Composition and dynamics in space and time of polychaete larvae in coastal waters of the North Sea

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CONTENT

Zusammenfassung

Meroplanktische Polychaetenlarven aus dem Lister Tidebecken (östliche Nordsee) wurden bestimmt, horizontale und vertikale Verteilungsmuster untersucht sowie zeitliche Abundanzschwankungen analysiert. Gezeiten verursachen starke Schwankungen der Wassertiefe innerhalb der Bucht und Jahreszeiten und Wetter eine hohe physikalische und biologische Variabilität. Die taxonomische Untersuchung der Larven erfolgte anhand von Proben einer fast täglichen Zeitreihe von einer festen Probenstelle (1996-2001) sowie von Proben, die innerhalb der gesamten Bucht während Ebbe und Flut zwischen 2000 und 2002 genommen wurden. Larven von insgesamt 46 Taxa, verteilt auf 18 Familien, wurden bestimmt. Artenreichste Familie waren die Spionidae (36% aller Taxa), gefolgt von Phyllodocidae (14%) und Polynoidae (9%). Die mittlere Abundanz der 1996-2001 Zeitreihe war $2.1 \cdot l^{-1}$ (±0.3). Die häufigste Art war *Pygospio elegans*, gefolgt von anderen Spioniden (*Spio martinensis* und *Polydora cornuta*) und *Lanice conchilega*. Die mittlere Abundanz aller Larven in der Bucht (2000-2002) betrug $3.7 \cdot l^{-1}$ (±0.2). Eine geringe Übereinstimmung zwischen der Artenzusammensetzung in Plankton und Benthos deutet auf einen bedeutenden Eintrag von Larven entfernteren Ursprungs hin. Eine unterschiedliche Artenzusammensetzung des Planktons an verschiedenen Stellen innerhalb der Bucht lässt vermuten, dass die Larven nicht durch Hydrodynamik zufällig gemischt werden. Räumliche Verteilungsmuster der Larven wurden zwischen 2000 und 2002 auf drei verschiedenen räumlichen Skalen (mehrere hundert Meter, ein Kilometer und mehrere zehn Kilometer) sowie während Hoch- und Niedrigwasser untersucht. Trotz des ständigen Wasseraustausches mit der Nordsee verbleiben Polychaetenlarven innerhalb der Bucht. Benthische Vorkommen und Küstenmorphologie könnten art-spezifische Verteilungsmuster verstärken. Explorative multivariate Methoden ergaben eine hohe Variabilität der Abundanz und Diversität der Larven zwischen den Jahren (1996-2001), jahreszeitliche Muster waren hingegen ähnlich und signifikant positiv korreliert mit einem Anstieg von Phytoplanktonbiomasse (Chl*a*), pH-Wert und Wassertemperatur (°C) zwischen Frühling und Sommer. Nicht-synchrone Schwankungen (<1-12 Monate) der °C-, NO_2-, PO_4- und Gesamt-Silikat-Werte waren mit der Larvenabundaz signifikant korreliert und sind wahrscheinlich an endokrinen Prozessen und der Reifung der Gonaden in adulten Polychaten beteiligt. Synchrone Schwankungen der Chl*a*-, NO_2-, pH-, PO_4-, Salinität- und °C-Werte waren signifikant mit der Larvenabundanz korreliert und vermutlich an der Auslösung des Laichens und der Nahrungsgewinnung der Larven und Adulten beteiligt.

Summary

Polychaete meroplanktonic larvae from the List tidal basin in the eastern North Sea were identified, their horizontal and vertical distribution patterns described, and temporal abundance fluctuations analyzed. Tides cause marked changes in the depth of this basin, while seasonality and weather dependence cause high environmental and biological variability. The taxonomic composition was analyzed from a quasi-daily time-series (1996-2001) obtained at a fixed point inside the basin, as well as samplings covering the basin during flood and ebb periods between 2000-2002. Larvae of 46 polychaete taxa belonging to 18 families were identified. Spionids were the most diverse (36% of the total number of taxa), followed by larvae of phyllodocids (14%), and polynoids (9%). The averaged abundance for the 1996-2001 time series was $2.1 \cdot l^{-1}$ (±0.3) with *Pygospio elegans* being the most abundant species, followed by other spionids (*Spio martinensis* and *Polydora cornuta*) and the terebellid *Lanice conchilega*. Between 2000-2002, the average abundance througout the basin was $3.7 \cdot l^{-1}$ (±0.2). A low correspondence between benthic and planktonic assemblages suggested a qualitatively important input of long-distance larval vagrants. Sites within the basin differed in species composition, suggesting that larvae are not randomly mixed by the tidal hydrodynamics. Spatial distribution patterns were described by sampling at three spatial scales (hundreds of m, 1 km, and tens of km) during flood and ebb periods between 2000-2002. In spite of tides continuously exchanging water with the North Sea, polychaete larvae are retained inside the basin. Benthic occurrence and coastal morphology may enhance species-specific distribution patterns. Explorative multivariate methods revealed high inter-annual variability (1996-2001) in larval abundance and diversity, but seasonality remained regular, being positively and significantly correlated with spring-summer increments in phytoplankton biomass (Chl*a*), pH-values, and water temperatures (°C). Lagged fluctuations (<1-12 months) of °C, NO_2, pH-values, PO_4, and total silicate were significantly related with larval abundances and are probably involved in endocrinal processes and gonadal maturation of adults. Instantaneous fluctuations of Chl*a*, NO_2, pH-values, PO_4, salinity, and °C were significantly related with larval abundances, being probably involved with triggering of spawning and feeding of larvae and adults.

Chapter 1. General introduction

The North Sea coastal zone shared between Germany and Denmark has a long history of research on marine biology and ecology. Zooplankton research started in this area during the 70's, focused on short-term descriptions of temporal dynamics of holoplanktonic copepods. Also meroplankton is a common and important component of marine zooplankton from neritic waters (Omori and Ikeda 1984). In this region, it is primarily represented by larval stages (transition stages between embryos and adults) of polychaetes, mollusks, and crustaceans (Hickel 1975; Martens 1980; Strasser and Guenther 2001). These must ensure the temporal and spatial persistence of populations, are important phytoplankton consumers, and represent a food source for other invertebrates and fish.

Due to the common occurrence and frequently high abundance of marine invertebrate larvae, ecologists became interested in them, consolidating the "larval ecology" as a discipline about a half-century ago (Young 1990). Young (1990) and McEdward (1995) have comprehensively revised the history, achievements, questions, and limitations of marine invertebrate larval ecology. From these contributions, it is concluded that larval studies have an enormous potential. They have become highly diverse, because different kinds of biologists seek for different kinds of information (morphology, behavior, physiology, life-history ecology, dispersal, recruitment, evolution, genetics, etc.) in descriptive, comparative, experimental, and theoretical studies, opening a wide variety of perspectives. Nevertheless, many intrinsic limitations still hamper the obtainment of clear results in this discipline.

The present study was undertaken inside one of the best-studied tidal basins of the German Wadden Sea, named the List tidal basin (see Gätje and Reise 1998). This is an enclosed bay, formed by the islands of Sylt and Rømø and causeways connecting these islands to the mainland; therefore, the water exchange is limited to a narrow tidal inlet between the islands. The depth of the basin varies with the tides, with a mean tidal range of 2 m. The water volume inside the basin at mean high tide is twice the mean low tide volume. One third of the basin area remains uncovered during low tides, and deep areas (depths >5 m) represent only 10% of its area. Particles are likely to settle only during slack water. Riverine discharges are negligible. Much of the local environmental and biological variability is produced by a pronounced seasonality and weather dependence.

Since polychaetes are one of the dominant groups of the macrozoobenthos inside the basin (Lackschewitz and Reise 1998), this study is focused on this group, attempting to assess three questions: *Which polychaete species occur as meroplanktonic larvae inside the basin? How do these distribute?* and *How large are their temporal abundance fluctuations?*

Larval identification is necessary in studies on recruitment and dispersal. The composition of polychaete larvae from the List tidal basin has remained unclear until now. Previous studies covered point locations, comprised short time periods, and did not perform detailed taxonomic analyses. In the present study, the local taxonomic composition was analyzed combining a time-series comprising 6 years (1996-2001) obtained at a fixed point inside the basin, as well as samplings covering almost the whole basin during flood and ebb periods between 2000-2002. The eastward and northward residual transport of water masses from The Netherlands, passing the Elbe estuary, may allow long-distance vagrants to join the species spectrum of the basin. This was analyzed in Chapter 2 (*Species identity and taxonomic remarks on polychaete larvae in the plankton of a tidal basin in the North Sea*). Low correspondence between local benthic and planktonic assemblages was found, suggesting that long-distance larval vagrants are qualitatively important. Since some taxa were captured at specific areas inside the basin, it seems that location is important for the taxonomic composition.

The study area is characterized by semi-diurnal tides and high wind stress, which together with the bottom topography produce strong currents (Backhaus *et al.* 1998). The water is in continuous movement and there is a strong exchange of energy and matter between the coast and the North Sea. Ecologists interested in marine invertebrate larval dispersal often perceived larvae as drifting bodies in a well-mixed water body, being at the mercy of currents, and subjected to wide dispersal. Nevertheless, macrozoobenthos do not distribute homogenously inside the basin. From the ecology of rocky shores it is known that larval supply determines to a large extent the distribution of benthic stages (see Ólafsson *et al.* 1994). In order to test this for soft-bottom fauna, the spatial patterns of larval abundance inside the basin were analyzed in Chapter 3 (*Spatial patterns of abundance in meroplanktonic polychaete larvae in a tidal basin*), sampling polychaete larvae at three spatial scales during a 3-year period and comprising flood and ebb periods (whenever possible). It was tested whether strong tidal mixing prevents the development of non-random spatial patterns within the waters of the basin, whether polychaete larvae show differential vertical distributions in the water column during flood and ebb flows, and whether they correspond to an onshore gradient of suspended particles of comparable size. Results obtained at three spatial scales point to larval retention as the dominant process inside the basin and suggest that a combination of benthic occurrence and coastal morphology enhances species-specific distribution patterns. These findings support recent studies (e.g. Kingsford *et al*. 2002 and Swearer *et al.* 2002), and illustrate that our understanding of marine invertebrate larval dispersal is changing.

The study of abundance fluctuations has been one of the most important tasks of ecology (Hanski 1997). Ecologists are interested in knowing when larvae occur and how large their abundance fluctuations are. The wide spectrum of morphologies, behaviors, and life histories of polychaetes complicates the picture on mechanisms of reproductive timing and synchrony. Reproductive synchronization can be achieved by coupled endogenous rhythms and environmental factors, but it is complicated by spatial changes and seasonal shifts in environmental parameters. The environmental variability of the Wadden Sea (e.g. strong winters and marked environmental seasonality) influences abundance fluctuations of benthic stages, but relationships between larval abundances and the environment have not been studied until now. Here, temporal dynamics and seasonality of polychaete larvae and environmental variables were analyzed with explorative multivariate methods, comprising 6 years (*Temporal dynamics of meroplanktonic polychaete larvae in a tidal basin of the North Sea: Are year-to-year fluctuations related to environmental variability?*). Locally, larval abundances show a high inter-annual variability. Lagged fluctuations of water temperature, NO_2, pH-values, PO_4, and total silicate have significant effects on larval abundances, being probably involved in endocrinal processes and gonadal maturation. Instantaneous fluctuations of phytoplankton biomass, NO_2, pH-values, PO_4, salinity, and water temperature affect larval abundances significantly, being probably related to the triggering of spawning, larval feeding, and feeding of adults to support ongoing spawning. The seasonality in larval abundance and diversity is rather regular, being positively and significantly correlated with increments in phytoplankton biomass, pH-values, and water temperatures during the spring-summer period.

Studying the ecology of planktonic larvae, in a variable environment like the Wadden Sea, was a challenge and not a trivial task.

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Chapter 2. Species identity and taxonomic remarks on polychaete larvae in the plankton of a tidal basin in the North Sea

Abstract

Meroplanktonic larvae of 46 polychaete taxa, belonging to 18 families, were identified from a set of water samples that covered the List tidal basin from 1996 to 2002. Larvae of spionids were the most diverse (36% of the total number of taxa), followed by larvae of phyllodocids (14%), and polynoids (9%). Based on the transport pattern of water masses by residual currents, at the scale of the German Bight, it is thought that long-distance vagrants could join the local species spectrum, since larvae from the Elbe estuary and the island of Helgoland could drift up to the area. Local records on polychaete taxa gathered during the last 75 years revealed that from 94 taxa with or presumably with larval stages, 45 are known from benthic stages only, 26 are only known as larval stages, and 23 have been found in both forms. This reveals a low correspondence between the benthic and planktonic species assemblages, and suggests that long-distance larval vagrants may be important. Twelve out of the 46 taxa encountered in this study were found at specific sites inside the basin, suggesting that location plays an important role for species composition.

1. Introduction

Polychaete larvae are worldwide components of coastal and open sea zooplankton. Their identification to species level is prerequisite for the analysis of recruitment processes and improves our knowledge about regional species richness. In polychaetes, the latter can substantially increase if plankton samples are included, since some species may locally occur only as larvae (Bhaud and Cazaux 1987).

The European Wadden Sea area is nursery for many marine invertebrates and fishes, and serves as feeding and resting ground for flocks of migratory birds. Polychaetes are an important diet of these consumers. Taxonomic studies on polychaete larvae from this region started with the description of material from Ringköbing (Denmark, 60 km north from the northernmost tip of the Wadden Sea) by Thorson (1946). Smidt (1951) described material from the Danish Wadden Sea. Finally, Plate and Huseman (1991 and 1994) described larvae from Helgoland. This short list is in marked contrast to an extensive literature on the benthic adults (see Hartmann-Schröder 1996).

Residual currents transport water masses from the Dutch coast eastward and, after passing the Elbe estuary, northward (Postma 1983). This may allow long-distance vagrants to join the local species spectrum. This was looked for, when the composition of polychaete meroplanktonic larvae inside the List tidal basin was studied.

2. Methodology

2.1. Sampling schemes

Three sampling strategies were undertaken, covering different temporal and spatial scales (Fig. 2.1). First, one surface water sample (10 l) was taken between January 1996 and December 2001 at List harbor during diurnal high tides, daily (spring to autumn) or weekly (winter). Second, at each of four sampling stations along the main tidal channel of Königshafen, five surface water samples (10 l each) were taken during diurnal high tides. Third, 11 stations distributed along the three main channels of the List tidal basin were sampled during diurnal high and low tides: four stations distributed along Lister Ley, four along Høyer Dyb, and three along Rømø Dyb. At each station, five water samples (10 l each) were taken from the surface, as well as three meters above the bottom. Sampling dates for the second and third schemes are given in Table 2.I. Königshafen is a shallow area (maximal depth of 5 m during high tides), while the rest of the sampled areas have maximal depths of 30 m. Water was filtered through a 80 μm mesh.

2.2. Identification of larvae

Identification was done following identification keys and/or comparing the material with illustrations and/or descriptions in the literature. The amount of taxonomic literature for polychaete larvae is much smaller than for adult stages, and less focused on geographical regions. In many cases, literature sources on adult stages were combined with notes on larval stages. Observations of live and fixed material were necessary in many cases (e.g. bands of cilia are easily detected in live material, but the shape of setae and hooks not). Larvae were fixed in seawater with 10% formol and preserved in methanol 70%. All species were schematized, and photographed under SEM when possible. Identities were corroborated by Dr. Michel Bhaud (Observatoire Oceanographique Banyuls-sur-Mer, France).

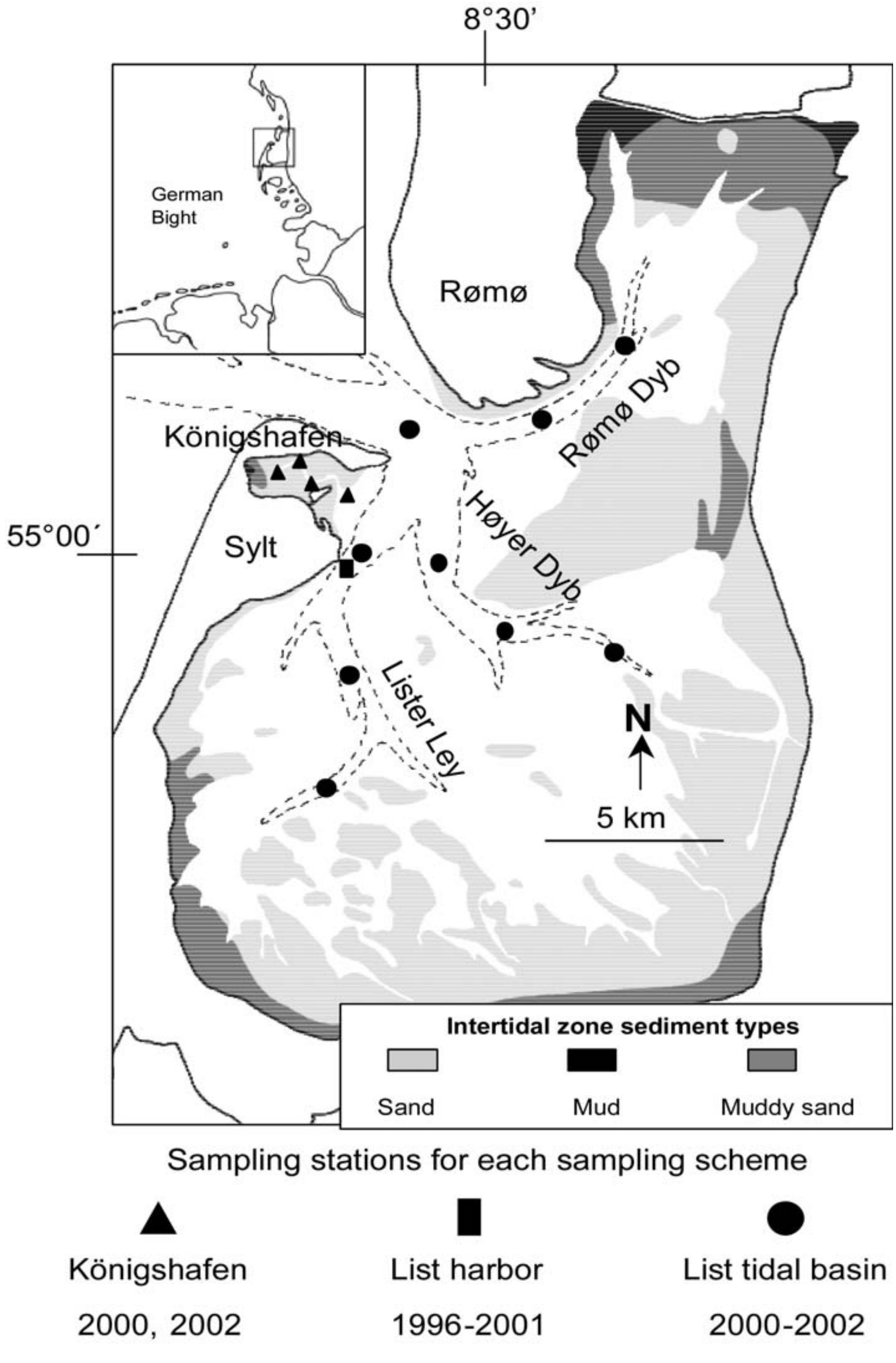


Fig. 2.1. Study area with sampling stations. Sediment types are taken from Strasser (2000).

Table 2.I. Sampling dates for polychaete larvae in Königshafen and the main gullies of the List tidal basin, between April 2000 and August 2002.

KÖNIGSHAFEN
Year 2000: April 20 and 28, May 8, 15, 25, and 31; June 13; July 3, 13, 24; Aug 7 and 22; Sep 12; Nov 20.
Year 2002: May 15; June 19; July 8; Aug 20.

LIST TIDAL BASIN			
	Channel		
	Lister Ley	Høyer Dyb	Rømø Dyb
High tide	Dec 6, 2000	Dec 7, 2000	Dec 11, 2000
	Feb 19, 2001	Feb 20, 2000	Feb 21, 2000
	July 2 and 17, 2001	July 3 and 18, 2001	July 4 and 19, 2001
	May 7 and 22, 2002	May 6 and 23, 2002	May 8 and 24, 2002
	July 2 and 17, 2002	July 3 and 18, 2002	July 4 and 19, 2002
Low tide	June 6, 2001	June 7, 2001	June 8, 2001
	Sep 3 and 10, 2001	Sep 4 and 11, 2001	Sep 5 and 12, 2001
	Apr 4, 2002	Apr 10, 2002	Apr 11, 2002
	May 27, 2002	May 28, 2002	May 29, 2002
	June 11, 2002	June 12, 2002	June 13, 2002
	July 24, 2002	July 25, 2002	July 26, 2002
	Aug 22, 2002	Aug 23, 2002	Aug 21, 2002

3. Results

Forty-six taxa were found, belonging to 18 families (Table 2.II). Spionids were the most diverse group (36% of the total number of taxa), followed by phyllodocids (14%), and polynoids (9%). Brief descriptions and taxonomic remarks are provided, followed by a key on the larvae encountered.

Family Orbiniidae Hartman 1942

Scoloplos (Scoloplos) armiger (O.F. Müller 1776) (Fig. 2.2)

Benthic stages of this species occur inside the basin and its larvae are common between March-May and October-December. Trochophore were about 360 µm in average length. The largest metatrochophore was 470 µm long with 8 setigers. Plate and Husemann (1991 and 1994) described meroplanktonic larvae from Helgoland. Based on the illustrations of larvae identified as *Heteromastus filiformis* by Smidt (1951) in the Danish Wadden Sea, it is very likely that he also observed meroplanktonic larvae of *S. armiger*. Non-pelagic larvae and juveniles released from egg-cocoons were first described by Thorson (1946). Populations in the List basin produce non-pelagic juveniles (about 360 µm in length) as well as pelagic larvae with well-developed setae and cilia. Non-pelagic juveniles are also commonly re-suspended in the water column.

Kruse (2002) recognized populations with pelagic and benthic larvae as belonging to separate species, termed as “S” and “I”, in reference to the subtidal and intertidal occurrence, respectively.

Family Spionidae Grube 1850

Aonides paucibranchiata Southern 1914 (Fig. 2.2)

Benthic stages occur inside the bight and their larvae are common between May-September. Only stages having 12-19 setigers were found, being 700-1000 µm long. Body without pigmentation. Long palpi are present and ventral hooded hooks have three teeth. A detailed description is in Hannerz (1956).

Laonice cirrata (M. Sars 1851) (Fig. 2.2)

Benthic stages have not been found inside the basin, but in the German Bight, and its larvae are very common between May-June. Sizes ranged from 580 to 1300 µm in length, with 4 to 12 setigers. Strong serrated setae in the posterior part of the body are characteristic. Descriptions in Hannerz (1956), Bhaud and Cazaux (1987), and Plate and Husemann (1994).

Malacoceros fuliginosus (Claparède 1868) (Fig. 2.3)

Benthic stages are known inside the basin, but its larvae were found only at Königshafen between May-July, being relatively rare. Sizes were about 800 µm in length. Palpi are long and the body lacks pigmentation. Description in Plate and Husemann (1994).

Polydora ciliata (Johnson 1838) (Fig. 2.3)

Benthic stages occur inside the basin and larvae are very common between March-July and September-November. Sizes ranged from 650 to 1230 µm in length with 11 to 18 setigers. Descriptions in Thorson (1946), Hannerz (1956), and Plate and Husemann (1994).

Polydora cornuta Bosc 1802 (Fig. 2.3)

Benthic stages occur inside the basin and larvae are very common between April-October. Sizes ranged from 550 to 1170 µm in length, with 9-17 setigers. The synonymy between *P. ligni* and *P. cornuta* was established by Hartmann-Schröder (1996). Smidt (1951) and Rasmussen (1973) discussed a synonymy between *P. ligni* (today *P. cornuta)* and *P. ciliata*, but Hannerz (1956), Michaelis (1978), Plate and Husemann (1994), and this work regard them as different species. Individuals lack ramified melanophores between the eyes described by Hannerz (1956) and Blake (1969).

Table 2.II. Polychaetes with meroplanktonic larval stages inside the List tidal basin, encountered in the period 1996-2002.

- Family Orbiniidae Hartman 1942
    - 1) *Scoloplos (Scoloplos) armiger* (O.F. Müller 1776)
- Family Spionidae Grube 1850
  - Genus *Aonides* Claparède 1864
    - 2) *Aonides paucibranchiata* Southern 1914
  - Genus *Laonice* Malmgren 1867
    - 3) *Laonice cirrata* (M. Sars 1851)
  - Genus *Malacoceros* Quatrefages 1843 emend. Pettibone 1963
    - 4) *Malacoceros fuliginosus* (Claparède 1868)
  - Genus *Polydora* Bosc 1802
    - 5) *Polydora (Polydora) ciliata* (Johnson 1838)
    - 6) *Polydora (P.) cornuta* Bosc 1802
    - 7) *Polydora (P.) hermaphroditica* Hannerz 1956
    - 8) *Polydora* Type I
    - 9) *Polydora* Type II
  - Genus *Pygospio* Claperède 1863
    - 10) *Pygospio elegans* Claperède 1863
  - Genus *Scolelepis* Blainville 1828 emend. Pettibone 1963
    - 11) *Scolelepis (Scolelepis) bonnieri* (Mesnil 1896)
    - 12) *Scolelepis (S.) squamata* (O.M. Müller 1806)
    - 13) *Scolelepis (S.) girardi* (Quatrefages 1866)
    - 14) *Scolelepis* Type I
  - Genus *Spio* Fabricius 1785
    - 15) *Spio martinensis* Mesnil 1896
    - 16) *Spio theeli* (Söderström 1920)
  - Genus *Spiophanes* Grube 1860
    - 17) *Spiophanes bombyx* (Claparède 1870)
- Family Magelonidae Cunningham & Ramage 1888
  - Genus *Magelona* F. Müller 1858
    - 18) *Magelona mirabilis* (Johnston 1865)
- Family Poecilochaetidae Hannerz 1956
  - Genus *Poecilochaetus* Ehlers 1875
    - 19) *Poecilochaetus serpens* Allen 1904
- Familiy Capitellidae Grube 1862
  - Genus *Capitella* Blainville 1828
    - 20) *Capitella* Type I
    - 21) *Capitella* Type II
- Family *Polynoidae* Malmgren 1867
  - Genus *Harmothoe* Kingber 1855
    - 22) *Harmothoe (Harmothoe) antilopes* McIntosh 1876
    - 23) *Harmothoe (Harmothoe) glabra* (Malmgren 1865)
    - 24) *Harmothoe (Harmothoe) impar* (Johnston 1839)
    - 25) *Harmothoe (Harmothoe) ljungmani* (Malmgren 1867)
    - 26) *Harmothoe* Type I
- Family Sigalionidae Malmgren 1867
  - Genus *Neolanira* Pettibone 1970
  - 27) *Neolanira* c.f. *tetragona* (Oersted 1845)

Table 2.II. Polychaetes with meroplanktonic larval stages inside the List tidal basin, encountered in the period 1996-2002 (continued).

- Family Phyllodocidae Oersted 1843
  - Genus *Phyllodoce* Lamarck 1818
    - 28) *Phyllodoce (Anaitides) mucosa* Oersted 1843
    - 29) *Phyllodoce (Anaitides) rosea* (McIntosh 1877)
  - Genus *Eteone* Savigni 1820
  - Subgenus *Eteone* Savigni 1820
    - 30) *Eteone (Eteone) longa* (Fabricius 1780)
  - Subgenus *Mysta* Malmgren 1865
    - 31) *Eteone (Mysta) barbata* Malmgren 1865
  - Genus *Eulalia* Savigni 1822
    - 32) *Eulalia viridis* (Linné 1767)
  - Genus *Pseudomystides* Bergström 1914 emend. Pleijel 1991
    - 33) *Pseudomystides limbata* (Saint-Joseph 1888)
  - Family Hesionidae Malmgren 1867
  - Genus *Microphtalmus* Mecznikov 1865
    - 34) *Microphtalmus aberrans* (Webster & Benedict 1887)
- Family Nereididae Johnston 1865
  - Genus *Nereis* Linné 1758
    - 35) *Nereis* Type I
    - 36) *Nereis* Type II
- Family Nephtyidae Grube 1850
  - Genus *Nephtys* Cuvier 1817
    - 37) *Nephtys caeca* (Fabricius 1780)
    - 38) *Nephtys hombergii* Savigny 1818
- Family Sphaerodoridae Malmgren 1867
    - 39) Sphaerodoridae Type I
- Family Flabelligeridae Saint-Joseph 1894
    - 40) Flabelligeridae Type I
- Family Dinophilidae Schultz 1902
  - Genus *Dinophilus* O.Schmidt 1848
    - 41) *Dinophilus gyrociliatus* O. Schmidt, 1857
- Family Pectinariidae Quatrefages 1865
  - Genus *Pectinaria* Lamarck 1818
  - Subgenus Pectinaria Lamarck 1818
    - 42) *Pectinaria (Lagis) koreni* (Malmgren 1865)
- Family Terebellidae Malmgren 1865
  - Genus *Lanice* Malmgren 1865
    - 43) *Lanice conchilega* (Pallas 1766)
- Family Sabellariidae Savigny 1818
  - Genus *Sabellaria* Savigny 1818
    - 44) *Sabellaria spinulosa* Leuckart 1849
- Familie Sabellidae Malmgren 1867
  - Genus *Chone* Kröyer 1856 emend. Banse 1972
    - 45) *Chone infundibuliformis* Kröyer 1856
    - 46) *Chone* Type I

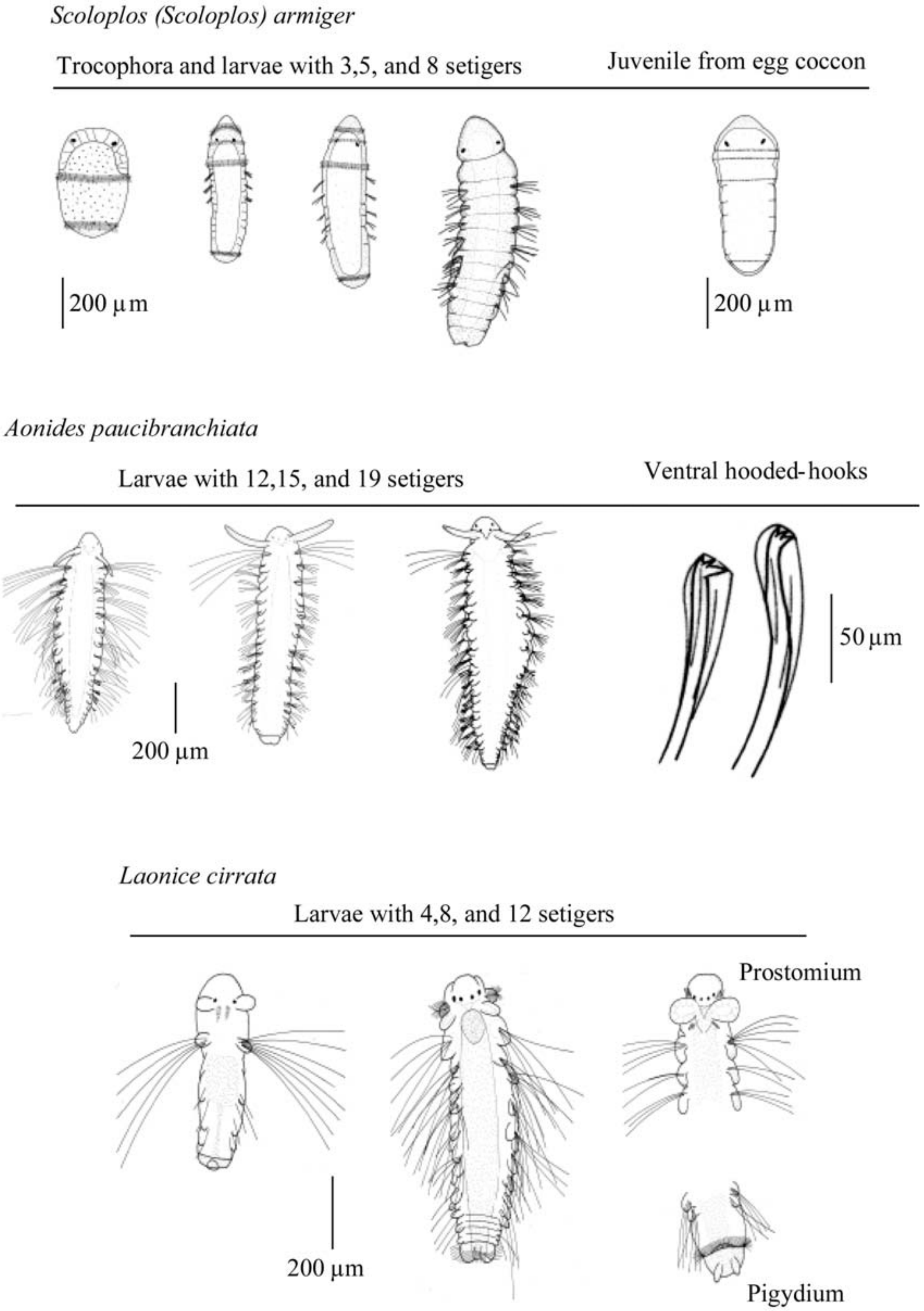


Fig. 2.2. Polychaete larvae from the List tidal basin: *Scoloplos armiger, Aonides paucibranchiata*, and *Laonice cirrata*.

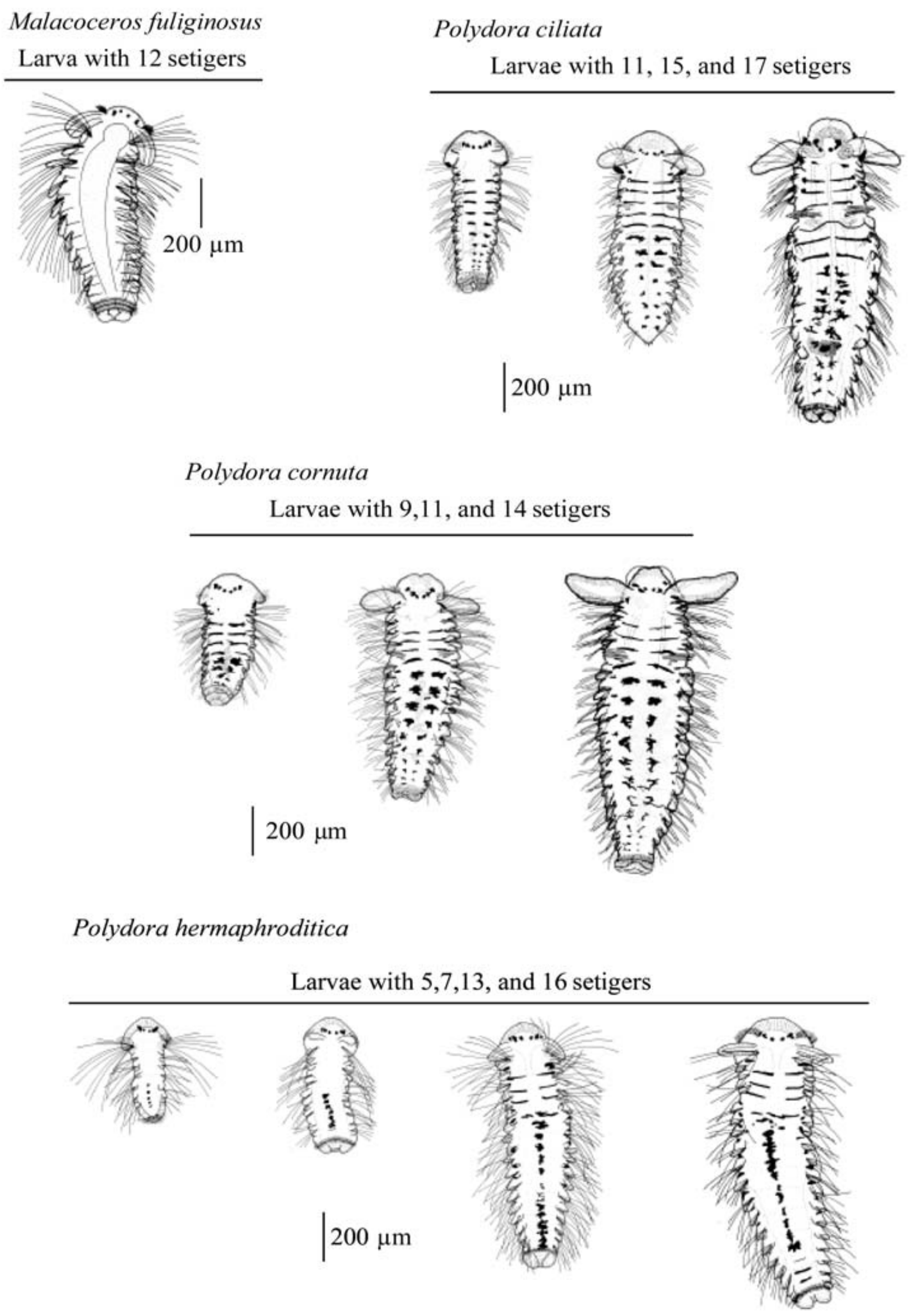


Fig. 2.3. Polychaete larvae from the List tidal basin: *Malacoceros fuliginosus, Polydora ciliata, P. cornuta*, and *P. hermaphroditica*.

Plate and Husemann (1994) stated that this species can be distinguished from *P. ciliata* only with more than 15 setigers. Here, it was possible to separate individuals from nine setigers onwards, based on the dorsal band-shaped melanophores. Descriptions as *P. ligni* are in Smidt (1951), Hannerz (1956), Blake (1969), Bhaud and Cazaux (1982), and Plate and Husemann (1994).

