# Positive Feedback of Consumer Population Density on Resource Supply

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*Recent studies demonstrate positive density-dependent feedbacks between animal populations and their resource supply that result in increased individual fitness at high densities. Such feedbacks occur in both terrestrial and aquatic organisms not showing strong social organization. A number of different mechanisms are involved. Detecting positive feedbacks in natural populations may not be possible from simple correlations between resource abundance and animal population density in space or time, but experimental manipulation of resource supply or animal density can reveal their presence. Positive feedbacks may result in higher equilibrium densities of animal populations, alter the density range over which intraspecific competition is detectable, and offer a resource-based explanation for the evolution of gregariousness and social organization.*

It is generally thought that the amount of resource supply to an individual consumer within a population decreases as population density increases[1,2]. Although exceptions to this relationship are known for some highly organized animal species – such as social Hymenoptera and termites where resource acquisition is dependent upon cooperative action – the usual assumption is that for most animal populations, intraspecific competition increases, and therefore per capita growth and fitness declines, as population density increases[1,2]. A number of studies demonstrate that these seemingly logical relationships are not always true. Resource supply, and growth and fitness of individuals, can increase as population density increases for animal species that do not show complex social organization[3–8].

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Here we review some examples of positive feedbacks, indicating where individual fitness has been demonstrated to increase, illustrating some of the mechanisms responsible, and briefly considering some general consequences for population theory. (We will not address effects of consumers on the fitness of living resources[9,10], nor will we examine effects of animal populations of one species on resource availability to another consumer species.)

The idea that animal feeding activity may have a positive feedback on resource supply to the consumer has been a topic of sporadic interest for over a decade[3–19]. For example, herbivory has been shown to increase overall primary productivity and, in some cases, enhance food quality or suitability at high compared to low levels of consumption in both aquatic and terrestrial environments[3,5,7,8,11,13,19]. Similarly, overall bacterial production can be increased at high versus low densities of bactivorous meiofauna (animals between 0.5 mm and 0.1 mm in length) in aquatic sediments and terrestrial soils[20–22]. Although the rate of production of detrital resources obviously cannot be altered by detritivores, the rate of supply of such non-living resources to individual organisms has been shown to be greater at higher densities of polychaetes on mudflats[23]. In most of these studies, correlations have been made between resource abundance and animal activity or density; positive feedbacks have only been inferred.

### Positive feedback in marine and freshwater environments

In nutrient-poor environments such as coral reefs, algal turfs grazed by the sea urchin *Diadema antillarum* can be ten times more productive per unit of chlorophyll than turfs not grazed by *D. antillarum*, because of more rapid nutrient recycling[17,18]. Similarly, the primary productivity of freshwater phytoplankton in experimental microcosms was also shown to increase because of nutrient regeneration following *Daphnia pulex* (water flea) feeding (Fig. 1)[12]. Although these studies clearly demonstrate that nutrient recycling, and not grazing *per se*, is responsible for increased resource production, consumer fitness as a consequence of greater food supply was not determined.

In a recent study on the marine intertidal sediments of Delaware Bay, USA, the effects of positive feedback on consumer fitness were addressed for a conveyor-belt feeder (an animal that ingests particles at depth and egests them on the sediment surface)[5]. In these intertidal sediments, the subsurface deposit feeder *Leitoscoloplos fragilis* (Orbiniidae: Polychaeta) mainly feeds on benthic diatoms[24]; these motile prey move vertically in the sediment on a light–dark cycle. The patchy distribution of *L. fragilis* is positively correlated with local differences in benthic diatom production.

Laboratory microcosm experiments showed that benthic diatom abundance, measured as chlorophyll *a*, significantly increased with increasing *L. fragilis* density in sandy sediments containing both high and low levels of fines (clay-sized particles) (Fig. 2). Using experimental exclosures that separated the worms from diatoms, it was demonstrated that *L. fragilis* stimulated diatom growth rates as a result of its feeding activities (Fig. 3). Diatom growth rates increased because of greater ammonia regeneration at depth in the pore water (interstitial water between sediment particles) (Fig. 4). This ammonia diffused upwards to the diatoms, increasing their production. Higher concentrations of finer clay-like particles in sandy sediments were negatively correlated with *L. fragilis* abundance in the field because these fine particles impeded the upward diffusion of regenerated ammonia to the primary pool of diatoms at the sediment–water interface, reducing the magnitude of the positive feedback. The fitness of *L. fragilis*, in this case measured as percentage growth, was greater in enclosures with high worm population densities than in those with low worm densities for both sediment types.

