

Density- and trait-mediated effects of fish predators on amphipod grazers: potential indirect benefits for the giant kelp *Macrocystis pyrifera*

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ABSTRACT: Indirect effects of predators on primary producers may arise when predators suppress herbivore abundance and/or alter the behaviour patterns of herbivores in ways that reduce grazing pressure. Most studies highlight the role of predators in reducing herbivore abundance (i.e. density-mediated interactions), while behavioural effects (i.e. trait-mediated interactions) induced by predators are less commonly considered and are often assumed to be of secondary importance. We used a mesocosm experiment to evaluate the consumptive and behavioural effects of 2 species of predatory fishes on amphipod grazers that feed and nest on the giant kelp *Macrocystis pyrifera*. Only one, *Notolabrus celidotus*, of the 2 predator species reduced grazer abundance. Although the second predator species, *N. fucicola*, did not affect grazer abundance directly, it significantly reduced the grazing efficiency of amphipods on blades of *M. pyrifera*. Our study illustrates how density- and trait-mediated interactions reduce grazer efficiency and provide potential indirect benefits to primary producers. To our knowledge, this is the first experimental evidence of a potential trophic cascade in kelp beds generated by consumptive and nonconsumptive effects. When considered alongside results of other studies that highlight positive effects of macroalgae on reef fish demographic rates, our results provide compelling evidence that mutualistic relationships may exist between kelp and associated predatory fishes.

KEY WORDS: Predation · Amphipods · Trait-mediated effects · Multiple predator effects · Reef fishes · Kelp beds · New Zealand

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INTRODUCTION

Predation is a pervasive process that can influence community organization (Paine 1966, Schmitz 1998, Duffy & Hay 2001) and ecosystem functioning (Schmitz 1998, Sih et al. 1998, Schmitz 2009). A fundamental component of predation is the direct removal of prey, leading to reductions in the numerical abundance of prey populations (Murdoch et al. 2003). Such reductions are considered density-mediated interactions (DMI) between predators and prey (Abrams 1995). Most food web studies have focused on DMIs, placing keystone predation, exploitative competition and cascade effects in the context of changes in densities of predators and/or prey populations (Sih et al. 1998, Duffy & Hay 2001). However,

predators can also induce phenotypic effects (i.e. trait-mediated interactions [TMI] on prey populations, Abrams 1995) (Main 1987, Lima 1998). These effects may induce morphological, physiological or behavioural responses from prey (Preisser et al. 2005). For example, when confronted with predators most prey seek refuge, which may result in a period of inactivity (Sih 1980, Lima & Dill 1990). This shift in behaviour patterns can alter the per capita effects of the prey species on other species (see Werner & Peacor 2003 and references therein). Though both density- and trait-mediated interactions can, in principle, affect the dynamics of other species in the local community (Abrams 1995), the relative importance of these 2 pathways is poorly known in most cases (but see Luttbeg et al. 2003).

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Many temperate subtidal areas are characterised by the presence of habitat-forming kelps (Dayton 1985), including *Macrocystis pyrifera*, which forms dense forests in the Northern and Southern hemispheres (Graham et al. 2007). Many seaweed populations are influenced by herbivory (Dayton 1985). Although several species of large invertebrates are known to be important grazers of *M. pyrifera* (for review see Steeneck et al. 2002), small mobile invertebrates (mesograzers), such as amphipods, are also potentially important in structuring seaweed populations (Duffy & Hay 2000, Graham 2002, Haggitt & Babcock 2003). Amphipods are one of the most abundant and diverse groups of small invertebrates inhabiting *M. pyrifera* (Coyer 1984) and other temperate brown macroalgae (Taylor & Cole 1994). The cumulative effects of grazing by amphipods may be similar to other herbivores on kelp beds (Sala & Graham 2002), and in some cases these effects may be stronger (see Haggitt & Babcock 2003). Furthermore, the high diversity of amphipod species suggests that feeding patterns may vary (Duffy 1990), implying a potential range of ecological consequences attributable to this group of mesograzers (Duffy & Hay 2000).

