Biol. Rev. (1997), **72**, *pp.* 349–364
Printed in the United Kingdom

THE TROPHIC ECOLOGY OF FRESHWATER *GAMMARUS* SPP. (CRUSTACEA: AMPHIPODA): PROBLEMS AND PERSPECTIVES CONCERNING THE FUNCTIONAL FEEDING GROUP CONCEPT

By CALUM MACNEIL, JAIMIE T. A. DICK and ROBERT W. ELWOOD

School of Biology and Biochemistry, The Queen's University of Belfast, Medical Biology Centre, 97 Lisburn Road, Belfast BT9 7BL, N. Ireland

(*Received* 4 *June* 1996; *revised* 4 *November* 1996; *accepted* 28 *November* 1996)

ABSTRACT

Gammarus spp. are widespread throughout a diverse range of freshwater habitats and can be the dominant part of many benthic macroinvertebrate assemblages, in terms of both numbers and/or biomass. Although the vast majority of studies have emphasized the herbivorous nature of *Gammarus* spp. and their 'shredder' functional feeding group (FFG) classification, we show that a far wider food base is exploited than has been previously acknowledged. This 'plasticity' as herbivore/predator is linked to the success of *Gammarus* spp. in persisting in and colonizing/invading disturbance-prone ecosystems. Intraguild predation and cannibalism are more common than previously realized. This behaviour appears to be a causal mechanism in many amphipod species replacements. Additionally, *Gammarus* spp. are major predators of other members of the macroinvertebrate community. Furthermore, while many studies have emphasized fish predation on *Gammarus* spp., we illustrate how this fish: amphipod, predator: prey interaction may be a two-way process, with *Gammarus* spp. themselves preying upon juvenile and wounded/trapped fish. We urge that a new realism be adopted towards the trophic ecology of *Gammarus* spp. and their role as predators and prey and that previously established FFG assumptions of both the food and the feeder be questioned critically.

Key words: Fish, freshwater, functional feeding group, *Gammarus* spp., macroinvertebrate, predation, shredder, trophic.

CONTENTS

I. INTRODUCTION

'Every species has its niche, its place in the grand scheme of things.'
(Paul Colinvaux, *Why Big Fierce Animals Are Rare*)

During the past two decades, a 'trophic' or 'functional' approach to studies of freshwater macroinvertebrate community structure has been increasingly emphasized, whereby taxa are assigned to a trophic or functional feeding group (FFG) based on their perceived dominant feeding mode. 'Scrapers' graze organic biofilms or 'aufwuchs' covering stones and plants, 'shredders' harvest allochthonous detritus and coarse particulate organic matter (CPOM, > 1 mm), sediment/deposit-feeding 'collector-gatherers' utilize fine and very fine particulate organic matter (FPOM, 50 μm–1 mm; VPOM, 0·05–50 μm), 'filterers' feed on suspended organic matter, 'herbivore shredders and piercers' feed on living macrophytes and, finally, 'predators' kill and eat members of other feeding groups (Cummins, 1973, 1974; Cummins & Klug, 1979; Merritt & Cummins, 1984). FFGs represent attempts to 'make the diversity of nature tractable to ecological analysis' (Duffy & Hay, 1994) and this trophic approach has been widely adopted by freshwater ecologists, allowing as it does some insight into energy flow and material cycling within ecosystems (Vannote *et al*., 1980). However, despite the fact that individual freshwater *Gammarus* species have been well studied as regards energy budgets (Mathews, 1967; Nilsson, 1974) and herbivorous diets (e.g. Barlöcher & Kendrick, 1973*a*, *b*; Moore, 1975; Willoughby & Sutcliffe, 1976; Marchant & Hynes, 1981; Chamier, Sutcliffe & Lishman, 1989), many investigations of the functional organization of benthic faunal assemblages have not advanced beyond a rigid reliance on a simple FFG designation of *Gammarus* spp. as shredders. This review examines this assumption critically in the light of accumulated ecological and behavioural evidence. We consider the role of *Gammarus* spp. as herbivores and carnivores, as well as predators and prey, operating in a diverse array of habitats. We attempt to form a rounded, coherent synthesis of the trophic ecology of this supposed 'shredder' to assess 'its [true] place in the grand scheme of things' (Colinvaux, 1980).

The crustacean sub-order Gammaridea comprises over 4500 species, that is, approximately 85 % of the order Amphipoda (Bousfield, 1973). In contrast to the three other amphipod sub-orders (the Hyperiidea, Ingolfiellidea and Caprellidea), which are highly specialized and ecologically restricted, the Gammaridea are widespread throughout a range of marine, freshwater and terrestrial habitats (Bousfield, 1973; Lincoln, 1979; Lincoln & Boxshall, 1987). The amphipod genus with the highest number of epigean freshwater species is *Gammarus*, which comprises over 100 freshwater species distributed widely throughout the northern hemisphere (Karaman & Pinkster, 1977). In freshwater ecosystems, abiotic factors such as temperature, salinity, oxygen, acidity and pollution influence the distribution of *Gammarus* species (Jeffries & Mills, 1990; Whitehurst & Lindsey, 1990). *Gammarus* spp. are often found in great abundance in or under any substratum that provides both shelter from predators and a supply of organic detritus and other foodstuffs, that is, under rocks, in gravel or coarse substrates and amongst living and dead vegetation (Fitter & Manuel, 1994). In many riverine communities, amphipod species such as *Gammarus pulex* (Linnaeus) can represent the dominant macroinvertebrate in terms of biomass, as in the Millstone Burn, Scotland, where Shaw (1979) and C. MacNeil (personal observation) found that *G. pulex* represented over 28 % and 38 %, respectively, of the total macroinvertebrate biomass.

II. THE FEEDING ECOLOGY OF *GAMMARUS*

In gammarids (= gammaridean amphipods), the third thoracic appendages, the gnathopods, are highly versatile limbs used for feeding, grooming, burrowing, agonistic encounters between males (Borowsky, 1984) and grasping females during amplexus/precopulatory pairing. In the laboratory, *Gammarus tigrinus* Sexton has been observed to use the gnathopods to carry strips of fish and to hold these strips up to the mandibles while feeding (C. MacNeil, personal observations). The mandibles are located lateral to the mouth and, in conjunction with the upper and lower lips, surround the mouth opening. The typical mandible consists of a strong chitinized incisor, a small accessory plate (the lacinia mobilis), a large medial molar and, in addition, a spine row between the molar and the lacinia. In the genus *Gammarus*, the molar is tough and ridged for crushing and grinding (Lincoln, 1979). Thus, the feeding apparatus of *Gammarus* spp. is clearly capable of coping with a wide variety of foodstuffs.

Evidence for a herbivorous lifestyle in freshwater *Gammarus* spp. comes from a variety of sources. *Gammarus pulex* is reported to sustain itself on decaying allochthonous leaf litter and its encumbent microbial community (Embody, 1911; Mottram, 1933; Hargrave, 1970; Barlöcher and Kendrick, 1973*a*, *b*; Cummins *et al.*, 1973; Moore, 1975; Marchant & Hynes, 1981; Barlöcher, 1982; Chamier *et al.*, 1989). Morphological studies of *G. pulex* gut structure indicate that plant material is digested in the foregut and fungi are digested in the hindgut (Agrawal, 1965), using enzymes identified as cellulases (Monk, 1977; Chamier & Willoughby, 1986; Chamier, 1991). In addition, the frequently observed congregations of *G. pulex* in leaf packs/accumulations of autumn shed leaves (Gee, 1982) and the apparent subjection of *G. pulex* populations to food limitation upon dissipation of the initial autumnal pulse of leaf litter (Gee, 1988), have been cited as evidence of a primarily herbivorous existence.

