Using food web model results to inform stock assessment estimates of mortality and production for ecosystem-based fisheries management

Sarah K. Gaichas, Kerim Y. Aydin, and Robert C. Francis

Abstract: Examining food web relationships for commercially important species enhances fisheries management by identifying sources of variability in mortality and production that are not included in standard single-species stock assessments. We use a static mass-balance model to evaluate relationships between species in a large marine ecosystem, the coastal Gulf of Alaska, USA. We focus on food web relationships for four case-study species: Pacific halibut (*Hippoglossus stenolepis*), longnose skate (*Raja rhina*), walleye pollock (*Theragra chalcogramma*), and squids (order Teuthoidea). For each, we present the species' position within the food web, evaluate fishing mortality relative to predation mortality, and evaluate diet compositions. We find that high trophic level (TL) species, whether commercially valuable (halibut) or incidentally caught (skates), have mortality patterns consistent with single-species assessment assumptions, where fishing mortality dominates natural mortality. However, assessments for commercially valuable (pollock) or incidentally caught (squids) mid-TL species can be enhanced by including food web derived predation information because fishing mortality is small compared with high and variable predation mortality. Finally, we outline food web relationships that suggest how production of species may change with diet composition or prey availability.

Résumé : L'examen des relations trophiques chez les poissons d'intérêt commercial améliore la gestion des pêches en identifiant les sources de variabilité de la mortalité et de la production qui ne sont pas incluses dans les évaluations monospécifiques courantes des stocks. Nous utilisons un modèle de bilan massique statique pour évaluer les relations entre les espèces dans un grand écosystème marin, la région côtière du golfe de l'Alaska, É.-U. Nous nous intéressons aux relations trophiques de quatre espèces représentatives, le flétan du Pacifique (*Hippoglossus stenolepis*), le pocheteau long-nez (*Raja rhina*), la goberge de l'Alaska (*Theragra chalcogramma*) et les calmars (ordre Teuthoidea). Pour chacune, nous présentons la position de l'espèce dans le réseau alimentaire, nous évaluons la mortalité due à la pêche par comparaison à la mortalité due à la prédation et nous déterminons la composition du régime alimentaire. Les espèces de haut niveau trophique, qu'elles soient commercialement intéressantes (flétan) ou capturées en passant (raies), ont des patrons de mortalité qui concordent avec les présuppositions des évaluations monospécifiques, lorsque la mortalité due à la pêche domine la mortalité naturelle. Cependant, les évaluations des espèces de niveau trophique intermédiaire d'importance commerciale (goberge) ou de capture accessoire (calmars) peuvent être améliorées en incluant les renseignements sur la prédation obtenus dans le réseau alimentaire, parce que la mortalité due à la pêche est basse par rapport à la mortalité due à la prédation qui est forte et variable. Nous soulignons, enfin, des relations trophiques qui indiquent comment la production des espèces peut changer en fonction de la composition du régime alimentaire et de la disponibilité des proies.

[Traduit par la Rédaction]

Introduction

How is a food web model useful to ecosystem-based fisheries management?

Historically, fisheries management has focused on individual commercially important species, and therefore fisheries science has focused on the population dynamics of those commercially important species as a basis for advising management on optimal harvesting (e.g., Beverton and Holt 1957). The idea behind optimal single-species harvesting was (and largely still is) that fished populations could be maintained in maximally productive states by regulating fishing mortality. When population dynamics models for optimal harvest were developed, simplifying assumptions were necessary to allow computation of fishing mortality. The first was that the only other source of mortality, "natural" mortality, was constant. The second was that the growth rate of the fished population was a function only of the size of that population (density dependence). While fisheries stock assessment models have increased considerably in

S.K. Gaichas[1] and K.Y. Aydin. Resource Ecology and Fisheries Management Division, NOAA NMFS Alaska Fisheries Science Center, 7600 Sand Point Way NE, Building 4, Seattle, WA 98115, USA.
R.C. Francis. University of Washington, School of Fisheries and Aquatic Sciences, 1122 NE Boat Street, Seattle, WA 98105, USA.

[1]Corresponding author (e-mail: Sarah.Gaichas@noaa.gov).

complexity and sophistication since the pioneering work of Beverton and Holt (1957), the assumptions of constant natural mortality and purely density-dependent growth remain. Under these assumptions, natural mortality parameterizes all predation mortality on a single species, and the intrinsic growth rate parameterizes all consumption of prey for that species. Most professional fisheries scientists recognize that these simplifications do not represent the real world but are hesitant to increase the complexity of models unnecessarily (e.g., Hilborn and Walters 1992). Because food web modeling explicitly takes predator–prey relationships into account, it can be used to evaluate when these simplifying assumptions are reasonable approximations in the ecosystem context and to suggest alternative approaches when they are not.

Using basic information gathered for stock assessment (biomass and population productivity), as well as supplemental information on predator–prey relationships (consumption rates and food habits data), a static food web model quantifies relationships between the species in an ecosystem in terms of energy or biomass flows. In quantifying biomass flows between species (and fisheries), the food web model explicitly partitions sources of mortality for a particular species among each of its predators, as well as fisheries. Similarly, the consumption by each species is quantified, suggesting whether a species is particularly dependent on any one source of prey.

Our objective in this paper is to outline the important insights for ecosystem-based fishery management that arise from a static food web model. While a static mass-balance model potentially quantifies thousands of relationships in a realistic food web, we focus on detailed "case studies" for selected species groups representing commercial and non-commercial species, predators, and prey specifically to demonstrate the relationships between species and fisheries currently managed separately on the continental shelf of the Gulf of Alaska (GOA; Fig. 1). Pacific halibut (*Hippoglossus stenolepis*) and walleye pollock (*Theragra chalcogramma*) were selected as commercially important species with different trophic roles. In addition to these commercially important species, longnose skate (*Raja rhina*) and squids (order Teuthoidea) were selected as groups of little current economic importance that are nevertheless encountered in fisheries and with different trophic roles. We briefly introduce each species here as background for our analyses.

Case-study species groups

Pacific halibut (family Pleuronectidae) are very large (2.7 m) predatory flatfish that range from Japan to Baja California in benthic North Pacific habitats from 6 m to 1100 m deep (Love et al. 2005). During spring and summer, adult halibut feed in continental shelf waters less than 200 m deep; during winter, they migrate to deeper (300 m) spawning grounds (International Pacific Halibut Commission (IPHC) 1998). Pacific halibut were first commercially fished in 1888 off British Columbia and Washington until populations there were depleted; since 1913, the majority of the halibut catch has been taken in Alaskan waters (Bell 1981). Pacific halibut were first managed by the IPHC starting in the 1920s and began to recover after regulations were applied in the 1930s. Landings reached a coast-wide peak of 31 752 t in 1962, dropped during the 1970s, but have since been maintained at over 20 000 t in the GOA (the most productive area) since 1997 (IPHC 1998, 2006).

Walleye pollock (family Gadidae) are medium-sized (<1 m) schooling groundfish. Pollock range throughout the North Pacific from Japan through the Bering Sea and down the US West Coast as far south as California, but their center of abundance is in the Bering Sea (Dorn et al. 2003; Ianelli et al. 2005). Pollock form massive schools over continental shelf habitats throughout their range, with annual migrations between spawning and feeding grounds driven by a combination of temperature, prey availability, currents, and day length (Browning 1980; Kotwicki et al. 2005). Though historically viewed as an undesirable species for its "soft" flesh quality (Eschmeyer et al. 1983), the development of at-sea processing capability eventually made pollock fishing attractive. Alaska pollock produced the highest single-species landings in the US in 2006 at 36% of total US landings. The Alaska pollock fishery comprised nearly two-thirds of the tonnage and one-fourth the value of the combined Alaska groundfish fishery valued at over US$753 million in 2006 (National Marine Fisheries Service (NMFS) Fisheries Statistics Division 2006; Hiatt et al. 2007). Most of the pollock catch comes from the eastern Bering Sea (EBS); GOA pollock accounted for less than 10% of 2006 Alaska pollock catches (NMFS Alaska Regional Office 2006).

Longnose skate (family Rajidae) is one of the most abundant skate species in the GOA according to NMFS bottom trawl surveys (Ormseth and Matta 2007), but little is known about its seasonal movements or breeding. This relatively large skate (1.7 m) is caught incidentally in fisheries targeting Pacific halibut, as well as Pacific cod (*Gadus macrocephalus*) and small flatfish. Since 2003, incidentally caught longnose skate have been retained and sold in the GOA as new markets have developed, and some targeted fishing on this species did occur in 2003 (Gaichas et al. 2003).

Squids (order Teuthoidea) are a functional group of cephalopod mollusks represented by many species throughout the North Pacific, but we focus on the medium-sized (<1 m) species most common in pelagic waters surrounding the outer continental shelf and slope. The 18 squid species found in the mesopelagic regions of the Bering Sea represent seven families and 10 genera (Sinclair et al. 1999). Less is known about which squid species inhabit the GOA, but the species there are likely to represent both Bering Sea species and more temperate species of the genus *Loligo*, which are regularly found on the US West Coast and in British Columbia, Canada, especially in warmer years (Ormseth and Gaichas 2008). There is no fishery for squids in Alaskan waters at present, but they are caught incidentally in pelagic trawl fisheries targeting pollock.

