Early post-settlement mortality of the scallop *Pecten fumatus* and the role of algal mats as a refuge from predation

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Early post-settlement mortality is one of the main processes determining distribution and abundance patterns of marine benthic invertebrates. Most scallops have an attached phase as spat before they release the byssus and move onto the soft sediments. Thus, spat differ from other stages of life in their use of microhabitat, lack of mobility, and therefore in their vulnerability to mortality processes such as predation. However, the contribution of predation to explain levels of mortality experienced by spat and early juvenile scallops is unknown. Complex habitats such as seagrasses and algae provide a substrate upon which spat can attach and might confer an advantage as a refuge from predation. This study investigates the contribution of early post-settlement predation on abundance of *Pecten fumatus* and determines the role of the algae *Hincksia sordida* as a refuge from predation. Data were collected using field observations, a predator exclusion experiment, and tethering techniques. Mortality of up to 85% during the first weeks after settlement appeared to have prevented the establishment of an adult population at our study site. Mats of the macroalgae *H. sordida* provided a settlement substrate for *P. fumatus* spat. However, increased algal biomass did not provide greater protection from predation to juvenile scallops than lower algal biomass. Our study suggests that prey survival in submersed vegetation is likely to be dynamic among years, and affected by prey behaviour and density as well as the characteristics of the submerged vegetation.

Keywords: bivalves, habitat complexity, macroalgae, predation, submersed vegetation.

Introduction

Early post-settlement survival is a key factor determining recruitment success in marine invertebrates with pelagic larvae (Olafsson et al., 1994; Hunt and Scheibling, 1997). Mortality during the first days to weeks after settlement is very high; often as much as 90% (see review in Gosselin and Qian, 1997). Post-settlement, marine invertebrates are subjected to a range of biotic and abiotic factors that influence survival such as predation (Thorson, 1966; Keough and Downes, 1982), competition for space (Connell, 1961; Menge, 1976), and environmental stresses, e.g. temperature and salinity (Denley and Underwood, 1979). The processes affecting newly settled invertebrates differ from those influencing older juveniles since the use of microhabitat and food resources change ontogenetically as does their vulnerability to external factors affecting survival (Gosselin and Chia, 1994). Predation is the most studied process and generally recognized as a key factor regulating distribution and abundance of newly settled invertebrates (Gosselin and Qian, 1997; Hunt and Scheibling, 1997). Predation pressure can be mediated by habitat complexity, with more complex habitats typically providing improved shelter opportunities and impacting predator efficiencies (Pohle et al., 1991; Carroll et al., 2014); therefore, it is essential that specific habitat characteristics are examined when explaining variation in abundances.

Complex habitats, such as seagrass and macroalgae, provide refuge and can reduce mortality by predation compared with unvegetated substrata (Peterson, 1982; Gribben and Wright, 2006; Hernández Cordero and Seitz, 2014). Blades of seagrass and macroalgae interfere with the mobility of predators (Gagnon et al., 2003) and their ability to detect prey visually (Hemminga and Duarte, 2000). Predation risk can decrease with increasing habitat complexity, e.g. increasing plant stem density (Stoner, 1982; Gotceitas, 1990). However, the role of vegetation on prey–predator dynamics...
is not straightforward and depends on predator and prey traits (James and Heck, 1994; Flynn and Ritz, 1999; Horinouchi et al., 2009), predator and prey density (Mattila et al., 2008; Scheinin et al., 2012), and predator and prey microhabitat use (Klecka and Boukal, 2014).

