An energy-based analysis of particulate-feeding and filter-feeding by blue tilapia, *Tilapia aurea*

Douglas W. Yowell[1] & Gary L. Vinyard[2,3]
[2] *Department of Biology, University of Nevada, Reno, NV 89557-0015, U.S.A.*
[1] *Present address: Commonwealth Edison, Environmental Services, P.O. Box 767, Chicago, IL, 60690–0767, U.S.A.*
[3] *Address for correspondence*

Synopsis

Adult blue tilapia, *Tilapia aurea*, employ filter-feeding as their primary feeding method, but feed as visual, particulate-feeding zooplanktivores as juveniles. We used measurements of oxygen utilization in enclosed chambers to assess filter-feeding energy costs, and videotaped observations of particulate-feeding to compute energy costs for this behavior. Weight-specific costs of filter-feeding are highest for smaller individuals, and decrease exponentially with fish size. Particulate-feeding costs increase with fish size and with distance travelled during attacks on zooplankton prey. These data were used in combination with published information to examine the energetics of the switch in feeding behavior in relation to the profitability of each feeding method. We develop a model which can be used to predict feeding behavior in relation to fish size and plankton array.

Introduction

Fishes which employ filter-feeding as their primary feeding method as adults are typically visual particulate-feeding planktivores as juveniles, and switch to filter-feeding as they grow. Associated with these behavioral changes are shifts in diet composition from a predominance of large zooplankton in juveniles to increasing reliance on phytoplankton and/or smaller, non-evasive zooplankton in adults (Kutkuhn 1957, Cramer & Marzolf 1970, Janssen 1976a, Durbin 1979, Drenner et al. 1982, Lazzaro 1987). Explanations of this behavioral switch have emphasized proximal mechanisms such as developmental changes in morphology of digestive tract or gill rakers (Bodola 1966, De Ciechomski 1967, Bowen 1982, Heidinger 1983, Drenner et al. 1984a,

Mummert & Drenner 1986). These explanations ignore the possibility that energy acquisition rates may also be important determinants of feeding mode.

Fishes may experience highly variable conditions of resource abundance. Because of this, it seems likely that relative energetic efficiencies of particulate and filter-feeding modes should be subject to strong selection and may vary with fish size (Calow 1985). It is likely that the shift from particulate-feeding to filter-feeding reflects changing net profitability of each feeding mode and that morphological changes are driven by energetic constraints. Although it has been suggested that energy maximization accounts for the facultative switch from particulate-feeding to filter-feeding in zooplanktivorous fish (Crowder & Binkowski 1983, Crowd-

er 1985), the energetics of each feeding method have not previously been examined in any species (Durbin 1979, Helfman 1990).

To investigate the energetics of feeding behavior in filter-feeding fishes, we began an analysis of feeding modes in blue tilapia, *Tilapia aurea*. As juveniles, they are visual zooplanktivores, but upon reaching 6 to 7 cm standard length they switch to pump filter-feeding on phytoplankton and zooplankton (Spataru & Zorn 1978, Gophen 1980, Gophen et al. 1983). Native to rift lakes and river systems of northern Africa and the Middle East, blue tilapia have established reproducing populations in several southeastern U.S. states (Germany & Noble 1979, Lee et al. 1980). Our experiments examined blue tilapia feeding profitability in relation to fish size for both particulate-feeding and filter-feeding.

Materials and methods

Three lines of investigation were used to examine metabolic rates of blue tilapia in relation to feeding behavior. We first determined routine metabolic rates of fish in relation to size. Second, we examined size-related energy costs of filter-feeding. Finally, particulate-feeding energy costs were assessed in relation to fish size and prey size.

Blue tilapia used in our experiments were progeny of individuals collected from a reservoir cooling pond in central Texas. In the laboratory they were housed in indoor aquaria maintained at approximately 20° C and fed live zooplankton and pelletized commercial trout chow. Sixty-three fish ranging from 2.0 to 16.1 cm standard length (SL) were used. Fish were deprived of food for 24 h prior to use in any procedure.

