Mechanisms underlying the effect of the chiton *Katharina tunicata* on the kelp *Hedophyllum sessile*: size escapes and indirect effects

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ABSTRACT: We monitored the population size-structure and demography of the intertidal kelp *Hedophyllum sessile* (C. Agardh) Setchell in areas of manipulated chiton *Katharina tunicata* (Wood) density to examine size-related 'escapes' and other mechanisms which may underlie the effects of this herbivore on *H. sessile*. This research was done on the west coast of Vancouver Island, British Columbia, Canada. We find that *K. tunicata* is associated with decreased juvenile *H. sessile* (<1 cm holdfast diameter) survivorship. While young adults of *H. sessile* (1–4 cm holdfast diameter) were found to survive significantly longer than juveniles between areas of low, control and high chiton density, adult (>4 cm holdfast diameter) survivorship did not differ among the density treatments. We argue that the mechanism underlying the effect of *K. tunicata* on young adult *H. sessile* survivorship is an indirect interaction wherein holdfast integrity is degraded, resulting in an increased susceptibility to wave-induced mortality. These findings provide a quantification of the mechanism of macrophyte size-escapes, may explain the geographically variable effects of *K. tunicata* and hold implications for studies which aim to assess the effects of wave exposure on macrophyte survivorship.

KEY WORDS: Kelp population dynamics · Herbivore density · Mechanisms · Size escapes · Interaction modification · Wave-induced mortality

INTRODUCTION

In the northeast Pacific, canopy forming kelps (Laminariales) play disproportionately important roles in determining the structure of rocky intertidal and shallow subtidal communities (Estes & Palmisano 1974, Dayton 1975, Reed & Foster 1984, Dean et al. 1989, Tegner et al. 1995). The primary sources of mortality of individual kelps are grazing by a variety of herbivores (Pearse & Hines 1979, Dayton et al. 1984, Duggins & Dethier 1985, Vadas et al. 1992) and the hydrodynamic forces associated with wave exposure (Koehl & Wainwright 1977, Harris et al. 1984, DeWreede 1986, Tegner et al. 1995). However, variation in the effects of these factors, and of ecological interactions in general, is widespread (Dethier & Duggins 1988, Foster et al.

1988, Menge et al. 1994, Estes & Duggins 1995) and consequently, much of community ecology is devoted to determining and quantifying the mechanisms involved in species interactions.

Marine herbivores are thought to have their greatest impact upon juvenile forms of kelp, and other algae, by creating 'herbivory bottlenecks' during which sporelings are highly susceptible to being grazed to mortality (Lubchenco 1983, DeWreede 1984, Harris et al. 1984, Dean et al. 1989). Three mechanisms may increase the probability that juvenile kelps survive through herbivory bottlenecks: (1) production of compounds which deter feeding (Lubchenco & Gaines 1981, Steinberg 1985, Duffy & Hay 1990), (2) spatial refuges or non-coexistence escapes in which herbivores are not encountered (Lubchenco & Gaines 1981, Menge & Lubchenco 1981, Pfister & Hay 1988, Farrell 1991), and (3) size-related escapes wherein the relative amount of tissue lost to herbivores by mature (large) kelps is

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unlikely to affect the survival of those individuals (Lubchenco & Gaines 1981, Harris et al. 1984, Duffy & Hay 1990). While the importance of chemical defenses and spatial refuges in mediating algal-herbivore interactions has been well examined, there are few estimates of the proportional value of size-related refuges to the survival of cohorts and populations (Vadas et al. 1992).

The importance and effectiveness of the mechanisms described above are directly dependent upon herbivore density (Lubchenco & Gaines 1981). For example, chemical deterrents and 'size-escapes' will be most important in areas of high herbivore density and the availability of spatial refuges will decrease with increasing herbivore density. However, while the effects of often extreme changes in herbivore density have been well documented (i.e. herbivore addition and removal experiments), smaller and more realistic changes in herbivore density remain less well understood (Andrew & Underwood 1993).

In this paper we examine the interaction between the intertidal kelp *Hedophyllum sessile* and the chiton *Katharina tunicata*. On semi-wave-exposed shores along the west coasts of Washington (USA) and British Columbia (Canada), from the mid to low intertidal, *H. sessile* forms a dominant, monospecific canopy which controls the diversity and abundance of understory algal and invertebrate species (Dayton 1975, Dethier & Duggins 1984, Paine 1984). *K. tunicata* is the principal herbivore in these areas and prefers to graze *H. sessile* (Himmelman & Carefoot 1975). In Washington, *K. tunicata* is capable of controlling the abundance of *H. sessile* and is therefore regarded as a strong interactor (Duggins & Dethier 1985). The mechanism underlying the effect of *K. tunicata* on *H. sessile* is presumed to be the consumption of juvenile sporophytes before they can reach refuges in size (Dayton 1975), resulting in a lack of replacement of adults lost to winter storms (Duggins & Dethier 1985). However, in a very similar community in south-eastern Alaska, Dethier & Duggins (1988) found this herbivore to have little or no effect on the dominant canopy forming kelp species found there, *Alaria marginata*.