Despite the high mortality documented for several marine invertebrate species, mortality estimates for bivalve species in the period immediately following settlement are scarce. Collecting this information is particularly challenging as newly settled bivalve spat are small and cryptic, making detection of recruitment events in the field difficult, although there has been success in using artificial habitats to obtain estimates for rates of recruitment and survival (Carroll et al., 2012). As a result, much of our data on predation in bivalves is about adults or juveniles (Bologna and Heck, 1999; Irlandi et al., 1999), and such knowledge cannot be extrapolated to newly settled spat. In bivalve populations, spat and juveniles are most vulnerable to predation until they attain a particular size (Garcia-Esquivel and Bricel, 1993; Pohle et al., 1991). Recently settled scallops (family Pectinidae) are particularly vulnerable to predation because of their thin shells, inability to close shells tightly near the auricles, and ability to keep the valves closed for prolonged periods (Brand et al., 1980). Moreover, scallops have distinct ontogenetic shifts in stage-specific habitat requirements; while most adults are free-living, spat secrete a byssus, using it to attach themselves to upright sessile organisms or structures such as hydroids (Bremec et al., 2008), filamentous algae (Harvey et al., 1993), seagrasses (Pohle et al., 1991), and polychaete tubes (Aguilar and Stotz, 2000). Then the spat of most scallop species, once reaching a specific size, release the byssus and the unattached juveniles move onto the soft substrate and are more mobile (Brand, 2006). Thus, scallop spat differ from other stages of life in their use of microhabitat, lack of mobility, and therefore in their vulnerability to different factors causing mortality.

The commercial scallop, Pecten fumatus, is an important species in the Australian scallop fishery, supporting substantial production since the early 1900s in the Derwent Estuary and the D’Entrecasteaux Channel, southeastern Tasmania. This species is a simultaneous hermaphrodite that has a protracted spawning period since the early 1900s in the Derwent Estuary and the D’Entrecasteaux Channel, southeastern Tasmania. This species is a simultaneous hermaphrodite that has a protracted spawning period during winter and spring (Sause et al., 1987; Young et al., 1999). Depletion of P. fumatus populations has occurred throughout the history of the fishery, with closures of fishing areas designed to allow stock recovery. Despite the commercial importance of P. fumatus, there is no information about early post-settlement processes affecting the abundance of this species. Spat of P. fumatus attach to filamentous substrate of algae and seagrass until they reach a size of ~4 mm, after which they tend to release the byssus (Gwyther et al., 1984) and recess into the sediment as juveniles. During summer, areas of fine sand sediment in the Derwent Estuary are covered by filamentous brown algal mats of Hincksia sordida, upon which larvae of several bivalves attach, including P. fumatus. These algal mats appear beneficial in providing a settlement substrate and potentially may extend this benefit to juvenile stages by providing refuge from predation. The objectives of this study were to examine the contribution of predation on abundance of spat of P. fumatus and to determine the role of H. sordida biomass as a refuge from predation in juveniles of P. fumatus. This was undertaken by field observations of spat and juvenile abundance across different macroalgal biomass levels, a predator exclusion experiment to assess the contribution of predation to abundance of spat, and a tethering experiment to assess differential survival of juveniles among different macroalgal biomass.

**Material and methods**

The study was undertaken at a site encompassing ~1 ha of sandy bottom in 10 m water depth, located in the Derwent Estuary, Tasmania, Australia (42.90639° S, 147.35170° W). The Derwent Estuary is a salt wedge estuary characterized by freshwater river input overlying marine saline waters, with a mean tidal amplitude of 0.8 m (Wild-Allen et al., 2009). During the austral summer (December–February) of 2011–2013, the substrate at this site was covered by mats of the brown algae H. sordida (mean ± s.e. 96.9 ± 14.5 g dry wt algae m⁻²) which can reach a height of ~20 cm off the substrate. Pecten fumatus spat were defined as individuals 0.5–4 mm shell height who were most likely to be attached to structures such as algae and seagrass (Gwyther et al., 1984; Hortle and Cropp, 1987), and juveniles were defined as individuals >4 mm who were likely to have detached from structures and moved onto sediment.

**Temporal changes in scallop density and size structure**

Densities of spat and juvenile P. fumatus could not be assessed in situ, so instead the H. sordida and the top 1 cm of sediment below the algal mat was removed from within 40.5 × 31.5 cm quadrats (total area = 0.1275 m²) haphazardly placed on the H. sordida mats. The algal mat was removed from the quadrats using scissors to cut the algae inside the quadrat and a hand shovel to collect both algae and the associated sediment. Mats and sediments were carefully transferred to a plastic bag underwater, sealed, and transported to the laboratory. All contents were passed through a 500 µm sieve and the retained material was fixed in 10% formalin for later analysis. A stereomicroscope was used to detect scallops (magnification 6.3×) and images were taken of each scallop to estimate shell height (largest distance perpendicular to the hinge) to the nearest 0.02 mm using Image 1 software. The H. sordida in each sample was oven-dried for 48 h at 60°C and weighed to estimate dry weight. Sampling at the site was done three times during the austral summer of 2011/2012: 30 December 2011 (n = 8 quadrats), 6 January 2012 (n = 5 quadrats), and 16 January 2012 (n = 8 quadrats), and on three occasions during the austral summer of 2012/2013: 13 January 2013 (n = 17 quadrats), 21 January 2013 (n = 10 quadrats), and 4 February 2013 (n = 22 quadrats).

