

N. DELLA CROCE¹ and P. VENUGOPAL

Chair of Hydrobiology, University of Genoa
Indian Ocean Biological Centre, National Institute
of Oceanography, Cochin

Penilia avirostris DANA in the Indian Ocean (Cladocera)

Abstract

The records of the marine cladoceran *Penilia avirostris* DANA in the Indian Ocean are discussed as a further contribution to studies on the features of its world distribution. The review has pointed out different aspects of the life cycle of the species and the influence of biological and environmental factors upon the mechanisms of the cycle itself. Production of *P. avirostris* is considered on a trophic basis. Observations carried out elsewhere are also discussed.

"*Penilia orientalis*" was first collected in the Indian Ocean on March 5, 1842 in the Sunda Strait (RICHARD, 1895). The species *Penilia avirostris* was then collected in the Zanzibar waters on 14 May 1885 (STEUER, 1933a); other early records concerned a "few scattered specimens" found in the plankton of Durban Bay (BRADY, 1915); later on "*Penilia schmackeri*" was found in Ceylon waters (RAMMNER, 1933-1934). In adjacent seas of the Indian Ocean, *Penilia avirostris* was collected in the Suez Canal (GURNEY, 1927), in the Red Sea (SANTUCCI, 1937) and in the Bangka Strait (STEUER, 1933a).

All these records, mainly related to the taxonomy and geographical distribution of the species, have to be considered "historical". It is now generally accepted that all the species included in this genus belong to the single species *Penilia avirostris* DANA, 1849 (CATTLEY & HARDING, 1949; DOLGOPOLSKAJA, 1958), which has a world-wide distribution approximately between latitude 40° N and S (DELLA CROCE, 1964).

In the Madras coastal waters, *P. avirostris* reaches peak numbers in October with temperature and salinity values of 29.5 °C and 30.92‰ respectively (RAJAGOPAL, 1962). In the Zanzibar area, the species is present from November until March with water temperatures ranging from 28.05 to 30.02 °C, and reaches peak numbers in January (WICKSTEAD, 1963). In the Sunda shelf *P. avirostris* mainly occurs in Singapore Strait at the monsoon change-over periods: second half of September and first half of April (WICKSTEAD, 1961). The species is present throughout the year in the waters of the Agulhas Bank with temperature and salinity values ranging from 14.99 to 21.79 °C and 35.22 to 35.51‰ respectively, and reaches high population densities from December to June (DELLA CROCE & ANGELINO, 1968-1969).

Previous and present records extend the upper temperature limit at which *P. avirostris* has been found (from 26.9 to 30.02 °C), while 8.7 °C remains the lower temperature limit (DELLA CROCE, 1958).

P. avirostris, which is a filter-feeding organism, occurs mainly in surface and coastal waters, frequently in swarms, and in a wide range of salinity and temperature conditions.

The appearance of the species is very abrupt. The population dynamics by which *P. avirostris* reaches peak numbers within a short time is based upon parthenogenetic

¹ Visiting Scientist to the Indian Ocean Biological Centre, Cochin, India, under UNESCO contract SC/2077/70-20579.

females hatched from resting eggs. These females have six large and successive broods which, in turn reproducing parthenogenetically at a fast rate, increase the population. At the time of population peak, depression factors have already appeared, and some parthenogenetic females produce males or resting eggs (sexual females), whilst other parthenogenetic females and their broods still reproducing parthenogenetically produce fewer and fewer parthenogenetic individuals.

According to WICKSTEAD's temperature threshold hypothesis (1963), if conditions become favourable, hatching of the resting eggs takes place before the old population disappears, and the remnants of the dying population will become mixed with the vigorous parthenogenetic females of the new population. This stage will be the valley between two population peaks which sometimes occur within a few months in some areas. As temperature is the factor most directly concerned with hatching of resting eggs, *P. avirostris* will have a single population in areas with a "regular annual temperature cycle" (Zanzibar), and two populations in areas with a "temperature cycle with two peaks" (Singapore).

