

## SPECIES INTERACTIONS IN INTERTIDAL FOOD WEBS: PREY OR PREDATION REGULATION OF INTERMEDIATE PREDATORS?

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**Abstract.** Most natural food webs have more than one predator species, and many have trophic interactions among these predators. When a top predator feeds on an intermediate predator and they both feed on a shared basal resource, a phenomenon labeled intraguild predation (IGP), the potential exists for complex food web dynamics due to predation and competitive effects. Here we investigate the relative importance of direct predation vs. competition by a top predator on an intermediate predator.

The study system is the rocky intertidal interaction web formed by the predatory seastar *Pisaster ochraceus*, the predatory whelks *Nucella emarginata* and *N. canaliculata*, and a shared resource species, the mussel *Mytilus trossulus*. Previous experiments documented strong negative effects of *Pisaster* on mussels and whelks, but the mechanisms responsible for the effects on whelks, whether competition or predation, were not identified. Here we report results of a field experiment that manipulated both *Mytilus* and *Pisaster* to determine the short- and longer-term changes in whelk populations. Using a simplified dynamic model for changes in abundance over the initial stages of the experiment, we separated and quantified the top-down effect of direct predation by seastars vs. the bottom-up effects of competition and food limitation. Short-term results were in agreement with longer-term responses. Results suggest that direct and indirect bottom-up influences of mussels were far stronger than predation, and thus, whelk increases in the absence of seastars were due to reduced competition with *Pisaster*. Large differences between the body sizes of seastars and whelks make it difficult to determine the ultimate nature of the resource under competition between predators. Small mussels may constitute only a food resource for seastars, but to some extent, they also represent a microhabitat for whelks. Differences in the magnitude of the response to mussel manipulations between *Nucella* species might be due to slight differences in the way the species utilize mussel beds. Some of the predictions of theoretical IGP models regarding coexistence and stability of species may not apply to this interaction web because it includes species with both “open” and “closed” populations, rather than just closed populations as assumed by the models.

**Key words:** bottom-up effects; effect sizes; exploitation competition; intraguild predation; mussels; *Mytilus*; *Nucella*; *Pisaster*; rocky intertidal; seastars; top-down effects; whelks.

### INTRODUCTION

Most food webs have more than one predator, and many also have a complex pattern of competitive and trophic interactions among these predators. In the simplest food webs, predators feed on the trophic level immediately below: a “top” predator feeds on an “intermediate” predator, which in turn feeds on herbivores or basal species. When this pattern of trophic interactions dominates food webs, the removal of species at the top trophic level results in a chain of effects producing a classic trophic cascade with alternation of positive and negative biomass responses between trophic levels (e.g., Hairston, Smith, and Slobodkin 1960,

Oksanen et al. 1981, Carpenter et al. 1985, Brönmark et al. 1992, Hunter and Price 1992, Moran et al. 1996). Specific predictions about the forces that regulate different trophic levels can then be made and some of them have been experimentally tested (e.g., Brönmark et al. 1992, Wootton and Power 1993, Wootton et al. 1996). However, this food web scenario can be substantially complicated by the existence of intraguild predation (IGP), in which a top predator feeds on an intermediate predator and both feed on a shared prey (Polis et al. 1989). In this case, predictions about the effects of predation will depend on the relative strengths of exploitation competition for prey, vs. direct predation of one predator on another (Spiller and Schoener 1990, Polis and Holt 1992, Holt and Polis 1997).

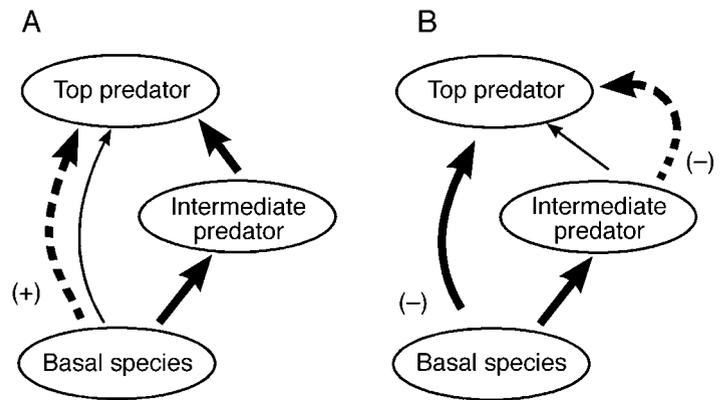
The widespread occurrence of intraguild predation and other forms of omnivory in natural food webs (e.g., Bradley 1983, ter Braak 1986, Menge and Sutherland

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FIG. 1. Two food webs with intraguild predation (IGP). In model A, the top predator feeds mostly on the intermediate predator, thus having a positive indirect effect on the shared basal prey. In model B, the top predator feeds mostly on basal prey, having a dominant negative direct effect on basal prey. Arrow thickness is proportional to the importance of the link. A solid line indicates a direct effect; a broken line indicates an indirect effect.



1987, Polis 1991, 1994, Diehl 1992, 1993) has led Polis and Strong (1996) to question the validity of the trophic level concept and the generality of trophic cascades. If intraguild predation among predators is strong, predation should keep predator densities low and prey abundance is predicted to be high (Fig. 1, model A). Alternatively, if intraguild predation is weak, but predator effects on shared prey are strong, exploitation competition may structure the higher trophic levels and prey should be subject to severe reductions (Fig. 1, model B; see Spiller and Schoener [1990], Diehl [1995]). A plethora of indirect effects, including resource competition, apparent competition, and mutual enhancement are possible in food webs with IGP (Polis et al. 1989). A simple theoretical analysis of a three species community with IGP, leads to the prediction that for an intermediate IG predator to coexist with a top IG predator (see Fig. 1), the former must be superior at exploiting shared prey resource (Polis and Holt 1992). Building on these simple models, Holt and Polis (1997) have recently formulated a basic theoretical framework for intraguild predation, leading to the identification of a series of conditions necessary for the stable coexistence of IG predators, IG prey and a basal resource species. Predictions from these models have not been experimentally tested.

In most marine intertidal food webs, several co-occurring predator species interact trophically (e.g., Dayton 1971, Menge 1983, Robles and Robb 1993, Navarrete and Menge 1996). The focus of most work in these systems has been on interactions affecting the basal trophic level (filter feeders and macroalgae), however, and relatively little experimental work has documented the effects of predation among trophically high species (but see Garrity and Levings 1981, Menge et al. 1986, Barkai and McQuaid 1988, Robles and Robb 1993).

