Growth, consumption and respiration by larvae of the kelp-fly *Fucellia capensis* (Diptera:Anthomyiidae)

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At 18 °C the eggs of the kelp-fly, *Fucellia capensis*, hatch in 24 – 32 h and the larval and pupal stages last 10 – 12 and 9 – 14 days respectively. The growth curve is discontinuous, with declining relative growth rates in successive larval instars. Food consumption is relatively independent of size, at 0,25 mg dry kelp mg^{-1} wet larva day^{-1}. Respiration rate is related to larval mass by the equation: Respiration rate ($\mu l\ O_2\ h^{-1}$) = 2,75 (wet mass larva)^{0,66}. In terms of energy an individual larva consumes 245,5 J over its lifespan, grows to the equivalent of 43,9 J and respires 51,6 J, indicating an assimilation efficiency of 30% and a gross growth efficiency of 17%. Kelp-fly larvae are probably less significant consumers of drift kelp than amphipods or isopods, but they promote the decay of wrack beds and are favoured as food by sea-shore birds.

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Die eiers van die seebamboesvlieg, *Fucellia capensis*, broei binne 24 – 32 h uit, terwyl die larwale en papie-vorms 10 – 12 en 9 – 14 dae onderskeidelik duur. Die groeikurwe is nie eenvormig nie weens 'n afname in relatiewe groei in opeenvolgende larwale stadia. Voedselinname is relatief onafhanklik van grootte, 0,25 mg droë seebamboes mg^{-1} nat larwe dag^{-1}. Respirasietempo is verwant aan larwale massa volgens die vergelyking: respirasietempo ($\mu l\ O_2\ h^{-1}$) = 2,75 (nat massa van larwe)^{0,66}. In terme van energie neem 'n indiwiduele larwe 245,5 J in binne sy lewensduur, groei tot die ekwivalent van 43,9 J en respireer 51,6 J. Dit is gelyk aan 'n assimilasiedoeltreffendheid van 30% en 'n bruto-groeidoeltreffendheid van 17%. Seebamboeslarwes benut waarskynlik minder uitgespoelde seebamboes as die amphipoda en isopoda maar hulle bevorder die verrotting van uitgespoelde seebamboes en word graag deur sekere seekus-voëls gevreet.

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Species of the genus *Fucellia* (Muscoidea, Anthomyiidae) are seashore flies that breed in wrack in both hemispheres. Like the related *Coelopa*, the adult flies sometimes become sufficiently numerous to become a public nuisance (Oldroyd 1954; Poinar 1977), while the larvae appear to be significant agents in the degradation of driftline algae. This function is particularly important where wrack is commercially collected, as is the kelp *Ecklonia maxima*, the principal algal species washed up along the west coast of South Africa.

The life-cycles of *Fucellia* species in the Northern hemisphere have been investigated by Egglishaw (1960b) and Kompfner (1974) and can be completed within a single lunar cycle, as can those of *Coelopa* species (Egglishaw 1960a; Dobson 1974). Nothing is known of the biology of the South African *F. capensis*, or of the less abundant sympatric *C. africana*, nor has the role of kelp-fly larvae as consumers and degraders of drift-line algae been quantified.

In the present study we report on the life cycle of *F. capensis* and measure production, consumption and respiration rates of the larvae. Since energy budget studies for the other major consumers in the wrack community, the amphipod *Talorchestia capensis* and the isopod *Ligia dilatata* have been completed (Muir 1977; Koop 1979), this will provide data necessary for quantitative assessment of the fate of beached kelp (Griffiths & Stenton-Dozey, in prep.).

Methods

Adult flies were collected from the beach at Kommetjie (34°08'S, 18°19'E) on the Cape Peninsula, and placed in batches of about 50 into 1-l glass jars containing fresh *Ecklonia maxima* on wet sand. The jars were covered with plankton netting and checked every four hours for the presence of eggs. As these were laid they were removed to separate jars held at 18 °C and containing excess moderately decomposed kelp.

Larval growth rates, as wet mass after draining on filter paper, were monitored with a Mettler ME 30 microbalance. Twenty larvae were weighed every four hours over the first six days of their development and at four-hourly intervals between 08h00 and 20h00 thereafter. Pupae were weighed daily until emergence of the adult fly.

