# *The effects of sampling gear and environmental conditions on the abundance estimates of freshwater zooplankton*

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## Summary

*Freshwater zooplankters (Rotifera, Cladocera and Copepoda) were counted in 96 plankton samples collected mainly from a small eutrophic reservoir in Córdoba, Argentina. Sampling gear used were two different nets (pushed ahead of the boat and towed behind it, with and without bridles), a submersible centrifugal pump, and a water bottle. The results suggest that neither net size nor bridles have measurable effects on the net yields. Disturbance of the upper layer during the daytime prior to collection engenders avoiding reactions which are responsible for conspicuously lower net, pump and bottle catches, while at night disturbance-related biases were not present. The zooplankters surveyed are more efficiently collected by nets in overcast weather and at night than under full sun; this is tentatively attributed to optomotor dodging reactions. As compared with net samples, both the stationary pump and the bottle underestimate densities; disturbance-related dispersion of the animals is partly responsible for this bias. In addition, all three groups studied have very strong positive rheotactic reactions and actively avoid the intake of the pump. The efficiency differences observed span, in some cases, several orders of magnitude.*

Key words : Zooplankton — Sampling — Escapement — Freshwater.

## Résumé

### Les effets du mode d'échantillonnage et de l'environnement sur l'estimation d'abondance du zooplancton d'eau douce

*L'abondance du zooplancton (Rotifères, Cladocères et Copépodes) a été évalué à partir de 96 échantillons, la plupart provenant d'un petit réservoir eutrophique de Córdoba, Argentine. Trois types d'échantillonneurs ont été employés : deux filets (placés en avant et en arrière du canot, avec et sans brides), une pompe centrifuge submersible et une bouteille. Les résultats suggèrent que ni la taille du filet ni les brides n'ont un effet mesurable sur la récolte. De jour, les perturbations de la couche d'eau supérieure provoquent des réactions d'échappement diminuant ainsi l'efficacité des échantillonneurs, par contre les perturbations nocturnes ne produisent pas tel effet. Le zooplancton a été capturé plus efficacement avec les filets pendant la nuit ou par temps nuageux que par temps ensoleillé; ceci peut s'attribuer aux réactions optomotrices d'évitement. Par rapport aux échantillons de filets, la pompe et la bouteille sous-estiment la densité; la dispersion causée par perturbation est en partie responsable de cette différence. De plus, les trois groupes étudiés montrent de fortes réactions rhéotactiles en évitant activement l'aspiration de la pompe. Les différences d'efficacité atteignent parfois plusieurs ordres de grandeur.*

Mots-clés : Zooplancton — Échantillonnage — Échappement — Eau douce.

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## INTRODUCTION

Present-day knowledge of the abundance of planktonic organisms is based upon counts of samples taken by means of a wide variety of equipment and techniques. Although many investigations have shown that the results of these abundance estimates are influenced by various factors (*i.e.*, sampling gear and procedures, size, anatomical and physiological characteristics of the organisms, vertical migrations, wind, space distribution patterns, etc. (see, for example, Barkley, 1964, 1972; Smyly, 1968; UNESCO, 1968; Wiebe & Holland, 1968; Beers, 1981; Boltovskoy, 1981; Boltovskoy, Pedrozo & Battistoni, 1984 ; Boltovskoy *et al.*, 1985; Omori & Hamner, 1982), too often the warnings reported are largely ignored in subsequent work.

Some of these biases can be quantified with relative precision without specific investigations. Among them are net filtration efficiency, estimation of volume of water filtered, estimation of towing depth, and counting errors (UNESCO, 1968; Sournia, 1978). Other problems, however, depend upon many changing variables and cannot be accounted for by introducing standardized corrections or using standardized techniques : avoidance of the sampling gear and planktonic patchiness are probably the most important of these. In this respect limited research has been done concerning plankton nets in marine environments (see review in Boltovskoy, 1981), but investigations on the performance of pumps and water bottles, as well as detailed comparative net-pump-bottle studies are scarce, fragmentary and their results often contradictory.

This report is an evaluation of the performance of three of the most commonly used plankton sampling devices : plankton net, submersible pump and water bottle. Our attention was centered on crustacean zooplankton, while Rotifera, dealt with in a previous report (Boltovskoy *et al.*, 1985) and some phytoplankters are included for comparative purposes.

## MATERIAL AND METHODS

Most of the samples were collected in "Embalse Cassafouths", an eutrophic reservoir located in Córdoba, Argentina, from a pneumatic boat equipped with an 8HP outboard motor. Bottom depths at the sampling site were between 20 and 30 m. Secchi disc readings at the times of our samplings were 1.7 to 2.25 m in December 1982, 3.25 m in July 1983, and 3.3 m in September 1983. Nine additional pump samples were taken in two different small ponds in May 1984 (not numbered and not included in Table I).

Both nets used were cylindro-conical and had a mesh opening of 0.044 mm, the larger one with a mouth diameter of 50 cm (250 cm long, porosity: 0.2, open area ratio: 2.2), and the smaller 20 cm (length: 100 cm, porosity: 0.22, open area ratio : 3.2) and were equipped with digital flowmeters. When towed, a minimum distance of 10 m was maintained between the net and the boat. Pushnets (small nets only) were installed at the end of a 5 m - long pole protruding from the boat's bow. For unbridled net tows the mouth-ring of the latter was fastened to a rectangular frame the upper side of which was attached perpendicularly to a 5 m - long pole. Towing speeds ranged between 60 and 75 meters per minute. Net tows were carried along a 100 m transect defined by means of two anchored buoys, in many cases in triplicate, travelling opposite directions. Two nets were used simultaneously in most tows. Preliminary trials indicated that flowmeter revolutions did not decrease consistently in tows up to 120 to 200 m long, thus confirming that clogging did not affect flowmeter readings.

Our comparative study required a fine mesh for retrieving all the organisms considered, but this

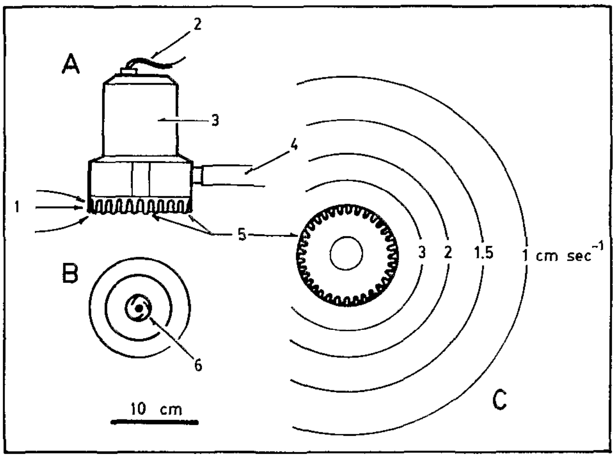

Fig. 1. — Diagrammatic scheme of the pump used seen from the side (A) and from below (B, protective cover removed). C : acceleration fields at different distances from the pump as shown by streaks of dyed water (pump viewed from below, protective cover on). The depth of the layer visibly influenced by the pump is about 10-15 cm. 1. Water intake; 2. Cable (to 12V battery); 3. Motor; 4. Discharge hose (to boat); 5. Slots in protective cover; 6. Intake and impeller's blades. *Schéma de la pompe utilisée : vue latérale (A) et vue inférieure (B, sans le couvercle protecteur). C : champs de vitesse à différentes distances de la pompe (vue inférieure, avec couvercle protecteur). L'épaisseur de la zone influencée par la pompe est de 10-15 cm. 1. Entrée d'eau; 2. Câble (branché à une batterie de 12V); 3. Moteur; 4. Tuyau de collecte (vers le canot); 5. Fentes du couvercle protecteur; 6. Orifice d'entrée et palette de prise d'eau*

resulted in a low filtration efficiency. Increasing the initial efficiency (*i.e.*, the ratio of the volume of water filtered to the volume swept by the mouth) would have been possible by reducing the diameter of the nets' mouths and/or lengthening their filtering surface; however, such nets would have been impractical and, especially, non-comparable to those normally used in routine surveys. Low efficiencies can, in some cases, account for imprecise flowmeter readings (UNESCO, 1968; BOLTOVSKOY, 1981). Several evidences allow us to conclude that our estimates are correct despite the low efficiency figures. At the towing speeds used the response (revolutions per meter) of the flowmeters was almost linear and well above their friction point. When comparing the volumes of water filtered by simultaneously towed and/or pushed nets, in 85% of the cases the differences between both nets were below 20%; this suggests a highly predictable, rather than erratic, flowmeter behavior. Finally, our net abundance estimates are similar to those performed independently in the same reservoir (collecting water with buckets and pouring it through nets).

The pump was centrifugal, submersible, battery-powered, with a 2.2 cm (internal diameter) plastic hose (fig. 1). Flow rates were around 50 liters per minute. The bottle was of the Niskin type, 6 l in volume, made of opaque (grey) PVC plastic.

