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The Effects of Parasitism on Energy Flow through Laboratory Shrimp Populations

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Abstract

I quantified the effects of parasitism by the isopod *Probopyrus pandalicola* on energy flow through the host *Palaemonetes pugio* by comparing secondary production, metabolism, ingestion, and egestion by unparasitized laboratory shrimp populations to the same parameters for parasitized groups during 10 months. The effects of parasitism on host growth and metabolism vary from month to month. Temperature, season, host age, sex, and reproductive condition affect energetics for host-parasite systems. *Probopyrus pandalicola* has little effect on host assimilation efficiency. However, tissue growth efficiences during most study months were higher for control shrimp than parasitized shrimp. These differences between groups were of lesser magnitude when parasite production was considered in the calculations. Trophic level energy intake efficiency for parasites was of the order of 6 to 10% throughout much of the study – the highest values were calculated during the parasites' reproductive months. Through parasitic castration, *P. pandalicola* significantly affects host energetics. Significantly, parasite reproduction was often of the same magnitude as reproduction by unparasitized hosts, although parasite biomass accounts for only about 4% of the total host-parasite system biomass.

Introduction

Although in recent years numerous workers have quantified energy flow through biological systems, few have investigated energy flow in host-parasite systems. Among the latter, Walkey and Meakins (1970) studied the energy demands of the endoparasitic tapeworm plerocercoids *Schistocephalus solidus* on the host *Gasterosteus aculeatus* by comparing energy budgets of infected fish to those of uninfected fish. In this host-parasite system, fish are frequently infected with more than one parasite; the host:parasite biomass ratio is variable. Hence, it was not possible for Walkey and Meakins to know prior to postmortem analysis the number, size, or individual growth rate of parasites present at the beginning of their experiment. Investigations with other cestodes have demonstrated that growth rate and maximum size may be significantly affected by parasite number. Walkey and Meakins concluded that energy intake is greater in infected fish than uninfected fish and that, under food-limiting circumstances, a heavy parasite burden could result in a considerable depletion of the host's endogenous food reserves. In another study, Castro (1971) used radiotracer techniques to demonstrate that the trophic level energy intake efficiency (after Odum, 1971) for female brachyurans, *Echinoecus pentagonus*, ingesting host fecal material and coelomocytes is 1.6%; for tissue-feeding males, the efficiency is 0.6%. Castro speculated that the nutritional requirement of females is too great to allow for tissue feeding, since displacement of females to the peristome, the normal habitat for male crabs, resulted in host death. In another study, Mace and Davis (1972) studied the energetics of the ectoparasitic leech *Malmiana nuda* and the host *Myoxocephalus scorpius*. Although these workers calculated the energy "burden" indirectly, they estimated the additional energy intake of the host due to parasitism, the increase in host metabolic rate due to parasite stress, and the energy utilization of the leech (2,240 cal/g of leech/week). In a fourth study, Kennedy (1972) attempted to quantify the effects of cestode larvae, *Caryophyllaeus laticeps*, on respiration, assimilation

and growth of the tubificid host *Psammoryctides barbatus*. He concluded that parasitism has a significant adverse effect on host tissue production: reductions of up to 60% during the host's life span are possible.

Most energetics ecologists, in attempting to characterize energy flow through biological systems, have used the following equation modified after Ricker (1968) as a framework:

$$I = P + R + F + U, \quad (1)$$

where I is the energy input into a system (ingestion); P is the energy incorporated as secondary production (growth, molting and reproduction); R is the energy utilized for maintenance (respiration); F is the energy egested (feces) and U is the energy excreted.

The pattern of energy flow through a host-parasite system may be visualized using the following modification of Eq. (1):

$$I_h - I_p = P_h + R_h + F_h + U_h. \quad (2)$$

The subscripts h and p refer to energy flow parameters for host and parasite, respectively. Energy flow through the parasite may be visualized as:

$$I_p = P_p + R_p + F_p + U_p. \quad (3)$$

The association between the isopod parasite *Probopyrus pandalicola* and the shrimp *Palaemonetes pugio* is amenable to an energetics approach. Adult parasites live in pairs within the branchial chamber of juvenile or adult hosts. The adult female parasite feeds on host hemolymph. The small adult male lives as a diminutive parasite of the female. Parasite biomass accounts for 3 to 4% of that of the host-parasite system. Although the host's cephalothorax becomes deformed due to the isopods' presence, no significant effects of parasitism on host vitality or activity are apparent. Due to the transparency of the host's exoskeleton, the size and reproductive state of parasites may be readily noted. Parasite growth may be accurately estimated due to the constancy of the host:parasite biomass ratio. *Probopyrus pandalicola* may be easily maintained in seawater for measurements of metabolism *in vitro*. Finally, the host-parasite system is well suited to laboratory maintenance.

Since parasitic castration of shrimp results from infection by *Probopyrus pandalicola*, one would expect the effects of parasitism on host energetics to be significant (Baudoin, 1975). Other studies have demonstrated that host metabolic rate (Baffoni, 1953; Anderson, 1975b), molting frequency (Callan, 1940), growth (Tucker, 1930; Morris, 1948) reproductive capacity (Tucker, 1930; Sansin, 1938; Hiraiwa and Sato, 1939; Callan, 1940; Reverberi, 1943; Baffoni, 1947; 1948; Morris, 1948) and biochemistry (Hughes, 1940; Reinhard *et al.*, 1947; Baffoni, 1953) may also be affected to a marked degree following infection by parasitic castrators.