This example demonstrates that density-dependent positive feedbacks exist that result in increased resource supply via enhanced resource production. However, density-dependent control of resource supply can occur without increases in resource production. For example, population-level control of sediment turnover and rate of sediment mixing in muddy sediments is probably important in maintaining relatively high populations of the polychaete (*Scoloplos*) *Leitoscoloplos robustus*[23], another conveyor-belt feeder. Unlike in the coarse sandy sediments of Delaware Bay, the feeding activities of both *Leitoscoloplos* species at high densities in the muddy sediments of Lowes Cove, Maine, USA, can significantly affect sediment turnover rates[23]. For example, when fed the same amounts of detritus (freeze-dried seaweed) in experimental enclosures containing muddy sediments, *L. robustus* showed higher individual growth rates at higher population densities[4]. The density-dependent increases in growth were probably due to increases in the burial and supply of food from the sediment surface down to the feeding depth (about 2 cm) because of a faster sediment turnover rate at higher polychaete densities.

The fitness of *Leitoscoloplos* species is increased in both sandy and muddy environments due to increased resource supply. However, two entirely different mechanisms are involved in the two sediment types. In the sandy sediments *L. fragilis* lives as a herbivore within a structured physical environment that is not altered by its conveyor-belt feeding activity – but where density-dependent nutrient recycling is responsible for enhanced resource production. Conversely, in muddy sediments, *L. robustus* alters the physical structure of its environment through greater sediment turnover, which results in an increase in the supply of resources at depth.

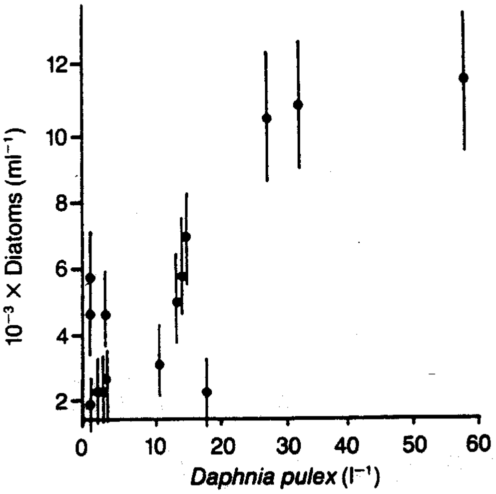


**Fig. 1.** Pennate diatom density inside grazer exclosures, where diatoms were shielded from direct grazing by *Daphnia pulex*, in treatments of different densities of *D. pulex*. [An ordinate axis value of $10^{-3}$ × diatoms (ml$^{-1}$) = 2, for example, denotes $2 \times 10^3$ diatoms ml$^{-1}$. The same form of notation is used in Figs 3 and 4.] This experiment demonstrated that fertilization of diatom production via nutrient recycling was responsible for the positive correlation between diatom density and grazing pressure by *D. pulex* observed in a previous experiment. Error bars denote 95% confidence intervals. *Redrawn from Ref. 12.*

## Positive feedback in terrestrial environments

Recent studies have demonstrated that grassland productivity is positively correlated with grazing intensity by African ungulates in the Serengeti grasslands[3,25,26]. Above-ground primary production was correlated more with grazing intensity than with rainfall, even though rainfall is a particularly important parameter affecting primary production in this system (Fig. 5). The positive feedback mechanisms responsible for increased productivity are recycling of nutrients (fecal and urine fertilization) and