Routine metabolism
Routine metabolic rates (Caulton 1977) were determined by continuously monitoring dissolved oxygen concentrations inside closed plexiglass chambers containing single fish. To insure adequate mixing, magnetic stir bars were slowly rotated inside each chamber with external power supplied by a water-powered stirring unit. Chamber volumes

ranged from 0.80 to 7.65 liters. Smaller chambers were used with small fish to increase measurement sensitivity. Dissolved oxygen values were automatically recorded at 5 second intervals by a microcomputer via an analog-to-digital conversion system.

Because preliminary measurements indicated elevated routine metabolic rates during 10–15 min after fish were placed in chambers, all fish were allowed to habituate to experimental conditions for at least 20–30 min prior to each observation series. Fish behavior was remotely monitored with a videotape system to limit disturbance from human observers.

After observations began, dissolved oxygen levels were recorded for 15–20 min. Then, with minimum disturbance and without removing fish, the chamber was flushed with aerated water and a second 15–20 min period was monitored using the same fish. Control trials without fish yielded no significant changes in dissolved oxygen concentration (ANOVA p = 0.58).

Because fecal material sometimes accumulated during trials, additional measurements were performed in chambers containing approximately 4 grams (wet weight) of fish feces. Although this mass was several times the accumulation during any trial, no significant change in dissolved oxygen was observed (ANOVA p = 0.97).

Routine metabolic rates were computed from linear regressions of dissolved oxygen concentration corrected for chamber volume and fish biomass. Oxygen values were converted to energy units (Joules) using a conversion factor of 13.68 J mg^{-1} O_2 (Caulton 1978).

Filter-feeding metabolism
Metabolic costs of filter-feeding were determined in the same chambers used for examination of routine metabolism. After the same acclimation procedures, blue tilapia were induced to pump filter-feed by injecting live plankton into each chamber. During plankton injection, care was taken to insure that fish were undisturbed and no air bubbles were introduced. Plankton were collected from a small, eutrophic pond on the campus of the University of Nevada, Reno using a 63 μm mesh plankton net. Plankton passing through a 200 μm mesh net but

retained by an 80 μm mesh net were used to induce filter-feeding.

During filter-feeding, dissolved oxygen concentrations were recorded and fish behavior was videotaped. Duration of feeding trials was approximately 15–20 min. Trials in which fish filter-fed for less than 10 min were excluded from analyses. Control trials in chambers without fish but containing plankton showed no significant changes in dissolved oxygen (ANOVA p = 0.27). Metabolic rates of filter-feeding fish were computed using the same procedures as for routine metabolism.

Particulate-feeding metabolism

Measuring dissolved oxygen to determine metabolic cost is impractical for single attacks by particulate-feeding fish and inappropriate if the particulate-feeding fish experience anaerobic metabolism during fast starts (Cech 1990). Therefore, we used data from videotaped observations to assess particulate-feeding energetics.

Groups of 2 to 4 blue tilapia were placed in a 75 × 12 × 6 cm plexiglass tank and allowed to acclimate for several hours. Single fish were isolated from the group into a 40 × 12 × 6 cm area by wire-mesh screen. Individual *Daphnia magna* were randomly chosen from one of four size classes and placed in the chamber outside the fish's reactive distance. Fish were videotaped during attack on *D. magna* prey. Analysis of videotapes allowed determination of attack distance and swimming velocities for each attack. Four size classes of *D. magna* produced by sorting with mesh netting were used in these trials ($\bar{x}$ = 1.08 mm, SD = 0.11; $\bar{x}$ = 1.51 mm, SD = 0.12; $\bar{x}$ = 2.48 mm, SD = 0.11; $\bar{x}$ = 3.58 mm, SD = 0.22).