Cummins (1973, 1974) and Cummins & Klug (1979) adopted an FFG (functional feeding group) approach to the perceived dominant feeding modes of freshwater macroinvertebrates, which encompasses assessment of morpho-behavioural adaptations, feeding methods, food particle size and food quality (see also Vannote *et al.*, 1980). This approach designates amphipods as shredders or facultative shredder-collectors (Cummins & Klug, 1979). In this FFG role, *Gammarus* spp. are regarded as major riverine processors or shredders of large amounts of coarse particulate organic matter such as leaf litter (Willoughby & Sutcliffe, 1976; Jenio, 1980; Herbst, 1982; Rosset, Barlöcher & Oertli, 1982; Griffith, Perry & Perry, 1994). *Gammarus pulex* and *Gammarus pseudolimnaeus* Bousfield reportedly processed up to 13% and 16% respectively of total litter input into low order (i.e. headstreams and tributaries) British and Canadian river systems (Mathews, 1967; Marchant & Hynes, 1981).

Not all leaves, however, are used easily as a food source. Cameron & LaPoint (1978) found that tannins in Chinese tallow (*Sapium sebiferum*: Euphorbiaceae) leaves greatly inhibited feeding in *Crangonyx shoemakeri* (Hubricht & Mackin), which is a member of the Crangonyctidae family closely related to the Gammaridae. Furthermore, C. MacNeil (personal observation) found that *Gammarus pulex* had a very low shredding capacity (only $2{\cdot}6 \times 10^{-4} \pm 5 \times 10^{-5}$ grams of leaf per 20 large *G. pulex* per day; mean $\pm$ s.e., $N = 10$) for oak *Quercus robur* (Linnaeus) litter that has both high lignin and tannin levels. Indeed, there is a 'processing continuum' or a hierarchy of leaf palatability for gammarids, in which leaves with high lignin and tannin levels, such as oak and beech, rank lower than softer, low tannin-level elm and maple leaves (Kaushik & Hynes, 1971; Petesen & Cummins, 1974; Malicky, 1990). In addition, Barlöcher & Kendrick (1973*a*, *b*) found that fungi influenced leaf palatability and were crucial modifiers of leaf material for *G. pulex* (Graca, Maltby & Calow, 1993, 1994). In feeding tests, the youngest stream-conditioned leaves with the highest viable fungal and bacterial densities invariably were preferred to older, more sterile specimens (Kostalos & Seymour, 1976; Barlöcher, 1990; Sridhar & Barlöcher, 1993).

The FFG shredder designation, however, is problematic, with the dilemma of whether it is the food or the feeder being categorized, resulting in macroinvertebrates such as amphipods being 'reluctantly forced' into FFGs (King *et al.*, 1988). As well as amphipods, difficulties have been experienced in assigning realistic FFGs to Plecoptera, Ephemeroptera and Trichoptera, with considerations of changing life-history strategies, the physical mechanisms of feeding and differing proportions of resources available all 'blurring' final FFG assignments (Wallace, Woodall & Sherberger, 1970; Short, Canton & Ward, 1980; Hawkins, Murphy & Anderson, 1982; Bunn, Edward & Loneragan, 1986; Chessman, 1986; King *et al.*, 1988; C. MacNeil, personal observations). For example, the physical feeding action on leaf material is highly age/body-size dependent (Feminella & Stewart, 1986). This is evident in Baetidae mayflies, commonly regarded as 'typical' collector-gatherers/scrapers (Cummins, 1973; Cummins & Klug, 1979) and also in Leuctridae stoneflies, which, like *Gammarus* spp., are also regarded as 'typical' shredders, with species such as *Leuctra hippopus* (Kempny) feeding as shredders when adult but as collector-gatherers when juvenile (Hildrew, Townsend & Henderson, 1980; Dobson & Hildrew, 1992; A. G. Hildrew, personal communication). Mouthpart specialization does not always mean obligate resource utilization (Minshall, 1988; Mihuc & Minshall, 1995) and, in reality, the mouthparts of such ephemeropteran and plecopteran families can cater for a wide range of food categories, ranging from CPOM such as leaf litter to aufwuchs and FPOM (Hawkins *et al.*, 1982; Chessman, 1986). The actual feeding methods reflect such ambiguities in that many Plecoptera do not 'shred' leaves but rather scrape away soft epidermal tissue (Wallace *et al.*, 1970; Short *et al.*, 1980). CPOM may ultimately be degraded by these methods, such that these macroinvertebrates are still termed shredders or rather 'micro-shredders' or 'skeletonizers' (King *et al.*, 1988). However, by such criteria, many ephemeropteran scrapers can also legitimately be termed shredders as they utilize CPOM in similar ways (Anderson & Sedell, 1979). Cummins (1973) also recognized that the study of aquatic macroinvertebrate feeding 'has been characterized by preoccupation with mature representatives'. To compensate for such difficulties, some studies (Hildrew *et al.*, 1980; Dobson & Hildrew, 1992) have arbitrarily divided *Leuctra* spp. and *Gammarus pulex* samples into 'large' (i.e. shredders) and 'small' (i.e. collectors) individuals when considering FFG designations. Such divisions may hamper legitimate distinctions being drawn between riverine assemblages of shredders and other groups based on the FFG concept. Friberg & Jacobsen (1994) argue that the 'feeding plasticity of detritivore-shredders is much greater than traditionally supposed', in that *Gammarus* spp. can eat fresh aquatic plant material as well as leaf litter. Marine trophic research (Duffy & Hay, 1991) also finds that designation of amphipods into FFGs based on feeding apparatus is too restrictive, when in reality there exist 'diverse feeding habits among herbivorous amphipods' (Duffy & Hay, 1994). Such herbivorous plasticity has been reflected in the apparent resource partitioning observed by Zimmerman, Gibson & Harrington (1979), who found four Florida lagoon gammarids, *Gammarus mucronatus* Say, *Cymadusa compta* (Smith), *Melita nitida* Smith and *Grandidierella bonnieroides* Stephenson, capable of using macro- and microphagous feeding modes to consume marine plant material ranging in size from large seagrass fragments to fine particle detritus. Many other studies have cited *Gammarus* spp. as capable of feeding on algae (Barlöcher & Kendrick, 1973*b*, 1975; Nilsson, 1974; Moore, 1975; Van Dolah, 1978; Anderson & Sedell, 1979; Willoughby, 1983; Moss, 1988; Aliyev, 1991; Steele & Whittick, 1991). Even in the FFG mode, algae and aufwuchs may both be just as legitimately 'shreddable' as leaf litter (Hawkins *et al*., 1982; Barlöcher & Murdoch, 1989). Hynes (1954) reports *Gammarus lacustris* Sars even destroying gill-nets and the bottoms of wooden fishing boats. Indeed, apart from cellulases, *Gammarus* spp. contain large amounts of amylases capable of digesting substantial quantities of a wide variety of detritus (Barlöcher & Howatt, 1986; Borowsky & Guarna, 1989). It has been hypothesized that released digestive amylases may play a role external to the amphipod, either in the predigestion of food or as an aid in locating food (Guarna & Borowsky, 1993). In addition, as Allan & Malmqvist (1989) found using traps baited with cheese, *Gammarus* spp. are not just attracted by plant material. Friberg & Jacobsen (1994) suggest three reasons for *Gammarus* spp. feeding plasticity. First, being highly mobile, individuals can move from unattractive to attractive food easily. Second, they speculate that *G. pulex* mouthparts are not adapted to handling some hard food items (citing Willer, 1922). Third, *Gammarus* spp. possess high respiration rates (Nilsson, 1974) such that, energetically speaking, individuals cannot afford to eat either difficult-to-handle material or food with low calorific value.

A number of authors have recently questioned the supposed herbivorous diets of gammarids. Schwartz (1992) complains that research on amphipod nutrition 'continues to be conducted with the assumption that amphipods feed only on decaying allochthonous material and fungi growing on such material'. Gee (1988) cited the apparent linkage between *Gammarus pulex* population dynamics and litter input/dissipation as good evidence of *Gammarus* herbivory. However, this cause-and-effect interpretation may be spurious if, for example, this reduction in allochthonous material is associated with reductions in populations of other macroinvertebrate species upon which *Gammarus* spp. prey (Dick, 1992). Indeed, one of the very few studies on *Gammarus* spp. gut contents found a high prevalence of animal material in both *Gammarus duebeni* Liljeborg and *G. pulex* from a variety of habitats in the Isle of Man (Hynes, 1954). Minshall (1967) noted that the indigenous population of *Gammarus minus* Say of Morgan's Creek, Kentucky, USA 'probably eats anything that is available' and, in reality, distinctions between FFGs remain arbitrary because the majority of macroinvertebrates are 'opportunistic generalists' or 'selective omnivores', feeding in direct proportion to the amount and quality of food available locally (Slack, 1936; Jones, 1949; Barnes, 1980; Gee, 1982).

