Consumer-food systems: why type I functional responses are exclusive to filter feeders

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ABSTRACT

The functional response of a consumer is the relationship between its consumption rate and the abundance of its food. A functional response is said to be of type I if consumption rate increases linearly with food abundance up to a threshold level at which it remains constant. According to conventional wisdom, such type I responses are more frequent among filter feeders than among other consumers. However, the validity of this claim has never been tested. We review 814 functional responses from 235 studies, thereby showing that type I responses are not only exceptionally frequent among filter feeders but that they have only been reported from these consumers.

These findings can be understood by considering the conditions that a consumer must fulfil in order to show a type I response. First, the handling condition: the consumer must have a negligibly small handling time (i.e. the time needed for capturing and eating a food item), or it must be able to search for and to capture food while handling other food. Second, the satiation condition: unless its gut is completely filled and gut passage time is minimal, the consumer must search for food at a maximal rate with maximal effort. It thus has to spend much time on foraging (i.e. searching for food and handling it).

Our functional response review suggests that only filter feeders sometimes meet both of these conditions. This suggestion is reasonable because filter feeders typically fulfil the handling condition and can meet the satiation condition without losing time, for they are, by contrast to non-filter feeders, able simultaneously to perform foraging and non-foraging activities, such as migration or reproduction.

Key words: filter feeders, foraging time, predators, searching effort, suspension feeders, time budgets, type I functional responses, type II functional responses, type III functional responses, dome-shaped functional responses.

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I. INTRODUCTION

(1) Functional responses

The functional response of a consumer is the relationship between its consumption rate (i.e. mean number of food items or biomass consumed per consumer per unit of time) and the abundance or the biomass of its food, respectively (Solomon, 1949). The consumer can be a carnivore, herbivore, or parasite/parasitoid with prey, plants, or hosts, respectively, as its food.

Functional responses are important for population biologists, evolutionary biologists, ethologists, and physiologists. They attract population biologists because they link together different trophic levels. Long-term responses averaged over many individuals are useful here. Evolutionary biologists can also utilize functional responses since these include the important fitness determinants energy intake and mortality risk. Evolutionary biologists are mainly interested in long-term responses of single individuals. Furthermore, ethologists also work with functional responses, for animal behaviour is often adaptive and thus influenced by energy intake or mortality risk. Ethologists primarily need short-term functional responses of single individuals. Finally and for obvious reasons, physiologists are interested in functional responses, too. They use short- as well as long-term responses of single individuals.

Theoretical ecologists have developed numerous functional response models (reviewed by Jeschke, Kopp & Tollrian, 2002). According to these models, functional responses are mainly affected by three consumer traits: success rate, handling time, and digestion time. The success rate is a parameter that summarizes a consumer's abilities to encounter (influenced by searching velocity and area or volume of perception), detect, and attack food items. Handling time is the period the consumer needs for attacking (including evaluating, pursuing, and catching; corrected for time wasted through unsuccessful attacks) and eating a food item. Lastly, a consumer's digestion time is the gut transit time of a food item corrected for gut capacity, i.e. the number of food items that can be digested simultaneously.

Holling (1959b) has categorized functional responses into three main types which he termed types I, II, and III (Fig. 1). They have in common a monotonic increase in consumption rate with food abundance. This is because at a higher food abundance, a consumer encounters more food items. The three response types differ in the way that consumption rate increases with food abundance: type II is characterized by a curvilinear increase, type III by a sigmoidal increase, and in type I, the increase is rectilinear. Type II is the most common. Since it is also the simplest to model (Jeschke et al., 2002), it could be seen as the basic type of functional response. A type II response becomes type III if the consumer is able to learn (including training) or if it switches between food types, patches, or foraging tactics, e.g. from ambushing to cruising (reviewed by Jeschke et al., 2002). A type II threshold functional response is intermediate between type II and III. Such a response looks like a type II response that is shifted to the right on the abscissa: below a certain threshold food abundance, the consumption rate remains zero. The third classical type of response, type I, is especially important to this review. A type I functional response has three characteristics: (1) a region of linear increase up to a certain threshold food abundance (i.e. the incipient limiting level); (2) a constant region: above the threshold, the consumption rate is constant; and (3) a sharp transition between these two regions. If a functional response has all three of these characteristics, it is of type I. If it has two, it is of an intermediate type. For example, a response with a linear increase and a constant region but no sharp transition between them is an intermediate type I/II response.

In some functional responses, consumption rate decreases at very high food abundances: i.e. the response is 'dome-shaped'. For example, if consumption rate rises sigmoidally up to a certain food abundance and decreases thereafter, the functional response is type III dome-shaped (Fig. 1). Dome-shaped responses can result from consumer confusion, early-warning by individual prey in a flock, simultaneous active defence by a number of prey individuals, accumulation of toxic substances produced by food items, or clogging of consumer filters. All these are swarming effects. With increasing food abundance, they diminish consumption rate more strongly. If they override the positive effect of the increasing number of encounters between consumer and food on consumption rate, the consumer shows a dome-shaped response (reviewed by Jeschke et al., 2002).

Finally, if an empirical functional response is linear or constant, it is incomplete, i.e. the range of food abundance that was investigated or that occurs naturally is too small to allow its precise classification. We call such a response a 'linear functional response' or a 'constant functional response', respectively. Only type I responses have a strictly linear and/or a strictly constant region, so if we were able to measure consumption rates without any error, we could say that a linear or a constant response must be part of a type I response. However, in practise the measured values for consumption rate will contain errors and linear or constant functional responses cannot be so classified with certainty.

