Fig. 3. Echo soundings of solitary waves formed above the sill crest during a flood tide, with current vectors. The waves are trapped just downstream of the internal hydraulic control at the sill crest. The upper image was made 2 hours before the lower image. (Top right) Upstream density profile.

trapped waves, because the convective speed $u_{conv} = (u_1 h_2 + u_2 h_1)/(h_1 + h_2)$ increases with distance downstream. Trapped solitary waves are therefore reverse rank ordered, as may be seen for the leading waves in Fig. 3.

Although the changing background current must be considered in any detailed model of stratified flow over topography, our observations show that such flows can be quite unstable, and this instability may play a role in the generation of internal solitary waves which propagate upstream or become trapped downstream of the control.

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become trapped ("B") in the supercritical flow $(F_1^2 + F_2^2 > 1)$. Trapping is more readily observed over the gentler lee slope during flood tide. The waves in Fig. 3 were trapped for more than 2 hours. Trapped waves maintain their amplitude for extended periods, implying that growth is balanced by dissipation, which in turn determines the trapping location. Only when

the tidal current decreases and hydraulic control is lost do they escape upstream. Amplification of waves moving up the subcritical interface as in Fig. 2B, and the resultant amplitude dispersion as they become nonlinear, ensures that waves formed in the subcritical flow tend to become rank ordered, such that the largest is in front. However, this result does not apply for

Paleolithic Population Growth Pulses Evidenced by Small Animal Exploitation

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Variations in small game hunting along the northern and eastern rims of the Mediterranean Sea and results from predator-prey simulation modeling indicate that human population densities increased abruptly during the late Middle Paleolithic and again during the Upper and Epi-Paleolithic periods. The demographic pulses are evidenced by increasing reliance on agile, fast-reproducing partridges, hares, and rabbits at the expense of slow-reproducing but easily caught tortoises and marine shellfish and, concurrently, climate-independent size diminution in tortoises and shellfish. The results indicate that human populations of the early Middle Paleolithic were exceptionally small and highly dispersed.

The size of a population has much to do with its long-term prospects for survival and the potential impact of random events on its evo-

lutionary history. It is difficult to appreciate or quantify just how small early Paleolithic populations were or how thinly they were

spread during much of the Pleistocene. Thus, to assess when human populations grew during the Late Pleistocene, we analyzed trends in the small animal species most commonly eaten by Paleolithic foragers.

Paleolithic humans relied on both small animals and ungulates for meat (*1*), but predator-prey relations between humans and small animals are more sensitive indicators of changes in human population density (*2*) because small prey species vary much more than ungulate species with respect to life history and predator avoidance characteristics. In the Mediterranean Basin (Israel and

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Italy), small animals were important to human diets throughout the Middle, Upper, and Epi-Paleolithic periods (Tables 1 and 2) (3). Most common in the Paleolithic refuse middens are the remains of tortoises (mainly *Testudo graeca*), shellfish (in Italy, *Patella* spp., *Mytilus galloprovincialis*, *Ostrea edulus*, *Callista chione*, *Glycymeris* spp., *Monodonta turbinata*, and others), partridges (*Alectoris chukar*, *Perdix perdix*, *Coturnix coturnix*), hares (*Lepus capensis*), and rabbits (*Oryctolagus cuniculus*). Other small-bodied species were also consumed on occasion, including doves, waterfowl, hedgehogs, marmots, squirrels, legless lizards, and large snakes as well as ostrich eggs. Damage from fire (Fig. 1), tool marks, and percussion fractures from stone hammers link the skeletal remains of small vertebrates and

invertebrates to the feeding activities of prehistoric humans (4). Littoral mollusks and tortoises, the most easily caught small prey species, are also the most sensitive to hunting pressure from humans.

