GROWTH, REPRODUCTION AND RECRUITMENT OF THE DOUGHBOY SCALLOP, MIMACHLAMYS ASPERRIMUS (LAMARCK) IN THE D'ENTRECASTEAUX CHANNEL, TASMANIA, AUSTRALIA

William F. Zacharin B.Sc. (Hons)

A thesis submitted to the University of Tasmania, Hobart in fulfilment of the requirements of the degree of Master of Science.

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma in any university, and that, to the best of my knowledge and belief, the thesis contains no copy or paraphrase of material previously published or written by another person, except where due reference is made in the text.

W E Zochorin

This thesis may be made available for load and limited copying in accordance with the Copyright Act 1968.

William F. Zacharin B.Sc. (Hons)



Minachlarys asperrimus

The doughboy scallop, *Chlamys* (*Mimachlamys*) asperrimus (Lamarck, 1819) is an abundant benthic bivalve mollusc found throughout south-eastern Australia. Large populations of doughboys extend over wide areas in Bass Strait, and a commercial fishery for the species has operated irregularly in the D'Entrecasteaux Channel in south-eastern Tasmania since the 1930's. This study describes the growth, reproduction and recruitment of the doughboy scallop in the D'Entrecasteaux Channel in southern Tasmania.

Growth rates were observed from monitoring populations of scallops in natural beds, reseeded populations, suspended culture and individual tagging. Values of L_{∞} and K from the von Bertalanffy model for a natural population were 94 mm and 0.578, and for the suspended culture population, 105 mm and 0.573 respectively. Aging was determined from external ring counts and von Bertalanffy growth curves. Observations of ring formation in *M. asperrimus* suggest that the major external rings are formed due to spawning stress. This is supported by the lack of a major ring in scallops < 40 mm that have grown through a winter season but not spawned.

Histological studies of gonad development determined the various stages in reproductive development. Males matured and released sperm earlier than females. Gonads began early development in late March - early April and immature oogonia are evident by May. Maturation continues through the winter months with a major spawning event occurring in late September to mid October. A minor spawning may be observed in December, but the significant decrease in GSI at this time may have been a consequence of oocyte lysis and re-absorption. *M. asperrimus* has some reproductive development in year 1 (0+) but the gonad does not mature past stage 3. Maturity is reached in the second year (1+). The smallest female observed with mature ova had a shell height of 57.5 mm. The collection and identification of two hermaphroditic individuals during this study had not been previously recorded for *M. asperrimus*.

Natural mortality estimates for *M. asperrimus* range between 0.23 to 1.04 yr⁻¹ for fully recruited year classes. Recruitment in *M. asperrimus* in the D'Entrecasteaux Channel region is both spatially and temporally erratic. For the six year period during 1987 to 1992, settlement of juveniles was only significant in two years (1988 and 1990), with the highest number of pre-recruits being observed in 1987.

Stock and recruitment parameters are discussed in relation to the change in population dynamics of the *M. asperrimus* fishery in the D'Entrecasteaux Channel.

ACKNOWLEDGEMENTS

The field studies for this research were conducted as part of a scallop fishery program undertaken by the Marine Resources Division, Department of Primary Industry and Fisheries, Tasmania.

I would like to thank the various people that assisted with the collection of specimens, tagging of scallops and diving during the D'Entrecasteaux Channel scallop surveys between 1989 and 1992, in particular Robert Green, Alex Schaap and Carl Waterworth.

To my supervisor Associate Professor Alastair Richardson, I convey my sincere thanks for his support over a long period, and his enthusiasm in discussing my project whenever I landed on his doorstep.

I also wish to thank Natasha for allowing me to disappear on regular occasions and escape from the boys to write up my thesis. Thanks also to Barry for providing a quiet office during the final drafting period.

CONTENTS

A hatmoot	Page
Abstract Acknowledgements	1 ii
Contents	iii
Figures, Tables and Plates	iv
Chapter 1 General Introduction	1
Chapter 2 Biology and Ecology	
 2.1 Distribution 2.2 Shell Morphology and Internal Organs 2.3 Behaviour 2.4 Predators 2.5 Parasites 	4 5 8 9
Chapter 3 Age and Growth	
 3.1 Introduction 3.2 Materials and Methods 3.3 Results 3.3.1 Incremental growth of cultured scallops 3.3.2 Incremental growth of a natural population 3.3.3 Calculation of age from external rings 3.4 Discussion 	11 12 14 17 17 20 26
Chapter 4 Reproduction	
 4.1 Introduction 4.2 Materials and Methods 4.3 Results 4.3.1 Histological staging of gonad development 4.5 Discussion 	31 31 32 33 46
Chapter 5 Recruitment	
 5.1 Introduction 5.2 Materials and Methods 5.2.1 Size frequency distribution 5.2.2 Relative abundance and natural mortality 5.2.3 Monitoring of spat settlement 5.3 Results 5.3.1 Size frequency distribution 5.3.2 Estimated relative abundance and natural mortality 5.3.3 Monitoring of spat settlement 5.3.4 Recruitment and Population Dynamics 	52 52 52 53 54 56 56 56 60 61
5.4 Discussion	61
Chapter 6 Conclusions	67
References	74
Appendix I Appendix II Appendix III Appendix IV Appendix V Raw growth data from cultured scallops Raw growth data from natural and reseeded scallops Gonosomatic index data Size frequency data for statistical areas from 1987 to 1992 Published paper	83 88 93 103 106

FIGURES

1.1	D'Entrecasteaux Channel study area
3.1	Relationship between shell height and shell width
3.2	Relationship between shell height and somatic weight
3.3	Growth of doughboy scallops in lantern cage culture
3.4	Seasonal growth curves for doughboy scallops in lantern cage culture
3.5	Von Bertalanffy growth curve for tagged scallops in lantern cage culture
3.6	Growth of juvenile doughboy scallops in spat collectors at Huon Island
3.7	Growth of juvenile doughboy scallops reseeded in Great Bay
3.8	Size frequency histograms of doughboy scallops from Satellite Island
3.9	Growth of doughboy scallops on a natural population at Satellite Island
3.10	Von Bertalanffy growth curve for the population at Satellite Island
3.11	Growth of reseeded scallops in Great Bay
3.12	Relationship between shell height and external shell rings at Satellite Island
4.1	Seasonal changes in mean GSI in the female doughboy scallop
4.2	Seasonal changes in mean GSI in the male doughboy scallop
4.3	Fecundity index shown as a relationship between shell height and gonad
	weight in 1988
4.4	Fecundity index shown as a relationship between shell height and gonad weight in 1989
5.1	Diagram of spat collection system deployed at Huon Island
5.2	Daily water temperature readings taken adjacent to the Huon Island spat collection site
5.3	Interannual changes in the size frequency distribution of M. asperrimus in
	the D'Entrecasteaux Channel between 1987 to 1992
5.4	Relative abundance of 30-40 mm scallops in each statistical area between
	1987 and 1992
5.5	Size frequency histograms for statistical areas 6, 7 and 8 in the
	D'Entrecasteaux Channel sampled between 1987 and 1992
5.6	Size frequency histograms for statistical areas 9, 10 and 11 in the
	D'Entrecasteaux Channel sampled between 1987 and 1992

TABLES

3.1	Summary of growth data for a population of M. asperrimus monitored at
	Satellite Island between March 1991 to May 1992
3.2	Number of prominent external shell rings compared to shell height and
	estimated age for M. asperrimus in the D'Entrecasteaux Channel
3.3	Relationship between age and shell height from the von Bertalanffy models
4.1	Description of gonads and distinct histological stages in the reproductive
	cycle of M. asperrimus in the D'Entrecasteaux Channel
5.1	Estimated relative abundance of M. asperrimus for statistical areas 6,7,8,9
	and 10 in the D'Entrecasteaux Channel for the years 1987 to 1991
5.2	Estimates of natural mortality from survey data of each recruited year class
	for M. asperrimus during the years 1988 to 1990
5.3	Results from spat collectors deployed at Huon Island during spring/summer
	of 1988/89
6.1	Summary of individual experiments at each site in the D'Entrecasteaux
	Channel
6.2	Growth rates for grouped data (5 mm) showing size specific growth
6.3	Comparison of reproductive season for M. asperrimus and other Chlamys sp
	PLATES
2.1	Range of colour variation in juvenile M. asperrimus
2.2	Female and male doughboy scallop showing internal morphology
2.3	Shell blisters on the ventral valve of M. asperrimus
3.1	Tagged doughboy scallops
3.2	External rings on the dorsal valve of a doughboy scallop
4.1	Photomicrographs of the gonad of a female M. asperrimus showing the
	characteristic stages of reproductive development

Photomicrographs of the gonad of a male M. asperrimus showing the

Photomicrographs of the gonad from a hermaphrodite M. asperrimus

characteristic stages of reproductive development

4.2

4.3

1 GENERAL INTRODUCTION

The doughboy scallop, *Chlamys* (*Mimachlamys*) asperrimus (Lamarck, 1819) is an abundant benthic bivalve mollusc found throughout south-eastern Australia. Large populations of doughboys extend over wide areas in Bass Strait, and a commercial fishery for the species has operated irregularly in the D'Entrecasteaux Channel in south-eastern Tasmania since the 1930's (Anon. 1981, 1984, 1985; Perrin and Croome 1988). It is intriguing that for such a prominent member of the southern Australian benthic community only scant information exists in the scientific literature on the life history or biology of this species.

Waller (1991) has distinctly separated this species from the *Chlamys* group, therefore future reference to the species in this study will be as *Mimachlamys asperrimus*. There are many species of *Mimachlamys*, but few have any commercial potential. The species is generally smaller than the *Chlamys* or *Pecten* species, and these larger scallops are targeted for exploitation in preference to the *Mimachlamys*.

The D'Entrecasteaux Channel is a narrow semi-enclosed waterway between the Tasmanian mainland and Bruny Island. The Channel has a maximum depth of approximately 30 metres, but the majority of the area and in particular the many bays and inlets, have a maximum depth of 15 metres (figure 1.1). Bottom sediments in the channel vary from deep mud to coarse sand. In the more sheltered shallow bays, seagrass beds proliferate, whilst the deeper areas support large stands of lattice bryozoans, sponges and sea pens (*Pennatulacea*). Doughboy scallops are found throughout the Channel area.

Water temperature in the Channel region may fluctuate between a low of 8° C in August to a high of 21° C in January. Salinity in the northern area ranges between 32 and 36 ppm, whereas the southern area around Huon Island and Little Taylors Bay experiences periodic drops in salinity to 28 ppm during winter due to the influence of the Huon River.

Commercial exploitation of the doughboy scallop in the D'Entrecasteaux Channel ceased in 1986 after about sixty years and the fishery remained closed until 1990 when a limited recreational dive fishery was introduced. This activity lasted for three seasons until 1993 when the survey results suggested that even this limited exploitation had reduced the populations to the lowest levels ever recorded (Zacharin 1986, 1987, 1988, 1991b, Zacharin *et al.* 1990). The fishery has remained closed to all fishers since 1993.

Regular surveys of the doughboy populations in the D'Entrecasteaux Channel have been conducted by the author since 1985 to monitor recruitment of the doughboy fishery. During these surveys it became evident that recruitment in the doughboy populations was very patchy from year to year, and in some years reproduction and spawning was observed to be distinctly different in timing and intensity.

To sustainably manage a scallop fishery subject to commercial or recreational exploitation, it is necessary to have information on the life history of the species. The level of success of annual reproductive events strongly influences the commercial survival of scallop populations and recruitment failure can have a serious impact on an exploited population (Caddy 1975, Orensanz 1986, Sinclair *et al.* 1985). Other factors such as temperature, density, environment, predation and larval distribution mechanisms all contribute to the growth, reproduction and survival of scallops, so an understanding of the local effects is also necessary in interpreting population dynamics (Butman 1987, Bricelj *et al.* 1987, Orensanz *et al.* 1991).

The larval and juvenile development of *M. asperrimus* was studied by Rose and Dix (1984), observations on epizooic sponge associations with the doughboy have been reported by Pitcher(1981) and Pitcher and Butler (1987), and some factors affecting mortality by Chernoff (1987). However, no studies have been conducted on the growth, reproduction or recruitment of this scallop species. These stock or population parameters, together with estimates of natural mortality, are important for making sound decisions on the management of any fishery.

This study describes the growth, reproduction and recruitment of the doughboy scallop in the D'Entrecasteaux Channel in southern Tasmania. Each topic has been treated in separate chapters with a broad discussion of the conclusions in chapter 6. Results presented on the life history and population dynamics of this species will assist in the future management of the doughboy scallop fishery.

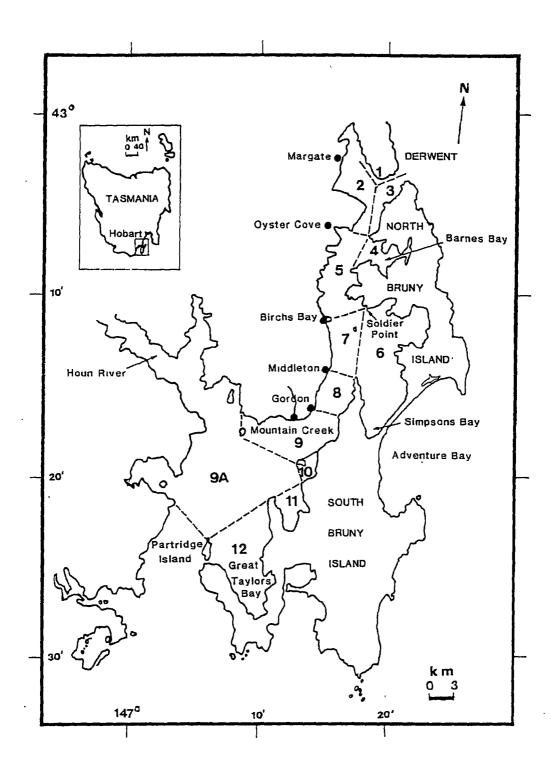


Figure 1.1: D'Entrecasteaux Channel as divided into statistical areas by Fairbridge (1953) for conducting scallop surveys. The same boundaries were used for the dredge and dive surveys between 1986 and 1992. (taken from Perrin and Croome 1988).

2 BIOLOGY and ECOLOGY

2.1 Distribution

M. asperrimus inhabits shallow waters throughout south-eastern Australia to a depth of about 160 metres. M. asperrimus prefers sandy bottom but is also found in areas of coarse sand, rock and muddy bottom. In sandy areas, the doughboy is usually 'free-living' in the sense that it is not attached by a byssal thread to any material. In muddy bottom, the scallop is usually found attached to bryozoans or sponge. This strategy provides for greater water flow, improved feeding conditions and some protection from fine sediments stirred up by other marine organisms.

The doughboy has been recorded from the coastal waters of Western Australia, South Australia, Victoria, New South Wales and Tasmania (Grant 1971a,b, Grant and Alexander 1973, Young and Martin 1990). Along the eastern boundary of Bass Strait and the north-east coast of Tasmania, the species in found in great abundance (>10 m⁻¹), usually in association with beds of the commercial scallop, *Pecten fumatus* (Reeve) and the queen scallop, *Equichlamys bifrons* (Lamarck). Distinct differences in the morphological characteristics of the shell exist between different geographical locations. The Bass Strait doughboy populations only grow to a maximal shell height¹ of 60 mm, whereas the D'Entrecasteaux Channel populations may grow to a shell height of 110 mm (Zacharin 1991a,b).

High density beds of *M. asperrimus* located in Eastern Bass Strait are found between 40 and 60 metres in depth, whereas high density beds in the D'Entrecasteaux Channel are found between 10 and 20 metres depth. A characteristic of scallop species is the patchiness of their distribution and *M. asperrimus* is no exception. High density beds (> 0.5 scallops m⁻²), usually of one distinct size class, are found scattered within the channel area, while the majority of the channel has a low density of scallops (< 0.1 scallops m⁻²) (Zacharin 1986, 1987, 1988). This patchiness of scallop distribution and spatial separation of size (year) classes has been reported for many scallop species and is assumed to be a consequence of the spatial and temporal differences in spawnings and settlement events between years (Caddy 1975, Heald and Caputi 1981, Gruffydd 1974, Mason 1983, Orensanz 1986).

Environmental factors recorded as affecting local scallop distribution are temperature, salinity, turbidity, depth, water currents and predation (Brand 1991). *M. asperrimus* forms high density populations in the D'Entrecasteaux Channel in areas of

¹ shell height being the distance from the umbo to the outer margin of the shell

increased water flow around prominent headlands, islands or steep changes in bottom topography. Increased water flow will generally provide better conditions for scallops as they are benthic filter feeders that rely on the currents for the transport of nutrients (Bricelj and Shumway 1991, Mason 1983). Turbidity does not appear to affect the survival of adult *M. asperrimus* as the ability to detach and form a new byssus allows the scallop to attach to any manner of material and lift itself clear of the sediment. However, the negative survival and growth effect of fine silt on juveniles is well documented and muddy areas tend not to support high density beds (Vahl and Clausen 1980, Wallace and Reinses 1984, Yamamoto 1960).