Videotapes of particulate-feeding fish were examined using a motion analyzer. Positions of attacking fish were determined at 1/60 second intervals to allow computation of attack velocities and accelerations. Determination of energy costs of particulate-feeding by blue tilapia is possible using fast start swimming equations provided in Webb (1975). Attack distance, velocity, and acceleration were determined from videotapes. Fish biomass was measured directly. Fish wetted surface area (FWSA) was computed using a regression
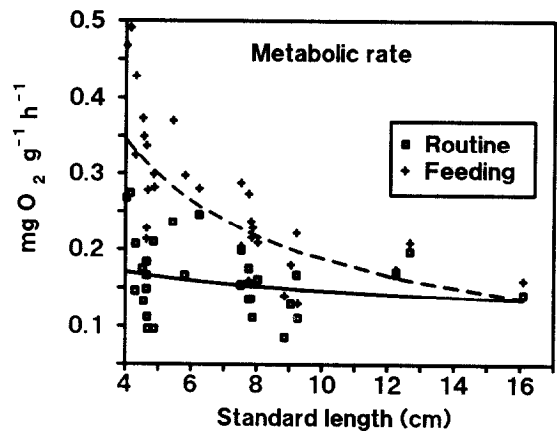

Fig. 1. Metabolic oxygen consumption rates of blue tilapia during routine metabolism and while filter-feeding. Oxygen consumption rates were determined for fish enclosed in chambers and either inactive or feeding. The upper regression line (y = 0.879 × SL$^{-0.671}$, n = 31, r^2 = 0.53) is derived from filter-feeding individuals, while the lower line (y = 0.215 × SL$^{-0.168}$, n = 31, r^2 = 0.04) is derived from routine metabolic rate measurements.

derived from digitized tracings of fish ranging from 23 to 125 mm standard length (FWSA = 0.213 × SL$^{2.152}$, r^2 = 0.99, n = 14).

Results

Routine metabolic rate

Routine metabolic rate per fish (RMRF), computed from oxygen consumption rates and expressed in J fish^{-1} h^{-1}, increased with fish size (RMRF = 0.105 × SL$^{2.823}$, r^2 = 0.94, n = 31). In contrast, weight-specific routine metabolic rate (RMRG), in J g^{-1} h^{-1}, declined only slightly in larger fish (RMRG = 2.946 × SL$^{-0.167}$, r^2 = 0.04, n = 31, Fig. 1).

Filter-feeding metabolic rate

Metabolic rates measured during filter-feeding include a component reflecting routine metabolism and an additional increment due to filter-feeding. Filter-feeding metabolic rate per fish (FMRF), derived from oxygen measurements and expressed in J fish^{-1} h^{-1}, increases with fish SL (FMRF = 0.348 × SL$^{2.368}$, r^2 = 0.92, n = 31). Weight-specific filter-feeding metabolic rate (FMRG, J g^{-1} h^{-1}), decreases with increasing standard length (FMRG =
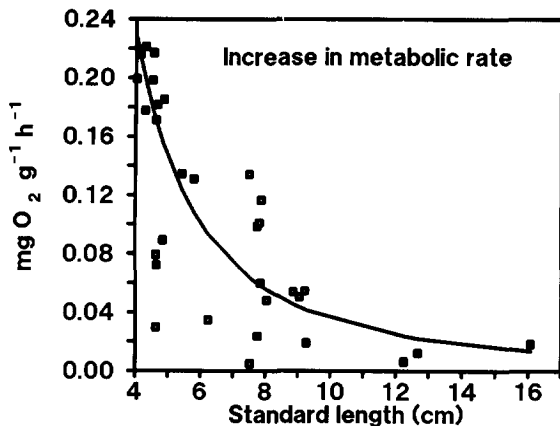
Fig. 2. Increase in metabolic oxygen consumption resulting from filter feeding in blue tilapia. Points plotted are differences between routine and filter-feeding metabolic rates for individual fish. The plotted regression line is derived from these points and is by the equation $y = 0.285 \times SL^{-0.667}$, $n = 31$, $r^2 = 0.75$.

$12.032 \times SL^{-0.671}$, $r^2 = 0.53$, $n = 31$, Fig. 1). Metabolic rate increases resulting from filter-feeding are inversely related to fish size (Fig. 2), demonstrating that the relative cost of using this feeding mode is much less for large fish, compared to small fish.