There is considerable contrast in the management and assessment of the four case-study species that we have selected, which primarily reflects the history of the commercial value for each species. Fisheries for the highly valued halibut and pollock are currently monitored intensively, with annual stock assessments based on comprehensive fishery-independent surveys and commercial catch monitoring (e.g., Dorn et al. 2008; Hare and Clark 2008). Catch of longnose skate has been monitored only since 2004 in the GOA in groundfish fisheries and remains unmo-

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Fig. 1. Geographic extent of the Gulf of Alaska (GOA) food web model.
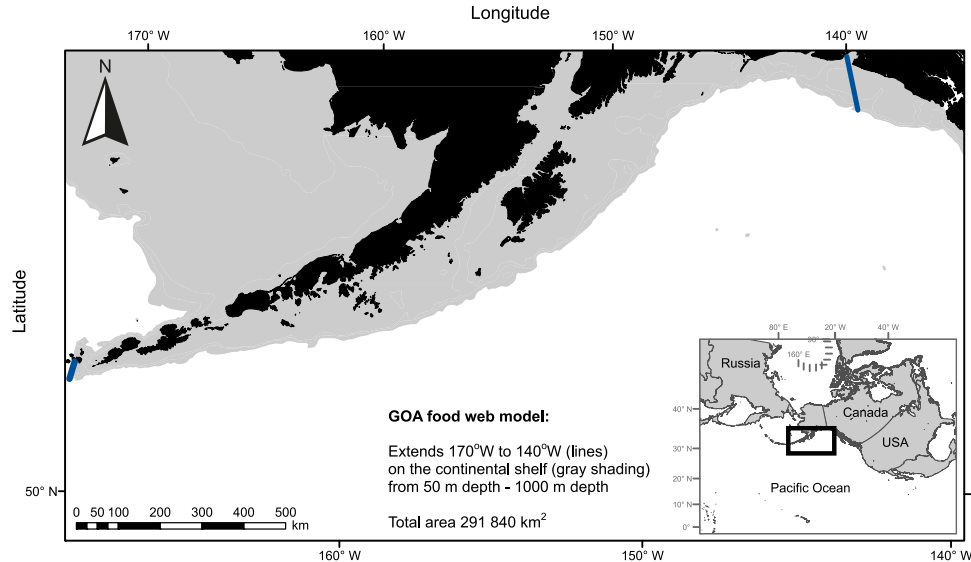
nitored in halibut fisheries. Catch of "squids" (in aggregate) is monitored only in groundfish fisheries, with no species-specific information. Fishery-independent information for longnose skate and squids is of variable to low quality. Rudimentary single-species stock assessments for longnose skate and squids have only recently been attempted (Gaichas et al. 2003; Ormseth and Matta 2007; Ormseth and Gaichas 2008). The use of static food web models to assess relationships between these species, fisheries, and the wider ecosystem both adds information to current single-species management approaches and may help identify whether single-species management tools and objectives are appropriate for different GOA species within the broader context of their food web relationships.

Materials and methods

Information was integrated from GOA field observations, single-species stock assessments, and primary literature using Polovina's (1984) static mass-balance food web model, Ecopath. We developed an independent version of this modeling framework to accommodate the large number of functional groups in the GOA and EBS food web models and included additional experimental functions (Aydin et al. 2007), but our method remains comparable with that implemented for the Ecopath portion of the software package Ecopath with Ecosim (EwE; Walters et al. 1997; Pauly et al. 2000; Christensen and Walters 2004). Although Ecopath is described in detail elsewhere, we highlight the components that provide useful comparisons with single-species assessments below.

Static mass-balance model

The static mass-balance model consists of a system of equations, one for each species or functional group, which are linear in the biomass (B, a density that we measured in tonnes per square kilometre, t·km^{-2}) terms. Each equation describes the balance of biomass gains and losses for each functional group (i) with predators (j):

$$(1) \quad B_i \left(\frac{P}{B} \right)_i \mathrm{EE}_i + \mathrm{IM}_i + \mathrm{BA}_i =$$

$$\sum_j \left[B_j \left(\frac{Q}{B} \right)_j \mathrm{DC}_{ij} \right] + \mathrm{EM}_i + C_i$$

The definition of the parameters in eq. 1, the derivation of additional parameters used below in eq. 2, and the general information used to input their group-specific values are described in detail (Table 1).

Equation 1 can be rearranged to demonstrate how static food web models usefully balance a functional group's annual production (P) with multiple sources of removal:

$$(2) \quad P_i = (F_i + M2_i + M0_i)B_i + E_i + \mathrm{BA}_i$$

In contrast with single-species models that account for only the known fishing (F) and the unknown nonfishing mortality rates (natural mortality, M), this food web model partitions nonfishing mortality into that accountable from predation ($M2$) and from unknown sources ($M0$). Specifically, predation mortality ($M2$) is calculated as the sum of the consumption of a group i by all of its predators, and all nonpredation mortality ($M0$) on group i is calculated as a remainder to account for production that is not directly consumed by predators or caught by fisheries. It is also possible to account for net migration (E) and known trends in biomass (BA; see Table 1).

After supplying the diet composition and three of the four key parameters (B, P/B, Q/B, and (or) EE) for all groups in the food web, the system of linear equations is solved by matrix inversion to estimate B or EE for each group. If EE is supplied to estimate B, this is termed "top-down" balance. In other words, the model supplies the information on how much biomass and productivity there must be for the group to give the observed diet compositions, consumption requirements, turnover rates, and upper trophic level (TL) biomasses (given the model assumption of static mass balance).

With the system of equations solved, it is simple to calcu-

Table 1. Parameters and calculation methods for mass-balance model master equations.

Parameter	Abbreviation (units)	Parameter source
Biomass	B (t·km^{-2})	Input or model estimate: survey estimates, sampling programs, stock assessments; estimated by fixing EE if no data available
Production/biomass	P/B (year^{-1})	Input: mortality rates, growth rates, bioenergetics models
Consumption/biomass	Q/B (year^{-1})	Input: bioenergetics models, gut content analysis
Diet composition	DC (proportion of the prey i in the diet (by mass) of consumer j; dimensionless)	Input: gut content analysis
Fisheries catch	C (t·km^{-2}·year^{-1})	Input: fisheries catch statistics
Biomass accumulation	BA (t·km^{-2}·year^{-1})	Input: biomass trend (only used if energetic demand requires it)
Immigration and emigration	IM and EM (t·km^{-2}·year^{-1})	Input: used to specify annual net migration imbalance (not used in this model)
Ecotrophic efficiency	EE (proportion; dimensionless)	Model estimate: derived as EE = $(C + M2)/P$; the ratio of "used" production to total production for a group. If no biomass data are available, EE is fixed at a standard level (0.8 here) to estimate biomass
Production	P (t·km^{-2}·year^{-1})	Model estimate: derived as $P = (P/B)B$
Consumption	Q (t·km^{-2}·year^{-1})	Model estimate: derived as $Q = (Q/B)B$
Fishing mortality	F (year^{-1})	Model estimate: derived as $F = C/B$
Predation mortality	$M2$ (year^{-1})	Model estimate: derived as $M2 = (\Sigma Q(\mathrm{DC}))/B$, where the sum is over all predators of the functional group
Unexplained mortality	$M0$ (year^{-1})	Model estimate: derived as $M0 = (P(1 - \mathrm{EE}))/B$
Net migration	E (t·km^{-2}·year^{-1})	Model estimate: derived as $E = \mathrm{EM} - \mathrm{IM}$ (not used in this model)

late which predators are responsible for what portion of each species group's mortality and consumption for each group. TL is also calculated at this point; primary producers have a TL = 1, and each successive consumer group has a TL equal to one higher than the average of the TLs of its prey, weighted by the proportion of prey in the diet (Lindeman 1942; Odum and Heald 1975).

Temporal and spatial scale

Our static food web model is designed with the same annual time scale and broad, basin-wide spatial scale as the single-species stock assessments used in fishery management in the North Pacific. The GOA model represents 291 840 km^2 of the continental shelf area ranging from 50 m to 1000 m in depth, from a western boundary at 170°W to an eastern boundary of 140°W (Fig. 1). Nine strata representing geographic regions and depth–habitats accounted for within-region variability for each modeled group (for full details, see Aydin et al. 2007). Modeling the food web on this broad scale allows for most of the data collected for single-species population models to be used in food web modeling and best accommodates the scale of current regional management needs. However, we recognize that important smaller-scale ecological processes may be lost in the spatial and temporal averaging for current regional fishery management, current stock assessment models, and this food web model.