Polydora hermaphroditica Hannerz 1956 (Fig. 2.3)

Benthic stages have not been found inside the basin. Larvae were found around Königshafen, being rare and occurring between April -July. Sizes ranged from 450 to 1200 µm in length with 7 to 19 setigers. They differ from other *Polydora* by having only one mid dorsal column of star-shaped chromatophores. Descriptions in Hannerz (1956) and Plate and Husemann (1994).

Polydora Type I (Fig. 2.4)

Benthic stages are unknown. Larvae were common between May-November, at all sampled areas. Specimens ranged from 750 to 1260 µm in length with 9 to 19 setigers. Prostomium rounded, with well-developed nuchal organs, and short prototroch. Three pairs of black eyes are arranged in “V” shape when viewed from above. Palpi are relatively short, distally rounded, robust, with black pigmentation at their basis. Nuchal crest is low. Five pairs of band-shaped dorsal melanophores are continued by two columns of large, bold, and intertwined star-shaped chromatophores. In large specimens, the notopodial lobes of the first setiger become fin-shaped and reach the second setiger in length (indicated by arrow in Fig. 2.4). Larval setae are not iridescent. Individuals with 9-14 setigers had ventral hooded hooks from the 9th setiger onwards, and those with 15-19 setigers had these hooks from the 7th setiger onwards. Notopodial lobes pigmented and telotroch well developed.

Polydora Type II (Fig. 2.4)

Benthic stages are unknown. Larvae were found along Høyer Dyb and Rømø Dyb, between November-February, being rare. Sizes ranged from 600 to 1200 µm in length with 3 to 20 setigers. Prostomium short, narrow, and rounded, with pigmentation restricted to the eyes. Six pairs of band-shaped dorsal melanophores are present, continued by two columns of small and diffuse star-shaped chromatophores. Prototroch absent and nuchal crest low. In individuals having up to 14 setigers, eyes are disposed in three pairs of spots, while in those with more than 18 setigers dorsal eyes are peduncle-shaped. Nuchal organs rudimentary. Palpi flat, long, blade-shaped, and delicate. When their blades brake off, only a long, slender, and cylindrical main stem remains. Larval setae iridescent. Ventral hooded hooks appear from the 7th setiger in individuals with more than 14 setigers. Notopodial lobes with one pigment spot. Telotroch absent. To my knowledge, the presence of peduncle shaped eyes in polychaete larvae is here reported for the first time. SEM observations indicate that they do not have a smooth surface, but are formed by small tubes. Juvenile and adult stages are required, to know whether eyes remain peduncle-shaped after metamorphosis.

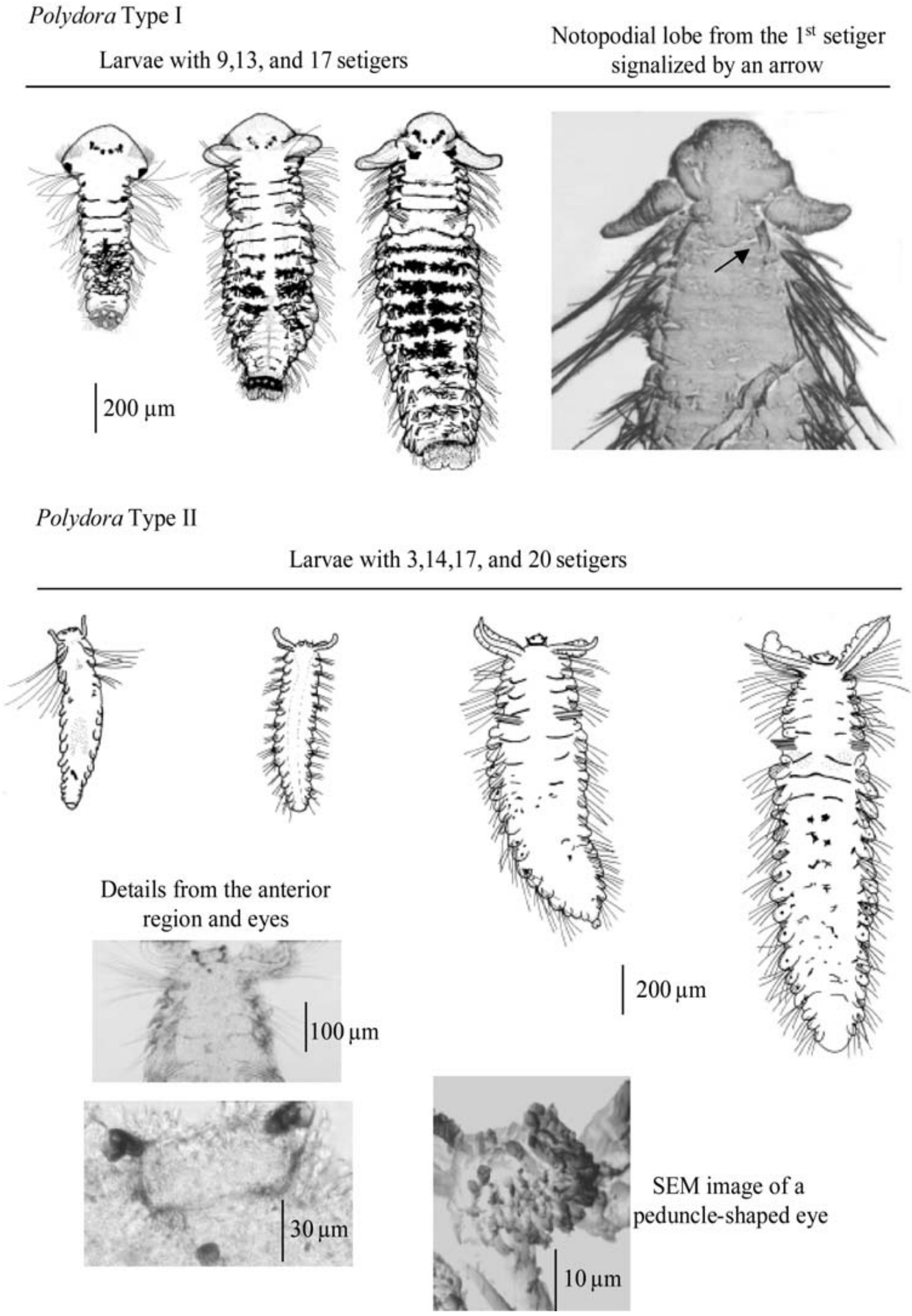


Fig. 2.4. Polychaete larvae from the List tidal basin: *Polydora* Types I and II.

Pygospio elegans Claperède 1863 (Fig. 2.5)

Benthic stages occur inside the basin and larvae are very common between March-December. Sizes ranged from 420 to 1000 µm in length, with 8 to 15 setigers. Descriptions in Thorson (1946), Smidt (1951), Hannerz (1956), Rasmussen (1973), and

Plate and Husemann (1994). This species is able to reproduce by larvae and asexually (Morgan *et al.* 1999). Sexual and asexual reproduction (poecilogony) has been also reported for populations from Sylt (Anger *et al.* 1986).

Scolelepis (S.) bonnieri (Mesnil 1896) (Fig. 2.5)

Benthic stages have not been found inside the basin, but larvae are common between May-June. Sizes were around 2.5 mm in length, with 19 setigers. Body without chromatophores. Description in Plate and Husemann (1994).

Scolelepis (S.) squamata (O.M. Müller 1806) (Fig. 2.5)

Benthic stages occur inside the basin and larvae are very common between June-August. Sizes ranged from 2 to 3.5 mm in length with 12 to 26 setigers. Pigmentation restricted to the prostomium (slightly red). Description in Plate and Husemann (1994).

Scolelepis (S.) girardi (Quatrefages 1866) (Fig. 2.6)

Benthic stages have not been found inside the bight. Larvae occurred between May-July, being relatively rare. Body short and wide (400 to 1000 µm in length, with 5 to 12 setigers). Early stages with thin black lines intertwined in the back and bold black spots close to the nuchal area. Larger individuals have scattered dorsal star-shaped chromatophores. Hoods from ventral hooks truncated. Description in Hannerz (1956).

Scolelepis Type I (Fig. 2.6)

Benthic stages unknown. Occurrence between May-July, being relatively rare. Body short and wide (600 to 1200 µm in length with 6 to 14 setigers). Early stages with two columns of bold rectangular chromatophores on the back. Older stages with irregularly distributed star-shaped chromatophores. Prostomium strongly rectangular and broad. Palpi are long. Ventral hooded-hooks have grooved hoods.

Spio martinensis Mesnil 1896 (Fig. 2.7)

Benthic stages occur inside the basin and larvae are very common between May-October. Sizes range from 200 to 1200 µm in length with 6 to 18 setigers. Two columns of circular chromatophores run along the body back. These chromatophores reflect the light. Larval setae markedly long and give the body a fluffy appearance. Descriptions in Hannerz (1956), and Plate and Husemann (1994). Probably, the “Spionid larva F” illustrated and described by Thorson (1946) corresponds to *S. martinensis*. Poecilogony was reported by Blake and Arnofsky (1999). Adults occur in the lower intertidal (Lackschewitz and Reise 1998).

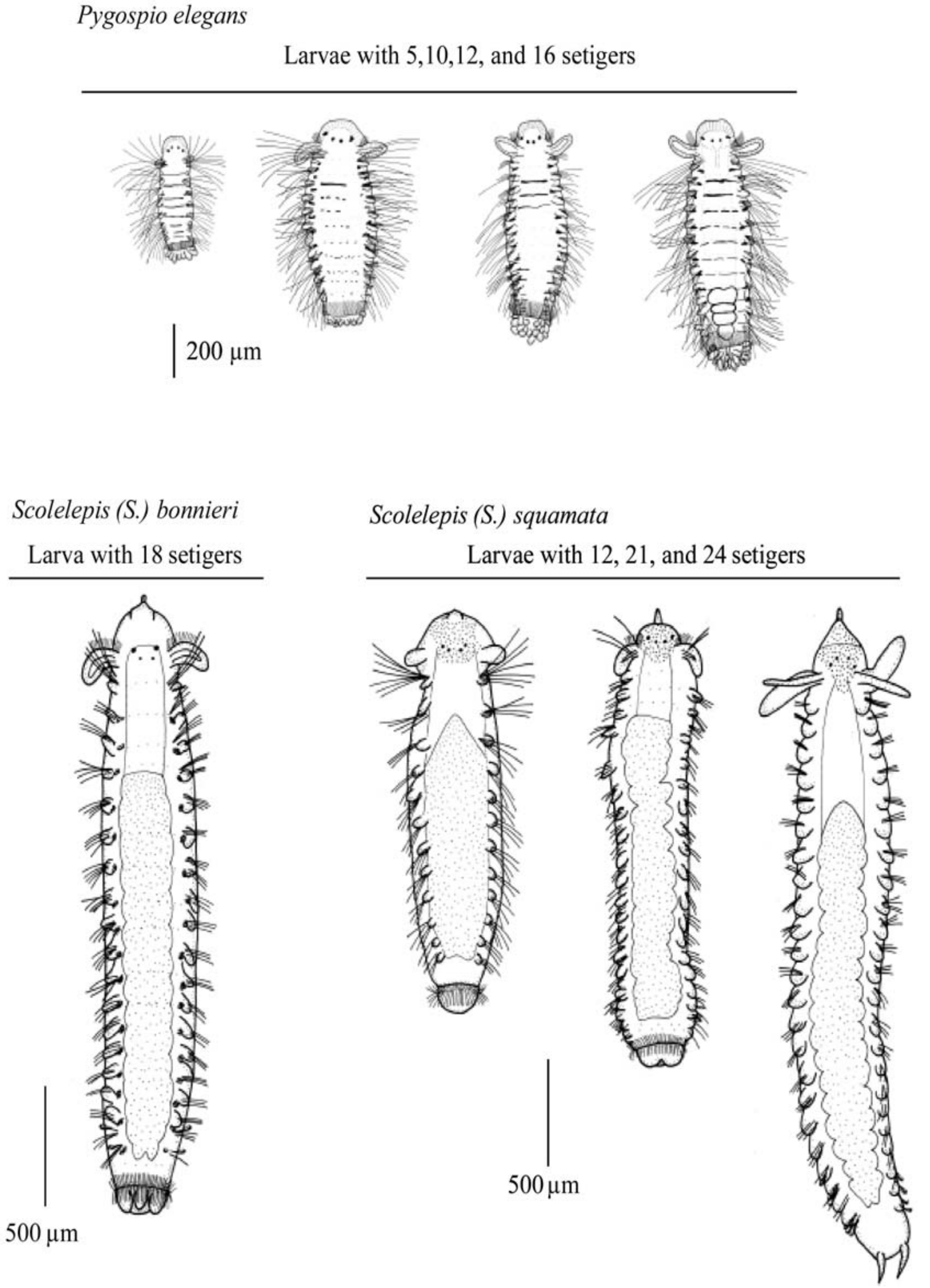
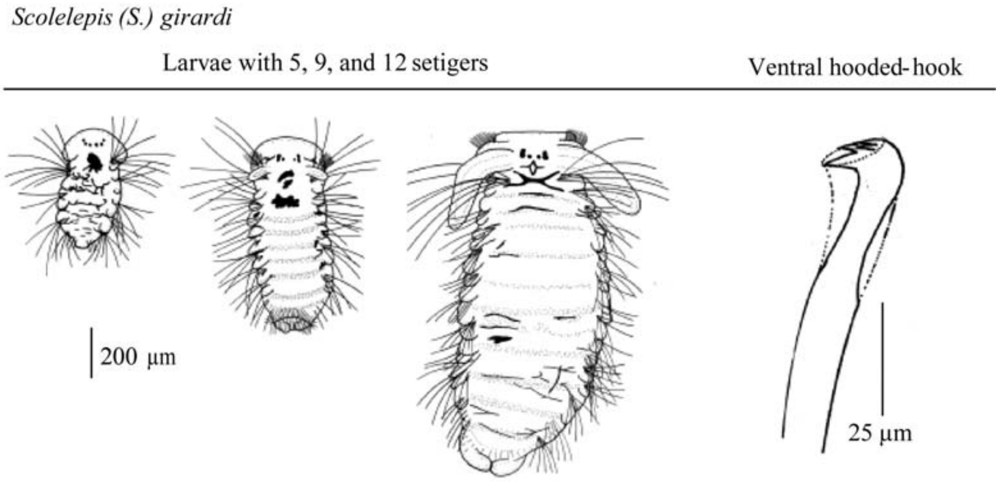


Fig. 2.5. Polychaete larvae from the List tidal basin: *Pygospio elegans, Scolelepis bonnieri*, and *S. squamata*.



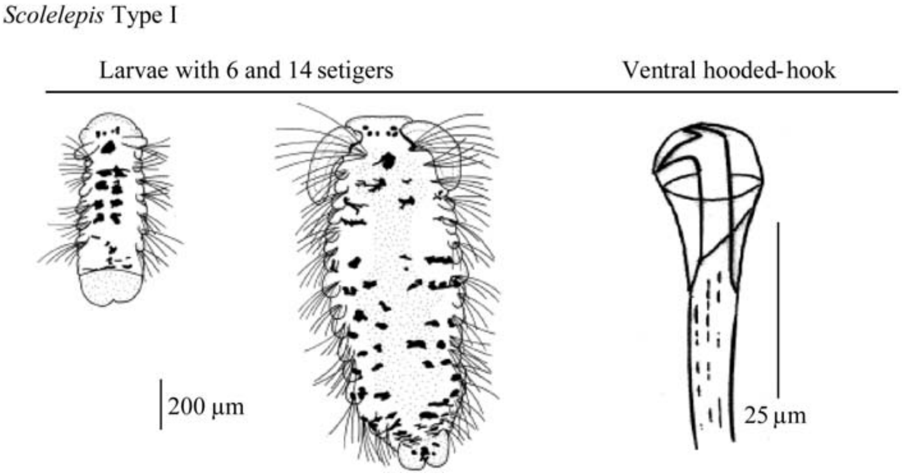


Fig. 2.6. Polychaete larvae from the List tidal basin: *Scolelepis girardi* and *Scolelepis* Type I.

Spio theeli (Söderström 1920) (Fig. 2.7)

Benthic stages have not been found inside the basin. Larvae present between May-October, being relatively rare. Size between 600 and 1400 µm in length with 10 to 23 setigers. Dorsal chromatophores composed by thin and diffuse horizontal bands. Larval setae are long, giving the body a fluffy appearance. Description in Hannerz (1956).

Spiophanes bombyx (Claparède 1870) (Fig. 2.7)

Benthic stages are known for the basin. Larvae are common between May-July. Sizes were about 1000 µm in length with 13 setigers. Neurosetae from the first setiger are curved and the prostomium has small horns in the anterior region. Back of the body with two columns of black chromatophores between the 2nd and 6th setigers. Descriptions in Thorson (1946), Hannerz (1956), and Plate and Husemann (1994).

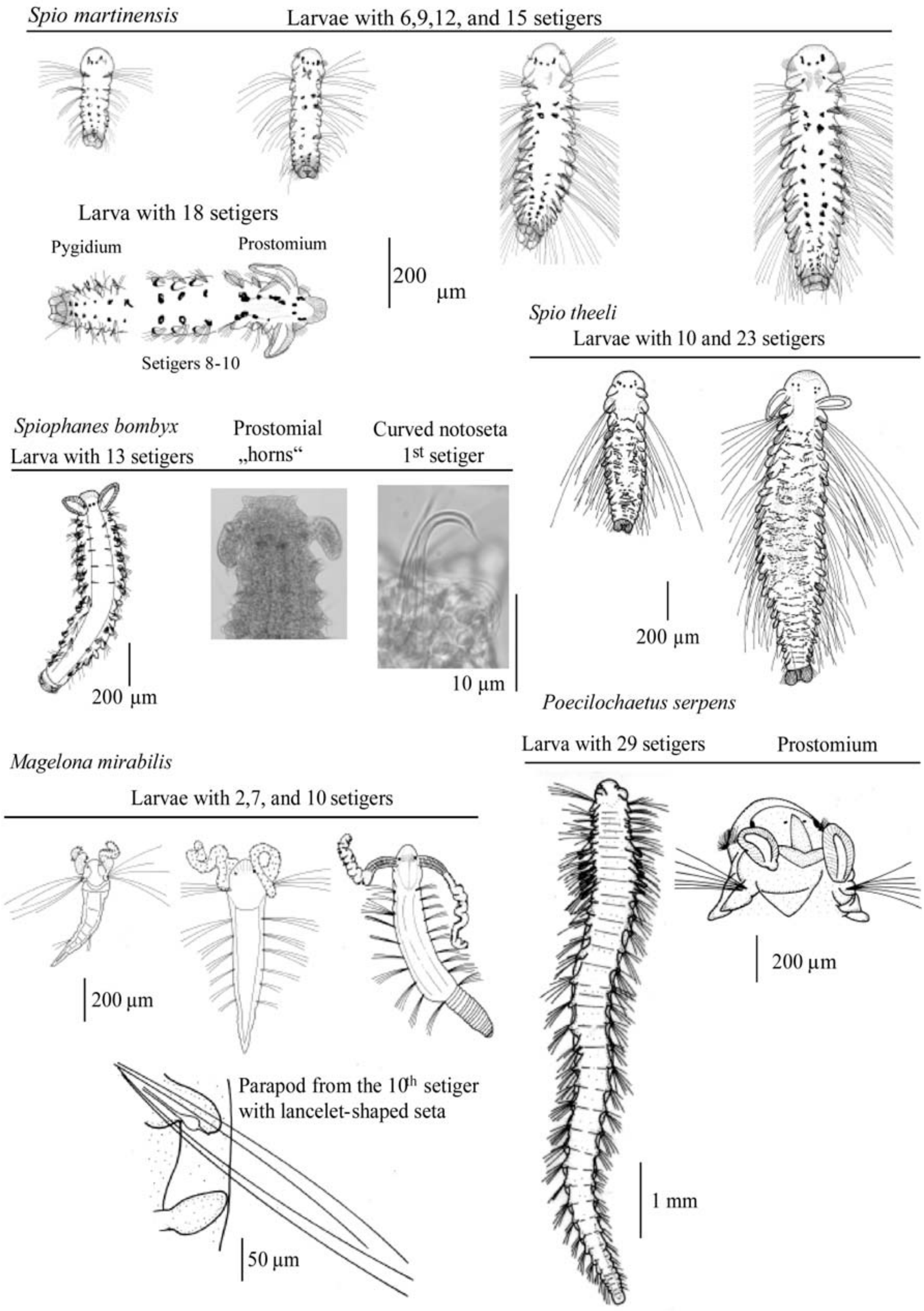


Fig. 2.7. Polychaete larvae from the List tidal basin: *Spio martinensis, S. theeli, Spiophanes bombyx, Magelona mirabilis*, and *Poecilochaetus serpens*.

Magelona mirabilis (Johnston 1865) (Fig. 2.7)

Benthic stages have been found inside the basin. Larvae are very common between May-June. Sizes ranged between 400 and 900 µm in length with 2 to 10 setigers. Tentacles are ciliated. One modified lancelet-shaped seta present in the 10th setiger. Descriptions in Smidt (1951), Bhaud and Cazaux (1982), Wilson (1982), and Plate and Husemann (1994). *M. papillicornis* is a synonymy of *mirabilis* (Hartmann-Schröder 1996).

Poecilochaetus serpens Allen 1904 (Fig. 2.7)

Benthic stages have not been found inside the basin. Larvae were rare, but present between June-July. Larvae were 7 mm in length with 29 setigers. Descriptions in Hannerz (1956), Bhaud and Cazaux (1982), and Plate and Husemann (1994). Bhaud (1983) described very similar larvae as paraonids.

Capitella Types I and II (Fig. 2.8)

Benthic stages of *Capitella capitata* occur inside the basin. Larvae of both types were common between March-October. In the first type, stages with lengths about 400 µm were found. The body lacking pigmentation. The anterior and posterior ends with rings of cilia. The length of the anterior and posterior regions is alike. Similar larvae were described by Plate and Husemann (1994). The second type had lengths between 300-400 µm. Small black chromatophores more or less homogeneously distributed over the body. Cilia restricted to the pigydium. The length of the anterior an posterior regions is similar. Gamenick *et al*. (1998) observed that *Capitella capitata* in Königshafen is represented by two sibling species.

Harmothoe (Harmothoe) antilopes McIntosh 1876 (Fig. 2.8)

Benthic stages have not been found inside the basin. Larvae were found around Königshafen, being relatively common between July-September. Larvae were 2 mm in length with 13 setigers. Six pairs of dorsal elytra were present with small papilla homogeneously distributed over the surface, bordering also the edge of the elytra. Four types of papilla present: simple nipple-shaped, nipple-shaped with peaks on the top, short and rounded with peaks on the top, and short globule-shaped with peaks on the top. Noto- and neurosetae serrated. Identification was based on features from adults given in Hartmann-Schröder (1996).

Harmothoe (H.) glabra (Malmgren 1865) (Fig. 2.8)

Benthic stages have not been found inside the basin. Larvae were found around Königshafen, being relatively common between July-September. Larvae were around 400 µm in length with 7 setigers. Body with four pairs of dorsal elytra with few papilla covering their surface. Elytra with smooth edges. Finger-like papilla and short and globular papilla with short cilia present. Notosetae longer than neurosetae, both with only one side of the blade serrated. Identification was based on the features from adults given in Hartmann-Schröder (1996). Three pairs of dorsal eyes arranged as triangles.

Harmothoe (H.) impar (Johnston 1839) (Fig. 2.9)

Benthic stages are known for the basin. Larvae were found around Königshafen, being common between July-September. Individuals were around 300 µm in length with 6 setigers. Body covered by four pairs of dorsal elytra, which were only covered with simple long papilla. Elytral edges smooth. Noto- and neurosetae similar in length. Neurosetae with one serrated edge. Two types of notosetae present: setae with both edges serrated and setae with only one serrated edge. Description in Plate and Husemann (1994).

Harmothoe (H.) ljungmani (Malmgren 1867) (Fig. 2.9)

Benthic stages have not been found inside the basin. Larvae were found around Königshafen, between July-September, being relatively rare. Sizes were about 1 mm in length with 6 setigers. Specimens lacked of elytra, but features from dorsal cirri and prostomium agree with those of adults described by Hartmann-Schröder (1996).

Harmothoe Type I (Fig. 2.9)

Benthic stages are unknown. Larvae were found around Königshafen, between July-September, being relatively rare. Sizes were about 1 mm in length with 11 setigers. Six pairs of dorsal elytra were present. The surface of the elytra has smooth and porous sections, and their edges are smooth. Tube-shaped papilla long and slender. Notosetae with one serrated edge, while neurosetae with both edges serrated.

Neolanira cf. *tetragona* (Oersted 1845) (Fig. 2.10)

Benthic stages have not been found inside the basin. Larvae were found around Königshafen, between July-September, being rare. Body delta-shaped. Sizes were around 900 µm in length with 8 setigers. Two pairs of large black eyes present. Tips of the parapodial lobes pigmented black. Four large and thin jaws, with one short tooth, present. Four pairs of dorsal elytra present, covered with large and thin tube-like papilla restricted to the superior left quarter of the edge. Neurosetae articulated and notosetae simple. Identification was based in the description of adults given in Hartmann-Schröder (1996).

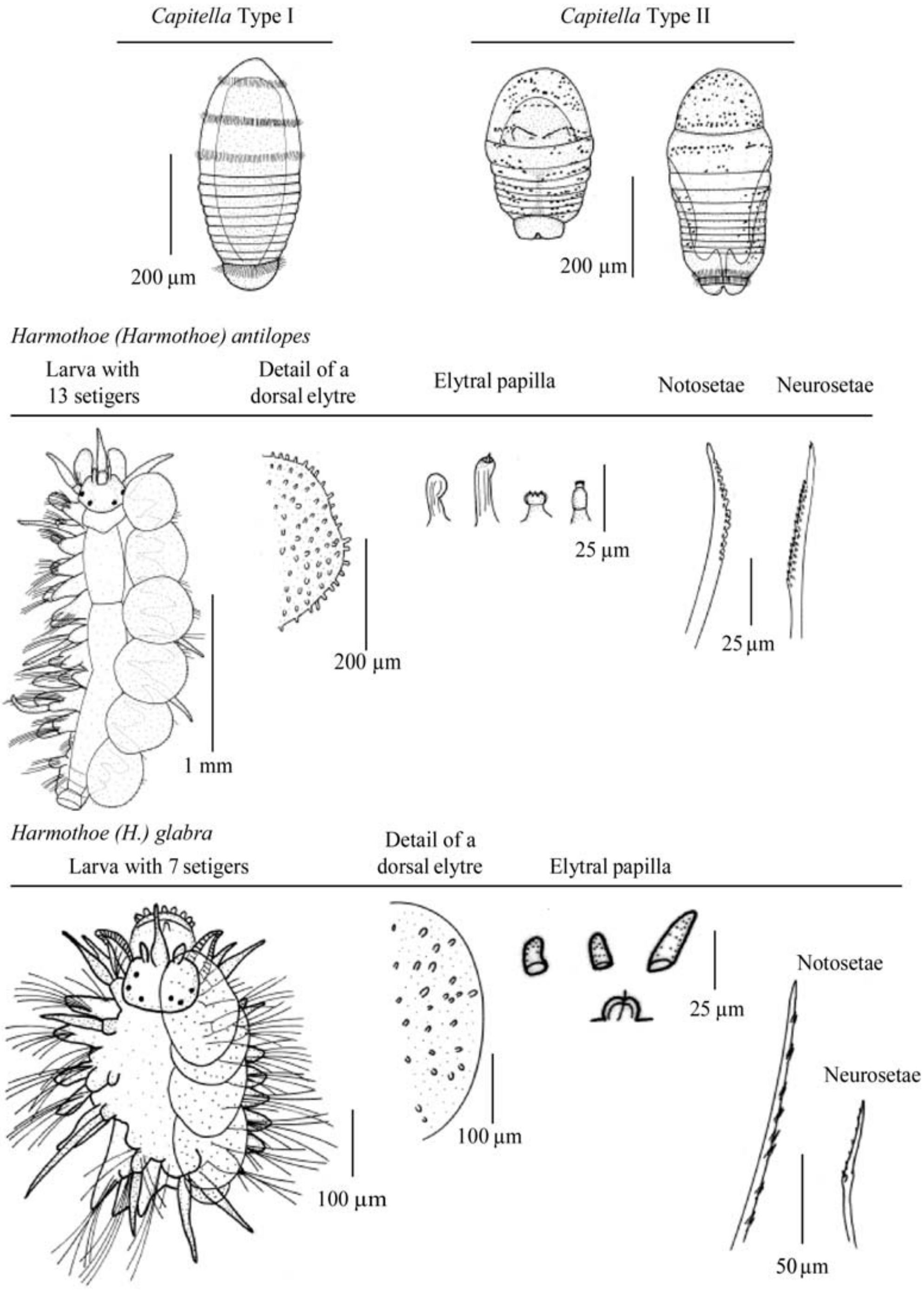


Fig. 2.8. Polychaete larvae from the List tidal basin: *Capitella* Types I and II, *Harmothoe antilopes*, and *H. glabra*.

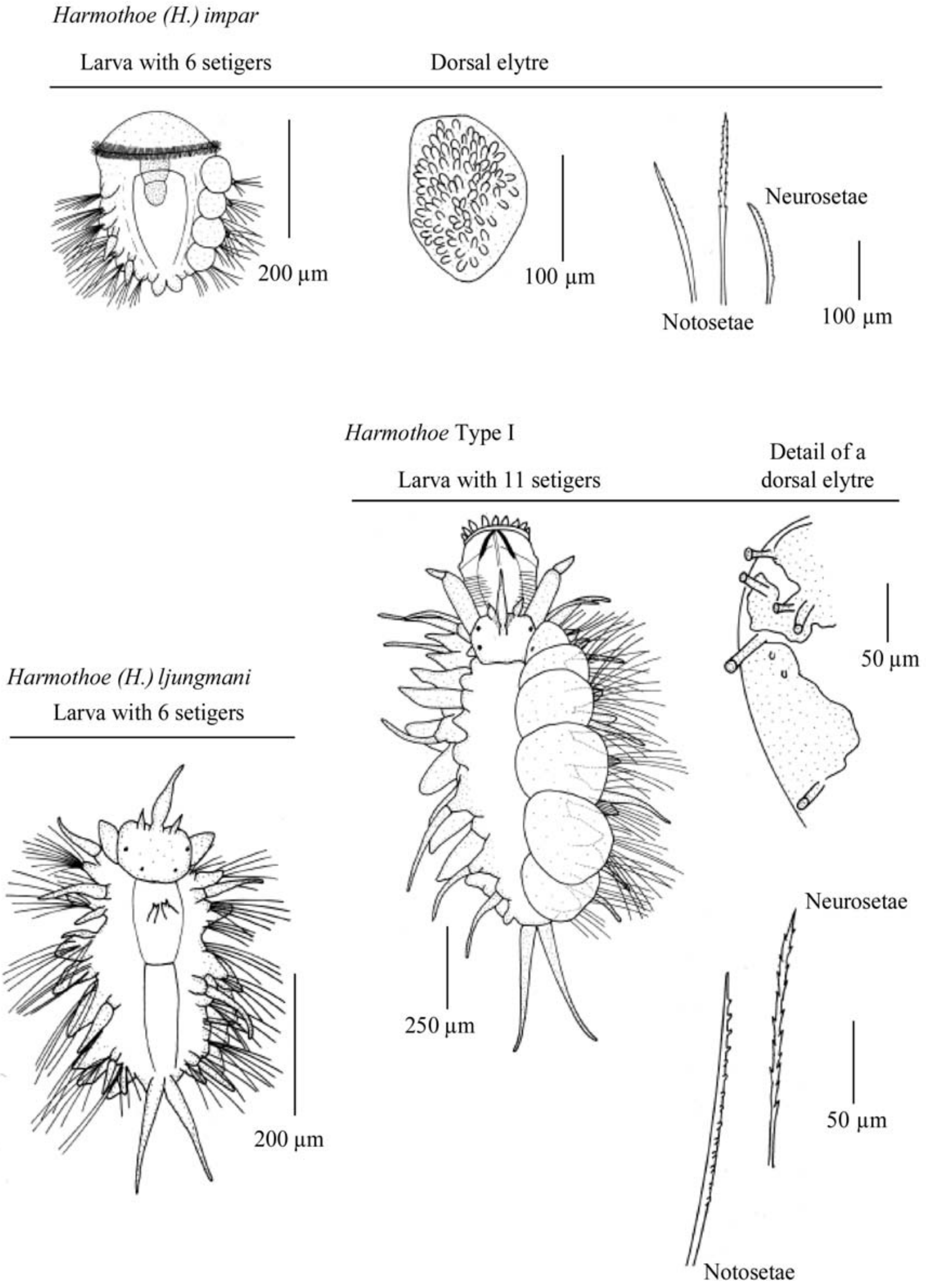


Fig. 2.9. Polychaete larvae from the List tidal basin: *Harmothoe impar, H. ljungmani*, and *Harmothoe* Type I.

Phyllodoce (Anaitides) mucosa Oersted 1843 (Fig. 2.10)

Benthic stages occur inside the basin. Larvae were very common between March-October. Sizes ranged from 600 to 900 µm in length with 7 to 17 setigers. Live larvae had greenish color. Early stages lack chromatophores, while older ones have rows of dorsal black chromatophores. Two pairs of black eyes present. Post-larval stages commonly found in the water column by re-suspension. Chromatophores vanish in post-larval stages. Descriptions in Smidt (1951), Bhaud and Cazaux (1987), and Plate and Husemann (1994).

Phyllodoce (Anaitides) rosea (McIntosh 1877) (Fig. 2.10)

Benthic stages have not been found inside the basin. Larvae occurred between March-October, being relatively rare. Sizes ranged from 500 to 1000 µm in length with 6 to 11 setiger. Live larvae with pale bodies. Spots of black chromatophores are present at the basis of each parapodial lobe from early stages on. Eyes red. Post-larval stages were commonly found in the water column by re-suspension. Chromatophores remain in post-larval stages. Description in Plate and Husemann (1994).

Eteone (Eteone) longa (Fabricius 1780) (Fig. 2.11)

Benthic stages are known for the basin. Larvae occurred between March-October, being very common. Individuals were about 900 µm in length with 6 setigers. Dorsal and ventral tentacular cirri similar in length. Descriptions in Thorson (1946), Smidt (1951), and Plate and Husemann (1994).

Eteone (Mysta) barbata Malmgren 1865 (Fig. 2.11)

Benthic stages have not been found inside the basin. Larvae occurred between March-October, being common, and ranging from 600 to 700 µm in length with 5 to 7 setigers. Dorsal tentacular cirri longer than ventral ones. Descriptions in Thorson (1946) and Plate and Husemann (1994).

Eulalia viridis (Linné 1767) (Fig. 2.11)

Benthic stages have been found inside the basin. Larvae present between March-October, being common. Sizes from 600 to 1100 µm in length with 8 to 12 setigers. Prostomium with 5 antenna, 3 tentacular cirri, and red eyes. Dorsal bands of red chromatophores present. Descriptions in Thorson (1946) and Plate and Husemann (1994).

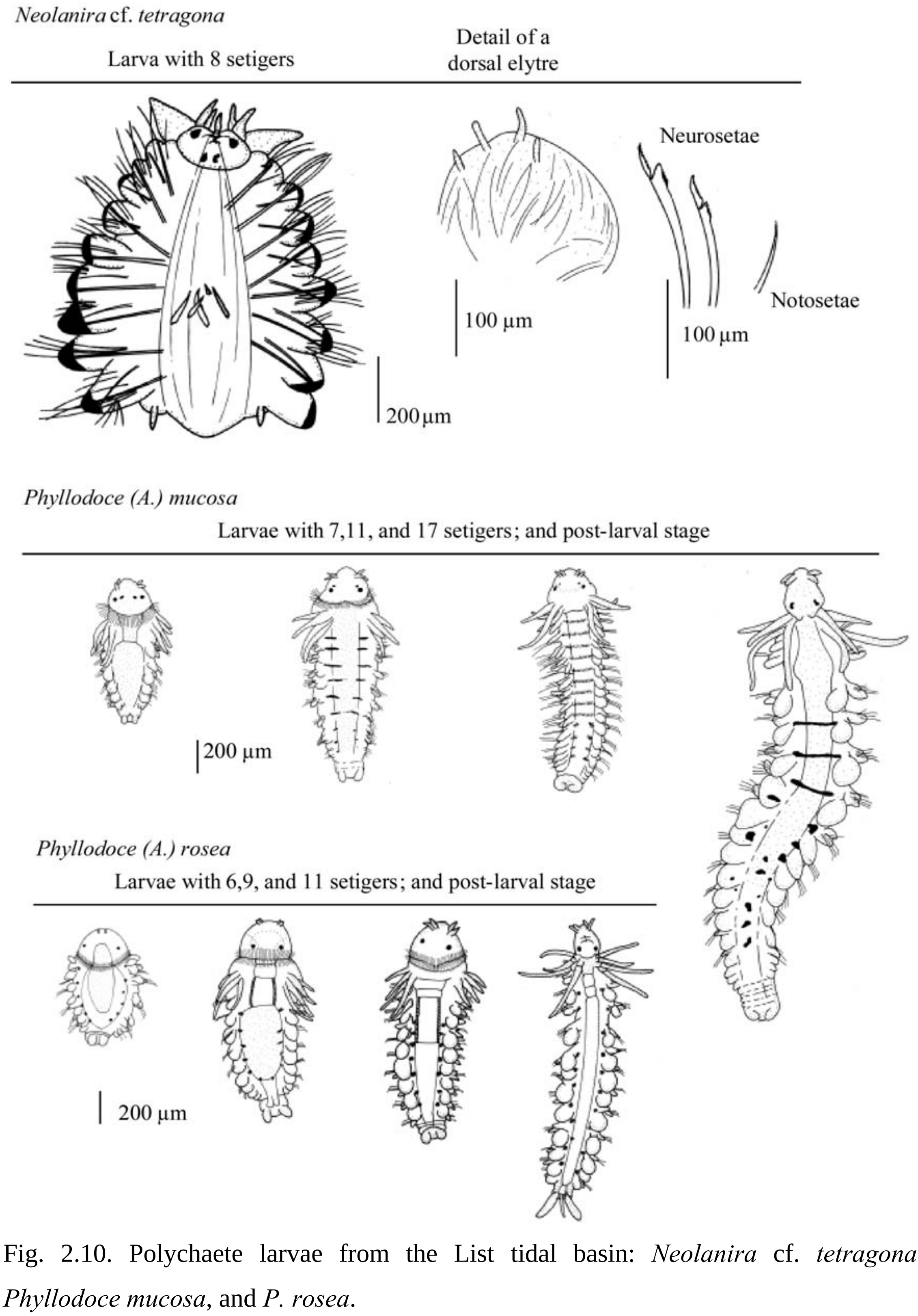


Fig. 2.10. Polychaete larvae from the List tidal basin: *Neolanira* cf. *tetragona*, *Phyllodoce mucosa*, and *P. rosea*.

