

## Intertidal mesograzers in field microcosms: linking laboratory feeding rates to community dynamics

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### Abstract

Mesograzers (herbivores < 2.5 cm) are both diverse and abundant, but their relative effects on intertidal communities have rarely been quantified. Here I examine the effects of crustacean and polychaete mesograzers on two intertidal resources, the red alga *Odonthalia floccosa* Esp. (Falkenb.) and the epiphytic diatom *Isthmia nervosa* Kütz. The mesograzers were hermit crabs (*Pagurus hirsutiusculus* (Dana) and *P. granosimanus* (Benedict)), amphipods (*Hyale frequens* Stout and *H. pugettensis* (Dana)), isopod (*Idotea wosnesenskii* (Brandt)), juvenile kelp crab (*Pugettia producta* (Randall)), and polychaete worm (*Platynereis bicanaliculata* (Baird)). Feeding rates on *Isthmia*, measured in the laboratory for different consumer species and size classes, scaled allometrically with body mass. Consumption rates were 2–23% of body mass daily on a fresh weight basis. However, feeding rates on *Odonthalia* did not scale, suggesting that size will not always indicate per capita effect. Mesograzer densities were measured on Tatoosh Island, Washington, USA. The mesograzer predicted to have the largest total effect (*P. hirsutiusculus*), based on density  $\times$  feeding rate, was neither the most abundant nor the most voracious. The validity of these sorts of predictions depends on how well feeding rates measured in the laboratory approximate per capita effects under field conditions. Predictions were compared to observed effects in field microcosms. Given known numbers of mesograzers, predictions were made about the amount of *Isthmia* biomass that should disappear over 2 weeks from microcosms ( $9 \times 9 \times 12$  cm) anchored in tidepools. Average per capita effects in field microcosms were correlated with laboratory feeding rates, but, for three species with significant feeding on *Isthmia*, effects were lower than feeding rates predicted. Feeding trials may overestimate community impact because they fail to account for alternative food, search times, resource productivity and stimulation of growth, or interference from other consumers. Nevertheless, densities of mesograzers can reach sufficiently high levels so that even feeble per capita effects combine to alter biomass of epiphytes and perhaps other small algae. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** Feeding rate; *Hyale frequens*; *Hyale pugettensis*; *Idotea wosnesenskii*; Interaction strength; *Pagurus hirsutiusculus*; *Pagurus granosimanus*; Per capita effect; *Platynereis bicanaliculata*; *Pugettia producta*; Total effect

## 1. Introduction

Intertidal community structure can be strongly influenced by the actions of large herbivores (e.g. chitons, sea urchins, limpets, crabs; Paine and Vadas, 1969; Sousa, 1979; Paine, 1992; Bustamante et al., 1995), but the role of mesograzers is less firmly established (Hawkins and Hartnoll, 1983). Mesograzers include crustaceans and molluscs less than 2.5 cm (Brawley, 1992). Although their individual effects must be small, the total effect of a mesograzer species could be substantial because densities regularly exceed thousands of individuals  $m^{-2}$  (see e.g. Brawley, 1992). Both per capita and total effects are crucial parameters in any prediction of trophic dynamics (Menge et al., 1994). Per capita effects, especially when disproportionate to biomass, reveal whether small perturbations in a species' density could alter community structure (Power et al., 1996). In contrast, total effects define the immediate consequence of complete loss of species.

The difficulty of identifying and manipulating small, mobile, often cryptic organisms makes their role difficult to assess. However, in a few studies, mesograzers have been manipulated in laboratory microcosms or field experiments, to compare treatments at two densities. These studies have focussed on limpets and snails, whose relative immobility makes density manipulation possible, and whose effects can be pronounced on abundance and composition of microalgae and sporelings (Castenholz, 1961; Nicotri, 1977; Lubchenco, 1978; Underwood, 1980; Hawkins and Hartnoll, 1983; Hunter and Russell-Hunter, 1983; Petraitis, 1983; Keser and Larson, 1984; Lein, 1984; Chapman, 1989; Jernakoff and Nielsen, 1997).

Feeding rates of many crustacean mesograzers are known (Zimmerman et al., 1979; Shacklock and Croft, 1981; Norton and Benson, 1983; Pederson and Cappuzzo, 1984; Hay et al., 1987), and their total effects have been examined in laboratory microcosms (Brawley and Adey, 1981; Brawley and Fei, 1987; Duffy, 1990; Williams and Ruckelshaus, 1993), fine-mesh cages (Chapman, 1989; Parker et al., 1993; Jernakoff and Nielsen, 1997), or indirectly by manipulating their predators (Warwick et al., 1982; Kennelly, 1983). Although these studies have indeed revealed effects from crustaceans to resource, the interaction may be as strong in the reverse direction, resulting in positive associations of mesograzers and epiphyte load (Norton and Benson, 1983; Jennings and Steinberg, 1997). In principle, total trophic effect should be a function of how much each individual eats (feeding rate) and how many individuals are present (density). However, there has been no test of how well feeding rates can be extrapolated to per capita effects in the field.