In kelp habitats, amphipods also provide a link between kelp and higher trophic levels, including fish, which are voracious predators of amphipods (Jones 1988, Holbrook et al. 1990, Taylor 1998). Top-down control of amphipods by fishes constitute a positive indirect effect in which fishes benefit the health and growth of kelp (Davenport & Anderson 2007, Newcombe & Taylor 2010). Some marine fishes are known to substantially reduce the local abundance of amphipods, but no studies (to our knowledge) have addressed possible trait-mediated effects of fishes on amphipod–kelp interactions. In freshwater systems, several studies have indicated that amphipods under threat of predation tend to reduce foraging time (Andersson et al. 1986), mate less frequently (Cothran 2004) and alter their mating decisions (Dunn et al. 2008). These phenotypic responses to predators may deleteriously affect prey populations and alter community structure via trophic cascades. How fishes in temperate kelp systems might affect interactions between amphipods and *Macrocystis pyrifera* remains unknown.

Many ecological communities are composed of multiple predators that may target a common prey item and contribute to density- and/or trait-mediated interactions (Schmitz 2007). In some cases, the presence of multiple predators may actually reduce the overall risk of predation when, for example, 2 or more predators interfere with each other, or when predators also prey on each other (i.e. intraguild predation). Alternatively, the presence of 2 or more predators may enhance their

individual effects (e.g. when the antipredator behaviour of prey to one predator increases its risk to other predators; see Hixon & Carr 1997, Van Son & Thiel 2006).

Here, we use a mesocosm study to evaluate the separate and joint effects of 2 common reef fishes, *Notolabrus celidotus* and *N. fucicola* (Family Labridae), on the interaction between amphipod grazers and the giant kelp *Macrocystis pyrifera*. Specifically, we evaluated the effects of fishes on the survival (DMI) and grazing efficiency (TMI) of amphipods. Both fish predators are common inhabitants of *M. pyrifera* kelp forests, and both feed upon invertebrates including amphipods. We hypothesised that similar feeding modes exhibited by these 2 fishes would not lead to risk enhancement for amphipod prey. Instead, we predicted that the 2 fish predators might interfere with each other, leading to enhanced prey survival in the presence of both predators (Schmitz 2007). Finally, we hypothesised that the effects of fishes on amphipods would be consumptive, such that fishes might alter amphipod–kelp interactions primarily via density-mediated interactions.

MATERIALS AND METHODS

Study species. The gammarid amphipods used in this study, *Pseudopleonexes lessoniae* and *Bircenna macayai*, live and feed upon blades of *Macrocystis pyrifera* as well as other brown macroalgae (Poore et al. 2008, Løerz et al. 2010). Our preliminary studies confirmed that both amphipods leave similar grazing marks when consuming *M. pyrifera* (A. Pérez-Matus unpubl. data); however, they differ in their sheltering behaviours (M. Thiel pers. comm.) (see Figs. S1 & S2 in the supplement at www.int-res.com/articles/suppl/m417p151_supp.pdf).

According to our preliminary surveys from a representative location within the study region, mean (\pm SD) amphipod densities can reach up to 11.52 ± 4.82 individuals frond⁻¹ of *Macrocystis pyrifera*. Amphipods are common prey items for fish predators including the locally common labrids *Notolabrus celidotus* and *N. fucicola* (Russell 1983, Jones 1984, Denny & Schiel 2001, Francis 2001). Juvenile and adult *N. celidotus* and *N. fucicola* are commonly found in association with *M. pyrifera* on rocky reefs around Wellington, New Zealand (Pérez-Matus & Shima 2010).

