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#### Part E: Invasive Alien Species

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## **D1.4 Meta analysis of the driver databases and development of new parameterisations relevant to the ecosystem models**

### **Part E: Invasive Alien Species**

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## 1. Overall introduction

The principal aim of the meta-analysis of invasive alien species (IAS) was to parameterize:

- a) IAS impacts on different elements of marine ecosystems for further application in ecosystem models;
- b) Ecological traits of benthic and pelagic invertebrate and fish IAS which have potential to spread to adjacent marine regions;
- c) Functional types and environmental tolerance limits for selected phytoplankton IAS.

The following products have been created as the result of the meta-analysis:

1. **IMPACTS**: parameterization of the IAS impacts. The meta-analysis covered abundance/distribution range of IAS and the magnitude of their impacts on community structure, habitats and ecosystem functioning in the Baltic Sea;
2. **ECOTRAITS**: parameterization of the ecological traits of benthic and pelagic invertebrate and fish IAS. The database on ecological traits of IAS was compiled that are widely distributed and are known to cause significant environmental impact within the Baltic Sea, and have potential to spread to the adjacent areas of the North Sea and/or North Atlantic;
3. **PHYTO-TYPES**: parameterization of the functional traits and environmental tolerance limits for phytoplankton species known to be established in the European regional seas.

## 2. IMPACTS: meta-analysis of bioinvasion impact in the Baltic Sea

### 2.1. Bioinvasion (biopollution) impact analysis methodology: introduction

An overall bioinvasion impact assessment at the scale of a large marine region, the Baltic Sea, as defined by the Helsinki Commission was performed. The methodology is based on a classification of the abundance and distribution range of alien species and the magnitude of their impacts on native communities, habitats and ecosystem functioning aggregated in a “Biopollution Level” index (BPL) which ranges from ‘no impact’ (BPL=0) to ‘massive impact’ (BPL=4). The assessment performed for nine pre-defined Baltic sub-regions: the Kattegat and the Belt Sea, Odra Lagoon, the Gulf of Gdansk and Puck Bay (hereafter – the Gulf of Gdansk), Vistula Lagoon, Curonian Lagoon, the Baltic Proper, the Gulf of Riga, the Gulf of Finland, and the Gulf of Bothnia (Fig.1). The selected assessment period covered two decades, 1990-2010. It was assumed that the most research effort was aimed at the Baltic Sea alien species in that

period, therefore data published in scientific papers during that time was considered for the analysis.

## **2.2. Data search and data management**

The extensive data-mining was conducted using the Google Scholar service. To collect data for the analysis, the search option with the input keywords including species name assessment unit name (e.g. *Acartia tonsa* Baltic Proper) was used. In order to secure that none of the relevant information sources were missed (since some geographical areas may be cited under another names, e.g. the Bothnian Sea or the Bothnian Bay instead of the Gulf of Bothnia), an additional search with a species name and the Baltic Sea as keywords was performed. The search results were scanned and all publications with relevant information were selected for the further analysis.

More than two-hundred peer-reviewed papers and scientific reports covering the period 1990-2010 were examined. Only those accounts that had reliable (medium to high levels of confidence for data) were selected for each assessment unit. High confidence level corresponded with the abundance and distribution range studied for the entire Baltic Sea or for each assessment unit where there were relevant detailed studies. A medium confidence level corresponded to the abundance and distribution range studied in a part of an assessment unit and then extrapolated to the entire assessment unit according to expert judgment. Impacts documented by field and/or experimental studies for a part of an assessment unit were treated in the same way. Should information of a species impact not be available (i.e. no relevant reference was found), it was assumed that the BPL magnitude was 0 (with a medium confidence level. Equal data mining effort distribution among the analyzed assessment units was ensured while performing information searches.

Data acquired from the literature sources for the each case were set into the on-line Bioinvasion Impact / Biopollution Assessment System (BINPAS), available at <http://www.corpi.ku.lt/databases/binpas>. Hereafter 'a case' corresponds to the one unique assessment of the species abundance and distribution range (ADR), or species impact on native community (C), habitat (H) or ecosystem functioning (E) in an assessment unit over the period 1990-2010.

Additional information (e.g. taxonomy, origin and pathways of introduction) on considered alien species was sourced from the Baltic Sea Alien Species Database (2010) and references therein.

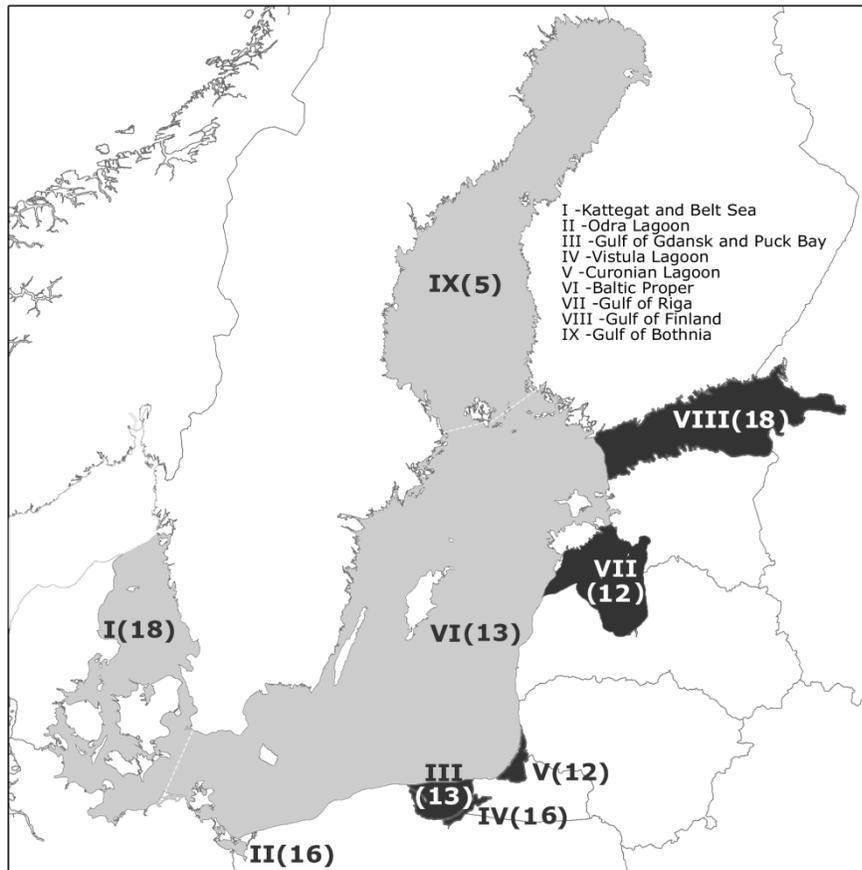


Figure.1. Assessment units defined in the Baltic Sea for the biopollution assessment procedure and their biopollution level (lighter regions are those with BPL=2, darker – with BPL=3). Numbers in parentheses indicate impacting alien species within a assessment unit (with BPL>0).