(2) Filter feeders

According to conventional wisdom, type I functional responses are more frequent among filter feeders than among other consumers. This claim is probably based on Holling's (1965) early review of empirical functional responses. The
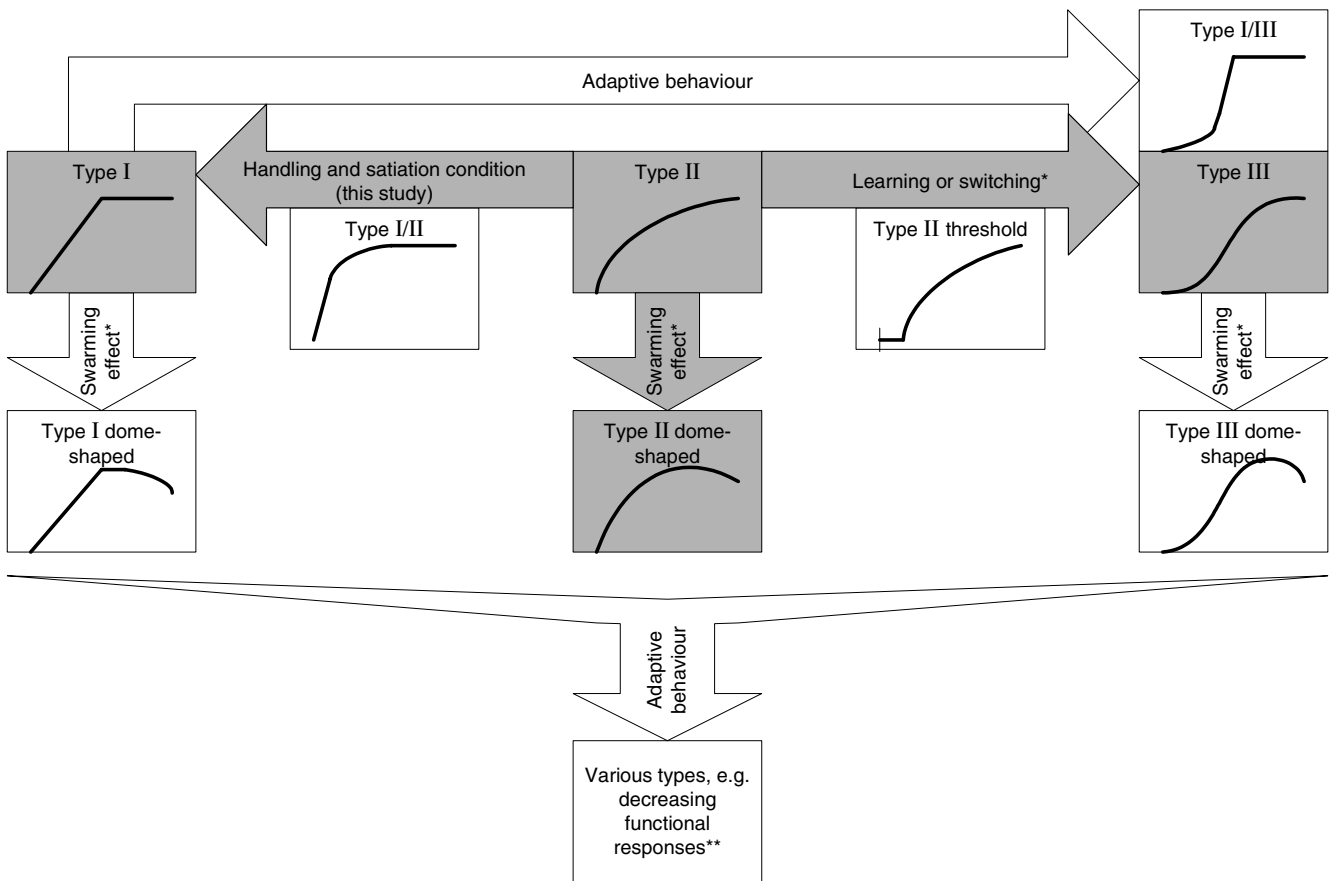
Fig. 1. Types of functional response and the relationships between them. Types I–III, and II dome-shaped are highlighted because they are the most common. *Switching is often the result of adaptive behaviour. **Reviewed by Jeschke *et al.* (2002).

only filter feeders included in it were crustaceans, and these showed type I responses.

We here define filter feeders in a very broad sense, to include: (1) suspension feeders (*sensu* Jørgensen, 1966), e.g. protozoans such as *Stentor* spp., sponges, rotifers such as *Brachionus* spp., bivalves such as *Mytilus* spp., crustaceans such as *Daphnia* spp., bryozoans, brachiopods, crinoids such as *Antedon* spp., tunicates, tadpoles, and baleen whales; (2) trap-builders, e.g. carnivorous plants, hydromedusae, web-building spiders; and (3) sediment filter feeders, e.g. lugworms and sea cucumbers such as *Holothuria* spp. All other consumers are defined as non-filter feeders. Of course, the classification of a consumer as a filter feeder or a non-filter feeder is often subjective. In some taxa, the distinction is based on food particle size, e.g. in protozoans, rotifers, copepods, or euphausiids. Furthermore, several animals switch to a filter feeding foraging strategy at high food abundances only, e.g. the thalassinidean decapod *Upogebia deltaura* (Lindahl & Baden, 1997); we have classified these as filter feeders.

Filter feeders can only capture food particles that flow through, or over, their filtering system. While some species actively produce these currents (i.e. active filter feeders), others use already existing ones (i.e. passive filter feeders). All trap-builders are passive filter feeders, all sediment filter feeders are active filter feeders, and the large group of suspension feeders contains passive (e.g. crinoids) as well as active filter feeders (e.g. bivalves) (Jørgensen, 1966; LaBarbera, 1984; Riisgård & Larsen, 1995, 2000).

Filter feeders have certain features in common: (1) while searching for food, they are able to perform other activities, e.g. food capture, migration, or reproduction. (2) They are also able simultaneously to capture several food items. (3) The food items they consume are relatively smaller than those of non-filter feeders. (4) Many are immobile or unable to move fast. (5) They are much more abundant in aquatic than in terrestrial habitats. (6) Suspension feeders, which form the largest of the three groups of filter feeders listed above, usually operate at small Reynolds numbers (LaBarbera, 1984).

The claim that type I functional responses are more frequent among filter feeders than among other consumers has never been tested. By reviewing empirical functional responses from the literature, we reveal that type I functional responses are not only extraordinarily frequent among filter feeders but that they have only been reported from these consumers. However, the majority of filter feeders does not show a type I response. To allow for a mechanistic understanding of these findings, we present the conditions that a consumer must fulfil in order to show a type I response.

Table 1. A review of empirical functional responses. References and information on the species investigated as well on the experimental conditions (see also Table 2) are given as a supplement to this review which is available from the authors or online at www.jeschke.tk.

Type of consumer	Are searching and handling mutually exclusive?*	Observed types of functional response		
		I	II	III
(1) Non-filter feeders				
(a) Carnivores				
(i) Non-queueing carnivores (see Juliano, 1989)				
(α) Invertebrates	Yes	−(0)	+(**188**)	+(28)
(β) Vertebrates	Yes	−(0)	+(**40**)	+(11)
(ii) Planktivorous fishes	Partly	−(1)	+(**16**)	+(2)
(iii) Queueing carnivores (e.g. *Notonecta* spp.; see Juliano, 1989)	Partly	−(0)	+(**15**)	+(4)
(b) Herbivores				
(i) Invertebrates				
(α) Protozoans that consume only one food item per generation	Not relevant	+(**2**)	−(0)	−(0)
(β) Aquatic microphagous molluscs	Partly	−(1)	+(2)	−(0)
(γ) Others	Yes	−(0)	+(**9**)	+(5)
(ii) Vertebrates	Partly	−(9)	+(**69**)	+(2)
(c) Parasites and parasitoids	Yes	−(0)	+(**23**)	+(5)
(2) Filter feeders				
(a) Protozoans				
(i) Non-giants	Partly	−(3)	+(**22**)	+(5)
(ii) Giants (e.g. *Stentor* spp.)	No	+(1)	−(0)	+(3)
(b) Carnivorous plants	Partly	+(3)	+(1)	−(0)
(c) Cnidarians and ctenophores	No	−(5)	−(5)	+(1)
(d) Rotifers	No	+(16)	+(17)	+(6)
(e) Molluscs	No	+(**23**)	+(14)	+(3)
(f) Polychaetes: arenicolids (lugworms)	No	−(0)	−(0)	+(**4**)
(g) Crustaceans				
(i) Branchiopods (e.g. *Artemia* spp., *Daphnia* spp.)	No	+(**57**)	+(19)	+(2)
(ii) Copepods (e.g. *Acartia* spp., *Calanus* spp.)	Partly	+(30)	+(32)	+(28)
(iii) Euphausiids (e.g. *Euphausia superba*)	Partly	+(2)	−(0)	+(**6**)
(iv) Thalassinidean decapods (e.g. *Upogebia* spp.)	Partly	−(0)	−(0)	+(1)
(h) Insect larvae: blackflies	Partly	+(**4**)	−(1)	−(0)
(i) Bryozoans	No	+(**4**)	−(1)	−(0)
(j) Echinoderms: crinoids	No	−(0)	+(1)	−(0)
(k) Tunicates				
(i) Ascidians	No	+(**6**)	+(2)	−(0)
(ii) Thaliaceans	No	+(2)	−(1)	−(0)
(l) Anuran larvae	No	−(0)	−(0)	+(**6**)

* If searching and handling are mutually exclusive then while handling a food item, consumers are not able to search for or capture another one; if they are partly overlapping then while handling one or a few food items, consumers can search for and capture another one (Juliano, 1989); 'no' in this column means that searching and handling completely overlap (while handling one or more food items, these consumers are able to search for and capture another one).

