

Literature review of
the “Blue Corridors” concept
and it’s applicability to
the Baltic Sea



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0 **PREFACE**

This report, which is a product of the BALANCE project (2006-2008), is a literature review focusing on the “Blue Corridor” concept and its applicability to the Baltic Sea.

The report discusses various aspects of connectivity among vulnerable marine areas and marine protected areas as an essential element of management of marine areas in order to contribute to maintaining the biological structure and function of the Baltic Sea ecosystem.

The elements included are:

- Connectivity among the marine habitats and ecosystems
- Biogeographic aspects of the Baltic Sea ecosystem
- Temporal and spatial differentiation in Life cycles of Baltic species
- Genetic aspects of connectivity in the conditions of the Baltic Sea
- Connectivity of populations, habitats, ecosystems used in MPA planning internationally. International examples.

This literature review is the first of two reports focusing on the blue corridor concept. The second report will be available during the autumn of 2006 on the Balance web site.

More information about BALANCE can be found at <http://www.balance-eu.org>.

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1 INTRODUCTION

The assessment of coherence and connectivity of MPA networks in the Baltic Sea requires the identification of possible ways of improvement of the current situation. This could be achieved either by enlarging the amount of the sea area covered by MPA network or improving the connectivity between the protected habitats by establishment of a so called “Blue corridors” system covering the entire sea area. This report is a first step in a set of activities directed towards implementation of the “blue corridors” concept in the Baltic Sea area aiming to collect the available international and local knowledge covering the topics relevant to illustrate the connectivity issues in marine environment which will be followed by more practical and technical manual on use of the concept.

1.1 Definitions:

Blue corridors:

A general definition of a Blue corridor could be as follow. A blue corridor can be considered as a channel or a route of particular importance for the population exchange between locations and of importance for the maintenance biogeographical patterns of species and communities. Blue corridors are shaped either by biological mechanisms thus describing the possible route, or the route of choice of migrating motile organisms or the corridors can be shaped by physical factors when biota is transported passively by currents. In the context of planktonic dispersal, passive transport, blue corridors should refer to non-random biogeographical patterns of benthic organisms established by routes of dispersal via currents.

Connectivity in the context of Blue Corridors

Connectivity refers to the effectiveness by which population exchanges occur along the trajectories of a blue corridor. The levels of connectivity should be considered as 1) high if population exchange between populations efficiently prevents local population dynamics. 2) Medium if populations are restored within reasonable time following extinction of subpopulations. 3) Low if local sub-population develops with population dynamics being unaffected by regional population dynamics and restoration takes very long time following extinction events. 4) Non-existing when endemism develops. At the ecosystem level connectivity could be quantified in a similar way depending on the degree to which the integrity of the ecosystems is regulated by regional or local processes.

2 CONNECTIVITY AMONG THE MARINE HABITATS AND ECOSYSTEMS

2.1 Connectivity of marine communities on habitat and landscape scales

The influence of habitat structure on species persistence at the landscape scale is receiving increasing attention as human activities continue to drastically alter the configuration of natural habitats. Generally, the conversion of continuous habitat to small isolated patches (i.e. habitat fragmentation) generally decreases the reproductive output (Temple & Cary 1988, Robinson et al. 1995), movement (van Appeldoorn et al. 1992), survival (Andr n 1992, Robinson et al. 1995), and population size (Brittingham & Temple 1983) of many species in terrestrial landscapes.

Benthic habitats have high structural variability at local (<1 to 10s of m) and landscape (100 to 1000s of m) scales and this variability is closely linked with physical setting. Identification of the relevant scales of variability in space and time is a prerequisite to understanding factors and processes generating patterns in biotic and abiotic components of ecosystems (Levin 1992). Macrobenthos is a key element of many marine and estuarine monitoring programmes, but usually these programmes do not (or cannot) explicitly take into account distribution patterns at different spatio-temporal scales.

The relative mix and intensity of factors controlling succession change varies between different spatial scales. As a result, successional dynamics may vary considerably as the spatial scale of disturbance increases. At small scales, factors at each level of the spatial hierarchy are important. The greater potential for biotic interactions at this scale may be particularly critical. At meso- to large scales population processes and environmental conditions have the most influence on successional dynamics. Due to these differences, responses to small-scale (<1 m²) as well as large-scale (>1 hectare) disturbances may be quite variable. Within this range (>1 m² < 1 hectare), short- and long-term responses to disturbance may be relatively more predictable and conform to current models of succession in benthic habitats (Zajac et al. 1998).

In general local- and landscape-scale habitat structure shape faunal communities in macrophyte habitats. However, the scale dependency of faunal responses to environmental variables may differ greatly between macrophyte landscapes. High variability in macrophyte landscape structure does not necessarily correspond to variability in faunal abundance. These findings are wholly unlike those of terrestrial ecosystems, where equivalent ranges of landscape structure might be expected to strongly influence faunal abundance and composition (Saunders et al. 1991, Andr n 1994).

As in fragmented forests, variation in sea grass habitat structure at the landscape scale (100s to 1000s of m) may influence large-scale processes that shape faunal abundance and structure communities (Hovel & Lipcius 2001). At the local scale (<1 to 10s of m), elements of sea grass structural complexity such as shoot density, shoot biomass or leaf surface area are the important determinants of faunal abundance (Orth 1992). Faunal abundance is enhanced in areas of high shoot density or biomass due to reduced preda-

tor foraging efficiency and enhanced living space and food. Structurally complex sea grass beds also may be actively selected by fauna (Orth 1992, Worthington et al. 1992). Though positive relationships between faunal abundance and structural components of sea grass beds such as shoot biomass and shoot density are common, few studies have measured the effects of large-scale habitat structure (e.g. percent cover, edge, patch size) and energy regime on faunal abundance in sea grass habitats (Turner et al. 1999, Hovel et al. 2002). Moreover, local- and landscape-scale sea grass habitat structure are strongly related to hydrodynamic activity, and this co-variation makes it difficult to determine which processes are chiefly responsible for shaping faunal communities.

Spatial patterning of habitats at the landscape scale often has strong effects on processes such as predation that influence faunal abundance. Landscape structure also may be an important determinant of faunal abundance and survival in marine systems. Bivalve survival was reduced in small sea grass patches (Irlandi 1997) and in areas of low sea-grass cover (Irlandi et al. 1995) in Back Sound, and the crab survival and density were lowest in seagrass patches of intermediate size in Chesapeake Bay (Hovel et al. 2002). Dense seagrass shoots interfere with predator search and capture of prey (see reviews by Orth et al. 1984, Heck & Crowder 1991) and thus areas of high structural complexity serve as refuges from predation for many species. In the Schelde estuary, however, the region scale spatial effects (104 m) on the dominant macroinvertebrate species were not significant (Ysebaert & Herman 2002). In the case of temporal variation between years, there was a number of dominant species showing significant synchronicity in temporal development between stations. Those species e.g. *Macoma balthica* and *Pygospio elegans* are also commonly found in the Baltic Sea area. It is suggested that climatic factors can synchronise population changes over wide geographical areas if they have a direct effect on recruitment or mortality. In general, the magnitude of recruitment was extremely variable between years, and rarely showed co-variation between different species within a given year. The potential causes and consequences of this variability, in conjunction with spatial scale, probably vary on a species-to-species basis.

In the previous study variations at the scale of stations was the most important component of variability for most species. The species composition of the assemblage and the abundance of the individual species are dependent on the abiotic characteristics of (mostly) the station. Spatial distribution of macrofauna at larger scales (hundreds of meters) appeared to be more related to physical factors (topography, current shear stress, wind stress) (Legendre et al. 1997), whereas at scales of meters adult-larva interactions seemed to be an important factor producing patches of macrofauna (Turner et al. 1997). Thrush et al. (1997) concluded that different processes operate at different spatial scales and that processes operating at small scales can influence large-scale patterns.

Subdivision of the environmental variables into a long-term average and a temporal component always shows that the long-term averages were much more important than the short-term deviations from this average. It is concluded, therefore, that species adapt to local (10 to 100 m scale) average conditions, but are relatively insensitive to short-term or very small-scale variations in their environment (Ysebaert & Herman 2002).

Hydrodynamic regime influences the density of a variety of fauna at various spatial scales. Hydrodynamic setting may influence faunal abundance indirectly by modifying seagrass (e.g. canopy geometry, percent cover, patch size) or sediment characteristics (e.g. sediment organic content and silt-clay; Fonseca & Bell 1998). Besides, waves and

currents may directly influence the density of some crustaceans and fishes, perhaps by influencing feeding rates (Bell et al. 1994), larval availability and settlement (Orth 1992, Worthington et al. 1992) or locomotion (Vogel 1994). Sea grasses often form extensive, continuous meadows in areas of low hydrodynamic activity but can be maintained as small, isolated patches by strong waves and currents and bottom feeding and burrowing animals (Hovel et al. 2002).

Faunal habitat associations at small spatial scales may not exist over larger scales, perhaps due to patchy distributions of settling larvae (Worthington et al. 1992) or faunal movement from patch to patch (Sogard 1989). Therefore, in contrast to many terrestrial landscapes, complex interactions between a variety of processes across several spatial scales may limit the extent to which faunal densities in macrophyte habitats are correlated with landscape- scale structure, even if strong relationships exist between structure and key interactions such as predation.

2.2 *Connectivity within habitats: implication of habitat fragmentation*

Habitat loss and isolation associated with land conversion for human activities pose perhaps the most severe threat to the earth's biological diversity. Because the study of habitat fragmentation provides an important link between the concepts of landscape ecology and the practice of landscape architecture and planning it becomes essential to study the ecological consequences of changes in the spatial characteristics of native habitats. 'Habitat fragmentation' is often defined as an increase in distance among habitable patches (habitat proximity) and/or a reduction in the number of remnant habitats (habitat number) (reviews in Andr en 1994, Zuidema et al. 1996). Two paradigms dominate current research, the species-area relationship, and the species isolation relationship (McArthur & Wilson 1967, Hanski 1994). Greater rates of extinction occur in landscapes with fewer or smaller patches of habitat. Rates of colonisation to distant patches of habitat may decrease because dispersal is diminished by increased risks associated with travelling larger distances through relatively inhospitable areas. Small populations are more likely to become extinct (review in Gilpin & Soul e 1986), hence rare species, either because they occupy a small number of habitats or because they make up a small proportion of total abundance among habitats, are likely to be sensitive to the adverse effects of modification of habitat.

2.3 *Importance of spatial characteristics of habitat fragments on colonisation success*

An important spatial factor, which can affect the succession of marine assemblages, is the size of the area or patch being colonised (e.g. Benedetti-Cecchi and Cinelli 1993). One of the longest-surviving mathematical relationships described in ecology is that relating the number of species to the available (or sampled) area (e.g. Arrhenius 1921). This relationship has been explained by "random placement hypothesis" (Arrhenius 1921, Coleman 1981), is that increases in area result in increases in the number of organisms and thus increases in the number of species, purely as a random process, an artefact of an increase in the size of the sample. Experimental tests on the validity of the species-area relationship showed that the concept should not necessarily be regarded as

a truism as it did not always hold in this system (Anderson 1998). The named study focused on small-scale effects of area on species colonisation in a very limited range. No biogeographic-scale models were tested. Besides, the initial timing of experiments with respect to recruitment and succession influenced the results. An alternative hypothesis is the "habitat diversity hypothesis", which suggests that the number of species is greater in larger areas because of a related increase in the diversity of habitats or niches available for colonisation by different species (Williams 1943; Connor and McCoy 1979). Another alternative hypothesis explaining the species-area relationship is the equilibrium theory of island biogeography (MacArthur and Wilson 1967). The (equilibrium) number of species is expected to be lower on smaller islands (or patches) because the immigration rates will be lower and the extinction rates will be greater than on larger islands. With the increasing fragmentation of habitat, and increasing concern for biodiversity (which often includes measures of species number), a re-examination of the species-area relationship, and its possible extension to include multivariate measures, is timely and important.

Many habitat fragmentation experiments make the prediction that animal population density will be positively related to fragment, or patch, size. So far the mechanism that is supposed to result in this prediction is unclear. Only a minority of possible scenarios produces positive density vs. patch size relationships. More commonly, these relationships are expected to be negative. These results demonstrate the importance of autecological mechanisms such as immigration behaviour when developing the predictions that is currently tested in habitat fragmentation or other experiments (Bowman et al. 2002).

2.4 *Effects of habitat fragmentation vs habitat loss on marine populations*

Recent studies have suggested that loss of habitat has a greater influence on population dynamics relative to habitat fragmentation (break up of continuous habitat) which only affects abundances in landscapes with a small amount of habitat. Results of empirical studies of habitat fragmentation are often difficult to interpret because many researchers measure fragmentation at the patch scale, not the landscape scale and most researchers measure fragmentation in ways that do not distinguish between habitat loss and habitat fragmentation per se, i.e., the breaking apart of habitat after controlling for habitat loss. Empirical studies to date suggest that habitat loss has large, consistently negative effects on biodiversity. Habitat fragmentation per se has much weaker effects on biodiversity that are at least as likely to be positive as negative (Andr n 1994, Fahrig 1998, Trzcinski et al. 1999, Fahrig 2003). Regardless of the scarcity of experimental studies about habitat fragmentation, the general conclusions drawn from the experimental study on grassland insect populations (Collinge 1998) are likely applicable for many other ecosystems. In this study the following generic effects of the habitat fragmentation were listed: (1) fragment size influenced species loss; small fragments lost species at a higher rate than did larger fragments; (2) corridors reduced rates of species loss, but only in medium-sized fragments; (3) corridors enhanced re-colonisation of medium-sized fragments, (4) one of the three insect species examined moved preferentially in corridors; and (5) spatial configuration of land conversion sequences significantly influenced species richness.

It has been demonstrated that plant species richness in eucalypt forest fragments of eastern Australia is determined by a complex interaction among patch size, age and disturbance history. Here, the nature of the disturbance plays a key role in determining native species richness, which may increase following a natural disturbance, such as fire, but decrease following anthropogenic disturbance (Ross et al. 2002, Drake et al. 2002).

Sea grass is often the dominant subtidal vegetation in near shore coastal marine environments, and supports large standing crops and high species diversity of organisms. Sea grass meadows may become fragmented through the feeding activities of epibenthic predators (e.g., crabs and rays) and herbivores (e.g., sea urchins), and through anthropogenic impacts such as damage from boat propellers and dredging (e.g., Peterson et al., 1987; Valentine and Heck, 1991; Fonseca, 1992). Effect of fragmentation of the sea-grass *Enhalus acoroides* meadow on its reproductive output was quantified in the reef flats off Bolinao (NW Luzon, The Philippines). *E. acoroides* and overall sea grass cover were correlated positively. The proportion of female flowers of *E. acoroides* that developed a fruit increased sharply as overall sea grass cover was around 50%. This threshold-type of relationship suggests that fragmentation of sea grass meadows can have a major effect on the reproductive output of this but potentially other similar species. A possible mechanism underlying these results would be a non-linear increase of the efficiency of trapping the surface-dispersed pollen with increasing sea grass canopy density (Vermaat et al. 2004).

The experimental study on macrophyte community in marine system showed that loss and fragmentation of habitat did not operate independently at many scales. Patterns of diversity responded markedly to decreases in number of habitats, but this effect was reduced when neighbouring habitats were proximate rather than distant i.e. the spatial pattern of habitat compensated for the decrease in diversity associated with loss of habitat per se. Rare rather than common taxa primarily responded to these varying aspects of fragmentation. Awareness that number and proximity of patches are not independent at local scales may provide insights needed to predict the effects of habitat fragmentation on biodiversity, particularly on components of assemblages that tend to be rare (Goodsell & Connell 2002). Earlier studies on benthic invertebrates have also reported that rare species are disproportionately affected by loss and fragmentation of habitat (Didham et al. 1998, Golden & Crist 1999). These studies indicate that identifying rarity within habitats may be a crucial component of understanding the effects of fragmentation on biodiversity. Unfortunately, it is common practice for ecologists to omit rare species from multivariate analyses of assemblage structure because they seldom affect their outcomes (Gauch 1982).

