

**Effects of environmental conditions on culturing scallop spat**  
*(Pecten maximus)*

By  
Gyda Christophersen

Department of Biology  
University of Bergen  
Bergen, Norway  
2005

ISBN 82-308-0006-5

Bergen, Norway 2005

## **PREFACE AND ACKNOWLEDGEMENTS**

Things take time...

This study was a part of the umbrella project “Spat production of great scallop”, which was initiated by Dr. Thorolf Magnesen, Centre for Studies of Environment and Resources (SMR), University of Bergen (UoB) in 1995. The Research Council of Norway (NFR) funded a Dr. scient. grant during the period from 1996 to 1998 (NFR project no. 110999/122), while later SMR has been of invaluable support. A 4-months stay in 1998 at the Marine Institute, Memorial University of Newfoundland (MUN), Canada, under the supervision of Cyr Couturier and Pat Dabinett, was funded by a Bergen-MUN exchange scholarship and a grant from NFR (no. 123398/120). My supervisor has been professor Dag L. Aksnes, Department of Fisheries and Marine Biology (IFM) (now Department of Biology (BIO)), UoB, and co-supervisors have been Dr. scient. Thorolf Magnesen, SMR, UoB and Dr. scient. Øivind Strand, Institute of Marine Research (IMR). I am grateful you have lasted all these years.

The experiments were performed at the facilities of the commercial scallop hatchery Scalpro AS in Øygarden and the land-based nursery Sealife AS at Tysnes in Hordaland. I highly appreciate the access I had to the “real world” when doing farm-based research. The experiments depended on scallops produced at Scalpro AS and the daily management and help of the Scalpro AS and Sealife AS staffs. I address special thanks to Anne Grete Dale, Eivind Rong, Johnny Rong, Else Rong, Annlaug Espevik and Alf Roald Sætre. The lab-work was carried out at IFM, UoB, Institute of Nutrition (now The National Institute of Nutrition and Seafood Research (NIFES)), and IMR, Austevoll. Sincere thanks are hereby expressed to everybody at these organisations who supported small or great help. I am also grateful to my co-authors for the collaboration at the different papers, Øivind Lie, Thorolf Magnesen, Øivind Strand, Lise Torkildsen and Terje van der Meer.

Aquaculture combines biology, ecology, production techniques, business, people and places in an excellent way, and was an obvious choice as academic direction considering my background from the food industry. It is rewarding that your study-animal finally may end up as a favourite on peoples plates. A conviction there is space and need for farming a more diverse range of aquaculture species along the Norwegian coast has been another driving force. My interest in scallops and bivalve spat production was initiated during a practical at the Biomarin AS bivalve hatchery (now Scalpro AS) in 1990. I am grateful to Lena Söderholm, Siri Hanson and Ruth Paulson who enthusiastically transferred their knowledge about the biology and production of early scallop life-stages to me.

Without help, enthusiasm, patience, encouragement and support from several others the thesis could not have been completed. This includes family, friends, past and present colleagues at SMR, SFU, IFM, BIO, NIFES and IMR, the Bergen scallop research group and the extended international Pectinid family. I thank you from the bottom of my heart!

Bergen, April 2005

Gyda Christophersen



**TABLE OF CONTENTS****page**

Preface and acknowledgements .....	3
Summary .....	7
List of papers .....	8
Introduction .....	9
The scallop <i>Pecten maximus</i> .....	9
Environmental impact on scallop physiology .....	11
Why culture scallops? .....	14
Constraints in scallop spat production .....	16
Objectives .....	20
Results and discussion .....	20
Influence of rearing environment on spat performance .....	20
Effects of temperature and salinity on growth and survival .....	20
Effects of food availability on growth and survival .....	24
Tolerance limits and sub-optimal conditions .....	27
Culture strategies .....	31
Site selection and growth systems .....	31
Acclimation and tolerance to environmental changes .....	35
Culling, handling and transfer .....	38
Perspectives .....	41
References .....	42
Appendix .....	57
Spelling and word corrections	
Papers I-V	



## **SUMMARY**

The great scallop, *Pecten maximus*, is a valuable bivalve species attractive for human consumption. Scallop aquaculture is increasing, but availability of spat is a bottleneck to the development of a viable culture industry in many countries. The collection of *P. maximus* spat from the wild has been insufficient, and intensive hatchery production is considered an optional strategy for a predictable spat supply to growers in Norway. Large variations in growth and survival during the post-larval stages are experienced, and temperature, salinity and food availability have been identified as critical environmental factors during the nursery growth stage. A nursery bridges the gap between intensive culture in the hatchery and grow-out in the sea, and covers the rearing from metamorphosis (ca. 0.25 mm) until the commercial spat size of 15-20 mm. Transfer between production stages and grow-out sites is required in scallop culture. The present study filled an information gap related to effects of environmental factors on small scallops (ca. 2 mm) in the transition phase between hatchery and nursery. Different transfer strategies were investigated to test the capability of scallop spat to tolerate transfer and adapt to new environmental conditions.

Experimental studies with hatchery reared *P. maximus* showed that viability through the various spat stages could be improved by employing adequate culture and transfer strategies. Transfer of spat of different settlement age to nursery was approved to further increase the spat yield. Site selection and timing of transfer are of major importance, and the observed sub-optimal and lethal environments should be avoided. Higher rearing temperature (18 vs. 15 °C) resulted in increased growth and survival, while salinity of 20 and 25 affected growth, survival and byssal attachment negatively. Exposure to low temperatures was a main factor affecting the performance of small spat. Acclimation of 1-2 mm spat to a lower temperature than in the hatchery improved post-transfer survival to seawater of <7 °C. So did transfer of larger (4 mm) spat. Alternatively, spat could be transferred to a land-based nursery using solar heated and fertilised "poll" water as food source to give an earlier start of the production season in the spring. The growth was similar to in sea-based nursery. Dry transportation of small spat was shown feasible up to 12-24 hours. The change to "poll" food conditions resulted in a significant decrease of lipids, but except for sterol content, the nutritional status at transfer was not associated with growth and survival in the land-based nursery. Increased water recirculation rates in the hatchery rearing tanks hardly affected the spat performance and the chemical composition, thus supporting more efficient utilisation of algae.

## **LIST OF PAPERS**

The thesis is based on the following individual papers and manuscript, which are identified by their Roman numerals in the text.

### **Paper I**

Christophersen, Gyda 2000. Effects of air emersion on survival and growth of hatchery reared great scallop spat. *Aquaculture International* 8(2/3):159-168.

### **Paper II**

Christophersen, Gyda & Magnesen, Thorolf 2001. Effects of deployment time and acclimation on survival and growth of hatchery-reared scallop (*Pecten maximus*) spat transferred to the sea. *Journal of Shellfish Research* 20(3):1043-1050.

### **Paper III**

Christophersen, Gyda & Strand, Øyvind 2003. Effect of reduced salinity on the great scallop, *Pecten maximus*, spat at two rearing temperatures. *Aquaculture* 215(1-4):79-92.

### **Paper IV**

Christophersen, Gyda & Lie, Øyvind 2003. Nursery growth, survival and chemical composition of great scallop, *Pecten maximus* (L.), spat from different larval settlement groups. *Aquaculture Research* 34:641-651.

### **Paper V**

Christophersen, Gyda, Torkildsen, Lise & van der Meeren, Terje. Effect of increased water recirculation rate on algal supply and post-larval performance of scallop (*Pecten maximus*) reared in a partial open and continuous feeding system. Manuscript accepted for publication in *Aquacultural Engineering*.



## INTRODUCTION

### **The scallop *Pecten maximus***

Scallops are invertebrate animals in the phylum Mollusca, class Bivalvia and family Pectinidae, and widely distributed. Worldwide about 40 scallop species belonging to the supragenera *Chlamys*, *Mimachlamys*, *Aequipecten*, *Palliolium*, *Decatopecten* and *Pecten* are commercially or potentially commercially exploited for human consumption (Waller 1991, Minchin 2003). A large adductor muscle is the most attractive part of the scallop and therefore the European great scallop, *Pecten maximus*, is one of the most sought-after species. The great scallop is distributed along the eastern coast of the North Atlantic Ocean, from northern Norway (Vesterålen) south to the Iberian Peninsula (Tebble 1966, Wiborg & Bøhle 1968, Høisæter 1986), but is also registered as far south as Cape Verde off West Africa and in the Mediterranean (Ansell et al. 1991, Peña 2001). *P. maximus* lives in subtidal areas from low water to more than 100 metres depth, and is found on bottoms of firm sand, fine or sandy gravel, sometimes with an admixture of mud (Tebble 1966, Brand 1991 and references therein). The food source is suspended phytoplankton, detritus, bacteria and other organic material which the scallop filters from the water (Bricelj & Shumway 1991, Beninger & Decottignies 2005).

*P. maximus* grow to a shell-height of 150 mm or more in most areas (Ansell et al. 1991), and may have a life length beyond 20 years (Tang 1941, Mason 1957, Orensanz et al. 1991). Reproductive age is reached after 2-3 years (Tang 1941) and commercial size of >100 mm shell-height after 4-6 years (Mason 1957) in the northern part of the geographical range, while in the southern part maturity may be reached after 1 year and minimum legal size (100 mm shell length = 91 mm shell-height) within 2 years (Acosta & Román 1994). The great scallop is a functional hermaphrodite where the gonad is divided in two compartments containing sperm and eggs respectively (Dakin 1909, Tang 1941, Mason 1958). The sperm and eggs are usually shed with a time-lag and fertilisation takes place in the water column. The annual reproduction cycle of *P. maximus* is influenced both by environmental and genetic factors, and the spawning period is mainly between April and October, but depends on location (Tang 1941, Mason 1958, Wilson 1987a, Paulet et al. 1988, Strand & Nylund 1991, Pazos et al. 1997, Duinker 2002).

Fertilised eggs develop into trochophore larvae and further to straight-hinged (D-shaped) veliger and pediveliger larvae (Le Pennec et al. 2003, Fig. 1). The velum is used for both food capture and movements, as suggested for the foot during the pediveliger stage (Cragg & Crisp 1991, Reid et al. 1992). The larval phase is planktonic, and as for marine bottom invertebrates in general, the length of the pelagic life and ocean currents determines the dispersal (Thorson 1961, Thouzeau 1991). At a size of 200-250  $\mu\text{m}$  competent *P. maximus* larvae are ready-to-settle and show the features required to undergo metamorphosis (Gerard et al. 1989, Fig. 1). Biological, chemical and physical factors affect settlement and metamorphosis (Le Pennec et al. 2003), and the scallops are able to settle and attach itself to a variety of substrates (Minchin 1992, Chauvaud et al. 1996). Byssus threads are secreted from a gland in the foot and the pediveligers can choose between crawling or attach to a suitable substrate (Cragg & Crisp 1991). During metamorphosis the D-shape is gradually lost and the velum degenerates along with development of the gills (Gruffyd & Beaumont 1972, Gerard et al. 1989). Consequently the feeding strategy changes during the early life stages (Reid et al. 1992, Kean-Howie et al. 1995). From 1 to 4 mm shell-height the post-larvae or spat develop into a miniature of an adult scallop with a functional gill apparatus (Beninger et al. 1994). The scallop stops producing byssus threads at approximately 15 mm, detaches, and continues a free life on the seabed (Minchin 1992).

During the early life stages the number of surviving scallops related to the number of eggs spawned is greatly decimated. Studies have estimated survival from egg to recruitment (age 2-4 years) of scallops in nature to  $1-5 \times 10^{-5}$  % survival of *Placopecten magellanicus* (McGarvey et al. 1992) and *Chlamys islandica* (Vahl 1981). Salaün (1994, cited in Le Pennec et al. 2003) reported 31-73 % survival of *P. maximus* during the veliger larval stage *in situ*, and Orensanz et al. (1991 and references therein) 4-10 % survival during the first months after settlement of *Patinopecten yessoensis*. Environmental conditions such as temperature, food availability and hydrodynamic may affect survival, and a variety of predators are likely to be encountered during the planktonic stage. Later in life the scallops are mainly vulnerable to predation by crab and starfish species (Barbeau et al. 1996, Fleury et al. 1996, Strand & Vølstad 1997, Cliche & Giguere 1998).

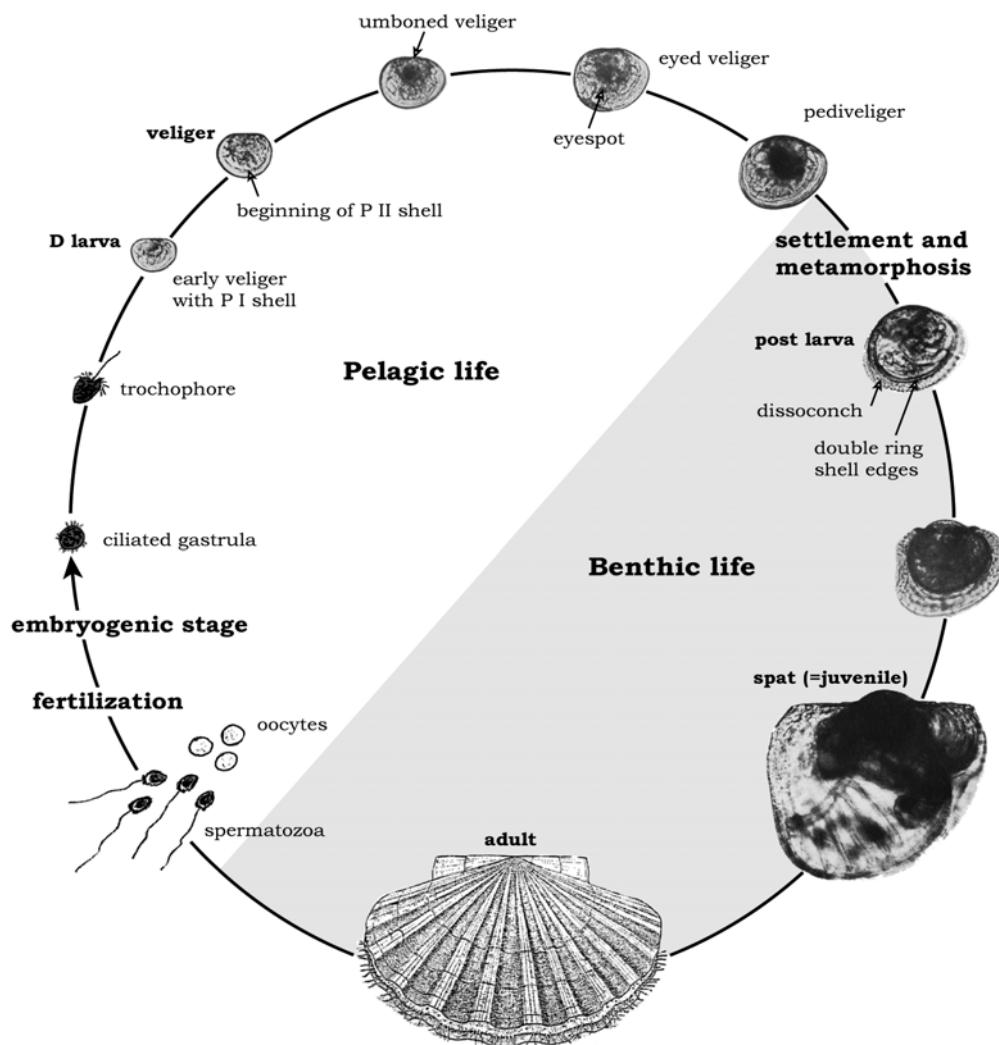


Figure 1. The life cycle of *Pecten maximus* (PI and PII = prodissoconch I and II). From Le Pennec et al. 2003.

### Environmental impact on scallop physiology

Scallops occur in most seas of the world and inhabit the range of climatic zones from polar to tropical (Brand 1991, Waller 1991, Peña 2001). How the environment affects the different scallop species depends on the climatic, oceanographic and ecological characterisation of the natural habitat (Lodeiros et al. 2001, Minchin 2003). *P. maximus* is adapted to a life in temperate to cold regions (Koeppen's climate classification), and the natural habitat is subtidal, where temperature, salinity and food levels are relatively constant (Brand 1991). Variations in salinity and temperature affect growth, survival and activity of marine species in

general (Kinne 1964), and it is shown that the functional activity and cellular mechanisms of marine molluscs are affected by altered salinity (Berger & Kharazova 1997). Pectinids are less adapted to large environmental variations compared to other bivalves like clams, oysters and mussels, which live in coastal and estuarine habitats exposed to tidal variations. The biological and physical processes in coastal waters are closely coupled and benthic filter feeders, including wild and cultured bivalves, play important roles in these ecosystems (Bayne 1998, Riisgård & Larsen 2000).

Recruitment depends on successful development and survival during the different life stages along with matching environmental conditions. While thermal stress is shown to increase the ratio of anomalies in *P. maximus* larvae and thus lower the viability (Salaun et al. 1991), favourable environmental conditions should result in normal development. Temperature and food availability are among the factors that affect the length of the larval stage, onset of metamorphosis, settlement and geographical distribution of scallops (Brand 1991, Thouzeau 1991, Le Pennec et al. 2003). The shell characters develop according to habitat, and the different scallop species have a morphology which reflects the ecological niche they occupy. The ecomorphological features have evolved due to characteristics of the water environment, substrate, type of competitors and predators (Minchin 2003). The shell valve design and muscle size and position determine the swimming ability, which for many scallops are reduced during ontogeny (Baird & Gibson 1956, Gould 1971). Shell thickness and strength have evolved as a response to environmental conditions such as temperature and salinity or to avoid predators (Vermeij 1993, Reimer & Harms-Ringdahl 2001). Adult *P. maximus* are sedentary and retracted but capable of swimming by clapping the valves and escape if predators threaten them or the environment deteriorates. Unfavourable environment can cause slower escape response and thus indirectly affect survival (Dickie 1958, Lafrance et al. 2003).

The bivalves are poikilothermal organisms (ectotherms), meaning their body temperature fluctuates with that of the surrounding environment (Holmes 1979). Metabolism in general varies with temperature and physiological processes are accelerated as a consequence of increased temperature (Schmidt-Nielsen 1990). The interrelationship between temperature and metabolism, development and behaviour of ectotherms is, however, complex and affects physiological processes at many levels (Wieser 1973). Marine bivalves respond to the quality of the surrounding seawater, and important processes related to feeding, digestion, respiration, circulation, excretion and osmoregulation are influenced by the environment (Bayne 1976,

Gosling 2003). Most energy requiring processes depend on available oxygen, and the body size affects the oxygen consumption of bivalves in general (Gosling 2003) and scallops in particular (Bricelj & Shumway 1991, Thompson & MacDonald 1991, Strickland & Dabinett 1993, Lu et al. 1999a, Frenette et al. 2002). Respiratory stress or aerial exposure is shown to affect the heart activity (Brand & Roberts 1973) and the acid-base status (Duncan et al. 1994) of *P. maximus* negatively, which reflects the sublittoral adaptation of scallops.

