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Post-settlement processes affecting Commercial Scallop recruitment in south-eastern Tasmania

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Executive summary

The D'Entrecasteaux Channel in south-eastern Tasmania supports an important recreational scallop fishery. However, stock size has varied widely between years due to inter-annual variability and spatial patchiness in recruitment as well as the direct impact of fishing. Low recruitment combined with high fishing pressure has the potential to result in stock collapse, a phenomenon that has been repeated several times throughout the history of the fishery.

Recruitment is influenced by a number of factors, including larval supply, settlement processes and post-settlement processes. Previous research has indicated that larval supply may not explain the abundance patterns of newly settled scallops and even if sufficient larvae are produced, the availability of suitable substrate may limit larval settlement and recruitment. Once settled, processes such as dispersal, growth and predation come into play in determining recruitment to the fishable stock.

The overall aim of this study was to examine the role of habitat and post-settlement processes on recruitment, as well as their effects on newly settled scallops. Specific objectives were to:

1. Examine the role of habitat structure and sediment type on scallop density.
2. Assess the relationships between dispersal and growth of recently settled scallops and site characteristics; and
3. Identify the main factors affecting survival of newly settled scallops.

Dive surveys were undertaken to examine the relationships between the distribution and abundance of three species of scallops - the Commercial Scallop *Pecten fumatus,* Queen Scallop *Equichlamys bifrons,* and Doughboy Scallop *Mimachlamys asperrima* - and associated habitat characteristics. At the scale of kilometres, the pattern of distribution for the three co-occurring species was aggregated rather than random or uniform, and thus typical of scallop species. Factors such as sediment type, habitat structural components and presence of predators were shown to influence distribution patterns, although the nature of these relationships differed markedly between species. Commercial Scallops were associated with finer sediments, Queen Scallops with coarse grain sediments, whereas Doughboy Scallops had a less selective association with sediment type, possibly because the species can use byssal attachment on a wide range of substrates. The associations between habitat characteristics and distribution of each species of scallop were discussed in the context of behavioural characteristics and predation pressure. Predation is an important factor regulating distribution and abundance and habitat characteristics have been demonstrated in other studies to influence predation efficiency and predator-prey encounter rates.

Laboratory experiments were conducted to examine whether juvenile Commercial Scallops actively select for particular sediment types, thereby providing further insight into preferences for sediment characteristics and potential post-settlement dispersal. Within the limitations of the experimental system, there was no evidence for active selection of sediment type. The association of Commercial Scallops with fine sediments observed in field may thus

be more related to relatively higher survival in fine sediments rather than an active behavioural choice or post-settlement movement.

In a series of field-based experiments the impacts of predation mortality on recently settled Commercial Scallop spat was examined. An eight-fold reduction in scallop densities was observed within a three week period which, when considered in the light of concurrent predator exclusion experiments, confirmed that predation pressure acting during the first weeks after settlement represents a major factor influencing the subsequent success of a recruitment event contributing to the adult stock. This means that good settlement is no guarantee of recruitment success.

Habitat complexity, specifically the density of the algae *Hincksia sordida* appear to offer a refuge from predation for juvenile scallops compared to spat that settled on bare sand. Our study showed that most of the scallop losses could be attributed to species which crush scallops, such as toadfish, crabs and rays, rather than sea star predation (evidence of which is empty shells or clappers). Our results also indicated growth was faster on sand substrate compared with algal mats, implying that recently settled scallops may be faced with a trade-off between growth and survival.

The relationship between scallop size and probability of sea star predation was examined in laboratory experiments. Results indicated that vulnerability to sea star predation was greater at smaller sizes and decreased with scallop size, supporting a size-refuge hypothesis. In addition, while the invasive northern Pacific sea star did not appear to pose a greater predation risk than the native eleven-arm sea star, it has the potential to contribute to the depletion of scallop populations especially when present in large numbers.

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1 General Introduction

The D’Entrecasteaux Channel in south-eastern Tasmania supports an important scallop fishery, however, due to inter-annual variability and spatial patchiness in recruitment, the stock size has varied widely between years. Low recruitment combined with high fishing pressure has the potential to result in stock collapse, a phenomenon that has been repeated several times throughout the history of the fishery. Recent assessments have indicated that the abundance of the Commercial Scallop *Pecten fumatus* in the D’Entrecasteaux Channel has declined by about 80% since 2006. This decline is due in part to the effects of fishing but is also related to poor recruitment success during this period (Tracey and Lyle, 2011).

Recruitment is influenced by several factors, including larvae supply, settlement and post-settlement processes. Previous research by Semmens et al. (2013) indicated that larval supply may not explain the abundance patterns of newly settled scallops in the D’Entrecasteaux Channel. Other studies have suggested that even if sufficient larvae are produced, the availability of suitable substrate may limit larval settlement and affect recruitment. While these observations provide a first indication of the importance of substrate, a strong effect of post-settlement dispersal and mortality has also been suggested in the D’Entrecasteaux Channel. For instance, during 2009 and 2010, cohorts of newly settled Commercial Scallops did not necessarily translate into successful juvenile recruitment (Semmens et al., 2013). The fate of those newly settled individuals was not determined.

1.1 Study Objectives

The current study aimed to build on Semmens et al. (2013) by examining processes occurring shortly after settlement and their influence on subsequent recruitment to adult populations. The primary objective was to examine the role of habitat and post-settlement processes such as dispersal, growth and survival, and their effects on newly settled scallops. Specific objectives were to:

1. Examine the role of habitat structure and sediment type on scallop densities.
2. Assess the relationships between dispersal and growth of recently settled scallops and site characteristics; and
3. Identify the main factors affecting survival of newly settled scallops.

Persistent poor recruitment of scallops throughout the study period (Tracey and Lyle, 2012; Semmens et al., 2013) hindered a number of anticipated activities, particularly some field based components of the project. The study, therefore, included a focus on laboratory experimentation to address issues of sediment preferences and relative predation rates of potential predators. Laboratory-based experiments were implemented to assess whether juvenile scallops showed preferences for different types of substrate commonly found in the D’Entrecasteaux Channel in order to provide insight as to whether patterns of settlement in the field are due to active behaviour (movement or dispersal) linked to sediment characteristics.

The lack of recruitment also hindered the evaluation of factors affecting survival in the D’Entrecasteaux Channel. However, in early 2011 and again in late 2011 a strong recruitment pulse of recently settled Commercial Scallops *Pecten fumatus* was discovered on *Hincksia sordida* algae mats in Nutgrove Beach, Derwent Estuary. This discovery allowed us to investigate post-settlement survival processes using full exclusion, partial exclusion and open plots to assess the relative contribution of predation on survival of newly settled scallops (2-4 mm in length).

This report is presented as four stand-alone data chapters and there is, therefore, some repetition of background information providing context to the study. Chapter 2 examines habitat characteristics and their links to the distribution and abundance of scallops in the D’Entrecasteaux Channel (Objective 1). Chapter 3 uses laboratory experimentation to examine whether juvenile scallops actively select for different substrate types (Objectives 1 and 2). Chapter 4 is based on field experiments and examines the influence of predation pressure on the survival of recently settled scallops and how this might influence the distribution and abundance of scallops (Objectives 2 and 3). Chapter 4 uses laboratory trials to examine the vulnerability of Commercial Scallops to predation by sea stars (Objective 3).

2 Habitat characteristics associated with distribution and abundance of scallops in the D’Entrecasteaux Channel

2.1 Introduction

The patterns of distribution and abundance at each life-cycle stage in scallops are influenced by habitat characteristics such as depth, substrate type, currents, turbidity, and salinity (see review by Brand 2006). At a finer spatial scale structural components of habitat, such as presence of polychaete tubes (Aguilar and Stotz 2000), hydroids (Harvey et al. 1993), sponges (Bremec et al. 2008), macroalgae (Cantillánez 2000) and/or shells (Pacheco and Stotz 2006), provide settlement substrates for settled scallop larvae or ‘spat’. Attachment by spat on structures can reduce predation rates (Pohle et al. 1991), enhance growth - as an elevated position in the water column provides access to better quality food (Eckman et al. 1989), and avoids smothering by soft sediments (Merrill and Edwards 1976).

The role of habitat structure in reducing risk of predation continues into the juvenile and adult phases. Habitat characteristics influence predation by affecting predation efficiency and/or predator-prey encounter rates (Heck et al. 1981; Myers et al. 1980). Predator encounters are reduced for juvenile bay scallops *Argopecten irradians* by attaching to the upper canopy of the eelgrass *Zostera marina* (Pohle et al. 1991). Complex habitats with greater numbers of horse mussels, sponges and ascidians provide refuge for *Pecten novaezelandiae* from predation by sea stars and gastropods (Talman et al. 2004). Beyond directly reducing scallop visibility to predators, structure may impact movement and foraging behaviours of predators, as is the case with the Queen Scallop *Equichlamys bifrons* which suffer less predation mortality in seagrass beds than on bare sand because starfish have reduced mobility within the seagrass (Wolf and White 1997).

Despite the role of specific habitat characteristics in influencing scallop distribution and abundance patterns, quantitative studies on scallop-habitat relationships are rare. Identifying the specific habitat characteristics to which scallops are associated is relevant in managing, conserving, and even restoring these habitats. This type of information is particularly necessary for the D’Entrecasteaux Channel (DEC), south-eastern Tasmania, where three species of scallops co-occur; the Commercial Scallop *Pecten fumatus*, Queen Scallop *Equichlamys bifrons*, and Doughboy Scallop *Mimachlamys asperrima*.

The DEC supported a significant commercial dredge fishery for scallops from the early 1920s to late 1960s, with catches peaking at around 4500 tonnes meat weight in the mid-1960s and declining rapidly thereafter (Perrin and Croome 1988). Significant depletions of scallop populations have occurred throughout the history of the fishery, resulting in area closures to allow for stock recovery. In 1990 the DEC was declared a recreational-only scallop fishery (Zacharin 1991) but the fishery was closed shortly afterwards due to the lack of scallops in the area. By the mid-2000s there was evidence for stock rebuilding, following more than a decade of fishery closure, that lead to the area being reopened as a dive-only fishery in 2005, with a reduced daily bag limit of 40 scallops per person. This limit was introduced for a trial period between 2005 and 2008 and was set in the fisheries rules at 50 scallops in 2008. Despite these controls on the fishery, the abundance of Commercial Scallops declined by approximately 80% between 2006 and 2010, due to the combined effects of fishing, natural mortality and poor recruitment during this period (Tracey and Lyle 2011).

The three co-occurring scallop species exhibited distinct and temporally consistent distribution patterns within the DEC during the 2000s, suggesting that species-specific habitat requirements may have an influence on their distribution. The abundance of scallops, however, has varied significantly from year to year, with variable and episodic recruitment experienced by each of the species. Commercial Scallops are mainly found in the mid and mid-west sections of the DEC (Tracey and Lyle 2008, Tracey and Lyle 2011) on a range of soft sediment substrates including silt-sand and coarse sand (Fairbridge 1953, Olsen 1955). Commercial Scallop spat bysally attach to filamentous substrate such as macroalgae until approximately 6-10 mm in shell length when they release the byssus and then recess in the substrate (Hortle and Cropp 1987). Queen Scallops do not tend to recess into the substrate and are often found in association with the seagrass *Heterozostera tasmanica* (Olsen 1955, Wolf and White 1997) and occur in greatest numbers in a narrow area in the middle of the Channel (Tracey and Lyle 2011). Doughboy Scallops are widely distributed in the middle and southern regions of the DEC (Tracey and Lyle 2011). They bysally attach throughout their lifetime to a wide range of substrates including bryozoans, seaweeds, sponges, oysters, mussels, old scallop shells, timber and rocks (Zacharin 1994).

An understanding of the distribution and abundance patterns of the three co-occurring species of scallops in relation to habitat characteristics will provide insight into the ecological processes regulating these populations. Being a relatively shallow and sheltered system, the D’Entrecasteaux Channel provides a unique opportunity to study the patterns of distribution by direct observation. In this study we have used dive surveys to examine the relationships between the distribution and abundance of each species and associated habitat characteristics, including structural components, sediment type, predator abundance and depth. We discuss how these relationships are mediated by the distinct behaviour of each species.

2.2 Materials and methods

2.2.1 Study area

The D’Entrecasteaux Channel, separates Bruny Island from the Tasmanian mainland. It was divided into four sections based on topography and bathymetry: a narrow northern section with an average depth of 20 m (Area 1 in Fig. 2.1), an extensive shallow mid-section with an average depth of 15 m (Area 2), a narrow central area with stronger currents than the other Areas and an average depth of 14 m (Area 3) and a southern region with an average depth of 40 m which opens to the Southern Ocean (Area 4) (Olsen 1955, Herzfeld et al. 2005). D’Entrecasteaux Channel system is micro-tidal, with a spring tide ranging up to one metre (Herzfeld et al. 2010).

