

Zooplanktivory in the Endemic Freshwater Sardine, *Sardinella tawilis* (Herre 1927) of Taal Lake, the Philippines

Rey Donne S. Papa^{1,*}, Roberto C. Pagulayan², and Alicia Ely J. Pagulayan¹

¹Department of Biological Sciences and Research Center for the Natural Sciences, University of Santo Tomas, Manila 1015, the Philippines

²Institute of Biology, University of the Philippines, Diliman, Quezon City 1101, the Philippines. Current Address: Center for Research and Development, Angeles University Foundation, Angeles City, Pampanga 2009, the Philippines

(Accepted February 29, 2008)

Rey Donne S. Papa, Roberto C. Pagulayan, and Alicia Ely J. Pagulayan (2008) Zooplanktivory in the endemic freshwater sardine, *Sardinella tawilis* (Herre 1927) of Taal Lake, the Philippines. *Zoological Studies* 47(5): 535-543. In this study, we compared the composition and relative abundance of zooplankton found in the vicinity of Napayun I., Taal Lake, the Philippines, with the zooplankton found in stomachs of the freshwater sardine *Sardinella tawilis* (Herre 1927) caught from the same location. Samplings were conducted monthly from July 2003 to June 2004. Ninety percent of the stomach contents were composed of relatively large-bodied adult copepods; the remaining 10% contained cladocerans and rotifers. Selectivity coefficients computed from comparing the fish diet with the available prey from the environment showed a high preference for copepods and a low to no preference for cladocerans and rotifers for all 10 mo sampled of the 12 mo study. A high preference for calanoid copepods noted in Apr.-June coincided with the peak spawning of *S. tawilis* according to previous studies. The preference for large prey such as calanoids, despite the dominance of small-bodied zooplankton present during that time may have been related to increased food intake during spawning. These results indicate a preference for larger zooplankton due to size-selective particulate feeding exhibited by clupeids such as *S. tawilis*. <http://zoolstud.sinica.edu.tw/Journals/47.5/535.pdf>

Key words: *Sardinella tawilis*, Taal Lake, Zooplanktivory, Size-selective predation, Copepods.

Fisheries biologists have long appreciated the importance of feeding and food habits to the ecology and production dynamics of fish stocks (Gerking 1994), which may have significant impacts on their prey (Northcote 1988). Predation is an important factor structuring prey communities such as zooplankton (Pagano et al. 2003). A degree of preference is often apparent among predators. The optimal foraging theory states that predators should select their prey based on the net energy gain, which is affected by prey type, search time, habitat type, and predator avoidance (Olson et al. 2003). Predators maximize the energetic gains available in relation to the energetic costs of prey capture, ingestion, and digestion (Nunn et al. 2007). Bigger

prey may produce higher energy yields, compared to much smaller ones; however, this comes with an increase in handling time (Nunn et al. 2007). Zooplanktivorous fish have been noted to visually select larger prey due to their particulate feeding habits (Good and Cargnelli 2004, Kahilainen et al. 2005, Lazzaro 1987). Selective predation is a common feature of most predators and can be studied by comparing predator diets with the prey available in the environment (Turesson et al. 2002). Zooplankton biomass and composition are regulated by size-selective predation by fish which select the largest, most visibly conspicuous prey in lakes and ponds. This leads to an increase in the density of small individuals or species such as

*To whom correspondence and reprint request should be addressed. Tel: 632-4061611 ext. 8297 or 4054.
E-mail:rspapa@mnl.ust.edu.ph; reypaps@yahoo.com

rotifers (Pagano et al. 2003, Rettig 2003, Wissel et al. 2003).

Sardinella tawilis (Herre 1927; Clupeidae) is an integral component of the Taal Lake ecosystem. It is regarded as the most important fish in Taal Lake in terms of biodiversity (Guerrero 2002), since it is one of the few freshwater *sardines* in the entire world, it is the only freshwater *Sardinella* in the Philippines (Froese and Pauly 2003), and it is endemic to Taal Lake, Luzon I. It is mainly pelagic with peak spawning in Mar.-May or May-July according to 2 separate studies conducted by Joson-Pagulayan (1999) and Aypa et al. (1991), respectively. The first recorded stomach content found in *S. tawilis* was the silverside *Hepsetia balabacensis* which was observed by Herre to be present in the stomachs of fish he had collected, which included the type specimen (Herre 1927). However, this seems to be the only record of *S. tawilis* ever being a piscivore, as more recent studies showed that the diet of *S. tawilis* was mostly comprised of zooplankton and ostracods (Castillo et al. 1975).