Field collections. We collected six 1 m apical lengths of fronds of adult *Macrocystis pyrifera* individuals using mesh collecting bags (0.5 mm mesh) designed to retain the associated epifauna (including the mesograzers *Pseudopleonexes lessoniae* and *Bircenna macayai*). We then used seawater to rinse the epifauna from each sampled *M. pyrifera* frond length into a

sieve. We collected 12 juvenile *Notolabrus celidotus* (each ~14 cm in total length, TL) and 12 juvenile *N. fucicola* (~20 cm TL) using baited traps. The traps were 75 cm in length, constructed with knotless 15 mm mesh with a mesh opening of 8 cm diameter, baited with mussels and deployed beneath kelp canopies for ~10 min. Before each experimental trial, newly collected individual fish were acclimatised (without food) for 24 to 32 h in indoor tanks with circulating seawater. Amphipods were acclimatised in separate tanks with aerated seawater only. All individuals (macroalgae, amphipods and fishes) were used only once (i.e. new organisms were collected for each trial).

Experimental design. Experiments were conducted in outdoor tanks (mesocosms) at the National Institute of Water and Atmospheric Research (NIWA, Greta Point, Wellington), and all organisms used for these studies were collected from a common location at Karaka Bay, Wellington New Zealand (41° 18' 31" S, 174° 49' 58" E). We constructed 5 experimental mesocosms using black plastic tanks (150 cm diameter, 45 cm height) supplied with recirculating water at a flow rate of 10 l min⁻¹ (Fig. 1a). Tanks were covered with 0.5 mm mesh that provided shade to *Macrocystis pyrifera* (to more closely match the light environment experienced by seaweeds in the ocean) and prevented fish from jumping out of the tanks. At the centre of each tank we constructed a cylindrical cage (60 cm diameter and 2 mm mesh size, spanning the full height of the tank). This cage structure facilitated our manipulation of fish access to *M. pyrifera* and amphipods, which was required for some experimental treatments. To evaluate potential cage artefacts (Steele 1996), we used mock cages (with an open panel) for a set of our

fish exclusion and control tanks (detailed below). Within each tank we added a single frond of *M. pyrifera* (~50 cm length), which included an average (\pm SD) of 20 \pm 3 blades and the apical meristem (Fig. 1b). To avoid the effects of grazing history on the experimental blades, we carefully selected fronds without grazing marks.

Experimental fronds were established with standardised densities of mesograzers. To ensure that all epifauna were removed from experimental fronds, the fronds were soaked in fresh water for 3 min immediately before their addition to the experimental tanks, which effectively removed any remaining epifauna not captured by the initial sieving. This treatment did not seem to adversely affect *Macrocystis pyrifera*. We then attached defaunated fronds to a rock at the bottom in the centre of each tank with a plastic cable tie. Finally, we supplied a standardised number and composition of amphipods to each mesocosm. The composition of amphipods added to each mesocosm was identical within trials. For all trials but one, we added 6 individuals of each species of amphipod. For the aberrant trial, we stocked mesocosms with 5 individuals of *Pseudopleonexes lessoniae* and 2 of *Bircenna macayai* (because we were limited by the total number of amphipods obtained from our prescribed collection regime). Amphipods were added to mesocosms 1 h before the addition of predatory fishes.

Using this basic configuration, we established 5 unique treatments to evaluate the direct and indirect effects of *Notolabrus celidotus* and *N. fucicola* (separately and in combination) on the survivorship, nesting behaviour and grazing efficiency of amphipods on *Macrocystis pyrifera*. Treatments were as follows: (1)

