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ORIGINAL PAPER

Specialized aquatic resource exploitation at the Late Natufian site of Nahal Ein Gev II, Israel

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Abstract

This paper investigates aquatic resource exploitation at the Late Natufian site (ca. 12,000 cal. BP) of Nahal Ein Gev II located 2 km east of the Sea of Galilee. Aquatic game, here fish and waterfowl, were an important component of the diverse small game resources that became important in the Late Epipaleolithic in Southwest Asia. We characterize local adaptations to the aquatic habitat and their economic and social implications at Nahal Ein Gev II. Taxonomic abundance and diversity, body-part representation, and fish body-size were investigated to evaluate the contribution of aquatic resources to human diets and butchery and transport strategies. Our results show that the residents of Nahal Ein Gev II were highly selective of the aquatic resources they captured and transported home. The hunters maximized foraging efficiency by nearly exclusively choosing the largest bodied species of fish and waterfowl and processing their carcasses to maximize meat utility before transporting them back to the site. The selectivity of these human foragers enables us to reconstruct rare details about the organization of forays for aquatic resources. When combined with evidence from other material classes from Nahal Ein Gev II and other sites, the results suggest that aquatic resource exploitation is only one of several specialized activities practiced at Nahal Ein Gev II. These along with other archaeological evidence provide evidence of task diversification that foreshadows the emergence of a more complex division of labor to come in the succeeding Neolithic period.

Keywords Zooarchaeology · Fishing · Hunting · Task specialization · Origins of agriculture · Division of labor

Introduction

The evolution of human diets and their relationship to larger patterns of human demography leading up to and across the transition to agriculture have been extensively explored in the southern Levant (Asouti 2006; Bar-Oz 2004; Davis 1987, 1991, 2005; Davis et al. 1994; Munro 2004; Stiner et al. 1999 2000 Stiner 2001; Tchernov 1991, 1994; Weiss et al. 2004). Although the expansion of human diets and small game resources have received significant attention, much less has been given to specific small game resources (but see, Bar-Yosef-Mayer and Zohar 2010; Lev et al. 2020; Simmons 2013; van Neer et al. 2005; Yeomans and Richter 2018; Zohar 2004; Zohar et al. 2018). This is true despite dramatic variation in the physiological, behavioral, and environmental characteristics of species within the small prey category which includes members from nearly all vertebrate classes, including small mammals, reptiles, birds, and fish. This wealth of variability offers an opportunity to glean new and detailed nuances of human behavior to enrich the current picture of human economic and social life at the end of the Pleistocene.

Aquatic resources (here, waterfowl and fish) play an important role in this diversification trend, although their role is more important at some sites than others (Bar-Yosef Mayer and Zohar 2010; van Neer et al. 2005). These resources are nearly universally present in Late Epipaleolithic and early Neolithic sites in the southern Levant when preservation allows (Bar-Yosef-Mayer and Zohar 2010). Aquatic resources provide important details about human foraging strategies and diet, as well as larger patterns of subsistence evolution and their social implications. For instance, they inform on human dietary change (Jones et al. 2016; Stiner and Munro 2011), early seafaring and colonization (Erlandson 2001), technological change (Colley 1987), task scheduling (van Neer 2004),

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human demography (Butler and Campbell 2004; Erlandson and Rick 2010), and the timing and intensity of human investment into the aquatic niche (Barrett et al. 2004; Erlandson 2001; O'Connor et al. 2011; Rick et al. 2001). Sites that feature aquatic resources can provide rich data about seasonality, technology, task-specific activities, and specialization.

Here, we delve into some of these topics by investigating aquatic resource exploitation at the Late Natufian site of Nahal Ein Gev II (NEG II) in the upper Jordan Valley (UJV) and its implications for the massive economic and social changes that accompanied Neolithization. Aquatic taxa are defined as species that spend a significant proportion of their life in or on water for locomotion, protection or feeding. They include fish, turtles, and birds typically referred to as waterfowl—those that swim or forage in water. By documenting which aquatic resources were exploited by humans, their costs and benefits, season of capture, processing and preparation, and hunting techniques and technologies, we characterize local adaptations to the aquatic niche and their implications for broader economic and social change. Importantly, our study goes beyond subsistence to consider the organization of foraging excursions to the Sea of Galilee, their timing and constraints. Within the context of task-specific forays to hunt and fish aquatic resources, we investigate task specialization by considering the execution of tasks that require specific knowledge, skillsets, and experience that were likely held by individuals or small subsets of the population (Costin 1991; Flad and Hruby 2007). The investigation of such task-specific activities is especially relevant on the eve of the Neolithic, a time when producer specialization emerges to play a central role in the intensification of social complexity (e.g., Bar-Yosef Mayer 2013; Quintero and Wilke 1995; Twiss 2006; Wright 2008; Wright et al. 2008).

The Upper Jordan Valley

NEG II is located in the Upper Jordan Valley (UJV), 2 km east of the Sea of Galilee (Fig. 1), the largest body of freshwater in the southern Levant. The unique ecology created by the Jordan Valley river system provided local residents with special aquatic foraging opportunities that gave a local character to the transition to agriculture in this area (see also Borvon et al. 2018; Zohar in Valla et al. 2007). The Jordan Valley differs from the Mediterranean Hills region of the southern Levant in its significant permanent freshwater system comprised of rivers and lakes that buffered the region against water stress and provided unique hunting and gathering opportunities in aquatic and wetland habitats. Diverse communities of aquatic vertebrates inhabit the UJV, which serves as a central corridor of the Mediterranean-Black Sea flyway connecting Eurasia and Africa. This corridor, one of highest traffic bird migration routes on earth, hosts an estimated 500 million birds each year (Frumkin et al. 1995). Many of these birds stop to feed, nest or winter along the way. Thus, the waterfowl populations of the UJV are abundant and diverse, but vary markedly from season to season. The freshwater bodies of the UJV currently host 26 species of native freshwater fish from six families. Nineteen of these reside in the Sea of Galilee (Goren and Ortal 1999).

Nahal Ein Gev II

Nahal Ein Gev II (NEG II; SW 261750–743280; NE 261978–743404; geographic coordinates collected by LG using GPS +/− 3 meter accuracy) is a large open-air habitation site located 120 m below sea level on the northern bank of the Nahal Ein Gev, a perennial stream fed by a spring in the western foothills of the Golan. Six seasons of excavation directed by LG, unearthed a large Natufian village (60 × 100 m^2) with a complex site plan, including several round structures, including one that encompasses a human burial area (Friesem et al. 2019; Grosman et al. 2016). NEG II is located primarily on the natural slope of a terrace cut by a meander in the stream's course, but also partially extends over the adjacent alluvial terrace. The excavation of the site focused on a portion of the eroded south section of the stream cut (ca. 540 m long).