The goals of this study were to (1) determine the interaction strength of *Katharina tunicata* in British Columbia using realistic herbivore densities, (2) test the unquantified mechanism of size-related escapes for this algal-herbivore interaction proposed by Dayton (1975) and Duggins & Dethier (1985), and (3) investigate additional potential mechanisms of direct interaction between this kelp and herbivore, including the effects of *K. tunicata* on adult *Hedophyllum sessile* survivorship. We did this by first manipulating densities of *K. tunicata* within the range of densities naturally occurring on the shore and predicted that *H. sessile*

percent cover and density would increase with decreasing *K. tunicata* density. Second, while most studies of herbivory monitor algal percent cover or density, in order to determine size-specific changes in survivorship we monitored *H. sessile* population size-structure and demography in areas of manipulated *K. tunicata* density, predicting that *H. sessile* survivorship would increase with increasing *H. sessile* size. While studies of algal population structure and demography are rare, none to our knowledge have been performed in concert with manipulation of herbivore density.

METHODS

Study site. The study area was the rocky low intertidal zone at Prasiola Point located in Barkley Sound on the west coast of Vancouver Island, British Columbia, Canada (48°49'N, 125°10'W). Experimental plots were located on rocky substratum with moderate to gentle slopes throughout the low intertidal zone (0.5 to 1.0 m above mean lower low tides; Canadian Chart Datum), and over a horizontal distance of approximately 100 m. The portion of Prasiola Pt. used for the experiment was semi-exposed to waves from the northwest. Biological indicators of consistent wave exposure, such as *Lessoniopsis littoralis* (Dayton 1975), are absent from this site. For descriptions of comparable communities found at similar sites see Dayton (1975), Paine (1984), Duggins & Dethier (1985).

Experimental design. Densities of the chiton *Katharina tunicata* were manipulated within density ranges observed in the field. To avoid using artificial barriers to maintain density manipulations, treatment areas within the *Hedophyllum sessile* zone were selected on the basis of the presence of natural topographic features which would limit herbivore emigration and immigration. *K. tunicata* is rarely found above or below the *H. sessile* zone, therefore, natural isolating features were required primarily to limit horizontal movement. These included small surge channels, isolated rocks and outcrops of the shoreline. Each of 18 selected treatment areas was between 2 and 4 m^2.

For each treatment area the number of potential locations for a 25 × 25 cm quadrat was determined using tape measures to construct a grid. Using the number of potential locations where a quadrat could be placed and a random number table, a location within each treatment area was randomly selected to place and mark a permanent 25 × 25 cm quadrat. Quadrat locations were marked by drilling approximately 5 cm deep and 0.6 cm diameter holes at 2 of the 4 corners using a Ryobi gas rock drill. A #8-10 plastic drywall anchor was hammered into each hole and a 6.4 cm stainless wood screw was screwed into each. In

this way quadrat positions were precisely re-located on each sampling date.

Naturally occurring densities of the chiton *Katharina tunicata* within each 25 × 25 cm permanent quadrat were recorded and averaged over the 18 treatment areas. The 25th and 75th percentiles of this mean were then used to determine density ranges for, respectively, low and high chiton density treatment areas.

A random block design was used to determine the treatment type for each treatment area and to control for small scale variation in physical factors such as wave exposure. Based on proximity, treatment areas were grouped into blocks of 3, and each treatment area within a block was randomly assigned as either a low, control, or high chiton density treatment area. In this way, each density treatment was replicated 6 times.

At the beginning of July 1995 chiton density treatments were applied by haphazardly placing 25 × 25 cm quadrats within treatment areas and either removing or adding chitons until the desired density ranges were achieved. Larger areas were treated then sampled and this acted to limit chiton emigration and immigration, thereby maintaining density manipulations within sampling areas. Control density plots were not manipulated, but to control for handling effects in the low and high chiton density areas, all chitons were picked up and placed down again. Manipulations were checked and maintained, relative to densities within control plots on that date, every 2 mo at regular sampling dates between July 1995 and November 1996. Thorough searching within haphazardly placed quadrats was performed to avoid affecting *Katharina tunicata* between-treatment size distributions.

Sampling. Initial sampling took place just prior to chiton manipulation in July 1995 and continued approximately bimonthly over the following year. At each permanent quadrat, the percent cover of *Hedophyllum sessile* was recorded. A 25 × 25 cm quadrat was divided with monofilament line at 2.5 cm intervals such that each 2.5 × 2.5 cm square represented 1% of total cover. The percent cover of *H. sessile* was recorded by counting the number of squares occupied by each individual. Within each quadrat the density of *H. sessile* was recorded as the number of individuals with distinctly independent holdfasts. For each individual of *H. sessile*, the maximum holdfast diameter, number of blades and lengths of blades were recorded.

Using a 25 × 25 cm quadrat and the monofilament grid described above as a coordinate system, a map of all *Hedophyllum sessile* individuals was created for each permanent plot and updated on each sampling date. By comparing maps between successive sampling dates a measure of survivorship was obtained for *H. sessile* populations in each chiton density treatment. Holdfast diameters at the initial sampling date were used to place all individuals into 3 size classes. Juveniles were defined as those plants with holdfasts <1 cm in diameter and adults were split into those with holdfasts 1–4 cm and >4 cm in diameter. For survivorship analysis, individuals of each size class were pooled over the 6 replicates of each chiton density manipulation.

Data analysis. Data for all measures except survivorship were compared between treatment groups on each sampling date using 1-way analysis of variance with 'treatment' and 'block' as independent variables. Tukey's HSD test was used for post hoc comparisons. For the sampling dates of April 1996 to July 1996, variables were compared using 2-tailed paired *t*-tests because there were no surviving *Hedophyllum sessile* individuals in the high chiton density areas. For blade number and blade length, the mean of each individual was averaged over each permanent plot. F_{max}-tests were used to check for homogeneity of variances (Sokal & Rohlf 1981). In some cases this assumption was violated and the transformations used have been indicated in the 'Results' section. Data were examined for approximate normality (Underwood 1981) by constructing probability plots. These data were analyzed using SYSTAT version 5.2.1 for Macintosh (Wilkinson et al. 1992).