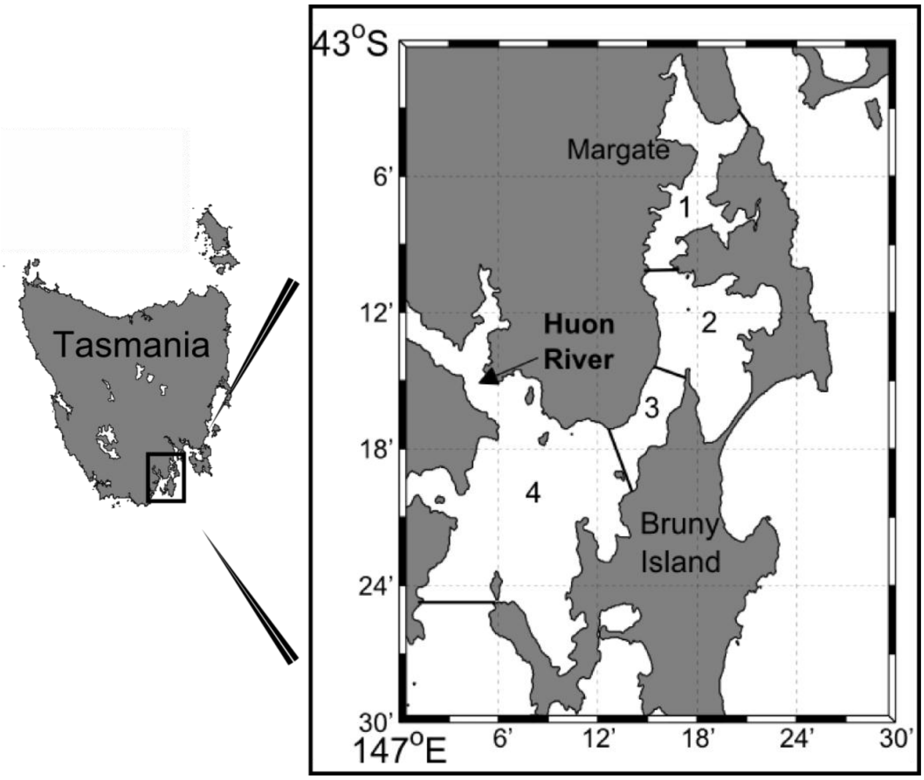

Fig.2.1 Map of the D'Entrecasteaux Channel. Numbers represent the Areas referred to throughout the text.

2.2.2 Distribution patterns

Scallop distribution and abundance in the Channel were quantified using dive surveys of 59 sites defined in Tracey and Lyle (2011). The survey sites were restricted to depths <20m and to soft sediments. Briefly, at each site, a 100 m transect was laid haphazardly and two divers searched and collected all scallops one metre either side of the transect line, covering an area of 200 m^2. The species and shell width (SW- largest distance parallel to the hinge) was recorded for each scallop collected. However, given the potential for very small scallops to be underrepresented due to collection bias based on size, analyses have been limited to include only individuals > 30 mm. The numbers of two known scallop predators, the native eleven-arm sea star *Coscinasterias muricata* and the invasive northern Pacific sea star *Asterias amurensis,* was also recorded for each transect.

Patterns of scallop abundance were analysed by comparing them to a Poisson (random) distribution, which assumes that the expected number of organisms is the same in all sampling areas and is equal to the mean (Krebs 1999). Agreement between observed and expected values was evaluated using a chi-square test of goodness-of-fit at the 5% level of significance, the null hypothesis being that the distribution did not differ significantly from a Poisson distribution (Elliott 1977). To evaluate if the distribution was aggregated, the standardised Morisita's Index of dispersion (I) was used because it is independent of population density and sample size (Myers 1978). This index ranges from -1 to +1, with zero indicating a random distribution pattern and negative values indicating a uniform distribution and positive values an aggregated distribution pattern (Krebs 1999). Values <-0.5 and >0.5 are significant at the 5% level.

2.2.3 Habitat structural components, sediment type and depth

The main habitat structural components of the surveyed sites were macroalgae species (including seagrass), sponges, and shell debris. To generate semi-quantitative estimates of coverage, these structural components were ranked using a three-point scale of relative abundance. Sponges were ranked “absent” when there were no individuals, “low” when there were 1–10 individuals and “medium” for > 10 individuals within the transect area. For macroalgae and shell cover the categories were “absent” when the component was not observed within the transect area, “low” when the cover was rated as <10% of the transect area and “medium” when the coverage was >10%. None of these components, however, had coverage levels in excess of 50%.

A sediment core, taken to a depth of approximately 2 cm, was collected by divers at each site for grain size assessment. Samples were dispersed using calgon (0.5% [mass:volume] sodium hexametaphosphate) (Gatehouse 1971) and then oven dried (60ºC, 48 hours), weighed and shaken through a series of eight sieves ranging from 63 μm to 8 mm. The sediment in each sieved fraction was weighed to the nearest 0.1 g and the cumulative percentage by weight of the eight fractions was calculated and the mean plotted against a phi ($\emptyset$) scale where:

$$\emptyset = log_2 d$$

where *d* is particle diameter in millimetres. Mean grain size (d_m) was estimated using phi values corresponding to the 16th, 50th and 84th percentiles of the cumulative proportion of weight using the formula:

$$d_m = \frac{\emptyset_{16}+\emptyset_{50}+\emptyset_{84}}{3} \text{ (Folk 1968)}$$

where larger d_m values correspond to finer grain sizes. Mean grain size was classified according to the Wentworth scale (Wentworth, 1922) which combines numerical intervals of grain size with rational definitions (pebble, sand, mud, etc.) (Eleftheriou and McIntyre 2008). Water depth was measured at each site using dive computers within 0.1 m precision.

2.2.4 Relationship between abundance patterns and explanatory variables

To visualize the spatial distribution of scallops, sea stars, mean grain size and depth, a triangle-based cubic interpolation algorithm was applied to fit an interpolated surface to the average value recorded for each site using Matlab (Version 7.2.0.232; The Mathworks Inc. 2006).

Scatterplots indicated than none of the continuous explanatory variables (mean grain size, depth, sea star counts) were correlated. Scallop abundance was modelled as a function of explanatory variables using Generalized Additive Models (GAMs) (Hastie and Tibshiarine, 1990). Generalized Additive Models provide a flexible framework to model the relationship between abundance and environmental variables and have been applied to several marine organisms (Swartzman et al. 1995, Hedger et al. 2004, Dalla Rosa et al. 2012). Generalized Additive Models were fitted using the mgcv package from the statistic software R (Version 0.06.331; Wood, 2001). Explanatory variables were selected if significant ($p<0.05$). As the data were over-dispersed a quasi-Poisson was used (Zuur et al, 2009). Due to the tendency of GAMs to overfit (when the generated model is so powerful that it faithfully models the noise associated with the data), the argument gamma = 1.4 was used (Kim and Gu, 2004) and the basis dimension parameter k was set to a maximum of 8 to correct for over fitting without compromising the model (Wood 2006). Categorical variables were analysed as ordered variables using orthogonal polynomial contrasts to examine trends and determine whether response variables changed linearly or nonlinearly as a function of habitat structural component cover (Crawley 2007).

Model selection was based on Generalized Cross Validation (GCV) (Wood 2006), percentage deviance explained and visual examination of residuals. Spatial autocorrelation in the models' residuals was investigated through Variogram analysis using the geoR package v 1.6-22 in R (Ribeiro 2001). One of the model assumptions is there is no spatial autocorrelation and violation of this assumption was tested by comparing a variogram of the deviance residuals with Monte Carlo envelope empirical variograms computed from 300 independent random permutations of the residuals (Diggle 2007). There was no evidence of significant spatial autocorrelation on the residuals of any model as the semi-variance was within the boundaries of the Monte Carlo envelopes in the variograms.

2.3 Results

2.3.1 Distribution patterns

Commercial Scallops were most dense in the eastern section of Area 2, with a maximum of 170 scallops per transect, but were very scarce in Areas 1, 3 and 4 (Fig. 2.2). Queen Scallops were most dense in Area 3, with as many as 65 scallops per transect, scarce in Areas 1, 2 and were absent in Area 4. Doughboy Scallops were found in the highest densities in Areas 2 and 3, with a maximum of 145 scallops per transect, but were absent in Area 4. All three species had aggregated, non-random distributions according to the Standardised Morisita's Index (Table 2.1).

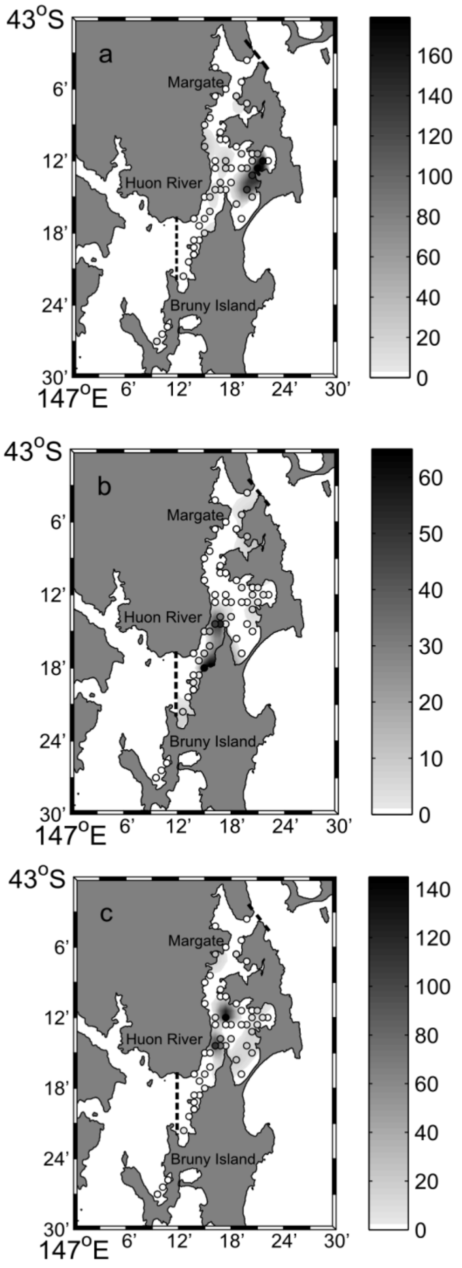

Fig. 2.2 The interpolated distribution and densities (scallops per 200 m^2 transect) of a) Commercial Scallops, b) Queen Scallops and c) Doughboy Scallops throughout the D'Entrecasteaux Channel in 2010. Circles indicate the survey sites and the colour intensity (white = no scallops) indicates the interpolated relative density of scallops. Note density scales (to the right of each map) differ among species. Areas located left of the dotted line were considered outside the model interpolation domain.

Table 2.1. Goodness of fit tests for a random (Poisson) or aggregated distribution (Morisita's Standardised Index of Dispersion).

* denotes significant difference from a Poisson distribution ($p<0.05$); ^ denotes a significant departure from randomness at $p<0.05$.

Test	Commercial Scallops	df	Queen scallops	df	Doughboy Scallops	df
Random distribution - Poisson	2976.5*	18	1350.6*	13	2131.3*	16
Test of Aggregation – Morisita's Index	0.555^	58	0.546^	58	0.558^	58

Size frequency distribution plots showed few juvenile scallops (<30 mm) during the study period (Fig. 2.3). This scarcity precluded an analysis of habitat association at different life history stages, i.e. attached spat, juveniles and adults. Most individuals were adults in each of the three species.

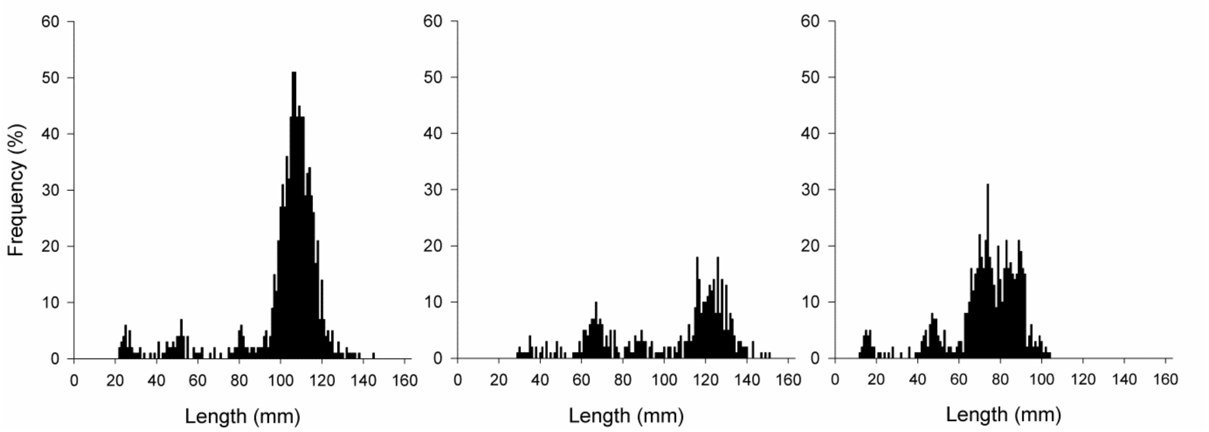

Fig. 2.3. The size frequency (per cent) distribution of Commercial Scallops (left), Queen Scallops (centre) and Doughboy Scallops (right) sampled from 59 sites within the D'Entrecasteaux Channel in 2010.

2.3.2 Habitat elements

The 59 sites ranged from 5.6-18.9 m in depth. The deepest survey sites were located in Area 1, with an average depth of 13.2 meters, while the Area 2 sites were shallowest, averaging 9 m depth (Fig. 2.4a). Sites located in Areas 1, 2 and 4 were characterized by fine to very fine sand, while the northern section of Area 3 had coarse sand (Fig. 2.4b). The invasive northern Pacific sea star was found mainly in Area 1 and in the south of Area 3, with up to 39 individuals per transect. The native eleven-arm sea star was found only in the northern end of the DEC, with up to 28 individuals per transect (Fig. 2.4c and d, respectively).