The objectives of the present study are to compare energy budgets for parasitized shrimp populations with those of unparasitized populations, to determine the energy "burden" of parasitism, to evaluate the influence of temperature on host and parasite energetics, and to calculate the efficiency of energy transfer from host to parasite.

Materials and Methods

Collection and Maintenance of Experimental Animals

Several hundred parasitized and unparasitized *Palaemonetes pugio* were collected monthly from September, 1972, through August, 1973 (except during February and March) by seining in North Inlet, a high-salinity estuary near Georgetown, South Carolina, USA. After collection, the shrimp were transported to the Belle W. Baruch Institute for Marine Biology and Coastal Research laboratory in Columbia, South Carolina, where subsequent experiments were conducted.

In the laboratory, 10 male and 10 female parasitized shrimp were blotted in tissue paper for 30 sec, weighed to the nearest 1.0 mg, and placed in a plastic box containing 1.5 l of 30‰ S filtered seawater. Uninfected shrimp of corresponding sizes and sexes were placed in a separate box. The boxes were aerated and maintained for 1 month at the temperature recorded on the date of collection. During this time I monitored ingestion, egestion, molting, and reproduction for each population.

The rest of the shrimp were sexed, weighed and oven-dried at 80°C for 48 h, whereafter dry weights and caloric contents were measured (see "Calorimetry"). Least-squares analysis was used to compute the empirical wet:dry weight relationships for parasitized males, parasitized females, control males and control females. The calculated wet:dry weight relationships and caloric values were used to estimate the total energy content present in the laboratory populations (initial standing stock) at the start of the energetics experiment.

The procedures described above were followed each study month. At the end of the month each laboratory population was sacrificed for determination of final standing stock. Freshly collected shrimp

were selected for the subsequent month's study.

Ingestion (I)

For each experimental population, the following 3 aspects of caloric intake were analyzed: ingestion of *Artemia salina* nauplii used as a food source, ingestion of reproductive products (shrimp and parasite larvae), and utilization of endogenous food reserves.

Shrimp populations were fed known volumes of concentrated newly hatched *Artemia salina* nauplii. The volume administered was adjusted daily to correspond to the maximum which could be ingested prior to the next day's feeding. Replicate, 1 ml concentrated *A. salina* samples were retained for dry weight and caloric content measurements (see "Calorimetry").

Reproductive products (shrimp and parasite larvae) were invariably ingested by shrimp. Hence, the estimated energy content of larvae produced during the reproductive season was considered as an additional component of ingestion. The methods used in estimating reproduction are given below (see "Secondary Production").

The final standing stock of some populations was less than the estimated initial standing stock. This suggested that endogenous food reserves had been depleted in these populations. Such reductions were considered as an additional component of ingestion (see "Secondary Production").

Secondary Production (P)

Somatic growth was estimated subsequent to metabolic rate determinations by measuring the total energy content (final standing stock) of each population (see "Calorimetry") and subtracting the estimated initial standing stock. When negative values were obtained, I considered growth to be zero and assumed the reduction of standing stock energy to represent utilization of endogenous food reserves. Such values were treated as a component of ingestion.

Molting losses for each population were quantified by pooling all exuviae produced by each population during the month and subsequently measuring the total energy content (see "Calorimetry").

Due to parasitic castration, only control populations reproduced. Reproduction was calculated by multiplying the estimated dry weight of larvae produced times the caloric value (cal/g dry weight). I weighed female shrimp as they became ovigerous and estimated the biomass of broods using the following formula relating brood size to ovigerous female size:

$$Y = 0.168X,$$

where Y is the dry weight of the shrimp brood and X is the total dry weight of the ovigerous female (brood plus female). This formula had been derived previously by removing larvae from the pleopods of 9 preweighed females, determining dry weights for shrimp and brood, and calculating the ratio. Subsequently, caloric content of shrimp larvae was determined.

Respiration (R)

Oxygen uptake was determined for both laboratory populations at the end of each month's experiment. Two methods were employed to measure rates: manometric techniques for individual shrimp (September - November), and a closed system with a polarographic oxygen electrode for entire laboratory shrimp populations (all other months). Shrimp were starved for 24 h prior to determinations.

For the September-November experiments, oxygen consumption rates were measured with a Gilson Differential Respirometer following established manometric procedures (Umbreit *et al.*, 1964). Each shrimp was placed into a 15 ml respirometer flask containing 5 ml of filtered seawater and with 0.2 ml of 20% KOH in the side arm to absorb metabolic CO_2. Readings were made over a 1 to 3 h period following an initial 30 min equilibration interval. Oxygen uptake data were converted to energy equivalents using an oxycalorific coefficient of 4.81 cal/ml O_2, assuming a mixed diet (Brody, 1945).

During the other study months, the rate of oxygen consumption was measured using a Beckman oxygen electrode/monitor sealed into a magnetically stirred 1.9 l respirometer vessel. Prior to measurements, the electrode was cleaned and calibrated in air. One experimental population at a time was placed in the respirometer vessel and it was filled with autoclaved filtered seawater from an aerated reservoir. Water was allowed to continue flowing through the vessel during a 30 min equilibration period, during which the experimental shrimp became less active. Inflow and outflow valves were then closed, the initial percentage O_2 saturation recorded, and the time noted. Percentage oxygen saturation was recorded at 15 min intervals over a 1 h period. Total oxygen uptake per hour was calculated for each group by converting

the percentage saturation data obtained during the runs to mg O_2/l using an oxygen solubility nomograph (Strickland and Parsons, 1972) and later to ml O_2. Values were corrected using data obtained during control runs and converted to energy equivalents as described previously.