The archaeological deposits at NEG II reach up to 2.5 m in depth in some places. The homogeneous nature of the material remains within these deposits suggests that the site was created by a single cultural entity. The stratigraphic relationship between the various architectural features suggests at least four occupation phases. The size of the site, the thick archaeological deposits, invested architecture, and multiple occupation sub-phases reveal a large, sedentary community (Grosman et al. 2016). The architecture at NEG II is constructed from local basalt and limestone blocks. Some walls are preserved to a height of ca. 1 m and are built from large stones up to 80 cm in length. One impressive wall reaches at least eight stone-courses in height and represents the remnant of a large, 6 m wide, semi-circular structure, that encompasses a multi-burial grave dug into the bedrock. Soil micromorphology and infrared spectroscopy indicate that some of the burials were covered by a massive layer of lime plaster of unprecedented quantity and quality (Friesem et al. 2019). The results demonstrate that the pyrotechnology that typifies the Neolithic had already been developed by the Late Natufian.

NEG II is radiocarbon dated to 12,000–12,200 cal. BP (Grosman et al. 2016). Interestingly, although these dates fall at the end of the Natufian period, some aspects of the architecture, technology, and other material culture are more similar to the succeeding Pre-Pottery Neolithic A (PPNA) tradition (Grosman et al. 2016). For example, although the lithic tool kit lacks PPNA attributes, the artistic style, and some architectural elements are more like those of the early

Fig. 1 **a** Map of southern Levant indicating the location of Nahal Ein Gev II and key comparative sites. **b** Aerial view of excavation area (2018)

PPNA, despite clear roots in Early Natufian traditions. Thus, in some respects, the site bridges the crossroads between the Epipaleolithic and Neolithic (Grosman et al. 2016).

Methods

The fauna from NEG II was identified using the vertebrate comparative collection from the National Collections in the Department of Ecology, Systematics and Evolution at the Hebrew University in Jerusalem. More specific identifications of some birds, namely geese and some raptors were undertaken using the avian collections of the Natural History Museum at Tring, UK. Fish were identified using the personal collections of Irit Zohar and the author. Only the fish and waterfowl components of the assemblage are treated in detail here.

Each faunal specimen was identified to the most specific taxonomic level possible. Although it is possible to identify many fish elements including vertebrae to the family level, far fewer elements (i.e., pharyngeal bones and teeth) can be identified to species. Of the commonly represented vertebrae, only the atlas and axis can be distinguished beyond the family level using diagnostic morphological criteria (Zohar 2004). Based on modern fish specimens, Zohar (2004) observed that the diameter of vertebral centra could be used to differentiate large from small Cyprinid species. Three Cyprinid species inhabiting the Sea of Galilee (*Luciocarpus longiceps*, *Carasobarbus canis*, *Capoeta damascina*) are significantly larger (greatest length 450–700 mm; Zohar et al. 2018) than the other five species. Only the vertebral centra of the large Cyprinids exceed 3.5 mm in diameter (~ 220 mm in greatest length) (Zohar 2004; Zohar et al. 2018). Cyprinid vertebral centra less than 3.5 mm in diameter may represent small Cyprinid taxa or young large cyprinids and thus are assigned only to a general Cyprinid category. The size distribution of the Cyprinid vertebrae is depicted using a histogram indicating the frequencies of centra with a spectrum of diameters.

Zohar (2004) also developed regression equations to estimate the range and average length (mm) and weight (kg) of large Cyprinids using the diameters of modern *L. longiceps* and *C. canis* atlas and axis centra. The measurements of the Cyprinid atlases and axes from NEG II were plugged into Zohar's (2004) regression equations for weight (atlas: $Y = -173.6 + 106.2 \times X$; axis: $Y = -163.6 + 1 - 4.1 \times X$) and body length (atlas: $Y = 20.6 + 37.3 \times X$; axis: $Y = 23.1 + 37 \times X$), and the resulting distributions were plotted.

Three relative abundance and two diversity indices were calculated to evaluate the contribution of aquatic resources to human diets at NEG II. These indices are compared to those from the Early Epipaleolithic site of Ohalo II and the Final Natufian site of Eynan (Ain Mallaha) to consider variation within the Epipaleolithic UJV. The relative abundance indices include (1) an aquatic resource index that measures the proportion of aquatic resources within the total assemblage, (2) an aquatic small game index that evaluates the importance of aquatic resources within the small game component, and (3) an aquatic bird index that presents the proportion of waterfowl in the avian assemblage. Two measures are also calculated to investigate diversity in the aquatic assemblage including (4) taxonomic richness (NTAXA), a raw count of the number of taxa within each aquatic assemblage, and (5) the inverse of Simpson's index ($1/P(r_i)2$) which combines measures of richness and evenness while taking sample size into account (Simpson 1949). The latter index ranges between 1 and the total number of species—values closest to zero indicate low diversity and higher values indicating higher diversity.

Body-part analyses were undertaken to determine the relative representation of the anatomical regions of the bird and fish carcasses to evaluate human hunting, butchering, and transport strategies. Fish are divided into low-utility (cranial elements) and high-utility (post-cranial elements) regions following the element divisions provided in Zohar and Biton (2011: Table 2). Special attention is given to the representation of the branchial region since this part is often removed during gutting and thus its presence or absence informs on fish processing strategies (Zohar 2004). Bird skeletons are divided into head and neck, pectoral, upper wing, lower wing, upper leg, and lower leg anatomical regions (elements listed in Levantine Upper Palaeolithic faunal recomentary Table S1). We also calculate a high-utility index which represents the relative abundance of the meat-rich pectoral and pelvic girdle (high-utility), in relation to lower-utility elements of the lower limb and feet.

Surface damage such as cutmarks (Blumenschine et al. 1996) and burning (Stiner et al. 1995) were recorded when present and are used to evaluate the butchering and processing of bird and fish carcasses, as well as food preparation strategies. The percentages of burned geese and fish specimens are compared to terrestrial prey. The percentage of burned bones is also calculated for the fish and bird anatomical regions to investigate cooking strategies.

The zooarchaeological sample

The faunal assemblage from the 2010–2017 excavations at NEG II totals 8475 identified specimens (Table 1). The sample includes all of the fauna recovered during excavation and from the 1.8 mm dry-sieve on site. Following dry-sieving, the sediments remaining in the screen were washed and then sorted (“picked”) for microartifacts and fauna in the lab. Picking is time consuming and at the time of analysis, had only been fully completed for the sediments from the 2012 and 2013 seasons (NISP = 751; 21% of the identified fauna from the 2012 and 2013 seasons). It is important to emphasize that the picked and dry-sieved samples were screened through the same sized mesh. Nevertheless, the picking process greatly improves the recovery of small items by increasing visibility and the scrutiny of the sediment under well-lit conditions. Because only two of the seven seasons of picked fauna are included in this study, we examine differences in the proportions of key taxonomic groups in the picked versus the total (picked plus field [excavation and sieved] samples) 2012 and 2013 sample to determine how this influenced our results (Fig. 2). Figure 2a shows that the relative abundance of most taxa are not impacted since the relative contribution of the picked sample to the total proportion of most taxa is more or less the same. Nevertheless, and not surprisingly, picking contributes proportionally fewer bones to the total ungulate sample than other taxa. Similarly, bones from the picking contribute a far greater proportion of the snake and especially fish elements to the totals for these taxa (Fig. 2a). Excluding five seasons of picking from our sample is thus expected to slightly over-represent the ungulates in the sample and more substantially under-represent snakes and especially fish. Since this paper concerns fish in particular, it is important to further explore how this will affect the results. The majority of fish elements from NEG II are small, compact vertebral centra that are easily hidden within small clumps of dirt in the dry-screen. Although many fish vertebrae were recovered in the screen, Fig. 2 b and c show that the smallest fish vertebrae (< 3.5 mm in diameter) were the most likely to be missed. Like the field-recovered sample, the majority of fish vertebrae from the picking fall into the large Cyprinid size category (> 3.5 mm), however, smaller Cyprinid vertebrae that could represent juvenile large Cyprinids or small Cyprinid species are more abundant in the picking than in the field fraction and are thus under-represented in the final assemblage. Given these potential discrepancies, we use the combined 2012 and 2013 sample as a completely recovered benchmark to compare the complete assemblage data in analyses where relative abundance of taxonomic groups matters.