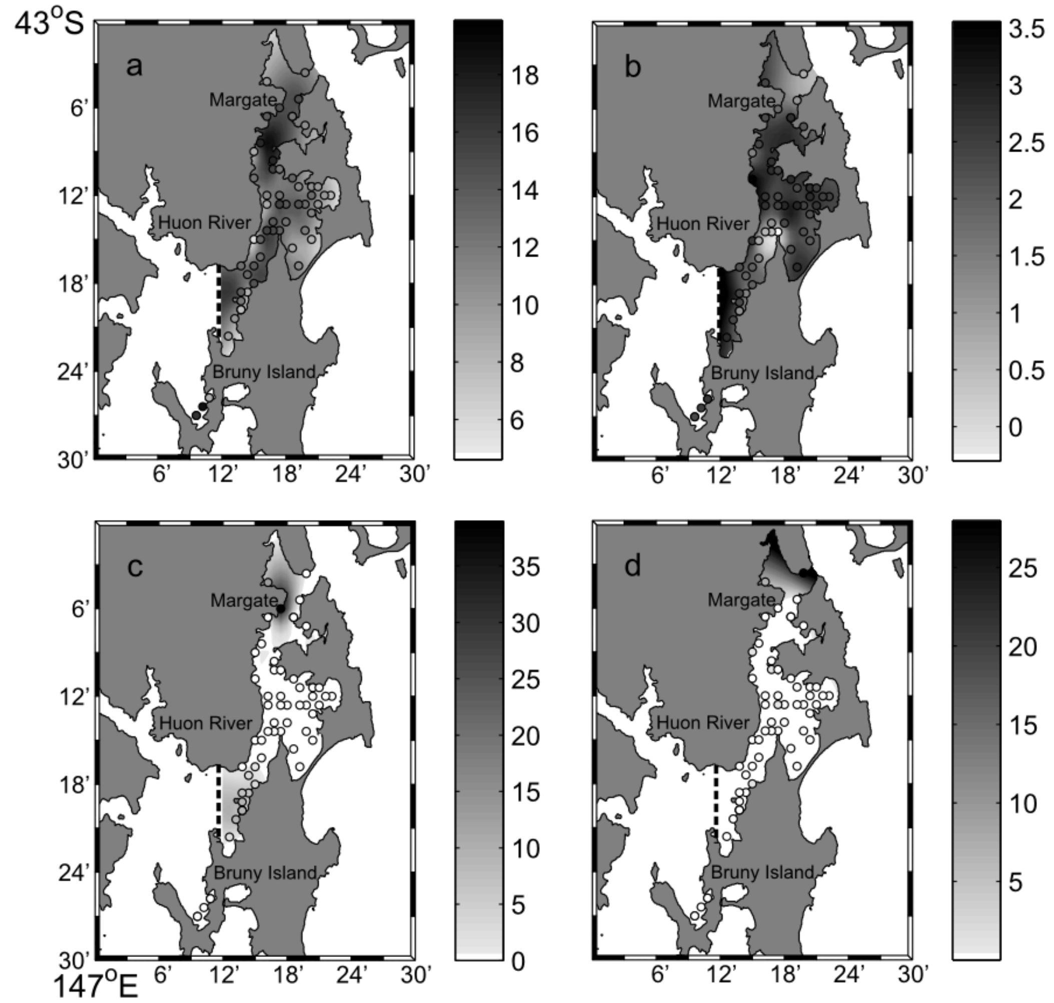

Fig. 2.4 The interpolated values of a) depth in meters, b) mean grain size (mm) and abundances (number per 200 m^2 transect) of c) northern Pacific sea star and d) eleven-arm sea star throughout the D'Entrecasteaux Channel in 2010. Circles indicate the survey sites and the colour intensity indicates the interpolated relative value. Note density scales vary between the starfish species. Areas located left of the dotted line were considered outside the model interpolation domain.

Area 3 was characterized by a greater cover of habitat structural components (Fig. 2.5). Area 2 had less algae/seagrass cover than Areas 1, 3 and 4. Shell cover had no clear pattern of distribution (Fig. 2.5).

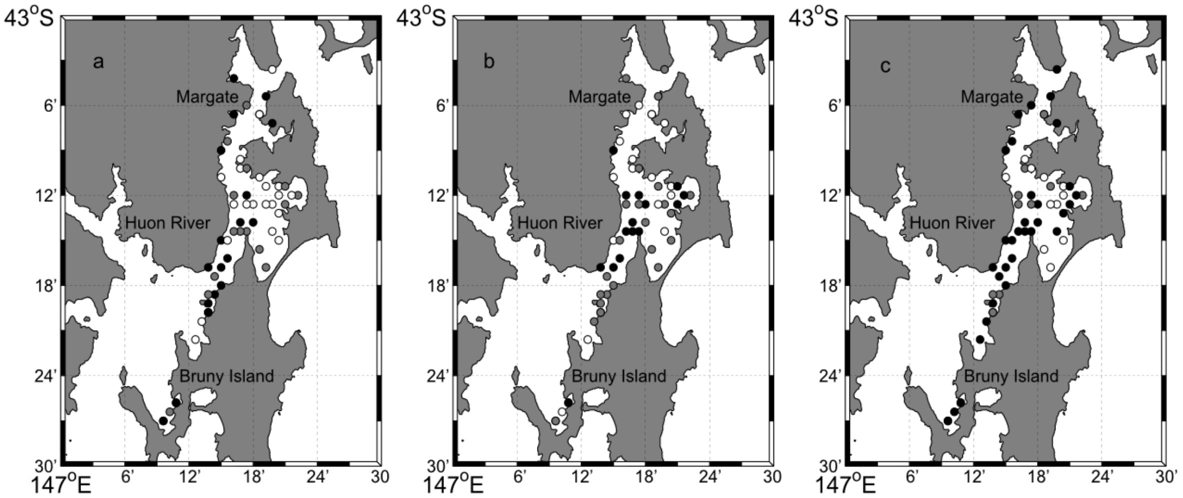

Fig. 2.6. Distribution of main structural components in the D'Entrecasteaux Channel: a) sponges; b) shells and c) algae. Circle colours indicate per cent cover, with absent (white), low (grey) and medium (black) cover.

2.3.3 Relationship between scallop abundance patterns and explanatory variables

Commercial Scallop

Sediment size, depth, northern Pacific sea star abundance, shell and macroalgae cover explained 72% of the variation in the Commercial Scallop abundance. Greatest numbers of the species occurred in areas of fine sand and in depths from 8 – 12 m (Fig. 2.6) and numbers increased with shell cover (significant 1st and 2nd -order orthogonal polynomial contrast, t=4.65, df 1, p<0.001, and t=2.31, df 1, p=0.024, respectively). In contrast, Commercial Scallop abundance decreased as macroalgae cover (significant 1st-order contrast t=-2.41, df 1, p<0.001) and northern Pacific sea star abundance increased (t=-2.29, df 57, p=0.026).

Queen Scallop

Mean grain size and macroalgae cover explained 68% of the variation in Queen Scallop abundance. The greatest numbers of were present in sites with medium to coarse sand (Fig. 2.7) and greater macroalgae cover (significant 1st-order polynomial contrast, t=3.37, df 1, p=0.001). There was no evidence that depth, shell, sponges and sea star abundances contributed to explaining variation in the Queen Scallop abundance patterns.

Doughboy Scallop

Mean grain size and sponge cover explained 70% of the variation in Doughboy Scallop abundance. Greater numbers were present in fine or coarse sand than in medium sand and the number of Doughboy Scallops was highest with medium sponge cover (significant 1st and 2nd -order orthogonal polynomial contrast, t = 3.73, df =1, p<0.001, and t=2.63, df 1, p=0.01, respectively) (Fig. 2.8). Depth, macroalgae, shells and sea star abundance did not contribute to explaining the patterns of variation in Doughboy Scallop distribution.

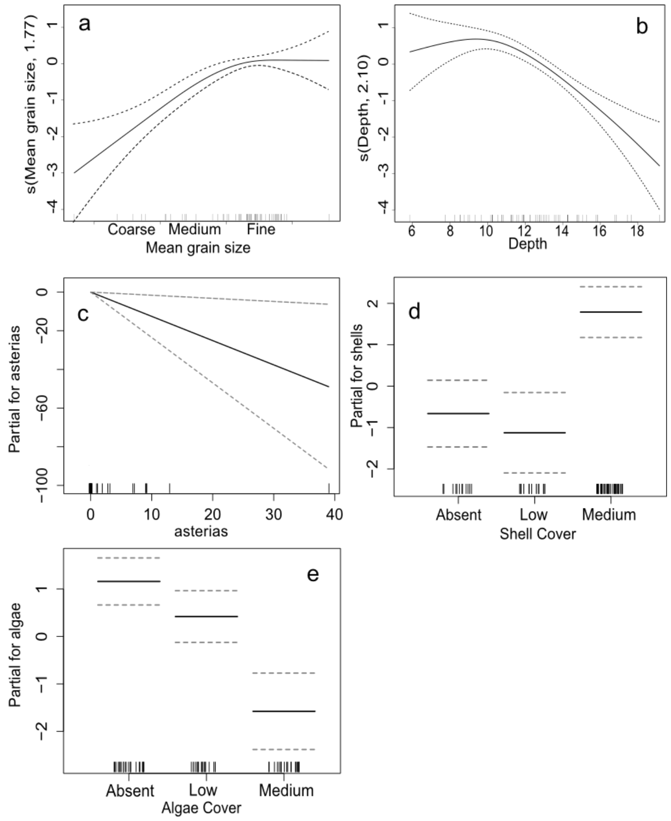

Fig. 2.6. Graphical results of the GAM model fitted to Commercial Scallop abundance. For the a) mean grain size, b) depth and c) northern Pacific sea star abundance, the smoother illustrates the partial effect of these continuous explanatory variables once the effects of all other explanatory variables or factors included in the model have been taken into account. For d) shell and e) algae/seagrass cover, the model also calculates their effect once the effects of all other explanatory variables have been taken into account. The y-axis shows the contribution of the smoother or of the category to the predictor function in the model. Dashed lines represent 95% confidence intervals and whiskers on the x-axis indicate data presence.

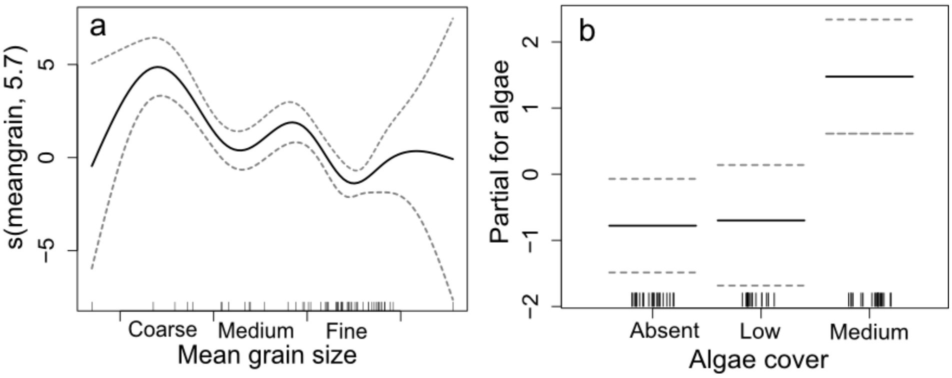

Fig. 2.7 Graphical results of the GAM model fitted to Queen Scallop abundance. Significant explanatory variables are a) mean grain size and b) algae/seagrass cover. See Fig. 2.6 for explanation.

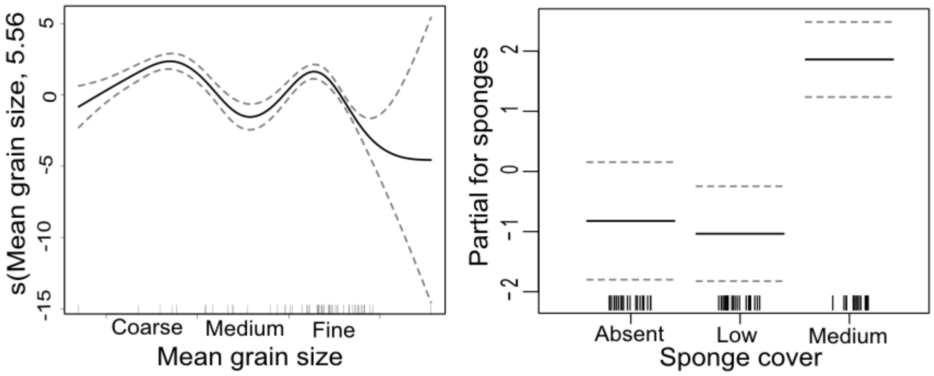

Fig. 2.8. Graphical results of the GAM model fitted to Doughboy Scallop abundance. Significant explanatory variables are a) mean grain size and b) sponge cover. See Fig. 2.6 for explanation.

2.4 Discussion

Each of the three scallop species exhibited aggregated rather than random or uniform patterns of distribution; aggregated distributions being typical amongst scallop species (Langton and Robinson 1990, Stokesbury and Himmelman 1993). Factors such as sediment type, habitat structural components and presence of predators were found to influence distribution, importantly the nature of the relationships between these factors and distribution patterns differed markedly among species.

Commercial Scallops were associated with finer sediments, Queen Scallops with coarse grain sediments, whereas Doughboy Scallops had a less selective association with sediment type, possibly because the species can use byssal attachment on a wide range of substrates (Zacharin 1995). Bearing in mind that these associations do not imply direct causal or functional relationships, these results highlight the close linkages between different species and their habitat, most probably a consequence of their particular life history traits. Habitat preferences are assumed to be adaptive, and associations between species and habitats potentially reflect natural selection on habitat choices (Martin 1998). Differential abundance of bivalves based on sediment type can be suggestive of differential refuge properties of each sediment type that may relate to physical properties of the sediment, food availability or changes in predator-prey relationships (Lipcius and Hines 1986, Eggleston et al. 1992).