Pseudomystides limbata (Saint-Joseph 1888) (Fig. 2.11)

Benthic stages have not been found inside the basin. Larvae present between March-October, being common. Sizes from 700 to 1000 µm in length with 8 to 11 setigers.

Prostomium with 5 antenna, 3 tentacular cirri, and black eyes. Black dorsal pigmentation present. Description in Plate and Husemann (1994).

Microphthalmus aberrans (Webster & Benedict 1887) (Fig. 2.11)

Benthic stages occur inside the basin. Larvae were relatively rare, occurring between July-September. Sizes were about 700 µm in length with 6 setigers. Body broadest in the anterior part. Prostomium with four small black eyes, a pair of short antennae, and short palpi. Notopodial cirri at the 1st, 2nd, 4th, and 6th parapods. Early larval stages were described by Westheide (1967) and the identification was aided with the description of adults given by Hartman-Schröder (1996).

Nereis Type I and II (Fig. 2.11)

Benthic stages unknown. Larvae of both types occurred between April-July, being very common. Those belonging to Type I ranged from 300 to 700 µm in length, with 3 to 6 setigers. Blue-green yolk grains present in all stages. Pigmentation restricted to four small black eyes. Individuals resemble those described as *N. (Nereis) pelagica* by Thorson (1946) and Plate and Husemann (1994). Larvae of Type II ranged from 500 to 1000 µm in length with 5 to 11 setigers. Yolk grains absent. Jaws and proboscis musculature present from the earliest stages onwards. Dorsal red spots were present. Larvae of Type II resemble those described as *N. (Neanthes) succinea* by Rasmussen (1973) and Plate and Husemann (1994).

Nephtys caeca (Fabricius 1780) (Fig. 2.12)

Benthic stages occur inside the basin. Larvae occurred between June-October and are common. Sizes were about 800 µm in length with 7 setigers. Prostomium large, broad, and rounded. Anal cirri short. Descriptions in Thorson (1946), and Plate and Husemann (1994).

Nephtys hombergii Savigny 1818 (Fig. 2.12)

Benthic stages occur inside the basin. Larvae occurred between June-October and were common. Sizes were around 900 µm in length with 9 setigers. Prostomium small, narrow, and rectangular. Anal cirri long. Descriptions in Thorson (1946), Smidt (1951), Rasmussen (1973), and Bhaud and Cazaux (1982).

Sphaerodoridae Type I (Fig. 2.12)

Benthic stages of this family have not been found inside the basin. Larvae found around Königshafen, in August, and were rare. Body around 1mm in length with 10 setigers. Bodies barrel-shaped covered with small papilla. Prostomium rudimentary and pigydium bifurcated. Eyes were not visible. Setae bundles long and rigid. Bhaud and

Cazaux (1982) illustrated another type that differs markedly from the one found inside the bight.

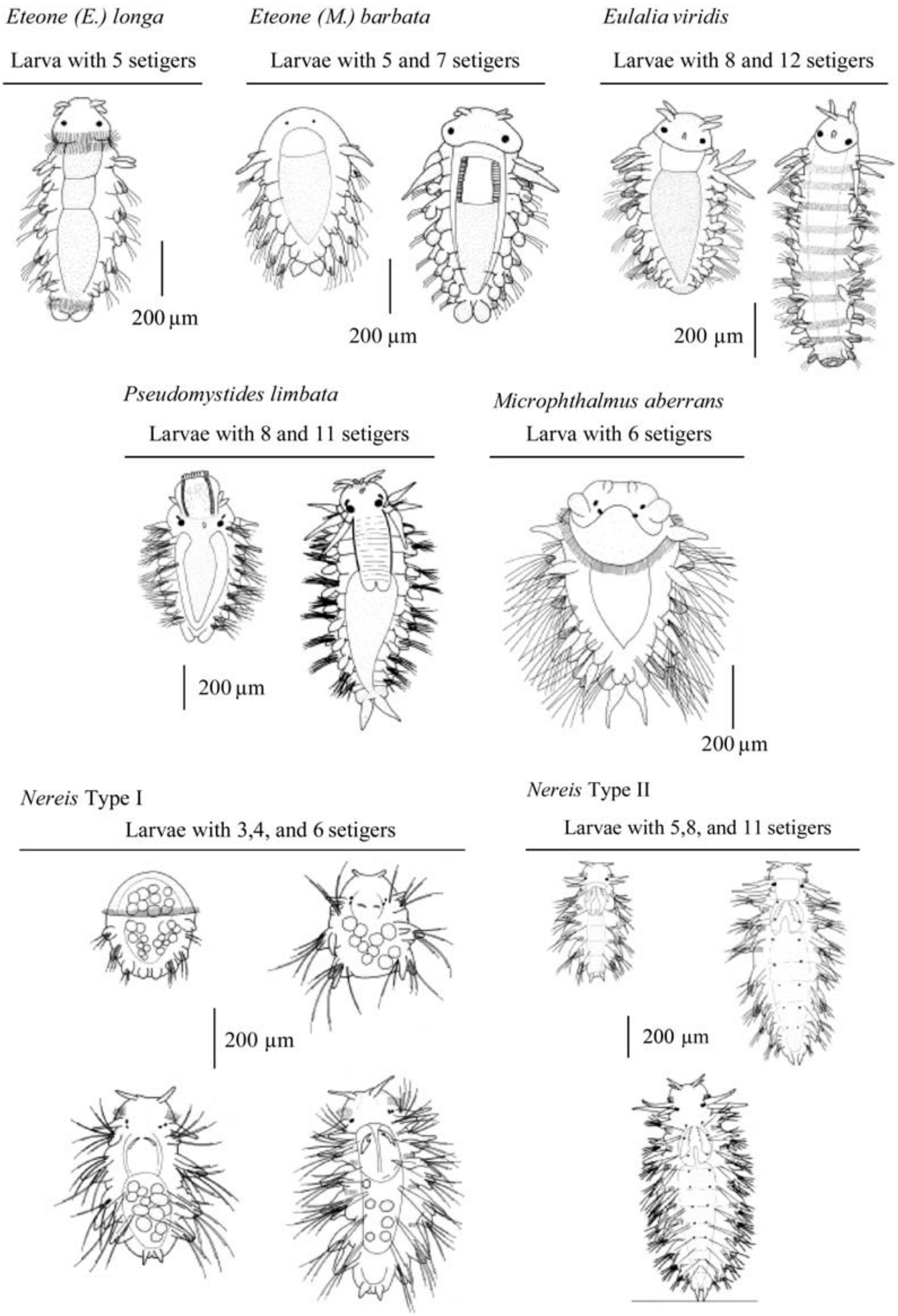


Fig. 2.11. Polychaete larvae from the List tidal basin: *Eteone longa, E. barbata, Eulalia viridis, Pseudomystides limbata, Microphthalmus aberrans*, and *Nereis* Types I and II.

Flabelligeridae Type I (Fig 2.12)

Benthic stages of this family have not been found inside the basin. Larvae found around Königshafen, in May, being rare. Body about 1 mm in length with 15 setigers. Body elongated with its anterior region wider that the posterior one. Setae of the first setiger directed anteriorly. The body was covered by simple papilla. Ventral hooded hooks present from the first setiger onwards. The prostomium has three small antennae, two laterals, and one in the middle. The pygidium has four long fin-like lobules. Identification based on the description of adults given by Hartman-Schröder (1996).

Dinophilus gyrociliatus O. Schmidt, 1857 (Fig. 2.12)

This species has no pelagic larvae (Hartmann-Schröder, 1996) but re-suspended juveniles were frequent between September and October, in spite that benthic stages have not been found inside the basin. Sizes were around 500 µm in length. Their appearance was similar to larvae of Protodrilidae described by Bhaud and Cazaux (1987) and Plate and Husemann (1994) but differ for having three complete cilia-rings and one pair of black eyes. The body lacked pigmentation. Ciliated rings from the 1st, 2nd, and last segments were incomplete. The prostomium is elongated and has cilia in its anterior region.

Pectinaria (Lagis) koreni (Malmgren 1865) (Fig. 2.12)

Benthic stages occur inside the basin. Larvae occurred between April-September and were relatively common. The body is protected by a tube, about 10 mm in length, with sand grains encrusted at its entrance. Larvae were about 800 µm in length with 10 setigers. Golden paleae are directed to the front. Black dorsal chromatophores occur at the basis of each parapod. Setae lancet-shaped. Dorsal avicular uncini present in the posterior part of the body. Descriptions in Thorson (1946) and Smidt (1951).

Lanice conchilega (Pallas 1766) (Fig. 2.13)

Benthic stages occur inside the basin. Larvae occurred between April-September and are very common. Sizes ranged from 80 µm to 15 mm in length, with 2 to 25 setigers. The body is enclosed in a hyaline tube. Descriptions in Thorson (1946), Smidt (1951), Bhaud and Cazaux (1987), Bhaud (1988a), Marcano and Bhaud (1995), and Plate and Husemann (1994).

Sabellaria spinulosa Leuckart 1849 (Fig. 2.13)

Benthic stages are probably gone from the basin. Larvae were found around Königshafen, between May-June, and were rare. Sizes were about 500 µm in length with 4 setigers. Setae of the first setiger serrated and long, giving the body a fluffy appearance. Bifurcated setae and uncini are present in the posterior part of the body. Palpi pigmented black. Body pigmented with black bands. Descriptions in Smidt (1951), Bhaud and Cazaux (1987), and Plate and Husemann (1994).

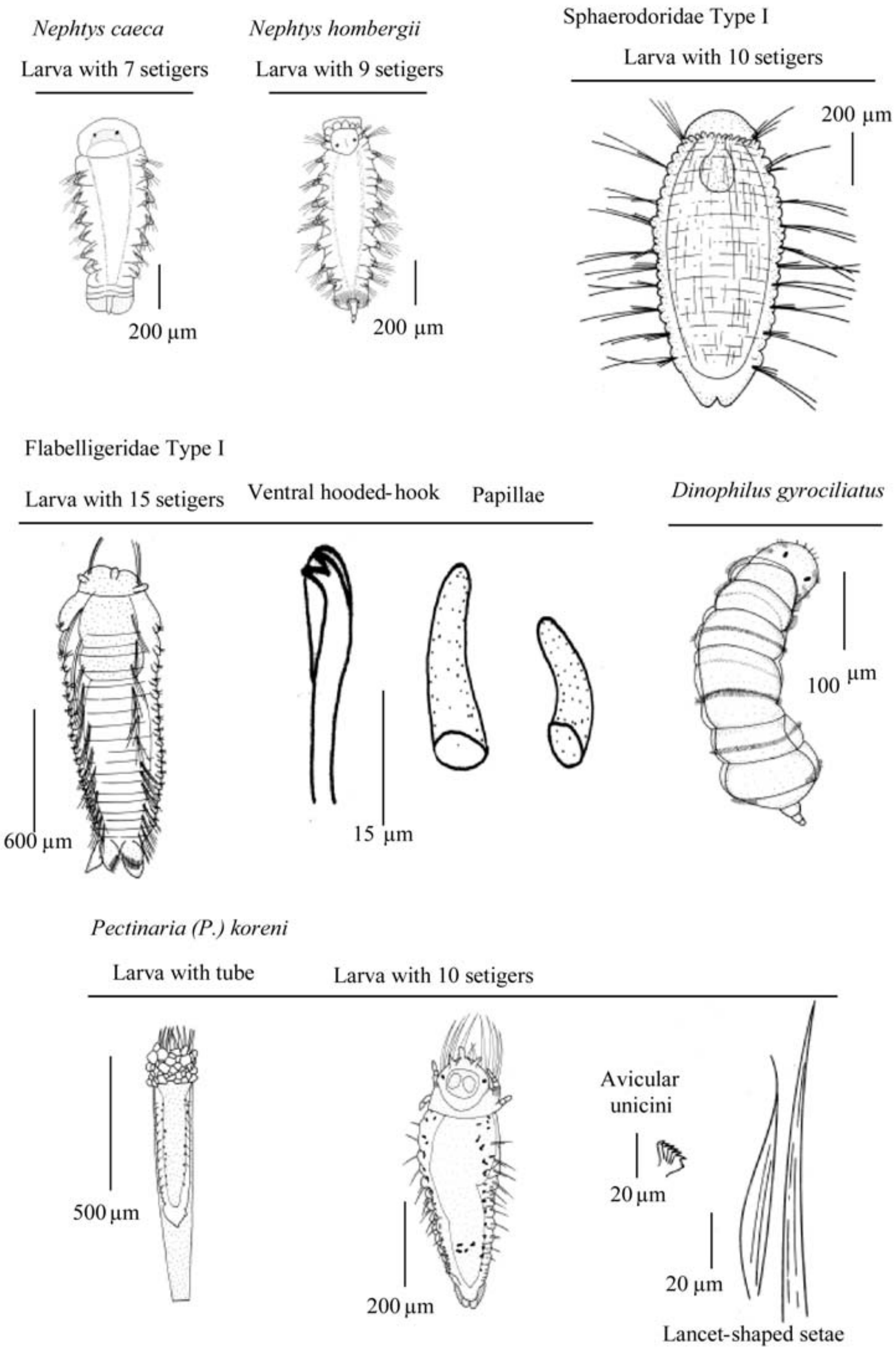


Fig. 2.12. Polychaete larvae from the List tidal basin: *Nephtys caeca, N. hombergii*, Sphaerodoridae Type I, Flabelligeridae Type I, *Dinophyllus gyrociliatus*, and *Pectinaria koreni*.

Chone infundibuliformis Kröyer 1856 (Fig. 2.13)

Benthic stages have not been found inside the basin. Larvae occurred between October-November, being common. Sizes were about 400 µm in length with 3 setigers. Bodies barrel-shaped. Prostomium with a distal bundle of cilia and one pair of eyes. Setae composed by avicular uncini, as well as sword- and leaf-shaped setae. Body lack pigmentation. Identification based on adult features given in Hartmann-Schröder (1996).

Chone Type I (Fig. 2.13)

Benthic stages are unknown. Larvae present between October-November, being common. Sizes were about 300 µm in length with 3 setigers. Bodies barrel-shaped and pigmented orange-red. Prostomium without distal cilia. One pair of eyes present. Leaf-shaped setae and avicular uncini present. Sword-shaped setae absent.

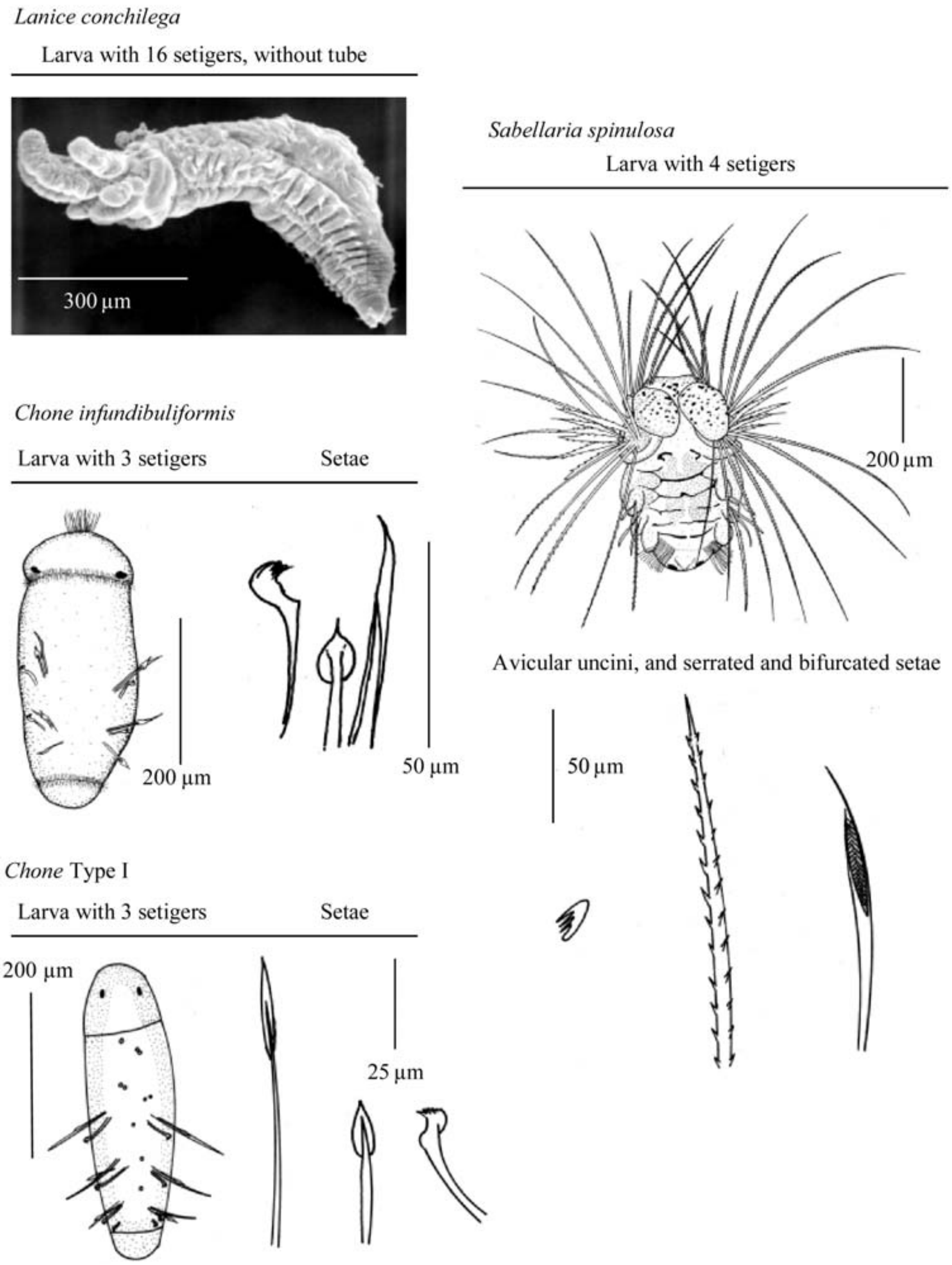


Fig. 2.13. Polychaete larvae from the List tidal basin: *Lanice conchilega, Sabellaria spinulosa, Chone infundibiliformis*, and *Chone* Type I.

IDENTIFICATION KEY FOR MEROPLANKTONIC POLYCHAETE LARVAE FROM THE LIST TIDAL BASIN

(1) Larvae with tube ……………………………………………………….……………..(2)
Larvae without tube ..…………...……………………………………...……….…(3)
(2) Prostomium with paleae……..……………………………*Pectinaria (Lagis) belgica*
Prostomium without paleae…………………...……...……………*Lanice conchilega*
(3) Body with elytra……………………...…………………………………………….(4)
Body without elytra……………………………...………………………….....(9)

(4) Dorsal cirri absent, notosetae simple and neurosetae compound, elytral papilla restricted to the superior left quarter of the elytra and over their edges.……………………………………………...……*Neolanira ca. tetragona*

Dorsal cirri present, dorsal and ventral setae simple……………………..……..….(5)

(5) With two pairs of dorsal cirri……..………..……...………..……………………(6)

With three to four pairs of dorsal cirri………………….……….…………………(7)

(6) Anal cirri long…… …...…………...…..………. *Harmothoe (Harmothoe) ljungmani*

Anal cirri short. Elytral surface with numerous papillae……………………………………………*Harmothoe (Harmothoe) impar*

(7) Elytral edge with numerous short papillae……..... *Harmothoe (Harmothoe) antilopes*

Elytral papilla scarce and elytral edges smooth…….……………………...………..(8)

(8) Elytral surface with smooth and porous areas and covered by long papillae…………………………………………………….....*Harmothoe* Type I

Elytral surface homogeneously smooth.…..…..……*Harmothoe (Harmothoe) glabra*

(9) Body without setigers ………………………...……………………..………(10)

Body with setigers …………….………...……….………...………………………..(12)

(10) Body without setae or hooks. One pair of eyes present…………………………………….……..Juvenile *Dinophilus gyrociliatus*

Eyes absent. Setae and hooks present…...…………………..………………..…(11)

(11) Body without chromatophores……...……………….…….………*Capitella* Type I

Body with black chromatophores……………...…………….…...*Capitella* Type II

(12) Body with no more than three setigers…..……………...……...………………..(13)

Body with more than three setigers……………………………………..………(14)

(13) Prostomium with cilia. Setae composed by avicular uncini as well as sword- and leaf-shaped setae............…………………………………*Chone infundibuliformis*

Prostomium without cilia. Setae composed only of avicular uncini and leaf-shaped setae ....…………………….……………………………….……….....*Chone* Type I

(14) Prostomium with very long ciliated tentacles……………..…...*Magelona mirabilis*

Prostomium without very long tentacles…………….……….………………(15)

(15) Neuropods with hooded hooks……………………………...………………...(16)

Neuropods without hooded hooks……………………………………..…………..(32)

(16) Hooded hooks starting since the first parapod. Body covered by papillae……………………………………...…………..Flabelligeridae Type I

Hooded hooks appearing after the 7th parapod. Body without papillae.…...…....(17)

(17) Two pairs of red eyes present...………...……………………………….……(18)

Three pairs of black eyes present...……………...……………………….………..(22)

(18) Prostomium bell-shaped ………………………………….………………….……………(19)

Prostomium rectangular or rounded ……………………...…...………….....(20)

(19) Prostomium orange……………………...…… *Scolelepis (Scolelepis) squamata*

Prostomium without pigmentation……………..…….*Scolelepis (Scolelepis) bonnieri*

(20) Prostomium rounded. Tentacular cirri thin and long …….*Aonides paucibranchiata*

Prostomium rectangular. Tentacular cirri short and wide …………...…………(21)

(21) Dorsal melanophores absent……………… ……………..…………*Laonice cirrata*

Band shaped melanophores in the anterior half of the body. Prostomium and pygidium yellow……….………….…..…………….………....*Spiophanes bombyx*

(22) With modified setae in the 5th setiger…...……………...…...………………..…(23)

Without modified setae in the 5th setiger absent……...………...…....………....(27)

(23) Body with only one column of star-shaped melanophores…………………………...……….*Polydora (P.) hermaphroditica*

Body with two columns of star-shaped melanophores……………...………..(24)

(24) Star-shaped chromatophores large, bold, and intertwined.....……...*Polydora* Type I

Star-shaped melanophores not intertwined...………………...…………………(25)

(25) Body with only four pairs of band-shaped melanophores……..….*Polydora cornuta*

Body with six pairs of band-shaped melanophores……………..…………....(26)

(26) Palpi flat, long, blade-shaped, and delicate. Star-shaped chromatophores small and diffused. Dorsal eyes peduncle-shaped..*Polydora* Type II

Palpi long but not flat nor blade-shaped. Star-shaped chromatophores small and well defined. Dorsal eyes not peduncle-shaped………...…...…. *Polydora ciliata*

(27) Pygidium with numerous large papillae.……………...…..….…*Pygospio elegans*

Pygidium without papillae……………………………...……...………..(28)

(28) Dorsal chromatophores absent…………………………..... *Malacoceros fuliginosus*

Dorsal chromatophores present………………..….………………...…………(29)

(29) Body robust, prostomium rectangular………………...…………….…..………(30)

Body slender, prostomium rounded…………………………………...……..(31)

(30) Dorsal chromatophores as transversal lines, diffused and irregular.…………………………………………………….*Scolelepis girardi*

Dorsal chromatophores as well marked and rectangular spots...…*Scolelepis* Type I

(31) Dorsal chromatophores as spots with white center……..……...…*Spio martinensis*

Dorsal chromatophores as diffused lines……………………..…..…..…*Spio thelli*

(32) Antennae present……………………………………………..…...………………(35)

Antennae absent……………………………………...……………………(43)

(35) Prostomium with two antennae …………………...…………………………(36)

Prostomium with four or five antennae ……………………………….…….(37)

(36) Larvae with up to six setigers. Blue-green yolk grains present…..…..*Nereis* Type I

Larvae develop more than six setigers. Yolk grain absent. Body broader in the frontal part. Palps short. Notopodial cirri in the 1st, 2nd, 4th, and 6th parapods…………………………...…………….…..…*Microphtalmus aberrans*

(37) Two pairs of tentacular cirri…...……...………………………………...……(38)

Three to four pairs of tentacular cirri……………………………...…………(40)

(38) Dorsal tentacular cirri longer than the ventral ones….……..*Eteone* (*Mysta) barbata*

Dorsal and ventral tentacular cirri of the same length……………………….……….(39)

(39) Pharynx with papilla. Body without chromatophores.............*Eteone (Eteone) longa*

Pharynx with jaws. Body with dorsal chromatophores as red spots....*Nereis* Type II

(40) Four pairs of tentacular cirri……………………...………….……………(41)

Three pairs of tentacular cirri……………………………………...……………(42)

(41) Body greenish. Dorsal black chromatophores in transversal bands…………………………………...………..*Phyllodoce (Anaitides) mucosa*

Body without color. Dorsal chromatophores as small spots at the basis of each parapod…………………...…………….……….*Phyllodoce (Anaitides) rosea*

(42) Dorsal chromatophores as broad transversal bands…………..……….. *Eulalia viridis*

Dorsal chromatophores absent……...……...…………….. *Pseudomystides limbata*

(43) Body long and slender. Parapodial lobes between segments 6 and 10 enlarged……………………………………...………. *Poecilochaetus serpens*

Body short and broad. Parapodial lobes of the same size all along the body......(44)

(44) Prostomium conical…………………………..….. *Scoloplos (Scoloplos) armiger*

Prostomium rounded or rectangular ……………………………..……………(45)

(45) Pygidium with anal cirrus…………………..……………………………..…(46)

Pygidium without anal cirrus……………………………………...………(47)

(46) Prostomium broadly rounded………………………..…..………. *Nephtys caeca*

Prostomium rectangular……………………...………………*Nephtys hombergii*

(47) Body covered with papillae. Ventral hooded-hoods present...Sphaerodoridae Type I

Body without papillae. Setae from the first setiger very long and serrated, companied by serrated paleae. Hooded-hooks absent………..*Sabellaria spinulosa*

4. Discussion

Plate and Husemann (1994) reported 54 polychaete species with meroplanktonic larval stages around Helgoland. In the present study, only 22 of those species were found inside the List tidal basin. This suggests that both sites share a small fraction of benthic stages and that the meroplanktonic composition of open and costal zones is different.

One of the applications of taxonomic studies is the identification of species representative for a region. Often, the dispersal capabilities between developmental stages in marine invertebrates diverge. Post-settlement dispersal capabilities of juvenile/adult benthic stages tend to be limited, due to their need of contact with the sediment, compared to the pelagic larval stages. These are often regarded as passive particles at the mercy of the currents (Banse 1986; Jackson 1986; Butman 1987; Possingham and Roughgarden 1990; Ellien *et al.* 2000), and the populations are consequently assumed to be open assemblages (Gaines and Lafferty 1995), implying that the larval production of one benthic population disperses far beyond from the adult site recruiting other populations but rarely itself. Therefore, larvae collected at one location could originate from distant regions. In that case, the species assemblage from benthic and planktonic compartments might differ in taxonomic composition, and the number of species increases if both are taken into account, since some species may locally occur only as larvae (Bhaud and Cazaux 1987).

Furthermore, we have to ask to what extend the assemblage of meroplanktonic stages could reflect the composition of the local benthic assemblage. Table 2.III summarizes research on polychaetes around the study area over a period of 75 years, and species are listed which were encountered as meroplanktonic larvae and/or as juvenile/adult benthic stages. This table comprises 113 species. From these species, 19 do not have pelagic larvae or are unlikely to do it (*Arenicola marina, Heteromastus filiformis, Scalibregma inflatum, Microphtalmus sczelkowii, M. similis, M. listensis, Hesionides arenaria, H. maxima, Exogone naidina, Streptosyllis websteri, Fabricia sabella*, *T. marioni, Manayunkia aestuarina, Dinophilus gyrociliatus, Psammodrilus balanoglossoides, Stygocapitella subterranea, Trilobodrilus axi, Protodrilus symbioticus,* and *P. chaetifer*). These are substracted from the total. From the 94 remaining species, 45 are only known as benthic stages, 26 are only known as pelagic larval stages, and 23 have been found in both stages. This indicates that the correspondence between the benthic and planktonic species assemblages is low, suggesting that meroplanktonic stages could include long distance vagrants.

Nevertheless, this approximation is too simple. It is likely that the species spectrum in the planktonic compartment is underestimated, because the effort dedicated to study pelagic larval stages was much lower than for benthic stages. Unfortunately, uncertainties on taxonomic identity in the polychaete fauna occur in both compartments. Records up to family and/or genus levels (see Wohlenberg 1937, Westheide 1966, Reise 1978, Wolter 1987, Armonies and Hellwig-Armonies 1987, Schories 1991, Beushausen 1994, Raddatz 1994, Reise *et al.* 1994, Pieloth 1996, Suhr 1996, and Wolf 2002) make it impossible to know if they refer to new species, unidentified juvenile stages, cases where the specific level was not intended, or mixtures of different reasons. Inaccurate taxonomic resolution in the benthic compartment could have also lumped the sources of several larval stages.

If long-distance vagrants are present in the larval stage, they could originate from England, Belgium, or the Netherlands, because the residual current flows west to east, and then north (Postma 1983). On the other hand, if such vagrants are continuously recorded inside the bight, they should not be considered as vagrants anymore, since they can also be part of the local representative species spectrum as larval forms (Bhaud and Cazaux 1987).

There are many reasons to explain why larvae of some benthic stages have not been found. Some have no or a short pelagic life and/or dispersal, their recruitment could be undertaken by re-suspended juvenile stages, and others may have multiple developmental modes (poecilogony).

Poecilogony is common in polychaetes (Hoagland and Robertson 1988; Chia *et al.* 1996; Willcox and Nickel 1998; Blake and Arnofsky 1999; Duchene 2000). Anger *et al.* (1986) proposed that populations of *Pygospio elegans* from the List tidal basin are poecilogonic and the same applies for *Polydora quadrilobata* (K. Reise pers. com.). Poecilogony may be switched on by environmental stress (Chia *et al.* 1996) and the study area is characteristic for that. Climatic factors are responsible for many fluctuations in benthic stages of invertebrates in the Sylt area (Strasser *et al.* 2001 a and b; Strasser and Pieloth, 2001), but we do not know how these affect meroplanktonic stages.

Finally, it should be noted that several taxa were found at specific areas (around Königshafen or along specific gullies). This suggests that location plays a role in the species composition. In benthic stages this occurs due to the natural patchiness in sediment types. Patchiness in abundance of plankton is a very common phenomenon as well (Brentnall *et al.* 2003), but the patchiness in composition of meroplanktonic organisms has not been recorded yet. The assumption that the List tidal basin is permanently well mixed, due to the tidal currents and strong wind effects, is not supported by the presence of certain species at specific areas. This suggests a non-homogeneous horizontal mixing. Mileikovsky (1968) found that the distribution of larvae and juveniles of bottom invertebrates from the Norwegian and Barents Seas resembled that of their parental forms, while currents influenced the larval distribution secondarily. Hadfield (1986) suggested that larval behavior would place the larvae above suitable bottoms along shores. Swimming behavior, biotic and abiotic features of the sediment, microbial layers, co-generic and/or co-specific chemical signals, presence of sympatric species and/or food could help to define larval distribution areas (Wilson 1981; Gallagher *et al.* 1983; Cuomo 1984; Woodin 1985; Barke 1986; Qian 1999). Buoyancy or vertical positioning can help larvae to maintain their position, a behavior being of more importance than horizontal swimming (Mileikovsky 1973; Cameron 1986). Bhaud (1998b) proposed that controlled occupation of space should soon substitute the idea of passive dispersal in polychaete larvae. In a certain way, the possibility that larvae may control their horizontal distribution is reasonable, because often polychaete larvae settle near or at their con-specifics (Wilson 1968; Meadows and Campbell 1972; Barke 1986; Woodin 1986; Qian 1999), and some species are able to maintain their distribution areas close to the adult population in spite of a highly advective and diffusive environment (see Thiébaut *et al.* 1998).

Oceanographic processes (e.g. eddies) may also enhance gregarious distributions of larval clouds. However, local current patterns were not addressed in this study. This should be attempted in the future, seeking for relationships between location-dependent distributions and hydrodynamic processes.

Table 2.III. List of species found as larval and juvenile/adult benthic stages around the study area. Species are listed following the phylogenetic scheme proposed by Fauchald (1977). Sylt=Wadden Sea side of the island; DWS= Danish Wadden Sea. References listed at the end of the table.

Species	**Pelagic larval stage**	**Location**	**Reference**	**Benthic stage**	**Location**	**Reference**
1. *Scoloplos (S.) armiger*	X	Sylt DWS	39 4	X	Sylt DWS	2,5,6,7,8,11,12,13,14,15,16,17,18,19,20,21,22,23,24,27,28,29,30,31,33,35,38 4
2. *Tharyx killariensis=T. marioni*				X	Sylt	6,7,8,11,12,13,14,15,17,20,22,23,24,28,29,33,38
3. *Aricidea minuta*				X	Sylt	13,14,18,27,28,29,33,35
4. *A. (Allia) suecica=A. jefreysii*				X	Sylt	5,13,19,30,33
5. *Paraonis fulgens*				X	Sylt	17,18
6.*Aonides paucibranchiata*	X	Sylt	39	X	Sylt	18,31
7. *Laonice cirrata*	X	Sylt	39			
8.*Malacoceros fuliginosus*	X	Sylt	39	X	Sylt	5,6,8,12,14,19,20,22,23,24,27,29,33,38
9. *Polydora (P.) ciliata*	X	Sylt	26,39	X	Sylt	1,3,8,12,20,24,28,29,33,37
10.*P.(P.)cornuta=P. ligni*	X	Sylt DWS	26,39 4	X	Sylt DWS	2,6,7,10,11,12,14,15,19,20,23,28,29,30,31,33 4
11*P. (P.) hermaphroditica*	X	Sylt	39			
12. *P. quadrilobata*				X	Sylt	7,14,20,22,23,29,33
13. *P. pulchra*	X	Sylt	26			
14. *Polydora* Type I	X	Sylt	39			
15. *Polydora* Type II	X	Sylt	39			
16. *Pygospio elegans*	X	Sylt DWS	26,39 4	X	Sylt DWS	2,5,6,7,8,9,11,12,13,14,15,16,17,18,19,20,21,22,23,27,28,29,31,33,35,38 4
17. *Scolelepis (S.) bonnieri*	X	Sylt	39			

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Species	**Pelagic larval stage**	**Location**	**Reference**	**Benthic stage**	**Location**	**Reference**
18. *S. (S.) squamata*	X	Sylt	39	X	Sylt DWS	2,5,13,16,17,18,27,29,35 4
19. *S. (S.) girardi*	X	Sylt	39			
20. *S. (S.) foliosa*				X	Sylt	2,8,13,27,29,33,35
21. *S. ciliata = Colobranchus ciliatus = Malacoceros tetracerus*				X	Sylt	2, 8,12,17,18,20,24,29,33,35,38
22. *Scolelepis* Type I	X	Sylt	39			
23. *Spio martinensis*	X	Sylt	39	X	Sylt	35
24. *S. theelli*	X	Sylt	39			
25. *S. filicornis*				X	Sylt	6,7,8,11,12,13,14,17,18,21,22,27,29,30,31,33
26. *S. mecznikowianus*				X	Sylt	18
27. *Spiophanes bombyx*	X	Sylt	39	X	Sylt	13,14,17,18,27
28. *Streblospio benedicti=S. shrubsolii*				X	Sylt	12,14,27,29,33
29. *Microspio wireni*				X	Sylt	2
30. *Magelona mirabilis=M. papillicornis*	X	Sylt	26,39	X	Sylt DWS	2,8,13,17,18,27,29,33,35 4
31.*Poecilochaetus serpens*	X	Sylt	39			
32. *Chaetozone setosa*				X	Sylt	18,33
33. *Cirratulus cirratulus*				X	DWS	4
34. *Capitella capitata*	X	DWS	4	X	Sylt DWS	2,6,7, 8,11, 12,13,14,15,16,17,19,20,21,22,24,27,29,31,32,33,34,35,38 4
35. *Capitella minima*				X	Sylt	33

Table 2.III. List of species found as larval and juvenile/adult benthic stages around the study area. Species are listed following the phylogenetic scheme proposed by Fauchald (1977). Sylt=Wadden Sea side of the island; DWS= Danish Wadden Sea. References listed at the end of the table (continued).