Particulate-feeding metabolic rate

Energy expenditures during individual attacks on *Daphnia magna* were computed over intervals of 1/60 second and summed over the period from initiation of the attack until the point the fish stopped moving after engulfing each prey. This procedure yields an estimate of total energy cost for each attack.

Energy expenditures during particulate-feeding are strongly correlated with fish size and distance traveled (Fig. 3). Multiple linear regression of work done during attacks against fish weight and distance traveled (multiple $R^2 = 0.636$, $p < 0.0001$, $n = 167$) shows significant effects of fish weight ($p < 0.0001$) and distance ($p < 0.0001$) on work done during attacks. Linear regressions indicate that reactive distance (RD) of fish for *D. magna* increased with prey length (DL, in mm, measured from top of head to base of tail spine, $RD = 46.91 \times DL^{0.812}$, $r^2 = 0.44$, $n = 169$), but that RD was uncorrelated with fish standard length ($p = 0.55$).

Discussion

Smaller blue tilapia experience a greater increase in metabolic rate during filter-feeding than do large fish (Fig. 2). In contrast, expenditures for particulate-feeding increase with fish size, and also in response to distance traveled during attacks (Fig. 3). These two observations lead to the prediction that small fish should be more likely to particulate-feed and larger fish to filter-feed. Furthermore, for any identifiable plankton array, fish smaller than some specific size should employ particulate-feeding most efficiently while those above that size should filter-feed. Because plankton composition varies substantially in size spectrum and density over both spatial and temporal scales, the relative energy efficiency of either feeding mode should also vary in response to local conditions.

Our data allow estimation of size-related feeding costs for both filter-feeding and particulate-feeding blue tilapia. This allows comparison of net feeding profitability in relation to fish size for both filter-feeding and particulate-feeding. By assuming that fish will employ the feeding tactic which provides the highest net energy return rate, these results can be used to predict expected feeding behavior of blue tilapia in relation to fish size and prey array. We have used these ideas to develop a predictive model of blue tilapia feeding behavior which can be used to identify the fish size at which there should be a shift between particulate-feeding and filter-feeding.

The model first computes net energy gain and costs for an arbitrary specified interval of filter-feeding. It then computes costs required to acquire an equivalent net energy gain by particulate-feeding. Examination of the ratio of particulate-feeding costs to filter-feeding costs, while achieving an equivalent net energy return, allows prediction of feeding behavior. The predicted behavior is responsive to SL and to local prey conditions.

Filter-feeding energy gain

Expected energy gain from filter-feeding can be estimated from the volumetric rate of water proces-

sing, the expected food content of the water, and the filtration efficiency. Water processing rates for pump-filtering fishes are determined from the product of fish buccal volume and pumping rates. Expected plankton concentration can be estimated with reference to the ambient plankton particle size-frequency distribution and the size-related filtering efficiency.

The minimum particle size retained by filtering blue tilapia is approximately 25 μm (Drenner et al. 1984b). Above the minimum size threshold, filter-feeding fishes are thought to retain phytoplankton with high efficiency. Lazzaro (1987) cites a possibly excessive retention efficiency value of nearly 100 percent.

The size-frequency distribution of particles in lentic ecosystems often exhibits distinct abundance peaks roughly corresponding to trophic levels. Sprules et al. (1983) documented particle size distributions in 26 north temperate lakes. We used their data to estimate a generalized planktonic food particle size-frequency distribution. Two biomass ranges representing 25–200 μm equivalent spherical diameter (ESD) and 200–2600 μm ESD size particles were identified from data provided by Sprules et al. (1983), and judged to comprise primarily phytoplankton and zooplankton, respectively. Mean total biomass for each size class was then calculated. The 25–200 μm ESD biomass peak yielded an estimated biomass of 1.89 mg l^{-1}, whereas the 200–2600 μm ESD size range yielded an estimate of 84.72 mg l^{-1}.

