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Lavnun abundance: how changes may affect consumption of Lake Kinneret zooplankton

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with 8 figures, 3 tables and 1 appendix

Abstract: The Israeli Water Commissioner has subsidized the removal from Lake Kinneret of lavnun, the endemic cyprinid *Acanthobrama terraesanctae,* since the 1994-1995 fishing season. One of the rationales for the removal program is that reduced consumption of zooplankton by lavnun will increase production of zooplankton and their subsequent consumption of phytoplankton. Here, we use acoustic measures of fish population distribution and abundance, and bioenergetic and spatial modeling to assess the effect of lavnun removal on potential consumption of zooplankton in Lake Kinneret. Two lakewide acoustic surveys were made (in April and June 1998) with a dual-beam acoustic system to measure the fish population. On each survey a salinity and temperature profiler was used to measure the water temperature field in the lake. We used these data and spatially explicit bioenergetic models to determine potential consumption by fish. The size distribution and abundance of the measured fish population were manipulated to calculate potential consumption under various scenarios. Geostatistical interpolation of spatial models provided lakewide measures of fish abundance and potential consumption. Our analysis suggests that the lavnun dilution program has the desired effect of substantially reducing potential zooplankton consumption by lavnun. Further, model scenarios indicated that targeting smaller fish in the removal program could produce an even greater decrease in potential zooplankton consumption than that so far achieved by either the dilution program or by commercial fishing.

Introduction

Lake Kinneret, Israel, is the nation's only natural body of freshwater and as such the lake is a classic example of a multi-purpose natural resource. Lake Kinneret supports fisheries, tourism, and recreation, and most importantly, it provides water for irrigation and domestic con-

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sumption. Waters from Lake Kinneret supply 25-35% of the total water needs of the state of Israel (BEN-TUVIA et al. 1992, BERMAN 1994). Although multiple stake-holders place demands on Lake Kinneret, the National Water Carrier primarily manages the lake as a source of drinking water (GOPHEN 1988, BEN-TUVIA et al. 1992), and therefore, maintaining high water quality in the lake is of utmost importance.

The dinoflagellate *Peridinium* and nanoplankton represent potential threats to water quality in Lake Kinneret (GOPHEN 1988, BERMAN 1994). At present, chlorination and damage inflicted to cells by the pumping process easily control *Peridinium*, while nutrient availability and grazing by zooplankton in the lake control the nanoplankton populations (GOPHEN 1988). Controlling inflows from the agricultural regions to the north of Lake Kinneret have reduced the amount of nutrients input to the lake in recent years and helped reduce nanoplankton abundance (BERMAN 1994). Planktivorous fishes dominate the Kinneret fishery and fishery management has attempted to achieve two seemingly contradictory goals: to optimize economic returns from fishing and to reduce the consumption of zooplankton by planktivorous fish so that high levels of zooplankton grazing on nanoplankton can be maintained.

Pelagic fish populations of Lake Kinneret are dominated by the endemic cyprinid, *Acanthobrama terraesanctae* Steinitz (previously *Mirogrex terraesanctae*), known locally as lavnun, bleak or the Kinneret sardine (here we use lavnun throughout). Lavnun are almost exclusively planktivorous (GOPHEN et al. 1990), and comprise >50% of total fish biomass, about 50% of fish catch and > 80% of total fish numbers (WALLINE et al. 1992, WALLINE et al. 1993). They are relatively short-lived and small fish, reaching maturity at an age of about 2 years and a size of 9-10 cm (OSTROVSKY & WALLINE 1999). Lavnun apparently have had a strong effect on the zooplankton population in Lake Kinneret. Decreases in the size of zooplankton and a long-term decline in zooplankton abundance have been attributed to increased predation by fish, particularly lavnun (GOPHEN et al. 1990).

Managers of the National Water Carrier are concerned with lavnun because of their effect on water quality through top-down or consumer-controlled effects on the ecosystem (CARPENTER & KITCHELL 1993). Lavnun populations have undergone unusual changes in the first half of the 1990's. A highly successful recruitment event during the flood winter 1991-1992 led to a two- to three-fold increase in the abundance of sub-commercial (< 12 cm) sized lavnun. It was feared that this large year-class would increase predation pressure on zooplankton. In 1993-1994 the annual average biomasses of Cladocera and large Copepoda, the main components of the lavnun diet, were at the lowest levels ever observed in Lake Kinneret (GOPHEN, pers. comm.). In addition, significant deterioration in lavnun body condition was found at the end of 1993 (OSTROVSKY & WALLINE 1999b), apparently due to poor feeding conditions.

Large lavnun ostensibly disappeared from Lake Kinneret in 1993 and their loss led to collapse of the lavnun fishery (HAMBRIGHT & SHAPIRO 1997). Commercial sized (length ≥ 12 cm) lavnun, which have higher energetic demands during the spawning/fishing season, were most strongly affected by the lack of food in 1993. Length-frequency data collected from purse seine sampling in 1993 and 1994 show a remarkable difference between the two time periods (Fig. 1). There is a clear loss of large fishes between 1993 and 1994 that coincides with the collapse of the lavnun fishery (OSTROVSKY & WALLINE 2000). Hereafter, we will refer to this collapse of the lavnun fishery and the appearance of large numbers of sub-commercial sized lavnun as the "lavnun crisis".

In an attempt to remedy this situation, the Israel Water Commissioner instituted a lavnun "dilution" program aimed at reducing the abundance of sub-commercial sized lavnun in the

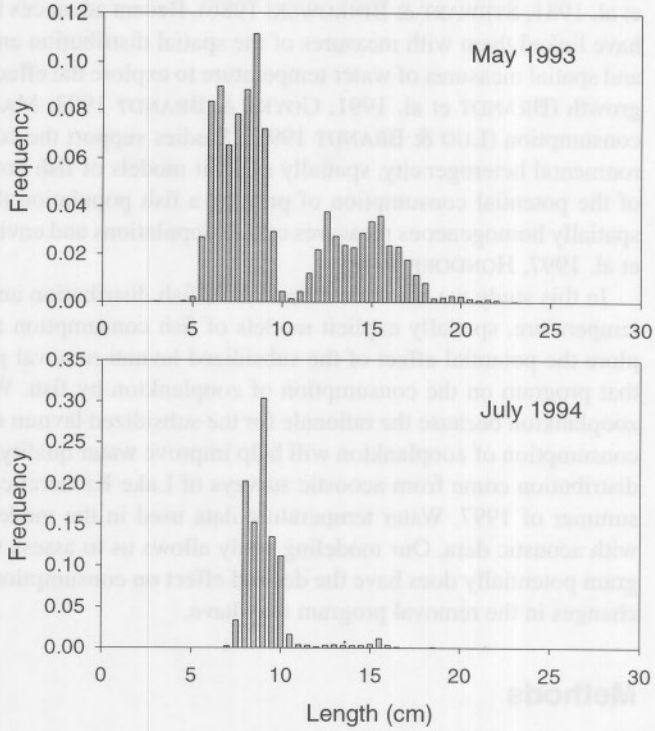

Fig. 1. Length frequency distributions of lavnun in May 1993 and June 1994. The loss of large fish in 1994 lead to the "lavnun crisis."

