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Life history and population dynamics of the marine cladoceran *Pleopis polyphemoides* (Leuckart)  
(Cladocera, Crustacea) in a shallow temperate Pärnu Bay (Baltic Sea)

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## Abstract

The seasonal cycle of parthenogenetic and gamogenetic reproduction modes of the marine cladoceran *Pleopsis polyphemoides* was studied in a shallow semi-enclosed Pärnu Bay, the NE Baltic Sea. Population development of *P. polyphemoides* was found to be very seasonal with a strong dominance of parthenogenetic females. The gamogenetic reproduction mode occurred almost throughout the whole reproductive season being the most intense during the population abundance peak. The change from parthenogenetic to gamogenetic reproduction was found to be neither influenced by water temperature, salinity nor Chl *a* concentration. Parthenogenetic fecundity was inversely correlated with water temperature and exhibited a positive relationship with total female body size, but showed no relationship with population density. In general, parthenogenetic females were larger just before or during the population peak. While the population development of *P. polyphemoides* in spring seemed to be associated with temperature, the drastic decline during the summer was a result of changes in the biotic conditions (predation) rather than in the abiotic environment. Significant fine-scale spatio-temporal variability in the population development and several vital rates of *P. polyphemoides* observed in the current study calls for caution when interpreting cladoceran multi-annual abundance dynamics from time series obtained with variable and/or low sampling frequencies.

Key words: Baltic Sea, fecundity, *Pleopsis polyphemoides*, reproduction, seasonal dynamics

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Introduction

Altogether, there are eight truly marine cladoceran species belonging to the families Podonidae (containing also *Pleopis polyphemoides* (Leuckart)) and Sididae, characterised by a very broad distribution range from tropical to subarctic waters (Gieskes, 1971a, 1971b, 1971c; Della Croce, 1974; Mordukhai-Boltovskoi and Rivier, 1987; Rivier, 1998). Phylogenetic analysis suggests the initial radiation of marine Podonidae during the Miocene or early Pliocene and start of their oceanic expansion via the Mediterranean at times when the Ponto-Caspian basin was connected with the world's oceans (Cristescu and Hebert, 2002; Durbin *et al.*, 2008). However, recent expansion (incl. transoceanic) of several species of marine and also brackish cladocerans might be a result of human intervention (Cristescu *et al.*, 2001; Durbin *et al.*, 2008; Pöllupüü *et al.*, 2008) as has been suggested for the freshwater predatory cladoceran *Bythotrephes cederstroemi* (Sprules *et al.*, 1990).

Cladocerans have high seasonal variability due to the alternation of parthenogenetic and gamogenetic reproduction modes (Egloff *et al.*, 1997; Rivier, 1998). A rapid increase in densities attained as a result of high rates of embryonic and postembryonic growth is characteristic of marine cladocerans, including *P. polyphemoides*. The density increase is accelerated by pädogenesis, namely, the development of parthenogenetic eggs beginning in the brood chambers of embryos before they are released from their parent, a phenomenon described commonly in marine Podonidae (Egloff *et al.*, 1997). The exponential growth of the parthenogenetically multiplying population is probably additionally accelerated by the development of new parthenogenetic eggs in the parent brood chamber before the previous embryos are fully developed and released.

Although cladocerans are often viewed as a 'secondary' constituent of marine zooplankton communities, they are widely distributed in marine ecosystems and may form a significant fraction in zooplankton communities in the Baltic Sea (Hessle and Vallin, 1934; Ackefors, 1969; Sandström, 1982; Kankaala, 1987; Lumberg and Ojaveer, 1991; Line and Sidrevics, 1995; Viitasalo *et al.*, 1995; Möllmann *et al.*, 2005; Ikauniece, 2006). Cladocerans possess an ability to increase their abundance by using parthenogenetic reproduction if the environment is favourable. This ability makes them especially adapted to opportunistic utilisation of seasonally changing resources (Brandl, 2002), enabling them to achieve seasonally very high abundances and play significant roles in the diet of various planktivorous fish and invertebrate predators at high densities (Hansson *et al.*, 1990; Rudstam *et al.*, 1992; Flinkman *et al.*, 1992, 1998; Egloff *et al.*, 1997; Lankov *et al.*, unpublished data). It has been also suggested that cladoceran populations (incl. Podonidae) are, in addition to key abiotic parameters and diet availability, regulated by top-down processes through

direct predation both by invertebrates and fish (e.g., Horsted *et al.*, 1988; Põllumäe and Kotta, 2007).

The cladoceran community of the Baltic Sea is dominated by five taxa: *Bosmina* spp., *Podon intermedius*, *Podon leuckarti*, *Pleopis polyphemoides*, *Evadne nordmanni* and the alien *Cercopagis pengoi*. *Pleopis polyphemoides* is a eurythermic species and prefers brackish and fresher parts of river estuaries. Unfortunately, in the quantitative analysis of most Baltic zooplankton studies which has included cladocerans, *P. polyphemoides* has not been distinguished from the morphologically relatively similar other podonids *Podon leuckarti* and *Podon intermedius* (e.g., Dippner *et al.*, 2000; Uitto, 2000; Möllmann *et al.*, 2002; Aleksandrov *et al.*, 2009) and there is no information about the reproduction of *P. polyphemoides* in this region. However, there are a number of relatively detailed investigations with high spatio-temporal resolution of annual density development, population structure, fecundity and production of *P. polyphemoides* elsewhere in the world, such as Chesapeake Bay (Bosch and Taylor, 1973a, 1973b), the North Atlantic and the North Sea (Gieskes, 1971a, 1971b, 1971c), the Inland Sea of Japan (Onbé, 1973, 1985; Onbe *et al.*, 1977), Narragansett Bay (Egloff *et al.*, 1997), Guanabara Bay in south-eastern Brazil (Marazzo and Valentin, 2003c; Valentin *et al.*, 2003) and a semi-enclosed bay in Hong Kong (Wong *et al.*, 2004).

The the lack of knowledge for the Baltic and the importance of cladocerans in the Baltic zooplankton communities as well as energy transfer to higher trophic levels led us to carry out detailed seasonal investigations on *P. polyphemoides*. The objective of the current study was to investigate the species in a shallow eutrophic Pärnu Bay during the ice-free season with respect to density dynamics, reproduction modes, individual fecundity and body length in relation to selected key environmental background parameters such as water temperature, salinity and chlorophyll *a* concentration.