The remains of all taxonomic groups that were likely to have been intentionally collected by humans were identified in the NEG II assemblage. This includes all ungulate and carnivore taxa, most small mammals and birds, fish, tortoises, turtles, and snakes. Excluded taxa include those typically considered microfauna—rodents, small lizards, and small Passeriforme birds. All of these taxa are rare at NEG II. Although the focus of this study is on aquatic taxa, other identified taxonomic groups are presented in Table 1 to illustrate the importance of aquatic taxa in the overall diet.

Results

As is typical of many Natufian assemblages, the NEG II fauna is nearly evenly divided between ungulates and small game, and carnivores play a less significant role (Table 1). The small game component is diverse and represented by sizeable samples of small mammals, mostly hares (*Lepus capensis*); birds, namely chukar partridge (*Alectoris chukar*), Falconiformes, and geese (*Anser* sp.); reptiles, including tortoises (*Testudo graeca*) and snakes; and fish, mostly large Cyprinids.

Aquatic taxa are quite common in the NEG II assemblage, (NISP = 739) constituting 8.7% of the total NISP. Together, they comprise 13.4% of small game, while waterfowl comprise 39.5% of the bird assemblage (Table 2). Waterfowl are represented by four species, three of which are geese. The greylag goose (*Anser anser*) (NISP = 198; 96% of waterfowl identified to species) is by far the most common. The remaining 4% of waterfowl are represented by the bean goose (*A. fabalis*; *n* = 6), and a single specimen each from the greater grey-fronted goose (*A. albifrons*), and the great crested grebe (*Podiceps cristatus*).

Only three fish species were identified, the Jordan Himri (*Carasobarbus canis*; binit gdolat cascas in Hebrew), the

Table 1 NISP values of taxonomic groups represented in the Nahal Ein Gev II assemblage from the 2010 to 2018 seasons

Common name	Latin name	NISP	Common name	Latin name	NISP
Small game			**Ungulates**		
Snake indeterminate	Colubridae	404	Equid indeterminate	*Equus* sp.	2
Mediterranean spur-thighed tortoise	*Testudo graeca*	2482	Cervid indeterminate	Cervidae	12
Starred gecko	*Stellagama stellio*	5	Roe deer	*Capreolus capreolus*	32
Fish indeterminate	Pisces indet.	91	Fallow deer	*Dama mesopotamica*	18
Minnows and carps	Cyprinidae indet.	15	Red deer	*Cervus elaphus*	10
Large barbels	Large Cyprinidae	331	Wild cattle	*Bos primigenius*	21
Jordan barbel	*Luciobarbus longiceps*	58	Wild boar	*Sus scrofa*	32
Jordan himri	*Carasobarbus canis*	9	Wild goat	*Capra aegagrus*	3
Levantine scraper	*Capoeta damascina*	5	Mountain gazelle	*Gazella gazella*	1730
Hedgehog	*Erinaceus europaeus*	8	Small ungulate indeterminate		641
Hare	*Lepus capensis*	1190	Medium ungulate indeterminate		55
Small bird indeterminate		13	Large ungulate indeterminate		31
Medium bird indeterminate		176	Huge ungulate indeterminate		3
Large bird indeterminate		114	Ungulate	Total	2590
Huge bird indeterminate		13			
Goose indeterminate	*Anser* sp.	23	**Carnivora**		
Bean goose	*Anser fabalis*	2	Wildcat	*Felis silvestris*	37
Greyleg goose	*Anser anser*	198	Jungle cat	*Felis chaus*	3
Greater white-fronted goose	*Anser albifrons*	6	Indet Canid	Canidae	9
Great bustard	*Otis tarda*	1	Red fox	*Vulpes vulpes*	289
Great crested grebe	*Podiceps cristatus*	1	Polecat	*Vormela peregusna*	13
Falconiformes indeterminate	Falconiformes	49	Marten	*Martes foina*	13
Large Falconiformes indeterminate	Large Falconiformes	2	Badger	*Meles meles*	3
Falcon indeterminate	*Falco* sp.	1	Mustelid Indeterminate	Mustelidae	4
Kestrel	*Falco tinunculus*	6	Small carnivore		18
Saker falcon	*Falco cherrug*	1	Carnivora	Total	389
Sparrowhawk	*Accipiter nisus*	1		Subtotal	8475
Buzzard	*Buteo buteo*	5			
Lesser spotted eagle	*Clanga pomarina*	1	Large mammal		2
Golden eagle	*Aquila chrysaetos*	10	Medium mammal		74
Tawny eagle	*Aquila rapax*	1	Small mammal		170
Vulture indeterminate		1			
Cinereous vulture	*Aegypius monachus*	1			
Owl indeterminate	Strigidae	2			
Barn owl	*Tyto alba*	1			
Eagle owl	*Bubo bubo*	8			
Chukar partridge	*Alectoris chukar*	232			
Pigeon/rock dove	*Columba livia*	17			
Eurasian skylark	*Alauda arvensis*	2			
Small perching bird indeterminate	Small Passeriforme	4			
Eurasian jackdaw	*Corvus monedula*	6			
Small game	Total	5496		**Grand total**	**8721**

Jordan barbel (*Luciobarbus longiceps*; binit arukat rosh in Hebrew), and the Levantine scraper (*Capoeta damascina*; hafaf in Hebrew). These are the three largest Cyprinid species that resided in the Sea of Galilee. They can be distinguished only by a few diagnostic elements including the pharyngeal bone and teeth and the atlas and axis (Zohar 2004). Of the