Pump samples were concentrated in the small net, lowering it into the water in order to avoid damaging the organisms and extruding them through the meshes due to pressure of the flow. The same net was used for concentrating the bottle samples, pouring gently the water into the net; the bottle was inverted (rather than drained through the lateral port) to overcome biases due to settling of the plankters (GARDNER, 1977).

In total, 1475 counts were performed. In most cases aliquots of the samples were counted usually enumerating between 100 and 200 individuals of each category considered. For the scarcest groups whole samples were counted in many instances. Duplicate counts were carried out occasionally in order to confirm the results.

In a few samples the dinoflagellate *Peridinium gatunense* (Nygaard), the desmidiacean *Staurastrum* spp., and the copepod *Tropocyclops prasinus* Fischer, were also counted.

Most of our subsequent discussions are based on ratios of the yields compared; for practical reasons, zero counts in the denominator were replaced by unity in these calculations. For statistical analyses raw data were normalized by means of logarithmic transformations: $x = \log(x+1)$ or, when this transformation proved still insufficient, $x = [\log(x+1) + 0.5]^{1/2}$.

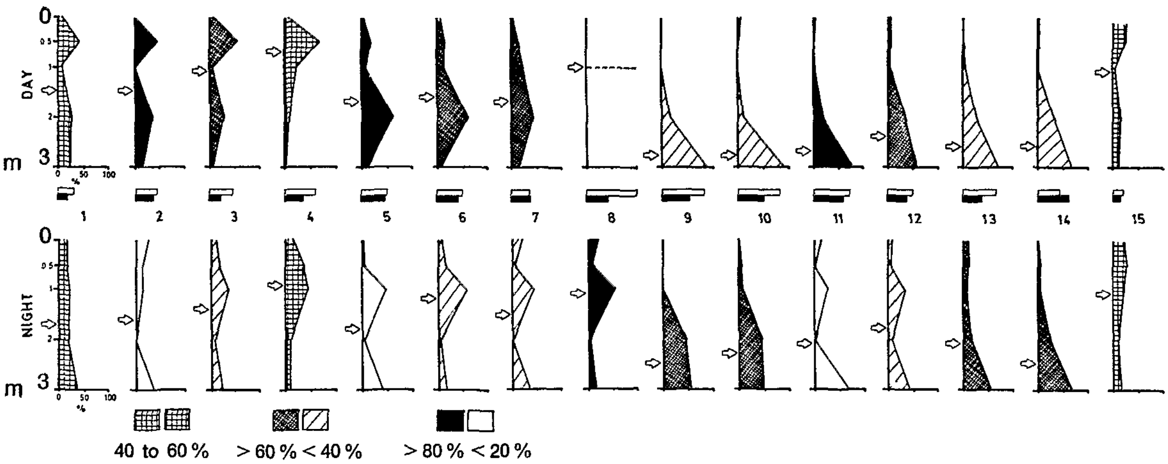

FIG. 2. — Vertical distribution (percentage data) of the groups studied in the 0-3 m layer as shown by pump samples #49-53 (day), and #57-61 (night). Shadings represent day vs. night relative abundance differences in 0-3 m layer (100% = sum of day + night totals). Arrows indicate position of average population depth ($\Sigma$ di . ni / $\Sigma$ ni, where di is depth i and ni is number of individuals at depth i). Lengths of horizontal bars at base of daytime profiles are proportional to standard deviations of concentrations in day (white bar) and night (black bar) profiles (based on percentages). See table I for group designations. *Distribution verticale (en pourcentages) des groupes étudiés dans la couche 0-3 m d'après les échantillons de pompe #49-53 (jour) et #57-61 (nuit). Les trames représentent les différences d'abondance jour-nuit (en %) dans la couche 0-3 m (100% = jour + nuit). Les flèches indiquent la position de la profondeur moyenne de la population ($\Sigma$ di.ni/$\Sigma$ni, ou di est la profondeur i, et ni est le nombre d'individus à la profondeur i). Les longueurs des barres horizontales en dessous des profils diurnes sont proportionnelles aux écarts-types des concentrations dans les profils de jour (blanc) et de nuit (noir), basés sur les pourcentages. Les groupes sont désignés dans le tableau I*

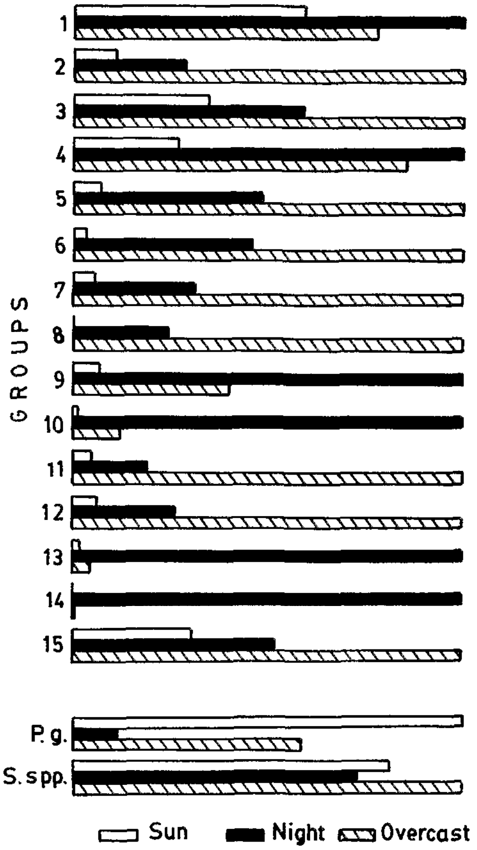

FIG. 3. — Relative abundance changes at the surface for each species group as shown by averaged yields of samples #1, 2, 3 (full sun, pushnets), #27-34 (night, pushnets), and #9-14 (overcast, pushnets). The algae *Peridinium gatunense* (P. g.) and *Staurastrum* spp. (S. spp.) were counted in samples #1, 11, 14, 27 and 33. See Table I for group designations. *Abondance relative, pour les différents groupe d'organismes. Changement d'abondance en surface (figures comparatives dans chaque groupe), montrés par les valeurs moyennes des échantillons #1, 2, 3 (voir le tableau I pour identification) en fonction des conditions d'éclairement : ensoleillé, nuageux et nuit. Valeurs moyennes des échantillons #1, 2, 3 (ensoleillé, filet avant), #27-34 (nuit, filet avant), et #9-14 (couvert, filet avant). Les algues* Peridinium gatunense *(P. g) et* Straurastrum *spp ont également été comptées dans les échantillons 1, 11, 14, 27 et 33*

## RESULTS AND DISCUSSION

### Vertical distribution

Although this survey was not aimed at the investigation of the vertical stratification of the plankters in the reservoir, an estimate of this pattern in the upper layers was necessary for the interpretation of subsequent results.

Fig. 2 and 3 suggest that most organisms studied performed diel vertical migrations. In clear weather, copepods, *Diaphanosoma brachyurum* and *Bosmina* spp. (groups 2-8, 11, 12) concentrated during the day between 0.5 and >3 m, while at night over 70% of their populations sank below 3 m. *Daphnia spinulata* and *Ceriodaphnia dubia* (groups 9, 10, 13 and 14) evaded the upper levels both in overcast and in sunny days (their concentrations in the 0-3 m stratum were several times higher at night than in the daytime), and peaked below 2 m at all times. Copepoda nauplii (group 1) and *Keratella cochlearis* (group 15), seemed to be less affected by diel cycles; abundances in the 0-3 m layer and at the surface varied within narrower limits. For comparative purposes in fig. 3 two algae are included: *Staurastrum* spp., which lacks the ability to perform diel

TABLE I

Summary of data and results of counts

All samples are surface unless otherwise indicated. Counting groups and their corresponding average lengths are as follows: 1. Copepoda nauplii (0.19 mm); 2. *Acanthocyclops robustus* (Sars), small copepodids (0.40 mm); 3. *A. robustus*, large copepodids (0.67 mm); 4. *A. robustus*, adults (1.02 mm); 5. *Notodiaptomus incompositus* (Brian), copepodids (0.68 mm); 6. *N. incompositus*, adults (1.20 mm); 7. *Diaphanosoma brachyurum* (Lievin), small (0.42 mm); 8. *D. brachyurum*, large (0.94 mm); 9. *Daphnia spinulata* (Biraben), small (0.81 mm); 10. *D. spinulata*, large (1.42 mm); 11. *Bosmina huaronensis* (Delachaux) and *Bosmina longirostris* (Mueller), small (0.32 mm); 12. *B. huaronensis* and *B. longirostris*, large (0.45 mm); 13. *Ceriodaphnia dubia* (Richard), small (0.38 mm); 14. *C. dubia*, large (0.62 mm); 15. *Keratella cochlearis* (Gosse), (0.18 mm). b: water bottle; d: day; fs: full sun; ln: large net; n: night; nb: no bridles; ov: overcast; p: pushnet; pm: pupm; sn: small net; t: towed; wb: with bridles.