Scallops are shown to be susceptible to small changes in temperature (Dickie & Medcof 1963, Strand et al. 1993, Chauvaud et al. 1998), but the tolerance limits vary with species and geographical range (Brand 1991). The capacity, rate and effect of adjustments to a different environment are affected by the animals' environmental history, genetic background, physiological condition, metabolism, age and size (Kinne 1963, Schmidt-Nielsen 1990). The rate of acclimatisation tends to follow the rate of metabolism, resulting in longer time needed for adjustment to a decrease in temperature than an increase. Both the ontogenetic and the physiological stage have impact on viability, and many of the scallop functions respond to temperature, salinity and food availability, which in turn affect growth and survival. For instance byssus formation in pectinids appears to be extremely sensitive to environmental changes (Brand 1991), specifically to reduction of salinity (Castagna & Chanley 1973, Paul 1980a, O'Connor & Heasman 1998, Rupp & Parsons 2004).

Feeding and digestion, in terms of filtration and digestive enzyme activity, are temperature dependent processes (Bayne 1976). The food availability in nature is related to fluxes of organic material and algae blooms which vary with season. In addition, water velocity and currents are important factors determining the growth environment and in turn affecting feeding behaviour (Wildish & Kristmanson 1997). Filter feeders capture suspended food particles from the water by the gills and transport them to the mouth with the help of cilia, mucus and surface currents on the gills (Bayne et al. 1976, Barker Jørgensen 1990, Beninger & Le Pennec 1991). Food quality, concentration, particle size and presence of toxic algae regulate the clearance- and ingestion rates of scallops (Vahl 1972, 1973, Winter 1978, Riisgård 1988, Bricelj & Shumway 1991, Cranford 1995, Bacon et al. 1998, MacDonald et al. 1998). The explanations of how the bivalve feeding mechanism functions and adapts to the environment are to some extent controversial. Studies of pre- and post-ingestive particle processing currently reveal new knowledge (Jørgensen 1996, Levinton et al. 1996, Bayne 1998, Hawkins et al. 1998, Brilliant & MacDonald 2000, Riisgård & Larsen 2000, Dufour &

Beninger 2001, Hawkins et al. 2001, Brillant & MacDonald 2002, 2003, Ward et al. 2003, Milke & Ward 2003, Beninger et al. 2004), and the research on particle selection in suspension- and deposit-feeding bivalves has recently been reviewed by Ward & Shumway (2004).

### **Why culture scallops?**

Culture of fish and marine molluscs has a considerable history and dates back several hundreds of years B.C. (Mann 1984, Gosling 2003). Production for human consumption is a main reason to initiate the culture of a species, and the advantage of culture should equal or exceed the benefits of ordinary fishery of the target species. The selection of a suitable species for aquaculture may be based on different criteria, and the first documentation of such is from China in about 500 B.C. where Fan Lee (cited in Mann 1984) determined a prime species to be tasty, hardy, not cannibalistic, inexpensive to culture, and of rapid growth. According to Mann (1984) bivalve species of the genera *Ostrea*, *Crassostrea* and *Mytilus* fit to Lee's criteria with the addition of adequate availability of juveniles, i.e. spat. In high-technology economies other criteria may predominate, and the trend is rather towards establishing culture techniques for species of high market price such as the molluscs, abalone and scallops.

Scallop aquaculture has shown an increasing trend during the last decades (Bourne 2000, FAO 2002). The landings (fishery and aquaculture) totalled 200 thousand tonnes in 1970 and have since increased ten-fold with 90 % now coming from culture. Environmental changes, habitat deterioration, pollution, irregular recruitment and heavy fishing pressure have led to collapse of fisheries and scallop populations in many countries (Gould & Fowler 1991, Orensanz et al. 1991, Bull 1994, Lu & Blake 1997b, Strand & Vølstad 1997, Stotz & Mendo 2001). To meet a general market demand aquaculture has to a large extent replaced scallop fisheries, i.e. in Japan, China and Chile (Ventilla 1982, Guo et al. 1999, Stotz 2000). In other countries reestablishment of populations for fishery, culture or restoration of endangered species are aimed at through stock enhancement and conservation programmes (Cliche & Giguère 1998, Dao et al. 1999, Arnold 2001, Stotz & Mendo 2001, Tettelbach et al. 2002, Drummond 2004). Such strategies require hatchery produced or wild collected scallops for transplantation to the target area. According to Bourne (2000) no large unexploited scallop stocks are known at present, and most of the fisheries are currently harvesting stocks at

maximum yield. Hence a further increase in scallop production will rely on culture operations.

Aquaculture is the most rapid growing food producing sector in the world (FAO 2002), and marine molluscs is an important source of highly nutritious animal protein. It is debated whether fish aquaculture *per se* will add to the net global fish supply in the future (Naylor et al. 2000, Tidwell & Allan 2002), as opposed to the farming of filter feeding bivalves which do not require input of wild fish for feed. Bivalves represent about 25 % of the total aquaculture production in the world, equivalent to ca. 12 million tonnes (FAO 2001).

Globally several scallop species are exploited through fisheries and culture. The total scallop production, wild and farmed, stands at 2 million tonnes (FAO 2001) of which China produces 50 % (Guo et al. 1999). Japan is the second largest producer (25 %) and in Asia culture is the dominating production form. In Europe most of the scallop production, 4 % of the world total, comes from fisheries (FAO 2001) as in the US (Shumway & Castagna 1994). UK and France are the largest producers in Europe with 28 and 23 thousand tonnes respectively (FAO 2001). The Norwegian scallop production of approximately 500 tonnes is *P. maximus*, harvested by divers. The domestic and export market is not yet satisfied and stimulate a larger output of scallops. Increased number of harvestable scallops in Norway is believed to come from sea-ranching of *P. maximus*, relying on release of hatchery produced seed scallops, i.e. spat or juveniles (Bergh & Strand 2001, Agnalt et al. 2003).

Availability of spat is a key factor in the development of an aquaculture industry. Spat is defined as the spawn or young of bivalve molluscs (Holmes 1979), and can be obtained by collection from wild or from production in hatcheries. Collection relying on natural spat fall is a viable option in many countries worldwide, but usually limited to specific species and areas (Shumway 1991 and references therein). Some countries rely solely on hatchery produced spat, others on spat collection from wild, and others again use a combination of the two methods (Dadswell 2001, Spencer 2002). In Europe the collection of sufficient *P. maximus* spat from nature has been unreliable and a year-to-year challenge (Dao et al. 1999). Spat settlement around the Isle of Man is reported to be generally very low, yet supporting a sustainable fishery (Beukers-Stewart et al. 2003). Attempts to obtain scallop spat from the wild in Norway and UK have resulted in low numbers of *P. maximus* spat per collector (Paul et al. 1981, Strand & Vølstad 1997). Consequently, intensive hatchery production is considered an optional strategy for a predictable spat supply in Norway (Bergh & Strand 2001).

To be sustainable a commercial scallop culture must satisfy economic, social and environmental requirements (Hishamunda & Ridler 2002), all factors implemented in the development of a scallop culture in Norway. Culturing scallops may be profitable as scallops obtain high market price and is a sought-after product for human consumption. Scallops are popular as fresh seafood, but also well suited to be freshly frozen which expand the market possibilities. The European species *P. maximus* is one of the most valuable species due to its large size (Dao et al. 1999) and reputation among chefs as a tasty and high quality ingredient. In general, sea based bivalve culture is regarded environmental friendly, as scallops do not need therapeutics or additional food to what is naturally occurring in the seawater. Norway has no tradition of harvesting *P. maximus* by conventional fishing gear mainly because of unsuitable bottom conditions (Strand & Vølstad 1997). The water environment and bottom substrate are however considered appropriate to scallop culture. The Sea Ranching Act (LOV-2000-12-21-118) adapted for the recapture right by concession holders of released scallops in a defined area, furthermore facilitating the development of scallop culture in western Norway.

### **Constraints in scallop spat production**

Successful scallop aquaculture depends on reliable growth and survival during the different production stages. Large variations in growth and survival during the different productions steps from larvae to spat is a worldwide experience (Ó Foighil et al. 1990, Bourne & Hodgson 1991, Heasman et al. 1994b, Couturier et al. 1995, Robert & Gérard 1999, Heasman et al. 2002, Le Pennec et al. 2003, Rupp et al. 2004b, Torkildsen & Magnesen 2004), and a bottleneck in the development of viable scallop culture industries. The scallops go through several critical stages in culture from broodstock conditioning to the size of 15-20 mm, which is the commercial spat size in Norway. The physical and nutritional environment is manipulated during conditioning and broodstock diet affects fecundity and viability of eggs and embryos (Utting & Millican 1998, Andersen & Ringvold 2000). Food quality and quantity are essential for larvae to successfully going through metamorphosis and survive the post-larval stages (Whyte et al. 1987, 1992, Delaunay et al. 1992, Farías et al. 1998, Lu et al. 1999b, Milke et al. 2004, Rupp et al. 2004b), and substrate type, water circulation, food availability, temperature and salinity are important factors determining larval settlement (Shumway 1991 and references therein). Temperature, salinity and food availability are



critical environmental factors during post-larval and spat growth. In hatcheries it is possible to enhance the output of scallop larvae and post-larvae, i.e. obtain higher spat yields than in nature (Loosanoff & Davis 1963, Le Pennec et al. 2003, Torkildsen & Magnesen 2004). Nevertheless, *P. maximus* spat yields are shown to be variable in culture (Robert & Gérard 1999, Bergh & Strand 2001).

A primary requisite in any culture operation is a reliable, plentiful and inexpensive supply of seed, i.e. spat or juveniles (Bourne 2000). Successful scallop culture industries exist, as in China and Japan, but spat are in short supply in several other countries. The information regarding environmental requirements of post-larvae and small spat is scarce, and Bourne (2000) emphasises the need for considerable research to be carried out in all phases of culture to develop large scallop industries. Descriptions of scallop spat culture procedures in large (commercial) scale systems exist primarily as hatchery manuals and confidential protocols, but also in more general literature as for *Placopecten magellanicus* (Couturier et al. 1995), *Pecten fumatus* (Heasman et al. 1994b, 2002), *Patinopecten yessoensis* (Ventilla 1982, Bourne et al. 1989, Bourne and Hodgson 1991), *Argopecten purpuratus*, *Argopecten ventricosus*, *Euvola ziczac*, *Nodipecten nodosus* and *N. subnodosus* (Uriarte et al. 2001, Merino et al. 2001), *Argopecten irradians irradians* (Widman et al. 2001), *Argopecten irradians concentricus* (Sastry 1965, Lu & Blake 1997b) and *P. maximus* (Millican 1997, Hardy 1991, Robert and Gérard 1999). Few findings of small spat in nature are reported (Baird 1956, Larsen & Lee 1978, Minchin 1992). Thus, published research on the biology of early life stages of scallops is for the most part obtained from studies in laboratory or hatchery situations, and related to reproduction, larval phase and grow-out of larger juveniles. Due to the development of scallop aquaculture industries over the last decades, the focus on the hatchery-nursery phase increases.

The post-larval growth stages are crucial in the spat production process, and adequate rearing conditions are fundamental. A nursery bridges the gap between intensive production in hatchery and grow-out in the sea (Claus 1981, Bourne et al. 1989), and covers the rearing of recently metamorphosed larvae (ca. 0.25 mm) until the juvenile size of 20-30 mm shell-height (Bourne 2000). Nursery growth may be divided into a primary and a secondary stage, with the primary nursery growth to approximately 2 mm usually in close connection with the hatchery. Due to rapid growth, the increase in food demand during the post-larval stage of bivalves is substantial, and facilitates the use of cost-effective semi-intensive secondary nurseries, which

can be sea- or land-based depending on natural or cultured algae as food source (Claus 1981, Manzi et al. 1986, Strand 1996, Hadley et al. 1999). The spat are kept in different kinds of enclosures (i.e. nets or trays) suspended from long-lines in the sea or in raceways or tanks with horizontal, downwelling or upwelling water flow. In 1981 the attention was paid to the use of semi-intensive growth systems or nurseries in bivalve production (Claus 1981). State of the art revealed few works dedicated to scallops at that time, but the use of nurseries as extensions to the hatchery has developed along with increased interest in cultivation (Claus 1981, Rhodes et al. 1981, Rosenthal et al. 1995, Gosling 2003). Therefore, most of the documented research on scallop nursery culture has been carried out during the last 10-15 years.

Major physiological and anatomical development takes place during the post-larval growth stages (Fig. 1), and thus small scallops are fragile and vulnerable to changes in the rearing conditions. Ontogenetic changes in response to the environment must be considered during stressful culture operations, as mortality associated with transfer and handling procedures may limit the spat yield (Maguire et al. 1999a,b,c, Maeda-Martínez et al. 2000). Limited information exists about nursery-sized scallops in general, and the knowledge concerning the smallest spat of  $\leq 2$  mm size is restricted to a few species of commercial interest. Regarding *P. maximus* of this size group, just a few parameters have been studied, i.e. the effect of food quantity, seawater flow and temperature on post-metamorphic development (Robert & Nicolas 2000, Nicolas & Robert 2001), and different diet compositions (Laing & Psimopoulos 1998). Diet and food availability are also studied for the species *P. magellanicus* (Ryan et al. 1998, Milke et al. 2004), *N. nodosus* (Rupp et al. 2004b), *P. yessoensis* (Ó Foighil et al. 1990) and *Argopecten* sp. (Martinez et al. 1995, Lu & Blake 1996, 1997a), and Shumway et al. (1997) compared particle clearance and selection in three of the species. Effects of rearing temperature and salinity are reported for small spat of *P. fumatus* (Heasman et al. 1994a, 1996) and *Amusium balloti* (Wang et al. 2002), while studies of deployment to sea-based nursery is reported for *A. purpuratus* (Martinez et al. 1992), *P. magellanicus* (Levy et al. 1998, Grecian et al. 2000, 2003) and *N. nodosus* (Rupp et al. 2004a, Rupp et al. 2005). The present study intends to fill the information gap related to effects of environmental factors on  $\leq 2$  mm *P. maximus* in the transition phase between hatchery and nursery. Such knowledge is crucial to improve culture methods and secure seed supply to scallop growers.

In cold and temperate water areas, like the North Atlantic, the length of the growth season in the sea is limited by environmental conditions such as low temperature in the spring (Grecian et al. 2000, 2003). The restricted period suitable for deployment to sea-based nursery is regarded a constraint in scallop spat production, and an extension of the production season compared to in nature is considered needed for scaling up scallop spat production in Norway (Bergh & Strand 2001). Hatchery production of *P. maximus* post-larvae is practiced on a year-round basis in Norway (Torkildsen & Magnesen 2004), while further growth in nurseries based on natural algal production is season dependent. However, it has been demonstrated that it is possible to produce juvenile scallops independently of season in land-based indoor nurseries (reported in Bergh & Strand 2001). The longer the period of the year, in which scallops can take advantage of the natural food production, the more beneficial it is to producers. If spat can be available earlier in the year, and larger spat provided the growers at the optimum time of the growth season, the yield can be increased. The use of different culture strategies, by modifying the husbandry methods or manipulating the scallop spat, is hypothesised to result in a prolonged growth season.

In Norway, *P. maximus* spat have been hatchery produced for a 10-15 years period (Bergh & Strand 2001). The post-larval and spat performance in the hatchery-nursery phase is variable and a lot of questions concerning rearing conditions remain unanswered to obtain a predictable spat production. A scaling-up of the spat production in Norway depends on an economic viable and biological stable production in the hatchery-nursery phase, and the search after more cost-effective production methods is a continuing process. The culture strategy of *P. maximus* proposed for Norway requires efficient transportation of different stages of scallops between different sites (Bergh & Strand 2001). As the growth conditions in spring-early summer are inadequate in Norwegian waters, strategies to increase the tolerance of spat to environmental changes and using alternative husbandry practice and nursery systems are considered possibilities to overcome the problem of variable survival. By increasing the survival through the different production stages, a viable production of scallop spat may be assured.

## **Objectives**

The objective of the study was to investigate effects of critical environmental factors on scallop post-larvae and small spat performance in culture. Experiments with hatchery reared *Pecten maximus* were designed on the purpose to study effects of temperature, salinity and food availability on growth, survival, byssal attachment and chemical composition. Different transfer strategies from the hatchery to sea- and land-based nurseries were to be investigated in order to improve the viability during the transition phase and after exposure to environmental changes. Pre-transfer acclimation of the spat to colder water temperature or transfer to nursery using "poll" water as food source was hypothesised to give an earlier start of the production season in the spring, and the investigations intended to extend the knowledge of scallop spat capability to tolerate transfer and adapt to new culture conditions.

## **RESULTS AND DISCUSSION**

### **Influence of rearing environment on spat performance**

#### *Effects of temperature and salinity on growth and survival*

Temperature and salinity are environmental factors that highly control the normal development of scallops (Shumway 1991, Gosling 2003). Exposure to low temperature and salinity clearly influenced the performance of small ( $\leq 2$  mm) *P. maximus* spat (Paper II, III). Temperature was stated the main environmental factor affecting growth and survival of small spat deployed to the sea (Paper II), in compliance with the results of Rupp et al. (2005) concerning small spat of the tropical species *Nodipecten nodosus*. Low temperature showed inhibited shell-height growth expressed as daily specific growth rate (SGR) averaging 1.6 % vs. 2.9 % of spat deployed to the sea at temperatures below and above 10 °C respectively (Paper II). Likewise, lower SGR (1.3 %) was shown for spat kept at 15 °C than for spat kept at 18 °C (2.3 %) in experimental indoor growth units (Paper III). The effect of higher temperature was in the same way seen (SGR 4.0 % vs. 6.2 %) for ash free dry weight growth (Paper III). Growth of larger (5-14 mm) *P. maximus* spat has been shown limited by temperature at 6.5 °C and by ration at 22.9 °C (Laing 2000), and based on condition index data a temperature of 17 °C was recommended the best nursery rearing temperature. Robert &

Nicolas (2000) suggest post-larval growth of *P. maximus* to take place at 15 °C even though a larger spat size was obtained at 18 °C after 5 weeks in micro-nursery. The temperatures used in the discussed papers (I-V) were for the most part kept within the range that should sustain growth according to Laing (2000), thus the results indicated a similar response to temperature of small ( $\approx 2$  mm) and larger ( $>5$  mm) spat. Post-larval growth in the hatchery was at 15 °C, while experimental temperatures were 12-19 °C except for the occasions where spat were transferred to the sea in early spring (Paper II, Table 1). An experimental rearing temperature of 18 °C gave higher spat survival during 25 days (92 % vs. 75 %) than a temperature of 15 °C (Paper III). At sea temperatures below 7 °C survival of 0.7-2.6 mm spat averaged less than 5 %, but survival increased substantially to 24-60 % when the temperature reached 10 °C (Paper II). Likewise, retrieval rates obtained of other scallop species are shown to vary with deployment date (i.e. temperature) to sea-based nurseries. Grecian et al. (2003) reported 53-97 % retrieval of *Placopecten magellanicus* spat  $>1.4$  mm deployed to the sea, and Rupp et al. (2005) obtained 1.5-42.8 % retrieval of *N. nodosus* deployed at a size of 0.5 mm.

