Note in this paper how population estimates made from catch per unit effort of gillnets + mark and recapture.

- Know definitions of:

biomass (= standing crop)

production → A. Net production
→ B. Gross production

yield (= harvest)

# Year-Class Abundance, Population, and Production of Walleye (*Stizostedion vitreum vitreum*) in Clear Lake, Iowa, 1948–74, with Varied Fry Stocking Rates[1,2]

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Carlander, K. D. and P. M. Payne. 1977. Year-class abundance, population, and production of walleye (*Stizostedion vitreum vitreum*) in Clear Lake, Iowa, 1948–74, with varied fry stocking rates. J. Fish. Res. Board Can. 34: 1792–1799.

Year-class abundance of walleye, *Stizostedion vitreum vitreum*, in Clear Lake from 1948 to 1974 was significantly correlated ($r = 0.613$) with annual fry stocking, which was varied from 0 to 6070 fry/ha. Abundance of young walleye seined along shore was even more highly correlated with fry stocking ($r = 0.819$) but not significantly correlated with year-class abundance ($r = 0.179$) indicating that year-class strength may change between the first summer and later years. No correlation was found between year-class abundance and temperature in summed degree-days, water levels, or abundance of yellow perch, *Perca flavescens*, as effects were probably masked by the fry stocking. Growth of age 0 and I walleye were negatively correlated with fry stocking ($r = -0.42$ and $r = -0.41$, respectively), but growth of age V walleye was positively correlated ($r = 0.70$). Growth was also correlated with water levels ($r = 0.79$). Annual mortality rate averaged 42%. Standing crop ranged from 2.63 to 16.52 kg/ha and annual production from 1.01 to 9.31 kg/ha. Production per biomass was low when water levels were low.

*Key words*: Percidae, walleye, *Stizostedion vitreum vitreum*, population dynamics, productions, Clear Lake, Iowa, stocking

Carlander, K. D., and P. M. Payne. 1977. Year-class abundance, population, and production of walleye (*Stizostedion vitreum vitreum*) in Clear Lake, Iowa, 1948–74, with varied fry stocking rates. J. Fish. Res. Board Can. 34: 1792–1799.

Il existe une corrélation significative ($r = 0.613$) entre l'abondance des classes d'âge du doré jaune, *Stizostedion vitreum vitreum*, dans le lac Clear, de 1948 à 1974 et les peuplements annuels d'alevins, variant de 0 à 6070 alevins/ha. L'abondance des jeunes dorés jaunes capturés à la senne le long du rivage est encore plus étroitement liée aux peuplements d'alevins ($r = 0.819$), mais il n'y a pas de corrélation significative avec l'abondance des classes d'âge ($r = 0.179$), ce qui indique que l'abondance des classes d'âge peut changer entre le premier été et les années subséquentes. Nous n'avons pas trouvé de corrélation entre l'abondance des classes d'âge et la température comme somme de degrés-jours, les niveaux d'eau ou l'abondance de la perchaude, *Perca flavescens*, étant donné que les effets sont probablement masqués par les peuplements d'alevins. La croissance des dorés jaunes d'âges 0 et 1 montre une corrélation négative avec les peuplements d'alevins ($r = -0.42$ et $r = -0.41$, respectivement), mais la corrélation est positive pour les dorés jaunes d'âge V ($r = 0.70$). La croissance est également liée aux niveaux d'eau ($r = 0.79$). Le taux de mortalité annuelle est de 42% en moyenne. La biomasse varie de 2.63 à 16.52 kg/ha, et la production annuelle de 1.01 à 9.31 kg/ha. La production par biomasse est faible quand les niveaux d'eau sont bas.

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Fish populations have been monitored at Clear Lake, Iowa, since 1942. In this paper, we relate the annual stocking of walleye, *Stizostedion vitreum vitreum* (Mitchill), fry to abundance of year-classes and estimate annual biomass and production of walleye. Numbers of walleye fry stocked from 1948 to 1972 were varied (Table 1) to evaluate the effect of stocking. An earlier report on the results of the 1948–57 stocking (Carlander et al. 1960) showed that walleye from years when fry were stocked were more abundant than in years dependent only upon natural spawning, but questions were raised about the effect of the regular alternation in stocking. The 1961–72 stocking rates were thus varied

[1]This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

[2]Journal paper J-8617 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa.

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TABLE 1. Numbers of walleye fry stocked per hectare, mean catches of walleye per gillnet-hour (C/f), year-class abundance indexes, and numbers of young-of-the-year walleye and yellow perch caught per standardized seine haul by calendar year.

| | | | | Young-of-the-year | |
|---|---|---|---|---|---|
| Year-class | Fry stocked | C/f[a] | Year-class abundance[b] | Walleye | Yellow perch |
| 1948 | 3870 | 0.180 | 1.44 | — | — |
| 1949 | 0 | 0.540 | 0.74 | — | — |
| 1950 | 3580 | 0.750 | 3.08 | — | — |
| 1951 | 0 | 0.200 | 0.67 | — | — |
| 1952 | 2205 | 0.460 | 2.82 | — | — |
| 1953 | 0 | 0.470 | 0.24 | — | — |
| 1954 | 2833 | 0.530 | 0.83 | — | — |
| 1955 | 0 | 0.498 | 0.13 | — | — |
| 1956 | 2860 | 0.215 | 0.17 | 22.75 | 8.47 |
| 1957 | 0 | 0.280 | 0.18 | 0.58 | 3.57 |
| 1958 | 2934 | 0.186 | 0.23 | 12.33 | 0.22 |
| 1959 | — | 0.236 | 0.26 | 6.00 | 5.92 |
| 1960 | 2152 | 0.104 | 0.29 | 19.66 | 0.20 |
| 1961 | 405 | 0.145 | 0.10 | 1.37 | 1.32 |
| 1962 | 202 | 0.156 | 0.13 | 0.25 | 0.16 |
| 1963 | 6070 | 0.036 | 1.50 | — | — |
| 1964 | 4047 | 0.097 | 1.39 | — | — |
| 1965 | 2024 | 0.318 | 0.75 | 3.00 | 2.65 |
| 1966 | 2024 | 0.287 | 1.21 | 20.66 | 6.90 |
| 1967 | 1012 | 0.352 | 0.67 | 2.44 | 2.07 |
| 1968 | 4047 | 0.471 | 1.43 | 9.11 | 2.93 |
| 1969 | 202 | 0.253 | 0.63 | 3.33 | 1.06 |
| 1970 | 405 | 0.256 | 0.40 | 1.77 | 0.83 |
| 1971 | 1012 | 0.184 | 0.55 | 4.66 | 1.08 |
| 1972 | 6070 | 0.129 | 10.21 | 32.33 | 6.35 |
| 1973 | — | 0.747 | | | |
| 1974 | — | 0.870 | | | |

[a]Data from Iowa Cooperative Fishery Research Unit Quarterly Reports. 1957–61 C/f values were reduced 8% to adjust for reduced water area those years.

[b]The mean C/f each year was multiplied by the percentages of the catch in ages I, II, and III. Individual C/f values in each age-group I–III were divided by the mean of that age-group (4.114, 9.403, and 7.590, respectively). The year-class abundance index is the mean of the adjusted C/f for the three age-classes representing that year-class.

according to an irregular pattern. The fry came from walleye gillnetted from spawning areas in the lake.

Clear Lake (44°N and 94°W) is a 1474-ha eutrophic lake (Table 2), and represents the original southern limit of walleye in lakes. Water levels were below the outlet from 1955 to 1960 (Fig. 1) and the area of the lake was reduced about 8% when the water was lowest, 1 m down (McCann and Carlander 1970). Bailey and Harrison (1945) listed 43 species of fish from the lake. The walleye is the most abundant predator species.

## General Methods

Graduate students from the Iowa Cooperative Fishery Research Unit collected scale samples and catch data each summer from 1947 to 1974 with a variety of gear. Gillnet sampling from 1947 to 1952 was concentrated in one area (Carlander 1954) but by 1958 it was standardized to include the entire lake (Bulkley 1970a). Gillnet catches showed a diel cycle (Carlander 1954) and were adjusted to represent equal sampling throughout the 24 h.

Ages and growth of walleye were determined from scale examination and measurement (Cleary 1949; Carlander and Whitney 1961).

## Relation Between Fry Stocking and Year-Class Abundance

Abundance indexes for year-classes 1948–72 (Table 1) were highly correlated with the number of fry stocked ($r = 0.613$, df 22). If the very abundant 1972 year-class is eliminated, the correlation is still significant ($r = 0.563$, df 21).