### 2.3. Analyses

The similarity of the assessment units in terms of impacting alien species and magnitude of their impacts was analyzed using a non-metric multidimensional scaling (NMDS) procedure and a similarity of percentages (SIMPER) analysis. Linear regression model was used to relate the number of impacting species with the total number of established alien species.

In order to overcome the potential bias in the assessment results, we took into account the heterogeneity in scientific interest (and consequently the amount of available information) on alien species issue in the different parts of the Baltic Sea. We considered separately the research effort (the number of literature sources available for alien species in a given assessment unit) and the level of knowledge. The later was estimated as:

Level of knowledge = (assessed cases/potential cases) x 100%,

where ‘assessed cases’ is the number of cases which were derived from literature sources where information on ADR and communities, habitats and ecosystem function was available, while ‘potential cases’ is the number of all possible cases which could be derived from the literature sources provided that they contain all necessary information, i.e. the number of alien species in an assessment unit multiplied by 4 (ADR, C, H, E). For instance, if there are 3 species selected for the analysis within an assessment unit, the number of ‘potential cases’ would be 12. If information on ADR, C, H and E was available for 2 of them, while for the third only ADR was assessed, it makes up 9 ‘assessed cases’ and consequently ‘level of knowledge’ equal 75%.

#### 2.4. Results

Among the 119 registered alien species in the Baltic Sea (listed in the Baltic Sea Alien Species Database by the last update, 25.10.2010), 79 were defined as established (sustaining self-reproducing populations) and 43 of the last were those having any documented ecological impact (see Appendix A for details). Others were considered having no or negligible effect and consequently BPL=0. Performing the assessment, only two alien species – *Balanus improvisus* and *Cercopagis pengoi* – were assigned the highest ADR class (E) for the Gulf of Finland, since they occurred in high numbers and were distributed throughout the assessment unit. Several other species, had a relatively high abundance and distribution range for at least one of the assessment units during the defined assessment period (i.e. occurred in moderate numbers in all localities, or in high numbers in many localities - ADR class D): *Bonnemaisonia hamifera*, *Carassius gibelio*, *Cercopagis pengoi*, *Dreissena polymorpha*, *Gammarus tigrinus*, *Gmelinoides fasciatus*, *Marenzelleria* spp., *Mnemiopsis leidyi*, *Mya arenaria*, *Neogobius melanostomus* (also known as *Apollonia melanostomus*), *Obesogammarus crassus*, *Palaemon elegans*, *Paramysis lacustris*, *Pontogammarus robustoides*, and *Potamopyrgus antipodarum*.

A strong impact on native species and communities (C3) was reported for *D. polymorpha*, *O. crassus* and *P. robustoides* in the Curonian Lagoon, and for *G. tigrinus* in the Vistula Lagoon. Sixteen of the 44 analyzed species have had any registered impact on habitat (*Balanus improvisus*, *Cercopagis pengoi*, *Chelicorophium curvispinum*, *Cordylophora caspia*, *Crassostrea gigas*, *Dasya baillouviana*, *Dreissena polymorpha*, *Ensis americanus*, *Eriocheir sinensis*, *Fucus evanescens*, *Gracilaria vermiculophylla*, *Marenzelleria* spp., *Mya arenaria*, *Mytilopsis leucophaeta*, *Potamopyrgus antipodarum* and *Sargassum muticum*). Yet there was only *D. polymorpha* with the referred strong impact on habitats (H3) in the Curonian Lagoon ecosystem.

For seven species (namely *N. melanostomus*, *O. crassus*, *P. robustoides*, *D. polymorpha*, *G. tigrinus*, *B. improvisus* and *C. pengoi*) high biopollution level (BPL=3) was defined in one or more analyzed sub-regions. None of the analyzed species has acquired the maximum (BPL=4) level of impact magnitude.

The mostly distributed species, observed nearly all around the Baltic Sea were *Marenzelleria* spp., *Potamopyrgus antipodarum*, *Eriocheir sinensis*, *Cercopagis pengoi*, *Mya arenaria* and *Balanus improvisus* (Fig. 2). Yet their magnitude of impact did not match in different assessment units (Fig. 3).