Sardinella tawilis is the dominant fish species caught in Taal Lake. It has been ranked first since 1996 with the highest annual fishery production recorded at 1120 metric tons in 1998 (Mutia et al. 2001). However, the catch of *S. tawilis* has been dwindling in recent years due to overfishing and changes in water quality (Mamaril 2001). Aside from those factors, human-mediated arrivals of commercial fish species such as the Nile tilapia *Oreochromis niloticus* have contributed to the decline of *S. tawilis* stocks (Villanueva et al. 1995; Mamaril 2001). A fish catch survey conducted in Taal Lake from 1996 to 1999 recorded 27 fish species from 32 families in the lake. This number is extremely low compared to records from the 1920s which indicated that 101 species from 32 families were present at that time in Taal Lake. About 87% of fish species had disappeared by 1996. This occurred during the same time that aquaculture flourished in the lake (Mutia et al. 2001). Conservation strategies in the lake have always been geared towards protecting organisms such as the freshwater sardine from overfishing; unfortunately, data on the feeding ecology of *S. tawilis* have been noted as being inadequate and fragmentary (Mamaril, 2001), in spite of the numerous studies conducted on its taxonomy, morphometrics, harvest rates, and reproductive biology, which are largely unpublished (Lagda et al. 2003). A better understanding of the biology

of *S. tawilis*, its diet, and its relationships with the zooplankton of Taal Lake would definitely help in creating better conservation strategies for the entire Taal Lake ecosystem.

This paper presents a 12-mo-long study on the diet of *S. tawilis*. We attempted to compare the diet of *S. tawilis* with the available prey in the immediate area where the fish were caught to update the available information on the food items consumed by the fish and establish its prey preference and food habits.

MATERIALS AND METHODS

Study area

Taal Lake (14°00'N, 121°19'E) formerly known as Lake Bombon, is the 3rd largest lake in the Philippine Archipelago. It is classified as an oligotrophic lake with a maximum depth of 180 m and drains through the Pansipit River into Balayan Bay to the southwest. It has a surface area of 24,356.4 ha (Guerrero 2002, Mutia et al. 2001). Taal Lake has multiple resource uses, but open water fishing and aquaculture of Nile tilapia (*Oreochromis niloticus*) and milkfish (*Chanos chanos*) are the most common. Taal Lake is also home to endemic, economic and ecologically important species such as the giant trevally (*Caranx ignobilis*) and the Lake Taal sea snake (*Hydrophis semperi*) (Mutia et al. 2001, Guerrero 2002, Lagda et al. 2003). It has been listed as a priority conservation area of extremely high importance and is in urgent need of further research (Ong et al. 2002).

We sampled at 2 sites at the southern tip of Napayun I. which is located on the northeastern side of Taal Lake in an area with an average depth of 25 m. Fishermen usually set up gill net sets with a float-line a short distance below the water surface (Herre 1927) to regularly catch *S. tawilis* in this area (Fig. 1).

Zooplankton

Sampling was done once a month from July 2003 to June 2004. Zooplankton were collected by making a vertical tow from a depth of 20 m to the surface using a conical plankton net (with a mesh size of 80 µm and a diameter of 0.254 m) between 05:00 and 07:00 at each sampling site. These were in the immediate area where fish were also collected during the same time. Collected samples

were fixed in 10% formalin.

Samples were brought to the laboratory for further analysis. Distilled water was added to make 50 ml subsamples. Three 1 ml replicates were taken separately and placed in a 1 ml Sedgewick-Rafter counting chamber. These were then analyzed under a low-power objective (10x). Organisms were counted in each replicate, and the average count was calculated. The total count was determined by multiplying the average by the original total volume of the liquid in the sample (Galbraith and Schneider 2000). Zooplankton density was computed by dividing the number of individuals in a sample by the volume of water filtered through the plankton net. The volume of water that passed through the plankton net was computed using the equation: $V = \pi r^2 h$, where r is 0.127 m and h is the depth of the tow. Identification was limited to genus level with the aid of illustrations and descriptions by Mamaril and Fernando (1978), except for the nauplii of cyclopoid and calanoid copepods, which were categorized together as nauplius larvae.

