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An energy budget for northern sand lance, *Ammodytes dubius*, on Georges Bank, 1977–1986

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The northern sand lance, *Ammodytes dubius*, is a small planktivorous fish, classified as a “ubiquitous shelf species” (Sherman et al., 1983) and is found off the northwest Atlantic coast from North Carolina to Greenland (Nizinski et al., 1990). Sand lance are consumed by many piscivorous marine vertebrates. They have been found in the stomachs of dogfish, *Squalus* spp., skates, *Raja* spp., Atlantic cod, *Gadus morhua*, haddock, *Melanogrammus aeglefinus*, pollock, *Pollachius virens*, sculpin, *Myoxocephalus* spp., Atlantic salmon, *Salmo salar*, various flatfishes, *Paralichthys*, *Limanda*, and *Pseudopleuronectes*, and other fishes (Scott, 1968; Reay, 1970; Meyer et al., 1979; Bowman and Michaels, 1981; Winters, 1981), as well as seabirds (Backus and Bourne, 1987). Humpback whales, *Megaptera novaeangliae*, have also been observed feeding on sand lance (Payne et al., 1986). Negative correlations have been shown between the abundance of sand lance and right whales, *Eubalaena glacialis*, and it has been suggested that in the northwest Atlantic these two animals may actually compete for their primary food source, the copepod *Calanus finmarchicus* (Kenney et al., 1986; Payne et al., 1990). Therefore, although the sand lance is not commercially important, as a plankton feeder and an important prey species, it may exert significant influence over the

efficiency of energy transfer from primary to higher trophic levels.

Georges Bank was chosen as a study area in which dramatic changes in the northern sand lance population might be examined in terms of the consumption and production of fish relative to the production of the region as a whole. This 41,809 km², 50-m deep plateau (Sherman et al., 1984) is located off the northeast coast of the United States and is a highly productive fishing ground with high annual primary production (350 g carbon·m⁻²·y⁻¹) owing to the retention of nutrients (Sherman et al., 1984; Backus and Bourne, 1987). Because of its commercial significance, Georges Bank has been well studied. Energy budgets have been developed for the entire Bank (Cohen et al., 1982; Jones, 1984; Sissenwine et al., 1984) and offer a convenient way to examine the significance of the consumption and production of an individual species within an important area of the Northeast Shelf ecosystem.

Individual energy budgets of fish have been developed for many species (Edwards et al., 1972; Adams, 1976; Kitchell et al., 1977; Kitchell and Breck, 1980; Cho et al., 1982; Kerr, 1982; Diana, 1983; Durbin and Durbin, 1983; Rice and Cochran, 1984; Kerr and Dickie, 1985; Cui and Wootton, 1989). In this study, the energy budget of the northern sand lance was developed

from experiments that measured the following parameters: growth, metabolism, feeding and assimilation efficiency (Larimer, 1992), and reproductive production. These parameters were assembled into an annual energy budget based on the daily activity of the fish in the field associated with temperature and food availability. Monthly growth was used to estimate annual ration and the budget was extrapolated to northern sand lance population abundance levels measured on Georges Bank from 1977 to 1986.¹ The potential predatory impact of the northern sand lance population on seasonal and annual zooplankton productivity on the bank² (Sherman et al., 1987) was examined. Finally, the annual production and consumption by these populations were compared with energy budget model values for Georges Bank.

Methods

Individual energy budget

An “average” adult northern sand lance was considered to be age 1+, the dominant age in a population of adults (Nelson, 1990). The average size was 142 mm fork length, 6.02 g wet weight, and 1.40 g dry weight based on the following wet-weight fork length relationship of Larimer (1992):

$$\text{weight} = 4.0665 e^{-4} \text{length}^{3.61}.$$

The annual energy budget for an individual northern sand lance was described by the following equation adapted from Winberg (1956):

¹ Kane, J. 1992. Macrozooplankton seasonal abundances on Georges Bank, 1977–1986. NOAA, Nat. Mar. Fish. Ser., Northeast Fish. Sci. Center, Narragansett Lab., Narragansett, RI 02882. Unpubl. data.