2.2 Shell Morphology and Internal Organs

Doughboy scallops are made up of anterior and posterior convex values joined by a hinge connected with a dark rubbery ligament called the resilium from which two 'ears' or auricles protrude. Predominant ridges fan out from the hinge to the shell margin and these ridges have protruding lamellae that gives the shell a rough exterior similar to sandpaper. These lamellae are thought to be deposited at the shell margin daily in younger scallops, but over longer periods in older scallops. This shell growth depends on whether the species is short-lived or relatively long-lived, and the water temperature and food availability (Broom and Mason 1978). The outer shell margins are variegated and close together precisely when shut. Shells are a reddish brown colour when not covered by orange, yellow or grey sponge. Spat can be many colours from purple to yellow, pink and orange (plate 2.1).

When one of the valves is removed the internal organs can be identified. The hinge area is the dorsal region and the outer shell margin is the ventral region. Inside the shells and positioned slightly off-centre is the large adductor muscle which is used to open the shell during feeding and provide locomotion for swimming. Surrounding the adductor muscle on one side is the gonad with a dark olive digestive gland situated at the gonad base, ventrally to the resilium. Running through the gonad is the intestine, while the stomach is enclosed in the digestive gland. A simple rectum and anus is situated around the base of the adductor muscle in the opposite direction from the gonad. Two small brown kidneys lie against the adductor muscle adjacent to the gonad. Lying in pairs over both shell are the gills and these are protected by the mantle that covers the whole inner surface of the shell to the outer margin. Pairs of bright blue fluorescent eyes are studded along the outer margin of the mantle. There is also a row of tentacles along this margin which are used as tactile organs and chemoreceptors (Wilkens 1981) (plate 2.2).

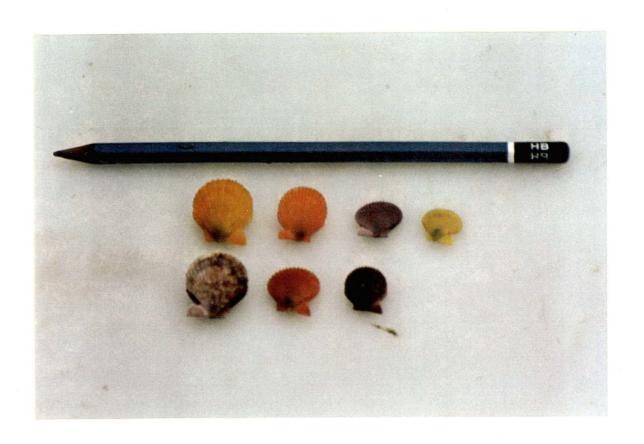


Plate 2.1: Juvenile M. asperrimus taken from spat collectors showing the range of different colours.

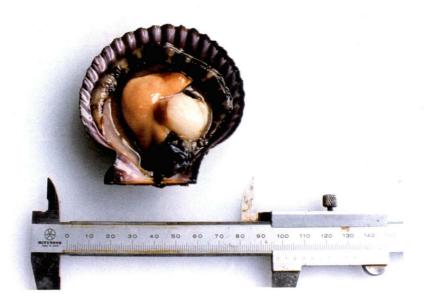




Figure 2.2: Female (top) and male (below) doughboy scallops displaying internal morphology. The mantle with its distinctive pairs of blue eyes and tentacles has withdrawn from the margin of the shell

At the base of the gonad, adjacent to the digestive gland, is the foot. It appears to serve no purpose in the adult, although the byssal gland has an opening on its anterior border, and byssal thread formation uses the foot for attachment (Beninger and Le Pennec 1991).

The circulatory system consists of a simple heart enclosed in a transparent pericardium situated next to the digestive gland dorsal to the adductor muscle. The majority of the nervous system is not readily seen without special chemical preparation (Beninger and Le Pennec 1991), however the visceral ganglia running from the base of the adductor muscle to the edge of the mantle are clearly visible without the aid of a microscope.

2.3 Behaviour

Adult and juvenile scallops are found both free-living or secured by a byssal attachment on a wide range of substrates and organisms. The author has observed M. asperrimus attached to bryozoan, seaweed (Zonia angustata and Lenormandia marginata), sponge, oysters, mussels, old scallop shells, timber and rock. Larvae have also been observed to settle on nylon bags, monofilament netting, plastic mesh, and various types of polypropylene ropes and meshes (Hortle and Cropp 1987, Fairbridge 1953, Olsen 1955, Rose and Dix 1984). M. asperrimus never loses the ability to form a byssus and either through forceful or passive release from attachment will secrete a new byssus and attach to a different surface. This has been observed during the study for both juveniles (>50 mm) and adults. Some other Chlamys species also exhibit the same characteristic (Brand 1991).

M. asperrimus is found to be free-living in areas where the substrate is predominantly sandy. These individuals are generally greater than 60 mm shell height and when disturbed will exhibit an escape response and swim a short distance. Older individuals that are usually covered in heavy sponges or worm (Galeolaria sp.) infestation of the external shell have difficulty in swimming, but tend to expel water in such a way so that the shell spins abruptly about 90°. Juvenile M. asperrimus are active swimmers and when disturbed release the byssus and may swim for a distance of up to 3 metres.

Epizooic sponge associations on the external shell are a characteristic of this species. Studies have shown this association to benefit the doughboy in regard to growth rate and mortality (Chernoff 1987, Pitcher 1981, Pitcher and Butler 1987). This commensal - protective mutualism has also been recorded for a number of scallops from the northern hemisphere, *Chlamys hastata* (Bloom 1975) and *Chlamys varia* (Forester

1979). Most of the doughboy spat caught in artificial collectors for the purpose of this study were not covered in epizooic sponges. However, when placed in hanging culture cages for growth experiments sponge growth was observed on all scallops after a two month period.

2.4 Predators

The effect of predation on scallop distribution has not been considered as important as some other factors such as temperature (Brand 1991), but there is increasing interest in the effects of predation, particularly its contribution to post-settlement mortality, as an important determinant for the spatial distribution of scallops. Predation rates can be very high in areas where certain predators are abundant (Brand *et al.* 1981, Volkov *et al.* 1983).

The major predator of juvenile and adult *M. asperrimus* is the eleven-armed seastar *Coscinasterias calamaria* (Grey). This voracious opportunistic predator has been observed in large numbers in areas of high scallop density, and has caused high levels of mortality on reseeded beds where enhancement studies have been conducted. Juvenile *M. asperrimus* are also susceptible to predation by crabs, skates, dog sharks and flathead (Chernoff 1987, Zacharin, this study).

2.5 Parasites

As mentioned, older animals in the D'Entrecasteaux Channel may be heavily infested with a species of *Polydora* that causes pronounced internal blistering of the shell. It is probable that heavy infestation contributes to natural mortality and predation in older individuals, but this hypothesis was not confirmed during this study (plate 2.3).

No infestation of the gonad by trematodes was observed, although commercial scallops (*P. fumatus*) in Bass Strait found among large doughboy populations were affected. The parasitic nematode, *Sulcarscaris sulcata* has been recorded in *M. asperrimus*. This nematode inhabits the stomach of sea turtles as an adult and is not thought to present any risk to human consumption (Getchell 1991).





Plate 2.3: Aged specimens of M. asperrimus showing heavy $Galeolaria\ sp.\ (top)$ and $Polydora\ sp.\ (bottom)$ infestation that has caused blistering of the internal shell.

3 AGE AND GROWTH

3.1 Introduction

Scallops exhibit typical characteristics of molluscan bivalve growth. Growth proceeds rapidly after settlement then slows dramatically, ceasing towards the end of life expectancy. This typical 's'-shaped or sigmoid growth curve is complicated by many environmental and biological factors over the scallop's life history. Major increases in shell growth are observed during summer, but this slows significantly during the autumn and winter months, when greater effort is directed towards gains in somatic weight and gonad development. This growth pattern has been demonstrated in many scallop species (Broom and Mason 1978, Ciocco 1991, Conan and Shafee 1978, Fairbridge 1953, Franklin and Pickett 1980, Orensanz 1986, Orensanz et al 1991, Paul 1981, Shafee 1980, Wallace 1982).

Variability in growth rates between individuals and size classes has also been well documented for scallops (Orensanz et al 1991) and for other mollusc species (Sainsbury 1982). Food availability and temperature have the greatest effect on growth, while density and depth have been shown to seriously affect growth at population extremes (Bricelj et al 1987, Broom and Mason 1978, Gruffydd 1974, MacDonald and Thompson 1985, Orensanz 1986, Sastry 1968, Schick et al 1987, Wallace and Reinsnes 1984). Environmental disturbance from storms or dredge fishing may also affect growth and survival.

The most common model used for describing the growth of scallops and other fish species is the von Bertalanffy equation (Conan and Shafee 1978, Gwyther and McShane 1988, Heald and Caputi 1981, Munro 1982, Orensanz 1986, Wolff 1987). However, as a number of researchers have pointed out, the von Bertalanffy equation does not take account of slower growth at the time of post-settlement, nor seasonal variations in the growth rate (Orensanz *et al* 1991). Seasonal changes in growth rates are more easily described by plotting incremental growth obtained from mark-recapture data.

Beside the need to analyse growth rates for a knowledge of population dynamics, the age structure of the population is important for investigating stock/recruitment processes. The age structure of a population can be assessed in three ways: (1) analysis of size frequency distributions to identify modal progression; (2) counting of external and internal 'disturbance' rings on the shell and in the resilium; and (3) tagging studies. Combining results from all the methods is the best approach as each method has a number of advantages and disadvantages. It is important when using size frequency distributions

to determine whether there is more than one annual recruitment event, as bimodal data will mask the true age structure of the population. Similarly, with disturbance rings it is necessary to determine if rings are due to environmental factors, winter growth checks or spawning stress rings (Orensanz *et al.* 1991).

3.2 Materials and Methods

Samples collected for analysis of reproductive condition were also used to establish the relationship between shell height and somatic weight. Scallops were returned to the laboratory and allowed to drain of all free-water before processing. All samples were processed the day of collection.

Juveniles used for growth experiments in cage culture and mark/recapture were taken from the spat collectors deployed adjacent to Huon Island in the D'Entrecasteaux Channel. Older and larger animals were collected by diving in Simpsons Bay (see figure 1.1). Scallops were removed from the water, tagged and immediately returned. Tags used were small wire strips approximately 5 centimetres long with one end coated in plastic displaying a particular colour and numerical code. The prominent ear on the scallop hinge was drilled with a high speed engraving tool using a 0.8 mm steel drill bit. The tag was threaded through one shell and twisted back on itself to be securely fastened. A small loop was left around the hinge to allow free movement of the shell (Plate 3.1).

Immediate post-tagging mortality (3 days) of tagged doughboy scallops held in circulating tanks was observed to be less than one percent. The doughboy is an extremely robust aquarium animal and a number of tagged individuals survived for over twelve months in an open aquarium system without the addition of any food supplements.

Age and growth were to be determined using four different procedures: (1) mark-recapture experiments; (2) incremental growth of cultured individuals and juveniles in spat collectors; (3) analysis of modal progression from size frequency data; and (4) counts of external shell rings. However, the loss of many of the tagged scallops through predation and poaching provided little data for analysis from the mark-recapture experiments.

Three hundred scallops ranging in size from 15 to 34 mm were individually tagged and suspended in typical "Japanese lantern" hanging culture cages (Hortle and Cropp 1987) at Birches Bay in the D'Entrecasteaux Channel as part of the experiment on growth. The lantern cages were held on a longline system at a depth of six metres. Scallops were at an initial density of 20 per section of the lantern cage to avoid density



Plate 3.1: *M. asperrimus* being tagged for release in growth trials and for validation of age. A high powered drill with a 0.8 mm bit was used to puncture the scallop 'ear' and the small tags are looped through the ear and twisted back on themselves leaving a small circle around the ear so as not to irritate the scallop.

dependent effects on growth. This density was later reduced to 15 per section. The lantern cages were regularly cleaned during data collection. If the lantern cage was heavily fouled, the scallops were removed and placed in a new lantern cage. Scallops were tagged on 1 July 1988 and the experiment was terminated on 2 November 1989 after a period of 489 days. Raw data measurements from this experiment are shown in Appendix 1.

For the collection of data on modal progression two separate populations were studied. A natural population at Satellite Island was observed over a period of 437 days and a reseeded² population near Great Bay over a period of 251 days. Growth of smaller scallops (<30 mm) was also monitored in the spat collectors deployed in 1990 and 1991 at Huon Island. Growth curves were fitted using the von Bertalanffy growth model fitted to the data using a non-linear regression program (an iteration of least squares using L_t and L_{t+1}) (SYSTAT 5). Raw data measurements are shown in Appendix 2.

Scallops collected for aging using external ring counts were returned to the laboratory and the ventral shell removed. Shells were soaked in hot water for about ten minutes and then scrubbed with a wire brush to remove sponge and other detritus. The ventral shell was used as this shell is less fouled and the major rings are more easily seen. The resilium were left on the dorsal shell and frozen until required. Fresh material was sectioned using a small scalpel and immersed in oil for observation under a dissection microscope. The rubbery nature of the resilium resulted in poor sections from dehydrated and embedded samples. Tagging of 1,800 individuals during 1988 and 1989 was to be used to validate aging data, but a lack of adequate tag returns resulted in other validation methods being used.

3.3 Results

The relationship between shell height and shell width is shown in figure 3.1, and the relationship between shell height and somatic weight is shown in figure 3.2. Seasonal changes in the height/weight relationship are pronounced post-spawning (summer), where there is a marked fall in somatic weight associated with a loss in condition of the adductor muscle. The adductor muscle appears yellowish, watery and flaccid. This condition is well documented, and is the result of energy reserves in the muscle being utilized for maintenance requirements after spawning. During the winter months shell growth slows and more energy is placed into somatic growth (Comely 1974, MacDonald 1986, MacDonald and Thompson 1985, 1986).

²spat obtained from collectors and placed back on the substrate to grow

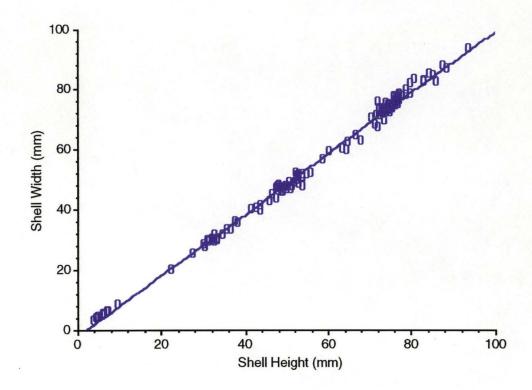


Figure 3.1 Relationship between shell height and shell width for *M. asperrimus* from the D'Entrecasteaux Channel, Tasmania. [$y = 1.0127x - 2.0836 R^2 = 9.96$]

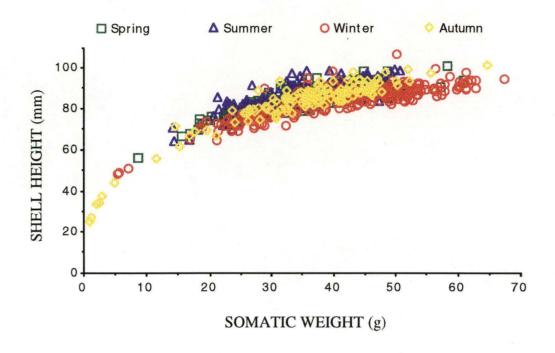


Figure 3.2 Seasonal relationship between shell height and somatic weight for *M. asperrimus* in the D'Entrecasteaux Channel, Tasmania.

Regression Analysis

Winter: $y = 0.57x + 60.32 \text{ r}^2 = 0.74$

Spring: $y = 0.63x + 62.46 \text{ r}^2 = 0.72$

Summer: $y = 0.64x + 63.44 \text{ r}^2 = 0.62$

Autumn: $y = 1.06x + 45.09 \text{ r}^2 = 0.82$

Shell growth rate in *M. asperrimus* in hanging culture is rapid over summer, the mean increase in shell height being 1.13 mm wk⁻¹. Over the winter months more energy is placed in somatic growth and reproductive conditioning, and this was evident from the increase in weight of the adductor muscle and the gonad. The shell growth rate over winter slowed to an average of 0.50 mm wk⁻¹ (figures 3.3 and 3.4). A von Bertalanffy function of the growth increments shows that doughboy scallops in a suspended culture system may reach 80 mm shell height in approximately 2.5 years (figure 3.5).

The growth rate for juvenile scallops sampled from spat collectors and subsequently reseeded is slower than that observed in the suspended culture system. During 120 days (1990) and 133 days (1991) over summer in the spat collectors at Huon Island, the young scallops were observed to have mean growth rates of 0.6487 mm wk⁻¹ and 1.0016 mm wk⁻¹ respectively (figure 3.6). After 186 days at release after reseeding in Great Bay (1990), the mean growth rate (during winter and early spring) was 0.4338 mm wk⁻¹ (figure 3.7). This growth rate is comparable with the 0.50 mm wk⁻¹ observed in the suspended culture system. No meaningful data were available for the 1991 reseeding experiment due to heavy predation.

3.3.2 Incremental growth of a natural population

Natural growth data from a large population were collected adjacent to Satellite Island. Scallops were irregularly sampled over a 437 day period between the 19 March 1991 and 28 May 1992 (table 3.1). Size frequency histograms of the random samples taken from the Satellite Island population show that by 6 February 1992 juveniles (30-40 mm) from the 1991 settlement are evident (figure 3.8).