Data and parameter derivations

The GOA food web model includes area- and time-specific production and consumption parameters based on research surveys and single-species stock assessments that characterized the state of the system in the early 1990s. The early

1990s period was selected for modeling because they were the earliest years with complete diet composition and biomass data for major GOA species. The GOA model used here includes 122 living groups (four producer and 118 consumer), five detritus groups, and 14 fisheries (Table 2). Details of model construction and parameterization for the entire GOA food web are documented in Aydin et al. (2007). (The model used here had 10 minor functional groups aggregated into related groups to reduce the size, but the underlying data are identical.)

Input parameters for the four case-study groups are presented (Table 3). In general, biomass estimates from standardized bottom trawl surveys (Britt and Martin 2001) were preferred as a consistent data source across species. Survey biomass was also used to weight spatial diet composition appropriately by the biomass in each model stratum as described in Aydin et al. (2007). Age-structured stock assessment based estimates of production rates (P/B) were preferred where available to represent early 1990s recruitment and population structure. Consumption rate (Q/B) was estimated by fitting a generalized von Bertalanffy growth function to weight-at-age data collected onboard trawl surveys and applying an empirical relationship between growth and consumption (Essington et al. 2001; Aydin 2004). Departures from these information sources and methods that were necessary for case-study species are described in detail in the section below.

Diet composition was primarily estimated from food habit collections made during the 1990 and 1993 bottom trawl surveys of the GOA. The sampling design for collecting fish stomachs aboard these surveys in the early 1990s emphasized pollock, cod, Pacific halibut, and arrowtooth flounder (*Atheresthes stomias*) collections during every sur-

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Table 2. Gulf of Alaska mass-balance model groups (for full details, see Aydin et al. 2007).

Category	Group	Juvenile group?
Toothed whales	*Orcinus orca*, transient killer whale	No
Toothed whales	*Physeter macrocephalus*, sperm whale	No
Toothed whales	*Orcinus orca*, resident killer whale	No
Toothed whales	Porpoises group	No
Baleen whales	*Eschrichtius robustus*, gray whale	No
Baleen whales	*Megaptera novaeangliae*, humpback whale	No
Baleen whales	*Balaenoptera physalus*, fin whale	No
Baleen whales	*Balaenoptera borealis*, sei whale	No
Baleen whales	*Eubalaena glacialis*, right whale	No
Baleen whales	*Balaenoptera acutorostrata*, minke whale	No
Otters and pinnipeds	*Enhydra lutris*, sea otter	No
Otters and pinnipeds	*Callorhinus ursinus*, northern fur seal	Yes
Otters and pinnipeds	*Eumetopias jubatus*, Steller sea lion	Yes
Otters and pinnipeds	*Phoca vitulina*, harbor seal	No
Birds	*Puffinus* sp., shearwaters	No
Birds	*Uria* sp., murres	No
Birds	*Rissa* sp., kittiwakes	No
Birds	Auklets group	No
Birds	*Fratercula* sp., puffins	No
Birds	*Fulmarus glacialis*, northern fulmar	No
Birds	Hydrobatidae, storm petrels	No
Birds	*Phalacrocorax* sp., cormorants	No
Birds	*Larus* sp., gulls	No
Birds	Albatross and Jaeger group	No
Sharks	*Somniosus pacificus*, sleeper shark	No
Sharks	*Lamna ditropis*, salmon shark	No
Sharks	*Squalus acanthius*, dogfish	No
Aged roundfish	*Theragra chalcogramma*, walleye pollock	Yes
Aged roundfish	*Gadus macrocephalus*, Pacific cod	Yes
Aged roundfish	*Clupea pallasi*, Pacific herring	Yes
Aged large flatfish	*Atheresthes stomias*, arrowtooth flounder	Yes
Aged large flatfish	*Hippoglossus stenolepis*, Pacific halibut	Yes
Small flatfish	*Limanda aspera*, yellowfin sole	No
Aged small flatfish	*Hippoglossoides elassodon*, flathead sole	Yes
Small flatfish	*Lepidopsetta polyxystra*, northern rock sole	No
Small flatfish	*Lepidopsetta bilineata*, southern rock sole	No
Small flatfish	*Pleuronectes quadrituberculatus*, Alaska plaice	No
Small flatfish	*Microstomus pacificus*, Dover sole	No
Small flatfish	*Glyptocephalus zachirus*, rex sole	No
Small flatfish	Misc. flatfish group	No
Skates	*Bathyraja* sp., other skates	No
Skates	*Raja rhina*, longnose skate	No
Skates	*Raja binoculata*, big skate	No
Aged deep roundfish	*Anoplopoma fimbria*, sablefish	Yes
Deep roundfish	Zoarcidae, Eelpouts	No
Deep roundfish	*Albatrossia pectoralis*, giant grenadier	No
Deep roundfish	*Coryphaenoides pacificus*, Pacific grenadier	No
Deep roundfish	Other Macrouridae group	No
Deep roundfish	Misc. deepwater fish group	No
Aged rockfish	*Sebastes alutus*, Pacific ocean perch	Yes
Rockfish	*Sebastes zacentrus*, sharpchin rockfish	No
Rockfish	*Sebastes polyspinis*, northern rockfish	No
Rockfish	*Sebastes variabilis*, dusky rockfish	No
Rockfish	*Sebastes borealis*, shortraker rockfish	No
Rockfish	*Sebastes aleutianus*, Rougheye rockfish	No
Aged rockfish	*Sebastolobus alascanus*, shortspine thornyheads	Yes
Rockfish	Other *Sebastes* sp.	No

Table 2 (*concluded*).

Category	Group	Juvenile group?
Aged shelf roundfish	*Pleurogrammus monopterygius*, Atka mackerel	Yes
Shelf roundfish	Other Hexagrammidae, greenlings	No
Shelf roundfish	Large sculpins group	No
Shelf roundfish	Other sculpins group	No
Shelf roundfish	Misc. shallow water fish group	No
Cephalopods	Octopoda, octopus group	No
Cephalopods	Teuthoidea, squid group	No
Forage fish	*Oncorhynchus* sp., salmon adults	No
Forage fish	*Oncorhynchus* sp., salmon juveniles	No
Forage fish	Bathylagidae, deepsea smelts	No
Forage fish	Myctophidae, lanternfishes	No
Forage fish	*Mallotus villosus*, capelin	No
Forage fish	*Ammodytes hexapterus*, sandlance	No
Forage fish	*Thaleichthys pacificus*, eulachon	No
Forage fish	Other forage group	No
Forage fish	Other pelagic smelts group	No
Shellfish	*Chionoecetes bairdi*, tanner crab	No
Shellfish	*Paralithodes camtschaticus*, red king crab	No
Shellfish	Pandalidae, commercial shrimp	No
Motile benthic epifauna	Non-pandalid shrimp	No
Motile benthic epifauna	Asteriodea, sea stars	No
Motile benthic epifauna	Brittle Stars	No
Motile benthic epifauna	Echinoidea (urchins) and Holothuroidea (sea cucumbers)	No
Motile benthic epifauna	Snails	No
Motile benthic epifauna	Paguridae, hermit crabs	No
Motile benthic epifauna	Other noncommercial crabs	No
Motile benthic epifauna	Barnacles, ostracods, cladocerans, isopods, etc.	No
Motile benthic epifauna	Benthic amphipods	No
Sessile benthic epifauna	Anemones	No
Sessile benthic epifauna	Corals	No
Sessile benthic epifauna	Hydroids	No
Sessile benthic epifauna	Urochordates	No
Sessile benthic epifauna	Sea Pens	No
Sessile benthic epifauna	Sponges	No
Benthic infauna	Bivalves	No
Benthic infauna	Polychaetes	No
Benthic infauna	Annelids, sipunculids, bryozoans, brachiopods	No
Pelagic zooplankton	Scyphozoan jellies	No
Pelagic zooplankton	Fish larvae	No
Pelagic zooplankton	Chaeteognaths, etc.	No
Pelagic zooplankton	Euphausiids	No
Pelagic zooplankton	Mysids	No
Pelagic zooplankton	Pelagic Amphipods	No
Pelagic zooplankton	Pelagic gelatinous filter feeders	No
Pelagic zooplankton	Pteropods	No
Pelagic zooplankton	Copepods	No
Microbial loop	Benthic bacteria	No
Microbial loop	Microzooplankton	No
Primary producers	Macroalgae	No
Primary producers	Large phytoplankton	No
Primary producers	Small phytoplankton	No
Primary producers	Outside production	No
Detritus	Fishery discards	No
Detritus	Fishery offal	No
Detritus	Pelagic detritus	No
Detritus	Benthic detritus	No
Detritus	Outside detritus	No

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Table 3. Input parameters and sources for case-study species groups.

| Input parameter	Case-study species group					
	Longnose skate	Pacific halibut	Pacific halibut juvenile	Squids	Walleye pollock	Walleye pollock juvenile
Biomass (t·km⁻²)	0.04974	1.519	0.1824	na	5.553	0.6718
Biomass source	Trawl survey	Trawl survey		Top-down balance	Stock assessment	
P/B (year⁻¹)	0.2	0.19	0.3824	3.2	0.41	2.669
P/B source	Literature	Stock assessment		Literature	Stock assessment	
Q/B (year⁻¹)	2.0	1.1	1.42	10.67	3.78	6.83
Q/B source	Literature	Weight at age, stock assessment	Weight at age, stock assessment	Literature	Weight at age, stock assessment	Weight at age, stock assessment
Diet composition source	Literature	Trawl survey	Trawl survey	Literature	Trawl survey	Trawl survey

Note: na, not available.

vey and rotated through secondary fish predators so that a complete set of species were collected over the course of two or three surveys. In the combined 1990 and 1993 surveys, 11 151 stomachs were collected from 13 groundfish predators, including 1026 halibut and 2317 pollock. The diet data are derived from laboratory examination of the preserved stomachs, with prey species recorded to the lowest possible taxonomic level (see Yang and Nelson 2000). The full GOA food web model includes diet data from other sampling years to include over 50 predators and over 450 species or species groups recorded as prey from over 35 000 fish stomachs (Aydin et al. 2007). For halibut and pollock, we also evaluate annual diets and changes in prey proportions over time using diet data collected between 1990 and 2007.