Because multiple species of mesograzers are rarely studied simultaneously, taxonomic variation in effect is largely unknown (but see Parker et al., 1993; Jernakoff and Nielsen, 1997). Per capita effects on a single resource vary widely among large-bodied invertebrate grazers, judging from experimental enclosures of each herbivore species (Paine, 1992). In comparison to these species, intertidal mesograzers are all likely to be 'feeble' interactors based on per capita effects (Lawton, 1992); they are individually simply too small to consume much tissue. However, even among mesograzers, body mass varies by one to two orders of magnitude, and per capita feeding rates could vary by almost as much (Peters, 1983). An open question is how often small per capita

impacts of numerous individuals may result in measurable consequences for community structure and function. Due to spatial and temporal variation in abundance (e.g. Underwood and Chapman, 1996, 1998), a species' role may be context-dependent, influencing community dynamics only under particular conditions.

In this study, I examine the relative trophic effects of several crustacean and polychaete mesograzers. The mesograzers are hermit crabs (*Pagurus hirsutiusculus* (Dana) and *P. granosimanus* (Benedict)), amphipods (*Hyale frequens* Stout and *H. pugettensis* (Dana)), isopod (*Idotea wosnesenskii* (Brandt)), juvenile kelp crab (*Pugettia producta* (Randall)), and polychaete worm (*Platynereis bicanaliculata* (Baird)). The resources are an epiphytic diatom (*Isthmia nervosa* Kütz) and its red algal host (*Odonthalia floccosa* (Esp.) Falkenb.). I consider both total and per capita effects of these mesograzers on two strongly-interacting resources and ask, first, do potential trophic effects vary among mesograzers, based on feeding rates and natural densities? The null hypotheses are that mesograzers occur at equal density, and that feeding rates scale allometrically with body size. Second, do actual effects observed in field microcosms differ from potential trophic effects of these mesograzers? If effects are predictable from feeding rate and density, then it becomes possible to define the conditions within which a mesograzers species affects community dynamics.

## 2. Methods

### 2.1. Study site and species

The study was carried out on Tatoosh Island, WA, USA, a wave-exposed rocky shoreline 0.6 km beyond the northwest point of the Washington state mainland (48°24'N 124°44'W). In bays around the island, the red alga *Odonthalia floccosa* is found at tide heights of  $-0.3$  to  $+0.3$  m above mean lower low water, often associated with crustose coralline algae and a sparse canopy of kelps. *Odonthalia* is also common in higher tidepools. Populations of *Odonthalia* become periodically epiphytized by a large chain-forming diatom, *Isthmia nervosa* (Ruesink, 1998a). The guild of mesograzers considered here includes all species (or stages)  $<2.5$  cm regularly associated with *Odonthalia*. I did not include snails (*Alia* spp., *Littorina* spp. and *Lacuna* spp.) because they were not observed to consume either resource.

### 2.2. Mesograzers densities

Most herbivores were counted at 22 sites around the periphery of Tatoosh Island seasonally from May 1994–June 1995. These sites were chosen in seven general locations, which varied in aspect and habitat (low intertidal zone, tidepools; Fig. 1). On each date, mesograzers were counted in 4–13 quadrats ( $20 \times 20$  cm) of high *Odonthalia* cover at each location. Amphipod densities were based on traps (2–14 per location per date) rather than quadrats because of the difficulty of counting individuals in situ. Amphipod traps were plastic pencil holders (10 cm length and 7 cm diameter, with 0.5 cm mesh size) that were filled with algae, deployed for one tidal cycle, and collected just