## Method

### Study area

Pärnu Bay, located in the northeastern part of the Gulf of Riga (Fig. 1), is a relatively enclosed and very shallow (maximum depth around 10 m) sea area covering approximately 700 km<sup>2</sup> with a volume of 2 km<sup>3</sup>. In most years Pärnu Bay is covered by ice from December/January to March/April. In summer, the average surface water temperature has reached 22–23°C during July–August. The salinity of the bay fluctuates from almost freshwater to 7.5 psu. The hydrographic

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2 conditions are formed under the complex influence of ice conditions, freshwater inputs from the  
3 Pärnu River and the water exchange with the Gulf of Riga. The bay suffers from extensive human  
4 pressures (recreation, eutrophication, fishing) (e.g., Kotta *et al.*, 2008). Based on the coastal  
5 morphology, associated hydrographic features and composition and seasonal dynamics of biota,  
6 Pärnu Bay falls into two parts, the inner and the outer basin.  
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13 Sampling

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16 Zooplankton samples were collected during daytime at two monitoring stations located in the inner  
17 and outer basins of Pärnu Bay during the ice-free period (April–November) in 2006. The sampling  
18 frequency was three times a month throughout the study period; the results obtained are considered  
19 as being representative of the 10-day periods per month. The inner bay sampling station (called  
20 hereafter the coastal station) is located in the vicinity of the Pärnu River estuary at 6–7 m depth and  
21 is directly and strongly under riverine freshwater inputs. The outer bay station (hereafter the open  
22 sea station) is located at a depth of 10 m. The conditions there are influenced by hydrological  
23 processes in the Gulf of Riga.  
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32 Sampling was performed using a Juday net (mouth opening 0.1 m<sup>2</sup>; mesh size 100 µm) integrating  
33 the whole water-column vertically. The samples were preserved immediately after sampling with  
34 formalin; final concentration ca 4%. Measurements of temperature, salinity and chlorophyll *a* (Chl  
35 *a*) were made by means of a CTD (model SAIV SD204). Zooplankton sampling and analysis  
36 followed the guidelines developed for the HELCOM COMBINE programme (HELCOM, 2006).  
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43 Sample analysis

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46 Body length of *P. polyphemoides* was measured from the top of the head to the end of the caudal  
47 outgrowths. Total length was determined from the top of the head to the end of the brood pouch  
48 (detailed information on conventional measurements of *Pleopis* is provided in Egloff *et al.*, 1997).  
49 All *P. polyphemoides* individuals were counted in the following categories: parthenogenetic  
50 females, gamogenetic females and males. Additionally, fecundity of parthenogenetic (number of  
51 embryos) and gamogenetic females (number of resting eggs) was determined. Embryonic  
52 development in *P. polyphemoides* was divided into four stages (I to IV), based on easily  
53 distinguishable external characteristics found in Podonidae (Wong *et al.*, 2004; Atienza *et al.*,  
54 2008). The body length of parthenogenetic embryos was measured by different developmental  
55 stages separately. Altogether, 8694 *P. polyphemoides* individuals were analysed.  
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Data analyses were performed by the statistical software “Statistica” version 8.0 and R. The R package relaimpo (relative importance of regressors in the linear models) method LMG was applied for tests between the total abundance (in 10-day periods), body size, fecundity of *P. polyphemoides* and different continuous abiotic variables. The relationship between the body size and fecundity of parthenogenetic females was estimated by a Spearman rank correlation analysis. The significance of differences in the body size of parthenogenetic females within and between the coastal and the open sea station was estimated by the post hoc Bonferroni test in repeated measures analysis of variance (ANOVA) where 10-day period was used as a time factor. The significance of differences in the body size of gamogenetic females and males between the coastal and the open sea station was estimated by one-way ANOVA. The difference between the body size of gamogenetic females and parthenogenetic females within and between stations was estimated by one-way ANOVA. The differences were considered significant at  $p < 0.05$ .

## Results

### Background conditions

In 2006, the retreat of the ice cover from Pärnu Bay was recorded at the end of April. At that time the water temperature exceeded 5°C at both the coastal and the open sea station. The seasonal temperature development was very similar at both stations with a sharp increase during the beginning of June and a peak in mid-July (25.5°C in the coastal and 23.1°C in the open sea station). A progressive decrease in water temperature was recorded for the rest of the season (Fig. 2A). There was a notable difference in salinity between the coastal and the open sea station, especially in spring with very low values at the coastal station. Salinity varied from 1.3 to 5.9 psu (mean 4.4 psu) at the coastal and from 3.6 to 5.9 psu (mean 5.0 psu) at the open sea station. In general, salinity values increased progressively during summer in both areas of the bay (Fig. 2B). The highest Chl *a* concentrations were recorded during the spring bloom: at the coastal station at the end of May (40.4 mg m<sup>-3</sup>) and at the open sea station at the beginning of May (26.9 mg m<sup>-3</sup>). After the spring bloom, Chl *a* concentrations dropped sharply, the values were mostly below 4 mg m<sup>-3</sup> during June–July. A moderate continuous increase in Chl *a* concentration (from 0.8 to 8.4 mg m<sup>-3</sup>) was observed at both stations from the end of July until the end of the season (Fig. 2C).

### Seasonal abundance dynamics



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2 The first individuals of *P. polyphemoides* appeared in Pärnu Bay at the beginning of May. At the  
3 coastal station, the densities reached the level of 1000 ind. m<sup>-3</sup> already by the end of May while at  
4 the open sea station, the density was substantially lower, around 600 ind. m<sup>-3</sup>. A rapid increase in  
5 the abundance of *P. polyphemoides* was observed from the beginning of June onward. The  
6 maximum abundance at the coastal station was registered in mid-June (6729 ind. m<sup>-3</sup>) while at the  
7 open sea station the maximum (7350 ind. m<sup>-3</sup>) was recorded 10 days later. The seasonal abundance  
8 peak was followed by a rapid decrease until mid-July (Fig. 3). Compared to the open sea station, the  
9 duration of the occurrence of *P. polyphemoides* was substantially more restricted at the coastal  
10 station: at the former, the species disappeared from the plankton community about two weeks later  
11 than at the latter. However, a few individuals were found at both stations as late as in December.

21 A strong positive relationship between the abundance of *P. polyphemoides* and water temperature  
22 was evident for parthenogenetic individuals ( $R^2 = 0.82$ ; relaimpo) as well as for gamogenetic  
23 females and males ( $R^2 = 0.9$ ; relaimpo). The relationship was weak and negative between  
24 abundance and Chl *a* concentration. Salinity and Chl *a* seemed to have no impact on *P.*  
25 *polyphemoides* abundance.

32 Reproduction mode

35 Parthenogenetic females of *P. polyphemoides* dominated in the population at both stations (Fig. 4).  
36 In May, only parthenogenetic females were found. Gamogenetic females and males appeared at the  
37 coastal station about 10 days earlier than at the open sea station (accounting for 2% and 11% of the  
38 total population abundance at the coastal and the open sea station, respectively). Gamogenetic  
39 reproduction was the most intense during or immediately after the *P. polyphemoides* population  
40 abundance peak (from the middle to the end of June) when the proportion of parthenogenetic  
41 females was already in a sharply decreasing phase (constituting 36% of the gamogenetic females  
42 and males at the coastal and 17% at the open sea station). In both areas, the abundance of  
43 gamogenetic individuals of *P. polyphemoides* rapidly decreased after their abundance peak. Males  
44 of *P. polyphemoides* disappeared from the plankton community in early July at the coastal station  
45 and about a month later at the open sea station. However, gamogenetic females were sporadically  
46 found also in autumn (in October) as was the case for parthenogenetic females.