Fish collection and stomach sampling

Fish samples were collected monthly from

July 2003 to June 2004 except in Oct. 2003 and Mar. 2004 due to bad weather and no fish being caught, respectively. Fish were collected using gill nets with a mesh opening of 10 mm. The nets were lowered to a depth of 3 m at 05:00-07:00 and were collected after 2 h. About 30-50 individuals were collected each month from the early morning catch of fishermen at each sampling site. A cut exposing the stomach of each fish was made before preserving it in 10% formalin. The total length (cm) and weight (g) were measured for each fish. Sex was determined by examining the gonads (Windell 1968).

Stomach contents were flushed and examined under a 10x (Low Power Objective) magnification light microscope. Only specimens with complete structures or with a prominent body part were counted and identified. Separated body parts like carapaces, spines, segments, and legs were not included in the analysis and were classified as digested material. The copepods were identified to the level of order, while cladocerans and rotifers were identified to genus. Each particular prey type was counted, while empty stomachs were also noted (Olson et al. 2003).

The percent frequency of occurrence (Liao et al. 2002, Windell 1968) and numerical method

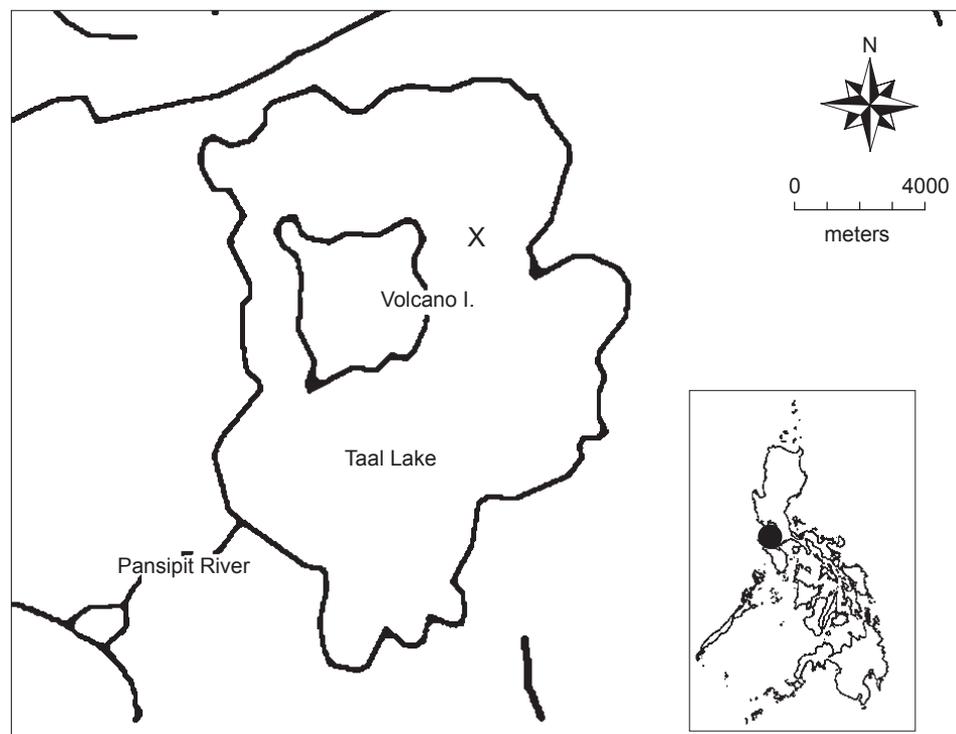


Fig. 1. Map of Taal Lake showing the location of Napayun I. (x).

(Windell 1968) were used to analyze the data. Vanderploeg and Scavia's (1979) selectivity coefficient, W'_i , calculated as $W'_i = \frac{(r_i / p_i)}{(r_i / p_i)_{pref}}$, where r_i is the percent number of food items, p_i is the percent abundance of the same element in the food complex of the environment, and $(r_i / p_i)_{pref}$ is the maximum value of (r_i / p_i) , was used to determine the prey preference by *S. tawilis*. W'_i varies between 0 for no ingestion of a prey type and 1 for preference (Pothoven et al. 2007).