TABLE 2. Physical and chemical characteristics of Clear Lake, Iowa.[a]

| | | |
|---|---|---|
| Physical | | |
| Lake area | (ha) | 1747 |
| Watershed area | (ha) | 3400 |
| Mean depth | (m) | 3.6 |
| Maximum depth | (m) | 6 |
| Shoreline development factor | | 1.58 |
| Littoral zone (< 2m) | | 25% |
| Little overflow most years | | |
| Not thermally stratified in summer | | |
| Chemical (as ppm) | | |
| Total alkalinity | | 143 |
| Total dissolved solids | | 230 |
| Calcium | | 23 |
| Magnesium | | 22 |
| Sulfate | | 13 |
| Chloride | | 7.8 |
| Nitrite nitrogen | | 0.004 |
| Phosphate | | 0.002 |
| Other | | |
| Transparency (summer mean, m) | | 1.4 |
| Specific conductivity (microhms) | | 306 |
| pH | | 8.6 |
| Morphoedaphic index (metric) | | 64 |

[a]The chemical data are mostly from Bachmann (1967) and the physical data from Pearcy (1953). The nitrogen, phosphate, and pH data came from Bailey and Harrison (1945). The total dissolved solids were reported by the State Hygienic Laboratory, Iowa City.

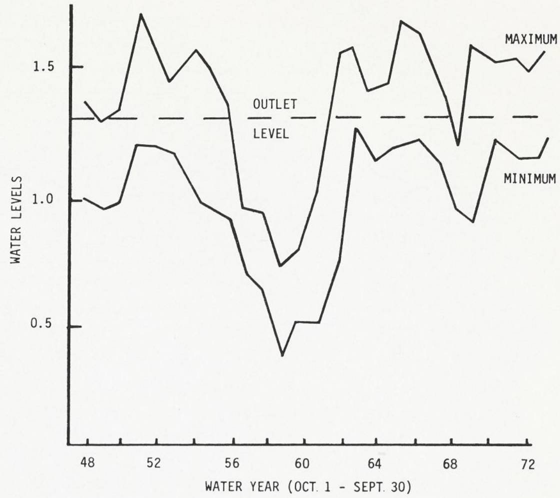


FIG. 1. Maximum and minimum water levels (m) at Clear Lake, Iowa, 1948–72.

During the low water years 1956–61, year-class strength was poor. Elimination of these year-classes improved the correlation with fry stocking ($r = 0.641$, df 17).

Numbers of age 0 walleye collected in a 9.1-m bag seine (7-mm mesh) from 1956 to 1972 (Table 1) were also highly correlated with the number of fry stocked ($r = 0.819$, df 13). Correlation between numbers of age 0 walleye and year-class abundance indexes (excluding the very abundant 1972 year-class) was only 0.179, indicating that year-class strength may change between the middle of the first summer and ages I to III.

## Year-Class Abundance and Other Factors

Success of walleye year-classes in western Lake Erie has been shown to be affected by water temperatures during spring spawning and incubation (Busch et al. 1975). However, time of ice-out, the rate of warming, total number of degree-days above 5.5°C (Ryder 1972), and the duration of ice cover the next winter after spawning showed no significant correlation with year-class abundance in Clear Lake. Although year-class abundance was low during drought years (1956–62), water levels were not significantly correlated with year-class abundance.

Success of walleye year-classes has been correlated with success of yellow perch, *Perca flavescens* (Mitchill), reproduction in two Minnesota lakes (Maloney and Johnson 1957), and in Lake Oneida (Forney and Noble 1970). Numbers of young walleye and yellow perch (Table 1) were significantly correlated in Clear Lake, 1956–72 ($r = 0.606$, df 13). Excluding 1972, the relationship is still significant ($r = 0.532$, df 12). Yellow bass, *Morone mississippiensis* Jordan and Eigenmann, were a more abundant prey for walleye than were perch from 1947 to 1968. Almost complete elimination of yellow bass in 1968 by an *Aeromonas salmonicida* infection (Bulkley 1970b) was followed by an increase in abundance and average size of yellow perch. Walleye fry in Clear Lake begin feeding on larval fish at approximately 31 mm in length (Bulkley et al. 1976). Yellow perch fry usually are available at this critical time whereas yellow bass fry do not emerge until considerably later.

The effects of fry stocking probably masked effects of climate or other factors. A step-down multiple regression analysis of year-class abundance to (1) number of fry, (2) C/f of yellow perch, (3) number of degree-days above 5.5°C, and (4) mean water levels failed to show any significance (at $P = 0.05$) except for fry stocking. Yellow perch C/f, however, approached significance ($r = 0.30$, $P < 0.10$) when the effects of fry stocking were removed.

TABLE 3. Mean calculated total lengths (mm) of walleyes at each annulus by year-classes, 1948–72.

| Year-class | Numbers in samples per age-group[a] | Length at each annulus | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| 1948 | 73, 116, 16, 28, 8, 4, 4, 1, 2, 1; 0, 1 | 166 | 298 | 384 | 436 | 479 | 573 | 551 | 606 | 618 | 659 | 655 | 670 | |
| 1949 | 16, 61, 69, 28, 5, 1, 2, 3; 0, 2, 2, 3, 4 | 176 | 264 | 349 | 434 | 493 | 533 | 553 | 577 | 604 | 605 | 605 | 625 | 640 |
| 1950 | 103, 340, 129, 40, 19, 17, 26, 4; 4, 9, 7, 1 | 171 | 265 | 363 | 442 | 487 | 520 | 546 | 576 | 576 | 606 | 607 | 609 | |
| 1951 | 49, 15, 13, 12, 15, 19, 1; 12, 6, 7, 0, 1 | 197 | 297 | 379 | 435 | 480 | 507 | 545 | 557 | 596 | 636 | 648 | 660 | |
| 1952 | 21, 82, 110, 41, 58, 7; 17, 8, 20, 5, 1 | 189 | 290 | 374 | 425 | 465 | 504 | 527 | 558 | 571 | 581 | 602 | | |
| 1953 | 1, 8, 14, 21, 8; 22, 14, 15, 5 | 186 | 289 | 378 | 427 | 468 | 496 | 514 | 548 | 490 | | | | |
| 1954 | 16, 38, 33, 7; 21, 10, 20, 7, 2, 0, 3 | 186 | 303 | 382 | 428 | 449 | 470 | 482 | 533 | 554 | 586 | 594 | | |
| 1955 | 6, 4, 1; 13, 8, 16, 4, 2, 0, 3, 1 | 188 | 285 | 386 | 431 | 464 | 485 | 540 | 566 | 627 | 640 | 648 | | |
| 1956 | 5, 2; 6, 2, 7, 7, 2, 0, 3 | 184 | 286 | 376 | 430 | 469 | 478 | 535 | 619 | 642 | | | | |
| 1957 | 3; 9, 2, 2, 8, 4, 0, 2, 2 | 190 | 287 | 354 | 394 | 429 | 486 | 520 | 539 | 561 | | | | |
| 1958 | 3, 3, 53, 26, 10, 0, 5, 8, 2, 0, 1 | 169 | 251 | 344 | 401 | 489 | 532 | 562 | 578 | 581 | 607 | 615 | | |
| 1959 | 4, 27, 16, 4, 0, 10, 5, 2, 1, 1, 1 | 175 | 265 | 336 | 411 | 477 | 512 | 551 | 588 | 619 | 640 | 653 | | |
| 1960 | 62, 49, 57, 0, 29, 14, 1, 7, 2, 1 | 172 | 263 | 332 | 416 | 472 | 486 | 534 | 559 | 638 | 668 | | | |
| 1961 | 14, 61, 0, 52, 42, 15, 10, 3 | 175 | 258 | 346 | 412 | 458 | 488 | 520 | 602 | | | | | |
| 1962 | 21, 0, 21, 20, 8, 9, 2, 0, 1 | 172 | 267 | 344 | 407 | 436 | 452 | 500 | 518 | 581 | | | | |
| 1963 | 0, 141, 68, 22, 22, 2, 1, 2 | 185 | 273 | 341 | 386 | 438 | 530 | 554 | 578 | | | | | |
| 1964 | 62, 116, 50, 32, 6, 6, 7 | 176 | 263 | 344 | 404 | 480 | 509 | 555 | | | | | | |
| 1965 | 56, 37, 14, 3, 7, 2, 1, 1 | 169 | 275 | 338 | 412 | 455 | 535 | 554 | 617 | | | | | |
| 1966 | 30, 72, 6, 25, 9, 1, 1, 3 | 163 | 249 | 304 | 377 | 454 | 522 | 565 | 584 | | | | | |
| 1967 | 16, 68, 42, 33, 2, 2 | 172 | 258 | 338 | 395 | 425 | 442 | | | | | | | |
| 1968 | 57, 95, 47, 7, 18, 3 | 169 | 260 | 321 | 381 | 427 | 498 | | | | | | | |
| 1969 | 27, 52, 15, 24, 1 | 176 | 260 | 352 | 427 | 472 | | | | | | | | |
| 1970 | 4, 22, 15, 6 | 191 | 261 | 338 | 469 | | | | | | | | | |
| 1971 | 12, 28, 3 | 187 | 272 | 340 | | | | | | | | | | |
| 1972 | 170, 185 | 163 | 256 | | | | | | | | | | | |

[a]The data on age-groups collected through 1958 are from Carlander and Whitney (1961) and are separated by semicolons from the data calculated by Payne.