The effect of size and proximity of a habitat to the diversity of neighbouring habitats is species specific. The composition of polychaetes differed between near and far habitats independent of habitat size, while copepod composition only differed between sizes of habitat when they were far apart (Russel et al. 2005). Passively dispersed epifauna respond to the shape and orientation of macrophyte patches when currents, the dispersal mechanism, are strong, but not when they are weak. Currents affect less taxa that actively disperse, or that are relatively sedentary (Tanner 2003). In the experimental study in Back Sound, North Carolina macrofauna responded to habitat patchiness in a complex manner that varied according to habitat type, site, species, taxon, functional group, and animal body size. There was a disproportionate reduction in macrofaunal abundance and diversity in small patches of oyster shell compared to sea grass and mixed habitat

treatments. The patterns observed in this study highlight the importance of scale- and habitat dependent responses by mobile organisms to complex benthic habitats, and, because of the disproportionate reduction in faunal density and diversity in small versus large patches of oyster shell, heightens concern over the negative impacts to biodiversity through large-scale fragmentation of subtidal oyster reefs in certain regions (Eggleston et al. 1999).

2.5 Artificial structures and habitat fragmentation

The progressive increase of a variety of artificial structures in shallow coastal waters, such as breakwaters, seawalls, jetties, groynes, pier-pilings and floating pontoons, has raised concern about their effects on natural assemblages of organisms. A number of studies have shown that subtidal and intertidal epibiota on artificial structures can be different from those occurring on adjacent natural rocky reefs, suggesting that the introduction of built structures can cause loss and fragmentation of natural habitats (Bulleri & Chapman 2004, Bulleri 2005). Few studies have attempted to identify the mechanisms underlying the establishment of different assemblages on natural and artificial structures, even though they could provide key information for management of urban waterways. Chapman and Bulleri (2003) have shown that, in Sydney Harbour (NSW, Australia), high- and mid-shore assemblages on seawalls were distinct from those found on adjacent vertical rocky reefs. Although seawalls and rocky shores supported similar suites of species, there were differences in terms of frequency of occurrence and relative abundances. Colonisation of cleared space differed between rocky shores and seawalls and it has been suggested that variation in the recruitment of algae and invertebrates between natural and artificial structures could have caused the occurrence of distinct mature assemblages. However, in another study the effects of the introduction of artificial substratum were negligible and the variability of other factors operating differentially between different habitats had stronger impact on the re-colonization and development of communities (Bulleri 2005). Understanding how physical features of artificial habitats affect ecological processes could enhance our ability to mitigate changes caused to natural assemblages, by designing artificial structures to better mimic natural rocky habitats.

2.6 Habitat fragmentation and dispersal of marine species

The effect of habitat fragmentation on biota is dependent on the dispersal mode of the species. In both terrestrial and marine ecosystems, most dispersing units move relatively short distances away from the source. Long distance dispersal events are typically rare in both plants (Willson, 1993) and animals (Paradis et al., 2002), although they are probably more prevalent in marine systems (Kinlan et al., 2005). Long distance dispersal can be highly case-specific and it is commonly greatly underestimated (Trakhtenbrot et al. 2005). Invertebrates with pelagic larval dispersal (e.g. polychaetes & echinoderms) are proposed to have better dispersive capabilities than do those with brooding or direct development (e.g. crustaceans) (Christie et al. 1998). Some filamentous ephemeral macroalgae have spatially and temporally much longer dispersal than perennial macroalgae, such as many kelps (Reed et al. 1988). Recent studies in sea grass systems suggest that many small sea grass patches may increase the overall probability of encounter by larvae or other immigrants, thereby increasing overall colonisation of the

patch, compared to larger patches (e.g., Sogard 1989; Worthington et al., 1992). Therefore it was proposed a conservation strategy for sea grass associates that attempts to preserve discrete sea grass beds within a larger area, rather than preserve one large contiguous bed (McNeill and Fairweather 1993). Differences in the response of organisms in terrestrial versus marine systems to habitat patchiness, if they prove to be general, may be due to greater dispersal limitation in terrestrial versus marine systems (e.g., Robbins and Bell, 1994), and the increased negative impacts that physical fluxes (e.g., radiation, wind, water) have across smaller patches in terrestrial systems (Saunders et al., 1991). In another study, where the relative effect of habitat fragmentation on benthic invertebrates was studied (Frost et al. 1999), the authors concluded that the infaunal community is the component least likely to be affected by fragmentation at small spatial scale whereas the significant difference in community composition is expected for more sensitive and high-profile parts of the biota (e.g. fish).

The effects of habitat fragmentation may be difficult to predict for many mobile benthic invertebrates such as shrimps and lobsters that have the changing habitat requirements during their life cycle. Sea grass and oyster beds are known to serve as settlement habitat for larval recruits. Vegetated substrates may function as movement corridors for juveniles but also predators and may facilitate dispersal to areas containing new resources. The effects of insularity on a population may be lessened by the nature of surrounding habitats if those habitats have important functional roles as larval settlement areas e.g. foraging grounds or movement corridors. An organism's response to habitat patchiness is species-specific, and that for a given species, the response is further modified by animal density and body size. Protection of a specific habitat may be ineffective if related habitats are left unprotected. Conservation strategies for mobile benthic species need to incorporate the protection of areas with heterogeneous habitats that are important to meet the changing habitat requirements of complex life cycles (Eggleston et al. 1998, Acosta 1999, Micheli & Peterson 1999, Russel et al. 2005).

The habitat fragmentation may indirectly favour the establishment of non-indigenous species in case negative biotic interactions by resident species may prevent successful invaders from becoming pests (Reusch & Williams 1999). The eelgrass affects the growth and survival of the non-indigenous mussels such as *Musculista senhousia* through reducing the available food inside the vegetation. Concurrent with the fragmentation of eelgrass canopy either due to extreme weather condition or human disturbance, the density of the suspension feeders increases. The dense beds of *Musculista* impede the rhizome growth and vegetative propagation of eelgrass and finally may pose the threat to the persistence of eelgrass beds.

When designing the networks of a MPA, species-specific effects of habitat loss and fragmentation, together with habitat composition, should be taken into account and based on these relationships the species probabilities of local occurrence should be computed. Sites are then chosen to represent all species with a given target probability. Earlier studies have shown that the results of computation depend on the number of species for which the spatial configuration plays an important role, and on the pattern and amount of habitat loss that is expected to follow around the reserves. The method represents a step towards taking better into account species persistence when selecting reserve networks in a changing world (Cabeza 2003).

To date there exist no descriptive and/or manipulative studies combining the effect of spatial orientation and fragmentation of habitats in the Baltic Sea area. Thus, it becomes necessary to evaluate the effect of spatial distribution of habitats at various spatial scales on benthic macroalgal, invertebrate and fish communities. In order to reveal the cause-effect relationships of observations these studies should be followed by manipulative experiments. This hierarchical design should enable to describe the effect of habitat fragmentation on different groups of marine organisms on different spatial scales.

3 BIOGEOGRAPHIC ASPECTS OF THE BALTIC SEA ECOSYSTEM

3.1 Hydrology

The Baltic Sea is the world's largest brackish water body. It covers approx. 415,000 km², having a volume of 21,000 km³. The catchment area comprises 1,671,000 km² (Kortum 1996). It is connected with the North Sea via the Kattegat and Skagerrak and stretches 1,200 km in east-west direction from the Kattegat to the Gulf of Finland and 1,300 km in south-north direction from the Odra Bight up to the Bothnian Bay, close to the Polar circle. The hydromorphology of the Baltic Sea is rather complex (Köster and Lemke 1996). Several underwater barriers and deep basins follow each other, subdividing the Baltic Sea into several districts. Roughly the main districts are: the Bothnian Bay in the outermost northern part of the Baltic, followed south by the Gulf of Bothnia. The easternmost part formed by the Gulf of Finland, the large semi-enclosed part between the Island of Saaremaa and the city of Riga the Gulf of Riga. The main water body, the Baltic Proper, stretches from westernmost Finland to the Danish Islands. The shallow regions south of the Danish Islands forms the Belt Sea, followed north of the Danish Islands by the Kattegat. The Baltic Proper divides into the Arkona Sea and the eastern and western Bornholm Sea. Irrespective of the fact that any of the different regional classification schemes are mainly orientated on the morphology of the Baltic Sea, they reflect also changes in the abiotic conditions, especially salinity. This is caused by the hydrological regime of the Baltic, having only one narrow connection to the fully marine habitat of the North Sea and being located in a humid climate zone. A water budget of the Baltic Sea has been given by Fennel (1996). River runoff was calculated by 483 km³ a⁻¹, whereby the Neva river with 77 km³ a⁻¹, located in the outermost eastern part of the Gulf of Finland, was by far the largest individual component, followed by the Wisła river (Poland) with 34 km³ a⁻¹. The precipitation above sea surface was estimated on 266 km³ a⁻¹, evaporation counts to 207 km³ a⁻¹, resulting in an effective direct freshwater input of approx. 60 km³ a⁻¹. The total freshwater input therefore sums up to 540 km³ a⁻¹. This surplus of freshwater input gets counteracted by inflow of marine water via the Skagerrak and Kattegat.

The mechanisms of the water exchange between the Baltic Sea and the North Sea are very complex. The brackish water originating from the Baltic Sea has a lower density and therefore moves on the surface relatively unhampered, driven by gravity because of the positive water budget mentioned above. Salt water inflow from the North Sea is hampered by the numerous underwater barriers and sills, most important ones are the Drogden Sill (the Sound) and the Darss Sill (the Arkona Sea) reaching just 7 m and 18 m, respectively, underneath surface. As a result of these preconditions, a steep salinity gradient along the Baltic Sea can be observed. From almost marine conditions in the Kattegat region, salinity drops within a short distance of approx. 300 km down to <10 psu in the Baltic proper.

Further east, salinity declines more slowly until the Bothnian Bay and the Gulf of Finland, exhibiting very low salinities of approx. 2-3 psu.

However, these statements about average salinities of the open water are of limited value, because it is superimposed by different ranges of irregular fluctuations of salinity at a certain location.

3.2 *Geology/morphology of coastline and seabed*

A survey about coastal structure of the Baltic Sea has been given by Klug (1985), differentiating the Baltic region into 12 coastal types. The pattern of their distribution is not uniform. Whereas the southern coastline is dominated by moraine material, along the northern coast occurrence of hard bottom is more common. It starts at the Jylland region with a rather small area of “seabed” coast, because the north of Jylland is still an uplift area. Further south moraine material becomes dominant, forming “Förden”, or, further south, a pattern of cliffs and shallow bights. The eastern Pomeranian coast is dominated by numerous small lagoons and enclosures, the so-called Bodden and Haffs, whereas the western Polish region is dominated by sandy material of high mobility, forming two large enclosures further eastwards. This coastal type, formed by massive sediment transport, ends at the Estonian coast, being again an uplift area, in which different types of hard bottom coasts predominates as for almost the whole Finnish and Swedish coast. These hard-bottom coasts cannot be seen as a single type, they consists of Fjärd and Fjord coasts, being characterised by bays stretching very deep into the mainland, in most of the cases accompanied by numerous Islands in front of the coast (archipelago), dominating the system in different extent. At the northernmost part of the Gulf of Finland and the Bothnian Bay again relative flat marsh-like regions, characterised by uplifted former seafloors, are dominant. At the Swedish coast, except for Scania, having moraine coast types, hard bottom coast types are predominant. The Danish Islands are dominated by coastal lagoons of the Bodden-type as present in the Pomeranian region of the eastern German coastline.

3.3 *Biological aspects*

Besides all this abiotic factors, also biotic ones differ largely along the Baltic Sea. The first investigations on zoobenthic diversity, done by Remane (1942) showed already the existence of a gradient in species number, related to salinity. The pattern drawn by Remane (1942) showed a decrease in species number until approx. 8 psu, the so-called “horohalinikum”, containing almost only the few brackish water species which can perform hyper- as well as hypotonic regulation, and followed by a steep increase in species number because of the freshwater species able to tolerate low saline conditions. Later surveys about phytobenthos diversity showed a slightly different picture. The decrease in species number was present as well but continued far behind the above-mentioned 8 psu border (Nielsen et al. 1995).

The biological communities of the Baltic Sea in their present state have been formed during a relatively short period. This is a most propable reason for not lack of truly endemic species in the area (Voipio, 1981). It is possible to group all organisms inhabiting present Baltic in the groups originating either from marine environment, fresh-water, or left in the area from previous geological periods (e.g. glacial relicts).

The flora and fauna of the Kattegat region includes most of the groups inhabiting the North Sea but moving further into the Baltic Sea decreases the number of marine species very fast. Several major groups of marine species not present in the Baltic Sea. The decrease in marine species from the southwestern Baltic towards the Gulf of Bothnia is partly compensated by an increase in species of freshwater origin (Leppäkoski et al. 2002).

Baltic Sea salinity gradient has strong effect on the number of species of marine origin. So the numbers of species decrease from almost 850 species of marine animals in the entrance area of the Baltic Sea to 50 in the Bothnian Bay and 10 in the Bothnian Bay and eastern Gulf of Finland, from almost 200 species of macroalgae in the Kattagat area to 10-15 species in the northernmost and easternmost parts of the sea (Nielsen et al, 1995). The number of marine fish species falls from about 70 in the south-western Baltic to about 20 in the Bothnian Sea and 6-10 in Bothnian Bay (Leppäkoski and Bonsdorff, 1989; Elmgren and Hill, 1997).

3.4 Environmental conditions determining the structure of animal and plant communities in the Baltic Sea region

Baltic Sea is a very complex system of environmental gradients of different scales with strong impact on the biological communities both on the regional and local scales where majority of living organisms are experiencing strong environmental stress in terms of salinity, low temperature, and high water turbidity (Waern, 1952; Schramm & Nienhuis, 1996). In the oceans the major structuring factors of communities inhabiting coastal areas are the competition for space, light, nutrients and water motion as well as interaction between different trophic levels (Kautsky & van der Maarel, 1990; Kiirikki 1996). In the Baltic Sea the role of the environmental forcing seems to be stronger and biotic factors have less importance (Kautsky & Kautsky, 1989; Kautsky & van der Maarel, 1990, Kiirikki, 1996, Martin 2000).

The effect of the salinity on the structure of benthic communities on the Baltic Sea scale is well described by several authors (e.g. Waern, 1952; Wallentinus, 1991). As the stable salinity gradient observed in the Baltic Sea on the S-N and W-E directions could create in defined localities favourable conditions for species originating from either fresh water or marine environment, the fluctuations of the salinity in a certain area could, on the contrary, eliminate a great number of species sensitive to extremely low or high salinity values.

Ice conditions can influence coastal biological communities more than open sea ones. Besides the ice scraping of the bottom, which can in several cases affect the bottom up to the depth of 2 (5) m (Waern, 1952), the length of the ice cover affects the length of the vegetation period. In the vicinity of major riverine inflows the severe ice conditions can cause a decrease of salinity in the phytobenthic zone during the winter period, preventing the wind-induced water mixing and formation of stable freshwater zone (1-3 m thick) below the ice (Martin, 2000). The positive effect of length of ice cover period on the biomass of the loose-lying *Furcellaria lumbricalis*-*Coccotylus truncatus* community in the inner sea of West Estonian archipelago was established by Martin & Kukk (1999).

Hydrological parameters in the form of wave action and water-level fluctuations can influence the development of shallow coastal communities in great extent (Kautsky, 1988; Kautsky & van der Maarel 1990). Wave activity affects the phytobenthic communities through the formation of substrate quality and direct physical disturbances (Kautsky, 1988).

Higher nutrient concentrations are supposed to favour fast growing and short living filamentous algae (Schramm & Nienhuis, 1996). The share of annual/perennial species in an area could be used as indicator of the trophic conditions as well as overall harshness of the environment (Kautsky, 1995).

Sedimentation rate is one of the most powerful factors regulating the biological diversity and structure of the communities on deeper edge of distribution of macroalgal vegetation (Kiirikki, 1996, Johansson, 2002, Eriksson & Johansson 2003).

