Drift

- downstream transport of benthos in water column
- common drifters

  Ephemeroptera (*Baetis*), Chironomidae, Simuliidae, some Plecoptera and Trichoptera, Gammaridae

  diatoms

  larval vertebrates

- ecological significance
  - mode of dispersal, emigration (Waters 1972)
  - food resource for drift-feeding fish and large filter-feeding invertebrates
- Waters (1965): behavioral drift, constant drift, catastrophic drift

Amount of drift

- mesh size
- fraction of benthos difting
  - at any moment - 0.01 - 0.5%
  - over 24h period - up to 100 × density
- drift density ~ 100-1000 ind./100 m^3
- drift rate ~ 10^4-10^5 ind./24 h

Colonization cycle (Müller 1954)

- larval populations move downstream
- Upstream larval movement of larvae ca 30% (Elliott 1971)
- compensations by upstream flight of adults
- egg-bearing females fly upstream for oviposition (Roos 1957)
- confirmed by number of studies (e.g., Otto & Svenson 1976)
- but Elliott (1967): flight of ETP according to the wind direction

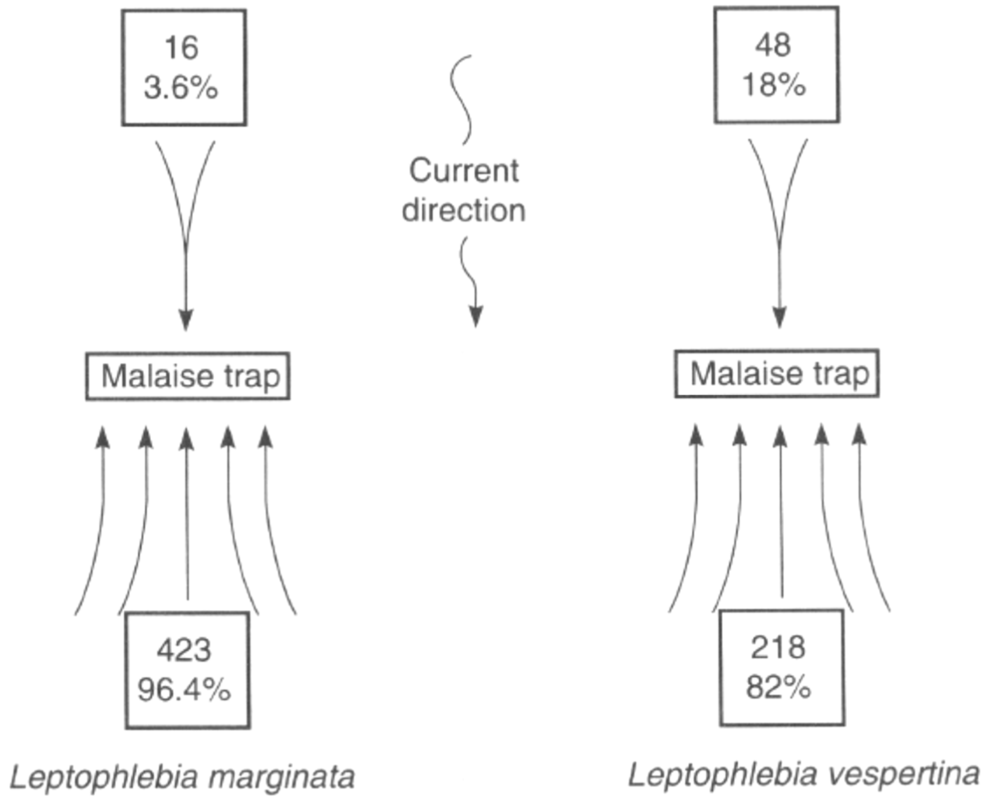


FIGURE 10.4 Flight directionality of two mayflies in the Gysinge rapids of the River Dalälven, showing predominantly upstream flight. (From Müller, 1982.)

Colonization cycle II

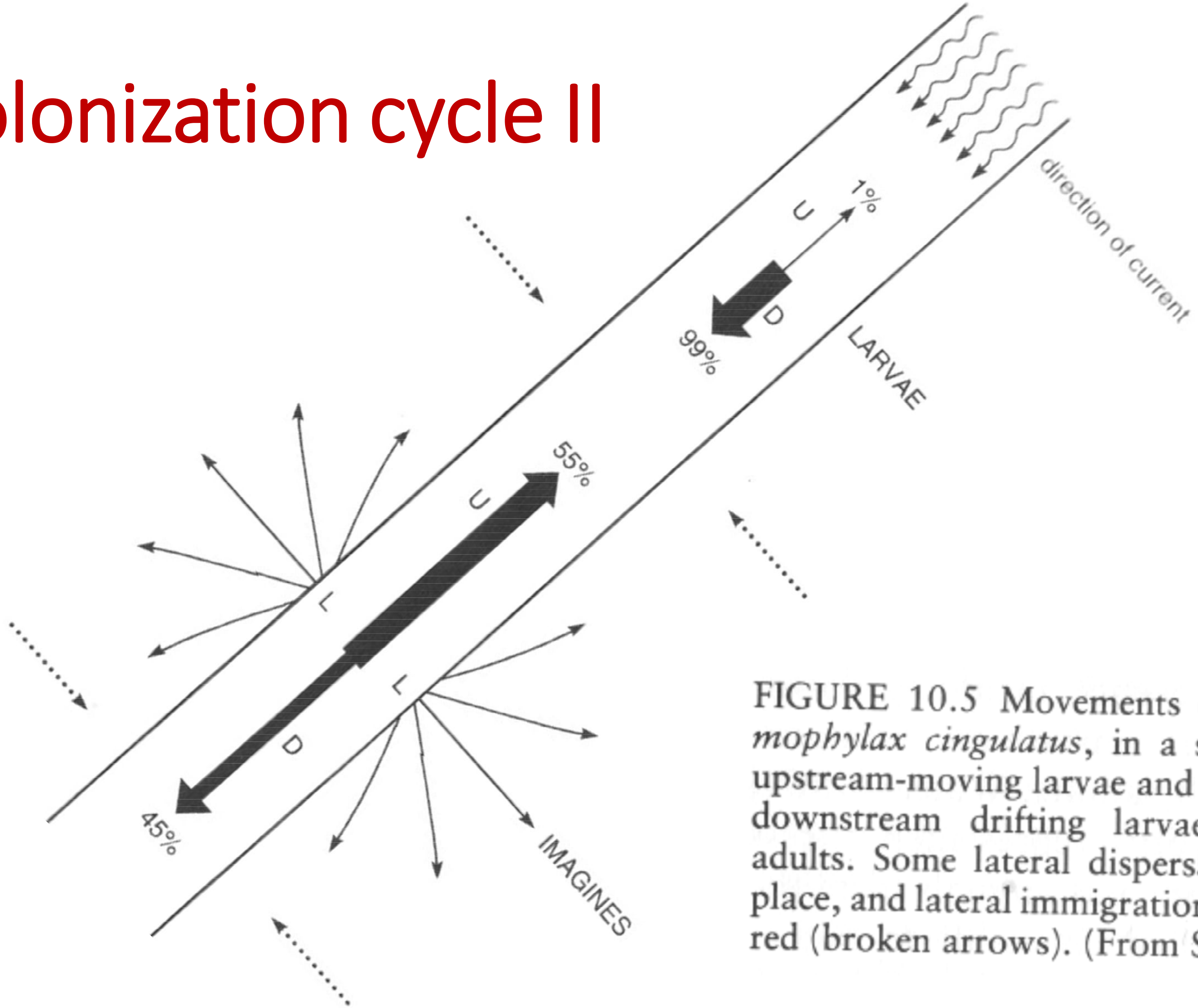


FIGURE 10.5 Movements of the trichopteran, *Potamophylax cingulatus*, in a south Swedish stream. U, upstream-moving larvae and upstream-flying adults; D, downstream drifting larvae and downstream-flying adults. Some lateral dispersal (L) of adults also took place, and lateral immigration of adults may have occurred (broken arrows). (From Svensson, 1974.)

Drift distance

- return to substrate
- experiments with live vs dead specimens
- traveling distance – nightly up to 75 m, life-time up to 10-15 km?
- little evidence for pools to trap drift

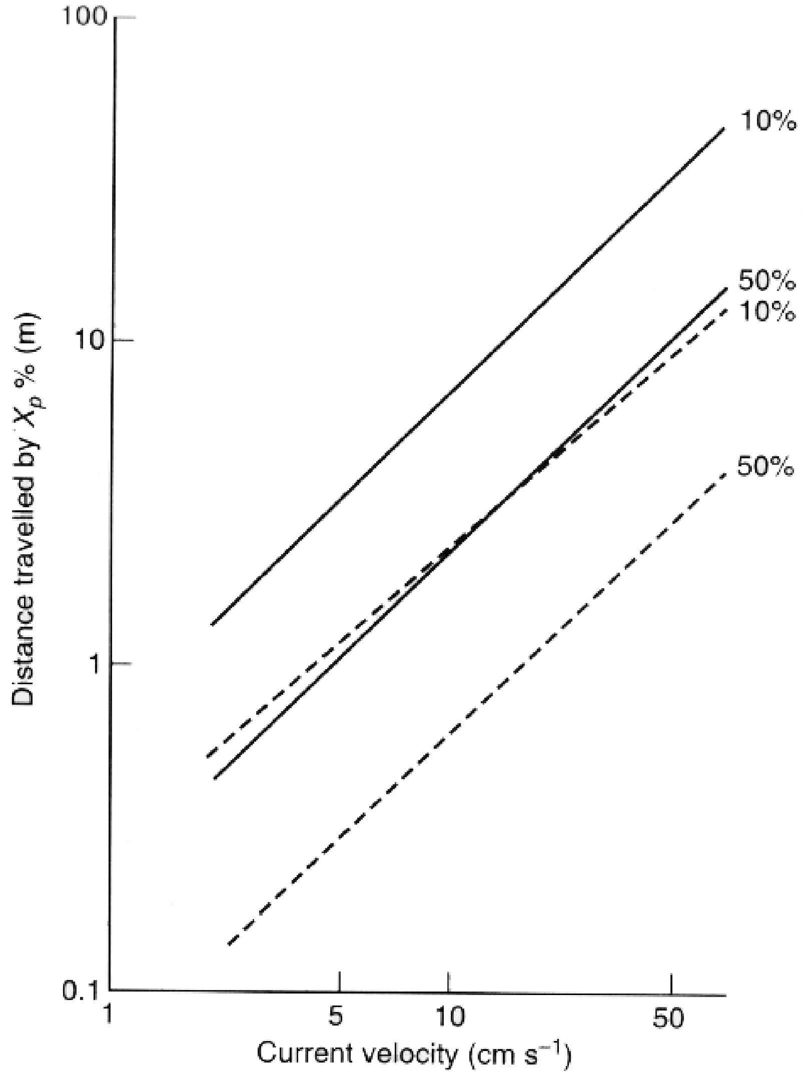


FIGURE 10.3 The distance traveled by drifting invertebrates as a function of water velocity, from Elliott's (1971b) equation 12 and Table 6. The solid lines depict taxa that regained the bottom no more rapidly alive than dead at all current speeds, or performed slightly better than this at slow currents only (a flatworm, chironomid and simuliid larvae, riffle beetles, several stoneflies and caddis larvae, and a heptageniid mayfly). The dotted lines depict *Baetis rhodani* and *Gammarus pulex*, which were the most adept at regaining the bottom. *Hydropsyche* spp. and *Ecdyonurus venosus* were intermediate. Note that $(100 - X_p)$% of individuals have settled out of the drift in the specified distance.