Table 1. Obtained growth of small scallop (*Pecten maximus*) spat reared at different environmental conditions based on raw-data from results presented in paper I-V from growth in hatchery (I and V), sea-based nursery (II), experimental system (III) and land-based nursery (IV). Size = initial shell-height, AFDW = ash free dry weight, na = data not available. Specific growth rate ( $\% \text{ day}^{-1}$ ) =  $(e^g - 1) \times 100$ ,  $g = (\ln \text{SH}/\text{AFDW}_{\text{final}} - \ln \text{SH}/\text{AFDW}_{\text{initial}})$  per number of days.

Paper no	Size mm	Temp °C	Salinity ‰	Time days	Season month	Shell height growth $\text{day}^{-1}$		AFDW growth $\text{day}^{-1}$	
						$\mu\text{m}$	%	$\mu\text{g}$	%
I	1.7-1.8	12-16	30-33	28	Dec-Apr	46-75	1.9-2.9	2.7-9.6	5.6-9.8
				19	Jun	113-128	4.3-4.8	14.9-19.6	14.2-15.7
II	0.7-5.6	5-15	28-33	52-134	Mar-Sep	46-128	0.9-3.3	na	na
III	1.4-2.3	15-18	30	23	Jul-Aug	23-57	1.2-2.5	1.7-5.5	3.6-7.3
IV	1.3-2.1	13-19	30-31	55-59	Jun-Oct	50-68	1.6-2.1	4.3-10.2	3.3-4.6
V	0.3-0.9	15	32-33	28-35	Jan-Mar	15-62	2.8-5.6	0.3-2.6	3.0-14.4

An interaction between temperature and salinity on scallop spat performance was shown under conditions likely to occur in shallow and landlocked coastal areas (Paper III). The growth decreased when the salinity was reduced from 30 to 20 and 25, and the growth was in general faster at 18 °C than at 15 °C (Paper III). The best growth result was obtained at the

combination of temperature 18 °C and salinity 30, while survival was equal of spat reared at salinity 25 and 30 (Paper III). Laing (2002) obtained highest growth of 6-10 mm *P. maximus* spat at a salinity of 30 compared to at 26 and 28 at 13-21 °C. No growth differences were found for 6-10 mm spat kept at temperatures between 13 and 21 °C at salinity 28-30 (Laing 2002). Larger *P. maximus* spat and juveniles are shown more sensitive to low salinity at low temperatures (Strand et al. 1993, Laing 2002), and juvenile scallops of other species are also shown to respond differently when exposed to various temperature and salinity combinations, namely *Chlamys opercularis* (Paul 1980b), *P. magellanicus* (Frenette & Parsons 2001, Frenette et al. 2002), *Argopecten irradians* (Mercaldo & Rhodes 1982), *Mimachlamys asperima* (O'Connor & Heasman 1998) and *N. nodosus* (Rupp & Parsons 2004).

A salinity of 20 was shown detrimental (Paper III) as reported for larger *P. maximus* spat (Laing 2002). In Laing (2002) it was concluded that salinity of 30-35 had no apparent effect on growth, condition, food consumption or survival. Growth rates of *P. maximus* spat surviving short-term exposure to salinity of 20-25 (6 hours per day) soon recovered to normal levels (Laing 2002). Levy et al. (1998) reports significant negative correlation of salinity with growth and retrieval of *P. magellanicus* spat transferred from hatchery to the sea, but they doubted the salinity to be causative as the salinity levels during the study were within the range of tolerance for juvenile sea scallops. Thus, growth and survival was probably not seriously affected by the salinity in the nursery studies (Paper I, II, IV and V, Table 1), although occasional drops below salinity of 30 were experienced in the sea (Paper II). Long-term exposure to low salinity, on the other hand, showed a clear negative impact on spat growth and survival (Paper III).

The *P. maximus* spat showed faster growth in summer compared to in winter and spring (Paper I, II) and the spat of the smallest initial size (Paper V) obtained higher specific growth rates compared to larger spat (Paper I-IV, Table 1). The seasonal fluctuation in growth rate could be related to the exposure time to high or low temperature (Paper II). The seasonal variation of seawater temperature has been shown to affect growth rates of other scallop species grown in the field, for instance of 1-year *Chlamys farreri* (Yang et al. 1999) and small *N. nodosus* (Rupp et al. 2005) and *P. magellanicus* spat (Grecian et al. 2000). The growth of *C. farreri* was slow at temperatures below 5 °C and declined rapidly above 23 °C (Yang et al. 1999). Between 5 and 23 °C the growth increased with increasing seawater temperature (Yang et al. 1999). Experimental studies of 5-14 mm *P. maximus* spat also showed increased

growth with temperature ranging from 5 to 23 °C (Laing 2000), while growth of <1 mm *P. maximus* was suppressed at 20 °C (Robert & Nicolas 2000).

The obtained shell growth varied from 15 to 128 µm per day (Paper I-V, Table 1) depending on initial size and treatment. The highest growth rates were within the range experienced for larger *P. maximus* spat in a study of Laing (2002) with 6-10 mm *P. maximus* spat, showing 78-229 µm growth per day increasing with temperature (9-21 °C) and salinity (30-35). An additional experiment with 8-16 mm spat obtained growth rates up to 370 µm per day at 18.3 °C (Laing 2002). Post-larval growth of ≈0.2-1.7 mm *P. maximus* was also affected by temperature as shell-length increased from 24 µm per day at 15 °C to 35 µm per day at 18 °C (Robert & Nicolas 2000). By comparison, the growth obtained during equal (4-5 weeks) time period in a commercial scale hatchery concerning the same size group of *P. maximus* (Paper V) was from 15 to 62 µm per day at 15 °C (Table 1). Experimental studies of 1 mm *P. fumatus* spat showed exponential growth during 4 weeks with growth rates increasing from approximately 20 to 110 µm per day within the temperature range of 13-27 °C (Heasman et al. 1996). Grecian et al (2000) also experienced seasonal and temperature dependent growth of *P. magellanicus* spat cultured in a sea-based nursery. A shell-height growth between 20 and 60 µm per day of spat of 1.4-2.9 mm initial size was obtained from October to July (Grecian et al. 2000), which was lower compared to *P. maximus* spat growth (46-128 µm per day) in the sea (Paper II, Table 1). The type of nursery growth system apparently affects the spat performance as different maximum shell growth was obtained in sea-based compared to land-based (128 vs. 68 µm per day) nursery (Paper II, IV, Table 1).

Reduced growth was shown for 1.7 mm *P. maximus* spat at salinity 25 compared to at 30 (Paper III). Larger *P. maximus* spat (6-10 mm) are shown to consume less algae food at salinity 26 than at 30, which also was reflected in growth rate (Laing 2002). This is in accordance with the study of Navarro & Gonzalez (1998) which demonstrated that reduction in salinity affected physiological processes like clearance rate, absorption, oxygen uptake and excretion of 25-100 mm *A. purpuratus*. They observed negative scope for growth values at salinities below 27, which implies growth highly affected by salinity stress (Navarro & Gonzalez 1998). Farming of juvenile *P. maximus* (30 mm) was recommended in areas where the salinity seldom drops below 29 (Strand et al. 1993), while on the basis of results in Paper III, small *P. maximus* spat should be kept in water of high salinity not less than 30. The tissue and shell growth did not correlate and the specific daily growth rate of AFDW was in general

higher than the shell growth (Paper I, III, IV, V, Table 1). The *P. maximus* spat kept at salinity of 20 showed a positive AFDW growth in contrast to a negative shell growth (Paper III), which indicates, that severely stressed scallops use the energy to maintain soft tissues instead of shell production. An uncoupling of the two growth processes was shown for the soft shell clam *Mya arenaria* (Lewis & Cerrato 1997), and these authors suggested shell growth to reflect metabolism and not the somatic production. The shell growth correlated with oxygen consumption (Lewis & Cerrato 1997) and thus with the temperature of the surrounding water. In agreement with this, daily shell growth variations of *P. maximus* were related to seasonal changes in temperature, but also food availability and quality (algae blooms) was shown to be factors regulating shell growth (Chauvaud et al. 1998, 2001).

#### *Effects of food availability on growth and survival*

One of the most critical functions during the early life stages of scallops is the ability to capture and ingest food particles of proper size and nutritional quality. The changes in gill morphology and functions are major during scallop post-larval growth from 0.3 to 4-14 mm (Sastry 1965, Beninger et al. 1994, Veniot et al. 2003). The numbers of gill filament increases during the *P. maximus* postlarval stage from metamorphosis (260 µm shell length) onwards, and the gill function of post-larvae up to 4 mm shell length is still different to that of adult *P. maximus* as differentiation of ordinary and principal filaments (heterorhabdic condition) begins beyond this size (Beninger et al. 1994). According to Beninger et al. (1994), particle capture was very inefficient for *P. maximus* smaller than 1 mm, but the efficiency increased during the growth from 1 to 4 mm. Most of the spat studied in Paper I-V were smaller than 4 mm (Table 1) and consequently of a vulnerable size at transfer time from the hatchery to nursery- or experimental conditions. A mismatch between stage, nutritional requirements and food availability reduces the feeding capacity of the scallops and hence growth and survival may have been affected by the changes in rearing environment.

During the post-larval stage in the hatchery and before experimental start (Paper I-V), the scallops were fed a similar mix of monocultured algae. The algae species supplied were the flagellates *Pavlova lutheri*, *Isochrysis galbana* and the diatoms *Skeletonema costatum*, *Chaetoceros calcitrans* and *C. mülleri*, all commonly used in bivalve hatcheries worldwide. The algae were of approximate sizes from 3 to 10 µm, a range expected to ensure efficient food uptake. Pectinid species commonly retain particles larger than 5-7 µm with 100 %



efficiency (Vahl 1973, Møhlenberg & Riisgård 1978, Palmer & Williams 1980, Riisgård 1988), while the retention efficiency decreases for smaller particles. Compared to other bivalve species (cockles, mussels, oysters and clams) scallops have limited ability to retain small sized particles of 1-4  $\mu\text{m}$  (Møhlenberg & Riisgård 1978). The diets during the experimental periods varied from using two algal species (Paper III) or continuing with the standard hatchery mix (Paper I and V) to rely on the production in a landlocked marine basin or “poll” (Paper IV) and in the sea (Paper II). In addition to the size and quality of the food particles, the quantity available to the scallops depends on the volume of water passing the gills, i.e. filtration rate and velocity, and the efficiency of which particles are retained (Bricelj & Shumway 1991). A mixed diet of cultured algae is supposed to have a quality that enhance growth of scallop spat and supply adequate quantities of lipid, carbohydrate and protein (Laing & Psimopoulous 1998, Milke et al. 2004), although the composition deviates from nature's own.

The lipid content of small *P. maximus* spat (1.3-2.1 mm) was significantly reduced after transfer from the hatchery to a land-based nursery using “poll” (described in Strand 1996) as water and food source (Paper IV). Lipids are important as energy reserves during critical stages from larvae to juvenile life (Whyte et al. 1987, 1992, Delauney et al. 1992, Farías et al. 1998, Lu et al. 1999b, Robert et al. 1999, Milke et al. 2004). Furthermore the physiological condition, i.e. the chemical content, and growth of scallop juveniles was shown to be influenced by diet and feeding regimen (Cahalan et al. 1989, Ó Foighil et al. 1990, Martínez et al. 1992, 1995, Parrish et al. 1995, Coutteau et al. 1996, Ryan et al. 1998, Uriarte & Farías 1999, Parrish et al. 1999, Milke et al. 2004, Paper IV), and thus food conditions during early life stages affect the success of transfer to a new environment. The total lipid content level after 8 weeks nursery growth (Paper IV) was comparable to lipid percentage found in *A. purpuratus* (Martinez et al. 1992) and *Crassadoma gigantea* (Whyte et al. 1992) grown in the sea. On the other hand, shell growth (55-71  $\mu\text{m}$  per day) in the land-based nursery (Paper IV) was lower than the growth rates (70-125  $\mu\text{m}$  per day) found for *P. maximus* spat of the same size transferred to the sea (Paper II). The obtained growth was comparable to growth of small scallop spat fed single-species and low ration diets (Lu & Blake 1996, Laing & Psimopoulous 1998, Laing 2000). Hence, it was suggested that the food conditions in the manipulated “poll” were qualitatively sub-optimal during the study (Paper IV).

Survival of the *P. maximus* spat transferred to the sea-based nursery early in the season was related to low temperature at transfer (Paper II), while food availability most likely impacted on growth of the surviving scallops. Algal abundance and temperature in the sea fluctuate with depth and season, which influences the food availability, and thus the growth of scallops (Kirby-Smith & Barber 1974, Vahl 1980, Sundet & Vahl 1981, Lodeiros & Himmelman 1994, Kleinman et al. 1996, Román et al. 1999, Lodeiros & Himmelman 2000). As the water temperature increases a larger ration is needed to sustain growth, and *P. maximus* spat (5-14 mm) consumed an increasing amount of algae when exposed to temperatures from 6.6 to 22.9 °C (Laing 2000). Higher growth rates of the smaller (ca. 1-5 mm) *P. maximus* spat were accordingly obtained later in the season (Paper II) after the diatom spring blooms, when temperature was higher and the species composition of algae and associated microbes changes (Larsen et al. 2004 and references therein). Likewise, the higher growth rates achieved for spat in the hatchery in June (Paper I) compared to in December, February and April can be explained by the seasonal changes in water conditions. The spat were supplied with coarser filtered seawater (sand filtered) in addition to seawater filtered through a 1 µm bag filter, which may have influenced the water quality and increased the available food amount. A seasonal change in the phytoplankton composition was seen in the poll-system (Paper IV) and the differences in AFDW growth between spat groups could be related to the change in food quality.

Increased water recirculation rate in the post-larvae rearing system (primary nursery) reduced the number of algal cells in the rearing sieves with up to 40-50 % of the amount (10 and 15 cells µl<sup>-1</sup>) introduced to the tanks (Paper IV), but growth and survival were not significantly affected. This indicated that food availability was not a limiting factor at the recirculation rates (67, 83 and 92 %) studied. The scallops were fed 10-15 algae cells µl<sup>-1</sup> when in the hatchery (Paper I-V), which was assumed adequate to support good growth, as optimum algal concentrations between 10 and 20 cells µl<sup>-1</sup> were suggested for *P. maximus* (6-63 mm) when fed a single cell diet of *Chaetoceros gracilis* (Skjæggestad et al. 1999). Likewise Lu and Blake (1996) found 10 cells µl<sup>-1</sup> of *Isochrysis galbana* optimal for 0.5-6.0 mm *Argopecten irradians concentricus*. Optimum food concentrations are shown to vary with stage and size (Lu & Blake 1996). A higher algal concentration was shown optimal for *A. irradians concentricus* larvae (20 cells µl<sup>-1</sup>) than for spat (10 cells µl<sup>-1</sup>) in the study of Lu & Blake (1996), while low algal concentrations, 7 and 4.7 cells µl<sup>-1</sup>, were shown to provide optimal food rations for *P. maximus* (Nicolas & Robert 2001) and *N. nodosus* (Rupp et al. 2004b)

post-larvae respectively. The clearance rates ( $\text{ml hour}^{-1}$ ) of *A. irradians concentricus* increased with spat shell size from 0.5 to 10 mm shell-height, but decreased with algal concentrations from 10 to 50 cells  $\mu\text{l}^{-1}$  (Lu & Blake 1997a). Similarly, the clearance percentage of algae from suspension of *P. maximus* spat (5-14 mm) decreased with food rations of 0.012-0.492 g (organic weight of algae)  $\text{g}^{-1}$  (live weight of spat)  $\text{week}^{-1}$  (Laing 2000). Maximum growth was obtained when the consumed proportion fell below ca. 80 % of the fed ration (Laing 2000), thus growth is limited by the feeding capacity of the scallop at high algal concentrations at the given temperature. In agreement, the effect of too high food abundance is shown in nature, where drops in growth rate of juvenile *P. maximus* have been associated with high densities of diatoms in the sea (Lorrain et al. 2000).

#### *Tolerance limits and sub-optimal conditions*

The rearing of scallops in artificial surroundings compared to the natural habitat may cause sub-optimal conditions and thus produce greater sensitivity to environmental changes (Bricelj & Shumway 1991, Thompson & Macdonald 1991, Maguire 1998, Lodeiros et al. 2001, Lafrance et al. 2003). Sub-optimal rearing conditions inhibited the growth potential of 2 mm *P. maximus* as seen at temperatures below 10 °C in the sea (Paper II) and below 18 °C in the hatchery (Paper III), and at reduced salinity below 30 (Paper III). Survival was not affected the same way (Paper II, III), while scallop spat may survive within a range of the different environmental parameters which is likely to occur during seasonal variations in the sea. Post-transport recovery showed reduced growth and survival after 24 hours emersion (Paper I), while temperatures of 5-7 °C and salinity of 20 was considered lethal to spat <3 mm (Paper II, III). Growth environment known to have lethal conditions should of course be avoided for culture, but of more concern are the sub-lethal stress levels. In culture, both the thermal and the nutritional conditions affect the scallop growth. Fouling organisms and predators are likely to compete for space and food and also disturb the water flow inside growth equipment. Abrupt and considerable changes in environmental conditions occur in an aquaculture situation during handling and transfer operations, further affecting the spat performance. Hence, lack of knowledge of tolerance limits and sensitivity to environmental variables could be detrimental to the scallop spat. Scallop (*C. opercularis* and *P. magellanicus*) spat (<10 mm) have demonstrated better tolerance to high temperature and low salinity than juveniles and adults (Paul 1980a,b, Rupp & Parsons 2004). A variation in tolerance to changes in salinity and temperature according to ontogenetic stage was also shown for *M. asperrima* as

mature juveniles (28 mm) were more sensitive than 18 mm juveniles (O'Connor & Heasman 1998). This implies a relative wide tolerance range for small spat, which is advantageous to sustain survival during the nursery growth phase.

Although it is well known that scallops are sensitive to variation in salinity and temperature, information about exact upper and lower lethal levels is scarce. Long term exposure (25 days) to salinity of 20 did not result in total mortality of 1.7 mm *P. maximus*, but growth had ceased (Paper III). The shell-growth was negative as the shell became very thin and fragile, and therefore easily damaged. A constant exposure to salinity of 20 is most likely fatal to small *P. maximus* spat, while salinity of 25 could be sub-lethal since survival was shown equal to survival at 30 but growth was lower (Paper III). No other published results was found regarding salinity tolerance of scallop spat less than 2 mm, but short term exposure (6 hours day<sup>-1</sup>, 1-3 days) of larger *P. maximum* spat (8-16 mm) to salinity 20 and 25 resulted in total mortality at 7.2 °C, and more than 80 % of the spat exposed to salinity 20 died at 10.7 °C (Laing 2002). Juvenile *P. maximus* suffered total mortality after 16 days exposed to a salinity of 20 at a temperature of 5 °C, while scallops held at salinity 23 died after 4 weeks exposure (Strand et al. 1993). The juveniles showed higher tolerance to salinities from 26 to 29, but the least mortality was shown at a salinity of 33 (Strand et al. 1993). The tolerance range is species specific and according to Singnoret-Brailovsky et al. (1996) *A. ventricosus-circularis* (23 mm) is restricted to a wide salinity range from 27 to 47, while *A. irradians* (10-30 mm) survive well at salinity 15 (Mercaldo & Rhodes 1982) and *M. asperrima* (18 mm) at salinities from 25 to 40 (O'Connor & Heasman 1998).