We examined two faunal series for changes in small prey composition, one compiled from archaeological sites on the western coast of Italy (Liguria and Lazio) and another from two sites 1 km apart in the Nahal Meged, an inland valley in the Galilee of Israel (Fig. 2). Each series spans the Middle through Epi-Paleolithic periods, beginning in Israel about 200,000 years ago (200 ka) at Hayonim Cave (5) and about 110 ka in Italy at Grotta dei Moscerini (6). Each series ends around the Pleistocene-Holocene boundary 10 ka. The Middle to Upper Paleolithic cultural transition occurred about 44 ka in Israel

and 36 ka in Italy. The Upper Paleolithic to Epi-Paleolithic transition in each region coincided roughly with the Last Glacial Maximum 20 to 18 ka. Neolithic cultures, which represent the transition from forager (Epi-Paleolithic hunter-gatherer) to food-producing economies began <10.5 ka in Israel and <8 ka in Italy.

The proportion of small to large game animals taken by Paleolithic humans in the two study areas shows no consistent trend over the past 200,000 years (Tables 1 and 2). However, the types of small animals most often consumed by prehistoric foragers—tortoises, shellfish, partridges, hares, and rabbits—shifted dramatically in both areas during the Upper and Epi-Paleolithic, even though the compositions of the biotic communities remained relatively stable (6, 7).

The small game species form two simple categories on the basis of how easy they are

Table 1. Relative abundances of small prey animals in the Paleolithic faunal series from Italy (Ligurian and Lazio sites combined) time-ordered from most recent to oldest. Shellfish are limpets and common Mediterranean bivalves such as mussels. Birds are mostly partridges, with lower frequencies of other game birds such as Columbiforms and Anseriforms. Other small mammals are marmots and hedgehogs. Major culture periods are Epi-Paleolithic (EP), 9 to 19 ka; Upper Paleolithic (UP), 19 to 36 ka; and Middle Paleolithic (MP), 36 to 200 ka; successive phases are indicated therein. Sites are Riparo Mochi (RM), Grotta Polesini (GPo), Grotta Palidoro (GPa), and Grotta dei Moscerini (GM).

Culture period (and site)	Age range (ka)	Small to large game (index)*	Total small game†	Tortoise (%)	Hares and rabbits (%)	Other small mammals (%)	Birds (%)	Shellfish (%)
EP Late Epigravettian (RM)‡	9 to 12	0.83	802	0	≪1	0	0	100
EP Late Epigravettian (GPo)§	10 to 11	0.02	889	0	41	1	58	0
EP evolved Epigravettian (GPa)§	15 to 16	0.01	30	0	17	0	83	0
EP Early Epigravettian (RM)	17 to 19	0.40	1176	0	45	6	34	14
UP Gravettian (RM)	24 to 28	0.21	767	0	23	15	43	19
UP Middle Aurignacian (RM)	27 to 32	0.46	416	0	2	9	12	76
UP Early Aurignacian (RM)	32 to 36	0.46	710	0	4	6	18	71
MP Middle Paleolithic (GM)	70 to 110	0.47	660	6	1	0	0	93

*Number of small game remains divided by sum of small game and ungulate remains.   †Counting units are number of identified skeletal specimens for vertebrate remains and minimum number of individuals for marine mollusks; the latter is used to correct for differences in average specimen size.   ‡Special purpose occupation based on paucity of terrestrial resources.   §Inland site for comparison with Late Epigravettian assemblage from Riparo Mochi.

Table 2. Relative abundances of small prey animals in the Paleolithic faunal series from Israel (Nahal Meged, Galilee) time-ordered from most recent to oldest. Birds are mostly partridges, with lower frequencies of other bird taxa; tortoise column includes scant remains of large lizards; hare column includes scant remains of Persian squirrels and hedgehogs. Culture periods are Epi-Paleolithic (EP), 10 to 19 ka; Upper Paleolithic (UP), 19 to 44 ka; and Middle Paleolithic (MP), 44 to 200 ka. Sites are Hayonim Cave (Hay) and Meged Rockshelter (Meg). bd, centimeters below datum. The Hayonim E 200- to 349-bd assemblage is omitted, because analysis is not complete except for the tortoise measurements in Fig. 5.