RESULTS

Fish sample statistics

In total, 449 individuals of *S. tawilis* ranging 5.77-14.54 cm in total length (TL) were collected from July 2003 to June 2004, except in Oct. 2003 and Mar. 2004 due to bad weather and no fish being caught, respectively. About 35-48 individuals were examined per month (Table 1).

Overall percent composition of the stomach contents

Stomach contents of *S. tawilis* consisted of various zooplankton (copepods, cladocerans, and rotifers), filamentous algae, and pennate diatoms. Partially digested and digested food, such as separated carapaces, legs and antennae of copepods, cladocerans, and rotifers, were also present. These body parts were not used in the diet analysis.

Calanoid copepods were the most abundant prey items comprising 58% of the total number of zooplankters found, followed by cyclopoids at 32%, thus making the copepods the dominant prey in the diet of *S. tawilis*, at 90%. The remaining 10% of the diet was made up of cladocerans and rotifers.

Temporal variations in diet composition

Cyclopoid copepods were the most common food item in the diet for 5 of the 10 sampled months: Aug., Sept., Nov., Jan., and Apr. Calanoid copepods were most common in May and June, but were also noted to be the 2nd most common for Apr., while in Feb., cyclopoid and calanoid copepods both had the highest percent frequency of occurrence at 75%. The cladoceran, *Bosmina* sp., however, was most frequent in Dec. The highest occurrence of rotifers in the diet of the fish was in Aug. at 17% (Fig. 2). Copepods also had the highest percent contribution to the diet of *S. tawilis* in terms of number (Fig. 3). Highest values were observed in Apr., May, and June when the percent compositions of this prey item were 97.33%, 96.7%, and 92.94%, respectively. The greatest number of empty stomachs was found in Feb. (6 stomachs), followed by July (5) and Dec. (3). One empty stomach was found in each of Aug., Sept., Nov., Jan., and June, while no empty stomachs were noted in Apr. or May.

Results from the analysis of Vanderploeg and Scavia's selectivity coefficient, W'_i , revealed that there was a high preference for cyclopoid copepods, calanoid copepods, and *Bosmina* in the different sampled months. The highest

Table 1. Number of *Sardinella tawilis* caught using gill nets from Napayun I. each mo

Mo	Sample size	Length groups (cm)				
		5.01-7.0	7.01-9.0	9.01-11.0	11.01-13.0	13.01-15.0
July	37	0	0	21	16	0
Aug.	48	2	1	23	21	1
Sept.	35	0	1	25	9	0
Nov.	48	1	1	34	12	0
Dec.	48	0	1	26	21	0
Jan.	48	0	0	2	46	0
Feb.	48	0	0	8	40	0
Apr.	47	0	1	12	33	1
May	45	0	0	12	33	0
June	45	1	0	12	31	1
Total	449					

preferences were observed for cyclopoid copepods in July, Aug., Nov., and May, while calanoid copepods showed the highest W'_i values in Jan., Feb., Apr., May, and June. *Bosmina* was noted to be the most preferred prey in Dec. A high preference for nauplii was observed in July ($W'_i = 0.84$), while low or no preference was shown in the remaining months. Low or no preference was

observed for the remaining 4 prey items (Table 2).

DISCUSSION

The diet of *S. tawilis* was dominated by zooplankton. This is similar to previous unpublished reports by Castillo et al. (1975), Flores

