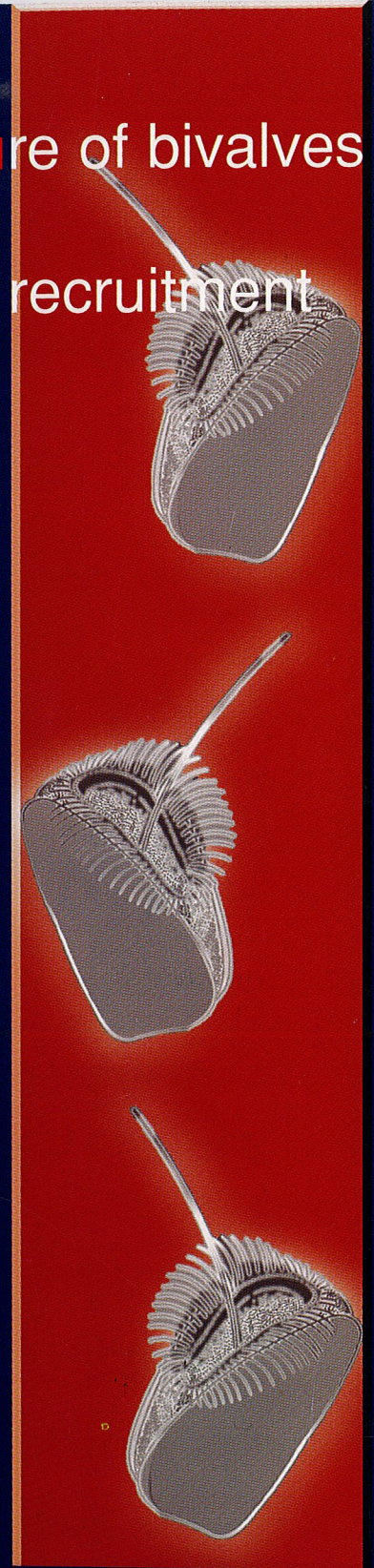


Spatial population structure of bivalves
in shallow sediments:
Hydrodynamic effects on recruitment
processes

Marine Zoology
Göteborg University
1996



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Göteborg University
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Dissertation

**Spatial population structure of bivalves in shallow marine
sediments: hydrodynamic effects on
recruitment processes**

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Akademisk avhandling för filosofie doktorsexamen i marin zoologi vid Göteborgs Universitet (examinator: professor Rutger Rosenberg), som enligt beslut av sektionstyrelsen för biologi kommer att försvaras offentligt fredagen den 15 mars 1996, kl. 13.00 på Tjärnö Marinbiologiska Laboratorium, 452 96 Strömstad.

Lindegarh, Mats 1996. Spatial population structure of bivalves in shallow marine sediments: hydrodynamic effects on recruitment processes
Marine Zoology, Göteborg University, Tjärnö Marine Biological Laboratory, S-452 96 Strömstad

Key words: bivalve larvae, settlement, larval behaviour, hydrodynamics, recruitment, spatial variability, spatial scale, juvenile transport, suspension-feeders, *Cerastoderma*, *Mya*, Sweden, flow, flume, larval staining, genetic markers, identification of larvae

ISBN 91-628-1929-1

Abstract: The abundance of marine invertebrate populations in general, and intertidal bivalves in particular, are highly variable and unpredictable in space and time. Life-histories of intertidal bivalves are generally characterised by high fecundity and dispersive larval stages. Much recent work is focused on how recruitment processes affect the formation of spatial and temporal patterns in these organisms.

The present thesis explores interactions between near-bottom hydrodynamics and larval and juvenile behaviour and how this may affect the spatial structure of populations of sediment-living intertidal bivalves. A field study revealed that the abundance and age structure of two common sediment-living species of bivalves varied predominantly on small spatial scales (<10³ m). Thus, it is suggested that small- and mesoscale processes must be incorporated in population dynamic models of marine invertebrate populations. Using a new method to visualize larvae macroscopically, larval settlement behaviour of the infaunal bivalve *Cerastoderma edule* was studied in flow tank experiments. Direct observations of settling larvae indicate that swimming behaviour is constrained by the steep velocity gradient in the bottom boundary-layer; when a larva reaches the bottom it is unable to swim up in the water column and consequently it will drift in the boundary-layer flow. An analytical model, based on hydrodynamic shear forces and larval morphology was proposed as an explanation of the observations.

Effects of flow on the risk of predation from filter-feeding adult *Cerastoderma edule* were studied in flow tank experiments. Although, settlement patterns around individual adult siphons indicated moderate effects on settlement intensity, observations of swimming larvae showed that the behavioural modifications induced by shear flow resulted in a higher probability of predator encounter and thus a considerable risk of predation. Both observations and numerical modelling indicated that the predation on larvae from adult filter-feeders may have a strong large-scale effect on the settlement intensity.

Hydrodynamic shear forces may also affect the distribution of already settled bivalve juveniles. When sediment transport is initiated, newly settled individuals may to some extent avoid transport. However, extensive sediment transport invariably leads to complete redistribution of juveniles.

Finally, a technique to identify field collected bivalve larvae is described and potential applications of genetic markers, to the study of population dynamics of marine invertebrates is discussed.

This thesis is based on the following papers, referred to by their Roman numbers:

I Mats Lindegarh, Carl André and Per R. Jonsson. (1995) Analysis of spatial variability in abundance and age structure of two infaunal bivalves, *Cerastoderma edule* and *C. lamarcki*, using hierarchical sampling programs. Marine Ecology Progress Series 116: 85-97

II Mats Lindegarh, Per R. Jonsson and Carl André. (1991) Fluorescent microparticles: a new way of visualizing sedimentation and larval settlement. Limnology and Oceanography 36: 1471-1476

III Per R. Jonsson, Carl André and Mats Lindegarh. (1991) Swimming behaviour of marine bivalve larvae in a flume boundary-layer flow: evidence for near-bottom confinement. Marine Ecology Progress Series 79: 67-76

IV Mats Lindegarh, Per R. Jonsson and Carl André. (Manuscript) A laboratory flume study and a hydrodynamic analysis of settlement patterns of inert particles around siphons of a suspension-feeding bivalve, *Cerastoderma edule*.

V Carl André, Per R. Jonsson and Mats Lindegarh. (1993) Predation on settling larvae by benthic suspension feeders: the role of hydrodynamics and larval behaviour. Marine Ecology Progress Series 97: 183-192

VI Curtis Roegner, Carl André, Mats Lindegarh, James E. Eckman and Jonathan Grant. (1995) Transport of recently settled soft-shell clams (*Mya arenaria* L.) in a laboratory flume flow. Journal of Experimental Marine Biology and Ecology 187: 13-26

VII Carl André, Mats Lindegarh, Per R. Jonsson and Per Sundberg. (Submitted) Species identification of bivalve larvae using random amplified polymorphic DNA (RAPD): distinguishing between the sibling species *Cerastoderma edule* and *C. lamarcki*.