Culture period (and site)	Age range (ka)	Small to large game (index)*	Total small game†	Tortoise (%)	Hares (%)	Ostrich eggshell (%)	Birds (%)
EP Natufian (Hay)	11 to 13	0.57	1154	35	30	0	35
EP Kebaran (Hay)	14 to 17	0.17	532	77	9	2	13
EP early Kebaran (Meg)	18 to 19	0.37	730	64	12	0	23
UP Pre-Kebaran (Meg)	19 to 22	0.27	160	77	6	0	16
UP Aurignacian (Hay)	26 to 28	0.28	2950	60	5	0	34
MP (Hay 350 to 419 bd)	~150‡	0.29	437	89	5	≪1	6
MP (Hay 420 to 469 bd)	~170‡	0.39	2625	95	<1	2	2
MP (Hay 470 to 539 bd)	~200‡	0.52	2371	97	<1	1	1

*Number of small game remains divided by sum of small game and ungulate remains.   †Counting unit is always number of identified skeletal specimens.   ‡Approximate age.
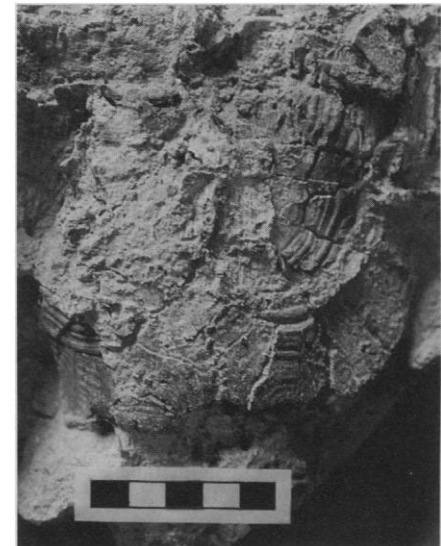

Fig. 1. Middle Paleolithic fractured tortoise (*T. graeca*) carapace preserved in cemented wood ash, from 200,000-year-old stratigraphic layer in Hayonim Cave, Israel.
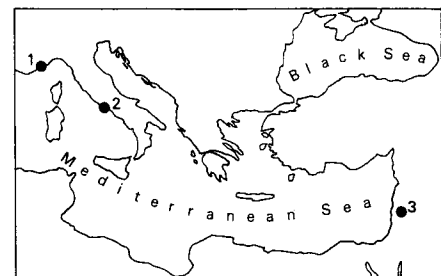

Fig. 2. Sources of archaeological sites in the Mediterranean Basin. Italy: Riparo Mochi on the northwestern coast, Province of Liguria (1), and Grotta dei Moscerini on the west-central coast and Grotta Polesini and Grotta Palidoro inland, Province of Lazio (2); Israel: Hayonim Cave and Meged Rockshelter, 1 km apart in an inland valley (Nahal Meged) in the western Galilee (3).

to catch and intrinsic potentials for population growth. We term these prey types "slow" and "quick." Tortoises and marine shellfish (in shoreline sites) dominate the Middle Paleolithic record of small game use (Fig. 3). Tortoises and most littoral shellfish are immobile or sluggish (essentially sessile) and, once discovered, are easy to collect. Because of their low metabolisms and long life-spans, these animals can exist at high densities in some habitats, where they become attractive prey. Tortoises and shellfish mature relatively slowly, however, requiring several years to reach reproductive age (2), and individuals continue to grow well into their adult years. Agile, warm-blooded animals that mature rapidly (<1 year)—mostly partridges and hares in our archaeofaunal samples—became important in human diets only later in each series (8): birds in the early Upper Paleolithic, followed by lagomorphs in the Epi-Paleolithic (Tables 1 and 2).