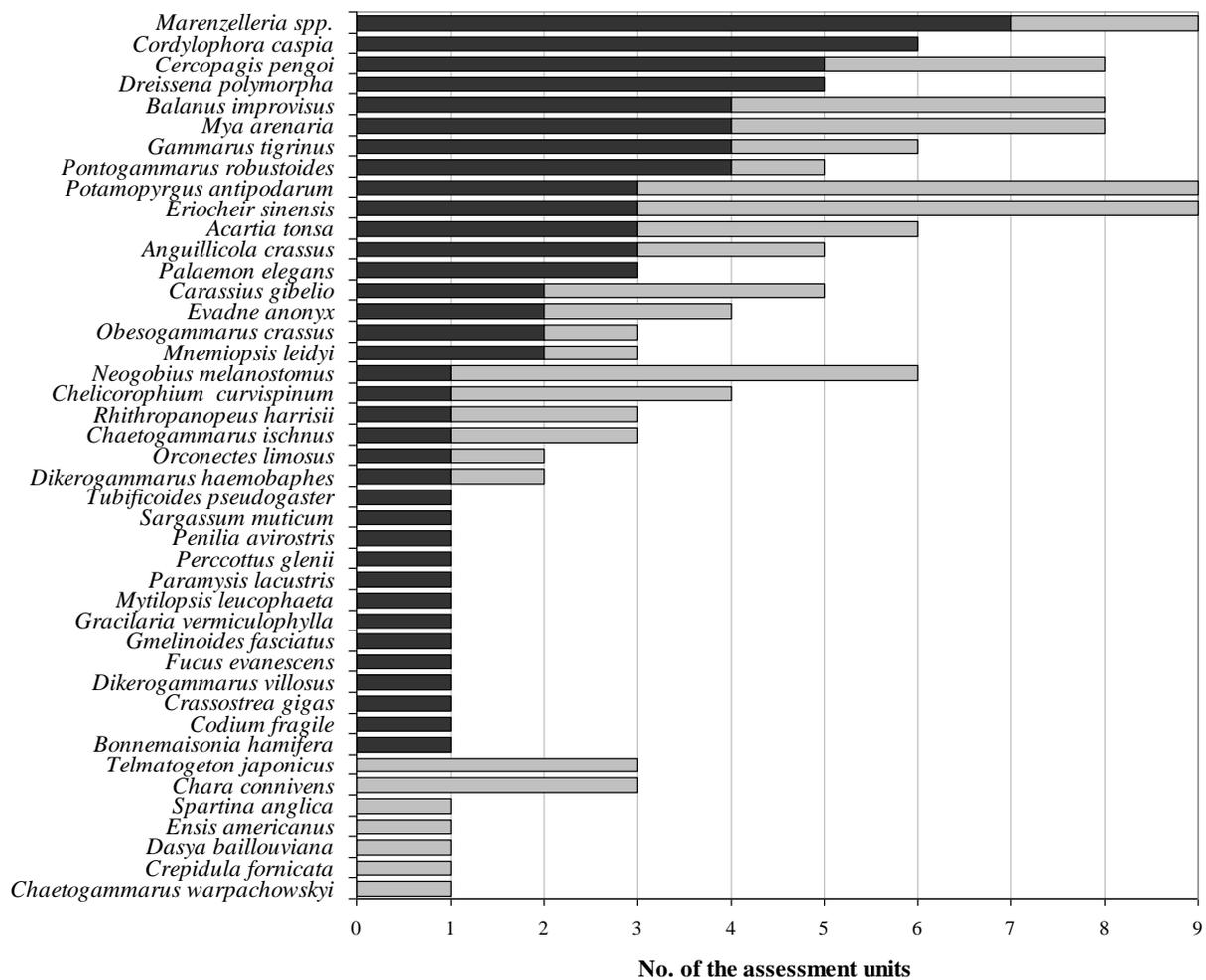


Figure 2. Number of the assessment units, where the species occur (grey bars) and have moderate to strong impact, BPL>1 (black bars).

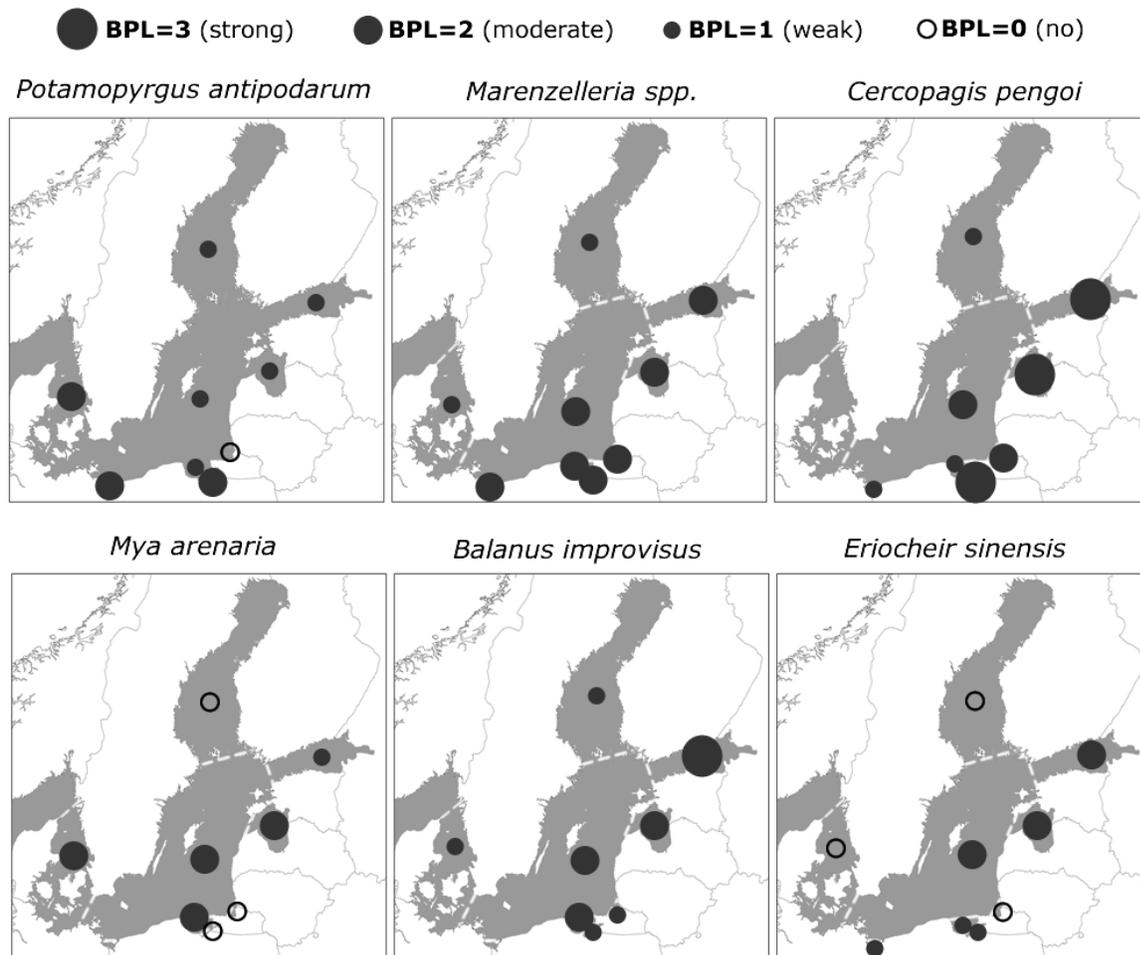


Figure 3. The magnitude of impacts of the 6 mostly distributed alien species in the Baltic Sea, assessed for the different assessment units, where the species is being reported.

The overall biopollution level (the highest value obtained for a certain assessment unit) ranged from “moderate” (BPL=2) to “strong” (BPL=3), being the highest in the coastal lagoons, inlets and gulfs, mainly in the eastern Baltic Sea (the Gulf of Riga, the Gulf of Gdansk and Puck Bay, the Curonian and Vistula Lagoons) and also in one of the larger sub-regions – the Gulf of Finland (Fig. 1).

Analysis of impacting alien species distribution and magnitude of their impacts revealed the highest similarity level (nearly 60%) among the three analyzed Baltic Sea lagoons (Odra, Vistula and Curonian). Three larger sub-regions having offshore areas – the Gulf of Finland, the Gulf of Gdansk and the Gulf of Riga showed greater resemblance with the open waters of the Baltic Proper. The most distinct were the Gulf of Bothnia and the Kattegat and Belt Sea.

The relationship of invasion pressure on the ecosystem to the amount of established alien species was tested via linear regression model. The analysis revealed a weak, statistically insignificant positive correlation ( $r=0.58$ ,  $p=0.10$ ) between the number of impacting alien species (with  $BPL>0$ ) and the total number of established alien species within an assessment unit.