Larvae both from the cultures and freshly collected from the field were used for feeding and respiration rate experiments. Feeding rates were measured for larvae held in glass vials covered by plankton netting and placed at 18 °C and 100% humidity in an enclosed waterbath. Up to 32 size-matched, weighed larvae, depending upon age, were placed in each tube together with a weighed disc of kelp cut with a cork-borer from an *E. maxima* frond. Similar discs cut from the same frond served as controls, both to obtain initial wet mass/dry mass conversions and to correct for changes in mass caused by autolysis or microbial activity during the feeding period. Since the larvae produce a copious watery faeces the discs were placed on the vertical walls of the chambers to maximize drainage. Both experimental and control discs were removed after 24 h, dried to constant weight (three days at 60 °C), then weighed. From these figures corrected dry mass of kelp eaten per larva per day was calculated.

Respiration rates were measured using a Gilson respirometer with 15 ml chambers and 10% KOH to absorb CO_2. Larvae were provided with discs of decaying kelp in an attempt to maintain normal feeding activity. Several controls were used in each run to correct for the small amount of oxygen used by the kelp discs.

Energy values for kelp frond and for *Fucellia* larvae were obtained with a ballistic bomb calorimeter.

Results

Adults mated readily in the culture jars, following which females laid eggs singly or in small batches on the surface of the kelp. Newly emerged larvae immediately burrowed into decaying areas of the fronds. Eggs, larvae and pupae were very similar in appearance to those of *Fucellia maritima*, as described by Egglishaw (1960b). The sizes and durations of the various stages are given in Table 1. First, second and third instar larvae may be distinguished by the presence of one, two and three posterior spiracular openings respectively.

Table 1 Size and duration of the stages in the life-cycle of *Fucellia capensis* at 18 °C

Stage	Length (mm)	Duration
Egg	1,0 – 1,2	24 – 32 h
First instar larva	1,0 – 2,2	15 – 20 h
Second instar larva	2,3 – 5,5	3 – 4 days
Third instar larva	5,6 – 11,2	6 – 7 days
Puparium	6,0 – 8,0	9 – 14 days
Adult	6,1 – 7,5	–

The growth rate of larvae is depicted in Fig. 1. The discontinuous growth curve is typical of insect larvae, the periodic declines in mass corresponding to loss of the old cuticle and of water during ecdysis (Wigglesworth 1965). Relative growth rate, expressed as percentage increase in wet mass per day, is a decreasing function of age, declining from 136% in first instar larvae to 69% in second, and 16% in third instar larvae. The wet mass of the puparium declines gradually over the nine days of metamorphosis.