On the Oregon coast, recent studies have suggested an inverse relation between predation by seastars, the "top" keystone *Pisaster ochraceus* and the size and local abundance of "intermediate" predators, the whelks *Nucella canaliculata* and *N. emarginata* (Menge et al. 1994, Navarrete and Menge 1996). The mech-

anism(s) underlying the increase in whelk density and, in some cases, average individual size following the removal of seastars was (were) not revealed by these experiments. Although seastars prey on whelks, frequencies of whelks in *Pisaster* diet are always low (Landenberger 1968, Menge 1972, Menge and Menge 1974, Sanford 1999). While this might suggest that predation by seastars on whelks is weak, the prevalence of prey items in the diet of predators is often not a good indicator of the actual impact of predators on prey populations (Paine 1980, Fairweather and Underwood 1983, Polis 1994). Steady predation on whelks, which are not abundant in the low intertidal zone where these consumers coexist, could have an important effect on whelk abundance or size. Alternatively, the changes could have been due to reduced exploitation competition. While *Pisaster* has a very broad diet that includes barnacles, limpets, snails, and chitons, mussels are its preferred prey (Paine 1974). Whelks, *Nucella* spp., feed almost exclusively on mussels and barnacles (Dayton 1971, Palmer 1984, Wieters and Navarrete 1998). Thus, whelks share a major prey resource with seastars, and both seastars and whelks have been documented to severely depress mussel abundance (Dayton 1971, Paine 1974, Menge et al. 1994, Navarrete and Menge 1996). Previous experiments found no detectable effects of whelks on seastars (Navarrete and Menge 1996), and thus if competition occurs, it is expected to be highly asymmetric in favor of seastars. Since both seastars and whelks feed most intensively on barnacles and mussels, they clearly co-occupy the predator guild in this community.

In this study we experimentally investigated the relative effects of intraguild predation vs. exploitation competition on the abundance of two species of whelks. We tested the effect of predation by manipulating seastar density, as in our earlier experiments. We evaluated the effect of exploitation competition by manipulating the abundance of small mussels that are available to both seastars and whelks. The relative sizes of seastars and whelks with respect to mussel prey makes it difficult to determine the ultimate nature of the resource under competition, however. The small mussels con-

sumed by whelks and seastars are similar in size to adult whelks, and both are much smaller than adult seastars. In addition to food resources and unlike adult seastars, whelks could find refuge from other predators (e.g., birds) or from environmental conditions by hiding amongst the mussels, although by doing so they are probably more exposed to incidental predation by seastars. Although our experimental areas provided abundant refuges for whelks under all treatment combinations, the experiments were not specifically designed to determine the relative importance of mussel beds as food or microhabitat. Thus, our evaluation of "exploitative competition" includes both the indirect effect of seastars on whelks through reducing food and, to some extent, through removing microhabitat.

By determining the responses of whelks to all combinations of seastar and mussel presence and absence and using a simple dynamic model that incorporates IGP, we were able to quantify and separate the effects of direct predation by and competition with seastars, as well as the direct bottom-up effect of prey resource. Our results suggest that the direct and indirect bottom-up influence of mussels was far stronger than predation, and thus that whelk increases in the absence of seastars were primarily due to reduced exploitation competition with *Pisaster*.

## METHODS

### *Study site*

This study was carried out from April 1994 to May 1995 at Strawberry Hill (44°15' N, 124°07' W; hereafter SH), located ~50 km south of Newport on the central Oregon coast, and described in Menge et al. (1994) and Navarrete and Menge (1996). Briefly, this site consists of a broad rocky bench whose numerous channels, tidepools, and outcrops break into a complex topography. Wave-exposed, low zone rocky surfaces are dominated at this site by sessile and mobile invertebrates; while seaweeds and surfgrass are present, they are a relatively minor component of community structure as compared to other sites along the coast of Oregon. Further, abundances of certain invertebrates vary annually in a predictable pattern (S. Navarrete, B. Menge, and B. Daley, *personal observation*). In late summer, *M. trossulus* are usually nearly absent; the barnacle *Chthamalus dalli* is typically the most abundant sessile invertebrate, while much rock surface is bare. Mussel settlement peaks in early fall (Menge et al. 1994), usually leading to the formation of large patches (from tens to hundreds of square meters in size) of *M. trossulus* in the low zone by mid- to late-winter. Another barnacle, *Balanus glandula*, typically settles from spring through autumn (Menge 2000), briefly reaching moderately high densities in the low zone. The gooseneck barnacle, *Pollicipes polymerus*, sometimes also settles heavily in the low zone, and can form extensive patches persisting for several years (B. Men-

ge, *unpublished data*). Seastar activity increases from late winter into summer, depleting the mussel patches by mid to late summer.

### *Seastar predator and mussel prey manipulations*

The mussel patches characteristic of the wave-exposed low zone at SH offered a satisfactory compromise between the conflicting needs for a relatively large area, with high predator densities, but an area small enough to make mussel removal feasible. The occurrence of mussels in relatively large patches permitted us to test the effects of predation and food on whelks using relatively (potential) artifact-free manual manipulative methods (as opposed to exclusion cages or fences).

Sixteen mussel patches (experimental plots) between 1.4 and 15.6 m<sup>2</sup>, relatively isolated from each other by surge channels and spread along a 500-m stretch of shore were located and marked with 10 × 10 cm Plexiglas plates engraved with treatment codes and plot number in March and April, 1994. Plot size varied according to the presence of surge channels and crevices and was not manipulated. The design included four replicates for each of the four combinations of seastar predator (present: +, or absent: -) and mussel prey (present, absent) treatments: +*Pisaster*+*Mytilus*, +*Pisaster*-*Mytilus*, -*Pisaster*+*Mytilus*, and -*Pisaster*-*Mytilus*. Each treatment combination was assigned randomly to plots, although in two cases we had to reassign treatments (nonrandomly). These reassignments were made because seastar-removal plots were so close to seastar-present plots that removal would have influenced densities in the neighboring nonremoval plots. Immediately above the experimental plots there were beds of the large mussel *Mytilus californianus*, which guaranteed the provision of refuge for whelks even in the absence of *M. trossulus*.

On 11 April 1994, abundance of mussels, other sessile invertebrates and whelks was estimated using 0.25-m<sup>2</sup> quadrats subdivided into a grid of 25 10 × 10 cm squares. Percent cover of sessile animals was estimated visually with the aid of the 10 × 10 cm grid. Density of whelks was estimated by counts of individuals in the entire quadrat. Since quadrats represented subsamples in each experimental plot, analyses used means of all quadrats for each plot. Seastar density was simply the number of individuals occurring in each experimental plot; divided by plot area. Plot area was estimated by measuring distances from the center of each plot to plot edge, estimated at 36° intervals, for a total of 10 measurements. These data were plotted on polar coordinate paper and area was estimated using a planimeter.

After these premanipulation estimates were made, seastars and mussels were removed from the corresponding removal plots. Seastars were pried from each removal plot and placed in appropriate habitat away from the plots. Mussels were removed using scrapers,

a process that necessarily also removed most acorn barnacles intermingled among the mussels. These were "press" perturbations (sensu Bender et al. 1984), so re-invading seastars and recruiting mussels were removed repeatedly. For seastars, removal frequency varied with seastar activity and season. In spring and summer, removals were done on most visits to this site, so ranged from daily to approximately every two weeks. In fall and winter, weather often prevented access to the site, but we were able to detach seastars at two to four week intervals. Due to time constraints, we were not always able to record seastar density in the seastar control plots during these visits.

Because we were unable to prevent re-invasion of seastars from removal plots during fall 1994 and because our design allowed whelks (and other predators) to prey on mussels in the patches, the mussel cover in the +*Mytilus* plots (unmanipulated mussel beds) decreased to the levels created in the -*Mytilus* plots. By late winter 1995, the mussel cohort from fall 1994 had again reached covers >50% in the +*Mytilus* plots, while rescraping the -*Mytilus* plots, after the fall mussel recruitment pulse, maintained mussel cover close to zero. Thus, the "mussel treatment" was effective during spring and summer 1994; it was not effective from late fall 1994 to late winter 1995, and then it was effective again in spring and summer 1995.