Behavioral drift

- nocturnal activity
- one or two peaks: after dusk, before dawn
- light intensity treshhold ~ 1 lux
- „risk of predator“ hypothesis (Allan 1978)
- Chironomidae – aperiodical
- Diatoms, water mites – daytime drift
- Palmer et al. (1992): strong nocturnal drift of copepods, oligochetes, rotifers and small chironomids

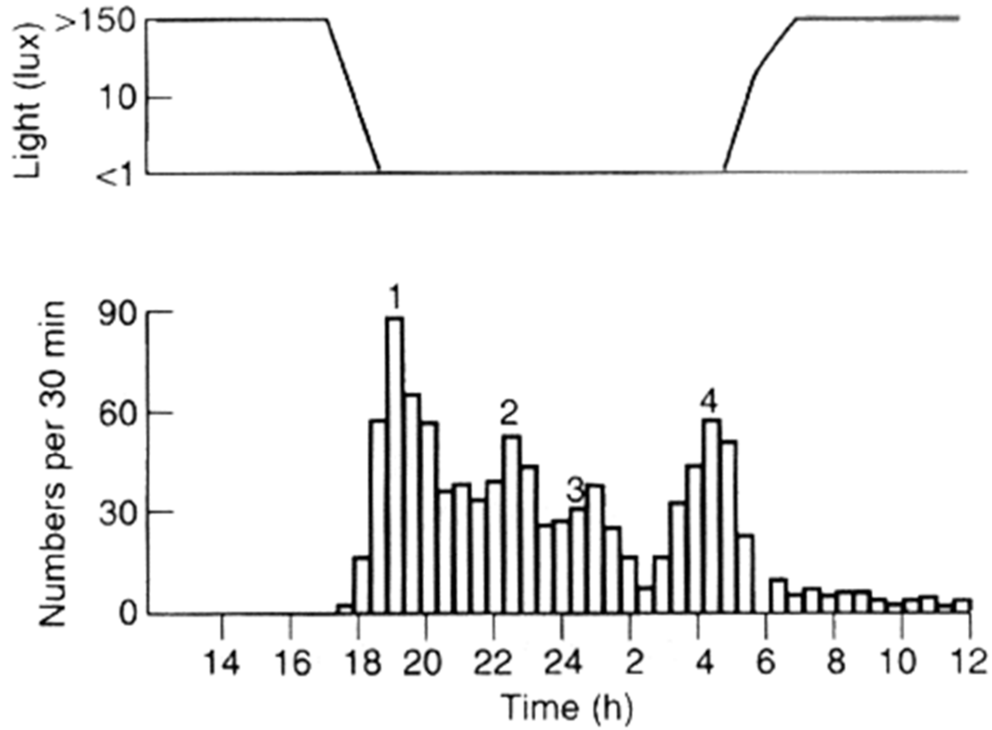


FIGURE 10.1 Diel variation in drift catches of *Baetis rhodani* at 30 min intervals over a 24 h period. Four apparent peaks are indicated (1–4). (From Elliott, 1969.)

Behavioral drift II

- exogenous vs. endogenous control
- negative phototaxis
- *Baetis*: constant light → no drift
- constant darkness: nocturnal periodicity lasts for ca a week

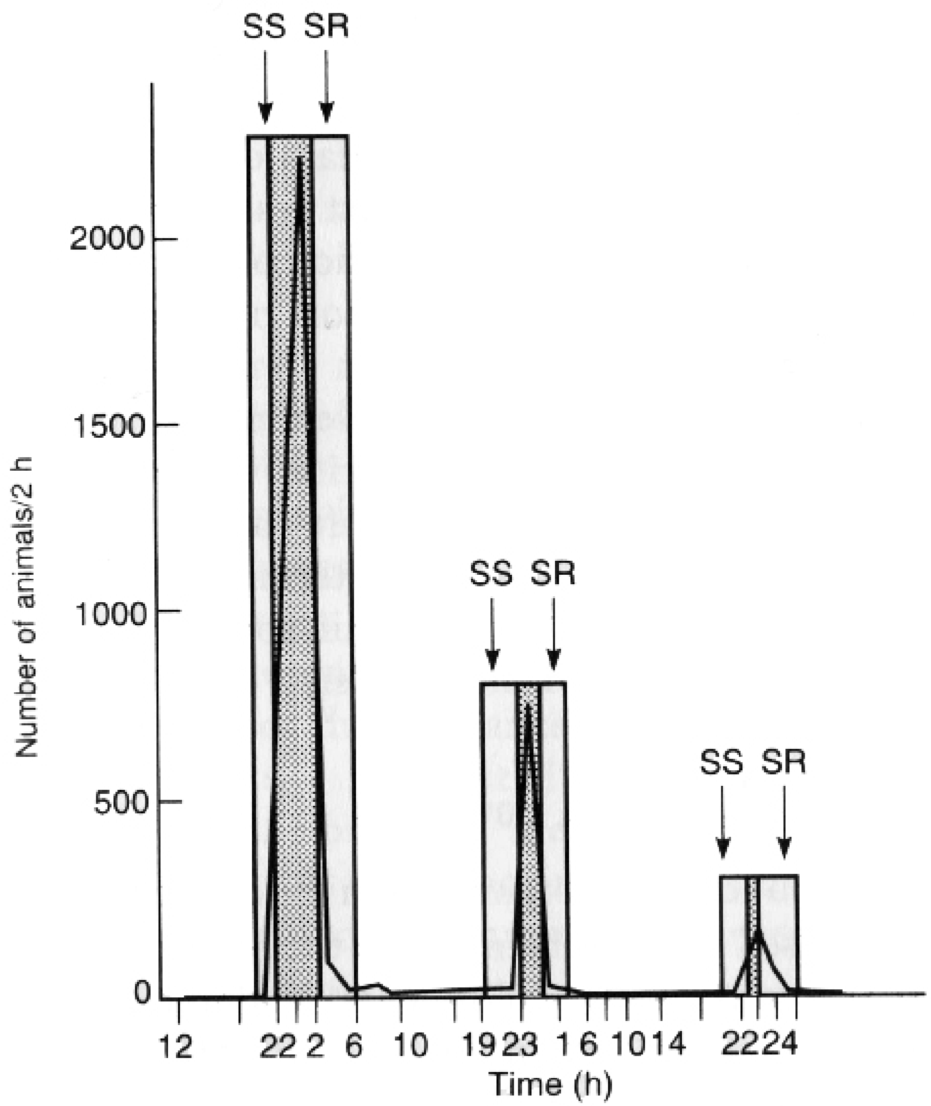


FIGURE 10.2 Drift activity of *Baetis* nymphs in artificially shortened nights. SS and SR denote natural sunset and sunrise, but artificial lights reduced the period of darkness to 4, 2 and 1 h, respectively (shaded regions). (From Müller, 1965.)

Drift as predation avoidance

- Allan (1978) – insect larvae drift more at night and are larger
- McIntosh & Peckarsky (2006) – night drift induced in Ephemeroptera in a fishless stream after introducing fish odor

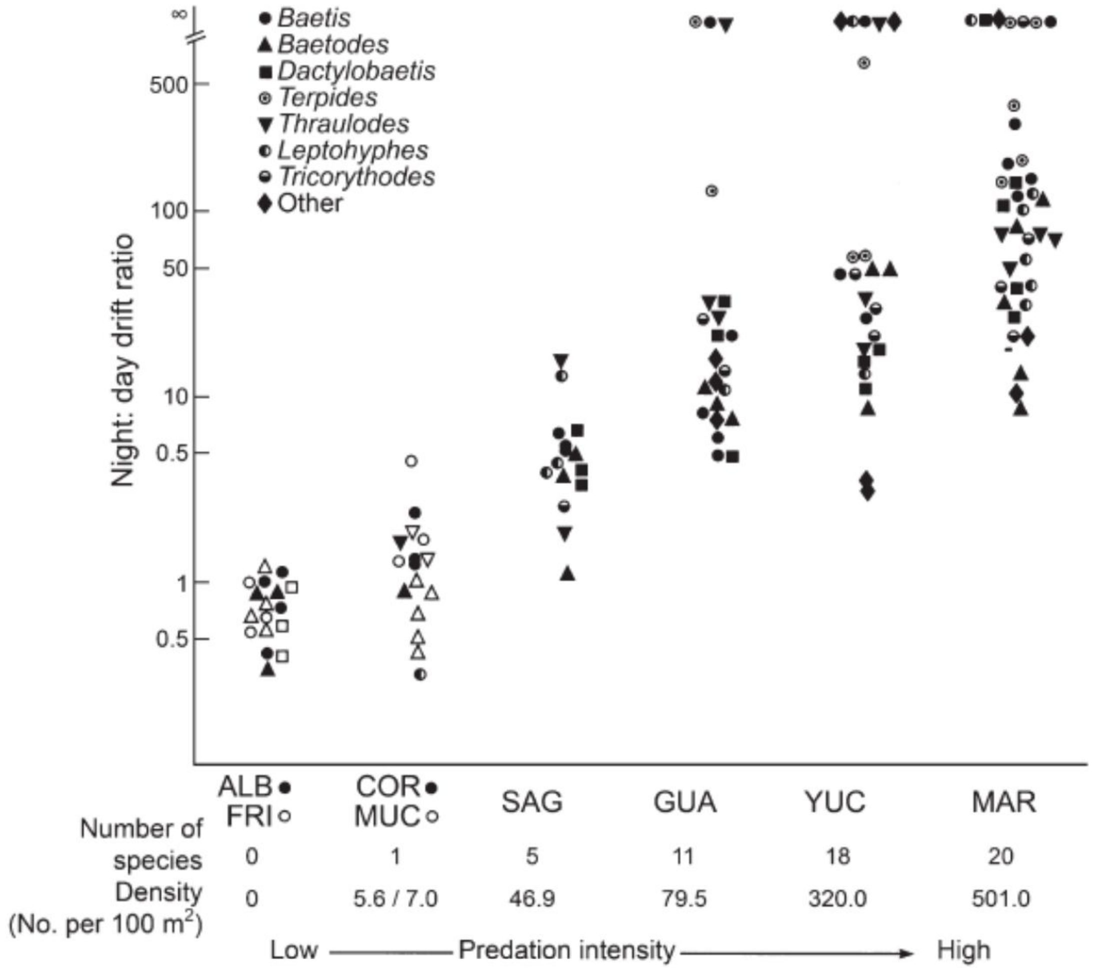


FIGURE 9.10 Night to day drift ratio of mayfly drift densities from a series of streams in the Venezuelan Andes representing a gradient from low to high predation. Note that drift is greater by day in high elevation streams lacking drift-feeding fish (Río Albarregas [ALB] and Quebrada La Fria [FRI]) compared to nearby streams containing introduced trout (Quebrada Coromoto [COR] and Mucunutan [MUC]). Other rivers are Río Saguas (SAG), Río Guache (GUA), Río la Yuca (YUC) and Río las Marías. (Reproduced from Flecker 1992b.)

Drift to search for food sources

- Kohler (1985)

  How does drift respond to starvation, access of food, and algal patchiness?

