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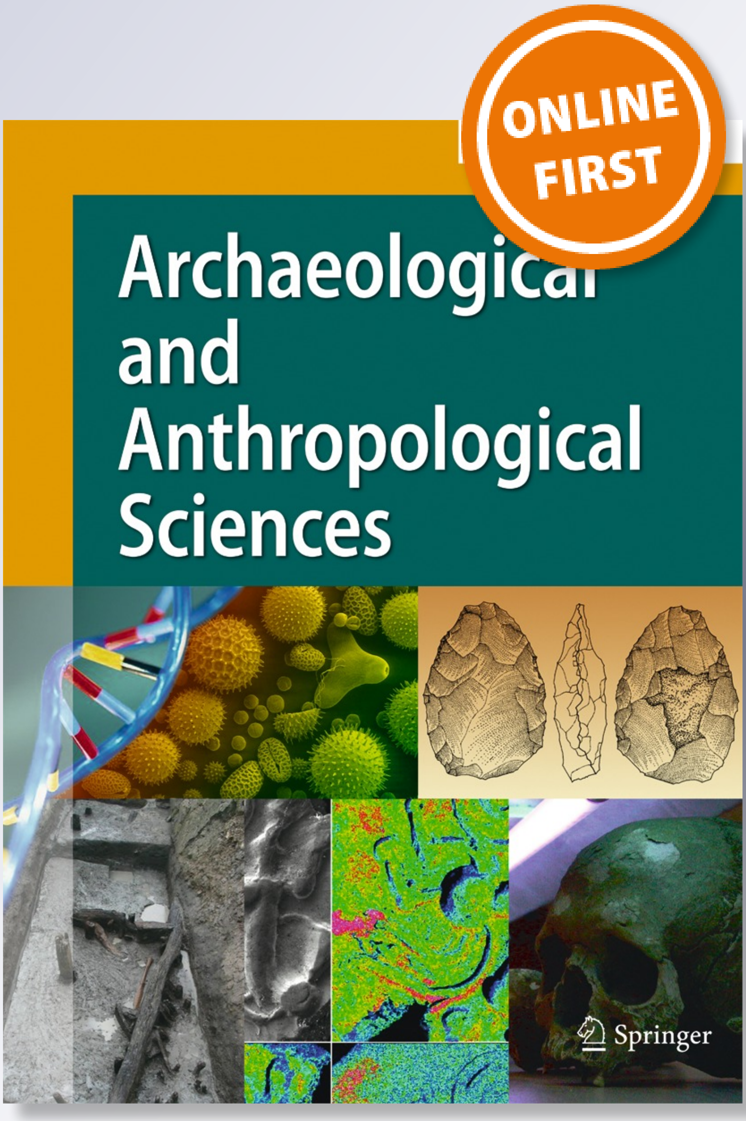

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ORIGINAL PAPER

Regional ecological variability and impact of the maritime fur trade on nearshore ecosystems in southern Haida Gwaii (British Columbia, Canada): evidence from stable isotope analysis of rockfish (*Sebastes* spp.) bone collagen

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Abstract The maritime fur trade (1785–1840s) led to the local extinction of sea otters (*Enhydra lutris*) in many parts of the northeast Pacific. On the basis of studies of extant sea otter populations, it has been established that they have a disproportionate effect on nearshore ecosystems by limiting sea urchin abundance and facilitating the establishment of nearshore kelp forests; in the absence of sea otters, a local reduction in kelp-derived carbon is therefore expected. We measured the isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) of rockfish (*Sebastes* spp.) bone collagen from late Holocene archaeological sites in southern Haida Gwaii, BC, Canada, using $\delta^{13}C$ as a proxy for kelp-derived carbon in the diet and $\delta^{15}N$ as a proxy for trophic position. We observed significant spatial variability in rockfish kelp-derived carbon ($\delta^{13}C$), but not trophic level ($\delta^{15}N$). Kelp-derived carbon varied largely as a function of site characteristics (wave exposure), suggesting that local oceanographic conditions are important factors with respect to consumer tissue isotopic compositions. Kelp-derived carbon decreased in post-European contact rockfish relative to pre-European contact rockfish, likely as a result of the reduction of kelp forests associated with the local extirpation of sea otters. Although we detected a reduction in kelp-derived carbon in rockfish diets, we found no shift in trophic level at sites occupied following the maritime fur trade. This implies a shift in local ecosystems, and particularly in carbon sources, following the maritime fur trade, likely due to a trophic cascade resulting from the local extirpation of sea otters. Stability in rockfish trophic levels, however, implies that rockfish continued to feed at similar trophic levels, consuming prey with similar nitrogen isotopic compositions.

Keywords Maritime fur trade · Tropic cascade · Stable isotopes · Historical ecology · Sea otter (*Enhydra lutris*) · Northwest coast

Introduction

The Pacific maritime fur trade, which peaked in the early part of the nineteenth century, was a time of massive change, in both social and ecological terms. The commercial maritime fur trade began in earnest with a surge in British presence between 1780 and 1800, followed by a period of American dominance with a large number of ships out of New England until the 1840s (Gibson 1988). By this time, fur-bearing marine mammal populations had markedly declined and there was a complete shift in the nature of the fur trade, which then became dominated by the Hudson's Bay Company and focused on terrestrial furs (Wolf 1982).

During the height of the Pacific maritime fur trade (1785–1825), the most sought after species was the sea otter (*Enhydra lutris*). One result of the fur trade was a massive decline in sea otter populations, possibly in excess of 99 % (Kenyon 1969; Riedman and Estes 1990), with otters

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extirpated from much of their pre-fur trade range. Sea otters were once distributed along the entire northwest coast of North America (NWC) from the Aleutian Islands to Baja California (Kenyon 1969), with the probable exception of the Salish Sea (Hanson and Kusmer 2001; but see McKechnie and Wigen 2011). After the unregulated hunting of sea otters ceased in 1919, only thirteen populations remained scattered along the coast (Jameson et al. 1982; Kenyon 1969). Beginning in the 1950s, sea otters were translocated to southeast Alaska, British Columbia (BC), Washington and Oregon, and established themselves in all locations (except Oregon), including the northwest coast of Vancouver Island (Bigg and MacAskie 1978; Breen et al. 1982; Morris et al. 1981). This BC population has increased markedly in both size and range, now occupying more than half of the west coast of Vancouver Island and a smaller area on the central BC mainland from Kildidt Sound to Aristizabal Island (Fig. 1; Nichol et al. 2009).

The local extirpation of sea otters from many regions of the NWC is particularly noteworthy because many regions have since experienced marked changes to nearshore food web structure and ecosystem dynamics. It has been demonstrated that sea otters have a disproportionately large impact on their communities relative to their abundance (Duggins 1980; Estes and Palmisano 1974; Estes et al. 1978, 1982; Simenstad et al. 1978). Because of its high per capita interaction strength, this keystone predator is well-known to trigger a cascade of indirect effects in nearshore ecosystems (Paine 1980). Through predation, sea otters limit grazing pressure by invertebrate herbivores, particularly sea urchins (*Strongylocentrotus* spp.). Sea urchins consume nearshore macroalgae (kelp), attacking the base (holdfast) and severing the structures, which then drift away (Leighton et al. 1966). When sea otters are present, urchins are limited to rock crevices and deeper habitats that are not easily accessible to otters, and dense stands of kelp proliferate (Estes et al. 1978). Conversely, when sea otters are absent, urchins are abundant, and the extent of kelp forests is reduced, although local oceanographic conditions play a major role in mediating this otter–urchin–kelp trophic cascade and its widespread applicability has been questioned, particularly for California (Foster 1990; Foster and Schiel 1988, 2010; Steneck et al. 2002).

Relatively few organisms consume kelp directly, but kelp can be a very significant source of biomass in nearshore

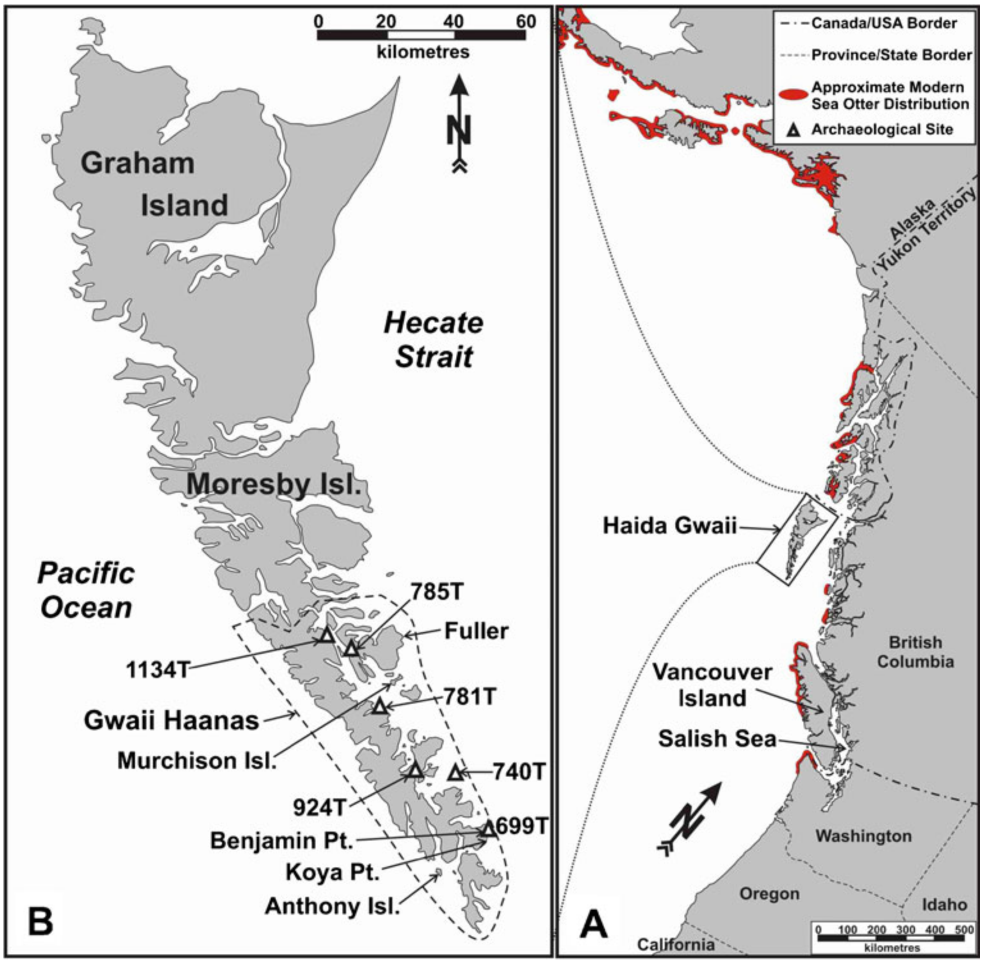

Fig. 1 Maps of the northwest coast of North America (**a**) and Haida Gwaii (**b**) showing locations of archaeological sites discussed in this paper and sampling areas for kelp. The pre-fur trade distribution of the sea otter spanned the entire coast illustrated here, with the exception of the Salish Sea region. The distribution of modern sea otter populations is based on Gregr et al. (2008), Laidre et al. (2009) and Nichol et al. (2009)

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food webs through detrital pathways (Mann 1973). Through the concentration and magnification of secondary production, kelp forests support a diverse and abundant assemblage of nearshore biota (Duggins et al. 1989). This includes species that: (1) feed directly on kelp (Bustamante et al. 1995; Steneck and Watling 1982), (2) use kelp as a substrate or feed on other kelp-based organisms (Hixon 1980; Holbrook and Schmitt 1984), (3) spawn in and/or utilize kelp beds as nurseries (Carr 1989, 1991, 1994; Dean et al. 2000; Ebeling and Laur 1985; Holbrook et al. 1990; Love et al. 1991), and (4) utilize the three dimensional habitat provided by kelp forests as adults (Bodkin 1988; DeMartini and Roberts 1990; Holbrook et al. 1990; Laur et al. 1988). Some of the relevant effects of the otter–urchin–kelp trophic cascade are summarized in Fig. 2.

The purpose of this study was to assess the extent to which the extirpation of sea otters from southern Haida Gwaii (BC, Canada) may have influenced the relative contribution of kelp-derived carbon to the nearshore foodweb by comparing the isotopic signature of consumer tissues (rockfish bone collagen) during and immediately following the maritime fur trade. Moreover, we sought to examine whether the foraging ecology of rockfish would be affected by ecological changes occurring as a result of the maritime fur trade. We hypothesized that kelp-associated rockfish would feed at a higher trophic level (with a significant contribution of juvenile rockfish to the diet) and assimilate a higher percentage of kelp-derived carbon than rockfish associated with urchin-dominated habitats or habitats with low kelp standing stock. Consequently, we expected proportionately more rockfish with kelp-associated isotopic compositions from archaeological contexts that predated European contact and the maritime fur trade.

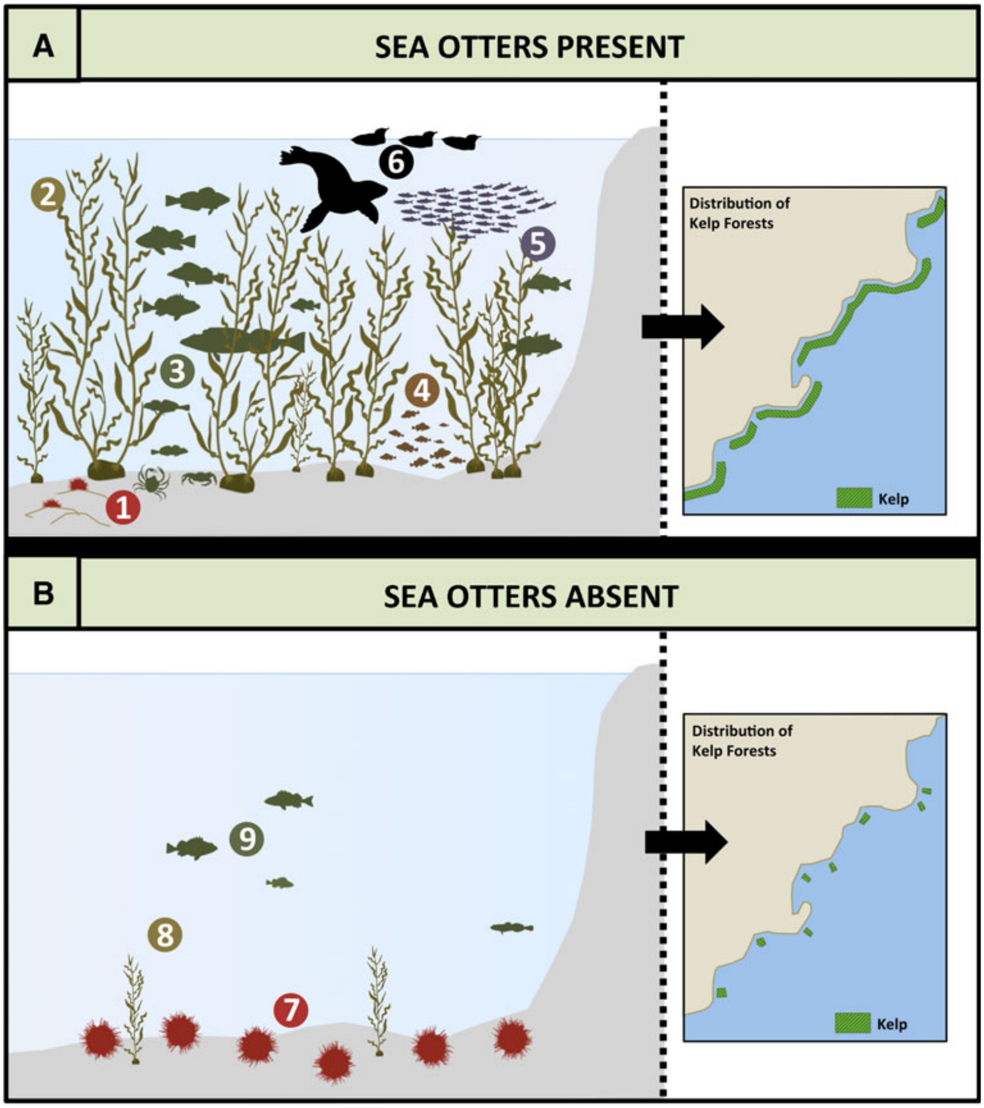

Fig. 2 Comparison of sea otter (**a**) and sea urchin (**b**) dominated communities. **a** Sea otters present: (*1*) Sea urchins are limited to small individuals, confined to crevices and deeper areas because of predation by sea otters. (*2*) Kelp forests are allowed to proliferate because herbivory by sea urchins is controlled by sea otter predation. (3) Kelp-associated species occur in greater abundance due to the increased secondary production and structure provided by the kelp-forest habitat. (*4*) Kelp forests provide important nursery areas for juvenile fish, which may positively influence the abundance of larger fish (3). (*5*) Small species (e.g. herring) may also use the kelp for spawning. (*6*) Large, predatory species (marine mammals and birds) are more abundant due to the increased productivity associated with kelp forests. **b** Sea otters absent: (*7*) Sea urchins are released from predation pressure; they are distributed fairly evenly and are of much larger size. (*8*) Kelp forests are either completely absent, or are limited to smaller areas because of overgrazing by sea urchins. (*9*) Consumer species are absent or less abundant

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Rockfish (*Sebastes* spp.)