The data presented in Fig. 1 suggest a different interpretation of the temperature threshold hypothesis. Moreover, the length of the cycle seems, to some extent, de-

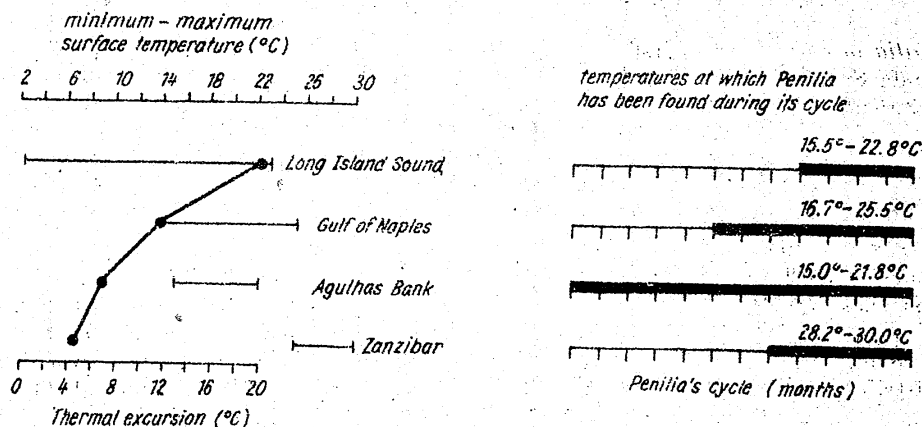


Fig. 1. *Penilia avirostris*. Temperature values and length of seasonal and annual cycles in different areas (For explanation see text).

pendent on minimum and maximum water temperatures observed throughout the year.

In temperate latitudes (Naples, Beaufort, Mediterranean and Atlantic waters) with a regular annual temperature cycle, *P. avirostris* has a single population, which appears abruptly, reaches its peak within a short time, and disappears slowly because of the gradual altering of the favourable environment. At higher (Narragansett, Sandy Hook, Atlantic waters) or lower latitudes (Zanzibar, Indian Ocean waters) a single population appears and disappears abruptly. There, the regular annual temperature cycle reaches low or high values which can limit the favourable ecological conditions severely in time and space. In these areas, the environmental situation does not allow the hatching of the resting eggs before the old population disappears.

In the waters of the Agulhas Bank, the annual thermal cycle is regular, with temperature values of the same order as those found at high and temperate latitudes during the *P. avirostris* cycle (Fig. 1). Here, as well as in the Algiers and Sierra Leone waters, where the species has been found throughout the year, a more steady continuity of favourable ecological factors can be regarded as supporting the annual

cycle of this cladoceran¹. Two populations corresponding to the two peaks in the temperature cycle can be considered typical of areas influenced by monsoon change-over periods (Singapore).

The abrupt increase in the population is related to the size and rate of deposition of the broods. WICKSTEAD (1963) suggests that a parent has 6 depositions in about 36 to 40 days, whilst a brood of young could develop and hatch within 3 to 4 days and, in turn, these young would bear broods in 2 to 3 days. According to DELLA CROCE & BETTANIN (1957), the eggs would require not less than 30 hours after deposition to develop into free-swimming young.