Mean growth rate for the natural Satellite Island population over the 437 days period was 0.4169 mm wk⁻¹ (figure 3.9). A von Bertalanffy function of the growth increments shows that *M. asperrimus* at Satellite Island may reach 80 mm shell height in approximately 3.4 years (Figure 3.10). This growth rate is very similar to the lower growth rate observed during winter in the suspended culture system (0.50 mm wk⁻¹), and the growth rate observed in the reseeded Great Bay population (0.4338 mm wk⁻¹). A von Bertalanffy function of the growth increments for the Great Bay population was not possible as only six months data was collected before the population was lost.

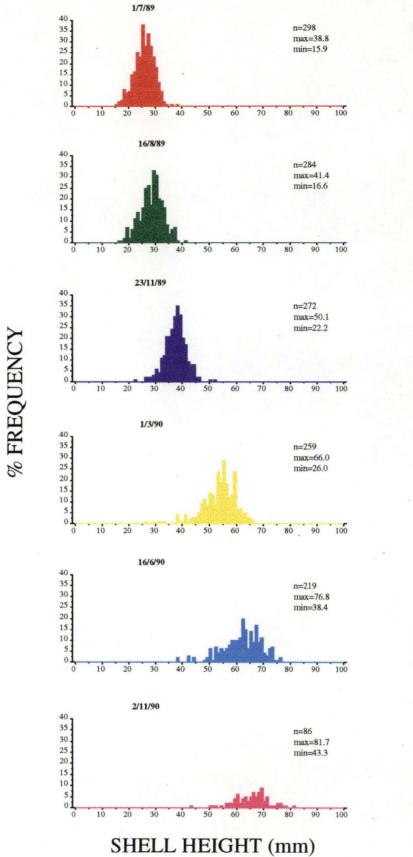


Figure 3.3 Growth of doughboy scallops in lantern cage culture over a period of seventeen months between the 1 July 1989 and 2 November 1990. (refer to Table 3.1)

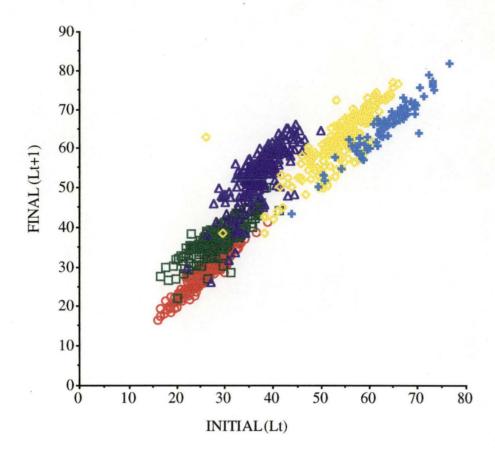


Figure 3.4: Growth curve from raw data of *M. asperrimus* grown in suspended cage culture in the D'Entrecasteaux Channel between 1 July 1989 and 2 November 1990.

- 1/7/91 to 16/8/91 (47 days) □ 16/8/91 to 23/11/91 (79 days) △ 23/11/91 to 1/3/92 (90 days)
- 1/3/92 to 16/6/92 (108 days) 16/6/92 to 2/11/92 (139 days)

The only successful method used to calculate age was the counting of the predominant external rings on the shell and the internal rings visible in the resilium (hinge). The predominant internal rings observed in the resilium corresponded to the number of major external rings, so the external rings were used for aging. There are many other less marked internal rings in the resilium and these are assumed to be the result of non-seasonal disturbance. In interpreting the data from external ring counts one needs to be able to identify whether the rings were caused by either some environmental stress factor, such as low salinity or turbidity, or whether they were winter rings resulting from the compressed distance between adjacent shell striae because of low water temperatures, or stress rings resulting from spawning.

No prominent external rings were observed in *M. asperrimus* below 40 mm shell height. These scallops had settled between October and December, and had experienced one winter. Juvenile scallops were also observed to have some maturation of the gonad in the first year (0+ age class), but no spawning was evident in these animals. The reproductive cycle is discussed in detail in Chapter 4, but it is important that this observation be noted because if the external ring was a result of winter stress, scallops below 40 mm shell height should have one prominent ring. This was not the case, but post-spawning scallops (1+ age class) all had one prominent ring. Therefore, it can be concluded that the major external rings are the result of spawning stress or shock (Table 3.2).

The appearance of one major disturbance ring on the external shell indicates that a scallop has completed its first major spawning and is approximately 1.75 years old (figure 3.11). For each successive ring a further 12 months is added to the age. If the rings were the result of winter stress (low water temperatures), the first major ring at approximately 45 mm shell height would indicate the scallops were only 10 months old. This is not supported by the recorded natural growth data or the spat collection data.

Spawning stress is dramatic and may result in significant mortality of older or environmentally stressed scallops. During regular field sampling periods many clappers³were observed in post-spawning beds, and on rare occasions clappers were observed having some somatic tissue still intact, suggesting recent death.

³a dead scallop with the shell valves still connected at the hinge

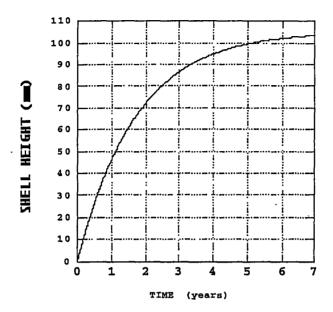
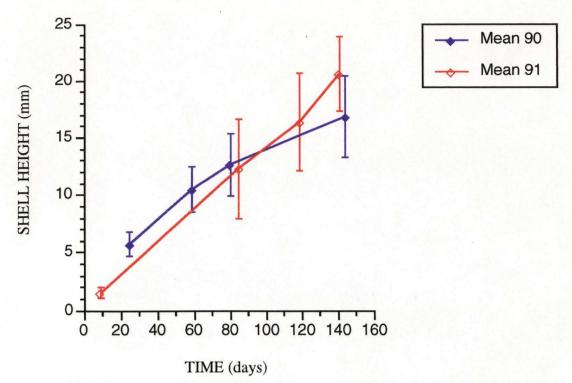


Figure 3.5 Von Bertalanffy growth curve for individually tagged M. asperrimus in lantern cage culture over a 16 month period in the D'Entrecasteaux Channel. [L ∞ = 105.289, K = 0.578]

Į

Table 3.1 Summary of growth data collected from a single population of doughboy scallops adjacent to Satellite Island between 19 March 1991 and 28 May 1992.

	·· ·· ·· ·· ·· ·· ·· ·· ·· ·· ·· ·· ··	SHELL HEIGHT (mm)				
Date	Mode	Mean	std	Number	Year-1	
19/3/91	50.0	47.59	6.09	268		
19/3/91 3/7/91	50.0 57.0	55.27	7.03	208 150	0.293	
27/9/91	62.2	60.92	2.99	39	0.239	
10/10/91	61.0	61.10	4.66	200	0.036	
6/2/92	64.2	62.46	9.19	200	0.326	
24/3/92	73.0	65.22	11.46	96	0.126	
28/5/92	71.0	73.62	8.221	103	0.181	



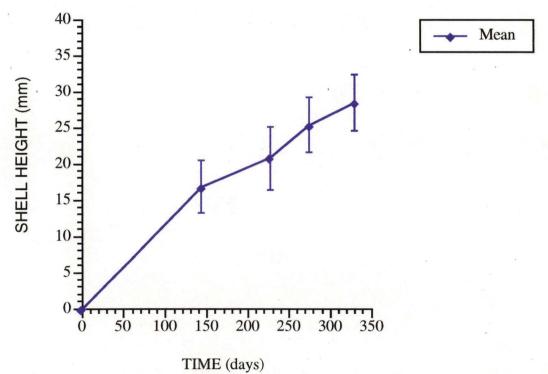


Figure 3.7 Growth of juvenile doughboy scallops taken from spat collectors and reseeded in Great Bay on 25 May 1990. {t 0 = 1 January}

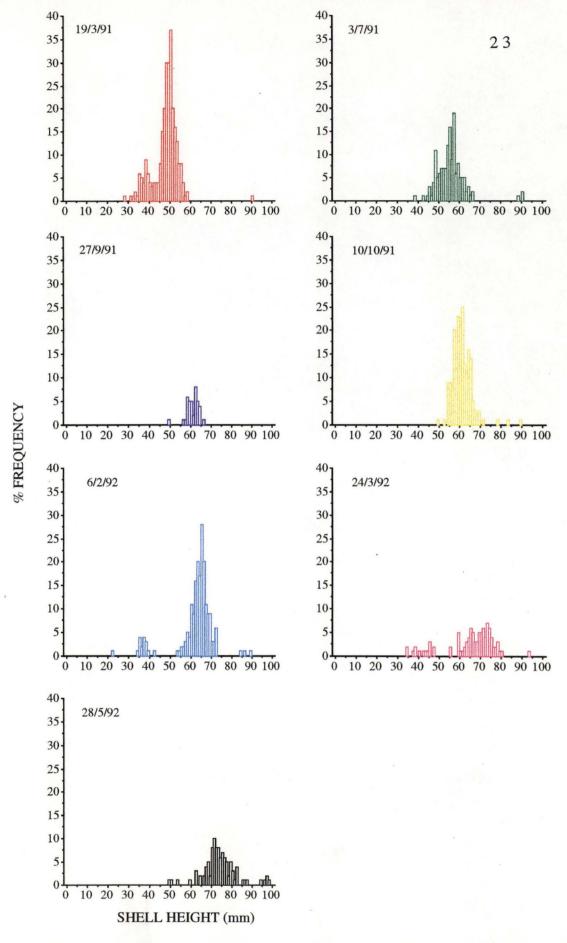


Figure 3.8: Growth of *M. asperrimus* over a 14 month period in an established natural bed at Satellite Island in the D'Entrecasteaux Channel.:

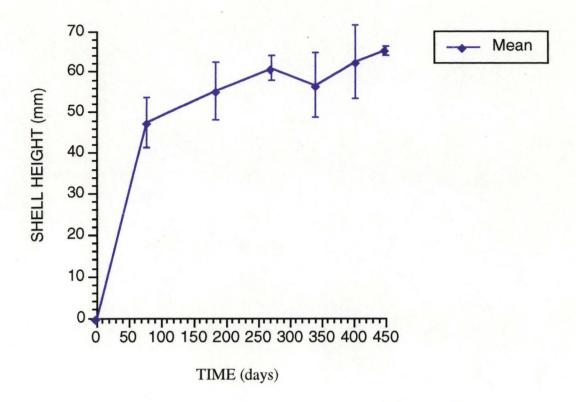


Figure 3.9 Growth curve for a natural population of *M. asperrimus* at Satellite Island, D'Entrecasteaux Channel between 19 March 1991 and 24 March 1992. [$t_0 = 1$ January] (Error bars represent one standard deviation)

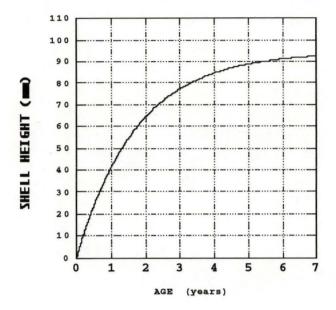


Figure 3.10 Von Bertalanffy growth curve for a natural population of *M. asperrimus* over a 14 month period at Satellite Island in the D'Entrecasteaux Channel. [$L \approx 94.053$, K = 0.573]

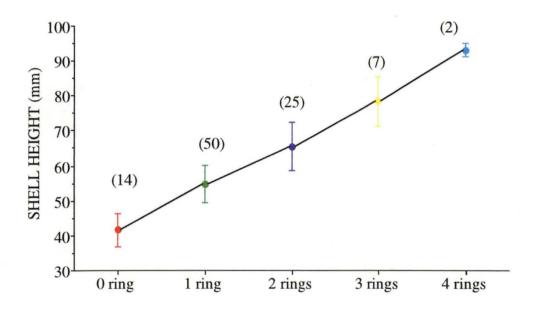


Figure 3.11 Correlation between the number of external rings and shell height for a sample of *M. asperrimus* from Satellite Island. [Error bars represent the range in shell height]

3.4 Discussion

Changes in the somatic weight of scallops are affected by the reproductive cycle and this in turn is affected by the physical environment (Barber and Blake 1981, Bricelj et al. 1987, MacDonald 1986, MacDonald and Thompson 1986). Doughboy scallops reach a maximal weight between late winter and early spring prior to spawning. As M. asperrimus is a suspension feeder, phytoplankton is its main food source. This weight increase coincides with the annual winter/spring phytoplankton blooms in the D'Entrecasteaux Channel (Hallegraeff and Sumner 1986, Hallegraeff - pers. comm., Harris et al. 1987). Post-spawning scallops lose gonad condition rapidly and a loss of somatic weight (adductor condition) follows over the next two to three months. This 'poor' condition persists through to late summer or early spring, the traditional 'closed season' for commercial scallop fishing.

The von Bertalanffy function has been widely used to describe the growth rates of scallops. Growth curves fitted with the model enable a comparison to be made between different populations of the same species and population growth rates of different species (Burnell and Rodhouse 1980, Ciocco 1991, MacDonald and Bourne 1989, Orensanz *et al.* 1991).

Growth in the cultured scallop population was significantly greater than in the natural populations, the shell height of 80 mm being reached in 2.5 years in the former compared to 3.4 years in the latter (t-test, P<0.02). This result is similar to that observed in the purple hinged rock scallop (*Crassadoma gigantea*) by MacDonald and Bourne (1989), where the same somatic weight could be gained from one year's less growth in suspended culture. Increased growth rates are a common characteristic of bivalves in suspended culture systems due to the higher temperatures and good food availability in the upper levels of the water column (Cropp and Hortle 1991, Hortle and Cropp 1987, MacDonald 1986, MacDonald and Bourne 1989, Wallace and Reinsnes 1984). However, for the variegated scallop *Chlamys varia*, Burnell and Rodhouse (1980) observed no obvious difference between suspended culture and bottom growth rates.

Values of L_{∞} and K from the von Bertalanffy model for the suspended culture population were 105 mm and 0.573, and for the natural population 94 and 0.578. These estimates are comparable with the observed mean L_{∞} of 97.5 mm from the D'Entrecasteaux Channel doughboy populations over a period of six years (Zacharin 1986, 1987, 1988, 1991b, Zacharin *et al.* 1990).

Table 3.2 Number of prominent external shell rings compared to the shell height and estimated age for *M. asperrimus* from a number of different populations in the D'Entrecasteaux Channel.

Site	Rings	Shell Height (mm)	Estimated Age (years)
Satellite Is.	0	0 - 47.3	0 - 1.75
	1	43.4 - 65.4	1.75 - 2.75
	2	53.0 - 77.4	2.75 - 3.75
	3	67.4 - 86.0	3.75 - 4.75
	4	91.8 - 94.4	4.75 - 5.75
Great Bay	3	78.0 - 91.0	3.75 - 4.75
	4	88.1 - 101.0	4.75 - 5.75
Huon Island	0	10.0 - 31.7	0 - 1.75

Ring formation occurs during growth from the compression of lamellae being deposited by the mantle to form striae on the external shell surface (plate 3.2). Observations of ring formation in *M. asperrimus* suggest that the major external rings are formed due to spawning stress. This is supported by the lack of a major ring in scallops < 40 mm that have grown through a winter season but not spawned. Bloom and Mason (1978) suggest that a winter ring occurs in *Chlamys opercularis* as a result of the deposition of striae close together during the colder winter months, and that the onset of spring increases the growth rate resulting in a prominent external ring on the shell. Their hypothesis for the lack of a ring in smaller scallops is that a smaller organism requires less food for its maintenance requirements, and thus small scallops can continue to grow throughout winter months. This hypothesis may be true for colder northern water species, such as *C. opercularis* and *P. maximus*, but is not consistent with the observed ring formation in *M. asperrimus* in suspended culture after the first spawning.

In *M. asperrimus* only one major external ring is deposited each year, but the first ring is deposited in the second year after the first major spawning event. The first major growth ring is also not evident in *Chlamys varia* (Conan and Shafee 1978), *Chlamys islandica* (Wallace 1982) or *Chlamys opercularis* (Paul 1981) until the second year, but the ring is still attributed to winter stress and not the result of spawning.

I would hypothesize that in *M. asperrimus* spawning stress and the use of stored metabolites in the adductor muscle for minimal maintenance requirements (Thompson and MacDonald 1991) leads to the formation of a major ring through the slowing of shell growth during this period. As there is no spawning in the first year, there is no necessity to use energy stored in the adductor muscle and no ring is deposited.

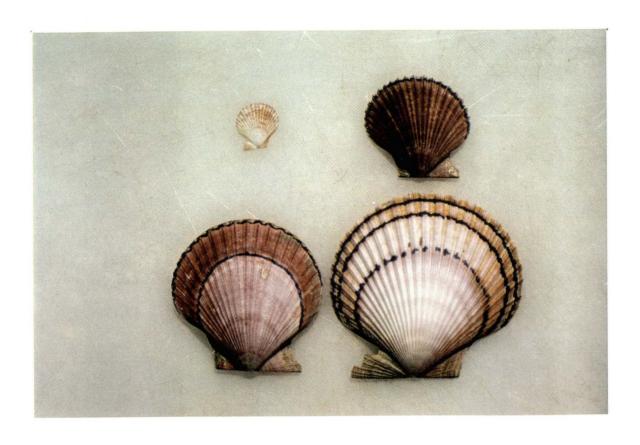


Plate 3.2: External rings on the dorsal value of M. asperrimus. The first ring from the hinge is the result of the first major spawning event at an age of approximately 18 to 20 months. Subsequent rings, also caused by spawning disturbance, occur at intervals of 12 months.