59 Body size

60 The body length of parthenogenetic females of *P. polyphemoides* significantly differed between the  
coastal and open sea stations ( $p < 0.01$ ; post hoc Bonferroni test, repeated measures ANOVA) with

larger individuals occurring at the coastal station. Such a difference was not evident for total length. The temporal dynamics of the total length of parthenogenetic females was similar at both stations with the largest values recorded prior to the population abundance peak (Table I). In general, parthenogenetic females were found to be the smallest in terms of the total length during or after the population peak. However, no clear patterns could be established for the body length of *P. polyphemoides* in terms of the population peak (Table I). A few large parthenogenetic females were found as late as October with total and body lengths of  $0.42 \pm 0.03$  and  $0.39 \pm 0.02$  mm, respectively. The highest total length/body length ratio was observed when the species first appeared in the plankton community. At that time, only parthenogenetic females were present. Subsequently, when intensive parthenogenetic reproduction began and in addition to large parthenogenetic females young individuals were also present, a lower total length/body length ratio was observed.

The total length of parthenogenetic females was inversely correlated with water temperature ( $R^2 = 0.72$ ; relaimpo) (Fig. 5). However, the body length was positively related to Chl *a* ( $R^2 = 0.82$ ; relaimpo). The total length and the body length of gamogenetic females, on the contrary, were both affected by water temperature,  $R^2 = 0.58$  and  $R^2 = 0.53$ , respectively (Table II). No relationship was found between the body size of males and abiotic environmental parameters, and we were not able to find any significant influence of salinity on the body length and total length of *P. polyphemoides* either.

In gamogenetic females of *P. polyphemoides* no significant difference was found in the total length or body length between the coastal and the open sea station. The total length and body length were greatest in June, when gamogenetic females first appeared to the plankton community. Although they generally disappeared in August, a few individuals were still observed in October with a total length of  $0.53 \pm 0.01$  mm and body length of  $0.43 \pm 0.00$  mm. The total length and body length of gamogenetic females significantly differed from that of parthenogenetic females at the coastal and open station ( $p < 0.01$ ; one-way ANOVA). Similarly to gamogenetic females, males with the maximum total length and body length occurred at the beginning of June, when they first appeared in the zooplankton community. Later in the season, males were significantly smaller (Table I). The body size of males did not differ between the coastal and the open sea station. On some occasions, the body length of males exceeded their total length.

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The fecundity of parthenogenetic females of *P. polyphemoides* was  $5.4 \pm 0.3$  at the coastal station and  $2.9 \pm 0.1$  embryos female<sup>-1</sup> at the open sea station. In both areas, the highest fecundity was associated with the first appearance of the species in the zooplankton community, which occurred at the beginning of May at the coastal station and about a month later at the open sea station (Table III). The maximum number of embryos in a brood pouch (10 embryos female<sup>-1</sup>) was observed also during the initial phase of population growth. The number of embryos per female correlated significantly with the total length at both the coastal ( $r = 0.77$ ;  $p < 0.01$ ) and the open sea station ( $r = 0.93$ ;  $p < 0.01$ ) (Fig. 6). However, there was no correlation between fecundity and body length. Parthenogenetic fecundity of *P. polyphemoides* was found to be higher at lower water temperatures ( $R^2 = 0.69$ ; relaimpo). No effect of Chl *a* concentration or salinity on fecundity was found.

During daytime most *P. polyphemoides* parthenogenetic embryos were at stage II (42%) or III (34%). Only 8% of the embryos were at early developmental stage I and 16% were determined as fully developed (stage IV). At both stations, the size of embryos increased with advancing developmental stage (Table IV). The maximum embryo size before its release from the brood pouch was 0.32 mm.

Gamogenetic females of *P. polyphemoides* carried only one resting egg in the brood pouch. The diameter of the resting egg was  $0.12 \pm 0.01$  mm on average both in the coastal and the open sea station. The gamogenetic female with the largest resting egg (0.2 mm) was recorded at the open sea station in July.

Discussion

In the Baltic Sea, the abundance dynamics of cladocerans (incl. *P. polyphemoides*) is characterised as extremely seasonal: they appear in spring, reach maximum densities in summer and disappear in autumn (Ackefors, 1969; Vuorinen and Ranta, 1987; Viitasalo *et al.*, 1995; Möllmann *et al.*, 2002). This was also confirmed by the current study. A similar seasonal distribution pattern of *P. polyphemoides* has been observed in several other areas of the world (Gieskes, 1971a, 1971b; Platt, 1977; Uye, 1982; Turner, 1992; Marazzo and Valentin, 2003c). However, there is evidence from the Chesapeake Bay (Bosch and Taylor, 1973b), Narragansett Bay (Egloff *et al.*, 1997) and the Marmara Sea (Isinibilir *et al.*, 2008) that this species may have a two-peak seasonal distribution pattern. Further, *P. polyphemoides* is usually a spring to early summer species in the Inland Sea of Japan (Onbé, 1985) and a winter to spring species in St. Andrew's Bay, Florida (Hopkins, 1966).

Thus, there is evidence to suggest that regional variability occurs in respect to seasonal development and duration of occurrence of *P. polyphemoides* in different seas of the world.

The densities of *P. polyphemoides* have been found to substantially differ in different marine areas. Very high densities (over 30 000 ind. m<sup>-3</sup>) of *P. polyphemoides* have been recorded in Chesapeake Bay (Bosch and Taylor, 1973a), in the Inland Sea of Japan (Onbé, 1985) and in Narragansett Bay (Egloff *et al.*, 1997). In the Dardanelles, *P. polyphemoides* is one of the most abundant cladoceran species (maximum over 10 000 ind. m<sup>-3</sup>) after *Penilia avirostris* (Buyukates and Inanmaz, 2007). Considerably lower densities (ca. 150 ind. m<sup>-3</sup>) have been observed in the Marmara Sea (Isinibilir *et al.*, 2008) and ca. 1 500–3 500 in Guanabara Bay, south-eastern Brazil, (Marazzo and Valentin, 2003c) and the west coast of Sweden (Eriksson, 1974), while the species was almost absent in the North Sea (Gieskes, 1971a). The densities of *P. polyphemoides* recorded within the current study were similar to those reported from the other areas of the Baltic Sea (below 10 000 ind. m<sup>-3</sup>), e.g., the northern Baltic Sea (Vuorinen and Ranta, 1987), Gulf of Finland (Pöllumäe and Kotta, 2007) and Pomeranian Bay (Chojnacki and Antończak, 2008).

