

**Influence of reproductive and post-settlement processes on
recruitment in scallops**

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Abstract

Knowledge about the key factors influencing recruitment of exploited benthic marine invertebrates is important, as it provides information necessary for sustainable fisheries management and population recovery. This information is especially relevant for stocks that have been severely depleted, such as the populations of *Pecten fumatus*, *Equichlamys bifrons* and *Mimachlamys asperrimus* in the D'Entrecasteaux Channel, Tasmania, Australia. Stock declines related to a combination of fishing pressure and recruitment failure have raised concerns about density related mechanisms that could influence recruitment. Correlations between numbers of recruits and numbers of adults have led to hypotheses that distribution patterns of adults might be explained by habitat-related characteristics. Therefore this study examined reproductive and post-settlement processes likely to contribute to patterns of recruitment in scallops, with a particular focus on *P. fumatus* to identify strategies for management and conservation of scallop populations in south-eastern Tasmania. This aim was addressed using a combination of field experiments, underwater observations and laboratory studies.

Spatial patterns of distribution and abundance for the three species of scallops were explained by sediment type, habitat structural components, and/or presence of predators. However, the nature of the relationships between these factors and the distribution patterns differed markedly among species. While *Pecten fumatus* was strongly associated with finer sediments and *Equichlamys bifrons* with coarse grain sediments, *Mymachlamys asperrima* had a less selective association, possibly related to its ability to attach on a wide range of substrates. Other habitat characteristics explaining the abundance of *P. fumatus* were depth, *Asterias amurensis* abundance, shell and macroalgae cover. *Equichlamys bifrons* was strongly associated with macroalgae and seagrass cover, whereas *M. asperrima* abundance was greatly explained by sponge cover. These relationships are likely mediated by predation pressure as well as the specific behavioural characteristics of each species. The findings highlighted the specific habitat characteristics relevant for spatial management and habitat restoration plans.

The role of predation during early post-settlement stages was explored by assessing the survival of recently settled *Pecten fumatus* using a range of field experiments and sampling. The role of the macroalgae *Hincksia sordida* as a settlement substrate and as a

refuge from predation for this species was examined. Predation on spat and juveniles was a major factor affecting local population sizes; mortality rates up to 95% during the first weeks after settlement appeared to have prevented the establishment of an adult population at the study site as few adults were found during three consecutive sampling years. While macroalgae provided settlement substrate for spat, higher macroalgal biomass did not offer increased protection from predation during the juvenile phase. This appears to be linked to the recessing behavior of *P. fumatus*, which may be hindered or prevented when algal biomass is high. When recessed into the sediment scallops are assumed to be less vulnerable to detection by predators. Thus the interplay between prey behavior and substrate characteristics was considered important in determining scallop survival.

Pecten fumatus is a simultaneous hermaphrodite with a protracted spawning season from October to March supported by stored energy reserves early in the spawning season, whereas later in the spawning period energy from oocyte breakdown provides an energy source for development of new oocytes when primary productivity levels were low. Protracted spawning represents a bet-hedging strategy that would ensure some recruitment by increasing the probability of offspring survival when environmental conditions are unpredictable. However, for low density populations the advantages of protracted spawning may not be fully realized because of the negative relationship between density of spawning stock, aggregation patterns, and synchronization of spawning. Areas with lower densities of scallops had less small scale aggregation and increased nearest neighbour distances. Spawning synchronization was highly variable throughout the season, with 3.5-59.8% of individuals spawning at a given time. *Pecten fumatus* was more likely to spawn when present in high density aggregations and when in closer proximity to conspecifics. Reducing densities not only reduces the number of individuals contributing to the production of gametes, but also reduces the synchronization of spawning and rate of gamete release. At density levels currently observed in the D'Entrecasteaux Channel it is probable that most individuals are at distances too great for fertilisation. Also, this study suggests that despite being a hermaphrodite, *P. fumatus* seems to be favouring cross-fertilization over self-fertilization.

By examining biological and ecological factors, this research identified a number of factors that may hinder the effective recovery of *Pecten fumatus* stocks within the area despite protracted closures to fishing. Specifically, this research highlights the benefits of

maintaining areas with a minimum density of 0.2 ind.m⁻² of *P. fumatus*, which could be achieved under the current rotational harvesting system in south-eastern Tasmania. In the case of the D'Entrecasteaux Channel, however, the populations are currently severely depleted and, being most likely self-recruiting, alternative restoration efforts such as transplantation or restocking may be warranted. These efforts would benefit from targeting species specific habitat characteristics, for example areas with greater sponge cover for *M. asperrima*, greater seagrass cover for *E. bifrons* and lower macroalgal cover for *P. fumatus*.

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Chapter 1. General Introduction

A major goal in ecology is to understand factors that determine the change of population size through time (Krebs 1972). Population size depends on survival and reproduction, which are fundamental processes for population persistence, as individuals contribute genes to the next generation only if they survive to reproduce (Goodman 1987). Understanding which factors influence survivorship from zygote to adult, is particularly important in marine populations where adult abundances have been reduced through anthropogenic impacts, such as fishing (Jackson et al. 2001, Baum et al. 2003, Atkinson et al. 2008) or habitat degradation (Lenihan & Peterson 1998, Wilson et al. 2008). These reductions can result in population collapses (Hutchings and Myers 1994; Myers 1997; Hutchings 2000; Safina and Klinger 2008), localised extinctions (see review in Carlton et al. 1999; Spotila et al. 2000; Dulvy et al. 2003), and generally affect the overall recovery dynamics of the population (Fogarty et al. 1991, Hutchings & Reynolds 2004) due to reductions in individual fitness (Shelton & Healey 1999, Keith & Hutchings 2012, Saha et al. 2013), changes concerning interactions among species (Swain & Sinclair 2000, Walters & Kitchell 2001) or modification of life history traits (Lorenzen & Enberg 2002, Jorgensen et al. 2009).

For benthic marine invertebrates, recruitment (defined here as the number of individuals that survive after a certain period of time) comprises different stages: larval production, larval dispersal, settlement and post-settlement (Hatton 1938; Thorson 1950; Connell 1961a; Gaines and Roughgarden 1985; Menge 2000). Determining which factors influence recruitment in marine benthic invertebrate is particularly challenging, because these species possess a complex life cycle that extends across multiple stages, often in different habitats, incorporating both the pelagic (larval) and benthic environment. Final numbers of recruits are affected by both pre-settlement (Thorson 1950; Loosanoff 1964; Underwood and Fairweather 1989) and post-settlement (Connell 1961a; Connell 1961b; Paine 1966; Dayton 1971; Paine 1974; Menge 1976) events, although the relative importance of each depends on factors such as density of settlers (Underwood and Denley 1984; Gaines and Roughgarden 1985; Roughgarden et al. 1988; Minchinton and Scheibling 1991; Menge 2000) and habitat type (Rowley 1989; Levin 1994; Olafsson et al. 1994; Eggleston and Armstrong 1995).

Marine benthic invertebrates are frequently broadcast spawners (Giese & Kanatani 1987), and produce large quantities of microscopic gametes that are hard to observe and quantify in the field, making our knowledge of timing of spawning and fertilization rates *in situ* very limited (Levitan 1995, Yund 2000). Marine benthic invertebrate larvae are small and can disperse over large distances (Scheltema 1986), making it difficult to quantify the extent of movement and connectivity between subpopulations (exchange of individuals among geographically separated subpopulations that comprise a meta-population) (Pineda et al. 2007, Cowen & Sponaugle 2009, Pineda et al. 2010). Determining the impact each different factor has on population dynamics is difficult as they do not necessarily act in a linear fashion. Rather, they operate and interact on different temporal and spatial scales making it difficult to predict or adequately describe changes in population abundances (Roughgarden et al. 1988; Fogarty et al. 1991). Moreover, the understanding of each stage requires a multidisciplinary approach between marine biologists and physical oceanographers, as the dispersive stage of larvae is greatly affected by physical processes (Johnson 1939; Thorson 1950).

Nevertheless, the growing number of species undergoing decline in population size and local extinctions in exploited populations of marine benthic invertebrates, such as abalone (Hobday et al. 2001, Stierhoff et al. 2012), gastropods (Leiva & Castilla 2001), scallops (Peterson & Summerson 1992, Tracey & Lyle 2011) and sea cucumbers (Purcell et al. 2013), warrants the effort to determine the causes that are likely to affect recruitment. Scarce information about the adult densities required for fertilization success and on the spawning season of the white abalone *Haliotis sorensen* resulted in severe reductions in population size (Hobday et al. 2001) and the listing of this species under the Endangered Species Act in the United States (NMFS 2001). Therefore, knowledge about the key factors influencing recruitment of exploited benthic marine invertebrates is important as it provides information necessary for sustainable fisheries management and conservation (Hobday et al. 2001). To assess which variables are exerting their influence on recruitment, it is convenient to divide the recruitment process into four stages (Fig. 1.1): production of larvae, larval dispersal, settlement, and post-settlement.

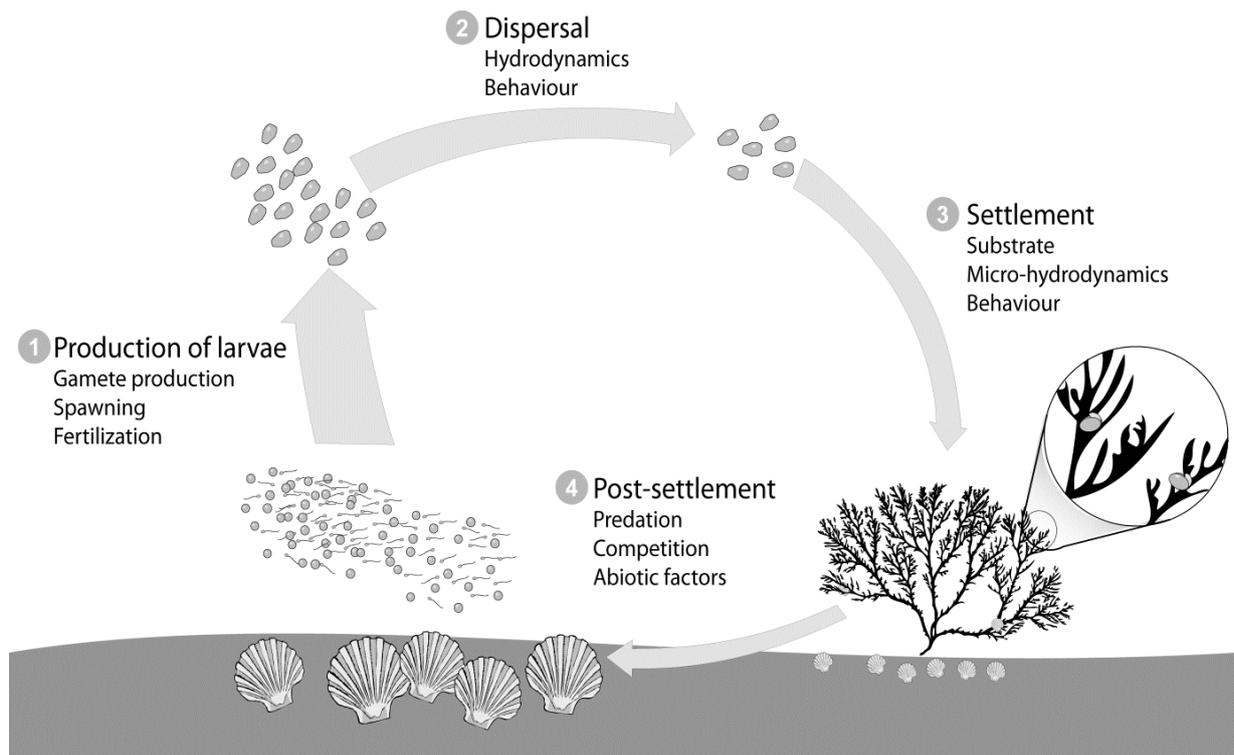


Fig. 1.1. Diagram showing different factors influencing recruitment in benthic marine organisms in different life cycle stages from gamete to adult. Arrow widths illustrate the relative reduction in individuals from one stage to the next one. Based on concepts by (Pineda et al. 2009) and (Underwood 2001).

1.1. Production of larvae

Production of larvae (Fig. 1.1, stage 1) is divided into three major phases: gamete production, spawning, and fertilization. Gamete production is an energy demanding process and the number of gametes produced will vary depending on food availability and quality (Bayne et al. 1978; Macdonald and Thompson 1986; Giese and Kanatani 1987; Qian and Chia 1991). Due to this high energy demand, benthic marine invertebrates use different strategies to acquire and allocate energy for reproduction: either they acquire energy from food available in the environment concurrently with breeding (income breeding) or they collect and store energy in advance until it is needed for reproduction (capital breeding), or a combination of both (Drent & Daan 1980, Stephens et al. 2009). Using a capital breeding strategy will provide an advantage in highly variable environments (Bonnet et al. 1998), such as temperate waters and allow the production of gametes to be independent of food

availability. The use of a particular strategy has implications on the timing of offspring production and the numbers of gametes produced (Drent & Daan 1980).

Regardless of breeding strategy (or combination of strategies), most benthic marine invertebrates will produce a large number of gametes per spawning event, however, not all eggs are fertilized. Manipulative studies have shown that many factors among them adult population density (Levitan 1991; Levitan et al. 1992), degree of synchronisation in spawning (Oliver & Babcock 1992, Babcock et al. 1994), distance from a sperm source (Pennington 1985; Babcock et al. 1992), time since sperm release (Gemmill 1900; Powell et al. 2001) and hydrodynamic processes (Coma and Lasker 1997; Levitan 2002) affect successful fertilization.

Fertilization success can be highly variable with estimates ranging from 0 to 100% for benthic marine organisms (Babcock et al. 1992, Brazeau & Lasker 1992, Sewell & Levitan 1992). In this context, the concept of sperm limitation was introduced, stating that extreme dilution of sperm in the sea would result in many eggs remaining unfertilized (Levitan & Petersen 1995). Organisms, however, have evolved a number of mechanisms that maximise the number of eggs and sperm in any one area (hence reducing sperm limitation), such as releasing gametes at times of lower water motion (Serrão et al. 1996), spawning from elevated surfaces to increase suspension and mixing (Himmelman et al. 2008), pseudocopulation (male superposed on a female, but no actual sexual union occurs) (Lawrence et al. 2011), forming dense aggregations during spawning seasons (Petersen et al. 1992, Sewell & Levitan 1992) and highly synchronized spawning (Coma & Lasker 1997). Moreover, several mechanisms exist in most marine organisms to avoid the contact of eggs with too many sperm (polyspermy) (Rothschild 1947; see review in Gould and Stephano 2003), as it results in embryonic death (Boveri 1901; Wilson 1928). A review on fertilization success in field studies showed that on average, fertilization success in the field was quite high, but greatly variable among taxa (Yund 2000).

Importantly, when compared to highly mobile broadcast spawners such as fish, the smallest estimates of fertilization success in the field are observed in sessile and sedentary broadcast spawners (see review in Yund 2000). These organisms cannot aggregate to reproduce, therefore changes in aggregation and population sizes reduce the probability of a sperm meeting an egg and hence the reproductive success of an individual (Pennington 1985;

Levitan et al. 1992; Levitan and Sewell 1998) . This deterioration in individual fitness (i.e. probability of reproducing or output of fertilized eggs) as either the number or density of conspecifics decreases is called an “Allee effect” (Allee 1931; Allee 1938; Stephens et al. 1999). Stephens et al. (1999) further clarified this concept by dividing Allee effects into ‘component’ (positive density dependence in some component of individual fitness) and ‘demographic’ (positive density dependence in the per capita population growth rate) Allee effects. In fisheries science the term depensation has been used to refer to positive density dependence mainly through predation or reproduction (Peterman and Gatto 1978; Hilborn and Walters 1992; Myers et al. 1995) and corresponds to a demographic Allee effect (Gascoigne and Lipcius 2004). Allee effects can have major consequences for population dynamics, because populations with few individuals and strong Allee effects will have a greater probability of decline and extinction than those with no or weak Allee effects (Stephens & Sutherland 1999). While there is considerable debate about the existence of Allee effects in marine systems (e.g. Myers et al. 1995; Liermann and Hilborn 1997; Shelton and Healey 1999; Stoner and Ray-Culp 2000; Keith and Hutchings 2012), there is increasing evidence that these effects are particularly relevant in sessile or semi-sessile marine broadcast spawners subjected to exploitation (e.g. Levitan et al. 1992; Shepherd and Brown 1993; Stoner and Ray-Culp 2000; Hobday et al. 2001; see review in Gascoigne and Lipcius 2004). Reducing harvesting mortality may be insufficient to allow prompt recovery of marine populations after abundance has been severely reduced (for a review see Hutchings 2000; Lotze et al. 2011), therefore considering Allee effects in exploited populations is critical for understanding population dynamics and for sustainable exploitation and management (Dennis 1989; Quinn et al. 1993; Berec et al. 2007).

1.2. Larval dispersal

Early studies on larval ecology in the 19th century recognized the importance of larval dispersal on distribution patterns of marine invertebrates (see Young 1990 for an historical overview). Dispersal distances in larvae are hard to measure directly, but recent studies show a pattern regarding dispersal in marine benthic organisms that can vary from tens of meters to hundreds of kilometres (see review in Kinlan & Gaines 2003). Producing larvae that can be dispersed away from the parental source is beneficial (see review in Pechenik 1999) because it reduces competition with adults for habitat and food (Istock 1967; Economou 1991), reduces predation by benthic predators (Lucas et al. 1979; Pechenik 1979; Pennington and

Chia 1984), reduces the likelihood of inbreeding (Jackson 1986; Knowlton and Jackson 1993), minimises the risk of extinction (Roff 1974) and facilitates colonization of new habitats (Mayr 1970; Scheltema 1971; Doherty et al. 1985). As a result, the population dynamics of a species might depend upon larvae originating from different subpopulations – these subpopulations are considered connected (Gaines et al. 2007). There is growing evidence that populations might be less open (or connected) than previously thought. Thus, larvae can be retained close to their natal site (Swearer et al. 1999; Pineda et al. 2007; Cowen and Sponaugle 2009) and recruit back to their source population (Jones et al. 1999; Swearer et al. 2002; Jones et al. 2005).

Knowledge of the degree of dispersal of larvae is important to understand the dynamics in a population because in ‘open’ populations, local reproduction might not affect local population dynamics (Gaines & Lafferty 1995, Adams et al. 2004) while in ‘closed’ populations a large degree of coupling between production of larvae and recruitment might occur (Peterson & Summerson 1992).

1.3. Settlement

Even if sufficient larvae are produced, the availability of suitable settlement substrate may limit larval settlement (Fig. 1.1, stage 3) (Meadows and Campbell 1972; Crisp 1974; Pawlik 1992) and ultimately affect recruit numbers. A range of senses allow larvae to encounter appropriate habitats (see review in Rodriguez et al. 1993; Young 1995), such as detecting variations in water chemistry (e.g. salinity (Sulkin et al. 1980; Tankersley et al. 1995)), sound and vibration (Kingsford et al. 2002; Simpson et al. 2005; Montgomery et al. 2006; Lillis et al. 2013), and changes in light (Thorson 1964; Crisp and Ritz 1973; Young and Chia 1982). As larvae encounter substrata, they may exhibit exploratory behaviours before metamorphosis, such as crawling or active re-suspension, in search of preferred habitat (Thompson 1830; Walters et al. 1999). This search may be affected by microhydrodynamics, substrate morphology (Wethey 1986, Pawlik et al. 1991), and chemical cues that trigger metamorphosis to acquire features appropriate with the new benthic phase (see review in Pawlik 1992; Hadfield and Paul 2001). Among such cues are the presence of conspecifics (Crisp and Meadows 1962; Scheltema 1974; Burke 1986; Jensen and Morse 1990; Slattery 1992), microbial films (Meadows and Williams 1963; Mueller 1969; Neumann 1979; Pearce and Scheibling 1991; Johnson et al. 1997) and prey species (Morse and Morse

1984; Hadfield and Scheuer 1985; Chia and Koss 1988). Therefore, habitat characteristics have a strong effect on patterns of distribution and abundance of settlers (Eggleston & Armstrong 1995, Moksnes 2002a).

1.4. Post-settlement

Post-settlement (Fig 1.1, Stage 4), up to 100% of the larvae die during the first few weeks after settlement (see review in Gosselin & Qian 1997). Post-settlement stages are subjected to biotic factors such as predation (Thorson 1966; Keough and Downes 1982; Stoner 1990; Gosselin and Chia 1995) and competition for space (Connell 1961a; Menge 1976; Davis 1987), and abiotic factors such as temperature, salinity, and desiccation (desiccation being relevant in intertidal organisms) (Denley and Underwood 1979; Moller 1986; Roegner and Mann 1995). The processes operating during this phase differ from those operating on adult phases since the use of microhabitat and food resources vary with ontogeny as does their vulnerability to external factors affecting survival (Wahle & Steneck 1991, Gosselin & Chia 1994). Mortality is generally greater during early post-settlement phases than when marine invertebrates reach adulthood (see review in Gosselin and Qian 1997), hence the importance of examining the magnitude of mortality at this stage to explain abundance of organisms.

Predation in juveniles is generally recognized as one of the key factors affecting post-settlement survival (see review in Hunt & Scheibling 1997), however, predation pressure can be mediated by habitat complexity, with more complex habitats typically providing improved shelter opportunities and impacting predator efficiencies (Paine 1976; Pohle et al. 1991; Smith and Herrkind 1992; Maldonado and Uriz 1998; Irlandi et al. 1999). Therefore, it is essential that specific habitat characteristics are examined when explaining variation in abundances.

1.5. Reducing complexity on a case by case analysis

Understanding the main factors influencing recruitment in marine benthic organisms is important for organisms subjected to exploitation, such as scallops, as it will inform managers on the vulnerability of the resource and on which intervention or management tactic will be likely to enhance population recovery (i.e. habitat manipulation, restocking,

predator control (Hobday et al. 2001, Orensanz et al. 2006)). This information is urgently required in populations that have been severely depleted, such as the population of *Pecten fumatus* in the D'Entrecasteaux Channel (DEC), Tasmania, Australia (Tracey & Lyle 2011).

To identify the most important factors influencing recruitment in marine benthic organisms, a coherent simplification in the number of factors influencing patterns of abundance and distribution is necessary (Pineda et al. 2009). Field observations provide a logical starting position from which to begin to propose hypotheses and/or describe functional processes (Underwood et al. 2000). This study was undertaken to determine critical factors influencing distribution and abundance in scallops, focusing on *P. fumatus* in the DEC. Available data on the population dynamics of the scallop were first analysed to provide a logical framework that aided in the decision process about which factors warranted more consideration.

The D'Entrecasteaux Channel is a semi-enclosed area between mainland Tasmania and Bruny Island. Historically, it has been a key area for the Australian scallop fishery, supporting a significant production since the early 1900s. Three species of scallops co-occur in the DEC: the commercial scallop *Pecten fumatus*, the queen scallop *Equichlamys bifrons*, and the doughboy scallop *Mimachlamys asperima* (Fig. 1.2). *Pecten fumatus* is a functional hermaphrodite that occurs in the coastal waters of southern Australia from central New South Wales in the East, around Tasmania, and beyond the border between South Australia and Western Australia (Young and Martin 1989). This species recesses (a behaviour that consists on a series of movements for semi-burying, in which the upper valve is level with or just below the surface of the sediment) and the upper valve is generally covered by sediment and epibiota (Olsen 1955). It can swim considerable distances (up to 15 feet in a single burst has been recorded (Olsen 1955)) usually when exposed to a predator species (Hamer and Jacobs 1987). This species usually attains 70-80 mm in the second year of life (Fairbridge 1953; Sause et al. 1987; Dredge 2006) and specimens of up to 16 years old have been reported (Fairbridge 1953). *Equichlamys bifrons* is a gonochoristic species found in New South Wales, Victoria, South Australia and Tasmania (MacPherson and Gabriel 1962). It is found free living on soft sediments and usually attains 70-80 mm in its second year of life (Wolf and White 1995). While *E. bifrons* can swim, they do not move great distances (about 20 m in 6 months) (Wolf and White 1997). *Mimachlamys asperima* is also gonochoristic species located from Western Australia to New South Wales and Tasmania (Young and Martin

1989). Juveniles and adults are usually attached by a byssus to hard substrates during most of their lifetime (Olsen 1955; Pitcher and Butler 1987). Nevertheless it can break the byssus and swim when exposed to predators (Pitcher and Butler 1987). This species reach smaller sizes than the other two and attains approximately 65-75 mm in its second year of life (Zacharin 1995).

The DEC supported a significant commercial dredge fishery for scallops from the early 1920s to late 1960s, with catches peaking at 4,500 tonnes of meat of *P. fumatus* in the mid 1960s, declining rapidly thereafter (Perrin & Croome 1988). Significant depletions of scallop populations have occurred at various times 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 low numbers of scallops. By the mid-2000s there was evidence of stock rebuilding, following more than a decade of closure, which led to the area being reopened as a recreational dive-only fishery in 2005. Several measures were put in place to reduce the impact of the recreational fishery such as reduction of daily bag limits (from 200 in 1993 to 40 scallops), increased minimum size limit and restriction of the fishery to dive only harvesting (Tracey & Lyle 2011).

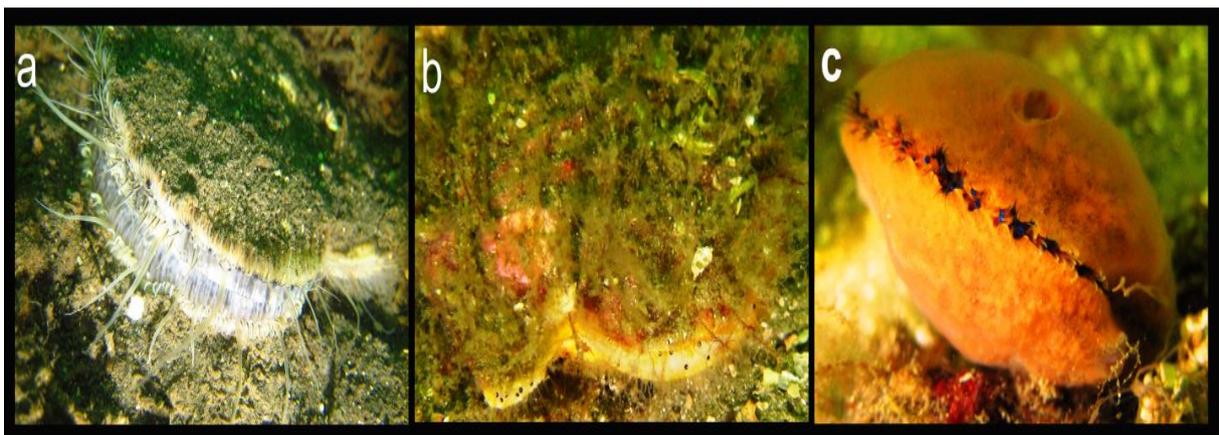


Fig. 1.2. Scallop species found in the D'Entrecasteaux Channel (DEC) a) *P. fumatus*, b) *E. bifrons* and c) *M. asperrima*

Despite this ostensibly 'conservative' approach to management, the abundance of scallops declined by approximately 90% between 2006 and 2012 (Tracey & Lyle 2012), due

in part to the effects of fishing coupled with natural mortality and poor recruitment during this period (Tracey & Lyle 2011). This decline in the population size and associated poor recruitment (Fig. 1.3) raised concern about positive density-dependent mechanisms that could be affecting recruitment.

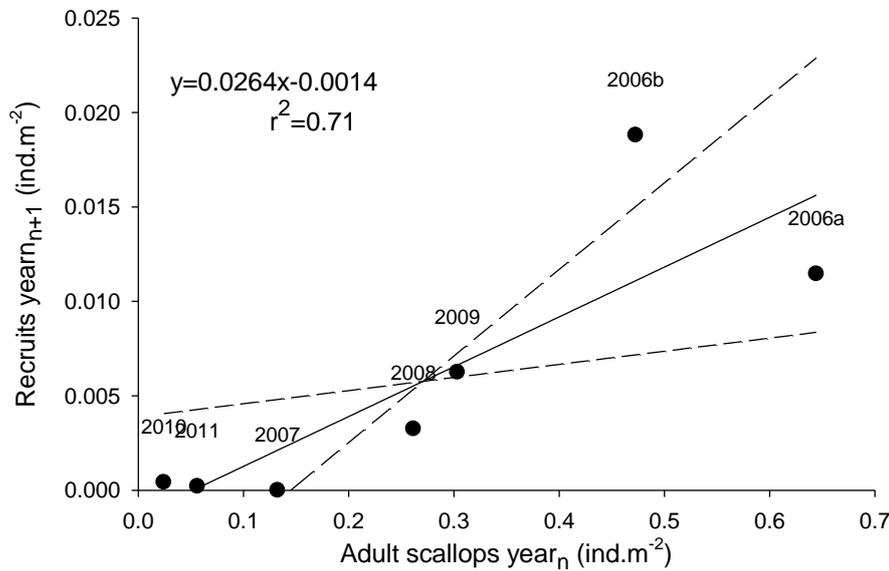


Fig. 1.3. Relationship between *P. fumatus* spawner density in year_n and recruits year_{n+1} in 24 sites in the DEC, from 2006 to 2012. 2006a refers to pre-season survey abundance (February 2006); 2006b refers to post-season abundance (July 2006). Major Axis regression model fitted lines (solid) and 95% confidence intervals (dashed) are shown. Relationship derived from unpublished data available from DEC scallop surveys (Tracey & Lyle 2012).

Habitat characteristics in the DEC might be important in influencing recruitment in scallops. Tracey & Lyle (2012) showed that these patterns were temporally and spatially consistent suggesting that habitat characteristics may be important for successful recruitment. Further evidence of the importance of habitat in regulating distribution and abundance in scallops was provided by a study on *Pecten fumatus* in Great Bay, DEC, where despite collections of large numbers of spat using artificial collectors, these spat did not necessarily translate into successful juvenile settlement to the benthos (Semmens et al. 2013a). Most juvenile scallops are present in sites with large numbers of adult scallops, suggesting that successful recruitment is a function of physical and biological site characteristics (Semmens et al. 2013a). However, even if a cohort of juveniles did settle in an area, few individuals survived to adulthood, suggesting that post-settlement processes are important in regulating

scallop populations (Semmens et al. 2013a). No information is available on habitat characteristics and early post-settlement processes affecting abundance of *P. fumatus*.