Temperature is a vital factor determining the salinity tolerance of scallops. A rapid rise in mortality occurred after nine days by the 1.7 mm spat kept at salinity 20 and temperature 15 °C, more than a week earlier than an increase in mortality rate was observed at 18 °C (Paper III). The mean mortality after 25 days was 59 % and 26 % respectively (Paper III). In accordance juvenile *P. maximus* (22-40 mm) showed increased tolerance to low salinity when the temperature was increased from 5 to 9 °C (Strand et al. 1993). The study by Rupp & Parsons (2004) likewise showed the lethal salinity of the tropical species *N. nodosus* to change with temperature and size. For instance the lethal salinities (LC<sub>50</sub>) of adult (50-60 mm), juveniles (20-30 mm) and spat (<10 mm) at 48-hours exposure to ambient temperature were 23.2, 23.6 and 20.1 respectively (Rupp & Parsons 2004). Salinities from 16 to 28 were in the same way shown lethal to *Chlamys opercularis* after a 24 hours exposure, depending on

temperature from 5 to 20 °C and scallop size from 5 to >60 mm (Paul 1980b). Salinities of 16 and below were lethal for juvenile (27-43 mm) *P. magellanicus*, but catatonic shock severe at the higher salinities 18 and 21 (Bergman et al. 1996). Results from another experiment with small (10-20 mm) and large (20-35 mm) *P. magellanicus* spat indicated required water conditions as salinity of 25 or higher and a temperature of 18 °C or lower (Frenette & Parsons 2001). A high temperature of 23 °C increased mortality of *P. magellanicus* remarkably (Frenette & Parsons 2001), which is concordant with results recorded for *A. irradians* (10-30 mm), showing the greatest mortality in combinations of low salinity ( $\leq 10$ ) and high temperatures (19-24 °C) (Mercaldo & Rhodes 1982).

Exposure to low water temperatures of <10 °C severely affected growth and survival of 0.7-2.6 mm *P. maximus* spat (Paper II). Less than 5 % of the spat survived direct transfer to the sea when the temperatures were between 5 and 7 °C (Paper II), indicating the lethal temperature close to 5 °C for small *P. maximus* spat. Exposure to cold water has been shown critical for other stages of *P. maximus* as well. High mortality of veliger larvae occurs at 7-8 °C and total mortality at 5 °C (Davenport et al. 1975, Beaumont and Budd 1982), while a 100 % mortality of juveniles at low winter temperature (<2-4 °C) is reported from growth trials in suspended intermediate culture in Norway (Strand & Brynjeldsen 2003). The low lethal tolerance temperature for *Patinopecten yessoensis* is also found to be about 5 °C (Ventilla 1982), while the sea scallop, *P. magellanicus* tolerate temperatures down to below 0 °C (Couturier et al. 1995). Laing (2000) found no growth or measurable uptake of food at 4.7 °C by larger (5-14 mm) *P. maximus* spat, in agreement with the reductions in filtration rate of 50-80 % recorded at 5 °C compared to at 9 °C for 20-30 mm juveniles (Strand et al. 1993). However, in Irish waters a higher threshold temperature (“biological zero”) than 5 °C, i.e. 9 °C, for shell growth was estimated from growth and temperature data of juvenile *P. maximus* in suspended culture (Wilson 1987b). Condition index was lower at 6.6 and 8.0 °C than at 10 °C or above in the laboratory studies of Laing (2000), indicating 5-10 °C sub-optimal temperatures for growth, as shown for the smaller *P. maximus* spat (Paper II).

Upper lethal temperatures for *P. maximus* are hardly documented, but a temperature exceeding 20 °C is likely to increase mortality (Román et al. 2001). The highest temperature exposure in the discussed papers was 19 °C (Paper IV, Table 1) well below lethal temperature. More information is available related to temperature ranges of interest to scallop

culturists, i.e. within ranges supporting growth and survival. *P. maximus* post-larvae ( $\approx 0.2$ -1.7 mm) showed decreased growth and survival at 20 °C compared to at 15 and 18 °C (Robert & Nicolas 2000), and given food was not a limiting factor, the study of Laing (2000) showed increased shell growth rate of *P. maximus* spat (5-14 mm) with temperature up to 23 °C. Higher growth rates were accordingly found for 2 mm spat at 18 °C than at 15 °C (Paper III). The filtration rate was similar for 17-19 mm spat between 10 and 17 °C (Laing 2004) which coincided with the optimum rearing temperature suggested for 5-14 mm *P. maximus* spat (Laing 2000, 2004). In accordance, survival and growth of smaller *P. maximus* spat deployed directly to the sea increased substantially after the sea temperatures had reached 7 °C and 10 °C respectively (Paper II). At 20 and 23 °C spat (5-14 mm) consumed a higher amount than the ration required for maximum growth (Laing 2000), furthermore indicating 20 °C sub-optimal. The upper lethal temperature for *P. magellanicus* has been determined to range from 20 to 23.5 °C depending on season (Dickie 1958), and from 19 to 24 °C and 24-25 °C for >30 mm and 5-10 mm *C. opercularis* respectively (Paul 1980a). Likewise, ontogenetic differences in tolerance to high temperatures were reported for *P. fumatus*. Temperatures above 20 °C were fatal to embryos and larvae, as opposed to small spat which showed reduced survival at 13-17 °C than at 21-27 °C (Heasman et al. 1996). The spat (ca. 1 mm) growth in the study of Heasman et al. (1996) was, however, substantially reduced at 27 °C compared to 24 °C after 5 weeks under experimental conditions.

If the environmental conditions are outside the tolerated limits, growth and survival will be seriously affected. Hence, exposing spat to extremes in temperature and salinity was fatal to 2 mm *P. maximus* spat (Paper II & III). The lower lethal temperature of scallop spat may rather be a temperature range than an absolute temperature. In nature the different scallop species is distributed within a certain geographical and bathymetric range where the environmental conditions support survival (Brand 1991). Tolerance limits therefore, will vary between populations of the same species due to the exposure of different local temperature ranges and seasonal variations. Within a population, a high temperature shown to be lethal to the animal during winter may be tolerated by the animal when exposed to summer conditions, and vice versa (Schmidt-Nielsen 1990). As an example, the scallop *N. nodosus* were more vulnerable to low salinity at summer temperatures (Rupp & Parsons 2004). The *P. maximus* spat investigated (Paper II) were of sizes between larvae and juveniles having lower lethal temperatures of 8 °C and 2 °C respectively (Beaumont & Budd 1982, Strand & Brynjeldsen 2003). Based on this information it was assumed that transfer of spat to sea temperatures >5

°C would not be critical. The observations (Paper II) showed that some *P. maximus* spat less than 2.5 mm were able to survive transfer to 5-7 °C, while others suffered high mortality. Likewise, some spat survived long term exposure to salinity 20, but were not considered able to recover (Paper III). Consequently, it was concluded that small spat should not be transferred from hatchery conditions to natural sea conditions at temperatures less than 7°C (Paper II) or to salinities below 25 (Paper III).

During the period when the spat produces byssus threads, byssal attachment reflects good growth conditions (Paul 1980a,b, Heasman et al. 1994a, 1996, O'Connor & Heasman 1998, Wang et al. 2002, Rupp & Parsons 2004, Paper III). In unfavourable environmental conditions the spat detach and growth may be affected due to a reallocation of energy expenditure. This is likely since marine bivalves from inshore and estuarine environments have been found to require a higher salinity for byssus production than is necessary for other activities (Castagna & Chanley 1973). *P. maximus* spat (1.7 mm) transferred to conditions holding salinity of 20 did not attach at all, while spat held at salinity of 30 showed 80-100 % attachment (Paper III). Salinity of 25 showed approximately 25 % attachment in the same study, indicating the condition sub-optimal, which was confirmed by the growth measurements. Similarly, rapid initial attachment, together with high and stable attachment rates, are found for other scallops in temperature and salinity conditions where high growth and survival appeared (Paul 1980a, Heasman et al. 1996, O'Connor & Heasman 1998, Rupp & Parsons 2004). The small *P. maximus* were shown to be more sensitive at a temperature of 15 °C compared to at 18 °C, resulting in reduction in numbers attached with time (Paper III). The number of reattached *P. fumatus* spat also showed a decline from a high level to 50 % and less after four weeks at sub-optimal growth temperatures (Heasman et al. 1996). Likewise Paul (1980a) found the maximum byssus attachment for *C. opercularis* to be temperature dependent, with attachment rate to decline and becoming more variable at higher and lower temperatures than the optimal temperature of 18 °C.

## **Culture strategies**

### *Site selection and growth systems*

Site selection is of major importance when culturing scallops, and growth and survival of

scallop spat is very much dependent on the grower's choice of culture method, system, equipment and nursery location (Grecian et al. 2000, Frenette et al. 2001, Rupp & Parsons 2004, Paper II, Paper IV). Suspension culture is a common rearing form for spat and juvenile scallops, and the vertical placement in the water column (depth) has significant influence on growth (Paul et al. 1981, Wallace & Reinsnes 1985, Thompson & MacDonald 1990, Côte et al. 1994, Thorarinsdóttir 1994, Kleinman et al. 1996, Lodeiros et al. 1998, Román et al. 1999, Grecian et al. 2000, Avendaño et al. 2001, Román et al. 2003). In a hatchery situation, scallops are held in a modified environment where the temperature and food availability are elevated compared with natural conditions. In suspended nursery and intermediate culture, the scallops are kept higher in the water column and exposed to more fluctuations in salinity and temperature. Cultivation sites at shallow depths in coastal waters, in landlocked basins or lagoons may occasionally be severely influenced by brackish water (Strand 1996, Frenette et al. 2001). As a result many culture localities of *P. maximus* experience a more variable environment compared to the natural habitat. Winter mortality has been reported of cultivated juveniles along the Norwegian coast, and a higher risk of low-temperature events was suggested to occur at sites located in the most southern and northern regions (Strand & Brynjeldsen 2003). As important as survival in a farming situation is the growth rate. The environment therefore should hold superior conditions to what is required to sustain the basal metabolism. In farming situations at shallower depths and in more protected sites compared to natural conditions on the seabed, the scallops take advantage of higher temperature and food availability. Sites in fertilized waters have shown increased primary (food) production and higher growth rates of *P. maximus* juveniles compared to at sea locations (Andersen & Naas 1993, Reitan et al. 2002).

In Europe the scallop spat are commonly grown to a size of approximately 2 mm shell-height in the hatchery, followed by growth to a size of 15-20 mm in a nursery (Millican 1997, Dao et al. 1999, Bergh & Strand 2001). Production of *P. maximus* spat is space consuming compared to production of for instance oysters and clams, which thrive in high densities at high temperatures and food levels. Special nursery systems were developed for the scallops (Buestel et al. 1982, Bourne et al. 1991, Karney 1991). One-layer growth on downwelling screens (sieves), as opposed to 3-dimensional settlement on collector bags, is the common method used for rearing the *P. maximus* post-larvae in Europe (Millican 1997, Robert & Gérard 1999), while small spat are kept in nets or plastic trays. Spat yield varies a lot regardless of settlement system. Gruffyd & Beaumont (1972) reported 4-14 % survival during



*P. maximus* larval rearing. In France 0-33 % post-larval (*P. maximus*) yield from screens is reported from a commercial hatchery, but better results are shown obtainable in research situations (Robert & Gérard 1999, Robert & Nicolas 2000, Nicolas & Robert 2001). Heasman (2002) reports 5-10 % spat (*P. fumatus*) yield from direct settlement on collector bags and up to 45 % yield when using different screen techniques. In Norway the average yield of 2 mm *P. maximus* post-larvae related to the amount of competent larvae has been 10-20 %, and the yield of 10 mm spat 0-80 % related to the number of post-larvae transferred to sea or land-based nursery (Paper II & IV, Magnesen & Christophersen unpublished data). Lu & Blake (1997b) showed a higher yield of 0.5 mm *A. irradians concentricus* post-larvae (33 and 60 %), but only 20 % yield of 10 mm spat after growth in the sea. Comparable yields obtained from collectors in tanks are documented from Brazil and Chile of the scallop species *N. nodosus* and *A. purpuratus* showing 3-16 % and 21-45 % respectively (Uriarte et. al. 2001). Similar results (<5-18 and 28-52 %) have been found in remote set trials with *P. magellanicus* in Newfoundland, Canada (Couturier & Christophersen unpublished data). The variation in spat yield may be explained by broodstock and larval quality together with the properties of the water, i.e. food availability, salinity, temperature and hydrodynamics in the tanks or at the site (Utting & Millican 1997, Wildish & Kristmanson 1997, Gosling 2003).

The use of a recirculation downwelling growth system in scallop post-larval production is an option to achieve a continuous supply and cost-effective reuse of water and food (Paper V). In the post-larval nursery in the hatchery the feeding regime may affect scallop growth and metabolism. Continuously feeding is experienced to give better growth and food assimilation in *A. purpuratus* larvae and early juveniles compared with feeding once or twice a day (Martínez et al. 1995). Juvenile bay scallops, *A. irradians*, fed four times per day are shown to have superior growth rates both to less (1 and 2 times) and more (8 times) frequent fed scallops (Smith & Wikfors 1998). In the hatchery, the incoming seawater is filtered and the scallops are usually fed a mixture of cultured algae rather than a single species diet to meet the required nutritional quality for good growth (Laing & Psimopoulous 1998). Algal concentration, ration, water flow and velocity are other factors affecting the growth of juvenile scallops (Wildish & Saulnier 1992, Lu & Blake 1996, Laing 2000, Robert & Nicolas 2000, Nicolas & Robert 2001). As there is a rapid increase in biomass during early life stages, the demand for algae and water increases correspondingly (Le Borgne 1981, Bourne et al. 1989, Millican 1997).

The cultivation of algae feed, seawater heating and pumping are major costs in bivalve production, and the mass production of live algae cells both a quantitative and a qualitative constraint (de Pauw 1981, Smith & Wikfors 1998, Robert & Gérard 1999, Wikfors & Ohno 2001, Heasman et al. 2002). An alternative to flow-through systems is recirculation systems where water and algae are reused. The use of closed recirculation systems is not common in bivalve rearing, but have been tried on experimental basis with nursery sized scallops, *A. irradians irradians* (Widman 1998), and clams, *Mercenaria mercenaria* (Pfeiffer & Rusch 2000). More commonly used in intensive bivalve aquaculture are batch (static) or flow-through (open) systems where a regular replacement of water avoids the build-up of organic matter and oxygen deficiency. The feeding amount must balance the food uptake by the scallops and the accumulation of debris that may reduce the water quality. Up to 92 % recirculation was shown feasible for growing *P. maximus* post-larvae, and no significant differences in growth and survival compared to 67 and 83 % were found (Paper V). On the basis of reported optimum algal concentrations for spat growth (Lu & Blake 1996, 1997a, Skjæggestad et al. 1999, Laing 2000, Nicolas & Robert 2001) it was assumed that the food amount was sufficient and not a limiting factor (Paper V). Partly recirculation of the water in post-larvae rearing tanks reduces the volume of new water with algae that has to be added per unit time, thereby increasing the utilisation of algae and lowering the expenses. In sea-based nurseries the scallop spat depend totally on the natural seawater quality. By growing scallop spat in the sea, adequate food and environmental conditions is likely to be ensured (Martínez et al. 1992, Pit & Southgate 2000). Consequently it is advantageous of biological and economical reasons to transfer the spat as early as possible to seawater based nurseries.

One strategy to extend the spat production period is to use a landlocked heliothermic marine basin or “poll” as water supply and food production system for a land based nursery (Strand 1996, Paper IV), allowing a 1-2 months earlier transfer of spat from the hatchery. In such an environment lower salinity and considerable higher temperatures, compared to sea conditions, are likely to occur (Gaarder & Bjerkan 1934, Strand 1996). Renewal of the poll water normally occurs during winter as saline and denser water from the fjord outside is allowed into the poll (Gaarder & Bjerkan 1934). Due to mixing of the water from the fjord, typically holding a salinity of 33, and the poll water, a salinity of 30 is commonly found during spring (Gaarder & Spärck 1932, Gaarder & Bjerkan 1934, Strand 1993). Runoff water and heavy rainfall may cause reduction in the salinity level during summer months (Strand 1993). Scallop cultivation is, however, broadly recommended to take place at sites of high salinity

and with a low rate of salinity fluctuations (Mercaldo & Rhodes 1982, Strand et al. 1993, Bergman et al. 1996, Singnoret-Brailovsky et al. 1996, Navarro & Gonzalez 1998, O'Connor & Heasman 1998, Frenette et al. 2001, Paper III).

Two important aspects in the development of growth systems for scallop spat are manipulated (i.e. land-based) versus natural conditions and small scale culture versus large scale. An efficient system is needed to scaling up the spat production, and land-based facilities simplify the husbandry due to easy access. Such systems, on the other hand require large space and volumes of water compared to sea-based nurseries taking advantage of the natural seawater flow. Keeping the spat enclosed is a balance between protection to predators and confinement limiting natural behaviour of the small spat which are active swimmers. The advantages of keeping spat in different types of equipment are that scallops are hindered in escaping and that predators to some extent are prevented from access to the spat. Problems may be planktonic larvae of starfish (Grecian et al. 2003) and crabs that settle and thrive within the equipment, and other fouling organisms that settle outside and reduce the water flow and thereby the food availability (Lu & Blake 1997b). In land-based nurseries this situation can be avoided, and the composition controlled by filtering the incoming water. The use of such land-based nursery facilities is shown to increase survival compared to sea-based nursery of *P. maximus* spat transferred at a size of <2 mm (Magnesen & Christophersen unpublished data). In France higher *P. maximus* post-larval yield was shown in research situations compared to results reported from a commercial hatchery (Robert & Gérard 1999, Robert & Nicolas 2000, Nicolas & Robert 2001). Caution is therefore needed when transferring the results obtained during small scale experimental conditions (Paper I & III) to large scale conditions. The disadvantage of carrying out experimental work in production conditions (Paper II, IV & V) is a less possibility to control every environmental factor. Nevertheless, the results may be more directly transferable to a farm site situation.