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Scope of this thesis

One of the fundamental themes in ecology is to develop models that can predict population growth and explain patterns of organism distribution in space and time. Implicit in this work is the quantification of patterns of distribution (Paper I), and identification of potentially important biological and physical processes that may account for the observed patterns. This thesis summarises a series of papers on hydrodynamic effects on recruitment processes and its importance for the population dynamics and distribution of some shallow water, sediment-living bivalves. A central feature of the thesis is to discuss questions of how hydrodynamic forces near the sediment surface interact with the behaviour of bivalve larvae and juveniles (Papers III, IV V and VI).

It is suggested that a better understanding of small- and mesoscale processes affecting larval and juvenile behaviour may be an important key in developing more powerful models on the population and community levels. A prerequisite for such studies is that we have the proper tools to observe individual behaviour and quantify the critical population parameters. Because of the small size of bivalve larvae and juveniles, the methodological difficulties are, however, not trivial. Therefore, a second theme in this thesis is to present new tools to observe larval behaviour in experimental situations (Paper II) and to identify larvae and juveniles to species in samples collected in the field (Paper VII).

Introduction

Population dynamics of benthic invertebrates. Marine populations, including populations of sediment-living intertidal bivalves, are notoriously unpredictable and variable (e.g. Beukema 1982; McArdle and Blackwell 1989; Thrush 1991; Morrissey et al. 1992a; Morrissey et al. 1992b). Irrespective of the

exact mechanisms, much of the variability and unpredictability of marine populations is probably a result of the life-history shared by many marine organisms.

The life cycles of most intertidal bivalves are characterised by high fecundity and a potentially highly dispersive larval stage. The outstanding dispersal capabilities causes practical problems when trying to measure vital parameters such as survival (Young and Chia 1987) and migration rates (Levin 1990). However, dispersal also has more conceptual implications for the dynamics (Roughgarden et al. 1985; Possingham and Roughgarden 1990) and evolution (Burton 1983; Ghiselin 1987) of these populations. Furthermore, with the enormous fecundity displayed by these organisms, even small differences in the survival during the early stages will result in large variability in surviving offspring (cf. Underwood and Fairweather 1989). Thus, for theoretical reasons there is a large potential for the early stages to have a profound effect on the temporal and spatial variability in abundance of these organisms (Thorson 1950), and consequently it is important that this is reflected in ecological models (Roughgarden et al. 1985; Underwood and Fairweather 1989).

Processes affecting recruitment in sediment-living benthic invertebrates. Assuming that we accept the importance of the early life-cycle stages as a determinant of variability in population size and structure: Which are the most important mechanisms and what generalisations can be made? Although much effort is put into this field and some progress have been made, these questions remain largely unanswered today (Olafsson et al. 1994).

A frequently debated issue in benthic ecology is whether the supply of larvae or post-settlement events limits the recruitment and subsequent population size. In some intertidal hard-substratum species several studies indicate that the supply of larvae may be a powerful predictor of subsequent population size

(e.g. Gaines et al. 1985; Gaines and Bertness 1992). Such demonstrations are, however, absent for sediment organisms (Olafsson et al. 1994).

In sediment habitats, more emphasis has been on settlement and post-settlement events. Recent work on hydrodynamic effects on settlement behaviour (e.g. Butman 1987) has shown that larval settlement is governed both by larval behaviour and hydrodynamic forces (e.g. Butman et al. 1988; Pawlik et al. 1991). It has also been suggested that settlement into populations of intertidal bivalves is regulated by filter-feeding by established adults ('adult-larval interactions'; Woodin 1976; André and Rosenberg 1991). There is also ample evidence of massive post-settlement mortality of intertidal bivalves (e.g. Muus 1973; Möller and Rosenberg 1983; Guillou and Tartu 1994). Although the relative importance of different mortality factors are not clear (Olafsson et al. 1994), several studies indicate that predation from epibenthic predators may be an important mortality factor (eg. Reise 1978; Pihl 1985). Furthermore, hydrodynamic disturbance has been suggested as an important source of post-settlement mortality and a structuring factor in intertidal habitats (Grant 1981; Emerson and Grant 1991; Hall 1994). The importance of hydrodynamic forces will be discussed more thoroughly below. The question whether settlement intensity or post-settlement mortality is the main determinant of recruitment is, however, still an open question although it seems probable that both pro-

cesses may be important (e.g. Peterson 1986).

Spatial structure of marine populations. Understanding the causes and consequences of temporal and spatial variability of abundance in populations is one of the most intriguing and important topics in ecology (e.g. Andrew and Mapstone 1987; Kareiva 1990; Hanski and Gilpin 1991; Levin 1992). Observations of spatial or temporal variability of abundance of an organism, is often the starting point which raises questions and generates hypotheses about important processes on the individual, population or community level (Levin 1992). However, it is evident that all populations vary differently on different temporal and spatial scales (Thrush 1991; Morrisey et al. 1992; Morrisey et al. 1992). This implies that different processes may be responsible for generating variability on different temporal and spatial scales and that patterns and processes must be assessed on several scales.

As previously described, there are several plausible processes which may affect spatial and temporal recruitment patterns. However, the importance of various settlement and post-settlement processes probably depend on the spatial and temporal scales considered (Butman 1987). Figure 1 shows a hypothetical case of how the intensity of two different processes, say larval supply and predation on settled juveniles, vary on different spatial scales and create spatially variable recruitment patterns. The concentration of larvae varies mainly among populations and the recruitment in population 2 is limited by larval sup-

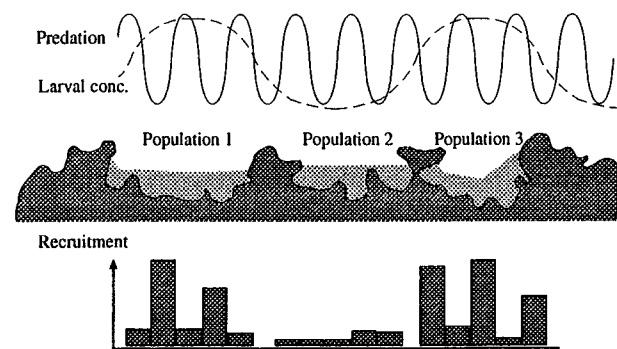


Fig. 1. Hypothetical example of regulating processes that vary in intensity on different spatial scales. The larval concentration varies on the scale of populations and limits the number of recruits in population 2. The recruitment in populations 1 and 3 is limited both by larval concentration and by predation which varies on a scale within populations.

ply. Populations 1 and 3, however, receive a large number of larvae but in some patches the recruitment is regulated by predation which varies on a within population scale. Although hypothetical, this example illustrates how different processes may act on different spatial scales, and act in concert to create complex patterns of variability. Furthermore, this example has far reaching implications for the design of ecological surveys and experiments, and emphasizes the need for studies that assess patterns of organisms at multiple spatial and temporal scales (Morrisey et al. 1992a; Morrisey et al. 1992b).