Case-study group parameters

Pacific halibut adult biomass is the average of 1990 and 1993 GOA NMFS bottom trawl survey estimates; this trawl survey is not used in the halibut stock assessment. The P/B was derived from the 1990–1993 recruitment and age structure in the halibut stock assessment for Area 3A (Clark and Hare 2003) and weight-at-age data collected on IPHC longline surveys (W. Clark, IPHC, personal communication, 2004). Because Pacific halibut weight at age has varied significantly over time (Clark et al. 1999), we used weight-at-age relationships from the early 1990s surveys only to estimate Q/B parameters for this model. Juvenile Pacific halibut were defined as fish less than 20 cm in length, roughly 0- and 1-year-olds. Estimating juvenile biomass using top-down methods was impractical because there is little predation mortality on juvenile halibut in the GOA according to available data. Therefore, we estimated juvenile mortality to be 0.5, a rate comparable with those estimated by multispecies virtual population analysis (MSVPA) model runs in the EBS (Jurado-Molina 2001). This estimated juvenile mortality rate was used to estimate the P/B for 1990–1993 based on stock assessment age structure and to estimate juvenile biomass given the numbers and weights at age estimated in the stock assessment for those years.

Walleye pollock adult biomass is the average of 1990–1993 stock assessment model estimated biomass for ages 2 through 10+ (Dorn et al. 2003). Bottom trawl survey estimates of adult pollock biomass are approximately half of those estimated by the stock assessment, which incorporates information from three surveys in addition to the bottom trawl survey. Because pollock are a schooling species distributed throughout the water column, bottom trawl surveys might underestimate biomass. The P/B for adults is derived from the age structure estimated for 1990–1993 in the stock assessment, with the additional assumption that the natural mortality rate for age-2 fish is 0.8 instead of 0.3, the assumption for all other age classes in the assessment. This adjustment is supported by previous multispecies modeling efforts specific to GOA pollock (Hollowed et al. 2000). The Q/B was estimated by the preferred method and scaled to the 1990–1993 age structure from the stock assessment. A biomass accumulation (BA) term of –1.25 t·km⁻² was included to balance the apparently high predation mortality on pollock. Pollock data quality was considered high and therefore unnecessary to adjust (see Discussion). Outmigra-

Fig. 2. Mortality of case-study species groups as partitioned by the Gulf of Alaska (GOA) food web model, with case-study groups arranged from highest (left, longnose skate) to lowest (right, squids) trophic level (TL): longnose skate, *Raja rhina*; Pacific halibut, *Hippoglossus stenolepis*; walleye pollock, *Theragra chalcogramma*; and squids, order Teuthoidea. (*a*) Fishing, predation, and unexplained mortality as a proportion of total mortality for each species (mortality sums to 1). (*b*) Fishing, predation, and unexplained mortality relative to the total annual production rate of each case-study species group (mortality sums to annual *P/B*, where *P/B* = accumulation + unexplained mortality + predation mortality + fishing mortality). Note that for pollock, the accumulation (BA) term is negative in this sum.
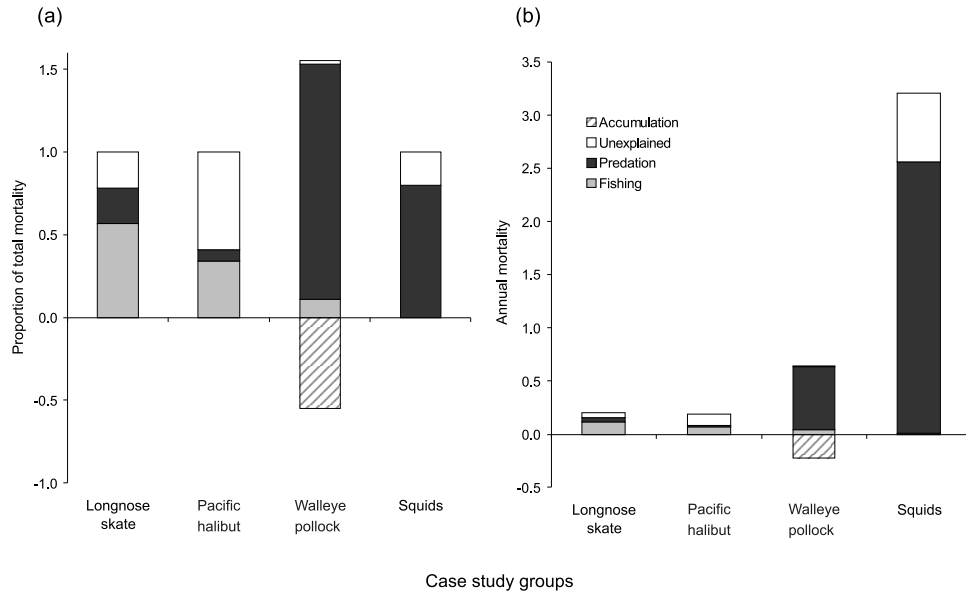
tion was not considered a factor, as the model encompasses the known range of pollock, and other sources of mortality (disease, etc.) have not been documented. This BA is within the range of estimated annual declines from the pollock stock assessment (Dorn et al. 2003), although greater than the maximum annual decline during the early 1990s. Juvenile walleye pollock were defined as fish less than 20 cm in length, roughly 0- and 1-year-olds. The juvenile *Q/B* was estimated by the preferred method. Juvenile pollock *P/B* was estimated based on stock assessment estimated age structure, and the biomass was then estimated by assuming that EE was 0.80 for the group.

Longnose skate biomass was computed from preferred survey estimates. Frisk et al. (2001) estimated that medium-sized (100–199 cm) elasmobranchs have a potential rate of population increase of 0.21. We used this to approximate *P/B* = 0.20, lacking other data. A growth efficiency intermediate between sharks and large teleost predators (Pacific halibut and arrowtooth flounder) seemed reasonable for skates. Growth efficiency (GE) is defined as production per unit consumption, so *Q/B* can be calculated as *P/B* divided by GE (Christensen and Walters 2004). We assumed a GE of 0.1, resulting in a *Q/B* estimate of 2.0 for all skate species. Diets of skates are derived from food-habit collections taken throughout the North Pacific range of these species because systematic sampling of skate food habits on NMFS GOA trawl surveys has only recently begun. In general, diets estimated from other areas were modified by the limited field observations available from Alaska. *Raja* diets evaluated from collections in Oregon (Wakefield 1984) were modified based on qualitative observations from the 2003 GOA trawl survey.

Squids are the most data-poor case-study group. The NMFS bottom trawl surveys are directed at groundfish species and therefore do not employ the appropriate gear or sample in the appropriate places to provide reliable biomass estimates for the generally pelagic squids (Ormseth and Gaichas 2008). Biomass for this group was estimated by assuming that EE was 0.80. Squids are highly productive and voracious predators, so a *P/B* of 3.2 and a *Q/B* of 10.62 were adapted from Radchenko (1992). Diet information is not available for GOA squids, so we substituted EBS diet composition based on information for *Berryteuthis magister* (Radchenko 1992). Although cannibalism is common in squids, we eliminated it from the diet (originally 12%) and reduced consumption of forage fish (from 5% to 2.5%) so that squids' high consumption would not result in excessive inflation of squid and forage fish top-down biomass estimates within the model. Consumption of euphausiids and copepods were increased by 12% and 10%, respectively, to compensate; this was intended to reflect the diet of smaller pelagic squid species not studied by Radchenko (1992).