Predation is an important factor regulating distribution and abundance of marine invertebrates (Gosselin and Qian 1997, Hunt and Scheibling 1997) and habitat characteristics can greatly influence predation by affecting predation efficiency and predator-prey encounter rates (Myers et al. 1980, Heck et al. 1981). Moreover, vulnerability to predation can vary in a species-specific manner within habitat types even between species that are morphologically and phylogenetically similar (Seitz et al. 2001). This seems to hold true in this study, where prevalence of Commercial Scallop adults in fine sediments suggest that abundances may depend, in part upon increased survival in those sediments. The semi-burying or recessing behaviour of the juveniles and adults, in which the upper valve is level with or just below the surface of the sediment (Brand 2006), is favoured in finer sediments compared to coarser sediments (Maguire et al. 1999). Such behaviour can provide protection from visual and non-visual predators, reduce fouling on the shell, and can anchor the individual in areas of strong currents (Brand 2006). Moreover, this behaviour does not interfere with active predator escape responses such as swimming (Minchin 1992). While greater abundances of Commercial Scallops occurred in areas with lower numbers of the invasive northern Pacific sea star, the nature of this relationship is unclear and needs to be examined cautiously. Northern Pacific sea star abundance and distribution patterns could for instance be related to other factors such as abundance of other epi-benthic bivalves rather than scallops (Ling et al. 2012).

Whereas there was a negative association between macroalgal cover and abundance in Commercial Scallops, Queen Scallops demonstrated a positive relationship that may be related to its use of this structural component as a refuge from predators. Field studies have demonstrated that in this species sea star predation rates are lower in seagrass beds compared to bare sand and can be attributed to reduced mobility of starfish within the seagrass (Wolf and White 1997). Similarly, the relation between Doughboy Scallop abundance and sponge cover might be linked to reduced predation pressure. There is an epizoic association between Doughboy Scallops and sponges, including the red sponge (Crellidae family), the yellowish sponge (Myxillidae family), and the purple honeycomb sponge (*Equinochlathria* sp.), and, since the presence of the sponges reduce the adhesion of the eleven-arm sea star tube feet on the scallop shell, vulnerability to sea star predation is reduced (Chernoff 1987, Pitcher and Butler 1987).

Identifying habitat characteristics to which scallops are associated and the life history stages at which these associations are developed has relevance in managing and restoring disturbed habitats. As scallop spat exhibit a distinct behaviour that involves byssal thread attachment to substratum elements, habitat characteristics associated with their distribution and abundance patterns might be quite different to those observed in adults, particularly in Commercial Scallops, where recessing into the sediment occurs. This was shown by Howarth et al, (2011), who found that macroalgae and dead coralline red algae cover were greatly associated with the abundance of juvenile (<10 mm) *Pecten maximus* and *Aequipecten opercularis*.

The current study provides insight into the relationships between habitat characteristics species-specific patterns of abundance in co-occurring scallop species; with sediment type and habitat structural components being of major importance. It highlights the importance of a suite of habitat characteristics that would potentially need to be considered in spatial management and/or restoration plans (i.e. fishing in a way that allows structure to re-establish) for the three species, in particular seagrass, sponge and shell cover. It also suggests potential behavioural mechanisms linking habitat and scallop abundances. However, the mechanisms or processes behind these associations are still not clear. Site variations in distribution patterns of adults may result from a number of factors such as among-habitat variation in larval arrival and settlement (Minchinton 1997, Moksnes 2002), differential availability of shelter from predation (i.e. habitat complexity) (Tupper and Boutilier 1995), or antagonistic interactions with conspecifics or competitors (Sweatman 1985). To understand the underlying mechanisms explaining distribution patterns the components of the recruitment process need to be examined concurrently. Manipulative experiments in which predation rates are compared amongst habitats for the three species could help understand the relative importance of predation and behavioural traits in regulating population size in different habitats. From this a better understanding of the relative importance of settlement and post-settlement processes in regulating population size in different habitats will be possible (Eggleston and Armstrong 1995).

3 Substrate selection of juvenile scallops: testing behavioural preferences and behaviour

3.1 Introduction

Marine organisms occur in varying densities within their distribution (Krebs 1994). Patterns of abundance and distribution may be affected by a series of processes and mechanisms involving larval supply, dispersal and mortality (Underwood 2001, Pineda et al. 2009). The effects of these processes may differ between habitats and explain particular patterns of habitat-related abundances. While external factors such as hydrodynamics, unfavourable abiotic conditions or higher vulnerability to predators are important, intrinsic factors such as behavioural choices can also affect patterns of distributions of organisms.

Larvae of several species show active selection for particular habitats or substrates; crawling and re-suspension into the water column in pursuit of an appropriate habitat is well documented (Morgan 2001, Underwood 2001). Habitat selection by juveniles also plays an important role in influencing distribution patterns and can lead to post-settlement re-distribution of the population (Moksnes 2002, Moksnes and Heck 2006). For many benthic marine invertebrates, significant mortality occurs in the early juvenile stages following settlement (see review in Gosselin and Qian 1997, Hunt and Scheibling 1997) and as juvenile growth and survivorship differs greatly among habitats, selection of favourable substratum can be critical (Herbert and Hawkins 2006).

Selection for particular substrate or habitat characteristics is likely to have evolved from benefits gained such as refuge from predation and access to food, enhancing settlement success and post-settlement survival (Pohle et al. 1991, Moksnes et al. 1998, Kamenos et al. 2004, Pacheco and Stotz 2006). Thus, understanding which substrates are actively chosen by organisms allow us to rank the substrates according to the likelihood that they enhance survival of that species. When a relationship between a particular habitat or substrate and distribution patterns of organisms is established it is often assumed that this reflects the animal's preference and therefore involves active selection. However, this relationship might be due to "accessibility" of the habitat in question rather than an active behavioural response to select that habitat (see Singer 2000, Olabarria et al. 2002). This makes it necessary to consider the role of post-settlement behaviour in contributing to the observed patterns of distribution as distinct from processes such as larval supply or differential mortality, and requires cautious experimental analysis to disentangle the role of the different drivers (Crowe and Underwood 1998, Underwood et al. 2004). In order to avoid misinterpreting habitat selection (preference) from other factors that influence distribution patterns, it is also necessary to determine the pattern of occupancy of each type of habitat when available alone (i.e. when there is no choice and therefore no preference) (Olabarria et al. 2002, Underwood et al. 2004).

The D'Entrecasteaux Channel (DEC) is a semi-enclosed area between the Tasmanian mainland and Bruny Island and is located in southeast Tasmania. Historically, it has been a key area for the Australian scallop fishery (the first commercial fishery was established here); supporting a significant production since the early 1900’s (Gwyther 1991). The main target species has been the Commercial Scallop, *Pecten fumatus*. Failure in recruitment combined with high fisheries pressure has resulted in protracted closures and a shift from a commercial to a recreational-only fishery in the DEC.

Scallops show an aggregated distribution which has been strongly associated with substrate type. Higher abundances are typically found on gravel and coarse to fine sand and generally areas with poor mud content (for a review see Thouzeau et al. 1991, Stokesbury and Himmelman 1993, Kostylev et al. 2003, Brand 2006). Thus, the Commercial Scallop has been associated with silt-sand and coarser substrata including shells (Fairbridge 1953, Olsen 1955), but highest numbers have been associated with fine to very fine sand (Chapter 2).

Whether or not certain habitats are preferred by juvenile scallops and whether or not ontogenetic shifts drive patterns of habitat preference are critical but poorly understood aspects of scallop ecology. This Chapter aims to investigate if juvenile Commercial Scallops have preferences among three different types of substrate commonly found in the DEC (medium sand, very fine sand and coarse sand) and hence to determine if the patterns of distribution in the field may be due to such preferences. It also aims to investigate whether or not preferences for particular substratum characteristics change during the juvenile stages.

3.2 Materials and methods

3.2.1 Preparation of substrates and collection of juveniles

Samples of different substrates, representing very fine, medium and coarse sand, were collected from the DEC. Before use, each were rinsed three times with fresh water to remove naturally occurring organisms and dried at 70 °C for 48 h to eliminate any source of food that could bias selection (Tapella et al. 2009). Sediments were sieved to determine grain size distributions and classified according to the Udden-Wentworth scale, with three readily available substrate types chosen to represent the range used by scallops (very fine sand, phi value=3.26; medium sand, phi value = 1.62 and coarse sand, phi value=0.97).

Collection of juveniles was attempted using spat collectors deployed in the DEC but very poor recruitment meant that very few recently settled spat and juveniles were available for the study. Juvenile scallops were, however, collected by divers from the DEC as well as from Nutgrove Beach in the nearby Derwent Estuary. These juvenile scallops were stored in 300 litre tanks with unfiltered seawater flow through systems until use in the experiments.

3.2.2 Experimental design and statistical analysis

Twenty-four tanks (four replicates for each treatment, Fig. 3.1) were divided into three equal sections using a plastic template; each section contained one of the three sediment types tested. Each container was supplied with flow through seawater at a rate of 3.5 L h^{-1}, the outflow was through a mesh (1 mm mesh size) covered standpipe (5 cm diameter) that was fixed centrally within the tank. Each experiment lasted less than five days to minimise the confounding effect of bio-films developing on clean substrates.

Three scallops were placed in one predetermined segment of the tank at the beginning of a daily light cycle (refer Fig. 3.1), and after a period of three hours the choice of substrate was recorded. Counts were repeated at 6, 9, 12 and 24 h from start of the experiment to obtain a general association pattern for a 24 hour period, and then counted every 24 hours for 5 days. Juveniles tested in Experiment 1 had an average length of 10.4 +/- 2.1 mm (called small juveniles) and in Experiment 2 an average length of 28.8 +/- 1.85 mm (mean+/- SD) (called large juveniles).

The number of juvenile scallops used in the tanks (three per tank) was in the density range observed for juveniles in the field (up to five individuals per m^{-2}). Preference was tested by using an experimental design (Fig. 3.1) which compares the proportion of scallops in each of the microhabitats when presented together (the *n* habitat choices) or alone (Olabarria et al. 2002). Thus, preference by Commercial Scallops for very fine sediments (Arena B) would be reflected by a greater proportion of scallops in these arenas at the end of the experiment compared to what is expected by chance if no preference is expressed. The chance of occurrence at the end of the experiment is estimated from the treatments where there is no choice (4-6, Fig. 3.1). Preferences for very fine sand means that the following hypothesis must be accepted: proportion of scallops in very fine sand B_t in treatment 2 and 5 must be greater than in treatment 1 and 3. The second hypothesis requires that the proportion in A_t and C_t in treatments 1 and 3, respectively are lower than in T4 and T6 because scallops are more likely to move from A_t and C_t to preferred sediment type B (very fine sand). These hypotheses were tested by analyses of variance which, when designs are balanced (as here), are robust to violations of assumptions of normality and homoscedasticity.

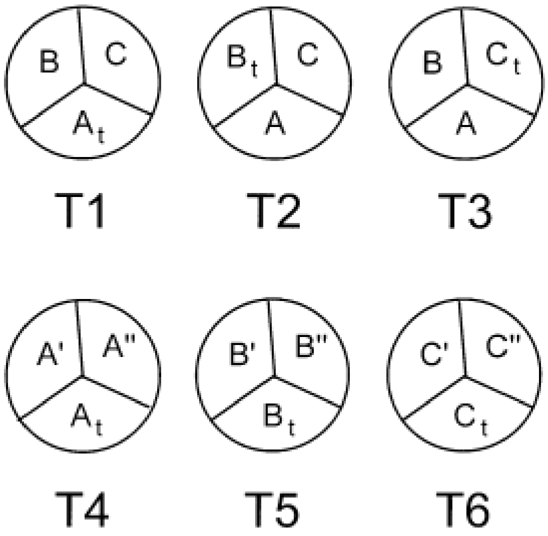

Fig. 3.1 treatment (T1-T6) used in the experiments. A is medium grain sediment, B is very fine size sediment and C is coarse grain sediment; t indicates the segment or arena where the scallops were placed at the beginning of the experiment.

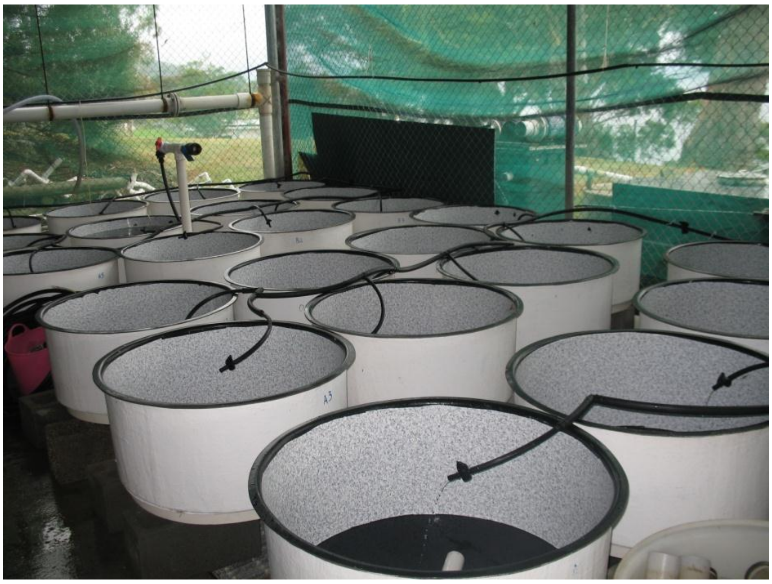

Fig. 3.2 Tanks used for the preference experiments at the IMAS-Taroona Aquarium Facility.

3.3 Results

3.3.1 Experiment 1 - Small juveniles

The small juveniles showed no selectivity among the sediment types offered. There was no evidence supporting a significant difference between treatments or of fewer individuals found in non-preferred sediments where there was a choice (Table 3.2, Fig. 3.3).