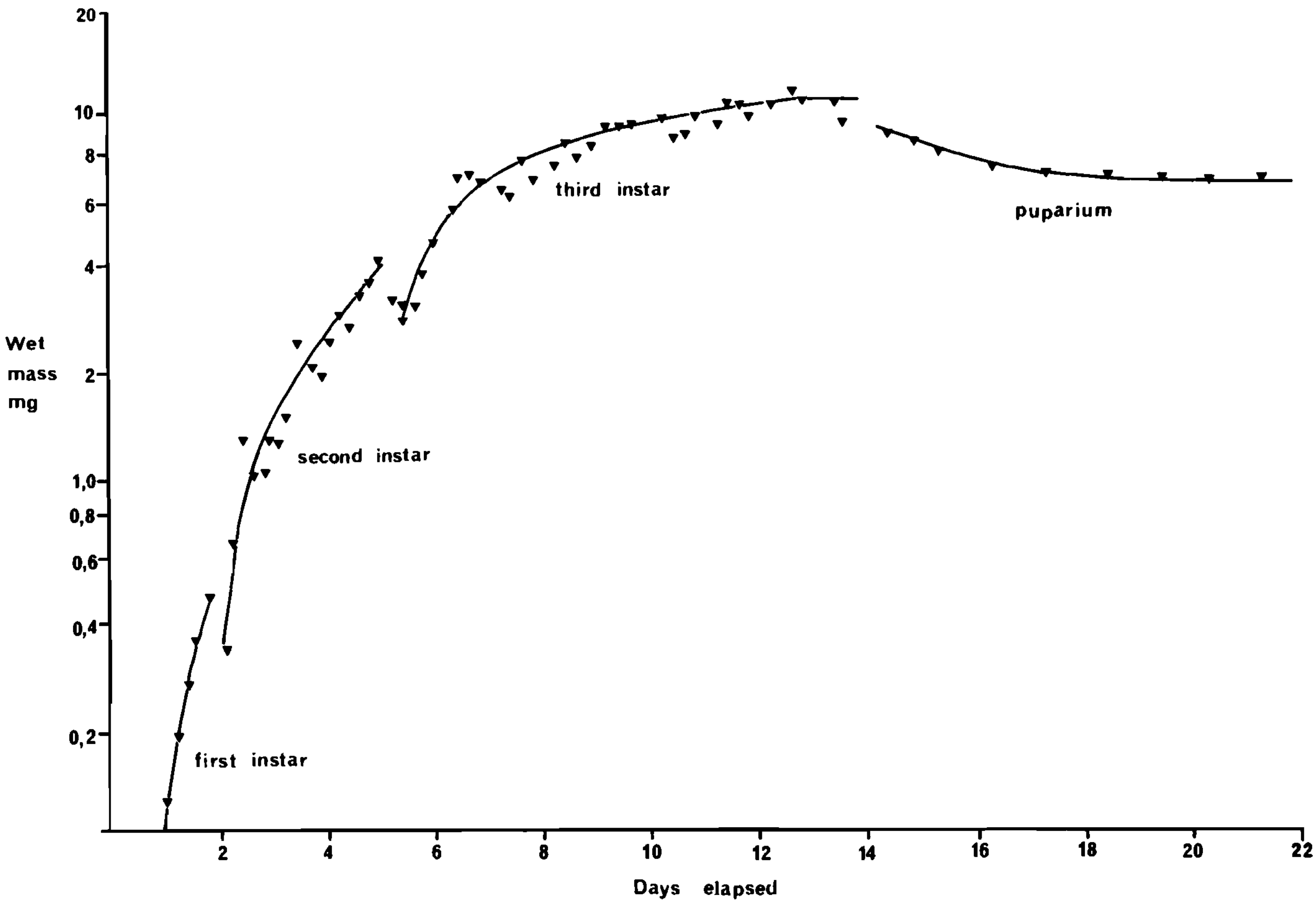

Fig. 1 The growth rate of *Fucellia capensis* larvae held in laboratory culture at 18 °C.

The relationship between larval mass and consumption rate is given in Fig. 2. There is a slight decline in the amount of food eaten per mg wet larval mass as growth proceeds, the parameters being related by the equation:

(Dry mass consumed, mg) = 0,27 (wet mass larva)^{0,95}
(r = 0,90, n = 43)

The mean consumption rate is thus approximately 0,25 mg dry kelp mg wet larva^{-1} day^{-1} (1,8 mg dry kelp per mg dry larva day^{-1}). The total mass of food eaten by an individual larva during its development is 18,7 mg dry. Of this the first instar consumes 2%, the second 24% and the third 74%.

Respiration rate is plotted as a function of wet larval mass in Fig. 3, the equation fitted to the data being:

(Respiration rate, μl O_2 h^{-1}) = 2,75 (wet mass larva)^{0,66}
(r = 0,95, n = 18)

There is a pronounced decrease in mass specific respiration rate with increasing size, the rate being, for example, 2,75 μl mg^{-1} at 1 mg and 1,26 μl mg^{-1} at 10 mg. The total oxygen consumed during development (based on mean daily mass) is 2,60 ml.

Discussion

The life cycle of *F. capensis* normally extends over 22 – 28 days (Table 1), although a few individuals in our cultures only emerged after six weeks. Development appears to be linked to the lunar cycle, the flies laying on kelp deposited high on the shore and maturing before high-water springs 28 days thereafter. If the wrack is inundated during development there is a good chance of both larvae and pupae surviving (Dobson 1974). Larvae of *F. capensis* certainly remain active for at least 24 h in water and the buoyant pupae may frequently be seen deposited alive along the drift line, often some distance from the wrack beds. The duration of the larval and pupal stages are similar to those of other wrack-flies, such as *F. maritima* (Egglishaw 1960b), *F. rufitibia* and *F. costalis* (Kompfner 1974) and also of *Coelopa* species (Egglishaw 1960a; Dobson 1974) held at similar temperatures. Some northern species over-winter as pupae (Egglishaw 1960b) but in the Cape *F. capensis* occurs year round, although numbers peak in early winter, when maximal amounts of kelp are beached (Koop 1979).