Within the order Amphipoda, herbivory is merely one of a diverse array of feeding modes ranging from ectoparasitism (Stock, 1977), filter-feeding (Holsinger & Langley, 1980; Blinn & Johnson, 1982), carnivory (Kozhov, 1963) and even coprophagy (Minckley, 1963). Keith (1969) found that skeleton shrimps (Caprellidae) had a diverse diet ranging from diatoms and carrion to live prey. These traits may also be found in *Gammarus* spp. Many authors cite *Gammarus* species as carrion feeders (Embody, 1911; Hynes, 1954; Kinne, 1959; Kozhov, 1963; Willoughby & Sutcliffe, 1976; Brown & Diamond, 1984) and Schwartz (1992) argues that other freshwater gammarids such as *Crangonyx shoemakeri* are 'at least facultatively predacious'. LeRoux (1933) used chopped earthworm to rear laboratory populations of gammarids, Oseid & Smith (1979) used dead fish as well as leaves to rear *Gammarus pseudolimnaeus* and Vassallo & Steele (1980) found that flesh supplements to an algal diet accelerated growth and maturation in *Gammarus lawrencianus* Bousfield. Delong, Summer & Thorp (1993) found that *Gammarus fasciatus* Say supplemented its leaf diet with dead chironomids. These latter authors argued that a diverse potential food base benefits riverine populations by allowing exploitation of seasonal changes in abundance of specific foods. In disturbance-prone ecosystems such as rivers, with their inherent 'feast and famine' resource conditions, invertebrates invariably switch between foods as they become available (Koslucher & Minshall, 1973; Kostalos & Seymour, 1976; Short, 1983). Ultimately, the ability to assimilate a 'diverse suite' of foods must contribute to the ability of the gammarids to persist in and colonize new and variable habitats (Schwartz, 1992). Indeed, Conlan (1994) provides numerous examples of how amphipods are themselves major creators of environmental disturbance by their exploitation of a variety of disparate food resources, arguing that large-scale destruction/alteration of food/physical resources by amphipods can affect the whole aquatic community.

III. CANNIBALISM AND INTRAGUILD PREDATION

Hunte & Myers (1983) note that cannibalism (i.e. the capturing, killing and devouring of an animal by a conspecific) has been reported in over 1300 animal species but 'has been viewed as an aberrant and occasional phenomenon' in orders such as the Amphipoda. Culver & Fong (1991), in their study of cave-dwelling amphipods, warn that 'a diversity of interactions may be lurking in apparently monotonous detritivore communities' and gammaridean cannibalism has been reported in many laboratory studies (Sexton, 1924, 1928; Clemens, 1950; Jones, 1951; Schmitz, 1967; Kostalos & Seymour, 1976; Jenio, 1980; Dick, 1995). Indeed, Jenio (1979) noted with surprise that when cannibalism commenced in *Gammarus minus pinicollis* Cole '...elm leaves (their preferred culture food source) were ignored'. Meijering (1972) found male predation on females in mixed species precopula pairs of *Gammarus pulex* and *Gammarus fossarum* Koch. Minshall (1967) found cannibalism in *Gammarus minus* in Morgan's Creek, Kentucky, USA and Jenio (1979, 1980) observed that *G. minus pinicollis* was both the most voracious of three sympatric *Gammarus* species in Elm Spring, Illinois, USA and the most abundant by over a factor of two compared to *Gammarus pseudolimnaeus* and *Gammarus troglophilus* Hubricht and Mackin. Both cannibalism and interspecific predation on injured, diseased and dead Elm Spring *Gammarus* spp. were observed, with Jenio (1979) concluding that cannibalism 'might turn out to be widespread with freshwater gammarids as more data become available'. Cannibalism of juveniles by adults is common in amphipods (e.g. Steele & Steele, 1969; Dennert, 1974; Kostalos & Seymour, 1976; Pinkster, Smit & Brandse-De Jong, 1977; Skadsheim, 1984; Dick, Montgomery & Elwood, 1993; Dick, 1995). Hunte & Myers (1983) even suggest that 'cannibalism may be an important agent of selection in the evolution of life histories', showing that changes in the phototactic behaviour of juveniles of three estuarine gammarid species, *Gammarus lawrencianus*, *Gammarus tigrinus* and *Gammarus mucronatus* coincided with juveniles becoming less vulnerable to cannibalism by adults (Hunte & Myers, 1984).

Within crustacean populations, the largest individuals are often the most dominant, aggressive and superior competitors (Bovbjerg, 1956; Lee & Fielder, 1983). Ward (1985), for example, found that large male *Gammarus duebeni* gain advantage over smaller males in aggressive interactions during the breeding season. This advantage in size often predisposes the cannibalism of smaller by larger individuals (e.g. Dick, 1995). Such cannibalism may, in turn, predispose individuals of one species towards the killing and eating of individuals of other species, particularly congenerics and/or members of the same ecological guild (see Polis, Myers & Holt, 1989 and below). Goedmakers & Roux (1975), for example, examining mixed species pairs of *Gammarus fossarum* Koch, *Gammarus wautieri* Roux and *Gammarus gauthieri* Karaman, found that females of some larger species consumed males of smaller species. The devouring of the gammarid *Crangonyx pseudogracilis* Bousfield (juvenile and adult forms) by the much larger *Gammarus pulex*, *Gammarus duebeni celticus* Stock and Pinkster and *Gammarus tigrinus* has also been identified and investigated (Dick, 1996). In addition, the vulnerability of individual *Gammarus* spp. at moult may allow predation on equally sized or even larger species, for example, predation by *G. tigrinus* on the larger *G. pulex* and *G. duebeni celticus* (Dick, 1996; Dick & Platvoet, 1996). Coupled with this, any one species may be inherently more aggressive than another, leading to smaller individuals killing heterotrospecifics (Dick, Elwood & Montgomery, 1995).

Predation such as that described above has been termed 'intraguild predation' or 'IGP' (Polis *et al.*, 1989), defined as predation occurring between potentially competing species that exploit the same class of environmental resources, regardless of different foraging strategies, and thus belonging to the same ecological 'guild' (Root, 1967; Colinvaux, 1986; Lincoln & Boxshall, 1987; Dick, 1992). Such IGP, together with cannibalism and interspecific competition, has been quantified and compared, producing evidence that this behaviour has wide-ranging community consequences, particularly in respect to species exclusions and replacements (Dick, Elwood & Irvine, 1990*a*; Dick, Irvine & Elwood, 1990*b*; Dick, 1992; Dick *et al.*, 1993).

Crustaceans face increased risks of predation during and shortly after the vulnerable moulting period, since moulted individuals are very soft, relatively inactive and thus easily victimized (Embody, 1911; Willoughby & Sutcliffe, 1976; Jenio, 1979, 1980; Ward, 1985; Dick *et al.*, 1990; Dick, 1992). In addition, water conductivities, with their ionic influence on the physiology of crustacean moult, influence the predatory interactions between *Gammarus* species (Dick & Platvoet, 1996). The expulsion of the indigenous *Gammarus duebeni celticus* from its niche by the apparently 'competitively superior' *Gammarus pulex* has been well documented (Pinkster *et al.*, 1970; Dennert, 1974; Strange & Glass, 1979). Dick (1992) and Dick *et al.* (1993), investigating the interactions underpinning this replacement, found that newly moulted females of both species are preyed upon heavily by congeneric males, but that significantly more *G. d. celticus* females are devoured by *G. pulex* males than in the reciprocal interaction. Coupled with this, 'clumping' feeding frenzies on congenerics can result in higher frequencies of congeneric predation on *G. d. celticus* females than on *G. pulex* females. The superior ability of *G. pulex* both to resist predation and to prey on moulted *G. d. celticus* results in an asymmetry of impact on populations of the two species. This perhaps constitutes the 'driving force' behind the ousting of *G. d. celticus* from many of its Irish and other European rivers by incursions of *G. pulex* (Dick, 1992, 1996; Dick *et al.*, 1993). Also in Ireland, the apparent segregation of *G. tigrinus* to the centre of Lough Neagh, with *G. d. celticus* greatly dominant in near-shore areas, could be the result of similar interactions occurring within changing habitat templets (i.e. changing physiochemical regimes that may moderate competitive/predatory interactions). Dick *et al.* (1993) put forward a model incorporating cannibalism, mutual predation and resource competition. This model indicates that, although cannibalism in the absence of predation may actually promote co-existence, cannibalism coinciding with predation of equal or greater magnitude results in rapid species eliminations and replacement. This may be a widespread phenomenon in amphipods and other taxa. Clearly, these reports of voracious cannibalism and intraguild predation do not fit well with the FFG image of *Gammarus* spp. as a somewhat passive shredder/detritivorous omnivore. Indeed, this FFG image is still stifling acceptance of research in the area of *Gammarus* spp. predation, because the fallacy of *Gammarus* spp. as almost totally reliant on allochthonous detritus and vegetation continues to be perpetuated in the literature.