TABLE 4. Instantaneous growth rates[a] in weight of walleye by age-group in Clear Lake, 1948–73.

| Year | I | II | III | IV | V |
|---|---|---|---|---|---|
| 1948 | 1.619 | 0.774 | 0.398 | 0.248 | 0.184 |
| 1949 | 1.636 | 0.858 | 0.363 | 0.276 | 0.143 |
| 1950 | 1.299 | 0.697 | 0.367 | 0.214 | 0.152 |
| 1951 | 1.361 | 0.919 | 0.408 | 0.206 | 0.191 |
| 1952 | 1.330 | 0.988 | 0.569 | 0.260 | 0.162 |
| 1953 | 1.382 | 0.832 | 0.483 | 0.259 | 0.189 |
| 1954 | 1.411 | 0.886 | 0.510 | 0.248 | 0.220 |
| 1955 | 1.483 | 0.842 | 0.396 | 0.302 | 0.238 |
| 1956 | 1.565 | 0.747 | 0.401 | 0.246 | 0.165 |
| 1957 | 1.376 | 0.760 | 0.350 | 0.232 | 0.160 |
| 1958 | 1.314 | 0.783 | 0.396 | 0.218 | 0.169 |
| 1959 | 1.219 | 0.752 | 0.308 | 0.225 | 0.164 |
| 1960 | 1.336 | 0.979 | 0.575 | 0.179 | 0.139 |
| 1961 | 1.286 | 0.734 | 0.602 | 0.263 | 0.155 |
| 1962 | 1.249 | 0.671 | 0.552 | 0.376 | 0.167 |
| 1963 | 1.269 | 0.885 | 0.543 | 0.304 | 0.278 |
| 1964 | 1.099 | 0.782 | 0.547 | 0.398 | 0.236 |
| 1965 | 1.217 | 0.726 | 0.549 | 0.318 | 0.170 |
| 1966 | 1.404 | 0.807 | 0.563 | 0.416 | 0.194 |
| 1967 | 1.386 | 0.720 | 0.389 | 0.286 | 0.128 |
| 1968 | 1.256 | 1.062 | 0.467 | 0.266 | 0.279 |
| 1969 | 1.412 | 0.764 | 0.370 | 0.260 | 0.152 |
| 1970 | 1.645 | 0.676 | 0.521 | 0.268 | 0.151 |
| 1971 | 0.944 | 0.696 | 0.431 | 0.278 | 0.195 |
| 1972 | 1.019 | 0.696 | 0.425 | 0.286 | 0.154 |
| 1973 | 1.415 | 0.890 | 0.687 | 0.249 | 0.169 |

[a]In calculating instantaneous growth, $G$, only the fish which completed the year's growth were used. e.g. Age I fish were not used in calculating the mean length at the first annulus in determining the increment in the second year. The mean lengths were converted to weights and $G = \log_e W_{n+1} - \log_e W_n$.

TABLE 5. Catches per gillnet-hour and population estimates of walleye in Clear Lake 1948–74.

| | | Walleyes over 305 mm | | Population estimates | | |
|---|---|---|---|---|---|---|
| Year | C/f | % | C/f | Over 305 mm[a] | All sizes | Rounded by 3's |
| 1948 | 0.180 | 68 | 0.122 | 8576 | 12612 | 24783 |
| 1949 | 0.540 | 85 | 0.459 | 31411 | 36954 | 33561 |
| 1950 | 0.750 | 93 | 0.697 | 47538 | 51116 | 34085 |
| 1951 | 0.200 | 49 | 0.098 | 6950 | 14184 | 32294 |
| 1952 | 0.460 | 75 | 0.345 | 23687 | 31583 | 25992 |
| 1953 | 0.470 | 91 | 0.428 | 29311 | 32210 | 33324 |
| 1954 | 0.530 | 96 | 0.509 | 34731 | 36178 | 34154 |
| 1955 | 0.498 | 90 | 0.408 | 30666 | 34073 | 28380 |
| 1956 | 0.215 | 94 | 0.202 | 13997 | 14890 | 22757 |
| 1957 | 0.280 | 96 | 0.269 | 18537 | 19309 | 15715 |
| 1958 | 0.186 | 94 | 0.175 | 12168 | 12945 | 16190 |
| 1959 | 0.236 | 97 | 0.229 | 15827 | 16316 | 12229 |
| 1960 | 0.104 | 89 | 0.093 | 6611 | 7425 | 11357 |
| 1961 | 0.145 | 64 | 0.093 | 6611 | 10330 | 9596 |
| 1962 | 0.156 | 63 | 0.098 | 6950 | 11032 | 8136 |
| 1963 | 0.036 | 48 | 0.017 | 1462 | 3046 | 8872 |
| 1964 | 0.097 | — | — | — | — | 12538 |
| 1965 | 0.318 | 62 | 0.197 | 13658 | 22029 | 18199 |
| 1966 | 0.287 | 55 | 0.158 | 11016 | 20029 | 22129 |
| 1967 | 0.352 | 67 | 0.236 | 16301 | 24330 | 25618 |
| 1968 | 0.471 | 56 | 0.264 | 18198 | 32496 | 24938 |
| 1969 | 0.253 | 36 | 0.091 | 6476 | 17989 | 22784 |
| 1970 | 0.256 | 59 | 0.151 | 10541 | 17866 | 16228 |
| 1971 | 0.184 | 79 | 0.145 | 10135 | 12824 | 13324 |
| 1972 | 0.129 | 53 | 0.068 | 4917 | 9277 | 24533 |
| 1973 | 0.747 | 36 | 0.269 | 18537 | 51492 | 41039 |
| 1974 | 0.870 | 11 | 0.096 | 6815 | 61955 | 61955 |

[a]Derived from the regression of C/f on five mark-and-recapture estimates, given in the text.

## Growth

The calculated growth rates for the various year-classes of Clear Lake walleye (Carlander and Whitney 1961) showed a negative correlation with year-class abundance for the years 1935–57. Such a correlation supports the evidence that, for fish in general, growth rate usually decreases as population density increases. Lengths calculated from scale measurements at each annulus (Table 3) were converted to weights using a weight–length regression based on 489 Clear Lake walleye collected in 1961–62 (Sriprasert 1974):

$$\log W = -5.4187 + 3.1413 \log L.$$

This procedure involved an underestimate of weight, and of the subsequent biomass estimates, "commonly in the order of 5%" (Ricker 1975, p. 211).

Negative correlations were found between numbers of fry stocked and instantaneous growth (Table 4) in the first ($r = -0.42$, $P < .05$) and second ($r = -9.41$, $P < .056$ years of life. This may have been related to increased density. The growth of age V walleye was positively correlated ($r = 0.70$, $P < .008$) with fry stocking. Chevalier (1973) stated that predation by age III and older (III+) walleyes was the most probable cause of mortality of young walleye in late summer and fall in Lake Oneida. A similar predation at Clear Lake may have resulted in an increased growth of older walleyes correlated with the numbers of fry stocked.

Carlander and Whitney (1961) reported a significant correlation ($r = 0.565$, df $= 21$) between summer temperatures and growth in Clear Lake for 1935–57; however, no correlation between temperature, in summed degree-days, and the average instantaneous growth rate was found for 1948–73. Instantaneous growth was significantly correlated with water levels ($r = 0.79$, $P < .0001$).

TABLE 6. Mark-and-recapture population estimates of adult walleye in Clear Lake and associated catch-per-effect for certain years.

| Source | Year of estimate | Walleye over 305 mm | |
|---|---|---|---|
| | | Number[a] | C/f[a] |
| Whitney (1958) | 1953 | 30,822 | 0.428 |
| McCann and Carlander (1970) | 1958 | 11,800 | 0.175 |
| | 1959 | 12,300 | 0.229 |
| Hollingsworth (1967) | 1966 | 11,716 | 0.158 |
| Schutte, S., I.S.C.C. Personal communication | 1972 | 6,600 | 0.068 |

[a]Except for 1953, the numbers are means of 2 to 4 estimates derived from the data by various modifications. Variation between the estimates was small within each year.
[b]Values (C/f) from Table 5.