'+' and '−' indicate whether a functional response of the type shown has been reported or has not, respectively; only pure types I, II, or III are relevant, intermediate types were not included. The most frequently observed type of functional response for each consumer is highlighted by a grey background. The numbers in parentheses indicate the numbers of observed functional responses; both pure and intermediate types of functional response are included. Type II dome-shaped functional responses were counted as type II functional responses; intermediate type I/II functional responses were counted as half type I and half type II; other dome-shaped and intermediate types were counted analogously. Type I threshold functional responses were classified as intermediate type I/III; type I/II threshold functional responses were classified as intermediate type I/II/III; the latter were counted as one-third type I, one-third type II, and one-third type III. Linear functional responses were ignored because they cannot be accurately classified with the exception of linear threshold functional responses which were counted as half unknown and half type III.

II. METHODS

Table 1 summarizes 814 empirically derived functional responses from 236 consumer species which are given in detail in a supplement to this review (available from the authors on request or online at www.jeschke.tk). Our review is based on 235 studies. It is the first review of functional responses since the 1970s (Holling, 1965; Murdoch & Oaten, 1975; and

Table 2. *The experimental conditions under which the functional responses summarized in Table 1 were obtained*

Experimental condition	Non-filter feeders	Filter feeders	All consumers
Laboratory/enclosure/field	70%/22%/9%	100%/0%/0%	83%/12%/5%
Competing consumers present/absent	28%/72%	87%/13%	55%/45%
Alternative food present/absent	19%/81%	1%/99%	11%/89%
Satiation effects included/excluded	62%/38%	84%/16%	72%/28%

Hassell, Lawton & Beddington, 1976). Since filter feeders are the main focus of this study, we included all 365 functional responses from 100 filter feeding species that we are aware of. The 449 functional responses from 136 non-filter feeding species used were chosen arbitrarily. In classifying functional responses, we usually follow the authors; exceptions are explicitly identified in the Supplement. If authors have not classified their functional response, we have done this by eye from the presented graph. Note that some responses may be misclassified; it is occasionally difficult to classify a functional response (Mullin, Stewart & Fuglister, 1975). Furthermore, it is probable that in some responses summarized here low or high food abundances were not tested in sufficient detail to reveal a type III or a dome-shaped response, respectively. Due to the large number of responses included in our analysis, however, we do not expect that these and similar problems severely bias our results.

In order to gain an understanding of why consumers differ in their tendency to show type I functional responses, in Table 1 we classify consumers according to the degree of overlap between two of their activities: searching for food and handling it. These two activities are either mutually exclusive, partly overlapping, or completely overlapping. Corresponding references are given in the Supplement.

Further information on each functional response integrated in Table 1 is provided in the Supplement. This includes the consumer and the food species involved. Furthermore, since functional responses are affected by the experimental conditions under which they are obtained (e.g. Ives *et al.*, 1999), the Supplement reports whether a response was obtained in the laboratory, in enclosures, or in the field, whether intra- or interspecifically competing consumers were present, whether alternative food was present, and whether the response includes satiation effects (long-term studies) or not (short-term studies). The spatial scale is usually small for laboratory studies, intermediate for enclosure experiments, and large for field studies.

III. RESULTS AND DISCUSSION

(1) The experimental conditions under which functional responses are obtained

The functional responses summarized in Table 1 were measured under different experimental conditions (Table 2). Below, we will compare the frequency distributions of functional response types between non-filter feeders and filter feeders. The results could be misleading if these frequency distributions were greatly affected by the experimental conditions under which the functional responses were obtained. This seems not to be the case, however: the frequency distribution of all data (i.e. mainly artificial experimental conditions) roughly matches that of field data (Fig. 2). This finding, furthermore, does not confirm the suggestion of Hassell, Lawton & Beddington (1977) that type III functional responses are severely underrepresented in artificial laboratory studies.

(2) Are type I functional responses extraordinarily frequent among filter feeders?

Type I functional responses have only been reported from filter feeders (Fig. 2); the small fraction of type I responses reported from non-filter feeders was derived from intermediate responses (e.g. type I/II responses) or protozoans that consume only one food item per generation. The majority of filter feeders does not show a type I response.

(3) The conditions for a type I functional response

We will discuss these findings by considering the conditions that a consumer must fulfil in order to show a type I functional response. We thereby take into account the three consumer traits that mainly affect functional responses (see Section I): success rate, handling time, and digestion time. A type I functional response requires that, below the incipient limiting level (ILL) of food abundance (see Section I), consumption rate is only determined by the consumer's success rate. In other words, below the ILL, neither the handling time nor the digestion time affects consumption rate, i.e. the consumer searches for food at a maximal rate with maximal effort. Above the ILL, though, digestion time determines consumption rate [see, for example, Rigler (1961) for branchiopods, Frost (1972) for copepods, and Rothhaupt (1990) for rotifers]; the consumer has a completely filled gut, digests its food in a minimal amount of time, and forages at a suppressed rate because it can only ingest as much food as it can digest per unit of time (see also Sjöberg, 1980). Hence, the handling time is either negligibly small or does not affect consumption rate (i.e. searching and handling completely overlap).