After initiation of the experiment, abundances of whelks and sessile invertebrates were estimated eight times between April 1994 and May 1995. In addition, we twice estimated average shell lengths per plot of each whelk species, once at initiation and once again in June 1994. This was done to ensure that size structures of the populations in each patch were initially comparable among the plots in the different treatments.

#### Data analysis

Because the effectiveness of the mussel treatment varied during the course of the experiment, data were divided into four time intervals for purposes of analysis: (a) early spring 1994, before manipulations were performed, (b) late spring and summer 1994, when the mussel treatment was effective, (c) fall and winter 1994–1995, when the mussel treatment was not effective but the plots continued to be monitored, and (d) spring and summer 1995, when the mussel treatment was again effective.

Whelk densities before manipulations were compared using two-way ANOVA with *Mytilus* and *Pisaster* densities as orthogonal treatments. Log-transformed data exhibited visually normal distribution and variance homogeneity according to Cochran's *C* test (Underwood 1997). Log transformation seemed appropriate not only to improve variance homogeneity, but because the mussels and seastars are expected to have multiplicative effects on whelk population size (Wilbur and Fauth 1990, Wootton 1994, Osenberg and Mittelbach 1995). Since it can be argued that *Nucella* species

might affect each other's densities within experimental plots, making separate ANOVAs nonindependent, we also compared densities before manipulations using a two-way MANOVA (Huberty and Morris 1989, Scheiner 1993) with the two *Nucella* species as dependent variables. Because the same experimental plots were followed over time, changes in whelk densities after application of treatments were analyzed using repeated-measures multivariate analysis of variance (RM-MANOVA; Crowder and Hand 1990, von Ende 1993), separately for both *Nucella* species.

Analyses were based on mean whelk densities per replicate during spring–summer 1994, fall–winter 1994–1995, and spring–summer 1995. Again, a multivariate analysis of variance considering both *Nucella* species simultaneously was conducted to compare the overall treatment means. Low degrees of freedom did not allow us to conduct repeated-measures MANOVA. Percent cover values of acorn barnacles (*Balanus* and *Chthamalus*) were similarly analyzed with RM-ANOVA, but only for the last three sample dates (January, April, and May 1995), because their abundances were near zero in all treatments until fall 1994. Arcsine transformation of percent cover data was necessary to meet the assumption of variance homogeneity (Underwood 1997). Since seastars might also respond to the mussel manipulations in the +*Pisaster* plots, we compared seastar abundance between +*Mytilus* and -*Mytilus* treatments using one-way RM-ANOVA. A one-way ANOVA was used to compare premanipulation seastar abundances.

Since whelks of the genus *Nucella* have no free swimming larval stage, their populations are "closed"; that is, local processes impinging on the reproductive potential of adults will directly affect local population abundance (Connell 1970, Spight 1974, Spight and Emlen 1976). Therefore, we used a simple difference equation model to fit the observed changes in local abundance of whelks. The model was

$$\log(N_t/N_0) = (f_1M - f_2P - m_N)t$$

where  $N_t$  is the abundance of whelks at time  $t$  and  $N_0$  the initial abundance of whelks in each experimental plot;  $f_1$  is a per-whelk scaling function that expresses the rate of acquisition and transformation of mussel prey into new whelk individuals;  $f_2$  is the seastar per capita consumption of whelks;  $m_N$  is the natural mortality and emigration rate of whelks; and  $M$  and  $P$  are the mussel and seastar abundances, respectively. An equation for the simultaneous changes in abundance of mussels allowed us to estimate the effect of seastars on mussel abundance and thus indirectly on whelks. Following Gaines and Lafferty's (1995, see also Gurney and Nisbet [1998]) modeling approach to completely open populations, mussel changes were expressed as follows:

$$\log(M_t/M_0) = (\Lambda - f_3N - f_4P - m_M)t$$

where  $M_t$  is the mussel abundance at time  $t$  and  $M_0$  that at the beginning of the experiment;  $f_3$  and  $f_4$  are the per capita consumption rates of mussels by whelks and seastars, respectively (equivalent to the alpha terms in Navarrete and Menge 1996),  $m_M$  is the mussel mortality rate in the absence of predators, and  $\Lambda$  is the mussel recruitment rate. Since experiments were started in spring, several months after the fall recruitment of mussels,  $\Lambda$  was assumed to be negligible during the course of the experiments. Because estimates of predation effects on mussels were done by comparing +*Mytilus* plots with and without seastars, relaxing the assumption about lack of mussel recruitment would not significantly alter our results, as long as recruitment was not biased by the removal of seastars from the -*Pisaster* plots. As a first approximation, we considered that at the beginning of the experiment *Pisaster* densities would remain relatively unchanged by application of the *Mytilus* treatment. This assumption proved to be partially wrong because of fast aggregative and emigration responses of seastars to *Mytilus* manipulations.

Using only data from the first 35 d of the experiment to minimize potential indirect effects due to species not considered in the experimental manipulations (Billick and Case 1994, Wootton 1994), yet allowing enough time to measure exploitation competition on the target whelk species, we regressed the natural logarithm of whelk abundance data ( $N_t/N_0$ ) over time in days. Estimates of the slopes of this relationship under each treatment combination were obtained using ordinary least squares. These slopes will be estimates of the following components of the dynamic equation for whelks under the different treatment combinations: (a) the slope in treatment -*Mytilus*-*Pisaster* will be an estimate of  $m$ , (b) the slope in treatment -*Mytilus*+*Pisaster* will estimate  $f_2P - m$ , (c) the slope in treatment +*Mytilus*-*Pisaster* will estimate  $f_1M - m$ ; and (d) the slope in +*Mytilus*+*Pisaster* will estimate  $f_1M - f_2P - m$ . Subtracting the natural mortality term, it was possible to estimate the per-population effect size of seastar predation,  $f_2P$ , and the direct bottom-up effect of prey,  $f_1M$ . Confidence intervals (95%) around the slope estimates were calculated from the least squares regression. Confidence intervals for the resulting parameter estimates were calculated using error propagation rules for random independent errors (Taylor 1982).

Similarly, to obtain an estimate of the effect of *Pisaster* on mussel abundance ( $f_4P$ ) during the same first 35 d of the experiment, we regressed the log-transformed proportional abundance of mussels ( $M_t/M_0$ ) in the +*Mytilus* plots against time. The least squares slope of this relationship in the +*Pisaster* treatment provided an estimate of the  $f_3N - f_4P - m_M$  term in the equation for mussel changes (assuming negligible mussel recruitment during the period). The slope under the -*Pisaster* treatment estimated  $f_3N - m_M$ . Since we have previously shown that predation by *Pisaster* on mussels

is unaffected by the presence of whelks (Navarrete and Menge 1996), subtraction of  $(f_3N - m_M)$  from  $(f_3N - f_4P - m_M)$  provided an estimate of  $f_4P$ , which multiplied by the effect of mussels on whelks ( $f_1M$ ) provided an estimate of the indirect effect of exploitative competition of *Pisaster* on whelks (see Fig. 1). It is important to note that all our estimates are dependent on the existing levels of predators and prey and that per capita coefficients of interaction strength (see Laska and Wootton 1998, Berlow et al. 1999) cannot be estimated because densities of prey and predators are expected to change during the course of the experiment.

