Abstract—Many highly exploited ecosystems are managed on the basis of single-species demographic information. This management approach can exacerbate tensions among stakeholders with competing interests who in turn rely on data with notoriously high variance. In this case study, an application of diet and dive survey data was used to describe the prey preference of lingcod (*Ophiodon elongatus*) in a predictive framework on nearshore reefs off Oregon. The lingcod is a large, fast-growing generalist predator of invertebrates and fishes. In response to concerns that lingcod may significantly reduce diminished populations of rockfishes (*Sebastes* spp.), the diets of 375 lingcod on nearshore reefs along the Oregon Coast were compared with estimates of relative prey availability from dive surveys. In contrast to the transient pelagic fishes that comprised 46% of lingcod diet by number, rockfishes comprised at most 4.7% of prey items. Rockfishes were the most abundant potential prey observed in dive surveys, yet they were the least preferred. Ecosystem-based fisheries management (EBFM) requires information about primary trophic relationships, as well as relative abundance and distribution data for multiple species. This study shows that, at a minimum, predation relative to prey availability must be considered before predator effects can be understood in a management context.

Prey preference of lingcod (*Ophiodon elongatus*), a top marine predator: implications for ecosystem-based fisheries management

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Ecosystem-based fisheries management (EBFM) has generated considerable interest over the last decade as a way of better managing depressed fisheries stocks (Pikitch et al., 2004; Gaichas et al., 2010). This interest has been in large part a reaction to the perceived failure of traditional single-species fisheries management to prevent the collapse of exploited and ancillary populations in many systems worldwide (Dulvy et al., 2003; Hutchings and Baum, 2005; Myers and Worm, 2005). One implication of EBFM is the capacity to forecast changes in managed populations in reaction to fluctuations in linked predator and prey populations. This requires understanding what species of interest consume in a given temporal and spatial context. An additional consideration is that many exploited fishes are generalist consumers and shifts in densities and distributions may produce complex top-down effects (Bruno and O'Connor, 2005). These are among numerous challenges in gathering the information required to describe even a subset of primary trophic relationships in a dynamic system.

Prey preference is the differential consumption of some prey types over others given equal availability. It is considered a fixed behavioral characteristic and, as a way of forecasting predation intensity on managed stocks, has received little attention. However, preference models may be both useful and efficient as an extension of food web models to aid management of exploited stocks (Gaichas et al., 2010). In this study I used an analysis of dive survey data with consumption data in a prey preference model to better understand the likely effects of a rapidly increasing predator population on managed prey. Consumption rates for generalist consumers like lingcod (*Ophiodon elongatus* Girard) may be either positively or negatively correlated among different prey types, or they may be uncorrelated, and these effects can be important in actively managed systems (Dill et al., 2003). If spatially and temporally transient prey species predominate in the diet of a resident predator, they may constitute subsidies to the local predator population (Anderson and Polis, 1998). When subsidies occur there may be a concomitant suppression of local prey species through apparent competition among prey types with a common predator (Holt, 1977; Chaneton and Bonsall, 2000). Especially in marine systems where trophic webs may be poorly defined (Thompson et al., 2007), initial consideration of predator-prey relationships requires dietary analysis (Heithaus et al., 2008). Diets of targeted fishery species provide necessary information for understanding food web structure, which is an important requirement for ecosystem-based fisheries science

and management (Francis et al., 2007). However, in addition to these basic trophic relationships, it is necessary to understand the context in which prey are being selected. The effects of predation on both predator and prey populations change as prey densities vary.

Although EBFM requires even more information than traditional single-species management approaches, managers, scientists, and stakeholders make use of less certain information both in less accessible systems and in those that are accessible but where temporal and spatial scales far exceed the capacity to collect local demographic data. For these reasons identifying specific management triggers based on comprehensive and collectable information has been proposed (Samhouri et al., 2010) and the case made that uncertain data and imperfect advice must be embraced, as long as they are appropriate data (Ludwig et al., 1993; Johannes, 1998; Frid et al., 2008). Challenges to the use of EBFM include "species conflicts," where management and stakeholder interest in one target species may interfere with other species and often involve the assumed effects of large generalist predator(s) on recovering high value prey species, sometimes in and out of marine protected areas. Examples of generalist predators involved in management conflicts are groupers (*Epinephelus* spp. [Ault et al., 2006; Coleman and Koenig, 2010]), red snapper (*Lutjanus campechanus* [Wells et al., 2008; Cowan et al., 2010]), cod (*Gadus morhua* [Link and Garrison, 2002]), and striped bass (*Morone saxatilis* [Paolisso, 2002; Walter et al., 2003]).

Marine reserves are becoming more widely considered as a management tool for protecting a portion of breeding populations as interest in EBFM increases. However, in addition to providing a refuge from fishing mortality, marine reserves can enhance local populations of large, resident, top-level predators (Martell et al., 2000; McClanahan and Arthur, 2001). Among possible effects of a local increase in predator biomass is a decrease in a particular prey type (Graham et al., 2003). For example, this kind of interaction has been proposed for lingcod predation on rockfishes (*Sebastes* spp.) within marine reserves (Beaudreau and Essington, 2007; 2009) and both are major targets of commercial fisheries.

