Chapter 8
Energetics of the Antarctic Silverfish, *Pleuragramma antarctica*, from the Western Antarctic Peninsula

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Abstract The nototheniid *Pleuragramma antarctica*, commonly known as the Antarctic silverfish, dominates the pelagic fish biomass in most regions of coastal Antarctica. In this chapter, we provide shipboard oxygen consumption and nitrogen excretion rates obtained from *P. antarctica* collected along the Western Antarctic Peninsula and, combining those data with results from previous studies, develop an age-dependent energy budget for the species. Routine oxygen consumption of *P. antarctica* fell in the midrange of values for nototheniids, with a mean of 0.057 ± 0.012 ml O_2 g^{-1} h^{-1} (χ ± 95% CI). *P. antarctica* showed a mean ammonia-nitrogen excretion rate of 0.194 ± 0.042 μmol NH4-N g^{-1} h^{-1} (χ ± 95% CI). Based on current data, ingestion rates estimated in previous studies were sufficient to cover the metabolic requirements over the year classes 0–10. Metabolism stood out as the highest energy cost to the fish over the age intervals considered, initially commanding 89%, gradually declining to 67% of the annual energy costs as the fish aged from 0 to 10 years. Overall, the budget presented in the chapter shows good agreement between ingested and combusted energy, and supports the contention of a low-energy lifestyle for *P. antarctica*, but it also resembles that of other pelagic species in the high percentage of assimilated energy devoted to metabolism. It differs from more temperate coastal pelagic fishes in its large investment in reproduction and its pattern of slow steady growth throughout a relatively long lifespan.

Keywords Fish metabolism • Energy budget • Antarctic fishes

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8.1 Introduction

8.1.1 Pelagic Lifestyle

Few Antarctic fishes have evolved to exploit the pelagic realm. Though a number of notothenioids display benthopelagic habits, or exploit the water column in early life, only one species, the Antarctic silverfish *Pleuragramma antarctica* Boulenger, 1902, retains a pelagic lifestyle through all its life stages (DeWitt 1970; DeVries and Eastman 1978; Eastman and DeVries 1982; Williams 1985; Hubold and Ekau 1987; Donnelly et al. 2004).

Notothenioids, including *P. antarctica*, do not possess a swim bladder. Near-neutral buoyancy in *P. antarctica* is achieved with reduced bone density, a characteristic trait of notothenioids (Eastman et al. 2014; Voskoboinikova et al. 2017), high water content (Reisenbichler 1993), and additional hydrostatic lift provided by a high lipid content (Hagen et al. 2000; Hagen and Kattner 2017). Lipids contributing to buoyancy are composed of triacylglycerols at various levels of saturation and are stored subcutaneously in lipid sacs surrounded by adipocytes (Eastman and DeVries 1989). Depending on the energetic state of the individual, the lipids providing buoyancy may also serve as energy fuel (DeVries and Eastman 1978; Eastman and DeVries 1989; Hagen and Kattner 2017).

P. antarctica dominates the pelagic environment in most regions of coastal Antarctica (Hubold 1984; Donnelly et al. 2004), comprising as much as 90% of the local ichthyofauna (Hubold and Ekau 1987). Comparable biomass dominance is usually only observed in highly productive areas such as the La Plata Estuary in Argentina, where early stages of the anchovy *Engraulis anchoita* range from 60–90% of total biomass (Hubold 1982). The dominance of *P. antarctica* in both numbers and biomass, its circumpolar distribution, and the lack of other pelagic fishes able to tolerate near-freezing waters (Cullins et al. 2011), combine to make *P. antarctica* a keystone species in the Antarctic coastal food web (DeWitt and Hopkins 1977; Hubold 1985; Kellermann 1987).

P. antarctica exploits a variety of habitats in the shelf waters of Antarctica during the course of its life. Floating eggs and early larval stages are associated with seasonal pack ice which provides structure, refuge, and a food source for early stages (Vacchi et al. 2004; Vallet et al. 2011; Guidetti et al. 2015). Post-larval and juvenile stages are found mainly in the upper 100 m of Antarctic shelf waters (Hubold 1984). Adults are found throughout the midwater at depths ranging from 0 to 900 m (Gerasimchuk 1986; Fuiman et al. 2002; Robison 2003). Larger individuals usually reside at greater depth, a size-dependent depth distribution that may reduce cannibalistic feeding on larvae and juveniles by adults (Hubold 1985, 1992; Hubold and Hagen 1997). A similar size-dependent segregation by depth is commonly observed in mesopelagic fishes (Marshall 1971).

Within its circumpolar distribution, *P. antarctica* is restricted to shelf waters. Further offshore, oceanic teleosts such as myctophids predominate (DeWitt 1970; Donnelly and Torres 2008). Though they are similar to *P. antarctica* in size, depth

profiles and feeding habits (Lancraft et al. 2004), myctophids lack the antifreezes required to survive in the frigid ice-shelf waters that typify most of the coastal Antarctic (Cullins et al. 2011). An exception to the clear-cut separation between oceanic and coastal faunal assemblages is found on the Western Antarctic Peninsula (WAP), where *P. antarctica* co-occurs with the myctophids *Electrona antarctica, Gymnoscopelus braueri, and G. nicholsi*, due to the presence of warm (2 °C) circumpolar deep water at mid-depths.

8.1.2 Vertical Migration

P. antarctica exhibits a range of different foraging strategies and daily behavior patterns. They have been observed feeding inshore in large schools (Daniels 1982; Daniels and Lipps 1982), as well as performing diel vertical migrations of 600 m and more in the deeper inshore troughs and fjords (Reisenbichler 1993; Robison 2003; Lancraft et al. 2004). Its migratory pattern allows *P. antarctica* to avoid visual predators such as penguins, seals and flighted-seabirds during the day and to capitalize on abundant prey such as *Euphausia superba* nearer the surface at night (Hopkins and Torres 1988; Robison 2003; Lancraft et al. 2004). Undoubtedly, vertical migration also incurs an energy expenditure as a result of the directed swimming to and from near-surface waters.

8.1.3 Feeding Habits

Larval *P. antarctica*, though primarily carnivorous, are capable of omnivory (Kellermann 1987; Vallet et al. 2011; Koubbi et al. 2007). The prey list of larval stages and juveniles includes diatoms, euphausiid eggs and larvae, copepods, pteropods, and tintinnids (DeWitt and Hopkins 1977; Kellermann 1987; Vallet et al. 2011; Tavernier and Giraldo 2017). Details of prey selection, if present at these stages, are not clear due to regional variations in the distribution and abundance of specific prey types.

