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# *Acineta nitocrae*: A new suctorian epizooic on nonindigenous harpacticoid copepods, *Nitocra hibernica* and *N. incerta*, in the Laurentian Great Lakes

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With 6 figures and 2 tables

**Abstract:** *Acineta nitocrae*, a suctorian ciliate previously known from Ukraine, was discovered in western Lake Erie in October 1997 and in the Detroit River in May 1999. Individuals were found inhabiting the body surface of *Nitocra hibernica* and *N. incerta*, nonindigenous harpacticoid copepods. *Acineta nitocrae* infested 64 % of *N. hibernica* in Lake Erie, whereas in Ukraine it infested between 24 and 80 % of *N. hibernica* populations. In Lake Erie, *N. hibernica* copepods suffered lower suctorian burdens than conspecific individuals in native habitats in Ukraine. In Ukraine, this suctorian was also found on two other harpacticoid species – *Nitocra lacustris* and *Canthocamptus staphylinus*. The highest preference of *A. nitocrae* was established for *N. hibernica*. *Acineta nitocrae* individuals from Lake Erie and Ukrainian populations of *N. hibernica* were similar with respect to dimensions of the lorica and stalk, but differed significantly in terms of the length and width of actinophores, with highest values observed for Lake Erie. Occurrence of *A. nitocrae* in the Great Lakes may be related to the introduction of its hosts, *N. hibernica* and *N. incerta*.

**Key words:** Ciliates, protists, potential invasions, Lake Erie, Ukraine.

## Introduction

Taxonomic diversity in the Protista has been studied insufficiently throughout many parts of the world, and new protist species continue to be described in

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many regions known for their long history of protistological research (TAYLOR & SANDERS 1991). Freshwater, sessile and sedentary protists appear to be restricted in their geographic ranges. For example, nearly 120 species of suctorian, chonotrich, and peritrich ciliates are endemic to Lake Baikal in Siberia (JANKOWSKI 1973, 1982). Conversely, many free-living protists are noted for their widespread or cosmopolitan geographic distributions (TAYLOR & SANDERS 1991). For many of these species, however, unrecognized historical transport may have led to false conclusions of their cosmopolitanism. Consequently, the occurrence of previously unrecognized species in regions impacted by ships' ballast discharge, such as the Laurentian Great Lakes, must be viewed critically as potential invasions (CARLTON & GELLER 1993).

The status of many protist species can be classified as cryptogenic since no reliable historical data are available to support their origin (CARLTON 1996). MILLS et al. (1994) inferred that the protists of the Laurentian Great Lakes "are likely to contain exotic species that remain undiscovered or have been mistakenly considered as Great Lakes natives..." because taxonomists had not studied this group until entry vectors had been in place for decades or even hundreds of years. Indeed, the actual number of introduced protist species may be highly underestimated in the Great Lakes, where they presently account for roughly 2 % (3 species) of all recognized introductions (MILLS et al. 1993, RICCIARDI & MACISAAC 2000). This insignificant fraction of exotic protists is in poor agreement with the enormous richness of the freshwater Protista, which amount to as much as 33.3 % (~30,000 species) of the global species diversity of fresh waters (COX 1997).

At least three species of parasitic protists are believed to have been transported to the Great Lakes with their fish hosts. The European native microsporidan, *Glugea hertwigi*, was probably introduced with the rainbow smelt, *Osmerus mordax*, in the 1950s (reviewed in MILLS et al. 1993). The Eurasian native kinetoplastid, *Trypanosoma acerinae*, invaded with the ruffe, *Gymnocephalus cernuus*, in the 1980s (PRONIN et al. 1998). *Myxosoma cerebrale* (synonym = *Myxobolus cerebralis*), a myxosporidian of unknown origin that is responsible for salmonid whirling disease, may have colonized the Great Lakes through the release of salmonid fishes in the 1960s (MILLS et al. 1993). No other protists have been recorded as introduced or cryptogenic taxa in the Great Lakes to date.

In this study, we describe the first record of the suctorian *Acineta nitocrae* from western Lake Erie in October 1997 and from the Detroit River in May 1999. We assess morphological characteristics of suctorians recovered from *Nitocra hibernica* in Lake Erie and contrast these patterns with comparable individuals from three host harpacticoid copepod species collected from Ukrainian basins – *N. hibernica, N. incerta* and *N. lacustris*. The occurrence of *A. nitocrae* on the Eurasian native harpacticoid copepods *Nitocra hibernica* and

*N. incerta* in the lower Great Lakes raises the possibility that this suctorian was introduced with its hosts in Eurasian ballast water released from trans-oceanic ships. We analyze the ecological and geographic aspects of *A. nitocrae* occurrence in North America to deduce its origin on that continent. As well, we assess the prevalence and intensity of *A. nitocrae* infestation on a population of *N. hibernica* from Lake Erie and compare these characteristics with those for *N. hibernica* populations from Ukraine. The potential significance of ciliate epibiosis in influencing pattern of *N. hibernica* occurrence in different geographic regions is briefly discussed.

## Materials and methods

### Study organisms

*Acineta nitocrae* is a commensal suctorian ciliate that lives on the exoskeleton of harpacticoid copepods (DOVGAL 1984, 1994). Life history in the genus *Acineta* was reviewed in MORADO & SMALL (1995). Its life cycle is composed of a free-swimming larval stage (swarmers, or tomites) and a sessile adult stage (trophonts). Trophonts adhere to the integument of substrate organisms by means of a stalk and an adhesive disc situated on its base. Swarmers, which develop in a brood pouch of the maternal cell, are mouthless and possess a ciliary field used for swimming.