In this context, this study examined reproductive and post-settlement processes likely to influence recruitment in scallops, with a particular focus on *P. fumatus* in order to identify factors that might be relevant for management and conservation of scallop populations in south-eastern Tasmania. Chapters 2 and 3 focused on settlement and post-settlement processes while Chapters 4 and 5 examined factors influencing the production of gametes. Dispersal of larvae in the DEC was not included within the scope of this study since the *P. fumatus* population within the DEC appears to be largely self recruiting, with negligible exchange of larvae with other populations from around Tasmania or southeastern Australia, presumably a consequence of the semi-enclosed nature of the DEC, (Woodburn 1988, Semmens et al. 2013b).

1.6. Thesis Structure

Each data chapter presents original data and is written in a style suitable for publication. Whilst I have attempted to maintain a logical flow of ideas throughout the thesis, each chapter can be read independently. This, however, has resulted in some repetition, particularly in the introductory sections of the chapters.

An understanding of the relationships between habitat characteristics and the distribution and abundance patterns in scallops provide insights into the ecological processes that regulate these populations. Chapter 2 examines the relationship between the distribution and abundance patterns of each of the three co-occurring scallop species in the DEC and associated habitat characteristics, including structural components, sediment type, predator abundance and depth.

Post-settlement processes in early post-settlement stages are generally poorly understood in scallops and in Chapter 3 the focus is on factors that influence whether settlement events result in successful recruitment to the adult population. This chapter also examines the role of macroalgae as a settlement structure and refuge from predation in early post-settlement stages.

Chapter 4 describes the reproductive biology of *P. fumatus* as a step to identifying spawning seasons and approximate timing of settlement. This chapter considers the sources of energy used to fuel the production of gametes and the underlying reproductive strategy adopted by the species. Chapter 5 builds on from Chapter 4 to examine two density-dependent mechanisms which affect the production of recruits: aggregation of spawners and synchronization of spawning.

Chapter 6 provides a general discussion of the key findings and implications of this study and the directions for future research. Identifying the importance of maintaining areas of minimum adult scallop densities, the influence of sediment and/or habitat characteristics and the role of early post-settlement mortality on survival of juvenile scallops represents a critical step towards understanding factors regulating patterns of distribution and abundance of scallops. This information has particular relevance to the future management of DEC scallop fishery since variability in settlement and subsequent recruitment to the adult stock will determine both the health of the scallop populations within the DEC and whether a recreational fishery can be supported without resulting in long-term stock collapse.

Chapter 2. Habitat characteristics associated with distribution and abundance patterns of scallops in D'Entrecasteaux Channel, Tasmania

2.1. Introduction

The distribution and abundance of 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 & Stotz 2000), hydroids (Harvey et al. 1993), sponges (Bremec et al. 2008), macroalgae (Cantillánéz 2000) and or shells (Pacheco & 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 & Edwards 1976).

The value of habitat structure in reducing risk of predation continues into the juvenile and adult phase. Habitat characteristics greatly influence predation by affecting predation efficiency and predator-prey encounter rates (Myers et al. 1980, Heck et al. 1981). 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 & White 1997).

Despite the apparent importance of specific habitat characteristics in influencing scallop distribution and abundance patterns, quantitative studies on scallop-habitat relationships are rare. Identifying the habitat characteristics to which scallops are associated is relevant in managing, conserving, and even restoring these habitats. This information is particularly necessary for the D'Entrecasteaux Channel (DEC), southeastern 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 4500 tonnes of meat in the mid 1960s and declining rapidly thereafter (Perrin & 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. By the mid-2000s there was evidence of stock rebuilding, following more than a decade of fishery closure, which led to the area being reopened as a dive-only fishery in 2005, with a reduced daily bag limit of 40 scallops per person. Despite this ostensibly ‘conservative’ approach to management, the abundance of commercial scallops declined by approximately 80% between 2006 and 2010, due in part to the effects of fishing coupled with natural mortality and poor recruitment during this period (Tracey & Lyle 2011).

The three co-occurring scallop species exhibited distinct and temporally consistent distribution patterns within the area during the 2000s (Tracey & Lyle 2011), 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. The ‘commercial’ scallop *Pecten fumatus* is found mainly on a range of soft sediment substrates including silt-sand and coarse sand (Fairbridge 1953, Olsen 1955). When at the spat stage, *P. fumatus* 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 & Cropp 1987). The ‘queen’ scallop *Equichlamys bifrons*, does not recess (Minchin 2003) and is often found in association with the seagrass *Heterozostera tasmanica* (Olsen 1955, Wolf & White 1997). The ‘doughboy’ scallop *Mimachlamys asperrima*, bysally attach throughout their lifetime to a wide range of substrates such as bryozoans, seaweeds, sponges, oysters, mussels, old scallop shells, timber and rock (Zacharin 1994).

An understanding of the relationships between habitat characteristics and the distribution and abundance patterns of each of these three species of scallops will provide insight into the ecological processes that regulate these populations. Being a relatively shallow and sheltered system, the DEC provided a unique opportunity to study the patterns of

distribution by direct observation. In this study we have used dive surveys to examine the relationship between the distribution and abundance patterns of each species and associated habitat characteristics, including structural components, sediment type, predator abundance and depth. We hypothesize that specific habitat features influence the patterns of distribution of each species in different ways and discuss how these relationships are possibly mediated by predation pressure and the behavioural characteristics of each species.

2.2. Materials and Methods

2.2.1. Study area

The DEC (147.33590 W and 43.22028 S), 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. 2010). The DEC system is micro-tidal, with a spring tide ranging up to 1 m (Herzfeld et al. 2010). The study was conducted under the Authority of the Department of Primary Industries, Parks, Water and Environment (DPIPWE) permit No. 10028.

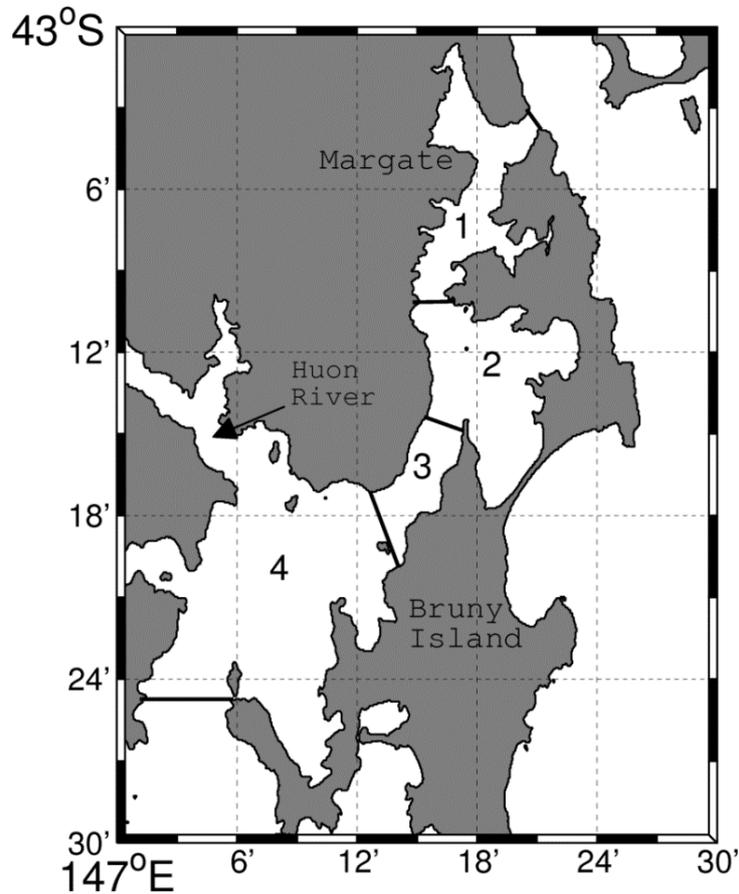


Fig. 2.1. Map of the D'Entrecasteaux Channel (DEC). Numbers represent the Areas referred to throughout the manuscript.

2.2.2. *Distribution patterns*

Scallop distribution and abundance in the DEC were quantified using dive surveys of 59 sites defined in Tracey & Lyle (2011). The survey sites were restricted to depths <20m and to soft sediments. Briefly, at each site, a 100 m transect was laid in a haphazard direction from the boat and two divers then searched and collected all scallops 1 m either side of the transect line covering an area of 200 m². The species and shell width (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 potential scallop predators, the native eleven-arm sea star *Coscinasterias muricata* and the introduced northern Pacific sea star *Asterias amurensis*, was also recorded for each transect.

Patterns of scallop abundance were analyzed 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 1994). 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 (Elliot 1971). To evaluate whether 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, 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 macroalgal 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 as being absent when none were recorded within the transect area, low when 1 – 10 sponges were counted and medium when more than 10 were present. Macroalgae and shell cover were estimated visually and when the component was not observed within the transect area it was ranked as absent, low when the coverage was judged to be less than about 10% 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 (60°C, 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 gram and the cumulative percentage by weight of the eight fractions was calculated and the mean plotted against a phi (Φ) scale where:

$$\Phi = \log_2 d$$

where d is particle diameter in millimeters. 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:

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

where larger d_m values correspond to finer grain sizes (Wentworth 1922). 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 & McIntyre 2008). Water depth was measured at each site using dive computers with 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 (MATLAB 2006). Coastlines for maps were extracted from the NOAA database (NOAA 2013).

Scatterplots indicated that none of the continuous explanatory variables (mean grain size, depth, *Asterias amurensis* and *Coscinasterias muricata* counts) were correlated. Scallop abundance was modelled as a function of explanatory variables using Generalized Additive Models (GAM) (Hastie & Tibshirani 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 (Wood 2006, R Development Core Team 2010). Explanatory variables were selected if significant ($p < 0.05$). As the data were overdispersed a quasi-Poisson distribution was used (Zuur et al. 2009). Due to the tendency of GAM to overfit 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 that there is no spatial autocorrelation. 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

Densest populations of *Pecten fumatus* were found in the eastern section of Area 2, with a maximum of 85 scallops per 100m² but were very scarce in Areas 1, 3 and 4 (Fig. 2.2). Densest populations of *Equichlamys bifrons* were found in Area 3 with as many as 33 scallops per 100m², scarce in Areas 1, 2 and were absent in Area 4. Highest densities of *Mimachlamys asperrima* were found in Areas 2 and 3, with a maximum of 73 scallops per 100m², but were absent in Area 4. All three species had aggregated, non random distribution according to the Standardised Morisita's Index (Table 2.1).

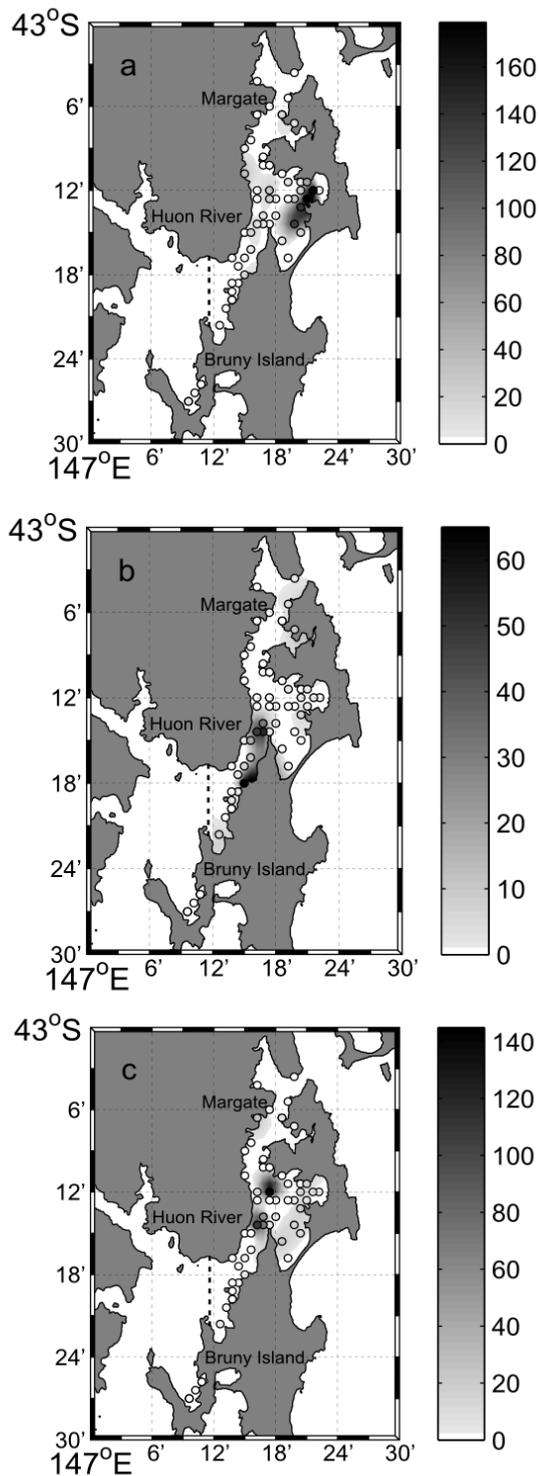


Fig. 2.2. The interpolated distribution and densities (scallops per 200 m² transect) of *P. fumatus* (a), *E. bifrons* (b) and *M. asperrima* (c) scallops throughout the DEC in 2010. Circles indicate the survey sites and the colour intensity (white = no scallops) indicates the interpolated relative density 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). Asterisks (*) denote significant difference from a Poisson or a negative binomial distribution ($p < 0.05$). A ^ denotes a significant departure from randomness at $p < 0.05$.

Test	<i>Pecten fumatus</i>	d.f	<i>Equichlamys bifrons</i>	d.f	<i>Mimachlamys asperrima</i>	d.f
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

The size frequencies of the three species of scallops consisted of multimodal distributions and were dominated by large (adult) scallops (Fig. 2.3).

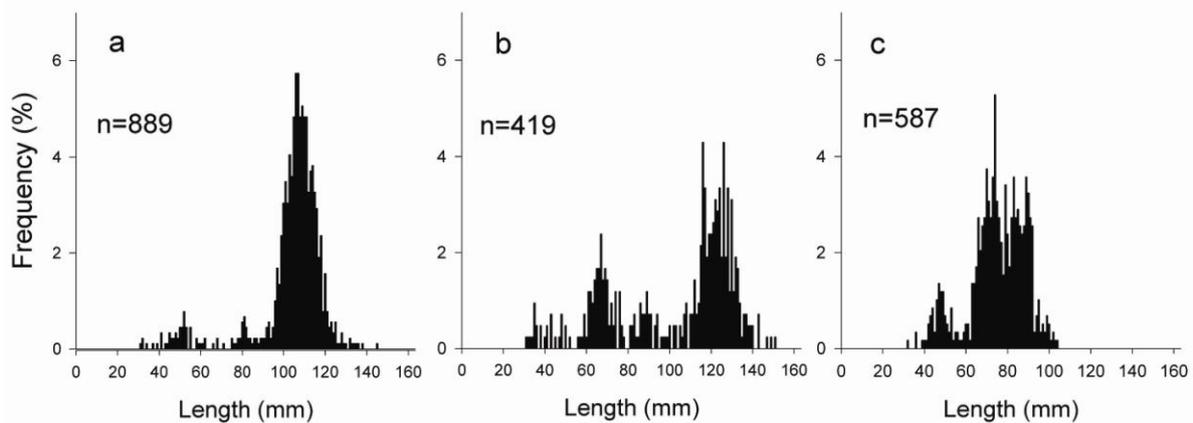


Fig. 2.3. The relative size composition of a) *P. fumatus*, b) *E. bifrons* and c) *M. asperrima* sampled from the 59 sites within the DEC in 2010.

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 *Asterias amurens* was found in 12 sites, mainly in the

north west of Area 1 and in the south of Area 3 with 1 – 39 stars per transect. The sea star *Coscinasterias muricata* was only found in the northern end of the Channel, in six out of the 59 sites surveyed and usually in very low numbers (one site with 28 individuals per transect and the other five with a single individual per transect) (Fig. 2.4 c and d, respectively).

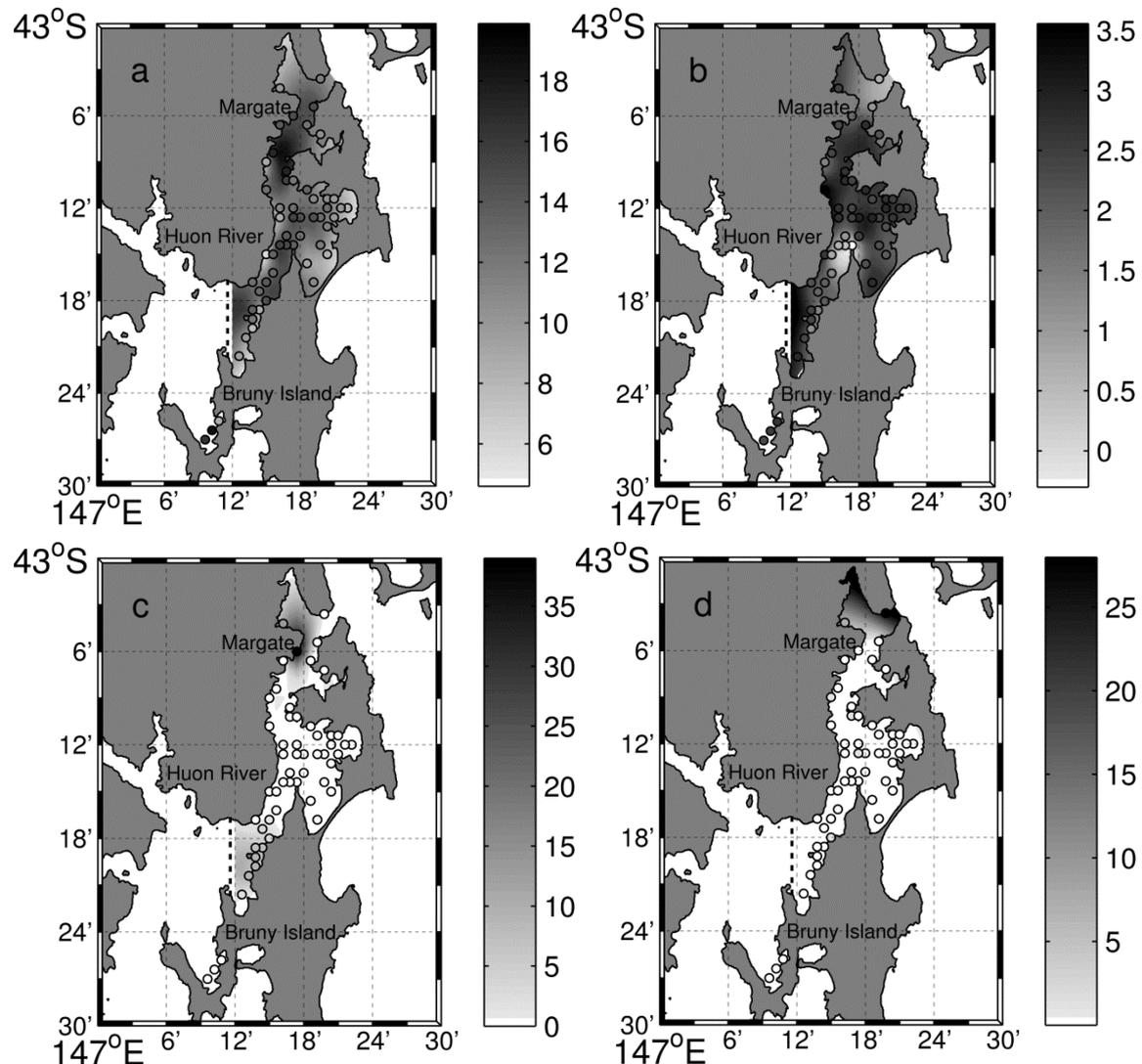


Fig. 2.4. The interpolated values of a) depth in meters, b) mean grain size, abundances (sea stars per 200 m² transect) of *A. amurensis* (c) and *C. muricata* (d) throughout the DEC in 2010. Circles indicate the survey sites and the colour intensity indicates the interpolated relative value. Note density scales vary between 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. Area 3 had more sites

showing medium sponge cover than the other 3 Areas. There was no clear pattern in the distribution of shell cover (Fig. 2.5).

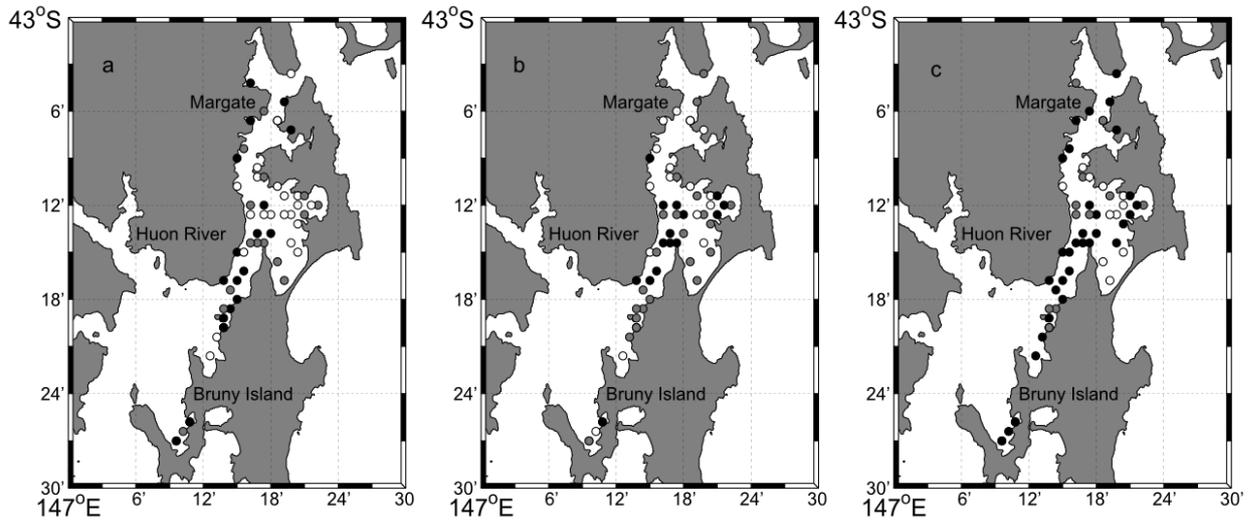


Fig. 2.5. Distribution of main structural components in the DEC: a) sponges; b) shells and c) algae. Circle colours indicate percent cover, with absent (white), low (gray) and medium (black) cover.

2.3.3. Relationship between scallop abundance patterns and explanatory variables

2.3.3.1. Commercial scallop *Pecten fumatus*

Sediment size, depth, *A. amurensis* abundance, shell and macroalgae cover explained 72% of the difference in the abundance of *P. fumatus*. Greatest numbers of the species occurred in areas of fine sand and in depths from 8 – 12 meters (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, *P. fumatus* abundance decreased as macroalgal cover (significant 1st-order contrast $t=-2.41$, $df=1$, $p<0.001$) and abundance of *A. amurensis* increased ($t=-2.29$, $df=57$, $p=0.026$).

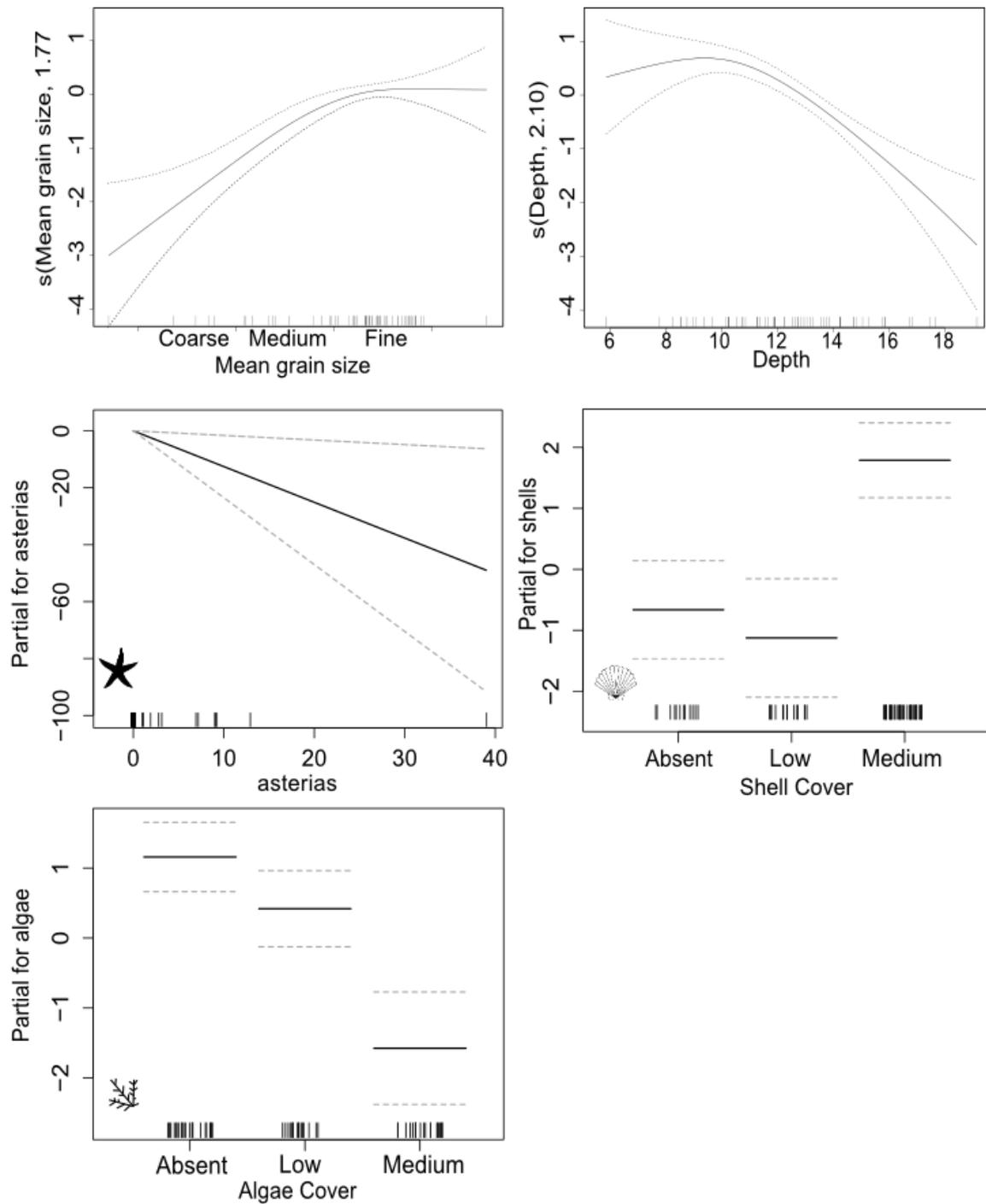


Fig. 2.6. Graphical results of the GAM model fitted to abundance of *P. fumatus*. Only significant variables are shown: a) mean grain size, b) depth, c) *Asterias amurensis* abundance, d) shell and e) algae/seagrass cover. The y-axis shows the relationship between the variable and scallops abundance, with effective degrees of freedom shown in brackets. Dashed lines represent 95% confidence intervals and whiskers on the x-axis indicate data presence.

2.3.3.2. Queen scallops *Equichlamys bifrons*

Mean grain size and algae and seagrass cover explained 68.3% of the variation in abundance of *E. bifrons*. The greatest numbers of *E. bifrons* were present in sites with medium to coarse sand (Fig. 2.7) and greater algae cover (significant 1st-order polynomial contrast, $t=3.37$, $df=1$, $p=0.001$). There was no evidence that depth, shell, sponges or sea star abundance contributed to explaining variation in the abundance patterns of *E. bifrons*.

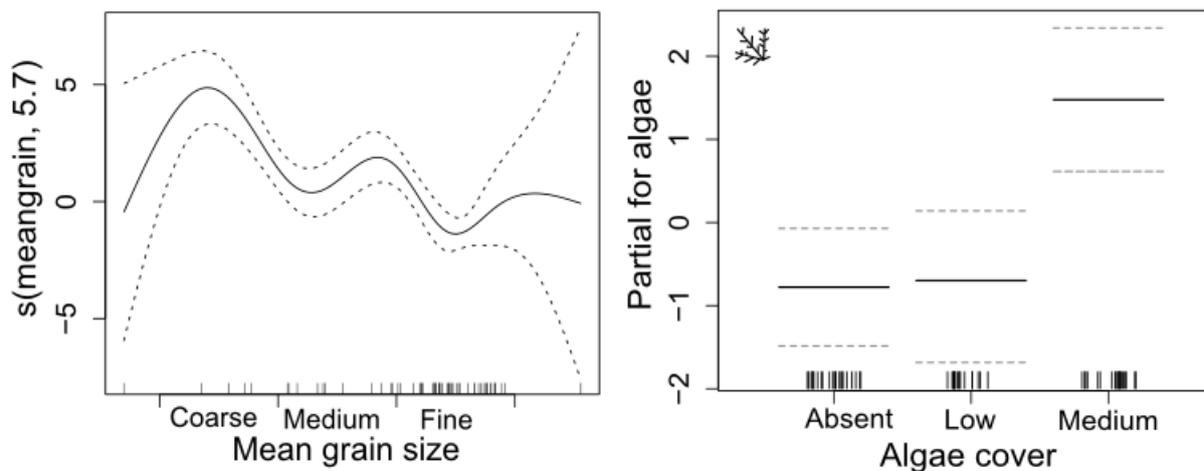


Fig. 2.7. Graphical results of the GAM model fitted to abundance of *E. bifrons*. Significant explanatory variables are a) mean grain size and b) algae/seagrass cover. See Fig. 2.6 for explanation

2.3.3.3. Doughboy scallop *Mimachlamys asperrima*

Mean grain size and sponge cover explained 69.7% of the variation in abundance of *M. asperrima* (Fig. 2.8). Greater numbers were present in fine or coarse sand than in medium sand and the number of *M. asperrima* 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). Neither depth, macroalgae, shells nor sea star abundance contributed to explaining the patterns of variation in *M. asperrima* distribution.