lake. The program's primary goal was to prevent deterioration of water quality caused by reduced abundance of zooplankton. Starting in the winter of 1994-95, the removal of small lavnun was accomplished by paying commercial fishermen to catch lavnun with a regular purse seine net (20-mm stretch with 28-mm stretch bunt), but with an added 10-mm stretch liner outside the bunt to retain fish smaller than commercial size. The plan was to remove a large fraction (at least 1,000 tons, or about 1/3) of the biomass during the winter, thus reducing predation pressure on zooplankton during the spring phytoplankton bloom. It was expected that this reduction would result in an enhanced zooplankton population during the period when phytoplankton production normally is highest.

Reducing the lavnun biomass in Lake Kinnerte appears to reduce predation on zooplankton and lead to increased zooplankton populations. In 1995 and 1996 lavnun were affected by a combination of enhanced natural mortality of large lavnun from low food resources, commercial fishing, and the subsidized lavnun dilution program. Simultaneously, the biomass of Cladocera and Copepoda increased by a factor of 1.5-2.0 (GOPHEN pers. comm.). The condition of lavnun remaining in the lake during this period of high zooplankton biomass was much improved over that seen during the immediately previous years (OSTROVSKY & WALLINE 2000). The improved condition of lavnun during 1995 and 1996 provides additional support for the hypothesis that the loss of large lavnun during the "lavnun crisis" of 1993 and 1994 could have resulted from low food availability.

Bioenergetic models that describe fish consumption, metabolic costs and growth have been valuable tools to study the role of fish in ecosystem dynamics (KITCHELL et al. 1977, STEWART

et al. 1981, STEWART & BINKOWSKI 1986). Recent advances in the use of bioenergetic models have linked them with measures of the spatial distribution and abundance of fish populations and spatial measures of water temperature to explore the effect of spatial heterogeneity on fish growth (BRANDT et al. 1991, GOYKE & BRANDT 1993, MASON & BRANDT 1996) and prey consumption (LUO & BRANDT 1993). Studies support the contention that by capturing environmental heterogeneity, spatially explicit models of fish growth produce different measures of the potential consumption of prey by a fish population than do studies that use average, spatially homogeneous measures of fish populations and environmental characteristics (RAND et al. 1997, HONDORP 1998).

In this study we combine measures of fish distribution and abundance, measures of water temperature, spatially explicit models of fish consumption and modeling simulations to explore the potential effect of the subsidized lavnun removal program and possible changes in that program on the consumption of zooplankton by fish. We focus on fish consumption of zooplankton because the rationale for the subsidized lavnun removal program is that reducing consumption of zooplankton will help improve water quality. The data on fish abundance and distribution come from acoustic surveys of Lake Kinneret conducted in the spring and early summer of 1997. Water temperature data used in the model were collected simultaneously with acoustic data. Our modeling study allows us to assess whether the lavnun removal program potentially does have the desired effect on consumption of zooplankton and what effect changes in the removal program may have.

Methods

Data Collection

We collected acoustic measures of fish biomass and water temperature profiles along fourteen transects covering the whole of Lake Kinneret on the nights of 6 April 1998 and 18 June 1998. The set of fourteen transects provided the best possible coverage of the lake that could be accomplished in a single night of sampling (KALIKHMAN et al. 1992, WALLINE et al. 1992). We collected data along twelve transects each 2.5 km long, perpendicular to the shoreline, and along two, 1.3 km, north-south transects sampled at locations near the center of the lake. Temperature profiles were recorded in the middle and at the end of each transect with an Applied Microsystems salinity-temperature-depth sampler.

During the June cruise, purse seine net samples were collected from a fishing vessel at 6 locations by the Israel Fisheries Department. The net used was the same as used for the dilution program (see above). Fish in these samples were identified and their total length measured to the nearest 0.25 cm.

We collected the acoustic data with a Biosonics 102 dual-beam echosounder operating at 120 kHz, pulse width 0.4 ms, and ping rate of 5 pings sec^{-1}. The transducer was towed on a fin from the RV Hermona at a speed of approximately 3 m sec^{-1}. The system was calibrated with a 33-mm diameter standard target with known target strength (-40.6 dB) before sampling (FOOTE 1982). Data from the wide and narrow beams were recorded on digital audio tape and replayed in the laboratory to convert the analog signal to digital data using a Biosonics PC-based digitizing card and software. Tapes analyzed for dual-beam target strength (TS) analysis (recorded with 40 $\log_{10}$ R TVG) were played back a second time and digitized using the echo integration module of the Biosonics program (BURCZYNSKI et al. 1987). For each transect the

echo integration data were analyzed to produce a two-dimensional array of relative fish biomass averaged within cells of a size 0.5 m depth X 12 m distance (20 pings).

Digitized acoustic data files were further analyzed with DEVIS (Digital Echo Visualization Information System, JECH & LUO in press) to produce data arrays of average fish length (mm) and density (number m^{-3}) for each 0.5 m X 12 m cell in the array. In order to convert acoustic size to fish length, we used the TS-fish length relationship (TS= 25 log (length) – 73, TS in dB, length in cm) currently in use in acoustic surveys of Lake Kinneret. This relationship was derived in earlier surveys from a comparison of TS distributions with length-frequency distributions of lavnun in purse-seine net samples (LINDEM & SANDLUM 1984).