Swarmers form the stalk to attach to a substrate suitable for settlement. Shortly after settling, they undergo further metamorphosis involving resorption of the cilia and differentiation of tentacles from the tentacle anlages. Our observations on live material in vitro suggest that intense *A. nitocrae* infestations are non-lethal. Although the effect of *Acineta* infestation on substrate organisms has not been investigated, heavy suctorian burdens likely affect the host's nutrient milieu and motility (e.g., MORADO & SMALL 1995). *Acineta nitocrae* infection may, however, result in deterioration of host integument owing to attachment by the suctorian adhesive disc and abrasion of host exoskeleton (I.V. DOVGAL, unpubl. data). Injured sections of integument may be prone to subsequent pathological infections.

*Nitocra hibernica* is a harpacticoid copepod native to Eurasia. It was first recorded in North America in 1973 from Lake Ontario, where it appeared to be introduced from Europe (HUDSON et al. 1998). The Eurasian populations of *N. hibernica* exhibit wide environmental tolerances, particularly with respect to salinity (APOSTOLOV & MARINOV 1988). It inhabits coastal and estuarine waters throughout the Arctic and Atlantic coasts of Europe, the Baltic, Black and Caspian seas, as well as fresh and brackish inland waters in southern, central and eastern Europe (APOSTOLOV & MARINOV 1988, MONCHENKO 1995). The distribution of this species also encompasses central Asia and the Caucasus. *Nitocra hibernica* was predominant among the near-bottom harpacticoid copepods in western Lake Erie (V. I. MONCHENKO, unpubl. data).

*Nitocra incerta* occurs naturally in fresh and brackish waters, at the salinities of 0.1–14.0‰, in the Ponto–Caspian region (MONCHENKO 1995). Its range also includes discrete localities in the Jordan River Valley, Southwest Asia, and Italy. This harpacti-

coid copepod was discovered in the mouth of the Detroit River in May, 1999 (V. I. MONCHENKO, unpubl. data). Seven live individuals were collected using a bottom sled dredge from sandy habitats. It is not clear whether *N. incerta* has established a reproducing population in the lower Great Lakes.

*Nitocra lacustris* is a cosmopolitan species, which ranges over a broad spectrum of salinity, from 0.2 to 60.0‰ (APOSTOLOV & MARINOV 1988). Its natural distribution extends through the Arctic, Atlantic and Indian oceans, and the North, Baltic, Mediterranean, Black, Azov, and Aral seas (APOSTOLOV & MARINOV 1988). The inland distribution of *N. lacustris* is thought to be limited by low water salinity. For example, in the Dnieper River basin its distribution is restricted mainly to the lower reaches and Kakhovka Reservoir (MONCHENKO 1995).

*Canthocamptus staphylinus* has an extensive natural distribution throughout freshwater habitats of the Palaearctic region. This species also occurs in North America (V. I. MONCHENKO, unpubl. data).

## Collection and processing of samples

During 1997 and 1998, *Nitocra hibernica* was collected on/in bottom sediments in western Lake Erie near Middle Sister Island. Collections were made using a ponar grab or a sled dredge and sieved through a 125-μm mesh net. An additional collection of *N. incerta* was obtained from the mouth of the Detroit River by trawling a sled dredge. We also utilized archived collections of *N. hibernica*, *N. incerta*, and two other harpacticoid copepod species made during 1963–1997 from eight Ukrainian habitats – Lake Nobel [Rovno region], a flood-plain lake [near Kiev city], the Kiev, Kanev and Kremenchug reservoirs, lower Dnieper River, Dnieper–Bug estuary, and Danube River delta. Ukrainian collections were gathered in near-bottom waters using plankton nets (mesh opening ≤ 220 μm). The geographic location of European and North American populations of harpacticoid copepods analyzed in this study are illustrated in Figs 1 and 2. All collections were preserved in 4% formalin or 70% ethanol (see Table 1).

In the laboratory, harpacticoid copepods were separated from other material and identified to species. Crustaceans were then examined for the presence of epibionts using a dissecting microscope. The suctorian ciliate *A. nitocrae* was observed adhered to harpacticoid copepods by means of its podite. Cells of *A. nitocrae* were recorded on each harpacticoid copepod.

Prevalence of *A. nitocrae* infestation of host species was calculated as the proportion of individuals infested in each harpacticoid copepod collection. Intensity of infestation, or burden, was calculated as the number of suctorian cells per individual host. Associations between *A. nitocrae* and a specific host species were analyzed using BEKLEMISHEV's specificity index, in which the number of suctorian cells detected on a given harpacticoid copepod species was divided by the total number of all suctorian cells found on all host species (BEKLEMISHEV 1961). This index characterizes the selectivity of epibionts' attachment to a specific substrate organism.

In order to produce permanent preparations of *A. nitocrae*, samples were placed in a concentrated BOUIN's fixative for 5 min., then stained with BÖHMER's or CLEVELAND's haematoxylin. Samples were then transferred to dioxan solvent and, finally,