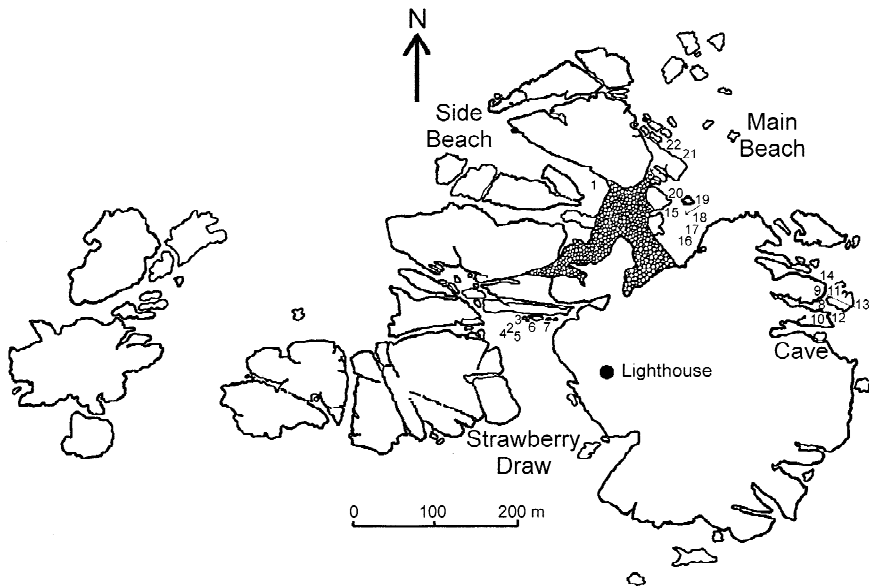


Fig. 1. Tatoosh Island showing locations where mesograzers were counted. Numbers 2, 3, 8–11, 15 and 22 represent surveyed tidepools; microcosms were anchored in nearby tidepools. Other numbers represent low intertidal sites.

as the tide left them exposed. Amphipods were counted and identified within 24 h, after they had been killed and dislodged from the algae with an arthropocide (Sevin: The Chas. H. Lilly Co., Portland, OR), and sieved through a mesh (1 mm). Although traps were usually filled with the fucoid alga *Fucus gardneri* Silva, densities of amphipods on *Fucus* were comparable to those observed when the traps were filled with *Odonthalia* (Ruesink, unpublished data). These traps provided an index of amphipod abundance, including individuals that utilized the intertidal zone during some portion of the tidal cycle. By using traps, I avoided destructive sampling of algae, and amphipods found on algae in traps should be similar in abundance to those on algae in situ.

To test the hypothesis of equal abundance among mesograzer species, a single-factor analysis of variance (ANOVA) was performed using counts from June 1994. Each location served as a replicate, based on average counts at that location, and the fixed effect was species. Combining samples in this way was necessary because many species were rare in quadrats (many zero counts). Although amphipods were sampled differently from other mesograzers, they were included in the analysis because algal volume in traps was similar to that of quadrats.

I focussed on a common species (*Pagurus hirsutiusculus*) to test the hypothesis of equal abundance within a species across seasons and locations. Fixed effects were location (two habitat types on four sides of Tatoosh Island) and date (May, August and October 1994, January and May 1995). To standardize sampling effort, I selected a random subsample ( $n = 5$ ) when  $> 5$  quadrats were available for a particular date and location. Because different quadrats were sampled on each date, a two-factor ANOVA

was used rather than repeated measures ANOVA. All densities were  $\ln(x + 0.1)$ -transformed prior to analysis. When ANOVA showed a significant main effect, post-hoc tests were performed using Scheffe's  $S$ .

### 2.3. Feeding rates

Feeding rates of all mesograzers on *Odonthalia* and *Isthmia* were measured over 2-day trials (occasionally to 6 days) that took place in a laboratory cold room (16:8-h light/dark, 10°C) in summer 1993 and 1994. Single individuals of most herbivore species were placed with pre-weighed resource in a  $9 \times 9 \times 5$ -cm volume of seawater. Amphipods (*Hyale frequens*) were placed as groups of three in smaller containers. I categorized individuals by size before calculating feeding rates for some species with wide size ranges (*Pagurus*, *Idotea*). Sample sizes ranged from five to 34 trials for each herbivore size class presented with each resource. *Odonthalia*, or *Isthmia* on *Odonthalia* was gently blotted with a paper towel and weighed ( $\pm 1$  mg) before and after each trial. Changes in weight represent maximum feeding rates (assuming negligible search time and no interference or facilitation from other herbivores), less weight change that would have occurred even in the absence of herbivores. Controls without herbivores were run concurrently with feeding trials. These controls involved *Odonthalia* alone ( $n = 29$ , 33–364 mg initial biomass) or *Odonthalia* with *Isthmia* ( $n = 8$ , 19–101 mg;  $n = 22$ , 120–855 mg). To account for losses not caused by herbivores, daily weight change in each feeding trial was adjusted by the amount expected for a no-herbivore control of that initial biomass. This no-herbivore weight change was based on the regression of biomass change on initial biomass, or, when this regression was not statistically significant, on the average weight change of controls.

Metabolic rates tend to scale allometrically with body size (Peters, 1983). Therefore, feeding rates should also scale with size. I tested whether mesograzers of different species and size classes showed an allometric relationship between body size (fresh weight,  $\pm 1$  mg) and feeding rate on *Isthmia* or *Odonthalia*.