Scallop densities were converted to the number of individuals per square metre before data analysis and analysis of variance (ANOVA) was used to assess if there were differences in scallop densities over time in each summer. A Shapiro test was used to check the assumption of normality of residuals and a Bartlett test to check for homogeneity of variances (Bartlett, 1937). An adjusted Welch’s test was used to test equality of means when variances were unequal (Welch, 1951). Pairwise t-tests with a Bonferroni correction method were used to determine which sampling dates differed (Wright, 1992).

**Scallop density and algal biomass**

The relationship between scallop densities and dry weights of H. sordida was assessed for spat and juveniles separately using either a linear regression model or a generalized additive model (GAM). Owing to the small number of juveniles found on the first three sampling occasions in 2012, an additional 37 quadrats were sampled on 27 January with only the juvenile scallops quantified to increase the replication to allow an estimate of the relationship between juvenile density and algal biomass. The GAM was fitted using the mgvc package from R (Wood, 2006; R Development Core...
Predation of spat
A predator exclusion experiment using cages was designed to estimate the loss of *P. fumatus* spat (0.5–4.0 mm total height) due to predation. Predator exclusion cages were rectangular plastic containers with tight-fitting lids and intact solid bottoms (40.5 cm length × 31.5 cm width × 20 cm depth) that were positioned on top of the sediment ~1 m apart. To completely prevent all predators, a full exclusion cage had a lid and all four sides of the container covered with 500 μm nylon mesh. A partial exclusion cage was designed to act as a cage control, with the same design as the full cage, but netting was absent from two of the four sides and the top to allow predators access to the cage. It was assumed that small fish and rays could forage on spat from above in the partial exclusion cages and crabs and starfish could enter from the two sides. Cages were made negatively buoyant using a metal bar secured on two sides. A no predator exclusion cage treatment was identified by a peg driven into the substrate at the start of the experiment to mark the area to be sampled at the end of the experiment.

Into each cage, a 40.5 × 31.5 cm area of algal mat and associated 1 cm of sediment below the algae was carefully placed (see *Temporal changes in scallop density and size* for details of removing the algal mat). It was possible that all or parts of the algal mat along with the attached spat could be lost due to water movement from the partial exclusion cages. To confirm that loss of scallops could be attributed to predation and not loss of algal mats, a time-lapse camera was positioned on a tripod 1.5 m above one of the partial cages to monitor algal mat loss. The camera took an image every minute for 24 h during the first and fifth day of the experiment with a tidal amplitude of 0.7 m, which was the average tidal amplitude for the site. The time-lapse photos revealed no movement of algal mats into or out of the cages; therefore, any reduction in scallop spat density in the partial exclusion cage was assumed to be due to predation. It was not possible to control for the effect of transplanting the *H. sordida* mat as the transplanted mat would float away unless confined by a cage. Therefore, it was assumed that the process of transplanting the *H. sordida* mat did not affect the survival of the spat attached to the *H. sordida*.

The experiment commenced on 30 December 2011 and lasted 17 d; this short duration was chosen to reduce potential cage artefacts that may contribute to changes in spat density, e.g. sedimentation and algae growth. As it was difficult to manipulate spat in situ, it was assumed that the density of spat estimated in sampled *H. sordida* mats at the beginning of the experiment was present in all treatments at the start of the experiment. Spat of *P. fumatus* attach to filamentous substrate via a byssus; therefore, it was assumed that any difference in densities between the start and the end of the experiment in the no exclusion plots was due to mortality and not movement of spat.