## RESULTS

### Initial conditions

Premanipulation patterns of community structure in the plots did not vary with treatment. Mussels (*Mytilus trossulus*) initially covered 40–60% of the substratum and were by far the most abundant sessile species, with average covers of the barnacles *Balanus glandula* and *Chthamalus dalli* ~15% and 10%, respectively (Fig. 2). Covers of the larger barnacle *Semibalanus cariosus*, the lepidomorph *Pollicipes polymerus*, and anemones *Anthopleura* spp. all averaged <5%. Similarly, no significant premanipulation differences in whelk densities were detected (Fig. 3, "Before manipulations"; Table 1), nor there were differences in densities of seastars between plots assigned to +*Pisaster* and -*Pisaster* treatments (Fig. 4A,  $F = 1.02$ ,  $P = 0.3507$ ,  $df = 1, 6$ ). Seastar densities did not differ among treatments before manipulations. Hence, experimental results were unlikely to be affected by any premanipulation differences in abundances of sessile invertebrates or the whelks.

### Treatment effectiveness

As in most such experiments, seastar "removal" did not result in the complete absence of *Pisaster*. Seastars commonly reinvaded the removal plots in a matter of days following the manual removals, particularly in spring and summer when seastars are most active (see also Menge et al. [1994]). Despite these reinvasions and considering that seastar densities were reduced to zero after each monitoring, the overall density of seastars in the +*Pisaster* treatment ( $2.12 \pm 0.24$  individuals/m<sup>2</sup> [mean  $\pm$  1 SE]) was  $>2.5\times$  the density in the -*Pisaster* treatment ( $0.84 \pm 0.31$  individuals/m<sup>2</sup>, Fig. 4). However, between September 1994 and February 1995, densities of seastars in the unmanipulated +*Pisaster* declined to levels similar to those in the seastar removal plots (Fig. 4), rendering the *Pisaster* treatment ineffective during that period.

Mussel removal was highly effective through September 1994, and only slightly less effective from then until the end of the experiment (Fig. 2). The modest increase in mussel cover in -*Mytilus* treatments was due to recruitment and growth, and our efforts to avoid

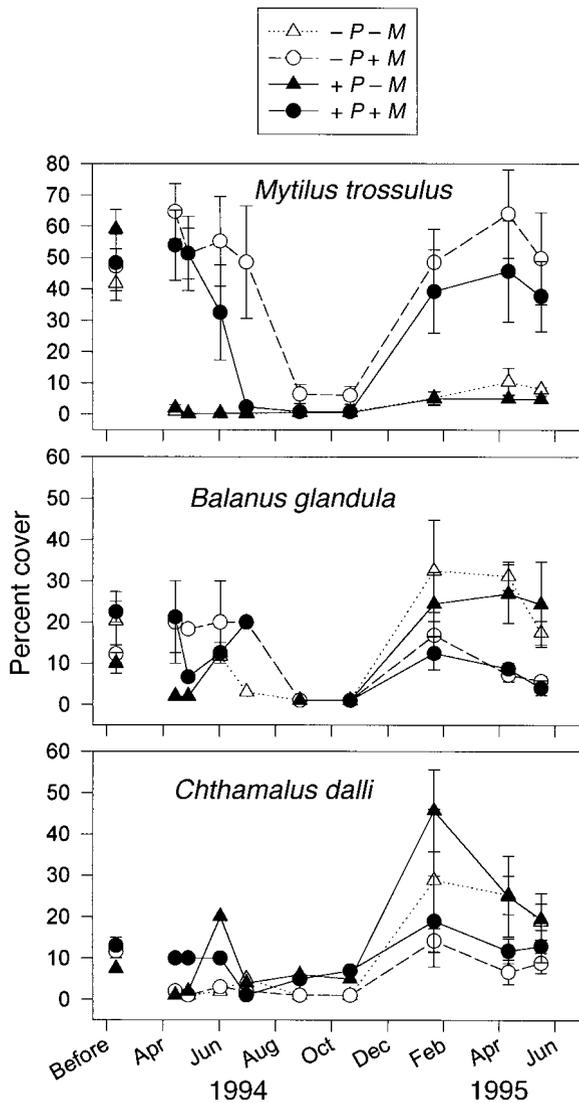


FIG. 2. Percent cover (mean  $\pm$  1 SE) of the mussel *Mytilus trossulus* and the barnacles *Balanus glandula* and *Chthamalus dalli*, the most abundant sessile species under the different combinations of *Pisaster* (P) and *Mytilus* (M) present (+) or absent (-). Cover of *M. trossulus* was reduced to near zero in the -*Mytilus* plots by manually scraping the rock, while mussel beds in +*Mytilus* plots were left undisturbed. Barnacles were inevitably removed with mussels in the initial mussel removal during April 1994, but they were undisturbed after that time.

removing barnacles while maintaining mussel removals. The effectiveness of the mussel treatment varied greatly over time, however. Mussel cover in +*Mytilus* plots decreased to the low levels maintained in the -*Mytilus* plots between late summer 1994 and early winter 1994–1995 (Fig. 2). During this period, seastar reinvasions evaded our control, resulting in near-elimination of mussels in these treatments for ~3 mo (Fig. 2). We continued to maintain the experiments, however, and by February 1995, mussel cover had largely re-

bounded, through recruitment and growth, to the levels seen in summer 1994 (Fig. 2).

#### Predation and prey effects

The manipulations led to strong responses by the whelks by spring 1994 (Fig. 3). Overall, whelk abundance increased in spring 1994, stayed high through the summer, decreased in winter 1994–1995, and increased again in spring 1995 (Fig. 3), following the typical seasonal changes reported previously for the Oregon coast (Berlow 1994, 1997, Navarrete 1996, Navarrete and Menge 1996). Changes in whelk abundance differed markedly with treatment and, to a lesser extent, with species of *Nucella*. In spring–summer 1994, densities of both *Nucella* species increased  $>3\times$  in the presence of mussels (+*Mytilus*) while they remained relatively unchanged when mussel beds were removed (Fig. 3). The proportional change was slightly lower and more variable for *N. emarginata*.

In winter 1994–1995, overall densities of both whelk species decreased, but for *N. canaliculata*, the differences between the +*Mytilus* and -*Mytilus* treatments were still evident and proportionally the same as those observed in spring–summer 1994 (Fig. 3). In contrast, differences between mussel treatments tended to disappear for *N. emarginata* toward the beginning of winter. In spring–summer 1995, densities of *N. canaliculata* again increased in the +*Mytilus* treatment, reaching the levels observed the previous year. Overall densities of *N. emarginata* also increased in spring–summer 1995, but they did not reach the values observed the previous spring–summer, nor were there the same proportional differences between +*Mytilus* and -*Mytilus* treatments (Fig. 3). No effect of *Pisaster* deletion was detected throughout the experiment for either *Nucella* species.

Statistical analyses indicated that high densities of *N. canaliculata* depended on *Mytilus* but not on *Pisaster* (Table 2, between-subjects main effects; *Mytilus* was significant, *Pisaster* was not). The effect of *Mytilus* did not vary with either *Pisaster* density (Table 2, no significant effect of *Pisaster*  $\times$  *Mytilus* interaction) or over time (Table 2, no significant *Mytilus*  $\times$  Time interaction). In partial contrast, densities of *N. emarginata* evidently varied independently of *Pisaster* density, and depended on *Mytilus* density but only at certain times (Table 2, significant within-subjects effect of *Mytilus*  $\times$  Time). Temporal variability in the response of *N. emarginata* to the treatments was so great (Fig. 3) that, despite trends similar to those for *N. canaliculata*, the overall between-subjects effect of *Mytilus* on density of this whelk was not significant (Table 2).