Eutrophication is considered to be Baltic Sea wide phenomenon having impact on all biological processes. At the same time conceptual models show that the eutrophication related consequences are different for different sub-basins of the Baltic Sea and are strongly dependent on local geomorphological and hydrological characteristics (Rönnberg & Bonsdorff, 2004).

Coastal plankton communities are supposed to be less stable and conservative in structure and function compared to open sea ones as in great extent the structure of the communities at given moment is dictated by the origin of water masses. So the type of the coastline plays a major role in stability and functioning of the coastal plankton communities. Generally in more sheltered inner archipelago or fjord-like coastal types the freshwater inflow determines the structure of the plankton community and exposed areas have a greater influence of open sea conditions. Such events as phytoplankton blooms and corresponding seasonal increase in zooplankton abundance have different mechanisms in such conditions. For the exposed coastal areas of the central Baltic the hydrological processes as upwelling events play major role in the short- and long-term variation in plankton communities. According to Kononen (1992) four main types of regulatory mechanisms operating in different spatio-temporal scales for these systems are identified:

- 1) Species-specific characteristics in nutrient uptake, assimilation, trophic links and growth play the major role in the temporal scales of minutes to days and spatial scales of cells to hundreds of meters.
- 2) In the temporal scale of one to several days and spatial scale of several kilometres, the dominant control is through the frequency and magnitude of the nutrient pulses as determined by the meteorological and hydrodynamical events.
- 3) In the temporal scales of years and spatial scales of sub-basins, the control is through quality (inorganic nutrient ratio) and magnitude of the nutrient reserves determined by nutrient loading and areal extension of the anoxic or low oxygen bottom layer i.e extension of the Baltic deep water.
- 4) At the scale of decades and the whole Baltic Sea, the magnitude of the phosphorus-rich nutrient reserves lying below the primary halocline controls the intensity.

The two main bloom forming organisms exhibit considerable differences as regards the bloom initiation (control by nutrients, temperature relationships) and the fate of the bloom (decomposition, sedimentation, and grazing). For *Aphanizomenon flos-aquae* sufficiently large nutrient inputs through wind induced mixing or upwelling are prerequisites for mass development. Bloom formation by *Nodularia spumigena* is mainly triggered by high temperature if sufficient phosphorus is available (Kononen 1992).

For zooplankton communities the salinity regime plays often more important role than nutrients. So according to Hänninen et al. (manuscript) the strong connection between seawater salinity and mesozooplankton community structure has been thoroughly demonstrated (Vuorinen ja Ranta 1987, Lumberg & Ojaveer 1991, Viitasalo et al. 1995, Flinkman et al. 1998, Ojaveer et al. 1998) in the Baltic Sea. Decreasing salinities during 1980s have brought a change in zooplankton species composition and abundance by favouring smaller mesozooplankton, which generally originates from freshwater (Vuorinen et al. 1998). This has a significant impact also on higher trophic levels.

Hydrological regime plays extremely important role for the spatial distribution of nektobenthos in the exposed coastline. It is shown that distribution of mysids is aggregated and related to the temperature conditions. Higher densities of mysids coincide with the areas where the thermocline boundaries touched the seafloor (Kotta and Kotta 2001). So zoobenthos as well as nektobenthos concentrates in the upwelling areas. While zoobenthos is favoured by in elevated nutrient concentrations nektobenthos follows the temperature gradient (Kotta et al. 2003).

The variation in quantitative and qualitative parameters in soft bottom macrozoobenthos is also mostly expressed through trophic conditions. In the northeastern Baltic Sea the dominating benthic invertebrates feed mainly on seston, i.e. small free-floating organisms and lifeless particles (Yarvekyulg 1979). In shallow waters the benthic suspension feeders are the main consumers of phytoplankton (Kotta & Mohlenberg 2002) whereas the deposit feeding invertebrates rely on the sedimented phytoplankton in the deeper sea (Kube et al. 1996). The addition of nutrients stimulates phytoplankton growth, which in turn provides better dietary conditions for both benthic suspension and deposit feeders.

It is shown that often interannual variation in coastal benthos, which could not be explained by variation in local environmental conditions, has better explanation if analysed at a larger scale. It could be illustrated by time series of abundance of several marine zoobenthos species which tend to show more or less parallel fluctuation patterns in the North Sea. Large climatic fluctuations are also having large-scale synchronisation. For instance the occurrence of severe winters in the Western Europe is synchronised over an area of >10 degrees latitude or about 2000 km extending from the Atlantic coast of France to the northern Baltic Sea (Beukema et al. 1996). Fluctuations of coastal biological parameters in relation to climatic variables of regional scale is shown also for the Baltic Sea (e.g. several biological parameters in Pärnu Bay, NE Baltic Sea had strong correlations with NAO (Kotta et al. 2004)). Relation of such events to variation in the open sea hydrological parameters is most often impossible due to the lack of data caused by differences in time scales of sampling and actual processes responsible for observed phenomena. At the same time very often such fluctuation in the benthic communities are overlooked as different groups of organisms can react to certain environ-

mental forcing in different way. So in an enclosed coastal lagoon (Szczecin Lagoon) the interannual variation in macrobenthos has been related to both climatic (severity of winter) and hydrological regime, while variation in meiobenthos could not be explained neither by local environmental data nor by any parameter of larger scale (Radziejewska & Chabior 2004).

One of the characteristic features of the coastal macroalgal communities is vertical zonation. In the Baltic Sea, disturbances caused by ice-scraping and irregular sea level fluctuations divide the vegetation into ephemeral and perennial. As a result of increased nutrient input, macroalgal mass occurrences or blooms frequently occur in eutrophied estuarine and coastal systems and have strong negative effects on fauna and perennial flora (Schramm and Nienhuis 1996, Raffaelli et al. 1998). These blooms are performed by fast-growing annual species which are characterised by high productivity rates and are strongly favoured by periodic nutrient enrichment (Duarte 1995). The extent, distribution, and species composition of these mass occurrences vary strongly among areas of similar nutrient regime and so far the nutrient status and loading alone are not sufficient to explain these events (Bonsdorff 1992, Schramm and Nienhuis 1996). Spring mass occurrences of filamentous algae, e.g. *Pilayella littoralis*, are proposed to arise from the direct effect of eutrophication level, while summer blooms of short-lived ephemeral algae are an effect of climatic and hydrological conditions and depend more on open sea conditions (Kiirikki 1996; Kiirikki & Lehvo, 1997). Seasonality (timing) of nutrient enrichment (upwelling events) is shown to determine the structure and extent of macroalgal bloom events (Kiirikki 1996, Lotze et al. 2000). Intensive upwelling events in the northern part of the Baltic Proper can occur frequently resulting in significant increase of nutrient concentration and salinity at the bottom but only slight increase at the very surface, hardly detectable by conventional monitoring methods (Haapala, 1994).

3.5 Alien invasive species

It is commonly accepted and agreed that invasion of alien species is one of the most serious and gradually increasing threats to aquatic ecosystems. This human-aided process has initiated significant, unpredictable, and irreversible changes to both abiotic and biotic environment in variety of waterbodies worldwide (e.g. Carlton 1996, 1999, Karatayev et al. 2002, Ojaveer et al. 2002, Vanderploeg et al. 2002) and may cause severe economic damage to man.

There are currently about 100 alien species found in the Baltic Sea. But only less than 70 of them have been recorded to be able to establish reproducing populations. About 60 alien species recorded in the Baltic Sea are unintentionally introduced. Besides the variety of ecological changes caused by alien species, several of them have also caused economic damage, incl. the hydrozoan *Cordylophora caspia*, the barnacle *Balanus improvisus*, the cladoceran *Cercopagis pengoi* and the bivalve *Dreissena polymorpha* (e.g. Olenin and Leppäkoski 1999, Leppäkoski et al. 2002).

No replacement of native species in the Baltic Sea ecosystem by invader has been observed. This could be explained by the availability of great number of free niches in the geologically young Baltic Sea ecosystem.

The dominant vectors for species introductions are shipping, including introductions via ballast water, tank sediments, and hull fouling, aquaculture (including unintentionally introduced nontarget species), and the opening of canals that have facilitated active or passive dispersal from adjacent fresh- and brackish-water systems (Leppakoski et al. 2002). Most often the colonisation of the new habitats takes place along the seashores and no colonisation patterns across the open sea areas are described so far.

3.6 Human pressure (pollution and eutrophication)

In the Baltic Sea, human influence has long history and the relatively vulnerable ecosystem had been altered by humans well before that was even acknowledged. Human pressure in the marine environment is no less effective than in the terrestrial one, but the factors causing disturbance differ. In contrast to terrestrial threats, where the habitat degradation is of the primary concern, the Baltic environment faces first of all decreased water quality, in terms of increased water turbidity, chemical pollution, and nutrient concentrations (Kautsky et al. 1986, Karlson et al., 2002, Lehtonen & Schiedek, 2006). Also habitat loss due to underwater construction, excavations and dredging and general disturbance by e.g. noise do affect the underwater environment. The factors causing reduced water quality and eutrophication are often interconnected and the interactions complex to predict. For example, a single factor, shipping, may cause, firstly, increased turbulence and wave action, which, in turn, mixes water layers and raises sedimented nutrients and toxins to water column or affects directly the littoral flora and fauna by increased water motion. Thirdly, the resuspended bottom sediment decreases light penetration into water column and inhibits the recruitment of macroalgae and sessile fauna. Finally, the resuspended nutrients increase phytoplanktonic primary production, thus, decreasing light conditions but, in shallow bays, may also shift the dominance in primary production from macrophytes to phytoplankton. On the other hand, also dredging, sand excavations, and river outflows cause enhanced nutrient concentrations and sediment loading.

Underwater noise has increased greatly during the last century. Many studies and observations have found that noise affects whales, also the harbour porpoise (*Phocoena phocoena*) in the Baltic Sea, and seals (Frankel & Clark 1994, Koschinski et al. 2003 and references therein). The animals avoid the noise source, the noise may mask their communication and echolocation and affect stress and auditory damage to the animals.

The increased nutrient input to coastal areas has altered the plant community structure and species composition in the Baltic Sea. Ephemeral fast-growing species have increased at an expense of perennial slowly-growing ones (Eriksson et al. 1998, 2002; Johansson et al. 1998; Rönnberg & Mathiesen 1998; Lotze et al. 1999; Vahteri et al. 2000) and vascular plant species vulnerable to water turbidity have decreased (Blindow 1992, Appelgren & Mattila, 2005). In coastal flads, semi-enclosed bays under land-uplift, the cover of vascular plants and particularly that of *Chara tomentosa* have decreased by increasing anthropogenic impact (Blindow, 1992, Appelgren & Mattila, 2005). Primary production in such bays is usually phosphorus-limited (Dahlgren & Kautsky 2004). Furthermore, the species composition of vascular plants commonly changes in eutrophicated bays as angiosperms (e.g. *Myriophyllum spicatum*, *Potamogeton perfoliatus*, and *Callitriche hermaphroditica*) outcompete charophytes (*Chara* spp.) due to the decreased light penetration to deeper depths (Blindow, 1992). *Chara tomentosa* has been suggested

as an indicator species of eutrophication in late-successional flads (Appelgren & Mattila, 2005). Dahlgren and Kautsky (2004) suggest that the threshold values for external loading in sheltered bays in the Baltic Sea are $<5 \mu\text{g l}^{-1} \text{ a}^{-1} \text{ P}$ and $<137 \mu\text{g l}^{-1} \text{ a}^{-1} \text{ N}$, below which the vascular plants would primarily dominate the primary production and the system would not switch to phytoplankton dominance.

The perennial slow-growing macroalgal species in the Baltic Sea have suffered from eutrophication. Zones of *Fucus vesiculosus* L. diminished greatly during 1970's and 80's, whereas the species has recently recolonized some of its former growing areas and depths (discussed in Nilsson et al., 2005). Obviously, the main factors in reducing the species are linked to the recruitment phase: the zygote settlement is shown to decrease on surfaces with sediment loading (Berger et al., 2003, Eriksson & Johansson 2003) and in nutrient-enriched water (Bergström et al. 2003). Dense cover of opportunistic algae reduce the recruitment success (Steen, 2004, Råberg et al., 2005) and snail grazing can be effective at post-settlement phase of the alga (Malm et al., 1999). Similar inhibition of recruitment by sediment and filamentous algae has been found also for *F. serratus* L. in the Baltic Sea (Isaeus et al., 2004). Eutrophication has also affected the full-grown individuals of *F. vesiculosus*: periodical bottom-up driven increases in the mesoherbivore densities have probably caused temporarily very strong grazing pressure on the species. The high biomass of grazers has potential to destroy even whole belts of *F. vesiculosus* (Kangas et al., 1982, Engkvist et al., 2000). However, the herbivores are usually not able to inhibit the growth of opportunistic macroalgae in the Baltic Sea, particularly in the eutrophicated coastal waters (Kotta et al., 2006).

The increase of nutrients has been found to affect also the microalgal assemblages. At the sea bottom, in eutrophicated environments, episammic microalgae have been shown to have lower primary production and altered species composition (Gerbersdorf et al., 2004). In an experiment in the Archipelago Sea, phytoplankton assemblages became dominated by few fast-growing and nitrogen-limited species, such as the diatom *Chaetoceros wighamii* (Brightwell) and the mixotrophic chrysophyte *Uroglena* sp. (Lagus et al., 2004). However, under experimentally induced phosphorus-limited conditions, the diatom *Skeletonema costatum* (Greville) Cleve and *Uroglena* sp. became dominating.

Ship traffic has increased greatly in the Baltic Sea. The effects of ship routes on plants have been predominantly negative (Rönneberg, 1981, Eriksson et al., 2004, Roos et al., 2004), probably due to increased sedimentation and water turbidity but also due to direct mechanical disturbances by motors and wave energy. The ship traffic has been demonstrated to increase water turbidity up to 50 % in lakes and rivers (Anthony & Downing, 2003). Also positive effects of ship routes have been found as the increased water motion enhances the macroalgal species richness on rocky shores very close to the ship routes and some vascular plants have benefited from the increased sediment load farther away from the routes (Roos et al., 2004). Eriksson et al. (2004) studied macrophyte cover and species distribution in recreational marinas and along routes of small ferries. They found that plant cover and species richness were significantly higher and reached much deeper along the shore in reference areas of scarce traffic than in the areas affected by boats and small ferries. Particularly, *C. tomentosa* and *Ruppia maritima* had lower abundances in the disturbed areas.

To summarise, the anthropogenic impact on the plants is obvious. This is also shown by modelling the effect of purification efforts in a wastewater treatment plant (Korpinen et al., 2004). By the model, the improvement of the purification efficiency of the waste water treatment plant in Helsinki, Finland, would have a great effect on the biomass of filamentous macroalgae and phytoplankton in the nearby sea area (Korpinen et al., 2004).

The effects of eutrophication on benthic animals are indirect and usually linked via complex interactions to several abiotic and biotic variables. To oversimplify, the increased nutrient availability enhances plant growth and thus by increased resources increases the faunal biomass (Worm et al., 1999). However, the higher plant biomass carries along other changes such as drifting algal mats, which alter oxygen and pH conditions on the sea floor (Norkko & Bonsdorff, 1996). Although the thick and large drifting algal mats have predominantly negative effects on the diversity of macrozoobenthos (Norkko & Bonsdorff, 1996, Norkko et al., 2000), thin mats may increase habitat complexity and, thereby, the diversity of macrozoobenthos (Norkko et al., 2000, Lauringson & Kotta 2004). Also Salovius et al. (2005) concluded that drifting mats of filamentous macroalgae create important temporary habitats for macrozoobenthos and that the floating mats can be of great importance in migration of benthic animals. Malm et al. (2004) reported of effects of mechanical removal of drifting algae from sandy beaches in Öland, the Baltic Proper. Intensive cleaning of the beaches caused reduction in abundance of bacteria, large ciliates, and littoral mysid shrimps. The cleaning procedure also decreased significantly the ammonia concentration in the shore water and the amount of organic material in the sediment (Malm et al., 2004). In macrozoobenthos, it is only the density of the polychaete *Hediste diversicolor* Müll. decreasing by the cleaning, but no statistically significant changes were found in the community structure of macrozoobenthos.