TABLE 7. Population estimates of walleye by age-groups each year based on numbers at age III computed from the regressions of the year classes and assuming an annual mortality of 42%.

| Year | I | II | III | IV | V | VI | Total[a] |
|---|---|---|---|---|---|---|---|
| 1948 | 24831 | 15121 | 4063 | 1935 | 831 | 462 | 48689 |
| 1949 | 10767 | 14402 | 8770 | 2357 | 1122 | 482 | 38647 |
| 1950 | 14138 | 6245 | 8353 | 5087 | 1367 | 651 | 36554 |
| 1951 | 46671 | 8200 | 3622 | 4845 | 2950 | 793 | 67781 |
| 1952 | 10648 | 27069 | 4756 | 2101 | 2810 | 1711 | 49950 |
| 1953 | 40678 | 6176 | 15700 | 2758 | 1218 | 1630 | 69653 |
| 1954 | 7803 | 23593 | 3582 | 4106 | 1600 | 707 | 48203 |
| 1955 | 11558 | 4526 | 13684 | 2078 | 5281 | 928 | 39515 |
| 1956 | 11008 | 6703 | 2625 | 7937 | 1205 | 3063 | 33926 |
| 1957 | 1650 | 6384 | 3888 | 1523 | 4603 | 699 | 21325 |
| 1958 | 1653 | 957 | 3703 | 2255 | 883 | 2670 | 14019 |
| 1959 | 6683 | 959 | 555 | 2148 | 1308 | 512 | 14821 |
| 1960 | 3098 | 3876 | 556 | 322 | 1246 | 759 | 11691 |
| 1961 | 3668 | 1797 | 2248 | 322 | 187 | 723 | 10530 |
| 1962 | 4703 | 2128 | 1042 | 1304 | 187 | 108 | 10763 |
| 1963 | 4257 | 2728 | 1234 | 604 | 766 | 108 | 10525 |
| 1964 | 19290 | 2469 | 1582 | 716 | 351 | 439 | 25390 |
| 1965 | 16843 | 11188 | 1432 | 918 | 415 | 203 | 31556 |
| 1966 | 5016 | 9769 | 6489 | 830 | 532 | 241 | 23332 |
| 1967 | 8038 | 2909 | 5666 | 3764 | 482 | 309 | 21564 |
| 1968 | 12970 | 4662 | 1687 | 3286 | 2183 | 279 | 24583 |
| 1969 | 13769 | 7522 | 2704 | 978 | 1906 | 1266 | 28542 |
| 1970 | 14524 | 7986 | 4363 | 1568 | 568 | 1106 | 31077 |
| 1971 | 10181 | 8424 | 4632 | 2473 | 910 | 329 | 28147 |
| 1972 | 3523 | 5905 | 4886 | 2687 | 1434 | 528 | 19848 |
| 1973 | 98274 | 2043 | 3425 | 2834 | 1558 | 832 | 109783 |
| 1974 | | 56999 | 1185 | 1987 | 1644 | 904 | 63201 |

[a]The totals for 1948 to 1960 include average numbers for the 1941 and earlier year-classes. The addition was 1135 to the 1948 collection and 42% less in each successive year.

## Standing Crop and Production of Walleye

To estimate annual biomass and production, C/f values were converted to population numbers (Table 5) by using mark and recapture estimates made in five of the years (Table 6). A correlation between these population estimates, $Y$, and adjusted C/f values, $X$, was significant ($r = 0.974$, df $= 3$) and the regression was

$$Y = 310 + 67759\,X.$$

Since most of the population in a given year

TABLE 8. Standing crops and annual production (kg/ha) of walleye in Clear Lake, 1948–74

| | Standing crop | | Annual Production | | |
|---|---|---|---|---|---|
| Year | III+ | I+ | III+ | I+ | 0+ |
| 1948 | 4.90 | 7.90 | 1.00 | 4.15 | 4.53 |
| 1949 | 6.06 | 8.35 | 1.51 | 4.62 | 5.38 |
| 1950 | 8.36 | 9.73 | 1.89 | 3.48 | 3.74 |
| 1951 | 8.30 | 10.39 | 1.63 | 5.36 | 5.77 |
| 1952 | 8.13 | 11.44 | 1.65 | 6.19 | 7.42 |
| 1953 | 9.99 | 12.42 | 3.07 | 7.26 | 9.31 |
| 1954 | 9.98 | 16.52 | 2.14 | 6.14 | 7.63 |
| 1955 | 11.30 | 12.33 | 2.91 | 4.64 | 4.91 |
| 1956 | 10.56 | 12.16 | 1.76 | 3.62 | 4.02 |
| 1957 | 8.90 | 9.88 | 1.34 | 2.28 | 2.68 |
| 1958 | 7.90 | 8.11 | 1.27 | 1.52 | 1.58 |
| 1959 | 5.70 | 6.03 | 0.72 | 1.14 | 1.20 |
| 1960 | 4.12 | 4.59 | 0.49 | 1.09 | 1.26 |
| 1961 | 3.42 | 3.74 | 0.59 | 0.95 | 1.04 |
| 1962 | 2.50 | 2.86 | 0.50 | 0.91 | 1.01 |
| 1963 | 2.25 | 2.63 | 0.46 | 0.99 | 1.12 |
| 1964 | 2.09 | 3.02 | 0.48 | 1.79 | 1.91 |
| 1965 | 1.88 | 3.67 | 0.42 | 2.35 | 3.00 |
| 1966 | 2.90 | 4.04 | 1.04 | 2.33 | 2.82 |
| 1967 | 3.63 | 4.16 | 0.97 | 1.64 | 1.77 |
| 1968 | 3.45 | 4.21 | 0.93 | 2.06 | 2.25 |
| 1969 | 3.86 | 4.95 | 0.64 | 2.16 | 2.51 |
| 1970 | 3.73 | 5.02 | 0.93 | 2.68 | 3.03 |
| 1971 | 3.94 | 5.30 | 0.88 | 2.13 | 2.55 |
| 1972 | 4.32 | 5.04 | 1.04 | 1.70 | 2.09 |
| 1973 | 4.27 | 6.77 | 1.32 | 6.98 | 6.98 |
| 1974 | 4.40 | 9.82 | — | — | — |
| Mean | 5.72 | 7.23 | 1.21 | 2.87 | 3.31 |
| without 1972 year-class | | | with 1972 | 3.08 | 3.53 |

must have been present the previous and following years, estimates were averaged by three's to reduce some of the irregularities. Population estimates were proportioned to age-groups on the basis of scale samples each year. Regressions of logarithms of numbers in each age-group (beginning with the most numerous age-group) within a year-class gave estimates of mortality rates (Ricker 1975) which ranged from 22 to 63% and averaged 42.5%. The combined data in one regression gave a mortality rate of 42%.

Numbers of age III walleye in each year-class were computed from the regression lines and the average mortality rate of 42% was applied to estimate numbers in each age-group (Table 7). Age III was selected since the average age of fish used in the regression was 3.2 yr. The numbers in each age-group were then converted to biomass by multiplying by the mean weight.

Standing crop ranged from 16.52 kg/ha in 1954 to 2.63 kg/ha in 1963 (Table 8). Even the peak standing crop of age III±, 11.30 kg/ha, was below the mean of 16 kg/ha for lakes summarized by Carlander (1977). The mean age II± standing crop was also below the lowest reported for those lakes, 6.1 kg/ha for West Blue Lake, Manitoba (Kelso and Ward 1972).

The morphoedaphic index for the lake is 64, in comparison with 40 for the optimum (Ryder et al. 1974) which indicates a more eutrophic condition than optimum. The number of competing species of fish in Clear Lake may be related to the low standing crop of walleye.

Annual production was estimated by multiplying the instantaneous growth rate by the mean biomass (i.e. the mean of the biomass at the

TABLE 9. Annual production per biomass at beginning of season ($P/B_o$ ratios) and per mean biomass[a] ($P/\bar{B}$ ratios) for walleye in Clear Lake, 1948–73.

| | $P/B_o$ | | $P/\bar{B}$ | | | $P/B_o$ | | $P/\bar{B}$ | |
|---|---|---|---|---|---|---|---|---|---|
| Year | III+ | I+ | III+ | I+ | Year | III+ | I+ | III+ | I+ |
| 1948 | 0.20 | 0.53 | 0.24 | 0.52 | 1961 | 0.17 | 0.25 | 0.21 | 0.29 |
| 1949 | 0.25 | 0.55 | 0.26 | 0.52 | 1962 | 0.20 | 0.32 | 0.22 | 0.34 |
| 1950 | 0.23 | 0.36 | 0.24 | 0.37 | 1963 | 0.20 | 0.38 | 0.23 | 0.40 |
| 1951 | 0.20 | 0.52 | 0.21 | 0.50 | 1964 | 0.23 | 0.59 | 0.26 | 0.56 |
| 1952 | 0.20 | 0.54 | 0.24 | 0.55 | 1965 | 0.22 | 0.64 | 0.26 | 0.62 |
| 1953 | 0.31 | 0.58 | 0.33 | 0.51 | 1966 | 0.36 | 0.58 | 0.40 | 0.58 |
| 1954 | 0.21 | 0.37 | 0.25 | 0.43 | 1967 | 0.27 | 0.39 | 0.29 | 0.41 |
| 1955 | 0.26 | 0.38 | 0.28 | 0.39 | 1968 | 0.27 | 0.49 | 0.27 | 0.47 |
| 1956 | 0.17 | 0.30 | 0.19 | 0.33 | 1969 | 0.17 | 0.44 | 0.19 | 0.45 |
| 1957 | 0.15 | 0.23 | 0.17 | 0.25 | 1970 | 0.25 | 0.53 | 0.27 | 0.54 |
| 1958 | 0.16 | 0.19 | 0.19 | 0.22 | 1971 | 0.22 | 0.40 | 0.25 | 0.42 |
| 1959 | 0.13 | 0.19 | 0.15 | 0.22 | 1972 | 0.24 | 0.30 | 0.27 | 0.36 |
| 1960 | 0.12 | 0.24 | 0.14 | 0.26 | 1973 | 0.31 | 1.03 | 0.34 | 0.84 |

[a]B was determined by taking the mean of the biomasses at the beginning of the year and at the beginning of the next year for the same year-classes.

beginning of the year and the beginning of the following year in each year-class). The annual production (Table 8) ranged from 1.01 to 9.31 kg/ha for fish age 0 through age VI or considering only age I+ from 0.91 to 6.98 or age III+ from 0.42 to 3.07 kg/ha.