The youngest (Late Epigravettian) assemblage from Riparo Mochi in coastal Italy presents an exception to the trend described above in that shellfish were practically the only prey consumed (isolated point in Fig. 3), but it is clear that birds and lagomorphs were important at contemporaneous inland sites (Table 1) such as at Grotta Polesini (6, 9) and Grotta Palidoro (6, 10). By contrast, where small game are present in Middle Paleolithic sites at all, the focus invariably was on the easily caught types.

Tortoises and shellfish continued to be consumed during the Upper and Epi-Paleolithic periods, but they figured less prominently with respect to total small game intake. The range of species targeted by human foragers changed little with time except as
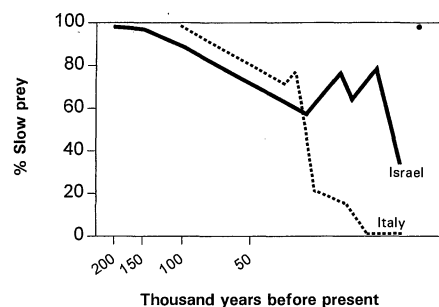
conditioned by the categorical increase in the exploitation of birds, an inherently diverse taxonomic group. Overall, however, few of the many bird and small mammal species known to have inhabited the Mediterranean Basin at the time were routinely taken (6, 7). More significant is increasingly even use of high-ranked (slow) and low-ranked (quick) small prey types with time.

Further evidence that the shifts in prey species resulted from hunting pressure and not simply climate or environmental change is that the mean sizes of slow-growing prey types decreased. Diminution was sudden for tortoises (T. graeca) in Israel (Fig. 4), beginning either in the late Middle Paleolithic or in the earliest Upper Paleolithic. Size suppression in the tortoises was sustained through the later periods. A hiatus in human occupations separates the end of the Middle Paleolithic and the Upper Paleolithic in the Nahal Meged series from Israel [Hayonim Cave and Meged Rockshelter (11) combined], however, which makes it difficult to pinpoint the onset of tortoise diminution in this faunal series. The late Middle Paleolithic (about 65 to 50 ka) and early Upper Paleolithic (Ahmarian phase, about 44 ka) levels from Kebara Cave (12) fill this gap, and, although this site is situated in a slightly richer vegetation zone where tortoises were always correspondingly larger, a significant decline in mean size is associat-

ed with the earliest Ahmarian (Upper Paleolithic) phase there. Mean size reduction in tortoises therefore took place at least 44 ka and probably earlier. Limpet (always dominated by Patella caerulea) diminution at Riparo Mochi in Italy began later, around 23 ka (Fig. 5). In each region an abrupt, significant decline in the average size of individual prey collected by foragers was sustained across major oscillations in world climate, as inferred on the basis of oxygen isotope stages and pollen and rodent chronologies (13). The diminution trends in tortoises and limpets thus are not explained by climate change or by local species replacement.

Predator-prey simulations (2) show that humans' decreasing emphasis on and coincident size suppression in slow-growing taxa could easily have resulted from overharvesting, especially if the intervals between exploitation events were shortened as human populations grew. The predator-prey simulations use life history parameters for modern Mediterranean tortoises (T. graeca and Testudo hermanni), partridges (P. perdix and A. chukar), and hares (Lepus europeaus, L. capensis, and certain North American species). Hunting offtake was increased incrementally as a percentage of the whole population until that population crashed. Population growth and the effects of hunting pressure were modeled under favorable and subaverage conditions, which produced a toler-

Fig. 3. Trend in the relative contribution of slow prey types (relative to quick prey) to the Pleistocene small game assemblages from Italy and Israel. These prey are immobile or slow-moving and population turnover rates are slow. In Italy they are primarily edible shellfish and low frequencies of tortoises; in Israel they are predominantly tortoises accompanied by scant remains of other large reptiles (legless lizards) and ostrich eggs. A mean time (ka) is used for each assemblage instead of the time range listed in Tables 1 and 2. Isolated point represents the anomalous Late Epigravettian assemblage in the Italian series; see explanation in text.