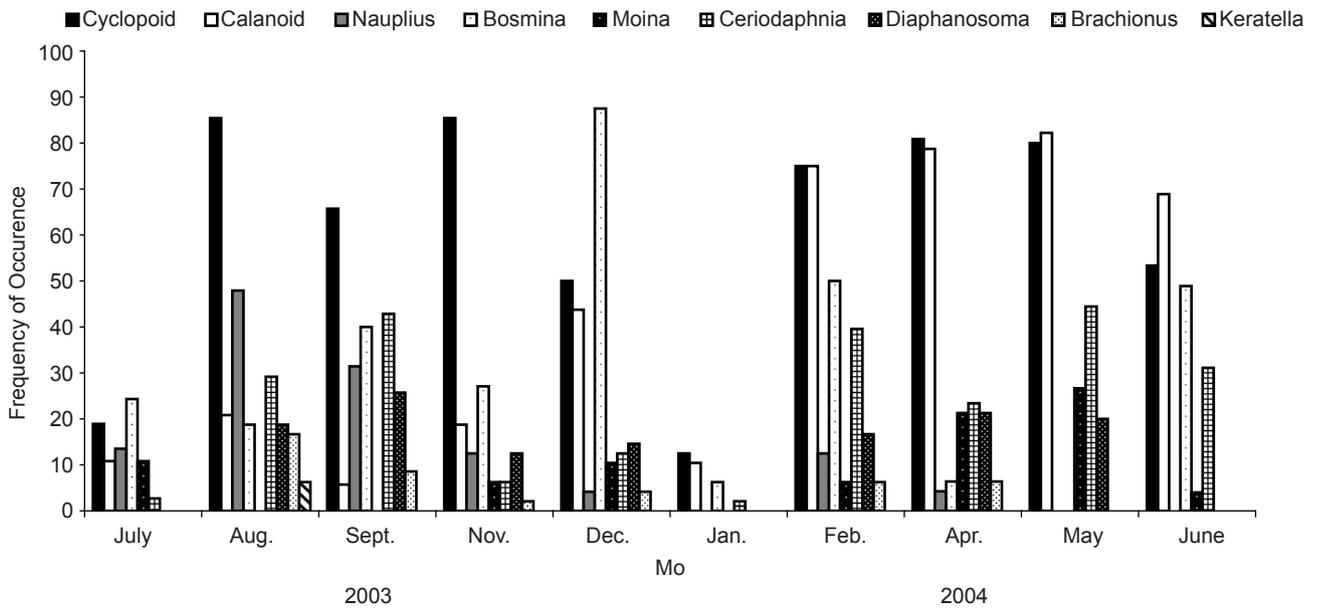


Fig. 2. Percent frequency of occurrence of the food items arranged by major taxonomic groups.

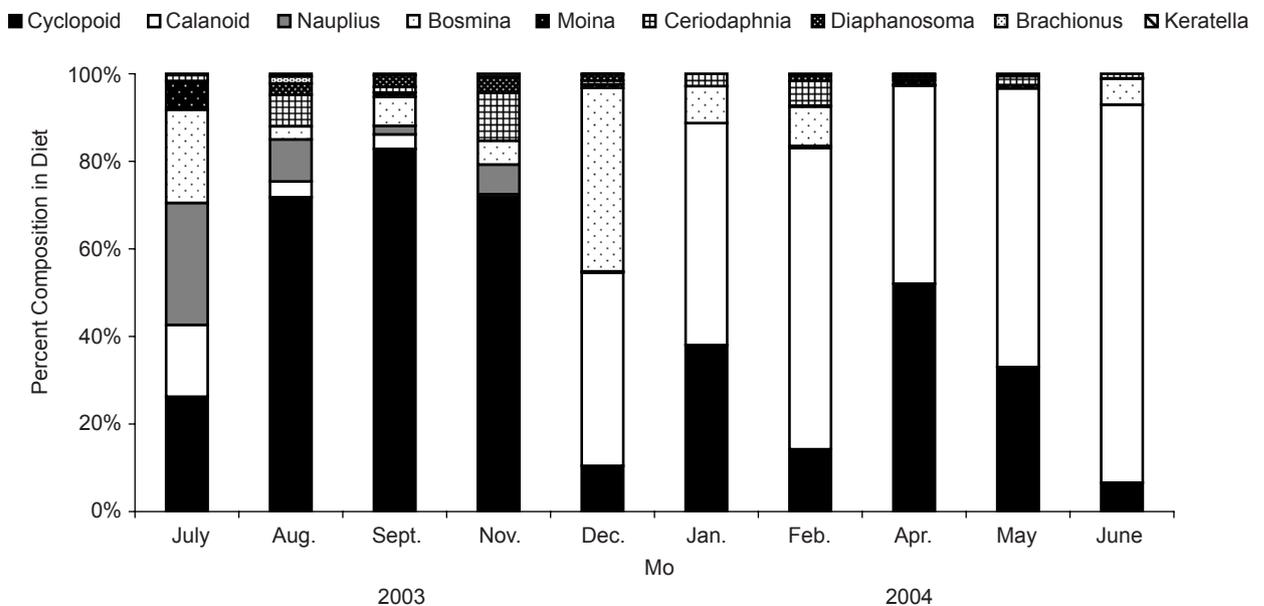


Fig. 3. Percent contribution of the different prey items found in the diet of *Sardinella tawilis*.