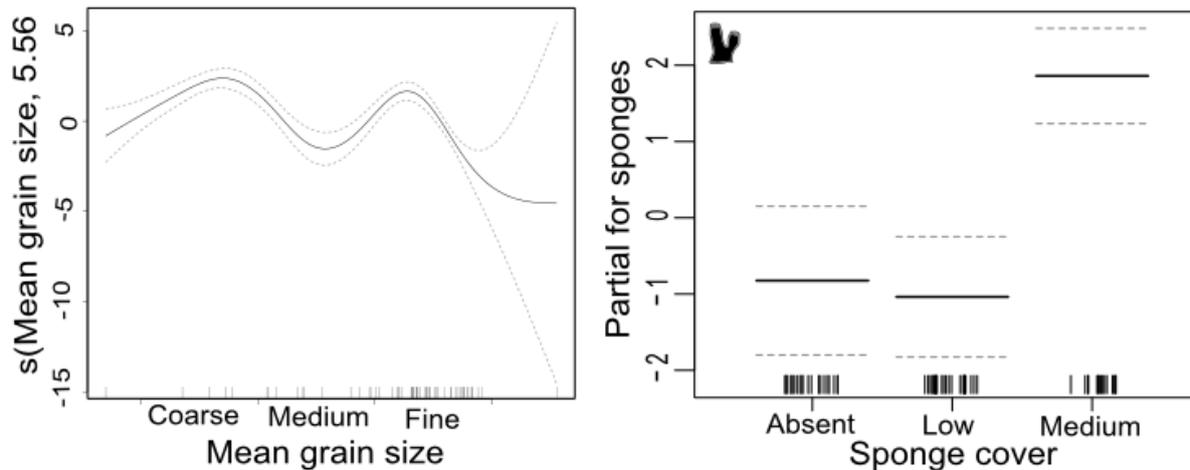


Fig. 2.8. Graphical results of the GAM model fitted to abundance of *M. asperrema*. Significant explanatory variables are a) mean grain size and b) sponge cover. See Fig. 2.6 for explanation.

2.4. Discussion

Within the study area, each of the three scallop species exhibited aggregated rather than random or uniform patterns of distribution; aggregated distributions being typical amongst scallop species (Langton & Robinson 1990, Stokesbury & Himmelman 1993). While the spatial distribution patterns for each species were explained by sediment type, habitat structural components and/or presence of predators, the nature of the relationships between these factors and the distribution patterns differed markedly among species.

Across all species, sediment type significantly explained scallop abundance. The commercial scallop *Pecten fumatus* was more strongly associated with finer sediments, *E. bifrons* with coarse grain sediments, whereas *M. asperrema* had a less selective association with sediment type, possibly because this species is able to use byssal attachment on a wide range of substrates (Zacharin 1995). Habitat preferences are assumed to be adaptive, which means that associations between species and their habitats reflect enhanced survival and reproductive success in these particular habitats (Martin 1998). Differential abundance of bivalves based on sediment characteristics suggests differing refuge properties related to physical properties of the sediment or changes in predator-prey relationships (Lipcius & Hines 1986, Eggleston et al. 1992).

Prevalence of *P. fumatus* in fine sediments suggests 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 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).

While the distribution of *P. fumatus* was negatively associated with macroalgal/seagrass cover, *E. bifrons* had a positive relationship with macroalgal/seagrass cover that may be related to its use of this structural component as a refuge from predation. Predation rates in *E. bifrons* by sea stars have been shown to be lower in seagrass beds compared to bare sand and this is linked to the reduced mobility of sea stars within seagrass compared with over bare sand (Wolf & White 1997). The positive relationship between *M. asperrima* and sponge abundances may be linked to the epizoic association between *M. asperrima* and sponges, including the red sponge (Crellidae family), the yellowish sponge (Myxillidae family), and the purple honeycomb sponge (*Equinochlathria* sp.) (Pitcher & Butler 1987). This association has the benefit that adhesion of the sea star *Coscinasterias muricata* tube feet on the scallop shell is reduced on sponges, effectively protecting the scallops from predation (Chernoff 1987, Pitcher & Butler 1987). To some extent the relationships between scallop abundance patterns and specific habitat characteristics can be explained in terms of the benefits that these relationships afford in reducing predation pressure for each species.

The abundance of *Coscinasteris muricata* did not explain distribution and abundance patterns of scallops. On the other hand, greater abundances of *P. fumatus* occurred where the introduced sea star *Asterias amurensis* was in relatively low numbers or absent. This sea star was first recorded in Tasmanian waters in 1986 (Byrne et al. 1997) and its expansion within the DEC raised concerns about their potential impact on the endemic scallop populations. Outbreaks of this species had detrimental impacts on the shellfish industry in Japan (Hatanaka & Kosaka 1958) and losses of *P. fumatus* spat over a settlement season due to *A. amurensis* predation may be as much as 50% in Tasmania (S. Crawford pers. comm. in (Hutson et al. 2005)). The negative relationship between the invasive *A. amurensis* and the scallop *P. fumatus*, but not the other two species of scallops may be due to habitat-mediated

changes in predation risk (Andruskiw et al. 2008). Vulnerability to predation can vary in a species-specific manner within habitat types even among species that are morphologically and phylogenetically similar (Seitz et al. 2001). For instance, the probabilities of encountering scallops and predation success rates for a related predator, *Asterias vulgaris*, were influenced by particle size (Wong & Barbeau 2003). In the present study, the nature of the relationship between *A. amurensis* and *P. fumatus* abundance is unclear and we cannot rule out preferential habitat use by *A. amurensis* or interactions with other sources of prey, such as the distribution of other epi-benthic bivalves (Ling et al. 2012), as explanatory factors for the sea star abundance.

This study has demonstrated that macroalgae and seagrass, shell and sponge cover have important roles in determining adult scallop distributions. It is uncertain, however, when these distribution patterns are established, whether at settlement and/or as a result of post-settlement processes. Scallop spat have distinct habitat requirements due to their need to attach to structural elements. Therefore, the habitat characteristics associated with settlement might be very different to those observed for the adults as observed by Howarth et al (Howarth et al. 2011) for *Pecten maximus* and *Aequipecten opercularis*. Information is needed about habitat specificity during the attached and unattached stage concurrently to determine whether habitat associations vary ontogenetically and therefore, if specific habitats need to be included in management plans.

This study provides clear descriptions of the relationships between habitat characteristics and species-specific patterns of abundance in three scallop species, with sediment type and habitat structural components being of major importance. These associations do not imply direct causal or functional relationships, however, and the mechanisms or processes behind these associations are not clear. Spatial variation 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 2002b), differential availability of shelter from predation (i.e. habitat complexity) (Tupper & Boutilier 1995), or agonistic interactions with conspecifics or competitors (Sweatman 1985). To understand the underlying mechanisms explaining distribution patterns the various components of recruitment 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 behaviour 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 & Armstrong 1995).

The spatial distribution patterns for the three species of scallops were explained by sediment type, habitat structural components and/or presence of predators, however, the nature of the relationships between these factors and the distribution patterns differed markedly among species. Generating predictive relationships between species and habitat characteristics is important because they provide insight into ecological processes that regulate populations as well as defining those habitat characteristics that need to be considered in developing spatial management and/or restoration plans (i.e. fishing in a way that allows structure to re-establish).

Chapter 3. Early post-settlement mortality of the scallop *Pecten fumatus* and the role of algae mats as a refuge from predation

3.1. Introduction

Early post-settlement survival is one of the main processes determining distribution and abundance patterns of marine invertebrates with pelagic larvae (Gosselin & Qian 1997, Hunt & Scheibling 1997). Mortality during the first days to weeks after settlement is very high, often as much as 90% (see review in Gosselin & Qian 1997). In ascidians and barnacles mortality rates of 38-78% during the first 24 hours after settlement have been estimated (Stoner 1990, Young 1991, Gosselin & Qian 1996). Despite the high mortality documented in marine invertebrates, estimates of early post-settlement mortality for bivalves are scarce and collecting this information is particularly challenging as newly settled bivalves (spat) are very small and cryptic, making detection of any recruitment event in the field difficult. Determining post-settlement mortality in bivalves is important because it greatly impacts recruitment success (Williams 1980; Olafsson et al. 1994; Roegner and Mann 1995; Strasser 2002; Flach 2003).

The main causes of mortality in marine invertebrates are physical disturbance and hydrodynamics, physiological stress caused by non/sub-optimal environmental conditions, predation, and competition (see review in Gosselin & Qian 1997). Predation is the most studied process and generally recognized as an important factor regulating distribution and abundance of newly settled invertebrates (Gosselin & Qian 1997, Hunt & Scheibling 1997, van der Veer et al. 1998). Much of our understanding of predation in bivalves is derived from studies on adults or juveniles (Arsenault & Himmelman 1996, Bologna & Heck 1999, Irlandi et al. 1999), and such estimates cannot be extrapolated to newly settled spat. In bivalve populations, spat and juveniles are most vulnerable to predation until they attain a particular size (Pohle et al. 1991, Garcia- Esquivel & Bricelj 1993). Recently settled scallops (family Pectinidae) are particularly vulnerable to predation because of their thin shells, inability to close shells tightly near the auricles and to keep them closed for prolonged periods of time (Brand et al. 1980, Wilkens 2006). Moreover, scallops have distinct ontogenic 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 & Stotz 2000). Most spat, once reaching a specific size, release the byssus and the unattached juveniles move onto the substrate with a relatively more mobile behaviour (see review in Brand 2006). Thus, 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, however, predation rates for spat and juvenile scallops in the field are essentially unknown.

Complex habitats, such as seagrass, play an important role in the persistence of marine invertebrate populations. Seagrass habitats provide refuge and can dramatically reduce predation rates compared to unvegetated substrata (Prescott 1990, Irlandi 1997, Bologna & Heck 1999, Heck & Orth 2006). Blades of seagrass plants can interfere with the mobility of predators (Wolf & White 1997) and their ability to detect prey visually (Coen et al. 1981, Hemminga & Duarte 2000). As a result, both the encounter rate with prey and the probability of capture upon encounter decrease as seagrass complexity (shoot density) increases (Wong 2013). Although macroalgae also offer a complex habitat with similar advantages for prey avoidance, our understanding of the role of macroalgal cover on the abundance of marine invertebrates is not as advanced as for seagrass. The macroalgae *Caulerpa taxifolia* enhances recruitment and survival of the Sydney cockle *Anadara trapezium* (Gribben and Wright, 2006), while in contrast drifting *Ulva lactuca* mats have a detrimental effect on survival and growth of the clam *Mercenaria mercenaria* (Tyler 2007). Most studies contrast abundance and predation mortality in bivalves between vegetated and unvegetated areas, however, the relationship between the algal biomass levels and bivalve abundance is unknown.

The commercial scallop, *Pecten fumatus*, is an important species in the Australian scallop fishery, supporting significant production since early the early 1900s in the Derwent Estuary and the D'Entrecasteaux Channel, south-eastern Tasmania. Significant depletions of populations of *P. fumatus* have occurred throughout the history of the fishery, resulting in area closures to allow for stock recovery. Despite the commercial importance of *P. fumatus*, there is no information about early post-settlement processes affecting the abundance of this species. Nutgrove Beach, located in the Derwent Estuary, 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 filamentous brown algal mats of *Hinckesia*

sordida, upon which larvae of several bivalves attach, including *P. fumatus*. Spat of *P. fumatus* spat attach to filamentous substrate until they reach a size of approximately 4 mm, after which they tend to release the byssus (Gwyther et al. 1984) and recess into the sediment as juveniles. Algal mats of *Hincksia sordida* appear to be beneficial to scallop recruitment, providing settlement substrate and may further extend this benefit to juvenile stages by providing refuge from predation.

The objectives of the present Chapter were to examine early post-settlement processes that are likely to affect abundance of spat and juvenile *Pecten fumatus* and determine the role of *H. sordida* biomass as a refuge from predation. 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 and growth of juveniles among different macroalgal biomass.

3.2. Materials and methods

Sampling was conducted at Nutgrove Beach, over an area of about 1 ha. (8 – 10 m deep) of sandy bottom. Nutgrove Beach is located in the Derwent Estuary, south-eastern Tasmania (42.90639 S., 147.35170 W.), 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). From 2011 to 2013 over the summer months, these sediments were covered by mats of the brown algae *Hincksia sordida* algae (mean +/- SE 96.9 +/-14.5 g.dry weight algae.m⁻²). Spat of *Pecten fumatus* were defined as 0.4- 4 mm shell height, which are most likely to be attached to structures such as weeds and seagrass (Gwyther et al. 1984), and juveniles as > 4 mm and more likely to have detached and moved to the sediment.

3.2.1. Temporal changes in scallop density and size

Spat and juvenile densities of *Pecten fumatus* were estimated on four occasions during the summer of 2011/12: 30 Dec 2011 (8 replicates), 06 Jan 2012 (5 replicates), 16 Jan 2012 (8 replicates), and 27 Jan 2012 (38 replicates) and on three occasions during the summer of 2013: 13 Jan 2013 (17 replicates), 21 Jan 2013 (10 replicates), and 04 Feb 2013 (22 replicates). Samples were collected by SCUBA divers at approximately 10 meters depth.

Each replicate consisted of a 40.5 x 31.5 cm quadrat (total area = 0.1275 m²) randomly placed on the bottom. Due to the difficulty associated with detecting scallop spat *in situ*, algal mats of *Hinckesia sordida* and the top 1 cm of sediment below the algal mat were 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 then 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 stereo microscope was used to detect scallops (magnification 6.3x) and images were taken of each scallop to estimate height (largest distance parallel to the hinge). Image J software was used to estimate total length (largest distance parallel to the hinge) of all scallops to the nearest 0.05 mm.

3.2.2. Contribution of predation to mortality rates

A predator exclusion experiment was designed to estimate the loss of spat of *P. fumatus* (>0.5 mm total length) due to predation. The experiment was started on the 30 Dec 2011 and lasted 17 days. This short duration was chosen to reduce potential cage artifacts that may contribute to changes in density of the spat, such as sedimentation, algae growth, and changes in density due to new scallop settlement events. The experiment compared the density of spat in four treatments: start of experiment (8 replicates), full exclusion (8 replicates), partial exclusion (6 replicates), and no exclusion (8 replicates). Estimates of spat density were obtained at the start of the experiment on the 30 Dec 2011 and for all other treatments on the 16 Jan 2011. Due to the difficulty associated with detecting and manipulating spat, the numbers of spat estimated at the beginning of the experiment were compared to the numbers of spat in the full exclusion container at the end of the experiment. No differences between these two treatments were found suggesting that no significant mortality had occurred inside our cages. Spat of *P. fumatus* attach to filamentous substrate until they reach a size of approximately 4 mm (Gwyther et al. 1984), therefore it was assumed that any difference in densities between the start and the end of the experiment in the no exclusion plots were due to mortality and not movement of spat.

The first day of the experiment, 8 replicates of 40.5 x 31.5 cm quadrats containing algal mats and associated 1 cm of sediment below the algae were carefully removed as described above and placed in plastic bags underwater for analysis in the laboratory. Using the same techniques, algal mats and associated sediments were placed with a hand shovel into full exclusion cages and partial exclusion cages. Predator exclusion cages were rectangular plastic containers with tight-fitting lids (40.5 cm length x 31.5 cm width x 20 cm depth, Fig. 3.1) positioned on top of the sediment approximately 1 m away from each other. In the full exclusion container, the lid and sides of the container were covered with 500 μ m nylon mesh (Fig. 3.1). The partial exclusion container acted as a cage control as it was the same design as the full cage, but the netting was removed from two sides and the top to allow predators to access the transplanted algal mat and associated sediments (Fig. 3.1). Containers were used to prevent access of potential predators, such as polychaetes, from the sediment. Small fish and rays could forage on spat from above the partial cages while crabs and starfish were observed passing through the openings in sides of the partial cages. The cages were made negatively buoyant using a metal bar secured on two sides. . In the no exclusion treatment, a peg was driven into the substrate at the start of the experiment to mark the area to be sampled at the end of the experimental period. Replicate units were placed haphazardly within the study area. Cages were cleaned of material clogging the mesh *in situ* by divers every three days using a brush. . At the end of the experiment (16 Jan 2012), the no exclusion treatment consisted of 8 replicates of 40.5 x 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 exclusion and partial exclusion containers were placed into plastic bags underwater and sealed, and transported to the laboratory. The algal mats and samples were treated as described above (See *Temporal changes in scallop density*).

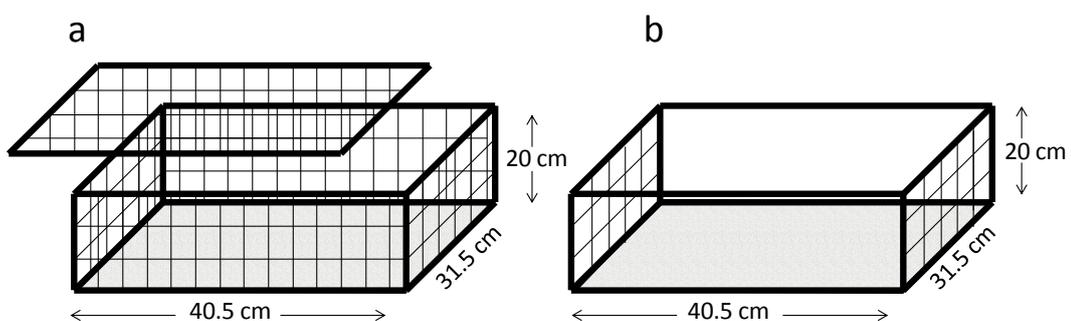


Fig. 3.1. Diagram of a) full exclusion containers and b) partial exclusion container

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. As scallop spat are attached to algae, loss of the algal mat would also result in loss of scallops. To ensure that loss of scallops could be attributed to predation and not due to 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 from the cages. The camera took an image every minute for 24 hours during the first and fifth day of the experiment. These days covered a tidal amplitude of 0.7 m, which was very close to the average tidal amplitude observed in Nutgrove Beach. The time lapse photos revealed no movement of algal mats into or out of the cages, therefore any reduction of scallops in the partial exclusion treatment was attributed to predation.

Although cages can induce experimental artefacts such as altered prey or predator behavior, altered water flow, and settlement patterns (Peterson 1979, Hall 1990, Miller 2007), they are still recognized as the most reliable way of assessing predation, provided that the experimental design and analysis are rigorous (Hall 1990, Beseres & Feller 2007). 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. As the partial exclusion cages mimic the 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. There was no evidence of cage artefacts in this study.

3.2.3. *Relationship between scallop abundance and biomass of *Hincksia sordida**

The relationship between biomass of *H. sordida* and scallops was assessed for spat and juveniles separately by comparing scallop densities and sizes across a range of algal dry weights. Samples collected on 30 Dec 2011 and 06 Jan 2012 were used to assess the relationship between spat and algal biomass for 2012, whereas samples from 27 Jan 2012 were used for juveniles. In 2013, samples from 21 Jan 2013 and 04 Feb 2013 were used to estimate the relationship between spat and algae and 13 Jan 2013 was used for juveniles. Algae were oven dried for 48 hours at 60 °C and then weighed to estimate dry weight. The differences between sampling dates in each year

3.2.4. Mortality and growth of juvenile *Pecten fumatus*

Two tethering experiments were undertaken to assess rates of predation and growth in juvenile scallops in ‘algal plots’ of differing algal biomass, one during January/February 2012 and the second during January/February 2013. Juveniles were collected from the study site and supplemented with juveniles collected using mesh bag spat collectors located off Eastern Tasmania and kept in aquaria until tethered. Each algal plot covered an area of 2.25 m² and between 24 - 31 juvenile (detached) scallops measuring from 4.6 - 24.4 mm were tethered individually to metal pins (15 cm long) which were inserted into the algal mat or the soft sediment, depending on algal cover. In 2012, six plots with varying amounts of algal biomass were assessed (ranging from 4.8 to 102.9 g dry wt.m⁻² of algal biomass), while in 2013 ten plots were studied (15.6 to 226.5 g dry wt.m⁻²). These levels were dependent on the actual algal biomass observed in the field, as we chose the plots underwater and tried to cover the greatest range of algal biomass. No bare sand plots were included for the experiment as the entire study area was covered by at least some strains of *H. sordida*. The plots chosen both years were placed inside an area of roughly 50 x 50 m.

The shell of the tethered scallops was cleaned and dried with absorbent tissue before a piece of 0.7 kg bracking strain monofilament was glued using cyanoacrylate (SuperGlue®) to the top valve, about 3 mm away from the umbo, to ensure that the valves were not glued together. Monofilament tethers were >15 cm to ensure that the scallop could easily move around within the plot. Each tether was attached to a numbered rectangular plastic label (2.5 x 4 mm) for scallop identification and then tied to a gardening mat pin. Images of each scallop were taken and then the software Image J was used to estimate scallop length to the nearest 0.05 mm. Survival of tethered scallops was assessed after 1, 3, 6, 10 and 14 days in 2012 and 3, 5, 8, 10 and 14 days 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). For the present study broken shells were assumed to be remains of scallops eaten by crabs and fish and clappers were assumed to be eaten by starfish (Stokesbury & Himmelman 1995). All scallops alive at the end of each experiment (day 14) were taken back to the laboratory and measured to estimate growth. To obtain estimates of mortality associated with tethering, each year five tethered scallops were placed in each one of three predator exclusion cages located inside the area of

the experiment. All tethered scallops survived the experimental period providing evidence that mortality of the tethered scallops placed on algal mats or soft sediments could be attributed to predation rather than an artefact of tethering or other natural causes such as disease or high temperatures, as these scallops would have been exposed equally to such factors.

The density of potential scallop predators was estimated by counting the number of all potential scallop predators (fish, rays, crabs, starfish) along six 30 x 2 m transects surveyed on the 20/01/12 and the 21/01/13 in the areas surrounding the tethering experiments. Potential predators included flathead (Platycephalidae), leatherjackets (Monocanthidae), rays (Urolophidae), porcupine fish (Diodontidae), toadfish (Tetraodontidae) and crabs (Cropp & Davidson 1988, Ambrose & Irlandi 1992, Barbeau & Scheibling 1994). To identify actual 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 in total length) in microhabitats with contrasting algal biomass. This was done on three occasions during 2012 (01/03/12, 06/03/12m and 12/03/12) and twice during 2013 (26/01/13 and 04/02/13). A single photograph was taken every minute for 46 hours, and image sequences spanned 23 hours from midnight to 2300h. The camera was equipped with red lighting to minimize disturbance of scallops and attraction of predators during the night (Veale et al. 2000).

3.2.5. *Statistical analyses*

Scallop densities were converted to number of individuals per m² prior to data analysis. Analysis of variance was used to assess if there were any differences in scallop densities over time in each year, differences between treatments in the predator exclusion experiment, and differences in average size of tethered scallops among different amounts of algal biomass in each year. 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).

To describe the relationship between algal biomass and scallop density each year, scallops were divided *a priori* into two groups for analysis: spat and juveniles. Either a linear regression model or a generalised additive model (GAM) was used. The GAM was fitted using the `mgvc` package from R (Wood 2006, R Development Core Team 2010). Explanatory variables were selected if significant ($p < 0.05$). Due to the tendency of GAM to over-fit, the basis dimension parameter k was set to a maximum of 8 to correct for over-fitting without compromising the model (Wood 2006). Model selection was based on Generalized Cross Validation (GCV) (Wood 2006), percentage deviance explained, and visual examination of residuals. To examine the relationship between *H. sordida* biomass and scallop sizes for spats and juveniles, a multiple linear regression model was used to assess the effect that density of scallops and algal biomass had on the scallop sizes. 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).

Mortalities of tethered scallops were treated as censored data (data for which the outcome is only partially known) and analyzed with the Cox proportional hazard model using algal biomass and size of scallops as covariates (Cox 1972) using the penalized spline to estimate the parameters in the model (Gray 1992). Variables were added and removed by stepwise selection using the Akaike's information criterion implemented in R (version 2.12.1). A χ^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 or fish (crushed shells). As none of the scallops in the exclusion cages were lost from the tethers, missing scallops 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 χ^2 was used to evaluate the goodness of fit of the model. Relative growth rates were estimated as the difference in shell length at the beginning and at the end of the tethering experiment, divided by the initial length and by the duration (in days) of the experiment. Variability of relative growth rates were examined as a function of *H. sordida* biomass using a linear regression where more than one value of Y is present for each value of X (Sokal & Rohlf 1969). An initial ANOVA

showed no significant differences in shell length for scallops located in different plots for 2012 and 2013 ($F = 0.271$, $df 5$, $p=0.928$ and $F = 1.72$, $df 9$, $p=0.08$, respectively). All statistical analyses used 0.05 as the critical probability level.

3.3. Results

3.3.1. Temporal changes in scallop density and size

There was a significant decline in the densities of scallops in 2011/12 ($F=7.94$, $df 3$, 52 , $p<0.001$). Over the 28 day study period there was a 72% reduction in average density on algal mats (Fig. 3.2). At the start of the experiment, on the 30/12/11, spat ranged from 0.4-3.6 mm in shell length with individuals predominantly 2-3 mm long (Fig. 3.3). After seven days, the surviving spat had grown as all scallops measured were 3-5 mm long and after 17 days, only four scallops were found and they were 2-5 mm long. Four weeks after the beginning of the experiment the average length of the scallops was 8.26 ± 0.35 mm ($\pm SE$).

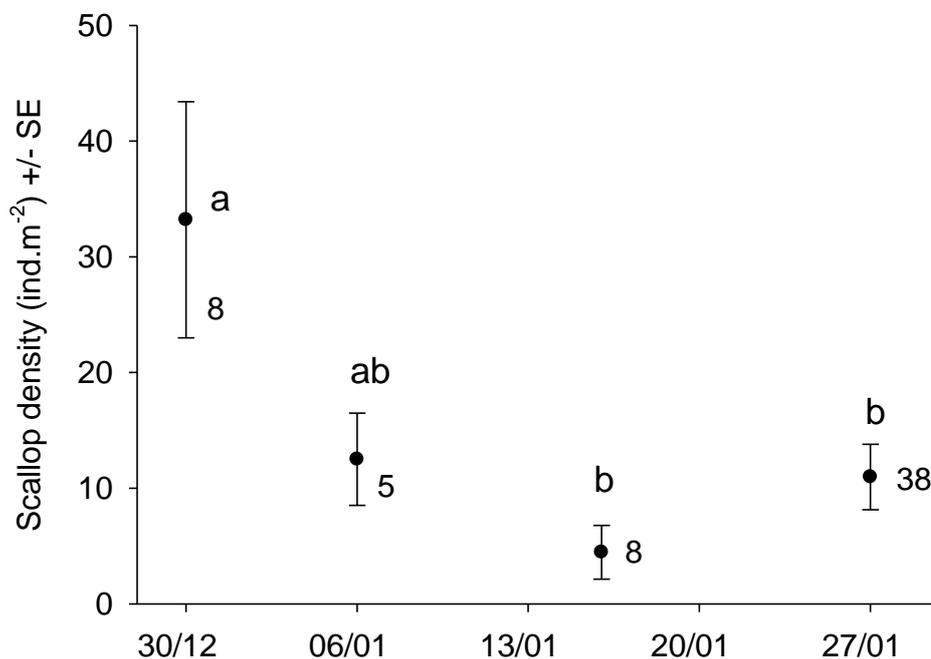


Fig. 3.2. Mean scallop density at Nutgrove Beach, Tasmania over four weeks in 2012. The mean densities on sampling days with different letters are significantly different from one another. Error bars represent standard errors (SE) and numbers next to the bars represent the sample size on each occasion.

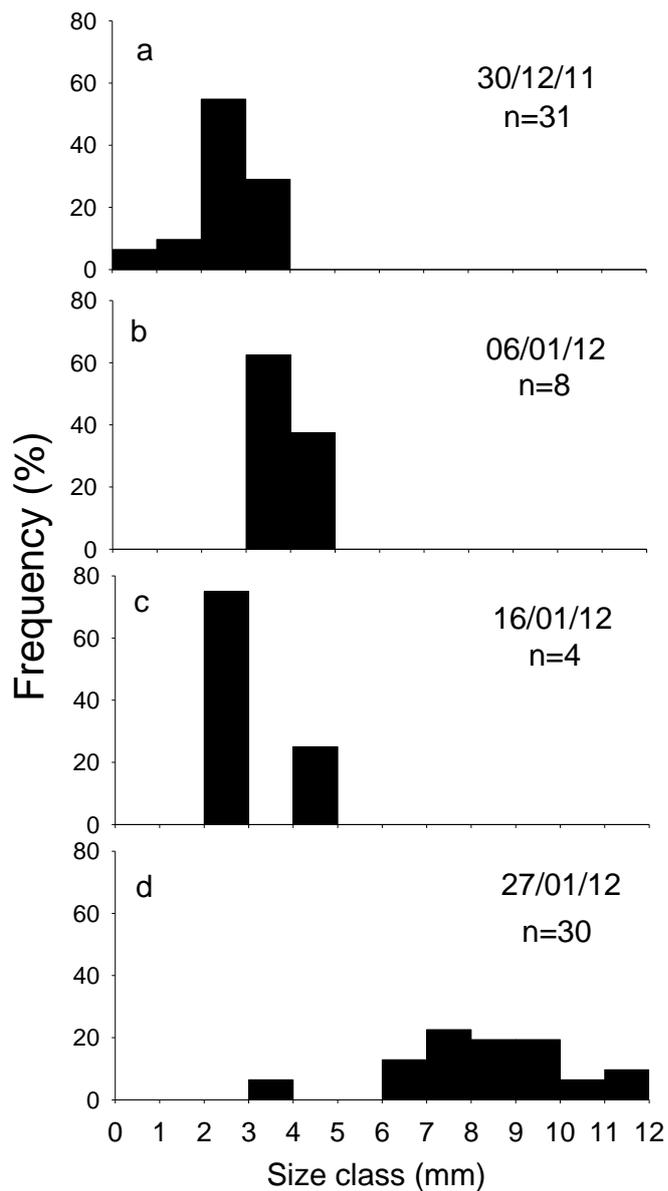


Fig. 3.3. Size frequency distribution of commercial scallop *P. fumatus* at a) start of experiment on 30.12.11; b) after seven days; c) after 17 days, and d) after 28 days; n = number of scallops measured on each sampling date.

No significant change in scallop densities was detected over the study period in 2013 ($F=1.85$, df 2,54, $p=0.168$), however, the size frequency distribution in this year suggested that this stability in scallop density though time was related to a recruitment event that occurred around January 21st 2013 (Fig. 3.4). Scallop density was re-calculated using only scallops > 4 mm long and this revealed a significant decrease of 95% in density for this size group over 22 days (Fig. 3.3, $F=9.00$, df 2, 22.9, $p=0.001$). At the beginning of the experiment, on the 13/01/13, scallops measured 2-11 mm (Fig. 3.5). After eight days, only a

few spat > 8 mm long were found and 70% of the scallops measured were 1–4 mm, indicating a possible new recruitment event. Fourteen days later, only 5% of the scallops found were > 4 mm, while 95% were 0.9–3.6 mm in length.