Fig. 4. Size reduction trend in spur-thighed tortoises (T. graeca) in the time-ordered assemblages from the Nahal Meged, Israel, based on mean values for the mediolateral dimension of the humeral diaphysis and standard deviations. Size decline does not coincide with changes in global climate as defined by Shackleton and Opdyke's (13) oxygen isotope stages (indicated in parentheses). A hiatus in human occupations lasting about 40,000 years separates these size groups in the Nahal Meged series. At Kebara Cave on Mount Carmel (not shown), a marked size decline in tortoises occurred about 44 ka, filling the gap in the Nahal Meged sequence. Hay, Hayonim Cave; Meg, Meged Rockshelter; *, generally colder and drier climate; ~, ages are preliminary, based on biostratigraphy, on thermoluminescence dating by E. Valladas and N. Mercier, and on electron-spin-resonance dating by J. Rink and H. P. Schwarcz.
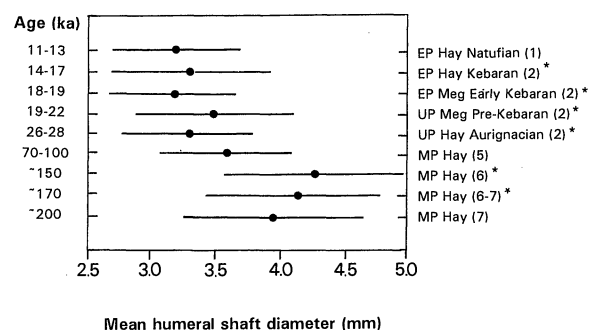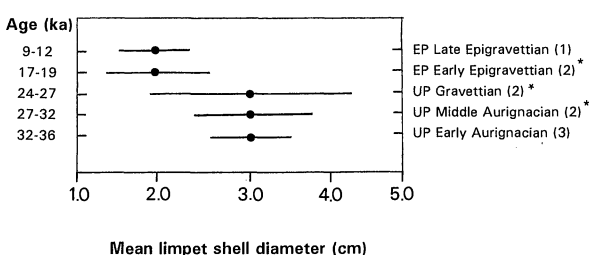

Fig. 5. Size reduction trend in limpets (mainly P. caerulea) in time-ordered Upper Paleolithic assemblages from Riparo Mochi (Liguria) in Italy, based on mean shell diameter and standard deviations. Size reduction occurred abruptly between the Gravettian and Early Epigravettian phases (about 23 ka). Although more than one limpet species is represented, there are no significant differences in species proportions among the cultural layers. Time ranges are in uncalibrated radiocarbon years based on direct and indirect dating. Symbols are as in Fig. 4.

ance range for each type of prey rather than a single, averaged measure of resilience. Differing maturation rates among the three kinds of prey proved crucial and, because of this, hare and partridge populations were minimally 7 to 10 times as resilient as tortoise populations to sustained hunting pressure (Fig. 6). Ease of capture accounts for the apparently high ranking of tortoises and littoral shellfish by Middle Paleolithic foragers. We did not model shellfish populations, but earlier studies suggest that, under conditions of intense predation, the marine mollusks normally eaten by humans are only somewhat more resilient than tortoises (14).

The prevalence of tortoise and shellfish remains in some Middle Paleolithic sites is remarkable in light of the simulation results. Shellfish and tortoises constitute at least 46% of the total number of large- and small-bodied animal remains in the early Middle Paleolithic site of Grotta dei Moscerini, Italy. Tortoises, along with a few large lizards and ostrich eggs, constitute as much as 52% of specimens identified in the early Middle Paleolithic layers of Hayonim Cave, Israel, and the tortoises collected by early Middle Paleolithic foragers were quite large on average. A high and sustained dependence on these slow-maturing animals for complete dietary protein and other nutrients implies that early human populations were exceptionally small, even by later Paleolithic standards, and that early Middle Paleolithic humans did not spend much time foraging in any one vicinity.