This hypothesis is supported by Ciocco (1991) and Orensanz (1986) who found that ring formation in *Chlamys techuelcha* is coincident with the spawning season, and that other less clearly marked 'disturbance' rings in some cohorts may appear in winter. Bricelj *et al* (1987) also found that shell growth in *Argopecten irradians* ceased during the reproductive period and that post-spawning there was a build-up of muscle reserves before a period of shell growth at a faster rate than tissue growth.

Age determination was difficult to describe accurately because of the wide variation observed in individual growth rates. The results show that care must be taken when interpreting growth rings as a reference to age. The use of spat collectors to identify the settling time of larvae (t₀) is important in the validation of age data. The highest number of spat observed under 5 mm were in December in most years (Chapter 4), so the date of 1 December was used as t₀ for the aging results (table 3.3).

The von Bertalanffy models of the growth of scallops in suspended culture and for natural populations shows the disparity in the growth rate as a result of increased food availability in suspended culture. This phenomena has been recorded for many scallop species grown in suspended culture (Cropp and Hortle 1991, MacDonald and Bourne 1987, Wallace and Reinsnes 1984).

The internal and external rings can only be used as an approximate measure of scallop age as the age calculated by this method may vary by \pm 8 months (table 3.2). As scallops age, it becomes increasingly difficult to identify disturbance rings along the shell margins, making this aging method unreliable for older scallops. Tagging studies of individual scallops over longer periods are required for more accurate age determination. Lack of tag return data during this study did not allow for any precision in age validation.

Table 3.3 Age vs shell height from the von Bertalanffy models.

Age	Suspended culture	Natural growth	
(yrs)	(mm)	(mm)	
0+	0 - 48	0 - 41	
1+	49 - 71	42 - 64	
2+	72 - 86	65 - 77	
3+	87 - 94	78 - 85	
4+	94 - 100	86 - 89	
5+	100+	90+	

M. asperrimus probably lives for a maximum of 6 years and is a relatively short lived species compared with the commercial scallop, Pecten fumatus, which is estimated to live for up to 12 years in the D'Entrecasteaux Channel (Fairbridge 1953). However, M. asperrimus terminal age is comparable with the more closely related Chlamys (Mimachlamys) varia (0-4 years) (Shafee and Conan 1984), and Chlamys tehuelcha (0-5 years) (Orensanz 1986).

In summary, *M. asperrimus* exhibits rapid growth in its first year and may attain a shell height of approximately 45 mm. The first major external ring is formed post-spawning in the second year and by that time *M. asperrimus* may attain a maximum shell height of approximately 70 mm. Growth rate and the relationship of shell height to age appears dependent on temperature and food availability. Scallops grown in suspended culture will grow faster than scallops in natural beds.

4 REPRODUCTION

4.1 Introduction

The majority of scallop species have an annual reproductive cycle that may result in a major, and in some years, a minor spawning event during spring and summer. This reproductive cycle is characteristic of pectinid molluscs and has been described for *Pecten fumatus* (Dix and Sjardin 1975, Sause *et al.* 1987a) and *Equichlamys bifrons* (Dix 1976) in southern Australian waters.

Generally as scallop gonads mature they increase in weight and size and change from a light brown translucent colour to orange, purple or red in the female and white in the male. The gonad becomes rounded as the gametes become more numerous with the tip of the gonad changing from being flat and pointed to cone shaped prior to spawning. In the immature and developing gonad the intestine can be clearly observed as a loop running the length of the gonad. On maturation the loop cannot be recognised due to the colour of the gametes. On spawning, the gonad becomes flatter and has a spotty appearance due to the loss of gametes and is very watery to the touch.

Quantitative changes in the condition of the gonad are calculated by a gonosomatic index (GSI) which is a relationship between gonad weight and total somatic weight:

Gross examination and GSI provides information on the gonad development under the assumption that weight is directly related to production of gametes, but histological examination is necessary to follow the gametogenic cycle.

The annual reproductive cycle of the doughboy M. asperrimus from the D'Entrecasteaux Channel is examined in this chapter. Macroscopic observations and histological sections of the male and female gonads were made to determine the time and frequency of the annual spawning events.

4.2 Materials and Methods

A sample of between 10 and 50 doughboys was collected from the same population in Simpsons Bay at 14 day intervals for a period of 28 months between 1 July 1988 to 27 November 1990. In the laboratory the animals were measured (shell height to the nearest 0.1 mm) and total somatic weight and gonad weighted to the nearest 0.1 g.

Sex was determined according to colour, males being white and the females orange. Gonosomatic Index (GSI) was calculated as a ratio of gonad weight to somatic tissue weight. A significant decrease in gonad index was considered to be an indication of spawning (Dredge 1981, Malachowski 1988, Sause *et al.* 1987a, West 1990).

Three animals of each sex macroscopically representative of the sample were fixed in Davidson's Solution for four days, then preserved in 70% alcohol before histological examination. Gonad tissue was dehydrated using serial dilutions of alcohol and xylene or toluene, then embedded in paraffin wax. Tissue sections 5 µm thick were stained with Harris's haematoxylin and eosin. Ripe female gonads were used from September and October samples to determine maximum egg size prior to spawning. Reproductive output was determined using an indirect method, in which the difference in gonad weight of mature female scallops immediately prior to spawning and after spawning was calculated. This weight loss on spawning can be used as an index of ova released from the gonad. The underlying assumptions are that mature ova prior to spawning have the same mass from year to year, and ova mass is the same across all size classes. Histological examination supports this assumption as gonad weight loss is due to a release of mature ova on spawning.

The terminology of stages in the gonad reproductive cycle was based on that of *P. fumatus* (Harrison 1961, Sause *et al.* 1987a), *Chlamys varia* (Shafee and Lucas 1980) and *Amusium balloti* (Dredge 1981).

4.3 Results

Macroscopic determination of gonad maturity can be categorised into four stages: spent or resting phase, early development, late development and running ripe or spawning. Microscopic examination of gamete development is, however, necessary in determining the exact stage of reproductive development and the timing of significant spawning events.

During late summer to autumn (January - March) gonads are completely spent and appear to be in a 'resting phase' with no cell division occurring. Accurate macroscopic identification of sex for the majority of individuals during the 'resting phase' proved to be impossible (Plates 4.1A and 4.2A). Early gonad development begins with gametogenesis in late autumn (April), corresponding with a drop in mean water temperatures. Follicular development proceeds steadily until late winter (August) when there is a rapid increase in gonad weight (Plates 4.1D and 4.2D). A significant decrease in gonad weight (suggestive of spawning) was observed between September and December in each year.

Fortnightly changes in gonosomatic index (GSI) for the 28 month period are shown in figures 4.1 and 4.2. Increases in gonad weight were attributed to follicular development and the production of gametes. A rapid decrease in gonad weight in September - October was indicative of spawning due to the release of gametes. This was confirmed by histological examinations. Mature females with a shell height of 90 mm may have a GSI = 45% of total flesh weight. The difference in gonad weights (being an index of ova number) for grouped samples (5 mm) indicated a significant increase in ova number for the older and larger scallops. With the exception of rare large doughboys, gonad weight increased with size and peaked in the 90 - 95 mm size class.

4.3.1 Histological Staging of Gonad Development

Six distinct stages of gonad development were recognised:

Stage 1- Resting (A)

Gonads composed of loose connective tissue (ct), interspersed with ciliated ducts (cd). The early formation of thin-walled follicles (f) may occur. No clear differentiation into ovary and testis. Sex determination not possible.

Stage 2 - Early Development (B)

Formation of follicles and appearance of primary oogonia and spermatogonia 'budding' from the follicle membrane (fm). Clear differentiation into ovary and testis. Oogonia with dark staining nucleus. Reduction in number of ciliated ducts. Connective tissue still the major tissue type, but decreases with advancing maturity.

Stage 3 - Late Development (C)

Lumen of the follicles fills with oocytes and spermatocytes. Small numbers of immature ova on the follicle walls with stalked oocytes being prominent. Ova size ranges from 45 to 55 μ m in diameter. In the male, spermatocytes (spc) line the follicle wall with spermatids and some spermatozoa (spo) towards the centre of the lumen. Little connective tissue still visible.

Stage 4 - Mature (Ripe) (D)

Follicle packed with irregular polygonal mature ova $60 \mu m$ in diameter (mo). Fewer stalked oocytes. Increase in spermatozoa with follicles becoming tightly packed. There is little connective tissue between the follicles.

Stage 5 - Spawning (E)

Maximum ova diameter of 60 μ m. Loss of ova and sperm from the centre of the follicles. Reappearance of ciliated ducts and connective tissue.

Stage 6 - Spent (F)

Connective tissue increasing with collapse of the follicles. Mature ova not expelled are undergoing lysis. No gametogensis evident along follicular wall. Clumps of sperm are scattered throughout the remaining follicles.

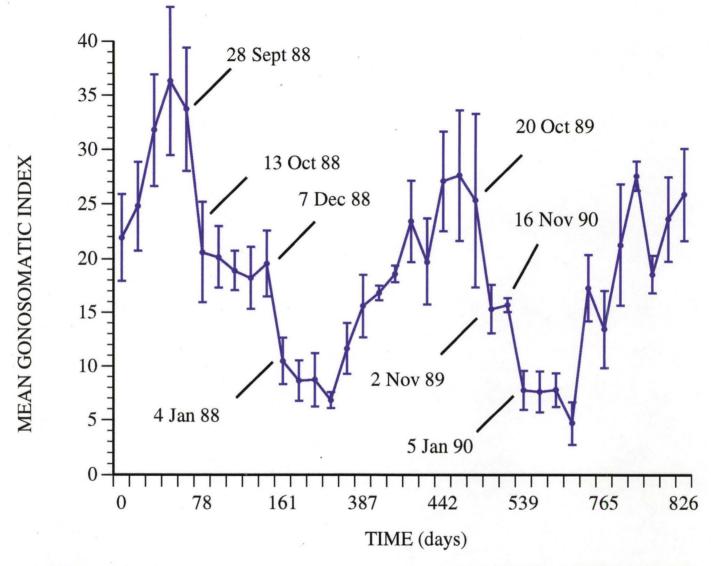


Figure 4. 1: Seasonal changes in mean gonosomatic index in the female doughboy scallop from the D'Entrecasteaux Channel, Tasmania. (Error bars represent one standard deviation)

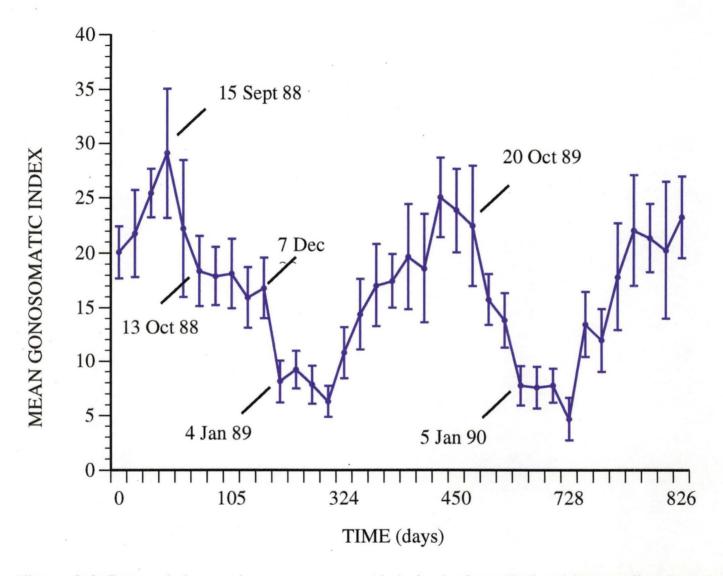


Figure 4. 2: Seasonal changes in mean gonosomatic index in the male doughboy scallop from the D'Entrecasteaux Channel, Tasmania. (Error bars represent one standard deviation)

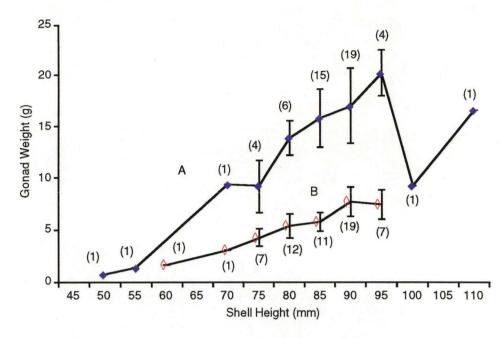


Figure 4.3 Reproductive output shown as a relationship between shell height (5 mm intervals) and gonad weight from running ripe samples (A) collected on 15 and 28 September 1988 and immediate post-spawning samples (B) on 13 and 20 October 1988. Number of scallops shown in brackets. [Error bars represent one standard deviation]

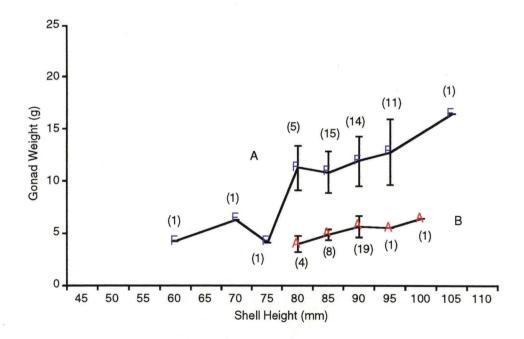
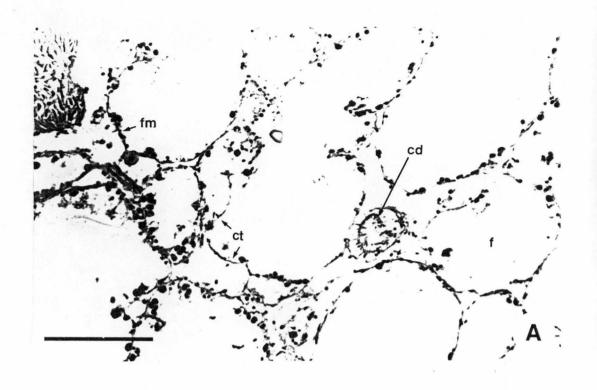
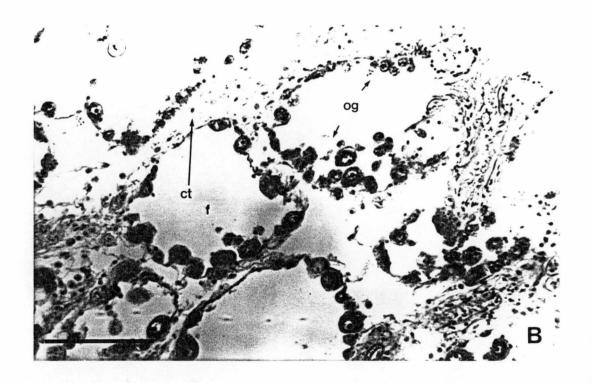


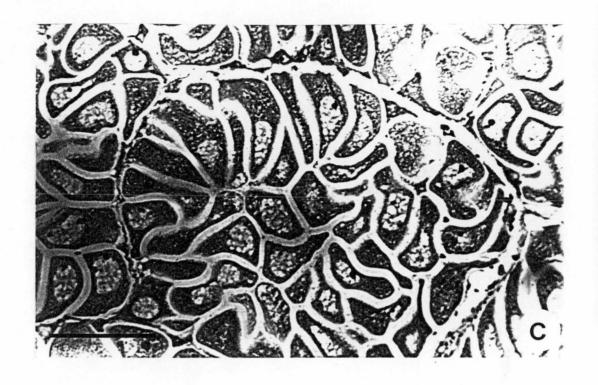
Figure 4.4 Reproductive output shown as a relationship between shell height (5 mm intervals) and gonad weight from running ripe samples (A) collected on 4 and 12 October 1989 and immediate post-spawning samples (B) on 2 and 16 November 1989. Number of scallops shown in brackets. [Error bars represent one standard deviation]

Plate 4.1 Photomicrographs of the gonad from a female M. asperrimus showing the characteristic stages of reproductive development: A, stage one (January - March) 'resting phase' showing empty follicles and ciliated ducts; B, stage two (April - June) early development with the appearance of primary oogonia; C, stage three (July - August) late development with elongated oocytes; D, stage four (September - October) mature gonads exhibiting irregular polygonal ova; E, stage five (October - December) spawning occurs with the release of ova from the centre of the follicles; F, stage six (November - January) spent gonads with lysis of remaining ova. [Bar lines represent 100 μm] Glossary: (ct) - connective tissue; (cd) - ciliated ducts; (f) - follicles; (fm) - follicle

membrane; (mo) - mature oocyte











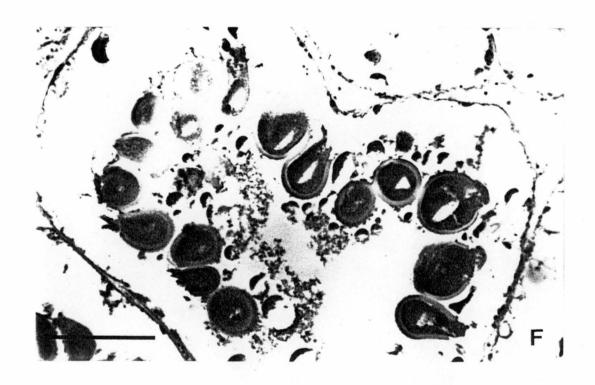


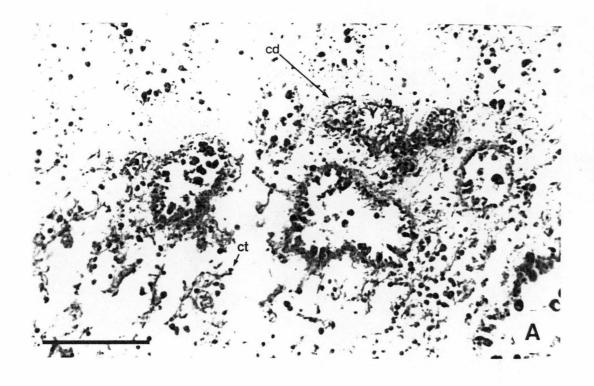
Table 4.1 Description of gonads and distinct histological stages in the annual reproductive cycle of the scallop, *Mimachlamys asperrimus* from the D'Entrecasteaux Channel, Tasmania.

