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Leptocephalus energetics: assembly of the energetics equation

Received: 25 May 2000 / Accepted: 8 January 2001 / Published online: 14 March 2001
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Abstract The principles of energetics were used to examine the energetic requirements of leptocephali. Respiration and excretion rates and daily growth rates combined with proximate composition were used to examine the allocation of energy into each of the three main components of energetics: metabolism, excretion and growth. The daily energetic requirements for leptocephali, referred to as type 2 larvae based upon their unique developmental strategy, were compared to the requirements of non-leptocephalus larvae, known as type 1. Leptocephalus daily energetic requirements were also compared to the energy available from the leptocephalus' proposed food sources. The four species of eel larvae selected were all from the order Anguilliformes: *Paraconger caudilimbatus* (Poey), *Ariosoma balearicum* (Delaroche), *Gymnothorax saxicola* Jordan and Davis, and *Ophichthus gomesii* (Castelnau). The allocation of energy to each of the components of energetics as well as the total energetic requirements for the leptocephali proved to be very different from those of type 1 larvae. Metabolism received the majority, 60–92%, of the energy required per day. Growth and excretion were allocated 4–39% and < 1–21%, respectively, of the total energy needed per day. Leptocephali required < 50% of the energy needed by type 1 larvae of equal dry mass. The unique growth strategy used by leptocephali allows them to increase rapidly in size while allocating the majority of their energy, not to growth as in most larval fish, but to metabolism.

Introduction

Two fundamentally different strategies characterize the early development of marine teleosts (Pfeiler 1986). The first and most common strategy (type 1) consists of a post-hatch period in which the yolk-sac is resorbed, after which exogenous feeding begins immediately and is continued throughout the larval period as the larva grows into a juvenile fish. Type 1 larvae increase in mass primarily by depositing protein as muscle (Ballbontin et al. 1973) and remain as larvae for days to a month or more (Fives et al. 1986; Leffler and Shaw 1992; Lang et al. 1994). In the second strategy (type 2), after a similar post-hatch period in which the yolk-sac is resorbed, the larval fish shows a dramatic increase in size. The increases in mass are accomplished by incorporating extracellular glycosaminoglycans (GAGs) into the body matrix (Pfeiler 1999). Type 2 larvae may remain in the plankton for several months, and are typical of five orders of bony fishes: the Albuliformes (the bonefishes), the Anguilliformes (the eels), the Elopiformes (the tarpon and ladyfishes), the Notacanthiformes (the spiny eels), and the Saccopharyngiformes (the gulper eels). The type 2 larva has an unusual morphology. It is decidedly laterally compressed, almost leaf-like in appearance, with a perfectly clear body and a slender head that gives it its name: the leptocephalus.

The GAGs deposited by leptocephali act as an energy depot that accumulates as they grow. As the larvae accumulate GAGs, the body walls separate to accommodate storage, creating a "mucinous pouch" (Smith 1989). Because GAGs are non-metabolizing compounds, they allow a substantial increase in size in late premetamorphic leptocephali without the costs accompanying cellular proliferation (Bishop and Torres 1999).

Development in the premetamorphic leptocephalus has been divided into two subphases, phase Ia and phase Ib (Donnelly et al. 1995; Bishop and Torres 1999). During phase Ia there is a high level of cellular proliferation, with preferential synthesis of protein and

Communicated by N.H. Marcus, Tallahassee

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carbohydrate over lipid. Growth is manifested in length rather than mass; up to 40% of the maximum length is attained over this period, while only 5–7% of the maximum mass (wet or ash-free dry) is accumulated. During phase Ib there is a leveling off of DNA and RNA content, an increase in the rate of lipid deposition, and an exponential increase in mass (wet and ash-free dry). Declines in DNA and RNA concentrations ($\mu\text{g g}^{-1}$) reflect the greater proportion of acellular tissue in phase Ib compared to phase Ia (Donnelly et al. 1995). The transition between subphases occurs at approximately 10% of the maximum premetamorphic mass of each species, coinciding with an otolith-derived age of approximately 20 days (Donnelly et al. 1995; Bishop et al. 2000).

From the discovery of leptocephali in 1763 until 1993, a period of 230 years, leptocephalus ingestion and diet had remained undescribed (Hulet 1978; Kracht and Tesch 1981). Where are the leptocephali acquiring material to form an extensive GAG reserve in an oligotrophic environment? Two potential sources of nutrition have been proposed for leptocephalus larvae: dissolved organic material and particulate organic matter in the form of zooplankton fecal pellets and larvacean houses.