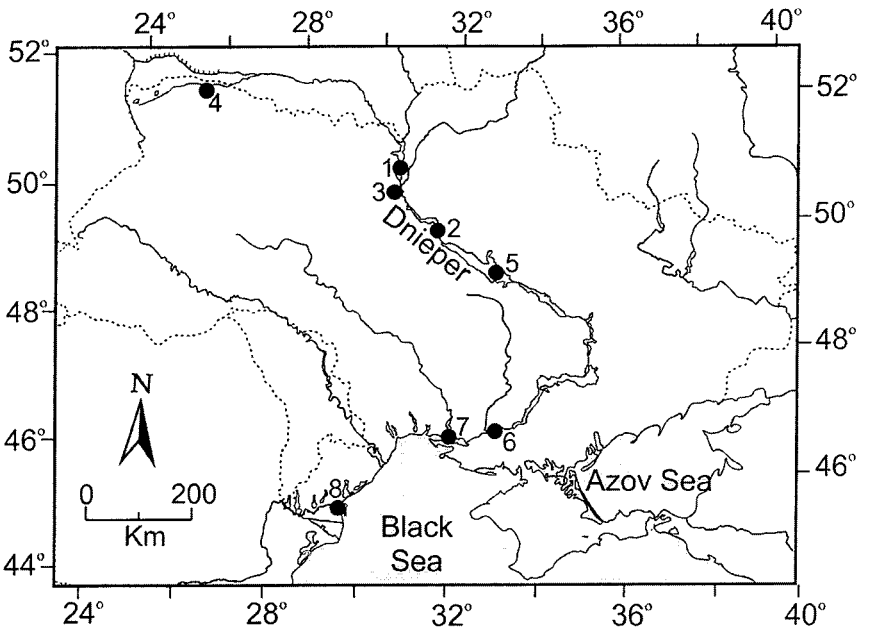


**Fig. 1.** Distribution of *Acineta nitocrae* in Ukraine. Numbers indicate habitats supporting *A. nitocrae*: Kiev reservoir (**1**); Kanev reservoir (**2**); flood-plain lake near Kiev city (**3**); Lake Nobel (**4**); Kremenchug reservoir (**5**); lower Dnieper River (**6**), Dnieper–Bug estuary (**7**); and Danube River delta (**8**).

mounted in dioxan balsam. Temporary preparations of *A. nitocrae* utilized in microscopy were stained with 1 % methyl green solution plus 1 % carbonic acid (DOVGAL 1996). To examine the external structures of *A. nitocrae*, non-stained specimens were placed in a solution of 20 % glycerin and 4 % formaldehyde (1 : 4) and surrounded with polystyrol (after JANKOWSKI 1975).

Dissecting and compound microscopes were employed for counting *A. nitocrae* and to examine its morphological characters. For individuals that were similarly oriented on the host body and had passed through complete metamorphosis we measured: 1) lorica length; 2) lorica width; 3) stalk length; 4) stalk width; 5) length of actinophores; 6) width of actinophores; 7) macronucleus length; and 8) the macronucleus width (Fig. 3). All measurements were taken using a calibrated optical micrometer.

Differences in mean size dimensions among *A. nitocrae* populations were examined using one-way ANOVA followed by BONFERRONI's multiple comparisons test when ANOVA was significant. Differences in size–frequency distribution among *A. nitocrae* populations were tested using a KOLMOGOROV-SMIRNOV two sample test. Collections gathered from sampling localities 4, 5, 8, and 10 were excluded from statistical comparisons as sample sizes were too small [$n \leq 3$]. Similarly, collections made from localities 3 and 7 were not used in these analyses because they had been preserved in a different fixative, formalin. Formalin is known to cause shrinkage in many aquatic taxa after a short period of preservation.

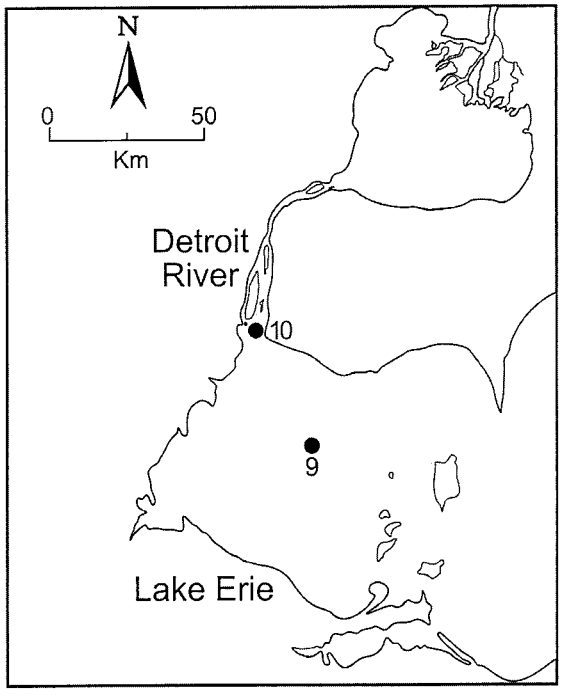


**Fig. 2.** Map of the lower Great Lakes showing localities of *Acineta nitocrae*: Lake Erie, Middle Sister Island (**9**); Detroit River mouth (**10**).

Differences in intensity of *A. nitocrae* infestation on *N. hibernica* and *N. incerta* among surveyed localities 1, 2, 6, and 9 were also tested using one-way ANOVA, followed by BONFERRONI's multiple comparisons test when ANOVA was significant. The t-test was employed following PESENKO (1982) to determine whether BEKLEMISHEV's specificity index differed among harpacticoid copepod species. This test was conducted using the software package STATISTICA for Windows, StatSoft, Inc. All other tests were conducted using Systat 8.0. All data were transformed as $\log_{10}(x + 1)$ prior to statistical analysis to stabilize variance.

Specimens of *N. incerta* and other *Nitocra* spp., preserved in ethanol, and trophonts of *A. nitocrae*, mounted on slides, were deposited in the invertebrate collection of the Schmalhausen Institute of Zoology, National Academy of Sciences, Kiev, Ukraine.