The trends in Paleolithic small game use can serve as a demographic barometer (2, 15). Human populations in the northern and eastern Mediterranean appear to have grown in a series of pulses, which began earlier in the east. Paleolithic foragers of the Mediterranean Rim could not dispense with small

Fig. 6. Comparison of hunting tolerance thresholds for tortoise (4 to 7%), partridge (22 to 65%), and hare (18 to 53%) populations in high (HGM) and low (LGM) growth models. Tortoise populations are far less resilient than partridges and hares to predator effects. Upper horizontal bars are crash thresholds, above which predators' dependence on that prey type is unsustainable; vertical bars represent range of variation in population resilience between the LGM and HGM; *, HGM threshold value is conservative and may be higher.

game when easily collected types were in short supply. What were once occasional shortages of highly ranked (slow) types in the Middle Paleolithic, evidenced by the rare presence of bird and lagomorph remains in the archaeofaunas, became chronic shortages 44 to 35 ka because of hunting pressure, which forced people's attention to fleeter (lower ranked) prey types. By contrast, early humans were uniformly interested in the large packages of meat that ungulates represent: there is remarkably little evidence for choosiness on the part of Paleolithic hunters when procuring ungulate species in our study areas (6, 16), apart from the elevations at which people were willing to travel to find them (17), and there are no trends in the relative contribution of ungulates to total game consumed. There appears to have been more room for adjustment in the exploitation of small animals.

Hunter-gatherers of the historic era normally obtain game birds and lagomorphs in quantity only with the help of special tools that take time to make and maintain [nets, snares, and barbed weapon tips (18)] or through communal game drives (19). We conclude that the key to ancient humans' lower ranking of birds and lagomorphs was the ability of these animals to escape quickly, which translates to a high work of capture that could be reduced only with trap-related technology. In western Asia, the timing of tortoise diminution shows that human populations increased substantially before the remarkable and rapid technologic innovations (radiations) that mark the Upper and Epi-Paleolithic periods (20). Our results show that the breadth of the human diet increased during the Upper and Epi-Paleolithic (21) and support the notion that population pressure played a significant role in the evolution of Late Pleistocene human cultures (22). Mobility was the preferred solution to local resource scarcity throughout much of prehistory. Any loss of mobility options is a grave matter for people who live by hunting and gathering. The changes in prey species during the Mediterranean Paleolithic nonetheless indicate demographic packing and associated reductions in mobility (22). The diversity of prey species consumed by humans did not substantially increase with time as supposed (23); rather, humans responded to differences in the defense mechanisms of a few key prey species as human population densities grew. Quite by accident, the differences in prey defense mechanisms to human predation correspond closely to differences in prey population resiliencies. These characteristics in turn affected the relative availability of slow and quick types as predator pressure increased. Intensified use of just a few species, a tendency also diagnostic of food-producing economies of the Neolithic, has its origins in the hunting and gathering lifeways of the later Paleolithic.

Anatomically modern humans are thought

to have evolved within the Middle Paleolithic period and overlapped for some time with human populations possessing archaic features (for example, the Neandertals). With so few people on earth, replacement of one human population with another could have involved minor differences in the intrinsic rate of increase, such as from a modest improvement in child survivorship. Low human population densities during most of the Middle Paleolithic imply that group sizes and social networks were small, which certainly limited the numeric scope of individual interactions. Under these conditions the possibilities for evolution of complex sharing and exchange behavior as ways to counter the effects of unpredictable resource supplies would also have been quite limited (20). The value of more diverse and efficient foraging equipment may have been lower as well.

Our data imply that Middle Paleolithic foragers simply did not experience the types of demographic and economic stresses that would tend to accelerate technological and social evolution of the sort typical of the Upper and Epi-Paleolithic. The zooarchaeological data, which can be dated and tied to region, clarify the timing and geographic centers of rapid population growth suggested by research on human molecular phylogenetics (24).