Similar results were obtained when the overall temporal means of both *Nucella* species were considered as dependent variables and compared using MANOVA (Table 3). Presence of *Mytilus* but not of *Pisaster* affected whelk abundance. Analysis of standardized ca-

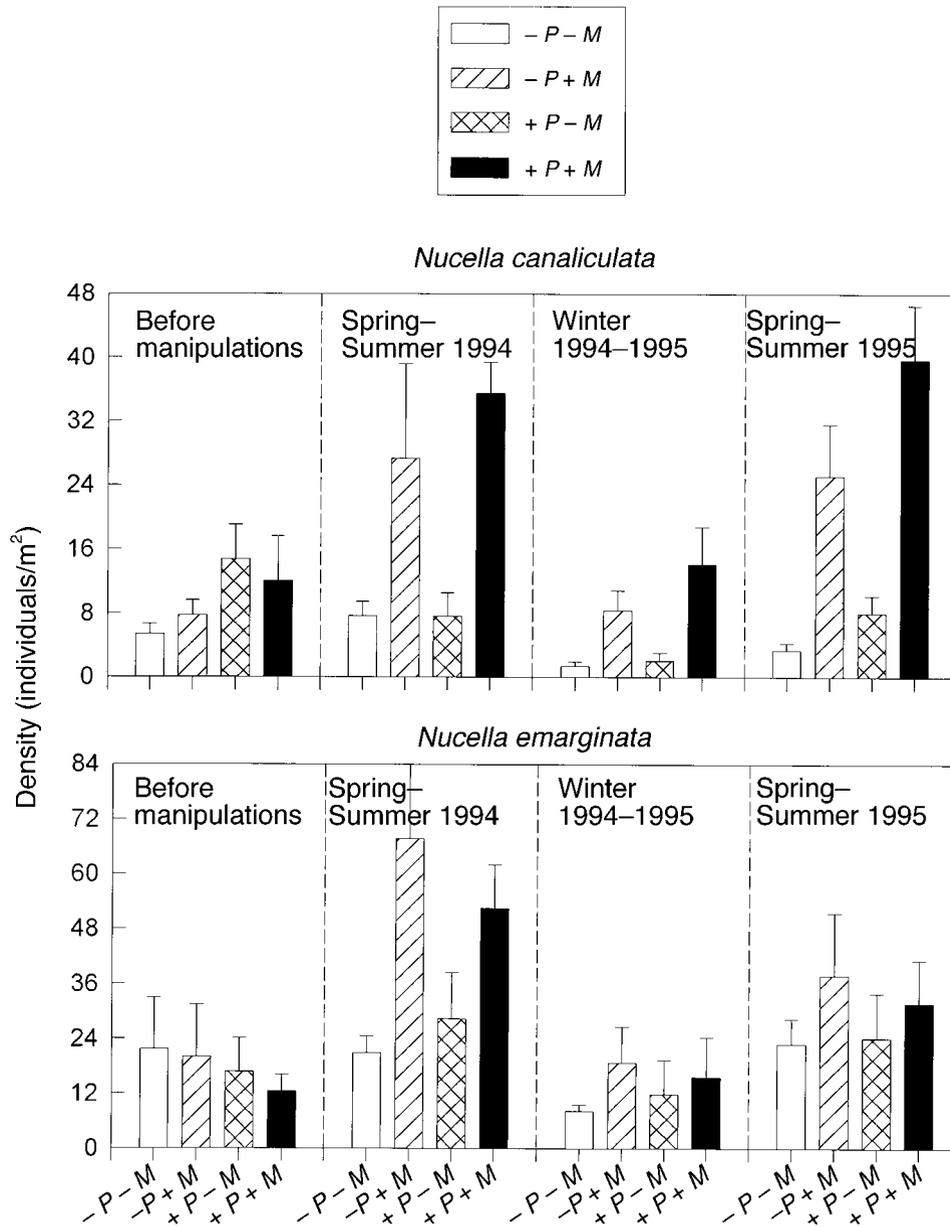


FIG. 3. Density (mean  $\pm$  1 SE) of whelks *Nucella canaliculata* and *N. emarginata* under the different combinations of *Pisaster* (*P*) and *Mytilus* (*M*) present (+) or absent (-). The time responses were divided into four time intervals, according to the effectiveness of the *Mytilus* treatment: (A) "Before manipulations" began in April 1994, (B) "Spring–Summer 1994," corresponded to April through September 1994, (C) "Winter 1994–1995," corresponded to October 1994 through February 1995, (D) "Spring–Summer 1995," corresponded to the months of April through June 1995.

nonical coefficients (see Scheiner 1993) suggests that the response was mostly due to *N. canaliculata*.

In summary, the *Mytilus*–*Nucella* link is a strong effect, the direct *Pisaster*–*Nucella* link is a very weak effect, and *N. canaliculata* was more affected by mussel manipulations than *N. emarginata*. Nevertheless, long-term treatment effects could have been affected, to some extent, by our failure to maintain complete *Pisaster* removals throughout the experiment and by

the natural decline in seastar abundance after the first 4 mo of the experiment (see Fig. 4).

Calculation of rates of change in whelk and mussel abundances during the first 35 d of the experiment, when seastar densities were high, were used to further evaluate prey and predation effects on whelks. These analyses also provide a way to estimate the magnitude of predation by, and competition with, *Pisaster* as well as food limitation by *Mytilus* and in general lend sup-

TABLE 1. Two-way ANOVA comparing *Nucella* densities among experimental plots before density manipulations on a rocky intertidal shore of the central Oregon coast. (A) Separate ANOVAs for each *Nucella* species. (B) MANOVA considering both *Nucella* species as dependent variables.

A) ANOVA							
Source	df	<i>Nucella canaliculata</i>			<i>Nucella emarginata</i>		
		MS	F	P	MS	F	P
<i>Pisaster</i>	1	0.440	2.08	0.1747	0.055	0.12	0.7345
<i>Mytilus</i>	1	0.010	0.05	0.8284	0.139	0.31	0.5903
<i>Pisaster</i> × <i>Mytilus</i>	1	0.109	0.51	0.4870	0.001	0.01	0.9615
Residual error	12						

B) MANOVA				
	Numerator df	Denominator df	Wilks' $\lambda$	P
<i>Pisaster</i>	2	11	0.7506	0.2065
<i>Mytilus</i>	2	11	0.9441	0.7290
<i>Pisaster</i> × <i>Mytilus</i>	2	11	0.9372	0.7001

port to the long-term results. Log-transformed whelk abundance data over the initial stages of the experiment followed reasonably linear trends, indicating that slope estimates are good descriptors of the changes in whelk abundance (Fig. 5, Table 4). Based on these slopes, the size of total effects per whelk indicate that prey (re-

source) limitation was the main factor driving changes in local abundance in both *Nucella* species (Fig. 6). The effect of direct predation by seastars was not significantly different from zero. The effect of competition with *Pisaster*, obtained by multiplying the negative effect of seastars on mussels,  $f_4P = -0.0346$  (95% confidence interval = 0.0039) by the positive effect that mussels had on whelks ( $f_1M$ , Table 4), was small but significant (nonzero) on both whelk species. The direct positive effect of mussels on *Nucella* was slightly different for each species. For *Nucella emarginata*, the positive bottom-up effect of mussel prey was slightly smaller than for *N. canaliculata* (Fig. 6).