Feeding rate multiplied by density gives a simple expectation of total effect. Given mesograzer density, feeding rate on *Odonthalia*, and feeding rate on *Isthmia*, it was possible to calculate expected total effect of each mesograzer on each resource on Tatoosh Island. For most species, each feeding rate measured in the laboratory was multiplied by the density at each location on Tatoosh Island in June 1994, giving a total sample size of (number of feeding trials)  $\times$  (seven). This calculation generates an overall average expected effect in the field, but it applies to a single season and year and integrates over all locations without incorporating smaller-scale variation in abundance. Thus, conclusions can only be drawn concerning the relative total effects of mesograzers averaged over a broad area at that time. For *P. hirsutiussculus*, the set of possible densities included each quadrat used in ANOVA testing for effects of location and date. I distinguished high-density ( $n = 67$  quadrats) from low-density locations ( $n = 85$  quadrats) and large from small individuals in quadrats. In principle, the calculation should involve every possible combination of large hermit crab feeding rate, small hermit crab feeding rate, and abundance in a quadrat, but, due to the large number of possible combinations, this calculation was performed on a random subsample of 500.

## 2.4. Microcosms

Using experiments in field microcosms, I measured how known species and numbers of herbivores affected the abundance of *Isthmia*. Microcosm containers (9 × 9 × 12 cm) were made of translucent plastic with 1-mm mesh on two sides and top (Ruesink, 1998a, b). Ten microcosms were anchored into each of three tidepools on Tatoosh Island. Many components of natural tidepool systems were present inside, including particulates, plant propagules, and small animals that could move through the mesh. Containers reduced water flow and light levels relative to field conditions. Experiments ran for 2 weeks during April to September 1993–1995. Replicate trials were carried out for each mesograzer: *Hyale* spp. ( $n = 24$ ), *Pugettia producta* ( $n = 9$ ), *Idotea wosnesenskii* ( $n = 22$ ), *Platynereis bicanaliculata* ( $n = 5$ ; 4 weeks), and *Pagurus hirsutiusculus* ( $n = 140$ ). *Hyale frequens* made up >85% of individual amphipods found in traps, but some experiments were carried out with *Hyale pugettensis*, which reaches an overall larger size and could be contained more effectively in microcosms. *Isthmia* biomass before and after each trial was estimated from the size of the host plant and its cover score (0–6 where the relationship between score and wet weight biomass of *Isthmia* is known; Ruesink, 1998a). These initial estimates had an average value of 1323 g (S.E. = 104 g,  $n = 200$ ). I placed single individuals of *Pugettia* and *Platynereis*, 5–20 *Hyale*, 1–5 *Idotea*, or 1–20 *Pagurus* in these microcosms.

Analyses addressed whether the actual change in diatom cover ( $\Delta I$ ) matched the loss expected based on the number of consumers present ( $C$ ), their per capita feeding rate in the laboratory ( $f_C$ ), and the duration of the experiment ( $d$ ), where a perfect match would imply:

$$\Delta I = C \cdot f_C \cdot d$$

The calculation of confidence limits (CL) for the expected loss assumes that feeding rates are correlated within individuals over time, but are not correlated among individuals, so that:

$$CL = t_{\alpha, \nu} \cdot \left( \frac{C \cdot (s_f \cdot d)^2}{n_f} \right)^{1/2}$$

where  $t$  is Student's  $t$  for the desired  $\alpha$ -level and degrees of freedom ( $\nu$ ) set by the number of microcosm experiments,  $s_f$  is the standard deviation of laboratory feeding rates, and  $n_f$  is the number of laboratory feeding trials. This formula concerns the variance of a sum of several uncorrelated variables (Sokal and Rohlf, 1995, p. 567). This formula combines variances of  $C$  individuals (assuming that rates of feeding are completely uncorrelated among individuals) feeding for  $d$  days (assuming that the rate of feeding of each individual is perfectly correlated from one day to another and that the variance among individuals stays constant from one day to another). If consumers feed in microcosms as they do in the laboratory, 95% of the experimental replicates should show biomass change within the 95% confidence limits of expected change (binomial test).

