Energy allocation in the threespine stickleback

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Energy is the basic currency of living organisms (Harold 1986). It gives the organism the potential to do the work required for maintenance, growth, and reproduction. Organisms are subject to the laws of thermodynamics (Brafield and Llewellyn 1982), making it possible to describe quantitatively the expenditure of energy. All forms of energy are interconvertible and so can be measured in common units of joules (J) (1 J = 4.18 cal).

A stickleback acquires its energy from the chemical bonds of the metabolizable components of food (or when an embryo, from the yolk provided by its mother), the proteins, lipids, and carbohydrates. Food also provides the basic chemical units for the synthesis of tissue. The total energy intake of an individual fish must be balanced by energy expended on maintenance plus any energy stored in the form of new tissue:

\[
\text{Intake} = \text{Maintenance} + \text{Growth.} \tag{5.1}
\]

Energy intake (C) is the energy content of the food consumed. Maintenance, used here in a wide sense, has several components. Some energy is lost in faeces (F), consisting of undigested or partly digested food, cells sloughed off from the alimentary canal, mucus, and other voided by-products of digestion. Energy is also lost in the nitrogenous excretory products (U) produced by the catabolism of protein. The major component of maintenance is the energy lost as heat generated by the metabolic processes as useful work is done. This loss can be partitioned into three components (Brett and Groves 1979). The first, resting or standard metabolism (R₀), is the work that has to be done to maintain the individual in a dynamic steady state. It is measured as the metabolic rate of a resting individual in a postabsorptive state. The second component represents the energy costs of swimming ('activity', Rₐ). The third is the energy cost of food processing ('digestion', Rₛ), often called specific dynamic action (SDA). This component may include the costs of synthesis of new tissue (Jobling 1985). Energy can be accumulated in new tissue through somatic growth and the deposition of storage products, (Pₛ), and as reproductive products (Pᵣ). The energy budget of an individual can be written as:
\[ C = F + U + R_s + R_a + R_d + P_s + P_r \]  \hspace{1cm} (5.2)

in which all components are measured in energy units, usually joules (Wootton 1990). The power generated by metabolism can be expressed in watts (W), equivalent to 1 J s\(^{-1}\).

Changes in the pattern of allocation of energy between components of the energy budget will often have important effects on the growth, reproductive output, and even the survival of an individual (Fig. 5.1). For example, an increased allocation to growth may reduce the time that an individual is vulnerable to a size-selective predator (Reimchen page 246 this volume). Because of these consequences for the components of fitness, energy allocation must be sensitive to natural selection (Alexander 1967; Calow 1985).

Selection will favour patterns of energy allocation that tend to maximize the lifetime production of young by individuals. Energy allocation provides the means by which reproductive success is achieved (see also Glebe and Leggett 1981), but that success is not defined in terms of energy. A successful energy allocation might be one that uses an energy income efficiently, but it might also be a pattern that uses a high rate of income relatively inefficiently but which generates a high rate of production of offspring. The laws of thermodynamics form a physical constraint within which natural selection operates. But the study of energetics taken on its own offers no guidance as to what patterns of allocation will maximize the lifetime production of offspring in specific environmental circumstances (see Baker Chapter 6 this volume).

**Fig. 5.1** Scheme of metabolic and possible fitness effects of energy allocation. (Modified after Calow 1985.)
The energy available to an individual is limited. Sometimes this limitation will result from a shortage of food. But even if food is plentiful, consumption rate is limited by the structures and mechanisms used to acquire and process food (Hart and Gill Chapter 8 this volume). Energy allocated to one component of the budget is at the expense of allocation to other components. Time is also a constraint. An individual may be able to increase its energy income by increasing the time it spends foraging, but this will be at the expense of the time spent in other activities such as sheltering from predators. Different activities have different energy costs, so that changes in the time spent in different activities will have implications for energy allocation.

The threespine stickleback, with its wide geographical range and its profusion of small variations on a common morphological and behavioural theme, offers great possibilities for understanding how patterns of energy and time budgeting relate to the reproductive success of individuals over a range of abiotic and biotic environmental conditions. Only a tentative start has been made on such a programme.

This essay reviews what is now known about energy allocation in the stickleback using data from both laboratory and field studies. It takes as its framework the energy balance equation, taking each term in that equation in turn and highlighting where important data are still required. An energy budget taken on its own is of little interest apart from demonstrating that the techniques used to measure each component are adequate. More important problems are these:

1. How do the patterns of energy allocation by individuals in a population change as environmental conditions change?
2. How do the patterns of allocation in different populations differ?
3. What are the consequences for growth, reproduction, and survival of differences in allocations?

CONSUMPTION

Prey selection and energy intake
The stickleback is catholic in its choice of prey (Wootton 1976, 1984a; Hart and Gill page 227 this volume), although its small body size restricts the size range of prey with which it can cope. Nevertheless, over a wide geographical range the diet tends to be dominated by two prey categories: zooplankton and the larvae and pupae of chironomids (Diptera) (Fig. 5.2). Interpopulation differences in the diet of the stickleback represent variations on a restricted theme. This restriction is emphasized even more by the similarity in the energy content of the typical prey (Table 5.1). Putting it crudely, a stickleback acquires approximately the same gross quantity of energy per unit dry weight of prey eaten, irrespective of which of the typical prey items are eaten. Prey will differ in their water content, ease of detection, and ease
Fig. 5.2 Examples of diet composition of stickleback populations from a wide geographical range. Sources: River Birket, north-west England (Hynes 1950); Llyn Frongoch, mid-Wales (Allen and Wootton 1984); San Pablo Creek, California, USA (Snyder 1984); Bothnian Sea, Sweden (Thorman and Wiederholm 1986); New Brunswick, Canada (Delbeek and Williams 1987a). Prey types are indicated in the figure (other components, including unidentified debris, make composition up to 100 per cent).

of capture, and so will differ in profitability (energy gained per unit time) (Hart and Gill Chapter 8 this volume).

Interpopulation differences in morphology and behaviour related to feeding (e.g. Bentzen and McPhail 1984; Lavin and McPhail 1985, 1986; Hart and Gill page 210 this volume) have consequences for the acquisition of energy. An example is given by a study in Scotland, UK, by Ibrahim and Huntingford (1988, 1989b) on the stickleback from a large lake, Loch Lomond, and a small adjacent pond. The pond stickleback had a larger gape and inter-raker distance than the loch fish. When provided with either benthic prey or zooplankton in densities similar to those occurring naturally, experimental pond fish acquired energy at the rate of 0.034 J s⁻¹ from zooplankton and at 0.026 J s⁻¹ from benthic prey. Compared with the pond stickleback, the loch fish were significantly more effective at exploiting
Table 5.1  Energy contents of typical prey of the stickleback.