Case-study evaluations

For the fisheries targeting halibut and pollock and for each case-study species, we use the results of the static food web model to evaluate the TL and role of the species to place it within the continuum of apex predator to low TL prey. Then, we evaluate fishing mortality *F* relative to predation mortality *M*2 and the remaining mortality *M*0 not explained by the food web model to determine the extent of potential control of mortality by fishery managers. We also evaluate the diet compositions of each group for the mass-balance period of the early 1990s and trends over 1990–2007 for halibut and pollock. We present these relationships visually within the food web by highlighting a fishery or

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Fig. 3. Food web of Gulf of Alaska (GOA) adult and juvenile Pacific halibut (pink boxes) in the early 1990s. The food web visualization shows predators of halibut highlighted in light blue and prey in yellow, with the strongest flows represented as thicker lines and weak flows represented only as highlighted group boxes with no lines. The significant predators of halibut (light blue boxes joined by light blue lines) include the longline fisheries for halibut and sablefish, trawl fisheries for flatfish, and dogfish, Steller sea lions, and longnose and big skates. Salmon sharks are significant predators of juvenile halibut. Significant prey of halibut (yellow boxes joined by yellow lines) are pollock, capelin, and crabs, with juvenile halibut preying more on shrimp and other benthic invertebrates. Green boxes indicate groups that are both predator and prey of halibut.
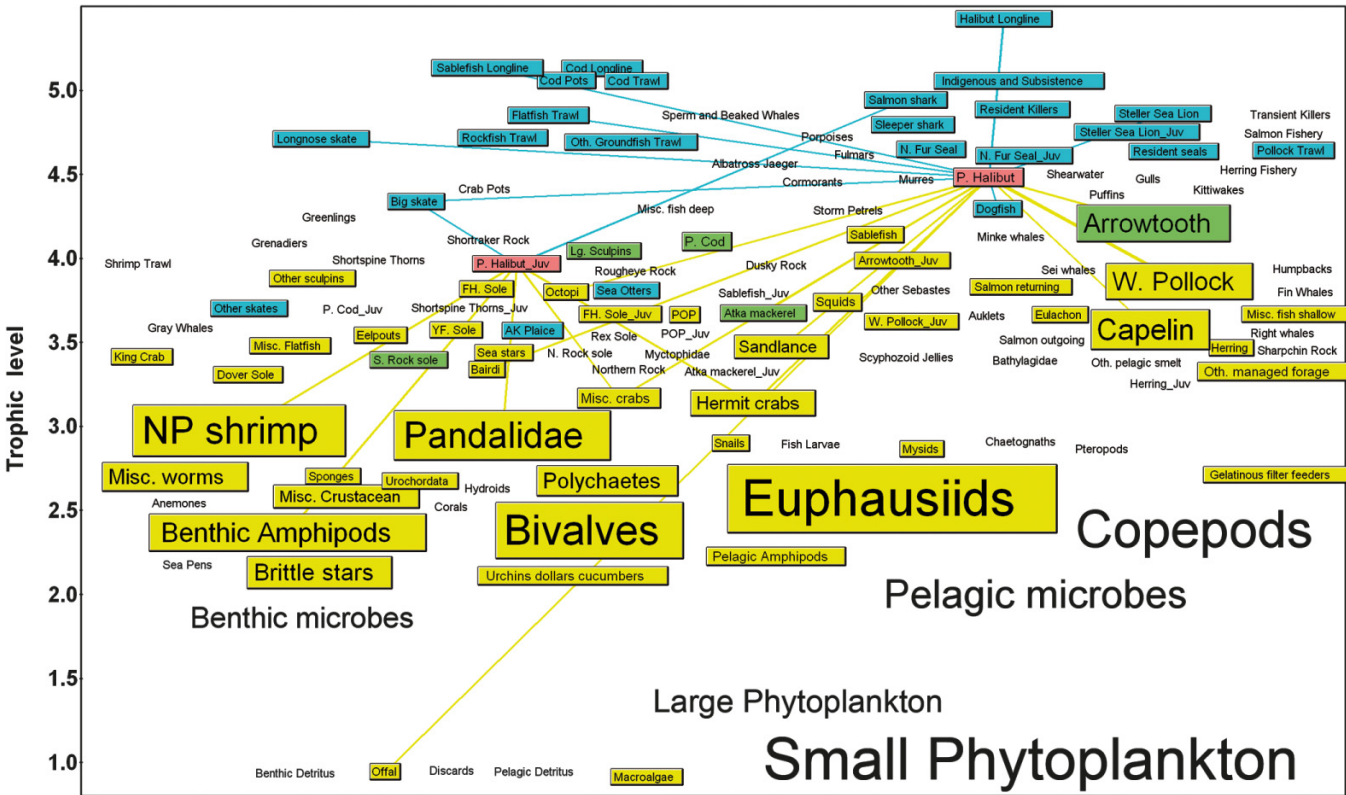
species group, each of its direct predators and prey, and the strength of the interaction. We then recommend management directions for each group that consider food web relationships, as well as fishing.

Results

Case-study groups within the full food web

The GOA food web quantifies biomass flow over 2969 pathways among its 141 total groups. Accounting for just the direct predators and prey of each of the case-study species, 354 of these ecosystem pathways are considered here. Adding the fisheries for halibut and pollock brings the total relationships examined in the case studies to 442, with connections between 68 groups. TLs calculated for each group, including fisheries, indicate that the halibut longline fishery is the apex "predator" in the GOA with a TL of 5.4. The pollock trawl fishery and the longnose skate have the next highest TL in the food web of the case-study groups at 4.7, followed by halibut at 4.5. Pollock and squids have the lowest TLs of the case-study groups, but are still at moderate to high positions in the food web with a TL of 3.7 each, suggesting that they represent important prey for higher predators but are significant predators themselves for low TL groups.

Partitioning mortality

Food web modeling suggests patterns in mortality sources by TL. Fishing mortality appears more important than predation mortality for high TL groups, regardless of commercial status. The high TL predators, longnose skate and Pacific halibut, experience the majority of their explained mortality from fishing (Fig. 2a). In contrast, the lower TL pollock and squids experience much larger predation mortality than fishing mortality, even though pollock are a commercially exploited species. The predation mortality estimated by the model for pollock exceeded the early 1990s production estimated from the stock assessment, thus the negative BA term, representing a declining biomass pool for the group, is apparent (Fig. 2a). Squid predation mortality appears dominant, while fishing mortality is not visible in Fig. 2a (although the estimate of "unexplained" mortality reflects a model assumption rather than an attempt at measurement of squid productivity and biomass, which is in contrast with the other case-study groups). Another view of the partitioned mortality reflects the different levels of productivity of each case-study species, showing that the higher TL predators are generally less productive than the lower TL groups, whose higher production supports high predation mortality (Fig. 2b). More detailed sources of mortality for

Table 4. Sources of mortality for case-study species groups.

	Percentage of total mortality caused by mortality source[a]					
Mortality source	Longnose skate	Pacific halibut	Pacific halibut juvenile	Squids	Walleye pollock	Walleye pollock juvenile
Halibut longline	29.59	28.86				
Pollock trawl	1.29	0.12		0.00	6.60	
All other fisheries	26.10	5.07		0.00	0.48	
All marine mammals	11.75	2.02	1.09	15.27	8.26	3.45
All sharks	9.54	1.60	33.52	0.49	0.87	0.19
Longnose skate		1.29	0.64		0.33	0.08
All other skates		2.01	1.00	0.07	0.22	0.05
Pacific halibut		0.00	0.04	0.10	22.88	0.13
Pacific cod		0.00	0.03	0.39	16.22	1.66
Arrowtooth flounder			0.15	0.62	32.79	47.10
Sablefish				5.07	5.13	1.07
Walleye pollock				3.32	4.82	10.98
Walleye pollock juvenile						4.21
All small flatfish			0.11			0.46
All rockfish				0.27		1.37
All salmon				50.06		
All other fish			0.25	1.87	0.41	1.00
All seabirds				2.45		9.80
All zooplankton				0.01		0.02
Unexplained	21.73	59.02	63.17	20.00	0.99	18.41
Total	100.00	100.00	100.00	100.00	100.00	100.00

[a]Blank spaces indicate that the source of mortality does not apply to the case-study group; 0.00% indicates a trace amount of mortality.

each case-study species are summarized (Table 4) and examined in detail below.

Halibut fishery food web, with longnose skate and halibut relationships

The food web model estimates that the halibut longline fishery is the apex predator in the GOA ecosystem because it catches both halibut and longnose skate (as well as other skates and sharks), which are high TL predators themselves (Fig. 3). The food web visualization shows the strongest flows as thicker lines, with weak flows represented only as highlighted group boxes with no lines; therefore, we see that the major flow to the halibut longline fishery is from halibut themselves. The halibut longline fishery appears as a primary predator of halibut, causing 29% of halibut mortality (Table 4). Halibut represent over 75% of the catch in this fishery, whereas longnose skate combined with other bycatch species represent less than 25% of the catch by weight (Table 5). (We note considerable uncertainty in halibut fishery bycatch estimates used in the food web model. Recent catches of skates in the halibut longline fishery from 1997 to 2004 appear to be a larger percentage of total halibut catch; see Gaichas et al. 2003; Ormseth and Matta 2007.)