Studies on the feeding habits of juvenile and adult *P. antarctica* suggest a diet mainly consisting of copepods, amphipods and euphausiids. Species and relative abundance of prey classes vary according to region, age class and season (DeWitt and Hopkins 1977; Moreno et al. 1986; Reisenbichler 1993). Overall, the feeding strategy of *P. antarctica* is that of a food-generalist throughout its life (Hubold and Hagen 1997). A generalist approach ensures energy acquisition throughout the year for a planktivore in a highly seasonal planktonic community. For recent reviews on diet and trophic ecology of Antarctic silverfish see Pinkerton (2017), and Tavernier and Giraldo (2017).

8.1.4 Growth Pattern

P. antarctica is a slow-growing species, reaching 45 g in 10–11 years (specimen collected in this study, based on growth curves in Reisenbichler 1993, Hubold and Tomo 1989, respectively). Growth rates of *P. antarctica* have been addressed in multiple studies. Region-dependent growth curves are subtly different, but all exhibit a low growth rate (Hubold and Tomo 1989; Radtke et al. 1993; Reisenbichler 1993; La Mesa and Eastman 2012). Reproductive maturity occurs at 13–16 cm (Hubold 1985; Duhamel et al. 1993, Faleyeva and Gerasimchuk 1990) or about 7–9 years of age (Hubold and Tomo 1989; Kock and Kellermann 1991). The observed slow growth and late reproductive maturity of *Pleuragramma* contrast with the life history strategies of temperate analogues such as the sardines and anchovies, which are often shorter-lived and may reproduce as early as the second year of life (e.g. *Sardinops caerulea*, Lasker 1970).

8.2 What Is an Energy Budget?

The energy budget of a species is a summary of how its food energy is utilized. It is grounded in the laws of thermodynamics, which, simply put, states that the "energy ingested by a fish (I) must turn up in one form or another through metabolism (M), growth (G), or excretion (E), where $I = M + G + E$" (Brett and Groves 1979). The amount of energy devoted to each category reflects a species' life history strategy as well as its current life stanza. Thus, active pelagic species such as tuna and sardines have a higher percentage of their ingested energy devoted to metabolism than sluggish species such as sargassum fish. Likewise, younger, quickly growing fish would be expected to devote a larger percentage of their energy intake to growth than older fish already at their maximum size. Comparisons between species are instructive in deducing aspects of species' life history that may be difficult to obtain otherwise, such as activity level.

It is important to recognize that each element of the energy budget represents a rate process that must be measured directly, either on the living fish (metabolism as oxygen consumption rate and nitrogen excretion as ammonium excretion rate), derived from compositional analyses of gut contents collected on a daily basis (ingestion rate or daily ration), or analyses of growth rate using the measured mass of individuals in conjunction with the ages recorded in their earbones (otoliths). The energy budget reported below combines new data for oxygen consumption and ammonium excretion with literature values for ingestion, growth and reproduction. It is a first cut at examining *Pleuragramma*'s energy usage.

8.2.1 Budget Components

The basic energy budget equation is usually stated as $I = M + G + E$, with its elements subdivided as needed to accommodate data sets within each component. For example, growth can be divided into somatic, or organismal growth, and reproductive growth, which refers to the increase in mass of the gonads as they mature prior to spawning. In this chapter the new (oxygen consumption and ammonium excretion) data will be presented first followed by a discussion of the literature-derived (ingestion, growth and reproduction) data used to assemble the budget, the budget itself and comparisons with similar species. Note that oxygen consumption, respiration, and metabolism are used interchangeably throughout the chapter.

8.3 Oxygen Consumption and Ammonium Excretion

8.3.1 Notes on Sampling and Methods

P. antarctica specimens were captured during multiple research cruises to the WAP in 2001, 2002 and 2010. Fishes were collected using a 10 m^2 multiple opening and closing net, with an environmental sensing system (MOCNESS) during two Global Ocean Ecosystem Dynamics (GLOBEC)-sponsored cruises aboard the R/V *Laurence M. Gould* and the R/V *Nathaniel B. Palmer* in the austral autumns and winters of 2001 and 2002. Additional specimens were collected during the austral autumn of 2010 aboard the R/V *Nathaniel B. Palmer*, using a 10 m^2 MOCNESS or a Tucker trawl. Immediately after collection, specimens were transferred to large flow-through tanks filled with 0 °C seawater. All specimens were placed in respiration chambers within 4 h of collection.

Oxygen consumption rates were determined using the methods of Torres and Somero (1988b). Specimens selected for measurements were in excellent condition, but had recently been captured in a midwater trawl. Rates should therefore be considered as estimates of routine metabolism; they are not comparable to rates determined on animals that can be maintained for long periods of time in the laboratory.

Ammonium (NH$_4$) excreted by each specimen during the respirometric trial was quantified by following the methods described in Jones (1991) as modified by Masserini and Fanning (2000). Briefly, frozen water samples (20 ml) collected before and after each respiratory run were thawed, diluted with deionized water and analyzed for ammonium with a Technicon® Auto Analyzer II. An ammonium-permeable membrane separated the water sample from a continuous flow of o-phthaldialdehyde reagent. The reagent binds to the permeating ammonium, forming a fluorescent product later quantified by the autoanalyzer. Ammonium concentrations in the respirometric chamber prior to each run were subtracted from the ammonium present in the final sample. Corrected ammonium concentrations were

Table 8.1 Oxygen consumption, nitrogen excretion, and O:N (atomic ratio) of *Pleuragramma antarctica* in three different mass ranges

| Mass (g) χ ± 95% CI (n) range	VO$_2$ (ml O$_2$ g^{-1} h^{-1}) χ ± 95% CI (n) range	Nitrogen excretion (μmol-N g^{-1} h^{-1}) χ ± 95% CI (n) range	O:N χ ± 95% CI (n) range
1.608 ± 0.327 (6) 1.024–2.187	0.058 ± 0.011 (6) 0.04–0.08	0.218 ± 0.033 (6) 0.161–0.277	23.352 ± 3.514 (6) 17.656–30.858
16.800 ± 2.856 (3) 14.1–19.1	0.059 ± 0.043 (3) 0.022–0.097	0.144 ± 0.073 (3) 0.096–0.218	34.108 ± 13.858 (3) 20.042–42.397
36.5 ± 9.510 (3) 28.7–45.4	0.051 ± 0.030 (3) 0.023–0.076	0.194 ± 0.144 (3) 0.057–0.309	26.657 ± 9.392 (3) 21.826–36.241
14.129 ± 8.729 (12) 1.024–45.4	0.057 ± 0.012 (12) 0.022–0.097	0.194 ± 0.042 (12) 0.057–0.309	26.967 ± 4.695 (12) 17.655–42.397

Bottom line is overall mean for data set

divided by the total run time to acquire an estimate of ammonium excretion per individual per hour.