IV. *GAMMARUS* AS PREDATORS OF OTHER TAXA

Gammarids are also predators of other invertebrate groups (Clemens, 1950; Forsman, 1951; Hynes, 1954; Borovitskaya, 1956; Martin, 1960; Fries & Tesch, 1965; Lubyanov & Zubchenko, 1970; Anderson & Raasveldt, 1974; Bengtsson, 1982). In particular, *Gammarus* spp. predation on members of the Isopoda is well reported (e.g. Fries & Tesch, 1965; Minshall, 1967; Williams & Moore, 1985). Oseid & Smith (1979) found exposure of *Asellus communis* to *Gammarus pseudolimnaeus* results in 'virtual elimination of the former by the latter'. Exudates of *Asellus aquaticus* (Linnaeus) trigger aggregative 'clumping' feeding-frenzy behaviour in *Gammarus pulex*, even without the physical presence of the isopod (Bengtsson, 1982). The isopod normally actively avoids *G. pulex via* chemotaxic mechanisms. Similar predation on an isopod has been noted in the cave-dwelling *Gammarus minus* (Culver & Fong, 1991). There is considerable niche overlap between *G. pulex* and *A. aquaticus* (Graca *et al.*, 1994) but Williams & Moore (1985) showed that the isopod is more important to the gammarid as prey than as a serious competitor. However, Oseid & Smith (1979) found that increasing cyanide pollution gradually shifts the competitive advantage from the aggressive *G. pseudolimnaeus* to the more passive *A. communis*, until, in extremely polluted areas, *G. pseudolimnaeus* is unable to compete with, let alone prey upon, the more resistant *A. communis*. This pollution-mediated amphipod:isopod predatory/competitive interaction has been exploited by Whitehurst (1988) and Whitehurst & Lindsey (1990), who found that the *Gammarus*:*Asellus* ratio is highly sensitive to organic pollution levels and could be employed as a monitoring tool of water quality.

The predatory repertoire of *Gammarus* spp. is often large, including chironomids (Jones, 1951; Minshall, 1967; Delong *et al.*, 1993; C. MacNeil, personal observations), baetine mayflies and trichopterans (Minshall, 1967), plecopterans (Hynes, 1954), annelids (Dick, 1992) and cladocerans (Hutchinson, 1937). Kortelainen (1991) found that *Gammarus lacustris* reduced the numbers of a cladoceran *Sida* sp. and a copepod *Eudiaptomus* sp. in a subarctic pond. Schwartz (1992) found that *Crangonyx shoemakeri* consumed mosquito larvae and a constant quantity of *Daphnia obtusa* Kurz, even over a 64-fold range of detritus availability, emphasizing the consistent predation pressure amphipods exert in ponds and pools. These predatory amphipods, which are particularly common in shallow woodland pools lacking vertebrate predators, therefore have the potential to regulate the density of their prey. A similar potential for *Gammarus* spp. to regulate prey populations has been found by Anderson & Raasveldt (1974) in certain North American lakes, where densities of zooplankton populations corresponded closely to variations in abundance of *Gammarus lacustris lacustris* Sars. Habitats lacking vertebrate predators may have amphipods as part of the plankton instead of their usual benthic habit (Hutchinson, 1937; Blinn & Johnson, 1982). Therefore, it is possible that macroinvertebrate prey experience a relatively constant predation pressure regardless of fluctuations in fish predation, because predatory gammarids exert a 'buffering' effect on prey community dynamics. Indeed, Roberts (1995), observing the predatory behaviour of *Gammarus duebeni* under laboratory conditions, found that they killed 4–8 mosquito larvae 24 h^{-1}, 'often killing larvae when not hungry'. He argues that predatory crustaceans could be successfully harnessed as effective biocontrols of salt-marsh mosquito larvae in preference to the use of toxic chemicals, and advocates enhancing their breeding and even release to control mosquito pests.

As well as being noted scavengers of dead vertebrates, principally fish (Kozhov, 1963), amphipods may also be active predators of vertebrates in marine and freshwaters. Although the importance of gammarids as fish food has long been stressed (Mottram, 1933; Hynes, 1956; Degani *et al.*, 1987; Ade, 1989; Andersen *et al.*, 1993; Friberg *et al.*, 1994), fish: amphipod predatory interactions are not exclusively one-way. Williamson (1950), for example, reports the hyperiid *Themisto* (= *Parathemisto*) *gracilipes* Norman eating part of the body wall of a live 7 mm post-larval fish and Logachev & Mordinov (1979) found gammarids feeding on round goby larvae *Neogobius melanostomus*. Similarly, Fries & Tesch (1965) report *Gammarus tigrinus* attacking guppies, *Lebistes reticulatus* and tadpoles, although both vertebrates were too large and active to be either seriously wounded or devoured. Pinkster *et al.* (1977) and Vader & Ramppainen (1985) report *Gammarus* spp. attacking fish trapped in nets. *G. tigrinus* has been observed attacking netted fish in Lough Neagh, N. Ireland (H. B. N. Hynes, personal communication; J. T. A. Dick & C. MacNeil, personal observations). In contrast to the difficulties that active prey present, fish eggs represent a rich static food source to amphipods. Brown & Diamond (1984), for example, found *Gammarus pulex* eating rainbow trout *Salmo gairdneri* Richardson eggs in the field.

These wide-ranging reports of *Gammarus* spp. and other amphipods as active predators of other macroinvertebrate and indeed vertebrate groups contradict with assigned FFGs, which designate them trophic roles as herbivorous shredders or, at best, generalist omnivores. The full role of gammarids in influencing community structure will only be clarified when the fallacy of applying a single rigid FFG designation is revised in the light of such reports.

V. CONCLUSIONS

(1) This review illustrates how *Gammarus* spp., typically viewed as archetypal shredders, utilize a much greater range of food resources than just allochthonous leaf material and its encumbent microbial community. These resources may be highly transitory in disturbance-prone aquatic ecosystems such as rivers, where stochastic and deterministic forces may be interacting constantly along very different spatial and temporal scales (Stanford & Ward, 1983; Hildrew & Townsend, 1987).

(2) Although *Gammarus* spp. are widely acknowledged as important fish food (e.g. Mottram, 1933; Degani *et al.*, 1987; Ade, 1989; Andersen *et al.*, 1993), we have shown that such vertebrate: gammarid predatory interactions are not exclusively one-way. Cannibalism, intra- and interguild predation are also at work and these can lead to species replacements and thus large-scale community change.