<table>
<thead>
<tr>
<th>Food item</th>
<th>Range of energy contents (kJ g^{-1} dry wt)</th>
<th>Range of energy contents (kJ g^{-1} wet wt)</th>
<th>Sources^a</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Oligochaeta</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tubificidae</td>
<td>21.63–23.34</td>
<td>3.18–3.60</td>
<td>1, 3, 4</td>
</tr>
<tr>
<td>Enchytraeidae</td>
<td>22.05–24.10</td>
<td>4.81</td>
<td>2, 5</td>
</tr>
<tr>
<td><strong>Insecta</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chironomidae</td>
<td>20.51–22.24</td>
<td>2.11–3.6</td>
<td>3</td>
</tr>
<tr>
<td><strong>Crustacea</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Copepoda</td>
<td>23.45–24.62</td>
<td>2.30</td>
<td>3</td>
</tr>
<tr>
<td>Cladocera</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Daphnidae</td>
<td>17.13–24.48</td>
<td>1.07–1.55</td>
<td>3</td>
</tr>
<tr>
<td>Bosminidae</td>
<td>21.49–22.27</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Chydoridae</td>
<td>22.62</td>
<td>3</td>
<td></td>
</tr>
</tbody>
</table>

^a Sources: 1, Cole (1978); 2, Cui and Wootton (1988a); 3, Cummins and Wuycheck (1971); 4, Walkey and Meakins (1970); 5, Wootton et al. (1980a).

the zooplankton, 0.059 J s^{-1}, and not significantly less effective at exploiting the benthos, 0.011 J s^{-1}. A regression model developed by Wootton et al. (1980b) for sticklebacks feeding *ad libitum* on enchytraeid worms (Oligochaeta) predicts a daily maximum consumption of 450 J for a fish weighing 1 g at 15 °C. Although the calculations are crude, they suggest that loch fish feeding on zooplankton can consume their maximum daily intake in only 2 h, whereas the same fish feeding on benthos would take about 11 h. These values suggest the potential effects on time and energy allocation that differences in foraging effectiveness could have. However, Ibrahim and Huntingford's (1988) data were obtained from feeding sessions of only 5 min. Consequently, they provide no direct evidence that the differences translate into differences in the rate of energy acquisition over longer periods, which would have consequences for the components of fitness of growth, reproduction, and survival.

**Maximum rate of consumption**

The daily, maximum rate of food consumption by the stickleback is a function of body size, water temperature, and possibly other environmental factors including salinity and pH. Over the temperature range of 3–19 °C, maximum consumption of enchytraeid worms by sexually immature fish was predicted by the relationship:

\[ \ln C_{\text{max}} = -4.28 + 0.93 \ln W + 0.91 \ln T \]  \hspace{1cm} (5.3)

where \( C_{\text{max}} \) is consumption in mg, \( W \) is fish weight in mg, and \( T \) is temperature in °C (Wootton et al. 1980b; Fig. 5.3). At higher temperatures, con-
Fig. 5.3  Predicted effect of body weight and temperature over range 7.0 to 20 °C on maximum daily food consumption, $C_{\text{max}}$, based on regression model in Wootton et al. (1980b).

Consumption probably declines sharply as in other teleost species (Elliott 1981).

Faris (1986) presented evidence that at pH lower than 6, appetite is depressed in freshwater residents. The effects of salinity are not known.

Under a defined set of environmental conditions, the maximum rate of consumption may change with the physiological condition of the fish. During a breeding season, sexually mature females readily consumed a daily ration of 16 per cent of their body weight of enchytraeid worms. At the end of the season, when egg production ceased, the same ration was only consumed over a period of several days, although neither temperature nor photoperiod changed. The females were still in a healthy condition two months later, so the changes in appetite were probably not due to senescence (Fletcher and Wootton unpubl. obs.). Such observations suggest that the fish do not always consume food at the maximum rate at which they can process it. Fish in a given physiological condition may have an optimal daily ration which is not necessarily the maximum possible ration. The regulation of appetite is an important but little-explored aspect of energy allocation in fishes.

**Natural rates of consumption**

There are several estimates of natural rates of food consumption. The use of different units to express consumption makes comparisons difficult, but the data suggest that a typical daily consumption is 2–10 per cent of body weight, depending on the temperature. Manzer (1976) estimated that planktivorous stickleback in Great Central Lake, Vancouver Island, Canada,
were eating 6–8 per cent of their body weight daily. Stickleback living in brackish water in the Baltic Sea had daily rations estimated at 24.2 mg per g of fish at 10 °C, 48.3 mg g⁻¹ at 14 °C, and 132 mg g⁻¹ at 18 °C (Rajasilta 1980). Assuming that the average energy content of the prey was 4.81 J mg⁻¹ wet wt (Cui pers. comm.) gives energy intake rates of 116, 232, and 634 J d⁻¹ respectively.

The population in Llyn Frongoch, a small reservoir in mid-Wales, UK, had an annual consumption estimated at 2700–4200 mg wet wt (13–20 kJ a⁻¹) per average fish as it grew from 65.8 to 552 mg wet wt (Allen and Wootton 1984). For this Welsh population, in most months, the rate of consumption estimated from observed growth rates was less than the maximum possible consumption estimated from laboratory studies (Allen and Wootton 1982b). If Allen and Wootton’s estimates are accurate, the growth rate of fish in the Frongoch population is energy limited, at least for portions of the year.

MAINTENANCE

Faecal and excretory losses
The proportion of ingested energy that is lost in faeces is largely determined by the quality of the food. Sticklebacks fed enchytraeid or tubificid worms, oligochaetes with soft cuticles, lost in faeces about 3–14 per cent of the energy ingested (Cole 1978; Allen and Wootton 1983). This proportion was lower in larger fish and at higher temperatures (Allen and Wootton 1983), but slightly higher when the intake rate was higher (Cole 1978). Similar research using prey with less digestible cuticles has yet to be done, although a field study suggests that the inclusion of such prey will increase the energy lost in faeces. The weight of faeces collected over 24 h from sticklebacks that had fed naturally in a Welsh lake was significantly higher than the weight produced by fish feeding at their maximum rate on an ad libitum supply of enchytraeid worms (Allen and Wootton 1983). For comparison, brown trout feeding on the isopod Gammarus lost 11–31 per cent of the energy in the food consumed, depending on temperature and ration size (Elliott 1979).

The major pathway of nitrogenous excretion is as ammonia/ammonium through the gills. The energy lost through nitrogenous excretion has yet to be estimated for the stickleback. A study of the European minnow, Phoxinus phoxinus (a small cyprinid), provides some comparable data. When fed on enchytraeid worms, the minnow lost 2–9 per cent of the ingested energy as nitrogenous wastes (Cui and Wootton 1988a). The loss tended to be proportionately greater at low rations and at higher temperatures. Brown trout fed Gammarus lost 3.6–15.1 per cent (Elliott 1979).

Metabolic expenditure
Energy lost neither in faeces nor in excretory products can be used to do useful work. The rate of energy expenditure can be directly measured by the
rate of heat production (direct calorimetry). Although some attempts have been made to measure energy expenditures in this way (Lowe 1978), the high heat capacity of water means that changes in its temperature caused by the metabolic activities of the fish are small and difficult to measure accurately. Indirect calorimetry is usually used (Brafield 1985). If the fish is respiring aerobically, the rate of energy expenditure is related to the rate of oxygen consumption. This latter rate can be converted to a rate of energy expenditure by an appropriate oxycalorific coefficient, which depends on the substrate being respired. For a carnivore such as the stickleback, a value of 13.61 \( \text{J mg O}_2^{-1} \) respired is appropriate (Brafield 1985). If rates of carbon dioxide and ammonia production by the fish are also measured, a more accurate rate of energy expenditure can be estimated because these rates will reflect the substrate being catabolized (Brafield 1985). The respirometer should allow the fish sufficient space to make voluntary movements and should, preferably, allow the experimenter to impose known rates of swimming on the fish whose respiration rate is being measured. Studies on the rate of metabolism of the stickleback often fall short of these requirements. One of the better respirometers used is Lester’s (1971). Unfortunately his presentation of the results makes it difficult to compare them with those from other studies that used less satisfactory respirometers.

**Standard metabolism, \( R_s \)**

Standard, or resting metabolism is difficult to measure accurately because the fish must be still and in a defined postabsorptive state. Lester (1971) and Meakins (1975) measured the decline in the oxygen concentration of water in a closed respirometer containing the fish. Meakins ensured that his fish were still by swimming them to exhaustion prior to measuring resting metabolism (although this procedure raises the possibility that the fish were repaying an oxygen debt incurred as they approached exhaustion). Meakins’ (1975) data could be expressed as:

\[
R(s) = aW^b
\]

(5.4)

where \( R(s) \) is the rate of oxygen consumption of the exhausted fish, \( W \) is body weight, and \( a \) and \( b \) are parameters with \( b \) taking values between 0.174 and 0.352 (Fig. 5.4). A weight exponent, \( b \), for standard metabolism is typically less than 1.0 in teleosts (Brett and Groves 1979), showing that the weight-specific energy cost of maintenance declines as the weight of the fish increases.