## Results

### Occurrence and identification

A single suctorian species, *Acineta nitocrae*, was detected from four harpacticoid copepod species collected in eight habitats in Europe and two habitats in

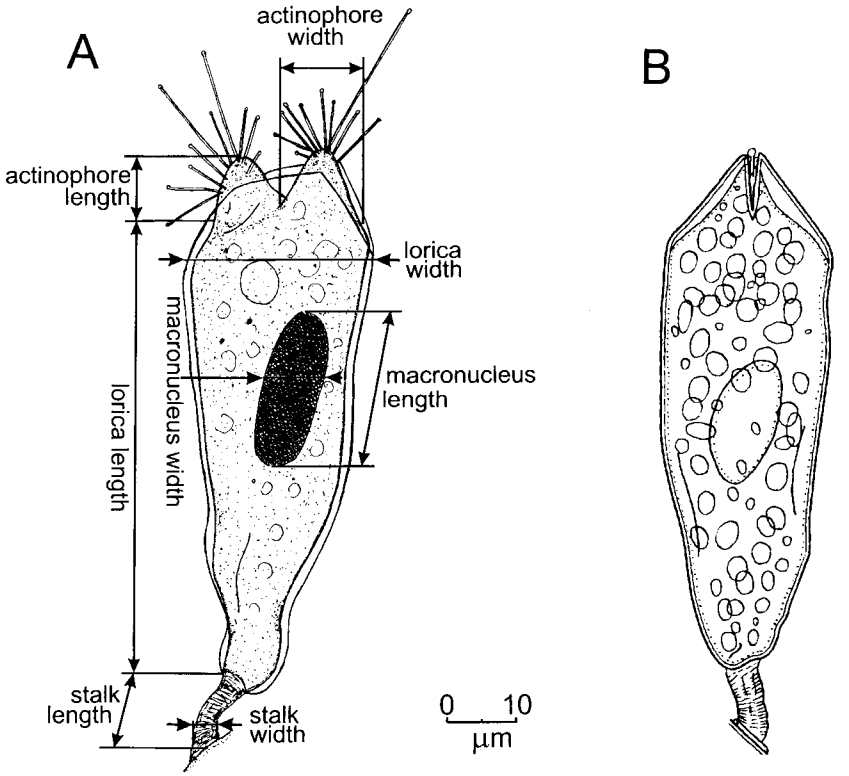


**Fig. 3.** Frontal view (**A**) of *Acineta nitocrae* trophont showing cell dimensions. Lateral view (**B**) of *Acineta nitocrae* trophont with tentacles drawn into cell body.

North America (see Figs. 1, 2). In each of these habitats, trophonts were generally found to conform to the diagnosis of *A. nitocrae* (DOVGAL 1984, 1996).

As a member of the ciliate family Acinetidae (Ciliophora: Suctoria), *A. nitocrae* possesses a rigid lorica, covering the cell body, and a series of clavate tentacles positioned on the actinophores at the body end opposite the podite (see Fig. 3). *Acineta nitocrae* differs from other members of the genus *Acineta* EHRENBERG, 1834 by its possession of a more elongated and less depressed body, more extensively developed triquetrous actinophores and a short, curved stalk (DOVGAL 1984, 1996, CURDS 1985). The ratio of the lorica length to the lorica width averaged nearly 2.9 : 1 (n = 70) in *A. nitocrae*. Another important feature, making separation of this species from North American congeners straightforward, is that its trophonts are specialized for epizooic existence with harpacticoid copepods and colonize predominantly the caudal rami. In contrast, the freshwater species of *Acineta* reported from North America, e.g., *A. fluviatilis* [as *A. tuberosa*] and *A. compressa* [as *A. papillifera*], generally do

not occur on crustaceans, but colonize aquatic macrophytes or inorganic substrates (e.g., LEE et al. 1985).

## Demography and morphometrics

We limit analysis of geographic size variation in *A. nitocrae* to four collections, which were recovered from two host species, *N. hibernica* and *N. incerta*, by using fairly similar collecting and processing techniques. These collections originated from four regions [localities 1, 2, 6, and 9], including, respectively, the Kiev and Kanev reservoirs and the lower Dnieper River in Europe and western Lake Erie in North America (Table 1).

*Acineta nitocrae* colonists on *N. incerta* were characterized by a higher proportion of individuals of 50–70 μm in the Kiev Reservoir and 60–80 μm in the Kanev Reservoir. Among colonists on *N. hibernica*, there was an apparent modal peak of trophonts with a lorica length of 70–80 μm (Fig. 4). However, size–frequency distributions were insignificantly different among these populations (pairwise KOLMOGOROV-SMIRNOV test, $P \geq 0.56$).

No significant geographic variation among *A. nitocrae* populations was observed with respect to length (ANOVA, $P = 0.23$) and width (ANOVA, $P = 0.39$) of the lorica, nor with respect to length (ANOVA, $P = 0.20$) and width (ANOVA, $P = 0.29$) of the stalk.

By contrast, significant differences among populations existed with respect to length (ANOVA, $P = 0.022$) and width (ANOVA, $P < 0.001$) of actinophores. The largest mean length and width of actinophores were recorded from *N. hibernica* in Lake Erie (15.9 and 18.3 μm, respectively), whereas the smallest values were observed from *N. incerta* in the Kiev Reservoir (11.7 and 10.0 μm, respectively). Significant differences among surveyed basins were also established for the length of macronucleus (ANOVA, $P = 0.004$), but not for the width of macronucleus (ANOVA, $P = 0.83$).

## Patterns of distribution and infestation occurrence

The natural distribution of *A. nitocrae* extends through the Dnieper drainage, Ukraine, where it was detected at eight localities (see Fig. 1). Western Lake Erie, in the vicinity of Middle Sister [41°51′N and 83°00′W], and the mouth of the Detroit River [42°20′N and 83°02′W] are the two North American habitats known to support *A. nitocrae* (Fig. 2). The contemporary North American distribution of its host *N. hibernica*, encompassing all the Great Lakes except Lake Superior (HUDSON et al. 1998), suggests that this suctorian is probably widely distributed in the lower Great Lakes.