Rockfish (*Sebastes* spp.) are a genus of nearshore and benthic fish species that are abundant along the north Pacific coast of North America (Heifetz et al. 2007; Love et al. 2002; Melteff 1987), being the most common group of bottom-dwelling and mid-water fish in many regions (Williams et al. 2010; Workman et al. 2008). Pacific rockfish are among the longest-lived fishes in the world, with many species living more than 50 years, and some well over 100 years (Love et al. 2002; Munk 2001; Parker et al. 2000). While a large number of rockfish species may be present in an area, typically one or a few species are extremely common (Murie et al. 1994; Nagtegaal 1983; Richards 1986). BC is home to a moderate number of rockfish species (Love et al. 2002), and the most common are: quillback rockfish (*Sebastes maliger*), copper rockfish (*Sebastes caurinus*), black rockfish (*Sebastes melanops*), yelloweye rockfish (*Sebastes suberrimus*), China rockfish (*Sebastes nebulosus*), and yellow tail rockfish (*Sebastes flavidus*) (Murie et al. 1994; Richards 1986; Yamanaka and Lacko 2008).

Morphologically, rockfish species are very similar (usually distinct on the basis of coloration), conforming to a generalized perciform body plan (Hallacher and Roberts 1985; Li et al. 2006); therefore, it is generally not possible to determine species-level identifications of rockfish skeletal material (Cannon 1987; Frederick and Crockford 2005; McKechnie 2007). Species recovered from BC archaeological assemblages are most likely to be one of the inshore (as opposed to shelf or deepwater) rockfish common to the region: yelloweye (*Sebastes rubrimus*), copper (*S. caurinus*), tiger (*Sebastes nigrocinctus*), China (*S. nebulosus*), quillback (*S. maliger*), black (*S. melanops*), redbanded (*S. babcocki*), rougheye (*S. aleutianus*) (Martin et al. 2006; Yamanaka and Kronlund 1997).

Most species of rockfish are generally sedentary, with relatively small home ranges, and do not undertake long migrations as adults (Larson 1980b; Love 1979; Mathews and Barker 1983; Matthews 1990b, c). Many species, particularly those associated with complex-relief habitats, have been observed to have home ranges on the order of 10 m^2 (Hannah and Rankin 2011; Matthews 1990c), and most other species tend to occupy home ranges of 10 km^2 or less, with a much smaller "core area" of highly concentrated activity (Jorgensen et al. 2006; Mitamura et al. 2009; Parker et al. 2007; Tolimieri et al. 2009). The vast majority of rockfish species are strongly associated with complex relief (kelp or rocky—specifically medium to large boulders) habitats (Larson and DeMartini 1984; Martin and Yamanaka 2004; Matthews 1990a; O'Connell and Carlile 1993; Richards 1986). While some species may *occur* on soft-bottom habitats (e.g. black, canary, copper, quillback, yellowtail), they still tend to be markedly more abundant in high-relief habitats (Johnson et al. 2003; Pearcy et al. 1989). Segregation of rockfish species, as well as size classes within species, by depth is also of considerable importance (Larson 1980a; Larson and DeMartini 1984; Love et al. 1990; Richards 1986).

Rockfish are important components in nearshore ecosystems in the North Pacific (Mills et al. 2007). Juveniles are significant or dominant prey items for numerous predatory species of anadromous fish (Brodeur 1991; Lowry et al. 1991; Mills et al. 2007), marine fish (Beaudreau 2009; Hallacher and Roberts 1985; Johnson 2006; Love and Westphal 1981; Love et al. 1991; Markel 2011), mammals (Lowry et al. 1991) and birds (Miller and Sydeman 2004; Sydeman et al. 2001; Thayer et al. 2008). Many rockfish species are closely tied to the nearshore ecosystems created by kelp forests (especially as juveniles), and are thus potentially sensitive to changes in those systems. Markel (2011), for example, has documented a close relationship between rockfish recruitment and the presence or absence of sea otters, and by extension the abundance of kelp forest cover, on the west coast of Vancouver Island. Using experimental removal of canopy-forming kelp forest, Bodkin (1988) found a marked reduction in the abundance of a number of species, including various rockfish.

Rockfish have long been an important economic resource for human populations in the northeast Pacific, and rockfish are abundant in faunal assemblages from archaeological sites representing human activities spanning the Holocene (Acheson 1998; Codding and Jones 2007; Colten 1994; Fedje et al. 2005; Gobalet and Jones 1995; Jones et al. 2008, 2009; McKechnie 2007; Orchard 2003, 2009). Increasingly, such archaeological records are seen as a useful source of data for examining long-term historical ecology (Braje and Rick 2011; Erlandson and Rick 2009; Jackson et al. 2001; Pitcher 2005; Rick and Erlandson 2008). Stable isotope analysis of zooarchaeological material has been used with increasing regularity to examine historical and paleoecological dynamics (Burton et al. 2001; Jones et al. 2011; Misarti et al. 2009; Moss et al. 2006; Newsome et al. 2007a; Szpak et al. 2009, 2012). Rockfish, then, provide a potentially useful, and abundant, source of insight into prehistoric ecological patterns along the NWC, and can also potentially provide a useful baseline from which to examine and understand ecological changes that may have accompanied the over-hunting and extirpation of sea otters from the region as a result of the maritime fur trade.

Stable isotope biogeochemistry of nearshore marine environments

In the nearshore marine environment, as in the terrestrial environment, the stable carbon isotopic compositions of

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consumer tissues have been regarded as an indicator of the source of primary production in the diet. On land, this distinction is possible because of the differences in carbon acquisition strategies between C_3 and C_4 plants, allowing the relative importance of graze vs. browse to be examined in some environments (e.g. Ambrose and DeNiro 1986; Cerling et al. 1999; Wittmer et al. 2010). In the northeast Pacific, the two most important sources of production are phytoplankton and kelp (Laminariales), which tend to be isotopically distinct. Kelps are relatively enriched in ^{13}C compared to phytoplankton (Dunton 2001; France 1995; Page et al. 2008; Schaal et al. 2010; Wainright et al. 1998), and numerous studies have demonstrated that the carbon isotopic composition of consumer tissues is informative with respect to the relative percentage of kelp-derived carbon in nearshore food webs (e.g. Bustamante and Branch 1996a; Duggins et al. 1989; Dunton and Schell 1987; Fredriksen 2003; Hill and McQuaid 2008; Kaehler et al. 2006; Kang et al. 2008; Schaal et al. 2009, 2010; Simenstad et al. 1993). The decomposition of fresh kelp appears to be associated with some degree of isotopic fractionation, leaving the decomposed kelp relatively depleted in ^{13}C and ^{15}N, thus making the isotopic composition of degraded kelp slightly less distinct from phytoplankton than fresh kelp (Kaehler et al. 2006).

The nitrogen isotopic composition (δ^{15}N) of consumer tissues is informative with respect to trophic level and foraging ecology. This is due to the consistent enrichment in consumer tissue ^{15}N of 3 to 5‰ that occurs at each trophic level (Minagawa and Wada 1984; Schoeninger and DeNiro 1984). Trophic discrimination factors for bone collagen fall within this range, with a recent survey of published literature finding $\Delta^{15}\mathrm{N}_{\text{bone collagen–diet}}$ to be +3.6±1.3‰ for mammalian bone collagen (Szpak et al. 2012). For most other tissues, it has been found, or at least assumed, that there is a comparatively smaller fractionation in ^{13}C that occurs between trophic levels (0 to +2‰), particularly higher trophic levels (DeNiro and Epstein 1978; Newsome et al. 2010; Wyatt et al. 2010). Bone collagen is somewhat unique in this respect as $\Delta^{13}\mathrm{C}_{\text{bone collagen–diet}}$ is generally appreciably larger, +3.7±1.6‰ (Szpak et al. 2012). This larger difference between consumer tissue and dietary δ^{13}C can be attributed to the glycine content of bone collagen, which accounts for approximately one third of all amino acid residues in the collagen of all vertebrates (Szpak 2011); glycine is characterized by a particularly large ^{13}C enrichment relative to the diet (Hare et al. 1991).

There are a number of environmental factors that have been correlated with aquatic producer carbon and nitrogen isotopic compositions. Salinity (Cornelisen et al. 2007), extracellular [CO_2] (Burkhardt et al. 1999; Kopczyńska et al. 1995), light intensity (Cornelisen et al. 2007), algal growth rate (Laws et al. 1995), water velocity (Osmond et al. 1981) and water temperature (Wiencke and Fischer 1990) have all been shown to influence the carbon isotopic composition at the base of the food web. Producer δ^{15}N varies according to N source (NO_3^-, NH_4^+, N_2), and the biogeochemical processes that occur prior to and during the assimilation into organic N (Ostrom et al. 1997). Oligotrophic (nutrient-poor) systems tend to be more dependent on recycled NH_4^+, which is relatively depleted in ^{15}N in comparison to upwelled NO_3^-. This results in producer δ^{15}N values being comparatively enriched in ^{15}N where the influence of upwelled nutrients is strong (Wu et al. 1997).

The number of factors that may influence the carbon and nitrogen isotopic composition at the base of the food web are numerous, complex and often difficult to isolate. Some generalizations, however, have been made with respect to the ways in which isotopic variation is reflected in higher-level consumers. Nearshore and benthic organisms tend to be comparatively enriched in ^{13}C and ^{15}N in comparison to offshore and pelagic organisms (Cherel and Hobson 2007; Hill et al. 2006; Hill and McQuaid 2008; Kang et al. 2003). Clementz and Koch (2001) outlined the differentiation of marine mammals living in distinct habitats (seagrass bed, kelp forest, nearshore marine, offshore marine) on the basis of the carbon isotopic composition of tooth enamel.

Materials and methods

Study region

Haida Gwaii, an archipelago composed of two large islands (Graham and Moresby) surrounded by hundreds of smaller islands and islets, is located off the northern coast of BC, Canada (Fig. 1). Haida Gwaii is located in a transitional area between an upwelling region to the south, and a downwelling region to the north (Peterson et al. 2007). The physical oceanography of the region is fairly well-described (Crawford and Thomson 1991; Crawford et al. 1988, 1995; Robinson et al. 2005). The eastern side of Haida Gwaii is bordered by Hecate Strait, a relatively well-mixed and shallow (40 to 300 m) stretch of ocean (Peterson et al. 2007), which separates the islands from the BC mainland. The southeast portion of Haida Gwaii, which is the focus of this study, consists of a series of shallow (40 to 60 m) and deep bays (200 m) (Peterson et al. 2007). Within the area, there is a diverse array of intertidal marine habitats, owing to the large variation in wave exposure and substrate, which are each characterized by their own set of marine plants and fauna (Harper et al. 1994).

Surveys conducted in the 1970s and 1980s found the distribution of urchin barrens (areas with abundant sea urchins lacking nearshore canopy-forming kelp) in southern Haida Gwaii to be patchy, often recording sites with rich algal diversity and no sea urchins within less than a

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kilometer of sites with large urchin populations and a very limited macroalgal community (Harper et al. 1994). Typically, these urchin barrens are located immediately sea-ward of narrow fringing extant kelp forests located between the 0–7 m depth contour and composed primarily of the annual canopy forming bull kelp (*Nereocystis luetkeana*), and a diversity of understory kelps of the order Laminariales (Harper et al. 1994; Sloan 2006). Harper and Morris (2006, p. 196) note that urchin barrens were observed along ~23 % of the coast, typically associated with rocky substrates, and semi-exposed or semi-protected wave energies. The abundance of urchin barrens in Haida Gwaii today is likely at least partly a result of the extirpation of sea otters from the region by the early 1900s (Sloan and Bartier 2000; Sloan 2006:260), although sea otter populations may have been locally depressed in the vicinity of villages as a result of First Nations hunting prior to the maritime fur trade (Szpak et al. 2012).

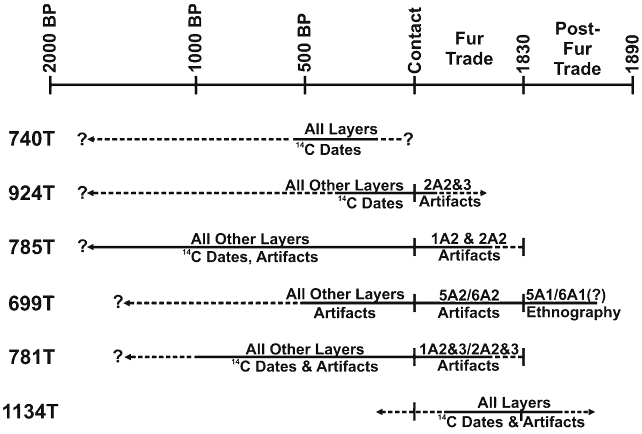

Fig. 3 Overview of the chronology of the sites included in the rockfish analysis (after Orchard 2009, p. 72). *Solid lines* represent established dates while *dashed lines* represent estimated spans of site occupations. Contexts (units and layers) representing each time period are listed above each line; data sources are listed *below each line*

Materials, archaeological and ecological context

Rockfish (*Sebastes* spp.) were sampled from six late-Holocene sites in southern Haida Gwaii (Fig. 1). The sites from which materials were sampled span the period from ca. 1500 BP to AD 1880 (Table 1; Fig. 3). These six sites were tested during recent archaeological excavations in Gwaii Haanas National Park Reserve and Haida Heritage Site (hereafter Gwaii Haanas), located in southernmost Haida Gwaii, and have produced a number of diverse faunal assemblages spanning Haida use of the region from the late Holocene (ca. 1,500 years before present [BP]) to the post-maritime fur trade period (Table 1; Orchard 2009). This project represents part of a larger research program aimed at better understanding the historical ecology of southern Haida Gwaii through a combined isotopic and zooarchaeological approach (Orchard and Szpak 2011; Szpak et al. 2009, 2012).

Faunal samples utilized in this study are derived from six shell midden sites located in eastern Gwaii Haanas (Fig. 1; Orchard 2009). Sites 781T, 785T and 924T represent small-to medium-sized villages (roughly two to six houses) that contain substantial shell-midden deposits containing diverse faunal assemblages which point to multi-season occupations and a range of activities. Similarly, site 699T contains a diversity of faunal remains from substantial shell midden deposits, but is significantly larger, containing 16 house depression features. Site 740T is a slightly smaller occupation, containing evidence of perhaps two house depressions, and producing a faunal assemblage that suggests a more limited, seasonal occupation aimed at harvesting small seabirds during nesting season. Finally, site 1134T appears to be a relatively short-lived and possibly entirely post-contact occupation, with two to three house depression features and a faunal assemblage that suggests a seasonally limited occupation focused on salmon harvesting.