*Day samples collected approximately between 10:00 and 17:00 hs., dusk samples: 18:00-19:00 hs., night samples: 23:00-03:00 hs.* First samples of each set of replicates are followed, in parentheses, by the corresponding subsequent tows; the latter are included in square brackets

*Données et résultats des comptages*

Tous les échantillons ont été pris en surface, sauf ceux qui sont indiqués. Les groupes comptés et leurs longueurs moyennes correspondantes sont comme suit : 1. copépode nauplii (0,19 mm) ; 2. *Acanthocyclops robustus* (Sars), petits copépodites (0,40 mm) ; 3. *A. robustus*, grands copépodites (0,67 mm) ; 4. *A. robustus*, adultes (1,02 mm) ; 5. *Notodiaptomus incompositus* (Brian), copépodites (0,68 mm) ; 6. *N. incompositus*, adultes (1,20 mm) ; 7. *Diaphanosoma brachyurum* (Lievin), petit (0,42 mm) ; 8. *D. brachyurum*, grand (0,94 mm) ; 9. *Daphnia spinulata* (Biraben), petit (0.81 mm) ; 10. *D. spinulata*, grand (1,42 mm) ; 11. *Bosmina huaronensis* (Delachaux) et *Bosmina longirostris* (Mueller), petit (0.32 mm) ; 12. *B. huaronensis* et *B. longirostris*, grand (0,45 mm) ; 13. *Ceriodaphnia dubia* (Richard), petit (0.38 mm) ; 14. *C. dubia*, grand (0,62 mm) ; 15. *Keratella cochlearis* (Gosse), (0,18 mm). b : bouteille ; d : jour ; fs : temps ensoleillé ; ln : filet-grand ; n : nuit ; nb : sans brides ; ov : temps nuageux ; p : filet placé en avant du canot ; pm : pompe ; sn : petit filet ; t : filet placé en arrière du canot ; wb : avec brides.

Les échantillons diurnes ont été recueillis entre environ 10 et 17 h, ceux du soir entre 18 et 19 h, et ceux de la nuit entre 23 et 3 h. Les échantillons de chaque série de replicats sont suivis, entre parenthèses, par les replicats correspondants ; ces derniers sont entre crochets