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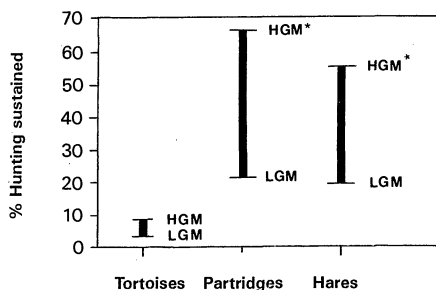
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Controlling Charge States of Large Ions

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The charge state of ions produced in electrospray ionization (ESI) was reduced in a controlled manner to yield predominantly singly charged species by exposure of the aerosol to a bipolar ionizing gas. Analysis of the resulting ions on an orthogonal time-of-flight mass spectrometer yielded mass spectra greatly simplified compared with conventional ESI spectra. The decreased spectral complexity afforded by the charge reduction facilitates the analysis of mixtures by ESI mass spectrometry.

The techniques of ESI (*1*) and matrix-assisted laser desorption/ionization (MALDI) (*2*) produce gas-phase ions of biomolecules for their analysis by mass spectrometry (MS). ESI and MALDI differ in a number of respects, including the complexity of the mass spectra produced: ESI produces a distribution of ions in various charge states, and correspondingly complex mass spectra, whereas MALDI yields predominantly singly charged ions and correspondingly simple mass spectra. This difference makes ESI generally unsuitable for the analysis of mixtures because of excessive overlap in the spectral features from the various components, in contrast to MALDI which is well suited for such analyses. MALDI, however, is less gentle and typically provides lower resolution of high-mass ions than does ESI (*3*).

In both MALDI and ESI desorption and ionization are closely intertwined, and it has not generally been possible to control the two processes independently. In ESI, buffer containing the analyte is passed through a capillary orifice maintained at a high electric potential. A stream of charged droplets is formed and subsequent desolvation leads eventually to a stream of charged ions. Previous work has explored the potential for charge reduction to simplify ESI mass spectra of large molecules. Several studies have shown that charge state complexity can be reduced by gas-phase reactions using merged gas streams containing oppositely charged species (*4*), by varying solution conditions (*5*), or by gas-phase ion-ion reactions in a quadrupole ion trap (*6–8*).

We describe here an approach that permits the charge state of ions generated in an electrospray plume to be reduced in a controlled manner, and for the resultant ions to be analyzed in an orthogonal time-of-flight (TOF) mass spectrometer (*9*). Charge reduction is achieved by exposure of the electrospray-generated aerosol to a neutralizing gas containing a high concentration of bipolar (that is, both positively and negatively charged) ions (*10*). Collisions between the charged aerosol and the bipolar ions present in the bath gas result in neutralization of the multiply charged electrospray ions (*11*). The rate of this process may be controlled by varying the concentration of bipolar ions in the bath gas, which in turn is controlled by the degree of exposure to a ^{210}Po α ionization source. This provides, in effect, the ability to "tune" the charge state of the electrospray-generated ions. A practical consequence is the ability to manipulate the charge distribution on electrospray-generated ions such that it consists principally of singly charged ions and neutrals, simplifying the mass spectra and thereby facilitating the analysis of mixtures.

The instrument has three basic components: a positive-pressure ESI source (*12*), a charge neutralization chamber (Fig. 1), and an orthogonal TOF mass spectrometer. The electrospray-generated aerosol containing analyte is swept into the neutralization chamber by a flow of medical air bath gas (4 liters/min). The neutralization chamber is cylindrical with a diameter of 1.9 cm and a length of 4.3 cm. The gas is ionized by exposure to a 5-mCi ^{210}Po α particle source, and reactions between the resultant ions and the aerosol droplets or analyte ions leads to neutralization (*13*). Two factors are important in determining the degree of charge neutralization occurring in the chamber: the α particle flux from the radioactive source and the residence time of the aerosol particles in the neutralization chamber. The α particle flux is readily controlled by placing thin brass disks with various numbers of holes punched in them between the ^{210}Po source and the neutralization chamber; the source is completely shielded by a brass disk with no holes and shielded proportionally to the exposed surface area when holes are present in the disks. The residence time of the aerosol particles is

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