Table 1 Summary of archaeological sites from which rockfish were sampled for stable isotope analysis (Orchard 2009)

Site	Wave exposure	*n* rockfish sampled	Dates
699T	Exposed	19	ca. AD 1500–1880
740T	Exposed	8	ca. AD 1400–1650
781T	Semi-protected	32	ca. AD 900–contact
785T	Protected	9	ca. AD 50–contact
924T	Protected	1	ca. AD 1500–contact
1134T	Protected	6	Post-contact

Dating of these archaeological sites (Table 1; Fig. 3) draws on a range of chronological indicators, including radiocarbon dates (Table 2), temporally diagnostic artifacts (particularly those associated with the maritime fur trade), and historic descriptions of the occupation of some locations (Orchard 2009). Site 699T was likely occupied from the late pre-contact through to the post-fur trade period, based on archaeological (Chinese coin, white glass button) and ethnohistoric evidence. Site 740T appears to represent a strictly pre-contact occupation, a temporal assignment that is supported by two radiocarbon dates (Table 2), and a lack of contact-period artifacts. The recovery of small assemblages of contact-period items (lead musket ball, glass fragment) from the upper layers of site 781T indicates that this site was occupied at least briefly during the early maritime fur trade period, while underlying deposits, characterized by dense shell midden, and two radiocarbon dates (Table 2) point to the late pre-contact period. Site 785T produced good evidence for both a lengthy pre-contact occupation, evident in a

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Table 2 Summary of relevant radiocarbon dates from sampled sites. Dates calibrated using Calib 6.0 (http://radiocarbon.pa.qub.ac.uk/calib/calib.html), using INTCAL09 or MARINE09 data sets. Marine shell dates corrected for marine reservoir effect using a local reservoir value (ΔR) of 250±50 (Southon and Fedje 2003). Note that the two samples from 740T1A2 and the two samples from 1134T3A1 represent shell-wood pairs (ie. shell and charcoal samples recovered in immediate association with each other) dated in conjunction with concurrent research examining the local marine reservoir effect (Southon and Fedje 2003)

Site	Context	Lab no.	Material	^{14}C age (BP)	Calibrate age range (95.4 % c.i.)	Source
740T	1A2	CAMS-70707	Marine shell	1090±40	cal AD 1392–1641	Mackie et al. 2001
	1A2	CAMS-70708	Charcoal	390±50	cal AD 1435–1635	Mackie et al. 2001
781T	4A3a	Beta-229459	Charcoal	550±40	cal AD 1304–1438	Orchard 2009
	4A4a	Beta-229460	Charcoal	1020±40	cal AD 898–1152	Orchard 2009
785T	1A3b	TO-10888	Charcoal	630±60	cal AD 1276–1415	Orchard 2009
	1A4b	TO-10889	Charcoal	850±60	cal AD 1040–1271	Orchard 2009
	2A2c	TO-10890	Charcoal	570±50	cal AD 1297–1431	Orchard 2009
	2A3c	TO-10891	Charcoal	1810±60	cal AD 74–380	Orchard 2009
924T	3A5b	UCIAMS-75530	Marine shell	925±20	cal AD 1490–1801	Orchard 2011
1134T	1A	CAMS-14421	Charcoal	160±60	cal AD 1655–1953	Mackie et al. 2001
	1A	CAMS-14422	Charcoal	240±60	cal AD 1481–1952	Mackie et al. 2001
	3A1	CAMS-70705	Marine shell	970±40	cal AD 1468–1691	Mackie et al. 2001
	3A1	CAMS-70706	Charcoal	190±40	cal AD 1645–1953	Mackie et al. 2001

series of four radiocarbon dates (Table 2), and a fur-trade period occupation, indicated by the recovery of historic artifacts (blue glass trade bead, rolled sheet-copper bead). Deposits tested at site 924T are somewhat more difficult to assign temporally. A single radiocarbon date from these deposits (Table 2) places this occupation in the late pre-contact period (ca. 270 to 380 BP; Orchard 2011). The only other chronological indicator recovered from the site is a very small fragment of glass from excavation unit 2. Though this is arguably a strong indicator of a contact-period occupation, the lack of supporting evidence suggests that the glass fragment may be intrusive. The final site, 1134T, contains no clear evidence of a pre-contact occupation, whereas numerous historic artifacts (four blue glass trade beads, white glass button, bottle glass, clay pipe stem, and miscellaneous fragments of glass, iron and ceramic) as well as several recent radiocarbon dates (Table 2) suggest a relatively intensive, if short-lived fur-trade period or post-fur trade period occupation (Orchard 2009).

As noted above, the six sites for which material was analyzed in this study have been classified by degree of wave exposure (Table 1; following Acheson 1998). The numerous islands and inlets that dominate the archipelago create a complex shoreline, which causes a wide variety of wave exposures, ranging from completely sheltered bays and inlets to exposed coasts that receive some of the strongest waves in the world (Harper et al. 1994). Drawing on Harper et al. (1994), Acheson (1998, 2005) presented a simplified classification of relative exposure of archaeological site locations. Specifically, Acheson defined three categories of site setting as follows: “Protected waters occur only within the upper reaches of the major inlets and deeper bays…Areas marginally affected by heavy seas, such as at the entrances to these bodies of water, and some stretches of coastline in the lee of smaller islands, are classed as semi-protected. Exposed coasts are those areas subject to incessant or frequent heavy seas and include linear stretches of shoreline, smaller islands, and points or bays” (Acheson 1998, p. 129). Based on this model, archaeological sites used in the current analysis are characterized as exposed, semi-protected or protected (Orchard 2009). Site 1134T is classified as protected, but is treated separately because it is the only site occupied entirely following European contact.

It is well established that wave exposure is among the most important factors with respect to kelp productivity, and the structuring of nearshore ecosystems in general (Bustamante and Branch 1996b). In fact, this variable ecology has been shown to greatly influence the composition of archaeological faunal assemblages from the study area, and by extension the nature of human foraging activities in Gwaii Haanas in the late Holocene (Orchard 2009). Specifically, among the sites analyzed here, protected localities tend to be dominated by small mussels and clams among the invertebrate remains, and are characterized by the greatest quantities of smelt, northern river otter and, to a lesser extent, dolphins and porpoises among the vertebrate remains. Exposed localities tend to be dominated by California mussel among the invertebrate remains and contain greater quantities of gunnels and pricklebacks, halibut, northern fur seals and, to a lesser extent, sea otters among the vertebrate remains. Semi-protected localities are intermediate between these two extremes.

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Kelp standing stock tends to be higher in more wave-exposed conditions when compared to sheltered conditions (Bustamante and Branch 1996b; Christie et al. 2003; Hurd 2000; Sjøtun and Fredriksen 1995; Wernberg and Connell 2008). While the amount of standing kelp may tend to be greatest at wave-exposed sites, this does not mean that proportionately more kelp-derived carbon will enter local food webs at these locations. Numerous studies have demonstrated that the amount of kelp-derived carbon entering the nearshore food web via direct grazing of living plants is minimal, largely because of the low nutritive quality of fresh kelp (Norderhaug et al. 2003) and the presence of polyphenolic compounds that deter grazers (Buchsbaum et al. 1991; Duggins and Eckman 1997; Steinberg 1988). The vast majority of kelp-derived carbon enters the food web through detrital pathways (as dissolved organic matter or particulate organic matter) (Mann 1973) after deterioration and bacterial degradation, which enhances the nutritive quality of the kelp (Duggins and Eckman 1997; Newell et al. 1980). Kelp detritus may be exported to other nearshore habitats (Britton-Simmons et al. 2009; Soares et al. 1997; Tallis 2009; Vanderklift and Wernberg 2008; Wernberg et al. 2006), beaches (Graeme 1989; Orr et al. 2005) or to other sites with topographies that may act to trap detritus (Krumhansl and Scheibling 2011; Vetter 1995). While wave-exposure and kelp standing stock may be positively correlated, kelp detritus (and also drift kelp) available to consumers may be negatively correlated with wave-exposure, with highly exposed conditions being associated with increased rates of detrital and drift kelp export (Schaal et al. 2009). Drift kelp and detritus are therefore more likely to settle in more sheltered locations (Crossman et al. 2001; Rodil et al. 2007). Gerard (1976) demonstrated that drifting *Macrocystis pyrifera* in central California tended to accumulate in larger quantities where water movement was slower. Rodríguez (2003) found higher levels of drift kelp at sites with calm conditions, compared to sites with intense wave action on the central Chilean coast. Moreover, Schaal et al. (2009) found a larger diversity of grazers feeding on *Laminaria digitata* at a sheltered, compared to a more exposed, site which they attributed to biochemical differences (higher protein content, lower C/N ratio) in *L. digitata* at the sheltered site. While comparatively few studies have assessed the differences in consumer isotopic composition between exposed and protected locations, those that have found the δ^{13}C values of consumers at exposed sites to be lower than those at protected sites in similar environments (Bode et al. 2006; Schaal et al. 2009), implicating the greater local accumulation of kelp-derived detrital matter at protected sites.

Selection of samples for analysis was based on a largely judgmental approach. Within sites and contexts that produced significant quantities of rockfish elements, samples for isotopic analysis were selected initially based on the size of the elements themselves, with the aim of providing enough bone, and by extension sufficient collagen, to facilitate isotopic analysis. Sampling always aimed, however, to avoid duplication of sampling of individuals by selecting, whenever possible, elements that clearly represented distinct individuals based on repetition of specific elements and on non-repetition of size classes. Finally, we aimed to select samples from diverse contexts (i.e. distinct stratigraphic units across multiple excavation units) within the available archaeological assemblages, to both further limit the possibility of re-sampling individuals, and to produce a general isotopic signature of the site as a whole, and not simply of specific contexts.

Bone collagen extraction and stable isotope analysis

Bone collagen was extracted using a modified Longin (1971) method, as previously described (Szpak et al. 2010). Entire skeletal elements (typically 200 to 800 mg) were demineralized in 0.5 M HCl at room temperature for several days. The insoluble collagen residue was then treated with 0.1 M NaOH for 15 min repeatedly, until the solution ran clear; this step aids in the removal of soil contaminants, particularly humic acids. The insoluble residue was rinsed to neutrality with MQ water, and heated in sealed glass vials in 10^{-3}M HCl at 80 °C for 18 h to solubilize the collagen. The water-soluble collagen was then transferred to 4 ml glass vials and air-dried at 80 °C. Dried collagen was weighed into tin capsules for isotopic analysis. Isotopic (δ^{13}C, δ^{15}N) and elemental compositions (%C, %N) were determined at McMaster University with a Thermo Finnigan Delta$^{\mathrm{PLUS}}$ XP continuous-flow isotope ratio mass spectrometer coupled to a Costech elemental analyzer. Accuracy for measurements was better than 0.2 ‰ for δ^{15}N and 0.1‰ for δ^{13}C.

Calculation of trophic level and kelp-derived carbon

Trophic level was calculated using the following equation (Hobson et al. 1994):

$$\mathrm{TL}_{\mathrm{consumer}} = 1 + \left(\delta^{15}\mathrm{N}_{\mathrm{consumer}} - \delta^{15}\mathrm{N}_{\mathrm{base}}\right)/\mathrm{TEF}$$

where $\mathrm{TL}_{\mathrm{consumer}}$ is the trophic level of the consumer, $\delta^{15}\mathrm{N}_{\mathrm{consumer}}$ is the nitrogen isotopic composition of the consumer tissue (in this case bone collagen), $\delta^{15}\mathrm{N}_{\mathrm{base}}$ is the nitrogen isotopic composition of the base of the food web, and TEF is the enrichment in ^{15}N at each trophic level. For $\delta^{15}\mathrm{N}_{\mathrm{base}}$, we used a value of 5.8‰, which represents an average of δ^{15}N values for particulate organic matter (POM) and kelp from southern Haida Gwaii—assuming a 50/50 contribution from each of these sources ($\delta^{15}\mathrm{N}_{\mathrm{kelp}}$=7.0‰, $\delta^{15}\mathrm{N}_{\mathrm{POM}}$=4.6‰; Salomon, unpublished data).

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The relative percentage of kelp-derived carbon was calculated using a simple two-source mixing model (modified from Duggins et al. 1989):

$$\%\text{Kelp Carbon} = \left(\delta^{13}\text{C}_{\text{consumer}} - \delta^{13}\text{C}_{\text{POM}} - \lambda\right) / \left(\delta^{13}\text{C}_{\text{kelp}} - \delta^{13}\text{C}_{\text{POM}}\right)$$

where $\delta^{13}C_{consumer}$ is the $\delta^{13}C$ value of rockfish bone collagen, $\delta^{13}C_{POM}$ is the $\delta^{13}C$ value for offshore particulate organic matter (POM), $\delta^{13}C_{kelp}$ is the $\delta^{13}C$ value of kelp, λ is the combined fractionations in ^{13}C between the base of the food web and bone collagen. The $\delta^{13}C$ values for POM and kelp were taken from modern surveys conducted in southern Haida Gwaii in 2011 (Salomon, unpublished data) and have been adjusted by +1‰ to account for changes in oceanic $\delta^{13}C$ due to the burning of ^{13}C-depleted fossil fuels (Newsome et al. 2007b). For each of the archaeological sites, site-specific $\delta^{13}C_{kelp}$ and $\delta^{13}C_{POM}$ values were used (Table 3). Each of the $\delta^{13}C_{kelp}$ values in Table 3 represent an average $\delta^{13}C$ value for the two dominant canopy-forming kelp species in the region, *M. pyrifera* and *Nereocystis luetkeana*.

The variable λ is somewhat complicated to derive because if the magnitude of fractionation in ^{13}C between the ultimate source (kelp or POM) and the consumer (rockfish) is dependent on trophic level, λ cannot be assumed to be constant between individuals. To account for potential variance in rockfish $\delta^{13}C$ caused by trophic level, rather than source carbon, we incorporated individual rockfish trophic level (calculated based on bone collagen $\delta^{15}N$ as described above) into the variable λ:

$$\lambda = \text{TEF}_{\text{collagen}} + \text{TL}_{\text{residual}}$$

where $\text{TEF}_{\text{collagen}}$ is 3.7‰, following the review by Szpak et al. (2012), and constant for all individuals. $\text{TL}_{\text{residual}}$ represents the residual trophic fractionation of ^{13}C after accounting for $\text{TEF}_{\text{collagen}}$ and will vary between individuals. $\text{TL}_{\text{residual}}$ is in turn comprised of two components:

$$\text{TL}_{\text{residual}} = (\text{TL})(x)$$

Table 3 Carbon isotopic compositions used for kelp and POM inputs in the mixing model (mean±one standard deviation). The $\delta^{13}C_{kelp}$ values represent the average carbon isotopic composition of the two dominant macroalgal species in the region: *M. pyrifera and N. luetkeana*. Kelp/POM sampling locations are depicted in Fig. 1

Site	$\delta^{13}C_{kelp}$ (‰)	$\delta^{13}C_{POM}$ (‰)	Kelp/POM sampling location(s)
699T	−14.5±2.3	−21.3±0.6	Benjamin Point, Koya Point
740T	−14.8±2.5	−21.4±0.3	Benjamin Point, Murchison Island
781T	−16.0±1.7	−21.1±0.2	Murchison Island
785T	−14.6±2.3	−20.8±0.1	Fuller
924T	−16.0±1.7	−21.1±0.2	Murchison Island
1134T	−14.6±2.3	−20.8±0.1	Fuller

TL is the calculated trophic level based on the rockfish bone collagen $\delta^{15}N$ values. To calculate x, we assumed that the lowest rockfish $\delta^{13}C$ value (−13.1‰) represented 0 % kelp-derived carbon in the diet (following Duggins et al. 1989) and solved the equation for x, which was determined to be 1.22. The assumption of 0 % kelp-derived carbon for this $\delta^{13}C$ value (−13.1‰) is not altogether unreasonable, as Pacific herring (a highly pelagic, but lower trophic level species) from the same contexts produced a mean $\delta^{13}C$ value of −13.6±0.9‰ (Szpak et al. 2009). This approach will tend to overestimate the amount of phytoplankton-derived carbon (Duggins et al. 1989), and is thus a fairly conservative estimate of kelp-derived carbon. It is important to point out that this estimation of kelp-derived carbon is associated with a high degree of uncertainty due primarily to estimation uncertainty and natural variation (kelp and POM $\delta^{13}C$ values). Therefore, while these estimations provide a reasonable means of making comparisons *within this dataset*, they are not likely to be directly comparable to other studies of this nature.

Statistical analyses

Differences in isotopic compositions between sites and between site types (wave exposures) were assessed with a one-way analysis of variance (ANOVA). Levene's test was used to assess homogeneity of variance; if variance was homoscedastic, a post hoc Tukey's honestly significant difference (HSD) test was applied and if variance was not homoscedastic, Dunnett's T3 test was applied. A significance level of $p<0.05$ was used for all statistical analyses. All statistical analyses were performed using SPSS 16 for Windows.

Results

The isotopic compositions ($\delta^{13}C$ and $\delta^{15}N$) of rockfish bone collagen, collagen yield, and C/N ratio are presented in Table 4. Three of the 75 samples analyzed produced C/N ratios outside of the acceptable range of 2.9–3.6 for unaltered bone collagen (DeNiro 1985; Szpak 2011), and have been discarded from all calculations, figures and statistical analyses, but are still presented in Table 4. Rockfish bone collagen $\delta^{13}C$ and $\delta^{15}N$ values ranged from −13.1 to −8.6 and 14.0 to 18.3‰, respectively.