Cages were cleaned of material clogging the mesh in situ by divers every 3 d using a brush. At the end of the experiment (16 January 2012), the no predator exclusion treatment consisted of 40.5 × 31.5 cm quadrats in which the algal mats and associated 1 cm of sediment below the algae were carefully removed as described above and placed in plastic bags underwater until analysis in the laboratory. Full predator exclusion and partial predator exclusion cages were placed into plastic bags underwater, sealed, and transported to the laboratory. Algal mats and samples were treated as described above (see *Temporal changes in scallop density and size*).

Predator exclusion cages are recognized as the most reliable way of assessing predation, if the experimental design and analysis are rigorous (Hall and Turrell, 1990). In this study, the treatments were replicated, the layout was randomized and the duration of the experiment was short to avoid the possibility of new early post-settled juveniles confounding results. Also, the density of scallops in the partial exclusion cages and no exclusion treatment did not differ, providing strong evidence that cage artefacts did not inflate estimates of mortality in this study. ANOVA was used to compare the density of spat at the beginning of the experiment (n = 8 cages), with the full exclusion (n = 8 cages), partial exclusion (n = 6 cages), and no exclusion (n = 8 cages) treatments after 17 d. A Shapiro test was used to check the assumption of normality of residuals and a Bartlett test to check for homogeneity of variances (Bartlett, 1937).

Predation of juveniles
Experiments using tethered juvenile scallops were used to assess the number of juvenile scallops that are predated on as a function of algal biomass; this was done twice, once in January/February 2012 and again in January/February 2013. Juveniles were collected from both the study site and from mesh bag spat collectors located off eastern Tasmania and kept in aquaria until tethered. On an algal plot (2.25 m²), 24–31 juvenile scallops (4.6–24.4 mm total height) were individually tethered to metal pins (15 cm long) inserted into the algal mat or the soft sediment, depending on algal biomass. The 2012 experiment used six plots with algal biomass of 4.8–102.9 g dry wt m⁻², while in 2013, ten plots with algal biomass of 15.6–226.5 g dry wt m⁻² were used. The range of algal biomass was determined on the actual algal biomass present at the time of the experiments. No bare sand plots were included for the experiment as the entire site was covered by *H. sordida*. The plots in both years were within an area of ~50 × 50 m.

The shell of each tethered scallop was cleaned and dried with absorbent tissue before a piece of 0.7 kg breaking strain monofilament was glued, using cyanoacrylate (SuperGlue®), to the top valve ~1 mm from the umbo ensuring that the valves were not glued together. Monofilament tethers were >15 cm to allow the scallop to move around within the plot. Each tether was attached to a numbered rectangular plastic label (2.5 × 4 mm) for scallop identification and then tied to a metal pin. Images of each scallop were taken and then the software Image J was used to estimate scallop height to the nearest 0.02 mm. Survival of tethered scallops was assessed after 1, 3, 6, 10, and 14 d in 2012 and 3, 5, 8, 10, and 14 d in 2013. Scallops were classified as alive, dead, or missing; dead scallops were classified as “broken shells” or “clappers” (the two shells still held together by the hinge). Clappers or open shells are usually associated with mortality due to disease, high temperature, and/or starfish predation (Hart, 2013). In this study, broken shells were assumed to be remains of scallops eaten by crabs or fish and clappers were assumed to have been eaten by starfish (Stokesbury and Himmelman, 1995). To obtain estimates of mortality associated with tethering, three replicates of five tethered scallops were placed in predator exclusion cages (see the *Contribution of predation to mortality* section) in each experiment. All tethered scallops in the predator exclusion cages survived the experimental periods.
Therefore, mortality of the tethered scallops in the experiment was attributed to predation and not an experimental artefact or other cause, e.g. disease or environmental stress.

To identify predation events and predators, a time-lapse camera was positioned on a tripod 1.5 m above 20 tethered scallops (5.0–24.4 mm total height) in microhabitats with very different algal biomass (4.5–148.1 g dry wt m$^{-2}$). In 2012, the time-lapse camera became available after the tethering experiment and was used in a trial separate from the tethering experiment on 1, 6, and 12 March; while in 2013, the camera was used at the time that the tethering experiment was undertaken on 26 January and 4 February. A single photograph was taken every minute, image sequences spanned 23 h from midnight to 23:00 h for a total of 46 h each time. The camera was equipped with red lighting to minimize disturbance of scallops and attraction of predators during the night (Veale et al., 2000).