### 3. Results

Densities of mesograzers showed dramatic variation both within and among species on Tatoosh Island. In general, large-bodied species were less abundant than smaller ones, often by several orders of magnitude (Species  $F_{5,23}=20.2$ ,  $P<0.001$ ; Table 1). Abundance of hermit crabs varied both spatially and temporally. In ANOVA, locations fell into two groups based on density of *P. hirsutiusculus* (Location  $F_{6,118}=34.3$ ,  $P<0.001$ ). High-density locations included both low intertidal zones and tidepools (2.9 per 0.04 m<sup>2</sup> [S.E.=2.4–3.5]; sites marked 1, 2–3, 8–11 in Fig. 1), as did low-density locations (0.2 per 0.04 m<sup>2</sup> [S.E.=0.1–0.2]; sites marked 4–7, 12–14, 15, 16–19 in Fig. 1). Sample date also showed a significant main effect in ANOVA ( $F_{4,118}=8.2$ ,  $P<0.001$ ), and hermit crab densities were generally higher in winter.

Feeding rates ( $f_c$ ) on *Isthmia* increased allometrically with mesograzer body size ( $B_c$ ) ( $F_{1,5}=22.9$ ,  $P=0.005$ ; Table 1):

$$f_c(\text{mg/day}) = 0.032 \cdot (B_c(\text{mg}))^{1.21}$$

The smallest mesograzers showed small average feeding rates, and, given variation among trials, feeding by *Hyale* and *Platynereis* could not be detected statistically. The exponent in the allometric equation ( $1.21 \pm 0.25$  S.E.) was indistinguishable from 2/3- or 3/4-power scaling (Peters, 1983; West et al., 1997). Feeding rates on *Odonthalia* did not scale allometrically, and feeding was confined to three (not necessarily the largest) mesograzer species ( $F_{1,4}=2.1$ ,  $P=0.2$ ; Table 1).

Smaller-sized species ate less but tended to be more abundant than were larger-sized species, which equalizes total effects among mesograzers relative to their per capita

Table 1

Wet weights, feeding rates, and densities of selected crustacean, molluscan, and polychaete mesograzers (mean (S.E.) [sample size])<sup>a</sup>

Species	Wet weight (mg)	Feeding rate (mg/day) on:		Density (no. per 0.04 m <sup>2</sup> )
		<i>Isthmia</i>	<i>Odonthalia</i>	
<i>Hyale frequens</i>	38 (13) [2]	0.74 (0.62) [10]		18.3 (10.2–32.8) [5] <sup>d</sup>
<i>Idotea</i> (<5 mm)		3.1 (0.5) [12]	3.2 (0.7) [12]	
<i>P. granosimanus</i> (small)		13.5 (8.5) [7]	1.8 (1.4) [10]	0.36 (0.22–0.57) [7] <sup>ab</sup>
<i>P. hirsutiusculus</i> (small)	89 (17) [9]	12.2 (3.0) [22]	2.3 (0.6) [30]	1.7 (1.1–2.8) [7] <sup>bc</sup>
<i>Platynereis</i>	100 [1]	22.7 (15.4) [9]	14.4 (2.7) [15]	0.23 (0.17–0.31) [6] <sup>a</sup>
<i>P. granosimanus</i> (large)	198 (45) [7]	38.4 (13.3) [8]	0.58 (0.59) [10]	
<i>Idotea</i> (adult)	294 (56) [5]	19.1 (4.0) [34]	10.1 (2.8) [15]	0.13 (0.11–0.15) [7] <sup>a</sup>
<i>P. hirsutiusculus</i> (large)	623 (68) [4]	66.7 (9.5) [10]	2.9 (1.5) [13]	
<i>Pugettia</i>	2333 (418) [3]	300 (66.9) [13]	103 (26.0) [5]	0.21 (0.16–0.28) [7] <sup>a</sup>

<sup>a</sup> Daily feeding rates were measured on two resources, the epiphytic diatom *Isthmia nervosa* and a red algal host *Odonthalia floccosa*. There is a significant allometric relationship between mesograzer size and feeding rate on *Isthmia*, but not on *Odonthalia*. Densities come from counts on Tatoosh Island in June 1994 and have been back-transformed from  $\ln(x+0.1)$ -transformed values. When letters presented after sample size are the same, densities of those species cannot be distinguished in ANOVA. Average values are given for *P. hirsutiusculus* even though densities also differed among locations.