Mean rockfish trophic level was calculated to be 3.9±0.2, with a range between 3.3 and 4.5. The calculated percentage of kelp-derived carbon for individual rockfish ranged from 0 to 86 %, with mean values for individual sites ranging between 15 and 50 % (Table 5). Mean rockfish carbon and nitrogen isotopic compositions, as well as calculated kelp-derived carbon and trophic levels are presented in Table 5, summarized according to site. Summary statistics for

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Table 4 Bone collagen isotopic and elemental data, and calculated kelp-derived carbon and trophic levels for all rockfish analyzed

Site	Site type (exposure)	Age	Sample no.	Context	δ^{13}C (‰)	δ^{15}N (‰)	Trophic level	% Kelp-derived C	C/N ratio	Collagen yield
699T	Exposed	Pre-contact	RF–003	6A3a	−11.3	15.7	3.8	25	3.43	10.8
			RF–009[1]	5A2c	−13.6	15.3	–	–	3.81	2.1
			RF–011	4A2b	−11.4	15.6	3.7	23	3.54	4.4
			RF–012	4A2b	−9.9	16.3	3.9	41	3.29	10.4
			RF–013	4A2c	−11.4	15.1	3.6	26	3.40	7.8
			RF–014	4A2c	−11.0	16.1	3.9	26	3.40	7.4
		Post-contact	RF–001	6A2a	−12.5	15.7	3.8	6	3.41	9.7
			RF–002	6A2D	−11.4	16.1	3.9	21	3.40	3.9
			RF–004	5A1b	−12.1	16.4	4.0	8	3.47	5.4
			RF–005	5A2a	−11.9	17.1	4.1	9	3.51	6.6
			RF–006	5A2a	−11.4	15.1	3.6	26	3.32	7.0
			RF–007	5A2b	−10.8	16.0	3.8	29	3.32	14.8
			RF–008	5A2b	−10.3	16.5	4.0	36	3.50	5.3
			RF–010[1]	4A2a	−12.5	14.8	–	–	3.94	1.9
			RF–104	5A2c	−11.5	14.9	3.5	25	3.08	6.9
			RF–105	5A2c	−10.3	16.1	3.8	37	2.99	12.2
			RF–106	5A2c	−12.2	15.2	3.6	14	3.11	5.4
			RF–111	5A2b	−11.5	15.0	3.6	25	3.13	6.4
			RF–112	5A2b	−10.0	15.0	3.6	47	3.05	7.5
740T	Exposed	Pre-contact	RF–136	2A2	−13.1	15.5	3.7	0	3.25	1.4
			RF–137	2A4	−11.5	15.3	3.6	24	3.21	8.7
			RF–138	2A4	−11.1	17.0	4.1	22	3.33	5.6
			RF–139	2A4	−12.1	15.5	3.7	14	3.13	7.7
			RF–300	2B2	−13.1	15.5	3.7	0	3.47	9.7
			RF–301	2A4	−11.5	15.3	3.6	25	3.39	6.5
			RF–302	2A5	−11.1	17.0	4.1	22	3.16	4.7
			RF–303	2A6	−12.1	15.5	3.7	14	3.36	6.1
781T	Semi-protected	Pre-contact	RF–036	2A4b	−10.5	16.5	4.0	41	3.35	10.7
			RF–037	2A4b	−10.4	16.7	4.0	42	3.31	10.4
			RF–038	2A4b	−10.4	18.3	4.5	31	3.39	7.9
			RF–015	4A2b	−11.2	16.8	4.1	26	3.28	8.5
			RF–016	4A3a	−10.1	16.0	3.8	53	3.35	5.4
			RF–122	4A3a	−10.1	15.7	3.8	54	3.36	4.3
			RF–017	4A3b	−10.0	16.5	4.0	51	3.32	11.2
			RF–018	4A3b	−10.3	15.7	3.8	51	3.36	6.8
			RF–019	4A3b	−10.3	16.6	4.0	45	3.34	9.3
			RF–020	4A3b	−10.5	16.8	4.1	40	3.31	5.5
			RF–116	4A3b	−10.2	16.0	3.8	50	3.56	1.6
			RF–117	4A3b	−10.3	16.1	3.9	48	3.55	11.6
			RF–022	4A3c	−10.7	15.8	3.8	42	3.09	6.0
			RF–023	4A3c	−11.2	14.0	3.3	44	3.28	8.6
			RF–123	4A3c	−10.2	15.5	3.7	54	3.36	12.0
			RF–124	4A3c	−10.1	16.2	3.9	51	3.30	8.0
			RF–125	4A3c	−10.5	15.9	3.8	47	3.45	2.8
			RF–024	4A4a	−9.4	17.6	4.3	56	3.15	6.7
			RF–025	4A4a	−10.5	16.3	3.9	43	3.17	4.2
			RF–026	4A4a	−9.8	16.6	4.0	55	3.40	7.7
			RF–027	4A4a	−9.8	15.9	3.8	59	3.38	8.0

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Table 4 (continued)

Site	Site type (exposure)	Age	Sample no.	Context	δ^{13}C (‰)	δ^{15}N (‰)	Trophic level	% Kelp-derived C	C/N ratio	Collagen yield
			RF–118	4A4a	−10.8	15.4	3.7	43	3.10	7.4
			RF–119	4A4a	−10.4	15.0	3.6	53	3.15	6.6
			RF–120	4A4a	−10.4	15.4	3.7	52	3.06	8.0
		Post-contact	RF–028	2A3a	−9.8	16.1	3.9	58	3.31	6.7
			RF–029[1]	2A3a	−11.3	15.6	–	–	3.65	1.6
			RF–030	2A3a	−10.1	17.0	4.1	45	3.28	8.0
			RF–031	2A3a	−10.5	17.8	4.3	33	3.29	6.3
			RF–032	2A3a	−9.8	17.3	4.2	50	3.29	5.4
			RF–033	2A3b	−10.4	17.1	4.1	40	3.09	7.8
			RF–034	2A3b	−11.1	16.4	3.9	31	3.24	8.2
			RF–035	2A3b	−10.4	17.4	4.2	38	3.10	5.5
785T	Protected	Pre-Contact	RF–039	1A3a	−10.8	16.7	4.0	34	3.37	7.0
			RF–040	1A3b	−9.5	17.1	4.1	57	3.46	8.0
			RF–041	1A3b	−10.4	16.7	4.0	41	3.42	6.1
			RF–042	1A3b	−9.6	16.1	3.9	62	3.33	10.8
			RF–043	1A3c	−8.6	15.3	3.6	86	3.35	8.3
			RF–044	1A3c	−11.0	16.3	3.9	33	3.38	5.9
			RF–045	1A3d	−10.6	16.7	4.0	39	3.33	7.2
			RF–046	1A4a	−10.0	16.5	4.0	52	3.38	4.4
			RF–047	1A4b	−10.3	16.5	4.0	45	3.19	11.5
924T	Protected	Pre-contact	RF–126	3A3b	−11.6	15.0	3.6	29	3.11	7.9
1134T	Protected	Post-contact	RF–200	2A2	−11.0	16.3	3.9	26	3.30	4.1
			RF–201	2A4	−11.8	16.9	4.1	11	3.30	6.7
			RF–202	2A4	−11.6	15.5	3.7	21	3.30	7.6
			RF–204	2A4	−10.9	16.1	3.9	28	3.30	6.6
			RF–205	2B2	−11.2	15.8	3.8	26	3.30	10.4
			RF–206	2A4	−11.7	17.5	4.3	9	3.40	4.5

comparisons between rockfish kelp-derived carbon with respect to site are presented in Table 6, and with respect to site type (exposure) in Table 7. Summary statistics for comparisons between rockfish trophic level with respect to site are presented in Table 8, and with respect to site type (exposure) in Table 9.

Rockfish kelp-derived carbon is plotted according to site in Fig. 4a. There were significant differences in kelp-derived

Table 5 Summarized isotopic data, and calculated kelp-derived carbon and trophic levels for rockfish by site

Site	Exposure	Period	*n*	δ^{13}C (‰)	δ^{15}N (‰)	% Kelp-derived C	Trophic level
740T	Exposed	Pre-contact	8	−11.9±0.8	15.8±0.7	15±10	3.8±0.2
699T	Exposed	All data	17	−11.2±0.8	15.8±0.6	25±12	3.8±0.2
		Pre-contact	5	−11.0±0.6	15.8±0.5	28±8	3.8±0.1
		Post-contact	12	−11.3±0.8	15.8±0.7	24±13	3.8±0.2
781T	Semi-exposed	All data	31	−10.3±0.4	16.3±0.9	46±8	3.9±0.2
		Pre-contact	24	−10.3±0.4	16.1±0.9	47±8	3.9±0.2
		Post-contact	7	−10.3±0.4	17.0±0.6	42±9	4.1±0.2
785T	Protected	Pre-contact	9	−10.1±0.8	16.4±0.5	50±17	4.0±0.1
924T	Protected	Pre-contact	1	−11.6	15.0	29	3.6
1134T	Protected	Post-contact	6	−11.4±0.4	16.4±0.7	20±8	3.9±0.2

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Table 6 Results of ANOVA for differences in rockfish kelp-derived carbon according to site

	Site	699T	740T	781T	785T	1134T
Kelp-derived carbon	699T	–	0.226	**<0.001**	**<0.001**	0.882
	740T	–	–	**<0.001**	**<0.001**	0.908
	781T	–	–	–	0.873	**<0.001**
	785T	–	–	–	–	**<0.001**

Values in boldface are statistically significant ($p<0.05$)

carbon between sites ($F_{[4,65]}=25.50$, $p<0.001$). In general, kelp-derived carbon was negatively related to site exposure, with rockfish from exposed sites being characterized by less kelp-derived carbon than rockfish from more sheltered sites (Table 6). Both exposed sites (699T and 740T) had significantly lower kelp-derived carbon than the semi-protected (781T) and protected (785T) sites, although this was not true for site 1134T, which is discussed in more detail below.

Rockfish kelp-derived carbon is plotted according to exposure in Fig. 4b–d. With respect to site exposure, there were significant differences in kelp-derived carbon ($F_{[2,68]}=24.27$, $p<0.001$). Exposed sites were characterized by significantly less kelp-derived carbon than protected ($p=0.03$) and semi-protected ($p<0.001$) sites; semi-protected and protected sites did not significantly differ ($p=0.30$). When rockfish were divided according to pre- and post-contact periods, there were still significant differences according to site exposure for pre-contact ($F_{[2,43]}=26.18$, $p<0.001$) and post-contact ($F_{[2,22]}=8.29$, $p=0.002$) groups. For the pre-contact period, exposed sites were characterized by significantly less kelp-derived carbon than protected ($p=0.002$) and semi-protected ($p<0.001$) sites; semi-protected and protected sites did not significantly differ ($p=0.99$). The lack of differentiation between exposed and protected sites in post-contact contexts ($p=0.81$) is driven by the unusually low kelp-derived carbon values for site 1134T, which are discussed in more detail below.

Rockfish kelp-derived carbon is plotted according to temporal period in Fig. 4e, f. Collectively, rockfish from pre-contact occupations were characterized by significantly more kelp-derived carbon than rockfish from post-contact occupations ($F_{[1,69]}=9.79$, $p=0.003$). Two sites (699T and 781T) contained sufficient numbers of pre- and post-contact rockfish for intrasite temporal comparisons. There were no significant differences in kelp-derived carbon between pre- and post-contact rockfish at 699T ($F_{[1,14]}=0.65$, $p=0.44$) or 781T ($F_{[1,29]}=1.99$, $p=0.17$).

Table 7 Results of ANOVA for differences in rockfish kelp-derived carbon according to site type (exposure)

		Semi-protected	Protected
All data	Exposed	**<0.001**	**0.027**
	Semi-protected	–	0.297
Pre-contact	Exposed	**<0.001**	**0.002**
	Semi-protected	–	0.999
Post-contact	Exposed	**0.004**	0.810
	Semi-protected	–	**0.005**

Values in boldface are statistically significant ($p<0.05$)

Rockfish trophic level is plotted according to site in Fig. 5a. In comparison to kelp-derived carbon, there were no obvious patterns with respect to rockfish trophic level. There were no significant differences in trophic level between sites ($F_{[4,65]}=2.21$, $p=0.08$). Rockfish trophic level is plotted according to site exposure in Fig. 5b–d. There were significant differences in rockfish trophic level according to site exposure ($F_{[2,68]}=3.99$, $p=0.02$), with rockfish from semi-protected sites at higher trophic levels than rockfish from exposed sites ($p=0.03$), although the magnitude of this difference was small (~0.15 trophic levels) and not present between other wave exposure categories (Table 9). Rockfish trophic level is plotted according to temporal period in Fig. 5e, f. There were no significant differences in rockfish trophic level between pooled pre- and post-contact occupations ($F_{[1,69]}=0.72$, $p=0.40$). Pre- and post-contact rockfish trophic level did not significantly differ at 699T ($F_{[1,14]}<0.01$, $p=0.98$), but did at 781T ($F_{[1,29]}=6.18$, $p=0.02$).

Discussion

General patterns in rockfish bone collagen δ^{13}C and δ^{15}N

The carbon and nitrogen isotopic compositions of rockfish bone collagen are consistent with what is known about present-day foraging habits. The calculated mean trophic level for southern Haida Gwaii rockfish is 3.9±0.2, which is higher than the value of 3.2 presented by Beattie (1999)

Table 8 Results of ANOVA for differences in rockfish trophic level according to site

	Site	699T	740T	781T	785T	1134T
Trophic level	699T	–	1.000	0.129	0.247	0.514
	740T	–	–	0.438	0.474	0.699
	781T	–	–	–	0.997	1.000
	785T	–	–	–	–	1.000

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Table 9 Results of ANOVA for differences in rockfish trophic level according to site type (exposure)

		Semi-protected	Protected
All data	Exposed	**0.027**	0.090
	Semi-protected	–	0.996
Pre-contact	Exposed	0.437	0.305
	Semi-protected	–	0.856
Post-contact	Exposed	**0.003**	0.234
	Semi-protected	–	0.227

Values in boldface are statistically significant ($p<0.05$)

for modern and historical Hecate Strait rockfish, and 3.4 and 3.7 for modern black and copper rockfish from Barkley Sound (Markel 2011). This suggests a secondary carnivore niche for rockfish in this region, with a diet composed primarily of juvenile rockfish, small forage fish (Pacific herring, sandlance, anchovy), benthic invertebrates (small cryptic crabs and shrimp, snails, brittle stars), and zooplankton (euphausiids, copepods, small crustaceans).

The high δ^{13}C values strongly suggest a relatively low reliance on pelagic carbon, which tends to have a more negative δ^{13}C value than benthic or kelp-derived carbon (France 1995). As a group, rockfish inhabit a wide variety of environments, with respect to depth, substrate-association, and proximity to the shore. The lack of pelagic offshore carbon in the tissues of these rockfish demonstrates that these fish were associated with nearshore habitats where there was potential for the contribution of significant amounts of kelp-derived carbon, which is discussed in more detail below.

Spatial variability in rockfish isotopic composition

Rockfish from exposed sites tended to have lower carbon isotopic compositions than rockfish from protected and semi-protected sites. The comparatively low δ^{13}C values for rockfish at exposed sites suggest a lower reliance on kelp-derived carbon (Table 7; Fig. 4a, b). Sites 1134T and 924T do not fit this pattern, but the former likely represents a temporal effect and the latter consists of only a single sample. The reasons for this spatial variability in carbon isotopic composition are likely complex, but we suggest two potential and related explanations.

The difference in rockfish kelp-derived carbon between the exposed and sheltered sites supports the assertion that hydrodynamic conditions can be important factors in determining the availability of different sources of organic matter in nearshore foodwebs (Norderhaug and Christie 2011), and that these differences may be reflected in higher trophic level consumers. Therefore, it is critical that interpretations of consumer δ^{13}C values (e.g. estimation of kelp or phytoplankton-derived carbon) take local hydrographic factors into consideration.

The bone collagen δ^{15}N values and calculated trophic levels of rockfish presented here did not systematically vary with respect to site (Table 8) or site exposure (Table 9). This suggests that rockfish at exposed and sheltered sites were feeding at very similar trophic levels. This supports the notion that the difference in rockfish δ^{13}C values between sites with different degrees of wave exposure is related to differences in the isotopic composition of the base of the food web, rather than differences in rockfish diets between these site types.

Fur trade era: reduction in kelp-derived carbon

The maritime fur trade in the northeast Pacific led to the local extinction of sea otters throughout much of this range. Although direct observations of ecological changes associated with the fur trade are absent, observations made during the last 40 years in areas with and without sea otters have generally demonstrated a positive association between sea otter presence and kelp forest size and depth—kelp forests being larger and extending deeper in the presence of sea otters (Estes and Palmisano 1974; Estes et al. 1978; Estes and Duggins 1995; Kvitek et al. 1989; Watson and Estes 2011). The comparison of rockfish living prior to and after the maritime fur trade period provides an opportunity to examine potential differences in the accumulation of kelp-derived carbon in nearshore ecosystems.