The long-term effects of eutrophication are seen as changes in macrozoobenthic community (Perus & Bonsdorff, 2004). In the Åland archipelago, the macrozoobenthos increased in biomass from 1970's to 1989 in middle and outer archipelago zones and this was linked to increased nutrient concentrations in the areas. In the inner archipelago zone the biomass was high already in the 1970's. In the 1990's, the biomass and abundance of macrozoobenthos showed a decreasing trend in the sea area (Perus & Bonsdorff, 2004). Similarly, in the Bothnian Sea, eutrophication has resulted increased the abundance and biomass of macrozoobenthos (Karlson et al., 2002). However, in the Gulf of Finland, the Baltic Proper, some coastal areas of the southern Baltic Sea, the Danish fjords, and the Kattegat, constant or periodical hypoxia or anoxia in the near-the-bottom waters has destructively affected the benthic fauna (Karlson et al. 2002). According to Diaz and Rosenberg (1995) hypoxia and anoxia cause the most drastic negative impacts on the benthic fauna worldwide. In the northern Baltic Sea, the structure of the macrozoobenthic communities is best explained by the amount of dissolved oxygen, but also by temperature and sediment organic matter content (Bonsdorff et al. 2003).

Man has a great impact on the Baltic fish populations. Aside from direct fisheries impact, the indirect effects of habitat losses and eutrophication-linked trophic changes have changed the coastal fish populations in the Baltic Sea (Rajasilta et al., 1999, Lappalainen et al. 2000). Densities of small littoral fish species have collapsed in the Archi-

pelago Sea (N Baltic) from 1970's to 1996 probably due to environmental changes in littoral habitats (Rajasilta et al., 1999) and the roach has increased rapidly in the outer archipelago of the Gulf of Finland most likely due to altered feeding conditions (Lappalainen et al. 2000). How this has affected lower trophic levels via top-down control is yet poorly known, but in oceanic environments trophic cascades have been found from predatory fish to phytoplankton (Frank et al., 2005).

There is experimental evidence that eutrophication, by increasing phytoplankton biomass, has negative effects on fish behaviour. Phytoplanktonic algal blooms, due to increased water turbidity, have been found to disturb mating behaviour of the sand goby (*Pomatoschistus minutus*) (Järvenpää & Lindström, 2004) and decrease feeding rates and the anti-predator behaviour of first-feeding pike (Lehtiniemi et al. 2005). However, the increased turbidity did not have effect on the consumption of mysid shrimps by perch (*Perca fluviatilis* L.) (Granqvist & Mattila, 2004).

The anthropogenic pollutants have been found from diverse marine fauna (Paasivirta, 1998) and are known to interact with the nutrient status of the area (Gunnarsson et al., 2000, Larsson et al., 2000, Skei et al., 2000). Although only little is known of effects of the vast amount of toxins in environment, the effects of some are relatively known covered (Lehtonen & Schiedek, 2006). Organochlorides (such as PCB and DDT) and oil have caused reproductive disorder in seals, fish-eating birds, and the amphipod crustacean *Monoporeia affinis* (Waldichuk, 1979, Jenssen, 1996, Breitholtz et al., 2001). PCBs and PAHs (polycyclic aromatic hydrocarbons) caused stress reactions in mussels (*Mytilus edulis*) (Olsson et al., 2004). The disappearance of Atlantic salmonids from polluted rivers and estuarine nursery grounds has also been linked to environmental pollution (Waldichuk, 1979). The imposex in gastropods has been linked to TBT and reproductive disorder and endocrine disruption in fish and molluscs to xenoestrogens and cadmium in the environment (Henson & Chedrese, 2004, Jobling et al., 2004, reviewed by Lehtonen & Schiedek, 2006).

4 **TEMPORAL AND SPATIAL DIFFERENTIATION IN LIFE CYCLES OF BALTIC SPECIES**

4.1 **Life cycles of fish**

Many marine species use different locations for spawning, larval development, larval and juvenile feeding, and adult feeding (Urho, 1999, Hinrichsen et al., 2005). Larval ontogeny, behaviour, and environmental conditions determine dispersal tactics, including when and how far to disperse (Urho, 1999). Species may disperse immediately after hatching or gradually after a certain hiding period in vegetation (Urho, 1999). The spawning habitats, larval tactics, and adult migrations largely determine how “connected” are different areas of the Baltic Sea and how vulnerable species are, if certain areas or habitats are lost. A literature survey was compiled in order to understand the applicability of the “blue corridor” concept on Baltic fish species. Literature notes of a total of 53 northern Baltic fish species were inspected in order to summarise the common life cycle modes in the area. Data was based on two databases: international Fish-Base (www.fishbase.org and the references therein) and, to a minor extent, a net site of the biota of Finnish coastal waters supported by a private consultancy company Alleco (www.alleco.fi, the database in Finnish). Details on some species were corrected according to Urho (1999) and Kjellman et al. (2001). The following characteristics were inspected: spawning in marine or freshwater, spawning habitat, environment of larval development, and adult migratory behaviour.

Of the fish species in the northern Baltic Sea, 10 out of 53 spawn only in freshwater, either by migrating there only for the spawning period (e.g. some cyprinids and nine-spined stickleback *Pungitius pungitius*) or to stay there for their juvenile period (e.g. Atlantic salmon *Salmo salar*, Sea trout *Salmo trutta*, European river lamprey *Lampetra fluviatilis*). Four species or species groups have populations, of which some spawn in freshwater and some in the Baltic Sea (white fish *Coregonus spp.*, grayling *Thymallus thymallus*, European smelt *Osmerus eperlanus*, and three-spined stickleback *Gasterosteus aculeatus aculeatus*). One species, European eel *Anguilla anguilla*, migrates outside the Baltic Sea to spawn.

The Baltic Sea supports more spawning areas for littoral-spawning species than the oceans due to the small size of the basin and the areas of dense archipelagos. The spawning of fish is a critical phase in their life cycle, particularly in terms of predation and environmental change. Eggs are vulnerable to altered environmental conditions, such as hypoxia/anoxia, pH, and salinity. According to the survey, the marine-spawning fish place their eggs mostly in shallow water, predominantly in the littoral zone: 33 out of 43 species leave their eggs either guarded or unguarded among seaweeds or under bivalve shells, stones, gravel or sand (e.g. gobies, sandeels, sculpins, bullhead *Cottus gobio gobio*, perch *Perca fluviatilis*, ruffe *Gymnocephalus cernuus*). Only one species, snakeblenny *Lumpenus lampretaeformis*, spawns on the sea floor in deep water. Four species produce pelagic buoyant eggs (flounder *Platichthys flesus*, turbot *Psetta maxima*, Atlantic cod *Gadus morhua*, and European sprat *Sprattus sprattus sprattus*).

Three fish species carry their eggs (pipefishes and viviparous blenny *Zoarces viviparus*).

The larval stage is of special interest when estimating the connectivity of the separate areas and considering the “blue corridor” concept. If fish have larvae that are confined to a local habitat, such as vegetation in a bay, the connectivity between distinct areas is estimated to be poor. Also, if fish species, in certain phase of its life cycle, is restricted to a certain area or habitat, the vulnerability of the population increases. According to Urho (1999), marine fish species mostly disperse immediately after hatching, whereas many species of freshwater origin (e.g. pike and cyprinids) start their dispersal gradually and as a response to environmental conditions, such as temperature, predation pressure, and food availability. According to the survey, the larvae of the examined marine-spawning fish species, which have a free-living larval stage, are mostly planktonic (26 out of 40); other larvae live among vegetation or otherwise in close association with sea bottom. The larvae living among vegetation belong mostly to species living in shallow bays (e.g. cyprinids and Eurasian minnow *Phoxinus phoxinus*) or more generally among seaweed and other vegetation (e.g. pike *Esox lucius*, spined loach *Cobitis taenia* and three-spined stickleback). Species spending their larval phase in the plankton include, for example, many gobies, sculpins, sandeels, lump sucker *Cyclopterus lumpus*, Baltic herring *Clupea harengus harengus*, European sprat, garpike *Belone belone*, flounder, and turbot. Surprisingly many of the species spending their adulthood in the littoral zone have planktonic larvae (e.g. rock gunnel *Pholis gunnellus*, spined-loach and striped seasnail *Liparis liparis liparis*, in addition to the species in the previous list). The classification is, however, very rough and even misleading, as two-spotted goby (*Gobiusculus flavescens*) has semiplanktonic larvae, the larvae of perch and pikeperch (*Sander lucioperca*) switch between planktonic mode and living among vegetation, and the larvae of burbot (*Lota lota*) and white fish (*Coregonus spp.*) return to the littoral zone as soon as the yolk-sac is consumed (Urho, 1999).

For the truly littoral fish species with a semiplanktonic or littoral larval stage, the ability to actively stay the vertical position in the water column or near the bottom is a matter of importance (Jahn & Lavenberg, 1986, Potts & McGuigan, 1986, Kobayashi, 1989). Some fish species, such as two-spotted goby (*Gobiusculus flavescens*), have semiplanktonic larval stage, as they remain in or close to the parental habitat during development (Marliave, 1986, Brogan, 1994). Two-spotted goby remains even in the same habitat as its adult stage, where it forms large larval and juvenile shoals (Folkestad, 2005 and references therein). Also cyprinid species often form schools of larvae, which may disperse along shore among vegetation depending on environmental conditions (Urho, 1999). Perch and pikeperch larvae, however, disperse after hatching to pelagic only to return back to the vegetated littoral zone at lengths of 7-20 (perch) and 8-18 (pikeperch) mm and to migrate again to deeper waters offshore at lengths of c. 48 mm (Urho et al., 1990, Urho, 1996, Kjellman et al., 1996, 2001). The back and return migrations are assumed to be linked to anti-predator and food-seeking behaviour (Kjellman et al., 2001).

The dispersal and/or drift from spawning grounds to suitable feeding grounds are among the key processes for the larvae to survive (Werner et al., 1996, Heath & Gallego, 1998, Hinrichsen et al., 2002). In concordance with the “blue corridor” concept, the drift of the planktonic larvae is dependent on water movements, such as currents or wind-induced waves (Hinrichsen et al., 2003, 2005). For example, larvae of the Baltic

sprat were accumulated to the southern and eastern coasts of the Baltic Sea by the prevailing western winds in the area (Hinrichsen et al., 2005). Nielsen et al. (1998) presents a correlation between abundance of plaice (*Pleuronectes platessa*) larvae and wind-induced surface flows in Kattegat. Plaice spawns along the Danish coasts to the western Kattegat. Its nursery grounds are on the east and West Coast of the Kattegat and in the Belt Seas. There are 10-20 fold differences in the abundance of plaice larvae in the nursery areas yearly and between sites. Nielsen et al. (1998) showed that these variations are caused by circulation patterns and the position of salinity front in the Kattegat. Strong winds bring north-spawned eggs and larvae to the 0-group nursery areas in the Kattegat, where the local and northern larvae become mixed. Using a baroclinic southerly flow, in the upper surface layer, at speed of 0.5 m s⁻¹ the drifting eggs or larvae may be transported as far as 300 km in about a week's time (Nielsen 2005). According to Nielsen (2005) a similar mechanism could be of importance in the southern part of the Kattegat in connection with outflow of Baltic water, and so here also the timing of spawning relative to outflow events would be of considerable interest.

The sprat larvae are, such as also many other species, able to change their vertical position in the water column and may thereby certainly affect their drifting and therefore it might be more accurate to talk about dispersal (active) rather than drifting (passive) (Urho, 1999, Voss, 2002). Although water motion obviously affects newly-hatched larvae, the larvae are able resist drifting also by active swimming, already after some weeks of growth (Urho, 1999). Hinrichsen et al. (2005) suggest that, as the eastern and northern Baltic Sea are characterized by weak northerly and easterly winds at the time of sprat spawning, the sprat larvae may stay in deeper water in order to avoid the drift to the deep basins in the Baltic Proper. Also smelt and the Baltic spring-spawning herring actively disperse to nursery areas in the River Vantaa estuary in the Gulf of Finland; the former from the river and the latter from the archipelago (Urho, 1999). Thus, the retention to estuary by the smelt and the use of near-bottom inshore flow by the herring indicate that both the species are actively choosing suitable nursery habitat by taking advantage of the opposite currents (Urho, 1999). However, Urho (1999) argues that the factors behind the dispersal are more complex than simple currents. He suggests that temperature, predation pressure, food availability, and shelter in the area as well as morphology and the behavioural responses of the species influence on the start and extent of dispersal (Urho, 1999). If retention and accumulation turn out to be common features of local marine population dynamics, areas important to these processes must be included in MPAs and in the designation of essential fish habitat.

Dispersal most likely mixes populations of fish species in the nursery grounds (Urho, 1999, Köster et al., 2003, Hinrichsen et al., 2005), whereas the larval tactics may also differ between populations: Urho (1999) suggests that larvae of the spring-spawning Baltic herrings stay closer to shores than those of the autumn-spawning ones.

Adult migratory behaviour was found from almost half of the examined fish species (25 out of 53) either between feeding and spawning grounds, between offshore and inshore, or between deep and shallow waters. Aside from the anadromous species and the cyprinid freshwater spawners, the migrating fish are mostly species of marine origin (e.g. lump sucker, Atlantic cod, rock gunnel, flounder, and Baltic herring). If the species are able to change their spawning grounds during the migrations, the connectivity of the sea area increases. Unfortunately very little is known about homing instincts of the non-

commercial species, but the migrations of Baltic herring probably lead to the mixing of different populations (Aro 1989).

In conclusion, fish species show large spatial dispersal at larval phase and, in case of migratory or pelagic species, at adult phase. How this connects different areas to each other remains, however, still largely unknown, because many larvae can be confined to certain nursery areas close to the spawning area by active use of local water circulation patterns rather than passively drift by the currents. Such an example was given from the River Vantaa estuary for the spring-spawning Baltic herring and the smelt. Also the semiplanktonic strategy, used by the two-spotted goby, suggested that planktonic larvae may retain near shoreline or littoral bottom and, thus, population mixing is probably not a rule and the connectivity of areas weak. However, as Urho (1999) pointed out, larval strategies are not straightforward and different abiotic and biotic factors may force larvae to switch to another strategy. For example, increased predation pressure or shortage of food drives cyprinid larvae from their nursery habitat to disperse along the shore line and find new habitats, as noted above. Although the retention may be a common strategy among larvae of many fish species, that does not lessen the importance of water movements in dispersal of larvae.

4.2 *Life histories, dispersal, and habitat requirements of marine invertebrates in Baltic waters*

In the marine realm habitats are often referred to as being related to either the pelagic or benthic environment. While some invertebrates spend their entire life either in the water masses (i.e. pelagic, holoplanktonic) or confined to the sea floor (benthic), most species spend part of their life in both environments. Among the latter, some may include pelagic stages (i.e. meroplankton) as reproducing adults (e.g. cnidarians, gastropods) or most commonly as larval offspring (most marine phyla). Some stages move freely in the interface between the water and the bottom, searching for food and shelter there (e.g. crustaceans). Moreover, many species may move between different habitats, at one or more stages during their lifetime or on a seasonal or daily basis.

Distribution of invertebrate species and their occurrence at a specific site is affected by a variety of physical and biological factors. In the Baltic region, hydrographic variation in salinity plays a major role in structuring the distribution of species in relation to their physiological requirements. Salinity changes both bathymetrically from the intertidal to the deeper waters, and geographically from the near oceanic North Sea and Skagerrak, through the Kattegat, the Belt Seas and the Sound, the brackish Western Baltic, and into the fresh waters of the Baltic.

Within the biogeographical areas, geological origin of benthic sediments modified by water action and currents are essential as habitat types and hence for distribution of the various species.

Temperature is of lesser importance, except at very shallow depths and in the fresh water areas. The Baltic region is influenced by coastal conditions and affected by considerable eutrophication that causes frequent events of local oxygen depletion, that are not endured by most species. Those unable to escape ultimately will die and this will lead to

short-circuit of the energy flow. Biological effects include inter-specific competition, symbiosis and commensalisms, parasitism and predation as well as availability of food and hide-outs.