Metabolic energy equivalents for each laboratory population were extrapolated for a 30 day period.

Egestion (F)

Fecal losses were quantified at 3 day intervals throughout the study. After shrimp were removed from the containers, the contents were centrifuged. The compacted fecal material was then collected and the energy content subsequently measured (see "Calorimetry").

Excretion (U)

I did not attempt to measure energy losses due to excretion, although the release of dissolved organic matter was demonstrated previously for *Palaemonetes pugio* by Johannes and Satomi (1967). Rather, I assumed that the magnitude of excretion would be apparent when I attempted to balance each population's energy budget (Eq. 1).

Parasite Energetics

Ingestion by *Probopyrus pandalicola* was estimated by adding secondary production to respiration. Since adult probopyrids lack an anus (Caullery, 1952), parasite egestion is probably negligible.

Following the metabolic rate determinations for parasitized shrimp, parasites were removed from the hosts' branchial chambers and oxygen uptake measured for each probopyrid pair within 1 h after removal. Each parasite pair was placed in a 4 ml respirometer flask containing 1 ml filtered seawater and with 0.05 ml KOH in the center well. Oxygen consumption was followed over an 8 to 12 h period. Total oxygen uptake volumes were computed, energy equivalents calculated as previously described, and values extrapolated for a 1 month period. Subsequently, the parasites were dried and their caloric values determined.

Growth of *Probopyrus pandalicola* closely parallels growth of the host (Tucker, 1930). The relationship between biomass of parasites and that of infected shrimp is rather constant: the parasite accounts for about 3.7% of the total weight of infected shrimp (Anderson, 1972). I estimated parasite growth by multiplying growth of the host-parasite system by 0.037 and then by the parasite caloric value (cal/g dry weight). The reliability of the resulting values may be questionable since I assumed that the growth rate of parasites on hosts fed *Artemia salina* conforms to the apparent growth rate for field-collected parasites.

Estimates of monthly parasite molting losses were based on the results of a previous study (Anderson, unpublished data) during which 23 intact parasite exuviae were recovered, rinsed in distilled water, pooled and weighed to the nearest 0.01 mg. Subsequently, the mean weight was calculated. Caloric values of exoskeletons could not be measured directly due to small sample size, rather, I assumed that parasite exuviae have the same energy content per unit weight as shrimp exuviae. Evidence suggests that parasites may molt in synchrony with hosts (Caroli, 1929; Walker, 1974). Hence, I calculated total molting losses by multiplying the estimated mean energy content per exuvium by the number of host exuviae recovered during the month.

The energy content of parasite larval broods was determined by removing broods from the marsupia of 18 parasites, measuring the energy content of each, and calculating the mean. Parasite reproduction was computed by multiplying the mean energy content per brood by the number of broods produced.

Calorimetry

A Phillipson Microbomb Calorimeter was used to determine energy content of whole grass shrimp and *Artemia salina* nauplii. For each whole shrimp sample, I burned 5 replicates. The samples contained at least 5 shrimp which had been oven-dried to constant weight at 80°C, powdered, and compacted into pellets weighing 15 to 25 mg each. Pellets were carefully weighed to the nearest 0.01 mg before being burned in the calorimeter which had been calibrated using benzoic acid as a standard. Subsequently, the mean energy content (cal/g dry weight) and standard deviation was calculated for each sample. Percentage ash was determined by burning the remainder of the sample in a muffle furnace at 500°C for 24 h. Ash-free caloric values were then determined. The energy content of *A. salina* nauplii was measured in the same manner, except that the replicate determinations were made for a dried sample of *A. salina* pooled from fifteen 1 ml aliquots of concentrated nauplii.

I used a wet combustion method as described by Winberg (1971) to measure the energy content of exuviae, shrimp and parasite larvae, feces, parasites, and some shrimp samples. Where possible, 5 replicates were combusted and mean ash-free energy content and standard deviation were calculated.

Treatment of Results

All energy flow data obtained for each population were mathematically adjusted to correspond to expected values for a 30 day experiment using a laboratory population of 20 shrimp weighing 1 g dry weight (= weight-adjusted values). For example, the estimated initial biomass of the parasitized population in September was 746.3 mg dry weight and its total ingestion was 9515 cal (Table 1). The estimated initial biomass of the October parasitized population was 366 mg dry weight and its total ingestion was 4752 cal. To correct these data to expected values for a population of 1 g dry weight, I performed the following calculations: September, 9515 cal ÷ 0.7462 g dry weight; October, 4752 cal ÷ 0.366 g dry weight; and obtained values of 12,751 and 12,984 cal/g dry weight as weight-adjusted intake values for parasitized populations in September and October, respectively. Such adjustments were necessary to allow for intermonthly data comparisons, since population biomass varied from month to month, the December experiment was shorter than others, and some mortality occurred during experiments. In addition, values for all energy flow parameters were calculated and expressed as percentages of ingested energy.

Ecological growth efficiencies (P/I x 100) were calculated for unparasitized populations. For parasitized groups, since hosts do not reproduce but parasites do, efficiencies were calculated both for the hosts (excluding secondary production by parasites from the calculation) and for the host-parasite system (including parasite production in the calculation).