#### *Acclimation and tolerance to environmental changes*

Acclimation was considered a successful way to adjust the scallops to new environmental conditions (Paper II). Though, the conditions must be inside the tolerated limits of the environmental factors. The adaptation to new surroundings can be described as a three-phase process consisting of an immediate response, a stabilisation of this response and a new steady state (Kinne 1963). By preparing the scallops to the environmental change, the possibility to

enhance survival from one production stage to another increases. The importance of behavioural acclimation of hatchery-reared fish, in order to prepare them for a life in the wild and improve post-release survival is emphasized by Brown & Day (2002), and they suggest implementing reintroduction techniques used by conservationists in fishery research and hatchery industries. Thermal acclimation is usual in bivalve rearing, and acclimation can be made in many ways by manipulating with different time- and temperature regimens. Scallops, like other marine bivalves, are demonstrated to be osmoconformers although the ability to adjust to ambient salinity may be restricted within a salinity tolerance range (Shumway 1977, Singnoret-Brailovsky et al. 1996). For other bivalve species, it has been found that acclimation is a useful method to increase the tolerance to extreme salinities (Chanley 1958, Castagna and Chanley 1973).

Too abrupt and large changes of the environmental conditions may be fatal, as shown for small spat transferred to a temperature 10 °C and more below ambient (Paper II) and from a salinity above 30 to 20 (Paper III). Acclimation may, on the other hand, skew the lethal toleration limits. Studies of the sea scallop have indicated that a rise or fall in acclimation temperature of about 5 °C may result in a corresponding change in lethal temperature of 1 °C (Dickie 1958). The rate of acclimation tends to follow the rate of metabolism, resulting in longer time needed for acclimation to a decrease in temperature than an increase. The animals' environmental history, genetic background, physiological condition, metabolism, age and size are all factors affecting the capacity, rate and effect of thermal acclimation (Kinne 1963, Schmidt-Nielsen 1990). The temperature response was measured as survival and shell- and organic growth (Paper II, III), while other methods, such as characterisation of stress protein responses may help in determination of the tolerance to acute temperature shocks (Brun et al. 2003).

The most common acclimation strategy used is by changing one environmental factor step by step during several days until the aimed conditions are acquired. Another method is to expose the animals to a major change, for then to stay in these surroundings until fully acclimated. The latter strategy was chosen in our work (Paper II) as the spat were transferred from a temperature of 15 °C in the hatchery to an environment of 10 °C for 1 and 3 weeks before deployment to temperatures between 5 and 10 °C in the sea. One week was regarded as sufficient for small scallop spat to adapt to 10 °C after transfer from 15 °C, since no

significant differences in survival and final shell-height were found between spat acclimated for 1 and 3 weeks (Paper II). A period of two weeks acclimation to a temperature change was however needed for mussels to physiologically compensate to initial levels of oxygen consumption and filtration rate (Bayne et al. 1976).

Small *P. maximus* spat (1-4 mm) could tolerate an abrupt change from 15 to 10 °C (Paper II). Exposure to a larger decrease in temperature, from 15 °C to 5-7 °C, on the other hand, seemed too stressful for the smallest spat of 0.7-2.6 mm shell-height (Paper II). Laing (2000) successfully acclimated *P. maximus* spat of 5-14 mm from a rearing temperature of 17 °C to 5 °C by temperature reduction rates of no more than 1 °C per day. Likewise *A. irradians irradians* spat (7-18 mm) could be acclimated from a rearing temperature of 22.5 °C to ambient seawater temperatures of 5, 11.5 and 14 °C by lowering holding temperatures at a rate of 2 °C every 2 days (Widman & Rhodes 1991). The constant and fluctuation temperature regime studied by Pilditch & Grant (1999) did not affect the shell growth rate of *P. magellanicus* differently, but limited ability to alter metabolic energy demands following temperature changes was shown. It is possible that *P. maximus* has similar limited capability to regulate its metabolism to sudden changes of low temperatures. Acclimation was shown to increase survival, but mean survival was in general low (<9 %) compared with the survival (24-60 %) obtained for spat transferred to sea temperatures more equal to the hatchery temperature (Paper II). Thus, the success of spat transfer to sea during cold-water seasons is highly dependent on deployment time, which also has been shown for the cold-water species *P. magellanicus* (Grecian et al. 2000) and the subtropical *N. nodosus* (Rupp et al 2005) spat.

The 1.7 mm *P. maximus* spat investigated in Paper III were directly transferred from high to low salinity (Paper III). The abrupt change in salinity from 30 to 20 and 25 did not show immediate mortality, but commenced after 10 and 14 days. Growth and behaviour on the other hand showed more immediate responses. Juvenile *A. irradians* and *P. magellanicus* are shown to survive short term low salinity exposure (Mercaldo & Rhodes 1982, Bergman et al. 1996), while rapid and dramatic falls in salinity which might happen in nature, for instance, during heavy rainstorms, have resulted in mass mortality of bay scallops (Tettelbach et al. 1985). Nevertheless, successful survival is recorded for several bivalves after direct transfer to salinity 10-15 lower than at the collection sites (Castagna & Chanley 1973), which was comparable to the salinity steps undertaken in the Paper III study. For other species studied by

Castagna & Chanley (1973) a rapid change in salinity of 15 was, however, shown to be lethal. The scallops that were transferred to a salinity of 20, more than 10 lower than the rearing environment, were severely impacted (Paper III). The retarded shell growth, heavy survival and lack of byssal attachment could well have been caused by the abrupt salinity change. In general, oceanic species show limited capacity for tolerance, regulation and adaptation to salinity stress in comparison to brackish or hypersaline forms (Kinne 1964).

#### *Culling, handling and transfer*

Successful scallop aquaculture is most likely to occur if stressful handling can be avoided, but during the production from larvae to spat handling and transport operations are required. Sampling frequency (Laing et al. 1999) and transport (Maguire et al. 1999a) have been shown to affect juvenile *P. maximus*, and 1.7-1.8 mm *P. maximus* spat (Paper I). During the early life stages the scallops are routinely cleaned, graded and relayed, with removal of poorly developed and slow growing animals as the result. The size variation is large for bivalve post-larvae and spat of the same age even when grown under the same conditions (Newkirk 1981, Deming & Russel 1999, Pit & Southgate 2003, Paper IV & V). Important questions for growers are whether the animals keep a constant growth rate for life and how the culling practice may affect the production result. If growth is constant, elimination of the slow growers as early as possible would be cost-effective, while if the opposite is the case, valuable stock may be thrown away (Newkirk 1981).

At water changes the scallop larvae are sieved through fine mesh screens, with increasing mesh size as the larvae grow (Millican 1997, Widman et al. 2001, Torkildsen & Magnesen 2004). The faster growing larvae retaining on the mesh are ready to settle at different times, resulting in different settlement groups from each larval batch. Our studies indicated that the *P. maximus* larval growth rate is unrelated to the spat stage growth (Paper IV), as shown for clams, oysters and mussels (Newkirk & Haley 1982, Strömngren & Nielsen 1989, Hilbish et al. 1993, Deming & Russell 1999). A clear conclusion, of which *P. maximus* spat originating from the second settlement group should be included in the production, was not drawn from the findings in the present studies. Lower survival of the slower growing larval group was shown in the hatchery settlement system (Paper V), while the results were contradictory for post-larvae transferred to land-based nursery relying on a different water source (Paper IV). Consequently it is left to conclude how the scallops will perform at later stages in the sea until

market size is attained. Newkirk (1981) claims that relative juvenile size of *Ostrea edulis* is a poor predictor of relative adult size. Likewise, Pit & Southgate (2003) showed that runts, given appropriate conditions, are capable of similar growth rates as larges spat. Rock oyster *Saccostrea commercialis* growth rate was not found affected by initial size class, implying the initial differences in size resulted from temporary environmental stunting (Mason et al. 1998). Deming & Russell (1999) even suggested the elimination of slow growing larvae from the production to be counterproductive, because they found an inverse growth relationship between larvae and post-settlement spat of hard clam *Mercenaria mercenaria*.

Scallop spat transport from hatchery to nursery, from one farm to another or to the market, is usually out of water (emersed) but in humid atmosphere (Paper I, IV). Alternatively the scallops can be transported in water (vivier trucks) but this method requires a large volume and increased cost (Maguire et al. 1999a). Transfer operations at the farm site are usually of short duration (<4 hours) while transfer of scallops to other growers may be of longer duration. Air emersion is stressful to the scallops and long-term exposure to air is fatal (Duncan et al. 1994), while short-term emersion and handling may be tolerated (Townsend et al. 1991, Dredge 1997, Laing et al. 1999, Maguire et al. 1999a, Lafrance et al. 2002, Paper I). Small *P. maximus* spat were capable of surviving 12-24 hours emersion in out of water transport conditions (Paper I). However, several authors have recommended transport time less than 12 hours (Fleury & Dao 1992, Maguire 1999a, Minchin et al. 2000). Transport of scallops will be a trade-off between the scallops' welfare and production costs. Maguire et al. (1999a) concludes that out-of-water transport of juvenile *P. maximus* is cost-effective up to 12 hours, while vivier transport must be used for journeys of longer duration. Storage in air for 12 hours and sprinkling or in-water storage for 12-34 hours were reported as feasible methods for transporting juvenile bay scallops, *A. irradians* (Liang 1996). Alternatively scallops can be transported in a modified atmosphere. Compared to air emersion, keeping scallop spat under a pure O<sub>2</sub> atmosphere was shown to increase the survival of *A. ventricosus* substantially (Maeda-Martínez et al. 2000).

Size at transfer was shown important to obtain predictable survival and growth (Paper II), but it seemed, however, of little advantage to keep the later settled spat of the same spawning for a prolonged period in the hatchery to reach a bigger size before transfer (Paper IV). As shown in paper II, it was demonstrated that pearl oyster, *Pinctada margaritifera*, spat transferred to an ocean-based nursery earlier after settlement, grew better in terms of shell-height than spat

transferred after being kept for a longer time in the hatchery (Pit & Southgate 2000). The environmental conditions in the nursery are essential, and Pit & Southgate (2000) suggested that their results reflected superior nutritional conditions in the sea compared to in the hatchery. Martínez et al. (1992) also concluded that the natural environment held a better balanced diet than could be offered in the hatchery. The scallops undergo major developmental changes as post-larvae which require adequate environmental conditions, and ontogenetic change in tolerance to environmental parameters for scallop egg, larvae and spat of *P. fumatus* and *M. asperima* have been shown (Heasman et al. 1996, O'Connor & Heasman 1998). Size of early *P. magellanicus* and *P. maximus* spat is likewise shown to be a critical factor at transfer from hatchery to colder water in sea based nursery, with sizes <3 mm showing lower survival than larger spat (Grecian et al. 2000, Paper II). These findings are supported by the anatomical development of the gill, which reach the adult form of spat >4 mm (Beninger et al. 1994, Veniot et al. 2003).

The timing of deployment to the sea is critical in obtaining commercial sized spat in the course of the first season (Grecian et al. 2000, Grecian et al. 2003, Paper II). During the window of opportunity of deployment of 1.5 mm *P. magellanicus* the seawater was characterised by high food density, high temperature and low sea star settlement (Grecian et al. 2003). On the contrary, a deployment temperature of 14 °C was shown disadvantageous to 8 mm *A. irradians* spat compared to deployment at 5 and 11.5 °C (Widman & Rhodes 1991). Biological aspects such as the initial spat condition, size, ontogenetic and physiological stage must also be considered to decide when the spat should be transferred to a new environment. Transfer of scallop post-larvae for further spat growth in a nursery is required to get a viable turnover in the hatchery. The transfer of post-larvae involves stress factors as detachment of byssus and aerial exposure. The stress effect was shown to be temperature and time dependent (Paper I and II) and the transfer strategy should differ according to season. A recent EU-project comprising *P. maximus* producing enterprises and research institutions in Norway, Ireland and Spain, has pursued the effects of handling and transport operations related to season, scallop size, temperature and time (Magnesen & Christophersen 2003, Magnesen, Roman, Gallagher & Christophersen unpublished data).



## Perspectives

Improvement of scallop culture in general requires knowledge of environmental conditions sustaining good growth and high survival. Progress in spat production depends to the greatest extent on information about the effects of different environmental variables to achieve optimum rearing conditions. Unfortunately, the early *P. maximus* life stages have rarely been observed in the wild such that the knowledge must be obtained from laboratory or hatchery studies. This study showed how certain aspects of the culture environment (i.e. temperature, salinity and food availability) influence scallop spat production. Many questions related to the interaction between the different variables, however, remain unanswered, and more knowledge on these aspects is required to further reduce the experienced variations in growth and survival. Temperature and salinity bioassays of narrower intervals than tested in the present study could be helpful in determining more exact tolerance limits. Though small scallop spat were shown capable of being prepared for transfer to cold water, the survival was low. A further increase in survival may be achieved by investigating a larger diversity of acclimation strategies.

Successful aquaculture depends on good quality spat produced at cost-effective methods, which secure high survival between production stages. The culling practice during the larval and spat phases may discard scallops viable for a life on the seabed. Poorly developed and slow growing scallops are successively eliminated through cleaning procedures or relaying onto growth equipment of larger mesh, leaving the fastest growers kept in production. It remains to reveal if fast growth during the early spat stages continues through the juvenile and adult stages. The timing of transfer is crucial to survival and the seasonal aspects need to be investigated in more detail. Transfers of spat to sea-based nursery depend highly on the annual changes in the sea, but also a seasonal effect was indicated for the transportation itself. Growth and survival are the result of complex environmental interactions that need further understanding. Spat age, size and nutritional status are all factors that may influence the tolerance to environmental changes, and comparable research should be carried out at several times of the year.

Efficient culture strategies are needed to develop an aquaculture industry. Intensive scallop culture is restricted to the larval and post-larval stages, while the intermediate culture in trays and the final culture at the bottom rely on natural food production. The traditional spat

production is space and labour intensive, and methods to reduce the time in the hatchery and in enclosures in the sea are aimed at. The study showed it was not feasible to keep post-larvae in the hatchery settlement system beyond reaching a shell-height of 2 mm. However, transfer of larger spat to the sea was shown to improve subsequent survival. Enhancement of post-transfer survival could be in prospect by introducing an intermediate step in the production before transfer of spat to the sea. A solution may be the use of a land-based nursery supplied with filtered seawater. In such a system the spat are protected against predators, and fouling on the equipment may be limited. Hence mortality and time needed for husbandry activities may be reduced.

Shellfish in general, and scallops in particular, are considered suitable aquaculture species in Norway. Compared to blue mussels, scallops are higher priced products, which justify the intensive production of spat. The domestic and export markets are not yet satisfied and stimulate a larger output of scallops. Hatchery production of spat is a prerequisite to the development of a sea-ranching industry of *P. maximus* in Norway, which relies on recapture of seeded scallops. In the Norwegian "Act relating to sea ranching" concession holders are demanded to release scallops of local origin. The present study was limited to spat from one local stock in Hordaland, but so far genetic differences in populations have not been identified along the western coast of Norway. Thus, it is likely that the gained results should be valid to scallops from a larger geographical area, but comparative studies are needed to reveal if stock-specific spat rearing methods are required.

## **REFERENCES**

- Acosta, C.P. & Román, G. 1994. Growth and reproduction in a southern population of scallop *Pecten maximus*. In: Bourne, N.F., Bunting, B.L. & Townsend, L.D. (eds.). Proceedings of the 9th International Pectinid Workshop, Nanaimo, B.C., Canada, April 22-27, 1993. Volume 1. Canadian Technical Report of Fisheries and Aquatic Sciences 1994, pp. 119-126.
- Agnalt, A.-L., Amodt, I., Haldorsen, M., Leikvoll, B., Strand, Ø. & Tvinnerheim, H. 2003. The new law on sea ranching in Norway ensuring property rights for invertebrates. In: Beyond Monoculture (ed. by Chopin, T. & Reinertsen, H.). Abstracts and extended communications, Aquaculture Europe 2003, Trondheim, Norway, August 8-12. European Aquaculture Society Special Publication No. 33, pp. 101-102.
- Andersen, S & Naas, K.E. 1993. Shell growth and survival of scallop (*Pecten maximus* L.) in a fertilized, shallow seawater pond. *Aquaculture* 110:71-86.
- Andersen, S. & Ringvold, H. 2000. Seasonal differences in effect of broodstock diet on spawning success in the great scallop. *Aquaculture International* 8:259-265.

- Ansell, A.D., Dao, J.-C. & Mason, J. 1991. Three European scallops: *Pecten maximus*, *Chlamys (Aequipecten) opercularis* and *C. (Chlamys) varia*. In: Shumway, S.E. (ed). *Scallops: biology, ecology and aquaculture*. Elsevier, Amsterdam, pp. 715-751.
- Arnold, W.S. 2001. Bivalve enhancement and restoration strategies in Florida, U.S.A. *Hydrobiologia* 465:7-19.
- Avendaño, M., Cantillán, M., Le Penec, M., Lodeiros, C. & Freitas, L. 2001. Cultivo de pectínidos Iberoamericanos en suspensión. In: A.N. Maeda-Martínez (ed.). *Los moluscos pectínidos de Iberoamérica: ciencia y acuicultura*, Editorial Limusa, México, pp. 193-211.
- Bacon, G.S., MacDonald, B.A., & Ward, J.E. 1998. Physiological responses of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicus*) bivalves to variations in the concentration and quality of suspended particles I. Feeding activity and selection. *Journal of Experimental Marine Biology and Ecology* 219:105-125.
- Baird, R.H. & Gibson, F.A. 1956. Underwater observations on scallop (*Pecten maximus* L.) beds. *Journal of the Marine Biological Association of the United Kingdom* 35:555-562.
- Barbeau, M.A., Hatcher, B.G., Scheibling, R.E., Hennigar, A.W., Taylor, L.H. & Risk, A.C. 1996. Dynamics of juvenile sea scallop (*Placopecten magellanicus*) and their predators in bottom seeding trials in Lunenburg Bay, Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2494-2512.
- Barker Jørgensen, C. 1990. Bivalve filter feeding: Hydrodynamics, bioenergetics, physiology and ecology. Olsen & Olsen, Fredensborg, Denmark, 140 pp.
- Bayne, B.L. (ed.) 1976. *Marine mussels: their ecology and physiology*. Cambridge University Press, 506 pp.
- Bayne, B.L. 1998. The physiology of suspension feeding by bivalve molluscs: an introduction to the Plymouth "TROPHEE" workshop. *Journal of Experimental Marine Biology and Ecology* 219:1-19.
- Bayne, B.L., Thompson, R.J. & Widdows, J. 1976. Physiology: I. In: Bayne, B.L. (ed.). *Marine mussels: their ecology and physiology*. Cambridge University Press, pp. 121-206.
- Beaumont, A.R. & Budd, M.D. 1982. Delayed growth of mussel (*Mytilus edulis*) and scallop (*Pecten maximus*) veligers at low temperature. *Marine Biology* 71:97-100.
- Beninger, P.G. & Decottignies, P. 2005. What makes diatoms attractive for suspensivores? The organic casing and associated organic molecules of *Coscinodiscus perforatus* are quality cues for the bivalve *Pecten maximus*. *Journal of Plankton Research* 27:11-17.
- Beninger, P.G., Decottignies, P. & Rincé, Y. 2004. Localization of qualitative particle selection sites in the heterorhabdic filibranch *Pecten maximus* (Bivalvia: Pectinidae). *Marine Ecology Progress Series* 275:163-173.
- Beninger, P.G., Dwiono, S.A.P. & Le Penec, M. 1994. Early development of the gill and implications for feeding in *Pecten maximus* (Bivalvia: Pectinidae). *Marine Biology* 119:405-412.
- Beninger, P.G. & Le Penec, M. 1991. Functional anatomy of scallops. In: Shumway, S.E. (ed). *Scallops: biology, ecology and aquaculture*. Elsevier, Amsterdam, pp. 133-223.
- Berger, V.J. & Kharazova, A.D. 1997. Mechanisms of salinity adaptations in marine molluscs. *Hydrobiologia* 355:115-126.
- Bergh, Ø. & Strand, Ø. 2001. Great scallop, *Pecten maximus*, research and culture strategies in Norway: a review. *Aquaculture International* 9:305-318.
- Bergman, C., Parsons, J. & Couturier, C. 1996. Tolerance of the giant sea scallop, *Placopecten magellanicus*, to low salinity. *Bulletin of the Aquaculture Association Canada* 96-3:62-64.