A more detailed comparison of the food web relationships for the high TL species caught in the halibut longline fishery, longnose skate and halibut, suggests both direct and indirect effects of that fishery on these species and the larger food web. Longnose skate, the unintended "prey" of the halibut longline fishery, are predatory fish with few other natural predators. The halibut longline fishery represents the

largest single source (29%) of mortality for longnose skate, although other fisheries also contribute to mortality (Table 4). Although the early 1990s catch of longnose skate in the GOA was roughly estimated to range from less than 1000 t to greater than 5000 t (Gaichas et al. 2003), predator consumption estimates are lower. Longnose skate consume primarily flatfish, pollock, capelin (*Mallotus villosus*), and sand lance (*Ammodytes hexapterus*) (Table 5).

Pacific halibut feed on more diverse and sometimes lower TL prey than the longnose skate, especially when juvenile halibut are considered separately (Table 5). Similar to longnose skate, the halibut longline fishery is also the largest single source (29%) of mortality for adult halibut (Table 4), with other fisheries, longnose skate, and Steller sea lions (*Eumetopias jubatus*) as weaker predator flows (Fig. 3). The great majority of halibut mortality is unexplained in the food web model, which is consistent with the role of halibut as a high TL predator subject to controlled fishing mortality. Adult halibut consume a mixture of demersal fish and benthic invertebrates, but a single species, pollock, comprises nearly half of the early 1990s adult halibut diet (Table 5; see strong flow in Fig. 3). However, the proportion of pollock in combined adult and juvenile halibut diet declined between 1990 and 2007, concurrent with a decline in assessed pollock biomass (Fig. 4). Juvenile halibut feed on benthic invertebrates (Table 5) and are fed upon by sharks and skates (Fig. 3).

Pollock fishery food web, with pollock and squid relationships

The food web model estimates that the pollock trawl fish-

Table 5. Catch and diet compositions for case-study fisheries and species groups.

| Catch or diet group	Percentage that each catch or diet group represents in the catch or diet of the fishery or predator[a]							
	Halibut longline fishery	Pollock trawl fishery	Longnose skate	Pacific halibut	Pacific halibut juvenile	Squids	Walleye pollock	Walleye pollock juvenile
All marine mammals		0.01						
All seabirds		0.00						
All sharks	4.17	0.31						
Longnose skate	2.66	0.05						
All other skates	3.68	0.09						
Pacific halibut	75.45	0.14	3.75	0.00				
Pacific cod	8.35	2.02	3.22	1.36			0.01	
Arrowtooth	2.10	1.60	15.57	3.69			0.06	0.18
Sablefish	3.07	0.17	0.01	0.26				
Walleye pollock		91.98	11.76	48.26			0.81	
Walleye pollock juvenile			1.42	0.14			0.94	1.65
Pacific halibut juvenile			0.45	0.00				
All small flatfish		2.26	30.63	0.79			0.13	
All rockfish	0.29	0.36		0.21				
All salmon		0.21	1.85	0.32				
Herring		0.02	1.86	0.73			0.02	
All other forage fish		0.16	21.53	4.10	0.09	15.00	6.56	
All other fish	0.22	0.47	5.83	3.28	2.99		0.20	
Squids		0.07		0.23			0.64	
All crabs		0.00		18.60	8.41		0.12	0.17
All shrimp		0.00	2.10	1.00	39.86		18.38	7.42
All other benthic inverts	0.02	0.01		13.93	47.29		8.06	14.55
Copepods						20.00	5.36	26.38
Euphausiids				0.52	0.17	42.00	50.03	44.60
All other zooplankton		0.08		0.00	1.18	23.00	8.61	5.06
Macroalgae				0.00				
Fishery offal				2.55			0.08	
Total	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

[a]Blank spaces indicate that the group is not caught or consumed by the case-study group; 0.00% indicates a trace amount of catch or consumption.

ery is a relatively high TL predator that interacts mostly with adult pollock, but also with many other species. Pollock fishery bycatch includes high TL predators such as salmon sharks (*Lamna ditropis*), sleeper sharks (*Somniosus pacificus*), and arrowtooth flounder, mid-TL pelagic forage fish and squid, and low TL benthic invertebrates such as crabs and shrimp, but all of these catches represent extremely small flows (Fig. 5). The pollock trawl fishery is more species-specific than the halibut longline fishery, with pollock representing over 90% of its total catch by weight; arrowtooth flounder and Pacific cod are next highest at 2% of total catch each (Table 5). Despite these low bycatch percentages, the high volume GOA pollock fishery catches the highest tonnage of certain pelagic species in the GOA, including smelts, salmon sharks, and squids (Gaichas et al. 1999; Ormseth and Gaichas 2008).

Food web modeling shows the importance of pollock as prey in the GOA ecosystem. When both adult and juvenile pollock food web relationships are included, over two-thirds of all GOA species groups are directly linked to pollock either as predators or as prey. The significant predators of pollock (light blue boxes joined by light blue lines in Fig. 5) include arrowtooth flounder, halibut, cod, sablefish (*Anoplopoma fimbria*), Steller sea lions, humpback whales (*Mega-*

ptera novaeangliae), and the pollock trawl fishery. Arrowtooth flounder, adult pollock, seabirds such as murres and puffins, and cod are significant predators of juvenile pollock. Significant prey of pollock (yellow boxes joined by yellow lines in Fig. 5) are euphausiids, copepods, benthic shrimps, and amphipods, with juveniles preying on the euphausiids and copepods. The majority of adult pollock mortality is caused by three groundfish predators: arrowtooth flounder (33% of total mortality), halibut (23%), and cod (16%) (Table 4). The pollock trawl fishery causes only 6.6% of adult pollock mortality, which is similar in magnitude to that caused by sablefish, Steller sea lions (adults and juveniles combined), and pollock cannibalism. The majority (47%) of mortality on juvenile pollock is also caused by arrowtooth flounder, followed by adult pollock cannibalism (11%) (Table 4). Seabirds cause the next highest juvenile pollock mortality (9% by murres, puffins, and kittiwakes combined). Both adult and juvenile pollock feed primarily on pelagic zooplankton, with euphausiids comprising 50% of the adult pollock diet and 45% of the juvenile pollock diet (Table 5). Although adult and juvenile pollock diets are similar, adult pollock prey more on pandalid and nonpandalid (NP) shrimp (18% of diet), and juvenile pollock prey more on copepods (26% of diet). The proportions of major

Fig. 4. Declining trend in the proportion of pollock in halibut diets (bars) and in pollock age 3+ biomass (diamonds joined by line) in the Gulf of Alaska, 1990–2008. Diet data collected by Alaska Fisheries Science Center (AFSC, Seattle, Washington: http://access.afsc.noaa. gov/REEM/WebDietData/DietTableIntro.php), pollock biomass trend from 2008 stock assessment (Dorn et al. 2008).
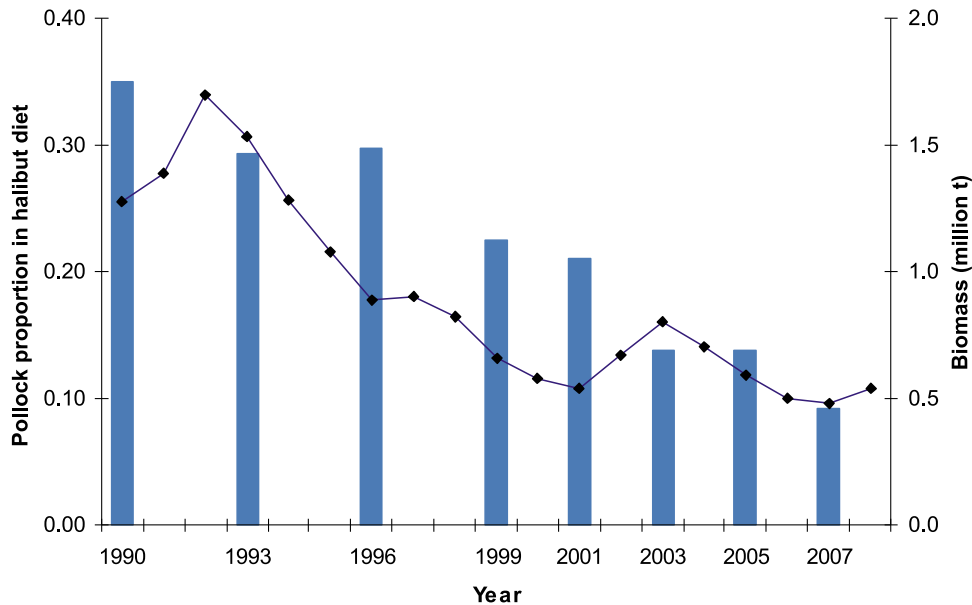
Fig. 5. Food web of Gulf of Alaska (GOA) adult and juvenile pollock (pink boxes) in the early 1990s. The food web visualization shows predators of pollock highlighted in light blue and prey in yellow, with the strongest flows represented as thicker lines and weak flows represented only as highlighted group boxes with no lines. The significant predators of pollock (light blue boxes joined by light blue lines) include halibut, arrowtooth, cod, sablefish, Steller sea lions, and the pollock fishery. The significant prey of pollock (yellow boxes joined by yellow lines) include euphausiids, copepods, shrimps, and other invertebrates. Green boxes indicate groups that are both predator and prey of pollock.