Site 1134T is located in a sheltered strait in close proximity to site 785T (Fig. 1), but is distinguished from all other sites analyzed in that it was occupied entirely following European contact (Orchard 2009), which occurred around 1774 in Haida Gwaii (Beals 1989; Blackman 1990). By the 1840s, the local sea otter population had been severely depleted, though otters were not completely extirpated from the region until the 1920s (Dick 2006). This rapid depletion of sea otter populations undoubtedly had a significant, though not necessarily instantaneous, impact on local ecosystems (Orchard 2009; Szpak et al. 2012). Therefore, it is at site 1134T that we would anticipate finding the best evidence of any potential differences in the amount of kelp-derived carbon represented in rockfish carbon isotopic compositions.

In comparison to rockfish from other protected (785T) and semi-protected (781T) sites, rockfish from 1134T are characterized by significantly lower δ^{13}C values (Table 6). Conversely, 1134T rockfish kelp-derived carbon values were not significantly different than rockfish from exposed sites (669T and 740T). This suggests that proportionately less kelp-derived carbon was entering the local foodweb, via detrital and/or grazing pathways, around the time of and slightly following European contact in the vicinity of this

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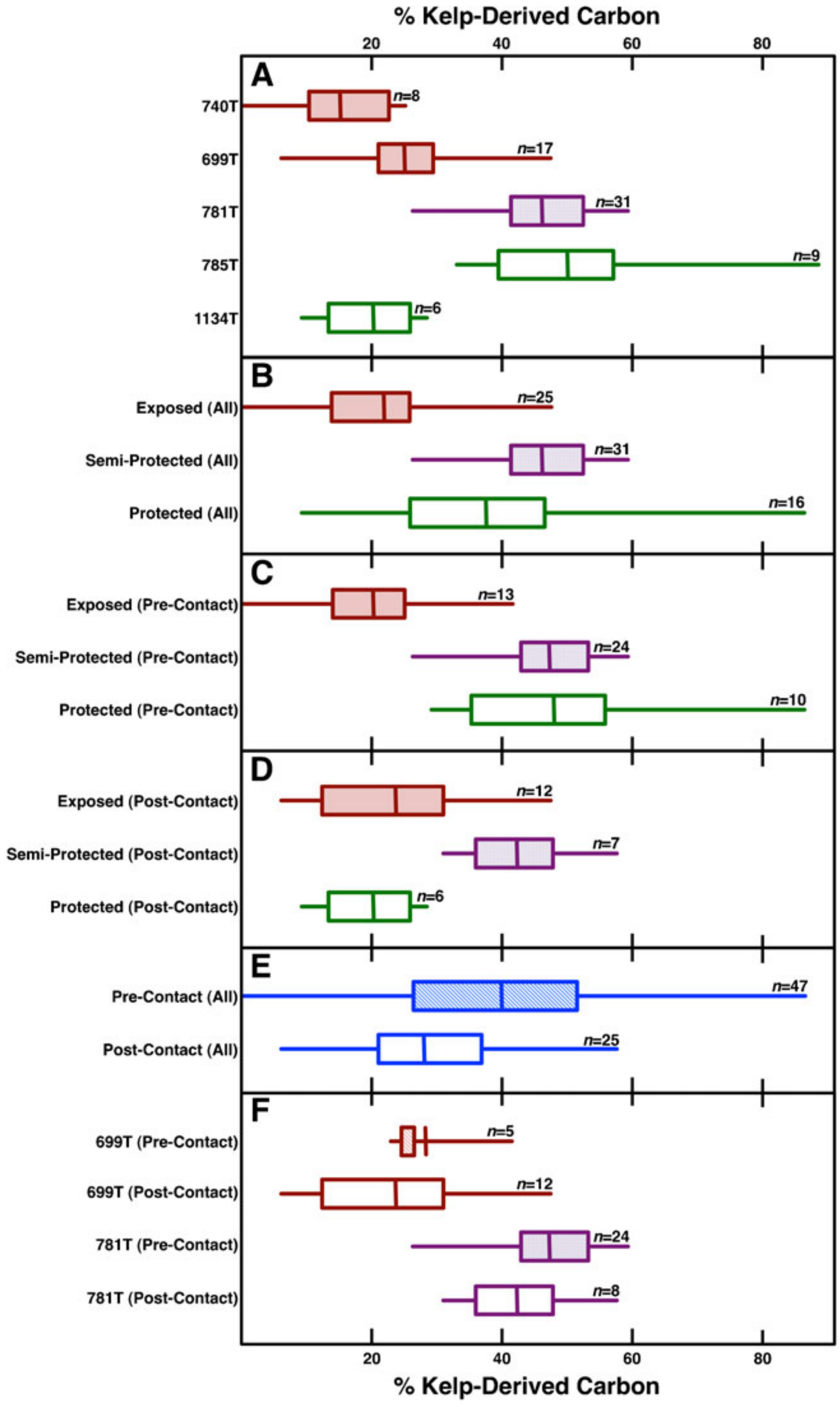
Fig. 4 Rockfish kelp-derived carbon by: **a** site, **b** site type (exposure), **c** site type for pre-contact rockfish only, **d** site type for post-contact rockfish only, **e** temporal period, **f** temporal period within sites 699T and 781T. *Vertical lines* represent means, *boxes* represent interquartile ranges (first to third) and *horizontal lines* represent ranges



particular site in southern Haida Gwaii. Based on the two-source mixing model, 1134T rockfish were on average characterized by 30 % less kelp-derived carbon compared to the other protected site (785T) located nearby, and 26 % less kelp-derived carbon compared to the semi-protected site (781T).

The magnitude of the difference between mean rockfish δ^{13}C values at 1134T and the protected (−1.3‰ for 785T) and semi-protected sites (−1.0‰ for 781T) is fairly small, but based on the results of similar studies, a small difference in consumer δ^{13}C values would be expected because kelp and phytoplankton carbon isotopic compositions usually differ by 4 to 6‰ (Duggins et al. 1989; Fredriksen 2003; Kaehler et al. 2006; Norderhaug et al. 2003), although the magnitude of this difference may be larger (Dunton and Schell 1987). The difference in δ^{13}C values between kelp and POM used in this study were fairly typical and ranged from 5.2 to 6.7. This contrasts to situations where consumer δ^{13}C values are used to interpret the relative contribution of C$_3$ and C$_4$ plants, which differ by ~14‰ with respect to

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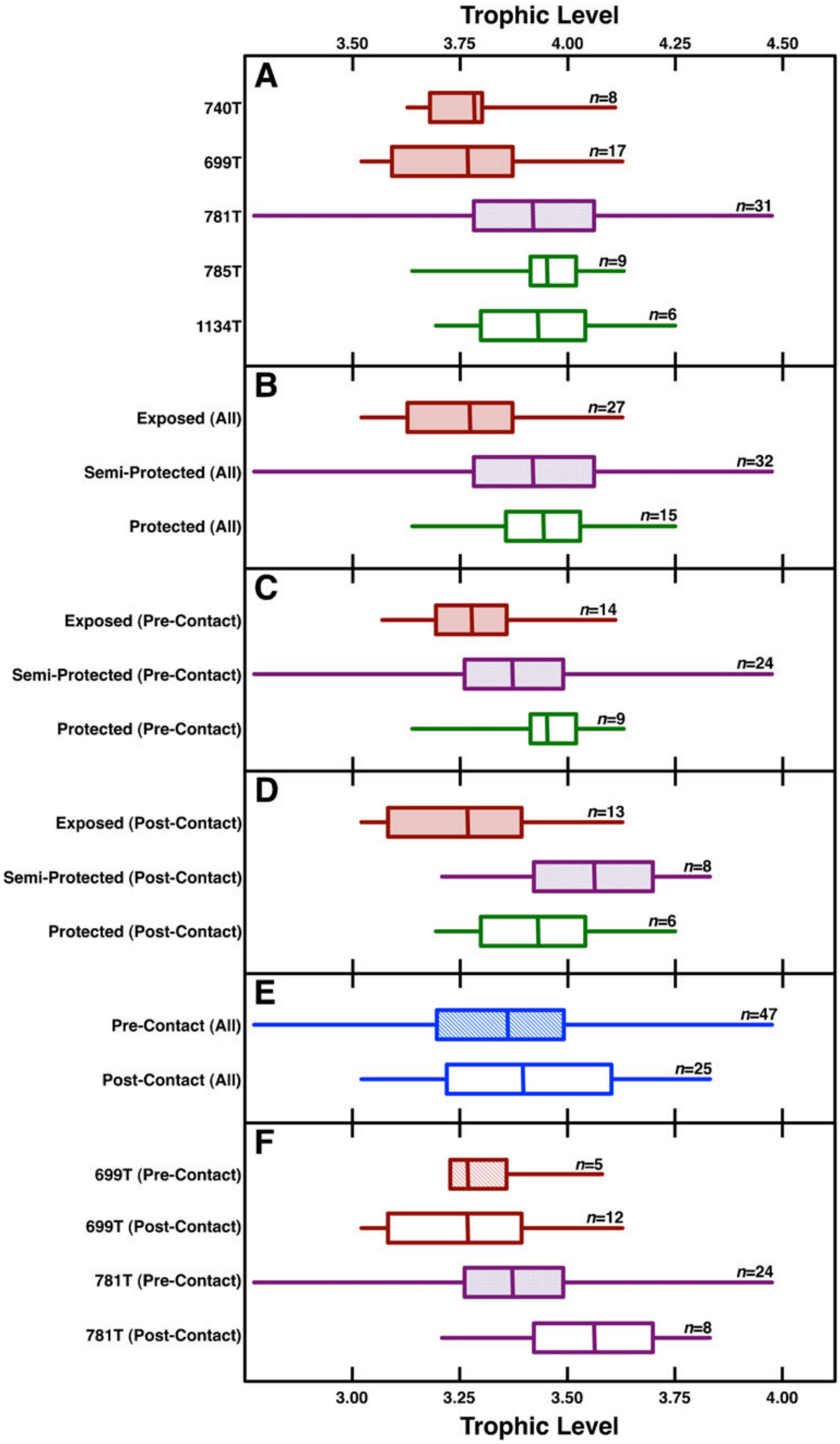
Fig. 5 Rockfish trophic level by: **a** site, **b** site type (exposure), **c** site type for pre-contact rockfish only, **d** site type for post-contact rockfish only, **e** temporal period, **f** temporal period within sites 699T and 781T. *Vertical lines* represent means, *boxes* represent interquartile ranges (first to third) and *horizontal lines* represent ranges



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their δ^{13}C values. In comparing islands in the Aleutians that were dominated by either kelp or sea urchins, Duggins et al. (1989) found 58 and 32 % kelp-derived carbon in the diets of primary consumers (a difference of 26 %), respectively. Using the mixing model provided by these authors, this equates to a mean difference in consumer δ^{13}C of 1.7‰ between kelp and urchin dominated islands. It is important to bear in mind that the consumers compared by these authors fed at trophic levels lower than rockfish. Assuming that the resolution of potential carbon sources is further dampened in long-lived species at higher trophic levels (Dunton et al. 1989; Simenstad et al. 1993), we would expect a similar, or likely even smaller difference in rockfish δ^{13}C.

The fact that there are still considerable amounts of kelp-derived carbon at all sites is not surprising given the scale at which kelp-derived carbon may be incorporated into near-shore food webs. Several studies have found significant quantities of kelp-derived carbon contributing to the diet of consumers in areas with low local kelp biomass (Duggins et al. 1989; Kaehler et al. 2006; Kang et al. 2008; Markel 2011; Salomon et al. 2008; Vanderklift and Wernberg 2008), demonstrating the importance of detritus at a more regional scale. Furthermore, surveys conducted within the last 30 years in Haida Gwaii have demonstrated that even though sea otters have been absent from the region for nearly 200 years, kelp stands still persist in some areas and the coastline is not completely dominated by urchin barrens (Harper et al. 1994; Jamieson and Campbell 1995; Sloan and Bartier 2000; Sloan 2006). In comparison to the west coast of Vancouver Island and Goose Island group (areas of the BC coast where sea otters are presently established), where kelp forests are quite extensive and composed primarily of *Macrocystis*, the kelp stands surrounding Haida Gwaii are very thin, shallow and composed primarily of *Nereocystis* (Salomon, unpublished data).

There was no significant difference in kelp-derived carbon between the pre- and post-contact rockfish at 699T ($F_{[1,14]}=0.65$, $p=0.44$) or 781T ($F_{[1,30]}=5.38$, $p=0.03$). There are several possible reasons why a reduction in kelp-derived carbon was not observed. First, because 699T and 781T are located in relatively exposed locations (especially 699T), the increased local water flow may create conditions that are conducive to a higher level of mixing of detritus at the regional scale than at sites located in more protected locations (e.g. 785T and 1134T). Following the observation that detritus tends to accumulate more in sheltered locations relative to exposed locations (Crossman et al. 2001; Rodil et al. 2007), the former may provide a much better opportunity to examine changes in detrital biomass. Second, it is very possible that the distribution of kelp forests throughout southern Haida Gwaii was relatively patchy before and after the fur trade. We have suggested previously that this may have been the case, possibly in connection with the local depression of sea otter populations in the vicinity of village sites (Szpak et al. 2012). This may have had the effect of mediating any changes in the relative abundance of kelp-derived carbon at the local scale, creating a situation that is not directly analogous to modern comparative studies of otter-present/otter-absent regions (e.g. Estes et al. 1978; Markel 2011; Watson and Estes 2011).

Site 699T also represents a somewhat unique cultural context from the other sites included in this analysis. As indicated above, this is a very large village site with clear evidence of at least 16 house features (Orchard 2009), though these houses may not have all been occupied contemporaneously throughout the occupation of the site. Based on ethnographic and ethnohistoric sources summarized by Acheson (1998), site 699T was occupied from the late pre-contact through the early contact period and into the post-fur trade period, before the remaining occupants resettled at Sgan Gwaii on Anthony Island in the mid-1800s. This represents one example of a wider process of amalgamation of small, dispersed villages into larger, more centralized villages. This process, which occurred throughout Haida Gwaii, may have begun in the latest pre-contact period but was certainly reinforced and accelerated after contact (Acheson 1998, 2005). Acheson (2005), for example, indicates that the large-scale settlement of site 699T emerged following European contact, likely a direct response to the new economic forces present with the onset of the maritime fur trade. A more detailed consideration of the factors driving this process of amalgamation is beyond the scope of this paper. Interestingly, while the invertebrate assemblage from 699T strongly reflects its exposed location, patterns in the vertebrate data are less distinct, and in some ways reflect a combination of exposed and protected resources (Orchard 2009). This pattern may suggest that the local environment was insufficient to meet the needs of a large, amalgamated village, forcing the occupants to range further afield on a seasonal basis to meet their subsistence needs. Haida that once occupied a series of smaller, dispersed villages in a variety of ecological settings would now return to those smaller village localities and resource gathering sites to meet at least a portion of their subsistence needs (Orchard 2009). The faunal assemblages at the large, amalgamated villages (e.g. 699T), now represented the combination of the previously locally variable aspects of the subsistence economy, combining exposed and protected resources. In terms of the current study, this process may have served to further dampen the apparent effects of local ecological variability by pooling rockfish remains from a larger catchment area that may not have been limited to the exposed contexts in which the site itself is located.

Finally, the assignation of particular materials as pre- or post-contact at 699T is somewhat problematic. Dating of

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these contexts, while based on multiple chronological indicators as discussed above, is largely based on the nature of the artifact assemblages in the excavated contexts, tracking a transition from purely traditional artifact styles to a combination of traditional and introduced European trade goods (Orchard 2009). While this site clearly contains an occupation that spans the pre-contact to post-contact periods, and while excavated stratigraphic layers can be confidently assigned relative ages, it is more difficult to conclusively identify the point at which the maritime fur trade began to influence the site occupants. As such, site 1134T, which contains numerous historic artifacts and has produced a series of radiocarbon dates, none of which point to a pre-contact occupation, provides the most reasonable means to examine the nature of post-contact rockfish isotopic compositions (Orchard 2009).

Further research will aid in clarifying the ecological impact of the maritime fur trade locally and regionally. With respect to stable isotope analysis in particular, there is potential to analyze the carbon isotopic composition of the organic component of invertebrate shells. The limited mobility and low trophic level of many species of filter feeders makes them very good candidates for understanding the relative contributions of different sources of organic matter. Unfortunately, there is a very small amount of organic material preserved in shell, which makes this type of analysis difficult (Hard and Katzenberg 2011).