Hydrodynamic processes in coastal habitats. Hydrodynamic processes have numerous important implications for the ecology of marine organisms (e.g. Vogel 1981; Denny 1988; Wolanski 1994). There are several mechanisms by which hydrodynamics may affect recruitment patterns at different temporal and spatial scales (Fig. 2). The possibility of interactions between larval behaviour and hydrodynamics during settlement and early juvenile stages has already been mentioned and will be further discussed below. However, recent methodological developments and the increasing interest in larval dispersal also justifies a brief cover of larger scale hydrodynamic processes.

Although planktonic larvae occasionally have the ability to migrate horizontally (e.g. Mann et al. 1991), the dispersal of planktonic larvae is largely a function of the time spent as plankton and hydrographic processes (Strathmann 1974). The duration of the planktonic phase of invertebrate larvae varies from a few hours in lecithotrophic species to more than a month in some planktotrophic species. Most intertidal bivalves have external fertilisation and a planktotrophic phase that lasts for 2-4 weeks. Thus, these species have a potential for large scale (10^4 - 10^6 m) dispersal with ocean currents and eddies. There are observations of ocean-scale dispersal in some species (e.g. Scheltema 1971; Scheltema 1979).

However, the existence of biogeographic zones and genetic differentiation (Avisé 1992; Karl and Avisé 1992) suggests that these observations are probably primarily of evolutionary importance.

Growing evidence suggest that the processes important for the recruitment of intertidal invertebrates act mainly in shelf or coastal waters. Several interesting findings relating mesoscale (10^2 - 10^4 m) hydrodynamic processes to larval abundance and recruitment have emerged (e.g. Shanks 1986; Farrell et al. 1991). Spatial variability in flushing rates caused by e.g. sea-grass beds or topographically controlled wakes (e.g. Peterson 1986; Sammarco and Andrews 1988) may enhance recruitment rates. Furthermore, both empirical studies (e.g. McShane et al. 1988; Sammarco and Andrews 1988; Gaines and Bertness 1992) and numerical models (Black et al. 1991; Black 1993) suggest that recruitment patterns may be affected by local coastal topography and that populations may be more dependent on the success of local recruits than previously anticipated.

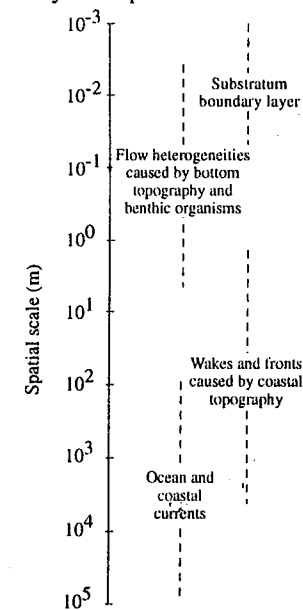


Fig. 2. Approximate spatial scales of hydrodynamic processes that may affect recruitment.

The interaction between settling larvae and near-bed flow is an example of hydrodynamic influence on recruitment acting on a much smaller spatial scale. These interactions occur on the scale of individual larvae and studies of these phenomena may help us to understand the mechanisms by which hydrodynamics influence larval and juvenile behaviour. During the last decade, increased use of laboratory flumes designed to study these processes have shed new light on the importance of larval habitat selection (Butman et al. 1988; Pawlik et al. 1991), passive sedimentation patterns (Eckman 1983; Hannan 1984; Mullineaux and Butman 1991; Harvey et al. 1995), flow around filter-feeding benthic organisms (Ertman and Jumars 1988; Monismith et al. 1990) and hydrodynamic disturbance (Eckman 1983; Eckman and Nowell 1984; Emerson 1990).

Central to the study of near-bed hydrodynamics is the 'no-slip' condition. This universal law postulates that a fluid immediately in contact with a solid surface does not slip in relation to the surface, i.e. at the substratum surface the flow velocity approaches zero (e.g. Nowell and Jumars 1984; Butman 1986).

Thus, whenever a fluid moves over a surface a velocity gradient (boundary-layer) develops (Fig. 3). In the intertidal zone, practically all flow regimes may be characterized as turbulent and one section of the velocity gradient (the logarithmic sub-layer) may be described by the 'law of the wall' (Schlichling 1979): where $U(z)$ is the flow velocity as a function

$$U(z) = \frac{u_*}{\kappa} \ln \frac{z}{z_0} \quad (1)$$

of height over the bottom, u_* , κ and z_0 are the friction (shear) velocity, von Karman's constant (≈ 0.4) and the roughness height respectively. The flow speed at a certain height above the substratum is thus a function of several parameters. The near-bed flow situation is often characterized by derivation of the parameters u_* and z_0 from measurements of flow speed at different heights in the logarithmic sub-layer.

Although the velocity profile is characterized as turbulent, there is always a layer close to the bottom (the laminar sub-layer) where flow is dominated by viscous forces (i.e. the flow is laminar). For a given turbulent regime, the depth of the laminar (viscous) sub-layer varies in time and space but generally it is on the order of 1-10 mm. The maximum swimming speed of most invertebrate larvae is less than a few mm s^{-1} (Chia et al. 1984), which is low compared to most natural flow velocities. Thus, it may be hypothesized that the volume of water, in which larvae can theoretically manoeuvre, is roughly restricted to the laminar sub-layer (Fig. 3). Furthermore, the depth of this layer is of the same order of magnitude as larval size. This indicates that shear forces in the velocity gradient may severely affect larval behaviour and that studies of larval behaviour in the benthic boundary-layer are crucial to understand the constraints imposed by flow on settling larvae.

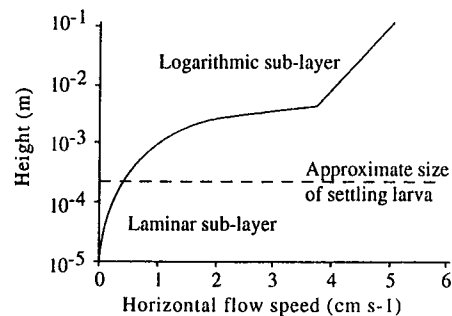


Fig. 3. Log-linear representation of a turbulent boundary-layer.

