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Proximate and Elemental Composition of Lanternfish (Pisces: Myctophidae) Larvae with Estimates of Energetic and Prey Requirements

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Abstract

The larvae of five species of myctophids [*Benthosema suborbitale*, *Ceratoscopelus townsendi*, *Hygophum taaningi*, *Myctophum selenops*, and *Notolychnus valdiviae*] from the eastern Gulf of Mexico were examined to estimate energetic and prey requirements during early growth. Age was determined from examination of sagittal otoliths. Larval period ranged from 36 days for the rapidly growing *C. townsendi* to 67 days for the diminutive *N. valdiviae*. Growth rate ranged from 0.14mmSL day^{-1} for *B. suborbitale* to 0.38 mmSL day^{-1} for *C. townsendi*. Energetic demands were estimated from a slightly modified version of the equation for the bioenergetic model where; Qc = Qg + Qs + Qm where Qc = energy consumed, Qg = food energy converted into potential energy through growth, Qs = includes energy lost in feces, excretions, and secretions, and Qm = includes energy consumed in routine metabolism [Qr] and energy consumed in active metabolism [Qa]. Proximate and elemental composition of larvae was measured and converted to calories using standard factors. Daily growth in calories was estimated from age and growth information combined with chemical composition [protein, lipid, and carbohydrate]. Time of active metabolism was determined from information on gut fullness evaluated during a diel cycle. Metabolic costs were then estimated from the measured respiratory activity of other Atlantic tropical-subtropical species. Caloric requirements for growth varied among species and size of larvae, but the greatest variation resulted from assumption regarding assimilation efficiency. Daily requirements ranged from less than one to 33 day^{-1}. Using known caloric value of preferred food, prey requirements were calculated for larvae by matching larval size to prey of the appropriate size and taxa. From these data, daily prey requirements ranged from <10 to >300 items.

Keywords: larval growth; bioenergetics; zooplankton; ichthyoplankton; lanternfish; Myctophidae; proximate composition; elemental composition; trophodynamics

Key Contribution: This research presents the first bioenergetic model of larval myctophids and for the larvae of any species of mesopelagic fish

1. Introduction

Mesopelagic fishes dominate the oceanic fish fauna in terms of the number of species and individuals [1–3]. Lanternfishes share this pelagic environment, are the most abundant of the vertically migrating mesopelagic fish groups [4–10], and play a primary role in the vertical transport of organic matter in the world's oceans [10–13]. Growth and development of vertically migrating myctophids is similar to that of ecologically and morphologically similar shallow water species [13,14]. Their populations support a wide variety of predators including cephalopods [15], other fishes [16–19], sea birds [20,21], penguins [22,23], pinnipeds [24,25], cetaceans [26,27], and some human populations indirectly as feed for our livestock [28–31].

As the most abundant vertical migrator in the world's oceans, understanding lanternfish ecology is critical in understanding the transfer of carbon and energy in the largest ecosystems on the planet, the ocean pelagial. Further, understanding the transfer of energy as Ash Free Dry Weight [AFDW], calories (cal), or energy density [ED]] and matter [as proximate and chemical composition] is essential for understanding the trophic transfer through pelagic habitats [32–35]. The ED of postmetamorphic lanternfishes has been reported from tropical-subtropical populations [33–35] to polar regions [32]. Energy content is variable, changing with food availability [33–37], depth of occurrence [35], and species within the family [32]. There is no comparable information for the larval stages of lanternfishes, a major component of pelagic ichthyoplankton assemblages.

Larval growth and survival have been identified as critical for understanding adult size and structure [38–45]. Because enhanced survival and growth can have a dramatic impact on adult year class strength [38,46–49] there has been a focus on early life history events to address problems in fisheries [50]. The emphasis on fisheries resulted in an emphasis on the temperate commercially important coastal species [51–58] that exhibit a wide range of growth rate [46]. Growth of these species varies because of a complex mixture of intrinsic [genetic] and extrinsic [temperature, food availability] factors [42]. Over the past several decades, we have learned much about the early life history of these important coastal species see [40,50,54,59] for reviews, but there are relatively few studies of open ocean ichthyoplankton.