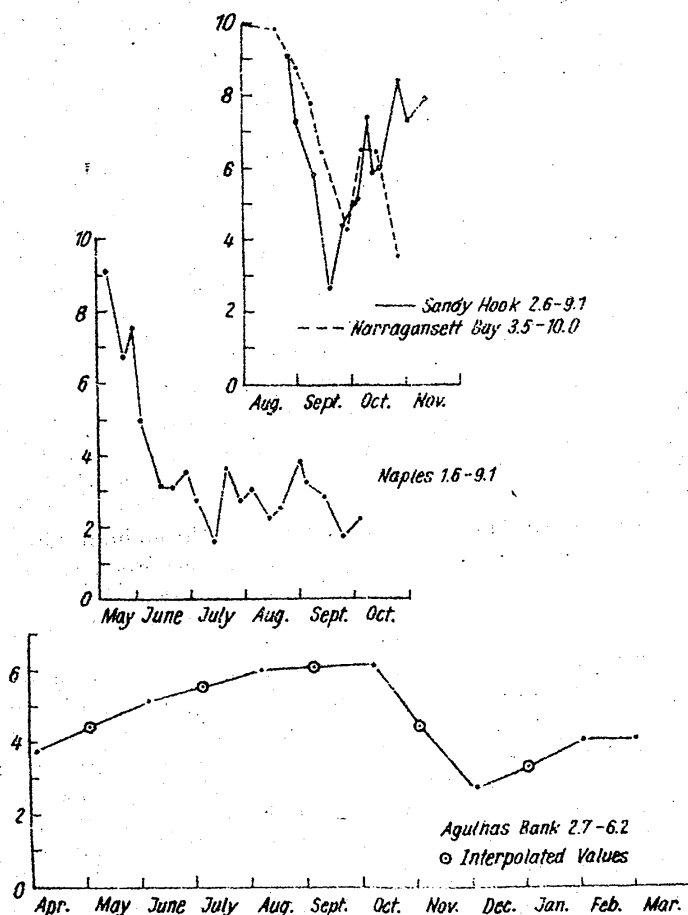


Fig. 2. *Penilia avirostris*. Mean number of eggs or embryos in parthenogenetic individuals through seasonal and annual cycles in different areas. Minimum and maximum numbers of eggs or embryos are given for each area.

¹ The annual cycle of *P. avirostris* in the Agulhas Bank waters is supported by parthenogenetic and sexual reproduction (DELLA CROCE & ANGELINO, 1968-1969). According to some authors, *P. avirostris* may reproduce only by parthenogenesis in Madras waters (RAJAGOPAL, 1962), in the Alboran Sea, and in the Algerian and Sierra Leone waters (CASANOVA, 1969). The hypothesis of LOCHHEAD (1954) by which the cycle may be supported exclusively by parthenogenetic reproduction has not yet been confirmed.

The data presented in Fig. 2 show that the brood size (reproductive potential) is very large at the beginning of the cycle, decreases at about the depression time, and increases again afterwards until the population suddenly disappears¹. Moreover, it has been shown (Fig. 3) that the larger the size of the parent, the larger is its brood

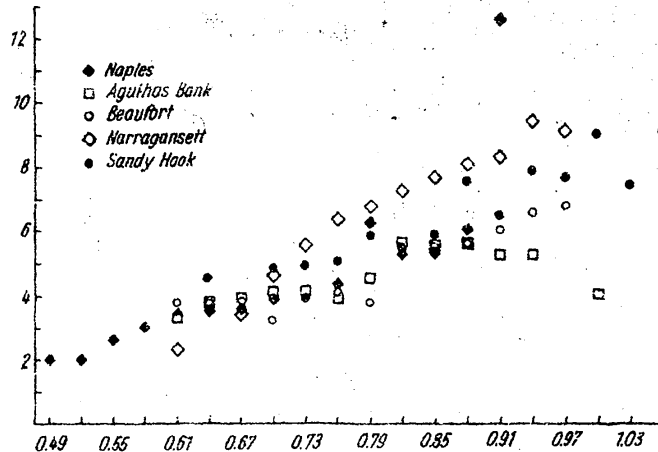


Fig. 3. *Penilia avirostris*. Mean number of eggs or embryos and size of parents, as represented by mid-points of size classes.

size (DELLA CROCE & ANGELINO, 1968–1969). However, high and low reproductive potentials of larger specimens seem mostly dependent on environmental conditions, as the larger specimens have a reproductive potential higher at the beginning than at the end of the cycle.

The composition of the parthenogenetic population throughout the cycle, as indicated by the number of eggs or embryos present in the brood pouch of parents, reveals that the mean reproductive potential is lower in the Bay of Naples, at Beaufort, and in Agulhas Bank waters, than in Narragansett Bay and the Sandy Hook area (Fig. 4).

The population dynamics, however, is far from being known. Research is needed to estimate the biological parameters of the species life cycle and to evaluate, among other factors, feeding, predation and dispersal, which affect the population.