² Fogarty, M. 1992. Survey biomass estimates for sand lance on Georges Bank. NOAA, Nat. Mar. Fish. Ser., Northeast Fish. Sci. Center, Water Street, Wood's Hole, MA 02543. Unpubl. data.

$$G + R = C - M - W, \quad (1)$$

where the components (in kilocalories) are

- G = somatic growth;
- R = reproduction;
- C = food consumption;
- M = metabolism;
- W = fecal loss.

Assimilated ration (A) equals consumption minus fecal losses. A small fraction of the assimilated energy is lost through nitrogenous excretion (Brett and Groves, 1979) but was not estimated in this study. The remaining portion of the assimilated energy was assumed available for growth and metabolism. The methods used to estimate each parameter are described below.

Growth

The northern sand lance growth rate is 0.87 yr^{-1} in grams, as determined by back calculation of length at age from otolith increments (Larimer, 1992). Multiplied by 6.02 g, the wet weight of an average fish, this is equivalent to a growth rate of $5.24 \text{ g}\cdot\text{yr}^{-1}$. Wet weight was converted to dry weight using the following equation (Larimer, 1992):

$$\text{dry wt.} = 0.309 \text{ wet wt.} - 0.286 \quad (r^2=0.859).$$

The growth rate (in dry grams) was $1.20 \text{ g}\cdot\text{fish}^{-1}\cdot\text{yr}^{-1}$. Growth in kilocalories was calculated based on a mean caloric content of $6.73 \text{ kcal}\cdot\text{dry gram}^{-1}$ (Larimer, 1992) and was $8.08 \text{ kcal}\cdot\text{fish}^{-1}\cdot\text{yr}^{-1}$.

Growth was also estimated on a monthly basis. Reay (1972) measured monthly growth in length of age 1+ *A. tobianus* off the coast of England. These fish and *A. dubius* are of similar size (range: 84–138 mm, Reay, 1972, versus 85–138 mm, Larimer, 1992) and seasonal temperatures in their habitats are similar (3–19°C off England, Reay, 1972; 3.4–14.4°C for Georges Bank, Hopkins and Garfield, 1981). Therefore, I assumed that their monthly growth rates would be similar. Reay (1972) found that *A. tobianus* grows from April to October; however, it spawns from February to March, later than the December to February spawning of *A. dubius* (Bigelow and Schroeder, 1953; Norcross et al., 1961; Reay, 1970; Colton et al., 1979; Sherman et al., 1984). Nelson and Ross (1991) found that gonadal development of *A. dubius* on Georges Bank was in progress by September. Thus, I assumed that *A. dubius* weight gain beginning in September is devoted to gonadal rather than to somatic growth, and therefore, their somatic growing season extends from April to August.

The percentage of annual growth occurring during each month of the growing season was calculated from two years of monthly growth data for *A. tobianus* as reported by Reay (1972). This monthly average was multiplied by the total annual growth measured for *A. dubius* ($8.08 \text{ kcal}\cdot\text{yr}^{-1}$, see above) to determine monthly net growth in caloric content.

Reproductive energetics

Gonad weight and caloric content were measured to estimate the portion of the northern sand lance annual energy budget devoted to reproduction. In December 1990, eight fish judged to be ripe (stage III, of Macer, 1966) were measured (fork length, mm), and wet weighed (g). The gonads were extracted, weighed and dried. The dried gonads were weighed, ground to a powder with mortar and pestle, and their caloric content measured with a Phillipson microbomb calorimeter (Phillipson, 1964).