DEVIS uses the TS-fish length relationship to report biomass and abundance in user-specified size classes. We divided targets into three size classes: the smallest was chosen to correspond to the size of juvenile lavnun (12-49 mm, -70 to -55.5 dB), the medium-sized class (50-180 mm, -55.5 to - 41.6 dB) to adult and juvenile lavnun, and the largest (length >180 mm, > -41.6 dB) to tilapia-like cichlids. The division between the lavnun and tilapia size groups was determined from considerations of the maximum size of lavnun observed in purse seine catches, and the maximum size of adult lavnun as determined from growth analysis (OSTROVSKY & WALLINE 1999). Nearly all were smaller than 18 cm and the largest ever observed were less than 25 cm.

The size-segregated fish length and density data were used in spatial models of fish consumption of zooplankton. We computed lakewide measures of fish abundance, water temperature and potential consumption of zooplankton (see below) by summarizing the data from all transects and using kriging methods (PETITGAS 1993) to interpolate lakewide measures. Areal measures of biomass and fish numerical abundance for each transect were calculated by summing over depth for each horizontal bin, to produce vectors of areal biomass (g m^{-2}) and density (number m^{-2}). Average biomass and density for each quarter transect was then computed. The four points for each transect were assigned their appropriate locations on a map of Lake Kinneret and these data provided the required inputs for the kriging interpolation of lakewide measures. We obtained the parameters for kriging (nugget = 0, range = 4) from variogram analysis of similar, previously collected data sets using EVA2 software (PETITGAS & LAFONT 1997). The analysis showed that a spherical variogram model fit the test data well and, therefore, this was used in all interpolations reported here. Summing biomass or numbers across all locations of the interpolated surface produced an estimate of total fish biomass and abundance for the entire lake.

Modeling zooplankton consumption by fish

The primary output of our modeling effort is an estimate of the total potential consumption of zooplankton by fish in Lake Kinneret. To model consumption of zooplankton by pelagic fishes, we applied spatially explicit bioenergetic models (BRANDT et al. 1992) to transect data of the April and June surveys of Lake Kinneret. Lake-wide estimates of maximum potential zooplankton consumption by fish were computed by interpolating the maximum consumption modeled for each transect using the same methods as described earlier for interpolating fish abundance and biomass. Summing the consumption of zooplankton across all locations of the interpolated surface produces an estimate of total potential consumption of zooplankton by fish in Lake Kinneret.

The spatial distribution of fish size and abundance and measured water temperatures in each of the fourteen transects of the April and June 1998 surveys of Lake Kinneret provided the input data used to model consumption of zooplankton by pelagic fish. The calculation of potential consumption used the "Wisconsin" bioenergetics models, specifically, maximum consumption (C_{max}) of fish in each cell of the transect (HANSON et al. 1997). C_{max} is a species-specific function of fish weight and water temperature (see Appendix) and represents grams wet weight of prey consumed per gram wet weight of fish body weight per day ($g\ g^{-1}\ d^{-1}$). We converted fish length (L, mm), derived from acoustic data, to fish weight (W, g wet weight) with the exponential relationship, $W = a \cdot L^b$, and parameter values appropriate for lavnun (a= $1.047 \cdot e^{-6}$, b=3.42); (OSTROVSKY & WALLINE 1999) and tilapia (a=$1.13 \cdot e^{-5}$, b=3.12); (OSTROVSKY, unpublished data) size classes. Fish weight in each cell of the acoustic transect was based on the average length of fish in each size class as determined by the TS-fish length relationship. Total consumption by fish within a transect cell (g wet weight d^{-1}) was calculated as the product of maximum consumption (C_{max}, $g\ g^{-1}\ d^{-1}$) and the measured biomass of fish (g). Spatial models of zooplankton consumption by fish were created for each transect surveyed in April and June 1998. The calculation of zooplankton consumption used in this research were made with GRP Map Maker software (TYLER 1998).

Model Simulations

To assess the effect of changes in the lavnun population on consumption of zooplankton, we adjusted the abundance of adult lavnun in selected size ranges and calculated lakewide maximum zooplankton consumption using the methods above. In doing this we kept the spatial distribution of fish and water temperature constant. We designed the adjustments in adult lavnun abundance and size distribution to estimate lavnun populations under four different scenarios: 1) the "lavnun crisis", 2) if the dilution program did not exist, 3) if neither the dilution program nor fishing existed, and 4) if the dilution program were adjusted to target smaller lavnun.

To adjust the lavnun population for each model simulation, we changed the biomass of fish in specified size ranges in all transects of the April and June lakewide surveys. All adjustments were made only in the adult lavnun size class (50-180 mm). Adult lavnun abundance (number m^{-3}) was altered in each cell so that total lake-wide biomass was changed to the desired level for the simulation. This procedure retained the length-frequency distribution of lavnun within the sizes of adult lavnun affected in the simulation and accounted for the fact that the relationship between fish number and biomass is not linear as fish size increases.

The four scenarios that we model represent past changes in the lavnun population and potential future changes that could result from altering management practices (Table 1). The size classes of adult lavnun affected in the model simulations differed between the April and June surveys to account for lavnun growth between the two sampling periods. The biomass added back in June was calculated by computing the number of fish that would have been in the population if no fish had been removed via the dilution program. The number of those fish remaining in June was determined by applying a mortality rate of 0.23 for the two month period (annual Z = 1.52, OSTROVSKY & WALLINE 1999) to the number of fish added to the population in April. The weight of individual lavnun was increased to account for a growth rate of 0.395 $g\ g^{-1}$ for the two month period. This growth rate was determined by the average difference in weight of lavnun measured in the April and June acoustic surveys. Total biomass added to the June data is the sum of the weights of survivors from the 750 tons returned in April.

Table 1. Summary of changes in the abundance and size distribution of lavnun (50-180 mm) from the baseline data to create the four modeling scenarios.

	biomass change from 1998 data (tons)		lavnun sizes affected (mm)	
Simulation name	April	June	April	June
"Lavnun Crisis"	0	0	100[1]	112[1]
No Dilution	750	920	85-155	85-155
No Dilution, No Fishing	1000	1227	85-180[2]	
85-180[2]				
New Dilution[3]	0	0	50-155	50-155

[1] To model the "lavnun crisis", the biomass of lavnun from sizes greater than that indicated is removed and the same biomass is added to lavnun of sizes below the indicated size.

[2] Lavnun biomass was added in two steps, first to in the size range indicated in the "no dilution" simulation, and an additional amount added in sizes susceptible to the commercial fishery (110 mm in April, 112 mm in June).

[3] For the "new dilution" simulation, the lavnun population from the "no dilution" simulation had biomass removed in the size range indicated to produce a simulated lavnun population of the same biomass as was measured in the 1998 April and June surveys.