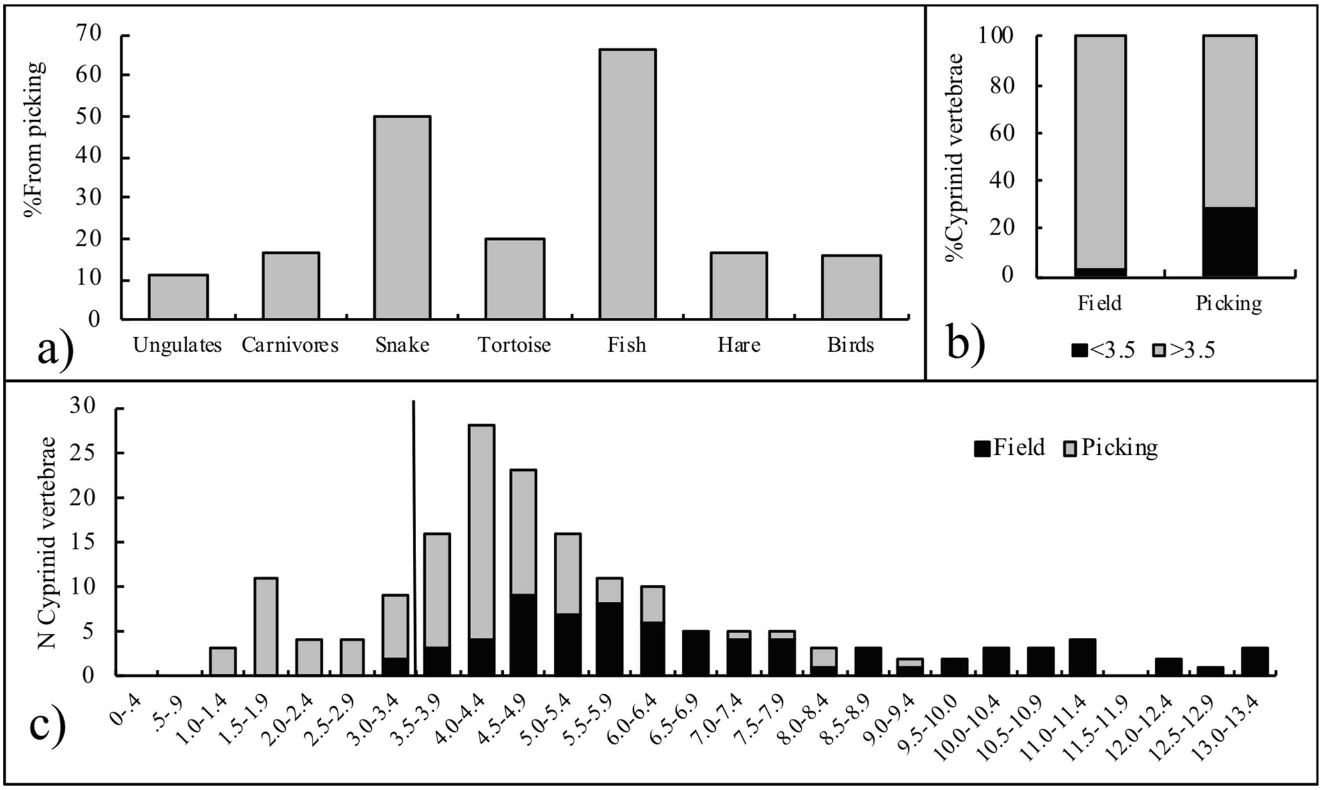

Fig. 2 **a** The proportion of each of the key taxonomic groups contributed by fauna recovered during picking. **b** The proportion of Cyprinid vertebrae < 3.5 mm and > 3.5 mm in diameter recovered in the field (1.8 mm dry sieve and during excavation) versus the picked sample. **c** Frequency distribution of Cyprinid vertebral diameter measurements (in mm) indicating field-recovered versus picked specimens

elements that could be assigned to species (NISP = 72), most were identified as *L. longiceps* (80.5%), although *C. canis* (12.5%) and *C. damascina* (7.0%) are also represented. All of the remaining fish specimens (mostly vertebrae) were less diagnostic and those that were sufficiently complete to be identified to the family level all belong to the family Cyprinidae. No other fish families that resided in the Sea of Galilee were identified.

The majority of the vertebral centra in the Cyprinid assemblage are wider than 3.5 mm in diameter (88.2%; Fig. 3) and derive from large Cyprinids. The remaining vertebrae with diameters < 3.5 mm may belong either to small Cyprinid species or juvenile large Cyprinids. The majority of these were recovered from the 2012 and 2013 picking, and thus are undoubtedly under-represented in the final assemblage. If the smaller vertebrae are equally abundant in the picked samples from other excavation seasons, the relative proportion of vertebrae < 3.5 mm could increase by up to 5% once the remaining picked fauna is added to the assemblage (see Fig. 2 b and c and comparison of picked and field recovered fauna below). The distribution of the centra measures (Fig. 3) form a more or less normal distribution concentrated in the 3–6.5-mm range with a very long tail extending to the right (larger) end of the graph. The left hand slope of the normal distribution dips into the < 3.5 mm size range, suggesting that many of the smaller vertebrae are part of this large Cyprinid distribution. An exception is the small peak at 1.5–1.9 mm which is separate from the dominant distribution and suggests that a small Cyprinid species may also be represented, though in significantly smaller quantities (see below). Thus far, no teeth, pharyngeal bones or atlases or axes of small Cyprinid taxa have been identified.

The distribution of Cyprinid body-lengths and body-weights (Fig. 4) estimated from the diameter of the atlas and axis centra (Zohar 2004), reflect a range of body sizes averaging about 1 kg in weight (963 g ± 421.1) and 316 mm in

Table 2 Relative taxonomic abundance and diversity indices for NEG II and the neighboring Epipaleolithic sites of Eynan (Ain Mallaha) and Ohalo II

Prey index	NEG II	Eynan	Ohalo II
%Aquatic of all fauna	8.7	N/A	N/A
%Aquatic of small game	13.4	N/A	N/A
%Waterfowl of all birds	25.6	60.9	92.5
Species richness waterfowl	4	18	46
Species richness fish	3	9	8
Inverse of Simpson's index waterfowl	1.09	5.65	6.17
Inverse of Simpson's index fish	1.5	N/A	1.99

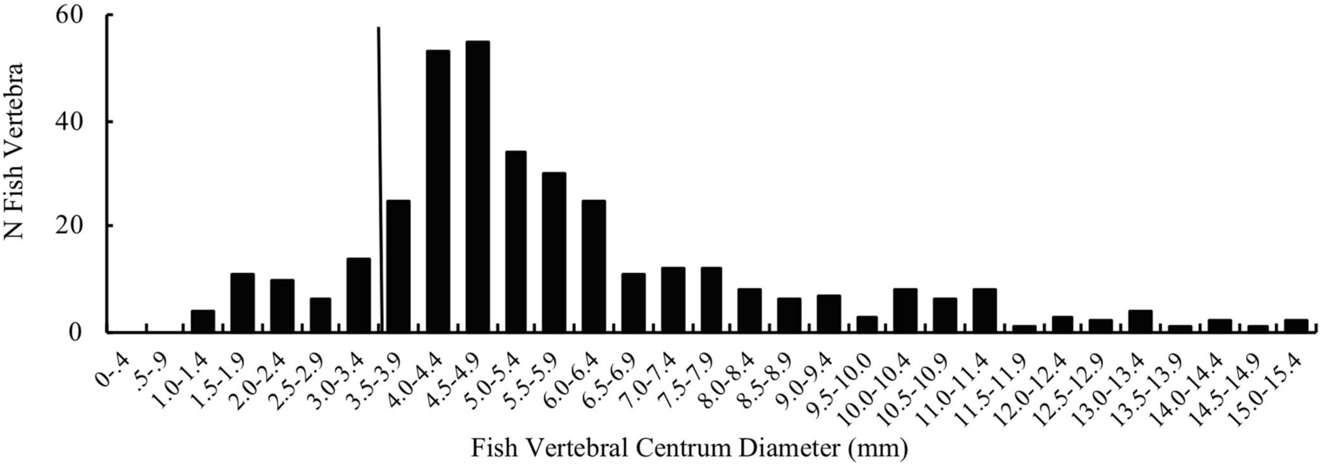

Fig. 3 Distribution of fish centrum diameters (in mm) recovered from complete sample from NEG II. Vertical line indicates > 3.5 mm dividing point for large Cyprinids

length (± 111 mm). All of the lengths fall within the large Cyprinid category (> 220 mm; Zohar et al. 2018, Table 1), except the smallest specimen which sits on the border (213 mm).