Metabolism

Metabolism was estimated for an "average" day in each month by using mean monthly water temperature calculated from averages of the top 40 m on Georges Bank (Hopkins and Garfield, 1981) and the number of hours of daylight at mid-month. I assumed the fish actively feed during half of the daylight hours. Thus, I divided a day into three periods: a nighttime resting period equivalent to the hours of darkness, a feeding period that is assumed to be half of the daylight hours, and a postfeeding period that is the remaining half of the daylight hours. Metabolic rates were estimated for each of these periods from the rates measured during similar periods at 6, 12, and 18°C (Larimer, 1992). The lowest temperature that could be maintained in the lab was 6°C so these temperatures were chosen as the best approximation of the annual temperature range on Georges Bank (Backus and Bourne, 1987). Because there was no clear relationship between metabolic rates and temperature evident in the respiration experiments (Larimer, 1992), the 6°C values were used for April, May, and December, the 12°C values were used for June, July, October, and November, and the 18°C values were used for August and September.

Assimilation efficiency

The efficiency of energy assimilation by sand lance was determined by the monthly temperature on Georges Bank (Backus and Bourne, 1987) and the relationship of assimilation efficiency to temperature found in Larimer (1992):

$$AE = 82.41 + 0.764 T, \quad (2)$$

where AE = assimilation efficiency (%);
 T = temperature ($^{\circ}C$).

Ration estimation

Annual ration was estimated by summing the metabolic requirements, somatic growth requirements, and reproductive requirements, and then by taking assimilation efficiency into account. Because assimilation efficiency was found to increase with increasing temperature (Larimer, 1992), ration was calculated on a monthly rather than an annual basis.

Seasonal water temperatures (and therefore fish activity levels) and food availability on Georges Bank were used to estimate a monthly ration for sand lance based on the energy budget requirements. I assumed that the fish are inactive during January, February, and March. Other species of *Ammodytes* (*A. tobianus*, Reay, 1970; *A. marinus*, Macer, 1966) are known to spend the winter months buried in the sand. This behavior has not been recorded for *A. dubius* but catches of these fish during the winter months are low (Nelson, 1990) and they have been observed to spend extended periods buried in the sand in the laboratory, apparently without feeding³ (personal observ., 1991). I assumed that the metabolic requirement for January, February, and March and the annual reproductive requirement were assimilated from May through September when food availability is high and water temperatures are still warm.

Monthly gross energy requirements were estimated by summing monthly energetic costs and multiplying by the percent of consumed calories lost as waste based on monthly assimilation efficiencies. These were divided by the caloric content of the ration ($6.11 \pm 0.77 \text{ kcal}\cdot\text{g}^{-1}$ for *Calanus finmarchicus*; Larimer, 1992) to determine the actual grams of ration required per month. The sum of these monthly estimates is the yearly ration requirement.

Population energy budget

The energy budget for individual adult northern sand lance was extrapolated to the population level by multiplying overall production (growth+reproduction) and consumption (predicted ration) by the number of individuals estimated to be present on Georges Bank from 1977 through 1986. Northern sand lance population size was estimated from spring sand lance biomass estimates for 1977–86.² Mean sand lance weight per tow was divided by mean individual adult fish wet weight (see above) and the average tow volume to estimate the number of indi-

viduals present per unit volume on the Bank. There were no sand lance abundance data for 1979. The energy budget parameters of the population were then compared with estimates of secondary production on Georges Bank.

Macrozooplankton production (including *Calanus finmarchicus*, *Pseudocalanus minutus*, *Centropages* species, and *Metridia lucens*) on Georges Bank was calculated from population estimates measured during the MARMAP surveys from 1977 to 1986 (Sherman et al., 1987). Zooplankton volumes were reported in Kane.¹ These were transformed into annual production values following Sherman et al. (1987) where volume is converted to biomass using the following equation (Wiebe et al., 1975):

$$\log_{10}(\text{dry weight}) = \log_{10}(\text{volume} + 1.828)/0.848.$$

A value of $5.25 \text{ kcal}\cdot\text{g}^{-1}$ (Laurence, 1976) and a production-to-biomass ratio (P:B) of 7 (Steele, 1974; Crisp, 1975) were used to convert zooplankton biomass to production. Annual production was estimated for each year of available zooplankton data (1977–86) and compared with the calculated annual consumption by northern sand lance.