The population survey carried out in Ukrainian basins suggests that *A. nitocrae* had epizooic associations with four species of harpacticoid copepods,

**Table 1.** Morphometric characteristics of *Acineta nitocrae* from 8 geographic localities.

| Locality | Fixative | Host Crustacean | Number of Crustaceans Examined | Number of Suctorians Recovered | Lorica Length | Lorica Width | Stalk Length | Stalk Width | Actinophore Length | Actinophore Width | Macronucleus Length | Macronucleus Width |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Alcohol | *N. incerta* | 21 | 10* | 66.8 (10.6) | 24.5 (3.9) | 5.3 (2.8) | 3.1 (1.2) | 11.7 (4.0) | 10.0 (2.7) | 11.3 (3.7) | 7.7 (1.8) |
| 2 | Alcohol | *N. incerta* | 9 | 10* | 73.4 (11.7) | 24.2 (2.7) | 7.1 (3.1) | 3.4 (1.3) | 13.7 (3.4) | 10.3 (2.3) | 18.7 (5.7) | 7.6 (1.5) |
| 3 | Formalin | *N. hibernica* | 30 | 10 | 83.1 (4.5) | 23.9 (2.6) | 6.3 (2.8) | 2.8 (0.6) | 16.0 (3.4) | 14.5 (1.4) | 21.0 (5.3) | 8.5 (1.7) |
| 5 | Alcohol | *N. incerta* | 2 | 2* | 59.2 (9.3) | 27.6 (1.9) | 5.3 (0.9) | 2.6 (0.4) | 14.5 (1.9) | 14.5 (1.9) | 10.5 (1.9) | 5.3 (1.9) |
| 6 | Alcohol | *N. hibernica* | 4 | 10* | 67.3 (11.6) | 24.3 (2.7) | 5.9 (0.9) | 3.6 (1.2) | 11.8 (4.7) | 14.5 (5.7) | 15.8 (4.8) | 7.5 (1.5) |
| 7 | Formalin | *N. lacustris* | 4 | 10* | 68.6 (11.5) | 25.3 (2.3) | 5.8 (1.6) | 2.9 (1.3) | 12.2 (4.7) | 12.4 (5.6) | 16.5 (5.7) | 7.4 (1.5) |
| 8 | Alcohol | *N. incerta* | 8 | 3* | 63.1 (7.0) | 20.2 (4.0) | 4.4 (1.5) | 2.7 (0.7) | 12.3 (1.5) | 9.6 (1.5) | 13.2 (4.6) | 7.0 (1.5) |
| 9 | Alcohol | *N. hibernica* | 53 | 20 | 73.4 (8.7) | 25.9 (3.1) | 5.6 (1.5) | 2.9 (0.7) | 15.9 (4.0) | 18.3 (4.6) | 17.6 (5.4) | 8.0 (1.7) |

Note: All dimensions are in µm. Localities designated as in Figs 1 and 2. Numbers represent mean and standard deviation (in parentheses) and sample sizes. *Acineta nitocrae* collections recovered from < 9 harpacticoid copepod individuals are indicated with *.

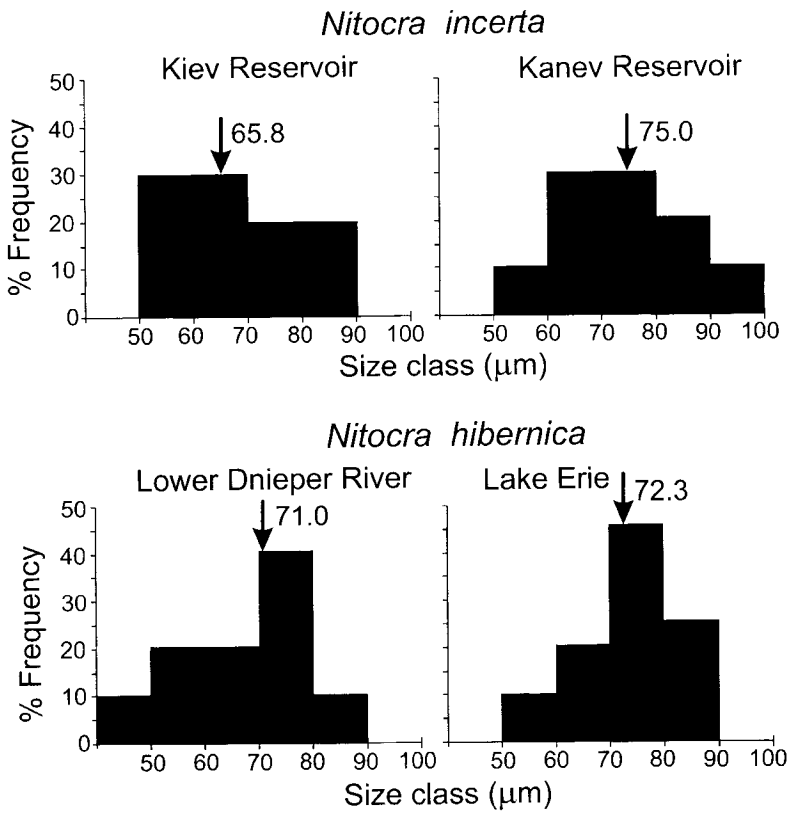


**Fig. 4.** Length–frequency histograms of *Acineta nitocrae* on *Nitocra incerta* from Kiev and Kanev reservoirs and on *Nitocra hibernica* from lower Dnieper River and western Lake Erie. Arrow indicates median lorica size.

namely, *Nitocra hibernica*, *N. incerta*, *N. lacustris*, and *Canthocamptus staphylinus*.

BEKLEMISHEV's specificity index differed among host species. The highest value of this index was established for *N. hibernica* (52 %), followed by that for *N. incerta* (29 %), *N. lacustris* (18 %) and *C. staphylinus* (1 %). Results of a t-test comparing BEKLEMISHEV's specificity index among host species indicated that *N. hibernica* was more attractive as settlement sites for *Acineta* than *N. incerta* (t-test, P = 0.01) and *N. lacustris* (t-test, P = 0.002). However, the difference in this index was not statistically significant between *N. incerta* and *N. lacustris* (t-test, P = 0.36).