| e # | Gear | Time and cloud coverage | Vol. water filt.(l) | Counts (indiv. per 100 l of water filtered) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| mber 1982 | | | | | | | | | | | | | | | | | | |
| 3) | sn,nb,p | d,fs | 365 | 36700 | 715 | 1835 | 404 | 700 | 280 | 171 | 0 | 62 | 15 | 31 | 78 | 62 | 0 | 184300 |
| | sn,nb,p | d,fs | 272 | 45200 | 287 | 686 | 187 | 174 | 50 | 25 | 0 | 25 | 37 | 25 | 0 | 12 | 0 | 110300 |
| | sn,nb,p | d,fs | 633 | 13200 | 117 | 357 | 54 | 305 | 62 | 14 | 2 | 18 | 18 | 14 | 23 | 8 | 0 | 75200 |
| 6) | sn,nb,t | d,fs | 390 | 34900 | 762 | 1494 | 164 | 314 | 299 | 120 | 45 | 15 | 0 | 0 | 15 | 30 | 0 | 127000 |
| | sn,nb,t | d,fs | 312 | 34500 | 346 | 870 | 227 | 712 | 633 | 109 | 49 | 30 | 40 | 30 | 30 | 10 | 10 | 195900 |
| | sn,nb,t | d,fs | 288 | 46200 | 482 | 1267 | 226 | 1176 | 618 | 105 | 75 | 30 | 45 | 60 | 45 | 15 | 30 | 239900 |
| | sn,wb,t | d,fs | 253 | 29300 | 172 | 317 | 49 | 81 | 26 | 16 | 0 | 10 | 10 | 23 | 3 | 13 | 3 | 131900 |
| | sn,wb,t | d,fs | 162 | 40400 | 103 | 385 | 18 | 9 | 0 | 13 | 0 | 0 | 0 | 4 | 0 | 13 | 0 | 126200 |
| ,11) | sn,nb,p | d,ov | 221 | 54400 | 4655 | 4240 | 771 | 9072 | 5781 | 1601 | 689 | 230 | 178 | 348 | 645 | 96 | 0 | 202800 |
| | sn,nb,p | d,ov | 221 | 43200 | 3208 | 3241 | 972 | 6838 | 8037 | 799 | 562 | 205 | 292 | 216 | 605 | 54 | 0 | 308200 |
| | sn,nb,p | d,ov | 221 | 49800 | 2820 | 1843 | 642 | 6143 | 3714 | 942 | 321 | 209 | 209 | 363 | 475 | 77 | 7 | 397600 |
| 3,14) | sn,wb,p | d,ov | 204 | 44500 | 4495 | 1917 | 595 | 5123 | 1025 | 1679 | 906 | 224 | 275 | 427 | 600 | 41 | 0 | 328000 |
| | sn,wb,p | d,ov | 189 | 38600 | 3727 | 3467 | 520 | 5547 | 5634 | 1647 | 347 | 238 | 173 | 693 | 542 | 43 | 0 | 321500 |
| | sn,wb,p | d,ov | 130 | 19300 | 2372 | 1779 | 516 | 2347 | 2733 | 1019 | 219 | 142 | 206 | 593 | 271 | 52 | 13 | 816100 |
| 6,17) | sn,nb,t | d,ov | 241 | 41000 | 4591 | 7880 | 1563 | 1726 | 2703 | 586 | 98 | 195 | 163 | 65 | 33 | 163 | 0 | 88500 |
| | sn,nb,t | d,ov | 226 | 24500 | 1775 | 3077 | 283 | 529 | 925 | 208 | 19 | 0 | 19 | 57 | 0 | 94 | 38 | 137300 |
| | sn,nb,t | d,ov | 212 | 16300 | 74 | 70 | 26 | 4 | 7 | 0 | 0 | 2 | 4 | 5 | 0 | 0 | 0 | 88000 |
| 9,20) | sn,wb,t | d,ov | 275 | 34300 | 5151 | 4717 | 372 | 3289 | 9495 | 1614 | 248 | 124 | 0 | 372 | 186 | 62 | 0 | 109600 |
| | sn,wb,t | d,ov | 245 | 30900 | 4761 | 5936 | 764 | 6171 | 11402 | 1352 | 353 | 176 | 59 | 353 | 59 | 0 | 117 | 180300 |
| | sn,wb,t | d,ov | 243 | 38100 | 3537 | 5777 | 1002 | 3537 | 8783 | 648 | 530 | 59 | 59 | 413 | 118 | 0 | 0 | 179600 |
| 2,23) | sn,wb,t | d,ov | 202 | 52500 | 4554 | 7525 | 1148 | 1941 | 1703 | 792 | 79 | 119 | 79 | 317 | 40 | 40 | 40 | 167200 |
| | sn,wb,t | d,ov | 243 | 34000 | 634 | 305 | 84 | 397 | 159 | 173 | 44 | 52 | 29 | 44 | 38 | 65 | 2 | 97900 |
| | sn,wb,t | d,ov | 252 | 12900 | 174 | 51 | 11 | 3 | 1 | 4 | 0 | 1 | 6 | 0 | 3 | 1 | 0 | 41400 |
| | sn,wb,t | d,ov | 265 | 20200 | 285 | 906 | 323 | 2419 | 1087 | 39 | 13 | 0 | 78 | 13 | 39 | 26 | 0 | 356800 |
| | sn,wb,t | dusk,ov | 276 | 59700 | 1630 | 7220 | 621 | 22205 | 14984 | 1009 | 233 | 0 | 78 | 233 | 0 | 78 | 78 | 260200 |
| | sn,wb,t | dusk,ov | 255 | 53000 | 4664 | 8720 | 608 | 19469 | 16528 | 1521 | 406 | 304 | 0 | 101 | 0 | 203 | 0 | 257300 |
| 8,29) | sn,nb,p | n | 259 | 46000 | 1218 | 1914 | 924 | 2958 | 2128 | 375 | 120 | 616 | 3212 | 27 | 134 | 1178 | 696 | 399600 |
| | sn,nb,p | n | 229 | 73200 | 1273 | 2162 | 888 | 3613 | 2458 | 385 | 148 | 474 | 2398 | 89 | 296 | 2102 | 655 | 190500 |
| | sn,nb,p | n | 216 | 53700 | 1715 | 1981 | 846 | 4977 | 2706 | 580 | 24 | 918 | 2126 | 145 | 48 | 1715 | 580 | 208800 |
| 1) | sn,nb,p | n | 224 | 53200 | 506 | 1244 | 822 | 1033 | 2172 | 675 | 274 | 105 | 105 | 105 | 42 | 443 | 105 | 156300 |
| | sn,nb,p | n | 274 | 48600 | 233 | 776 | 207 | 491 | 1008 | 233 | 284 | 52 | 181 | 0 | 26 | 1396 | 879 | 114400 |
| 3,34) | sn,wb,p | n | 271 | 36400 | 1227 | 1373 | 915 | 2122 | 1820 | 291 | 94 | 551 | 2445 | 94 | 187 | 967 | 437 | 207500 |
| | sn,wb,p | n | 266 | 45600 | 996 | 2115 | 935 | 3539 | 1973 | 366 | 0 | 793 | 1952 | 102 | 224 | 1362 | 549 | 179800 |
| | sn,wb,p | n | 216 | 71100 | 1046 | 1430 | 747 | 3905 | 2155 | 341 | 64 | 640 | 2262 | 107 | 149 | 1366 | 355 | 201500 |
| 6) | sn,nb,t | n | 282 | 39500 | 398 | 605 | 778 | 519 | 1608 | 259 | 104 | 17 | 17 | 138 | 104 | 259 | 69 | 101100 |
| | sn,nb,t | n | 312 | 32100 | 177 | 467 | 306 | 177 | 1257 | 226 | 322 | 32 | 81 | 16 | 0 | 1112 | 419 | 126300 |
| 8,39) | sn,wb,t | n | 363 | 43100 | 1986 | 2368 | 306 | 7220 | 3667 | 611 | 38 | 1031 | 1413 | 115 | 38 | 1261 | 573 | 203600 |
| | sn,wb,t | n | 323 | 45300 | 2223 | 6114 | 1240 | 4104 | 3848 | 898 | 214 | 556 | 1026 | 85 | 128 | 2266 | 470 | 221000 |
| | sn,wb,t | n | 360 | 44400 | 1690 | 2976 | 857 | 3690 | 2381 | 1000 | 24 | 809 | 1190 | 190 | 48 | 1976 | 309 | 110900 |
| 1) | sn,wb,t | n | 255 | 41900 | 2454 | 5693 | 1118 | 10497 | 16969 | 780 | 1118 | 1003 | 1898 | 224 | 109 | 1788 | 447 | 318700 |
| | sn,wb,t | n | 270 | 51200 | 1460 | 2921 | 1015 | 3505 | 4439 | 1285 | 526 | 935 | 2044 | 0 | 58 | 1285 | 467 | 157000 |
| 3) | sn,wb,t | n | 400 | 63100 | 2934 | 2616 | 1031 | 12131 | 25054 | 476 | 476 | 476 | 317 | 0 | 0 | 951 | 634 | 226100 |
| | sn,wb,t | n | 308 | 66700 | 1861 | 3205 | 982 | 7445 | 6256 | 931 | 569 | 931 | 1086 | 52 | 0 | 2171 | 310 | 233500 |
| | ln,wb,t | d,ov | 1594 | 31900 | 3665 | 5956 | 1031 | 3436 | 13515 | 1718 | 573 | 229 | 0 | 229 | 114 | 0 | 0 | 116500 |
| | ln,wb,t | d,ov | 1341 | 42700 | 4659 | 4765 | 1271 | 8789 | 15884 | 1059 | 741 | 0 | 529 | 318 | 0 | 106 | 0 | 160300 |
| | ln,wb,t | d,ov | 1270 | 36900 | 5144 | 7769 | 2205 | 3674 | 12493 | 1785 | 945 | 105 | 0 | 210 | 105 | 315 | 0 | 132800 |
| | ln,wb,t | n | 1963 | 103600 | 2232 | 3780 | 936 | 2016 | 3276 | 828 | 360 | 540 | 1440 | 144 | 180 | 720 | 576 | 369300 |
| | ln,wb,t | n | 2353 | 27200 | 1201 | 1018 | 435 | 732 | 1012 | 360 | 82 | 265 | 567 | 26 | 88 | 1092 | 321 | 116200 |
| | pm | d,fs | 240 | 1000 | 5 | 33 | 5 | 8 | 53 | 3 | 0 | 3 | 5 | 3 | 3 | 3 | 3 | 29700 |
| | pm (0.5 m) | d,fs | 240 | 11700 | 171 | 429 | 52 | 466 | 159 | 29 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 26900 |
| | pm (1 m) | d,fs | 240 | 2300 | 9 | 39 | 16 | 267 | 135 | 59 | 14 | 2 | 0 | 5 | 2 | 5 | 0 | 6900 |
| | pm (2 m) | d,fs | 240 | 7400 | 125 | 229 | 5 | 1544 | 645 | 94 | 0 | 52 | 10 | 31 | 26 | 68 | 31 | 18000 |
| | pm (3 m) | d,fs | 264 | 6900 | 74 | 57 | 0 | 292 | 90 | 34 | 0 | 341 | 105 | 121 | 43 | 183 | 65 | 15900 |
| | pm | d,ov | 142 | 6600 | 105 | 234 | 57 | 303 | 153 | 18 | 0 | 9 | 15 | 21 | 0 | 9 | 6 | 145000 |
| | pm | d,ov | 280 | 1200 | 44 | 38 | 10 | 46 | 86 | 3 | 2 | 1 | 7 | 1 | 2 | 5 | 2 | 9800 |
| | pm | dusk,ov | 300 | 3400 | 156 | 278 | 35 | 828 | 580 | 30 | 15 | 5 | 5 | 25 | 10 | 0 | 0 | 4100 |
| | pm | n | 300 | 2900 | 18 | 22 | 8 | 7 | 29 | 15 | 13 | 8 | 2 | 3 | 2 | 45 | 5 | 21600 |
| | pm (0.5 m) | n | 300 | 3400 | 9 | 43 | 24 | 14 | 73 | 4 | 6 | 3 | 11 | 0 | 1 | 59 | 16 | 27400 |
| | pm (1 m) | n | 360 | 4300 | 11 | 81 | 30 | 189 | 229 | 32 | 34 | 15 | 28 | 6 | 9 | 49 | 19 | 21900 |
| | pm (2 m) | n | 300 | 3900 | 0 | 19 | 6 | 23 | 13 | 0 | 2 | 383 | 163 | 0 | 2 | 95 | 81 | 11000 |
| | pm (3 m) | n | 300 | 7500 | 31 | 56 | 5 | 153 | 71 | 25 | 10 | 439 | 184 | 15 | 10 | 271 | 255 | 15700 |
| | pm | n | 643 | 3000 | 55 | 157 | 42 | 224 | 229 | 110 | 42 | 102 | 161 | 0 | 8 | 97 | 30 | 22200 |
| | pm | n | 600 | 1200 | 10 | 19 | 11 | 19 | 170 | 9 | 8 | 2 | 7 | 1 | 0 | 9 | 6 | 11700 |
| | b | d,fs | 232 | 6400 | 43 | 51 | 5 | 16 | 13 | 0 | 0 | 0 | 3 | 0 | 0 | 5 | 3 | 19700 |
| | b | n | 232 | 2900 | 13 | 45 | 20 | 50 | 333 | 20 | 18 | 8 | 25 | 5 | 2 | 55 | 38 | 10100 |
| · 1983 | | | | | | | | | | | | | | | | | | |
| | sn,wb,t | d,ov | 173 | 10000 | 212 | 478 | 64 | 181 | 0 | 0 | 0 | 0 | 0 | 11 | 159 | 11 | 21 | 189100 |
| | sn,wb,t | d,ov | 9 | 4100 | 164 | 340 | 0 | 47 | 0 | 0 | 0 | 0 | 0 | 23 | 153 | 47 | 23 | 256300 |
| | sn,wb,t | d,ov | 16 | 4300 | 601 | 679 | 67 | 278 | 33 | 0 | 0 | 11 | 0 | 44 | 67 | 11 | 0 | 200400 |
| | sn,wb,t | d,ov | 20 | 4300 | 291 | 947 | 91 | 164 | 0 | 0 | 0 | 0 | 0 | 36 | 109 | 55 | 0 | 251600 |
| | sn,wb,t | d,ov | 29 | 6000 | 998 | 752 | 82 | 654 | 0 | 0 | 0 | 0 | 0 | 180 | 327 | 147 | 0 | 278200 |
| | sn,wb,t | d,ov | 40 | 6600 | 225 | 494 | 9 | 171 | 0 | 0 | 0 | 0 | 0 | 108 | 162 | 9 | 18 | 202700 |
| | sn,wb,t | d,ov | 90 | 7900 | 513 | 1099 | 37 | 183 | 0 | 0 | 0 | 0 | 0 | 55 | 220 | 73 | 0 | 202800 |
| | ln,wb,t | d,ov | 181 | 2900 | 163 | 438 | 23 | 292 | 3 | 0 | 0 | 0 | 0 | 31 | 103 | 37 | 9 | 147900 |
| | ln,wb,t | d,ov | 209 | 10200 | 799 | 587 | 0 | 1036 | 37 | 0 | 0 | 0 | 0 | 87 | 100 | 87 | 0 | 214400 |
| | b | d,ov | 6 | 3000 | 138 | 121 | 17 | 86 | 17 | 0 | 0 | 0 | 0 | 17 | 34 | 0 | 0 | 88200 |
| | b | d,ov | 6 | 1900 | 52 | 86 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 17 | 34 | 0 | 0 | 16300 |
| | b | d,ov | 12 | 1100 | 60 | 103 | 17 | 60 | 0 | 0 | 0 | 0 | 0 | 17 | 9 | 17 | 0 | 20800 |
| | b | d,ov | 29 | 800 | 65 | 26 | 0 | 78 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 18600 |
| | b | d,ov | 58 | 800 | 64 | 46. | 2 | 17 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 5 | 0 | 11300 |
| | b | d,ov | 116 | 600 | 53 | 67 | 3 | 30 | 0 | 0 | 0 | 0 | 0 | 1 | 7 | 9 | 1 | 14000 |
| tember 1983 | | | | | | | | | | | | | | | | | | |
| | sn,wb,t | d,ov | 903 | 2200 | 51 | 76 | 8 | 93 | 2 | 0 | 0 | 2 | 0 | 34 | 8 | 544 | 145 | 300 |
| | pm | d,ov | 5 | 4500 | 60 | 80 | 0 | 100 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 480 | 260 | 3700 |
| | pm | d,ov | 10 | 3600 | 60 | 70 | 0 | 120 | 10 | 0 | 0 | 0 | 0 | 10 | 10 | 670 | 130 | 3900 |
| | pm | d,ov | 20 | 3800 | 50 | 70 | 5 | 130 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 445 | 130 | 1400 |
| | pm | d,ov | 50 | 1800 | 78 | 52 | 0 | 65 | 6 | 0 | 0 | 0 | 0 | 0 | 6 | 751 | 168 | 500 |
| | pm | d,ov | 100 | 2200 | 40 | 67 | 20 | 113 | 7 | 0 | 0 | 0 | 0 | 7 | 7 | 647 | 380 | 300 |
| | pm | d,ov | 200 | 1800 | 101 | 53 | 0 | 128 | 11 | 0 | 0 | 0 | 0 | 11 | 0 | 656 | 405 | 300 |