In the epipelagic zone, larvae of the family Myctophidae are abundant members of the ichthyoplankton, ranging from about 45-70% of all larvae collected [60–66]. Lanternfish larvae are at least an order of magnitude greater in abundance than adults in the eastern Gulf of Mexico [67] suggesting that larval mortality is an important factor in determining adult population size and structure, thus meeting energetic requirements during early growth is essential. Although there is still much to learn, information on larval feeding ecology, [68–71] and age and growth [14,72,73] have increased our understanding of this ecologically important group of vertebrates, but energy flow has not been examined.

The purpose of this study is to estimate the energetic demand for metabolism and growth during early life of larval myctophids and in turn, the prey required for larval growth to metamorphosis of representative members of the family. The trophodynamics of abundant larval lanternfishes in the eastern Gulf of Mexico were assessed from the examination of larval feeding chronology [69] age and growth [14] combined with proximate and chemical composition as reported here. Estimates from these combined studies can also be used to evaluate larval recruitment to the resident myctophid populations. Additionally, from the energetic information, we can generate approximations of energy available in myctophid ichthyoplankton to tertiary consumers, which will lead to a better understanding of energy flow in oceanic ecosystems. This is a companion study the ecology of postmetamorphic lanternfishes [6,12,13,67,74–76]. Thus, these results are part of a larger project initiated to provide a detailed analysis of the myctophid assemblage in the eastern Gulf of Mexico. This research adds an estimate of the calories required for growth towards transition to juveniles when these fishes begin their diel vertical migrations.

2. Materials and Methods

All samples were collected within 20 nautical miles of 27°N, 86°W. The hydrographic conditions are typical of vertically stratified oligotrophic environments [77]. The zooplankton and micronekton communities of the area have been extensively studied [see 75, 74-80 and references therein]. Net tows were made hourly during four summer cruises over a period of four years, representing over a month of daily sampling [14,69]. Ichthyoplankton was collected using two 505 µm mesh plankton nets, suspended side by side within a modified Tucker trawl frame [81]. These nets had a mouth opening of 0.56m^2 per net, and a length to mouth ratio of 7:1. Investigations in other areas [62,63] and preliminary investigations in the eastern Gulf of Mexico revealed that myctophid larvae were concentrated within the upper 200m of the water column, therefore, sampling was concentrated within this zone. Fish larvae were sorted immediately from the catch, identified, measured to the nearest 0.1mm standard length [SL], and frozen in individually sealed Nalgene® capsules. Larvae were separated into three groups. One group of larvae was used for estimates of age and growth [14], the second for dry weight measurement, and the third for proximate and elemental composition.

To estimate the energetic demands [Qc] of lanternfish larvae, the bioenergetics of the most abundant species [*Benthosema suborbitale, Ceratoscopelus townsendi*, H*ygophum taaningi, Myctophum selenops,* and *Notolychnus valdiviae*, [hereafter referred to as representative species] was evaluated. Bioenergetic models have been used to determine the energy budget of both adult [82,83] and larval [85–91] fishes. The following is a slightly modified [92] version of the equation for the bioenergetic model which has been discussed in detail [93–95]:

$Qc = Qg + Qs + Qm$

where.

Qc = energy consumed

Qg = food energy converted into potential energy through growth

Qs = energy lost in feces, excretions, and secretions

Qm = energy consumed in routine metabolism [Qr] and energy consumed in active metabolism [Qa].

The calculation of energy converted to potential energy through growth [Qg] requires knowledge of growth rate [14], increase in biomass, and chemical composition. Protein, lipid, and carbohydrate composition were determined for larvae of the representative species. Protein content was determined by a slightly modified version [see 92] of the method developed by Lowrey *et al***.** [96]. Lipid content was quantified following the methods of Bligh & Dyer [97] and carbohydrates by the methods of Dubois *et al.* [98]. Dry weight was measured by drying formerly frozen larvae at 60°C and weighing individuals on a Perkin-Elmer Autobalance AD-2 in a temperature and humidity-controlled chamber. Larvae were measured to the nearest 0.1mmSL and weighed to the nearest 0.001mg. Daily growth in calories [Qg] was estimated from age and growth information [14] combined with chemical composition [protein, lipid, and carbohydrate] using the following conversions; proteins contain 5.7 calories mg^{-1}, lipids contain 8.7 calories mg^{-1}, and carbohydrates 4.2 calories mg^{-1} [99].