Table 3.2, Analysis of proportions of Commercial Scallops in experimental treatments. (S)

	Experiment 1				Experiment 2			
Source of variance	df	MS	F	p	df	MS	F	p
Hypothesis 1. Bt2, Bt5 > At1,Ct3 (more in preferred sediments)								
Among treatments	1	0.4027	1.943	0.194	3	0.9091	71.77	<0.001
Residuals	10	2.0731			8	0.0127		
Hypothesis 2a: Nt3<Nt6 (fewer in non-preferred microhabitats where there is a choice)								
Among treatments	1	0.7156	3.616	0.13	1	0.1179	1	0.374
Residuals	4	0.1979			4	0.1179		
Hypothesis 2b: Nt1<Nt4								
Among treatments	1	0.1179	0.5	0.519	1	0.1179	1	0.374
Residuals	4	0.9432			4	0.1179		

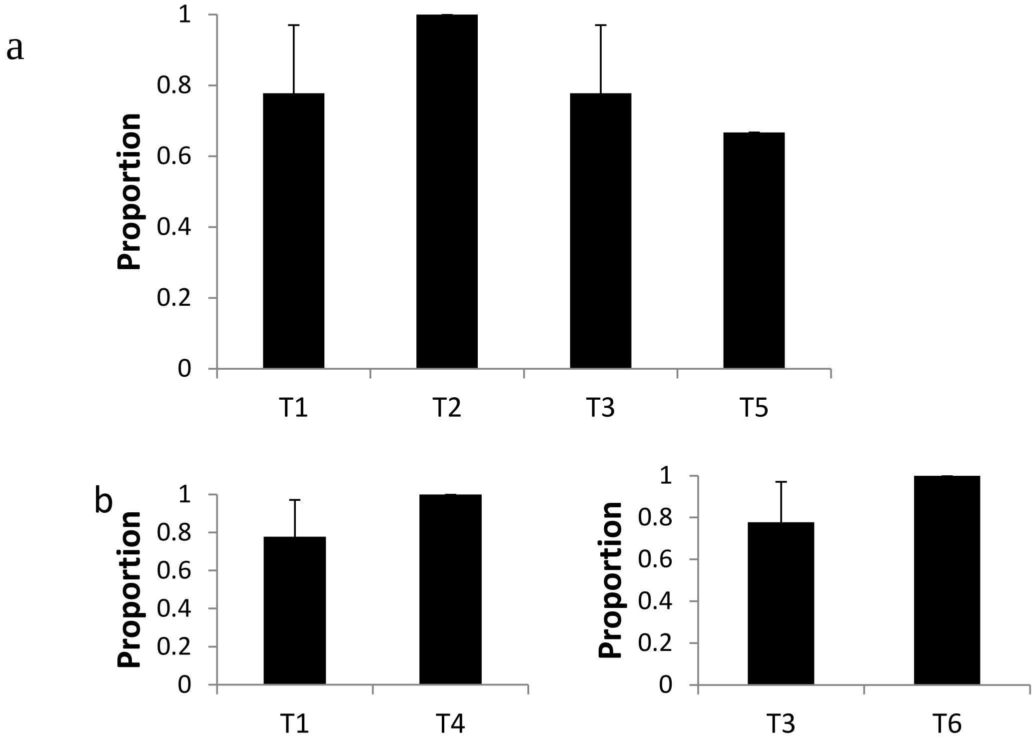

Fig. 3.3 Mean (SE) proportion of Commercial Scallops in Experiment 1 for small juveniles; a) proportion of individuals remaining in treatments in the sediments where they were initially placed; b) proportion of individuals staying in medium and coarse sediments in treatment 1 and 4 and 3 and 6. Smaller proportions are expected where animals have a choice to move to preferred sediment types (A_t and C_t in treatment 1 and 3 compared to Treatments 4 and 6, respectively. Error bars represent one standard error.

3.3.2 Experiment 2 – Large juveniles

Large juveniles showed no preference among the different sediment types offered (Table 3.2, Fig. 3.4). Large juveniles mainly recessed (semi-burying behaviour in which upper valve is level with or just below the surface of the sediment, Fig. 3.5).

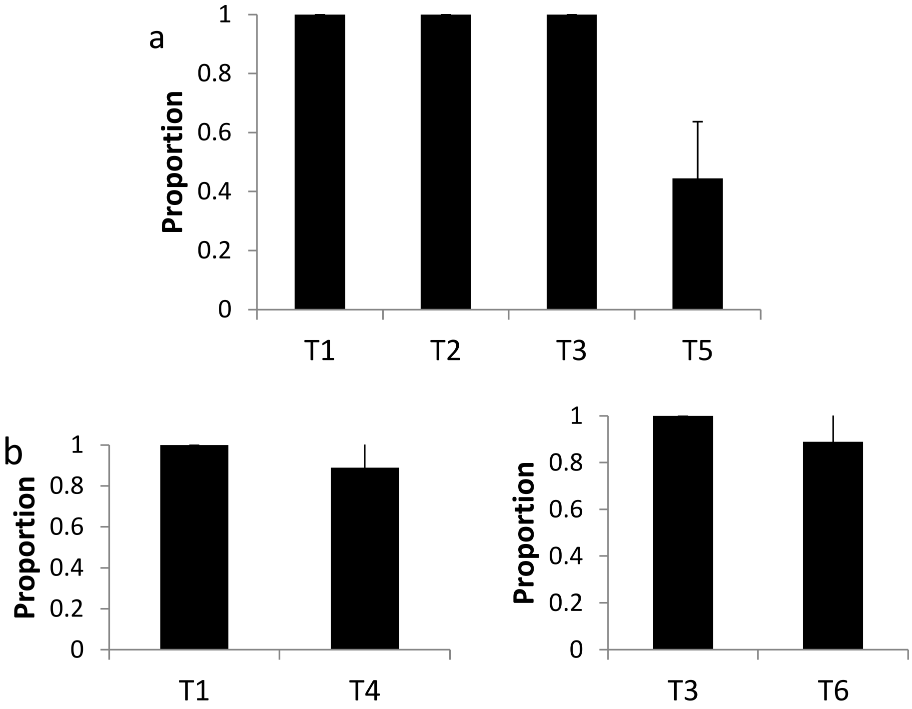

Fig. 4. Mean (SE) proportion of Commercial Scallops in Experiment 2 for large juveniles; a) proportion of individuals remaining in treatments in the sediments where they were initially placed; b) proportion of individuals staying in medium and coarse sediments in treatment 1 and 4 and 3 and 6. Smaller proportions are expected where animals have a choice to move to preferred sediment types (A_t and C_t in treatment 1 and 3 compared to Treatments 4 and 6, respectively. Error bars represent one standard error.

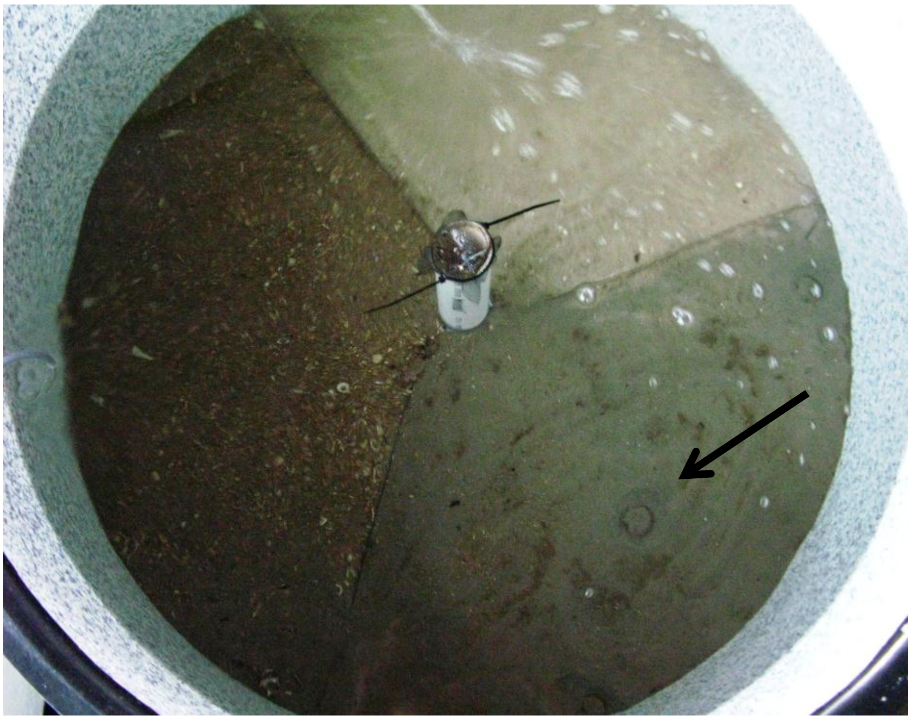

Fig. 3.5. Picture of experimental units with three different types of sediment. Scallop is recessed (arrow) in very fine sediment.

3.4 Discussion

The experimental data clearly supported the hypothesis that within the context of the experimental system juvenile Commercial Scallops did not actively select for a preferred sediment type. The association of Commercial Scallops and fine sediments observed in the D’Entrecasteaux Channel (Chapter 2) may, therefore, be more related to relatively higher survival in fine sediments rather than generated from an active behavioural choice or post-settlement movement. The semi-burying or recessing behaviour of the juveniles and adults, in which the upper valve is level with or just below the surface of the sediment (Brand 2006) is favoured in finer sediments compared to coarser sediments (Maguire et al, (1999) and provides protection from visual and non-visual predators, reduces fouling on the shell, and can anchor the individual in areas of strong currents (Brand 2006). Moreover, this behaviour does not interfere with active predator escape responses such as swimming (Minchin 1992).

As animals grow, the benefits of a particular habitat can change. It may become advantageous for those animals to migrate to different habitats, disguising initial settlement patterns (Moksnes and Heck 2006). In the current experiment we reduced the possibility of ontogenetic post-settlement migrations confounding the results by examining small and large juvenile scallops separately. The results show no pronounced selectivity among sediment types and therefore, it is unlikely that scallops strongly select a particular sediment type to the extent exhibited by other species, such as *Placopecten magellanicus*, which have been shown to select pebble and granule substrates over glass and sand (Wong et al. 2006b).

As with all laboratory experiments, there is a risk that results do not necessarily extend to natural situations because the animals were subject to artificial conditions. Predators such as sea stars, crabs and fish were absent from the arena and these artefacts may have caused scallops to behave differently to the wild populations.

4 Early post-settlement processes affecting scallop distribution and abundance

4.1 Introduction

Early post-settlement mortality is usually very high in marine invertebrates and can be an important process shaping distribution and abundance patterns of organisms (Gosselin and Qian 1997, Hunt and Scheibling 1997). Studies focused mainly on barnacles and ascidians have highlighted the magnitude of early post-settlement mortality, especially during the first days or weeks after settlement (Stoner 1990b, Hurlbut 1991, Gosselin and Qian 1996). In barnacles, the newly settled *Balanus glandula* and *Chthamalus fragilis* suffer about 38% and 53-78% mortality, respectively during the first day after settlement (Young 1991, Gosselin and Qian 1996). In ascidians, only 50% of individuals of *Diplosoma similis* survive the first day after settlement (Stoner 1990a). Estimates of early post-settlement mortality for bivalves are scarce, but for the oyster *Crassostrea virginica* are reported to be as much as 80-100% during the first seven days after settlement (Roegner and Mann 1995). Nevertheless, little is known about predation at early life stages in scallops, most studies focusing on predation in adults (Hunt and Scheibling 1997).

The main causes of mortality are physical disturbance and hydrodynamics, physiological stress caused by non/sub-optimal environmental conditions, predation and competition (see review in Gosselin and Qian 1997). Predation is the best documented process and generally recognized as an important factor regulating distribution and abundance of newly settled invertebrates (Gosselin and Qian 1997, Hunt and Scheibling 1997). In bivalve populations, newly settled juveniles are especially vulnerable to predation until they attain a particular size (Pohle et al. 1991, Garcia- Esquivel and Bricelj 1993). Scallops (family Pectinidae) are particularly vulnerable because of their thin shells, inability to close shells tightly near the auricles, and inability to maintain valves closed for prolonged periods of time (Brand et al. 1980, Wilkens 2006).

Studies on processes influencing distribution and abundance of newly settled organisms, particularly those with a planktonic larvae stage such as bivalves, are challenging because spat are very small (e.g. 250 μm for *Pecten fumatus*) and cryptic (but see McArthur 1998, Hiddink et al. 2002). Despite most scallops having free-living adults the spat secrete a byssus, using it to attach themselves to upright sessile epifauna such as hydroids, filamentous algae, and polychaete tubes (Harvey et al. 1993, Aguilar and Stotz 2000, Bradshaw et al. 2003, Bremec et al. 2008). Most scallop species, once reaching a specific size, release the byssus and individuals move to the sand (see review in Brand 2006). Thus, spat differ from other stages of life in their use of microhabitat, mobility and therefore in their vulnerability to different processes.

Habitat complexity is an important factor controlling animal abundances and predation rates. Several structural components of the habitat, such as polychaete tubes (Aguilar and Stotz 2000), hydroids (Harvey et al. 1993), sponges (Bremec et al. 2008), macroalgae (Cantillánez

2000) and or shells (Pacheco and Stotz 2006), provide settlement substrates for settled scallop larvae or ‘spat’. Attachment by spat on structures can reduce predation rates (Pohle et al. 1991), enhance growth - as an elevated position in the water column provides access to better quality food (Eckman et al. 1989), and avoids smothering by soft sediments (Merrill and Edwards 1976). The value of habitat structure in reducing risk of predation continues into the juvenile and adult phase. Juvenile Bay scallops *Argopecten irradians* reduce predator encounters by attaching to the upper canopy of the eelgrass *Zostera marina* (Pohle et al. 1991). Complex habitats with greater numbers of horse mussels, sponges and ascidians provide refuge for *Pecten novaezelandiae* from predation by sea stars and gastropods (Talman et al. 2004).