The following case study exemplifies necessary considerations for EBFM. Lingcod are targeted by both recreational and commercial fishermen along the west coast of North America. The 2000 stock assessment of lingcod from British Columbia to northern California estimated biomass at 11% of precommercial exploitation levels (Jagielo, et al.[1]) and management substantially reduced fishing mortality to allow recovery of this stock. By 2006, lingcod stocks were declared fully recovered by the Pacific Fisheries Management Council. Lingcod are

large (up to 152 cm total length [TL] and 59 kg) and fast growing. They are relatively site-attached, demersal, generalist predators, found on shallow northeastern Pacific rocky reefs. They roam across both rocky habitat and soft-bottom over distances of at least hundreds of meters, yet they demonstrate a high degree of site fidelity for time scales of at least weeks to months (Jagielo, 1990; Smith et al., 1990; Mathews, 1992; Yamanaka and Richards, 1993; Jagielo, 1999; Starr et al., 2004).

Although lingcod population dynamics have been studied from a fisheries perspective, very little is understood about how this predator affects the structure of fish populations and assemblages on rocky reefs. A previous study of diet and habitat associations of demersal fishes on nearshore reefs along the Oregon Coast revealed that 282 adult lingcod had consumed 27 identifiable species of fish and invertebrates. Of those 134 prey items, no adult rockfishes were found and the contribution to total biomass by all rockfish prey was less than one percent (Steiner, 1979). However, no prior lingcod studies have described diet in relation to prey abundance. In order to assess differential selection, and thus characterize which prey types will most likely be selected, there must be an estimate of prey availability relative to consumption (Manley et al., 2002). The goal of this study was to describe the diet of adult lingcod off the coast of Oregon, to characterize relative patterns of consumption of transient and resident prey species by lingcod, and describe whether or not preference, defined as the differential consumption of one prey type over others in relation to availability, was evident. Specifically, by using lingcod diet and prey abundance estimates off the coast of Oregon, I addressed the following questions: 1) Do lingcod prefer particular prey species, and 2) do lingcod preferentially target rockfishes? The answers to these questions were yes and no, respectively. This information can be used to more effectively manage a reserve system where both predator and prey populations are the focus of conservation efforts.

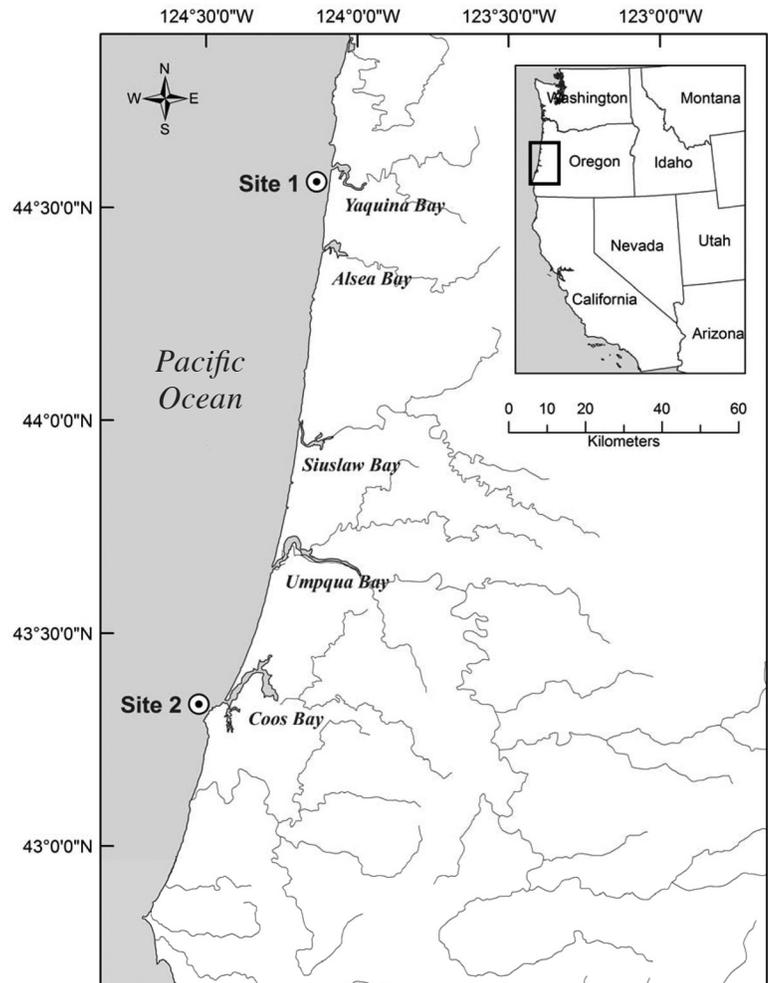## Materials and methods

Study area

The nearshore zone off Oregon is generally exposed, has relatively high wave energy, and is influenced by longshore currents. I sampled lingcod from two nearshore subtidal sites along the coast of Oregon: one south of Newport, referred to as site 1 (44°31′N lat.; 124°08′W long.), and another south of Coos Bay, referred to as site 2 (43°16′N; 124°25′W) (Fig. 1). Both sites comprised high relief rocky reef, rocky flats, cobble, and sand at depths of 20 to 50 m. The reefs varied from small pinnacles encompassing <10 m^2 to large boulder fields and bedrock flats that may exceed one km^2 in area. The area of exposed rock changes on temporal scales of months to decades, however, sand transport is greatest during the stormy winter months and relatively stable during the summer (Kulm et al., 1968).