The estimates of Lester (1971) and Meakins (1975) are similar. Meakins’ (1975) equations predict that a 1 g stickleback has a minimum rate of energy expenditure of about 80 J d\(^{-1}\) at 15 °C (fish caught in August). Lester (1971) gives the standard metabolic rate for a fish 60 mm in length as 52 J d\(^{-1}\) at 10 °C. These values are about 17 per cent of the maximum rate of energy intake (311 J d\(^{-1}\) at 10 °C and 450 J d\(^{-1}\) at 15 °C) predicted for a 1 g fish by the model of Wootton et al. (1980b).
Fig. 5.4 Predicted effect of body weight on standard, routine, and maximum rates of metabolism, $R_s$, $R_{rout}$, and $R_{max}$, at 15 °C in fish collected in February and August, based on regressions in Meakins (1975).

Standard metabolism includes the energy costs of active osmotic and ionic regulation. For freshwater sticklebacks, such costs will remain almost constant, but for anadromous populations the costs will change as the fish move into waters of different salinities during migration. Gutz (1970) compared the respiratory rates of phenotypes that differed in the number of their lateral plates. When the low-plated morph was moved from fresh water into seawater, it adapted passively by increasing the pool of free amino acids and did not increase its energy expenditure. The completely and partially plated morphs adopted an active regulatory mechanism signalled by an increase in the rate of oxygen consumption. Calculations based on the respiration data of Gutz (1970) suggest that for a 1 g fish, the rate of energy expenditure in salt water was about 65–90 J d$^{-1}$ higher in salt water than in fresh water at 20 °C. At 4 °C, the difference was about 45 J. However, these differences may also partly reflect differences in the level of spontaneous activity in fresh and salt water. McGibbon (1977) found that at 12 °C, a low-plated, freshwater stickleback showed no increase in the rate of oxygen consumption over a salinity range of 1.7–27.2‰ but there was a significant increase at 32.3‰.

The effects of other abiotic factors, including temperature, oxygen concentration, and pH, on the standard metabolism of the stickleback have yet to be quantified.
Activity metabolism, $R_a$

The energy costs of swimming can be estimated in two ways. In the first, the fish is provided with sufficient room in the respirometer to allow for spontaneous movement. Under these conditions, the routine rate of respiration is measured. This is the value commonly reported in studies of fish respiration rates (Brett and Groves 1979). The cost of swimming is the difference between the routine rate and the standard rate under the same conditions. Meakins (1975) and Wootton et al. (1980a) estimated the routine rate for fish held in a closed respirometer (Fig. 5.4, 5.5). At 15 °C, the routine rate predicted for 1 g fish was 153 J d$^{-1}$ or about double the standard rate by Meakins, but 105 J d$^{-1}$ by Wootton et al. (1980a). The effect of temperature on routine rate is also illustrated in Fig. 5.5. In a simultaneous comparison of routine metabolism by direct and indirect calorimetry, Lowe (1978) obtained estimates of 84 J g$^{-1}$ d$^{-1}$ (direct) and 80.9 J g$^{-1}$ d$^{-1}$ (indirect) (Brafield 1985). These studies did not define the amount of swimming shown by the spontaneously active fish, so any comparison of the results is difficult.

A second and better approach is that of Lester (1971), who forced fish to swim at a defined speed while the rate of respiration was measured. The range of speeds was from 0.9 to 1.8 body lengths per second (BL s$^{-1}$). Calculations based on Lester's (1971) data suggest that the rate of energy expenditure for a fish swimming at 0.9 BL s$^{-1}$ ranges from 60 to 142 J d$^{-1}$. The range partly reflects differences in fish size. Assuming a fish of 55 mm,
this represents the energy cost (including standard metabolism) of swimming just over 4 km in a day.

Stickleback usually swim with a labriform mode of locomotion using the large pectoral fins. This mode is often associated with fish that live in complex environments such as rocky reefs or weed-beds and is correlated with manoeuvrability, rather than speed in cruising or fast starts and turns (Webb 1984). When sprinting, stickleback switch to a body and caudal fin mode of swimming. However, Taylor and McPhail (1986) and Whoriskey and Wootton (1987) found that stickleback using the labriform mode could swim for long periods at speeds as high as 5 BL s\(^{-1}\). Taylor and McPhail (1986) describe morphological differences between the anadromous and freshwater stickleback which suggest that the former is better adapted for cruising. Anadromous forms may migrate upstream for many kilometres in spring. The energy cost of such prolonged swimming may be lower in stickleback with the morphology typical of anadromous (or limnetic) forms (Taylor and McPhail 1986). Well-designed experiments on sustained swimming of the anadromous, limnetic, and benthic forms are needed to relate the energy costs to the morphological adaptations, including differences in the number of lateral plates.

The small size of the stickleback means that swimming speeds of 5 BL s\(^{-1}\) represent absolute speeds of only 25–30 cm s\(^{-1}\). This limitation essentially restricts sticklebacks to the slow-moving waters of lakes, ponds, lowland streams, or rivers (Wootton 1976). In coastal waters, tidal currents may aid onshore and offshore movements, with some of the energy required for transportation being provided by the motion of the water rather than the metabolism of the fish (Whoriskey \textit{et al.} 1986). Adult and juvenile sticklebacks can occur many kilometres from the coast both in the North-west Pacific (Quinn and Light 1989) and in the West Atlantic (Cowen \textit{et al.} 1991). The relative contributions of active and passive transport to these oceanic distributions are not known.

\textbf{Apparent specific dynamic action, }R_4\textbf{ }

When a fish is fed, its rate of respiration increases to a peak, then declines as the meal is processed. This increase in energy expenditure associated with feeding has a small component attributable to the muscular work done during feeding and digestion, but the major portion is related to the biochemical processing of the food and the products of digestion (Jobling 1983). A portion of this expenditure may represent the energy costs of the synthetic processes involved in growth, particularly protein growth (Jobling 1985). \(R_4\) typically accounts for 9–20 per cent of the energy of the food consumed, the value partly depending on the chemical composition of the food (Jobling 1983). Although an increase in respiration associated with feeding has been observed in the stickleback (Wootton pers. obs.), quantitative analysis of the effect has not been completed.
Power budgeting

Priede (1985) has presented a stimulating if speculative analysis of energy expenditure in fishes. He notes that the total sustainable power output (i.e. energy per unit time) of a fish may be less than the maximum possible power demands of the three components, standard metabolism ($R_s$), activity metabolism ($R_a$), specific dynamic action ($R_d$) (see also Goolish 1991). Under these circumstances, the fish must regulate the allocation of the available power. Priede (1985) further argues that this allocation should, as far as possible, allow the fish to stay well within the limits of its scope for

![Graph](a)

![Graph](b)

**Fig. 5.6** Predicted scope (a) and normalized (relative) scope (b) for activity at 15 °C for fish collected in February and August. (Values based on regressions presented in Meakins 1975.)
activity. This scope is defined as the difference between the maximum and standard rates, i.e. \( R_{\text{max}} - R_s \), where \( R_{\text{max}} \) may be measured as the rate of metabolism of a fish swimming at its maximum sustainable speed (Fry 1971). Meakins (1975) provides some data on scope (Fig. 5.6). Priede (1985) defines a normalized scope \( (S) \) as:

\[
S = \frac{(R - R_s)}{(R_{\text{max}} - R_s)}
\]  

(5.5)

where \( R \) is the observed metabolic rate. In Meakins' experiments, fish that were collected in winter but acclimated and tested at 15 °C had \( S \) values ranging from 0.16 for the smallest fish (50 mg dry wt) up to 0.63 for the largest fish (300 mg dry wt). In contrast, fish collected in summer had an almost constant \( S \) value of about 0.3 irrespective of their size. Priede (1985) argues that the probability of dying increases greatly if a fish is forced to maintain very low or very high \( S \) values for long periods of time, and that evolutionary adaptations that tend to ensure that fish avoid such states are favoured.