8.3.2 Metabolism

Mean oxygen consumption of *P. antarctica* for the entire data set was 0.057 ± 0.012 ml O2 g^{-1} h^{-1} (χ ± 95% CI) (Table 8.1). VO$_2$ scaled with mass according to the equation $y = aX^b$, where y = oxygen consumption (μl O$_2$ individual^{-1} h^{-1}) and X = mass in mg (Fig. 8.1), with a slope or "b-value" of 0.932, indicating a nearly direct scaling with mass.

The fish sizes shown in Fig. 8.1 include standard lengths from 60 to 174 mm and masses from 1 to 45 g, roughly corresponding to year classes of 2–10 years (Reisenbichler 1993). Experimental subjects reflected the size structure of the silverfish population during the time of sampling (Parker et al. 2015). Smaller fish dominated the 2001–2002 cruises while larger fish were more abundant in 2010.

Routine oxygen consumption of *P. antarctica* fell in the midrange of values for nototheniids normalized to a mass of 10 g (low: 0.037 ml O$_2$ g^{-1} h^{-1} for *Trematomous hansoni*; high: 0.175 ml O$_2$ g^{-1} h^{-1} for *T. bernacchii*; Table 8.2) and likewise for the (non-nototheniid) notothenioids in general (0.036–0.061 ml O$_2$ g^{-1} h^{-1} for *Harpagifer georgianus* and *Gymnodraco acuticeps* respectively, Table 8.2). Interestingly, *P. antarctica* respiration was quite similar to that of *Pagothenia borchgrevinki* (0.050–0.069 ml O$_2$ g^{-1} h^{-1}). Mesopelagic fishes, normally excluded from coastal regions by the very cold (−2 °C) Antarctic shelf waters (DeWitt 1970; Donnelly and Torres 2008) and a lack of endogenous antifreezes, are well represented on the WAP shelf, largely due to the presence of warm (2 °C) circumpolar deep water at mid-depths (Klinck et al. 2004). *P. antarctica* and the myctophid *E. antarctica* exhibit a similar vertical migration pattern where they co-occur on the WAP shelf, and have a similar diet (Lancraft et al. 2004). The metabolic rate of
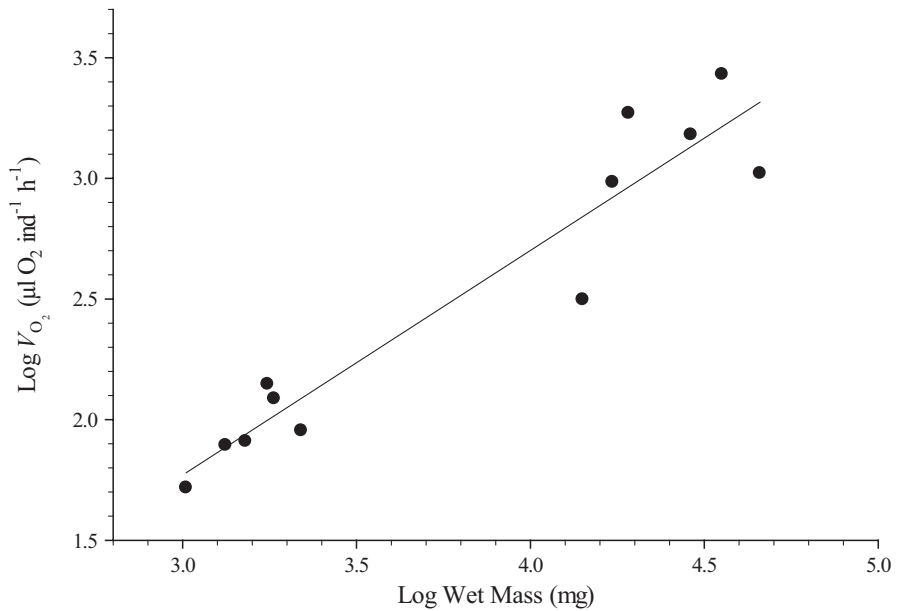
Fig. 8.1 Whole-individual respiration rate as a function of wet mass in *Pleuragramma antarctica* from the Western Antarctic Peninsula. Data were fitted to the equation Log y = −1.0208 + 0.9306 Log x; where y is the whole individual respiration rate and x is wet mass ($r^2 = 0.91$). Oxygen-consumption rates were determined following the methods described by Torres and Somero (1988b)

Electrona is slightly less (0.039 vs 0.050 ml O_2 g^{-1} h^{-1}; Table 8.2) than that of *P. antarctica* but its foraging strategy and vertical profile are quite similar. The deeper living myctophids, *G. braueri* and *G. opisthopterus*, are more similar to *P. antarctica* in size. They also vertically migrate, but remain at greater depth in their daily vertical excursions (Torres and Somero 1988a; Lancraft et al. 1989). The two deeper-living myctophids and the bathylagid, *Bathylagus antarcticus,* exhibited metabolic rates less than half those of *Electrona* and *Pleuragramma*.

A comparison of *P. antarctica* respiration with temperature- and mass-corrected rates of coastal pelagic species from other regions revealed similar rates to those of the two anchovies (Table 8.2), but about half that of the California sardine, a species it more closely resembles in size. Overall, its routine respiration rate, like that of its benthic relatives, suggests a capability for modest activity but not a lifestyle that involves continuous swimming (cf. La Mesa and Eastman 2012). The ratio of the maximum rate recorded in each run to the routine rate (see methods) produced an overall mean of 2.25 ± 0.59 (χ ± 95% CI) for the data set, suggesting a factorial scope of at least 3 for the ratio between minimum and maximum rates. Forster et al. (1987) reported a range of 3.94 to 5.68 for *P. borchgrevinki,* which is believed to alternate periods of activity with periods of rest in the near-surface platelet ice.