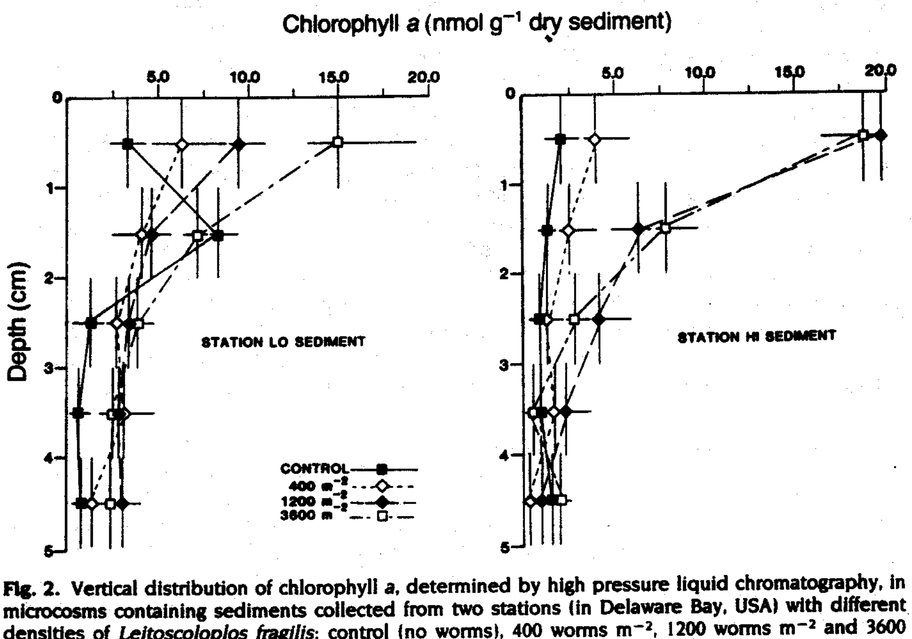


**Fig. 2.** Vertical distribution of chlorophyll *a*, determined by high pressure liquid chromatography, in microcosms containing sediments collected from two stations (in Delaware Bay, USA) with different densities of *Leitoscoloplos fragilis*: control (no worms), 400 worms m$^{-2}$, 1200 worms m$^{-2}$ and 3600 worms m$^{-2}$. Station LO sediment contains more clay-sized particles (fines) than station HI sediment. Laboratory microcosms containing one of the two sediment types were inoculated with the same amount of cultured diatoms. On termination of the experiment (60 days) sediments from each of the microcosms were collected and analysed for chlorophyll *a*. Horizontal error bars denote 95% confidence intervals. Vertical bars indicate depth intervals in the sediment. *Redrawn from Ref. 5, with permission.*

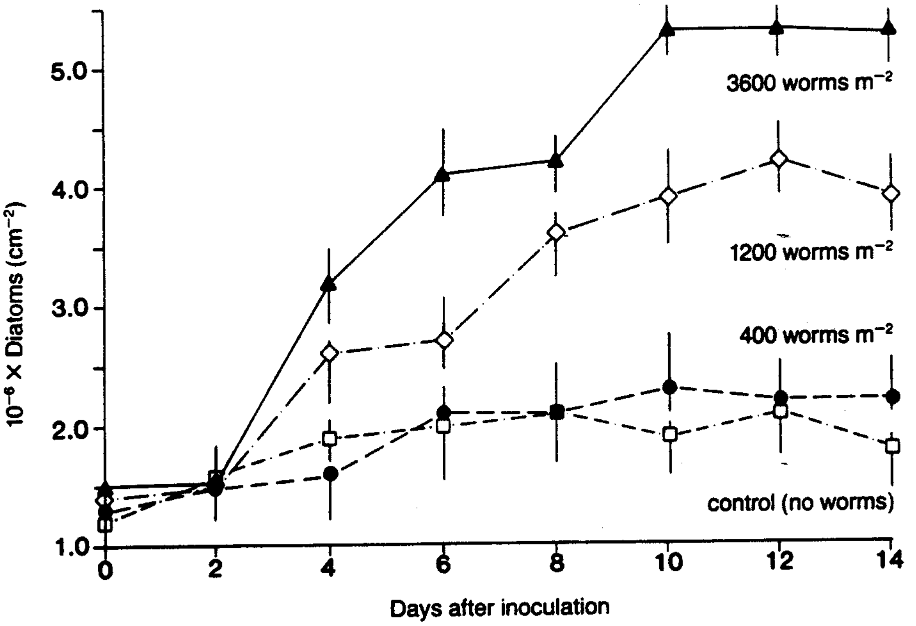


**Fig. 3.** Diatom standing stocks (determined by epifluorescence microscopy) in sandy sediments from Delaware Bay, USA, in laboratory exclosures surrounded by different densities of *Leitoscoloplos fragilis*. Diatoms were shielded from direct grazing by *L. fragilis* yet experienced different levels of nutrient recycling in treatments with different worm densities. Error bars denote 95% confidence intervals. *Redrawn from Ref. 5, with permission.*

direct grazing (grazed plants have higher production)[3]. At higher densities of ungulates, foraging efficiency of the individual grazer is enhanced because the productivity (and perhaps forage quality) of vegetation is higher. Secondary production of African ungulates is positively related to primary productivity of plants in these savanna systems[3]. Thus, individual animals may gain substantial increases in fitness, via increased foraging efficiency, when they occur in gregarious herds.