**GROWTH**

In energy terms, growth \( (P = P_s + T_r) \) is the difference between the energy income and the energy expended in maintenance:

\[
P = C - (F + U) - R.
\]  

(5.6)

Clearly, \( P \), measured in units of energy, can be either positive (growth) or negative (degrowth). Growth is used in reference to individual fish, while the term ‘production’ refers to the new tissue generated by a population (Wootton 1990). Individual fish are not homogeneous masses. The allocation of growth energy to different components of the fish must be analysed, as well as the total growth energy. A simple classification of these components would be:

1. Structural components, forming the soma: these are organs and tissues essential for the immediate survival of the individual, including organs such as the heart and circulatory system, the central nervous system, skeleton, muscle, alimentary canal, etc.

2. Reproductive components: these are the organs that either produce the gametes or play some role in reproduction, and so include secondary sexual characteristics. These components are not essential for the survival of the individual, and could in times of energy shortage be exploited to maintain the soma. But, unless at some stage priority is given to investment in the reproductive components, the individual will leave no offspring.

3. Storage components: these act as reservoirs, which can be filled during times when the energy income greatly exceeds the maintenance costs and emptied when costs exceed income, thus buffering both the reproductive and
somatic components from the effects of temporary energy imbalances. The storage materials are usually lipids or glycogen.

The allocation of energy among these three components will depend on the phase of the life cycle and on the immediate environmental conditions. In practice, most studies of growth report only growth in length, a measure of axial size, and weight, a measure of bulk. These measures give only a crude picture of the growth dynamics.

**Experimental studies on growth**

Experimental studies can quantify the effects of environmental factors on growth rates. Ration size and temperature are the factors that have received most attention. The relationship between specific growth rate and ration is curvilinear, with growth rate tending towards an asymptotic value (Fig. 5.7) (Allen and Wootton 1982c). Although Pascoe and Mattey (1977) fitted a straight line to the relationship between growth rate and ration, visual inspection of their graphs shows clearly that the relationship was curvilinear. In both of these experiments growth was measured as change in weight.

When weight is used to measure growth, there is a complicating factor: the energy content per unit dry weight varies with the age and condition of the fish. Stickleback weighing 0.030 g dry wt had an energy content of 14.23 kJ

![Fig. 5.7 Relationship between mean specific growth rate and ration, illustrated at three temperatures (N = 3) (Allen and Wootton 1982c).](image)
g\(^{-1}\), but this had increased to 19.87 kJ g\(^{-1}\) for fish weighing 0.270 g dry wt (Walkey and Meakins 1970). Sexually mature females had a higher energy content than mature males (24.27 v. 19.66 kJ g\(^{-1}\) dry wt, Meakins 1974). The difference represents the effect of the enlarged ovaries in the females. It is probable that fish receiving different rations also have different energy contents (Cui and Wootton 1988b), but growth measured as changes in weight will not reveal this difference.

In analysing the relationship between growth and rate of feeding, it is useful to define four ration levels: zero \((C_0 = \text{starvation})\), maintenance \((C_{\text{main}})\), optimum \((C_{\text{opt}})\), and maximum \((C_{\text{max}})\) (Brett 1979). The weight (or energy) loss at \(C_0\) defines the resistance of the fish to starvation. \(C_{\text{main}}\) is that ration which allows the fish to maintain a stable weight (or total energy content). \(C_{\text{opt}}\) is that ration at which the fish maximizes its weight (or energy) increase per unit of food consumed. \(C_{\text{max}}\) defines the maximum voluntary rate of consumption, so that the difference, \(C_{\text{max}} - C_{\text{main}}\), defines a scope for growth, which is analogous to the scope for activity as described above. Gross growth efficiency (GGE) is defined as:

\[
\text{GGE} = 100 \left( \frac{P_t}{C} \right) \tag{5.7}
\]

and is maximized at the optimum ration. Net efficiency (NGE) measures the growth per unit of food consumed after the requirements for maintenance have been subtracted, i.e.

\[
\text{NGE} = 100 \left\{ \frac{P_t}{(C - C_{\text{main}})} \right\}. \tag{5.8}
\]

The curvilinear relationship between growth and ration means that \(C_{\text{opt}}\) is less than \(C_{\text{max}}\) (Brett 1979). The individual can maximize either growth rate (by consuming \(C_{\text{max}}\)) or growth efficiency (by consuming \(C_{\text{opt}}\)), but not both, except at low temperatures when the growth rate even at \(C_{\text{max}}\) is low.

At 15 °C, \(C_{\text{main}}\) for a stickleback weighing 250 mg wet wt was about 1.9 per cent of its body weight of enchytraeid worms per day (Allen and Wootton 1982c). This consumption is approximately 22 J d\(^{-1}\), assuming that the energy content of enchytraeid worms is 23 J mg\(^{-1}\) dry wt, and their dry weight is 20 per cent of wet weight (Cui pers. comm.). This value is lower than \(R\), predicted by Meakins' (1975) equations or the routine metabolic rate predicted by Wootton \textit{et al.} (1980a), and may indicate that the fish adapt physiologically to the low rations.

The effect of ration (expressed in J d\(^{-1}\)) and temperature on specific growth rate (expressed in terms of wet weight) is shown in Fig. 5.8. These relationships are based on an empirical regression model developed by Allen and Wootton (1982c) relating growth rate to ration, temperature, and body weight. This model can be used to predict the effect on growth rate of a change in foraging behaviour that leads to a measurable change in the daily ration. The same model also provided the basis for predictions of the effect of temperature on \(C_{\text{main}}\), \(C_{\text{opt}}\), and \(C_{\text{max}}\) (Fig. 5.9).
Fig. 5.8  Predicted effect of ration and temperature on specific growth rate, for a 250 mg fish. (Based on regression in Allen and Wootton 1982c.)

Fig. 5.9  Predicted effect of temperature on maintenance, $C_{\text{main}}$, optimum, $C_{\text{opt}}$, and maximum, $C_{\text{max}}$, rations. (Based on regressions in Allen and Wootton 1982c.)
At $C_{\text{min}}$, GGE is, by definition, zero. With a further increase in consumption, GGE increases up to a maximum at $C_{\text{opt}}$ and then declines slightly between $C_{\text{opt}}$ and $C_{\text{max}}$. Although slightly dependent on temperature, the maximum mean GGE for a stickleback fed on enchytraeid worms was 15–16 per cent, when both growth and food consumption were measured in wet weights (Allen and Wootton 1982e). Estimates of the growth and food consumption for the population in Llyn Frongoch suggested a GGE of about 15 per cent averaged over a year (Allen and Wootton 1982b). Lower values for GGE were found when Tubifex (Oligochaeta) was the food, and both growth and consumption were measured in energy units. Cole (1978) measured a GGE of 7.7 per cent at 7 °C and 12.5 per cent at 20 °C, whereas Walkey and Meakins (1970) estimated the GGE at 6.7 per cent at 15 °C. The effect of ration size on GGE makes a direct comparison of these results difficult.