Table 8.2 Mass specific oxygen consumption rates in Antarctic pelagic and coastal species at intermediate weight and a standardized 10 g individual

Refs.	Species (Family)	Habits and depth distribution	IW (g)	OCR at 0.5 °C (μl O_2 mg wet weight^{-1} h^{-1})		Slope (b)	Intercept (a)
				IW V_{O_2}	10-g V_{O_2}		
[1]	*Pleuragramma antarctica* (Nototheniidae)	Pelagic planktivore	22.5	0.048	0.050	0.932	0.059
[2]	*Bathylagus antarcticus* (Bathylagidae)	Deep pelagic planktivore	25	0.015	0.016	0.889	0.021
	Electrona antarctica (Myctophidae)	Pelagic planktivore	5	0.040	0.039	0.946	0.044
	Gymnoscopelus braueri (Myctophidae)	Pelagic planktivore	–	–	0.026	1.029	0.024
	Gymnoscopelus opisthopterus (Myctophidae)	Pelagic planktivore	20	0.021	0.022	0.942	0.025
[3]	*Pagothenia borchgrevinki* (Nototheniidae)	Cryopelagic active	50	0.040	0.050	0.825	0.075
[4]	*Chaenocephalus aceratus* (Channichthyidae)	Hemoglobin-free ice fish	1048	0.019	0.061	0.750	0.108
	Pseudochaenichtys georgianus (Channichthyidae)	Benthic, 70–200 m	36	0.028	0.039	0.750	0.069
	Parachaenichthys charcoti (Bathydraconidae)	Ice fish, benthic 120–150 m	557	0.017	0.047	0.750	0.083
[5]	*Chaenocephalus aceratus* (Channichthyidae)	Benthic 90–160 m	~1000	0.016	0.051	0.750	0.090
	Notothenia gibberifrons (Nototheniidae)	Benthic, 90–160 m	470	0.016	0.042	0.750	0.074
	Notothenia neglecta (Nototheniidae)	Shallow water benthic	1000	0.020	0.063	0.750	0.112
[6]	*Harpagifer georgianus* (Harpagiferidae)	Nearshore benthic-sedentary	4	0.040	0.036	0.670	0.076
	Notothenia angustifrons (Nototheniidae)	Nearshore bentho-demersal	20	0.067	0.088	0.861	0.121
	Notothenia nudifrons (Nototheniidae)	Nearshore bentho-demersal	15	0.049	0.061	0.888	0.079
	Notothenia rossii (Nototheniidae)	Off-shore demerso-pelagic	350	0.023	0.108	0.616	0.262

Table 8.2 (continued)

Refs.	Species (Family)	Habits and depth distribution	IW (g)	OCR at 0.5 °C (µl O$_2$ mg wet weight^{-1} h^{-1}) IW V_{O_2}	10-g V_{O_2}	Slope (b)	Intercept (a)
	Trematomus hansoni (Nototheniidae)	Nearshore and off-shore bentho-demersal	45	0.019	0.037	0.693	0.075
[7]	*Notothenia neglecta* (Nototheniidae)		1000	0.037	0.143	0.785	0.234
	Notothenia rossii (Nototheniidae)		500	0.027	0.046	0.958	0.051
[8, 9]	*Pagothenia borchgrevinki* (Nototheniidae)		108	0.038	0.069	0.750	0.123
	Gymnodraco acuticeps (Bathydraconidae)		74	0.037	0.061	0.750	0.108
	Rhigophila dearborni (Zoarcidae)		32	0.012	0.016	0.750	0.029
[10, 11, 12]	*Trematomus bernacchii* (Nototheniidae)		148	0.064	0.175	0.752	0.309
	Trematomus hansoni (Nototheniidae)		30	0.072	0.092	0.845	0.132
	Trematomus loennbergii (Nototheniidae)		106	0.051	0.043	0.997	0.043
	Rhigophila dearborni (Zoarcidae)		30	0.018	0.026	0.965	0.028
[13]	*Sardinops caerulea* (Clupeidae)	Pelagic filter feeder	85	0.075	0.128	0.75	0.228
[14]	*Engraulis mordax* (Engraulidae)	Pelagic filter feeder	9	0.055	0.053	0.750	0.095
[15]	*Engraulis capensis* (Engraulidae)	Pelagic filter feeder	6	0.067	0.059	0.750	0.105

Slopes (b) and intercepts (a) correspond to the equation $y = aX^b$ relating whole individual oxygen consumption rate (y; ml O$_2$ individual^{-1} h^{-1}) and the total wet body weight (x; g). Values for b and a came from the reference cited except in Hemmingsen and Douglas (1970) and Holeton (1970), where b = 0.75 was arbitrarily assigned for purposes of calculation. Temperature conversion to 0.5 °C was necessary only in the case of Morris and North (1984), whose rates were determined at 3 °C and in James et al. (1989), whose rates were determined at 16.2 °C; a Q$_{10}$ of 2.0 was used. Information on Antarctic fish habits and depth distribution from Targett (1981) and Morris and North (1984). For information on additional species see Macdonald et al. (1987). *OCR* Oxygen Consumption Rate, *IW* Intermediate Weight. References: [1] Present study; [2] Torres and Somero (1988a); [3] Forster et al. (1987); [4] Hemmingsen and Douglas (1970); [5] Holeton (1970); [6] Morris and North (1984); [7] Ralph and Everson (1968); [8] Wells (1987); [9] Steffensen (2005); [10] Wohlschlag (1960); [11] Wohlschlag (1963); [12] Wohlschlag (1964); [13] Lasker (1970); [14] Childress and Somero (1979); [15] James et al. (1989)
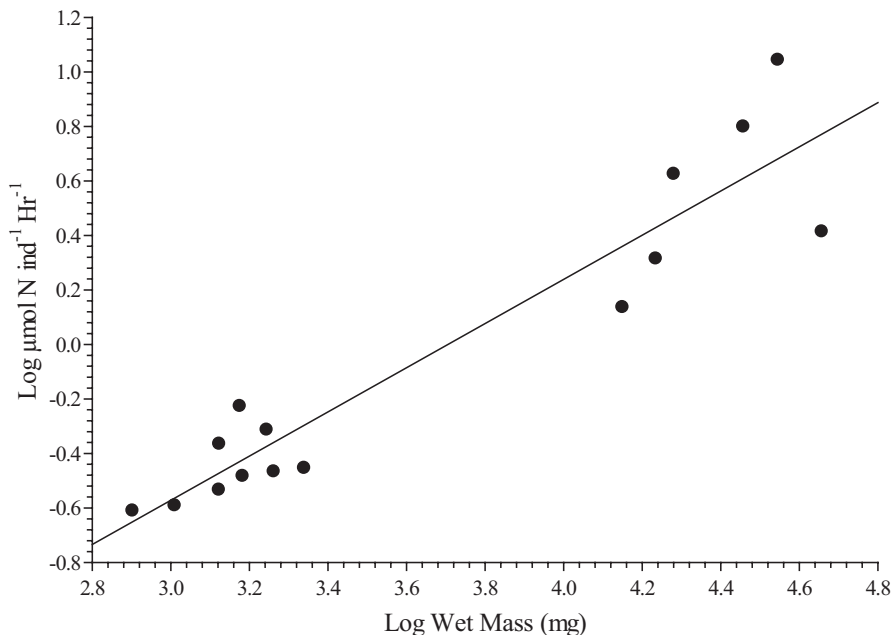
Fig. 8.2 Whole-individual nitrogen excretion rate as a function of individual wet mass of *Pleuragramma antarctica* from the Western Antarctic Peninsula. Data were fitted to the equation Log y = −3.004 + 0.8105 Log x; where y is the whole individual nitrogen excretion rate and x is wet mass ($r^2 = 0.89$)