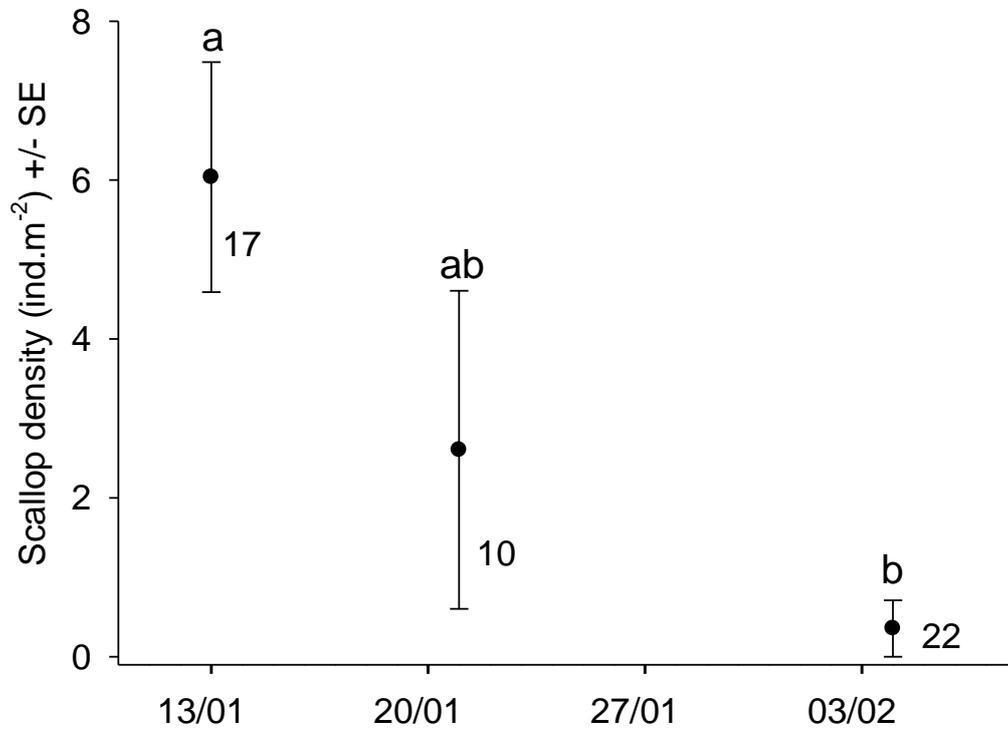


Fig. 3.4. Mean scallop density at Nutgrove Beach, Tasmania over 22 days in 2013. The mean densities on sampling days with different letters are significantly different from one another. Only scallops > 4 mm in length were used to in this analysis. Error bars represent standard errors (SE) and numbers next to the bars represent the sample size on each occasion.

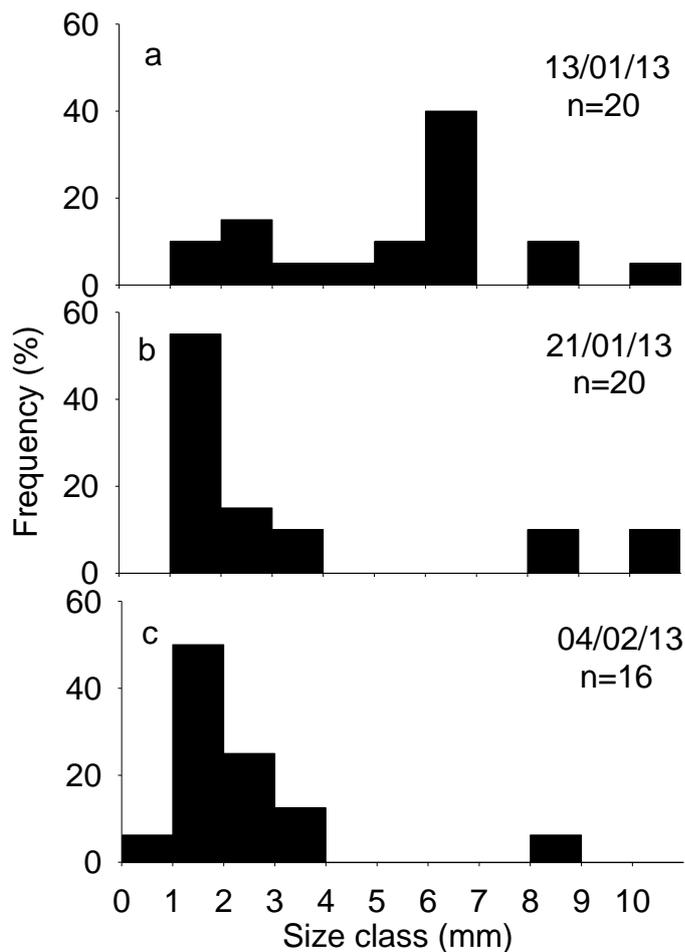


Fig. 3.5. Size frequency distribution of commercial scallop *P. fumatus* in a) beginning of experiment, b) after eight days; c) after 22 days. n = number of scallops measured on each sampling date.

3.3.2. Contribution of predation to mortality rates

The average densities of scallops significantly differed among treatments ($F=6.45$, df 3,26, $p=0.002$). The partial exclusion and no exclusion treatments had approximately 85% fewer scallop spat than the full exclusion treatment (Fig 3.6). In contrast, the full exclusion treatment at the end of the experiment had densities of scallop spat similar to that observed at the start of the experiment. There was no evidence of cage artefacts, as scallop densities were similar in the partial exclusion and the no exclusion treatments (Fig. 3.6).

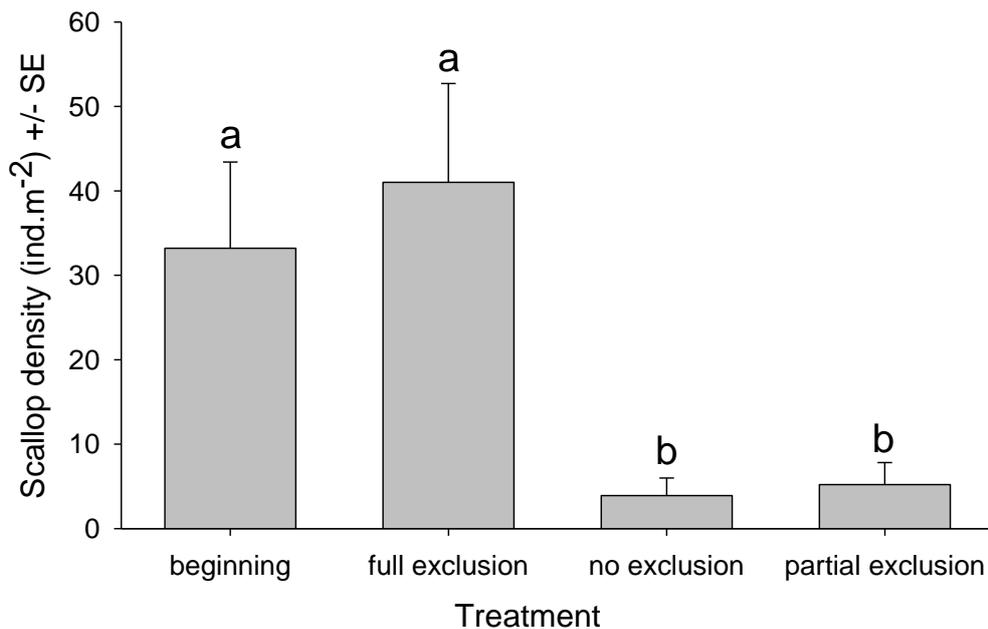


Fig. 3.6. Density of scallops.m⁻² at the beginning of the experiment on 30 Dec 2011, and full exclusion (no predators present), no exclusion and partial exclusion (cage control) treatments at the end of the experiment on 16 Jan 2012. Treatment means with different letters are significantly different from one another. Error bars represent standard errors (SE).

3.3.3. Relationship between scallops abundance and *Hincksia sordida* biomass

In 2012, no significant relationship was found between *H. sordida* biomass and spat density (Fig. 3.7 a&b; $F=3.025$, $df\ 1,11$, $p=0.109$). *Hincksia sordida* biomass explained 31.2% of the deviance in juvenile scallop density (Fig. 3.7a; $F=2.752$, $edf\ 3.40$, $p=0.0461$). Scallop densities increased as algal biomass increased up to a threshold of approximately 80 g dry wt.m⁻², peaking at 48 juveniles.m⁻². Densities then decreased in algal biomasses of 80-180 g dry wt.m⁻² before increasing again with algal levels > 200 g dry wt.m⁻² (Fig. 7.6b). In 2013, no significant relationship was found between *H. sordida* biomass and spat density (Fig. 3.7c; $F=0.868$, $edf\ 2.169$, $p=0.462$) or juvenile density (Fig. 3.7d; $F=0.3$, $edf\ 1.319$, $p=0.687$).

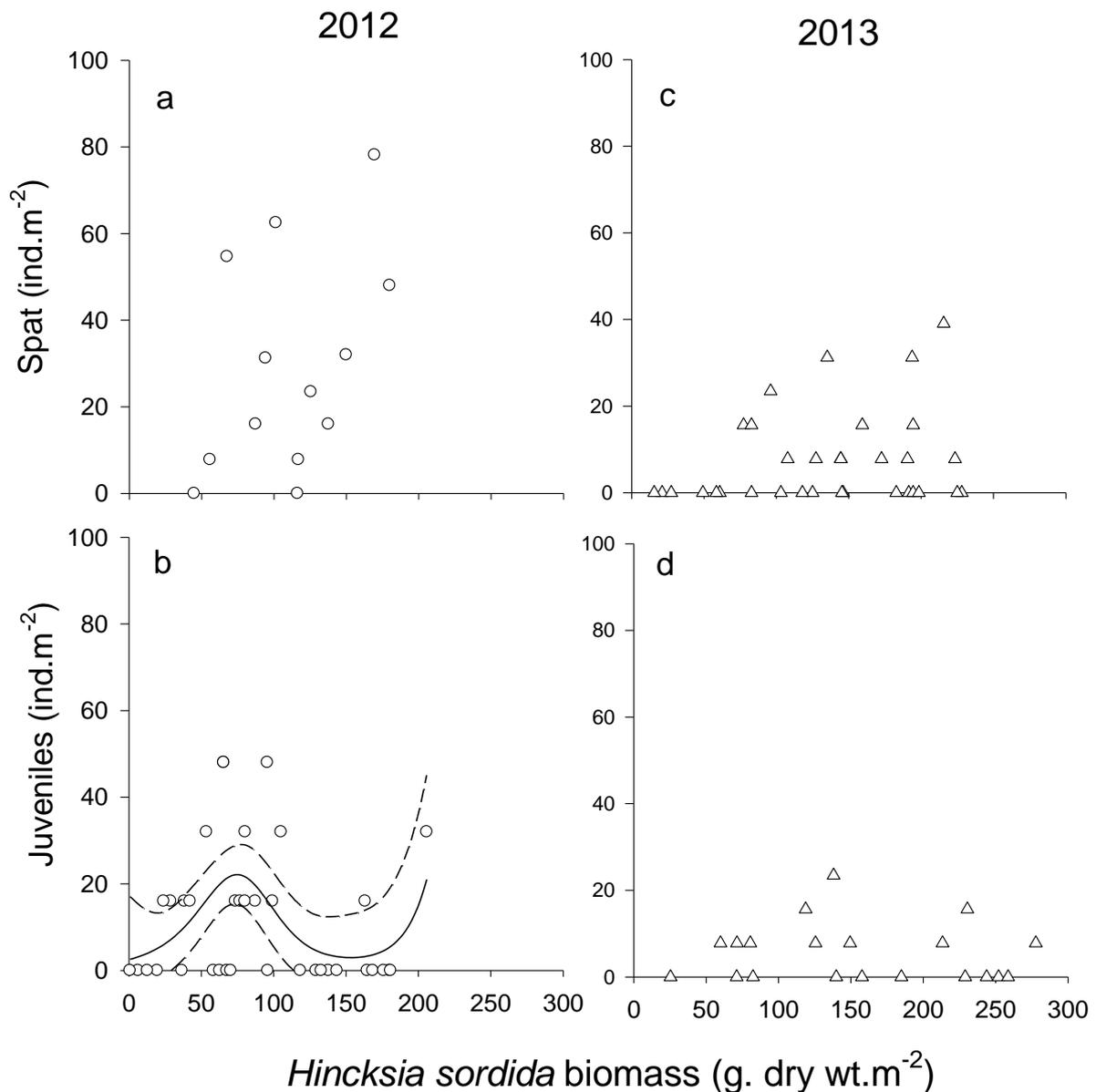


Fig. 3.7. Relationship between *Hincksia sordida* biomass and scallop densities. a) Scallop spat in 2012 (n=13); b) scallop juveniles in 2012 (n=37), c) scallop spat in 2013 (n=33) and d) scallop juveniles in 2013 (n=20). n equals number of sampling replicates. Fitted lines (solid) and confidence intervals (dashed) from the generalized additive model are shown when a significant relationship was found.

No significant relationship between spat size and *H.sordida* biomass was evident in 2012 (Fig. 3.8a; $F=1.69$, df 1,35, $p=0.202$) or 2013 (Fig. 3.8c; $F=0.359$, df 1,31, $p<0.553$). Smaller spat sizes were related to greater scallop densities in both years ($F=14.3$, df 1,35, $p<0.001$ and $F=13.23$, df 1,31, $p<0.001$, respectively), and this relationship is probably explained by greater numbers of scallops arriving to the mats and gradually being subjected

to mortality. No significant relationship between juvenile scallops and *H. sordida* biomass was detected for 2012 (Fig. 3.8b; $F=1.54$, $df\ 1,27$, $p=0.224$) or 2013 (Fig. 3.8d; $F=0.262$, $df\ 1,8$, $p=0.622$).

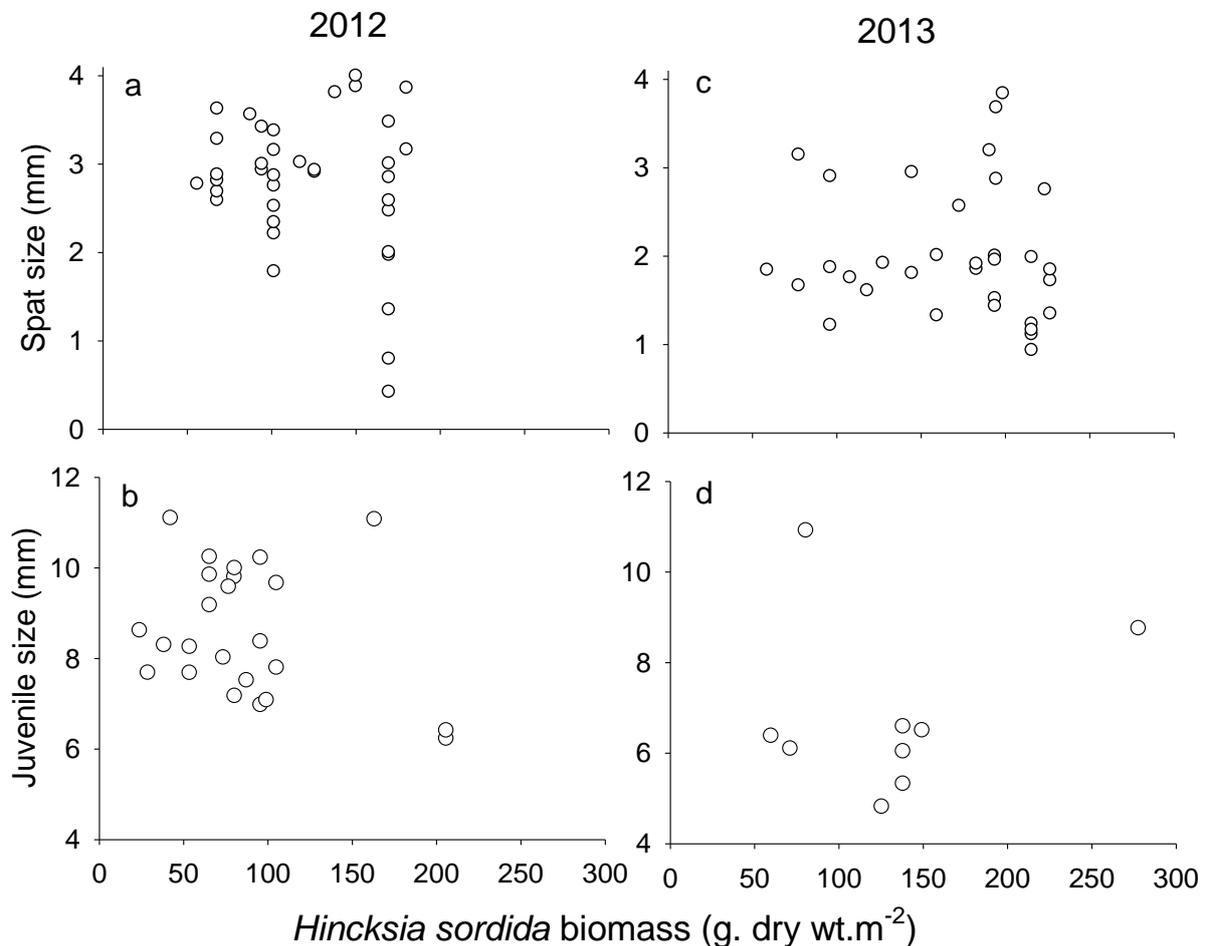


Fig. 3.8. Relationship between *Hincksia sordida* biomass and scallop size. a) Scallop spat size in 2012; b) scallop juveniles in 2012; c) scallop spat in 2013, d) scallop juveniles in 2013. No significant relationship was found.

3.3.4. Mortality and growth on *Hincksia sordida*

There was strong evidence of a difference in the rates of mortality between years ($\chi^2=44.1$, $df\ 1$, $p<0.001$). In 2012, 40% of the mortality occurred in the first three while in 2013, more than 80% of the mortality occurred in the first three days of the experiment (Fig. 3.9). The risk of dying in 2013 was 2.3 times greater than in 2012 ($Z=5.911$, $df\ 2$, $p<0.001$, Fig. 3.10). In 2012, there was a significant effect of algae on the relative risk of dying (Fig. 3.10; $\chi^2=11.49$, $df\ 1.96$, $p<0.003$). The relative risk of dying increased from 4.8 towards 23 g

H. sordida, decreased towards 72 g of algae weight and then increased again until algal biomass reached 102 g. dry weight biomass (Fig. 3.10). Size (total length 5.1 – 24.4 mm) did not influence the risk of dying ($Z=0.78$, $df\ 2$, $p=0.67$). In 2013, no significant effect of size or algal biomass on the risk of dying was evident ($Z=2.89$, $df\ 2$, $p=0.235$).

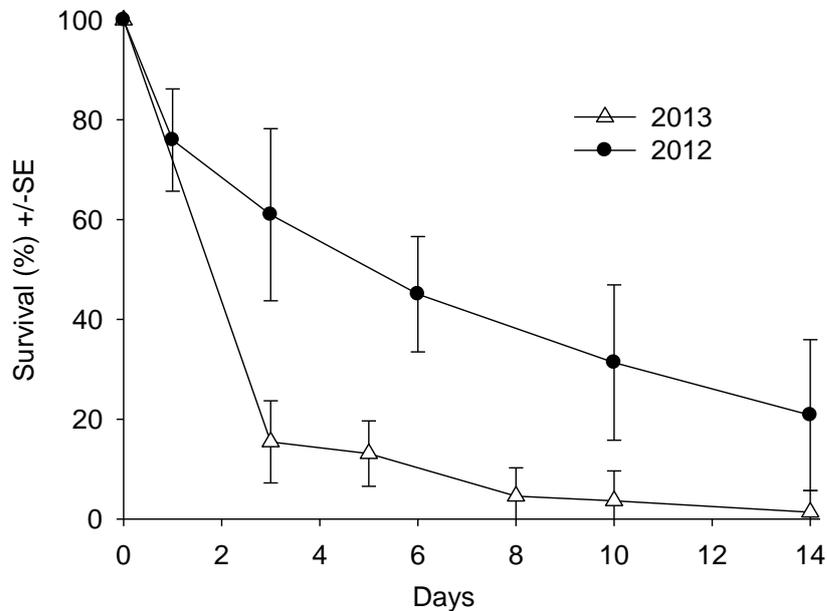


Fig. 3.9. Changes in the average survival of tethered scallops with the number of days that they were tethered for in 2012 ($n=6$ algal plots, total number of scallops = 151) and 2013 ($n=10$ algal plots, total number of scallops=221). Error bars represent standard errors (SE).

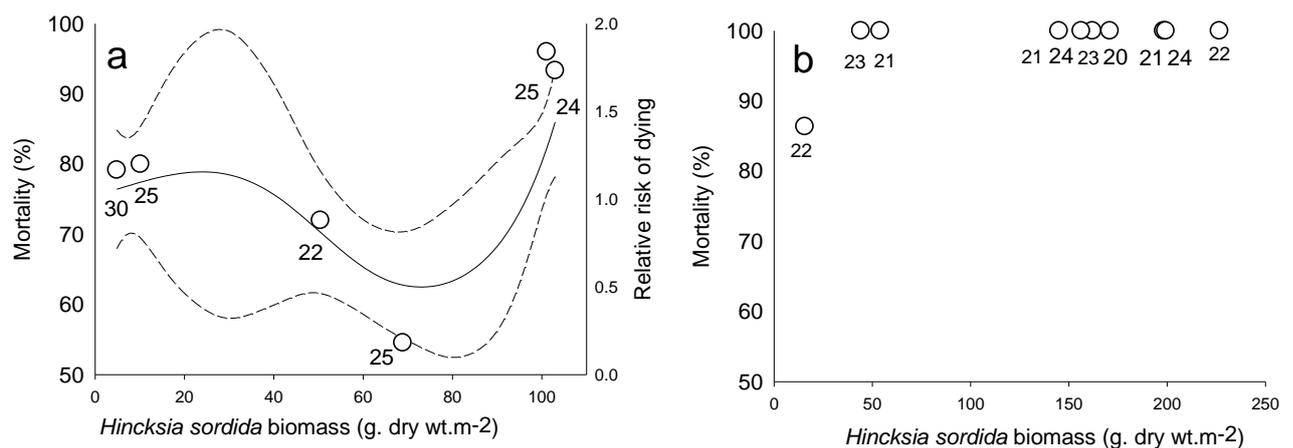


Fig. 3.10. Mortality (% , circles) of juvenile scallops on *Hincksia sordida* biomass during tethering experiments in a) 2012 and b) 2013. Fitted line (solid) and 95% confidence intervals (dashed) show the relative risk of dying on *H. sordida* biomass estimated from the Cox model. In 2013, the relative risk of dying could not be explained by algae or scallop size, therefore no model was fitted.

Potential predators considered capable of crushing the valves of the scallops included the banded stingaree *Urolophus cruciatus*, flathead *Platycephalus* sp., ringed toadfish *Omegophora armilla*, and spider crab *Leptomithrax gaimardii*. Although spider crabs were not observed during transect surveys, once in 2012 an aggregation of approximately 20 crabs per m² was observed in the study area. The only species of starfish observed was the invasive northern Pacific starfish *Asterias amurensis*. There was no significant difference in the densities of *Platycephalus* sp. (F=0.024, df 1,17, p=0.88) or *U. cruciatus* (F=0.86, df 1,17, p=0.367) between 2012 and 2013 (Fig. 3.11). Densities of *A. amurensis* were not compared between the years, because in 2013 almost exclusively only recruits < 20 mm in length were recorded, while in 2012 only adults were found.

Time-lapse photography identified one predator, the ringed toadfish *Omegophora armilla*. This species crushed the scallops, leaving only broken pieces of shells behind, and was observed to forage in sandy bottoms and in plots covered by different amounts of algal cover. The scallops consumed ranged from 5-24 mm in length.

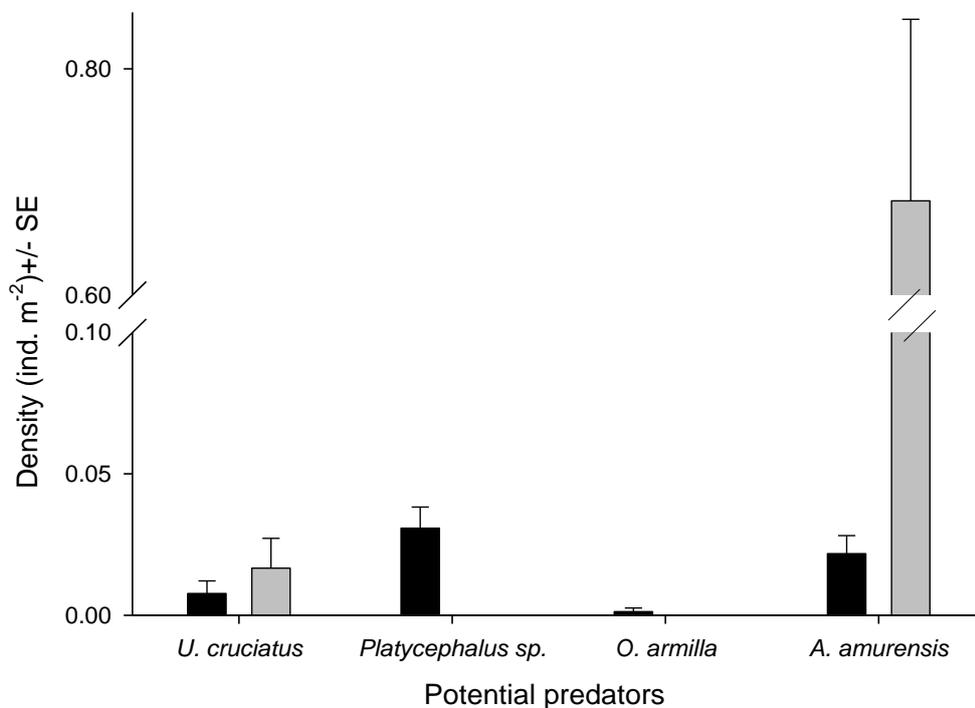


Fig. 3.11. Density of potential predators observed during transect counts in 2012 (black bars) and 2013 (gray bars).

Predation by crabs and fish occurred three times more often than by starfish ($\chi^2=46.83$, df 2, $p<0.001$). For every increase in 1 mm in scallop length, 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 ($Z=3.10$, df 1, $p=0.001$). The probability of being eaten by starfish or crabs and/or fish, did not differ between years ($Z=1.82$, df 1, $p=0.069$) or between levels of algal biomass ($Z=-1.25$ df 1, $p=0.210$).

Relative growth of the scallops was negatively affected by algal cover ($F=7.94$, df 1, 6 $p=0.030$), however, only 33% of the variability in relative growth is explained by algal biomass (Fig. 3.12).

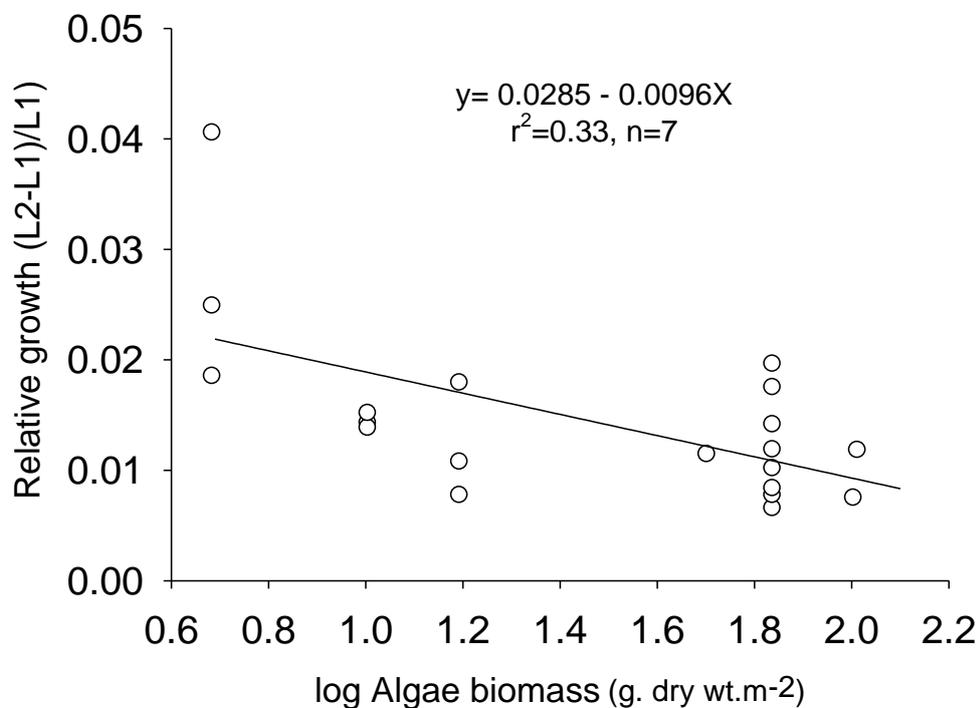


Fig. 3.12. Relationship between the *Hincksia sordida* biomass and relative scallop growth.

3.4. Discussion

Predation on spat and juveniles is a major factor affecting local population sizes of commercial scallop *P. fumatus*; mortality rates of up to 95% during the first weeks after settlement appeared to have prevented the establishment of an adult population at our study site. In fact, fewer than five adult scallops were observed in the study area despite considerable dive effort over two years (>40 hours searching). These findings highlight the

importance of predation in regulating recruitment success to adulthood as observed in other bivalve populations (Beukema et al. 1998, Flach 2003, Shank et al. 2012).

Mats of the macroalgae *Hinckesia sordida* acted as settlement substrate for *P. fumatus* spat. In other scallop species, filamentous algae also provide substrate for larvae settlement (Harvey et al. 1993, Cantillánéz 2000), as well as providing a refuge from predation (Pohle et al. 1991), enhancing growth due to the elevated position in the water column (Eckman et al. 1989), and avoidance of smothering of spat in soft sediments (Merrill & Edwards 1976). While no significant relationship between spat density and algal biomass was evident, no spat were recorded in areas where the biomass of *H. sordida* was less than 50 g dry wt.m⁻². The reasons for the apparent lack of spat at lower algal biomass are not clear and warrant further examination to determine whether there is a minimum threshold of algal biomass for effective spat settlement.