Routine respiration [Qr] was not directly measured for lanternfish larvae but respiration rates for the larvae of a variety of other tropical to subtropical species were in close agreement [34,87,88,91]. To approximate the respiratory rates of the five representative lanternfishes, the respiration during routine metabolism for larvae of similar morphology and diet [69] were matched to the measured values [91] of other tropical-subtropical species. Respiration [$\mu l\ O_2\ \mu gDW^{-1}\ hour^{-1}$] was converted to calories using the oxycalorific equivalent of 0.0046 calories $\mu l^{-1}\ O_2$ [99]. It was assumed that active [=feeding] metabolism was twice routine metabolism [99], estimated mean ratio of active to routine metabolic rate [1.7 ± 0.4] [99] and an estimated factor of 2.5 to convert routine to active metabolism for pelagic fishes [100]. Time of active metabolism was estimated from feeding incidence determined from gut fullness evaluated during a diel cycle [69]. Daily cost of metabolism was estimated from the equation [91]:

$Qm = [2m[t1] + m[t2]]W$

where;

Qm = the 24-hour metabolic cost in calories

m = routine metabolic rate [cal $\mu g^{-1}\ h^{-1}$]

W = dry weight of larvae [μg]

t1 = hours in feeding activity

t2 = non-feeding hours.

Energy lost through feces, excretions, and secretions [Qs] can be a major source of energy loss for fish larvae [91,101,102]. Thus, prey assimilation, or the percentage of food energy used for growth and activity, is highly variable. An average loss through defecation of 27% was measured for young carnivorous fishes [99]. Losses as high as 83% [91,103] and as low as 8% [87] have been reported for some marine fish larvae. Therefore, rather than choose one value, calculations of daily ration included minimum, average, and maximum values for this energy loss. Caloric requirements of the larvae [Qc values] were calculated at three levels according to the range of published assimilation values where the calculation of QcMin assumes a high assimilation [thus a lower prey requirement] of 92%, QcAvg assumes an average assimilation of 73%, and QcMax assumes a low assimilation of 18%. Losses due to metabolic excretions [urine and other metabolic fluids] are reported to be considerably lower, ranging from 1-10% [99]. This potential loss was not separately included in these calculations because of the wide range of loss calculated for assimilation values.

Caloric value of prey was determined from gut analysis [69]. Individual prey items were counted, measured, and identified. Wet mounts were made by pipetting small organisms [< 200µm] onto glass slides for measurement at 100 or 400X magnification. Volume of organisms was estimated from the closest geometric form. Calculated volume was converted to dry weight using a standard relation to volume [104] for soft bodied [non- crustacean] organisms. Dry weight of copepods and other crustaceans was calculated from dry weight to cephalothorax length relations of copepods collected from the same location in the eastern Gulf of Mexico [Conley & Hopkins, unpublished data]. Caloric value was determined from an average conversion factor of 0.0059 calories μgDW^{-1}.

3. Results

Growth of the representative lanternfish larvae was previously detailed [14]. Food energy converted to potential energy through growth [Qg] was estimated using the daily increase in standard length [from otolith microincrements], the relationship of biomass [as dry weight] to length, and the energetic value of tissue from its chemical composition [Table 1]. Analysis of chemical composition [Table 1] revealed that AFDW as percent of carbon ranged from 80.5% [*Hygophum taaningi*] to 94.3% [*Benthosema suborbitale*]. Expressed as a percentage of AFDW, protein ranged from 48.9% [*Ceratoscopelus townsendi*] to 58.4% [*Notolychnus valdiviae*], lipids ranged from 11.7% [*N. valdiviae*] to 22.8% [*B. suborbitale*], and carbohydrates ranged from 0.8% [*N. valdiviae*] to 1.3% [*Myctophum selenops*]. Combining the information on age and growth [14], dry weight [14], and chemical composition [Table 1] resulted in an estimate of average daily increase in the caloric content of tissues [Figure 1]. Daily increase in the caloric

Table 1. Chemical composition of the five representative species of lanternfish larvae.