  Baetis enter drift to find food

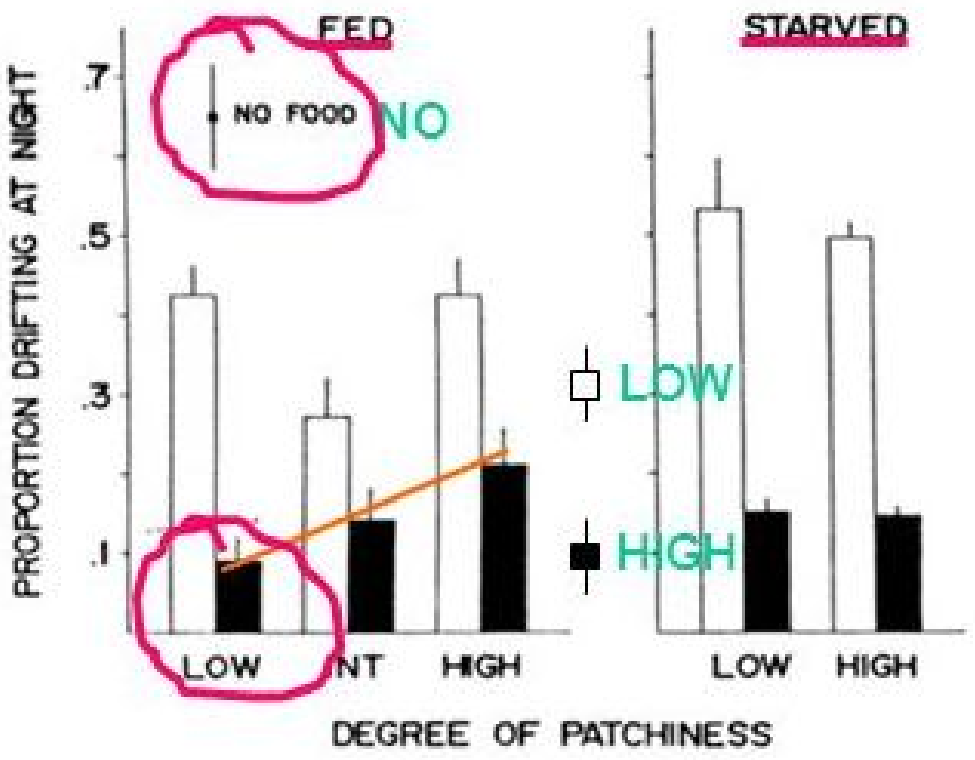


FIG. 3. The proportion of *Baetis* drifting at night ($\bar{X}$ + SE, n = 3 replicates) under control (no food), low-food (□), and high-food (■) conditions, as a function of the degree of periphyton patchiness.

Cost and benefits of drift

- Advantages
  - finding food – increased fitness
  - avoid tacticle invertebrate predators (*Baetis*)
- Disadvantages
  - landing in poor habitat
  - exposure to visual drif-feeding predators (% zero fitness)
- Ecological rule – minimizing „µ/g“

  µ ... mortality risk

  g .... growth rate
- Production compensation model (Waters 1961) – drift represents the production exceding the carrying capacity, entry to drift is disadvatageous, upstream movement unnecessary, drift low if the population under carrying capacity
- Hildebrand (1974) – drift is a constant % of benthic density

Predation

- ubiquitous
- „key stone predation“ (Paine 1966, 1969, Allan 1982)
- effects
  - reduction of abundance, elimination of species
  - restrictions on habitat use and foraging efficiency
  - adaptation through natural selection
  - cascade of interactions in trophic webs
  - changes in energy pathways
- predator preference
- prey vulnerability

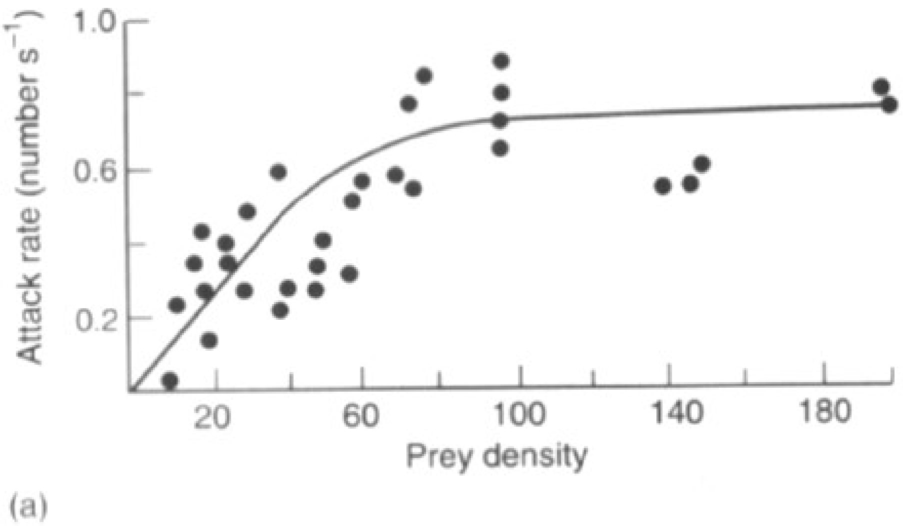


FIGURE 7.2 Functional response curves, or number of prey consumed per predator within a restricted time period, of two predator species over a range of prey densities. (a) Rainbow trout feeding on the amphipod *Hyallela* in aquaria, from Ware (1972).

Trophic guilds of stream fishes

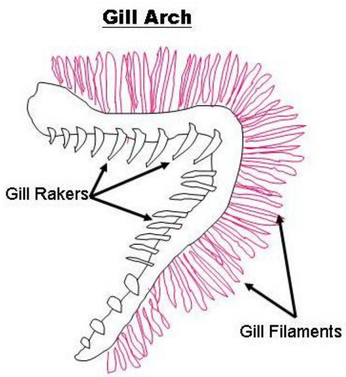
TABLE 8.3 Trophic guilds of stream fishes, for temperate North America (modified from Horwitz 1978) and tropical South America (modified from Welcomme 1979).

Guild	*Description for temperate streams*	*Occurrence[a] by species (%)*	*Comments for tropical streams*
Piscivore	Consumes primarily fish and/or large invertebrates, but includes smaller invertebrates	16	Piscivores may consume entire fish or specialize on parts of fish
Benthic invertebrate feeder	Feeds on benthic invertebrates, primarily immature insects	33	Most common in small to midorder streams
Surface and water column feeder	Consume surface prey (mainly terrestrial and emerging insects) and drift (zooplankton and invertebrates of benthic origin)	11	Diverse surface foods occurring in forested headwaters and during seasonal flooding
Generalized invertebrate feeder	Feeds at all depths	11	Similar category
Planktivore	Midwater specialists upon phytoplankton and zooplankton	3	Seasonally important in larger rivers
Herbivore-detritivore	Bottom feeders ingesting periphyton and detritus; includes mud feeders with long intestinal tracts	7	Herbivory may be subdivided into microphytes and macrophytes, and detritus feeders separated from mud feeders
Omnivore	Ingest a wide range of animal and plant foods, and detritus	6	Similar category
Parasite	Ectoparasites (e.g., lampreys)	3	Ectoparasites (e.g., candirú catfishes)

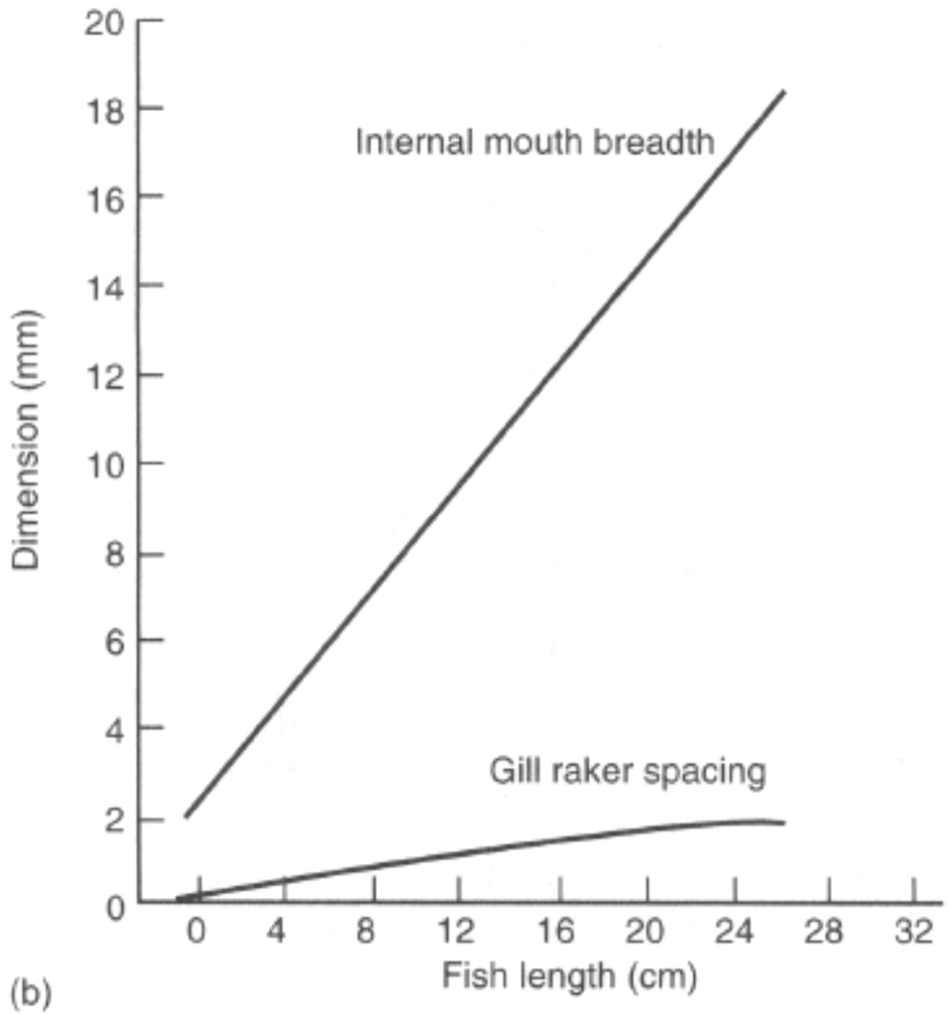
[a] Percentages are based on the number of species, rather than the number of individuals, from the central United States only, based on Horwitz' (1978) study of 15 US river systems. An additional 9% of species could not be categorized, and one species (*Lepomis microlophus*) fed on snails

Fish predators

- vision, olfaction
- bottom vs. midwater dwellers
- bottom vs. drift feeding
- adaptations of mouth, gill arches, fins
- most studied: salmon and trout
- strong predictors: fish abundance and size
- predator size vs. prey size



Salmo salar



(b)

Size preference in fish

- with increasing prey size
  - predation intensity increases
  - reaction distance increases