- Beukers-Stewart, B.D., Mosley, M.W.J. & Brand, A.R. 2003. Population dynamics and predictions in the Isle of Man fishery for the great scallop (*Pecten maximus*, L.). ICES Journal of Marine Science 60:224-242.
- Bourne, N.F. 2000. The potential for scallop culture – the next millenium. Aquaculture International 8:113-122.
- Bourne, N. & Hodgson, C.A. 1991. Development of a viable nursery system for scallop culture. In: Shumway, S.E. and Sandifer, P.A (eds.). An international compendium of scallop biology and culture. Selected Papers from the 7<sup>th</sup> International Pectinid Workshop, The World Aquaculture Society, USA, pp. 273-280.
- Bourne, N., Hodgson, C.A. & Whyte, J.N.C. 1989. A manual for scallop culture in British Columbia, Canadian Technical Report of Fisheries and Aquatic Sciences No. 1694, 215 pp.
- Brand, A.R. 1991. Scallop ecology: distribution and behaviour. In: Shumway, S.E. (ed). Scallops: biology, ecology and aquaculture. Elsevier, Amsterdam, pp. 517-584.
- Brand, A.R. & Roberts, D. 1973. The cardiac responses of the scallop *Pecten maximus* (L.) to respiratory stress. Journal of Experimental Marine Biology and Ecology 13:29-43.
- Bricelj, V.M. & Shumway, S. 1991. Energy acquisition and utilization. In: Shumway, S.E. (ed). Scallops: biology, ecology and aquaculture. Elsevier, Amsterdam, pp. 305-346.
- Brillant, M.G.S. & MacDonald, B.A. 2000. Postingestive selection in the sea scallop, *Placopecten magellanicus* (Gmelin): the role of particle size and density. Journal of Experimental Marine Biology and Ecology 253:211-227.
- Brillant, M.G.S. & MacDonald, B.A. 2002. Postingestive selection in the sea scallop (*Placopecten magellanicus*) on the basis of chemical properties of particles. Marine Biology 141:457-465.
- Brillant, M.G.S. & MacDonald, B.A. 2003. Postingestive sorting of living and heat killed *Chlorella* within the sea scallop, *Placopecten magellanicus* (Gmelin). Journal of Experimental Marine Biology and Ecology 290:81-91.
- Brown, C. & Day, R.L. 2002. The future of stock enhancements: lessons for hatchery practice from conservation biology. Fish and Fisheries 3:79-94.
- Brun, N.T., Bricelj, V.M., Egbosimba, E.E., MacRae, T.H. & Ross, N.W. 2003. Stress responses in scallops and hard clams to heat and cold shock. Journal of Shellfish Research 22:321.
- Buestel, D., Cochard, J.-C., Dao, J.-C. & Gérard, A. 1982. Production artificielle de naissain de coquilles Saint-Jacques *Pecten maximus* (L.). Premier résultats en rade de Brest. Vie Marine 4:24-28.
- Bull, M.F. 1994. Enhancement and management of New Zealand's "southern scallop" fishery. In: Bourne, N.F., Bunting, B.L. & Townsend, L.D. (eds.). Proceedings of the 9th International Pectinid Workshop, Nanaimo, B.C., Canada, April 22-27, 1993. Volume 2. Canadian Technical Report of Fisheries and Aquatic Sciences 1994, pp. 131-136.
- Cahalan, J.A., Siddall, S.E. & Luckenbach, M.W. 1989. Effects of flow velocity, food concentration and particle flux on growth rates of juvenile bay scallops *Argopecten irradians*. Journal of Experimental Marine Biology and Ecology 129:45-60.
- Castagna, M. & Chanley, P. 1973. Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginia waters on the western mid-Atlantic coast. Malacologia 12:47-96.
- Chanley, P.E. 1958. Survival of some juvenile bivalves in water of low salinity. Proceedings of the National Shellfisheries Association 48:52-65.
- Chauvaud, L., Donval, A., Thouzeau, G., Paulet, Y.-M. & Nézan, E. 2001. Variations in food intake of *Pecten maximus* (L.) from the Bay of Brest (France): Influence of environmental factors and phytoplankton species composition. Comptes Rendus de

- l'Academie des Sciences, Serie III. Sciences de la Vie/Life Sciences 324:743-755.
- Chauvaud, L., Thouzeau, G. & Grall, J. 1996. Experimental collection of great scallop postlarvae and other benthic species in the Bay of Brest: settlement patterns in relation to spatio-temporal variability of environmental factors. *Aquaculture International* 4:263-288.
- Chauvaud, L., Thouzeau, G. & Paulet, Y.-M. 1998. Effects of environmental factors on the daily growth rate of *Pecten maximus* juveniles in the Bay of Brest (France). *Journal of Experimental Marine Biology and Ecology* 227:83-111.
- Christoffersen, G. 2000. Effects of air emersion on survival and growth of hatchery reared great scallop spat. *Aquaculture International* 8:158-168.
- Christoffersen, G. & Lie, Ø. 2003. Nursery growth, survival and chemical composition of great scallop *Pecten maximus* (L.) spat from different larval settlement groups. *Aquaculture Research* 34:641-651.
- Christoffersen, G. & Magnesen, T. 2001. Effects of deployment time and acclimation on survival and growth of hatchery-reared scallop (*Pecten maximus*) spat transferred to the sea. *Journal of Shellfish Research* 20:1043-1050.
- Christoffersen, G. & Strand, Ø. 2003. Effect of reduced salinity on the great scallop (*Pecten maximus*) spat at two rearing temperatures. *Aquaculture* 215:79-92.
- Claus, C. 1981. Trends in nursery rearing of bivalve molluscs. In: Claus, C., De Pauw, N. & Jaspers, E. (eds.). *Nursery culturing of bivalve molluscs*. European Mariculture Society Special Publication No. 7, Bredene, Belgium pp.1-33.
- Cliche, G. & Giguère, M. 1998. Final report of the research program on scallop culture and restocking (REPERE), 1990-1997. *Canadian Industry Report of Fisheries and Aquatic Sciences* 247, 74 pp.
- Côté, J., Himmelman, J.H. & Claereboudt, M.R. 1994. Separating effects of limited food and space on growth of the giant scallop *Placopecten magellanicus* in suspended culture. *Marine Ecology Progress Series* 106:85-91.
- Couturier, C., Dabinett, P. & Lanteigne, M. 1995. Scallop culture in Atlantic Canada. In: Boghen, A.D. (ed.). *Cold-Water Aquaculture in Atlantic Canada*. The Canadian Institute for Research on Regional Development, Canada, pp. 297-340.
- Coutteau, P., Castell, J.D., Ackman, R.G. & Sorgeloos, P. 1996. The use of lipid emulsions as carriers for essential fatty acids in bivalves: a test case with juvenile *Placopecten magellanicus*. *Journal of Shellfish Research* 15:259-264.
- Cragg, S.M. & Crisp, D.J. 1991. The biology of scallop larvae. In: Shumway, S.E. (ed). *Scallops: biology, ecology and aquaculture*. Elsevier, Amsterdam, pp. 75-132.
- Cranford, P.J. 1995. Relationships between food quantity and quality and absorption efficiency in sea scallops *Placopecten magellanicus* (Gmelin). *Journal of Experimental Marine Biology and Ecology* 189:123-142.
- Dadswell, M.J. 2001. A review of the status of sea scallop (*Placopecten magellanicus*) aquaculture in Atlantic Canada in the year 2000. *Aquaculture Association of Canada Special Publication Number 4*, pp. 72-75.
- Dakin, W.J. 1909. *Pecten*. The edible scallop. *Liverpool Marine Biology Committee Memoirs* No 17. *Proceedings and transactions of the Liverpool Biological Society* 23:333-468 and plate I-IX.
- Dao, J-C., Fleury, P-G. & Barret, J. 1999. Scallop sea bed culture in Europe. In: Howell, B.R., Moksness, E. & Svåsand, T. (eds.). *Stock enhancement and sea ranching*. Fishing News Books, Blackwell Science, Oxford, UK, pp. 423-436.
- Davenport, J. Gruffyd, L.I.D. & Beaumont, A.R. 1975. An apparatus to supply water of fluctuating salinity and its use in a study of the salinity tolerances of larvae of the scallop *Pecten maximus* L. *Journal of the Marine Biological Association of the United*

- Kingdom 55:391-409.
- Delaunay, F., Marty, Y., Moal, J. & Samain, J.-F. 1992. Growth and lipid class composition of *Pecten maximus* (L.) larvae grown under hatchery conditions. *Journal of Experimental Marine Biology and Ecology* 163:209-219.
- Deming, C.J. & Russell, M.P. 1999. Assessing manipulations of larval density and culling in hatchery production of the hard clam, *Mercenaria mercenaria*. *Journal of Shellfish Research* 18:99-105.
- de Pauw, N. 1981. Use and production of microalgae as food for nursery bivalves. In: Claus, C., De Pauw, N., Jaspers, E. (eds.). *Nursery culturing of bivalve molluscs*. European Mariculture Society Special Publication No. 7, Bredene, Belgium, pp. 35-69.
- Dickie, L.M. 1958. Effects of high temperature on survival of the giant scallop. *Journal of the Fisheries Research Board of Canada* 15:1189-1211.
- Dickie, L.M. & Medcof, J.C. 1963. Causes of mass mortalities of scallops (*Placopecten magellanicus*) in the Southwestern Gulf of St. Lawrence. *Journal of the Fisheries Research Board of Canada* 20:451-482.
- Dredge, M.C.L. 1997. Survival of saucer scallop, *Amusium japonicum balloti*, as a function of exposure time. *Journal of Shellfish Research* 16:63-66.
- Drummond, K. 2004. The role of stock enhancement in the management framework for New Zealand's southern scallop fishery. In: Leber, K.M., Kitada, S., Blankenship, H.L. & Svåsand, T. (eds.). *Stock enhancement and sea ranching. Developments, pitfalls and opportunities*. Blackwell Publishing Ltd., Oxford, UK, pp. 397-411.
- Dufour, S.C. & Beninger, P.G. 2001. A functional interpretation of cilia and mucocyte distributions on the abfrontal surface of bivalve gills. *Marine Biology* 138:295-309.
- Duinker, A. 2002. Processes related to reproduction in great scallops (*Pecten maximus* L.) from Western Norway. Dr. scient. thesis, University of Bergen, Norway, 43 pp.
- Duncan, P., Spicer, J.I., Taylor, A.C. & Spencer Davies, P. 1994. Acid-base disturbances accompanying emersion in the scallop *Pecten maximus* (L.). *Journal of Experimental Marine Biology and Ecology* 182:15-25.
- FAO 2001. Food and Agriculture Organization of the United Nations. FAOSTAT fisheries database <http://apps.fao.org/page/collections?subset=fisheries>, Rome, Italy.
- FAO 2002. The state of World fisheries and Aquaculture, part 1, Rome, Italy, 52 pp.
- Fariás, A., Uriarte, I. & Castilla, J.C. 1998. A biochemical study of the larval and postlarval stages of the Chilean scallop *Argopecten purpuratus*. *Aquaculture* 166:37-47.
- Fleury, P.G. & Dao, J.C. 1992. De la pêche à l'aquaculture: l'élevage de la coquille Saint-Jacques. *Equinoxe* 38:20-27.
- Fleury, P.-G., Mingant, C. & Castillo, A. 1996. A preliminary study of the behaviour and vitality of reseeded juvenile great scallops, of three sizes in three seasons. *Aquaculture International* 4:325-337.
- Frenette, B. & Parsons, G.J. 2001. Salinity-temperature tolerance of juvenile giant scallops, *Placopecten magellanicus*. *Aquaculture Association of Canada Special Publication Number 4*, pp. 76-78.
- Frenette, B., Parsons, G.J. & Davidson, L.-A. 2001. Growth and survival of giant sea scallops, *Placopecten magellanicus* in shallow water embayments of Southeastern New Brunswick. *Aquaculture Association of Canada Special Publication Number 4*, pp. 79-81.
- Frenette, B., Parsons, G.J. & Davidson, L.-A. 2002. Influence of salinity and temperature on clearance rate and oxygen consumption of juvenile sea scallops *Placopecten magellanicus* (Gmelin). *Aquaculture Association of Canada Special Publication Number 5*, pp. 17-19.
- Gaarder, T. & Bjerkan, P. 1934. Østers og østerskultur i Norge. John Griegs Boktrykkeri,

- Bergen (in Norwegian), 96 pp.
- Gaarder, T. & Spärck, R. 1932. Hydrographische-biochemische untersuchungen in Norwegischen austern-pollen. Bergens Museums Årbok 1932, Naturvid. Rekke No. 1, 144 pp.
- Gerard, A., Salaun, M. & Tritar, S. 1989. Critères de compétence des larves à la métamorphose chez *Pecten maximus*. *Haliotis* 19:373-380.
- Gosling, E. 2003. Bivalve molluscs. Biology, ecology and culture. Fishing News Books, Blackwell Publishing, Oxford, UK, 443 pp.
- Gould, S.J. 1971. Muscular mechanics and the ontogeny of swimming in scallops. *Palaeontology* 14:61-94.
- Gould, E. & Fowler, B.A. 1991. Scallops and pollution. In: Shumway, S.E. (ed). *Scallops: biology, ecology and aquaculture*. Elsevier, Amsterdam, pp. 495-515.
- Grecian, L.A., Parsons, G.J., Dabinett, P. & Couturier, C. 2000. Influence of season, initial size, depth, gear type and stocking density on the growth rates and recovery of sea scallop, *Placopecten magellanicus*, on a farm-based nursery. *Aquaculture International* 8:183-206.
- Grecian, L.A., Parsons, G.J., Dabinett, P. & Couturier, C. 2003. Effect of deployment date and environmental conditions on the growth rate and retrieval of hatchery-reared sea scallops, *Placopecten magellanicus* (Gmelin, 1791), at a sea-based nursery. *Journal of Shellfish Research* 22:101-109.
- Gruffyd, L.I.D. & Beaumont, A.R. 1972. A method for rearing of *Pecten maximus* in the laboratory. *Marine Biology* 15:350-355.
- Guo, X., Ford, S.E. & Zhang, F. 1999. Molluscan aquaculture in China. *Journal of Shellfish Research* 18:19-31.
- Hadley, N.H., Baldwin, R.B., Devoe, M.R. & Rhodes, R. 1999. Performance of a tidal-powered upwelling nursery system for northern quahogs (*Mercenaria mercenaria*) in South Carolina. *Journal of Shellfish Research* 18:555-560.
- Hardy, D. 1991. *Scallop farming*. Fishing News Books, Oxford, England, 237 pp.
- Hawkins, A.J.S., Bayne, B.L., Bougrier, S., Héral, M., Iglesias, J.I.P., Navarro, E., Smith, R.F.M. & Urrutia, M.B. 1998. Some general relationships in comparing the feeding physiology of suspension-feeding bivalve molluscs. *Journal of Experimental Marine Biology and Ecology* 219:87-103.
- Hawkins, A.J.S., Fang, J.G., Pascoe, P.L., Zhang, J.H., Zhang, X.L. & Zhu, M.Y. 2001. Modelling short-term responsive adjustments in particle clearance rate among bivalve suspension-feeders: separate unimodal effects of seston volume and composition in the scallop *Chlamys farreri*. *Journal of Experimental Marine Biology and Ecology* 262:61-73.
- Heasman, M.P., O'Connor, W.A. & Frazer, A.W. 1994a. Detachment of commercial scallop *Pecten fumatus*, spat from settlement substrates. *Aquaculture* 123:401-407.
- Heasman, M.P., O'Connor, W.A. and Frazer, A.W. 1994b. Improved hatchery and nursery rearing techniques for *Pecten fumatus* Reeve. *Memoirs of the Queensland Museum* 36:351-356.
- Heasman, M.P., O'Connor, W.A. & Frazer, A.W.J. 1996. Ontogenetic changes in optimal rearing temperatures for the commercial scallop, *Pecten fumatus* Reeve. *Journal of Shellfish Research* 15:627-634.
- Heasman, M.P., O'Connor, W.A., Frazer, A.W., Languet, Y & O'Connor, S.J. 2002. Alternative means of nursery culture for commercial scallop (*Pecten fumatus* Reeve) spat. *Aquaculture* 213:323-338.
- Hilbish, T.J., Winn, E.P & Rawson, P.D. 1993. Genetic variation and covariation during larval and juvenile growth in *Mercenaria mercenaria*. *Marine Biology* 115: 97-104.