There are not enough data available to discuss the biological and environmental factors which determine the production of resting eggs in *P. avirostris*. WICKSTEAD (1963), on the basis of his observations in Zanzibar and Singapore waters, suggests that a great increase in number of diatoms coincident with the population "explosion" of *P. avirostris* maintains the oxygen and the carbon dioxide concentrations at acceptable levels for the cladocerans in relation to the oxygen consumed and the carbon dioxide produced by the zooplankton. The disappearance of the diatoms will destroy the balance between zooplankton, oxygen and carbon dioxide. Lowering the oxygen or raising the carbon dioxide concentrations in the water may cause parthenogenetic females to produce both resting eggs and males.

It has been shown that the morphological development of the resting eggs in *P. avirostris* takes place through 9 stages (DELLA CROCE & BETTANIN, 1969). Recent studies have shown that males can be recognized as such at the level of the last

¹ The only data available on the brood size of an annual population (Agulhas Bank) are also shown in Fig. 2.

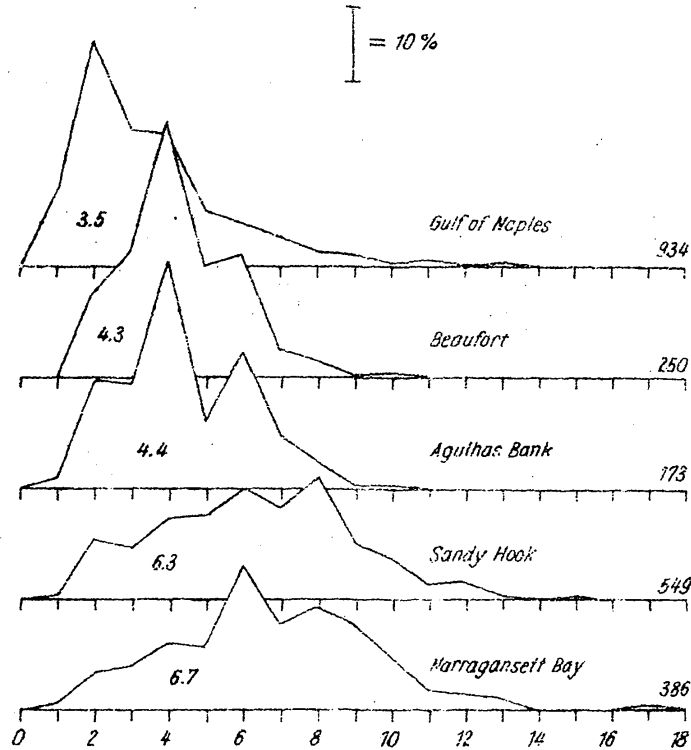


Fig. 4. *Penilia avirostris*. Percentage frequency distribution of number of eggs or embryos per brood during seasonal and annual cycles in different areas. For each area, mean number of eggs or embryos (left-hand side) and number of individuals (right-hand side) are given.

embryo stage (GAINO, 1971). The posterior end of the male gonads join to form a sac (DELLA CROCE & GAINO, 1971), which should function as a temporary receptacle for the spermatozoa during daytime, when males and sexual females of the same population inhabit different water layers. According to RUBINSTEIN (see DOLGOPOLSKAJA, 1958), males are photopositive, and prevail in daylight at the surface, whilst sexual females are found in deeper waters.

Diurnal migration is a poorly known aspect of the life history of this cladoceran. In Japanese waters, in September, the population density at the surface was higher immediately after sunset, and decreased at night, but was still higher at dawn than in the early afternoon (KIKUCHI, 1936). In the Mediterranean Sea, *P. avirostris* was more abundant at the surface by night than during the daytime in the Provençal waters (THIRIOT, 1970); in the Bay of Naples, in July, *P. avirostris* had reached high densities at sunset and lower ones at night, but this behaviour was not confirmed in August. In the Zanzibar waters no significant differences were found in the numbers of cladocerans in day and night samples (WICKSTEAD, 1963); such results were only partially in agreement with observations carried out in the waters of the Sunda shelf (WICKSTEAD, 1961).