*Canthocamptus staphylinus* was excluded from comparison because only one of > 40 specimens was infected by *A. nitocrae*. The occurrence of *A. nitocrae* on this harpacticoid copepod species appeared to be incidental.

**Table 2.** Prevalence and intensity of *Acineta nitocrae* infestation on harpacticoid copepods from 6 geographic localities.

| Locality | Host Crustacean | Prevalence (%) | Intensity (Cells per host) | |
|---|---|---|---|---|
| | | | Mean | Range |
| 1 | *N. incerta* | 38 | 2.2 (0.3) | 1–3 |
| 2 | *N. incerta* | 74 | 3.0 (0.4) | 1–5 |
| 3 | *N. hibernica* | 80 | 5.1 (0.5) | 1–17 |
| 6 | *N. hibernica* | 24 | 4.2 (0.6) | 1–6 |
| 8 | *N. incerta* | 57 | 1.3 (0.3) | 1–2 |
| 9 | *N. hibernica* | 64 | 3.2 (0.3) | 1–5 |

Note: Localities designated as in Figs 1 and 2. Standard errors are given in parentheses.

The prevalence of *A. nitocrae* infestation on *N. hibernica* was variable in Ukraine, ranging from a high of 80 % in a flood-plain lake near Kiev to 24 % on copepods from the lower Dnieper River (Table 2). In western Lake Erie, *Acineta* infested 64 % of the *N. hibernica* population. Intensity of *Acineta* infestation on *N. hibernica* differed significantly among habitats (ANOVA, $P = 0.027$), with a higher value observed from the flood-plain lake near Kiev. In this habitat, the amount of *Acineta* attached to individual *N. hibernica* varied during the year from 1 to 17. By comparison, only 1–5 suctorians infested each copepod in western Lake Erie (Table 2).

A similar pattern of geographic variation in the prevalence of *Acineta* infestation was established for *N. incerta*, however differences in the burden were not significant among basins (ANOVA, $P = 0.084$).

*Acineta nitocrae* was found predominantly on the caudal rami of adult harpacticoid copepods. However, at heavier infestation, the area of colonization increased in an anterior direction and suctorians also colonized copepod limbs, urosomal and metasomal segments, antennae and even setae (Fig. 5). A 12-month population survey conducted in the flood-plain lake near Kiev revealed a seasonal pattern of *A. nitocrae* burden on *N. hibernica* (Fig. 6). The highest intensities of *A. nitocrae* infestation occurred during April at surface temperature of 11.3 °C and oxygen concentration of 14.3 mg/l and during November at surface temperature of 4.0 °C and oxygen concentration of 15.1 mg/l. With surface temperature warming to 19–23 °C and at oxygen concentration of 6.0–8.8 mg/l during June-August, intensity of infestation dropped, to an average of 3–4 suctorians per copepod (see Fig. 6).

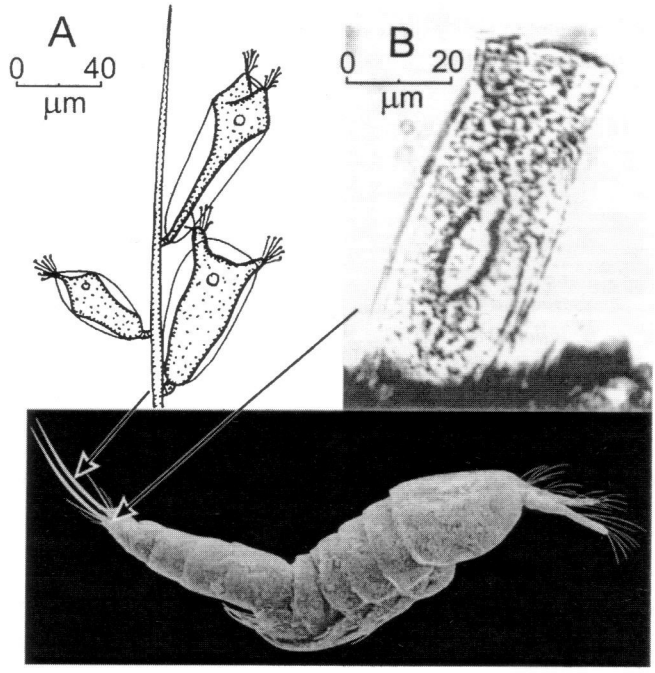


**Fig. 5.** Site locations of *Acineta nitocrae* on the harpacticoid copepod *Nitocra hibernica*: apical seta on caudal ramus (**A**); caudal ramus (**B**).

## Discussion

The present study established the identity of the Great Lakes' suctorian as *A. nitocrae*. Our results demonstrated that size dimensions of the lorica and stalk of *A. nitocrae* individuals do not differ significantly by sampling locality, nor by host species. Similarities in these morphometric characteristics among *Acineta* populations were observed despite the fact that surveys were conducted during different seasons and under differing environmental conditions. This is probably due to the outer tectinous covering that maintains the form and dimensions of individuals' cell and stalk.

In contrast, actinophores that stick out the apical atrium and lack the tectinous covering exhibited a high degree of variability among *Acineta* populations. Significant variability was also existed in terms of macronucleus length. We do not know if the location of the waterbodies or specialization to host species are responsible for this variation. Length and width of actinophores among *A. nitocrae* populations showed no consistent relationships to host species (Table 1). By comparison, intraspecific races of the suctorian *Discophrya lichtensteinii* associated with different host species were distinct with respect to size dimensions of the lorica and stalk and vacuole numbers (Matthes 1954).