Tissue growth efficiencies (P/A x 100, where A is the energy assimilated) were also calculated for control shrimp, hosts, and host-parasite systems.

Finally, I calculated the trophic level energy intake efficiency (I_t/I_{t-1} x 100, where I_t and I_{t-1} represent ingestion for parasite and host, respectively) for each parasitized population.

Results

Ingestion

Oven-dried concentrated *Artemia salina* nauplii weigh 111.6 ± 6.2 mg/ml and have a caloric value of 4860 ± 67 cal/g dry weight (5813 ± 79 cal/g ash-free dry weight), which is in close agreement with the value of 4.8 Kcal/g given by Khmeleva (1968). Hence, I used the value of 542 cal/ml to convert the total volume of *A. salina* ingested by each group to an energy equivalent.

Palaemonetes pugio broods average 16.8% of the total dry weight of ovigerous females. Mature shrimp larvae have a caloric value of 6070 ± 34 cal/g dry weight (7167 ± 42 cal/g ash-free dry weight). These values are somewhat lower than those for newly-deposited larvae (6210 ± 20 cal/g dry weight and 7513 cal/g ash-free dry weight, respectively). I used the former data to estimate the energy content of mature shrimp larvae liberated and ingested by unparasitized populations during each reproductive month.

Mature epicaridian larval broods weigh 1.64 ± 0.07 mg dry weight and have a caloric value of 6230 cal/g dry weight (7426 cal/g ash-free dry weight), in contrast to the higher value for immature larvae (see "Reproduction" section below). I used 10.2 cal/brood to estimate hosts' energy intake due to ingestion of parasite larvae.

During September, December, June, and July the standing stock (in cal) of shrimp populations decreased during the experiment. These reductions were considered as depletion of endogenous food reserves and are recorded as an additional component of ingestion. All ingestion data are summarized in Tables 1 and 2.

Secondary Production

Growth

The empirically derived equations used to estimate shrimp dry weight (to calculate initial standing stock) are: Parasitized males, $Y = 0.243X + 1.11$; Parasitized females, $Y = 0.257X - 0.22$; Control males, $Y = 0.240X + 1.60$; Control females, $Y = 0.268X - 1.50$; Ovigerous females, $Y = 0.277X - 4.30$; where X is the live weight and Y the dry weight (in mg). These data, along with caloric values for shrimp (Anderson, 1974), were used to determine the initial standing stocks for shrimp populations. By subtracting from these values the directly measured final standing stock values for

Table 1. *Palaemonetes pugio*. Ingestion (cal) of *Artemia salina* nauplii and reproductive products [shrimp larvae and parasite larvae for control (C) and parasitized (P) populations, respectively] and utilization of endogenous reserves by laboratory shrimp populations. Final column shows monthly values, calculated for shrimp populations containing 20 individuals totaling 1 g dry weight

Month and temperature	Population	Total intake of *A. salina* nauplii	Total intake of reproductive products	Utilization of endogenous food reserves	Weight-adjusted total
1972					
September (25°C)	P	8732	613	170	12751
	C	7457	0	0	10820
October (23°C)	P	4691	61	0	12984
	C	4702	0	0	13599
November (18°)	P	4529	0	0	5982
	C	3851	0	0	5523
December (14°C)	P	1356	0	160	4590
	C	1101	0	0	3415
1973					
January (11°C)	P	1600	0	0	2753
	C	1600	0	0	2734
April (15°C)	P	5125	194	0	4593
	C	4963	542	0	4225
May (23°C)	P	8271	449	0	6955
	C	8352	256	0	6985
June (30°C)	P	10250	541	1700	10137
	C	12149	1161	40	9995
July (31°C)	P	12176	520	360	10063
	C	12392	1481	1310	10543
August (30°C)	P	11458	490	0	15090
	C	10683	462	0	14245

Table 2. *Palaemonetes pugio*. Energy balance sheet for parasitized and non-parasitized shrimp. Weight-adjusted values (cal/g dry weight shrimp biomass) and values expressed as percentages of caloric intake (in parentheses) are given for ingestion, egestion, respiration, and secondary production (growth, molting, and reproduction). Comparison between "Total utilization" column (sum of egestion, respiration, and secondary production) and "Ingestion" column shows extent to which the budgets balanced for each population