vertical displacements, showed similar concentrations at all sampling times, while *Peridinium gatunense*, which is motile, tended to dwell near the surface during the day. This figure also suggests that for almost all the zooplankters counted contrasts in near-surface concentrations are as great for day vs. night patterns, as for overcast vs. sunny weather: with the only exception of group 11 and the two algae, all the clear vs. cloudy averages shown in fig. 3 were significantly different at levels $\leq 5\%$ (t-tests for log- transformed data).

## Factors not affecting the catches: net size and bridles

Several authors suggested that bridles ahead of the nets' mouths and small mouth diameters are responsible for underestimates of some zooplankters (McGowan & Fraundorf, 1966; Clutter & Anraku, 1968). Our results suggest that, within the framework of the experiments carried out, these two parameters do not affect the catches measurably.

Comparison of the yields of simultaneously collected small net — large net samples #18,19,20 vs. #44,45,46; #38 vs. #47; and #66-72 vs. #73-74 (the latter collected within a 2 hour interval) showed that, despite some differences, neither a clear trend nor significant and consistent disagreements were present. The scarce number of comparative data preclude us from further analyses of this relationship.

In total, 18 samples were collected in simultaneous unbridled-bridled pairs, each pair being repeated three times, both during the day by means of townets (#15,21; 16,22; 17,23), and pushnets (#9,12; 10,13; 11,14), and at night (pushnets only, #27,32; 28,33; 29,34). Although in most cases unbridled nets yielded slightly higher catches (overall ratio approx. 1.2 to 1), only 1 out of the 45 t-tests performed (3 experiments with 15 groups of organisms each) yielded a significant value at the 5% level, and neither during the day nor at night were there clear trends favoring either gear.

## Disturbance-related avoidance: bottle and net yields

Six bottle samples of variable size (6 to 116 liters) were taken in July 1983. Increasing volumes were achieved by repeatedly submerging the apparatus at the same site. The results obtained (table II) showed significant negative correlations for nauplii and *Bosmina* spp. (groups 1, 11 and 12). Most other groups present in these samples also correlated negatively with sample size, but the figures in question were not significant.

The fact that zooplankters evade foreign objects in their environment was suggested by several authors (e.g., Smyly, 1968; Langeland & Rognerud, 1974; Orr, 1981). Smyly *(op. cit.)*, concluded that cladocerans start moving away from the bottle as soon as it is placed in the water, and most of the swiftest ones will be out of reach within the first 30 seconds. In our case the time interval between arrival at the sampling site and actual collection of the samples was over several minutes; thus, most large zooplankters had probably fled the area even before the series was started. The negative significant correlations for nauplii and *Bosmina* spp. suggest that these poor swimmers were constantly moving away at a rate slow enough as to be recorded by consecutive samples (see below: "Disturbance-related avoidance and rheotactic responses: pump yields").

Table II

Correlation coefficients between organisms pet unit volume retrieved and bottle sample size, samples #75-80 (groups 6-10 and 14 were practically absent from these samples). Based on log-transformed data. See Table I for group designations

*Coefficients de corrélation entre les organismes comptés (par unité de volume) et la taille des échantillons de bouteille #75-80 (les groupes 6-10 et 14 ont pratiquement été absents dans ces échantillons). Les données sont transformées en logarithmes. Les groupes sont désignés dans le tableau I*

| Group number | Correlation index |
|---|---|
| 1 | -0.905** |
| 2 | -0.440 |
| 3 | -0.560 |
| 4 | -0.217 |
| 5 | -0.223 |
| 11 | -0.840* |
| 12 | -0.850* |
| 13 | 0.510 |
| 15 | -0.628 |
| Average | -0.412 |

* P < 0,05; ** P < 0,01

Small net samples of the December 1982 series were collected by means of tows 100 m long, between buoys. In most cases replicate samples for each gear and conditions were taken, towing in opposite directions at short intervals. These replicates were almost identical in all aspects, except for the fact that second and third tows of each set were performed in progressively more disturbed waters by the passage of nets, boat and, especially, motor. A comparison of the corresponding yields very strongly suggested that, during the daytime, recent disturbance of the medium influenced the catches of successive tows (fig. 4, day). In all cases, with the exception of *K. cochlearis* (group 15) and large *C. dubia* (group 14, present in very low densities)

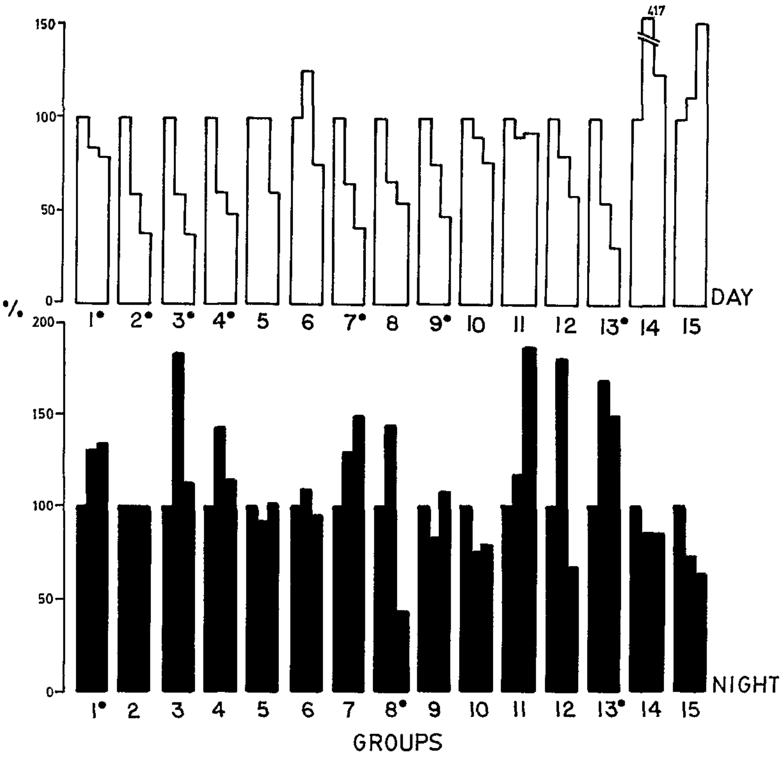

FIG. 4. — Comparative yields of second and third tows as referred to the first tow of the same set of replicates (based on averaged data of replicate net samples indicated in table I). Black dots denote differences between first and third tows at the 10 % or lower level of significance (t-test based on log-tranformed data). See table I for group designations. *Captures comparatives du second et troisième trait de filet par rapport au premier du même ensemble d'après les moyennes des replicats indiquées dans le tableau I). Les points noirs indiquent les différences significatives (P < 0.1, test de Student, données transformées en logarithmes) entre le premier et le troisième passage. Les groupes sont désignés dans le tableau I*

averaged data for third tows were lower than those for first ones, and in 11 cases second tows yielded intermediate figures. A similar analysis for nighttime samples showed no definite trend, the percentages in question oscillating at random around the mean of the first tow (fig. 4, night). It should be noticed that most consistent first tow/third tow daytime differences (denoted with a black dot in fig. 4) always involved lower yields in the latter, while at night there was no such relationship.