Larval size at pupation depends largely upon conditions during development, particularly food availability and crowding (Dobson 1974). Larvae of up to 40 mg have been recorded from Kommetjie, but in laboratory culture mass at pupation did not rise above 11 mg wet. In the course of development these larvae consumed an average of 18,7 mg dry kelp and respired 2,60 ml O_2. Given the wet mass/dry mass ratio of *Fucellia* larvae (7,04:1, after 3 days at 60 °C) the energy equivalents of larvae (25,8 kJg^{-1} dry) and of kelp frond (13,1 kJg^{-1} dry) as determined by bomb calorimetry and an oxycalorific equivalent (19,85 J ml^{-1} O_2), it is possible to calculate an energy budget for an individual larva over its lifespan. Using the standard energy budget equation of

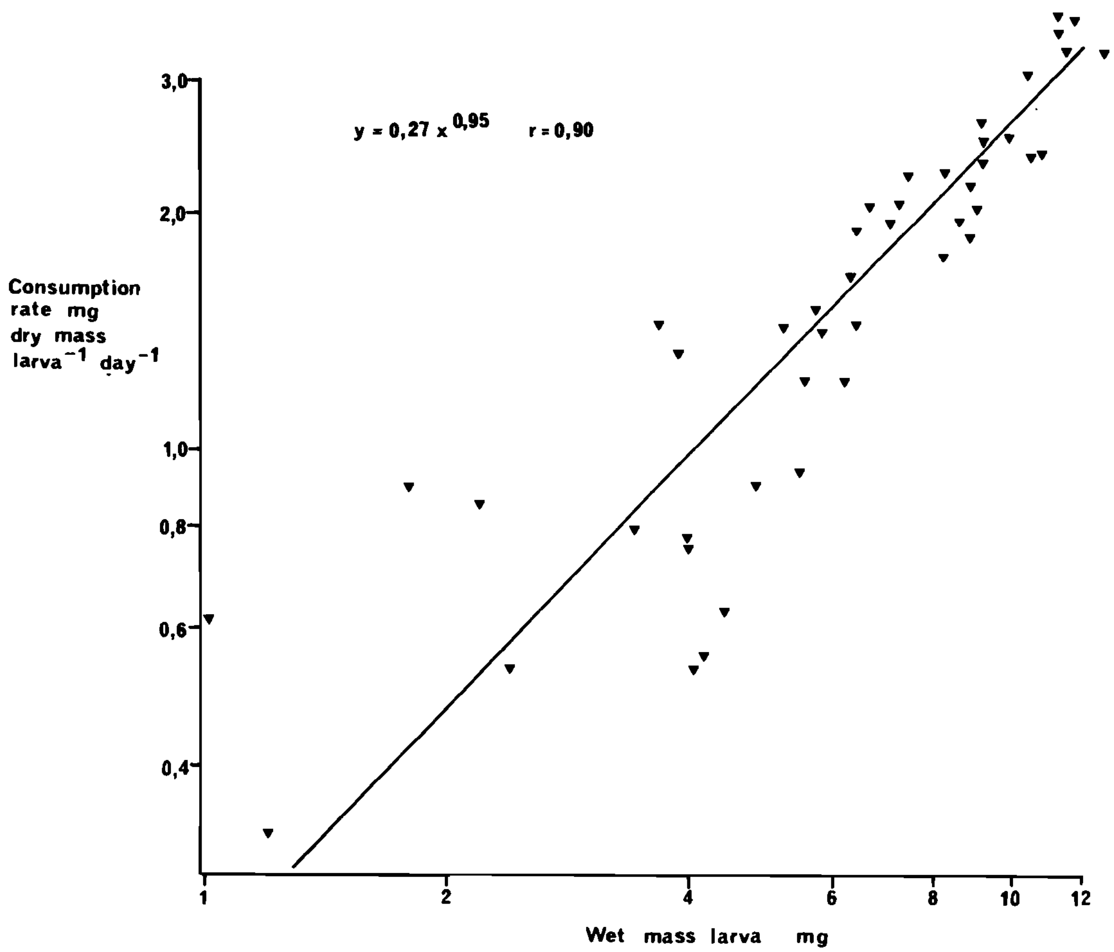

Fig. 2 Daily consumption rates of *Fucellia capensis* larvae fed on *Ecklonia maxima* frond and held at 18 °C.