Species	**Pelagic larval stage**	**Location**	**Reference**	**Benthic stage**	**Location**	**Reference**
36. *Capitella* Type I	X	Sylt	39			
37. *Capitella* Type II	X	Sylt	39			
38. *Capitomastus minimus*				X	Sylt	5,12,17
39. *Arenicola marina*				X	Sylt	2,5,6,9,11,12,14,17,19,20,21,23,24,27,28,29,33,35
					DWS	4
40. *Heteromastus filiformis*				X	Sylt	2,5,7,8,11,12,13,14,17,20,23,24,27,28,29,31,35,38
					DWS	4
41. *Ophelia limacina*				X	Sylt	8,17,18,
					DWS	4
42.*O.rathkei=O.cluthensis*				X	Sylt	2,5,12,14,15,16,17,18,24,27
43. *Scalibregma inflatum*				X	Sylt	8
44. *Phyllodoce (A.) mucosa*	X	Sylt	39	X	Sylt	6,7,8,11,12,14,17,19,21,23,24,27,28,29,30,31,33,35,37,38
45. *P. (A.) rosea*	X	Sylt	39			
46. *P. (A.) maculata*	X	DWS	4	X	Sylt	2,31
					DWS	4
47. *Eteone (E.) longa*	X	Sylt	39	X	Sylt	5,6,7,8,11,12,13,14,17,18,19,20,21,23,24,27,28,29,30,31,33,35,38
		DWS	4		DWS	4
48. *E. (E.) spetsbergensis*				X	Sylt	17
49. *E. (M.) barbata*	X	Sylt	39			
50. *Eulalia viridis*	X	Sylt	39	X	Sylt	2,8,20,29,33,37
51. *E. bilineata*				X	Sylt	31
52.*Pseudomystides limbata*	X	Sylt	39			
53. *Eumida sanguinea*				X	Sylt	8,20,30

Table 2.III. List of species found as larval and juvenile/adult benthic stages around the study area. Species are listed following the phylogenetic scheme proposed by Fauchald (1977). Sylt=Wadden Sea side of the island; DWS= Danish Wadden Sea. References listed at the end of the table (continued).

Species	**Pelagic larval stage**	**Location**	**Reference**	**Benthic stage**	**Location**	**Reference**
54. *E. punctifera*				X	Sylt	29
55. *Harmothoe (H.) antilopes*	X	Sylt	39			
56. *H. (H.) glabra*	X	Sylt	39			
57. *H. (H.) impar*	X	Sylt	39	X	Sylt	8,17,20,37
58. *H. (H.) ljungmani*	X	Sylt	39			
59. *H. (H.) imbricata*				X	Sylt	6,8,12,20,27,29,33,37
					DWS	4
60. *H. (Antionella) sarsi*				X	Sylt	6,12,13,27,29,31,33,35
61. *H. lunata*				X	Sylt	30
62. *Harmothoe* Type I	X	Sylt	39			
63. *Lepidonotus squamatus*				X	Sylt	2,5,8,20,24,27,29,33,37
					DWS	4
64. *Gattyana cirrosa*				X	Sylt	5,2,8
					DWS	4
65. *Pholoe minuta*				X	Sylt	6,20,29
66. *Neolanira* c.f. *tetragona*	X	Sylt	39			
67. *Keferestenia cirrata*				X	Sylt	20,24
68. *Microphtalmus aberrans*	X	Sylt	39	X	Sylt	5,6,11,12,13,14,29,33
69. *M. sczelkowii*				X	Sylt	5,11,12,14,15,21,22,23,27,29
70. *M. similis*				X	Sylt	5,14
71. *M. listensis*				X	Sylt	5,14,23
72. *Hesionides arenaria*				X	Sylt	5,15

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Species	**Pelagic larval stage**	**Location**	**Reference**	**Benthic stage**	**Location**	**Reference**
73. *H. maxima*				X	Sylt	5
74. *Exogone naidina*				X	Sylt	29
75. *Streptosyllis websteri*				X	Sylt	29
76.*Nereis (Nereis) pelagica*				X	Sylt	2,4,8
77.*N. (Neanthes) succinea*				X	Sylt	8,20,29,33,37
78. *N. (Neanthes) virens*				X	Sylt	5,6,8,9,12,13,14,17,18,23,24,27,29,33,37,38
					DWS	4
79.*N.(Hediste)diversicolor*	X	DWS	4	X	Sylt	2,5,6,9,12,14,15,16,17,18,19,20,21,23,24,27,29,31,33,35,37
					DWS	4
80. *Nereis* Type I	X	Sylt				32
81. *Nereis* Type II	X	Sylt				32
82. *Goniada maculata*				X	Sylt	14
83. *Goniadella bobretzkii*				X	Sylt	8,14
84. *Nephtys caeca*	X	Sylt	39	X	Sylt	5,8,12,13,17,18,23
85. *N. hombergii*	X	Sylt	39	X	Sylt	2,5,6,8,11,13,14,17,23,24,27,28,29,30,31,33,35
		DWS	4		DWS	4
86. *N. ciliata*				X	Sylt	13
87. *N. longosetosa*				X	Sylt	13
88. *N. cirrosa*				X	Sylt	25
89. *Sphaerodorum balticum*				X	Sylt	5,30
90. *S. minimum*				X	DWS	4
91. Sphaerodoridae Type I	X	Sylt	39			
92. *Ophryotrocha gracilis*				X	Sylt	14

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Species	**Pelagic larval stage**	**Location**	**Reference**	**Benthic stage**	**Location**	**Reference**
93.*Parapodrilus psammophilus*				X	Sylt	14
94. Flabelligeridae Type I	X	Sylt	39			
95. *Sabellaria spinulosa*	X	Sylt	39	X	DWS	4
96. *Pectinaria (L.) koreni*	X	DWS	4	X	Sylt	5,6,8,9,13,29,33
		Sylt	39		DWS	4
97. *Lanice conchilega*	X	Sylt	26,39	X	Sylt	2,5,6,7,8,12,14,17,24,27,29,31,33,35,38
					DWS	4
98. *Ampharete acutifrons = A. grubei*				X	Sylt	2,6,8,12,23,24,26,27,29,33
99. *A. baltica*				X	Sylt	38
100. *A. finmarchica*				X	Sylt	20
101. *Amphitrite johnstoni*				X	Sylt	2
102.*Neoamphitrite figulus*				X	Sylt	20,37
103. *Fabricia sabella*				X	Sylt	15,28,29
104. *Chone infundibuliformis*	X	Sylt	39			
105. *Chone* Type I	X	Sylt	39			
106. *Pomatoceros triqueter*				X	DWS	4,36
107. *Manayunkia aestuarina*				X	Sylt	12,14
108. *Dinophilus gyrociliatus*				X	Sylt	39

Table 2.III. List of species found as larval and juvenile/adult benthic stages around the study area. Species are listed following the phylogenetic scheme proposed by Fauchald (1977). Sylt=Wadden Sea side of the island; DWS= Danish Wadden Sea. References listed at the end of the table (continued).

Species	**Pelagic larval stage**	**Location**	**Reference**	**Benthic stage**	**Location**	**Reference**
109.*Psammodrilus balanoglossoides*				X	Sylt	14,29
110. *Stygocapitella subterranea*				X	Sylt	14
111. *Trilobodrilus axi*				X	Sylt	14
112. *Protodrilus symbioticus*				X	Sylt	14
113. *P. chaetifer*				X	Sylt	14

[1]Hagmeier and Kändler (1927); [2]Wohlenberg (1937); [3]Linke (1939); [4]Smidt (1951); [5]Westheide (1966); [6]Reise (1978); [7]Debus (1979); [8]Riesen and Reise (1982); [9]Reise (1981); [10]Reise (1983a); [11]Reise (1983b); [12]Buchholz (1984); [13]Wolter (1987); [14]Armonies and Helwig-Armonies (1987); [15]Hellwig-Armonies and Armonies (1987); [16]Reise (1989); [17]Schülke (1989); [18]Sander (1989); [19]Siebert (1989); [20]Ditmann (1990); [21]Majewski (1990); [22]Reise (1991), [23]Schories (1991); [24]Albrecht and Reise (1994); [25]Beushausen (1994); [26]Raddatz (1994); [27]Reise *et al.* (1994); [28]Guenther (1996); [29]Lackschewitz (1996); [30]Pieloth (1996); [31]Suhr (1996); [32]Buschbaum (1997); [33]Rasel (1997); [34]Gamenick *et al.* (1998); [35]Lackschewitz and Reise (1998); [36]Reise (1998); [37]Saier (2002); [38]Wolf (2002); [39]This study.

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Chapter 3. Spatial patterns of abundance in meroplanktonic polychaete larvae in a tidal basin

Abstract

The analysis of abundance patterns in meroplanktonic polychaete larvae inside the List tidal basin (northern Wadden Sea) revealed that highest larval abundances were concentrated at the innermost parts of the three main tidal channels of the bight. This was a recurrent pattern during both tidal phases, and occurred at a 10-km scale. At a 1-km scale, the same phenomenon was apparent during high tides along the main channel of a bay completely exposed at low tides. At the species level, larvae of *Pygospio elegans* and *Lanice conchilega* showed different spatial patterns around a sandy hook, resembling the pattern of their benthic stages. Polychaete larvae distribution resembled that of suspended particulate organic matter of similar size inside the basin, suggesting that they distribute like passive suspended particles. With regard to vertical position, there was no preference at high water, but at low water highest abundance were significantly more frequent close to the bottom. However, species diversity and species richness in the polychaete larval plankton showed only random spatial patterns at all locations. The results suggest that larval retention is the dominant local process and indicate that benthic occurrence of adult stages and coastal morphology may also influence species-specific distribution patterns.

1. Introduction

Why benthic marine invertebrates have pelagic larvae is a controversial issue. They may either constitute an escape of small life stages from a plenitude of predators and competitors at the bottom or they are essential for long-distance dispersal (Strathmann *et al.* 2002; Young 1990). In spite of the potential of wide dispersal for pelagic larvae, there is growing evidence that larval retention in localized areas may be a common phenomenon (Swearer *et al.* 2002). This has implications on the theory of open vs. closed marine populations as well as implications on the areal size and the potential effects of marine reserves (Warner and Cowen 2002).

Studies have shown that the supply of larvae is often a crucial factor in explaining distribution and abundance of recruitment to the rocky shore fauna (Ólafsson *et al.* 1994; Gaines and Lafferty 1995). To what extend this also applies to the sediment fauna is a controversial matter. It may be the case in some species (Strasser and Pieloth 2001). Not only the amount of larval supply may be important, but also their dispersal in the coastal waters to explain benthic patterns (Ólafsson *et al.* 1994; Gaines and Lafferty 1995). Therefore, the spatial distribution of larvae within a sedimentary embayment has been studied. In the shallow, eastern North Sea, polychaetes are a dominant component in the benthic macrofauna (Hartmann-Schröder 1996) as well as in the meroplankton (Hickel 1975; Martens 1980; Jak 1999). Accordingly, the polychaete larvae have been selected for this study.

The study area constitutes an artificially semi-enclosed embayment. Two adjacent barrier islands are connected by causeways to the mainland, thus enclosing a lagoon of 410 km^2, with a 2.5 km wide tidal inlet, flushing about half of the high water volume offshore with each ebbing tide. Consequently, the first question to be analyzed is whether strong tidal mixing prevents the development of any non-random spatial patterns in the meroplanktonic larvae within the tidal basin. This was assumed by Hickel (1975). He conducted the first quantitative survey of the zooplankton in the area. He selected a single sampling station at List harbor, close to the tidal inlet, and described the seasonal variability. Later, Martens (1980) sampled three stations, one in each of the major tidal channels of the List basin, but subsequently lumped the data to produce average values on zooplankton biomass. Thus, there is no knowledge whether differences in the composition and abundance of the polychaete larval plankton occur between branches of the tidal inlet, and between the inlet and the innermost parts of the channels. Fransz (1981) suggested that such differences occur in the western Dutch Wadden Sea. He found that biomasses of polychaete larvae were lowest near the tidal watershed of the Marsdiep tidal basin. Such a pattern may result in spite of the tidal mixing when zooplankton is mainly imported from the sea and subjected to severe predation and/or settling on the tidal flats.

Non-random distributions of polychaete larvae within a tidal basin may also result when larvae modify their vertical position within the tidal flow. Staying high in the water column during flooding tide and lower during ebbing tide might result in retention of larvae within the basin, assuming swifter flood currents close to the surface than ebb currents close to the bottom. This has been inferred for gelatinous zooplankton in the List tidal basin (Kopacz 1994). Consequently, the second question to be analyzed is whether polychaete larvae show differential vertical distributions in the water column during high and low tides in the channels.

Polychaete larvae might show a spatial pattern similar to passive suspended particles in a tidal basin. Particle transports have been described for tidal basins in general (Oost and De Boer 1994), and in particular for the List tidal basin on both small (1 km) and large (10 km) scales (Austen 1994; Austen *et. al.* 1998). Based on these descriptions, the third question to be analyzed is whether polychaete larvae correspond to the onshore gradient of suspended particles of comparable size.

If polychaete larvae distribute like passive particles, one would not expect to encounter species-specific patterns. On a small scale (1 km), the pattern of larvae of the terebellid *Lanice conchilega* and the spionid *Pygospio elegans* were compared with respect to adult populations and coastal morphology. The surrounding of a sandy hook separating a small and sheltered bay was studied. The final corresponding question to be assessed is, whether only benthic processes cause species-specific benthic patterns, or whether the availability of pelagic larvae generates the benthic pattern.

2. Methods

Attempts were made to obtain quasi-synoptic samples of polychaete larvae from the tidal waters to get snapshots of the spatial distribution at three scales (Fig. 3.1 and Table 3.I).

10-km scale: Samplings were undertaken inside the List tidal basin (410 km^2), sheltered by the islands of Sylt (Germany) and Rømø (Denmark) (Fig. 3.1), which are connected to the mainland by causeways. Tidal channels occupy 10% of the basin area with maximal depths of 30 m during high-water conditions; shallow subtidal sands occupy 60%, and tidal flats the remaining 30%. Tides are semidiurnal (range ≈2 m) and cause the exchange of roughly half of the high water volume. Detailed information is given in Gätje and Reise (1998). The ship followed the advancing peak of tidal high water, from the tidal inlet along one of the three main tidal channels of the List tidal basin. As there was only one ship available, the three channels were sampled at successive days. The same route was also taken at peak tidal low water. At each of 3 to 4 stations along the channels, a 30-l Van Dorn bottle was repeatedly used and its volume fractioned in order to collect five 10-l water samples from the surface, and five more from 3 m above the bottom. Depths for each sampling station during high water conditions are shown in Fig. 3.1. Samples were fixed on board, immediately after being filtered through a 80 µm mesh. Wind flow patterns and tidal current speeds are shown for each sampling date in Appendix 3.I. Mean velocities for superficial tidal currents ranged between 0.3-0.6 m·s^{-1} during high tides, and 0.3-0.8 m·s^{-1} during low tides.

1-km scale: Sampling was undertaken in the sheltered sandy intertidal back barrier bay Königshafen (6 km^2; see Austen 1994 and Reise and Gätje 1994), inide the List tidal basin (Fig. 3.1). Tides are semidiurnal with average amplitude of 1.8 m (Armonies 1994). This bay has a curved tidal creek with maximal depths of 4-5 m during high water conditions (Austen 1994). Four sampling stations we chosen, about 300 m apart along the tidal creek (Fig. 3.1). Five 10-l samples from the surface were taken at each station during the peak diurnal high tide. Water samples were taken from a ship, using a 10 l bucket, and were immediately fixed on board after being filtered through a 80 µm mesh. This sample gear was also used by Martens (1995) in the same locality. Wind flow patterns during each sampling date are shown in Appendix 3.II.

100-m scale: Sampling was undertaken at Oddewatt, which is a small bay (<1 km^2) in the outer Königshafen (Fig. 3.1). The sandy island of Üthorn in the north and a dike in the west provide shelter. During low water conditions the site is exposed, and during high water conditions maximal depths are 2 m. Six sampling stations were chosen (Fig. 3.1). Four 2-l samples were taken with a bucket at each station during the peak of diurnal high tides. Samples were fixed on the field immediately after being filtered through a 80 µm mesh. Data of the three outer stations were pooled representing "Outside" (O) conditions and those of the inner part pooled to represent "Inside" (I) conditions (Fig. 3.1). Distribution patterns of larvae of *Pygospio elegans* and *Lanice conchilega* were compared versus those of their juvenile and adult benthic stages. The spatial distribution of benthic stages of *Lanice,* during autumn 2001 was kindly provided by Dr. Matthias Strasser (Alfred Wegener Institute) and was part of an ongoing mapping program to study spatio-temporal dynamics (Strasser and Pieloth 2001). Spatial distribution patterns for *Pygospio* were obtained from sediment samples (three replicates at each sampling point, Fig. 3.1) taken with a tube (sampling area=13 cm^2, volume=50 ml) during low water conditions between May and August 2001. Abundances were estimated by sorting the samples under a stereomicroscope without sieving, to avoid the loss of juvenile stages.

In all sampling schemes, One-way ANOVA was applied to assess significant differences in abundance. In order to test the significance of patterns shown by groups of sampling dates, a Sign Test was used for the significance of recurrent patterns.

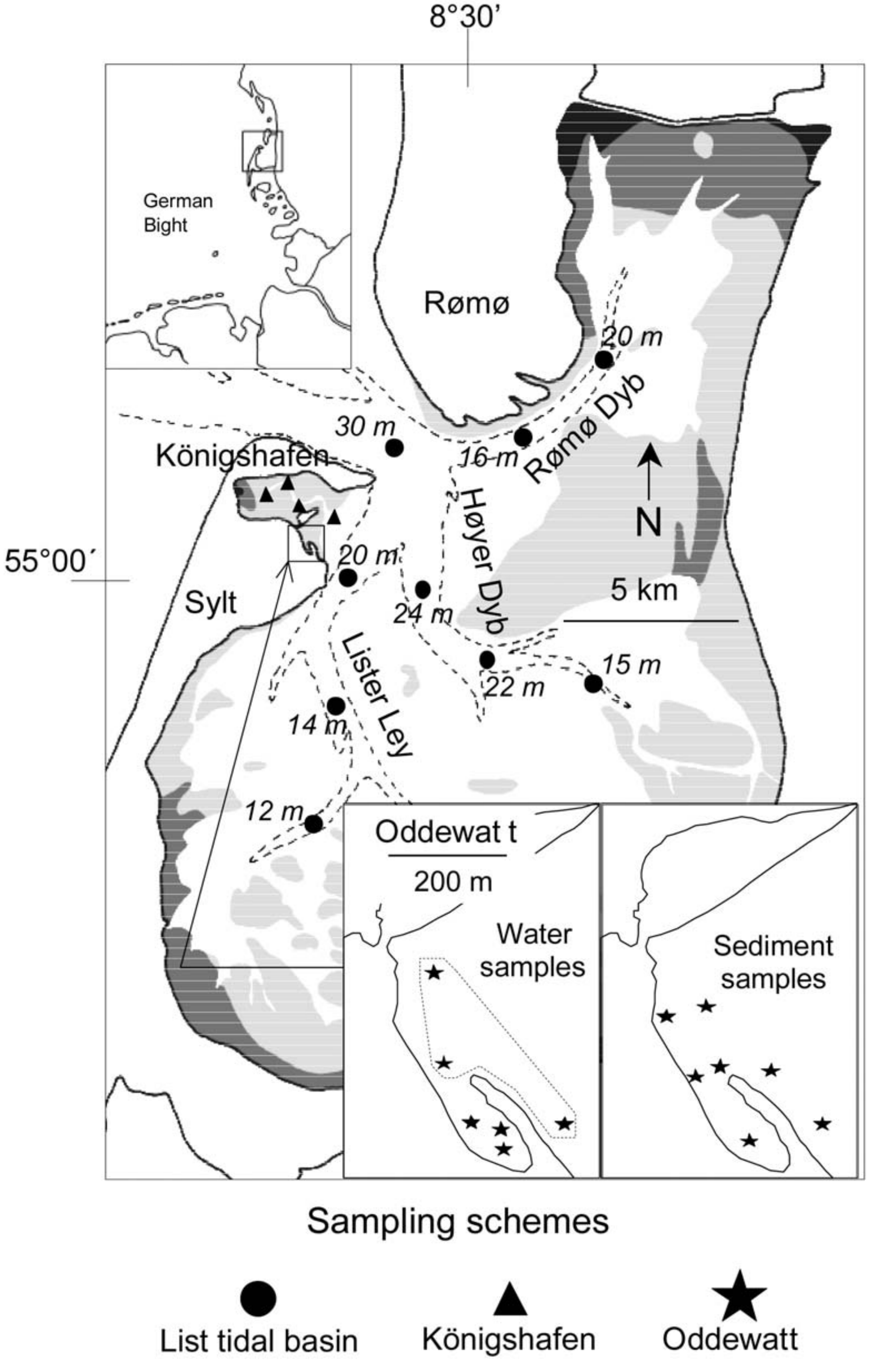


Fig. 3.1. Study area and position of sampling stations for three spatial scales in the List tidal basin. Numbers in italics at each sampling point along the main gullies of the basin show the depth during high tides.

Table 3.I. Sampling dates for three spatial scales chosen in the List tidal basin.

10-km scale: List tidal basin			
	Channel		
	Lister Ley	Høyer Dyb	Rømø Dyb
High tide	Dec 6, 2000	Dec 7, 2000	Dec 11, 2000
	Feb 19, 2001	Feb 20, 2000	Feb 21, 2000
	July 2 and 17, 2001	July 3 and 18, 2001	July 4 and 19, 2001
	May 7 and 22, 2002	May 6 and 23, 2002	May 8 and 24, 2002
	July 2 and 17, 2002	July 3 and 18, 2002	July 4 and 19, 2002
Low tide	June 6, 2001	June 7, 2001	June 8, 2001
	Sep 3 and 10, 2001	Sep 4 and 11, 2001	Sep 5 and 12, 2001
	Apr 4, 2002	Apr 10, 2002	Apr 11, 2002
	May 27, 2002	May 28, 2002	May 29, 2002
	June 11, 2002	June 12, 2002	June 13, 2002
	July 24, 2002	July 25, 2002	July 26, 2002
	Aug 22, 2002	Aug 23, 2002	Aug 21, 2002

1-km scale: Königshafen
Year 2000: May 8, 15, 25, and 31; July 3, 13, 24; Aug 7 and 22; Sep 12; Nov 20.
Year 2002: May 15; June 19; July 8; Aug 20.

100-m scale: Oddewatt
Year 2001: May 19,23, and 30; June 12,17,22, and 28; July 8.

3. Results

3.1. Overall abundance data

The overall mean larval density of all samples taken within the List tidal basin, between May 2000-August 2002, was 36.7 larvae·10 l^{-1} (±2.5; number of samples=2452). As this mean is strongly affected by the unequal seasonal coverage of sampling, the mean for the most intensively studied summer (May-August 2002) is given as well: 26.0 larvae·10 l^{-1} (±2.0; number of samples=960).

There was a significant difference in overall larval densities during high water conditions between areas within the List tidal basin (“Tidal inlet” (Lister Ley, Høyer Dyb, and Rømo Dyb station 1); “Main channels” (Lister Ley stations 2-4, Høyer Dyb stations 2-4, and Rømo Dyb stations 2-3); “Channel in Königshafen” (Königshafen stations 1-4); and “Tidal flat” (Oddewatt stations 1-6)) during the most intensively sampled periods from May-August 2001 for Oddewatt, and May-August 2002 for the other locations (Fig. 3.2).

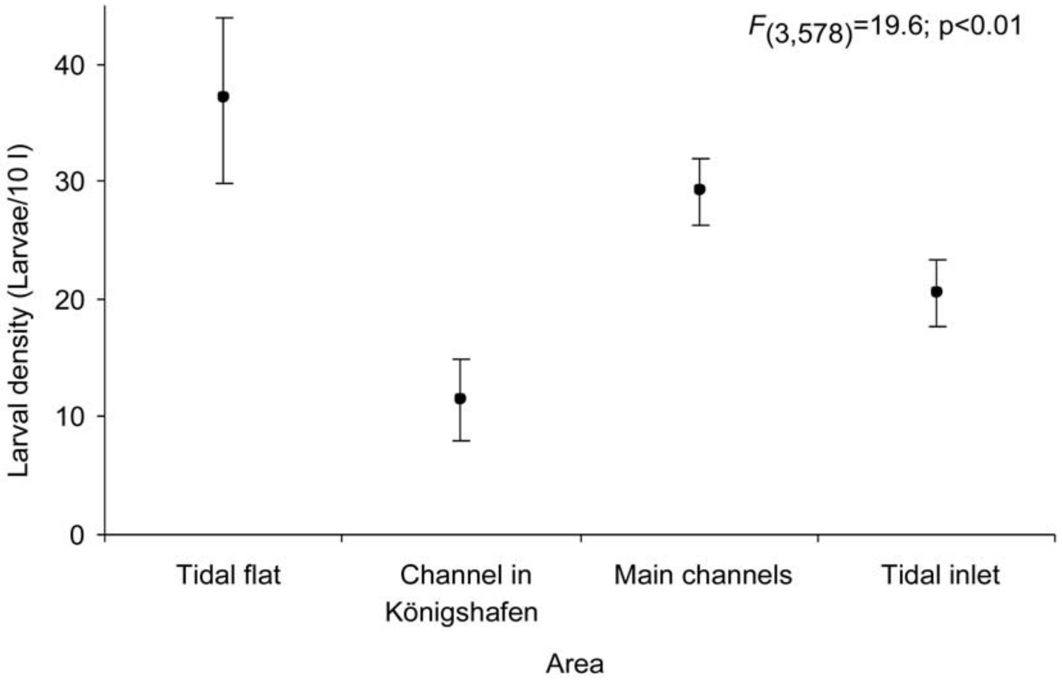


Fig. 3.2. Overall mean larval densities and 95% confidence intervals, during high water conditions, between areas within the List tidal basin. *F*-value refers to ANOVA test assessing significant differences in mean values between areas.

3.2. Spatial patterns at the 10-km scale

Differences in total larval abundance between channels were significant in 6 out of 15 cases during high-tide conditions (Table 3.II). In these cases, abundances were always highest at Lister Ley. During low-tide conditions, differences were more frequent with 10 out of 16 cases (Table 3.III), and highest abundances also occurred at Høyer Dyb and Rømø Dyb.

There was a recurrent spatial pattern, with highest abundances at the middle and inner intervals in each channel, at both depth levels of the water column during both tidal conditions (Figs. 3.3-3.5). In 69% (64 out of 93) of all cases, differences in abundance along each channel were significant. Significant deviations from random patterns dominated also when tidal phases and depth intervals were considered separately. In Lister Ley, the frequency of cases with highest abundances at stations from the middle and inner intervals was significantly higher than from the tidal inlet station (Sign test; $Z_{(31)}$=3.8, p<0.01). The same occurred in Høyer Dyb (Sign test; $Z_{(31)}$=3.9, p<0.01) and Rømø Dyb (Sign test; $Z_{(31)}$=4.7, p<0.01). Most apparent was, that the tidal inlet (Station 1) often showed low abundances. In 64% of all cases the lowest abundance occurred at that site.

Diversity and species richness showed no consistent pattern between and along the three channels, during both tidal conditions, and at both levels of the water column. H´ and S had the same probability (50%) of being highest at the inner- and outermost parts of the bight, during both phases of tide, and both levels of the water column (Sign test for Lister Ley: $Z_{(28)}=-0.2$, $p>0.05$ for H´ and S; for Høyer Dyb $Z_{(28)}=2.1$, $p>0.05$ for H´ and $Z_{(28)}=0.6$, $p>0.05$ for S; for Rømø Dyb $Z_{(28)}=0.6$, $p>0.05$ for H´ and $Z_{(28)}=1.3$, $p>0.05$ for S). Neither were there any consistent differences between high- and low-tide conditions as well as between surface and near bottom samples.

Table 3.II. Comparisons of mean larval densities (Larvae/10 l) between tidal channels, during high tides, for each sampling campaigns. The channel deviating significantly with a high mean is shaded (after Tukey HSD-test). *=p<0.05; **=p<0.01.

Period (Days/Month/Year)	Water level	Tidal Channel			ANOVA *F*-value (d.f.=2,52)
		Lister Ley	Høyer Dyb	Rømø Dyb	
6-7-11/VII/00	Surface	8.6±2.2	6.5±2.2	5.1±2.3	2.1
19-20-21/II/01	Surface	3.8±1.2	4.6±1.2	4.7±1.4	0.4
	Bottom	5.1±1.6	4.5±0.4	4.8±2.0	0.2
2-3-4/VII/01	Surface	17.0±5.8	17.8±5.4	11.6±6.2	1.2
	Bottom	21.7±3.4	10.9±7.2	19.2±8.2	2.4
17-18-19/VII/01	Surface	15.1±3.8	20.2±3.8	21.0±4.4	2.5
	Bottom	25.9±4.6	24.5±4.6	26.7±5.2	0.9
6-7-8/V/02	Surface	28.4±8.0	12.5±8.0	20.2±9.0	4.0*
	Bottom	25.4±3.0	14.5±5.0	21.3±6.0	4.8**
22-23-24/V/02	Surface	34.1±13.2	34.7±13.6	29.9±14.7	0.1
	Bottom	53.4±13.4	66.6±13.4	51.1±16.8	1.4
2-3-4/VII/02	Surface	27.3±2.8	19.2±2.8	4.3±3.2	59.9**
	Bottom	26.3±4.6	24.2±4.6	11.8±3.4	92.0**
17-18-19/VII/02	Surface	26.3±15.6	13.2±5.0	11.3±4.8	8.1**
	Bottom	42.1±9.8	21.0±8.6	17.0±8.6	8.3**

Table 3.III. Comparisons of mean larval densities (Larvae/10 l) between tidal channels, during low tides, for each sampling campaigns. The channels deviating significantly with a high mean are shaded (after Tukey HSD-test). *=$p<0.05$; **=$p<0.01$.

Period (Days/Month/Year)	Water level	Tidal Channel			ANOVA *F*-value (d.f.=2,52)
		Lister Ley	Høyer Dyb	Rømø Dyb	
6-7-8/VI/01	Surface	68.4±12.0	51.0±12.4	61.2±14.0	2.0
	Bottom	60.5±10.6	65.1±10.6	62.0±12.8	0.2
3-4-5/IX/01	Surface	17.4±5.4	25.2±5.4	16.8±6.8	2.7
	Bottom	32.4±6.0	42.7±6.2	21.3±7.0	10.3**
10-11-12/IX/01	Surface	26.2±8.8	21.6±9.0	41.6±10.0	4.6*
	Bottom	37.2±8.8	37.4±8.8	44.4±10.0	0.7
4-10-11/IV/02	Surface	19.2±7.6	6.2±1.6	30.3±9.0	8.5**
	Bottom	18.7±4.2	4.8±4.0	8.2±4.6	12.0**
27-28-29/V/02	Surface	52.2±11.2	36.3±11.4	39.3±13.2	2.1
	Bottom	132.5±21.8	55.4±21.8	42.2±25.2	18.5**
11-12-13/VI/02	Surface	64.7±20.5	28.5±20.0	16.2±14.0	5.5**
	Bottom	75.1±18.8	32.6±18.8	17.6±12.6	9.6**
21-22-23/VIII/02	Surface	10.1±3.6	19.9±3.6	13.1±4.4	6.8**
	Bottom	25.0±4.4	19.9±3.6	13.1±4.4	1.5
24-25-26/VII/02	Surface	14.5±2.8	5.9±2.8	8.7±3.2	9.4**
	Bottom	35.0±3.4	9.0±3.4	10.4±4.0	65.4**

3.3. Vertical distribution of the total abundance of polychaete larvae

Mean larval abundances at the surface and near-bottom levels in the water column at stations along the three main channels of the List tidal basin, during both tidal phases, are shown in Figs. 3.6-3.8. During high tide conditions, significant differences between both levels of the water column were detected in 18 out of 62 cases. Differences were more common during low tide conditions with 35 significant cases out of 72. In most of the significant cases, abundances close to the bottom were the highest. During high-water conditions, abundance had the same probability (50%) of being highest at either of the two levels in the water column. On the other hand, during low-water conditions the frequency of cases with highest larval abundances at the lower level in the water column was significantly higher than that of cases with highest abundances at the upper level, in two of the three main channels (Sign tests for high-tide conditions: Lister Ley, $Z_{(6)}=1.5$, $p>0.05$; Høyer Dyb, $Z_{(7)}=1.5$, $p>0.05$; Rømø Dyb, $Z_{(6)}=1.2$, $p>0.05$. Sign tests for low-tide conditions: Lister Ley, $Z_{(11)}=0.6$, $p>0.05$; Høyer Dyb, $Z_{(14)}=3.5$, $p<0.01$; Rømø Dyb, $Z_{(10)}=2.2$, $p<0.05$).

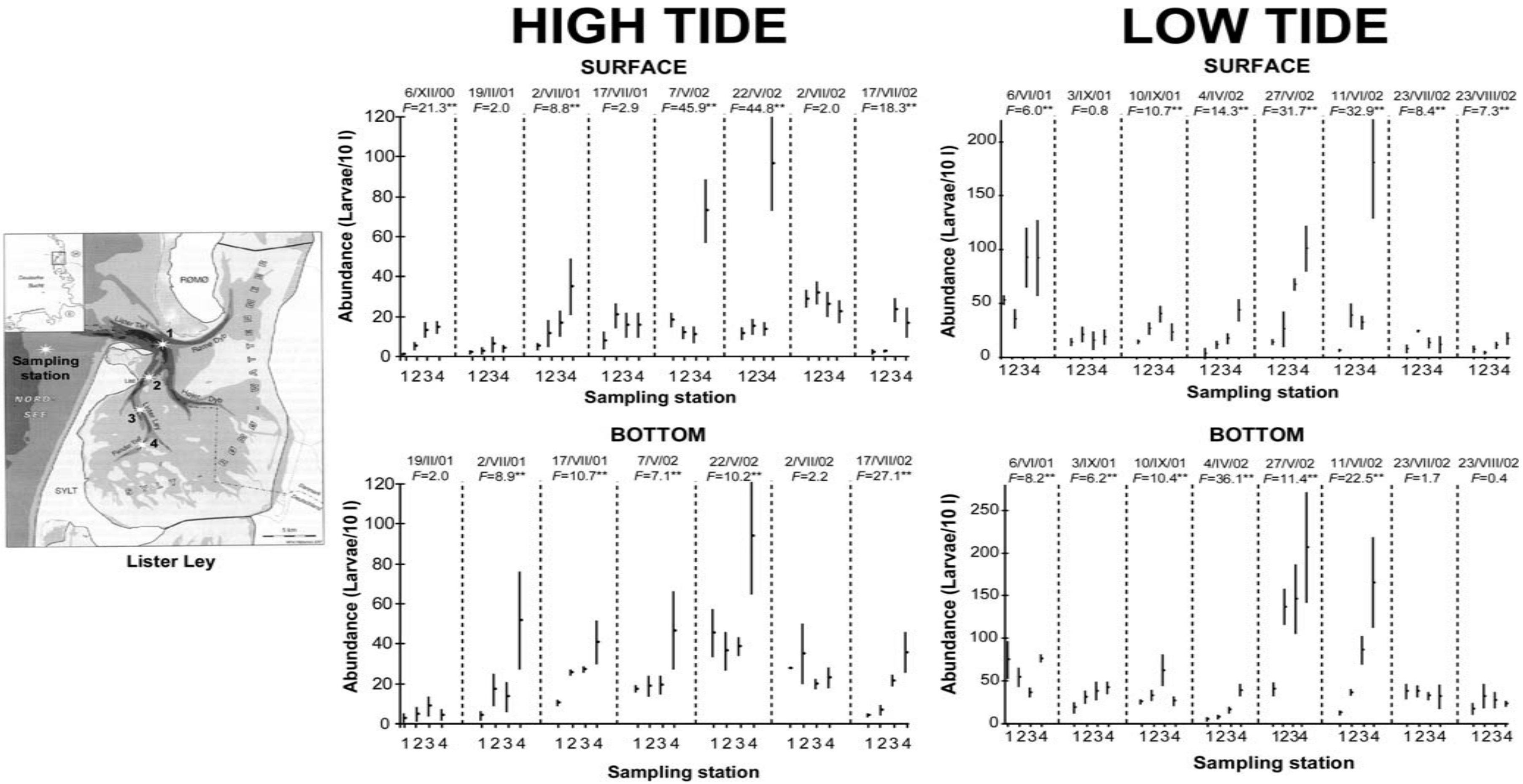


Fig. 3.3. Total abundances (Mean and S.E.) of polychaete larvae at four stations, from the tidal inlet to the inner channel along Lister Ley during high and low tide phases, and near the surface and 3 m above the bottom (below). Sets of samples were taken at irregular intervals between December 2000 and August 2002. *F*-values refer to ANOVA tests indicating significant differences in mean values between stations at each sampling date (**=$p<0.01$).