The Present Thesis

Background. Possibly because of commercial interest, there is a comparatively large number of surveys on abundance, recruitment and growth of several intertidal bivalves. For the cockle, *Cerastoderma edule*, which is the most studied organism in this thesis, several temporally and spatially extensive studies of abundance and recruitment in western Europe are available (e.g. Baggerman 1953; Kristensen 1957; Hancock and Urquhart

1965; Beukema 1982; Möller and Rosenberg 1983; Ducrotoy et al. 1991; Guillou and Tartu 1994). Unfortunately, because of insufficient spatial and temporal replication many of these surveys are unsuitable for tests of hypotheses about patterns of distribution in time and space (Underwood 1990; Underwood 1991).

The general pattern that emerges from these studies is that there is no discernible positive relation between local stock size and subsequent recruitment (Hancock 1973), the local population density fluctuates widely among years (e.g. Beukema 1982; Ducrotoy et al. 1991), and local populations consist of few 'strong' year classes (e.g. Evans and Tallmark 1976; Brock 1979; Ducrotoy et al. 1991; Jensen 1992). This pattern is fully consistent with what may be predicted from an organism with high fecundity and dispersive larvae, and are attributed to variable recruitment success and occasional severe adult mortality.

Several biological and physical processes may be suggested as causes of recruitment variability and adult mortality. The most frequently discussed causes of recruitment variability in *Cerastoderma edule* are adult-larval interactions (Hancock 1973; Brock 1980; André and Rosenberg 1991), post-settlement predation (Reise 1978; Möller and Rosenberg 1983; Pihl 1985) and post-settlement transport (Baggerman 1953; Kristensen 1957). Although, predation by birds and humans (Hancock 1970) and parasitic infestations (Hancock 1970; Jonsson and André 1992) have been shown to cause significant mortality in adult cockles, perhaps the most widely discussed mortality factor is the effects of cold winters (e.g. Hancock 1973; Beukema 1982; Möller and Rosenberg 1983; Ducrotoy et al. 1991). From time series data it is often inferred that massive winter mortality enhances recruitment the following season by decreasing the effects of adult-larval interactions.

Without denying the existence of winter mortality and adult-larval interactions, the general importance and explanatory power of

this model may be questioned. Firstly, recruitment is sometimes higher in years not preceded by a severe winter (cf. Fig. 1, *Cerastoderma edule*; in Beukema 1982). Secondly, recruitment and population density may fluctuate highly asynchronously among different sites separated by less than 10^3 - 10^4 m (cf. Fig. 2 in Ducrotoy et al. 1991). In other words, the spatial component and the component resulting from the interaction between time and space (i.e. the trajectories in time develop differently among places) is as large as the temporal component of variability. This indicates that the concept of 'severe winters' has limited explanatory power and that annual variations of some variable, e.g. temperature, is unlikely to explain a significant part of the spatial and temporal variability in abundance or recruitment for *C. edule*. Furthermore, the considerable small-scale spatial variation suggests that a better understanding of small- and mesoscale processes and individual behaviour may be an important step towards more powerful models to explain patterns of abundance in time and space.

Spatial population structure of cockles on the west coast of Sweden. The previous sections emphasize the need to relate the effects of different processes to different temporal and spatial scales and it is suggested that the understanding of small- and mesoscale processes may have serious consequences to our views on the large-scale dynamics of benthic organisms. This implies that spatial patterns must be assessed on multiple scales which also allows tests of the generality of spatial patterns (Underwood 1991).

In order to quantify spatial patterns of variability in abundance and age structure of the two cockles *Cerastoderma edule* and *C. lamarki* on the Swedish west coast, a field study was performed in 1992 (Paper I). The scales investigated ranged from 1 m to 10^4 - 10^5 m and the results showed that abundance and age structure varied significantly on several spatial scales (Fig. 4). Interestingly, the

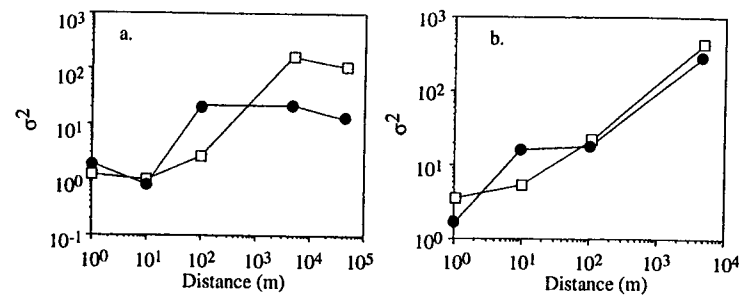


Fig. 4. Variability in abundance (a) and age (b) as a function of spatial scale in populations of *Cerastoderma edule* (●) and *C. lamarcki* (□) on the Swedish west coast (Paper I).

abundance of both *C. edule* and *C. lamarcki* varied significantly among sites located c. 100 m apart. This indicates that processes varying within bays are of major importance to the recruitment and survival of these two species. However, in *C. lamarcki* the variability among bays located 10^3 - 10^4 m apart was even more pronounced and consequently processes varying on this scale may be more important in explaining patterns of abundance for this species.

The analyses of spatial patterns in age structure of the two species also showed significant variability on several scales. In general it may be concluded that individuals living close to each other are more similar in age than individuals living further apart (Fig. 4). For both species the age structure varied considerably among bays located 10^3 - 10^4 m apart, but there were also differences among patches within bays. Different year classes may thus dominate in different parts of a bay. The picture that emerges from this study is a pattern of a hierarchical mosaic where population structure in different bays are dominated by different year classes and where individuals are non-randomly distributed within bays.

This sort of study does not provide any answers to what mechanisms are important to the population dynamics of *Cerastoderma edule* and *C. lamarcki*. However, it provides us with quantitative estimates of variability and allows us to test for significant patterns of distribution. Furthermore, whether the observed patterns are due to variability in recruitment, juvenile or adult mortality, the results

show that models based on processes acting on spatial scales $<10^3$ m are most likely to be powerful predictors of population variability.

Interactions between near-bottom flow and behaviour of recruits. Experimental evidence of habitat selection and gregarious settlement implies that larvae have the ability to respond to various chemical and biological cues during settlement (Crisp 1974; Pawlik 1992). These behavioural mechanisms are, however, most likely to be important on small spatial scales (Butman 1987) and it is not clear whether models based on these processes have any explanatory power on larger spatial scales. Nevertheless, it is evident that small- and mesoscale processes may be important in explaining spatial patterns of abundance of these organisms (Paper I).