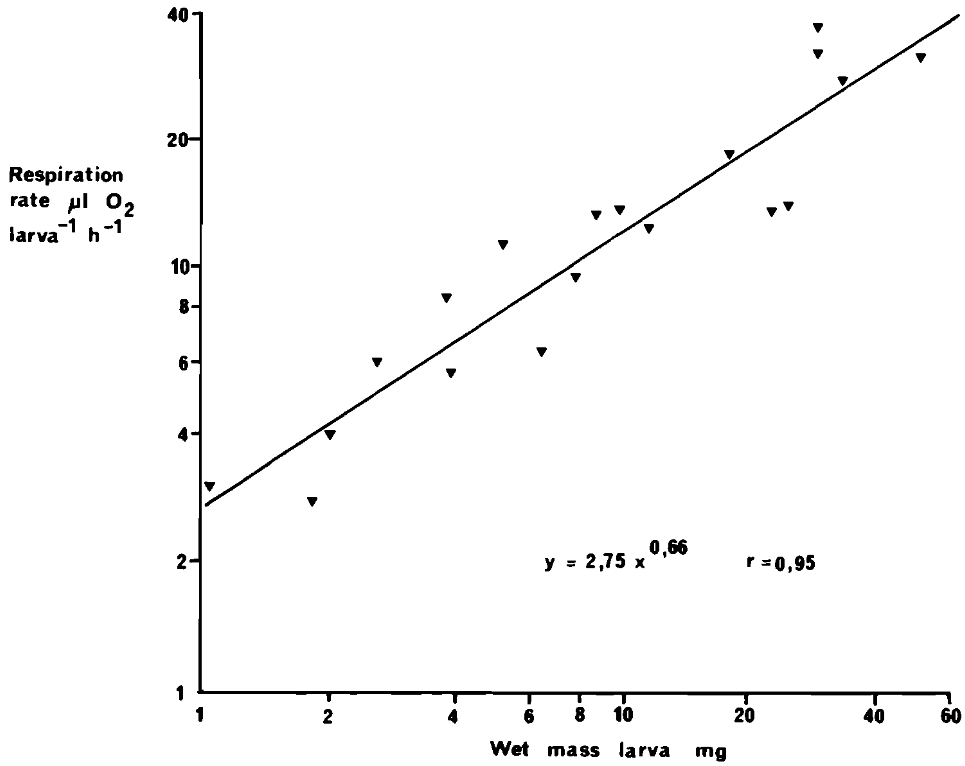

Fig. 3 Respiration rates of *Fucellia capensis* larvae at 18 °C.

the International Biological Programme:

Consumption = Production + Respiration + Faeces + Urine
or C = P + R + (F + U), this gives us:
245,5 = 43,9 + 51,6 + (150,0) Joules
F + U being obtained by subtraction.

This would suggest that 30% of ingested food is assimilated [A = (P + R)/C] and 17% utilized in growth (the gross growth efficiency, P/C). These figures omit the energy value of exuvia, which was not determined.

Kelp fly larvae are rapid feeders, eating 1,8 times their dry mass in kelp per day. The other major consumers, the amphipod *Talorchestia capensis* and the isopod *Ligia dilatata*, by comparison, eat 0,2 – 0,7 and 0,6 – 2,2 times their own dry mass per day, depending upon body size (Muir 1977; Koop 1979). The standing stocks of these crustacea, are, however, extraordinarily high — sometimes exceeding 2 000 g dry mass per m beach for *T. capensis* alone (Muir 1977). The overall mass of kelp they take thus overshadows that eaten by fly larvae, which seldom achieve a standing stock of more than 10 g dry mass per m beach (Stenton-Dozey & Griffiths, unpublished data). The effects of the larvae may, however, be greater than indicated by consumption figures alone. Rowell (1969) has, for example, shown that decay is more rapid, and of a different type than normal, in wrack containing *Coelopa* larvae, possibly as a result of the transfer and spread of micro-organisms by the larvae. Fly larvae, moreover, form a high-energy, readily accessible food resource for waders such as the curlew sandpiper. Such birds appear to be able to fulfil their food requirements much more rapidly by feeding upon larvae than by taking other invertebrates in nearby wetlands (Puttick 1979).

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