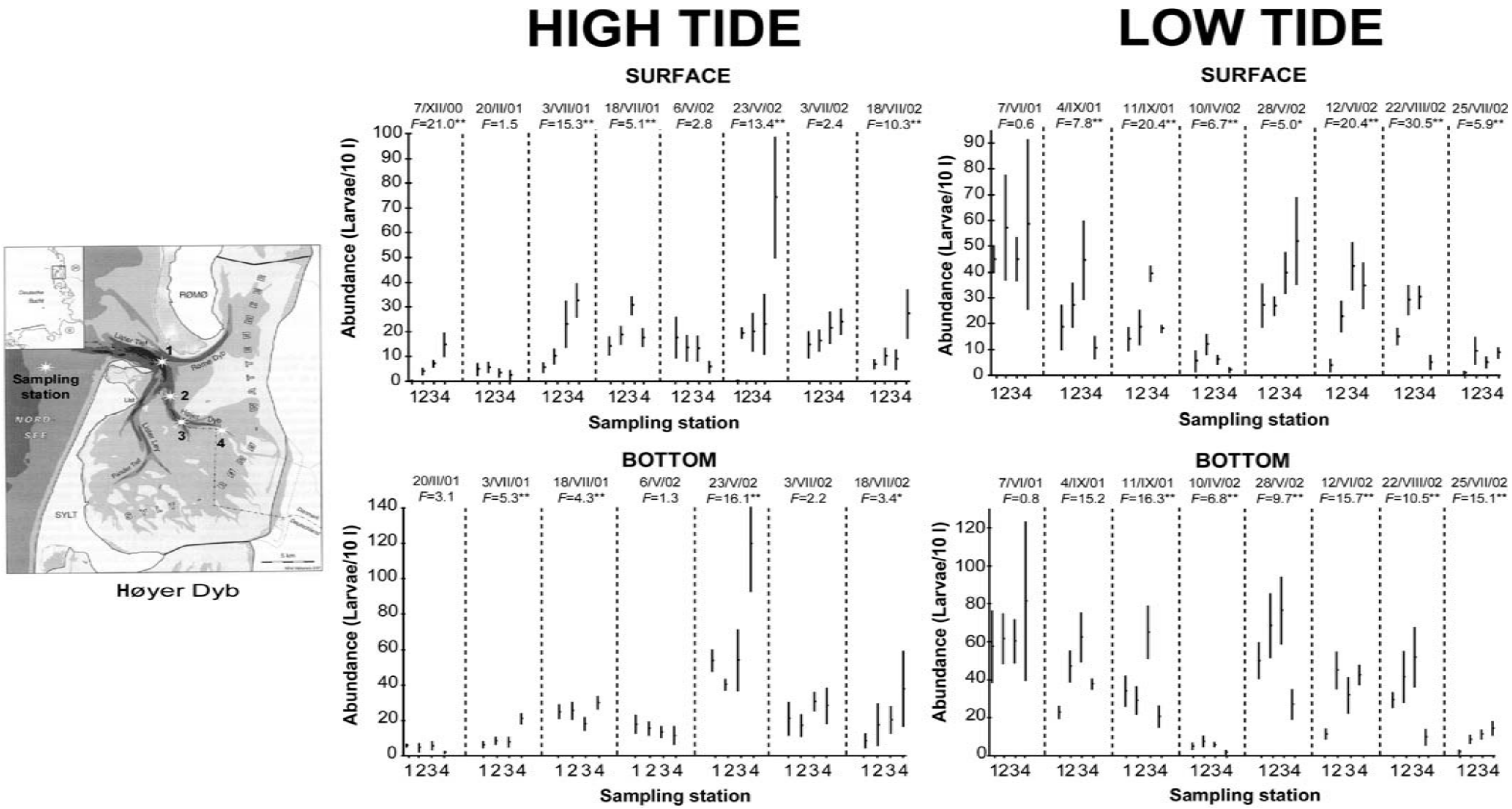


Fig. 3.4. Total abundances (Mean and S.E.) of polychaete larvae at four stations, from the tidal inlet to the inner channel along Høyer Dyb during high and low tide phases, and near the surface and 3 m above the bottom (below). Sets of samples were taken at irregular intervals between December 2000 and August 2002. *F*-values refer to ANOVA tests indicating significant differences in mean values between stations at each sampling date (**=p<0.01; *= p<0.05).

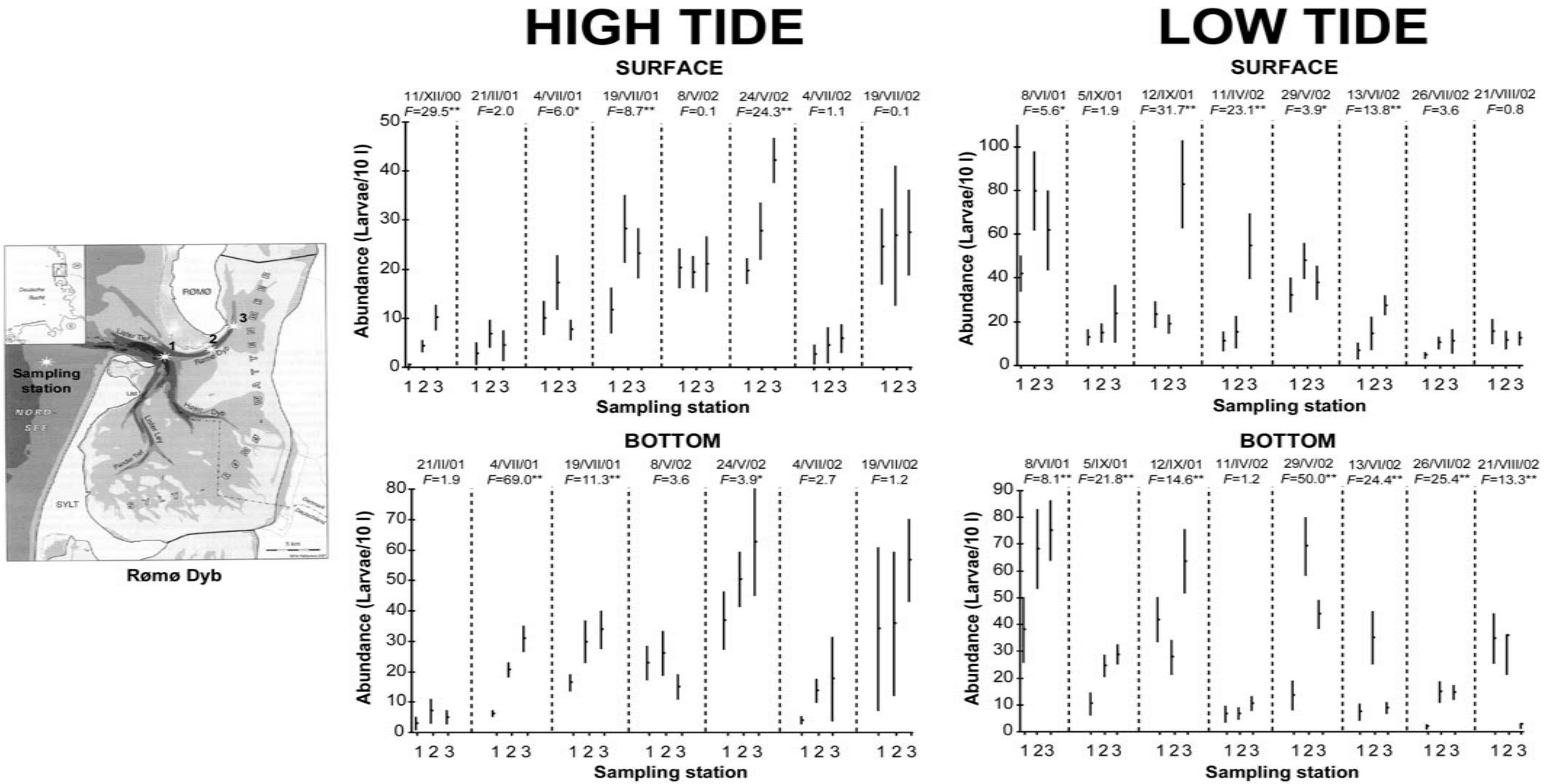


Fig. 3.5. Total abundances (Mean and S.E.) of polychaete larvae at three stations, from the tidal inlet to the inner channel along Rømø Dyb during high and low tide phases, and near the surface and 3 m above the bottom (below). Sets of samples were taken at irregular intervals between December 2000 and August 2002. *F*-values refer to ANOVA tests indicating significant differences in mean values between stations at each sampling date (**=p<0.01; *= p<0.05).

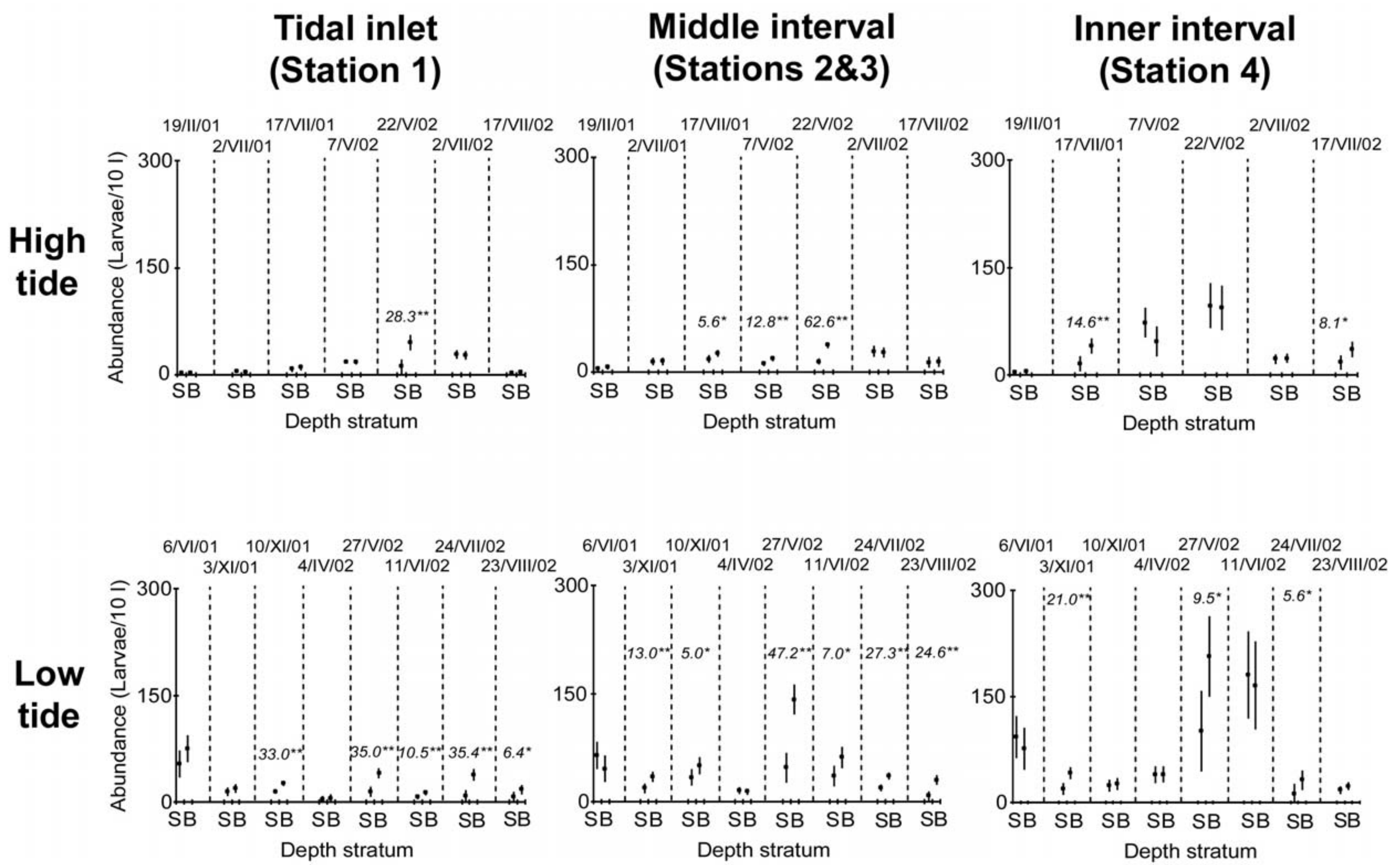


Fig. 3.6. Vertical distribution of polychaete larvae (Mean and S.E.) at stations along Lister Ley, during high and low tide, and at various dates in 2001 and 2002. S=Surface level; B=Bottom level. Numbers in italics refer to *F*-values of ANOVA tests indicating significant differences between surface and bottom levels (*=p<0.05; **=p<0.01, only significant cases are indicated).

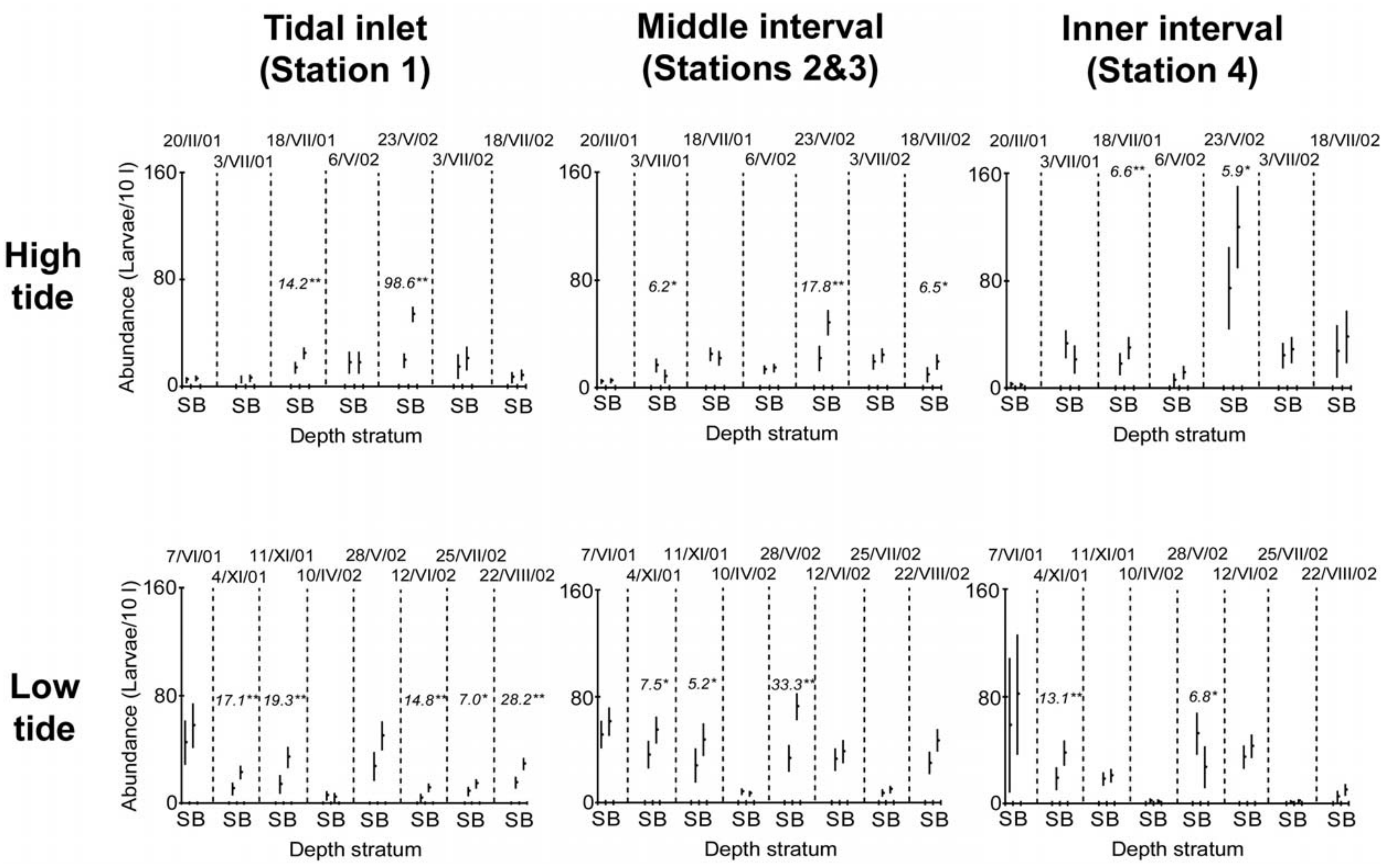


Fig. 3.7. Vertical distribution of polychaete larvae (Mean and S.E.) at stations along Høyer Dyb, during high and low tide, and at various dates in 2001 and 2002. S=Surface level; B=Bottom level. Numbers in italics refer to *F*-values of ANOVA tests indicating significant differences between surface and bottom levels (*=p<0.05; **=p<0.01, only significant cases are indicated).

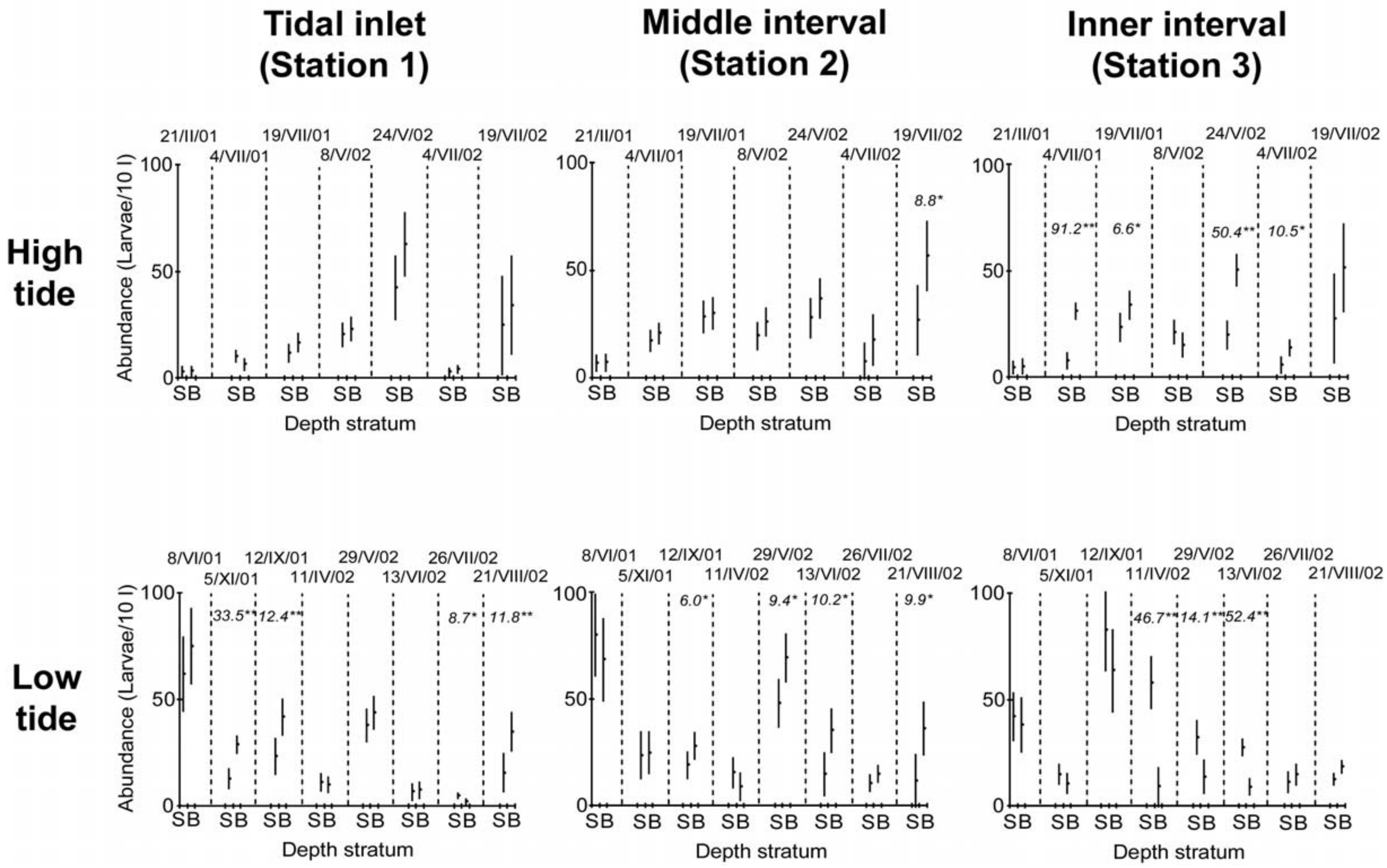


Fig. 3.8. Vertical distribution of polychaete larvae (Mean and S.E.) at stations along Rømø Dyb, during high and low tide conditions, and at various dates in 2001 and 2002. S=Surface level; B=Bottom level. Numbers in italics refer to *F*-values of ANOVA tests indicating significant differences between surface and bottom levels (*=p<0.05; **=p<0.01, only significant cases are indicated).

3.4. Spatial patterns at the 1-km scale

Along the main tidal channel in Königshafen, about 3 km in length, highest abundances were repeatedly found at the two innermost stations (Fig. 3.9). In 11 out of 14 cases, differences in abundance along the tidal creek were significant. The probability of finding highest abundances at the inner part was significantly higher than by chance (Sign test; $Z_{(12)}=2.6$, $p<0.01$).

Diversity and species richness showed no consistent pattern. Highest values had the same probability (50%) of occurring in the inner (Stations 1-2) or outer (Stations 3-4) parts of Königshafen (Sign tests; for H': $Z_{(15)}=0.3$, $p>0.05$, and for S: $Z_{(15)}=0.5$, $p>0.05$).

3.5. Spatial patterns at the 100-m scale.

To explore whether small-scale shore topography, such as a sandy hook 500 m in length, might have effects on polychaete larval abundances, comparisons between outside and inside this sheltering structure in Oddewatt were undertaken. Significant differences between larval abundances inside and outside this area were detected at 7 out of 12 sampling dates (Fig. 3.10). Both locations (I and O) did not differ significantly in the probability of having highest larval abundances ($Z_{(12)}=0.3$, $p>0.05$). However, in 6 of the 7 significant cases, abundances in the inner area were higher. Diversity and species richness showed no consistent spatial pattern between inside and outside (Sign test for H`: $Z_{(8)}=0.7$, $p>0.05$, and for S: $Z_{(8)}=-0.35$, $p>0.05$).

Abundances of *Pygospio elegans* were significantly higher at the inner area ($X^2_{(1)}=48.1$, $p<0.01$). Larvae of *Lanice conchilega*, on the other hand, were always absent from the inner area but usually present outside (Fig. 3.11). Distribution patterns of larvae of both species were in agreement with those of their benthic stages (Fig. 3.11). Benthic stages of *P. elegans* were abundant outside as well as inside, while those of *L. conchilega* were absent from the inner part of Oddewatt.

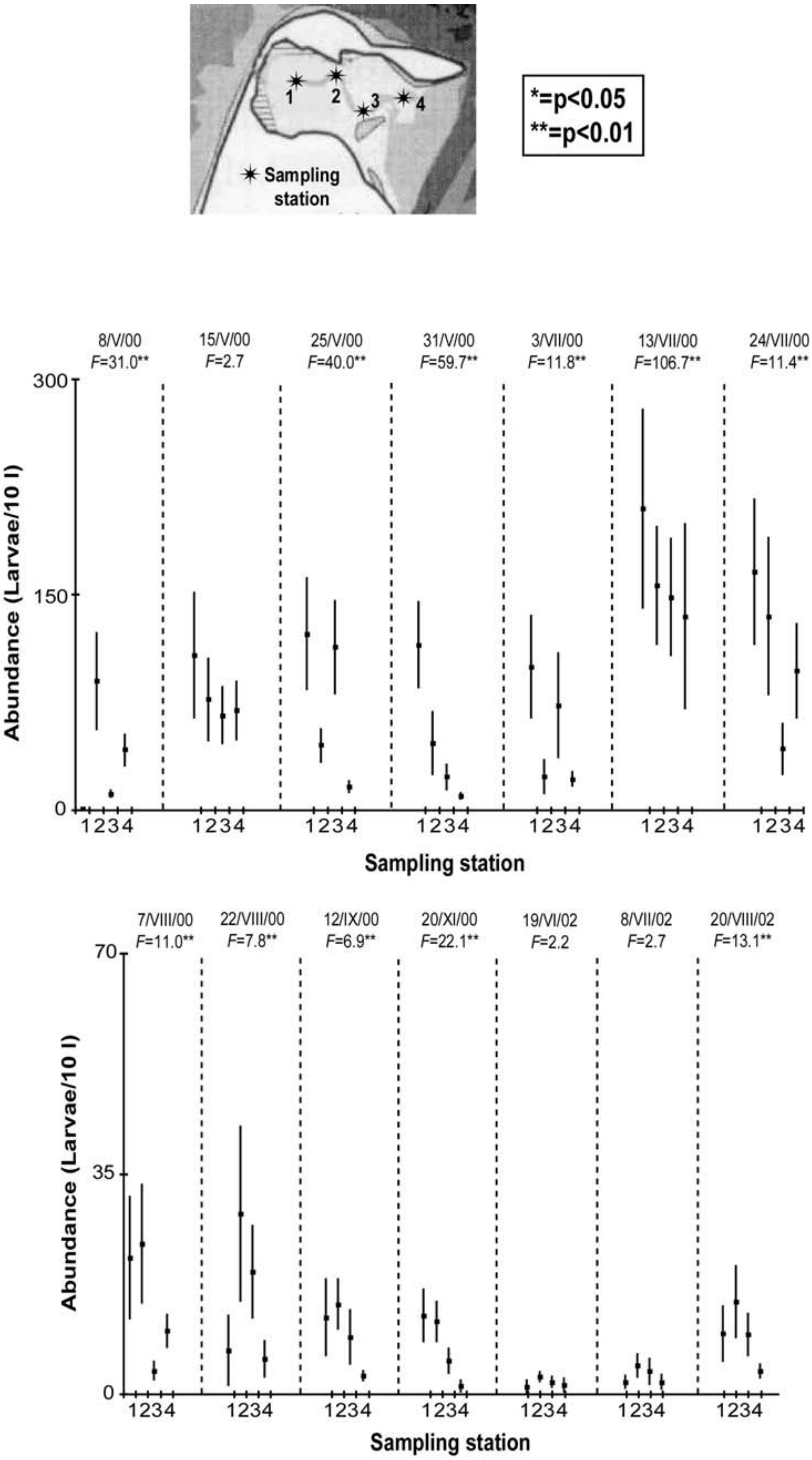


Fig. 3.9. Total abundances (Mean and S.E.) of polychaete larvae in Königshafen during high tides. Samples were taken from the surface with a 10-l bucket at intervals between May-November 2000 and at three dates in 2002. *F*-values refer to ANOVA tests indicating significant differences in mean values between stations at each sampling date.

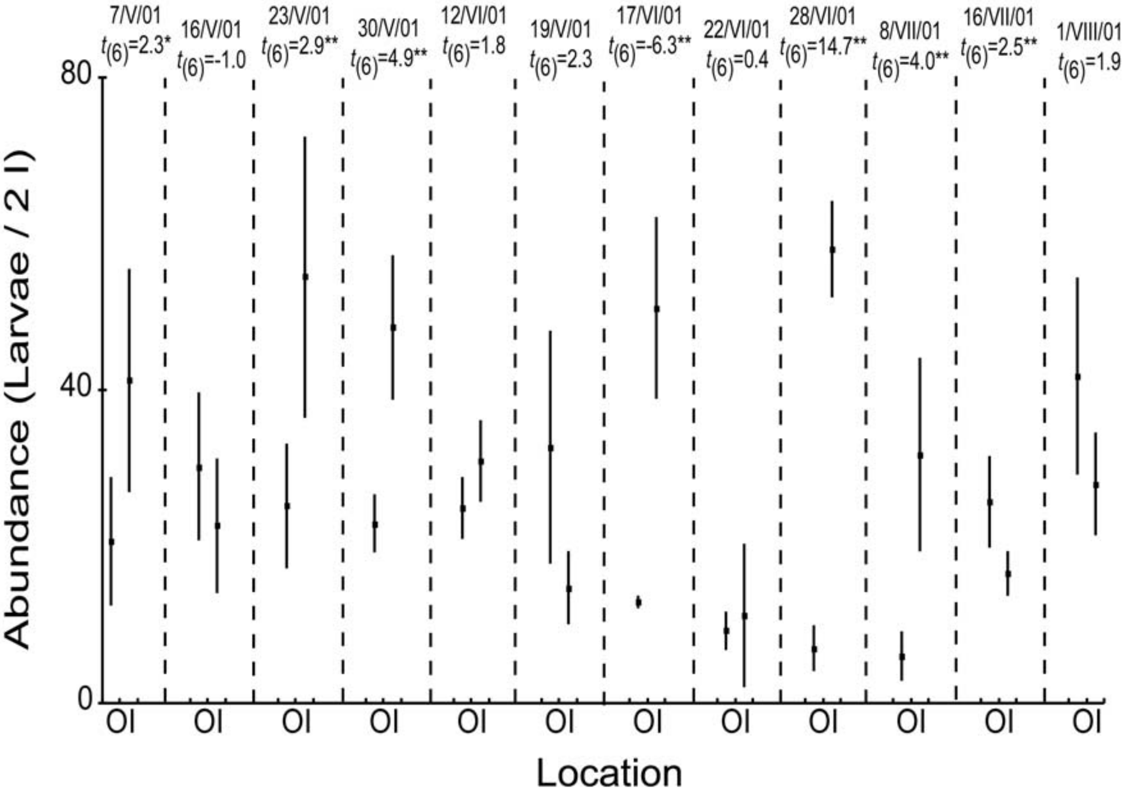
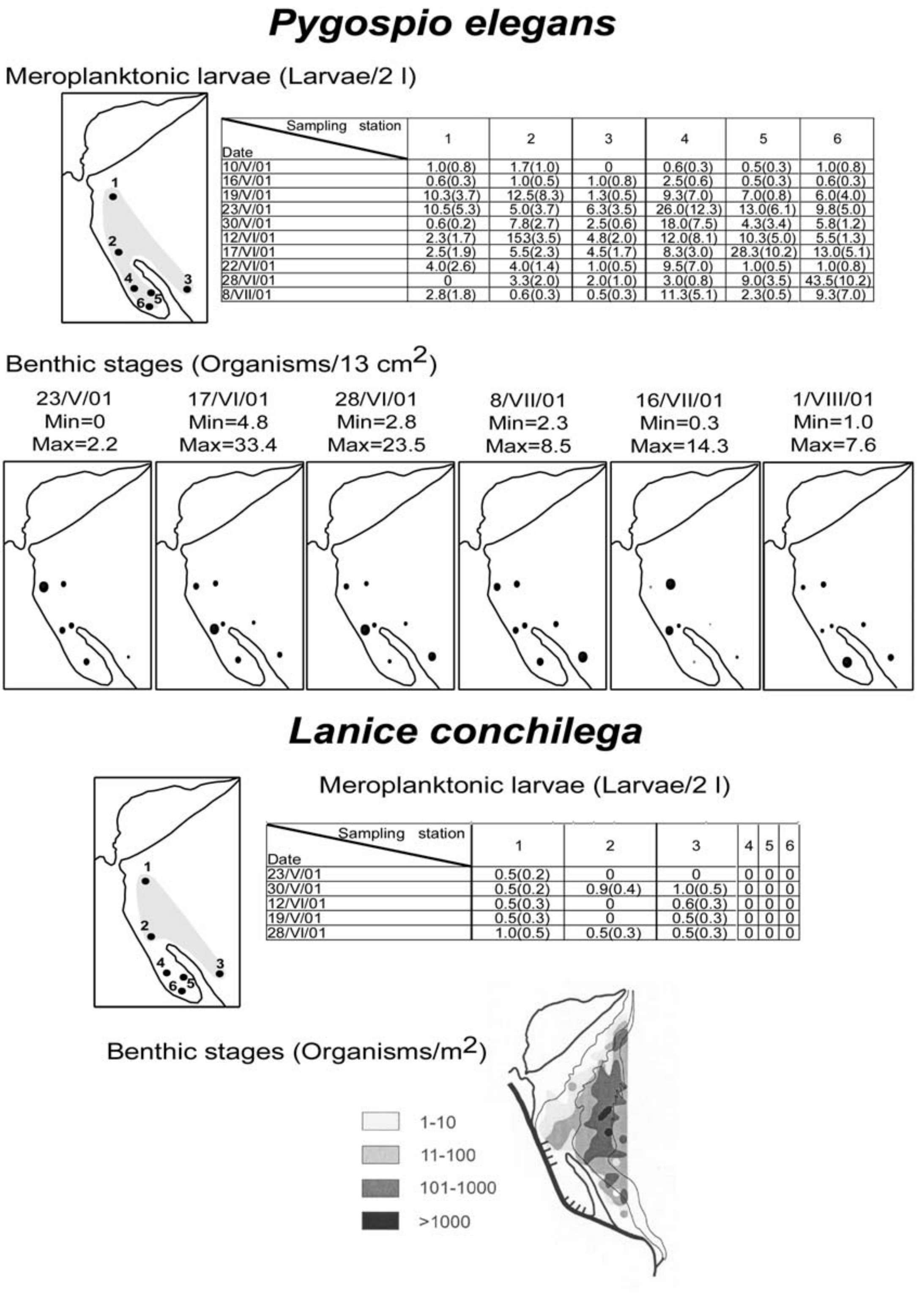


Fig. 3.10. Abundance of polychaete meroplanktonic larvae outside (O) and inside (I) a small embayment formed by a sandy hook. *=p<0.05; **=p<0.01.



Date \ Sampling station	1	2	3	4	5	6
10/V/01	1.0(0.8)	1.7(1.0)	0	0.6(0.3)	0.5(0.3)	1.0(0.8)
16/V/01	0.6(0.3)	1.0(0.5)	1.0(0.8)	2.5(0.6)	0.5(0.3)	0.6(0.3)
19/V/01	10.3(3.7)	12.5(8.3)	1.3(0.5)	9.3(7.0)	7.0(0.8)	6.0(4.0)
23/V/01	10.5(5.3)	5.0(3.7)	6.3(3.5)	26.0(12.3)	13.0(6.1)	9.8(5.0)
30/V/01	0.6(0.2)	7.8(2.7)	2.5(0.6)	18.0(7.5)	4.3(3.4)	5.8(1.2)
12/VI/01	2.3(1.7)	153(3.5)	4.8(2.0)	12.0(8.1)	10.3(5.0)	5.5(1.3)
17/VI/01	2.5(1.9)	5.5(2.3)	4.5(1.7)	8.3(3.0)	28.3(10.2)	13.0(5.1)
22/VI/01	4.0(2.6)	4.0(1.4)	1.0(0.5)	9.5(7.0)	1.0(0.5)	1.0(0.8)
28/VI/01	0	3.3(2.0)	2.0(1.0)	3.0(0.8)	9.0(3.5)	43.5(10.2)
8/VII/01	2.8(1.8)	0.6(0.3)	0.5(0.3)	11.3(5.1)	2.3(0.5)	9.3(7.0)

Date \ Sampling station	1	2	3	4	5	6
23/V/01	0.5(0.2)	0	0	0	0	0
30/V/01	0.5(0.2)	0.9(0.4)	1.0(0.5)	0	0	0
12/VI/01	0.5(0.3)	0	0.6(0.3)	0	0	0
19/V/01	0.5(0.3)	0	0.5(0.3)	0	0	0
28/VI/01	1.0(0.5)	0.5(0.3)	0.5(0.3)	0	0	0

Fig. 3.11. Distribution of meroplanktonic larvae during high tides (see stations 1-6 on map), and benthic stages during low tide, of *Pygospio elegans* (dot sizes indicate relative abundances) and *Lanice conchilega* (shading refers to abundance) in Oddewatt around a sandy hook in 2001. Values in tables are means (S.E.) for each sampling station.

4. Discussion

In the List tidal basin, polychaete larvae are not evenly or randomly distributed and tend to be most abundant at the inner and shallow parts, and close to the bottom. This overall pattern suggests that there is some process of larval concentration or retention in the innermost areas of the basin, and implies a disproportional supply of larvae to these areas.

Polychaete larvae are an important part of the Wadden Sea meroplankton (Hickel 1975, Martens 1980, Martens 1995, Jak 1999). Unfortunately, data on total abundances of polychaete larvae in offshore areas of the North Sea, for the same period covered in this study are not available. During this study, it was only possible to take samples in the open North Sea in front of Sylt at one date (July 10, 2001) obtaining a mean larval abundance of 5.5 larvae·10 l^{-1} (±3.7). This value is roughly half of the mean density present at the same time along the main tidal channels inside the tidal basin. This suggests that larval polychaetes are more abundant in the basin than further offshore.

The idea of larval retention inside the basin is supported by: 1) recurrently highest abundances on tidal flats (Oddewatt) and lowest abundances at the tidal inlet, showing an apparent sequence from shallow inner areas to deep outer areas during both tidal phases; 2) the presence of higher abundances in the channels at low tide near the bottom than at high tide at the surface; 3) the low incidence of high-density patches close to the inlet of the bight, suggesting that massive larval export or import are not the rule. These snapshots patterns were rather consistent, in spite of the fact that patterns vary from one day to another (see also Armonies 1994). Mathivat-Lallier and Cazaux (1990) also found higher densities of polychaete larvae close to the bottom than at the surface of the Bay of Arcachon.

Highest abundances and biomasses of barnacle and polychaete larvae at inner parts of the Dutch Wadden Sea were also reported by De Wolff (1974) and Fransz (1981), respectively. Significantly higher abundances of zooplankton at the inner parts of four embayments of different size and degree of exposure were interpreted as larval retention by Archambault *et al.* (1998) at the Lower St. Lawrence Estuary (Canada).

The amount of evidence indicating that the coastal retention of zooplankton may be frequent has been increasing (at scales of 1 to 10 km and even for species with long larval durations) (see Swearer *et al.* 2002; Warner and Cowen *et al.* 2002). Gagnon and Lacroix (1983) observed that the exchange of zooplankton between the inner and outer sections of the St. Lawrence estuary is not proportional to the exchange of water between both sections, and Mathivat-Lallier and Cazaux (1990) found that large water fluxes produced by tides at the Bay of Arcachon are not always associated with polychaete larval transport. A similar phenomenon was suggested to occur in the Wadden Sea since the 70's (de Wolff 1974). Modern hydrographic models also indicate that, in areas with non-unidirectional currents (e.g. the List tidal basin), a significant proportion of larvae might not be transported away from their natal place (Swearer *et al.* 2002). Basically all physical factors resulting in the departure from unidirectional and depth-uniform water flows provide the opportunity for larval retention (Sponaugle *et al.* 2002) (e.g. tidal currents driven by semi-diurnal cycles over the irregular bottom of the List tidal basin).