The density of potential scallop predators was estimated by counting the number of all potential scallop predators (fish, rays, crabs, starfish) along six 30 × 2 m transects surveyed on 20 January 2012 and the 21 January 2013 in the areas surrounding the tethering experiment. Potential predators included flathead (Platycephalidae), leatherjackets (Monocanthidae), rays (Urolophidae and Dasyatidae), porcupine fish (Diodontidae), toadfish (Tetraodontidae), crabs, and starfish (Asterias amurensis and Coscinasterias muricata; Cropp and Davidson, 1988).

Mortalities of tethered scallops were treated as censored data (censoring occurs when we do not know the time of death for all the individuals, because some individuals will outlive the experiment) and analysed with the Cox proportional hazard model using algal biomass and size of scallops as covariates (Cox, 1972). This model was used because it has the advantage that the effect of the covariate (i.e. algal biomass) is assessed throughout the study period allowing the survival of scallops to be evaluated several times rather than at a given point of time. A penalized spline was used to estimate the parameters in the model (Gray, 1992). Covariates were added and removed by stepwise selection using the Akaike’s information criterion (AIC) implemented in R (version 2.12.1). All statistical analyses used 0.05 as the critical probability level.

A $\chi^2$ goodness-of-fit test, with equal expected frequencies, was used to test for differences in the frequency of predation events by starfish (clappers) or crab and/or fish (crushed shells). As none of the scallops in the control cages were lost from the tethers, missing scallops in algal plots were assumed to have been eaten by crabs or fish as observed by Ambrose and Irlandi (1992). A multiple logistic regression was used to examine the effect of size, algal biomass, and year on the probabilities of a scallop being eaten by a starfish or a crab and/or fish. A Wald test was used to test the null hypothesis that there is no relationship between the binary response variable and the predictors (Agresti, 1996). Variables that were non-significant were removed and a reduced model refitted. Pearson’s $\chi^2$ was used to evaluate the goodness of the model fit.

**Results**

**Temporal changes in scallop density and size**

During the 17-d study period in summer 2011/2012, there was an 87% reduction in average density of scallops (spat and juveniles together) on algal mats ($F = 7.94$, d.f. 3, 52, $p < 0.001$, Figure 1a). At the start of the experiment, scallops were 0.4–3.6 mm in shell height with the 2–3 mm size class having the greatest proportion of individuals (Figure 2a). After 7 d, the surviving scallops had grown as all scallops measured were 3–5 mm long and by 16 January 2012, only four individuals remained, measuring 2–5 mm (Figure 2b and c). No significant change in scallop density was detected in 2013 ($F = 16.81$, d.f. 2, 50, $p = 0.103$); however, the size frequency distribution in this year suggested that this stability in scallop density through time was related to a settlement event that occurred after 13 January 2013 (Figure 2d–f). When the data were separated into spat and juveniles, density of juveniles (>4 mm) decreased by 95% over 22 d (Figure 1b, $F = 9.00$, d.f. 2, 22.9, $p = 0.001$). On 13 January 2013, scallops were 2–11 mm total height (Figure 2d). After 8 d, few juveniles were found and 70% of all the scallops found were 1–4 mm standard height (Figure 2e). Fourteen days later, only 5% of the scallops found were >4 mm, while 95% were 0.9–3.6 mm in height (Figure 2f).

**Scallop density and algal biomass**

No significant relationship was found between H. sordida biomass and density of scallop spat in either year (Figure 3a and c; in 2012 $F = 3.025$, d.f. 1, 11, $p = 0.109$; 2013 $F = 0.868$, edf 2.169, $p = 0.462$). Algal biomass did explain 31.2% of the deviance in juvenile scallop density in 2012 (Figure 3b; $F = 2.752$, edf 3.40, $p = 0.0461$).

![Figure 1](https://academic.oup.com/icesjms/article-abstract/72/8/2322/2458752)

**Figure 1.** Mean density of P. fumatus over time for (a) summer of 2011/2012 and (b) summer 2013. In each year, the mean densities of scallops on sampling days with different letters are significantly different from each other. Numbers next to the means represent the number of quadrats. Note the difference in scale between graphs.
but no significant relationship was detected in 2013 (Figure 3d; $F = 0.3$, edf 1.319, $p = 0.687$). Juvenile scallop densities in 2012 increased as algal biomass increased up to a threshold of $\approx 80$ g dry wt m$^{-2}$, peaking at 48 juveniles m$^{-2}$ and then decreased when algal biomass was 80–180 g dry wt m$^{-2}$ (Figure 3b). While there was evidence that when algal biomass was $> 200$ g dry wt m$^{-2}$, juvenile density increased again (Figure 3b), very few replicates were found with such levels of algal biomass; therefore, the evidence for a positive relationship between algal biomass and juvenile scallop density at the greater densities of algal biomass was considered weak.