Species	AFDW (% DW)	Protein (% AFDW)	Lipid (% AFDW)	Carbohydrate (% AFDW)
Benthosema suborbitale	94.3	55.4	22.8	1.0
Ceratoscopelus townsendi	86.7	48.9	13.6	1.2
Hygophum taaningi	80.5	54.0	14.5	1.0
Myctophum selenops	83.9	55.4	13.3	1.3
Notolychnus valdiviae	83.5	58.4	11.7	0.8

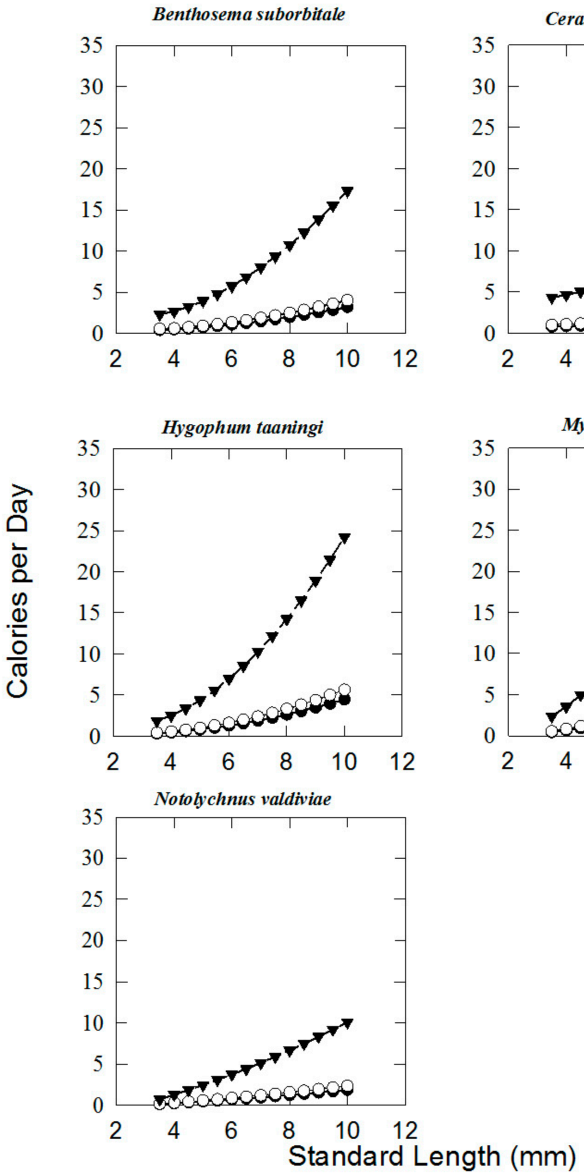

Figure 1. Relationship between dry weight and caloric content for larvae of the five representative species of myctophids [*Benthosema suborbitale*, *Ceratoscopelus townsendi*, *Hygophum taaningi*, *Myctophum selenops*, and *Notolychnus valdiviae*] from the eastern Gulf of Mexico. MinQ$_c$ cal day^{-1} = AvgQ$_c$ cal day^{-1} = MaxQ$_c$ cal day^{-1} =

Table 2. Calculation of caloric and numerical prey requirements for larvae of *Benthosema suborbitale*. Column headings refer to the variables of the bioenergetic and respiratory equations; SL = standard length of larvae, W = dry weight of larvae, R = respiratory rate, m = routine metabolic rate, Q_m = includes energy consumed in routine and active metabolism, Q_g = food energy converted into potential energy through growth, Q_c = total energy cost.