In recent years, much experimental work (e.g. Butman et al. 1988; Grassle and Butman 1989; Pawlik et al. 1991) and modelling (Denny and Shibata 1989; Eckman 1990) has been directed to understand the effects of boundary-layer flow on larval settlement. These studies suggest that flow may enhance settlement due to increased vertical fluxes. Furthermore, flow does not generally prohibit active habitat selection although it may impose constraints on larval behaviour and cause resuspension of settled individuals. Papers II, III, IV, V and VI represent further attempts to elucidate the small-scale hydrodynamic effects on recruitment processes in the sediment-living bivalves, *Cerastoderma edule* and *Mya arenaria*.

Visualization of settlement and sedimentation patterns. One approach to investigate the effects of near-bed hydrodynamics on small-scale settlement patterns is to use inert particles as larval mimics (e.g. Butman et al. 1988; Ertman and Jumars 1988). To increase the utility of this technique, we developed an inexpensive method to produce large quantities of fluorescently stained larval mimics (Paper II). These particles allow continuous observations and a better resolution in studies of small-scale sedimentation patterns (Paper IV; Harvey et al. 1995).

Larvae of *Cerastoderma edule* are approximately 250 μ m in size by the time they are competent to settle and metamorphose. This means that, in a flowing environment, it is very difficult to study larval behaviour for any longer periods of time (>10 s). To circumvent this problem we developed a technique to visualize larvae by feeding them fluorescent particles (Paper II). This labelling allows macroscopic observations of the behaviour of individual larvae during settlement (Papers III and V), and settlement patterns can easily be studied with high spatial resolution. The fluorescent particles appear to be non-toxic to the larvae. However, the use of this technique is restricted to experiments lasting less than 10 h as the gut contents are eventually replaced with 'natural' food particles.

Flow effects on settlement behaviour in *Cerastoderma edule*. To evaluate the impor-

tance of active habitat selection, gregarious settlement and adult-larval interactions, it is crucial to understand the constraints imposed by near-bed flow on larval settlement behaviour. Previous models of larval settlement behaviour in flowing water (Keough and Downes 1982; Hannan 1984) have suffered from the inability to study swimming behaviour directly. Settlement behaviour have instead been inferred from settlement patterns and circumstantial observations. However, the labelling technique described in paper II provided new opportunities to study how larval behaviour interacts with boundary-layer flow. Thus, the behaviour of competent larvae were observed and quantified as a function of shear flow (Paper III).

The observations of settling larvae in shear flow revealed qualitative differences in swimming behaviour as compared to behaviour in still water (Fig. 5). In still water bivalve larvae typically swim up and down in helices (e.g. Mann et al. 1991).

When larvae are exposed to flow they are transported downstream with the current and at low flow velocities (free-stream velocities ≤ 2 cm s^{-1} ; $u_* \leq 0.19$ cm s^{-1}) they show the same kind of upward and downward swimming as in still water. At a free stream velocity of c. 2 cm s^{-1} , however, the behaviour was changed into sequences of upward swimming interrupted by sequences of near-bed swimming. When the flow was further increased (free-stream velocity = 5 cm s^{-1} ; $u_* \leq 0.22$ cm s^{-1})

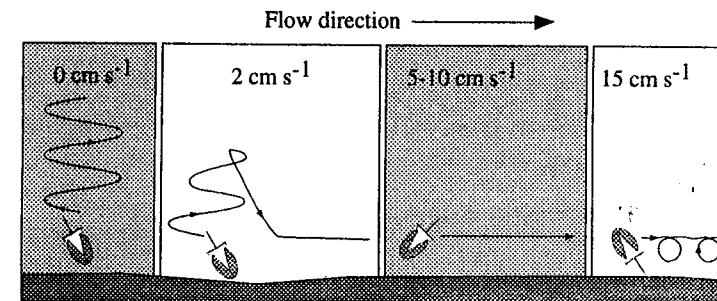


Fig. 5. Schematic drawing of the behaviour of larvae in different flow regimes (Paper III).

the swimming behaviour altered qualitatively and larvae were seemingly trapped in the boundary-layer, unable to swim upwards. Close observations in a dissecting microscope revealed that at flow velocities of 5 and 10 cm s⁻¹ the larvae were swimming upwards in a tilted position less than 1 mm above the surface. Furthermore, the change in behaviour was reversible; when the flow ceased the larvae were able to swim up in the water column again. Finally, when the flow velocity exceeded 15 cm s⁻¹ ($u_* \geq 0.57$ cm s⁻¹) the larvae began to tumble along the bottom.

To account for the observed larval behaviour we proposed a model based on the interaction between larval morphology and the physical forces that act on the larva in the boundary-layer. The model proposes that the near-bed confinement of larvae is caused by a dynamic balance of two opposing torques: (1) a gravitational torque, T_{grav} , and (2) a viscous torque, T_{visc} (Fig. 6).

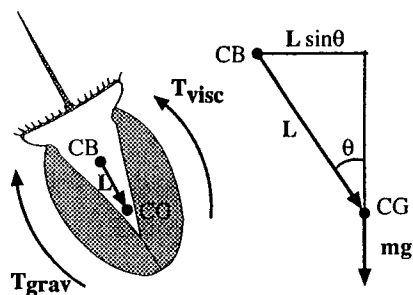


Fig. 6. Schematic illustration of the proposed model of larval behaviour in the benthic boundary-layer. For further explanations see text.

Observations of anaesthetised larvae indicate that there is a gravitational torque which tends to reorient a falling larva until the umbo is pointing downwards. It is hypothesized that the gravitational torque is due to a separation of the centres of buoyancy and gravity, because of an asymmetry in the density distribution of the larva. The gravitational torque is calculated as:

$$T_{grav} = m g L \sin\theta \quad (2)$$

(Kessler 1986) where m is the larval mass, g is gravitational acceleration, L is the separation distance between the centres of buoyancy and gravity and θ is the angle between the vectors L and mg (Fig. 6). Our calculations showed that a separation distance on the order of 1 μ m is sufficient to account for observed reorientation rates of falling larvae. Further, it is suggested that this mechanism, apart from consequences in the boundary-layer, generally may serve as a mechanism for negative geotaxis in bivalve larvae.