The expectation that structural complexity in the habitat, specifically increasing levels of algal cover would provide greater protection from predation than areas with less algal cover to juvenile scallops was not evident in our study. Tethering trials indicated that in 2012, at algal levels greater than 100 g dry wt.m⁻², mortality rates were consistently above 93%, whereas at low levels of biomass (4.8 – 68.8 g dry wt.m⁻²), mortality rates were highly variable but consistently lower, ranging from 54-80%. During 2013, at algal levels greater than 44 g dry wt.m⁻², mortality rates were 100%, whereas at 15 g dry wt.m⁻², the mortality rate was 86%. This finding is perhaps unexpected given the capacity of macrophytes to provide protection from predators (Heck Jr & Thoman 1981, Hovel & Lipcius 2001, Adams et al. 2004). For instance, seagrasses provide protection from predation compared to bare sand areas for the closely related *E. bifrons*, a scallop species co-occurring with *P. fumatus* (Wolf & White 1997). The higher mortality rates of *P. fumatus* juveniles in more complex habitats may be influenced by the escape tactics used by this species not matching the physical structure of the habitat (Lima 1993). *Pecten fumatus* juveniles and adults display a semi-burying or recessing behavior, in which the upper valve is level with or just below the surface of the sediment (Brand 2006). Recessing provides protection from both visual and non-visual predators and does not interfere with active predator escape responses such as swimming (Minchin 1992, Brand 2006). Faster growth of juvenile *P. fumatus* in sand compared to algae supports this observation, as selection for a particular substrate is likely to have evolved from substrate benefits gained such as refuge from predation and access to food

(Pohle et al. 1991, Moksnes et al. 1998, Kamenos et al. 2004, Pacheco & Stotz 2006). Predation on *Pecten maximus*, which also displays recessing behavior, is reduced when spat leave sites of byssal attachment and start to recess (Buestel & Dao 1978). Thus for species that recess, areas of dense algal cover may hinder this behaviour and result in greater vulnerability to predators. While earlier research suggested that increasing vegetation density has a positive effect on prey survival (Nelson 1979, Heck et al. 1981, Nelson & Bonsdorff 1990) recent studies question this paradigm and suggest that the impact of vegetation on prey survival depends on relative densities of interacting organisms at each vegetation level and predator traits such as foraging tactics (James & Heck 1994, Grabowski 2004, Mattila et al. 2008, Horinouchi et al. 2009, Scheinin et al. 2012). Ryer (1988) proposed that only when spaces between the leaves matched the size of the prey did a substantial refuge exist. In this regard, the nature of *H. sordida*, which has filaments that intertwine to form mats might have precluded spaces large enough for scallops to get into especially at the higher levels of biomass. Therefore, predator traits, prey behavior as well as the characteristics of the submerged vegetation appear to be important in determining prey survival.

Predation rates varied greatly between years but could not be explained by the abundance of potential predators and even the substantial increase in densities of the starfish *A. amurensis* (a known predator of *P. fumatus*) in 2013 did not alter the proportion of scallops eaten by starfish between years. This may be a function of differences in starfish size, predominantly adults in 2012 whereas in 2013 they were mostly juvenile recruits. However 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 & Hixon 1995, Kinoshita et al. 2013). Also, predator foraging rates can be affected by prey density levels (Hines et al. 1997, Knights et al. 2012): the settlement event detected in 2012 had an average of 33.2 ind.m⁻², the one detected in 2013 had an average of 13.0 ind.m⁻². Additionally, the levels of biomass of *H. sordida* encountered at the time of sampling were greater for 2013 than 2012. This may involve greater areas of dense algal cover which may affect the probability of *P. fumatus* to find a suitable sand substrate to recess. Also, predators can alter their behaviour in response to spatial patterning in seagrass habitats, for example, increased exposure associated with patchy seagrass beds might alter predation rates on scallops (Irlandi et al. 1995; Bologna and Heck 1999; Irlandi et al. 1999; Carroll et al. 2012). The role of density of scallops and algal spatial patterning on predation mortality were not assessed in this study and require further research.

Scallop size had an impact on the likelihood of being eaten by each of the specific predator groups, a finding consistent with previous laboratory studies (Barbeau & Scheibling 1994). Specifically, the probability of predation by starfish decreased with increasing scallop size, and this is most likely related to size-related differences in prey vulnerability, as capture upon encounter success is greater for starfish feeding on small scallops (5-8.5 mm) than on bigger ones (10-25 mm) (Barbeau & Scheibling 1994). In contrast, the probability of being eaten by crabs and/or fish increased with scallop size. Again, predator behaviour could explain this result, as crabs actively select bigger scallops (Barbeau & Scheibling 1994). Therefore, predator ensembles and their associated prey size preferences are likely to be important determining the predation risk associated to a particular ontogenetic phase in the scallop prey.

While predation rates were identified as an important factor affecting the survival of spat and juveniles of *Pecten fumatus*, the lack of information about optimal initial densities of spat necessary to sustain a population precludes the assessment of the relative contribution of pre-settlement versus post-settlement factors affecting recruitment. Limited larval numbers might be responsible for the patterns of population abundance, as suggested for *Argopecten irradians concentricus* in North Carolina (Peterson and Summerson 1992) and for *Argopecten irradians irradians* in Long Island, New York (Tettelbach et al. 2013). A series of observations and manipulative experiments examining mechanisms underlying recruitment success at intra and inter-annual scales such as larval supply, habitat selection and habitat and density-dependent mortality are required to understand which factors regulate the dynamics of adult populations in marine organisms with pelagic larvae (Doherty 1981; Gaines and Roughgarden 1985; Eggleston and Armstrong 1995; Menge 2000; Moksnes 2002).

Tethering techniques can be useful to infer the fate of individual organisms, especially when information on predator behaviour is available (Barbeau et al. 1994). Tethering is generally used to compare predation rates of mobile organisms between sites or habitats, however, tethering influences normal behaviour of prey, making it more vulnerable to specific predators (Barbeau and Scheibling 1994) and in some cases even vulnerable to predators that would not otherwise succeed in an attack on an untethered prey (Adams et al. 2004; Mills et al. 2008). Despite criticism about the technique (Barshaw and Able 1990; Kneib and Scheele 2000), tethering is still acknowledged as a useful method to gather

information on predation provided that rigorous tests on the artefact effects of tethering and complementary data on predator assemblages are investigated (Barshaw and Able 1990; Aronson and Heck 1995; Aronson et al. 2001; Mills et al. 2008). In this study, the length and weight of the tether were sufficiently long and light enough to preclude obvious effects on the normal mobility of scallops. Transect counts and camera observation of potential predators showed that one of the main predators, the toad fish *Omegophora armilla*, was unlikely to be affected by tethering procedures as it chewed on the scallops it encountered. Scallops would only close valves upon encounter (no active escape response such as swimming was observed). Also, no differences between the likelihood of being eaten by different predators among algal biomass was observed, and *O. armilla* foraged in sandy and algae covered bottoms, suggesting that the predator affected the different algae biomasses in a similar manner. However, we can not rule out interactions between the tether and levels of algal biomass and this interaction would need to be explored experimentally.

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 precluding the establishment of an adult population in the study area. *Hincksia sordida* was used as a settlement substrate but as the spat progressed to the juvenile phase individuals in the areas of lower algal density experienced greater survival and growth rates possibly due to their recessing behaviour which provided a degree of protection from predation. The manner in which vegetation provides protection for prey therefore needs to be considered 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.

Chapter 4. Reproductive strategies and energy sources fuelling protracted spawning in *Pecten fumatus*, D'Entrecasteaux Channel Tasmania

4.1. Introduction

Strategies for energy acquisition and allocation for reproduction fit within the continuum between income or opportunistic breeding, where organisms acquire energy from food available in the environment concurrently with breeding, and capital or conservative breeding, where organisms collect and store food or energy in advance until it is needed for reproduction (Drent and Daan 1980; Tuomi et al. 1983; Stephens et al. 2009). Using the income-capital classification is useful to explore aspects of physiology, behaviour and population dynamics (for examples see Stephens et al. 2009; McBride et al. 2013). Fuelling reproductive growth directly from ingested food is a better strategy when costs associated with establishment, maintenance and use of stored energy are substantial or food is reliably available. Capital breeders, in contrast, have an advantage in highly variable environments with unpredictable or limited food supply which allows feeding and reproduction to be decoupled spatially and temporally (Cherel et al. 1994; Jonsson 1997; Trexler and DeAngelis 2003; Johnson 2006). The disadvantage of this strategy is that capital breeders may have to pay energetic costs to defend the stored food and also risk the loss of potential food items to other competitors (Vander Wall & Jenkins 2003) and that the ability to avoid predators can be affected (Hedenstrom 1992; Bonnet and Naulleau 1996; Lee et al. 1996). Given the particular advantages and disadvantages of each strategy in some instances a combination of strategies is observed, depending on environmental conditions or food availability (Jonsson 1997; Stephens et al. 2009; McBride et al. 2013).

Considerable research into breeding strategies has focused on birds and mammals, and therefore much of the discussion regarding them has been in the context of endothermy (Bonnet et al. 1998). For some endothermic animals, large internal energy stores might affect their mobility, therefore increasing vulnerability to predation and the cost of locomotion (Witter & Cuthill 1993, Gosler et al. 1995). In ectotherms, the energetic and demographic costs associated with storage, maintenance and utilisation of body reserves are less, leading Bonnet et al. (1998) to conclude that income breeders are likely to be rare among ectotherms. Their conclusion however, was based on examples from amphibians and reptiles. This

postulate, however, was not accurate for fishes (see review in McBride et al. 2013) and its general applicability for marine invertebrates has yet to be tested. Marine ectotherms typically experience highly variable environments and in the case of broadcast spawners, fertilization success generally increases with greater synchronization of spawning events in the population (Babcock et al. 1994, see Levitan 1995 and references therein). A capital breeding strategy, where energy is stored until the appropriate environmental (Cantillanez et al. 2005b) or conspecific (Barber & Blake 2006) cues occur, would therefore seem to be more favourable for synchronisation of gametogenesis.

In scallops (family Pectinidae), which are broadcast spawners, an array of different breeding strategies are observed. These appear to vary greatly among different species and locations, for example, *Chlamys septemradiata* and *Placopecten magellanicus*, which have a single spawning event per year appear to follow an income breeding strategy, with food in the water column sustaining gametogenesis in optimal environmental conditions (Ansell 1974; Thompson 1977). In contrast, the semelparous *Argopecten irradians concentricus* has a capital breeding strategy, where energy is stored for their 'once in a lifetime' reproductive event, before dying (Barber & Blake 1981; Epp et al. 1988). A combination of the two strategies is also possible, as is the case for *Chlamys varia* and *Pecten maximus*, where the energy necessary to support two spawning events per year results from a combination of stored energy and food available in spring (Shafee 1981; Pazos et al. 1997). Likewise, the protracted spawner *Aequipecten opercularis* uses a combination of both breeding strategies to support gametogenesis during several months (Roman et al. 2002). These studies suggest some flexibility in terms of particular breeding strategies relative to reproductive mode (single spawner, semi-annual spawner, protracted spawner), however, a comprehensive review of available literature for scallops is necessary to test this statement.

When following a capital breeding strategy, scallop reproduction is supported by the adductor muscle and digestive gland as the main storage tissues providing energy required for gonad maturation (see review in Brokordt & Guderley 2004). Energy substrates, however, seem to vary between species and geographic locations, with glycogen, lipids, and/or protein being used as the main energy source in scallops (Barber & Blake 1981, Epp et al. 1988, Strohmeier et al. 2000) whereas others may use all three sources simultaneously (Roman et al. 2002). Therefore, to understand the breeding strategy from an energetics perspective it is necessary to assess each energy substrate in the various storage tissues concomitantly.

Scallops are a useful marine invertebrate study group to explore energy allocation associated with reproduction because the gonad and the main energy storage sites such as the adductor muscle, digestive gland and mantle are easily isolated. Physiological indices (Barber & Blake 1985b), respiratory quotient (Barber & Blake 1985b) and radiotracer experiments (Barber & Blake 1985a) support the hypothesis that changes in somatic tissue weights in scallops indicate sites of energy storage and that changes in energy sources such as glycogen, lipid and protein levels indicate which of the energy sources contribute to energy use (Barber & Blake 2006).

This study focuses on the scallop *Pecten fumatus*, which occurs in the coastal regions of southern Australia and supports a significant commercial fishery (Young et al. 1999). *Pecten fumatus* is a simultaneous hermaphrodite which usually spawns during winter and spring (Harrison 1961, Sause et al. 1987, Fuentes 1994, Young et al. 1999), and is characterised by a protracted spawning season with several partial spawning events throughout the year (Sause et al. 1987, Fuentes 1994). With spawning lasting five months on average, the question arises as to whether these animals have adopted a capital, income or combination of capital and income breeding strategies to support this protracted spawning period. If the latter, it is hypothesised that gametogenesis is fuelled from stored energy reserves, while later maturation of gametes is supported by the increased availability of food in the environment. Recently, studies focusing on fish with protracted spawning and asynchronous oocyte development have highlighted the difficulty associated with analysing energy use and allocation based on a temporal pattern, as several oocytes stages might be present in a single sampling occasion (Domínguez-Petit et al. 2010; Alonso-Fernández and Saborido-Rey 2012). Therefore, it was deemed appropriate to analyse the dynamics of energy storage and reproduction based on both, a temporal pattern and by reproductive stage. Energy use and allocation was analysed for each microscopically determined ovarian reproductive stage. With the information generated from this study and a review of existing literature on scallop reproduction and energy allocation, I further examine the hypothesis that scallops are more likely to be capital breeders and explore how the reproductive mode (ie single spawner, semi-annual spawner, protracted spawner) affects which breeding strategy is being used.

4.2. Methods

4.2.1. Case study

4.2.1.1. Reproductive cycle

Every 15-20 days between August 2010 and late March 2011, approximately 25 adult scallops (shell length > 100 mm) were collected by divers from Great Bay in the D'Entrecasteaux Channel, southern Tasmania (147.33590 W and 43.22028 S, 12 meters depth). Scallops were maintained in seawater-filled plastic containers (40x40x30 cm) until processed in the laboratory. Each scallop was measured for shell height and width (to the nearest 1 mm), total weight, gonad weight, adductor muscle weight, shell weight, and digestive gland weight (to the nearest 0.1 g). The gonad was divided into halves longitudinally so that both the female and the male structure were present in both halves, one half was fixed in FAACC (formalin, acetic acid and calcium chloride) for gonad histology (Winsor 1994) and the other half frozen at -40°C for proximal analysis.

To estimate spawning time and reproductive effort, the gonadal mass index of *Pecten fumatus* was estimated for each specimen using the approach described by Bonardelli and Himmelman (1995). First, the slope b was obtained from the log-linear regression of the width and gonad mass of *P. fumatus* for each collection date. This slope b was then used to calculate the gonad mass Y' for a standard scallop measuring 105 mm (the average length of scallops sampled in this study):

$$\text{gonad mass for a standard scallop}_{ij} = (Y_{ij}) / (H_{ij}^b) * (105^b)$$

where i represents the i^{th} scallop, j is the collection date, Y is the gonad mass in g, H is the shell length in mm, b is the slope from the regression of log₁₀ gonad mass on log₁₀ shell length (Bonardelli & Himmelman 1995). Muscle and digestive gland mass indices were calculated following the same procedure as described above.

Histological examination of gonads was used to identify causes of the changes in gonad mass associated with gametogenesis and spawning. A decrease in the gonad mass index may be due to either spawning or resorption of gametes, and this can only be

determined histologically. Fixed gonad tissue was transferred to 70% ethanol and stored for at least 48 hours, before being embedded in paraffin and sectioned to 6µm. Sections were stained with Haemotoxylin and Eosin and mounted with a mixture of distyrene, tricesyl phosphate and xylene (DPX synthetic resin mountant) (Kiernan 2008).

To determine maturity stage of individuals, a reproductive stage frequency distribution of the gametes was generated for each gonad using 50 random points distributed in the female part of the gonad with Coral Point Count with Excel extensions (CPCe) version 4.1 (Kohler & Gill 2006). The gonad contains a large number of acini, with walls composed of connective tissue and primary germ cells. The lumen of the acini is more or less filled with gametes in varying stages of gametogenesis, depending on the reproductive stage of the gonad (Fig. 4.1). Reproductive stages were identified for female gonads following a modified scale from Sauce et al, (1987) and Cantillanez et al, (2005b) (Table 4.1; Fig. 4.1). When the acini structure was clearly evident (i.e. Fig 1a) under the random point the reproductive stage was classified using the appearance of the acini (Table 4.1; Stages 1, 4 & 5). When the acini structure had broken down and its wall was hard to observe, the appearance of the oocyte under the random point was assigned a reproductive stage (Stages 2 & 3). For each female the maturity stage was assigned as the most frequently observed reproductive stage of the acini and oocytes, excluding atretic acini, because this provided an assessment of the stage of gametogenesis. Atresia was analysed separately, the percentage of atretic oocytes in each scallop was recorded from the random point assessment and these data was incorporated in the MANOVA analysis detailed below to determine if any limitation in energy sources in the muscle, digestive gland and gonad could explain the occurrence or extent of atretic oocytes.

Table 4.1 - Classification scale for gametic reproductive maturity stages in *P. fumatus*. Stages modified from (Mason 1958; Harrison 1961; Sause et al, 1987)

Stage no.	Gonad stage	Description of stage
1	Developing	Gonadal acini small. Previtellogenic oocytes of various sizes adhering to acini wall. This stage includes the formation of oocytes in acini but inter-acinal tissue is still present (Fig. 4.1a).
2	Mature	Large gonadal acini, completely filling the gonadal space, with a predominance of fully developed vitellogenic oocytes (Fig. 4.1b).
3	Atresia	Oocytes are deformed (jigsaw-puzzle appearance) and staining affinities change (Fig. 4.1c).
4	Partial spawning	Initiation of gamete release, decrease in free vitellogenic oocytes in the lumen (Fig. 4.1d).
5	Fully spawned	Very few free vitellogenic oocytes in the lumen, most remaining oocytes are pedunculated (Fig. 4.1e).

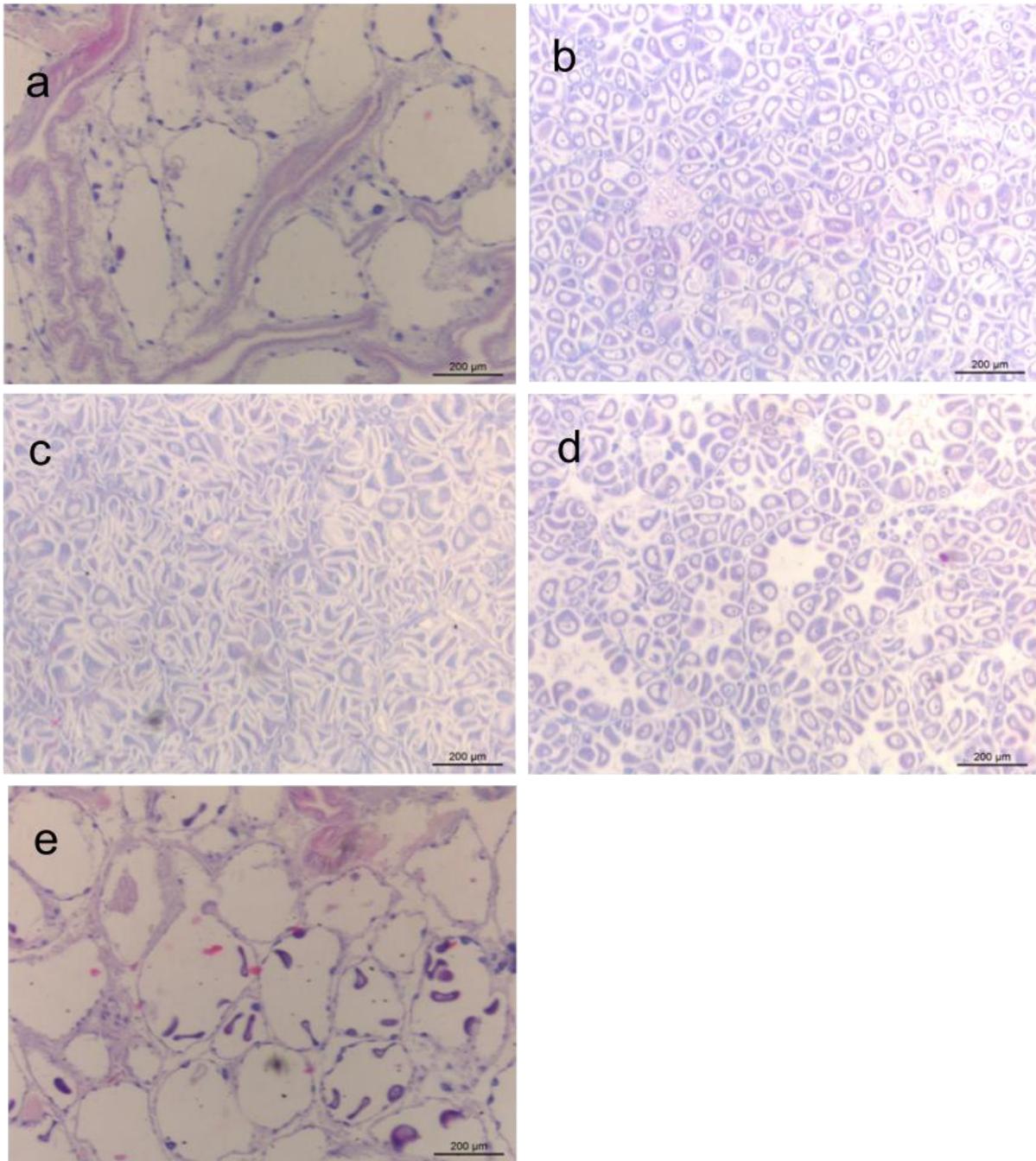


Fig. 4.1. Histological sections of *P. fumatus* female gonads showing the different reproductive stages (scale 200 µm). a) developing stage, b) mature, c) atresia, d) partial spawning and e) fully spawned. See Table 4.1 for the description of the reproductive stages.

4.2.1.2. Proximal composition

Proximal analyses were conducted on muscle, gonad and digestive gland tissue from 4-6 randomly selected individuals per month. These tissues were initially frozen and then freeze-dried, weighed and ground with a mortar and pestle. Subsamples of each tissue were

used to calculate glycogen, protein and lipid concentration. These values were then multiplied by the total dry weight of each tissue to estimate total content per tissue. Glycogen concentration was quantified by subtracting free glucose from glycogen derived glucose using amyloglucosidase (from *Aspergillus niger*) to breakdown glycogen to glucose (Burton et al. 1997). Glucose concentration was measured using an Amplex Red Glucose/Glucose Oxidase Assay kit (Life Technologies). Glycogen standards from oyster (Type II, Sigma Cat. N G8751) were prepared concomitantly with tissue samples to generate a standard curve for glycogen concentration (Simon and Jeffs 2011). Total nitrogen was determined using a Thermo Finnigan EA 1112 Series Flash Elemental Analyser. Samples were combusted using tungstic oxide on alumina as an oxidising agent followed by reduced copper wires as a reducing agent. The results were calibrated using a certified sulphanilamide standard and total protein from total nitrogen was calculated using the factor 6.25 (Giese 1967). The concentration of total lipids was determined by the method of Bligh and Dyer (1959) using chloroform:methanol (2:2) and estimated gravimetrically. Energy conversion factors to estimate the total energy content per gram of dry tissue were 17.14 KJ.g⁻¹ for glycogen (Brody 1945); 17.97 KJ.g⁻¹ for proteins (Beukema & De Bruin 1979), and 35.20 KJ.g⁻¹ for lipids (Beukema & De Bruin 1979).

4.2.1.3. *Environmental variables*

Monthly average data of Sea Surface Temperature (SST) and Chlorophyll-*a* (Chl-*a*) for the study area were obtained from the MODISA satellite imagery (<http://oceandata.sci.gsfc.nasa.gov/MODISA/Mapped/Monthly/>) at 4 km scale and processed using MATLAB v. 7.2 (R2006a) (The MathWorks, Natick, Massachusetts). Sea surface temperature data were retrieved from the closest information pixel to the study area, while the chlorophyll-*a* concentration (mg.m⁻³) was retrieved from an average of the five closest pixels to the study area. These data was used as proxies for temperature (SST) and food availability (Chl- *a*) in the area during the study period.

4.2.1.4. *Data analysis*

To assess if the frequency distribution of scallops in each reproductive stage was the same on each sampling date, a chi-square test of independence was used. If the analysis was significant, standardised residuals were used to determine where differences between

observed and expected frequencies were large (>2). Differences in the mean standard mass of different tissues at the different sampling dates and in total energy content in each tissue were assessed using an ANOVA. Normality of residuals was assessed visually by plotting the residuals. Homogeneity of variances was assessed using the Bartlett's test (Bartlett 1937). An adjusted Welch's test was used to test equality of means when variances were unequal (Welch 1951). Post hoc pairwise t-tests with a Bonferroni correction method were used to determine which sampling dates differed (Wright 1992)

To determine the dynamics of energy use and storage by reproductive stage, average energy content of gonad, digestive gland and adductor muscle and average percent atresia among the reproductive stages were examined for differences using a MANOVA test. The fully spawned and the developing reproductive stages were combined for this analysis, as the acini structure is very similar. There were strong correlations among some of the energy sources in muscle, digestive gland and gonad, therefore only six variables (glycogen in muscle, protein in muscle, protein in gonad, lipid in gonad, lipid in digestive gland and percent atresia) were used. A sequential Bonferroni (Holm's method) was used to adjust the p-values from the pairwise contrasts among the reproductive stages (Quinn & Keough 2002). The Shapiro-Wilk Multivariate Normality Test was used to assess multivariate normality and the Box's M test was used to test homogeneity of covariance matrices using a p-value < 0.005 to reject the null hypothesis (Huberty & Petoskey 2000). For all other statistical analyses a p-value of 0.05 was used to test the significance of the results. A canonical discriminant analysis followed the MANOVA to identify the variables that explained the differences in the centroid means for each maturity stage. Statistical analysis was conducted using the R software package (R development core team 2011, version 2.12.1).

4.2.2 Literature review

The ISI Web of Knowledge electronic data base (1975–2013, <http://portal.isiknowledge.com>) was used to identify literature about breeding strategies of scallops, using the keywords scallop, biochemical, energetic, reproductive, reproduction, energy, storage and cycle. References cited in each of the resulting studies were reviewed for the presence of any additional studies that could have been missed in the previous search step. Scallop from wild populations and from aquaculture were included in the review only if no addition of food to the system was reported. As most studies do not specifically state

which breeding strategy is being used by a particular species, data on gonad indexes, reproductive stages, glycogen, protein and lipids in the muscle and digestive gland (in the form of Tables or Figures) were carefully analysed to determine which breeding strategy was likely to be used. It was assumed that a decrease in an energy source such as glycogen, lipid or protein either in the muscle or the digestive gland during gametogenesis (which was determined either by histological analysis or by an increase in the gonad index) was used to fuel the development and maturation of gametes.

4.3. Results

4.3.1. *Temporal patterns of gonad mass and reproductive stages*

Muscle, digestive gland and gonad mass standardised for size (105 mm scallop) varied significantly during the study period ($F=52.44$, df 15, 146.54, $p<0.001$; $F=39.08$, df 15, 146.55, $p<0.001$; $F=6.77$, df 15, 146.64, $p<0.001$, respectively). Mean muscle mass was least between August and October 2010 (about 9 g) after which it increased steadily until January 2011, remaining at around 16 g for the remainder of the study period (Fig. 4.2a). Digestive gland mass was also lowest between August and September (about 2 g) but increased rapidly during October to remain at around 4 g between November and January before declining to an intermediate level in February and March (Fig. 4.2b). Gonad mass was most variable early in the study period, especially from August to November, and apart from a small increase in January, tended to decline thereafter (Fig. 4.2c).

The proportion of females in the different reproductive stages changed through time ($\chi^2=183.15$, df 36, $p<0.001$) and a greater percentage of individuals in the developing stage (88%) were observed at the beginning of October and in mid-December 2010 (44%) (Fig. 4.2d). Mature individuals occurred in more or less the same proportions (averaging 73%) throughout the study period apart from at the beginning of October (12.5%) and mid-December (25%), when a high proportion of developing individuals were present, and during February (22.5%), when most individuals had fully spawned. From November until late March a greater percentage (47% in average) of individuals with partially spawned and fully spawned stages were observed (Fig. 4.2d).

Reproductive stage and the gonad mass index revealed a reproductive cycle that could be divided into an initial maturation (Aug-Sep) phase followed by a protracted spawning season. Adductor muscle and digestive gland mass were at their lowest during maturation phase (Fig. 4.2a&b). Spawning was detected in October and was associated with an increase in the muscle and digestive mass index. Lowest average gonad mass was observed from January to late March 2011, and 30-63% of individuals showed fully spawned gonads (Fig. 4.2c&d).

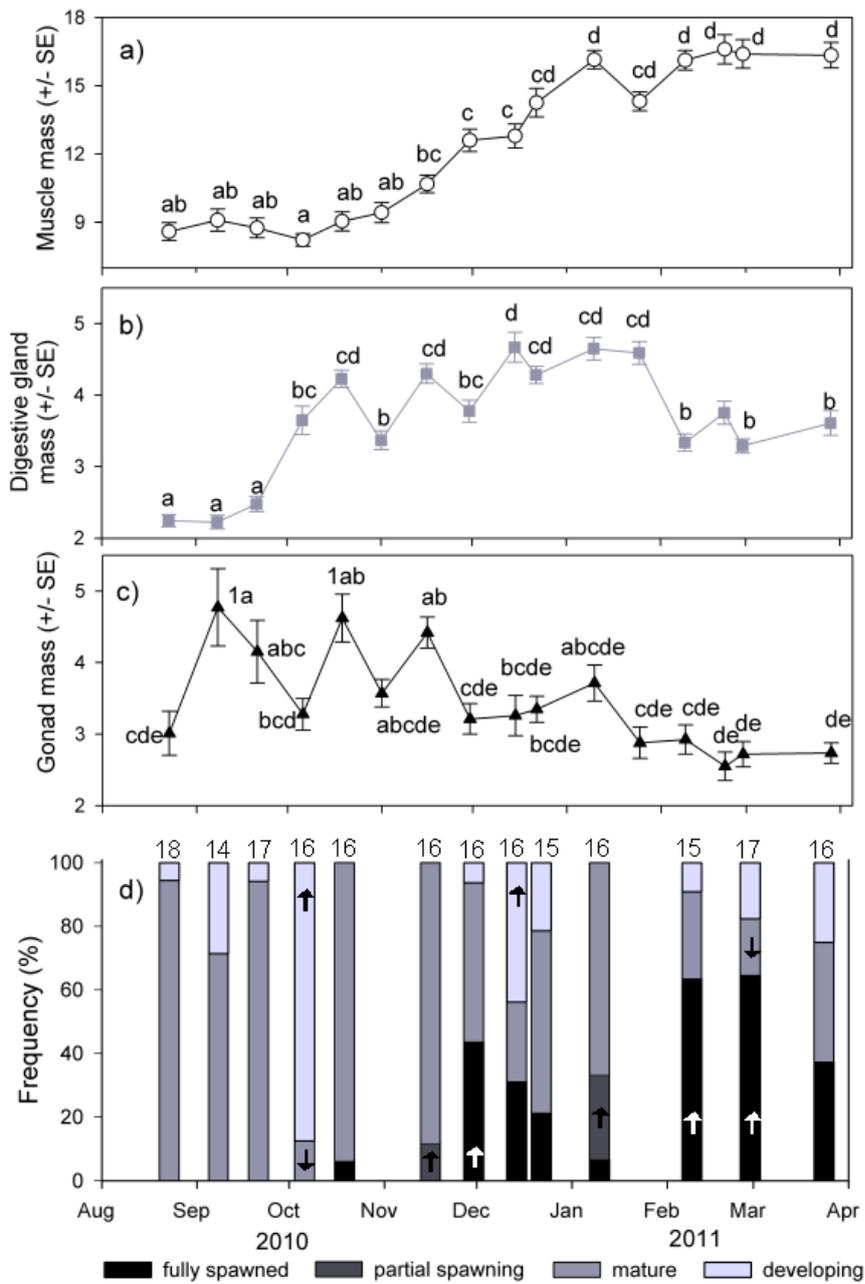


Fig. 4.2. Mean a) muscle, b) digestive gland and c) gonad mass (g) standardised for a 105 mm scallop. Different letters/numbers in panels a, b and c indicate significant differences between sampling dates. Panel (d) illustrates the frequency of females in each reproductive stage from August 2010 to March 2011. Arrows indicate where frequencies were more (↑) or less (↓) than expected in each reproductive stage under the hypothesis that the frequency of individuals in each stage was independent of time. Numbers above the bars indicate the sample size from each sampling date.