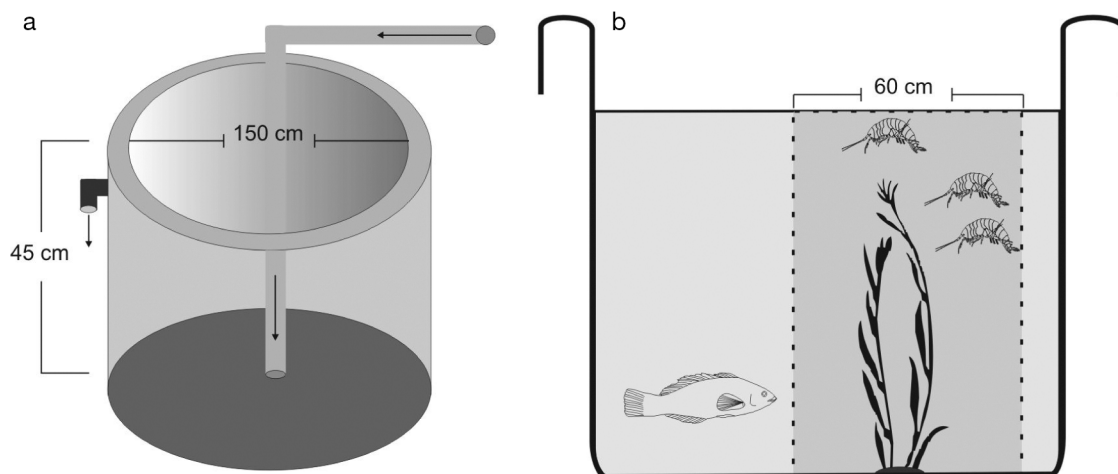


Fig. 1. Diagrammatic representation of mesocosm design. (a) Mesocosm dimensions and arrows representing flow of seawater. (b) Mesocosm shown in cross-section to illustrate placement of organisms relative to internal cage. Each mesocosm contained one cage. Each cage contained a single frond of *Macrocystis pyrifera*. For all treatments except the 'Autogenic' treatment, an initial population of amphipods was introduced to the kelp frond. Fish were then added to the cage as prescribed in the treatments (refer to 'Materials and methods'). Organisms within tanks are not shown to scale

'*N. celidotus* predator': 6 juvenile *N. celidotus* and amphipods were added to the central cage of the mesocosm (i.e. with *M. pyrifera*); (2) '*N. fucicola* predator': 6 juvenile *N. fucicola* and amphipods were added to the central cage of the mesocosm; (3) 'Both predators': 3 juvenile *N. celidotus* and 3 juvenile *N. fucicola* and amphipods at ambient densities were added to the central cage of the mesocosm; (4) 'Fish exclusion': 3 individuals of *N. celidotus* and 3 of *N. fucicola* were added to the tank but outside the cage (i.e. fish had no direct access to kelp and amphipods, which were inside the cage); (5) 'Autogenic': kelp was included without either fish or amphipods. This last treatment served as a control that enabled us to evaluate the overall performance of the kelp (e.g. background tissue accumulation or degradation) under experimental mesocosm conditions in the absence of grazing pressure; this treatment also helped us to develop protocols to distinguish between natural decay and grazing marks caused by amphipods.

We employed a 'substitutive design' that held the overall predator density constant, because one of our primary goals was to evaluate interspecific interactions (Sih et al. 1998). Because we were constrained by the number of available tanks for mesocosms, we replicated treatments in time (i.e. 'trials'; rotating the assignment of treatments across tanks for each trial). The duration of each experimental trial was 6 d. We carried out a total of 8 trials ($n = 8$ replicates) for each treatment, and all trials were completed between 10 February and 22 April 2009.

Density-mediated effects of fishes on amphipods.

Lethal effects (i.e. predation) of the fishes on amphipods were estimated as the proportion of amphipods surviving after each trial. After each trial period, we removed the fish and sieved the contents of each tank, and recorded the number of remaining amphipods.

We used generalized linear models (GLM) (Crawley 2007) to analyse our data because our response variable (proportions based upon counts) had unequal variances and non-normally distributed errors. We contrasted all predator access treatments against the fish exclusion treatment (i.e. '*N. celidotus* predator', '*N. fucicola* predator', 'Both predators' versus 'Fish exclusion'), using the proportion of amphipods surviving as the response variable. For this GLM we specified a binomial error distribution and a logit link function. Data were overdispersed (residual deviance model = 43.7, $df = 28$) and were corrected using a quasibinomial error distribution (Crawley 2007). We conducted a second set of contrasts to detect emergent effects of multiple predators (Sih et al. 1998). We contrasted the proportion of amphipods surviving in the treatment with both fishes present against treatments with either *Notolabrus celidotus* or *N. fucicola*