### Contribution of predation to mortality of spat

The average densities of scallops differed significantly among treatments in the predator exclusion experiment ($F = 6.45$, d.f. 3, 26, $p = 0.002$). The partial predator exclusion and no predator exclusion treatments both had $\approx 85\%$ fewer spat than the full predator exclusion treatment at the end of the experiment (Figure 4). In contrast, the full predator exclusion treatment had spat densities no different from that observed at the start of the experiment (Figure 4).

#### Mortality of tethered juveniles on H. sordida

An initial ANOVA showed no significant differences in shell height for scallops located in different plots for 2012 and 2013 ($F = 0.271$, d.f. 5, $p = 0.928$ and $F = 1.72$, d.f. 9, $p = 0.08$, respectively). There was strong evidence of a difference in the number of tethered individuals that died between years ($\chi^2 = 44.1$, d.f. 1, $p < 0.001$). In the first 3 d after tethering in 2012, $\approx 40\%$ of the individuals died, compared with $> 80\%$ in 2013 (Figure 5). The mortality risk in 2013 was 2.3 times greater than in 2012 ($Z = 5.911$, d.f. 2, $p < 0.001$). In 2012, variability in the number of individuals dying due to predation was explained by algal biomass ($\chi^2 = 11.49$, d.f. 1, $p < 0.003$). The risk of dying due to predation decreased around 72 g of algae weight and then increased until algal biomass reached 102 g dry weight biomass (Figure 6). There was no evidence that size of the individuals (total height 5.1–24.4 mm) explained the risk of dying ($Z = 0.78$, d.f. 2, $p = 0.67$). In 2013, nearly all the individuals died within the first 8 d, which resulted in no significant contribution of size or algal biomass on the risk of dying ($Z = 2.89$, d.f. 2, $p = 0.235$).

Two predators of juvenile scallops were identified using a time-lapse camera, the ringed toadfish *Omegophora armilla* and the porcupine fish *Diodon hystrix*, which crushed juvenile scallops (5–24 mm in height) leaving broken pieces of shells behind and foraged in sandy bottoms and in plots covered by different amounts of algal cover. Diving observations during transect counts further revealed the presence of the northern Pacific starfish *A. amurensis*. This species was seen manipulating scallops assuming a humped, feeding position and then leaving empty shells (still bound by the dorsal hinge). Densities of *A. amurensis* were not compared between the years, because in 2012, only adults were found, whereas in 2013, the species was almost exclusively present as new recruits (<20 mm longest arm length). Regarding other potential

### Figure 2.

Size frequency distribution of *P. fumatus* spat (0.5–4.0 mm total height) and juveniles (>4.0 mm total height) on (a) 30 December 2011, (b) 6 January 2012, (c) 16 January 2012, (d) 13 January 2013, (e) 21 January 2013, and (f) 4 February 2013; $n$, number of scallops measured on each sampling date.
predators, there was no significant difference in the densities of *Platycephalus* sp. ($F = 0.024, \text{d.f.} 1, 17, p = 0.88$) or *Urolophus cruciatus* ($F = 0.86, \text{d.f.} 1, 17, p = 0.367$) between 2012 and 2013 (Table 1). *Omegophora armilla* was only detected during transect counts in 2012 (Table 1), while *D. nicthermerus* was not encountered.

Broken shells, indicative of predation by crabs and/or fish, were present three times more often than clappers, indicative of predation by starfish ($\chi^2 = 46.83, \text{d.f.} 2, p < 0.001$). For every 1 mm increase in scallop height, the odds of being eaten by a crab or a fish increased 1.2 times, whereas the odds of being eaten by a starfish decreased 0.8 times ($Z = 3.10, \text{d.f.} 1, p = 0.001$). The probability of being eaten by starfish or crabs and/or fish did not differ between years ($Z = 1.82, \text{d.f.} 1, p = 0.069$) or with amount of algal biomass ($Z = -1.25, \text{d.f.} 1, p = 0.210$).