4.3.2. Atresia during reproductive period

The percentage atresia in the female part of the gonads varied significantly over time ($F=4.64$, $df\ 12,195$, $p<0.001$) but showed no particular trend during the study period apart from declining from 76% in February to 22% towards the end of the study (Fig. 4.3).

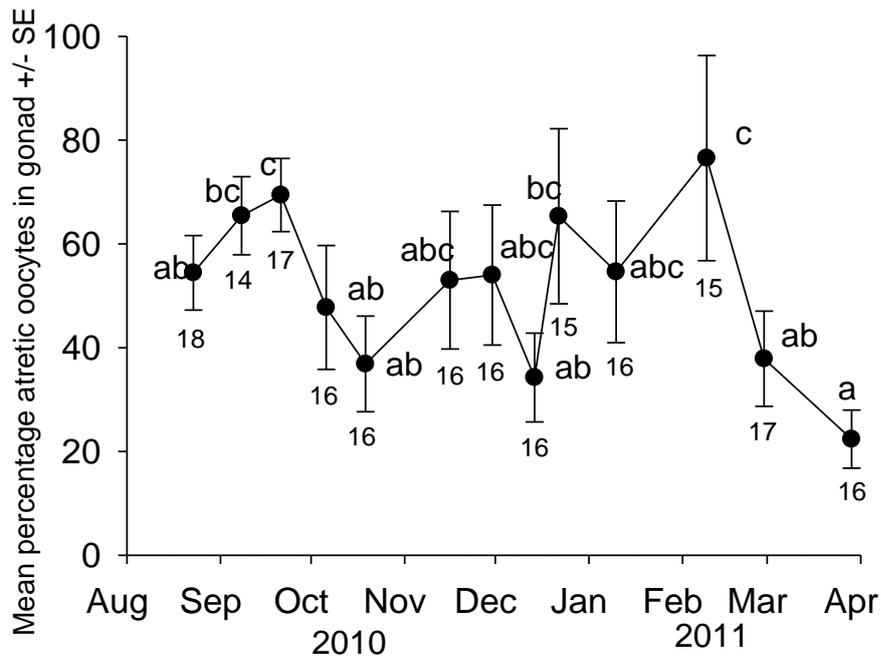


Fig. 4.3. Mean percentage values of atretic oocytes in the female gonad for each individual during each sampling date from August 2010 to March 2011. Different letters indicate significant differences between sampling dates. Error bars represent one standard error. Numbers below error bars indicate the sample size from each sampling date

4.3.3. Energy content

The adductor muscle had the greatest energy content among the tissue types ($F=134.60$, $df\ 2, 82.73$, $p<0.001$; Fig. 4.4), this energy was accumulated in the form of protein and glycogen with a very small contribution from lipids (2.8 to 4.5 kJ). Average energy content derived from glycogen varied significantly over time ($F=68.82$, $df\ 8,13.03$, $p<0.001$); on average 1.3 kJ was estimated during August to October, after which an increase occurred with up to 58 kJ in February and then a decline in late March (26.4 kJ). Average energy derived from muscle protein also varied during the study period ($F=3.38$, $df\ 8, 35$, $p=0.005$) and was significantly higher in late February (57.6kJ) than during the months of

August to October (31.1 kJ on average). Energy from the lipid in the muscle did not show significant differences during the study period ($F=1.95$, df 8, 35, $p=0.084$).

Less energy was found in the gonad than in the muscle, mainly accumulated in the form of protein and lipids (Fig. 4.4). Average energy content in the gonad from protein, lipids and glycogen changed significantly during the study period ($F=5.26$, df 8, 35, $p<0.001$; $F=2.90$, df 8, 35, $p=0.013$; $F=4.11$, df 8, 35, $p=0.001$, respectively). Average protein values peaked during maturation (20.7 kJ on in September), and then declined steadily during spawning reaching a low of 5.8 kJ. Average lipid values were significantly different between the beginning (5.3 kJ) and the end of the spawning phase (1.2 kJ, Fig. 4.4). Average glycogen levels were very low in the gonad (0.25 kJ) and showed a similar pattern to lipid content in the gonad. Energy content from lipids in the digestive gland varied significantly over time ($F=11.29$, df 8, 35, $p<0.001$) and showed a similar pattern to glycogen in the muscle, with low levels (1.5 kJ on average) during maturation and higher levels during the spawning phase (9.8 kJ on average, Fig. 4.4).

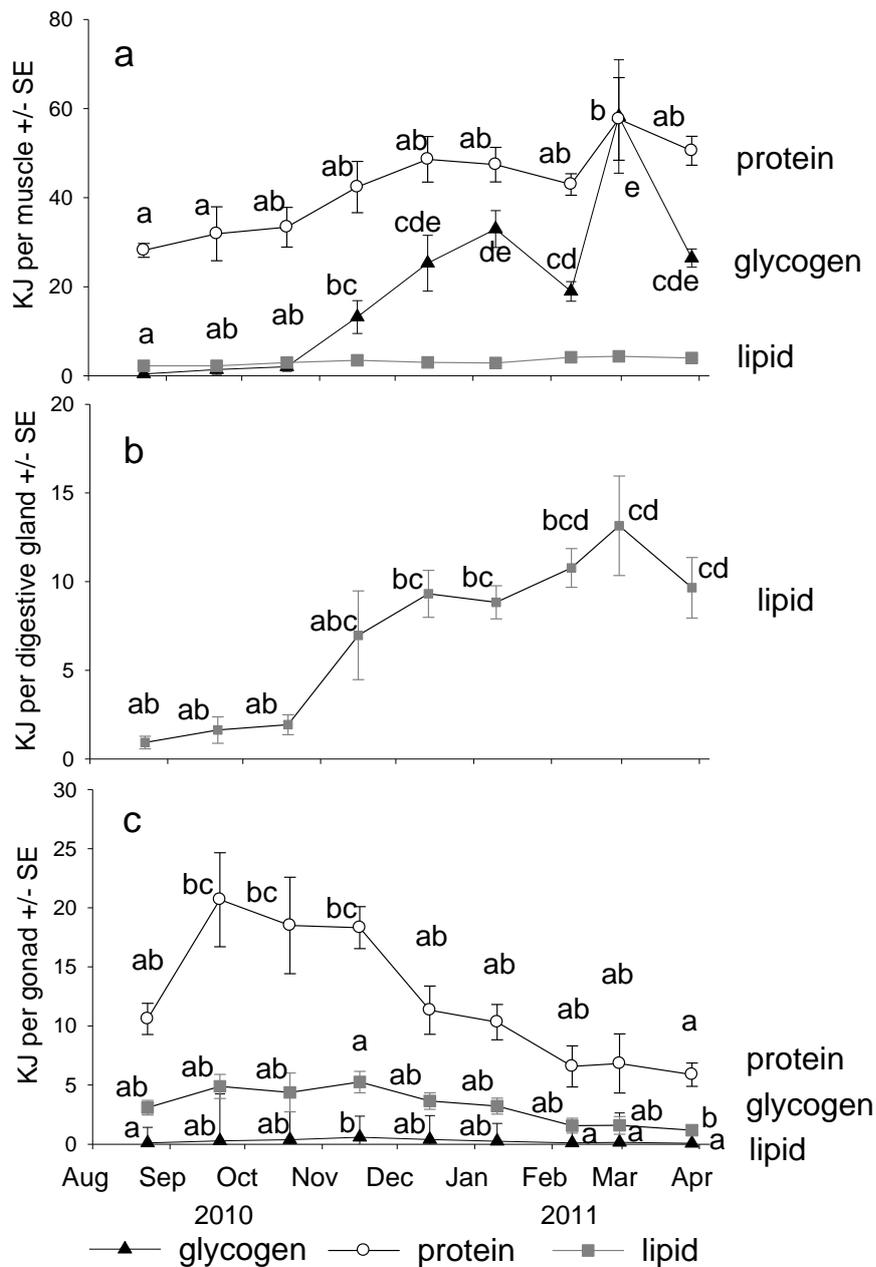


Fig. 4.4. Seasonal changes in mean contribution of energy content in glycogen, protein and lipid (total kJ per tissue) in a) muscle, b) gonad and c) digestive gland. Note y-axis scales differ between graphs, n= 4-6 per sampling date. Different letters in a graph denote significant differences for each energy source through time and not comparisons amongst the different proximal elements.

4.3.4. Environmental variables

Sea surface temperatures were coolest during August and September and started to warm in October, being warmest in February and cooling thereafter (Fig. 4.5). Chlorophyll-a concentration increased from August to a peak in September, after which a gradual decrease was observed until December and lowest values were recorded thereafter (Fig. 4.5). Spawning started when temperatures were rising and chlorophyll values were decreasing and continued throughout the warmer months (Fig. 4.5).

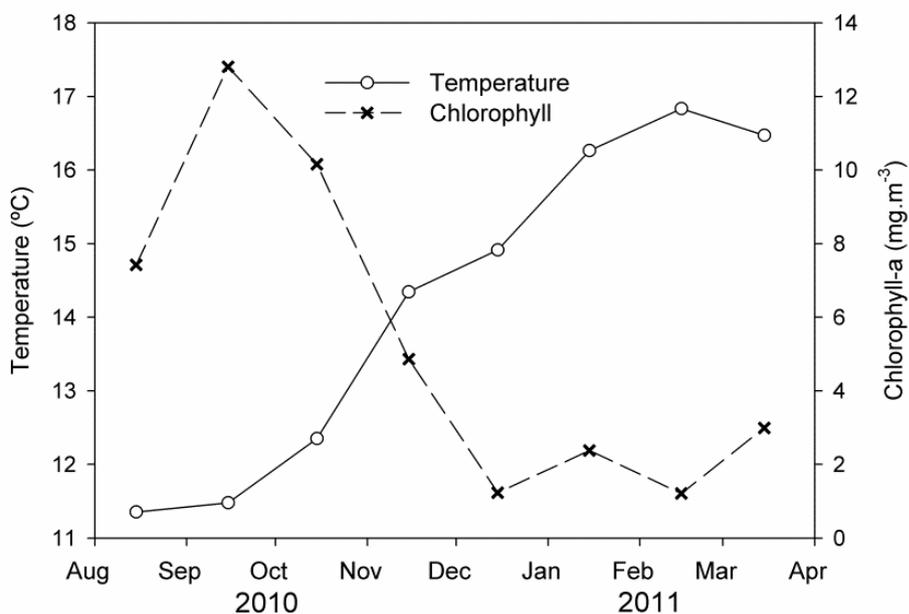


Fig. 4.5. Monthly average variations in Sea Surface Temperature (°C) and Chlorophyll-a (mg.m⁻³) in Great Bay, DEC, from August 2010 to March 2011.

4.3.5. Dynamics of energy use and storage by reproductive stage

Energy storage showed a clear fluctuation pattern related to reproduction as the reproductive stages of the scallops were significantly different in terms of glycogen, protein and lipid levels ($F=3.982$, $df\ 2,12$, $p<0.001$). However, pairwise contrasts showed that only the mature and fully spawned stages were significantly different ($F=10.429$, $df\ 6,30$; $p<0.001$) (Fig. 4.6). Differences among the two reproductive stages were driven by the percentage of atresia, glycogen and protein content in the muscle and lipid content in the digestive gland. The percentage of atresia was greatest in scallops with mature gonads but lowest in fully spawned individuals. Mature scallops were most associated with greater

values of lipid and protein in the gonads; while partial spawning and fully spawned individuals were more associated with higher values of glycogen and protein in muscle and lipid in the digestive gland (Fig. 4.6).

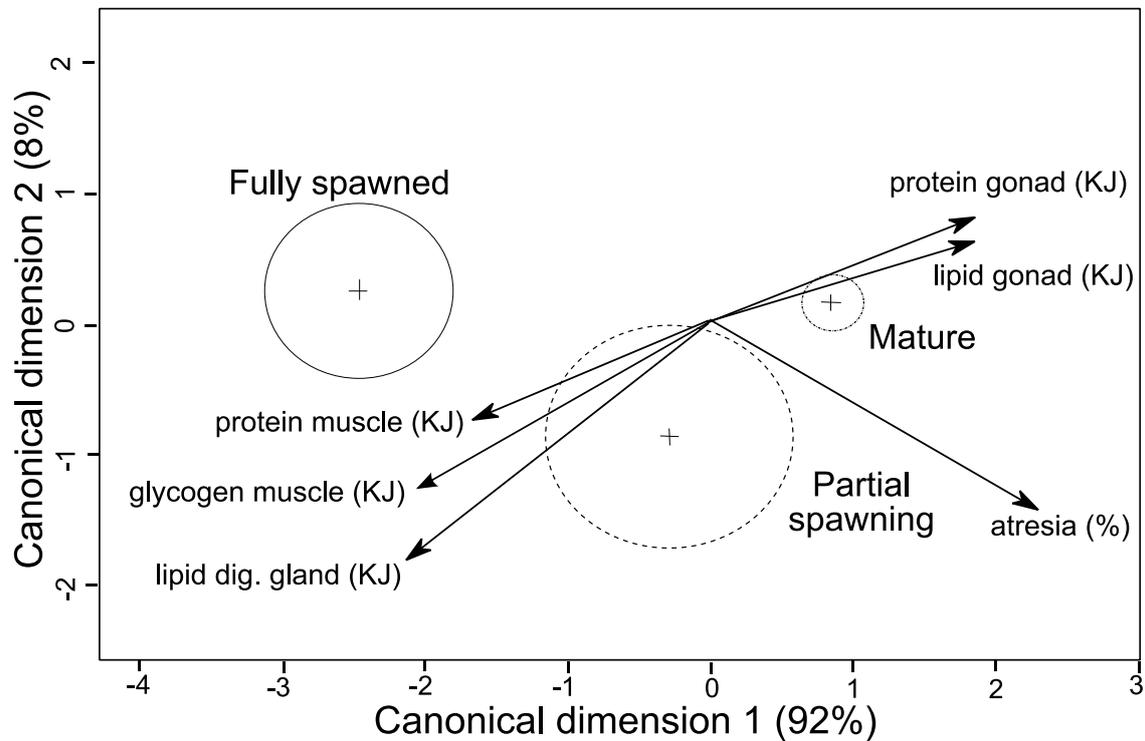


Fig. 4.6. The centroid means for each of three reproductive stages plotted in the first two canonical discriminant dimensions. The direction and length of the vectors show the strength and nature of the correlation with each variable and the canonical discriminant axes. The percent values for each axis is the percentage of variability among the three centroid means explained by each of the two axes.

4.3.6. *Breeding strategies in scallops*

Twenty one scallop populations were identified for which information on reproduction and energy use and storage was available (Table 4.2). This information included eleven species, five of them hermaphrodites and six dioecious. Most populations were located in the northern hemisphere (19 out of 21), mostly at latitudes greater than 40 degrees (16 populations). Only six studies analysed all energy sources concomitantly (glycogen, protein and lipid in the muscle and the digestive gland). Maturation of gonads occurred during any season of the year, and was not species specific (Table 4.2). Reproductive mode did not seem to be species specific, as observed for *Aequipecten opercularis* (Taylor and Venn 1979;

Román et al. 2002) and *Pecten maximus* (Comely 1974; Faveris and Lubet 1991; Lubet et al. 1995; Pazos et al. 1997; Strohmeier et al. 2000). Most populations of scallops appeared to use a capital breeding strategy to fuel maturation, although a combination of both strategies is also possible (Table 4.2).

1 Table 4.2. Changes in proximal composition in the muscle and digestive gland during maturation months in 21 species of scallops.
 2 H=hermaphrodite, D= Dioecious; less/more = refers to a decrease/increase in the energy substrate of a particular storage tissue during maturation; NCT=no clear trend. A
 3 decrease in energy would be indicative of capital breeding while no clear trend or an increase would suggest an income breeding strategy.
 4 a =only few comparative sampling dates; * cultured organisms. Breeding strategy 1=income breeding, 2 = capital breeding
 5 N.A. = No information available; Mode P= protracted S= single or Se=Semi-annual spawning; Life history I=iteropareous, S=semelpareous
 6

Species	location	lat (°)	sex	maturation season	Muscle			digestive gland			months spawning	Mode	Life history	Breeding strategy	Reference
					glycogen	protein	lipid	glycogen	protein	lipid					
<i>Aequipecten opercularis</i>	Spain	42	H	winter-spring	less	less	N.A.	N.A.	N.A.	less	6	P	I	1 and 2	Roman et al, 2002
<i>Aequipecten opercularis</i>	U.K.	55	H	spring-summer	less	less	NCT	N.A.	N.A.	N.A.	2	S	I	2	Taylor and Venn, 1979
<i>Argopecten irradians irradians</i>	U.S.A	28	H	autumn	less	less	less	NCT	NCT	NCT	1	S	S	2	Barber and Blake, 1981
<i>Argopecten irradians irradians</i>	U.S.A	40	H	spring-summer	NCT	less	less	NCT	NCT	NCT	1	S	S	2	Epp et al, 1988
<i>Argopecten purpuratus</i>	Chile	-30	H	spring-summer	less	less	NCT	N.A.	N.A.	N.A.	N.A.	N.A.	I	2	Martinez, 1991*
<i>Chlamys islandica</i>	Norway	69	D	spring-early summer	less	less	less	NCT	NCT	NCT	1	S	I	2	Sundet and Vahl, 1981
<i>Chlamys islandica</i>	Canada	50	D	summer	less	NCT	N.A.	N.A.	N.A.	N.A.	N.A.	S	I	2	Brokordt et al, 2000 ^a
<i>Chlamys islandica</i>	Canada	50	D	summer	less	NCT	NA	NCT	NCT	less	N.A.	S	I	2	Brokordt and Gurdeley, 2004
<i>Chlamys septemradiata</i>	U.K.	55	D	spring-summer	NCT	more	NCT	N.A.	N.A.	N.A.	2	S	I	1	Ansell, 1974
<i>Chlamys varia</i>	France	48	D	spring	more	more	more	N.A.	N.A.	N.A.	2	Se	I	1	Shafee 1981
				summer	less	less	less	N.A.	N.A.	N.A.				2	
<i>Euvola ziczac</i>	Venezuela	11	H	spring	less	NCT	N.A.	N.A.	N.A.	N.A.	N.A.	Se	I	2	Brokordt et al, 2000 ^a
				summer	less	NCT	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.			
<i>Nodipecten subnodosus</i>	Mexico	27	H	summer-autumn	less	less	N.A.	more	more	less	3	S	I	2	Arellano et al, 2004
<i>Nodipecten subnodosus</i>	Mexico	24	H	winter-spring	more	more	N.A.	NCT	NCT	more	N.A.	S	I	1	Racotta et al, 2003*
<i>Pecten fumatus</i>	Australia	-43	H	summer-autumn	less	NCT	NCT	N.A.	N.A.	less	6	P	I	2	this study
<i>Pecten maximus</i>	U.K.	55	H	autum-winter-spring	less	less	N.A.	NCT	NCT	less	2	S	I	2	Comely, 1974
<i>Pecten maximus</i>	Spain	42	H	winter	less	less	NCT	less	less	less	1	Se	I	2	Pazos et al, 1997*
				spring	more	more	NCT	more	more	more					
<i>Pecten maximus</i>	Norway	60	H	spring-early summer	less	less	NCT	less	less	less	3	S	I	2	Strohmeier et al, 2000
<i>Pecten maximus</i>	France	49	H	winter-spring	less	NCT	less	N.A.	N.A.	N.A.	3	S	I	2	Faveris and Lubet, 1991
<i>Pecten maximus</i>	France	49.5	H	winter-spring	less	N.A.	N.A.	N.A.	N.A.	N.A.	5	P	I	1? and 2	Lubet et al, 1995
<i>Placopecten magellanicus</i>	Canada	46	D	spring-summer	NCT	NCT	NCT	N.A.	N.A.	N.A.	3	S	I	1	Thompson, 1977
<i>Placopecten magellanicus</i>	U.S.A	44	D	summer	less	N.A.	NCT	NCT	N.A.	less	3	S	I	2	Robinson, 1981

7
8
9

4.4. Discussion

Pecten fumatus spawned over a protracted period, with evidence of gamete production fuelled from stored energy reserves indicative of a capital breeding strategy. However, the sources of stored energy fuelling spawning appear to vary through time. The initial peak of egg production in winter-spring was most probably fuelled by stored energy substrates, while later on the spawning phase appeared to be fuelled by recycling of mature oocytes that failed to be released during the beginning of the spawning event. Analysing energy reserves over monthly patterns as well as by reproductive stages showed that in mature *P. fumatus*, muscle glycogen and protein and digestive gland lipid content are lower when compared to fully spawned scallops. These findings support the conclusion that these energy substrates in the muscle and digestive gland are providing energy for gametogenesis in pectinids (Taylor and Venn 1979; Barber and Blake 1981; Strohmeier et al. 2000, Arellano-Martinez et al. 2004, Brokordt & Guderley 2004). Conversely, maturing of oocytes in the latter part of the spawning season occurred when these energy substrates in the muscle and digestive gland were increasing and chlorophyll-a concentration (a proxy of food availability) was low, suggesting that these energy substrates were not used and also that income breeding was unlikely to have been the primary strategy used to support gametogenesis over this period. Rather, the presence of substantial numbers of atretic oocytes throughout the spawning period suggests that metabolites produced by the recycling of gonad products via atresia (oocyte lysis) may have been used to supplement the energy demands for gametogenesis, as suggested for a deep-water population of *Placopecten magellanicus* (Barber et al. 1988) and for *Pecten maximus* (Duinker and Nylund 2002; Lubet et al. 1987). Mature oocytes have a relative short life span in the ovary and if they are not spawned they enter into atresia, initiated by putative lysosomes present in mature oocytes (Dorange & Lepennec 1989). This process has been examined in *Pecten maximus*, where the energy for the production of successive cohorts of developing gametes is supplied through resorption of atretic material (Le Pennec 1991).

The reproductive cycle in *Pecten fumatus* was characterised by the presence of atretic oocytes during the whole study period. Atresia has been reported for *Pecten fumatus* in the Bass Strait (Young et al. 1999) and also for several scallop species such as *Pecten maximus* (Tang 1941; Dorange and Lepennec 1989; Motavkine and Varaskine 1989; Duinker and

Nylund 2002), *Placopecten magellanicus* (Barber et al. 1988), *Argopecten irradians* (Epp et al. 1988), *Argopecten purpuratus* (Cantillanez et al. 2005). Rates of atresia has been associated to water temperature and food availability in *Pecten maximus* (Soudant et al. 1996; Lubet et al,1987; Paulet et al. 1988), and food availability in *Placopecten magellanicus* (Barber et al, 1988). In this study, there was no apparent temporal pattern in the percentage of atresia in the gonads of *P. fumatus*, suggesting that atresia was not associated with temperature. Additionally, analysing energy use and storage by reproductive stage in each scallop suggested that the percentage of atresia in the gonad was not related to energy content in the muscle and digestive gland. These results are similar to those for *Pecten maximus*, where atretic oocytes are found throughout the year and under different nutritional conditions (Pazos et al 1996; Strand and Nylund, 1991). As studies on reproductive cycles in scallops begin to incorporate the quantification of atresia in their reproductive stage analysis we will increase our understanding of the adaptive significance of this process and its role in supplementing energy demands for gametogenesis (and hence its effect on breeding strategies used).

Spawning in *P. fumatus* in the DEC involves the continuous partial release of mature oocytes, similar to that described for populations of the same species in the D'Entrecasteaux Channel, Tasmania (Harrison 1961), Jervis Bay, New South Wales (Fuentes 1994), Port Phillip Bay, Victoria (Sause et al. 1987), and Bass Strait (Young et al. 1999). While there are differences in the timing of spawning for these three populations, the spawning cycle seems to be described by extended periods of partial spawning activity and re-development of gonads with resorption through atresia occurring during several months (Sause et al. 1987, Fuentes 1994). It seems plausible that protracted spawning is the main if not only reproductive mode in this species. Spawning in the DEC lasted for approximately five months over spring and summer, presumably with progressively fewer oocytes released as gonad mass decreased, a common pattern for scallops with protracted spawning periods (Román et al. 2002, Arellano-Martinez et al. 2004). Protracted spawning is considered a bet-hedging strategy to prevent complete recruitment failure, whereby a continuous release of small numbers of larvae increases the probability that environmental conditions supporting good survival will be experienced by some larvae (Murphy 1968, Philippi & Seger 1989). Bet-hedging may further benefit recruitment, as juveniles arrive at different times to the settlement habitat reducing competition among offspring and increasing survival during early stages (Nakayama et al. 2011).

Scallops with protracted spawning can either combine a capital breeding strategy with later oocytes lysis-derived energy to sustain maturation - as suggested in this study - or use a combination of capital and income strategies during the reproductive cycle (Román et al. 2002). No other studies assessing reproductive and reserve storage cycles for scallop species with protracted spawning were found in the literature but for fish, a combination of both strategies has also been observed for batch spawners with asynchronous oocytes development (McBride et al. 2013). For scallops with two pronounced spawning seasons when maturation occurred in periods of low food availability, a capital breeding strategy was used, while if maturation occurred in spring, a period associated with high food availability, an income breeding strategy was used (Shafee 1981, Pazos et al. 1997) (Table 4.2). Differences in reproductive strategies between populations of the same species of scallops strongly suggest that location or time of the year when spawning occurs is important and would agree with the idea that the breeding strategy acquired by an individual is not species related but depends on the organism's interaction with the environment (Stephens et al. 2009). The effect of inter-annual differences in the timing of maturation and spawning on the breeding strategy used and associated reproductive output in *P. fumatus* needs to be further elucidated.

A capital energy strategy to fuel reproduction is common among scallops, based on this study and a review of information about breeding strategies for other scallop populations (Table 4.2). Most populations (18 of 21) use this strategy, supporting the hypothesis that ectotherms are rarely income breeders (Bonnet et al. 1998), however, our conclusions are based on mainly temperate species. Such a strategy makes sense in highly variable habitats such as the marine environment, where primary productivity varies seasonally and the temporal separation of feeding and gonad maturation allows animals to store energy at one time and reproduce at another (Bonnet et al. 1998). The almost sessile nature of scallops would mean that the mass of stored energy is unlikely to have a negative effect on survival. Increased vulnerability to predation, due to reduced mobility, a potential consequence of storing energy (Hedenstrom 1992, Gosler et al. 1995), does not appear applicable in this group of species since stored glycogen in the muscle increases the capacity of these animals to recover from exhaustive escape responses (Brokordt et al. 2000a, Brokordt et al. 2000b). Furthermore, food intake is not affected by stored energy, as scallops are suspension-feeders and do not actively pursue their food (MacDonald et al. 2006). Finally, the storage of reserves should not have any effect on the effectiveness at courtship (Bonnet et al. 1998), as

scallops are broadcast spawners that release eggs and sperm into the water column where fertilization occurs. These physiological and behavioural characteristics seem to favour the occurrence of a capital breeding strategy in scallops.

In conclusion, our results support the hypothesis that scallops are more likely to use a capital rather than income breeding strategy, presumably because of a scallop-specific set of physiological and behavioural characteristics that seem to favour the occurrence of capital breeding. However, the occurrence of one over another is likely to be dynamic within a species and to depend on the interaction between the organism and the environment. Metabolites produced from oocyte lysis appear to be at least partly sustaining later maturation during protracted spawning in *P. fumatus*, probably ensuring a continuous release of larvae over a long period of time, to bet-hedge against reproductive failure under adverse conditions. These findings also stress the importance of quantifying atresia for studies on the reproductive cycle as it has to be considered a possible energy source fuelling reproduction in marine invertebrates.

Chapter 5. Importance of density on aggregation patterns and synchronization of spawning the hermaphroditic scallop *Pecten fumatus*

5.1. Introduction

Broadcast spawning, where individuals release gametes into the water column prior to fertilization, is a common reproductive mode in marine invertebrates (Strathmann 1990). The likelihood that a sperm finds and fertilizes an egg is, however, very low (Levitan & Petersen 1995), as the gametes are highly diluted and the lifespan of sperm is relatively short (Pennington 1985, Levitan 1995). Successful fertilization from a broadcast spawning strategy depends on factors that maximise the number of eggs and sperm in any one area, such as localised hydrodynamic processes that retain eggs and sperm together (Lasker et al. 1996, Simon & Levitan 2011), synchronization of spawning between individuals (Oliver & Babcock 1992, Babcock et al. 1994) and a high density of spawners (Levitan et al. 1992, Babcock & Keesing 1999, Metaxas et al. 2002).