Dissolved organic carbon (DOC), either absorbed through the intestine or across the epithelial layer of the integument, has been proposed as a source of nutrition for leptocephali (Otake et al. 1993; Otake 1996). The uptake of DOC across the integument has been observed as a mode of supplemental nutrition in the eggs and yolk-sac larvae of fish (Siebers and Rosenthal 1977; Korsgaard 1991). In fact, the pronounced laterally compressed morphology and soft body wall make uptake of DOC an attractive hypothesis for leptocephalus nutrition. Hulet (1978) examined the epidermis of the leptocephalus *Ariosoma balearicum* and found the surface to be covered with microvilli-like structures similar to those found in fish digestive tracts. These structures, combined with the rapid increase in length compared with mass during phase Ia observed in four species of leptocephali (Donnelly et al. 1995; Bishop and Torres 1999), may potentially serve as mechanisms for increasing the surface to volume ratio, facilitating epithelial absorption. Though not demonstrated, the uptake of DOC appears to be a feasible source of leptocephalus nutrition.

Particulate organic carbon (POC) has also been hypothesized as a possible source of nutrition for leptocephali. POC, in the form of gelatinous feeding structures of appendicularians and attached zooplankton fecal pellets, has been observed in the leptocephali of eight eel species spanning five families (Otake et al. 1990, 1993; Mochioka and Iwamizu 1996). Pfeiler (1999), however, points to an inconsistency in this hypothesis. The stable isotope ratios ($\delta^{15}\text{N}$) found in both *Conger myriaster* (Otake et al. 1993) and *Albula* sp. (Pfeiler et al. 1998) were lower than ratios in POC samples, indicating that the leptocephali were feeding primarily at an even lower trophic level than POC.

The principles of energetics are useful tools for describing the allocation of energy in the developing leptocephalus and quantifying the nutritional requirements of the larvae with respect to metabolism, excretion, and growth (Brett and Groves 1979). The feasibility of different proposed diets for leptocephali can be tested, and differences in the allocation of energy between the type 1 and type 2 developmental strategies can be examined. The larvae selected for the assembly of the energetics equations are four of the most abundant eel larvae in the Gulf of Mexico: *Paraconger caudilimbatus* (Poey), *Ariosoma balearicum* (Delaroche), *Gymnothorax saxicola* Jordan and Davis and *Ophichthus gomesii* (Castelnau).

Materials and methods

Daily metabolic requirements were determined from respiration analysis (Bishop and Torres 1999). Oxygen uptake measurements were routine rates and obtained using closed-vessel respirometry. Predicted wet mass-specific oxygen consumption ($\mu\text{l O}_2 \text{g}^{-1} \text{WM h}^{-1}$) was converted to joules (J) using the oxycaloric coefficient (Brett and Groves 1979; Pennycuik 1988) of $0.0194 \text{ J } \mu\text{l}^{-1} \text{ O}_2$.

Nonfecal excretion values (NH_3) (Bishop and Torres 1999) in the form of wet mass-specific excretion rates ($\text{NH}_3 \text{g}^{-1} \text{WM h}^{-1}$) were converted to joules using a value of $0.0204 \text{ J } \mu\text{g}^{-1} \text{NH}_3$ (Elliot and Davidson 1975). Fecal energy is not reported due to the small amounts produced in larval fish (Brett and Groves 1979) and apparent absence in leptocephali.

Larval wet mass was converted to joules using the proximate composition ($\mu\text{g g}^{-1} \text{WM}$) (Bishop and Torres 1999 for *Paraconger caudilimbatus*, *Gymnothorax saxicola*, and *Ophichthus gomesii*; Donnelly et al. 1995 for *Ariosoma balearicum*) and the caloric equivalents in Brett and Groves (1979) for protein ($0.020 \text{ J } \mu\text{g}^{-1}$), lipid ($0.0397 \text{ J } \mu\text{g}^{-1}$), and carbohydrate ($0.0172 \text{ J } \mu\text{g}^{-1}$). Larval wet mass-specific values ($\text{J g}^{-1} \text{WM}$) and daily growth rates of larvae ($\text{g}^{-1} \text{WM day}^{-1}$), determined from growth models (Bishop et al. 2000) for each of the species, were combined to yield daily growth in joules ($\text{J g}^{-1} \text{WM day}^{-1}$). Table 1 shows by species the energy in joules required per day regressed on mass (g WM) for each of the components and the corresponding P and r^2 values.