Body-part representation

The postcranial elements, namely vertebrae, of the large Cyprinid skeletons are significantly more abundant at NEG II (77.9% of NISP) than expected in a complete fish skeleton (33%) ($\chi^2 = 122.94$, $p < 0.00001$; Table 3; observed values from Zohar and Biton 2011). The bias against the cranial region is even more notable given that the dense pharyngeal teeth of the post-branchial arch located immediately caudal to the cranium but are included in the cranial group in this analysis. This is true despite the fact that the pharyngeal teeth are especially resistant to post-depositional processes and thus are often over-represented in archaeological contexts (Marder et al. 2015; Zohar and Biton 2011).

Elements from the pectoral (breast) region, particularly the coracoid, dominate the goose body-parts from NEG II (Fig. 5; Supplementary Table S1). Wing and upper limb bones are present, but in much lower quantities. Elements from the head, axial, and foot regions are nearly absent. Other than the wing bones, this profile is very similar to that of the terrestrial

Fig. 4 Body mass and body length distribution of Cyprinids estimated from centrum diameter of atlases and axes

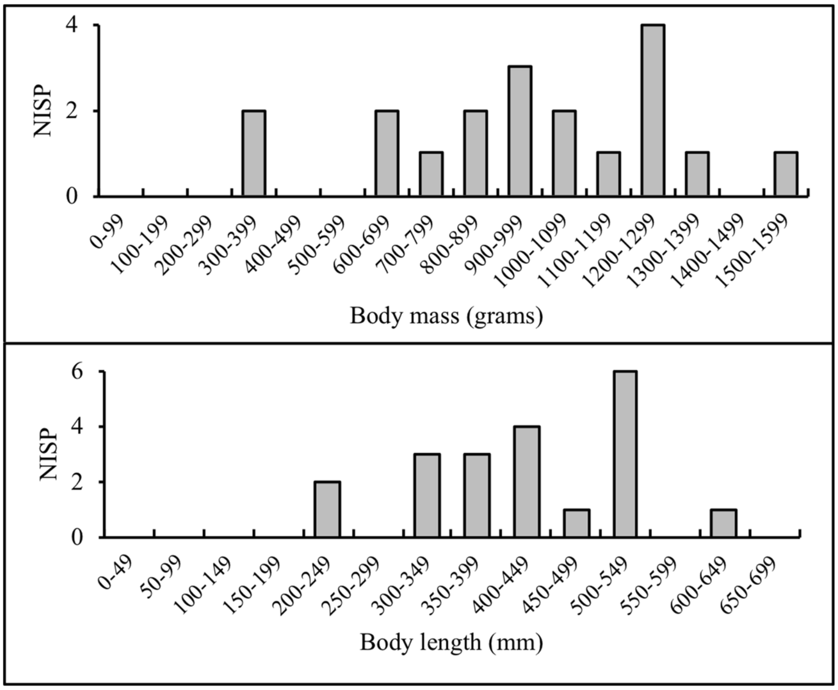

Table 3 Observed and expected values of Large Cyprinid cranial and post-cranial body-parts from NEG II. Expected values from Table 2 in Zohar and Biton 2011

Taxon	Cranial	Postcranial	Total	%Postcranial
Cyprinid expected	145–155	59–69	204–224	32.0
Fish indeterminate	31	59	90	65.6
Cyprinid indeterminate	2	13	15	86.7
Large Cyprinid	89	314	403	77.9
Total fish	122	386	508	76.0

chukar partridge, which is also common at NEG II (Fig. 5), but it differs dramatically from the Falconiformes which are represented nearly exclusively by elements of the lower limbs, feet, and wing tips (Fig. 5). An index comparing high-utility elements—those associated with the most meat (scapula, humerus, coracoid, furculum, pelvis, and femur)—with low-utility elements associated with no meat (phalanges and tarsometatarsus), highlights the sharp discrepancy in the representation of these taxa—while the partridge and goose skeletons are nearly entirely dominated by bones associated with the meaty breast, the Falconiformes are nearly exclusively represented by low-utility foot bones (Fig. 6; Supplementary Table 2).

Cultural modifications

Cutmarks are scarce in the aquatic game assemblages. One goose humeral fragment bears a series of short parallel incisions across the deltoid crest, and one possible cut was observed on a proximal goose coracoid (cutmarks 0.9% of geese). Cutmarks are rare in the NEG II assemblage in general—only 1% of specimens were affected in total.

Burning damage is far more common. It may have occurred during cooking or through indirect heating of the archaeological sediments following disposal. Four percent of goose bones and 7.5% of large Cyprinids were burned (Table 4). The proportion of burning on goose bones is identical to partridges (3.9%) and slightly lower than other small game taxa like tortoises and snakes (Table 4). Burning on the goose skeleton is highest on the neck, upper wing, and upper leg regions, while the bones of the pectoral girdle, are burned only 2.3% of the time (Table 5). Burning is nearly twice as common on the Cyprinid cranial elements (11.9%) than on the post-cranial skeleton (6.1%; Table 5).

Discussion

That aquatic resources contributed to human diets at NEG II (9% of total NISP) is not surprising given the site's location immediately adjacent to a permanent spring and 2 km from the largest permanent freshwater body in the Levant. More interesting is that, despite high fish and bird diversity in local aquatic habitats, very few fish and waterfowl species were selected and transported to the site. Over 98% of the aquatic taxa identified to species derive from only three fish and one waterfowl species. Although a minor peak of small Cyprinid vertebrae suggests the presence of a small, as of yet unidentified, Cyprinid taxon in the NEG II assemblage, the vast majority of the fish assemblage belong to the largest Cyprinid species in the region (*Carsobarbus canis*, *Luciobarbus longiceps*, and *Capoeta damascina*). This is true even though 19 species of fish from six families (Zohar et al. 2018, Table 1) inhabit the Sea of Galilee. The same is true of the bird assemblage. Although four species of waterfowl are represented, 96% of them derive from the greylag goose, despite the fact that myriad large waterfowl species are available in the Jordan Valley at different times of year.