Sponaugle *et al.* (2002) recognized two types of retention: a) physical, where larvae remain passive and the whole process is driven by physical processes, and b) biophysical, involving active behavioral input from larvae. Results disclosed here do not allow to know which kind is more frequent inside the bight, but at least some physical processes enhancing the retention of suspended particles (and probably larvae) can be recognized:

a) Strong (>8 m·s^{-1}) westerly onshore winds that raise the high-tide level (Backhaus *et al.* 1998) and partially prevent the ebbing flow.

b) Increased residence time of water by the combined effect of (a) with water stagnation caused by topographically influenced circulation at scales of tens of km (Sponaugle *et al.* 2002). Tidal currents and residual currents inside the List tidal basin are strongly modified by topography (Backhaus *et al.* 1998) and the average residence time of water is 25 tidal cycles (pers. com. J. van Beusekom, Alfred Wegener Institute).

c) Asymmetrical flood-tide waves. Tidal waves become asymmetrical in the inner parts of the Wadden Sea, causing a net transport inwards (Oost and de Boer 1994). Similar landward accumulation of larvae and other particles was reported at Californian mudflats by Levin (1986).

d) The permanent presence of eddies inside the List tidal basin powered by residual tidal currents (Fig. 3.12). These delay water in its way out of the basin during ebb periods. Residual tidal currents are locally ruled by topography (Backhaus *et al.* 1998), and according to Thorrold *et al.* (2002) the mixture of irregular bottom topography and eddies is decisive for enhancing retention.

Factors enhancing biophysical retention could be chemical cues (Gallagher *et al.* 1983; Cuomo 1984; Barke 1986; Qian 1999), active vertical movements (Mileikovsky 1973; Cameron 1986; Thiébaut *et al.* 1998), coupling of vertical and horizontal movements with mesoscale circulation features and wind induction (Cowen *et al.* 2000), and active larval swimming behavior (Mileikovsky 1968, Hadfield 1986, Mathivat-Lallier and Cazaux 1990, Young 1990, Wiafe and Frid 1996, Bhaud 1998, Qian 1999, Cowen *et al.* 2000).

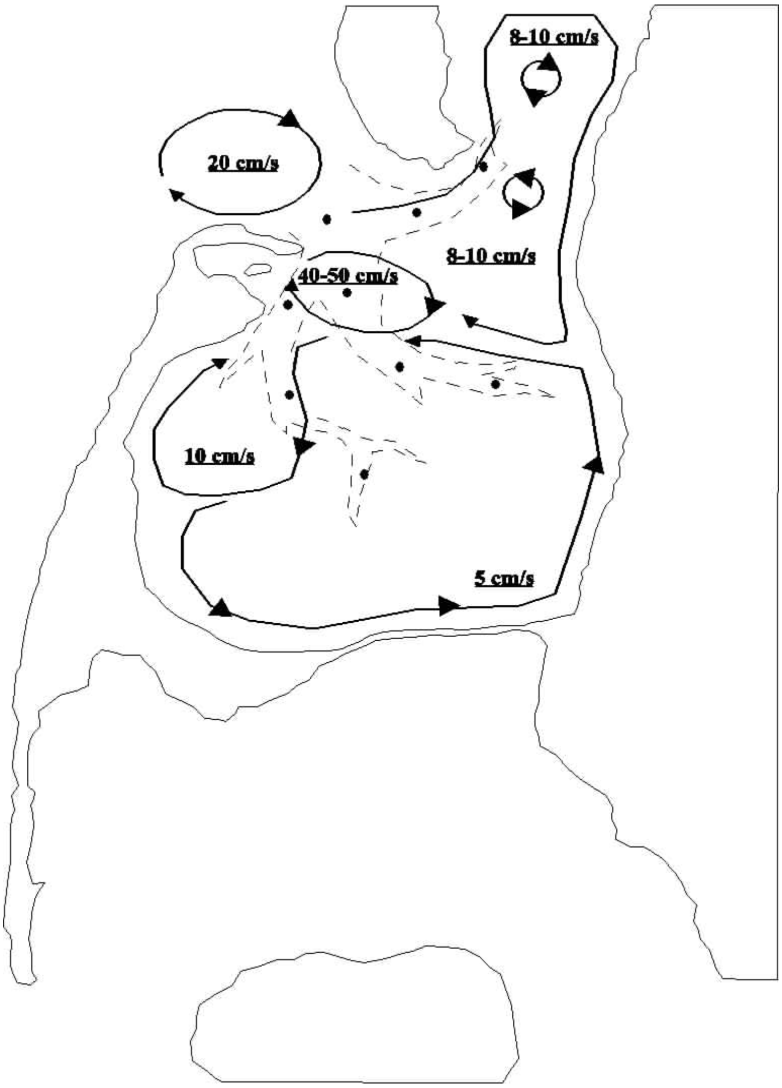


Fig. 3.12. Residual currents in the List tidal basin (modified from Backhaus *et al.* 1998).

The most common consequence of retention is auto-recruitment (Swearer *et al.* 2002; Kingsford *et al.* 2002; Thorrold *et al.* 2002), which may be understood as levels of retention that substantially enhance the abundance of local populations (Sponaugle *et al.* 2002). This implies that retention should be measured and not only detected, and this still needs to be done in the study area. The only accurate and robust choice to do it is mark-recapture techniques using natural or artificial markers (see Thorrold *et al.* 2002). In spite that significant differences in abundance between the three gullies were not persistent, they occurred and abundances at Lister Ley and Høyer Dyb were higher in both tidal phases. Therefore, it could be speculated that retention at these gullies is stronger than at Rømø Dyb.

Highest abundances of polychaete larvae occurred repeatedly at the inner parts of the main channels of the List tidal basin, as well as along the inner part of the main channel in Königshafen. These patterns correspond well with those of particulate organic matter described by Austen (1994) and Austen *et al.* (1998). De Wolff (1974) found that abundances of barnacle larvae and the amount of suspended matter were correlated inside the Dutch Wadden Sea and suggested that physical processes should rule their distributions. This reflects the concept of larval dispersal as a passive phenomenon, entirely dependent on current patterns, and larvae acting as neutrally buoyant bodies (see Banse 1986, Possingham and Roughgarden 1990, and Ellien *et al.* 2000). On the other hand, current knowledge on marine invertebrate larvae rejects the assumption of passive behavior and transport (Swearer *et al.* 2002; Thorrold *et al.* 2002). The problem resides in differentiating between behavior and fine-scale hydrographic phenomena (Thorrold *et al.* 2002). The correspondence between larval concentration areas and particulate organic matter could also reflect the presence of favorable conditions for polychaete larvae.

Results show that in spite of tidal mixing, highest larval densities were frequently close to the bottom than at the surface of the channels. This could reflect active vertical movements, but another sampling design with frequent sampling during a tidal cycle at a fixed point would allow to obtain more reliable results. Position control by vertical migration potentially provides a means to affect transport to specific locations or promote retention in particular areas (see Hill 1991). Active vertical movements are usually thought to be undertaken only in stagnant waters. However, Kopacz (1994) demonstrated that gelatinous zooplankton performs vertical movements in the tidal currents of the Lister Ley.

In Oddewatt, larvae of *Pygospio* and *Lanice* showed different distribution areas that resemble those of their benthic stages, suggesting that coastal morphology and/or benthic adult occurrence could enhance species-specific distribution patterns. Larvae are usually thought not to be able to influence their distribution patterns actively (see Banse 1986; Jackson 1986; Butman 1987; and Armonies 1996). Nevertheless, resemblances between distributions of larval and parental forms were suggested since the 60's (see Mileikovsky 1968). Posteriorly, behavioral traits (Hadfield 1986), chemical signs (see Wilson 1981, Gallagher *et al.* 1983, Cuomo 1984, and Woodin 1985), and active vertical movements (Mileikovsky 1973, Wiafe and Frid 1996, Bhaud 1998, Thiébaut *et al.* 1998, Qian 1999) were proposed as mechanisms enhancing controlled horizontal distributions. The discovery of navigation and orientation capabilities of polychaete larvae (see Kingsford *et al.* 2002), mixed with the interplay of larval behavior and physically induced retention, can lead to non-random larval distributions reflected by species-specific distribution patterns (Sponaugle *et al.* 2002).

5. References

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6. Appendices

Appendix 3.I. Wind flow patterns and superficial tidal current velocities (Mean±S.E.) inside the List tidal basin (Wind data provided from the German Meteorological Service). Tidal velocities were estimated using the hydrographic model of Behrens *et al.* (1997).

Date	Wind conditions		Tidal cycle	Tidal channel	Current speed ($m \cdot s^{-1}$)
	Direction	Velocity ($m \cdot s^{-1}$)			Mean±S.E.
Dec 6, 2000	S	7.5	High tide	Lister Ley	0.3±0.02
Dec 7, 2000	SE	8	High tide	Høyer Dyb	0.6±0.09
Dec 11, 2000	SE	11.5	High tide	Rømø Dyb	0.3±0.06
Feb 19, 2001	W	8.5	High tide	Lister Ley	0.4±0.08
Feb 20, 2001	N	9	High tide	Høyer Dyb	0.35±0.06
Feb 21, 2001	N	11	High tide	Rømø Dyb	0.3±0.07
June 6, 2001	SW	5	Low tide	Lister Ley	0.8±0.06
June 7, 2001	SW	15	Low tide	Høyer Dyb	0.8±0.04
June 8, 2001	W	8	Low tide	Rømø Dyb	0.7±0.05
July 2, 2001	N	8	High tide	Lister Ley	0.6±0.1
July 3, 2001	N	3	High tide	Høyer Dyb	0.7±0.07
July 4, 2001	E	7.5	High tide	Rømø Dyb	0.6±0.05
July 17, 2001	N	5.5	High tide	Lister Ley	0.4±0.1
July 18, 2001	SE	9.5	High tide	Høyer Dyb	0.6±0.09
July 19, 2001	S	5	High tide	Rømø Dyb	0.4±0.05
Sep 3, 2001	W	5	Low tide	Lister Ley	0.7±0.1
Sep 4, 2001	W	2.5	Low tide	Høyer Dyb	0.5±0.02
Sep 5, 2001	N	5.5	Low tide	Rømø Ley	0.3±0.05
Sep 10, 2001	N	8.5	Low tide	Lister Dyb	0.8±0.1
Sep 11, 2001	N	4.5	Low tide	Høyer Dyb	0.6±0.07
Sep 12, 2001	W	3.5	Low tide	Rømø Dyb	0.5±0.02
Apr 4, 2002	E	9.0	Low tide	Lister Ley	0.6±0.07
Apr 10, 2002	N	6.5	Low tide	Høyer Dyb	0.1±0.04
Apr 11, 2002	E	6.0	Low tide	Rømø Dyb	0.6±0.05
May 6, 2002	NE	5.0	High tide	Høyer Dyb	0.6±0.05
May 7, 2002	E	5.5	High tide	Lister Ley	0.6±0.1
May 8, 2002	E	4.0	High tide	Rømø Dyb	0.5±0.05
May 22, 2002	SE	7.5	High tide	Lister Ley	0.7±0.03
May 23, 2002	SW	5.0	High tide	Høyer Dyb	0.4±0.05
May 24, 2002	SW	8.0	High tide	Rømø Dyb	0.1±0.03
May 27, 2002	S	6.5	Low tide	Lister Ley	0.6±0.05
May 28, 2002	E	2.0	Low tide	Høyer Dyb	0.5±0.05
May 29, 2002	W	7.0	Low tide	Rømø Dyb	0.7±0.05
June 11, 2002	W	8.0	Low tide	Lister Ley	0.4±0.08
June 12, 2002	SW	9.0	Low tide	Høyer Dyb	0.8±0.04
June 13, 2002	NW	6.5	Low tide	Rømø Dyb	0.1±0.03
July 2, 2002	SW	10.0	High tide	Lister Ley	0.4±0.07

Appendix 3.I (Continued). Wind flow patterns and superficial tidal current velocities (Mean±S.E.) inside the List tidal basin (Wind data provided from the German Meteorological Service). Tidal velocities were estimated using the hydrographic model of Behrens *et al.* (1997).

Date	Wind conditions		Tidal cycle	Tidal channel	Current speed ($m \cdot s^{-1}$)
	Direction	Velocity ($m \cdot s^{-1}$)			Mean±S.E.
July 3, 2002	S	9.0	High tide	Høyer Dyb	0.6±0.04
July 4, 2002	N	8.0	High tide	Rømø Dyb	0.4±0.06
July 17, 2002	N	9.5	High tide	Lister Ley	0.6±0.1
July 18, 2002	N	10.0	High tide	Høyer Dyb	0.3±0.06
July 19, 2002	N	11.0	High tide	Rømø Dyb	0.3±0.07
July 24, 2002	NW	12.0	Low tide	Lister Ley	0.6±0.02
July 25, 2002	NW	11.0	Low tide	Høyer Dyb	0.6±0.02
July 26, 2002	W	7.5	Low tide	Rømø Dyb	0.7±0.05
Aug 21, 2002	E	5.0	Low tide	Rømø Dyb	0.6±0.05
Aug 22, 2002	SE	3.5	Low tide	Lister Ley	0.7±0.02
Aug 23, 2002	N	5.0	Low tide	Høyer Dyb	0.5±0.03

Appendix 3.II. Wind flow patterns and superficial tidal current velocities (Mean±S.E.) during maximal diurnal high tides in Königshafen.

	1 h before the maximum diurnal high tide		During the maximum diurnal high tide		Current speed ($m \cdot s^{-1}$)
Sampling date	Velocity ($m \cdot s^{-1}$)	Direction	Velocity ($m \cdot s^{-1}$)	Mean±S.E	Mean±S.E.
April 20, 2000	8.3	E	8.7	E	0.07±0.01
May 8, 2000	7.0	E	6.0	E	0.07±0.01
May 15, 2000	4.4	S	4.4	S	0.04±0.008
May 25, 2000	8.7	E	7.1	E	0.07±0.01
July 3, 2000	3.0	E	2.7	E	0.07±0.01
July 13, 2000	7.5	W	7.5	W	0.2±0.02
July 24, 2000	4.0	N	4.4	N	0.02±0.001
Aug 7, 2000	9.9	NW	9.6	NW	0.08±0.01
Aug 22, 2000	5.8	NW	7.0	NW	0.08±0.01
Sep 12, 2000	7.2	SE	7.5	SE	0.2±0.05
Nov 20, 2000	8.7	SE	9.5	SE	0.2±0.05
May 15, 2002	9.0	SW	8.4	SW	0.1±0.02
June 19, 2002	7.0	SW	7.0	SW	0.1±0.02
July 8, 2002	9.0	S	8.3	S	0.1±0.02
Aug 20, 2002	3.5	SE	4.0	SE	0.07±0.01

Chapter 4. Temporal dynamics of meroplanktonic polychaete larvae in a tidal basin of the North Sea: Are year-to-year fluctuations related to environmental variability?

Abstract

The temporal variability between the years 1996-2001 in meroplanktonic polychaete larvae of the List tidal basin (northern Wadden Sea) is described. Environmental variables significantly affecting abundance fluctuations and a description of the seasonality in abundances and environmental variables are presented as well. Significant fluctuations in larval abundances and diversity are detected, with outstanding changes occurring after 1998. Larvae of *Pygospio elegans*, *Spio martinensis, Polydora cornuta*, and *Lanice conchilega* were the most abundant. The inter-annual variability in abundance was high. Environmental variability was characterized by significant fluctuations in salinity and PO_4, both apparently decreasing over the years; by significant fluctuations in NO_2 and Si, both apparently increasing over the years; by significant fluctuations in phytoplankton biomass and pH-values without an apparent trend; by a reduced incidence of N- and NE-winds and increased incidence of S- and SE-winds; and by a restored influence from the Elbe River plume after the winter 1995/1996. Cross-correlations and multiple linear regressions detected significant lag effects (<1-12 months) of water temperature, NO_2, pH-values, PO_4, and total silicate on larval abundances. These may be related to effects on endocrinal processes and gonadal maturation. Canonical Correspondence Analysis detected the significant instantaneous effect on larval abundances by phytoplankton biomass, NO_2, pH-values, PO_4, salinity, and water temperature fluctuations. These variables might be related to the triggering of spawning, larval feeding, and feeding of adults to support ongoing spawning. The seasonality in abundance and diversity was rather regular, with maximal values during spring and summer, positively correlated with increments in phytoplankton biomass, pH-values, and water temperatures.

1. Introduction

The study of abundance fluctuations is one of the most important tasks of ecology (Hanski 1997), and the analysis of relationships between abundance fluctuations and the environment has direct application in ecosystems modeling. Marine invertebrate populations in shallow coastal waters undergo strong abundance fluctuations in their benthic stages (see Niermann 1996; Strasser and Pieloth, 2001; Strasser *et al.* 2001 a and b).

The effect of climatic factors on the abundance fluctuations of benthic stages in the List tidal basin has been demonstrated for several species (e.g. the polychaete *Lanice conchilega*, see Strasser and Pieloth 2001; several bivalves, see Reise 1985 and Strasser *et al.* 2001b; and *Arenicola marina*, see Reise *et al.* 2001), while on pelagic stages have not been studied up to now.

The first studies on temporal dynamics in zooplankton of the Wadden Sea were conducted by Hickel (1975) and Martens (1980), describing short-term (seasonal) fluctuations of copepod and mesozooplankton biomass. Martens (1995) found that water temperatures, rainfall, and nitrogen affected the seasonality of mesozooplankton inside the List tidal basin. Jak (1999) concluded that the between-year composition and biomass of zooplankton in the Wadden Sea fluctuate irregularly in response to shifts in spring phytoplankton blooms, driven by unknown stochastic factors. It is known that severe winters, characterized by increased salinities and low nitrite concentrations are followed by exceptional diatoms blooms (Martens 2001), but it is unknown if this could also affect meroplanktonic larvae. Colebrook (1985) and Greve *et al.* (2001) analyzed the relationships between zooplankton and environmental variables in the North Sea, suggesting that temperature might be a key factor.

Zooplankton studies in the List tidal basin never have covered a time span longer than one year, and the effort focused on holoplanktonic copepods. However, meroplankton is a dominant component, being mainly represented by polychaete larvae (Hickel 1975; Martens 1980; Jak 1999). Polychaete larvae are an important food item for fish, and their temporal fluctuations may affect local food chains and other ecological processes (Martens 1995). Locally, there are no quantitative data on polychaete larvae. In 1996 a regular zooplankton-sampling program started, and the polychaete component of this ongoing data series constitutes the basis of this study.

Polychaetes are thought to spawn under species-specific “optimal” conditions (Bhaud 1972; Clark and Olive 1973; Todd and Doyle 1981; Fisher 1999; Andries 2001). Nevertheless, relations between the time of spawning and environmental factors have been mainly studied in species lacking meroplanktonic larvae (see Schiedges 1979, Franke 1999), mainly focusing on physiological experiments (see Clark and Olive 1973; Hauenschild 1974; Olive and Garwood 1979; Franke and Pfannnestiel 1984; Bentley and Pacey 1992). Larval abundances of polychaetes are often positively correlated with phytoplankton biomass considering some time lag (see Zajac 1991 a and b; Hansen 1999; Calbet *et al*. 2001). Geographical variations in the time of spawning are common (see Bentley and Pacey 1992).

The scope of this study is to analyze abundance fluctuations of meroplanktonic polychaete larvae inside the List tidal basin between 1996 and 2001, and to find environmental variables significantly affecting abundances, as well as to describe the seasonality in larval abundances and environmental variables.

Based on the references mentioned above, abundances of meroplanktonic polychaete larvae are expected to be affected by fluctuations in water temperature, salinity, and nitrogen compounds. These three factors potentially affect the production of phytoplankton, which is food for many adult and larval polychaetes, and also triggers the secondary productivity, so it could be expected that phytoplankton also affects the larval abundances of carnivore larvae. The study area is characterized by marked seasonal differences in the environment. Therefore, considerable seasonality in larval production is expected, because species should take advantage of “optimal conditions” for reproduction.

2. Methodology

2.1. Study site and sampling

A fixed sampling station was located at List harbor, inside the List tidal basin, on the eastern shore of the northern tip of the island of Sylt. The mean depth at this station is 10 m. It is influenced by a permanent eddy located in front of Königshafen Bay, powered by tidal currents (0.5-1 $m \cdot s^{-1}$) (Behrens *et al.* 1997). The water column at this station is well mixed (Martens 1980, 1995).

Between January 1996 and December 2001, one surface water sample (10 l) was taken during peak diurnal flood, daily (spring to autumn) or weekly (winter), as part of a regular zooplankton-monitoring program (contact person: Dr. M. Strasser, Alfred-Wegener-Institute). Each sample was filtered through an 80 μm mesh and fixed in filtered seawater with 10% formol. Abundances of meroplanktonic polychaete larvae were obtained from these samples (1463 samples in total). For the same period, measurements of physical and chemical water properties at the sampling site were obtained from an environmental and phytoplankton monitoring program (contact person: Dr. J. van Beusekom, Alfred-Wegener-Institute). The German Meteorological

Service (DWD) provided mean wind speeds and directions for each sampling date, measured 2 km south of List harbor.

The environmental data set consists of measurements of wind speed ($W_{m/s}$, in $m \cdot s^{-1}$) and direction (NE, E, SE, S, SW, W, NW, and N); water temperature (°C); phytoplankton biomass (Chl*a* in $mg \cdot l^{-1}$); salinity (*Sal* in PSU); pH-value (pH); concentration of dissolved nitrite (NO_2), phosphate (PO_4), and total silicate (Si), all in $\mu mol \cdot l^{-1}$; and records of full moon (FM) and new moon (NM). This set of environmental variables was selected, because only these have been measured without interruption along the six-year span analyzed here.

2.2. Statistical analyses

Relationships between total larval abundance, abundances of 14 taxa comprising 90% of the total larval abundance, and the environmental data were calculated in two ways.

1) Combining cross-correlation and multiple linear regressions (Legendre and Legendre 1995): This technique is suitable when the interval between consecutive sampling dates is short (1 day during spring-autumn and 8 days during winter in the present study), and it is assumed that abundance responds to events that occurred at a previous time (lag). Cross-correlation is used to identify time lags that maximize the correlation between abundance and environmental variables. Of course, it is also possible that the correlation gets maximized with a time lag of 0, if so, an instantaneous effect is considered. Once the optimal lag for each variable was found, multiple regression is applied, with each environmental variable lagged by the appropriate number of sampling intervals. These procedures were applied to raw data and progressive changes in the environmental characteristics (trends) were retained, because it was considered that they had an effect on larval abundances. Data series were equispaced, using averages for intervals of 8 sampling dates along the whole six-year span, independently of the season. Wind directions and moon phases (qualitative variables) were not included in these analyses.
2) Canonical Correspondence Analysis (CCA): (Legendre and Legendre 1995; Lepš and Šmilauer 2003). This multivariate technique allows the definition of models describing the instantaneous effect of environmental variables on larval abundances. Significance is evaluated through Monte Carlo permutation tests. Here, qualitative variables (wind directions and moon phases) were included as

nominal dummy variables. Analyses were performed using CANOCO for Windows 4.5. Data series were not equispaced and temporal autocorrelation was removed applying permutations designed for time-series designs, available in the software. Only the first pair of canonical axes was taken into account. Statistically significant pair-wise dependences of abundances on environmental variables were assessed using *t*-value biplots with Van Dobben circles (Ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003) (see Fig. 4.1 for an example). These specialized ordination diagrams are formed by *t*-values of multiple regression coefficients, obtained from regressions between abundances and the set of environmental variables, taking into account the model defined by the CCA-analysis. Arrows represent species. Two circles enclose areas where positive and negative effects of a particular environmental variable are significant (one circle for the positive effect and another for the negative effect). Species of which arrows end inside these circles depend significantly on that environmental variable. Results derived from this method should be interpreted in terms of regression. There are as many *t*-value biplots with Van Dobben circles as environmental variables.

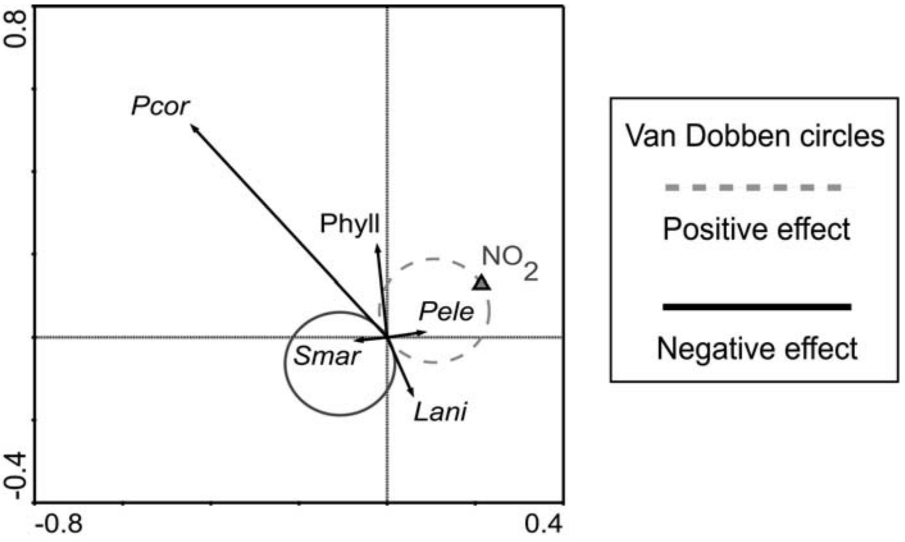


Fig. 4.1. Example of a *t*-value biplot with Van Dobben circles. Arrows represent five taxa: *Polydora cornuta* (*Pcor*), *Spio martinensis* (*Smar*), *Lanice conchilega* (*Lani*), *Pygospio elegans* (*Pele*), and Phyllodocidae (Phyll). Circles represent areas where the effect of NO_2 is significant. Since only arrows of *Pele* and *Smar* end inside the circles, the increase of NO_2 is only significantly positive for *Pele,* while decreases are only significantly negative for *Smar.*

2.3. Assumptions behind the analyses

Abundance fluctuations could reflect the effect of environmental changes on the performance of larvae inside the bight and/or on egg production, temporal changes in larval import/export from/to the North Sea, as well as dislocations inside the bight. No data on egg production are available, and it is unknown if the water exchange between the bight and the open sea fluctuated significantly between 1996-2001. Results shown in Chapter 3 indicate that larval retention inside the bight is a dominant process and that larval inputs from the North Sea may be quantitatively negligible. Therefore, it will be assumed here that larval retention leads to local auto-recruitment and that larval sources are mainly located inside the bight. It is important to make this *a priori* assumption in this chapter; because it is believed that temporal fluctuations in larval abundances and diversity are responses to processes occurring inside the basin, and not in the adjacent North Sea.

3. Results

3.1. Inter-annual variability of larval abundances and environmental variables

Within the study period, the mean abundance of polychaete larvae was rather similar between years, except for the year 2000, when the mean abundance (42 larvae·10 l^{-1} ±6.0; number of samples=250) was more than twice as high as the average of the other five years (17 larvae·10 l^{-1} ±1.2; number of samples=1213) (Fig. 4.2a). This exceptional abundance was caused by coinciding peaks of several taxa (see below). Because of the exceptional year 2000, inter-annual fluctuations over the 6-year period are significant (after Tukey-HSD Post hoc-Tests). Annual diversity also fluctuated significantly but was not correlated with mean abundance (r=0.8, p>0.05), The high r-value suggests that the lack of significance was caused by the shortness of the time series. However, the year 2000 with the highest abundance also showed the highest diversity (Fig. 4.2b). Of the 14 most abundant taxa, most peaked in annual abundance either in 1998 or in 2000, and these were the years with the highest diversity. Neither total abundance, nor diversity, showed significant linear trends over the study period (total abundance: β=0.4, $F_{(1,4)}$=1.0, p>0.05; diversity: β=0.4, $F_{(1,4)}$=0.6, p>0.05).

The 14 most abundant taxa comprised a grand total of 31,462 larvae. Their monthly sums over the six-year span, abbreviations of their names used in the text, and the percentage of the grand total of each taxa are shown in Fig. 4.3.

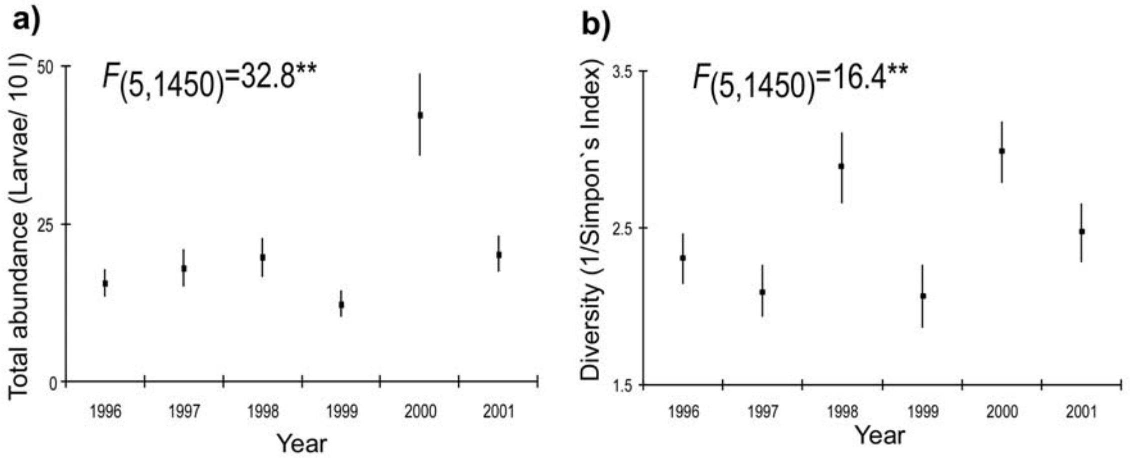


Fig. 4.2. Annual means and 95% confidence limits of (a) total abundance and (b) species diversity (1/Simpson diversity index). *F*-values refer to tests for significant temporal fluctuations with ANOVA, $^{**}=p<0.01$.

Averaged over 1996 to 2001, the most abundant taxa were *Pygospio elegans*, followed by other spionids (*Spio martinensis* and *Polydora cornuta*), and the terebellid *Lanice conchilega* (Table 4.I). *Magelona mirabilis*, *L. conchilega*, *Laonice cirrata*, *Nereis* Types I and II, *Nephtys* spp. and *Chone* spp. showed the highest inter-annual variability in abundance (Relative variation coefficients between 25-52%), while the rest of taxa showed coefficients between 4-18%. Most of the taxa (Phyllodocidae, *Polydora ciliata, Scoloplos armiger*, *Chone* spp., *Scolelepis* spp., and *Nephtys* spp.) had abundance peaks during 1998.

Yearly mean abundances of *S. armiger, Chone* spp., *L. conchilega, P. cornuta, L. cirrata*, and nereidids showed no significant overall temporal fluctuations (Fig. 4.4). In all cases, except that of *P. cornuta*, high intra-annual variability may have concealed the detection of significant temporal fluctuations.

Some of these taxa showed some suggestive temporal patterns: abundances of *S. armiger* increased between 1996-1998, with posterior decrements; those of *L. conchilega* increased between 1996-1999, decreasing after; and those of *L. cirrata* were characterized by two increasing cycles, one between 1996-1998, and another between 1999-2001.

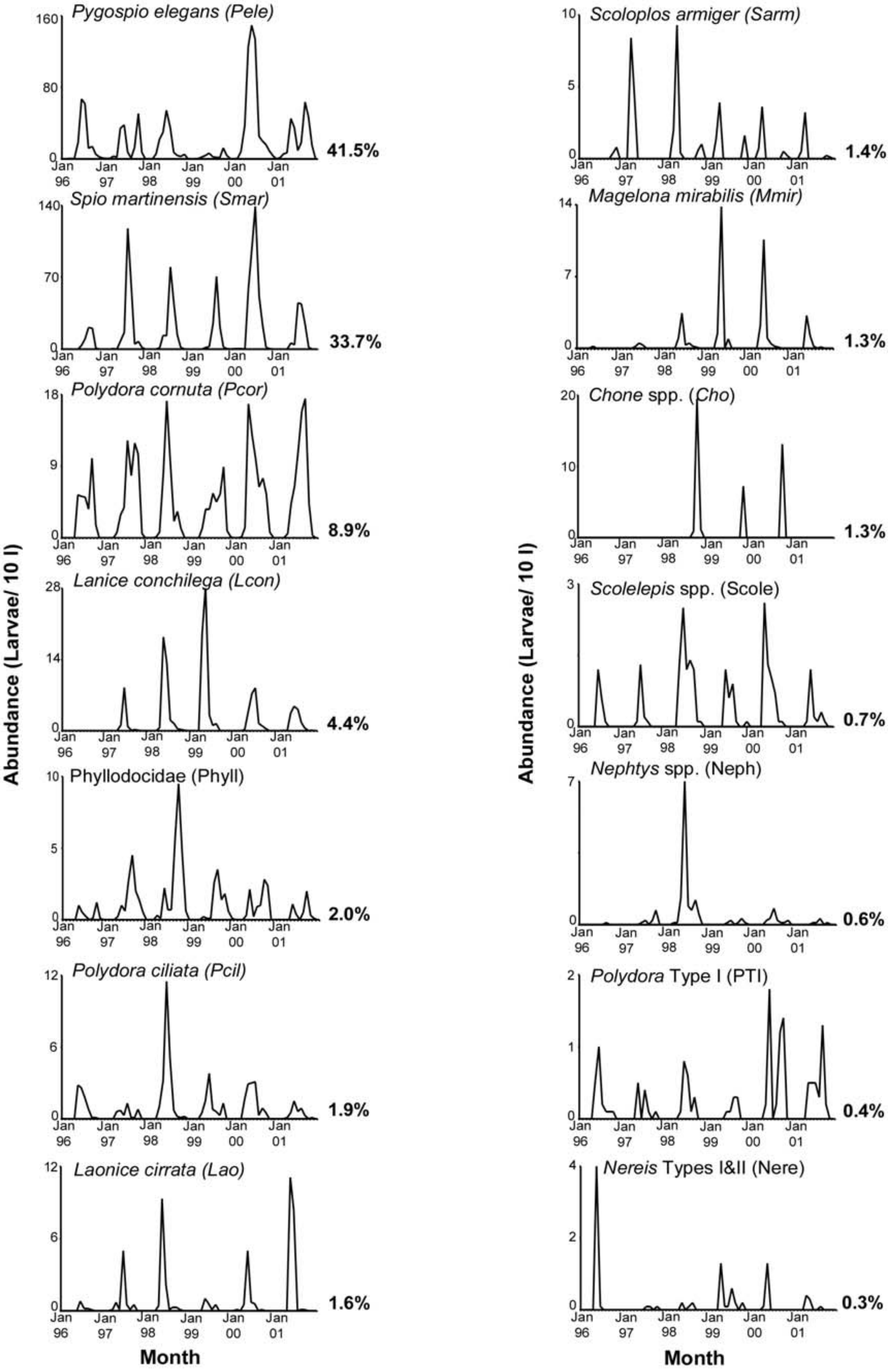


Fig. 4.3. Monthly sums of the 14 taxa comprising 90% of the grand total, as well as their percentage (%) of the grand total (31,462 larvae).

Table 4.I. Averaged abundances (larvae/ 10 l) and 95% confidence limits of polychaete larvae in the List tidal basin for the period 1996-2001, relative variation coefficients (CV_r), and years of peak abundance of the 14 most abundant taxa.

Taxa	Overall mean 1996-2001	CV_r (%)	Year of peak abundance
Pygospio elegans	7.00±0.70	10.70	2000
Spio martinensis	5.20±0.70	13.00	2000
Polydora cornuta	1.40±0.10	9.00	2001
Lanice conchilega	0.60±0.20	25.80	1999
Phyllodocidae	0.30±0.04	12.70	1998
Polydora ciliata	0.30±0.04	14.50	1998
Scoloplos armiger	0.24±0.06	4.20	1998
Magelona mirabilis	0.20±0.05	25.50	1999
Chone spp.	0.20±0.10	51.10	1998
Laonice cirrata	0.20±0.06	25.80	2001
Scolelepis spp.	0.11±0.01	14.30	1998
Nephtys spp.	0.08±0.03	33.10	1998
Polydora Type I	0.07±0.01	17.60	2000
Nereis Types I&II	0.05±0.01	31.00	1996

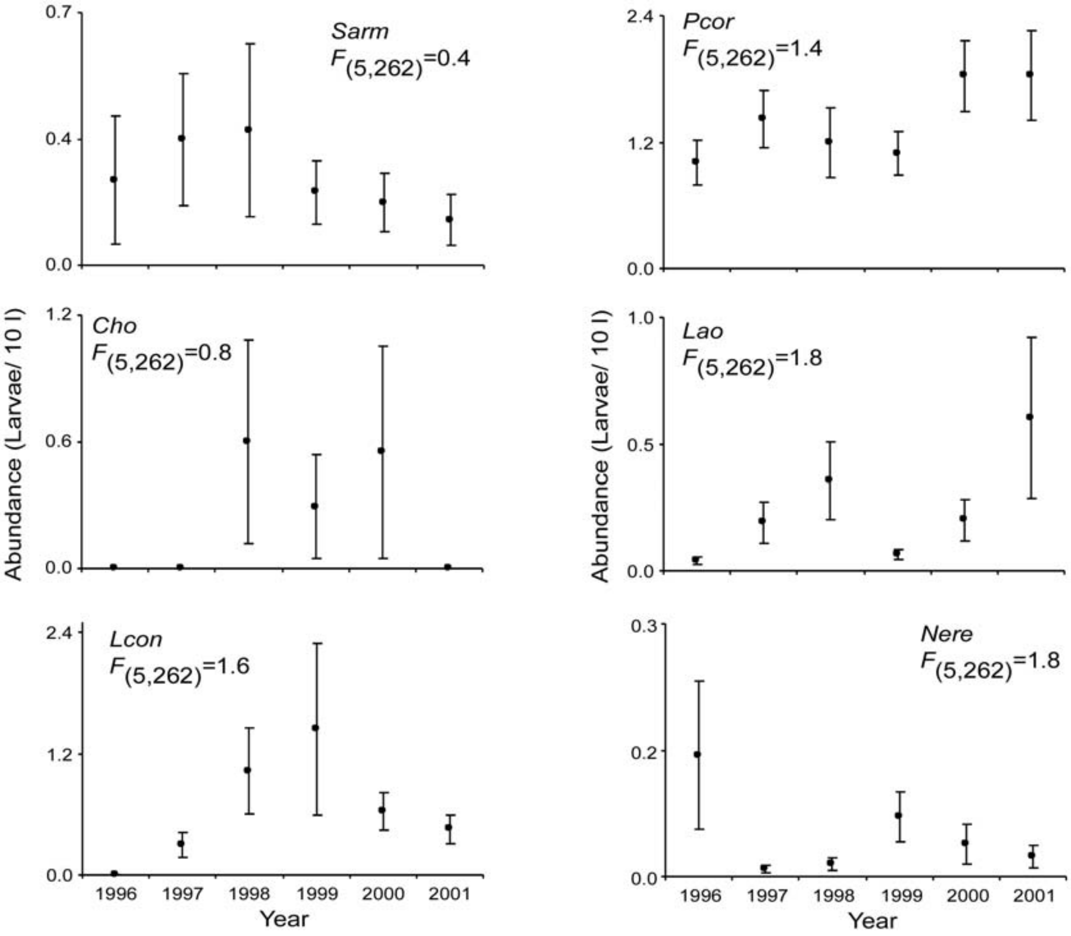


Fig. 4.4. Annual mean abundances and 95% confidence limits of taxa without significant abundance fluctuations between years. F-values refer to tests on temporal fluctuations with ANOVA. Abbreviations as in Fig. 4.3.