- Hishamunda, N. & Ridler, N.B. 2002. Macro policies to promote sustainable commercial aquaculture. *Aquaculture International* 10:491-505.
- Holmes, S. 1979. Henderson's dictionary of biological terms, ninth edition. Longman, London, Great Britain, 510 pp.
- Høisæter, T. 1986. An annotated check-list of marine molluscs of the Norwegian coast and adjacent water. *Sarsia* 71:73-145.
- Jørgensen, C.B. 1996. Bivalve filter feeding revisited. *Marine Ecology Progress Series* 142:287-302.
- Karney, R.C. 1991. Ten years of scallop culture on Martha's Vineyard. In: Shumway, S.E. & Sandifer, P.A (eds.). An international compendium of scallop biology and culture. Selected Papers from the 7<sup>th</sup> International Pectinid Workshop, The World Aquaculture Society, USA, pp. 308-312.
- Kean-Howie, J.C., O'Dor, R.K. & Scarrat, D.J. 1995. Evolution of feeding strategies throughout the life histories of bivalve molluscs, with emphasis on ontogeny and phylogeny. *ICES Marine Science Symposia* 199:5-12.
- Kinne, O. 1963. The effects of temperature and salinity on marine and brackish water animals. I. Temperature. *Oceanography and Marine Biology: an Annual Review* 1:301-340.
- Kinne, O. 1964. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature salinity combinations. *Oceanography and Marine Biology: an Annual Review* 2:281-339.
- Kirby-Smith, W.W. & Barber, R.T. 1974. Suspension-feeding aquaculture systems: effects of phytoplankton concentration and temperature on growth of the bay scallop. *Aquaculture* 3:135-145.
- Kleinman, S., Hatcher, B.G., Scheibling, R.E., Taylor, L.H. & Hennigar, A.W. 1996. Shell and tissue growth of juvenile sea scallops (*Placopecten magellanicus*) in suspended and bottom culture in Lunenburg bay, Nova Scotia. *Aquaculture* 142:75-97.
- Lafrance, M., Cliche, G., Haugum, G.A. & Guderley, H. 2003. Comparison of cultured and wild sea scallops *Placopecten magellanicus*, using behavioral responses and morphometric and biochemical indices. *Marine Ecology Progress Series* 250:183-195.
- Lafrance, M., Guderley, H. & Cliche, G. 2002. Low temperature, but not air exposure slows the recuperation of juvenile scallops, *Placopecten magellanicus*, from exhausting escape responses. *Journal of Shellfish Research* 21:605-618.
- Laing, I., 2000. Effect of temperature and ration on growth and condition of king scallop (*Pecten maximus*) spat. *Aquaculture* 183:325-334.
- Laing, I. 2002. Effect of salinity on growth and survival of king scallop spat (*Pecten maximus*). *Aquaculture* 205:171-181.
- Laing, I., 2004. Filtration of king scallops (*Pecten maximus*). *Aquaculture* 240:369-384.
- Laing, I., Millican, P.F. & Earl, N.H. 1999. Effect of sampling frequency on growth and survival of juvenile scallops (*Pecten maximus*). In: Strand, Ø. (ed.). Book of abstracts, 12<sup>th</sup> International Pectinid Workshop, Bergen, Norway, pp. 47-48.
- Laing, I. & Psimopoulous, A. 1998. Hatchery cultivation of king scallop (*Pecten maximus*) spat with cultured and bloomed algal diets. *Aquaculture* 169:55-68.
- Larsen, A., Flaten, G.A.F., Sandaa, R.-A., Castberg, T., Thyraug, R. Erga, S.R., Jacquet, S. & Bratbak, G. 2004. Spring phytoplankton bloom dynamics in Norwegian coastal waters: Microbial community succession and diversity. *Limnology and Oceanography* 49:180-190.
- Larsen P.F. & Lee, R.M. 1978. Observations on the abundance, distribution and growth of postlarval sea scallops, *Placopecten magellanicus* on Georges Bank. *The Nautilus* 92:112-116.



- Le Borgne, Y. 1981. Nursery culturing of postlarvae key to further development for bivalve molluscs hatcheries. In: Claus, C., De Pauw, N. & Jaspers, E. (eds.). Nursery culturing of bivalve molluscs. European Mariculture Society Special Publication No. 7, Bredene, Belgium, pp. 141-149.
- Le Pennec, M., Paugam, A. & Le Pennec, G. 2003. The pelagic life of the *Pecten maximus* – a review. ICES Journal of Marine Science 60:211-223.
- Levinton, J.S., Ward, J.E. & Thompson, R.J. 1996. Biodynamics of particle processing in bivalve molluscs: models, data, and future directions. Invertebrate Biology 115:232-242.
- Levy, L., Parsons, G.J. & Dabinett, P. 1998. Effect of deployment date and environmental conditions at a farm-based nursery on growth and recovery of hatchery-reared sea scallops (*Placopecten magellanicus*). Bulletin of the Aquaculture Association Canada 98-2:73-75.
- Lewis, D.E. & Cerrato, R.M. 1997. Growth uncoupling and the relationship between shell growth and metabolism in the soft shell clam *Mya arenaria*. Marine Ecology Progress Series 158:177-189.
- Liang, Y. 1996. The study on the feasible transport environmental condition for bay scallop juvenile. Marine Environmental Science/Haiyang Huanjing Kexue 15:44-50 (In Chinese with summary in English).
- Lodeiros, C.J. & Himmelman, J.H. 1994. Relations among environmental conditions and growth in the tropical scallop *Euvola (Pecten) ziczac* (L.) in suspended culture in the Golfo de Cariaco, Venezuela. Aquaculture 119:345-358.
- Lodeiros, C.J. & Himmelman, J.H. 2000. Identification of factors affecting growth and survival of the tropical scallop *Euvola (Pecten) ziczac* (L.) in suspended culture in the Golfo de Cariaco, Venezuela. Aquaculture 182:91-114.
- Lodeiros, C., Maeda-Martínez, L.F., Freitas, L., Uribe, E., Lluch-Cota, D.B. & Sicard, M.T. 2001. Ecofisiología de pectínidos Iberoamericanos. In: A.N. Maeda-Martínez (ed.). Los moluscos pectínidos de Iberoamérica: ciencia y acuicultura, Editorial Limusa, México, pp. 77-88.
- Lodeiros, C., Rengel, J.J., Freitas, L., Morales, F. & Himmelman, J.H. 1998. Growth and survival of the tropical scallop *Lyropecten (Nodipecten) nodosus* maintained in suspended culture at three depths. Aquaculture 165:41-50.
- Loosanoff, V.L. & Davis, H.C. 1963. Rearing of bivalve mollusks. Advances in Marine Biology 1:1-136.
- Lorrain, A., Paulet, Y.-M., Chauvaud, L., Savoye, N., Nézan, E. and Guérin, L. 2000. Growth anomalies in *Pecten maximus* from coastal waters (Bay of Brest, France): relationship with diatom blooms. Journal of the Marine Biological Association of the United Kingdom 80:667-673.
- Lu, Y.T. & Blake, N.J. 1996. Optimum concentrations of *Isochrysis galbana* for growth of larval and juvenile bay scallops, *Argopecten irradians concentricus* (Say). Journal of Shellfish Research 15:635-643.
- Lu, Y.T. & Blake, N.J. 1997a. Clearance and ingestion rates of *Isochrysis galbana* by larval and juvenile bay scallops, *Argopecten irradians concentricus* (Say). Journal of Shellfish Research 16:47-54.
- Lu, Y.T. & Blake, N.J. 1997b. The culture of the southern bay scallop in Tampa Bay, an urban Florida estuary. Aquaculture International 5:439-450.
- Lu, Y.T., Blake, N.J. & Torres, J.J. 1999a. Oxygen consumption and ammonia excretion of larvae and juveniles of the bay scallop, *Argopecten irradians concentricus* (Say). Journal of Shellfish Research 18:419-423.
- Lu, Y.T., Blake, N.J. & Torres, J.J. 1999b. Biochemical utilization during embryogenesis and

- metamorphosis in the bay scallop, *Argopecten irradians concentricus* (Say). *Journal of Shellfish Research* 18:425-429.
- MacDonald, B.A., Bacon, G.S. & Ward, J.E. 1998. Physiological responses of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicus*) bivalves to variations in the concentration and quality of suspended particles II. Absorption efficiency and scope for growth. *Journal of Experimental Marine Biology and Ecology* 219:127-141.
- Maeda-Martínez, A.N., Sicard, M.T. & Reynoso-Granados, T. 2000. A shipment method for scallop seed. *Journal of Shellfish Research* 19:765-770.
- Magnesen, T. & Christophersen, G. 2003. Improving the Quality of Scallops to Ensure a Viable Aquaculture Production (SCALQUAL) [EU CRAFT project no. Q5CR 2000-70310]. In: Book of Abstracts, 14<sup>th</sup> International Pectinid Workshop, St. Petersburg, Florida, USA, pp. 50-51.
- Maguire, J.A. 1998. Aspects of the biology of cultured scallops (*Pecten maximus* L.) with particular reference to stress. Ph.D. thesis, National University of Ireland, 152 pp.
- Maguire, J.A., Cashmore, D. & Burnell, G.M. 1999a. The effect of transportation on the juvenile scallop *Pecten maximus* (L.). *Aquaculture Research* 30:325-333.
- Maguire, J.A., Fleury, P.G. & Burnell, G.M. 1999b. Some methods for quantifying quality in the scallop *Pecten maximus* (L.). *Journal of Shellfish Research* 18:59-66.
- Maguire, J.A., O'Connor, D.A. & Burnell, G.M. 1999c. An investigation into behavioural indicators of stress in juvenile scallops. *Aquaculture International* 7:169-177.
- Mann, R. 1984. On the selection of aquaculture species: a case study of marine molluscs. *Aquaculture* 39:345-353.
- Manzi, J.J., Hadley, N.H. & Maddox, M.B. 1986. Seed clam, *Mercenaria mercenaria*, culture in an experimental-scale upflow nursery system. *Aquaculture* 54:301-311.
- Martínez, G., Caceres, L.A., Uribe, E. & Diaz, M.A. 1995. Effects of different feeding regimens on larval growth and the energy budget of juvenile Chilean scallops, *Argopecten purpuratus* Lamarck. *Aquaculture* 132:313-323.
- Martínez, G., Torres, M., Uribe, E., Diaz, M.A. & Pérez, H. 1992. Biochemical composition of broodstock and early juvenile Chilean scallops, *Argopecten purpuratus* Lamarck, held in two different environments. *Journal of Shellfish Research* 11:307-313.
- Mason, C.J., Reid, D.D. & Nell, J.A. 1998. Growth characteristics of Sydney rock oysters *Saccostrea commercialis* in relation to size and temperature. *Journal of Experimental Marine Biology and Ecology* 227:155-168.
- Mason, J. 1957. The age and growth of the scallop, *Pecten maximus* (L.), in Manx waters. *Journal of the Marine Biological Association of the United Kingdom* 36:473-492.
- Mason, J. 1958. The breeding of the scallop, *Pecten maximus* (L.), in Manx waters. *Journal of the Marine Biological Association of the United Kingdom* 37:653-671.
- McGarvey, R., Serchuk, F.M. & McLaren, I.A. 1992. Statistics of reproduction and early life history survival of the Georges Bank sea scallop (*Placopecten magellanicus*) population. *Journal of North West Atlantic Fishery Science* 13:83-99.
- Mercaldo, R.S. & Rhodes, E.W. 1982. Influence of reduced salinity on the Atlantic bay scallop *Argopecten irradians* (Lamarck) at various temperatures. *Journal of Shellfish Research* 2:177-181.
- Merino, G., Cortés-Monroy, J., Abarca, A. & Barraza, J. 2001. Diseño y operación de sistemas de cultivo. In: A.N. Maeda-Martínez (ed.). *Los moluscos pectínidos de Iberoamérica: ciencia y acuicultura*, Editorial Limusa, México, pp. 375-404.
- Milke, L.M., Bricelj, V.M. & Parrish, C.C. 2004. Growth of postlarval sea scallops, *Placopecten magellanicus*, on microalgal diets, with emphasis on the nutritional role of lipids and fatty acids. *Aquaculture* 234:293-317.
- Milke, L.M. & Ward, J.E. 2003. Influence of diet on pre-ingestive particle processing in

- bivalves II. Residence time in the pallial cavity and handling time on the labial palps. *Journal of Experimental Marine Biology and Ecology* 293:151-172.
- Millican, P.F. 1997. The hatchery rearing of king scallop (*Pecten maximus*). The Centre for Environment, Fisheries & Aquaculture Science, Lowestoft, UK, 40 pp.
- Minchin, D. 1992. Biological observations on young scallops, *Pecten maximus*, *Journal of the Marine Biological Association of the United Kingdom* 72:807-819.
- Minchin, D. 2003. Introductions: some biological and ecological characteristics of scallops. *Aquatic Living Resources* 16:521-532.
- Minchin, D., Haugum, G.A., Skjæggestad, H. & Strand, Ø. 2000. Effect of air exposure on scallop behaviour, and the implications for subsequent survival in culture. *Aquaculture International* 8:169-182.
- Møhlenberg, F. & Riisgård, H.U. 1978. Efficiency of particle retention in 13 species of suspension feeding bivalves. *Ophelia* 17:239-246.
- Navarro, J.M. & Gonzalez, C.M. 1998. Physiological responses of the Chilean scallop *Argopecten purpuratus* to decreasing salinities. *Aquaculture* 167:315-327.
- Naylor, R.L., Goldberg, R.J., Primavera, J.H., Kautsky, N., Beveridge, M.C.M., Clay, J., Folke, C., Lubchenco, J., Mooney, H. & Troell, M. 2000. Effect of aquaculture on world fish supplies. *Nature* 405:1017-1024.
- Newkirk, G.F. 1981. On the unpredictability of bivalve growth rates: is a slow growing juvenile oyster a runt for life? In: Nursery culturing of bivalve molluscs. Claus, C., De Pauw, N & Jaspers, E. (eds.). European Mariculture Society Special Publication No. 7. Bredene, Belgium, pp. 211-218.
- Newkirk, G.F. & Haley, L.E. 1982. Phenotypic analysis of the European oyster *Ostrea edulis* L.: Relationship between length of larval period and postsetting growth rate. *Journal of Experimental Marine Biology and Ecology* 59:177-184.
- Nicolas, L. & Robert, R. 2001. The effect of food supply on metamorphosis and post-larval development in hatchery-reared *Pecten maximus*. *Aquaculture* 192:347-359.
- O'Connor, W.A. & Heasman, M.P. 1998. Ontogenetic changes in salinity and temperature tolerance in the doughboy scallop, *Mimachlamys asperrima*. *Journal of Shellfish Research* 17:89-95.
- Ó Foighil, D., Kingzett, B., Ó Foighil, G. & Bourne, N. 1990. Growth and survival of juvenile japanese scallops, *Patinopecten yessoensis*, in nursery culture. *Journal of Shellfish Research* 9:135-144.
- Orensanz, J.M., Parma, A.M. & Iribarne, O.O. 1991. Population dynamics and management of natural stocks. In: Shumway, S.E. (ed). *Scallops: biology, ecology and aquaculture*. Elsevier, Amsterdam, pp. 625-713.
- Palmer, R.E. & Williams, L.G. 1980. Effect of particle concentration on filtration efficiency of the bay scallop *Argopecten irradians* and the oyster *Crassostrea virginica*. *Ophelia* 19:163-174.
- Parrish, C.C., McKenzie, C.H., MacDonald, B.A. & Hatfield, E.A. 1995. Seasonal studies of seston lipids in relation to microplankton species composition and scallop growth in South Broad Cove, Newfoundland. *Marine Ecology Progress Series* 129:151-164.
- Parrish, C.C., Wells, J.S., Yang, Z. & Dabinett, P. 1999. Growth and lipid composition of scallop juveniles, *Placopecten magellanicus*, fed the flagellate *Isochrysis galbana* with varying lipid composition and the diatom *Chaetoceros muelleri*. *Marine Biology* 133:461-471.
- Paul, J.D. 1980a. Upper temperature tolerance and the effects of temperature on byssus attachment in the Queen scallop, *Chlamys opercularis* (L.). *Journal of Experimental Marine Biology and Ecology* 46:41-50.
- Paul, J.D. 1980b. Salinity-temperature relationships in the Queen scallop *Chlamys*

- opercularis*. Marine Biology 56:295-300.
- Paul, J.D., Brand, A.R. & Hoogesteger, J.N. 1981. Experimental cultivation of the scallops *Chlamys opercularis* (L.) and *Pecten maximus* (L.) using naturally produced spat. Aquaculture 24:31-44.
- Paulet, Y.M., Lucas, A. & Gerard, A. 1988. Reproduction and larval development in two *Pecten maximus* (L.) populations from Brittany. Journal of Experimental Marine Biology and Ecology 119:145-156.
- Pazos, A.J., Román, G., Acosta, C.P., Abad, M. & Sánchez, J.L. 1997. Seasonal changes in condition and biochemical composition of the scallop *Pecten maximus* L. from suspended culture in the Ria de Arousa (Galicia, N.W. Spain) in relation to environmental conditions. Journal of Experimental Marine Biology and Ecology 211:169-193.
- Peña, J.B. 2001. Taxonomía, morfología, distribución y hábitat de los pectínidos Iberoamericanos. In: A.N. Maeda-Martínez (ed.). Los moluscos pectínidos de Iberoamérica: ciencia y acuicultura, Editorial Limusa, México, pp. 1-25.
- Pfeiffer, T.J. & Rusch, K.A. 2000. An integrated system for microalgal and nursery seed clam culture. Aquacultural Engineering 24:15-31.
- Pilditch, C.A. & J. Grant. 1999. Effect of temperature fluctuations and food supply on the growth and metabolism of juvenile sea scallops (*Placopecten magellanicus*). Marine Biology 134:235-248.
- Pit, J.H. & Southgate, P.C. 2000. When should pearl oyster, *Pinctada margaritifera* (L.), spat be transferred from the hatchery to the ocean? Aquaculture Research 31:773-778.
- Pit, J.H. & Southgate, P.C. 2003. Should slow growing pearl oyster (*Pinctada margaritifera*) spat ("runts") be discarded? Journal of Shellfish Research 22:773-775.
- Reid, R.G.B., McMahon, R.F., Ó Foighil, D. & Finnigan, R. 1992. Anterior inhalant currents and pedal feeding in bivalves. The Veliger 35:93-104.
- Reimer, O. & Harms-Ringdahl, S. 2001. Predator-inducible changes in blue mussels from predator-free Baltic Sea. Marine Biology 139:959-965.
- Reitan, K.I., Øie, G., Vadstein, O. & Reinertsen, H. 2002. Response on scallop culture to enhanced nutrient supply by experimental fertilisation of a landlocked bay. Hydrobiologia 484:111-120.
- Rhodes, E.W., Goldberg, R. & Widman, J.C. 1981. The role of raceways in mariculture systems for the bay scallop, *Argopecten irradians irradians*, and the surf clam, *Spisula solidissima*. In: Nursery culturing of bivalve molluscs. Claus, C., De Pauw, N & Jaspers, E. (eds.). European Mariculture Society Special Publication No. 7. Bredene, Belgium, pp. 227-251.
- Riisgård, H.U. 1988. Efficiency of particle retention and filtration rate in 6 species of Northeast American bivalves. Marine Ecology Progress Series 45:217-223.
- Riisgård, H.U. & Larsen, P.S. 2000. Comparative ecophysiology of active zoobenthic filter feeding, essence of current knowledge. Journal of Sea Research 44:169-193.
- Robert, R. & Gérard, A. 1999. Bivalve hatchery technology: The current situation for the pacific oyster *Crassostrea gigas* and the scallop *Pecten maximus* in France. Aquatic Living Resources 12:121-130.
- Robert, R. & Nicolas, L. 2000. The effect of seawater flow and temperature on metamorphosis and postlarval development in great scallop. Aquaculture International 8:513-530.
- Román, G., Campos, M.J., Acosta, C.P. & Cano, J. 1999. Growth of the queen scallop (*Aequipecten opercularis*) in suspended culture: influence of density and depth. Aquaculture 178:43-62.
- Román, G.C., Cano, J.P., Campos, M.J.L. & López, J.I.L. 2001. Biología y cultivo de la vieira