The four primary aquatic taxa targeted by the Natufians all fall at the large-bodied end of the spectrum of available aquatic taxa. Other than catfish, which have not been found at NEG

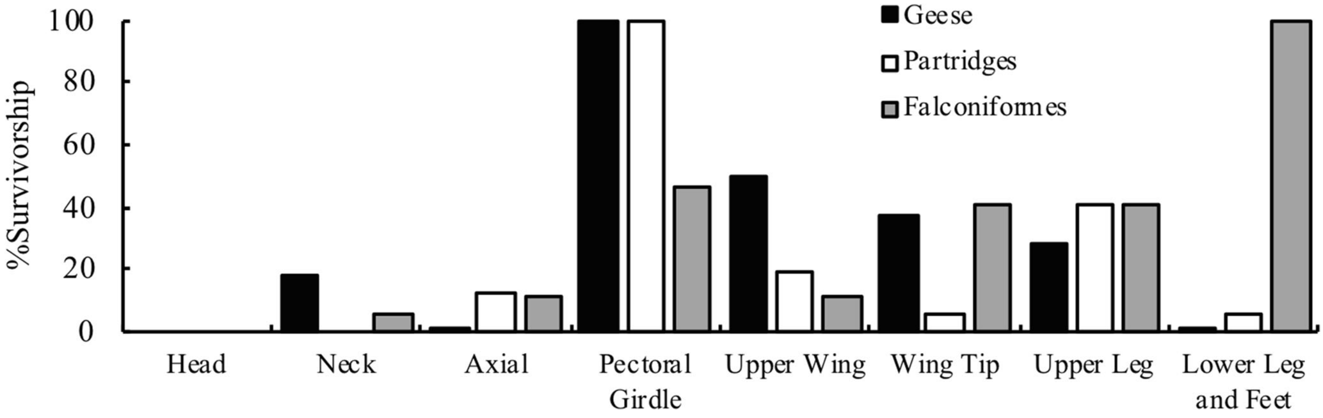

Fig. 5 Body-part representation of geese, partridges, and Falconiformes from NEG II

Table 4 Proportion of burned bones from common taxa represented at NEG II

Taxon	NISP	Burn NISP	%Burn
Deer	72	8	11.1
Aurochs	21	4	19.0
Wild boar	32	3	9.4
Gazelle	1730	136	7.9
Fox	289	20	6.9
Felids	40	4	10.0
Mustelids	33	3	9.1
Snakes	404	22	5.4
Tortoise	2482	145	5.8
Large Cyprinids	389	29	7.5
Hare	1190	99	8.3
Geese	229	9	3.9
Chukar partridge	232	9	3.9
Falconiformes	77	4	5.2
Total	7220	495	6.7

II, the three Cyprinids would have been the largest fish in the Sea of Galilee during the Epipaleolithic. All reach reproductive maturity at around 200 mm in length. Adult *L. longiceps* are the largest, growing to 500–700 mm, while *C. canis* commonly reaches 400–660 mm in length (Fishelson et al. 1996) and *C. damascina* grows to about 500 mm (Krupp and Schneider 1989). Furthermore, vertebral measurements show that many of the individual fish represented at NEG II fall into the upper half of the body-size range with estimated lengths between 326 and 625 mm

Table 5 Proportion of burning on goose and fish skeletons by anatomical region

Anatomical region	NISP	N Burned	%Burned
Geese			
Head	0	0	0.0
Neck	28	2	7.1
Axial	1	0	0.0
Pectoral girdle	87	2	2.3
Upper wing	44	4	9.1
Wing tip	47	0	0.0
Upper leg	15	1	6.7
Lower leg and feet	4	0	0.0
Total	226	9	4.0
Fish			
Cranial	75	8	10.7
Postcranial	386	23	6.0
Teeth	47	2	4.3
Total	508	33	6.5

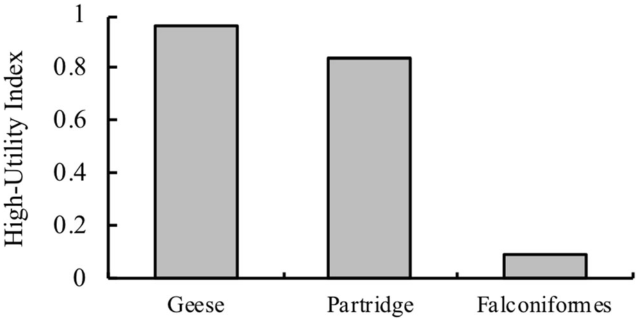

Fig. 6 High-utility index of geese and partridge and Falconiformes skeletal elements from NEG II high-utility bones include elements of the pectoral girdle. Low-utility bones include the lower limb and feet.

A similar pattern is true of the waterfowl recovered at NEG II. Geese are large birds; the greylag goose averages 3.3 kg in weight but can reach up to 4.5 kg (Dunning 1992). Geese were not the biggest waterfowl available in the region, but they fall at the large end of the spectrum. The large size of the goose is more apparent when compared to the most commonly hunted terrestrial avian species at NEG II, the chukar partridge, which weighs about 0.5 kg on average. The results clearly show that the Natufians who visited the Sea of Galilee to fish and fowl were highly selective in their choice of large-bodied species.

The representation of Cyprinid and goose body-parts at NEG II diverges strongly from a complete skeleton model. In the case of Cyprinids, cranial elements are strongly underrepresented in comparison to post-cranial parts, particularly vertebrae. The cranium group includes elements from the branchial region which because it includes the dense pharyngeal teeth, should preserve well in the archaeological record. The underrepresentation of the branchial and cranial elements in the fish body-part profiles strongly suggests that many of the NEG II fish were processed before they were transported to the site. Processing fish the size of the large Cyprinids typically involves cleaning and gutting which keeps the flesh fresh for later consumption. Gutting is achieved by slitting the fish ventrally along its sagittal plane which often dislodges the bone elements from the branchial region (Zohar et al. 2001). The head has limited nutritional value and is often intentionally removed (Zohar and Cooke 2019). The disposal of body-parts with little nutritional value including the crania and guts at the place of acquisition, reduces carcass weight, increasing the energetic value of the fish that can be carried back to the site.

The goose assemblage is also dominated by high-utility anatomical regions. The pectoral girdle (the shoulder and breast) are the meatiest parts of the carcass (Tchernov 1994) and the best represented anatomical region, followed by the upper wing, the lower wing, and the upper leg. The rarity of lower limb, foot, neck, and head elements suggest that like fish, the low-utility parts were trimmed from the carcasses prior to transport. The pattern contrasts sharply with the body-part representation of birds of prey at NEG II which clearly were not consumed. The raptors are represented nearly exclusively by toe and lower limb bones, especially the terminal phalanges—none of which associated with meat. This is a well-known pattern for raptors whose feathers and foot bones most often served symbolic purposes in the Paleolithic and early Neolithic periods (Kuhn et al. 2004; Rabinovich 2003; Stiner 2005). Like the Cyprinids, the body-part profiles of geese, provide clear evidence for processing to remove low-utility body-parts and the selective transport of body-parts associated with the largest meat yields.

Seasonality

The Cyprinid taxa targeted by the Natufians are predatory or omnivorous species that often forage in shallow waters. Because the shallows along the east coast of the Sea of Galilee are narrow, the part of the lake closest to NEG II is one of the least productive fishing areas in the lake (Troche 2016). Historic documents indicate that fisheries were operated only on the central east coast during winter and early spring (Jan-April) (Masterman 1908; Troche 2016). In this season, the large Cyprinids and other species, liked to forage close to the coast when small fish (especially *Acanthobrama terraesanctae*; Kinneret "sardine") were abundant in shallow waters, feeding on algae blooms fed by the influx of nutrient-saturated water into the lake following the winter rains (Troche 2016). The large Cyprinids are also easily caught when spawning in the shallows of the Sea of Galilee during winter (December through March; Fishelson et al. 1996). Although the large Cyprinids could have been exploited at any time of the year, fish were most accessible when they were close to the shore in the winter months.