In summary, a consumer must fulfil two conditions in order to show a type I functional response. First, the handling condition: the consumer must have a negligibly small handling time, or it must be able to search for and to capture food while handling other food. Second, the satiation condition: Unless its gut is completely filled and gut passage time is minimal, the consumer must search for food at a
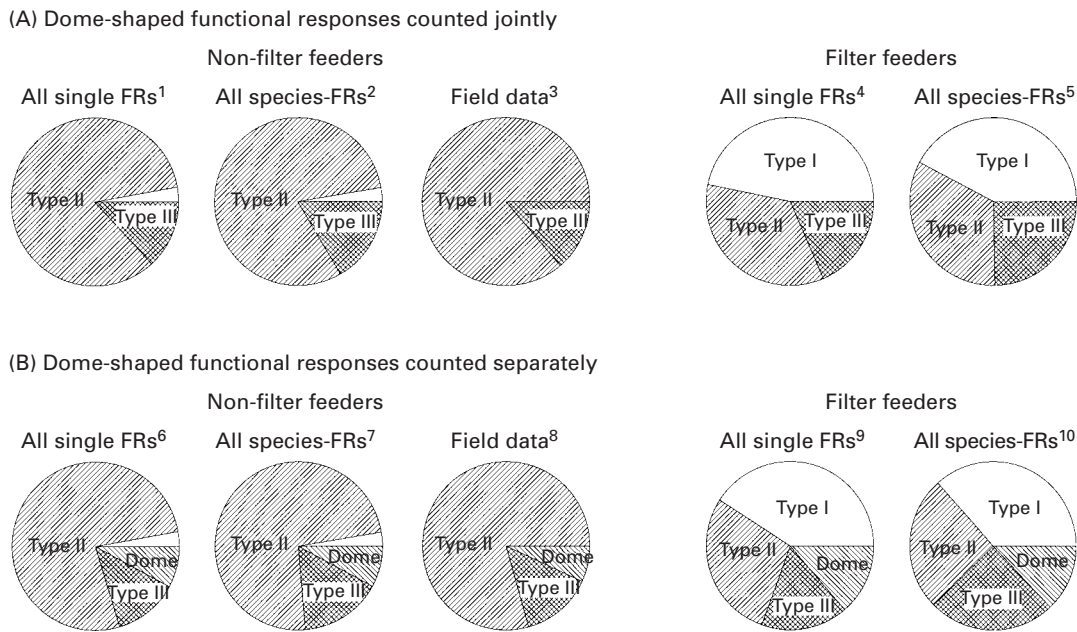
Fig. 2. Graphical summary of our review of functional responses (FRs). (A) Dome-shaped functional responses are included in the appropriate category, e.g. type II dome-shaped functional responses were counted as type II functional responses. Charts headed 'All single FRs' or 'Field data' are based on the individual functional responses given in the Supplement (see also Tables 1, 2 and Fig. 4). Here, each consumer species may be included multiple times, one for each time its functional response was reported. Pie charts headed 'All species-FRs' include each consumer species only once, either because only one response was found in the literature or, if two or more responses were reported, by inclusion of the more typical response. These typical response types are given in the Supplement. 'Field data' pie charts include only functional responses that were obtained in the field. Data corresponding to the pie charts: [1]$N_{type\,I}=12$ (2.8%), $N_{type\,II}=360.5$ (84.0%), $N_{type\,III}=56.5$ (13.2%), $N_{linear}=20.0$, $N_{total}=449.0$; [2]$N_{type\,I}=3.5$ (2.6%), $N_{type\,II}=107.5$ (80.8%), $N_{type\,III}=22.0$ (16.5%), $N_{linear}=3.0$, $N_{total}=136.0$; [3]$N_{type\,I}=0.0$, $N_{type\,II}=25.0$ (86.2%), $N_{type\,III}=4.0$ (13.8%), $N_{linear}=7.0$, $N_{total}=36.0$; [4]$N_{type\,I}=153.8$ (46.8%), $N_{type\,II}=114.3$ (34.8%), $N_{type\,III}=60.8$ (18.5%), $N_{linear}=36.0$, $N_{total}=365.0$; [5]$N_{type\,I}=41.0$ (42.3%), $N_{type\,II}=32.0$ (33.0%), $N_{type\,III}=24.0$ (24.7%), $N_{linear}=3.0$, $N_{total}=100.0$; [6]$N_{type\,I}=12$ (2.8%), $N_{type\,II}=329.5$ (76.8%), $N_{type\,III}=53.5$ (12.5%), $N_{dome\text{-}shaped}=34.0$ (7.9%), $N_{linear}=20.0$, $N_{total}=449.0$; [7]$N_{type\,I}=3.5$ (2.6%), $N_{type\,II}=98.0$ (73.7%), $N_{type\,III}=21.0$ (15.8%), $N_{dome\text{-}shaped}=10.5$ (7.9%), $N_{linear}=3.0$, $N_{total}=136.0$; [8]$N_{type\,I}=0.0$, $N_{type\,II}=23.0$ (79.3%), $N_{type\,III}=4.0$ (13.8%), $N_{dome\text{-}shaped}=2.0$ (6.9%), $N_{linear}=7.0$, $N_{total}=36.0$; [9]$N_{type\,I}=134.3$ (40.8%), $N_{type\,II}=94.3$ (28.7%), $N_{type\,III}=55.3$ (16.8%), $N_{dome\text{-}shaped}=45.0$ (13.7%), $N_{linear}=36.0$, $N_{total}=365.0$; [10]$N_{type\,I}=35.5$ (36.6%), $N_{type\,II}=25.0$ (25.8%), $N_{type\,III}=24.0$ (24.7%), $N_{dome\text{-}shaped}=12.5$ (12.9%), $N_{linear}=3.0$, $N_{total}=100.0$.
  Intermediate types of functional response were included and counted as described in Table 1.

maximal rate with maximal effort. It thus has to spend much time on foraging. See the Appendix for a more formal justification of these conditions. The two conditions are necessary, not sufficient, i.e. a consumer showing a type I functional response must have met both conditions but a consumer meeting both conditions does not necessarily show a type I response. For example, if a consumer meets both conditions but additionally suffers from a swarming effect, its functional response will not be of pure type I but is expected to be type I dome-shaped. An exception to the conditions are consumers that consume only one food item during their lifetime, e.g. some protozoans (we here define lifetime as the period between cell divisions). They show type I functional responses without fulfilling the two conditions. This is because, first, handling food does not prevent such a consumer from searching for its next meal since there is no next meal and, second, for the same reason, satiation cannot lower the searching effort of such a consumer.

Sjöberg (1980) has offered a further condition for a type I functional response: the digestion condition. The consumer must be able simultaneously to digest many (ideally: an infinite number of) food items. For example, *Daphnia magna* typically show type I functional responses (Table 1) and are able simultaneously to digest 10^5–10^6 cells, depending on body size and cell size (Evers & Kooijman, 1989). As well as the other two conditions, the digestion condition implies that consumers are relatively large compared to their food. Consumers fulfilling the handling and the satiation condition should therefore automatically also meet the digestion condition. As was mentioned in Section I, filter feeders are characteristically large compared to their food.

Holling (1966) has claimed that his invertebrate model produces type I functional responses when the 'reactive field' of the consumer is constant (this corresponds to our satiation condition). However, simulations by ourselves (results not shown) indicate that two additional conditions must be fulfilled for a type I functional response in the invertebrate model: handling time must be negligibly small (our handling condition), and consumers must be relatively large compared to their food. Thus, Holling's invertebrate model

is not in contradiction to our conditions for a type I response.

(4) Filter feeders *versus* non-filter feeders

Combining the handling and the satiation condition with our finding that type I functional responses are restricted to filter feeders, it follows that all consumers evidently fulfilling both conditions in our study are filter feeders. Indeed, the handling condition is generally fulfilled by filter feeders, but not by non-filter feeders (see Section I and Table 1). The satiation condition is hard to investigate directly. The Appendix, however, offers an indirect method: if a consumer fulfils the satiation condition, it should show a type I or an intermediate type I/II functional response, respectively, depending on whether or not it fulfils the handling condition. This statement refers to functional responses that include satiation effects; other responses are by definition inappropriate for testing the validity of the satiation condition. Admittedly, this method is hampered by the empirical difficulty involved in discriminating between type I/II and II responses. Moreover, it neglects consumer learning, switching, confusion, and other factors that can qualitatively alter the shape of a functional response. We apply the method with these drawbacks in mind. For non-filter feeders, type I/II functional responses that include satiation effects have almost never been reported (see Supplement). Hence, almost all non-filter feeders seem not to fulfil the satiation condition. On the contrary, about half of the filter feeders appear to meet this condition. In conclusion, non-filter feeders usually show type II functional responses (Table 1, Fig. 2) since they neither fulfil the handling condition nor the satiation condition and because learning or switching effects leading to type III responses are infrequent. On the other hand, filter feeders typically meet the handling condition. They show type I functional responses when they additionally fulfil the satiation condition; they show type II responses when they decrease their filtration rate (i.e. searching effort) with increasing gut fullness in a strictly monotonic way; and they show type III responses when they reduce their filtration rate in times of low food abundance.

To fulfil the satiation condition, a consumer must spend much time foraging. Fig. 3 illustrates that consumers showing type I responses (these fulfil the satiation condition) spend more time foraging (i.e. searching and handling) than consumers that show type II responses (these do not fulfil the satiation condition). Non-filter feeders are not able simultaneously to perform foraging and non-foraging activities, such as avoidance of top predators, migration, reproduction, or territorial behaviour. They probably would not have enough time for essential non-foraging activities, were they fulfilling the satiation condition. Filter feeders, on the other hand, can meet the satiation condition without conflict. Why many of them nevertheless do not fulfil this condition may be clarified in future studies. Copepods, for example, show almost all imaginable types of functional response (Table 1) and are present in both marine and freshwater environments. According to Fig. 4 (see also Paffenhöfer & Stearns, 1988), copepod functional responses seem to be qualitatively influenced by habitat type. Perhaps one or more factors coupled with habitat type, e.g. the level or the variability of food abundance, ultimately determines the fulfilment of the satiation condition and consequently the type of functional response.