**Growth in natural populations**

The threespine stickleback is typically a short-lived, seasonal breeder (Baker Chapter 6 this volume). In many populations, few or no fish survive much longer than a year (Wootton 1976, 1984a). This means that somatic and reproductive growth, plus any increase or depletion of stored reserves, are compressed into a single reproductive cycle. The species conforms to the typical teleostean growth pattern, with a high specific growth rate early in life, and the rate declining as the fish increases in size and approaches an asymptotic size (Allen and Wootton 1982b; Crivelli and Britton 1987).

The asymptotic size and size at sexual maturity reflect both genetic and environmental effects. McPhail (1977) reared the progeny of fish from populations taken from ten lakes on Vancouver Island, British Columbia, Canada. He demonstrated heritable differences among the populations for size at maturity of females. Similarly, Snyder and Dingle (1989) found differences in the size and age at maturity between the laboratory-raised offspring from an anadromous and a freshwater population from the Navarro River in California, USA. It is not clear whether these population differences are caused by differences in appetite, in the allocation of different proportions of the energy income to growth, or are the result of differences in the timing of the onset of reproduction.

An example that probably reflects environmental rather than genetic effects on growth is provided by a population living in a small backwater of the Afon Rheidol in mid-Wales, UK. In the period between 1972 and 1986, the mean size of fish aged about 15 months varied from 45 mm to 58 mm (Wootton pers. obs.).

Growth rates also reflect seasonal changes in the environment. In Llyn Frongoch in mid-Wales, the growth of the stickleback ceased during the late autumn and winter and resumed in the following spring (Allen and Wootton 1982b). In a population in southern England, the growth rate slowed in
winter, but some growth was maintained (Mann 1971). For a population in the Camargue delta region in southern France, there was no check to growth in winter (Crivelli and Britton 1987). At the onset of maturation, the males stopped growing, although growth of females continued.

**Growth of body components**

Both field and laboratory studies of growth in total body weight may conceal differences in growth rates of the body components. Such differences can mean that some components maintain a positive growth rate while others are losing weight (or total energy content) (Wootton *et al.* 1978; Allen and Wootton 1982a). Prior to first spawning, almost all the investment in gonadal growth may be recouped and reallocated either to somatic growth or to storage if necessary. However, the structures required for the production and release of gametes have to be in place to take advantage of an opportunity to reproduce, so it may be advantageous to maintain some investment in the gonads during temporarily unfavourable conditions. The failure to invest adequately in gonadal maturation is illustrated in a population in Scotland, UK (Ukegbe 1986). A portion of the adult fish fail to spawn when they are a year old. Such fish survive up to their second winter of life, but die before the next breeding season (see also Chellappa *et al.* 1989).

**Laboratory studies**

Allen and Wootton (1982a) found that under experimental conditions, the soma (excluding the liver), liver, and ovaries of females from the Llyn Frongoch population differed in their sensitivity to the size of the food ration. Females were taken at month intervals directly from the field and exposed for a 21 d period to a range of rations from 0 per cent of body weight to *ad libitum*. For most of the year, ration size had no significant effect on the growth of the ovaries over the 21 d period, but the growth of both the soma and the liver was sensitive to ration. This sensitivity varied during the year. The liver was relatively insensitive to ration level during the breeding season in spring and summer, but highly sensitive in autumn and winter. The results suggest that the liver acts as a short-term buffer, ameliorating the effects of a food shortage on the soma and ovaries. The liver is also the site of synthesis of the precursors of the yolk deposited in the maturing oocytes, and so in this role mediates between the soma and the ovaries.

**Field studies of the growth of components**

In two Welsh populations, ovarian growth was maintained over the first winter of life even when the hepatic and other somatic growth slowed or ceased (Wootton *et al.* 1978). Because of the small size of the ovaries, this growth did not represent a large absolute rate of increase in energy (Table 5.2). In the winter months, food consumption was low and ovarian growth represented a high proportion of the energy remaining after the losses in
Table 5.2  Estimates of the components of the overwintering energy allocation of an average female stickleback from Llyn Frongoch and the Afon Rheidol (mid-Wales, UK) (from Wootton et al. 1980a). $R$, respiration rate; $C$, consumption rate; $F$, faecal losses.

<table>
<thead>
<tr>
<th>Site and month</th>
<th>Temp. ($^\circ$C)</th>
<th>Mean length (mm)</th>
<th>Change in energy in Soma (J d$^{-1}$)</th>
<th>Change in energy in Ovaries (J d$^{-1}$)</th>
<th>$R$ (J d$^{-1}$)</th>
<th>$C$ (J d$^{-1}$)</th>
<th>$F$ (J d$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frongoch</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sept.</td>
<td>13.0</td>
<td>31.8</td>
<td>5.8</td>
<td>0.2</td>
<td>32.8</td>
<td>47.8</td>
<td>1.5</td>
</tr>
<tr>
<td>Oct.</td>
<td>9.5</td>
<td>33.8</td>
<td>0.2</td>
<td>0.2</td>
<td>30.0</td>
<td>38.0</td>
<td>1.6</td>
</tr>
<tr>
<td>Nov.</td>
<td>6.5</td>
<td>35.0</td>
<td>-5.2</td>
<td>0.2</td>
<td>25.4</td>
<td>42.5</td>
<td>2.0</td>
</tr>
<tr>
<td>Dec.</td>
<td>5.8</td>
<td>35.6</td>
<td>-1.8</td>
<td>0.3</td>
<td>26.3</td>
<td>31.1</td>
<td>1.8</td>
</tr>
<tr>
<td>Jan.</td>
<td>6.5</td>
<td>35.7</td>
<td>0.3</td>
<td>0.4</td>
<td>26.3</td>
<td>38.0</td>
<td>1.9</td>
</tr>
<tr>
<td>Feb.</td>
<td>4.0</td>
<td>35.8</td>
<td>23.6</td>
<td>0.3</td>
<td>24.0</td>
<td>45.4</td>
<td>2.4</td>
</tr>
<tr>
<td>Mar.</td>
<td>5.0</td>
<td>36.4</td>
<td>3.6</td>
<td>2.1</td>
<td>26.5</td>
<td>61.0</td>
<td>2.7</td>
</tr>
<tr>
<td>Apr.</td>
<td>7.0</td>
<td>37.2</td>
<td>4.9</td>
<td>2.0</td>
<td>34.3</td>
<td>78.9</td>
<td>2.9</td>
</tr>
<tr>
<td>Total (kJ)</td>
<td></td>
<td></td>
<td>0.897</td>
<td>0.173</td>
<td>6.83</td>
<td>11.59</td>
<td>0.507</td>
</tr>
<tr>
<td>Per cent of $C$</td>
<td></td>
<td></td>
<td>7.8</td>
<td>1.5</td>
<td>59.1</td>
<td>100</td>
<td>4.4</td>
</tr>
<tr>
<td>Rheidol</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sept.</td>
<td>12.5</td>
<td>36.8</td>
<td>12.3</td>
<td>0.2</td>
<td>48.4</td>
<td>64.4</td>
<td>1.9</td>
</tr>
<tr>
<td>Oct.</td>
<td>10.0</td>
<td>38.6</td>
<td>-0.2</td>
<td>0.0</td>
<td>46.3</td>
<td>55.8</td>
<td>1.9</td>
</tr>
<tr>
<td>Nov.</td>
<td>6.0</td>
<td>39.6</td>
<td>-31.6</td>
<td>0.2</td>
<td>37.0</td>
<td>44.1</td>
<td>2.1</td>
</tr>
<tr>
<td>Dec.</td>
<td>6.5</td>
<td>40.0</td>
<td>16.6</td>
<td>0.5</td>
<td>35.5</td>
<td>62.8</td>
<td>2.4</td>
</tr>
<tr>
<td>Jan.</td>
<td>6.5</td>
<td>40.0</td>
<td>1.2</td>
<td>0.9</td>
<td>39.7</td>
<td>46.7</td>
<td>2.1</td>
</tr>
<tr>
<td>Feb.</td>
<td>5.0</td>
<td>40.0</td>
<td>1.5</td>
<td>0.9</td>
<td>34.0</td>
<td>72.1</td>
<td>2.9</td>
</tr>
<tr>
<td>Mar.</td>
<td>4.5</td>
<td>40.8</td>
<td>0.2</td>
<td>4.6</td>
<td>35.0</td>
<td>84.8</td>
<td>3.2</td>
</tr>
<tr>
<td>Apr.</td>
<td>10.0</td>
<td>42.2</td>
<td>10.3</td>
<td>9.6</td>
<td>53.6</td>
<td>147</td>
<td>4.2</td>
</tr>
<tr>
<td>Total (kJ)</td>
<td></td>
<td></td>
<td>0.324</td>
<td>0.511</td>
<td>9.97</td>
<td>17.44</td>
<td>0.625</td>
</tr>
<tr>
<td>Per cent of $C$</td>
<td></td>
<td></td>
<td>1.9</td>
<td>2.9</td>
<td>57.2</td>
<td>100</td>
<td>3.6</td>
</tr>
</tbody>
</table>