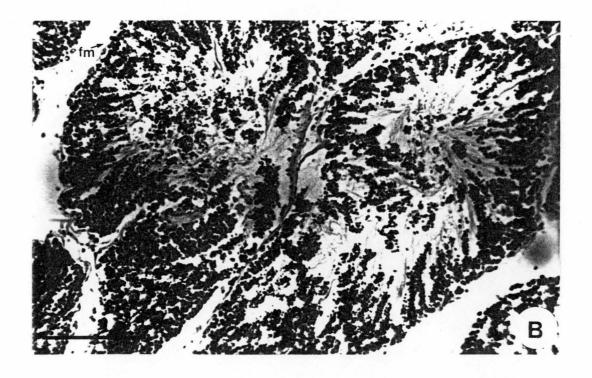
Stage	Female	Male	
(1) Resting	Gonad small, flat and yellow brown. Composed of loose connective tissue. Intestinal loop visible. Ciliated ducts present.		
(2) Early development	Slight increase in gonad size. Follicles with primary oogonia or spermatogonia. Clear differentiation of male and female gonads. Intestinal loop not visible.		
(3) Late development	Gonad increased in volume, tip being tapered.		
	Oocytes fill the follicle. Oocytes small and elongate. Oocyte size $45-55 \mu m$. Gonad orange.	Spermatocytes line the follicle. Spermatids towards the centre of the follicle. Small number of spermatozoa. Gonad white.	
(4) Mature	Gonad volume large with rounded tip. Little connective tissue.		
	Follicle packed with mature irregular polygonal oocytes.	Large number of spermatozoa. Follicles tightly packed.	
(5) Spawning	Free space in the centre of the follicles as gametes are expelled. Appearance of more connective tissue. Loss of gonad colour.		
	Ova size 50-60 μ m.	Gaps between rows of spermatozoa.	
(6) Spent	Follicles nearly empty of all gametes. Increase in connective tissue. Phagocytes predominate.		
	Lysis of remaining oocytes.	Small dense clumps of spermatozoa occupy the lumen.	

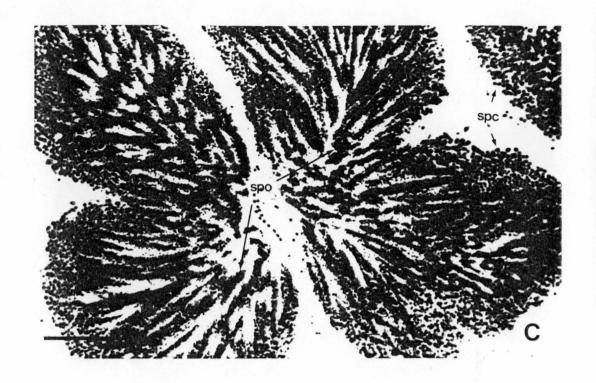
Male GSI peaked earlier than females, and males appeared to commence releasing sperm earlier than females shed ova (figure 4.1, 4.2). GSI peaked earlier in 1988 (September) than in 1989 (October). The index of fecundity was significantly higher in 1988 with the average gonad weight of the 90 - 95 mm size class being 38 percent higher than in 1989 (t-test, P < 0.02). Gonad weight loss on spawning in 1988 for the 90 - 95 mm size class was 63.12 percent of total gonad weight compared to 56.83 percent in 1989 (figures 4.3, 4.4). A significant decrease in gonad weight (suggestive of spawning) was observed between September and December in each year.

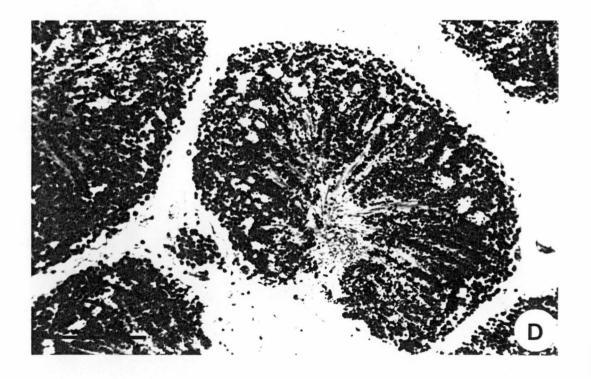
In both years there was a second rapid decline in gonad weight in late Decemberearly January. This has been interpreted as being indicative of partial spawning. Microscopic examination shows that further gametes may be released in some years, but gametes not released undergo lysis and are reabsorbed (Plates 4.1F and 4.2F). Plate 4.2 Photomicrographs of the gonad from a male *M. asperrimus* showing the characteristic stages of reproductive development: **A**, stage one (January - March) 'resting phase' showing early follicle formation and ciliated ducts; **B**, stage two (April - June) early development with the appearance of primary spermatogonia and clear follicular structure; **C**, stage three (July - August) late development with an increase in spermatocytes; **D**, stage four (September - October) mature spermatozoa fill the follicles; **E**, stage five (October - December) early spawning with the release of sperm from the centre of the follicles; **F**, stage six (November - January) spent gonads showing collapse of follicles and presence of phagocytes. [Bar lines represent 100 µm] Glossary: (ct) - connective tissue; (cd) - ciliated ducts; (f) - follicles; (fm) - follicle

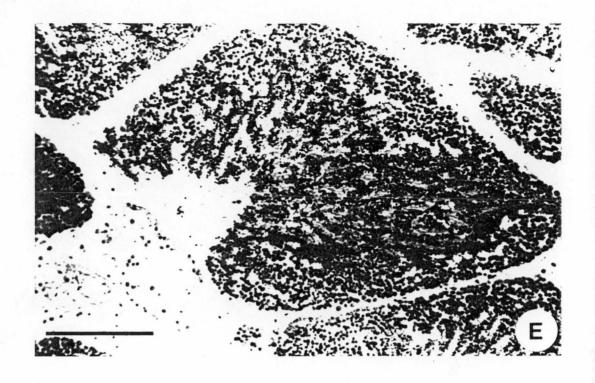
Glossary: (ct) - connective tissue; (cd) - ciliated ducts; (f) - follicles; (fm) - follicle membrane; (spc) - spermatocytes; (spo) - spermatozoa













Data obtained from spat collectors also supports this concept. It is not known what percentage of gametes released through earlier partial or late spawnings are competent; or their contribution to recruitment. However, spat collectors placed at a number of locations in the D'Entrecasteaux Channel and Bass Strait between September and April suggest that minor settlement occurs over a number of months, but only one major event is observed. The highest spat numbers (< 5 mm) observed in spat collectors in December of 1988 and 1989 suggests the major spawning in September/October contributes to greater spat settlement (see Chapter 5).

Sex ratio for all samples collected was 1:1. There was no change in sex ratio observed between different ages or shell height. Gonad maturity for males and females occurs in their first year (0+ year class), but the first major spawning occurs in their second year when most animals are > 55 mm shell height.

From a total of 300 gonad histological samples, two animals macroscopically identified as male were found to contain eggs and appeared to be functional hermaphrodites. This condition has not been previously reported for *M. asperrimus* (Plate 4.3).

4.5 Discussion

Sustainable management of a scallop fishery is dependent in part on an understanding of the reproductive cycle and environmental influences that may change or alter the timing and frequency of spawning. An important objective of the fishery manager is to identify the minimum size and age at first maturity, to reduce the potential for recruitment overfishing⁴. Knowledge of the reproductive cycle is also important in determining when, and to a lesser extent, where recruitment to the fishery may occur (Orensanz 1986).

M. asperrimus is a synchronous spawner, as is P. fumatus (Sause et al. 1987a) and E. bifrons (Dix and Sjardin 1975). M. asperrimus is similar to E. bifrons in that sexes are separate, the male and female individuals readily identified for the majority of the year. Males have a white, creamy appearance from early development through to maturity, whereas the female exhibits a rosy pink to bright orange gonad when mature.

Males matured and released sperm earlier than females. Gonads began early development in late March - early April and immature oogonia are evident by May.

⁴ Recruitment overfishing occurs when individuals are removed from a population or unit stock before reproductive maturity has been reached.

Maturation continues through the winter months with a major spawning event occurring in late September to mid October. A minor spawning may be observed in December, but the significant decrease in GSI at this time may have been a consequence of oocyte lysis and re-absorption. Rose and Dix (1984) collected mature ova from individuals in the D'Entrecasteaux Channel during September/October in their study of the larvae of *M. asperrimus*, which is consistent with the results of this study.

M. asperrimus has some reproductive development in year 1 (0+) but the gonad does not mature past stage 3. Maturity is reached in the second year (1+). The smallest female observed with mature ova had a shell height of 57.5 mm. Fecundity generally increases with shell height and age, peaking in the 90 to 95 mm size class. Few ripe scallops were found larger than 95 mm, but of the two located, one 101 mm individual found in 1989 had the highest gonad weight recorded of 16.4 g.

The results illustrate the need to monitor populations over a number of seasons to accurately establish the timing, frequency and level of ova release during spawning. The major spawning in 1988 occurred between 15 September and 20 October with the maximum mean GSI being 37.72 percent on 15 September. In 1989 the major spawning occurred four weeks later between 4 October and 16 November on the basis of GSI changes, with the maximum mean GSI being 27.59 percent on 12 October. Spawning in 1990 was observed to be later than 31 October. Maximum gonad index and ova diameter is reached two to three weeks prior to spawning and some gamete 'leakage' does occur prior to the main spawning event. This was revealed by early spat settlement in the collectors.

Gonad weight loss was used as a measure of fecundity, as the number of ova released in any year may fluctuate widely. A count of total ova number, as is performed in many fecundity studies, may not have highlighted this difference. Nash (1985) points out that the total ova number released annually is preferable to the number of mature ova contained in the ovary. Research into stock/recruit relationships may be clearer to interpret if the former and not the latter measure is more widely used.

The collection and identification of two hermaphroditic individuals during this study had not been previously recorded for *M. asperrimus*. This phenomenon is not unique to this gonochoristic species, having been recorded in *Placopecten magellanicus* (Merrill and Burch 1960), *Patinopecten caurinus* (Hennick 1971), *Amusium japonicum balloti* (Dredge 1981) and *Hinnites giganteus* (Malachowski 1988). Both hermaphrodites were macroscopically male but on histological examination mature oocytes were scattered along the boundaries of the follicles (Plate 4.3). Whether these mature oocytes are

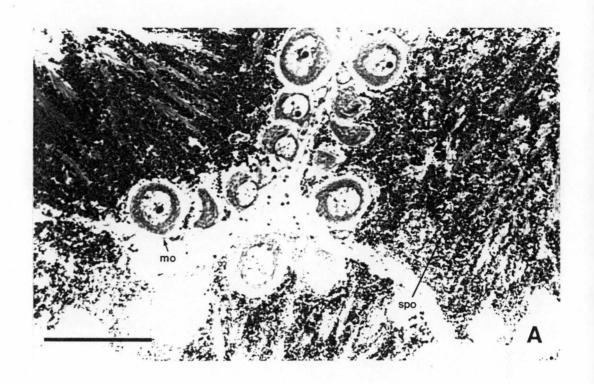
released during spawning, and whether these oocytes are competent was not determined during this study.

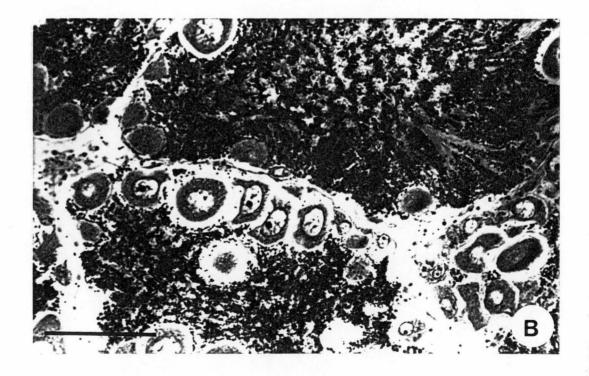
Spat collection was an important process used to validate identification of both the peak spawning period and secondary or minor spawning events. During the two year period from 1988/89 to 1989/90, highest spat numbers were recorded in December, with shell height frequency histograms indicating a further minor settlement in February. Spat < 5 mm are continually observed in spat collectors during November to March, indicating some partial spawning or 'leakage' of gametes at a low level over a 5 month period. This gamete leakage has been reported for a number of other scallop species (Brand *et al.* 1981, Ciocco 1991, Hortle and Cropp 1987, Sause *et al.* 1987a,b; Wolff 1988).

Rose and Dix (1984) indicated that the larval period exhibited by *M. asperrimus* in the laboratory at a temperature of 17 - 18° C was between 20 and 23 days. Analysis of the time of spawning from histological examination, and the appearance of 5 mm spat in collectors during this study, suggests that the natural larval period is longer than observed in the laboratory. As water temperature (at 12 metres) is between 11.5-14.5° C in the D'Entrecasteaux Channel during October to December (figure 5.6), larval growth would be slower than in the laboratory. Results from this study suggest the natural larval period for *M. asperrimus* ranges between 30 to 40 days.

Delay mechanisms influencing spat settlement are the result of complex water temperature, food availability and substrate interactions, and have been recorded for other scallop species (Broom and Mason 1978, Hodgson and Bourne 1988, Mann 1988) and other bivalves such as mussels (Bayne 1976). However, it is difficult to accurately determine the time of natural spat settlement as spat may not be detected until the artificial collectors are randomly hit by the planktotrophic 'pools' of scallop larvae from different populations. Models of larval advection show that strength and the direction of wind at the time of spawning is an important determining factor in the distribution of scallop larvae (Butman 1987, Orensanz et al. 1991, Young et al. 1992). The length of the natural larval period for M. asperrimus requires further investigation. There may be considerable implications in this for scallop fisheries management, as commercial fishing dredges may disturb the substrata to such a degree that spat settlement and survival is severely affected.

Plate 4.3 (A and B) Photomicrographs of the gonad from a macroscopically identified male C. asperrimus with a shell height of 85 mm. Mature oocytes occur along the follicle walls surrounded by spermatozoa. [Bar lines represent 100 μ m] mo - mature oocyte, spo - spermatozoa.





 $M.\ asperrimus$ is a gonochoristic species. Gonad development is initiated with a decrease in the mean water temperature during late April - early May each year. Mature ova and sperm are observed during early September to December, with a major spawning event occurring during September to October. At the time of spawning, maximum ova diameter is 60 μ m. Gonad development and spawning is synchronous, but males mature and release sperm earlier than females release ova. Doughboy scallops reach reproductive maturity in their first year, but the first major spawning occurs in their second year at a shell height > 55 mm. Macroscopic examination of gonads is not a valid method for determining the reproductive cycle, as spawning animals take up water which fills the empty lumen creating the illusion of ripe gonads.

5 RECRUITMENT

5.1 Introduction

The Pectinidae are characterised by their extreme variability in recruitment and *M. asperrimus* is no exception. Doughboys grow, mature and usually spawn each year, but settlement of spat and subsequent recruitment⁵ of juveniles to the fishery is an irregular event that only occurs at high densities once every few years. To effectively study population changes in age classes, recruitment processes need to be studied over an extended period, both in unfished and fished populations. There are many different methods for determining the population structure of a scallop stock. Regular surveys by diving, dredging or trawling provide good information on size frequency distributions, modal progression and an indication of mortality (Ciocco 1991, Gwyther and McShane 1988, Orensanz 1986, Zacharin 1986, 1987, 1988, 1991a,b). Other methods that have been effectively used are commercial fishing data, mark-recapture techniques and age determination models based on 'disturbance' or growth rings on the external shell (Caddy 1975, Ciocco 1991, Dickie 1955, Dredge 1985a,b, Hancock 1979, Orensanz *et al.* 1991, Sause *et al.* 1987).

To interpret the dynamics of a population or unit stock, information needs to be available on the reproductive cycle, the life history of the larvae (larval advection processes affecting recruitment), factors affecting settlement, the effect of temperature and food availability, and natural mortality. These interactions are discussed in association with the observed recruitment and populations dynamics of *M. asperrimus* in the D'Entrecasteaux Channel region.

5.2 Materials and Methods

5.2.1 Size frequency distribution

Regular surveys of doughboy scallops in the D'Entrecasteaux Channel have been conducted by the author since 1985. Between 1985 and 1988, 110 to 119 random stations within each statistical area were sampled using a 2.5 m wide toothed scallop dredge (Zacharin 1986, 1987, 1988). Since 1989, scallop surveys have been conducted by diving, to more accurately sample doughboys in the size range 30 - 40 mm (Zacharin 1991b, Zacharin *et al.* 1990).