Results and discussion

Predicted ration and individual budget

The ratio of production to consumption (P:C) determined from an individual energy budget represents the gross ecological growth efficiency of an animal within a trophic level (Slobodkin, 1960). This ratio was determined from the individual energy budget for the northern sand lance. Monthly growth estimates calculated from Reay's (1972) data range from 0% from September to March to 36% dry body weight in May (Table 1) and from 0.00 kcal, from Septem-

Table 1

Monthly somatic growth of northern sand lance, *Ammodytes dubius*, on Georges Bank estimated from measurements of *A. tobianus* growth rates in length (Reay, 1972) and the availability of food on the Bank. Reay measured no net growth September through March.

Month	% Growth (wt)	Growth (kcal)
April	0.14	1.15
May	0.36	2.90
June	0.19	1.50
July	0.07	0.56
August	0.24	1.97

³ Halavik, T. NOAA, Nat. Mar. Fish. Ser., Northeast Fish. Sci. Center, Narragansett Lab, Narragansett, R.I. 02882. Personal commun., September 1991.

Table 2

Monthly energy requirements for northern sand lance, *Ammodytes dubius*, on Georges Bank. Fish are assumed to be inactive in January, February, and March; therefore metabolic energy requirements for those months ("nonfeed metabolism"), as well as annual reproductive energy requirements, were divided equally over the months of highest temperature and food availability.

Month	Metabolic cost (kcal)	Somatic growth (kcal)	Reproductive growth (kcal)	Nonfeed metabolism (kcal)	Energy required (kcal)
January	2.23	0.00	0.00	0.00	0.00
February	2.02	0.00	0.00	0.00	0.00
March	2.23	0.00	0.00	0.00	0.00
April	3.90	1.15	0.00	0.00	5.05
May	4.15	2.90	0.49	1.29	8.83
June	3.33	1.50	0.49	1.30	6.62
July	3.38	0.56	0.49	1.30	5.73
August	3.57	1.97	0.49	1.30	7.33
September	3.33	0.00	0.49	1.29	5.11
October	3.07	0.00	0.00	0.00	3.07
November	2.91	0.00	0.00	0.00	2.91
December	3.44	0.00	0.00	0.00	3.44

Table 3

Gonad weight and energy content of northern sand lance, *Ammodytes dubius*, from Georges Bank.

	Males	Females	Total mean
<i>N</i>	1	7	8
Fork length (mm)	132	127±7.4	128±7.1
Dry weight (g)	1.23	1.22±0.35	1.23±4.94
Gonad (% dry body weight)	14.33	26.36±2.72	24.85±4.94
Gonad (kcal/g)	6.4	7.12±0.52	7.03±0.54

ber to March, to 2.90 kcal in May (Table 2). The mean percent of body weight accounted for by the ripe gonads, 24.85%, is similar to the 20–30% measured for age 1+ *A. personatus* (Okamoto et al., 1989) and the 25–28% measured for both male and female *A. americanus* (Smigielski et al., 1984), (Table 3). Estimated monthly metabolic requirements range from a low in February of 2.03 kcal to a high in May of 4.15 kcal (Table 4). The annual individual energy requirement was 37.56 kcal (Table 4). Monthly assimilation efficiencies and daily rations are shown in Table 5, and the predicted annual ration is 52.62 kcal·fish⁻¹ or 8.60 g·fish⁻¹ (assuming a caloric content of 6.11 kcal·g⁻¹ for *C. finmarchicus*; Larimer, 1992). The energy assimilated from that ingested is 48.09 kcal·fish⁻¹ so the annual individual energy budget in terms of kilocalories is approximated by

$$(G) + (R) = (AR) - (R), \quad (3)$$

Table 4

Calculated monthly respiration requirements in kilocalories for northern sand lance, *Ammodytes dubius*, on Georges Bank. Fish are assumed to be inactive from January to March.