- en Málaga. Recursos pesqueros, Pesca y acuicultura, Consejería de Agricultura y Pesca, Junta de Andalucía, Spain, 75 pp.
- Román, G., Louro, A. & De la Roche, J.P. 2003. Intermediate culture of king scallop (*Pecten maximus*) in suspension in cages: effect of stocking density and depth. *Journal of Shellfish Research* 22:647-654.
- Rosenthal, H., Allen, J.H., Helm, M.M. & McInerney-Northcott, M. 1995. Aquaculture technology: Its application, development and transfer. In: Boghen, A.D. (ed.). *Cold-Water Aquaculture in Atlantic Canada*. The Canadian Institute for Research on Regional Development, Canada, pp. 393-450.
- Rupp, G.S. & Parsons, G.J. 2004. Effects of salinity and temperature on the survival and byssal attachment of the lion's paw scallop *Nodipecten nodosus* at its southern distribution limit. *Journal of Experimental Marine Biology and Ecology* 309:173-198.
- Rupp, G.S., Parsons, G.J., Thompson, R.J. & de Bem, M.M. 2004a. Effect of depth and stocking density on growth and retrieval of the postlarval lion's paw scallop, *Nodipecten nodosus* (Linnaeus, 1758). *Journal of Shellfish Research* 23:473-482.
- Rupp, G.S., Parsons, G.J., Thompson, R.J. & de Bem, M.M. 2005. Influence of environmental factors, season and size at deployment on growth and retrieval of postlarval lion's paw scallop, *Nodipecten nodosus* (Linnaeus, 1758). *Aquaculture* 243:195-216.
- Rupp, G.S., Thompson, R.J. & Parsons, G.J. 2004b. Influence of food supply on postmetamorphic growth and survival of hatchery-produced lion's paw scallop, *Nodipecten nodosus* (Linnaeus, 1758). *Journal of Shellfish Research* 23:5-13.
- Ryan, C.M., Parsons, J. & Dabinett, P. 1998. Effect of algal harvest phase on larval and post-larval growth of giant scallops (*Placopecten magellanicus*) in a commercial hatchery. *Bulletin of the Aquaculture Association of Canada* 98-2:65-67.
- Salaun, M., Boucher, J. & Le Penec, M. 1991. Prodissoconch shell characteristics as indicators of larval growth and viability in *Pecten maximus* (Linnaeus, 1758). *Journal of Shellfish Research* 10:37-46.
- Sastry, A.N. 1965. The development and external morphology of pelagic larval and post-larval stages of the bay scallop, *Aequipecten irradians concentricus* Say, reared in the laboratory. *Bulletin of Marine Science* 15:417-435.
- Schmidt-Nielsen, K. 1990. *Animal physiology: Adaptation and environment*. 4th ed. Cambridge University Press, 602 pp.
- Shumway, S.E. 1977. Effect of salinity fluctuation on the osmotic pressure and Na<sup>+</sup>, Ca<sup>2+</sup> and Mg<sup>2+</sup> ion concentrations in the hemolymph of bivalve molluscs. *Marine Biology* 41:153-177.
- Shumway, S.E. (ed.) 1991. *Scallops: biology, ecology and aquaculture*. *Developments in Aquaculture and Fisheries Science*, 21, Elsevier, Amsterdam, 1095 pp.
- Shumway, S.E. & Castagna, M. 1994. Scallop fisheries, culture and enhancement in the United States. *Memoirs of the Queensland Museum* 36:283-298.
- Shumway, S.E., Cucci, T.L., Lesser, M.P., Bourne, N. & Bunting, B. 1997. Particle clearance and selection in three species of juvenile scallops. *Aquaculture International* 5:89-99.
- Singnoret-Brailovsky, G., Maeda-Martinez, A.N., Reynoso-Granados, T., Soto-Galera, E., Monsalvo-Spencer, P. & Valle-Meza, G. 1996. Salinity tolerance of the catarina scallop *Argopecten ventricosus-circularis* (Sowerby II, 1842). *Journal of Shellfish Research* 15:623-626.
- Skjæggstad, H., Andersen, S. & Strand, Ø. 1999. The capacity of the great scallop, *Pecten maximus*, to exploit enhanced food levels. In: Strand, Ø. (ed.). *Book of abstracts, 12<sup>th</sup> International Pectinid Workshop*, Bergen, Norway, pp. 49-50.
- Smith, B.C. & Wikfors, G.H. 1998. An automated rearing chamber system for studies of shellfish feeding. *Aquaculture Engineering* 17:69-77.

- Spencer, B.E. 2002. Molluscan shellfish farming. Fishing News Books, Blackwell Publishing, Oxford, UK, 274 pp.
- Stotz, W. 2000. When aquaculture restores and replaces an overfished stock: Is the conservation of the species assured? The case of the scallop *Argopecten purpuratus* in Northern Chile. *Aquaculture International* 8:237-247.
- Stotz, W. & Mendo, J. 2001. Pesquerías, repoblamiento y manejo de bancos naturales de pectínidos en Iberoamerica: su interacción con la acuicultura. In: A.N. Maeda-Martínez (ed.). Los moluscos pectínidos de Iberoamérica: ciencia y acuicultura, Editorial Limusa, México, pp. 357-374.
- Strand, Ø. 1996. Enhancement of bivalve production capacity in a landlocked heliothermic marine basin. *Aquaculture Research* 27:355-373.
- Strand, Ø. & Brynjeldsen, E. 2003. On the relationship between low winter temperatures and mortality of juvenile scallops, *Pecten maximus* L., cultured in western Norway. *Aquaculture Research* 34:1417-1422.
- Strand, Ø. & Nylund, A. 1991. The reproductive cycle of the scallop *Pecten maximus* (Linnaeus, 1758) from two populations in western Norway, 60°N and 64°N. In: Shumway, S. & Sandifer, P.A. (eds.). An international compendium of scallop biology and culture, The World Aquaculture Society, USA, pp. 95-105.
- Strand, Ø., Solberg, P., Andersen, K.K. & Magnesen, T. 1993. Salinity tolerance of juvenile scallops (*Pecten maximus* L.) at low temperature. *Aquaculture* 115:169-179.
- Strand, Ø. & Vølstad, J.H. 1997. The molluscan fisheries and culture of Norway. NOAA Technical Report NMFS 129. US Department of Commerce, pp. 7-24.
- Strickland, J. & Dabinett, P. 1993. Rates of feeding, oxygen consumption and ammonia excretion as a function of size for hatchery reared spat of the sea scallop *Placopecten magellanicus*. *Bulletin of the Aquaculture Association Canada* 93-4:125-127.
- Strömngren, T. & Nielsen, M.V. 1989. Heritability of growth in larvae and juveniles of *Mytilus edulis*. *Aquaculture* 80:1-6.
- Sundet, J.H. & Vahl, O. 1981. Seasonal changes in dry weight and biochemical composition of the tissues of sexually mature and immature Iceland scallops, *Chlamys islandica*. *Journal of the Marine Biological Association of the United Kingdom* 61:1001-1010.
- Tang, S.-F. 1941. The breeding of the scallop [*Pecten maximus* (L.)] with a note on the growth rate. *Proceedings and transactions, Liverpool Biological Society* 54:9-28.
- Tebble, N. 1966. British bivalve seashells. A handbook for identification. Trustees of the British Museum (Natural History), Oxford, UK, 212 pp.
- Tettelbach, S.T., Auster, P.J., Rhodes, E.W. & Widman, J.C. 1985. A mass mortality of northern bay scallops, *Argopecten irradians irradians*, following a severe spring rainstorm. *Veliger* 27:381-385.
- Tettelbach, S.T., Smith, C.F., Wencel, P. & Decort, E. 2002. Reproduction of hatchery-reared and transplanted wild bay scallops, *Argopecten irradians irradians*, relative to natural populations. *Aquaculture International* 10:279-296.
- Thompson, R.J. & MacDonald, B.A. 1990. The role of environmental conditions in the seasonal synthesis and utilisation of biochemical energy reserves in the giant scallop, *Placopecten magellanicus*. *Canadian Journal of Zoology* 68:750-756.
- Thompson, R.J. & MacDonald, B.A. 1991. Physiological integrations and energy partitioning. In: Shumway, S.E. (ed). *Scallops: biology, ecology and aquaculture*. Elsevier, Amsterdam, pp. 347-376.
- Thorarinsdóttir, G.G. 1994. The Iceland scallop, *Chlamys islandica* (O.F. Müller), in Breidafjörður, west Iceland. III. Growth in suspended culture. *Aquaculture* 120:295-303.
- Thorson, G. 1961. Length of pelagic larval life in marine bottom invertebrates as related to

- larval transport by ocean currents. *Oceanography*. Publication of the American Association for the Advancement of Science 67:455-474.
- Thouzeau, G. 1991. Déterminisme du pré-recrutement de *Pecten maximus* (L.) en baie de Saint-Brieuc: processus régulateurs de l'abondance, de la survie et de la croissance des post-larves et juvéniles. *Aquatic Living Resources* 4:77-99.
- Tidwell, J.H. & Allan, G.L. 2002. Fish as food: aquaculture's contribution. Ecological and economic impacts and contributions of fish farming and capture fisheries. *World Aquaculture* 33:44-48.
- Torkildsen, L. & Magnesen, T. 2004. Hatchery production of scallop larvae (*Pecten maximus*) – survival in different rearing systems. *Aquaculture International* 12:489-507.
- Townsend, L.D., Kingzett, B.C. & Bourne, N. 1991. An improved method for handling large numbers of juvenile scallops. *Aquaculture* 92:389-392.
- Uriarte, I. & Farías, A. 1999. The effect of dietary protein content on growth and biochemical composition of Chilean scallop *Argopecten purpuratus* (L.) postlarvae and spat. *Aquaculture* 180:119-127.
- Uriarte, I., Rupp, G. & Abarca, A. 2001. Producción de juveniles de pectínidos Iberoamericanos bajo condiciones controladas. In: A.N. Maeda-Martínez (ed.). Los moluscos pectínidos de Iberoamérica: ciencia y acuicultura, Editorial Limusa, México, pp. 147-171.
- Utting, S.D. & Millican, P.F. 1997. Techniques for the hatchery conditioning of bivalve broodstocks and the subsequent effect on egg quality and larval viability. *Aquaculture* 155:45-54.
- Utting, S.D. & Millican, P.F. 1998. The role of diet in hatchery conditioning of *P. maximus* L.: a review. *Aquaculture* 165:167-178.
- Vahl, O. 1972. Particle retention and relation between water transport and oxygen uptake in *Chlamys opercularis* (L.)(Bivalvia). *Ophelia* 10:67-74.
- Vahl, O. 1973. Efficiency of particle retention in *Chlamys islandica* (O.F. Müller). *Astarte* 6:21-25.
- Vahl, O. 1980. Seasonal variations in seston and in the growth rate of the Iceland scallop, *Chlamys islandica* (O.F. Müller) from Balsfjord, 70 °N. *Journal of Experimental Marine Biology and Ecology* 48:193-204.
- Vahl, O. 1981. Age-specific residual reproductive value and reproductive effort in the Iceland scallop, *Chlamys islandica* (O.F. Müller). *Oecologia* 51:53-56.
- Veniot, A., Bricelj, V.M. & Beninger, P.G. 2003. Ontogenetic changes in gill morphology and potential significance for food acquisition in the scallop *Placopecten magellanicus*. *Marine Biology* 142:123–131 and Erratum 827–832.
- Ventilla, R.F. 1982. The scallop industry in Japan. *Advances in Marine Biology* 20:310-382.
- Vermeij, G.J. 1993. A natural history of shells. Princeton University Press, New Jersey, USA, 207 pp.
- Wallace, J.C. & Reinsnes, T.G. 1985. The significance of various environmental parameters for growth of the Iceland scallop, *Chlamys islandica* (Pectenidae), in hanging culture. *Aquaculture* 44:229-242.
- Waller, T.R. 1991. Evolutionary relationships among commercial scallops (Mollusca:Bivalvia:Pectinidae). In: Shumway, S.E. (ed). *Scallops: biology, ecology and aquaculture*. Elsevier, Amsterdam, pp. 1-73.
- Wang, S., Duncan, P.F., Knibb, W. & Degnan, B.M. 2002. Byssal attachment of *Amusium balloti* (Bernardi, 1861) (Bivalvia:Pectinidae) spat. *Journal of Shellfish Research* 21:563-569.
- Ward, J.E., Levinton, J.S. & Shumway, S.E. 2003. Influence of diet on pre-ingestive particle processing in bivalves I: Transport velocities on the ctenidium. *Journal of*

- Experimental Marine Biology and Ecology 293:129-149.
- Ward, J.E. & Shumway, S.E. 2004. Separating the grain from the chaff: particle selection in suspension- and deposit-feeding bivalves. *Journal of Experimental Marine Biology and Ecology* 300:83-130.
- Whyte, J.N.C., Bourne, N., Ginther, N.G. & Hodgson, C.A. 1992. Compositional changes in the larva to juvenile development of the scallop *Crassadoma gigantea* (Gray). *Journal of Experimental Marine Biology and Ecology* 163:13-29.
- Whyte, J.N.C., Bourne, N. & Hodgson, C.A. 1987. Assessment of biochemical composition and energy reserves in larvae of the scallop *Patinopecten yessoensis*. *Journal of Experimental Marine Biology and Ecology* 113:113-124.
- Wiborg, K.F. & Bøhle, B. 1968. Forekomster av matnyttige skjell (muslinger) i norske kystfarvann (med et tillegg om sjøsnegler). *Fisken og havet* nr. 1, Havforskningsinstituttet/Institute of Marine Research, Bergen, Norway, pp. 1-20. (In Norwegian with English summary).
- Widman, J.C. 1998. Design of a recirculating nursery culture system for the bay scallop, *Argopecten irradians irradians*. *Journal of Shellfish Research* 17:364 (abstract only).
- Widman Jr., J.C., Choromanski, J., Robohm, R.A., Stiles, S., Wikfors, G. & Calabrese, A. 2001. Manual for hatchery culture of the bay scallop, *Argopecten irradians irradians*. National Marine Fisheries service/Northeast Fisheries Science Center, Milford Laboratory, Milford, Connecticut 06460, USA, 50 pp.
- Widman, J.C. & Rhodes, E.W. 1991. Nursery culture of the bay scallop, *Argopecten irradians irradians*, in suspended mesh nets. *Aquaculture* 99:257-267.
- Wieser, W. 1973. Temperature relations of ectotherms: A speculative review. In: Wieser, W. (ed.). *Effects of temperature on ectothermic organisms. Ecological implications and mechanisms of compensation*, Springer-Verlag, Germany, pp. 1-23.
- Wikfors, G.H. & Ohno, M. 2001. Impact of algal research in aquaculture. *Journal of Phycology* 37:968-974.
- Wildish, D. & Kristmanson, D. 1997. *Benthic suspension feeders and flow*. Cambridge University Press, UK, 409 pp.
- Wildish, D. & Saulnier, A.M. 1992. The effect of velocity and flow direction on the growth of juvenile and adult giant scallops. *Journal of Experimental Marine Biology and Ecology* 133:133-143.
- Wilson, J.H. 1987a. Spawning of *Pecten maximus* (Pectinidae) and the artificial collection of juveniles in two bays in the west of Ireland. *Aquaculture* 61:99-111.
- Wilson, J.H. 1987b. Environmental parameters controlling growth of *Ostrea edulis* L. and *Pecten maximus* L. in suspended culture. *Aquaculture* 64:119-131.
- Winter, J.E. 1978. A review on the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture* 13:1-33.
- Yang, H., Zhang, T., Wang, J., Wang, P., He, Y. & Zhang, F. 1999. Growth characteristics of *Chlamys farreri* and its relation with environmental factors in intensive raft-culture areas of Sishiliwan Bay, Yantai. *Journal of Shellfish Research* 18:71-76.



**APPENDIX****Spelling and word corrections**

Changes made to the thesis text originally submitted for evaluation to the degree dr. scient.

<b>Page</b>	<b>Original text</b>	<b>Corrected</b>
7	...from wild...	...from <b>the</b> wild...
7	...intensive culture in hatchery...	...intensive culture in <b>the</b> hatchery...
7	...transferred to land-based nursery...	...transferred to <b>a</b> land-based nursery...
10	...to a variety of substrate...	...to a variety of substrates...
12	...lover the viability...	...lower the viability...
13	...the tolerance limits varies...	...the tolerance limits vary...
13	...functions and adapt...	...functions and adapts...
14	...aquaculture have to a large extent...	...aquaculture has to a large extent...
15	...if fish aquaculture per se...	... <b>whether</b> fish aquaculture <i>per se</i> ...
15	...stands for 2 million tonnes...	...stands <b>at</b> 2 million tonnes...
15	...of which China produce...	...of which China produces...
15	...spat from wild...	...spat from <b>the</b> wild...
16	...adapt for the recapture right	...adapted for the recapture right...
16	...furthermore approving the development	...furthermore <b>facilitating</b> the...
16	...broodstock diet affect fecundity...	...broodstock diet affects fecundity...
17	...are shown variable...	...are shown <b>to be</b> variable...
17	Descriptions of...systems exists...	Descriptions of...systems <b>exist</b> ...
17	...be divided in...	...be divided <b>into</b> ...
21	...experimental temperatures was...	...experimental temperatures <b>were</b> ...
22	...showed soon recovery...	... <b>soon recovered</b> ...
22	...salinity levels during the study was...	...salinity levels during the study <b>were</b> ...
23	The highest growth rates was...	The highest growth rates <b>were</b> ...
23	...cultured in sea-based nursery...	...cultured in <b>a</b> sea-based nursery...
24	...consequently of vulnerable sizes	...consequently of <b>a</b> vulnerable <b>size</b> ...
25	Lipids are important as energy reserve	Lipids are important as energy reserves
25	...food conditions in the...was	...food conditions in the... <b>were</b>
26	This indicated that that food...	This indicated <b>that</b> food...
29	...showing greatest mortality...	...showing <b>the</b> greatest mortality...
30	Temperatures above 20 °C was...	Temperatures above 20 °C <b>were</b> ...
31	The small <i>P. maximus</i> was...	The small <i>P. maximus</i> <b>were</b> ...
33	...feeding ones or twice a day...	...feeding <b>once</b> or twice a day...
34	The uses of closed...	The <b>use</b> of closed...
38	...removal of poor developed...	...removal of poorly developed...
40	...spat are likewise shown a critical	...spat <b>is</b> likewise shown <b>to be</b> a critical
40	...further spat growth in nursery...	...growth in <b>a</b> nursery
40	...was shown temperature and...	...was shown <b>to be</b> temperature...
41	...observed in wild...	...in <b>the</b> wild...
	References	
43	Bayne, B.L. 1976.	Bayne, B.L. (ed.) 1976.
46	Duinker, A. 2002. Peocesses....	...Processes
53	Shumway, S.E. 1991.	Shumway, S.E. (ed.) 1991.