present (i.e. 'Both Predators' versus '*N. celidotus* predator' and 'Both Predators' versus '*N. fucicola* predator'). A significant difference between treatments was interpreted as evidence of emergent multiple predator effects (MPE). Data were overdispersed (residual deviance model = 72.16, $df = 28$) and were corrected using a quasibinomial error distribution (Crawley 2007). Moreover, we calculated the expected survival (E) of amphipods assuming independence in the presence of both fish predators (Vonesh & Osenberg 2003) as:

$$E_{N. celidotus, N. fucicola} = \frac{\sigma_{N. celidotus} \times \sigma_{N. fucicola}}{\sigma_{\text{Fish-exclusion}}} \quad (1)$$

where σ is the mean proportion (%) of amphipods that survived in each treatment. This was further compared with the mean number of survivors from the treatment when both fish predators were together to detect risk reduction or enhancement on survivorship of amphipods (Vonesh & Osenberg 2003).

Trait-mediated effects of fishes on the grazing efficiency of amphipods. Grazing marks left by amphipods are indicative of their direct consumption of *Macrocystis pyrifera* tissue. We characterised grazing marks inflicted by the 2 amphipod species in our focal study. Undamaged portions of *M. pyrifera* blades were individually immersed in indoor aquaria with seawater and with specimens of amphipods. These observations enabled us to identify grazing marks in our mesocosm experiment (and to differentiate these from algal decay).

We assessed grazing activity on 6 randomly selected blades taken from each treatment/trial in our mesocosm experiment. We counted all apparent grazing marks, and to estimate grazing efficiency, we standardised these counts by the effective densities of amphipods; i.e. we multiplied the observed number of grazing marks by the ratio between the number of amphipods (initial number of individuals) and the number of blades within the mesocosm.

We conducted a preliminary analysis to validate our estimates of grazing marks, by contrasting our 'Fish exclusion' treatment (i.e. amphipods present) and our 'Autogenic' control (i.e. amphipods absent). Following this initial assessment, we used GLM (with Poisson error distribution and log link function) to evaluate variation in amphipod grazing efficiency, contrasting each of the predator access treatments against the 'Fish exclusion' treatment (i.e. '*N. celidotus* predator', '*N. fucicola* predator', 'Both predators', versus 'Fish exclusion'). Data were overdispersed (residual deviance model = 1183, $df = 235$) and were corrected using a quasipoisson error distribution (Crawley 2007). All statistical tests were performed using R v. 2.11.1 (R Development Core Team 2010).

RESULTS

Density-mediated effects of fishes on amphipods

When fish were excluded from the inner cage of mesocosms, amphipods persisted at ~50% of their initially stocked densities. We attributed these losses of amphipods to emigration from the kelp fronds (mesh size of 0.5 mm did not prevent movement of amphipods). Where *Notolabrus celidotus* was present alone, amphipods were reduced to ~10% of their initial stocked densities (Fig. 2a), and relative to the 'Fish exclusion' treatment, this suggests an 80% decrease in amphipod survival ($t = 3.12$, $df = 28$, $p < 0.001$). A similar reduction in survival (i.e. populations were reduced to ~12% of initial densities) was observed in the treatment where both fish species had access to amphipods ($t = 2.63$, $df = 28$, $p < 0.01$). When only *N. fucicola* had access, amphipod populations persisted at ~40% of initial stocking densities, and relative to the 'Fish exclusion' treatment, this does not reflect a significant reduction in amphipod survival ($t = 0.55$, $df = 28$, $p = 0.55$) (Fig. 2a).