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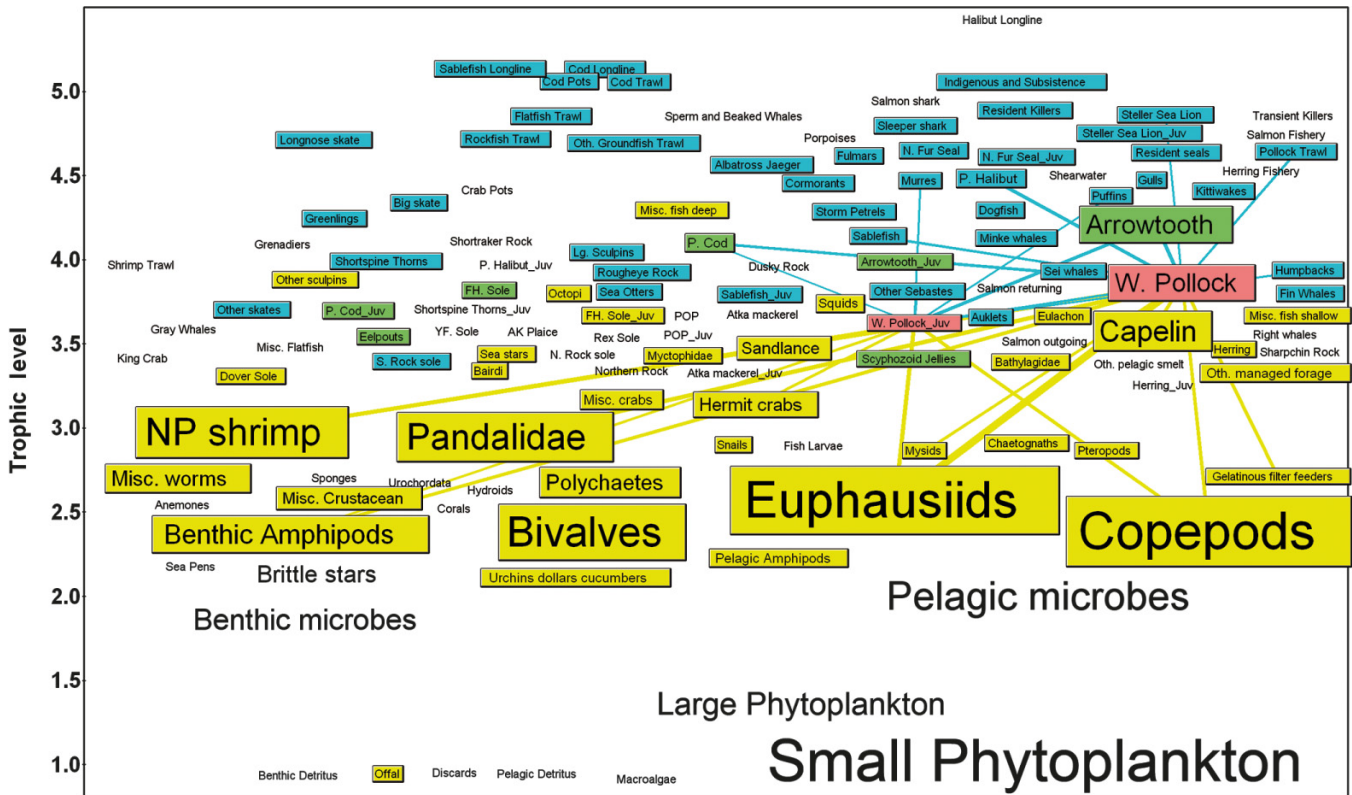
Fig. 6. Proportion of copepods, euphausiids, pandalid shrimp, and nonpandalid (NP) shrimp in pollock diets, 1990–2007. Diet data collected by Alaska Fisheries Science Center (AFSC, Seattle, Washington: http://access.afsc.noaa.gov/REEM/WebDietData/DietTableIntro.php).
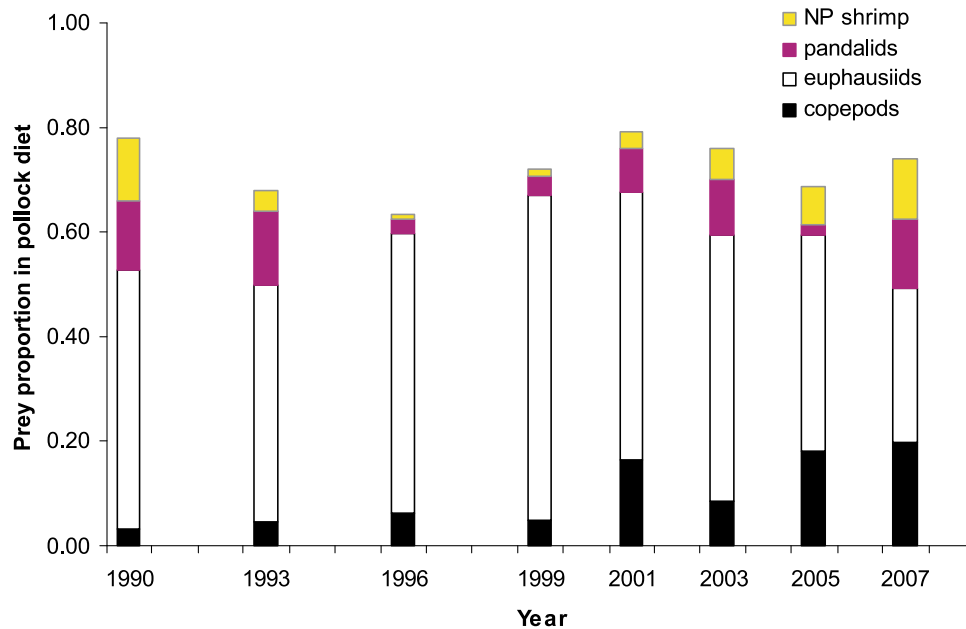
prey in pollock diets remained stable from 1990 to 2007, aside from a recent increase in copepods (Fig. 6). The combination of pollock diet composition along with high biomass within the system results in high estimated flows from pelagic zooplankton and benthic shrimp to pollock (Fig. 5).

The food web model estimates that squid are also important prey for several species groups in the GOA food web, despite relatively poor data. The predators of squids in the GOA are primarily salmon, which account for nearly half of the squid mortality in the ecosystem model (Table 4). Marine mammals such as sperm whales (*Physeter macrocephalus*) and other toothed whales account for a total of 14% of squid mortality, and the primary groundfish predators of squids are sablefish, pollock, and grenadiers (Macrouridae, labeled "other fish" in Table 4), which combined account for another 10% of squid mortality. We know little about GOA squid diets at present, so we assumed (based on limited Bering Sea data) a generalized diet dominated by euphausiids, copepods, and other pelagic zooplankton in the GOA (Table 5). Although Pacific salmon (genus *Oncorhynchus*) have the highest consumption of squids in the GOA, squid are not dominant in salmon diets, so salmon do not appear to be as dependent on squids as some other predators are. Squid make up about 20% of the diet of GOA salmon, 86% of the diet of GOA sperm whales, 67% of the diet of other toothed whales, and 21% of the diet of sablefish (Aydin et al. 2007).

Discussion

The case studies developed here from the detailed static food web model of the GOA marine ecosystem (Aydin et al. 2007) provide important insights for fishery management on multiple levels. First, the simple "accounting exercise" of assembling information for all species in the same units

for the same time period forces reconciliation of multiple, sometimes conflicting, sources of information: survey data, food habits data, and production, consumption, and biomass estimates based on stock assessment results from multiple agencies. Second, viewing fisheries within the context of predator–prey relationships provides a comprehensive view of fishing impacts beyond target species. Third, evaluating the predator–prey relationships for commercially important species improves fishery sustainability through a fuller accounting of mortality sources and prey species contributing to production, which may enhance single-species management. Finally, evaluating the predator–prey relationships for noncommercial species incidentally caught in fisheries shows which indirect effects of fishing might eventually affect target species or even the entire food web. We expand on each of these points below.

Comprehensive accounting and consistency check for management

Food web modeling organizes multispecies information into an internally consistent framework. However, information for each species may not be consistent. Stock assessments are generally conducted independently for each species, and separate agencies maintain survey and fishery databases with diverse goals, time frames, and collection methods. Because regulations based on separate analyses and information sources are implemented simultaneously in the ecosystem, inconsistencies could lead to unexpected (and undesirable) management outcomes. Therefore, a food web model provides information not otherwise available for management in that it implicitly checks for consistency in assumptions across species. In the GOA, the information was consistent enough for each species group's estimated annual production to adequately supply the estimated annual catch and consumption by predators (see Aydin et al. 2007).

However, many instances in which the information was not consistent indicated where current field sampling efforts might be adjusted to improve biomass, diet, or other estimates if this is a priority for management.