8.3.3   Nitrogen Excretion

P. antarctica showed an ammonium-nitrogen excretion rate ranging from 0.057 to 0.309 μmol $NH4$-N g^{-1} h^{-1} (Table 8.1) and an overall mean of 0.194 ± 0.042 μmol $NH4$-N g^{-1} h^{-1} (χ ± 95% CI). Nitrogen excretion scaled with mass according to the equation $y = aX^b$, where y represents ammonium-nitrogen excretion rate (μmol $NH4$-N individual^{-1} h^{-1}) and X represents mass in mg (Fig. 8.2). The intermediate slope or "b-value" of 0.808 indicated a more pronounced decrease in nitrogen excretion rate with increasing mass than was observed with oxygen consumption rate, and is in the mid-range of b-values reported for other species (Boyce 1999).

An index that is useful for determining the biological substrate being oxidized is the O:N ratio, the ratio of the moles of oxygen consumed to the moles of ammonia N excreted. If all amino acids resulting from protein catabolism are deaminated with all N excreted as NH_4, and all C-skeletons go to CO_2 and H_2O, then the theoretical O:N minimum is 9.3; generally for carbohydrates 20–30; lipids >30. Since metabolizable carbohydrates are only present in minute quantities outside of the algal community (cf. Donnelly et al. 1994; Torres et al. 1994), the metabolic substrates encountered by carnivorous pelagic species such as *Pleuragramma* will

Table 8.3 Summary of ammonium-Nitrogen excretion rates for *Pleuragramma antarctica* and other marine fishes with disparate life histories

Family	Species	Habit location	AE	WMR	Refs.
Nothotheniidae	*Pleuragramma antarctica*	Pelagic zooplanktivore Antarctic	0.194	1–45	[1]
Harpagiferidae	*Harpagifer antarcticus*	Benthic Antarctic	0.066	6–36	[2]
Blenniidae	*Blennius pholis*	Benthic intertidal North Atlantic	0.045	5	[3]
Clupeidae	*Brevoortia tyrannis*	Pelagic planktivore North Atlantic	0.046	302	[4]
Engraulidae	*Engraulis capensis*	Pelagic planktivore South Africa coastal	0.187	200–600	[5]
	Engraulis mordax	Pelagic planktivore California coastal	0.17	9	[6]
Cottidae	*Taurulus bubalis*	Intertidal North Atlantic	0.207	27	[7]
Labridae	*Crenilabrus melops*	Intertidal North Atlantic	0.156	109	[7]
Salmonidae	*Oncorhynchus nerka*	Ne pacific	0.191	29	[8]
	Oncorhynchus mykiss	Temperate fresh water	0.094	129	[8]

AE Ammonium Excretion (μmol g wet mass^{-1} h^{-1}), *WMR* Wet Mass Range (g). References: [1] present work (Table 8.1); [2] Boyce (1999); [3] Sayer and Davenport (1987); [4] Durbin and Durbin (1981); [5] James et al. (1989); [6] McCarthy and Whitledge (1972); [7] Sayer and Davenport (1987); [8] Brett and Groves (1979)

be a mix of protein and lipid, with the O:N value indicating which, if either, predominates.

The O:N ratio (NH$_4$-N) ranged from 17.66 to 42.40 with a mean of 26.97 (Table 8.1) suggesting a prey spectrum including some items with high lipid levels, such as *Euphausia crystallorophias* for the larger fish, and lipid-rich copepods such as *Calanoides acutus* and *Calanus propinquus* for the smaller specimens (Torres et al. 1994; Donnelly et al. 1994). Crystal krill and the two calanoids are well established as important in the diets of silverfish at the sizes addressed in the present study (La Mesa and Eastman 2012). Since all rates were obtained in the austral autumn, overwintering lipid deposition would have been well underway in the copepods.

Few data on nitrogen excretion in Antarctic fishes are available for comparison. The benthic plunderfish, *Harpagifer antarcticus,* exhibits a rate about a third that of *P. antarctica* (Table 8.3), which is fairly typical of comparisons between benthic and pelagic species (Handy and Poxton 1993; Brett and Groves 1979). *H. antarcticus* exhibits a low VO$_2$ as well (Table 8.2), suggesting a sedentary life-style. Temperature-corrected values from other species are the only other available comparisons, but they are informative. The two anchovies showed rates very similar to that of the

silverfish (Table 8.3), but another pelagic species, the Atlantic menhaden (*Brevoortia tyrannus*), was about 25% of that in *P. antarctica* (Durbin and Durbin 1981). Techniques employed for measurement in the two anchovies were most similar to that used in the present study, with determinations made on fishes in individual chambers. Menhaden determinations were taken on a small school of fish in a controlled laboratory setting, a near-ideal situation. For all species but *P. antarctica* in Table 8.3, experimental subjects were starved for a minimum of 36 h, and most for 6 days or more. Overall, silverfish NH4 excretion most closely resembled that of moderately active species of similar size.

8.4   Energy Budget Components

A simple energy budget that uses a combination of the best, and in many cases the only, information available for each budget category is presented in Tables 8.4 and 8.5. Table 8.4 shows data presented in kcal; Table 8.5 shows the budget broken down in terms of percent of assimilated energy. For a species that must be manipulated only in the field, usually on board ship due to its limited longevity after capture, the information is reasonably good. In Table 8.4 data are presented in kcal for ease of comparison with previous literature. To convert to kJ multiply by 4.19.