Prey availability

Prey availability was compared with observed prey consumption to evaluate prey preference. Lingcod are highly generalized visual predators and visual surveys provide an estimate of relative prey density within a visual field. I evaluated prey availability with dive surveys in the areas where lingcod were collected for gut analyses (Starr et al., 2010). Dive surveys were conducted from a relatively small boat equipped with standard electronics. Ocean conditions had to be sufficiently benign for both safe boat handling and diver deployment and recovery. Weather conditions were a limiting factor for dive surveys. In general, combined seas (wave and swell height) of less than two to three meters and wind velocities of less than 20 knots are necessary. Additionally, fog and strong currents at times prohibited safe dive and boat operation near shallow reefs. A single dive survey consisted of a single 100×4 m visual-count transect (Bohnsack, 1996) during daylight between 1000 and 1500 hours. I conducted surveys at site 1 in January and June 2004, and in June 2005 (three surveys total), and at site 2 in January and October 2004, and in June (three surveys) and September 2005 (six surveys total) (Table 1). The exact locations of transects were determined haphazardly from the surface by dropping a weighted line in an area as close as possible to where fishing for lingcod occurred and where depths were sufficiently shallow so that single dive surveys could be completed within one scuba dive (<35 m). Visibility was variable but was always sufficient to identify fish within two meters of the transect line, and fishes and invertebrates were approachable. I surveyed three basic habitat types within each transect: high-relief rocky reef, boulder mixed with cobble, and broken shell mixed with sand. I quantified the relative abundance of potential prey within the foraging range of lingcod, estimating age groups of rockfishes (year 1, 1–2, 3+) from estimated total lengths. During dives I estimated fish lengths by comparing them against objects of similar shape and color of known lengths at various distances. I observed only adult lingcod on rocky reef habitat. Relative prey availability between sites 1 and 2 were compared by one-way analysis of similarity (ANOSIM; Clark, 1993). The ordination, associated tests, and species accumulation curves were produced with PRIMER analytical software (vers. 6.1.6, PRIMER-E Ltd., Plymouth, U.K.[2]) by using an included ANOSIM method (Clark and Gorley, 2006). Additionally, a rank concordance test of prey category abundance was

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[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Figure 1
Map of study region (inset) and study sites (1 and 2) within the Oregon nearshore zone where stomach samples of lingcod (*Ophiodon elongatus*) were collected and dive surveys of potential prey were conducted.

conducted for sites 1 and 2 (Sokal and Rohlf, 1995). For comparisons of two groups, *t*-tests were used unless a Shapiro-Wilk test for normality, equal variance, or both, failed, in which case a Mann-Whitney rank sum test was used. The Michaelis-Menten equation (MME) was used to generate species accumulation curves to evaluate how quickly the number of new species became asymptotic (curve stability) with additional sampling effort (Willott, 2001; Williams et al., 2007). The beta value for the MME represents the number of samples required to detect 50% of the total number of species, or groups.

Dietary composition

Multiple anglers using lines with a single hook and attractor on a chartered recreational fishing vessel in July (19 and 17 fish in two sampling trips), August (12 fish), and September (12 fish) of 2003 (one trip each) collected a total of 60 lingcod at site 1. The lingcod collected at Site

2 were by a commercial fisherman in the months of May (21 fish), June (48 fish), and October (59 fish) of 2004, and May (49 fish), June (45 fish), August (46 fish), and October (40 fish) of 2005 (Table 1). The commercial gear used was a "dingle-bar"—an iron bar trolled just off the seafloor with a set of three rubber jigs with large hooks and an attractor. An additional set of three jigs with hooks was trolled mid-water (about 10–20 m off-bottom). When multiple lingcod hit the jigs, they generally did so simultaneously on both the bottom and mid-water sets.

In the first year, lingcod stomachs were labeled, placed in cloth bags, and preserved in ethanol. In subsequent years, stomachs were labeled, wrapped in cheesecloth, packed in ice, and examined within 24 hours. The number and identity of items in each stomach were identified to the lowest possible taxon. When the identification of a prey fish was not possible from external characteristics, I attempted to identify the prey by otoliths or skeletal elements (or both). A second, blind reading of a subsample of otoliths and skeletal elements was done by a recognized expert who confirmed prior determinations. When possible, beaks were used to estimate size and infer species of octopus by comparison with other samples that were identified to species from external characteristics.

Observed consumption provides a description of a local prey base if sample sizes are large enough to cap-

ture the diversity within a population and incorporate representative temporal and spatial scales. Although lingcod are highly generalized, the incidence of new prey types in gut samples was asymptotic with increasing sample size. The MME was used to generate a species-accumulation curve and test for sufficiency of sampling effort. A rank concordance test of prey category abundance was conducted for sites 1 and 2 (Sokal and Rohlf, 1995). For comparisons of two groups, t-tests were used unless a Shapiro-Wilk test for normality or equal variance test (or both) failed, in which case a Mann-Whitney rank sum test was used. Additionally, one-way analysis of variance (ANOVA) was used to test for differences among sampling trips for differences in stomach fullness and for differences in consumption of transient and resident prey types.

Stomach content data were analyzed by frequency of occurrence, $\%F_o = (n \cdot 100)/N_s$; and percentage of prey, $\%N = (n'-100)/N_p$; where n=the number of stomachs containing a particular prey type, N_s=the total number of lingcod stomachs examined, n'=the total number of individuals of a particular prey type, and N_p=the total number of prey items (Hyslop, 1980).