Annual production is obviously dependent upon the biomass available at the beginning of the season ($B_0$), and the effects of other factors upon production will be masked by the differences in available biomass. Annual comparisons may be more evident with the $P/B_0$ ratio, the production per unit of biomass at the beginning of the year (Table 9). The production per biomass was low from 1956 to 1962, the low water years. The production per biomass also decreased with age:

| Age-group | I | II | III | IV | V | V+ |
|---|---|---|---|---|---|---|
| $P/B_o$ | 2.24 | 1.00 | 0.43 | 0.24 | 0.16 | 0.11 |

Age-groups I and II accounted for 59% of the annual production; 78% by I–III; and 87% by I–IV. The usual $P/B$ ratios using mean biomass are aquivalent to instantaneous growth rates of all year-classes (since $P = \bar{B}G$).

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# Biomass, Production, and Yields of Walleye (*Stizostedion vitreum vitreum*) and Yellow Perch (*Perca flavescens*) in North American Lakes[1,2]

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CARLANDER, K. D. 1977. Biomass, production, and yields of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) in North American lakes. J. Fish. Res. Board Can. 34: 1602–1612.

Compilation of available data indicated that walleye (*Stizostedion vitreum vitreum*) biomass in lakes averaged 16 kg/ha, but the data were not adequate to show relationships with mean depth, alkalinity, latitude, or morphoedaphic indexes of the lakes. Yellow perch (*Perca flavescens*) biomass also failed to show relationships with these factors. In small lakes and ponds with only perch, biomass ranged from 39 to 215 kg/ha, but in lakes with other species, perch biomass was under 65 kg/ha. Annual production of walleye was from 1.2 to 4.1 $kg \cdot ha^{-1} \cdot yr^{-1}$ and that of yellow perch was 21.9 $kg \cdot ha^{-1} \cdot yr^{-1}$. Average commercial yields of walleye ranged up to 3.06 $kg \cdot ha^{-1} \cdot yr^{-1}$, and sport fish yields averaged 3.7 $kg \cdot ha^{-1} \cdot yr^{-1}$. Annual commercial and sport yields decreased with latitude. Area of lake was negatively correlated with sport yield, but positively with commercial yield. The latter situation is believed to be an artifact of the sample and not a general trend. Commercial yield increased with total dissolved solids of the lakes. Lack of other correlations may be related to the fact that walleye biomass and yield do not bear a constant relationship to total biomass and yield.

*Key words*: Percidae, *Stizostedion*, *Perca*, biomass, production, yield

CARLANDER, K. D. 1977. Biomass, production, and yields of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) in North American lakes. J. Fish. Res. Board Can. 34: 1602–1612.

Une compilation des données disponibles indique que la biomasse des dorés jaunes (*Stizostedion vitreum vitreum*) dans les lacs était en moyenne de 16 kg/ha, mais ces données sont insuffisantes pour montrer les relations avec la profondeur moyenne, l'alcalinité, la latitude ou les indices morphoédaphiques des lacs. La biomasse des perchaudes (*Perca flavescens*) ne montre pas, elle non plus, de relations avec ces facteurs. Dans les petits lacs et les étangs ne contenant que des perchaudes, la biomasse varie de 39 à 215 kg/ha, mais dans les lacs contenant d'autres espèces, la biomasse des perchaudes est inférieure à 65 kg/ha. La production annuelle de dorés jaunes varie de 1.2 à 4.1 $kg \cdot ha^{-1} \cdot a^{-1}$, et celle des perchaudes est de 21.9 $kg \cdot ha^{-1} \cdot a^{-1}$. Les rendements commerciaux moyens en dorés jaunes vont jusqu'à 3.06 $kg \cdot ha^{-1} \cdot a^{-1}$, et les rendements de la pêche sportive sont en moyenne de 3.7 $kg \cdot ha^{-1} \cdot a^{-1}$. Les rendements commerciaux et sportifs diminuent tous deux en fonction de la latitude. Il y a une corrélation négative entre la superficie du lac et le rendement de la pêche sportive, mais une corrélation positive avec le rendement commercial. On croit que cette dernière situation est une erreur systématique d'échantillonnage plutôt qu'une tendance générale. Le rendement commercial augmente avec les solides totaux dissous des lacs. Il se peut que l'absence d'autres corrélations soit liée au fait que la biomasse et le rendement des dorés jaunes ne comportent pas de relation uniforme avec la biomasse et le rendement totaux.

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EVEN though information on production of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) would be helpful in management of the resources, few data are available. Data on 136 populations of walleye or yellow perch in North American lakes were compiled from a search of published, and some unpublished, reports. These data were reported as biomass, production, and yield.

Biomass, or standing crop, is weight of the population at any specified time. It is the result of the previous production, as affected by natural and fishing mortality. It is also somewhat a mea-

[1]This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

[2]Journal Paper No. J-8699 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa.

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sure of the productivity, or carrying capacity, of the environment. As biomass approaches carrying capacity net production (addition to biomass) decreases. Production is the tissue elaborated by the organisms through reproduction or individual growth within a specified period, whether or not that tissue survives to the end of the period. Yield means the number or weight of the organisms harvested from the population within a specified period of time.

For comparative purposes in this paper, these measures are expressed as kilograms per hectare (and per year for yield and production).

## Biomass

Biomass is usually estimated by mark-and-recapture methods or by draining or chemical treatment of a lake or pond to recover all of the fish. Well-balanced, healthy populations are rarely estimated by chemical treatment. Mark and recapture usually is limited to fish above a given size; thus, the estimates do not include the younger fish. Biomass may also be estimated by determining numbers or weight of fish per area with gear that effectively captures all the fish in a given area; but gear is rarely consistent or effective in enough areas to adequately determine biomass in a lake. *selectivity of gear

*Walleye* — Comparatively few estimates of walleye biomass (Table 1) were found, and most of them do not apply to typical walleye lakes. Walleyes are most abundant in large unstratified lakes where the annual growing season has 500–720 degree-days above 12.8°C (Schneider 1973a).

In the three lakes with <3.3 kg/ha, walleye were not the principal predators. The lake trout, *Salvelinus namaycush*, was the major predator in Nipigon Bay; the northern pike, *Esox lucius*, in Burnt Camp Lake; and the smallmouth bass, *Micropterus dolomieu*, in East Twin Lake. Long Lake, with a biomass of 3.9 kg/ha, originally was noted as a smallmouth bass lake.

Biomass in the other lakes ranged from 5.7 to 37.0 kg/ha and the mean was 16.0, considering only the estimates for walleye longer than 300–350 mm. The three lakes under 100 ha had 18.7–37.0 kg/ha with a mean of 26.8; the nine lakes between 100 and 1000 ha, 6.1–15.5 kg/ha with a mean of 10.5; and the seven lakes over 1000 ha, 5.7–37.0 kg/ha with a mean of 18.4. The correlation between area and biomass was only 0.385 ($P > .05$), even eliminating the lakes <100 ha.

Correlation of biomass with mean depth of the lakes with latitude or length of growing seasons was not evident. The three Canadian lakes had a lower mean biomass, 8.2 kg/ha, than the eight Michigan, Minnesota, and Wisconsin lakes at 17.1 kg/ha and the eight Iowa, Ohio, and New York lakes at 17.3 kg/ha; but this is not sufficient to show latitudinal effects. There also is no evidence of correlation with alkalinity or with the morphoedaphic index, MEI (Ryder et al. 1974).

Standing crops within a lake change from year to year and from season to season as the result of harvest, reproductive success, and environmental changes. The estimates also have sampling variation even if there were no changes in biomass. For example, the range in estimated biomass was 1.65 times the mean of 27 annual estimates in Clear Lake, 1.35 times the mean of 16 annual estimates in Escanaba Lake, 0.92 times the mean of 6 annual estimates in Wilson Lake, and 0.52 times the mean of 5 estimates in 1 yr in West Blue Lake (citations as in Table 1).

*Yellow perch* — More biomass estimates (Tables 2–4) were found for perch than for walleye, but only three of those found were for percid lakes, or lakes in which walleyes were the major predator: Storm Lake, Iowa, with 7 kg perch/ha; East Twin Lake, Michigan, with 22 kg/ha; and Oneida Lake, New York, with 36 kg/ha.

The data from the other lakes do not add to our knowledge of percid lakes but give some information on perch populations. They are considered in three categories. The first (Table 2) is for lakes in which perch were < 20% of the fish biomass. Other estimates in which perch were a minor part of the population are available, but this listing includes most estimates in which perch were at least 2 kg/ha. In lakes in which perch were at least 20% of the fish biomass, the mean biomass of perch was 27 kg/ha (Table 3). Several of the lakes in both these lists were chemically treated because they contained undesirable populations of stunted perch, and the results from these lakes are thus not representative of lakes as a whole.