SL (mm)	W µgDW	R µg O_2 h^{-1}	m x 10^{-6} cal µg^{-1} h^{-1}	Q_m cal day^{-1}	Q_g cal day^{-1}	Q_m + Q_g cal day^{-1}	AvgQ_c cal day^{-1}	MinQ_c cal day^{-1}	MaxQ_c cal day^{-1}	AvgPrey no. day^{-1}	MinPrey no. day^{-1}	MaxPrey no. day^{-1}
3.5	80	0.70	40	0.13	0.27	0.39	0.54	0.42	2.30	7	5	29
4.0	130	1.05	37	0.19	0.27	0.45	0.62	0.49	2.67	8	6	34
4.5	210	1.56	35	0.28	0.27	0.55	0.75	0.60	3.22	9	8	41
5.0	320	2.23	32	0.40	0.27	0.67	0.91	0.73	3.92	12	9	50
5.5	460	3.02	30	0.55	0.27	0.81	1.11	0.88	4.77	9	7	60
6.0	630	3.93	29	0.71	0.27	0.97	1.34	1.06	5.73	10	8	45
6.5	830	4.95	28	0.89	0.27	1.16	1.59	1.26	6.82	12	10	53
7.0	1060	6.08	27	1.10	0.27	1.36	1.87	1.48	8.02	15	12	62
7.5	1320	7.31	26	1.32	0.27	1.58	2.17	1.72	9.32	17	13	72
8.0	1610	8.63	25	1.56	0.27	1.82	2.50	1.98	10.72	19	15	80
8.5	1930	10.04	24	1.81	0.27	2.08	2.85	2.26	12.23	21	17	91
9.0	2280	11.55	23	2.09	0.27	2.35	3.22	2.56	13.83	24	19	103
9.5	2660	13.14	23	2.37	0.27	2.64	3.61	2.87	15.52	27	21	115
10.0	3070	14.82	22	2.68	0.27	2.94	4.03	3.20	17.30	30	24	129

Table 3. Calculation of caloric and numerical prey requirements for larvae of *Ceratoscopelus townsendi*. Column headings refer to the variables of the bioenergetic and respiratory equations; SL = standard length of larvae, W = dry weight of larvae, R = respiratory rate, m = routine metabolic rate, Q_m = includes energy consumed in routine and active metabolism, Q_g = food energy converted into potential energy through growth, Q_c = total energy cost.

SL (mm)	W µgDW	R µg O_2 h^{-1}	m x 10^{-6} cal µg	Q_m cal day^{-1}	Q_g cal day^{-1}	Q_m + Q_g cal day^{-1}	AvgQ_c cal day^{-1}	MinQ_c cal day^{-1}	MaxQ_c cal day^{-1}	AvgPrey no. day^{-1}	MinPrey no. day^{-1}	MaxPrey no. day^{-1}

			$^{-1}$ h $^{-1}$									
3.5	199	1.36	32	0.24	0.49	0.74	1.01	0.80	4.34	15	12	64
4.0	243	1.65	31	0.30	0.49	0.79	1.08	0.86	4.65	16	13	68
4.5	297	2.01	31	0.36	0.49	0.86	1.17	0.93	5.03	17	14	74
5.0	363	2.44	31	0.44	0.49	0.93	1.28	1.02	5.49	21	16	89
5.5	444	2.97	31	0.54	0.49	1.03	1.41	1.12	6.06	23	18	98
6.0	543	3.62	31	0.65	0.49	1.15	1.57	1.25	6.74	25	20	109
6.5	664	4.40	31	0.79	0.49	1.29	1.76	1.40	7.58	29	23	123
7.0	811	5.36	31	0.97	0.49	1.46	2.00	1.59	8.59	32	26	139
7.5	992	6.52	30	1.18	0.49	1.67	2.29	1.82	9.82	37	29	159
8.0	1213	7.93	30	1.43	0.49	1.93	2.64	2.09	11.32	42	33	178
8.5	1483	9.65	30	1.74	0.49	2.24	3.06	2.43	13.15	48	38	207
9.0	1813	11.74	30	2.12	0.49	2.61	3.58	2.84	15.38	56	45	242
9.5	2216	14.29	30	2.58	0.49	3.07	4.21	3.34	18.08	66	53	285
10.0	2709	17.39	30	3.14	0.49	3.63	4.98	3.95	21.37	78	62	336

Table 4. Calculation of caloric for larvae of *Hygophum taaningi*. Column headings refer to the variables of the bioenergetic and respiratory equations; SL = standard length of larvae, W = dry weight of larvae, R = respiratory rate, m = routine metabolic rate, Q_m = includes energy consumed in routine and active metabolism, Q_g = food energy converted into potential energy through growth, Q_c = total energy cost.