(3) Future work should not be 'strait-jacketed' into accepting only one established functional role for *Gammarus* spp. and, indeed, other macroinvertebrate genera in the community or assemblage being studied. Concepts such as the FFG are admittedly superficially attractive because 'stereotyping a species by classifying its feeding behaviour fits comfortably with a natural desire to name or label organisms' (Gerking, 1994). However, this invariably presents the dilemma of whether it is the assumed food or the feeder being assigned, with the result that some studies have reluctantly 'forced' taxa into FFGs (e.g. King *et al.*, 1988). Thus, in many cases, 'functional feeding groups' may actually be 'fictional feeding groups'! A compromise in accounting for all of these often contradictory considerations is the use of joint-assignments of FFGs to certain 'problem' taxa such as *Gammarus*; however, this serves only to blunt the sensitivity in detecting any differences in functional or trophic organization of assemblages between habitats, which defeats the principal purpose of the FFG concept (King *et al.*, 1988). Friberg & Jacobsen (1994) argue that the FFG concept should not be applied 'too rigorously' and indeed, Mihuc & Minshall (1995) note 'the prevalence of generalist trophic function among benthic macroinvertebrates' and that FFGs should not be used as 'trophic guilds'. Consequently, they conclude that the concept 'should be used with caution to infer systems-level trophic dynamics in streams (e.g. system autotrophy or heterotrophy derived from scraper or shredder abundance or biomass)'. Such strong reservations call into question the whole purpose of the FFG concept. Perhaps unsurprisingly, workers studying the feeding of other animals, such as fish, are reaching similar conclusions. Gerking (1994) argues that 'what the fish should be eating should be cast aside and in its place researchers must accept gracefully what they are eating' and therefore 'the notion of broad trophic adaptability should be adopted'. Trophic classifications such as the FFG concept, when applied to potentially omnivorous macroinvertebrates such as gammarids, should thus be treated with great caution, otherwise they mislead and oversimplify our understanding of riverine ecosystem processes. Indeed, unless precautions are taken, much otherwise valid and worthwhile freshwater research may be marred. Strict adherence to FFG designations, regardless of changing habitat templets, may establish erroneous linkages between macroinvertebrate assemblage composition and implied food resources. Therefore, we argue that designations of FFGs to potentially omnivorous groups such as amphipods must reflect both the versatility and transitory nature of dominant feeding modes. Thus, *Gammarus* spp. may be mainly shredders in one habitat in one season, collector-gatherers in the same habitat in a different season, mainly predators in a third ecosystem and probably generalist-detritivores under many more habitat templets.

(4) To accompany trophic studies we recommend widespread adoption of gut dissection of *Gammarus* and other taxa at the locality being studied and at the time in question (e.g. Jones, 1951; Hynes, 1954; Barmuta, 1989; Dittrich, 1992; Dobson & Hildrew, 1992). If this is coupled with laboratory observations of macroinvertebrate feeding behaviour on possible food sources collected from the same locality, this may

ascertain what is actually eaten and by what method by the amphipod or macroinvertebrate in question, and not what is assumed it should be eating. Only then, and regardless of established FFG designations, can one make a realistic attempt at assessing a species' true dominant feeding mode and 'its place in the grand scheme of things' (Colinvaux, 1980).

VI. ACKNOWLEDGEMENTS

This study was undertaken during a Department of Education for Northern Ireland (D.E.N.I.) Research Studentship awarded to C. MacNeil. J. T. A. Dick acknowledges support under the Natural Environment Research Council (N.E.R.C.) Fellowship scheme. Thanks to the anonymous referee whose comments greatly improved this manuscript. Many thanks are due to Mike Jeffries, Chris Gibbons, David Turnbull, Sandy Milner, Jimmy Nail, Scott Mathieson, Peter Beardsley, Sam Felinus, Terry Clough and Alan Hildrew who have all, knowingly or unknowingly, shaped my (C. MacNeil) ideas on freshwater ecology over recent years. Thanks also to Andy Bridge, Johnny 'P' Prenter, Gillian Bell, Sarah Faloon and Ian Montgomery for creating an encouragingly nonchalant laboratory atmosphere in which to work.

VII. REFERENCES

Ade, R. (1989). *The Trout and Salmon Handbook. A Guide to the Wild Fish*. Blackwell, Oxford.

Agrawal, V. P. (1965). Feeding appendages and the digestive system of *Gammarus pulex*. *Acta Zoologica* **46**, 67–81.

Aliyev, R. I. (1991). Ecology and biology of *Gammarus matienus* (Crustacea, Amphipoda) in the waters of Azerbaijan. *Hydrobiologia* **27(1)**, 91–94.

Allan, J. D. & Malmqvist, B. (1989). Diel activity of *Gammarus pulex* (Crustacea) in a south Swedish stream: comparison of drift catches vs baited traps. *Hydrobiologia* **179(1)**, 73–80.

Andersen, T. H., Friberg, N., Hansen, H. O., Iversen, T. M., Jacobsen, D. & Krojgaard, L. (1993). The effects of introduction of brown trout (*Salmo trutta* L.) on *Gammarus pulex* L. drift density in two fishless Danish streams. *Archiv für Hydrobiologie* **126(3)**, 361–371.

Anderson, N. H. & Sedell, J. R. (1979). Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology* **24**, 351–377.

Anderson, R. S. & Raasveldt, L. G. (1974). *Gammarus* and *Chaborus* predation. *Canadian Wildlife Service Occasional Papers* **18**, 1–23.

Barlöcher, F. (1982). The contribution of fungal enzymes to digestion of leaves by *Gammarus fossarum* Koch (Amphipoda). *Oecologia* **52**, 1–4.

Barlöcher, F. (1990). Factors that delay colonization of fresh alder leaves by aquatic hyphomycetes. *Archiv für Hydrobiologie* **119(3)**, 249–255.

Barlöcher, F. & Howatt, S. L. (1986). Digestion of carbohydrates and protein by *Gammarus mucronatus* Say (Amphipoda). *Journal of Experimental Marine Biology and Ecology* **104(1–3)**, 229–237.

Barlöcher, F. & Kendrick, B. (1973*a*). Fungi in the diet of *Gammarus pseudolimnaeus*. *Oikos* **24**, 295–300.

Barlöcher, F. & Kendrick, B. (1973*b*). Fungi and food preferences of *Gammarus pseudolimnaeus*. *Archiv für Hydrobiologie* **72**, 501–516.

Barlöcher, F. & Kendrick, B. (1975). Leaf conditioning by micro-organisms. *Oecologia* **20**, 359–362.

Barlöcher, F. & Murdoch, J. R. (1989). Hyporheic biofilms – a potential food source for interstitial animals. *Hydrobiologia* **184(1–2)**, 61–67.

Barmuta, L. A. (1989). Habitat patchiness and macrobenthic community structure in an upland stream in temperature Victoria, Australia. *Freshwater Biology* **21**, 223–236.

Barnes, R. D. (1980). *Invertebrate Zoology*. Holt – Saunders Japan Ltd., U.S.A.

Bengtsson, G. (1982). Energetic costs of amino acid exudation in the interaction between the predator *Gammarus pulex* L. and the prey *Asellus aquaticus* L. *Journal of Chemical Ecology* **8**, 1271–1281.

Blinn, D. W. & Johnson, D. B. (1982). Filter feeding of *Hyalella montezuma*, an unusual behaviour for a freshwater amphipod. *Freshwater Invertebrate Biology* **1**, 48–52.

Borovitskaya, M. P. (1956). Biology of *G. pulex* in water-bodies of the Leningrad district and its importance in fish-farming. *Trudÿ Leningradskogo obshchestva estestvoispÿtateleî* **7**, 99–122. (*Freshwater Biological Association Translations* (N.S.) No. 102).

Borowsky, B. (1984). The use of the males' gnathopods during precopulation in some gammaridean amphipods. *Crustaceana* **47(3)**, 245–250.

Borowsky, R. & Guarna, M. M. (1989). Excess amylase in *Gammarus palustris* (Crustacea: Amphipoda); its release into and possible roles in environment. *Marine Biology* **10(4)**, 529–534.

BOUSFIELD, E. L. (1973). *Shallow-water Gammaridean Amphipoda of New England*. Cornell University Press, Ithaca and London.

BOVBJERG, R. V. (1956). Some factors affecting aggressive behaviour in crayfish. *Physiological Zoology* **29**, 127–136.

BROWN, A. F. & DIAMOND, M. (1984). The consumption of rainbow trout (*Salmo gairdneri* Richardson) eggs by macroinvertebrates in the field. *Freshwater Biology* **14**, 211–215.

BUNN, S. E., EDWARD, D. H. & LONERAGAN, N. R. (1986). Spatial and temporal variation in the macroinvertebrate fauna of streams of the northern jarrah forest, Western Australia: community structure. *Freshwater Biology* **16**, 67–92.