Prey-preference model

A preference model describes the relative selection of resources in relation to the availability of those resources. If a particular prey type is selected more or less frequently than would be predicted by relative availability, that prey type is said to be either preferred or avoided relative to other prey types. The general formulation of the preference model (Johnson, 1980) is as follows. Let r_{ij} be the rank of some measure of consumption of prey component (i) by an individual predator (j) and s_{ij} be the rank of an observed measure of the availability of prey component (i) to individual predator (j). The individual differences in these ranks, $t_{ij} = r_{ij} - s_{ij}$, are then averaged across animals to indicate the relative preference of all prey types across all predators, as given in Equation 1 below. The advantage of this nonparametric approach is that information about prey preference can be gleaned from imperfect field data. The use data and availability data are ranked for each animal and even if a particular prey type is not observed, those data can be used in the analysis. If a known prey type was not observed, the availability of that particular prey type would be considered low by comparison with other prey types in the analysis.

$$\bar{t}_i = \sum_{j=1}^{J} (r_{ij} - s_{ij}) / J. \quad (1)$$

Results

Prey availability

Observed fish abundance was overwhelmingly dominated (over 90%) by demersal rockfishes (*Sebastes* spp.) at both

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Table 1

Dates and locations of dive surveys and stomach collections for diet samples of lingcod (*Ophiodon elongatus*) in the nearshore zone off the Oregon Coast. Site 1 is located south of Newport, OR, and site 2, south of Coos Bay, OR. An X indicates that data were collected. Data used for prey preference analysis are within-season.

Dive survey	Diet samples	Site	Date
	X	1	16/07/03
	X	1	23/07/03
	X	1	25/08/03
	X	1	24/09/03
X		1	09/01/04
X		2	22/01/04
	X	2	24/05/04
X		1	09/06/04
	X	2	24/06/04
	X	2	05/10/04
X		2	22/10/04
	X	2	13/05/05
X		2	03/06/05
	X	2	08/06/05
X		1	22/06/05
X		2	26/06/05
X		2	27/06/05
	X	2	17/08/05
X		2	28/09/05
	X	2	20/10/05

sites. Aggregations of black rockfish (*S. melanops*) typically exceeded 100 individual adults and were the most common rockfish species. There was no evidence of a group effect between sites 1 and 2 (one-way ANOSIM, global $R=-0.115$; significance of sample stat.=64.2%). An MME for species accumulation indicated sampling effort was sufficient to achieve a stable asymptotic curve (S_{max}=17.94; β=0.72). In the pooled data, black rockfish were 41.1% of a total of 2640 fish recorded in nine dive surveys. When *Sebastes* species were aggregated into a single prey category (demersal rockfishes) there was no difference in mean abundance between sites (two-sided *t*-test, P=0.84, df=7) or of lingcod abundance between sites (Mann-Whitney U=26.5, P=1.0). There was a mean of 177.7 (standard error [SE]=14.8) demersal rockfish and 4.3 (SE=0.33) lingcod observed at Site 1 and a mean of 148.8 (SE=37.8) rockfish and 3.8 (SE=0.98) lingcod at site 2. A rank concordance test of prey common to both sites was significant with respect to abundance of potential prey species between sites (Kendall's rank concordance test, P<0.01, n=16, s=1.91). Striped surfperch (*Embiotoca lateralis*) and yellowtail rockfish (*S. flavidus*) were recorded only at site 1, whereas canary rockfish (*S. pinniger*) were observed only at site 2. Besides those species, the sites did not differ with respect to either the presence of potential prey species or relative abundance by genus, with the exception of significantly more sculpins (family Cottidae) at site 1 than site 2 (Mann-Whitney U=18.0, P=0.3). Geographic ranges of all species in this study are known to overlap both sites.

The smallest lingcod sampled or observed on a reef was 42 cm TL. Lingcod may be retained by the fishery at 61 cm TL and larger. Although undersized lingcod were sampled by special permit at both sites, the commercially caught samples were biased toward larger lingcod and most of the lingcod sampled were within a relatively narrow size range, likely because the local lingcod population was rebuilding and was dominated demographically by only a few cohorts. Lingcod juveniles settle onto a variety of habitats but were not observed on reefs. This is not surprising because lingcod are periodically cannibalistic, as shown in this and other studies.

Dietary composition

Of the 60 lingcod stomachs sampled at site 1, 12 were empty and 48 contained prey that were aggregated into 10 categories. At site 2, of the 315 lingcod stomachs sampled, 177 were empty and 138 contained the same 10 prey categories plus Pacific sandlance (*Ammodytes hexapterus*) as a major prey item, as well as market squid (*Loligo opalescens*), Pacific lamprey (*Lampetra tridentata*), and northern anchovy (*Engraulis mordax*) as minor items (Table 2). Because both the number of samples and sampling effort was much greater at site 2, it was expected that more prey types were found in

Figure 2

Lingcod (*Ophiodon elongatus*) total length (cm) and frequency of occurrence for empty and nonempty stomachs sampled at sites 1 and 2 off Oregon, 2003–05. Gear types were: multiple fishermen with single hooks and lines at site 1 (gray), and a commercial fisherman with multiple hooks and lines for site 2 (black). Lingcod under the legal limit for total length (<61 cm) were retained by permit at both locations, but were proportionately more abundant among sampled lingcod at site 1, and proportionately more lingcod stomachs were empty at site 2.

lingcod from there (see Bock, 1987). There were proportionately fewer empty stomachs among captured lingcod, and lingcod were smaller on average at site 1 than at site 2 (Fig. 2). Among prey categories common to both sites, there were significantly more Pacific herring (*Clupea pallasii*) consumed by lingcod sampled at site 1 than at site 2 (two-sided *t*-test, P=0.01, df=373). A rank concordance test was significant, indicating that prey consumption by category did not differ between sites (Kendall's rank concordance test, P<0 .01, n=15, s=2.03) and therefore the data were pooled for the preference analysis.