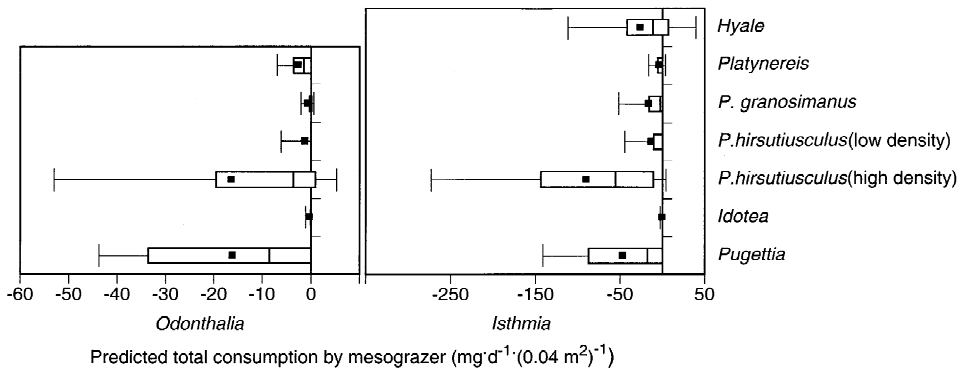


Fig. 2. Predicted effects of mesograzers on Tatoosh Island, based on actual densities and feeding rates observed in the laboratory. Effects are given in terms of fresh weight of *Odonthalia* or *Isthmia* consumed in one quadrat ( $0.04 \text{ m}^2$ ) per day. For *Pagurus hirsutiusculus*, quadrats were divided into low- and high-density locations, and small and large individuals in these quadrats were accorded separate feeding rates. Effects of all other species were calculated from samples used to generate Table 1. All combinations (or 500 random subsamples) of feeding rate and density were multiplied for each species. The box plots show the average combination (■), and the box itself represents the median, lower and upper quartiles. Lines show the most extreme observation within 1.5-box-lengths of the end of each box.

effects. For comparative purposes, Fig. 2 presents the predicted total consumption by each species on Tatoosh Island. Among mesograzers, hermit crabs were expected to have the largest total effect on *Isthmia*, due to a combination of moderate feeding rates and locally high densities. Variation in these predicted effects was high because each feeding rate from the laboratory was incorporated separately, which assumes that all consumers in an area would feed as did the single individual. Direct consumption of *Odonthalia* was predicted to be much lower than of *Isthmia*, consistent with per capita feeding by mesograzers.

In the absence of these mesograzers in microcosms, 72% of 188 ‘control’ replicates maintained or increased diatom biomass (Ruesink, 1998b). In treatment replicates with mesograzers, the relative ability of different species to deplete diatoms was correlated with feeding rate. Average daily per capita effect of each mesograzers species in these experiments ( $e_c$ ) was predictable from average laboratory feeding rate on *Isthmia* ( $f_c$ ) ( $e_c = 4.19 + 0.34 \cdot f_c$ ;  $F_{1,4} = 113.8$ ,  $P < 0.001$ ). However, less biomass was lost than feeding rates of three species (*P. hirsutiusculus*, *I. wosnesenskii*, *P. producta*) would suggest, even when cases where the resource was completely eliminated (and therefore no more diatoms could be consumed) were censored from the analysis (Fig. 3).

## 4. Discussion

### 4.1. Per capita effects

This study advances our understanding of the roles played by marine mesograzers in