Today, the greylag and white-fronted goose are rare winter visitors in the UJV (Paz 1987). Their abundance in prehistoric assemblages from the region suggests that they were regular winter visitors in the past. The same may be true of *A. fabalis* which, although it is a vagrant today, may have been an occasional visitor during the Epipaleolithic. The great-crested grebe is much more common but also frequents the Sea of Galilee only in winter (Paz 1987). Thus, regardless of how often and in what numbers these taxa visited the region, they were only available in winter, limiting the hunting season. The waterfowl and potentially the fish thus provide a similar seasonal signal, suggesting that the residents of NEG II obtained aquatic resources from the Sea of Galilee in winter and early spring (January–April). Over-wintering birds also dominate the waterfowl assemblage at Ohalo II and both the EN and Final Natufian components at Eynan.

Although there are few opportunities to assess seasonality in the NEG II assemblage, the evidence does not signal an exclusively winter occupation. Some fish may have been captured in other seasons, and the gazelle tooth wear data indicate summer or early autumn presence (early stage II [3–7 months]; Munro et al. 2009). In addition, the small Cyprinids indicated by the minor peak on the vertebral centrum histogram, may have been captured in the Nahal Ein Gev immediately adjacent to the site at any time of year.

Fishing technology

In combination with technological evidence, the taxonomic composition, and body-size of fish represented at NEG II provide clues about fishing techniques. A range of technologies with different manufacture, maintenance, and handling costs were available to Epipaleolithic people, including bare hands, lines and hooks, barbed points, and nets and traps such as weirs and baskets (Colley 1987; Bar-Yosef Mayer & Zohar 2010; Nadel et al. 1994). Because many of the components of fishing technologies are organic and thus perishable (i.e., fishing lines, traps, nets), we must rely on the few primary technological parts such as bone fish hooks, in combination with secondary technological components such as line or net sinkers to reconstruct past fishing techniques.

No fish hooks, the most direct evidence for prehistoric fishing, have been recovered from NEG II although they were found at other Natufian sites located adjacent to permanent waterbodies in the UJV such as Eynan and Jordan River Dureijat (Sharon et al. 2020; Stordeur 1988; Valla et al. 2004, 2007). Some researchers (Bar-Yosef and Tchernov 1970; Campana 1989; Stordeur 1988) have argued that the small bone bipoints (often called gorges) commonly found in Natufian sites, served as hooks, citing ethnographic examples. Nevertheless, others have suggested that these may have served other functions, such as fasteners for clothing (Klein et al. 2017). A small sample of bone gorges (< 5) were recovered at NEG II. Other well-preserved evidence for fishing comes in the form of grooved stones that likely served as sinkers that pull a hook and line or a net under the water (Fig. 7). The groove circling these stones provides a recess into which a line can be fitted and tied. To date, 22 grooved stones averaging 56 ± 22.6 g have been recovered at NEG II. Their variability in size and weight suggest that they served as sinkers for fishing nets (e.g., gill nets) rather than fishing lines (line weights usually weigh less than 30 g; Cavulli and Scaruffi 2011).

The ethnographic and historic information, the biology, taxonomic representation, and body-size range of the fish from NEG II suggest that selective fishing techniques were likely used to target only the largest fish. A likely candidate is a net, such as a cast or gill net, with a large mesh size designed to entrap larger-bodied fish. The size of the mesh determines the size of the fish that can be captured (Galili et al. 2013). Gill or vertical nets are especially selective, since they allow smaller-bodied fish to pass through, while preventing larger

Fig. 7 Grooved stone from Nahal Ein Gev II, possible fishing weight

fish from penetrating the net far enough to get trapped (Morales 2007). Cast nets with larger meshes could have easily been deployed by wading fishermen to selectively target large-bodied Cyprinids while they were breeding in the littoral zone of the Sea of Galilee during the winter months, although gill nets are also potential candidates given the size of the net sinkers and the narrow size range of most fish captured at NEG II.

Specialized hunting and fishing of aquatic taxa at Nahal Ein Gev II

The taxonomic data indicates that the hunter-fishers of NEG II were highly selective when it came to aquatic resources. This selectivity is even more pronounced when compared to the much more diverse fish and waterfowl assemblages from Ohalo II and Eynan which have eight and four times the respective number of aquatic species than NEG II (Table 2; Borvon et al. 2018; Bouchud 1987; Bridault et al. 2006, Desse 1987; Pichon 1987; Simmons 2013; Simmons and Nadel 1998; Zohar et al. 2018). The same is true of the inverse of Simpson's Diversity Index for birds which is nearly five times greater at Eynan and 6 times greater at Ohalo II than at NEG II. Unlike NEG II, the waterfowl at these two sites is not limited to over-wintering taxa. Fish diversity is also 50% higher at Ohalo II (Table 2) than at NEG II. A detailed analysis of the fish has not yet been completed for the new excavations at Eynan, but in progress work on a single Final Natufian structure (228) revealed thousands of fish bones (NISP = 7475 and counting; Borvon et al. 2018). At least six species of fish representing a wide spectrum of body-sizes have been identified thus far.

The fundamental differences in species diversity and the importance of aquatic species in the diet are likely related to the proximity of aquatic opportunities offered by different site locations. Ohalo II sat literally on the shore of the Sea of Galilee, while Eynan was located very close to the wetlands associated with Paleolake Hula. In contrast, although residents had access to smaller fish in the Nahal Ein Gev immediately next to the site, NEG II was located 2 km from the much larger catchment of the Sea of Galilee. The focus on large-bodied taxa, high-utility body-parts and the restriction of fishing and waterfowling to seasons when resources were most concentrated and abundant, mitigated travel and transport costs. The distance clearly limited more opportunistic exploitation of the Sea of Galilee by the residents of NEG II at most times of year.

In summary, these data reveal that many of the decisions made by the residents of NEG II regarding the taxa, body-size, processing, and transport of aquatic resources were guided by efficiency. They selectively fished and hunted large taxa that provided the highest returns; they invested in field processing, and then transported the higher-utility body-parts back to NEG II. Furthermore, they nearly exclusively engaged in the acquisition of aquatic resources in the seasons when they were most accessible, abundant, and concentrated, thus minimizing capture costs.