Low spawner densities are associated with reduced fertilization success (see review in Levitan 1995). Likewise, poor synchronization among spawning individuals also reduces fertilization success (Babcock et al. 1994). Interestingly, less attention has been dedicated to the interaction between density and spawning synchronization despite several laboratory studies indicating that synchrony could be affected by localised spawning cues from conspecifics (Beach et al. 1975, Miller 1989, Hardege & Bentley 1997, Soong et al. 2005). Observations of spawning in wild populations of corals, scallops and ascidians suggest that individuals in close proximity tend to spawn more synchronously than those further apart (Marshall 2002, Styan & Butler 2003, Levitan et al. 2011). This implies that declines in marine broadcast spawner densities may directly impact gamete production and in addition, indirectly reduce pheromone signalling among spawning individuals. Therefore, at lesser densities or greater distance between conspecifics, spawning might be less synchronous and individuals too far apart would not receive the cue to spawn (Babcock & Keesing 1999, Levitan et al. 2011).

Several marine broadcast spawners such as the white abalone *Haliotis sorenseni* in California (Hobday et al. 2001), the Iceland scallop *Chlamys islandica* in Breidafjordur, West

Iceland (Jonasson et al. 2007), and the oyster *Crassostrea gigas* in Chesapeake Bay (Rothschild et al. 1994) have experienced population declines and associated density reduction due to fishing; however, the intensity of the effect of these declines on fertilization success will vary depending on the reproductive behaviour of the species. While sessile organisms will not be able to aggregate, aggregative behaviour related to reproduction has been documented in some starfish (Himmelman et al. 2008), abalone (Seamone & Boulding 2011) and sea urchins (Simon & Levitan 2011). For scallops, there is no evidence of aggregative behaviour related to reproduction, however, the clumped-like aggregations of *Placopecten magellanicus* suggests they may aggregate, possibly to increase fertilization success (Langton and Robinson 1990; MacDonald and Bajdik 1992; Stokesbury and Himmelman 1993). Therefore, knowledge of the aggregation patterns of scallops is important in identifying their potential to recover from population declines. In scallops, maturation of gonads is achieved in response to environmental cues such as temperature and food (Sastry and Blake 1971; Sastry 1979) and it is suggested that precise spawning synchrony relies upon chemical cues from neighbouring conspecifics (Beninger et al. 1995) that are detected by specific chemical receptors and communicated to the gonad to induce spawning (Barber & Blake 2006). Consequently, in areas with greater densities, mature, ready to spawn adults would receive stronger chemical signals that could result in a greater synchronization of spawning.

The scallop *Pecten fumatus* is a commercially and recreationally important species that once supported a significant dredge fishery in the D'Entrecasteaux Channel (DEC), Tasmania. Commercial catches peaked at 4,500 tonnes of meat in mid-1961 and declined rapidly to 100 tonnes in 1963 (Perrin & Croome 1988), further significant depletions of the scallop population have occurred since that time. Area closures, the cessation of the commercial fishery, and recently the closure of the recreational fishery have occurred in a so far unsuccessful effort to allow for stock recovery (Tracey & Lyle 2011). The abundance of *P. fumatus* in the DEC is distinctly lower than 50 years ago, and recent assessments suggest a decline by approximately 80% between 2006 and 2010 resulting from the impact of recreational fishing coupled with high natural mortality and poor recruitment during this period (Tracey & Lyle 2011). This decline in the population size and associated poor recruitment raised concern about positive density-dependent mechanisms that could be affecting recruitment. The population within the DEC appears to be largely self-recruiting, with negligible exchange of larvae with other populations, presumably a consequence of the

semi-enclosed nature of the DEC, (Woodburn 1988, Semmens et al. 2013b). Maintaining areas of high scallop density might prove important for recruitment, due to greater synchronization of gamete release (Styan & Butler 2003) and consequent improved fertilization rates at greater densities (Claereboudt 1999; Smith and Rago 2004).

This study aimed to assess the importance of adult density on aggregation patterns and synchronization of spawning in *Pecten fumatus*. This species is a simultaneous hermaphrodite with broadcast spawning that usually spawns during winter and spring (Olsen 1955, Harrison 1961, Sause et al. 1987, Fuentes 1994, Young et al. 1999), and is characterised by a protracted spawning season (Sause et al. 1987, Fuentes 1994). This species usually attains sexual maturity during its second year (Dredge 2006) and individuals of up to 16 years were recorded during the early fishery history (Fairbridge 1953). The study explored a number of specific questions: 1) whether there was a relationship between density, small scale aggregation patterns and nearest neighbour distance between individuals; 2) whether there is a the temporal pattern of spawning synchronization in two spawning seasons, and 3) whether site density and within-site con-specific proximity affect the probability of spawning.

5.2. Materials and methods

The first step to study spawning synchronization consisted in identifying the spawning season of *Pecten fumatus* in Great Bay. Every 15-20 days between August 2010 and late March 2011, approximately 25 adult scallops (shell length > 100 mm) were collected by divers at three sites (C,D and E in Fig. 5.1) in Great Bay in the D'Entrecasteaux Channel, southern Tasmania (147.33590 W and 43.22028 S, 12 meters depth). This sampling regime identified a protracted spawning season that lasted from October to late March, and from November until late March a greater percentage of individuals with partially spawned and fully spawned stages were observed (Chapter 4). Density was identified as a significant factor affecting the probability of spawning in 2010/11, therefore, it was decided to increase the number of sampling sites in 2012 to increase the range of densities and sample until a strong spawning event was detected. Site C, which had the lowest density of scallops in spawning season 2010/11, did not have enough scallops to provide sufficient samples for season 2012. Therefore, sites A, B, D, E, F, and G were sampled in spawning season 2012,

and only three months were sampled, as in December a strong spawning event was detected by assessing the gonad index (Chapter 4) and by histological techniques.

5.2.1. Aggregation patterns, densities and conspecific distances

Density (ind.m⁻²) was estimated at three sites (C,D and E in Fig. 5.1) in Great Bay, DEC in August 2010 by dividing the number of scallops encountered 1 m either side of a 100m transect by the total transect area (200 m²). In 2012, densities were estimated at six sites in Great Bay, during October 2012 (A, B, D, E, F, and G in Fig. 5.1). At each site, six 25 m transects were laid randomly and two divers collected all scallops 2m either side of the transect line. The site density was then calculated by averaging the transect densities. To examine patterns of distribution across densities, approximately eighteen 8 x 4 m quadrats were sampled haphazardly in sites A-F. To evaluate if the distribution of scallops was aggregated, the Morisita's Index of dispersion (I) was used because it is independent of population density (Morisita 1962)(Myers 1978). Morisita's index is strongly influenced by quadrat size (Elliot 1971), therefore, we estimated the position (+/- 20 cm) of each scallop inside each quadrat using an 8 m transect line marked every 10 cm and a 2 m long graduated PVC pipe which was placed perpendicular to the line every time a scallop was found on either side. The position of each scallop at the Y and X axis was recorded. To evaluate the effect of quadrat size, the area of the quadrat was sequentially reduced by half five times, obtaining quadrats of 16, 8, 4, 2 and 1 m², respectively. For each quadrat size, the number of scallops was estimated and the Morisita's Index was calculated (Elliot 1971). Each index was tested against a chi-squared based probability for the null hypothesis of random distribution. The aggregation patterns were examined using the *dispindmorisita* function in the *vegan* package version 2.0-9 in R version 3.0.2 (R Development Core Team 2010).

Nearest neighbour distance (NND) was estimated in sites A, B, D, E, F, and G during October 2012 for 22-34 scallops per site, and again during December 2012 for 17-23 scallops at three sites A, E and F. A 2m long graduated PVC pipe was used to determine the distance between each scallop to the nearest conspecific +/-10 cm within a 2 m radius. A 2 m radius was chosen based on *in situ* results of fertilization success for the abalone *Haliotis laevis* and the scallop *E. bifrons* where males and females had to be close (< 2 meters) to overcome gamete dilution effects and reproduce successfully (Styan 1998, Babcock & Keesing 1999). A chi-square test of independence was used to assess whether the NND frequency

distributions differed across the density estimates from the six sites. If the chi-square test of independence was significant, standardised residuals ($> \pm 2$) were used to determine where differences between observed and expected frequencies were significant.

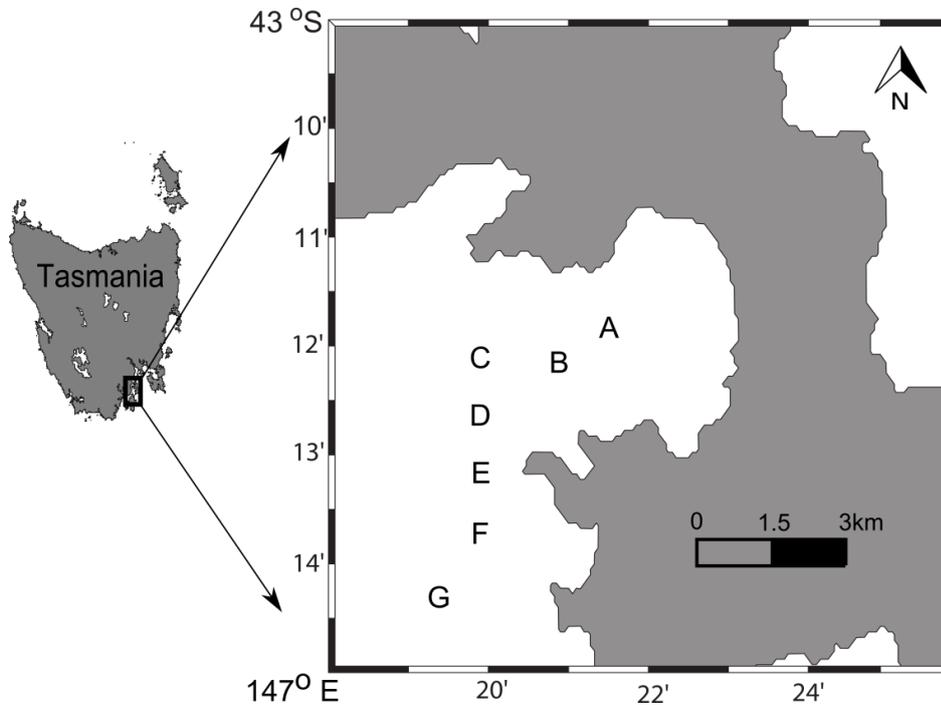


Fig. 5.1. Location of sampling sites (A, B, C, D, E, F, and G) in Great Bay, DEC.

5.2.2. Temporal pattern of synchronization of spawning

The effect of density on the synchronization of spawning was examined for two protracted spawning seasons: season 2010/11, from September 2010 to late March 2011 at monthly or fortnightly intervals at three sites (Fig 1, Sites C, D and E) and season 2012 at monthly intervals from October to December 2012 at five sites (A, B, D, E and F). Densities were estimated as described in the section *Aggregation patterns, con-specific distances and densities*.

Approximately 25 adult scallops (shell length > 80 mm) were collected at each sampling date from each site. Scallops were kept alive in seawater filled plastic containers (40x40x30 cm) until processing in the laboratory (within 1 day of capture). Each scallop was measured for shell length (to the nearest 1 mm), gonad weight, adductor muscle weight, and digestive gland weight (to the nearest 0.1 g). The gonad was fixed in FAACC (formalin,

acetic acid and calcium chloride) for histological sectioning. Fixed gonad tissue was transferred to 70% ethanol and stored for > 48 hours, before being embedded in paraffin and sectioned to 6 µm. Sections were stained with haemotoxylin and eosin and mounted with a mixture of distyrene, tricesyl phosphate and xylene (DPX synthetic resin mountant).

Gonadal reproductive stage was determined for each individual by assessing reproductive stage frequency distribution of the oocytes within each gonad using 30-50 random points (Coral Point Count with Excel extensions, version 4.1, (Kohler & Gill 2006)) distributed in the female part of the gonad in histological sections. Gonads contain a large number of acini whose walls are composed of connective tissue and primary germ cells. The lumen of the acini contains gametes in varying stages of gametogenesis, depending on the reproductive stage of the gonad. Reproductive stages were identified for female gonads following Mason (1958) and Harrison (1961). When the acini structure was clearly evident under the random point the reproductive stage was classified using the appearance of the acini (stages: developing, partial spawning and fully spawned). When the acini wall structure had broken down, the appearance of the oocyte under the random point was assigned a reproductive stage (stages: mature and atresia). The reproductive stage for each female was assigned as the most frequently observed reproductive stage. Partially spawned and fully spawned acini were pooled and categorised as “spawning stage” for analysis.

Data on reproductive stage were used to determine the proportion of individuals spawning over time. To assess if the proportion of spawned individuals was the same across sampling dates, a chi square test of independence was used. If the analysis was significant, standardised residuals ($> \pm 2$) were used to determine where differences between observed and expected frequencies were significant.

5.2.3. *Modelling the probability of spawning*

A multiple logistic regression was constructed to examine the effect of site density, nearest neighbour distance, gonad mass, scallop width, muscle mass and temperature on the probability of scallop having spawned (reproductive stage: spawning or not spawning) in spawning seasons 2010/11 and 2012. Strong collinearity between variables was checked with plots among all explanatory variables and variables removed if necessary. There was strong correlation between shell width, gonad, muscle and digestive gland weight, therefore

only gonad mass was used as an explanatory variable in the model (Table 5.1). Three different models were constructed, one for spawning season 2010/11, which included density as a categorical factor because only three sites were sampled (Table 5.1a), one for the spawning season 2012, which included three sampling months and where density was incorporated as a continuous variable (Table 5.1b) and finally a model to examine the effect of nearest neighbour distance on the probability of spawning, that included two sampling months (October and December 2012) (Table 5.1c). We re-analysed the first model using density as a continuous variable to explore if density remained a significant variable in our alternative model. Density was still significant; therefore our model seemed to be robust to the differences between the types of variables (categorical or continuous). When nearest neighbour distance was >2 m, an arbitrary value of 2.5 was entered in the model. Monthly average sea surface temperature (SST) for the study area were obtained from the MODISA satellite imagery (<http://oceandata.sci.gsfc.nasa.gov/MODISA/Mapped/Monthly/>) at 4 km scale and processed using MATLAB v. 7.2 (R2006a) (The MathWorks, Natick, Massachusetts). Sea surface temperature data were retrieved from the closest information pixel to the study area and used as a proxy for temperature (SST) in the area during the study period.

Table 5.1 - Variables used in multiple logistic regressions in a) spawning season 2010/11, b) 2012 and c) in October and November 2012 with nearest neighbour distance data

a) Spawning season 2010/11				
Predictor	Type	Average/Level	Min. value	Max. value
Density (ind.m ⁻²)	categorical	1.455, 0.59 and 0.255	NA	NA
Temperature (°C)	continuous	14.64	11.35	16.83
Gonad (g)	continuous	4.02	0.7	12.44
b) Spawning season 2012 (October, November and December)				
Density (ind.m ⁻²)	continuous	0.094	0.021	0.203
Temperature (°C)	categorical	11.23, 13.13 and 15.58	NA	NA
Gonad (g)	continuous	4.85	0.1	14.7
c) October and December 2012				
Density (ind.m ⁻²)	continuous	0.094	0.021	0.203

Month	categorical	Oct and Dec	NA	NA
Gonad (g)	continuous	4.22	0.1	10.7
Nearest Neighbour distance (m)	continuous	1.54	0.1	2.5

In a logistic regression, the natural logarithm of the odds of an event occurring are modelled as a linear function of the explanatory variables. If we want to understand the effect of each explanatory variable on the odds of an event occurring we need to apply an equation of the form:

$$\text{Odds of event occurring} = e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n}$$

Where β_0 = the intercept of the model, i.e. the odds of spawning occurring relative to not occurring when all predictors are equal to zero, and $\beta_1, \beta_2, \beta_n$ = the partial regression coefficients for the variables X_1, X_2 and X_n , respectively. Each coefficient estimate β_n was interpreted as usual for logistic regression: a z-unit increase in an explanatory variable result in an exponential ($e^{z\beta^i}$) increase in the odds of spawning occurring. For categorical variables, the reference level was shown as the intercept in the model output table and each level categorical variable was compared to this corresponding reference level. As $e^0 = 1$, which represents the effect of no change, the following formula gives the percentage increase or decrease in the odds due to a one-unit change in the explanatory variable: $(e^\beta - 1) * 100$ (Zuur et al. 2007).

A Wald test (Z) was used to test the null hypothesis that there is no relationship between the response variable (spawning or not spawning) and the predictors (density, nearest neighbour distance, gonad mass, and temperature) (Agresti 1996). Variables that were non-significant were removed and a reduced model refitted. Pearson's χ^2 was used to evaluate the goodness of fit of the model. Significant levels of all statistical procedures were set at $p=0.05$. Predicted probabilities of spawning occurring were calculated for three gonad weights (1, 3 and 5 grams in Figure 5.4) for easier visualization of results by using the following formula: $\text{predicted probability} = \frac{\text{odds}}{(1+\text{odds})}$.

It was assumed that nearest neighbour distance did not change between the spawning episode and the sampling date, i.e scallops did not move. This assumption is based on observations of adults of *P. fumatus* in the field (Gwyther and McShane 1988) and in aquaria (Mendo, pers. obs), in which individuals, once recessed into the sediment, only moved if a predator came in close vicinity of the scallop. Lack of movement has also been observed for other scallop species that recess such as *Pecten maximus*, which did not move for 27 days when recessing and moved only when approached by predators (Hartnoll 1967). Further, during reproduction *P. fumatus* uses energy from the muscle to support gamete production (Chapter 2), so energy in the muscle would probably not support consistent swimming behaviour, as observed for the scallops *Euvola ziczac* and *Chlamys islandica*, which need more time to recover from escape responses when they have mature and spawning gonads compared to developing or immature (Brokordt et al. 2000a; Brokordt et al. 2000b). Finally, it was assumed that an individual of *P. fumatus* scored as spawning based on gonad histology would have done so recently, as other scallops species such as *Placopecten magellanicus* and *Pecten novaezelandiae* show fast rates of gonad redevelopment after spawning (at the scale of days) (Bonardelli et al. 1996, Williams 2005).

5.3. Results

5.3.1. Relationship between density and aggregation patterns

In 2012 distribution patterns differed with scallop density. For densities ranging from 0.021 to 0.075 ind.m⁻², scallops did not show an aggregated pattern, while at greater densities (0.085, 0.103 and 0.203 ind.m⁻²) an aggregated pattern was apparent (Table 5.2). Generally, as quadrat area decreased, the scallop distribution became less aggregated. Aggregated patterns were detected mostly with 16 and 8 m² size quadrats.

Table 5.2 - Standardized Morisita Index of Dispersion (I) and significance levels calculated for each site with varying densities in October 2012. A chi square based probability (χ^2) tested the null hypothesis of random distribution pattern.

Density	Site	Quadrat size	Morisita's Index	χ^2	df	p	Distribution
0.021	C	32	1.363	21.00	17	0.2263	Not aggregated
		16	0.461	28.538	35	0.771	Not aggregated
		8	0.923	70.076	71	0.5087	Not aggregated
		4	0	131	143	0.755	Not aggregated
		2	0	283	295	0.682	Not aggregated
		1	0	563	575	0.631	Not aggregated
0.053	A	32	0.967	16.375	17	0.4974	Not aggregated
		16	1.333	44	35	0.1415	Not aggregated
		8	1.142	61.85	59	0.374	Not aggregated
		4	0.993	142.8	143	0.489	Not aggregated
		2	1.324	296.4	287	0.338	Not aggregated
		1	1.367	488.55	479	0.371	Not aggregated
0.075	F	32	1.031	18.268	17	0.3721	Not aggregated
		16	1.018	35.8	35	0.4307	Not aggregated
		8	0.956	69.18	71	0.5388	Not aggregated
		4	0.797	134.48	143	0.682	Not aggregated
		2	1.594	311.97	287	0.148	Not aggregated
		1	0.634	556.65	572	0.669	Not aggregated
0.085	G	32	1.058	19.941	17	0.2772	Not aggregated
		16	1.634	63.56	35	0.002	Aggregated
		8	1.600	98	71	0.018	Aggregated
		4	1.391	160.60	143	0.149	Not aggregated
		2	1.391	304.60	287	0.227	Not aggregated
		1	2.226	630.17	575	0.055	Not aggregated
0.103	E	32	1.272	32.830	17	0.0118	Aggregated
		16	1.646	71.21	35	0.0002	Aggregated
		8	1.524	100.89	71	0.0136	Aggregated
		4	1.430	157.98	143	0.0752	Not aggregated
		2	1.337	304.55	285	0.203	Not aggregated
		1	1.346	595.10	575	0.272	Not aggregated
0.203	F	32	1.114	26.895	16	0.0426	Aggregated
		16	1.198	50.043	32	0.0220	Aggregated
		8	1.248	72.4	54	0.0480	Aggregated
		4	1.599	150.75	107	0.0034	Aggregated
		2	1.907	295.75	225	0.0010	Aggregated
		1	2.000	643.08	547	0.0028	Aggregated

5.3.2 *Relationship between density and nearest neighbour distance*

The frequency distribution of nearest neighbour distances differed among densities ($\chi^2=85.29$, df 20, $p<0.001$). The site with the greatest density of scallops (0.203 ind.m⁻²) had a greater proportion of scallops with a nearest neighbour distance < 0.5m and smaller proportion of scallops with a nearest neighbour distance > 2 meters than expected (Fig. 5.2). In contrast, the sites with the lowest scallop density (0.053 and 0.021), had a greater proportion of scallops with a nearest neighbour distance > 2 m than expected (Fig. 5.2). Average nearest neighbour distances decreased with increasing densities (Table 5.3) and the average width of scallops in each site varied from 111 to 115 mm (Table 5.3).

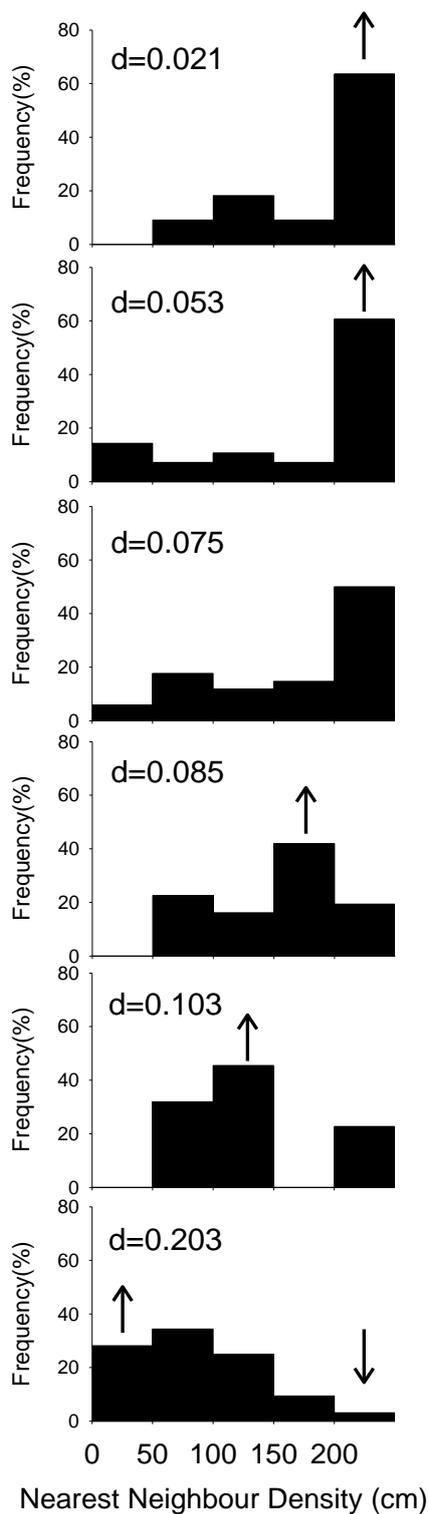


Fig. 5.2. Frequency of nearest neighbour distances (NND) for scallops at different densities (d) in October 2012. Arrows indicate where frequencies scallops were more (↑) or less (↓) than expected in each nearest neighbour class under the hypothesis that the frequency of individuals in each distance class was equal across densities.

Table 5.3. Summary data for nearest neighbour distances (NND) calculated for each site with varying densities and associated scallop size (width) and standard deviations (sd). When nearest neighbour distance was > 2 m, an arbitrary value of 2.5 was entered for calculations

Density (ind.m ⁻²)	Number of scallop pairs measured	Average NND (cm)	sd	Average width (mm)	sd
0.021	16	194	0.68	114.62	7.91
0.053	21	186	0.84	115.97	7.10
0.075	19	180	0.77	115.89	6.98
0.085	18	160	0.51	111.11	6.22
0.103	15	142	0.56	112.76	7.38
0.203	20	98	0.64	114.38	10.49

5.3.2. Temporal pattern of synchronization of spawning

During the 2010/11 spawning season (October to late March), the proportion of individuals spawning at each site differed among months ($\chi^2=31.42$, df 5, $p<0.001$). A lesser proportion of spawning individuals was observed in October and January (3.5 and 8.1%, respectively) compared to mid-December and late February 2011 (35.4 and 39.6%, respectively; Fig. 5.3a). The proportion of individuals spawning in 2012 was also affected by month ($\chi^2=81.15$, df 2, $p<0.001$), with a peak occurring in December (59.8% of individuals spawned; Fig. 5.3b) and lowest spawning activity recorded in November (2.5% of individuals spawned, Fig. 5.3b).

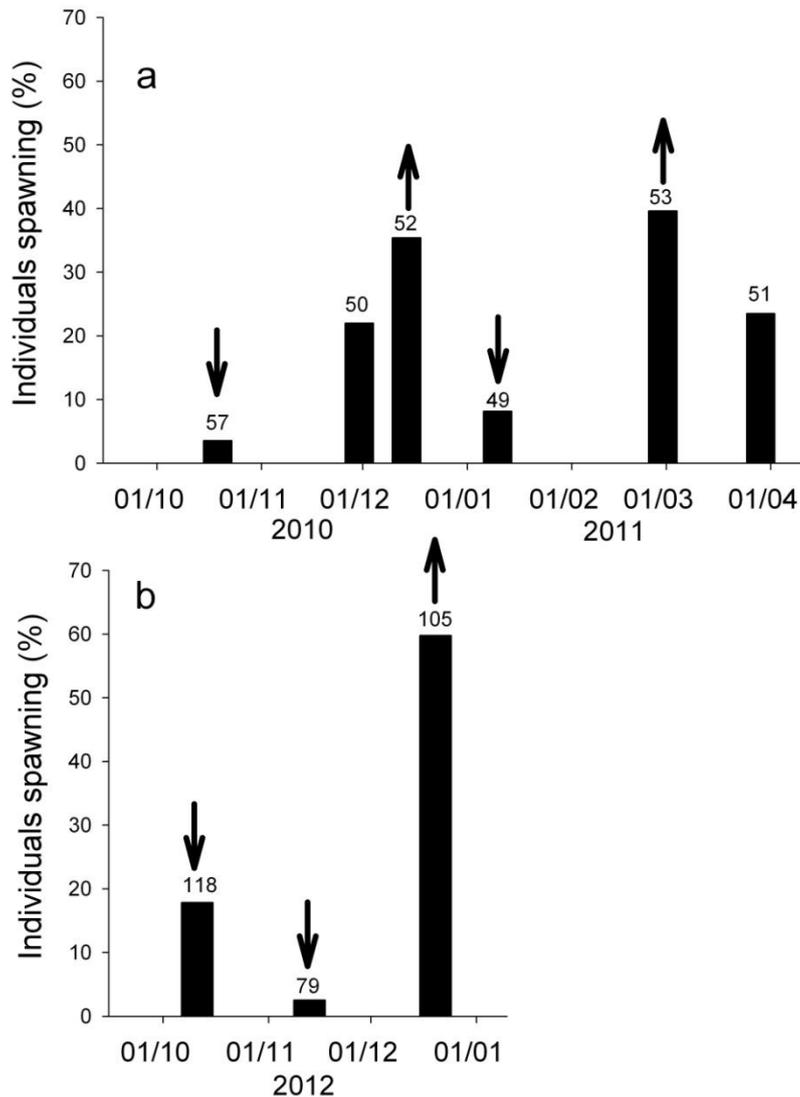


Fig. 5.3. Percentage of individuals spawning in a) spawning season 2010/11, and b) spawning season 2012, numbers above the bars indicate sample size (n) per sampling date. Arrows indicate where frequencies of spawned scallops were more (↑) or less (↓) than expected in each sampling date under the hypothesis that the frequency of individuals in each sampling opportunity was equal across dates.

5.3.3. Modelling the probability of spawning

The probability of a scallop having spawned in 2010 was explained by scallop density, SST, and gonad mass ($\chi^2=39.71$, $p<0.001$, for specific odds ratios, confidence intervals and Wald statistics refer to Table 5.4). The model predicted that for each 1°C increase in temperature the odds of scallops having spawned would increase by 39.8%, and for every 1g increase in gonad weight, the odds of scallops having spawned would decrease by 31.4% (Table 5.4).

The odds of scallop having spawned was 284.6% greater at the site with 1.45 ind.m⁻² and 165% greater at the site with 0.59 ind.m⁻² when compared to the site with 0.255 ind.m⁻² (Table 5.4). The probability of a scallop having spawned in 2012 was explained only by SST ($\chi^2=78.93$, $p<0.001$, for specific odds ratios, confidence intervals and Wald statistics refer to Table 5.4). The model predicts that when the SST is 15.58 °C, the odds of spawning are 953.8% greater than the odds of spawning occurring when the SST was 11.2 °C (Table 4).

Table 5.4 – Odds ratio, confidence intervals and Wald test statistics (Z-value) from logistic regressions for spawning season 2010/11 and 2012

Spawning season 2010/11

Term	Odds ratio	Confidence interval	Z-value	p-value
SST (°C)	1.398	1.266 - 1.543	3.358	<0.001
Gonad (g)	0.685	0.607 - 0.774	-3.111	0.002
Density0.59	2.651	1.724 - 4.075	2.266	0.023
Density1.45	3.845	2.531 - 5.841	3.221	0.001
Null deviance: 322.68 on 346 df				
Residual deviance: 282.97 on 342 df				

Spawning season 2012

Term	Odds ratio	Confidence interval	Z-value	p-value
SST - 13.3°C	0.241-	0.110 - 0.529	-1.811	0.07
SST - 15.58°C	10.538	7.192 – 15.440	6.163	<0.001
Null deviance: 292.52 on 272 df				
Residual deviance: 213.59on 270 df				

5.3.4. *Nearest Neighbour Distance and probability of spawning*

The probability of a scallop having spawned was explained by SST and the interaction between gonad mass (g) and nearest neighbour distance (NND, m) ($\chi^2=45.4$, df 4, $p<0.001$). The model predicted that the odds of a scallop having spawned in December are

530% greater than for October (Table 5.5). In smaller gonads, an increase in nearest neighbour distance is associated with a decrease in the probability of a scallop having spawned (Fig. 5.4a,b), e.g., when a gonad weighs 1 g, an increase of 1 m in the nearest neighbour distance is associated with a 77% decrease in the odds of spawning (Table 5.5). As gonad weight increases, the probability of a gonad having spawned decreases and an increase in nearest neighbour distances is associated with a greater probability of a scallop having spawned (Fig 5.4c).