However, the initial key to the spatial and temporal distribution of specific species is to understand their mobility and capacity to disperse during the different stages of their life. The mobility of the benthic stages varies greatly between species, and it is often correlated with the mode of development. For many species the only possibility to become dispersed are larvae or drifting juveniles. Therefore the distribution of a species of the latter kinds heavily depends on the current systems as a medium for transport of eggs, larvae, juveniles, and even in some cases of the adults.

4.2.1 Life-histories and modes of reproduction

The life-history of marine invertebrates includes several stages, depending on their phyletic ancestry. There are three principal modes of development as defined for bivalve life-histories (Ockelmann 1965), and used for e.g. gastropods (Todd & Doyle 1981), polychaetes (Hartman-Schröder 1996), and many others (e.g. Thorson 1946, Mileikovsky 1971). Two of the modes involve one or more pelagic larval stages, either as planktotrophic (feeding) or lecithotrophic (non-feeding). Both require metamorphosis into the juvenile stage. The separation between these two modes is unclear in only a few species where lecithotrophic larvae are facultatively planktotrophic (e.g. Todd & Doyle 1981). In the third mode, direct development, a free larval stage is lacking and the hatching offspring resemble the adults.

Although the mode of development is described for many Baltic molluscs, polychaetes, crustaceans, and echinoderms, there is no list available for the developmental mode of the more than 3000 marine macro-invertebrate species described from the Baltic region. The numbers listed below includes those for marine and brackish waters species described from Danish waters, unless other is mentioned.

Of the bivalves in Danish waters (123+ spp.), most develop by way of planktotrophic larvae (92 spp.). Bivalves with lecithotrophic larvae (21 spp.) are e.g. species of the genera *Nucula*, *Nuculana*, and *Thyasira*. These lecithotrophic larvae are common in the autumn when the temperature decreases (e.g. in November in the Sound, 10-15 minutes dredged using plankton net 150 µm with bottle 1.5 m above the bottom). The juveniles and adults are deposit feeders and hence more indirectly dependent on the primary production than are filter- and suspension feeding species. Species with direct development (10 spp.) is e.g. *Musculus discors* where the early progeny disperse by drifting over the bottom (perhaps including preferential settlement). Other species with direct development are those of *Astarte* (embryos develop in sticky eggs that drifts along the bottom). In all Scaphopods and Polyplachophorans where the development is known, it is non-planktotrophic (several with lecithotrophic larvae).

Of all classes of marine invertebrates the polychaetes (brittle worms) probably exhibit the greatest variation between species as to biology and morphology. This also applies to modes of reproduction and dispersal (cf. Thorson 1946, p. 146). Attempts to quantify the occurrence of these modes in relation to different biotope types are hampered by lack of basic information for very many species. Moreover, in a number of polychaetes, transition from planktonic to benthic life is not distinctly marked by a change in mor-

phology but rather by a change in behaviour. Another feature of many polychaete larvae is the fact that they are capable of fast swimming in any direction. This allows a much more efficient way for the late larvae to find a suitable place for settlement. Post-settlement migration is known in several species. Generally, the early stages of polychaetes suffer a lower mortality than do e.g. the bivalve species with planktotrophic larval development. Hence, female polychaetes produce fewer but larger eggs than bivalves (e.g. Thorson 1952). The more efficient way of polychaete offspring to find a suitable habitat may explain the fact that there are relatively many species in the same environment with lecithotrophic larval development as compared with e.g. echinoderms and bivalves. Polychaete families that comprise species with lecithotrophic larvae are e.g. Spaeodoridae, Pholoididae, Spirorbidae, Terebellidae, and Nereidae. In fact, while it is easy enough to identify planktotrophy in polychaetes, the distinctions between lecithotrophic larvae and direct development may become a matter of taste. One example is non-feeding, briefly swarming stage after hatching of *Ophryotrocha socialis* which appears not to differ morphologically from the juvenile stage (Ockelmann & Åkesson 1990). Stolon-formation in e.g. *Autolytus* with non-feeding swarming individuals, brooding embryos in the plankton, are another special case of reproduction. The mobility of many polychaetes species and their potential for a differential reproductive behaviour greatly influences population structure.

The echinoderms are sensitive to low salinity and oxygen concentration and most require some water agitation for respiration. Many adults are mobile during their adult benthic stage. Among the asteroids (sea stars, 19+ spp.), (see Thorsen 1946, Mortensen 1927) most have lecithotrophic larvae or develop directly (12 spp.), some have planktotrophic larvae (6 spp.) or modus is unknown (1+ spp.). Shallow water species often develop by planktotrophic larvae, while species living at greater depths develop by way of lecithotrophic larvae (e.g. *Crossaster*, *Solaster*, *Leptasterias*) or direct. In the ophiuroid-eans (brittle stars, 14+ spp.) most have planktotrophic larvae (8 spp.), while some have lecithotrophic larvae (2 spp.) or direct development (3 spp.), or unknown (1 sp.). All echinoids (sea urchins, 9+ spp.) have planktotrophic larvae. The holothuroideans (sea cucumbers, 10+ spp.) have either lecithotrophic (4 spp.) or planktotrophic (1 sp.) larvae or development is unknown (5 spp.). The single crinoid species have lecithotrophic larvae.

Also, many gastropods and crustaceans are mobile during all the stages of their life, including when on the bottom. They often attach to substrate types that may loosen and drift occasionally. In the gastropods all three types are present. Direct development and planktotrophic larvae dominate, while lecithotrophic larvae are comparatively rare. In the crustaceans direct development is not possible due to exoskeleton grow. Few species are lecithotrophic (often parasitic species) and the majorities develop by way of one or more free living planktotrophic larvae.

In Bryozoans most species develop by way of lecithotrophic larvae, a few by way of planktotrophic larvae. The tadpole larvae of Ascidiaceans are usually rather short-lived and all lecithotrophic. The cnidarians differ from most other fauna groups in having life histories with metagenesis, normally including one pelagic and one benthic generation, either on hard faces or in muddy substrates. Most Baltic species have a planula larva, which is always lecithotrophic. In the anthozoans the benthic polypoid stage releases the planula. In the hydrozoans either the pelagic medusa stage or the benthic polypoid stage

(with retained medusa stage) releases the planula. In the scyphozoans the pelagic medusa releases the planula, and the small sized polypoid stage is often overlooked in its benthic habitat on hard faces.

4.2.2 *Patterns of dispersal and population connectivity*

The advantages and disadvantages of larval stages are many (reviewed by Pechenick 1999). The dispersal potential of pelagic larvae varies greatly between species, depending on the length of the pelagic phase and the advection capacity of the water layers they inhabit (reviewed in Scheltema 1986). In itself dispersal may not be selected for in evolution (Strathmann 1985). Any specific species that reproduces by planktotrophic larvae will not change modus based on costs alone. Some suggests that in an environment with seasonal variability of resources, when solutions are equal energetically for the species, favour is towards that of the three strategies planktotrophic, lecithotrophic, or direct, that best matches the optimal time for respectively spawning and settling (Todd & Doyle 1981).

It is an apparent energetic paradox than in common invertebrates with planktotrophic larval development practically the whole reproductive effort goes to sustain other organisms. This fact is a consequence of interdependent recruitment in a system of scattered co-specific populations. The claim that species with planktotrophic larvae generally have a wider geographical distribution than species with a non-planktotrophic development does not hold. Quite many species with lecithotrophic development - planktonic or direct - have a very wide distribution.

Until achieving a better understanding of the mechanisms driving shifts in mode of reproduction and development, mode specific implication together with current speeds and patterns may aid in developing tools for spatial planning of connectivity of populations and habitats in and between marine protected areas in the Baltic region.

The implications of the three principal modes of development are listed in Table 1. Each individual species has its own set of answers for its existence and persistence of the species. The recruitment of benthic populations of macro-invertebrates depends on a specific co-action of a number of factors. The first is the production of very many viable larvae at any given time. These larvae have to grow if they are planktotrophic - to become competent for settling. Meanwhile they have been carried by surface currents far away from their origin. Within the span of some weeks they then must get to the right place for settling. With the delay of this event larval mortality increases very much. If these larvae find a suitable place for settling, their number must be much larger than the number of larvae settled which grew up to become their parents. Implicit in this fact is that many populations of such species depend on recruitment from other populations. If human activities affect this pattern negatively the result will be a general decline of the species affected. This is a parallel to what is happening with a number of commercial fish species.

In the outer Baltic region, populations of species with planktotrophic larvae are subject to a current system that determines recruitment patterns and exchanges between populations. Populations in the Western North Sea supply the Eastern North Sea as well as the Skagerrak and the Kattegat (and vice versa). Depending on the wind systems and gyre patterns of the Kattegat and the Skagerrak, populations may circulate recruits within the

area. The Kattegat and the North Sea also supply larvae to the Belt Seas and the Sound, while the opposite occurs rarely, if at all.

4.2.3 *Reproductive surplus*

In species with planktotrophic larvae, recruitment is dependent of other populations. This implies that for such species there will be areas, which for one reason or another contribute differently to the persistence of the species. It can be difficult to distinguish between migration and mortality in nature. Some areas will provide off spring with a surplus, some will be neutral, and yet others and the larger part will contribute negatively. Areas that provide surplus to the meta-population are not necessarily identical with the optimal site for the species, if hydrographical circumstances prevent successful dispersal and settlement of the off spring. Also, low densities (i.e. reproductively isolated) of large-sized individuals do not reflect an optimum site for a given species rather it indicates that the reproductive output in this area is low or even zero. Broadcasting species with planktotrophic larvae will probably use synchronised reproduction, at least locally. Such species will often benefit from pheromone induced settlement.

As an example of the complexity of the factors determining successful recruitment, our observations from the Sound on that of the important bivalve *Spisula subtruncata* show an enormous variation between years in the numbers of settled early spat. The same pattern is known from the North Sea. This is evidence for the interdependence between different populations as to recruitment. This is also a consequence of the short adult life-span of little more than a year. Moreover, the species distribution may vary greatly between generations.

Table 1.

Life-histories of invertebrates in boreal marine and brackish water. The three principal modes of development and associated implications based on data for bivalve, polychaete, and echinoderm species with adult stages living on or in the bottom sea floor (Ockelmann & Dinesen).

MODE OF DEVELOPMENT	DIRECT	LARVAL LECITHOTROPHY	LARVAL PLANKTOTROPHY
Larval stages	Lacking	One	One to several
Egg size	Large	Medium	Small
Egg numbers female-1	Few	10 ² - 10 ⁴	10 ³ - 10 ⁷
Place of fertilization	In or close to female	Most often free spawning	Most often free spawning
Complexity of larval morphology	%	Feeding structures not functioning	Alimentary system functional
Direction of development when modus is changed	(\Rightarrow)	\Leftarrow (\Rightarrow)	\Leftarrow
Duration of development	Variable, in most species determined	Determined, from less than 1 hr to about 10 days	Variable
Seasonal limitation for reproduction	In the benthic stage only	Indirectly dependent on primary production	Directly dependant on primary production

MODE OF DEVELOPMENT	DIRECT	LARVAL LECITHOTROPHY (sedimentation)	LARVAL PLANKTOTROPHY
Range of dispersal	Often quite small (determined by own mobility and bottom currents)	Intermediate (determined by fixed embryonic reserves and bottom currents)	Highly variable, often considerable, 102-103 km (104 km teleplanic)
Water layer where major dispersal occur	Near-bottom water (except for floating embryos and egg masses)	Near-bottom water	Surface waters (partly in near bottom water)
Possibility of substrate choice	Highly limited or absent	Common, but time-limited (by fixed developmental time)	Common, and not very time-limited
Occurrence on main bottom types	Coarse bottoms on sand, gravel, shell gravel, vegetation	Level bottoms, on fine sand to fine mud	Level bottom sediment, stones, solid rocks and algae and plants
Size of free, initial bottom stage	Highly variable between species, frequently large compared with adult	Determined	Variable, often related to mode of feeding
Area of distribution, occurrence	Small sized areas, often in high-energy environments	Areas of large coverage	Areas of frequent occurrence, but discontinuous
Evolutionary change and speciation	High, many endemisms	Slow, often cline formation	Most often slow
Recruitment to any given population	Self-recruitment, most often to local areas	Self-recruitment, but to larger areas	Mainly from other populations
Ability to re-establish and colonize new areas	Low	Intermediate, mostly not very important due to occurrence in large and uniform areas	High
Importance for ecosystem structure and complexity	High, often at a higher trophic level (many carnivores)	Intermediate, important in deeper waters	Low, often important consumers at lower trophic levels
Importance as productive input to fisheries (fish, crustaceans, bivalves)	Often low	Intermediate, but widespread and important as food for fish and crustaceans in deeper waters	High, includes the most productive food species for fish

Such short life histories are viewed as an r-strategy, and may be an adaptation to highly varying environments and/or predator avoidance. This differs from long-lived species which mature only after several years, the so-called K-strategy, such as e.g. infauna bivalves (*Arctica islandica*), heart urchins (*Echinocardium cordatum*, *Brissopsis lurifera*), and crustaceans (*Nephrops norvegicus*), semi-infauna brittle stars (*Amphiura spp.*), sea feathers (*Virgularia mirabilis*, *Pennatula phosphorea*), tube-building crustaceans (*Haploopsis spp.*), and the epibenthic, reef-forming horse mussel, *Modiolus modiolus*, sponges, and coral reefs (in Swedish waters *Lophelia pertusa*). The latter bottom structuring species which live a K-strategy life are much more vulnerable to habitat destruction than are the r-strategy species.

Protection of the areas with a reproductive surplus is highly important. For the r-strategy species these areas changes in time at a high rate (often annually), whereas for the K-strategy species such areas may be spatial stable for decades or even centuries. The areas are most likely to be recognized by having a high number of reproductive adult individuals of medium sizes for the species (and including also juveniles and young adults), and a current regime that is connected with surrounding areas (Figure 1A).

In species with lecithotrophic development the larval stage is brief (short-lived) because the availability (and/or accessibility) of a suitable substrate is not a master factor in determining the distribution, since it comprises large coherent areas (Figure 1B).

In species with direct development, dispersal depends on either the drifting capacity of any stage from egg capsule to adult and or locomotion of juveniles and adults (Figure 1C). There is no possibility of habitat selection until after hatching of the juveniles. Such species have low dispersal powers and are often restricted to specific areas. If the habitat at a given site is destroyed the species is in high risk of becoming locally extinct.

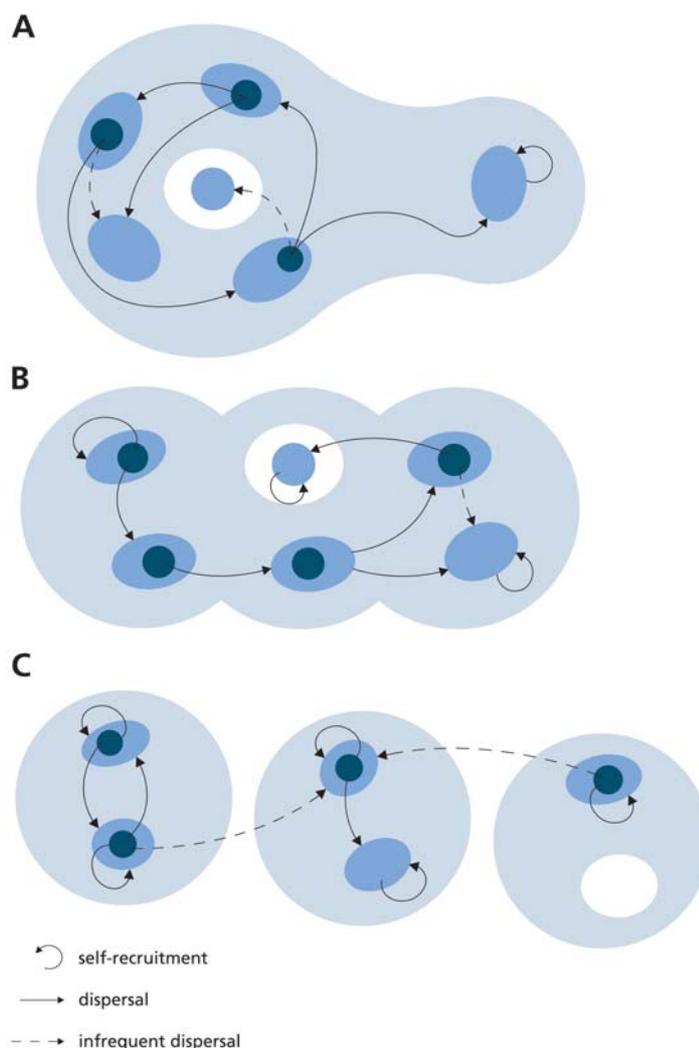
4.2.4 Triangular meshes in the food web

The feeding modes and distributions of Baltic invertebrates are known only in some species (e.g. synopsis in Hansson 1998, K oie et al. 2000). The early offspring may require a different type of food than do larger juveniles and adults. The precise food requirements (quality as well as quantity) of the juveniles of most marine benthic invertebrates are unknown.