Fur trade era: consistency in rockfish trophic level

Rockfish are important components in nearshore ecosystems in the North Pacific (Mills et al. 2007). Juveniles are significant or dominant prey items for numerous predatory species of anadromous fish (Brodeur 1991; Lowry et al. 1991; Mills et al. 2007), marine fish (Beaudreau 2009; Hallacher and Roberts 1985; Love and Westphal 1981; Love et al. 1991), mammals (Lowry et al. 1991) and birds (Miller and Sydeman 2004; Sydeman et al. 2001; Thayer et al. 2008). Kelp forest canopies may serve as important habitats for juvenile rockfish (Dean et al. 2000; Love et al. 1991; Markel 2011), which in turn may strongly influence the abundance of other kelp forest fishes (Bodkin 1988). More generally, several authors have noted a positive relationship between kelp and nearshore fish abundance (Bodkin 1988; DeMartini and Roberts 1990; Ebeling and Laur 1988; Laur et al. 1988; Markel 2011; Reisewitz et al. 2006). On the west coast of Vancouver Island, Markel (2011) found that adult (but not juvenile) black and copper rockfish in habitats with sea otters and abundant kelp forests fed at higher trophic levels (based on muscle $\delta^{15}N$) than conspecifics in habitats without sea otters and sparse kelp forests (black rockfish trophic level 3.44 sea otters present, 3.14 sea otters absent; copper rockfish trophic level 3.72 sea otters present, 3.38 sea otters absent). As such, we expected a reduction in the quantity of kelp-derived carbon (lower $\delta^{13}C$) in rockfish to be coincident with a reduction in trophic level (lower $\delta^{15}N$) due to decreased availability of forage fish (Pacific herring) and juvenile rockfish.

We did not find any evidence of a reduction in trophic level in the post-fur trade rockfish (Fig. 5e, f). This does not suggest, however, that rockfish diets were unchanged. Shifts between similar trophic level prey (e.g. juvenile forage fish to predatory amphipods) may be functionally significant, but due to a lack of isotopic differentiation between these prey, may not be detectable using conventional isotopic analysis. The general lack of differentiation at the level of sites or site exposure with respect to rockfish trophic level lends further support to the notion that the differences in rockfish $\delta^{13}C$ values are related to differences in isotopic composition at the base of the food web (kelp vs. phytoplankton), rather than differences in feeding ecology.

The lack of any differentiation in rockfish $\delta^{15}N$ values in pre- and post-fur trade contexts may be partially explained by the long temporal record represented by bone collagen. Many species of fish, including rockfish, are characterized by large ontogenetic differences in diet and trophic level, with shifts of one trophic level or more occurring through life; these age-related dietary differences have been recorded in fish tissue nitrogen isotopic compositions, mostly muscle and other tissues with relatively short turnover times (Cummings et al. 2010; Hamilton et al. 2011; Markel 2011; Morinière et al. 2003; Vizzini and Mazzola 2002). Because bone collagen remodels at a much slower rate and represents a much larger temporal window than tissues typically used in ecological analyses, there may be a significant blurring of consistent patterns in adult trophic level. This is especially true since there is no control over the sizes and ages of the fish that were sampled for isotopic analysis, where the nitrogen isotopic composition of some individuals may reflect more or less juvenile diet depending on the age/size of the fish. Carbon isotopic composition less strongly reflects trophic level (relative to nitrogen isotopic composition), these ontogenetic effects may be more prevalent in bone collagen $\delta^{15}N$ values.

Conclusion

Rockfish from exposed sites had significantly lower kelp-derived carbon ($\delta^{13}C$ values) than rockfish from sheltered sites, while semi-protected sites were intermediate, suggesting a greater amount of kelp-derived carbon was assimilated by rockfish at the sheltered sites. Rockfish bone collagen $\delta^{15}N$ values did not vary with respect to site exposure. The results of this study highlight the importance of regional ecological variability in structuring the isotopic composition of animal tissues. These results also provide considerable

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insight into human foraging patterns in late Holocene Haida Gwaii. The generally high $\delta^{13}C$ values for the analyzed rockfish, as discussed above, strongly suggest a low reliance on pelagic carbon, and indicate that the Haida were targeting rockfish primarily in nearshore waters. More specifically, the relatively close correlation between site setting and rockfish $\delta^{13}C$ values suggests that these rockfish were all harvested in the immediate vicinity of the sites from which these faunal remains were recovered. This provides additional evidence for a very locally focused subsistence harvesting regime among the Haida in eastern Gwaii Haanas in the late Holocene, a pattern that has been previously recognized through numerous other faunal indicators (Orchard 2009).

Post-contact data suggest a decline in the quantities of kelp-derived carbon assimilated by rockfish in at least some locations, likely reflecting a decline in local kelp standing stock biomass and productivity as urchin barrens increased in size and abundance following the local extirpation of sea otters during the maritime fur trade. Rockfish from the entirely post-contact site 1134T had significantly lower carbon isotopic compositions, and hence kelp-derived carbon, than rockfish from sites in similar environmental settings. At the two individual sites with both pre- and post-contact occupations (699T and 781T), kelp-derived carbon decreased following European contact, although this difference was not statistically significant. This lack of differentiation may be partly related to coarseness in temporal resolution, though these are clearly chronologically distinct deposits based on stratigraphic data, and clearly date generally to the pre-contact to early contact period transition. In fact, this transitional period itself may contribute to the lack of isotopic distinction, as the early contact period may be a time when these ecological changes were just beginning, whereas there may be a delay of years or decades for the increase in sea urchins and decrease in kelp to occur. Moreover, at site 699T specifically this lack of an apparent reduction in kelp-derived carbon may reflect an increasing foraging radius for the Haida occupants of this site, which was by far the largest village site in our sample, representing the results of the amalgamation of smaller, regional villages into larger, more centralized villages in the late pre-contact and early contact period (Acheson 1998, 2005). As discussed elsewhere by Orchard (2009:119), the large populations at villages such as 699T may not have been able to meet their subsistence needs in local environments alone, and may thus have drawn on more dispersed foraging locations.

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References

Acheson SR (1998) In the wake of the *Ya'aats' xaatgaay* ['Iron People']: a study of changing settlement strategies among the Kunghit Haida. British Archaeological Reports International Series 711. John and Erica Hedges, Oxford

Acheson SR (2005) Gwaii Haanas settlement archaeology. In: Fedje DW, Mathewes RW (eds) Haida Gwaii: human history and environment from the time of loon to the time of the iron people. UBC Press, Vancouver, pp 303–336

Ambrose SH, DeNiro MJ (1986) The isotopic ecology of east African mammals. Oecologia 69(3):395–406. doi:10.1007/BF00377062

Beals HK (1989) Juan Pérez on the northwest coast: six documents of his expedition in 1774. Oregon Historical Society Press, Portland

Beattie A (1999) Report of the BTF workshop on reconstruction of the Hecate Strait Ecosystem. In: Haggan N, Beattie A, Pauly D (eds) Back to the future: reconstructing the Hecate Strait Ecosystem, vol. 7, vol 3, The Fisheries Centre. University of British Columbia, Vancouver, pp 1–12

Beaudreau AH (2009) The predatory role of lingcod (*Ophiodon elongatus*) in the San Juan Archipelago, Washington. Unpublished Ph.D. Dissertation, University of Washington, Seattle

Bigg MA, MacAskie IB (1978) Sea otters reestablished in British Columbia. J Mammal 59(4):874–876

Blackman M (1990) Haida: traditional culture. In: Suttles W (ed) Handbook of North American Indians, vol 7, Northwest Coast. Smithsonian Institution, Washington, D.C., pp 240–260

Bode A, Alvarez-Ossorio MT, Varela M (2006) Phytoplankton and macrophyte contributions to littoral food webs in the Galician upwelling estimated from stable isotopes. Mar Ecol Prog Ser 318:89–102. doi:10.3354/meps318089

Bodkin JL (1988) Effects of kelp forest removal on associated fish assemblages in central California. J Exp Mar Biol Ecol 117 (3):227–238. doi:10.1016/0022-0981(88)90059-7

Braje TJ, Rick TC (eds) (2011) Human impacts on seals, sea lions, and sea otters: integrating archaeology and ecology in the Northeast Pacific. University of California Press, Berkeley

Breen PA, Carson TA, Foster JB, Stewart EA (1982) Changes in subtidal community structure associated with British Columbia sea otter transplants. Mar Ecol Prog Ser 7:13–20

Britton-Simmons KH, Foley G, Okamoto D (2009) Spatial subsidy in the subtidal zone: utilization of drift algae by a deep subtidal sea urchin. Aquat Biol 5(3):233–243. doi:10.3354/ab00154

Brodeur RD (1991) Ontogenetic variations in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon. Environ Biol Fishes 30(3):303–315. doi:10.1007/bf02028846

Buchsbaum R, Valliela I, Swain T, Dzierzeski M, Allen S (1991) Available and refractory nitrogen in detritus of coastal vascular plants and macroalgae. Mar Ecol Prog Ser 72:131–143

Burkhardt S, Riebesell U, Zondervan I (1999) Effects of growth rate, CO_2 concentration, and cell size on the stable carbon isotope fractionation in marine phytoplankton. Geochim Cosmochim Acta 63(22):3729–3741. doi:10.1016/s0016-7037(99)00217-3

Burton RK, Snodgrass JJ, Gifford-Gonzalez D, Guilderson T, Brown T, Koch PL (2001) Holocene changes in the ecology of northern

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fur seals: insights from stable isotopes and archaeofauna. Oecologia 128(1):107–115. doi:10.1007/s004420100631

Bustamante RH, Branch GM (1996a) The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. J Exp Mar Biol Ecol 196(1–2):1–28. doi:10.1016/0022-0981(95)00093-3

Bustamante RH, Branch GM (1996b) Large scale patterns and trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure. J Biogeogr 23(3):339–351. doi:10.1046/j.1365-2699.1996.00026.x

Bustamante RH, Branch GM, Eekhout S (1995) Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. Ecology 76(7):2314–2329. doi:10.2307/1941704

Cannon DY (1987) Marine fish osteology: a manual for archaeologists. Department of Archaeology, Simon Fraser University, Burnaby

Carr MH (1989) Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. J Exp Mar Biol Ecol 126(1):59–76. doi:10.1016/0022-0981(89)90124-x

Carr MH (1991) Habitat selection and recruitment of an assemblage of temperate zone reef fishes. J Exp Mar Biol Ecol 146(1):113–137. doi:10.1016/0022-0981(91)90257-W

Carr MH (1994) Effects of macroalgal dynamics on recruitment of a temperate reef fish. Ecology 75(5):1320–1333. doi:10.2307/1937457

Cerling TE, Harris JM, Leakey MG (1999) Browsing and grazing in elephants: the isotope record of modern and fossil Proboscideans. Oecologia 120(3):364–374. doi:10.1007/s004420050869

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281–287. doi:10.3354/meps329281

Christie H, Jørgensen NM, Norderhaug KM, Waage-Nielsen E (2003) Species distribution and habitat exploitation of fauna associated with kelp (*Laminaria Hyperborea*) along the Norwegian Coast. J Mar Biol Assoc U K 83(04):687–699. doi:10.1017/S0025315403007653h

Clementz MT, Koch PL (2001) Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. Oecologia 129(3):461–472. doi:10.1007/s004420100745

Codding BF, Jones TL (2007) History and behavioral ecology during the middle-late transition on the Central California Coast: findings from the Coon Creek Site (CA-SLO-9), San Luis Obispo County. J Calif Gt Basin Anthropol 27(2):125–151

Colten RH (1994) Prehistoric animal exploitation, environmental change, and emergent complexity on Santa Cruz Island, California. In: Halvorson WL, Maender GJ (eds) The fourth California Islands Symposium: update on the status of resources. Santa Barbara Museum of Natural History, Santa Barbara, pp 201–214

Cornelisen CD, Wing SR, Clark KL, Bowman MH, Frew RD, Hurd CL (2007) Patterns in the δ^{13}C and δ^{15}N signature of *Ulva pertusa*: Interaction between physical gradients and nutrient source pools. Limnol Oceanogr 52(2):820–832

Crawford WR, Huggett WS, Woodward MJ (1988) Water transport through Hecate Strait, British Columbia. Atmosphere-Ocean 26(3):301–320. doi:10.1080/07055900.1988.9649305

Crawford WR, Thomson RE (1991) Physical oceanography of the western Canadian continental shelf. Cont Shelf Res 11:669–683. doi:10.1016/0278-4343(91)90073-f

Crawford WR, Woodward MJ, Foreman MGG, Thomson RE (1995) Oceanographic features of Hecate Strait and Queen Charlotte Sound in summer. Atmosphere-Ocean 33(4):639–681. doi:10.1080/07055900.1995.9649549

Crossman DJ, Choat JH, Clements KD, Hardy T, Jason M (2001) Detritus as food for grazing fishes on coral reefs. Limnol Oceanogr 46(7):1596–1605

Cummings D, Booth D, Lee R, Simpson S, Pile A (2010) Ontogenetic diet shifts in the reef fish *Pseudanthias rubrizonatus* from isolated populations on the north-west shelf of Australia. Mar Ecol Prog Ser 419:211–222. doi:10.3354/meps08827

Dean TA, Haldorson L, Laur DR, Jewett SC, Blanchard A (2000) The distribution of nearshore fishes in kelp and eelgrass communities in Prince William Sound, Alaska: associations with vegetation and physical habitat characteristics. Environ Biol Fishes 57(3):271–287. doi:10.1023/a:1007652730085

DeMartini EE, Roberts DA (1990) Effects of giant kelp (*Macrocystis*) on the density and abundance of fishes in a cobble-bottom kelp forest. Bull Mar Sci 46:287–300

DeNiro MJ (1985) Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction. Nature 317(6040):806–809. doi:10.1038/317806a0

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42(5):495–506. doi:10.1016/0016-7037(78)90199-0

Dick L (2006) The maritime fur trade in Southern Haida Gwaii (Queen Charlotte Islands), ca. 1787–1920. Western and Northern Service Centre, Parks Canada. Vancouver, British Columbia

Duggins DO (1980) Kelp beds and sea otters: an experimental approach. Ecology 61(3):447–453. doi:10.2307/1937405

Duggins DO, Eckman JE (1997) Is kelp detritus a good food for suspension feeders? Effects of kelp species, age and secondary metabolites. Mar Biol 128(3):489–495. doi:10.1007/s002270050115

Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245(4914):170–173. doi:10.1126/science.245.4914.170

Dunton KH (2001) δ^{15}N and δ^{13}C measurements of Antarctic Peninsula Fauna: trophic relationships and assimilation of benthic seaweeds. Am Zool 41(1):99–112. doi:10.1668/0003-1569(2001)041[0099:NACMOA]2.0.CO;2

Dunton KH, Saupe SM, Golikov AN, Schell DM, Schonberg SV (1989) Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. Mar Ecol Prog Ser 56:89–97

Dunton KH, Schell DM (1987) Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an arctic kelp community: δ^{13}C evidence. Mar Biol 93(4):615–625. doi:10.1007/bf00392799

Ebeling AW, Laur DR (1985) The influence of plant cover on surfperch abundance at an offshore temperate reef. Environ Biol Fishes 12(3):169–179. doi:10.1007/BF00005148

Ebeling AW, Laur DR (1988) Fish populations in kelp forests without sea otters: effects of severe storm damage and destructive sea urchin grazing. In: VanBlaricom GR, Estes JA (eds) The community ecology of sea otters, vol 65, Ecological Studies. Springer-Verlag, Berlin, pp 169–191

Erlandson JM, Rick TC (2009) Archaeology meets marine ecology: the antiquity of maritime cultures and human impacts on marine fisheries and ecosystems. Annu Rev Mar Sci 2(1):231–251. doi:10.1146/annurev.marine.010908.163749

Estes JA, Duggins DO (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecol Monogr 65(1):75–100. doi:10.2307/2937159

Estes JA, Jameson RJ, Rhode EB (1982) Activity and prey selection in the sea otter: influence of population status on community structure. Am Nat 120(2):242–258

Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. Science 185(4156):1058–1060. doi:10.1126/science.185.4156.1058

Estes JA, Smith NS, Palmisano JF (1978) Sea otter predation and community organization in the western Aleutian Islands, Alaska. Ecology 59(4):822–833. doi:10.2307/1938786

Fedje DW, Mackie AP, Wigen RJ, Mackie Q, Lake C (2005) Kilgii Gwaay: an early maritime site in the south of Haida Gwaii. In: Fedje DW, Mathewes RW (eds) Haida Gwaii: Human History and

Author's personal copy

Environment from the Time of Loon to the Time of the Iron People. UBC Press, Vancouver, pp 187–203

Foster MS (1990) Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. Hydrobiologia 192(1):21–33. doi:10.1007/BF00006225

Foster MS, Schiel DR (1988) Kelp communities and sea otters: keystone species or just another brick in the wall? In: VanBlaricom GR, Estes JA (eds) The community ecology of sea otters, vol 65, Ecological studies. Springer, Berlin, pp 92–115