Although our mussel manipulations were performed to observe the response of whelks to prey availability, seastars in the +*Pisaster* plots also responded to mussel removal (Fig. 4, Table 5). In spring 1994, seastar density increased in +*Mytilus* plots (Fig. 4), following the spring–summer increase in activity and abundance typical for the Oregon coast (Menge et al. 1994, Navarrete and Menge 1996). Seastar density in these plots remained high until late summer 1995, when it sharply decreased to winter levels. In contrast, seastars tended to abandon –mussel plots, and never reached the densities observed in +mussel plots (Fig. 4). By late winter, after seastars had eliminated mussels in the +*Mytilus* plots, seastar densities in +mussel and –mussel plots became indistinguishable. In spring 1995, seastar density began to increase again, but no clear differences between +mussel and –mussel plots was apparent when the experiment was terminated (Fig. 4). Thus, the initial removal (spring and summer 1994) of mussels from the –*Mytilus* plots prevented the typical spring increase in seastar abundance, probably because *Pisaster* concentrated on +mussel beds.

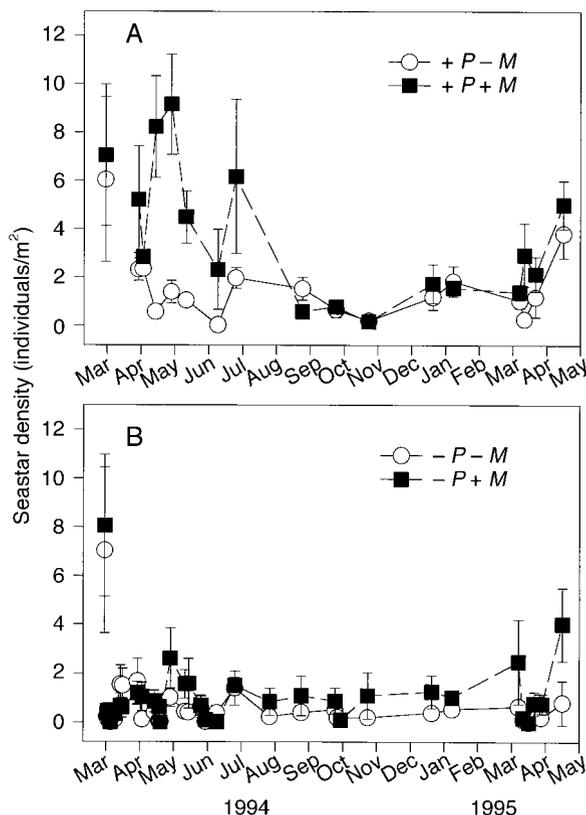


FIG. 4. Density (mean  $\pm$  1 SE) of the seastar *Pisaster ochraceus* observed in areas where *Mytilus trossulus* was either removed (–M) or left undisturbed (+M). (A) Density of seastars in +*Pisaster* plots. (B) Mean density in *Pisaster* removal plots. The first data point, in April 1994, corresponds to the density before mussel beds were removed from –M plots.

## DISCUSSION

Of the alternative interaction web models (Fig. 1), this experiment supports an indirect-competition interpretation of the interactions between seastars and whelks at Strawberry Hill. Removal of mussels sup-

TABLE 2. Repeated-measures ANOVA comparing the responses of *Nucella* species to predators (*Pisaster*) and prey (*Mytilus*) treatments.

Source of variation	df	<i>Nucella canaliculata</i>			<i>Nucella emarginata</i>		
		MS	F	P	MS	F	P
Between subjects							
<i>Pisaster</i>	1	0.949	3.43	0.0886	0.010	0.01	0.9345
<i>Mytilus</i>	1	14.37	51.97	0.0001	2.610	1.67	0.2202
<i>Pisaster</i> × <i>Mytilus</i>	1	0.17	0.65	0.4373	0.007	0.01	0.9495
Error	12	0.27			1.56		
Within subjects							
Time	2	2.800	24.59	0.0001	3.810	44.59	0.0001
Time × <i>Pisaster</i>	2	0.086	0.75	0.4813	0.095	1.11	0.3467
Time × <i>Mytilus</i>	2	0.158	1.39	0.2687	0.337	3.95	0.0328
Time × <i>Pisaster</i> × <i>Mytilus</i>	2	0.059	0.52	0.5996	0.017	0.20	0.8229
Error (Time)	24	0.114			0.085		

Notes: The sphericity test showed no significant deviations from the assumption of circularity of the treatment differences matrix for both *Nucella* species (see von Ende [1993] for an explanation of the test and assumption; chi-square = 1.12,  $P = 0.5702$  for *N. canaliculata*, and chi-square = 0.678,  $P = 0.7123$  for *N. emarginata*). Thus, the uncorrected univariate probabilities are presented here.

pressed the spring increase in whelk abundance (Fig. 3). Further, when mussel abundances declined due to natural causes, either from reductions by seastars in +*Pisaster* plots or as a response to direct predation by whelks, whelk densities dropped to near zero. No significant direct response to *Pisaster* density was observed, suggesting that consumption of *Nucella* by seastars does not have an effect on the local abundance of whelks (Fig. 6). Our previous demonstration of strong negative effects of *Pisaster* on *Nucella* abundance and size (Menge et al. 1994, Navarrete and Menge 1996) was evidently caused by indirect effects mediated by mussels, and not by intraguild predation.

There are at least two important consequences of these results for our view of marine intertidal communities. First, our results reinforce the idea that "food chain" omnivory (consumers feeding on more than one trophic level, like seastars feeding on mussels and whelks; Fig. 1b) is the most important trophic interaction in this intertidal community and one that dominates its dynamics. Our work, with that of Paine (1969) suggests that three potentially important food chains in this community all involve weak predation (*Pisaster* → *Nucella* → *Mytilus*; *Pisaster* → *Nucella* → *Balanus*; *Pisaster* → *Tegula* → macroalgae). Paine (1969), for example, showed that the trophic interaction between *Pisaster ochraceus* and the herbivorous gastropod *Tegula funebris* did not seem to have important consequences for the rest of the community. In our study, the direct trophic interaction between *Pisaster* and the principal predatory species in their diet, *Nucella* spp., also appears of minor consequence for the rest of the community. Thus, although *Pisaster* is the top predator of three important intertidal food chains, it preys on species in three trophic groups (whelks, herbivorous gastropods, sessile animals) and two trophic levels (primary carnivores, herbivores) and is therefore an omnivore. The direct links to herbivores and to primary carnivores are weak, however, so the direct omnivorous link to sessile animals is the central dynamic of this web. The indirect effect of *Pisaster* on *Nucella* mediated through mussels, however, does have important effects on populations of *Nucella* and on the local structure of low-intertidal communities (Menge et al. 1994, Navarrete and Menge 1996). Others have argued that the existence and prevalence of omnivory (sensu Pimm and Lawton 1977) in marine communities may effectively prevent the manifestation of trophic cascades under natural conditions (see Strong 1992, Polis and Strong 1996). In our system, while predation by top predators on both intermediate predators and herbivores does occur, the intensity of these links is too weak to modify the overall direct negative effect of top pred-

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TABLE 3. Multivariate analysis of variance to compare the effects of the *Pisaster* (predator) and *Mytilus* (prey) treatments on both *Nucella* species simultaneously (dependent variables).