(5) The adaptive significance of type I functional responses

For a given success rate and digestion time, and at each food abundance, a consumer has a maximal consumption rate if it shows a type I functional response. Compared to a type II response, the advantage is greatest at intermediate food abundances (Fig. 5). Combining this observation with our finding that filter feeders often show type I functional responses suggests that a filter feeding foraging strategy helps to increase consumption rate, especially at intermediate food abundances. Thus, besides an aquatic habitat and small food particles as an energy source (see Section I), a third environmental condition favouring filter feeding may be an intermediate food abundance (for passive filter feeders, it is not the food abundance that should be intermediate, but the encounter rate with food, which is proportional to the product of food abundance and ambient velocity, see models reviewed by Jeschke *et al.*, 2002). What 'intermediate' means in practice depends on the characteristics of the focal consumer. For example, *Daphnia* spp. are more typical filter feeders than copepods: in contrast to copepods, *Daphnia* spp. have a foraging strategy in which searching and handling completely overlap (see Supplement). They more often show type I functional responses (Table 1), and their filtering system is less selective. Daphnids are therefore unable to avoid toxic or other unpalatable particles. This disadvantage of an unconditional filter feeding foraging strategy counteracts the benefits of a higher consumption rate [according to Muck & Lampert (1984), the mass-specific consumption rate of *Daphnia longispina* exceeds that of *Eudiaptomus gracilis*]. Moreover, the *Daphnia* spp. filtering system has higher energetic demands than that of copepods (Schmink, 1996). It is thus expected to be adaptive at intermediate food abundances, whereas the copepod performs better at low and high food abundances. Muck & Lampert (1984; see also Mookerji *et al.*, 1998) found that in oligotrophic and heavily eutrophic lakes and ponds, copepods usually dominate over daphnids, whereas in mesotrophic lakes and ponds, daphnids dominate over copepods. Similarly, copepods generally dominate in marine habitats which typically have a low food abundance. In freshwater copepods, an intermediate foraging strategy between *Daphnia* spp. and marine copepods seems to have evolved: freshwater copepods collect food like marine copepods but fulfil the satiation condition like *Daphnia* spp. Finally, this pattern can be affected by the higher susceptibility of *Daphnia* spp. to predation because they are less agile than copepods (Mookerji *et al.*, 1998). In summary, a filter feeding foraging strategy increases a consumer's energy input, especially at intermediate food abundances. On the other hand, it decreases the consumer's ability to select food, it increases its energy output by an amount that is roughly independent of food abundance, and it may increase the consumer's vulnerability to predation because it is
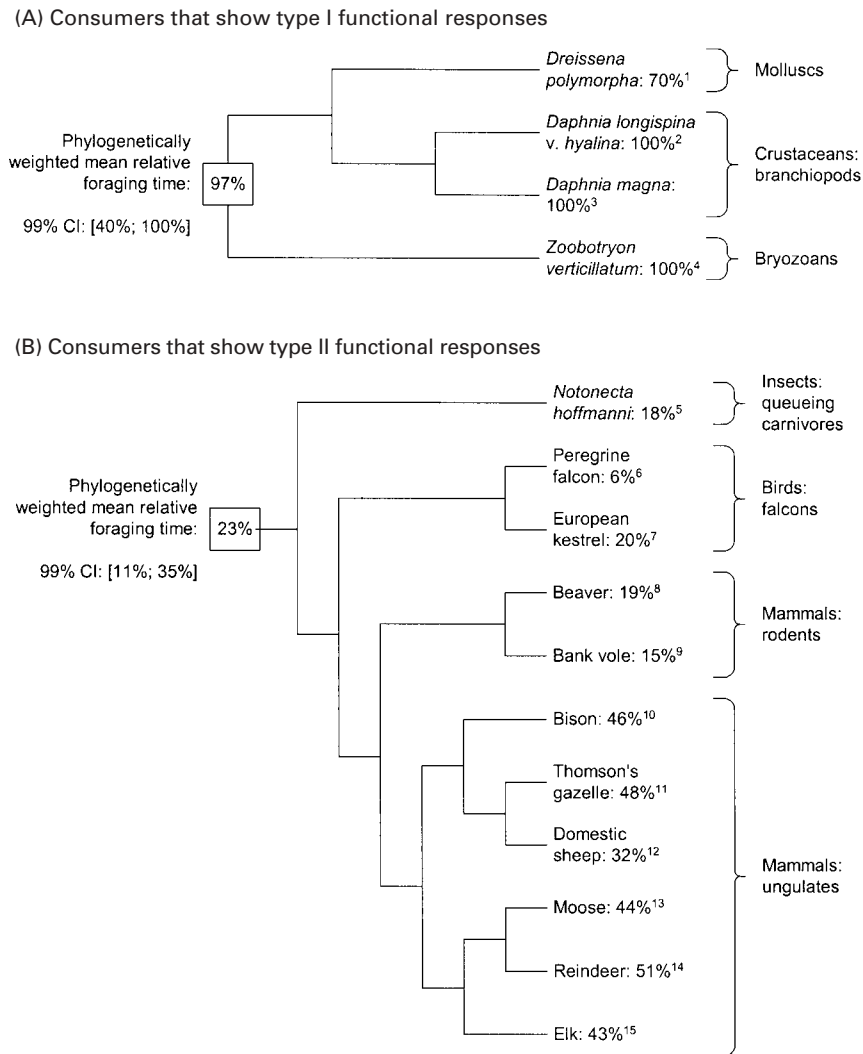
(A) Consumers that show type I functional responses

Phylogenetically
weighted mean relative
foraging time: **97%**

99% CI: [40%; 100%]

Dreissena polymorpha: 70%[1] — Molluscs

Daphnia longispina v. hyalina: 100%[2]
Daphnia magna: 100%[3] — Crustaceans: branchiopods

Zoobotryon verticillatum: 100%[4] — Bryozoans

(B) Consumers that show type II functional responses

Phylogenetically
weighted mean relative
foraging time: **23%**

99% CI: [11%; 35%]

Notonecta hoffmanni: 18%[5] — Insects: queueing carnivores

Peregrine falcon: 6%[6]
European kestrel: 20%[7] — Birds: falcons

Beaver: 19%[8]
Bank vole: 15%[9] — Mammals: rodents

Bison: 46%[10]
Thomson's gazelle: 48%[11]
Domestic sheep: 32%[12]
Moose: 44%[13]
Reindeer: 51%[14]
Elk: 43%[15] — Mammals: ungulates

Fig. 3. A comparison of foraging times between consumers that show type I functional responses and consumers that show type II responses (foraging time is the proportion of a 24 h period spent searching for food and handling it). Note that type I functional response consumers spend more time foraging than type II consumers.

The phylogenies are based on Pérez-Barbería & Gordon (1999 *a, b*) and Maddison (2003). We have calculated the means and the confidence intervals (CI) with independent contrasts analyses (Felsenstein, 1985; Garland *et al.*, 1993; Garland, Midford & Ives, 1999) by using Pagel's (1992) arbitrary branch lengths and arcsine-transformed data (Sokal & Rohlf, 1995).