Blade lengths and blade numbers of the 1–4 cm holdfast size class of each treatment group were further analyzed by extracting them from the original analysis and pooling them on each sampling date. This was done in an effort to eliminate some of the variation associated with comparing blade lengths and numbers of all 3 holdfast size classes simultaneously. However, in treating these data in this way we have committed pseudo-replication and therefore the conclusions drawn from this analysis should be viewed with caution (Hurlburt 1984). Where necessary, some replicates were randomly removed from the analyses to have equal sample sizes in all treatments.

Survivorship of *Hedophyllum sessile* was compared between the treatment groups in 3 ways. First, depletion curves for each size class were constructed by calculating and plotting as a percentage the proportion of individuals of the initial cohort surviving to each sampling date. Second, a Kaplan-Meier survival analysis (Collett 1994) was used to determine the mean survival time with 95% confidence intervals of individuals within each size class for each treatment group. Finally, the Cox proportional hazards model (Collett 1994; Cox regression model, Norusis 1994) was used to compare survival times of *H. sessile* between chiton density manipulations. The assumption of proportional hazards for the Cox regression was tested by constructing the model using the independent variable 'chiton density' as a time-dependent covariant. This
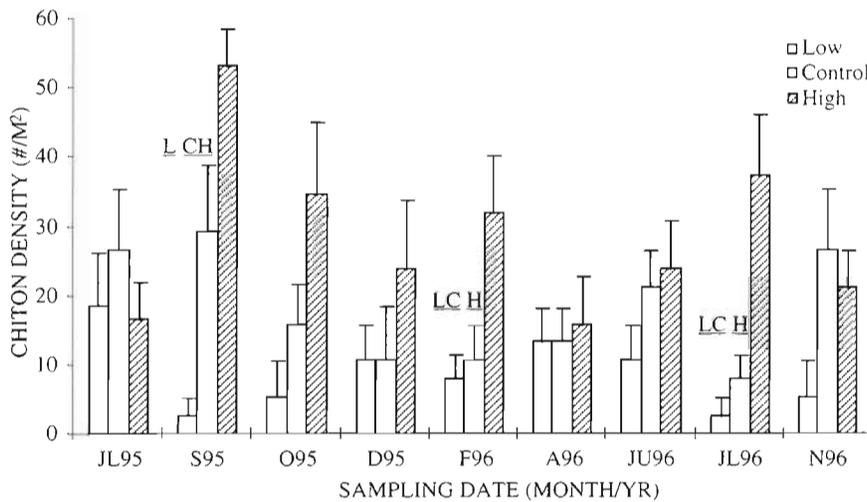
Fig. 1. *Katharina tunicata* density (no. m^{-2}) within chiton density manipulation areas on each sampling date (mean + SE, n = 6). Letters of means sharing an underline are not significantly different (p > 0.05)

assumption was met in all cases. All survivorship analyses were performed using SPSS version 6.0 for Macintosh (Norusis 1994).

Table 1 Results of ANOVA comparing *Katharina tunicata* densities between chiton density treatment areas on those sampling dates with significant differences

Source	df	MS	F	p
Sep 1995 (square-root transformed)				
Treatment	2	55.207	15.056	0.001
Block	5	2.157	0.588	0.710
Error	10	3.667		
Feb 1995				
Treatment	2	1038.222	7.766	0.009
Block	5	389.689	2.915	0.071
Error	10	133.689		
Jul 1996				
Treatment	2	8.167	8.448	0.007
Block	5	0.400	0.414	0.829
Error	10	0.967		

RESULTS

Katharina tunicata density

Densities of *Katharina tunicata* in each permanent plot were expressed on a per m^2 basis. Data were square-root transformed to equalize variances for the sampling date of September 1995. Chiton density manipulations were intended to represent small differences in densities naturally occurring throughout the intertidal. Consequently, *K. tunicata* densities between low, control and high *K. tunicata* treatment areas were significantly different on only 3 of the 9 sampling dates between July 1995 and November 1996 (Fig. 1, Table 1).

Hedophyllum sessile percent cover

No differences in *Hedophyllum sessile* canopy cover were present prior to chiton manipulation in July 1995
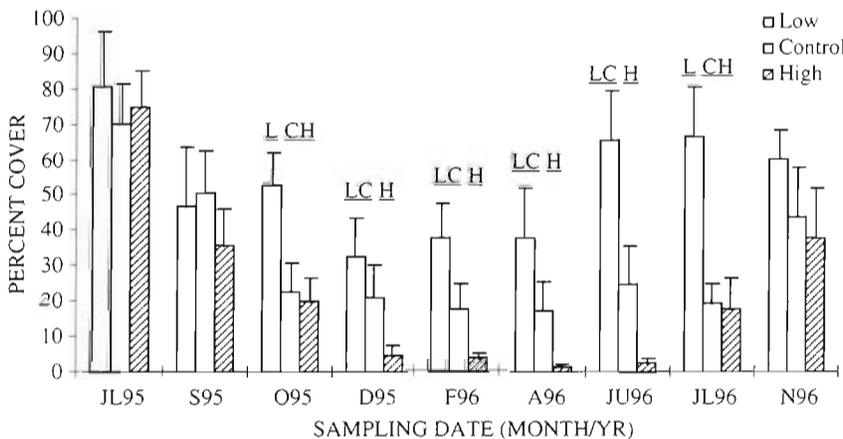