The scarce observations about the reaction of *P. avirostris* to artificial light are contradictory. LOCHHEAD (1954) found no reaction under experimental conditions, whilst PORUMB & PORUMB (1966) reported *P. avirostris* to be strongly photopositive to artificial light. It is felt that, in future studies, the "age" of the population has to

be considered, as the reaction to light may differ for parthenogenetic and sexual individuals, at different period of the cycle.

P. avirostris feeds on bacteria and phytoplankton but mainly on detritus¹, which, in some areas, has been thought to constitute over 95% of the food ingested (PAVLOVA, see MULLIN, 1969). Because of the abundance of this material, the relationship found between numbers of *P. avirostris*/m³ and water transparency in the Gulf of Naples (DELLA CROCE, 1962) suggests that a coastal area, with an increasing degree of eutrophication, may support a new or more intense colonization by *P. avirostris*, provided that other environmental conditions are favourable; thus, *P. avirostris* could be considered as an indicator of high productivity areas in coastal waters.

Production has been mainly estimated as numbers of *P. avirostris*/m³. In a previous paper (DELLA CROCE & BETTANIN, 1964-1965) it has been pointed out that, in some areas of the Black Sea, *P. avirostris* prevails (50%) over other plankton organisms seasonally, and constitutes the main food of the fishes feeding on plankton. According to WICKSTEAD (1963), *P. avirostris* and *Eoadne tergestina* are ideal food for fish larvae in Zanzibar waters.

Recently, SHMELEVA (1965) has estimated the biomass of *P. avirostris* from the Adriatic Sea as equal to 0.0024 to 0.025 mg for specimens 0.480 to 0.880 mm long. MULLIN (1959) has used, among others, data concerning *P. avirostris* populations from the Black Sea to evaluate the rate at which organic matter is transformed into or produced by zooplankton populations. *P. avirostris* populations were calculated to ingest daily in the same month 2.8 mg C/m² in the central part, and 111 mg C/m² in the northwestern coastal area of the Black Sea. The calculated rates of production, not corrected for concurrent losses, were 1.1 and 44 mg C/m²/day. Another study has revealed that the carbohydrate content in *P. avirostris* from the Mediterranean Sea was equal to 0.27% (ranging from 0.24 to 0.35%) of its wet weight (RAYMONT & LINFORD, 1966).

Production, however, can be markedly reduced by various events. MIRONOV (1969) has found that *P. avirostris* is sensitive to the presence of oil in sea water. Oil concentrations of 0.001 ml/l accelerated death, whilst concentrations of 0.1 ml/l killed this cladoceran within the first day of the experiment.

Parasitism by bacteria has been already found to inhibit egg production in *Daphnia magna* (GREEN, 1957). ST EUER (1933b) described the only recorded case of helminth parasitism in *P. avirostris*, which was caused by a nematode. Recently, ZELEZINSKAJA (1966) reported that *P. avirostris* in the northwestern part of the Black Sea suffered mass mortality by an unclassified fungus which was found to be a parasite of this cladoceran. Numerous specimens of *P. avirostris* from the Japanese waters of Hokkaido and those of the Great Australian Bight have been found with knobstick-like elements affixed in great number all over its body, but it was not possible to ascertain any effect of this fungus on the populations².

In the Indian Ocean, *P. avirostris* can be considered endemic in the Zanzibar and Agulhas Bank waters, where old records are confirmed by recent ones showing *P. avirostris* carrying resting eggs (WICKSTEAD, 1963; DELLA CROCE & ANGELINO, 1968-1969). According to previous records and those gathered during the International Indian Ocean Expedition Cruise no. 8 of the R./V. "A. Bruun" in the Western

¹ Studies on feeding of *P. avirostris* have been carried out in the laboratory (PAVLOVA, 1959) and at sea (DELLA CROCE & GALNO, 1968-1969).

² Observations carried out by N. DRAGO at the University of Genoa. TREGOUBOFF (personal communication to DELLA CROCE in 1967) believed that the fungus parasite of *P. avirostris* from the Black Sea belonged to the phycomycetes, but he pointed out that the parasite of the specimens from Japanese and Australian waters was a fungus not yet recorded as a parasite of Crustacea.