Foster MS, Schiel DR (2010) Loss of predators and the collapse of southern California kelp forests (?): alternatives, explanations and generalizations. J Exp Mar Biol Ecol 393(1–2):59–70. doi:10.1016/j.jembe.2010.07.002

France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar Ecol Prog Ser 124:307–312. doi:10.3354/meps124307

Frederick G, Crockford SJ (2005) Analysis of vertebrate fauna from Ts'ishaa village, DfSi 16, Benson Island. In: McMillan AD, Claire DE (eds) Ts'ishaa: archaeology and ethnography of a Nuu-chah-nulth origin site in Barkley Sound. Archaeology Press, Simon Fraser University, Burnaby, pp 173–205

Fredriksen S (2003) Food web studies in a Norwegian kelp forest based on stable isotope (δ^{13}C and δ^{15}N) analysis. Mar Ecol Prog Ser 260:71–81. doi:10.3354/meps260071

Gerard VA (1976) Some aspects of material dynamics and energy flow in a kelp forest in Monterey Bay, California. Unpublished Ph.D. Dissertation, University of California, Santa Cruz

Gibson JR (1988) The maritime trade of the north Pacific coast. In: Washburn WE (ed) Handbook of North American Indians, vol 4, History of Indian-White Relations. Smithsonian Institution, Washington, D.C., pp 375–390

Gobalet KW, Jones TL (1995) Prehistoric native American fisheries of the Central California Coast. Trans Am Fish Soc 124:813–823

Graeme I (1989) The colonisation and degradation of stranded *Macrocystis pyrifera* (L.) C. Ag. by the macrofauna of a New Zealand sandy beach. J Exp Mar Biol Ecol 125(3):203–217. doi:10.1016/0022-0981(89)90097-x

Gregr EJ, Nichol LM, Watson JC, Ford JKB, Ellis GM (2008) Estimating carrying capacity for sea otters in British Columbia. J Wildl Manag 72(2):382–388. doi:10.2193/2006-518

Hallacher L, Roberts D (1985) Differential utilization of space and food by the inshore rockfishes (Scorpaenidae: *Sebastes*) of Carmel Bay, California. Environ Biol Fishes 12(2):91–110. doi:10.1007/BF00002762

Hamilton SL, Caselle JE, Lantz CA, Egloff TL, Kondo E, Newsome SD, Loke-Smith K, Pondella DJ II, Young KA, Lowe CG (2011) Extensive geographic and ontogenetic variation characterizes the trophic ecology of a temperate reef fish on southern California (USA) rocky reefs. Mar Ecol Prog Ser 429:227–244. doi:10.3354/meps09086

Hannah RW, Rankin PS (2011) Site fidelity and movement of eight species of Pacific rockfish at a high-relief rocky reef on the Oregon Coast. N Am J Fish Manag 31(3):483–494. doi:10.1080/02755947.2011.591239

Hanson DK, Kusmer KD (2001) Sea otter (*Enhydra lutris*) scarcity in the strait of Georgia, British Columbia. In: Gerlach SC, Murray MS (eds) People and Wildlife in Northern North America: Essays in honor of R. Dale Guthrie. British Archaeological Reports International Series 944. Archaeopress, Oxford, pp 58–66

Hard RJ, Katzenberg MA (2011) Stable isotope study of hunter-gatherer-fisher diet, mobility, and intensification on the Texas Gulf Coastal Plain. Am Antiq 76(4):709–751

Hare PE, Fogel ML, Stafford TW, Mitchell AD, Hoering TC (1991) The isotopic composition of carbon and nitrogen in individual amino acids isolated from modern and fossil proteins. J Archaeol Sci 18(3):277–292. doi:10.1016/0305-4403(91)90066-X

Harper JR, Austin WT, Morris M, Reimer PD, Reitmeier R (1994) A Biophysical Inventory of the Coastal Resources in Gwaii Haanas. Coastal and Ocean Resources, Inc., Calgary

Harper JR, Morris MC (2006) Living Marine Legacy of Gwaii Haanas V: Coastal Zone Values and Management around Haida Gwaii. In: Sloan NA (ed) Coastal thematic summaries. Gwaii Haanas National Park Reserve and Haida Heritage Site, Queen Charlotte, pp 181–215

Heifetz J, DiCosimo J, Gharrett AJ, Love MS, O'Connell VM, Stanley RD (eds) (2007) Biology, assessment, and management of North Pacific Rockfishes. Alaska Sea Grant, University of Alaska, Fairbanks

Hill JM, McQuaid CD (2008) δ^{13}C and δ^{15}N biogeographic trends in rocky intertidal communities along the coast of South Africa: evidence of strong environmental signatures. Estuar Coast Shelf Sci 80(2):261–268. doi:10.1016/j.ecss.2008.08.005

Hill JM, McQuaid CD, Kaehler S (2006) Biogeographic and nearshore-offshore trends in isotope ratios of intertidal mussels and their food sources around the coast of southern Africa. Mar Ecol Prog Ser 318:63–73. doi:10.3354/meps318063

Hixon MA (1980) Competitive interactions between California reef fishes of the genus *Embiotoca*. Ecology 61(4):918–931. doi:10.2307/1936761

Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. J Anim Ecol 63(4):786–798

Holbrook SJ, Carr MH, Schmitt RJ, Coyer JA (1990) Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. Bull Mar Sci 47:104–114

Holbrook SJ, Schmitt RJ (1984) Experimental analyses of patch selection by foraging black surfperch (*Embiotoca jacksoni* Agazzi). J Exp Mar Biol Ecol 79(1):39–64. doi:10.1016/0022-0981(84)90029-7

Hurd CL (2000) Water motion, marine macroalgal physiology, and production. J Phycol 36(3):453–472. doi:10.1046/j.1529-8817.2000.99139.x

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293(5530):629–637. doi:10.1126/science.1059199

Jameson RJ, Kenyon KW, Johnson AM, Wight HM (1982) History and status of translocated sea otter populations in North America. Wildl Soc Bull 10(2):100–107

Jamieson GS, Campbell A (1995) Red sea urchins and kelp in northern British Columbia. In: Skjoldal HR, Hopkins C, Erikstad KE, Leinaas HP (eds) Ecology of fjords and coastal waters. Elsevier, Amsterdam, pp 537–547

Johnson DW (2006) Predation, habitat complexity, and variation in density-dependent mortality of temperate reef fishes. Ecology 87(5):1179–1188. doi:10.1890/0012-9658(2006)87[1179:phcavi]2.0.co;2

Johnson SW, Murphy ML, Csepp DJ (2003) Distribution, habitat, and behavior of rockfishes, *Sebastes* spp., in nearshore waters of Southeastern Alaska: observations from a remotely operated vehicle. Environ Biol Fishes 66(3):259–270. doi:10.1023/a:1023981908146

Jones TL, Culleton BJ, Larson S, Mellinger S, Porcasi JF (2011) Toward a prehistory of the southern sea otter (*Enhydra lutris nereis*). In: Braje TJ, Rick TC (eds) Human Impacts on Seals, Sea Lions, and Sea Otters: Integrating Archaeology and Ecology in the Northeast Pacific. University of California Press, Berkeley, pp 243–271

Author's personal copy

Jones TL, Garza SC, Porcasi JF, Gaeta JW (2009) Another trans-Holocene sequence from Diablo Canyon: new faunal and radiocarbon findings from CA-SLO-585, San Luis Obispo County, California. J of Calif and Great Basin Anthropol 29(1):19–31

Jones TL, Porcasi JF, Gaeta JW, Codding BF (2008) The Diablo Canyon Fauna: a coarse-grained record of trans-holocene foraging from the Central California Mainland Coast. Am Antiq 73(2):289–316

Jorgensen SJ, Kaplan DM, Klimley AP, Morgan SG, O'Farrell MR, Botsford LW (2006) Limited movement in blue rockfish *Sebastes mystinus*: internal structure of home range. Mar Ecol Prog Ser 327:157–170. doi:10.3354/meps327157

Kaehler S, Pakhomov EA, Kalin RM, Davis S (2006) Trophic importance of kelp-derived suspended particulate matter in a through-flow sub-Antarctic system. Mar Ecol Prog Ser 316:17–22. doi:10.3354/meps316017

Kang C-K, Choy E, Son Y, Lee J-Y, Kim J, Kim Y, Lee K-S (2008) Food web structure of a restored macroalgal bed in the eastern Korean peninsula determined by C and N stable isotope analyses. Mar Biol 153(6):1181–1198. doi:10.1007/s00227-007-0890-y

Kang C-K, Kim JB, Lee K-S, Kim JB, Lee P-Y, Hong J-S (2003) Trophic importance of benthic microalgae to macrozoobenthos in coastal bay systems in Korea: dual stable C and N isotope analyses. Mar Ecol Prog Ser 259:79–92. doi:10.3354/meps259079

Kenyon KW (1969) The sea otter in the Eastern Pacific Ocean. North American Fauna, No. 68. U.S. Government Printing Office, Washington, D.C

Kopczyńska EE, Goeyens L, Semeneh M, Dehairs F (1995) Phytoplankton composition and cell carbon distribution in Prydz Bay, Antarctica: relation to organic particulate matter and its δ^{13}C values. J Plankton Res 17(4):685–707. doi:10.1093/plankt/17.4.685

Krumhansl KA, Scheibling RE (2011) Detrital production in Nova Scotian kelp beds: patterns and processes. Mar Ecol Prog Ser 421:67–82. doi:10.3354/meps08905

Kvitek RG, Shull D, Canestro D, Bowlby EC, Troutman BL (1989) Sea otters and benthic prey communities in Washington state. Mar Mamm Sci 5(3):266–280. doi:10.1111/j.1748-7692.1989.tb00340.x

Laidre KL, Jameson RJ, Gurarie E, Jeffries SJ, Allen H (2009) Spatial habitat use patterns of sea otters in coastal Washington. J Mammal 90(4):906–917. doi:10.1644/08-mamm-a-338.1

Larson RJ (1980a) Competition, habitat selection, and the Bathymetric segregation of two rockfish (*Sebastes*) species. Ecol Monogr 50 (2):221–239. doi:10.2307/1942480

Larson RJ (1980b) Territorial behavior of the black and yellow rockfish and gopher rockfish (Scorpaenidae, *Sebastes*). Mar Biol 58 (2):111–122. doi:10.1007/bf00396122

Larson RJ, DeMartini EE (1984) Abundance and vertical distribution of fishes in a cobble-bottom kelp forest off San Onofre, California. Fish Bull 82(1):37–53

Laur DR, Ebeling AW, Coon DA (1988) Effects of sea otter foraging on subtidal reef communities off Central California. In: VanBlaricom GR, Estes JA (eds) The community ecology of sea otters, vol 65, Ecological studies. Springer, Berlin, pp 151–168

Laws EA, Popp BN, Bidigare RR, Kennicutt MC, Macko SA (1995) Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO_2]_{aq}$: theoretical considerations and experimental results. Geochim Cosmochim Acta 59(6):1131–1138. doi:10.1016/0016-7037(95)00030-4

Leighton DL, Jones LG, North W (1966) Ecological relationships between giant kelp and sea urchins in southern California. In: Young EG, McLachlan JL (eds) Proceedings of the 5th International Seaweed Symposium, Oxford, England. Pergamon Press, Oxford, pp 141–153

Li Z, Gray AK, Love MS, Asahida T, Gharrett AJ (2006) Phylogeny of members of the rockfish (*Sebastes*) subgenus *Pteropodus* and their relatives. Can J Zool 84(4):527–536. doi:10.1139/z06-022

Longin R (1971) New method of collagen extraction for radiocarbon dating. Nature 230(5291):241–242. doi:10.1038/230241a0

Love M, Carr M, Haldorson L (1991) The ecology of substrate-associated juveniles of the genus *Sebastes*. Environ Biol Fishes 30(1):225–243. doi:10.1007/bf02296891

Love MS (1979) Isolation of olive rockfish, *Sebastes serranoides*, populations off southern California. Fish Bull 77(4):975–983

Love MS, Morris P, McCrae M, Collins R (1990) Life history aspects of 19 rockfish species (Scorpaenidae: *Sebastes*) from the Southern California Bight. In. NOAA Technical Report NMFS 87

Love MS, Westphal WV (1981) Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, of central California. Fish Bull 79(3):533–545

Love MS, Yoklavich MM, Thorsteinson L (2002) The rockfishes of the Northeast Pacific. University of California Press, Berkeley

Lowry MS, Stewart BS, Heath CB, Yochem PK, Francis JM (1991) Seasonal and annual variability in the diet of California sea lions *Zalophus californianus* at San Nicolas Island, California, 1981–86. Fish Bull 89(2):331–336

Mackie Q, Orchard TJ, Lake C (2001) The Environmental Archaeology Pilot Project in Gwaii Haanas. Report to the British Columbia Heritage Trust, Victoria, British Columbia

Mann KH (1973) Seaweeds: their productivity and strategy for growth. Science 182(4116):975–981. doi:10.1126/science.182.4116.975

Markel RW (2011) Rockfish recruitment and trophic dynamics on the west coast of Vancouver Island: Fishing, ocean climate, and sea otters. Unpublished Ph.D. Dissertation, University of British Columbia, Vancouver

Martin JC, Lacko LC, Yamanaka KL (2006) A pilot study using a remotely operated vehicle (ROV) to observe inshore rockfish (*Sebastes* spp.) in the southern Strait of Georgia, March 3–11, 2005. Can Tech Rep Fish Aquat Sci 2663:36

Martin JC, Yamanaka KL (2004) A visual survey of inshore rockfish abundance and habitat in the southern Strait of Georgia using a shallow-water towed video system. Can Tech Rep Fish Aquat Sci 2566:52

Mathews SB, Barker MW (1983) Movements of rockfish (*Sebastes*) tagged in northern Puget Sound, Washington. Fish Bull 83 (1):916–922

Matthews KR (1990a) A comparative study of habitat use by young-of-the-year, subadult, and adult rockfishes on four habitat types in central Puget Sound. Fish Bull 88(2):223–239

Matthews KR (1990b) An experimental study of the habitat preferences and movement patterns of copper, quillback, and brown rockfishes (*Sebastes* spp.). Environ Biol Fishes 29(3):161–178. doi:10.1007/bf00002217

Matthews KR (1990c) A telemetric study of the home ranges and homing routes of copper and quillback rockfishes on shallow rocky reefs. Can J Zool 68(11):2243–2250. doi:10.1139/z90-312

McKechnie I (2007) Investigating the complexities of sustainable fishing at a prehistoric village on western Vancouver Island, British Columbia, Canada. J Nat Conserv 15(3):208–222. doi:10.1016/j.jnc.2007.05.001

McKechnie I, Wigen RJ (2011) Toward a historical ecology of pinniped and sea otter hunting traditions on the coast of southern British Columbia. In: Braje TJ, Rick TC (eds) Human impacts on seals, sea lions, and sea otters: integrating archaeology and ecology in the Northeast Pacific. University of California Press, Berkeley, pp 129–166

Melteff BR (ed) (1987) Proceedings of the International Rockfish Symposium. Anchorage, Alaska, October 20–22, 1986. Alaska Sea Grant Report No. 87–2. University of Alaska, Anchorage

Miller AK, Sydeman WJ (2004) Rockfish response to low-frequency ocean climate change as revealed by the diet of a marine bird over multiple time scales. Mar Ecol Prog Ser 281:207–216. doi:10.3354/meps281207

Author's personal copy

Mills KL, Laidig T, Ralston S, Sydeman WJ (2007) Diets of top predators indicate pelagic juvenile rockfish (*Sebastes* spp.) abundance in the California Current System. Fish Oceanogr 16 (3):273–283. doi:10.1111/j.1365-2419.2007.00429.x

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochim Cosmochim Acta 48(5):1135–1140. doi:10.1016/0016-7037(84)90204-7

Misarti N, Finney BP, Maschner H, Wooller MJ (2009) Changes in northeast Pacific marine ecosystems over the last 4500 years: evidence from stable isotope analysis of bone collagen from archaeological middens. Holocene 19(8):1139–1151. doi:10.1177/0959683609357824

Mitamura H, Uchida K, Miyamoto Y, Arai N, Kakihara T, Yokota T, Okuyama J, Kawabata Y, Yasuda T (2009) Preliminary study on homing, site fidelity, and diel movement of black rockfish *Sebastes inermis* measured by acoustic telemetry. Fish Sci 75 (5):1133–1140. doi:10.1007/s12562-009-0142-9

Morinière EC, Pollux BJA, Nagelkerken I, Hemminga MA, Huiskes AHL, Velde G (2003) Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. Mar Ecol Prog Ser 246:279–289. doi:10.3354/meps246279