Fig. 2. *Hedophyllum sessile* percent cover within chiton density manipulation areas on each sampling date (mean + SE, n = 6). Letters of means sharing an underline are not significantly different (p > 0.05)

Table 2. Results of ANOVA on the treatment effect of *Katharina tunicata* density on *Hedophyllum sessile* percent cover on those sampling dates with significant differences

Source	df	MS	F	p
Oct 1995 (square-root transformed)				
Treatment	2	1992.667	4.218	0.047
Block	5	312.533	0.662	0.661
Error	10	472.400		
Dec 1995 (log transformed)				
Treatment	2	10.419	7.172	0.012
Block	5	2.911	2.004	0.164
Error	10	1.453		
Feb 1996 (log transformed)				
Treatment	2	12.111	15.736	0.001
Block	5	1.941	2.522	0.100
Error	10	0.770		
Apr 1996 (log transformed)				
Treatment	2	15.871	8.499	0.007
Block	5	2.857	1.530	0.265
Error	10	1.867		
Jun 1996 (log transformed)				
Treatment	2	16.975	6.413	0.016
Block	5	2.805	1.060	0.436
Error	10	2.647		
Jul 1996				
Treatment	2	4578.722	5.324	0.028
Block	5	152.222	0.174	0.960
Error	10	874.856		

but by October 1995 there were significant (p = 0.047) differences between the treatment groups which continued until November 1996. Data were log transformed to equalize variances for the sampling dates of February, April and June 1996 (Fig. 2, Table 2).

Hedophyllum sessile density

The number of individuals within each permanent plot was expressed on a per m² basis on each sampling date. New recruits appearing after the initial sampling date were not included in the analysis. By February 1996 differences in *Hedophyllum sessile* density between low and high treatment areas approached significance (p = 0.080). By April 1996 there were no surviving individuals in any of the 6 replicate high chiton density treatment areas. Transformations were not required for analysis on any sampling date (Fig. 3).

Blade length and blade number

There were no significant differences in cumulative blade number prior to April 1996 when there were no longer any surviving *Hedophyllum sessile* individuals from the initial cohort in the high chiton density areas (Fig. 4). Cumulative blade lengths differed only in February 1996, just prior to this event ($F_{2,5,10}$ = 7.4, 1.5; p = 0.011, 0.275; Fig. 5). Examined in isolation, blade numbers of the 1–4 cm holdfast size class did not differ among the 3 treatment groups prior to the disappearance of the 1–4 cm holdfast size class in high chiton density areas by December 1995. In July 1995, blade lengths of 1–4 cm holdfast individuals were initially longer in the control group than the low and high chiton density groups (n = 14, $F_{3,38}$ = 5.0, p = 0.012), but did not differ again until December 1995 when *H. sessile* in the high chiton density areas disappeared completely (Fig. 6). At this date, individuals in the control and low chiton density areas did not differ in blade length or blade number (2-tailed paired *t*-test, n = 5).

Hedophyllum sessile survivorship

Depletion curves for the 3 size classes of *Hedophyllum sessile* holdfasts (Fig. 7) indicate that survivorship of individuals in the <1 cm and 1–4 cm size classes, but not the >4 cm size class, was less in the high than in the control and low chiton density treatment areas. Sample
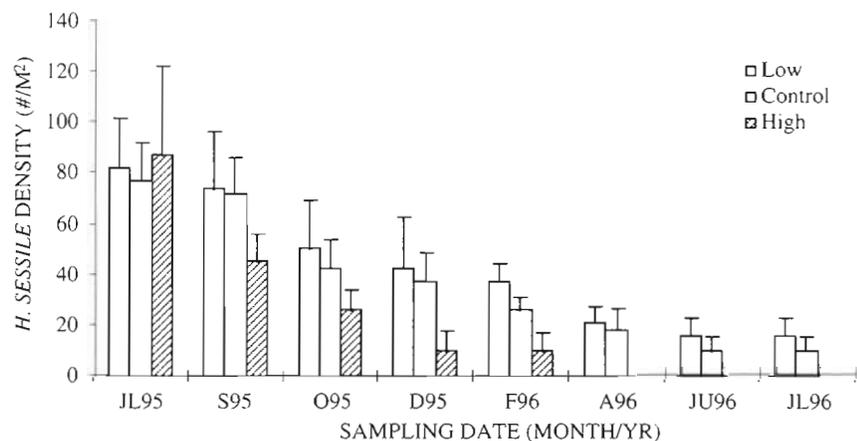
Fig. 3. *Hedophyllum sessile* density (no. m⁻²) within chiton density manipulation areas on each sampling date (mean + SE, n = 6). No significant differences (p < 0.05) were found between treatment groups on sampling dates prior to April 1996
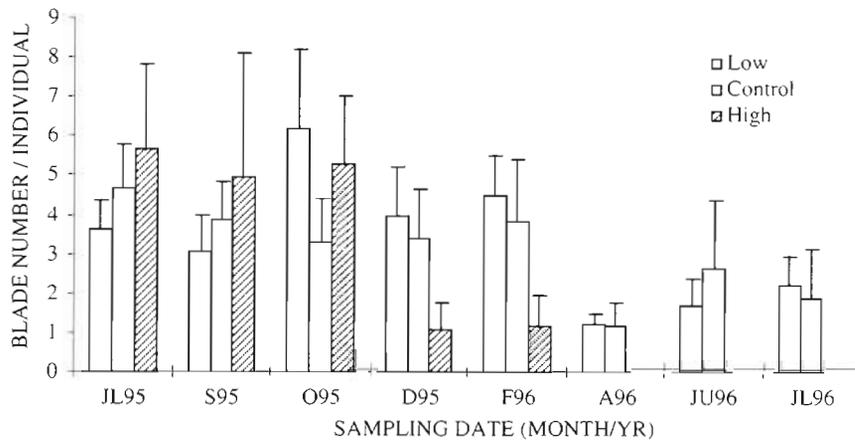
Fig. 4. *Hedophyllum sessile* mean blade number per individual within chiton density manipulation areas on each sampling date (mean + SE, n = 6). No significant differences (p < 0.05) were found between treatment groups on sampling dates prior to April 1996