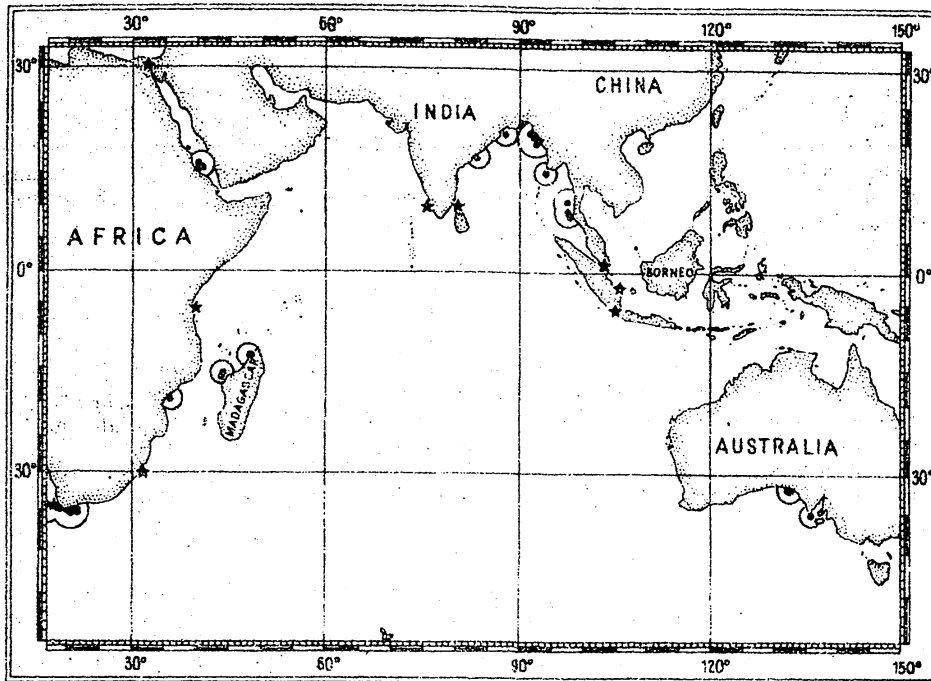


Fig. 5. *Penilia avirostris*. Geographical distribution in the Indian Ocean. Black stars: previous records. Black dots in semi-circles: present records.

Indian Ocean¹, the species has a seasonal (from September until March) distribution which can be considered geographically continuous from Cape Agulhas to Zanzibar (Fig. 5).

P. avirostris collected during Cruise no. 1 of the same research vessel in the Eastern Indian Ocean¹, and previous records in this area have revealed a seasonal (between March and April) but continuous distribution from the Bay of Bengal to the Singapore Strait, at the monsoon change-over period (Fig. 5). No endemic areas were located, but sexual females were found at Station 48, on April 5, 1963 (19° 41' N—93° 06' E).

Although recent observations (TREGOUBOFF, 1963; CASANOVA, 1964; 1965) show that *P. avirostris* has been found at great depths in the Mediterranean Sea, the species normally inhabits the surface layers.

Distribution is not merely a problem of transport, as subsequent survival and colonization are related to the mode and degree of biological tolerance and reaction of the species to environmental conditions.

Acknowledgement

The authors wish to thank Dr. N. K. PANIKKAR, Director National Institute of Oceanography, Panaji, India; Dr. M. VANNUCCI, UNESCO Curator at the Indian Ocean Biological Centre, and Dr. T. S. S. RAO for facilities provided. The senior author is grateful to UNESCO, which made this work possible.

¹ Observations by DELLA CROCE on samples from the Smithsonian Sorting Center, Washington D. C.

Summary

Earlier and current records of *Penilia avirostris* DANA in the Indian Ocean are reviewed. The temperature requirements of this species and the influence of temperature on its cycle are discussed. The mechanism of the explosive population cycle and the influence of environmental factors on the reproductive potential and on the deposition of the resting eggs are also discussed. Laboratory and field work on diurnal migrations, photosensitivity to artificial light and feeding are considered. The contribution of *P. avirostris* to production and its place in the trophic chain is reviewed. Cases of parasitism on this species are recalled.