Month and temperature	Population	Ingestion	Egestion	Respiration	Production (*P*)			Total utilization
					Growth[a]	Molting	Reproduction	
1972								
September (25°C)	P	12750	540(4)	7560(59)	-230 (-)	560(4)	1020[b](8)	9680(76)
	C	10820	510(5)	9070(84)	460 (4)	540(5)	-	10580(98)
October (23°C)	P	12980	460(4)	9570(74)	540 (4)	700(5)	210[b](2)	11480(89)
	C	13600	490(4)	10450(77)	1310 (10)	750(6)	-	13000(97)
November (18°C)	P	5980	280(5)	6660(111)	400 (7)	330(5)	-	7670(128)
	C	5520	400(7)	7880(143)	550 (10)	370(7)	-	9200(167)
December (14°C)	P	4590	340(7)	5480(119)	-220 (-)	280(6)	-	6100(133)
	C	3420	380(11)	3690(108)	150 (4)	210(6)	-	4430(129)
1973								
January (11°C)	P	2750	160(6)	5060(184)	1050 (38)	160(6)	-	6430(234)
	C	2730	120(4)	5120(187)	840 (31)	200(7)	-	6280(229)
April (15°C)	P	4590	160(3)	3780(82)	630 (14)	220(5)	210[b](5)	5000(109)
	C	4230	130(3)	3420(81)	760 (18)	330(8)	690 (16)	5330(126)
May (23°C)	P	6960	320(5)	6150(82)	630(9)	630(9)	440[b](6)	8170(117)
	C	6990	310(4)	5740(82)	590 (8)	620(9)	280 (4)	7540(107)
June (30°C)	P	10137	700(7)	6160(61)	-1130 (-)	720(7)	560[b](6)	8140(80)
	C	9995	790(8)	6510(65)	-30 (-)	750(8)	890 (9)	8940(89)
July (31°C)	P	10063	590(6)	6480(64)	-230 (-)	680(7)	500[b](5)	8250(82)
	C	10543	530(5)	7610(72)	-790 (-)	680(6)	1190 (11)	10010(95)
August (30°C)	P	15090	610(4)	8700(58)	900 (6)	670(4)	770[b](5)	11650(77)
	C	14250	520(4)	8110(57)	680 (5)	780(6)	600 (4)	10690(76)

[a] Negative values in this column represent utilization of endogenous food reserves and are treated as ingestion (see Table 1).

[b] For parasitized groups, values represent reproductive losses by parasites.

each population, I determined whether growth or utilization of endogenous food reserves occurred during the month (Table 2).

Molting

Caloric values for molted exuviae ranged from 2863 ± 17 (December) to 5506 ± 48 (May) cal/g dry weight (ash-free). Each month's values (Anderson, 1974) were used to determine molting losses (Table 2).

Reproduction

Newly emerged larval broods of *Palaemonetes pugio* average 16.8% of the total weight of ovigerous females. The energy content of larvae is 6210 ± 20 cal/g dry weight (7513 cal/g ash-free). These data were used to estimate reproductive losses by control shrimp populations (Table 2). Larval energy content decreases somewhat during the incubation period (see "Ingestion" section above).

The mean biomass of newly emerged parasite broods is 1.64 ± 0.07 mg dry weight; larvae have an energy content of 7720 cal/g dry weight (7858 cal/g ash-free). Energy content of larvae declines during embryogenesis. Since monthly parasite reproduction is frequently of the same magnitude as shrimp reproduction, parasite reproduction has been included in Table 2 as well as in Table 3 (see below).

Respiration

Maintenance losses were considerable for all populations (Table 2): values of 57 to 88% of the total monthly energy intake were usually recorded. However, during November, December, and January, values exceeded 100% of the total measured caloric intake. Such overestimates, while unfortunate, are not surprising, since oxygen uptake rates were measured over a brief time span and the results extrapolated for a 30-day period. Furthermore, manipulation (i.e., moving the shrimp from the temperature incubator to respirometer flasks) of animals may have stressed them, thereby resulting in overestimates of hourly uptake.

Egestion

The caloric value (cal/g dry weight) of fecal material was found to vary little from month to month. Hence, I used the mean of 3550 cal/g dry weight (5171 cal/g ash-free dry weight) to estimate fecal losses for each population. Egestion data as weight-adjusted values and percentages of ingestion are presented in Table 2.

Parasite Energetics

Table 3 summarizes energy flow data for laboratory populations of *Probopyrus pandalicola*. All data are expressed as weight-adjusted values (assuming a host population of 1 g dry weight) and as percentages of estimated parasite ingestion.

Efficiencies

Ecological growth efficiencies and tissue growth efficiencies for control shrimp, hosts, and host-parasite systems are given in Table 4. Trophic level energy intake efficiencies for parasites are presented in Table 5.

Table 3. *Probopyrus pandalicola*. Elements of energy flow for laboratory populations of parasites. For all parameters data are expressed as expected values (in cal/month) for parasites infecting a host population of 1 g dry weight (first value under each category). Numbers in parentheses are expressed as percentage of estimated parasite ingestion

Month and temperature	Ingestion ($R_p + P_p$)	Respiration	Reproduction	Growth	Molting
1972					
September (25°C)	1288	240 (19)	1020 (79)	3 (0)	26 (2)
October (23°C)	477	230 (48)	210 (44)	10 (2)	27 (6)
November (18°C)	125	105 (84)	0	4 (3)	16 (13)
December (14°C)	53	40 (75)	0	3 (6)	10 (18)
1973					
January (11°C)	150	140 (94)	0	6 (4)	4 (3)
April (15°C)	344	120 (35)	210 (61)	5 (1)	9 (3)
May (23°C)	658	200 (30)	440 (67)	0 (0)	18 (3)
June (30°C)	813	225 (28)	560 (69)	0 (0)	28 (3)
July (31°C)	677	150 (22)	500 (74)	0 (0)	27 (4)
August (30°C)	1302	510 (39)	770 (59)	6 (0)	16 (1)

Table 4. *Palaemonetes pugio* and *Probopyrus pandalicola*. Ecological growth efficiencies ($\frac{P}{I}$) and tissue growth efficiencies ($\frac{P}{A}$) for control shrimp, parasitized shrimp and host-parasite systems