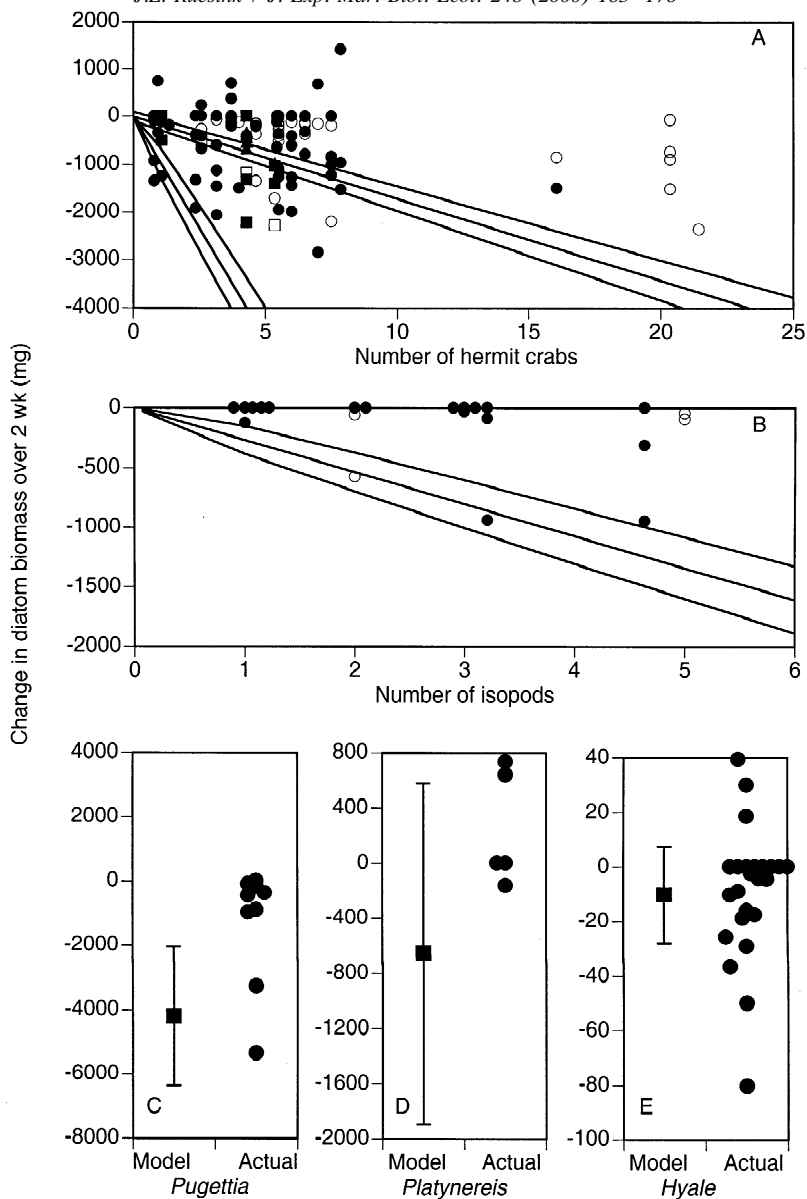


Fig. 3. Expected (mean  $\pm$  95% CL) and observed effects of mesograzers in microcosms. Each point represents one replicate, showing change in diatom biomass over 2 weeks (4 weeks for *Platynereis*). The probability that the observed number of replicates would by chance fall above the 95% CL of predicted effects was calculated, using only those replicates in which resource was in excess and therefore persisted for 2 weeks (filled symbols). (a) *Pagurus hirsutiusculus* (binomial test:  $P < 0.001$ ). The binomial test was applied conservatively by comparing expected effects of small- and medium-sized individuals (upper lines) to actual effects regardless of size (squares = large individuals, circles = medium, triangles = small). (b) *Idotea wosnesenskii* ( $P < 0.001$ ), (c) *Pugettia producta* ( $P < 0.001$ ), (d) *Platynereis bicanaliculata* ( $P > 0.1$ ), (e) *Hyale* spp. ( $P > 0.1$ ). For *Hyale*, microcosms contained five to 20 individuals, so results could be presented as in (a) and (b) but instead show calculated per capita effects because *Isthmia* was not significantly reduced in feeding trials. In the graphs, points are offset to account for trials slightly longer or shorter than 2 weeks and to show overlapping points.

linking feeding rates (relatively well-studied) to community-level impacts of particular species (newly-explored). For the six taxa considered here, feeding rates generally increased with body size both within and among species (Table 1). Consumers ingested 2–23% of their body weight daily, which is consistent with other studies (Shacklock and Croft, 1981; Peters, 1983) except that amphipods have been found to ingest >100% of their body weight of some resources (Zimmerman et al., 1979; Norton and Benson, 1983; Pederson and Cappuzzo, 1984).

The combination presented here of laboratory feeding trials and microcosm experiments suggests that maximum feeding rates will tend to overestimate trophic interaction strength in the field (Fig. 3). However, the relative (as opposed to absolute) effects on *Isthmia* of mesograzers species remained consistent from laboratory to field. Furthermore, body size provided a proxy measure of relative per capita effect, because of the allometric relationship with feeding rate on *Isthmia* (Table 1).

Feeding rates on *Isthmia* gave little insight into the rates at which mesograzers consumed other resources, specifically the red alga *Odonthalia*. *Odonthalia* contains iodine and bromine compounds that may defend it against consumption by some species (Hofsten and Pedersen, 1980 in Westlund et al., 1981). Mesograzers that have strong trophic effects on the epiphyte may not similarly affect its host. In fact, species that consume *Isthmia* but not *Odonthalia* may act as indirect mutualists, because *Odonthalia* is cleaned of an epiphyte that would otherwise interfere with photosynthesis (Ruesink, 1998a). As a consequence, these species which, based on trophic mode and size, might be considered a single functional group, are actually not functionally redundant. One species cannot necessarily be replaced or compensated by another that would maintain the same relative effect on *Odonthalia* and *Isthmia*.

#### 4.2. Total effects

Ranking mesograzers by their potential total effect differed from rankings by per capita effect because of interspecific variation in densities on Tatoosh Island. Amphipods and the hermit crab *P. hirsutiusculus* were significantly more abundant than other mesograzers species (Table 1). This pattern conforms to prior observations in a variety of benthic marine systems that, in relationships between body size and abundance, the most abundant species tend to be about the size of amphipods (Warwick and Clarke, 1996). At almost half of the sampled locations, hermit crabs were expected to have total effects two to ten times higher than those of any other mesograzers (Fig. 2). Hermit crabs reach locally high densities as a function of shell supply (Vance, 1972; Abrams, 1987). In these areas of high density, their total effect appears to have community-level consequences, based on field manipulations of hermit crabs and large-scale patterns that show *Isthmia* is rare, where *Pagurus* is common (Ruesink, unpublished data). Although *Isthmia* is seasonally rare in winter (Ruesink, 1998a), its absence is more likely a function of phenology than of particularly high hermit crab densities at that time of year.