⁵adult population above the legal minimum size that is exposed to fishing mortality

As scallops in the D'Entrecasteaux Channel are characteristically distributed at low densities over large areas, and at high densities forming 'commercial beds' over discrete areas, sampling techniques must compensate for this fact. To adjust for this pattern of distribution, diver surveys were conducted using the following procedure. A number of random sampling points are distributed over an area to give an indication of scallop distribution and density. Further non-random sampling points were chosen based on previous catch history of the area and from reported sightings by recreational divers. At each site a 100 m transect line weighted with lead and buoyed at each end is deployed parallel to the current. Two divers swam along the transect line collecting all scallops within 1 m of the weighted line (200 m²). It is important to deploy the line with the current and to swim with the current, as any scallops disturbed by the deployment of the line may move. As scallops tend to swim off the bottom and then free-fall to the substrate the majority are more likely to remain in the transect area if deployment is parallel to the current.

Diver experience is important in surveying *M. asperrimus* populations, however, small doughboys are easier to identify than *P. fumatus* as doughboys are usually attached by a byssal thread (particularly as juveniles), and do not depress themselves in the sediment when free-living as does *P. fumatus*.

The survey data from 1987 to 1992 is presented and assembled as both total size frequencies for those statistical areas of the D'Entrecasteaux Channel surveyed each year (see figure 1.1), and as size frequencies of scallops in the various statistical areas. This interpretation provides spatial information on annual scallop settlement and recruitment events.

5.2.2 Relative abundance and natural mortality

Estimates of relative abundance for *M. asperrimus* in the statistical areas for the years 1987 to 1992 were calculated from survey data. The total area of each statistical area to low water mark was calculated using a geographical information system at the Department of Environment and Land Management, Hobart. These "statistical areas" were devised in the 1950's by the Fisheries Division, Department of Primary Industry for the recording of commercial scallop catches (see figure 1.1). The areas have a fairly constant depth so no further stratification was considered necessary. To calculate relative

⁶ A scallop bed is defined as a circular patch of scallops from a single cohort whose density falls off with distance from the centre.

⁷ The statistical area boundaries were determined primarily by geographic features such as headlands or islands, but coincidentally the areas are reasonably homologous in their depth strata.

abundance, the mean scallop density of each statistical area is multiplied by the available ground area. However, because of the patchiness of scallop distribution, high density areas are treated separately from low density areas, and the two estimates then added, to reduce the potential for over-estimation of the relative abundance. Within each statistical area, there are numerous areas where no scallops were observed during the dive surveys, but to calculate a better estimate would involve a considerably greater number of sample sites and perhaps finer stratification of the areas. Both strategies do reduce the confidence intervals about the relative abundance estimate, but do not significantly alter the mean abundance estimate. A balance is required between the cost and time of sampling against the expected gain in robustness of the abundance estimate.

Natural mortality was estimated from the changes in mean abundance of the year classes from survey data between 1988 and 1991. These data were from an unfished population, therefore total mortality (Z) can be assumed to equal natural mortality (M). Total mortality was calculated from the expression $N_{t+1} = N_t \, e^{-z}$, where N_t is the number of scallops at age t and N_{t+1} the number of scallops at age t+1. This expression can be transformed using natural logarithms to:

$$ln N_{t+1} = -Z$$

$$N_t$$
 (Gulland 1983)

No estimate of natural mortality was possible from tagged scallops due to the low number of recaptures.

5.2.3 Monitoring of spat settlement

Spat collection in the D'Entrecasteaux Channel was conducted using small orange coloured onion bags (5 mm mesh) with dark monofilament mesh filling as a settlement substrate. Collectors were attached to sub-surface longlines between 6 and 15 m (figure 5.1). Spat collectors were deployed in September 1988 adjacent to Huon Island in the southern channel region. This site was selected as tidal flow is greater around prominent headlands and islands, and large catches of *P. fumatus* spat had been observed at Huon Island in previous years. Collectors were observed each month to assess the time and intensity of spat settlement. Further spat collectors were deployed adjacent to Huon Island in 1990 and 1991 to catch juveniles for growth trials. Water temperature at the Huon Island site was recorded over a six month period between 1 September 1988 to 24 January 1989 using an automatic temperature recorder at a depth of 12 metres (figure 5.2).

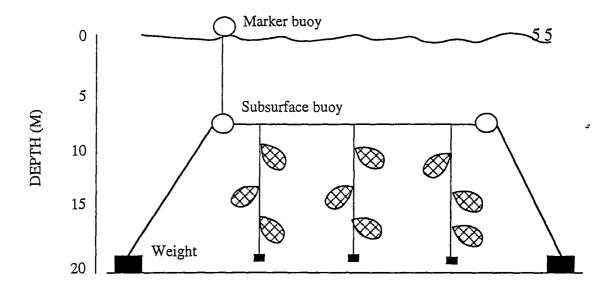


Figure 5.1: Diagram of the spat collection system deployed at Huon Island.

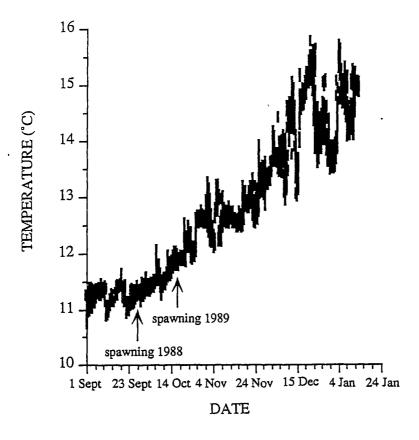


Figure 5.2 Daily temperature reading taken adjacent to the Huon Island spat collection line at a depth of 12 metres between 1 September 1988 and 24 January 1989.

5.3.1 Size frequency distribution

Inter-annual changes in the size frequency distribution of *M. asperrimus* in the D'Entrecasteaux Channel during 1987 to 1992 are shown in figures 5.3 (total data) and 5.4 (individual years). As the diver surveys were conducted between March and April each year, an index of potential recruitment is represented by the numbers of the 0+ year class (30 - 40 mm size range). Survey results indicate that there was strong settlement in 1988, 1990 and 1991 (Zacharin 1988, 1991b, Zacharin *et al.* 1990).

Size frequency histograms for each statistical area demonstrate the spatial patchiness of scallop settlement by the relative abundance of 30 - 40 mm scallops (figures 5.5, 5.6). In areas 7, 8 and 9 30 - 40 mm scallops were relatively abundant in 1989 and 1991, but in areas 6 and 10, 30 - 40 mm scallops were rare except in the 1991 samples. Area 11 supported few such scallops throughout the entire study period.

The *M. asperrimus* population(s) in the D'Entrecasteaux Channel were much larger and older in 1988 compared with other years and the majority of these older scallops were in area 8. These older scallops are more fecund than younger scallops (see Chapter 4) and this appears to have led to a major spawning event in 1988, and good subsequent settlement and pre-recruit numbers in 1989 (table 5.1). However, this result is markedly different from the situation in 1990, when there was a much lower number of older, more fecund scallops, but a significant settlement event was also recorded in 1991. These results suggest that factors other than spawning population size are interacting to influence recruitment. The remaining statistical areas (2,3,4,5,12) historically have low scallop density and were not sampled with sufficient regularity to give meaningful data.

5.3.2 Estimated relative abundance and natural mortality

During 1987 and 1988, relative abundance estimates were calculated assuming the scallop dredges used for sample collection were 100 % efficient, therefore these estimates should be considered as minimum values as scallop dredge efficiency may range between 10 and 100 % (McLoughlin *et al.* 1991). Estimates for 1989 to 1991 are based on mean density results from dive surveys (diver efficiency 95%) and should be considered as more accurate mean values.

Using the estimates of relative abundance for the years 1988 to 1990, and knowing the approximate age of the scallops, an estimate of natural mortality can be

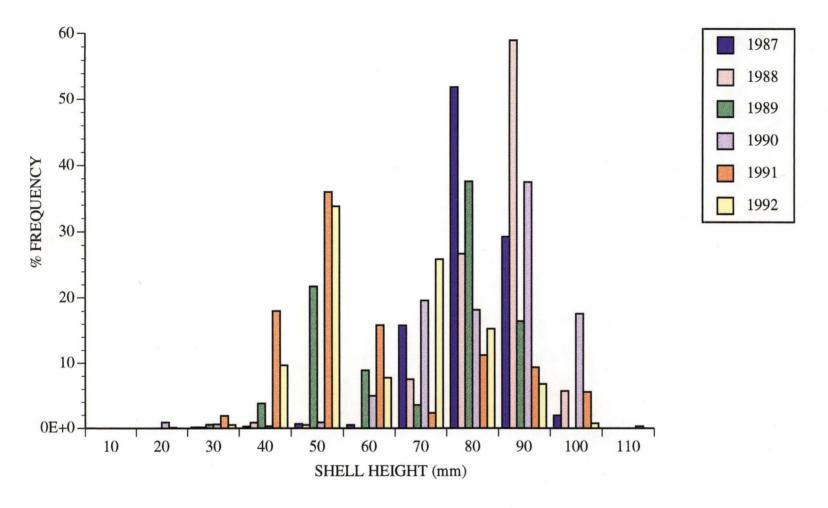


Figure 5.3: Size frequency histogram for all doughboy scallops measured from all statistical areas during the 1987 to 1992 surveys. The 1987 and 1988 surveys were conducted using a dredge, while the 1989 to 1992 surveys were conducted by divers. Values indicate percentage frequency of size calssess in each year.



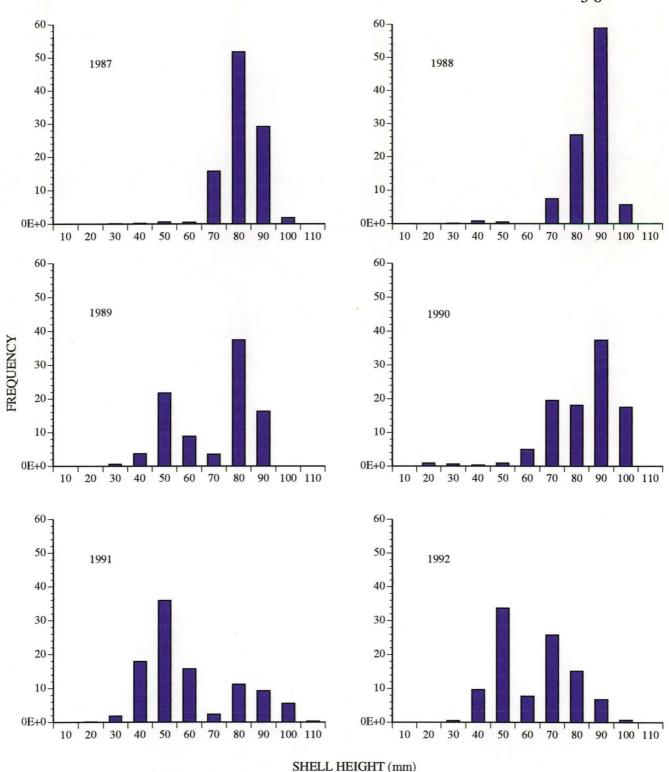


Figure 5.4: Size frequency histograms for all doughboy scallops measured for all statistical area for the years 1987 to 1992.

calculated as the instantaneous mortality rate between fully recruited size classes in each year. The years 1988 to 1990 were chosen as no legal fishing (commercial or recreational) was permitted during this period (or before the survey was completed in 1990), therefore total mortality (Z) = natural mortality (M) (table 5.2).

Natural mortality estimates range between 0.23 to 1.04 yr⁻¹ for fully recruited year classes. The results suggest that natural mortality decreased with increasing age/size in *M. asperrimus*, but as it was not possible to determine age with an acceptable degree of accuracy for scallops larger than 90 mm, the low mortality estimate of 0.23 may be the result of a combination of factors. Firstly, there would be some bias in the aging by the 'bunching' of older age classes into the one (5+) age category, and secondly, the 1988 abundance estimate was calculated from a dredge survey, and dredge efficiency has been demonstrated to show significant variation.

Table 5.1 Estimated relative abundance of *M. asperrimus* for statistical areas 6,7,8,9 and 10 in the D'Entrecasteaux Channel for the years 1987 to 1991.

Size range	1987	1988	1989	1990	1991
(mm)	(Scallop Number x 10 ³)				
10-20	0	0	0	33.43	12.04
20-30	15.61	35.35	42.48	22.27	240.86
30-40	68.95	58.58	297.19	11.15	2,348.35
40-50	1,144.88	29.29	1,719.65	33.43	4,696.69
50-60	98.88	81.81	636.87	189.32	2,059.51
60-70	2,464.09	825.17	275.99	746.19	301.07
70-80	8,357.62	4,765.18	700.63	690.50	145.92
80-90	1,821.40	3,975.36	2,972.18	1,425.55	1,216.06
90-100	68.95	331.28	1,295.01	668.23	722.57
100-110	0	0	0	0	36.13
Total (x 10 ⁶)	13.67	11.09	7.94	3.82	13.09

Table 5.2 Estimates of natural mortality (Z=M) from survey data of each recruited age class for M. asperrimus in the D'Entrecasteaux Channel for the years 1988 to 1990.

Size range	Age	1988	1989	1990	M
(mm)	(yrs)		$(x 10^3)$		(coefficient)
78-85	3+	a3,365.11	b1,379.97	567.99	-
86-89	4+	c1,629.89	d1,188.85	e590.27	ad1.04,be0.85
90+	5+	331.28	f1,295.01	g668.23	cf0.23,dg0.58

5.3.3 Monitoring of spat settlement

Spat settlement at Huon Island was first observed in early December. The three scallop species located in the D'Entrecasteaux Channel settled in the spat collectors at about the same time. Monitoring the spat collectors between December and April in 1988/89 showed there was only one major spawning event that led to spat settlement (table 5.3). This is supported by the gonad index data for 1988 (see chapter 3).

The primary objective was to collect data on spat settlement to assist in determining the major spawning season, peak settlement period and validation of the age/shell height relationship. Samples of three to five collectors were sorted and counted each period. Spat number was observed to vary between collectors and water depth, but no comparative analysis was conducted due to the small number of collectors deployed. All the doughboys were abyssally attached to the inner mesh or surface of the spat collector whereas the majority of the *P. fumatus* spat was found in the bottom of the collector bags. *M. asperrimus* spat do not have the characteristic covering of sponge in the collector bags and this made identification and removal easier.

Table 5.3 Results from spat collectors deployed adjacent to Huon Island in the D'Entrecasteaux Channel (statistical area 9) during 1988/89.

Date	Number/Collector	Mean Shell	std
		Height (mm)	
9/12/88	158-208	4.26	1.59
25/1/89	316	5.75	0.99
28/2/89	230	10.43	1.97
21/3/89	226-306	, 12.65	2.69
30/4/89	130-176	16.43	4.29

5.3.4 Recruitment and Population Dynamics

An index of recruitment (70-80 mm size class) for each of the six successive years for areas 6, 7 and 8 show that pre-recruit numbers were relatively high in 1987 and 1988 (areas 6 and 8 only), but the number decreased significantly in each successive year from 1989 to 1992 (figure 5.4). As there was no fishing of doughboys in the D'Entrecasteaux Channel (prior to the surveys) during 1987 to 1990, these fluctuation in the size distribution of the population are the result of the species interaction with its environment. In 1990, the Channel region was opened to recreational divers for a limited scallop season, and although the legal minimum size was set at 80 mm (shell height), one suspects that scallops below the minimum size were taken. The mean abundance of pre-recruits observed during the 1991 survey was very low (<0.1 m⁻¹) and suggests the population may have been subject to recruitment overfishing⁸. However, there was also a strong year class of 1+ scallops in 1992 in area 6, and these are expected to recruit to the fishery (as 3+ scallops) in 1994. Raw data of the size frequency distributions is located in Appendix IV.

Little Taylors Bay (area 11) was found to have minimal 0+ scallops in all years, but there were large numbers of pre-recruits in 1987, 1988 and 1991. There must be immigration to this area from the northern regions of the D'Entrecasteaux Channel; an observation supported by the strong currents that flow from the Huon River and south from Satellite Island into Little Taylors Bay.

Statistical area 6 consistently supported a greater abundance of scallops than any other area (figure 5.5). This may have been a consequence of the vast size of area 6, but the semi-enclosed nature of this area also may contribute to the retention of larvae in the area by providing a physical barrier to larval dispersal from resident spawning populations. Emigration of juvenile scallops from the southern region of area 6 to other areas is also less likely to occur.

5.4 Discussion

The population dynamics of scallop stocks are affected by a vast array of physical and environmental factors, but it is the environmental factors affecting spawning and the subsequent settlement and survival of the pelagic larvae that determine to a larger extent the size of the population (Orensanz 1986, Peterson and Summerson 1992, Tremblay and Sinclair 1992). Increases in population size on a large scale are driven by periodic recruitment events, while increases on a smaller scale are affected by immigration,

⁸ the depletion of the reproductive population resulting in poor recruitment

emigration and mortality. Growth and natural mortality are known to be affected by density dependent processes, but this is not attributed to food limitation among benthic suspension feeders, rather the chaotic nature of their food supply (Orensanz *et al.* 1991).

Recruitment in *M. asperrimus* in the D'Entrecasteaux Channel region is both spatially and temporally erratic. For the six year period during 1987 to 1992, settlement of juveniles was only significant in two years (1988 and 1990), with the highest number of pre-recruits being observed in 1987. Some areas, such as Little Taylors Bay, appear to rely on immigration to boost scallop populations. Movement of scallops due to the affects of prevailing currents was observed during monitoring of juvenile populations over many years. When an escape response is illicited due to some perceived threat, the scallop will swim up into the water to a height of approximately 3 metres, then drift downwards in the direction of the currents, sometimes landing at least 10 metres from their original position if currents are 2 to 3 knots.