When considering clear and overcast weather samples jointly, neither during the day nor at night did the yields of simultaneous pushnets and townets show any particular trend. However, when separating sunny and overcast weather samples a suggestive pattern emerged (fig. 5). Under full sun the rear net yielded higher numbers than the front one, while in cloudy conditions the front net retrieved more organisms than the rear one. The averaged pushnet /townet ratio for all groups in full sun (0.41) differed significantly ($P<0.01$, t-test) from the same in overcast weather (1.46) (night average pushnet/townet ratio, samples #30-34 vs. #35-39: 1.1). The explanation of these differences should probably be sought in the combined effects of different clear day vs. overcast day concentrations at the surface and avoiding reactions of the disturbance which preceded townets. Under full sun the uppermost stratum was underpopulated, most plankters peaking at or below 0.5 m (fig. 2). The yields of towed nets were higher than those of pushnets because the waters they fished were enriched by admixture from subsurface, more densely populated strata, brought up to the surface by the action of front net, boat, and especially motor. The drop due to disturbance-avoiding reactions on the yields of townet samples were in this case overcompensated by the abovementioned artificial enrichment. On the other hand, in overcast weather zooplankton concentration at the surface were conspicuously higher than in clear days (fig. 3), and vertical profiles most probably lacked a sharp subsurface (0.5 – 1 m) drop (which was absent even at night, most taxa peaking at 0.5 to 2 m, rather than at the surface; see fig. 2). Thus, the catch drop in townets due to avoidance was not compensated by admixture of the deeper waters (see fig. 6 for a diagrammatic interpretation).

The time elapsed between the passage of front net and rear net at the same place was usually approx. 15 to 20 seconds. Estimates of the swimming velocities of Copepoda range from 2-3 up to 100 cm per second (Clutter & Anraku, 1968; Strickler, 1975); while those for Cladocera are somewhat slower (Smyly, 1968; and our observations). Even assuming the lowest values as a conservative estimate, most plankters should have had enough time to escape the waters disturbed (and subsequently sampled).

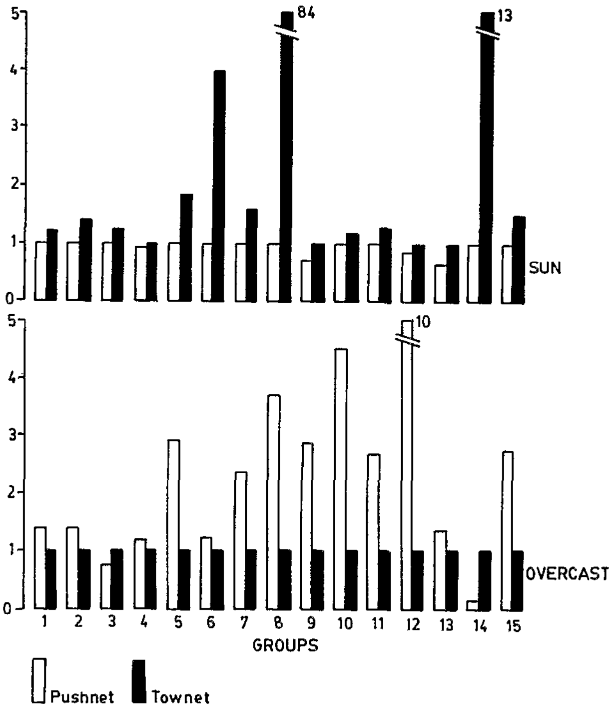

Fig. 5. — Pushnet and townet yields, comparative figures within each group. Based on averaged data of samples #1, 2, 3 vs. #4, 5, 6 (full sun), and #9-14 vs. #15-24 (overcast). See table I for group designations. *Captures par filet avant et filet tracté pour les différents groupes d'animaux, en utilisant les moyennes des échantillons #1, 2, 3 vs. #4, 5, 6 (temps ensoleillé) et #9-14 vs. 15-24 (temps nuageux). Les groupes sont désignés dans le tableau I*

These results suggest that, during the daytime, disturbance of the upper layer is a strong stimulus for evading the area of turbulence. Since at night evasion of townets was not evidenced, it is probable that light constitues the main clue which allows the organisms to flee the area disturbed. Our results also indicate that the animals tend to swim downwards (or settle passively), rather than move at random in any direction. These behavior patterns, derived on the basis of sampling biases, are confirmed by some previous ethologically oriented studies. Anderson (1974) showed that *marine* copepods that swim horizontally more than vertically are captured by predators 10 times more frequently than those that employ vertically oriented swimming modes. Singarajah (1975, and references therein), found that several marine copepods react to turbulence either seeking contact with solid surfaces or settling quickly to the bottom. He also observed that a few species (e.g., the copepod *Temora longicornis*) did so only in illuminated conditions, while in the darkness the tendency to sink was not present. Several authors proposed and tested pushnet systems for marine fish larvae (Herke, 1969; Kriete & Loesch, 1980; Gallagher & Conner, 1983), and in some cases pushnet vs. townet ratios were in excess of 20 (e.g., Kriete & Loesch, *op. cit.*). Our results suggest that, despite the much smaller size and lower motility of freshwater Copepoda and Cladocera (as compared to fish larvae), their efficient dodging behavior is responsible for the fact that townet systems underestimate their abundances.

## Disturbance-related avoidance and rheotactic responses: pump yields

Pump samples #82-87 are replicates taken within a <30 min. period, where volumes of water filtered were purposefully increased. The corresponding correlations between sample size and catch (Table III) strongly suggest that the abundance estimates of Copepoda nauplii and *K. cochlearis* were severely biased by this procedure, either because of disturbance of the sampling site prior and during the collection, or due to positive rheotactic reactions of the plankters swimming against the suction current, or both. In order to check the relative importance of these two factors, 9 additional samples were collected in May 1984. All of them were taken from the shore turning the pump on as soon as it was placed in the water; disturbance of the medium was also minimized by taking successive probes several meters apart. In both cases all correlations between sample size and numbers of organisms retrieved per unit volume were negative, and in 50 % of the cases significant (table III). These results confirm those illustrated in table II suggesting that, when disturbance prior to sampling was present most larger zooplankters fled the area much before the series was completed. On the other hand, nauplii, *K. cochlearis* and *Bosmina* spp. (the poorest swimmers of the cladocerans considered) were moving away at slower

TABLE III

Correlation coefficients between organisms per unit volume retrieved and pump sample size, samples #82-87 (groups 7-10 were absent from these samples). Based on transformed data : $x = [\log(x+1) + 0.5]^{1/2}$. See table I for group designations

*Coefficients de corrélation entre les comptages (par unité de volume) et la taille des échantillons de pompe #82-87 (les groupes 7-10 ont pratiquement été absents dans ces échantillons). Les donnés ont été transformés :* $x = [\log(x + 1) + 0.5]^{1/2}$*.Les groupes sont désignés dans le tableau I*

| Pooled groups | With disturbance prior to sampling | No disturbance prior to sampling | |
|---|---|---|---|
| | Samples #82-87 | May 1984 samples<br>5 samples | 4 samples |
| Nauplii (1) | -0.910* | -0.884* | -0.951* |
| Cyclopoida (2-4) | 0.733 | -0.882* | -0.483 |
| Calanoida (5-6) | 0.232 | -0.838 | -0.632 |
| *Bosmina* spp. (11,12) | 0.706 | --- | -0.836 |
| *C. dubia* (13,14) | 0.706 | --- | --- |
| *K. cochlearis* (15) | -0.969** | --- | -0.988** |

* $P < 0.05$; ** $P < 0.01$. Volumes filtered for samples in last two columns: 43, 86, 129, 215, 430 liters, and 9, 18, 72, 94 liters. In these samples the cyclopoids were represented by *Tropocyclops prasinus*, and the calanids by *Notodiaptomus incompositus*

* $P < 0{,}05$; ** $P < 0{,}01$. Les volumes filtrés des échantillons des deux dernières colonnes : 43, 86, 129, 215, 430 litres ; et 9, 18, 72, 94 litres. Dans ces échantillons les cyclopides ont été représentés par *Tropocyclops prasinus*, et les calanoides par *Notodiaptomus incompositus*

rates thus showing decreasing abundances in consecutive samples. Repeating the same experiment without prior disturbance, i.e., starting sampling and disturbance simultaneously, both large and small plankters showed negative correlations with sample size (table III).