Most of the lakes are too shallow for the morphoedaphic indexes to be meaningful, and the data gave no indication of correlation between alkalinity and the biomass.

There are standing crop estimates for several ponds and small lakes in which yellow perch were the only species of fish (Table 4), and these ranged from 39 to 215 kg/ha. The biomass in some experimental ponds in Illinois (Buck and Thoits 1970) were 2–3 times as high as those of smallmouth or largemouth bass (*M. salmoides*) populations in the same ponds in other years.

## Production

Annual production is the most meaningful measure of a population's response to the environ-

TABLE 1. Biomass (kg/ha) of walleye, other predators, and all fish in 23 North American Lakes, arranged according to increasing biomass.

| Lake and citation | Area (ha) | Mean depth (m) | TDS (ppm) | MEI | Biomass: Walleye | Biomass: Other predators | Biomass: All species[a] |
|---|---|---|---|---|---|---|---|
| Nipigon Bay, Ont. Ryder 1968 | 34,200 | 10.8 | 71 | 7 | 1.1 | — | — |
| East Twin, Wis. O'Donnell 1943 | 5 | 3.0 | 28[b] | 9 | 2.3[c] | 3.9 | 208 |
| Burnt Camp, Minn. Maloney 1956 | 4 | 5.0 | 45 | 9 | 2.8 | 7.8 | 142 |
| Long, Wis. O'Donnell 1943 | 11 | 3.0 | 76[b] | 79 | 3.9[c] | 0 | 151 |
| West Blue, Man. Kelso and Ward 1972, 1977 | 162 | 11.3 | 18 | 16 | 6.1 | — | — |
| Clear, Iowa Carlander and Payne 1977 | 1,474 | 3.6 | 230 | 64 | 5.7<br>7.2(age I+) | — | — |
| Dexter, Ont. Moenig 1975 | 368 | 1.8 | — | — | 7.2 | — | — |
| Cadillac, Mich. Schneider 1973a | 465 | 3.3 | 100[b] | 30 | 8.2[d] | 1.6[d] | 28 |
| East Okoboji, Iowa Rose 1957 | 764 | 2.8 | 272[b] | 97 | 9.9[d] | — | — |
| Clear, Iowa McCann and Carlander 1970 | 1,474 | 3.6 | 230 | 64 | 10.4[d] | 0.6 | 80 |
| Many Points, Minn. Olson 1958 | 694 | 9.1 | 168 | 18 | 11.0[d] | — | — |
| Savanne, Ont. P. J. Colby personal communication 1975 | 364 | 2.6 | 65 | 25 | 11.2 | 8.5 | — |
| Escanaba, Wis. Kempinger et al. 1975 | 119 | 4.3 | 43 | 10 | 12.3 | 6.0 | — |
| Spirit, Iowa Jennings 1968, 1969, 1970 Moen 1963, Rose 1955, 1957 | 2,168 | 5.2 | 271[b] | 52 | 12.4[d] | — | — |
| East Twin, Mich. Schneider 1973a | 336 | 6.7 | 119[b] | 18 | 13.5 | 3.4 | 54 |
| Hoover, Ohio Momot et al. 1977 | 1,143 | 6.5 | 199 | 31 | 13.6 | — | — |
| Wilson, Minn. Johnson 1977 | 245 | 6.6 | 51[b] | 8 | 15.5<br>23.4(>200 mm) | — | — |
| Erickson, Wis. Helm 1958 | 44 | 3 | 65[b] | 22 | 18.7[d] | — | — |
| West Okoboji, Iowa Rose 1957 | 1,540 | 12.0 | 261[b] | 22 | 24.6[d] | — | — |
| Oneida, NY Forney 1967 | 20,640 | 6.8 | 165 | 24 | 25.0 | — | — |
| Little John, Wis. Helm 1958 | 62 | 4 | 94 | 24 | 28.0[d] | — | — |
| Spauldings, Wis. Threinen and Helm 1952 | 11 | 2.5 | 102[b] | 41 | 33.6 | — | — |
| Storm, Iowa Rose 1950 | 1,238 | 2.0 | 185[b] | 93 | 37.0 | 2 | 305 |

[a]All that were estimated; usually other species were present but not included.
[b]Converted from total alkalinity measures by the formula of Ryder (1964): TDS (total dissolved solids) = 1.1913 (total alkalinity) + 23.5 ppm. The alkalinity values for some Iowa lakes came from Bachmann (1967).
[c]Treated with rotenone. All other estimates were by mark-and-recapture techniques, usually for walleyes over 300 or 350 mm.
[d]Numbers converted to weights on the assumption that mean weight was 0.68 kg (1.5 lb) except that in Little John Lake a mean weight of 0.45 kg was used since this was judged to be a better average by Helm (correspondence).

TABLE 2. Biomass (kg/ha) of yellow perch and all fish in 18 lakes where they were less than 20% of the fish biomass.

| Citation and lake | Area (ha) | Mean depth (m) | Alkalinity (ppm) | Biomass Perch | Biomass Total | Method[a] |
|---|---|---|---|---|---|---|
| Nova Scotia, Smith 1940 | | | | | | |
| Trefry's | 22 | — | — | 1 | 19 | p |
| Tedford | 21 | 2.5 | — | 2 | 40 | p |
| Minn., Hooper 1951 | | | | | | |
| Demming | 5 | 3.5 | 25 | 2 | 22 | p |
| Indiana, Ricker 1942 | | | | | | |
| Shoe | 17 | 4 | — | 2 | 180 | m |
| Mass., Stroud 1953 | | | | | | |
| Ponkapoog Pond | — | — | — | 4 | 48 | p |
| Iowa, Rose 1950 | | | | | | |
| Storm | 1238 | 2 | 136 | 7 | 305 | m |
| Wis., O'Donnell 1953 | | | | | | |
| West Twin | 5 | 6 | — | 9 | 103 | p |
| Mich. Schneider 1973a | | | | | | |
| O'Brien | 4 | 4.5[b] | 167 | 2 | 50 | p |
| Deep | 6 | 9[b] | — | 2 | 71 | p |
| Howe | 5 | 3.5[b] | 51 | 2 | 71 | p |
| Scaup | 2.4 | 2 | 121 | 3 | 50 | m |
| Walsh | 4 | 3[b] | 138 | 3 | 171 | p |
| Cub | 11.3 | 3.3 | 10 | 11 | 70 | m |
| Kimes | 2.8 | 2.7 | — | 12 | 256 | p |
| Mill | 55 | 1.6 | 140 | 16 | 130 | m |
| Pond 4 | 0.6 | — | — | 20 | 127 | p |
| Cassidy | 19 | 1 | 127 | 27 | 162 | m |
| Wintergreen | 16 | — | — | 36 | 404 | m |

[a]p = estimate by chemical treatment; m = mark-and-recapture estimate.
[b]Mean depth not available, estimates at 0.5 maximum depth.

ment. However, production estimates involve data on standing crop by size or age-groups, individual growth rates, and mortality rates. Therefore, very little annual production information (Table 5) is available on walleye or perch populations. Because sustained harvest cannot exceed annual production, walleye yields from these lakes should not exceeds 1–3 kg/ha.

## Yield

Annual yield statistics are the most readily available indicators of fish production. If yields only from lakes subjected to moderately intensive or intensive fishing are used and if the fishery is maintained several years, the yield statistics probably are representative of production (Ryder et al. 1974).

Perch yield data were not analyzed. Few perch populations are subject to consistently intensive fishing because the perch fishery is secondary to that for other species. The data that I analyzed cover a wider range of lake types than those reported by Adams and Olver (1977), but the yields were recorded in a less standardized manner and did not always cover enough years to indicate sustained yields. My search was not exhaustive, and yield data are scattered, often in reports with limited distribution or in unpublished files.

The annual commercial yields of walleye (Table 6) ranged from 0.04 to 3.06 kg/ha. Hebden and Contact lakes had larger yields of lake trout than of walleye and perhaps should not be included as percid lakes. Lakes Michigan and Ontario had their largest yields of walleye only after lake trout had been largely eliminated. Perhaps only Lake of the Woods, Lake St. Claire, Red Lake, and Lake Erie, lakes with yields of 1.35–3.06 kg/ha, are representative of percid populations. With these four lakes there is no correlation between yield of walleye and area, mean depth, total dissolved solids, or MEI.