sizes in Fig. 7 refer to the total number of individuals of each size class within each treatment group. The results of the Kaplan-Meier survival analysis agree with these observations (Fig. 8). Ninety-five percent confidence intervals for mean survival time of the <1 cm and 1–4 cm size classes in high chiton treatment areas do not overlap with those for the low and control treatment areas.

The Cox regression analysis further supports and adds to the certainty of these differences in survivorship. The Cox regression uses one dependent variable as a reference variable to which other dependent variables can be compared. For analysis of survival time of *Hedophyllum sessile* size classes between chiton density treatments, low chiton density was the reference variable (Table 3). The relative risk of mortality, denoted Exp(B), describes the percentage change in the relative hazard rate associated with each *H. sessile* holdfast size class (Norusis 1994). For <1 cm holdfast diameter individuals in the high chiton density areas, the relative risk of mortality was 2.25 times that of <1 cm individuals in the low chiton density areas (Table 3). The 95% confidence intervals for Exp(B) are

interpreted as being significant when they do not include 1 (Collett 1994, Norusis 1994). Positive regression coefficients indicate decreased survival as compared to the reference variable whereas negative values indicate increased survival. The significance level of B, the regression coefficient, was determined using the Wald statistic which has a chi-square distribution (Norusis 1994). The Wald statistic is B, divided by its standard error, squared [i.e. $(B/SE)^2$]. *H. sessile* individuals of the 1–4 cm holdfast size class in the high chiton density areas were 1.72 times more likely to die than the same size class individuals in the low chiton treatment areas. The 95% confidence interval of this value did not include 1 and the positive regression coefficient was significant. No differences in survival time for individuals in the >4 cm holdfast size class were found between treatment groups.

DISCUSSION

The dramatic decline in *Hedophyllum sessile* percent cover and density in the high *Katharina tunicata*
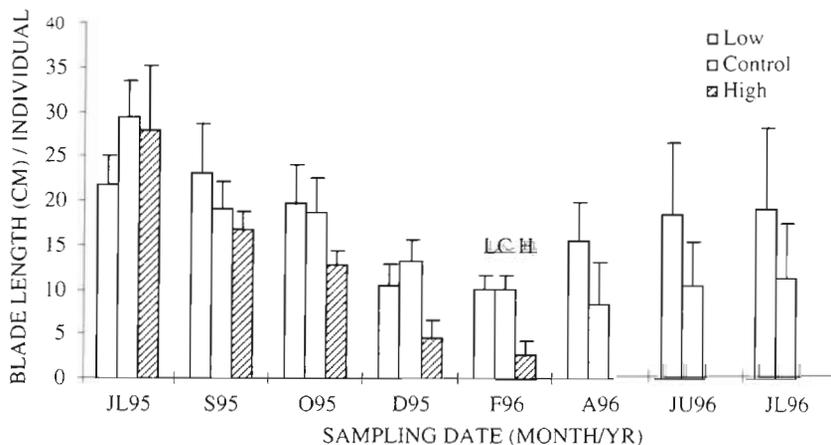

Fig. 5. *Hedophyllum sessile* mean blade length per individual within chiton density manipulation areas on each sampling date (mean + SE, n = 6). Letters of means sharing an underline are not significantly different (p > 0.05)
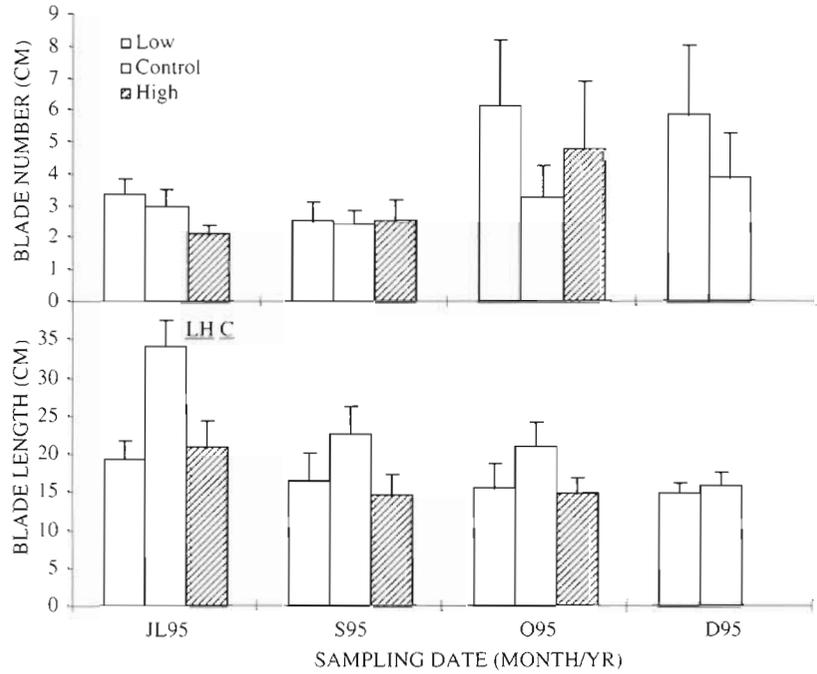
Fig. 6. Blade number and blade length of *Hedophyllum sessile* individuals of the 1–4 cm maximum holdfast diameter size-class within chiton *Katharina tunicata* density manipulation areas. Data are means + SE (JL95, n = 14; S95, n = 11; O95, n = 5) pooled over chiton density manipulation areas between July and December 1995. Letters of means sharing an underline are not significantly different (p > 0.05)