Lavnun Crisis: We adjusted the April and June 1998 lavnun biomass data to model the "lavnun crisis." We removed the biomass from all lavnun of lengths >100 mm for the April survey and >112 mm for the June survey. An equal biomass of lavnun was then returned to the model adult lavnun population in sizes <100 (April) and <112 mm (June), thus producing a shift in the size distribution of lavnun during the "crisis." We assumed no net change in model adult lavnun biomass between the "lavnun crisis" and the 1998 data because there are no data on actual biomass of adult lavnun in Kinneret during the crisis of '93-'94 that could be used for this scenario.

No Dilution: Biomass was added back to the1998 adult lavnun population data to simulate cancellation of the dilution program. To model the effect of halting the subsidized lavnun dilution program, we increased the biomass of adult lavnun in the 85-155 mm size range by 750 tons in April and 920 tons in June. We added biomass to adult lavnun in this size range because it was the same as the size range of lavnun removed through the subsidized dilution program in 1998 (J. SHAPIRO, Israel Department of Fisheries, pers. comm.). Also, we added back 750 tons of adult lavnun biomass because the dilution program is designed to remove 750-1,000 tons from Lake Kinneret between December and March each year according to protocols of the Kinneret Fishery Management Committee, Israel Department of Agriculture.

No Dilution, No fishing: To model the effect of discontinuing dilution and fishing effort on the lavnun population, we added lavnun biomass to the model adult lavnun populations generated for the "no dilution" simulation described above. An additional 250 tons (April) and 307 tons (June) were added to the data already adjusted to account for discontinuing the dilution program. The amount added back in April was the commercial catch of lavnun during the preceding fishing season (Israel Fishery Department) and the amount in June was the same 250 tons after applying mortality and growth as described above. The additional biomass was added to adult lavnun in the size range 110-180 mm, sizes typically taken by the lavnun fishery. Thus a total increase of 1,000 tons (April) and 1,227 tons (June) was added to the 1998

data on adult lavnun abundance to produce the model lavnun population for the no-dilution and no-fishing simulations.

New Dilution: To simulate the effect of changing the sizes of fish removed in the dilution program, we first returned the biomass removed by the current dilution program to the adult lavnun population and then removed the same biomass in a different size range. The adult lavnun population created in the "no dilution" scenario, i.e. adding 750 and 920 tons of lavnun back to the population measured in April and June 1998, respectively, provides our estimate of an "undiluted" adult lavnun population. To simulate a change in the mesh size of nets used in the dilution program, we then removed 750 and 920 tons of adult lavnun in the size range of 50-155 mm respectively from the April and June "undiluted" adult lavnun populations.

Results

Fish Biomass in Lake Kinneret

Acoustic surveys of fish abundance in April and June 1998 showed considerable differences in the biomass of fish in the three size classes (Fig. 2). In both April and June surveys, the lowest biomass fell into the juvenile size class (12-49 mm). The lavnun size class (50-180 mm) accounted for the greatest biomass of fish in April, but accounted for the second greatest biomass of fish in Lake Kinneret in June. The total biomass of fish in the lake was five times greater in June (3,688 tons) than it was in April (729 tons) (Fig. 2). The kriging analysis resulted in a coefficient of variation of 13% in April and 18% in June for the mean biomass of fish (all sizes combined).

The distribution of fish in Lake Kinneret varied considerably by size class in April, but the variation in distribution was much less noticeable in June (Fig. 3). Areas of highest fish biomass in April were generally in the southern half of the lake, but the transect with highest biomass differed among the three size classes of fish. In June, the northeast areas of the lake contained the highest biomass of fish for all size classes.

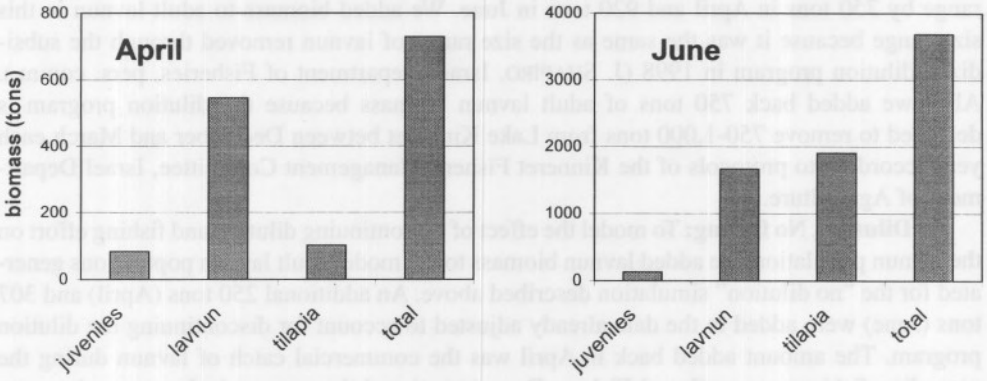

Fig. 2. Biomass of fish in three different size classes as determined from acoustic surveys conducted on 6 April 1998 and 18 June 1998. Fish population is separated into three size classes, juveniles (12-49 mm), lavnun (50-179 mm), and tilapia (≥180 mm).