We made observations on the reactions of *K. cochlearis, Notodiaptomus incompositus, Tropocyclops prasinus* and *Bosmina* spp. to currents and pressure changes. Swiftest responses to any kind of disturbance (shaking, approach of foreign objects, currents) were displayed by copepods and cladocerans. Clearest reactions were observed when siphoning liquid (flow rates were approx. 0.3 to 5 cm per second) from a beaker which contained the plankters. Adult copepods would hardly ever be drawn into the siphon : as soon as they sensed the current they would perform several powerful strokes which carried them invariably away from the intake. Copepodids reacted in a similar manner, as well as *Bosmina*

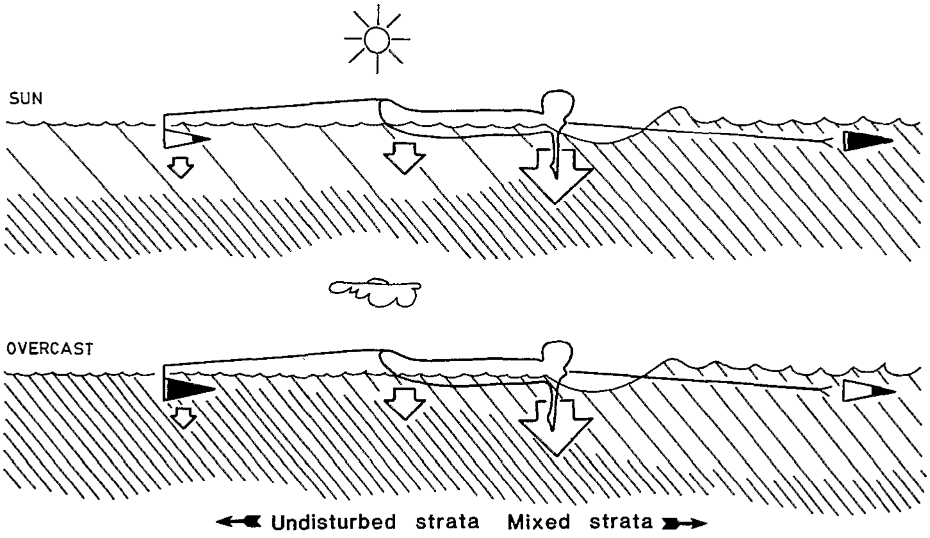

FIG. 6. — Diagrammatic interpretation of the differences in townet vs. pushnet ratios. Shadings represent different plankton concentrations ; arrows : avoiding reactions ; and comparatively higher catches are filled nets. Not to scale (see text for explanation).

*Schéma d'interprétation (sans échelle) des différences entre filet avant et filet arrière. Les ombrages représentent des différentes concentrations du plancton ; flèches : réactions d'évitement ; les filets noircis représentent les captures relatives. (Voir les explications dans le texte)* spp.; if drawn into the siphon in over 90% of the cases they swam rapidly against the current. In several instances we observed copepodids and cladocerans swimming frantically at the tip of the siphon for periods of over 30 seconds, until they would either be drawn inside or succeed in escaping the intake. Also *K. cochlearis* swam mostly against the current; this was best seen inside the transparent glass tube, behind its tapering end where current velocities were lower than at the intake.

In order to estimate quantitatively the evasion observed we devised the following experiment: freshly collected plankton was placed in a small (150 ml) beaker; from its central part a horizontally oriented siphon tube 3.5 mm in cross section connected the beaker with another container placed somewhat lower. Part of the liquid was then siphoned away into the lower container at rates ranging between 0.4 and 5 ml per second; thus, the current velocities at the tapering end of the siphon were about 6 to 60 cm per second. Subsequently both samples were fixed and counted. In all cases concentrations of organisms were higher in the original beaker than in the second one. Using the slowest current velocity (approx. 6 cm per second), at the end of the experiment we recorded 48.7 times more Copepoda (adults + copepodids) in the former than in the latter, *Bosmina* spp. : 8.1, and nauplii : 5.5. Increasing the intake velocity lowered these figures; at approx. 60 cm per second they were, Copepoda : 10.9, *Bosmina* spp. : 1.6, nauplii : 3.1, and *K. cochlearis* : 2.9 - 4.0. Repeating the same test in complete darkness (at 60 cm per second) lowered the latter figures even further : Copepoda : 4.8, nauplii : 1.1, and *K. cochlearis* : 1.1.

These tendencies to swim against the current are probably an adaptation to avoid planktivorous organisms that suck in water to catch their prey (Clutter & Anraku, 1968), and/or to avoid being expatriated from their habitats, as in the case of inflowing or outflowing streams. Fig. 1C is a diagrammatic scheme of the pump used which shows the zone visibly influenced by the apparatus. According to the diameter and depth of the layer where the streaks of dyed water indicate measurable displacements, the volume influenced by >3 cm per second velocities does not exceed approx. 15-20 liters. Most of our pump samples filtered over 200 liters; thus, usually over 80-90% of the water analysed came from an area which most positively rheotactic plankters could have fled before being sucked into the pump. Altough evasion from a pump is obviously a function of the capacity of the apparatus (e.g., Beers, 1981), it is probable that even high-capacity stationary systems in marine environments are subject to this type of bias because the overall proportions (i.e., flow rate, velocity fields, concentration of the organisms in the medium, volume required for a representative sample) are comparable to smaller systems in more densely populated waters.

Since our pump samples were taken from an anchored boat, the pump filtered at exactly the same place. It is probable that underway pump sampling can reduce avoidance considerably (Beers, 1981; Miller & Judkins, 1981; Taggart & Leggett, 1984). However, underway pump sampling does not allow the investigation of small scale spatial distributions, especially in oligotrophic, sparsely populated environments. In addition, in small and/or narrow water bodies anchoring is a necessity since pump sampling is usually a time consuming operation in the course of which winds and currents can displace the vessel considerably.

## Pump and bottle underestimation

Fig. 7 shows that nets always retrieved higher numbers of organisms than the pump. These figures,

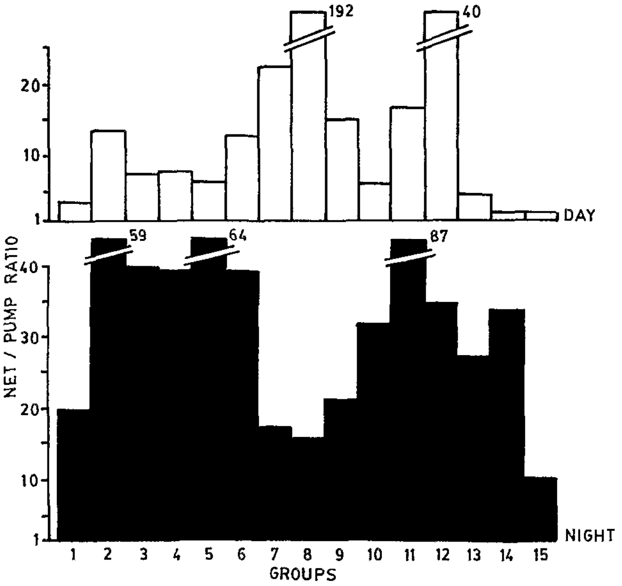

Fig. 7. — Averaged ratios of net vs. pump yields. Samples used : #1-24 vs. #49, 50, 54, 55, and #81 vs. #82-87 (day); #27-43 vs. #57, 58, 62, 63 (night). Since the abundances of some groups were negatively correlated with pump sample size, only the highest yield of the #82-87 series for each group was considered. See table I for group designations. *Rapport moyen entre les captures par filet et avec la pompe. Échantillons utilisés : #1-24 vs. #49, 50, 54, 55, et #81 vs. 82-87 (jour); #27-43 vs. #57, 58, 62, 63 (nuit). Étant donné que les abondances de certains groupes présentent une corrélation négative avec la grandeur des échantillons de pompe, seules les plus fortes valeurs du groupe #82-87 ont été utilisées. Les groupes sont répertoriés dans le tableau I*

which represent overall averages for many samples, are in good agreement with a more detailed comparison involving the 5 net vs. pump sets collected within short ($<1$ hour) intervals : in 71 out of 75 comparisons (15 groups by 5 closely comparable sets) nets collected higher numbers of plankters. Fig. 7 also illustrates that nighttime differences were considerably higher than daytime ones (according to a t-test the means of the two series of ratios differed significantly, $P<0.01$); and that *K. cochlearis* had the lowest net/pump ratios (see also below : « Daytime net underestimation »). Altough pump samples did contain slightly higher proportions of damaged specimens than net and bottle samples (especially Cladocera), partial destruction of the fragile organisms cannot account for the different day vs. night net/pump ratios, and for underestimates of the more resistant categories counted, such as nauplii.