density manipulation areas shows that in low intertidal communities along the west coast of Vancouver Island the chiton *K. tunicata* is a strong interactor, much as it is in Washington State. Duggins & Dethier (1985) describe similar changes in *H. sessile* percent cover between their *K. tunicata* addition and removal areas. In this study, however, the manipulated changes in chiton density were much smaller, giving a more precise indication as to the range of chiton densities that are required to cause significant declines in *H. sessile* abundance. It is worth noting here that in general, using natural topographic features to limit chiton movements was quite successful. However, following removal of the *H. sessile* canopy in the high chiton density areas, rates of emigration and/or mortality were high and required more frequent addition of chitons. This pattern is also described by Dayton (1975) and Duggins & Dethier (1985).

This study supports the previously unquantified mechanism termed size escape (Duffy & Hay 1990), refuge in size, or coexistence escape (Lubchenco & Gaines 1981). In the high chiton density areas, individuals of the 1–4 cm maximum holdfast diameter size class survived significantly longer than <1 cm holdfast individuals and significantly less than those in the >4 cm holdfast size class. This process is regarded as a
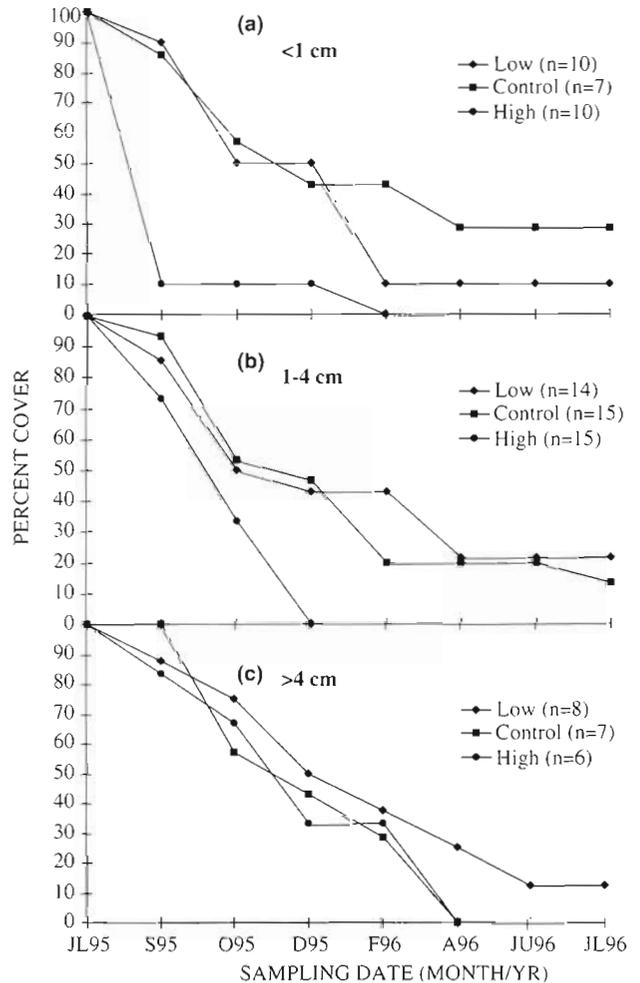
Fig. 7. Comparison of depletion curves of the July 1995 cohort of *Hedophyllum sessile* (a) <1 cm, (b) 1–4 cm, and (c) >4 cm maximum holdfast diameter size-classes as a function of time and chiton *Katharina tunicata* density
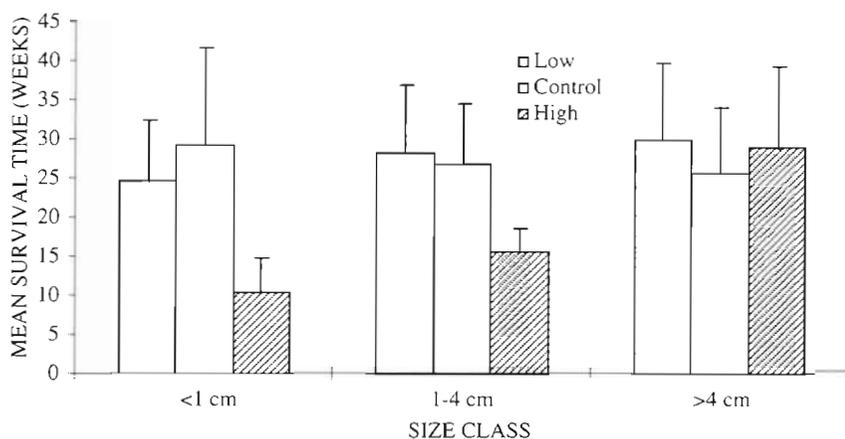
Fig. 8. Results of the Kaplan-Meier analysis of the *Hedophyllum sessile* <1, 1–4 and >4 cm maximum holdfast diameter size-classes as a function of chiton *Katharina tunicata* density. Data are mean survival times (wk) with upper 95% confidence intervals. Refer to Fig. 7 for respective sample sizes