numerous of the prey items seen in the stomachs of the *S. tawilis*, respectively. Visual cues and large sizes might have caused the preference of *S. tawilis* for cyclopoid and calanoid copepods in spite of their having greater swimming speeds and escape abilities compared to cladocerans and rotifers. Copepods are more visible to fish compared to cladocerans (Nunn et al. 2007). Planktivorous fish were also noted to feed on the largest, most visibly conspicuous prey, which includes large cladocerans and copepods (Brooks and Dodson 1965). This was also observed in the alewife *Alosa pseudoharengus* when it was observed to selectively feed on larger zooplankton species and the largest individuals within a species (Good and Cargnelli 2004). This was further noted to drastically reduce zooplankton size, abundance, and community structure through intense size-selective predation. The result was a zooplankton community dominated by smaller-bodied organisms. The zooplankton samples collected from Taal Lake in this study were also observed to be dominated by small-bodied organisms such as nauplius larvae and the rotifer, *Brachionus* sp., particularly during the latter sampling months. Predators can reduce the abundance of their prey to the point of exclusion and may facilitate the establishment of other species (Brooks and Dodson 1965). A similar effect on the zooplankton community was observed in Black Pond, NY, USA, when alewives were introduced as forage for landlocked Atlantic salmon, *Salmo salar*. The larger zooplankton that were abundant in 1958 had been replaced by small forms by 1966, which indicated that the alewives were able to eliminate large zooplankton species from the pond through selective feeding (Good and Cargnelli 2004).

The sardine consumed the highest amounts of cyclopoid and calanoid copepods during Apr. and May, in spite of the abundance of *Brachionus* sp. in the environment and the lower numbers of copepods observed during those months. The high selectivity coefficients for calanoids in Jan., Feb., Apr., May, and June could also be 1 cause for the lower percent contribution of calanoids to the overall zooplankton density compared to earlier months, when the preference for calanoids was not as high. Zooplankton biomass and composition are regulated by size-selective predation, and fish are known to select the largest, most visibly conspicuous prey in lakes and ponds. This can lead to an increase in the density of small individuals or species such as rotifers (Pagano et al. 2003, Rettig 2003, Wissel et al. 2003).

This coincided with months noted in previous studies to be the peak spawning season of *S. tawilis* (Aypa et al. 1991, Joson-Pagulayan 1999). Calanoid copepods were more preferred by *S. tawilis* compared to other prey during that time. The importance of consuming larger prey in preparation for spawning is evident by the preference of *S. tawilis* for calanoid copepods during these months. Aside from this, calanoid copepods swim longer and more consistently than cyclopoid copepods, making them easier to capture (Nunn et al. 2007). This may be 1 advantage in consuming more calanoids since they provide maximum energy gain per unit of handling time (Nunn et al. 2007), and fish would then be able to use most of their energy reserves for spawning. Adipose tissues were found to be bigger in gravid *S. tawilis* compared to spent individuals (Joson-Pagulayan, pers. comm.).

Visual cues such as eyespots and pigmentation patterns can also guide planktivores in selecting prey (Drenner and McComas 1980). *Sardinella tawilis* may rely on such cues as it feeds on cladocerans which possess conspicuous eyespots. Of the 3 genera of cladocerans found in the diet of *S. tawilis*, *Bosmina* was observed to be the most preferred prey. Bosminids have been noted to be bigger and less transparent than other daphniids, and their circular shapes are also more efficiently detected by chasing fish (Eggers 1977). A preference for *Bosmina* was also observed to have occurred at a time of a lower preference for calanoid and cyclopoid copepods.

This study provides more insights into the zooplanktivory of *Sardinella tawilis* which was observed from samples obtained in 10 mo of a 12 mo period. We also established that *S. tawilis* has a preference for copepods. This was attributed to its ability to select its prey based on its large size and other visual cues regardless of the abundance of smaller alternatives.

Acknowledgments: The main author would like to thank Drs. Pedro and Rosalinda Papa, the Office of the Vice Rector for Academic Affairs and the College of Science, University of Santo Tomas, Manila, the Philippines for financial support during various stages of this research. We would also like to express our gratitude to Mr. Enzo Ingle, of Balete, Batangas for assistance during fieldwork; the Research Center for the Natural Sciences and the Department of Biological Sciences, University of Santo Tomas, Manila, the Philippines for the use of their laboratories and equipment; and to Dr. Jodi

Sedlock of Lawrence Univ., U.S.A. for valuable comments on and suggestions for the manuscript.