After sites were pooled, there were 21 identified species aggregated into 14 ecologically similar prey categories. Among the 342 prey items found in 375 stomachs (50.4% of lingcod stomachs were empty) major prey items were Pacific herring, Pacific sandlance, unidentified fishes, two-spotted octopus (*Octopus bimaculatus*), and pandalid shrimps (*Pandalus* spp.). All other prey groups, including rockfishes, each comprised less than five percent of the total gut contents (Fig. 3). A MME for species accumulation indicated that sampling effort was sufficient (S_{max}=14.91; β=17.21). Of the prey items that were measurable to total length, 14 were confirmed to be rockfishes. The largest of those was 28 cm (the only potential adult), and none was estimated to be more than three years old based on published length-at-age curves (Love et al., 2002). Of the identified young-of-year rockfishes, five were of the "black-spot" group and one was a stripetail (*S. saxicola*). Nearly all rockfishes identified to species were *S. melanops* and less than two years old as inferred by length (Love et al., 2002).

Table 2

Prey found in stomachs of 375 lingcod (*Ophiodon elongatus*) collected off Oregon, where *n* is the number of stomachs containing a particular prey type and *n'* is the total number of individuals of a particular prey type; $\%F_o$ is the frequency of occurrence, and $\%N$ is the percentage of prey items. The preference rank for each of 14 aggregated prey categories is also provided, where 1=most preferred prey and 14=least preferred prey.
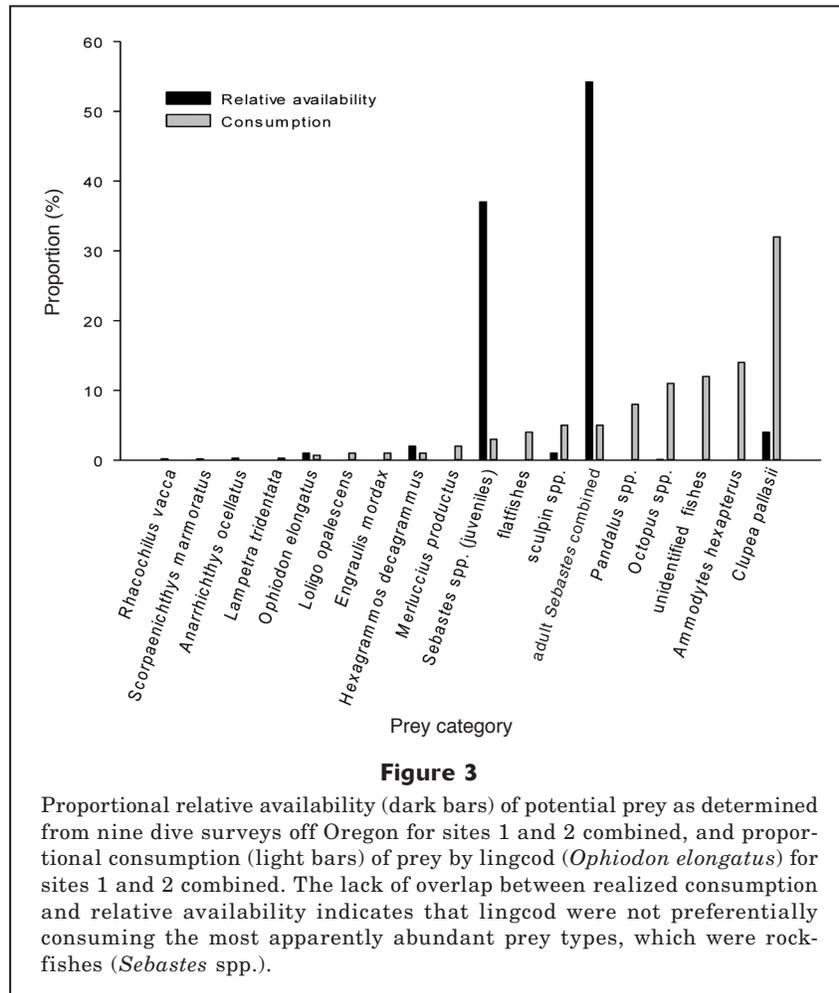
Prey species	*n*	*n'*	$\%F_o$	$\%N$	Preference rank
Transient and pelagic fishes					
Lampetra tridentata	1	1	0.27	0.31	8
Engraulis mordax	2	2	0.53	0.62	6
Clupea pallasii	37	109	9.87	33.64	7
Merluccius productus	7	8	1.87	2.47	4
Ammodytes hexapterus	15	49	4	15.12	2
Skates and flatfishes (soft bottom)				3	
Raja spp.	1	1	0.27	0.31	
Hippoglossus stenolepis	1	1	0.27	0.31	
Citharichthys sordidus	3	3	0.8	0.93	
Parophrys vetulus	1	1	0.27	0.31	
Platichthys stellatus	2	2	0.53	0.62	
unidentified flatfishes	5	5	1.33	1.54	
Reef-dwelling fishes					
Rockfishes					13,14
Sebastes melanops	6	6	1.6	1.85	
Sebastes saxicola	1	1	0.27	0.31	
unidentified rockfishes	7	9	1.87	2.78	
Greenlings					12
Hexagrammos decagrammus	3	3	0.8	0.93	11
Ophiodon elongatus	2	2	0.53	0.62	
Unidentified fishes	28	33	7.47	10.19	
Sculpins					10
Hemilepidotus hemilepidotus	3	3	0.8	0.93	
Scorpaenichthys marmoratus	2	2	0.53	0.62	
Unidentified sculpins	9	9	2.4	2.78	
Invertebrates					
Octopus					9
Octopus bimaculatus	26	30	6.93	9.26	
Octopus dofleini	5	5	1.33	1.54	
Loligo opalescens	3	3	0.8	0.93	5
Pandalus spp.	23	27	6.13	8.33	1
Cancer magister	2	6	0.53	1.85	

The dominant prey type was Pacific herring ($\%F$=9.87, $\%N$=33.64), a transient and pelagic species. Other prey types were clustered and far less dominant in the diet (Fig. 4). Among sampling periods, empty stomachs ranged from 8–81% (mean 56% empty, *n*=10 sampling periods, SE=5.7). Among sampling months, May–October, the presence of consumed prey among lingcod was unpredictable, regardless of the sampling month (ANOVA, $F_{1,9}$=1.77, P=0.22) and consumption of resident prey appeared to be independent of consumption of transient prey (ANOVA, $F_{1,9}$=2.46, P=0.15).