Source of variation	Numerator df	Denominator df	Wilks' $\lambda$	P	Standardized canonical coefficients	
					<i>N. canaliculata</i>	<i>N. emarginata</i>
<i>Pisaster</i>	2	11	0.846	0.3985	2.257	-0.536
<i>Mytilus</i>	2	11	0.227	0.0003	2.286	-0.587
<i>Pisaster</i> × <i>Mytilus</i>	2	11	0.982	0.9054	2.295	-0.527

Notes: Standardized canonical coefficients are a measure of the relative importance of each whelk species to the significance of that effect.

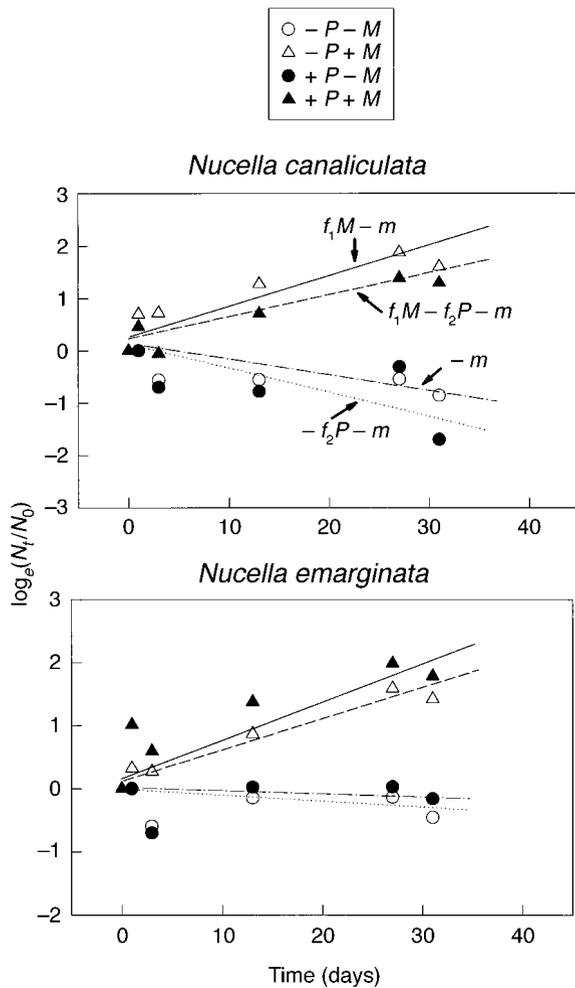


FIG. 5. Mean rate of change in the density of the whelks *Nucella canaliculata* and *N. emarginata*, expressed as the natural logarithm of the ratio of the density at time  $t$  ( $N_t$ ) to the initial density ( $N_0$ ), over the first 35 d of the experiment. Ordinary least-squares regression lines were fitted to these data for each combination of *Pisaster* ( $P$ ) and *Mytilus* ( $M$ ) present (+) or absent (-).

ators on basal prey species or to significantly affect population abundance at intermediate trophic levels.

Diehl (1993) has shown that in most food webs with omnivorous links experimentally examined, the direct negative effect of the top predator in the system offsets any indirect positive effects mediated by the intermediate predator. He argues that this is at least partly a consequence of the relative body sizes of the top and intermediate predators with respect to the shared prey resource. The pattern of body sizes in our rocky intertidal subweb lends support to Diehl's argument. A much larger seastar top predator feeds on similarly sized whelks and mussels, and the release from predation pressure accrued by mussels when seastars include whelks in their diet does not offset its direct negative effect. We suggest that the empirical pattern of body sizes found in most food webs, including the

intertidal zone, may often introduce a bias when comparing the impact of prey resource between top and intermediate predators. Besides providing food/energy for both predators, the basal resource may also provide important microhabitat for the intermediate predator. Our evaluation of "exploitative competition" between predators may thus be influenced by intrinsic differences in the way seastars and whelks perceive mussel beds. Experimental separation of these types of prey effects may be very challenging in most systems.

Secondly, these results offer further insights into discussions about the relative importance of the ecological processes that regulate trophic levels in natural communities (e.g., Hairston et al. 1960, Menge and Sutherland 1976, 1987, Oksanen et al. 1981, Menge and Olson 1990, Strong 1992). While many studies have quantified the top-down effect of predators on prey populations (see reviews by Sih et al. 1985, Kerfoot and Sih 1987, Menge and Farrell 1989, Holt and Lawton 1994, Menge 1995), there are few examples of studies in which both top-down and bottom-up factors (e.g., prey effects) have been simultaneously quantified at intermediate and higher trophic levels (Diehl 1993; but see Power 1992, Wootton and Power 1993, Osenberg and Mittelbach 1995). Most studies that experimentally quantified bottom-up factors have concentrated on the influence of nutrients on algal or plant growth. Experimental quantification of the effect of prey on herbivore or carnivore predators is generally more rare (Sih et al. 1985, Kerfoot and Sih 1987) and almost nonexistent in the marine realm (but see Fairweather [1988], and the elegant study of Robles et al. [1995]). The scarcity of studies quantifying prey effects on predators is probably due to the logistical difficulties of incorporating the usually larger temporal and spatial scales over which prey affect predator population dynamics. For instance, while predation can be viewed as a quasi-instantaneous reduction in per capita growth rate of the prey, gains from predation by the predator population need to be assimilated and then converted into new predators through reproduction.

At least two approaches have been used to get around this problem to enable comparison of prey and predation effects on intermediate trophic levels. First, population changes induced by predators and changes in individual body mass induced by the prey can be transformed into biomass as a common currency (e.g., Osenberg and Mittelbach 1995). The assumption made here is that individual body mass of predators is correlated positively and monotonically with fitness (Osenberg and Mittelbach 1995). A second approach is to simply quantify the short-term aggregative responses induced by prey manipulations and assume that population level responses would follow a similar trend (e.g., Robles et al. 1995, Diehl 1995).

This latter approach, in combination with observations of longer-term (>14 mo) population responses, is the one followed here. Overall there was good agree-

TABLE 4. Results of least-squares linear regressions analysis for (A) log-transformed whelk abundance ( $N_t/N_0$ ) and (B) mussel abundance ( $M_t/M_0$ ) over time in days.