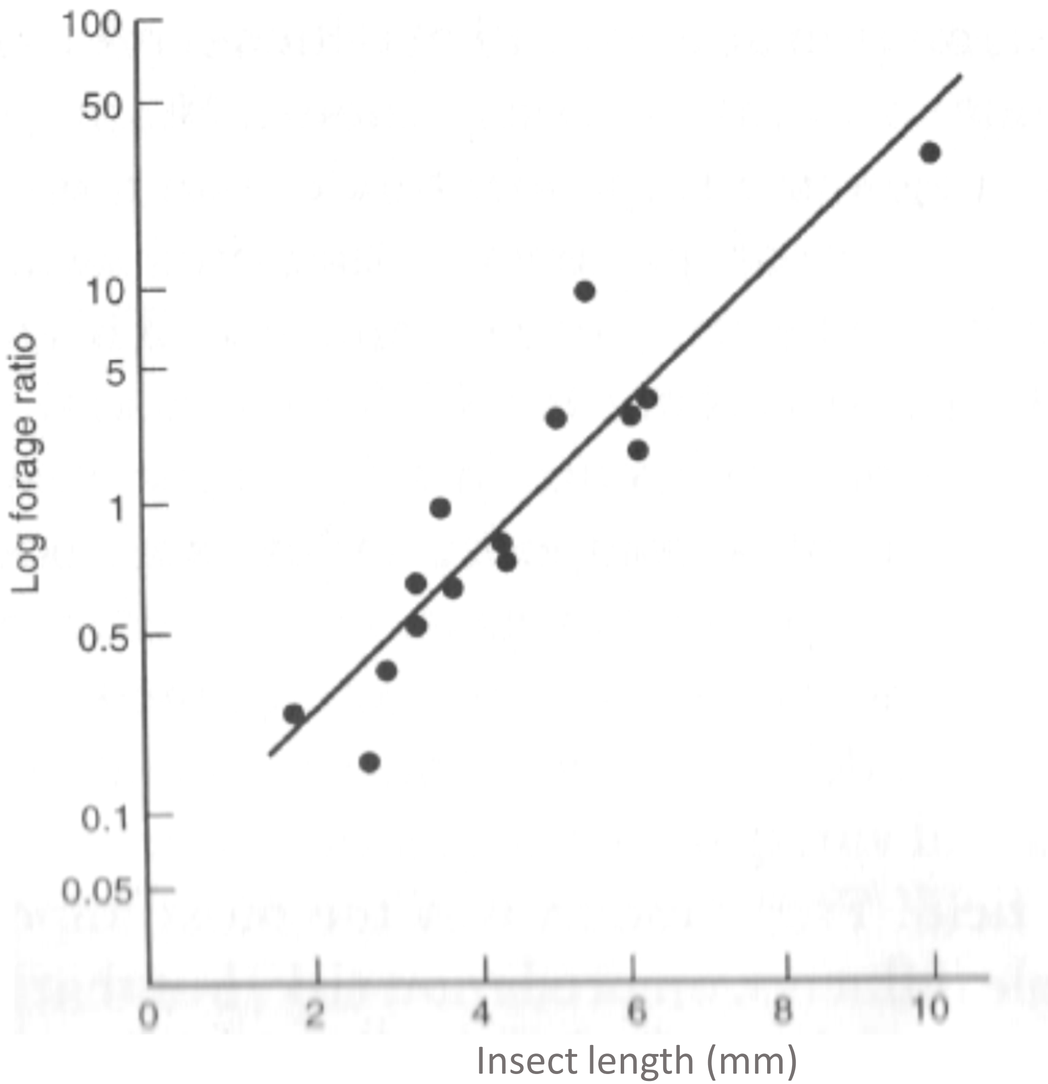


FIGURE 7.3 The size preference of trout for large prey. (a) Rainbow trout consuming surface drift in a German stream, mainly emerging insects and adults of Ephemeroptera and Chironomidae. (From Metz, 1974.)

Prey choice in fish

- gut content vs. prey community composition
- „availability factor“ (Allen 1941)
- diet composition resembles the composition of fauna
- common items over-represented
- availability vs. true selection
- field vs. laboratory studies
- specialization on the most frequently feeded prey

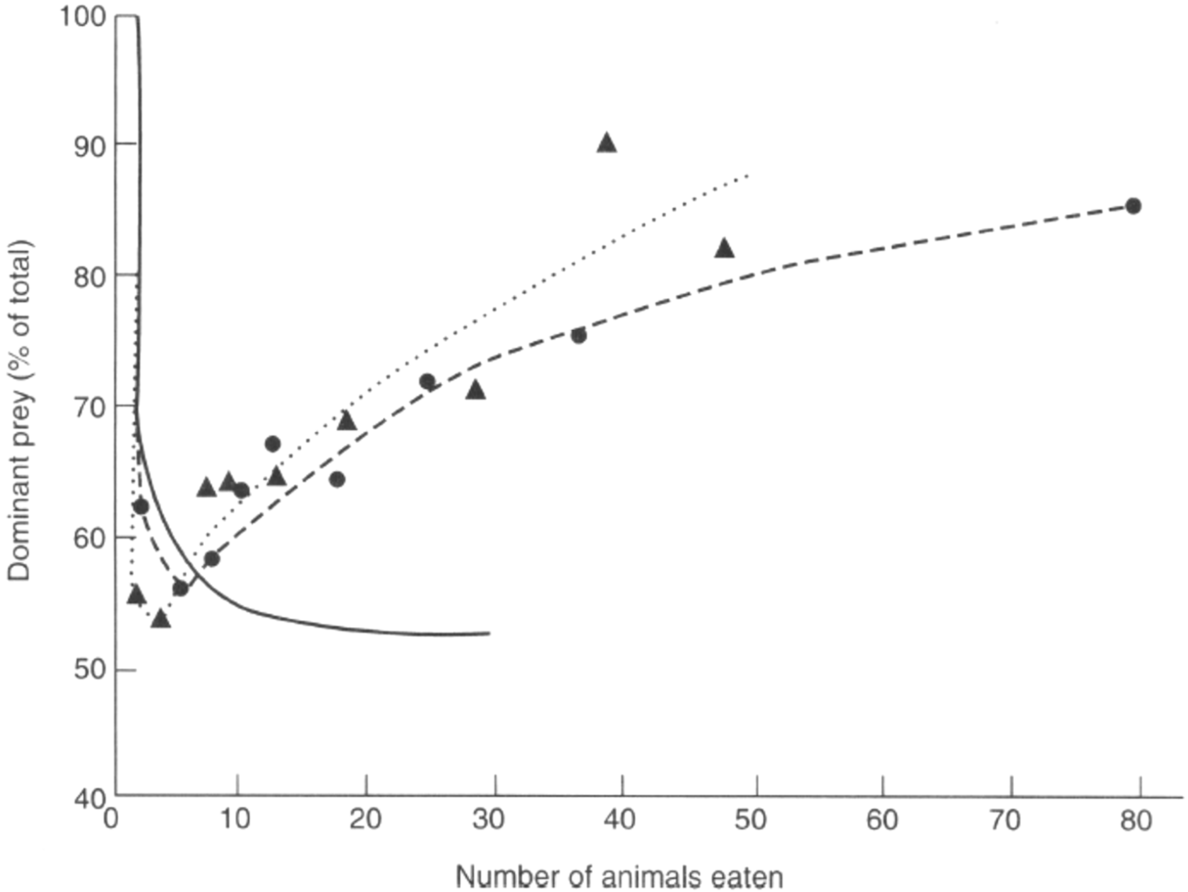
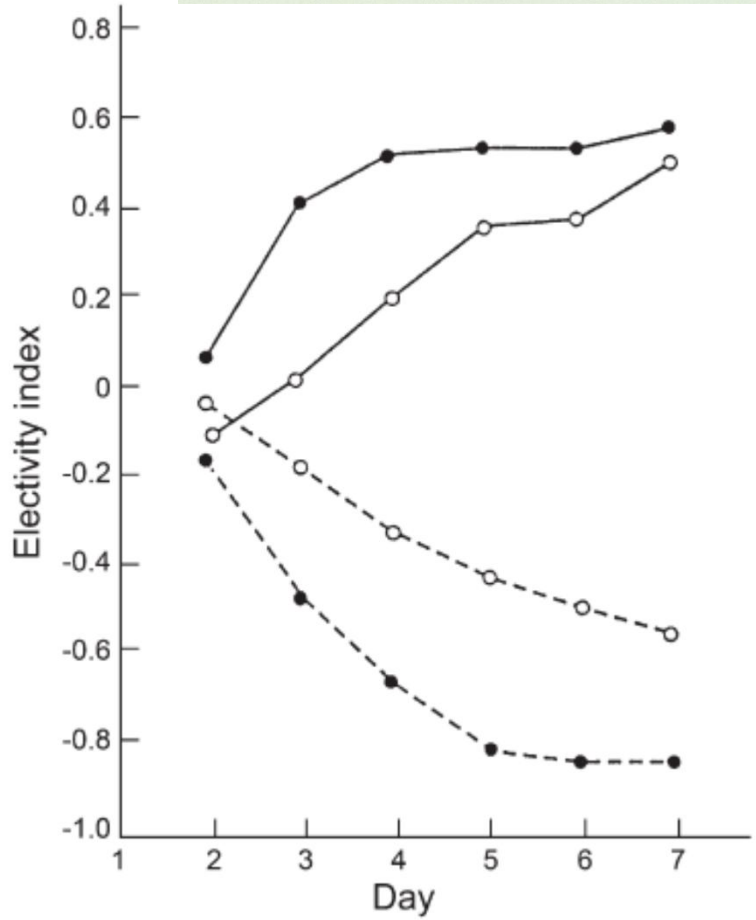


FIGURE 7.1 The percentage of total stomach contents that the dominant prey item constituted in the diet of young Atlantic salmon in two Scottish rivers. Dotted line, River Thurso; dashed line, River Eden; solid line, theoretical expectation from random feeding. (From Allen, 1941.)

Learned specialization

- predatory behavior changes with experience
- increases rates of predation/foraging efficiency
- „training bias“
- variation in individual feeding responce (Bryan & Larkin 1972)
- capture rate varies with hunger level

FIGURE 9.6 The size preference for large prey of drift-feeding brown trout in a laboratory stream. Wild trout were maintained on a diet of brine shrimp. In this experiment, brine shrimp (dashed lines) only were provided on day 1, and the larger mealworms (solid lines) were added on day 2. Drift rates were 5 (open circles, low) and 10 (solid circles high) per minute. "Electivity" is a measure of preference based on prey consumed in relation to prey available. (Reproduced from Ringler 1979.)



Energy maximization

- searching, handling
- energy gain = $\frac{\text{dry mass or calories obtained}}{\text{energy expended in prey acquisition}}$
- optimal prey size
- rejection of superoptimal prey
- no upper limit to prey size in nature (optimal prey size for a 20 cm salmon/trout: 10-12 mm)

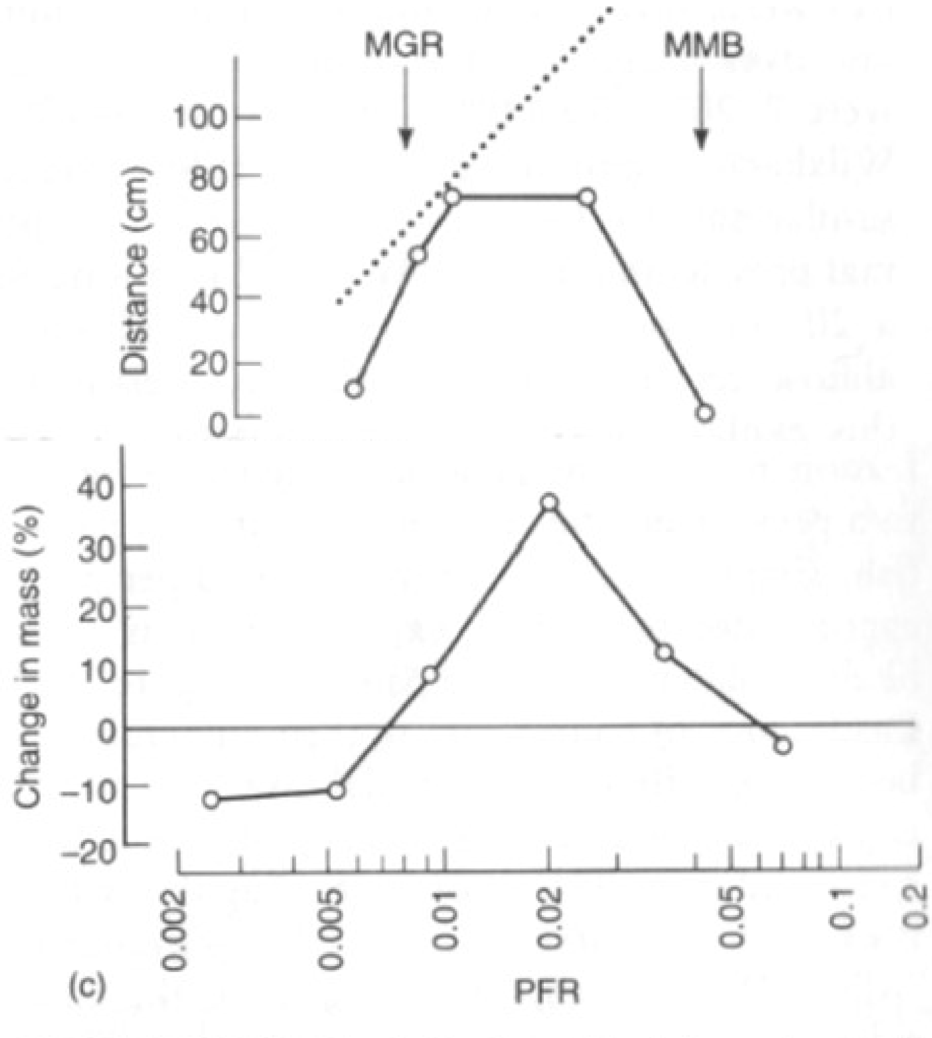
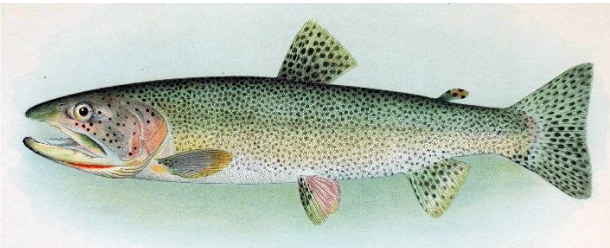