Hydrodynamic processes also play a major role in the transportation of larvae (Butman 1987, Orensanz et al. 1991, Young et al. 1992). This is well illustrated by the spatial changes in the distribution of juvenile scallops in the D'Entrecasteaux Channel. Area six is the most enclosed bay within the D'Entrecasteaux Channel region, and this area was consistently found to have higher abundance and a greater range of year classes than other more exposed or less enclosed areas. Larvae transported to, or produced by, spawning scallops in area six, are more likely to be trapped in the area thus resulting in increased scallop density. This result has been well documented for numerous scallop fisheries world-wide, and entrapment of larvae appears to be a primary determinant in the annual survival of many commercial scallop fisheries (Caddy 1975, Peterson and Summerson 1992, Tremblay and Sinclair 1992).

The potential for the population to recover to the abundance of 1988 (Zacharin 1988) must in part rely on the capacity of a greater number of the larger scallops to escape capture by the annual recreational fishery. The size frequency distributions for all scallops sampled during the surveys show that the percentage of scallops above the scallop legal minimum size (80 mm) decreased from 91.32 percent of the population in 1988 to 22.65 percent in 1992. Collapse of the scallop fishery in the D'Entrecasteaux Channel since 1990 may be attributed to recruitment overfishing, but during 1988 and 1989 the number of scallops above 80 mm decreased by 37.58 percent with no fishing. This decrease in abundance may have been the result of senescence due to the age of the population in 1988 or to illegal fishing activity.

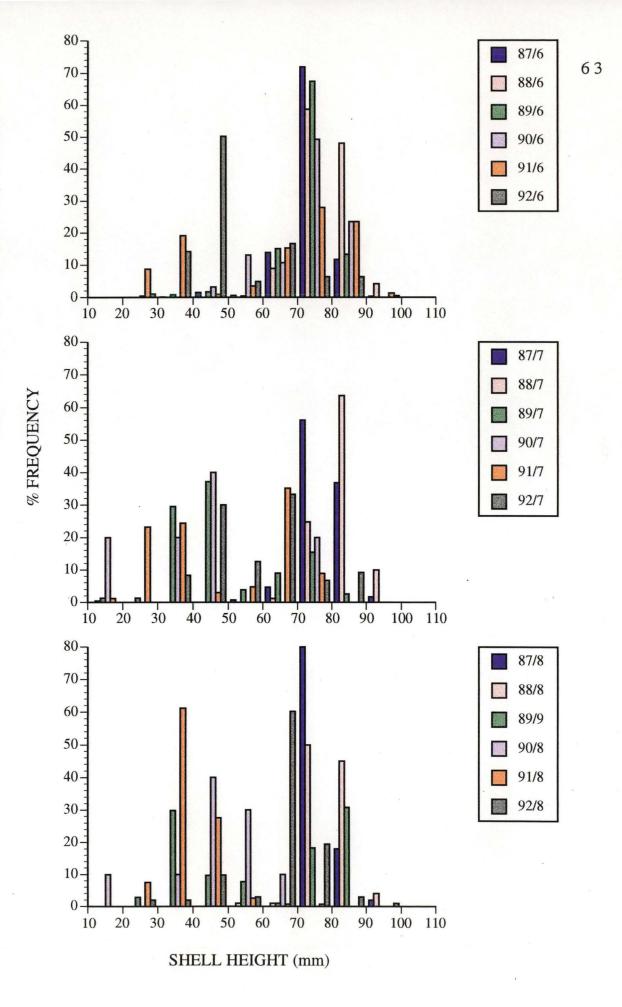


Figure 5.5: Size frequency histograms for statistical areas 6, 7 and 8 in the D'Entrecasteaux Channel sampled between 1987 and 1992

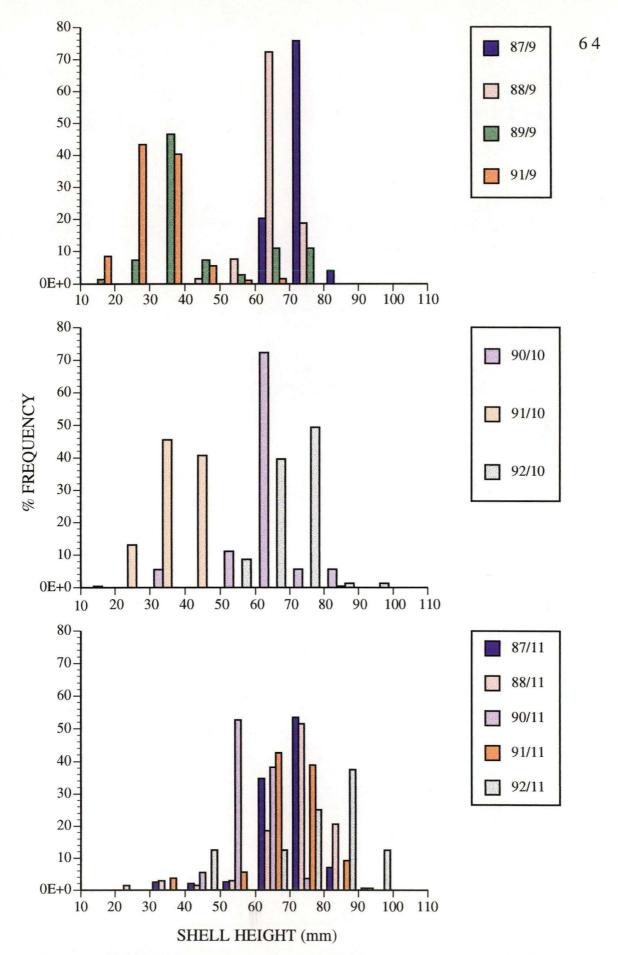


Figure 5.6: Size frequency histograms for statistical areas 9, 10 and 11 in the D'Entrecasteaux Channel sampled between 1987 and 1992.

Area 10, adjacent to Satellite Island, supported a high density bed of M. asperrimus during 1990 and 1991 but a heavy concentration of fishing effort on this population during the subsequent limited fishing seasons decimated this population. Scallop density at some sample sites were 0.64 scallops m^2 , the highest recorded for M. asperrimus in the D'Entrecasteaux Channel between 1987 and 1992. No recovery had occurred by April 1993 (Zacharin - pers. obs.).

The range of natural mortality estimates between 0.23 and 1.04 yr⁻¹ are comparable with other mortality estimates for *Chlamys* species. Shafee and Conan (1984) found natural mortality in *C. varia* to range between 0.71 and 1.19 yr⁻¹, and Orensanz (1986) calculated a natural mortality range of 0.62 to 1.99 yr⁻¹ for *C. techuelcha* in Chile. Both these estimates were calculated from a change in the abundance of a cohort over time, as used in this study. Sources of natural mortality were not specifically investigated as part of this study, but senescence, predation by the seastar *Coscinasterias calamaria*, and shell borers of the genus *Polydora* were observed as likely causes of mortality. Small scallops were frequently being attacked by *C. calamaria*, and on occasion a number of larger scallops were found with gapping shells, with the viscera attached, in difference stages of decay. This was assumed to be the result of senescence because of their size.

Other sources of mortality such as strandings, low salinity, dissolved oxygen depletion and algal blooms have been recorded as major causes of mortality for some scallop species (Gruffydd 1974, Orensanz 1986, Orensanz et al. 1991, Vahl 1982). None of these sources of mortality were evident during this study, except for separate algal blooms in the D'Entrecasteaux Channel during 1989 and 1991. Biotoxin testing of scallop tissue did not indicate that scallops were affected (R. Brown - unpub. data), and no mortality was observed.

The natural mortality estimates for fully recruited year classes of *M. asperrimus* from 1989 to 1990 were 0.85 and 0.58 respectively. Natural mortality is more likely to be closer to these two estimates, as the relative abundance estimates used to determine scallop numbers for each age class are probably more robust for 1989 and 1990 because of the better sampling efficiency of dive surveys. Dredges tend to bias the data towards larger scallops as their efficiency is highly variable, and the mesh size of 70 mm fails to trap small scallops unless rubbish (rock, sponge) is also trapped in the rear of the dredge. Although scallops smaller than 15 mm are extremely difficult to locate using most sampling methods, diver efficiency is significantly better than dredge efficiency. Diver surveys should be used for scallop abundance estimates where water depth is below 20 metres.

Extreme recruitment variability showing no relationship with spawning stock is characteristic of many scallop fisheries (Orensanz *et al.* 19991). *M. asperrimus* is no different from other scallop fisheries, recruitment appearing to be driven more by physical and environmental factors that influence the transport of larvae and juvenile survival, than the number of spawning animals within the population. Langton *et al.*(1987) suggests that if environmental conditions are not ideal for successful spawning in a given year, scallop may adopt a 'dribble' spawning strategy thus ensuring that some larvae will find favourable conditions and survive. This may explain the continuous observation of small doughboys in the spat collectors between November and May in some years.

Peterson and Summerson (1992) suggest that variation in the pattern of population abundance may be a function of the number of successful larval colonists in a year, rather than subsequent post-settlement processes such as predation. This phenomenon has been described as 'recruitment limitation' and contrasts with the common assumption that marine invertebrates release so many larvae that subsequent year class strength is not limited by spawning stock size (Hancock 1973). I would agree that increases in population size must be initially driven by the number of successful larval colonists, but environmental affects together with post-settlement predation, would appear to exert greater influence in determining the number of recruits to a scallop fishery. A number of juvenile reseeding trials using *M. asperrimus* and *P. fumatus* in the D'Entrecasteaux Channel have been spectacularly unsuccessful, survival after one year being less than two percent because of predation (Zacharin - unpub. data).

If the level of the spawning population falls below some undetermined threshold size, the capacity of the population (or stock) to produce sufficient larvae for population growth may be severely affected. However, for *M. asperrimus* the spawning population in 1990 (table 5.1) was the lowest recorded since 1987, but this resulted in a massive settlement event in early 1991. Over 2 million 30 - 40 mm scallops resulted from the low 1990 spawning population. This result supports the observations of many researchers that stock - recruit relationships for scallops do not exist, or can not be detected, at average population sizes (Orensanz *et al.* 1991). The relationship may only become evident at low stock levels, and again this relationship may be masked by environmental affects. Recruitment to the *M. asperrimus* populations in the D'Entrecasteaux Channel was only observed to be significant in two years (1988 and 1989) between 1987 and 1992. Recruitment to the populations after 1989 would appear to have been affected by recreational fishing activities. A large recruitment event is expected to occur in 1994.

⁹ slow, prolonged release of ova

6 CONCLUSIONS

The reproduction, growth, mortality and recruitment rates of *M. asperrimus* are of considerable importance to our understanding of scallop fishery management and the potential of *M. asperrimus* for aquaculture. There have been many studies of scallop populations world-wide which show considerable variability between species in reproductive capacity, growth and recruitment, and these differences appear to be determined as a result of interaction with the local environment (Barber and Blake 1983, Burnell and Rodhouse 1980, Caddy 1989, Dredge 1985b, Fifas *et al.* 1990, Hancock 1973, MacDonald and Thompson 1988, Monical 1980, Naidu 1988, Orensanz 1986, Orensanz *et al.* 1991, Sastry 1968, Sause *et al.* 1987, Shafee and Lucus 1980).

It is evident from the results presented on *M. asperrimus* that scallop growth in suspended culture is faster than growth observed in natural beds. This increased growth rate for *M. asperrimus* in suspended culture suggests the species has potential for aquaculture. In Japanese lantern hanging culture, shell growth over summer was as high as 1.13 mm wk⁻¹ with winter growth reducing to 0.5 mm wk⁻¹. *M. asperrimus* in suspended culture may reach a commercial size of 80 mm in about 2.5 years. This growth rate is comparable to growth of the larger scallop *P. fumatus* in Tasmanian waters which has a growth rate in suspended culture ranging between 0.54 and 1.38 mm wk⁻¹ (Cropp and Hortle 1991). Growth on the seabed at two sites during this study, both from a natural and a reseeded population, indicated that natural growth rate during winter and spring was 0.42 mm wk⁻¹(table 6.1). At this rate *M. asperrimus* would take an average of 3.4 years to reach a size of 80 mm.

In all growth experiments maximal shell growth occurred during summer and autumn, whilst somatic condition and peak reproductive capacity was reached during late winter to early spring. Estimates of L∞ ranged between 105 (in suspended culture) to 94 (natural population) with K being 0.578 and 0.573 respectively. This seasonal pattern in growth may vary inter-annually and has been demonstrated to be dependent on water temperature and food availability for other scallop species (MacDonald and Bourne 1989, Sastry 1968, Wallace and Reinsnes 1984). As the energy available for shell growth decreases with size due to increasing metabolic requirements, shell growth will slow with age (MacDonald 1986).

There was considerable individual variation in growth characteristics for M. asperrimus in suspended culture and this is apparent in the data. However, if the growth data are grouped into 5 mm samples, it is clear that the individual differences in growth rate are just a function of size/age, but also the seasonal variation in water temperature and

food supply (Table 6.2). Small, young scallops generally grow faster than larger, old scallops; although there was an exception with the 66-70 mm size class. The lack of shell growth in this size class between June and November may have been because these scallops were transporting more energy into reproductive conditioning. Ciocco (1991) reported similar differences in individual growth rate among *C. techuelcha* populations in Argentina.

Table 6.1 Summary of individual experiments at each study site in the D'Entrecasteaux Channel.

Site	Study Period	Method Used	Shell Height (mm)	Growth (mm wk ⁻¹)
Simpsons Bay Simpsons Bay Huon Island Birches Bay	1987-1992 1/7/88-27/11/90 1989/90-1990/91 1/7/88-2/11/89	size frequency gonad condition spat collection cage culture	0-105 70-105 0-35 20-90	0.64-1.0 summer 1.13 summer 0.50 winter
Satellite Is. Great Bay	19/3/91-28/5/92 25/5/90-11/9/90	natural growth reseeded	40-70 15-30	0.42 0.43 winter

The slowing of shell growth in older scallops makes scallop aging using external rings considerably more difficult for older individuals. External rings become crowded together as the number of striae laid down in the shell decreases with age (Crabtree et al. 1980, Franklin and Pickett 1980), and it is possible in older scallops that no shell growth occurs during the last one or two years of life. Tagging experiments during this study were to provide a validation method for age determination, but this was not possible due to poor tags returns from the 1,800 scallop tagged during 1988 and 1989. However, the age structure as presented using ring counts was verified using incremental growth measures from size frequency analysis, size at known age for juvenile scallops from spat collectors and growth of cultured scallops.

The reported size/age relationship is dependent on the hypothesis that external rings are the result of spawning stress and not a slowing of shell growth due to low water temperatures over winter. There is evidence in the literature to support either hypothesis (Orensanz et al. 1991), but it is important in this study that microscopic evaluation of reproductive maturity showed that no spawning occurs in the first year, and subsequently no external ring is apparent. Low water temperatures during winter may result in a slight stress ring in M. asperrimus, but these rings are not comparable to the pronounced spawning rings laid down after the second year. M. asperrimus probably has a maximum life expectancy of six years.

Table 6.2 Growth rates observed in suspended culture presented in 5 mm groupings to show differences in size and age classes.

Size Class	Age (yrs)	Growth Period (days)	Season	Observed growth range (mm)
16-20 21-25 26-30 31-35	0+	489	July'88-Nov'89	31.8-46.2 30.6-47.7 34.4-52.1 32.9-43.1
36-40 41-45	0+	. 205	Nov'88-Jun'89	13.9-24.8 19.5-31.7
46-50 51-55 56-60 61-65	1+	246	Mar'89-Nov'89	8.2-12.4 6.7-14.3 7.0-12.3 9.1-16.7
66-70	1+	155	Jun'89-Nov'89	0.5-2.8
71-75	2+	155	Jun'89-Nov'89	1.1-6.1
76-80	2+	155	Jun'89-Nov'89	4.9

Note: scallops grown in suspended culture attain a larger size at a younger age

Reproduction in *M. asperrimus* is an annual event with synchronous spawning occurring during September and October. Synchronous spawning is a feature of many benthic invertebrates as this strategy is critical for the reproductive success of species with external fertilisation (Caddy 1975, Hancock 1973). The peak spawning period for other scallop species reported in the literature appears to be dependent on prevailing environmental conditions, particularly water temperature and food supply (MacDonald and Thompson 1985, 1988, Sastry 1968). A comparison of spawning season for closely related *Chlamys* species is shown in Table 6.3.

Gonad weight is representative of the number of ova, and ova number is exponentially related to shell height (Vahl 1984). The relationship within size classes may change from year to year, but in *M. asperrimus* ova number is greatest in the 90 to 95 mm size class. Older individuals observed with ripe gonads usually had lower GSI showing that reproductive effort is not a linear function of age, as suggested by Langton *et al.* (1987) for *Placopecten magellanicus*. It has been shown by MacDonald and Thompson (1985, 1986 and 1988) that older, larger scallops cannot accumulate enough food reserves to direct maximum effort into reproductive capacity. They require energy to maintain basic functions and this energy requirement increases with somatic weight.