Month	°C	Hours of light	Kcal used per month
January	6.1	9.5	2.23
February	4.3	10.5	2.02
March	3.4	12.0	2.23
April	3.4	13.5	3.90
May	7.7	14.5	4.15
June	10.9	15.5	3.33
July	13.0	15.0	3.38
August	14.4	14.0	3.57
September	14.3	12.5	3.33
October	13.2	11.0	3.07
November	11.0	10.0	2.91
December	8.8	9.0	3.44
Annual total			37.56

where growth $(G) = 8.08 \text{ kcal}\cdot\text{yr}^{-1}$;
 reproduction $(R) = 2.45 \text{ kcal}\cdot\text{yr}^{-1}$;
 assimilated ration $(AR) = 48.09 \text{ kcal}\cdot\text{yr}^{-1}$;
 respiration $(R) = 37.56 \text{ kcal}\cdot\text{yr}^{-1}$.

If the budget is converted into percentage of total consumption accounted for by each parameter, the following relationship results:

Table 5

Predicted daily ration of adult northern sand lance, *Ammodytes dubius*, on Georges Bank based on monthly growth (Table 1) and assimilation efficiency for *Calanus finmarchicus* (Equation 2).

Month	Assimilation efficiency (%)	Required energy (kcal/month)	Ration (kcal/month)	Ration (g/month)	Daily ration (% body wt)
January	87.07	0.00	0.00	0.00	0.00
February	85.70	0.00	0.00	0.00	0.00
March	85.01	0.00	0.00	0.00	0.00
April	85.01	5.05	5.81	0.95	2.26
May	88.29	8.83	9.86	1.61	3.72
June	90.74	6.62	7.23	1.18	2.82
July	92.34	5.73	6.17	1.01	2.33
August	93.41	7.33	7.81	1.28	2.95
September	93.34	5.11	5.45	0.89	2.12
October	92.49	3.07	3.30	0.54	1.24
November	90.81	2.91	3.18	0.52	1.24
December	89.13	3.44	3.81	0.62	1.44
Annually		48.09	52.62	8.60	

Table 6

Annual consumption of adult northern sand lance, *Ammodytes dubius*, on Georges Bank, based on individual energy budget requirements extrapolated to population levels from 1977 through 1986. These values are compared to average annual zooplankton productivity for each year. The percent of production consumed by sand lance is shown for each year.

Year	Sand land abundance (no. per m ³)	Annual consumption (kcal/m ³ /yr)	Zooplankton production (kcal/m ³ /yr)	% consumed by sand lance
1977	0.0198	1.03	45.56	2.27
1978	0.0261	1.63	32.07	5.08
1980	0.0782	4.07	21.16	19.24
1981	0.0143	0.74	22.89	3.24
1982	0.0261	1.36	16.25	8.37
1983	0.0091	0.48	12.77	3.76
1984	0.0056	0.29	14.56	1.99
1985	0.0032	0.17	21.58	0.79
1986	0.0081	0.42	18.49	2.27

$$100C = 15G + 5R + 71M + 9W, \quad (4)$$

where C = consumption;

G = growth;

R = reproduction;

M = metabolic requirement;

W = waste (that portion of the predicted ration that is not assimilated based on Equation 2 above).

For an individual adult northern sand lance on Georges Bank, total production is $10.53 \text{ kcal}\cdot\text{yr}^{-1}$ (growth+reproduction), and total consumption is $52.62 \text{ kcal}\cdot\text{yr}^{-1}$ (Table 5); therefore, ecological efficiency is 20.0%.

Population energy budget

Northern sand lance consumed a significant proportion of total annual zooplankton production of Georges Bank from 1977 through 1986. Population abundance of northern sand lance from 1977 through 1986 was negatively correlated with zooplankton abundances during the same period ($r^2=0.683$, $P<0.05$; Fig. 1). Northern sand lance consumed 0.79–19.24% of the annual zooplankton production from 1977 to 1986 (Table 6; Fig. 2).