The average yield ($Y$) decreases with latitude in degrees north ($L$) if Lakes Michigan, Huron, Ontario, Hebden, and Contact are left out:

TABLE 3. Biomass (kg/ha) of yellow perch and all fish in lakes where they were at least 20% of the fish biomass.

| Citation and lake | Area (ha) | Mean depth (m) | Alkalinity (ppm) | Biomass Perch | Biomass Total | Method[a] |
|---|---|---|---|---|---|---|
| Nova Scotia, Smith 1961 | | | | | | |
| Boar's Back | 22.6 | 2.5 | — | 4.5 | 19 | p |
| New Brunswick, Smith 1939 | | | | | | |
| Jessie | 18.2 | 2.4 | 10 | 5.2 | 23 | p |
| Ont., Chadwick 1976 | | | | | | |
| Red Deer | 6.2 | 3.7 | 26 | 10 | 15 | p |
| Mass., Stroud 1953 | | | | | | |
| Wineconnet | — | — | — | 17 | 62 | p |
| N.Y., Vashro 1975 | | | | | | |
| Oneida | 20,640 | 6.8 | 90 | 35 | — | m |
| Wis., O'Donnell 1943 | | | | | | |
| Long | 11 | 3 | — | 39 | 155 | p |
| Minn., Peterson 1955 | | | | | | |
| Camp 4[c] | 6.7 | 4.5 | — | 40 | 71 | p |
| Mich., Schneider 1973a | | | | | | |
| Fitzek | 2.5 | — | — | 9 | 36 | p |
| Twin | 8.7 | 13.7[b] | 5 | 11 | 19 | p |
| Linnbeck | 2.1 | 3.8[b] | 190 | 12 | 54 | p |
| Booth | 6.5 | 4.7[b] | 125 | 17 | 40 | p |
| East Twin | 33.6 | 2.0 | — | 22 | 54 | m |
| Airport | 2.8 | 4.2[b] | 5 | 26 | 27 | p |
| Pike #4 | 1.9 | 2.7 | 153 | 27 | 82 | p |
| East Fish | 5.5 | 6.5[b] | 196 | 35 | 56 | p |
| Swanzy | 8.2 | 7[b] | 20 | 46 | 58 | p |
| Grebe | 29 | 2 | 75 | 48 | 131 | m |
| Marsh | 27 | 5 | 6 | 53 | 59 | m |
| Ford | 4.7 | 5[b] | 127 | 65 | 96 | p |
| Mean | | | | 27 | 59 | |

[a]p = estimate by chemical treatment; m = mark and recapture estimate.
In Lake Wineconnet only one cove was rotenoned.
[b]Mean depth not available; estimated at 0.5 maximum depth.
[c]The estimate, given as 64 kg/ha of littoral area, was corrected to the area of the entire lake to be comparable with data from the other lakes.

$$Y = 6.36 - 0.096\ L;\ r = -0.58,\ P < 0.05$$

Yield also increases with total dissolved solids ($T$):

$$Y = 0.29 + 0.008\ T;\ r = 0.61,\ P < 0.05$$

However yield also shows a trend to increase with mean depth ($r = 0.32$, $P > 0.05$) which is the reverse of the expected relationship and therefore for this series of lakes, MEI is not as good a predictor of yield as is the total dissolved solids.

The yield also increases with the area (A) of the lakes in this series:

$$Y = 1.17 + 0.0007\ A;\ r = 0.58,\ P < 0.05$$

Rounsefell (1946) found the yield to decrease with increasing area of lakes. The fact that the eight lakes under 86,000 ha were all in Saskatchewan probably influenced the positive correlation in the data.

Multiple regression analysis indicated that the following would account for 55% for the variation in yield compared with 37% accounted for by total dissolved solids:

$$Y = 0.359 + 0.0063\ T + 0.00058\ A$$

Addition of latitude, mean depth, and MEI did not materially improve the regression.

The annual yield to sport fishing averaged 3.7 kg/ha (Table 7) which was greater than the average commercial yield. Many of these data are for a single year of fishing rather than averages over several years, but the available averages

TABLE 4. Biomass (kg/ha) in lakes with only yellow perch.

| Citation and lake | Area (ha) | Mean depth (m) | Alkalinity (ppm) | Biomass | Method[a] |
|---|---|---|---|---|---|
| Mich., Schneider 1973a | | | | | |
| Cassidy | 19 | 1 | 127 | 39 | m |
| Section 4 pond | 1.3 | 11+ | 149 | 53 | p |
| South Twin | 1.7 | 0.7 | 106 | 65 | p |
| Jewett | 5 | 2 | 33 | 70 | m |
| Mass., Mullan and Tompkins 1959 | | | | | |
| Round Pond | 1.4 | — | — | 56 | p |
| N.Y., Regier 1962 | | | | | |
| Vann Pond | 0.2 | — | — | 63 | 2 y |
| Mich., Schneider 1973b | | | | | |
| Cattail ponds | — | — | — | 94 | |
| Plankton ponds | — | — | — | 121 | |
| Ill., Buck and Thoits 1970 | | | | | |
| Iota Pond | 0.4 | — | 149 | 106 | 1 y |
| | | | | 112 | 2 y |
| Alpha Pond | 0.4 | — | 203 | 161 | 1 y |
| | | | | 215 | 2 y |
| Theta Pond | 0.4 | — | 117 | 206 | 3 y |

[a]p = estimate by chemical treatment; m = mark and recapture estimate; y = population when drained after 1, 2, or 3 yr growth.

TABLE 5. Annual production ($kg \cdot ha^{-1} \cdot yr^{-1}$) of walleye and of yellow perch.

| Lake and citation | Ages included | Production Mean | Range | Years |
|---|---|---|---|---|
| *Walleyes* | | | | |
| West Blue, Man. | | | | |
| Kelso and Ward 1977 | I–VI | 2.1 | — | 1969 |
| Dexter, Ont. | IV+ | 4.1 | — | — |
| Moenig 1975 | IV + a | 7.8 | — | |
| Clear, Iowa | III+ | 1.21 | 0.42–3.07 | 1948–73 |
| Carlander and Payne 1977 | I+ | 3.08 | 0.91–6.98 | 1947–73 |
| Hoover Reservoir, Ohio | II+ | 2.16 | 1.31–4.05 | 1967–73 |
| Momot et al. 1977 | | | | |
| *Perch* | | | | |
| Red Deer, Ont. | | 21.9 | — | 1974 |
| Chadwick 1976 | | | | |

[a]Including reproductive products.

are similar to those from single years. Additional data on mean depths and on water chemistry and other factors may be available, but there is no indication that these would provide significant correlations.

There is, however, a significant correlation between yields and latitude, $r = -0.395$, $P < 0.02$, and between yields and area of the lake, $r = -0.366$, $P < 0.03$. Multiple regression analysis gave

$$Y = 18.52 - 0.3197\,L - 0.00002\,A$$

The combined regression, $r = 0.476$, accounts for 22.6% of the variance, whereas simple regression on latitude accounted for 15.6%. Increased yields to the south are to be expected because the growing seasons are longer, and yield is a function of production more than of biomass. Data on growth

TABLE 6. Annual yield (kg/ha) of walleye and all fish to commercial fishing

| Citation and lake | Area (1000 ha) | Lat. (°N) | Mean depth (m) | TDS (ppm) | MEI | Yield | | Years |
|---|---|---|---|---|---|---|---|---|
| | | | | | | Walleye | All species | |
| Baldwin and Saalfeld 1962[a] | | | | | | | | |
| Michigan | 5802 | 44 | 84 | 118 | 1.4 | 0.04 | 1.95 | 1951–60 |
| Ontario | 1948 | 44 | 80 | 155 | 1.9 | 0.06 | 0.5 | 1951–60 |
| Huron | 5960 | 45 | 59 | 195 | 3.3 | 0.17 | 1.6 | 1891–1900 |
| Sask., Rawson 1957a | | | | | | | | |
| Churchill[b] | 43 | 56 | 9 | 136 | 15 | 0.4 | 2.7 | 1941–55 |
| Ille a la Crosse | 45 | 55 | 8 | 185 | 23 | 0.5 | 3.2 | 1951–55 |
| Frobisher | 31 | 56 | 6 | 79 | 13 | 0.7 | 2.35 | 1966–55 |
| Little Peter Pond | 19 | 56 | 5 | 44 | 29 | 1.2 | 6.9 | 1941–55 |
| Big Peter Pond | 55 | 56 | 14 | 137 | 10 | 1.6 | 6.2 | 1941–55 |
| Sask., Rawson 1957b | | | | | | | | |
| La Range | 124 | 55 | 13 | 149 | 11 | 0.2 | 1.1 | 1946–50 |
| Sask., Koshinsky 1965 | | | | | | | | |
| Hebden | 0.47 | 55 | 8 | 45 | 6 | 0.04 | 1.23 | 1956–64 |
| Contact | 1.42 | 55 | 7 | 55 | 8 | 0.11 | 2.1 | 1956–64 |
| Little Deer | 0.36 | 55 | 6 | 55 | 9 | 0.44 | 2.8 | 1956–64 |
| Sulphide | 0.43 | 55 | 4 | 55 | 14 | 0.71 | 4.25 | 1956–64 |
| Sask., Atton and Kallemeyn unpublished data | | | | | | | | |
| Peter Pond | 74 | 56 | 11 | 140 | 12 | 1.7 | 9.2 | 1956–72 |
| Churchill | 43 | 56 | 9 | 128 | 13 | 2.2 | 12.6 | 1956–72 |
| Ont., Chevalier 1977 | | | | | | | | |
| Rainy | 86 | 48 | 10 | 57 | 6 | 1.0 | 4.4 | 1924–74 |
| Minn., Heyerdahl and Smith 1972 | | | | | | | | |
| Lake of the Woods | 357 | 49 | 8 | 83 | 10 | 1.35 | 4.88 | 1930–70 |
| Minn., Heyerdahl and Smith 1971 | | | | | | | | |
| Red | 117 | 48 | 6 | 275 | 32 | 2.71 | 4.57 | 1930–69 |
| Minn., Smith 1977 | | | | | | | | |
| Red[b] | 117 | 48 | 6 | 275 | 32 | 2.1 | 4.09 | 1954–75 |
| | | | | | | 2.65 | 4.19 | 1930–53 |
| Baldwin and Saalfeld 1962 | | | | | | | | |
| St. Claire | 119 | 42 | 3 | 208 | 69 | 1.75 | 5.92 | 1891–1900 |
| Erie | 2572 | 42 | 18 | 196 | 11 | 3.06 | 7.25 | 1931–60 |

[a]Yields for the decades with the highest average walleye catch. Bluepike and/or sauger were included with walleye in Ontario, Huron, Erie, and St. Clare data.
[b]Not used in further calculations.

of walleye tabulated by Carlander (1953) and Colby et al. (1977) indicate that growth rates increase from the north to the south. The negative correlation between yield and area of the lake may be related to decreased fishing effort per hectare as distance from shore increases.