A.						
Treatment	<i>Nucella canaliculata</i>			<i>Nucella emarginata</i>		
	Slope (CI)	$r^2$	$P$	Slope (CI)	$r^2$	$P$
- <i>Pisaster</i> - <i>Mytilus</i> [- $m$ ]	-0.0194 (0.0048)	0.91	0.0009	-0.0076 (0.0046)	0.68	0.0226
- <i>Pisaster</i> + <i>Mytilus</i> [ $f_1M - m$ ]	+0.0219 (0.0073)	0.85	0.0012	+0.0244 (0.0195)	0.61	0.0224
+ <i>Pisaster</i> - <i>Mytilus</i> [ $f_2P - m$ ]	-0.0204 (0.0134)	0.72	0.0157	-0.0003 (0.0087)	0.09	0.9394
+ <i>Pisaster</i> + <i>Mytilus</i> [ $f_1M - f_2P - m$ ]	+0.0197 (0.0075)	0.49	0.0576	+0.0149 (0.0089)	0.49	0.0540

B.			
Treatment	<i>Mytilus trossulus</i>		
	Slope	$r^2$	$P$
- <i>Pisaster</i> + <i>Mytilus</i> [ $f_3N - m$ ]	-0.0033 (0.0007)	0.85	0.0255
+ <i>Pisaster</i> + <i>Mytilus</i> [ $f_3N - f_4P - m$ ]	-0.0313 (0.0039)	0.91	0.0008

Notes: Estimated terms of dynamic equations are indicated in square brackets under each treatment. A model without intercept was used to force the regression through the origin. Numbers in parentheses show the 95% confidence interval centered around each slope estimate.

ment between the long term results and the analysis of rates of change at the beginning of the experiment, and this led us to the conclusion that the intermediate predators of the genus *Nucella* are primarily limited by bottom-up (prey) factors (Fig. 6). The two *Nucella* species responded with slightly different intensities to

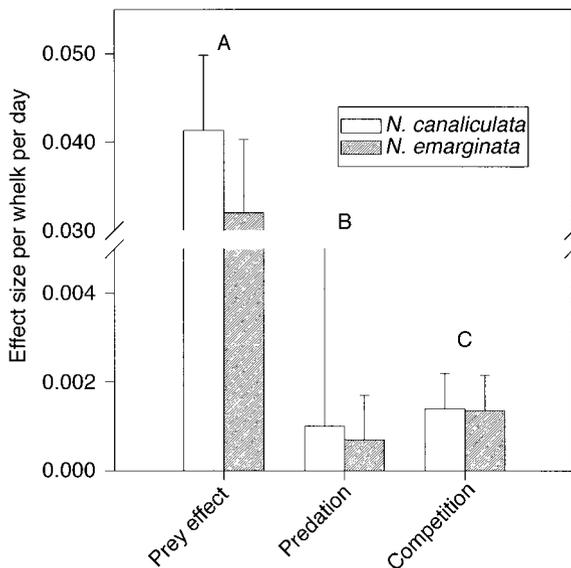


FIG. 6. Estimates of the mean change (with upper portion of 95% CI) in whelk density per whelk per day, produced by (A) the direct effect of *Mytilus trossulus* ("prey"), (B) the direct effect of predation by the seastar *Pisaster ochraceus* ("predation"), and (C) exploitation competition with the seastar ("competition"). Estimates were based on slopes presented in Fig. 5 and the estimated direct effect of seastars on mussels.

mussel manipulation. Differences in whelk responses are not likely explained by differences in food preferences. Both species show remarkably similar feeding preferences when subjected to a choice of mussel and barnacle species (Palmer 1984, Wieters and Navarrete 1998). Yet, there might be differences in terms of their ability to switch to less preferred prey species as the abundance of the preferred prey is reduced ("predator switching", Murdoch and Oaten 1975). If *Nucella emarginata* is able to more rapidly switch to the barnacle *Balanus glandula* after the removal of *Mytilus* (see the increase in *B. glandula* in -*Mytilus* treatments on the second summer, Fig. 2), it could maintain higher densities than *N. canaliculata* in the face of a drastic increase of the most abundant prey. We have, however, no data on diet of *Nucella* species through the exper-

TABLE 5. Repeated-measures ANOVA comparing the density of seastars *Pisaster ochraceus* in plots with and without beds of *Mytilus trossulus*.

Source of variation	df	MS	F	P
Between subjects				
<i>Mytilus</i>	1	0.461	6.23	0.0468
Error	6	0.074		
Within subjects				
Time	2	0.206	6.61	0.0116
Time × <i>Mytilus</i>	2	0.016	0.50	0.6164
Error(Time)	12	0.031		

Notes: The sphericity test showed no significant deviations from the assumption of circularity of the treatment differences variance matrix for both *Nucella* species (see von Ende 1993; chi-square = 1.95,  $P = 0.3761$ ). Thus, the uncorrected univariate probabilities are presented here.

iment. Another possibility is related to the way both species use mussel beds. While both whelks are found in patches in mussel beds and exhibit similar patterns of spatial and temporal variation (Navarrete 1996), field observations suggest that individuals of *N. canaliculata* are more often found within and underneath the *Mytilus trossulus* mat than are *N. emarginata*, which more often occur within open gaps. The apparently differential use of alternative mussel-associated microhabitats could also cause differences in whelk responses to the mussel bed removals and could explain the slightly larger mussel effect on *N. canaliculata* as compared to *N. emarginata* (Fig. 6). Further studies designed to quantify the relative effect of mussels as food and microhabitat for whelk species are warranted.

Meaningful quantification of the strength of interactions among species is one of the major goals of community ecologists, yet agreement on how this should be done is elusive (Laska and Wootton 1998, Berlow et al. 1999). Here, we used a simple model that includes terms for changes in whelk and mussel abundances over relatively short periods of time to quantify the total population strength of direct and indirect links in the subweb. Because in food webs with omnivory the abundances of all species are expected to be coupled, our absolute estimates of interaction strength are dependent on the existing levels of prey and predators in the system. However, the relative sizes of the different factors (prey effect, predation, and competition) should not be greatly affected. The observed rapid changes in seastar abundance following the removal of mussels could lead to an underestimation of the total (population) predation effects on whelks. However, comparisons of predation effects in the presence of mussels (bottom two curves in Fig. 5) suggest that this was not the case. The effect of seastars in presence of mussels, when they have both a direct negative effect due to predation and an indirect negative effect due to competition, was rather small and can be accounted for by competition alone.

Using a series of simple models, Holt and Polis (1997; see also Polis and Holt 1992) formulated a basic theoretical framework for the study of intraguild predation. Assuming that prey and predator species have population dynamics dominated by constraints on local reproduction of adults (i.e., are "closed"), they reached the general conclusion that for an IG predator to coexist with an IG prey, the latter must be a superior competitor at exploiting the basal resource. In the present case the IG predator, not the IG prey, was a superior competitor. However, these models maybe inappropriate for understanding the conditions for coexistence among *Pisaster*, *Nucella* spp., and *Mytilus*. *Nucella* spp. have closed populations due to their deposition of benthic egg cases that produce crawl-away juveniles, and therefore their populations should respond directly to local conditions (Spight 1974, Spight and Emlen 1976). In contrast, both *Pisaster* and *Mytilus* have free-swim-

ming, pelagic, widely dispersing larval stages that spend several weeks in the water column, and their populations are thus "open" (Gaines and Lafferty 1995). This means, for instance, that the population growth rate of *Pisaster* is not strictly dependent on the local gains accrued by exploiting either *Nucella* or *Mytilus*, but depends on settlement rate and available space (Gaines and Lafferty 1995). Thus, Holt and Polis' (1997) criterion for coexistence—at resource equilibrium ( $R^*$ ), per capita resource exploitation of IG predator ( $fP(R^*) < \text{per capita resource exploitation of IG prey } fN(R^*)$ )—may not strictly hold. The large empirical differences in relative body sizes of IG predators and IG prey, typical of many food webs, are another reason why theoretical predictions may not hold in real systems (Diehl 1993). Much more theoretical work is needed to incorporate the life history features of most marine organisms (complex life cycles, Roughgarden et al. [1988]) into models and predictions of food webs with intraguild predation. We are just starting to unveil its consequences in natural communities.

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