Significant temporal fluctuations in abundance among years were detected in the other eight taxa (Fig. 4.5). Four groups were defined, based on their fluctuation patterns: 1) Taxa with a decrease until 1999, but sudden increase after 2000: *P. elegans*, *Polydora* T1, and *S. martinensis*; 2) Taxa with peaks between 1998-1999: Phyllocidae and *M. mirabilis*; 3) Taxa with sudden increments in 1998: *Nephtys* spp.; and 4) Taxa with apparently random fluctuations: *P. ciliata* and *Scolelepis* spp.

The temporal variability of environmental variables shows significant fluctuations in salinity and phosphate which seem to have decreased, but their trends were not significant (salinity:β=-0.4, $F_{(1,4)}$=0.7, p>0.05; phosphate:β=-0.4, $F_{(1,4)}$=0.8, p>0.05) (Fig. 4.6). Significant fluctuations in phytoplankton biomass and pH-values also have no significant trend (phytoplankton:β=0.3, $F_{(1,4)}$=0.3, p>0.05; pH:β=-0.3, $F_{(1,4)}$=0.3, p>0.05.

Significant fluctuations in nitrite and silicate concentrations occurred. Both seem to have increased, but the trends were not significant (nitrite:β=0.3, $F_{(1,4)}$=0.3, p>0.05; silicate:β=0.2, $F_{(1,4)}$=0.2, p>0.05). Annual water temperatures show no significant fluctuations between years. Winds >6 $m \cdot s^{-1}$ were more common between 1997-2000, but temporal differences between modes were not significant. Percentages of S- and SE-winds increased between 1999 and 2001, while those of N- and NE-winds decreased.

Significant correlations between the fluctuation patterns of the environmental variables are shown in Table 4.II. In general, most of the temporal patterns are not significantly correlated (21 out of 56 cases are significant). Correlation coefficients are low and negative correlations slightly dominated among the significant cases (13 out of 21). This implies that most of the environmental variables did not covary in the same way in the period 1996-2001.

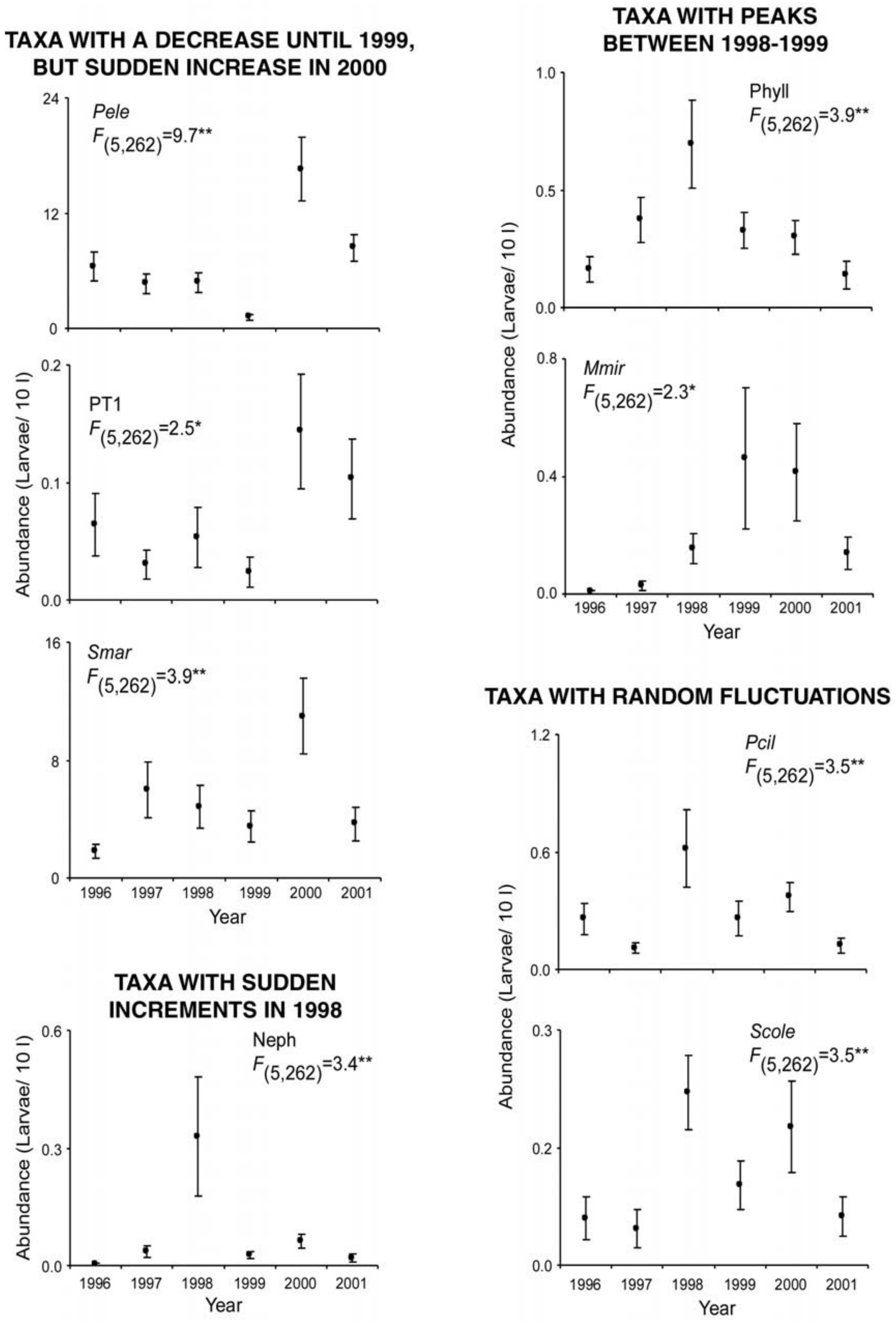


Fig. 4.5. Annual mean abundances and 95% confidence limits of taxa with significant overall temporal fluctuations. *F*-values refer to tests on temporal fluctuations with ANOVA. *=p<0.05, **=p<0.01. Abbreviations as in Fig. 4.3.

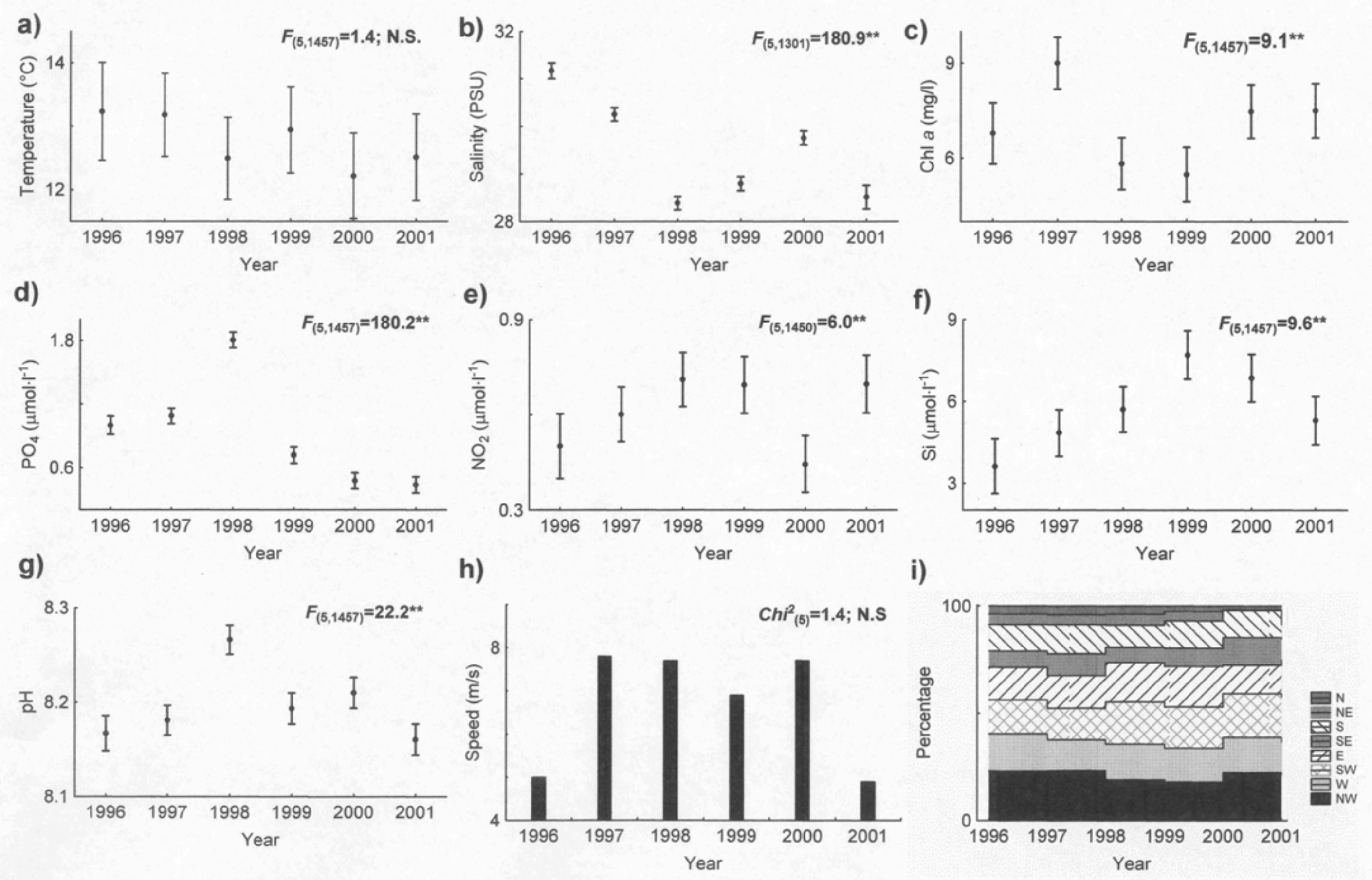


Fig. 4.6. Temporal patterns (1996-2001) of environmental variables. a) Water temperature; b) Salinity; c) Phytoplankton biomass; d) Phosphate; e) Nitrite; f) Silicate; g) Water pH; h) Annual modal wind speeds (the *Chi*^{2}-value refers to the assessment of significant temporal changes); i) Annual percentages of the incidence of wind directions. From a-g, mean values and 95% confidence limits are shown. *F*-values refer to tests on temporal fluctuations with ANOVA, N.S.=Non-significant; **=p<0.01.

Table 4.II. Significant Pearson' correlation coefficients ($p<0.05$) between environmental variables for the period 1996-2001.

(+) Correlations (-) Correlations	$W_{m/s}$	°C	Chl*a*	*Sal*	pH	NO_2	PO_4	Si
Wind speed							0.21	0.18
°C	-0.23			0.46	0.23			
Chl*a*		-0.19			0.41			
Salinity								
PH	-0.13			-0.14				
NO_2		-0.65		-0.29	-0.45		0.45	0.60
PO_4		-0.40			-0.20			0.30
Si		-0.62	-0.23	-0.45	-0.48			

3.2. Relationships between larval abundances and environmental variables

Multiple regressions involving the total abundance, and abundances of *Pele, Smar*, Phyll, *Pcorn*, and *Scole* show the highest adjusted coefficients of determination (Table 4.III). Regressions for abundances of the other 9 taxa have $R_a^2 \leq 0.3$ and are not taken into account, since in most of the cases these are non-significant. Most of the significant cases involve short- and long-term time lags (<1-12 months), while phyllodocids show only long-term lags (8-12 months). Water temperature and silicate show the highest cross-correlation coefficients, while the speed of the wind has the lowest ones. pH-values, water temperature, nitrite, and silicate are the most frequent environmental variables with significant lag effects on larval abundances.

The CCA-model describing instantaneous relationships between environmental variables and total larval abundances, as well as abundances of the 14 most abundant taxa is statistically significant ($F=11.7$, $p<0.01$), but explains only 18% of the total variance. Environmental variables significantly related to the first two canonical axes are shown in Table 4.IV. The highest significances were found with water temperature, salinity, PO_4, and phytoplankton biomass.

Statistically significant pair-wise dependences of abundances on particular environmental variables are shown in Fig. 4.7. Phytoplankton biomass, NO_2, pH, PO_4, salinity, and water temperature have significant effects. Abundances of larvae of *P. elegans* are significantly favored by increments in phytoplankton, nitrite, and salinity; while increments in pH, PO_4, and water temperature are significantly negative for its abundance. Abundances of phyllodocid larvae are significantly favored by pH and PO_4 increments, while salinity increments significantly reduce its abundance. Larval abundances of *L. conchilega* are significantly favored by PO_4 increments but negatively affected by salinity increments.

Table 4.III. Cross-correlations and multiple regressions between larval abundances and environmental variables. The “Cross-correlation” section shows Pearson’s correlation coefficients (r±S.E, all significant at $p<0.01$) and the optimal time lag in months (in parenthesis). The “Multiple regression” section shows variables with significant partial regression coefficients (β, $p<0.05$), adjusted coefficients of determination (R_a^2), and F-values of ANOVAs testing the significance of the multiple regressions. **=$p<0.01$.

	Cross-correlation								Multiple regression		
	$W_{m/s}$	°C	Chl*a*	*Sal*	pH	NO_2	PO_4	Si	Significant β	R_a^2	ANOVA
Total abund.	0.30±0.06 (5)	0.60±0.06 (<1)	0.30±0.06 (3)	0.40±0.06 (2)	0.50±0.06 (1)	0.50±0.06 (6)	-0.40±0.07 (12)	0.50±0.06 (7)	°C (0.80) NO_2 (0.40)	0.50	$F_{(8,50)}$=7.80**
Pele	0.30±0.06 (7)	0.40±0.07 (10)	0.20±0.06 (9)	0.40±0.06 (12)	0.40±0.06 (1)	0.5±0.06 (7)	-0.40±0.06 (<1)	-0.40±0.06 (7)	*Sal* (-0.3) pH (0.40) PO_4 (-0.40) Si (0.30)	0.51	$F_{(4,85)}$=24.50**
Smar	0.30±0.06 (5)	0.50±0.06 (<1)	0.40±0.07 (12)	-0.50±0.06 (4)	0.40±0.06 (8)	0.50±0.06 (8)	-0.40±0.06 (12)	0.50±0.06 (5)	$W_{m/s}$ (0.20) pH (0.30) Si (0.20)	0.50	$F_{(6,183)}$=26.30**
Phyll	0.30±0.06 (10)	0.50±0.07 (10)	0.60±0.06 (12)	-0.50±0.06 (8)	0.40±0.06 (12)	0.50±0.06 (12)	0.40±0.06 (8)	0.50±0.06 (12)	NO_2 (0.60) Si (0.20)	0.50	$F_{(4,96)}$=24.20**
Pcorn	0.30±0.06 (12)	0.60±0.06 (0)	0.30±0.06 (12)	0.30±0.06 (1)	0.40±0.06 (12)	0.40±0.06 (8)	0.30±0.06 (12)	0.50±0.06 (6)	°C (0.60) pH(0.10) PO_4 (-0.10)	0.41	$F_{(5,133)}$=20.00**
Scole	0.20±0.06 (10)	0.40±0.06 (1)	0.30±0.06 (12)	-0.40±0.06 (9)	0.50±0.06 (1)	0.40±0.06 (11)	0.30±0.06 (10)	0.50±0.06 (6)	°C (0.20) pH (0.20) NO_2 (0.30)	0.40	$F_{(6,193)}$=22.00**

Table 4.IV. Environmental factors significantly related to the first pair of canonical axes of the CCA-model describing instantaneous relationships between environmental variables and larval abundances. Values shown are *t*-values of regression/canonical coefficients for standardized variables ($t_{\mathrm{crit}(\alpha=0.05)}$=1.6, d.f.≥90).

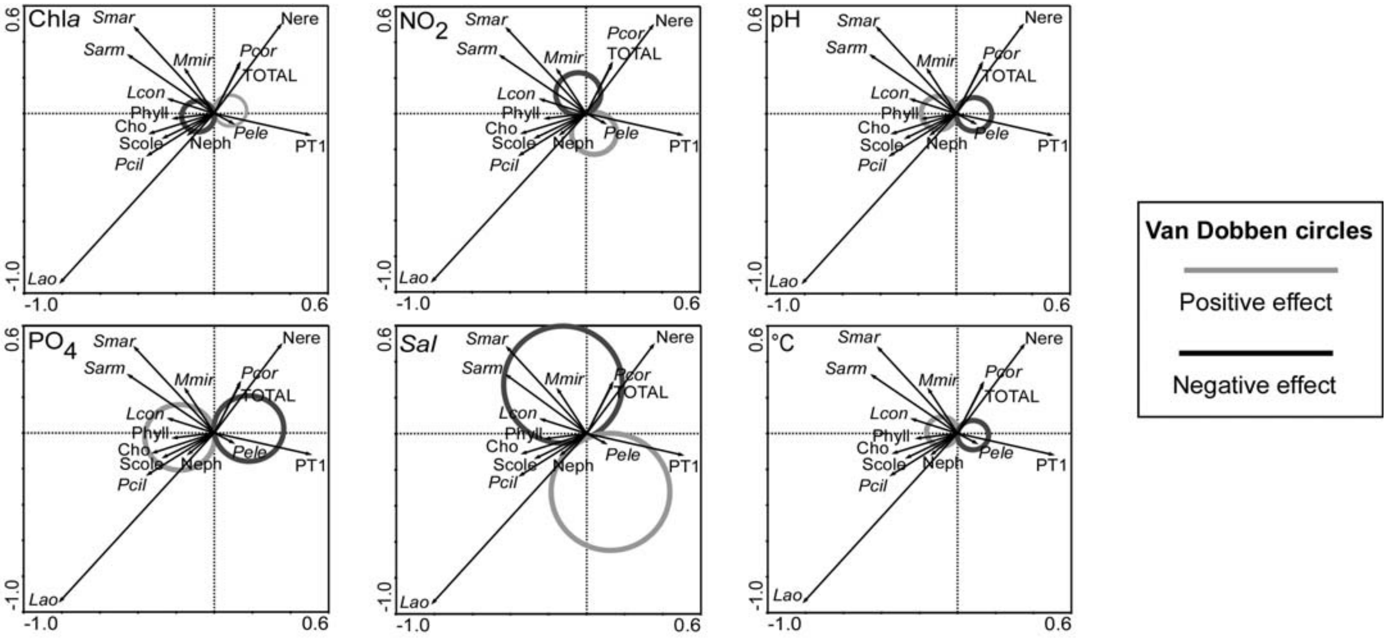
Canonical axis Environmental variable	1^{st}	2^{nd}
°C	116.8	53.9
Salinity	72.2	33.5
PO_4	39.3	62.0
Chl*a*	52.4	40.3
NO_2	59.9	27.9
SE-wind direction	10.7	15.4
Wind speed	0.4	24.1
SW-wind direction	17.9	0.7
Si	13.4	0.4
E-wind direction	11.4	0.8

Abundances of larval *Scolelepis* spp., *Nephtys* spp., and *Chone* are significantly favored by PO_4 increments. Salinity increments affect significantly and negatively the total larval abundances, and abundances of *P. cornuta*, *S. armiger*, and *M. mirabilis*. Larvae of *L. cirrata, Polydora* Type I*, Nereis* spp.*, S. martinensis, and P. ciliata* are not significantly affected by this set of environmental variables. Instantaneous effects of silicate, wind speed, both lunar phases, and any wind direction are not significant (Fig. 4.8).

3.3. Seasonality of the environmental variables and larval abundances

Environmental variables and abundances show a marked seasonality. pH-values, phytoplankton biomass, and larval abundances of *L. conchilega, P. ciliata*, nereid, nephtids*, L. cirrata, S. armiger*, and *M. mirabilis* peaked during spring (Fig. 4.9). The seasonal counts of *L. conchilega, P. ciliata*, and nereid significantly correlate with pH-values, while seasonality of *L. cirrata, S. armiger*, and *M. mirabilis* correlate significantly with phytoplankton biomass. The seasonal pattern of *Nephtys* spp. shows no significant correlation with either of the measured environmental parameters.

Water temperature, salinity, the total polychaete larval abundance, and abundances of *P. cornuta*, *S. martinensis*, and *Scolelepis* spp. peaked during the summer season (Fig. 4.10). Significant correlations are only found between the total larval abundance and abundance of *P. cornuta* with water temperature.



	Environmental variable					
Abundance	Chl*a*	NO$_2$	pH	PO$_4$	*Sal*	°C
Pygospio elegans	+	+	-	-	+	-
Phyllodocidae	None	None	+	+	-	None
Lanice conchilega	None	None	None	+	-	None
Scolelepis spp.	None	None	None	+	None	None
Nephtys spp.	None	None	None	+	None	None
Chone spp.	None	None	None	+	None	None
TOTAL	None	None	None	None	-	None
Polydora cornuta	None	None	None	None	-	None
Scoloplos armiger	None	None	None	None	-	None
Magelona mirabilis	None	None	None	None	-	None
Laonice cirrata	None	None	None	None	None	None
Polydora Type I	None	None	None	None	None	None
Nereis spp.	None	None	None	None	None	None
Spio martinensis	None	None	None	None	None	None
Polydora ciliata	None	None	None	None	None	None

Fig. 4.7. *t*-value plots with van Dobben circles showing significant pair-wise dependences of abundances on environmental variables. The table shows the type of effect (positive or negative) of each environmental variable over the taxa. TOTAL=Abundance comprised by the 14 most abundant taxa.

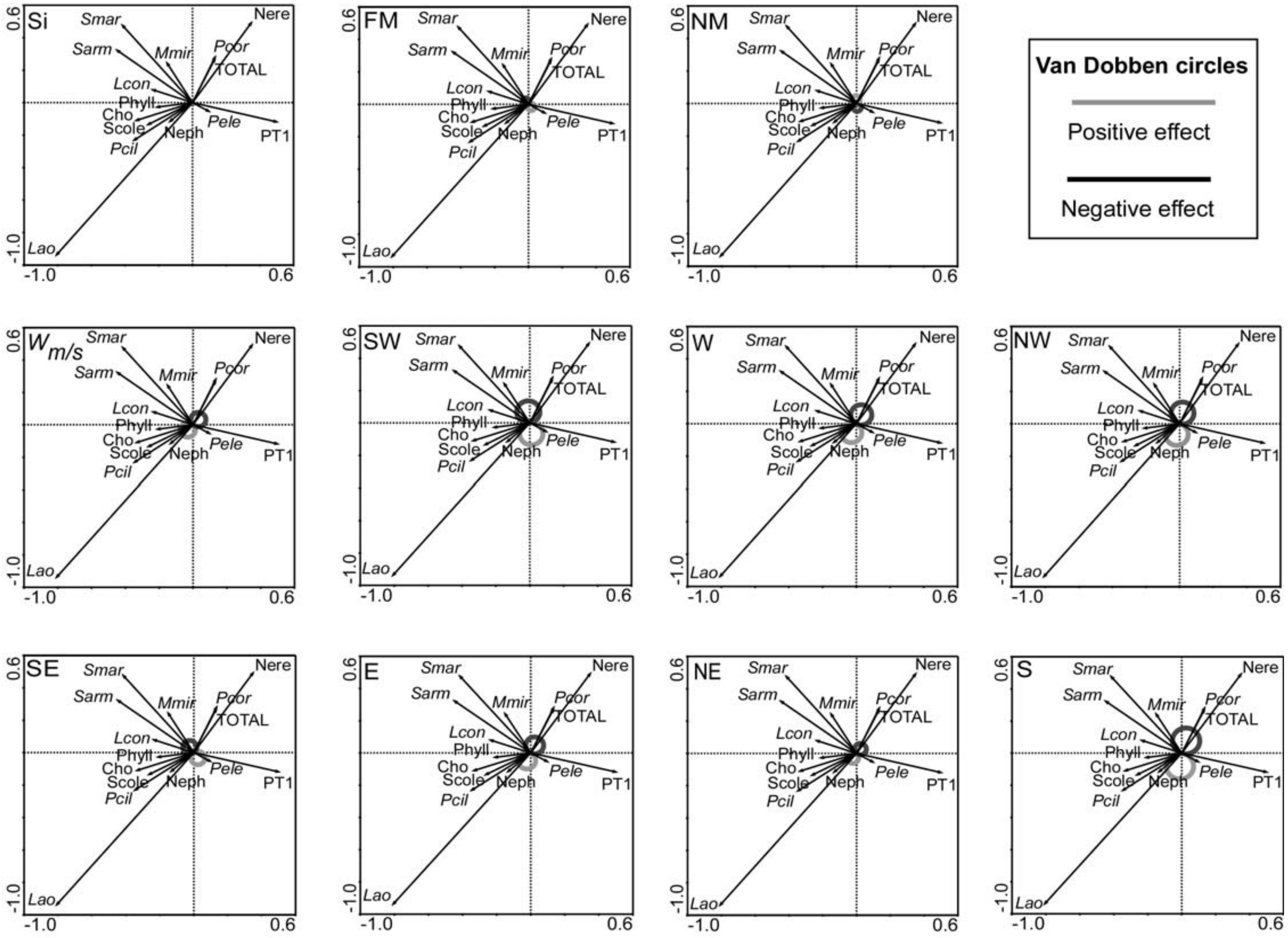


Fig. 4.8. *t*-value plots with van Dobben circles showing non-significant pair-wise dependences of abundances on environmental variables. TOTAL=Abundance comprised by the 14 most abundant taxa.

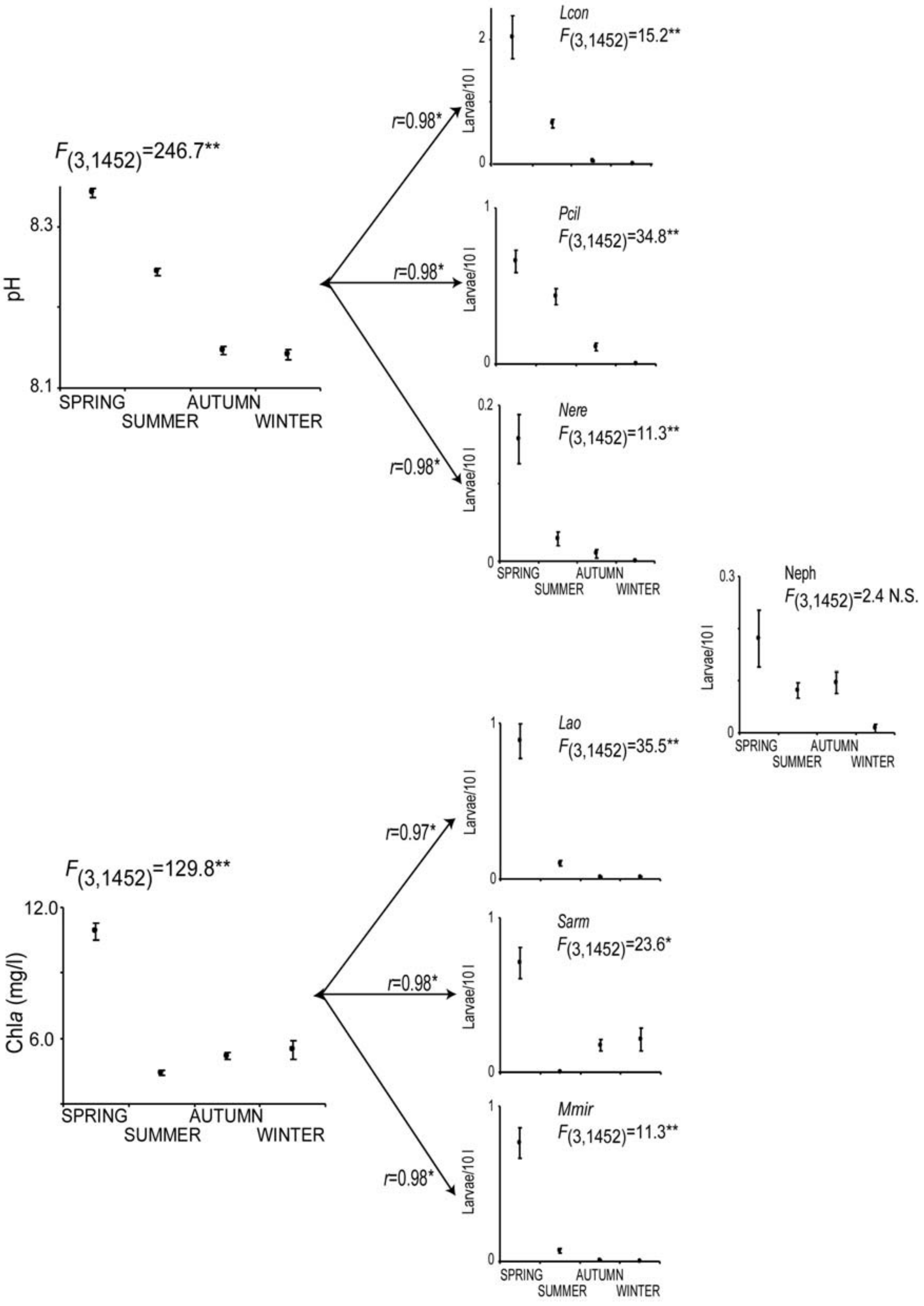


Fig. 4.9. Seasonality of means and 95% confidence limits of environmental variables and abundances peaking during the spring season. *F*-values refer to tests on significant differences between seasons with ANOVA, and *r*-values refer to significant Pearson' correlation coefficients between environmental variables and larval abundances. *=p<0.05, **=p<0.01.

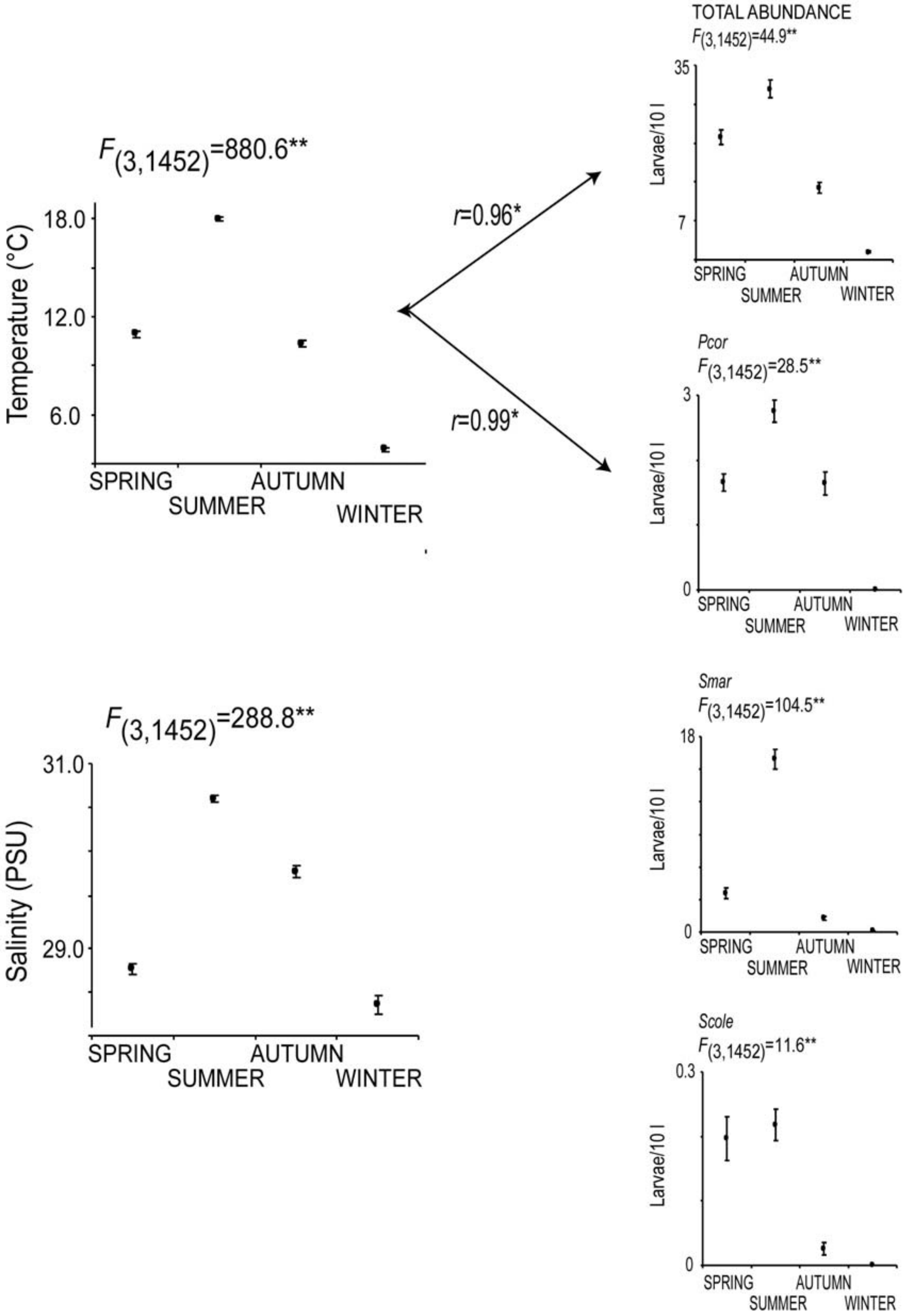


Fig. 4.10. Seasonality of means and 95% confidence limits of environmental variables and abundances peaking during the summer season. *F*-values refer to tests on significant differences between seasons with ANOVA, and *r*-values refer to significant Pearson' correlation coefficients between environmental variables and larval abundances. *=p<0.05, **=p<0.01.

PO_4, Si, NO_2, and wind speed peaked during winter and seasonality of none of the taxa correlated significantly with these (Fig. 4.11). Diversity and larval abundances of *P. elegans* and *Polydora* Type I were high between spring-autumn, showing no significant correlation with the seasonal patterns of any environmental variable. Larval abundances of phyllodocids and *Chone* sp. peaked during autumn and were not significantly correlated with the seasonal pattern of any environmental variable.

The frequency of NE-, N-, and NW-wind directions remained almost constant over the seasons (Fig. 4.12). Those of W-, SW-, S-, and SE-winds increased during autumn, while the frequency of E-winds was maximal during spring, and decreased gradually over the year. No taxon was significantly correlated with the seasonal patterns of wind directions.

Based on the seasonal distribution of abundance the following reproductive periods were assumed (Table 4.V): (1) Species with continuous reproduction throughout the year and reproductive peaks in spring (*P. elegans, L. conchilega, P. ciliata, L. cirrata, Nepthys* spp., *P. cornuta,* and *Polydora* Type I.); (2) Species with continuous reproduction during the year and reproductive peaks during summer (*S. martinensis* and *Scolelepis* spp.); (3) Species with seasonally limited reproduction and reproductive peaks in spring or autumn (Phyllodocidae, *S. armiger, Chone* spp., *M. mirabilis*, and *Nereis* spp.).