Data from the Minnesota Department of Natural Resources indicated sport fishing yields of walleye from 15 lakes classified by W. J. Scidmore (personal communication) as warmwater rather than percid lakes averaged 2.4 $kg \cdot ha^{-1} \cdot yr^{-1}$ and ranged from 0.04 to 7.25. The yield from one other lake was considered as exceptional, 21.3 kg/ha, and not included in the mean. Walleye may be quite abundant even where other predators are more abundant.

## Conclusion

The available data point to our lack of information and suggest merely the probable magnitude of walleye and perch production. The lack of correlation between biomass or yields and the usual indicators of productivity probably is largely because walleye or perch populations do not bear a constant relationship to the total fish biomass or yield. The morphoedaphic index may indicate the potential yield from a body of water, but the proportion of the yield varies according to the

TABLE 7. Annual yield (kg/ha) of walleye, other predators, and all fish to sportfishing in 48 percid lakes arranged in order of increasing yield

| Lake and citation | Area (ha) | Lat. (°N) | Mean depth (m) | TDS (ppm) | MEI | Yield: Walleye | Yield: Other predators | Yield: Total | Yrs covered |
|---|---|---|---|---|---|---|---|---|---|
| LaRonge, Sask. Rawson 1957b | 123,616 | 52 | 13 | 149 | 11 | 0.15 | — | — | 6 |
| St. Clair, Ont. Johnston 1977 | 119,139 | 42 | 3 | 208 | 69 | 0.19 | — | — | 6 |
| Seagull, Minn. Micklus 1959 | 1,512 | 46 | — | — | — | 0.5 | — | — | 1 |
| Eagle, Ont. Chevalier 1975 | 27,692 | 48 | 3 | — | — | 0.8 | 0.9 | — | 1 |
| Lake of the Woods, Minn. Scidmore[a] | 122,316 | 49 | 7 | 83 | 12 | 1.0 | 0.2 | — | 3 |
| Cutfoot Sioux, Minn. Moyle and Franklin 1953 | 953 | 47 | — | — | — | 1.0 | 5.9 | — | 1 |
| Nipissing, Ont. Anthony and Jorgensen 1977 | 85,500 | 46 | 4.6 | 80 | 11 | 1.0 | 1.2 | 2.9 | 1 |
| Lost Island, Iowa Moen 1960a | 510 | 43 | 2.5 | 290[b] | 116 | 1.1 | — | 285 | 1 |
| Pike, Minn. Scidmore[a] | 328 | 47 | 7 | 99 | 14 | 1.2 | — | 1.3 | 2 |
| Kegonsa, Wis. Frey et al. 1939 | 1,273 | 42 | — | — | — | 1.3 | — | 10.7 | 1 |
| Green, Minn. Moyle and Franklin 1953 | 2,244 | 45 | — | — | — | 1.3 | 3.8 | — | 1 |
| Waubesa, Wis. Frey et al. 1939 | 823 | 43 | — | — | — | 1.5 | — | 2.0 | 1 |
| Winnibigoshish, Minn. Schneider 1977 | 28,256 | 46 | 4.6 | 169 | 45 | 1.7 | — | 5.0 | 2 |
| Clear, Iowa Moen 1959, 1960a | 1,474 | 43 | 3.6 | 230 | 64 | 1.8 | — | 16.8 | 2 |
| Edward, Minn. Scidmore[a] | 822 | 45 | 11 | — | — | 2.0 | — | — | 3 |
| Cass, Minn. Scidmore[a] | 6,313 | 47 | 7.6 | 180 | 24 | 2.1 | — | 6.2 | 5 |
| Leech, Minn. Scidmore[a] | 45,123 | 47 | 5.1 | 172 | 34 | 2.1 | — | 4.8 | 3 |
| Splithand, Minn. Scidmore[a] | 575 | 47 | 5.5 | 137 | 25 | 2.4 | — | 5.6 | 3 |
| Toad, Minn. Scidmore[a] | 679 | 46 | 6.4 | 183 | 29 | 3.0 | — | 10.9 | 2 |
| Lac des Mille Lacs, Ont. Elsey and Thomson 1977 | 24,114 | 48 | 6.8 | 68 | 10 | 3.1 | 1.3 | 5.2 | 4 |
| Moose, Minn. Scidmore[a] | 485 | 46 | 7.9 | 163 | 21 | 3.2 | — | 4.6 | 5 |
| Many Point, Minn. Scidmore[a] | 694 | 47 | 9.1 | 168 | 18 | 3.3 | — | 8.5 | 3 |
| Andrusia, Minn. Scidmore[a] | 611 | 46 | 7.9 | 177 | 22 | 3.3 | — | 9.5 | 5 |

TABLE 7. (*Concluded*)

| Lake and citation | Area (ha) | Lat. (°N) | Mean depth (m) | TDS (ppm) | MEI | Yield: Walleye | Yield: Other predators | Yield: Total | Yrs covered |
|---|---|---|---|---|---|---|---|---|---|
| Norris, Tenn. 1974 Fitz and Holbrook Unpublished data | 13,840 | 36 | 18 | 127 | 7 | 3.5 | — | — | 1 |
| Ingham, Iowa Moen 1959 | 170 | 43 | 25 | 163[b] | 65 | 3.6 | 5.6 | — | 1 |
| Detroit, Minn. Moyle and Franklin 1953 | 1,223 | 47 | — | — | — | 3.7 | 5.1 | — | 1 |
| Mille Lacs, Minn. Scidmore[a] | 53,420 | 46 | 6.2 | 133 | 21 | 4.0 | — | 6.0 | 2 |
| Wolf, Minn. Scidmore[a] | 425 | 47 | 8.5 | 167 | 20 | 4.8 | — | 15.2 | 5 |
| Wilson, Minn. Johnson 1977 | 245 | 47 | 6.6 | 51 | 8 | 4.9 | 0.5 | — | 3 |
| Little Pine, Minn. Scidmore[a] | 824 | 46 | 8.5 | 222 | 26 | 6.1 | — | 11.6 | 3 |
| West Okoboji, Iowa Moen 1960b | 1,594 | 43 | 12 | 261[b] | 22 | 6.2 | — | 62 | 3 |
| Oneida, N.Y. Grosslein 1961 | 20,640 | 43 | 6.8 | 90 | 13 | 6.5 | — | — | 3 |
| Black Hawk, Iowa Moen 1960a | 387 | 42 | 2 | 260[b] | 103 | 6.7 | — | 117 | 1 |
| Big Bearskin, Wis. Bersing 1940 | 229 | 44 | — | — | — | 7.3 | — | — | 1 |
| Spirit, Iowa Moen 1960a | 2,168 | 43 | 5.2 | 271[b] | 52 | 7.7 | — | 26.5 | 4 |
| East Okoboji, Iowa Moen 1960b | 567 | 43 | 2.8 | 272[b] | 97 | 8.0 | — | 77 | 3 |
| Escanada, Wis. Kempinger and Carline 1977 | 119 | 45 | 4.3 | 43 | 10 | 9.0 | — | 19.8 | 27 |
| Norris, Tenn. 1963 Fitz and Holbrook Unpublished data | 13,840 | 36 | 18 | 127 | 7 | 10.8 | — | — | 1 |
| Escanaba, Wis. Churchill 1957 | 119 | 45 | 4.3 | 43 | 10 | 12.9 | — | 21 | 8 |

[a]Data from files and reports of Minnesota Department of Natural Resources by W. J. Scidmore, 1976.
[b]Calculated from total alkalinity by the formula from Ryder et al. (1974).

species composition of the population and catch. In many of the lakes covered in this report there is evidence of overfishing for walleye, and in few cases was the yield sustained over a sufficient number of years for the average yields to be valid measures of annual production.

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