FIGURE 7.5 Feeding behavior, selectivity and growth in Atlantic salmon of mean length 8.6 cm in June, as a function of the ratio of prey diameter to fish fork length (PFR). (a) MGR, mean gill raker spacing; MMB, mean mouth breadth; expected response distance (dotted line); striking distance (solid line). (c) Growth, measured as percentage change in mass. (From Wankowski, 1979.)

Influence of light on predation by fish

- treshhold for effective visual location of prey ~ 0.1 lux
- role of shading



pstruh žlutohrdlý

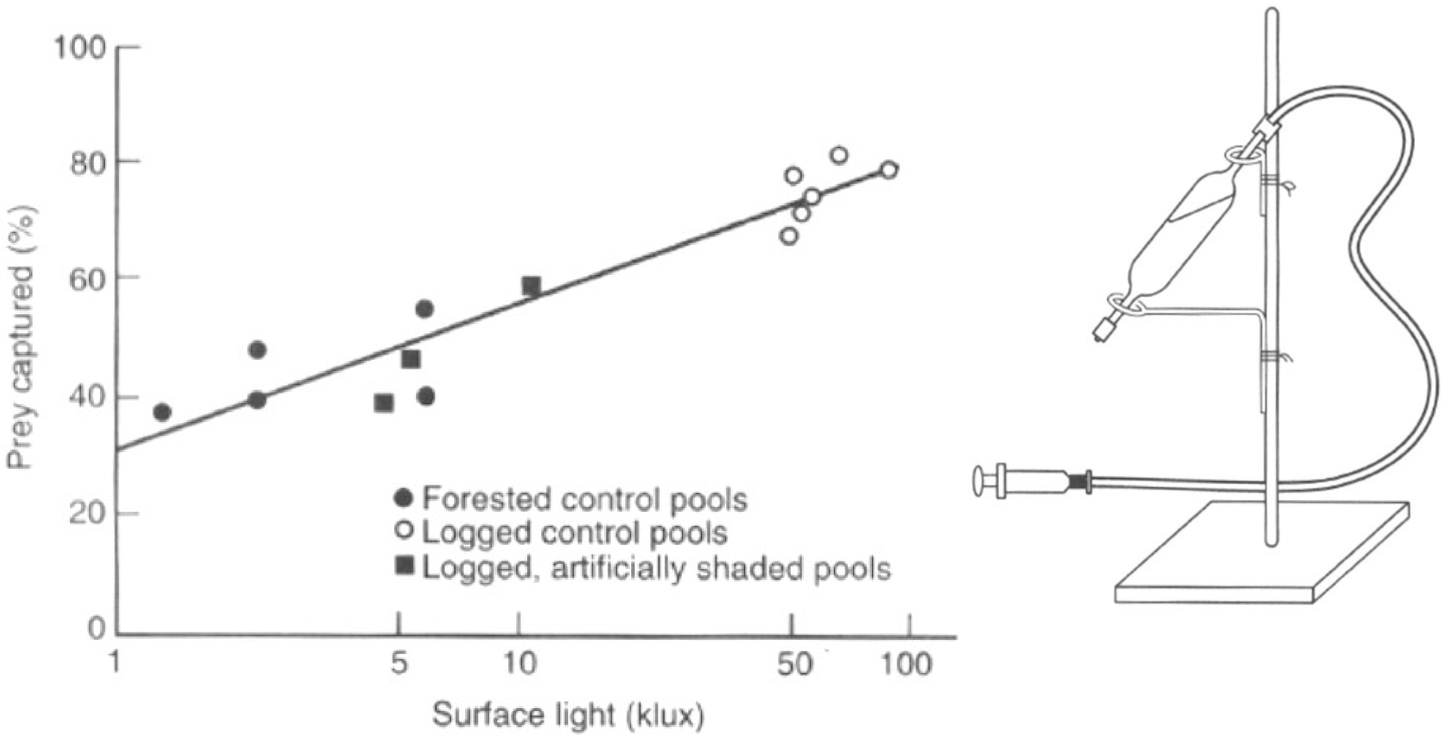


FIGURE 7.4 The percentage of prey captured by cutthroat trout (*Oncorhynchus clarki*) as a function of light intensity at the water surface. Prey were mosquito larvae introduced with a syringe apparatus and captures were recorded by underwater observation. (From Wilzbach, Cummins and Hall, 1986.)

Invertebrate predators

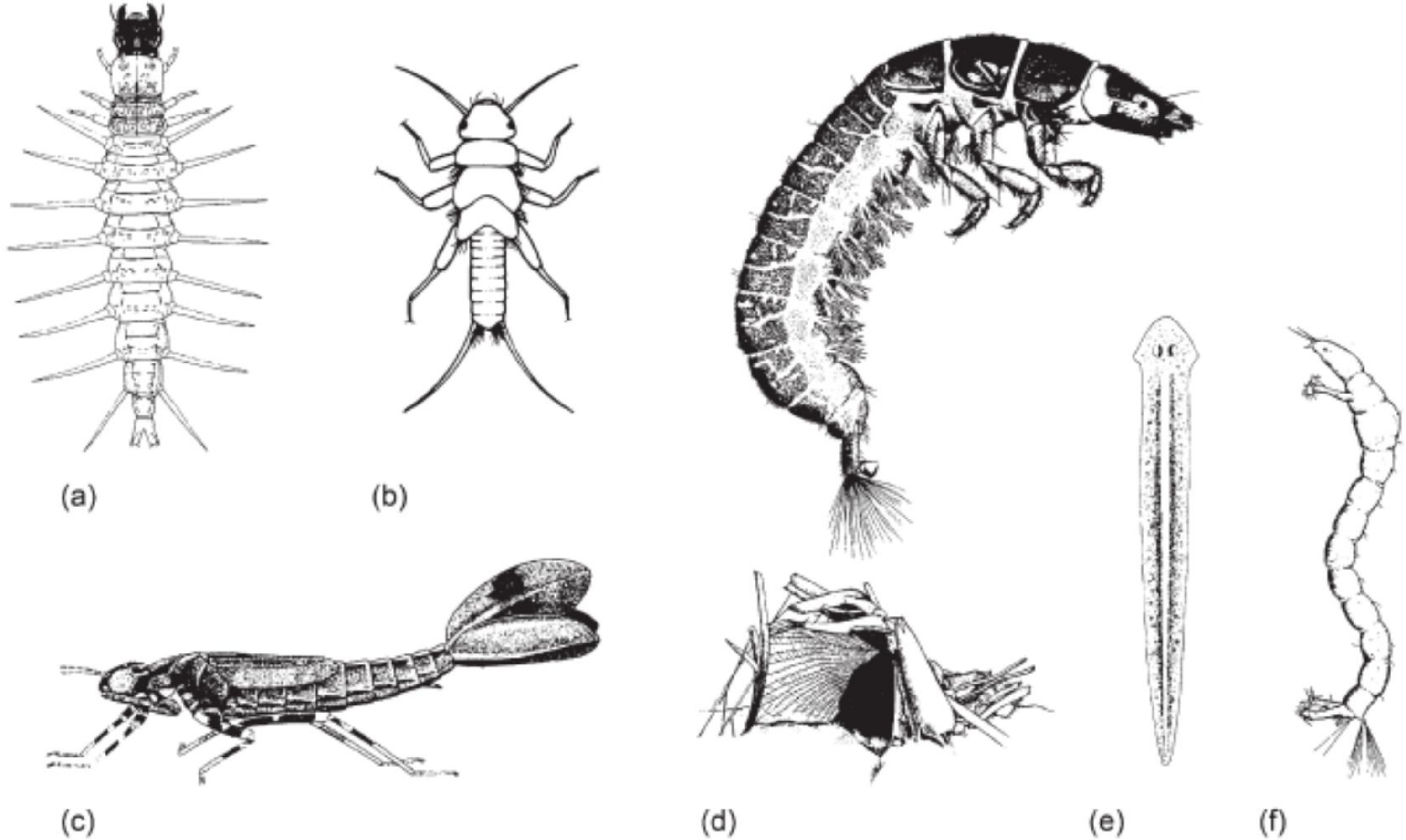


FIGURE 8.9 Examples of predaceous invertebrates, including those consuming large prey, illustrated by nymphs of (a) Megaloptera (Corydalidae) and (b) Plecoptera (Perlidae); those consuming prey of intermediate size, illustrated by (c) Odonata (Zygoptera) and (d) Trichoptera (Hydropsychidae); and those consuming small prey, illustrated by (e) Turbellaria (Tricladida) and (f) Chironomidae (Tanypodinae). (Figures a and d reproduced from Merritt and Cummins 2004; figures b, c, e, and f reproduced from Pennak 1989.)