Month and temperature	Control population		Parasitized population		Host-parasite population	
	$\frac{P}{I}$	$\frac{P}{A}$	$\frac{P}{I}$	$\frac{P}{A}$	$\frac{P \quad P_p}{I_h}$	$\frac{P \quad P_p}{A_h}$
1972						
September (25°C)	9	10	4	5	13	13
October (23°C)	15	16	10	10	11	12
November (18°C)	17	18	12	13	12	12
December (14°C)	11	12	6	7	6	6
1973						
January (11°C)	38	40	44	47	44	47
April (15°C)	42	43	19	19	23	24
May (23°C)	21	22	18	19	25	26
June (30°C)	16	18	8	9	15	15
July (31°C)	19	20	7	7	12	13
August (30°C)	14	15	10	11	16	16

Table 5. *Probopyrus pandalicola*. Trophic level energy intake efficiencies $\left(\frac{I_{\text{parasite}}}{I_{\text{host}}}\right)$ during various months of the year (in percentages)

Month and temperature	Efficiency
1972	
September (25°C)	10
October (23°C)	4
November (18°C)	2
December (14°C)	1
1973	
January (11°C)	6
April (15°C)	8
May (23°C)	10
June (30°C)	9
July (31°C)	7
August (30°C)	9

Discussion and Conclusions

Ingestion

As expected, ingestion by *Palaemonetes pugio* is generally temperature-dependent (Table 1). However, it is highest in August (30°C) rather than July (31°C); an additional peak was observed in October (23°C). These findings are in contrast to those of Ivleva (1970) who showed that the ingestion rate for *Leander adspersus* increases with increasing temperature and reaches a maximum at the upper temperature limit for the species. The present findings indicate that weight-adjusted ingestion during June was substantially lower than for August although both experiments were conducted at the same temperature. Similarly, May's values were lower than October's, despite an identical experimental temperature (23°C). These findings may be related to intermonthly variations in shrimp size and age-class distribution. Shrimp collected in May and June were older and larger than those used during August and October. Similarly, Wood (1966) reported that the largest grass shrimp in the Galveston Bay (Texas, USA) system occur in spring and summer, but are replaced by progressively smaller individuals in August and September. Since weight-specific metabolic rate (and therefore, energy requirements) generally decreases as weight increases (Zeuthen, 1953), the weight-adjusted ingestion values reflect size as well as temperature effects. Had shrimp of uniform sizes and ages been available throughout this study, intermonthly comparisons would not show such size effects.

The daily ingestion rate, considered as a percentage of population biomass, ranged from 2% in January to 10% in August. Similarly, Ivleva (1970) found that the daily ingestion rate of *Leander adspersus* equals 2.5 to 15% of body weight; the highest value is characteristic of consumption near the upper temperature limit.

Except during October, May, and July, parasitized populations ingested more than control groups (Table 1). The difference noted during May is inconsequential. The results observed in July and October may be due to the noted higher maintenance requirements and secondary production in the control groups compared with parasitized groups during these months (Table 2). The generalization that parasitized groups ingest more than control groups is in agreement with the findings of Walkey and Meakins (1970), and Mace and Davis (1972), all of whom studied host-parasite energetics and demonstrated higher ingestion rates for infected than noninfected hosts.

Secondary Production

Growth

Shrimp growth varied greatly from month to month and showed little temperature dependence (Table 2). During several months, population standing stocks decreased. Such reductions resulted from weight or caloric value losses by shrimp populations. Shrimp size and age may have been responsible for the most significant standing stock decreases (June and July), since field-collected shrimp were old

and many did not survive these months' experiments. Lasker (1966) recorded weight losses for euphausiids maintained in the laboratory and noted that such losses were frequently followed by death, as in the present study. An alternate hypothesis for the noted decreases is that *Artemia salina* is not an adequate food for adult shrimp. Broad (1957) demonstrated that larval growth is more rapid and metamorphosis more likely for *Palaemonetes* spp. reared on *A. salina* nauplii than shrimp reared on unicellular algae. However, adult *P. pugio* are detritivores in nature (Adams and Angelovic, 1970; Welsh, 1973). Possibly the dietary restrictions imposed in the present study resulted in the reductions observed.

The effect of parasitism on growth is variable throughout the year (Table 2). In some months, growth is lower for parasitized than control populations (April; September-December); during other months the opposite is true (January, May, and August). During September and December, control populations grew while parasitized ones did not. Similarly, Walkey and Meakins (1970) and Mace and Davis (1972) reported losses in caloric content for parasitized fish but not for control fish.

Growth for experimental populations declined from January to July. This is not surprising, since these groups represent the same age class. It is known that growth efficiencies are higher for young animals than older ones (Phillipson, 1966). A similar trend was not observed for the age class represented by the August-December groups. For example, growth values obtained during October were higher than both the previous and subsequent month's values (Table 2). The reason for this finding may be that October follows the shrimps' reproductive season. One would expect that a higher proportion of assimilated energy would be available for somatic growth during this month than previous months. A similar finding was made by Fuji (1967) who noted that, for the sea urchin *Strongylocentrotus intermedius*, two distinct growing seasons occur: one in which energy is used for somatic growth and another in which energy is used for gonadal growth. His finding is in close agreement with the present one, since gross growth efficiency for control *Palaemonetes pugio* is generally high when gross reproduction efficiency is low (Table 2).