Triangular trophic relations in the food web consist of a consumer species, which feeds on another consumer species lower in the food web plus on the food of the latter (Figure 2A-C). High numbers of this type of trophic relations are characteristic for biologically mediated ecosystems. In marine environments they are most common in e.g. corals reefs or in and on stable level bottoms (Figure 2C).

On sandy bottoms (Figure 2B) not only plaice and other flatfish depend on *Spisula* as prey but also many other invertebrate species which them self serve as food for the same species of flatfish. Food preferences may often change depending on availability,

e.g. the gastropod *Polinices alderi* may prefer *Spisula substuncata* from *Venus striatula*



as prey.

Figure 1. The three principal modes of development and associated dispersal patterns. Macroinvertebrate species with (A) free spawning and planktotrophic larval development, populations are interdependent of each other; (B) lecithotrophic larval development, populations either self sustained and or interdependent of each other; and (C) direct development, where populations most commonly are self sustained and rarely interdependent. The black areas represent populations (1) in right place and on which the existence of the species in the area is based. The dark grey areas represent populations (2) temporarily in balance but with no surplus contribution to the main distribution of the species. The light grey areas represent populations (3) with greater losses than contribution to the persistence of the species as well as populations (4) with too little recruitment and too little connection with the main current pattern. White areas represent areas (5) where the species is found as juveniles only, or not at all (Ockelmann & Dinesen).

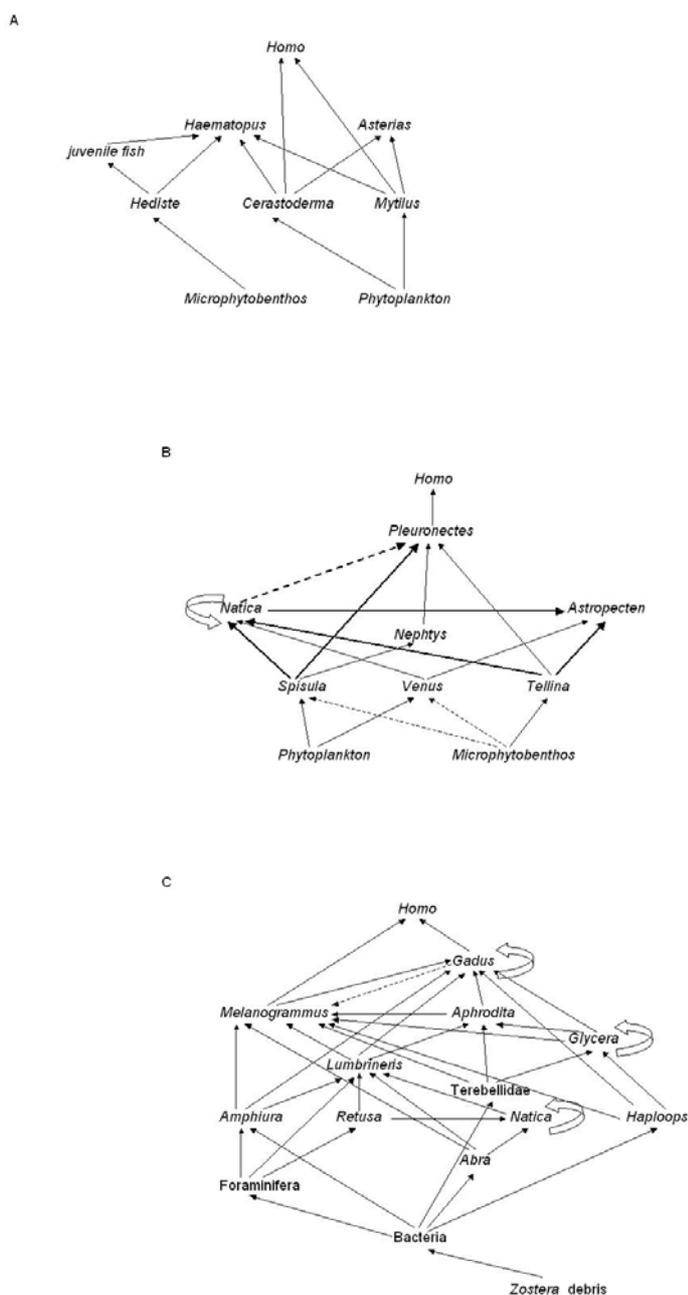


Figure 2. Simplified representation of main food web components responsible for the energy flow from primary producer to top predator. (A) Exposed, shallow water habitats (photic zone, e.g. shallow bays, mud flats, 0 - 2 m) where the energy flow is fast from the primary production to the top predator, triangular meshes in the food web are few or non-existing; (B) Moderate exposed, shallow waters (photic zone, e.g. NW Kattegat, sand, 5 - 10 m) where the energy flow is slightly more complex and triangular network begin to appear (bold lines indicate two triangular meshes); and (C) deeper waters on most substrates (aphotic zone), where the food web is highly complex and multiple triangular food webs are found (i.e. in the low or non-disturbed condition). Cannibalism may occur when density is high or food is scarce (Ockelmann & Dinesen).

Triangular meshes are also present in pelagic food webs where several carnivorous species occur. Among the larvae of polychaetes, approximately 50% are carnivores and hence placed higher in the food web (this is reflected in e.g. that these polychaetes have

larger eggs than for example bivalves in which the veliger larvae feed on phytoplankton).

The one main reason for habitat destruction in the Baltic region is the heavy bottom trawling fisheries, with supple side effects from periodically oxygen depletion and extraction of raw material. The massive disturbance of the stable level bottom due to intensive trawl fishing must lead to an overall reduction in the efficiency to utilize the available energy input. The possibility exists that trawl fishing accentuates oxygen deficiency.

4.2.5 Habitat requirements and connectivity

Essential sediment habitats for marine invertebrates with benthic adult stages are shallow water sand flats (intertidal to 2 m, subtidal from 2 to 15 m), deeper sand flats (below the pycnocline), gravel, sandy silt, silt (mud), and biogenic sediments, in Danish waters primarily including shell gravel (fine sorting, coarse sorting) and lime stone. Essential hard bottoms comprise mainly boulder reefs (bed rock only around Bornholm, Denmark), bobbling reefs, and man made structures (e.g. break waters, wrecks). Last but not of least importance are biogenic substrates of plants (eel grass meadows), algae (*Laminaria* sp. and *Fucus* sp. forests, red algae beds) and animals. The latter includes both intertidal and shallow reefs of blue mussels (*Mytilus*) and polychaetes (*Sabellaria*), and subtidal aggregations of horse mussels (*Modiolus*), crustaceans (*Haploops*) and perhaps also of sponges and corals. Biogenic reefs of animals function as both substrate for others and sediment traps. Particularly those of bivalves are engines for organic enrichment of the sediment, in the form of pseudo-faeces, which provides basis for life of other species.

Species with direct development occur in areas of strong current regimes, with much water agitations or eddies-formation, in shallow waters associated with vegetation or gravel bottoms, and in deeper waters below the pycnocline associated with gravel or hard substrates.

All pelagic larvae change habitat when settling on the bottom. Habitat requirement of juveniles and adults may differ. Examples of adults occurring at greater depth are juvenile *Pagurus bernhardus* that are much more common in shallow water while the adults are more common in deeper waters. Examples of juveniles occurring in deeper waters than the adults, are *Mytilus edulis*, *Asterias rubens*, and *Littorina littoria* juveniles that occur among red algae at 5-10 m, whereas the adults are found at more shallow depths. Juveniles of *Arenicola marina* and the byssally attached *Mya arenarea* occur in the algal belt around 8 m of depths (the Sound) whereas the adults are found in sandy silt bottoms in the intertidal. The early juveniles of *Aequipecten opercularis* and some other pectinid bivalves live byssally attached to hydroid stolons while later become free-living on level bottom substrates. At same depths, juveniles of *Mya truncata* live as epifauna byssally attached below the pycnocline, later they live as infauna of deep mud and sand-mixed bottoms. Adult *Carcinus maenas* migrate to deeper water in the winter, commonly where shelter can be found. Adults of other portunids, such as *Liocarcinus depurator*, migrate from the Kattegat into the Sound in the autumn. The day and night rhythm governs the activity period of many benthic species, particularly among polychaetes (e.g. nereids) and crustaceans (e.g. cumaceans).

4.2.6 **Passive transport of invertebrates along Blue corridors**

Juvenile and adult invertebrates may also drift along with surface currents, as well as bottom currents especially those living in the tidal zone as observed for the bivalve *Macoma baltica* (Norkko et al. 2001). Passive dispersal can also result from diurnal migration up in the water column of benthic crustacean (Saigusa 2001) and of planktotrophic larvae of most fauna groups, or by means of rafting when organisms attach to substrates drifting in the water column (e.g. Grantham et al. 2003).

It has been hypothesised that certain species may adjust the size of the egg and thereby the duration of the pelagic phase (Marchall & Keough 2003). The completion of the pelagic stage in the Baltic region varies typically in the time scale of weeks (Ockelmann & Muus 1978, Anger et al. 1986, Lastra et al. 1993, Pedersen et al. manuscript.)

The residence time of the water in the Baltic basins exceeds the duration of the larval stages and suggests a much smaller range of dispersal. However, the main vector for current-mediated transport of larvae is the wind-systems (e.g. larvae transport into the Sound, Ockelmann pers. obs.) Direct measurements of the range of dispersal are few in the literature as the sources of planktonic larval cohorts are largely unknown. Hansen et al. (2004) found that the abundances of echinoderm larvae in the water column roughly matched the distribution of the adult population in the inner Danish coastal waters at the entrance to the Baltic Sea. This suggested dispersal range in the scale of 100 km. Drifting juvenile and adults may disperse the population in the scale of meters (Norkko et al. 2001). Gunther (1992) categorised the range of dispersal of larvae, juveniles, and adults as large-scale, mesoscale and small respectively. However, rafting may enable long-distance dispersal of adults, especially when the animal utilises the substrate both as raft and for food, such as drifting macroalgae (Thiel 2003). Drifting algal mats are a medium of dispersal for many invertebrate species (Salovius et al. 2005).

Pelagic larval stages provides an efficient dispersal of recruits but, on the other hand, pelagic dispersal also imply considerable loss due to advection of the population over areas that do not fulfil the requirements of the species to complete the life cycle also termed sterile areas (Bhaud 2000). Dispersal over sterile areas may especially constrain recruitment of species with a limited geographically range. For these species dispersal will result in a dramatically increased mortality.

In closed estuaries dispersion may have little influence on the recruitment for larvae released inside the estuaries. Mortality rates have been reported in the range between 0.15 and 0.3 d⁻¹ (reviewed in Rumrill 1990), which means that few percent survives the planktonic life stage. Transport of larvae from one place to another will be reduced due to both mortality and dilution. In a system where dispersal occurs by simple diffusion a patch of larvae will be diluted to an extent, which scales with the distance cubed and time for needed to travel a certain distance scales with distance squared and finally mortality will scale with time. However, if the larval patch is transported by currents the loss rates could be significantly reduced which emphasis the potential role of blue corridors. As an example, it has been hypothesised that the Corsica channel act as at “gate” which can be either open or closed for the transport of larvae from the Tyrrhenian Sea to the Ligurian Sea through depending on the on the current speed (Aliani & Meloni 1999).

Josefson and Hansen (2004) observed that species richness of species with planktonic larval stages in Danish estuaries correlated with water exchanges with open areas. The authors argue that species richness was maintained by larval imported from adjacent open areas, which serves as species pools. The community composition and diversity of polychaetes on an isolated oceanic island in the Canary Archipelago could in a similar way be related to larval import from the open ocean. Here there was an overall a dominance of species with broad geographical range and pelagic dispersal (Herrando-Perez et al. 2001). Such pattern are in agreement with the hypothesis that certain populations are not self-reproducing but should be regarded as meta-populations (Botsford et al. 1998) that rely on import of larval recruits from other places. In this context such populations depend on connection to a “blue corridor”. Yet, there is no consensus on the existence of meta-population as a general phenomenon (sensu Hummel 2003)

The possibility that certain populations are in fact composed of meta-populations is an important aspect to consider when designing marine protected areas. Botsford et al. (2001) argues that in order to achieve sustainability of reserves the size of the reserve should be larger than the mean larval dispersal distance. The dependence of larval import in the case-study of Danish estuaries (Josefson & Hansen 2004) emphasises that the sustainability of populations locally in one area depend on it’s connectivity with populations elsewhere, which should be considered in the design of MPAs.

The dependence of openness for planktotrophic larval import from outside could however be modelled as with 3-D models and could lead to quantification of the planktotrophic larval exchanges between sites which could be ranked in an “upstream-downstream” hierarchy of donor and acceptor sites.

5 GENETIC ASPECTS OF CONNECTIVITY IN THE CONDITIONS OF THE BALTIC SEA

5.1 Importance of genetic considerations in MPA planning

Genetic variation among and within species is an essential part of biodiversity, nature protection and resource management, as stated e.g. in the definition of biodiversity in Article 2 of the Convention of Biological Diversity: "Biological resources includes genetic resources, organisms or parts thereof, populations, or any other biotic component of ecosystems with actual or potential use or value for humanity."

It has sometimes been argued that at least in a short time perspective, ecological and behavioural considerations should be more important than genetic considerations in biological conservation. This is may not always be the case - depletion of genetic variation within a population or species may be an extremely rapid process, and the effects of such diversity losses may also express itself within a few generations. Certainly if the goals of a network of MPAs are set with a longer time perspective of tens to hundreds of generations, genetically considerations are essential to ensure the survival and continued evolution of populations and species.

The maintenance of genetic variation is thus a conservation or resource management goal in itself, but genetic information is also together with ecological and life-history data a powerful tool when designing MPAs. Genetic considerations may be important for the selection and management of protected areas from at least three perspectives

- Genetic information can contribute to the knowledge about what type of biological values are present in an MCPA
- Genetic information can give data on the performance of an MCPA
- Genetic information can aid in the design and management of an MCPA, or a network of MCPAs

It is sometimes argued that genetic information is expensive and difficult to collect, compared to other types of biological data. Although this may sometimes be true, the cost, skill, and time necessary for making genetic analyses are rapidly decreasing with the development of ready-made kits. The skills and equipment needed are today standard among most biological laboratories, and not necessarily more demanding than e.g. analyses of environmental pollutants. Genetic data may in some situations be easier to obtain than the corresponding ecological or behavioural data needed to address a problem. For example, genetic data may be a faster and more rapid way to get information on connectivity among populations than alternative ecological methods (e.g. tagging studies). Some problems are only addressed by using genetic analyses, e.g. separating species of a sibling species complex (see below), quantifying differentiation between populations and levels of genetic exchange, and estimating rates of inbreeding and loss of genetic diversity.

If genetic data are not available or possible to collect, genetic considerations can still be incorporated in MPA decisions. As an example, although genetic data on population

connectivity may be lacking, data on dispersal mechanisms and life expectancy may be used to guide management that includes genetic considerations. If other concerns (ecological, demographic, social, practical) indicate that there is no difference between protecting either one large or two smaller areas, genetic concerns may point to preserving two smaller area instead as a means of preserving two populations with potentially different genetic structure.