The obvious reason behind the abrupt increase of cladoceran populations in spring/early summer is rapid and intense parthenogenetic reproduction, associated with rising water temperature (Egloff *et al.*, 1997; Rivier, 1998; Marazzo and Valentin, 2003a, 2003b, 2003c). The population of *P. polyphemoides* in Pärnu Bay in spring and early summer, i.e., before the abundance peak when the water temperature increased rapidly, was characterised by the presence of relatively large parthenogenetic individuals, which were found to be generally more fecund than smaller individuals. This was shown not only by a significant positive correlation between parthenogenetic fecundity and total female length, but also by a negative correlation between parthenogenetic fecundity and water temperature. A positive relationship between total length and fecundity was expected, as total length is mainly determined by the reproductive phase and number of embryos in a brood pouch (Marazzo and Valentin, 2003c). However, body length, was not related to fecundity characteristics. Remarkably, some very large (and highly fecund: 10 embryos female<sup>-1</sup>) parthenogenetic individuals, probably hatched from resting eggs, were found during the very initial stages of population development. Overall, the parthenogenetic females exhibited significant seasonal variability in their total length, achieving the largest values just prior to the population abundance peak and having usually smaller values afterwards with lowered individual fecundity. In general, the fecundity of marine cladocerans typically appears to be higher during the initial phases of population growth, decreasing rapidly as the population increases (Platt and Yamamura, 1986; Mullin and Onbé, 1992; Egloff *et al.*, 1997; Rivier, 1998). In contrast, we found no clear relation

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between parthenogenetic fecundity and *P. polyphemoides* density. The observed parthenogenetic fecundity of *P. polyphemoides* in Pärnu Bay seems to be comparable to that of this species in other areas (Murakami and Onbé, 1967; Onbé, 1974; Marazzo and Valentin, 2003c).

The eyes of the embryos of marine cladocerans become pigmented at the final stage when the embryos are fully developed (Platt and Yamamura, 1986). Because planktivorous fish select for the pigmented structures (Zaret and Kerfoot, 1975; Flinkman *et al.*, 1992), it has been suggested that the reason for the release of neonates by cladocerans at night is the decrease in fish predation (Wong *et al.*, 2004). Our observations showed that during the daytime, most of the embryos in the female brood pouch were in stages II and III while the share of fully developed embryos (i.e., stage IV) was very low. However, whether this was due to nocturnal release of neonates and predation remains unclear and should be investigated in the future.

Marine cladocerans attain high population abundances very rapidly, but these are generally sustained only for a very short time. Reasons for a sudden decrease of cladoceran populations are relatively poorly understood. However, this decrease is typically accompanied by an intensive gamogenetic reproduction (Onbé, 1978) resulting in the production of diapausing (resting) eggs at the end of the reproductive season. This has been suggested to be triggered by changes in environmental conditions and aimed at ensuring survival of the species over the winter (Egloff *et al.*, 1997; Rivier, 1998). In contrast to this, in the current study no strong and significant relationships were found between the appearance of gamogenetic females carrying resting eggs and the abiotic variables measured. This is probably because no clear shift between the two reproduction modes was detected and the species was found to reproduce both parthenogenetically and gamogenetically almost during the whole reproductive season, with relatively intense gamogenetic reproduction lasting for about a month. It has been suggested earlier that the onset of sexual reproduction in podonids generally follows a sharp reduction in parthenogenetic fecundity (Bainbridge, 1958; Onbé, 1974; Egloff *et al.*, 1997; Rivier, 1998). Although no clear shift in reproduction modes was detected in this study, we did observe substantially intensified gamogenetic reproduction at the population abundance maximum or soon after it, which was accompanied by decreasing fecundity of parthenogenetic females. After intense production of resting eggs begins, the population of *P. polyphemoides* may almost disappear but parthenogenetic reproduction may still continue for several months (Della Croce and Venugopal, 1973; Rivier, 1998). This pattern was also observed in our study.

The sexual reproduction process may be terminated by water temperature. It has been found that gamogenetic females are not present in cladoceran communities above certain water temperatures.



For instance, in the Chesapeake Bay, gamogenetic females disappeared at water temperatures exceeding 23°C (Bosch and Taylor, 1973b) and in Narragansett Bay at 22.5°C (Egloff *et al.*, 1997). Temperature control may serve as a possible explanation for the disappearance of gamogenetic females of *P. polyphemoides* from Pärnu Bay at water temperatures exceeding 22°C.

It was found that gamogenetic females of *P. polyphemoides* carried one resting egg in Pärnu Bay. In other studies gamogenetic females of *P. polyphemoides* with more than one resting egg have not been seen either (Onbé, 1974; Egloff *et al.*, 1997). The maximum recorded percentages of gamogenetic individuals in a population range from less than 10% for *P. polyphemoides* in the Inland Sea of Japan (Onbé, 1978) and in the Chesapeake Bay (Bosch and Taylor, 1973b) to 46% in Narragansett Bay (Egloff *et al.*, 1997). In a tropical Guanabara Bay, characterised by substantially lower densities of *P. polyphemoides*, the share of gamogenetic individuals was remarkably more stable (20–50%) (Marazzo and Valentin, 2003c), indicating that a smaller population continuously sustains higher production of resting eggs throughout the reproductive season. In contrast, the proportion of gamogenetic females of *P. polyphemoides* in Pärnu Bay varied over a very wide range. It has been suggested that low incidences of gamogenetic reproduction may result from the failure of parthenogenetic females to be transformed to gamogenetic females, as was the case for *P. polyphemoides* in Narragansett Bay (Egloff *et al.*, 1997).

Several investigators have argued that the environment plays a key role in declines of cladoceran populations. Amongst others, temperature, salinity, food availability, water transparency and predation have been indicated as regulating factors (Calbet *et al.*, 2001; Marques *et al.*, 2006; Atienza *et al.*, 2008). Further, it is possible that instead of any single factors, interaction of several ones (such as stratification of the water column, higher water temperatures and associated prey availability) are important (Atienza *et al.*, 2008). In the Baltic Sea, temperature, salinity and predation by planktivorous fish as well as predatory invertebrates have been indicated to influence the abundance dynamics of small-sized cladocerans at various spatio-temporal scales (Ikauniece, 2001; Möllmann *et al.*, 2002; Kotta *et al.*, 2004; Ojaveer *et al.*, 2004; Pöllumäe and Kotta, 2007; Casini *et al.*, 2009; Kotta *et al.*, 2009). In the current study, it was found to be unlikely that temperature triggered the observed sharp density drop because the *P. polyphemoides* population started to decline at the time when water temperature was at its maximum. Neither was there any relationship between salinity and population abundance. Most investigators assume that podonids primarily feed on dinoflagellates because of the observed high abundance of podonids during dinoflagellate blooms (Bainbridge, 1958; Egloff *et al.*, 1997). This, however, could not be the case in Pärnu Bay, because in this bay dinoflagellates form an insignificant fraction of the phytoplankton

community during summer (A. Jaanus, Tallinn, personal communication) when *P. polyphemoides* is present. Besides, in the current study, population abundance correlated negatively with Chl *a* concentration. We suggest that it was rather predator–prey interactions that were responsible for the observed decline as the predation pressure on zooplankton should be high in the study area, which is biologically a very productive region and acts as an important spawning and nursery ground for several fish species (Simm and Ojaveer, 2000; Lankov *et al.*, 2006). As there is evidence on the predation-induced mortality of small-sized cladocerans in the Baltic Sea (Kotta *et al.*, 2004; Ojaveer *et al.*, 2004; Põllumäe and Kotta, 2007) as well as for other regions (Gliwicz, 2001; Marazzo and Valentin, 2003c), we hypothesize that predation should be an important factor behind the sharp drop of the abundance of *P. polyphemoides* during summer. This hypothesis is backed by the fact that the size of parthenogenetic females was significantly lower at and/or soon after the seasonal population peak, potentially indicating predation mortality of larger individuals.