Molting

Molting by grass shrimp is greater at high than low temperatures (Table 2), although as a percentage of energy intake, molting remained fairly constant throughout the year. Generally, monthly molting losses were greater for control than parasitized populations. This is surprising, since Callan (1940) showed accelerated molting for parasitized shrimp during the reproductive season. Similarly, previous findings for *Palaemonetes pugio* (Anderson, in preparation) indicate that molting during the reproductive season is accelerated in parasitized females. However, since the molting rate apparently decreases during the same months for parasitized males, it is possible that the two effects balanced one another during the present study.

Previous workers (review by Hughes, 1940) have suggested that parasitism may result in a reduction in the host's capability to store glycogen and therefore an inability to mobilize organic matter for incorporation into the exoskeleton during molting. No differences between either energy content/unit weight of exuviae or total monthly energy losses via molting of parasitized and control shrimp were noted in the present study.

The energy content of molted exuviae varies from month to month but apparently is not affected by parasitism. The highest values were recorded during May. Ivleva (1970) found that, although monthly molting losses are correlated with temperature for *Leander adspersus*, the caloric value (cal/g dry weight) of exuviae does not vary significantly with temperature. He reported the mean caloric value of exuviae to be 1140 ± 370 cal/g dry weight which is significantly lower than the values determined for *Palaemonetes pugio*.

Molting occurred in all experimental groups, although it was not always accompanied by somatic growth (Table 2). Similarly, Lasker (1966) reported that some euphausiids maintained in the laboratory molted but failed to grow despite "adequate" food availability. He concluded that molting is a metabolic necessity which may continue at the expense of an animal's organic reserves.

Reproduction

Newly deposited shrimp larvae have a higher energy content (7513 cal/ g ash-free dry weight; 11% ash) than mature larvae (7167 cal/g ash-free dry weight; 15.3% ash). Clutter and Theilacker (1971) demonstrated that ash-free caloric content decreases from 7620 cal/g dry weight (6% ash) to 6200 cal/g dry weight (6.6% ash) during larval development of the mysid *Metamysidopsis elongata*. Hence,

both studies indicate that, during embryogenesis, percentage ash increases while energy content decreases as stored energy is used for maintenance, protein biosynthesis, structural differentiation, and exoskeleton development.

Shrimp reproduction accounts for up to 16% of the total estimated energy intake (Table 2). The present study's demonstration of early and late summer reproductive peaks is in agreement with Wood's (1966) findings for Gulf Coast shrimp populations. Reproduction in parasitized shrimp does not occur. However, it is significant that reproduction by parasites, when expressed as a percentage of host intake (Table 2) is often greater than reproduction by uninfected shrimp. Furthermore, parasites reproduced during September and October, non-reproductive months for *Palaemonetes pugio*. The reproductive energy output by *Probopyrus pandalicola* is remarkable in light of its small size.

Since parasitic castration of shrimp hosts results from infection by *Probopyrus pandalicola*, reproduction is the energy flow parameter affected most significantly by parasitism. However, since the incidence of parasitism does not exceed 3% in North Inlet Estuary, the impact of parasitism is probably negligible with respect to shrimp recruitment. Populations in areas such as Biscayne Bay, where there is a high incidence of *Probopyrus* sp. (Joseph Simon, personal communication), are undoubtedly dramatically affected by parasitism. The density-dependent effects of parasitic castrators on host populations have been discussed by Kuris (1971).

Respiration

Respiratory energy expenditure consistently exceeded secondary production (Table 2). Likewise, Welsh (1973) estimated the caloric demand for respiration to be $4\frac{1}{4}$ times that for production. Maintenance always accounts for over 57% of the total energy input (Table 2). Lasker (1966) reported that 62 to 87% of the carbon assimilated by *Euphausia pacifica* is used for maintenance. During at least November, December, and January of the present study, maintenance was overestimated (Table 2) as evidenced by higher maintenance values than ingestion values during these months. Any overestimate for hourly respiration would have been magnified 720 times when monthly values were computed. Probably, more reliable estimates could have been obtained using flow-through respirometry and making oxygen determinations over a 24 h period for each experimental group. In addition to reducing the error magnification, such a method would have allowed measurement of possible rhythms in oxygen uptake, although McFarland and Pickens (1965) considered such rhythmicity to be nonexistent in *Palaemonetes vulgaris*.

Surprisingly, weight-adjusted metabolic rate showed little consistent temperature dependence (Table 2) during the present study. Different findings were reported by Welsh (1973), who noted that Q_{O_2} for Rhode Island populations of *Palaemonetes pugio* increases up to 18°C, but then decreases with increasing temperature. Undoubtedly, a number of variables such as size, age, temperature, reproductive stage, etc. interact to influence metabolic rates of shrimp.

Generally, maintenance is greater for control than parasitized shrimp. The exceptions noted during April, May and August are probably insignificant, while that noted for December is more likely the result of a gross overestimation of metabolism for the parasitized group than an effect of parasitism. The finding that Q_{O_2} for control shrimp generally exceeds that of infected shrimp is in agreement with previous work (Anderson, 1975b).

Egestion

Fecal production for shrimp populations is also temperature-dependent. However, relatively little (generally 3 to 8%) ingested energy is unassimilated (Table 2). Hence, the assimilation efficiency for grass shrimp maintained on *Artemia salina* nauplii averages 94 to 95%. A lower estimate (78 to 79%) was given by Johannes and Satomi (1966) for *Palaemonetes pugio* fed on *Nitzschia closterium*. Assimilation efficiency has frequently been found to be diet-dependent (e.g. Fuji, 1967; Carefoot, 1970; Schindler, 1971).