Riassunto

Gli A. A. prendono in esame i ritrovamenti passati e recenti di *Penilia avirostris* DANA nello Oceano Indiano. Le esigenze termiche di questa specie e l'influenza della temperatura sul suo ciclo vengono discusse unitamente al meccanismo dell'esplosione di popolazione ed all'influenza dei fattori ambientali sul potenziale riproduttivo e sulla deposizione delle uova durature. Gli A. A., inoltre, prendono in esame aspetti interessanti le migrazioni diurne, la sensibilità alla luce artificiale, l'alimentazione, la produttività, nonché alcuni casi di parassitismo, in base ad osservazioni condotte su questa specie anche in altre aree oceaniche.

References

- BRADY, G. S., 1915: Notes on the pelagic Entomostraca of Durban Bay. — Ann. Durban Mus. 1: 134–146.
- CASANOVA, J. P., 1964: Pêches planctoniques, superficielles et profondes, en Méditerranée occidentale (Campagne de la „Thalassa” — janvier 1961 — entre les îles Baléares, la Sardaigne et l'Algérois). V. Cladocères. — Rev. Trav. Inst. Pêches marit. 28: 265–270.
- 1965: *Penilia avirostris* DANA, indicateur d'eaux diluées. — Ibid. 29: 197–204.
- 1968: *Penilia avirostris* DANA en Méditerranée occidentale, sa valeur d'indicateur écologique. — Ann. Fac. Sc. Marseille 41: 95–119.
- CATTLEY, J. G., and J. P. HARDING, 1949: *Penilia*, a cladoceran normally found off tropical and subtropical coasts, recorded in North Sea plankton. — Nature 164: 238–239.
- DELLA CROCE, N., 1958: Considerazioni biologiche su un cladocero marino, *Penilia avirostris* DANA. — Atti Acc. Lig. Sc. Lett. 15: 311–325.
- 1962: Zonazione zooplanctonica nel Golfo di Napoli. — Publ. Sta. zool. Napoli 32 (suppl.): 368–379.
- 1964: Distribuzione e biologia del cladocero marino *Penilia avirostris* DANA. — Bull. Inst. océanogr. Monaco 62, no. 1301: 1–16.
- , M. I. ANGELELLO, 1968–69: *Penilia avirostris* DANA nelle acque del Banco Agulhas. — Boll. Mus. Ist. biol. Univ. Genova 36: 5–14.
- , S. BETTANIK, 1964–65: Osservazioni sul ciclo biologico di *Penilia avirostris* DANA del Golfo di Napoli. — Boll. Mus. Ist. biol. Univ. Genova 33: 49–68.
- , — 1967: Accrescimento embrionale in *Penilia avirostris* DANA. — Lincoi — Rend. Sc. fis. mat. e nat. 43: 590–596.
- , 1969: Formazione delle uova durevoli in *Penilia avirostris* DANA. — Cah. Biol. Mar. 10: 95–102.
- , E. GAING, 1968–69: Alcune osservazioni sul ritmo di alimentazione in *Penilia avirostris* DANA. — Boll. Mus. Ist. biol. Univ. Genova 36: 15–21.
- , — 1970: Osservazioni sulla biologia del maschio di *Penilia avirostris* DANA. — Cah. Biol. Mar. 11: 361–365.
- DOLGOPOLSKAYA, M. A., 1958: Cladocera of the Black Sea. — Trud. Sevastopol. biol. Stants. 10: 27–75 (in Russian).
- GAING, E., 1971: Dimorfismo sessuale a livello embrionale in *Penilia avirostris* DANA. — Cah. Biol. Mar. 12: 283–289.

