest. The $^{15}\text{N}:$ ^{14}N isotope data indicate that the species investigated have a low trophic position in the food web (cf. Dunton 2001). The $^{13}\text{C}:$ ^{12}C isotope data suggest that kelp forest POM is mainly kelp derived, and is an important constituent of the diet of these species (cf. Rau et al. 1989), i.e. it is not derived from the majority of the epiphytic red algae upon which these species live. However, fresh kelp and the red alga *Palmaria palmata* have isotope values similar to POM, and only fresh kelp has been ruled out as a food source in this study. The observed differences in isotope signal between the various macroinvertebrate species also suggest that other food sources are utilised, perhaps in mixed diets. This is common in kelp forest macrofauna and in related species elsewhere (Nair & Anger 1979a, Shillaker & Moore 1987, Cruz-Rivera & Hay 2000b).

CONCLUSIONS

This study has shown that kelp derived POM with a high C:N ratio is unsuitable as food for many, but not all, consumers until it has gone through an ageing process. It demonstrates the great importance of bacterial degradation in making kelp available as food for the kelp forest consumers and thereby giving them access to a large food source. The results indicate that kelp provides abundant food resources to consumers, and that its large POM production is important to the coastal ecosystem.

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