CAMERON, G. N. & LAPOINT, T. W. (1978). Effects of tannins on the decomposition of Chinese tallow leaves by terrestrial and aquatic invertebrates. *Oecologia* **32(3)**, 349–366.

CHAMIER, A. C. (1991). Cellulose digestion and metabolism in the freshwater amphipod *Gammarus pseudolimnaeus* Bousfield. *Freshwater Biology* **25**, 33–40.

CHAMIER, A. C. & WILLOUGHBY, L. G. (1986). The role of fungi in the diet of the amphipod *Gammarus pulex* L.: an enzymatic study. *Freshwater Biology* **16**, 197–208.

CHAMIER, A. C., SUTCLIFFE, D. W. & LISHMAN, J. P. (1989). Changes in Na, K, Ca, Mg and Al content of submersed leaf litter, related to ingestion by the amphipod *Gammarus pulex* (L). *Freshwater Biology* **21**, 181–189.

CHESSMAN, B. C. (1986). Dietary studies of aquatic insects from two Victorian rivers. *Australian Journal of Marine and Freshwater Research* **37**, 129–146.

CLEMENS, H. P. (1950). Life cycle and ecology of *Gammarus fasciatus* Say. *Contributions. Stone Laboratory Ohio University* **12**, 1–63.

COLINVAUX, P. (1980). *Why Big Fierce Animals Are Rare*. Penguin, London.

COLINVAUX, P. (1986). *Ecology*. John Wiley and Sons, London.

CONLAN, K. E. (1994). Amphipod crustaceans and environmental disturbance: a review. *Journal of Natural History* **28**, 519–554.

CULVER, D. C. & FONG, D. W. (1991). Species interactions in cave stream communities: experimental results and microdistribution effects. *American Midland Naturalist* **126**, 364–379.

CUMMINS, K. W. (1973). Trophic relations of aquatic insects. *Annual Review of Entomology* **18**, 183–206.

CUMMINS, K. W. (1974). Structure and function of stream ecosystems. *Bioscience* **24**, 631–641.

CUMMINS, K. W. & KLUG, M. J. (1979). Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* **10**, 147–172.

CUMMINS, K. W., PETERSEN, R. C., HOWARD, F. O., WUYCHECK, J. C. & HOLT, V. I. (1973). The utilization of leaf litter by stream detritivores. *Ecology* **54**, 336–345.

DEGANI, G., BROMLEY, H. J., ORTAL, R., NETZER, Y. & HARARI, N. (1987). Diets of rainbow trout (*Salmo gairdneri*) in a thermally constant stream. *Vie Milieu* **37(2)**, 99–103.

DELONG, M. D., SUMMER, R. B. & THORP, J. H. (1993). Influence of food type on the growth of a riverine amphipod, *Gammarus fasciatus*. *Canadian Journal of Fisheries and Aquatic Science* **50(9)**, 1891–1896.

DENNERT, H. G. (1974). Tolerance differences and interspecific competition in three members of the amphipod genus *Gammarus*. *Bijdragen tot de Dierkunde* **44**, 83–99.

DICK, J. T. A. (1992). The nature and implications of differential predation between *Gammarus pulex* and *G. duebeni celticus*. *Journal of Zoology, London* **227**, 171–183.

DICK, J. T. A. (1995). The cannibalistic behaviour of two *Gammarus* species (Crustacea:Amphipoda). *Journal of Zoology, London* **236**, 697–706.

DICK, J. T. A. (1996). Post-invasion amphipod communities of Lough Neagh, N. Ireland: influences of habitat selection and mutual predation. *Journal of Animal Ecology* **65**, 756–767.

DICK, J. T. A. & PLATVOET, D. (1996). Intraguild predation and species exclusions in amphipods: the interaction of behaviour, physiology and environment. *Freshwater Biology*, **36**, 375–383.

DICK, J. T. A., ELWOOD, R. W. & IRVINE, D. E. (1990*a*). Displacement of the native Irish freshwater Amphipod *Gammarus duebeni* by the introduced *Gammarus pulex*. *Irish Naturalists' Journal* **23**, 313–316.

DICK, J. T. A., ELWOOD, R. W. & MONTGOMERY, W. I. (1995). The behavioural basis of a species replacement: differential aggression and predation between the introduced *Gammarus pulex* and *G. duebeni celticus* (Amphipoda). *Behavioral Ecology and Sociobiology* **37**, 393–398.

DICK, J. T. A., IRVINE, D. E. & ELWOOD, R. W. (1990*b*). Differential predation by males on moulted females may explain the competitive displacement of *Gammarus duebeni* by *G. pulex* (Crustacea:Amphipoda). *Behavioral Ecology and Sociobiology* **26**, 41–45.

DICK, J. T. A., MONTGOMERY, I. & ELWOOD, R. W. (1993). Replacement of the indigenous amphipod *Gammarus duebeni celticus* by the introduced *G. pulex*: differential cannibalism and mutual predation. *Journal of Animal Ecology* **62**, 79–88.

Dittrich, B. U. (1992). Functional morphology of the mouthparts and feeding strategies of the parasitic amphipod *Hyperia galba* (Montagu, 1813). *Sarsia* **77(1)**, 11–18.

Dobson, M. & Hildrew, A. G. (1992). A test of resource limitation among shredding detritivores in low order streams in southern England. *Journal of Animal Ecology* **61**, 69–77.

Duffy, J. E. & Hay, M. E. (1991). Amphipods are not all created equal: a reply to Bell. *Ecology* **72**, 354–358.

Duffy, J. E. & Hay, M. E. (1994). Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. *Ecology* **75(5)**, 1304–1319.

Embody, G. C. (1911). A preliminary study of the distribution, food and reproductive capacity of some freshwater Amphipods. *International Revue der Gesamten Hydrobiologie und Hydrographie* Supplement **3**, 1–35.

Feminella, J. W. & Stewart, K. W. (1986). Diet and predation by three leaf-associated stoneflies (Plecoptera) in an Arkansas mountain stream. *Freshwater Biology* **16**, 521–538.

Fitter, R. & Manuel, R. (1994). *Collins Photo Guide to Lakes, Rivers, Streams and Ponds*. Harper Collins, London.

Forsman, B. (1951). Studies on *Gammarus duebeni* Lillj., with notes on some rockpool organisms in Sweden. *Zoologiska bidrag från Uppsala* **29**, 215–237.

Friberg, N. & Jacobsen, D. (1994). Feeding plasticity of two detritivore-shredders. *Freshwater Biology* **32**, 133–142.

Friberg, N., Andersen, T. H., Hansen, H. O., Iversen, T. M., Jacobsen, D., Krojgaard, L. & Larsen, S. E. (1994). The effect of brown trout (*Salmo trutta* L.) on stream invertebrate drift, with special reference to *Gammarus pulex* L. *Hydrobiologia* **249(2)**, 105–110.

Fries, G. & Tesch, F. W. (1965). Der Einfluss des Massenvorkommens von *Gammarus tigrinus* Sexton auf Fische und niedere Tierwelt in der Weser. *Aus dem Niedersachsischen Landesverwaltungsamt* **16**, 133–150.

Gee, J. H. R. (1982). Resource utilization by *Gammarus pulex* (Amphipoda) in a Cotswold stream: a microdistribution study. *Journal of Animal Ecology* **51**, 817–832.

Gee, J. H. R. (1988). Population dynamics and morphometrics of *Gammarus pulex* L.: evidence of seasonal food limitation in a freshwater detritivore. *Freshwater Biology* **19**, 333–343.

Gerking, S. D. (1994). *Feeding Ecology of Fish*. Academic Press, London.

Goedmakers, A. & Roux, A. L. (1975). Essais d'hybridation entre plusieurs populations de gammares du groupe *pulex* (Amphipoda). *Crustaceana* **29**, 99–109.

Graca, M. A. S., Maltby, L. & Calow, P. (1993). Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus*. 1. Feeding strategies. *Oecologia* **93**, 139–144.