Filter-feeding capture efficiency on zooplankton is reduced by zooplankton evasion (Janssen 1976b, Ehlinger 1989). Using a suction device to simulate pumping currents generated by filter-feeding fishes, Drenner et al. (1978) and Drenner & McComas (1980) determined an average capture efficiency of 51 percent for pump-filtering fish consuming an assemblage of cladoceran and copepod zooplankton.

Expected net energy content of plankton are estimated using carbon assimilation efficiency values of 43 percent for phytoplankton (Moriarty & Moriarty 1973), and 85 percent for zooplankton (Solomon & Brafield 1972). Mean caloric equiv-
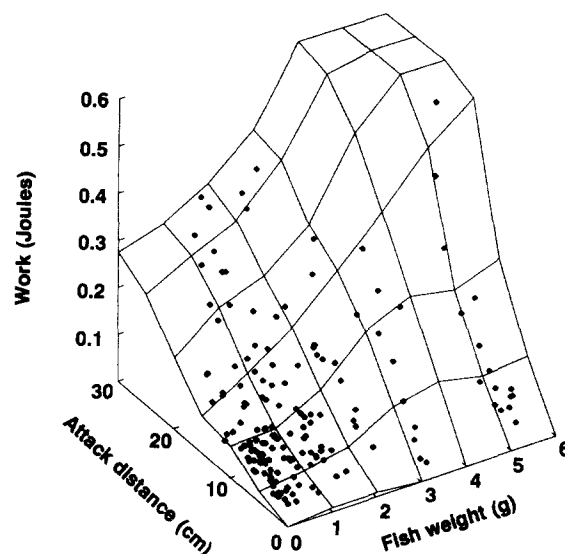

Fig. 3. Three dimensional plot showing the relationship between attack distance, fish weight and work performed during attacks on zooplankton prey. Results of individual observations are plotted as points on the figure. The surface was produced by a distance weighted, least squares fit of the data (Wilkinson 1987).

alent values of 695.8 cal g^{-1} wet weight for phytoplankton and 432.0 cal g^{-1} wet weight for zooplankton (Cummins & Wuycheck 1971) allow computation of estimated net energy yield from biomass consumed.

Particulate-feeding energy gain

The expected energy gain from particulate-feeding is affected by prey capture efficiency, assimilation efficiency, zooplankton abundance, and mean zooplankton size. Because capture efficiency ranges from 50 percent to nearly 100 percent for various zooplankton types (Vinyard 1982), we use a mean particulate-feeding capture efficiency value of 75 percent. Average zooplankton biomass within the 200–2600 μm (ESD) size class was estimated at 0.387 mg using a length-weight regression for *Daphnia* (Edmondson 1971). Zooplankton caloric equivalents can be computed using mean value of
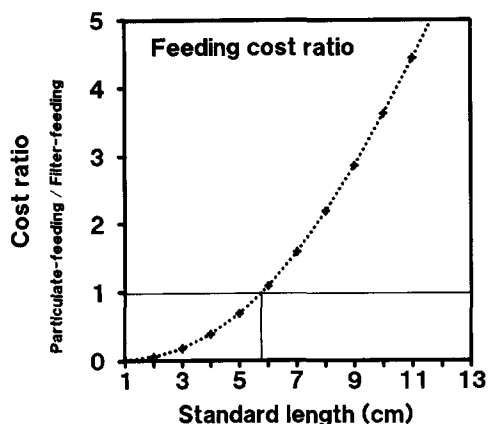
Fig. 4. Results from simulation of filter-feeding and particulate-feeding blue tilapia showing relative cost ratio of each feeding mode while acquiring equivalent net caloric intake values. The horizontal line at y = 1 indicates the level at which net profitability of each feeding mode are equivalent. For ratios < 1 particulate-feeding is most profitable, at ratios > 1 filter-feeding is most efficient. This simulation predicts that for the initial conditions, summarized in the text, fish less than approximately 5.7 cm should behave as particulate-feeders, while those larger should filter-feed. The size at which the behavior shift is predicted to occur varies with changes in plankton density and size distribution.