Despite these economic constraints, the taxonomic representation of aquatic resources indicates that Epipaleolithic foragers also made choices unrelated to economics. Interestingly, like at NEG II, a single species also comprises a significant component of the waterfowl assemblage at Ohalo II and Eynan, though the species differs at the three sites. At Ohalo II, the great crested grebe (*Podiceps cristatus*) is most common, while the mallard duck (*Anas platyrhynchos*) is most numerous in EN and FN Eynan (more so in the EN). Like the geese of NEG II, these species are winter visitors; all three congregate in large groups and were likely present in large numbers. This pattern could be related to differential availability of waterfowl related to local variability in ecological conditions, but it may equally relate to cultural tradition. The same is true of the fish assemblage. Though people focused on large-bodied Cyprinids, the largest fish inhabiting the Sea of Galilee (1500 g maximum), the catfish (*Clarias gariepinus*), is absent from NEG II. This could be related to more practical issues such as seasonality, catfish are easiest to catch when breeding in shallow nearshore lagoons in spring and summer (Goren and Gasith 1999), to food preferences related to its taste or the texture of its meat, or for more esoteric reasons related to group identity or beliefs. Scholars of the Natufian (Belfer-Cohen et al. 1995; Le Dosseur and Marèchal 2013; Valla 1999) have long noted pronounced differences in the representation of certain artifacts at Natufian sites. For example, the relative abundance of personal ornament types varies dramatically from site to site—with certain types abundant at some sites, but absent from others (i.e., distal partridge tarsometatarsi at Hayonim Cave and Eynan; pierced fox teeth at Hayonim Cave, distal gazelle phalanx beads at Eynan and Wadi Hammeh 27). Belfer-Cohen et al. (1995) argued that this relates to group identity and variation in cultural tradition among local groups. Potential preferences for food species add a novel dimension to such arguments, especially given the conservative, yet powerful role of tradition and identity in human food choices (MacClancy 1992).

Task-specific activities and task specialization at NEG II

The importance of aquatic resources at NEG II is undoubtedly linked to broader evolutionary shifts in resource acquisition that typify the Natufian period. As average foraging efficiency declined across the Upper Paleolithic and Early and Middle Epipaleolithic periods (Stiner et al. 2000), it ultimately became cost-effective to hunt small, and quick animal taxa despite reduced foraging efficiency. After the threshold to accept these animals into the diet was crossed, a wide range of taxa became available for more routine human consumption including small mammals, birds, reptiles, and fish. With these resources came a new and diverse array of behavioral characteristics, ecologies, and escape strategies that had to be learned and overcome by human hunters—geese and large Cyprinids at NEG II are only two of many very different prey types in which the Natufians invested (Munro et al. 2018; Tchernov 1994). The capture of such a wide array of taxa necessitated sophisticated scheduling, knowledge, technological improvements, and decision-making related to prey acquisition. Accordingly, the knowledge and skills required to undertake each foraging task became increasingly specialized as foraging diversified.

Aquatic resource acquisition at NEG II reflects engagement in planned, specialized, task-specific subsistence activities (Erlandson and Fitzpatrick 2006). The residents of the site traveled to the Sea of Galilee with the goal of capturing geese and large Cyprinids in winter. These activities required knowledge of the ecological characteristics of the relevant species—their seasonal schedule, foraging territories, distribution, and escape behavior among other things. Both fishing and fowling require sophisticated and invested technologies such as bows and arrows, traps and nets that require skill and practice to operate (Erlandson and Fitzpatrick 2006). The modest contribution of fish and geese to the NEG II diet, the skillset required, and the seasonally restricted nature of this activity suggest that this knowledge and skill was exercised only occasionally, likely by a subset of the population.

Fishing and waterfowling are only two of several task-specific activities visible in the material record at NEG II. Another example is provided by flint perforators (borers and awls) used for drilling. These are typically found in Natufian assemblage but are unusually abundant at NEG II and the neighboring contemporary sites of Huruq Musa and Gilgal II, where they are by far the most common tool types (24–38%; Dag and Goring-Morris 2010; Grosman et al. 2016; Rosenberg et al. 2010). Other material evidence from NEG II shows that once produced, these perforators were used for other tasks including the manufacture of shell beads and piercing soft limestone pebbles. The flint perforators are not only numerous, they are also unusually uniform in their dimensions and retouch modifications, indicating a more standardized manufacture process. The shell beads from NEG II were made from *Cerastoderma* shells collected from the Mediterranean Sea and from fossil beds located within 500 m of the site (Shaham and Grosman 2019). The recovery of shells in all stages of manufacture—unmodified, undrilled bead pre-forms, partially drilled specimens and finished products—clearly demonstrates that the beads were produced at NEG II. In addition, like the perforators, the uniform dimensions of the finished shell beads, and similarities in the shapes of the pre-forms suggest a standardized manufacture process directed toward a specific outcome (Grosman et al. 2016).

Importantly, evidence for the manufacture of very high-quality plaster is also found in several installations, and burial contexts at NEG II (Friesem et al. 2019). Chemical analyses (FTIR) and micromorphological observations indicate that the plaster is of uniformly high-quality—it was produced at very high temperatures from pure calcium carbonates (Friesem et al. 2019) and differs from the plasters made with clay inclusions in the succeeding Pre-Pottery Neolithic periods (Goren and Goldberg 1991). The process required to manufacture this kind of high-quality plaster involves heating limestone at high temperatures beyond that of a typical campfire (> 700 °C), maintaining this temperature for a few hours, and slaking the limestone with water for long enough to complete the chemical reaction needed to transform limestone into plaster (Friesem et al. 2019). This complex task requires knowledge of the properties of limestone and experience producing high temperature conditions for long periods of time (Kingery et al. 1988). The high, uniform quality of the plaster indicates that this was achieved consistently. The scale of plaster production that took place at NEG II could have been completed on a part-time irregular basis, and would not have required full-time specialists (Goren and Goldberg 1991) as has been previously suggested (Kingery et al. 1988), but manufacture was likely undertaken by a limited number of individuals with the necessary knowledge and experience.

The material evidence from NEG II thus demonstrates that diverse task-specific activities were carried out as expected for a large habitation site with invested architectural features, thick site deposits, and a large burial area (Grosman et al. 2016; Hitchcock 1987). Because some of these tasks required a specialized set of knowledge and skills, they were likely carried out by subsets of the population. In hunter-gatherer societies specific task groups are most often divided by sex or age (Isaac 1978). Nevertheless, as tasks diversify, it becomes more difficult to master all of the required skills and knowledge. That the task-specific activities documented above at NEG II required this special knowledge and skill is apparent in the uniformity and quality of the products. Ultimately, certain tasks become more specialized and a smaller subset of individuals is able to master the task (Barzilai 2010; Baysal 2013; Costin 1991; Costin and Hagstrum 1995). This kind of task specialization can lead to the emergence of product specialists—individuals who produce a commodity for folks outside their immediate household (Clark 1995).

The emergence of specialized production and the division of labor are fundamental changes typically associated with the emergence of full-fledged agricultural societies. There is no sign of these social changes at NEG II, but evidence for many task-specific activities indicate task diversification, while the standardization in the size of drills, fish, and architectural elements and the specialized knowledge required for the production of high-quality plaster suggests the specialization of some tasks. This suggests an incipient division of labor—a kind of evolutionary precursor to producer specialization (Arnold 2000, Clark and Parry 1990; Flad and Hruby 2007) in which certain tasks are increasingly carried out by individuals or subsets of the population who possess the necessary skills and experience. Evidence for these kinds of specialized tasks become more entrenched as we move into the Neolithic. For example, the naviform blades of the Pre-Pottery Neolithic B show great standardization and skilled craftsmanship (Barzilai 2010; Quintero and Wilke 1995) and stone bead workshops are proposed for early Neolithic sites in the Wadi Jilat, Jordan (Wright and Garrard 2003). Our research shows that precursors of this behavior were present in the Late Natufian deposits at NEG II and are likely present in other Natufian sites as well.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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