REFERENCES

- Ayza S, A Jr Galicia, ES Lapasaran. 1991. A contribution to the biology of *Harengula tawilis* in Taal Lake, Batangas. Quezon City, The Philippines: Bureau of Fisheries and Aquatic Resources Completion Report to the Department of Agriculture, Bureau of Agricultural Research.
- Brooks JL, SI Dodson. 1965. Predation, body size and composition of the plankton. *Science* **150**: 28-35.
- Cabalona R, E Estrella, A Navalta, A Oplado, E Sanchez. 2003. A study of the stomach contents of *Sardinella tawilis*. BS Biology thesis, Univ. of Santo Tomas, Manila, the Philippines.
- Castillo BB, AS Castillo, CL Gonzales. 1975. Tawilis fishery resources investigation of Taal Lake. *In* Philippine Council for Agriculture and Resources Research Fisheries Forum. Philippine Council for Agriculture and Resources Research, Los Baños, Laguna, the Philippines, pp. 75-98.
- Drenner RW, SK McComas. 1980. The role of zooplankton escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. Evolution and ecology of zooplankton communities. Special Symp. Am. Soc. Limnol. Oceanogr. **3**: 587-595.
- Eggers DM. 1977. The nature of prey selection by planktivorous fish. *Ecology* **58**: 46-59.
- Flores CB. 1997. Stomach contents of the freshwater *Sardinella*, *Sardinella tawilis* (Family Clupeidae) caught at night from Lake Taal (Batangas, Philippines). BS Biology thesis, Univ. of the Philippines, Diliman, Quezon City, the Philippines.
- Froese R, D Pauly, eds. 2003. FishBase. World Wide Web electronic publication. Available at <http://www.fishbase.org> vers. 26.
- Galbraith M, J Schneider. 2000. Sampling zooplankton in lakes. *In* JC Schneider, ed. Manual of fisheries survey methods II with periodic updates. Ann Arbor, MI: Michigan Department of Natural Resources, Fisheries Special Report 25, pp. 1-4.
- Gerking SD. 1994. Feeding ecology of fish. San Diego, CA: Academic Press.
- Good S, L Cargnelli. 2004. Alternative strategies for the management of non-indigenous alewives in Lake St. Catherine, Vermont. Pittsford, VT: Department of Fish and Wildlife, 74 pp.
- Guerrero R III. 2002. The fisheries of Lake Taal and its management for sustainability. Proceedings of the FISHSTRAT Users Meeting in Bangkok, Thailand. Bangkok, Thailand, 36 pp.
- Herre AW. 1927. Four new fishes from Lake Taal (Bombon). *Phil. J. Sci.* **34**: 273-279.
- Joson-Pagulayan AE. 1999. Aspects of the reproductive biology of the *Sardinella tawilis* (Herre, 1927) (Pisces: Clupeidae). MS Biology thesis, Univ. of the Philippines, Diliman, the Philippines.
- Kahilainen K. 2004. Ecology of sympatric whitefish (*Coregonus lavaretus* (L.)) forms in a subarctic lake. PhD Biology dissertation, Univ. of Helsinki, Helsinki, Finland.
- Kahilainen K, E Alajarvi, H Lehtonen. 2005. Planktivory and diet-overlap of densely rakered whitefish (*Coregonus lavaretus* (L.)) in a subarctic lake. *Ecol. Freshw. Fish* **14**: 50-58.
- Lagda M, N Tresnado, A Diesmos. 2003. Biology, exploitation and conservation assessments of endemic vertebrate species in Lake Taal, Luzon Island, Philippines. Technical paper. Project funded by North England Zoological Society and Fauna and Flora International, 50 pp.
- Lazzaro X. 1987. A review of planktivorous fishes: their evolution, feeding behaviors, selectivities and impacts. *Hydrobiologia* **146**: 97-167.
- Liao H, CL Pierce, JG Larscheid. 2002. Diet dynamics of the adult piscivorous fish community in Spirit Lake, Iowa, USA 1995-1997. *Ecol. Freshw. Fish* **11**: 178-189.