Several studies have dealt with the role that complex habitats such as seagrasses play in the persistence of bivalve populations. These studies showed decreased rates of predation and increased survivorship of soft sediment bivalves in seagrasses compared to unvegetated substrata (e.g. Irlandi and Peterson 1991, Pecon-Slattery et al. 1991, Irlandi 1994, Skilleter 1994). In seagrasses, the above and below components provide protection from predation for a variety of animals (Reise 1978, Peterson 1982, Orth et al. 1984, Summerson and Peterson 1984). The seagrass blades interfere with the mobility of consumers and the visual detection of prey (e.g., Nelson 1979, Coen et al. 1981, Heck and Thoman 1981) while the below-ground roots and rhizomes act as a barrier to digging predators (Blundon and Kennedy 1982, Peterson 1982). Despite representing complex structures, the effect of macroalgae cover on patterns of abundance and distribution of bivalves is not yet clear. While the macroalge *Caulerpa taxifolia* enhances recruitment and survival of the Sydney cockle *Anadara trapezium* (Gribben and Wright, 2006), drifting *Ulva lactuta* mats have a detrimental effect on the clam *Mercenaria mercenaria* (Tyler, 2007).

The Commercial Scallop *Pecten fumatus* is a key species for the Australian scallop fishery, supporting a significant production since the early 1900’s in the Derwent Estuary and the D’Entrecasteaux Channel in Tasmania. The population size, and hence the fishery, is affected by inter-annual variation in stock size, with frequent and protracted closures of the fishing grounds needed to protect populations from depletion. Despite the commercial importance of the species, there is no information about early post-settlement processes affecting the patterns of abundance in the Commercial Scallop.

Nutgrove Beach, located in south-eastern Tasmania (42.90639 S., 147.35170 W.) is a sheltered beach characterized by fine sand sediments. Over the summer months, these sediments are covered by mats of *Hincksia sordida* algae, upon which larvae of several bivalves attach. Among these bivalves, major settlement events for Commercial Scallops have been identified (Mendo, pers. obs.). However, these settlement events have not resulted in significant recruitment to adult populations. The aim of this study was to examine the hypothesis that predation on spat is a key mechanism explaining patterns of abundance and distribution of scallops and that predation pressure can prevent successful recruitment into scallop spawning stock. The goals of this study were to: (1) identify patterns of abundance and distribution of scallops in algae mats and (2) determine whether differential predation and growth are explaining these patterns.

4.2 Materials and methods

4.2.1 Temporal changes in scallop density and size

Densities of scallops in the field were estimated on four occasions during a major settlement event in 2011-12: 30/12/11 (8 replicates), 06/01/12 (5 replicates), 16/01/12 (8 replicates) and 27/01/12 (35 replicates). The *Hincksia sordida* algae mat and 1 cm of sediment below the algal mat were removed from 0.1275 m^2 (40.5 x 31.5 cm) areas using a small hand shovel. The *Hincksia sordida* and sediments were transferred to a plastic bag, sealed, and transported to the laboratory. All contents were sieved through a 500μm sieve and the retained material was fixed in formalin 10% for later analysis. A stereoscope was used to count scallops (magnification 6.3x) and photographs of each scallop were taken. The Image J software was used to estimate the size (total length) of all scallops to the nearest 0.1mm.

4.2.2 Contribution of predation to early post-settlement mortality rates

A predator exclusion experiment was designed to estimate the loss of Commercial Scallop spat (>500μm total length) due to predation. The experiment was initiated on the 30th December 2011 and lasted for 17 days. This short duration was chosen to reduce potential cage artefacts such as sedimentation, algae growth, and changes in density due to new scallop settlement events. The predator exclusion cages were rectangular plastic containers with tight-fitting lids (40.5 cm length x 31.5 cm width x 20 cm depth). The lid and sides of the containers were covered with 500 μm nylon mesh. On two sides of the cages, a piece of a metal bar was secured to make cages negatively buoyant.

The experiment consisted of three treatments; full exclusion (8 replicates) which completely excluded predators; partial exclusion (6 replicates) which acted as a cage control as it was the same design as the full cage, but the netting was removed from sides and top to allow predator access; and no exclusion (8 replicates) which was the same area as the cage areas and open to predators. As the partial exclusion cages mimic physical effects of the full exclusion cage but allow predator access, if there is no cage artefact then the density of scallops in partial exclusion cages and in no exclusion treatments should not differ. The experiment was conducted over a large area (about 1 ha.) covered by layers of *Hincksia sordida* algae (96.9 +/-14.5 g. dry weight algae.m^{-2} [average +/- standard error]), with replicate units randomly placed throughout the area, not grouped by treatment (Hurlbert 1984, Quinn and Keough 2002).

Algae mats (40.5 x 31.5 cm) were cut with scissors and the algal and associated sediment were carefully placed into the full and partial exclusion cages. In the no exclusion treatment, a peg was driven into the substrate to mark the location of sampling area at the end of the experiment. Cages were cleaned every three days using a brush to remove material clogging the mesh. At the end of the experiment (16th January 2012), each cage was placed into a plastic bag underwater, sealed to prevent loss of the algal mat scallops, and transported to the laboratory. The no exclusion algal mats and samples were treated as described above (section 4.2.1).

As the partial exclusion cages were open on the sides and the top it was possible that all or parts of the algal mat could be lost due to water movement, loss of the algal mat would also result in loss of scallops. Therefore examine whether there was any evidence of loss of scallops that could be attributed to algal mat loss rather than predation a time lapse camera was positioned on a tripod one meter above one of the partial exclusion cages. The camera took an image every minute for 24 hours during the first and fifth day of the experiment. The time lapse photos revealed no movement of algae mats into or out of the cages, therefore reduction of scallops in the partial exclusion treatment was assumed to be attributable to predation.

4.2.3 Patterns of scallop distribution on Hincksia sordida *mats*

On 27th January 2012 thirty-five algae mat samples were taken to estimate scallop distribution among algae biomass (refer section 4.2.1 for details). Scallops and other organisms were removed from algae and counted and then the algae samples were oven dried for 48 hours at 60 ºC and weighed.

4.2.4 Predation and growth

A tethering experiment was undertaken during January-February 2012 to assess differential predation and growth in different levels of algae biomass. Scallops were tethered to gardening mat pins which were inserted into the algae mat and/or the soft sediment. Twenty – four to thirty one scallops were used in each treatment (algae biomass.m^{-2}). Six different plots with varying levels of algae biomass were assessed. Initial size analysis showed no significant differences in shell height among algae biomass levels (χ^2 = 1.9022, df 5, p=0.862).

Scallops were tethered in the following manner: the top valve was cleaned and allowed to dry, and then a piece of monofilament was glued to the top valve. This technique ensured that the valves were not accidentally glued together. Monofilament tethers were at least 20 cm to ensure that the scallop could easily move around within each plot. Each monofilament had a rectangular plastic label (3 x 5 mm) with a number attached for identification. The scallop tethers were then tied to steel pins which were inserted into the algae mat and/or the soft sediment. Survival of tethered scallops was assessed after 24 hours, 3, 6, 10 and 14 days in the field. Scallops were classified as alive, dead or missing. When dead scallops were found they were further classified as “broken shells” or “clappers”. Predation by crabs and fish are usually associated with broken shells whereas clappers or open shells are usually left following sea star predation (Barbeau and Scheibling 1994a). Fifteen tethered scallops were positioned in three exclusion cages and used as tethering mortality controls.

4.2.5 Potential predators in the field

To identify potential scallop predators, a time lapse camera was positioned on top of algae mats on a tripod above 20 tethered scallops in habitats with contrasting algae biomass. The camera took an image every minute for 48 hours during the first and fifth day of the experiment.

4.2.6 Statistical analysis

Scallop density data were converted to numbers per square metre prior to data analysis. Variances were not homogeneous so a Welch's test was used to assess differences in densities between sampling dates and differences between treatments in the predator exclusion experiment. Scallop density was square root-transformed because of heterogeneous variances determined using a Barlett's test. All statistical analyses used 0.05 as the critical probability level.

4.3 Results

4.3.1 Temporal changes in scallop density and size

There was a significant decline in the densities of scallops in Nutgrove Beach (χ^2=12.776, df 3, p<0.01; Fig. 4.1). Over the four week period there was a reduction of around 72% in scallop density on the algae mats, almost all of this reduction occurred during the first seven days after initiation of sampling; there was no significant difference in densities between subsequent sampling dates after day seven.

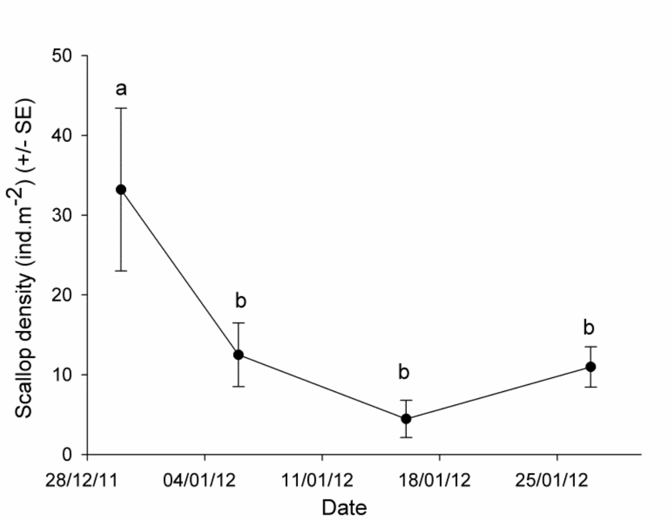

Fig. 4.1: Mean Commercial Scallop density at Nutgrove Beach, Tasmania over four weeks. Sampling days with different letters are significantly different. Error bars represent one standard error.

At the beginning of the experiment, on the 30th December 2011, most scallops measured between 2 - 3 mm, with individuals ranging from 0.4 mm to 3.6 mm in shell length (Fig. 4.2). After seven days, there was evidence that the surviving spat had grown as all scallops measured were between 3 - 5 mm in length. After 17 days, only four scallops were found in the samples and they ranged between 2 - 5 mm. Four weeks after the beginning of the experiment the average length of the scallops was 8.2 mm. On average, this represented a growth rate of 0.20 mm.day^{-1} over the four week period.

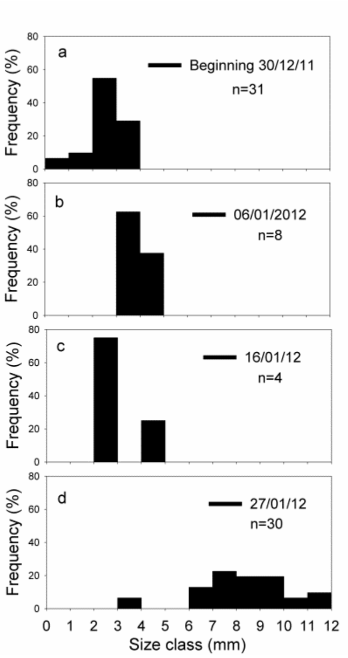

Fig. 4.2. Size frequency distribution of Commercial Scallop in a) beginning of experiment (30 December 2011); b) after seven days; c) after 17 days, and d) end of experiment.
n denotes the number of scallops measured in each sampling date.

4.3.2 Predator exclusion experiment

There was a significant difference among treatments in the average densities of scallops (F=6.45, df 3, p<0.002). At the completion of the experiment the partial and no exclusion treatments each had approximately 85% fewer scallop spat alive than the full exclusion treatment and there was no evidence of cage artefacts, as final scallop densities for the partial and the no exclusion treatments did not differ significantly (Fig 4.3). In addition, there was no significant difference between spat densities in at the start and end of the experiment in the full exclusion treatment.

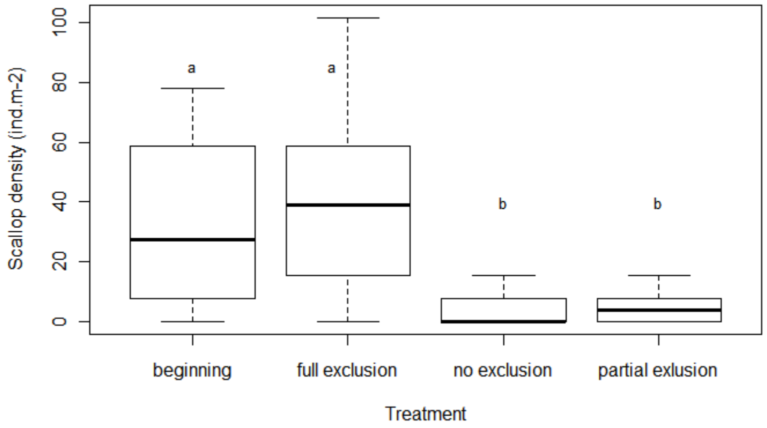

Fig.4.3. Mean density of scallops.m^{-2} at the beginning of the experiment on 30 December 2011), full exclusion (no predators present), no exclusion and partial exclusion (cage control) treatments at the end of the experiment on 16 January 2012. Treatments with different letters were significantly differed.

4.3.3 Patterns of scallop distribution on Hincksia sordida mats

Juvenile scallop densities were highly variable at the Nutgrove Beach study site, generally increasing with increasing *H. sordida* biomass to a threshold of approximately 100 g dry wt.m^{-2}, decreasing when the algal biomass was between 120 and 200 g dry wt.m^{-2}. Greater densities of juvenile scallops were found above the 200 g dry wt.m^{-2} of algae biomass (Fig.4.4). The sizes of the scallops did not differ with algae biomass and ranged between 6 and 12 mm in total length.

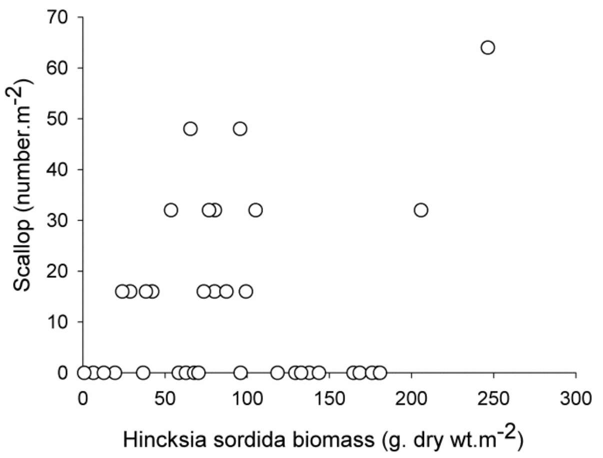

Fig. 4.4. Relation between *Hincksia sordida* biomass and Commercial Scallop densities.