**Discussion**

Predation on spat and juveniles was a major mortality process: mortality of up to 85% of individuals in the first weeks after settlement may explain why adult populations were not established at this site. Fewer than five adult scallops were observed in the study area, despite >40 h searching over 2 years. These findings highlight the importance of predation in regulating recruitment success to adulthood in *P. fumatus*, as observed in other bivalve populations (Flach, 2003; Shank et al., 2012).

While *P. fumatus* will settle on a range of different species of algae (Gwyther et al., 1984; Hortle and Cropp, 1987), at this site over 2 years mats of the macroalgae *H. sordida* provided a settlement substrate for *P. fumatus* spat. In other scallop species, such as *Chlamys islandica* and *Argopecten purpuratus*, filamentous algae also provide substrate for
larvae settlement (Harvey et al., 1993; Cantillán, 2000). Although there was no significant relationship between spat density and algal biomass, *P. fumatus* spat were not recorded in areas where the biomass of *H. sordida* was < 50 g dry wt m$^{-2}$. For juveniles, increased levels of structural complexity in the habitat (increasing levels of algal biomass) were not associated with greater densities; despite an expectation that this would provide greater protection from predation. However, using a metric of cover quality (e.g. Bartholomew, 2002) may provide an alternative assessment of the capacity of the settlement substrate to protect spat from predators. Mortality in the tethering experiment in 2012 was less when there was less algal biomass, suggesting that while the algal mats provided an attractive substrate for attachment, this did not directly translate into a refuge from predation for juvenile scallops. The tethering techniques used in this experiment explicitly allowed for comparisons of relative mortality between sites or habitats by mobile organisms, as the tethers were sufficiently long and light enough to preclude obvious effects on the normal mobility of scallops. However, tethering may influence normal behaviour of prey making individuals more vulnerable to predators (Barbeau and Scheibling, 1994b) and in some cases even vulnerable to predators that would not otherwise succeed in an attack on an untethered prey (Mills et al., 2008). While perhaps the number of individuals eaten in this study was inflated, it did provide valuable data on the influence of habitat on mortality.

Increasing vegetation density does have a positive relationship with prey survival for some marine invertebrates (Heck and Thoman, 1981; Nelson and Bonforsdorff, 1990). However, the generality of this paradigm is not supported and the impact of vegetation on prey survival depends on relative densities of interacting organisms at each vegetation level and predator traits, particular foraging tactics (James and Heck, 1994; Mattila et al., 2008). Perhaps only when spaces between the leaves match the size of the prey does a substantial refuge exist (Ryer, 1988). In forming mats and especially at the higher levels of biomass, *H. sordida* filaments may intertwine sufficiently tight to prevent scallops from finding refuge beneath the surface of the mat. The escape behaviours used by *P. fumatus* may be limited in dense algal mats translating into greater mortality, because both juveniles and adults use a recessing behaviour, in which the upper valve is level with or just below the surface of the sediment (Brand, 2006). This limits detection by visual and non-visual...
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Table 1. Average density of potential predators in 2012 and 2013.

| Predator          | Average density (ind. m$^{-2}$ ± s.e.) |
|-------------------|---------------------------------------|
| Urolophus cruciatus | 0.008 (0.004) 0.017 (0.010)           |
| Platyccephalus sp. | 0.031 (0.007) 0.033 (0.017)           |
| Omegophora armilla | 0.001 (0.001) 0.022 (0.006)           |
| Asterias amurensis | 0.683 (0.161)                           |

predators, while also allowing active predator escape responses such as swimming (Minchin, 1992). In areas of dense algal cover, recessing behaviour may be prevented resulting in greater vulnerability to predators. Conversely and as demonstrated in this study, mortality was reduced at lower algal biomass, presumably because the juveniles would be able to recess into the substrate. These observations agree with previous negative relationships found between abundance of P. fumatus and algal/seagrass cover (Mendo et al., 2014). In contrast, a closely related species, Equichlamys bifrons, which co-occurs with P. fumatus and does not recess (Styan and Butler, 2003), has been positively associated with algal/seagrass cover (Mendo et al., 2014) and obtains greater protection from predation in seagrass than is provided by bare sand (Wolf and White, 1997). The interaction between behaviour and the structure of the vegetation may determine the role of vegetation in reducing the risk of predation with predation risk being greater when escape tactics do not match the habitat physical structure (Lima, 1993).