crucial mechanism which determines in part the influence of grazing on algal distribution and intertidal community structure (Hawkins & Hartnoll 1983). Lubchenco & Gaines (1981) calculate a theoretical measure of 'expected herbivore damage' by multiplying the probability that a plant will be encountered by a herbivore, by the conditional probability the herbivore will eat at least part of the plant, by the expected change in fitness of the plant given that it is encountered and at least partially consumed. Algal size-related escapes impact this equation directly, affecting both the conditional probability that the herbivore will feed and the expected change in fitness. In the case of adult *Hedophyllum sessile*, the probability that *Katharina tunicata* will feed when it encounters adult blades is high, but the expected change in algal fitness is low. Juvenile sporophytes, on the other hand, are likely to suffer dramatic changes in fitness should grazing occur. The finding of survivorship increasing for successively larger sizes of *H. sessile* individuals in this

study represents an important quantification of this ecologically important mechanism which mediates the outcome of many plant-animal interactions.

Over most winters *Hedophyllum sessile* populations are dramatically reduced by storms which either remove entire individuals or leave only perennating holdfasts with a few blades of greatly reduced length (Duggins & Dethier 1985). Previous investigators of this community (Dayton 1975, Duggins & Dethier 1985) have speculated that *Katharina tunicata* inhibits the annual recovery of the *H. sessile* canopy by grazing juvenile sporophytes before they are able to grow and reach a refuge in size. Grazing of adult sporophytes, particularly during low tides when blades are most accessible, also occurs. However, adults were thought to be tolerant of *K. tunicata* grazing as a result of their size. Following this scenario, lack of replacement of adult *H. sessile* lost annually to wave force by juveniles consumed by *K. tunicata* would eventually lead to the differences in canopy cover observed between areas of low and high *K. tunicata* density (Duggins & Dethier 1985). Although juvenile survivorship was found to be lower in high chiton density areas, this scenario is not completely supported by the results of this study.

The survivorship analysis showed that although the *Hedophyllum sessile* canopy does decline dramatically each winter due to battering by waves, the system is not completely reset every year. In fact, during the 1994/95 winter, the canopy showed little sign of deterioration at all. However, during the 1995/96 winter over which the experiment was performed, the particularly inclement weather resulted in an approximately 60% decline in *H. sessile* percent cover in

Table 3. Results of Cox regression analysis comparing *Hedophyllum sessile* maximum holdfast diameter size-class survivorship between chiton density treatment areas. Refer to 'Results: *Hedophyllum sessile* survivorship' for explanation of column headings. Significant differences indicated by bold type

Variable comparison	Exp(B) (relative risk)	95% CI for Exp(B) Lower	Upper	B (regression coefficient)	p
Size class: <1 cm					
Control vs low	0.576	0.289	1.148	−0.552	0.117
High vs low	2.251	1.207	4.197	0.811	**0.011**
Size class: 1–4 cm					
Control vs low	0.811	0.516	1.278	−0.208	0.368
High vs low	1.716	1.070	2.751	0.540	**0.025**
Size class: >4 cm					
Control vs low	1.254	0.671	2.343	0.226	0.478
High vs low	0.972	0.508	1.8589	−0.029	0.932

the control chiton density treatment areas. Survivorship data for individuals within the low and control chiton density treatment areas show that many plants survived the winter and contributed to the recovery of the canopy the following spring. However, the survivorship analysis of individuals within high chiton density areas shows that young adults with maximum holdfast diameters of 1–4 cm at the start of the study survived significantly fewer weeks than comparable adults in the control and low chiton density areas. All of these 1–4 cm holdfast diameter individuals were lost by December 1995. The mechanism by which *Katharina tunicata* can affect juvenile (<1 cm size class) *H. sessile* survivorship is clear: the small delicate blades are easily grazed to mortality. However, the mechanism by which chitons can affect adult individuals, which have supposedly reached a refuge in size from grazing, is less obvious.

Circumstantial evidence strongly suggests that the 1–4 cm holdfast individuals in the high chiton density areas were lost due to the combined effects of *Katharina tunicata*-induced degradation of holdfast integrity and increased wave force from September 1995 to December 1995. The rate at which these individuals were lost strongly suggests that some factor in addition to chiton grazing must have played a contributing role in their demise. It is not plausible to expect that these metabolically low and slow moving molluscs could have consumed this entire size class between July 1995 and December 1995. If this were the case, one would expect to have found evidence of grazing at sampling dates prior to December 1995 in the form of declining or significant decreases in blade number and/or blade length. However, comparison of blade lengths and numbers of 1–4 cm holdfast individuals clearly shows there was no treatment effect of *K. tunicata* density on *Hedophyllum sessile* blade number or length prior to their disappearance from the high chiton density areas by December 1995 (Fig. 6). This indicates that at the time these individuals were lost they were morphologically identical to their counterparts in the low and control chiton density areas. Finally, the period of time over which these events occurred coincides precisely with the seasonal increase in wave exposure during October and November. Thus, we suggest here that *K. tunicata*'s behaviour of burrowing into or edging underneath the holdfasts of *H. sessile*, likely for protection from desiccation or waves (Duggins & Dethier 1985, Stebbins 1988), was indirectly responsible for the loss of the 1–4 cm holdfast size class from the high chiton density areas by degrading holdfast integrity and making these individuals extremely susceptible to wave-induced mortality. In this way, *H. sessile* survival can be described quantitatively as a function of both grazing and wave exposure: the com-