No correlation between assimilation efficiency and temperature is evident (Table 2). Similarly, Ivleva (1970) could show no correlation between temperature and assimilation efficiencies for *Leander adspersus*.

In contrast to Ivleva's (1970) demonstration that energy content of shrimp fecal material increases with temperature, no temperature dependence was noted during the present study. The energy content of shrimp feces is similar to values obtained for stoneflies (McDiffett, 1970) and aquatic dipterans (Stockner, 1971).

The assimilation efficiencies calculated for grass shrimp may have been

overestimated since I made no attempt to collect feces immediately following defecation. Johannes and Satomi (1966) demonstrated coprophagy by *Nitzschia closterium*-fed shrimp. They found that reingested feces show a 40% reduction in organic carbon. Furthermore, during the present study, fecal material may have been degraded somewhat by bacterial action. Assimilation efficiencies reported here represent final rather than initial values.

The high energy content of *Palaemonetes pugio* fecal material is not unreasonable. Welsh (1973) speculated that protein-rich fecal material packed with bacteria derived from the hindgut of grass shrimp continues to increase in nutritional value in the presence of dissolved organic matter (Johannes and Satomi, 1966). Since fecal material was not collected daily in the present study, it is likely that such a process could have occurred, thus resulting in energy-rich fecal material.

The finding that parasitism has little effect on egestion is in agreement with that of Mace and Davis (1972), who failed to demonstrate a significant effect of parasitism by leeches on assimilation efficiencies of fish. However, they speculated that a change in conversion efficiency could perhaps be reflected by a change in nitrogenous waste excretion rather than a change in fecal production. No attempt was made to quantify excretion during the present study.

Parasite Energetics

It should be noted that many of the data presented as parasite energy flow parameters (Table 3) are estimates and may not accurately reflect conditions *in vivo*. For example, parasite ingestion was estimated by summation of other parasite energy flow parameters (respiration + secondary production); respiration was measured for parasites *in vitro* with no attempt made to measure parasite respiratory quotients; energy content of parasite exuviae could not be measured directly; it has not been shown conclusively that parasites always molt in synchrony with hosts, although I assumed that they do for the present study. However, I feel that the data presented are the best estimates which could have been made within the limitations of the experimental procedures used.

Parasite ingestion was estimated to be 1 to 10% of the total energy intake for the host-parasite system (Table 5). Hence, the magnitude of the parasite "energy burden" is frequently near that for host growth. In September, parasite ingestion equalled the quantity of energy used by hosts for secondary production. Ingestion by *Probopyrus pandalicola* is substantially greater than that for brachyuran symbionts of sea urchins, which consume 1.6% (female crab) or 0.6% (male crab) of the hosts' caloric intake (Castro, 1971).

During their reproductive season, parasites use a smaller proportion of assimilated energy for maintenance than do hosts (Tables 2 and 3). Such low maintenance requirements are probably related to parasites' easily assimilable food (host hemolymph) and low activity level.

Parasite molting and growth estimates are low relative to metabolism and reproduction for all study months (Table 3).

The high ash-free caloric values measured for eggs and larvae of *Probopyrus pandalicola* (7858 and 7426 cal/g dry weight, respectively) support my earlier hypothesis that epicaridian larvae contain a high proportion of stored energy-rich lipids which may be catabolized during this active non-feeding stage (Anderson, 1975a). Calow and Jennings (1974) have noted that a different reproductive strategy, that of using glycogen for energy storage, characterizes parasitic Platyhelminthes. The values obtained here are similar to those obtained by Clutter and Theilacker (1971) for *Metamysidopsis elongata*. Although the decrease in energy content noted during larval development of *P. pandalicola* is accompanied by a dramatic increase in percentage ash (newly deposited larvae contain 1.8% ash and mature larvae contain 16.2% ash), such an increase was not noted for *M. elongata*.

Parasite reproduction constitutes a significant proportion of intake from April-October (Table 3). Gross reproductive efficiency ranges from 44 to 79% during these months. Mace and Davis (1972) reported that reproductive efficiencies for leeches often approached 76%.

Efficiencies

Both tissue growth efficiency and ecological growth efficiency are consistently higher for control shrimp than parasitized shrimp, except during January (Table 4). However, the differences between efficiencies for control shrimp and host-parasite systems are not as great. Furthermore, in September, January, May, and August, efficiencies for host-parasite systems exceeded those for control shrimp. These findings suggest

that *Probopyrus pandalicola* are remarkably efficient at utilizing host tissues as a source of energy for secondary production. Walkey and Meakins (1970) demonstrated that the mean ecological growth efficiency is lower for parasitized fish than control fish although the mean efficiency for the host-parasite system is greater than that for uninfected fish.

The ecological growth efficiencies calculated during January are rather high in light of the known range of values (6 to 37%) given by Phillipson (1966). High values for this parameter point to efficient assimilation of food energy with little being voided as feces or used in respiration.

Calculation of trophic level energy intake efficiencies revealed that, via parasitic castration of hosts, *Probopyrus pandalicola* may obtain as high a proportion of its host's intake energy (up to 10%) as many predators obtain via predation (Slobodkin, 1964). Other than Castro's study (1971) which demonstrated a maximum trophic level energy intake efficiency of 1.6% for a brachyuran-echinoderm system, the present study is the only one for which such data have been provided for a host-parasite system. It would be interesting to determine the maximum transfer efficiency possible in this and related systems.

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