SL (mm)	W µgDW	R µg O_2 h $^{-1}$	m x 10^{-6} cal µg $^{-1}$ h $^{-1}$	Q_m cal day^{-1}	Q_g cal day^{-1}	$Q_m + Q_g$ cal day^{-1}	AvgQ_c cal day^{-1}	MinQ_c cal day^{-1}	MaxQ_c cal day^{-1}
3.5	100	1.09	51	0.20	0.12	0.32	0.43	0.34	1.86
4.0	160	1.70	49	0.31	0.12	0.43	0.58	0.46	2.51
4.5	240	2.49	48	0.45	0.12	0.57	0.78	0.62	3.35
5.0	340	3.46	47	0.62	0.12	0.74	1.02	0.81	4.37
5.5	460	4.60	46	0.83	0.12	0.95	1.30	1.03	5.58
6.0	600	5.91	46	1.07	0.12	1.19	1.62	1.29	6.97
6.5	760	7.38	45	1.33	0.12	1.45	1.99	1.58	8.54
7.0	940	9.01	44	1.63	0.12	1.75	2.39	1.90	10.27
7.5	1140	10.81	44	1.95	0.12	2.07	2.84	2.25	12.18
8.0	1360	12.76	43	2.30	0.12	2.42	3.32	2.63	14.25
8.5	1600	14.87	43	2.69	0.12	2.80	3.84	3.05	16.50
9.0	1860	17.14	43	3.09	0.12	3.21	4.40	3.49	18.90
9.5	2140	19.55	42	3.53	0.12	3.65	5.00	3.97	21.47
10.0	2440	22.13	42	4.00	0.12	4.11	5.64	4.47	24.20

Table 5. Calculation of caloric and numerical prey requirements for larvae of *Myctophum selenops*. Column headings refer to the variables of the bioenergetic and respiratory equations; SL = standard length of larvae, W = dry weight of larvae, R = respiratory rate, m = routine metabolic rate, Q_m = includes energy consumed in routine and active metabolism, Q_g = food energy converted into potential energy through growth, Q_c = total energy cost.

SL (mm)	W µgDW	R µg O_2 h^{-1}	m x 10^{-6} cal µg $^{-1}$ h $^{-1}$	Q_m cal day^{-1}	Q_g cal day^{-1}	Q_m + Q_g cal day^{-1}	AvgQ_c cal day^{-1}	MinQ_c cal day^{-1}	MaxQ_c cal day^{-1}	AvgPrey no. day^{-1}	MinPrey no. day^{-1}	MaxPrey no. day^{-1}
3.5	153	1.20	36	0.27	0.14	0.40	0.55	0.44	2.36	5	4	22
4.0	300	2.11	33	0.47	0.14	0.60	0.83	0.66	3.55	8	6	33
4.5	493	3.20	30	0.71	0.14	0.85	1.16	0.92	4.97	11	8	46
5.0	730	4.45	28	0.99	0.14	1.12	1.54	1.22	6.61	9	7	40
5.5	1013	5.85	27	1.30	0.14	1.43	1.97	1.56	8.44	12	9	51
6.0	1340	7.40	26	1.64	0.14	1.78	2.44	1.93	10.47	15	12	63
6.5	1713	9.09	25	2.02	0.14	2.15	2.95	2.34	12.67	18	14	76
7.0	2130	10.91	24	2.42	0.14	2.56	3.51	2.78	15.06	21	17	91
7.5	2593	12.86	23	2.86	0.14	2.99	4.10	3.25	17.61	25	20	106
8.0	3100	14.94	22	3.32	0.14	3.46	4.73	3.76	20.33	28	22	120
8.5	3653	17.14	22	3.81	0.14	3.95	5.40	4.29	23.21	32	25	137
9.0	4250	19.47	21	4.33	0.14	4.46	6.11	4.85	26.24	36	29	155
9.5	4893	21.90	21	4.87	0.14	5.00	6.85	5.44	29.43	40	32	173
10.0	5580	24.46	20	5.44	0.14	5.57	7.63	6.05	32.77	45	36	193

Table 6. Calculation of caloric and numerical prey requirements for larvae of *Notolychnus valdiviae*. Column headings refer to the variables of the bioenergetic and respiratory equations; SL = standard length of larvae, W = dry weight of larvae, R = respiratory rate, m = routine metabolic rate, Q_m = includes energy consumed in routine and active metabolism, Q_g = food energy converted into potential energy through growth, Q_c = total energy cost.