Table 8.4 Energy budget for *Pleuragramma antarctica*

A	SL	WM	GE	I	Met	Gr	NH_4 exc	Tot N exc	RE (kcal year^{-1}) GSI 15	GSI 25	GSI 45	O:N
1	46.73	0.27	0.09	2.65	1.88	0.09	0.16	0.20				24.43
2	63.62	1.28	0.58	7.61	5.04	0.49	0.37	0.46				24.63
3	79.91	3.18	1.85	15.77	9.95	1.27	0.67	0.83				25.01
4	95.60	6.07	4.31	27.42	16.65	2.46	1.05	1.30				25.59
5	110.69	10.01	8.41	42.78	25.20	4.10	1.50	1.87				26.38
6	125.18	15.07	14.62	62.03	35.63	6.21	2.03	2.52				27.39
7	139.07	21.30	23.43	85.35	47.98	8.81	2.63	3.26	3.51	5.86	10.54	28.64
8	152.36	28.74	35.35	112.87	62.25	11.92	3.29	4.08	5.30	8.84	15.91	30.12
9	165.05	37.44	50.92	144.73	78.49	15.56	4.03	4.99	7.64	12.73	22.91	31.86
10	177.14	47.42	70.66	181.05	96.70	19.75	4.82	5.98	10.60	17.67	31.80	33.86

Values for caloric growth and ingested energy from equations in Reisenbichler (1993). Metabolism, excretion, and O:N calculated from data acquired in the present study. Reproductive energy was estimated using gonadosomatic indices (GSIs) of 15%, 25%, and 45% (Kock and Kellermann 1991) and age-specific caloric densities (kcal g wm^{-1}) from Reisenbichler (1993). Reproductive energy values assumed that the caloric densities for the gonads were equivalent to that of whole *P. antarctica*.

A Age (years), *SL* Standard Length (mm), *WM* Wet Mass (g), *GE* Gross Energy (kcal ind^{-1}), *I* Ingestion (kcal year^{-1}), *Met* Metabolism (kcal year^{-1}), *Gr* Growth (kcal year^{-1}), *NH4 exc* NH_4 excretion (kcal year^{-1}), *Tot N exc* Total N excretion (kcal year^{-1}), *RE* Reproductive Energy

Table 8.5 Energy budget for *Pleuragramma antarctica*

A	M	Gr	NH$_4$ exc	Total N exc	RE GSI 15	GSI 25	GSI 45
1.00	88.98	4.09	7.51	9.31			
2.00	82.82	8.05	6.13	7.60			
3.00	78.81	10.06	5.33	6.60			
4.00	75.90	11.23	4.79	5.94			
5.00	73.64	11.98	4.40	5.45			
6.00	71.80	12.51	4.09	5.08			
7.00	70.26	12.90	3.85	4.77	5.15	8.58	15.44
8.00	68.94	13.20	3.65	4.52	5.87	9.79	17.62
9.00	67.78	13.44	3.48	4.31	6.60	10.99	19.79
10.00	66.76	13.63	3.33	4.13	7.32	12.20	21.95

Caloric values from Table 8.4 expressed as percent of total annual assimilated energy

8.4.1   Ingestion (I)

Data for ingestion in calories come from Reisenbichler (1993), whose values for ingestion (1.22 ± 0.38% wet mass: χ ± SD for ages 4–9) agree well with those of Olaso et al. (2004) (1.03% over the same age interval), although Reisenbichler (1993) provided caloric values for the stomach contents. Based on the results of both studies, the gastric evacuation rate was assumed to be once per day for purposes of generating the value for ingestion. Using the general equation of Brett and Groves (1979; see below) assimilated energy was assumed to be 80% of the ingested energy listed in Table 8.5.

8.4.2   Somatic Growth (G)

Caloric growth for WAP silverfish was obtained from Reisenbichler (1993) whose growth curve is nearly superimposable on that of Hubold and Tomo (1989), but who also provided equations for calculating yearly caloric (kcal g WM^{-1}) values for ages 1–10. As in Hubold and Tomo (1989), Reisenbichler's ages were determined using the annular rings of otoliths (sagittae). Landmark ages, such as onset of reproduction at age 7, were the same as those reported in Hubold and Tomo (1989) and Kock and Kellermann (1991).

8.4.3   Reproductive Investment

In the absence of data on reproductive output, energy used in reproduction was estimated using gonadosomatic index (GSI: mass of the gonad as a percent of total mass) values of 15%, 25%, and 45% (Kock and Kellermann 1991); caloric values for the gonad were calculated based on the caloric value of whole-fish tissue for that age interval. Values of 15% to 40% have been recorded for other nototheniids (Kock 1992), and what data are available suggest that *P. antarctica* is a particularly fecund species (La Mesa and Eastman 2012; La Mesa et al. 2014).

8.4.4   Metabolism (M)

Oxygen consumption rates were collected as previously described in *8.4.1*. Yearly values were estimated for the age interval preceding the listed age, e.g. for age 2, between ages of 1 and 2. Mid-year values of mass were used to compute the metabolism and excretion numbers for the age interval. Oxygen consumption rates were converted to kcal g WM^{-1} day^{-1} using an oxycalorific equivalent of 4.63 kcal l^{-1} O_2, assuming mixed metabolic substrates (Brett and Groves 1979).

8.4.5   Excretion (E)

Ammonium excretion rates were collected as previously described in *8.4.1*. As with metabolism, yearly values were generated for the age interval preceding the listed age, e.g. for age 2, between ages of 1 and 2. Mid-year values of mass were used to compute the excretion numbers for the age interval. In studies where nitrogen excretion values are reported (e.g. Durbin and Durbin 1981; James et al. 1989), values are usually given for excreted ammonium, or total ammonium nitrogen (TAN), and, if measured, dissolved organic nitrogen (DON). For marine fishes, TAN is 70 to 80% of the total nitrogen excreted, and the remainder is mainly urea and a differing suite of other nitrogenous compounds including creatine, creatinine and tri-methyl amine oxide (McCarthy and Whitledge 1972; Durbin and Durbin 1981). The values for *P. antarctica* in Table 8.4 used our data for TAN only, using the caloric conversion for the combustion of ammonia (5.94 kcal g^{-1} ammonia) obtained from Elliot and Davison (1975). Durbin and Durbin (1981) give a ratio for DON to TAN of 0.437, i.e. DON-N / TAN-N = 0.437, or 69.6% TAN to 30.4% DON by mass. If it is assumed that the TAN is 70% of the total excreted N, their equation provides a useful way of arriving at a total N if DON data are unavailable. Further, if the remaining 30% is assumed to be solely composed of urea (cf. James et al. 1989) a caloric value for a hypothetical total N excretion can be estimated. Working within these assumptions and using a caloric conversion of 2.57 kcal g^{-1} urea, an estimated value for

total N excreted is reported in Table 8.5 both in terms of kcal year^{-1} and % of assimilated energy. O:N uses only the TAN data for the ratio. If hypothetical total N were used, the ratio would be adjusted downward by 26%.