Invertebrate predators

- Pecarsky (1982,1984)
- mechanical, visual, chemical detection, and their combinations
- functional groups by Cummins (1973):
  - engulfers
  - piercers (Athericidae, some Chironomidae and Hemiptera)
- means of hunting
  - sit-and-wait
  - searching
  - combinations of both
- occasional predation

Dinocras cephalotes
(Sjöström 1985)

Ryacophila nubila
(Otto 1993)

Unionicola crassipes
(Proctor & Pritchard 1990)

Prey preference

- gut analyses, head width mesurement
- good correlation of proportion of prey in gut content and faunal community
- average size of prey increases with increasing size of predator
- diet change during development (e.g., stoneflies – Allan 1982)
- size refuge

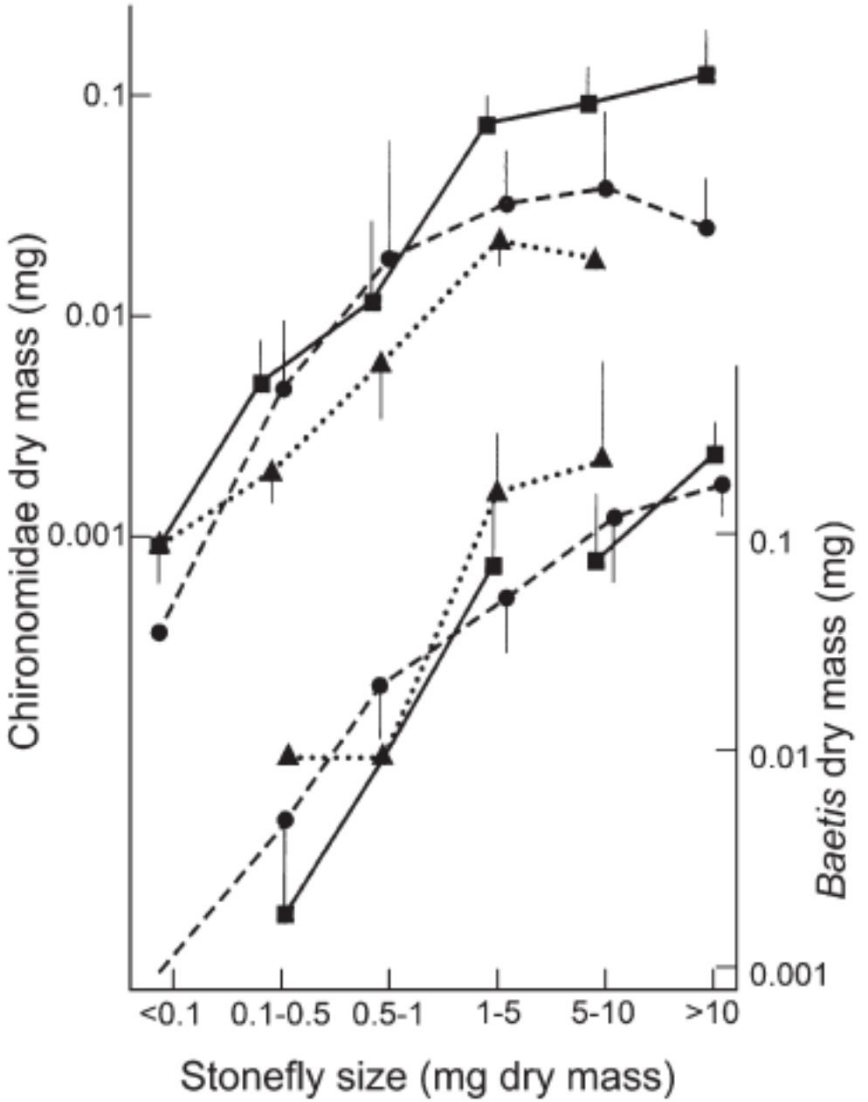


FIGURE 8.10 Average dry mass of prey found in the foreguts of three species of predaceous stoneflies, as a function of size groupings of predators. stoneflies of a particular size consumed prey of the same size for both prey species. Means and 95% confidence limits are shown for *Megarcys signata* (■), *Kogotus modestus* (▲), and *Hesperoperla pacifica* (●). (Reproduced from Allan 1982a.)

Prey availibility, predator aggregation, and body size relationships

- prey availibility – may override differences between predators in foraging mode → dietary overlap
- patch use
    - aggregation of predators in patches of high prey density – correlative and experimental studies
    - *e.g. Plectrocnemia conspersa* (Hildrew & Townsend 1980)
    - absence of aggregative behaviour in predacious stoneflies (Peckarsky & Dodson 1980, Peckarsky 1985)
- body size relationship - mutual predation and canibalism among predator species (Woodward & Hildrew 2002)

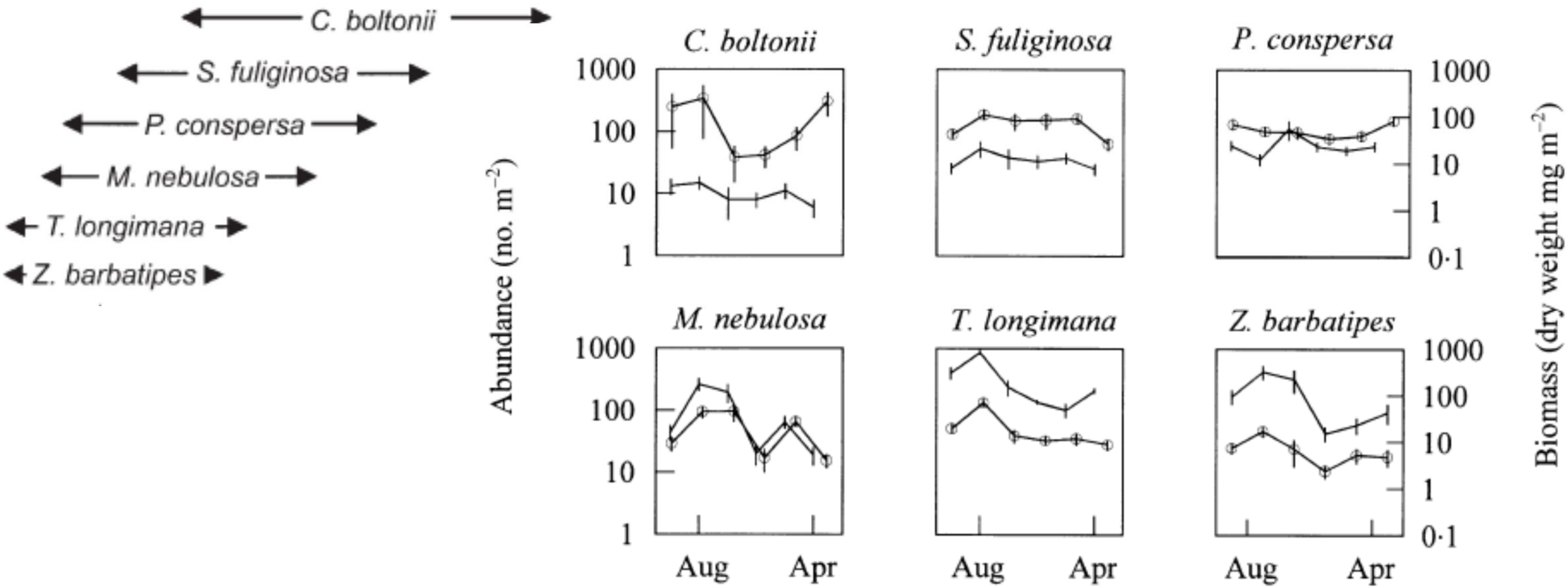


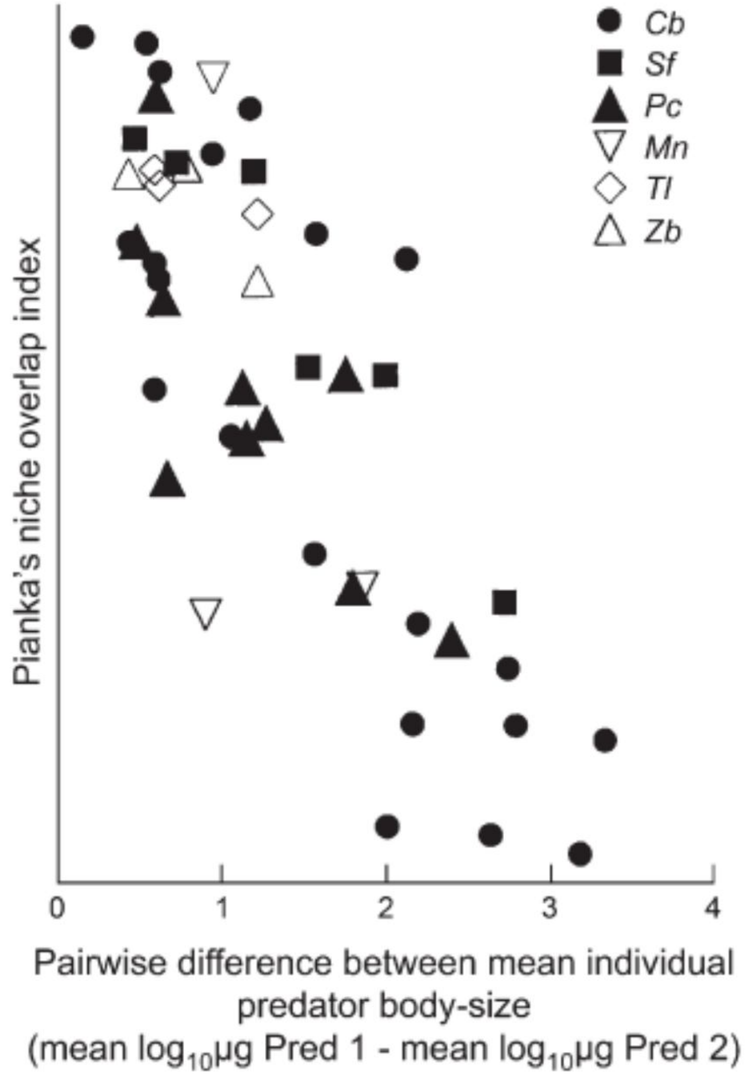
Fig. 1. Seasonal variations in the abundance and biomass (open circles) of the six dominant predator species in Broadstone Stream between 1996 and 1997. Note logarithmic *y*-axes.

From largest to smallest the predators include the dragonfly *Cordulegaster boltonii*, the alderfly *Sialis fuliginosa*, the caddisfly *Plectrocnemia conspersa*, and three tanypod midges *Macropelopia nebulosa*, *Trissopelopia longimana*, and *Zavrelimyia barbatipes*. (Reproduced from Woodward and Hildrew 2002a.)

Dietary overlap in invertebrates

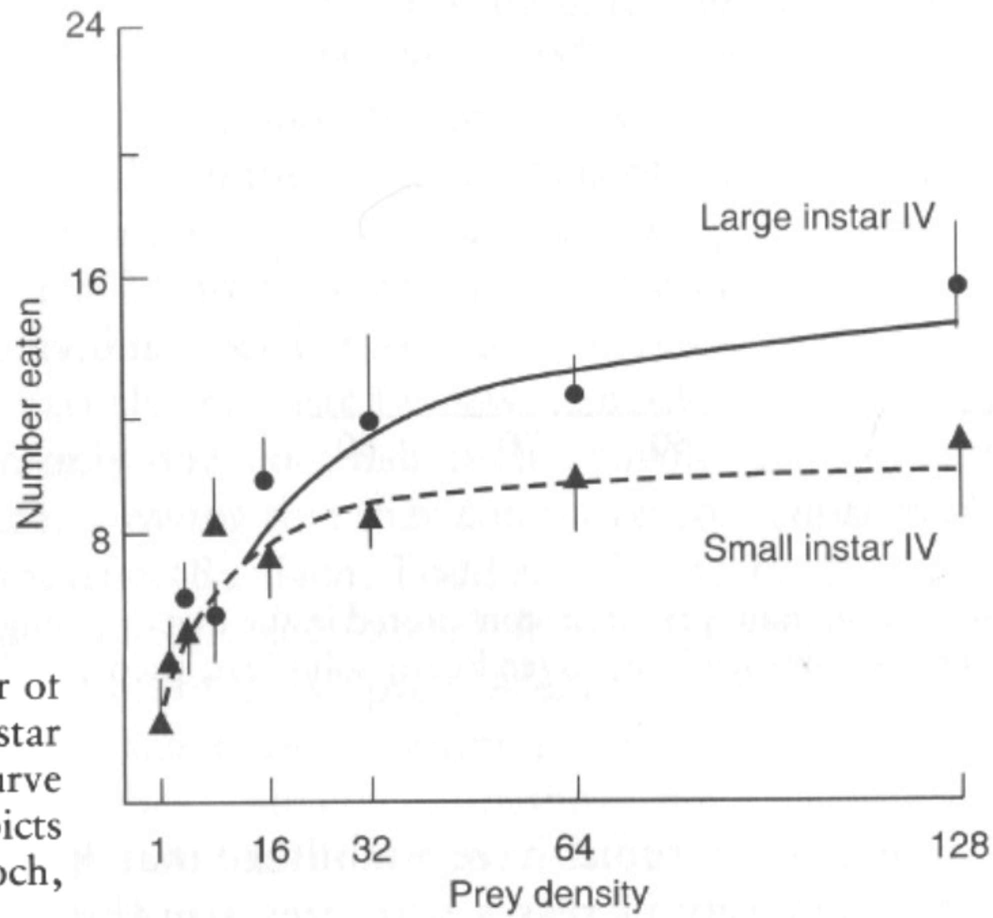
- small predators – narrow niche
- niche overlap highest when predator sizes strongly overlapped
- niche overlap decreased with increasing difference in predator size

FIGURE 9.8 Pair-wise dietary overlap among invertebrate predators as a function of differences in individual predator body size using mean log dry mass of pairs of predators among size classes within each species. See Figure 9.7 for species codes. (Reproduced from Woodward and Hildrew 2002a.)