Predictions of total effects are limited in this study by the lack of information for most species on spatial and temporal variation in abundance. In fact, the predictions of total effect represent an average across Tatoosh Island in a single season and year. In a study explicitly addressing scales of variation in abundance of intertidal invertebrates,

Underwood and Chapman (1996) recorded that gastropods could differ by one to three orders of magnitude in abundance over 5–50 cm. Although many of the crustaceans studied here can rapidly move several meters, their distribution and therefore effect may nevertheless be patchy. For instance, numbers of amphipods on algae can differ from one individual plant to another of the same species (Gunnill, 1984).

Temporal variation in abundance would be expected for amphipods, which are short-lived and seasonally reproductive (Edgar, 1983; Strathmann, 1987; Parker et al., 1993). Other studies have demonstrated annual spawning in *P. bicanaliculata* (Roe, 1975), and annual fluctuations in *P. producta* (Hines, 1982) and *I. wosnesenskii* (Ruesink, 2000), but these species were not at sufficiently high abundances on *Odonthalia* to make such an analysis possible. Variation in abundance increases the chance that a mesograzer at some place and time reaches densities at which expected effects imply a measurable community role.

#### 4.3. Why do predicted and observed effects differ?

Because *Isthmia* (on *Odonthalia*) and unepiphytized *Odonthalia* were presented separately to mesograzers, I cannot define preference as a function of availability (e.g. Hawkins and Hartnoll, 1983; Arrontes, 1990; Poore, 1994). Feeding rates on single resources indicate herbivores' potential effects. However, these effects were realized quite differently within the complicated food webs of field situations: mesograzers had much smaller impacts than expected from feeding rates. Brawley (1992) lists some of the reasons that laboratory feeding trials should be extrapolated with caution to field impacts. Often, feeding trials do not account for natural size-frequency distributions, densities, or sex ratios of consumers. As in the current study, they may not allow herbivores to choose among different resources. Herbivores may respond differently to whole plants than they would to portions or plugs; also, many plants in the field may be protected from herbivory by epiphytes. Laboratory feeding trials may use starved individuals, and they may take place under unnatural light or temperature conditions in areas that are too small to accommodate natural foraging behavior.

To the Brawley (1992) list, I would add that feeding trials will tend to underestimate effects of consumers that remove more biomass than is actually consumed. They will tend to overestimate effects when consumers spend substantial time in the field searching for resources, when diets include multiple foods, or when intra- and interspecific interactions slow consumption. For instance, the presence of predators is well-known to reduce feeding by their prey (McCollum et al., 1998). Interference competition with conspecifics or other species could also slow rates of resource acquisition (Gunnill, 1984; Creel and Creel, 1996; Faragher and Jaeger, 1998). Consumers can stimulate plant growth, either by reducing competition or by releasing nutrients (Lehman, 1980; McNaughton et al., 1997), which would allow a resource to compensate for some consumption. In the current study, grazing may increase the availability of resources (light or nutrients) to remaining diatom cells. These cells may then replace consumed cells by dividing, reducing the apparent amount of consumption by mesograzers. In fact, below threshold densities of consumers, effects on a growing resource will be negligible (Sommer, 1997; Ruesink, 1998b); that is, effects may

increase nonlinearly with density. There is increasing evidence that effects of small consumers may be restricted to a narrow window of time when the resource is newly-recruited and therefore small, vulnerable, and slow-growing (Kennelly, 1983; Lein, 1984; Osman et al., 1990; Cervin and Åberg, 1997).

Because of the difficulty of altering densities of mesograzers in the field, few studies have examined their effects experimentally (see references in Introduction and also, Brawley, 1992). Yet by ignoring small invertebrates, we run the risk of misrepresenting community dynamics. In these experiments, actual changes rarely matched effects predicted from feeding rates and densities. Nevertheless, mesograzers had the capacity to alter the abundance of an epiphytic diatom in microcosms. Measuring feeding rates and field densities can help focus attention on those species that are likely to have the strongest community impacts. Even if these direct impacts only extend to small ephemeral plants, mesograzers have potential indirect effects on major community processes such as succession, regeneration, and the performance of dominant plants colonized by epiphytes.

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