There are also positive feedbacks between asocial insect herbivores and their resources. Per capita growth and fecundity of the cabbage aphid (*Brevicoryne brassicae* L.) is higher when aphids aggregate because the amount of photosynthate flowing to the leaf is increased above that available to individuals or small groups of aphids[7]. Mass attack by many species of bark beetles (*Dendroctonus* spp.) on conifers makes it possible for beetles to overcome tree defenses, which is not readily accomplished at low beetle densities[19]. The beetles use attractant pheromones to produce a mass attack and then repellent pheromones to prevent further colonization, thereby minimizing subsequent intraspecific competition[19]. Similar feedbacks may also exist with the shoot-galling *Euura* sawflies on willows. High densities of galls result in shoot mortality and an increase in the number of susceptible juvenile shoots for subsequent generations of sawflies[8] – although in this case, per capita fitness of these sawflies as a function of density has not, to our knowledge, been examined.

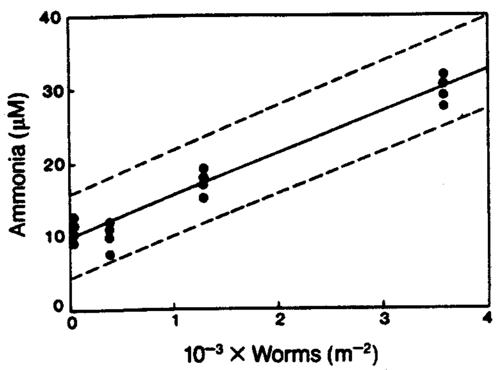


**Fig. 4.** Relationship between pore-water ammonia concentration and density of *Leitoscoloplos fragilis*; the regression is significant ($r = 0.93$, $P<0.05$; the dashed lines indicate 95% confidence intervals). Ammonia was measured using the phenol–hypochlorite method. *From Ref. 5, with permission.*

Density-dependent control of abiotic resource supply can also lead directly to greater fitness of the consumer. For example, water is a limiting resource for many animals living in deserts. In the Negev Desert, Israel, individual isopods (*Hemilepistus reaumuri*) have an increased fitness when living in dense populations, because the efficiency with which water can be obtained is controlled by density-dependent processes[6]. The greater the number of individual isopods burrowing at a particular site, the greater the probability of locating water. Failure to find water results in death. The isopods offer an interesting parallel to the subsurface 'conveyor-belt' feeding polychaetes in muddy sediments. In both situations a greater fitness is gained, per capita, at higher densities due to increases in resource supply, which both result from alteration in the physical environment where the resource is located (i.e. soil excavation or sediment turnover). The difference is that the isopods are using the excavating efficiency of higher animal densities to reach a resource that is below the soil surface, whereas the polychaetes enhance sediment turnover and resource supply from the surface at high densities. In both cases greater fitness is conferred without affecting resource production.

### Implications of positive feedback

These examples show that in some circumstances increases in per capita fitness can occur with increases in population density as a result of increases in the supply of the resource at high population densities. A number of mechanisms are involved: rapid recycling of nutrients that would otherwise be supplied at slower rates, leading to higher resource productivity (polychaetes and ungulates; stimulation of production by maintenance of highly productive stages of the resource (ungulates and sawflies); diversion of resources to the consumer (aphids); changes in resource suitability (bark beetles); and modification of the physical environment to increase the probability of finding a supply of the resource (isopods) or its rate of supply (polychaetes). All of these examples involve aggregation of individuals, but do not involve complex social organization.

Two interesting observations that arise from the studies in these systems are illustrated for two hypothetical populations in Fig. 6: one with density-dependent positive feedback ($P_F$) and one without feedbacks ($P_N$). Both populations show an overall decrease in per capita resource supply as the population grows; however, $P_F$ shows increases in supply at certain densities. The equilibrium density for each population ($ED_N$ and $ED_F$), i.e. the density at which the population is neither increasing nor decreasing, occurs at the level of per capita resource supply necessary for maintenance of growth and/or reproduction of individuals ($S_M$). First, it can be seen that the equilibrium density of the population with feedback is greater than that of the population without feedback ($ED_F > ED_N$) at the same $S_M$. Second, over a considerable range of densities, the per capita resource supply of the population with feedback is greater than that of the population without feedback, at the same density; for example at $D_1$, $S_F >> S_N$.

Thus, density-dependent positive feedback mechanisms may permit animal populations to exist at higher densities than would be expected in the absence of positive feedback. Furthermore, per capita resource supply is greater for populations with feedback than without feedback, at the same population density, for a portion of the population density range. If increased per capita resource supply results in increased individual growth and/or reproduction then, all other factors being equal, per capita fitness will also be greater. Density-dependent positive feedbacks between consumers and their resources are a form of 'Allee effect'[27], in which different equilibrium densities can occur even though both types of population are constrained to upper limits by intraspecific competition.