5.2 Genetic information can contribute to the knowledge about what to protect

Biogeographic analyses. Genetic and phylogenetic information can aid in assessing the representativeness of a site, and to identify biogeographical regions. If several species show a similar geographic population differentiation pattern, then this can be used to design a network of MPAs, with representative areas protected in each such biogeographic area

Sibling species. It has been shown that sibling species, i.e. species difficult or impossible to distinguish by external characters, are common in the marine environment (Knowlton 1993). Often the only way to identify siblings is by genetical methods. Sibling species are not necessarily rare or seldom studied species: examples include well studied and commercially used genera such as blue mussels (genus *Mytilus*) and periwinkle snails of the genus *Littorina*. For the Baltic, another important example is the recently discovered algal species *Fucus radicans*, where genetic studies were essential for showing that it was not just a local growth form of the more common species *Fucus vesiculosus*. If an MPA or a network of MPAs aims to protect a species, then without information about the proper systematic status of the species complex there is a risk protecting only one of several sibling species. Not properly identifying sibling species can be especially dangerous if they are used as indicators of environmental status or conservation performance, or if they are to be used for restocking organisms to other areas.

Genetic variation among populations. A species is seldom ecologically or genetically homogenous over its entire distribution. It has been argued that the presence of larval transport should limit spatial genetic differentiation in marine populations. However, genetic studies show that genetic sub-structuring of marine species is commonly observed in fish and invertebrates, even in wide-ranging species such as cod (Ruzzante et al. 2001). Both nature conservation (e.g. the CBD) and fisheries management recognise the importance for protecting not only species but also genetically different populations of a species. There are several important reasons to preserve separate populations of most species: to maintain overall genetic diversity of a species, to retain local adaptations to various conditions specific for each locality, and to preserve both present differential adaptation and the possibilities for future adaptation and in this way preserve an evolutionary potential for the future. These are powerful arguments not only for a network of MPAs, but also for replicated areas within a network of MPAs, i.e. that there should be several protected sites of the same type. In the absence of genetic data, ecological or even geographical considerations may be used to make decisions about how to allocate protected areas to preserve different populations. However, most of the variations among populations are difficult or even impossible to detect ecologically, and then

genetic studies may be the only option. Fortunately, the main conclusions from ecological and genetic considerations suggest some similar design of MPAs. For both ecological and a genetic reasons, it is desirable to keep populations within an MPA large, and maintain a network of MPAs. For ecological reasons, increasing the number of MPAs decreases the risk of chance extinctions and catastrophes (storms, accidents, pollution, invasion of alien species). Chance events in local populations can be a problem also for genetic reasons and thus increasing the numbers of populations of a species promotes species sustainability. However, for genetic reasons keeping several separate populations (i. e. a network of MPAs) is desirable in itself, since this makes it possible to protect populations with different genetic set-ups.

Genetic variation within populations. Genetic diversity within populations is fundamental in the sense that the ability to adapt to changing conditions, either man-made or natural, relies on genetic variation. With small population sizes, the risk of inbreeding and loss of genetic variation increases, this may have both short-term and long-term ecological consequences.

5.3 Performance of an MPA and genetic information.

Forensic possibilities. Genetic methods can aid in detecting violations against MPA regulations. It can often be difficult to prove if marketed products originate from a protected area. If populations occurring within an MPA (or are protected everywhere) have a specific genetic signature, molecular genetic studies can be a powerful method to identify their origin, even in commercial products (Baker and Palumbi 1994, Hoelzel 2001).

Genetic monitoring. Just as the success of MPAs can be monitored by counting individuals of a species, the genetic structure of a population can be monitored to assess if genetic diversity and/or distinctiveness is maintained. For instance, if genetic diversity decreases while the population size is maintained, conservation objectives are not met. In this particular example, probable causes may be a change in the reproductive ecology of the species (changed sex ratio or size distribution), or a disruption of the gene flow from other populations, possibly outside the MPA.

5.4 Management of genetic resources

Kenchington et al. (2003) give the following suggest that management objectives for genetic diversity should target:

- 1) Population structure. A proposed management objective could be to maintain the number of populations
- 2) Genetic diversity among populations. A proposed management objective could be to maintain the relative size of populations.
- 3) Genetic diversity within populations. Two proposed management objectives could be to (i) maintain large abundance of individuals in populations, and (ii) to minimise human-induced selection (e.g., through pollution, fisheries or aquaculture)

5.5 Genetic structure of Baltic populations

A recent scientific review (Johannesson & André, manuscript) analyses the difference in genetic composition between Baltic and North Sea populations of 30 species. The result was that many species showed a marked genetic discontinuity around the Sound and the Belt Seas, indicating that Baltic populations differ from North Sea populations, and that there is a limited gene flow between the Baltic and the North Sea. Examples of such species are Herring, Cod, Salmon, blue mussels and the bivalve *Macoma balthica*.

Several species also exhibit genetic structure within the Baltic, including several algal species (e.g. *Fucus vesiculosus* and *Fucus serratus*) and commercial fish species such as salmon and Northern pike (Johannesson and André, Laikre et al. 2005). Some Baltic species (e.g. *Macoma balthica*, blue mussels *Mytilus trossulus*) are unique for the NE Atlantic, in being genetically more closely related to populations from the Pacific or the White sea than to the rest of the NE Atlantic, possibly reflecting conditions conserved since the last ice age (Johannesson & André, manuscript).

5.6 Genetic information can aid in the design and management of a MPA, or a network of MPAs

Population connectivity. The amount of exchange between populations in different areas are of profound importance for the implementation and design of MPAs, both for preserving biodiversity and for the export of biological resources to other areas. Data on population connection can be obtained with ecological methods (e.g. tagging studies), but also with genetic studies of differentiation among and within populations. This latter approach is an area of intense basic and applied research, e.g. within fisheries.

Conventional tagging studies have the advantage of following individuals at temporal and spatial scales that are relevant for management purposes. Disadvantages of tagging studies include that they are expensive and complicated to perform, and that they mainly are applicable on adult individuals. For MPA and other conservation purposes, however, investigating the flow of larvae is just as important. A coarse way of estimating larval transport distances is to map current patterns and speeds, and to combine this with estimate of larval stage duration times to get a potential for larval transport. However, although few studies have been done so far comparing potential larval transport distances with results from genetic studies, the emerging pattern is that realised larval transport distances are much lower than the potential distances (Palumbi 2003).

Palumbi (2003) gives a suggestion of how genetic studies could concretely be used to assist in the design of a network of MPAs. In short, if there is no direct ecological information on connectivity (e.g. from tagging studies), an investigation on genetic differences among populations separated by different distances can be combined with oceanographic information to estimate the average dispersal distance. If this estimated mean dispersal distance is e.g. 150 km, then either the MPA should be this large (perhaps not likely), or the distance between individual MPAs should be of this magnitude.

Changed population connectivity. A potential disadvantage of genetic studies of population connectivity is that current patterns of genetic structure are the integrated result of

past and present processes, i.e. they need not reflect the current ecological setting if the conditions for the population have changed significantly. The combination of genetic and ecological studies is therefore important. If genetic and ecological data are analysed together, it may be possible to assess changes in the history of a species (population), and if current conditions (e.g. migration measured by tagging studies) are different from previous conditions. This can be of great value for designing a proper conservation strategy. From a genetic point of view, it is important to maintain natural levels of connectivity, rather than increasing it beyond natural levels. If connectivity is increased above natural levels, e.g. through restocking or the creation of new biotopes (such as artificial reefs), this may erase the present genetic population structure and thus destroy local populations and adaptations.

Restocking. Sometimes it may be desirable to increase the population of a species within an MPA by introducing individuals from other areas. This is a situation where genetic and ecological considerations may differ. From an ecological perspective it may be desirable to take the introduced individuals from a location with a large and healthy population, possibly even with some desirable production characteristics. From a genetic perspective, however, it is very important that the introduced individuals are taken from a population which is genetically similar to the population to be restocked, in order to prevent the introduction of "alien" alleles and thus destroy genetic distinctiveness (Laikre et al. 2003).

Alien invasive species. Genetic methods (molecular markers) can be very helpful in studying and monitoring invasions of alien species, especially if the invading species is small and cryptic such as larvae introduced via ballast water.

6 CONNECTIVITY OF POPULATIONS, HABITATS, ECOSYSTEMS USED IN INTERNATIONAL MPA PLANNING

6.1 Principles of MPA planning

According to the Johannesburg Summit (2002) we should globally have a comprehensive network of marine protected areas by 2012. In the HELCOM/OSPAR ministerial declaration in 2003 it was further stated that the network in the Baltic Sea and the NorthEast Atlantic should be completed already by 2010.

What does this network mean? It was a hot topic in the previous COP-meeting for the Biodiversity Convention in Kuala Lumpur in 2004. The only clear statement by contracting parties was that it is not only the list of existing marine protected areas, but also a real functioning network. Setting up a network is a very large experiment and has often also important political and social implications additionally to the basic need to protect marine biodiversity. That's why the basis for MPA network should be thoroughly studied.

Marine protected areas are usually selected in ad hoc manner, especially in the past that was the case (e.g. Stewart et al. 2003). Only in the recent years scientists all over the world have started to study comprehensiveness and representativeness of marine protected areas and their networks and in the basis of these analysis to develop tools for systematic marine reserve design systems.

Even in Australia, in a country which is one of the leading countries in protecting marine environment, the selection of marine reserves and protected areas have largely been ad hoc, rather than the outcome of a state-wide strategy to represent marine biodiversity, and is thus thought to be inadequate to meet current conservation objectives (Government of South Australia 1998, ANZECC 1999). Stewart et al. (2003) studied the marine reserves in the Southern Australia to clarify how efficiently they contribute to quantitative biodiversity conservation targets.

There are some general MPA planning principles, which are derived from existing scientific theory and expert opinion. According to Stewart et al. (2003) these principles serve to inform the reserve selection process by providing a clear statement about what, reserve systems aim to achieve. These principles are complementarity, comprehensiveness and representativeness, adequacy and self-sustainability, systems, replication and spatial cohesion and flexibility.

In the following the principles described by Stewart et al. (2003) are given in more details:

Sites complement each other well if the species or habitats they contain are quite different, so their selection provides a combination of sites that together achieve the ultimate goals of comprehensiveness in the most efficient way. Thus planning for marine reserve systems should be informed by what is already contained within the existing reserves

(Kirkpatrick 1983, Vane-Wright et al. 1991, Pressey et al. 1993). In the light of results by Margules & Pressey (2000) this means that the conservation value of an area is dynamic and will change as the reserve system is established.

Comprehensiveness of the marine MPA system should cover the full range of biodiversity composition (species and genetic diversity), structure (physical organisation, e.g. habitats, patches) and function (ecological and evolutionary processes, e.g. reproduction, recruitment), providing for shifts in habitats and preferences of marine species at different life stages (Noss 1990).

Persistence and long-term viability rely upon the degree of connectivity between reserves which is a function of patch size, patch quality, recruitment, mortality and dispersal (Crowder et al. 2000). According to Stewart et al. (2003) marine protected areas should be configured so that they can interact in a positive fashion. Reserves located at source populations should ideally retain sufficient recruits to sustain local populations, with surplus larvae exported to other areas. Reserves, which are located at sink populations, are likely to depend upon replenishment from elsewhere, thereby diminishing prospects for long-term viability (Pulliam & Danielson 1991, Roberts 1998).

Stewart et al. 2003 state that because different ecological processes operate across several scales, marine populations are best supported by well-designed reserve systems in which the whole is more than the sum of the parts. A system-based approach is considered superior to the creation of isolated individual reserves for it can provide meaningful spatial relationships amongst sites for the maintenance of ecosystem linkages and connectivity, as well as offsetting effects from localised catastrophes (Ballantine et al. 2003, Roberts et al. 2003). Reserves should be also both compact and contiguous, with some level of replication (Pressey & Nicholls 1989, Ballantine 1997, Possingham et al. 2000).

The principle of flexibility arises from the non-unique occurrences of many biodiversity features. This has important implications for selection procedures for it means that conservation goals can be met in different ways. Having a variety of possible configurations gives scopes for sensible resolutions of resource use conflicts (Keller & Kenchington 1992). According to Stewart et al. 2003 equally important is the implication that we lose flexibility when sites with unique features are lost.

Most marine populations are thought to be well connected via long-distance dispersal of larval stages. The knowledge of larval exchange among populations of many marine organisms is vital to the study of marine population dynamics, management of fishery stocks and the design of marine MPAs (Cowen et al. 2000, Gaines et al. 2003). Decisions based on the assumption that larvae are widely dispersed may lead to erroneous actions if the assumption is wrong. For this reason Cowen et al. 2003 studied if the connectivity of marine populations is open (general assumption) or closed. They found that coastal marine populations may not be as open as has been thought and furthermore that management decisions based on open population models might overestimate the level of population exchange. This, in turn, can lead to a false sense of security among managers of downstream resources. This finding is extremely important and needs to be considered also in the Baltic Sea before establishing new MPAs.

6.2 *International examples of involving connectivity issues in MPA planning*

Connectivity among MPAs is one of the most poorly understood aspects of MPA function (Palumbi 2001). There are a growing number of studies in the world describing the function of marine protected areas (MPA), but most of the studies are confined to no-take reserves, their size, form, location and function. Most likely the comparisons between marine no-take reserves and areas outside are easier to interpret than in case of MPAs. To establish a marine reserve has been thought to benefit particularly fisheries, but there is almost a complete lack of knowledge of the effects on invertebrates or algae (however, see for example Shears & Babcock, 2003). The reserve networks may improve the status of exploited populations, reduce the risks of overexploitation of fish populations, and protect the functional attributes of marine ecosystems (Murray et al., 1999). According to model predictions (Nowlis & Roberts, 1999) and field observations (Mumby, 2004, 2006) the nature reserves enhance catches of overexploited fish populations, and will reduce annual catch variation in surrounding fishing grounds. However, nature reserves will not secure species if fishing is not limited outside the reserves (Botsford, 2001).

Most marine populations receive larval propagules through ocean dispersal from hundreds of kilometres away (Roughgarden et al., 1988, Robinsson et al., 2005) and the larvae of invertebrates may live from some days to as long as 1-2 months in the plankton (Kingsford et al., 2002, Appeldoorn & Lindeman, 2003, Grantham et al., 2003). In the text below the attention has been given to larval dispersal of fish (the bulk of studies are dealing with fish larvae) and invertebrates (only implicit information) and international examples are presented in favour and in contrast to “blue corridor” concept.

6.2.1 *Connectivity of Caribbean reef fishes*

In the Caribbean, Roberts (1997) considered the larval dispersal of coral reef fish in a network of reefs. He assumed in his model that larvae drift passively by currents; he called the recipient end as the “downstream area” and the source area as the “upstream area”. For 18 locations with coral reefs, Roberts mapped “transport envelopes” from which larvae spawned elsewhere could potentially arrive and to which larvae spawned locally could potentially be transported. He found that there is an order of magnitude variation in both the upstream and downstream reef areas. Roberts (1997) concluded that there is a high connectivity between the reef areas and that the upstream areas supported the abundance of coral reef fish species in the downstream reefs, because depletion of local populations may be offset by inputs of offspring spawned elsewhere. He further discussed that the size of the upstream area would positively affect the tolerance of the downstream area to local human management and that those downstream areas with large upstream areas would be more resilient to recruitment overfishing (that is, fishing at intensities high enough that populations are limited by insufficient reproduction) and less susceptible to species loss than areas with small upstream areas.

For example, Jamaica's reefs have been intensively fished since the end of the last century (Jackson, 1997); populations of many fish species on the north coast are almost entirely nonreproductive, as virtually all individuals are caught before sexual maturity (Pears & Sary, 1997). According to Roberts (1997) such populations must be maintained by spawning elsewhere. The north coast of Jamaica has a relatively large up-

stream reef area, notably containing lightly fished reefs of the Turks and Caicos Islands. In contrast, places with small upstream area, such as Barbados and Saba, are very vulnerable to overfishing. A lack of larval supply is probably responsible for the slow rate of recovery of populations of large groupers after the establishment of a no-take marine reserve in Saba (Roberts, 1995).