Multiple assays were conducted on each larva. Metabolism, excretion, and proximate composition values were determined for each individual. Analysis-specific preservation techniques prevented the use of the same larvae for age determination. The ages of individual larvae were predicted for each species using larval mass. All equations were obtained using least-squares regressions of ln-transformed data. Maximum and minimum values were obtained using the maximum and minimum joules needed per species across all sizes. Graphs depict the regressions fitting the raw data, and values in the tables have been back-transformed.

Results

The total individual energy required per day ($\text{J ind.}^{-1} \text{day}^{-1}$) increased in an allometric relationship with increasing wet mass (g WM) (Fig. 1). The total energetic requirement per day for the four larvae ranged from $15.7 \text{ J ind.}^{-1} \text{day}^{-1}$ for *Gymnothorax saxicola*, to $198.49 \text{ J ind.}^{-1} \text{day}^{-1}$ for *Ariosoma balearicum*, the largest of the four species examined (Table 1). In contrast, the total energy required per gram of mass ($\text{J g}^{-1} \text{WM day}^{-1}$) decreased precipitously with increasing mass (Fig. 2),

Table 1 Energy in joules required per day for each of the components of energetics regressed on wet mass (g WM) for each species. General formula: $\text{joules day}^{-1} = a(\text{g WM})^b$. * $P < 0.01$; ** $P < 0.001$

Species	Metabolism					Growth					Excretion				
	<i>a</i>	<i>b</i>	<i>r</i> ²	<i>P</i>	<i>n</i>	<i>a</i>	<i>b</i>	<i>r</i> ²	<i>P</i>	<i>n</i>	<i>a</i>	<i>b</i>	<i>r</i> ²	<i>P</i>	<i>n</i>
<i>Paraconger caudilimbatus</i>	40.445	0.172	0.925	**	46	6.114	0.302	0.633	**	46	0.368	-1.093	0.856	**	45
<i>Ariosoma balearicum</i>	67.094	0.427	0.823	**	27	23.713	0.688	0.831	**	27	0.124	-1.031	0.823	**	27
<i>Gymnothorax saxicola</i>	48.689	0.471	0.887	**	37	26.996	0.953	0.583	**	37	0.133	-1.132	0.669	**	37
<i>Ophichthus gomesii</i>	31.802	0.050	0.965	**	25	21.396	0.893	0.821	**	25	0.258	-1.752	0.963	**	25

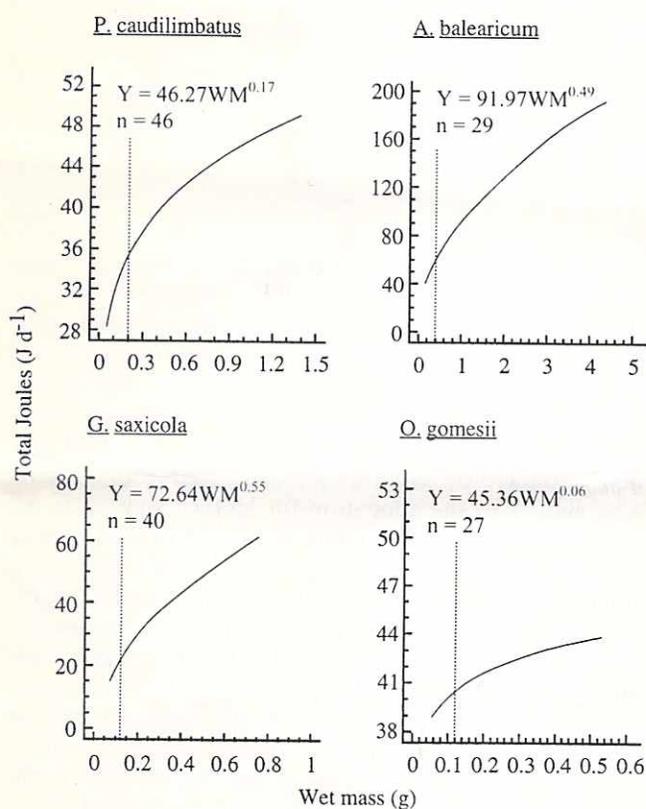


Fig. 1 Least-squares regressions of the total joules required by each species per day ($\text{J ind.}^{-1} \text{day}^{-1}$) against wet mass (g WM). The formula is $Y = a(\text{g WM})^b$; *n* indicates the number of larvae examined. Since the equations result from predicted age values, standard errors and coefficients of determination are not reported. The dashed line indicates the transition from phase Ia (left) to phase Ib (right)