faeces and routine maintenance were subtracted. In some months, the total energy content of the soma declined (Table 5.2), probably because of depletion of its lipid content. February marked the start of a period of rapid growth of the carcass, and March an acceleration in ovarian growth rate. Thus in spring, food consumption was sufficient to support investment in both the soma and the ovaries. After the start of the breeding season in May, somatic growth slowed or ceased, and the lipid content of the soma and liver declined.

A study of male stickleback in a Scottish population provides a comparable picture. During early winter, the lipid and glycogen contents of the liver and carcass were depleted, but then recovered in a period of growth in the spring. Over the breeding season, reproductively active males showed massive depletion of liver glycogen, liver lipid, and somatic glycogen, and to a lesser extent somatic lipid (Chellappa et al. 1989). The depletion of
glycogen preceded lipid depletion. Males that did not reproduce entered their second autumn with higher lipid and glycogen contents than the few reproductively active males that survived. But the former then suffered rapid depletion of both lipid and glycogen during the autumn and had disappeared from the population by January.

Both the Welsh and Scottish populations were effectively annual. Gonadal growth was maintained over the first winter of life even at times when the soma and liver were being depleted. In the annual population in the Camargue (Crivelli and Britton 1987), the testes grew rapidly between September and December, and the ovaries between December and February. For both sexes, the soma grew rapidly between October and January, growth slowing or ceasing after the onset of breeding in February or March. No studies have been published on the pattern of growth of soma and gonads in those populations in which sexual maturity is reached at two or more years, nor on anadromous populations in which sexual maturity is reached at two or more years, nor on anadromous populations in which the energy costs of migration have to be met.

REPRODUCTION

The main pathways of energy expenditure on reproduction are the energy invested in the released gametes, plus any increased metabolism associated with the synthesis of the gametes or secondary reproductive characteristics and with the behavioural activities associated with reproduction. In the female stickleback, the expenditure is dominated by the eggs. In the males the main expenditure is probably associated with reproductive behaviour plus the energy content of the glue secreted during nest building. In terms of the energy budget (eqn 5.2), the expenditure of the female is measured principally by the $P_r$ term, but that of the male by the $R_s$ term.

Energy expenditure by females

In the laboratory, the female stickleback can spawn several times during the breeding season, at intervals of a few days. The energy represented by the eggs produced by a female is the product of the average energy content per egg, average clutch size, and the number of times the female spawns.

Energy costs of egg production

The energy costs of egg production can be met from two sources: from the food ingested, or by depletion of the soma, including the storage components. If insufficient food is consumed in the interval between successive spawnings to meet the cost of the next clutch, the cost of egg production is subsidized from the female's soma (Wootton 1977; Fletcher 1984).

Wootton (1977, 1979) estimated the daily energy intake that a female needed if she was to avoid losing weight during the breeding season (Table
Table 5.3  Predicted egg production per spawning in energy units, ration required for no net somatic weight loss, and efficiency of egg production of female stickleback during a breeding season (from Wootton 1979). (Ration as per cent body weight (% BW) is calculated assuming 1 J = 0.217 mg wet weight of food.)

<table>
<thead>
<tr>
<th>Weight of female (mg)</th>
<th>Interval between spawns (d)</th>
<th>Egg production per spawning (kJ)</th>
<th>Ration (kJ d(^{-1}))</th>
<th>Efficiency of egg production (% BW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>800</td>
<td>4</td>
<td>0.501</td>
<td>0.683</td>
<td>18.6</td>
</tr>
<tr>
<td>800</td>
<td>5</td>
<td>0.470</td>
<td>0.597</td>
<td>16.2</td>
</tr>
<tr>
<td>800</td>
<td>6</td>
<td>0.447</td>
<td>0.512</td>
<td>13.9</td>
</tr>
<tr>
<td>1200</td>
<td>4</td>
<td>0.789</td>
<td>0.862</td>
<td>15.6</td>
</tr>
<tr>
<td>1200</td>
<td>5</td>
<td>0.741</td>
<td>0.777</td>
<td>14.1</td>
</tr>
<tr>
<td>1200</td>
<td>6</td>
<td>0.704</td>
<td>0.691</td>
<td>12.5</td>
</tr>
<tr>
<td>1600</td>
<td>4</td>
<td>1.089</td>
<td>1.041</td>
<td>14.1</td>
</tr>
<tr>
<td>1600</td>
<td>5</td>
<td>1.023</td>
<td>0.956</td>
<td>13.0</td>
</tr>
<tr>
<td>1600</td>
<td>6</td>
<td>0.972</td>
<td>0.870</td>
<td>11.8</td>
</tr>
</tbody>
</table>

5.3). Expressed in terms of the weight of enchytraeids consumed as a percentage of female body weight, the values in Table 5.3 range from 18.6 to 11.8 per cent. (In the experiment, the fish had been fed either minced beef or *Tubifex* worms.) In a subsequent experiment in which the females were fed enchytraeids alone, Fletcher (1984) estimated that females would have to consume about 8 per cent per day to avoid losing weight. These rations compare with a maintenance ration for a non-breeding female of about 2 per cent. The energy demands of egg production probably explain why somatic growth slows or stops during the breeding season (Wootton *et al.* 1978; Crivelli and Britton 1987), and explain the depletion of lipids and glycogen over the breeding season described above (Wootton *et al.* 1978).

Giles (1987a) provided indirect evidence of demands on metabolism that are imposed by the synthetic processes associated with multiple spawning. As fish were subjected to progressively decreasing oxygen concentrations, gravid females started using the oxygen-rich surface film (aquatic surface respiration) at significantly higher oxygen concentrations than did non-gravid females. The behaviour of the gravid females resembled that of females infested with plerocercoids of the cestode *Schistocephalus solidus*, a parasite that makes substantial energy demands on its host (Walkey and Meakins 1970; Lester 1971; Meakins 1974; see also Hart and Gill page 217, Huntingford *et al.* page 281 this volume).

The proportion of energy income invested in eggs over a breeding season, a measure of reproductive effort, can also be calculated from measurements of the total food consumption and total egg production (Wootton 1977;
Fletcher 1984). Fletcher (1984) found an inverse relationship between ration size and reproductive effort (see also Wootton 1985a). Although they produced fewer eggs over a breeding season than the females on high rations, the females on low rations were investing a higher proportion of their energy income in eggs. The high reproductive effort of females on low rations resulted from the subsidy from the soma and storage components for egg production, because rate of food consumption was insufficient to meet the costs of egg production. A more complete index of reproductive effort would be given by the ratio: (total energy content of eggs produced) (energy in food consumed + energy losses of soma and storage components). There was a weak but significant inverse correlation between reproductive effort and growth rate (Fletcher 1984; Wootton 1985a) over the breeding season. That is, at the phenotypic level, there was a trade-off between growth and breeding season fecundity. This inverse correlation was strongest for females receiving a 2 per cent daily ration, but not significant for females on daily rations of 8 and 16 per cent of body weight.