The analysis of the taxonomic composition, origin and pathway of introduction performed for impacting *versus* established alien species also revealed a certain degree of likeness (e.g. in dominant groups). However, the “group-portrait” of the most common alien species in the case with ‘impacting’ ones was more apparent: crustaceans from the Ponto-Caspian region, introduced by shipping activities (Fig. 4). It is also noteworthy that the second most common group among impacting aliens in the Baltic Sea was macrophytes (including macroalgae) - nine of the established ten species were affecting the Baltic Sea ecosystem in one or another way. Meanwhile among eleven established oligochaete and polychaete worms, only two (*Marenzelleria spp.* and *Tubificoides pseudogaster*) are known to have caused impact to the Baltic Sea communities, habitats or ecosystem functioning.

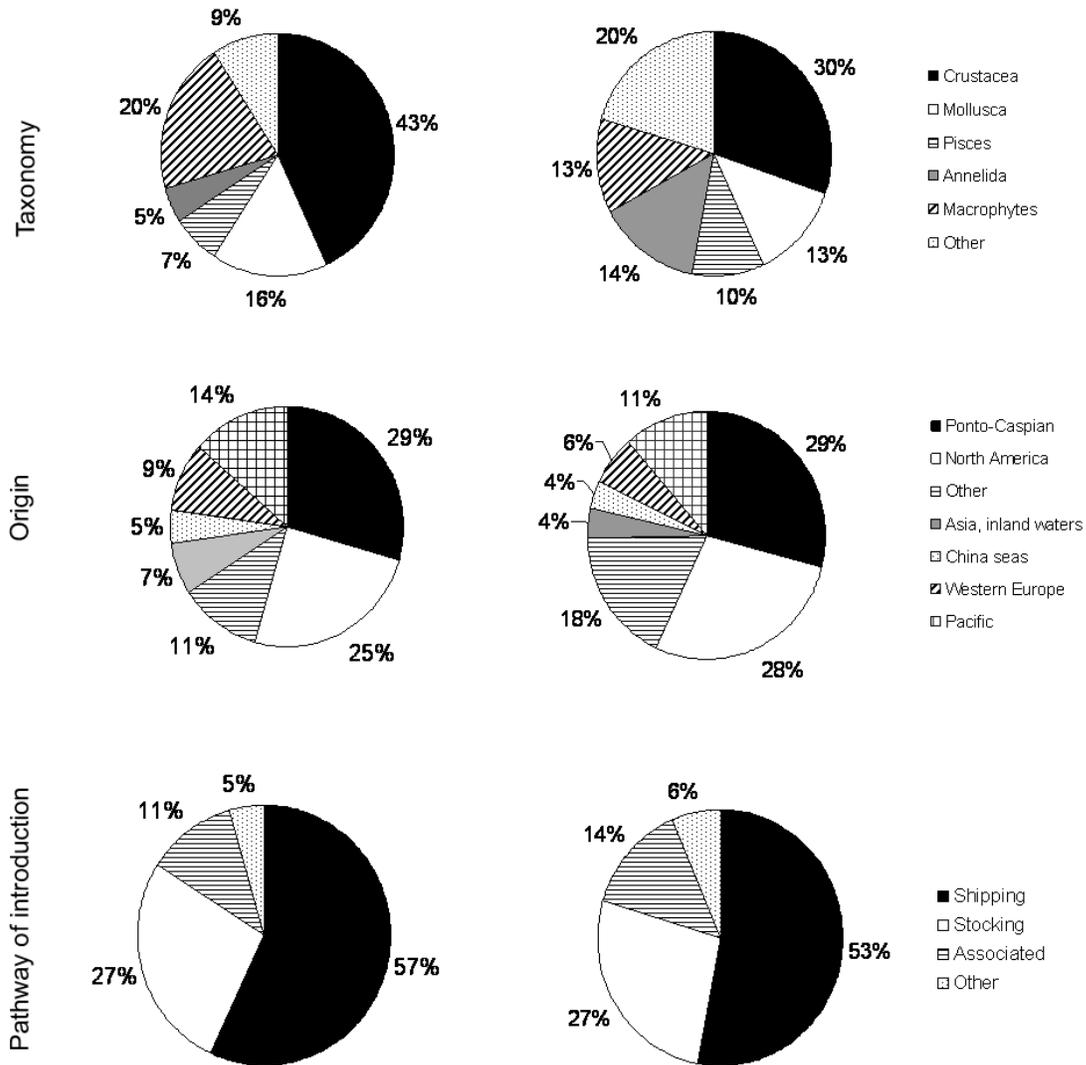


Figure 4. Taxonomic composition, areas of origin and pathways of introduction, characterizing the established (right column) and impacting (BPL>0) (left) alien species in the Baltic Sea.

The extent of the literature for each assessment unit varied from the Gulf of Bothnia (13) to the Baltic Proper (48). On the other hand, the Gulf of Bothnia hosted the least number of both alien and impacting species, while in the Baltic Proper those numbers were among the five highest within the entire Baltic Sea. The meta-analysis of the literature sources revealed that the research effort did not necessarily coincide with the level of knowledge gained from the analyzed literature.

Also we found that information was unevenly distributed among the analyzed categories (ADR, C, H and E). For example, it was possible to assess the ADR in all cases, while the impact on communities (C) was known in 65%, impact on habitats (H) - 30% and impact on ecosystem functioning (E) - in 43% of the cases. Similarly, the percentage of information with high confidence level obtained differed for these categories: 29% for ADR, 20% for C, 5% for H and 4% for E.

## 2.5 Conclusions

- We found the BPL method could be sufficiently robust when using both raw datasets and extractions from the published literature.
- Based on the presented results, we would suggest to define species into 'alien' (BPL=0), 'impacting' (BPL>0), i.e. the 'potentially invasive' (BPL=1) (since these species may distribute further and their weak, but measurable impacts may proliferate over the time), and the 'invasive' (BPL>1) ones.
- The most numerous (in terms of alien species richness) and most impacting taxa in the Baltic Sea are crustaceans.
- Ponto-Caspian and North-American species makes the prevailing group among all established alien species; most of them get the invasive species status (BPL>1) and should be listed as potential invaders in other ecosystems within and outside the studied region.
- Estuaries, coastal lagoons and inlets generally harbor more alien invertebrate species than open sea areas and bioinvasion impacts tend to be more apparent in these areas.
- Assessing alien species impacts on a larger scale (like we did for the extended sub-regions, having offshore areas – the Baltic Proper, Gulf of Finland, Gulf of Bothnia and Gulf of Riga) may result in underestimation of some local effects.
- The BPL approach is a convenient tool for assessing both ecological status of a waterbody that could be employed in EU Marine Strategy Framework Directive and risk assessments required in the IMO Ballast Water Management Convention
- The relevant data on alien species impacts, properly entered into BINPAS and stored in the database, can assist researchers to unify their assessments, compare the invasiveness of a species in different ecosystems, track the dynamics of biopollution level over time, *etc.*

### **3. ECOTRAITS: parameterization of the ecological traits of benthic and pelagic invertebrate and fish IAS**

#### **3.1 Introduction to methodology**

The performed bioinvasion impact (biopollution) analysis for the Baltic Sea (see 2. IMPACTS) non-indigenous has indicated that there are at least 29 species that could be qualified as "invasive" (assessed impact magnitude from medium to strong) widely distributed and/or spreading intensively and having significant environmental impact). Eight of these species have not been reported yet from the North Sea or North East Atlantic. Since the species may spread to these regions in the nearest future due to extensive shipping, we have proposed them for the consideration in the North East Atlantic Shelf Model in order to predict whether a NIS will establish itself in the area provided that environmental tolerance limits are known (identify "envelopes" - areas to be invaded).