To demonstrate the inter-annual variation in ova release, grouped size classes were used. The significant change in the number of ova released between 1988 and 1989 (ttest, P < 0.02) is important as it gives a good comparative measure of reproductive output from a population (or stock) in any year. This parameter may explain or qualify processes operating to cause changes in recruitment and population dynamics. Fecundity estimates were not determined during this study as total egg production is not considered as useful a measure of spawning success as a measure of reproductive output. There are examples of other scallop species where spawning has been minimal or has not occurred due to unfavourable environmental conditions (Barber and Blake 1983, Barber *et al.* 1988, Yamamoto 1950). Therefore, reproductive output is of more value to a fishery manager where a resource is being exploited. Fecundity estimates for *M. asperrimus* were determined by Rose and Dix (1984), induced females producing between 9.5 x 10^5 and 2 x 10^6 ova.

M. asperrimus was observed to be in spawning condition ("running ripe") for a number of weeks prior to the observed major spawning event. Individuals collected for sampling in September would begin spawning if left out of water for about five minutes. This was probably a response to the shock of handling and also the higher air temperature.

In both 1988 and 1989 spawning in *M. asperrimus* was over a short period of approximately two months. It has been reported for other scallop species that GSI may gradually decline over a period of five months, or that a secondary spawning event occurs later in the year. This strategy is thought to be adopted where environmental conditions are not suitable for spawning (Bricelj *et al* 1987). This strategy may be adopted by *M. asperrimus* in some years, but was not observed during this study.

The secondary decrease in GSI in *M. asperrimus* observed in 1989 was due to lysis and reabsorption of gametes and not ova release. Lysis of oocytes is detectable by the breakdown of the vitelline membrane and the presence of oocytes fragments in the follicles (see Plate 4.1F). The mechanisms operating that determine firstly, the extent of a spawning in terms of the percentage of mature ova released, and secondly, whether remaining mature ova are released later or reabsorbed, were not investigated during this study, but water temperature and food supply are again thought to be the primary determinants (Barber and Blake 1981, 1991; Sastry 1968).

Species	Spawning Season	Location	Reference
C. islandica	summer	Norway	Sundet and Lee (1984)
C. (Mimachlamys) varia	summer-autumn	France	Shafee and Lucus (1980)
C. opercularis	summer	U.K	Broom and Mason (1978)
C. tehuelcha	summer	Chile	Orensanz (1986)
C. septemradiata	summer	U.K	Ansell (1974)
M. asperrimus la	te spring-early summer	Australia	Zacharin (this study)

Lysis and reabsorption of mature oocytes has been reported in Argopecten irradians, Pecten maximus and Placopecten magellanicus (Dupaul et al. 1989). Spawning activity by individuals in the immediate area may also influence further ova release.

There is one predictable effect of a significant spawning event, and that is, an increased likelihood of recruitment to the stock. Unless there are unseasonal or unfavourable environmental conditions, or heavy predator activity on post-settlement juveniles, small scallops (30-40 mm) will be observed in *M. asperrimus* populations around March each year. However, no assumptions can be made on year class strength from the reproductive output data as other factors are interacting to determine spat settlement and subsequent recruitment.

The size of the 0+ year class is an important determinant of recruitment for future years. As *M. asperrimus* does not recruit to the fishery in the D'Entrecasteaux Channel until 80 mm shell height (this being the legal minimum size), there is a lag time of three years. In the six years between 1987 and 1992 in the D'Entrecasteaux Channel strong 0+ year classes were recorded in 1989, 1991 and 1992. The low adult spawning biomass in 1990 resulted in a large settlement event in 1991 providing a good example of the lack of a stock-recruit relationship (at the observed population level).

Recruitment to the *M. asperrimus* population(s) in the D'Entrecasteaux Channel has been demonstrated to be both spatially and temporally variable. Factors independent of adult spawning stock size are responsible for these affects. Larval advection processes, such as water currents, wind, the trapping characteristics of bays, inlets and other physical features, and substrates all determine resultant spat settlement (Brand *et al.* 1981, Butman 1987, Caddy 1989, Eckman 1987, Kaatvedt *et al.* 1987, Mann 1988).

In spat collection experiments with *P. fumatus* in the D'Entrecasteaux Channel, the author conducted larval sampling studies to track larvae movement, and observed that moderate winds and prevailing currents have a strong effect on the transport of scallop larvae (Zacharin, unpub. data). It was possible to predict where larvae may settle-out from the water column when current and wind direction and strength was monitored for three days prior to settlement. Whether the larvae survive once they make contact with the substrate depends on the suitability of that substrate and other disturbance mechanisms (Caddy 1975, Hancock 1979). Closed fishing seasons during peak settlement periods may, however, provide further protection for juvenile scallops and assist in boosting recruitment. This strategy warrants closer investigation.

The Japanese use larval monitoring data to predict settlement time and position with considerable success in many areas of Japan for scallop reseeding operations (Ventilla 1982, Zacharin, pers. obs.). In a semi-enclosed area like the D'Entrecasteaux Channel, modelling larval advection in combination with known annual reproductive output data may allow some level of prediction in the scallop fishery.

For some statistical areas in the Channel recruitment was present each year (area 6), whereas other areas were only observed to have recruitment in one of the four years sampled (area 9). It is possible that pre-recruit scallops in area 9 (which were observed in 1988 and 1989) may have been transported by the strong currents from the Huon River into area 11. This movement of adult beds was observed when *M. asperrimus* were disturbed by divers. When scallops are positioned on the bottom and feedings, the scallop hinge is positioned away from the water current so feeding potential is maximised, and when disturbed the scallop's swimming action tends to be with the current, increasing the distance of the escape response. Scallop beds in strong current locations were found to move frequently and had a crescent shape probably as a result of these current effects.

Another important parameter for the fishery manager is the natural mortality rate. The allowable level of exploitation of a scallop stock to ensure sustainable management is dependent inpart on the minimum size at first maturity and the natural mortality rate. The instantaneous mortality rate for *M. asperrimus* for fully recruited year classes ranged between 0.23 and 1.04 yr⁻¹. This indicates that between 36 and 98 percent of the scallop age classes available for legal harvest may die in each year, therefore, a level of fishing effort that removes the majority of scallops greater than 80 mm is an appropriate strategy, so long as reproductive output is not adversely affected. As the minimum size at first maturity is approximately 57 mm, a high level of egg production is maintained by the existing legal size limit of 80 mm. There is probably limited scope to reduce the legal

minimum size as *M. asperrimus* spawns for a second time between 65 and 77 mm shell height.

Variations in the mortality rate probably occur year to year and may be influenced by a number of factors (Gosling and Burnell 1988). Mortality observed during this study appeared due primarily to senescence and predation, although heavy *Polydora* infection on older individuals may have contributed to their death. Reseeded *M. asperrimus* became a tasty target for many species of groundfish, such as flathead, shark, skates and the major seastar predator *C. calamaria*. Other significant mortality events caused by *C. calamaria* has been observed for *P. fumatus* in Bass Strait (Zacharin, unpub. data). Some protection from seastar predation is given to *M. asperrimus* by epibionts, particularly sponges (Family Crellidae and Myxillidae) (Butler and Pitcher 1987, Chernoff 1987, Pitcher 1981).

The life history of the doughboy scallop, *M. asperrimus* is greatly influenced by local environmental and physical effects. These variables, in particular water temperature, determine the growth, reproduction, mortality and distribution of the species. Further understanding of the recruitment processors and population dynamics of *M. asperrimus* may be gathered by regular monitoring of the marine environment. The combined effects of variations in water temperature, local hydrographic influences and prevailing wind conditions appear to have a profound impact on the growth, reproduction and recruitment of scallops.

A majority of 'fishery managers' tend to depend heavily on results from studies of a species' biological parameters, with little or no information on the marine environment in which the animal must live and compete. More emphasis needs to be placed on a holistic approach to fishery research if the correct sustainable management decisions are to be made in the future.

REFERENCES

Allen, D.M. and T.J. Costello (1972) The Calico Scallop, Argopecten gibbus. Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish. 656.

Ansell, A.D. (1974) Seasonal changes in biochemical composition of the bivalve *Chlamys septemradiata* from the Clyde Sea area. *Mar. Biol.* 25, 85-99.

Anon. (1981) Channel scallop survey results. FINTAS 4(1), 22.

Anon. (1984) Channel season an Amateur picnic. FINTAS 7(3), 14.

Anon. (1985) Channel scallop season opens on July 6. FINTAS 8(2), 5.

Barber, B.J. and N.J. Blake (1981) Energy storage and utilisation in relation to gametogensis in Argopecten irradians concentricus (Say) J. Exp. Mar. Biol. Ecol. 52, 121-134.

Barber, B.J. and N.J. Blake (1983) Growth and reproduction of the bay scallop, Argopecten irradians (L) at its southern distributional limit. J. Exp. Mar. Biol. Ecol. 66, 247-256.

Barber, B.J, S. Getchell, S. Shumway and D. Schick (1988) Reduced fecundity in a deep water population of the giant scallop *Placopecten magellanicus* in the gulf of Maine, USA. *Mar. Ecol. Prog. Ser.* 42, 207-212.

Bayne, B.L. (1976) (Editor) Marine Mussels, their Ecology and Physiology. Cambridge University Press, London.

Benninger, P.G. and M.Le Pennec (1991) Functional Anatomy of Scallops. *In*:: S.E. Shumway (Editor) Scallops: Biology, Ecology and Aquaculture. *Developments in Aquaculture and Fisheries Science*, Vol. 21, 133-224.

Bloom, S.A (1975) The Motile Escape response of a Sessile Prey: A Sponge-Scallop Mutualism. J. Exp. Mar. Biol. Ecol. 17, 311-321.

Booth, J.D. (1983) Studies on twelve common bivalve larvae, with notes on bivalve spawning seasons in New Zealand. N.Z. Mar. Freshw. Res. 17, 231.

Brand, A.R. (1991) Scallop Ecology: Distributions and Behaviour. In *Scallops: Biology, Ecology and Aquaculture*. Ed S.E. Shumway. p517-569.

Brand, A.R, J.D. Paul and J.N. Hoogester (1981) Spat settlement of scallops *Chlamys opercularis* (L.) and *Pecten maximus* (L.) on artificial collectors. *J. Mar. Biol. Ass. U.K.* **60**, 379-390.

Bricelj, V.M, J. Epp and R.E. Malouf (1987) Intraspecific variation in reproductive and somatic growth cycles of bay scallops *Argopecten irradians*. *Mar. Ecol. Prog. Ser.* 36, 123-137.

Bricelj, V.M and S.E. Shumway (1991) Physiology: Energy acquisition and utilization. *In*: S.E. Shumway (Editor) Scallops: Biology, Ecology and Aquaculture. *Developments in Aquaculture and Fisheries Science*, Vol 21, 305-346.

Broom, M.J. and J. Mason (1978) Growth and Spawning in the Pectinid *Chlamys opercularis* in relation to Temperature and Phytoplankton Concentration. *Mar. Biol.* 47, 277-285.

Bull, M. (1974) The Biology of Scallops (*Pecten novaezelandiae*). Second Report - April 1974. University of Wellington, New Zealand.

Burnell, G.M. and P.G. Rodhouse (1980) Growth and Reproduction of the Variegated Scallop, *Chlamys varia* (L.). 3rd Scallop Workshop Port Erin, Isle of Man. *Mimeo*.

Butman, C.A. (1987) Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamic processes. *Oceanogr. Mar. Biol. Ann. Rev.* 25, 113-165.

Caddy, J.F. (1975) Spatial model for an exploited shellfish population, and its application to the Georges Bank scallop fishery. Fish. Res. Board Can. 32, 1305.

Caddy, J.F (1989) A perspective on the population dynamics and assessment of scallop fisheries, with special reference to the sea scallop, Placopecten magellanicus Gmelin. *In*. Marine Invertebrate Fisheries: Their Assessment and Management. Wiley - Interscience, New York.p 559-590.

Chernoff, H. (1987) Factors affecting mortality of the scallop *Chlamys asperrima* (Lamarck) and its epizooic sponges in South Australian waters. *J. Exp. Mar. Biol. Ecol.* **109**, 155-171.

Ciocco, N.F (1991) Differences in individual growth rate among scallop (*Chlamys techuelcha* (d'Orb)) populations from San Jose Gulf (Argentina). Fish. Res. 12, 31-42.

Cloern, J.E. and F.H. Nichols (1978) A von Bertalanffy growth model with a seasonally varying coefficient. J. Fish. Res. Bd. Can. 35, 1479-1481.

Cochard, J.C. and N. Devauchelle (1991) Spawning fecundity and larval growth in relation to controlled conditioning in five populations of *Pecten maximus* (L.) *J. exp. mar. exp. biol.* **144**.

Conan, G. and M. Syed Shafee (1978) Growth and Biannual Recruitment of the Black Scallop *Chlamys varia* (L.) in Lanveoc area, Bay of Brest. *J. Exp. Mar. Biol. Ecol.* 35, 59-71.

Comely, C.A. (1974) Seasonal variations in the flesh weights and biochemical content of the scallop *Pecten maximus* L. in the Clyde Sea area. *J. Cons. int. Explor. Mer.* 35, 281-295.

Crabtree, D.M., C.D. Clausen and A.A. Roth (1980) Consistency in growth line counts in bivalve specimens. *Palaegeogr. Paleoclimatol. Palaeoecol.* **29**, 323-340.

Cropp, D.A and M.E. Hortle (1991) Midwater cage culture of the commercial scallop *Pecten fumatus* Reeve 1852 in Tasmania. *Aquaculture* 102, 55-64.

Devauchelle, N and C. Mingant (1991) Review of the Reproductive physiology of the scallop, *Pecten maximus*, applicable to intensive aquaculture. *Aquat. Living Resour.* 4, 41-51.

Dickie, L.M. (1955) Fluctuations in abundance of the giant scallop, *Placopecten magellanicus* (Gmelin), in the Digby area of the Bay of Fundy. *J. Fish. Res. Bd. Canada*. **20**, 451-482.

Dix, T.G. (1976) Larval development of the Queen Scallop, Equichlamys bifrons. Aust. J. Mar. Freshw. Res. 27, 399-403.

- Dix, T.G. and M.J. Sjardin (1975) Larvae of the Commercial Scallop (Pecten meridionalis) from Tasmania, Australia. Aust. J. Mar. Freshw. Res. 26, 109-112.
- Dredge, M.L.C. (1981) Reproductive Biology of the Saucer Scallop Amusium japonicum balloti (Bernardi) in Central Queensland waters. Aust. J. Mar. Freshwater Res. 32, 775-787.
- Dredge, M.L.C. (1985a) Growth and Mortality in an isolated bed of saucer scallops, Amusium japonicum balloti (Bernardi). Queensland J. Agr. Animal Sci. 42, 11-21.
- Dredge, M.L.C. (1985b) Estimates of Natural Mortality and Yield-per Recruit for Amusium japonicum balloti Bernardi (Pectinidae) based on tag recoveries. J. Shellfish Res. 5(2), 103-109.
- Dorange, G and M. LePennac (1989) Ultrastructural study of oogensis and oocytic degeneration in *Pecten maximus* from the Bay of St. Brieuc. *Mar. Biol.* **103**(3), 339-348.
- Dupaul, W.D., J.E. Kirkley and A.C. Schmitzer (1989) Evidence of a Semiannual Reproductive Cycle for the Sea Scallop, *Placopecten magellanicus* (Gmelin 1791) in the Mid-Atlantic region. *J. Shellfish Res.* 8(1), 173-178.
- Eckman, J.E. (1987) The role of hydrodynamics in recruitment, growth and survival of Argopecten irradians (L.) and Anomia simplex (D'Orbigny) within eelgrass meadows. J. Exp. Mar. Biol. Ecol. 106, 165-191.
- Fairbridge, W.S (1953) A population study of the Tasmanian 'commercial' scallop *Notovola meridionalis* (Tate) (Lamellibranchiata, Pectinidae) *Aust. J. Mar. Freshw. Res.* 4, 1-40.
- Forester, A.J. (1979) The Association between the Sponge *Halichondria panicea* (Pallas) and Scallop *Chlamys varia* (L.): A Commensal-Protective Mutualism. *J. Exp. Mar. Biol. Ecol.* **36**, 1-10.
- Franklin, A. and G.D. Pickett (1980) Shell growth increments in scallops (Pecten maximus) from the English Channel. *Int. Council Explor. Sea.* cm 1980/K13. *Ministry of Agriculture, Fisheries and Food, U.K* p 1-7.
- Getchell, R.G (1991) Diseases and parasites of scallops. In:: S.E. Shumway (Editor) Scallops: Biology, Ecology and Aquaculture. Developments in Aquaculture and Fisheries Science, Vol. 21, 471-494.
- Gosling, E.M. and G.M. Burnell (1988) Evidence for selective mortality in *Chlamys varia* (L.) transplant experiments. *J. mar. biol. Ass. U.K* 68, 251-258.
- Grant, J.F. (1971a) Scallop survey north-west coast, Tasmania 23 Feb 3 March 1971. Tasmanian Fish. Res. 5(2), 14.
- Grant, J.F. (1971b) Scallop survey D'Entrecasteaux Channel, Tasmania 11-14 May 1971. Tasmanian Fish. Res. 5(2), 8.
- Grant, J.F. and K.R. Alexander (1973) The scallop resources of Bass Strait below latitude 39° 12' south, 1972/73. Tasmanian Fish. Res. 7(2), 1.
- Gruffydd, L.L. (1974) An estimate of natural mortality in an unfished population of the scallop *Pecten maximus* (L.) *J. Cons. Int. Explor. Mer.* 35(2), 209-210.