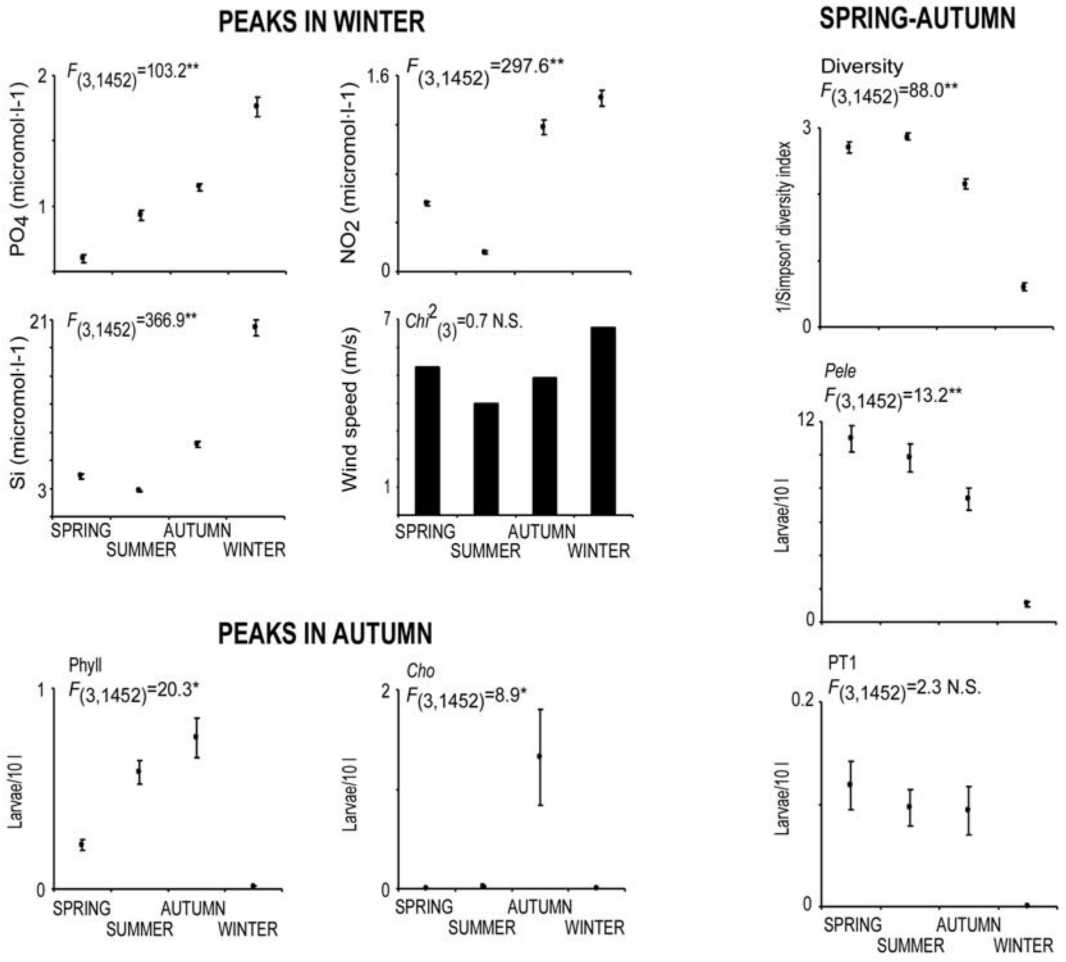


Fig. 4.11. Environmental variables, taxa abundances, and diversity values (means and 95% confidence limits) peaking during autumn, winter, and the spring-autumn period. *F*- and Chi^2-values refer to tests of significant differences between seasons. *=p<0.05, **=p<0.01, N.S.=non-significant.

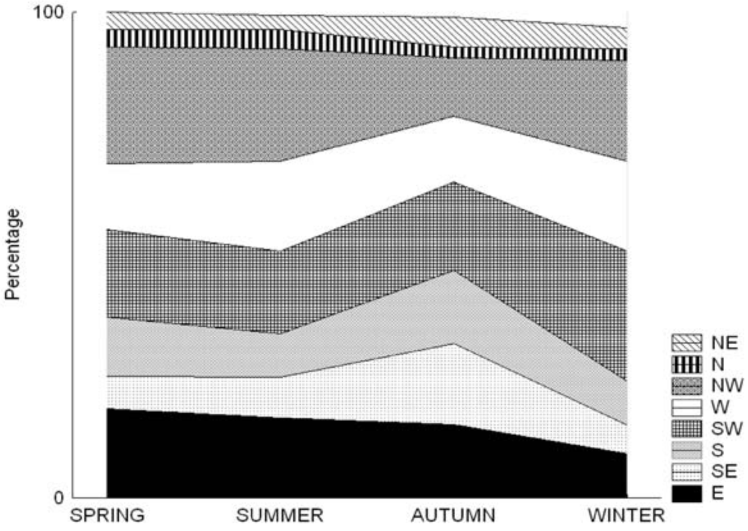
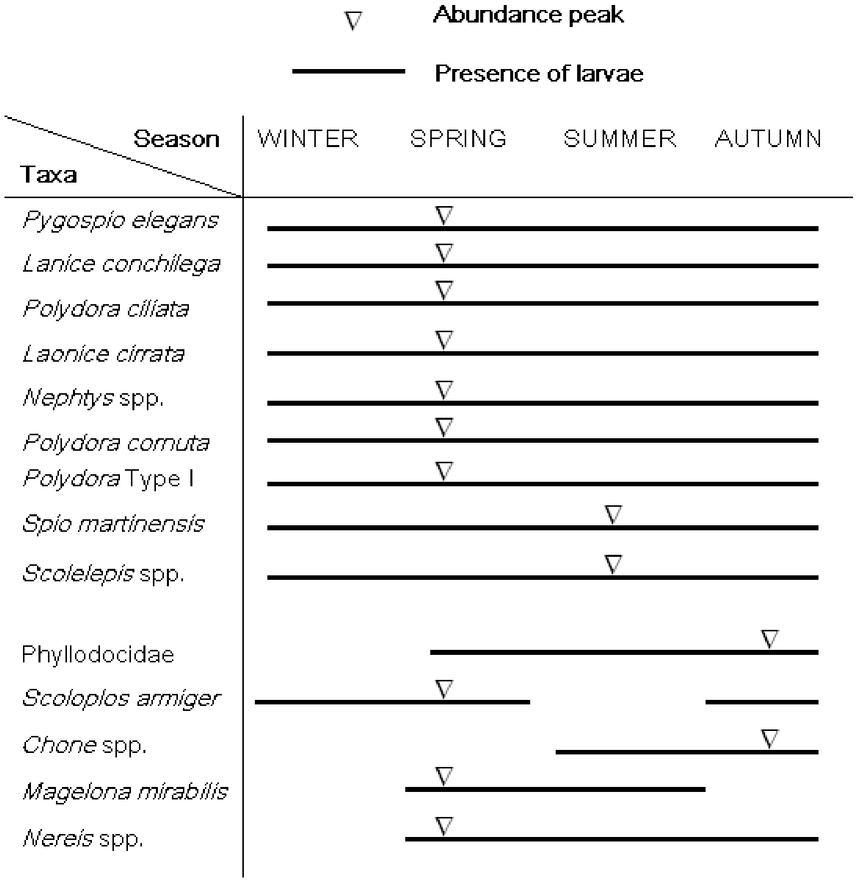


Fig. 4.12. Seasonal patterns of the percentual frequency of wind directions.

Table 4.V. Reproductive periods for the 14 polychaete taxa analyzed.



4. Discussion

The study period was characterized by significant annual fluctuations in salinity, phytoplankton biomass, pH-values, and concentrations of NO_2, PO_4, and Si. Apparent reductions in salinity and increments of NO_2 occurred due to the restored influence of the Elbe River plume, when the strong offshore winds during the winter 1995/1996 ceased; and increased salinities during 1996 occurred due to low precipitation and ice formation inside the basin during the same winter (Martens 2001). The apparent increase in total silicate may be interpreted as increased freshwater runoff into the basin. The reduction in PO_4 would suggest an increased phytoplankton production.

Environmental fluctuations coincided with significant fluctuations in abundance and diversity. Water temperature, NO_2, pH-values, PO_4, and total silicate had significant time lag effects on larval abundances; while significant instantaneous effects were those of phytoplankton biomass, NO_2, pH-values, PO_4, salinity, and water temperature. This study provides no experimental evidence for cause-effect relationships.

Similar relationships between environmental variables and larval abundances of polychaetes have been recognized since the 70`s (see Bhaud 1972), and have been demonstrated in temporal development of populations of copepods and phytoplankton in the List tidal basin (water temperature, see Martens 1995, 2001). They have been also found in non-gelatinous zooplankton from the Caribbean Sea (nutrient inputs from rainfall, see García and López 1989), zooplankton and polychaete larvae from the Mediterranean Sea (water temperature and nutrients, see Siokou-Frangou *et al.* 1998). Salinity and water temperature are known to affect the larval abundance of *Marenzelleria viridis* from the Baltic Sea (Bochert *et. al.* 1996). Positive correlations between abundances of polychaete larvae and phytoplankton biomass (Chl *a*) have been reported by Calbet *et al*. (2001) in the Mediterranean Sea. It is interesting to note that, although the previous references included species inhabiting different habitats at other regions of the world (e.g. Mediterranean and tropical environments), such relationships are common.

A schematic and hypothetic description of how environmental variables may influence larval abundances is shown in Fig. 4.13. Variables with time lag effects may be related to endocrinal processes and gonadal maturation of adults. This is exemplified by the seasonal pattern of the total larval abundance, since it becomes maximal in summer, after the winter and spring algal blooms. Zajac (1991a and b) reported that adult *Polydora* use winter phytoplankton blooms in order to maturate their gonads, start to spawn in early spring, and produce maximal larval abundances in summer. Summer phytoplankton blooms would support the ongoing spawning and settlement (Todd and Doyle 1981; Zajac 1991*a* and 1991*b*). The advantage of producing the highest larval abundances during spring-summer is, that larval cohorts experience the highest water temperatures, shorten their development and residence times with low starvation risk (although *Polydora* larvae seem to cope well with fluctuations in food availability, see Winging-Hansen 1999). Larvae spawned in autumn/winter have longer egg-juvenile periods (Todd and Doyle 1981).

Environmental variables with significant instantaneous “effects” may be related to the triggering of spawning, larval feeding, and feeding of adults to support ongoing spawning. The triggering effect of water temperature over polychaete gametogenesis has been reported by Lawrence (1996) and Bentley and Pacey (1992). The role of water temperature in gonadal maturation of polychaetes was described by Clark and Olive (1973), Schiedges (1979), Todd and Doyle (1981), Franke (1983), Franke and

Pfannenstiel (1984), and Bentley and Pacey (1992). Water temperature as spawning trigger was reported by Clark and Olive (1973), Todd and Doyle (1981), Franke (1983), Bentley and Pacey (1992), Fischer (1999), Franke (1999), and Andries (2001). The triggering effect of salinity over spawning was reported by Clark and Olive (1973), and its influence over larval performance was reported by Mathivat-Lallier and Cazaux (1990) and Bochert *et. al.* (1996). The importance of food supply for gonadal maturity was reported by Clark and Olive (1973) and Schiedges (1979), and for spawning by Bentley and Pacey (1992). Omori and Ikeda (1984), and DeMott (1989) mentioned that fluctuations of salinity, temperature, and pH affect zooplankton fitness (performance) by depressing feeding and growth rates and influencing the balance between energy intake and metabolic demands.

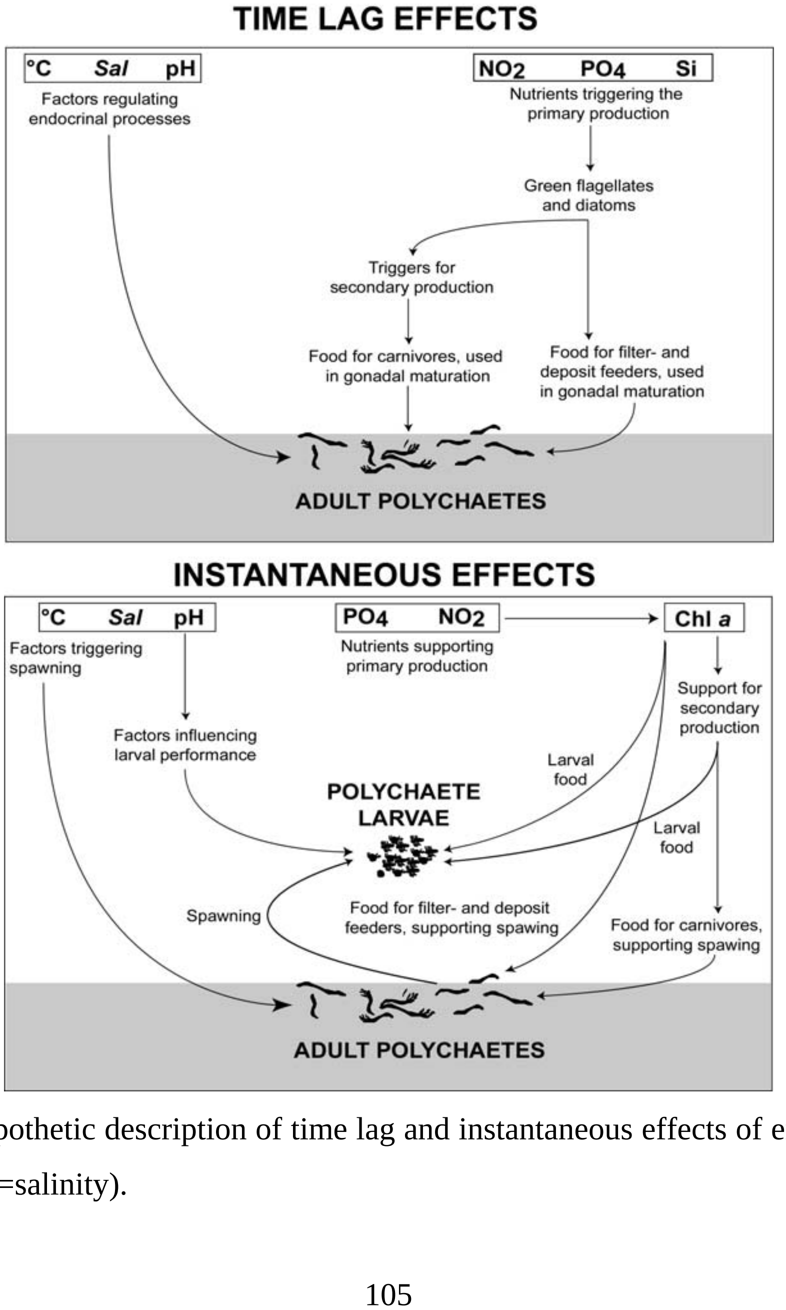


Fig. 4.13. Hypothetic description of time lag and instantaneous effects of environmental variables (*Sal*=salinity).

Apparently, the environmental fluctuations did not affect all taxa to the same extend. This is exemplified with the larval abundances of *P. cornuta* and *M. mirabilis.* Larvae of both species occur during the whole year, but abundances of *P. cornuta* have not significantly fluctuated between 1996 and 2001, while the larval abundance of *M. mirabilis* was low between 1996-1998 and increased significantly between 1999-2001. Severe winters have effects on many components of the Wadden Sea fauna (see Strasser and Pieloth 2001) and it may be speculated that the low larval abundance of *M. mirabilis* between 1996-1998 was related to the severe winter 1995/1996. The same applies to larvae of *L. conchilega*. Their absence during 1996 may have been caused by the massive adult mortality during that winter (Strasser and Pieloth 2001). However, the decline observed in its larval abundance after 1999 cannot be related to the occurrence of another severe winter. On the other hand, nereid larval abundances were maximal during 1996 and decreased thereafter. These differences suggest that taxa differ in their response to severe winters in terms of their larval production. In most of the taxa analyzed, outstanding changes in abundance occurred after 1998, suggesting that processes other than severe winters may be controlling their abundance fluctuations.

How much of this variability was produced by the influence of environmental fluctuations inside the bight? How much was contributed by external processes (e.g. temporal/seasonal fluctuations in the larval input from the open sea)? Unfortunately, it is not possible to answer these questions, because the appropriate information is not available. The larval input (*sensu stricto*) from the open sea has never been measured. Measurements performed by Raddatz (1994) were done in a zone affected by permanent eddies; thus, it is possible that he was continuously sampling the same larval set. Water masses cannot be used as proxy for larval exchange because detailed descriptions of water movements at different depths of the water column are not available, and their use might be valid only at short temporal scales. After using the available data of water temperature and salinity to create T-S diagrams, describing the movement of water masses inside the bight, only the restored influence from the Elbe River plume after 1996 is observed (Fig. 4.14). This was demonstrated by Martens (2001). Seasonal differences in the water movement shown in these diagrams are expected, since local hydrodynamics are highly affected by winds, and seasonal changes in wind patterns were previously shown.

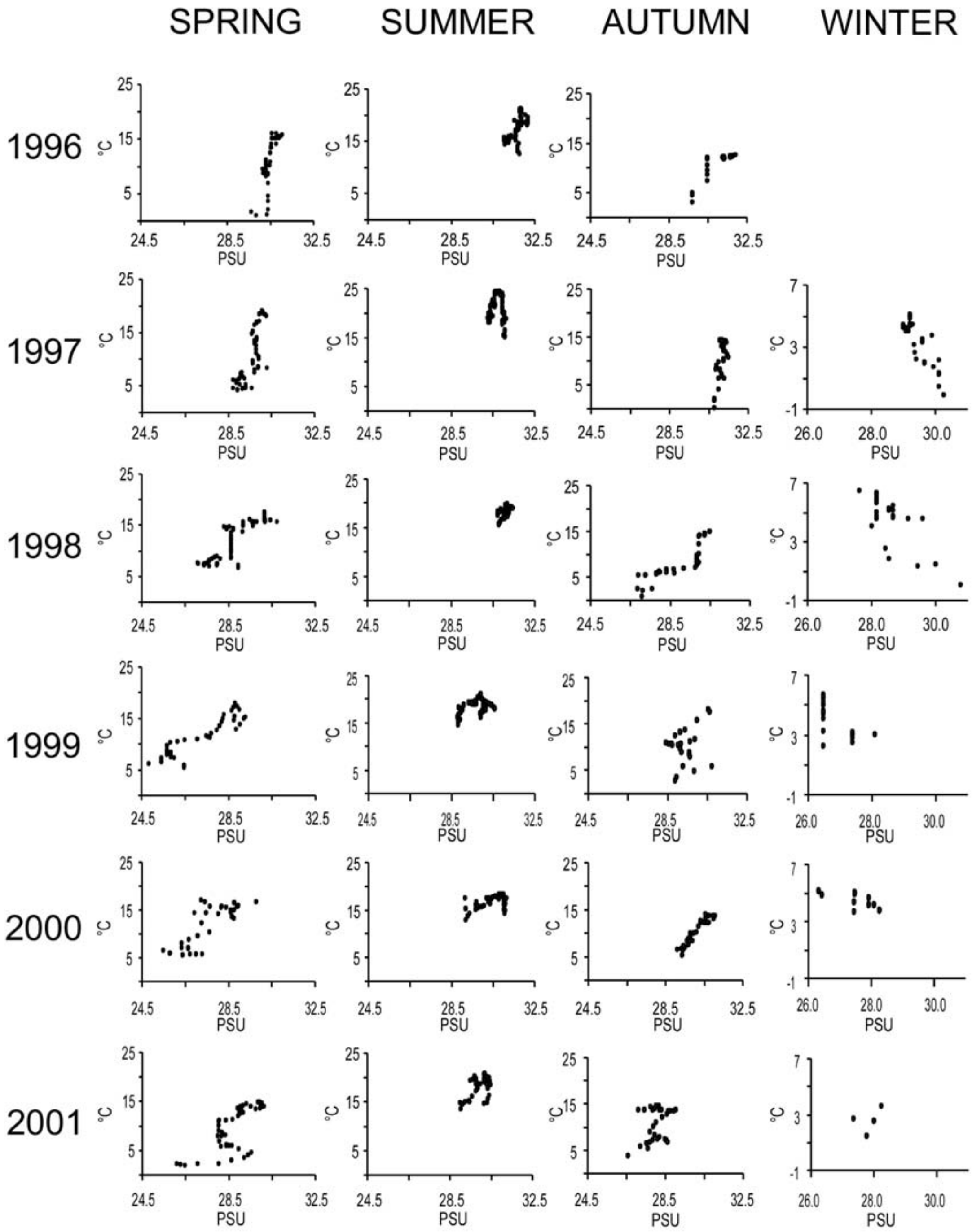


Fig. 4.14. Seasonal T-S diagrams for the period 1996-2001 (°C=Temperature in celcius degrees, PSU= Salinity in PSU units).

Abundances of oceanic taxa (e.g. Appendicularia) could be used as proxy for intrusions of North Sea water into the bight (temporal increments in their abundance could be interpreted as increased intrusions of offshore water), but the risk is, that we may be measuring real population fluctuations and not temporal fluctuations in the water exchange. In this sense, intrusions of North Sea water would be easier detected during the winter (which is usually harsh at this coast due to freezing), because no taxon reaches its highest larval abundance inside the bight during this season, and if high amounts of larvae would suddenly show up, it may be speculated that they have come from the open sea. Available models of superficial current patterns (e.g. Behrens *et al.* 1997) and waves do not necessarily reflect water exchange between the coast and the open sea. Thus, the unique solution for this problem is to get real measurements of the larval exchange and to undertake the adequate oceanographic research.

Assuming a dominance of local larval production, environmental variables significantly affecting the larval abundance in time lagged and instantaneous ways, show different combinations for different taxa, in agreement with the supposition that factors affecting the reproduction of polychaetes are taxa-specific (Bhaud 1972; Clark and Olive 1973; Todd and Doyle 1981; Fisher 1999; Andries 2001).

Methods applied in the present study revealed a negligible instantaneous effect of wind direction and full- and new-moon phases on larval abundances. In the case of the wind, an artifact could have been present by using wind directions over all speeds. Winds <3-4 $m \cdot s^{-1}$ have weak effect on the local hydrodynamics (W. Armonies, pers. com.), thus the use of all wind situations may bring much noise in the data, particularly if direction and speed are treated separately. The direction of wind driven flow has been found to be important during 1991 for copepod abundances inside the List tidal basin (Martens 1995). Westerly winds have positive influence on the North Sea zooplankton (Colebrook 1985; Greve *et al.* 2001), and some gastropods spawn under certain wind directions and stormy conditions (Sasaki and Shepherd 1995). Moon phases are important for the gonadal maturation in lumbrinerids (Clark and Olive 1973), and for spawning in nereids and syllids (Schiedges 1979, Bentley and Pacey 1992, Franke 1999).

Another probable artifact affecting these results is, that the significance of some environmental factors varies depending on the pooling of abundance data (e.g. total abundance, families, single or groups of species, etc.) (Martens 1995), and environmental variables not considered here may show better correlations.

Strasser and Pieloth (2001) and Strasser *et al.* (2001a and b) have shown that climatic fluctuations may induce abundance fluctuations of marine invertebrates on tidal flats. Abundance of larvae has been taken as the traditional sign of reproductive activity in polychaetes (Bhaud 1972), but environmental fluctuations may also induce poecilogony (Gudmundsson 1985; Hoagland and Robertson 1988; Young and Ebert 1996; Chia *et al.* 1996), and we do not know if this occurred in the study area. Some locally important species are potential sibling species or poecilogonic (e.g. *Scoloplos armiger* (Plate and Husemann 1991, Kruse *et al.* 2003), *Pygospio elegans* (Anger *et al.* 1986; Gibson and Harvey 2000), and *Capitella* (Gamenick *et al*. 1998).

The sampling program is ongoing, and in the future it will be possible to reach a higher certainty on the influence of environmental factors on larval abundances. A longer temporal coverage would lead to the smoothing of variability induced by exceptional conditions (e.g. winter 1995/1996), because more samples would represent "normal periods". Nevertheless; the identification of the larval sources, regular oceanographic research to clarify temporal variability in water exchange, and an appraisal of the set of environmental variables are inevitable. On the other hand, monitoring programs running for more than 20 years can lead to the situation, where no significant correlation between environmental factors and zooplankton abundances is found (see Kane 2003).

Several open questions are prompted by the results, for example: 1) A deeper analysis on effects of wind directions on larval abundances, transforming the wind data to represent an index of turbidity; 2) The environmental variability at the offshore area can be expected to be lower than inside the Wadden Sea. Larvae produced inside the basin should be adapted to the prevailing conditions there, while those coming from the offshore area may be more sensitive to the harshness inside the basin. Therefore, the search for reliable representative taxa of both environments should be intensified in order to test for this "lack of adaptation"; 3) Up to now, the influence of single environmental variables on the taxa was analyzed. This is certainly too simplistic. "Optimum curves" might allow the analysis of the interplay of several environmental variables on one taxon; 4) It might be useful to re-analyze specific periods or seasons, in order to distinguish better between remarkable events (e.g. severe vs. mild winters), or specific seasons (e.g. limiting the analyses to spring/summer periods, when larval abundances are the highest).

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Chapter 5. General discussion

Once the basis of a description of species composition, distribution, and temporal abundance fluctuations of meroplanktonic polychaete larvae inside the basin is settled, we may ask, to what extent the local polychaete plankton is representative for coastal waters of the North Sea.

Martens (1998) found at the scale of the List tidal basin that the abundance of spionid polychaete larvae in inner surface waters increases during low tides and decreases during high tides, concluding that an important proportion of meroplankton is exported to the open sea during ebb periods, but based on the copepods found inside the basin it was proposed that holoplankton is imported during flood periods. Reise *et al.* (1998) suggested that only few zooplankters could be considered local for the bight (e.g. the copepod *Acartia* spp. and medusas). *Acartia* reproduces in the basin and medusas perform vertical movements that allow them to remain inside the basin. Based on the low coherence observed between benthic and planktonic assemblages in the present study, it seems that the qualitative input from the North Sea enlarges the species spectrum. Larvae of *Laonice cirrata, Polydora hermaphroditica, Poecilochaetus serpens,* and *Pseudomystides limbata*, of which benthic stages are not known from the benthic surveys are candidates of the meroplankton potentially imported during flood periods. Nevertheless, evidence for larval retention as the dominant process suggests that the effect of the quantitative imput from offshore on overall abundance is small.

Since a large proportion of the total larval abundance was comprised by species with benthic stages well known from inside the basin (e.g. *P. elegans, S. martinensis, P. cornuta, and L. conchilega*), it may be assumed that a large proportion of the polychaete larval production is local.

The study of Smidt (1951) is the only other investigation on species composition of meroplanktonic polychaete larvae for the northern Wadden Sea. Species and types of spionids, polynoids, and phyllodocids found here indicate that the species composition of these groups has not remained static and that periodic taxonomic studies are still necessary. In the long-term, the species composition of the Wadden Sea has continuously changed, due to the loss of particular habitats (e.g. *Sabellaria*-reefs and sublitoral seagrass-beds) and the establishment of alien species (Reise *et al.* 1998). Since these changes have been common for all the tidal basins along the Wadden Sea, it could be expected that the biota of the List tidal basin would not differ from the rest of the tidal flats (Reise *et al.* 1999), but it would be interesting to test this using the meroplanktonic compartment.

Martens (1998) proposed that the large tidal exchange of water volume causes larvae to enter and leave the bight with each tide. However, his data could also be interpreted as follows: Abundances of spionid larvae increased during the ebb phase, because they were retained inside the bight and the reduction in water volume was concentrating them. On the other hand, their abundance decreased during flood tides, because they were diluted in a larger volume of water.

One may assume that the tidal mixing is enough to induce random larval distributions. However, the occurrence of particular taxa in specific areas of the basin and the persistent detection of highest larval abundances at its innermost parts indicate that polychaete larvae are not simply homogenized and washed-out by tides. The List tidal basin is unique along the Wadden Sea, by being separated from other tidal basins by causeways, leaving only one connection open to the North Sea. It would be interesting to examine whether abundance patterns are similar to those basins not enclosed by causeways.

The occurrences of particular taxa at specific areas of the basin and the persistent detection of highest larval abundances at its innermost parts have implications for the ongoing regular zooplankton-sampling program. It should be analyzed if zonations of abundance and species composition inside the basin occur in other meroplanktonic groups. If so, additional sampling points distributed inside the basin should complement the fixed sampling station from List harbor. Nevertheless, the List harbor station should be maintained, since a large amount of valuable information has been obtained there over the last seven years. This information is necessary to discuss physical variability and zooplankton population dynamics, from the point of view of long-term physical and biological data sets. Up to now, such discussions have been undertaken for the whole North Sea, but the coastal zones should not be left aside. The analysis of year-to-year fluctuations in the production of meroplanktonic polychaete larvae and some environmental variables at the List tidal basin (Chapter 4) is only one example of a wide spectrum of possible analyses. The continuation of the time-series from List harbor will lead to the achievement of higher certainty on the influence of environmental factors on the meroplankton. Although Biologische Anstalt Helgoland has produced the 25 years long zooplankton time-series of Helgoland Roads, representative for the German Bight, similar time series are also necessary for shallow coastal areas, and there lies the importance of the List harbour time series.

An important quantitative role of polychaete larvae in zooplankton has been mentioned for the study area by Hickel (1975), Martens (1980), and Jak (1999). Bosselman (1989) also recorded a numerical dominance of polychaete larvae at one subtidal area of the German Bight. Archambault *et al.* (1998) noted the numerical dominance throughout the year at four bays of the Lower St. Lawrence Estuary (Canada). Shanks *et al.* (2002, 2003) reported the numerical dominance at Cape Hatteras. On the other hand, polychaete larvae are a minority at the Faroe shelf (Gaard 1999) and some locations of the NW-Mediterranean Sea (Calbet *et al*. 2001). It would be desirable to know, how comparable are local abundances of polychaete larvae with those of other zooplankters, and if their abundance levels are similar at other regions. Data from the literature make such a comparison difficult due to temporal mismatch and differences in sampling gears and methodologies. Furthermore, abundance data of polychaete larvae are not often provided. They are commonly pooled together in groups such as “macrobenthic larvae”, “total zooplankton”, or “others”; or are expressed as biomasses.

The averaged abundance of polychaete larvae along gullies in the bight as well as inside Königshafen and Oddewatt, was 37.0 larvae·10 l^{-1} (±2.0). The averaged abundance for the 1996-2001 time series obtained at List harbor was 21.5 larvae·10 l^{-1} (±3.0). Table 5.I shows maximal abundances reported for several zooplankters from the bight and other areas. Averaged abundances from the present study compare well to the maximal abundances reported for haparticoid copepods, appendicularia, medusae, and crab larvae inside the bight; nevertheless, abundances of the copepod *Acartia* and bivalve larvae can be higher. Averaged abundances from the present study are higher than the maximal larval abundances reported for polychaete taxa at Kiel Bay, German Bight, Caribbean Sea, Mediterranean Sea, and Atlantic Ocean. Nevertheless, some polychaete taxa from Japan, U.S.A., and the Baltic Sea can reach extremely high abundances.

The contribution of Hamers (2001) provides the opportunity of compare recent larval abundances of particular polychaete taxa at open waters around Helgoland and inside the bight. The maximal abundance of larvae of *P. ligni, S. martinensis, S. squamata* and *S. bonnieri* around Helgoland, between 1996-1998, were 0.5-20 times lower than the maximal values measured inside the List tidal basin during the same years (24 and 144 larvae·10 l^{-1} for *P. ligni* and *S. martinensis,* respectively; and 5 larvae·10 l^{-1} for *Scolelepis* spp.) (Table 5.I). In the case of *P. ciliata,* its maximal larval abundance around Helgoland during 1998 was 10 times higher than the maximal value measured inside the List tidal basin during the same year (16 larvae·10 l^{-1}) and the averaged abundance of larval *Magelona mirabilis* inside the List tidal basin between 1996-2001 (0.3 larvae·10 l^{-1} ±0.1) is five times lower than the maximal value measured at one subtidal location of the German Bight between 1985-1986 (Table 5.I). These differences correspond well with the respective benthic occurrences at Helgoland and Sylt (see Ziegelmeier 1978 and Gillandt 1979).

The data reaffirm the numerical importance of polychaete larvae in the local zooplanton, suggest that their abundances inside the List tidal basin are higher than at neighboring offshore waters, and partially support the assumption that the quantitative input from open water might be low. The present study showed that the highest abundance of polychaete larvae occurs between spring-summer. In the Dutch Wadden Sea, densities and biomass of macrozoobenthos become maximal during this period also (Beukema 1974; Beukema *et al.* 1999). Buchholz (1984) found at the muddy intertidal of the List tidal basin, that densities of polychaetes (dominated by *Scoloplos armiger*) were higher during spring than during autumn. These references suggest, that the occurrence of the highest larval abundances relates well to those of benthic stages. A similar seasonal coupling between larval and benthic abundances was observed by Zajac (1991 a and b) at the east coast of the U.S.A.

To conclude, the present study shows that the composition of polychaete taxa occurring as meroplanktonic larvae inside the List tidal basin is representative of the coastal waters of the North Sea. An important qualitative input from the open sea may be responsible for this. However, the quantitative input seems to be low because highest larval abundances were continuously detected at the innermost parts of the bight. Therefore, larval retention seems to be a locally dominant process. Benthic presence and costal morphology may enhance non-random and species-specific distribution patterns inside the bight. The annual variability in production of polychaete larvae is high with a conspicuous and regular seasonality. Temporal fluctuations in larval abundances are significantly related to time lag and instantaneous fluctuations of some environmental variables, which may influence gonadal maturity and spawning activity of adult stages as well as performances and feeding of larval stages.

Table 5.I. Maximal abundances of several zooplankton taxa, from different regions of the world.

Taxa	**Location**	**Reported abundance**	**Abundance (Number·l^{-1})**	**Sampling device**	**Mesh size (μ)**	**Depth (m)**	**Data**	**Year**
Harpacticoid copepods	List tidal basin	$5.00\cdot l^{-1}$	5.00	?	150	Surface	Mar-Nov	1972[1]
Polychaete larvae	List tidal basin	$3.00\cdot l^{-1}$	3.00	?	150	Surface	Mar-Nov	1972[1]
Appendicularia	List tidal basin	$2.00\cdot l^{-1}$	2.00	?	150	Surface	Mar-Nov	1972[1]
Larvae of Magelonidae	Volcano Bay, Japan	$12550.50\cdot 100\ l^{-1}$	125.50	Funnel cone	40	0-0.5	Feb-Apr	1982[2]
Larvae of *Phyllodoce groenlandica*	Kiel Bay	$32500.00\cdot l^{-1}$	0.06	Pump	110	21.0	May/Sep	1953[3]
Larvae of *Pseudopolydora paucibranchiata*	Mission Bay, California	$300000.00\cdot m^{-3}$	300.00	Plastic jars	63	0.2-0.5	Apr	1980[4]
Magelona spp.	Subtidal of the German Bight	$150.00\cdot m^{-3}$	0.15	Net	150	25.0-35.0	Monthly samplings	1985-1986[5]
Polychaete larvae	Caribbean Sea	$617.00\cdot m^{-3}$	0.60	Pump	200	0.5-1.0	Monthly sampling	1985/1986[6]
Larvae of *Lanice conchilega*	Arcachon Bay	$300.00\cdot 10\ m^{-3}$	0.03	Cylindrical net	200	30.0	May/June	1988[7]
Rathkea octopunctata	List tidal basin	$5000.00\cdot m^{-3}$	5.00	Hand net	500	1.0	May	1991[8]
Larvae of *Marenzeriella viridis*	Southern Baltic	$21000000.00\cdot m^{-3}$	21000.00	?	120	Surface	Sep-Apr	1992-1994[9]
Total bivalve larvae	Schleswig-Holstein Wadden Sea	$100000.00\cdot m^{-3}$	100.00	Paired Bongo nets	150	Surface	Weekly-monthly samplings	1990-1992[10]
Polychaete larvae	Bay of Blanes	$120.00\cdot m^{-3}$	0.12	Pump	80	7.0-8.0	Apr	1995[11]
Acartia spp.	List tidal basin	$49000.00\cdot m^{-3}$	49.00	Bucket/Bongo net	80/150	Surface	Winter	1986[12]
Pseudocalanus elongatus	List tidal basin	$1200.00\cdot m^{-3}$	1.20	Bucket/Bongo net	80/150	Surface	Winter	1986[12]
Larvae of spionids	List tidal basin	$9000.00\cdot m^{-3}$	9.00	Bucket/Bongo net	80/150	Surface	Summer	1986[12]
Larvae of *Polydora ciliata*	Helgoland	$20000.00\cdot m^{-3}$	20.00	Hydro-bios net	75	4-12	Two times/week	1998[13]

Table 5.I. Maximal abundances of several zooplankton taxa, from different regions of the world (continued).

Taxa	**Location**	**Reported abundance**	**Abundance (Number·l^{-1})**	**Sampling device**	**Mesh size (μ)**	**Depth (m)**	**Data**	**Year**
Larvae of *P.ligni*	Helgoland	810.00·m^{-3}	0.80	Net	75	4-12	Two times/week	1996[13]
Larvae of *Spio martinensis*	Helgoland	590.00·m^{-3}	0.60	Net	75	4-12	Two times/week	1997[13]
Larvae of *Scolelepis squamata*	Helgoland	21.00·m^{-3}	0.02	Net	75	4-12	Two times/week	1996[13]
Larvae of *Scolelepis bonnieri*	Helgoland	100.00·m^{-3}	0.10	Net	75	4-12	Two times/week	1998[13]
Total bivalve larvae	List harbor	2400.00·0.01 m^{-3}	240.00	Bucket	80	Surface	Quasy-daily	May 96-Dec 98[14]
Carcinus maenas	List harbor	2400.00·m^{-3}	2.40	Bucket	80	Surface	Quasy-daily	May 96-Dec 98[14]
Polychaete larvae	Coastal NW-Mediterranean Sea	3000.00·m^{-3}	3.00	Net	200	0-25	Weekly samplings	Aug 95-Oct 96[15]
Phyllodocid larvae	Cape Hatteras	2062.00·m^{-3}	2.00	Pump	100	2-5	Aug	1994[16]
Spionid larvae	Cape Hatteras	1269.00·m^{-3}	1.30	Pump	100	2-5	Aug	1994[16]
Spionid larvae	Cape Hatteras	947.00·m^{-3}	0.90	Pump	100	2-5	Aug	1994[16]

[1]Hickel (1975)1; [2]Yokouchi (1984); [3]Banse (1986); [4]Levin (1986); [5]Bosselmann (1989); [6]García and López (1989); [7]Mathivat-Lallier and Cazaux (1990); [8]Kopacz (1994); [9]Bochert *et al.* (1996); [10]Pulfrich (1997); [11]Martin *et al.* (1997); [12]Martens (1998); [13]Hamers (2001); [14]Strasser and Günther (2001); [15]Calbet *et al.* (2001); [16]Shanks *et al.* (2002).

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