Interannual variation in estimates of mortality of juvenile P. fumatus by predators was not explained by abundance of potential predators. This was despite an increase in densities of the starfish A. amurensis (a known predator of P. fumatus) in 2013, probably because in 2013, they were mostly juveniles which may have different consumption rates of scallops compared with adults. In the light of this outcome, future work seeking to explain the spatial distribution patterns of scallop could explore the roles of estuarine dynamics, specifically salinity changes, which can affect predation rates on bivalves (Stickle et al., 1985; Agüera et al., 2015), predator assemblages (Martino and Able, 2003), and prey selection (Aronhime, 2010). Also, this study was not able to track predators that may have passed through the study area or night-time predators, which could lead to localized depletions (Carr and Hixon, 1995; Kinoshita et al., 2013). Levels of mortality are not just a function of predator density, but also prey density (Hines et al., 1997; Knights et al., 2012) and the densities of scallops in the 2 years of this study differed almost sixfold (average of 33.2 ind. m$^{-2}$ in 2012 vs.6.0 ind. m$^{-2}$ in 2013). There was also greater H. sordida biomass in 2013 than 2012, which may affect the probability of P. fumatus to find a suitable sand substrate to recess. The exclusion cages we used had the lid and sides covered with 500 μm nylon mesh which would prevent most predators > 500 μm from entering the cage, although small invertebrates in the algal mats would have been introduced to the cages when the algal mats were translocated. At the end of the experiment, scallop densities in the full exclusion cage were not different from densities in the algal mats at the start of the experiment, and the absence of scallops <3 mm shell height suggested that a settlement event did not occur to replace eaten scallops. Therefore, we concluded that predation by small predators is unlikely to be contributing to patterns of mortality in newly settled scallops. Finally, the effect of algal spatial patterning on predation mortality was not assessed in this study and requires further research. Spatial patterning in seagrass habitats has been shown to alter predator—prey dynamics, for example, increased exposure associated with patchy seagrass beds might alter predation on scallops (Irlandi et al., 1995; Bologna and Heck, 1999; Carroll et al., 2012).

The size of juvenile scallops (>4 mm total height) explained the likelihood of being eaten by each of the specific predator groups. This is most likely related to size-related differences in vulnerability to different predators, as the probability of predation by starfish decreased with increasing scallop size. In contrast, the probability of being eaten by crabs and/or fish increased with scallop size. These findings agree with laboratory studies on Placopesten magellanicus, which showed that starfish apparent preference for smaller scallops was explained by size-related changes in scallop vulnerability (Barbeau and Scheibling, 1994a). Conversely, crabs preference for larger scallops resulted from an active choice by crabs and low encounter rates with smaller scallops (Barbeau and Scheibling, 1994a). Therefore, predator assemblages and their associated prey size preferences are likely to be important in determining the predation risk associated with a particular ontogenetic phase in the scallop prey.

This study suggests that early post-settlement predation on spat and juvenile P. fumatus represents a major factor determining small-scale patterns of abundance, and in the study area is sufficiently high as to ultimately preclude the establishment of an adult population. Hinckia sordida was used by the scallops initially as a settlement substrate, but as the spat grew and became juveniles, those individuals in the areas of lesser algal density experienced greater survival. This suggests a change in the role and importance of a habitat structure with ontogeny. Therefore, while this alga provided a settlement structure for scallop spat, as individuals grew greater algal biomass became detrimental to survival, possibly by hindering the recessing behaviour in juvenile P. fumatus. These findings are consistent with recent laboratory studies showing that increased vegetation density will not consistently lead to proportionally greater prey survival (Mattila et al., 2008; Scheinin et al., 2012; Klecka and Boukal, 2014). The manner in which vegetation provides protection for prey will therefore vary according to prey traits/behaviour as well as predator feeding strategies, since structurally complex habitats may negatively influence survival at different stages during their ontogeny.

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