Predation rate in invertebrates

- predation rate increases with
  - increasing prey density (functional response curve)
  - increasing predator size
- predation rate decreses
  - before emergence and molting
  - with satiation
  - with habitat complexity and presence of refuge
- little or no evidence for the role of learning and experience



(b) Number of mosquito larvae eaten in 3 h by a single IVth instar *Notonecta hoffmanni* (means ± 2 S.E.). Solid curve depicts large instar IV predators, broken line depicts small instar IV predators. (From Fox and Murdoch, 1978.)

Prey vulnerability

- mobility

  highly mobile prey (e.g., Baetis) is vulnerable to sit-and-wait predators

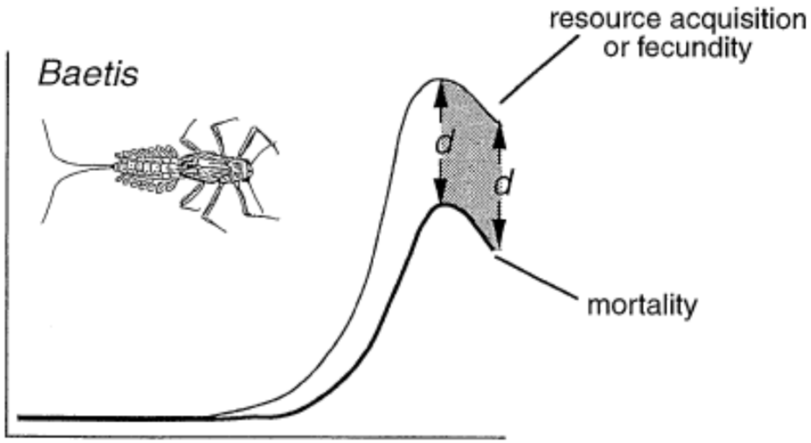
  but can escape from large searching predators (overestimation of predation rate in cage experiments)

- anti-predator adaptations
  - some reduce the likelihood of encounter
  - fixed – protective armor, nocturnal activity, case building
  - induced – escape after encounter, visual contact or smell perception

    – different habitat use (Gerridae, *Orconectes propinquus*)

- trade-off between minimizing predation risk and maximizing food aquisition

Alternative predator avoidance (Peckarsky 1996)



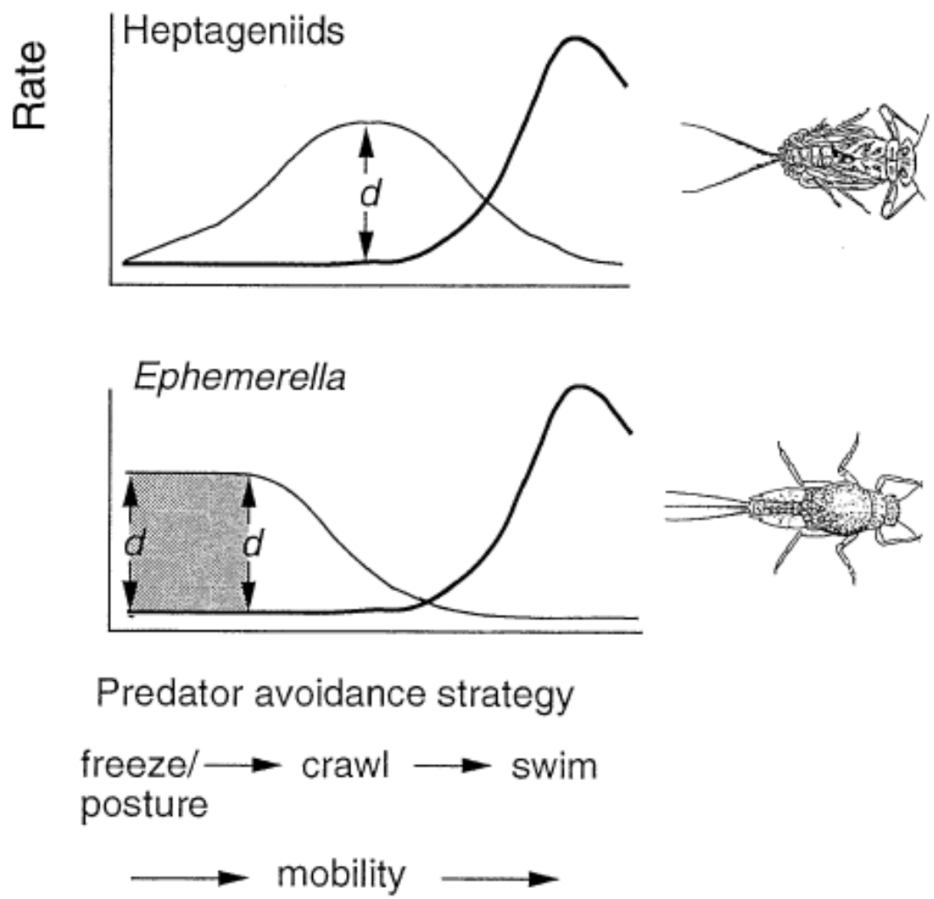


FIG. 7. Conceptual model contrasting changes in rates of mortality, resource acquisition, and fecundity of different mayfly species along an axis of increased prey mobility to avoid predation by stoneflies. Alternative predator avoidance syndromes of *Baetis* (upper), heptageniids (center), and *Ephemerella* (lower) illustrate different solutions to the evolutionary problem of foraging under risk of predation. Each predator avoidance syndrome maximizes fitness, represented as the difference (*d*) between rates of resource acquisition (and consequent fecundity) and mortality due to predation.

Effects of predation on prey populations

- inverse relationship between piscivores and their prey
- different relationships for invertivores
  - inverse correlation between fishes and invertebrate predators (Hildrew 1984)
  - no difference in invetebrate abundance between trout and troutless stream sections (Edwars 1986)
  - only *Baetis* abundances higher in troutless stream (Meissner & Muotka 2006)
  - manipulations of fish abundance using cages – different or no effect on invertebrate abundance
- total prey consumption by trout ~ all available production (Allan 1983, Huryn 1996)
- invertebrate predators usually consume less production than fish
- when fish absent, invertebrate predators consume all secondary production at lower trophic levels

Indirect effect on predation

- predator avoidance → reduction of fitness
- predator risk reduces foraging
  - *Baetis* and stoneflies with glued mouhtparts in microcosmos (Peckarsky et al. 1993)
- inducible life history shift
  - *Baetis* had faster maturation at smaller body size as reaction to trout odor (Peckarsky & McIntosh 1998)
- drift as anti-predatory adaptation

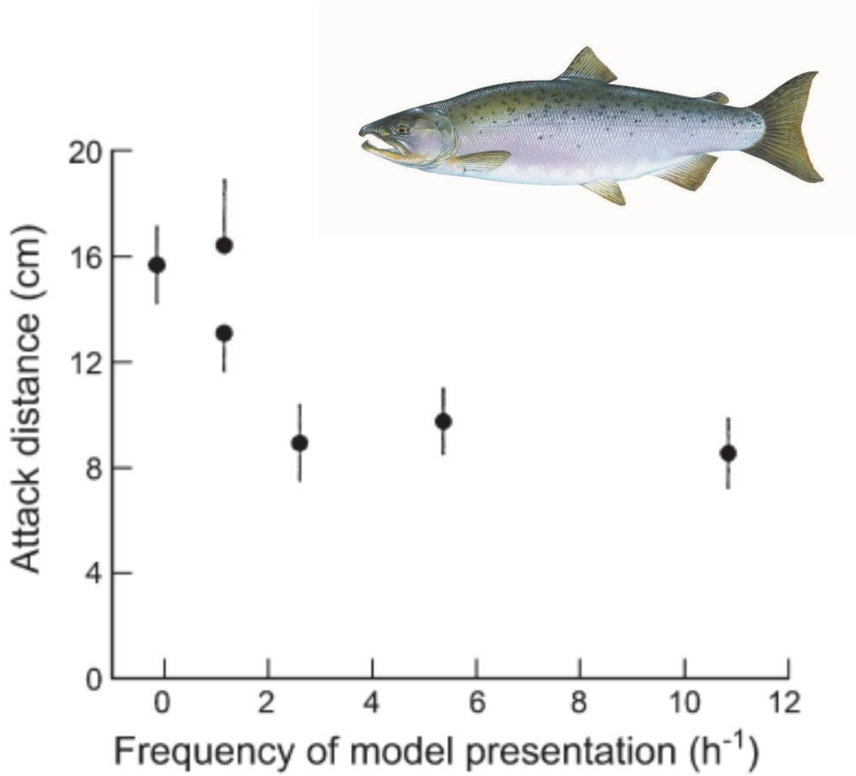


FIGURE 9.9 Attack distance of Coho salmon responding to medium-sized flies, as a function of frequency of presentation of a model rainbow trout. Values are means ±1 standard error. (Reproduced from Dill and Fraser 1984.)