There are obviously high rates of gene flow among Caribbean reefs leading to genetic similarity at a regional scale (Lacson, 1992, Gold et al., 1993, Hateley & Sleeter, 1993). However, Shulman and Bermingham (1995) found that genetic similarity among populations of eight fish species from six areas of the Caribbean did not obviously reflect current patterns, but the species were most likely good dispersers. Also, a few studies have shown regional genetic differentiation (Katz et al., 1983, Campton et al., 1992), suggesting the existence of population-isolating mechanisms such as limited larval dispersal (Roberts, 1997).

A contrasting example from the Caribbean is given by Cowen et al. (2000), who argue that retention is more likely for fish larvae. The larvae, which disperse by currents, face heavy mortality and dilution in the way that the downstream areas receive larvae reduced by five (and potentially greater than nine) orders of magnitude. Cowen et al. (2000) argue that mesoscale and sub-mesoscale circulations may minimize long-distance dispersal by retaining larvae for a portion of or throughout their pelagic stage (Boehlert et al., 1992, Werner et al., 1993, Cowen & Castro, 1994, Lee & Williams, 1999). The existence of endemic species around isolated oceanic islands also suggests successful retention (Robertson & Allen, 1996). Cowen et al. (2000) used a high resolution model in the eastern Caribbean and noticed a great capacity for dispersal, but also a dilution effect on density, which, they think, would make the support of fish community in downstream areas impossible. They conclude that larvae stay in the area by taking advantage of layered water flows in the water column and that coastal marine populations may not be as open as previously thought. Though, Cowen et al. (2000) admit that there is also the potential for long-range dispersal to occur due to short-term climatic variations.

The third example in Caribbean describes how different habitats close to each other may enhance the fish species richness and abundance. A number of reef fish, representing herbivores (e.g., *Scarus iserti*, *Scarus guacamaia*), invertivores (*Haemulon sciurus*, *Haemulon flavolineatum*, *Haemulon plumieri*), and piscivores (*Lutjanus apodus*, *Sphyraena barracuda*) use mangroves and seagrass beds as juveniles and coral reefs as adults (Mumby et al., 2004, 2006). Mumby et al. (2004) found that some fish species use seagrass habitat first, then move to mangroves and finally as adults to coral reefs. However, only one of the species was functionally dependent on the coral reefs. Thus, the vicinity of the other habitats greatly enhanced the fish species richness and abundance in the coral reefs.

6.2.2 Metapopulation in the Great Barrier Reef

In the Great Barrier Reef, James et al. (1990) and Armsworth (2002) suggest that a subregion of the reef, a collection of reefs in the northern part of the Cairns Section, supports other parts of the larger reef area, at least for some species. Recruitment rates in the area show a large degree of spatial variability, with some sites consistently receiving lower numbers of recruits than others (Doherty and Fowler 1994, Caselle 1999). According to Armsworth (2002) it is important for the Great Barrier Reef metapopula-

tion persistence that somewhere within the system there exist a larval connectivity pathway that permits intergenerational feedback from some local population to itself. The recruitment limitation hypothesis (Doherty, 1981) supports this by stating that many local reef fish populations are undersaturated with larvae, and that recruitment is therefore an important determinant of subsequent population size.

6.2.3 Design of the MPAs

Isolated reserves will not necessarily maintain biodiversity over the long term, and there is a need to establish networks of interdependent reserves (Roberts, 1997). The study by Roberts (1997) suggests that reserves located in areas with large downstream reef area may be highly effective at supporting populations and fisheries elsewhere. As a corollary, Gaines et al. (2003) found that advection can play a dominant role in determining the effectiveness of different reserve configurations. They predicted that with strong currents, multiple reserves can be markedly more effective than single reserves of equivalent total size and that, in the presence of strong currents; reserves can significantly outperform traditional, effort-based management strategies in terms of fisheries yield, and do so with less risk. But how large a fishery reserve is enough to support sustainable fisheries? According to Mangel (2000) the answer is not numeric but a procedure, where the following questions must be met: sustainability criterion (the risk of the population to crash), planning horizon (how flexible planning in the area), and what is managed (how much one can control the populations). Mangel (2000) underlines that the decision is in most cases based on social requirements rather than sound science.

6.2.4 Connectivity of MPAs in case of invertebrates

Marine invertebrate species may show surprisingly weak population mixing indicating retention instead of dispersal (Barber et al., 2000). Although studies by passive drifters show great potential for larvae to drift far in Indonesian coastal waters, the genetic structure of the mantis shrimp *Haptosquilla pulchella* showed distinct differences even across distances as short as 300 km (Barber et al., 2000). Barber et al. (2000) suggest that past geographical isolations have caused the differentiations of the populations, which have lasted in the present state of the area despite the strong currents. They underline that connectivity of the areas is also dependent on the local biogeographic and oceanographic history.

Grantham et al. (2003), in their review of invertebrate larvae on North-American West coast, have provided valuable information of dispersal distances and life-time of invertebrate larvae. They found that species staying their adulthood in sand habitats had relatively few planktonic larvae and therefore poor dispersal capability. However, in other habitats, there are more species with planktonic larvae and their duration in plankton is long; thus, the recruitment from nearby sites is probably important. Many invertebrate species in North-American West coast and Caribbean Sea have a larval duration on c. 1-2 months (Appeldoorn & Lindeman, 2003, Grantham et al. 2003), whereas some molluscan larvae may stay in plankton only for days (Appeldoorn & Lindeman, 2003).

In their comprehensive review of larval abilities for dispersal, Kingsford et al. (2002) list the sensory means of many taxa based on literature search. The invertebrate larvae may use "partial navigation" i.e. sense cues in the water and position themselves vertically in the water column to be drifted by currents (Pineda, 1999, Kingsford et al., 2002). The cues can be of organic origin or abiotic. Kingsford et al. (2002) suggest that the distance to sense the biotic cues is most often short, because of the degradation of

the cue molecules in the environment, the fact which augments the dense design of MPA network. Abiotic stimuli, such as changes in turbidity, temperature, salinity, and minerals or sound of breaking waves, can reach farther away. For example, the sound of crash of breaking waves may exceed the background noise as far as 4-20 km away from the source. However, there are no reports of hearing ability among invertebrates. The estuaries are a good example of multiple cues; organisms can possibly sense changes, in addition to above-mentioned abiotic cues, also in plankton abundance and diversity (Kingsford et al. 2002). The chemical cues from an estuary can reach as far as hundreds of kilometres. Habitats of 'habitat-forming' organisms, such as kelps, may have unique chemical signatures.

Also transport by rafting appears to be common among sessile species like barnacles, snails, amphipods, and ascidians, but it is unclear how much this has an effect on the recruitment of the species (Grantham et al., 2003). Even less is known of adult mobility or egg and sperm dispersal (Johannesson, 1988). Grantham et al. (2003) suggest, based on larval life-time and dispersal distance, that a small reserve protects a greater proportion of the taxa in a sandy habitat than in the others i.e. that small reserves can protect assemblages of taxa with limited dispersal.

6.2.5 Connectivity of macroalgal populations

The algal spores and gametes are relatively short-lived due to the lack of protective outer covering. However, the kelp species *Pterygophora californica* can spread spores across distances as long as 4 km and the spores of the filamentous brown alga *Ectocarpus siliculosus* did not decrease in density after a distance of 500 metres from the source (Reed et al. 1988). There is also high variation in dispersal range among the species: the zoospores of the kelp *Macrocystis pyrifera* reached only 10 metres from the parent (Reed et al., 1988). Similarly, the gametes of *Fucus vesiculosus* disperse only some meters and the range is negatively dependent on salinity (Serrao et al. 1996). Therefore, the recolonization of *F. vesiculosus* is very slow from an area to another in oceanic shores and particularly in the Baltic Sea and the distance between the areas should be short ("stepping stone colonization"). Perhaps, the recolonization of *F. vesiculosus*, after its destructive decline in 1980' (Kangas et al., 1982), would need active establishment of new populations or active enhancement of potential areas by clearing substrates for the settlement. Although the theoretical estimates of macroalgal dispersal range show short-distance dispersal (e.g. Serrao et al. 1996), stochastic factors, such as storms, may carry the propagules very far from the parent population (Ebeling et al. 1985). However, in general, the species-specific dispersal capabilities of the Baltic filamentous algae are inadequately known.

How open or closed are the marine populations? Recent studies by Barber et al. (2000), Cowen et al. (2000), and Kinlan et al. (2005) stress that dispersal across pelagic areas is often overemphasized issue, whereby the connectivity of distinct populations is probably less frequent and intense. A growing number of studies has shown that species-specific differences are much more significant a factor in determining the dispersal than the sole existence of the currents. This means that species may more or less actively choose, probably by means of sensory organs, the water flows they use in the water column (Leis, 1991, Cowen & Castro, 1994, Urho, 1999, Kingsford et al., 2002, Rawlinson et al., 2004, Hinrichsen et al., 2005). In estuaries, this behaviour has long been recognized as a part of some species' life cycle (e.g. Baeta et al., 2005 and references therein). Aside fish and decapod species, also meroplankton (i.e. larvae of littoral spe-

cies) are able to migrate vertically and thus to orientate to certain layers and currents (Rawlinson et al., 2004), whereas the age of the fish larvae affects their mobility (Urho 1999): Newly-hatched larvae are more easily carried by currents. However, many fish species produce early fins very soon, which help them in orientating vertically in the water column. Thus, the results of this literature survey indicate that, in addition to detailed hydrographical information, also understanding of species-specific behaviour is required in order to estimate the functioning of the MPA network in the Baltic Sea.

7 GENERAL CONCLUSIONS

The Baltic Sea with its unique and peculiar complex of ecological conditions and diversity of environmental gradients offers a great challenge in understanding and utilizing the information on connectivity matters for MPA planning purposes.

Identification of the relevant scales of variability in space and time is a prerequisite to understanding factors and processes generating patterns in biotic and abiotic components of ecosystems. Different processes operate at different spatial scales and that processes operating at small scales can influence large-scale patterns.

There are both supporting and rejecting evidence for the blue corridors. The support or objection depends on the role active behaviour the organisms are expected to show. Models based on passive behaviour predict high connectivity between MPAs, whereas active behaviour seems to lead to retention in the upstream area. Thus, the connectivity of the areas seems to depend on the characteristics of the organisms and, if one is active, on the choice on the organism to disperse downstream. Also the invertebrates are partially active in choosing their direction of drift; they are shown to be able (as are fish also) to sense cues from distant habitats.

The conversion of continuous habitat to small isolated patches (i.e. habitat fragmentation) generally decreases the reproductive output, movement, survival, and population size of many species. The following conclusions have been drawn for different habitats: fragment size influenced species loss, small fragments lost species at a higher rate than did larger fragments, corridors reduced rates of species loss, but only in medium-sized fragments, corridors enhanced re-colonization of medium-sized fragments, the preferential movement in corridors is species specific, and spatial configuration of land conversion sequences significantly influenced species richness.

Protection of a specific habitat may be ineffective if related habitats are left unprotected. Conservation strategies for mobile benthic species need to incorporate the protection of areas with heterogeneous habitats that are important to meet the changing habitat requirements of complex life cycles. When designing the networks of a MPA, species-specific effects of habitat loss and fragmentation, together with habitat composition, should be taken into account and based on these relationships the species probabilities of local occurrence should be computed. Sites are then chosen to represent all species with a given target probability. To date there exist no descriptive and/or manipulative studies combining the effect of spatial orientation and fragmentation of habitats in the Baltic Sea area. Thus, it becomes necessary to evaluate the effect of spatial distribution of habitats at various spatial scales on benthic macroalgal, invertebrate and fish communities.

Organism's response to habitat fragmentation is dependent on its life history and distribution traits and may vary on different temporal and spatial scales. Rare species are likely to be more sensitive to the adverse effects of modification of habitat. Protection of a specific habitat may be ineffective if related habitats are left unprotected. Conservation strategies need to incorporate the protection of areas with heterogeneous habitats

that are important to meet the changing habitat requirements of complex life cycles. Corridors between habitat fragments reduce the rate of species loss and enhance the recolonization of habitat fragments. To date there exist no descriptive or manipulative studies combining the effect of spatial orientation and fragmentation of habitats in the Baltic Sea area. Thus, it becomes necessary to evaluate the effect of spatial distribution of habitats at various spatial scales on benthic macroalgal, invertebrate and fish communities.

Baltic Sea species show large spatial dispersal at larval phase and, in case of migratory or pelagic species, at adult phase. How this connects different areas to each other remains, however, still largely unknown, because many larvae can be confined to certain nursery areas close to the spawning area by active use of local water circulation patterns rather than passively drift by the currents. Also the semiplanktonic strategy, suggested that planktonic larvae may retain near shoreline or littoral bottom and, thus, population mixing is probably not a rule and the connectivity of areas weak. However, larval strategies are not straightforward and different abiotic and biotic factors may force larvae to switch to another strategy.

International research and experiences show that the maintenance of genetic variation can be a conservation or resource management goal in itself. Furthermore, genetic information is also together with ecological and life-history data a powerful tool when designing MPAs. Genetic considerations may be important for the selection and management of protected areas from at least three perspectives

- Genetic information can contribute to the knowledge about what type of biological values is present in an MPA. A Baltic example of this is the existence of genetically specific populations in the Baltic.
- Genetic information can give data on the performance of an MCPA (e.g. through the identification of migrating individuals in and out of the MPA)
- Genetic information can aid in the design and management of an MCPA, or a network of MCPAs (e.g. together with oceanographic modelling it can be used to assess the connectivity among locations inside or outside a network of MPAs).

There are plenty of international examples of involvement of connectivity matters in MPA planning but this approach has so far been very weakly implemented in the Baltic Sea area. The aim of further work in BALANCE WP3 should direct towards direct proposals of application of the connectivity issues and “Blue corridor” principle in the Baltic Sea MPA planning.

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 7. General conclusions. *By Georg Martin, Per Nilsson, Jonne Kotta, Kristjan Herekül and Samuli Korpinen*
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About the BALANCE project:

This report is a product of the BSR INTERREG IIIB project "BALANCE".

The BALANCE project aims to provide a transnational marine management template based on zoning, which can assist stakeholders in planning and implementing effective management solutions for sustainable use and protection of our valuable marine landscapes and unique natural heritage. The template will be based on data sharing, mapping of marine landscapes and habitats, development of the blue corridor concept, information on key stakeholder interests and development of a cross-sectoral and transnational Baltic zoning approach. BALANCE thus provides a transnational solution to a transnational problem.

The BALANCE partnership is composed of the following institutions based in 10 countries: The Danish Forest and Nature Agency (Lead), The Geological Survey of Denmark and Greenland, The National Environmental Research Institute, The Danish Institute for Fisheries Research, WWF Denmark, WWF Germany, Institute of Aquatic Ecology at University of Latvia, Estonian Marine Institute at University of Tartu, Coastal Research and Planning Institute at Klaipeda University, Metsähallitus Natural Heritage Service, The Finnish Environment Institute, The Geological Survey of Finland, WWF Finland, The Swedish Environmental Protection Agency, The National Board of Fisheries – Department of Research and Development, The Geological Survey of Sweden, County Administrative Board of Stockholm, Department of Marine Ecology at Gothenburg University and WWF Sweden.

The following institutes contribute as consultants to the partnership: The Geological Survey of Norway, Norwegian Institute for Water Research, DHI Water and Environment, The Leibniz Institute of Marine Sciences, The Sea Fisheries Institute, The Finnish Game and Fisheries Research Institute, Metria Miljöanalys and The Nature Conservancy.

The **BALANCE Report Series** included at the 1st of July 2006:

BALANCE Interim Report No. 1 "Delineation of the BALANCE Pilot Areas".

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BALANCE Interim Report No. 3 "Feasibility of hyperspectral remote sensing for mapping benthic macroalgal cover in turbid coastal waters of the Baltic Sea".

BALANCE Interim Report No. 4 "Literature review of the "Blue Corridors" concept and its applicability to the Baltic Sea".

BALANCE Interim Report No. 5 "Evaluation of remote sensing methods as a tool to characterise shallow marine habitats".

BALANCE Interim Report No. 6 "BALANCE Cruise Report – The Archipelago Sea".

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