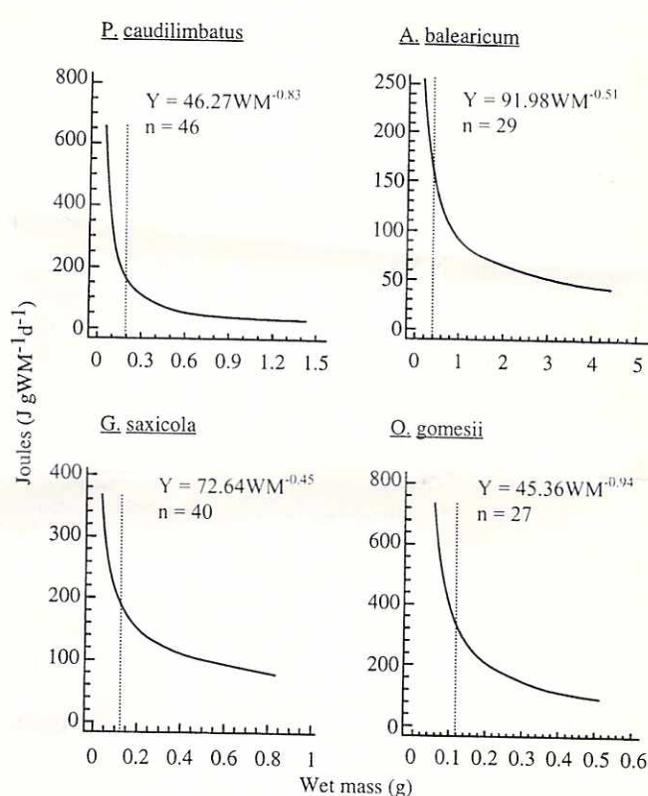


Fig. 2 Least-squares regressions of the mass-specific joules expended per day ($\text{J g}^{-1} \text{WM day}^{-1}$) against wet mass (g WM). The formula is $Y = a(\text{g WM})^b$; *n* indicates the number of larvae examined. Since the equations result from predicted age values, standard errors and coefficients of determination are not reported. The dashed line indicates the transition from phase Ia (left) to phase Ib (right)

with the phase Ia larvae (larvae < 10% of the maximum premetamorphic mass) requiring the most energy per gram, followed by a gradual decrease to an asymptote.

The greatest amount of energy in all four species was allocated to metabolism. The total energy needed to maintain the leptocephalus metabolic rate ranged from 11.1 to 125.6 $\text{J ind.}^{-1} \text{day}^{-1}$ (Table 2). The total energy needed decreased allometrically in phase Ia larvae and remained fairly constant for phase Ib larvae. The percent of the total energy necessary to maintain the metabo-

lism ranged from a minimum of 60% to a maximum of 92% for *G. saxicola* and *Paraconger caudilimbatus*, respectively.

Growth received the second greatest allocation of energy: 1.4 to 74.0 $\text{J ind.}^{-1} \text{day}^{-1}$. The energy allotted to growth increased allometrically with the greatest rate of increase occurring in larvae of < 0.2 g WM. Percentages of the total energy devoted to growth ranged from 3.8% (*Ophichthus gomesii*) to 39.2% (*G. saxicola*) (Table 2).

The smallest fraction of the energy budget, in all larvae, at all sizes, was the energy lost to excretion,

Table 2 Ranges of total joules ($\text{ind.}^{-1} \text{ day}^{-1}$) and percent of total energy (%) allocated to metabolism, growth, and excretion for the four species (NA not applicable)