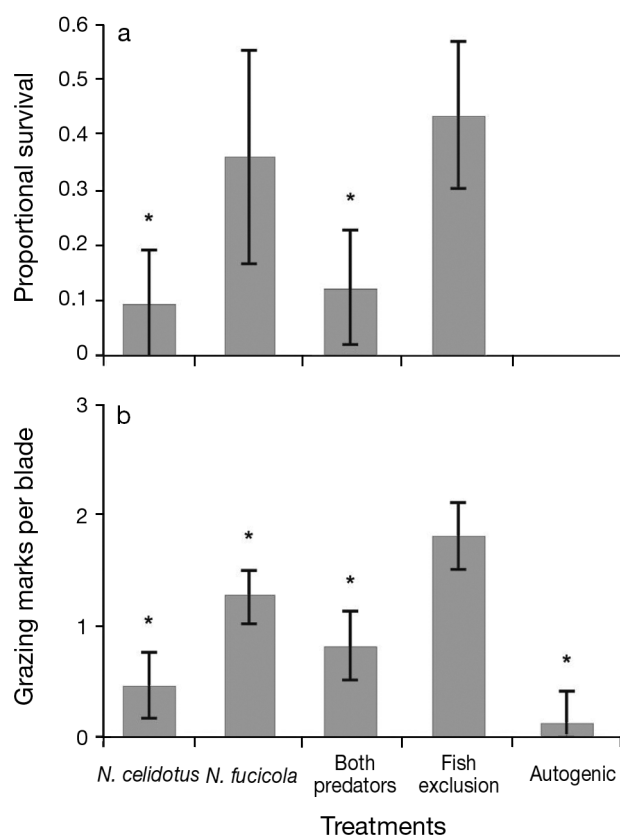


Fig. 2. (a) Proportional survival (mean \pm 95% CI) of amphipods. (b) Per capita number of grazing marks per blade (mean \pm 95% CI). Treatments are as follows: '*N. celidotus*' present, '*N. fucicola*' present, 'Both predators' present, 'Fish exclusion' and 'Autogenic' control. Asterisk (*) denotes significant ($p < 0.05$) differences relative to the treatment 'Fish exclusion'

Our results do not suggest emergent multipredator effects. The expected proportion of amphipod survivors (determined to be 8.6%, assuming the effects of predators were independent of one another) did not differ significantly from the observed proportion of $12.3 \pm 10.1\%$ (mean \pm 95% CI), indicating an absence of emergent multipredator effects (or our inability to detect such effects given our level of replication) when both predatory fishes were together ($t = -0.57$, $df = 28$, $p > 0.05$). In this case, the absence of an emergent multipredator effect is not surprising because only one predator (*Notolabrus celidotus*) appeared to be an effective consumer of amphipods in our mesocosm experiment (e.g. Fig. 2a).

Trait-mediated effects of fishes on the grazing efficiency of amphipods

Both *Pseudopleonexes lessoniae* and *Bircenna macayai* caused visible marks on *Macrocystis pyrifera* in our preliminary aquarium experiment, and marks concordant with these observations were readily identifiable in both the mesocosm experiment and our casual field observations. Both amphipod species damaged only the blade lamina of *M. pyrifera* and left no grazing marks on pneumatocysts. Both species generated deep bites on the blades that can result in complete holes. However, only *P. lessoniae* inflicted substantial lateral damage and bites along the blades, such that within 3 d blades routinely became detached from the pneumatocyst. In contrast, grazing by *Bircenna macayai* more commonly resulted in the formation of a 'gallery' of ~1 cm long, and within this structure grazing appeared to proceed primarily beneath the blade surface (e.g. from within a 'burrow' structure). *P. lessoniae* constructed nests within a period of hours, and they can also leave grazing marks inside the nests (see supplement for photographs of grazing marks, nests and galleries).

After 3 d with *Macrocystis pyrifera* blades in aquaria, both amphipod species consumed substantial amounts of algae, and their activity gave us a very clear 'search image' for grazing marks (see supplement for details). These observations improved our estimates of grazing efficiency in our mesocosm treatments.

Grazing efficiency of amphipods increased 15-fold in the absence of fish predators (i.e. relative to the 'Autogenic' treatment in which amphipods were not added; $t = -6.27$, $df = 235$, $p < 0.001$). We believe this significant difference validates our identification of grazing marks left by amphipods.