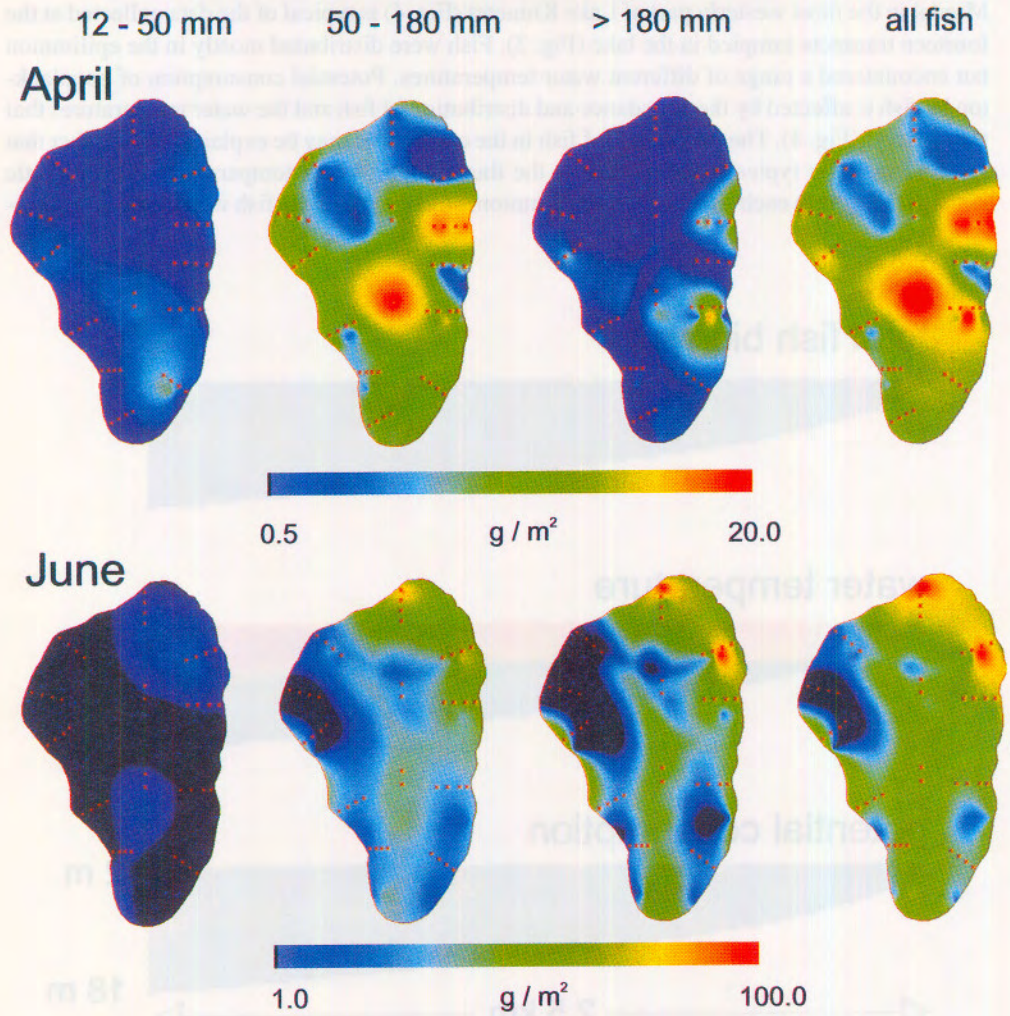

Fig. 3. Biomass distribution of fish in Lake Kinneret during the surveys of 6 April 1998 and 18 June 1998. Survey transects are indicated with red ≠ that indicate the quarter transects. Data are shown on a log scale.

As expected, nearly all fish in the purse seine samples were lavnun (92%). One of 2011 lavnun measured was greater than 18 cm in length (18.75). The mean and mode length of lavnun in the purse seine samples was 12.2 cm. The average TS measured at the 6 stations was –45.7 dB, equivalent to 12.4 cm when the TS-length equation we used was applied.

Potential consumption of zooplankton

Potential consumption of zooplankton by fish showed the effects of variation in the distribution and abundance of fish and variation in water temperatures. The transect collected near

Migdal in the most westerly part of Lake Kinneret (Fig. 4) is typical of the data collected at the fourteen transects sampled in the lake (Fig. 3). Fish were distributed mostly in the epilimnion but encountered a range of different water temperatures. Potential consumption of zooplankton by fish is affected by the abundance and distribution of fish and the water temperatures that they inhabit (Fig. 4). The prevalence of fish in the epilimnion may be explained by the fact that Lake Kinneret is typically anoxic below the thermocline. Water temperatures differed little among transects in each survey. In the epilimnion, where most of the fish were found, tempera-

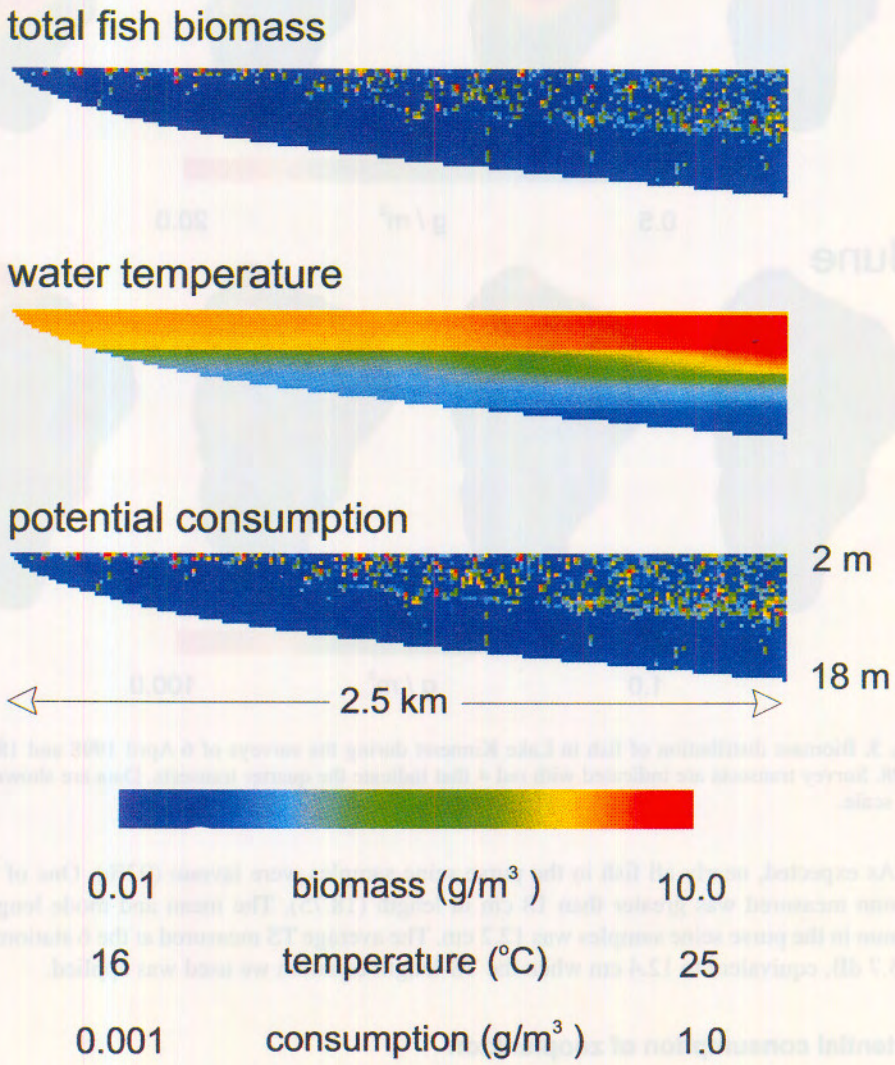

Fig. 4. Lavnun biomass, water temperature and potential consumption of zooplankton by lavnun on the Migdal transect (western most transect in Lake Kinneret) on 18 June 1998. Data are shown on a log scale.

tures were quite different between the surveys, with April temperatures up to 10°C colder than June temperatures.