As an opposing force to gravitational torque we propose a viscous torque, T_{visc} , which is induced by the velocity gradient in the benthic boundary-layer. The presence of a velocity gradient means that the lower part of the larva will experience a lower flow velocity than the upper part. This induces a shear force which will tend to rotate the larva (Fig. 6) and, assuming a spherical shape, this viscous torque is:

$$T_{visc} = 4 \pi \mu a^3 \left(\frac{du}{dz} - 2 \omega \right) \quad (3)$$

where μ is the dynamic viscosity, a is the radius of the sphere, du/dz is the velocity gradient over the larval body and ω is the angular velocity of the larva (Kessler 1986). By substituting m (in eq. 2) by $4 \pi a^3 \rho / 3$ where ρ is larval density, and equating the two opposing torques we arrive at an analytical expression for a stable equilibrium orientation ($\omega = 0$):

$$\sin\theta = \frac{3\mu}{L\rho g} \frac{du}{dz} \quad (4)$$

The equilibrium orientation will result in retention of larvae in the boundary-layer if $\theta \geq 90^\circ$, which occurs when the near-bottom velocity gradient is greater than 3.5 s⁻¹. This result is within the range of the velocity gradients in our experiments, although the predicted critical gradient was slightly steeper than the observed.

To evaluate the effects of helical motion displayed by bivalve larvae (which is not included in the analytical expression), a set of numerical simulations was performed. By

varying the magnitude of two rotational parameters and L , the sensitivity of the critical velocity gradient was examined. The results show that for a helical motion the critical velocity gradient decreased, compared to the analytical expression (at $L = 1 \mu$ m), which indicates that some of the discrepancy between observed and predicted critical velocity gradient may be explained by the absence of rotational components in the model. However, the conclusion was that adding helical motion does not affect the plausibility of the proposed mechanism.

The model correctly predicts the qualitative behavioural shifts and is reasonably successful in predicting the critical parameter values resulting in behavioural shifts. Thus, we conclude that the observed behaviour is explained as a passive consequence of physical forces and not an active behaviour by the larvae. This does, however, not exclude the possibility for active larval choice. On the contrary, this may even enhance the possibilities for larvae to select micro-scale patches because they can scan the sediment while drifting less than a millimeter above the sediment surface.

Interactions between settling larvae and adult Cerastoderma edule. The potential importance of adult bivalves as predators of settling larvae and regulators of recruitment has been inferred both from negative correlations between adult stock and recruitment (Hancock 1973), and from manipulative experiments (e.g. Hancock 1973; André and Rosenberg 1991). Several manipulative studies, however, have failed to demonstrate any negative effects on recruitment and some studies have even recorded enhanced recruitment with higher densities of adult bivalves (reviewed by Olafsson et al. 1994). Mechanisms have been hypothesised that either decreases or increases settlement around individual bivalve siphons (Ertman and Jumars 1988). The potential decrease is obviously attributed to predation whereas an increase could be caused by flow

interactions between siphon currents and ambient horizontal flow. Furthermore, it has also been proposed that enhancement of settlement in dense beds of conspecific adults may be caused by gregariousness, with respect to adult conspecifics (Peterson and Black 1993). The visualization technique described in paper II provided new opportunities to detect small-scale settlement patterns and to assess the importance of hydrodynamics and larval behaviour as potential mechanisms for settlement heterogeneities within populations of suspension-feeding bivalves. In papers IV and V we thus quantified and modelled flow fields and settlement patterns around individual cockle siphons, and assessed the predation risk of individual larvae as a function of adult density and flow regime.

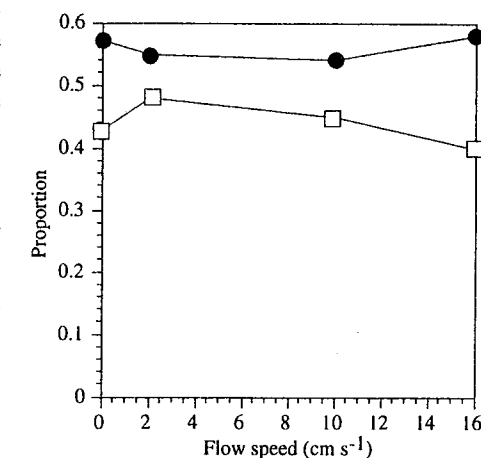


Fig. 7. Interaction plot of the proportion of settled particles in the inner area (□) and the outer area (●) as a function of flow.

The primary aim of paper IV was to quantify settlement patterns of fluorescently stained larval mimics as a means to model the hydrodynamic conditions near bivalve siphons. A series of flume experiments showed that passive sedimentation intensity decreased about 20% close (≈ 1 cm) to the inhalent siphon of adult *Cerastoderma edule* and that changes in the ambient flow speed (0-16 cm s⁻¹) had minor effect on the observed sedi-

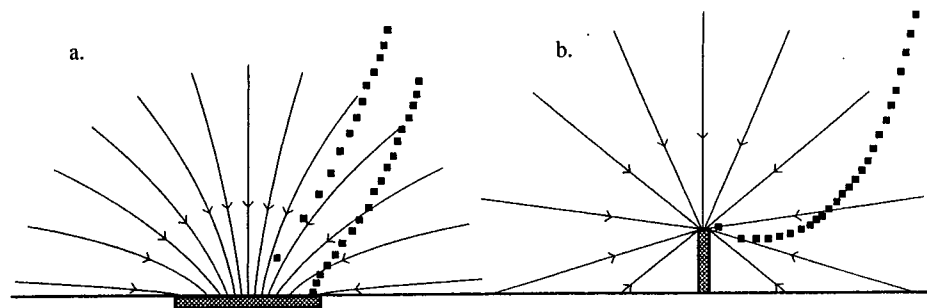


Fig. 8. Schematic drawing of the impact of the two different hydrodynamic models of inhalant siphonal currents on settling particles in still water. Arrows show inhalant flow lines in the plane of the paper. (a) Model with siphon orifice flush with the substratum surface, (b) model with a protruding point sink. Particle trajectories are indicated with dots separated by a constant time interval.

mentation patterns (Fig. 7).

Attempts to numerically model small-scale sedimentation patterns suggested that the observed decrease in sedimentation near inhalant siphons is not an automatic consequence of suspension-feeding. Thus, decreased sedimentation was only observed when the model siphon was located a few mm above the sediment surface where inhalant flow lines are directed away from the sediment surface (Fig. 8). Possibly, this may explain some of the inconsistencies among previous field experiments (Young 1990; Olafsson et al. 1994).