- Mamaril AC. 2001. Translocation of the clupeid *Sardinella tawilis* to another lake in the Philippines: a proposal and ecological considerations. *In* CB Santiago, ML Cuvin-Aralar, ZU Basiao, eds. Conservation and Ecological Management of Philippine Lakes in relation to Fisheries and Aquaculture. Quezon City, the Philippines: SEAFDEC; PCAMRD, and BFAR, pp. 133-147.
- Mamaril AC, CH Fernando. 1978. Freshwater zooplankton of the Philippines: Rotifera, Cladocera and Copepoda. *Nat. Appl. Sci. Bull.* **30**: 109-221.
- Mummert JR, RW Drenner. 1986. Effect of fish size on the filtering efficiency and selective particle ingestion of a filter-feeding clupeid. *Trans. Am. Fish. Soc.* **115**: 522-528.
- Mutia MT, L Magistrado, F Muyot. 2001. Assessment of Lake Taal fisheries. Taal, Batangas, the Philippines: National Fisheries Biological Center, pp. 1-17.
- Northcote TG. 1988. Fish in the structure and function of freshwater ecosystems: a top-down view. *Can. J. Fish. Aquat. Sci.* **45**: 361-379.
- Nunn AD, JP Harvey, IG Cowx. 2007. The food and feeding relationships of larval and 0+ year juvenile fishes in lowland rivers and connected waterbodies. II. Prey selection and the influence of gape. *J. Fish Biol.* **70**: 743-757.
- Olson NW, CP Paukert, DW Willis, JA Klammer. 2003. Prey selection and diets of bluegill *Lepomis macrochirus* with differing population characteristics in two Nebraska natural lakes. *Fisheries Manage. Ecol.* **10**: 31-40.
- Ong PS, LE Afuang, RG Rosell-Ambal, eds. 2002. Philippine biodiversity conservation priorities: a second iteration of the National Biodiversity Strategy and Action Plan. Quezon City, the Philippines: Department of Environment and Natural Resources – Protected Areas and Wildlife Bureau, Conservation International-Philippines, Biodiversity Conservation Program – Univ. of the Philippines Center for Integrative and Development Studies, and Foundation for Philippine Environment, 113 pp.
- Pagano M, MA Koffi, P Cecchi, D Corbin, G Champalbert, L Saint-Jean. 2003. An experimental study of the effects of nutrient supply and *Chaoborus* predation on zooplankton communities of a shallow tropical reservoir (Lake Brobo, Ivory Coast). *Freshwater Biol.* **48**: 1379-1395.
- Papa RS. 2005. A study on the zooplankton diet of freshwater sardine, *Sardinella tawilis* (Herre 1927) in Lake Taal, Batangas. MS Biological Sciences thesis, Univ. of Santo Tomas, Manila, the Philippines, 74 pp.
- Pothoven SA, HA Vanderploeg, JF Cavaletto, DM Krueger, DM Mason, SB Brandt. 2007. Alewife planktivory controls the abundance of two invasive predatory cladocerans in Lake Michigan. *Freshwater Biol.* **52**: 561-573.

- Rettig JE. 2003. Zooplankton responses to predation by larval bluegill: an enclosure experiment. *Freshwater Biol.* **48**: 636-648.
- Turesson H, A Persson, C Bronmark. 2002. Prey size selection in piscivorous pikeperch (*Stizosteidon lucioperca*) includes active prey choice. *Ecol. Freshw. Fish* **11**: 223-233.
- Villalobos H, R Rodriguez-Sanchez. 2002. Pattern of increase in gill raker number of the California sardine. *J. Fish Biol.* **60**: 256-259.
- Villanueva LS, AP Luistro, CS Calabig. 1995. Assessment of Lake Taal capture fisheries with emphasis on the exploitation of *Harengula tawilis*. Tanauan, Batangas, the Philippines: STIARC-Experimental Farm for Fisheries.
- Windell JT. 1968. Food analysis and rate of digestion. *In* WE Ricker, ed. *Methods for assessment of fish production*. Oxford, UK and Edinburgh: International Biological Programme. Blackwell Scientific Publications, pp. 197-198.
- Wissel B, WJ Boeing, CW Ramcharan. 2003. Effects of water color on predation regimes and zooplankton assemblages in freshwater lakes. *Limnol. Oceanogr.* **48**: 1965-1976.