Positive feedbacks in natural populations are likely to be more common than one might think because, as can be seen from Fig. 6, they cannot be detected without measuring per capita resource supply at different population densities over time (either as individual growth/reproduction or individual consumption – assuming resource quality to be the same). If resource abundance is simply correlated (as standing crop) with animal population density at different spatial locations at one point in time, or if standing crop at one spatial location is correlated with population density over time, as is often the case in the literature, per capita supply (or growth/reproduction) over time in relation to population density will be unknown. Any increases in resource supply are likely to be obscured by the myriad of non-resource factors affecting population dynamics. If, however, resource supply is measured or experimentally manipulated at different population densities, and individual fitness (as growth or reproductive output) is measured, as in some of the case studies we have reviewed, positive feedbacks – together with their effects on equilibrium density and individual fitness – can be detected.

Future studies may show that positive feedbacks are common. If so, there may be important implications for our understanding of factors regulating population density. For example, the presence of positive feedbacks is likely to change the density range over which density-dependent intraspecific competition is a factor influencing population dynamics of species that lack social organization. Furthermore, the potential fitness advantages in aggregated populations that have positive feedbacks may be a strong selective force in the evolution of gregariousness and complex social organization.

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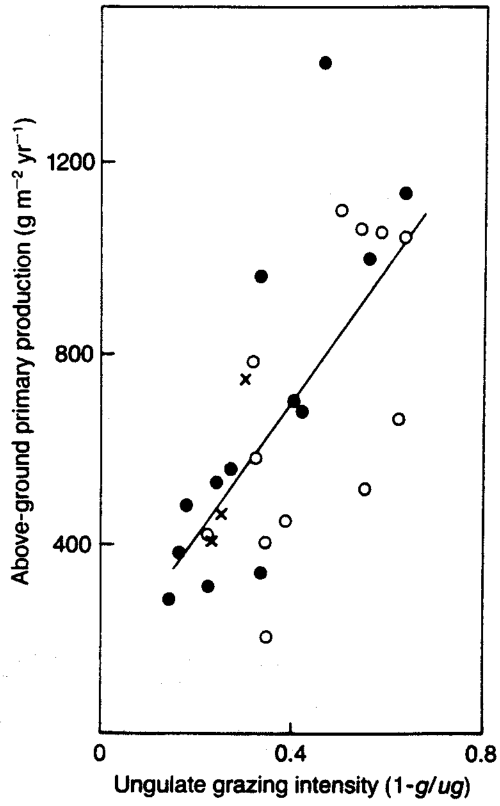


**Fig. 5.** Relationship between above-ground primary production and ungulate grazing intensity calculated as (1 – *g*/*ug*), where *g* was the biomass in grazed areas unprotected by fencing and *ug* was the biomass in the permanent exclosure. Above-ground productivity (g m$^{-2}$ d$^{-1}$) was calculated from positive biomass increments. Grazing accounted for 46.5%, and rainfall for 13.2%, of the variance in above-ground primary production. Open circles, short grasslands; filled circles, medium-height grasslands; crosses, tall grasslands; $r^2 = 0.465$, $P < 0.001$. *Redrawn from Ref. 3, with permission.*

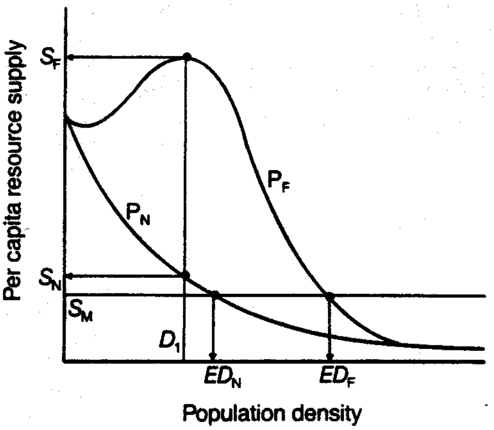


**Fig. 6.** Hypothetical relationships between per capita resource supply and population density for two populations – one ($P_F$) with density-dependent positive feedback on resource supply and one ($P_N$) without feedback. $S_M$ is the per capita resouce supply necessary for maintenance of individual growth/reproduction. $ED_N$ and $ED_F$ are the equilibrium densities (population growth = 0) for the populations $P_N$ and $P_F$, respectively. $S_N$ and $S_F$ are the resource supply values for $P_N$ and $P_F$, at density $D_1$.

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