#### **3.2 Considered variables and data search**

The parameters chosen to be considered were:

- Species taxon
- Functional group
- Origin
- Year of introduction into the Baltic Sea
- Location where registered first in the Baltic
- Most probable pathway of introduction into the Baltic Sea
- Possible vector of introduction
- Current distribution within the Baltic Sea
- Occurrence in the proximity of the harbor areas
- Biopollution level in the Baltic
- Salinity tolerance range (in the wild)
- Experimentally defined salinity limits (if available)
- Temperature tolerance range (optimal population range, lethal, optimal for reproduction)
- Preferable depth of occurrence
- pH tolerance limits
- min O<sub>2</sub> tolerance

The extensive data-mining was conducted using the Google and Google Scholar service. Data both from the web-resources (official databases, on-line reports) and peer-reviewed scientific papers were considered. If available, preference was given to scientific publications, where data were based either on field observations or experimental studies.

### 3.3 Summarized results

Seven of the eight considered species were crustaceans (5 nektonic and 2 zooplankton predators), and one – predatory demersal fish *Perccottus glenii*. Six species were intentionally introduced (either for stocking or for ornamental purposes) and two arrived occasionally via shipping. Currently all of them occur near the harbor areas within coastal lagoons, gulfs and inlets.

The fishhook waterflea *Cercopagis pengoi* is widely distributed and appears in high abundances all over the Baltic Sea. Other species are restricted to coastal areas within gulf and lagoons. The crustaceans intentionally introduced for stocking purposes occurs exceptionally in the shallow waters, others may be observed up to 60m depths.

Crustaceans *Chaetogammarus ischnus* and *Gmelinoides fasciatus* as well as the fish *Perccottus glenii* are oligohaline species, with restricted salinity tolerance limits up to 3 PSU. Others are mesohaline, however only *Pontogammarus robustoides* and *Obessogammarus crassus* may withstand up to 18 PSU. The annual salinity mean range for *Evadne anonyx* is set as 0.6-1 PSU, in the wild population maximum observed at 5.4 PSU, yet according to the experimental results, its maximum salinity limit is 30 PSU. All of the species are eurythermic, able to tolerate temperatures up to 30°C, yet optimal range for successful reproduction is narrower. All of the considered species can tolerate poorly oxygenated water (<2 mg/l O<sub>2</sub>). The information on pH tolerance for most of the species was unavailable from the literature.

## 4. PHYTO-TYPES: parameterization of the functional traits and environmental tolerance limits for phytoplankton species known to be established in the European regional seas

### 4.1 Introduction

The meta-analysis of the invasive phytoplankton types have been performed in order to develop the database on their trophic status, eco-morphology and motility, bloom formation, toxicity, life cycle, environmental tolerance limits and adaptive strategy. These data may be used further for the analysis of successful invader traits and development of "super-invader plankton species" model.

### 4.2 Data search and quality control

The existing databases (DAISIE, NOBANIS, Baltic Sea Alien Species Database) were critically analysed, and established alien species selected.

DAISIE Database records 45 marine phytoplankton species (DAISIE, 2009; Olenin and Didžiulis, 2009). Of them, 12 species should be excluded because: the same species are listed twice (under the valid name and as a synonym), native species are misidentified and listed as aliens (Gomez, 2008), the same alien species is listed by two different names (the *Gyrodinium aureolum* case, Hansen et al. 2000). Out of 33 species left, 23 are listed as established, most of them being dinoflagellates (12 species) and diatoms (6 species) as well as raphidophytes (4), and dictyochophytes (1) (Fig. 5).

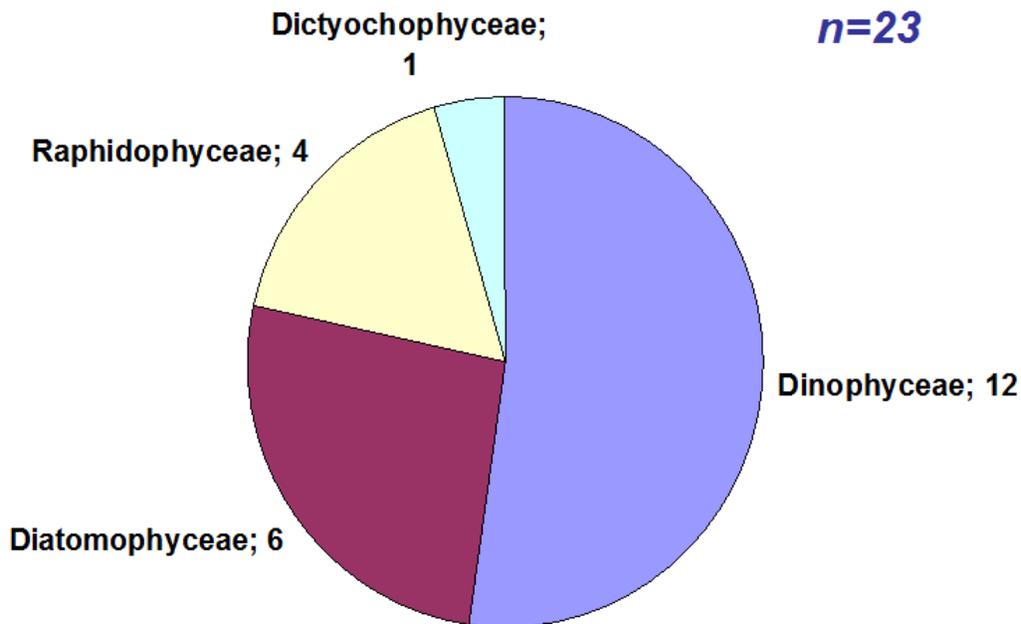


Figure 5. Taxonomic composition of established non-native phytoplankton species in the European seas; number of the recorded species

The list of non-indigenous phytoplankton is unlikely to be complete. Moreover, the classification of non-indigenous, cryptogenic (i.e. species of unknown origin which cannot be ascribed as being native or alien are termed cryptogenic, *sensu* Carlton, 1996) and cosmopolitan species and the discovery of new species to science make it difficult to apportion the status of a species (Gomez, 2008) and this may vary according to personal opinion. In this meta-analysis, we focused only on established in the recipient areas and truly invasive species (*sensu* Occhipinti-Ambrogi and Galil, 2004), which have been documented to increase in abundance and spread over large areas (without taking into account their origin, which in many cases remains uncertain). These species are listed in Table 1.