bination of these 2 factors results in mortality when neither alone would be sufficient. This represents an example of an 'interaction modification' indirect effect, as described by Wooton (1993). We can offer no alternative explanation for the rapid and differential loss of these morphologically similar individuals during a period of increasingly high wave exposure. One additional line of evidence to support this hypothesis is that in the low and control treatment groups, several individuals of *H. sessile* survived as only holdfasts which vegetatively regrew new blades in the spring. No such individuals were found in high chiton density treatment areas, further suggesting that some mechanism was responsible for the loss of entire thalli.

Herbivory and hydrodynamic forces represent the 2 primary sources of mortality to benthic algal populations of wave-swept, low intertidal and shallow subtidal communities. Critical investigations of the roles that hydrodynamic forces play in shaping benthic algal communities of wave-swept shores are relatively recent and few (Denny 1988, Gaylord et al. 1994, Shaughnessy et al. 1996, Blanchette 1997). By directly impacting survivorship, and therefore reproductive output, the combined effects of drag, lift and acceleration resulting from water movement are strong selective agents acting on both form (Shaughnessy et al. 1996) and reproductive strategies (DeWreede & Klinger 1988). Similarly, marine herbivores are well known for their effects on benthic algal population and community structure and several investigations also have attempted to attribute morphological, structural, chemical and reproductive features of algal thallus forms to their effects (Littler & Littler 1980, Padilla 1984, Paul & Hay 1986, Hay & Fenical 1988, Hay 1996). However, recent attention to the indirect relationship between herbivores and macroalgae by way of wave exposure (Biedka et al. 1987, DeWreede et al. 1992, Padilla 1993, Tegner et al. 1995) suggests that determining the relative importance of these factors separately may be inappropriate, if not impossible (i.e. studies examining the effects of wave exposure on algal survivorship *in situ* must control for the indirect effects of herbivores in order to assess only the effects of hydrodynamic forces).

As pointed out by Tegner et al. (1995), the hydrodynamic models of Gaylord et al. (1994) predict that as individual macroalgae increase in size the probability of mortality due to holdfast failure or breakage becomes much higher. The finding in this study that smaller adults (1–4 cm holdfast size class), not the largest adults (>4 cm holdfast size class), are lost first contradicts this prediction and may give some insight as to the trade-offs that macroalgae face. Specifically, *Hedophyllum sessile* juveniles (<1 cm holdfast size class) may reach an escape in size from significant her-

bivore damage to blades when they reach the 1–4 cm holdfast size class; however, at this size they are still susceptible to the direct and indirect effects of holdfast degradation by high densities of *Katharina tunicata*. Growing larger yet into the >4 cm holdfast size class may make these algae less susceptible to the actions of *K. tunicata*, but may also push them past the maximum size at which they can tolerate local and seasonal hydrodynamic forces.

Duggins & Dethier (1985; and Dethier & Duggins 1988) point out the importance of abiotic disturbance in this community and the geographic variation of *Katharina tunicata*'s interaction strength: the seasonal increase in hydrodynamic forces imposed upon low-intertidal canopy-forming kelps is directly responsible for population attrition and *K. tunicata* is a strong interactor in Washington but not Alaska. The indirect effects, however, of *K. tunicata* on the population dynamics of *Hedophyllum sessile* were not realized. The proposed mechanism of interaction between *K. tunicata* and the holdfast of *H. sessile* may explain the geographic variation in the interaction strength of this herbivore. Although Dethier & Duggins (1988) describe differences between the Washington and Alaskan communities communities as 'subtle', dramatic morphological differences exist between the dominant kelp species found in these areas. Based on their descriptions, the community studied in Washington was dominated by *H. sessile* and is very similar to that found at Prasiola Point. However, the Alaskan community was dominated by the winged kelp *Alaria marginata*. Functionally, *A. marginata* appears to play an ecologically equivalent role in Alaska to that of *H. sessile* in Washington and British Columbia: a competitively dominant canopy is formed that supports a diverse algal and invertebrate understory community. However, whereas *H. sessile* individuals possess a large (occasionally >10 cm), perennating holdfast composed of interwoven haptera which supports a diverse infaunal invertebrate community, *A. marginata* possesses a small, stout, annual holdfast (Scagel 1972) which appears impenetrable to most burrowing invertebrates. In light of the mechanism proposed here, this difference in penetrability provides a plausible explanation of *K. tunicata*'s variable effects on these kelp communities. Tegner et al. (1995) describe a similar interaction between sea urchins *Stronglylocentrotus* spp. and the holdfasts of *Macrocystis pyrifera*, in which cavitation, or burrowing into the large holdfasts, resulted in a higher probability of dislodgment by wave action.

This study capitalized on the advantages of monitoring benthic algal population structure and demography in combination with experimental manipulation of herbivore densities to determine the mechanisms by which a principal herbivore affects a temperate low intertidal kelp community. As a result, we have revealed the combined importance of hydrodynamic forces subsequent to herbivore-induced tissue damage, and have offered explanation for geographic variation in interaction strength of the herbivore *Katharina tunicata*. Finally, the importance of algal size was emphasized with the quantification of the ecologically important mechanism of size-related escapes.

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