Graca, M. A. S., Maltby, L. & Calow, P. (1994). Comparative ecology of *Gammarus pulex* (L.) and *Asellus aquaticus* (L.). 2. Fungal preferences. *Hydrobiologia* **281(3)**, 163–170.

Griffith, M. B., Perry, S. A. & Perry, W. B. (1994). Secondary production of macroinvertebrate shredders in headwater streams with different baseflow alkalinity. *Journal of the North American Benthological Society* **13(3)**, 345–356.

Guarna, M. M. & Borowsky, R. L. (1993). Genetically controlled food preference: biochemical mechanisms. *Proceedings of the National Academy of Sciences U.S.A.* **90(11)**, 5257–5261.

Hargrave, B. T. (1970). The utilization of benthic microflora by *Hyalella azteca* (Amphipoda). *Journal of Animal Ecology* **39**, 427–437.

Hawkins, C. P., Murphy, M. L. & Anderson, N. H. (1982). Effects of canopy, substrate composition and gradient on the structure of macroinvertebrate communities in Cascade streams of Oregon. *Ecology* **63**, 1840–1856.

Herbst, G. N. (1982). Effects of leaf type on the consumption rates of aquatic detritivores. *Hydrobiologia* **89(1)**, 77–87.

Hildrew, A. G. & Townsend, C. R. (1987). Organization in freshwater benthic communities. In *Organization of Communities Past and Present* (eds. J. H. R. Gee and P. S. Giller). Blackwell, Oxford.

Hildrew, A. G., Townsend, C. R. & Henderson, J. (1980). Interactions between larval size, microdistribution and substrate in the stoneflies of an iron-rich stream. *Oikos* **85**, 387–396.

Holsinger, J. R. & Langley, G. (1980). The subterranean amphipod crustacean fauna of an artesian well in Texas. *Smithsonian Contributions to Zoology* **308**, 1–62.

Hunte, W. & Myers, R. A. (1983). Intraspecific predation and the evolution of phototaxis in amphipods. *Proceedings Association Island Marine Laboratories Caribbean* **17**, 12.

Hunte, W. & Myers, R. A. (1984). Phototaxis and cannibalism in gammaridean amphipods. *Marine Biology* **81**, 75–79.

Hutchinson, G. E. (1937). Limnological studies in Indian Tibet. *International Revue der Gesamten Hydrobiologie und Hydrographie* **35**, 134–177.

HYNES, H. B. N. (1954). The ecology of *Gammarus duebeni* Lilljeborg and its occurrence in freshwater in western Britain. *Journal of Animal Ecology* **23**, 38–84.

HYNES, H. B. N. (1956). British freshwater shrimps. *New Biology* **21**, 25–42.

JEFFRIES, M. & MILLS, D. (1990). *Freshwater Ecology: Principles and Applications*. Belhaven Press, London.

JENIO, F. (1979). Predation on freshwater gammarids (Crustacea: Amphipoda). *Proceedings of the West Virginia Academy of Sciences* **51**, 67–73.

JENIO, F. (1980). The life-cycle and ecology of *Gammarus troglophilus* Hubricht and Mackin. *Crustaceana* (*Supplement*) **6**, 204–215.

JONES, J. R. E. (1949). A further ecological study of calcareous streams in the 'Black Mountain' district of South Wales. *Journal of Animal Ecology* **18**, 142–159.

JONES, J. R. E. (1951). An ecological study of the River Towy. *Journal of Animal Ecology* **20**, 68–86.

KARAMAN, G. S. & PINKSTER, S. (1977). Freshwater *Gammarus* species from Europe, North Africa and adjacent regions of Asia (Crustacea-Amphipoda). Part 1. *Gammarus pulex*-group and related species. *Bijdragen tot de Dierkunde* **47(1)**, 1–97.

KAUSHIK, N. K. & HYNES, H. B. N. (1971). The fate of dead leaves that fall into streams. *Archiv für Hydrobiologie* **68**, 465–515.

KEITH, D. E. (1969). Aspects of feeding in *Caprella californica* Stimpson and *Caprella equilibria* Say (Amphipoda). *Crustaceana* **16**, 119–124.

KING, J. M., DAY, J. A., HURLY, P. R., HENSHALL-HOWARD, M. P. & DAVIES, B. R. (1988). Macroinvertebrate communities and environment in a Southern African stream. *Canadian Journal of Fisheries and Aquatic Science* **45**, 2168–2181.

KINNE, O. (1959). Ecological data on the amphipod *Gammarus duebeni*. A monograph. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* **6**, 177–202.

KORTELAINEN, I. (1991). *Gammarus lacustris*: herbivore or predator? *Annales Universitatis Turkuensis Series A II Biologica-Geographica-Geologica* **0(76)**, 31–34.

KOSLUCHER, D. G. & MINSHALL, G. W. (1973). Food habits of some benthic invertebrates in a northern cool-desert stream (Deep Creek, Curlew Valley, Idaho–Utah). *Transactions of the American Microscopical Society* **92**, 441–452.

KOSTALOS, M. & SEYMOUR, R. L. (1976). Role of microbrial enriched detritus in the nutrition of *Gammarus minus* (Amphipoda). *Oikos* **27**, 512–516.

KOZHOV, M. (1963). Lake Baikal and its life. *Monographiae Biologicae*, **2**.

LEE, C. L. & FIELDER, D. R. (1983). Agonistic behaviour in the development of dominance hierarchies in the freshwater prawn *Macrobrachium australiense* Holthius (Crustacea: Palamonidae). *Behaviour* **83**, 1–17.

LEROUX, M. L. (1933). Recherches sur la sexualité des Gammariens. *Bulletin biologique de la France et de la Belgique* **16**, 1–138.

LINCOLN, R. J. (1979). *British Marine Amphipoda: Gammaridea*. (British Museum (Natural History), London.

LINCOLN, R. J. & BOXSHALL, G. A. (1987). *The Cambridge Illustrated Dictionary of Natural History*. Cambridge University Press, Cambridge.

LOGACHEV, V. S. & MORDINOV, Y. E. (1979). The swimming speed and the activity of larval round goby and of some predatory crustaceans from the Black Sea. *Biologiya Morya* **3**, 77–80.

LUBYANOV, I. P. & ZUBCHENKO, I. A. (1970). Fundamental aspects of the feeding of the amphipod *Gammarus* (R.) *balanicus* (Crustacea, Amphipoda). *Freshwater Biological Association Translations. New Series*, **86** (1975). Russian original in: *Nauchnye Doklady Vysshei Shkoly Biologicheskie Nauki* **7**, 99–122.

MALICKY, H. (1990). Feeding tests with caddis larvae (Insecta: Trichoptera) and amphipods (Crustacea: Amphipoda) on *Platanus orientalis* (Platanaceae) and other leaf litter. *Hydrobiologia* **206**, 163–173.

MARCHANT, R. & HYNES, H. B. N. (1981). Field estimates of feeding rate for *Gammarus pseudolimnaeus* (Crustacea: Amphipoda) in the Credit River, Ontario. *Freshwater Biology* **11**, 27–36.

MARTIN, A. L. (1960). On the feeding, digestion and some aspects of food storage of gammarids (Amphipoda). PhD thesis, University of London.

MATHEWS, C. P. (1967). The energy budget and nitrogen turnover of a population of *Gammarus pulex* in a small woodland stream. *Journal of Animal Ecology* **36**, 62–69.

MEIJERING, M. P. D. (1972). Physiologische beiträge zur frage der Systematischen stellung von *Gammarus pulex* (L.) und *Gammarus fossarum* Koch (Amphipoda). *Crustaceana*, Supplement **3**, 313–325.

MERRITT, R. W. & CUMMINS, K. W. (eds). (1984). *An Introduction to the Aquatic Insects of North America*, 2nd ed. Kendall/Hunt Publishing Company, Dubuque.

MIHUC, T. B. & MINSHALL, G. W. (1995). Trophic generalists vs. trophic specialists: implications for food web dynamics in post-fire streams. *Ecology* **76(8)**, 2361–2372.

Minckley, W. L. (1963). The ecology of a spring stream Doe Run, Meade County, Kentucky. *Wildlife Monographs* **11**, 1–124.

Minshall, G. W. (1967). Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology* **48(1)**, 139–149.