Potential consumption of zooplankton by fish was more than three times greater during June (360 tons) than in April (97 tons) (Fig. 5). Adult lavnun had the greatest potential zooplankton consumption in both surveys even though they did not always constitute the greatest biomass (Fig. 2). The potential consumption of zooplankton by the tilapia class (>180 mm) was notably low in both April and June.

Model Simulations

Lavnun Crisis: Our modeling scenarios of the "lavnun crisis" attempted to simulate the loss of large adult lavnun from the population and the change in potential consumption of zooplankton resulting from a change in the size distribution of lavnun. Total biomass in the adult lavnun size class, which was the only class manipulated, remained the same before and after our manipulation. Shifting the biomass of adult lavnun from large to small fish caused an increase in the potential consumption in both surveys (Fig. 6). The increase in potential consumption was larger during June (28.7 tons) than during April (13.3 tons). However, the percentage increase was greater in April (24.3%) than in June (10.9%). This occurred despite the fact that in the April simulation only 8.6% of the total biomass was moved from large (>100 mm) to small fish while in June 11.1% of the total biomass was moved from large (>112 mm) to small fish.

No Dilution: Adding biomass of adult lavnun to the population sampled in April and June 1998 to simulate the absence of a dilution program increased the potential consumption of zooplankton (Fig. 7). For the simulation with no lavnun dilution program, a greater biomass of fish in the adult lavnun size class was added back to the measured June biomass than to the April biomass (920 tons as compared to 750 tons), but the relative increase was lower for June than for April (Table 2).

No Dilution, No Fishing: The simulation in which adult lavnun biomass was added to the 1998 data to replicate conditions with neither lavnun dilution nor fishing produced a change in

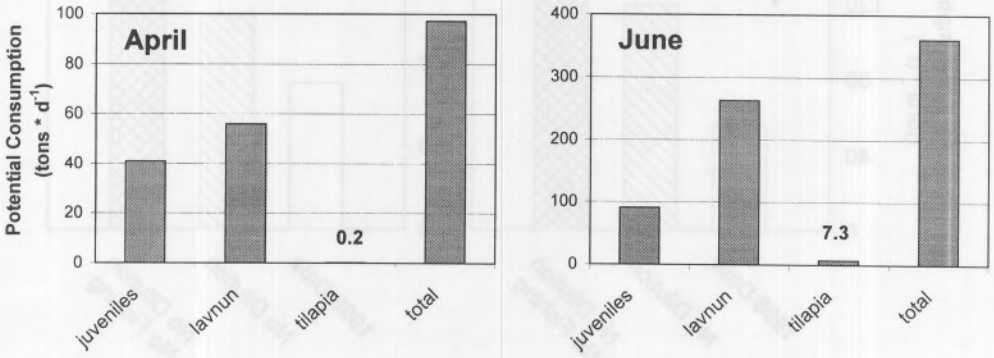

Fig. 5. Potential consumption of zooplankton by fish calculated for the whole of Lake Kinneret in the 6 April 1998 and 18 June 1998 surveys. Potential consumption presented for fish in each of the three size classes and for the total pelagic fish population.

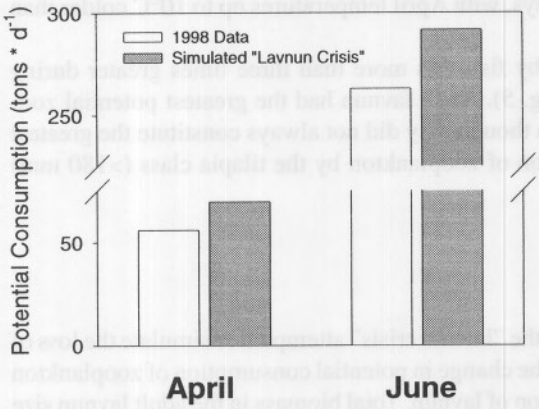

Fig. 6. Potential consumption of zooplankton by lavnun for the "lavnun crisis" model simulation.

the potential consumption of zooplankton that was generally similar to that observed for the No Dilution simulation (Fig. 7). The biomass added to the June data (1227 tons) was higher than that added to the April data (1000 tons), but the relative increase in biomass was lower in June than in April (Table 2). The increased lavnun biomass increased potential zooplankton consumption, but the relative increase in consumption was lower than the relative increase in biomass.

New Dilution: We simulated a change in the dilution program that targeted fish for removal from the lake smaller (50-155 mm) than those targeted currently (85-155 mm). The model simulation produced a decrease in the potential maximum consumption even though the biomass of lavnun removed was the same (Fig. 8). Again, the absolute difference in potential zooplankton consumption was greater for June (18.9 tons) than for April (6.0 tons), but the relative difference was greater in April (20.7% decrease) than in June (17.2% decrease).

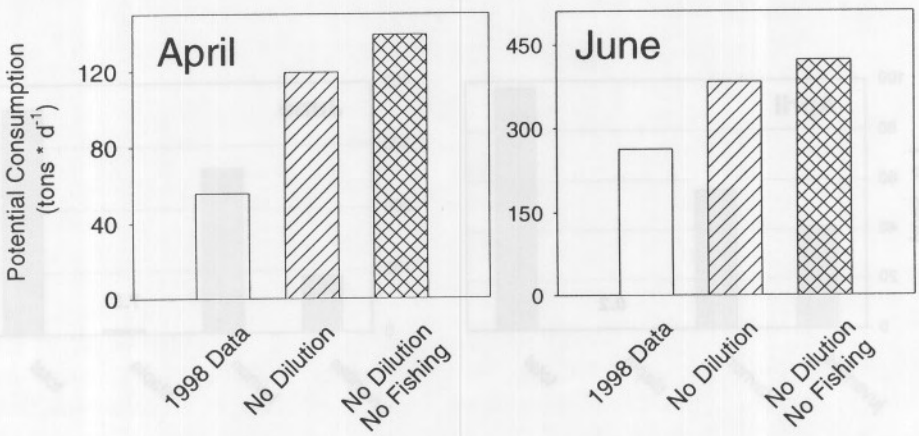

Fig. 7. Potential consumption of zooplankton by lavnun for the No Dilution and the No Dilution, No Fishing model simulations.