There were 41 unidentified prey items, 33 of which were confirmed not to be rockfishes. Lingcod eat parts of animals they cannot swallow whole by tearing prey apart (e.g., Pacific giant octopus; personal observ.) and are thus not considered gape-limited with respect to prey preference. Larger lingcod consumed larger prey (Fig. 5) but not distinctly different prey types (adjusted coefficient of determination r^2=0.29, one-way ANOVA $F_{1,71}$=30.3, $P < 0.01$, n=72 measurable prey items). Typically, a single prey item (but as many as 17) was found in a stomach containing prey, and among those stomachs containing more than one prey item, as many as four different species were found.

Numerically, 52% of prey were transient and pelagic, 4% were associated with soft-bottom seafloors, 44% were demersal reef-dwelling species, and of the latter, half were invertebrates. The importance of macroinvertebrates among local prey species is different from what was found in previous studies. Sand

Figure 3
Proportional relative availability (dark bars) of potential prey as determined from nine dive surveys off Oregon for sites 1 and 2 combined, and proportional consumption (light bars) of prey by lingcod (*Ophiodon elongatus*) for sites 1 and 2 combined. The lack of overlap between realized consumption and relative availability indicates that lingcod were not preferentially consuming the most apparently abundant prey types, which were rockfishes (*Sebastes* spp.).

consistently occurred in lingcod stomachs containing both octopus and shrimps, but never with flatfishes of any species. This pattern suggests that these lingcod did not forage for flatfishes directly over the seafloor, but were eating them in the water column. Because lingcod were captured on mid-water lures, they are apparently capable of foraging in the pelagic as well as the benthic zones.

Prey preference

Analysis of identified prey in the pooled data showed that prey selection was not proportional to availability (Johnson's preference, $F_{13,132}=943$, $P<<0.001$). Rockfishes were significantly "avoided" among prey categories (Waller-Duncan [1969] multiple comparisons, $P=0.01$, $n=145$). In order of preference, adult rockfishes were ranked last followed by subadult rockfishes (Fig. 6). Preference ranking also indicated that transient and pelagic prey (Pacific herring and Pacific sandlance) were among the most preferred prey. The January surveys could not be temporally matched with consumption data and therefore were excluded from this analysis, as were empty stomachs. However, because of the inherent tem-

poral and spatial patchiness of transient prey, as well as the difficulty in comparing very different types of prey, it was not possible to differentiate prey preference ranks among Pacific herring, Pacific sandlance, shrimps, and octopus. Other categories fell between these extremes (Fig. 6).

Discussion

These data indicate that lingcod off the coast of Oregon 1) are highly generalized predators of both fish and invertebrates in multiple habitats; 2) select prey disproportionately to prey abundance; and 3) do not differentially target rockfish as prey. Rockfishes may not be preferred because, unlike any other identified prey items, they have robust, venomous spines (Smith and Wheeler, 2006). In this case, experimental manipulation of predator and prey densities at meaningful temporal and spatial scales is not possible. For this reason it is necessary to use consumption and relative density estimates in a static model to find evidence of an effect. If consumption is very low relative to prey abundance, as is the case with predation on rockfishes, then any

direct effects on the population dynamics of either are unlikely to be strong.

There is incomplete spatial and temporal overlap between prey availability and consumption data sets and the variance may be greater than it otherwise would be because the dive surveys are disjunct. Still, the MME beta value and asymptotic curve stability of the combined surveys suggest that the heterogeneity of available prey can be detected with this level of effort and that the data are representative at this spatial and temporal scale. The prey availability data are not intended to reflect regional abundance. When a prey type such as Pacific herring is ranked low with respect to availability relative to rockfishes, it suggests rockfishes have more constant (less patchy) temporal and spatial overlap with lingcod. In this way the potential for encounter is much higher between lingcod and rockfishes.
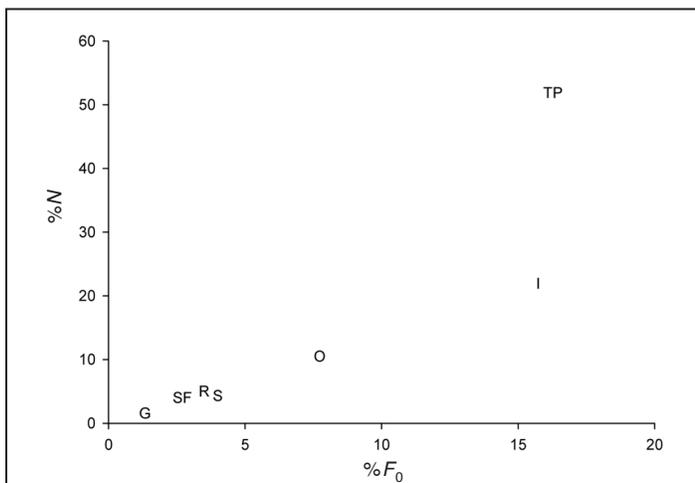
Large, highly generalized predators eat many different prey types and often do so infrequently, and therefore sample sizes must be relatively large to adequately capture the heterogeneity of the consumption data (e.g., Kingsford, 1992). With 375 samples, the dietary data reported here describe the relative abundance of prey categories in the diet of lingcod over a limited geographical area during half the year. However, Steiner (1979) collected summer and winter stomach samples and did not show an increase in lingcod consumption of rockfishes in winter and the number of samples collected appears to have captured the heterogeneity in the consumption data. The primary sources of error in these data include potential misidentification of prey and undefined rates of egesting stomach contents. Additionally, the digestion rates for free-living lingcod are unknown. Although they do reflect the relative temporal distributions of different prey types, the data from dive surveys were biased by both the spatial and temporal patchiness of transient prey, and by asymmetric sampling accuracy among habitats for prey types that were difficult to observe. However, rockfishes are highly observable and there was clearly a strong negative preference (or avoidance) for rockfishes than for all other prey types. Hydro-acoustic tracking studies of black rockfish have shown they move less than a few hundred meters over periods of months (Parker et al., 2008).