Essentially because of a very short generation time, cladoceran abundance is highly variable at the fine-scale level, stressing thus the importance of spatio-temporal scale considerations when designing studies on cladocerans. The current investigation provides additional information on the spatio-temporal dynamics of vital rates of one of the most abundant cladoceran species in the Baltic Sea, *P. polyphemoides*, which is, amongst others, one of the most important diet items for several pelagic fish species in the Gulf of Riga (Lankov *et al.*, unpublished data.). Also, it was suggested (Põllumäe and Kotta, 2007) that in the Gulf of Finland the non-indigenous *C. pengoi* may suppress *P. polyphemoides* abundance and significantly modify its density dynamics. While only a few measured parameters (e.g., abundance, parthenogenetic and gamogenetic fecundity, body size of gamogenetic individuals) were relatively stable across the sampled stations in Pärnu Bay, several key characteristics (such as timing, duration as well as the body size of *P. polyphemoides*) exhibited differences between the coastal and the open sea station. It should be noted that both stations are in fact relatively coastal, shallow and sheltered from strong winds. Further studies should resolve some of the important issues discussed in the study, like causes of the abundance drop in summer, mechanisms behind the dissimilar performance of *P. polyphemoides* in the inner and the outer bay as well as annual-scale variability in the seasonal dynamics of *P. polyphemoides*. Finally, results of the current study provide additional considerations for limitations of interpretation of analysis of long-time datasets based on a relatively coarse time-scale sampling design.

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2 Table and Figure legends  
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5  
6 Table I. Dynamics of the body length (BL) and total length (TL) (mm; mean  $\pm$  SE) of *Pleopis*  
7 *polyphemoides* in the coastal and the open sea station in Pärnu Bay by 10-day periods (D) during  
8 May–August 2006  
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12 Table II. Relative importances ( $R^2$ ) of different environmental variables for the total length (TL)  
13 and the body length (BL) of *Pleopis polyphemoides*  
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18 Table III. Fecundity (embryos female<sup>-1</sup>; mean  $\pm$  SE) of parthenogenetic females of *Pleopis*  
19 *polyphemoides* in the coastal and the open sea station in Pärnu Bay by 10-day periods (D)  
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23 Table IV. Length (mm; mean  $\pm$  SE) of parthenogenetic embryos of *Pleopis polyphemoides* by  
24 different developmental stages in the coastal and the open sea station in Pärnu Bay  
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29 Fig. 1. Location of the sampling sites, coastal station in the inner bay (empty circle) and open sea  
30 station in the outer bay (filled circle) in Pärnu Bay (Baltic Sea).  
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34 Fig. 2. Dynamics of sea surface temperature (A), salinity (B) and chlorophyll *a* concentration (C) in  
35 the coastal (solid line) and the open sea station (bold line) in Pärnu Bay in 2006.  
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39 Fig. 3. Abundance dynamics of *Pleopis polyphemoides* in the coastal (solid line) and the open sea  
40 station (bold line) in Pärnu Bay in 2006.  
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44 Fig. 4. Abundance dynamics of parthenogenetic females (solid line, left scale) and gamogenetic  
45 females (black columns, right scale) and males (white columns, right scale) of *Pleopis*  
46 *polyphemoides* in the coastal (A) and the open sea station (B) in Pärnu Bay in 2006.  
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51 Fig. 5. Seasonal dynamics of the total length of parthenogenetic females of *Pleopis polyphemoides*  
52 and surface water temperature (dotted line) in Pärnu Bay in 2006.  
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57 Fig. 6. Scatterplot of total length and fecundity (number of embryos female<sup>-1</sup>) of *Pleopis*  
58 *polyphemoides* in the coastal (empty circles) and the open sea (filled circles) station in Pärnu Bay.  
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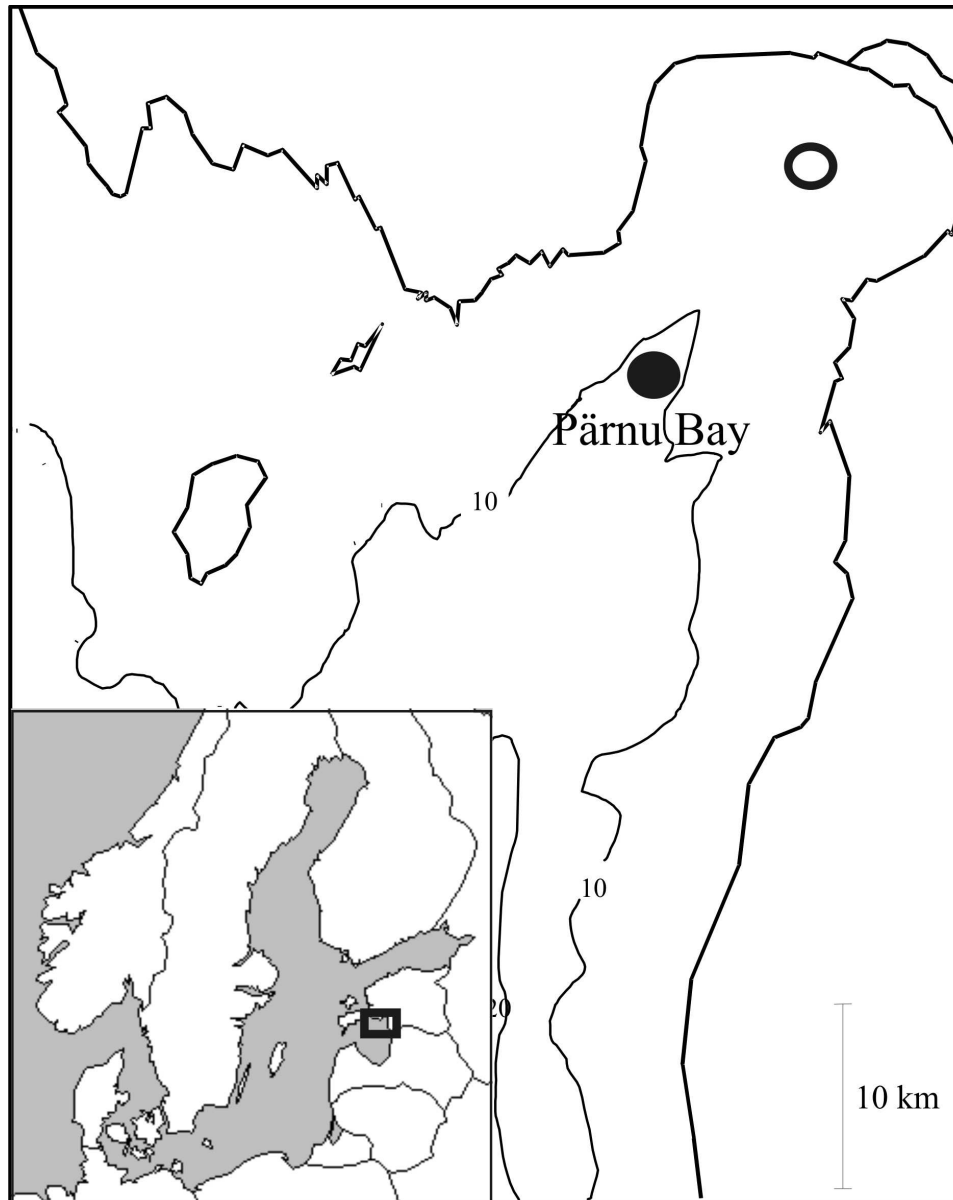