Table 2. Ratio of changes in lavnun biomass and potential consumption of zooplankton between 1998 data and model scenarios without lavnun dilution or fishing.

	No Dilution		No Dilution, No Fishing	
	April	June	April	June
Biomass	2.38	1.56	2.83	1.75
Consumption	2.13	1.46	2.48	1.61

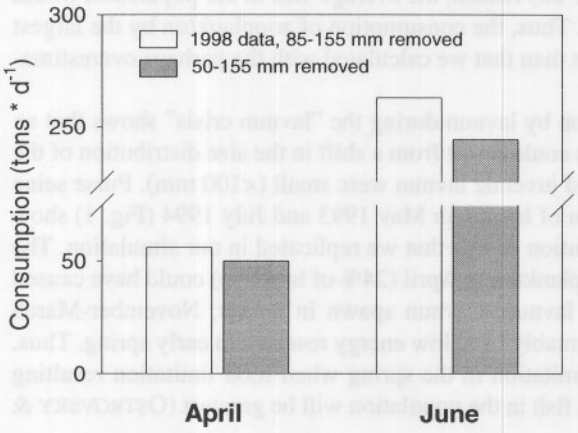

Fig. 8. Potential consumption of zooplankton by lavnun for the New Dilution model simulation.

Discussion

The data and model presented here show that of the three size classes of fish in Lake Kinneret, the middle size class (50-180 mm), comprised primarily of adult lavnun, has the greatest potential to affect zooplankton abundance. In both April and June 1998, the potential consumption of zooplankton was dominated by the fraction resulting from consumption by adult lavnun (April: 58%; June: 73%). Potential consumption of zooplankton by the largest class of fish (>180 mm) accounted for a trivial amount of the total consumption. This finding suggests that the effect of fish on zooplankton populations in Lake Kinneret will be dominated by the feeding of lavnun.

The division of the fish targets into size groups depends on the TS-length relationship. In recent years the length-frequency distribution of fish caught in the purse seine has been nearly always unimodal (for example, see bottom half of Fig. 1), as has the target strength frequency distribution. Thus, each survey produces only a single point for determination of this relationship by comparison of peaks in length and TS frequency distributions. This was the case also in June 1998. The length-frequency distribution was dominated by lavnun around 12 cm in length. Since the modes in the frequency distributions differ by only a few centimeters or dB's between seasons and years, the points are close to one another. As a result the TS-length relationship we used is most reliable for fish with lengths corresponding to those of the bulk of the adult lavnun population, that is around 10 to 12 cm total length. Future revisions of the TS-length relationship may result in changes affecting the largest size class as we have defined it, but should have only minor effects on the lavnun size class.

Clearly, criteria based solely on size cannot cleanly discriminate between species. The lavnun group will contain juveniles and small adults of other species, and the tilapia group will contain other large fish, such as silver carp. However, based on observations from purse seine catches, it was expected that the middle size class should be comprised mostly of lavnun and should include nearly all of the juvenile and adult lavnun population. This was certainly the case in June 1998, as can be seen from the dominance of lavnun in the purse seine catches.

The TS-length relation we used may have overestimated the population of large fish. Although the acoustic estimate of mean size (12.4 cm) in the population in June was close to the mean size (12.2 cm) observed in the purse seine net samples, the purse seine does not adequately sample fish smaller than 10 cm. For this reason, the average size in the population would be expected to be smaller than 12.2 cm. Thus, the consumption of zooplankton by the largest size class should be even less significant than that we calculated with the perhaps overestimated biomass of fish in this class.

Our model simulation of consumption by lavnun during the "lavnun crisis" shows that an increase in consumption of zooplankton could result from a shift in the size distribution of the lavnun population such that all adult and juvenile lavnun were small (<100 mm). Purse seine data of the length-frequency distribution of lavnun in May 1993 and July 1994 (Fig. 1) show the shift in the length-frequency distribution of fish that we replicated in our simulation. The increased potential consumption of zooplankton in April (24% of baseline) could have caused a short-term food limitation for adult lavnun. Lavnun spawn in winter, November-March (BEN-TUVIA et al. 1992), and will presumably have low energy reserves in early spring. Thus, large fish may be vulnerable to food limitation in the spring when food limitation resulting from an increase in the number of small fish in the population will be greatest (OSTROVSKY & WALLINE 2000).

Our simulation of the "lavnun crisis" did not include a change in the total fish biomass because data on the biomass of lavnun in Lake Kinneret during that period were not available. We consider our simulation to be a conservative approach to modeling the "lavnun crisis" because we affected a small fraction of the lavnun biomass. The 1993 purse seine data show that 35% of the lavnun had a length > 100 mm (OSTROVSKY & WALLINE 2000). The biomass affected in our scenarios is 9% (April) and 11% (June). Thus, even if total adult lavnun biomass did change during the "lavnun crisis," the chance that we have overestimated the effect of changing the size structure of the lavnun population on consumption of zooplankton is minimal. Most likely, our scenario underestimates the effect of the shift to small fish that was observed in 1993.

The model simulations of adding biomass back to the lavnun population in the size range affected by the dilution program suggest that the dilution program has the intended effect of decreasing zooplankton consumption by lavnun. Potential zooplankton consumption by lavnun in 1998 was 56 tons $\cdot d^{-1}$ in April and 263 tons $\cdot d^{-1}$ in June (Fig. 5) which is substantially lower than the potential consumption if the dilution program had not removed 750 tons of lavnun from Lake Kinneret (Fig. 7). The level of zooplankton consumption, if the dilution program did not exist, could likely cause a substantial reduction in the standing stock of zooplankton. Annual production of zooplankton in Lake Kinneret has been reported at 263,000 tons per year (WALLINE et al. 1993) which averages out to 720 tons d^{-1}. Our model simulations with no lavnun removal calculated maximum potential zooplankton consumption at 119 tons $\cdot d^{-1}$ in April and 384 tons $\cdot d^{-1}$ in June; 17% and 53% of the daily production respectively. Zooplankton production in Lake Kinneret has fluctuated in recent years (GOPHEN, pers.

comm.). The maximum potential consumption values calculated here are at levels that should cause lavnun consumption to affect zooplankton standing stocks under current lake conditions.