The gape-limitation hypothesis predicts that prey-size selection is consistent with optimal diet theory at the lower bound and the physical constraint of mouth size at the upper bound (Schmitt and Holbrook, 1984) and can be useful for predicting foraging behavior in fish (e.g., Persson et al., 1996). Larger lingcod tend to consume larger prey, but the gape-limitation hypothesis, or size-spectrum hypothesis (Scott and Murdoch, 1983), is not particularly useful for predicting prey selection in these animals because all sizes of lingcod eat small prey and lingcod consume parts of larger prey. Gape-limitation does not effectively predict which prey species or functional groups adult lingcod of different sizes will prefer to consume, nor do these data show a distinct shift to larger prey with increasing lingcod size.

In relatively long-lived generalist predators such as lingcod, dietary sampling at temporal scales over two years may be required for meaningful patterns in consumption to emerge. The variance in consumption by local predators of transient prey is high and may be independent of regional prey abundance. If consumption of resident prey is relatively even over time, the resident prey types may provide a maintenance resource and more ephemeral prey may provide sporadic opportunities for enhanced growth and reproduction. Additionally, indirect effects can be important to the distribution of predators. Besides direct consumption, risk effects (modification of prey distribution or behavior because of a perceived predation risk) may have an important influence on community structure (Creel and Christianson, 2007; Madin et al., 2010).

There is concern that lingcod predation may reduce the efficacy of marine reserves in the recovery of some overfished populations of rockfishes. In a recent study that addressed this issue in Puget Sound, Washington, Beaudreau and Essington (2007) found that in 560 lingcod (<30–108 cm TL) sampled inside and outside marine reserves, 6.8% of the total number of prey items were rockfishes. All individual rockfish identified to species were Puget Sound rockfish (*S. emphaeus*) and 0.4% of all prey were confirmed to be other species of *Sebastes*. The Puget Sound rockfish is a

Figure 4

Percentage of lingcod (*Ophiodon elongatus*) prey (%N) as a function of frequency of occurrence in the diet (%F_o). Prey categories are as follows: TP=transient-pelagic fishes (predominantly Pacific herring [*Clupea pallasii*]); SF=skates (*Raja* spp.) and flatfishes; S=sculpins (family Cottidae); R=rockfishes (*Sebastes* spp.); G=greenling (family Hexagrammidae)(including cannibalism by lingcod); I= invertebrates; O=other (including uncategorized, unidentified fishes). TP, for example, was both a relatively large percentage of the overall diet, and also commonly occurred as a prey type among lingcod sampled.
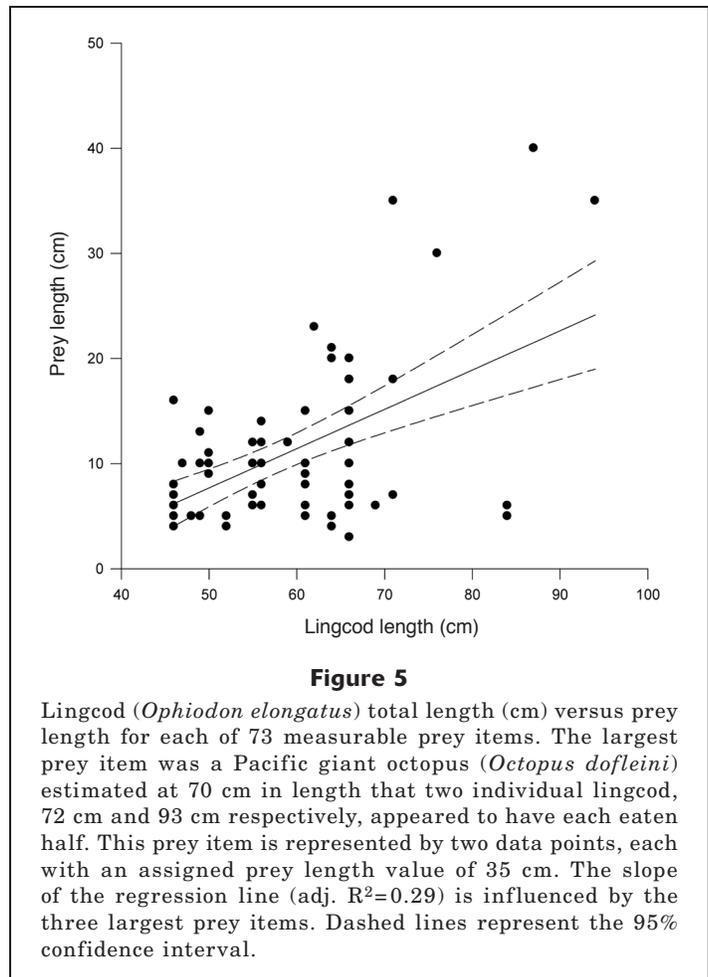
very small species that matures in 1–2 years. It is a schooling species and is often found in high densities. It is not fished either recreationally or commercially and thus is not the focus of recovery efforts. The largest measurable rockfish in Beaudreau and Essington's (2007) study was 16.6 cm. Combined with the results from Steiner (1979) and this study, lingcod of any size rarely prey on larger-body rockfishes. Beaudreau and Essington (2007) state that model results suggest intensive lingcod fishing is likely to disproportionately alleviate predation pressure on larger rockfishes. However, combined empirical evidence from this study and the two studies cited immediately above does not support this assertion.