8.5 Energy Budgets: *Pleuragramma* and Other Coastal Pelagic Fishes

Brett and Groves (1979) reviewed the literature on energy budgets in fish up until the time of publication, and, based on data available from 15 studies, presented a general energy budget for young, fast-growing carnivorous fishes:

$$100\,I = (44 \pm 7)\,M + (29 \pm 6)\,G + (27 \pm 3)\,E\,(all\,\text{values}\,\chi \pm 95\%\,CI)$$

This equation provides an excellent standard of comparison for fishes in general and carnivorous fishes in particular. From the total calories ingested (I) 27% of those calories are lost through excretory processes (E) including energy lost as feces (20%) and as excreted nitrogen (7%). Growth (G) included only somatic growth; no reproductive losses were noted. Metabolism (M) was derived from respirometric analysis and, as above, converted to kcal g WM^{-1} day^{-1} using an oxycalorific equivalent of 4.63 kcal l^{-1} O$_2$. The spectrum of life-styles covered did not include any pelagic species, but did include salmonids, a variety of freshwater species including pike and perch, and the cod *Gadus morhua*. Most species used were moderately active ambush predators. Metabolism ranged from 36 to 76.5%; growth ranged from 3 to 74% and excretion from 1.3 to 49.4%. Most of the values for each budget category were within 10% of the figures in the equation above.

A few characteristics stand out in *Pleuragramma*'s acquisition and use of energy (Tables 8.4 and 8.5). First, the ingestion rate is fairly low relative to other species. Results from two studies, Reisenbichler (1993) and Olaso et al. (2004), reported nearly identical values for ingestion as a percent of wet mass (1.2% and 1.0% respectively). Field-based estimates of the daily ration for a variety of oceanic fishes were in the range of 2–6% of wet body mass (Gartner et al. 1997), with fishes of comparable size to *P. antarctica* in the range of 2–4%. Most of these were from subtropical temperatures. Laboratory based measurements of daily ration are available for brown trout (Elliott 1975a, b) in closely controlled conditions. Elliot reported a maintenance ration level for brown trout of 1.4% of wet mass per day at a fish mass of 50 g and a mid-range temperature for the species of 10 °C. A maintenance ration provides enough energy for survival, but not enough for growth. The optimum ration for growth (maximum growth per unit ration) was 2.4% of wet mass per day, and the maximum ration was 2.8%. Experiments were conducted with the amphipod, *Gammarus pulex,* as food. Similar experiments were conducted on sockeye salmon (Brett et al. 1969) using a variety of prepared feeds as well as marine zooplankton (frozen *Calanus plumchrus)*. The maintenance ration for the highest calorie diet was about 0.6% of wet mass per day, and the maximum ration was 2.1%

of wet mass per day for a 50 g fish at 15 °C. The maximum ration of the commercial feed produced a daily growth rate of 3% of body mass per day. In contrast, the maintenance ration for the marine zooplankton diet was 1.8% of wet mass and the maximum ration was 4.2% per day. Corresponding daily growth for maximum ration using the copepods was only 1% per day, a big drop from the 3% observed with the commercial feed.

Despite the fact that the daily ration for *P. antarctica* was in the low end of the continuum for oceanic fishes, ingestion was sufficient to cover the metabolic requirements over the age intervals considered here (Tables 8.4 and 8.5). Metabolism stands out as the highest energy cost to the fish, commanding between 89% and 67% of the annual energy costs as the fish aged from 0 to 10 years. Though clearly quite high, the California sardine, *Sardinops caerulea,* showed a similar high cost of respiration, only in a reverse pattern with age. Metabolism consumed 81.5–97.9% of the total energy used by the fish between the year classes of 0 and 6 (Lasker 1970). The main difference between the two species was in the pattern of growth and its share of the energy budget.

The sardine grows most rapidly in its first 4 years of life, reaching 78% of the species' maximum length (280 mm; Butler et al. 1996) and exhibiting a rapidly declining investment in assimilated energy from years 1 to 4 (18.5–3.0%; Lasker 1970) as growth in length and mass levels off at the asymptotic size. In contrast, though the silverfish shows large annual increases in length from years 2–5 (36% declining to 16%, Table 8.5) and similarly in mass (373% declining to 65%), it only reaches 44% of its maximum length (maximum about 250 mm; La Mesa and Eastman 2012) by age 5 and it shows the opposite pattern of energy devoted to growth. Investment in growth increases annually from 8 to 12% of assimilated energy and remains within 2% of that level for the entire age interval considered here (Table 8.5). Low-cost growth is achieved with a low caloric density in the first 4 years and a steady low energy of investment and low rate of growth until death (Hubold and Tomo 1989; Reisenbichler 1993).

Sexual maturity occurs in *P. antarctica* at a length of 13–16 cm (La Mesa and Eastman 2012) corresponding to an age of 7–10 years in Table 8.5 (Reisenbichler 1993; Hubold and Tomo 1989). The literature provides good agreement on size at maturity, less so on age at maturity, which is the result of discrepancies in size at age. The majority of growth curves agree well with the size at age in Table 8.5, which come from Reisenbichler (1993). Data from Hubold and Tomo (1989) are essentially identical and like Reisenbichler (1993), were generated for fishes from the WAP. Sutton and Horn (2011), using fishes from Ross Sea, put the 13–16 cm size range at ages of 6–10 years, whereas Gerasimchuk (1992) puts the size at maturity at ages of 4–5 years for females and 4–7 years for males. All studies on reproductive output agree on the time of spawning as July–August (e.g. Kock and Kellermann 1991; Ghigliotti et al. 2017), time of hatch at October–November (Hubold and Tomo 1989; Vacchi et al. 2004) and a very high fecundity (Gerasimchuk 1987; La Mesa et al. 2014). Gerasimchuk reported 4315–17,774 eggs per female for

silverfish captured in the Mawson Sea, scaling directly with fish mass (124.9 ± 4.4 eggs g^{-1}; χ ± SD) (Gerasimchuk 1987). More recently, fecundity of silverfish captured on the WAP shelf was reported by La Mesa et al. (2014) to be between 3000 and 12,000 eggs per female and between 80 and 190 eggs g^{-1}, also scaling directly with fish size.