The trophic efficiency of the northern sand lance is 20%, according to the present energy budget model. Jones's (1984) Georges Bank energy model found that

the primary productivity of the Bank adequately accounted for fish production only if a trophic transfer efficiency of greater than 10% was assumed. This may be a valid assumption for the model at the trophic level of the northern sand lance.

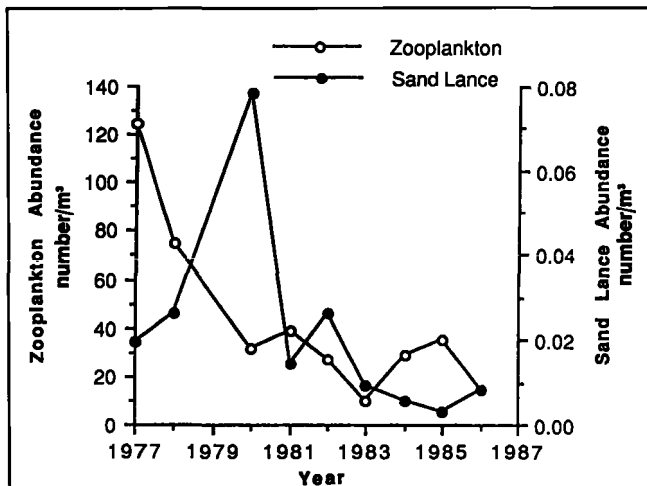


Figure 1

Average annual copepod abundance of *Calanus finmarchicus*, *Pseudocalanus minutus*, *Centropages hamatus*, *C. typicus*, *Metridia lucens*, and of adult northern sand lance, *Ammodytes dubius*, on Georges Bank from 1977 through 1986.

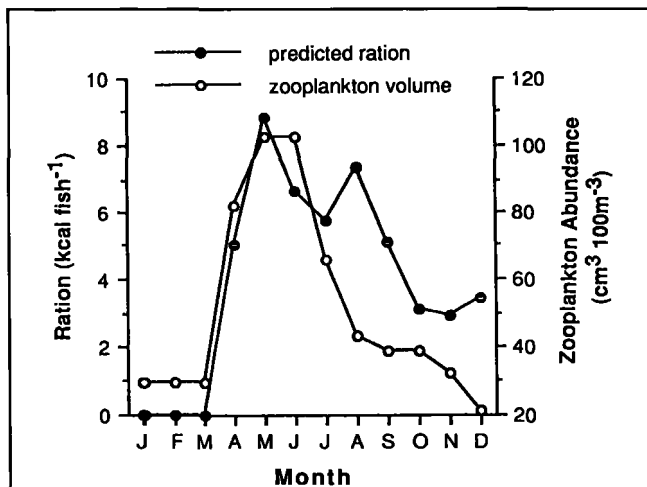


Figure 2

Mean monthly zooplankton biomass of *Calanus finmarchicus*, *Pseudocalanus* species, *Paracalanus parvus*, and *Centropages* species on Georges Bank (Sherman et al., 1987) and monthly ration required for an individual adult northern sand lance, *Ammodytes dubius*, based on the individual energy budget.

In their budget of Georges Bank bioenergetics, Sissenwine et al. (1984) place sand lance in their "other finfish" compartment (all nonfished species that are vulnerable to fishing gear). From 1973 to 1975 a consumption of $9.3 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ was attributed to this category. Sissenwine et al. (1984) suggested that the impact of the sand lance population was underestimated in their budget, and it appears from the present study, based on the individual energy budget and population size, that this error was potentially significant. By converting population energetic consumption on Georges Bank (Table 6) to consumption per square meter (assuming a mean depth on the Bank of 50 m; Backus and Bourne, 1987), sand lance consumed from 8.5 to $203.5 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ from 1977 to 1986. This represents nearly all the consumption attributed to the "other finfish" at low northern sand lance abundances and over 20 times the total "other finfish" consumption at high northern sand lance abundances. The results of this study suggest that the budget estimates of annual consumption by exploitable but commercially undesirable fishes may need to be revised upward.

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