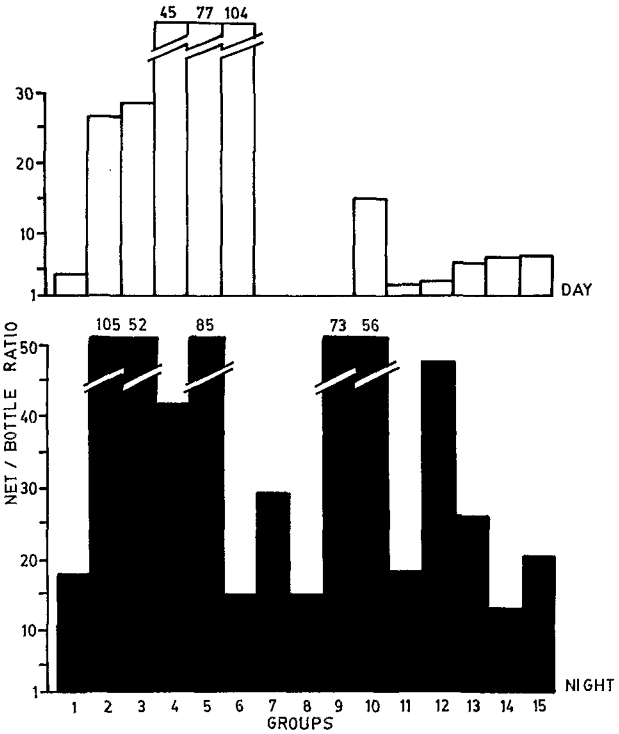

FIG. 8. — Averaged ratios of net vs. bottle yields. Samples used: #1-24 vs. #64, and #66-72 vs. #75-80 (day); #27-43 vs. #65 (night). Since the abundances of some groups were negatively correlated with bottle sample size, only the highest yield of the #75-80 series for each group was considered. See Table I for group designations. *Rapport moyen entre les captures avec filets et avec bouteille. Échantillons utilisés : #1-24 vs. #64, et #66-72 vs. #75-80 (jour) ; #27-43 vs. #65 (nuit). Étant donné que les abondances de certains groupes présentent une corrélation négative avec la grandeur des échantillons de pompe, seules les plus grandes captures des séries #75-80 ont été considérées. Les groupes sont désignés dans le tableau I*

Fig. 8 presents the ratios for the net vs. bottle samples compared. With almost no exceptions nets retrieved much higher numbers of organisms per liter than bottles. The average net/bottle ratio was significantly higher at night than during the day ($P<0.01$).

It should be pointed out that the ratios illustrated in figs. 7 and 8 are partly based on underestimated results of second and third net tows of sets replicates (fig. 4), and on probably somewhat overestimated pump and bottle yields (see captions to figs. 7 and 8). Thus, it is conceivable that in reality the ratios are even higher than indicated.

Several previous investigations reported similar net-pump-bottle efficiences, and some concluded that bottle and/or pump performance are better than net sampling (e.g., BEERS, 1981 ; RUTTNER-KOLISKO, 1977 ; MAKAREWICZ & LIKENS, 1979). However, patchiness, extrusion through the meshes, diel vertical migrations, clogging, are some of the phenomena that can obscure evidences of avoidance and engender wrong interpretation of the results. For example, according to CLUTTER & ANRAKU (1968), extrusion through the meshes might have been responsible for the apparently lower density of copepods in nets as compared with the suction pump used by ARON (1958). RUTTNER-KOLISKO's (1977) net sample results were most probably biased by clogging. MAKAREWICZ & LIKENS (1979) compared bottle samples filtered through a 0.035 mm mesh with 0.158 mm mesh nets ; the gauze of the latter was large enough as to retrieve very few or no Rotifera, and most probably allowed many Crustacea to be extruded through the meshes.

## Daytime net underestimation

Pump samples underestimate abundances conspicuously at all times, therefore direct comparison with net yields beyond the ratios shown on fig. 7 are difficult. However, the different pump and net biases can be standardized referring them to the efficiency of the same gear at the same time. This was done in fig. 9, standardizing pump and net catches in clear and cloudy weather on the basis of their corresponding night yields. In overcast weather both gears behave in a roughly similar manner. On the other hand, under full sun nets showed considerably lower ratios than the pump. Since « oversampling » (by the pump) is a hardly conceivable event, we conclude that this difference is due to net undersampling. In other words, direct sunlight (as opposed to diffuse light in overcast conditions) might constitute an important factor which substantially lowers the catchability of the net.

Clogging (due to higher abundances of plankton at

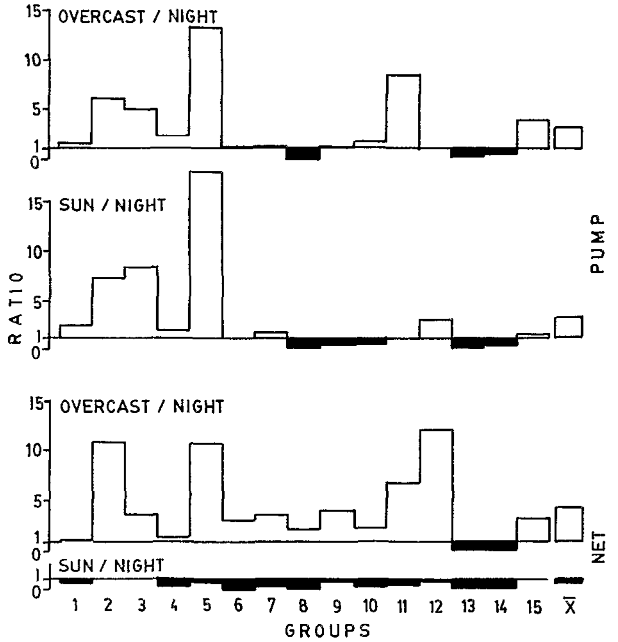

FIG. 9. — Daytime/nightime ratios of net and pump yields in sunny and in cloudy weather. Samples used : #9-14 (net, overcast); #30, 31, 35, 36 (net, night); #54, 55 (pump, overcast); #57, 58, 63 (pump. night); #49, 50 (pump, full sun). Samples were collected in the same overcast day, same sunny day, and same night. See table I for group designations. *Rapport entre les captures nocturnes et diurnes avec filet et avec pompe selon les conditions d'éclairement. Échantillons utilisées : #9-14 (filet, temps nuageux); #30-31, 35, 36 (filet, nuit); #54-55 (pompe, temps nuageux); #57, 58, 63 (pompe, nuit); #49, 50 (pompe, temps ensoleillé); et #1, 2, 3 (filet, temps ensoleillé). Ces échantillons ont été recueillis le même jour nuageux ou ensoleillé, et la même nuit. Les groupes sont désignés dans le tableau I*

the surface, see figs. 2 and 3) and, therefore, pressure fronts ahead of the nets must have been higher in overcast weather than under full sun : this supports the assumption that enhanced net evasion in clear weather is more closely linked to vision or light/vision-related physiological changes, than to pressure fronts. Several previous observations, most of which were performed in marine environments (e.g., BRINTON, 1967; WIEBE *et al.*, 1982; OMORI & HAMNER, 1982; THAYER *et al.*, 1983; etc.) commented on the effects of light (in general) on the dodging behavior of zooplankters. The above-discussed results also link highest escapement with lowest densities (under full sun). It is probable that the number of animals per unit volume plays some role in this respect as well. FLEMINGER & CLUTTER (1965) observed that at higher densities the evading reactions of Mysidacea were lower than in sparser populations. In nature, pressure fronts are generated by a wide variety of factors, including the organisms themselves (STRICKLER, 1975); if the latter are very numerous, the overabundance of signals might obscure those generated by the approaching net.

## CONCLUSIONS

Three of the most commonly used plankton sampling devices (nets, pushed ahead of the boat and towed behind it; a submersible pump, fig. 1; and a water bottle) were used in a comparative study of their efficiency for collecting freswater zooplankton, including Rotifera *(Keratella cochlearis)*, Copepoda *(Acanthocyclops robustus* and *Notodiaptomus incompositus)*, and Cladocera *(Diaphanosoma brachyurum, Daphnia spinulata, Ceriodaphnia dubia* and *Bosmina* spp.). In total about 1500 counts were carried out of the 15 categories (copepods and cladocerans divided into size-classes) considered in the approx. 100 samples collected (table I). The results of our analyses show that :

1. Within the framework of this survey, neither net size (mouth diameters 20 and 50 cm), nor bridles ahead of nets' mouths affect the catches measurably.
2. During the daytime, especially under full sun, zooplankters react to disturbance of the medium by sinking to deeper strata ; this behavior is responsible for lower net catches in recently disturbed waters (fig. 4). Disturbance-generated mixing of surface waters with lower more densely populated layers can obscure avoidance yielding higher catches in the disturbed (and enriched) area (rear net), rather than in the undisturbed one (front net; see figs. 5 and 6). Bottle and pump samples are also affected by disturbance; most organisms move away from the sampling site fast enough as to flee the area in the interval between reaching the site and starting the collection, thus successive samples do not show decreasing concentrations. On the other hand, smaller and slower organisms escape the area of disturbance at a rate slow enough as to show a consistent and gradual decrease (tables II and III). At night disturbance-related avoiding reactions were not detected.
3. All the zooplankters studied have very strong rheotactic reactions (swimming against the current) which greatly enhance their pump-dodging capabilities (table III).
4. Avoidance of disturbance and rheotactic behavior are responsible for consistently underestimated bottle and net yields. The bias involved is, in general terms, more conspicuous for the larger and more active organisms, and significantly higher at night than during the day (figs. 7 and 8).

5. In clear (sunny) weather nets are considerably less efficient than in overcast conditions (fig. 9); this difference is most probably due to enhanced net-dodging capabilities under full sun.

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