Relative to the 'Fish exclusion' treatment, the presence of *Notolabrus celidotus* and *N. fucicola* alone resulted in a 5-fold decrease ($t = -5.72$, $df = 235$, $p <$

0.001; Fig. 1b) and a 2-fold decrease ($t = -2.11$, $df = 235$, $p < 0.01$), respectively, in the number of grazing marks. Relative to the 'Fish exclusion' treatment, the presence of both predators together resulted in 2.5-fold decrease in the number of grazing marks ($t = -4.175$, $df = 235$, $p < 0.001$; Fig. 1b).

DISCUSSION

Our study suggests that 2 temperate reef fishes exert positive indirect effects on seaweeds via consumption or behavioural modification of grazers, and that these 2 fish species do not interfere with one another or otherwise enhance the risk of their prey.

Specifically, we found that both fish species in our study independently reduced the grazing pressure of amphipods on *Macrocystis pyrifera*, and importantly, they appeared to produce this effect via different mechanisms. *Notolabrus celidotus* exerted a direct effect on the amphipod–algae interaction by reducing the numerical abundance of amphipods grazers via consumption. In contrast, *N. fucicola* did not appear to directly consume our focal amphipod species (at least in the context of our experimental mesocosms). Instead, *N. fucicola* exerted an indirect effect on amphipod–algae interactions, perhaps by altering the behaviour of amphipods.

In the presence of *Notolabrus celidotus*, amphipods survived poorly and this may explain their reduced grazing activities on blades of *Macrocystis pyrifera*. Thus, *N. celidotus* appears to affect amphipod–algae interactions via a density-mediated interaction (DMI). In contrast, the presence of *N. fucicola* appears to induce a behavioural change in amphipods that also results in reduced grazing activity, and this is consistent with *N. fucicola* provisioning benefits to *M. pyrifera* via a trait-mediated interaction (TMI). The strength of the DMI in our system appears to be twice as strong as the TMI. Some authors have argued that DMIs are more important in magnitude than TMIs (but see Huang & Sih 1990). The strength of both DMIs and TMIs depends on the foraging behaviour of predators and risk effects posed to prey species (Schmitz & Suttle 2001). In short, prey species may trade off risks of starvation with risk of being eaten (both are functions of foraging time) (Schmitz et al. 1997). Both DMIs and TMIs must be considered when evaluating predatory effects on communities.

The importance of trait-mediated effects is apparent across a range of environments. Turner (1996, 1997) demonstrated the effects of a TMI involving molluscivorous fish and snail grazer on periphyton dynamics in a freshwater system. Similarly, Trussell et al. (2002, 2004) found that TMIs could be even more important than the direct consumption by predators in some marine tide pools. Most studies of TMIs, however, have

been conducted with predators on target prey. Non-consumptive effects are important in community dynamics and few have documented the induced behavioural changes of predators in nontargeted prey whilst reducing the strength of herbivory on plants (see Walzer & Schausberger 2009).

Our study confirms that the mere presence of a predator (e.g. *Notolabrus fucicola*) can reduce herbivore damage by a nontarget prey. Reduced foraging activity and increased use of shelters to decrease detection by predators are common antipredator behaviours. These have been described previously in several amphipod–fish predator interactions (Williams & Moore 1985, Andersson et al. 1986, Bollache et al. 2006). According to the trait compensation hypothesis, prey with poor morphological defence might show stronger antipredator behaviours than morphologically well-defended prey (Dewitt et al. 1999). Amphipods may initiate a series of behavioural actions to avoid natural enemies (e.g. *N. celidotus*) or unusual predators (e.g. *N. fucicola* in our study). First, both amphipod species and both sexes of amphipods examined here have the ability to construct 'nests' (in the case of *Pseudopleonexes lessoniae*) by curling the blades of macroalgae (see Appadoo & Myers 2003, Cerda et al. 2010 for details on amphipod nesting behavior), or they may generate 'galleries' (*Bircenna macayai*) that provide sites for reproduction and refuge from predators while feeding. Nest occupancy is short, usually less than 4 d within a single nest, and amphipods exhibit high mobility within a single sporophyll (Cerda et al. 2010). Secondly, like many crustaceans, amphipods may use chemical cues to detect and escape from predators (Hazlett 1999). We observed losses of amphipods of close to 50% when predators were present in our experimental mesocosm but unable to access their prey. One possible explanation for these losses is that the prey (i.e. amphipods) may detect chemical cues from fish predators and, subsequently, attempt to emigrate to a safer location. Unfortunately, our design did not include a treatment with amphipods present and fish absent, so we are unable to address this possibility directly.