The relevance to natural populations of these laboratory studies will only become evident with studies of the fecundity and rates of food consumption in natural populations. Some circumstantial evidence—a decline in growth rate and a depletion of lipids and glycogen over the breeding season observed in natural populations (Wootton et al. 1980; Crivelli and Britton 1987) and high postbreeding mortality (Hagen and Gilbertson 1973b)—suggests that the energy demands of reproduction exert a cost.

Breeding season fecundity

Food supply is an important determinant of the total number of eggs spawned in a breeding season by a female because of its effect on the number of spawnings (Wootton 1973a, 1977; Fletcher 1984). Under laboratory conditions, a well-fed female may spawn 15–20 times at intervals of 3–6 d, whereas a poorly fed female may not spawn. Figure 5.10 shows the predicted increase in breeding season fecundity with ration size (J d−1) based on experiments with females fed enchytraeid worms.

Do females in natural populations express this physiological capacity to produce multiple clutches? Bolduc and Fitzgerald (1989; see also Baker page 170, Whoriskey and Fitzgerald page 199 this volume) showed that individually marked females in salt-marsh pools spawned between zero and three times before leaving a pool. In this habitat, where suitable food was judged to be abundant, egg production does not seem to be limited by energy but by the short time the females spend on the breeding grounds (Whoriskey et al. 1986). In contrast, Foster (pers. comm.) observed marked females spawning at approximately weekly intervals over a three month breeding season at Crystal Lake, British Columbia, Canada. Some females produced clutches throughout the season, although the majority did so for a shorter (≤ 2 month) period.
Clutch size

The number of eggs in a clutch is a function of female size at the start of the breeding season (Wootton 1973b). The relationship between length ($L$) or weight and clutch size ($F$) takes the general form:

$$ F = aL^b \quad \text{or} \quad F = cW^d. $$

(5.9)

The length exponent, $b$, is typically about 3.0 (as expected from the relationship between linear dimensions and volume), and the weight exponent, $d$, about 1.0 (Wootton 1973a; 1976). Both parameters $a$ and $b$ (or $c$ and $d$) may show interpopulation variation (Hagen 1967; Wootton 1973a; Snyder and Dingle 1989; reviewed in Baker Chapter 6 this volume, Fig. 6.4). Such interpopulation differences suggest different levels of investment in egg production. Crivelli and Britton (1987) report the high length exponent ($b$) of 5.28 for the Camargue population, which lives close to the southern limit of the stickleback in Europe.

Unlike breeding season fecundity, clutch size is little affected by the amount of food eaten during the breeding season. Wootton (1977) found no significant relationship between the food eaten in the interval between successive spawnings and clutch size. In a larger series of experiments, Fletcher (1984) found that differences in daily ration accounted for only 4 per cent of the variance in clutch size, although the effect was statistically significant. In contrast, body size accounted for 50 per cent of the variance. This contrast suggests that food supply exerts its major effect on clutch size.
indirectly through its effect on growth and hence size at maturity (Wootton 1973b). Other studies have found that clutch size is little influenced by temperature fluctuations (Boulé and FitzGerald 1989), pH (Faris 1986), and a range of physicochemical variables including temperature, dissolved oxygen, and salinity (Bolduc and FitzGerald 1989). Both food and temperature have important effects on the components of the energy budget, so the insensitivity of batch fecundity to these factors is unexpected. Once a female is committed to producing a clutch, the size of that clutch is not adjusted to the level of energy income from the food consumed.

Clutch size varies among individuals within a population (even after correcting for differences in female size) and between clutches produced by the same female in the breeding season, but the causes of this variation are not known.

Energy content of eggs
The mean energy content of eggs from the Afon Rheidol population of mid-Wales is 22.6 J mg⁻¹ dry wt (Wootton and Evans 1976), giving a mean energy content per egg of 7–9 J. Meakins (1974) gives a higher value of 26.2 J mg⁻¹ dry wt for ovarian tissue. Interpopulation variation in egg size is discussed by Baker (page 160 this volume), and there may also be variation in the energy content.

Reproduction in the male
Under laboratory conditions, the energy accounting for reproductively active females is not technically demanding. But for males the situation is different, because the energy costs of reproduction are predominantly imposed by the behavioural activities associated with successful reproduction: territoriality, nest building, and parental care. In the absence of direct measurements of the energy costs of reproductive behaviour, two approaches have suggested that the costs are substantial. The first investigates the effect of different levels of energy income on reproductive behaviour (Stanley 1983; Stanley and Wootton 1986; Wootton 1985a). The second measures the depletion of the energy content of body components (Chellappa and Huntingford 1989; Chellappa et al. 1989; FitzGerald et al. 1989).

Males with a large body size may achieve greater reproductive success. Rowland (1989a) introduced pairs of sexually mature males into a tank simultaneously and found that the larger male usually dominated the smaller in the contest for a territory (see also Rowland page 302 this volume). A weight difference of 15 per cent was sufficient to give the heavier male a distinct advantage. In more complex experimental designs in which several males competed for territories, size has not always emerged as an important variable (van den Assem 1967; Sargent and Gebler 1980). Dufresne et al. (1990) examined the effect of size and age by keeping groups of small and large mature males in wading pools. Only when the mean size difference
between large and small males was 16 mm or more were the larger males significantly more successful in obtaining territories.

Two aspects of size need to be considered: the first is absolute size; the second is the size of the energy reserves on which the fish can draw to meet the energy demands of the establishment and defence of a territory and of the subsequent courtship and parental activities.

Several effects of ration size on the reproductive biology of the male are recorded. As a male matures, its kidneys enlarge and start to synthesize the glue used in nest construction. When comparisons were made between sexually mature males of the same length, the kidneys of males on a low ration (2 per cent body wt d\(^{-1}\)) were significantly smaller than those of males on higher rations (6 per cent or 18 per cent d\(^{-1}\)) (Stanley 1983).

In large tanks, at a given density of males, proportionately fewer males on low rations held territories than in tanks holding males on higher rations. When males were transferred from the large tanks into smaller, individual tanks, a significantly smaller proportion of the males on low rations built nests (Stanley and Wootton 1986). After each isolated male with a nest was

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**Fig. 5.11** Effect of ration on fanning by males fed rations of enchytraeid worms of 2 per cent (\(N = 6\)), 6 per cent (\(N = 5\)), and 18 per cent (\(N = 10\)) of body weight during a parental cycle from fertilization to hatching. Stage of cycle: 1, day after fertilization; 2, 25 per cent of cycle completed; 3, 50 per cent of cycle completed; 4, 75 per cent of cycle completed; and 5, 100 per cent of cycle completed (from Stanley 1983).
allowed to fertilize one clutch, the low-ration males spent less time fanning their eggs than males on higher rations (Fig. 5.11). This difference in fanning did not translate into a difference in the proportion of fertilized clutches that hatched (Stanley 1983).