Notes on foraging times and corresponding references: [1]Shell opening time (Walz, 1978); [2]Nauwerck (1959); [3]Porter, Gerritsen & Orcutt (1982); [4]Bullivant (1968); [5]moving time (Sih, 1992); [6]*Falco peregrinus*, reviewed by McGowan (1997); [7]*Falco tinnunculus*, females $\approx 17.9\%$ [4.6% flight-hunting + 2.0% flying including soaring + $\approx 11.3\%$ perch-hunting (=half of total perching time)], males $\approx 21.2\%$ (6.7% flight-hunting + 3.8% flying including soaring + $\approx 10.7\%$ perch-hunting [=half of total perching time]), Masman, Daan & Dijkstra (1988); [8]*Castor canadensis*, Belovsky (1984); [9]*Clethrionomys glareolus*, reviewed by Ashby (1972); [10]*Bison bison*, sum of searching time (i.e. moving time, 34%) and cropping time (12%) Belovsky & Slade (1986); [11]*Gazella thomsonii*, sum of searching time (i.e. moving time, 12%) and cropping time (36%), Walther (1973); [12]*Ovis aries*, average of values reported from Allden & Whittaker (1970; $\approx 31\%$) and reviewed by Trudell & White (1981; $\approx 30\%$, $\approx 35\%$); [13]*Alces alces*, sum of searching time (i.e. moving time, 23%) and cropping time (21%), Belovsky & Jordan (1978); [14]*Rangifer tarandus tarandus*, average of values reported from Trudell & White (1981): 53% [sum of searching time (i.e. moving time, 27%) and cropping time (26%)] and reviewed by Trudell & White (1981; 49%); [15]*Cervus elaphus*, sum of searching time (i.e. moving time, 30%) and cropping time (13%), Belovsky & Slade (1986).

frequently correlated with immobility or the inability to move fast (see Section I). Our finding that type I functional responses are extraordinarily frequent among filter feeders is thus not only important for population biologists but also for evolutionary ecologists.

IV. CONCLUSIONS

(1) Type I functional responses have only been reported from filter feeders. This is because only filter feeders
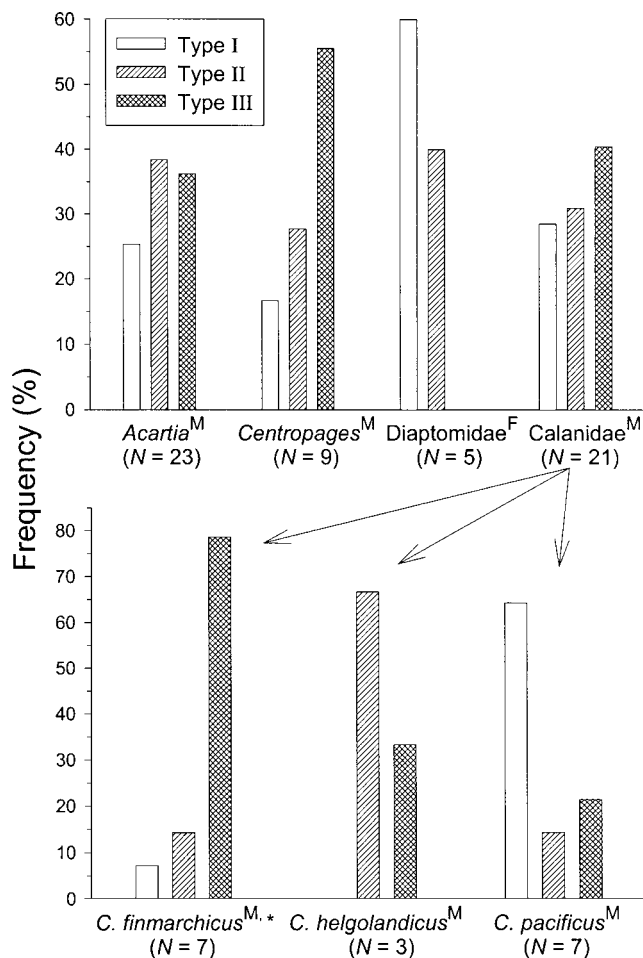
Fig. 4. Functional response types of calanoid copepods relative to phylogeny and habitat type (^Ffreshwater, ^Mmarine). Most marine copepods show type II or III functional responses [*Acartia*: type II or III; *C. finmarchicus*: type III (*$P < 0.05$, χ^2-test against uniform distribution, 2 df); *C. helgolandicus*: type II or III; *Centropages*: type III], whereas *C. pacificus* and freshwater copepods usually show type I functional responses.

Data are from Table 1; *Acartia* species: *A. clausi*, *A. erythraea*, *A. hudsonica*, and *A. tonsa*; *Centropages* species: *C. chierchiae*, *C. hamatus*, *C. typicus* and *C. yamadai*; Diaptomidae: *Diaptomus oregonensis*, *Diaptomus sicilis* and *Eudiaptomus gracilis*; Calanidae: *Calanus finmarchicus*, *Calanus helgolandicus*, *Calanus pacificus*, *Calanus plumchrus*, *Calanus sinicus* and *Calanoides carinatus*. Dome-shaped functional responses were excluded. Intermediate types of functional response were included and counted as described in Table 1.

sometimes meet both handling condition and the satiation condition. For the handling condition to be met a consumer must have a negligibly small handling time, or it must be able to search for and to capture food while handling other food. Filter feeders typically meet this condition. To meet the satiation condition, unless its gut is filled completely and gut passage time is minimal, the consumer must search for food at a maximal rate with maximal effort. Filter feeders can meet this condition because they are able simultaneously to perform foraging and non-foraging activities.
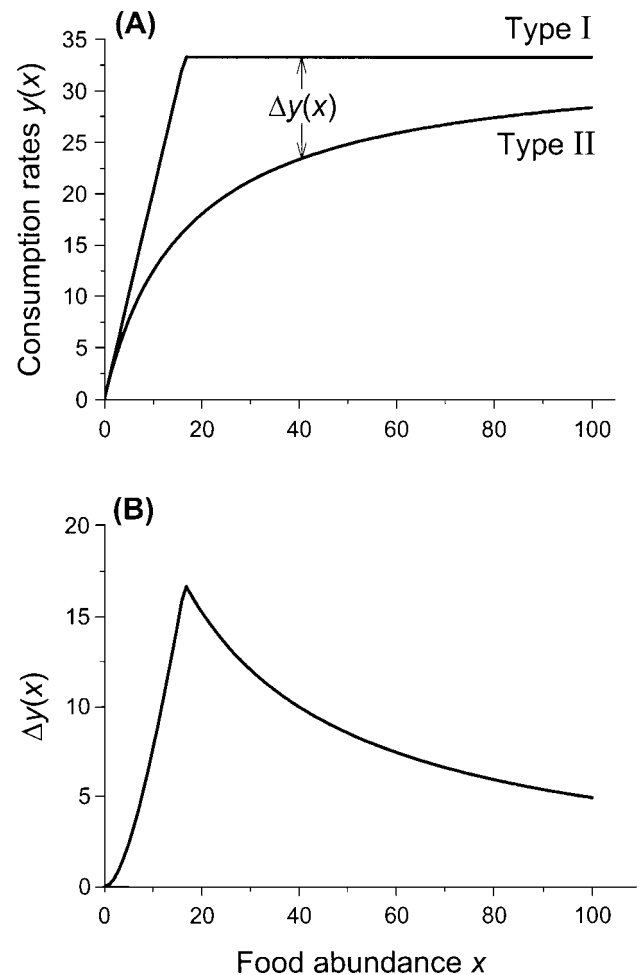

Fig. 5. (**A**) Comparison of type I and II functional responses. The difference between the curves, $\Delta y(x)$, is plotted against food abundance in (**B**) to show how type I functional responses maximize consumption rate, especially at intermediate food abundances.