We were unable to identify a significant emergent multiple predator effect (MPE) on amphipod survival when both fish predators were present. We found neither risk reduction nor enhancement of prey consumption, suggesting that when they are together, these predators do not interfere with each other. Amphipod survival was low when *Notolabrus celidotus* was present alone. Amphipod survival was similarly low when *N. celidotus* was present with *N. fucicola*; this is considered to be a trivial MPE (Sih et al. 1998). This agrees with the majority of MPE studies, which have found that multiple predators are not substitutable in their consumption of prey (reviewed by Sih et al. 1998). Al-

though amphipods frequently occur in the diet of both fishes (Russell 1983, Denny & Schiel 2001), the lack of substitutable predatory effects between *N. fucicola* and *N. celidotus* may be explained by a combination of a lack of competition for prey resources (suggesting resource partitioning) and a narrow habitat domain of amphipods (i.e. occurring only on fronds of *Macrocystis pyrifera*). For example, if in the field one predator forages more commonly on fronds while the other forages on the holdfast, as have been suggested (Jones 1984, Denny & Schiel 2001), MPEs would be expected to be trivial (or else dependent upon the degree to which amphipods move between these microsites within *M. pyrifera*). Hence, spatial partitioning of prey and predator activities could simplify, effectively, to 2 separate single predator–prey systems, where only one predator is able to reduce amphipods numerically in each microsite (Schmitz 2007).

Reported ontogenetic changes in the diet of the fish predators offer another explanation for the observed differences between fish species in their propensity to consume amphipod prey. Both *Notolabrus celidotus* and *N. fucicola* undergo dietary shifts in their preferences for small crustaceans such as amphipods (Jones 1984, Denny & Schiel 2001). According to Denny & Schiel (2001), large *N. fucicola* (such as those used for this study) consume more hard-shelled prey than do smaller size classes (~150 mm TL), which more regularly consume amphipods. While large *N. fucicola* may no longer target amphipods as prey, amphipods may be unable to distinguish between size classes of known fish predators.

Grazing activities of amphipods may have substantial effects on many marine communities. At least one study suggests that grazing pressure increases following El Niño events, when amphipod populations have been observed to increase (Tegner & Dayton 1987). Grazing by amphipods may be severe enough to limit recruitment (Tegner & Dayton 1987, Graham 2002) and lead to compensatory growth of kelp (Cerde et al. 2009). Fish are known to mediate amphipod populations by consumptive effects that can reduce local densities of amphipods. Thus, fish may also be expected to regulate grazing pressure and benefit *Macrocystis pyrifera* via DMIs. In our study area, fish densities are elevated in vegetative structures (Pérez-Matus & Shima 2010) and may be sufficiently high to suppress amphipod populations. Our results are partially consistent with other experiments conducted in mesocosms (Duffy & Hay 2000, Newcombe & Taylor 2010) and caging experiments in the field manipulating fish predators (Davenport & Anderson 2007, Korpinen et al. 2007), in that they revealed a significant effect of amphipods on benthic biota in the absence of fish predators. Our experiments also suggest that fish may similarly benefit *M. pyrifera* via a non-consumptive (i.e. TMI) effect on prey behaviour.

The data provided in this study may motivate future research into the behaviour, ecology and evolution of possible mutualistic relationships between kelp and their associated fish fauna.

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