SL (mm)	W µgDW	R µg O_2 h^{-1}	m x 10^{-6}cal µg $^{-1}$ h $^{-1}$	Q_m cal day^{-1}	Q_g cal day^{-1}	Q_m + Q_g cal day^{-1}	AvgQ_c cal day^{-1}	MinQ_c cal day^{-1}	MaxQ_c cal day^{-1}	AvgPrey no. day^{-1}	MinPrey no. day^{-1}	MaxPrey no. day^{-1}
3.5	20	0.22	50	0.04	0.08	0.12	0.16	0.13	0.68	3	2	12

4.0	90	0.77	40	0.14	0.08	0.22	0.30	0.23	1.27	5	4	23
4.5	170	1.31	36	0.24	0.08	0.31	0.43	0.34	1.85	8	6	33
5.0	260	1.87	33	0.34	0.08	0.41	0.57	0.45	2.44	8	7	36
5.5	360	2.46	32	0.44	0.08	0.52	0.71	0.57	3.06	10	8	45
6.0	470	3.07	30	0.56	0.08	0.63	0.87	0.69	3.72	13	10	54
6.5	590	3.72	29	0.67	0.08	0.75	1.03	0.81	4.40	15	12	64
7.0	720	4.40	28	0.79	0.08	0.87	1.19	0.95	5.12	17	14	75
7.5	860	5.10	27	0.92	0.08	1.00	1.37	1.08	5.87	20	16	86
8.0	1010	5.84	27	1.05	0.08	1.13	1.55	1.23	6.65	20	16	86
8.5	1170	6.60	26	1.19	0.08	1.27	1.74	1.38	7.47	22	18	97
9.0	1340	7.40	26	1.34	0.08	1.41	1.94	1.54	8.31	25	20	108
9.5	1520	8.22	25	1.48	0.08	1.56	2.14	1.70	9.19	28	22	119
10.0	1710	9.08	25	1.64	0.08	1.72	2.35	1.86	10.09	30	24	131

value of fish tissue [AvgQ$_c$ cal day^{-1}] for mid-size (6.5 mm SL) larvae ranged from 1.03 calories for *N. valdiviae*, the slowest growing species represented, to 2.95 calories for *M. selenops*, the heaviest of the species represented [Tables 2 – 6].

Diurnal activity patterns were determined from an analysis of larval feeding activity, assuming that non-feeding larvae are quiescent [69]. Unlike adult lanternfishes, larvae are primarily diurnal predators. Four of the five species revealed a similar diel pattern; feeding commenced between 0600 and 0800 hours and terminated between 1700 and 2100 hours [69]. Time of peak feeding incidence varied and there was no consistent pattern among species. Unlike the other representative species, larvae of *Myctophum selenops* apparently always fed, regardless of light availability.

The weight-specific energy cost for activity [Qm], estimated from the relationship of oxygen consumption to larval dry weight and activity level for mid-sized larvae, ranged from 0.67-2.02 calories per day [Tables 2 - 6]. Larval size and assimilation efficiency [choice of Qs] resulted in greater differences than among species.

The number of individual zooplankters required daily was calculated from the caloric value of known preferred prey items and the size of prey ingested by each size class of larvae [69]. The number of prey ingested also varied more according to size and assimilation efficiency within a species than among species. The average number of prey required daily for larvae 5.0 mm SL or less ranged from 3-23 [Tables 2-6]. For larvae in the second size category [> 5.0-7.5mmSL], average daily prey requirements ranged from 9 to 37. The average number of prey required daily for species greater than 7.5mmSL ranged from 19 - 78.

4. Discussion

There are no other comprehensive evaluations of the bioenergetics of myctophid larvae. Most studies on shallow water larval species [83–90] employ comparable evaluations, assumptions, and results. Since lanternfish larvae are essentially shallow water species pre-transformation, we have utilized similar methodology and assumptions with some adaptations. The amount of energy required for daily growth and maintenance [Qc] by the five representative species of lanternfishes was estimated from a bioenergetic equation. The modeling efficiency of bioenergetics can be quite high [90,96], but variations in each of the three major parameters used to calculate Qc affect the final determination of energy requirements. The estimate of prey energy converted into potential energy through growth [Qg] was evaluated from analysis of age and growth [14], plus measurement of dry weight and chemical composition. Age was determined from microincrement analysis of sagittal otoliths.