432.0 cal g^{-1} wet weight for cladocerans and copepods (Cummins & Wuycheck 1971).

In conjunction with our data indicating costs of filter-feeding and of particulate-feeding, our model yields the prediction that blue tilapia should switch from particulate-feeding to filter-feeding at approximately 5.7 cm SL (Fig. 4). This value is within the size range reported for the primary change in feeding behavior for blue tilapia, 4 to 8 cm (Spataru & Zorn 1978, Gophen 1980, Gophen et al. 1983). However, the model is sensitive to changes in each parameter used in its development, and can be used to yield predictions of behavior under varying conditions of prey size distribution and abundance. Changes in zooplankton density and size most strongly affect predicted behavior. For example, if zooplankton biomass is doubled, the model predicts that fish should shift to filter-feeding at approximately 4.1 cm SL. Reduction of zooplankton biomass by half results in a prediction that filter-feeding should occur at approximately 7.2 cm SL. Increases of mean zooplankton size are predicted

to determine the size at which filter-feeding is most profitable to shift toward larger fish. The model predicts that increased phytoplankton biomass should result in a shift to filter-feeding at smaller sizes. Our model is less sensitive to changes in biomass of phytoplankton than of zooplankton. We are presently testing predictions produced by the model under a range of fish sizes and plankton distributions.

Many fishes which are filter-feeders or piscivores as adults begin their independent foraging early in life as visual particulate-feeding zooplanktivores. As they grow, filter-feeding fish may continue to exploit zooplankton while adding phytoplankton to the diet. By contrast, piscivores continually increase the size range of acceptable prey as they shift to higher trophic levels (Durbin 1979). Production in large piscivores may thus become energy limited. For filter-feeding fish, the consumption of primary producers and primary consumers offers access to more abundant energy resources (Durbin 1979, Lazzaro 1987). Success of this style is reflected in the large individual sizes observed in the whale shark, *Rhincodon typus*, and basking shark, *Cetorhinus maximus*, and by the large total biomass attained by populations of many filter-feeding fishes (Moyle & Cech 1982, Sanderson & Wassersug 1990). In reservoirs in the central U.S., two filter-feeding clupeids account for 45 percent of fish standing crop. Filter-feeders also support the largest commercial marine fisheries (Ryther 1969, Lazzaro 1987). The apparent advantages of filter-feeding to fish are also demonstrated by the independent derivation of this foraging behavior in numerous orders and families (Lazzaro 1987).

Small filter-feeders may be restricted to zooplanktivory because of their relatively high weight-specific routine metabolism (Fig. 1). Because filtering cost is inversely related to fish size, filter-feeding may yield insufficient net gain to meet the energy requirements of small fish. However, as fish grow, volumetric filtering capacity increases and weight-specific routine metabolic and filter-feeding costs decrease. These changes result in a shift in the relative energy efficiency of the two feeding tactics, with filter-feeding becoming more efficient for larger fish.

Minimization of feeding costs while maximizing net energy return may have been important in the development of filter-feeding. We suspect that energy maximization on a proximal level determines short-term feeding mode shifts by blue tilapia. Facultative planktivores that may utilize both feeding modes interchangeably (Leong & O'Connell 1969, Crowder & Binkowski 1983, Ehlinger 1989, Helfman 1990) usually filter-feed on small, abundant zooplankton and particulate-feed on larger, less abundant forms. We suggest this is a tactic which maximizes net energy return in response to a changing prey base.

Acknowledgements

References cited

Bodola, A. 1966. Life history of the gizzard shad, *Dorosoma cepedianum* (LeSueur), in Western Lake Erie. U.S. Fish and Wildlife Serv. Fish. Bull. 65: 391–425.

Bowen, S.H. 1982. Feeding, digestion and growth – qualitative considerations. pp. 141–156. *In:* R.S.V. Pullin & R.H. Lowe-McConnell (ed.) The Biology and Culture of Tilapias, ICLARM Conference Proceedings 7, International Center for Living Aquatic Resources Management, Manila.