Fig. 1. Location of the sampling sites, coastal station in the inner bay (empty circle) and open sea station in the outer bay (filled circle) in Pärnu Bay (Baltic Sea).  
79x99mm (600 x 600 DPI)



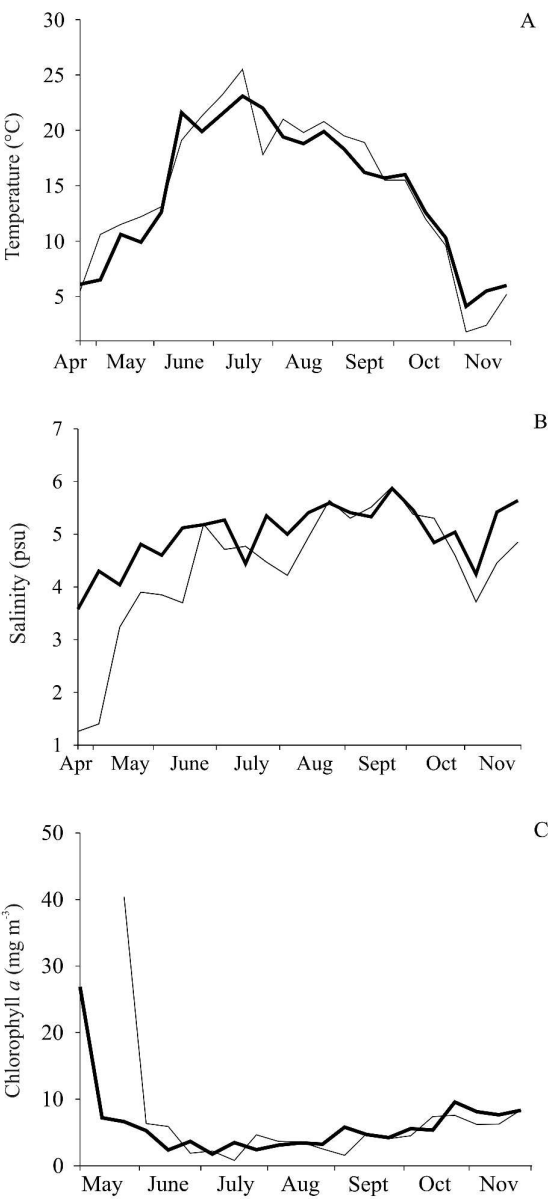


Fig. 2. Dynamics of sea surface temperature (A), salinity (B) and chlorophyll *a* concentration (C) in the coastal (solid line) and the open sea station (bold line) in Pärnu Bay in 2006.  
79x169mm (600 x 600 DPI)

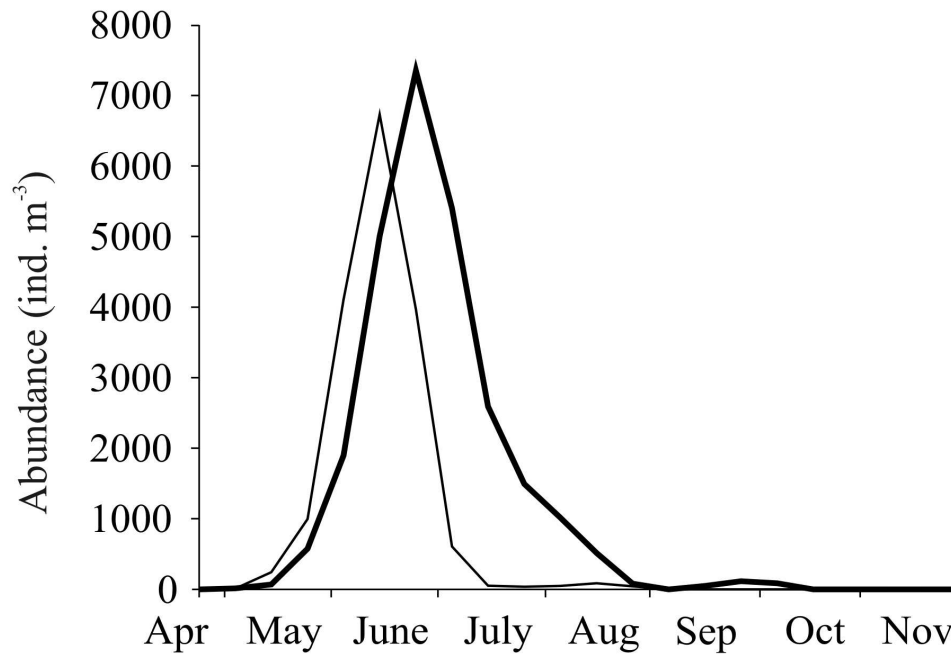


Fig. 3. Abundance dynamics of *Pleopis polyphemoides* in the coastal (solid line) and the open sea station (bold line) in Pärnu Bay in 2006.  
79x57mm (600 x 600 DPI)