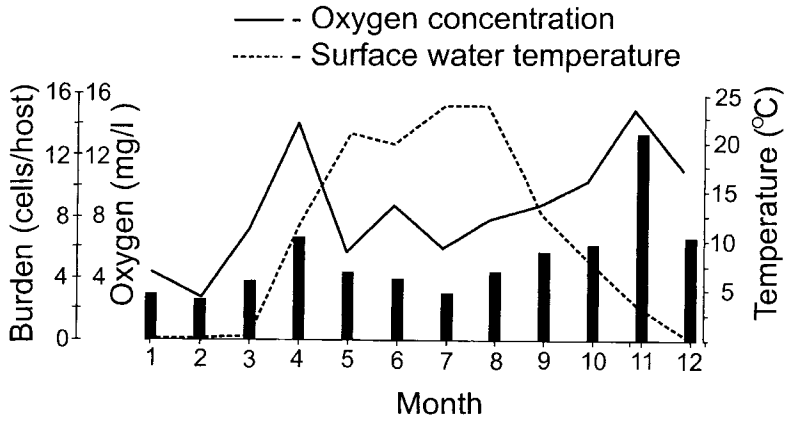


**Fig. 6.** Seasonal occurrence of *Acineta nitocrae* on *Nitocra hibernica* in flood-plain lake near Kiev city during 1985.

Our observations, however, revealed significant geographic variability in length and width of actinophores among *Acineta* populations from the same host species. Hence, consideration of both environmental responses and commensal–host relationships is required to explain size variability of actinophores.

Our study demonstrated that *A. nitocrae* associations with copepod hosts are not species-specific, as this suctorian was found on four harpacticoid copepod species – *N. hibernica*, *N. incerta*, *N. lacustris* and *C. staphylinus*. However, the preference for *N. hibernica* was significantly higher than for other host species. *Acineta nitocrae* infestation was limited mainly to the genus *Nitocra*.

The inland distribution of *A. nitocrae* in Ukraine suggests that this species is probably native to Europe. Its hosts, *Nitocra hibernica* and *N. incerta*, are thought to have been introduced to the Great Lakes in ballast water from Europe (HUDSON et al. 1998, V. I. MONCHENKO, pers. communication). The wide geographic distributions and salinity tolerances of *N. hibernica* and its other host species make them ideal vectors of *A. nitocrae* dispersal. Although *A. nitocrae* is known to tolerate salinity fluctuations from 0.1 to 5.0‰ in the Dniepr–Bug estuary, the species' tolerances to ocean salinity are not known. Therefore, it is difficult to determine whether *A. nitocrae* can survive in the ballast tanks of ocean-going vessels that have completed ballast water exchange. As with its hosts *N. hibernica* and *N. incerta*, *A. nitocrae* may have invaded the Great Lakes through the release of its free-swimming larval stage or a sessile adult stage attached to host species. The latter mechanism of transfer has been implicated for other introduced protists in the Great Lakes (MILLS et al. 1993). *Acineta nitocrae* association with several host species, which have extensive geographic distributions and broad environmental tolerances, may facilitate the dispersal and range extension of this suctorian. Similar inferences

have been drawn for invading parasites and disease agents (KARPEVICH 1975). The origin and occurrence of *A. nitocrae* in North America has been insufficiently studied, therefore this species must be considered cryptogenic in North America (CARLTON 1996).

The present study documented substantial variability in prevalence and intensity of *A. nitocrae* infestation of copepods among surveyed basins (Table 2). Environmental conditions, specifically temperature and oxygen concentration, in conjunction with life history characteristics of the hosts, are factors most often implicated as regulators of suctorian occurrence and abundance (DOVGAL 1994, MORADO & SMALL 1995). Indeed, a seasonal pattern of *A. nitocrae* occurrence suggested cold-water affinities of this species (see Fig. 6).

Our results demonstrated that intensity of *A. nitocrae* infestation may be significantly higher in native populations of *N. hibernica* than in introduced ones, while geographic variation in suctorian burden among the native populations of *N. incerta* was not significant. In western Lake Erie, introduced *N. hibernica* outnumbered native harpacticoid copepod species (V. I. MONCHENKO, unpubl. data). Since its first discovery in Lake Ontario in 1973, *N. hibernica* has expanded its distribution to other lower Great Lakes (HUDSON et al. 1998). It is not clear why this copepod has been so successful in invading the Great Lakes, although a number of possibilities invite examination. Intra-basin movement of ballast water may facilitate rapid dispersal of zooplankton. For example, *Cercopagis pengoi* spread to Lake Michigan only one year after it was initially discovered in the Great Lakes in Lake Ontario; this range extension was almost certainly due to movement of ballast water to the former from the latter lake (MAKAREWICZ et al., 2001). Alternatively, it is possible that epibionts mediate competition between native and exotic zooplankton taxa, particularly if the species differ with respect to vulnerability to epibiosis.

A previous study revealed that *Acartia hudsonica* copepods infected with peritrich ciliates experienced reduced egg production and lower nauplii survival rates, though egg hatching rate and nauplii developmental rate were not affected (WEISSMAN et al. 1993). Epibionts may affect the movement, feeding, respiration, reproduction and survival of host populations (e.g., WILLEY et al. 1990, THRELKELD et al. 1993, WEISSMAN et al. 1993, MORADO & SMALL 1995). Whether *A. nitocrae* epibiosis affects life history attributes of copepod hosts in either North America or Europe remains to be determined.

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## References


APOSTOLOV, A. M. & MARINOV, T. M. (1988): Fauna of Bulgaria. Vol. **18**. Copepoda, Harpacticoida (marine harpacticoids). 1–384. – Izdatelstvo Balg. Akad. Nauk., Sofia. (in Bulg.)

BEKLEMISHEV, V. N. (1961): Notions and terms used in the quantitative studies on populations of ectoparasites and nidicoles. – Zool. Zhurn. **40:** 149–158. (in Russ.)