Calow, P. 1985. Adaptive aspects of energy allocation. pp. 13–31. *In:* P. Tytlet & P. Calow (ed.) Fish Energetics – New Perspectives, Johns Hopkins University Press, Baltimore.

Caulton, M.S. 1977. The effect of temperature on routine metabolism in *Tilapia rendalli* Boulenger. J. Fish Biol. 11: 549–553.

Caulton, M.S. 1978. The effect of temperature and mass on routine metabolism in *Sarotherodon (Tilapia) mossambicus* (Peters). J. Fish Biol. 13: 195–201.

Cech, J.J., Jr. 1990. Respirometry. pp. 335–362. *In:* C.B. Schreck & P.B. Moyle (ed.) Methods for Fish Biology, American Fisheries Society, Bethesda.

Cramer, J.D. & G.R. Marzolf. 1970. Selective predation on zooplankton by gizzard shad. Trans. Amer. Fish. Soc. 99: 320–322.

Crowder, L.B. 1985. Optimal foraging and feeding mode shifts in fishes. Env. Biol. Fish. 12: 57–62.

Crowder, L.B. & F.P. Binkowski. 1983. Foraging behaviors and the interaction of alewife, *Alosa pseudoharengus*, and bloater, *Coregonus hoyi*. Env. Biol. Fish. 8: 105–113.

Cummins, K.W. & J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Int. Ver. Theo. Ang. Limnol. 18: 1–158.

De Ciechomski, J.D. 1967. Investigations of food and feeding habits of larvae and juveniles of the Argentine anchovy, *Engraulis anchoita*. Calif. Coop. Oceanic Fish. Invest. Rep. 11: 72–81.

Drenner, R.W., F. deNoyelles Jr. & D. Kettle. 1982. Selective impact of filter-feeding gizzard shad on zooplankton community structure. Limnol. Oceanogr. 27: 965–968.

Drenner, R.W. & S.R. McComas. 1980. The roles of zooplankter escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. pp. 587–593. *In:* W.C. Kerfoot (ed.) Evolution and Ecology of Zooplankton Communities, University Press of New England, Hanover.

Drenner, R.W., J.R. Mummert, F. deNoyelles Jr. & D. Kettle. 1984a. Selective particle ingestion by a filter-feeding fish and its impact on phytoplankton community structure. Limnol. Oceanogr. 29: 941–948.

Drenner, R.W., S.B. Taylor, X. Lazzaro & D. Kettle. 1984b. Particle-grazing and plankton community of an omnivorous cichlid. Trans. Amer. Fish. Soc. 113: 397–402.

Drenner, R.W., S.B. Taylor, G.L. Vinyard, K.W. Kratz & M. Gophen. 1983. Filtering rates and particle size selectivities of planktivorous *Sarotherodon*. pp. 00–00. *In:* XX (ed.) International Symposium on Tilapia in Aquaculture, Nazareth.

Drenner, R.W., J.R. Strickler & W.J. O'Brien. 1978. Capture probability: the role of zooplankter escape in the selective feeding of planktivorous fish. J. Fish. Res. Board. Can. 35: 1370–1373.

Durbin, A.G. 1979. Food selection by plankton feeding fishes. pp. 203–218. *In:* R.H. Stroud & M. Clepper (ed.) Predator-Prey Systems in Fisheries Management, International Symposium on Predator-Prey Systems in Fish Communities and their Role in Fisheries Management, Sport Fishing Institute, Washington. D.C.

Edmondson, W.T. 1971. Methods of processing samples and developing data. pp. 127–169. *In:* W.T. Edmondson & G.G. Winberg (ed.) A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters, IBP Handbook No. 7, Blackwell Scientific Publications, Oxford.

Ehlinger, T.J. 1989. Foraging mode switches in the golden shiner (*Notemigonus crysoleucas*). Can. J. Fish. Aquat. Sci. 46: 1250–1254.