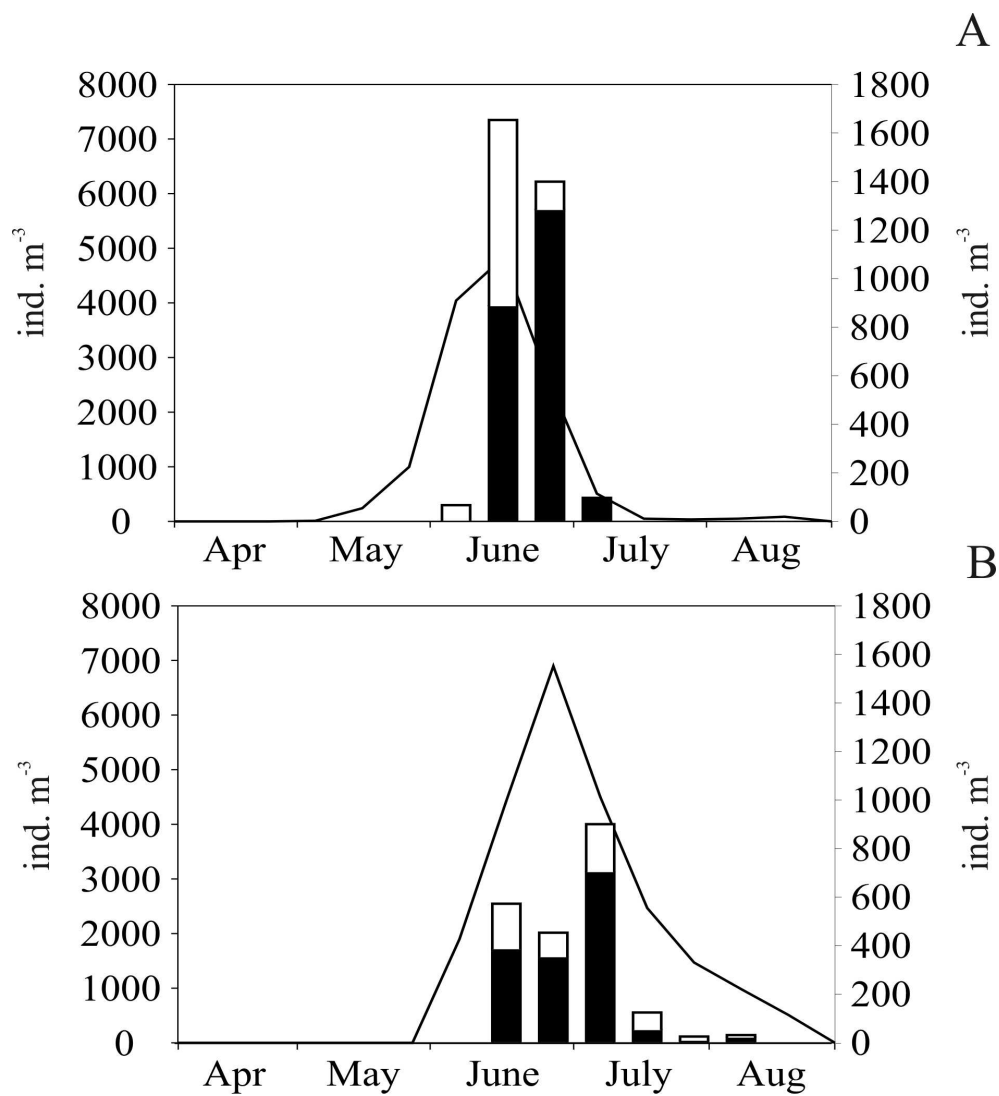


Fig. 4. Abundance dynamics of parthenogenetic females (solid line, left scale) and gamogenetic females (black columns, right scale) and males (white columns, right scale) of *Pleopis polyphemoides* in the coastal (A) and the open sea station (B) in Pärnu Bay in 2006. 79x97mm (600 x 600 DPI)

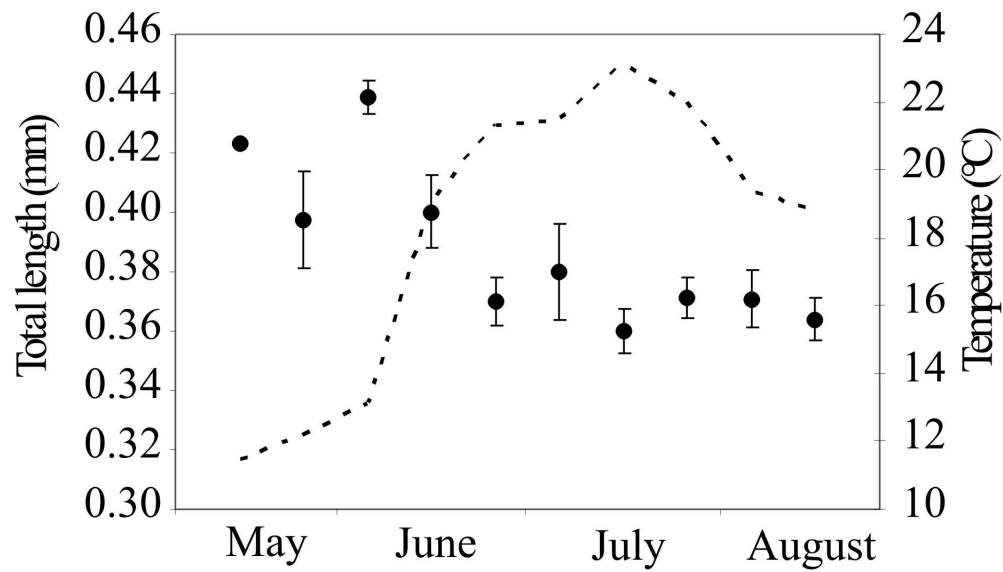


Fig. 5. Seasonal dynamics of the total length of parthenogenetic females of *Pleopis polyphemoides* and surface water temperature (dotted line) in Pärnu Bay in 2006.  
79x47mm (600 x 600 DPI)

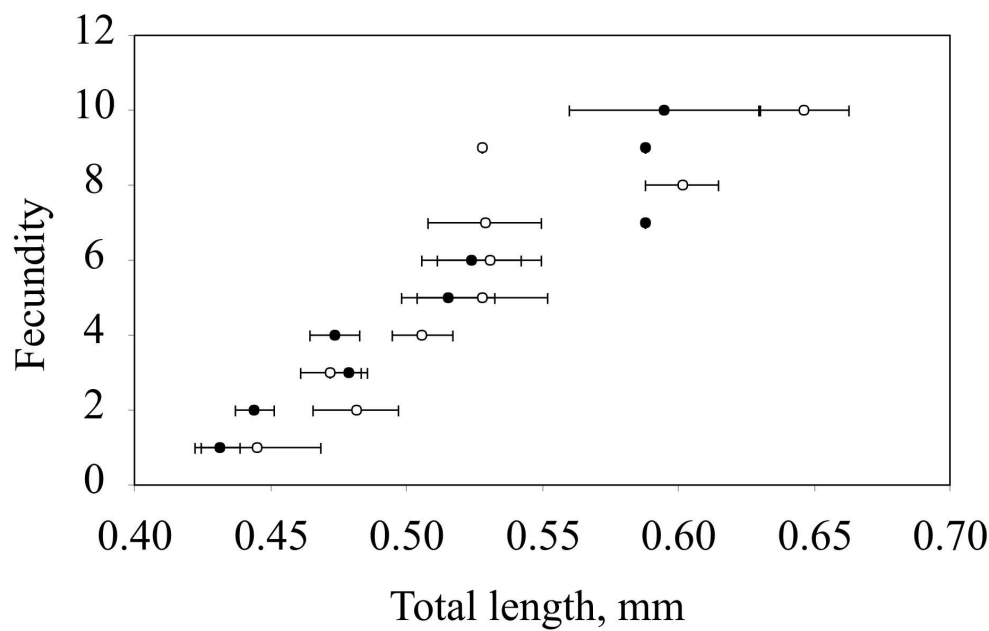


Fig. 6. Scatterplot of total length and fecundity (number of embryos female-1) of *Pleopis polyphemoides* in the coastal (empty circles) and the open sea (filled circles) station in Pärnu Bay. 79x51mm (600 x 600 DPI)