**Table 1.** List of non-indigenous phytoplankton species known to be established in different European marine regions.

<b>Dinoflagellates</b>
• <i>Alexandrium angustitabulatum</i> F. J. R. Taylor in Balech 1995
• <i>Alexandrium catenella</i> (Whedon & Kofoid) Balech 1985
• <i>Alexandrium leei</i> E. Balech
• <i>Alexandrium minutum</i> Halim, 1960
• <i>Alexandrium taylori</i> Balech, 1994
• <i>Alexandrium tamarense</i> (Lebour) E Balech 1995
• <i>Dicrroerisma psilonereia</i> Taylor & Cattell
• <i>Gymnodinium catenatum</i> L. W. Graham
• <i>Gyrodinium corallinum</i> Kofoid & Swezy, 1921
• <i>Karenia mikimotoi</i> (Miyake & Kominami ex Oda) G. Hansen & Ø. Moestrup
• <i>Noctiluca scintillans</i> (Macartney) Kofoid et Swezy, 1921
• <i>Prorocentrum minimum</i> (Pavillard) J. Schiller
<b>Diatoms</b>
• <i>Coscinodiscus wailesii</i> Gran & Angst
• <i>Odontella sinensis</i> (Greville) Grunow
• <i>Pleurosigma simonsenii</i> Hasle 1990 *
• <i>Pseudo-nitzschia seriata</i> (Cleve) H. Peragallo
• <i>Thalassiosira punctigera</i> (Castracane) Hasle 1983
• <i>Thalassiosira tealata</i> Takano 1980
<b>Raphidophytes</b>
• <i>Chattonella marina</i> var. <i>antiqua</i> (Hada) Demura & Kawachi in Demura et al. 2009**
• <i>Chattonella marina</i> (Subrahmanyam) Hara & Chihara 1982
• <i>Fibrocapsa japonica</i> S. Toriumi & H. Takano 1973
• <i>Heterosigma akashiwo</i> (Y. Hada) Y. Hada ex Y. Hara & M. Chihara 1967
<b>Dictyochophytes</b>
• <i>Pseudochattonella farcimen</i> (W. Eikrem, B. Edvardsen, & J. Throndsen) W. Eikrem in W. Eikrem, B. Edvardsen & J. Throndsen 2009**

\* In DAISIE database the species is listed under synonym name *Pleurosigma planctonicum* R. Simonsen 1974;

\*\* Acc. to DAISIE (2009) this species is known as alien from the North Sea (German and Norway waters) and from the Baltic Sea (Kattegat area). Firstly it was identified as raphidophyte *Chattonella* sp. or *Chattonella cf. verruculosa*. This was later transferred to the class Dictyochophyceae and renamed firstly as *Verrucophora farcimen* Eikrem, Edvardsen et Throndsen (Edvardsen et al., 2007), and then as *Pseudochattonella farcimen* Riisberg (Riisberg, 2008)

### 4.3 Traits of the selected non-indigenous phytoplankton species

In order to compile the PHYTO-TYPES database nearly one hundred research papers, online databases and environmental reports have been screened. The following groups of alien phytoplankton traits were distinguished (Table 2).

**Table 2.** Traits of alien phytoplankton species selected for development of the PHYTO-TYPES database

Group of traits	Traits, features	Explanation
Taxonomy	Class Species	Taxonomic group and Latin name of the species
Morphology	Cell shape	Important for calculation of biovolume, total biomass, carbon content, etc
	Max dimension range	Important for calculation of biovolume, total biomass, carbon content, etc
	Max cell volume	Important for calculation of total biomass, carbon content, etc. One of the key features to identify adaptive strategy type of the species.
Population growth and life cycle characteristics	Max growth rate	Measured in cell divisions per day. One of the key features to identify adaptive strategy type of the species
	Resting spore form	Ability to form resting spores, which allows species to withstand critical environmental conditions and survive during transportation in ship ballast water
Ecomorphology and trophology	Motility	Ability of cells to move. Important feature to identify competitive abilities of species (consumption of nutrients)
	Trophic status	Division into autotrophic (only photosynthetic), heterotrophic (only organic material is used) and mixotrophic (both photosynthetic and organic material) way of nutrition of phytoplankton species
	Life-form	Solitary or colonial forms. Forming of colonies improves buoyancy and protection against grazing
Harmfulness	Bloom formation	Division into species which are known to form outbreaks (blooms) and those which are not forming blooms
	Toxicity	Species which are able to excrete phytotoxins which may poison aquatic biota and cause human health problems
Environmental tolerance limits	Temperature range	
	Salinity range	
	Nutrients	Phosphorus, nitrogen and silicium (for diatoms) compounds
	Irradiance	Data limited to few species only. Shows their requirements to solar radiation
Adaptive strategy	C-S-R strategy	The integrative characteristics of phytoplankton based on the ecomorphology, growth rate and tolerance to environmental stress of the phytoplankton (see more detailed explanation below).

The C-S-R classification is based on works of Reynolds (1988), Reinolds et al. (2002) and Smayda (2002), identifying types of the phytoplankton species as follows :

**C** - colonist species are primarily invasive species which often predominate following onset of elevated nutrient conditions, i.e. chemically-disturbed waters; they are generally smaller than R and S species, have faster growth rates and achieve greater abundances. When toxic, they are primarily ichthyotoxic.

**S** - nutrient stress tolerant species are primarily acquisitive species, typically very large, often highly ornamented, and capable of depth-keeping through motility alone or in combination with auto-regulated buoyancy. They are typically K-selected species which achieve modest but persistent abundance, and they often possess endosymbionts, or mixotrophically supplement their photo-autotrophy.

**R** - species occur in physically-disturbed water masses and are primarily attuning or acclimating strategists tolerant of, or dependent upon, entrainment within actively-mixed or circulating water layers. Among their traits are: pre-adaptations to shear/stress effects; effective light-harvesting antennae and cellular shape; or related adaptive form achieved through chain formation. Their abiding attributes enable their growth to be light saturated at lower aggregate light levels than apply to other types of phytoplankton. They are anticipated to have slightly higher growth rate than other dinoflagellates to counterbalance windinduced washout. Their counterparts among diatoms are the spring-bloom species.

Data on the phytoplankton traits and types are compiled in Table 3. The results of our meta-analysis show that most of the alien phytoplankton species belong to R-strategists (Fig. 6).