Morris R, Ellis DV, Emerson BP (1981) The British Columbia transplant of sea otters *Enhydra Lutris*. Biol Conserv 20(4):291–295. doi:10.1016/0006-3207(81)90015-X

Moss ML, Yang DY, Newsome SD, Speller CF, McKechnie I, McMillan AD, Losey RJ, Koch PL (2006) Historical ecology and biogeography of north Pacific pinnipeds: isotopes and ancient DNA from three archaeological assemblages. J Isl Coast Archaeol 1(2):165–190. doi:10.1080/15564890600934129

Munk KM (2001) Maximum ages of groundfishes in waters off Alaska and British Columbia and considerations of age determination. Alaska Fish Res Bull 8:12–21

Murie DJ, Parkyn DC, Clapp BG, Krause GG (1994) Observations on the distribution and activities of rockfish, *Sebastes* spp., in Saanich Inlet, British Columbia, from the *Pisces IV* submersible. Fish Bull 92:313–323

Nagtegaal DA (1983) Identification and description of assemblages of some commercially important rockfishes (*Sebastes* spp.) off British Columbia. Canadian Technical Report of Fisheries and Aquatic Sciences. Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo

Newell RC, Lucas MI, Velimirov B, Seiderer LJ (1980) Quantitative significance of dissolved organic losses following fragmentation of kelp (*Ecklonia maxima* and *Laminaria pallida*). Mar Ecol Prog Ser 2:45–59

Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Mar Mamm Sci 26(3):509–572. doi:10.1111/j.1748-7692.2009.00354.x

Newsome SD, Etnier MA, Gifford-Gonzalez D, Phillips DL, van Tuinen M, Hadly EA, Costa DP, Kennett DJ, Guilderson TP, Koch PL (2007a) The shifting baseline of northern fur seal ecology in the northeast Pacific Ocean. Proc Natl Acad Sci 104 (23):9709–9714. doi:10.1073/pnas.0610986104

Newsome SD, Etnier MA, Kurle CM, Waldbauer JR, Chamberlain CP, Koch PL (2007b) Historic decline in primary productivity in western Gulf of Alaska and eastern Bering Sea: isotopic analysis of northern fur seal teeth. Mar Ecol Prog Ser 332:211–224. doi:10.3354/meps332211

Nichol LM, Boogaards MD, Abernethy R (2009) Recent trends in the abundance and distribution of sea otters (*Enhydra lutris*) in British Columbia. Canadian Science Advisory Secretariat Research Document 2009/016, vol 2009/016. Fisheries and Oceans Canada, Nanaimo, British Columbia

Norderhaug KM, Christie H (2011) Secondary production in a *Laminaria hyperborea* kelp forest and variation according to wave exposure. Estuar Coast Shelf Sci 95(1):135–144. doi:10.1016/j.ecss.2011.08.028

Norderhaug KM, Fredriksen S, Nygaard K (2003) Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of bacterial degradation to food quality. Mar Ecol Prog Ser 255:135–144. doi:10.3354/meps255135

O'Connell VM, Carlile DW (1993) Habitat-specific density of adult yelloweye rockfish *Sebastes ruberrimus* in the eastern Gulf of Alaska. Fish Bull 91(2):304–309

Orchard TJ (2003) An application of the linear regression technique for determining length and weight of six fish taxa: the role of selected fish species in Aleut Paleodiet. British Archaeological Reports, International Series 1172. Archaeopress, Oxford

Orchard TJ (2009) Otters and urchins: continuity and change in Haida economy during the Late Holocene and maritime fur trade periods. British Archaeological Reports International Series 2027. Archaeopress, Oxford

Orchard TJ (2011) Mid- to Late Holocene Subsistence and Settlement in Gwaii Haanas: Analysis of Auger, Column, and Faunal Samples from 2009 and 2010 Fieldwork. Report submitted to Parks Canada, Cultural Resource Services, Western & Northern Canada Services Centre, Victoria and Vancouver, B.C.

Orchard TJ, Szpak P (2011) Identification of salmon species from archaeological remains on the northwest coast. In: Moss M, Cannon A (eds) The archaeology of North Pacific fisheries. University of Alaska Press, Fairbanks

Orr M, Zimmer M, Jelinski DE, Mews M (2005) Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. Ecology 86(6):1496–1507. doi:10.1890/04-1486

Osmond CB, Valaane N, Haslam SM, Uotila P, Roksandic Z (1981) Comparisons of δ^{13}C values in leaves of aquatic macrophytes from different habitats in Britain and Finland; some implications for photosynthetic processes in aquatic plants. Oecologia 50 (1):117–124. doi:10.1007/BF00378804

Ostrom NE, Macko SA, Deibel D, Thompson RJ (1997) Seasonal variation in the stable carbon and nitrogen isotope biogeochemistry of a coastal cold ocean environment. Geochim Cosmochim Acta 61(14):2929–2942. doi:10.1016/S0016-7037(97)00131-2

Page HM, Reed DC, Brzezinski MA, Melack JM, Dugan JE (2008) Assessing the importance of land and marine sources of organic matter to kelp forest food webs. Mar Ecol Prog Ser 360:47–62. doi:10.3354/meps07382

Paine RT (1980) Food webs: linkage, interaction strength and community infrastructure. J Anim Ecol 49(3):667–685. doi:10.2307/4220

Parker SJ, Berkeley SA, Golden JT, Gunderson DR, Heifetz J, Hixon MA, Larson R, Leaman BM, Love MS, Musick JA, O'Connell VM, Ralston S, Weeks HJ, Yoklavich MM (2000) Management of Pacific rockfish. Fisheries 25(3):22–30. doi:10.1577/1548-8446(2000)025<0022:mopr>2.0.co;2

Parker SJ, Rankin PS, Olson JM, Hannah RW (2007) Movement patterns of black rockfish (*Sebastes melanops*) in Oregon coastal waters. In: Heifetz J, DiCosimo J, Gharrett AJ, Love MS, O'Connell VM, Stanley RD (eds) Biology, assessment, and management of North Pacific rockfishes. Alaska Sea Grant, University of Alaska, Fairbanks, pp 39–57

Pearcy WG, Stein DL, Hixon MA, Pikitch EK, Barss WH, Starr RM (1989) Submersible observations of deep-reef fishes of Heceta Bank, Oregon. Fish Bull 87:955–965

Peterson TD, Toews HNJ, Robinson CLK, Harrison PJ (2007) Nutrient and phytoplankton dynamics in the Queen Charlotte Islands (Canada) during the summer upwelling seasons of 2001–2002. J Plankton Res 29(3):219–239. doi:10.1093/plankt/fbm010

Author's personal copy

Pitcher TJ (2005) Back-to-the-future: a fresh policy initiative for fisheries and a restoration ecology for ocean ecosystems. Philos Trans: Biol Sci 360(1453):107–121

Reisewitz S, Estes J, Simenstad C (2006) Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian archipelago. Oecologia 146(4):623–631. doi:10.1007/s00442-005-0230-1

Richards LJ (1986) Depth and habitat distributions of three species of rockfish (*Sebastes*) in British Columbia: observations from the submersible PISCES IV. Environ Biol Fishes 17(1):13–21. doi:10.1007/BF00000397

Rick TC, Erlandson JM (eds) (2008) Human impacts on ancient marine ecosystems: a global perpsective. University of California Press, Berkeley

Riedman ML, Estes JA (1990) Sea otter (*Enhydra lutris*): behavior, ecology, and natural history. US Department of Interior Biological Report 90–14

Robinson CLK, Morrison J, Foreman MGG (2005) Oceanographic connectivity among marine protected areas on the north coast of British Columbia, Canada. Can J Fish Aquat Sci 62(6):1350–1362. doi:10.1139/f05-088

Rodil I, Lastra M, López J (2007) Macroinfauna community structure and biochemical composition of sedimentary organic matter along a gradient of wave exposure in sandy beaches (NW Spain). Hydrobiologia 579(1):301–316. doi:10.1007/s10750-006-0443-2

Rodríguez SR (2003) Consumption of drift kelp by intertidal populations of the sea urchin *Tetrapygus niger* on the central Chilean coast: possible consequences at different ecological levels. Mar Ecol Prog Ser 251:141–151. doi:10.3354/meps251141

Salomon AK, Shears NT, Langlois TJ, Babcock RC (2008) Cascading effects of fishing can alter carbon flow through a temperate coastal ecosystem. Ecol Appl 18(8):1874–1887. doi:10.1890/07-1777.1

Schaal G, Riera P, Leroux C (2009) Trophic significance of the kelp *Laminaria digitata* (Lamour.) for the associated food web: a between-sites comparison. Estuar Coast Shelf Sci 85(4):565–572. doi:10.1016/j.ecss.2009.09.027

Schaal G, Riera P, Leroux C (2010) Trophic ecology in a Northern Brittany (Batz Island, France) kelp (*Laminaria digitata*) forest, as investigated through stable isotopes and chemical assays. J Sea Res 63(1):24–35. doi:10.1016/j.seares.2009.09.002

Schoeninger MJ, DeNiro MJ (1984) Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. Geochim Cosmochim Acta 48(4):625–639. doi:10.1016/0016-7037(84)90091-7

Simenstad CA, Duggins DO, Quay PD (1993) High turnover of inorganic carbon in kelp habitats as a cause of δ^{13}C variability in marine food webs. Mar Biol 116(1):147–160. doi:10.1007/BF00350742

Simenstad CA, Estes JA, Kenyon KW (1978) Aleuts, sea otters, and alternate stable-state communities. Science 200(4340):403–411

Sjøtun K, Fredriksen S (1995) Growth allocation in *Laminaria hyperborea* (Laminariales, Phaeophyceae) in relation to age and wave exposure. Mar Ecol Prog Ser 126:213–222. doi:10.3354/meps126213

Sloan NA (2006) Kelp forests. In: Sloan NA (ed) Living marine legacy of Gwaii Haanas V: coastal zone values and management around Haida Gwaii. Gwaii Haanas National Park Reserve and Haida Heritage Site, Queen Charlotte, pp 256–262

Sloan NA, Bartier PM (2000) Living marine legacy of Gwaii Haanas I: marine plant baseline to 1999 and plant-related management issues. Parks Canada-Technical Reports in Ecosystem Science, No. 27, Gwaii Haanas National Park Reserve/Haida Heritage Site, British Columbia

Soares AG, Schlacher TA, McLachlan A (1997) Carbon and nitrogen exchange between sandy beach clams (*Donax serra*) and kelp beds in the Benguela coastal upwelling region. Mar Biol 127(4):657–664. doi:10.1007/s002270050056

Southon JR, Fedje DW (2003) A post-glacial record of ^{14}C Reservoir Ages for the British Columbia Coast. Can J Archaeol 27:95–11

Steinberg PD (1988) Effects of quantitative and qualitative variation in phenolic compounds on feeding in three species of marine invertebrate herbivores. J Exp Mar Biol Ecol 120(3):221–237. doi:10.1016/0022-0981(88)90003-2

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ Conserv 29(04):436–459. doi:10.1017/S0376892902000322

Steneck RS, Watling L (1982) Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. Mar Biol 68(3):299–319. doi:10.1007/bf00409596

Sydeman WJ, Hester MM, Thayer JA, Gress F, Martin P, Buffa J (2001) Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997. Prog in Oceanogr 49(1–4):309–329. doi:10.1016/s0079-6611(01)00028-3

Szpak P (2011) Fish bone chemistry and ultrastructure: implications for taphonomy and stable isotope analysis. J Archaeol Sci 38(12):3358–3372. doi:10.1016/j.jas.2011.07.022

Szpak P, Gröcke DR, Debruyne R, MacPhee RDE, Guthrie RD, Froese D, Zazula GD, Patterson WP, Poinar HN (2010) Regional differences in bone collagen δ^{13}C and δ^{15}N of Pleistocene mammoths: implications for paleoecology of the mammoth steppe. Palaeogeogr Palaeoclimatol Palaeoecol 286(1–2):88–96. doi:10.1016/j.palaeo.2009.12.009

Szpak P, Orchard TJ, Gröcke DR (2009) A Late Holocene vertebrate food web from southern Haida Gwaii (Queen Charlotte Islands, British Columbia). J Archaeol Sci 36(12):2734–2741. doi:10.1016/j.jas.2009.08.013

Szpak P, Orchard TJ, McKechnie I, Gröcke DR (2012) Historical ecology of late Holocene sea otters (*Enhydra lutris*) from northern British Columbia: isotopic and zooarchaeological perspectives. J Archaeol Sci 39(5):1553–1571. doi:10.1016/j.jas.2011.12.006

Tallis H (2009) Kelp and rivers subsidize rocky intertidal communities in the Pacific Northwest (USA). Mar Ecol Prog Ser 389:85–96. doi:10.3354/meps08138

Thayer JA, Bertram DF, Hatch SA, Hipfner MJ, Slater L, Sydeman WJ, Watanuki Y (2008) Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: synchrony and relationships with sea surface temperature. Can J Fish Aquat Sci 65(8):1610–1622. doi:10.1139/F08-076

Tolimieri N, Andrews K, Williams G, Katz S, Levin PS (2009) Home range size and patterns of space use by lingcod, copper rockfish and quillback rockfish in relation to diel and tidal cycles. Mar Ecol Prog Ser 380:229–243. doi:10.3354/meps07930

Vanderklift M, Wernberg T (2008) Detached kelps from distant sources are a food subsidy for sea urchins. Oecologia 157(2):327–335. doi:10.1007/s00442-008-1061-7

Vetter EW (1995) Detritus-based patches of high secondary production in the nearshore benthos. Mar Ecol Prog Ser 120:251–262. doi:10.3354/meps120251

Vizzini S, Mazzola A (2002) Stable carbon and nitrogen ratios in the sand smelt from a Mediterranean coastal area: feeding habits and effect of season and size. J Fish Biol 60(6):1498–1510. doi:10.1111/j.1095-8649.2002.tb02443.x

Wainright SC, Haney JC, Kerr C, Golovkin AN, Flint MV (1998) Utilization of nitrogen derived from seabird guano by terrestrial and marine plants at St. Paul, Pribilof Islands, Bering Sea, Alaska. Mar Biol 131(1):63–71. doi:10.1007/s002270050297

Watson JC, Estes JA (2011) Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. Ecol Monogr 81(2):215–239. doi:10.1890/10-0262.1

Wernberg T, Connell SD (2008) Physical disturbance and subtidal habitat structure on open rocky coasts: effects of wave exposure,

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extent and intensity. J Sea Res 59(4):237–248. doi:10.1016/j.seares.2008.02.005

Wernberg T, Vanderklift M, How J, Lavery P (2006) Export of detached macroalgae from reefs to adjacent seagrass beds. Oecologia 147(4):692–701. doi:10.1007/s00442-005-0318-7

Wiencke C, Fischer G (1990) Growth and stable carbon isotope composition of cold-water macroalgae in relation to light and temperature. Mar Ecol Prog Ser 65(3):283–292

Williams GD, Levin PS, Palsson WA (2010) Rockfish in Puget Sound: an ecological history of exploitation. Marine Policy 34(5):1010–1020. doi:10.1016/j.marpol.2010.02.008

Wittmer MHOM, Auerswald K, Schönbach P, Schäufele R, Müller K, Yang H, Bai YF, Susenbeth A, Taube F, Schnyder H (2010) Do grazer hair and faeces reflect the carbon isotope composition of semi-arid C3/C4 grassland? Basic Appl Ecol 11(1):83–92. doi:10.1016/j.baae.2009.10.007

Wolf E (1982) Europe and the people without history. University of California Press, Berkeley

Workman GD, Stanley RD, Olsen N, Rutherford KL (2008) West coast Queen Charlotte Islands groundfish bottom trawl survey, September 11th to October 17th, 2007. Can Manuscr Rep Fish Aquat Sci 2823

Wu J, Calvert SE, Wong CS (1997) Nitrogen isotope variations in the subarctic northeast Pacific: relationships to nitrate utilization and trophic structure. Deep-Sea Res I Oceanogr Res Pap 44(2):287–314. doi:10.1016/S0967-0637(96)00099-4

Wyatt ASJ, Waite AM, Humphries S (2010) Variability in isotope discrimination factors in coral reef fishes: implications for diet and food web reconstruction. PLoS One 5(10):e13682. doi:10.1371/journal.pone.0013682

Yamanaka KL, Kronlund AR (1997) Inshore rockfish assessment for the west coast of Canada in 1996 and recommended yields for 1997. Can Tech Rep Fish Aquat Sci 2175:80

Yamanaka KL, Lacko LC (2008) Research catch and effort data on nearshore reef-fishes in British Columbia Statistical Area 12. Can Tech Rep Fish Aquat Sci 2803:45