The most important inconsistency revealed by food web modeling in the GOA is the apparent excess consumption of pollock relative to their estimated production, which is difficult to attribute to inadequate sampling. Pollock is one of the best-studied and assessed species in the ecosystem (e.g., Dorn et al. 2008). The predators causing the excess consumption, arrowtooth flounder, halibut, and cod, are also well studied and assessed in the GOA because of their commercial importance (Turnock and Wilderbuer 2007; Hare and Clark 2008; Thompson et al. 2008). The food habits of all four of these species are well sampled. Consistent estimation methods for consumption rates across species make it unlikely that substantial bias affects only the three major predators of pollock. In an early version of the GOA food web model with only 40 functional groups and lacking adult and juvenile age structure, pollock production and biomass were found inadequate to support the estimated consumption by their predators. The current GOA food web model was designed, in part, to address the problem of too many predators for too few pollock by attributing predation appropriately between age groups and all possible alternative prey. Even with this careful attention to detail, the estimated consumption of adult pollock still exceeds their estimated production, so a negative BA had to be included to balance the model.

The magnitude of the BA required to balance predator consumption of pollock suggests where single-species assessment assumptions might be investigated further. Food web modeling suggests that either the early 1990s pollock decline was substantially greater than that estimated by all recent stock assessments (e.g., Dorn et al. 2003, 2008) or that the stock assessment underestimated adult pollock biomass, or both. Alternatively, if the pollock assessment is accurate, then the food web model suggests that biomass of arrowtooth flounder, Pacific halibut, and (or) Pacific cod must be lower than both the NMFS bottom trawl survey and their respective stock assessments estimates. The GOA food web model itself cannot be used to determine which single- or multiple-species survey biomass, diet data, or consumption rate estimates are responsible for the inconsistency between pollock production and consumption. However, food web modeling may suggest alternative assumptions for testing within individual stock assessments (e.g., survey catchability, often assumed to be 1, may be assumed to be higher or lower based on compatibility of resulting biomass with food web consumption and production estimates). Using any inconsistencies discovered in a food web modeling context, we may begin to reconcile the independent stock assessment assumptions that are implemented together in the real world.

Fisheries as predators

Food web modeling expands the conventional view of a fishery and its direct effect on the population of its target species by picturing fisheries as predators within the system, which can be assigned a TL and characterized in terms of their prey, including both intended catch and incidental catch. Contrasts between fisheries and other predators are also instructive. At the apex of the food web, the halibut longline fishery is a highly selective predator on halibut that also catches less selective apex predators such as skates and sharks. Similarly, the pollock trawl fishery shares a high TL with longnose skate but with a more focused diet of pollock relative to longnose skate's diverse fish diet. Although similarities in specialization and trophic position might be expected for fisheries, the effect of these fisheries on their prey differs due to the (correlated) productivity and TL of those prey. For example, the halibut longline fishery represents the largest single source of mortality for both halibut and the incidentally caught longnose skate. Both halibut and longnose skate are high TL predators themselves, with few natural predators, so fishing mortality is a larger component of total explained mortality than predation mortality. However, the high-volume pollock fishery causes relatively little of the lower TL pollock's total mortality. Further, despite being responsible for the largest catch of squids of any GOA fishery (Ormseth and Gaichas 2008), the pollock trawl fishery contributes an insignificant portion of squids' estimated total mortality in the GOA. These food web derived comparisons of TL and the relative contributions of fishing mortality and predation mortality to total mortality may help prioritize management efforts to control fishing mortality where it matters most (high TL commercial and nontarget species) and allow consideration of alternative strategies where changing fishing mortality may not contribute greatly to changes in total mortality (lower TL commercial and nontarget species).

Commercial species in the food web

Understanding food web relationships for a fished species suggests potential sources of variability in mortality and production that might be included in single-species stock assessments. For a fished predator species such as halibut, food web modeling generally supports the single-species stock assessment assumption of constant natural mortality, because halibut have few natural predators and the majority of explained halibut mortality is from fishing. However, adult halibut's dependence on pollock for nearly half of its diet suggests that future halibut production might be negatively affected by declining pollock populations. Recent data supports this insight from food web modeling: the steady decline in the proportion of pollock in halibut diet concurrent with the decline in pollock biomass suggests that pollock have become a less important energy source for halibut over time. Although halibut biomass remained steady over the course of the 1990s, a dramatic reduction in halibut weight at age was observed (Clark et al. 1999); this decline in production was attributed to a climate regime shift. Food web modeling suggests that further investigation of the relationship between halibut production, pollock stock size, and the availability and quality of alternative prey might be important to sustainable halibut fishery management.

For fished prey species such as pollock, food web modeling shows that the overwhelming majority of explained mortality is from predation, rather than fishing. This suggests that reducing fishing mortality may have little overall positive impact on their population trajectory and (or) that increased fishing mortality might have a greater than expected effect under the combined effects of high predation mortality and increased fishing mortality. Further, if pollock's predator populations change substantially, then predation mortality

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could change with them, making a stock assessment assumption of constant natural mortality incorrect. The impact of variable predation mortality on the GOA pollock stock assessment has been explored by Hollowed et al. (2000) and more recently by A'mar et al. (2010). In both studies, including increased predation mortality resulted in higher estimates of pollock biomass in the ecosystem and (or) lower estimates of survey catchability, either of which would resolve the pollock supply inconsistency found in the GOA food web model. However, the pollock-centered modeling of these studies could not address alternative assumptions for the predator stock assessments or subtle trends in pollock diet that might affect the outcome as well.

Insights from food web modeling may prioritize the next steps in enhancing single-species assessment and management by suggesting coordinated monitoring and management efforts for interacting commercial species. At present, halibut and pollock fisheries are managed separately by different agencies (IPHC and NMFS), with independent stock assessments and little formal monitoring of diet trends. With key predator–prey relationships and diet components identified by complex static food web models, the most important interactions can be monitored in survey data and captured in models with fewer species but more detailed population dynamics and alternative management scenarios. This would build on the predation mortality analyses of Hollowed et al. (2000) and A'mar et al. (2010), which were unable to consider feedbacks from pollock to predator production or effects of pollock diet trends on pollock production. As a next step, alternative management policies for halibut might be examined for effects on pollock (and vice versa) using a two-species assessment model with full predator–prey feedback.

Nontarget species in the food web

Food web models can help prioritize monitoring and management for nontarget species by evaluating the relative importance of fishing and other food web interactions. For example, the food web model shows that longnose skate feed on both commercially important fish species and noncommercial shrimp and forage fish but show no strong dependence on any single prey (unlike halibut). Therefore, management practices that promote the sustainability of commercial fish, as well as forage species, should support continued longnose skate production. However, monitoring skate food habits for major changes would be somewhat important as fishing continues and evolves. The GOA food web model estimates that longnose skate are similar to halibut in occupying a relatively high TL and experiencing higher fishing mortality than predation mortality. The life history of skates, with relatively slow growth to large size and late maturity with low fecundity, indicates that they might be vulnerable to overfishing even as bycatch (King and McFarlane 2003). Therefore, food web modeling suggests that developing a conventional single-species approach to the assessment of skate population dynamics and response to fishing would be a high priority for management.

Although there is little information available to conduct a stock assessment for the squid complex in the GOA (Ormseth and Gaichas 2008), the food web model estimates squid incidental fishing mortality to be extremely small relative to predation mortality. Therefore, developing a conventional stock assessment might be given low priority as long as the catch remains very small. Overall, the relatively low impact of fisheries on squid estimated by the GOA food web model appears to mean low impacts to squid predators as well. However, the food web relationships for squid suggest that researching potential interactions between incidental squid catch and the timing and location of foraging by salmon, sablefish, sperm whales, and other toothed whales would be a higher priority for maintaining production of those predators. Some separation of the squid species complex into size or habitat-associated components may be useful for further clarification of potential fishery–food web interactions with particular predators.

Food web models and fishery management

The case studies developed here from the full GOA food web model demonstrate how considering relationships between species in the ecosystem may enhance single-species stock assessments and help prioritize monitoring and research for ecosystem-based fishery management. Food web modeling provides a framework for assessing the consistency of survey data and individual stock assessments that are analyzed independently for multiple species but implemented simultaneously in the ecosystem. A consistency check for relationships between managed species can help verify stock assessment assumptions regarding survey catchability, natural mortality, or other parameters. Further, the case studies suggest that both commercial and incidentally caught species at high TLs are more likely to have mortality patterns generally consistent with single-species assessment assumptions, that is, that fishing mortality is a dominant force over relatively constant "natural" (predation) mortality. Conversely, both commercial and incidentally caught species at mid-TLs are unlikely to have mortality patterns consistent with single-species assessment assumptions, because fishing mortality may be a very small proportion of overall mortality, which is dominated by variable "natural" (predation) mortality. The case studies suggest that for groups throughout the food web, species production may change with diet composition or prey availability. Monitoring diet information in stock assessments might forewarn of changing production which is now determined mostly retrospectively. All of these insights contribute to an ecosystem-based fishery management objective of maintaining the relationships in a marine ecosystem, including the economic relationships based on present and future commercial species sustainability.

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