CARLTON, J. T. (1996): Biological invasions and cryptogenic species. – Ecology **77:** 1653–1655.

CARLTON, J. T. & GELLER, J. B. (1993): Ecological roulette: the global transport of nonindigenous marine organisms. – Science **261:** 78–82.

COX, G. W. (1997): Richness of the life on earth. – In: COX, G. W.: Conservation Biology: Concepts and applications. – Wm. C. Brown, Dubuque, IA, pp. 35–37.

CURDS, C. R. (1985): A revision of the Suctoria (Ciliophora, Kinetophragminophora). 1. *Acineta* and its morphological relatives. – Bull. Br. Mus. nat. Hist. Zool. Ser. **48**(2): 75–129.

DOVGAL, I. V. (1984): *Acineta nitocrae* sp. n. (Ciliophora, Suctoria): A commensal of *Nitocra hibernica*. – Vest. Zool. 4: 75–76. (in Russ.)

– (1994): Seasonal changes in the faunistic complexes of freshwater suctorians (Ciliophora, Suctoria) in Ukrainian waters. – Vest. Zool. 1: 53–58. (in Russ.)

– (1996): Keys for identification of tentaculous ciliates of the fauna of Ukraine. – Vest. Zool./Suppl. 2: 1–42. (in Russ.)

HUDSON, P. L., REID, J. W., LESKO, L. T. & SELGEBY, J. H. (1998): Cyclopoid and harpacticoid copepods of the Laurentian Great Lakes. – Ohio Biol. Surv. Bull. New Ser. **12** (2): 1–50.

JANKOWSKI, A. W. (1973): Fauna of the USSR. Infusoria. Subclass Chonotricha. Vol. **2**. Fasc. 1: 1–353. – Nauka, Leningrad, Russ. (in Russ.)

– (1975): A new method for producing glycerin preparations. – Vestn. Zool. 3: 80–81. (in Russ.)

– (1982): New genera of symbiotic protozoans of Baikal fauna. – In: GALAZII, G.I., Novel idea of Baikal fauna. – Nauka, Moscow, Russ., pp. 35–37. (in Russ.)

LEE, J. J., HUTNER, S. H. & BOVEE, E. C. (eds.), (1985): An illustrated guide to the Protozoa. 1: 620. – Allen Press, Lawrence.

KARPEVICH, A. F. (1975): Theory and practice of acclimatization of aquatic organisms. 1–432. – Pishchevaya Promyshlennost, Moscow, Russ. (in Russ.)

MAKAREWICZ, J. C., GRIGOROVICH, I. A., MILLS, E. L., DAMASKE, E., CRISTESCU, M. E., PEARSALL, W., LAVOIE, M. J., KEATS, R., RUDSTAM, L., HEBERT, P. D. N., HALBRITTER, H., KELLY, T., MATKOVICH, C. & MACISAAC, H. J. (2001): Distribution, fecundity, and genetics of *Cercopagis pengoi* (OSTROUMOV) (Crustacea: Cladocera) in Lake Ontario. – J. Great Lakes Res. **27:** 19–32.

MATTHES, D. (1954): Suktorienstudien. 3. *Discophrya lichtensteinii* (CLAPAREDE and LACHMANN 1858) COLLIN 1912, ein an Halipliden und Dytisciden gebundenes Suktor. – Zool. Anz. **152:** 252–262.

MILLS, E. L., LEACH, J. H., CARLTON, J. T. & SECOR, C. L. (1993): Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. – J. Great Lakes Res. **19:** 1–54.

– – – – (1994): Exotic species and the integrity of the Great Lakes. – Bioscience **44:** 666–676.

MONCHENKO, V. I. (1995): Harpacticoids (Copepoda, Harpacticoida) of the Dnieper: Results of faunistic investigations. – Gidrobiol. Zhurn. **31** (5): 33–37. (in Russ.)

MORADO, J. F. & SMALL, E. B. (1995): Ciliate parasites and related diseases of crustaceans: A review. – Rev. Fish. Sci. **3:** 275–354.

PESENKO, Y. A. (1982): Principles and methods of qualitative analysis of faunistic investigations. 1–284. – Nauka, Moscow. (in Russ.)

PRONIN, N. M., SELGEBY, J. H., LITVINOV, A. G. & PRONINA, S. V. (1998): Comparative ecology and parasitic fauna of exotic invaders in the great lakes of the world: the rotan goby (*Perccottus glehni*) in Lake Baikal and the ruffe (*Gymnocephalus cernuus*) in Lake Superior. – Sibir. Ekol. Zhurn. **5:** 397–406. (in Russ.)

RICCIARDI, A. & MACISAAC, H. J. (2000): Recent mass invasion of the North American Great Lakes by Ponto–Caspian species. – Trends Ecol. Evol. **15:** 62–65.

TAYLOR, W. D. & SANDERS, R. W. (1991): Protozoa. – In: THORP, J. H. & COVICH, A. P. (eds.): Ecology and classification of North American freshwater invertebrates. – Academic Press, San Diego, pp. 37–93.

THRELKELD, S. T., CHIANVELLI, D. A. & WILLEY, R. L. (1993): The organization of zooplankton epibiont communities. – Trends Ecol. Evol. **8:** 317–321.

WILLEY, R. L., CANTRELL, P. A. & THRELKELD, S. T. (1990): Epibiotic euglenoid flagellates increase the susceptibility of some zooplankton to fish predation. – Limnol. Oceanogr. **35:** 952–959.

WEISSMAN, P., LONSDALE, D. J. & YEN, J. (1993): The effect of peritrich ciliates on the production of *Acartia hudsonica* in Long Island Sound. – Limnol. Oceanogr. **38:** 613–622.

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