(2) The majority of functional responses reported from filter feeders is not of type I. This is probably due to a failure to meet the satiation condition which should be adaptive for filter feeders that, for example, consume food of highly variable abundance.

(3) Non-filter feeders usually show type II functional responses since they normally neither fulfil the handling nor the satiation condition and because learning or switching effects leading to type III responses are infrequent. Non-filter feeders do not meet the handling condition, for their handling times are seldom negligibly small and, more importantly, they are characteristically not able to search for or to capture a food item while handling another one. They are furthermore unable simultaneously to perform foraging and non-foraging activities and thus would be unable to perform essential non-foraging activities, were they fulfilling the satiation condition.

(4) An intermediate food abundance may favour a filter feeding foraging strategy because, all other things being equal, a consumer showing a type I functional response

gains more energy per unit time than one showing a type II response, and this difference is largest at an intermediate food abundance.

(5) We have focused this paper on two questions: which consumers show type I functional responses and why is this the case? We have reported that only filter feeders show type I responses and offer a theoretical explanation for this finding. It is hoped that this review encourages researchers to look for further factors that qualitatively influence functional responses.

V. ACKNOWLEDGEMENTS

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VII. APPENDIX: A FORMAL JUSTIFICATION OF THE TWO CONDITIONS FOR A TYPE I FUNCTIONAL RESPONSE

(1) Searching and handling are mutually exclusive

A basic functional response model designed for consumers for which the processes of searching for food and handling it are mutually exclusive is Holling's (1959a) disc equation. It includes the two parameters success rate a (dimension in SI units: $\mathrm{m^2\,s^{-1}}$ for two-dimensional habitats and $\mathrm{m^3\,s^{-1}}$ for three-dimensional habitats) and handling time b (s):

$$y(x) = \frac{ax}{1+abx}, \qquad (A1)$$

where x is food abundance ($\mathrm{m^{-2}}$ or $\mathrm{m^{-3}}$, respectively) and $y(x)$ is consumption rate ($\mathrm{s^{-1}}$). [Note that the dimension of food abundance x given in Jeschke *et al.* (2002) is incorrect: to allow correct cancellation of units, the unit 'individuals' must either be excluded from or included in the dimensions of all relevant parameters. Since we, the authors of Jeschke *et al.* (2002), originally gave the dimensions in SI units, 'individuals' was excluded from all dimensions. Without our permission, however, the dimension of food abundance x was changed to individuals/$\mathrm{m^2}$ or individuals/$\mathrm{m^3}$, respectively, without changing the other dimensions.]

The disc equation (equation A1) considers only two kinds of behaviour: the search for food or the handling of it. In other words, the searching effort $\alpha(h(x))$ [$0 \leqslant \alpha(h(x)) \leqslant 1$; $h(x)$ is hunger level (dimensionless)] of a consumer that is not handling food is unity. To allow values below unity, $\alpha(h(x))$ has to be incorporated explicitly into the disc equation (see also Jeschke *et al.*, 2002):

$$y(x) = \frac{\alpha(h(x))ax}{1+\alpha(h(x))abx}. \qquad (A2)$$

Searching effort is the product of searching probability (of a consumer that is currently not handling food) and searching intensity. Hence, for consumers that do not vary the intensity of searching (this is approximately true for cruising carnivores), searching effort equals searching probability. It is reasonable to assume that searching effort depends on hunger level $h(x)$. We are, however, not aware of any empirical data illustrating the form of this dependency. Jeschke *et al.* (2002) assumed the simplest possible case, i.e. $\alpha(h(x)) = h(x)$. With $h(x) = 1 - cy(x)$ (see Jeschke *et al.*, 2002), we have

$$\alpha(h(x)) = h(x) = 1 - cy(x), \qquad (A3)$$

where c is the digestion time of the consumer (s). Inserting this equation into equation (A2) leads to the steady-state satiation (SSS) equation which is presented and explained in Jeschke *et al.* (2002). Here, we want a more flexible and therefore more realistic assumption for searching effort $\alpha(h(x))$:

$$\alpha(h(x)) = \frac{eh(x)}{1+(e-1)h(x)} = \frac{e(1-cy(x))}{1+(e-1)(1-cy(x))}, \qquad (A4)$$

where e [$0 \leqslant e < \infty$] is a dimensionless shape parameter (Fig. A1 A–C): for $e = 1$, equation (A4) is identical to equation (A3) (the graph of $\alpha(h(x))$ is linear, see Fig. A1 A); for $e < 1$, $\alpha(x)_{A4} \leqslant \alpha(x)_{A3}$ (the graph of $\alpha(h(x))$ is accelerating); and for $e > 1$ (which might be valid for
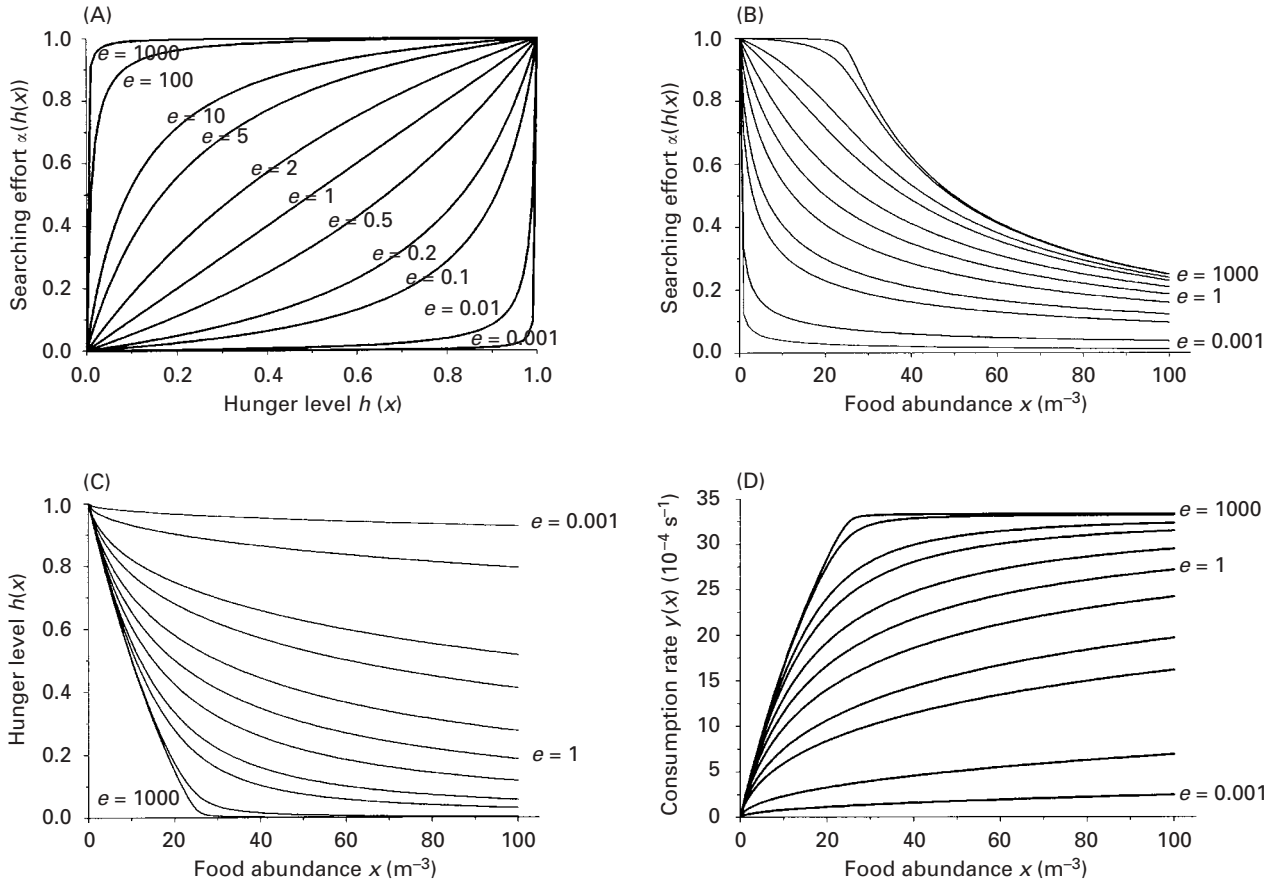
Fig. A1. Graphical representations of equations A4 (**A**, **B**) and A5 (**C** [note that $h(x) = 1 - cy(x)$, where $h(x)$ is hunger level, c is digestion time and $y(x)$ is consumption rate], **D**) with different values for the shape parameter e. In (**A**), e determines the gradient at the origin. For $e = 1$, equation (A4) is identical to (A3), and consequently, equation (A5) is identical to the SSS equation given in Jeschke *et al.* (2002). Other model inputs: success rate $a = 2 \times 10^{-4}\,\mathrm{m^3\,s^{-1}}$, handling time $b = 100\,\mathrm{s}$, digestion time $c = 300\,\mathrm{s}$.