- GREEN, J., 1957: Parasites and epibionts of Cladocera in rock pools of Tvärmlane archipelago. — Arch. Soc. „Vanamo“ 12: 5–12.
- GURNEY, R., 1927–29: Zoological results of the Cambridge expedition to the Suez Canal, 1924. VIII. Report on the Crustacea: Copepoda and Cladocera of the plankton. — Trans. Zool. Soc. Lond. 22: 139–172.
- KIKUCHI, K., 1930: Diurnal migration of plankton crustacea. — Quart. Rev. Biol. 5: 189–206.
- LOCHHEAD, J. H., 1954: On the distribution of a marine cladoceran, *Penilia avirostris* DANA (Crustacea, Branchiopoda), with a note on its reported bioluminescence. — Biol. Bull. 107: 92–105.
- MIRONOV, O. G., 1969: Effect of oil pollution upon some representatives of the Black Sea zooplankton. — Zool. Zh. 48: 980–984 (in Russian).
- MULLIN, M. M., 1969: Production of zooplankton in the ocean: the present status and problems. — Oceanogr. Mar. Biol. Ann. Rev. 7: 293–314.
- PAVLOVA, E. V., 1959: Feeding of *Penilia avirostris* DANA. — Trud. Sevastopol. biol. Stants. 11: 63–71 (in Russian).
- PORUMB, F. I., and I. I. PORUMB, 1966: Cercetări asupra migrațiilor nietemerale a zooplanctonului marin de vară. — St. si. cerc. biol. Seria zoologie 18: 65–76.
- RAJAGOPAL, P. K., 1962: Notes on the occurrence of Cladocera in the Madras coastal waters. — Current Science, 31: 467–468.
- RAMMNER, W., 1933–34: Die Cladoceren der „Meteor“ — Expedition. — Wiss. Ergebn. Dtsch. Atlant. Exped. — „Meteor“ 12: 111–121.
- RAYMONT, J. E. G., and E. LINFORD, 1966: A note on the biochemical composition of some mediterranean zooplankton. — Int. Revue ges. Hydrobiol. 51: 485–488.
- RICHARD, J., 1895: Révision des Cladocères. — Ann. Sc. Nat. Zool. et Paléontol., 7^e ser. 18: 279–389.
- SANTUCCI, R., 1937: Ricerche sulla fauna del Mar Rosso (Dicembre 1932–Giugno 1933): II Plankton dei banchi madreporici. Contributo alla conoscenza del microplankton di superficie. — Boll. Musei. Lab. Zool. Anat. Comp. Univ. Genova 17: (92): 1–45.
- SHMELEVA, A. A., 1965: Weight characteristics of the zooplankton of the Adriatic Sea. — Bull. Inst. océanogr. Monaco, 65, no. 1351: 1–24.
- STEUER, A., 1933a: Die „Arten“ der Cladoceren-gattung *Penilia* DANA. — Mitt. Zool. Mus. Berlin 19: 80–83.
- 1933b: Zur Fauna des Canal di Leme bei Rovigno. — Thalassia 1 (4): 1–44.
- THIRIOT, A., 1970: Cycle et Distribution de Crustacés Planctoniques de la Région de Banyuls-sur-Mer (Golfe du Lion). 2. Étude Spéciale des Cladocères. — Thèse de doctorat: 121–308.
- TREGOUBOFF, G., 1963: La distribution verticale des Cladocères a large de Villefranche-sur-Mer. — Bull. Inst. océanogr. Monaco, 61, no. 1279: 1–23.
- WICKSTEAD, J. H., 1961: A quantitative and qualitative study of some Indo-West Pacific plankton. — Fish. Publ. Lond. no. 16: 1–200.
- 1963: The Cladocera of the Zanzibar area of the Indian Ocean, with a note on the comparative catches of two plankton nets. — East. Afr. Agr. For. Jour. 29: 164–172.
- ZELEZINSKAJA, L. M., 1966: On mass mortality of *Penilia avirostris* DANA in the northwestern part of the Black Sea. — Gidrobiol. Zhurn. 2: 53–55 (in Russian).

Prof. Dr. NORBERTO DELLA CROCE
Cattedra di Idrobiologia e Piscicoltura,
Facoltà di Scienze, Fisiche, Matematiche
e Naturali, Università di Genova
16126 Genova, Via Balbi 5