Of all prey items found in this study, only one was a potentially reproductive rockfish and it apparently had been ingested within 24 hours of capture. This ratio simplifies to less than one adult rockfish consumed per adult lingcod per year, whereas the dive surveys revealed an average of 40 adult rockfishes living in the vicinity of each lingcod. If these ratios are representative, they suggest that lingcod predation is not a primary source of mortality for nearshore adult rockfishes off the coast of Oregon. Nor do lingcod appear to be a primary source of mortality of juvenile or young-of-the-year rockfishes because they were only slightly more likely than adult rockfishes to be eaten by lingcod. Hobson et al. (2001) found predation by black rockfish, blue rockfish, and kelp greenling was the primary source of mortality for postsettlement juvenile rockfishes in northern California.

Figure 5

Lingcod (*Ophiodon elongatus*) total length (cm) versus prey length for each of 73 measurable prey items. The largest prey item was a Pacific giant octopus (*Octopus dofleini*) estimated at 70 cm in length that two individual lingcod, 72 cm and 93 cm respectively, appeared to have each eaten half. This prey item is represented by two data points, each with an assigned prey length value of 35 cm. The slope of the regression line (adj. $R^2=0.29$) is influenced by the three largest prey items. Dashed lines represent the 95% confidence interval.

Conclusions

The results of this study show that lingcod are highly generalized predators that consume a broad variety of prey in terms of taxa, body form, and habitat. Lingcod are mobile, opportunistic, ambush predators that do not appear to be individually specialized. On the basis of the number of empty stomachs, they frequently go at least several days without eating, indicating there may be large differences between local prey abundance and prey availability (see Menge, 1972; Kelly, 1996). Better information is required on foraging range in relation to differences in habitat and prey availability to better understand lingcod foraging behavior as it relates to prey density. Nevertheless, this study strongly indicates that lingcod do not pose a threat to rockfish populations.
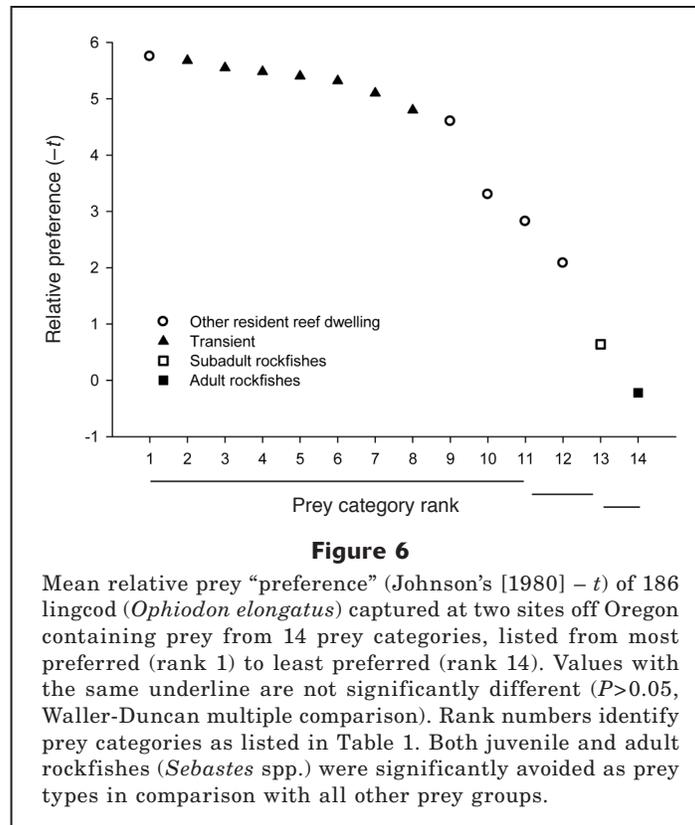
EBFM requires more information than single-species management approaches. In data poor systems, and particularly those that are difficult to access, higher echelon data describing interactions among both targeted and nontargeted species will be very difficult to develop. However, this study shows that untested assumptions about trophic relationships may lead to counterproductive management decisions, particularly with respect to large predatory species (Baum and Worm, 2009). Marine reserves can be an effective management tool for the conservation and recovery of exploited and other species, and particularly so where species of particular interest have relatively site-attached adult populations. In these cases trophic relationships, especially among resident and transient species, are a critical uncertainty and these relationships can only be fully understood through both consumption and relative prey availability measures. In this case, a preference index provides much more information about the likely result of fluctuations in predator and prey populations than would be the case with diet data alone.

Figure 6

Mean relative prey "preference" (Johnson's [1980] $-t$) of 186 lingcod (*Ophiodon elongatus*) captured at two sites off Oregon containing prey from 14 prey categories, listed from most preferred (rank 1) to least preferred (rank 14). Values with the same underline are not significantly different ($P>0.05$, Waller-Duncan multiple comparison). Rank numbers identify prey categories as listed in Table 1. Both juvenile and adult rockfishes (*Sebastes* spp.) were significantly avoided as prey types in comparison with all other prey groups.

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