The chemical composition of lanternfish larvae [Table 1], with proteins and lipids predominant over carbohydrates, is similar to that exhibited by the larvae of shallow water fish species [88,89,106]. In addition, results for these larvae fall within the range reported for postmetamorphic lanternfishes from the eastern Gulf of Mexico [35], except that the unusually high lipid level that they reported in adult *Notolychnus valdiviae* was not found in the larvae of this species, which had the lowest percent lipid content of all species examined.

Four of the representative species were actively feeding for approximately 15 hours a day except larvae of *Myctophum selenops,* which appeared to feed continuously [69]. Energy spent during routine metabolism was estimated from an examination of respiration by the larvae of a variety of tropical-subtropical species [92]. These authors concluded that oxygen uptake [R] related strongly to biomass [dry weight] and did not differ significantly among species. Further, analysis of respiration by larval redfish [*Sciaenops ocellatus*] was similar to the respiratory requirements of other tropical-subtropical species [89,108]. It is likely, therefore, that the equations generated by Houde & Schekter [92] are applicable for approximating the metabolic requirements of lanternfish larvae.

Whereas the values for energy funneled into growth [Qg] and burned for activity [Qm] were either measured or derived from corroborated values in the literature, the amount of energy lost through non-assimilation is contentious. The ability to capture and measure the amount of prey energy lost in feces [unassimilated food] is difficult, thus it is often measured indirectly [107,108]. Even when direct measurement of prey assimilation was attempted [102], assimilation levels were shown to be highly variable within a species and were not significantly related to age, standard length, or dry weight. Results of assimilation calculations range from 17-92% in marine larvae, with an average value of 73%. Because of the high degree of variability associated with this parameter, Qc was determined for the lowest, average, and highest levels for assimilation reported for marine fish larvae.

Larval fishes probably have lower assimilation levels than adults because of the lack of development of gut tissues and digestive organs [103,109], but the values are probably not as low as indicated by some experimental results. Among the factors contributing to the variability of measured assimilation levels are prey availability and type. The maintenance of larvae in the laboratory requires prey densities much higher than those available *in situ* [39]. Under such conditions larvae pack their guts, forcing prey items through more quickly than would probably occur naturally [108]. Lack of retention within the gut would result in lower assimilation efficiencies. Houde and The poor assimilation of prey by bay anchovy [*Anchoa mitchilli*] may be related to a residence time in the gut of only a few minutes duration [92]. Although high prey concentrations are likely encountered by marine larvae [69,110–113], these do not match the high levels of prey consistently provided to laboratory-reared larvae [39]. It is likely, therefore, that the minimum and average prey requirements calculated herein are closer to the natural feeding requirements of larvae, which assumes a relatively high assimilation rate.

The digestibility of prey also affects assimilation efficiencies. It was suggested that the high assimilation of rotifers by redfish larvae to the relative ease at which these prey can be digested [87,88]. It may be more difficult to extract energy from other prey items, such as phytoplankton and crustacean prey. *Hygophum taaningi* is particularly problematic in this regard. Larvae of this species have a diet dominated by gelatinous prey, primarily tunicates [69]. Because of the difficulty in both determining actual prey size and the lack of caloric conversion information, we did not feel confident that we could accurately estimate numerical prey consumption. Most marine larvae feed upon a variety of prey, especially during the early part of larval development [69,115–117]. The average assimilation rate of 73% [99] is likely the best estimate for assimilation of prey for larvae over a range of sizes.

Although variation exists among the five species reported herein, the change in growth rate is minor when compared to other families. The larval period is variable among tropical - subtropical species, ranging from a few days to months [118–121]. Lanternfish growth is not unlike that of several species of Gulf of Mexico clupeids and sciaenids [14,119,120]. Thus, even though post-metamorphic myctophids reside at mesopelagic depths, their larval life history, spent in epipelagic waters, most closely resembles that of normally epipelagic and shallow water fish species. It was suggested that except for some differences related to diel vertical migrations [e.g. feeding chronology, otolith microincrement deposition periods], basic myctophid biology [age, growth and reproduction patterns] in general does not reflect unique adaptation to their deep-sea residence, but in fact resembles that of shallow water species [13]. Our early life history data support this concept. Despite many morphological and physiological adaptations to their deep-sea homes, myctophids have not lost the basic shallow water life history patterns of their ancient ancestors.

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