The model results support a claim that targeting a size range of adult lavnun for the dilution program smaller (50-155 mm) than are currently removed from the population (85-155 mm) would lead to a decrease in the potential zooplankton consumption (Fig. 8). Simulated removal of 750 tons of adult lavnun biomass in this smaller size class caused about a 10% greater reduction in potential zooplankton consumption (April: 11%, June: 8%) than does the removal of the same 750 tons by the fishery. Targeting smaller fish could be accomplished by using nets with smaller mesh sizes in the dilution program, and therefore is quite feasible. However, this option would be precluded if the use of smaller mesh nets resulted in increased by-catch of stocked, commercially valuable fish.

A general result of this modeling effort is that the same biomass of smaller fish consumes more zooplankton than does the same biomass of larger fish. This finding stems directly from the construction of the bioenergetic models used to compute consumption (see Appendix). Maximum consumption (C_{max}) is a simple exponential function of weight ($C_{max} = aW^b$) with exponent (b) taking negative values (HEWETT & JOHNSON 1992, HANSON et al. 1997). Although this result seems obvious from the construction of the bioenergetics model, similar analysis has shown that this is not always the case. The spatial heterogeneity in water temperatures and fish distributions included in this model can affect estimates of planktivore consumption. In fact, including the spatial distribution of planktivores has been shown to cause a greater than two-fold difference in estimates of potential consumption (RAND et al. 1995, HONDORP 1998).

The acoustic data indicated a large increase in the biomass of adult lavnun (50-180 mm) and tilapia (>180 mm) size classes between the April and June 1998 surveys which was likely caused by fish growth. However, April biomass measures appear unusually small. In particular, the "tilapia" size class was comprised largely of St. Peter's fish, which spawn in the nearshore areas of Lake Kinneret in the spring (BEN-TUVIA et al. 1992). During the spawning period St. Peter's fish are found in areas too shallow to be sampled by the acoustic gear. The inability of downward looking echosounders to sample these fish is likely to cause an underestimate of biomass in the largest size class of fish in April. A return of large fish to deep water sometime between the April and June surveys would appear as a sudden increase in the biomass of these fish, which is what we observed.

The abundance of fish in the two smaller size classes may also have been underestimated in April. The vertical distribution of smaller fish (12-50 mm and 50-180 mm) on the two sampling dates differed. In June, fish were distributed in a mid-water layer which makes them most reliably measured by acoustic techniques (MACLENNON & SIMMONDS 1992). At some stations in the April survey, fish numbers were greatest at the shallowest depths (2 m) that can be monitored with the acoustic system. Fish abundance could have been underestimated on those transects if there were many fish in the upper 2 m of the water column. Although in general, biomass in April may be at its lowest level of the year because of fishing and relatively high natural mortality in winter, the biomass actually measured acoustically, and thereby potential consumption calculated for April, were probably underestimates.

The analysis we have presented here assumes that fish consumption plays an important role in determining zooplankton abundance, an assumption which stems from the well-known "Trophic Cascade" hypothesis (CARPENTER & KITCHELL 1993). However, much about the aquatic food web in Lake Kinneret remains to be learned and basing the value of the lavnun

dilution program on a relatively simple interpretation of the trophic cascade hypothesis may not lead to the best management of the ecosystem. The strength of connections between planktivores and zooplankton and between predatory invertebrates and zooplankton can affect the importance of different predator populations in controlling zooplankton populations (RAMCHARAN et al. 1995). Good data on the actual consumption of zooplankton by planktivores and predatory invertebrates would be of considerable benefit. These data would increase our understanding of the strength of food web linkages in Lake Kinneret and allow for better management of the lake.

The research approach that we have used here allows us to provide estimates of the potential maximum consumption of zooplankton by planktivorous fish in a way that incorporates high resolution measures of the environment and fish populations on a whole-lake basis together with bioenergetic models of fish consumption. This represents a new combination of techniques and makes use of high resolution, whole-lake data in a way not previously accomplished. Previous use of this method studied large aquatic ecosystems such as Chesapeake Bay (BRANDT et al. 1992, BRANDT & KIRSCH 1993) and the Great Lakes of North America (GOYKE & BRANDT 1993, MASON et al. 1995) that required weeks to sample effectively. Lake Kinneret is an ecosystem where changes in fish populations can be measured on a short timescale. Because Lake Kinneret can be sampled in its entirety during a single night, ongoing and future research will include frequent sampling of the fish population in Lake Kinneret to explore changes in the annual biomass, production and zooplankton consumption. This research will allow us to examine the seasonal change in the fish population and how those changes may affect the pelagic ecosystem. The issues addressed with the future research may provide critical insight to the ecological processes of the aquatic community in Lake Kinneret and allow for more informed management of this important resource.

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Appendix

We used the Wisconsin bioenergetics model (HEWETT & JOHNSON 1992, HANSON et al. 1997) as the foundation for the spatially-explicit model of consumption of zooplankton. The three size classes are modeled as juvenile lavnun, adult lavnun and tilapia. The bioenergetics parameters for the two classes of lavnun do not differ and are both calculated with a model adapted from that published for dace (OSTROVSKY, unpublished data). Below are listed the model parameters used to compute the maximum consumption (C_{max}, g g^{-1} d^{-1}) of lavnun and tilapia. Both models use the same C_{max} equation and C_{max} is a function of the fish weight (W, g) and water temperature (T, °C):

$$C_{max} = a\, W^b f(T)$$

The function $f(T)$ describes the temperature-dependent component of C_{max} and is itself comprised of four components, V, X, Y, and Z described below.

$$f(T) = V^X e^{(X(1-V))}$$

$$V = \frac{T_m - T}{T_m - T_o}$$

$$X = \frac{(Z^2 (1+(40/Y)^{0.5})^2}{400}$$

$$Z = \ln(\theta)(T_m - T_o)$$

$$Y = \ln(\theta)(T_m - T_o + 2)$$

Parameter values used to calculate C_{max} for lavnun and tilapia may be found in Table A1.

Table A1. Parameters for C_{max} calculations for lavnun and tilapia (OSTROVSKY, unpublished data; HANSON et al. 1997).

Parameter	lavnun	tilapia
a	0.36	0.15
b	-0.31	-0.36
θ	2.3	2.5
T_O	27	30
T_M	30	37