Table 5.5 - Odds ratio, confidence intervals and Wald test statistics (Z value) estimated for the logistic regression for October and December 2012 including gonad weight and Nearest Neighbour Distance (NND)

Predictor variable	Odds ratio	Confidence interval	Z-value	p-value
Month: December	6.309	3.803 - 10.464	3.649	<0.001
Gonad weight	0.174	0.098 – 0.310	-3.023	0.002
NND	0.064	0.025 – 0.164	-2.942	0.003
Gonad:NND	2.164	1.676 – 2.792	3.028	0.002
Null deviance: 164.56.65 on 152 df				
Residual deviance: 119.16 on 148 df				

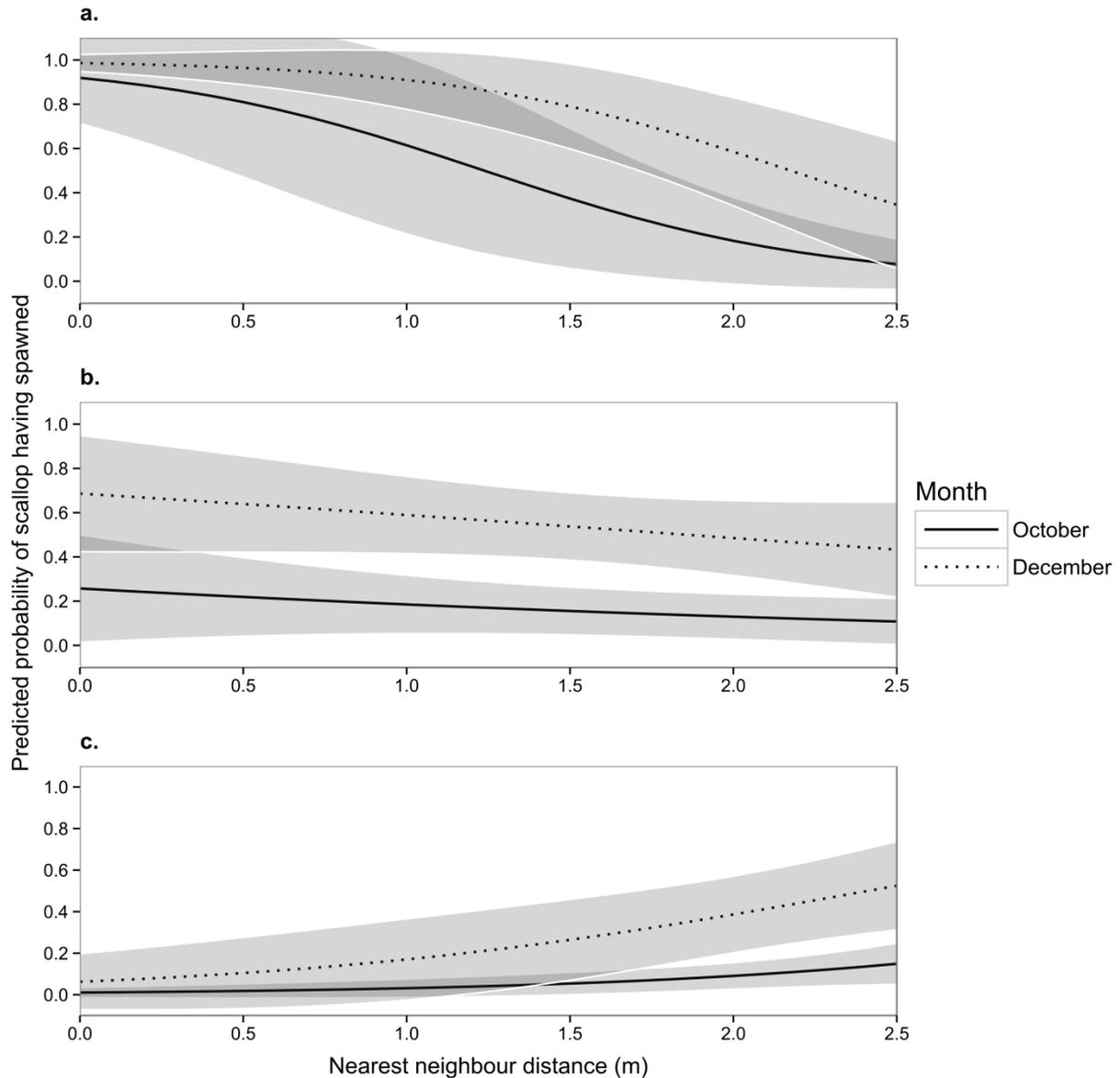


Fig. 5.4. Predicted probability of a scallop having spawned with nearest neighbour distance (cm) in a) small (1g), b) medium (3 g) and c) large (5g) gonads in October (11.2 °C) and December (15.6°C) 2012. Gray areas show 95% confidence intervals.

5.4. Discussion

This study suggests that *Pecten fumatus* will be more likely to engage in spawning activity when at greater densities and at closer proximity to conspecifics. This situation will also increase the potential encounter rates between gametes, having a net effect of an increased probability of spawning success. The findings support the idea postulated by Levitan et al, (2011) that a density decrease will indirectly reduce synchronization of spawning. Maintaining regions of high scallop density is therefore considered important for

enhancing recruitment success, partly due to the improved fertilization rates at greater densities (Smith & Rago 2004), but also due to indirect effect on synchronization of spawning or actual engagement of scallops in the spawning activity.

Greater densities of *Pecten fumatus* were associated with aggregated rather than random small scale patterns and smaller distances between conspecifics, both of which are extremely important for successful fertilization of gametes (Levitan et al. 1992, Babcock & Keesing 1999). The small scale distribution of *Pecten fumatus* was aggregated at densities ranging from 0.085-0.203 ind.m⁻², comparable to the patterns observed in the gonochoristic (separate sexes) scallop *Placopecten magellanicus*, at densities ranging from 0.16 – 0.57 ind.m⁻². (Langton and Robinson 1990; MacDonald and Bajdik 1992; Stokesbury and Himmelman 1993). Nearest neighbour distances were also similar; in this study 87.5% of the scallops were located less than 150 cm apart at a density of 0.203 ind.m⁻², and at similar densities, two gonochoristic scallop species *Placopecten magellanicus* (0.34 ind.m⁻²) and *Chlamys bifrons* (0.24 ind.m⁻²) showed 90% and 85% of the individuals located less than 150 cm apart, respectively (Stokesbury and Himmelman 1993; Styan 1998). These similarities in aggregation patterns and nearest neighbour distance suggest that the hermaphroditic nature of *P. fumatus* does not have an effect on aggregation patterns observed in scallops. While hermaphrodites have the capability to self-fertilise, outcross mating seems to be the predominant mode of successful fertilization for many hermaphroditic marine invertebrates (Heyward and Babcock 1986; Knowlton and Jackson 1993). In *P. fumatus*, fewer self-fertilized embryos develop to D-veliger stage and show lower growth rates compared to cross-fertilized ones (Heasman et al, 1996). This reduction in survival of *P. fumatus* embryos and the lower probability of releasing gametes when at lower densities strongly suggest that *P. fumatus* is not favouring self-fertilization over cross-fertilization, however, we can not rule out that self-fertilization might occur at lower densities as a strategy to avoid complete reproductive failure when no mates are in close proximity, as observed for other invertebrate species with no or limited mobility (Ghiselin 1987; Yund and McCartney 1994; Manriquez and Castilla 2005).

For marine broadcast spawners with external fertilization, distances of only a few meters between individuals may be sufficient to cause sperm limitation, reducing fertilization success (Levitan et al. 1992, Levitan & Petersen 1995, Babcock & Keesing 1999). Large egg production by *P. fumatus* (1.2×10^6 eggs per spawning event in wild scallops (Heasman et al.

1994)) may not guarantee successful fertilization if scallop densities are too low or proximities between individuals are too great. The relationship between distances between conspecifics and fertilization success in *P. fumatus* is unknown, but for another Pectinid, the scallop *E. bifrons*, males and females need to be very close (<0.5 m) to overcome gamete dilution effects (Styan 1998). Using 0.5 m as an estimate for effective cross-fertilization in the *P. fumatus* population in the study area, then even in the site with the greatest density in 2012 (0.203 ind.m⁻²), most individuals would have incurred gamete dilution effects, as only 25% of the individuals were within the optimum distance.

Densities of scallops explained the probability of a scallop having spawned in 2010 but not in 2012. In 2010 only three sites were examined, however, site specific characteristics are unlikely to explain this relationship, given the similarity and proximity of the sites (~1.5 km apart, silty sandy bottom, ~12 metres depth) and considering the increased effect of density on the probability of scallop having spawned, with a greater probability at the high density site than at medium density site, which was in turn greater than the low density site. This suggests the existence of a conspecific cue that triggers spawning in scallops as evidenced for several marine invertebrates such as the oyster *Ostrea virginica* (Galtsoff 1938), the moon scallop *Amusium pleuronectes* (Belda and Del Norte 1988), the giant clam *Tridacna maxima* (Gwyther and Munro 1981), abalone (Babcock & Keesing 1999), starfish (Beach et al. 1975, Miller 1989) and polychaetes (Hardege & Bentley 1997). For example, spawning induction trials of solitary *Haliotis laevigata* resulted in only a few individuals actually spawning, while individuals located in tubs with conspecifics spawned simultaneously (Babcock & Keesing 1999). During 2012 density did not explain the probability of spawning and this may be due to the different range of densities observed among sites. The greatest density in this spawning season was less than the smallest density recorded in spawning season 2010/11 and suggests the existence of a threshold density below which the cues remained undetected. Laboratory studies are needed to confirm the presence of spawning cues in *P. fumatus* and the effect of density on detection levels.

Spawning synchrony (the proportion of individuals spawning at a particular sampling date) was highly variable, ranging between 3.5-59.8% in this study, which is similar to values estimated for the scallop *Pecten novaezelandiae* (Williams 2005). Frequency of sampling and differences between sampling regimes in both spawning seasons might have missed strong spawning events and made between year comparisons difficult, however, the

observations of synchronization in both years suggest that it may not be appropriate to assume that population density is equal to spawner density in scallops with protracted spawning. Spawning observations *in situ* in bivalves such as the scallop *Mimachlamys asperima* and the mussel *Mytilus californianus* show that spawning can occur in small specific areas, while individuals located in areas meters or tens of meters away do not spawn (Styan & Butler 2003, Gosselin 2004). These observations and low fertilization rates observed for individuals located further apart (Levitan et al. 1992) suggest that variation in synchronization of spawning should probably be assessed within a spatial context and within small distances, i.e inside a patch or at 1-10's cm scales.

Small scale aggregation patterns were observed at greater densities of adults of *Pecten fumatus* but not at low densities. The reasons underlying these patterns (i.e. habitat selection, differential predation mortality, reproduction) are still unclear in scallops, and while small scale 'clumps' or patches have been detected (MacDonald and Bajdik 1992; Stokesbury and Himmelman 1993), there is no evidence of aggregative behaviour related to reproduction. While this study assessed aggregation patterns during the spawning season, to make better conclusions about aggregative behaviour, further studies on scallops should incorporate the assessment of aggregation patterns in several occasions before, during and after spawning as conducted for other species such as sea stars (Minchin 1987), limpets (Coleman et al. 2006) and abalone (Shepherd 1986). Acoustic methods may also provide useful information to evaluate aggregative behaviour, as evidenced for the abalone *Haliotis corrugata* (Coates et al. 2013).

While it is well known that reducing densities in a sessile or semi-sessile marine broadcast spawner reduces the number of individuals contributing to the production of gametes, this study suggests that these reductions also decrease the synchronization of spawning and rate of gamete release. The results of this study support the establishment or maintenance of regions with high scallop densities to enhance recruitment success. These management regimes have already proven beneficial for other scallop populations, for example, the establishment of spawner sanctuaries (harvest-free areas planted with high densities of adults) had a positive effect on recruitment for several populations such as *Pecten maximus* in Bay of Brest (Dao and Carval 1999), *Pattinopecten yessoensis* in Japan (Ventilla 1982), *Argopecten irradians concentricus* in North Carolina (Peterson et al. 1996), *Argopecten irradians* in Florida (Arnold et al. 2005) and *Argopecten irradians irradians* in

New York (Tettelbach et al. 2013). Closing areas to fishing activities have proven successful in increasing population numbers for *Placopecten magellanicus* in Georges bank and Southern New England, United States of America (Murawski et al. 2000) and *Pecten maximus* in the Isle of Main, United Kingdom (Beukers-Stewart et al. 2005) and rotational management systems where areas of a scallop population are subjected to periodic fishing while maintaining others unfished can increase harvest yield and maintain higher spawning stock biomass (Caddy and Seijo 1998; Myers et al. 2000).

Chapter 6. General discussion

This thesis examined reproductive and post-settlement factors likely to influence recruitment in a marine benthic invertebrate and has highlighted the importance of habitat requirements, predation at juvenile stages and density dependent reproductive processes in impacting recruitment. By considering both biological and ecological processes, this study contributes to our understanding of the factors that affect recruitment in benthic marine invertebrates. Specifically, habitat (Chapter 2), early post-settlement predation (Chapter 2 &3) and density dependent reproductive processes (Chapter 4 &5) have been identified as key factors influencing recruitment success in the scallop *P. fumatus*.

Prior to undertaking this study, little was known about role of these factors in influencing recruitment in spite of significant depletions in scallop populations within the study area, the D'Entrecasteaux Channel (DEC), over many years. This research identified a number of factors that may hinder the effective recovery of *P. fumatus* stocks within the area despite protracted closures to fishing. Sediment type and habitat characteristics were found to explain much of the variability in the abundances of the three co-occurring scallop species, including *P. fumatus*, found in the study area (Chapter 2). By establishing the shape and direction of these scallop-habitat relationships it is suggested that habitat-mediated predation and specific behavioural characteristics of each of the scallop species are most likely driving the observed abundance (a proxy for recruitment) patterns (Chapter 2 and 3). This was confirmed by experimental manipulation *in situ*, where predation rates on *P. fumatus* of up to 95% during the first weeks after settlement were recorded (Chapter 3). The reproductive strategy also affected recruitment patterns in *P. fumatus* as partial release of gametes during the spawning season ensures some progeny survive, despite adverse environmental conditions. However, in populations with reduced spawner densities this advantage may not be fully realized (Chapter 4 & 5), due in part to the relationship between spawner density and synchronization of spawning which can ultimately affect fertilization success (Chapter 5).

6.1 Implications of the findings

6.1.1 The importance of habitat characteristics

The patterns of distribution and abundance of adult scallops in three co-occurring species in the DEC could be explained by species-specific habitat characteristics (Chapter 2). Habitat is critical in determining abundance patterns in many benthic marine organisms as they depend on particular habitat features for settlement (Harvey et al. 1993, Rodriguez et al. 1993), attachment to structures (Bell & Gosline 1996, Brand 2006), access to prey (Sebens 1991) and protection from predators (Orth et al. 1984, Wolf & White 1997). Despite the importance of habitat to the survival of organisms, little is known about the basic habitat requirements of the vast majority of marine organisms (Hutchings & Reynolds 2004). Such an understanding is particularly important given that, after exploitation, habitat modification and degradation represent a major driver of species depletions in coastal areas (Munday 2004, Lotze et al. 2006). For example, a significant reduction in seagrass cover, predominantly of *Heterozostera tasmanica* has occurred in the last few decades in the DEC (Mount & Otera 2011). The implications of these reductions on the patterns of distribution and abundance of scallops are unknown, although for *Argopecten irradians*, loss of seagrass habitat has been associated with population declines (Milne and Milne 1951; Pohle et al. 1991; Orth et al. 2006; Hernandez et al. 2012). Therefore, it is possible that a reduction in seagrass cover could have had an effect on *E. bifrons* abundance (Chapter 2), probably due to increased vulnerability to predation outside these vegetated habitats (Wolf & White 1997).

Another important factor contributing to habitat change or degradation in south-eastern Tasmania are introduced marine species. The New Zealand screwshell *Maoricolpus roseus* is a gastropod introduced into Tasmania most likely during the 1920s (Bax et al. 2003) and now occupies vast areas of benthic habitats, including within the study area, at densities up to 2500 ind.m⁻² (Reid 2003; Gunasekera et al. 2005). This gastropod modifies habitat structure, often completely covering soft substrates (with shells of live and dead individuals) and impacting on the abundance and condition of *P. fumatus*, possibly through competition for space and food (Reid 2010). While the current study showed a positive relationship between shell cover and *P. fumatus* abundance (Chapter 2), levels of shell coverage (including dead scallops, screwshells, among others) were always below 50%, which may not

correspond to the densities where a significant impact was detected by Reid (2010). Another introduced species in Tasmania is the northern Pacific starfish, *Asterias amurensis*. The expansion of *A. amurensis* numbers within the study area has raised concerns about their potential impact on the endemic scallop populations: outbreaks of this species had a detrimental effect on the shellfish industry in Japan (Hatanaka & Kosaka 1958) and losses of spat of *P. fumatus* over a settlement season due to *A. amurensis* predation are reported to be as high as 50% in Tasmania (S. Crawford pers. comm. in Hutson et al. 2005). The negative relationship between the abundances of *P. fumatus* and *A. amurensis* (Chapter 2) could be explained by predation, as this starfish was responsible for about a quarter of predation mortality recorded in juveniles of *P. fumatus* (Chapter 3). Therefore, habitat modification and degradation, not only through changes in structure or complexity but also by the addition of invasive species can have significant effects on recruitment in scallops, although the magnitude of these effects is hard to determine.

6.1.2 *Early post-settlement predation: a driver of recruitment success*

In *Pecten fumatus* early post-settlement predation may prevent the establishment of local populations (Chapters 2 & 3). Thus, even if sufficient larvae are produced and then settle at a given site, post-settlement processes mediated by habitat appear to be extremely important in determining the successful establishment of a scallop population, a phenomenon observed in fish and other bivalve species (Tupper & Boutilier 1995, Seitz et al. 2001, Juanes 2007).

The high predation rates recorded at the Nutgrove Beach study site appear to have been mediated by macroalgal biomass (Chapter 3). Macroalgal filaments act as settlement substrate for *P. fumatus* spat but the expectation that macroalgal cover would provide greater protection from predation than bare sand to juvenile *P. fumatus* was not evident (Chapter 2&3). Rather, field-based evidence suggest that increasing structural complexity in submerged vegetation did not necessarily result in increased survival, as has been reported in experimental studies observed under controlled conditions (Mattila et al. 2008, Lannin & Hovel 2011). The specific mechanisms underlying predator-prey interactions in scallops, as influenced by substrate structural complexity, require further attention. While macroalgae may act as settlement substrate for several scallop species (Harvey et al. 1993, Cantillán 2000), species specific behaviour needs to be taken into account following byssal

detachment. For example, a possible explanation for the observation that survival rates in juvenile *P. fumatus* were higher in sand may relate to decreased vulnerability to predation related to recessing behaviour or, conversely, increased vulnerability if unable to use this behaviour to avoid predator detection when in dense macroalgae beds. The precise nature of such responses are, however, likely to depend on the structure and patchiness of the vegetation (Irlandi et al. 1995).

6.1.3 Reproductive processes influencing recruitment

A detailed knowledge about the reproductive processes leading to the recruitment is necessary to understand the dynamics of a population (Ramirez Llodra 2002). In *P. fumatus*, protracted spawning was primarily fuelled by stored energy substrates and energy derived by the resorption of mature oocytes (Chapter 4). Egg resorption is a process better studied in parasitoid insects, and has been advanced as an important adaptive trait that can act as a energy insurance at times of irregular food availability and starvation, comparable to the hoarding behaviour in vertebrates (Richard & Casas 2009). In fish, it is suggested that the number and quality of oocytes are reduced by atresia to optimize reproductive investment (McBride et al. 2013) and is generally associated with species with indeterminate fecundity (fecundity is not fixed before spawning and oocytes continue to be matured and spawned during spawning season) (Murua & Saborido-Rey 2003). In scallops, atresia is suggested to provide energy for oogenesis in *Pecten maximus* (Duinker & Nylund 2002) and *P. fumatus* (Chapter 4), however, the reasons for atresia in scallops are still unclear, for instance energy content in the muscle and digestive gland do not appear to explain observed levels of atresia (Chapter 4). As studies on reproductive cycles in scallops incorporate the quantification of atresia in their reproductive stage analysis we will start to understand if atresia is an adaptive mechanism for protracted spawners or if there are other reasons responsible such as environment or food availability.

Pecten fumatus is more likely to spawn at greater densities with and at closer proximity to conspecifics (Chapter 5), implying a form of reproductive facilitation similar to that observed for highly synchronized spawning corals (Levitan et al. 2011). Reproductive facilitation occurs when individuals are more likely to reproduce if able to perceive others reproducing (Berec et al. 2007). This mechanism can generate an Allee effect (Berec et al. 2007), especially when densities drop to levels where individuals are unable to perceive each

other, and can hinder the recovery of a population at low densities (Stierhoff et al. 2012). Reproductive facilitation is mostly reported for mammals and insects (see review in Gascoigne et al. 2009), and recently for the asexual freshwater snail *Potamopyrgus antipodarum*, where waterborne substances produced by the snail are most likely the cue causing facilitation (Neiman et al. 2013, Zachar & Neiman 2013). The present study represents the first demonstration that reproductive facilitation may occur in scallops and implies that reduction in spawner densities will reduce the numbers of eggs and sperm produced, increase nearest neighbour distances (Chapter 5) and therefore decrease the chances of sperm and eggs meeting (Pennington 1985, Levitan 1995), and indirectly affect the synchronization of spawning in a population (Chapter 5).

6.2 Recommendations for scallop management in south-eastern Tasmania

Overfishing is a serious threat to benthic marine populations worldwide, with a third of the major stocks overexploited or closed (Anderson et al. 2011). Fisheries closures have not always led to rapid recovery of populations (this study, Hobday et al. 2001), therefore identifying important factors influencing the recruitment of exploited benthic marine invertebrates can provide information necessary for sustainable fisheries management and persistence of populations (Hobday et al. 2001). This is particularly important in this group of species, since the rate at which invertebrate fisheries are expanding is currently not met by basic scientific research for appropriate management (Anderson et al. 2011).

Habitat characteristics (Chapter 2), early post-settlement predation (Chapter 2 &3) and density dependent reproductive processes (Chapter 4 &5) have been identified as key factors influencing recruitment success in the scallop *P. fumatus*. The findings of this study provide further evidence that restocking operations and maintaining areas of high spawning stock densities closed to fisheries will be essential to enhance spawning activity and fertilization leading to population recovery. Closing areas to fisheries had a positive effect on populations of *Placopecten magellanicus* (Murawski et al. 2000), *Pecten maximus* (Beukers-Stewart et al. 2005), several populations of *Argopecten irradians* in New York, Florida and North Carolina (Peterson et al. 1996; Arnold et al. 2005; Tettelbach et al. 2013) and *Patinopecten yessoensis* in Japan (Masuda and Tsukamoto 1998). Restocking of wild populations in South eastern Tasmania with hatchery produced stock is currently not an option for *P. fumatus* as no hatcheries are producing commercial numbers of spat. Rotational

management systems that are currently applied in Tasmanian commercial scallop fisheries, where only small areas of known stocks are opened to commercial harvesting (Harrington et al. 2007), leaving high density areas unfished might prove a more viable alternative for fisheries management, provided that the links between source and sink subpopulations are better understood (Caddy and Defeo 2003; Lipcius et al. 2008) and that the scale and closure time of the areas and densities therein are optimal (Chapter 5, Kassner and Malouf 1982; Hart 2003). The positive experience in Queensland, where closing some areas to fishing and applying a rotational harvesting strategy for *Amusium japonicum balloti* increased the yield per recruit and biomass per recruit (O'Sullivan et al. 2005; Jebreen et al. 2006), further supports this management strategy.

Establishing the optimal densities for scallop reproduction and spawning synchronization would be highly beneficial for scallop stock management. Styan (1998) estimated the optimal distance for successful fertilization for *Equichlamys bifrons* as <0.5 m. If we used this estimate for *Pecten fumatus* then at densities of 0.203 ind.m⁻², only 25% of the individuals would not have incurred gamete dilution effects (Chapter 5). Additionally, at this distance, the probability of spawning of *Pecten fumatus* ranges between 50-95 % in optimal temperature conditions (as observed in December, 15.6° C). Maintaining areas with densities > 0.2 ind.m⁻² might therefore prove valuable for population increases in *P. fumatus*. Rather than proposing absolute biomass levels below which the population will be vulnerable to overfishing, critical densities and associated nearest neighbour distances should be used and incorporated into management plans as has been proposed for other bivalves such as the clam *Macoma balthica* (Luttikhuizen et al. 2011) and abalone *Haliotis laevigata* (Dowling et al. 2004).

A positive relationship between spawner density and recruit density the following year was found for *Pecten fumatus* in the DEC. Observations of high recruitment levels in scallop populations at times when spawning stock is at very low levels has led to conclusions that there is no apparent relationship between spawning stock and recruitment (Naidu 1991; Román 1991; Ciocco and Monsalve 1999). However, a review by Orensanz et al 2006 clearly showed that for self-sustaining scallop stocks, recruitment is positively correlated with stock size. This study supports Orensanz et al. (2006) conclusion and suggests that efforts should be directed to restock areas in the DEC such as Great Bay, where adults were consistently found in greater quantities before the recreational fishery was re-opened in 2006 (Tracey and

Lyle 2011), which suggests that this Bay has favourable conditions for survival after settlement.

Potential re-stocking operations should consider the species-specific habitat characteristics that are most suitable for post-settlement survival (Chapter 2 and 3). Selecting appropriate habitat characteristics is an important factor to consider for restocking of scallops because predation can have significant effects on released scallop numbers (Chapter 3, Hatcher et al. 1996). The findings of this study suggest that restocking programs for the three species of scallops in the DEC would benefit from targeting different habitat characteristics, i.e. areas with greater sponge cover for *M. asperrima*, greater seagrass cover for *E. bifrons* and lower macroalgal cover for *P. fumatus*. Re-seeding trials of juveniles of *P. fumatus* (> 33.5 mm height) in enclosures in the late 1980s were encouraging albeit labour intensive, as frequent removal of the starfish *Coscinasterias calamaria* was necessary to obtain survival rates of 64% after almost two years (Cropp 1988). The suitability of spat collection and subsequent re-seeding or transplantation still needs to be carefully assessed for the DEC, as the success of restoration efforts in bivalves depends on several factors such as habitat characteristics, planting season and density, and predator abundance (Morgan et al. 1980; Peterson et al. 1995). Also, transplanting may affect population attributes, for example, animals might not spawn when local conditions are at best for larval survival (Bell et al. 2005) with differences in reproductive timing observed for transplanted *Pecten maximus* (Cochard and Devauchelle 1993; Mackie and Ansell 1993). All these factors still need careful consideration in the DEC.

6.3 Future research directions

From a conservation and management perspective, knowledge of particular habitat requirements of benthic marine organisms is valuable for target species, since the threats of anthropogenic stressors to habitats are increasing (Lotze et al. 2006, Halpern et al. 2008). Moreover, benthic marine invertebrates are commonly fished with bottom trawlers and dredges, which are fishing techniques that not only reduce the stock but also affect associated habitat characteristics (Collie et al. 2000). The impact and recovery times after dredging depend on the magnitude of the fishing disturbance relative to environmental disturbances or variability and the nature of the habitat (Collie et al. 2000, Henry et al. 2006, Sciberras et al. 2013). Several studies have highlighted the impact of dredging techniques on abundances of

erect sessile organisms such as sponges, bryozoans and anemones (McConnaughey et al. 2000, Guijarro Garcia et al. 2006, Hinz et al. 2011). If certain physical elements or structure are important to the survival of benthic marine organisms as this (Chapter 2 and 3) and several other studies (Sebens 1991, Seitz et al. 2001, Talman & Keough 2001) suggest then exploited benthic marine invertebrates may be subjected to greater habitat disturbance and consequently slower rates of recovery than pelagic species for which critical habitat components are not equally impacted during fishing (Hutchings & Reynolds 2004). Therefore, a thorough examination of the habitat requirements of benthic marine invertebrates is needed, not only for adults as in this study (Chapter 2), but for the different life stages (settled larvae, juveniles and adults) as requirements can vary during ontogeny (Chapter 3, Snover 2008, Howarth et al. 2011, Vasconcelos et al. 2013). Habitat can influence vulnerability to predation, and the different mechanisms by which habitat affects predation still need to be determined. Additionally, differences in predation rates between years showed that post-settlement processes are dynamic (Chapter 3), and further work is needed to understand the effect of initial spat density on the functional response of predators, especially as prey density can significantly alter the survival rates in marine organisms (Seitz et al. 2001, Lannin & Hovel 2011).

Protracted spawning is usually regarded as a bet-hedging strategy, where individuals ‘spread the risk of dying’ among different environmental conditions (Philippi & Seger 1989). Bet-hedging usually occurs in unpredictable environments and increases the chances of at least some of the progeny experiencing optimal conditions for growth and survival (Nakayama et al. 2011). However, in populations that exhibit protracted spawning, rapid reductions in abundance caused by human activities or natural events might put populations at risk of reproductive failure if individuals have traits that are poorly adapted to reproduce at fewer numbers (Levitan 2012). Reproductive asynchrony or protracted spawning might result in reduced population growth in populations where densities have been reduced to levels lower than have consistently occurred during evolutionary history (Calabrese & Fagan 2004). Therefore, we need to assess if a protracted spawning strategy in *P. fumatus*, characterised by partial spawners and where high levels of atresia are present throughout the spawning season, is optimal for population growth or recovery.

Long term monitoring of reproductive cycles in populations with protracted spawning such as *P. fumatus* may help identify which factors influence the degree of population

synchronization of spawning and atresia. There is still a knowledge gap related to reproductive mode in scallops, which appears to be a response to environmental conditions rather than set (Chapter 4). In *Placopecten magellanicus* greater recruitment was observed after a highly synchronized spawning than when the scallop followed a protracted spawning with partial gamete release strategy (Claereboudt & Himmelman 1996). Therefore we need to examine which factors other than spawner density (Chapter 5) are likely to influence the synchronization of spawning in marine broadcast spawners.

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