Similar experiments were then performed with competent, laboratory reared larvae of *Cerastoderma edule* (Paper V) thus incorporating larval behaviour. These experiments suggested that despite the characteristic swimming behaviour described in paper III, the settlement patterns around individual cockles were similar in range and intensity to those displayed by passive particles (Paper IV). This relatively modest reduction in settlement does, however, not reflect the intensity of predation over a bed of adult cockles. Observations of settling larvae revealed that the rate of predation on larvae was considerable in flow speeds of 5 and 10 cm s⁻¹. The drifting settlement behaviour made larvae extremely susceptible to adult predation and approximately 70% of the larvae were inhaled during passage over the 40 cm long working section which was stocked with adult cockles (380 m⁻²). The

average larval survival time in the flow tank working section was c. 1 min. Furthermore, direct observations of larval movement did not provide any evidence of active microhabitat selection or tendencies towards gregariousness on the scale of individual cockles.

The risk of predation is to a large extent a function of predator encounter rate. To evaluate the risk of predation under a wider set of flow speeds and adult densities, a numerical model was formulated. Using the measured pumping rates, near-bed velocity profiles and drifting velocities, larvae were exposed to different densities of adults and flow speeds in an

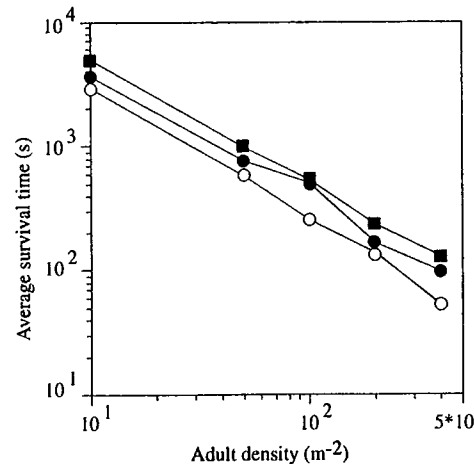


Fig. 9. Average survival time as a function of adult density at 2 (■), 5 (●) and 10 cm s⁻¹ (○). Redrawn from fig. 7a in paper V.

infinite space. As a first validation, the predicted average survival times at a density of 400 m⁻² and 5 and 10 cm s⁻¹ were in the same range as observed in the flow tank experiments (Fig. 9). The model predicts that survival times are highly dependent on adult density. A 40-fold increase in adult density decreases the average survival time by two orders of magnitude. Increasing the flow speed, and thus the encounter rate, also affects the survival time of larvae but to a lesser extent.

In conclusion, the experiments and models show that small-scale settlement behaviour of *Cerastoderma edule* larvae interacts strongly with boundary-layer flow and that this has implications for the risk of predation by suspension-feeding adult bivalves. Furthermore, it is suggested that variability in the settlement of larvae caused by adult consumption is manifested mainly on larger spatial scales rather than around individual adult bivalves.

Hydrodynamic transport of juvenile *Mya arenaria*. In contrast to sessile invertebrates populating hard substrata, sediment-living organisms such as burrowing bivalves do not necessarily remain at the site of initial settlement. Although adult bivalves may have the ability to migrate short distances it is reasonable to assume that early post-settlement movements are more important in redistributing settled individuals. Especially in high-energy tidal flats, field experiments have shown that post-settlement hydrodynamic transport of bivalve juveniles may be important in redistributing and structuring populations spatially (e.g. Baggerman 1953; Emerson and Grant 1991). The purpose of paper VI was to investigate the susceptibility of newly settled juvenile soft-shell clams, *Mya arenaria*, to hydrodynamic sediment transport. More specifically we wanted to define under what flow regimes settled individuals may persist and to assess the importance of juvenile behaviour to prevent bed-load transport.

The experiments revealed that newly settled juveniles have some possibilities to avoid

post-settlement transport. Observations showed that larvae burrowed immediately and unless there was extensive sediment movements this behaviour protected them from being transported. Thus the transport of larvae is largely governed by the magnitude of sediment movements.

Sediment movements are initiated when the shear velocity exceeds a certain sediment-specific critical shear velocity. The critical shear velocity depends on grain size but may also be greatly affected by biological processes; e.g. benthic microflora will increase the critical shear velocity (Madsen et al. 1993). This means that the critical shear velocity is a better predictor of juvenile transport rather than the absolute values of the shear velocities reported in this study.

Genetic markers in larval ecology. In this thesis I have argued that small- and mesoscale processes may be of key importance to population dynamic models of marine organisms in general, and to populations of intertidal bivalves in particular. The papers presented here deal mainly with small-scale hydrodynamic processes, but as emphasized above it is crucial to assess variability and processes on a broad range of spatial and temporal scales. The small size of larvae in combination with their potentially large-scale dispersal capabilities, however, makes it a very difficult task to quantify vital population parameters for these organisms.

A partial solution to this problem may be the recent developments of PCR (Polymerase Chain Reaction) based DNA-techniques which are becoming increasingly accessible as standard tools. Due to the small amount of tissue needed for genetic analyses and due to the wealth of information contained in the genome, these techniques offer new possibilities to analyze single larvae. Using these techniques it will be possible to approach problems in larval ecology that previously were hardly feasible: e.g. identify and monitor large- and mesoscale movements and patchiness of lar-

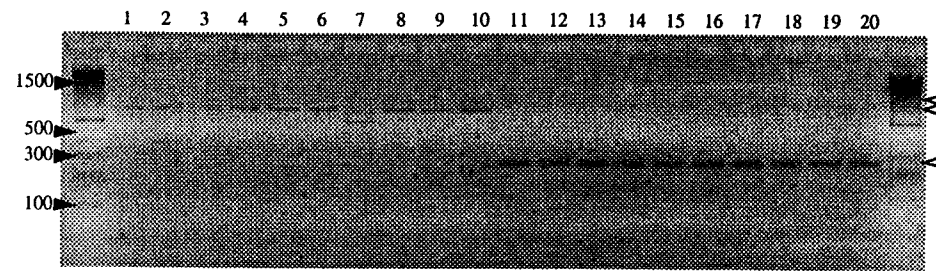


Fig. 10. Photo of agarose gel showing RAPD banding patterns of larvae of *Cerastoderma edule* (lanes 1-10) and *C. lamarcki* (lanes 11-20). Black arrows indicate the position of 4 DNA fragments with known base pair length and white arrows indicate the position of diagnostic DNA fragments.

val cohorts, assess differences in reproductive success and safely identify early larval stages to the species level (Paper VII).

Identification of bivalve larvae. To resolve questions about various recruitment processes, important to population regulation in benthic marine invertebrates, it is imperative to have reliable methods which can identify larvae and early juveniles to the species level. Today the inability to identify larvae of marine invertebrates considerably limits the testing of hypotheses about various recruitment processes in the marine environment (e.g. Olson et al. 1991). Consequently, more reliable identification techniques would be an important contribution to a better understanding of the processes that structure and regulate populations of benthic marine invertebrates.