4.3.4 Survival of scallops on Hincksia sordida mats

Significant differences in survival between algae biomass levels were obtained after 14 days of initiating the experiment (χ^2= 15.58, df =5, *p*=0.008). The standardized residuals showed that there were more scallops alive in the 68 g dry weight algae than expected and fewer live scallops than expected in the high cover algae levels (Fig. 4.5).

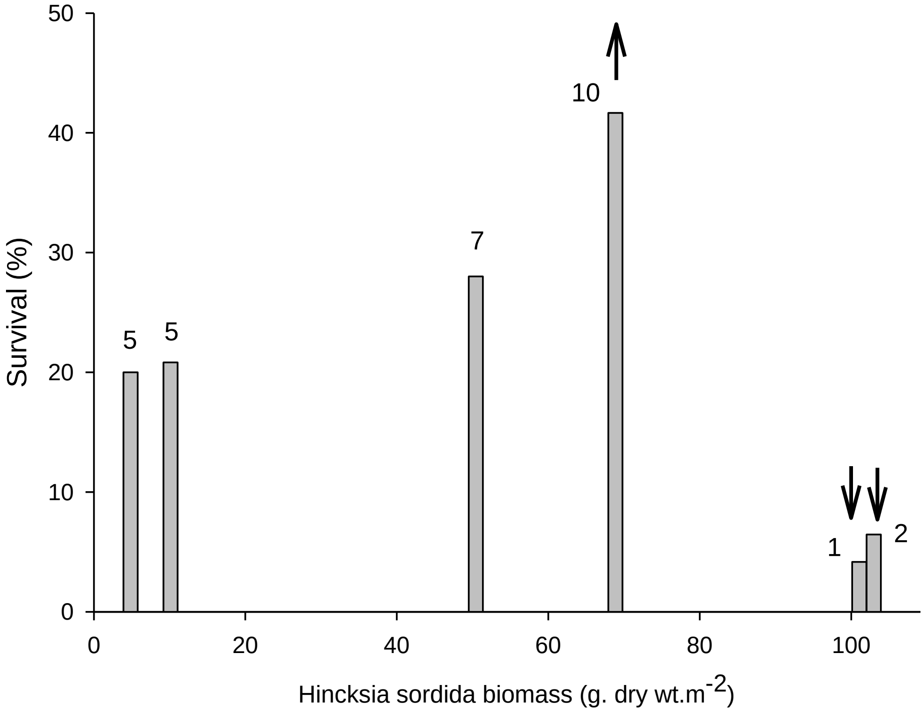

Fig. 4.5. Proportion of Commercial Scallops alive in each plot after 14 days of initiating the experiment. The number above the bar indicates the number of scallop alive after 14 days of initiating the experiment. Arrows indicate when proportions were greater (↑) or less (↓) than expected.

4.3.5 Possible contribution of predators

Predation by crabs and fish seemed to play a more important contribution to predation mortality than predation by starfish (Fig. 4.6). Potential predators observed during SCUBA diving that might crush the shell valves included the banded stingaree *Uropholus cruciatus*, the ringed toadfish *Omegophora armilla* and the spider crab *Leptomithrax gaimardii*. The only species of sea star observed in the study area was the invasive northern Pacific sea star *Asterias amurensis* (Fig. 4.7). Time lapse photography only identified one actively feeding predator - the ringed toadfish.

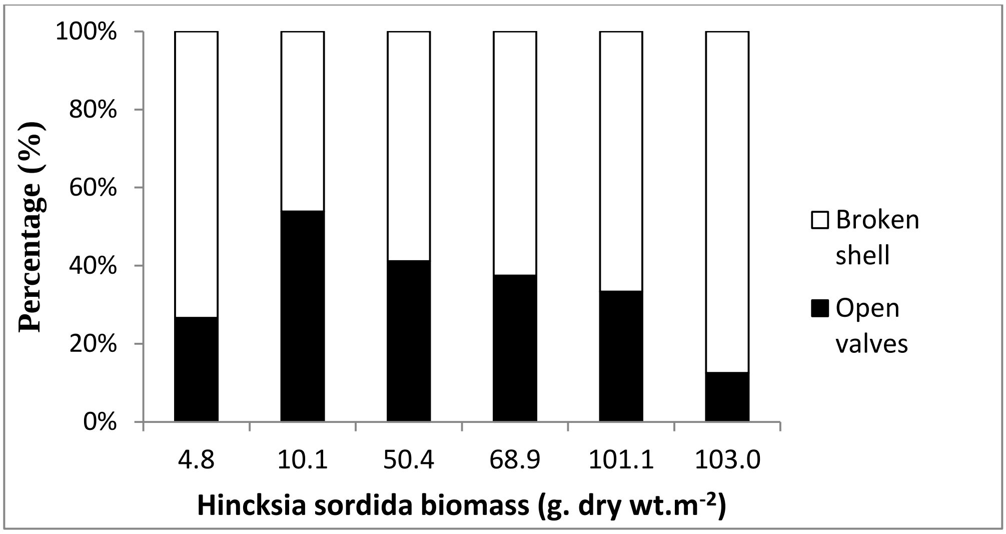

Fig. 4.6 Relative contribution of sea stars (open valves) and crabs or fish (broken shells) to predation mortality.

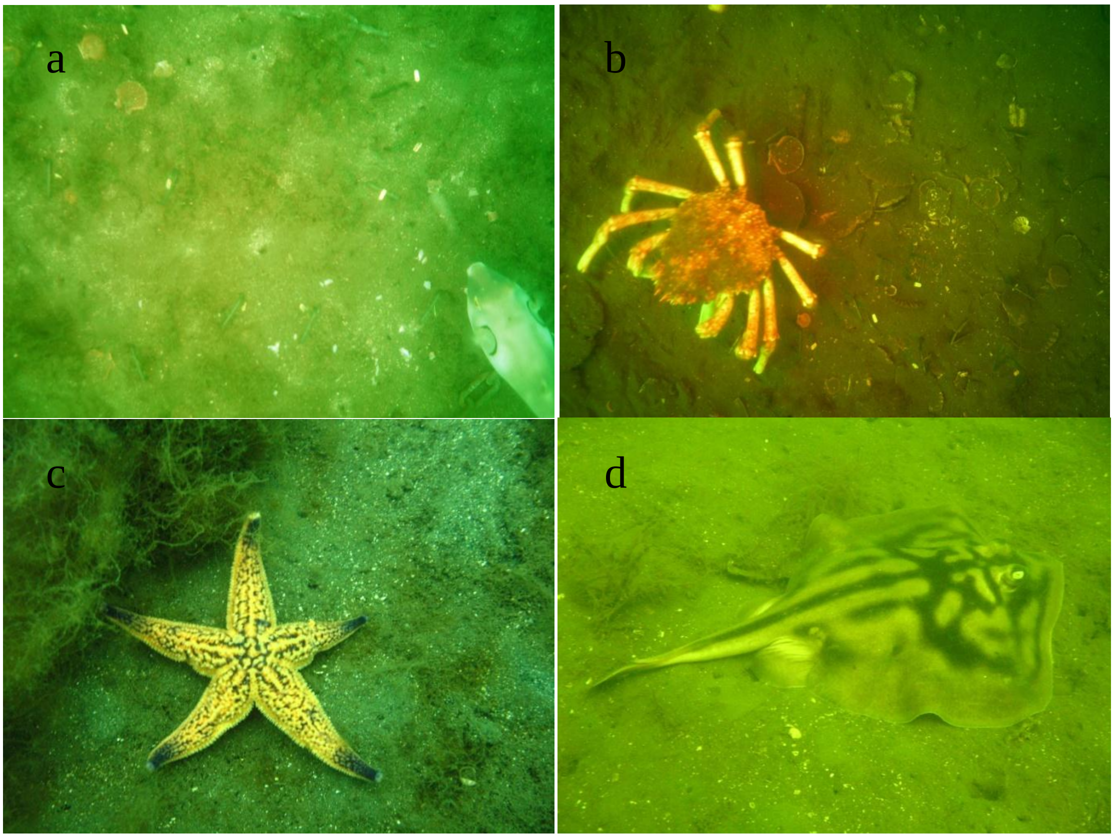

Fig. 4.7. Potential predators observed in the field during the experiments. a) ringed toadfish *Omegophora armilla,* b) spider crab *Leptomithrax gaimardii,* c) invasive northern Pacific sea star and d) banded stingaree *Uropholus cruciatus*

4.3.6 Growth

There were significant differences between relative growth rates for the different treatments (F=4.487, df 2, *p*= 0.037) (Fig. 4.8). Pairwise comparisons revealed that growth was greater in the sand treatment than in the other treatments (*p*<0.04).

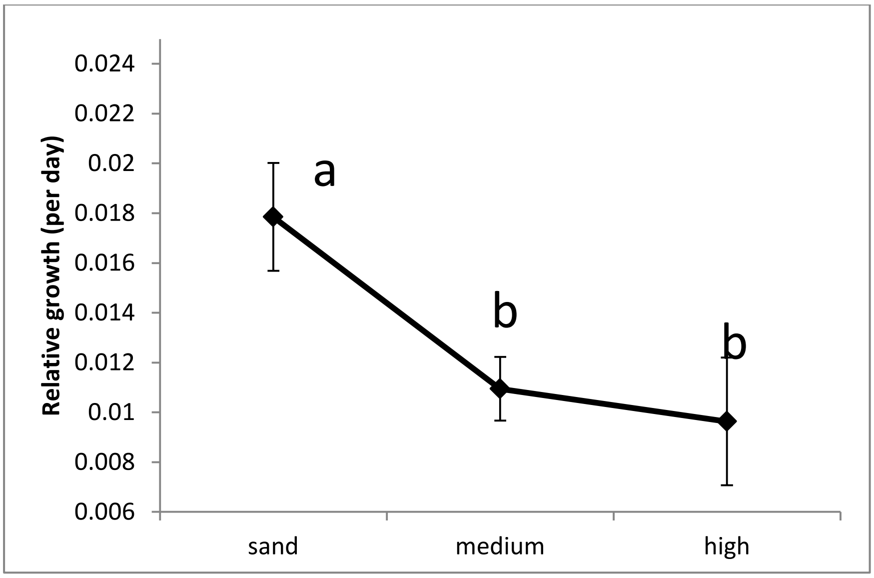

Fig. 4.8 Average relative growth ($(L_2-L_1)/L_1$) of Commercial Scallops in three different microhabitats. Error bars represent one standard error.

4.4 Discussion

This represents the first study to directly examine the impacts of predation mortality on recently settled scallop spat for sizes ranging between 0.4 - 4 mm. An eight-fold reduction (~85%) in scallop densities was observed over 17 days which, when considered in the light of the predator exclusion experiments, suggests that predation pressure acting during the first weeks after settlement represents a major factor in the subsequent failure of settlement events, in this case onto *Hincksia sordida* algae mats, to result in recruitment to the juvenile and adult stock. That is to suggest that ostensibly good settlement is no guarantee of recruitment success. In fact, despite detecting strong recruitment pulses in 2010 (Mendo pers. obs., no quantitative data available) and again in 2011 (up to 100 individuals.m^{-2}), we encountered only five adult scallops during approximately 30 hours of diving in the Nutgrove Beach study area. Our results therefore provide strong evidence that predation on spat represents a major ecological process affecting local population sizes in the Commercial Scallop. High mortality rates appear to have prevented the establishment of an adult population of Commercial Scallops at our study site.

The importance of predation in shaping abundance patterns in bivalves is supported by Van der Veer et al., (1998) who reported a 65% reduction in numbers of the clam *Macoma balthica* (Tellinidae) due to predation during the first two weeks after a strong settlement pulse. Predation pressure has also been show to significantly reduce recruitment success in *Mya arenaria* (Myidae) and *Cerastoderma edule* (Cardiidae) in soft-bottom bays (Flach 2003).

Field experiments using cages can induce experimental artefacts such as changing prey or predator behaviour, altering water flow and settlement patterns (Peterson 1979, Hall 1990, Miller 2007). Despite these concerns they are still recognized as the most reliable way of directly assessing predation, provided that the experimental design and analysis are rigorous (Hall 1990, Beseres and Feller 2007). In our study, the treatments were replicated (at least 6 replicates), the layout was randomized and the duration of the experiment was short to reduce the possibility of new, early post-settled juveniles confounding results. Also, partial cages designed to mimic full cages were used as cage artefact controls for any physical effect caused by cages. All of these conditions probably precluded artefacts associated with the use of cages, as we found no evidence of cage artefacts in our study.

The differences in survivorship among levels of *Hincksia sordida* biomass indicate that the algae mats may offer a refuge from predation for juvenile scallops compared to sand, and this protection is greater in medium levels of algae biomass. Our study showed that most of the scallop losses could be attributed to species which crush scallops such as toadfish, crabs and rays. These findings are consistent with preliminary studies on predation (scallop sea farming feasibility study; Cropp and Davidson, 1988), which found that between 23 and 49% of dead scallops consisted of empty shells (possibly due to starfish predation) but the majority of recorded predation left dead scallops fragmented. Predators such as flathead, leatherjackets, skates, rays, porcupine fish, toadfish and crabs were assumed to be responsible. Laboratory observations during the sea farming feasibility study also confirmed that the spider crab *Leptomithrax gaimardii* and the north Pacific sea star, were both common predators of scallops, consuming juvenile scallops of the size tethered for the current study.