Minshall, G. W. (1988). Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society* **7**, 263–288.

Monk, D. C. (1977). The digestion of cellulose and other dietary components, and pH of the gut in the amphipod *Gammarus pulex* (L.). *Freshwater Biology* **7**, 431–440.

Moore, J. W. (1975). The role of algae in the diet of *Asellus aquaticus* L. and *Gammarus pulex* L. *Journal of Animal Ecology* **44**, 719–730.

Moss, B. (1988). *Ecology of Fresh Waters*, 2nd ed. Blackwell Scientific Publications, Oxford.

Mottram, J. C. (1933). Some observations on the life history of the freshwater shrimp. *Transactions. Newbury District Field Club* **7**, 2–4.

Nilsson, L. M. (1974). Energy budget of a laboratory population of *Gammarus pulex* (Amphipoda). *Oikos* **25**, 35–42.

Oseid, D. M. & Smith, C. L. (1979). The effects of hydrogen cyanide on *Asellus communis* and *Gammarus pseudolimnaeus* and changes in their competitive response when exposed simultaneously. *Bulletin of Environmental Contamination and Toxicology* **21(4–5)**, 439–447.

Petersen, R. C. & Cummins, K. W. (1974). Leaf processing in a woodland stream. *Freshwater Biology* **4**, 343–368.

Pinkster, S., Dennert, A. L., Stock, B. & Stock, J. H. (1970). The problem of European freshwater populations of *Gammarus duebeni* Lilljeborg, 1852. *Bijdragen tot de Dierkunde* **40**, 116–147.

Pinkster, S., Smit, H. & Brandse-de Jong, N. (1977). The introduction of the alien amphipod *Gammarus tigrinus* Sexton, 1939, in the Netherlands and its competition with indigenous species. *Crustaceana Supplement* **4**, 91–105.

Polis, G. A., Myers, C. A. & Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**, 297–330.

Roberts, G. M. (1995). Salt-marsh crustaceans, *Gammarus-duebeni* and *Palaemonetes-varians* as predators of mosquito larvae and their reaction to *Bacillus-thuringiensis* subsp *israelensis*. *Biocontrol Science and Technology* **5(3)**, 379–385.

Root, J. B. (1967). The niche exploitation pattern of the blue-grey gnat catcher. *Ecological Monographs* **37**, 317–350.

Rosset, J., Barlöcher, F. & Oertli, J. J. (1982). Decomposition of conifer needles and deciduous leaves in two Black Forest and two Swiss Jura streams. *International Revue der Gesamten Hydrobiologie und Hydrographie* **67(5)**, 695–711.

Schmitz, E. H. (1967). Visceral anatomy of *Gammarus lacustris lacustris* Sars (Crustacea: Amphipoda). *American Midland Naturalist* **78**, 1–54.

Schwartz, S. S. (1992). Benthic predators and zooplanktonic prey: predation by *Crangonyx shoemakeri* (Crustacea: Amphipoda) on *Daphnia obtusa* (Crustacea: Cladocera). *Hydrobiologia* **237(1)**, 25–30.

Sexton, E. W. (1924). The moulting and growth-states of *Gammarus*, with descriptions of the normal and intersexes of *G. chevreuxi*. *Journal of the Marine Biological Association U.K.* **13**, 340–341.

Sexton, E. W. (1928). On the rearing and breeding of *Gammarus* in laboratory conditions. *Journal of the Marine Biological Association U.K.* **15**, 33–35.

Shaw, G. (1979). Prey selection by breeding dippers. *Bird Study* **26**, 66–67.

Short, R. A. (1983). Trophic ecology of three winter stoneflies (Plecoptera). *American Midland Naturalist* **105**, 341–347.

Short, R. A., Canton, S. P. & Ward, J. V. (1980). Detrital processing and associated macroinvertebrates in a Colorado mountain stream. *Ecology* **5**, 105–115.

Skadsheim, A. (1984). Coexistence and reproductive adaptations of amphipods: the role of environmental heterogeneity. *Oikos* **43**, 94–103.

Slack, H. D. (1936). The food of caddis fly (Trichoptera) larvae. *Journal of Animal Ecology* **5**, 105–115.

Sridhar, K. R. & Barlöcher, F. (1993). Seasonal changes in microbial colonization of fresh and dried leaves. *Archiv für Hydrobiologie* **128(1)**, 1–12.

Stanford, J. A. & Ward, J. V. (1983). Insect species diversity as a function of environmental variability and disturbance in stream systems. In *Stream Ecology* (ed. J. R. Barnes and G. W. Minshall). Plenum, New York.

Steele, D. H. & Steele, V. J. (1969). The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. 1. *Gammarus duebeni* Lillj. *Canadian Journal of Zoology* **53**, 1116–1126.

Steele, D. H. & Whittick, A. (1991). Seasonal variation in *Pilayella littoralis* (Phaeophyceae) and its consequences as a food source for the amphipod *Gammarus lacustris* in the intertidal of Newfoundland. *Journal of the Marine Biological Association U.K.* **7(4)**, 883–887.

STOCK, J. H. (1977). Whale-lice (Amphipoda, Cyamidae) on *Lagenorhynchus albirostris* in Dutch waters. *Crustaceana* **32**, 206.

STRANGE, C. D. & GLASS, G. B. (1979). The distribution of freshwater gammarids in Northern Ireland. *Proceedings of the Royal Irish Academy* (*B*) **79**, 145–153.

VADER, W. & RAMPPAINEN, K. (1985). Notes on Norwegian marine Amphipoda. 10. Scavengers and fish associates. *Fauna norvegica*. Series **A(6)**, 3–8.

VAN DOLAH, R. F. (1978). Factors regulating the distribution and population dynamics of the amphipod *Gammarus palustris* in an intertidal salt marsh community. *Ecological Monographs* **48**, 191–217.

VANNOTE, R. L., MINSHALL, G. W., CUMMINS, K. W., SEDELL, J. R. & CUSHING, C. E. (1980). The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Science* **37**, 130–137.

VASSALLO, L. & STEELE, D. H. (1980). Survival and growth of young *Gammarus lawrenicus* Bousfield, 1956, on different diets. In Buikema, A. L. and Holsinger, J. R. (eds) *Studies-On-Gammaridea* 2. Supplement **6**, 118–125.

WALLACE, J. B., WOODALL, W. R. & SHERBERGER, F. F. (1970). Breakdown of leaves by feeding of *Peltoperla maria* nymphs (Plecoptera: Peltoperlidae). *Annual of Review of Entomology* **63**, 562–567.

WARD, P. I. (1985). The breeding behaviour of *Gammarus duebeni*. *Hydrobiologia* **121**, 45–50.

WHITEHURST, I. T. (1988). Factors affecting the *Gammarus* to *Asellus* ratio in unpolluted and polluted waters. Unpublished Ph.D. thesis, Brighton Polytechnic.

WHITEHURST, I. T. & LINDSEY, B. I. (1990). The impact of organic enrichment on the benthic macroinvertebrate communities of a lowland river. *Water Research* **24(5)**, 625–630.

WILLER, A. (1922). Untersuchungen zur Kenntnis der Ernährungsphysiologie von *Gammarus pulex* L. *Schrifter Physikalis* **63**, 60.

WILLIAMS, D. D. & MOORE, K. A. (1985). The role of semiochemicals in benthic community relationships of the lotic amphipod *Gammarus pseudolimnaeus*: a laboratory analysis. *Oikos* **44**, 280–286.

WILLIAMSON, D. I. (1950). Note on *Themisto gracilipes* Norman. *Annual Report of the Marine Biological Station, Port Erin* **62**, 26.

WILLOUGHBY, L. G. (1983). Feeding behaviour of *Gammarus pulex* (L.) (Amphipoda) on *Nitella*. *Crustaceana* **44**, 245–250.

WILLOUGHBY, L. G. & SUTCLIFFE, D. W. (1976). Experiments on feeding and growth of the amphipod *Gammarus pulex* (L.) related to its distribution in the River Duddon. *Freshwater Biology* **6**, 577–586.

ZIMMERMAN, R., GIBSON, R. & HARRINGTON, J. (1979). Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. *Marine Biology* **54(1)**, 41–47.