The depletion over the breeding season of the lipid and glycogen in the carcass and liver of males in a Scottish population is also evidence of the energy costs incurred by breeding compared with non-breeding males (Chellappa et al. 1989). Even fights between pairs of males lasting between 11 and 204 s caused depletion of liver glycogen. The depletion increased the longer the fight lasted. At the end of the fight, the liver glycogen of the victorious males was significantly higher than in the losers (Chellappa and Huntingford 1989). Growth over a 12 d period was significantly lower in nest-holding males than in others (Stanley 1983). The energy costs of parental behaviour were indicated by the changes in the weight of males relative to their weight on the day they fertilized eggs (Fig. 5.12). FitzGerald et al. (1989) also noted a decline in the dry weight of males that completed a parental cycle compared with non-parental males over the same period. One-year-old breeding males lost more weight than non-breeding males over the same time period, although inexplicably for two-year-old fish, there was no significant difference between the two groups (Dufresne et al. 1990).

The consequences of the energy demands made on the reproductive male

![Graph showing changes in weight of parental males](image)

**Fig. 5.12** Effect of ration on per cent weight change by parental males held at different rations (per cent body wt) during a parental cycle from fertilization to hatching. For further explanation see Fig. 5.11 (from Stanley 1983).
for other aspects of its biology may be illustrated by the study of Bentzen and McPhail (1984) on the foraging behaviour of the limnetic form of the stickleback in Enos Lake on Vancouver Island, British Columbia. When presented with a substrate containing benthic prey, only the males of the limnetic form fed. The females would strike at stray zooplankters in the water column, but did not exploit the abundant benthic prey. Bentzen and McPhail (1984) noted that the male limnetics must spend the summer months in a benthic environment to breed. This may impose a compromise on the males between pure planktivory and benthic feeding. In contrast, the females need only visit the benthic environment for the short time required for spawning and can then return to foraging on zooplankton in the water column.

Although a value can be calculated for the effect of an increase in the daily ration of a female on her breeding season fecundity (Fig. 5.10), it is not yet possible to relate the total number of eggs fertilized by a male to his energy income. Nor is it possible to compare the energy allocations of males and females until more is known about the rates of food consumption of the two sexes and the metabolic costs of reproductive behaviour.

DISCUSSION AND CONCLUSIONS

A central aim of studies of bioenergetics on species such as the threespine stickleback must be to relate the patterns of energy allocation described to the reproductive success of the fish. The study of energetics charts one pathway which causally relates both individual variation and the effects of environmental factors to differences in reproductive success. This is because these differences are likely to be related to differences in the patterns of energy allocation (Fig. 5.1). These differences may also relate to other patterns of allocation, such as those for nitrogen, calcium, or phosphorus, which are not considered here but could, in some circumstances, be important (Giles 1983a).

For stickleback above about 20 mm in length, there is now the clear possibility of describing the rates of energy income and expenditure and the pattern of allocation between maintenance, growth, and reproduction (Wootton et al. 1980a). Using the quantitative relationships between environmental factors, including food availability, temperature, and salinity, and the patterns of energy allocation, it will become possible to develop models that allow predictions of the likely effects of environmental change on reproductive success. The next step will be to describe, in quantitative terms, the ontogenetic changes in rates of income and expenditure and the pattern of allocation for a variety of populations, from a range of climatic zones (the stickleback is found from Arctic to Mediterranean zones) and for both resident and anadromous forms within the same watersheds. The patterns of energy allocation must then be related to the demographic characteristics of
the populations. Such analyses would in turn be related to the predictions of life-history theory (see Wootton 1990; Baker Chapter 6 this volume) and those studies which explore the consequences of alterations in the life-table traits of age-specific survival and age-specific fecundity (e.g. Roff 1984; Stearns and Crandall 1984).

Such studies need to be carried out within protocols that allow comparisons to be made between groups of workers working in different parts of the world. The protocols need to agree on how the rate of food consumption, in energy units, can be accurately measured both in laboratory and field studies. The analyses of Wootton et al. (1980b) and Allen and Wootton (1984) suggest approaches to this problem. The measurement of the rates of energy expenditure at realistic levels of behavioural activity requires that particular attention be paid to the design of respirometers that allow simultaneous recording of oxygen consumption and activity. These recordings must be coupled with laboratory and field studies on the time spent by fish in different activities, both inside and outside the breeding season. A satisfactory estimate of the daily rates of energy expenditure by the free-living stickleback has yet to be obtained (Wootton et al. 1980a). Changes in the levels of its activity potentially provide the fish with an effective method of regulating its pattern of energy allocation (Priede 1985).

For biological traits, including those related to energy and time budgeting, there are two sources of variation: environmental and genetic (for reviews see Falconer 1989; Maynard Smith 1989). Some of the variation may be fortuitous, but the working hypothesis must be that much of the variation is adaptive. In the stickleback, there is good evidence for the adaptive significance of phenotypic variation in morphological and behavioural traits (Bell 1984; Wootton 1984a; Chapters by Bell and Foster, Reimchen, Huntingford et al., Foster, McPhail this volume), and the same is likely to be true for variations in energy allocation.

At one level, the adaptive variation will reflect phenotypic plasticity. Fish with similar genotypes respond to changing environmental conditions with alterations in their time and energy allocations which minimize the consequences of the changes for the reproductive success of the fish (Slobodkin and Rapoport 1974). The range of phenotypic plasticity for such traits is not well known in the stickleback. Well-controlled breeding experiments are required to show that some of the variation in patterns of time and energy allocation has a genetic basis. The way ahead has already been pointed by the studies of McPhail (1977) on the age of first reproduction, and of Snyder and Dingle (1989) for several life-history traits.

The levels of parasitic infestation and predation experienced by populations are likely to be reflected in the patterns of energy (and time) allocation. Giles (1987b) found that exposure to a disturbing stimulus (being netted and placed in a strange tank) inhibited feeding of healthy sticklebacks for at least 96 h. In contrast, fish infested with Schistocephalus resumed feeding within
48 h of the disturbance. Calculations provide a crude estimate that the fright response in healthy fish had a total energy cost of 1.3 kJ (metabolic losses over 96 h plus income losses through failure to feed), whereas for infested fish this loss was only 0.24 kJ. The earlier resumption of feeding by the infested fish probably reflects the effects on the hunger of the fish of the energy demands made by the parasite (Walkey and Meakins 1970; Meakins 1974; Giles 1987b). But if the fright was caused by exposure to a predator, the earlier resumption of feeding could increase the risk of predation. The impact of size-selective predation on a stickleback population is also relevant (Reimchen 1980, 1988, 1990; Werner and Gilliam 1984). If a fish can grow rapidly through the sizes that make it vulnerable to predation, its chances of survival will increase. Large size also allows a faster absolute swimming speed, which may aid escape from predators. In other situations a slow growth rate may be advantageous if it ensures that the fish does not grow into a vulnerable size class (McPhail 1977). The nature of the predation to which a population is exposed will determine which size classes should be grown through quickly and which slowly (Reimchen Chapter 9 this volume). Predation by invertebrates such as dragonfly naiads is heaviest on small fish (Reimchen 1980, page 261 this volume). But under some circumstances, large sticklebacks could be at a disadvantage because of size-selective predation by fish, birds, and mammals (McPhail 1977).

An unexplored area is the effect on survival of maintaining investment in the gonads at the expense of the soma in times of energy shortage. The temporal patterns of energy availability will differ between populations (compare growth patterns noted by Mann 1971; Allen and Wootton 1982b; Crivelli and Britton 1987). Do the patterns of mortality within and between populations reflect the priority given to gonadal versus somatic growth as food supplies vary?

Two important unifying principles of biology are bioenergetics and the adaptive evolution through natural selection of life forms with Mendelian genetic systems. The studies of the past three decades on the biology of the threespine stickleback have encompassed physiological, behavioural, ecological, and evolutionary problems. These studies show that a programme of research can be mapped out which will give a coherent account of the way in which a complex organism uses energy and time to achieve reproductive success over a wide range of environmental conditions. The crux of such a programme will be the integration of studies on energetics with studies on the crucial demographic variables of size-specific mortality and fecundity.

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