most consumers), $\alpha(x)_{A4} \geqslant \alpha(x)_{A3}$ (the graph of $\alpha(h(x))$ is decelerating). Activities that are mutually exclusive to foraging are not explicitly considered in our model. However, the relationship between searching effort $\alpha(h(x))$ and hunger level $h(x)$ for a consumer that does not have to trade off activities against each other will probably correspond to $e \to \infty$, whereas where such trade-offs occur $e < \infty$.

Inserting equation (A4) into equation (A2) gives the following functional response equation:

$$
y(x) = \begin{cases}
\dfrac{e(1 + ax(b+c)) - \sqrt{e(4acx + e(1 + ax(b-c))^2)}}{2c(e(1 + abx) - 1)}, \\
\qquad c > 0,\ x \neq \dfrac{1-e}{abe}, \\[2mm]
\dfrac{ax}{1 + abx}, \qquad c = 0,\ x \neq \dfrac{1-e}{abe}, \\[2mm]
\dfrac{1-e}{b + c(1-e)}, \qquad x = \dfrac{1-e}{abe}.
\end{cases}
$$

(A5)

For the SSS equation and equation (A5), the gradients at the origin and the asymptotic maximal consumption rates are identical:

$$
\frac{\mathrm{d}y(0)}{\mathrm{d}x} = a,
$$
$$
\lim_{x \to \infty} y(x) = \min\left(\frac{1}{b}, \frac{1}{c}\right).
$$

(A6)

As the SSS equation, equation (A5) generally produces type II functional responses (Fig. A1 D). For large values of the shape parameter e, however, equation (A5) produces type I-like curves. This results from a step-like relationship between searching effort and hunger level at high values of e (Fig. A1 A). For the limiting case $e \to \infty$, this relationship (equation A5) becomes a real step function:

$$
\alpha(x) = \begin{cases}
1, & x \leqslant x^*, \\
\dfrac{1}{ax(c-b)}, & x > x^*
\end{cases}
$$

(A7)

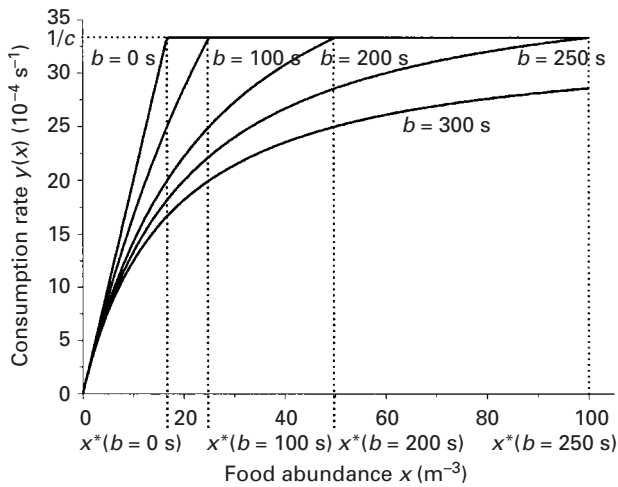with the incipient limiting level $x^* = 1/a(c-b)$.

Fig. A2. A continuum (handling time $b = 100$ s, 200 s, 250 s) between type I ($b = 0$ s) and type II ($b = 300$ s) functional responses (according to equation A8). Note that, if searching and handling are mutually exclusive (as assumed by equation A8), a consumer can only show a type I functional response if its handling time is negligibly small. Other model inputs: success rate $a = 2 \times 10^{-4}$ m^3 s^{-1}, digestion time $c = 300$ s. For $b = c$ ($= 300$ s here), equation (A8) equals the disc equation (equation A1). The incipient limiting levels x^* are according to equation (A8): $x^*(b = 0$ s$) = 16.67$ m^{-3}, $x^*(b = 100$ s$) = 25$ m^{-3}, $x^*(b = 200$ s$) = 50$ m^{-3}, and $x^*(b = 250$ s$) = 100$ m^{-3}. For all curves, the asymptotic maximal consumption rate is 33.33×10^{-4} s^{-1} (equation A6).

The functional response equation (A5) then simplifies to

$$y(x) = \begin{cases} \dfrac{ax}{1 + abx}, & x \leqslant x^*, \\[2mm] \dfrac{1}{c}, & x > x^* \end{cases} \qquad (A8)$$

or

$$y(x) = \min\left(\frac{ax}{1 + abx}, \frac{1}{c}\right).$$

The gradients at the origin and the asymptotic maximal consumption rates of the SSS equation, equation (A5), and equation (A8), are identical (see equation A6). Equation (A8) can also be derived by extending the disc equation by a digestive capacity constraint (Schmitz, 1995).

Depending on handling time b, equation (A8) produces functional responses of type I, I/II, or II (Fig. A2). Since equation (A8) is based on the assumption that $e \to \infty$, all curves have a sharp transition between their rising and their constant regions (if there is a constant region at all). (1) For $b = 0$, handling time does not affect consumption rate. The functional response therefore has a linear increase ($x \leqslant x^*$). Above the incipient limiting level ($x > x^*$), digestion time limits consumption rate which is now constant. Thus, the functional response is of type I. (2) For $0 < b < c$, increasing handling time gradually decreases the slope of the curves, and the increase is therefore not linear. However, the curves do have a constant region determined by digestion time. Thus, these curves are intermediate between types I and II. (3) Finally, for $b \geqslant c$, handling time gradually decreases the slope of the curve. The region of increase is therefore not linear. In addition, no constant region exists because consumption rate becomes limited by handling time before it can be limited by digestion time (mathematically, x^* is negative and has therefore no biological meaning). Thus, the curve is of type II.

In summary, when searching and handling are mutually exclusive, a consumer must fulfil two necessary but not sufficient conditions to show a type I functional response: (1) handling condition – it must have a negligibly small handling time ($b = 0$); (2) satiation condition – unless its gut is completely filled and gut passage time is minimal, it must search for food at a maximal rate with maximal effort ($e \to \infty$).

(2) Searching and handling completely overlap

If searching and handling completely overlap, the consumer is able to search for and to capture food while handling other food. Therefore, handling time does not affect consumption rate. The handling condition for a type I functional response must therefore be extended as follows: the consumer must have a negligibly small handling time, or it must be able to search for and to capture food while handling other food.