Hypothetical values for reproductive investment are presented in Tables 8.4 and 8.5 for ages between 7 and 10 years, using GSI values proposed for silverfish by Kock and Kellermann (1991) and assuming that increases in mass due to gonad development are equivalent in energy density to that of the whole fish (likely an underestimate). Values for reproductive investment as a percentage of assimilated calories range from 5.2% at a GSI of 15 at age 7, to 22% for a GSI of 45 at age 10. Enough latitude exists within the budget to accommodate a GSI of about 30 at ages 7 and older, supporting a case for high fecundity in *P. antarctica*, even with the many assumptions used to generate the numbers.

GSI for the California sardine was assumed to be 10 in the energetics study of Lasker (1970), representing an energetic investment of between 0.7% and 1.2% of assimilated calories between the ages of 1 and 6. Depending on latitude, young sardines are capable of reproduction in their first or second year of life (Butler et al. 1996), a very different reproductive strategy than that exhibited by *P. antarctica*. A GSI of 10 is also typical of the gadoids (Kock 1992).

Nitrogen excretion, whether as computed total N or measured NH4, is a continuous low level energy loss originating from protein breakdown and tissue maintenance. In a laboratory setting, N excretion can be monitored with precision, and it spikes for a few hours after feeding before returning to a fairly consistent endogenous, or maintenance level (Durbin and Durbin 1981). The excretion rates reported here most closely resemble the endogenous values, as any feeding in the recently captured fish would have taken place hours before data acquisition. N excretion when combined with VO$_2$ as the O:N ratio is also useful in producing insights on composition of ingested prey, since it reflects their protein-lipid composition. For *P. antarctica*, the O:N ratio produces the fairly unremarkable conclusion of a diet high in protein and lipid, typical of the chemical composition of known prey such as *E. crystallorophias*.

Overall, the budget in Tables 8.4 and 8.5 shows good agreement between ingested and combusted energy despite the fact that the data come from a variety of sources. It supports the contention of a low budget lifestyle for *P. antarctica*, but it also resembles that of other pelagic species in the high percentage of assimilated energy devoted to metabolism, particularly when compared to the general energy budget of Brett and Groves (1979). It differs from more temperate coastal pelagics in its large investment in reproduction, its slow pattern of steady growth throughout its life, and its fairly long life.

8.6   Concluding Remarks

Pleuragramma's lifestyle most closely resembles that of a mesopelagic vertically migrating fish, with a few caveats. First, the fact that it spawns *en masse* under the fast ice in Terra Nova Bay (Vacchi et al. 2004) points to a shoaling and schooling component to its behavioral repertoire that is never observed in other oceanic migrators. Schooling behavior involving thousands of individuals was observed first-hand by Daniels (1982) while diving under fast-ice on the WAP shelf, and was believed to be associated with feeding on biota associated with the underside of the ice. Whether schooling is the norm and vertical migration only occurs at low population densities is difficult to resolve with the data available. Certainly *P. antarctica* is capable of purposeful horizontal movement; it has been directly observed (Daniels 1982) and must be inferred from the data of Vacchi et al. (2004, 2012). In addition, the presence of benthic fauna in its gut reported by Daniels (1982) suggests occasional interaction with the shallow benthos on the WAP shelf.

Mesopelagic vertical migrators, which include myctophids and *P. antarctica* (at least part of the time), are found pan-globally (Robison 2003). They typically spend their daytime hours at depths from 400 to 800 m and swim to near-surface waters at night. Submersible observations indicate that migrating fishes exhibit a greatly reduced activity level ("lethargic behavior") at depth (Barham 1971), reminiscent of that reported by Fuiman et al. (2002) and La Mesa and Eastman (2012) for *P. antarctica* using critter-cams and ROVs. A diel rhythmicity in activity level greatly reduces energy expenditure, particularly for near-neutrally buoyant species that are able to reduce swimming activity to very low levels when not actively hunting or migrating. Vertical migration to depths of 400 m or greater effectively reduces their predator spectrum for part of the day to deep-diving species such as emperor penguins, seals, and toothfish (Williams 1995; Ainley and DeMaster 1990; Robison 2003). *Pleuragramma*'s center of distribution during the day is below 500 m in waters of sufficient depth (e.g. Croker Passage, Lancraft et al. 2004) and between 300 and 500 m at normal shelf depths (Parker et al. 2015).

A few characteristics of *P. antarctica* that are considered unusual for both nototheniids and the Antarctic marine ecosystem are a result of its pelagic lifestyle, and are mirrored in other mesopelagic species. High water (80%; Reisenbichler 1993) and high lipid (48% dry weight; Reinhardt and Van Vleet 1986) levels in their tissues confer near-neutral buoyancy (Near et al. 2009). *E. antarctica*, a vertically-migrating myctophid that co-occurs with *P. antarctica* in the WAP system and has a similar daily vertical excursion, exhibits a lipid level ranging from 57 to 73% of dry weight (Reinhardt and Van Vleet 1986), though with the lower water level of 66%. In the cold temperate waters of the California borderland, the tissue composition of vertically-migrating myctophids ranged from 66.1 to 80.4% water (72.9 ± 5.7; χ ± SD) and 10.0 to 58.1% lipid (38.7 ± 17.7; χ ± SD) as a function of dry weight (Childress and Nygaard 1973): in the same range as that of silverfish. The quest for neutral buoyancy is a universal one, and the mechanisms employed are similar from system to system. None of the myctophids considered here has a functional

swimbladder as an adult, so their buoyancy is a function of their compositional attributes.

The co-occurrence of *P. antarctica* and *E. antarctica* on the WAP shelf, their similar migratory habit and diet (Lancraft et al. 2004), and their similar compositional attributes begs for a comparison between the two species. From a life history perspective, they are quite different. *E. antarctica* is believed to live for about 4 years reproducing at the end of its life, though the nature of the reproductive event, i.e., repetitive spawning over the productive season or one *big bang* is unknown (Greely et al. 1999). If it is similar to myctophids from warmer climates, it would be multiple spawnings (Gartner 1993). A simple energy budget for year 3 of its life suggests a rough breakdown of 56% of assimilated energy for metabolism, 34% for growth, and 10% for nitrogen excretion, a much higher investment in somatic growth than that observed for *P. antarctica* at any time in its first 10 years of life. Faster growth, a low reproductive age, a broadcast spawning reproductive strategy and high lipid accumulation for energy security during winter make *E. antarctica* a successful species on the WAP shelf. However, its lack of antifreeze (Cullins et al. 2011) excludes it from all low temperature shelf systems, that is, all but that of the WAP, which coincidentally is experiencing the most rapid warming of any marine ecosystem (Vaughan et al. 2003).

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