Trophic cascades

- influence of top predator on the whole food web
- increase of algal abundance after reduction of grazers
- algal blooms in New Zealand streams after introduction of non-native trout which excluded weaker competitor fish of native fam. Galaxiidae (Huryn 1996, Townsend 2003)
- reduction of Lestidae → increase of Chironomidae → decrease of algae; fish removal → increase of algae
- suppression of cascade if modest predatory effect– e.g. trout feeds mainly on terrestrial insect infall (Nakano et al. 1999)

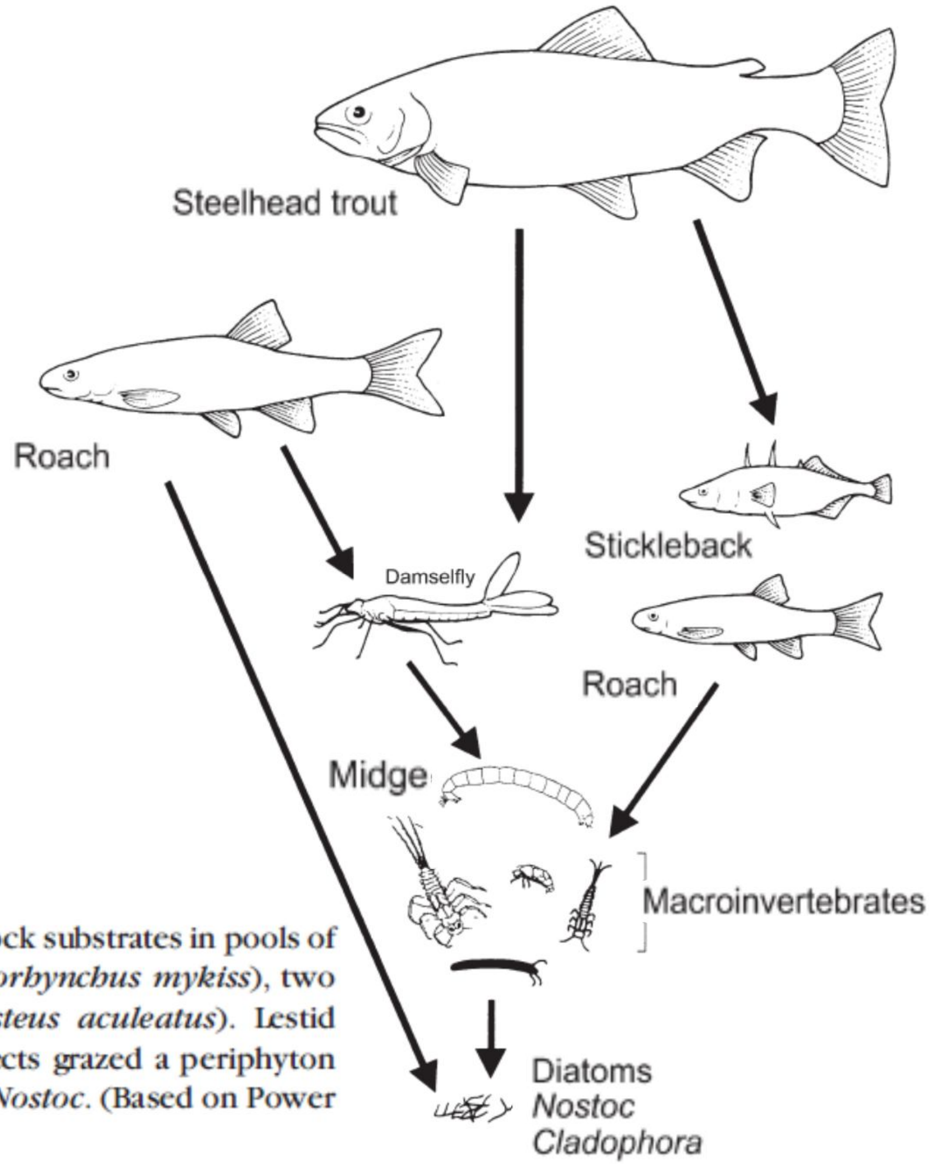


FIGURE 9.11 Trophic relations of dominant biota in and around algal turfs on boulder-bedrock substrates in pools of a California river during the summer low-flow period. Fishes include steelhead trout (*Oncorhynchus mykiss*), two size classes of the roach (*Hesperoleucas symmetricus*), and the stickleback (*Gasterosteus aculeatus*). Lestid damselflies fed on midge larvae and a number of other aquatic insects. In turn, these insects grazed a periphyton turf consisting of filamentous green algae (*Cladophora*), diatoms, and the cyanobacterium *Nostoc*. (Based on Power 1990.)

Predation as disturbance

- intermediate disturbance hypothesis
- equilibrium vs. non-equilibrium communities

Competition

- shared limited resources
- competition usually assymetrical
- exploitative competition
- interference competition – e.g. Simullidae vs. Blephariceridae, *Hydropsyche siltalai* (Englund 1993)
- diffuse competition
- **niche specialization**: habitat, dietary or temporal segregation (Schoener 1074)
- correlative studies, field and laboratory experiments
- many studies on algae indicate competition (for light and space)
- competition in filter feeders - Hydropsychidae
  - resource partitioning: food particle (Wallace et al. 1977), microhabitat (Hildrew & Edington 1979, longitudinal distribution (Lowe & Hauer 1999), life cycle (Mackay 1977)
  - but no evidence that food and space are limiting

Competition in grazers

- combination of exploitative and interference competition
- snails (Hill 1992)
- *Glossosoma* – dominant grazer, robust and slow
    - vs. Baetis (Kohler 1992)
    - collapse induced by microsporidian pathogen (Kohler & Wiley 1997)

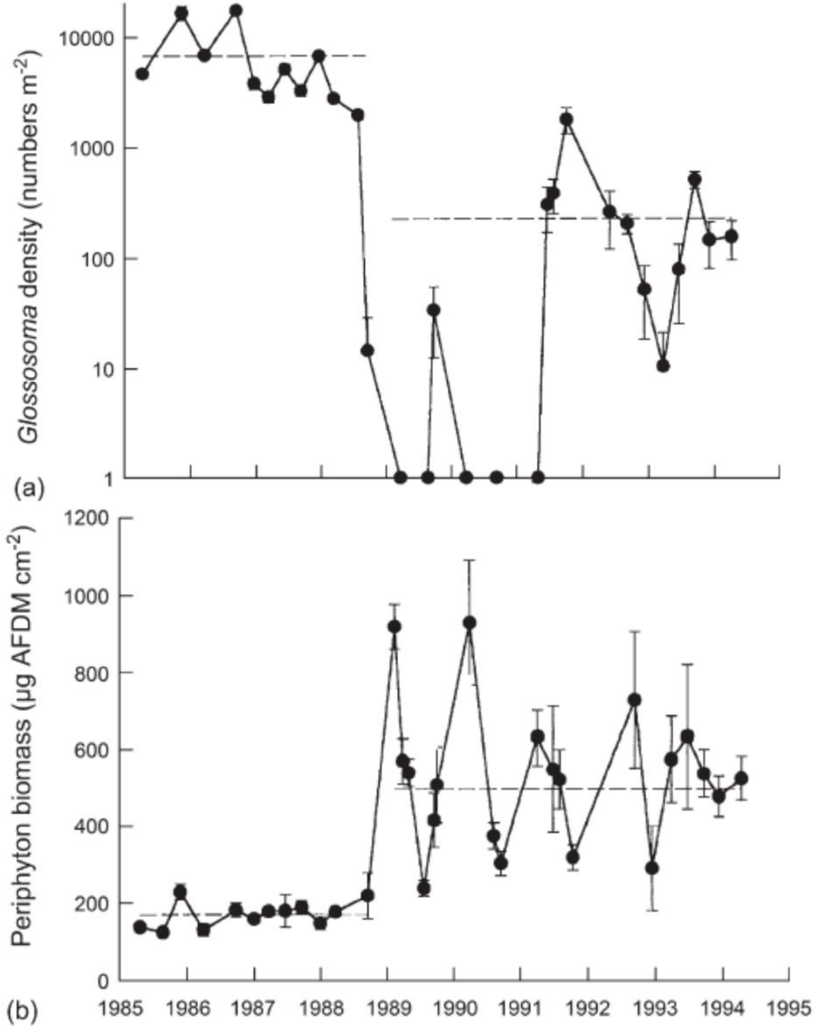


FIGURE 9.14 Density of *Glossosoma nigrior* (a) and biomass of periphyton (b) in Spring Brook, Michigan. Horizontal dashed lines are the overall mean density or biomass for the periods before and after *Glossosoma*'s collapse in 1988. Values are means + 1 SE. (Reproduced from Kohler and Wiley 1997.)

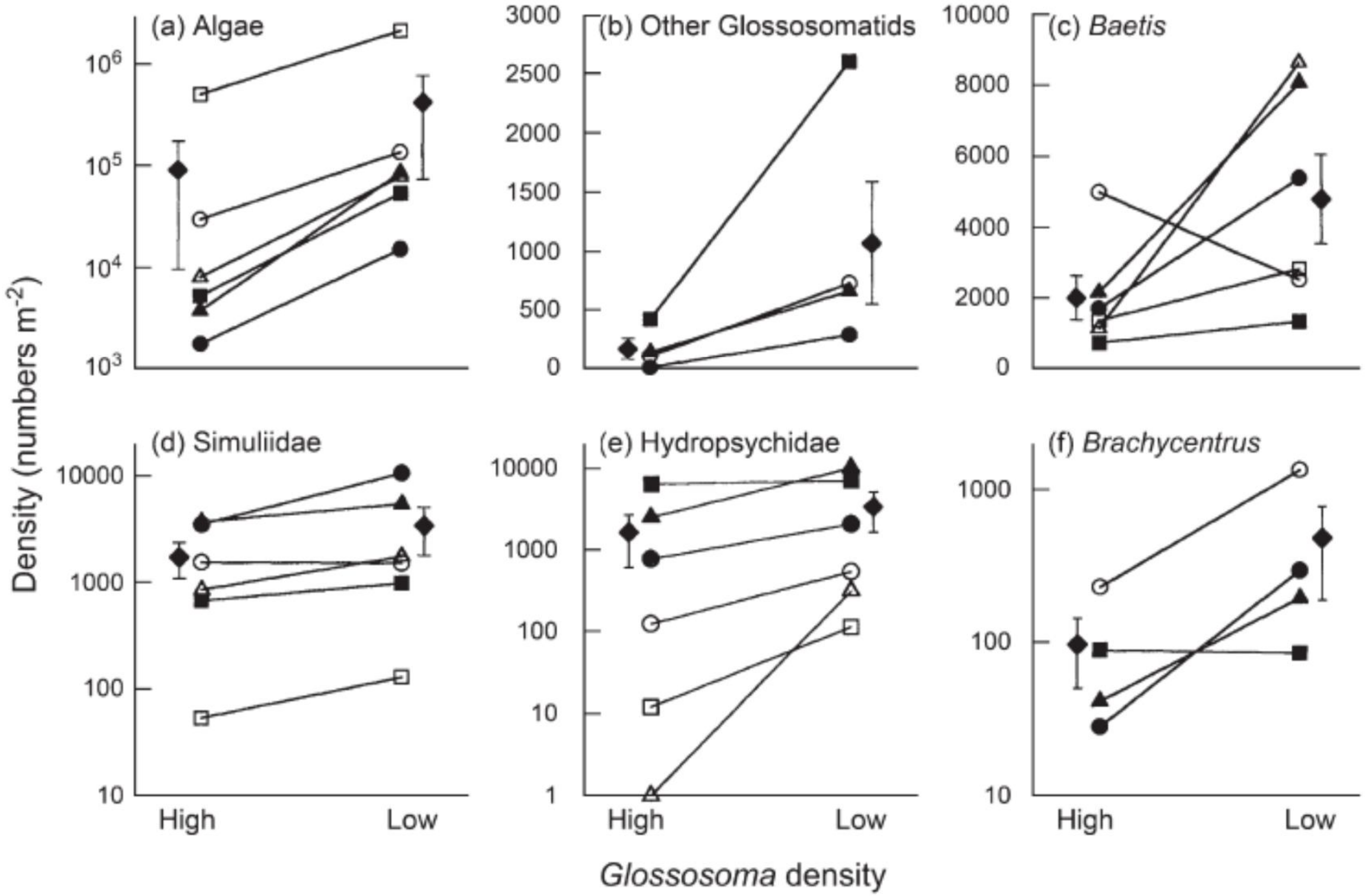


FIGURE 9.15 Mean abundances of periphyton (as algal cells cm^{-2}) (a), periphyton-grazing insects (b, c) and filter feeders (d–f) as a function of *Glossosoma* density (high, low = prior to or during recurrent pathogen outbreaks, respectively) in six streams from southwest and northern lower Michigan. Invertebrate densities are expressed as number of individuals per square meter. Symbols denote the six streams. (Reproduced from Kohler and Wiley 1997.)