Species	Total joules ($\text{ind.}^{-1} \text{ day}^{-1}$)		Percent energy (%)	
	Minimum	Maximum	Minimum	Maximum
<i>Paraconger caudilimbatus</i>				
Metabolism	23.27	42.89	80.89	91.5
Growth	2.31	7.64	7.19	16.58
Excretion	0.08	3.26	0.18	11.12
Total	28.76	50.15	NA	
<i>Ariosoma balearicum</i>				
Metabolism	30.72	125.57	62.72	82.73
Growth	7.17	73.97	17	37.27
Excretion	0.03	0.82	1.41	21.19
Total	38.71	198.49	NA	
<i>Gymnothorax saxicola</i>				
Metabolism	11.12	91.21	60.21	91.21
Growth	1.43	21.81	8.35	39.19
Excretion	0.15	3.17	0.26	20.19
Total	15.72	62.64	NA	
<i>Ophichthus gomesii</i>				
Metabolism	32.86	36.77	65.38	90.59
Growth	1.56	17.22	3.85	34.08
Excretion	0.24	2.45	0.54	6.01
Total	38.99	50.53	NA	

ranging from 0.03 to 3.3 $\text{J ind.}^{-1} \text{ day}^{-1}$ (Table 2). The percent of the total energy lost to excretion ranged from a low of 0.2% in *P. caudilimbatus* to 21.2% in *A. balearicum* (Table 2).

Discussion

Leptocephali use a unique growth strategy that allows them to increase rapidly in size while devoting the majority of their energy, not to growth as in most larval fish (Houde and Schekter 1983; Yamashita and Bailey 1989; Keckeis and Schiemer 1992) but to metabolism. The incorporation of GAGs provides a mechanism for rapid growth in wet mass. In addition, the GAGs serve as a gelatinous skeleton (Hulet 1978; Hascall and Hascall 1981). This material provides structure for the muscles to work against in place of a skeleton, conserving energy that would potentially be expended in ossification. It allows for a well-developed anguilliform locomotory ability and a very large larval size with no bony skeleton.

In leptocephali, metabolism received 60–92% of the total ingested energy, much higher than reported values for other larval fish at similar temperatures (Houde and Schekter 1983; Houde 1989; Torres et al. 1996). The high percentages allocated to metabolism may be explained by the mode of nutrition of leptocephali. Transport of DOC across the integument, either as a main nutritional source or supplemental one, is energetically expensive (Withers 1992). The amount of POC required to power the leptocephalus, whether generally in the form of POC, or more specifically as larvacean houses, would require substantial energy expenditure for collection and consumption. Locomotion is energetically expensive and can account for up to 30% of a fish's total energy expenditure (Ware 1975). Either mode of nutrition could theoretically result in elevated metabolic rates.

The amount of energy attributable to excretion losses in young fishes varies among studies. Brett and Groves (1979) obtained nonfecal excretion values equal to 7% of ingested calories. In larval fish, the amount lost to excretion is thought to decrease with ontogeny as assimilation efficiencies increase (Klumpp and von Westernhagen 1986). Torres et al. (1996) found that the energy excreted by red drum larvae ranged from 0.5% to 21%, similar to the allocation for leptocephali.

With the exception of metabolism, the percentages of total energy allocated to each element of the energy budget are comparable to other larval fish, but total energetic requirements of the four species of leptocephalus examined are very different from those of larval fish using the type I developmental strategy. Brightman et al. (1997) determined that the energetic requirements of growing red drum larvae ranged from 0.23 to 0.25 $\text{J ind.}^{-1} \text{ day}^{-1}$ for 14-day-old larvae (0.109 mg DM). If the energy required per day for red drum larvae and *Paraconger caudilimbatus* are both standardized to a dry mass of 0.05 g DM, the red drum larvae would require $96.03 \pm 22.94 \text{ J ind.}^{-1} \text{ day}^{-1}$ compared to $42.48 \pm 10.15 \text{ J ind.}^{-1} \text{ day}^{-1}$, more than double the energy required by the leptocephalus.

DOC in marine ecosystems represents a very large pool of potential energy to organisms adapted for the uptake of these compounds from dilute solution (Manahan and Crisp 1982), leading to the theory that certain aquatic animals acquire nutrients through direct absorption of DOC via the integument. Marine DOC represents one of the largest active reservoirs of organic carbon in the biosphere (Hedges 1992). It contains substances representative of the main biochemical classes: amino acids, carbohydrates, lipids, and vitamins. The amount of DOC usually exceeds the particulate organic fraction by a factor of 10–20. DOC concentrations in the western Gulf of Mexico at a bottom depth of

1550 m and a sampling depth of 2 m are approximately 83 μM (Guo et al. 1994). Using the carbon values of Guo et al. (1994) for DOC, a 0.5 g WM *P. caudilimbatus* would need to absorb and utilize all of the DOC in 1 l of water to obtain the energy it requires each day.