Table I. Dynamics of the body length (BL) and total length (TL) (mm; mean  $\pm$  SE) of *Pleopis polyphemoides* in the coastal and the open sea station in Pärnu Bay by 10-day periods (D) during May–August in 2006

| Parthenogenetic females |   |     |                 |                 | Gamogenetic females |                 |                 | Males |                 |                 |
|-------------------------|---|-----|-----------------|-----------------|---------------------|-----------------|-----------------|-------|-----------------|-----------------|
| Month                   | D | n   | BL              | TL              | n                   | BL              | TL              | n     | BL              | TL              |
| Coastal station         |   |     |                 |                 |                     |                 |                 |       |                 |                 |
| May                     | 2 | 26  | 0.35 $\pm$ 0.01 | 0.42 $\pm$ 0.02 | —                   | —               | —               | —     | —               | —               |
|                         | 3 | 163 | 0.24 $\pm$ 0.00 | 0.40 $\pm$ 0.01 | —                   | —               | —               | —     | —               | —               |
| June                    | 1 | 57  | 0.38 $\pm$ 0.01 | 0.44 $\pm$ 0.01 | —                   | —               | —               | 3     | 0.45 $\pm$ 0.00 | 0.48 $\pm$ 0.00 |
|                         | 2 | 67  | 0.39 $\pm$ 0.01 | 0.40 $\pm$ 0.01 | 9                   | 0.46 $\pm$ 0.01 | 0.50 $\pm$ 0.01 | 18    | 0.43 $\pm$ 0.01 | 0.44 $\pm$ 0.01 |
|                         | 3 | 7   | 0.35 $\pm$ 0.02 | 0.37 $\pm$ 0.02 | 4                   | 0.40 $\pm$ 0.02 | 0.46 $\pm$ 0.02 | —     | —               | —               |
| Open sea station        |   |     |                 |                 |                     |                 |                 |       |                 |                 |
| June                    | 1 | 95  | 0.34 $\pm$ 0.01 | 0.42 $\pm$ 0.01 | —                   | —               | —               | —     | —               | —               |
|                         | 2 | 572 | 0.37 $\pm$ 0.00 | 0.40 $\pm$ 0.00 | 38                  | 0.44 $\pm$ 0.00 | 0.49 $\pm$ 0.01 | 34    | 0.42 $\pm$ 0.01 | 0.46 $\pm$ 0.01 |
|                         | 3 | 89  | 0.33 $\pm$ 0.00 | 0.34 $\pm$ 0.01 | 3                   | 0.42 $\pm$ 0.02 | 0.45 $\pm$ 0.01 | 3     | 0.35 $\pm$ 0.02 | 0.33 $\pm$ 0.01 |
| July                    | 1 | 43  | 0.37 $\pm$ 0.01 | 0.38 $\pm$ 0.01 | 4                   | 0.41 $\pm$ 0.02 | 0.43 $\pm$ 0.01 | 6     | 0.34 $\pm$ 0.02 | 0.35 $\pm$ 0.02 |
|                         | 2 | 49  | 0.35 $\pm$ 0.01 | 0.36 $\pm$ 0.01 | —                   | —               | —               | —     | —               | —               |
|                         | 3 | 59  | 0.34 $\pm$ 0.01 | 0.37 $\pm$ 0.01 | 1                   | 0.40            | 0.46            | 2     | 0.34 $\pm$ 0.02 | 0.35 $\pm$ 0.03 |
| August                  | 1 | 59  | 0.36 $\pm$ 0.01 | 0.37 $\pm$ 0.01 | 4                   | 0.42 $\pm$ 0.01 | 0.46 $\pm$ 0.01 | 2     | 0.32 $\pm$ 0.01 | 0.34 $\pm$ 0.00 |
|                         | 2 | 6   | 0.36 $\pm$ 0.02 | 0.36 $\pm$ 0.03 | —                   | —               | —               | —     | —               | —               |

Table II. Relative importances ( $R^2$ ) of different environmental variables for the total length (TL) and the body length (BL) of *Pleopis polyphemoides*

|                            | Parthenogenetic females |      |      | Gamogenetic females |      |
|----------------------------|-------------------------|------|------|---------------------|------|
|                            | n                       | TL   | BL   | TL                  | BL   |
| Chl <i>a</i> concentration | 15                      | 0.13 | 0.82 | 0.08                | 0.09 |
| Temperature                | 15                      | 0.72 | 0.12 | 0.58                | 0.53 |
| Salinity                   | 15                      | 0.14 | 0.05 | 0.34                | 0.39 |

Table II. Fecundity (embryos female<sup>-1</sup>; mean  $\pm$  SE) of parthenogenetic females of *Pleopis polyphemoides* in the coastal and the open sea station in Pärnu Bay by 10-day periods (D)

| Month            | D | n   | Embryos female <sup>-1</sup> |
|------------------|---|-----|------------------------------|
| Coastal station  |   |     |                              |
| May              | 2 | 23  | 7.7 $\pm$ 0.4                |
|                  | 3 | 7   | 5.9 $\pm$ 0.3                |
| June             | 1 | 21  | 5.6 $\pm$ 0.3                |
|                  | 2 | 19  | 2.3 $\pm$ 0.2                |
| Open sea station |   |     |                              |
| June             | 1 | 13  | 4.0 $\pm$ 1.0                |
|                  | 2 | 105 | 3.2 $\pm$ 0.1                |
| July             | 1 | 16  | 1.6 $\pm$ 0.2                |
|                  | 2 | 12  | 1.5 $\pm$ 0.2                |
|                  | 3 | 27  | 3.0 $\pm$ 0.3                |
| August           | 1 | 17  | 1.2 $\pm$ 0.1                |



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Table III. Length (mm; mean  $\pm$  SE) of parthenogenetic embryos of *Pleopis polyphemoides* by different developmental stages in the coastal and the open sea station in Pärnu Bay

| Embryo stage     | n  | avg $\pm$ SE    | min – max   |
|------------------|----|-----------------|-------------|
| Coastal station  |    |                 |             |
| I                | 8  | 0.13 $\pm$ 0.01 | 0.08 – 0.17 |
| II               | 22 | 0.18 $\pm$ 0.01 | 0.11 – 0.24 |
| III              | 17 | 0.21 $\pm$ 0.01 | 0.14 – 0.27 |
| IV               | 24 | 0.26 $\pm$ 0.00 | 0.19 – 0.31 |
| Open sea station |    |                 |             |
| I                | 12 | 0.11 $\pm$ 0.01 | 0.05 – 0.17 |
| II               | 87 | 0.16 $\pm$ 0.00 | 0.08 – 0.24 |
| III              | 73 | 0.21 $\pm$ 0.00 | 0.14 – 0.27 |
| IV               | 19 | 0.23 $\pm$ 0.01 | 0.15 – 0.32 |