The two sibling species *Cerastoderma edule* and *C. lamarcki* are both common on the Swedish west coast but in general they differ in the kind of habitat that they live in. A first step towards elucidating the processes behind these differences is to investigate whether larvae from both species are available in the two habitats. Based on morphological criteria, however, larvae of the two species are indistinguishable and thus this question would hardly be possible to address without any other identification criteria.

Using random amplified DNA polymorphisms (RAPD) (Williams et al. 1990) larvae

of the two species could, however, be readily distinguished from each other and from 5 other common intertidal bivalves (Paper VII). After screening some 30 different primers we selected one primer which was diagnostic for both species and gave easily detectable banding patterns (Fig. 10). This demonstrates that RAPD is promising tool for identification of field collected larval samples. For identification purposes we selected a primer which had minimal intra-specific and maximum inter-specific variation. Most primers, however, yielded much intra-specific variation which opens prospects for analysis of low level phylogenetic relationships such as population divergence and paternity even for single larvae.

Conclusions. This thesis presents experimental evidence of hydrodynamic influence on the behaviour of marine bivalve larvae and juveniles (Papers III, V and VI). A physical model which predicts larval behaviour in different regimes of shear flow is proposed (Paper III), and the implications of this behaviour to interactions with suspension-feeding adult bivalves are explored in subsequent experiments (Papers IV and V). Summing up these results, it is appropriate to consider them in a wider perspective: What conclusions can be drawn from these experiments, in the context of the observed spatial population structure of sediment-living marine bivalves (Paper I)? What implications do the observed hydrodynamic

effects have for the importance of various ecological interactions previously proposed to involve larvae?

It is beyond the scope of this thesis to evaluate the relative importance of pre- and post-settlement processes to the population ecology of shallow water sediment-living bivalves, which is still much of an open question. Throughout this thesis I have, however, argued for the importance of relating processes to relevant temporal and spatial scales. Obviously, this has implications also on the results presented in this thesis.

The patterns observed in paper I indicate that most of the variability in abundance and age structure of cockles on the west coast of Sweden occur among and within bays on spatial scales equal to or smaller than 10^3 m. This means that the processes likely to account for most of the variability is likely to vary in intensity on those spatial scales. Thus, if hydrodynamics is in any sense important in structuring these populations it should be attributed to small- and mesoscale processes (Fig. 2) and not to large-scale currents.

Flume observations of individual larvae and juveniles indicating hydrodynamic influence on settlement behaviour, predation risk and post-settlement transport are by definition reflecting small-scale events ($<10^1$ m). The models proposed here are mainly aimed at predicting small-scale spatial patterns of variability. However, if critical parameters, e.g. the near-bed velocity gradient or the abundance of filter-feeding adult bivalves, vary on larger scales, these small-scale mechanisms may also mediate the formation of large-scale recruitment patterns.

Furthermore, the studies of small-scale larval and juvenile behaviour have shed new light on previously proposed processes regulating the recruitment of marine sediment-living bivalves. Although we did not observe or quantify any habitat selection behaviour of larvae, the model of larval swimming behaviour predicts under what flow regimes larvae may be able to actively manoeuvre in the

near-bed velocity gradient and thus potentially perform habitat selection (Paper III). The observations did not reveal any evidence of gregariousness on the scale of individual cockles as previously proposed (Paper V). The possibilities of gregariousness on larger scales, however, still remain.

Previous field experiments on predation from adult suspension-feeders have yielded inconsistent results. Our studies indicate that weak effects on small-scale settlement patterns are expected and may depend on the location of feeding structure (Paper IV). Effects on larger spatial scales may, however, occur and due to the hydrodynamic modification of larval behaviour, predation rates may be substantial (Paper V).

The experimental procedures used in this thesis allowed detailed observations and quantification of larval behaviour and hydrodynamic conditions. To be able to evaluate the importance of settlement variability as a function of near-bed flow in a wider context, a necessary development of these studies is to move into field observations and experiments. Using high-resolution optics it may be possible to reproduce the detailed observations of larval behaviour and quantification of near-bed flow conditions also in the field. Furthermore, it may be suggested that studies of small- and mesoscale circulation patterns in the coastal zone and how this affects spatial and temporal variability of larvae may prove to be a fruitful approach in further studies of the role of hydrodynamic effects on recruitment. In this context the development and application of new genetic markers (e.g. Paper VII) may be of key importance.

Acknowledgements

I wish to express my deepest gratitude to Per Jonsson who has been a super supervisor, friend and personal ostrich consultant during these years. I also thank Carl André who has been a super 'co-

supervisor' and friend during the same years: Working with you two has been a great pleasure, even though I still don't understand your bizarre interest in Swiss army knives, small torches and water-proof clothing!

Many friends and colleagues have made Tjärnö Marine Biological Laboratory a very special place for me. I am very grateful to all of you!! To mention a few I would like to thank Lars Afzélius for creating such a positive and generous working atmosphere; Hans G. Hansson for his assistance in computer chaos and for generously sharing the crops of his garden and carboys; Benno Jönsson for always being extremely helpful and for introducing me to Fransson, Strindberg and Sigrid; Per Nilsson for many interesting discussions and for not playing too much 'Sven-Ingvars'; Fredrik Pleijel for being a good friend and for his never ending belief in the ecological significance of plastic particles and Eva-Marie Rödström for being a dear friend and for tolerating my bad language and computer abuse (together with Bonnie and Rasmus).

I thank the people at Kristineberg Marine Research Station and the Marine Research Institute in Lysekil connected to Marine Zoology for the constructive working spirit in trying to develop the new 'department' and I also thank my friends at the Department of Zoology for inspiring nights at the 'Gyllene Prag'. I thank Per Sundberg and the people in the 'Gaza-remsan' for introducing us to DNA-methods. Many friends and colleagues at the Department of Marine Botany have also been very helpful during these years. Especially, I would like to thank Henrik Pavia and his family for their friendship and support.

I think that my parents and the rest of my family have for a long time wondered when I will stop 'school'. This is it! Anyway, I would like to thank you all for your support and care.

Per Jonsson, Carl André and Rutger Rosenberg commented on earlier drafts of this thesis and I thank Bob Scott for designing the cover and for giving me all sorts of advice in how to layout the thesis. Vladimir Kostylev and Tomas Dahlgren also assisted in attempts to recover lost files.

Susanne Svensson commented on me during the last two years and I love her for that among many other things. You mean very much to me!

Financial support was provided by Göteborg

University Marine Research Centre. Additional support was provided by the foundations of Colliander, Helge Ax:son Johnsson, Lars Hiertas Minne, Wilhelm och Martina Lundgren and Hierta Retzius.

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