During the present study southern sand flathead were observed to capture tethered scallops but in each case these scallops were then rejected, possibly an artefact of the tether. In overseas studies, toadfish (*Opsaus tau*) have been observed to feed on tethered Bay Scallops, removing the entire animal (Ambrose and Irlandi 1992). This could explain the relatively large numbers of missing scallops during our experiments, while in control cages all tethers remained attached to the scallops. More field and laboratory observations on the behaviour of scallop predators are needed to better understand the mechanism of how the algae mat functions as a refuge from predators for juvenile scallops.

While the probability of predation of recently settled scallops may have been lower on algae mats compared to sandy bottoms, there may be other factors explaining the association between algae mats and juvenile scallops. Elevation off the bottom could avoid sediment deposition and place them in flow regimes more favourable for growth (Eckman et al. 1989). Our results indicate fastest growth occurred on sand substrate and appear to contradict this observation. The present findings suggest that juvenile scallops may be faced with the trade-off between growth and survival, since on the bare sand substrate survival rates were lowest whilst growth was fastest. Slower growth, however, increases the risk of predation since it prolongs the time before the individual reach a size that lowers the predation probability.

5 Size dependent vulnerability of scallops to predation by native and invasive sea stars

5.1 Introduction

Predation is an important factor regulating abundance of newly settled invertebrates (Gosselin and Qian 1997, Hunt and Scheibling 1997). In bivalve populations, juveniles are particularly vulnerable until they reach a size that allows them to escape from most predators (Pohle et al. 1991, Garcia- Esquivel and Bricelj 1993). Scallops are particularly vulnerable because of their thin shells, inability to seal the two shell valves near the auricles, and inability to seal the shell valves for long periods (Brand et al. 1980, Wilkens 2006). Nevertheless, most knowledge about predation in scallops is for adults, few studies have considered predation on juveniles (Hunt and Scheibling 1997), despite juveniles being more susceptible to predators because of their small size and lower swimming capability (Brand 2006)

Sea stars represent a major predator of juvenile scallops (see review in Ciocco 2001), they are slow and non-visual predators that use chemosensory receptors located on the tip of their arms to detect prey (Feder 1966). Prey are digested extraorally or intraorally and for bivalve prey items the empty intact shells (clappers) are left behind after consumption. Sea stars spend considerable time searching for prey and the probability of capturing a scallop on encounter is low because scallops are able to move and escape. Nevertheless, once captured, prey items rarely escape (Barbeau and Scheibling 1994a, Wong et al. 2006a, Wong et al. 2010).

The D'Entrecasteaux Channel (DEC) is an area that has supported large populations of scallops through time. Three species of sea stars are found in the area, two native sea stars, the granular sea star *Uniophora granifera,* and the eleven-arm sea star *Coscinasterias muricata* and one invasive species, the northern Pacific sea star *Asterias amurensis* (Tracey and Lyle 2008). The expansion of the invasive sea star numbers within the DEC has raised concerns about their potential impact on the endemic scallop populations: outbreaks of this species have had a detrimental effect on the shellfish industry in Japan (Hatanaka and Kosaka 1958) and losses of Commercial Scallop spat (*Pecten fumatus*) over a settlement season due to north Pacific sea star predation are reported to be as high as 50% in Tasmania (S. Crawford pers. comm. in Hutson et al. 2005). Nevertheless, little is known about sea star-scallop interactions in the DEC.

Hutson et al. (2005) showed significantly fewer active escape responses (swimming) in Commercial Scallops to the invasive sea star when compared to the native eleven-arm sea star and suggested that the scallop did not recognise the invasive sea star as a predator. If this is the case, then the capacity of scallops to evade invasive sea stars would be lower and therefore the predation risk of the invasive species would be higher and have a higher impact on scallop populations than native sea star species.

Another approach to understanding the interaction between the native and the invasive sea star and scallops, is by dividing the predation process into discrete behavioural units. This systematic approach has proven useful to understand underlying mechanisms of foraging behaviour and size selection (Barbeau and Scheibling 1994a, Nadeau et al. 2009). Predation can thus be assessed and compared between species by comparing probabilities (encounter rate between predator and prey, probability of capture upon encounter, and probability of consumption upon capture) and behavioural time budgets (searching, handling, not foraging) (Holling 1966, Osenberg and Mittelbach 1989).

This study examined the effect of predator species (invasive and native sea stars) and prey size on predation rates, predator foraging behaviours and scallop escape responses. This objective of the study was to evaluate the capacity of juvenile scallops to evade predation by the various sea star species by comparing sea star consumption rates, foraging and non-foraging behaviours and scallop escape response to approaching sea stars. This study also aimed to determine whether the vulnerability of being consumed changed with scallop size.

5.2 Materials and methods

5.2.1 Experimental procedures

An experiment was run during February 2013 using tanks mounted with flow-through water (10 L.min^{-1}) at ambient temperature and natural daylight. Juvenile scallops, caught in spat collectors deployed in Great Bay, D’Entrecasteaux Channel, were held in separate tanks (300 litres) for a month prior to the experiment and no additional food was added to the natural seston in sea water. Eleven-arm and northern Pacific sea stars were collected from the Derwent Estuary. Each species of sea star was maintained in separate tanks and fed blue mussels until five days prior to the experiment (see Barbeau and Scheibling 1994b). Experimental tanks had sediment to allow scallops to recess (scallops enter into a saucer-shaped depression in the seabed, typically so that the upper valve is level with or just below the surface of the sediment).

One scallop was added to each tank prior to the beginning of the experiment to give them enough time to recess. After 24 hours, one sea star was added to the centre of the tank. The experimental design consisted of a randomized block design with two predictors, a categorical predictor: sea star species and continuous predictor: scallop size.

To obtain information on behaviour, six cameras were used to continuously record six tanks during the length of each predation event (Fig. 5.1). If a scallop was consumed, the camera was moved to another tank. From these video observations, foraging and non-foraging times were estimated for each species and the probabilities of sea stars capturing scallops after an encounter was recorded (i.e. success rates). Escape responses of scallops to sea star encounters were also recorded.

Fig. 5.1. Left:Video camera recording sea star behaviour (at night red light was used). Right: Invasive sea star leaving empty shells after predating on Commercial Scallops

5.2.2 Statistical analysis

A logistic regression was used to assess the effect of sea star species and scallop size on the vulnerability of scallops to predation or the probability of being eaten. Mann-Whitney tests were used to compare proportion of time spent foraging and not foraging, the probabilities of capture after encounter and escape responses of scallops after encounter.

5.3 Results

Scallop vulnerability to predation did not differ significantly between the two sea star species (Z=-3.578, df 1, $p<0.001$) but did decrease with increasing scallop size. Scallops ranging from 14-30 mm in length had a predation probability of about 0.8; this decreased less than 0.2 for 105 mm scallops (Fig. 5.2).

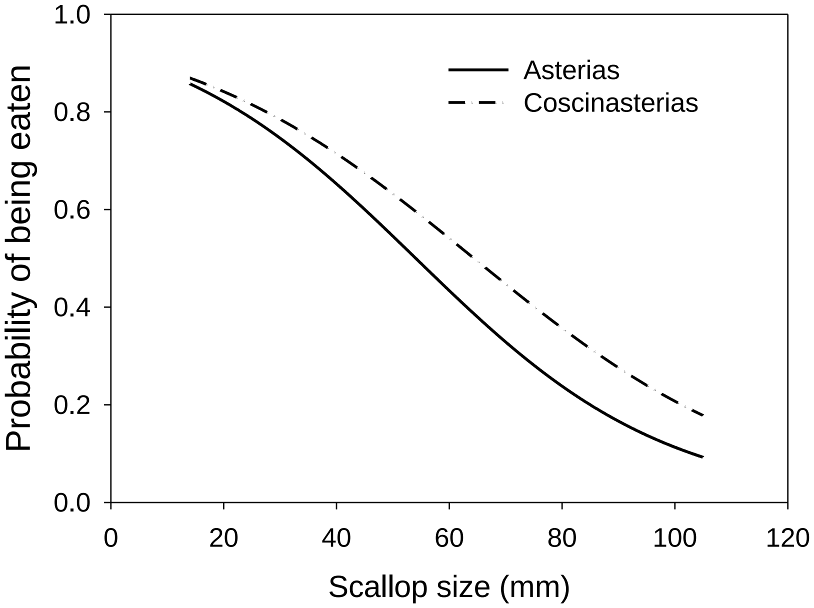

Fig. 5.2 Probability of being eaten by northern Pacific (*Asterias*) and eleven-arm (*Coscinasterias*) sea star by scallop sizes.

The behavioural analysis showed no differences in the proportion of time spent foraging (40% of the time on average) versus non-foraging between the two species of sea star (Fig. 5.3; U=4, df 2, *p*>0.8)

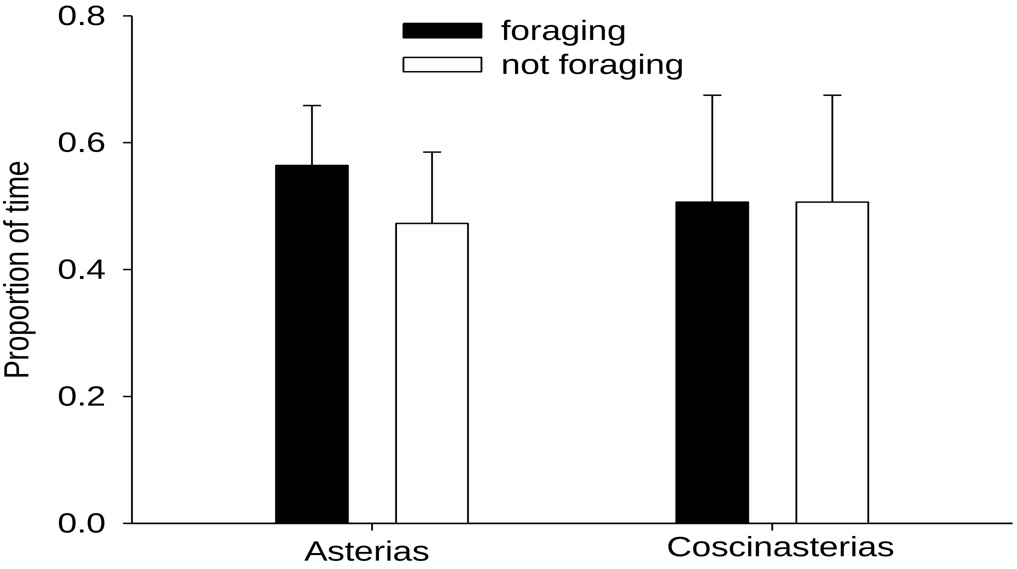

Fig 5.3. Proportion of time a predator spent foraging or not foraging. Error bars represent one standard error.

For both species of sea star, on average, three out of four encounters with scallops did not result in the scallop being captured and consumed (U=2, df 2, *p*>0.5). For both species, scallops showed a similar active escape response (swimming) probability (60% on average) (U=1, df 1, *p*>0.1) (Fig. 5.4).

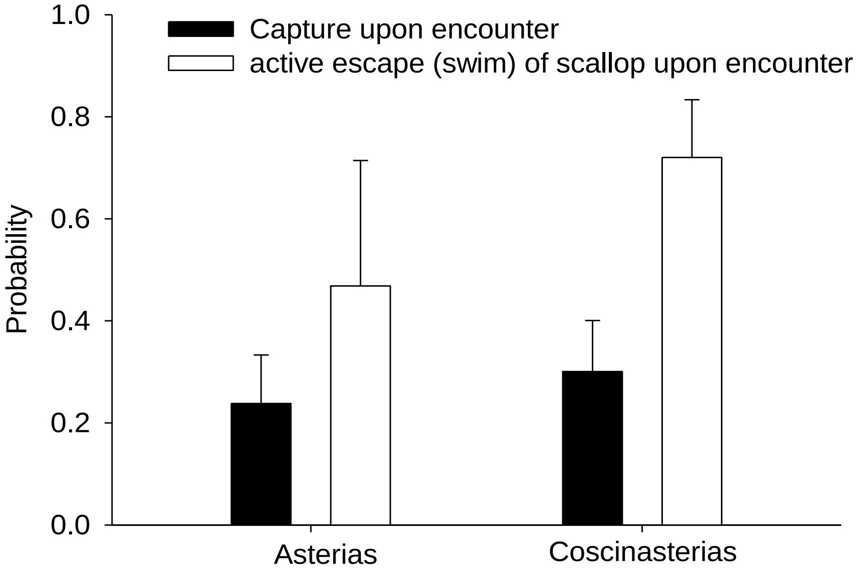

Fig 5.4. Probability of capture upon encountering a scallop and scallop response to each sea star. Error bars represent one standard error.

5.4 Discussion

We hypothesised that Commercial Scallops would be more vulnerable to the invasive sea star species than the native eleven-arm sea star. This hypothesis built on findings by Hutson et al. (2005) who found a lower frequency of escape responses in scallops when held in contact with the invasive sea star compared to the native sea star. Our trials found no evidence to support this hypothesis; the probability of a scallop being eaten was not significantly different between the two predator sea stars. While the active escape response (swimming away) of scallops was proportionally greater when in contact with the native sea star, this difference was not statistically significant and did not affect the overall risk of predation in scallops. Alternatively, escape behaviours of scallops to the invasive sea star could have evolved to some extent over a very short periods, a phenomenon observed for barnacles and whelks (Rochette et al. 1998).

Vulnerability to sea star predation was greater at smaller sizes and decreased with scallop size, supporting the size-refuge hypothesis. Prey handling constraints was a major factor; both sea stars showed very similar behaviours and the amount of time spent foraging and not foraging did not differ between species. While encounter rates were greater between sea stars and scallops, the appropriate humped position for consumption in sea stars was only achieved after several attempts.

Sea stars can have a significant negative impact on bivalve populations. Our study indicates that small scallops are more vulnerable to starfish predation than large individuals and, while the invasive sea star does not appear to pose a greater predation risk than the native sea star, it has the potential to contribute to the depletion of scallop populations where present.

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