Germany, R.D. & R.L. Noble. 1979. Population dynamics of the blue tilapia in Trinidad Lake. Texas. Proc. Southeast. Assoc. Fish Wildl. Agencies 31: 414–417.

Gophen, M. 1980. Food resources, feeding behavior and growth rates of *Sarotherodon galilaeum* (Linnaeus) fingerlings. Aquaculture 20: 101–115.

Gophen, M., R.W. Drenner & G.L. Vinyard. 1983. Cichlid stocking and the decline of the Galilee Saint Peter's fish (*Sarotherodon galilaeus*) in Lake Kinneret, Israel. Can. J. Fish. Aquat. Sci. 40: 983–986.

Heidinger, R.C. 1983. Life history of gizzard shad as it relates to the ecology of small lake fisheries. pp. 1–18. *In:* D. Bonneau

& G. Radonski (ed.) Pros & Cons of Shad: Proceedings of Small Lakes Management Workshop, Iowa Conserv. Comm. & Sport Fishery Institute, Ames.

Helfman, G. 1990. Mode selection and mode switching in foraging animals. Adv. Stu. Behav. 19: 249–298.

Janssen, J. 1976a. Feeding modes and prey selection in the alewife (*Alosa pseudoharengus*). J. Fish. Res. Board Can. 33: 1972–1975.

Janssen, J. 1976b. Selectivity of an artificial filter feeder and suction feeders on calanoid copepods. Amer. Midl. Nat. 95: 491–493.

Kutkuhn, J.H. 1957. Utilization of plankton by juvenile gizzard shad in a shallow prairie lake. Trans. Amer. Fish. Soc. 87: 80–103.

Lazzaro, X. 1987. A review of planktivorous fishes; their evolution, feeding behaviours, selectivities, and impacts. Hydrobiologia 146: 97–167.

Lee, D.S., C.R. Gilbert, C.H. Hocutt, R.E. Jenkins, D.E. McAllister & J.R. Stauffer, Jr. 1980. Atlas of North American freshwater fishes. NC State Mus. Nat. Hist., Raleigh. 854 pp.

Leong, R.J.H. & C.P. O'Connell. 1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Board Can. 26: 557–582.

Moyle, P.B. & J.J. Cech Jr. 1982. Fishes: an introduction to ichthyology. Prentice-Hall, Englewood Cliffs. 593 pp.

Moriarty, D.J.W. & C.W. Moriarty. 1973. The assimilation of carbon from phytoplankton by two herbivorous fishes: *Tilapia nilotica* and *Haplochromis nigripinnis*. J. Zool. Lond. 171: 41–55.

Mummert, J.R. & R.W. Drenner. 1986. Effect of fish size on the filtering efficiency and selective particle ingestion of a filter-feeding clupeid. Trans. Amer. Fish. Soc. 115: 522–528.

Ryther, J.H. 1969. Photosynthesis and fish production in the sea. Science 166: 72–76.

Sanderson, S.L. & R. Wassersug. 1990. Suspension-feeding vertebrates. Sci. Amer. 262(3): 97–101.

Solomon, D.J. & A.E. Brafield. 1972. The energetics of feeding metabolism and growth of perch (*Perca fluviatilis* L.). J. Anim. Ecol. 41: 699–718.

Spataru, P. & M. Zorn. 1978. Food and feeding habits of *Tilapia aurea* Steindachner (Cichlidae) in Lake Kinneret (Israel). Aquaculture 13: 67–69.

Sprules, W.G., J.M. Casselman & B.J. Shuter. 1983. Size distribution of pelagic particles in lakes. Can. J. Fish. Aquat. Sci. 40: 1761–1769.

Vinyard, G.L. 1982. Variable kinematics of Sacramento perch (*Archoplites interruptus*) capturing evasive and non-evasive prey. Can. J. Fish. Aquat. Sci. 39: 208–211.

Webb, P.W. 1975. Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Board. Can. 190. 159 pp.

Wilkinson, L. 1988. Sygraph. Systat, Evanston. 822 pp.