Ingestion of POC by leptocephali has been demonstrated by several authors (Otake et al. 1990, 1993; Mochioka and Iwamizu 1996). Suspended POC in the upper layers of the sea consists mainly of detritus and phytoplankton. The concentration of POC in the euphotic zone is usually considerably higher than in the underlying water. POC occurs in concentrations varying between 0.02×10^{-3} and 0.2×10^{-3} g C l^{-1} , and is an extremely important part of the marine food chain, providing food for organisms at several trophic levels (Parsons 1975). Applying Parsons' (1975) carbon content values for POC to the leptocephalus' energetic requirements, a 0.5 g WM *P. caudilimbatus*, would need to consume and utilize all of the POC in 1 l of seawater.

Appendicularians are important macrozooplankton throughout the world's oceans, episodically reaching very high densities (Alldredge 1976a). They consistently occur in the zooplankton fauna of the oligotrophic central regions of the subtropical convergence, locations of suspected eel spawning. These pelagic tunicates filter particles through a "house", a unique feeding structure secreted around the animal by glandular epithelium on the body. When the external filters become clogged with phytoplankton or particulate matter, the house is discarded but remains in the water column as an organic aggregate (Alldredge 1976b). Houses, macroscopic mucus aggregates ranging from a few millimeters to 2 m in diameters, are highly concentrated energy sources for grazers (Alldredge 1976a). The house constructed by *Oikopleura rufescens*, a larvacean species that produces a house slightly larger than those observed by Mochioka and Iwamizu (1996), combined with attached zooplankton fecal pellets, contains 5.4 ± 1.3 μg C per discarded house (Alldredge 1976a). A 0.5 g WM (80 mm TL) *P. caudilimbatus*, requiring 41.17 J ind.^{-1} day^{-1} , would need to consume 181 larvacean houses and attached particulate matter, sweeping clear on average > 1 m^3 water day^{-1} (Alldredge 1976a). During larvacean blooms densities of houses from *Oikopleura* spp. in the Florida current reach 1130 m^{-3} (Alldredge 1976a), and could theoretically support the leptocephali.

The estimates of required larval consumption presented above are assuming an unlikely assimilation efficiency of 100%. Assimilation efficiency varies with larval fish ontogeny. A literature survey by Govoni et al. (1986) revealed assimilation efficiencies ranging from 44% to 99%. For protein-bound radio-labeled nutrients, larval assimilation efficiencies have been shown to range from 30% to 92% (Rust et al. 1993). There are very few measurements of assimilation efficiencies for detritivorous zooplankton. Ferguson (1973, in Raymont 1983) determined that the assimilation efficiency for marine mysids feeding on algal detritus and cellulose ranged from 10% to 50%. Steinberg (1995) presented an

assimilation efficiency of 60% for copepods feeding on larvacean houses. Regardless of the assimilation efficiency, it is possible for leptocephali to obtain their nutrition solely from DOC, but the amount of POC that the larvae would need to consume, in particular larvacean houses, seems remarkably high. The most likely scenario is that the leptocephali are utilizing a combination of DOC and POC to meet their energetic requirements.

The accumulation of GAGs serves a threefold purpose in leptocephali. First, the larvae grow rapidly with minimal energy expenditure. The large mucopolysaccharides (GAGs) are resistant to compressive forces, thereby providing structural support to the larvae in the absence of ossification. At the same time, the leptocephali avoid the increased energy demands associated with increased size by growing primarily in non-metabolizing mass. The final benefit of the type 2 developmental strategy is the establishment of an energy depot, which in conjunction with lipid stores (Pfeiler 1996), helps fuel the larvae through the complex metamorphic period. The type 2 developmental strategy used by leptocephali allows the larvae to avoid some of the risks incurred by the type 1 larvae trying to avoid visual predators. The developmental strategy of leptocephalus larvae takes advantage of the benefits of increased size while circumventing many of its potential drawbacks.

Acknowledgements The authors would like to express their appreciation to the captains and crews of the R.V. "Hernan Cortez", R.V. "Suncoaster", R.V. "Bellows" and R.V. "Tommy Munro" for their assistance at sea. Thanks also to S. Geiger and J. Donnelly for their assistance and valuable advice, and to numerous volunteers for their shipboard assistance. Ship-time was generously provided by T. Hopkins, the Florida Institute of Oceanography and Gulf Coast Research Laboratories. This research was funded by NSF grant OCE-9712572 to J.J. Torres.

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