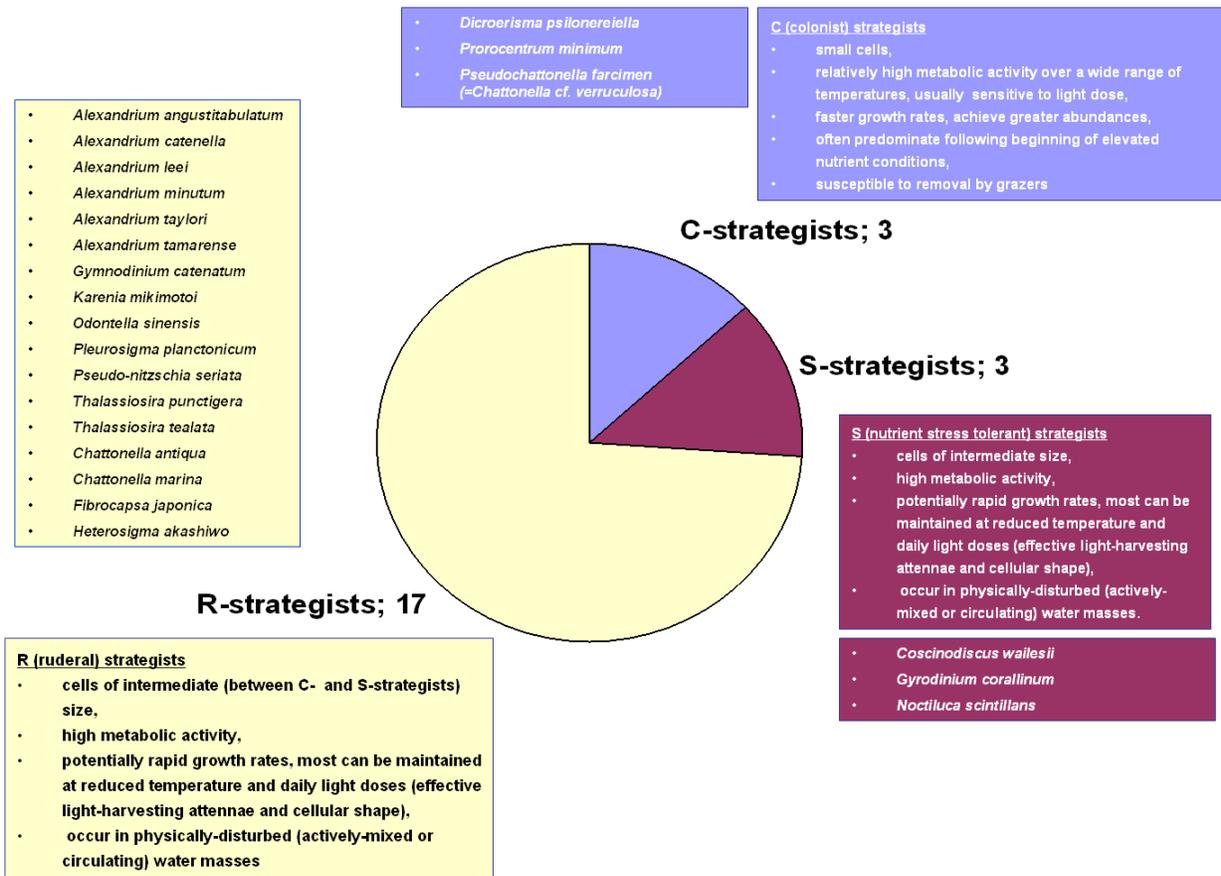


Figure 6. Functional classification of established alien phytoplankton according to C-S-R strategies (sensu Reynolds 1988; Smayda & Reynolds 2001 and Smayda 2002)

### 4.3 Summary

23 alien phytoplankton species are known to be established in the European regional seas; 14 of them are known to have impact either on environment or uses of the sea, or both. Most of the established alien species (52%) are dinoflagellates, followed by diatoms (26%); most of them (74%) belong to R (ruderal) strategists.

**Table 3.** Summarized information on traits of the non-indigenous phytoplankton species known to be established in different European marine regions.

Class	Species	Cell shape	Max dimension range, $\mu\text{m}$	Max cell volume, $\mu\text{m}^3$	Max. cell growth rate, divisions $\text{day}^{-1}$	Resting spore form.	Motility	Trophic status	Life-form	Bloom formation	Tox.**	T °C range	S‰ range	Nutrients, $\mu\text{M}$	Irradiance	C-S-R strat.
Dinophyceae	<i>Alexandrium angustitabulatum</i>	Rotational ellipsoid	17-24	5,000	0.5	+	Vertically migrate	AU	Solitary	No blooms observed	Toxic, PSP	10-30	3-37.5			R
Dinophyceae	<i>Alexandrium catenella</i>	Rotational ellipsoid	20-25	25,700	0.47 (0.55 in culture)	+	Vertically migrate	AU	In short chains of 2, 4 or 8 cells	Toxic blooms	Toxic, PSP	12-28	15-37	NH <sub>4</sub> (0.4–2.8); NO <sub>3</sub> (1–5.4); PO <sub>4</sub> (0.2–0.6) SiO <sub>4</sub> (1.4–4.2)		R
Dinophyceae	<i>Alexandrium leei</i>	Cone+half sphere	35–50	48,400	No data	+	Vertically migrate	AU	single or two-cell chains	No blooms observed	Ichthyotoxic	15-25	10-35			R
Dinophyceae	<i>Alexandrium minutum</i>	Rotational ellipsoid	15-30	9,000	0.5	+	Vertically migrate	AU	Solitary	Abundant, but no blooms observed	Toxic, PSP	4-24	3-30			R

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Dinophyceae	<i>Alexandrium taylori</i>	Pyriform	33–37	31,000	0,5 (1,48 in culture)	+	Vertically migrate	AU	Solitary	Blooming	Toxic, PSP	N/A	N/A			R
Dinophyceae	<i>Alexandrium tamarense</i>	Rotational ellipsoid	22-51	51,700	0.33	+	Vertically migrate	AU	Solitary or in pairs	Blooming	Toxic, PSP	8-20	21-30	Nitrate limitation	230 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$	R
Dinophyceae	<i>Dicroerisma psilonereia</i>	Cone+half sphere	23-32	4,000	N/A		Vertically migrate	AU	Solitary	No blooms observed		N/A	N/A			C
Dinophyceae	<i>Gymnodinium catenatum</i>	Circular to squarish	38-53	36,500	0.33	+	Swimming	AU	In long, chains of tiny cells, with up to 64 cells in a chain	Blooming	Toxic, PSP	4-30	15-34	Able to exploit the nutrient rich layer of the pycnocline. Better growth using $\text{NH}_4$		R
Dinophyceae	<i>Gyrodinium corallinum</i>	Rotational ellipsoid	124-158	264,600	N/A	N/A	Vertically migrate	AU	N/A	N/A	N/A	N/A	N/A			S?
Dinophyceae	<i>Karenia mikimotoi</i>	Rotational ellipsoid	18-40	9,400	1.2	N/A	Vertically migrate	AU	Solitary	The most common red-tide	Ichthyotoxic (brevetoxin)	5-27	12-35	Limited by ammonium. Blooms in	Suffer from photo	R

									species	traits	habitat	phenology	ecology	impacts	management	
Dinophyceae	<i>Noctiluca scintillans</i>	Sphere	200-2000	523.333,000	0,3	Not observed	Vertically migrate	HT	Solitary	Red-tide species	Not toxic (high biomass effect: discoloration, anoxia)	10-28	19-36	nutrient poor inshore waters	inhibition	S
Dinophyceae	<i>Prorocentrum minimum</i>	Rotational ellipsoid	14-22	1,100	0.52	+	Vertically migrate	MX	Solitary	Blooming	Toxic (non-toxic in the Baltic Sea)	3-33	0.7-35	P nutrition have an important role. NH <sub>4</sub> supporting blooms. Effectively take up DON, DOP	High irradiance (30 - 500 μmol photons m <sup>-2</sup> s <sup>-1</sup> )	C
Diatomophyceae	<i>Coscinodiscus wailesii</i>	Cylinder	175-500	13.203,000	1.06	+	Non-motile	AU	Solitary		Harmful (Mucilage; high biomass effect on nori)	0-32	10-35	NO <sub>3</sub> (0.24-0.97); PO <sub>4</sub> (0.26-0.68)	10 - 150 μmol photons m <sup>-2</sup> s <sup>-1</sup>	S

Diatomophyceae	<i>Odontella sinensis</i>	Oval cylinder	120-170	1.000,000	1.5	Resting spores unknown, auxospore formation may take place	Non-motile	AU	Solitary or in pairs, chains	Blooming	No harmful effects observed	1-27	2-35	Limited by inorganic nitrogen	High light conditions	R
Diatomophyceae	<i>Pleurosigma planctonicum</i> (valid name: <i>Pleurosigma simonsenii</i> )	Parallel piped/2		N/A	N/A	Not observed	Limited movement by secretion of mucilaginous material	AU	Solitary or in pairs, chains	Rare (abundant in the Western English Channel, but no blooms) observed	No harmful effects observed	N/A	N/A			R
Diatomophyceae	<i>Pseudonitzschia seriata</i>	Parallel piped	80-120	9,200	N/A	Not observed	Limited movement by secretion of mucilaginous material	AU	In chains	Blooming	Toxic (DA)	5-30	6-48			R

Diatomophyceae	<i>Thalassiosira punctigera</i>	Cylinder	40-186	107,800	0,26	Not observed	Non-motile	AU	In chains	Rare (abundant in the Western English Channel, but no blooms observed)	No harmful effects observed	11 – 22 – 22 – 33		R
Diatomophyceae	<i>Thalassiosira tealata</i>	Cylinder	6-10	92	N/A	Not observed	Non-motile	AU	In chains	No blooms observed	No harmful effects observed	N/A N/A		R
Raphidophyceae	<i>Chattonella antiqua</i>	Rotational ellipsoid	80-90	37,700	0,97	+	Vertically migrate	AU	Solitary	Blooming	Ichthyotoxic	15-28	15-41	R
Raphidophyceae	<i>Chattonella marina</i>	Rotational ellipsoid	30-40	9,000	1,08	+	Vertically migrate	AU	Solitary	Blooming	Ichthyotoxic	10-30	15-45	R
Raphidophyceae	<i>Fibrocapsa japonica</i>	Rotational ellipsoid	20-30	4,700	0.4	+	Vertically migrate	AU	Solitary	Blooming	Toxic	4-32	>15	R

Raphidophyceae	<i>Heterosigma akashiwo</i>	Rotational ellipsoid	15-25	4,200	0.35	+	Swimming, vertically migrate	AU	Solitary	Blooming	Toxic	9-30	4-35	Blooms initiated by nitrogen substrates (NH <sub>4</sub> <sup>+</sup> > NO <sub>3</sub> > urea)	100 μmol photons m <sup>-2</sup> s <sup>-1</sup>	R
Dictyochyceae	<i>Chattonella cf. verruculosa</i> (valid name: <i>Pseudochattonella farcimen</i> )	Rotational ellipsoid	10-40	5,800	1.74	No data	Vertically migrate	AU	Solitary	Blooming	Ichthyotoxic	5-30	10-35			C

\* AU- autotrophic; HP- heterotrophic; MX- mixotrophic

\*\* DA- domoic acid; PSP- Paralytic Shellfish Poisoning

#### 4. References

- Carlton JT (1996). Biological invasions and cryptogenic species. *Ecology* 77: 1653-1655
- DAISIE (2009). DAISIE. Handbook of Alien Species in Europe. *Invading Nature – Springer Series In Invasion Ecology*. Vol. 3, Springer, 399pp.
- Edvardsen B, Eikrem W, Shalchian-Tabrizi K, Riisberg I, Johnsen G, Naustvoll L & Thronsen J. (2007). *Verrucophora farcimen* gen. et sp. nov. (Dictyochophyceae, Heterokonta) - a bloom-forming ichthyotoxic flagellate from the Skagerrak, Norway. *Journal of Phycology* 43(5): 1054-1070.
- Gómez F (2008). Phytoplankton invasions: comments on the validity of categorizing the non-indigenous dinoflagellates and diatoms in European Seas. *Mar. Pollut. Bull.* 56, 620–628.
- Occhipinti-Ambrogi A, Galil B (2004). A uniform terminology on bioinvasions: a chimera or an operative tool? *Mar. Pollut. Bull.* 49, 688–694.
- Olenin S, Didziulis V (2009). Introduction to the list of alien taxa. In: DAISIE. Handbook of Alien Species in Europe. *Invading Nature – Springer Series In Invasion Ecology*. Vol. 3, Springer, pp. 129–132.
- Reynolds et al. (2002). Towards a functional classification of the freshwater phytoplankton. *J. Plankton Res.*, 24(5), 417-428.
- Reynolds (1988). Functional morphology and the adaptive strategies of freshwater phytoplankton. In: Sandgren, C.D. (Ed.), *Growth and Reproductive Strategies of Freshwater Phytoplankton*. Cambridge Univ. Press, Cambridge, UK, pp. 388– 433
- Smayda (2002). Adaptive Ecology, Growth Strategies and the Global Bloom Expansion of Dinoflagellates. *J. Oceanography*, 58 (2), 281-294
- Riisberg I (2008). Genetic characterization of the marine ichthyotoxic flagellate *Pseudochattonella farcimen* (Heterokonta) and phylogenetic relationships among heterokonts, Ph.D. thesis, Univ. Oslo, Oslo, pp. 1–33.